LAND PLANTS OF THE NORTHERN ROCKY MOUNTAINS BEFORE THE APPEARANCE OF FLOWERING PLANTS

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ABSTRACT

Evidence of land plants before the appearance of flowering plants near the end of the Early Cretaceous is spotty. Seas covered much of the land during the Paleozoic and early Mesozoic, but certain areas were exposed, perhaps as islands. Evidence of Devonian vegetation from Beartooth Butte, Wyoming includes rhyniophytes, trimerophytes, zosterophylls, and lycopsids. Fossils from several different deposits show Late Mississippian to Pennsylvanian age vegetation like that of coal swamps to the east. The floras include lepidodendrids, calamites, ferns, seed ferns, and cordaites, with conifers present at some localities. Triassic and Early Jurassic land vegetation is poorly known in the region, as most strata are marine; but Late Jurassic sediments reflect the general emergence of the land concurrent with uplift along the Nevadan orogenic zone at the western edge of the present northern Rocky Mountains. The interior basin supported bryophytes, horsetails, cycads, caytonialeans, ginkgoes, and conifers, with bennettitaleans and ferns dominating. This was followed in the Early Cretaceous by similar flora but with the swamp vegetation dominated by conifers. These plants apparently grew under a generally arid but seasonally wet frost-free climate. It was into this environment that the first flowering plants of the region migrated.

The object of this paper is to give an overview of the types of vegetation that occurred in the northern Rocky Mountain region before the appearance of flowering plants there. This region extends along the Rocky Mountains from central Colorado and Utah north into southern Alberta and British Columbia. The time span involved extends from the Early Devonian Siegenian, about 385 million years ago, to the Early Cretaceous Aptian, about 110 million years ago (Fig. 1). During the intervening 275 million years both the vegetation and the land it occupied changed radically, keeping pace with similar vegetational and land mass changes elsewhere in the world.

In fact, evidence of vegetation within the present northern Rocky Mountain region is spotty (Fig. 2). The best records of Paleozoic vegetation come from deposits in Europe and eastern and midwestern North America. Similarly, early Mesozoic, i.e., Triassic and Jurassic, floras are more abundant and better preserved in Europe and the southwestern United States than in the northern Rocky Mountains. It isn't until the Late Jurassic and Early Cretaceous that records within the region are as good as those found elsewhere. The Paleozoic and Mesozoic sites that are known in the northern Rocky Mountains, however spotty, show that the types of plants in the region are similar to those elsewhere and that they probably were organized in similar communities which occupied similar habitats. Thus, while the deposits within the region fail to provide conclusive evidence, they nonetheless permit inference based on our knowledge of nearby vegetation outside the area.

DEVONIAN

During the Early Devonian, the only part of the period for which we have evidence, the present northern Rocky Mountains was an area of lowlands and shallow seas along the western margin of the early land mass Laurussia (Bambach et al., 1980). This continent lay across the equator, extending from about 10° south latitude to about 40° north latitude, with the present northern Rocky Mountains situated at about 12° north latitude (Ziegler et al., 1981, fig. 7.5). Because of its position, the area had a tropical climate with warm temperatures and abundant rainfall throughout the year. This, combined with the location of the northern Rocky Mountains in the Devonian along the western coast of the continent where sharp changes in climate were moderated by ocean currents, resulted in what must have been ideal growing conditions.

Two deposits of Early Devonian plant fossils have been recorded in the Beartooth Butte Formation in the northern Rocky Mountains. The classic site at Beartooth Butte, Wyoming (Fig. 1A) has been known for over 50 years. Five taxa were described by Dorf (1933, 1934a, 1934b)

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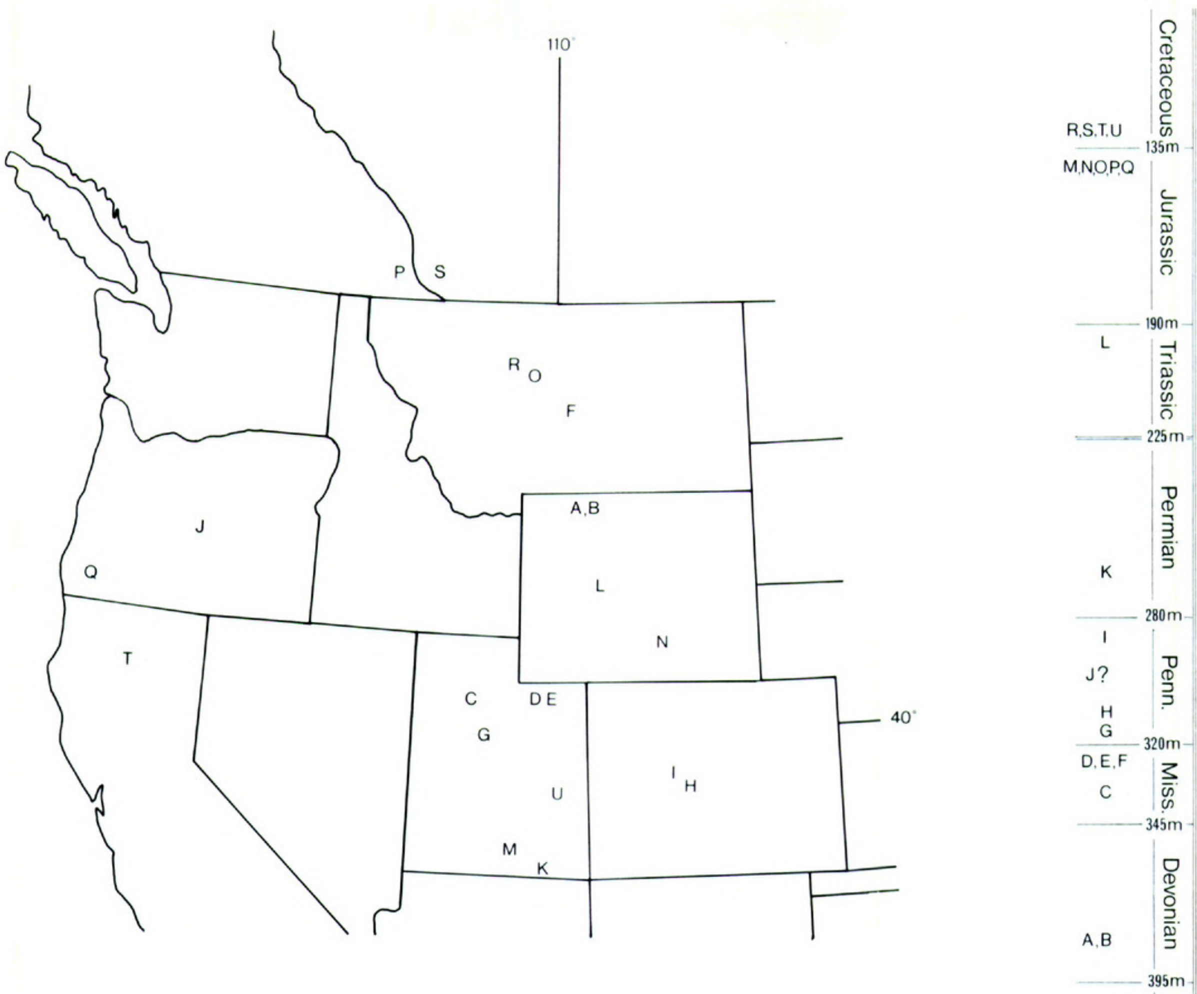

FIGURE 1. Index map and geologic time column showing the approximate locations and ages of the localities mentioned in the text.—A. Beartooth Butte, Early Devonian.—B. Cottonwood Gulch, Early Devonian.—C. Deseret Limestone, Utah, Early Mississippian.—D. Uinta Mountains, Late Mississippian.—E. Daggett County, Utah, palynoflora, Late Mississippian.—F. Bear Gulch Palynoflora, Late Mississippian.—G. Manning Canyon Shale, Early Pennsylvanian.—H. Weber Formation, Early Pennsylvanian.—I. McCoy Formation, Late Pennsylvanian.—J. Spotted Ridge Flora, Pennsylvanian.—K. Cutler Formation, Permian.—L. Wyoming Red Beds, Triassic.—M. Morrison Flora, Utah, Late Jurassic.—N. Morrison Flora, Wyoming, Late Jurassic.—O. Morrison Flora, Montana; Late Jurassic.—P. Kootenay Formation, Late Jurassic.—Q. Douglas County, Oregon, Late Jurassic.—R. Kootenai Formation, Early Cretaceous.—S. Lower Blairmore, Early Cretaceous.—T. Shasta Flora, Early Cretaceous.—U. Burro Canyon Formation and Cedar Mountain Formation, Early Cretaceous.

based on imprints of plant fragments. More recently, Hueber (1972) and Tanner (1982, 1983) described additional remains from the locality. The deposit is regarded as Emsian in age, about 375 million years old.

Tanner (1982, 1983) described fossils from the new Beartooth Butte Formation locality near Cottonwood Gulch (Fig. 1B) in northcentral Wyoming, about 50 km east of the original site (Fig. 1A). It is believed to be Siegenian in age, about 385 million years old, and thus somewhat older than the Beartooth Butte locality. Locating a second deposit in the region raises hope that these are not isolated occurrences and that further search will turn up more deposits.

Five taxa were originally described by Dorf (1933) from the Beartooth Butte locality. These include *Psilophyton wyomingense* Dorf for flattened branch systems bearing numerous spines (Fig. 2A, B), (?) *Psilophyton* sp. for an elongated presumed sporangium, *Bucheria ovata* Dorf (see note on change in name below) for narrow axes bearing numerous lateral sporangia (Fig. 2C, D), *Hostimella* sp. for flattened branch systems lacking spines, and (?) *Broggeria strobiformis* for a cylindrical strobiluslike structure. Hueber (1970)

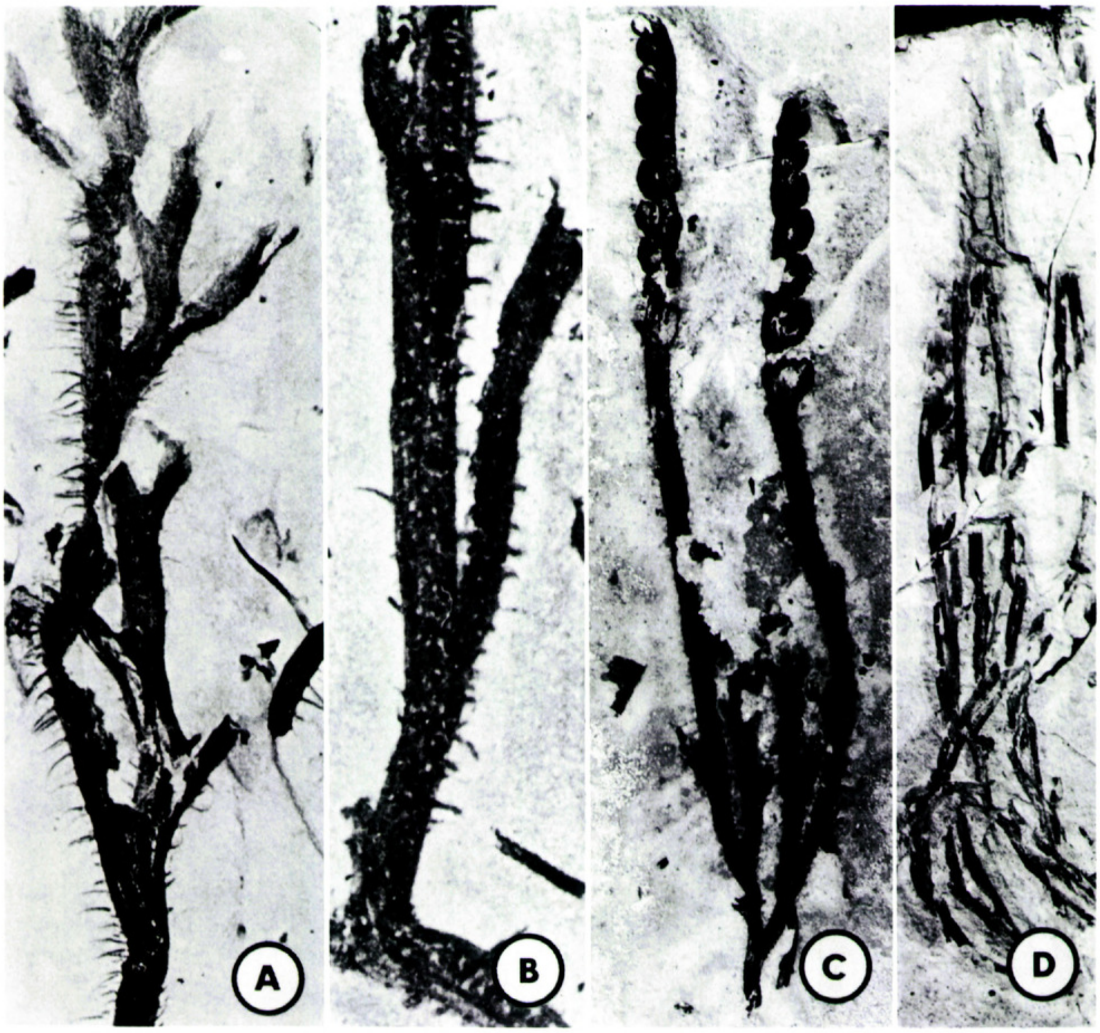

FIGURE 2. Examples of plant fossils from the Early Devonian Beartooth Butte Formation. A, B. *Psilophyton wyomingense* Dorf.—A. Holotype, from Dorf (1933, plate V, fig. 3), ×2.5.—B. from Dorf (1933, plate V, fig. 5), ×2.5.—C. *Rebuchia ovata* (Dorf) Hueber, USNM 168991B counterpart, ×1.3.—D. *Rebuchia ovata* (Dorf) Hueber, USNM 168992, ×1.3. (Figs. A, B reproduced by permission of the University of Chicago Press; Figs. C, D from photographs courtesy of F. M. Hueber.)

changed the name of *Bucheria ovata* to *Rebuchia ovata* and later (1972) described its vegetative axes linked with the fertile stems (Fig. 2C, D). These clearly show the affinity of the plant with the Zosterophyllophytina.

More recently Tanner (1982, 1983) described additional taxa from both sites of the Beartooth Butte Formation, bringing the total known to 14. Six of these are based on vegetative axes with attached fertile parts, five are known from vegetative axes alone, while one taxon is based on a sporangial pair. Present are rhyniophytes, trimerophytes, zosterophylls, and the early lycopsids *Drepanophycus* and *Leclercquia* (Tanner, 1983). There are also two taxa of undetermined botanical affinities.

Discussion. Even though the two localities occur in the same formation, palynological evidence indicates that they may be separated by as much as 20 million years. Such a gap is not apparent in the megafossils or the fish fauna preserved at both, although the Cottonwood Creek assemblage lacks definitive marker species (Tanner, 1983).

In comparison with other Early Devonian assemblages in North America and Europe, the Wyoming flora shows a surprising lack of trimerophytes and a richness in zosterophylls and early lycopsids. The new information about the floristic diversity of the Beartooth Butte Formation does not support the floristic zones proposed by Gierlowski (Ziegler et al., 1981) in which the western North America zone is characterized by relatively low generic diversity of two to six taxa per assemblage and a lack or restriction of zosterophylls. Including the unnamed sporangial pair and two morphotypes of sterile axes, the Wyoming assemblage has ten genera, three of which belong to the Zosterophyllaceae.

Early Devonian plants share an architectural plan that with few exceptions consists of relatively naked aerial branches up to a meter tall, which branch from rhizomes that bear adventitious roots or rhizoids (Gensel & Andrews, 1984). This is often interpreted as implying that these plants grew in marshy habitat. Since many of the known Early Devonian plant assemblages, and particularly the Wyoming sites, are from near equatorial paleolatitudes with equable temperatures and moisture, transpiration stress may not have been enough to require actual growth in standing water or even saturated soil as would be found in coastal marshes. Occurrence at more inland and upland sites may have been possible.

MISSISSIPPIAN

While movement of other continental plates between the Early Devonian and Mississippian was significant, the position of Laurussia, and thus the present northern Rocky Mountains, was relatively unchanged. There was an apparent increase in mountain building activity west of Laurussia and an increase in the amount of shallow seas and evaporite formation (Bambach et al., 1980, fig. 11). Much of the northern Rocky Mountains was an evaporitic basin in which limestone was deposited. However, some land was exposed within this zone of shallow seas, for plant remains are recorded as petrifactions in northwestern Utah (Fig. 1C; Tidwell & Jennings, 1986), as impressions and as pollen and spores in northwestern Utah (Fig. 1D, E; Arnold & Sadlick, 1962; Schemel, 1950), and as pollen and spores associated with exceptionally well-preserved fish and invertebrates at Bear Gulch (Fig. 1F) near Lewistown, Montana (Cox, 1986).

Deseret Limestone petrifactions. Tidwell & Jennings (1986) described a new lycopod, *Stansburya,* from the Early Mississippian Deseret Limestone near Grantsville, Utah, south of Great Salt Lake. Six stem specimens were included in a single carbonate concretion. The stems are about 1.4 cm in diameter and are dichotomously branched. Scalelike leaves are tightly appressed helically around the stems. None of the axes contain secondary tissues, and this led the authors to interpret the fossils as representing an herbaceous plant. Much remains to be learned about this new genus, but discovery of these fossils in the Deseret Limestone suggests that further search may be rewarding.

Daggett County, Utah, Palynoflora. Schemel (1950) reported several different types of pollen and spores isolated from a coal sample from Late Mississippian sediments in northwestern Utah (Fig. 1E). Over 90% of the palynomorphs belong to *Densosporites.* Similar spores have been found in Pennsylvanian age sediments both dispersed and in strobili of presumed arborescent lycopods (Taylor, 1981). Several other types of spores occur in the Utah coal in small amounts and suggest that sphenopsids, ferns, pteridosperms, and cordaitaleans grew in the vicinity.

Uinta Mountains Flora. The megafossil assemblage reported from a locality in the Uinta Mountains in northeastern Utah (Fig. 1D) is a small one based on poorly preserved imprints of vegetative remains (Arnold & Sadlick, 1962). *Archaeocalamites* was identified from pith casts. These show ribs continuous across the nodes rather than alternate as in *Calamites.* The occurrence of *Lepidodendron* is documented by imprints of characteristic stems, leafy twigs, and detached leaves. Defoliated axes, probably of seed fern fronds, identified as *Caulopsis,* are present, as are detached fern or seed fern pinnules of *Fryopsis* (formerly *Cardiopteris*). Lastly, *Rhodea,* frond portions of a seed fern characteristic of the Late Mississippian and Early Pennsylvanian, has also been identified.

Arnold & Sadlick (1962) interpreted the plant remains as representing streamside vegetation with fragments washed into an estuary or bay by river currents. The plant fragments are small and are imprints with occasional flecks of carbon. However, the siltstone matrix contains numerous flecks of black material that presumably represent macerated plant debris (Arnold & Sadlick, 1962).

The assemblage is regarded as Chesterian in age based on associated invertebrates (Arnold & Sadlick, 1962) and is correlated with the Late Visean or Early Namurian stages in Europe. The plant assemblage compares well with floras of similar age in the Appalachian trough.

Bear Gulch palynoflora. Palynomorphs are also preserved in rocks that have given up exceptionally well-preserved vertebrate and invertebrate fossils at Bear Gulch, near Lewistown, Montana (Fig. 1F; Melton, 1971). The palynomorphs (Cox, 1986) include: *Acanthotriletes, Anapiculatisporites, Chaetosphaerites, Convolutispora, Cyclogranulatisporites, Denosporites,* *Endosporites, Lycospora, Procoronospora, Punctatisporites, Raistrickia, Rotaspora, Savitrisporites, Tripartites,* and *Verrucosisporites.* The assemblage indicates a Chesterian age for the deposit and correlates with the Namurian A stage of Europe.

Furthermore, the palynoflora indicates that a diverse assemblage of ancient vascular plants inhabited the land that then surrounded the bay in which the Bear Gulch sediments were deposited. Although the correlation of the pollen and spore species found here with the plants that produced them remains uncertain, other species of some of these genera have been found in sporangia. By analogy the following megafossil forms may have been present: lepidodendrids (*Denosporites* and *Lycospora*), zygopterid ferns (*Convolutispora*), progymnosperms (*Cyclogranisporites*), cordaitaleans (*Endosporites*), filicalean ferns (*Raistrickia*), marattialean ferns (*Verrucosisporites*), and seed ferns (*Punctatisporites* and *Schulzospora*) (Kosanke, 1950; Millay & Taylor, 1979; Taylor, 1981).

Discussion. The two palynofloras and the Uinta Mountain megaflora combine to give solid evidence that vegetation similar to that occurring in eastern North America and Europe was present in the northern Rocky Mountains during the Late Mississippian.

PENNSYLVANIAN

By Pennsylvanian time Laurussia was connected to Gondwana in the process of forming Pangaea, but the present northern Rocky Mountains remained at about 10° north latitude (Bambach et al., 1980; Ziegler et al., 1981). More of the present land surface was covered by shallow seas than earlier, but sufficient land was exposed to support vegetation characteristic of the period.

Early Pennsylvanian vegetation is well in evidence in the Manning Canyon Shale flora from northern Utah (Fig. 1G). Similar remains, though not as extensive, are known from the Weber Formation in central Colorado (Fig. 1H). Late Pennsylvanian plant remains are known from the McCoy Formation in central and northern Colorado (Fig. 1I), and additional fossils have been reported from a locality in central Oregon (Fig. 1J) of uncertain stratigraphic placement within the Pennsylvanian.

Manning Canyon Shale. Plant fossils recovered from the Manning Canyon Shale in northern Utah (Fig. 1G) are well-preserved imprints that show considerable variety of plant form (Tidwell, 1962, 1967; Tidwell et al., 1974). While the strata were once thought to straddle the Mississippian–Pennsylvanian boundary, the flora best correlates with Early Pennsylvanian Namurian B or possibly late Namurian A stages of Europe.

The plants are like those of coal swamps to the east. Arborescent lycopods were numerous (Tidwell et al., 1974). *Lepidodendron* (Fig. 3D), *Lepidophloios,* and *Sigillaria* are known to have been present based on stem imprints. In addition, remains of the presumed reproductive organs of these plants are represented by *Lepidostrobus, Lepidocarpon,* and *Sigillariostrobus,* with *Stigmaria* (Fig. 3C) representing the underground parts and *Lepidophyllum* and *Cyperites* the foliage.

Both *Archaeocalamites* and *Calamites* (Fig. 3A) were present, as were three species of calamitalean foliage of the *Asterophyllites* type (Fig. 3B). A poorly preserved *Calamostachys* has been found, but details of its construction and the type of spores it produced remain unknown.

Ferns and seed ferns are represented by 11 species of foliage assigned to the genera *Adiantites, Cornypteris, Crossopteris* (Fig. 3F), *Diplothmema, Mariopteris, Neuropteris, Rhodea, Sphenopteridium, Sphenopteris* (Fig. 3E), and *Zeilleria* (Fig. 3G). In addition, the pollen organs *Aulacotheca* and *Telangium* are present, as well as seeds of *Cornucarpus, Holcospermum, Lagenospermum, Rigbycarpus,* and *Trigonocarpus.*

Cordaitales are represented by three species of foliage, a *Cordaianthus* (Fig. 3H), and six species of seeds.

Thus, the Manning Canyon Shale flora represents vegetation similar to that of coal swamps in the midwestern and eastern United States. The setting is interpreted as a coastal swamp community at the margin of a fresh or brackish water embayment that underwent several transgressive–regressive cycles (Tidwell, 1967). Some of the taxa have stratigraphic ranges suggesting a Mississippian age for the flora, but most indicate a Pennsylvanian age correlating with the Namurian B stage in Europe.

Weber Formation, Colorado. Scattered plant remains are known from the Weber Formation in Colorado (Fig. 1H), which Read & Mamay (1964) treated as Early Pennsylvanian Zone 6. *Lepidodendron johnsonii* Arnold (1940) represents the westward extension of typical coal swamp vegetation into central Colorado. The

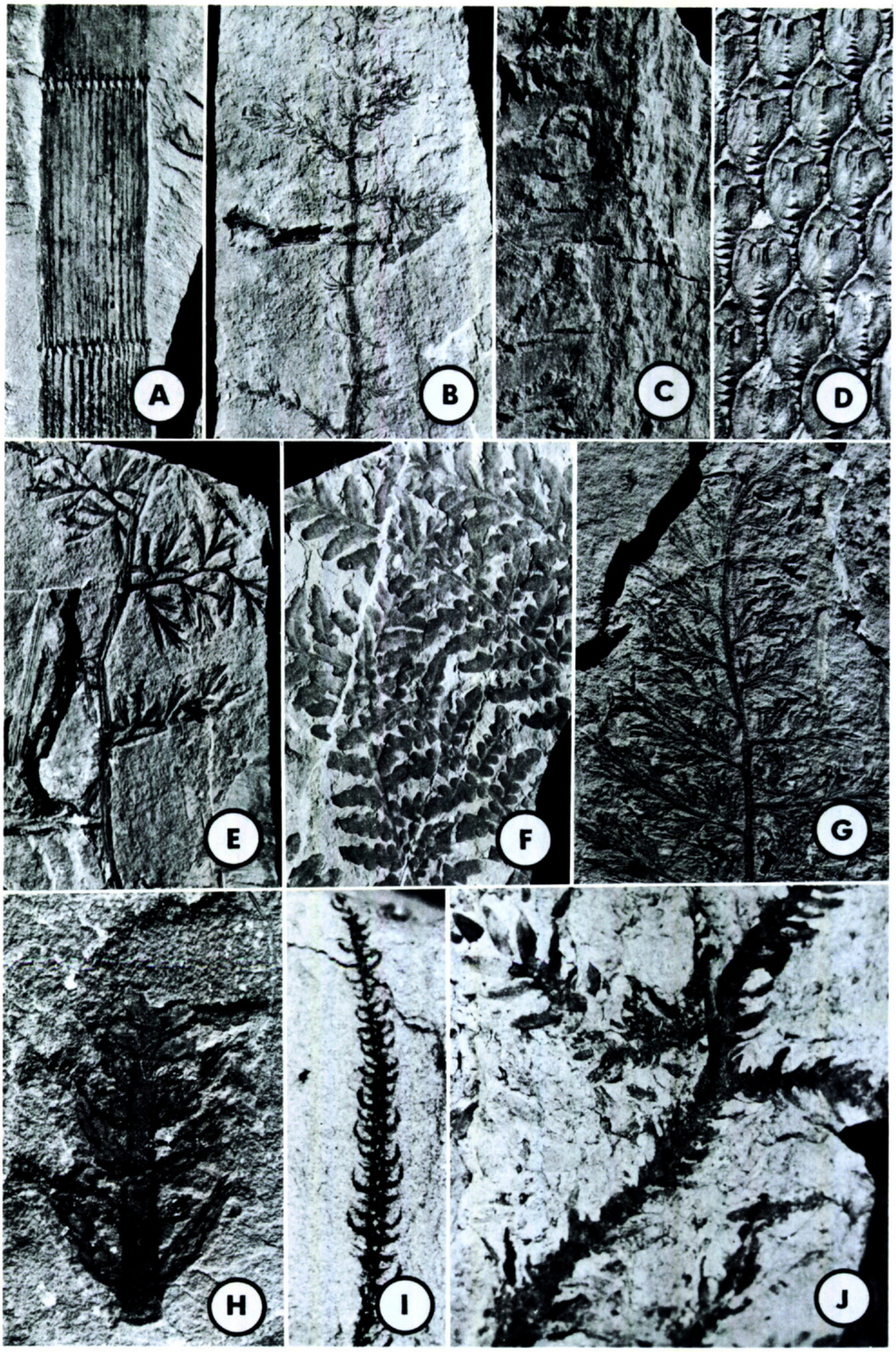

FIGURE 3. Example Pennsylvanian plant fossils from the northern Rocky Mountains.—A. *Calamites,* ×0.6.—B. *Asterophyllites,* ×1.0.—C. *Stigmaria,* ×0.5.—D. *Lepidodendron,* ×0.95.—E. *Sphenopteris,* ×0.7.—F. *Crossopteris,* ×0.6.—G. *Zeilleria,* ×1.1.—H. *Cordaianthus,* ×0.9.—I. *Walchia* sp., UMMP 22131, ×1.0.—J. *Lecrosia gouldii* Arnold, UMMP 21005, ×1.0. (Figs. A–H from photographs courtesy of W. D. Tidwell.)

small amount of coal in the Weber Formation suggests, however, that the coal swamp was of limited development and of short duration (Arnold, 1940). Read (1933) reported imprints of *Trichopitys whitei* from the Weber Formation and in 1934 added *Lepidostrobus, Stigmaria, Calamites, Asterophyllites, Adiantites, Dactylophyllum, Neuropteris, Sphenopteris, Diplomema, Cordaites,* and *Cordaianthus.*

McCoy Formation. Several localities within the McCoy Formation in Colorado (Fig. 1I) have yielded imprints of plant remains (Arnold, 1941). Examples are: *Calamites gigas* Brongn., *Odontopteris mccoyensis* Arnold, *Cordaites anguloso-striatus* Grand'Eury, *Samaropsis hesperius* Arnold, *Lecrosia gouldii* Arnold (Fig. 3J), *Walchia stricta* Florin, and *Walchia* sp. (Fig. 3I; Arnold, 1941). Arnold commented on the arid environment evidenced by the plants and by desiccation features in the rocks. Thus, the fossils may represent forms that grew on drier sites than the coal swamp represented by the plants from the Weber Formation. The McCoy Formation is regarded as Late Pennsylvanian Zone 10 by Read & Mamay (1964), and the drier setting may correlate with similar events in coal swamps to the east (Phillips et al., 1985) or may reflect some early uplift of the ancestral Rocky Mountains (Pfefferkorn & Gillespie, 1980).

Spotted Ridge flora, Oregon. The position of this plant megafossil assemblage (Fig. 1J) within the Pennsylvanian has not been determined; none of the fossils found to date in this flora are reliable stratigraphic indicators. The flora has the distinction of being the westernmost deposit of Paleozoic plants in the conterminous United States and is thought to have grown on an island arc or microcontinent that was some distance west of the North American craton (Pfefferkorn & Gillespie, 1980). The following taxa have been reported: an unnamed lepidodendrid branchlet, *Mesocalamites hesperius* (Arnold) Mamay & Read, *M. crookensis* Mamay & Read, *Mesocalamites* sp., *Phyllotheca paulinensis* Mamay & Read, cf. *Asterophyllites equisetiformis* (Schlotheim) Brongn., *Pecopteris oregonensis* Arnold, *Dicranophyllum rigidum* Mamay & Read, cf. *Cordaianthus longibracteatus* Florin, and cf. *Schizopteris trichomanoides* Goeppert (Arnold, 1953; Mamay & Read, 1956; Read & Merriam, 1940). Of these, *Mesocalamites hesperius, Phyllotheca paulinensis, Pecopteris oregonensis,* and *Dicranophyllum rigidum* are the most common, with the others represented in the collection by one to a very few specimens (Mamay & Read, 1956). The large size of the collection rules out sampling bias, and the numbers of specimens are thought to reflect plant abundances with reasonable accuracy (Mamay & Read, 1956).

Mamay & Read (1956) commented that the plant remains occur in sandstone and mudstone and show little evidence of transport. In fact, some *Calamites* stems appear to have been preserved in growth position. Most of the sediments are terrestrial in origin or some possibly originated in a marine or brackish water estuary. Thus, the vegetation represented does not appear to be directly comparable with any of the coal swamp communities of the eastern and midwestern United States. While the plants probably grew in a moist habitat, the latter was not a coal swamp.

Discussion. In addition to the fossil assemblages described above, fragmentary plant remains are known from subsurface samples in Montana (Pfefferkorn & Gillespie, 1980), and a small collection of fossils has been reported from Pennsylvanian sediments in Wyoming (Sando et al., 1975). These indicate that the type of vegetation present in eastern North America during the Pennsylvanian also occurred on exposed land surfaces in the present northern Rocky Mountain region. Nonetheless, Pfefferkorn & Gillespie (1980) recognized the vegetation of the region as belonging to a distinct floral province, the Cordilleran, of which *Crossopteris* (Fig. 3F) is a characteristic endemic.

PERMIAN

The Permian was a pivotal period of geologic time from the standpoint of plant evolution and from the types of vegetation that occurred. Toward the end of the Pennsylvanian, eastern and midwestern coal swamps reflect a change in community structure from domination by arborescent lycopods to domination by marattiaceous tree ferns (Phillips et al., 1985). This perhaps foretells of changes to come with breakup of Pangaea and the movement of continents poleward during the early Mesozoic.

Deposits of Permian age plant remains in the region are few, and none that are known provide the quantity of well-preserved fossils typical of earlier periods. One occurrence of Permian age plant remains has been reported by Mamay & Breed (1970) from the southern periphery of the present northern Rocky Mountains. They reported eight specimens from the Cutler Formation in southern Utah (Fig. 1K). From these are identified *Taeniopteris* sp., *Supaia rigida* White, *Protoblechnum bradyi* Mamay & Breed, and *Callipteris* sp. This represents the northernmost occurrence of *Supaia. Protoblechnum bradyi* is most similar to a species from eastern Asia and suggests the possible affinities of the Utah assemblage with the Asian flora (Mamay & Breed, 1970).

Similar remains are found in deposits in Texas, New Mexico, and Arizona, and we can only speculate that exposed land surfaces in the present northern Rocky Mountains supported similar plants.

Triassic

The only plant fossils reported from the Triassic in our region are an *Equisetum,* two species of *Pterophyllum,* two of *Zamites* and one *Podozamites* (Berry, 1924). These come from the so-called "red beds" in westcentral Wyoming (Fig. 1L). These fossils are similar to those found in the Chinle Formation in the Southwest (Ash, 1972; Daugherty, 1941) and suggest that a similar vegetation occurred in the northern Rocky Mountains.

Jurassic

During the Early and Middle Jurassic, the present northern Rocky Mountain region was covered by an inland sea in which marine limestone and sandstones were deposited (Imlay, 1984; Silverman & Harris, 1967). Uplift in the Nevadan orogenic belt south and west of the present northern Rocky Mountains resulted in a broad interior basin of low relief that was poorly drained by rivers northward and received sediments from highlands to the southwest and from the Canadian shield to the east (Brenner, 1983; Walker, 1974). The large size of the interior basin is reflected by the widespread deposition of shales and sands of the Late Jurassic Morrison Formation and its equivalents, which are recognized from southern Utah and Colorado north into southern Canada (Walker, 1974).

Geologic studies suggest that a somewhat arid but seasonally wet climate prevailed during the Late Jurassic (Walker, 1974), supporting a savannalike vegetation with many shallow lakes and swamps. There were probably dry periods during which water tables dropped and exposed accumulated debris to oxidation and decay. This may explain why plant fossils are not more abundant in the region (Walker, 1974).

Plant fossils are known from scattered localities throughout the region (Delevoryas, 1969; Tidwell, 1975), but large assemblages of remains that reflect vegetation are known only from central Montana (Fig. 1O) and southern Canada (Fig. 1P). South of the northern Rocky Mountain region are a number of occurrences of silicified remains from the Late Jurassic Morrison Formation (Fig. 1M). Some noteworthy examples are: *Hermanophyton kirkbyorum* Arnold (1962), a *Rhexoxylon*-like log, *Osmundacaulis wadei* Tidwell & Rushforth (1970), the only species of petrified osmundaceous rhizome known from the Jurassic of North America, as well as several different coniferous woods (Medlyn & Tidwell, 1975, 1979).

Within the region there are reports of foliage imprints of the two cycadophytes *Nilssonia nigricollensis* Wieland and *Zamites arcticus* Goeppert (Knowlton, 1916) and of petrified cycadeoid trunks (Delevoryas, 1960; Ward, 1905), both from Wyoming (Fig. 1N).

The most extensive Late Jurassic flora (Table 1) in the northern Rocky Mountains is that preserved in shales of the Morrison Formation in central Montana (Silverman & Harris, 1967; Brown, 1972). Plant remains have been found at six localities, one near Lewistown and the rest south of Great Falls near the town of Belt (Fig. 1O).

While three of the six localities in central Montana are close to one another, the most distant sites are over 170 km apart. *Zamites arcticus* (Fig. 4A), *Nilssonia* cf. *compacta* (Fig. 4D), *Podozamites lanceolatus* (Fig. 4G), and *Pityophyllum lindstromii* (Fig. 4F) occur at all six localities; and these taxa probably represent the dominants of the regional vegetation. *Pagiophyllum* sp. (Fig. 4F) and *Cladophlebis virginiensis* (Fig. 4C) occur at five of the sites and were thus also widespread. *Sagenopteris elliptica* (Fig. 4E), leaflets of a caytonialean seed fern, and *Coniopteris hymenophylloides* (Fig. 4B), foliage of a dicksoniaceous fern, are locally abundant at certain localities. Nowhere are remains of conifers as abundant as those of cycadophytes. Ginkgophytes (Brown, 1975) are present but rare. Thus, the vegetation appears to have been a relatively open one with scattered conifers, more closely spaced cycadophytes and tree ferns, occasional ginkgophytes, and an understory of ferns.

One of the localities clearly represents material

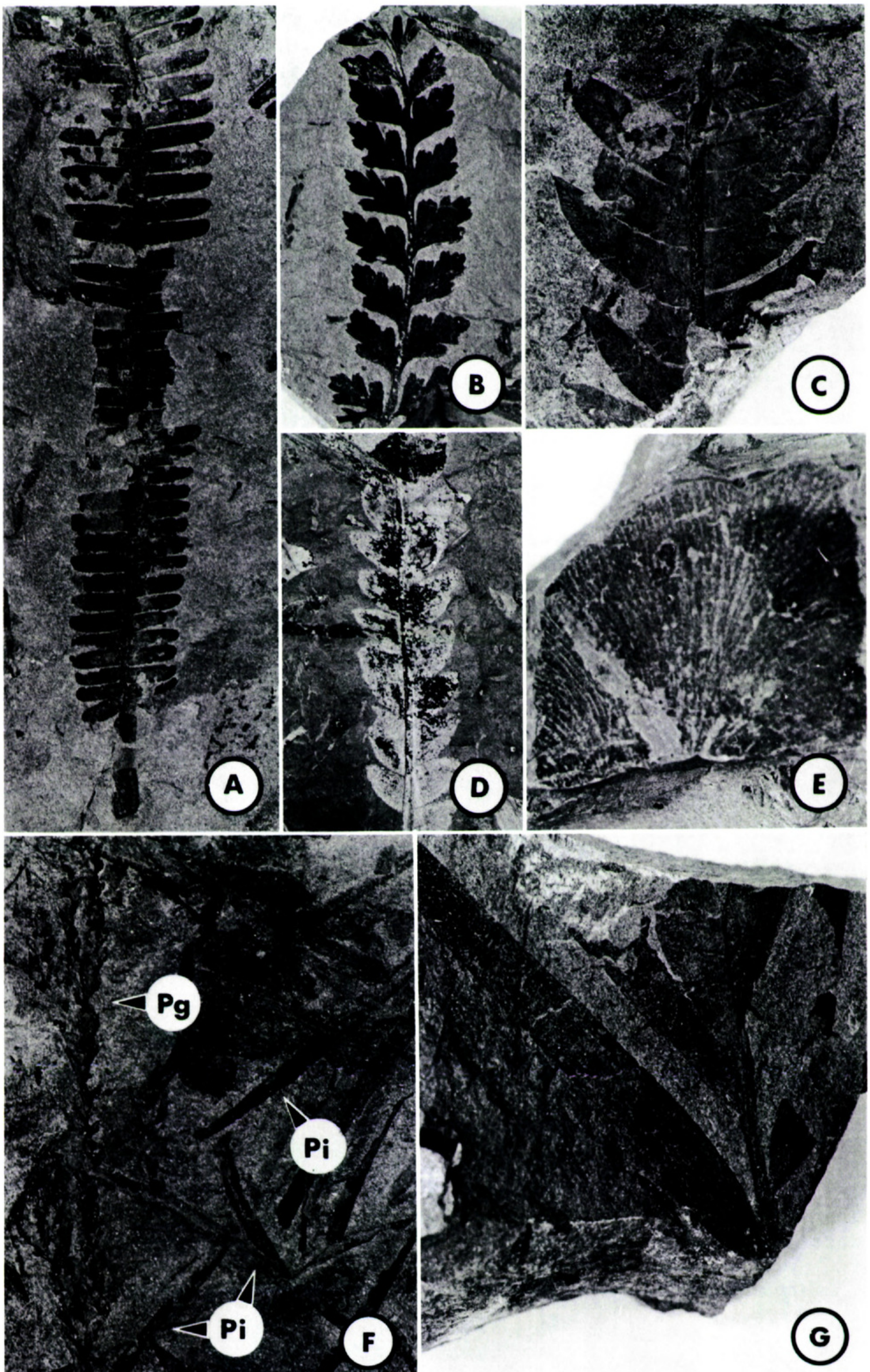

FIGURE 4. Typical plant fossils from the Late Jurassic Morrison Formation, Montana.—A. *Zamites arcticus* Goeppert, UMPM 1091, ×1.2.—B. *Coniopteris hymenophylloides* (Brongn.) Seward, UMPM 1092, ×1.5.—C. *Cladophlebis virginiensis* Fontaine, UMPM 1094, ×1.4.—D. *Nilssonia* cf. *compacta* (Phill.) Bronn., UMPM

washed in from surrounding areas, and others provide evidence of an extensive swamp and swamp margin community stable enough to result in a thin but mineable seam of low grade coal (Silverman & Harris, 1967). While coal formation indicates deposition of plant debris in water having oxygen low enough to retard degradation of remains by aerobic bacteria, some areas of the swamp were above water level and supported growth of marchantioid liverworts.

A similar vegetation extended northward into Canada (Fig. 1P) where megafossils are preserved in sediments of the Kootenay Formation (Bell, 1956), and microfossils are known from the Upper Vanguard Formation (Pocock, 1962). However, there is no reason to assume that a given swamp extended over that distance. Rather, there were probably many swamps that formed and disappeared over the several million years represented by the Late Morrison Formation and the Kootenay and Upper Vanguard formations in Canada. Thus, it is doubtful that direct correlation of these strata is possible.

Furthermore, the Canadian flora appears more diverse than that in Montana (Bell, 1956). While some of this apparent diversity is simply more species of the same genera and is probably due to taxonomic splitting, several genera occur in the Canadian flora that are absent in Montana. These are the fern *Klukia,* the seed fern *Czekanowskia,* the cycadophytes *Ctenis, Pseudoctenis,* and *Ptilophyllum,* and the ginkgophyte *Baieria* (Bell, 1956).

There is another Late Jurassic flora close to but outside the northern Rocky Mountain region (Fig. 1Q). Over 60 taxa have been reported from 20 localities in Douglas County, Oregon (Ward, 1905), and essentially no research has been done on this assemblage since it was treated in the *Status of the Mesozoic floras of the United States, 2nd paper* over 80 years ago. A modern study of these fossils has great potential to advance substantially our knowledge of Jurassic vegetation.

TABLE 1. Fossil plants from the Morrison Formation of central Montana.

Bryophytes
Marchantiolites sp.
Ferns and fern allies
Equisetum laterale Phillips
Hausmannia fisheri (Knowlton) Oishi & Yamasita
Coniopteris hymenophylloides (Brongn.) Seward
Adiantites montanensis (Knowlton) Brown
Cladophlebis alberta (Dawson) Bell
C. heterophylla Fontaine
C. virginiensis Fontaine
Cycadophytes
Nilssonia cf. *compacta* (Phillips) Bronn.
Zamites arcticus Goeppert
Cycadolepis spp.
Weltrichia sp.
Anomozamites sp.
Sagenopteris elliptica Fontaine
Ginkgophytes
Ginkgoites cascadensis Brown
G. pluripartita (Schimper) Seward
Conifers
Pagiophyllum sp.
Podozamites lanceolatus (Lindley & Hutton) Braun
Pityophyllum lindstromii (Heer) Nathorst
Pityocladus sp.
Schizolepis sp.

EARLY CRETACEOUS

The broad interior basin in which sediments of the Late Jurassic Morrison Formation were deposited persisted into the Early Cretaceous. Sedimentation was not continuous, however. It ceased for a time and then resumed. This cessation resulted in a disconformity overlain by a layer of coarse sandstone which occurs throughout the region (Walker, 1974). The disconformity is regarded as the boundary between the Jurassic and the Cretaceous (Brown, 1956).

Sometime after the resumption of deposition, plant remains were deposited. In central Montana this was not until what is believed to be the Aptian stage of the Early Cretaceous (LaPasha & Miller, 1984) even though invertebrates in the basal sandstone of the Kootenai Formation indicate a Neocomian age for those strata (Walker, 1974).

The plant-bearing layers of the Kootenai For-

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1093, ×1.7.—E. *Sagenopteris elliptica* Fontaine, UMPM 1095, ×2.7.—F. *Pagiophyllum* sp. (Pg) and *Pityophyllum lindstromii* (Heer) Nathorst (Pi), UMPM 1096, ×1.5.—G. *Podozamites lanceolatus* (Lindley & Hutton) Braun, UMPM 1097, ×1.4.

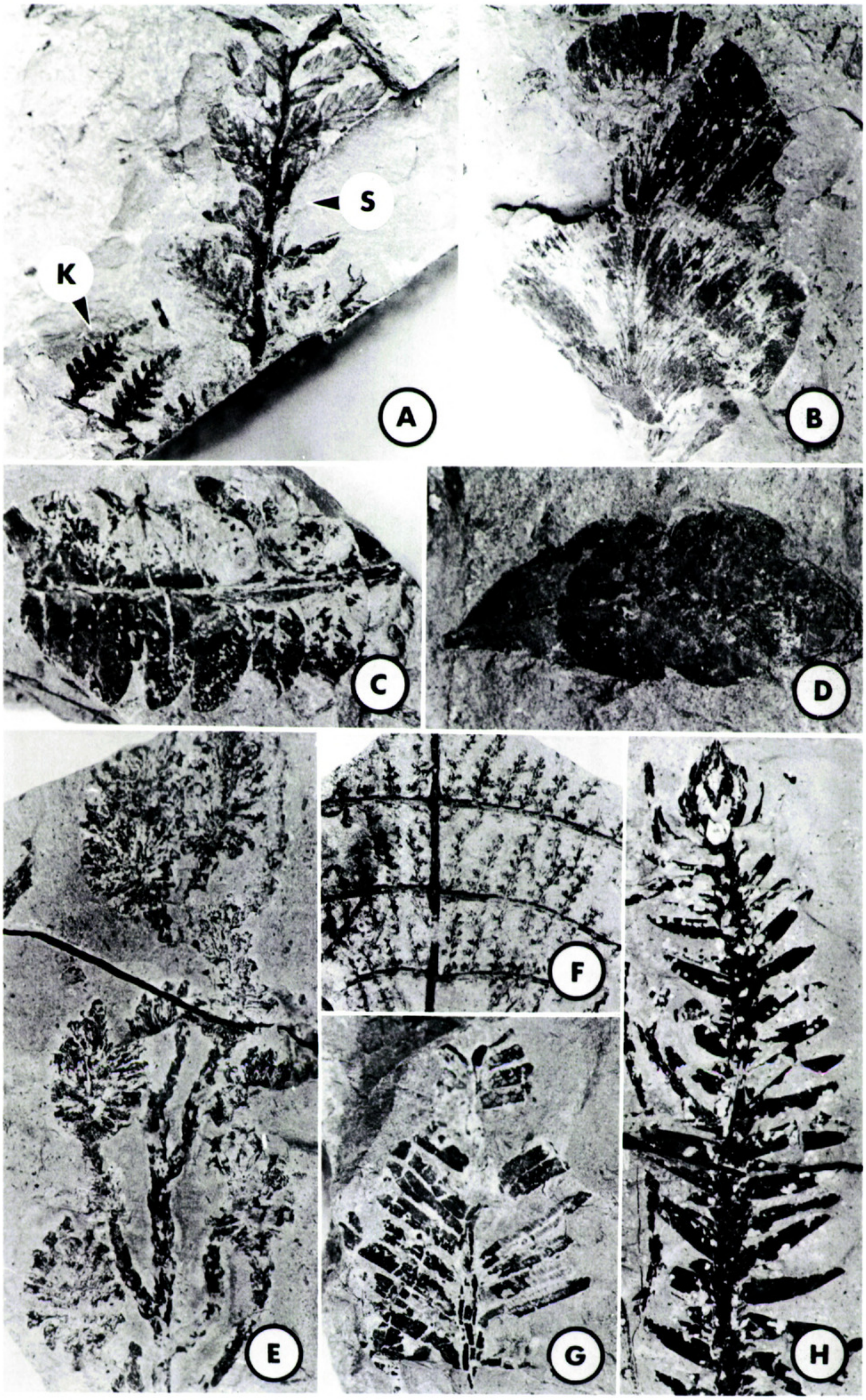

FIGURE 5. Typical plant fossils from the Early Cretaceous Kootenai Formation.—A. *Klukia canadensis* Bell (K) and *Sphenopteris latiloba* Fontaine (S), UMPM 1098, ×1.6.—B. *Sagenopteris williamsii* (Newberry) Bell, UMPM 1099, ×1.3.—C. *Cladophlebis oblongifolia* Fontaine, UMPM 1100, ×3.5.—D. *Sagenopteris mclearnii*

mation represent deposition of sediments and plant remains in poorly drained swamps that formed from infilling of lakes. Evidence suggests that the swamps contained standing water throughout the year. Some areas were above water level as indicated by the occurrence of liverworts, which were probably preserved in place (Brown & Robison, 1974, 1976; LaPasha & Miller, 1984, 1985). However, the water table at these sites was high enough to keep the soil saturated.

Certain plants (Table 2) probably grew in the swamps in which their remains were deposited. This is indicated by the occurrence of large, locally abundant remains in low diversity assemblages in a wide variety of sediment size classes (LaPasha & Miller, 1984). Fossils that fit this category are *Marchantiolites, Diettertia, Coniopteris simplex* (Fig. 5F), *Acrostichum, Sagenopteris williamsii* (Fig. 5B), and *Athrotaxites berryi* (Fig. 5E). Remains of other plants are generally found as abundant, small fossils occurring in high diversity assemblages and in narrow ranges of sediment size classes, particularly coarse sediments suggesting slight transport. Examples of these are *Coniopteris, Cladophlebis* (Fig. 5C), *Sphenopteris* (Fig. 5A), *Sagenopteris elliptica, S. mclearnii* (Fig. 5D), *Ginkgo* (Brown, 1975), *Elatides* (Fig. 5H), and *Elatocladus* (Fig. 5G). The same reasoning, combined with the relative scarcity of fossils, suggests that remains of *Equisetum, Klukia* (Fig. 5A), *Hausmannia, Zamites,* and other bennettitaleans were transported some distance, but exactly how far is unknown.

While certain species are common to both the Morrison flora and the Kootenai flora (Tables 1, 2), the two represent different types of vegetation. The Kootenai flora appears to have been dominated by conifers, especially *Athrotaxites,* with bennettitaleans relatively rare (Miller & LaPasha, 1983, 1984). Ferns formed the understory; and although *Sagenopteris* is abundant at certain localities, the stratum of vegetation it occupied remains unknown.

The Kootenai Formation is widespread in Montana and has equivalents in adjacent states, but plant fossils are known in abundance only near Great Falls. Permineralized cycadeoid trunks have been reported from the Burro Canyon For-

TABLE 2. Fossil plants from the Kootenai Formation of central Montana.

Bryophytes
Marchantiolites blairmorensis (Berry) Brown & Robison
Megzgeriites montanensis LaPasha & Miller
Diettertia montanensis Brown & Robison
Sphenopsids
Equisetum montanensis LaPasha & Miller
E. cascadensis LaPasha & Miller
Lycopsids
Minerisporites sp. A
Minerisporites sp. B
Pteropsids
Coniopteris hymenophylloides (Brong.) Seward
C. simplex (Lindley & Hutton) Harris
Klukia canadensis Bell
Hausmannia montanensis LaPasha & Miller
Acrostichum longipennis Fontaine
Cladophlebis constricta Fontaine
C. inclinata Fontaine
C. oblongifolia Fontaine
C. oerstedii (Heer) Seward
C. virginiensis Fontaine
Sphenopteris brulensis Bell
S. latiloba Fontaine
S. mclearnii Bell
S. goeppertii Dunker
Arcellites sp.
Parazollopsis cascadensis LaPasha & Miller
Cycadophytes
Sagenopteris elliptica Fontaine
S. mclearnii Berry
S. williamsii (Newberry) Bell
Zamites arcticus Goeppert
Pseudocycas douglasii LaPasha & Miller
Ginkgophytes
Ginkgo pluripartita (Schimper) Heer
Conifers
Athrotaxites berryi Bell
Elatides curvifolia (Dunker) Nathorst
Elatocladus dunnii Miller & LaPasha
E. montanensis Miller & LaPasha
Masculostrobus montanensis Miller & LaPasha
Conites sp.

←

Berry, UMPM 1101, ×2.3.—E. *Athrotaxites berryi* Bell, UMPM 894a, ×1.8.—F. *Coniopteris simplex* (Lindley & Hutton) Harris, UMPM 1102, ×1.3.—G. *Elatocladus montanensis* Miller & LaPasha, holotype UMPM 914, ×1.7.—H. *Elatides curvifolia* (Dunker) Nathorst, UMPM 907, ×1.4.

mation (Fig. 1U) in Colorado (Brown, 1950). *Frenelopsis varians* and *Tempskya* are known from the Cedar Mountain Formation (Fig. 1U) in Utah (Tidwell et al., 1976), although the upper parts of both of these formations are regarded by some as younger than the Kootenai Formation (Ash & Read, 1976; Tschudy et al., 1984).

An extensive assemblage of plant remains (Fig. 1S) is known from the Lower Blairmore Formation of Alberta (Bell, 1956), and the Kootenai flora compares best with this assemblage. The Lower Blairmore flora is of special interest because it contains the earliest convincing flowering plant megafossils in the region, leaf imprints identified as *Sapindopsis angusta* (Heer) Seward & Conway (Bell, 1956). While it is possible that the sites these leaves come from are in fact somewhat younger than the Kootenai flora, it is also possible that the leaves indeed represent some of the earliest flowering plant migrants into the region.

Another extensive Early Cretaceous assemblage is known from outside the northern Rocky Mountain region, but it is nonetheless of special interest. Like the Jurassic plants from Douglas County, Oregon, those from the Shasta Series in northern California (Fig. 1T) represent a large and diverse assemblage that has received no further work since the flora was described over 80 years ago (Ward, 1905). These fossils should be the subject of a modern study.

SUMMARY

This report deals with the record of terrestrial vegetation in the northern Rocky Mountains prior to the appearance of flowering plants. The span of time involved covers the Early Devonian 385 million years ago to the Early Cretaceous about 110 million years ago. Before the Late Jurassic the evidence, with few exceptions, is discontinuous and spotty. At best, it permits inferences about the type of vegetation present in the region.

Recent work on plant remains from the original and a second collecting site in the Early Devonian Beartooth Butte Formation of northern Wyoming has added considerably to the forms known. Represented are rhyniophytes, trimerophytes, zosterophylls, and early lycopsids. These compare well with plants of similar age known from eastern North America and western Europe, making the Beartooth Butte assemblage one of the better known Early Devonian floras of the world.

Several deposits of Late Mississippian and Early Pennsylvanian fossils show that vegetation like that of coal swamps of Appalachia and the North American interior occurred in the northern Rocky Mountain region as well. The latter vegetation was composed of arborescent lycopsids, arborescent sphenopsids, tree ferns, seed ferns, and cordaites like that of the Interior-Appalachian Province to the east, but the presence of unique forms is grounds for treating the western vegetation in the distinct Cordilleran Province. Similarly, because of species unique to it, the Spotted Ridge flora of Oregon is treated as representing the Oregonian Province.

Our record of vegetation is spotty in sediments of the Permian, Triassic, and Early and Middle Jurassic in the northern Rocky Mountains. By comparison, evidence of Late Jurassic and Early Cretaceous vegetation is relatively abundant and informative. Much of the present northern Rocky Mountains was then a broad interior basin of low relief that supported an open savanna type of vegetation interspersed with shallow lakes, swamps, and rivers. During the Late Jurassic conifers appear to have been widely scattered, cycadophytes and ferns were more closely spaced, and ginkgophytes and caytonialean seed ferns were more rare and occasional. This vegetation presumably grew under somewhat arid conditions with seasonal wet periods. Temperatures were equable, and there is no evidence of freezing conditions.

While the interior basin persisted into the Early Cretaceous and was the site of deposition of plant fossils, the vegetation represented had an entirely different aspect. Conifers were abundant and dominated the vegetation, with cycadophytes rare and widely scattered. Ferns formed the understory and caytonialean seed ferns were locally abundant. Rainfall and temperatures were like those of the Late Jurassic.

There is no evidence of flowering plants in the flora of the Early Cretaceous Kootenai Formation in Montana, which is regarded as Aptian in age. However, imprints of flowering plant leaves are present but rare in sediments of presumably equivalent age in adjacent Canada. Whether or not the sediments containing the leaves are somewhat younger than Aptian, as some believe, these imprints represent some of the first flowering plants in the northern Rocky Mountain region.

Thus, angiosperms made their first appearance in the northern Rocky Mountains toward the end

of the Early Cretaceous, and it is important to know about the vegetation that occurred on the land as they migrated into the region. Unlike problems confronting the first land plants in the Early Devonian that colonized relatively barren land, the establishment of flowering plants required their successful competition with vegetation that was already in place. This is indeed a remarkable feat; however, this survey shows that replacement of one form of vegetation by another has been the rule throughout the 275 million years discussed in this paper.

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