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A flora from the Dakota sandstone formation (Cenomanian) near Westwater, Grand County, Utah

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**A FLORA FROM THE DAKOTA SANDSTONE
FORMATION (CENOMANIAN)
NEAR WESTWATER, GRAND COUNTY, UTAH**

by

Samuel R. Rushforth



**BIOLOGICAL SERIES — VOLUME XIV, NUMBER 3
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A FLORA FROM THE DAKOTA SANDSTONE FORMATION (CENOMANIAN) NEAR WESTWATER, GRAND COUNTY, UTAH

by

Samuel R. Rushforth¹

ABSTRACT

A Cretaceous (Cenomanian) flora from the Dakota Sandstone Formation near Westwater, Grand County, Utah contains an admixture of ferns and angiosperms. The ferns of this flora are representative of an older Jurassic-Wealden vegetational type, whereas the angiosperms are typical of the modern vegetational type. Species of *Gleichenia* and *Matonidium* and *Astralopteris*

coloradica represent the dominant forms in this flora.

The Westwater flora contains fourteen genera including nineteen species and one variety. New species described from this flora include *Asplenium dakotensis*, *Coniopteris westwaterensis* and *Ilex serrata*.

INTRODUCTION

A fern-angiosperm flora from the Cretaceous (Cenomanian) Dakota Sandstone Formation has been under study for some time. This flora was collected from an ash seam and sandstone in the Dakota Sandstone Formation from Rabbit Valley, Grand County, Utah, and along the road and surrounding areas between U.S. Highway 50 and Westwater, Grand County, Utah.

This Dakota flora is significant for three reasons. First, it contains several new species of fossil plants. Second, it extends the known

distribution patterns of many previously described species. The Westwater flora is one of few paleofloras which illustrates an admixture of an older Jurassic-Wealden floristic type with a modern angiospermous floral type. Third, this flora provides new information on a time of the earth's history when angiosperms were expanding from a position of little floristic importance to a position of dominance in Cretaceous and later floras.

GEOLOGICAL BACKGROUND

LITHOLOGICAL CHARACTERISTICS.— Two early workers, Marcou (1864) and Capellini (Capellini and Heer, 1867), considered the Dakota Group of Meek and Hayden (1856, 1861) to have been deposited in fresh water. This determination was based primarily upon the included leaf flora. However, Hayden (1867) stated that together with F.B. Meek, he had collected well-preserved marine invertebrate remains mingled with the leaves of the Dakota Group. Hayden concluded that the Dakota Group was marine in origin. This conclusion was adhered to by Lesquereux (1874, and others) and by subsequent workers.

Lesquereux (1874) presented an excellent discussion on the probable origin of the Dakota Group. Based upon studies of recent depositional facies and comparing them to the Dakota, Lesquereux stated: "They are beach formations, like those in progress at the present time along the shore of the North Sea, in Holland and Belgium, where the widely extended muddy shores are formed of a soft substance of the red color." Lesquereux further mentioned that the presently forming North Sea beaches are characteristic and similar to Dakota beds by being composed of sands borne by the sea intermixed with muds borne by the sea inter-

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mixed with muds borne by nearby rivers. In mentioning that the leaves of some species often exhibit a clumped rather than a random distribution in Dakota strata, Lesquereux (i.e.) postulated:

A distribution of this kind can result only from the proximity of the trees from which the leaves have been derived, and confirms the opinion that the formation of the Dakota group is the result of muddy flats whose surface, raised perhaps in hillocks above water-limits, and already solid ground, was cut like an immense swamp, here and there interspersed by rare groups of trees and bushes.

In support of Lesquereux's hypothesis, it should be mentioned that within the Dakota Sandstone Formation there are deposits indicative of fresh and brackish water. Evidence for this comes from lignite seams, fossil assemblages, stratigraphy and lithology. These sediments could have been deposited in embayments, estuaries, and on flood plains (Chaney, 1954; Repenning and Page, 1956.). However, because of frequent lignite beds and carbonaceous shales, and the great number of leaf impressions, which, due to their excellent state of preservation, do not appear to have been transported for any great distance, these deposits appear to have been laid down in paludal environments close to the sea, similar to those described by Lesquereux (1874).

In discussing the nomenclature used in connection with the Dakota Sandstone (as used by Meek and Hayden, 1856, 1861), Tester (1931) preferred the useage of the term Dakota Stage. His reasoning for the application of this term sheds some light on the nature of the beds referred to the Dakota Sandstone. Tester stated in part:

Geologic events which are of considerable magnitude, and which have some effect over a large area, or which constitute a normal progression of rocks, are considered responsible for the deposition of rocks comprising a stage. The widespread marine advance, with its shoreline variations due to minor retreats and advances of the waters and to the lands being built out into the oceans, or the migration of faunas and shifting of ocean currents, all have their effect on the character of the rocks. The rocks deposited under such conditions on an extensive scale, as they were during Dakota time, are classed as a stage. It might be said that a stage is indicative of a set of conditions of rock deposition rather than of a distinct lithological or paleontological division.

From Tester's discussion, several important concepts are apparent. First, the geologic event

responsible for the deposition of the Dakota Sandstone was of considerable magnitude and had effect over a large area. Second, this geological event was the extensive marine advance during Dakota times. Third, the Dakota Sandstone Formation indicates a set depositional characteristics rather than conforming to a distinct lithological or paleontological division.

From the foregoing discussion, a working definition of the Dakota Sandstone Formation may be given. This formation is a Cretaceous time transgressive sequence of marine, fresh or brackish water, clastic sediments of various colors (with red, yellow, and white being common) deposited under fluvial and paludal conditions, often with interbedded lignite, shale and ash sequences. This formation can not be defined on the basis of paleontological similarities, although included fossil plants may be correlated to some extent. Strata comprising the Dakota Sandstone Formation are related throughout their geographical extent in that they were similarly deposited as the result of the invading Cretaceous sea. The Dakota Sandstone Formation exhibits continuity throughout much of the western and midwestern United States, although sediments of this formation from different regions need not be of the same age due to the deposition of Dakota strata at the edge of a coastline which changed with time.

Tester (1931) pointed out that a wide variety of names had been used for discussing Dakota strata including Dakota Group (originally used by Meek and Hayden in 1861 in referring to their Formation No. 1 of 1856), Dakota Series, Dakota Stage, Dakota Formation, Dakota Sandstone, and Dakota without any additional term. Tester (1931) preferred the use of Dakota Stage which he used synonymously with the term group, since he restricted the usage of group for the rocks of an entire era.

The term group or stage usage is useful in delimiting the rocks of more than one closely related formation when the distinction between them is either difficult or unnecessary. However, later workers (Jenney, 1899; Darton, 1905; Stanton, 1905) showed that the Dakota Group of the Black Hills and Rocky Mountain regions could be divided into Lower and Upper Cretaceous formations; these workers restricted the Dakota Sandstone to formational status. Furthermore, the original Dakota Group from the midwestern United States is similar stratigraphically and floristically (although some variation may be noted in floras from different regions) to the restricted Dakota Sandstone

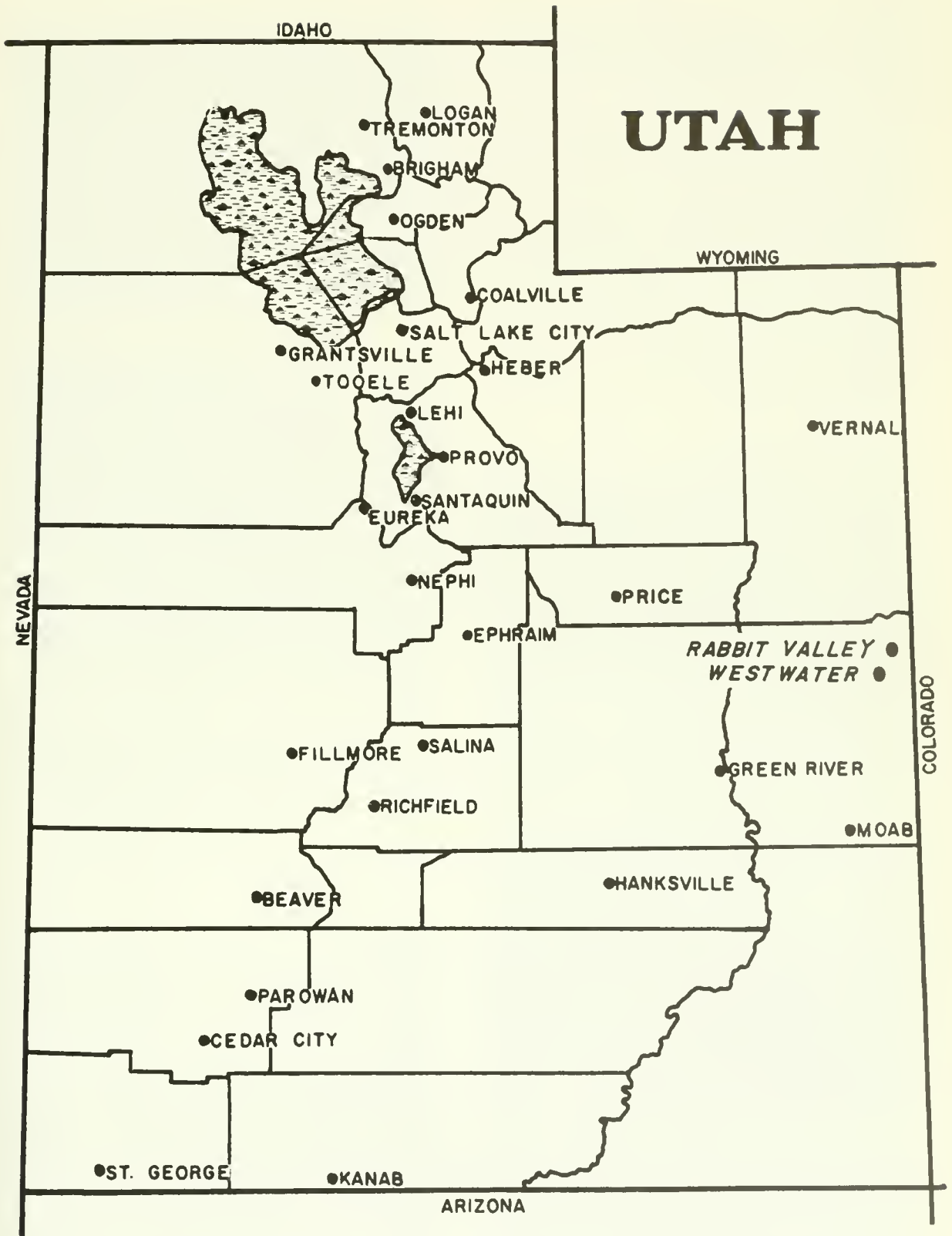


FIG. 1. Index map of collecting localities.

Formation of the Black Hills and Rocky Mountain regions. In light of this, the term Dakota Sandstone Formation will be used by the author for discussion of Dakota strata.

GEOLOGY.—Stanton (1905) in working with the Jurassic Formation and its relationship with the Comanche Series and the Dakota Formation in Southern Colorado, New Mexico, and Oklahoma, demonstrated that the Dakota Sandstone of this region, as originally defined, contains both Lower and Upper Cretaceous strata. Thus, Stanton pointed out that the true Dakota Sandstone Formation of these widely separated regions overlies Lower Cretaceous deposits which overlie the Morrison Formation.

Similar conditions have been observed in several other regions of the western United States. In Montrose County, Colorado, the Dakota Sandstone Formation occupies a position between the Jurassic Morrison Formation (McElmo Formation of Coffin, 1921) and Upper Cretaceous Mancos Shale Formation. Careful examination of these strata (Coffin, 1921) indicated that the Jurassic Morrison Formation is overlain by a Lower Cretaceous sequence. This sequence was given formational status by Coffin (1921) who named it the Post-McElmo Formation. Stokes (1948) changed the name of this Lower Cretaceous sequence to the Burro Canyon Formation.

Plants of this Lower Cretaceous sequence in Colorado were studied by Brown (1950). Brown concluded that floristic evidence agreed with the findings of Coffin (1921). A Lower Cretaceous flora was described by Brown from

the Burro Canyon Formation, and a somewhat atypical Dakota flora was described from the Dakota Sandstone Formation. This Dakota flora is atypical in that the incidence of ferns with angiosperms is high.

Jurassic and Cretaceous stratigraphy near Westwater, Grand County, Utah, is similar to that of Montrose County, Colorado. The Jurassic Morrison Formation from this region of Utah is overlain by the Lower Cretaceous Cedar Mountain Formation. This formation is correlated to the east with the Burro Canyon Formation. However, no plants have been collected from the Cedar Mountain Formation of Grand County. This Lower Cretaceous formation is overlain by the Dakota Sandstone Formation (Plate 3.) This formation from this region is composed of three lithological units. The basal unit is a massive, buff-colored sandstone of approximately thirty feet in thickness. This unit is overlain by a shale-coal-sand sequence which is approximately thirty feet thick. Fossil plants collected near Westwater are obtained from this unit. This shale-coal-sand unit is in turn overlain by a massive buff-colored sandstone unit. This is the uppermost unit of this formation near Westwater, and it is approximately thirty to forty feet in thickness. This formation is overlain by the Upper Cretaceous Mancos Shale Formation. Most leaf compressions collected from the Dakota of this region are obtained from an ash seam approximately forty to forty-five feet beneath the *Gryphaea newberryi* zone in the overlying Mancos Shale.

THE AGE OF THE DAKOTA SANDSTONE

Much of the earliest work concerning the Dakota Sandstone Formation was concerned extensively with the age of these rocks. Briefly, the Dakota was the first considered as a Cretaceous group (Meek and Hayden, 1856, 1858). This interpretation was refuted by Hawn (1858) who supposed that Dakota strata belonged in the Triassic. Heer (1859, 1861) proposed that the Dakota was of Tertiary age, and Marcou (1855) stated that the original Dakota was composed of rocks of both Tertiary and Jurassic age. Later work (Marcou, 1864; Capellini and Heer, 1867) demonstrated that Dakota rocks indeed belong to the Cretaceous, as originally postulated by Meek and Hayden. This age determination has been adhered to by all follow-

ing workers, and the only subsequent controversy has been concerning the proper Cretaceous epoch to which Dakota strata should be assigned.

An accurate ascertainment of the age of the Dakota Sandstone Formation (whether early or late Cretaceous) has been complicated by two problems. The first concerns a poor usage of the term, "Dakota flora." This term has been used loosely by some workers, and as pointed out by Berry (1920), "Any Cretaceous formation containing dicotyledonous leaves and known or thought to be older than the Benton . . ." was said to contain a Dakota flora. In other words, Dakota flora became an adjectival term rather than delimiting a flora which had been ob-



FIG. 2. A. Southeast view down canyon towards Westwater, Grand County, Utah. The Dakota Sandstone Formation forms the hills and slopes in the foreground and is exposed along the roadcut. Original collections from the Dakota Sandstone of this region were made in the roadcut (A). The Mancos Shale Formation overlies the Dakota in this region. B. Close-up of collecting site (A) in Fig. 1. This site yielded the best collections of fossil plants from this area.

tained from the Dakota Sandstone. This problem became so acute that Berry (1920) further stated, "It has become increasingly clear of late years that Dakota flora was not a unit and had no precise stratigraphic value." Berry (1920) proposed that in order to eliminate this problem, a true Dakota flora may be defined as "meaning thereby the equivalent of that of the Woodbine Formation of Texas, and those of corresponding age elsewhere. . . ." This interpretation, however, has one inherent difficulty. That is, it does not allow for the possibility that within the same formation, fossil assemblages may differ sufficiently to render their comparison with the flora from another formation difficult. This may result either from a non-random geographical distribution of fossils

within the formation or from evolutionary changes in plant communities over a period of time synchronous with deposition.

An alternative to the proposal of Berry (1920) is that in delimiting a true Dakota flora, only plants from the Dakota Sandstone Formation be considered. That is, the only valid application of the term Dakota flora can be in the discussion of plants from the Dakota Sandstone *sensu stricto*. It is neither valid nor prudent to delimit a Dakota flora, merely in the sense of a Cretaceous dicotyledonous flora, from any other geological entity.

This suggestion, however, leads to a discussion of the second problem which is somewhat less easily treated. It is that the Dakota Sandstone is a time transgressive formation and

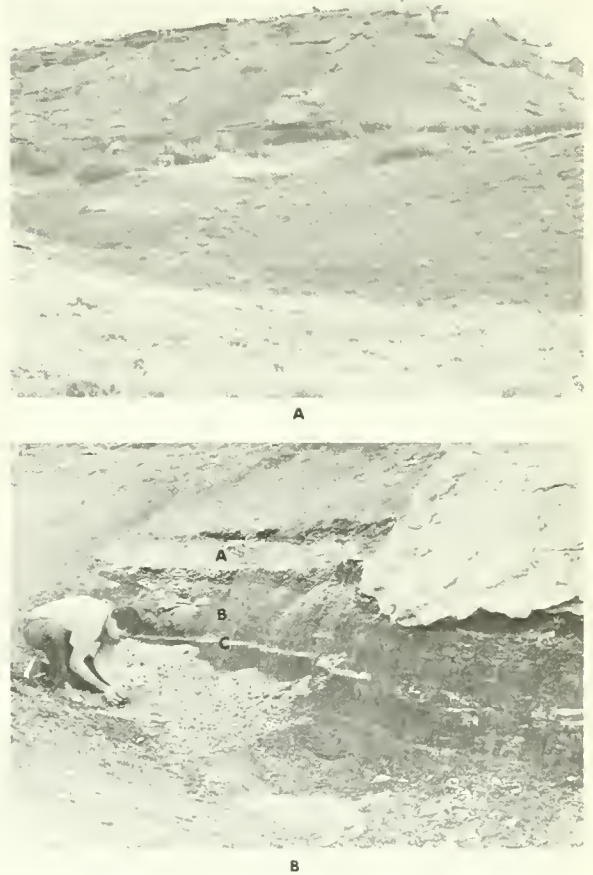


FIG. 3. A. Overview of Dakota Sandstone Formation showing massive upper sandstone unit resting upon shale-coal-sand unit. The arrow points to a collecting excavation. B. Close-up of excavation in Fig. 1 illustrating lithology of shale-coal-sand unit. The upper coal (B) and unfossiliferous ashes (A and C) have been removed in this excavation exposing the fossiliferous ash upon which the worker is kneeling.

was deposited over a range of time that witnessed a vast floristic change in the dominant vegetation of the earth. That is, although all formations are time transgressive, many are deposited within a period of time wherein little change in the contemporaneous flora or fauna occurred, and therefore the included fossils of that formation would be expected to exhibit homogeneity. However, the Dakota Sandstone Formation was deposited over a period of time when the predominant vegetational type of the earth changed from a fern-gymnosperm alliance typical of the older Mesozoic to an angiosperm dominated flora typical of the Late Cretaceous, Tertiary, and present times. Therefore it is possible to collect within this formation, fossil assemblages which appear to be indicative of different ages. This is particularly the case when the Dakota Sandstone Formation from west and east of the Rocky Mountains are compared, and the floras from the western portion of this formation appear to be older than their counterparts from the east. Further discussion on both microfloral and megafloreal evidence bearing on this situation will be considered later.

Earliest detailed estimates (Lesquereux, 1874, 1883, 1892) concerning the age of the Dakota Sandstone Formation placed it as Cenomanian. This concept has been generally adhered to since that time, although some geologists have disagreed with it based chiefly upon stratigraphy. In connection with this, Twenhofel (1920) assigned the Dakota to a Lower Cretaceous age. Tester (1931) in studying the type locality of the Dakota Sandstone considered it to be older than Cenomanian and placed Washita-Kiowa-Mentor-Dakota rocks of Kansas at the base of the Cretaceous, with the Dakota being at least as old as the Mentor Formation of this region (midAlbian). However, the conclusions of Twenhofel and Tester were drawn based upon stratigraphic evidence alone and are not substantiated by floristic evidence.

Cobban and Reeside (1952) assigned the Dakota Group to various ages ranging from early Aptian to middle Cenomanian. However, the lower members of this group (Lakota Sandstone and Fuson Shale of Darton, 1905) were assigned to ages earlier than late Albian, and the restricted Dakota Sandstone Formation was considered by these workers to range from late Albian through middle Cenomanian.

Berry (1920) was opposed to the determination of Twenhofel (1920) that the Dakota Sandstone Formation was of Lower Cretaceous age. In this paper Berry cited floristic evidence



FIG. 4. A. Roadcut exposure of Dakota Sandstone Formation. The upper massive sandstone unit (A) of this formation from this region rests upon the middle shale-coal-sand unit (B). C delimits an unfossiliferous ash, and D represents the chief fossiliferous ash seam. B. Contact between Dakota Sandstone and Cedar Mountain-Morrison Formation. The Dakota forms the slope and ledge (A) which rests upon the slope of the Cedar Mountain-Morrison Formation (B).

that the Dakota was of Upper Cretaceous (Cenomanian) age and could be correlated with the Woodbine Formation of Texas. However, Berry (1922) later considered the Woodbine Formation to be of Turonian age, although still to be correlated with the Dakota Sandstone Formation. This determination was based upon a detailed analysis of the flora of the Woodbine Formation from Lamar County, Texas, wherein it was noted by Berry that this flora had three species in common with Turonian floras of Europe.

MacNeal (1956) restudied the Woodbine flora from collections made in Denton County, Texas. Based upon examination of more and better material, MacNeal disagreed with the age determination of Berry, and assigned the

Woodbine flora to a Cenomanian age. MacNeal did, however, agree with Berry (1920) that the Woodbine flora is closely related to the flora of the Dakota Sandstone.

A Cenomanian age for the Woodbine was also agreed upon by Stephenson (1952) based upon a study of the invertebrate fauna from this formation.

Brown (1952) agreed with Berry (1920) that the Woodbine flora is very similar to the flora of the Dakota Sandstone of Kansas. One apparent difference, however, was the conspicuous absence of gymnospermous species in the Woodbine flora. This difference was eliminated by MacNeal (1958) in his Woodbine studies and recently by Hedlund (1966) in his palynological studies on the Red Branch Member of the Woodbine.

Hedlund (1966) also confirmed the Cenomanian age of the Woodbine Formation. In this paper, Hedlund treated many species of fern and gymnosperm palynomorphs indicating that this segment of the flora, even though poorly represented by macrofossils, nonetheless, represents an important floristic component of the Woodbine.

Pierce (1961), Hall (1963), and Agasie (1967) in reporting on microfloral assemblages from the Dakota Sandstone Formation of Minnesota, Iowa, and Arizona, respectively, assigned this formation to a Cenomanian age. The present author agrees with this Cenomanian assignment of the Dakota Sandstone Formation, although in part this formation may be of late Albian age (Cobban and Reeside, 1952).

A CONCEPT OF A DAKOTA FLORA

It was recognized from earlier plant collections from the Dakota Sandstone Formation that plants from this formation were rather closely related to plants growing on the earth at the present time. Fossils from these collections were representatives of dicotyledonous families and genera most of which are still represented in the earth's flora. As Meek and Hayden (1859) commented, Dakota fossils "belong to a higher and more modern type of dicotyledonous trees. . . ."

As more collections were made from this formation throughout the midwestern United States from such diverse localities as Kansas, Nebraska, North Dakota, South Dakota, Wyoming, New Mexico, etc., a floristic picture of the Dakota began to evolve. This picture was essentially that of Meek and Hayden (1859), and later of Lesquereux (1874, 1883), that the flora of the Dakota was essentially a modern type of flora without many fossils representing antecedent floristic types. As mentioned by Lesquereux (1874) only one specimen collected to that time could be referred to the Cycadophyta (*Pterophyllum* (?) *haydenii*), and even this reference was doubtful. Conifers were rare from these early studies, both in number of species and number of specimens, and represented a very limited portion of the flora. Likewise, ferns were few in number and appeared to make up a very limited part of the total Dakota vegetation.

On the other hand, even from earliest studies, it was apparent that plant fossils refer-

able to the modern angiospermous vegetational type were exceedingly common and comprised by far the dominant part of Dakota vegetation. Indeed, Lesquereux (1874) noted that dicot species represented in the Dakota floras could be referred to "genera to which belong most of the living arborescent plants of this country (North America) and of our present climate."

When these facts were considered by Lesquereux (1874), he wrote a section dealing with the disconnection of Dakota floras with antecedent types. In this chapter, Lesquereux wrote:

. . . it is evident that the flora of the Dakota Group is as widely disconnected from that of the Jurassic, even of the Lower Cretaceous, or as distinctly original, as are the flora of the Carboniferous compared to that of the Devonian, or the Permian types compared to those of the Cretaceous.

Later studies (Lesquereux, 1883, 1892) indicated that although ferns and gymnosperms were more common than indicated by earliest studies, these floral types were still present in limited numbers. Thus, Lesquereux (1892) in his final work on the flora of the Dakota Group summarized the relative importance of the different components of this flora. Of a total of 460 species identified from the Dakota Sandstone flora, Lesquereux recognized six species of ferns, representing 1.3 percent of the total flora; twelve cycadean species representing 2.6 percent; fifteen species of conifers representing 3.5 percent; and 437 species of angiosperms representing 92.6 percent of the total flora.

In the light of the above discussion, it may be summarized that the prevailing early concept of the flora of the Dakota Sandstone Formation was that it was essentially a modern flora composed principally of dicotyledonous leaves related to modern arborescent genera. The apparent paucity of antecedent floral types (Jurassic-Wealden ferns and gymnosperms) common in earlier Mesozoic floras is noteworthy, although somewhat enigmatic to some early paleobotanists. It must be remembered, however, that this concept grew out of studies by Lesquereux and others of macrofossils from the midwestern portion of North America and was drawn without the aid of data from two sources to be added later. These two sources are microfloral analysis of the Dakota, and megafloal analysis of this formation from many new localities, especially those further west than original collection sites.

As more data accumulate concerning the Dakota Sandstone Formation, particularly data dealing with regions west of the Rocky Mountains, it becomes clear that a valid concept of a Dakota flora must be modified somewhat from early views. While this early concept is essentially for megafloal assemblages from that portion of this formation east of the Rocky Mountains, it does not fit well for the formation as a whole. In this respect, it is significant that the incidence of species representative of the antecedent Jurassic-Wealden vegetational type, particularly Middle Mesozoic ferns, is much higher in megafloal assemblages from several localities in the Dakota Sandstone Formation west of the Rocky Mountains. That is not to say that dicotyledonous species are not present at these localities. They are not only present, but they are directly related to the dicotyledonous species from this formation further to the east. Indeed, at some of these collection sites, angiospermous fossils comprise the dominant floristic component of the fossil assemblage. However, from many localities in the Dakota Sandstone Formation in Utah, Colorado, and Arizona, fossils representative of the older antecedent vegetational type are relatively more important than their counterparts east of the Rockies, both in number of species and number of specimens present. Indeed, at some western localities, representatives of this ancient floral type dominate the floral assemblage.

The Dakota flora from Montrose County, Colorado, represents an admixture of representatives of the Jurassic-Wealden vegetational type with modern angiospermous forms. Early

work by Cockerell (1916) and Berry (1919a) indicate the presence of matoniaceous ferns from this region. Ferns referable to this family are representative of an earlier floral type, as they are common in the European Wealden and other Middle Mesozoic strata. Matoniaceous ferns are uncommon from rocks younger than Early Cenomanian, and are unknown from Tertiary strata. Brown (1950) made further studies on the plants from several localities in the Dakota of Montrose County. This author also treated matoniaceous ferns, as well as ferns of the family Gleicheniaceae, which are also indicative of a preangiospermous floral type. Several other ferns from the Dakota of this region were also discussed by Brown. The author has had occasion to study the Dakota collections from Montrose County reported by Brown. It is apparent that the fern families Matoniaceae and Gleicheniaceae were very well developed in this region during Dakota times. Indeed, ferns of these two families are so common that they make up the predominant part of the fossil vegetation, although they are collected in association with angiospermous forms which, as mentioned by Brown (1950),

... include chiefly species that occur in the large flora described by Lesquereux, Newberry and others from the brownish Dakota Sandstone of Kansas and Nebraska, in the Woodbine Formation of Texas, the Dakota of the Black Hills, South Dakota, and the Upper Cretaceous rocks of Greenland.

Therefore, during Dakota times in southwestern Colorado, the vegetation was composed of typical Dakota angiospermous species, but with a large proportion of plants representative of a more ancient floristic type.

A somewhat similar situation existed in Grand County, Utah, during Dakota times. Similar to the fossils from Colorado, the Dakota flora from this part of Utah is comparable to Dakota floras from other localities. However, it is both significant and apparent that the flora from the Grand County Dakota Sandstone Formation is very much dominated by ferns representative of the older Jurassic-Wealden vegetational type. Indeed, it is almost impossible at some localities in Grand County to crack open a rock without exposing at least one specimen of a fern representative of the families Matoniaceae or Gleicheniaceae. Dicotyledonous species are reduced both in number of species and number of specimens present. Gymnosperms represent a rather minor part of the flora from this region as far as number of species present, although quantitatively they are represented by large amounts

of silicified wood. Therefore, the Grand County Dakota flora may be characterized as a fern-dominated, fern-angiosperm-gymnosperm alliance, similar to what could be expected during a time which directly preceded the much discussed "population explosion" of angiosperms during Cenomanian times (Seward, 1927).

This same vegetational aspect has been observed by the author from several other Dakota localities of the western United States. Floras from Longhouse Valley and Kayenta, Navajo County, Arizona, both exhibit characteristics discussed above in connection with Colorado and Utah Dakota floras. That is, ferns representative of the old Jurassic-Wealden vegetational type dominated the Dakota vegetation of these regions, and angiosperms represented a rather limited vegetational type.

The Dakota Sandstone Formation from Coal Canyon, Coconino County, Arizona, as discussed by Ágasie (1967) exhibits similar floristic characteristics. Microfloral analysis from this region indicates that Dakota vegetation was composed of a fern-angiosperm alliance with a minor gymnospermous component. Fern spores represent the dominant microfloral component, especially forms related to the family Selizaceae. This fern family is often represented in pre-angiospermous floras (Harris, 1961), and preliminary collection of megafossils from the area also indicates the presence of many ferns related to an old Jurassic-Wealden vegetational type.

In addition to the data presented above, it has been shown by Pierce (1961) and Hall (1963)

from microfloral analysis of two localities in the Dakota from Minnesota and Iowa respectively, that ferns and gymnosperms represented more important components of the eastern Dakota flora than indicated by the megafossil record. With respect to this, Pierce reported 24 species of palynomorphs representative of angiospermous species, 36 species of gymnospermous palynomorphs, and approximately 20 species of fern palynomorphs. Based on this, Pierce postulated that angiospermous species are not as important in this formation as indicated by the megafossil record. However, a more precise conclusion would be that rather than the angiosperms representing a less important floral component, the gymnosperm-fern floral component represents a more important part of the flora than previously thought.

From the above discussion, a more accurate concept of the flora of the Dakota Sandstone Formation as a unit may be formed. In western America, the Dakota flora is a fern-angiosperm alliance with a relatively small gymnospermous component. At several localities west of the Rockies, ferns dominate the megafloora as well as the microflora. To the east, this flora changes character somewhat, becoming an angiosperm-dominated flora with a fern and gymnosperm component. This fern-gymnosperm component was originally thought to be of very minor importance in the eastern Dakota, but recent microfloral studies (Pierce, 1961) have demonstrated that this component of Dakota vegetation was more important than had been previously supposed.

PALEOECOLOGY

The plants from the Dakota Sandstone Formation near Westwater are preserved in a light tan ash layer from five to ten inches in thickness. This layer was deposited directly upon a coal seam and is overlain by another. These plants are extremely well preserved with many of the leaf compressions illustrating cuticle, vascular tissue, and reproductive structures. In addition, many of these fossils are disposed in the strata in such a manner as to indicate that the plants were preserved in growth position, suggesting that deposition of the ash was rapid.

The ash layer is uniform in color and composition throughout, with the exception of a one- to two-inch portion directly beneath the upper coal seam. Laterally throughout the ash, distribution of the plants is differential. Thus, within a local area, most of the plants are

of the same species, and laterally the species change abruptly within a distance of a very few feet. In certain outcroppings of the ash, dense mats of leaves are found within a relatively small area. These mats are normally found in the lower portion of the ash, and if one traces them laterally, they appear to follow definite channels indicating possible stream channels.

Peels of the foliage of the channel areas were prepared to aid in identifying the angiosperms. On one of these peels a well-preserved diatom and several spores of either algal or fungal origin were found, indicating the likelihood that the depositional environment of matted leaves in these areas was aquatic.

More detailed study of the fossiliferous ash brought to light several other important factors.

In all areas near Westwater where the plant-bearing ash has been examined, the contact between the ash and the underlying coal seam is very sharp and easily distinguished (Fig. 5). In addition, the lowermost portion of the ash contains large numbers of root and rhizoid-like structures, often in such profusion as to form dense mats of these structures (Fig. 6). Leaves are scarce in the lower portion of the ash with the exception of poorly preserved, often broken specimens. One of the more important identifiable fossils common in this region of approximately one inch in thickness is the rhizome of *Equisetum lyelli* Mantel with attached tubers.

Immediately above this rhizome region is a horizon containing numerous well-preserved leaf impressions. This region contains foliage belonging almost exclusively to the three fern genera *Matonidium*, *Astralopteris*, and *Gleichenia*. This zone is approximately five to eight inches thick and is literally full of beautifully preserved specimens.

At the upper portion of this dense foliage region, the color and composition of the ash changes somewhat (Fig. 5). The ash becomes noticeably darker in color and somewhat silty-carbonaceous in composition. Many of the fossils found in this region differ taxonomically from those found lower in the ash. While the three genera *Matonidium*, *Astralopteris* and *Gleichenia* are still present as leaf impressions in this region, they are not as dominant as they were in the lower portions of the ash.

Plant fossils in this upper region represent several different genera. The greatest taxonomic diversity in the Westwater flora occurs within this zone. Significantly, *Equisetum* rhizomes reoccur in this upper region after being noticeably rare in collections from the middle portion of the ash.

The contact between the ash and the upper coal seam is not as sharp as the lower contact (Fig. 5). From the point where the ash becomes carbonaceous in nature and diversity in the flora appears, the ash layer gradually becomes more carbonaceous until within a distance of one to two inches it grades into a well-defined lignitic coal.

Several explanations for the above described phenomena have been considered and rejected. The sharp contact between the lower coal and ash indicates that the ash fell directly upon a coal swamp and preserved the plants that were growing at the time. Further evidence in support of this is noted when it is recalled that at the base of the ash a region rich in rootlike



A



B

FIG. 5. A. Collecting site exhibiting characteristic lithology of Dakota Sandstone near Westwater. The upper massive sandstone unit forms the cliff, and the weathered shale-coal-sand sequence forms the talus slope in the foreground. B. Close-up of fossiliferous ash seam illustrating rhizome region (1), leaf region (2), and diversity region (3).

structures, rhizomes, partially decomposed leaves, stream channels, etc., occurs. Above this is a region extremely rich in matoniaceous, gleicheniaceus, and astralopteroid fossils which appear to be in growth position. This evidence would tend to support the hypothesis that the ash was deposited rapidly upon a coal swamp which was composed chiefly of ferns of the three genera *Matonidium*, *Gleichenia* and *Astralopteris*. If this indeed occurred, the rhizome region would contain mostly rhizomes and roots of these three genera.

The upper portion of the ash where the diversity appears contains plants which may represent forms that began to grow upon the previously deposited ash. That is, the plants of the upper part of the ash represent forms that repopulated the swamp following ash deposition. The likely reason for the diversity in taxonomy of these plants is that they are forms

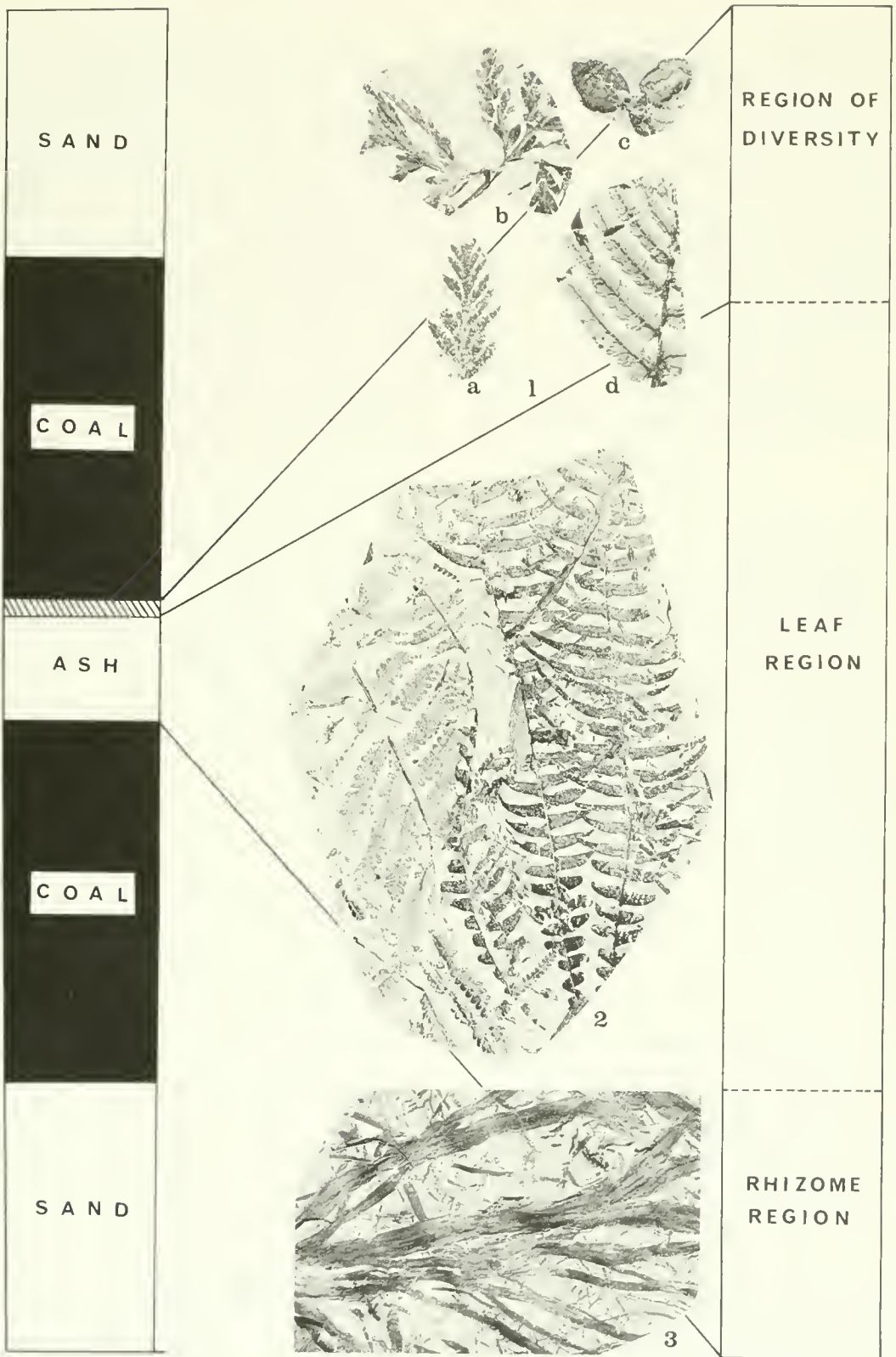


FIG. 6. 1. Representative forms found in region of diversity: *Coniopteris* (a); *Asplenium* (b); *Equisetum* (c); and *Cladophlebis* (d). 2. Single specimen collected from leaf region illustrating *Gleichenia* and *Matonidium*. 3. Rhizome and rootlike structures collected from rhizome region.

from seral communities in secondary succession. It is likely that the climax vegetation growing in the coal swamp was a *Matonidium-Gleichenia-Astralopteris* association. Further evidence in support of this conclusion was obtained by the author from study of macerations of the lower and upper coals. Even though palynomorphs from these coals were poorly preserved, it was evident that matoniaceous fern spores were the dominant microfossils from both, indicating that species of *Matonidium* were prevalent both prior to and subsequent to ash deposition.

To test the above hypothesis, thin sections of the ash were made from the three discussed regions (rhizome region, leaf region, and diversity region). The ash of the rhizome and leaf

regions shows no difference when examined microscopically. However, the ash of the region of diversity is much more silty and carbonaceous than the ash of the two lower regions. This evidence would tend to support the theory that the plants of the rhizome and leaf regions were preserved in one ash fall. The silty carbonaceous region (region of diversity) represents a region of increased silt and carbon deposition due to the initial deposition of enough soil to support plant growth, population of this soil by new plants (secondary succession), and subsequent carbon deposition as these plants died and were deposited. These plants probably represent stages in seral succession toward the climax coal swamp vegetation of *Matonidium*, *Gleichenia* and *Astralopteris*.

PALEOCLIMATE

It is sometimes possible, particularly when working with late Mesozoic and Tertiary paleofloras, to reconstruct the presumed climate under which these fossil floras existed. Two basic methods used in determination of paleoclimates are the comparison of fossil genera to their nearest living relatives existing under known climatic conditions (extrapolation through uniformitarianism), and the determination of dicotyledonous leaf characteristics and comparison of these characteristics with those found in species growing in known climatic conditions.

It was first recognized by Bailey and Sinnott (1915) that leaves of arborescent dicotyledonous species growing in tropical regions exhibit a higher incidence of entire margins than do their counterparts growing under non-tropical conditions. These authors pointed out that there is a correlation between the number of entire margins of arborescent dicot species to climatic conditions under which these species exist. Thus, from seventy to ninety percent of tropical woody dicot species exhibit entire leaf margins, whereas only twenty to forty percent of woody dicots of cold temperature regions exhibit entire margins. Further studies (Sinnott and Bailey, 1915; Chaney and Sanborn, 1933) pointed out that large leaves, thick leaves, compound leaves, and leaves with attenuated apices are more abundant in tropical regions, decreasing proportionately into temperate regions.

Chaney (1954) applied these characteristics in analyzing 200 species of leaves from the Dakota flora in an effort to determine the paleoclimate of Dakota times. He noted that 73 percent of the leaves from this flora exhibit entire

margins, 44 percent are over 10 cm long, and 74 percent are thick in texture. From these data, Chaney concluded that the Dakota flora lived under conditions "more subtropical than temperate." Chaney further pointed out that 72 percent of Dakota leaves exhibit camptodrome venation patterns which, according to Chaney, also indicates that the climate during Dakota times was tropical or subtropical in nature. Chaney suggested that this angiosperm flora existed in a lowland forest, and that some highland regions were to be found nearby.

Pierce (1961) discussed the Cretaceous climate of Minnesota based upon a fossil pollen assemblage from this region. He concluded that the flora could be characterized as a coniferous rain forest growing under warm temperate climatic conditions similar to conditions found presently in the Pacific Northwest of the United States or the coastal regions of eastern Asia. This was based upon an unusually high frequency of gymnospermous pollen encountered which, Pierce argued, could not have come from nearby upland regions. Based upon this information, Pierce agreed with Lesquereux (1874) who suggested that the Dakota flora was similar to the modern flora growing between 30° and 45° north latitude. However, Lesquereux never assumed that the Dakota flora was a coniferous forest, or that it even contained a large number of gymnosperms. Indeed, just the opposite was the case as Lesquereux (1874) discussed the noteworthy absence of gymnospermous and fern species from the Dakota flora. The work of Pierce, however, does point out that both the gymnospermous and the fern

component of the Dakota flora are larger than indicated by megafloreal analysis.

Hedlund (1966), in considering the pollen flora from the Red Branch Member of the Woodbine Formation which is closely related to the flora from the Dakota Sandstone, compared component members with their modern counterparts and concluded that the climate of this region during Woodbine times was warm temperate to tropical. His determination was based upon the high incidence of palynomorphs related to modern plants which are presently distributed chiefly in warm temperate-subtropical regions.

A Dakota pollen flora from Coal Canyon, Arizona, indicates subtropical to tropical climatic conditions for this region during Dakota times (Agasie, 1967). This is based upon relatively high frequency of palynomorphs from genera related to extant taxa growing under wet tropical or subtropical conditions. The relatively high frequency of gymnospermous pollen present in this flora indicates that well-drained, low upland regions existed near the lowland swampy depositional basins.

Several species and hundreds of specimens of *Matonidium* are present in the Westwater flora. These ferns are probably the best climatic indicators present in this flora. These fossils are related to the fern family Matoniaceae which is presently a monotypic (Bower, 1923) or ditypic (Holtman, 1947) family containing the genus *Matonio*. This genus is extremely limited geographically and climatically in the present world's flora and grows only in the humid tropical upland regions of the Malayan Peninsula. As mentioned by Mahabale (1954) matoniaceous ferns are among a select group of ferns that are accurate climatic indicators.

Gleicheniaceae ferns are well represented in the Westwater flora, although these fossils are somewhat less valuable than matoniaceous ferns as climatic indicators. Of 80 extant species the majority are of tropical distribution, although some species extend well into southerly latitudes (Bower, 1923).

The fern family Dipteridaceae is also repre-

sented in the Grand County flora. This family is monotypic containing the genus *Dipteris*, which is presently restricted to five species all of which are found in the Indio-Malayan region of the world (Bower, 1923). Thus, this family also may be cited as an excellent example of a tropical or subtropical climatic indicator.

In addition to the above evidence, most observed angiospermous fossils exhibit entire leaf margins and two species show long attenuated apices (drip points) which are thought to function in facilitating the run off of excess moisture. As mentioned previously, these characteristics are found more frequently in tropical regions, and thus, the Dakota angiosperms from Westwater substantiate the conclusion that the Westwater Dakota flora grew under subtropical to tropical conditions.

Topography at the time of deposition of the shale-coal-sand unit of the Dakota Sandstone Formation of this region was likely a broad swampy mudflat near the shore of the Cenomanian Sea. Pockets of dense vegetation composed basically of ferns and *Equisetum* developed in some of these regions, often accumulating enough volume, under proper conditions, to comprise a large component of the coal deposits which occurred between sandy or shale sequences. Well-drained highland areas existed nearby with gymnosperms and angiosperms present. Streams ran from the upland regions into the lowland swampy areas carrying leaves and other debris in various stages of decomposition. The vegetative deposits from these streams (gymnosperm and angiosperm leaves, and likely wood) probably formed a large portion of the coals, with the remainder being added from the ferns and associated plants of the fern swamps.

Following a period of time when deposition occurred as outlined above, the shoreline of the sea changed, and the shale-coal-sand sequence in the Dakota of the Westwater region was overlain by a massive sand sequence. Following this, the entire formation was overlain by deposits from the Mancos Sea.

SYSTEMATICS

Division ARTHROPHYTA

Genus EQUISETUM L.

Harris (1961) discussed the usage of *Equisetum* and *Equisetites* for fossils exhibiting similarities to the extant *Equisetum*. Harris elected

to use *Equisetum* since "No morphological difference has ever been proved between *Equisetum* and *Equisetites*. . . ." This statement is completely accurate, and furthermore, the fossil and living forms exhibit striking morphological similarity. In view of this, the author

has followed Harris (1961) and others in using *Equisetum* for placement of fossils which exhibit characteristics similar to those of the extant genus.

Equisetum lyelli Mantel

Figs. 7-3, 7-5; 15-5. 15-9.

1889 *Equisetum marylandicum* Fontaine—U.S. Geol. Surv. Mon. 15, p. 65, Pl. 170, Fig. 8.

1893 *Equisetum lyelli* Mantel, Dawson—Trans. Roy. Soc. Can. v. 10, pt. 4, p. 83, text-Fig. 1.

1956 *Equisetites lyelli* (Mantel) Unger, Bell—Geol. Surv. Can. Mem. 285, p. 76. Pl. 28, Figs. 5-8.

DESCRIPTION.—Rhizome horizontal, unbranched, 2-4 mm in diameter, smooth to slightly ribbed, bearing short tuber-bearing branches at intervals as close as 8 mm; tubers ovoid to globose, commonly wrinkled, subtended by leaflike bracts, 13 mm long by 6 mm wide, borne in pairs; upright stems unknown.

OCCURRENCE.—Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1807-1810.

DISCUSSION.—Many specimens of *Equisetum* have been collected from the Westwater flora. These specimens may be easily identified by their attached tubers, although positively identified stem material is absent. Specimens obtained from this flora are collected for the most part from the lowermost and uppermost portions of the ash.

It is rather difficult to assign this plant to any known species since no aerial stems have been observed. However, rhizomes of *Equisetum* are not uncommon in the fossil record, and the Westwater material rather closely resembles some described specimens.

Fontaine (1889) described *Equisetum virginicum* based upon both aerial stem and rhizome material. The aerial stem was highly branched, and tubers (called imperfect buds by Fontaine) were borne individually along the rhizome. This specific name was used again later by Fontaine (1899) for placement of a specimen from the Black Hills Lower Cretaceous. Bell (1956) noted that in overall morphology, *E. virginicum* is very similar to *E. lyelli* Mantel.

Equisetum marylandicum was described in 1889 by Fontaine. The aerial stem of this

species was highly branched, although a rhizome questionably attributed to this species (op. cit., Pl. 179, Fig. 8) is very much similar to rhizomes collected from Westwater.

Bell (1956) illustrated tuber-bearing rhizomes of *Equisetites lyelli* (Mantel) Unger (*Equisetum lyelli* Mantel). These rhizomes differ from the Westwater specimens by being branched and exhibiting strongly ribbed internodes. Other differences are the whorled disposition of tubers and the apparent lack of bracts subtending tubers on the Canadian specimens. However, the dimensions of the Canadian material compare well with those noted for Westwater specimens, although the tubers are commonly somewhat larger in the latter.

Other citations of *E. lyelli* are incomparable to the Utah specimens since only aerial stems are described. Thus, Schenk (1871) described aerial stems of *E. lyelli* as being much branched, and with larger dimensions than would be expected for aerial stems of the Westwater *Equisetum*, and Fontaine (1889) noted that characteristics of aerial stems of *E. lyelli* from Virginia agreed closely with those of this species from Europe as noted by Schenk (1871).

Division FILICOPHYTA

Genus ASPLENIUM L.

This genus is rather large and is well represented both in the modern and fossil flora. Bower (1923) reported *Asplenium* to contain 429 extant species, and Jongmans (1957) listed 96 fossil species of this genus with three varieties and listed ten as *Asplenium* sp. In addition, *Asplenites* has been used for placement of asplenioid ferns resembling the modern *Asplenium*; this genus contains several additional species.

Most of the fossil species of *Asplenium* are based upon sterile foliage, and undoubtedly many are synonyms. This problem is further complicated by the fact that sterile foliage of this genus rather closely resembles foliage of several other fern genera such as *Anemia*, *Onychiopsis*, *Sphenopteris*, *Acrostichopteris*, *Coniopteris*, and *Dicksonia*. There is no adequate way of determining between some species of these genera and between species of *Asplenium*, based upon sterile foliage alone. Clarification of resulting taxonomic problems awaits further collection and study of existing specimens.

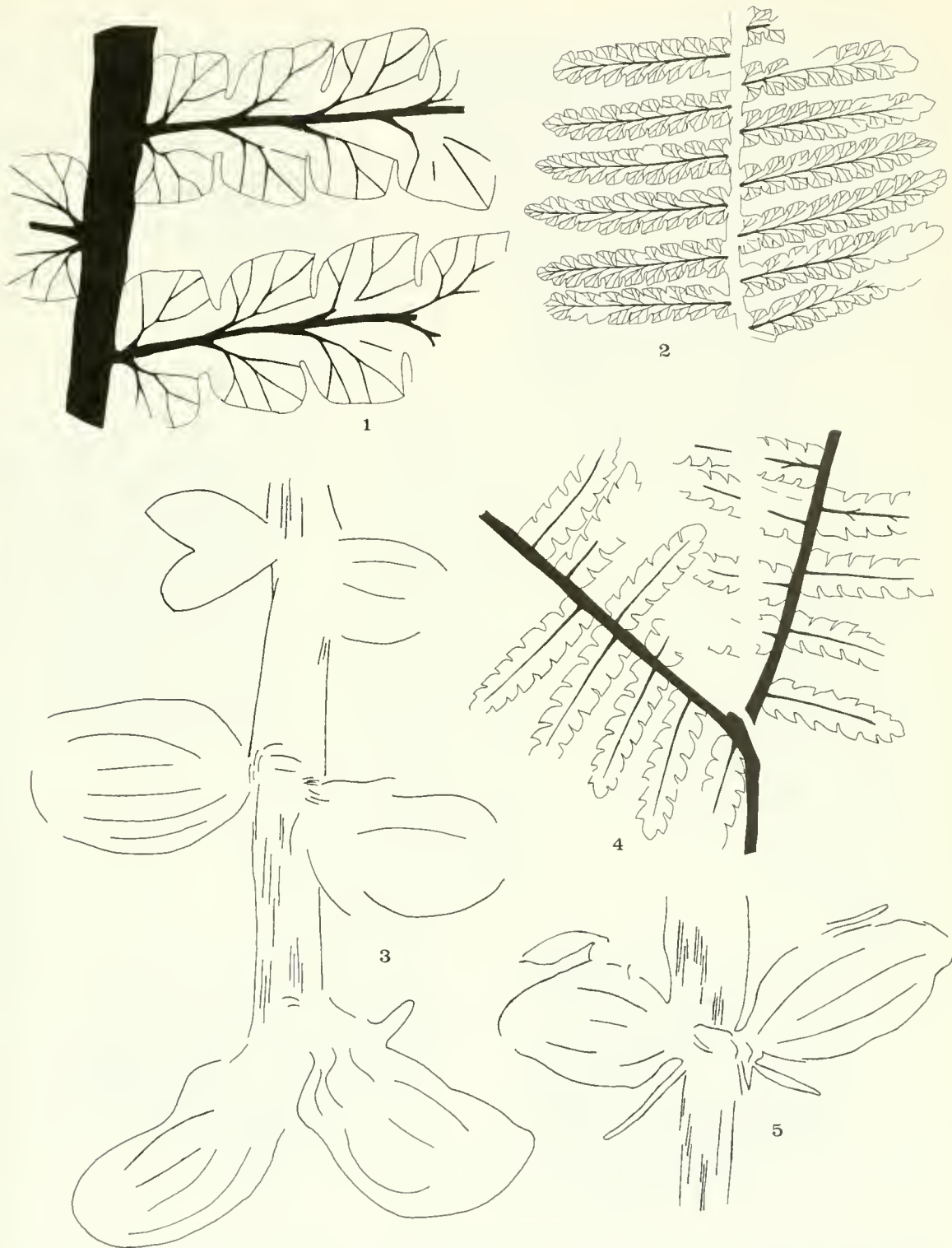


FIG. 7. 1. *Gleichenia delicatula* Heer. Portions of pinnae illustrating pinnule shape and disposition. (X12:5). BYU 1829. 2. *Gleichenia delicatula* Heer. Portions of pinnae illustrating pinnule shape and disposition. (X3). BYU 1829. 3. *Equisetum lyelli* Mantel. Portion of rhizome illustrating shape and disposition of tubers. (X3). BYU 1809. 4. *Gleichenia delicatula* Heer. Pinna fragment illustrating characteristic branching. (X3). BYU 1830. 5. *Equisetum lyelli* Mantel. Portion of rhizome illustrating tubers with subtending bracts. (X3). BYU 1810.

Asplenium dicksonianum Heer

Figs. 8-1: 11-3; 12-2; 15-4.

1874 *Asplenium dicksonianum* Heer—Flor. Foss. Arct., v. 3, pt. 2, p. 31, Pl. 1, Figs. 1 (excl. b, c), laa, 2-1, 5 (excl. a, b).

1899 *Asplenium dicksonianum* Heer, Ward—U.S. Geol. Surv. 19th Ann. Rept., pt. 2, p. 704, Pl. 170, Fig. 1.

1950 *Asplenium* sp. Brown—U.S. Geol. Surv. Prof. Paper 221-D, p. 48, Pl. 10, Fig. 4.

DESCRIPTION.—Entire leaf unknown, at least bipinnate; ultimate pinnae alternate, up to 90 mm or more long by 50 mm wide; pinnules lanceolate, entire to deeply cut, alternate, up to 40 mm long by 9 mm wide; attachment basal to single point; midvein strong at point of origin, not extending to pinnule apex, dividing; secondary veins repeatedly divided, free throughout; fertile specimens unknown.

OCCURRENCE.—KNOWN from the Dakota Sandstone Formation near Hot Springs, South Dakota, near Naturita, Montrose County, Colorado, and near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1811-1814.

DISCUSSION.—The author has elected to follow Ward (1899) who collected an asplenioid fern from the Dakota Sandstone of the Black Hills region and placed it in *A. dicksonianum*. However, Brown (1950), in describing a similar fern collected by Stokes from the Dakota Sandstone of Montrose County, Colorado, noted that both the Colorado and the South Dakota specimens appeared to be somewhat smaller and more delicate than typical specimens of *A. dicksonianum*. However, based upon material in his possession, Brown (1950) was hesitant to name a new species of this genus and so ascribed the material to *Asplenium* sp.

The observations of Brown were accurate for some specimens of *Asplenium* from Colorado. However, with the smaller forms mentioned by Brown (1950) are many which are larger and resemble rather closely *A. dicksonianum*. Westwater specimens of *Asplenium* are also like *A. dicksonianum*, although positive identity of this fern awaits collection of specimens illustrating soral and sporangial characteristics.

Asplenium dakotensis Rushforth, sp. nov.

Figs. 11-5, 12-6.

DESCRIPTION.—Entire leaf unknown, bipinnate; petiole smooth, 1-2 mm in diameter, bifurcat-

ing to give rise to two rachi; pinnae alternate, 35 mm or more long by 11 mm wide, lanceolate; pinnules ovoid, up to 9 mm long by 3.5 mm wide, alternate, attachment basal with rounded sinuses, to nearly single point, apices obtuse to rounded, margins entire; midvein strong at point of origin, not extending to pinnule apex, dividing; secondary veins mostly obscure, free, extending to pinnule margin; fertile specimens unknown.

OCCURRENCE.—KNOWN from the Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, holotype; BYU 1806.

DISCUSSION.—*Asplenium dakotensis* is proposed for a small, rather delicate *Asplenium* from the Westwater flora. It differs from *A. dicksonianum* Heer from the same locality by being much smaller, both in pinnule and pinna size, and by pinnules being entire and rather strap-shaped, rather than dentate or deeply cut and lanceolate as are pinnules of *A. dicksonianum* (Table 1). *A. dakotensis* Rushforth is also much smaller than most other species of *Asplenium* and differs from many by having pinnules with entire margins. It is also rather unique in its bifurcated petiole which gives rise to two rachi. This last characteristic coupled with pinnule shape and margination led the author to consider this fern closely related to *Knoultonella* Berry (1911). However, examination of the type specimens of *Knoultonella* indicates that the branching habit of the two differs, as does pinnule shape. Fertile specimens of neither *Knoultonella* nor *A. dakotensis* have been discovered, and for the present, the author prefers to assign this fern to the Aspleniaceae as *Asplenium dakotensis*, rather than to the Matoniaceae under *Knoultonella*.

Table 1

Comparative Morphology of *Asplenium dicksonianum* Heer and *Asplenium dakotensis* Rushforth

	<i>A. dicksonianum</i>	<i>A. dakotensis</i>
Length of pinna	90 mm	35 mm
Width of pinna	50 mm	11 mm
Length of Pinnule	40 mm	9 mm
Width of Pinnule	9 mm	3.5 mm
Pinnule shape	Lanceolate	Strap-shaped
Pinnule margin	Entire to deeply cut	Entire



FIG. 8. 1. *Gleichenia delicatula* Heer. Pinna fragment illustrating characteristic branching. (X1.2). BYU 1827. 2. *Matonidium brownii* var. *magnipinnulum* Rushforth. Pinna fragment illustrating long, linear pinnules. (X1.2). Holotype: 1566. 3. *Gleichenia delicatula* Heer. Pinna fragment illustrating pinna and pinnule disposition. (X1.2). BYU 1828. 4. *Asplenium dicksonianum* Heer. Pinna illustrating ultimate pinnae disposition. (X1.2). BYU 1811. 5. *Cladophlebis parva* Fontaine em. Berry. Pinna fragment illustrating pinnule disposition. (X1.2). BYU 1842. 6. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna fragment illustrating characteristic branching. (X1.2). BYU 1817. 7. *Asplenium dicksonianum* Heer. Pinna fragment illustrating disposition of ultimate pinnae. (X1.2). BYU 1812.

Family DICKSONIACEAE

Genus CONIOPTERIS Brongniart

Coniopteris is probably the best known fossil genus of the fern family Dicksoniaceae. As listed by Jongmans (1959) this genus contains approximately 45 species and three varieties. However, as discussed by Harris (1961) this genus is in need of revision, and fewer than 45 species are likely to be valid.

Coniopteris westwaterensis Rushforth, sp. nov.

Figs. 10-2; 11-4; 13-5.

DESCRIPTION.—Entire leaf unknown, at least bipinnate, some divided into a sterile portion below and fertile portion above; sterile pinnae lanceolate, up to 20 mm wide by greater than 60 mm long; pinnules subopposite to alternate, up to 12 mm long by 3 mm wide, lanceolate, margins entire near pinna apex to strongly dentate further down the pinna, apices generally acute but range to somewhat obtuse, attachment basal to constricted basal, sinuses rounded (pinnules connected along rachis); midvein prominent; secondary veins mostly obscure; fertile foliage consists of sterile pinnae below and fertile pinnae above; fertile portion of frond up to 65 mm long or longer above highest sterile pinna; fertile pinnules highly reduced, alternate, connected along the rachis; venation obscure; sori, sporangia and spores not observed.

OCCURRENCE.—KNOWN from the Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, holotype: BYU 1803.

DISCUSSION.—This fern is known from several specimens collected from the Westwater locality. A few of these are rather complete, illustrating fertile as well as sterile foliage. However, even though fertile specimens have been collected none illustrate sori or sporangia.

C. westwaterensis is similar in some respects to several other species of *Coniopteris*. It perhaps approaches most closely *C. burejensis* (Zalessky) Seward which is a common species from the Mid Jurassic of Asia and has also been collected from Alaska and Europe. *C. westwaterensis* differs from *C. burejensis* (Zalessky) Seward in having less crowded pinnae and by having the fertile portion of the foliage separated from the sterile portion, often occurring as much reduced pinnae apically to sterile pinnae.

C. bella Harris, which is similar to *C. burejensis* (Zalessky) Seward also is similar to *C. westwaterensis*. *C. bella* is only separated from *C. burejensis* based on pinnule margination and fine soral details, and *C. westwaterensis* differs from this fern as from *C. burejensis*. *C. westwaterensis* also differs from both of these ferns in that it exhibits secondary pinnae which are consistently larger, being up to 20 mm wide, whereas the pinnae of *C. burejensis* and *C. bella* are typically 10 mm wide.

Family DIPTERIDACEAE

Genus HAUSMANNIA Dunker

Dunker (1846) proposed this genus for sterile leaf fragments collected from the Wealden of Germany. These fragments were divided by nearly equal dichotomies to form strap-shaped leaf segments. Subsequent to this time, several other specimens of this genus have been collected, and a rather adequate generic diagnosis has evolved (Harris, 1961).

Hausmannia rigida Newberry

Figs. 9-2, 9-3, 13-4.

1895 *Hausmannia rigida* Newberry—U.S. Geol. Surv. Mon. 27, p. 35, Pl. 1, Figs. 2, 3, 5.

1910 *Newberryana rigida* Berry—Jour. Geol., v. 18, p. 254.

1911 *Newberryana rigida* Berry—Geol. Surv. New Jersey Bull. 3, p. 220.

DESCRIPTION.—Entire leaf unknown, divided to form tongue-shaped pinnules; pinnules typically 9 mm long by 3 mm wide, apices rounded, margins entire, attachment basal with rounded sinuses; midrib prominent, apparently not extending to pinnule apex; secondary veins obscure if present; fertile specimens unknown.

OCCURRENCE.—KNOWN from near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1815.

DISCUSSION.—The botanical affinity of *Hausmannia* has been in question in the past. Some early workers considered this plant to be a hepatic. Newberry (1885) said in this connection:

I have been led to think it possible it was a higher kind of hepatic, a *Marchantia*, for example, lifted from its creeping condition into an independent and erect plant, trained and disciplined into symmetry by the occult in-



FIG. 9. 1. *Astradopteris coloradica* (Brown) Reveal, Tidwell, and Rushforth. Near apical pinna fragment. (X1.2). BYU 1839. 2. *Hausmannia rigida* Newberry. Near apical pinna fragment illustrating tongue-shaped pinnales. (X1.2). BYU 1815. 3. *Hausmannia rigida* Newberry. Enlargement of Fig. 2. (X3). BYU 1815. 4. *Gleichenia delicatula* Heer. Pinna fragment illustrating disposition of ultimate pinnae. (X1.2). BYU 1826. 5. *Cladophlebis crenata* Fontaine. Pinnule fragment illustrating venation. (X3). BYU 1841. 6. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna fragment illustrating disposition of ultimate pinnae. (X1.2). BYU 1816. 7. *Astradopteris coloradica* (Brown) Reveal, Tidwell, and Rushforth. Pinnac fragment. (X1.2). BYU 1840.

fluence which has given such grace and exactness to the foliage of ferns, lycopods, and some conifers.

Later studies have shown that *Hausmannia* is a fern of the family Dipteridaceae (Richter, 1906), although fertile specimens demonstrating soral characteristics are still unknown. The Westwater *Hausmannia* does not shed any light on this problem since fertile specimens are unknown.

Hausmannia was first treated in America by Newberry (1885) who described *H. rigida*. This species was proposed for several plant fragments collected from the Amboy Clays of New Jersey.

Berry (1910) later transferred *Hausmannia rigida* to the new genus *Newberryana* without description, discussion, or illustration, and hence, his reasons for this move were unknown. However, Berry (1911, p. 220-221) further discussed *Hausmannia rigida* and stated that Newberry had referred this plant to the Hepaticae, and due to this:

It is, obviously, not related to the genus *Hausmannia*, Dunker, which has been definitely proven to be a fern genus of the family Dipteridaceae, so that I have selected to propose a new generic name. . . .

However, Berry gave no reasons why this plant should not be considered to be related to *Hausmannia*, and further went on to say that indeed it is probably a fern. It is the opinion of the present author that Newberry was justified in placing his material in *Hausmannia* as a new species since this material agrees rather well with the generic diagnosis of *Hausmannia*. Further collections and reevaluation of Newberry's material should, however, be undertaken.

H. rigida Newberry (1895, p. 35, Pl. I, Figs. 2, 3, 5.) is probably most closely related to the Westwater *Hausmannia*. This species lacks dichotomous leaf divisions, and more regular divisions of the frond-forming tongue-shaped segments is also found in the Westwater species. As discussed by Newberry (1895), the midrib in *H. rigida* gives rise to numerous fine secondary veins, although his illustrations do not demonstrate this feature. These secondary veins cannot be observed in the specimen from Westwater.

H. dichotoma Dunker is a common species of this genus from the Jurassic and Lower Cretaceous of Europe. This species usually has been well described and, as mentioned by Newberry (1895), is closely related to *Hausmannia rigida*. *H. rigida* differs from *H. dichotoma* in

that the divisions of the leaf are not dichotomous, and are more regular in the former.

Family GLEICHENIACEAE

Genus GLEICHENIA Smith

Berry (1924) discussed the usage of *Gleichenites* and *Gleichenia*. In this paper, Berry rather strongly supported the use of *Gleichenia* rather than *Gleichenites* and stated in this regard, "It is surely nothing but a mental illusion to imagine that the use of an objectionable term like *Gleichenites* indicates a conservation of judgment." However, Seward (1927) disagreed with Berry and used the name *Gleichenites* for placement of several Greenland species. Seward stated that in his opinion it is a sound practice to use an *ites* ending for a generic name when "either our ignorance or the occurrence of some character in which a fossil species differs from any existing type" may apply to an extinct taxon.

Harris (1961) pointed out that the practice of using genera with an *ites* ending is being dropped by most paleobotanists in recent times. Harris, however, rightfully suggested that when a question exists as to whether a fossil taxon may with equal validity be placed with more than one living taxa, a different generic name for the fossil must be used.

It is my opinion that it is sound to use the *ites* ending under certain circumstances when evidence of the sameness of a fossil and living genus is suggested but not definite. However, the use of this ending merely because of the older age of a fossil is not valid. When there is little or no question that a fossil may be placed in an extant genus, it is both acceptable and desirable to use the modern generic name for its placement.

The fossil section of the genus *Gleichenia* is in urgent need of revision and reevaluation. Many species are undoubtedly synonyms and could be more correctly placed. In addition, this genus affords an excellent opportunity to follow the evolution and migration of a fern genus from Paleozoic to recent times, and its study could contribute greatly to botanical knowledge.

Gleichenia comptoniaefolia (Deb. and Ett.) Heer

Figs. 8-6; 10-1, 10-6; 12-1, 12-3; 13-1, 13-3; 14-3; 20a.

1859 *Didymosarus comptoniaefolia* Deb. and



FIG. 10. 1. *Gleichenia comptoniacifolia* (Deb. and Ett.) Heer. Pinna fragment illustrating disposition of ultimate pinnae. (X1.2). BYU 1821. 2. *Coniopteris westwaterensis* Rushforth, sp. nov. Pinna fragment illustrating disposition of fertile pinnae. (X1.2). Paratype BYU 1804. 3. *Matonidium brownii* Rushforth. Pinna fragment illustrating pinnule disposition. This fragment is somewhat atypical and resembles some species of *Selenocarpus* Schenk. (X1.2). BYU 1833. 4. *Gleichenia delicatula* Heer. Pinna fragment illustrating ultimate pinnae disposition and pinnule shape. (X1.6). BYU 1829. 5. *Matonidium brownii* Rushforth. Pinna fragments and fiddle head. (X1.2). BYU 1834. 6. *Gleichenia comptoniacifolia* (Deb. and Ett.) Heer. Pinna fragment illustrating ultimate pinnae disposition and pinnule shape. (X1.2). BYU 1822.

Ett.—Denksch. K. Akad. Wiss. Wien., 17, Pl. 1, Figs. 1-5.

1868 *Gleichenia gieseckiana* Heer, pro parte—Flor. Foss. Arct., v. 1, p. 78, Pls. 43, Figs. 1a, 2a, 3a; 44, Figs. 2-3.

1868 *Pecopteris borealis* Brong., Heer, pro parte—Flor. Foss. Arct., v. 1, p. 81, Pl. 44, Fig. 5.

1868 *Gleichenia zippei* (Corda) Heer—Flor. Foss. Arct., v. 1, p. 79, Pl. 43, Fig. 4.

1868 *Pecopteris arctica* Heer, pro parte—Flor. Foss. Arct., v. 1, p. 80, Pl. 43, Fig. 5.

1868 *Pecopteris rinkiana* Heer—Flor. Foss. Arct., v. 1, p. 81, Pl. 44, Fig. 4.

1874 *Gleichenia longipennis* Heer, pro parte—Flor. Foss. Arct., v. 3, pt. 2, p. 46, Pl. 6, Figs. 4-6.

1874 *Gleichenia thulensis* Heer—Flor. Foss. Arct., v. 3, pt. 2, p. 48, Pls. 5, Fig. 9b; 10, Fig. 18.

1874 *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer, pro parte—Flor. Foss. Arct., v. 3, pt. 2, p. 49, Pl. 11, Figs. 1-2.

1874 *Gleichenia gracilis*, Heer, pro parte—Flor. Foss. Arct., v. 3, pt. 2, p. 52, Pl. 10, Fig. 5.

1874 *Gleichenia gieseckiana* Heer—Flor. Foss. Arct., v. 3, pt. 2, p. 43, Pls. 3, Id. 8; 7, Fig. 1.

1874 *Gleichenia nauckhoffi* Heer—Flor. Foss. Arct., v. 3, pt. 2, Pl. 25, Fig. 4.

1874 *Gleichenia zippei* (Corda) Heer, pro parte—Flor. Foss. Arct., v. 3, pt. 2, p. 44, 90, 97, Pls. 4-7; 25, Figs. 1-3.

1874 *Pecopteris hyperborea* Heer—Flor. Foss. Arct., v. 3, pt. 2, p. 41.

1874 *Gleichenia kurriana* Heer, Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 47, Pl. 1, Figs. 5, 5b, 5c.

1882 *Gleichenia gieseckiana* Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 6, Pl. 2, Fig. 9.

1882 *Gleichenia zippei* (Corda) Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 7, Pl. 3, Fig. 2.

1882 *Gleichenia longipennis* Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 7, Pl. 2, Fig. 5.

1882 *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 8, 36, Pl. 46, Fig. 25.

1883 *Gleichenia nordenskioldi* Heer, Lesquereux—U.S. Geol. Surv. of Terr. Repts., v. 8, p. 26, Pl. 1, Figs. 1, 1a.

1889 *Gleichenia nordenskioldi* Heer, Fontaine

—U.S. Geol. Surv. Mon. 15, p. 119, Pl. 21, Fig. 11.

1889 *Gleichenia zippei* (Corda) Heer, Fontaine—in Ward, U.S. Geol. Surv. 19th Ann. Rept., p. 664, Pl. 162, Fig. 9.

1927 *Gleichenites gieseckiana* (Heer) Seward—Phil. Trans. Roy. Soc. London B, v. 215, p. 69, Pl. 5, Figs. 1-4, 6-14, 16, 17; Pl. 10, Fig. 96; Pl. 12, Fig. 118; text-Fig. 2.

1950 *Gleichenia kurriana* Heer, Brown—U.S. Geol. Surv. Prof. Paper 221-D, p. 48, Pl. 10, Figs. 5-6.

1956 *Gleichenia gieseckiana* (Heer) Seward, Bell—Geol. Surv. Can. Mem. 285, p. 61, Pl. 17, Figs. 1, 2; Pl. 18, Fig. 5.

DESCRIPTION.—Entire leaf unknown, at least bipinnate; rachis stout, slightly greater than 1 mm in diameter, smooth, appearing dichotomously branched (although not truly dichotomizing [Bower, 1926]), with a bud in the axil of dichotomy; ultimate pinnae alternate, occasionally subopposite, nearly linear, approximately 80 mm long by 10 mm wide; pinnules arising obtusely from rachis, narrow elliptic to deltoid near pinna apex, oriented slightly toward pinna apex, ranging from 1 mm wide by 2 mm long at apex of pinna to 3 mm wide by 6 mm long near pinna base, margins entire, apices obtuse; major vein strong at point of origin, not extending to pinnule apex; secondary veins numerous, dividing, extending to pinnule margins; sori commonly three per pinnule, round; sporangia and spores unknown.

OCCURRENCE.—Near Westwater, Grand County, Utah, and Rabbit Valley, Grand County, Utah. REPOSITORY.—Brigham Young University, BYU 1816-1825, 1853a.

DISCUSSION.—As may be deduced from the synonymy for *G. comptoniaefolia*, Heer proposed many species of *Gleichenia* in the late 1800s based upon material collected from several Greenland localities. Heer treated any form that illustrated any variation whatsoever as a new species. Seward (1927) reviewed the work of Heer and studied many of his original collections. Based upon his studies, Seward concluded that many of the species proposed by Heer merely represent variations of a few species.

In discussing the synonymy for *G. gieseckiana*, into which Seward (1927) lumped many of Heer's (1868, 1874, 1872) species, Seward mentions two names which predate *G. gieseckiana*. The first of these *Pecopteris borealis* Brongniart, was applied by Brongniart (1828). Seward ex-



FIG. 11. 1. *Cladophlebis constricta* Fontaine em. Berry. Pinnules illustrating deeply lobed margins. (X3). BYU 1941. 2. *Cladophlebis parva* Fontaine em. Berry. Pinna fragment illustrating pinnule shape and venation. (X3). BYU 1842. 3. *Asplenium dicksonianum* Heer. Pinna fragment illustrating shape and venation of pinnules. (X3). BYU 1814. 4. *Coniopteris westwaterensis* Rushforth, sp. nov. Portion of pinna illustrating pinnule shape and margination. (X3). Paratype: BYU 1805. 5. *Asplenium dakotensis* Rushforth, sp. nov. Portion of frond illustrating pinnae and pinnule disposition. (X3). Holotype: BYU 1806.

amined the type specimen of this fern and concluded that it was not possible to determine if it is synonymous with *G. gieseckiana*. Later collections from the probable locality where *P. borealis* was collected have turned up specimens which are identical with *G. gieseckiana*. However, since the original type specimen is not identifiable, Seward chose to retain Heer's specific epithat.

Didymosarus comptoniaefolius Deb. and Ett. that.

(1859) is also an older name which has been applied to *G. gieseckiana* Heer. Heer recombined *D. comptoniaefolius* Deb. and Ett. as *Gleichenia gieseckiana* since the former is undoubtedly gleicheniaceus. Seward (1927) placed *G. comptoniaefolia* (Deb. and Ett.) Heer in synonymy with *G. gieseckiana* Heer. Seward did not use the oldest specific epithat because "evidence of identity is not convincing." However, Seward in the same paper noted that some of the ferns Heer had placed in *G. comptoniaefolia* were, without question, referable to *G. gieseckiana*. Furthermore, the illustrations of Debey and Ettinghausen (1859) indicate that it is very likely that the ferns referred by them to *Didymosarus comptoniaefolius* are identical to *G. gieseckiana*. In view of this, it is preferable to use the oldest specific epithat, and therefore the most acceptable binomial applied to *G. gieseckiana* of Heer, is *G. comptoniaefolia* (Deb. and Ett.) Heer.

Lesquereux (1874) figured a gleichenious fern from the Dakota Group of Kansas. These ferns agree in every detail with *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer, but were placed in *Gleichenia kurriana* Heer by Lesquereux. However, it is important to note that Lesquereux considered the Dakota ferns closely allied to *Didymosorus comptoniifolius* Deb. and Ett., and in fact noted that in pinnule shape, disposition, and venation, "our American species or variety would be more closely related to *Didymosorus comptoniifolius* Deb. and Ett. . ."

Lesquereux (1883) again treated gleichenious ferns in his work on the Cretaceous and Tertiary of the Western Territories. Pinna fragments of *Gleichenia* from the Dakota Group were placed by Lesquereux in *G. nordenskioldi*. However, as noted by Seward (1927) the fern examined by Lesquereux agrees in all respects with *G. gieseckiana* (*G. comptoniaefolia*).

Fontaine (1889) discussed *Gleichenia nordenskioldi* Heer as known from the Potomac Group. However, this fern agrees with *G. comptoniaefolia* closely, and should be placed in this species.

In discussing Lower Cretaceous plants from the Black Hills region, Fontaine (1899) again

discussed gleicheniaceus ferns. He placed a specimen of *Gleichenia* in *G. zippei* (Corda) Heer. This fern likewise is very similar to *G. comptoniaefolia*, and can be correctly considered in this species.

Velenovsky (1888) described and illustrated several fossil ferns with gleichenious affinities collected from the European Cretaceous. Two of these which are very similar to *G. comptoniaefolia* are *G. zippei* (Corda) Heer and *G. multivervosa* Velen.

Brown (1950) reported on gleichenious fossils from the Dakota Sandstone of southwestern Colorado. He placed these ferns in *Gleichenia kurriana* following Lesquereux (1874). Recent examination of these ferns by the present author indicates that they are indeed very similar to those figured by Lesquereux (1874) as *G. kurriana* which are correctly placed with *G. comptoniaefolia*.

Bell (1956) described *Gleichenites gieseckianus* Heer em. Seward from several localities in western Canada. These ferns agree with the Westwater *Gleichenia* in all respects except that the pinnules on the Canadian specimens are often somewhat reflexed. Again, these ferns are correctly classified as *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer.

Seward (1927) discussed *Gleichenites nordenskioldi* Heer, and retained it as a valid species which differs from *G. comptoniaefolia* by having long pinna of uniform breadth and pinnules with somewhat more frequent veins. Soriation in the two species is similar, but Seward noted that *G. nordenskioldi* has more sori per pinnule. All of these features are extremely variable, and specimens from Westwater may be found intermediate to all of these species-differentiating characteristics. However, the author has elected not to make any changes in classical usage of *G. nordenskioldi* and *G. comptoniaefolia* until further review.

Gleichenous fossils from the Westwater locality are similar to those figured by Heer (1868, 1874, 1882), Seward (1927), and others. Similar problems of classification have been encountered with these ferns in that they exhibit rather wide morphological variation. However, the present author has elected to be more conservative than Heer and Seward, and many fossils which exhibit some degree of variation are nonetheless placed in *G. comptoniaefolia* (Deb. and Ett.) Heer.

This species of fern is the most common element from the Westwater area and it is present in such profusion that at certain outcroppings one can scarcely break open a rock without exposing at least one beautiful specimen. It is in-



FIG. 12. 1. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna illustrating ultimate pinnae and pinnules. (XI.2). BYU 1818. 2. *Asplenium dicksonianum* Heer. Pinna fragment illustrating disposition of ultimate pinnae and pinnules. (XI.2). BYU 1812. 3. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna illustrating ultimate pinnae and pinnules. (XI.2). BYU 1819. 4. *Salix newberryana* Hollick. Leaf demonstrating characteristic shape and margination. (XI.2). BYU 1851. 5. *Ilex serratus* Rushforth, sp. nov. Leaf illustrating shape and margination. (XI.2). Paratype: BYU 1802. 6. *Asplenium dakotensis* Rushforth, sp. nov. Pinna illustrating shape and disposition of ultimate pinnae and pinnules. (XI.2). Holotype: BYU 1806.

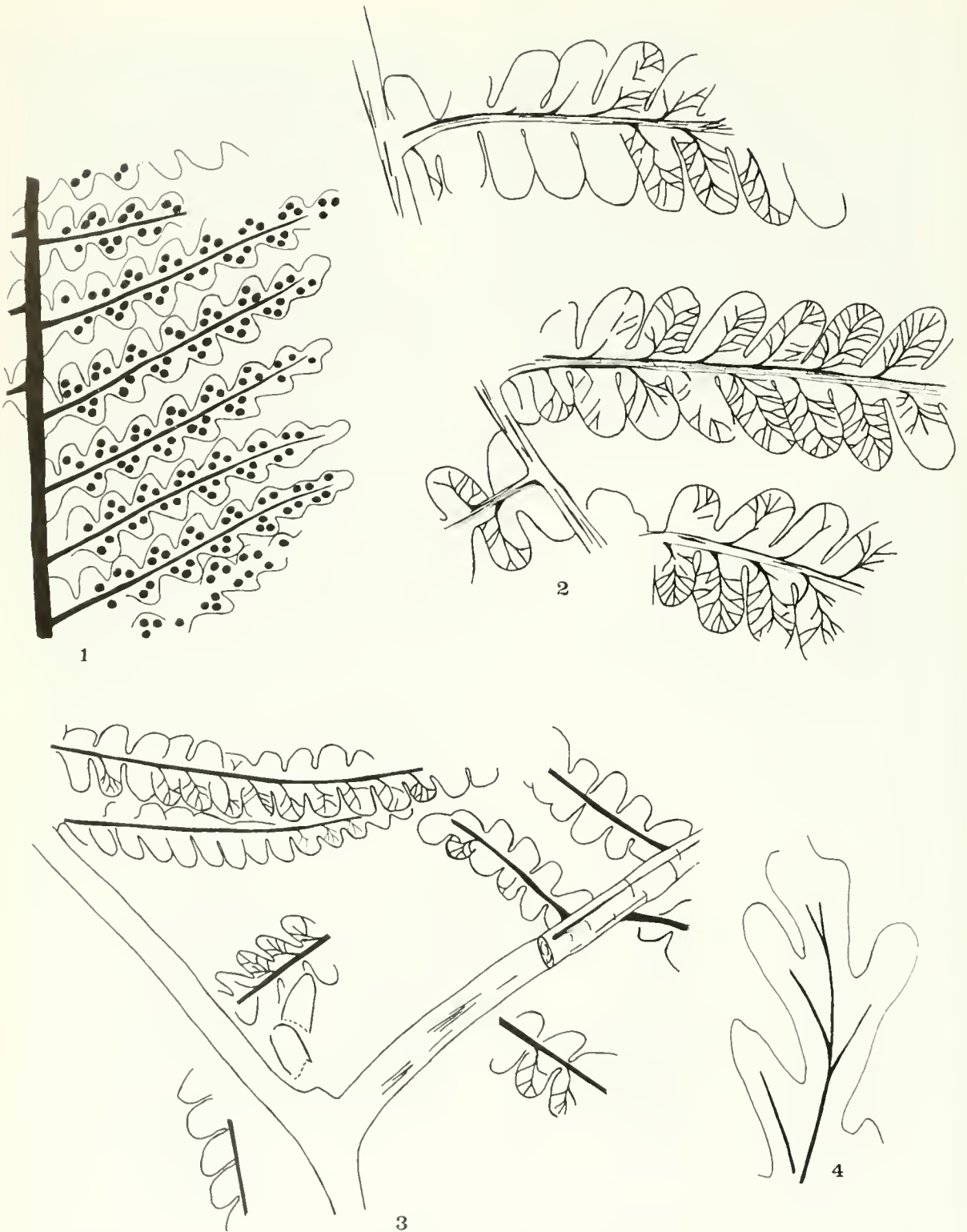


FIG. 13. 1. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna fragment illustrating soral disposition. (X3). BYU 1823. 2. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinnae fragments with pinnules exhibiting venation. (X3). BYU 1824. 3. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna fragment illustrating characteristic branching. (X3). BYU 1825. 4. *Hausmannia rigida* Newberry. Pinnae fragment demonstrating tongue-shaped pinnules. (X3). BYU 1815.

teresting to note that gleicheniaceus ferns are also most common from the Greenland Cretaceous flora. Indeed, as mentioned by Seward, ". . . part of the country was occupied by a vertiable *Gleichenietum*."

Gleichenia delicatula

Figs. 7-1, 7-2, 7-4; 8-1, 8-3; 9-4; 10-4.

1874 *Gleichenia delicatula* Heer—Flor. Foss. Arct., v. 3, pt. 2, p. 54, Pl. 9, Figs. 11e, 11f; Pl. 10, Figs. 16, 17.

1882 *Gleichenia delicatula* Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 9.

1888 *Gleichenia delicatula* Heer, Velenovsky—Abh. K. Bohm. Ges. der Wiss., Math.-Natw., ser. 7, v. 1, p. 7, Pl. 3, Figs. 12-14.

1910 *Gleichenites delicatula* (Heer) Seward—Fossil Plants: v. 2, p. 354, Fig. 262b.

1919 *Gleichenia delicatula* Heer, Berry—U.S. Geol. Surv. Prof. Pap. 112, p. 54.

DESCRIPTION.—Entire leaf unknown, at least bipinnate; petiole less than 1 mm in diameter, smooth, appearing dichotomously branched with a bud in the axis of dichotomy; ultimate pinnae alternate, linear, up to 15 mm long by 2 mm wide; pinnules tending toward ovate but with truncated edge toward pinna apex, oriented slightly toward pinna apex, approximately 1 mm long by 1.2 mm wide, attachment basal with rounded sinuses, margins entire, apices acute to obtuse, directed apically; primary vein dividing immediately upon arising from rachis; secondary veins dividing, giving rise to three to five ultimate veinlets which extend to pinnule margin; fertile specimens unknown.

OCCURRENCE.—Near Westwater, Grand County, Utah, and Rabbit Valley, Grand County, Utah

REPOSITORY.—Brigham Young University, BYU 1826-1730.

DISCUSSION.—*Gleichenia delicatula* was proposed by Heer in 1874 for placement of several pinna fragments collected from the Greenland Cretaceous. This fern was originally described by Heer (1874) as follows:

G1. fronde gracillima, dichotoma, bipinnata, racchi tenuissima, pinnis approximatis, patentibus. linearibus, pinnulis minutissimis, rotundatus.

This description, and the illustrations of Heer agree rather well with the Westwater specimens. One readily apparent difference is

the pinnule shape, which as described by Heer is round in the Greenland specimens, but tends toward ovate with an angular apex in the Westwater material. In the oblong pinnule shape, the Utah material resembles *Gleichenia micromera* Heer, a contemporaneous species with *G. delicatula*. However, the westwater material is dissimilar to *G. micromera* in that the pinnules in the latter are not attached to the rachis with their entire base, whereas, they are broadly attached and with rounded sinuses in the Utah *Gleichenia*.

Velenovsky (1888) discussed and figured two specimens of *Gleichenia delicatula*. These specimens agree in all details with Heer's (1874) specimens, and differ from the Westwater specimens only in pinnule shape. Pinna morphology and size of Velenovsky's specimens is identical to that of the Utah *Gleichenia*.

Seward (1910) used the generic name *Gleichenites* for the placement of *Gleichenia delicatula*. He made no changes in description, and figured a specimen of *Gleichenia delicatula* which appears very close to those of Heer (1874), Velenovsky (1883), and the material from Utah. Again, the pinnule shape varies between Seward's specimens and those from Utah.

Berry (1919) reported on *Gleichenia delicatula* collected from the Tuscaloosa Formation of Fayette County, Alabama. This fern was placed with *G. delicatula* based upon the pinnules being united to the rachis along their entire base. Berry further mentioned that Fontaine (1895) had wrongly placed pinna fragments collected from the Raritan Formation in *G. micromera*. Berry placed these in *G. delicatula* based upon their completely basal attachment. Again, this fern is similar in size to the Westwater fern, but pinnule shape differs somewhat.

Even though in pinnule shape the Westwater *Gleichenia* differs somewhat from other small pinnuled species of this genus, for the present time the author has elected to place it with *G. delicatula* Heer. This placement is based upon similar pinna morphology and pinnule size and disposition.

Family MATONIACEAE

Genus MATONIDIUM Schenk

Schenk (1871) was the first to use the generic name *Matonidium* for placement of fossil ferns exhibiting similar characteristics as the extant *Matonia pectinata* R. Br. Fossil ferns placed in this genus are morphologically very similar



FIG. 14. 1. *Matonidium brounii* Rushforth. Pinna fragment illustrating venation and soriation of pinnules. (X1.2). BYU 1563. 2. *Matonidium brounii* Bushforth. Enlargement of Fig. 1. (X2.7). BYU 1563. 3. *Gleichenia comptoniaefolia* (Deb. and Ett.) Heer. Pinna fragment illustrating ultimate pinnae disposition. (X1.2). BYU 1820. 4. *Astralopteris coloradica* Reveal, Tidwell, and Rushforth. Pinna fragment illustrating pinnule attachment and shape. (X1.2). BYU 1838. 5. *Coniopteris westwacensis* Bushforth, sp. nov. Sterile and fertile pinnae. (X1.2). Holotype: BYU 1803. 6. Angiosperm leaf base possibly belonging to *Ficus* sp. (X1.2). BYU 1847.

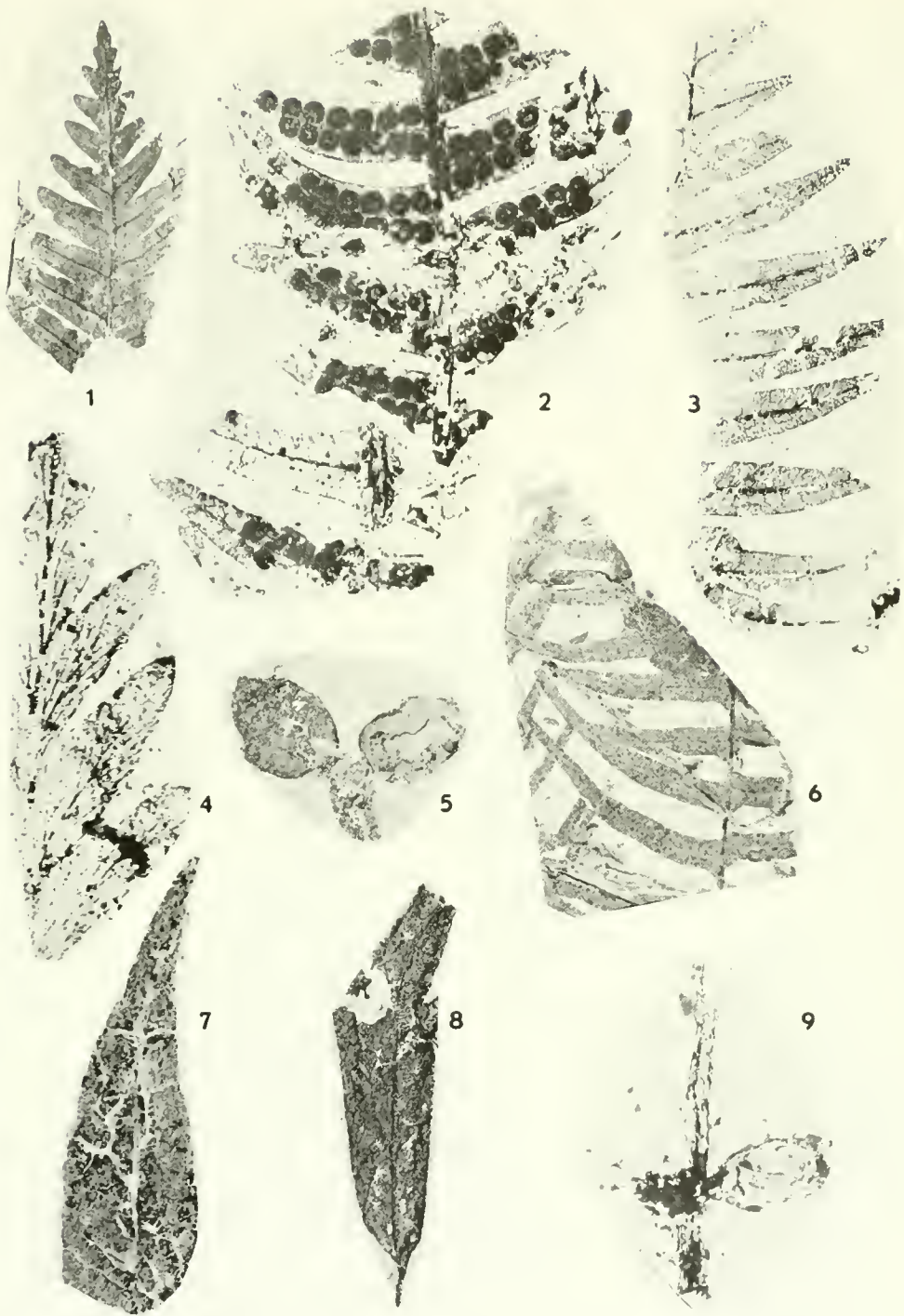


FIG. 15. 1. *Matonidium brownii* Rushforth. Pinna apex demonstrating disposition of pinnules. (X1.2). BYU 1832. 2. *Matonidium brownii* Rushforth. Pinna fragment demonstrating venation and soriation. (X2.8). Paratype: BYU 1559. 3. *Matonidium* (?) *lanicipinnulum* Rushforth. Pinna transfer illustrating pinnule shape and disposition. (X1.5). Holotype: BYU 1569. 4. *Asplenium dicksonianum* Heer. Pinna transfer illustrating pinnule disposition and venation. (X2.4). BYU 1813. 5. *Equisetum lyelli* Mantel. Portion of rhizome with two tubers attached. (X1.2). BYU 1807. 6. *Matonidium brownii* var. *magnipinnulum* Rushforth. Pinna fragment showing long, linear pinnules. (X1.2). BYU 1836. 7. *Salix neuberryana* Hollick. Leaf demonstrating characteristic shape and size. (X1.2). BYU 1850. 8. *Eucalyptus dakotensis* Lesquereux. Leaf of characteristic size and shape. (X1.2). BYU 1848. 9. *Equisetum lyelli* Mantel. Rhizome transfer with attached tubers. (X1.2). BYU 1808.

and often essentially identical to modern matoniaceous ferns.

Matonidium is often difficult to differentiate from other members of the Matoniaceae, particularly *Phlebopteris*. However, *Matonidium* is separated from *Phlebopteris* based upon the presence of an indusium in the former. This difference is often very difficult to determine even in fertile specimens, and is impossible to ascertain in sterile material. Furthermore, to compound this problem, *Matonidium* and *Phlebopteris* are often very similar in venation. Further work dealing with this family will likely show that the distinction between these two genera is unnatural and that ferns variously placed in the two should be classified under a single genus.

Matonidium americanum Berry em. Rushforth

Figs. 18-3, 18-4: 19-5.

1916 *Matonidium althausii* (Dunker) Ward, Cockerell-J. Wash. Acad. Sci., v. 6, p. 111, Fig. 2.

1916 *Cycadospadix* sp. Cockerell-J. Wash. Acad. Sci., v. 6, p. 111, Fig. 1.

1918 *Matonidium americanum* Berry—Bull. Torrey Bot. Club, v. 46, p. 287, Fig. 2. Pls. 12, Figs. 1-12; 13, 3-6.

1970 *Matonidium americanum* Berry, Rushforth—BYU Geol. Stud., v. 16, pt. 3, p. 25, Pl. 8, Fig. 1; Pl. 13, Fig. 2.

DESCRIPTION.—Fronds pedate, petiole stout, to approximately 1 cm in diameter, furrowed (?), dividing to form a collar from which pinnae are born; pinnae lanceolate to linear, 20 cm to 25 cm long, up to 39 per frond; pinnules inserted near the upper margin of the rachis, up to 9 mm long by 3 mm wide, coriaceous, more or less falcate; apices rounded; margins entire or revolute; midvein prominent to near the pinnule apex; secondary veins prominent, bifurcate approximately one-half to two-thirds of the way to margin, remain free; sori biseriate, round (except where crowded), decrease in size toward pinnule apex, indusiate; indusium peltate; sporangia and spores unknown.

OCCURRENCE.—Near Cutthroat Gulch and Hovenweep Canyon west of Dolores, Montrose County, Colorado, and Rabbit Valley, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1572, 1831.

DISCUSSION.—As mentioned by Berry (1919) the pinnules of *M. americanum* are coriaceous. This

feature is easily discerned in the specimens examined by the present author and may be the reason that venation in this species is poorly preserved. Berry also described the pinnules of this species as having revolute margins. While this is possible, it is likely that this appearance is due to the coriaceous nature of the pinnules. This feature is quite unique within the Matoniaceae.

This species also differs from other species of *Matonidium* in the large number of pinnae borne on a single frond. In addition, the open venation pattern is somewhat uncommon although not unprecedented within the Matoniaceae.

Matonidium brownii Rushforth

Figs. 10-3, 10-5; 14-1, 14-2; 15-1; 17; 18-2; 18-1, 18-3. 18-6.

1950 *Matonidium americanum* Berry, Brown—U.S. Geol. Surv. Prof. Paper 221-D, p. 48, Pl. 10, Figs. 7-8.

1970 *Matonidium brownii* Rushforth—BYU Geol. Stud. 16(3), p. 9, Pl. 1, Fig. 2; Pls. 2-5; Pl. 6, Fig. 2; Pl. 8, Fig. 2; Pl. 11, Fig. 1.

DESCRIPTION.—Petiole stout, between 5 mm and 15 mm in diameter, divided apically into two short arms; pinnae four to ten or more per frond, lanceolate, up to 14 cm in length, pinna rachis between 0.5 mm and 2.5 mm in diameter; pinnules opposite to alternate, basal in attachment, decurrent but free from each other, up to 30 mm in length by 9 mm in width, arise nearly perpendicular to the rachis but become oriented toward pinna apex; margins entire; apices rounded; midrib prominent to pinnule apex; secondary veins arise from midrib, divide to form costal areoles; tertiary veins arise from costal areole and other secondary veins and anastomose in the pinnule lamina; costal areoles absent in fertile specimens; secondary veins form an arch above placenta; tertiary veins arise from this arch and extend to the placenta; upper epidermal cells more or less isodiametric, average 45 μ in diameter; lower epidermal cells unknown; sori round, biseriate 1.7 mm to 2.9 mm in diameter, with a single ring of from ten to fourteen sporangia; indusia present, peltate, persistent; sporangia cuneate sessile or nearly so; annuli oblique; spores trilete, laesurae three quarters of the distance to the equator, rounded-triangular, 57 μ in diameter, with a weak margo.

OCCURRENCE.—Known from near Naturita, Montrose County, Colorado, and near Westwater, Grand County, Utah.



FIG. 16. 1. *Magnolia boulayana* Lesquereux. Leaf of characteristic size and shape. (X1.2). BYU 1843. 2. *Ilex serrata* Rushforth sp. nov. Angular-ovate leaf with typical serrate to spinose margin. (X1.2). Holotype: BYU 1801. 3. *Ficus daphnogenoides* (Heer) Berry. Cuneate leaf base exhibiting cuneate base. (X1). BYU 1845. 4. *Ficus daphnogenoides* (Heer) Berry. Leaf exhibiting drip point, shape and margination. (X1). BYU 1846. 5. Poorly preserved angiosperm leaf possibly of *Magnolia* sp. (X1). BYU 1844. 6. *Platanus newberryana* Heer. Portion of leaf exhibiting characteristic venation. (X1.5). BYU 1849.

REPOSITORY.—Brigham Young University, holotype: BYU 1557; paratypes: BYU 1559, 1563; BYU 1832-1835.

DISCUSSION.—*M. brownii* was first described by Brown (1950) from specimens collected from the Dakota Sandstone of southwestern Colorado. However, Brown placed this fern in *M. americanum* Berry. The present author examined the specimens collected from this locality and concluded that these specimens should not be placed with *M. americanum*. Due to this, *M. brownii* Rushforth (1970) was proposed.

M. brownii differs from *M. americanum* by being much larger; by having fewer pinnae per frond; by having anastomosing rather than open venation; and in soriation (Rushforth, 1970).

M. brownii differs from a related species, *M. wiesneri* Krasser, by having anastomosing rather than open venation; by being larger in overall size; and by having more numerous sori. *M. althausii* (Dunker) Ward differs from *M. brownii* in pinnule shape and habit, and in venation. Soriation of *M. althausii* also differs from *M. brownii* in that the former exhibits sori born to the extreme pinnule apex decreasing in size as the apex is approached.

In venation *M. brownii* is similar to *Phlebopteris* (Schenk) Schenk.

Matonidium brownii var. *magnipinnulum*
Rushforth

Figs. 15-6; 18-2; 21b.

1970 *Matonidium brownii* var. *magnipinnulum* Rushforth—BYU Geol. Stud., v. 16, pt. 3, p. 11, Pl. 6, Fig. 1; Pl. 7, Fig. 2; Pl. 14, Fig. 2.

DESCRIPTION.—Entire leaf unknown, pedate; pinnae observed up to 30 cm long, longer in growth, lanceolate; rachis up to 1.5 mm in diameter; pinnules opposite to alternate, basal in attachment, often decurrent, free, up to 60 mm in length by 6 mm in width, arise at 90° but become oriented toward pinna apex; margins entire; apices rounded; midvein prominent to pinnule apex; secondary veins prominent, forming costal areoles in sterile pinnules, progressing directly to placenta in fertile forms; tertiary veins often anastomose except in pinnule tips; lower epidermal cells large (up to 95u by 45u), lobed; fertile specimens not observed.

OCCURRENCE.—Known from the Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, holotype: BYU 1566; BYU 1836.

DISCUSSION.—*M. brownii* var. *magnipinnulum* was described by Rushforth (1970) for matoniaceous frond fragments from the Westwater flora. In pinnule habit and venation *M. brownii* var. *magnipinnulum* is very similar to *M. brownii* var. *brownii*. However, the pinnules of var. *magnipinnulum* are consistently longer and narrower than those of var. *brownii*. In addition, the disposition of the pinnules on the rachis is farther apart in var. *magnipinnulum*.

As mentioned by Rushforth (1970), this fern may be distinguished from other matoniaceous ferns due to its large pinna and pinnule size. However, long, linear pinnules are not unknown within the Matoniaceae. Bell (1956) reported on *Phlebopteris* (?) *elongata* for sterile pinna fragments from the Cretaceous of Canada, and *P. muensteri* also exhibits long linear pinnules.

Matonidium (?) *lancipinnulum* Rushforth

Figs. 15-3; 18-1; 19-2.

1970 *Matonidium* (?) *lancipinnulum* Rushforth BYU Geol. Studies, v. 16 pt. 3, p. 24, Pl. 7, Fig. 1; Pl. 9; Pl. 10; Pl. 13, Fig. 1.

DESCRIPTION.—Entire leaf unknown; pinnules sub-opposite, linear-lanceolate, 60 mm long by 12 mm wide, essentially perpendicular to rachis except at extreme pinnule apex, attachment basal with rounded sinuses; midvein prominent to pinnule apex; secondary veins prominent, forming costal areoles, anastomosing above costal areoles except near laminar edge, composed of tracheids with annular, helical and reticulate wall thickenings; guard cells 40u long by 15u wide, leaving stomata 10u wide; fertile specimens unknown.

OCCURRENCE.—Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, holotype: BYU 1569; paratype: BYU 1579.

DISCUSSION.—Rushforth (1970) placed this fern in the Matoniaceae based upon pinnule venation and shape. However, the assignment of this fern to this family must remain provisional until fertile specimens are collected.

One interesting fact concerning this fern is that it seems to be somewhat intermediate in venation pattern between well-defined members of the Matoniaceae and another Westwater fern, *Astralopteris* (Polypodiaceae). This latter genus illustrates venation which would tend to align it with the Matoniaceae, but soral characteristics align it with the Polypodiaceae. Further at-



FIG. 17. *Matonidium brownii* Rushforth. Portion of a frond illustrating pinnae and pinnule disposition, (X1.2).
Holotype: BYU 1557.

tempts to locate more specimens of *M. lancipinnulum* are presently under way.

Family POLYPODIACEAE

Genus *ASTRALOPTERIS* Reveal, Tidwell and Rushforth

Astralopteris coloradica (Brown) Reveal, Tidwell and Rushforth

Figs. 9-1, 9-7; 14-4; 19-4; 20.

1950 *Bolitis coloradica* Brown—U.S. Geol. Surv. Prof. Paper 221-D, p. 49, Pl. 12, Figs. 6-7.

1967 *Astralopteris coloradica* (Brown) Reveal, Tidwell and Rushforth, Tidwell *et al.*—BYU Geol. Studies, v. 14, p. 239, Pl. 2, Fig. 1; Pls. 3-6.

1968 *Astralopteris coloradica* (Brown) Reveal, Tidwell and Rushforth, Rushforth and Tidwell—BYU Geol. Studies, v. 15, p. 109, Pls. 1-3.

DESCRIPTION.—Entire frond unknown; pinnae incomplete, large, ovate, tapering to rather acute apices; pinnules coriaceous, pinnate, alternate to opposite on rather stout rachises; lower pinnules linear-lanceolate, about 7 to 11 times as long as broad, sessile to short stalked attachment; margins entire; apices acute to rounded; upper pinnules similar to lower ones, 4 to 5 times as long as broad, basal attachment with rounded sinuses in the uppermost pinnules; midvein prominent to the pinnule apex or nearly so, arising decurrently from rachis; lateral veins numerous arising acutely and then becoming nearly at right angles to the midvein (or divaricate) for nearly their entire length, simple for one-half to three-quarters or more of their length then usually bifurcating two or three times (or rarely trifurcating at the first fork); ultimate veins finer, anastomosing, often obscure; sori round, biseriate between the main lateral veins, about one-fourth of the distance from the midrib to the margin, fed from a costal areole and other secondary veins which extend to the placenta; sporangia 12 to 15, arranged in a ring around a central placenta; annuli vertical; spores unknown.

OCCURRENCE.—Known from the Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1415-1422; 1837-1840.

DISCUSSION.—*A. coloradica* was originally described as *Bolbitis coloradica* by Brown (1950). This placement was based upon sterile specimens collected from Naturita, Montrose County, Colorado. Brown encountered difficulty in placing this fern and consequently he conferred

with extant fern workers from the Smithsonian Institute. These workers suggested that in overall gross morphology (pinnule shape, size, venation, etc.) the Naturita fossils are similar to ferns of the extant genus *Bolbitis*.

Tidwell *et al.* (1967) reported fertile specimens of this fern and illustrated that this fern could not be placed in the extant *Bolbitis*. Furthermore, since no living or fossil genus allowed for the placement of this fern the new genus *Astralopteris* was proposed.

A. coloradica is one of the most common elements of the Westwater flora. In some collecting sites it is collected almost exclusively, although it is most commonly collected in association with *Matonidium* and *Gleichenia*. Collections of fertile specimens of this fern are rare at the Westwater locality but, from recent examinations by the author, appear to be somewhat more common from the Dakota Sandstone of southwestern Colorado and Arizona.

UNCLASSIFIED FERNS

Genus *CLADOPHLEBIS* Brongniart

This generic name was originally proposed by Brongniart (1849) but Saporta (1873) first defined (*Cladophlebis*) as follows:

Fronde pinnately divided; pinnules separate from one another, or slightly united, attached by the entire base.

Schimper (1874) emended this diagnosis to:

Fronde pinnately divided; pinnae spreading; lobes or pinnules attached by the entire base, sometimes confluent, rarely slightly auriculate, acuminate or obtuse, occasionally dentate, especially at the apex, not rarely subfalcately curved upwards; midnerves pretty strong; secondary nerves departing at a more or less acute angle, dichotomous; slender to very slender.

Fontaine (1889) modified this diagnosis only in regard to venation by saying, ". . . midnerve strong at base, and towards the summit dissolving into branches."

Fontaine (1889) discussed the usage of *Cladophlebis* and concluded that it is a useful genus for placement of sterile foliage which may be described as above. This is indeed the case, as foliage assigned to *Cladophlebis* could fit well into a number of different genera. Therefore, *Cladophlebis* has become a useful, though unnatural genus which is very characteristic of the Mesozoic, particularly of Jurassic times. Thus Berry (1912) mentioned that *Cladophlebis* is essentially a form genus and includes species



FIG. 18. 1. *Matonidium* (?) *lancipinnulum* Rushforth. Pinna fragment illustrating pinnule disposition. (X1.2). Paratype: BYU 1570. 2. *Matonidium brownii* Rushforth. Trilete spore illustrating weakly defined margo. (X1200). Paratype: BYU 1561. 3. *Matonidium americanum* Berry em. Rushforth. Two pinna fragments. (X1.2). BYU 1572. 4. *Matonidium americanum* Berry em. Rushforth. Portions of two pinnae illustrating venation. (X3.6). BYU 1572.

which when fertile may be placed into several different genera and even families.

Fontaine (1889) treated 23 species and several varieties of *Cladophlebis* from the American Potomac Group. However, Berry (1912) revised this genus, as known from the Potomac, and recognized eight species. As mentioned by Berry, Fontaine recorded this high number of species:

. . . altogether losing sight of variation and changes due to age or to position of the fossils with regard to the frond as a whole, as well as changes due to the direct action of the environment.

Seward (1894) in treating Wealden fossils in the British Museum of Natural History accepted the generic diagnosis of Schimper (1874) as emended by Fontaine (1889). Berry (1912) also followed this same generic diagnosis, and most workers subsequent to Berry have done likewise.

The literature dealing with *Cladophlebis* is voluminous and is in need of reviewing. Many species are recognized, although this is to be expected in any unnatural genus as reproductive morphology may not be compared. However, many species appear to be identical, and the genus should be monographed.

Cladophlebis constricta Fontaine em. Berry

Figs. 9-5; 11-1.

1889 *Cladophlebis constricta* Fontaine—U.S. Geol. Surv. Mon. 15, p. 68, Pl. 2, Fig. 11; Pl. 3, Fig. 2; Pl. 6, Figs. 5, 6, 8-14; Pl. 21, Figs. 9, 13; Pl. 169, Fig. 2.

1888 *Cladophlebis latifolia* Fontaine—U.S. Geol. Surv. Mon. 15, p. 68, Pl. 3, Fig. 1; Pl. 6, Fig. 4.

1904 *Cladophlebis constricta* Fontaine, in Ward—U.S. Geol. Surv. Mon. 48, p. 197, Pl. 71, Fig. 26.

1905 *Cladophlebis virginensis* Fontaine, pro parte, in Ward—U.S. Geol. Surv. Mon. 48, p. 512, Pl. 111, Fig. 7.

91 *Cladophlebis constricta* Fontaine, Berry—Proc. U.S. Nat. Mus., v. 41, p. 314.

DESCRIPTION.—Entire leaf unknown; pinnules typically greater than 27 mm long by 10 mm wide, margins deeply lobed up to one-half of the distance to the midvein, lobe margins entire, lobe apices obtuse; midvein very strong; secondary veins repeatedly forked, open to the margin; fertile specimens unknown.

OCCURRENCE.—Near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1841.

DISCUSSION.—This fern is known from the Westwater flora only from a single specimen. This specimen illustrates fragments of two pinnules each of which is rather well preserved, exhibiting venation well.

This specimen agrees well with some specimens placed by Fontaine (1889) in *Cladophlebis constricta*, especially Pl. 2, Fig. 11a. However, due to the paucity of fossil material from Westwater, it is not known if the Utah specimens agree in all details with the specimens from Virginia. Even though this is the case, venation, overall size, and pinnule lobing, are all in agreement with *C. constricta* Fontaine em. Berry, and the author believes these similarities are sufficient to warrant the placement of the Westwater fern in this species.

Cladophlebis parva Fontaine em. Berry

Figs. 8-5; 11-2.

1889 *Cladophlebis parva* Fontaine—U.S. Geol. Surv. Mon. 15, p. 73, Pl. 4, Fig. 7; Pl. 6, Figs. 1-3.

1899 *Cladophlebis parva* Fontaine, in Ward—U.S. Geol. Surv. 19th Ann. Rept., pt. 2, p. 657, Pl. 160, Fig. 18.

1904 *Cladophlebis parva* Fontaine, in Ward—U.S. Geol. Surv. Mon. 48, p. 125, Pl. 65, Figs. 5-8.

1911 *Cladophlebis parva* Fontaine, Berry—Maryland Geol. Surv., Low. Cret., p. 250, Pl. 27, Figs. 1-2; Pls. 39-31.

1912 *Cladophlebis parva* Fontaine, Berry—Proc. U.S. Nat. Mus., v. 41, p. 316.

1956 *Cladophlebis parva* Fontaine, Bell—Geol. Surv. Can. Mem. 285, p. 56, Pl. 11, Figs. 3-5; Pl. 12, Fig. 3; Pl. 13, Figs. 1-2; Pl. 14, Fig. 3; Pl. 14, Fig. 3.

DESCRIPTION.—Entire leaf unknown; pinnae probably lanceolate; rachis about 1 mm in diameter; pinnules alternate, linear-lanceolate, up to 26 mm long by 6 mm wide, lobed approximately one-half of the way to the midrib, margins of lobes slightly undulate, apices acute, attachment basal to somewhat constricted basal; midvein prominent, undivided to pinnule apex; secondary veins divide from one to three times, remain free; fertile specimens unknown.

OCCURRENCE.—Near Westwater, Grand County, Utah.

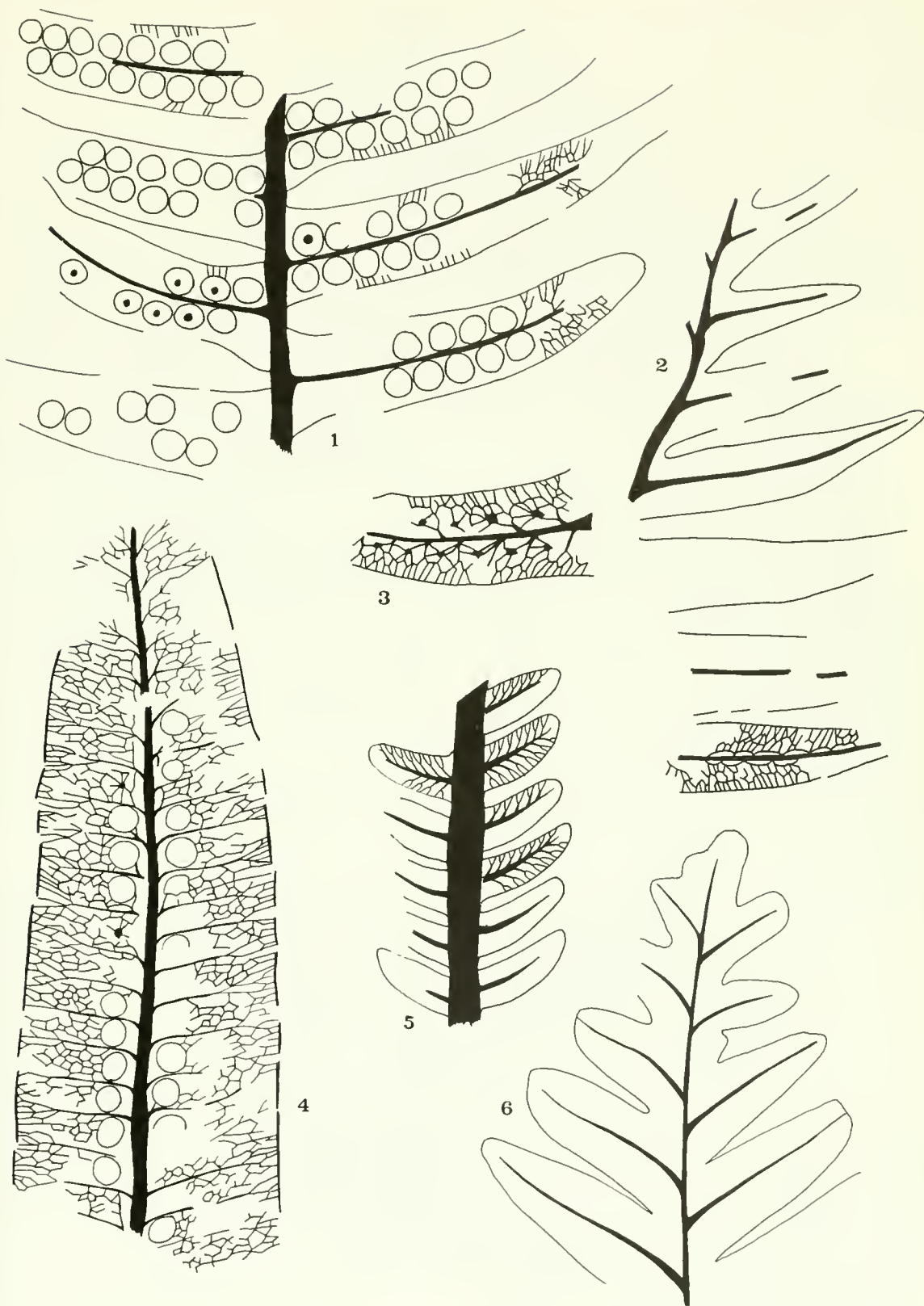


FIG. 19. 1. *Matonidium brownii* Rushforth. Pinna fragment illustrating sori and venation. (X3). Paratype: BYU 1563. 2. *Matonidium* (?) *lancipinnulum* Rushforth. Pinna fragment illustrating pinnule disposition and venation. Holotype: BYU 1569. 3. *Matonidium brownii* Rushforth. Pinnule exhibiting venation. (X3). Paratype: BYU 1559. 4. *Astralopteris coloradensis* Reveal, Tidwell, and Rushforth. Pinnule exhibiting venation. (X3). BYU 1837. 5. *Matonidium americanum* Berry em. Rushforth. Pinna fragment exhibiting venation. (X3). BYU 1831. 6. *Matonidium brownii* Rushforth. Pinna apex illustrating pinnule disposition. (X3). BYU 1835.

REPOSITORY.—Brigham Young University, BYU 1842.

DISCUSSION.—*Cladophlebis parva* Fontaine em. Berry is known only from one specimen in the Westwater flora. This specimen illustrates several pinnules on a pinna fragment, a few of which are rather complete. This fern from the Westwater locality has been assigned to *Cladophlebis parva* based upon venation, pinnule shape and habit, and size. However, it is always difficult to place fragments of *Cladophlebis* accurately, and this fern resembles several other species of *Cladophlebis*.

Division

ANTHOPHYTA (MAGNOLIOPHYTA)

Family AQUIFOLIACEAE

Genus ILEX L.

Ilex serrata Rushforth, sp. nov.

Figs. 12-5; 16-2.

DESCRIPTION.—Leaves vary from fairly short and wide (3.5 cm long by 1.7 cm wide) to longer and thinner (4 cm long by 1 cm wide), somewhat coriaceous, angular-ovate; apex acute to acuminate; base narrowing to the petiole; margins serrate to somewhat spinose; petiole short; midvein weak, continuing to apex; secondary veins mostly obscured, borne at acute angles, progressing to margin.

OCCURRENCE.—Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, holotype: BYU 1801; paratype BYU 1892.

DISCUSSION.—Leaves assigned to this species from near Westwater are somewhat similar to *Ilex dakotensis* Lesquereux in shape and size. However, the leaf originally placed in *I. dakotensis* does not exhibit serrate margins, and venation differs somewhat from Utah specimens. In overall shape, the Westwater material agrees rather closely with *Ilex stenophylla* Unger from the Tertiary of Europe, as does *Ilex dakotensis*. However, Lesquereux (1892) pointed out that these two species differ in size and somewhat in shape. In addition, *I. stenophylla* is not serrate to spinose as is the Utah *Ilex*.

Ilex serrata differs from other species of *Ilex* in its small size coupled with spinose margins. In margination, *I. serrata* is similar to *I. armata* Lesquereux, although the latter is much larger and of different shape than *I. serrata*.

Family MAGNOLIACEAE

Genus MAGNOLIA L.

Magnolia boulayana Lesquereux

Fig. 16-1.

1792 *Maglonia boulayana* Lesquereux—U.S. Geol. Surv. Mon. 17, p. 202, Pl. 60, Fig. 2.

1894 *Magnolia glaucoides* Hollick—Bull. Torrey Bot. Club, v. 21, p. 60, Pl. 175, Fig. 1-7.

1895 *Magnolia glaucoides* Hollick, Newberry—U.S. Geol. Surv. Mon. 26, p. 74, Pl. 47, Figs. 1-4.

1995 *Magnolia glaucoides* Hollick—U.S. Geol. Surv. Mon. 50, p. 67, Pl. 19, Fig. 6; Pl. 20, Fig. 6.

1909 *Magnolia boulayana* Lesquereux, Berry—Bull. Torrey Bot. Club, v. 36, p. 254.

1911 *Magnolia boulayana* Lesquereux, Berry—New Jersey Geol. Surv. Bull. 3, p. 131, Pl. 14, Fig. 2.

DESCRIPTION.—Leaf greater than 7.5 cm long by 4 cm wide, narrowly elliptic in outline, coriaceous; base rounded to bluntly rounded; margins entire; midvein strong, bearing somewhat infrequent secondaries; secondary veins pinnate, parallel, progressing to near margin and then bending to unite with vein above to form rounded areoles near the margin; tertiary veins connecting the secondaries.

OCCURRENCE.—Near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1843.

DISCUSSION.—Berry (1911) noted that leaves of *Magnolia boulayana* Lesquereux are remarkably constant in size and shape. This is particularly noteworthy when it is recalled that this constancy extends over wide geographical areas and for a good deal of time.

Berry (1911) noted that leaves assigned to *Magnolia glaucoides* Hollick by Hollick and Newberry are identical to leaves of *M. boulayana*. In view of this, Berry placed *M. glaucoides* in synonymy under *M. boulayana*.

Placement of the Utah *Magnolia* in *Magnolia boulayana* Lesquereux may be made without hesitation, as size, shape, and venation are all identical between the two.

Family MORACEAE

Genus FICUS L.

This genus in regard to the Mesozoic has become more of a form genus than a natural



FIG. 20. *Astralopteris coloradica* Reveal, Tidwell, and Rushforth. Pinna exhibiting pinnule disposition. (X1.2).
BYU 1415.

unit. Into this genus are placed leaves which are somewhat similar in that they exhibit lauraceous characteristics. However, Cretaceous leaves placed in this genus often could be placed with equal logic in various other genera such as *Salix* or *Laurus*.

Ficus daphnogenoides (Heer) Berry

Figs. 16-3, 16-4.

1867 *Proteoides daphnogenoides* Heer, in Capellini and Heer—Denksch. Allgem. Schweiz. Ges. Naturwiss., v. 22, p. 17, Pl. 4, Figs. 9-10.

1874 *Proteoides daphnogenoides* Heer, Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 85, Pl. 15, Figs. 1-2.

1905 *Ficus daphnogenoides* (Heer) Berry—Bull. Torrey Bot. Club. v. 32, p. 329, Pl. 21.

1921 *Ficus daphnogenoides* (Heer) Berry—U.S. Geol. Surv. Prof. Paper 129, p. 163, Pl. 39, Fig. 1.

1959 *Ficus daphnogenoides* (Heer) Berry, Brown—U.S. Geol. Surv. Prof. Paper 221-D, p. 50, Pl. 11, Figs. 1, 2, 4.

DESCRIPTION.—Leaves typically greater than 12 cm long by 3 cm wide, more or less oblanceolate; apex acuminate, forming a rather long drip point; base cuneate; margins entire; midvein strong at point of origin, becoming weaker towards leaf apex; secondary veins pinnate, arising acutely, bending to parallel margin; tertiary veins obscured.

OCCURRENCE.—Near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1844-7846.

DISCUSSION.—Lesquereux (1874) described *Proteoides daphnogenoides* Heer (*Ficus daphnogenoides*) as follows:

Leaves ovate-lanceolate near the base, gradually tapering upward to a long, acute, scythe-shaped point, entire, smooth, and coriaceous; medial nerve narrow; secondary veins obsolete, few, ascending under a very acute angle from the medial nerve and following the borders.

This description fits the Westwater *Ficus* in all respects, and the identity of the two may be fairly certain.

Berry (1905) transferred *Proteoides daphnogenoides* Heer to the genus *Ficus*. This transfer was valid, although Brown (1950) remarked:

These entire-margined leaves have been referred to many different genera with little

satisfaction, as might be expected for entire leaves, the internal venation structure of which tends in many toward similarity. I regard this reference to *Ficus* as makeshift. Many similar leaves from the Dakota Sandstone have been referred with little evidence to *Andromeda*. All are perhaps examples of lauraceous species that are difficult to separate.

Family MYRTACEAE

Genus EUCALYPTUS L. Herit
Eucalyptus dakotensis Lesquereux

Fig. 15-8.

1892 *Eucalyptus dakotensis* Lesquereux—U.S. Geol. Surv. Mon. 17, p. 137, Pl. 37, Figs. 14-19.

1895 *Eucalyptus angustifolia* Newberry—U.S. Geol. Surv. Mon. 26, p. 111, Pl. 32, Figs. 1, 6, 7.

1895 *Eucalyptus* (?) *nervosa* Newberry—U.S. Geol. Surv. Mon. 26, p. 111, Pl. 32, Figs. 3-5, 8.

DESCRIPTION.—Leaf linear, 4.5 cm long by 1.1 cm wide, somewhat coriaceous; base cuneate; margins entire; midvein strong; secondary veins pinnate, arising obtusely, extending to leaf margin.

OCCURRENCE.—Near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1848.

DISCUSSION.—Lesquereux (1892) described *Eucalyptus dakotensis* as follows:

Leaves coriaceous, linear, or gradually narrowed from an obtuse apex to the base, decurring into short, alate petiole; borders recurved, median nerve strong; secondaries thin, oblique, proximate, parallel, camptodrome.

Lesquereux further pointed out that the margin of some specimens was flat rather than recurved.

Eucalyptus angustifolia Newberry and *E.* (?) *nervosa* Newberry appear to be specifically identical both with each other and with *E. dakotensis* Lesquereux. The only apparent difference is that the petiole of *E. angustifolia* is naked rather than alate.

The Westwater *Eucalyptus* also agree well with the description of Lesquereux (1892), except that the petiole of the Utah specimen is not winged. However, this difference does not warrant specific separation, and *E. dakotensis* is used for placement of the Westwater specimen.

As mentioned by Lesquereux (1892) *E. dakotensis* differs from an apparently closely related form, *E. geinitzi* in that the former is smaller and linear in shape as opposed to larger and broadly spatulate in shape.

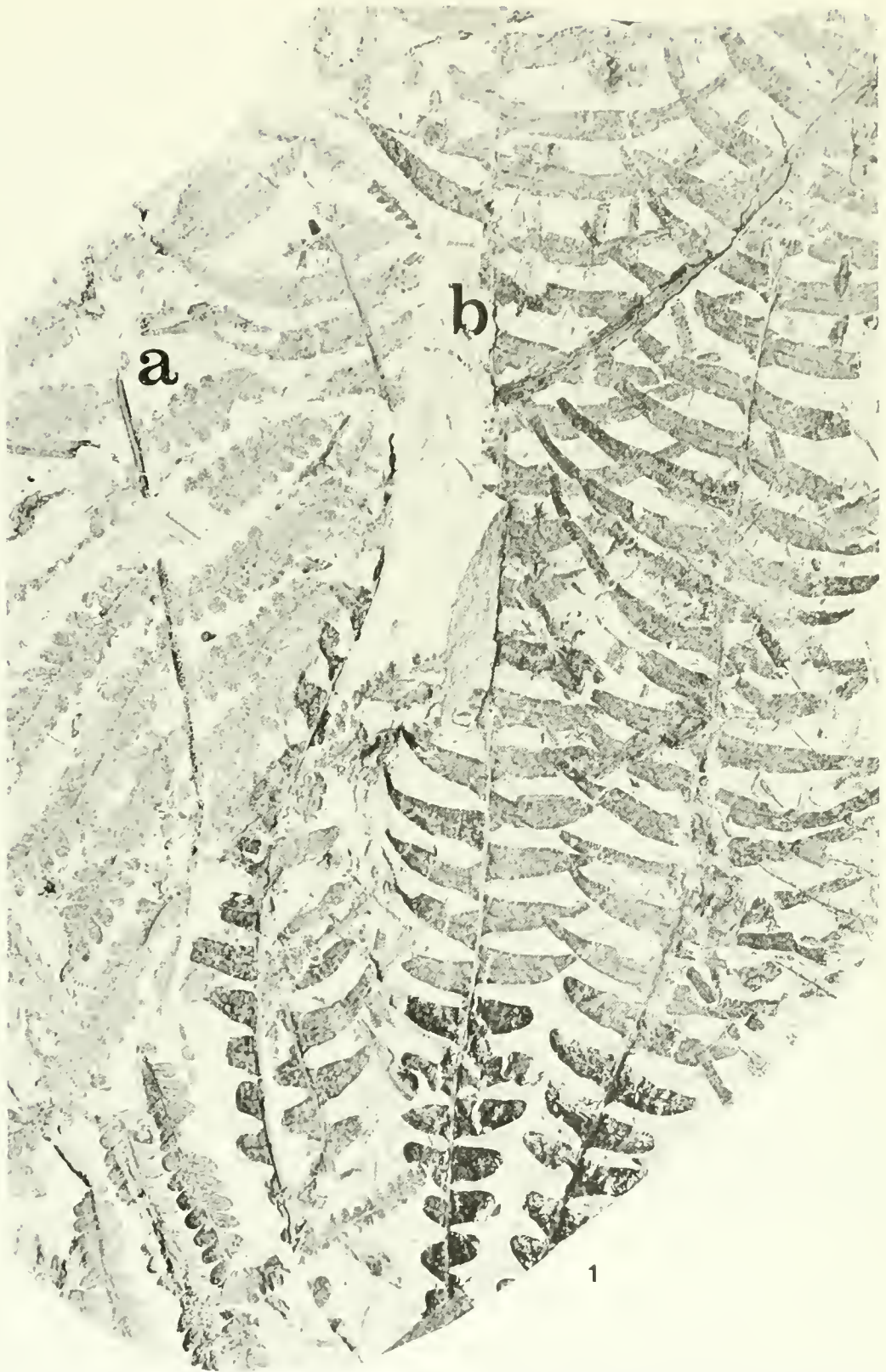


FIG. 21. A. *Gleichenia comptoniacifolia* (Deb. and Ett.) Heer, Pinna fragments exhibiting pinnule disposition. (X1.5). BYU 1853a. B. *Matonidium brownii* var. *magnipinnulum* Rushforth. Pinna fragments. (X1.5). BYU 1853b.

Family PLATANACEAE

Genus PLATANUS L.

Leaves of the genus *Platanus* from the Cretaceous are well known and rather common. Many of these leaves are essentially indistinguishable from those of extant species (Seward, 1927).

Platanus newberryana Heer

Fig. 16-6.

1867 *Platanus newberryana* Heer, in Capellini and Heer—Denksch. Allgem. Schweiz. Ges. Naturwiss., v. 22, p. 16, Pl. 1, Fig. 4.

1868 *Platanus newberryana* Heer. Lesquereux—Amer. Jour. Sci., v. 46, p. 97.

1874 *Platanus newberryana* Heer, Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 72, Pl. 8, Figs. 2-3; Pl. 9, Fig. 3.

1874 *Platanus affinis* Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 71, Pl. 4, Fig. 4.

1873 *Protophyllum minus* Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 194, Pl. 27 Fig. 1.

1874 *Protophyllum nebrascense* Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 6, p. 103, Pl. 27, Fig. 3.

1882 *Platanus affinis* Lesquereux, Heer—Flor. Foss. Arct., v. 6, pt. 2, p. 73, Pl. 18, Figs. 16-17.

1883 *Platanus newberryana* Heer, Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 8, p. 28, Pl. 59, Figs. 1-6; Pl. 60, Fig. 1.

1883 *Cissites affinis* Lesquereux—U.S. Geol. Surv. Terr. Rept., v. 8, p. 67.

1927 *Platanus newberryana* Heer, Seward—Phil. Trans. Roy. Soc. London B, v. 215, p. 128, Pl. 11, Fig. 116; Text-Fig. 30.

DESCRIPTION.—Leaf greater than 5 cm long by 3 cm wide, coriaceous; base rounded; midvein strong bearing numerous secondary veins at acute angles; secondary veins apparently extend to margin (caspodrome); tertiary veins numerous, borne at nearly 90° angles to secondary veins, connecting secondaries.

OCCURRENCE.—Dakota Sandstone Formation near Rabbit Valley, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1849.

DISCUSSION.—This leaf agrees in all details with *Platanus newberryana* Heer, and is very similar to leaves figured under this species by Lesquereux and Seward. In addition, it is very similar to leaves described as *Platanus affinis*, *Protophyllum minus*, and *Protophyllum nebrascense* by Lesquereux (1874, 1882). The Westwater leaf exhibits a rounded to angular base, which agrees with the description of *Platanus newberryana* by Lesquereux (1874), although in this respect it differs somewhat from specimens placed in this species by Seward (1927) which exhibited very rounded bases.

Seward (1927) noted that leaves of *Platanus newberryana* "agree very closely with the recent *Platanus mexicana* Moric."

Family SALICACEAE

Genus SALIX L.

Salix newberryana Hollick

Figs. 12-4; 15-7.

1895 *Salix newberryana* Hollick, in Newberry—U.S. Geol. Surv. Mon. 26, p. 68, Pl. 14, Figs. 1-7.

1911 *Salix newberryana* Hollick, Berry—New Jersey Geol. Surv. Bull. 3, p. 113, Pl. 11, Fig. 2.

DESCRIPTION.—Leaves greater than 6 cm long by up to 2.5 cm wide, lanceolate; base rounded; apex acuminate to form a rather well defined drip point; margins finely crenate to dentate; midvein fairly strong; other veins obscure.

OCCURRENCE.—Dakota Sandstone Formation near Westwater, Grand County, Utah.

REPOSITORY.—Brigham Young University, BYU 1850-1851.

DISCUSSION.—This leaf from Westwater is essentially identical to those described by Hollick (in Newberry, 1895) and Berry (1911). It may be placed with confidence in *Salix newberryana* Hollick.

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