The Lower Cretaceous Flora of the Gates Formation from Western Canada

A Thesis Submitted to the College of

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by

Zhihui Wan

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College of Graduate Studies and Research

SUMMARY OF DISSERTATION

Submitted in partial fulfillment

of the requirements for the

DEGREE OF DOCTOR OF PHILOSOPHY

ZHIHUI WAN

Department of Geological Sciences
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Fall 1995

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The LOWER CRETACEOUS FLORA OF THE GATES FORMATION FROM WESTERN CANADA

The Lower Cretaceous Gates Formation (late Early Albian) of western Canada is a set of paralic coal-bearing strata composed of siltstone, sandstone and coal. Macrofossil plants are abundant in the Gates Formation; most of those are impressions; others include casts and molds of tree trunks. No permineralized fossils are found.

Examination of macrofossil plants from the Gates indicates that the flora consists of bryophytes (*Marchantiolites* and *Thallites*), *Equisetites*, ferns (*Gleichenites* of Gleicheniaceae, *Acanthopteris* and *Coniopteris* of Dicksoniaceae, *Cladophlebis*, *Sphenopteris* and a new genus), seed-ferns (*Sagenopteris* and a new genus), conifers (*Pityocladus* and *Pityophyllum* of Pinaceae, *Athrotaxites* and *Elatides* of Taxodiaceae, *Elatocladus*), cycads (*Chilinia*, *Ctenis*, *Pseudocycas* and *Pterophyllum* and two new genera), *Ginkgo* and *Ginkgoites*: leptostrobans (a new genus), *Taeniopteris* and angiosperms. In total, 52 species from 28 genera are described, including 5 new genera, 15 new species and 3 new combinations.

Most plants of the Gates flora appears to have been deciduous. Only *Elatides curvifolia* and *Elatocladus manchurica* are convincingly evergreen. The interpreted paleoclimate is strongly seasonal with winter minimum temperature possibly below -15^0 C. Rainfall appears to have been abundant since coal deposits are common in the Gates Formation. Although low winter minimum temperature appears to be the main factor causing deciduousness of the Gates flora, low winter light levels may have also contributed to the deciduousness of the Gates flora, as the paleolatitude of the study area was situated at 50^0-60^0 N.

Three floral provinces are recognized: the Arctic Province, which lacks Cheirolepidiaceae; the Equatorial Province, which has Cheirolepidiaceae; and the Antarctic Province, which also lacks Cheirolepidiaceae. Similar floras have been reported from throughout the Arctic Province, including Montana, the western Interior of Canada, the Bowser Basin, Alaska, western Greenland, Spitzbergen, Siberia, northern Mongolia, northeastern China and the Inner Zone of Japan. The Pacific-rim areas are excluded from the Arctic Province. Plant deciduous habit appears to have prevailed within the Arctic Province during the Early Cretaceous.

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The Lower Cretaceous Flora of the Gates Formation from Western Canada

ABSTRACT

The Lower Cretaceous Gates Formation (late Early Albian) of western Canada is a sequence of paralic coal-bearing strata composed of siltstone, sandstone and coal. Macrofossil plants are abundant in the Gates Formation: most fossils are impressions: others include casts and molds of tree trunks. No permineralized fossils are found.

The Gates flora consists of bryophytes (*Marchantiolites* and *Thallites*), *Equisetites*, ferns (*Gleichenites*, *Acanthopteris* and *Coniopteris* of Dicksoniaceae, *Cladophlebis*, *Sphenopteris* and a new genus), seed-ferns (*Sagenopteris* and a new genus), conifers (*Pityocladus* and *Pityophyllum* of Pinaceae, *Athrotaxites* and *Elatides* of Taxodiaceae, *Elatocladus*), cycads (*Chilinia*, *Ctenis*, *Pseudocycas* and *Pterophyllum* and two new genera), *Ginkgo* and *Ginkgoites*; leptostrobans (a new genus), *Taeniopteris* and unidentified angiosperms. In total, 52 species from 28 genera are described, including 5 new genera, 15 new species and 3 new combinations.

Most plants of the Gates flora appears to have been deciduous. Only *Elatides curvifolia* and *Elatocladus manchurica* are convincingly evergreen. The interpreted paleoclimate based on the Gates flora is strongly seasonal with winter minimum temperature possibly below -15^0 C. Rainfall appears to have been abundant since coal deposits are common in the Gates Formation. Although low winter minimum temperature appears to be the main factor causing deciduousness of the Gates flora, low winter light levels may have also contributed to the deciduousness of the Gates flora, as the paleolatitude of the study area was situated at 50^0-60^0 N.

Three Early Cretaceous floral provinces are recognized: the Arctic Province, which lacks Cheirolepidiaceae: the Equatorial Province, which has Cheirolepidiaceae: and the Antarctic Province, which also lacks Cheirolepidiaceae. Floras similar to the Gates flora have been reported from throughout the Arctic Province, including Montana, the western Interior of Canada, the Bowser Basin of northwestern Canada, Alaska, western Greenland, Spitzbergen, Siberia, northern Mongolia, northeastern China and the Inner Zone of Japan. The Pacific-rim areas are excluded from the Arctic Province. Plant deciduous habit appears to have prevailed within the Arctic Province during the Early Cretaceous.

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Chapter 1

Introduction

This chapter briefly reviews previous paleobotanical work of Early Cretaceous within the western Interior of North America, presents an overview of the global Early Cretaceous vegetation, and addresses the significance of this study.

1.1 Previous paleobotanical work

Lower Cretaceous macrofloras are widespread but poorly understood in western North America, especially in Canada. Bell's (1956) publication marks the beginning of systematic floral research in the Early Cretaceous of the western Interior of Canada. The history of paleobotanical research in the western Interior of North America can be roughly divided into three stages. The first is before Bell's publication. During this stage paleobotanical work was restricted to sporadic reports of fossil plant discoveries, usually with simple descriptions, with or without photo plates. Reported species were few. Principal publications, relevant to the Northern Rocky Mountain area, are Dawson (1886, 1892), Newberry

(1891), Fontaine (1892, 1905f, i), Knowlton (1907) and Berry (1929a, b), and those relevant to the Central and Southern Rocky Mountain area are Newberry (1861, 1898), Brown (1933), Read and Brown (1937), Arnold (1945), Andrews and Kern (1947) and Spackman (1948). All are cited in McClammer and Crabtree's (1989) list of fossil localities.

The second stage is marked by Bell's (1956) publication. Bell was the first person to systematically describe the macroflora of the Lower Cretaceous of western Canada. He summarized previous work and studied the fossil plants that were collected from non-marine Upper Jurassic-Lower Cretaceous rocks at 365 localities, which covered the following strata: the Kootenay Formation, the Nikanassin Formation, the Hazelton Group, the Tantalus Formation, the Blairmore Group, the Luscar Formation, the Bullhead Group, the Uslika Formation, the Jackass Mountain Group, the Spence Bridge Group, the Pasayten Group, the Kingsvale Group, the Crowsnest Formation, and the Commotion Formation. Most of those materials were gathered by officers of the Geological Survey of Canada from 1883-1955, and some by companies engaged in oil exploration. Bell's publication covered the floras from the Late Jurassic to Albian; 140 species were described and the age and correlation of the relevant strata were discussed. However, Bell's work was limited to only the specific descriptions; generic circumscriptions were not given, and some of the specific diagnoses are ambiguous. Not only were some former existing taxonomic problems perpetuated, but some new ones were also introduced.

One paleobotanical investigation of the Gates Formation was of a flora (only a species list) which was identified by Bell, Hueber and McGregor as the equivalent flora of Lower Blairmore-Luscar-Gething "Aptian" floras (Stott, 1968). However, since Early to Middle Albian marine faunas occur below the Gates and in laterally equivalent beds (Stott, 1982), the "Aptian" age of the Gates needs reconsideration.

The third stage followed Bell's work. During this stage, no major systematic study of the Lower Cretaceous was initiated in Canada except for that of MacLeod and Hills (1992a) on the Bowser Basin flora from northern British Columbia. MacLeod and Hills (1990, 1992b) also demonstrated the stratigraphic value of fossil plants in the western Interior of Canada. Other recent paleobotanical studies were restricted to rocks mainly within the United States. Crabtree (1983, 1987, 1988), for example, contributed significantly to the knowledge of Aptian and younger floras of the western Interior of North America. In particular, McClammer and Crabtree (1989) reevaluated the chronostratigraphic positions of all major plant megafossil collections in the Rocky Mountain regions of post-Barremian age. Studies by LaPasha and Miller (1983, 1984, 1985), and Miller and LaPasha (1984) on the Aptian Kootenai Formation of Montana have helped to solve some of the taxonomic problems inherent in Bell (1956) as well as to demonstrate the potential of fossil macrofloras for understanding the paleoecology of this period in western North America. Miller (1987) provided a similar overview of vegetation types of the northern Rocky Mountains for the Devonian to Early Cretaceous interval. No systematic paleobotanical investigation has been done in the Lower Cretaceous rocks along the foothills of the western Interior of Canada since Bell's publication (1956).

1.2 Lower Cretaceous floras of the world

Mesozoic floras differ from Paleozoic floras in having different dominant groups. A typical Mesozoic flora is characterized by abundant cycads, conifers, ginkgoes and Czekanowskiales, while a typical Paleozoic flora is dominated by lycopsids, articulates, ferns and seed-ferns. Although cycads, conifers, ginkgoes and Czekanowskiales might have originated in the Carboniferous or earlier, they did not become abundant until the Late Permian or early Mesozoic.

Cycads, conifers, ginkgoes and Czekanowskiales played dominant roles in many Triassic to Early Cretaceous floras. Distinct floral change occurred between the Early and the Late Cretaceous. In the Late Cretaceous many of the plants that determined the aspect of earlier floras disappeared or decreased greatly in number of genera and species, or decreased in distribution and the angiosperms became the dominant group. Therefore, Late Cretaceous floras are frequently referred to as the Cenophytic. A typical Cenophytic flora differs from a typical Mesophytic flora in having angiosperms as its dominant group.

Although Early Cretaceous floras have been reported from all over the world, significant research on the Lower Cretaceous has been restricted in Northern Hemisphere; extensively researched areas including Europe and the Far East (Figure 1.1). Dominant groups of the Early Cretaceous floras are cycads, conifers, ginkgoes and Czekanowskiales. Angiosperms are rare in Early Cretaceous floras, but are significant in differentiating between most Early Cretaceous floras and Jurassic floras or earliest Cretaceous floras which do not contain angiosperms. Therefore, the earliest Early Cretaceous floras are typical Mesozoic floras regarding their dominant groups. The Gates flora mainly consists of ferns, cycads, and conifers.

A few ginkgoes and Czekanowskiales also occur in the Gates flora. Two species of angiosperms have been recovered from the Gates Formation. Therefore, the Gates flora is typical of the Early Cretaceous floras but not the earliest.

Early Cretaceous floras of the world can be divided into three floral provinces (Figure 1.1). In the Arctic Province, dominant components of the Early Cretaceous floras include ferns of the Dicksoniaceae and Gleicheniaceae, cycads (*Chilinia*, *Ctenis*, *Cutchiphyllum*, *Pseudocycas*, *Pterophyllum* and *Nilssonia*), ginkgoes, Czekanowskiales, Pinaceae and Taxodiaceae. In the Equatorial Province, Early Cretaceous floras are characterized by *Weichselia*, Cheirolepidiaceae, Cupressaceae, and cycads (*Ptilophyllum*, *Zamites*, *Otozamites* and *Dictyozamites*). In the Antarctic Province, floras are characterized by having Dicksoniaceae, Osmundaceae, *Zamites*, Podocarpaceae and Araucariaceae.

The Gates flora of the Early Albian (Figure 1.1, No. 1) lies within the Arctic Province. Other relevant western Canadian floras include the Bowser basin flora (MacLeod and Hills, 1992a), which is Tithonian to pre-Aptian, and the Late Jurassic-Early Cretaceous floras described by Bell (1956). The Western Canadian floras, together with the Montana flora (Miller and LaPasha, 1984; LaPasha and Miller, 1985), the Alaska floras (Figure 1.1, No. 26), and the Kome flora from the western Greenland (Figure 1.1, No. 8) represent the North American part of the Arctic Province.

Representative Early Cretaceous fossil sites (Figure 1.1):

1. Western Canadian floras (Berry, 1929; Bell, 1956; MacLeod and Hills; 1992a; **Present study**).
2. Queen Charlotte flora (Ward, 1905, p. 209).

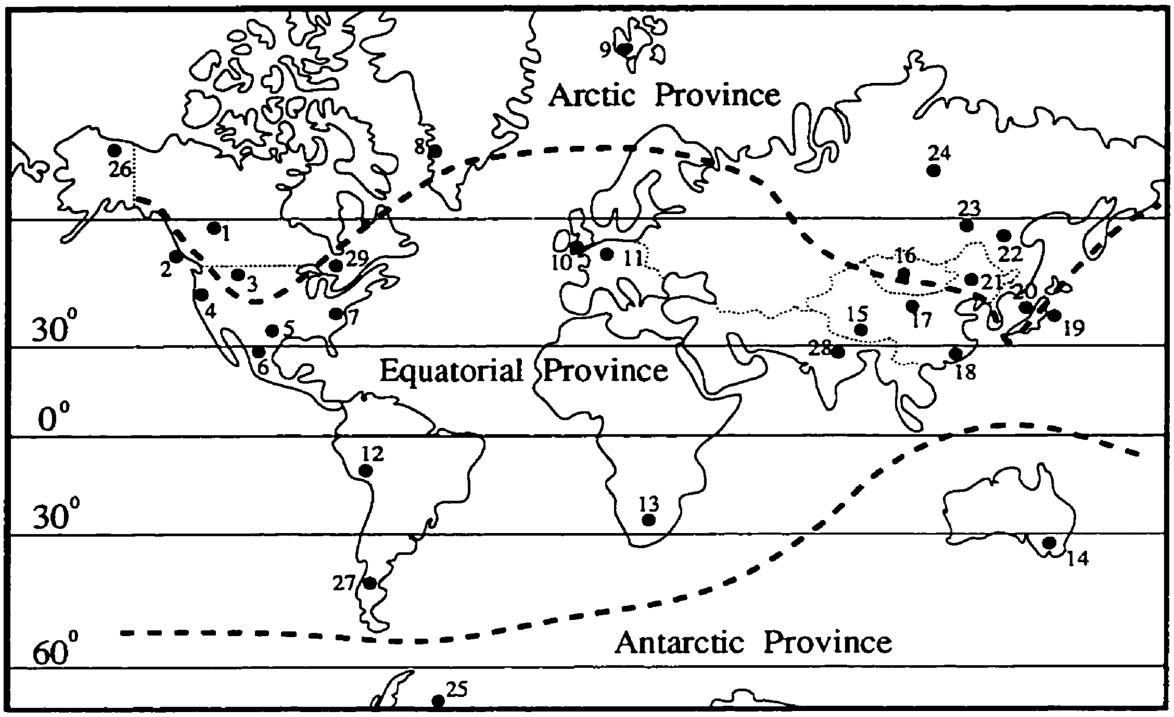


Figure 1.1: Map showing the three Early Cretaceous floral provinces and the representative flora sites of the Early Cretaceous. (See text for data sources)

3. Montana flora (Fontaine, 1905f, i; Miller and LaPasha, 1984; LaPasha and Miller, 1985).
4. Shasta flora (Fontaine, 1905e, g, h).
5. Glen Rose flora (Watson, 1977; Watson and Fisher, 1984).
6. Mexico flora (Nathorst, 1893 listed in Berry, 1911, p. 126).
7. Potomac flora (Fontaine, 1889; Berry, 1911).
8. Kome flora (Heer, 1874; 1882; 1883; Seward, 1926).
9. Spitzbergen flora (Heer, 1876; Nathorst, 1897 and DeGeer, 1882 listed in Berry, 1911, p. 117; Vassilevskaya, 1980).
10. English Wealden flora (Seward, 1894, 1895; Watson, 1969, 1977, 1982; Watson and Sincock, 1992).
11. European floras (All the floras of the European Province except those from England, Vakhrameev, 1991, p. 130).
12. Peru flora (Steinmann, 1903-1904 in Berry, 1911, p. 114).

13. South Africa flora (Seward, 1903, 1907 listed in Berry, 1911, p. 113; Anderson and Anderson, 1985).
14. Australian flora (Douglas, 1969, 1973; Douglas and Williams, 1982).
15. Tibet flora (Duan et al., 1977; Li, 1982; Chen and Yang, 1983).
16. Mongolian flora (Krassilov, 1982).
17. Inner Mongolian flora (Tan and Zhu, 1982) (Cited from Chen et al., 1988, p. 118).
18. South China flora (Li, 1948; Cao, 1983; Sze, 1942; Zhou, 1923) (Cited from Chen et al., 1988, p. 120).
19. Ryoseki flora (intensively researched, detailed reference list is given in Kimura, 1987, p. 95).
20. Tetori flora (intensively researched, detailed reference list is given in Kimura, 1987, p. 95).
21. Northeast China flora (Zhang et al., 1980; Li, 1981; Zheng and Zhang, 1982, 1983; Cao, 1983; Shang, 1987; Chen et al., 1988).
22. Sungari flora (Cited from Vakhrameev, 1991, p. 123, Fig. 3.13).
23. Amur flora (Vakhrameev and Doludenko, 1961; Vakhrameev and Lebedev, 1967; Koshman, 1969, 1970; Krassilov, 1972a, 1973b) (Cited from Vakhrameev, 1991, p. 104).
24. Lena flora (Vassilevskaya, 1959, 1966; Vassilevskaya and Pavlov, 1963; Vassilevskaya and Abramova, 1966; Vakhrameev, 1958; Samylina, 1963) (Cited from Vakhrameev, 1991, p. 95) .
25. Antarctic flora (Jefferson, 1982; 1987).
26. Alaska flora (Fontaine, 1905b-d; Smiley, 1966, 1967, 1969a, b, 1972; Parrish and Spicer, 1988).
27. Patagonia flora (Archangelsky and Gamerro, 1967; detailed reference list is given in Vakhrameev, 1991, p. 170).
28. India flora (Detailed reference list is given in Vakhrameev, 1991, p. 178).
29. James Bay flora (Martison, 1952).

1.3 Purposes of study

The study area is restricted to the western Canadian part, or northern Foothills part, of the western Interior of North America and includes northeastern British Columbia (Tumbler Ridge) and west-central Alberta area (Grande Cache and Cadomin) (Figure 1.2). The whole Interior extends along the eastern side of the Rocky Mountains from the Alaska to the Gulf of Mexico. During Early Cretaceous time, the Interior was occupied by transgressing seaways from both the Gulf of Mexico and the Arctic Ocean from time to time. Those two seaways were separated for most of the Early Cretaceous, except for a short period of coalescence in the Late Albian (Williams and Stelck, 1975).

The Lower Cretaceous rocks, representing sediments of two major marine transgression-regression cycles, are widely distributed in the Western Interior Basin (Stott, 1982). Those rocks were deposited along the eastern side of the Rocky Mountains, that is, the western side of the Interior sea, as sequences of intercalated marine shales and coal-bearing strata.

The correlation of the various stratigraphic units in the western Interior has been based on lateral continuity and index fossils. Dramatic facies changes make lateral correlation of the non-marine deposits very difficult. Fossils of macrofaunas are not abundant within the succession, and fossils of microfaunas are rare in non-marine strata, especially in coal-bearing strata. Palynological investigations are very limited, although Singh (1971, 1976) has demonstrated the stratigraphic value of this approach. The abundant macrofossil plants within the Gates Formation have not been thoroughly studied. Bell's (1956) publication is the only major taxonomic work on the macrofloras of this age in western Canada, but his work

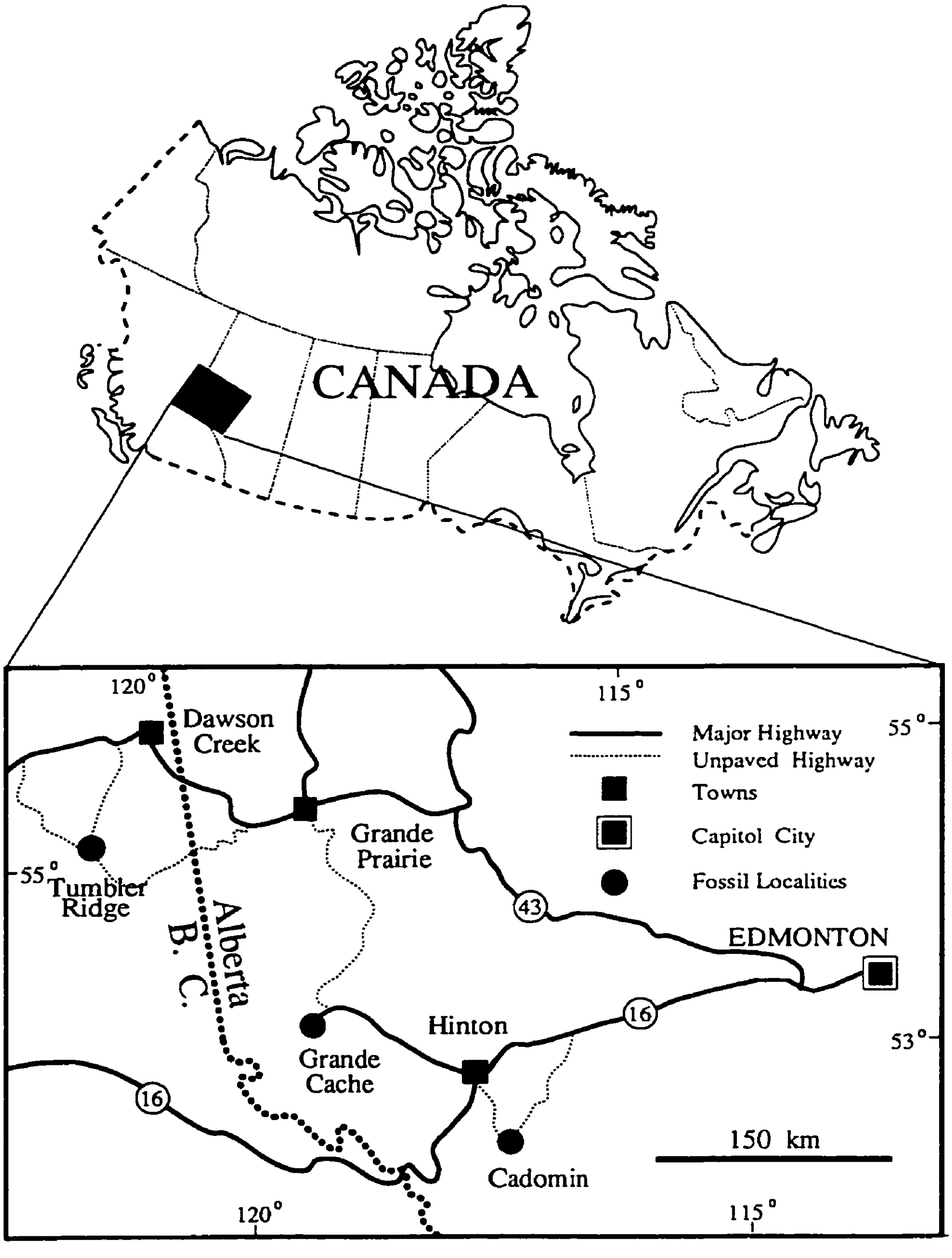


Figure 1.2: Map showing fossil localities.

was preliminary and many taxonomic problems remained unsolved. It has been necessary to refine and reevaluate his research results. A number of operating open-cut coal mines provide excellent opportunity to collect large quantities of fossil plants. The present research addresses this need, and provides a revision of part of Bell's work.

Because of the advantages of the intercalations of marine shales and coal-bearing strata in the study area, the present study helps our understanding of the relationships between fossil floras and fossil faunas, which are important in the correlation of marine strata to non-marine strata.

Plants are very sensitive to climate change, and it follows that fossil plants are useful as paleoclimatic indicators. The present study improves our understanding of Early Cretaceous climate change, which is of considerable importance to the understanding of Cretaceous extinction events and angiosperm evolution.

Chapter 2

Geological Background

This chapter reviews the global Early Cretaceous paleogeography, discusses the tectonic background, sedimentary history and the age of the Gates Formation, and introduces the materials and methods used in this study.

2.1 Tectonics

Paleogeography

The paleogeography of the Early Cretaceous as reconstructed by Barron et al. (1981, Pl. 5; 1987, Fig. 6; Hallam, 1985; Smith et al., 1994) was significantly different from the present. North America was still connected to Europe, as was South America to Africa and Australia to Antarctica. India was an island continent in the southern subtropics (Figure 2.1). Sea level appears to have been much higher than at present and about 20% of the continental area was flooded (Barron et al., 1980), creating one of the greatest epicontinental seas known in the Phanerozoic. Extensive marine transgression occurred on every major continent.

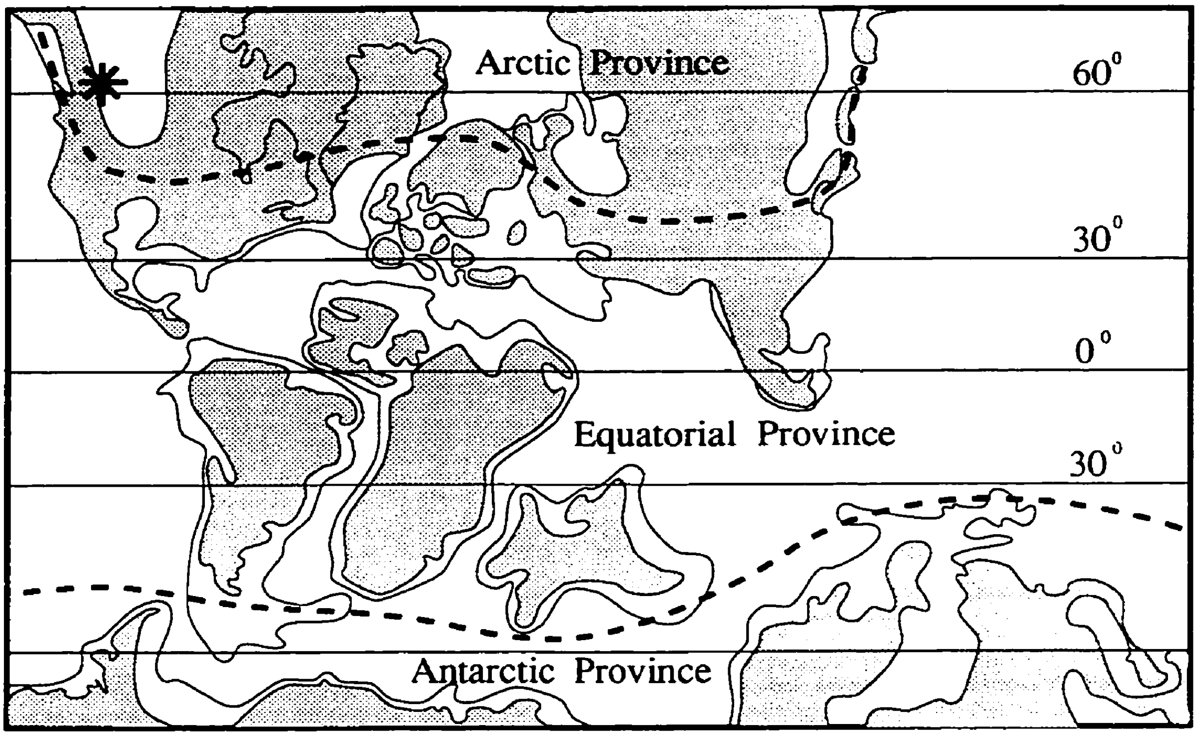


Figure 2.1: Paleogeographic Map of Early Cretaceous (Albian). Modified after Barron el al. (1981, Pl. 5; 1987, Fig. 6), Hallam (1985), and Smith et al. (1994). (Asterisk marks the study area; shadowed areas represent continents; dashed lines are floral provincial boundaries)

The Interior seaway on the North American continent is an example of those epicontinental seas. The paleolatitude of the working area (Asterisk in Figure 2.1) is almost the same as the present latitude, although the orientation of the North American continent was slightly different from that of the present.

Regional Tectonics

Convergence of the Pacific Ocean plate and the Canadian craton began in the Late Jurassic and continues to the present. Several large, exotic terranes collided with the western margin of craton and compressed miogeosynclinal strata in an eastward-verging fold and thrust belt. To the east of the fold and thrust belt

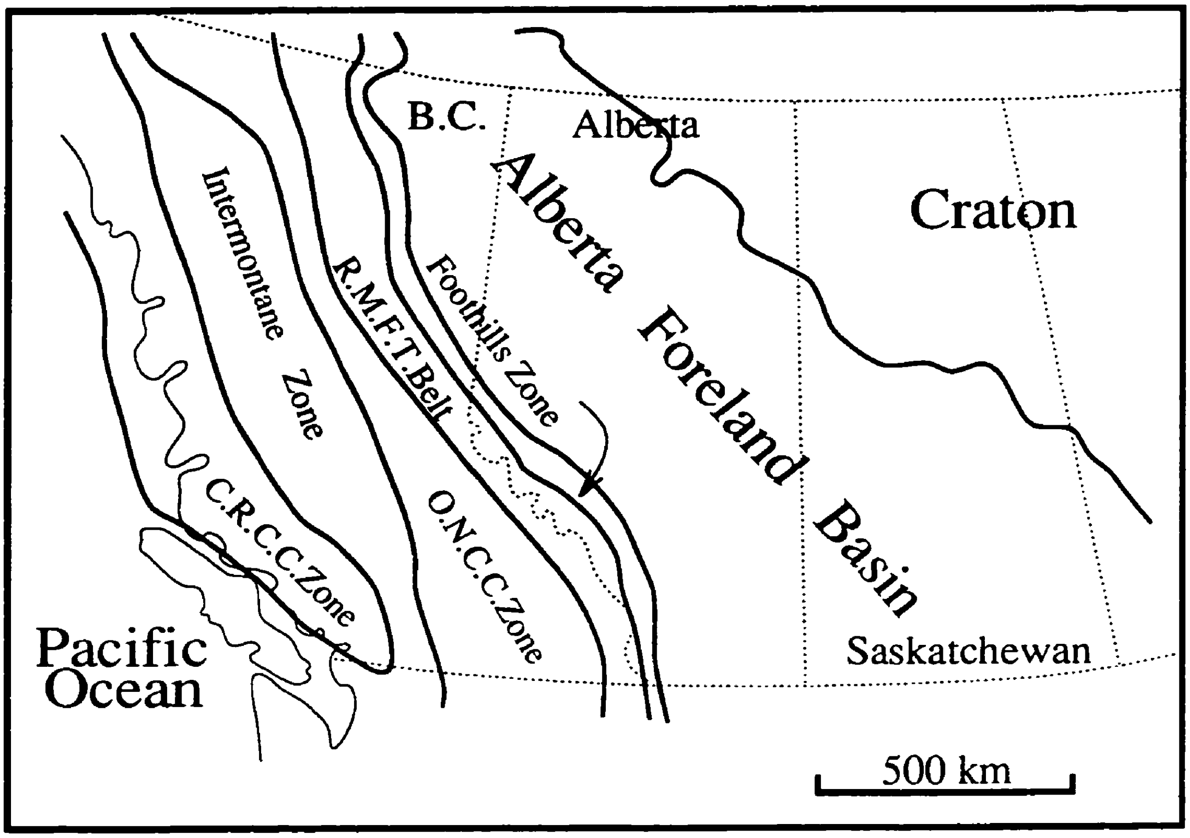


Figure 2.2: Schematic diagram showing tectonic features of Western Canada. Modified after Beaumont (1981, p. 302, Fig. 4). (C.R.C.C = Coast Range Crystalline Core; O.N.C.C. = Omineca-Nelson Crystalline Core; R.M.F.T. = Rocky Mountain Fold Thrust).

was a foreland basin, the Alberta Foreland Basin. The detailed structures of the Alberta Foreland Basin have been modelled by Beaumont (1981).

The Alberta Foreland Basin was bordered on the west by the northwesterly trending Omineca-Nelson Crystalline Core Zone (Fig. 2.2) and on the east by the Canadian craton. Within the basin, there is an off-lapping sequence of eastward-tapering clastic wedges. Each represents a period of rapid telescoping and uplift within the Cordillera. The two oldest wedges are Late Jurassic through earliest Cretaceous in age (the Kootenay Formation, the Nikanassin Formation, or the Minnes Group) and Early Cretaceous through mid-Cretaceous age (the Bullhead and the Fort St. John) (Leckie, 1986a, b). The Fort St. John Group consists of a set of intercalated marine shales and paralic sandstones (including the Gates Formation), and records a period of recurrent pulses of mountain building in the Cordillera region. These pulses are part of the mid-Columbian Orogeny (Stott, 1982).

Basin Structure

Within the Alberta foreland basin, structural units include: the Alberta Trough and Liard Trough (Stott, 1982), also called the West Alberta Basin and Keg River-Hay River Low, respectively (Stelck, 1975); the Peace River Arch; the Sweetgrass Arch and the McDonald Fault (Stelck, 1975) (Fig. 2.3). The Peace River Arch is a northeasterly trending structure lying in the vicinity of Pine and Peace rivers in British Columbia. It is bounded on the south by the Alberta Trough and on the north by the Liard Trough. These troughs were strongly negative elements bordering the interior Platform. The Peace River Arch was active during much of Albian time and had influence on the deposition of both the Fort St. John and Bullhead Groups. Its up and down oscillations created the intercalated sequence of marine shales and coal measures in the Fort St. John Group. The Sweetgrass Arch parallels the Peace River Arch, on the southern border of Alberta trough. The McDonald Fault was considered by Stelck (1975) to mark the southern limit of the Scatter deltaic complex and also the main southern limit of the conglomeratic facies of the Dunvegan Formation.

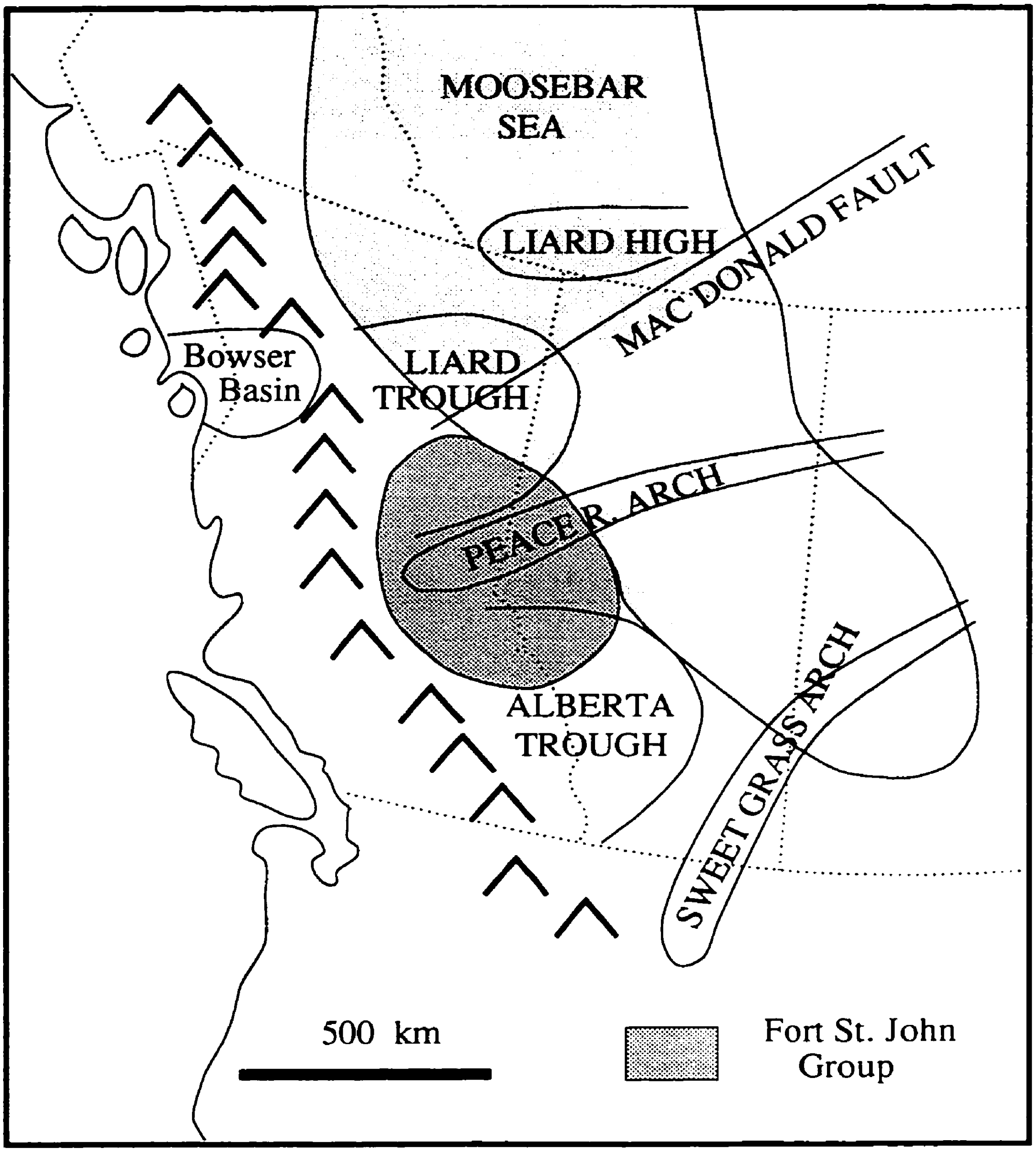


Figure 2.3: Schematic diagram showing basement structures of western Canada. Modified after Stelck, 1975, Text-figure 1. Note: The shown Fort St. John Group area only includes the Peace River area, in which all four cycles of the Fort St. John Group are present. The whole Fort St. John Group is much more widespread.

2.2 Depositional history

According to Stott (1982), three major clastic sequences of Late Jurassic-Cretaceous age were deposited along the western margin of the Alberta Foreland Basin during the Cretaceous (Figure 2.4). Within the lower sequence(the Fernie-Minnes Sequence), marine shales of the Fernie Formation, deposited during Jurassic transgressions, were succeeded by prograding sandstones and mudstones of the Minnes Group of latest Jurassic to early Neocomian age. Later tectonic movement uplifted and bevelled those rocks in a northward and eastward direction. A regional erosional unconformity truncates those strata (Pre-Bullhead unconformity).

The middle sequence (The Bullhead-Fort St. John-Dunvegan Sequence) comprises sediments deposited within an elongate embayment that gradually transgressed from boreal regions into the mid-continent during late Neocomian (?) to early Cenomanian time. That seaway was bordered south of Peace River by a broad, low-lying alluvial plain, which is represented by the carbonaceous sandstones and shales in the Blairmore Group. Coarse clastic material consisting mainly of older sediments spread eastward and was trapped in the rapidly developing basin. The alluvial-deltaic sediments of the Bullhead Group were deposited during the initial transgression. Renewed subsidence within the basin permitted the gradual advance from boreal regions of a major seaway that extended toward the Peace River area. Several large deltas developed along the embayment and were repeatedly overridden by the expanding seaway. Expansion of the seaway, accompanied by several up and down oscillations of the Peace River Arch, resulted in the development of four cyclical successions in which marine shale

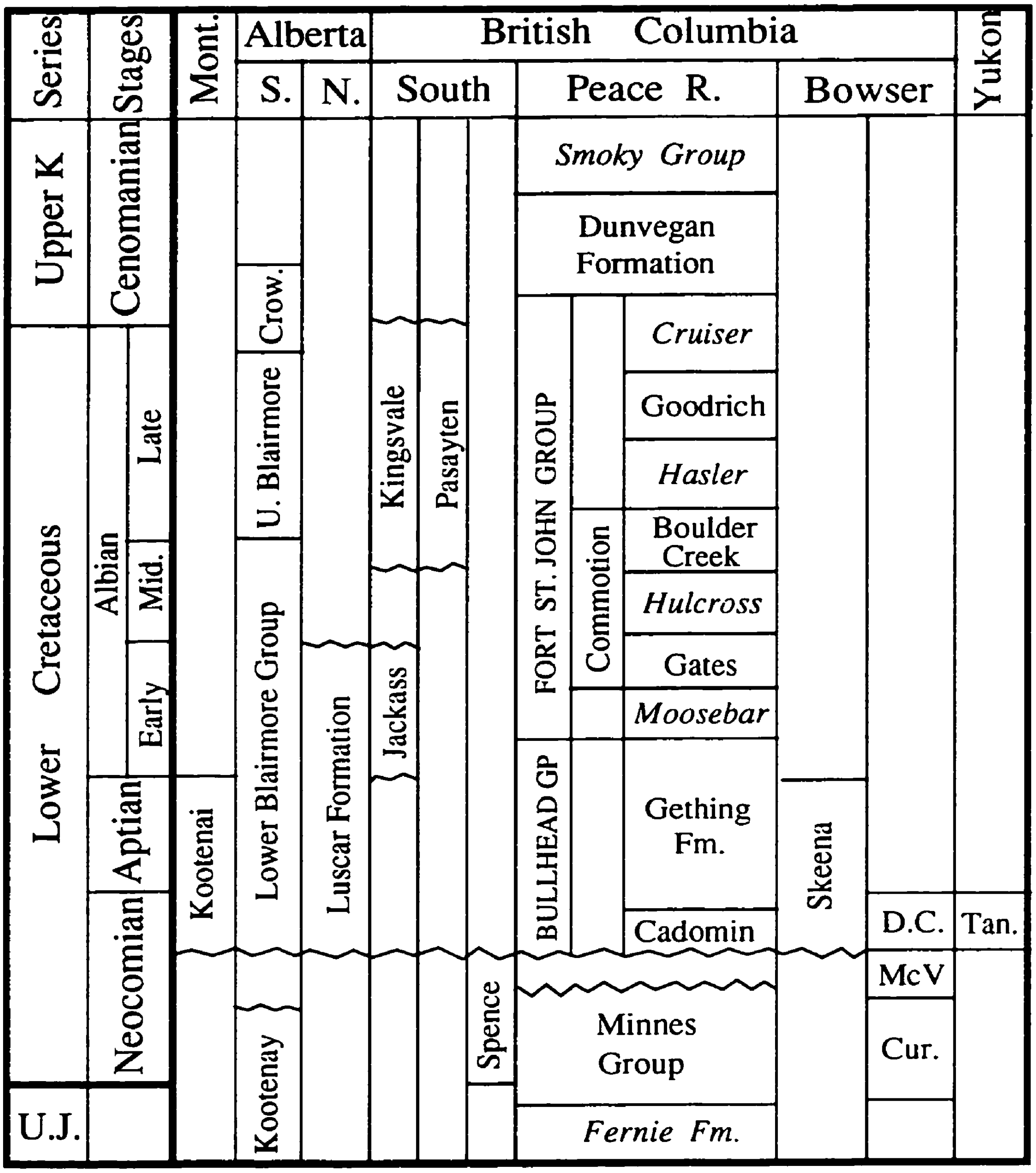


Figure 2.4: Correlation Chart of Plant-Bearing Units of the Northwestern Interior. Modified after Stott (1982, p. 13, Table 1), MacLeod and Hills (1990, p. 996, Fig. 8; 1992, p. 13, Fig. 3). D.C. = Devils Claw, McV = McEvoy, Cur. = Currier, Tan. = Tantalus, Mont. = Montana, Spence = Spence Bridge Group, Jackass = Jackass Mountain Group, Crow. = Crowsnest. Italics indicate marine shales (non plant-bearing).

grades laterally and vertically into alluvial-deltaic sandstone, mudstone, coal, and conglomerate. Those sediments are included in the Fort St. John Group and Dunvegan Formation.

The upper sequence is represented by the Smoky Group and Wapiti Formation. The Smoky Group consists of marine strata that record the two vast transgressions of the boreal seaway in Turonian and Santonian time, which coalesced with the Gulf of Mexico seaway. The succeeding coarse clastic sediments of the Wapiti Formation represent Campanian to Maastrichtian regressive deposits.

Fort St. John Group

The Fort St. John Group is exposed along the Foothills belt of the Rocky Mountains in northeastern British Columbia and western Alberta. It also occurs in the subsurface of the Interior Plains, and extends under the Liard Plateau of the Yukon Territory and District of Mackenzie. However, the complete four cycles of transgression-regression sequences within the group are shown only in the Peace River Arch area (Pine and Peace River area) (Fig. 2.3). Deposition in this area was related to tectonism during the Columbian Orogeny and was influenced by the up-and-down movements of the Peace River Arch (Stott, 1968, 1982).

The Fort St. John Group consists of four major sequences; each contains marine shale at the base which grades vertically upward into near-shore, deltaic, or alluvial deposits. The first marine transgression from the north began in early Early Albian. The Interior was inundated in late Early Albian time by a broad gulf of the Boreal ocean, which flooded the old Interior drainage basin some 2400 km inland to as far south as the present location of Calgary in southern Alberta (Stott, 1968, Jeletzky, 1971). This marine transgression is represented by the widely distributed Moosebar Formation (corresponding rocks in the northern part of the basin are the Buckinghorse and the Garbutt formations), which is composed of marine shale and siltstone. It falls mainly within the Early Albian *Arcthoplites* Zone (Jeletzky, 1971; Stott, 1982). Deltaic deposits and alluvial deposits developed to the south of the Moosebar sea. With the northward progradation of these deltas and the alluvial plain, a major regression process began. This regression process was recorded in the Gates Formation, of which the corresponding rocks in the northern part of the basin are the Bulwell Member of the Scatter Formation.

Overlying shales (representing the second marine transgression), extending upward in the Middle Albian *Pseudopulchellia pattoni* Zone (Jeletzky, 1971; Stott, 1982) are assigned to the Hulcross Formation, of which the corresponding rocks are lower middle Buckinghorse Formation and the Wildhorn Member of the Scatter Formation. Marine sandstone included in the basal Boulder Creek Formation, corresponding to the Cadotte Member of the Peace River Formation and the Tussock Member of the Scatter Formation, lies within the *Gastroplites* Zone (Jeletzky, 1971; Stott, 1982).

Younger marine shales of the Hasler Formation, the middle Buckinghorse and the Lepine Formation, representing the third marine transgression, lie within the Late Albian *Stelckiceras liardense* Zone (Jeletzky, 1971: Stott, 1982). Those shales grade upward into epineritic deposits of the Goodrich Formation and the Sikanni Formation in the north, both composed of sandstones and deposited during the Late Albian *Neogastroplites* Zone (Jeletzky, 1971; Stott, 1982).

Representatives of the fourth relative marine transgression, the Cruiser Formation and the Sully Formation of Albian to Cenomanian age, grade transitionally upward into the Cenomanian (earliest Late Cretaceous) Dunvegan Formation.

Among the four transgression-regression cycles, all except the first one appear to be confined to the Peace River Arch area and to have been caused by the up and down oscillation of the Peace River Arch. Supporting evidence for this includes the observation that the trends of maximum accumulation of the Gates and Boulder Creek sandstones are parallel the major structural trend related to the Peace River Arch (Stott, 1982; Leckie, 1986b).

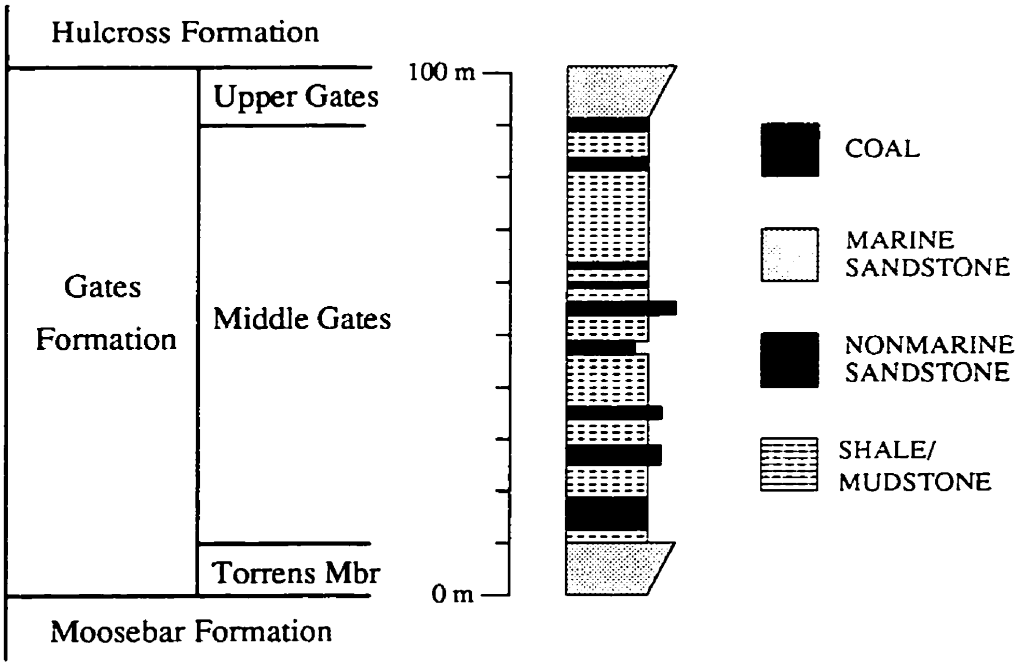
Gates Formation

As defined by Stott (1982), Gates Formation refers to the lowest of three members of the Commotion Formation (Fig. 2.5), which was earlier defined by Wickenden and Shaw (1943) as a sequence of sandstone, shale and conglomerate that overlies the Moosebar shale in Pine River valley. The middle and upper members were renamed Hulcross Formation and Boulder Creek Formation, respectively, by Stott (1982).

Lithologically, as described by Stott (1982), the Gates Formation is a set of alluvial, deltaic, and epineritic sediments, which at its type locality (Pine River valley) consists primarily of massive- to thin-bedded fine-grained, well-sorted sandstone. The basal part is characterized by fine-grained, fairly well-sorted sandstone: the middle part consists of a cyclic succession of carbonaceous sandstone, mudstone, siltstone, coal, and some conglomerate; the top is typically marked by thick-bedded sandstone. Informally, the Gates Formation is commonly divided into the Torrens Member, the Middle Gates and the Upper Gates (Lamberson et

SERIES	STAGES	GROUPS		FORMATIONS
Upper Cretaceous	Cenomanian			Dunvegan (sandstone, 107-300m)
Lower Cretaceous	(97.5 Ma) Albian (113 Ma)	Fort St. John Group		Cruiser (marine shale, 107-244 m)
				Goodrich (sandstone, 15-411 m)
				Hasler (marine shale, 152-459 m)
			Commotion Formation	Boulder Creek (sandstone, 73-171 m)
				Hulcross (marine shale, 0-131 m)
				Gates (sandstone, 67-274 m)
				Moosebar (marine shale, 30-304 m)
	Aptian	Bullhead Group		Gething (sandstone and shale, 22-549 m)
				Cadomin (conglomerate, 14-214 m)

(A)



(B)

Figure 2.5: Diagram showing the Gates stratigraphy. A. Modified after Stott, 1982, Table 1. B. Modified after Lamberson et al., 1991, Fig. 3: Geologic Column of the Gates is from Quintette area, Tumbler Ridge and appears to be typical of the study area.

al., 1991). The Torrens Member refers to the basal thick-bedded sandstone; the Upper Gates, the top thick-bedded sandstone; and the Middle Gates, the cyclic succession of carbonaceous sandstone, mudstone, siltstone and coal (Fig. 2.5).

Coal seams of economic thickness occur only in the Middle Gates and are as thick as 10 meters. The number of economic coal seams varies from place to place. In the Quintette area, nine coal seams are recognized; only six seams are present at the Bullmoose area (Lamberson et al., 1991); and only two coal seams occur in Grande Cache. Each coal seam is named locally, and their relationships are difficult to determine.

Sandstones of the Gates Formation are characterized by typical delta-front sandstones (Stott, 1982; Leckie, 1986b) and can be traced laterally into coal-bearing beds of the delta-plain environment. Coals accumulated in strandplain setting (Kalkreuth and Leckie, 1989), and in general, directly overlie beach deposits and occur within flood plain deposits (Stott, 1968, 1982; Leckie, 1986b). Terrestrial origin of parts of this formation is indicated by the abundance of carbonaceous material. The well preserved delicate flora, rootlets, fallen logs, and upright stumps are indicative of preservation in place. Studies of Gates deposits have indicated that sediment supply was from the west and southwest (Stott, 1968). The source area was regionally extensive, and extended well into the Omineca Crystalline Belt and eastern margins of the Intermontane Belt (Fig. 2.2) (Leckie, 1968a, b).

2.3 Geological age of the Gates Formation

Thanks to the intercalations of marine shales and paralic coal-bearing measures in the Fort St. John Group, the Gates Formation can be precisely dated by reference to its underlying and overlying marine strata, which have been well dated on the basis of both macrofaunas and microfaunas.

The Moosebar Formation, underlying the Gates Formation, was dated as Early to Middle Albian on the basis of microfaunal assemblage, which includes *Marginulinopsis collinsi* Mellon & Wall, *Saracenaria trollopei* Mellon & Wall, and *Quadimorphina albertensis* Mellon & Wall (Stelck et al., 1956; Mellon et al., 1963; Chamney in Stott; 1968, p. 55).

Caldwell et al. (1978) established the *Gaudryina nanushukensis* foraminiferal zone, which was subdivided into six subzones; the third subzone *Marginulinopsis collinsi-Verneuilinoides cummingensis* occurred in the Moosebar Formation of the Foothills and was considered to be the equivalent of the late Early Albian *Arcthoplites irenensis* and *Arcthoplites mcconnelli* ammonite subzones of the *Beudanticeras affine* zone (Jeletzky, 1968).

Since *Arcthoplites* cf. *A. indicum* Spath, *Arcthoplites belli* McLearn and *Arcthoplites irenensis* (*Lemuroceras*) (McLearn and Kindle, 1950) occur in the upper Moosebar shale near Peace River, and fauna of the late Early Albian *Arcthoplites* spp. zone (Jeletzky, 1968) also occurs in the overlying Gates Formation (Stott, 1982), the Gates Formation appears to be of late Early Albian age (Stott, 1982, Fig. 5).

Irish (in: Stott, 1982, p. 16) collected cf. *Arcthoplites* spp., and cf. *Beudanticeras* sp. from the lower part of the Hulcross Formation, which is above the

Gates Formation; from the upper part of the Hulcross Formation, *Gastroplites* spp. were found. *Pseudopulchellia pattoni*, representative of an early Middle Albian zone, was collected from the uppermost 31 meters of the Hulcross Formation in the Peace River Foothills (Jeletzky, 1980).

Stelck et al. (1956) reported that the early Middle Albian *Haplophragmoides multiplum* zone (Caldwell et al., 1978) occurred in the Hulcross Formation. Later paleontological research (Stelck and Leckie 1988; 1990) further confirmed that the Hulcross Formation is of early Middle Albian age.

In terms of contact relationships, the Gates Formation is much more closely related with the Moosebar Formation than the Hulcross Formation, because the Moosebar shales grade continuously, vertically and laterally into the Gates Formation, whereas there is always a distinct lithological change between the Gates and the Hulcross Formation, although there is no obvious hiatus (Stott, 1982, p. 14; Plate 4). On the basis of faunal information and the contact relations, the Gates flora can be precisely determined as late Early Albian.

2.4 Materials and Methods

All fossil materials were collected in two field trips. The first trip, made in 1990, covered two localities: Tumbler Ridge and Cadomin. In Tumbler Ridge, fossils were collected from the Quintette coal mine and the Bullmoose coal mine. In Cadomin, fossils were collected from the Greg River mine. The second trip, made in 1991, covered Grande Cache and Cadomin. Most fossils were collected from the Gates Formation; only a few were from the younger Boulder Creek Formation.

The details of fossil localities are given in appendix A. All the fossils were collected by the author, Dr. James F. Basinger, Cathy Greenwood and Loreleen Britton. About 5000 specimens in total were collected.

Most fossils are preserved as impressions or compressions on fine-grained sandstones or siltstones. Very delicate features of some plant remains are rarely preserved. In general, Gates fossils are not well-preserved in terms of the delicate structures. Some of the impressions may bear some carbon compressions; others are impressions, lacking organic remains.

Differences between two types of impressions have been neglected by paleobotanists. These differences can be very significant when plant leaves present different dorsal features from ventral ones. Two kinds of impressions are recognized in this study. The first will be referred to as **eu-impressions**. An original carbon compression or a mineral replica entirely remains within rocks while its surface features are imprinted on the enclosing rocks, which are the eu-impressions. Eu-impressions include both dorsal and ventral impressions. The dorsal and ventral features of a leaf can be recognized from dorsal or ventral impressions.

The second will be referred to as **sub-impressions**. Sub-impressions form when plant remains have been entirely lost, leaving only their imprints on the sediment; diagenesis and geological history cause mingling of dorsal and ventral features, commonly with loss of features. The two parts of a sub-impression fossil are identical, and present the same information. It is impossible to interpret the dorsal and ventral features of a leaf on the basis of sub-impressions. Both types of impression fossils are recovered from the Gates Formation.

A few fossilized tree trunks have been found. These are actually mineralfilled replicas. No permineralized fossils, so far, have been found or reported from the Lower Cretaceous rocks in the western Interior of Canada. This fact might be related with the low temperatures and humid climate of the area during the Early Cretaceous. Low temperatures and plentiful rain would produce an unsaturated C_aCO_3 environment in the sedimentary basin, which would have been unfavourable to permineralizing processes. Water permeating plant remains would be unable to deposit minerals on cell walls. Those cell walls would soon decompose without the protection of fine mineral layers (Schopf. 1975). When the Boreal seaway coalesced with the Gulf of Mexico in the Late Cretaceous, permineralized fossils began to appear (e.g. McIver and Aulenback. 1994).

Effort has been made to extract cuticles from the fossil plants, but there appears to be no extractable cuticles preserved on the Gates materials. Morphological analysis appears to be the only possible approach for systematic study of the Gates flora.

Chapter 3

The Gates Flora

This chapter describes the fossil plants from the Gates Formation, discusses their distributions, and compare them with the fossil plants from other parts of the world.

All specimens illustrated are deposited in the University of Saskatchewan, Paleobotanical Collection. A specimen number consists of two parts, locality and specimen numbers; for example, 921-7195 refers to locality 921, specimen 7195. All locality numbers refer to the University of Saskatchewan, Paleobotanical Collection. All localities are within the Gates Formation unless they are indicated otherwise as within the Boulder Creek Formation.

Efforts have been made in strict application of the ICBN (1994) as the basis for nomenclature. Where original spelling of specific epithets differs from that now acceptable to the ICBN (1994), spelling has been corrected without further explanation.

Not all materials in synonymy lists have been seen, judgement has been made on the basis of published illustrations and descriptions: only those considered adequately described and clearly illustrated are listed.

Whenever the term "northwestern Interior" is used in the text, it refers to the western Interior of Canada plus northern Montana.

When a new species is established, the holotype for the species is explicitly indicated; other illustrated specimens of the new species are all paratypes.

Division Bryophyta

Class Hepaticae

Order Marchantiales

Family Marchantiaceae

Genus *Marchantiolites* Lundblad

Comments: According to Lundblad (1954), *Marchantiolites* is characterized by air-pores in the preserved cellular structure resembling those in Marchantiineae of the Marchantiales. There are few species being reported within this genus because of difficulty in preserving the delicate lamina of the plants. The differentiation of species within the genus is on basis of the size of thallus and the pattern of cell layers (Brown and Robison, 1976). Two species are currently included within the genus: the type species, *M. porosus* Lundblad, and *M. blairmorensis* (Berry) Brown & Robison. Both were recovered from Early Cretaceous strata.

Marchantites was proposed by Brongniart in 1849 for vegetative thalli similar. in both morphology and habit, to the recent thalloid Hepaticae, as represented by a genus such as *Marchantia* (Seward, 1898). Walton, in 1925, claimed that *Marchantites* should only include one species, *Marchantites sezannensis* Saporta, which has both reproductive organs and vegetative thalli similar to recent *Marchantia*, and that most other species included within *Marchantites* should be transferred to *Thallites* when their affinities were uncertain (Sze et al., 1963). Instead, Walton proposed *Hepaticites* for fossils which showed features exclusive to the hepatics (Hepaticae) (Harris, 1961; Sze et al., 1963).

Because only the vegetative thalli are recovered in the Gates materials, it is impossible to compare the Gates materials with *Marchantia*, and therefore *Marchantites* is not appropriate for the Gates materials. Because the Gates materials are very similar to *Marchantiolites blairmorensis*, which was reported by Brown and Robison (1976) from the area adjacent to the Gates Formation, the Gates materials appear to belong to *Marchantiolites.* Although it is also correct to assign the Gates materials to *Hepaticites*, *Marchantiolites* appears to be a more appropriate name than *Hepaticites* because *Hepaticites* is a form-genus.

Generitype: *Marchantiolites porosus* Lundblad

Marchantiolites blairmorensis (Berry) Brown & Robison

(Pl. 1, fig. 1)

Basionym: *Marchantites blairmorensis* Berry, 1929, p. 34, Pl. 4, figs. 1, 2.

Thallites blairmorensis (Berry) Lundblad, 1954, p. 409; Bell, 1956, p. 46, Pl. I, fig. 1.

Marchantiolites blairmorensis (Berry) Brown & Robison, 1976, p. 309, Text-figs. 1, 2; LaPasha and Miller, 1985, p. 117, Pl. 1, fig. 1-3; Chen et al., 1988, p. 31, Pl. 3, fig. 1.

Description: Thallus dichotomously branched at an acute angle, laminae ribbon-like, 5 to 15 mm wide. Medially there is a vein-like, microscopically striated band, 0.5-1.5 mm wide. Although the consistency of the lamina is thin, that of the vein-like band appears very thick. Laminae typically smooth, rarely with hair-like striae.

Materials: Total 7 specimens. Locality no.: 851, 858 (Boulder Creek Fm.), 877, 920.

Distribution: This species has been reported from the Early Cretaceous in the Fuxin Formation of northeastern China and the northwestern Interior strata, the Gates, Boulder Creek and Kootenai formations, and the Blairmore Group (lower flora). The distribution of *M. blairmorensis* appears confined to the Aptian-Albian in the Arctic Province.

Discussion: *Marchantiolites blairmorensis* was originally described as *Marchantites blairmorensis* Berry (1929). Lundblad (1954) transferred this species to *Thallites* because of its uncertain affinity. Bell (1956) also indicated that the superficial resemblance of this species to living species of the genus *Marchantia* does not necessarily indicate affinity, as suggested by Berry (1929).

Brown and Robison (1976) studied the cuticles of this species and transferred it to *Marchantiolites*. *Marchantiolites blairmorensis* differs from the type species *M. porosus* in having a larger thallus than the type species, which is not more than 2.6 mm wide, and in that the former species commonly has only a single series of smaller cells surrounding the air pore, while in the latter the cells appear to form two or three rows (Brown and Robison, 1976).

All specimens of this species available from the Gates Formation are impressions; it is impossible to detect lamina cell structures. However, because the Gates materials are morphologically identical to the type of the species, which was recovered from the adjacent area to the Gates Formation, it is reasonable to assign the Gates materials to *M. blairmorensis.*

Chen et al. (1988, p. 31, Pl. 3, fig. 1) reported the occurrence of *M. blairmorensis* from the Fuxin Formation of the Early Cretaceous in northeastern China. Although their only photo is not clear and the width of the lamina was not provided in their description, they claimed that their specimen was very similar to the Montana materials described by LaPasha and Miller (1985), and concluded that their specimen was in accordance with the Montana materials in thallus form, branching manner and medial band. Most likely, their specimens are conspecific with the Gates materials.

Division Incertae Sedis (Bryophyta ?)

Class/Order/Family Incertae Sedis

Genus *Thallites* Walton

Comments: According to Sze et al. (1963), Walton instituted this genus in 1925 for all plant bodies in thalloid form, potentially including algae, bryophytes and even fern prothalli. The differentiation of species within the genus is based on the size of the thallus, the branching patterns, and the size of the medial band. Numerous species within this genus have been reported from the Carboniferous to Quaternary.

Generitype: *Thallites erectus* (Leckenby) Walton

Thallites sp.

(Pl. 1, figs. 2, 3)

Description: Preserved lamina up to 5 cm long, dichotomously branched once at an acute angle, laminae ribbon-like, average width about 2 mm. maximum 3.5 mm. Laminae have a distinct and broad midrib, which comprises about 1/3 of the lamina width. The lamina on either side of the midrib is thin and filmy.

Materials: Only one specimen. Locality no.: 858 (Boulder Creek Fm.).

Distribution: Boulder Creek Formation.

Discussion: The morphology and size of complete thalli are unknown because the preserved lamina is only part of a thallus; the size of a complete thallus may have been more than 5 cm in length.

Macroscopically, this species is distinguished from *Marchantiolites blairmorensis* and *Marchantites sezannensis* Saporta (Seward, 1898) by its small lamina width. *Thallites erectus* (Leckenby) Walton, *T. pinghsiangensis* Hsü and *T. zeilleri* (Seward) Harris are different from the Gates species in their even smaller size of thallus and profuseness of branching. There appears no suitable species that the Gates materials can be assigned to, yet it is not appropriate to institute a new species on the basis of a single incomplete specimen.

Division Tracheophyta

Class Sphenopsida

Order Equisetales

Family Incertae Sedis

Genus *Equisetites* Sternberg

Comments: Some authors prefer to use *Equisetum* for *Equisetum*-like Mesozoic fossils (Harris, 1961; LaPasha and Miller, 1985), others prefer *Equisetites* (Sze et al., 1963; Chen et al., 1988). Seward (1898) justified retention of *Equisetites* as follows:

"The generic name *Equisetites* was proposed by Sternberg in 1838 as a convenient designation for fossil stems bearing a close resemblance to recent species of *Equisetum*. Some authors have preferred to apply the name *Equisetum* to fossil and recent species alike, but in spite of the apparent identity in the external characters of the fossil stems with those of existing Horse-tails, and a close similarity as regards the cones, there are certain reasons for retaining Sternberg's generic name. **It is important to avoid such nomenclature as might appear to express more than the facts admit.**" (Seward, 1898, p. 257) (Bold face is added by the author, Z. Wan).

In my opinion, *Equisetum*-like fossils of post-Late Cretaceous can be assigned to *Equisetum*, but those of pre-Early Cretaceous had better be assigned to *Equisetites* because the Late Cretaceous vegetation is quite different from that of the Early Cretaceous so that there a chance that pre-Early Cretaceous *Equisetum*-like fossils differ from *Equisetum*. Therefore, *Equisetites* appears to be more appropriate than *Equisetum* for the Gates materials.

Many species are recognized on the basis of the size of stem, the length of internode, and the number, size and morphology of teeth in a leaf-sheath. When only diaphragms are available, species are separated on the basis of the shape of diaphragms, and number and length of the spokes. The underground rhizomes provide little information for species recognition. Species reported range from Carboniferous to Quaternary in age (Cenozoic species are generally assigned to the living genus *Equisetum*).

Generitype: *Equisetites muensteri* Sternberg

Equisetites montanensis (LaPasha & Miller) comb. nov.

(Pl. 2, figs. 1-3)

Basionym: *Equisetum montanensis* LaPasha &Miller, 1985. Palaeontog., Abt. B, Bd. 196, p. 119, Pl. 2, figs. 7, 8, text-fig. 4B.

Original Diagnosis: "Stems 2.0-4.0 mm wide, 2-3 ridges seen in surface view of compressions and about 5 prominent ridges and 5 furrows in entire stem, internode length 4 cm or more; leaves about 5.0 mm long, 1.0-2.0 mm wide, fused basally forming a leaf sheath, free part of leaf about 2.0 mm long, apex acuminate; leaf sheath tightly appressed to the stem, sometimes slightly bulging but with leaf apices appressed to stem (LaPasha and Miller, 1985, p. 119)".

Emended Diagnosis: Aerial shoots articulated, 2-4 mm wide; internode 2 cm or more in length; about 5-8 ridges in an entire stem; secondary branches arising from the nodes. Leaves about 5 mm long, 1-2 mm wide, fused basally to form a leaf sheath, 5-8 leaves per sheath, free part of leaf 1-2 mm long, apex acuminate; leaf sheath tightly appressed to the stem, sometimes slightly bulging but with leaf apices appressed to stem.

Tuber-bearing rhizomes articulated, 3 mm wide; internode 1-5 cm long. Tubers oval, ovate or globose, up to 1 cm in diameter, paired on node, their surfaces generally wrinkled.

Materials: Specimens numerous. Locality no.: 926, 950, 951, 952.

Distribution: This species has been reported from the Gates Formation and Kootenai Formation. Its distribution appears confined to the Aptian-Albian in the northwestern Interior of North America.

Discussion: The Gates materials are similar to those reported from Montana by LaPasha and Miller (1985), except the length of the internode is shorter and the number of leaves in a sheath is slightly greater than reported for Montana specimens. These differences are considered as normal variation within a species.

As discussed under generic comments, *Equisetites* is preferred over *Equisetum* for the Gates materials. Therefore the species is transferred from *Equisetum* to *Equisetites*. The gender of *Equisetum* is neuter. The gender of the specific epithet *montanensis*, chosen by LaPasha and Miller (1985), is not in accordance with *Equisetum* in gender but happens to be the same as that of *Equisetites*. Therefore, the suffix of the specific epithet does not need to be changed.

This species differs from most other Mesozoic *Equisetites* by its small size. Among smaller *Equisetites*-like species, *Equisetum filum* Harris (1979) is similar to the present species in stem size, but differs in having obtuse teeth. LaPasha and Miller (1985) also indicated that the leaves of *Equisetum filum* Harris were less extensively fused. *Equisetum virginicum* Fontaine (1889) is similar in almost every aspect to the present species except that it has a stem twice as wide. *Equisetum marylandicum* Fontaine (1889) differs from the Gates species mainly in having shorter leaves.

Although no connections of aerial shoots with the underground rhizomes are found in the Gates material, it is concluded that both parts are from one type of plant, because among the very numerous specimens found in the Gates Formation, only one type of aerial organs, and one type of rhizome are recognized.

Class Filicopsida

Order Filicales

Family Dicksoniaceae

Genus *Acanthopteris* Sze emend. Chow

Generic Diagnosis: Frond pinnately divided; sterile pinnules pecopteroid, or *Cladophlebidium*-type; sori terminal, situated on apices of fertile pinnules, wrapped in indusia; indusium bivalved like that of the living *Dicksonia*.

Comments: *Acanthopteris* was instituted by Sze in 1931 to designate pinnate fronds characterized by having more or less triangular pecopteroid pinnules and intercalated pinnules (Sze et al. , 1963). Chow supplemented the reproductive organ information in 1974, which, together with the vegetative pinnae, was summarized by GIW (1978). Since there was originally only the type species *A. gothanii* in the genus, the generic diagnosis of *Acanthopteris* was not explicitly given and was assumed to be the same as the specific diagnosis of *A. gothanii*. The above given generic diagnosis is summarized by the author on the basis of GIW (1978) and Chen et al. (1981).

Acanthopteris has been generally accepted as a natural genus in the family Dicksoniaceae. However, Zhang et al. (1980, p. 250) listed the genus under Incertae Sedis instead of under Dicksoniaceae. They also claimed that the fertile pinnae of the genus were the same as those of *Coniopteris*, which was included in the Dicksoniaceae by them. There is inconsistency in their point of view.

The genus *Birisia*, established by Samylina in 1972, is a synonym of *Acanthopteris* (Chen et al., 1981; Zheng and Zhang, 1983; Cao, 1983; Chen et al., 1988).

Kylikipteris Harris (1961) differs from *Acanthopteris* in having cup-shaped indusia rather than bivalved indusia (Figure 3.1). In practice, it is difficult to show the nature of the indusium, so that recognition of *Acanthopteris* is mainly on the basis of sterile pinnae. Therefore, it is quite possible that specimens of *Kylikipteris* are included in *Acanthopteris*.

Eboracia Thomas (Harris, 1961) mainly differs from *Acanthopteris* in having marginal sori rather than terminal ones (Figure 3.1). Also, indusia of *Eboracia*

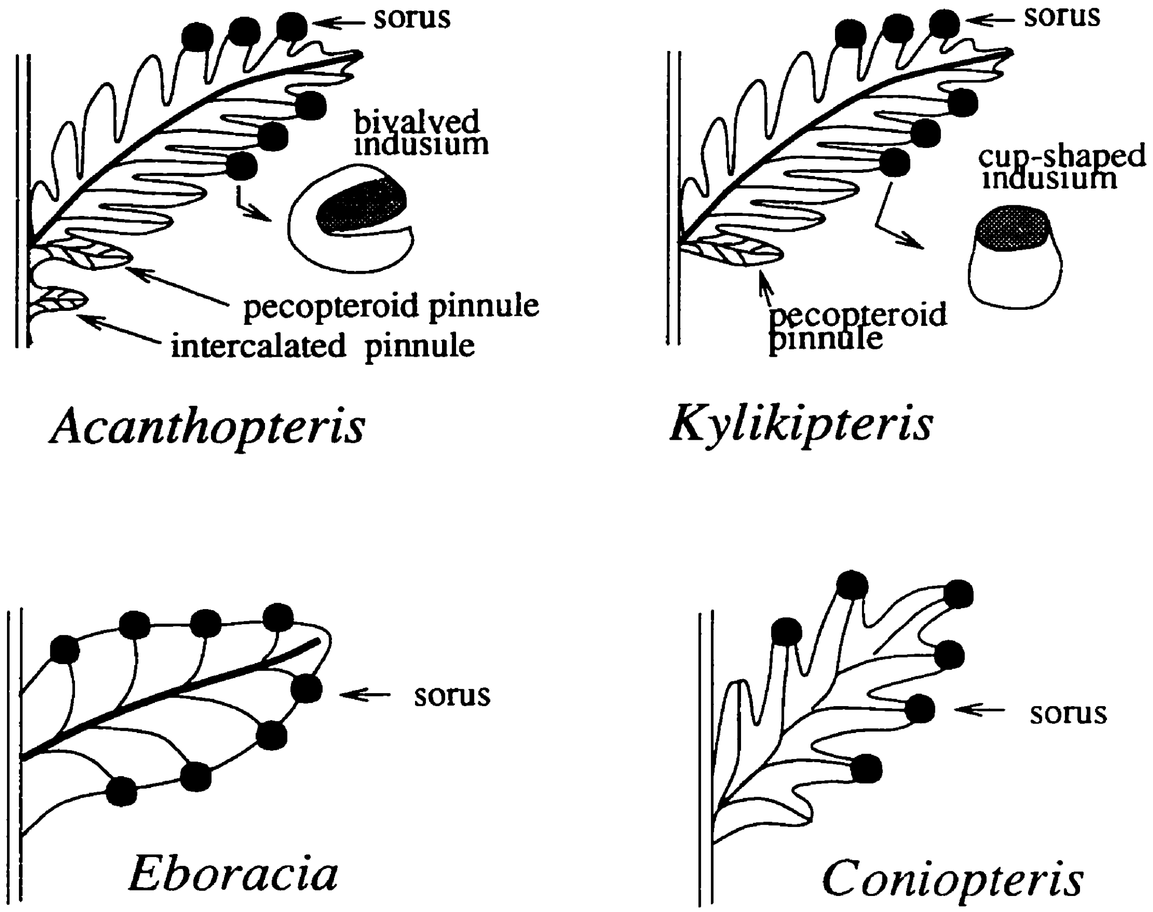


Figure 3.1: Morphology of similar fossil genera of Dicksoniaceae

are cylindrical rather than bivalved.

Coniopteris Brongniart differs from *Acanthopteris* in having sphenopteroid sterile pinnae rather than pecopteroid pinnae (Figure 3.1). Although Chen et al. (1981) indicated that the indusia of *Acanthopteris* were similar to those of *Dicksonia*, which has bivalved indusia, and that indusia of *Coniopteris* were similar to those of *Thyrsopteris*, which has cup-shaped indusia, Krassilov (1978, p. 21, Pl. 8, figs. 72-81) showed that some species of *Coniopteris* may have bivalved indusia, too. Therefore, the indusium of *Coniopteris* may be like that of *Acanthopteris*.

A concise generic definition of *Acanthopteris* was given by Chen et al. (1981, p. 46) to be: "*Cladophlebidium*-type sterile pinnae plus *Dicksonia*-type fertile pinnae" (translated from Chinese by the author).

Zhang et al. (1980) and Cao (1983) claimed that the fertile pinnae of *Acanthopteris* were of the *Coniopteris* type. As the indusia of *Coniopteris* include both bivalved and cup-shaped forms (Harris, 1961; Krassilov, 1978), the definition of *Acanthopteris* given by Zhang et al. and Cao appears to overlap that of *Kylikipteris*.

It is, hereby, suggested that *Kylikipteris* Harris be restricted to plants having cup-shaped indusia; *Acanthopteris* Sze refers to both plants having bivalved indusia and plants whose indusium nature is imperfectly known.

Although five species have been reported within the genus, only two of them are generally accepted, *A. gothanii* Sze and *A. onychioides* (Vassilevskaya & Kara-Mursa) Zhang. Differentiation between these species is on the basis of size of pinnae and pinnules, venation, and the existence of intercalated pinnules.

Generitype: *Acanthopteris gothanii* Sze

Acanthopteris gothanii **Sze**

(Pl. 2, figs. 4-6; Pl. 3, figs. 1-4)

Cladophlebis alata Fontaine *sensu* Fontaine, 1905d, p. 158, Pl. XXXIX, figs. 9-11, Pl. XL; [*non*] Fontaine, 1889, p. 77, Pl. XIX, Fig. 5; [*non*] Fontaine, 1905h, p. 229, Pl. LXV, Figs. 17-21.

Coniopteris pachyphylla (Fontaine) Berry, 1929, [*pro parte*] p. 42, Plate VII, figs. 1, 2 [*only*].

Coniopteris brevifolia (Fontaine) Bell, 1956, [*pro parte*] p. 47, Pl. I, fig. 3, Pl. II, figs. 1, 3, Pl. III, fig, 1, Pl. VI, fig. 2 [*only*].

Acanthopteris gothanii Sze, 1931, p. 53, Pl. 7, figs. 2-4 (type not seen; reference cited from Chen et al., 1988, p. 39); Sze et al., 1963, p. 125, Pl. 46, figs. 1, 2; GIW, 1978, p. 170, Text-fig. 3-29; Chen et al., 1981, p. 46, Pl. I, figs. 1-3; Yang and Sun, 1982, 5, p. 589, Pl. I, figs. 1, 2; Chen and Yang, 1982, p. 577, Pl. I, fig. 3; Cao, 1983, p. 30, Pl. II, figs. 3, 3a; Chen et al., 1988, p. 39, Pl. 9, figs. 1-5, Pl. 10, figs. 1, 2, Pl. 12, fig. 1, Pl. 62, figs. 5-7.

Sphenopteris sp. "*d*"; Douglas, 1973, p. 81, Pl. 22, Figs. 7, 17.

Coniopteris frutiformis Douglas, 1973, p. 24, Pl. 27, Pl. 28; Figs. 7, 24, 25.

Coniopteris inenarabilis (Hollick) Scott & Smiley, 1979, Pl. 2, fig. 1.

Acanthopteris alata (Fontaine) Zhang, 1980, p. 251, Pl. 158, figs. 6-7, Pl. 159, figs. 1-3.

Coniopteris hymenophylloides (Brongniart) Seward *sensu* LaPasha and Miller, 1985, [*pro parte*] p. 121, Pl. 4, figs. 5, 6, Text-fig. 5-I [*only*]; [*non*] Seward, 1910, p. 367, Figs. 271, 271, 275 B; [*non*] Harris, 1961, p. 152, Text-figs. 53, 54; [*non*] Sze et al., 1963, p. 75, Pl. 24, fig. 6, Pl. 46, fig. 3.

Sphenopteris maclearnii Bell *sensu* LaPasha and Miller, 1985, p. 131, Pl. 7, figs. 5, 6, Text-fig. 10 (D-F); [*non*] Bell, 1956, p. 73, Pl. XXIII, fig. 3, Pl. XXIV, fig. 2, Pl. XXVII, fig. 3.

Description: Frond large, at least tripinnate; rachis longitudinally ridged, up to 2 mm broad, winged distally. Pinnae linear up to 2.5 cm long by 0.5 cm wide, with acuminate apices; base decurrent; pinna rachis winged. Intercalated pinnae morphologically same as normal pinnae.

Pinnules up to 5 mm long and 1 mm wide, oblique, pecopteroid, variable, generally deltoid to linear lanceolate, more or less curving forward; the posterior margin convex, the anterior margin slightly concave, pinnule having acute-pointed apex; base decurrent, neighbouring pinnules connected at base; pinnule arising in katadromic order, basal pinnule decurrent on pinna rachis, forming an intercalated pinnule; intercalated pinnules morphologically the same as normal pinnules; those on the main rachis modified into triangular shape.

Venation pecopteroid, veins slender, 3-4 pairs of simple or once-divided lateral veins arising at acute angle from the midvein.

Fertile pinnae appearing in the upper part of frond; pinnule membrane strongly reduced; sori subcircular, large, up to 1.5 mm in diameter, enclosed in indusia, borne on ends of midveins; details of the indusia and sporangia unknown.

Materials: Specimens numerous. Locality no.: 875, 878, 925, 950-951, 956, 957.

Distribution: This species has been reported from the northwestern Interior (Bell, 1956, LaPasha and Miller, 1985), Alaska (Fontaine, 1905d; Scott and Smiley, 1979), northeastern China (Chen et al., 1988) and Siberia GIW (1978). It also apparently occurs in the Early Cretaceous of the Antarctic Province (Douglas, 1973). Its distribution appears confined to both the Arctic Province and the

Antarctic Province from the Neocomian to Albian. Occasionally it occurs in the Late Jurassic.

Discussion: The Gates materials show apparent intercalated pinnules and/or pinnae. Intercalated pinnules in the upper part of the frond look like decurrent pinnules (Pl. 2, fig. 4; Pl. 3, fig. 4); in the lower part of the frond, the intercalated pinnule is attached to the main rachis (Pl. 2, fig. 5 A). The vegetative pinnae are very similar to the Chinese materials figured as *A. gothanii* (Sze, 1931; Sze et al., 1963), and there is no doubt that they are conspecific.

One of the specimens from the Luscar Formation figured by Bell (1956, p. 47, Pl. III, fig. 1) as *Coniopteris brevifolia* shows apparent intercalated pinnules and appears to be referrable to *A. gothanii.* Furthermore, *Coniopteris brevifolia* (Fontaine) Bell appears to be an invalid species name, since Bell did not explicitly indicate the basionym of this species at the time of transfer.

The Montana materials figured by LaPasha and Miller (1985, p. 131, Pl. 7, figs. 5, 6) as *Sphenopteris maclearnii* also show apparent intercalated pinnules, which are absent on the holotype of *Sphenopteris maclearnii* Bell (1956, p. 73, Pl. XXIV, fig. 2, Pl. XXVII, fig. 3); the Montana specimens appear to be conspecific with *A. gothanii.*

The best fertile specimen shows only part of a fertile pinna (Pl. 2, fig. 6). Although the basal intercalated pinnule can not be observed, the size and morphology of this fertile pinna fit those vegetative pinnae quite well. Sterile pinnules at the base of this specimen are consistent with those of vegetative pinnae. Therefore, it is concluded that this kind of fertile pinna is also conspecific with

A. gothanii. Similar specimens from the Luscar Formation figured by Bell (1956, p. 47, Pl. I, fig. 3; Pl. II, figs. 1, 3; Pl. VI, fig. 2) as *Coniopteris brevifolia* have terminal sori rather than marginal ones and appear to be conspecific with *A. gothanii.* The Montana materials figured by LaPasha and Miller (1985, p. 121, Text-fig. 5-I, Pl. 4, figs. 5, 6) as *Coniopteris hymenophylloides* have terminal sori rather than marginal ones; they also appear to be conspecific with *A. gothanii.*

The Alaska materials identified by Fontaine (1905d) as *Cladophlebis alata* appear to be conspecific with *A. gothanii* in terms of vegetative pinna morphology, although there are no fertile pinnae reported from Alaska. They differ from the type specimen of *Cladophlebis alata* (Fontaine, 1889; p. 77, Pl. XIX, fig. 5) from the Potomac Group in having obvious intercalated pinnules or pinnae, which are absent on the Potomac materials.

Zhang et al. (1980) created a new combination on the basis of the Alaska materials and Chinese materials, *A. alata* (Fontaine) Zhang. Fertile pinnae were reported as of the *Coniopteris* type. Zhang et al. (1980) indicated that *A. alata* differs from *A. gothanii* in having larger pinnules (15-20 mm long and 2-3 mm wide), but they also mentioned that this difference was not so apparent and the two might belong to one species. Chen et al. (1988) indicated that the delimitations of those two species were not clear, and showed that a frond of the *A. alata* type formed part of the upper frond of *A. gothanii.*

In addition, there appears to be some nomenclatural problem with *A. alata* (Fontaine) Zhang. The basionym of *A. alata* (Fontaine) Zhang is *Cladophlebis alata* Fontaine, which was typified by the Potomac material. What Zhang et al. (1980) referred to was probably the Alaska materials, because only the Alaska materials were cited in their synonym list, rather than the Potomac material. In fact, the Potomac material (Fontaine, 1889, p. 77, Pl. XIX, Fig. 5) is different from the Alaska materials (Fontaine, 1905d, p. 158) in lacking intercalated pinnules. Therefore, *A. alata* (Fontaine) Zhang is an invalid combination.

Another Alaska specimen figured by Scott and Smiley (1979, Pl. 2, fig. 2) as *Coniopteris inenarabilis* shows no difference from *A. gothanii* and therefore is treated as synonymous.

Zhang et al. (1980) established three new species of *Acanthopteris*, *A. acutata* (Samylina) Zhang, *A. alata* (Fontaine) Zhang and *A. onychioides* (Vassilevskaya et Kara-Mursa) Zhang. Cao (1983) instituted another new species, *A. szei* Cao, which lacked intercalated pinnules. Although five species have been reported, only two species have generally been accepted : *A. gothanii* Sze and *A. onychioides* (Vassilevskaya & Kara-Mursa) Zhang; the former has intercalated pinnae, the latter does not (Sze et al., 1963,; Zhang el al., 1983; Cao, 1983).

Chen et al. (1981) claimed that all the reported species of *Acanthopteris*, including the North American, Russian, Chinese and Japanese materials, were possibly only one species, *A. gothanii*. Accordingly, the differences among various species would represent variations found in different parts of a frond. Later on Chen et al. (1988) changed their point of view and indicated that *Coniopteris onychioides* Vassilevskaya & Kara-Mursa, the basionym of *A. onychioides* (Vassilevskaya et Kara-Mursa) Zhang, differed from *A. gothanii* in lacking intercalated pinnules in the middle and lower part of the frond and in having a curving rachis. Therefore, only *A. gothanii*, *A. onychioides* and *A.* sp. are accepted as distinct species in this study.

The two specimens from the Kootenay Formation figured as *Coniopteris pachyphylla* (Berry, 1929, p. 42; Pl. VII, figs. 1, 2) are identical to those of *A. gothanii.* The basionym of *Coniopteris pachyphylla* (Fontaine) Berry, *Dicksonia pachyphylla* Fontaine, is a fertile fragment from the Shasta Formation (Fontaine, 1905h, p. 224, Pl. LXV, fig. 1). Similar fertile fragments can be found among remains of either *A. gothanii* or some species of *Coniopteris*, like *C. bidens* (Bell) comb. nov, and *C. simplex* (Harris, 1961). Because the pinna base of the Shasta material can not be observed, it is uncertain if intercalated pinnule exists. Therefore, the identity of the Shasta material can not be confirmed.

The materials from the Kootenai Formation figured as *Dicksonia pachyphylla* Fontaine (1905i, p. 288, Pl. LXXI, figs. 5-11) appear to belong to more than one species. The specimen in Pl. LXXI, fig. 11 (Fontaine, 1905i) may be conspecific with *A. gothanii* judging from the general shape of that specimen, but the pinna base is not preserved and the information about intercalated pinnules is absent. Therefore, its identity can not be confirmed.

Other fertile pinnae from the Kootenai Formation (Fontaine, 1905i, p. 288, Pl LXXI, figs. 7-10) do not show enough features to confirm their identity. The sterile specimen in Pl. LXXI, figs. 5, 6 (Fontaine, 1905i) is quite different from *A. gothanii* in having bifurcated pinnules, a feature that is, however, characteristic of *Coniopteris bidens* (Bell) comb. nov.

The materials from the Kootenai Formation figured as *Dicksonia montanensis* Fontaine (1905i, p. 286, Pl. LXXI, figs. 1-4) were cited by Berry (1929, p. 42) as a synonym of his *Coniopteris pachyphylla* (Fontaine) Berry. None of those specimens shows intercalated pinnules. The specimen in Pl. LXXI, figs. 1, 2

(Fontaine, 1905i), which is from the upper part of a frond, does, however, show the existence of intercalated pinnules. The one in Pl. LXXI, figs. 3, 4, which appears to be from the middle and lower part of a frond, does not show any intercalated pinnules. Considering that the rachis is curving, as shown on Fontaine's Pl. LXXI, fig. 3, *Dicksonia montanensis* is most likely conspecific with *A. onychioides*.

All the Australian specimens figured as *Sphenopteris* sp. "*d*" and *Coniopteris frutiformis* Douglas (1973) are morphologically similar to *A. gothanii* and are treated as conspecific.

Acanthopteris sp.

(Pl. 3, fig. 5)

Coniopteris brevifolia (Fontaine) Bell, 1956, [*pro parte*] p. 47, Pl. III, fig. 2 [*only*].

Sphenopteris warragulensis McCoy *sensu* Douglas, 1973, p. 73, Pl. 20, figs. 1-2; Figs. 7, 6-9.

Description: Frond at least bipinnate; pinna linear, up to 4 cm long by 0.5 cm wide, apex acute, base decurrent on rachis, winged. Pinnules up to 10 mm long and 2 mm wide, oblique, inserted on rachis at acute angle, pecopteroid, variable, generally linear lanceolate to linear elliptic, more than 2/3 part of the posterior side free, about 1/3 part of the anterior side free; apex acute-pointed; base decurrent, neighbouring pinnules connected at base; pinnules arising in katadromic order, basal pinnule decurrent to the primary pinna rachis, appearing to be an intercalated pinnule. Venation pecopteroid, veins slender, 2-3 pairs of simple or once-divided lateral branches arising at acute angle from the midvein.

Fertile pinnules unknown.

Materials: 3 specimens. Locality no.: 853.

Distribution: This species has been recovered from the Gates Formation and The Bullhead Group in the northwestern Interior and from the Lower Cretaceous of Victoria, Australia. It distribution appears confined to the Lower Cretaceous of both the Arctic and the Antarctic Provinces.

Discussion: These materials are morphologically similar to vegetative pinnae of *A. gothanii*, but its pinnules are about as twice large as those of *A. gothanii*. As there were no intermediate forms between *A.* sp. and *A. gothanii* in the Gates Formation, *A.* sp. appears to be a distinct species. Because of the fragmentary nature of the specimens and the absence of fertile materials, it is not appropriate to institute a new species.

Bullhead material figured as *Coniopteris brevifolia* (Bell, 1956, p. 47, Pl. III, fig. 2) is morphologically identical with *A.* sp. and appears to be conspecific.

The Victoria specimens figured as *Sphenopteris warragulensis* (Douglas, 1973) are morphologically identical with *A.* sp and appear to be conspecific. The Victoria specimens include both fertile and sterile pinnae. Since the type material of *Sphenopteris warragulensis* was not available for examination, it is uncertain whether the Victoria specimens are correctly identified as *Sphenopteris warrag-*

ulensis and should therefore be recombined, or if they should represent a new species of *Acanthopteris*.

Genus *Coniopteris* Brongniart

Comments: The nomenclatural difficulties of *Coniopteris* have been discussed in detail by Harris (1961). *Coniopteris* was founded by Brongniart in 1849 for the sterile leaf *Sphenopteris murrayana* and for what he regarded as its fertile leaf *Tympanophora racemosa* (which probably belong to another separate species). Curiously, Brongniart did not include *Sphenopteris hymenophylloides* within the genus. Subsequently *Coniopteris* was only used intermittently until Seward adopted it in 1900 since when it has been in general use.

Seward (1910) treated the type species *C. murrayana* (Brongniart) Brongniart as a synonym of *C. hymenophylloides* (Brongniart) Seward, but he gave no nomenclatural reasons why *C. hymenophylloides* was employed as the binomial name for the species instead of *C. murrayana*. Harris (1961) considered *C. hymenophylloides* and *C. murrayana* as two distinct species after careful comparisons. Sze et al. (1963) also claimed that *C. hymenophylloides* did not include *C. murrayana*. Sze et al. (1963, p. 74) were incorrect in citing *C. hymenophylloides* as the generitype; *Coniopteris murrayana* appears to be the correct generitype.

Although *Coniopteris* was instituted by Brongniart in 1849 for fossil fronds characterized by pinnules more or less intermediate between the *Pecopteris* and *Sphenopteris* types and agreeing in the form of the sori with the leaves of recent species of *Dicksonia* (Seward, 1910), there was only one species, *C. arguta* (Lindley

& Hutton) Seward (1910) that possessed *Pecopteris*-type pinnules. This species was, later on, transferred to *Kylikipteris arguta* (Lindley & Hutton) Harris (1961). Therefore, the sterile pinnae of *Coniopteris* refer only to those of *Sphenopteris* type.

Harris (1961) gave an emended diagnosis of *Coniopteris* and described the sori of *Coniopteris* as having a short placenta and a cup-shaped indusium, or sometimes an indusium flattened in the plane of the lamina and then more or less divided into upper and lower lobes. Although Harris' emended diagnosis is contradictory with the original diagnosis (Seward, 1910) in having cup-shaped indusia, instead of bivalved indusia, he did show some species of *Coniopteris* having cup-shaped indusia (Harris, 1961, p. 145, Fig. 50-E, F; p. 157, Fig. 54-E, F).

Some species of *Coniopteris* have been found with bivalved indusia like those of the living *Dicksonia* (Krassilov, 1978; Chen et al., 1988). Species having flattened or lobed indusia (Harris, 1961, Fig. 51-I, J) appear to be intermediate forms between the bivalved and the cup-shaped.

Although species having bivalved indusia should be included in a genus distinct from those having cup-shaped according to the classification criteria for living plants (Bower, 1926), it is difficult to apply such criteria in fossil plants because indusia of fossil plants are not always available for examination. In fact, most specimens have been assigned to the genus *Coniopteris* simply on the basis of macroscopic similarity without regard for the details of their indusia. The present trend is to assign the name of *Dicksonia*, a extant genus, to those having demonstrably bivalved indusia (Krassilov, 1978; Chen et al., 1988). Therefore, *Coniopteris* appears to include two kinds of fossils; plants that fit Harris' (1961) emended diagnosis and plants whose indusia are imperfectly known.

Berry (1911) proposed *Dicksoniopsis* as a convenient name for fern fronds which showed an undoubted relationship with the modern ferns of Dicksoniaceae, but were impossible to correlate positively with any of the existing genera of the subfamily. *Dicksoniopsis* appears to have no major difference from *Coniopteris* in definition and is treated as a synonym of the latter.

Differentiation among species is based on the morphology of both vegetative and fertile pinnae, and on the venation of pinnules.

Generitype: *Coniopteris murrayana* (Brongniart) Brongniart

Coniopteris bidens (Bell) comb. nov.

(Pl. 4, figs. 1-4)

Dicksonia pachyphylla Fontaine, 1905i, [*pro parte*] p. 288, Pl. LXXI, figs. 5. 6 [*only*].

Basionym: *Sphenopteris bidens* Bell, 1956, Geol. Surv. Canada, Memoir 285, p. 71; Pl. XXXII, fig. 2, Pl. XXXIII, fig. 5.

Original Diagnosis: "Frond, at least bipinnate and probably tripinnate. Penultimate rachis, long, stout, about 2 mm diameter, obscurely ribbed longitudinally. Ultimate pinnae, alternate to subopposite, contiguous, linear-acuminate, inserted at open angles to parent rachis, of about equal breadth for more than half their length, then narrowing gradually to a very acute termination, up to 7 cm or more long and 1 cm wide; rachis, winged. Pinnules, oblique to rachis, alternate to subopposite, decurrent on wing of rachis, closely set, obovate-cuneate to subrectangular, generally bifid or obtusely bidentate or emarginate at broad anterior end; the largest are occasionally trifid by emargination or division of the anterior lobe. A single, oblique vein enters each pinnule, gives off a posterior branch where pinnule connects with wing of rachis, whereas the anterior branch generally bifurcates a short distance beyond; the posterior branch of the main vein is generally single, terminating in a posterior, bluntly pointed lobe of the pinnule, or in largest pinnules divides once to enter the two segments of a bifid lobe. The anterior, once-divided branch of the main vein supplies the anterior distal lobe of the pinnule, which may have a subordinate marginal lobe at the end or the forward vein. The pinnules approaching the apex of a pinna are subrectangular, emarginate or bifid at their extremities, each segment provided with a single branch of the main vein.

Fertile pinnae, unknown (Bell, 1956, p. 71)".

Emended Diagnosis: Sterile pinnae are the same as described in the original diagnosis.

Fertile pinnae morphologically similar to vegetative ones, showing no reduction of pinnule lamina. Sori borne on the apices of pinnule lobes; sori up to 1 mm in diameter, enclosed by an indusium; details of the indusium and sporangia unknown.

Materials: Specimens more than 40. Locality no.: 950, 951, 956.

Distribution: The species has been recovered from the Gates Formation, the Kootenai Formation, and the lower Blairmore Group. Its distribution appears confined to the Aptian-Albian in the northwestern Interior.

Discussion: Sterile specimens are numerous, but only one fertile specimen was found (Pl. 4, figs. 3, 4); fortunately, this fertile specimen shows connection between fertile pinnae and sterile pinnae. As the fertile specimen (Pl. 4, figs. 3, 4) is from the upper part of a frond, most of its pinnules do not bifurcate; this phenomenon is also common in sterile pinnae (Pl. 4, fig. 2 A). However, the basal pair of pinnules of every fertile pinna shows the characteristic bifurcation. Therefore, the fertile specimen (Pl. 4, figs. 3, 4) is morphologically identical with sterile specimens.

The specimen figured as *Dicksonia pachyphylla* Fontaine (1905i. p. 288. Pl. LXXI, figs. 5, 6) has bidentate pinnules in the upper part of a pinna and unified pinnules in the lower part of the pinna. A pinnately divided pinna of *C. bidens* in the apex of a frond can present this morphology. Therefore, Fontaine's specimen is considered to be conspecific with *C. bidens*.

Specimens included within *Dicksonia montanensis* Fontaine (1905i, p. 286. Pl. LXXI, figs. 1-4) are all fertile pinnae, which provide little taxonomic information because their fertile pinna laminae are strongly reduced. The only valuable taxonomic information is provided on Pl. LXXI, fig. 2 of Fontaine (1905i), on which every pinnule has an apical sorus except the two basal pinnules. Each basal pinnule (lobe) together with the neighbouring pinnule (lobe) appears to constitute a bifid pinnule, a feature typical of *C. bidens* (Pl. 4, fig. 4 B). Therefore, the Kootenai materials may belong to *C. bidens*.

On the other hand, each of those basal bifid pinnules can also be interpreted as two independent pinnules (Fontaine, 1905i, Pl. LXXI, fig. 2). in which case it would differ from *C. bidens*. Besides, the fertile pinna laminae of the Kootenai specimens appear strongly reduced while those of *C. bidens* are not reduced. Therefore, a definite conclusion can not be made until more information is available.

Coniopteris ermolaevii (Vassilevskaya) Meng & Chen

(Pl. 5, figs. 1-5)

Basionym: *Scleropteris ermolaevii* Vassilevskaya, 1963, Pl. 23. (type not seen; reference cited from Chen et al., 1988, p. 36)

Coniopteris brevifolia (Fontaine) Bell, 1956, [*pro parte*] p. 47., Pl. I, fig. 4, 5, Pl. II, fig. 2, 4, Pl. III, fig. 6 [*only*].

Coniopteris hymenophylloides (Brongniart) Seward *sensu* LaPasha and Miller, 1985, [*pro parte*] p. 121, Pl. 3, fig. 6-13, Pl. 4, fig. 1-4, 7, Text-fig. 5, A-H [*only*]; MacLeod and Hills, 1992a, [*pro parte*] p. 20, Fig. 5 b [*only*]; [*non*] Seward, 1910, p. 367, Figs. 271, 271, 275 B; [*non*] Harris, 1961, p. 152, Text-figs. 53, 54; [*non*] Sze et al., 1963, p. 75, Pl. 24, fig. 6, Pl. 46, fig. 3.

Coniopteris ermolaevii (Vassilevskaya) Meng et Chen; Chen et al., 1988, p. 36, Pl. 6, fig. 9, Pl. 7, figs 1-7, Pl. 8, figs 1-5, Pl. 62, figs. 2, 3.

Description: Frond at least bipinnate, rachis up to 1.5 mm wide, ridged longitudinally; winged distally. Pinnae up to 8 cm long and 1.3 cm wide, alternate to subopposite, attached at about 45 degrees to rachis, linear, acutely pointed; pinna rachis winged distally. Pinnules up to 7 mm long and 3 mm wide, alternate in anadromic order, oblique, decurrent, variable according to position in frond, elliptical to lanceolate, subrhomboidal, generally with narrowly rounded or acute apices; lobes 3 pairs in the well-developed pinnules, oblique, rounded to bluntly pointed, contracted at base by a narrow anterior sinus and cut halfway to center; less-developed pinnules only marginally lobed or crenulate; distal pinnules, more elongate, crenulate or entire. Venation sphenopteroid; veins one to each pinnule, giving off a simple or once divided branch to each lobe.

Fertile pinnae morphologically similar to vegetative ones; laminae slightly to strongly reduced, having marginal sori; sorus subcircular, about 1 mm in diameter, borne on the apex of each lobe, apparently enclosed in an indusium; details of indusia and sporangia unknown.

Materials: Specimens numerous. Locality no.: 851, 853, 874, 902, 925, 950-952, 956, 957.

Distribution: This species has been reported from the Kootenay Formation of Alberta and British Columbia, the Kootenai Formation of Montana, and the Gates Formation; it is also reported from Siberia and northeastern China (Chen et al., 1988). Its distribution appears to have been restricted to the Arctic Province from the Late Jurassic to Early Cretaceous.

Discussion: *Coniopteris ermolaevii* is characterized by an anadromic branching pattern. Comparisons with other similar species were presented in detail by Chen et al. (1988).

Most specimens assigned by Bell to *C. brevifolia* (Pl. I, fig. 4, 5, Pl. II, fig. 2, 4, Pl. III, fig. 6.) are morphologically identical with *C. ermolaevii* and are treated as conspecific. Although Bell's materials are somewhat similar to those of the Potomac species *Thyrsopteris brevifolia* Fontaine (1889, p. 121, Pl. XXIV, figs. 5, 10), the possible basionym of *Coniopteris brevifolia* (Fontaine) Bell, the Potomac materials appear to have katadromic order and acute pinnule apices, while Bell's materials have anadromic order and rounded pinnule apices. Fontaine's materials probably are *Coniopteris*, and therefore should be transferred to this genus. Bell's transfer should be considered invalid, as he failed to cite the basionym and the type, as required by ICBN (Greuter et al., 1994).

Most specimens assigned to *C. hymenophylloides* (e.g. LaPasha and Miller,1985, Pl. 3, fig. 6-13, Pl. 4, fig. 1-4, 7, text-fig. 5, A-H) are also conspecific with *C. ermolaevii* . Although LaPasha and Miller (1985) described the branching style to be katadromic, their specimens and text-figures all show apparent anadromic style, which is contradictory to Harris' description for *C. hymenophylloides* (Harris, 1961). The filiform processes of the basal pinnules, which exist throughout the whole frond in Harris' materials, are absent in LaPasha and Miller's materials.

Although three Montana specimens (LaPasha and Miller,1985, Pl. 3, fig. 6-8, text-fig. 5-A, G) slightly differ from other normal Montana specimens, they appear to represent the young stage of normal fronds and therefore are considered to be conspecific with other normal Montana specimens.

Although LaPasha and Miller (1985) claimed that the Montana materials showed continuous variation between sterile pinnule forms like those treated by Harris (1961) as *C. burejensis* and *C. bella* (Harris 1961), curiously, they assigned the Montana materials to *C. hymenophylloides*. *C. burejensis* appears to be different from the Montana and the Gates materials in having katadromic branching (Harris, 1961; Krassilov, 1978; Chen et al., 1988). *Coniopteris bella* is also different from the Montana and the Gates materials in having opposite basal pinnules and aphlebiform lobes on the the first pinnule on the basiscopic side.

The Bowser specimen figured as *C. hymenophylloides* by MacLeod and Hills (1992a, p. 20, Fig. 5 b) shows no differences from *C. ermolaevii* and is treated as conspecific.

Coniopteris simplex (Lindley & Hutton) Harris

(Pl. 6, fig. 1)

Basionym: *Tympanophora simplex* Lindley & Hutton, 1835, The fossil flora of Great Britain, 3: p. 57, Pl. 170a, London. (type not seen, reference cited from LaPasha and Millar, 1985, p. 121)

Coniopteris berryi Bell, 1956, [*pro parte*] p. 49, Pl. V, fig.4, Pl. VI, fig. 6 [*only*].

Coniopteris simplex (Lindley & Hutton) Harris, 1961, p. 142, Text-figs. 49, 50 A-G; LaPasha and Miller, 1985, p. 121, Pl. 4, figs, 8-11, Pl. 5, figs. 1-3. Text-fig. 6.

Description: Pinnae linear lanceolate. Pinnules 7 mm long and 3 mm wide, inserted at right angles to rachis, divided into about 4 pairs of slender lobes which are almost like pinnules rather than lobes; lobe apex round, base slightly contracted; veins unclear.

Fertile pinnules unknown.

Materials: 3 specimens. Locality no.: 878.

Distribution: This species has been recovered from the Early Cretaceous floras of the northwestern Interior, and the English Jurassic Yorkshire flora (Harris, 1961). Its distribution appears confined to the Middle Jurassic to Lower Cretaceous in North America and Europe.

Discussion: Frond dissection pattern of *C. simplex* resembles that of *C. quinqueloba* (Phillips) Seward (1910, fig. 273 A), but the former species appears to have 4 or more pairs of lobes on each pinnule; the latter, only 2 pairs of lobes.

Most specimens of *Coniopteris berryi* Bell (1956) have no substantial differences from *C. simplex* (Harris, 1961) and are treated as conspecific. The specimen in Pl. III, fig. 3 of Bell (1956) is only part of a fertile pinna. Because of the strong reduction of lamina of fertile pinnae in *Coniopteris* and *Acanthopteris*, similar fertile pinnae may appear in different taxa (e.g. *C. bidens* and *A. gothanii*). Therefore, the identity of this specimen can not be confirmed.

Bell (1956) included parts of *Coniopteris pachyphylla* (Berry, 1929, Pl. VII, fig. 3, 4) in *C. berryi* on the basis of resemblance of the fertile pinnae. Again, their identities can not be confirmed.

Although the type specimen of *C. berryi* (Bell, 1956, Pl. V, fig. 4) was considered by Harris (1961)to be conspecific with *C. hymenophylloides*, it is actually more like *C. simplex* because there appears no aphlebiform process on the first pinnule on the basiscopic side, which is common in *C. hymenophylloides*.

LaPasha and Miller (1985) included *C. pachyphylla* (Berry, 1929) within *C. simplex*. Nevertheless, earlier in the same paper, *C. pachyphylla* had been included within their *C. hymenophylloides*, an apparent contradiction.

Coniopteris tatungensis (Sze et al., 1963) appears to differ from *C. simplex* in having acute lobe apices, while *C. simplex* appears to have round lobe apices.

Family Gleicheniaceae

Genus *Gleichenites* Seward (non Goeppert)

Comments: *Gleichenites* was instituted by Goeppert in 1836 for some Carboniferous plants which were later on demonstrated to have no close relationship with Gleicheniaceae, and were subsequently included in *Sphenopteris* and *Neuropteris*. *Gleichenites* Goeppert would then be treated as a synonym of *Sphenopteris* (Sze et al., 1963).

Seward (1910; 1926) used *Gleichenites* Goeppert in a quite different sense for fossil ferns with sori similar to *Gleichenia*. Harris (1931, p. 67) assigned authority of *Gleichenites* to Seward, instead of Goeppert and stated: "Berry (1924) criticised this use of *Gleichenites* because it is contrary to the rules of nomenclature and because he considers it unnecessary, the fossils being in his opinion generically identical with *Gleichenia*. It has not, however, been proved that the species described here is identical with *Gleichenia*, but at the same time, the material does not justify a revision of the nomenclature of this group. The name *Gleichenites* Seward is therefore used here".

Although Andrews (1955) insisted on retaining Goeppert as the authority of *Gleichenites*, he accepted the new meaning assigned to *Gleichenites* by Seward and chose *Gleichenites porsildii* Seward, which is consistent with Seward's definition for *Gleichenites*, as the generitype.

Although *Gleichenites* Seward is an ill-defined genus in terms of nomenclature. Harris' way (1931) is followed here to deal with the Gates materials.

Generitype: *Gleichenites porsildii* Seward

Gleichenites nordenskioeldii (Heer) Seward

(Pl. 7, figs. 1, 2)

Basionym: *Gleichenia nordenskioeldii* Heer, 1874, p. 48, Pl. VIII, figs. 4, 5, Pl. IX, figs. 1-4.

Gleichenites nordenskioeldii (Heer) Seward, 1926, p. 74, Pl. 6, figs. 22, 25, 26, Pl. 10, fig. 97; Bell, 1956, p. 62, Pl. XV, fig. 2, Pl. XVI, fig. 3, Pl. XVIII, figs. 1, 3, 7, Pl. XIX, fig. 7, Pl. XX.

Description: Frond large, at least bipinnate; rachis up to 2 mm wide. Pinnae linear, at very open angles or normal to parent rachis, up to 8 cm long and 1 cm wide, of almost equal breadth for about 3/4 of length, then tapering to acute apex. Pinnules at wide angles or normal to pinna rachis, most commonly directed a little forwards, up to 6 mm long and 2.5 mm wide, lingulate, generally parallel-sided and obtuse, base attached at the whole width; distal pinnules, connate at base and form a wing to rachis. Midveins continuous to apex or bifurcated close to it; lateral veins up to 7 pairs in largest pinnules, commonly once divided, curving forward to meet margin at open angles.

Fertile pinnae unknown.

Materials: 18 specimens. Locality no.: 851, 914, 915, 925.

Distribution: The species has been reported from only the western Interior of Canada and western Greenland; its distribution appears confined to the Early Cretaceous of North America and Greenland.

Discussion: Although the Gates materials are all sterile pinnae, they are morphologically similar to those assigned by Bell (1956) to *G. nordenskioeldii*. As Bell's materials include both fertile and sterile pinnae which were recovered from areas (e.g. Luscar Formation) adjacent to the Gates Formation, it is reasonable to assign the Gates materials to *G. nordenskioeldii*.

Bell (1956) indicated that *Gleichenia gilbert-thompsonii* Fontaine (1889, p. 232, Pl. 66, fig. 11) (Bell, 1956, p. 63, mistaken as fig. 10 of Fontaine which is not *G. gilbert-thompsonii*) is conspecific with *G. nordenskioeldii*. I agree that both are morphologically similar, but there are no fertile pinnae in Fontaine's materials. It is better to treat Fontaine's *G. gilbert-thompsonii* as indeterminate, as Seward did (1926).

Family Incertae Sedis

Genus *Cladophlebis* Brongniart

Comments: Although *Cladophlebis* was instituted by Brongniart in 1849 as a transitional form between *Pecopteris* and *Neuropteris* from both the Paleozoic and Mesozoic (Sze, 1963), Brongniart did not provide any definite diagnosis for the genus. Fontaine (1889) referred to Saporta as the first who defined the features of the genus *Cladophlebis* and cited Schimper's fuller analysis of the generic features. Seward (1894) reviewed the history of *Cladophlebis* and gave a modified definition based on that of Schimper.

Sze et al. (1963, p. 97) summarized Seward's definitions of 1894 and 1910, Zeiller's of 1900, and Halle's of 1927 and characterized *Cladophlebis* as follows: "Frond pinnately divided 2-4 times; pinnules commonly large, more or less falcate; pinnules entire or toothed, attached on rachis by full base; base sometimes slightly contracted or auriculate; apex acute or round; venation pinnate, midvein conspicuous, often extending to near pinnule apex, lateral veins often bifurcate" (translated by the author).

It is sometimes difficult to distinguish *Cladophlebis* from *Pecopteris* if the pinnules of *Cladophlebis* are not strongly falcate. In practice, *Cladophlebis* is commonly assigned to Mesozoic fossils and *Pecopteris* is used for Paleozoic fossils. *Pecopteris* foliage is commonly found to belong to ferns of the Marattiales, while

Cladophlebis is more commonly found to be related to the Osmundaceae and other Leptosporangiatae ferns.

Numerous species have been included within *Cladophlebis*. The differentiation of species is on the basis of the size and morphology of pinnules, venation, and characters of the rachis.

Generitype: *Cladophlebis albertsii* (Dunker) Brongniart

Key to the *Cladophlebis* and *Cladophlebis*-like species of the Gates:

1. Pinnule margin entire................................2
   pinnule margin toothed.............................*C. serrata*

2. lateral veins simple, curving inward...........*C. simplexa*
   lateral veins forked, curving outward..........3

3. pinnule base constricted.............................*C. constricta*
   pinnule base not constricted........................4

4. pinnule apex round ....*G. nordenskioeldii*
   pinnule apex acute ....*C. virginiensis*

Cladophlebis constricta Fontaine

(Pl. 6, figs. 3, 4)

Cladophlebis constricta Fontaine, 1889, p. 68, Pl. II, fig. 11, Pl. III, fig. 2, Pl. VI, figs. 5, 6, 8-14, Pl. XXI, figs. 9, 13, Pl. CLXIX, fig. 2; Fontaine, 1905i,

p. 297, Pl. LXXI, fig. 26; LaPasha and Miller, 1985, p. 126, Pl. 6, fig. 2, 3, Text-fig. 9 A, B; [*non*] Berry, 1911, p. 249, Pl. XXIX, fig. 3.

Description: Frond large, at least bipinnate. Pinnae linear, alternate, acutely pointed, up to 10 cm long and 1.3 cm wide, attached at 40 degrees or so on parent rachis, basal pinnae of frond nearly normal to parent rachis. Pinnules alternate, linear lanceolate to triangular, more or less falcate; apex acute to rounded acute; base more or less constricted, cut more deeply on the acroscopic side than on the basiscopic. Midvein rapidly diminishing in size, generally extending only half way to apex; lateral veins 5 pairs on well-developed pinnules, dichotomizing twice in basal part of pinnule, and only once or simple when approaching the apex, having a narrow angle with the midvein, and appearing flabellate.

Fertile pinnules unknown.

Materials: Specimens numerous. Locality no.: 874, 875, 877-879, 925, 950, 957.

Distribution: This species has been recovered only from the Early Cretaceous of North America.

Discussion: *Cladophlebis constricta* was instituted on the basis of Potomac materials (Fontaine, 1889). It is characterized by its constricted pinnule base and less forked lateral veins. *Cladophlebis latifolia* Fontaine (1889, p. 69; Pl. III, fig. 1; Pl. VI, fig. 4) is similar to *C. constricta* in overall pinnule morphology but differs in having copiously forked lateral veins; the lower lateral veins are 3-4 times forked, the upper lateral veins only once bifurcate or simple.

Berry (1911) apparently viewed *C. constricta* and *C. latifolia* as a single species. The sole specimen that Berry assigned to *C. constricta* (Berry, 1911, p. 249, Pl. XXIX, fig. 3) is typical of *C. latifolia*. As *C. constricta* is a form-taxon, there is no sense to modify its definition. *Cladophlebis constricta* and *C. latifolia* are treated as distinct in this study.

The Gates specimens are very similar to the Montana materials. The variation of pinnule base, size and morphology were discussed in detail by LaPasha and Miller (1985).

I would, however, exclude the specimen figured by Fontaine (1889: Pl. IV, figs. 4, 4a, 4b) as *C. virginiensis* that LaPasha and Miller (1985) included in their treatment, because the pinnule bases of Fontaine's material are not contracted like the type specimen of *C. constricta*.

In the original diagnosis for *C. constricta* (Fontaine, 1889; p. 68), the explanation of Pl. II does not match the figures in the plate. The explanation of Pl. II, fig. 11 should be applied to Pl. II, fig. 12; that of Pl. II, fig. 11a to Pl. II, fig. 11; that of Pl. II, fig. 11b to Pl. II, fig. 11a.

Cladophlebis serrata sp. nov.

(Pl. 7, figs. 3, 4)

Basionym: *Pecopteris denticulata* Brongniart, 1828, Hist. vég. foss. p. 301, Pl. XCVIII, figs. 1, 2. (type not seen; reference cited from Seward, 1910, p. 343)

Cladophlebis denticulata (Brongniart) Nathorst non Fontaine; Fontaine, 1905a, [*pro parte*] p. 68, Pl. XI, figs. 3-6 [*only*]; [*non*] *Cladophlebis denticulata* Fontaine, 1889, p. 71, Pl. IV, figs. 2, 2a, Pl. VII, figs. 7, 7a..

C. denticulata (Brongniart) Seward, 1910, [*pro parte*] p. 343, Figs. 257, 256A in part (right hand pinnule) [*only*].

C. denticulata (Brongniart) Fontaine; Harris, 1961, p. 78, Text-figs. 25-27 (sterile pinnae); Doludenko and Svanidze, 1969, p. 13; Pl. I, figs. 1-5.

Todites denticulata (Brongniart) Krasser; Sze et al., 1963, p. 64, Pl. 20, fig. 3, 4; Zhang et al., 1980, p. 234, Pl. 120, figs. 1, 2, text-fig. 172.

Emended Diagnosis: Frond large, at least bipinnate; rachis strong, up to 3 mm wide. Pinnae linear lanceolate, alternate, up to 9 cm long and 2.5 cm wide, closely spaced or just touching, attached at open angles on parent rachis. Pinnules, lanceolate, up to 20 mm long and 5 mm wide, exceptionally up to 25 mm long and 8 mm wide, falcate, alternate; apex acute to bluntly pointed; margin sparsely serrate, fine acutely pointed teeth directing forward, teeth becoming smaller toward the base of a pinnule, sometimes the basal part of the margin appearing entire; attached to rachis along full base, pinnules situated near the pinna base rarely having slightly constricted base. Midveins moderately strong; lateral veins, 7 pairs, commonly dichotomizing once, proximal veins may divide twice, distal veins simple; veins reach margin through teeth, with each tooth host to one vein.

Fertile pinnules unknown.

Etymology: The epithet *serrata* originates from Latin *serratus*, referring to the serrate pinnule margins.

Materials: 13 specimens. Locality no.: 875, 889, 950, 955.

Distribution: This species has been reported from the Triassic to Cretaceous in the Northern Hemisphere.

Discussion: The name *C. serrata* sp. nov. is, hereby, instituted to replace the commonly used name *C. denticulata* (Brongniart) Fontaine (Harris, 1961), or *C. denticulata* (Brongniart) Nathorst non Fontaine (Fontaine, 1905a, p. 68, 69), or *C. denticulata* (Brongniart) Seward (1910), which appear to be all nomenclaturally invalid.

Nathorst (1876, p. 19) appears to be the first author who used the name *Cladophlebis denticulata* Brongniart. Nathorst's usage was later on cited by Fontaine (1905a, p. 68) as *C. denticulata* (Brongniart) Nathorst non Fontaine. Fontaine interpreted Nathorst's usage of the name to be a new combination from *Pecopteris denticulata* Brongniart. Since Nathorst did not explicitly indicate any sources that *C. denticulata* Brongniart referred to, other interpretations are possible. Therefore, Nathorst's usage, *C. denticulata* (Brongniart), appears to be invalid, as indicated by the ICBN (Greuter et al., 1994),. Although the ICBN (Greuter et al., 1994) is enforced for publications on or after Jan. 1, 1953 regarding basionym citation, the same principle can be used to judge the validity of publications prior to Jan. 1, 1953.

Fontaine (1889) instituted the name *C. denticulata* Fontaine as a new species designating some finely dentate "pinnules" from the Potomac Group (Fontaine, 1889, Pl. IV, figs. 2, 2a; Pl. VII, figs. 7, 7a). Fontaine's publication is valid, should *C. denticulata* (Brongniart) Nathorst be invalid.

Seward (1910) ignored Fontaine's publication (1889, p. 71) and created a new combination *C. denticulata* (Brongniart) Seward in 1900, which referred to *Pecopteris denticulata* Brongniart (1828, p. 57, p. 301, Pl. XCVIII, figs. 1, 2). *C. denticulata* (Brongniart) Seward is obviously a later homonym of *C. denticulata* Fontaine.

Harris (1961) misinterpreted *C. denticulata* Fontaine as a new combination referring to *Pecopteris denticulata* Brongniart and cited it as *C. denticulata* (Brongniart) Fontaine. Harris also indicated that the Potomac materials were different from *Pecopteris denticulata* Brongniart. Later authors followed Harris' usage (e.g. Doludenko and Svanidze, 1969, p. 13).

Therefore, *C. denticulata* Fontaine appears to be the valid name to refer to the Potomac materials as his was not a transfer of the type, but a new species. Transfer of *Pecopteris denticulata* Brongniart into *Cladophlebis* will therefore produce a later homonym. Article 55(a) of the ICBN (Greuter et al., 1988) provides a solution for such a problem, allowing transfer with a new epithet. *Cladophlebis serrata* sp. nov. is, hereby, created to refer to a new combination of *Pecopteris denticulata* Brongniart.

Cladophlebis raciborskii (Sze et al., 1963) is similar to some specimens of the present species in having teeth on the distal 1/3 of the pinnule margin, but differs from *C. serrata* in having blunt teeth and twice forked lateral nerves.

The specimens included in *C. serrulata* Samylina (Vakhrameev and Doludenko, 1961, p. 70; Pl. XXI, figs. 2-4; text-fig. 17) are similar to *C. serrata* in every aspect except the twice forked lateral veins. *Cladophlebis tongusorum* Prynada (Vakhrameev and Doludenko, 1961; p. 71; Pl. XXII, fig. 1; Pl. XXIII, fig. 1; text-fig. 18) also differs from *C. serrata* in having twice forked lateral veins.

Part of the Jurassic specimens from Oregon assigned by Fontaine (1905a, p. 68, Pl. XI, figs. 3-6) to *C. denticulata* (Brongniart) Nathorst non Fontaine appear to be conspecific with *C. serrata*; nevertheless, others are different.

The Late Jurassic specimens from Georgia of the former Soviet Union described by Doludenko and Svanidze (1963) as *C. denticulata* are conspecific with *C. serrata.*

Chinese specimens assigned to *Todites denticulata* (Sze et al., 1963, p. 64. Pl. 20, figs. 3, 4; Zhang et al., 1980, p. 234. Pl. 120, figs. 1, 2, text-fig. 172) are morphologically similar to *C. serrata.* Because the Chinese specimens are all sterile pinnae, designation as *C. serrata* appears to be more appropriate than *Todites denticulata.*

Cladophlebis simplexa sp. nov.

(Pl. 8, figs. 1, 2)

Cladophlebis parva Fontaine *sensu* Bell, 1956, [*pro parte*] p. 56, Pl. XI, fig. 5, Pl. XII, fig. 3, Pl. XIII, fig. 1, Pl. XV, fig. 3 [*only*]; [*non*] Fontaine, 1889. p. 73, Pl. IV, fig. 7, Pl. VI. figs. 1-3; [*non*] Berry, 1911. p. 250. Pl. XXXI. figs. 5, 6.

Diagnosis: Frond large, at least bipinnate. Pinnae linear lanceolate, alternate, acutely pointed, up to 6.5 cm long and 1.5 cm wide, those holding a basal position nearly normal to parent rachis, whereas those near apex are oblique, more or less falcate; length of pinnae variable, proximal pinnae shorter than distal ones; rachis winged. Pinnules alternate, up to 9 mm long and 3 mm wide, pecopteroid, more or less decurrent, triangular to long elliptical, slightly falcate; apex bluntly or more sharply pointed; base connate, fusion of adjacent pinnules more pronounced distally; margin appears slightly toothed because of the strong lateral veins. Veins moderately thick; midvein slightly flexuous, thick; lateral veins 5 pairs in largest pinnules, fewer in small pinnules, simple, strongly ascending curved backwards, reaching pinnule margins at acute angles.

Fertile pinnule unknown.

Etymology: The epithet *simplexa* is used to suggest the simple later veins.

Materials: 5 specimens. Locality no.: 855 (Boulder Creek Fm.), 952, 957.

Holotype: Pl. 8, fig. 2; specimen no.: 855-7283.

Distribution: This species has been recovered from the lower Blairmore Group, the Hazelton Group in British Columbia, the Boulder Creek Formation and the Gates Formation. Its distribution appears confined to the Aptian-Albian in the northwestern Interior.

Discussion: This species is characterized by having simple and backward curving lateral veins. *Cladophlebis suniana* (Sze et al., 1963; p. 109) from the Late Triassic of northern China is similar to the present species but differs in having flatly rounded pinnule apices and sub-oblong pinnule shape.

Most the specimens assigned to *C. parva* by Bell (1956; p. 56; Pl. XI, fig. 5; Pl. XII, fig. 3; Pl. XIII, fig. 1; Pl. XV, fig. 3) are considered to be conspecific with *C. simplexa.*

Cladophlebis parva (Fontaine, 1889) was originally defined as having mostly once forked lateral nerves. Bell's materials are not in accordance with Fontaine's definition. Therefore, Fontaine's' materials are excluded from *C. simplexa.* Two specimens (Berry, 1911; p. 250; Pl. XXXI, figs. 5, 6) figured as *C. parva* are similar to the present species but differ in having forward curving lateral veins and therefore are excluded from *C. simplexa.*

Cladophlebis virginiensis **Fontaine**

(Pl. 6, fig. 2)

Cladophlebis virginiensis Fontaine, 1889, p. 70, Pl. III, figs. 3-8, Pl. IV, fig. 1, 3-6; LaPasha and Miller, 1985, p. 129, Pl. 6, fig. 10; [*non*] *C. virginiensis* Fontaine *sensu* MacLeod and Hills, 1992 p. 17, Pl. 1, figs. 1-4, 6.

Cladophlebis virginiensis Fontaine emend. Berry *sensu* Bell, 1956, [*pro parte*] p. 50, Pl. V, figs. 1-3, Pl. VI, figs. 3-5, 7, Pl. VII, fig. 2, Pl. VII, Pl. IX, fig. 4 [*only*]; [*non*] *C. virginiensis* Fontaine emend. Berry, 1911, p. 248, Pl.

XXIX, figs. 4-6.

Description: Frond large; pinnae linear lanceolate. Pinnules linear lanceolate, up to 11 mm long and 4 mm wide, the ratio of length to width to length 2:1-3:1, subopposite to alternate, conspicuously falcate, attached at almost right angles to rachis; apex acutely or bluntly pointed; base attached to rachis along full base. Midvein moderately strong, almost reaching apex; lateral veins 11 pairs or so, ascending at low angles from midvein, commonly dichotomizing once, resulting branches reaching the pinnule margin.

Fertile pinnules unknown.

Materials: Total 3 specimens. Locality no.: 875.

Distribution: The species has been reported from the Early Cretaceous of North America.

Discussion: *Cladophlebis virginiensis* was instituted on the basis of Potomac materials (Fontaine, 1889, p. 70, Pl. III, figs. 3-8; Pl. IV, figs. 1, 3-6), and is characterized by having falcate pinnules, acute pinnule apex, and once-bifurcated lateral veins (basal ones may bifurcate twice). Similar species from the Potomac include: *C. parva* Fontaine (1889), *C. falcata* Fontaine (1889), *C. oblongifolia* Fontaine (1889), *C. inclinata* Fontaine (1889) and *C. acuta* Fontaine (1889).

Cladophlebis parva has a pinnule length to width to ratio close to 1:1 and appears to be a distinct species. Berry (1911) viewed *C. falcata*, *C. oblongifolia* and *C. acuta* as synonyms of *C. virginiensis*. The type specimens of *C. virginiensis* had pinnule length to width ratio between 2:1-3:1, which differs from 3:1-4:1 of other species. Therefore, *C. virginiensis* should be recognized as a distinct species. There appear no specific differences among *C. frigida* (Heer) Bell (1956, p. 52, Pl. VII, fig. 1; Pl. IX, fig. 1), *C. falcata*, *C. oblongifolia*, *C. acuta*, and *C. inclinata*; these are regarded as synonyms of *C. inclinata*.

A simplified key to those above species can be as follows:

1. L/W ratio > 2:1 2
   L/W ratio < 2:1 ....*C. parva*

2. L/W ratio 2:1–3:1 ....*C. virginiensis*
   L/W ratio 3:1–4:1 ....*C. inclinata*

The Potomac specimens illustrated by Berry in his emendation of *C. virginiensis* (Berry, 1911, p. 248, Pl. XXIX, figs. 4-6) are different from Fontaine's type materials and should be included within *C. inclinata*.

Although Bell (1956) used *C. virginiensis* Fontaine emend. Berry instead of *C. virginiensis* Fontaine, all specimens figured by Bell except one (Bell, 1956, Pl. VII, fig. 4) are consistent with Fontaine's original definition.

LaPasha and Miller (1985) used *C. virginiensis* in the strict sense following Fontaine's original definition. Their only figured specimen from Montana is conspecific with the Gates material, but their text-figure (LaPasha and Miller (1985, p. 127, text-fig. 9 F) does not show the falcate features of the species and appears to be inconsistent with the figured specimen (LaPasha and Miller, 1985, p. 127, Pl. 6, fig. 10).

The Bowser basin materials figured as *C. virginiensis* by MacLeod and Hills

(1992, p. 17, Pl. 1, figs. 1-4, 6) differs from the Gates materials in having twice-bifurcated lateral veins. MacLeod and Hills' usage of *C. virginiensis* appears to have excluded the type materials of this species and is different from the original definition of this species.

Genus *Pseudophlebis* gen. nov.

Generic Diagnosis: Frond pinnately divided. Pinnules pecopteroid or cladophleboid, margin entire or toothed; venation pinnate, midvein obvious; lateral veins arising from midvein, bifurcating a few times, resulting veins reach pinnule margin, extending along the margin and fusing with adjacent veins, fused vein to form a marginal vein ring.

Etymology: The generic name consists of *Pseudo-* and *-phlebis*; the second part is from part of *Cladophlebis*, because the new genus is similar to *Cladophlebis* in pinnule morphology.

Discussion: The new genus is distinct from other genera in having a peculiar marginal vein ring. The species that belong to the genus can be distinguished on the basis of pinnule size, shape, margin, apex and the existence of petiole.

Generitype: *Pseudophlebis gatesii* sp. nov.

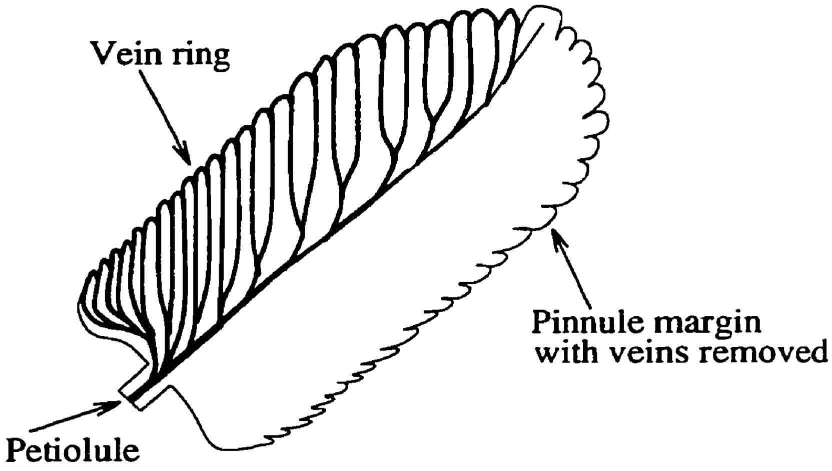


Figure 3.2: Venation of *Pseudophlebis gatesii* sp. nov.

Pseudophlebis gatesii **sp. nov.**

(Pl. 8, figs. 3, 4)

Diagnosis: Frond pinnately divided. Pinnules lanceolate, petiolate, up to 3 cm long by 1.2 cm wide; petiolule 1.5 mm long, winged on both side; apex obtuse: base cordate; margin crenulate; pinnules attached alternately at right angles by the short petiolule on parent rachis, distal pinnules may attach at narrow angles along full base on parent rachis, dropping at maturity.

Midveins slender, extending over 3/4 of the pinnule; lateral veins up to 12 pairs, the basal pair of lateral veins dichotomizing three times, lateral veins in the lower part of a pinnule dichotomizing once or twice, lateral veins in the middle part of a pinnule dichotomizing once, distal lateral veins maybe simple, resulting arms ascending at 45 degrees or so and reaching sinus between teeth, and then extending along pinnule margin, fusing with adjacent arms to form a marginal vein ring.

Fertile pinnules unknown.

Etymology: The epithet *gatesii* originates from the "Gates"(Formation).

Materials: 16 specimens. Locality no.: 915, 921, 925, 950, 957.

Holotype: Pl. 8, fig. 3; specimen no.: 921-7195.

Distribution: This species has been recovered only from the Gates Formation.

Discussion: The relationships between the lateral veins and marginal teeth are unique in this species. Commonly, the lateral veins extend into teeth in species of *Cladophlebis*, but the lateral veins of this species extend into the sinuses and then fused with neighbouring lateral veins along the pinnule margin (Figure 3.2). The pinnules near the lower part of a frond have well developed petiolules. Detached pinnules were commonly encountered in the field. *Pseudophlebis gatesii* appears to have been a deciduous plant.

Genus *Sphenopteris* (Brongniart) Sternberg

Comments: According to Sze et al. (1963), *Sphenopteris* was a subgenus name instituted by Brongniart in 1822; Sternberg promoted it to the rank of genus in 1825. *Sphenopteris* is a form genus whose members can be found from Paleozoic and Mesozoic strata. Most Paleozoic *Sphenopteris* are related to pteridosperms, while most Mesozoic *Sphenopteris* have been found to belong to true ferns, especially Dicksoniaceae.

A brief diagnosis of this genus given by Seward (1910, p. 530) is as follows: "The lobed lamina, contracted and often wedge-shaped at the base, the dichotomously branched veins radiating from the base or given off from a median rib at an acute angle; the lamina may be divided into a few bluntly rounded lobes or deeply dissected into linear or cuneate segments".

The differentiation of species within the genus is on the basis of morphology of pinnules and pinnae. The morphology of the first pinnule on the basiscopic side of a pinna is often important.

Generitype: *Sphenopteris elegans* (Brongniart) Sternberg

Sphenopteris acrodentata Fontaine

(Pl. 10, figs. 2, 3)

Sphenopteris acrodentata Fontaine, 1889, p. 90. Pl. XXXIV, fig. 4: Bell. 1956. p. 68, Pl. XXII, figs. 4, 6, Pl. XXII, fig. 2.

Ruffordia goeppertii var. *latifolia* Seward, 1894, p.85, Pl. VI, figs. 1, 1a.

Ruffordia goeppertii (Dunker) Seward, 1894, [*pro parte*] p. 76, Pl. V, fig. 4 [*only*]: Berry, 1911, p. 231, Pl. XXIII, figs. 3, 4.

Cf. *Ruffordia goeppertii* (Dunker) Seward; Sze et al., 1963, p. 69, Pl. 22, figs. 4, 4a.

Description: Frond large, at least tripinnate; rachis commonly about 1 or 1.5 mm wide, and generally appearing canaliculate or with pronounced central cord, distally winged. Pinnae elliptical, alternate to subopposite, up to 3 cm long by 2 cm wide. Pinnules obovate-cuneate to subquadrate to elliptical, up to 1.5 cm long and 0.5 cm wide, constricted at base to short, stout footstalk, and more or less deeply divided into obtuse lobes, which are sometimes like pinnules; lobe apices obtusely rounded, minutely toothed. A single, stout vein enters each pinnule, and by successive dichotomous divisions results in a flabelliform pattern, the arms of each division running subparallel, a vein entering each tooth.

Materials: 5 specimens. Locality no.: 952, 958.

Distribution: This species has been reported from the Jurassic to Early Cretaceous in the Northern Hemisphere.

Discussion: Seward (1894) found a collection of forms intermediate between *S. acrodentata* and *S. goeppertii*. *Sphenopteris acrodentata* and *S. goeppertii* represent the two extremes among those intermediate forms; pinnules of *S. acrodentata* are barely dissected while those of *S. goeppertii* are strongly dissected. In dealing with the difficulty of drawing a definite line between those two extreme forms, Seward combined both forms in *Ruffordia goeppertii*. Although there were forms intermediate between *S. acrodentata* and *S. goeppertii*, those two forms were very distinct. To show the difference between the two extreme forms, Seward considered *S. acrodentata* to be a variety of *Ruffordia goeppertii*, namely, *Ruffordia* *goeppertii* var. *latifolia* Seward.

Most authors (e.g. Berry, 1911; Bell, 1956; LaPasha and Miller, 1985) continue to accept *S. acrodentata* as a distinct species and their approach is followed here simply because those two extreme forms are quite distinct. In dealing with the definite line between those two species, it is suggested that height of a minute tooth of *S. acrodentata* should be less than 1/3 of a lobe of the pinnule.

Incidently, an error exists in the labelling of figures in Berry (1911). The two specimens labelled as *Ruffordia goeppertii* were described under *Ruffordia acrodentata* (Berry, 1911, Pl. XXIII, figs. 3, 4). The two specimens labelled as *Ruffordia acrodentata* (Fontaine) Berry were described under *Ruffordia goeppertii* (Berry, 1911, Pl. XXIII, figs. 5, 6).

Sphenopteris brulensis **Bell**

(Pl. 10, fig. 4; Pl. 11, figs. 1, 2)

Sphenopteris brulensis Bell, 1956, p. 71, Pl. XXXI, figs. 3, 4; LaPasha and Miller, 1985, p. 130, Pl. 7, figs. 1, 2, Text-fig. 10 A, B.

Description: Frond at least bipinnate. Pinnae alternate, linear-acuminate, up to 7 cm long and 1.5 cm wide, inserted at almost right angles to parent rachis; rachis, distally winged, 0.5 mm wide. Pinnules elliptic to rhomboid, with bluntly acute to narrowly rounded apices, contracted at base in well-developed pinnules, more or less deeply cut into 3 pairs of alternate lobes in addition to the terminal lobe. Veins intermediate between sphenopteroid and pecopteroid; in well-developed pinnules a branch arises from the midvein close to its base and bifurcates once in the basal lobes; vein branches to remaining lobes bifurcate once or are simple.

Fertile pinnules morphologically similar to the vegetative ones; sori borne under lateral veins, one sorus per pinnule lobe; sorus composed of numerous sporangia, up to 1 mm in diameter, details of the sporangia and indusia unknown.

Materials: 17 vegetative specimens; locality no.: 950-952, 955, 957. 20 fertile specimens; locality no.: 952, 957.

Distribution: This species is known from the Neocomian to the Albian in the northwestern Interior.

Discussion: Although the direct connection between the fertile pinnae and the vegetative pinnae has not been found, both are very similar in pinnule morphology. The fertile pinnae differ from *Coniopteris* in having non-marginal sori. Although the fertile pinnae are somewhat similar to *Gleichenites*, sporangial details are unknown. Therefore, *Sphenopteris* remains the most suitable generic designation.

Sphenopteris erecta **Bell**

(Pl. 9, figs. 1-3)

Sphenopteris (Gleichenites ?) erecta Bell, 1956, p. 65, Pl. XIX, fig. 6, Pl XXII, figs. 1, 7.

Description: Frond at least tripinnate. Pinnae lanceolate, up to 7 cm long and 2.5 cm wide, opposite to alternate, moderately spaced or touching, attached at right angles to parent rachis; apices acute. Pinnules pinnately lobed, alternate, contiguous or nearly so, inserted at almost right angles to rachis, lanceolate, apically obtuse, basally constricted to midvein or nearly so, up to 1.3 cm long and 4 mm wide, having up to 7-8 pairs more less deeply-cut lobes; lobes obtuse, pinnule-like, suborbicular to subovate. Midvein strong and thick; lateral veins one to each lobe, bifurcating 1-4 times, resulting branches curving backward and the ends reaching the lobe margins.

Fertile pinnules morphologically similar to vegetative pinnules, often appearing in the upper part of the frond. Sori circular, up to 0.75 mm in diameter, one on each lobe, located under lateral vein on abaxial side at about half way to margin, with numerous sporangia in each sorus; no indusium observed; details of the sporangia unknown.

Materials: Specimens numerous, No. 658 (Boulder Creek Fm.), 674, 750-752, 756, 757.

Distribution: This species has been reported from the Luscar Formation and the upper Blairmore Group by Bell (1956); its distribution appears to be confined to the Albian in the western Interior of Canada.

Discussion: The Gates specimens are a little larger in size than Bell's materials (Bell, 1956), but there is no doubt that they all belong to one species. Although the fertile pinnae are somewhat similar to *Gleichenites*, sporangial details are unknown and comparison is limited. Therefore, *Sphenopteris* remains the most suitable generic designation.

Sphenopteris goeppertii **Dunker**

(Pl. 9, figs. 4, 5; Pl. 10, fig. 1)

Sphenopteris goeppertii Dunker, 1846, Monographie der Norddeutschen Wealdenbildung, p. 4, Pl. 1, fig. 6, Pl. 9, figs. 1-3. (type not seen; reference cited from LaPasha and Miller, 1985, p. 131)

Ruffordia goeppertii (Dunker) Seward, 1894, [*pro parte*] p. 76, Pl. III, figs. 5, 6, Pl. IV, Pl. V, figs. 1-3 [*only*].

Ruffordia acrodentata (Fontaine) Berry, 1911, p. 230, Pl. XXIII, figs. 5, 6.

Sphenopteris goeppertii Dunker; LaPasha and Miller, 1985, p. 131, Pl. 7, fig. 7, Text-fig. 10 G.

Description: Frond at least quadripinnate, broadly deltoid. Primary (?) pinnae, up to 5 cm long by 2 cm wide, deltoid. Secondary pinnae up to 1.7 cm long and 1.2 cm wide, deltoid. Pinnae 1 cm long and 6 mm wide, rhomboid, commonly with two lateral subopposite flabellately dentate pinnules in addition to a terminal group of segments. Pinnules 8 mm long and 2 mm wide, narrow flabelliform, lobed or dissected into several linear segments, each segment is bluntly or acutely pointed and commonly with one or more blunt or more sharply pointed apical teeth. Veins thin, single vein entering each pinnule, dividing by successive dichotomies so as to provide a simple vein to each ultimate segment or tooth.

Materials: 30 specimens. Locality no.: 875, 889, 896, 914, 950-952, 956.

Distribution: This species has been reported from the Late Jurassic to the Early Cretaceous in the Northern Hemisphere.

Discussion: The Gates specimens of *S. goeppertii* closely resemble most of the vegetative specimens described under *Ruffordia goeppertii* by Seward (1894; p. 76; Pl. IV; Pl. V, figs. 1-3). Because there is no information on fertile pinna available for the Gates materials, *Sphenopteris* appears to be the most suitable generic designation for the Gates materials.

Class Gymnospermopsida

Order Caytoniales

Family Incertae Sedis

Genus *Caytoniopteris* gen. nov.

Generic Diagnosis: Leaflets petiolate, possibly palmately arranged on a petiole. Each leaflet having an apparent midrib; lateral veins reticulate, forming narrow simple meshes.

Etymology: The generic name is a combination of *Caytonia* and *-pteris*.

Generitype: *Caytoniopteris williamsii* (Newberry) comb. nov.

Discussion: Earlier authors used the terms frond (Newberry, 1891), pinnule (Newberry, 1891; Fontaine, 1890) or pinna (Berry, 1911) in describing *Sagenopteris*-type leaves on the belief that *Sagenopteris* was a fern. Seward used the word "leaflet" describing the Caytoniales leaves (Seward, 1900) and indicated that the assignment of *Sagenopteris* to the ferns lacked sufficient evidence. After discovery of the fertile organs of Caytoniales (Thomas, 1925), most authors followed Thomas in using "leaflet" to describe Caytoniales leaves (Berry, 1929; Harris, 1940, 1963; Bell, 1956; LaPasha and Miller, 1985; Kimura, 1987) on the assumption that *Sagenopteris*-type leaves were compound.

Caytoniopteris vs. Normal *Sagenopteris* leaves

The leaves of *Caytoniopteris* appear to be similar to those originally assigned to *Sagenopteris* in their compound structure, for Bell (1956, p. 80) stated: "In G.S.C No. 5337 (Pl. XXXIV, fig. 2) the petiole of a leaflet may be followed downwards to junction with at least two and apparently three other leaflets at top of a stout axis". The "petiole" in Bell's description is equivalent to the petiolule in this study; his "axis", is equivalent to the petiole.

Leaflets previously attributed to *Sagenopteris* include both sessile and the petiolate types. Although the materials of the type species *S. nilssoniana* were not available for examination here, Harris (1932) redescribed this species according to materials from East Greenland. Those leaflets are sessile according to his diagram (Harris, 1932, fig.1). Species that have sessile leaflets include:

Sagenopteris nilssoniana (Brongniart) Ward
S. mantellii (Dunker) Seward
S. spatulata Sze
S. undulata Nathorst
S. ilekensis Brick
S. elliptica Fontaine
S. phillipsii (Brongniart) Presl.
S. maclearnii Berry
S. goeppertii Zign
S. paucifolia (Phillips) Ward
S. alaskensis Fontaine
S. heterophylla Doludenko & Svanidze

The number of leaflets in each leaf could be an important feature for each species. *Sagenopteris nilssoniana*, *S. spatulata* and *S. phillipsii* were described as tetra-foliate; *S. mantellii* and *S. elliptica*, with five leaflets in each leaf. Leaflet number in *S. maclearnii* can be as many as nine (Pl. 12, fig. 2). On the other hand, it is quite possible that variation of leaflet number was a result of incomplete preservation. Therefore, the number of leaflets in each leaf proves of limited practical use.

Another group of plants, which was attributed to *Sagenopteris* but differs in having petiolate leaflets, is represented by *S. williamsii* (Newberry) Bell. Species included within in this group are as follows:

Sagenopteris williamsii (Newberry) Bell
S. colpodes Harris
S. serrata Harris
Caytonia orientalis Krassilov

The existence of petiolules in these plants appears quite consistent. The only exception is a specimen which was assigned to *S. phillipsii* by Harris (1963). This specimen is minutely petiolate, differing from the other specimens in the species, which have sessile leaflets. Such minor variation of sessile to minutely petiolate leaflets is quite possible within a genus, or even within a species. Nevertheless. the presence of petiolules as long as 5 cm in *S. williamsii* apparently suggests that *S. williamsii* represents a different evolutionary lineage from that of *Sagenopteris*. Therefore, it is reasonable to establish a new genus *Caytoniopteris* for those petiolate leaflets. *Sagenopteris* should include only plants with sessile leaflets.

It is certainly a problem to distinguish sessile leaflets from petiolate leaflets when the petiolules are very short. In my opinion, decisions can be made on the basis of two points. First of all, an obvious petiolule should not be less than 2 mm in length: and then the presence of petiolules should be a consistent feature on all or most specimens of a species. Otherwise, the leaflets should be considered to be sessile.

Caytoniopteris vs. Abnormal *Sagenopteris* leaves

The specimen figured as *Sagenopteris phillipsii* var. *cuneata* Seward (1900, p. 167, Pl. XVIII, Fig. 3) is similar to a leaflet of *Caytoniopteris* but differs in lacking a midrib. Thomas (1925, Pl 15, fig. 52) indicated that Seward's specimen was a simple leaf, and suggested that it represented the vegetative leaf of *Caytonia sewardii* Thomas because of their cuticle resemblance.

Among Harris' specimens of *S. phillipsii* (Harris, 1963), there are a series of small leaves, each of which has a short petiole and a blade which may be entire or lobed. Harris (1963) claimed that these small leaves were merely leaves produced in a particular region of the stem, because their cuticles were identical to those of normal *S. phillipsii*. Therefore, Harris (1963) assigned these small leaves to *S. phillipsii* var. *cuneata*, conspecific with Seward's specimen (Seward, 1900, p. 167, Pl. XVIII, Fig. 3). Harris believed that *S. Phillipsii* var. *cuneata* was the leaves of *Caytonia nathorstii (Gristhorpia)* Thomas, while Thomas (1925) suggested that it was associated with *Caytonia sewardii* Thomas. The inconsistency between Harris (1963) and Thomas (1925) should be noted.

These small leaves assigned to *S. phillipsii* var. *cuneata* are all petiolate and have entire or lobed blades, which have several major palmate veins and lack midribs. Morphologically, these small leaves fall within the definition of *Chiropteris* and differs from normal *Sagenopteris* leaves in lacking well-developed sessile leaflets; they also differs from *Caytoniopteris* in lacking well-developed petiolate leaflets. *Chiropteris* is a form genus and may includes leaves of Caytoniales, but because Harris (1963) demonstrated the cuticle resemblance between normal leaves of *S. phillipsii* and these small leaves, these small leaves should be included within *Sagenopteris*.

I disagree with Harris' interpretation that these small leaves were produced in a particular region of the stem. Instead, these small leaves are most likely the young stage of normal *Sagenopteris* leaves or poorly developed *Sagenopteris* leaves.

Caytoniopteris vs. Other similar genera

Chiropteris is characterized by having petiolate leaves which are entire or lobed. and lack midribs; some species of *Chiropteris* may have a midrib in each lobe or segment (Sze et al., 1963). A leaf of *Chiropteris* is somewhat similar to a leaflet of *Caytoniopteris*, but differs in lacking a midrib.

Lower Cretaceous specimens from the Inner Zone of Japan described as *Tetoriophyllum reniformis* (Oishi) Kimura (1991) differ from *Caytoniopteris* in having pinnately arranged pinnules and in the absence of midribs in pinnules.

Key for Caytoniales leaves and analogues:

1. leaf not pinnately compound..2
   leaf pinnately compound..*Tetoriophyllum*
2. leaf lobed or divided but without detachable leaflets.....*Chiropteris*
   leaf divided, leaflet detachable.......................................3
3. leaflets petiolate...*Caytoniopteris*
   leaflets sessile..*Sagenopteris*

Caytoniopteris williamsii (Newberry) comb. nov.

(Pl. 11, figs. 3-5)

Basionym: *Chiropteris williamsii* Newberry, 1891, Am. J. Sci., 3rd., vol. 41, p. 198, Pl. XIV, fig. 10, 11.

Sagenopteris williamsii (Newberry) Bell, 1956, p. 80, Pl. XXXI, fig. 2, Pl. XXXIII, fig. 4, Pl. XXXIV, figs. 1-3, Pl. XXXVI, fig. 1; LaPasha and Miller, 1985, p. 134, Pl. 10, figs. 1-6; [*non*] MacLeod and Hills, 1992a, p. 41, Fig. 11a.

Original Diagnosis: "Fronds orbicular, oblong or lobed, two to four inches in diameter; petiolate, margins entire, venation radiate, dichotomously forked and somewhat reticulated" (Newberry, 1891, p. 198).

Emended Diagnosis: Leaf palmately compound; leaflets petiolate, up to four or more, palmately arranged. Blades of leaflets orbicular or oblong, 5 to 10 cm in diameter, more or less symmetrical; base broadly rounded, or truncate or rarely cordate; apex broadly rounded to more elongate-obtuse; margins entire, smoothly curved to undulating. Midrib broad in basal quarter, diminishing and then disappearing above middle. Lateral veins well defined, strongly ascending, dichotomizing repeatedly and anastomosing moderately to sparingly; mean maximum distance between nerves in central parts of a blade about 1 mm, but variable from 0.75 to 1.5 mm. Petiolule up to 5 cm long and 4 mm wide; base slightly swollen and curving, having traverse striae on surface.

According to LaPasha and Miller (1985, p. 134-135): Adaxial cuticle: "cells polygonal to circular, walls straight, 35 μm diameter". Abaxial cuticle: "cells over midrib axially elongate, 30-35 μm long, 13-21 μm wide, arranged in longitudinal files, walls straight; cells between veins polygonal, walls straight, about 40 μm diameter, very thin; stomata sunken, aperture oval to circular, 12-16 μm diameter".

Materials: Specimens numerous. Locality no.: 875, 914, 956, 920, 954.

Distribution: This species has been reported from the Kootenai Group of Montana (Newberry, 1891), Kootenai Formation of Montana (LaPasha and Miller, 1985), Lower Blairmore Group, Luscar Formation of Alberta, Bullhead Group and Hazelton Group of British Columbia (Bell, 1956), middle and upper floras of Belcourt Ridge (Mellon et al., 1963) and the Gates Formation. The distribution of the species appears to have been restricted to the Aptian-Albian in the northwestern Interior.

The only possible exception is that Newberry's collections contains fossils from both the Morrison and the Kootenai formations. The age of the Morrison Formation is Late Jurassic and the age of the Kootenai Formation is Aptian. Because the origin of Newberry's specimens cannot be accurately determined (LaPasha and Miller, 1985), it is uncertain if Newberry's specimens were Late Jurassic (Morrison Formation) or Aptian (Kootenai Formation). Most likely, Newberry's specimens were from the Kootenai Formation, since the presence of the species elsewhere is in Aptian or younger strata.

Discussion: The species was originally described as *Chiropteris williamsii* by Newberry (1891, p. 198, Pl. 14, figs. 10,11). Newberry included this plant in the genus *Chiropteris* with much hesitation, for it differs from the type species of *Chiropteris* in having an orbicular or elliptical blade. Fronds of *Chiropteris* are commonly flabellate and deeply lobed. The venation of Newberry's materials were described by Newberry as to be typical of *Chiropteris*, but it appears that Newberry erred in describing the venation of the plant. Although Newberry claimed the nervation was radiate, apparent midribs can be observed on both specimens (Newberry, 1891, Pl. 14, figs. 10,11). Bell (1956), LaPasha and Miller (1985) also referred to the existence of midribs, and the Gates materials also show clear midribs (Pl. 11, figs. 3-5). The existence of a midrib in each leaflet is a key point that separates *Caytoniopteris* leaflets from *Chiropteris* leaves.

The Potomac specimens figured as *Sagenopteris virginiensis* Fontaine (1889, p. 150, Pl. CXXXVIII, Fig. 13; Pl. CXXXIX, Fig. 1) also can be referred to *Caytoniopteris*. Unfortunately, those two specimens are too fragmentary to determine their specific identity. Although Fontaine's *Sagenopteris virginiensis* resembles *Caytoniopteris williamsii* in petiolule length, the leaflet size and shape of Fontaine's materials are unknown, and therefore the relationships between those two species can not be confirmed.

The specimen from Bowser Basin figured as *Sagenopteris williamsii* (MacLeod and Hills, 1992a) is only the upper part of a leaflet blade. It is uncertain if this specimen is petiolate or not, but the external outline of the blade in the Bowser specimen appears to be elliptic (estimated 7 cm long and 2.5 cm wide) rather than round as in *C. williamsii*, and therefore the Bowser specimen appears to be distinct.

On the basis of available information, the following species can be transferred into *Caytoniopteris* from *Sagenopteris*.

Caytoniopteris colpodes (Harris) comb. nov

Basionym: *Sagenopteris colpodes* Harris, 1964, The Yorkshire Jurassic flora. 2. Caytoniales, Cycadales and Pteridosperms. British Museum (Natural History). p. 4, Text-figs. 1-3.

Original Diagnosis: "Upper leaflets almost symmetrical, lower part with midrib considerably nearer the distal margin. Leaflets varying from small ones of broadly ovate shape and twice as long as broad to large ones of long lanceolate shape and five times as long as broad. Apex of leaflet obtuse, margins entire, base minutely stalked. Midrib usually disappearing considerably below the apex. Vein meshes 0.75-nearly 1.0 mm wide on larger leaves"(Harris, 1964, p. 4).

Diagnosis not emended.

Caytoniopteris serrata (Harris) comb. nov.

Basionym: *Sagenopteris serrata* Harris, 1932, The fossil flora of Scoresby Sound, east Greenland. Part 3: Caytoniales and Bennettitales. *Meddelelser om Grønland*, 85(5), p. 11, Pl. 1, fig. 9; Text-fig. 3.

Original Diagnosis: "Leaf probably composed of four leaflets. Leaflets lanceolate, typically 7 cm long and 3 cm wide, apex acute, margins irregularly serrate, base contracted, with a distinct stalk. Midrib situated in middle of leaflet, giving off veins traversing lamina at an angle of -60^0 to midrib. Lateral veins dichotomizing freely but only occasionally anastomosing, adjacent veins usually about 1.2 mm apart midway between midrib and margin. Mesophyll substance consisting of fine granules evenly distributed between veins. Resin absent"(Harris, 1932, p. 11).

Diagnosis not emended.

Caytoniopteris orientalis (Krassilov) comb. nov.

Basionym: *Caytonia orientalis* Krassilov, 1967, Early Cretaceous flora of southern Far East near sea area and its significance for stratigraphy., p. 137, Pl. XXXI, figs. 1-4. Moscow: Nauka. (in Russian)

Emended Diagnosis: Leaflet elliptic, 6 cm long and 3.3 cm wide; apex acute, margins entire, base contracted; petiolule 6 mm long; midrib extending to the apex; lateral veins reticulated.

Discussion: *Caytonia orientalis* should be transferred into *Caytoniopteris* because *Caytonia*, as originally defined, referred to reproductive organs of Caytoniales; leaflets of *C. orientalis* are petiolate and fall within the definition of *Caytoniopteris.*

Key to *Caytoniopteris* species

1. Petiolule long, up to 5 cm..*C. williamsii*
   Petiolule short, less than 1 cm..................................2
2. Margins serrate...*C. serrata*
   Margins entire..3
3. Length/width 2–3:1, elliptic, midrib to apex..............*C. orientalis*
   Length/width 5:1, lanceolate, midrib below apex......*C. colpodes*

Genus *Sagenopteris* Presl

Original Diagnosis: "Frons pinnata, pinnis ternatim rarius binatim compositis. Venae tenuissimae, ramosissimae, aequales, in maculas irregulariter hexagonoideas elongatas confluentes. Costae crassae usque ad apicem pinnularum excurrentes" (Cited from Berry, 1911, p. 284).

Emended Generic Diagnosis: Leaflets sessile, palmately arranged on the petiole. Each leaflet having an apparent midrib; lateral veins dichotomizing and reticulate, forming narrow simple meshes.

Comments: The generic comparisons among *Sagenopteris*, *Caytoniopteris* and *Chiropteris* have been presented in the discussion under *Caytoniopteris*. As petiolate leaflets are excluded from *Sagenopteris*, emendation of the generic diagnosis is necessary.

Generitype: *Sagenopteris nilssoniana* (Brongniart) Ward

Key to well-defined *Sagenopteris* species of Early Cretaceous:

1. Leaflet lobed ....*S. maclearnii*
   Leaflet margin entire...2

2. Widest at middle of leaflet................................*S. elliptica*
   Widest in upper third of leaflet.........................3

3. Midvein extending > 3/4 of leaflet length.........*S. newensis*
   Midvein extending < 1/2 of leaflet length.........*S. oregonensis*

Sagenopteris maclearnii Berry

(Pl. 12, figs. 2, 3)

Sagenopteris maclearnii Berry, 1929, p. 36, Pl. 4, fig. 3, Pl. 5, figs. 8, 9; Bell, 1956, [*pro parte*] p. 81, Pl. XXIX, figs. 4, 5, Pl. XXXII, fig. 3 [*only*]; LaPasha and Miller, 1985, p. 134, Pl. 9, figs. 4-10.

Description: Leaflet sessile, obovate in outline, 1.5-3 cm wide and 6-9 cm long; pinnately lobed, having about 7 pairs of rounded lobes, separated by acute sinuses, the lobing being most pronounced medially and diminishing toward both the base and the apex; apex may be broadly rounded or narrowly extended; base narrowly cuneate. Midrib conspicuous except in upper quarter, becoming thin distally; lateral veins diverge from the midrib at acute angles, curving outward, abundantly reticulate and terminating in the margin.

Materials: Specimens numerous. Locality no.: 852, 874, 875, 877, 914, 950, 952.

Distribution: This species has only been reported from the Lower Blairmore Group (Berry, 1929), Kootenai Formation, Luscar Formation, and the Gates Formation. Its distribution appears confined to the Aptian-Albian in the northwestern Interior.

Discussion: *Sagenopteris maclearnii* is similar to *S. newensis* in shape and size range; and there exist intermediate forms between the two species. LaPasha and Miller (1985) studied the cuticle structure of both species and indicated that stomata in *S. elliptica* (actually *S. newensis*) are smaller and mostly sunken as compared to the larger, superficial stomata of *S. maclearnii*; cell walls of the adaxial epidermis of the former species are more sinuous than the nearly straight walls of the latter species. Therefore *S. maclearnii* appears to be a distinct species.

Sagenopteris newensis **sp. nov.**

(Pl. 12, figs. 1, 4-6)

Basionym: *Chiropteris spatulata* Newberry, 1891, Am. J. Sci., 3rd., vol. 41, p. 199, Pl. XIV, fig. 1, 2.

Sagenopteris maclearnii Berry; Bell, 1956, [*pro parte*] p. 81, Pl. XXIX, fig. 3 [*only*].

Sagenopteris elliptica Fontaine *sensu* Bell, 1956, p. 82, Pl. XXXIII, fig. 6, Pl. XXXVI, fig. 5; LaPasha and Miller, 1985, p. 133, Pl. 8, figs. 8, 9; [*non*] Fontaine, 1889, p. 149, Pl. XXVII, figs., 9, 11-17; [*non*] Fontaine, 1905h, p. 236, Pl. LXV, figs. 19, 40.

Sagenopteris mantellii (Dunker) Schenk *sensu* Krassilov, 1967, p. 138, Pl. XXXI, figs. 5-10; [*non*] Seward, 1894, p. 131, Pl. IX, figs. 4, 5.

Original Diagnosis: "Pinnules 1.5-2 inches long, spatulate in outline, midrib strong, lateral nerves well defined, coarsely reticulated" (Newberry, 1891, p. 199).

Emended Diagnosis: Leaflet sessile, spatulate in outline, 3.5-5 cm long and 1.2-2.2 cm wide, with the greatest breadth of a leaf most commonly above the middle; margins entire; apex obtuse to rounded, base broadly cuneate. Midrib strong, persistent for at least three-fourths of the leaflet; lateral veins diverging from the midrib at acute angles, curving outward, abundantly reticulate and terminating in the margin.

Etymology: Because a new epithet is given to Newberry's (1891) type materials, the epithet is termed "new".

Materials: Specimens numerous. Locality no.: 851, 875, 950, 920, 954, 956.

Distribution: This species has been reported widely from the Early Cretaceous of the Arctic Province.

Discussion: *Sagenopteris newensis* was originally described as *Chiropteris spatulata* by Newberry (1891). As mentioned above in the generic discussion of *Caytoniopteris*, *C. spatulata* should be transferred into *Sagenopteris*. The resulting binary name *Sagenopteris spatulata* happens to be a later homonym of a Late Triassic plant from northern China (Sze, 1956). According to Article 55 (a) of the ICBN (Greuter et al., 1988), a new specific name must be given to this transferred species.

Sagenopteris newensis is different from *S. spatulata* Sze in having an entire leaflet margin, the latter species having a wavy leaflet margin.

The materials assigned to *S. mantellii* by Krassilov (1967) differ from specimens described as *S. mantellii* by Seward (1894) in a having distinct and strong midrib and having the greatest breadth of a leaf above the middle. Krassilov's materials are, however, very similar to *S. newensis* and are treated as conspecific.

Sagenopteris elliptica Fontaine (1889) differs from *S. newensis* in having an elliptical outline, with the greatest breadth at or near the middle of the leaflet. Both Bell (1956), and LaPasha and Miller (1985) described their *S. elliptica* as having the greatest breadth of a leaf above the middle; their descriptions are, therefore, inconsistent with the definition of *S. elliptica* but do match that of the *S. newensis* and therefore are treated as conspecific. The specimen attributed by Bell (1956, Pl. XXIX, figs. 3) to *S. maclearnii* has an entire margin and is conspecific with *S. newensis*.

Order Coniferales

Family Pinaceae

Genus *Pityocladus* Seward

Comments: *Pityocladus* was used originally as a subgenus of *Pinites* by Nathorst in 1897 designating branches bearing short shoots similar in habit to those of *Cedrus* and *Larix*. Seward (1919) was the first to treat it as a generic name and attributed its authority to Nathorst. Andrews (1955) rightly names Seward as the author, although Seward gave no diagnosis and named no type species. Andrews (1970) selected *Pityocladus longifolius* (Nathorst) Seward as the type species, which was the first described species of the genus by Seward. Harris (1979) gave an appropriate diagnosis as follows:

"Long shoots slender and woody, bearing caducous foliage leaves and persistent short shoots, short shoots bearing bud scales and foliage leaves in a crowded helix. Foliage leaves simple, linear, single-veined; bud scales small, persistent" (Harris, 1979, p. 93).

The Gates materials resemble the vegetative shoots of *Pityites solmsii* Seward (1919, p. 374, fig. 772) in outline appearance, but *Pityites*, founded by Seward (1919) to designate specimens which showed a direct connection between cones and foliage-shoots, is not suitable for Gates materials as there are no reproductive parts with the Gates materials. *Pityocladus* appears to be the most appropriate name for the Gates materials.

Generitype: *Pityocladus longifolius* (Nathorst) Seward

Pityocladus magnifolius sp. nov.

(Pl. 13, fig. 3)

Basionym: *Leptostrobus longifolius* Fontaine, 1889, U. S. Geol. Surv., Mon. XV, p. 228, Pl. CI, Figs. 2, 3, Pl. CII, Figs. 1-4, Pl. CIII, Figs. 6-12, Pl. CIV, Fig. 6; Fontaine, 1905k, p. 506, Pl. CX, fig. 11; Fontaine, 1905k, p. 551, Pl. CXVI, fig. 1.

Abietites longifolius (Fontaine) Berry, 1911, p. 407, Pl. LXVII, Fig. 7.

Original Diagnosis: "Trees or shrubs with stout and long primary leafy branches, which contain the leaves attached singly and scattered along the stem, as now seen attached to the under surface or to the sides of the stems, but most probably originally found spirally arranged and attached to the stem on all sides. The primary leafy branches have lateral and terminal short shoots, on the ends of which the leaves are arranged in tufts; leaves very long and narrowly linear or needle-shaped, with their extremities in no case seen, attached by the entire bases, not narrowed; nerves several, parallel, slender, and obscure (Fontaine, 1889, p. 228)".

Emended Diagnosis: Trees or shrubs with stout and long leafy shoots; long shoot at least 9 cm long and 8 mm wide, bearing spirally arranged leaves on all sides of the long shoot, or densely covered with leaf scars if leaves detached. Long leafy shoots with lateral and terminal short shoots, which bear numerous linear leaves arranged in fascicles. Leaves very long and narrowly linear or needle-shaped, attached by the entire base, at least 7 cm long and 1.5 wide, apparently uninerved.

Etymology: The new epithet is used to suggest the large size of the leaves.

Materials: 3 specimens. Locality no.: 956.

Distribution: This species has been reported from the Potomac Group and the Gates Formation. Its distribution appears confined to the Early Cretaceous in North America.

Discussion: *Leptostrobus* was instituted by Heer for strobili from Jurassic strata in Siberia agreeing closely in habit and in the form of the seed cone scales with those of *Voltzia* (Seward, 1919). Because all the Potomac specimens included in *Leptostrobus* by Fontaine (1889) are vegetative shoots, Fontaine's usage of *Leptostrobus* appears to be inappropriate. Berry (1911) also indicated that the Potomac materials were not *Leptostrobus.*

Later study showed that *Leptostrobus* is related to *Czekanowskia* and appears to be independent of the conifers (Harris, 1935). *Czekanowskia* was instituted by Heer for fascicles of long and narrow, filiform, leaves with a simple or occasionally forked lamina born on a short supporting axis covered with broader and shorter scale-leaves (Seward, 1919). An important feature of *Czekanowskia*, the dichotomous branching of lamina, has never been observed on the Potomac nor the Gates materials. *Czekanowskia* may also have more than one vein in each leaf. Although the leaves of the Potomac materials were described by Fontaine (1889) as having several nerves, Berry (1911) indicated that those nerves were most likely surface striae. The true venation of the Potomac and the Gates materials is unclear, but most likely uninerved. Therefore, the Potomac and the Gates materials do not belong to *Czekanowskia.*

Berry (1911) was correct in assigning the Potomac materials to *Abietites* Nilsson, which was used as a replacement of *Pinites* Lindley & Hutton (Berry, 1911), but *Pityocladus* appears to be a more precise name for both the Potomac and the Gates materials. The new combination, *Pityocladus longifolius*, happens to be a later homonym of *Pityocladus longifolius* (Nathorst) Seward (1919, p. 378). According to Article 55 (a) of the ICBN (Greuter et al., 1988), a new specific epithet is given to this species.

Pityocladus magnifolius sp. nov. differs from most other species within the genus in having numerous leaves on each short shoot. *Pityocladus schenkii* and *P. kobukensis* (Seward, 1919) also have numerous leaves on each short shoot, but they appear to have narrower leaves (1 mm wide) than *P. magnifolius* (1.5 mm wide).

The leaves of this species, if preserved separately, fall within the size range of *Pityophyllum nathorstii* Seward.

Genus *Pityophyllum* Nathorst

Comments: *Pityophyllum* has been applied to detached leaves of needle-like form similar to those of recent pines as well as to long linear leaves broader and flatter than the needles of *Pinus* (Seward, 1919). This name appears to be useful for some Gates materials.

The differentiation of species within the genus is based on the size of leaves and the leaf base and apex morphology. Sze et al. (1963) gave a useful key to commonly seen species within the genus.

Generitype: *Pityophyllum staratschinii* (Heer) Nathorst

Pityophyllum staratschinii (Heer) Nathorst

(Pl. 13, fig. 2)

Basionym: *Pinus staratschinii* Heer, 1874, p. 129, Pl. 38, figs. 6, 7.

Pityophyllum cf. *P. nordenskioeldii* (Heer) Krystofovich; Bell, 1956, p. 112, Pl. LXI, fig. 3, Pl. LXII, figs. 1, 4, 5.

Pityophyllum cf. *P. longifolium* (Nathorst) Moeller; Bell, 1956, p. 113, Pl. LXVI, fig. 3, Pl. LXIX, fig. 1.

Pityophyllum staratschinii (Heer) Nathorst; Sze et al., 1963, p. 279, Pl. 92, fig. 11.

Pityophyllum var. 1, Scott and Smiley, 1979, Pl. 5, fig. 3.

Marskea sp. 1; Chen et al., 1988, p. 89; Pl. 55, figs. 4-8.

Description: Leaves linear, commonly curving, clustered on short shoots, 5-8 cm long and 3 mm wide, maximum width situated at the upper part of a leaf; apex bluntly acute; base gradually contracted into a narrow stalk almost the same width as the midrib; uninerved.

Materials: Specimens many. Locality no.: 951.

Distribution: This species appears to have been distributed from the Jurassic to Early Cretaceous in the Northern Hemisphere.

Discussion: The leaves included within the species resemble those of *Pseudolarix*. Although LaPage (per. comm. 1993) claimed that the morphological features of such leaves were sufficient evidence to assign them to *Pseudolarix*, it is perhaps better to include them in the form genus *Pityophyllum* until evidence about reproductive organs is available.

The two specimens from northeastern China assigned to *Marskea* by Chen et al. (1988, p. 89, Pl. 55, figs. 4, 5) are morphologically different from *Marskea* but the same as the Gates materials. *Marskea* Florin (1958) was originally defined as having persistent leaves and long decurrent leaf bases. Both of these Chinese specimens were preserved in detached states. Chen et al. (1988) must have noticed the morphological difference between the Chinese materials and *Marskea*, and indicated that their attribution of the Chinese materials to *Marskea* was because of the cuticular resemblance between the Chinese materials and *Marskea*. As cuticles of the Gates materials are not available, comparisons of cuticle structures between the Gates and the Chinese materials can not be done. On the basis of external morphology, the Chinese materials are treated as conspecific with the Gates materials.

The specimens assigned to *Pityophyllum* cf. *P. nordenskioeldii* and *Pityophyl-*

lum cf. *P. longifolium* (Bell, 1956) are identical to the Gates materials. The so-called medial grooves on the upper surfaces of leaves included within *P.* cf. *P. nordenskioeldii* are, most likely, the impressions of the midrib. According to the species key given by Sze et al. (1963), *P. longifolium* appears to have a larger leaf width (4.5-5 mm) than the Gates materials; leaves of *P. nordenskioeldii* appear to be shorter (up to 55 mm) than those of the Gates materials. On the basis of the size and the falcate feature of the Gates materials, *P. staratschinii* appears to be the only possible choice for the Gates materials.

The two specimens from the Luscar Formation (Bell, 1956, Pl. LXVI, fig. 3; Pl. LXIX, fig. 1) show that these kinds of leaves are borne on short shoots. Therefore, the Gates materials are most likely a member of Pinaceae.

One Alaska specimen figured as *Pityophyllum* var. 1 (Scott and Smiley, 1979) is very similar to the present species, but this specimen was not described in the publication. By examining the photo of the specimen, leaves are found to be 4 or 5 in a bundle clustered on a short shoot, more or less falcate, 7-8 cm long and 3 mm wide, apex bluntly acute, base gradually contracted to a stalk. All the features of the specimen indicate that it is conspecific with *P. staratschinii*.

Another Alaska specimen figured as *Pityophyllum* var. 2 (Scott and Smiley, 1979, Pl. 5, fig. 1) is also very similar to the Gates materials in external outline, but has a larger leaf width (6 mm) than that of the Gates materials and therefore perhaps belongs to another species.

The specimen figured as *Oleandra graminaefolium* Berry (1929, p. 38, Pl. V, figs. 5, 6) is similar to the Gates materials, but the bases and apices of Berry's materials are not preserved and therefore their relationships with the Gates materials can not be confirmed. I agree with Bell (1956) in his assessment that Berry (1929) mistook transverse wrinkles on his specimens for lateral veins so that Berry's figure 6 is baseless.

The specimen figured as *Cephalotaxopsis ramosa* (Fontaine, 1905j, p. 311, Pl. 73, fig. 8) is also similar to the Gates materials. Again, because the bases and apices of Fontaine's materials are not preserved, their relationship with the Gates materials can not be confirmed.

Family Taxodiaceae

Genus *Athrotaxites* Unger

Comments: According to Seward (1919), this name was proposed by Unger in 1849 for cone-bearing shoots resembling recent *Athrotaxis* Don. Schimper tried, in 1874, to substitute for *Athrotaxites* a new genus *Echinostrobus* to get rid of the implication of relationship to recent *Athrotaxis*. Without adequate reason Schimper altered Unger's type species name *lycopodioides* to *sternbergii*. Seward (1919) disagreed with Schimper and suggested that *Athrotaxites* be retained, and restricted its use to the sense only of a natural genus. Seward's view is followed in this study. Miller and LaPasha (1984) indicated that there is no difference between *Athrotaxites* and *Athrotaxopsis* Fontaine (1889), and that the former has priority.

Generitype: *Athrotaxites lycopodioides* Unger

Athrotaxites berryi **Bell**

(Pl. 14, figs. 1-5; Pl. 15, figs. 1-5)

Athrotaxites berryi Bell, 1956, p. 115, Pl. LVIII, fig. 5, Pl. LX, fig. 5, Pl. LXI, fig. 5, Pl. LXII, figs. 2, 3, Pl. LXIII, fig. 1, Pl. LXIV, figs. 1 5, Pl. LXV, fig. 7; Miller and LaPasha, 1983, p. 772-779, Figs. 1-25; Miller and LaPasha, 1984, p. 6, Pl. 1, figs. 1-5, Pl. 2, figs. 1-9; Chen et al., 1988, p. 79, Pl. 69, figs. 4, 4a, 4b, 8.

Description: Shoots irregularly branched, most but not all branches in a single plane, branches from large shoots commonly at open angles, whereas the small ones are at more acute angles. Leaves scale-like, rhomboid, spirally arranged, occurring typically in a 3/8 phyllotactic order; leaves about 2.5 mm long and 2 mm wide; apex acutely pointed; veins unknown.

Seed cones terminal on shoots, elliptical, oval to globose, up to 15 mm long and 10 mm wide. Pollen cones terminal, elliptical, up to 10 mm long and 5 mm wide.

Materials: Specimens numerous, found in almost every fossil site (see Appendix A).

Distribution: This species was reported from the Kootenai Formation of Montana (Miller and LaPasha, 1983; 1984), the Lower Blairmore Group of Alberta, the Hazelton Group and the Bullhead Group of British Columbia (Bell, 1956), and the middle flora of Belcourt Ridge (Mellon et al., 1963). Chen et al. (1988)

reported the occurrence of the species from the upper part of the Fuxin Formation of northeastern China. Although Krassilov (1967) reported the occurrence of the species from the southern Primoriya near Vladivostok, Maritime Territory, southeastern former USSR, Miller and LaPasha (1984) indicated that the Russian specimens should be assigned to a different species. *Athrotaxites berryi* appears to have been distributed throughout the Arctic Province in the Early Cretaceous.

Discussion: This species was well-described and studied by Miller and LaPasha (1983, 1984). The differences between *Athrotaxites berryi* and other similar species, including both fossil and living materials, were discussed in detail by Miller and LaPasha (1983, 1984). I have little to add to their interpretation except some ecological features.

Stems are found either covered with leaves or leaf scars (Pl. 14, fig. 4), or even smooth (Pl. 14, fig. 2). The specimen in Pl. 14, fig. 3 shows two different kinds of leaf scars on a single stem; the leaf scars on the lower part of the stem are round and closely spaced, and appear to be reformed by later growth process; the ones on the upper part are in the shape similar to that of leaves. This fact may suggest that growth was seasonal and that leaf abscission was a periodic event rather than a progressive process. In other words, those scars were, most likely, caused by leaf fall in winter rather than leaf replacement or leaf aging. Therefore, *Athrotaxites berryi* appears to have been a deciduous plant.

Lateral branches are always found covered with leaves; they might have had a habit similar to that of some members of recent Taxodiaceae such as *Metasequoia*, *Glyptostrobus* and *Taxodium*, and shed leafy twigs.

Genus *Elatides* Heer

Comments: According to Seward (1919), this genus was proposed by Heer in 1876 for shoots bearing spirally disposed falcate leaves and cones similar externally to those of *Picea*, *Abies*, and other Abietineae (Antiquated term for Pinaceae). Harris (1979, p. 66) restricted the leaves of the genus to those that are "borne helically and diverging radially, free part falcate and isodiametric, rhomboidal in section".

As both falcate helically arranged isodiametric rhomboidal leaves and flat pseudo-distichous leaves appear in one plant in the Gates materials, Harris' diagnosis needs to be modified to include both type of leaves.

Differentiation of species within *Elatides* is based on both vegetative and reproductive organs. Cuticle structure appears to be a useful tool in distinguish similar species, although epidermal structure is known for only four species. The differences among those four species were discussed by Miller and LaPasha in detail (1984). Unfortunately, cuticles are not preserved in the Gates materials.

Generitype: *Elatides ovalis* Heer

Elatides curvifolia (Dunker) Nathorst

(Pl. 16, figs. 1-4; Pl. 17, figs. 1-4; Pl. 22, 1A)

Basionym: *Lycopodites curvifolous* Dunker, 1846, Monographie der Norddeutschen Wealdenbildung, p. 20, Pl. 7, fig. 9. (type not seen; reference cited from Jongmans and Dijkstra, 1973, p. 329)

Elatides curvifolia (Dunker) Nathorst; Seward, 1919, p. 273, Fig. 743; Bell, 1956, p. 110, Pl. LIV, figs. 1, 3, 4, 5, Pl. LVII, figs. 2-4, 6, Pl. LVIII, figs. 1, 4, Pl. LIX, fig. 3, Pl. LX, fig. 4; Miller and LaPasha, 1984, p. 7, Pl. 3, figs. 1-8, Pl. 4, figs. 1-8.

Elatides splendida Bell, 1956, [*pro parte*] p. 111, Pl. LIX, fig. 4, Pl. LX, figs. 2, 3, 6, Pl. LXI, figs. 1, 4, Pl. LXIII, figs. 2, 3 [*only*].

? Abietites sp., Scott and Smiley, 1979, Pl. 5, fig. 5.

Description: Leafy twigs, up to 1 cm thick, branching irregularly. Leaves dimorphic; one kind of leaves is isodiametric and helically arranged; the other, flat and pseudo-distichously arranged.

Flat leaves helically attached, more or less pseudo-distichous, linear lanceolate, on average 7mm long and 1.5 mm wide but up to 10 mm long and 2 mm wide, obliquely attached at angles generally greater than 45 degrees,narrowing gradually to bluntly acute apices; base decurrent to the stem forming rhomboidal cushions; upper surface of a leaf commonly concave; lower surface appearing to have a rounded median keel, which is also decurrent to leaf cushions and may be absent in very young leaves; veins unclear.

Isodiametric leaves spirally arranged, acicular, strongly falcate, square or rhomboidal in cross section, size range same as that of the flat leaves; apex acuminate.

Seed cones terminal, elliptical to oval up to 3 cm long and 1 cm wide.

Materials: Specimens numerous, found in almost every locality (see Appendix A).

Distribution: This species has been reported from the Kootenai Formation of Montana (Miller and LaPasha, 1984), the Lower Blairmore Group and the Luscar Formation of Alberta, the Bullhead Group, the Hazelton Group, the Jackass Mountain Group and the Spence Bridge Group of British Columbia (Bell, 1956), the Nanushuk Group of the Alaska (Scott and Smiley, 1979) and the Gates Formation. This species has also been reported from the Jurassic of Siberia and the Wealden flora of Spitzbergen (Seward, 1919). This species appears to have been distributed in Jurassic to Early Cretaceous deposits throughout the Northern Hemisphere.

Discussion: Two kinds of foliages have been found in this species. One is pseudodistichously arranged flat leaves; the other is spirally arranged isodiametric falcate leaves. Both kinds of leaves are commonly found on the same specimen. Flat leaves are commonly borne on lateral branches (Pl. 17, fig. 1 A; Pl. 22, 1 A) while the isodiametric leaves are commonly seen on stems, or leading branches (Pl. 17, fig. 1 B; Pl. 22, 1 A). Isodiametric leaves are also commonly seen on the shoot joints (Pl. 16, fig. 4 B); in this case these isodiametric leaves might function like bud bracts in winter. Such a wrapping bud mechanism was considered to be a feature of high latitude plants (Spicer and Chapman, 1990).

Hundreds of specimens have been examined, and none has shown any evidence of leaf abscission. However, leafy twigs may have been shed intact (Miller and LaPasha, 1984), especially twigs with flat leaves, which might grow annually because flat leaves are never seen associated with old branches or stems. Isodiametric leaves appear to have been persistent on old branches or stems all year around.

Some leafy twigs having flat leaves were assigned by Bell to *E. splendida* Bell (1956) when preserved in isolation. Miller and LaPasha (1984) indicated that both *E. splendida* and *E. curvifolia* could be included in *E. curvifolia* because the leaf size of both species fell in same range.

Miller and LaPasha (1984) doubted the generic identification of *E. splendida* in that the holotype and two of the paratypes (Bell, 1956, Pl. LIX, fig. 1; Pl. LX, fig. 1 and Pl. LXI, fig. 2 respectively) appeared to have needles that are narrow at the base rather than broad. I agree with them in that those three specimens show features inconsistent with Harris' (1979) definition of *Elatides*; therefore those three specimens are not included within *E. curvifolia.*

Two specimens of Bell (1956, Pl. LXVI, figs. 1, 4) have exceptionally large leaves which are not seen in either the Montana or the Gates materials; besides, their leaves appear to diverge spirally rather than in two rows like the flat leaves of *E. curvifolia*; therefore they are excluded from *E. curvifolia.* Other specimens included in *E. splendida* by Bell all belong to *Elatides curvifolia.*

The Alaska specimen figured as *? Abietites* sp. (Scott and Smiley, 1979) shows great resemblance to the Gates materials in leaf size, morphology and branching manner and therefore is treated as conspecific. This specimen only shows vegetative shoots; both isodiametric and flat leaves can be observed clearly in a single specimen (Scott and Smiley, 1979, Pl. 5, fig. 5).

Family Incertae Sedis

Genus *Elatocladus* Halle

Comments: This genus was proposed by Halle (1913) for sterile coniferous branches of the radial or dorsiventral type which do not show any features that permit them to be included in one of the genera instituted for more particular forms. This name is appropriate for some Gates materials.

Generitype: *Elatocladus heterophylla* Halle

Elatocladus brevifolia (Fontaine) Bell

(Pl. 18, figs. 1-4)

Cephalotaxopsis brevifolia Fontaine, 1889, p. 238, Pl. CV, fig. 3, Pl. CVI, fig. 5, Pl. CVII, fig. 5; Berry, 1911, p. 379, Pl. LX, fig. 2.

Elatocladus brevifolia (Fontaine) Bell, 1956, p. 109, Pl. LIII, fig. 2, Pl. LIV, fig. 2, 7, Pl. LVII, fig. 1, Pl. fig. 7.

Elatocladus brevifolia forma *lata* Bell, 1956, p. 110, Pl. LIX, fig. 2, Pl. LX, fig. 7.

Description: Shoots pseudo-dichotomizing or sub-oppositely branching. Leaves, pseudo-distichous, alternately arranged, linear, up to 2.3 cm long and 2 mm wide, uninerved; base contracted and rounded to a very short, decurrent footstalk; apex acute.

Materials: 81 specimens. Locality no.: 874, 915, 950, 952.

Distribution: Early Cretaceous of North America.

Discussion: The Gates specimens are morphologically similar to the Potomac materials called *Cephalotaxopsis brevifolia* by Fontaine (1889). *Cephalotaxopsis* was originally a form genus. Berry (1929) was the first who attributed *Cephalotaxopsis* to the Taxaceae on the basis of cuticle features of this genus. Seward (1919), Florin (1958) and NCIGS (1976) agree with Berry in attributing *Cephalotaxopsis* to the Taxaceae. Recognition of the genus should not be only on the basis of the morphology of vegetative shoots but also on cuticle features, because the vegetative shoots of the genus are similar to those of other genera such as *Cephalotaxus*, *Torreya* and *Taxus*.

Although NCIGS (1976) gave some morphological criteria for recognition of *Cephalotaxopsis*, those criteria may be useful only when very well-preserved specimens are available.

Bell (1956) was reasonable to assign this kind of vegetative shoot to *Elatocladus* and to institute the new combination *E. brevifolia* (Fontaine) Bell, although he did not explicitly list the basionym for *E. brevifolia* (Fontaine) Bell as required by ICBN (Greuter et al., 1994). However, because Bell (1956) so commonly neglected to give the sources of basionyms for new combinations, invalidation of all Bell's new combinations would cause extensive nomenclatural change, which might lead to further confusion. Therefore, *E. brevifolia* (Fontaine) Bell is retained in this study to avoid nomenclatural confusion. Presumably, the basionym of *E. brevifolia* (Fontaine) Bell (1956) is *Cephalotaxopsis brevifolia* Fontaine (1889). As cuticles are not preserved in the Gates materials, *E. brevifolia* appears to be the most appropriate name.

There do not appear to be any external differences between *E. brevifolia* and *E. montanensis* Miller and LaPasha (1984) except for the branching. The two species differ in that the stomata are arranged in regular longitudinal files in *E. montanensis* while they are not in regular files in *E. brevifolia*; cells of the adaxial epidermis are commonly rounded in the former, rather than square as in the latter species (Miller and LaPasha, 1984). Unfortunately, the shoot branching manner of *E. montanensis*, which might differ from that of *E. brevifolia*, is unclear. Judging from the specimen of Miller and LaPasha (1984, Pl. 5, fig. 4), the branching pattern of *E. montanensis* does not appear to be pseudo-dichotomizing, and if so, would represent a significant morphological difference between the two species.

Elatocladus manchurica (Yokoyama) Yabe

(Pl. 19, figs. 3, 4)

Basionym: *Palissia manchurica* Yokoyama, 1906, Journ. Coll. Sci. Imp. Univ. Tokyo, Vol. 21., Art. 9, p. 32, figs. 2, 8. (type not seen; reference cited from Chen et al., 1988, p. 86)

Elatocladus manchurica (Yokoyama) Yabe; Sze et al., 1963, p. 297, Pl. 95, fig. 1, 2, Pl. 96, figs. 3, 4, Pl. 97, figs. 10, 11; Chen et al., 1988, p. 86, Pl. 49, figs. 6A, 7, 8, Pl. 50, figs. 1A, 2, 3A, Pl. 51, figs. 1, 2, 4-6, Pl. 52, figs. 1-3, Pl. 66, figs. 1-4, Pl. 68, fig. 3.

Description: Shoots thick. Leaves helically arranged and spirally diverging, 1.5-2 cm long and 1.5-2 mm wide, lanceolate, decurrent, base broad, apex acuminate; uninerved.

Seed cones, cylindrical, 3-3.5 cm long and 1-1.5 cm wide, details unknown.

Materials: Specimens many. Locality no.: 865, 874, 914, 920, 950, 953.

Distribution: Jurassic to Early Cretaceous in Northern Hemisphere.

Discussion: *Elatocladus manchurica* differs from *E. smittiana* (Heer) Seward in that the latter species has spirally attached but distichously diverging leaves (Seward, 1926) while the former species has spirally diverging leaves; the other possible difference is that the former species has thick branches while the latter, slender branches. The Gates materials appear to belong to *E. manchurica* because of their thick branches and spirally diverging leaves.

Elatocladus sp.

(Pl. 13, fig. 1)

Elatocladus sp.; Chen et al., 1988, p. 87; Pl. 58, figs. 1-3.

Description: Specimen is part of a leafy twig. Leaves pseudo-distichously arranged, opposite, lanceolate, up to 12 mm long and 1.5 mm wide; base rounded, contracted to a very short stalk; rather gradually narrowed to an acutely pointed apex.

Materials: 2 specimens, No. 915, 921.

Distribution: This species appears confined to the Early Cretaceous of the Arctic Province.

Discussion: The Gates materials resemble the specimens from northeastern China described as *Elatocladus* sp. (Chen et al., 1988), but are slightly larger. Leaves arranged in this pattern are seen only in *Metasequoia*. which is a natural genus in Taxodiaceae. Because the Gates materials are vegetative shoots. *Elatocladus* appears to be appropriate name as recommended by Christophel (1976).

Unidentified conifer seeds ?

(Pl. 19, figs. 1, 2)

Description: Seeds paired, borne on a 2 mm long stalk; seed obovate, 5 mm long and 3 mm wide.

Materials: 14 specimens. Locality no.: 951.

Distribution: This species has only been recovered from the Gates Formation.

Discussion: The seeds are very similar in shape to those of living *Cephalotaxus*. Unfortunately, no connection with leafy twigs have been found. The seeds were found only in one site; other plants preserved together with the seeds are *Elatides curvifolia* and *Pityophyllum staratschinii.*

Order Cycadales

Family Incertae Sedis

Genus *Chilinia* Lee & Yeh

Comments: According to Chen et al. (1988), *Chilinia* was instituted by Lee and Yeh in 1964 to designate fronds similar to *Ctenis* in general morphology, venation and cuticle structures, but differing from *Ctenis* in having forward directed teeth all along the pinna margin. Zhang (1980) reported two additional species of the genus and indicated that the fronds of the genus were spirally arranged or clustered.

Encephalartopsis, instituted by Fontaine (1889), is similar to *Chilinia* in pinna morphology and venation. Zhang (1980) and Chen et al. (1988) noted that, because Fontaine's specimens were too fragmentary to show the way that pinnae were inserted on rachis and lacked of cuticle information, it was therefore difficult to compare them to *Chilinia*. Therefore *Encephalartopsis* appears to be an unusable genus in this study.

Ctenis exilis Harris (1964) appears to be a member of *Chilinia*. Harris indicated that *Ctenis exilis* differs from all species of *Ctenis* in its small, dentate pinnae and realized that it could be separated generically from *Ctenis*. Because of the fragmentary nature of the specimens, Harris (1964) did not institute a new genus. Although *Ctenis exilis* may be transferable to *Chilinia*, it is difficult to compare with other species of *Chilinia* because of the fragmentary nature of Harris' specimens.

Two species from the Stanovy Ridge of the former Soviet Union are apparently also members of *Chilinia*. *Ctenis stanovensis* Vakhrameev & Blinova (1971) is characterized by having less conspicuously toothed pinnae which measure 15-18 mm long and 6-7 mm wide. The pinnae of *Ctenis harrisii* Vakhrameev & Blinova (1971) measuring 25 mm long and 3-5 mm wide are conspicuously toothed and a little longer and narrower than those of *Ctenis stanovensis*. Both species are in accordance with the definition of *Chilinia* and should be included within *Chilinia*.

Chilinia stanovensis (Vakhr. & Blinova) comb. nov.

Basionym: *Ctenis stanovensis* Vakhrameev & Blinova, 1971, Paleontol. Journ., 1, p. 91, Pl. X, fig. 1; Text-fig. 1. (In Russian)

Diagnosis not emended.

Chilinia harrisii (Vakhrameev & Blinova) comb. nov.

Basionym: *Ctenis harrisii* Vakhrameev & Blinova, 1971, 1971, Paleontol. Journ., 1, p. 93, Pl. X, figs. 2, 3; Text-fig. 2. (In Russian)

Diagnosis not emended.

Since all the species within the genus have once pinnately divided fronds, It is recommended that *Chilinia* be restricted to once pinnate fronds.

Differentiation of species within the genus is based on the size and morphology of fronds and pinnae. A key to the species within the genus is given as follows.

Key of *Chilinia* species:

1. Pinna length >8 cm ....*C. magnifolia*
   Pinna length < 5 cm 2

2. Pinna length 4-5 cm 3
   Pinna length < 4 cm 4

3. Pinna width about 1 cm ....*C. fusinensis*
   Pinna width about 0.5 cm ....*C. elegans*

4. Pinna length about 3 cm 5
   Pinna length < 3 cm 6

5. Pinna width about 1.5 cm ....*C. ctenioides*
   Pinna width 0.3 - 0.5 cm ....*C. harrisii*

6. Pinna length 1.5-1.8 cm ....*C. stanovensis*
   Pinna length about 1.3 cm ....*C.* sp.

Generitype: *Chilinia ctenioides* Lee & Yeh

Chilinia magnifolia sp. nov.

(Pl. 20, figs. 1, 2)

Diagnosis: Frond large; rachis narrow, 2 mm wide. Pinna at least 8 cm long and about 1.6 cm wide, ribbon-like, subopposite; attached on rachis along full pinna base; apex digitately dentate; lateral margins of pinna sparsely toothed; venation reticulate.

Etymology: The new epithet is used to suggest the large size of the frond.

Materials: 5 specimens. Locality no.: 877, 950.

Holotype: Pl. 20, fig. 1; specimen no.: 877-7079.

Distribution: This species is restricted to the Gates Formation.

Discussion: This species is distinguished from other species within *Chilinia* by its exceptionally large pinna size.

Chilinia sp.

(Pl. 20, fig. 3)

Description: Frond small, length unknown, 2.6 cm wide; rachis thin, 1 mm wide. Pinnae alternate to subopposite, 1.3 cm long and 5 mm wide, oblong, having teeth all around pinna margin, attached to rachis along entire base. Teeth on the apex are more closely spaced than on the lateral margins. Venation most likely reticulate.

Materials: 2 specimens. Locality no.: 921.

Distribution: This species is restricted to the Gates Formation.

Discussion: This species is distinguished from other species within the genus by its small size. Although the venation system is not clear for this species, it is assigned to *Chilinia* on the basis of the overall resemblance to other members of *Chilinia*.

Genus *Ctenis* Lindley & Hutton

Comments: *Ctenis* is one of the least controversial genera. *Ctenis* as employed here basically follows Harris' translation (Harris, 1964) of Florin's diagnosis of 1933. This genus should only include forms having entire pinna margins.

Many species within the genus have been reported from the Northern Hemisphere. The differentiation of species within this genus is on the basis of the pinna size and morphology. It appears that all the species can be grossly divided into two groups, a linear-pinna group and an elliptical-pinna group. The linear pinna group is represented by the following species:

1. *Ctenis sulcicaulis* (Phillips) Ward; Harris, 1964, p. 103, Text-figs. 44-46C.

2. *Ctenis reedii* Harris, 1964, p. 109, Text-figs. 46A, B, 47.

The Gates species, *Ctenis rotundata* sp. nov., is a representative of the elliptical-pinna group. A key to well defined elliptical-pinna species is given below.

Key to the *Ctenis* species having elliptical pinnae:

1. Pinna base not connate..2
   Pinna base connate..*C. lyrata*

2. Pinna apex rounded...3
   Pinna apex acute..*C. burejensis*

3. Pinna width > 2.5 cm...*C. rotundata*
   Pinna width < 2.5 cm...4

4. Pinna width > 1 cm..5
   Pinna width < 1 cm..*C. nana*

5. Pinna vein meshes in regular elongate hexagons....*C. szeiana*
   Pinna vein meshes in irregular polygons................6

6. Pinna more or less oblong....................................*C. yokoyamae*
   Pinna more or less deltoid...................................*C. uwatokoi*

Generitype: *Ctenis sulcicaulis* (Phillips) Ward

Ctenis rotundata **sp. nov.**

(Pl. 20, fig. 4; Pl. 21, fig. 1)

Ctenis burejensis f. typica Prynada; Samylina, 1963, [*pro parte*] p. 82, Pl. XI [*only*].

Diagnosis: Frond large, over 11 cm wide; rachis slender, 2 mm wide. Pinnae at least 5.5 cm long, 2.5 cm wide, obovate in shape, alternately to suboppositely attached on the sides of the rachis, maximum width in the upper part of a pinna; apex rounded, base slightly contracted. Venation reticulate.

Etymology: The new epithet originates from the Latin *rotundus*, suggesting the shape of pinna apex.

Materials: 5 specimens. Locality no.: 915, 921.

Holotype: Pl. 21, fig. 1; specimen no.: 915-7199.

Distribution: This species has been reported from the Gates Formation and the Jurassic to Early Cretaceous deposits of Siberia (Samylina, 1963) and appears to have been distributed throughout the Arctic Province from the Jurassic to Early Cretaceous.

Discussion: One of the Siberian specimens figured as *Ctenis burejensis* Prynada by Vakhrameev and Doludenko (1961, p. 89, Pl. XXXIX, fig. 2) is similar to

Ctenis rotundata in pinna size. Differences between this Siberian specimen and *C. rotundata* seem to be that the pinnae of this Siberian specimen have bluntly acute apices (Vakhrameev and Doludenko, 1961, p. 90, text-fig. 26) and the maximum width of a pinna is in the lower part of the pinna, while pinnae of *C. rotundata* has round apices and the maximum width of a pinna is in the upper part of the pinna. Therefore, this Siberian specimen is distinct from *C. rotundata*.

Other specimens included within *C. burejensis* by Vakhrameev and Doludenko (1961, p. 89) appear to have much smaller pinna size and therefore are distinct.

The specimen described as *C. latiloba* by Samylina (1963, p. 83, Pl. XIII, fig. 1) is similar to the new species in pinna apex and pinna width but differs in having much longer pinna length than that of the new species and should be left as a distinct species.

One specimen described as *C. burejensis f. typica* Prynada by Samylina (1963, p. 82; Pl. XI) is similar to the new species in pinna shape and size, and is treated as conspecific with the new species. Other specimens under *C. burejensis f. typica* Prynada have much smaller pinna size and appear to be distinct.

Genus *Multipinnia* gen. nov.

Generic Diagnosis: Frond at least bipinnate; pinnae attached on the sides of the rachis, margin toothed, venation reticulate.

Etymology: The generic name is a combination of Latin *Multi-* and *pinnatus*, referring to fronds which pinnately divide more than once.

Generitype: *Multipinnia interior* sp. nov.

Discussion: This genus differs from *Chilinia* only in having at least bipinnate fronds. *Chilinia* has been found to have spirally arranged or clustered fronds (Zhang, 1980; Chen et al., 1988), all of which are once pinnate. *Multipinnia* is also very similar to Potomac *Ctenopteris* Brongniart of Fontaine (1989) in all aspects except for the reticulate venation in the former genus. Nevertheless, *Ctenopteris* is not nomenclaturally valid (Harris, 1964, p. 89). *Multipinnia* differs from *Ctenozamites* Nathorst in having reticulate venation.

Multipinnia interior sp. nov.

(Pl. 21, figs. 2-4)

Diagnosis: Frond large, at least bipinnate. Pinna rachis subopposite to alternate, at least 8 cm long. Pinnae alternate, elliptic to ovate, up to 13 mm long and 4 mm wide, base slightly contracted and then winged; distal pinnae with entire margin; basal pinnae toothed, the posterior margin entire, the anterior margin with a single large acute tooth, apex of pinna consisting of two apical teeth. Two primary veins arise from the rachis and enter the pinna, dichotomizing once and then reticulate.

Etymology: The new epithet refers to the northwestern "Interior".

Materials: Only one specimen. Locality no.: 875.

Holotype: Pl. 21, fig. 4; specimen no.: 875-7082.

Distribution: This species is restricted to the Gates Formation.

Discussion: Two specimens attributed by Bell (1956, p. 108, Pl. LII, figs. 1, 2) to *Ctenopteris insignis* Fontaine are very similar to the new species in pinna morphology. Unfortunately, neither of Bell's specimens is complete, so it can not be determined if they are conspecific with the new species.

Order Cycadeoidales (Bennettitales)

Family Incertae Sedis

Comments: Compressions and impressions of bennettitalean leaves are the most abundant fossils of the Cycadeoidales and have a worldwide Mesozoic distribution. The leaf genera system which is generally accepted was developed over the years by Halle (1913), and Harris (1949, 1969). This system "provides little more than an essential handle on which to hang the specific epithet", as stated by Watson and Sincock(1992). The following key to the leaf genera of the Bennettitales is modified after Watson and Sincock(1992) to accommodate the classification of the Gates flora.

Key to the leaf genera of the Bennettitales:

1. Leaf simple (entire)..*Nilssoniopteris*

   Leaf divided pinnately...2

2. Venation reticulate..*Dictyozamites*

   Venation free, parallel or diverging.....................................3

3. Pinna rhomboid or diamond-shaped..................................*Sphenozamites*

   Pinna non-rhomboid...4

4. Pinna margin toothed...*Neozamites*

   Pinna margin non-toothed...5

5. Pinna having basal auricle..*Otozamites*

   Pinna without basal auricle...6

6. Lower basal angle of pinna decurrent.................................*Ptilophyllum*

   Lower basal angle of pinna non-decurrent............................7

7. Basal angle of pinna symmetrically contracted.....................*Zamites*

   Basal angle of pinna never contracted.................................8

8. Pinna detachable..9

   Pinna non-detachable..10

9. A single central stomata groove on lower surface.................*Pseudocycas*

   No stomata groove or more than one stomata groove...........*Cutchiphyllum*

10. Pinna about as wide as long..*Anomozamites*

    Pinna longer than wide...*Pterophyllum*

Genus *Ptilophyllum* Morris emend.

Original Diagnosis: "Stem — ? Fronds pinnate; pinnae closely approximated, linear, lanceolate, more or less elongate, imbricate at the base, attached obliquely; base semicircular or rounded; veins equal, slender, parallel" (Morris, in: Grant, 1840, captions of Plate XXI).

Emended Diagnosis: Frond pinnate. Pinnae linear, **borne** on the upper surface of rachis along full pinna base, having parallel veins; base asymmetric, basiscopic side decurrent on rachis, acroscopic side rounded.

Generitype: *Ptilophyllum acutifolium* Morris

Lectotype: Plate XXI, fig. 1 of Morris, in: Grant, C.W. 1840, Transactions of the Geological Society of London, 2nd ser., V, pp. 289-330. .

Discussion: *Ptilophyllum* was founded by Morris (in: Grant, 1840) to designate some pinnate fronds which were characterized by having semicircular or round and imbricate pinna bases and obliquely attached pinnae. Seward (1917) indicated that Halle (1913) employing *Ptilophyllum* in Feistmantel's sense was incorrect, i.e. Halle (1913) and Feistmantel claimed that the decurrence of the pinnae by their lower edges was an important distinguishing feature of *Ptilophyllum* . Seward (1917) expressed the opinion that the pinnae of *Ptilophyllum* were characterized by their attachment to the upper face of the rachis; both the upper and the lower angles of the pinna base were rounded. This point was shown on the clear drawing of Morris' type-specimen (Seward, 1917, p. 518, fig. 591). Halle's (1913) *Sub-*

Zamites section was included by Seward (1917) in his *Ptilophyllum*. Seward (1917) also mentioned that in a few cases, (which, I think, belong to *Otozamites*), both the upper and the lower angles of the pinna base were auriculate (Seward, 1917, p. 519, fig. 592, 593).

Harris (1969) agreed that features of Seward's drawing (1917, p. 518, fig. 591) were visible on the type. However, Harris found the counterpart of the specimen on which Seward's drawing based, and suggested that the pinna bases might be in fact decurrent. On the other hand, Harris defined *Zamites* in the sense of Halle's *Eu-Zamites* section. Halle's *Sub-Zamites* section, therefore, seemed to be rejected from both *Ptilophyllum* and *Zamites* by Harris (1969). Although it appears that species conforming to Halle's *Sub-Zamites* section are not accommodated within Harris' taxonomic system, Harris' approach is still accepted by most authors (e.g. Watson and Sincock, 1992). It is necessary, however, to create a generic category for *Sub-Zamites* type species.

Seward (1917) claimed that the pinna base of *Ptilophyllum* was round on both the lower and upper angles while Harris(1969) claimed that pinna base was decurrent. This seems to be a contradiction. However, the meaning of "decurrent" in Harris' definition probably only suggests that the pinnae are attached obliquely on the rachis, so that the basiscopic side of a pinna base might correspondently extend down slightly. Among all Harris' diagrams (Harris, 1969, p. 58, fig. 26, A-E; p. 60, fig. A, B; p. 62, fig. A-D; p. 65, fig. 30, A-G; p. 66, fig. A-F, H, I), only part of diagrams from one species, *Ptilophyllum pecten* (Phillips) Harris (1969, p. 66, fig. A-F, H, I), barely show pinna bases extending downward slightly. Harris' usage of the word "decurrent" is probably equivalent to Seward's "rounded base angles". The difference between Seward's definition and Harris' appears to be an insubstantial verbal dispute, but the word "rounded base angles " appears to be more appropriate.

Later authors who accept Harris' (1969) definition, however, generally use the word "decurrent" in a way different from Harris' (1969) meaning. For example, all the *Ptilophyllum* species from the Wealden flora were claimed to have decurrent pinnae (Watson & Sincock, 1992); nevertheless, they are quite different from the plants described by Seward (1917) as having pinna bases with round angles, and by Harris (1969) as having "decurrent" pinna bases.

The Wealden *Ptilophyllum* species of Watson and Sincock (1992) appear to be in accordance with Halle's (1913) definition for *Ptilophyllum*, which is in the sense of Feistmantel's definition (Halle, 1913, Pl. 9, fig. 1). Feistmantel's recognition of *Ptilophyllum* was apparently based on *P. acutifolium* Morris, but that of Seward (1917) was on *P. cutchense* Morris. Those two species were established at the same time by Morris (1840) as the only species under his new genus *Ptilophyllum*, but Morris did not designate either type species or holotype. I agree that the specimen in Pl. XXI, fig. 1 (Morris, 1840) under *P. acutifolium* has decurrent bases. Plate XXI, fig. 2 (Morris, 1840), also under *P. acutifolium*, does not provide any information about the pinna base. Another specimen under *P. acutifolium* (Morris, 1840, Pl. XXI, fig. 3) shows rounded basiscopic pinna bases rather than decurrent bases. It is believed that Feistmantel's drawing (Halle, 1913, Pl. 9, fig. 1) was on the basis of the specimen in Morris, 1840, Pl. XXI, fig. 1, while Seward's drawing (Seward, 1917, p. 518, fig. 591) must have been on the basis of the sole specimen under *P. cutchense* (Morris, 1840, Pl. XXI, fig. 4). Therefore, the dispute between Seward (1917) and Halle (1913) appears to have arisen as a result of Morris' (1840) inclusion of two different kinds of fronds in one genus.

The Gates materials agree with Seward's *Ptilophyllum*, whereas the Wealden materials are in accordance with Halle's *Ptilophyllum.* Those two kinds of materials are quite distinct and should not be included in one genus.

Morphologically, a pinna base with "round angles" should have an obvious boundary between tissue of pinna base and the rachis. This feature is well shown in Gates materials (Pl. 23, figs. 3, 4). The structural explanation is that a pinna having rounded base angles is "jointed" on the rachis and can more easily be shed from the rachis under unfavourable conditions (Pl. 23, fig. 2). This inference also pertains to other Gates taxa, including *Pseudocycas*, which has rounded pinna base angles similar to the Gates "*Ptilophyllum*" (*Cutchiphyllum*).

For a "decurrent" pinna base there should not be any abrupt change between tissue of pinna base and the rachis. The Wealden materials show this form clearly (Watson & Sincock, 1992, p. 92, text-fig.60, fig. A, B). Structurally, a pinna having a "decurrent" base is broadly fused with the rachis, forming an coherently entire structure. The Wealden materials (all species described under *Ptilophyllum* by Watson and Sincock, 1992) have never been reported as having detached pinnae. Watson and Sincock (1992, p. 101) also discovered that there was no perceptible change in the epidermis structure when pinna base passed into rachis for a "decurrent" base, noting that "the exact limits of the pinna bases are difficult to ascertain".

Given the above-mentioned morphological definition and structural interpretation of the pinna base, the differences between "rounded base angles" (Figure 3.3.

Cutchiphyllum) and "decurrent" base (Figure 3.3, *Ptilophyllum*) reflect significant differences in plant structures. Because the original definition of *Ptilophyllum* included different type of plants, it is necessary to split *Ptilophyllum* to two genera. It is suggested that the *Ptilophyllum* species conforming to Feistmantel's or Halle's (1913) definition continue to use the name *Ptilophyllum.* Because Morris (1840) did not designate type species and holotype for *Ptilophyllum*, it is necessary to designate a type for *Ptilophyllum. Ptilophyllum acutifolium* Morris (in: Grant, 1840) is the only possible type species for *Ptilophyllum.* Plant XXI, fig. 1 (Morris, in: Grant, 1840) under *P. acutifolium* is the only possible specimen to be the holotype for *Ptilophyllum.*

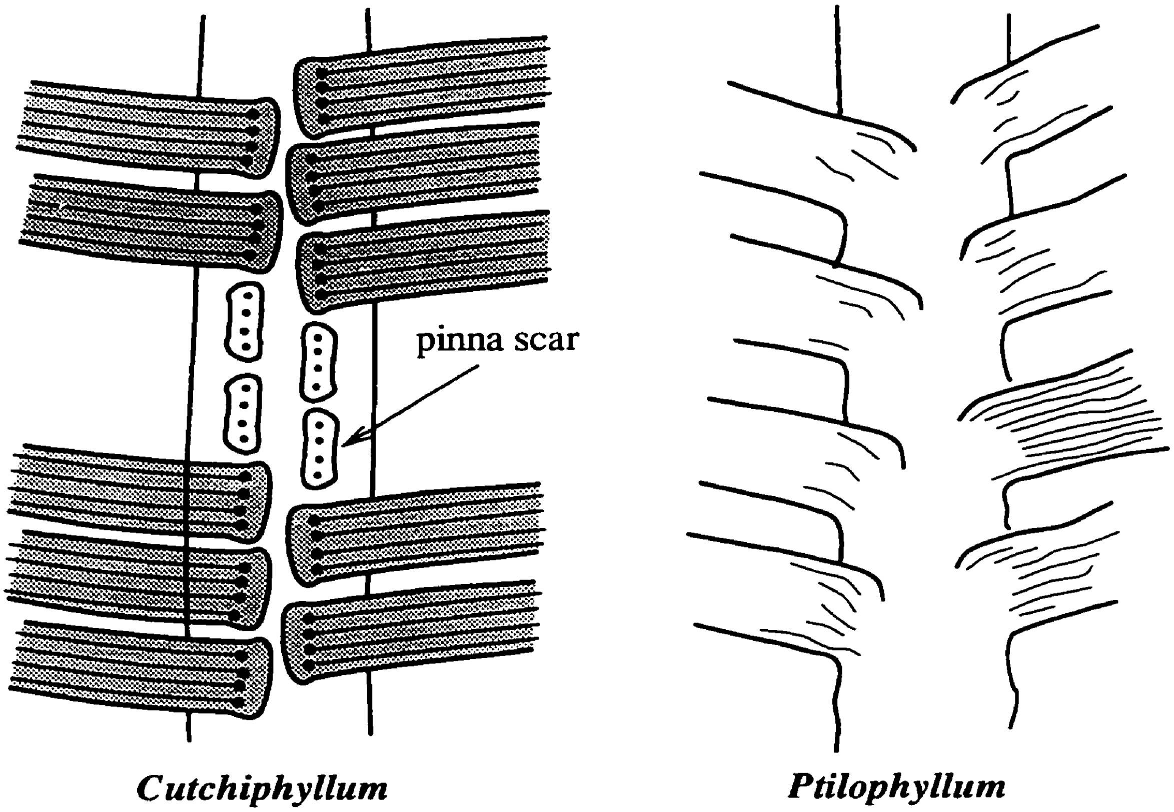
A new genus *Cutchiphyllum* is instituted here for designation of species conforming to Seward's (1917) definition of "*Ptilophyllum*". Because the Gate materials are better preserved, *Cutchiphyllum* will be typified upon the Gates materials.

Genus *Cutchiphyllum* gen. nov.

Generic Diagnosis: Frond pinnate. Pinnae linear, **jointed** on the upper surface of rachis along the entire pinna base; base maybe slightly swollen, base angles rounded on both acroscopic and basiscopic sides; veins parallel.

Etymology: The generic name originates from the fossil locality of *Ptilophyllum*: Cutch (Morris, 1840).

Generitype: *Cutchiphyllum canadensis* sp. nov.



Cutchiphyllum ***Ptilophyllum***

Figure 3.3: Pinna base morphology of *Cutchiphyllum* vs. *Ptilophyllum.*

Discussion: The name *Cutchiphyllum* is instituted for designation of those former "*Ptilophyllum*" species that accord with Seward's definition (1917), including Halle's *Sub-Zamites.* Because the pinnae of *Cutchiphyllum* are jointed on the rachis along the full pinna base, the concept "jointed" is the key point separating *Cutchiphyllum* from *Ptilophyllum* Morris emend. Pinnae of *Pterophyllum* are borne on the sides of the rachis, and therefore differ from those of either *Cutchiphyllum* and *Ptilophyllum* Morris emend.

Bell (1956) apparently did not make this distinction in his assignment of materials to *Ptilophyllum.* Vakhrameev and Doludenko (in: Vakhrameev, 1991, p. 124) indicated that Bell's *Ptilophyllum* were all *Pterophyllum.* Their opinion is correct, with one exception. The specimen in Pl. XLIV, fig. 3 of Bell (1956) under *Ptilophyllum arcticum* (Goeppert) Seward is, indeed, a *Ptilophyllum*, now *Cutchiphyllum*.

Zamites differs from *Cutchiphyllum* in that venation is derived from one point. The use of *Zamites* by LaPasha and Miller (1985) was apparently in the sense of Halle's *Sub-Zamites*. Their *Zamites arcticum* Goeppert is equivalent to Bell's *Ptilophyllum arcticum*, and is included in *Cutchiphyllum* in this study. In addition to the morphological differences between *Zamites* and *Cutchiphyllum*, *Cutchiphyllum* appears to have been widely distributed in the Arctic Province, whereas *Zamites*, appears to have been common in the Equatorial and the Antarctic provinces. Therefore, *Cutchiphyllum* should be treated as a separate genus from *Zamites*.

In terms of pinna base morphology, there is no difference between *Cutchiphyllum* and *Pseudocycas*. Because *Pseudocycas* is a generally accepted genus (Seward, 1917; Bell, 1956; Watson and Sincock, 1992), it is treated as an independent genus in this study. *Pseudocycas* includes all species whose pinnae have a central stomatal groove on the lower surface; *Cutchiphyllum* includes the species that can not be assigned to *Pseudocycas* (Figure 3.4).

Geographically, *Cutchiphyllum* is common in the Arctic Province and rare in the Equatorial Province, but has never been reported from the Antarctic Province. *Ptilophyllum* appears to have been common in the Equatorial Province. Many specimens under *Dioonites* from North America (Fontaine, 1889; 1905h; Berry, 1911), especially, those from the Potomac Group, are actually *Ptilophyllum*.

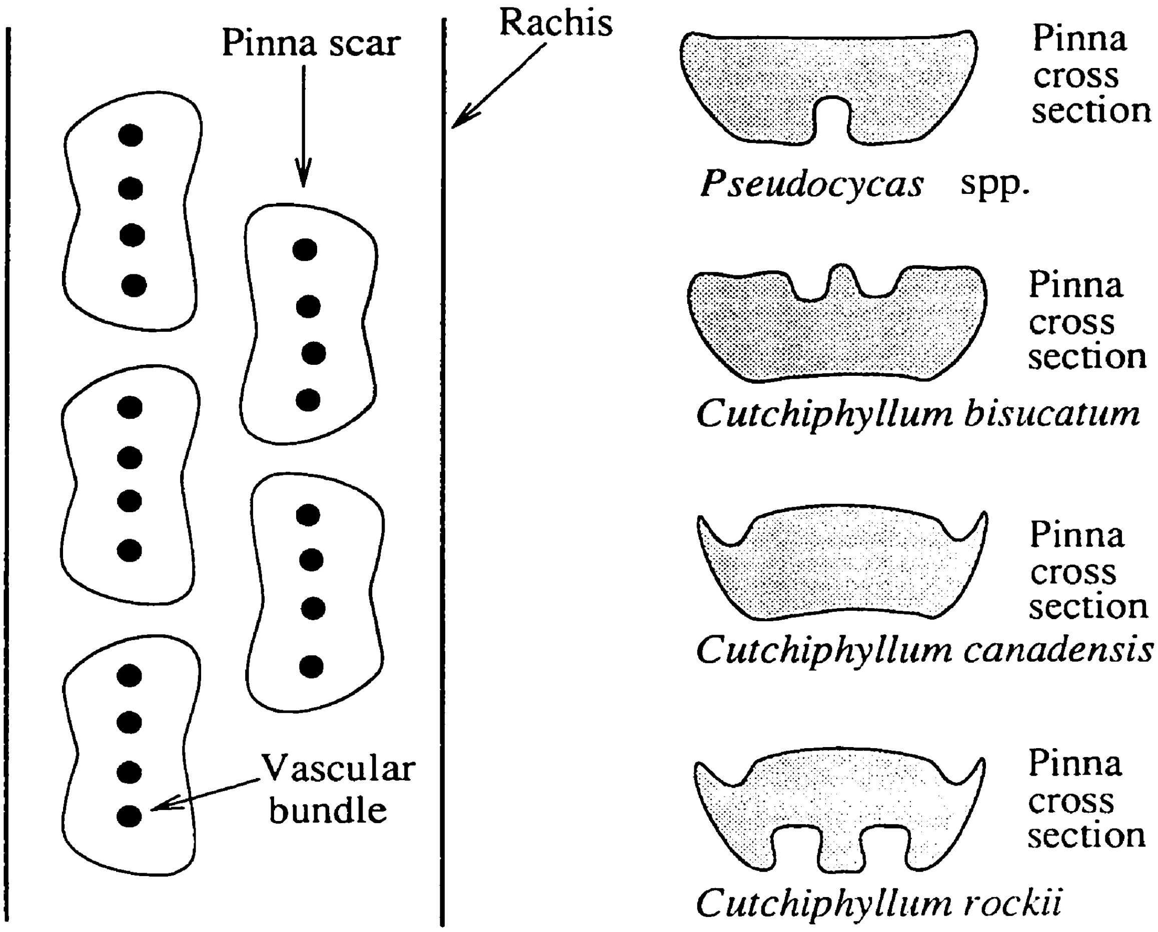


Figure 3.4: Pinna cross section morphology of *Cutchiphyllum* and *Pseudocycas*.

Cutchiphyllum bisulcatum sp. nov.

(Pl. 24, figs. 1-4; Pl. 25, fig. 1)

Ptilophyllum (Anomozamites) montanense (Fontaine) Bell, 1956. [*pro parte*] p. 91, Pl. XLI, fig. 1 [*only*].

Diagnosis: Frond petiolate, up to 50 cm long and 8 cm wide, long elliptic in shape; apex rounded; base cuneate; petiole 3 cm long and 4 mm wide. Rachis 4 mm wide; dorsal surface appearing smooth, the ventral surface having a central ridge and two grooves, one on each side of the ridge. Pinnae linear, commonly falcate, up to 4 cm long and 2 mm wide, alternately to suboppositely jointed on the ventral surface of the petiole; apex acuminate; base rounded and slightly swollen. Dorsal surface of pinna appearing flat; ventral surface having two narrow furrows running parallel to the pinna length. Veins inconspicuous, appearing to be four.

Etymology: The new epithet originates from Latin *sulcatus*, suggesting the two ventral furrows on pinna.

Materials: Specimens many. Locality no.: 874, 915, 921, 950, 952

Holotype: Pl. 24, fig. 2: specimen no.: 921-7018.

Distribution: This species has been recovered only from the Gates Formation and the Luscar Formation. Its distribution appears confined to the Early Albian of the western Interior of Canada.

Discussion: This species is one of the most common fossils in the Gates Formation. Pinnae of this species commonly produce impressions similar to those of *Pseudocycas* and it is difficult, sometimes even impossible, to distinguish them from *Pseudocycas* on the impressions (sub-impressions) alone. The two narrow furrows on the ventral (upper) surface of a pinna typically are cast as two ridges bounding a flat central groove on the ventral (upper surface) impression, which is somewhat similar to the ventral (upper surface) impression of *Pseudocycas*. In the occurrence of compressions together with its impressions, it is not difficult to distinguish ventral (upper surface) features of *C. bisulcatum* with the dorsal (lower surface) features of *Pseudocycas*. Without the preservation of compressions, a ventral impression is simply the counterpart of the dorsal impression, and it is difficult to tell the difference between *Pseudocycas* and *Cutchiphyllum bisulcatum* (Figure 3.4); in this case, specimens may be assigned to either cf. *Pseudocycas* sp. or cf. *Cutchiphyllum bisulcatum*.

The function and nature of the two ventral (upper surface) furrows are unknown. They are not part of the venation and do not appear to have connection with the vein system. The venation does not show any traces on the ventral (upper) surface; four inconspicuous parallel veins are apparent on the dorsal (lower) surface. Pinnae of *Cutchiphyllum bisulcatum* appear to have been very thick, so that veins leave no mark in the ventral (upper) surface.

One specimen figured as "*Ptilophyllum (Anomozamites) montanense*" by Bell (1956, p. 91, Pl. XLI, fig. 1) appears to be conspecific with the present species. Although the two ventral (upper surface) grooves were not described by Bell, they can be observed on the photo; besides, the size of the frond and the falcate feature of its pinnae match the present species very well. Other specimens included by Bell (1956) within *Ptilophyllum (Anomozamites) montanense* are distinct and appear to belong to *Pterophyllum* (see discussion of *Pterophyllum albertense*).

Bell (1956) did not explicitly indicate the basionym for his new combination *Ptilophyllum (Anomozamites) montanense* (sic) (Fontaine) Bell, as required by the ICBN (Greuter et al., 1994). Nevertheless, the basionym is evidently *Zamites montanensis* Fontaine (1892), which differs from *C. bisulcatum* in lacking the two ventral (upper surface) grooves.

Cutchiphyllum canadensis sp. nov.

(Pl. 22, figs. 1-3; Pl. 23, figs. 1-4)

Pseudocycas sp. A cf. *Pseudocycas unjiga* (Dawson) Bell, 1956, [*pro parte*] p. 98, Pl. XLVI, fig. 2 [*only*].

Diagnosis: Frond large (possibly exceeding 100 cm long and 16 cm wide), oblanceolate, once pinnate; apex rounded; petiolate, petiole about 5.5cm long and 8 mm wide, petiole base swollen. Pinnae linear, alternately or suboppositely jointed at almost right angles to the ventral (upper) surface of the petiole, leaving one third of the petiole visible, commonly crowded in the lower part of the frond, but less crowded in the upper part of the frond, never overlapping, variable in size, the largest pinnae in the upper part of a frond, 8 cm long and 4 mm wide, progressively narrowing and shortening towards both the frond apex and the frond base, average pinna width 2-2.5 mm, abnormally wide pinnae (up to 5 mm wide) rarely present; apices acute; bases rounded and slightly swollen; marginal groove composed of revolute pinna edge on each side of pinna, merging at pinna apex, disappearing at pinna base.

Veins parallel, four, distinct in pinna base, becoming less clear towards pinna apex, no evidence of vein dichotomizing.

Pinnae shed from rachis, leaving pinna scar. Pinna scars appearing as ob-trapezoids. The ventral (upper surface) side of the ob-trapezoid flat, 4 mm long;

the dorsal (lower surface) side concave inwards, 1.5 mm; thickness of pinnae, as measured from pinna scar, up to 2 mm. Four vein traces present in pinna scar.

Etymology: The new epithet originate from the country (Canada) in which the new species has been found.

Materials: Specimens many. Locality no.: 874, 877, 951, 950, 952, 915.

Holotype: Pl. 22, fig. 1; specimen no.: 874-7010.

Distribution: This species has been reported from the Gething Formation of British Columbia (Bell 1956) and the Gates Formation. Its distribution appears confined to the Aptian-Albian in the northwestern Interior.

Discussion: This species is one of the most common elements in Gates Flora. Pinnae appear very thick. Venation can be seen only near the pinna base. This new species is characterized by its large size and the marginal grooves on pinnae (Figure 3.4). None of the species within the genus is of this size.

The specimen described as *Pseudocycas* sp. A cf. *Pseudocycas unjiga* (Dawson) Bell (1956, p. 98; Pl. XLVI, fig. 2) appears to be conspecific. The marginal grooves of pinnae can be observed on the photo of that specimen and there appears no central stomatal grooves. Other features, including general shape and size, are consistent with those of the new species.

The specimen from the Kootenay Formation (Late Jurassic) figured as *Ptilo-*

phyllum arcticum (Goeppert) Seward (Bell, 1956, p. 94, Pl. XLIV, fig. 3) is very similar to the present species in terms of pinnae structure, but the Kootenay material is much smaller in size than the present species (only about one fifth of the size of the present species).

Cutchiphyllum rockii sp. nov.

(Pl. 25, figs. 2-4)

Diagnosis: Frond large, probably over 1 m long and 9 cm wide, ribbon-like, pinnately divided. Pinnae about 4.5 cm long and 2 mm wide, jointed on the ventral (upper surface) side of the rachis along the full pinna base; apex rounded; base rounded on both acroscopic and basiscopic sides. Ventral (upper) surface of pinna appearing flat except for marginal grooves; dorsal (lower) surface having a medial ridge parallel pinna length, with a furrow on each side of the medial ridge; cross-section of furrow appearing square. Veins four, inconspicuous, no evidence of dichotomy.

Etymology: The new epithet originates from "Rocky" (Mountains).

Materials: 3 specimens. Locality no.: 952.

Holotype: Pl. 25, fig. 2; specimen no.: 952-7089.

Distribution: Only known from the Gates Formation.

Discussion: This species is similar in all aspects to *C. canadensis*, except for the two dorsal (lower surface) grooves (Figure 3.4). The two dorsal (lower surface) grooves have a square cross section and are not evident on the ventral (upper) surface of a pinna. They are definitely not folds between veins and appear unrelated to the venation. Venation can not be seen throughout a pinna, but at the pinna base four veins are seen to arise from the rachis in a manner like those of *C. canadensis*. Although the nature and function of these two grooves are unknown, the most similar structure in cycads is the dorsal (lower surface) groove of *Pseudocycas*-type pinnae. Nevertheless, *Pseudocycas* is characterized by only one dorsal stomatal groove on each pinna (Seward, 1917; Watson & Sincock, 1992). On the basis of pinna base morphology, it is appropriate to include the Gates materials within *Cutchiphyllum*.

The Yorkshire Jurassic specimens named by Harris (1964) as *Paracycas* are also very similar to *C. rockii*. The pinna of *Paracycas* was described as having a midrib and two dorsal (lower surface) grooves, one on each side of the midrib. The two dorsal (lower surface) grooves were proved to be two stomatal bands by cuticular analysis. Morphologically, *Paracycas* appears to differ from the Gates materials primarily in having midribs in the pinnae. If similar midribs existed on the Gates materials, they would be assigned to *Paracycas*. I have carefully checked the Gates materials, and concluded that they have no such midribs. The pinnae of the Gates materials appear thick; the upper surface of the pinna is flat except for the marginal grooves, and there are no traces of midrib or veins; the lower surface of the pinnae shows clearly two grooves separated by a highly-raised medial ridge; four veins can be observed only at the pinna base. On the basis of those observations, the Gates materials should not be included in *Paracycas*.

On the other hand, I do not think that the presence of midribs in pinnae of *Paracycas* has been fully demonstrated. The pinnae of the type species of *Paracycas* were described as "surface of pinna flat, but with a sightly thickened midrib. midrib more prominent below" (Harris, 1964, p. 67). The external appearance of pinnae of *Paracycas* appears to be very similar to that of the Gates Materials. It is quite possible that the midrib does not exist on those Yorkshire specimens described as *Paracycas*. The so-called midrib may be just the medial ridge on the lower surface of pinna. If so, the diagnosis of *Paracycas* is incorrect. *Paracycas* should be conspecific with the new species. Because the Yorkshire materials were not available for me to examine. this hypothesis has not been verified in this study.

Genus *Pseudocycas* Nathorst

Comments: Among the form genera in the Cycadeoidales. the best defined genus is *Pseudocycas*. *Pseudocycas* was originally defined by Nathorst (Seward. 1917) as having a double midrib bounding a central furrow. Halle in 1915 demonstrated that the so-called double midribs were in fact elevated margins bordering a stomatal groove. thus giving the appearance of two parallel veins (Watson and Sincock. 1992). The actual venation of these pinnae has remained unknown until the present study.

One specimen of *Pseudocycas alberta* has pinna scars on the frond rachis. There are four dots in a row within each pinna scar. representing vascular bundle traces (Figure 3.4). Four veins enter the pinna from the rachis; it is unlikely that these four veins branch because the pinnae are very narrow, and do not expand beyond the base. The significance of this discovery is that it demonstrates that the arrangement and distribution of stomata in *Pseudocycas* are independent of venation. In another words, the morphology of the surface cells over the veins does not reflect internal anatomy. The reasonable anatomical explanation is that the pinnae of *Pseudocycas* are very thick and the veins are situated too far from the surface to affect the development of surficial cells. This inference explains why venation is never apparent in hand specimens. It is believed that this phenomenon is common to all species of *Pseudocycas*.

The same phenomenon also occurs on *Cutchiphyllum bisulcatum*, *Cutchiphyllum canadensis* and *Cutchiphyllum rockii* (Figure 3.4), which are all very similar to *Pseudocycas* in terms of venation and pinna base structures

The differentiation of species in *Pseudocycas* is primarily on the basis of cuticular features (Watson and Sincock, 1992). Some species have been defined solely on the basis of cuticular features (LaPasha and Miller, 1985). These facts make species identification of hand specimens very difficult. Nevertheless, it appears possible to identify various species on the basis of pinna morphology. Pinna bases of different species in *Pseudocycas* are very similar and appears less helpful in specific recognition. Macroscopic features of the central stomatal groove are difficult to observe in detail and therefore are less helpful. Pinna size and apex morphology appear important in species identification. The following key has been developed as a guide for species recognition.

Generitype: *Pseudocycas insignis* Nathorst

Key for well-defined *Pseudocycas* species:

1. Pinna length > 8 cm 2
   Pinna length < 8 cm 3

2. Pinna length $= 9$ cm, width $= 2$-3 mm ....*P. insignis*
   Pinna length $= 10$ cm, width $= 2.5$ mm............................*P. dunkeriana*
   Pinna length $= 11$ cm, width $= 2$ mm...............................*P. lesleyae*

3. Pinna width > 3 mm ....*P. roemerii*
   Pinna width < 3 mm 4

4. Pinna length $= 6$-7 cm, width $= 1$-1.5 mm ....*P. saportae*
   Pinna length $= 5$ cm, width $= 1.5$ mm ....*P. alberta*
   Pinna length $= 3$ cm, width $= 2$ mm ....*P. manchurensis*

Pseudocycas alberta sp. nov.

(Pl. 26, figs. 1-3; Pl. 27, figs. 1, 2)

Pseudocycas dunkeriana (Goeppert) Florin; Bell, 1956, p. 97, Pl. XLIII, fig. 6, Pl. XLVII, figs. 2, 6.

Diagnosis: Frond large, about 100 cm long and 9 cm wide; ribbon-like in shape, petiolate; petiole 5.5 cm long and 1 cm wide; rachis at least 8 mm wide. Pinnae linear and rigid, up to 5 cm long and 1.5 mm wide; apex acute; base rounded and slightly swollen, attached along the entire pinna base on the ventral (upper) surface of the rachis; central narrow groove about 0.25 mm on the dorsal (lower) surface of each pinna. Veins four, apparently unbranched.

Etymology: The new epithet originates from the name of the sedimentary basin, the "Alberta" Foreland Basin.

Materials: Specimens many. Locality no.: 851, 874, 887, 878.

Holotype: Pl. 26, fig. 1; specimen no.: 874-7019.

Distribution: Early Cretaceous of the western Interior of Canada.

Discussion: The specimens included within *P. dunkeriana* by Bell (1956) are conspecific with the present species. *Pseudocycas dunkeriana* as described by Seward (1917) appears to have a much larger size and therefore is distinct.

Pseudocycas douglasii LaPasha and Miller (1985) is probably conspecific with *P. alberta* in terms of their pinna width, which is the only comparable feature between the two species. Although *P. douglasii* was described as having a single vein per pinna, this important feature was never illustrated by LaPasha and Miller (1985). Their description of the single vein was probably a misinterpretation of the central stomatal groove. Most likely, the Montana specimen has four veins per pinna, like the Gates materials, although this can not be confirmed because of the incompleteness of the Montana specimen.

Pseudocycas saportae (Seward) Holden (Watson and Sincock, 1992) is similar to the new species but differs in having larger pinna size; another important difference is that the former species has cuspidate pinna apices, while the Gates materials have acute pinna apices.

Pseudocycas sp.

(Pl. 27, fig. 3)

Description: Frond pinnate; rachis at least 6 mm wide: pinnae 3 mm wide, length unknown; stomatal groove very narrow, approximately 1/3 mm wide.

Materials: Only one specimens. Locality no.: 855 (Boulder Creek Fm.).

Distribution: Recovered only from the Boulder Creek Formation.

Discussion: The stomatal groove of this specimen is extremely narrow in comparison with the pinna width. This specimen differs from *P. alberta* in having much broader pinnae.

Most specimens figured as *Pseudocycas* sp. A cf. *P. unjiga* (Bell, 1956, p. 98, Pl. XLIV, fig. 2; Pl. XLV, fig. 3; Pl. XLVII, fig. 4) are similar to the present species, but differ in having narrower pinnae (2-2.5 mm). The specimen figured as *Pseudocycas* sp. B cf. *P. unjiga* (Bell, 1956, p. 99, Pl. XLIV, fig. 1) is also similar to the present species, but differs in having wider pinnae (4-4.5 mm).

Because of the fragmentary nature, further comparisons with other species of *Pseudocycas* are not possible.

Genus *Pterophyllum* Brongniart

Comments: The name *Pterophyllum* was first applied by Brongniart in 1825 to fronds which were subsequently removed by Nathorst in 1881 to *Anomozamites* (Seward, 1917). *Pterophyllum* originally included fronds of both the *Pterophyllum* and *Anomozamites* types. Thomas and Bancroft (1913) indicated that *Anomozamites* Schimper was as independent genus on the basis of cuticle structural differences. The present usage of *Pterophyllum* appears to be consistent to the later use of *Pterophyllum* by Brongniart in 1828 (Seward, 1917; Harris, 1969), i.e., species conforming to *Anomozamites* are excluded from *Pterophyllum*. It was Andrews (1955) who selected *P. longifolium* Brongniart as the type species.

Thomas (1930) indicated that certain Paleozoic leaves placed in *Pterophyllum* had non-Bennettitalean cuticles and ought therefore to be excluded from the genus. This was fully summarized together with morphological features in Harris (1932).

Harris (1969) presented an emended diagnosis for *Pterophyllum* which is still generally accepted, and discussed the morphological differences between *Pterophyllum* and other Bennettitalean form genera. Harris' (1969) definition was designed to restrict the use of *Pterophyllum* to leaves having syndetocheilic stomata (agreeing with Cycadeoidales). Harris' definition (1969, p. 92) is followed in the present study.

Numerous species have been reported within the genus. The differentiation of species is on the basis of both the pinna morphology as well as cuticular structures. In the absence of cuticles, it is difficult to compare many species. A key to the Gates species of *Pterophyllum* is given as follows.

Generitype: *Pterophyllum longifolium* Brongniart

Key to the Gates *Pterophyllum*:

1. Pinna length < 1 cm..................................2
   Pinna length > 1 cm..................................4

2. Pinna width about 2 mm............................*P. plicatum*
   Pinna width about 1 mm............................3

3. Pinna sessile...*P. smallifolium*
   Pinna petiolate ....*P.* sp. 1

4. Pinna width > 4 mm.................................*P.* sp. 2
   Pinna width < 4 mm.................................5

5. Pinna length < 2 cm.................................*P. rectangulare*
   Pinna length > 2 cm.................................*P. albertense*

Pterophyllum albertense sp. nov.

(Pl. 27, figs. 4-6)

Basionym: *Zamites montanensis* Fontaine, 1891, U.S. Nat. Mus., Proc., Vol. 15, p. 494, Pl. LXXXIV, Fig. 4.

Ptilophyllum (Anomozamites) montanense (Fontaine) Bell, 1956, [*pro parte*] p. 91, Pl. XL, fig. 2; Pl. XLI, figs. 2, 3; Pl. XLVII, fig. 1 [*only*].

Original Diagnosis: "The leaf (compound) is narrowly elliptical in outline and small. it is abruptly pinnate, with a stout rigid midrib. The lower leaflets are lancet-shaped, short, remote, and stand at right angles with the midrib. In ascending towards the tip of the compound leaf, the leaflets become linear in shape and are more closely approximate, until they touch. They are also non-falcate, and toward the end of the leaf are obliquely attached to the midrib. The leaflets of the central part of the leaf are longest, giving the elliptical outline. Nerves, three in number, strong, parallel with each other and the margins of the leaflets" (Fontaine, 1891, p. 494).

Emended Diagnosis: Frond pinnate, oblong, obtuse at base and apex; rachis 1.5 mm wide. Pinnae normal or openly oblique to rachis, alternate to subopposite, linear, up to 25 mm long and 2 mm wide, attached on the lateral sides of the rachis; apex acute. Veins parallel, usually four, unbranched.

Etymology: The new epithet originates from the name of the sedimentary basin, the "Alberta" Foreland Basin.

Materials: 15 specimens. Locality no.: 852, 853, 874, 875, 914, 951.

Distribution: This species has been reported from the Kootenai Formation of both Alberta and British Columbia, the Nikanassin Formation of Alberta, the Hazelton Group of British Columbia (Bell, 1956), and the middle flora of Belcourt Ridge (Mellon et al., 1963). The age of the middle flora of Belcourt Ridge is probably equivalent to the Gates. The species appears to have been distributed from the Late Jurassic to the Albian in the northwestern Interior.

Discussion: As mentioned above in the discussion of *Cutchiphyllum bisulcatum*, Bell did not specify type and basionym in his transfer, as required by the ICBN (Greuter et al., 1994), and therefore *Ptilophyllum (Anomozamites) montanense* (Fontaine) Bell would be an invalid species name. Nevertheless, the basionym of *Ptilophyllum (Anomozamites) montanense* (Fontaine) Bell is most likely *Zamites montanensis* Fontaine (1891), because other species published by Fontaine with the specific epithet "montanensis" are not related to the present species at all. The type specimen of *Zamites montanensis* Fontaine (1891, Pl. LXXXIV, Fig. 4) appears to be conspecific with both Bell's materials and the Gates materials. These materials are apparently neither *Zamites*, because their pinna bases are not contracted, nor *Ptilophyllum* because their pinna bases are not decurrent. These materials apparently belong to *Pterophyllum*, and therefore transfer is necessary.

Transfer of *Zamites montanensis* to *Pterophyllum* happens to produce a later homonym of *Pterophyllum montanense* Knowlton. According the Article 55 (a) of the ICBN (Greuter et al., 1988), *P. albertense* is instituted for the present new combination.

Pterophyllum plicatum Bell

(Pl. 28, figs. 4, 5)

Pterophyllum plicatum Bell, 1956, p. 93, Pl. XL, fig. 4, Pl. XLII, figs. 1, 5, Pl. XLIII, figs. 2, 5.

Pterophyllum rectangulare Bell, 1956, [*pro parte*] p. 92, Pl. XLII, fig. 3 [*only*].

Description: Frond 6 cm long and 1 cm wide; rachis slender, 0.5 mm wide. Pinnae up to 6 mm long and 2 mm wide, attached along the full pinna base on the rachis; apex rounded. Veins four, parallel, inconspicuous. Space between veins marked by a fold that gives a conspicuous, plicated appearance to the pinna.

Materials: Only 1 specimen. Locality no.: 952.

Distribution: This species has been reported from the Bullhead Group of British Columbia, the Luscar Formation of Alberta (Bell, 1956) and the Gates Formation. The species appears to have been confined to the Aptian-Albian within the western Interior of Canada.

Discussion: The Gates specimen is fully in accordance with the original definition of the species (Bell, 1956).

Pterophyllum rectangulare Bell

(Pl. 28, figs. 1-3)

Pterophyllum rectangulare Bell, 1956, [*pro parte*]p. 92, Pl. XLII, figs. 4, 6 [*only*].

Description: Frond petiolate, pinnate, with elongate rectangular-elliptical blade, truncate at base and summit; petiole up to 2 mm wide. Pinnae more or less rectangular, about 3 cm wide and 10 cm long, attached at right angles or nearly so, except near summit where obliquely ascending and at base where lowest pair is slightly descending, alternate to subopposite, free except near frond apex where pinnae are basally connate, up to 15 mm long and 3 mm wide, decreasing very gradually in length distally, abruptly and obtusely rounded at apex. Veins commonly four, inconspicuous, or moderately defined, parallel, rarely forked.

Materials: 23 specimens. Locality no.: 852, 857 (Boulder Creek Fm.), 950, 914, 952.

Distribution: This species has been reported from the Luscar Formation of Alberta, the Bullhead Group, Hazelton Group and Jackass Mountain Group of British Columbia (Bell, 1956) and the Gates Formation. It appears to have been distributed from the Neocomian to Albian in the western Interior of Canada.

Discussion: One specimen included within *P. rectangulare* Bell (1956, p. 92; Pl. XLII, fig. 3) is inconsistent with the type (Bell, 1956, p. 92; Pl. XLII, fig. 4) and appears to belong to *P. albertense* according to frond size and pinna morphology.

Pterophyllum smallifolium sp. nov.

(Pl. 28, figs. 6, 7)

Description: Frond sessile, linear, 7.5 cm long and 1.3-1.5 cm wide; base wedge-shaped; rachis 1 mm thick. Pinnae 6-7 mm long and 1 mm wide, alternately to suboppositely attached on the lateral side of the rachis; apex rounded. Veins not apparent.

Etymology: The new epithet is used to suggest the small pinna size of the new species.

Materials: 4 specimens. Locality no.: 952

Holotype: Pl. 28, fig. 7; specimen no.: 952-7183.

Distribution: Recovered only from the Gates Formation.

Discussion: The new species is distinguished from all other known species by its small size. The specimen assigned to *Ptilophyllum arcticum* (Goeppert) Seward by Bell (1956, p. 94, Pl. XLIII, fig. 3) is similar to the new species in size but differs in having a short petiole. *Pterophyllum* sp. 1 is also similar to the new species in size but differs in having an even longer petiole.

Pterophyllum sp. 1

(Pl. 29, fig. 1)

Description: Frond petiolate, base wedge-shaped, length unknown, 11 mm wide; rachis 1 mm wide; petiole 12 mm long and 1.5 mm wide. Pinnae 5.5 mm long, 1 mm wide, alternately to suboppositely attached on the lateral side of the rachis; apex rounded. Veins not apparent.

Materials: Only 1 specimen. Locality no.: 952.

Distribution: Recovered only from the Gates Formation.

Discussion: The present species is characterized by its small size and petiolate leaf; it differs from the specimen assigned to *Ptilophyllum arcticum* (Goeppert) Seward (Bell, 1956, p. 94, Pl. XLIII, fig. 3) in having a longer petiole. Since the only specimen (Pl. 29, fig. 1) is only the lower part of a leaf, it is inappropriate to institute a new name for it.

Pterophyllum sp. 2

(Pl. 29, figs. 2, 3)

Description: Frond pinnate. Pinnae up to 2 cm long, 5 mm wide, thick, opposite to subopposite attached on the two sides of the rachis; apex rounded. Veins 5-6, commonly separated by conspicuously folds.

Materials: 7 specimens. Locality no.: 696.

Distribution: Only found in the Gates Formation

Discussion: The present species is characterized by its conspicuously folding of pinna surface. Because all the specimens found are fragmentary, it is inappropriate to institute a new name for it.

Order Czekanowskiales

Family Incertae Sedis

Genus *Phoeniphyllum* gen. nov.

Generic Diagnosis: Leaves fascicled like those of *Phoenicopsis*, oblanceolate to wedged-shaped, sessile, distal margin toothed. Veins subparallel, inconspicuous.

Etymology: The generic name originates from the first half of *Phoenicopsis* to suggest the close relationship between *Phoenicopsis* and *Phoeniphyllum*.

Generitype: *Phoeniphyllum tumblericum* sp. nov.

Discussion: *Phoeniphyllum* is believed to be similar to *Phoenicopsis* in almost every aspect except that *Phoeniphyllum* has toothed pinna margin. The fascicled leaves were observed in the field, but collecting of those fascicled leaves as a whole failed because of the fragile nature of rocks.

Phoeniphyllum tumblericum sp. nov.

(Pl. 31, fig. 10; Pl. 13, fig. 1)

Diagnosis: Leaves fascicled, asymmetrical, oblanceolate to wedge-shaped, up to 10 cm long and 2 cm wide, having a sub-medial groove, distally dentate; teeth, acuminately pointed, directing forward. Veins subparallel, possibly dichotomizing once, each resulting vein branch entering a tooth;

Etymology: The new epithet refers to the fossil locality of the new species: Tumbler Ridge.

Materials: 12 specimens. Locality no.: 915, 921.

Holotype: Pl. 31, fig. 10; specimen no.: 915-7108.

Distribution: This species is specific to the Gates Formation.

Discussion: The asymmetrical shape of the holotype may have resulted from its position within the fascicle, and therefore is not considered of taxonomic value. Some smaller leaves having entire margins (Pl. 13, fig. 1), with rounded apices cleft in the middle, may be leaves which were situated in different positions within the fascicle.

Order Ginkgoales

Family Ginkgoaceae

Genus *Ginkgo* Linnaeus

Comments: Diagnosis of the genus presented by Sze et al. (1963) is followed in the present study. Harris et al. (1974) dropped the name *Ginkgoites* because it was not used in a consistent way (see discussion of *Ginkgoites*). All *Ginkgo*-like fossils have been included by Harris et al. (1974) in the genus *Ginkgo*.

It is true that the common usage of *Ginkgoites* is ill-defined, but including all *Ginkgo*-like fossils in the recent genus *Ginkgo* will cause confusion, because some fossils are found to be quite different from recent *Ginkgo*, as noted by Florin in 1936 and some fossils are imperfectly known.

I would like to limit the use of *Ginkgo* to those specimens which show resemblance with recent *Ginkgo biloba* in both morphology and cuticular structures. Although cuticles are not available on the Gates materials, it is possible to morphologically compare the Gates materials to some well-studied *Ginkgo* species which have been reported from areas adjacent to the Gates Formation.

Generitype: *Ginkgo biloba* Linnaeus

Ginkgo pluripartita (Schimper) Heer

(Pl. 31, figs. 1-5)

Basionym: *Baiera pluripartita* Schimper. 1869. Traité de paleontologie végétale ou la flore du monde primitif. J. B. Baillière et tils. Paris, 1: p. 423, Pl. 31, fig. 12. (type not seen; reference cited from LaPasha and Miller, 1985, p. 137).

Ginkgoites pluripartita (Schimper) Seward, 1926, p. 93, Pl. 9, figs. 65, 66, 71, 74, 83, 83A, 84, 86.

Ginkgo pluripartita (Schimper) Heer; Bell, p. 85, Pl. XXXVI, figs. 2, 3, Pl. XXXVII, figs. 2, 3, Pl. XXXVIII, fig. 1; Brown, 1975, p. 724, Text-figs. 1A, C, D; LaPasha and Miller, 1985, p. 137, Pl. 13, figs. 4-8, Pl. 14, figs. 1-3; Chen et al., 1988, p. 67, Pl. 65, fig. 1.

Description: Leaves petiolate; petiole up to 3 cm long and 1.5 mm wide; lamina up to 3.5 cm long and 6 cm wide, more or less hemispherical, divided more or less deeply from summit to lower half of lamina into basically four primary segments, the two outside primary segments may be divided again, but not so deeply as the primary division; base truncate, more or less concave. Segments of lamina all obtusely rounded to rounded-truncate. Veins strong, subparallel in mid-region, concentration about 16 per cm, dichotomizing generally once or twice.

Materials: Specimens numerous. Locality no.: 950, 951, 957.

Distribution: The species appears to have been distributed from the Late Jurassic to Early Cretaceous in the Northern Hemisphere.

Discussion: The cuticles of this species were well-studied by Brown (1975) and

LaPasha and Miller (1985) from materials from the Kootenai Formation of Montana. The morphological resemblance of the Gates materials to the Montana materials strongly suggests that they are conspecific.

The differences between *G. pluripartita* and other similar species were discussed in detail by Brown (1975), LaPasha and Miller (1985).

Genus *Ginkgoites* Seward emend. Florin

Comments: *Ginkgoites* was instituted for fossil leaves which were believed to be generically identical with *Ginkgo* or very closely allied (Seward, 1919). Seward's primary purpose for adopting *Ginkgoites* was to get around troublesome taxonomic problems caused by absence of necessary information about cuticles and/or reproductive organs. Seward did not indicate the type for his new genus. Andrews (1955) selected *Ginkgoites obovata* (Nathorst) Seward as the type in his "Index of Generic Names of Fossil Plants".

Florin's work in 1936 demonstrated that some of the *Ginkgoites* did have quite different cuticle structure from the recent *Ginkgo*. He used *Ginkgoites* for both species which he judged differed significantly from *Ginkgo* and those species which were too imperfectly known, mostly because their cuticles were uninvestigated. Florin's usage of *Ginkgoites* mixed the sense of form genus with that of natural genus. Although accepted by many authors, such a usage is problematic and confusing. It is preferred to retain *Ginkgoites* as a form genus in the sense of Seward's (1919) definition, which includes Florin's imperfectly known specimens. *Ginkgo*-like leaves proven to be different from recent *Ginkgo* should perhaps be included in a new genus. Because of poor preservation, this job can not be done on the basis of the Gates materials. In the present study, the name *Ginkgoites* is employed in the sense of Florin's definition of 1936 because there appears no other better way to deal the problem.

Harris et al. (1974) tried to avoid confusion by dropping the name *Ginkgoites* and included all the *Ginkgo*-like leaves in the recent genus *Ginkgo*. Harris et al.'s (1974) approach does not appear to be helpful in clarifying the confusion between form-genus and natural genus.

Generitype: *Ginkgoites obovata* (Nathorst) Seward

Ginkgoites cascadensis Brown

(Pl. 31, figs. 6-9)

Ginkgoites cascadensis Brown, 1975, p. 727, Text-fig. 2.

Description: Leaves petiolate; petiole up to 8 cm long and 2 mm wide; lamina hemispherical, the base generally truncate, divided more or less deeply from summit to half of the lamina or beyond into six primary segments, each of which may divide again into 2-4 secondary segments. Ultimate segments all obtusely rounded to rounded-truncate, each 3-4 mm wide. Veins, strong, subparallel, concentration almost 18 per cm, dichotomizing generally once, rarely twice, within segment area.

Materials: Specimens numerous. Locality no.: 852, 875, 950, 951, 957.

Distribution: This species has only been reported from the Morrison Formation on Montana (Brown, 1975) and the Gates Formation. It appears to have been distributed from the Late Jurassic to Early Cretaceous in the northwestern Interior.

Discussion: The present specimens differ from those of *Ginkgo pluripartita* in having a much longer petiole and greater number of subdivisions of the leaf lamina. The Gates materials are identical to the type specimen of *Ginkgoites cascadensis* Brown (1975, p. 728, Text-Fig. 2A), although the petiole of *Ginkgoites cascadensis* was described as 2 cm in length by Brown (1975). Nevertheless, neither the holotype nor other specimens on which *Ginkgoites cascadensis* was based showed a complete petiole, so that the actual length of the petiole was probably unknown by Brown (1975). The Gates materials reveal a petiole as long as 8 cm.

The cuticles of the type material for this species were well-studied by Brown (1975): generic comparisons with *Ginkgo* and specific comparisons with other similar *Ginkgoites* species were discussed in detail by Brown (1975). *Ginkgoites* is employed in the sense of a natural genus in this case.

Class/Order/Family Incertae Sedis

Genus *Taeniopteris* Brongniart

Comments: This name was instituted by Brongniart in 1828 for simple linear or broadly linear leaves with a prominent midrib from which secondary veins are given off (Seward, 1910).

Cuticle studies of *Taeniopteris*-type specimens from Greenland by Harris (1932) showed that they belonged to several very different genera, including *Marratiopsis*, *Nilssoniopteris*, *Macrotaeniopteris*, *Doratophyllum* and *Nilssonia*. Specimens whose cuticles are unknown were still included within *Taeniopteris* (Harris, 1932).

Although *Taeniopteris* was originally referred to simple leaves, it has been difficult to distinguish simple leaves from compound leaves because of the fragmentary nature of fossil plants. In practice, *Taeniopteris* is used to refer to all ribbon-shaped leaves with a midrib and pinnate venation without considering if the leaves are simple or compound. Therefore, *Taeniopteris*, in fact, includes both simple and compound leaves.

Numerous species have been reported within the genus. The differentiation of species is on the basis of leaf shape and the density of lateral veins.

Generitype: *Taeniopteris vittata* Brongniart

Taeniopteris canmorensis (Dawson) Bell

(Pl. 29, fig. 4)

Angiopteridium canmorense Dawson, 1892, p. 83, text-fig. 2.

Taeniopteris canmorensis (Dawson) Bell, 1956, p. 75, Pl. XXXIII, fig. 1.

Description: Pinnae lanceolate, averaging 6.5 cm long and 1.5 cm wide, sessile, narrowly attached on rachis; apex acute; base rounded. Midvein stout, up to 2 mm wide at base, reaching pinna apex; lateral veins almost normal to midvein, dichotomizing once near the midvein, resulting venation dense, concentration about 26/cm at the pinna margin.

Materials: 8 specimens. Locality no.: 856 (Boulder Creek Fm.), 950, 952.

Distribution: The Late Jurassic to Early Cretaceous of the northwestern Interior.

Discussion: The type material of the species (Dawson, 1892, text-fig. 2) is apparently a compound leaf; pinnae are oppositely attached on the rachis. The Gates specimens are preserved as detached pinnae and therefore it can not be confirmed that the pinnae from the Gates were attached oppositely on the rachis. Although pinnae of the Gates specimens are slightly larger in size than those of the holotype, both the type material and the Gates materials appear consistent in shape, length to width ratio (4:1), and are considered conspecific.

Taeniopteris gatesensis sp. nov.

(Pl. 29, fig. 5; Pl. 30)

Diagnosis: Pinnae petiolate, oblanceolate, averaging 26 cm long and 3.6 cm wide; apex varying from acute to mucronate; base oblique: petiole about 3.5 cm long and up to 5 mm wide. Midvein stout, reaching apex of pinna: lateral veins almost normal to midvein, simple or dichotomizing once near the midvein or halfway from the midvein, resulting venation dense, concentration about 28/cm at the pinna margin.

Etymology: The new epithet originates from the "Gates" (Formation).

Materials: Specimens numerous. Locality no.: 853, 874, 950-952.

Holotype: Pl. 30; specimen no.: 952-7136.

Distribution: Found only in the Gates Formation.

Discussion: A single complete specimen and numerous fragments from the Gates Formation are available. The new species is characterized by petiolate pinnae, large size and high concentration of lateral veins. It is uncertain if the Gates materials are simple leaves or compound leaves. To keep consistency of descriptions within *Taeniopteris canmorensis*, the word "pinnae" is used in the diagnosis instead of "leaf". Most species within *Taeniopteris* were instituted on the basis of pinna fragments, such as *T. richthofenii* (Schenk) Sze (Sze et al., 1963). Therefore, those species names are unusable in the present study.

Few species within *Taeniopteris* are described on complete specimens, but even so appear incomparable to the Gates materials. *Taeniopteris canmorensis* differs from *T. gatesensis* in having smaller sessile pinnae.

Class Angiospermopsida

Subclass Dicotyledonea

Order/Family/Genus Incertae Sedis

Comments: A few specimens of angiosperms have been recovered from the Gates Formation. Two of them are complete leaves and appear to belong to the same species. Other two specimens are fragmentary, but they appear to represent two different species. Therefore, the total number of angiospermous species within the Gates Formation is estimated as 3.

Unidentified angiospermous leaf **1.**

(Pl. 32, figs. 1, 2)

Description: Leaf small, petiolate; blade round, 22 mm long and 15 mm wide; petiole winged, 8 mm long, tapering toward the base until almost the same width as midrib. Midrib reaching the middle of the blade; lateral veins are unclear but appear reticulate.

Materials: 2 specimens. Locality no.: 925, 952.

Distribution: Recovered only from the Gates Formation.

Discussion: The present specimens are like angiosperm leaves more than those of any other plant groups, and appear to represent a undescribed species. As it is difficult to determine the generic attribution of the specimens, they are treated as unidentified angiospermous leaves in this study. In terms of external morphology, the Gates materials are very similar to a specimen reported by Crabtree (1987, Fig. 38).

Unidentified angiospermous leaf **2.**

(Pl. 32, fig. 3)

Description: Leaf elongate elliptical, greatest breadth about midpoint, 3 cm wide, 10 cm long; apex acuminate; base unknown. Midrib reaches apex.

Materials: 1 specimen. Locality no.: 952.

Distribution: Recovered only from the Gates Formation.

Discussion: In terms of external morphology and size, this leaf resembles the Blairmore specimen assigned to *Dicotylophyllum* sp. by Bell (1956, p. 138, Pl. LXXXIV, fig. 1). It is difficult to make any definite comparison between the two because of poor preservation.

The Gates materials are also very similar to *Magnoliaephyllum* sp. of Crabtree (1987, Fig. 33).

Unidentified angiospermous leaf 3.

(Pl. 32, fig. 4)

Description: Leaf shape unknown; venation reticulate. complex. with several vein orders.

Materials: 1 specimen. Locality no.: 921.

Distribution: Recovered only from the Gates Formation.

Discussion: The specimen is only a leaf fragment. Reticulate venation of this type is seen in some Mesozoic ferns like *Hausmania*, *Clathropteris* and *Dictyophyllum* as well as in angiosperms. Because of the fragmentary nature of the specimen, further evaluation is impossible.

Chapter 4

Early Cretaceous Floras of the Interior

This chapter discusses the deciduous habits of the Early Cretaceous floras in the northwestern Interior, analyzes the paleoclimates on the basis of floral habits and other evidence, and then demonstrates the stratigraphic significance of the floras in the correlation of plant-bearing strata in the northwestern Interior.

In interpreting paleoclimate on the basis of pre-Cenomanian floras, two difficulties are encountered. The first is that living floras are commonly dominated by angiosperms, while the pre-Cenomanian floras are dominated by non-angiospermous groups; therefore, there are few grounds for comparisons between pre-Cenomanian floras and living floras. The second is that plants of the pre-Cenomanian flora may have had different habits from those of the living floras even if they belong to the same taxonomic group, such as cycads.

Morphological or physiognomic analysis on recent plants has been used as an effective method to interpret paleoclimates on the basis of angiosperm-dominated floras (e.g. Wolfe, 1978; 1979; 1980; 1987; Basinger et al., 1994). As such paleoclimatic interpretations have relied on analogy to living floras, the methods are best applied to post-Albian angiosperm-dominated floras. Comparisons between pre-Cenomanian non-angiosperm plants and their living analogues are possible only when the habits of the fossil plants are well known and even then uncertainty may be great.

4.1 Early Cretaceous Climate of the Interior

4.1.1 Deciduousness of the Gates Flora

Habits of the Gates Ferns

Most true ferns of the Gates flora belong to Dicksoniaceae (inclusive of Thyrsopterideae and Dicksonieae) (Bower, 1926). Some ferns of the Gates flora are related to Gleicheniaceae.

Modern members of the Dicksoniaceae are distributed throughout tropical and temperate areas. They vary from low creeping stocks to lofty tree-ferns (Bower, 1926). Distribution of the Early Cretaceous Dicksoniaceae is quite different from that of the living. The Early Cretaceous species of Dicksoniaceae have been abundantly reported from throughout the Arctic Province, including the northwestern Interior, northern slope of the Alaska (Scott and Smiley, 1979), Siberia and northeastern China. The Early Cretaceous species of Dicksoniaceae have also been reported in abundance from the Antarctic Province. In the Equatorial Province, Dicksoniaceae has only been reported from those areas adjacent to the Arctic Province (e.g. Crabtree, 1983; Fontaine, 1989) and are missing from most of the Equatorial Province.

Unfortunately, the habits of the Gates Dicksoniaceae are not well known. In fact, there are no satisfactory reports regarding habits of the Lower Cretaceous Dicksoniaceae from anywhere within the Arctic Province. Because tree ferns have never been reported from the Gates Formation or equivalent strata in the Arctic Province, the Gates Dicksoniaceae were most likely shrubs, with fronds arising from underground rhizomes. Because living ferns having underground rhizomes are widely distributed all over the world, the Early Cretaceous Dicksoniaceae may be a poor indicator of climate zones. LaPasha and Miller (1984) apparently interpreted the Lower Cretaceous Dicksoniaceae of Montana as having similar habits to living Dicksoniaceae and concluded that the temperatures were probably moderate, with rare or no freezing periods. It is presently unclear whether the Gates Dicksoniaceae grew seasonally or all year around, or whether perhaps Early Cretaceous Dicksoniaceae of the high paleolatitude had climate tolerances that differed from modern species.

Modern members of the Gleicheniaceae are distributed throughout the tropics and are absent from the northern temperate zone. Creeping habit is common for these ferns. Although little is known about the habits of the Gates Gleicheniaceae, they appear not to have been comparable with living Gleicheniaceae regarding their climate tolerance. Faunal evidence indicates that the Early Cretaceous coral reef northern boundary was situated in the middle of Texas, far south of the Arctic Province (Kauffman, 1984). Typical tropical deposits like red beds and carbonates are missing from the Gates Formation and indeed from all Lower Cretaceous strata in the northwestern Interior (the Late Albian is excluded). It is unlikely that the Early Cretaceous climate of the northwestern Interior was as warm as present tropics, so that the Gleicheniaceae, like the Dicksoniaceae, appears to have inhabited a wider range of climatic conditions than do living members of the family.

Pseudophlebis gatesii is very peculiar among the Early Cretaceous ferns in having petiolate pinnules which appear to have been detachable from the rachis, as detached pinnules are often seen in the Gates Formation. It appears that *Pseudophlebis gatesii* grew seasonally and that the fronds fell apart, shedding pinnules in a deciduous manner.

Habits of the Gates Gymnosperms

All species of Caytoniales appear to have been deciduous. Leaves of Caytoniales have had well-developed petioles, and leaflets of *Sagenopteris* were detachable from their petioles. *Caytoniopteris* in particular has a well developed long petiolule on each leaflet which is slightly swollen at base and morphologically similar to recent deciduous broad leaves of the angiosperms. It is believed that members of the Caytoniales were all deciduous.

All remains of ginkgoes recovered from the Gates are detached leaves. Because these leaves are morphologically very similar to the living *Ginkgo biloba*, it is reasonable to assume that they had similar deciduous habits.

Leaves of *Phoeniphyllum* were observed borne in fascicles on short shoots, as are those of *Czekanowskia* and *Phoenicopsis*. It is generally accepted that they had similar deciduous habits, as do some other gymnosperms with fascicled leaves on short shoots, such as *Pseudolarix* and *Larix*.

Zhang (1980) and Chen et al. (1988) observed the radiate arrangement of several *Chilinia* leaves and inferred that they might be clustered on the end of the stem. Chen et al. (1988) also reported the fascicled habit of *Ctenis* leaves. Nevertheless, pinnae of *Chilinia* and *Ctenis* appear un-detachable from their rachis. It is not known if fronds of *Chilinia* and *Ctenis* were deciduous. If *Chilinia* and *Ctenis* were evergreen plants. their petioles would have remained attached to the stem like living *Cycas*. Such stems fully covered with persistent petioles have been extensively reported from the Equatorial Province and have been generally referred to *Cycadeoidea*. Since *Cycadeoidea*-type fossils have never been reported from the Lower Cretaceous of the northwestern Interior, fronds of *Chilinia* and *Ctenis* were likely borne on some other type of stem. and may well have been deciduous.

Multipinnia differs from *Chilinia* and *Ctenis* mainly in having fronds at least bipinnate. It is believed that *Multipinnia* was similar to *Chilinia* and *Ctenis* in having a deciduous habit.

Bennettitaleans of the Gates include two kinds of plants: one has small leaves. such as *Pterophyllum plicatum*, which is about 10 cm long; the other has large leaves, such as *Cutchiphyllum canadensis*, which is more than 100 cm long. The small-sized bennettitaleans include all the species of *Pterophyllum*; some species of Gates *Pterophyllum* have petiolate leaves while others have sessile leaves. Pinnae of *Pterophyllum* appear un-detachable from their rachis, but all the Gates *Pterophyllum* have been found in a detached state with leaf base intact. It is believed that the small-sized bennettitaleans had a deciduous habit similar to the Early Cretaceous deciduous plant, the vine-like *Nilssonia* from the Tetori Basin of Japan (Kimura and Sekido, 1975).

The large-sized bennettitaleans include all the species of *Cutchiphyllum* and *Pseudocycas* in the Gates flora. They have petiolate, pinnate leaves, some up to 2 meters in length. Pinnae of these large-sized bennettitaleans are jointed on their rachis, and are detachable from the rachis. It is believed that these large-sized bennettitaleans dropped their pinnae from the rachis and petioles from the stem in winter, because complete detached petioles of *Cutchiphyllum* and *Pseudocycas* have been commonly seen in the Gates Formation (Pl. 22, fig. 3; Pl. 27, fig. 1).

The conifers of the Gates flora are mainly composed of members of the Pinaceae (*Pityophyllum staratschinii* and *Pityocladus magnifolius*) and Taxodiaceae (*Elatides curvifolia* and *Athrotaxites berryi*). *Elatocladus brevifolia*, *Elatocladus manchurica* and *Elatocladus* sp. are form-taxa, but possibly also belong to Taxodiaceae.

The Gates *Pityophyllum staratschinii* are all detached leaves, which were fascicled on short shoots in the manner of *Pseudolarix*; it is believed that they, too, were, deciduous. *Pityocladus magnifolius* has both long and short shoots; needle leaves are found aggregated on short shoots, while long shoots are fully covered with leaf scars. While some of these features are found in evergreen taxa, they are more typical of a deciduous habit.

Elatides curvifolia has dimorphic leaves and was probably evergreen. Its falcate leaves were isodiametric in cross section and are consistent with many evergreen Pinaceae and Taxodiaceae elements, some of which resist low temperatures in winter, as their smaller surface to volume ratio would help to reduce frost draught (Woodward, 1987). The falcate leaves of *Elatides curvifolia* are helically arranged and appressed on the stem to further reduce evaporation. These falcate isometric leaves appear to be persistent on stems, because no leaf scars or detached falcate leaves have been observed from the Gates materials. Flat leaves of *Elatides curvifolia* are pseudo-distichous in arrangement and may have been less hardy than falcate isometric leaves. These flat leaves are typically borne on twigs which may have been shed as intact leafy twigs, as they are extremely abundant as fossils.

Athrotaxites berryi on the other hand appears to be both a leaf dropper and a shoot dropper in winter; its deciduous habit has been discuss in detail together with its description.

Leaves of *Elatocladus brevifolia* and *Elatocladus* sp. have rounded bases, which are contracted to very short petioles. As leafy shoots are most commonly incomplete, they most likely dropped both leaves and leafy shoots in winter.

Elatocladus manchurica appears to have been evergreen, as leaves are firmly attached to twigs along the full width of the base. It probably had a habit similar to that of *Elatides curvifolia.*

Summary of the Habits of the Gates Flora

In summary, plants of the Gates flora can be divided into the following groups:

1. **True ferns**, which includes Filicopsida. The habits of the true ferns of the Gates flora are not well-known. Because many seed plants of the Gates Formation were deciduous, it is likely that the Gates true ferns grew seasonally, too.

2. **Deciduous non-needle-leaved**, which include ginkgoes, Czekanowskiales, *Pterophyllum*, Caytoniales, Cycadales, *Taeniopteris* and "Unidentified angiosperm leaf 1". Most plants of this group have typical deciduous features

and were likely deciduous.

3. **Deciduous needle-leaved**, which include *Pityocladus*, *Pityophyllum*, *Athrotaxites berryi*, *Elatocladus brevifolia*, *Elatocladus* sp., *Cutchiphyllum* and *Pseudocycas*. Note: Pinnae of*Cutchiphyllum* and *Pseudocycas* are compared with needle-leaved conifers. Plants of this group are all typical deciduous plants.

4. **Evergreen needle-leaved**, which include *Elatides curvifolia* and *Elatocladus manchurica*.

4.1.2 The Climate reflected by the Gates Flora

There is no sedimentary evidence of seasonal drought in the Early Cretaceous northwestern Interior basin. On the contrary, thick and abundant coal deposits are clearly indicative of humid climate and abundant rain fall. The deciduous habit of the Gates flora appears not to be an adaption to seasonal drought.

Seasonality of light can cause deciduousness in high latitude floras. The paleolatitude of the study area can be estimated at between 50^0-60^0 N on the basis of reconstructions of Hallam (1985), Barron et al. (1981, 1987), and Smith et al. (1994). This is roughly equivalent to the present latitude of approximately 53^0 N. Winter darkness above the Arctic Circle (65^0-70^0 N) would certainly contribute to polar deciduousness (Axelrod, 1984; Wolf, 1987; Basinger et al., 1994). At 50^0-60^0 N, the Gates flora would still be effected by low winter light levels; McIver and Basinger (1993) predicted deciduousness at these paleolatitudes based upon their study of the Paleocene Ravenscrag flora at 58^0 N. However, some evidence suggests that additional factors may have contributed to the Gates deciduousness.

Firstly, because the Montana Aptian flora is very similar to the Gates flora, it is believed that the climates of these two areas were very similar, with little change from the Aptian through to Middle Albian throughout the northwestern Interior. By the Late Albian, there was a distinct climate change in the western Interior as indicated by drastic vegetational change. As an example, the tree fern *Tempskya* has been found to extend from Arizona to northern Montana in the Late Albian (Ash and Read, 1976); commonly seen Aptian-Middle Albian elements such as Caytoniales, ginkgoes and Czekanowskiales, are missing in the Late Albian. This climate change was local to the Interior, and appears related to the joining of the seaways from the Gulf of Mexico and the Arctic Ocean. Because the paleolatitude of the Interior changed little from the Aptian to the Late Albian, day length conditions should not have changed. It is assumed that tree ferns like *Tempskya* were non-deciduous plants and grew all year around. The replacement of the deciduous Montana Aptian flora by a non-deciduous Late Albian flora appears to have been caused by temperature increase. That is to say that winter light levels at the paleolatitude of Montana permitted the non-deciduous plants to grow were the climate to be warm enough. Therefore, temperature appears most likely the key factor that contributed to deciduousness in the Montana Aptian flora.

The study area was situated about 10^0 poleward of the Montana fossil sites. The winter temperature of the study area in pre-Late Albian time would have been somewhat lower than that of Montana because of the latitudinal temperature gradient, and therefore, would have, in and of itself, caused deciduousness of the

Gates flora. Of course, winter day length in the study area was certainly shorter than that in Montana and would have had some influence on the Gates flora, but low minimum temperature appears to have been the overriding factor that caused the deciduousness of the Gates flora.

Secondly, it is apparent that deciduousness was a feature common throughout the Arctic Province, and climate throughout the region may have been similar. In Asia, southeast area of the Arctic Province extended into what is now northeast China, with paleolatitude between 40^0 to 45^0 N on the basis of reconstruction (Hallam, 1985; Barron et al., 1981; 1987; Smith et al., 1994). Deciduousness of the Lower Cretaceous floras of northeast China would not have been caused by seasonality of light at that latitude. Neither does drought explain deciduousness, as sedimentary evidence indicated that the climate was humid in the Early Cretaceous (Chen et al., 1988). Low temperature appears the only possible factor causing deciduousness of these Chinese floras.

Another piece of evidence is the Early Cretaceous floral zonation in Japan. The boundary between the Arctic Province and the Equatorial Province splits the Japanese Archipelago along a line almost perpendicular to latitude. It appears that this boundary was determined not by the seasonality of light, which would result in a boundary more nearly parallel to latitude.

It is difficult to determine the precise temperature of the Albian climate in the Interior, because the Gates flora is so different from modern vegetation that there is little basis for direct comparison. It is known that different plants have quite different abilities to resist low temperature. According to Woodward (1987), broad-leaved evergreen living angiosperms are unable to survive minimum temperature below about -15^0 C, although the precise physiological nature of this limitation is unclear; when the minimum temperature falls below about -15^0 C. the characteristic vegetation becomes broad-leaved winter deciduous. Representatives of both evergreen and deciduous living conifers are able to survive minimum temperature below -40^0 C, although it is clear that frost resistance of non-deciduous conifers is widely variable. Thus frost resistance of conifers, whether evergreen or deciduous is impossible to estimate.

According to Woodward (1987), low temperature causes two possible effects on living plants, cell membrane injury and frost drought. It appears that the cell membrane is the primary site of both chilling (temperatures greater than 0^0 C and less than 10^0 C) and freezing injury. Cell membrane injury may lead to leakage of ions and amino acids, quickly followed by cell death. Frost drought is caused by formation of extracellular ice within a leaf when temperature drops below 0^0 C: the formation of ice removes liquid water from cells so that solute concentration increases: in addition, the vapour pressure over ice is lower than over liquid water at the same temperature. Increases in solute concentration will be accompanied by large changes in pH and in ionic strength, leading to irreversible denaturation of proteins and other macromolecular structures. It follows that freezing injury could be a significant end result. The deciduousness of the Gates flora appears to be an adaption to deal with such freezing injury.

The general absence of broad-leaved evergreen gymnosperms such as cycads in the Gates flora may be a result of the same physiological constraints that limit distribution of broad-leaved evergreen angiosperms today. If so. there was most probably some period of freezing during the winter, and minimum winter temperature below -15^0 C may therefore have existed.

4.1.3 The Climate reflected by other evidence

Considerable geological evidence indicates that the Early Cretaceous represents a period of warm global temperatures and absence of permanent ice at low elevation anywhere on the Earth. Evidence summarized by Crowley and North (1991) includes latitudinal poleward displacement of invertebrates (coral reefs, large foraminifera, gastropods, rudist bivalves, ammonites and belemnoids), the presence of dinosaurs above the Arctic Circle, and the high temperature (15^0 C higher than the present) of intermediate-deep ocean waters based on oxygen isotope records.

However, there is some data that indicates that parts of the Earth were cool during the Early Cretaceous. Reports of apparently ice-rafted deposits in high-latitude regions during the Late Jurassic and the Early Cretaceous have been used to suggest that freezing conditions occurred near the poles and that glaciers may possibly have existed periodically (Frakes et al., 1992). Crowley and North (1991) also indicated that there were some problems with the oxygen isotope measurements because many published records have not been sufficiently examined to test for alteration effects (diagenesis), which significantly modify oxygen isotope values. Also the depth habitat of some of the measured organisms (e.g., belemnoids) is not well known; oxygen isotope values can vary with depth, and are also significantly modified in coastal regions. Many of the oxygen isotope measurements listed by Barron and Washington (1982) are from shallow-water marine realms. Bakker (1975, 1980) argued that dinosaurs were warm-blooded and therefore might have been able to tolerate cool winters. Some dinosaurs may also have migrated seasonally to warmer climates (Axelrod, 1984; Parrish et al., 1987).

There are no published oxygen isotope records within the northwestern Interior in the Lower Cretaceous. Fauna of the Fort St. John Group have no relationship with those from the Gulf of Mexico because there were no connections for most of the Early Cretaceous between the two seaways. Therefore, it is unknown if the climate of the Early Cretaceous would have allowed warm-loving fauna to extend poleward. Dinosaur footprints occur in Gates rocks at Grande Cache and have been seen in coal mines during the present study, but small to intermediate-sized reptiles like turtles are apparently absent from the northwestern Interior in the Early Cretaceous (pre-Late Albian).

4.1.4 Summary of the Interior Climate

In conclusion, summers of the Early Cretaceous (pre-Late Albian) in the northwestern Interior appears warm and humid, with abundant rainfall. Winter temperatures likely dropped below freezing, at least periodically, to a point that would inhibit development of broad-leaved evergreen gymnospermous vegetation. Existing evidence from both plants and animals and oxygen isotope records argue against prolonged deep frost. Minimum winter temperature may have been as low as -15^0 C to -20^0, but cold month mean temperature were probably much higher, perhaps close 0^0 C.

4.2 Floral assemblages of the Interior

As stated earlier in the section on "Geological age of the Gates Formation", the age of the Gates Formation can be precisely determined as late Early Albian. The advantage of intercalated coal-bearing strata and marine shales in the study area will help to build up Early Cretaceous floral assemblages, which are stratigraphically significant in the correlation of the plant-bearing strata in the northwestern Interior.

4.2.1 The Aptian assemblage

The Aptian assemblage of the northwestern Interior is represented by the Gething flora of British Columbia (Bell, 1956) and the Kootenai flora from Montana (Miller and LaPasha, 1985; LaPasha and Miller, 1985). The Aptian assemblage is characterized by the following features.

1. Absence of angiosperms.
2. Main body of the assemblage consisting of the following elements:
   (a) *Acanthopteris gothanii* (Neocomian-Albian)
   (b) *Coniopteris ermolaevii* (Late Jurassic-Early Cretaceous)
   (c) *Cladophlebis virginiensis* (Early Cretaceous)
   (d) *Caytoniopteris williamsii* (Aptian-Middle Albian)
   (e) *Sagenopteris maclearnii* (Aptian-Middle Albian)
   (f) *Sagenopteris newensis* (Aptian-Middle Albian)
   (g) *Pterophyllum albertense* (Late Jurassic-Early Cretaceous)
   (h) *Ptilophyllum arcticum* (Late Jurassic-Early Cretaceous)
   (i) *Elatides curvifolia* (Jurassic-Early Cretaceous)
   (j) *Athrotaxites berryi* (Early Cretaceous)
   (k) Ginkgoes

3. *Podozamites*, which is common in earlier strata, is rare in the Aptian assemblage.

According to Retallack and Dilcher (1986), angiosperms occurred in the coastal plain of eastern North America during the latest Barremian or early Aptian, reaching California by the Albian or perhaps as early as Aptian. Reports of angiosperm macrofossils from the northwestern Interior earlier than the Albian are all unreliable. The presence of *Phyllites* sp. in the Gething flora in Bell's (1956) fig. 1 appears to be a mistake, because the species was indicated to occur within the Luscar Formation in both the species description and plate captions in Bell's original text (1956, p. 139). MacLeod and Hills (1990; 1992b) appear to have inherited the mistake in Bell's publication in illustrated the Gething flora as an angiosperm-bearing flora.

Culmites sp., which occurs in the Kootenay Formation (Late Jurassic) (Bell. 1956), is only a stem having longitudinal striae. Its attribution to the angiosperm is inappropriate.

Definite presence of angiosperms in the northwestern Interior includes the "Unidentified angiospermous leaves 1 and 2" from the Gates Formation, *Phyllites* sp. from the Luscar Formation and *Sapidopsis angusta* from the Lower Blairmore Group (Bell, 1956), which appear all to be Early Albian.

Crabtree (1987) also reported the earliest presence of angiosperms of the northwestern Interior from the Gates Formation. The Gates Formation was regarded by Crabtree (1987) as lower Middle Albian in reference to the earlier works of Bell (1956), Mellon et al. (1963), Stott (1960, 1968) and Singh (1971).

On the basis of the three above features of the Aptian assemblage, the floras from the following floras are considered to be Aptian: the Kootenai Formation. the Gething Formation, lower part of the Luscar Formation, lower part of the lower Blairmore Group, and the Hazelton Group (Skeena beds) (Figure 2.4).

The Skeena beds were dated by MacLeod and Hills (1990, Fig. 9) as Neocomian, although this is inconsistent with their assignment of most Skeena beds to the Aptian-Albian in their Fig. 8.

The Bowser flora from the Devils Claw, McEvoy, and Currier formations was determined as pre-Albian (MacLeod and Hills, 1990, 1992a, 1992b). In fact, the only typical Aptian element in the Bowser flora, *Caytoniopteris (Sagenopteris) williamsii*, appears to be misidentified (see discussion of *C. williamsii*). *Cladophlebis virginiensis* of the Bowser flora is different from both the type materials of this species and the Gates specimens assigned to this species in the present study. *Elatides curvifolia* appears to have ranged from the Jurassic to the Early Cretaceous, and therefore is of little biostratigraphic significance. *Coniopteris hymenophylloides* of the Bowser flora appears to be the same as *Coniopteris ermolaevii* of the Aptian assemblage; it also is long ranging, from the Late Jurassic to the Early Cretaceous.

Many other elements of the Bowser flora suggest that the Bowser flora is in fact pre-Aptian, rather than pre-Albian. *Nilssonia brongniartii* of the Bowser flora occurs in Neocomian strata of the Hazelton Group and Tantalus Formation (Bell, 1956). *Cladophlebis heterophylla* and *Ctenis borealis* of the Bowser flora have been documented in the Late Jurassic Kootenay Formation (Bell, 1956). *Nilssonia schaumburgensis* of the Bowser flora has been reported from pre-Aptian strata of the Kootenay Formation and the Hazelton Group. *Nilssonia tenuicaulis* and *Baiera furcata* of the Bowser flora (MacLeod and Hills, 1992a, b) are similar to specimens described as *Nilssonia* cf. *N. tenuicaulis* and *Baiera* cf. *B. furcata* from pre-Aptian strata of the Hazelton Group, the Tantalus Formation and the Kootenay Formation (Bell, 1956).

MacLeod and Hills (1992a, b) made worldwide stratigraphic analysis on some selected elements of the Bowser flora in their determination of the age of the Bowser flora as Tithonian to pre-Albian. Inherent in such worldwide stratigraphic analysis is the assumption that all plants of a species were contemporaneous and become extinct simultaneously throughout their geographical region. Due to plant migration and regional variation, this assumption may not hold all the time. Therefore, worldwide biostratigraphic comparison based on fossil plants may be less precise. Nevertheless, within a single region or sedimentary basin such as the northwestern Interior, the migration time of plants is negligible. Therefore, in determining the age of the northwestern Interior floras, comparison is in the first instance restricted to within the northwestern Interior Basin. It is expected that such comparison will produce more precise results than worldwide stratigraphic analysis. Although the Bowser Basin does not belong to the northwestern Interior, the northwestern Interior basin appears to be the closest area and both basins belong to a single floral province, the Arctic Province. Therefore comparison between the northwestern Interior floras and the Bowser Basin floras is considered to be appropriate.

4.2.2 Early Albian assemblage

The Early Albian assemblage of the northwestern Interior is well represented by the Gates flora. The Albian assemblage is characterized by the following features.

1. Presence of 2-3 species of angiosperms.
2. Main body of the assemblage includes most of the principal Aptian assemblage elements:
    (a) *Acanthopteris gothanii* (Neocomian-Albian)
    (b) *Coniopteris ermolaevii* (Late Jurassic-Early Cretaceous)
    (c) *Cladophlebis virginiensis* (Early Cretaceous)
    (d) *Caytoniopteris williamsii* (Aptian-Middle Albian)
    (e) *Sagenopteris maclearnii* (Aptian-Middle Albian)
    (f) *Sagenopteris newensis* (Aptian-Middle Albian)
    (g) *Pterophyllum albertense* (Late Jurassic-Early Cretaceous)
    (h) *Elatides curvifolia* (Jurassic-Early Cretaceous)
    (i) *Athrotaxites berryi* (Early Cretaceous)
    (j) Ginkgoes
3. Presence of elements specific to the Early Albian:
    (a) *Coniopteris bidens*
    (b) *Sphenopteris erecta*
    (c) *Pseudophlebis gatesii*
    (d) *Cutchiphyllum bisulcatum*
    (e) *Cutchiphyllum canadensis*
    (f) *Cutchiphyllum rockii*
    (g) *Chilinia magnifolia*
    (h) *Multipinnia interior*
    (i) *Phoeniphyllum tumblericum*
4. *Podozamites*, which is common in Triassic and Jurassic strata, is absent in the Early Albian assemblage.

On the basis of features of the Early Albian assemblage, the equivalent floras of the Early Albian assemblage include those from the upper part of the Lower Blairmore Group, the upper part of the Luscar Formation and the Jackass Mountain Group.

Although Bell (1956) did not recover any angiosperms from the Jackass Mountain Group, Crabtree (1987) reported the presence of 2 species, which makes the Jackass Mountain Group more likely to be of an Early Albian in age, rather than Aptian as reported by Bell (1956) and MacLeod and Hills (1990, 1992a, 1992b).

The Albian Spence Bridge flora summarized by MacLeod and Hills (1990, Fig. 9; 1992b, Fig. 3) appears to be distinct from the Spence Bridge flora of Bell (1956). Bell's (1956) Spence Bridge flora consists of Late Jurassic elements and lacks angiosperms, and therefore appears to be pre-Aptian in age (Figure 2.4). MacLeod and Hills list about 10 species of angiosperms in their Spence Bridge flora, which are characteristic of the Late Albian assemblage, or at least Middle Albian. Because MacLeod and Hills did not give the source of that Spence Bridge flora, further comparison is impossible.

4.2.3 Middle Albian assemblage

Well-dated Middle Albian strata in the study area include the Hulcross Formation and the lower Boulder Creek Formation (Stelck and Leckie, 1990a). Nevertheless, there are no well-studied Middle Albian floras in the northwestern Interior. Mellon et al. (1963, youngest flora) reported a species list for the Boulder Creek flora. In comparison with the Early Albian assemblage, the Boulder Creek flora shows little change in floral composition except for the angiosperms, which increased to 8 species. The Middle Albian assemblage can be characterized as follows:

1. Presence of about 8 species of angiosperms.
2. Main body of the Middle Albian assemblage is similar to that of the Early Albian in having:
   (a) *Cladophlebis* cf. *C. virginiensis*
   (b) *Caytoniopteris williamsii*
   (c) *Sagenopteris* cf. *S. maclearnii* (Aptian-Middle Albian)
   (d) *Ptilophyllum* aff. *P. montanense*, which may be similar to *Pterophyllum albertense*
   (e) *Elatides* cf. *E. curvifolia* (Jurassic-Early Cretaceous)
   (f) Ginkgoes
3. The Middle Albian assemblage also differs from the Early Albian assemblage in lacking those elements specific to the Early Albian assemblage plus the following species:
   (a) *Acanthopteris gothanii* (Neocomian-Albian)
   (b) *Coniopteris ermolaevii* (Late Jurassic-Early Cretaceous)
   (c) *Sagenopteris newensis* (Aptian-Middle Albian)
   (d) *Athrotaxites berryi* (Early Cretaceous)

There appears no abrupt change between the Early and the Middle Albian assemblages. The most important difference between the two assemblages is that there are more angiosperms in the Middle Albian assemblage. Therefore, it is possible that equivalent strata include the uppermost beds of some otherwise typical Early Albian units like the lower Blairmore Group and the Jackass Mountain Group, and the lowermost beds of some typical Late Albian units like the Pasayten Group and the Kingsvale Group.

4.2.4 Late Albian assemblage

Major climatic change within the Interior occurred when the Interior seaway from the north coalesced with that from the Gulf of Mexico. This change was manifest by the extensive distribution of the tree fern *Tempskya* within the Interior from Arizona and New Mexico to northern Montana (Ash and Read, 1976, p. 7, fig. 3). The climate of the Late Albian is believed to have been significantly warmer than the Early Albian, possible frost free, but it is unknown how far north the influence of the warm climate affected vegetation, as there is an absence of sufficient paleobotanical data.

The upper Blairmore flora (Bell, 1956) was dominated by angiosperms (up to 15 species); other elements of the flora are quite different from those of the Early-Middle Albian assemblages. *Cladophlebis virginiensis* is the only element common to both the upper Blairmore flora and the Early-Middle Albian assemblages. Because of the form-taxon nature of *Cladophlebis virginiensis* and its long stratigraphic range, its presence in the upper Blairmore flora is of little stratigraphic significance. Other well-defined, easily recognized Aptian-Middle Albian elements are missing from the Upper Blairmore flora, including:

1. *Acanthopteris gothanii*
2. *Coniopteris ermolaevii*
3. *Caytoniopteris williamsii*
4. *Sagenopteris maclearnii*
5. *Sagenopteris newensis*
6. *Pterophyllum albertense*
7. *Elatides curvifolia*

8. *Athrotaxites berryi*
9. Ginkgoes

Therefore, the upper Blairmore flora appears to be younger than the Middle Albian. On the other hand, the upper Blairmore Group is quite different from the overlying Dunvegan Formation (Cenomanian), in which angiosperms are as many as 43 species (Bell, 1963). Therefore, it is reasonable to assign a Late Albian age to the upper Blairmore flora.

The Crowsnest flora and the Commotion flora described by Bell (1956) consist of only a few plants taxa, of which all are angiosperms except one, so that the age of these beds can be no older than Late Albian. However, the "upper flora" (flora 3) from the Commotion Formation of Belcourt Ridge reported by Mellon et al. (1962) is different from the Commotion flora described by Bell (1956) in having many Aptian-Middle Albian elements. A possible explanation is that Bell's Commotion flora was from the uppermost beds of the Commotion Formation. On the other hand, one or both of these "Commotion" floras may actually represent different and misidentified strata.

The Pasayten and Kingsvale floras are basically similar to the upper Blairmore flora, but there is one Aptian-Early Albian element, *Sagenopteris newensis*, in these floras. Therefore, the Pasayten and Kingsvale groups are largely of Late Albian age, although the lowermost beds of the Pasayten and Kingsvale might be the Middle Albian.

Chapter 5

Early Cretaceous Floral Provinces

This chapter discusses the Early Cretaceous global floral provinces. A new scheme of floral provinces is proposed; provincial boundaries are discussed in detail.

Vakhrameev was the only paleobotanist to systematically study the global distribution of Jurassic and Cretaceous floras (Vakhrameev, 1988; 1991). He distinguished four paleofloristic provinces for the Early Cretaceous: the Siberio-Canadian province, the European-Sinian province, the Equatorial province, and the Notal province (Meyen, 1987, p. 319, fig. 90). Vakhrameev (1991) later referred to these four provinces as regions, and subdivided these regions into several provinces. In the following discussion, the four regions of Vakhrameev will be referred to as provinces, and his provinces in each region will be referred to as sub-provinces to accommodate the more customary usage of "province". Vakhrameev's publication (1991) is the most complete summary of global Jurassic and Cretaceous floras. Nevertheless, Vakhrameev's recognition of four provinces is problematic.

First of all, the boundaries of Vakhrameev's four provinces are more or less parallel to paleolatitude and appear to be based in part on the assumption that climate across continents was influenced mainly by latitudinal temperature gradients (Frakes et al., 1992). Of course, latitude would have had an important influence on plant distribution, but other influences, like land and sea distribution and ocean currents, also significantly influenced plant distribution. The Early Cretaceous floral zonation of the Japanese archipelago is a good example of the effects of such non-latitudinal influences. Kimura and Hirata (1975) recognized two types of Early Cretaceous floras in Japan: the Ryoseki flora of the eastern or outer side opening into the Pacific Ocean, which is similar to the European floras; and the Tetori flora of the inner or western side. Although the Tetori flora has mixed features of both the Ryoseki flora and the Siberian floras, it is more like the Siberian floras than the Ryoseki flora, as there are no typical Ryoseki taxa like *Frenelopsis* reported in the Tetori flora. Vakhrameev (1991) was the only paleobotanist who insisted that the Tetori flora was a special plant community of the Euro-Sinian province; other paleobotanists have considered it to be comparable to the Siberian floras (e.g., Kimura and Hirata, 1975; Chen et al., 1988; MacLeod and Hills, 1992b).

Sloan and Barron (1990) have shown, on the basis of their global climate simulation, that zonation as Vakhrameev claimed was unlikely because of the large sizes of the continents. They predicated that continental interiors would have experienced more seasonal extremes than marginal areas. Contrast between the Ryoseki and Tetori floras is compatible with this interpretation. On the eastern side of the Pacific Ocean, this phenomenon is not so obvious because of absence of floristic data. It is known that the Queen Charlotte flora (listed by Ward in 1905, p. 209; Berry, 1911, p. 125), the northernmost known Pacific-rim Early Cretaceous flora, is more like the Equatorial floras rather than the Arctic floras. It is possible that the whole of the Pacific-rim might have hosted floras similar to those of the Equatorial Province because the latitudinal temperature gradient might have been overwhelmed by the warm ocean currents.

Secondly, the criteria for recognition of Vakhrameev's four provinces are not clearly stated. The difference between the European-Sinian province and the Equatorial province is unclear. In fact, there appears no conspicuous floral change across this boundary. It is also difficult to understand why the Notal Province should include Patagonia and India, which produce floras different from the Australian floras.

In this study, provinces are primarily recognized on the basis of the presence and absence of Cheirolepidiaceae (*Frenelopsis* and/or *Classopollis*). Accordingly, only three floral provinces are here recognized in the Early Cretaceous (Figure 2.1):

The Arctic Province, which does not have Cheirolepidiaceae and is situated to the North of the Equatorial Province.

The Equatorial Province, which has Cheirolepidiaceae.

The Antarctic Province, which does not have Cheirolepidiaceae and is situated to the South of the Equatorial Province.

Although this provincial scheme presents a good overview on the global floral zonation, it relies on the correct recognition of the Equatorial Province. In practice, more detailed analysis is needed, especially when floras are from near provincial boundaries and may not be typical of any single province. The following elements are selected as typical of the Equatorial Province (in order of importance):

1. Cheirolepidiaceae (*Frenelopsis* and/or *Classopollis*)
2. *Weichselia*, *Cycadeoidea*
3. Cupressaceae.
4. *Tempskya* and other tree ferns.
5. *Ptilophyllum*, *Zamites*, *Dictyozamites*, and *Otozamites*.

5.1 The Arctic Province

The Arctic province mainly includes Alaska, the northwestern Interior of North America, Greenland, Spitzbergen, Siberia, northern Mongolia, northeastern China and the Inner Zone of Japan (Figure 2.1). The Pacific-rim area is excluded from the Arctic province. The Arctic province is characterized by having the following features:

1. Typical elements which are common in the Arctic Province, but are rare or absent in either of the other two provinces, include:
    (a) *Equisetites*
    (b) *Dicksoniaceae*
    (c) *Acanthopteris gothanii*
    (d) Pinaceae
    (e) Taxodiaceae

   (f) *Chilinia*
   (g) *Cutchiphyllum*
   (h) *Ginkgo*, *Ginkgoites* and *Baiera*.
   (i) Czekanowskiales

2. Elements which are absent from , or at least very rare in, the Arctic Province, include:
   (a) *Weichselia*
   (b) Cheirolepidiaceae, Cupressaceae, Podocarpaceae and Araucariaceae.
   (c) *Ptilophyllum*, *Zamites* and *Otozamites*.
   (d) *Cycadeoidea*.
   (e) *Tempskya* and other tree ferns.
3. Floras in the province are diverse.
4. Deciduous habit prevailed within the province (Spicer and Parrish, 1986; Chen et al., 1988; this report). Climate appeared to have been seasonal, with the possibility of winter frost.

5.1.1 Boundary on the North American continent

Few fossil plants are reported from the Queen Charlotte Islands (listed by Ward in 1905, p. 209; Berry, 1911, p. 125). The presence of *Ginkgo* appears to indicate a resemblance of the Queen Charlotte flora to the floras of the Arctic Province, but other evidence also indicates a resemblance to the Equatorial Province. Dicksoniaceae appears to be absent from the Queen Charlotte flora; *Zamites tenuinervis* of the Queen Charlotte flora was reported from the Shasta Formation (Fontaine, 1905h). Other plants of the Queen Charlotte Islands flora are less indicative. Nevertheless, the general impression of the flora is that it is much more like the Equatorial than Arctic floras. *Ginkgo* is common in the Arctic, but rare presence in the Equatorial floras is quite possible, especially for floras adjacent to the boundary, as for example the presence of *Baiera* in the Potomac flora (Berry, 1911) and *Ginkgo* in English Wealden flora (Watson. 1969). The Bowser flora is basically similar to the Gates flora (MacLeod and Hills, 1990; 1992a, b) in terms of the major groups within the flora. Therefore, in North America the western boundary of the Arctic Province can be drawn between the Queen Charlotte Islands and the Bowser Basin.

To the southwest, the boundary between the Arctic Province and the Equatorial Province can be drawn somewhere between the Shasta Formation of northern California (Fontaine, 1905h) and the Montana Aptian flora (Miller and LaPasha. 1984; LaPasha and Miller, 1985). The Shasta flora appears different from the Gates flora in lacking ginkgoes and in having *Cycadeoidea*, the so-called *Dioonites* (= *Ptilophyllum*), and *Zamites*. *Cycadeoidea* is common in the Potomac flora (Berry, 1911), the Wealden flora (Seward, 1894. 1895; Watson and Sincock. 1992) and central U.S.A. (Weiland, 1906). The so-called *Dioonites* is the same as many plants described as *Ptilophyllum* in the Wealden flora. *Dioonites dunkerianus* of the Shasta Formation was also found in the Glen Rose beds of Texas (Fontaine, 1905h); *Dioonites buchianus* of the Shasta was also reported from the Potomac flora (Berry, 1911, p. 332). Both the Glen Rose and Potomac flora are typical of the Equatorial Province. Various members of the Cheirolepidiaceae and *Cycadeoidea* from the Glen Rose Formation of Texas indicate their affinity to the Equatorial Province (Berry, 1911; Watson, 1977; Watson and Fisher. 1984).

The boundary between the Arctic and the Equatorial provinces in the North American continent can therefore be drawn between the seaway from Gulf of Mexico to the south and the northwestern Interior seaway to the north. That is.

between the Glen Rose beds of Texas and the Montana Aptian beds.

The Aptian flora of the Lakota Formation from the Black Hills of western South Dakota, studied mainly by Ward and listed in Berry (1911, p. 137), is quite different from those of the Gates, the Bullhead Group (Bell, 1956) or the Kootenai Formation (LaPasha and Miller, 1985; Miller and LaPasha, 1984) in having *Cycadeoidea*, which is the dominant element in the flora. Other features of the Equatorial Province seen in the Lakota flora include the absence of Dicksoniaceae and ginkgoes and the presence of *Zamites*. The presence of *Czekanowskia* was considered questionable by Ward and appears to be unlikely to me. There is no doubt that the Aptian flora of the Black Hills belongs to the Equatorial Province, and that there are no elements transitional between the Black Hills flora and the other northwestern Interior floras, although they are in such close proximity. There appears to be very little latitude difference between the Kootenai Formation of Montana and the Lakota Formation of Black Hills. Continental topography appears to be the main factor causing such an abrupt change.

The boundary between the Arctic and the Equatorial provinces can be drawn, therefore, between the Kootenai area of Montana and the Black Hills during the Aptian.

The Albian flora from the Black Hills, listed in Berry (1911, p. 141) was from the upper part of the Lakota Formation, called by Cobban and Reeside (1952) the Fuson Formation. The Fuson flora appears to be approximately the same age as the Gates flora in that both floras have few angiosperms. Cobban and Reeside (1952) attributed the Fuson Formation to the Aptian on the basis of comparison with the Canadian floras (Bell, 1956; Berry, 1929). Nevertheless, the Fuson flora is so different from the lower Blairmore flora as to make comparison meaningless. Although *Cycadeoidea*, the dominant element of the Lakota flora did not occur in the Fuson, other typical Equatorial elements, such as *Weichselia*, occur within the Fuson flora, and there is an absence of Arctic sphenopterids and ginkgoes. *Leptostrobus* is typical element of the Arctic Province. The Fuson specimens figured as *Leptostrobus alatus* Ward as listed by Berry (1911, p. 141) are not available for examination. Nevertheless, Potomac specimens referred to as *Leptostrobus* by Fontaine (1889, 1905k) are all *Pityocladus*. Because the Fuson flora was described by Fontaine and Ward, it may be predicated that their *Leptostrobus alatus* from the Fuson flora also belongs to *Pityocladus*. In addition, presence of *Leptostrobus* in the Fuson Formation appears unlikely to me. Therefore, the boundary between the Arctic and the Equatorial provinces changed little through the Aptian and Albian.

The Potomac flora (Fontaine, 1889; Berry, 1911) is a typically Equatorial flora in spite of the occasional presence of some Arctic elements such as *Baiera* and Pinaceae. Typical Equatorial elements of the Potomac flora include: *Tempskya*, *Cycadeoidea*, *Dioonites* (same as *Ptilophyllum*), *Zamites*, and Cheirolepidiaceae.

The James Bay flora (Martison, 1952) appears to have belonged to the Equatorial Province, although there are some mixed features of both the Arctic and the Equatorial provinces. *Pityophyllum*, a common element of Arctic Province, is abundant and widespread in the James Bay flora. *Brachyphyllum*, most likely a member of Cheirolepidiaceae is common in the James Bay flora. Therefore, James Bay flora appears be have been in close proximity to the boundary between the Arctic and the Equatorial provinces.

The Kome flora of Greenland (Heer, 1874; 1882; 1883; Seward, 1926) can be included within the Arctic Province, although the Kome flora has mixed features of both the Arctic Province and Equatorial Province. Most taxa of the Kome flora are typical Arctic elements, including *Czekanowskia*, *Ginkgo*, *Gleichenia*, and *Sphenopteris*. The usage of *Zamites* in the Greenland flora (Heer, 1874) is in Halle's *Sub-Zamites* sense; therefore, those *Zamites* are equivalent to *Cutchiphyllum*. The specimen described as *Cycas steenstrupii* is most likely *Cutchiphyllum bisulcatum* or *Pseudocycas* sp. However, the presence of two typical Equatorial elements, *Frenelopsis* and *Cupressinocladus*, suggests that the Kome flora must have been situated near the provincial boundary between the Arctic and Equatorial provinces.

The Spitzbergen flora as listed by Berry (1911, p. 116) appears to be similar to the Arctic floras but can not be considered typical; the dominant group in the flora appears to be Pinaceae, a common element in the Arctic floras. Other elements of the Spitzbergen flora are of little significance in floral geography.

5.1.2 Boundary on the European-Asian continent

The Ural Mountains appear to approximate the boundary between the Arctic and Equatorial provinces within the European-Asian continent. The various floras to the west of the Ural were summarized by Vakhrameev (1991). Those floras have many features in common, including the occurrence of Cheirolepidiaceae, the fern *Weichselia*, and *Cycadeoidea*. Generally speaking, these European floras are more like the Equatorial type, but there are some Arctic elements like *Ginkgo*, as the European floras are adjacent to the provincial boundary. Palynological investigations also suggested the existence of such a boundary (Herngreen and Chnolova, 1981).

The Mongolia flora (Krassilov, 1982) has elements indicative of the Arctic Province, including Czekanowskiales. There are also some Equatorial elements like *Otozamites* and *Cycadeoidea* in the Mongolia flora. Vakhrameev (1991) discussed the transitional features of the Mongolia floras and attributed Mongolia to his Euro-Sinian province. In this study, the boundary is drawn across Mongolia, with northern Mongolia attributed to the Arctic Province, and southern Mongolia, to the Equatorial.

The boundary between the Arctic and Equatorial provinces within the Asian continent is essentially the boundary between the northern and the southern floral areas of China (Guo, 1986; Chen et al., 1988). The eastern boundary of the Arctic Province splits Japan; the Tetori-type floras from the western side of Japan belong to the Arctic Province: the Ryoseki-type floras from the eastern side of Japan belong to the Equatorial Province (Kimura, 1980, p. 398: 1984, p. 339: 1987, p. 94).

The main factors that governed the distribution of the Japanese floras appeared to have been paleogeography. This point may not be easy to see in the far east region without reconstruction of paleogeographic relationships. According to Vakhrameev (1987), there was a deep marginal sea during the Aptian between Japanese archipelago and the main land Asia (Figure 2.1). This marginal sea was connected with the Arctic Ocean through a narrow channel called the Anyui Strait, and therefore this marginal sea is somewhat similar to the northwestern Interior seaway. This paleogeographic feature may well explain the distribution of the Tetori-type floras, which were influenced by this polar seaway, and the Ryoseki-type floras, where climate was controlled by the Pacific Ocean.

5.2 The Equatorial Province

The Equatorial Province includes most of the continental USA, Europe, South America, Africa, the Middle East region, India, southern Mongolia, most of China, eastern side of Japan and the Pacific-rim areas. The province is characterized by having the following features:

1. Typical elements which are common in the Equatorial Province, but are rare in either of the other two provinces, include:
    - (a) *Weichselia*
    - (b) Cheirolepidiaceae, Cupressaceae.
    - (c) *Ptilophyllum*, *Zamites* and *Otozamites*.
    - (d) *Cycadeoidea*.
    - (e) *Tempskya* and other tree ferns.
2. Elements which are absent from , or at least rare in the Equatorial Province, include:
    - (a) Typical elements of the Arctic Province.
    - (b) Typical elements of the Antarctic Province except *Zamites*.
3. Floras adjacent to the other two provinces may have some Typical elements of other two provinces
4. Climate of the province was quite warm and appeared to be frost free. Most areas of the province were dry. Plants are either evergreen in humid environments, or possibly deciduous because of drought.

Vakhrameev (1991) included the southern ends of the African and South American continents together with India within the Notal province. In fact, there appear to be no abrupt floral compositional changes from the equator to the Antarctic Province. Since the typical elements, including Cheirolepidiaceae, occur in the

Patagonia flora (cited from Vakhrameev, 1991, p. 170), and *Weichselia* occurs in the India floras (cited from Vakhrameev, 1991, p. 178), South America and India are better included within the Equatorial Province. Because *Zamites* and *Dictyozamites* have been abundantly reported from South Africa (Anderson and Anderson, 1985), and typical elements of the Antarctic Province such as ginkgoes and *Acanthopteris gothanii* are absent, South Africa is better included within the Equatorial Province.

5.3 The Antarctic Province

The Antarctic Province includes the Antarctic and Australian continents. The province is characterized by having the following features:

1. Typical elements which are common in the Antarctic Province, but are rare or absent in either of the other two provinces, include:
    - (a) *Equisetites*
    - (b) *Dicksoniaceae*
    - (c) *Acanthopteris gothanii*
    - (d) Podocarpaceae and Araucariaceae.
    - (e) *Zamites* (= *Ptilophyllum* of Douglas, 1969; 1973).
    - (f) *Ginkgo*, *Ginkgoites* and *Baiera*.
    - (g) Tree ferns.
2. Elements which are absent from , or rare in the Antarctic Province, include:
    - (a) *Weichselia*
    - (b) Cheirolepidiaceae, Cupressaceae, Pinaceae and Taxodiaceae.
3. Floras in the province are diverse.
4. Both evergreen (e.g. araucarians, cycads, tree ferns) and deciduous or semi-deciduous forms (e.g. pteridosperms and Ginkgoales) appear to have been represented. Climate was apparently warmer than that of the Arctic.

Few floras have been reported from the Antarctic Province. Jefferson (1982) reported some fossil forests composed of silicified trunks from the Lower Cretaceous of Alexander Island, Antarctica. The well-preserved growth patterns of those trunks are different from those of modern high-latitude trees and are closest to some species of living trees growing in warm temperate areas with a long growing season.

The Victoria flora reported by Douglas (1969, 1973), and Douglas and Williams (1982) is representative of the Antarctic Province. The Victoria flora appears to be a diverse fossil flora, including cryptograms, pteridosperms, Cycadales, Cycadeoidales, Ginkgoales, Coniferales and angiosperms. The climate has been interpreted as was warm- to cool-temperate, relatively equable and with moderate seasonality and no widespread winter freezing (Douglas and Williams, 1982).

Bennettitaleans of the Victoria flora are common, but monotonous; only one genus, with 11 species, was recognized by Douglas (1969, 1973). It must be noted that Douglas' (1969, p. 115) usage of *Ptilophyllum* is incorrect; all 11 species of *Ptilophyllum* belong to *Zamites*.

It appears that the climate of the Antarctic as a whole was warmer than that of the Arctic, because tree ferns were able to survive there. This temperature difference could have been caused by different patterns of land-sea distribution in the south polar regions. The Antarctic Province appears open toward the Equatorial oceans, but the Arctic Province was basically separated to the Equatorial oceans.

Conclusions

Examination of macrofossil plants from the Gates Formation indicates that the flora consisted of bryophytes (*Marchantiolites* and *Thallites*), *Equisetites*, ferns (*Gleichenites* of Gleicheniaceae, *Acanthopteris* and *Coniopteris* of Dicksoniaceae, *Cladophlebis*, *Pseudophlebis* gen. nov., and *Sphenopteris*), seed-ferns (*Sagenopteris* and *Caytoniopteris* gen. nov.), conifers (*Pityocladus* and *Pityophyllum* of Pinaceae, *Athrotaxites* and *Elatides* of Taxodiaceae, *Elatocladus*), cycads (*Multipinnia* gen. nov., *Chilinia*, *Ctenis*, *Cutchiphyllum* gen. nov, *Pseudocycas* and *Pterophyllum*), *Ginkgo* and *Ginkgoites*; leptostrobans (*Phoeniphyllum* gen. nov.), *Taeniopteris* and angiosperms.

In total, 52 species from 28 genera are described, including 15 new species and 3 new combinations. The new species are: *Cladophlebis simplexa*, *Cladophlebis serrata*, *Pseudophlebis gatesii*, *Sagenopteris newensis*, *Pityophyllum magnifolius*, and *Pterophyllum albertense*, *Chilinia magnifolia*, *Ctenis rotundata*, *Multipinnia interior*, *Cutchiphyllum bisulcatum*, *Cutchiphyllum canadensis*, *Cutchiphyllum rockii*, *Pseudocycas alberta*, *Phoeniphyllum tumblericum*, and *Taeniopteris gatesensis*. The new combinations are: *Equisetites montanensis*, *Coniopteris bidens*, *Caytoniopteris williamsii*.

Most plants of the Gates flora appears to have been deciduous. Only *Elatides* *curvifolia* and *Elatocladus manchurica* are convincingly evergreen. The interpreted paleoclimate is strongly seasonal with winter minimum temperature possibly below -15^0 C. Rainfall appears to have been abundant, because coal deposits are thick and extensive in the Gates Formation. Although low winter minimum temperature appears to be the main factor causing deciduousness of the Gates flora, daylight shortage may have also contributed to the deciduousness of the Gates flora, as the paleolatitude of the study area was 50^0-60^0 N.

The age of the Gates flora can be determined as Early Albian on the basis of faunal evidence. With in the northwestern Interior, four floral assemblages, ranging from the Aptian to Late Albian, are recognized. Floral assemblages from the Aptian to Middle Albian changed very little in their compositions; the most obvious change is the increase of angiosperms. Dramatic floral change occurred between the Middle and the Late Albian, when non-angiospermous Middle Albian elements were replaced by angiospermous Late Albian elements. Strata equivalent to the Gates Formation include the upper part of the Lower Blairmore Group, the upper part of the Luscar Formation and the Jackass Mountain Group.

Globally, three floral provinces are recognized in this study. They are the Arctic Province, which lacks Cheirolepidiaceae, the The Equatorial Province, which has abundant Cheirolepidiaceae, and the Antarctic Province, which also lacks Cheirolepidiaceae. The Gates flora is typical of the Arctic Province. Similar floras have been reported from throughout the Arctic Province, including Montana, the western Interior of Canada, the Bowser Basin, Alaska, western Greenland, Spitzbergen, Siberia, northern Mongolia, northeastern China and the Inner Zone of Japan. A deciduous habit appears to have prevailed within the Arctic Province.

Climate appears to have been strongly seasonal, with the probability of winter frost.

The Equatorial Province includes most of USA, Europe, South America, Africa. Middle East region, India, southern Mongolia, most of China, the eastern side of Japan and the Pacific-rim areas. Dry, warm climate prevailed in most of the Equatorial Province.

The Antarctic Province included Antarctica and Australia; dominant plants were Araucariaceae, Podocarpaceae, ginkgoes and cycads. Leptostrobans and Cheirolepidiaceae are absent. Climate of the Antarctic Province appears to have been humid and somewhat warmer than that of the Arctic.

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Appendix A

Fossil Sites

Fossils collected in the summer of 1990 are as follows:

No. 850 Quintette Coal Limited, Mesa Pit, close to coal seams D+E in Gates Formation.

No. 851-853 Quintette Coal Limited, Wolverine Pit, in Gates Formation.

No. 855-862 Quintette Coal Limited, Wolverine Pit, in Boulder Creek Formation.

No. 863-865 Quintette Coal Limited, Wolverine Pit, in Gates Formation.

No. 866-873 Quintette Coal Limited, Mesa Pit, in Boulder Creek Formation.

No. 874 Bullmoose Corporation, from above E coal seam in the Gate Formation.

No. 875 Bullmoose Corporation, from between C and D coal seams in the Gates Formation.

No. 876-78 Bullmoose Corporation, from above A coal seam in the Gates Formation.

No. 879-896 From section I in Quintette Coal Limited, Wolverine Pit in the Gates Formation.

No. 897-913 From section II in Quintette Coal Limited by the main road in the Gates Formation.

No. 914 Quintette Coal Limited, by the main road cut in the Gates Formation.

No. 915 Quintette Coal Limited. Shikano Pit, from the Gates Formation.

No. 916-919 Quintette Coal Limited, from section III by the main road in the Gates Formation.

No. 921-926 Cardinal River Coals Limited, in the Gates Formation in Luscar.

Fossils collected in the summer of 1991 are as follows:

No. 950 Smoky River Coals Limited, in the Gates close to No.4 coal seam at Mine 12 in Grande Cache.

No. 951 Smoky River Coals Limited, in the Gates at Mine 9 in Grande Cache.

No. 952-953 Cardinal River Coals Limited, in the strata about 50 meters above the Jewel Coal Seam in the Gates Formation, in the 50-A-4 Pit.

No. 954-955 Gregg River Coals Limited, in the Gates Formation in PQ1.

No. 956-957 Gregg River Coals Limited, in the Gates Formation in HI1.

No. 958 Cardinal River Limited, in the Gates Formation in 50-B-4 Pit.

Appendix B

Plates

Plate 1

Fig. 1. *Marchantiolites blairmorensis* (Berry) Brown & Robison.

1. Bifurcating, strap-shaped thallus with midrib. No. 858-7365, X1.

Figs. 2, 3. *Thallites* sp.

2. Bifurcating, strap-shaped thallus with midrib. No. 858-7360. X2.
3. Strap-shaped thallus showing midrib. No. 858-7360, X2

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Plate 1

Plate 2

Figs. 1-3. *Equisetites montanensis* (LaPasha & Miller) comb. nov.

1. Articulated stem with branches, No. 950-7357. X3.
2. Articulated stem with leaf sheaths. No. 950-7358. X3.
3. Articulated tuber-bearing rhizome, No. 926-7324. X3.

Figs. 4-6. *Acanthopteris gothanii* Sze.

4. Upper part of frond. showing intercalated pinnule. No. 951-7334. X2.
5. Lower part of frond, showing modified intercalated pinnule (A). No. 950-7329. X3.
6. Fertile pinna. No. 958-7339. X3.


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Plate 2

Plate 3

Figs. 1-4. *Acanthopteris gothanii* Sze.

1. Tripinnate portion of frond, No. 956-7337, X1.
2. Frond with conspicuous intercalated pinna (A), No. 950-7337, X1.
3. Close-up of an intercalated pinna (A), No. 950-7127, X2.
4. Intermediate forms between pinnae and pinnules, No. 950-7328, X2.

Fig. 5. *Acanthopteris* sp.

5. Bipinnate portion of frond, No. 853-7130, X2.

Plate 3

Plate 4

Figs. 1-4. *Coniopteris bidens* (Bell) comb. nov.

1. Bipinnate portion of frond, showing bifurcate pinnules. No. 951-7351, X2.
2. Pinnae showing non-bifurcate pinnules (A). No. 951-7342, X2.
3. Fertile pinna. No. 951-7349, X2.
4. Close-up of Fig. 3: showing terminal sorus (A) and bifurcate basal pinnules (B). No. 951-7349. X4.

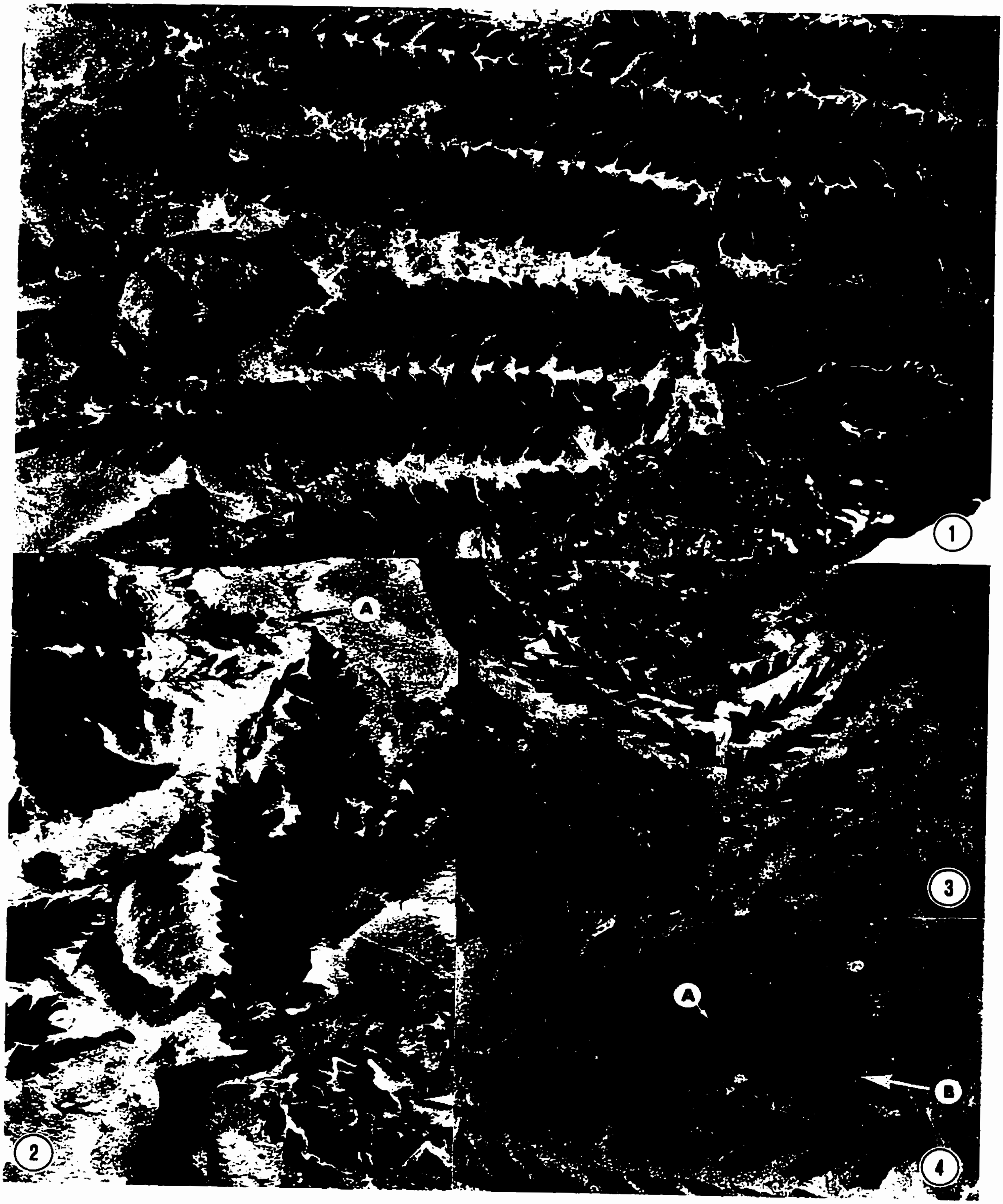

Plate 4

Plate 5

Figs. 1-5. *Coniopteris ermolaevii* (Vassil.) Meng & Chen.

1. Sterile pinna; note rounded to bluntly pointed lobes, No. 878-7344. X2.
2. Sterile pinnae; note rounded lobes. No. 878-7347, X2.
3. Fertile pinnae; note that the reverse pinna (A) is less reduced. No. 851-7354. X2.
4. Sterile pinnae; note bluntly pointed lobes. No. 878-7346, X2.
5. Close-up of a fertile pinna, showing terminal sori. No. 851-7356. X5.

Plate 5

Plate 6

Fig. 1. *Coniopteris simplex* (Lindley & Hutton) Harris.

1. Bipinnate portion of frond. No. 950-7127. X3.

Fig. 2. *Cladophlebis virginiensis* Fontaine.

2. Pinna. No. 875-7162. X2.

Figs. 3, 4. *Cladophlebis constricta* Fontaine.

3. Bipinnate portion of frond. showing smaller pinnules. No. 952-7100. X2.
4. Bipinnate portion of frond. showing larger pinnules. No. 952-7094. X2.


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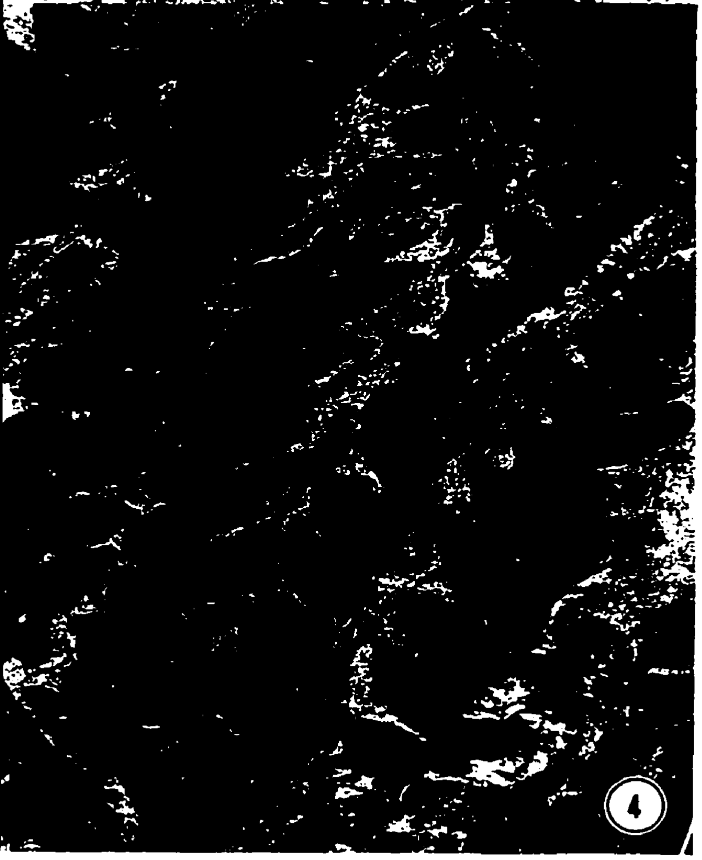
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Plate 6

Plate 7

Figs. 1, 2. *Gleichenites nordenskioeldii* (Heer) Seward.

1. Bipinnate portion of frond, No. 851-7278. X1.
2. Close-up of another bipinnate portion of frond. No. 925-7273. X2.

Figs. 3, 4. *Cladophlebis serrata* sp. nov.

3. Bipinnate portion of frond; showing slightly contracted bases of pinnules. No. 950-7070. X1.
4. Bipinnate portion of frond; showing full bases of pinnules. note serrate margin in distal half of pinnules. No. 874-7022. X2.


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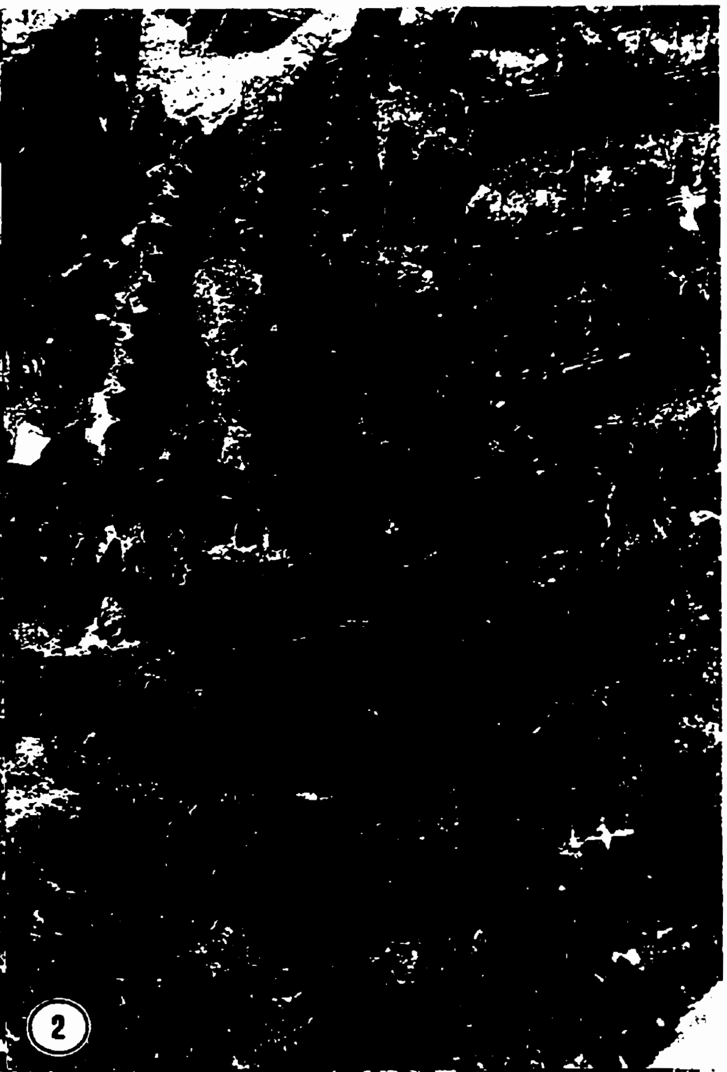
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Plate 7

Plate 8

Figs. 1, 2. *Cladophlebis simplexa* sp. nov.

1. Pinna showing pinnule venation. No. 855-7286, X3.
2. Bipinnate portion of frond. No. 855-7283, X3.

Figs. 3, 4. *Pseudophlebis gatesii* sp. nov.

3. Distal part of a pinna. No. 921-7195. X3.
4. Proximal part of a pinna. No. 915-7146. X2.

Plate 8

Plate 9

Figs. 1-3. *Sphenopteris erecta* Bell.

1. Bipinnate portion of frond, with both fertile (A) and sterile (B) pinnules. No. 950-7282. X1.
2. Fertile pinna. No. 950-7274, X2.
3. Fertile pinnae, showing both entire and lobed pinnules. No. 958-7275. X2.

Figs. 4, 5. *Sphenopteris goeppertii* Dunker.

4. Tripinnate portion of frond. No. 956-7326. X2.
5. Close-up of a tripinnate portion of frond, No. 956-7325. X3.

Plate 9

Plate 10

Fig. 1. *Sphenopteris goeppertii* Dunker.

1. Tripinnate portion of frond, showing less lobed pinnules. No. 956-7319. X2.

Figs. 2, 3. *Sphenopteris acrodentata* Fontaine.

2. Bipinnate portion of frond. No. 958-7343. X2.
3. Close-up of a bipinnate portion of frond. No. 952-7309. X6.

Fig. 4. *Sphenopteris brulensis* Bell.

4. Sterile bipinnate portion of frond. No. 955-7999. X2.

Plate 10

Plate 11

Figs. 1, 2. *Sphenopteris brulensis* Bell.

1. Fertile bipinnate portion of frond, No. 952-7324, X2.
2. Close-up of fertile bipinnate portion of frond, No. 958-7315, X3.

Figs. 3-5. *Caytoniopteris williamsii* (Newberry) comb. nov.

3. Complete leaflet; the white-coloured area on the left is a mineral stain. No. 920-7058. X1.
4. Small leaflet, possibly unmature or aberrant. No. 954-7037. X1.
5. Another complete leaflet. No. 914-7039, X1.


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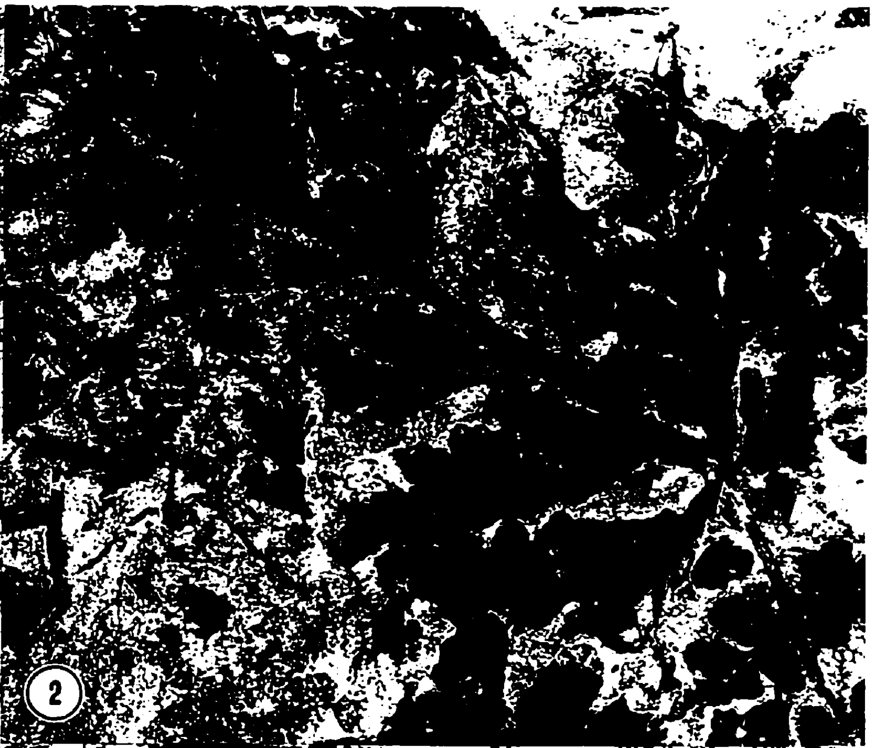
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Plate 11

Plate 12

Figs. 1, 4-6. *Sagenopteris newensis* sp. nov.

1. Four palmately attached sessile leaflets. No. 950-7040. X2.

4. Five palmately attached sessile leaflets on a petiole. No. 954-7031. X1.

5. Two attached leaflets. No. 954-7048. X2.

6. Detached leaflet. No. 954-7060. X1.

Figs. 2, 3. *Sagenopteris maclearnii* Berry.

2. Nine palmately attached leaflets. No. 852-7052. X2.

3. Detached leaflet. No. 875-7050. X2.

Plate 12

Plate 13

Fig. 1A. *Elatocladus* sp.

1A. Leafy twig, No. 921-7103, X2.

Fig. 1B. *Phoeniphyllum tumblericum* sp. nov.

1B. Upper part of a leaf, No. 921-7103, X2.

Fig. 2. *Pityocladus magnifolius* sp. nov.

2. Twig, with large terminal fascicle of leaves, No. 956-7001, X1.

Fig. 3. *Pityophyllum staratschinii* (Heer) Nathorst.

3. Detached leaves, No. 951-7259, X3.

Plate 13

Plate 14

Figs. 1-5. *Athrotaxites berryi* Bell.

1. Leafy twigs. No. 926-7240. X1.
2. Leafy twigs borne on leafless axis, No. 953-7007, X2.
3. Branch covered with leaf scars; leaf scars on the upper part (A) are elliptical: leaf scars on the lower part (B) are round, No. 950-7167, X3.
4. Close-up of Fig. 5, showing leaf scars. No. 853-7003. X10.
5. Branch covered with leaf scars. No. 853-7003. X2.5.

Plate 14

Plate 15

Figs. 1-5. *Athrotaxites berryi* Bell.

1. Detached pollen cones. No. 957-7256. X1.5.
2. Round terminal seed cone. No. 957-7258. X2.
3. Terminal pollen cone. No. 957-7239. X4.
4. Round seed cone borne terminally on shoot branch. No. 865-7237. X2.
5. Cylindrical seed cone. No. 957-7260. X2.

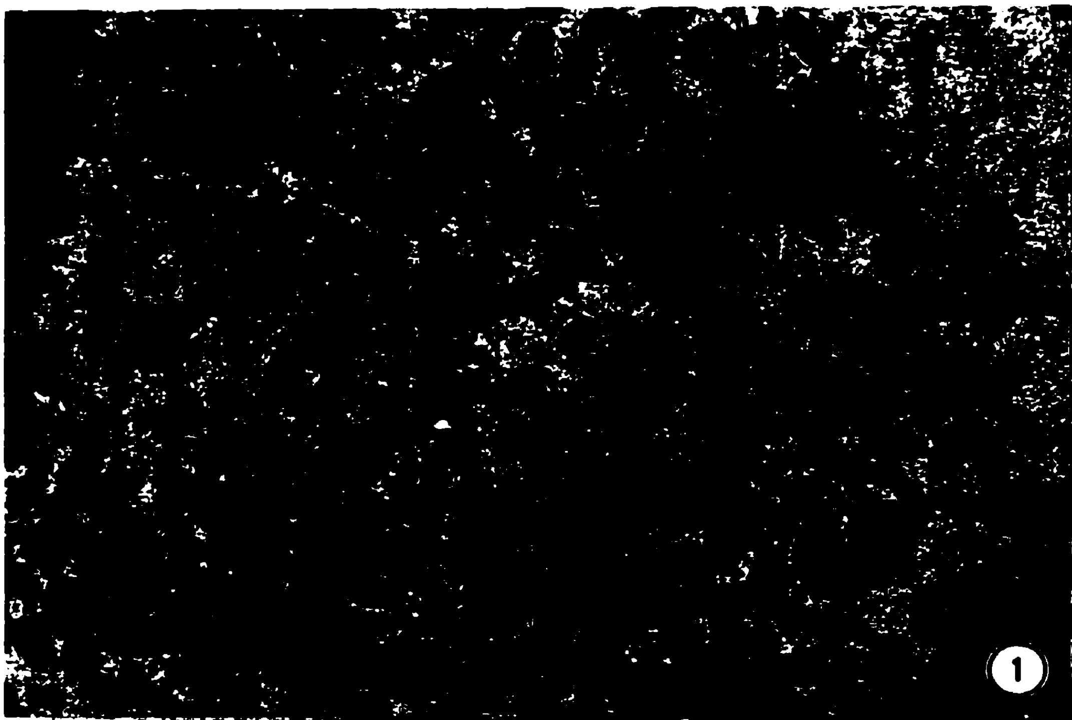

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Plate 15

Plate 16

Figs. 1-4. *Elatides curvifolia* (Dunker) Nathorst.

1. Leafy twigs bearing primarily flat leaves, No. 957-7227, X1.
2. Leafy twigs bearing falcate leaves, No. 952-7224, X1.
3. Upper part of leafy twigs with falcate leaves, No. 876-7230, X1
4. Close-up of Fig. 1: note that both flat leaves (A) and falcate leaves (B) exist on the same shoot. No. 957-7227, X2.

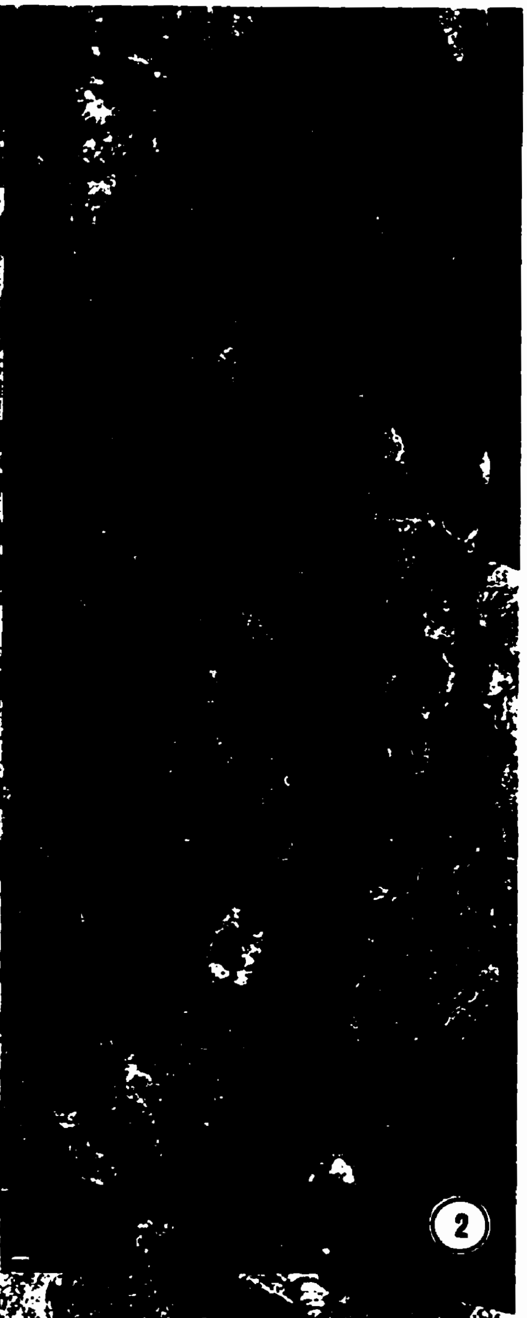

Plate 16

Plate 17

Figs. 1-4. *Elatides curvifolia* (Dunker) Nathorst.

1. Leafy twigs, showing both flat leaves (A) and falcate leaves (B) on the same branch. No. 954-7226, X2.
2. Main branch with falcate leaves, No. 950-7234, X2.
3. Close-up of Fig. 2, showing falcate leaves, No. 950-7234, X4.
4. Terminal seed cone, No. 921-7222, X2.

Plate 17

Plate 18

Figs. 1-4. *Elatocladus brevifolia* (Fontaine) Bell.

1. Leafy twig, showing branching pattern, No. 950-7245, X1
2. Leafy twig, terminal branch pseudo-bifurcate, No. 950-7255, X2.
3. Leafy twig with relatively small leaves, No. 874-7253, X2.
4. Leafy twig, note the contracted leaf bases, No. 952-7251, X2.

Plate 18

Plate 19

Figs. 1, 2. Unidentified conifer seeds ?

1. Unidentified seeds preserved together with *Elatides curvifolia* (Dunker) Nathorst and *Pityophyllum staratschinii* (Heer) Nathorst. No. 951-7259. X2.
2. Close-up of Fig. 1. No. 951-7259. X6.

Figs. 3, 4. *Elatocladus manchurica* (Yokoyama) Yabe.

3. Leafy twig with cylindrical seed cones. No. 920-7209. X1.
4. Leafy twig, showing helically arranged leaves. No. 874-7213. X1.

Plate 19

Plate 20

Figs. 1, 2. *Chilinia magnifolia* sp. nov.

1. Upper part of frond. No. 877-7079. X1.
2. Upper part of pinnae, showing digitate teeth. No. 950-7081. X1.

Fig. 3. *Chilinia* sp.

3. Once pinnate frond. No. 921-7075. X2.

Fig. 4. *Ctenis rotundata* sp. nov.

4. Once pinnate frond. pinna base contracted. No. 921-7198. X1.

Plate 20

Plate 21

Fig. 1. *Ctenis rotundata* sp. nov.

1. Once pinnate frond, pinna apex round; lower part of the frond is mineral-stained. (A) indicating the frond rachis, No. 915-7199, X1.

Figs. 2-4. *Multipinnia interior* sp. nov.

2. Close-up of Fig. 4, showing penultimate pinnae and both entire and dentate pinnae. No. 875-7082, X1.8.
3. Close-up of Fig. 2, showing pinna venation and marginal teeth. No. 875-7082, X6.
4. Bipinnate portion of frond, No. 875-7082, X1.3.

Plate 21

Plate 22

Fig. 1A. *Elatides curvifolia* (Dunker) Nathorst.

1A. Branchlets having flat leaves arising from branches covered with falcate leaves, No. 874-7010, X0.6.

Figs. 1B, 2, 3. *Cutchiphyllum canadensis* sp. nov.

1B. Central portions of a leaves. No. 874-7010. X0.6.

2. Lower part of leaf. No. 952-7204. X1.

3. Basal part of leaf, showing swollen base of petiole. No. 952-7888. X1.

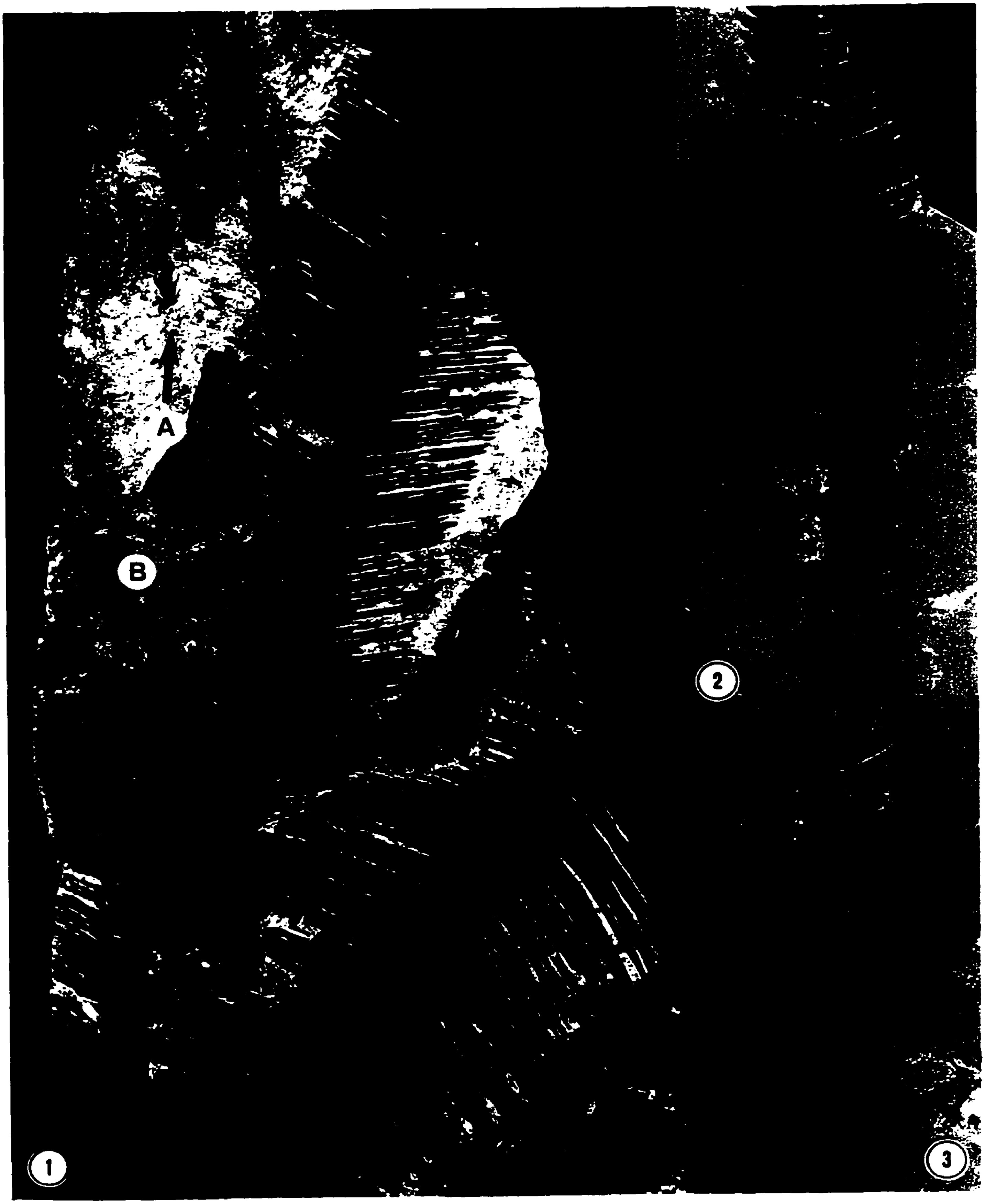

Plate 22

Plate 23

Figs. 1-4. *Cutchiphyllum canadensis* sp. nov.

1. Middle part of a leaf with having aberrant, wide pinna (A). No. 952-7203. X1.
2. Rachis covered with pinna scars. No. 952-7208. X3.
3. Lower part of a leaf, showing pinna apices and bases attached to ventral (upper) surface of rachis. No. 952-7205. X2.
4. Middle part of a leaf, showing pinna bases attached to ventral (upper) surface of rachis. No. 952-7204. X2.

Plate 23

Plate 24

Figs. 1-4. *Cutchiphyllum bisulcatum* sp. nov.

1. Lower part of a leaf, No. 915-7017, X2.
2. Upper part of a leaf, No. 921-7018, X2.
3. Leaf showing the two ventral grooves on each pinna, No. 921-7013. X2.
4. Close-up of a pinna, showing two ventral grooves, No. 874-7023. X25.

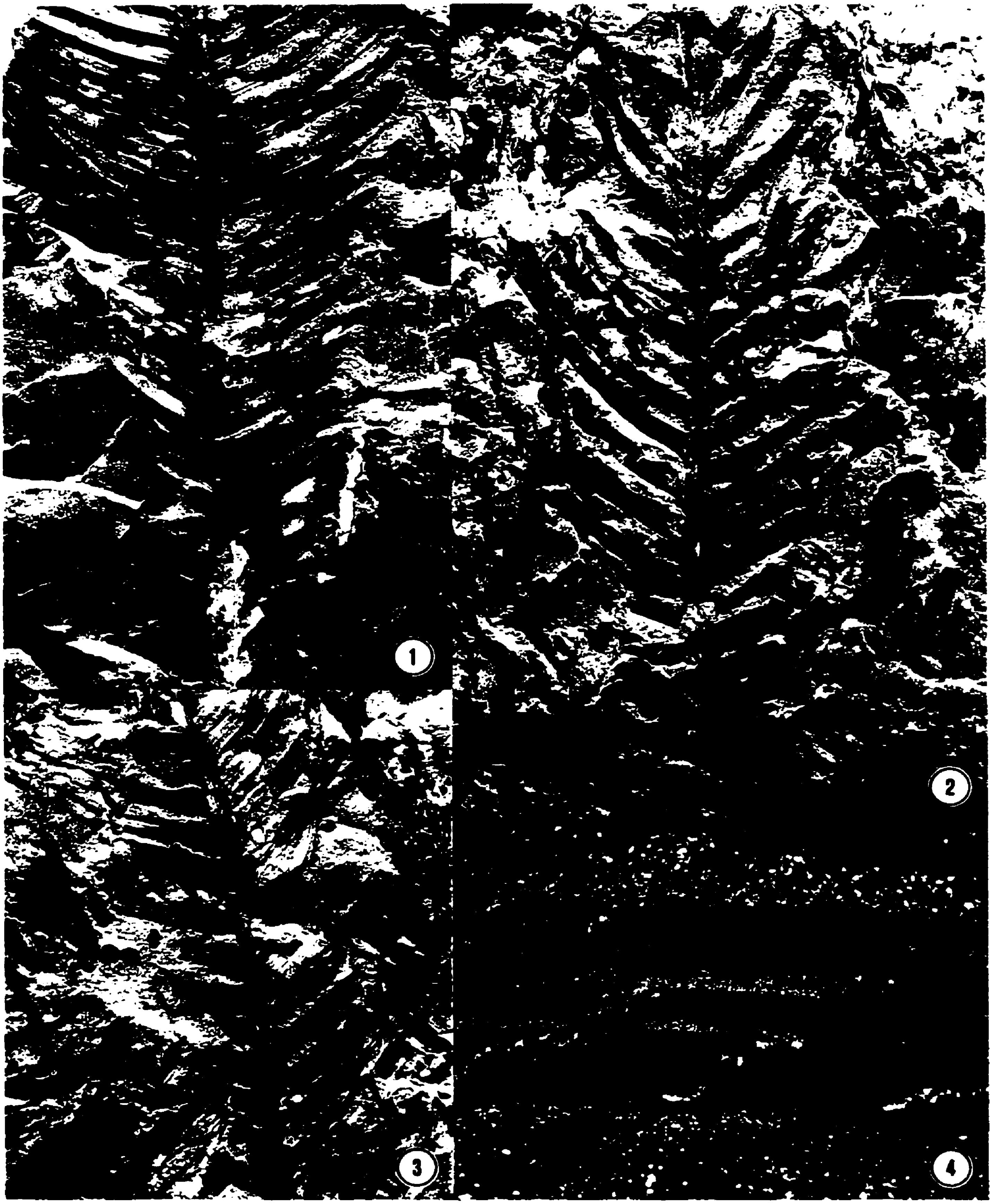

Plate 24

Plate 25

Fig. 1. *Cutchiphyllum bisulcatum* sp. nov.

1. Petiolate leaf, No. 952-7012, X1.

Figs. 2-4. *Cutchiphyllum rockii* sp. nov.

2. Middle part of a leaf, showing pinnae attached to ventral (upper) surface of rachis No. 952-7089, X1.
3. Close-up of Fig. 2, showing the two dorsal (lower surface) grooves and the two marginal ventral (upper surface) grooves on each pinna. No. 952-7089. X2.
4. Leaf showing the two dorsal (lower surface) grooves on each pinna. No. 952-7091. X2.

1

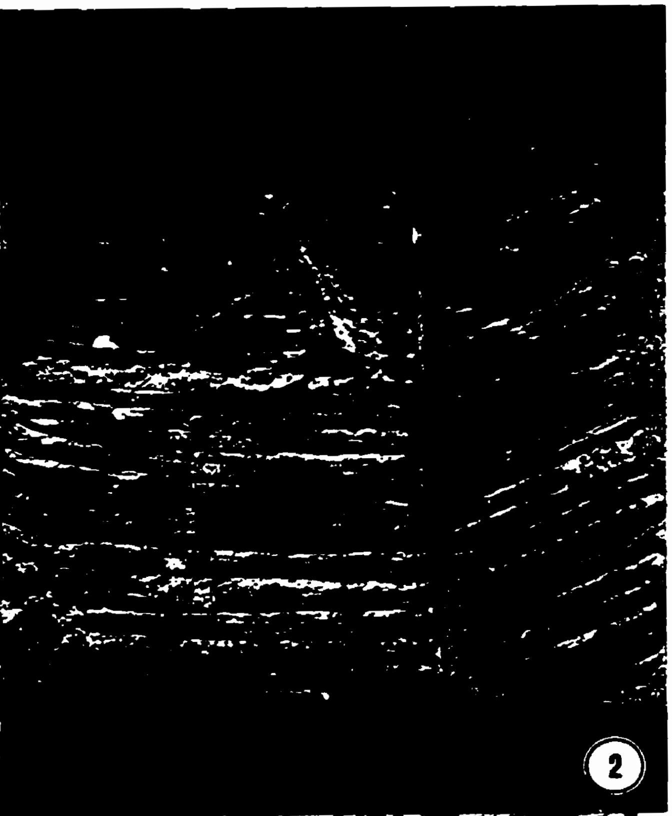

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Plate 25

Plate 26

Figs. 1-3. *Pseudocycas alberta* sp. nov.

1. Upper part of a leaf. No. 874-7019. X1.
2. Lower part of a leaf. No. 851-7030. X1
3. Leaf showing the dorsal (lower surface) groove on every pinna: note that the specimen is a dorsal impression. No. 874-7025. X2.

Plate 26

Plate 27

Figs. 1, 2. *Pseudocycas alberta* sp. nov.

1. Petiolate leaves. (A) indicating an intact, swollen base of petiole. No. 874-7052. X1.

2. Leaf showing the pinna bases and the dorsal grooves. No. 851-7027. X2.

Fig. 3. *Pseudocycas* sp.

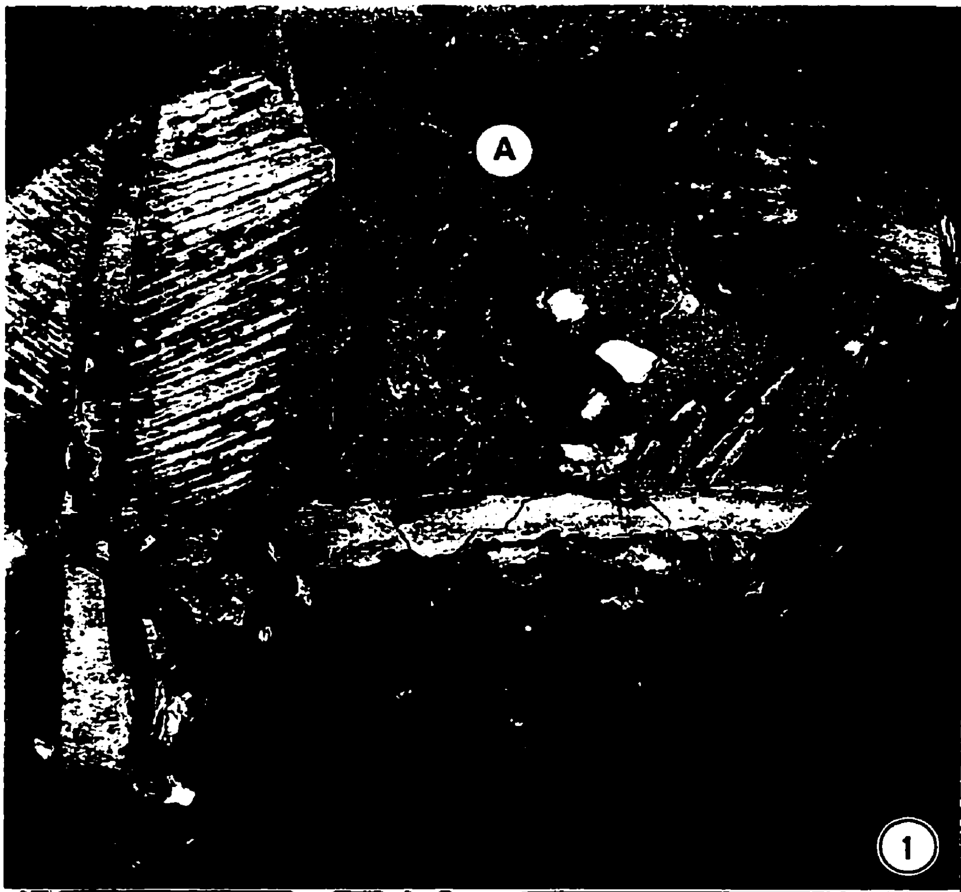
3. Part of leaf. No. 855-7029. X1.5.

Figs. 4-6. *Pterophyllum albertense* sp. nov.

4. Upper part of leaf: note that pinnae are attached to the sides of the rachis. No. 914-7188. X1.

5. Upper part of leaf: note that pinnae are attached to the sides of the rachis. No. 874-7197. X1.

6. Lower part of leaf: note that the leaf is sessile, and that pinnae are attached to the sides of the rachis. No. 874-7190. X1.



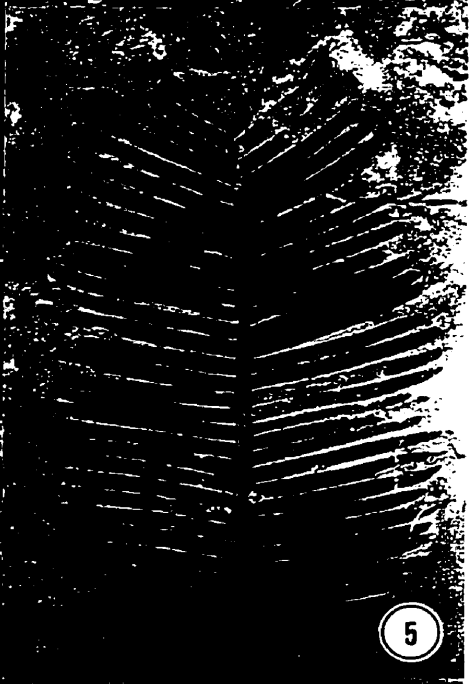


Plate 27

Plate 28

Figs. 1-3. *Pterophyllum rectangulare* Bell.

1. Lower part of leaf, No. 952-7174, X1.
2. Upper part of leaf, No. 950-7167, X1.5.
3. Petiolate leaf, No. 952-7186, X1.

Figs. 4, 5. *Pterophyllum plicatum* Bell.

4. Sessile leaf. No. 952-7191. X1.
5. Counterpart of Fig. 4. No. 952-7006. X2.

Figs. 6, 7. *Pterophyllum smallifolium* sp. nov.

6. Part of leaf with intact base. No. 952-758. X2.
7. Complete leaf. sessile. No. 952-7183. X1.

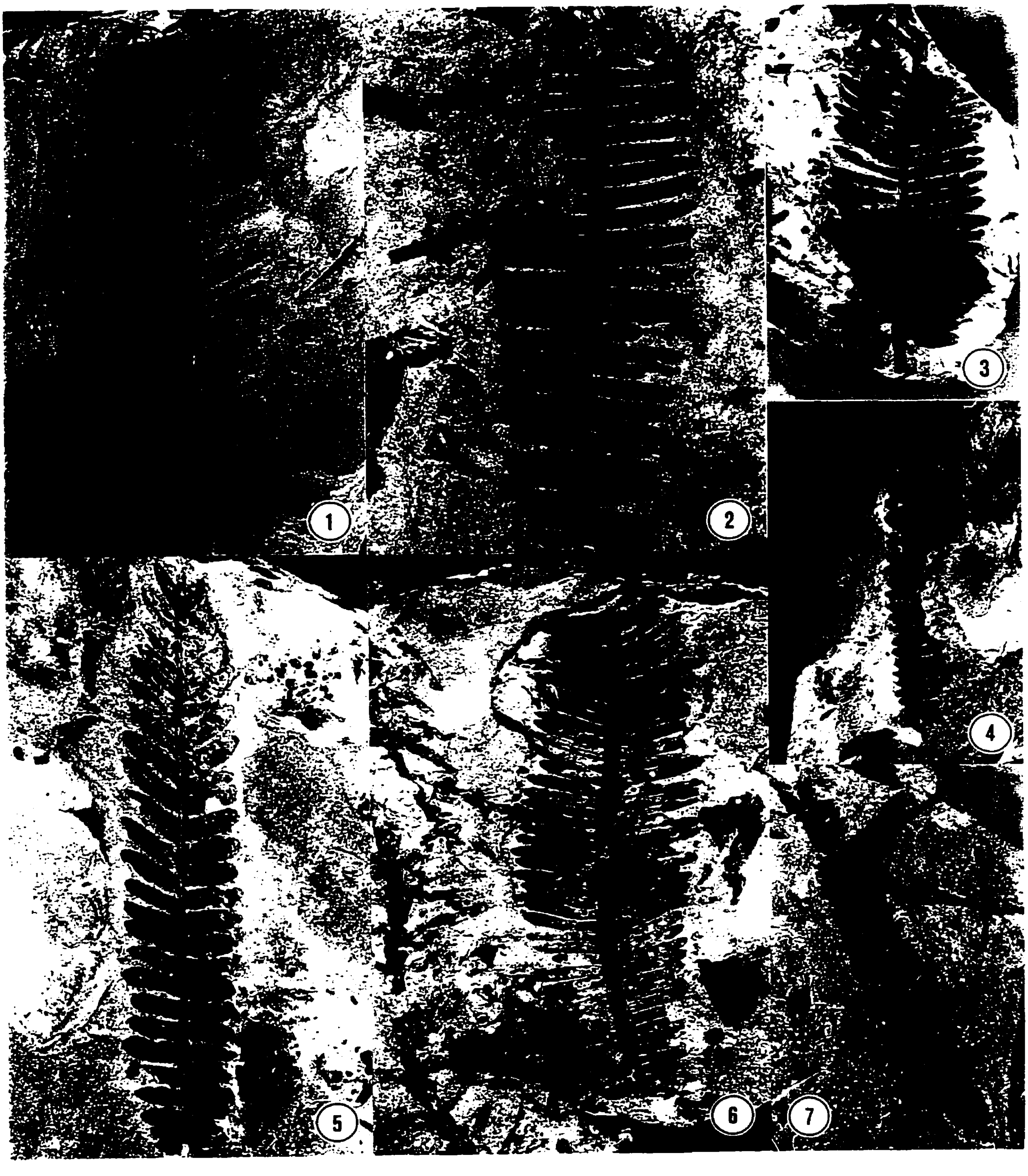


Plate 28

Plate 29

Fig. 1. *Pterophyllum* sp. 1

1. Lower part of leaf, showing the petiole, No. 952-7181, X2.

Figs. 2, 3. *Pterophyllum* sp. 2

2. Lower part of leaf, No. 896-7192, X1.
3. Upper part of leaf, No. 896-7193, X1.

Fig. 4. *Taeniopteris canmorensis* (Dawson) Bell.

4. Complete sessile pinna, showing intact base, No. 952-7287, X2.3.

Fig. 5. *Taeniopteris gatesensis* sp. nov.

5. Middle part of pinna, No. 950-7135, X1.


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Plate 29

Plate 30

Taeniopteris gatesensis sp. nov.

Complete petiolate pinna. No. 952-7136, X0.8.

Plate 30

Plate 31

Figs. 1-5. *Ginkgo pluripartita* (Schimper) Heer.

1. Complete leaf, No. 951-7120, X1.
2. Complete leaf, No. 951-7113, X1.
3. Complete leaf, No. 951-7112, X1.
4. Complete leaf, No. 951-7116, X1.
5. Lower part of leaf, No. 951-7118, X1.

Figs. 6-9. *Ginkgoites cascadensis* Brown.

6. Leaf, No. 951-7169, X1.
7. Leaf, No. 852-7114, X1.
8. Complete petiole, No. 958-7179, X1.
9. Leaf, No. 958-7176, X1.

Fig. 10. *Phoeniphyllum tumblericum* sp. nov.

10. Leaf showing forward pointing teeth, No. 915-7108, X1.


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Plate 31

Plate 32

Figs. 1-2. Unidentified angiosperm leaf 1.

1. Complete petiolate leaf, No. 925-7266, X1.
2. Leaf blade, No. 952-7201, X1.

Fig. 3. Unidentified angiosperm leaf 2.

3. Upper part of leaf, No. 952-7262, X1.5.

Fig. 4. Unidentified angiosperm leaf 3.

4. Fragment of leaf, No. 921-7265, X2.

Plate 32