A Morphotype Catalogue, Floristic Analysis and Stratigraphic Description of the Aspen Shale Flora (Cretaceous–Albian) of Southwestern Wyoming

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Abstract

We describe 28 fossil plant morphotypes from the Aspen Shale flora (Cretaceous: middle to late Albian) in southwestern Wyoming. This impression flora includes 6 ferns, 1 sphenopsid, 2 conifers, 17 dicotyledonous angiosperm (dicot) leaves and 2 dicot reproductive structures. The Aspen Shale megaflora is most similar to that of Subzone IIB of the Potomac Group of the eastern United States. Analysis of the Aspen Shale sedimentology and botanical composition shows occupation of open, paludal sites by a succession of progressively more complex plant communities. Like other middle Cretaceous floras, these data suggest that early angiosperms were weedy, herbaceous to shrubby, early successional competitors to ferns on open substrates. The description and illustration of the Aspen Shale morphotypes is presented as an example of how an entire flora can be described and analyzed before full taxonomic determinations have been made.

Keywords

Paleobotany, morphotype, Aspen Shale, early angiosperm, early succession, Albian, Early Cretaceous, Wyoming, floral catalogue.

Introduction

Fossil floras can provide important insights into land-plant evolution, paleocology, biogeography and climate (e.g., Hickey and Doyle 1977; Graham 1999; Hoffman and Stockey 1999; Manchester 1999; Wilf, Johnson et al. 2003; Peppe et al. 2007). A traditional floristic monograph includes taxonomic and systematic descriptions of all entities in a flora. However, taxonomic and systematic identifications are seldom completed, because the assignment of each entity to its correct systematic group and taxon requires knowledge of: (1) plant morphology; (2) the systematic distribution of plant characters; (3) phylogenetic relationships; (4) the detailed taxonomy of a wide range of plant groups; and (5) extensive research into the nomenclature of each taxon. There are also inherent difficulties in dealing with fossil plant material: preservation is always incomplete, organs are often separated, characters are often enigmatic, and many extinct species and genera have no modern relative to alleviate these problems. Furthermore, a large proportion of older paleobotanical literature is full of nomenclatural errors, misidentifications and imprecise, inaccurate and missing descriptions and illustrations of species (see discussions in Hickey 1973; Dilcher 1974; Hickey and Wolfe 1975). Thus, any taxonomic study of a fossil flora is a tedious and time-consuming process that greatly impedes the timely realization of the flora's broader potential.

Despite these difficulties, once operational taxonomic units have been established for a fos-

Table 1. Lithostratigraphic section for Aspen Shale locality. Unit is the stratigraphic bed; unit thickness is the total thickness of the stratigraphic unit and total thickness is the measure of the stratigraphic section. Stratigraphic levels of floral localities are indicated in bold.

Unit	Unit thickness (cm)	Total thickness (cm)	Lithologic description of each stratigraphic unit
1	400	400	Medium grey silty shale, with 2 to 4 cm interbeds of tuffaceous siltstone or rusty grey-brown, fine-grained sandstone.
2	100	500	Medium grey tuff, porcellaneous, aphanitic. Parallel bedded. Unit forms a resistant shoulder.
3	90	590	Medium grey claystone, porcellaneous with parallel interbeds of yellowish grey, fine-grained, tuffaceous sandstone from 5 to 20 cm-thick.
4	560	1150	Tannish grey silty shale, with a tannish grey, resistant (tuffaceous), porcellaneous bed 3.1 m above the base that thickens from 10 cm to 40 cm westward in the outcrop.
5	50	**1200**	Sandstone, very fine-grained, tuffaceous, downcut 0.5 m into underlying shale laterally. Trough cross-bedded at base; becoming plane-bedded at top. Thins westward in outcrop. Flora 0026α
6	60	1260	Yellow-grey siltstone, porcellaneous, blocky, hackly, with some vertical limonite staining.
7	20	1280	Light yellowish grey siltstone, porcellaneous, massive, blocky.
8	60	**1340**	Light grey tuff, blocky. Upper 15 cm weathers to a punky texture, with limonite staining and poorly preserved rhizomorphs. Flora 0026a
9	60	1400	Medium grey porcellinite, with vertical and horizontal rhizomorphs.
10	120	**1520**	Light yellow-grey siltstone, massive, blocky weathering, tuffaceous. Has parallel and low-angle cross-lamination in the basal 40 cm. A 20-cm bed of light grey, tuffaceous siltstone, with vertical rhizomorphs occurs 0.8 m above the base. The uppermost 20 cm is a tuff with vertical and horizontal rhizomorphs and mats of fern rachises. Flora 0026b
11	30	1550	Light yellowish grey silty tuff, chippy, with small plant fragments and a twisted pinna of a AS1 at the base of the unit.
12	290	1840	Greenish grey siltstone, blocky weathering, with carbon films and irregular bedding. Becomes medium greenish grey with rhizomorphs and poorly preserved plant scraps laterally.
13	20	1860	Light yellowish grey siltstone.
14	130	1990	Greenish grey siltstone, blocky weathering, with carbon films and irregular bedding.
15	200	2190	Greenish grey claystone, blocky, aphanitic. Mottled with limonite and has disrupted texture, but contains no peds or rhizomorphs. Poorly resistant.
16	90	2280	Greenish grey tuff, blocky weathering but massive, forms a ledge.
17	30	**2310**	Olive grey to light grey tuff, aphanitic. Flora 0026c.
18	70	2380	Olive grey siltstone, poorly resistant. Becoming more resistant and aphanitic 50 cm above the base, with the uppermost 10 cm consisting of a light grey silty tuff.
19	10	2390	Siltstone, tuffaceous.
20	170	**2560**	Medium olive grey, siltstone. Becomes more resistant in the topmost 40 cm. Flora 0026d occurs in uppermost 15 cm.
21	60	2620	Sandstone, very fine-grained, with low angle cross-lamination at the base, which appears to be downcutting.

sil flora a range of methods can be applied to them. These include: inference of paleoclimatology (e.g., Bailey and Sinnot 1915; MacGinitie 1953; Wolfe 1979; Wing and Greenwood 1993; Wolfe 1993; Wilf 1997; Wilf et al. 1998; Forest et al. 1999; Burnham et al. 2001; Jacobs 2002; Huff et al. 2003; Kowalski and Dilcher 2003; Greenwood et al. 2004; Greenwood et al. 2005; Royer et al. 2005; Miller et al. 2006; Meyer 2007); paleoecology (e.g., Spicer 1989; Wing et al. 1993; Wilf, Cuneo et al. 2003; Green and Hickey 2005; Royer et al. 2005; Wilf et al. 2005; Royer et al. 2007); and biostratigraphic zonation (e.g., Crabtree 1987; Johnson and Hickey 1990; Johnson 2002; Wilf and Johnson 2004). These studies can be especially informative when the biotic data are analyzed in relation to the sedimentologic and stratigraphic framework of the deposit in which the plants occur. However, precisely because of the difficulties involved in their taxonomic identification, studies of whole floras have lagged seriously over the last 40 years or so, just as these powerful new tools have been developed.

Because the methods described above can be used even when only morphologic operational taxonomic units are employed, one solution to the taxonomic problem is to handle paleobotanical data outside of a Linnaean framework. In palynology (e.g., Potonié 1956–1975; Hughes 1970, 1976; Traverse 1988) and in megafloral paleobotany (Ferguson 1971) researchers have designed non-Linnaean systems for floral analysis. However, these systems are all still hierarchical and rank-based and, in the case of the Ferguson (1971) study, the system placed species level operational taxonomic units in the lowest Linnaean taxonomic rank possible (class to genus).

Our approach is based on the morphotype concept described in Johnson (1989). This method is independent of the Linnaean system and uses morphological characteristics of the various categories of plant organs, such as leaves or fruits, to differentiate a flora into operational taxonomic units. Morphotypes are "selected to express the total variety of distinct topologic entities present in a flora" (Johnson 1989:70). There can be multiple morphotypes within one species (e.g., *Cercidiphyllum genetrix*: Brown 1939, 1962; Hickey 1977) and multiple species or even genera in a single morphotype (e.g., *Sabalites*: Read and Hickey 1972). When the work of establishing morphotypes has been carefully done on large collections of fossil plants, the resulting categories will often, but not always, coincide with biologic species. Morphotypes are unique to the study site, study area or formation, and to the researchers working on a particular collection. The morphotype system allows for rapid classification of floras and makes it possible to focus on questions of interpretation rather than on taxonomic issues. As time permits, the morphotypes can later be attributed to a Linnaean taxon.

In this paper we provide a catalogue of the Aspen Shale flora for the use of the morphotype method for the rapid documentation of an entire flora. In our view, a floral catalogue should, at a minimum, include descriptions and illustrations of all morphotypes in a flora. It should also give sufficiently detailed geographic and stratigraphic information to identify the site and the age of the flora. In this catalogue we have also included preliminary taxonomic information, limited synonymies and detailed sedimentological and environmental interpretations of the site. The morphotypes described in this catalogue are divided into three categories: (1) those identified strictly as numerical morphotypes; (2) those recognized as morphotypes whose previously published taxonomic name we regard as invalid or illegitimate, or whose assignment is incorrect or doubtful; and (3) those that can be assigned to valid and legitimate species with a reasonable degree of certainty.

The Aspen Shale flora is significant as one of the few Early Cretaceous angiosperm floras in the Rocky Mountain region (Crabtree 1987; McClammer and Crabtree 1989). Because of its potential to provide a window on the timing, rates and ecology of early angiosperm occupation of the region, we feel that it is important to publish what we know of the flora in advance of its full taxonomic study.

Locality and Geologic Setting

The Aspen Shale plant locality (designated LJH9918 and LJH0026; the latter is used throughout the remainder of this paper) is on the south side of the junction of Roney (formerly Everly) Creek and Fontenelle Creek (lat 42.08°N, long 110.16°W), approximately 30 km north of

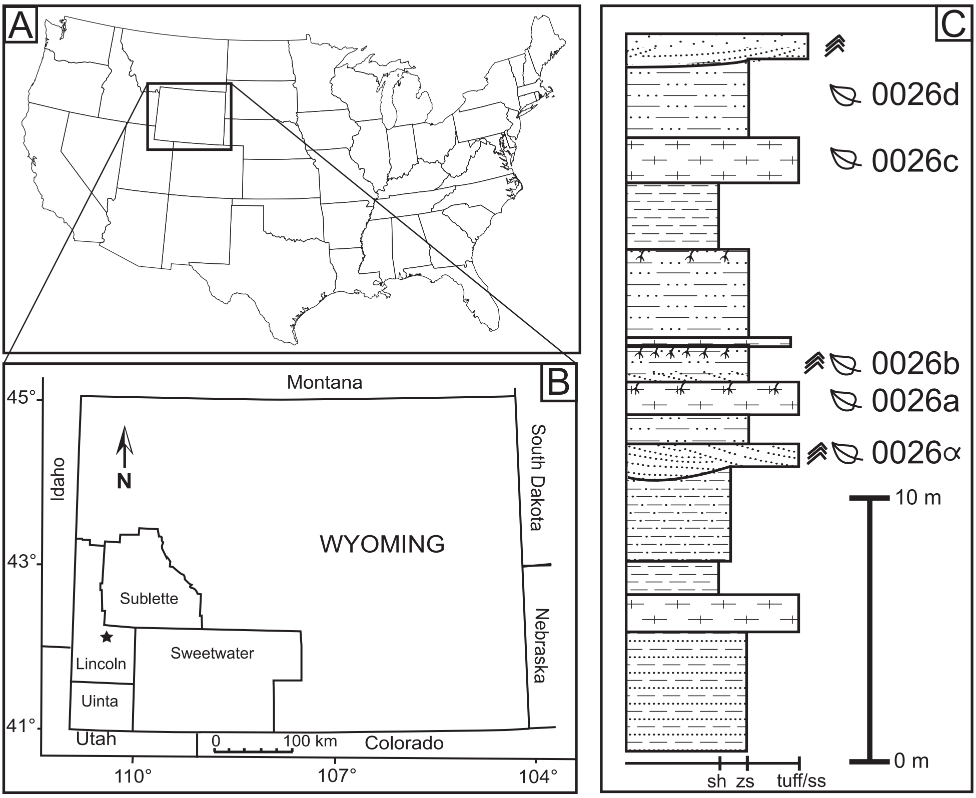

FIGURE 1. **A, B.** Fossil leaf locality, indicated by star in B. **C.** Stratigraphic section of locality LJH0026. The stratigraphic position of floral levels is shown on the right (sh, shale; zs, siltstone; tuff/ss, tuffaceous unit/sandstone).

Kemmerer, in Lincoln County, Wyoming, USA, in the so-called Overthrust Belt (Figure 1). Roland W. Brown visited the site in 1930 and wrote the only published report on it 3 years later (Brown 1933). To our knowledge, no major collecting occurred at this locality until its rediscovery by Hickey in 1999 and a subsequent visit by Hickey and Green in 2000. A small collection made by S. Manchester, P. Crane and M. Collinson and is housed at the Field Museum in Chicago (S. Manchester, personal communication 2008).

The fossil plant locality lies within 40 m of the upper contact of the Aspen Shale. This formation consists of black shale, dark grey arenaceous shale and drab grey sandstone between 400 and 600 m thick (Schultz 1914). Its strata dip westward and form a series of rounded, elongate, north–south trending hills west of a high, continuous ridge of the overlying Frontier Formation. The Aspen Shale is thought to be predominately marine, because of the presence of abundant fish scales and rare linguloid brachiopods, ammonites and pelecypods (Schultz 1914; Reeside and Weymouth 1931). However, the Aspen Shale strata at the plant site seem to have been deposited in a paludal setting and contain a significant component of volcaniclastic sediment. The Aspen Shale overlies the Bear River Formation. The dark-colored shale, thin-bedded limestone and sandstone of the marine Bear River Formation form a belt of topographically more subdued landscape to the east of the Aspen outcrop (Schultz 1914). These formations range in age from Albian for the Bear River and the Aspen to Cenomanian for the Frontier (e.g., Nichols and Jacobson 1982; M`Gonigle et al. 1995).

Stratigraphy and Sedimentology

The stratigraphic section at the Aspen Shale plant locality (see Figure 1; Table 1), contains a high concentration of volcaniclastic material, with several beds of porcellaneous tuff. The basal 11 m of the section consists of parallel-bedded, fissle shale with 2 to 4 cm interbeds of tuffaceous siltstone. This is separated into two units (1 and 4) by a 2 m thick interval of tuff (unit 2) and interbeds of tuffaceous sandstone and siltstone (unit 3). The upper shale bed also contains a lens of tuff (up to 40 cm thick). Weathering colors in the lower sequence are predominantly medium grey.

The plant-bearing interval comprises the upper 14 m of the section and lies above a downcut surface at the base of the sandstone designated as unit 5 (see Figure 1; Table 1). Although the strata above that level are still highly tuffaceous, there is a marked change in the type of sedimentary structures, with disrupted bedding, vertical and horizontal rhizomorphs, carbon films, mottling and yellow grey to greenish grey weathering in various intervals (especially toward the upper boundaries of units) throughout the sequence. While Brown (1933) only described one fossiliferous bed, we found fossil plants in 5 distinct beds. One of these (unit 5) is a tuffaceous sandstone, 3 are tuffs (units 8, 11 and 17) and the uppermost (unit 20) is a massive siltstone. Units 17 and 20 are probably the main sources of Brown's published flora.

Sedimentary Interpretation

The stratigraphic section seems to represent a change from predominantly marine to terrestrial sedimentation after a lowering of base level that allowed incipient soils to develop before being inundated by ash falls or debris flows. The floras here are interpreted as representing a series of early successional fern-dominated, and later angiosperm-dominated, communities that colonized a bare substrate and grew until they were destroyed by an episode of sedimentation. Tuff beds in the terrestrial part of the section are frequently laminated and are barren of plant remains, except toward their bases and tops. The basal few centimeters of a typical tuff bed often contain comminuted plant matter that sometimes seems to have been charred or burned. The upper 10 to 40 cm of a typical tuff frequently show a steady increase in brownish coloration and an increase in carbon content. Rhizomorphs and limonite staining, especially on incipient cutans, are present in the upper interval of typical tuff beds. Recognizable plant fossils in mats of plant remains occur in the uppermost 15 to 20 cm of the plant-bearing beds. Each of these assemblages seems to represent a pioneer plant community that was colonizing an incipient soil developing on the upper surface of an ash flow or, in the case of unit 20, on a floodplain soil.

Methods

Stratigraphic and Floral Collection Methods

The section was measured by first exposing bedrock and bedding contacts, then systematically logging the beds to the nearest centimeter using an Abney level and a Jacob staff. During logging of the section, the lithology, lithologic unit thickness, sedimentary structures, fossil content and Munsell color were recorded. Beds were physically traced laterally to determine the extent of the floral deposits.

During fossil collecting, the floral levels were logged into the measured section in stratigraphic order: flora LJH0026α was collected from unit 5, flora LJH0026a from unit 8, LJH0026b from unit 11, LJH0026c from unit 17 and LJH0026d from unit 20 (see Figure 1, Table 1). A preliminary floral collection was made in 1999 and floral census collections were made in 2000 from floras LJH0026b, LJH0026c and LJH0026d. During the census collection, all identifiable leaf specimens were tallied and examples of each morphotype were collected, and the distribution and abundance of specific morphotypes among the designated stratigraphic intervals was tabulated (Table 2). The specimens are curated at the Peabody Museum of Natural History at Yale University.

Floral Description

In this treatment, we include descriptions and figures of all morphotypes. The morphotypes are ordered according to broad taxonomic category (i.e., ferns and sphenopsids, conifers and dicotyledonous angiosperms [dicots]). The dicots are first classified by organ type. The leaves are grouped by their organization and margin. We have included limited synonymies. However, note that, for all synonymies, the described morphotype can only be related to the cited publications and not necessarily to the type specimen or to other references to the species. The morpho-

Table 2. List of morphotypes, their presence or absence, and census data for Aspen Shale flora. *Abbreviations:* For affinity into taxonomic category (Affinity): FER, fern; SPH, sphenopsid; CON, conifer; DIC, dicotyledon. For plant organ (Plant): L = leaf; R = reproductive structure. For organization of angiosperm leaf (Org): S, simple leaf; C, compound leaf; –, absent. For dicotolydon angiosperm leaf margin type (Margin): E, entire; T, toothed; –, absent. For fossil leaf levels at Aspen Shale locality (LJH0026α, LJH0026a, LJH0026b, LJH0026c, LJH0026d) ×, presence; –, absence; the number of specimens tallied in the census collection is given in parentheses.

						Locality levels				
Affinity	**Plant**	**Org**	**Margin**	**Morphotype number**	**Taxon**	**LJH 0026α**	**LJH 0026a**	**LJH 0026b**	**LJH 0026c**	**LJH 0026d**
FER	L	–	–	AS1	"*Amenia*" *freemontii*	–	×	×(75)	×(23)	–
FER	L	–	–	AS2	*Baieropsis* sp.	–	×	×(54)	×(5)	–
FER	L	–	–	AS3	*Cladophlebis readii*	×	×	×(14)	×(1)	×(0)
FER	L	–	–	AS4		–	–	×(0)	–	×(0)
FER	L	–	–	AS5	"*Microtenia paucifolia*"	–	–	–	–	×(25)
FER	L	–	–	AS6	"*Asplenium*" *occidentale*	–	–	–	×(0)	–
FER	L	–	–	AS26	*Housemania* sp.	–	–	–	–	×(0)
SPH	L	–	–	AS12	*Equisitites* sp.	–	–	×(0)	–	×(12)
CON	L	–	–	AS7		–	–	–	×(18)	–
CON	L	–	–	AS8		–	–	–	–	×(1)
DIC	R	–		AS9	"*Sparganium*" *aspensis*	–	–	–	×(12)	×(1)
DIC	R	–		AS33		–	×	–	–	–
DIC	L	S	E	AS16		–	–	–	×(9)	×(0)
DIC	L	S	E	AS17		–	–	–	×	–
DIC	L	S	E	AS20		–	–	–	–	×(1)
DIC	L	S	E	AS34		–	–	–	×	–
DIC	L	S	T	AS10	"*Sassafras*" *bradleyii*	–	–	–	×(0)	×(1)
DIC	L	S	T	AS11		–	–	–	–	×(1)
DIC	L	S	T	AS13	"*Populus*" *aspensis*	–	–	–	×(6)	×(0)
DIC	L	S	T	AS18	"*Prunus*" *aspensis*	–	–	×(2)	×(25)	×(0)
DIC	L	S	T	AS25		–	–	×(0)	×(1)	–
DIC	L	S	T	AS27		–	–	–	–	×(4)
DIC	L	S	T	AS28		–	–	–	×(0)	×(0)
DIC	L	S	T	AS29		–	–	×(1)	–	×(1)
DIC	L	S	T	AS31		–	–	–	–	×(3)
DIC	L	S	T	AS32	*Sapindopsis shultzii*	–	–	–	×(2)	×(2)
DIC	L	C	E	AS19	*Sapindopsis magnifolia*	–	–	×(0)	×(25)	×(65)
DIC	L	C	T	AS14, AS30	*Sapindopsis belviderensis*	–	–	–	×(51)	×(5)

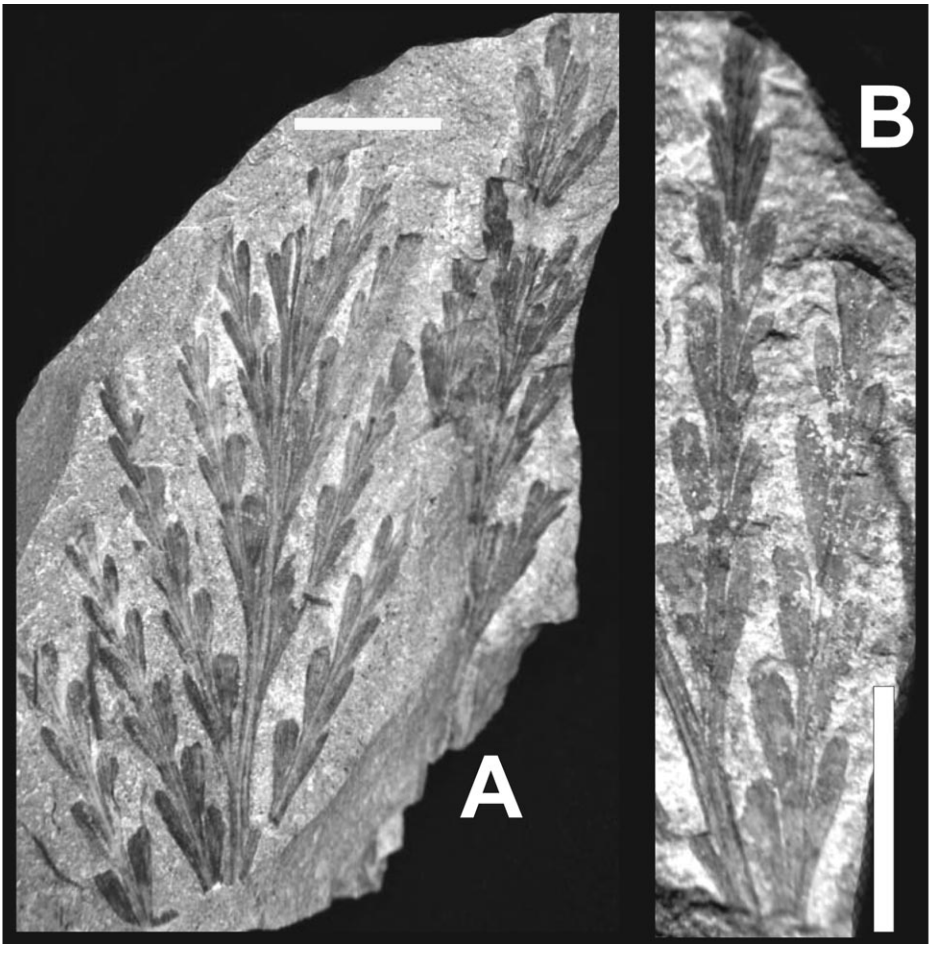

FIGURE 2. "*Anemia*" *fremontii* Brown, 1933, AS1. **A.** YPM 56068, bipinnate frond, showing alternate to subalternate arrangement. **B.** YPM 56068, close-up of frond showing pinnatasect, subopposite pinnules. Scale bars = 1 cm.

types described below have been placed into 3 categories on the basis of the certainty of taxonomic identification (see Introduction, above, for a complete description of these categories):

1. No previous description is known and no name is proposed (e.g., AS2).
2a. Genus is incorrect or invalid, but the species name is valid (e.g., "*Anemia*" *fremontii* Brown, 1933).
2b. Those associated with a previously published but uncertain or incorrect identification (e.g., "*Microtaenia paucifolia*").
3. As far as is known, this is a correct identification to a valid and legitimate genus and species (e.g., *Cladophlebis readii* Brown, 1933).

Format of Floral Description

The descriptions follow the format of Johnson (1996), which is a modification of Hickey (1977). The terms used are based on Ash et al. (1999) and Hickey (1973). Each morphotype is described in the following format:

Morphotype number.

Taxonomic name.

Systematic affinity.

Previous identification.

Synonymy.

Description. Organization of laminae. Lamina shape and preservation. Lamina length; lamina width; length-to-width ratio; apex shape; base shape; margin type; other characters of the lamina (e.g. petiole, glands, etc.). Category and preservation of primary ve-

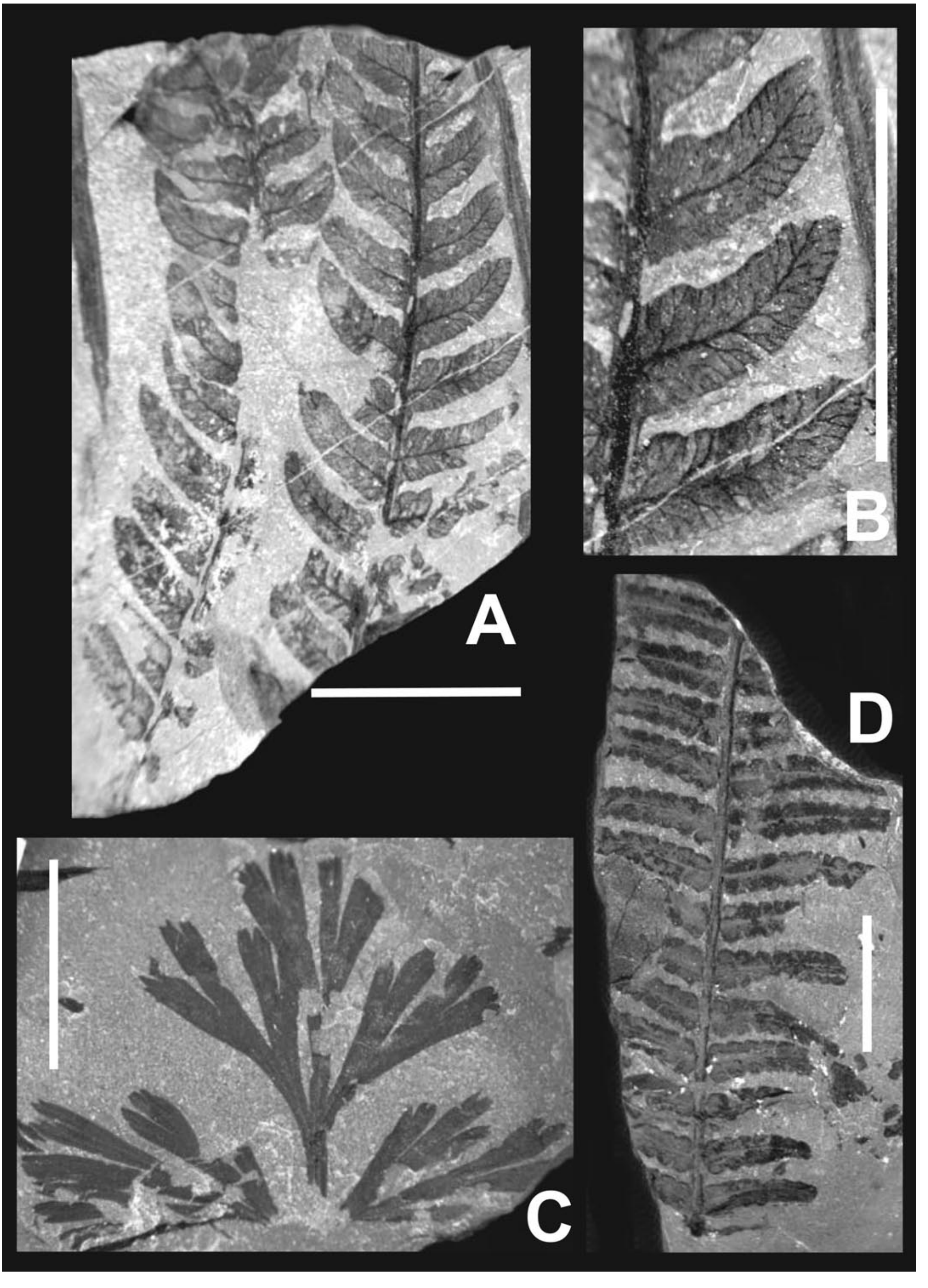

FIGURE 3. **A, B.** *Cladophlebis readii* Brown, 1933, AS3. **A.** YPM 55897, frond showing subalternate to alternate arrangement of pinnules. **B.** YPM 55897, close-up of pinnule showing bifurcated venation. **C.** *Baieropsis* sp., AS2, YPM 55913, frond showing subopposite, irregular dissection to even pinnate arrangement of pinnules. **D.** AS4, YPM 56096, pinnate frond with stout rachis. Scale bars = 1 cm.

nation; thickness of primary vein(s); presence of agrophic veins; category and preservation of secondary venation; arrangement and spacing of secondary veins on primary; number of secondary vein pairs; angle of secondary vein departure from primary; secondary vein course; nature of intersecondary veins. Category and preservation of tertiary venation; tertiary vein course; position and orientation of tertiary veins for the primary and secondary veins; tertiary vein spacing. Higher order venation. Areolation; tooth type, tooth venation; tooth shape.

Morphotype exemplar.

Discussion.

Terms and Definitions Used in Floral Description

The following systematic descriptions use these terms: "Morphotype number" is a numerical designation that distinguishes an entity with a unique morphology within the flora; using the convention established by Johnson (1989), this is a 2-letter prefix based on the formation name plus a number starting from one. "Previous identification" indicates that this morphotype has been identified and published before, but that the identification is incorrect or uncertain; this term will only be used for morphotypes in category 2b. "Morphotype exemplar" is the specimen that best exemplifies the characters of the morphotype and may be changed if a better specimen is found.

Description of Morphotypes

Ferns and Sphenopsids

AS1
Figure 2A, B

"*Anemia*" *fremontii* Brown 1933

Systematic affinity: Class Filicopsida; Order Filicales; Family and Genus *incertae sedis.*

Synonymy: *Anemia fremontii* Brown, 1933:3, pl. 1, fig. 3 (USNM 39136).

Description: Frond bipinnate; pinnules typically arranged alternately to subalternately, occasionally odd-pinnate. Pinnules pinnatisect, subopposite, forming a low angle with the rachilla. Venation dichotomizing, no reticulation. Margin irregularly toothed, veins appear to end in tooth sinus.

Morphotype exemplar: YPM 56058.

AS2
Figure 3C

Baieropsis aff. *B. expansa* Fontaine 1889

Systematic affinity. Class Filicopsida; Order Filicales; Family Schizeaceae.

Description. Pinnules irregularly dissected; arrangement of pinnules subopposite to even pinnate. Venation open dichotomous. Irregular, terminally bifurcated veins give appearance of an irregularly toothed margin.

Morphotype exemplar. YPM 55913, YPM 55976 (part and counterpart).

Discussion. This morphotype belongs to Fontaine's (1889) genus *Baieropsis.* It likely belongs to the species *B. expansa,* which is the type species of *Baieropsis.* However, the Aspen Shale material does not have sporangia, making the species assignment uncertain. Berry (1911) later made *B. expansa* the type of his genus *Schizaeopsis.* Under Article 11.3 of the Code

Figure 4. "*Microtaenia paucifolia*," AS5, YPM 56058, fertile frond showing subopposite to opposite attachment of fertile material. Scale bar = 1 cm.

of Botanical Nomenclature (Greuter et al. 2000), *Baieropsis* Fontaine (1889) is the correct name for this taxon and Berry's genus *Schizaeopsis* is an illegitimate junior synonym. The complex of fern species recognized by Fontaine (1889) as *Baieropsis* is most abundant in Potomac Group Zone I, but extends upward to Subzone IIC (Clark et al. 1911:90–91; Hickey and Doyle 1977).

AS3
Figure 3A, B

Cladophlebis readii Brown, 1933

Systematic affinity. Class Filicopsida; Order Filicales; Family Osmundaceae.

Synonymy. *Cladophlebis readii* Brown, 1933:4, pl. 1, fig. 2 (USNM 39138).

Description. Frond bipinnate, rachis stout. Pinnule arrangement subalternate to alternate. Pinna broadly attached to rachis; pinnules pinnatisect, asymmetrical, falcate, bending toward apex of frond. Veins bifurcate twice and terminate at the margin.

Morphotype exemplar. YPM 55897, YPM 55969 (part and counterpart).

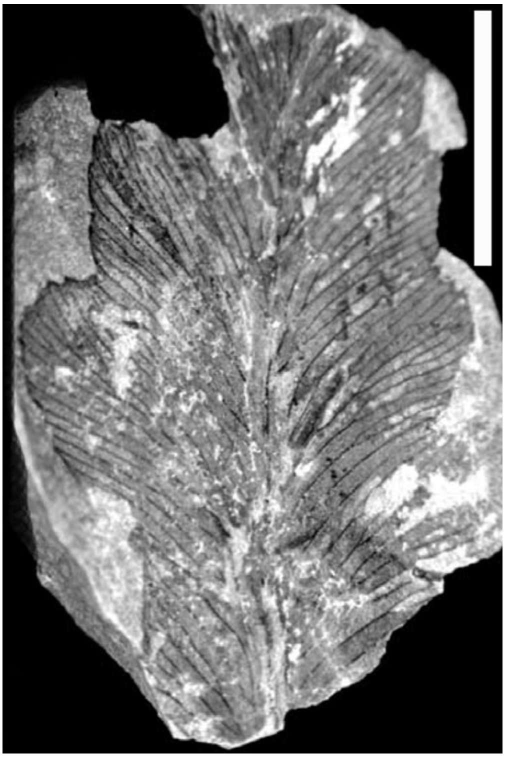

FIGURE 5. "*Asplenium*" *occidentale,* AS6, YPM 56132, pinna showing bifurcated venation. Scale bar = 1 cm.

AS4
Figure 3D

Systematic affinity. Class Filicopsida; Order Filicales; Family, Genus and species *incertae sedis.*

Description. Frond once-pinnate, deeply pinatifid, rachis stout. Pinnules opposite to alternate; dissected part way to the rachilla, forming lobes; rachilla perpendicular to the rachis. Midrib of pinnule distinct; secondary veins bifurcate up to two times. Margins of pinnules entire.

Morphotype exemplar. YPM 56906.

AS5
Figure 4

"*Microtaenia paucifolia*"

Systematic affinity. Class Filicopsida; Order Filicales; Family Matoniaceae; Genus and species *incertae sedis.*

Previous identification. *Microtaenia paucifolia* (Hall) Knowlton, Brown 1933:4, pl. 1, fig. 4 (USNM 39139).

Description. Fertile frond. Opposite to subopposite attachment of reproductive fertile material. Fertile material orbicular. Venation of frond pinnate.

Morphotype exemplar. YPM 56058.

AS6
Figure 5

"*Asplenium*" *occidentale*

Systematic affinity. Class Filicopsida; Order, Family and Genus *incertae sedis.*

Synonymy. *Asplenium occidentale* Brown, 1933:3, pl. 1, fig. 5 (USNM 39137).

Description. Shape of pinnule uncertain. Pinnae lobed. Veins bifurcate at least twice, no reticulation, veins curved abaxially and ending at the margin. Margin toothed, teeth sharp-pointed with rounded sinuses, veins go to tips of teeth.

Morphotype exemplar. YPM 56132.

AS26
Figure 6

Hausmannia sp.

Systematic affinity. Class Filicopsida; Order Filicales; Family Dipteridaceae.

Description. Leaf small, less than 5 cm wide by 5 cm long. Margin serrate and highly dissected; multi-lobed. Pinnate primary

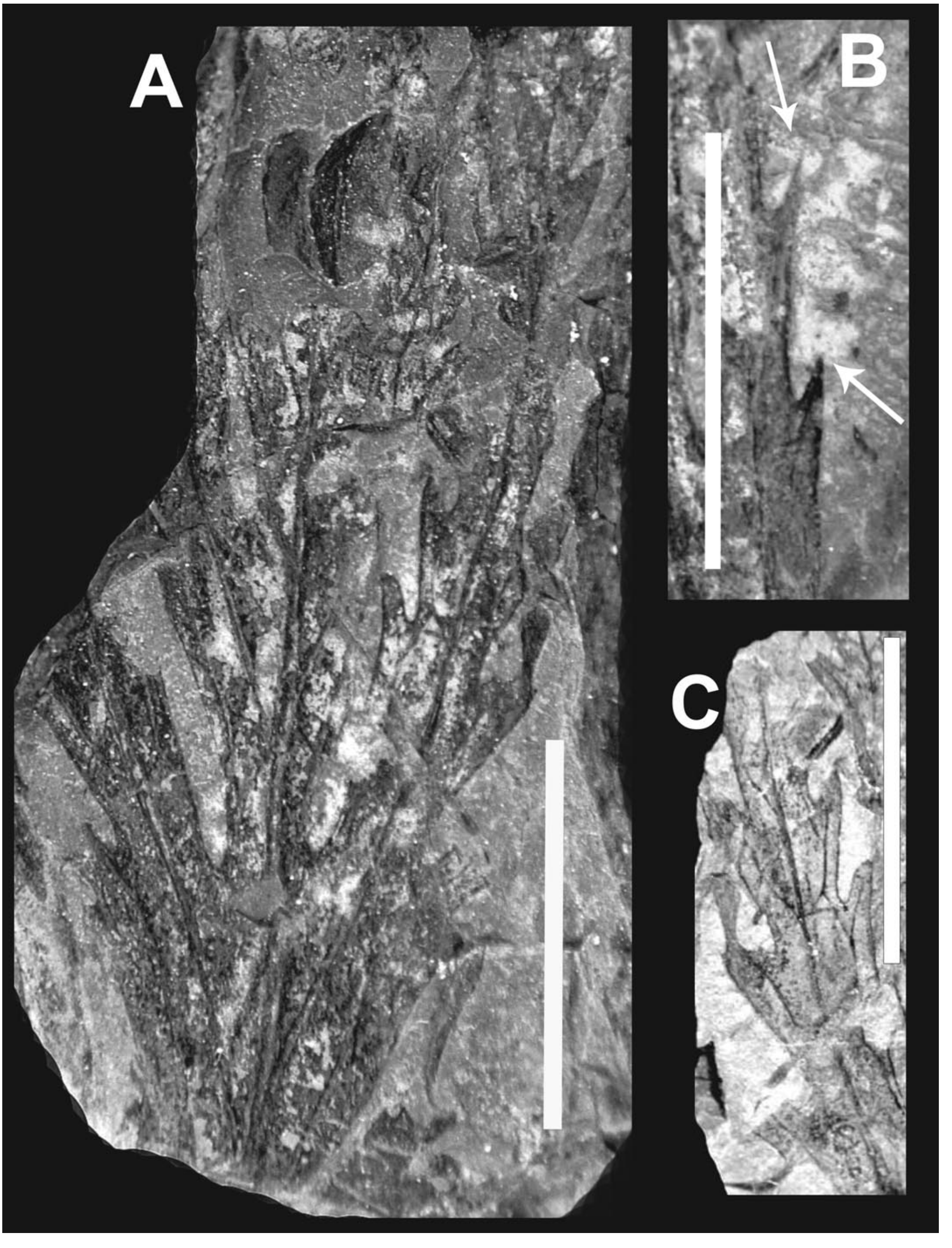

FIGURE 6. **A–C.** *Hausmania* sp., AS26. **A.** YPM 56082, small multi-lobed leaf showing serrate, highly dissected margin. **B.** YPM 56129, close-up of margin showing serrate teeth, arrows indicate spinose gland at end of tooth. **C.** YPM 56129, close-up of end of lobe showing serrate teeth that do not have spinose glands. Scale bars = 1 cm.

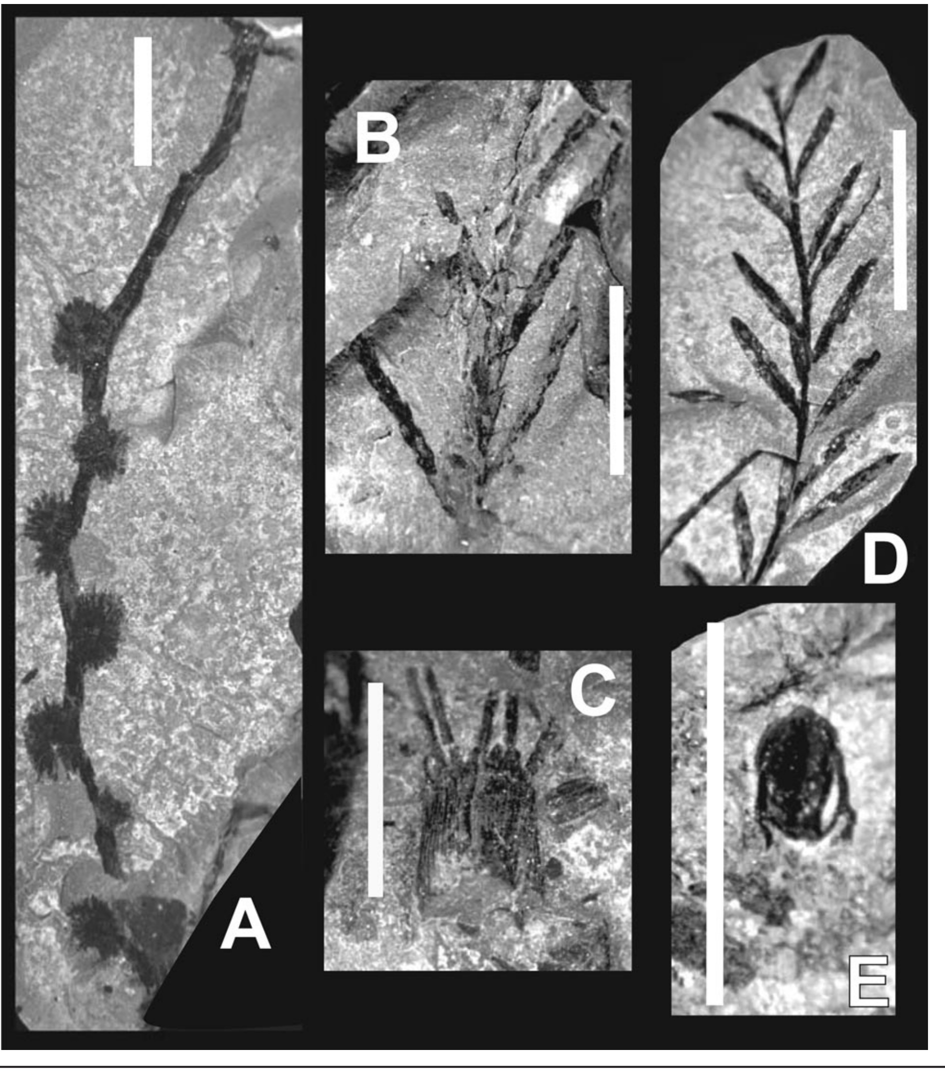

Figure 7. **A.** "*Sparganium*" *aspensis* Brown, 1933, AS9, YPM 56001, inflorescence showing alternate attachment of probably flower heads. **B.** AS8, YPM 56069, conifer showing adpressed, spirally arranged scales. **C.** *Equisetites* sp., AS12, YPM 55878, whorled leaves around stem. **D.** AS7, YPM 55782, branch showing 1 to 2 cm long needles. **E.** AS33, YPM 56151, angiosperm (see D). Scale bars = 1 cm.

venation; secondary veins semicraspedodromous or reticulodromous. One order of teeth, 2 teeth per centimeter, spacing irregular, shape irregular, sinus rounded, some teeth spinose.

Morphotype exemplar. YPM 56129, YPM 56082 (part and counterpart).

AS12
Figure 7C

Equisetites sp.

Systematic affinity. Class Sphenopsida; Order Equisetales; Family Equisetaceae.

Description. Whorled leaves at nodes; leaves linear with no evident venation. Stem 0.5 to 1.0 cm wide; vertical, linear striations on stem.

Morphotype exemplar. YPM 55996.

Conifers

AS7
Figure 7D

Systematic affinity. Class Coniferopsida; Order, Family, Genus and species *incertae sedis*.

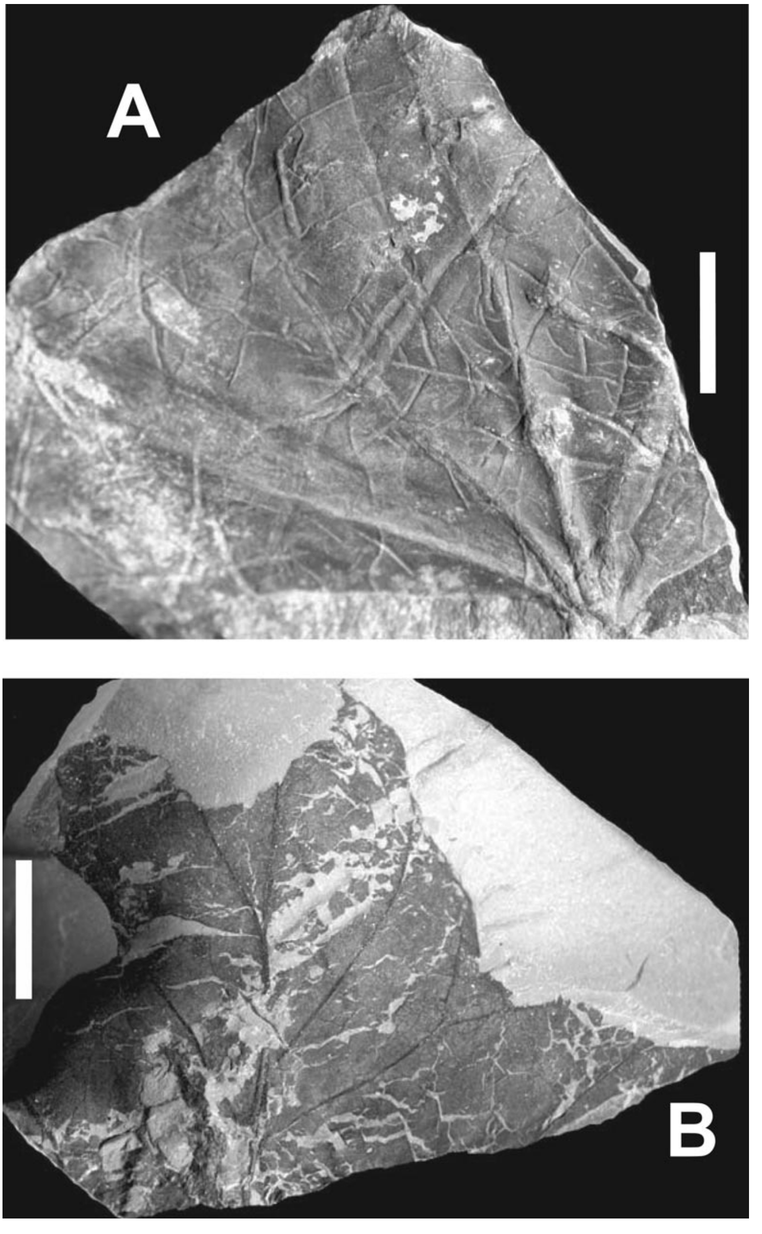

FIGURE 8. AS16. **A.** YPM 56095, base of leaf showing 5 basal veins. **B.** YPM 55883, apex of leaf showing entire margin and opposite percurrent tertiary veins. Scale bars = 1 cm.

Description. Needles alternate, possibly spirally arranged. Needles 1 to 2 cm long, dorsiventrally flattened; bases clasping branchlet; single vein in each needle.

Morphotype exemplar. YPM 55782.

Discussion. This morphotype resembles *Glyptostrobus* Endlicher (1847), which is known from other Early Cretaceous floras (e.g., LePage 2007), but was not confirmed by cones or cone scales.

AS8
Figure 7B

Systematic affinity. Class Coniferopsida; Order, Family, Genus and species *incertae sedis*.

Description. Adpressed, spirally arranged scales. Scales 1 to 3 mm, sharp-pointed.

Morphotype exemplar. YPM 56069

Discussion. This morphotype resembles *Brachyphyllum* Brongniart (1828), but the generic assignment was not confirmed by cones or cone scales.

Dicot Angiosperm Reproductive Structures

AS9
Figure 7A

"*Sparganium*" *aspensis*

Systematic affinity. Class Magnoliopsida; Order, Family, and Genus *incertae sedis.*

Synonymy. *Sparganium aspensis* Brown, 1933:4, pl. 2, fig. 2 (USNM 39140).

Description. Inflorescence consisting of orbicular, alternately attached heads of probable flowers.

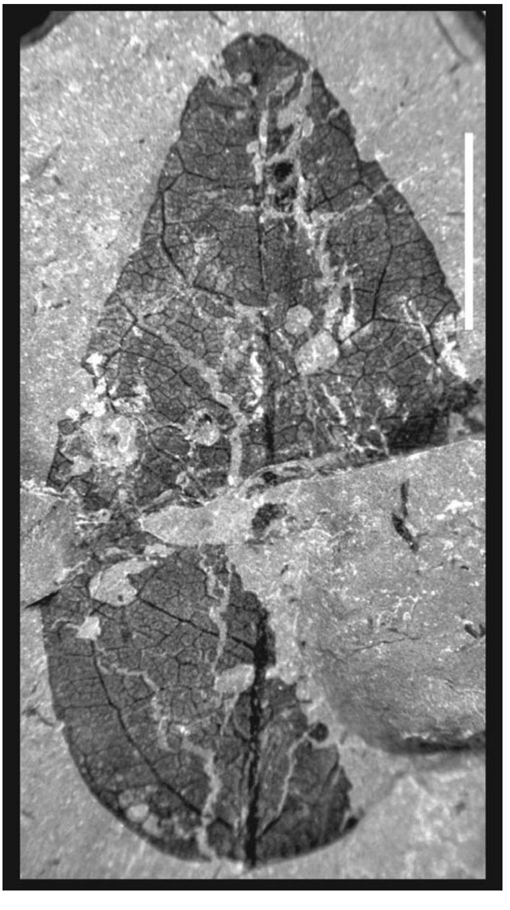

Figure 9. AS17, YPM 56018, ovate, microphyll-sized leaf. Scale bar = 1 cm.

Morphotype exemplar. YPM 56001, YPM 56064 (part and counterpart).

Discussion. "*Sparganium*" *aspensis* (AS9) can likely be assigned to the genus *Platanocarpus* Friis, Crane, and Pederson (1988)

AS33
Figure 7E

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Elliptic, 0.5 cm long seed.

Morphotype exemplar. YPM 56151.

Simple, Entire, Dicot Leaves

AS16
Figure 8A, B

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Leaf simple, mesophyll-sized. Leaf symmetrical; base rounded to obtuse, base angle obtuse; petiolar attachment marginal; margin entire at base. Primary venation actinodromous, at least 5 basal veins; secondary veins likely brochidodromous; tertiary veins opposite percurrent; fourth-order veins opposite percurrent. Leaf may be lobed.

Morphotype exemplar. YPM 56095.

AS17
Figure 9; Figure 10B

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Leaf simple, ovate, microphyll-sized. Leaf symmetrical; apex rounded, apex angle acute; base rounded, base angle obtuse; apex may be glandular; margin entire. Primary venation pinnate; secondary veins festooned brochidodromous, secondary vein spacing irregular; basal secondary vein angle irregular; intersecondary veins absent; tertiary veins alternate percurrent, obtuse to primary vein, inconsistent angle variability; fourth-order venation polygonal, regular reticulate; fifth-order venation dichotomizing; areoles moderately well developed; freely ending veinlets branched.

Morphotype exemplar. YPM 56018.

Discussion. The festooned brochidodromous secondary venation, the regular polygonal reticulate fourth-order venation, the dichotomizing fifth-order venation, the moderately well-developed areolation, and the branched freely ending veinlets suggest that this morphotype is likely a species of the genus *Ficophyllum* Fontaine (1889).

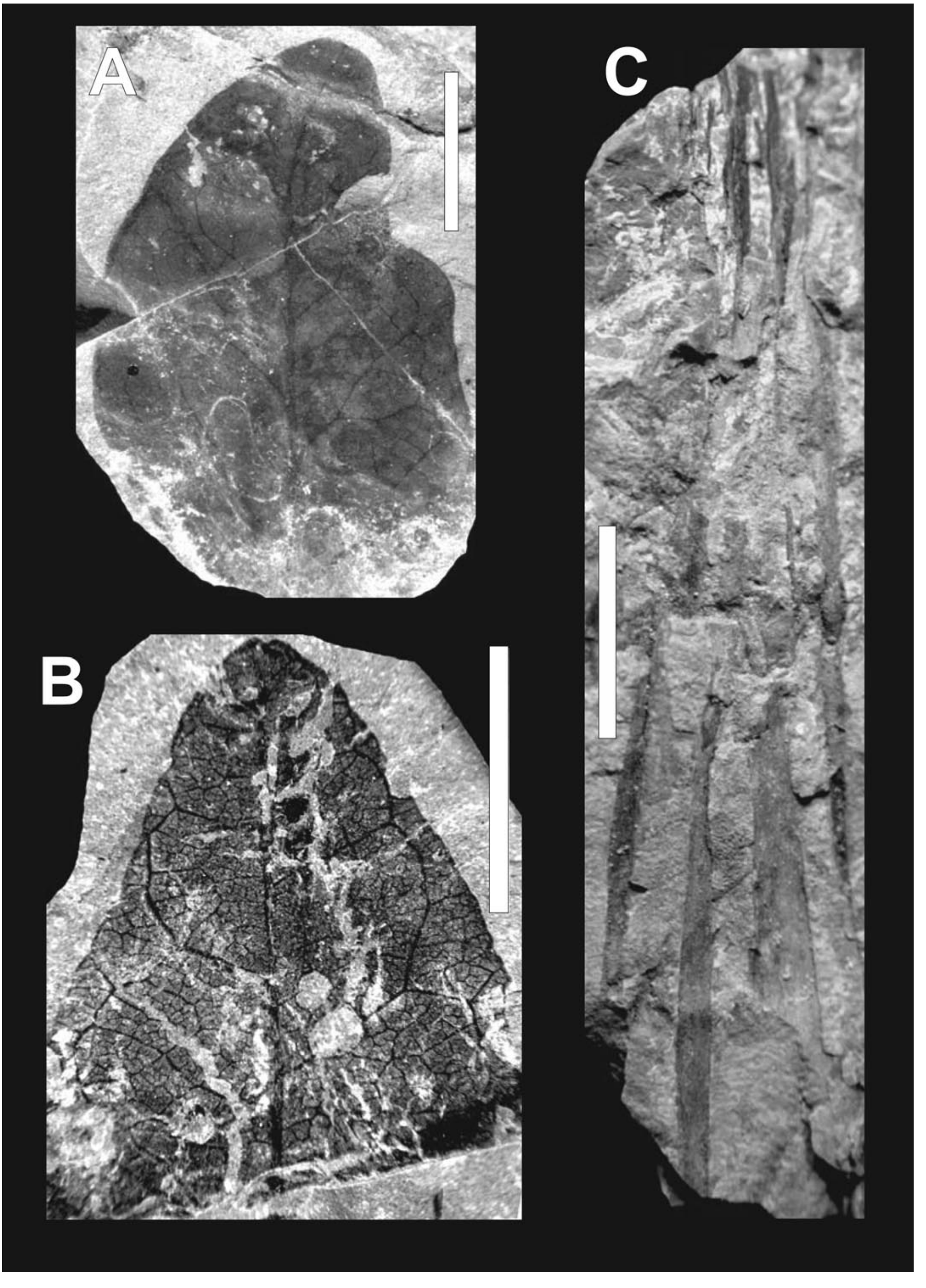

Figure 10. **A.** AS20, YPM 56063, apex of ovate leaf showing reticulodromous venation. **B.** AS17, YPM 56018, close-up of apex of leaf showing higher order venation. **C.** AS34, YPM 56138, long, linear leaves. Scale bars = 1 cm.

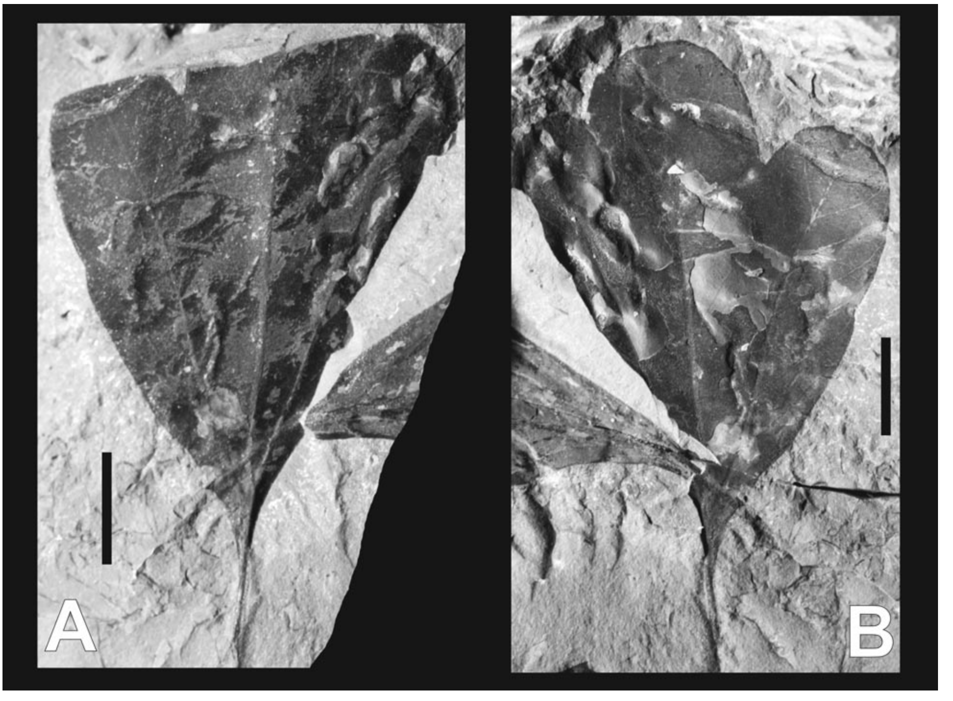

FIGURE 11. "*Sassafras*" *bradleyii* Brown, 1933, AS10. **A.** YPM 56073b, base of leaf showing suprabasal actinodromous primary venation. **B.** YPM 56073a, 3-lobed leaf showing lobes with round apices. Scale bars = 1 cm.

FIGURE 12. "*Sassafras*" *bradleyii* Brown, 1933, AS10, YPM 56077a, leaf showing suprabasal actinodromous venation. Scale bar = 1 cm.

AS20
Figure 10A

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis*.

Description. Simple, ovate, microphyll-sized leaf. Leaf asymmetrical; margin entire. Primary venation pinnate; secondary venation reticulodromous.

Morphotype exemplar. YPM 56063

AS34
Figure 10C

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis*.

Description. Long, linear, thin leaf. Margin entire. One prominent midvein.

Morphotype exemplar. YPM 56138.

Simple, Toothed Dicot Leaves

AS10
Figure 11; Figure 12

"*Sassafras*" *bradleyi*

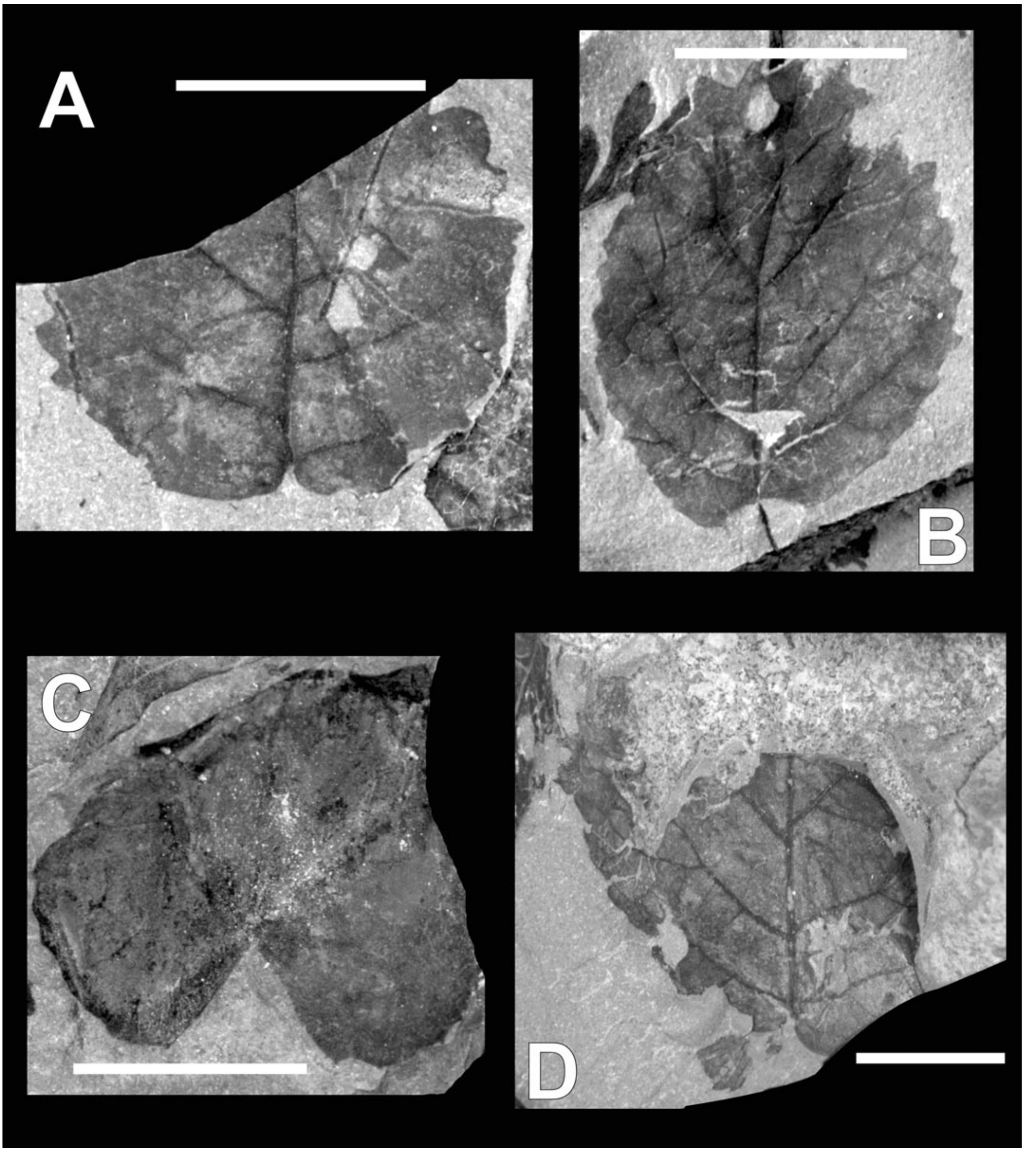

FIGURE 13. **A–B.** "*Populus*" *aspensis* Brown, 1933, AS13. **A**. YPM 56003, nanophyll-sized with showing cordate base. **B.** YPM 5906, nanophyll-sized leaf with rounded apex. **C.** AS11, YPM 55996, base of leaf with deeply cordate base. **D**. "*Prunus*" *aspensis* Brown, 1933, AS18, YPM 56008, leaf with cordate base and pinnate primary venation. Scale bars = 1 cm.

Systematic affinity. Class Magnoliopsida; Order, Family, and Genus *incertae sedis.*

Synonymy. *Sassafras bradleyi* Brown, 1933:7, pl. 2, fig. 5 (USNM 39144).

Description. Leaf ovate, notophyll- to mesophyll-sized. Leaf symmetrical; apex acute to rounded; base acute to decurrent; margin toothed or entire; 3 lobes, lobes rounded to acute at apices; intrafoliar glandular dots present. Primary venation suprabasal actinodromous; 3 or more basal veins; secondary veins festooned brochidodromous to weakly brochidodromous, irregularly spaced, secondary vein angle approximately 45° to the primaries; tertiary venation random reticulate, vein course and vein angle to primary random; fourth-order venation random reticulate. When toothed, one order of teeth, shape convex/concave (CV/CC), sinus rounded, apex rounded.

Morphotype exemplar. YPM 56077a, b.

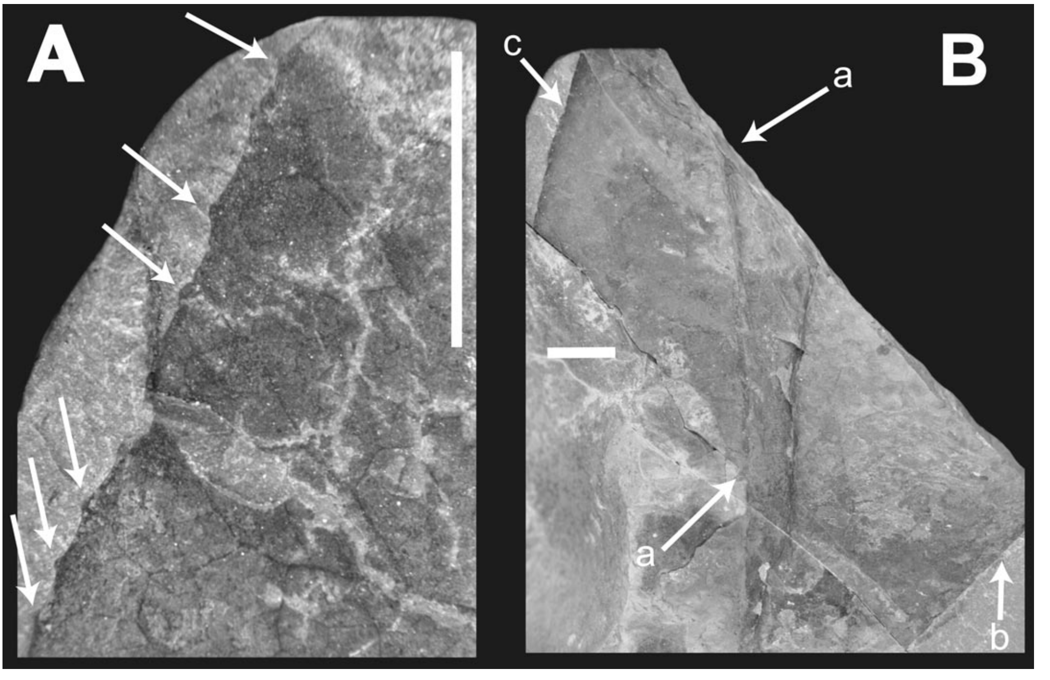

FIGURE 14. AS25, YPM 56178. **A.** Close-up of margin of leaf showing teeth and higher order venation. Arrows indicate position of crenate teeth. **B.** Large leaf (a, position of midvein; b, margin near base; c, toothed margin shown in A). Scale bars = 1 cm.

AS11
Figure 13C

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Leaf simple, very broad ovate, microphyll-sized. Leaf symmetrical; apex rounded, angle obtuse; base deeply cordate; petiolar attachment marginal; margin crenate. Primary veins basal actinodromous; 5 basal veins; one pair of weak agrophic veins; secondary veins semicraspedodromous. One order of teeth, 3 to 4 teeth per centimeter, tooth spacing regular, tooth shape convex/convex (CV/CV), sinus sharp, apex rounded.

Morphotype exemplar. YPM 55996.

AS13
Figure 13A, B

"*Populus*" *aspensis*

Systematic affinity. Class Magnoliopsida; Order, Family, and Genus *incertae sedis.*

Synonymy. *Populus*? *aspensis* Brown 1933:5, fig. 1 (USNM 39141).

Description. Simple, ovate to elliptic, nanophyll-sized leaf. Leaf symmetrical; apex rounded, angle acute; base cordate, angle obtuse; margin serrate. Primary vein pinnate; secondary veins craspedodromous, basally crowded, secondary vein angle slightly increasing to base; tertiary veins mixed opposite–alternate, vein course irregular, angle to primary vein obtuse, angle variability inconsistent; fourth-order veins roughly orthogonal to tertiary veins. One order of teeth, irregular spacing, tooth shape CV/CC, sinus rounded, apex glandular.

Morphotype exemplar. YPM 55906.

Discussion. The teeth and higher order venation suggest that this morphotype may be a member of the Trochodendraceae.

AS18
Figure 13D

"*Prunus*" *aspensis*

Systematic affinity. Class Magnoliopsida; Order, Family, and Genus *incertae sedis.*

Synonymy. *Prunus aspensis* Brown 1933:9, pl. 2, fig. 4 (USNM 39147).

Description. Simple, ovate, mesophyll-sized leaf. Leaf asymmetrical; apex acute; base cordate; margin crenate to serrate. Primary vein pinnate; secondary veins semicraspedodromous; no higher order venation preserved. Teeth crenate to serrate, one order of teeth, tooth shape CV/CV, sinus angular, simple to possibly glandular apex.

Morphotype exemplar. YPM 56008.

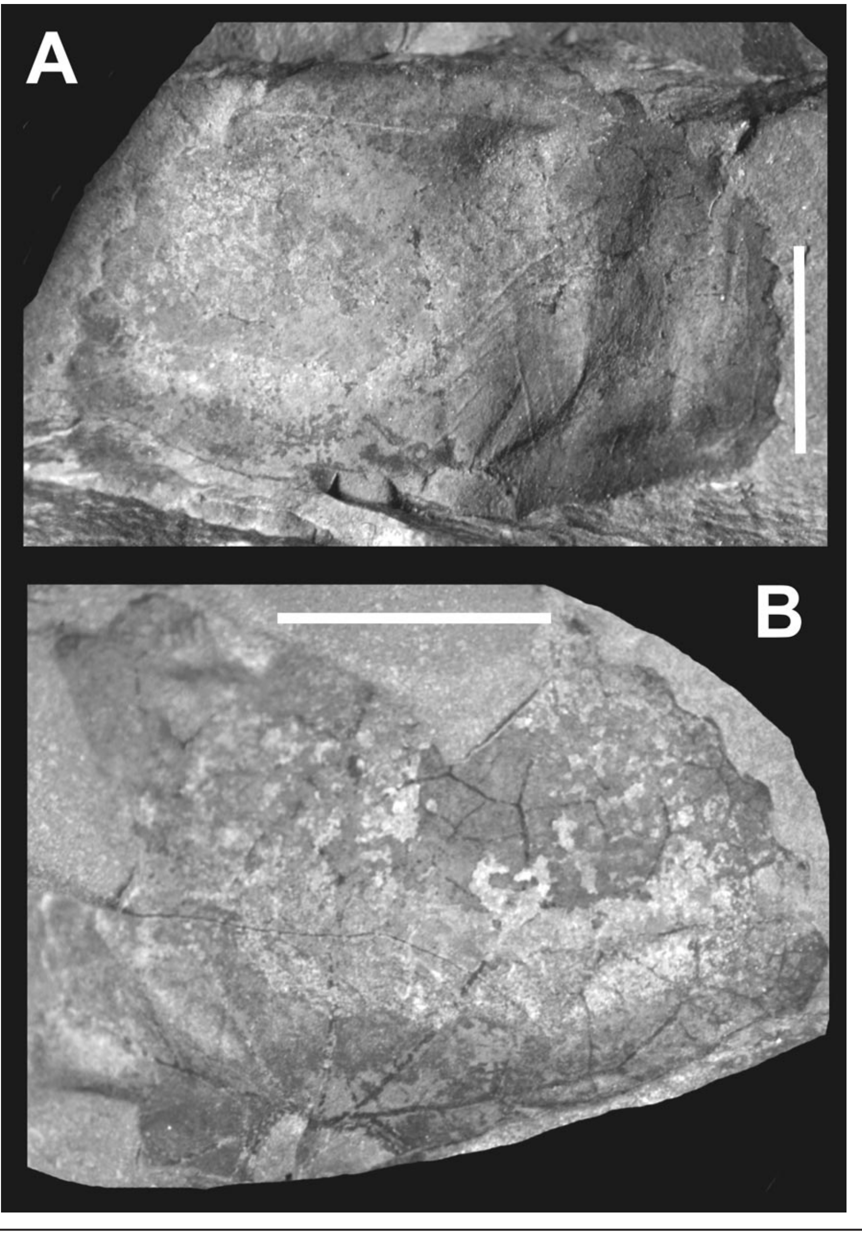

Figure 15. AS27. **A.** YPM 56077b, leaf with rounded apex and cordate base. **B.** YPM 56007a, leaf with actinodromous primary venation and one pair of agrophic veins showing crenate margin. Scale bars = 1 cm.

AS25
Figure 14

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Megaphyll-sized leaf. Margin crenate. Primary venation pinnate; secondary venation weakly brochidodromous; tertiary veins random reticulate. One order of teeth, 4 teeth per centimeter, spacing regular, shape concave/concave (CC/CC), sinus rounded, apex pointed.

Morphotype exemplar. YPM 56178.

AS27
Figure 15

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Simple, elliptic, microphyll-sized leaf. Leaf symmetrical; length-to-width ratio 1:1; apex rounded, angle acute; base cordate, angle obtuse; petiolar attachment marginal; mar-

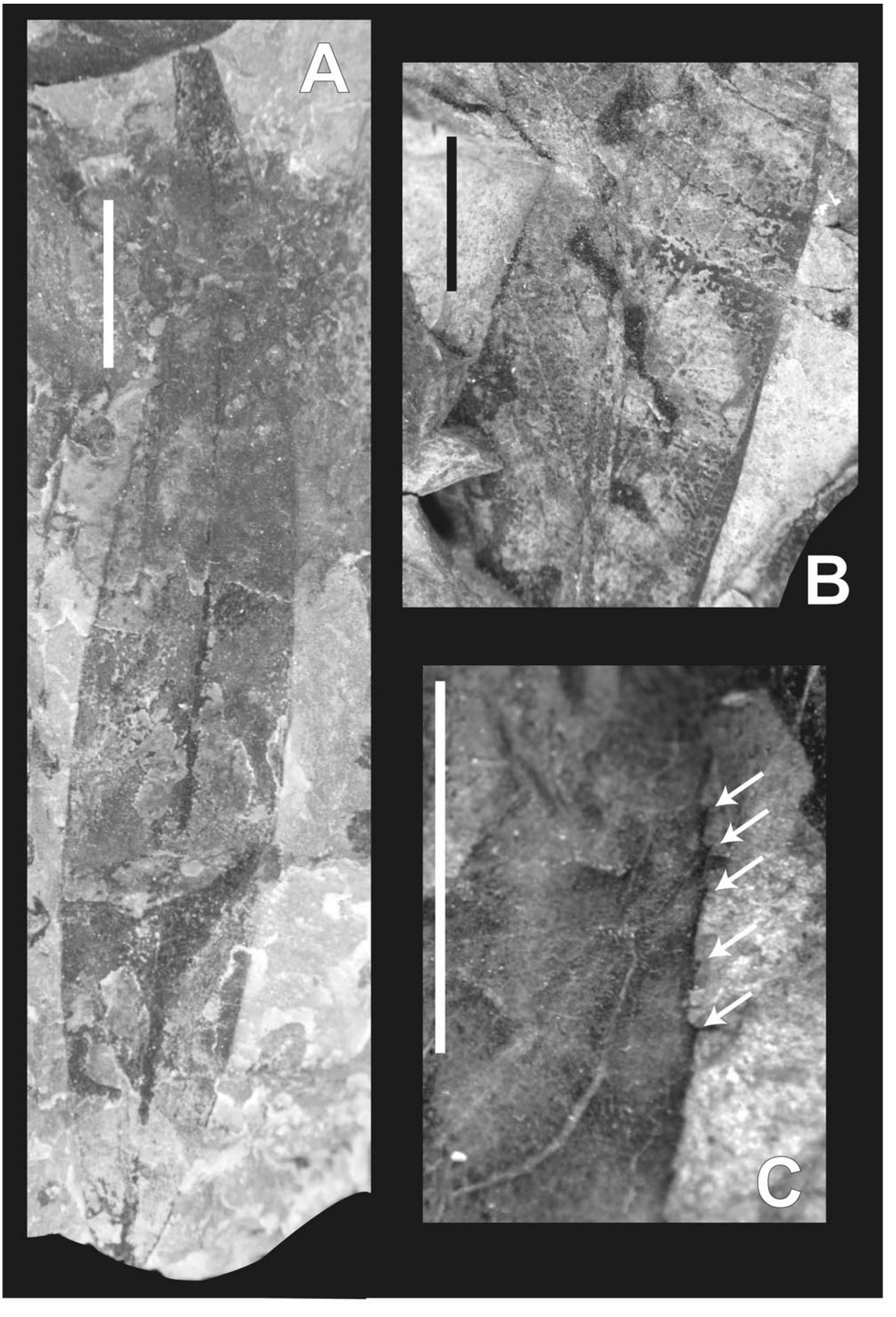

FIGURE 16. AS28. **A.** YPM 56073b, ovate leaf with acute apex and base. **B.** YPM 56099, close-up of leaf showing highly ascending secondary veins. **C.** YPM 56076, close-up of margin of leaf showing closely spaced serrate teeth. Arrows indicate position of teeth. Scale bars = 1 cm.

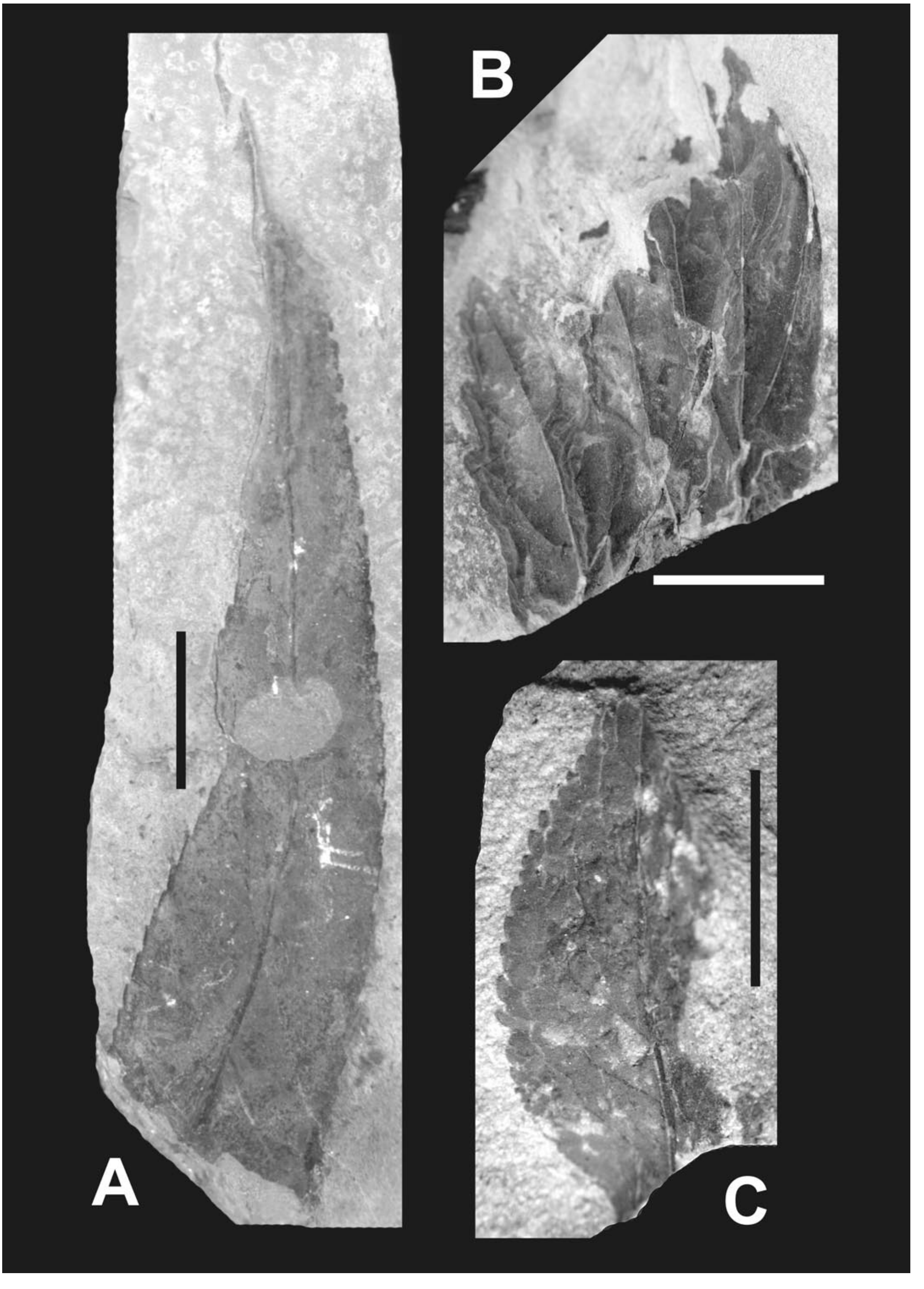

FIGURE 17. **A.** "*Sapindopsis*" *schultzii* Brown, 1933, AS32, YPM 56116b, ovate leaf with straight apex and serrate margin. **B.** AS29, YPM 55899, leaf with lobes and large teeth. **C.** AS31, YPM 55877, microphyll-sized leaf with serrate margin. Scale bars = 1 cm.

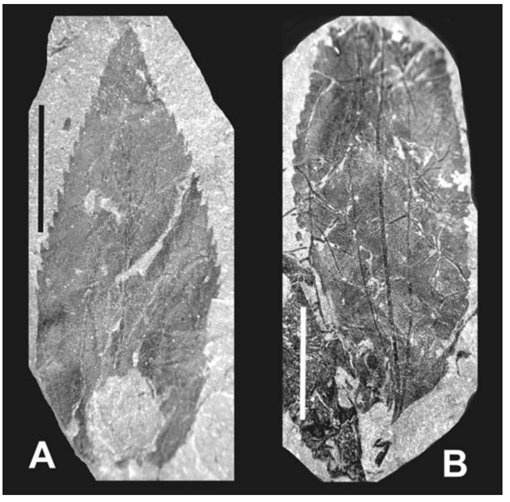

Figure 18. AS31. **A.** YPM 55975, leaf with serrate margin and acute apex. **B.** YPM 56052, leaf with rounded base and acrodromous secondary venation. Scale bars = 1 cm.

Figure 19. *Sapindopsis magnifolia* Fontaine, 1889, AS19, YPM 56073a, bi-lobed terminal leaflet. Scale bar = 1 cm.

gent crenate. Primary venation actinodromous to palinactinodromous; one pair of agrophic veins; secondary veins festooned brochidodromous to reticulodromous; tertiary veins random reticulate. One order of teeth, 3 to 4 teeth per centimeter, tooth spacing regular, shape CV/CV, sinus rounded, apex rounded and glandular.

Morphotype exemplar. YPM 56077.

AS28
Figure 16

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Simple, ovate to linear, notophyll- to mesophyll-sized leaf. Leaf symmetrical; length-to-width ratio 7:1; apex acute, angle acute; base acute, angle acute; petiolar attachment marginal; margin minutely serrulate, but in most specimens appearing entire, perhaps due to marginal enrollment. Primary venation pinnate; secondary veins craspedodromous, veins highly ascending toward margin; tertiary veins opposite percurent. Teeth very small, in one order, 3 to 5 teeth per centimeter, spacing irregular, shape CV/CC to CV/CV, sinus rounded.

Morphotype exemplar. YPM 56076

Discussion. This morphotype can be distinguished from AS31 and AS32 ("*Sapindopsis*" *shultzii*) by the size and shape of its teeth and a much greater length-to-width ratio of the lamina.

AS29
Figure 17B

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species *incertae sedis.*

Description. Notophyll-sized leaf. Apex angle acute; margin serrate; multi-lobed. Primary venation pinnate; secondary veins craspedodromous to semicraspedodromous; tertiary veins loosely and irregularly percurrent, vein course irregular and slightly sinuous; fourth-order venation random reticulate. Two orders of teeth, 3 to 4 teeth per centimeter, spacing irregular, shape CV/CV, sinus rounded to acute, apex rounded to sharp, tooth glandular, chloranthoid tooth. Lamina has glandular dots.

Morphotype exemplar. YPM 55899, YPM 56023 (part and counterpart).

AS31
Figure 17C; Figure 18

Systematic affinity. Class Magnoliopsida; Order, Family, Genus and species incertae sedis

Description. Simple, ovate, microphyll-sized leaf. Leaf symmetrical; length-to-width ratio 3:1; apex acute, angle acute; base rounded; petiolar attachment marginal; margin serrate. Primary venation acrodromous; one pair of agrophic veins; secondary veins craspedodromous; higher order venation random reticulate. One order of teeth, 6 to 8 teeth per centimeter, spacing regular, shape CV/CV, sinus rounded, apex sharp and glandular.

Morphotype exemplar. YPM 56052.

Discussion. This morphotype can be distinguished from AS28 and AS32 ("*Sapindopsis*" *shultzii*) by is acrodromous primary venation and the size and shape of its teeth.

AS32
Figure 17A

"*Sapindopsis*" *shultzii*

Systematic affinity. Class Magnoliopsida; Order, Family, Genus *incertae sedis.*

Synonymy. *Sapindopsis shultzii* Brown, 1933:10, pl. 1, fig. 7 (USNM 39149).

Description. Simple, ovate, notophyll- to mesophyll-sized leaf. Leaf symmetrical; length-to-width ratio 3:1 to 6:1; apex straight, angle acute; margin serrulate. Primary venation pinnate; secondary veins semicraspedodromous; higher order venation random reticulate. One order of teeth, 4 to 6 teeth per centimeter, spacing regular, shape CV/CV, sinus acute, apex rounded to sharp.

Morphotype exemplar. YPM 5611a, b.

Discussion. The teeth and venation of this morphotype suggest that it may be a species of *Crassidenticulum.* This morphotype can be distinguished from AS28 and AS31 by its pinnate primary venation and the size and shape of its teeth.

Compound, Entire Dicot Leaves

AS19
Figure 19; Figure 20; Figure 21

Sapindopsis magnifolia

Systematic affinity. Class Magnoliopsida; Order and Family *incertae sedis.*

Synonymy. *Sapindopsis magnifolia* Fontaine 1889:297, pl. 151, fig 2–3, pl. 152, fig. 2–3, pl. 153, fig. 2, pl. 154, fig. 1, 5, pl. 155, fig. 6.
Laurus aspensis Brown 1933:6, pl. 2, fig. 1 (USNM 39143).

Description. Leaf odd-pinnate compound, oppositely attached. Leaflets lanceolate to elliptic, notophyll-sized, except the terminal leaflet, which is obovate and notophyll-sized. Leaf symmetrical to rarely asymmetrical; apex rounded to acute; base acute

FIGURE 20. *Sapindopsis magnifolia* Fontaine, 1889, AS19, YPM 56070, odd-pinnate compound leaf showing attached leaflets. Scale bar = 1 cm.

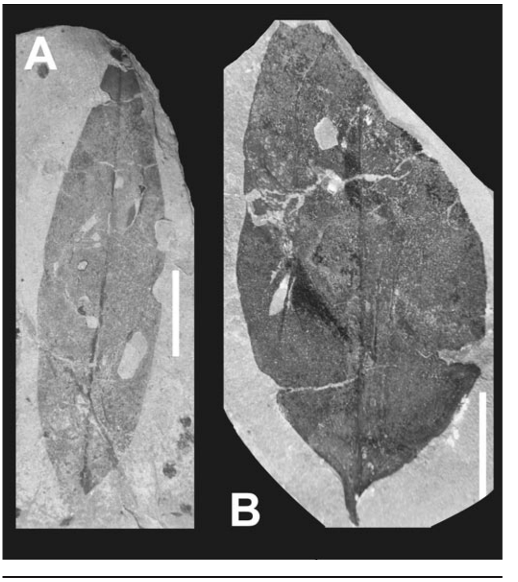

FIGURE 21. *Sapindopsis magnifolia* Fontaine, 1889, AS19. **A.** YPM 56077a, elliptic leaflet with pinnate primary venation. **B.** Slightly asymmetrical leaflet. Scale bars = 1cm.

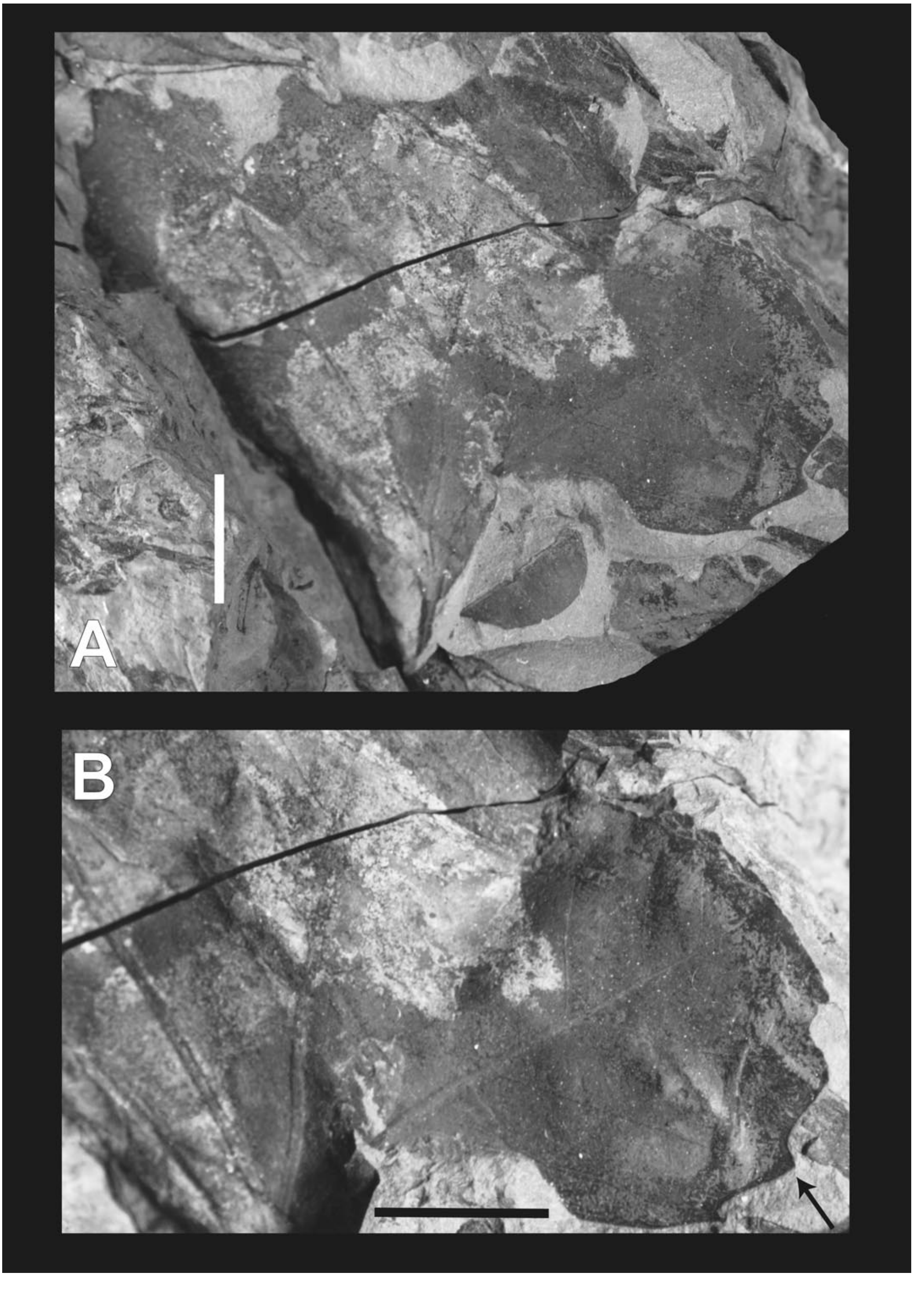

FIGURE 22. *Sapindopsis belvedierensis* Berry, 1922, AS14, YPM 56077a. **A.** Terminal leaflet with 3 lobes. **B.** Close-up of margin of leaf showing crenate margin. Arrow indicates tooth. Scale bars = 1 cm.

to decurrent; margin entire; terminal leaflet unlobed to bilobed. Primary venation in unlobed leaves pinnate, primary venation in lobed leaves suprabasal actinodromous; secondary venation weakly brochidodromous, vein spacing irregular, vein angle decreasing to base; inter-secondary veins present; tertiary veins random reticulate.

Morphotype exemplar. YPM 56070.

Compound, Toothed Dicot Leaves

AS14
Figure 22

Sapindopsis belvedierensis

Systematic affinity. Class Magnoliopsida; Order and Family *incertae sedis.*

Synonymy. Berry 1922:216–217, pl. 49, fig 1–7, pl. 50, fig. 1, pl. 51, fig. 1, pl. 52, fig. 1, pl. 53, fig. 1–2, pl. 54, fig. 2.

Description. Leaflet obovate, mesophyll-sized. Apex acute; base acute; margin crenate, typically 3-lobed. Primary veins suprabasal actinodromous to palinactinodromous, 5 basal veins; secondary veins craspedodromous, vein spacing irregular; no higher order venation preserved. Large teeth. One order of teeth, 2 to 3 teeth per centimeter; spacing regular, shape CV/CC to CV/CV, sinus rounded, apex acute to rounded, teeth become rounded and more symmetrical to leaf apex.

Morphotype exemplar. YPM 56076, YPM 56099 (part and counterpart).

Discussion. The diagnostic features of this leaf are its large teeth and its primary venation pattern. This is likely the terminal leaflet of a compound *Sapindopsis belvedierensis* Berry (1922) leaf.

AS30
Figure 23; Figure 24

Sapindopsis belvedierensis

Systematic affinity. Class Magnoliopsida; Order and Family *incertae sedis.*

Synonymy. Berry 1922:216–217, pl. 49, fig 1–7, pl. 50, fig. 1, pl. 51, fig. 1, pl. 52, fig. 1, pl. 53, fig. 1–2, pl. 54, fig. 2.

Description. Leaflet elliptic to obovate, notophyll-sized. Leaflet symmetrical; length-to-width ratio 3:1; apex rounded, angle acute; base cuneate to decurrent, angle acute; margin serrate. Primary venation pinnate; secondary veins semicraspedodromous, vein angle decreases towards base. One order of teeth, 1 tooth per centimeter, spacing regular, shape flexuous/convex (FL/CV), flexuous/concave (FL/CC), CC/CC, sinus rounded, apex rounded, apex occasionally glandular.

Morphotype exemplar. YPM 55882, YPM 55884 (part and counterpart).

Discussion. This is likely a lateral leaflet of *Sapindopsis belvedierensis*. It can be distinguished from AS14 by its pinnate primary venation, leaf shape, and tooth type.

Biostratigraphic Correlation and Paleoecological Interpretation

The presence of *Sapindopsis belvedierensis* and the petiolulate form of *S. magnifolia,* combined with the presence of palmately lobed leaves, the variety of dicot angiosperm leaf types and the

Figure 23. *Sapindopsis belvedierensis* Berry, 1922, AS14, YPM 55884, obovate leaflet with large teeth. Scale bar = 1 cm.

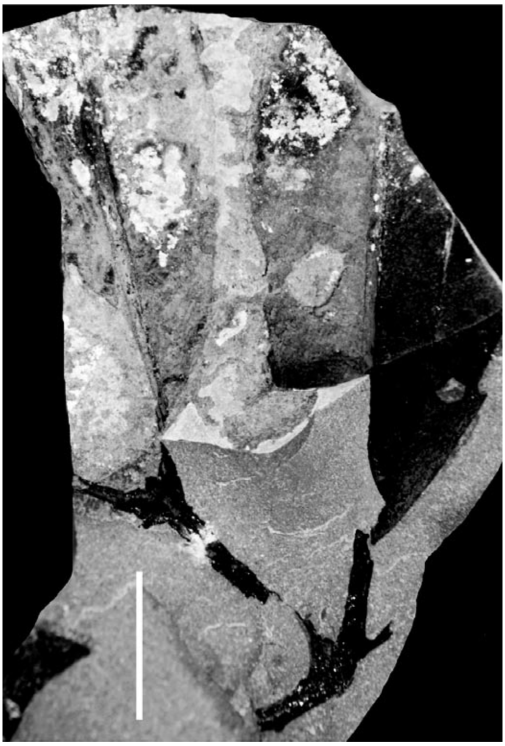

FIGURE 24. *Sapindopsis belvedierensis* Berry, 1922, AS14, YPM 55907, odd-pinnate compound leaf showing attached leaflets with teeth. Scale bar = 1 cm.

presence of AS7, "*Sparganium*" *aspensis,* allows us to correlate the Aspen Shale flora with the upper part of Subzone IIB of the Potomac Group of the Middle Atlantic United States (Doyle and Hickey 1976). This indicates a middle to late Albian age (Doyle and Hickey 1976). In addition, the occurrence of toothed, pinnatifid leaves of *Sapindopsis* in middle to late Albian strata in the Pacific northwest (Bell 1956), the Cheyenne Sandstone of Kansas (Berry 1922) and the upper Lakota and Fall River formations of the Black Hills (Hickey and Doyle 1977) supports this chronostratigraphic estimate.

At the outcrop scale, the floral composition of the plant beds changes significantly upward in the sequence (see Table 1). Ferns dominate the lowest 3 floral levels. In the basalmost level, LJH0026α, only a single fern species, *Cladophlebis readii* (AS3), is present. In the next two levels, LJH0026a and LJH0026b, *C. readii* (AS3) also occurs with "*Anemia*" *fremontii* (AS1) and "*Asplenium*" *occidentale* (AS6). Angiosperms are rare in the third level, LJH0026b, but become dominant in the fourth level, LJH0026c. In this level *Sapindopsis belvedierensis* (AS14, AS30) is the most abundant component of the flora. *S. magnifolia* (AS19) and *S. belvedierensis* dominate the angiosperm assemblage of the fifth and uppermost floral level (LJH0026d), where *C. readii* is the only fern present.

The trends toward increasing angiosperm abundance and diversity are similar to trends found in other early angiosperms assemblages (e.g., the Potomac flora, Hickey and Doyle 1977), suggesting three possible interpretations. The first, and least likely, is ecological succession. The strata are disturbed, but there are not patterns of seral succession within these beds. A second interpretation is that there is progressive ecological displacement of early successional ferns by early successional angiosperms through evolution and immigration. Given typical continental sedimentation rates, this interpretation seems unlikely because the restricted thickness of the section (about 13 m between lowermost and uppermost floral levels; see Figure 1; Table 1) likely represents little time.

We favor a third interpretation, in which ferns and angiosperms colonized disturbed environments. We infer that the relative abundance of ferns and angiosperms in each floral bed is due to heterogeneity of the fluvial environment (see Figure 1; Table 1). The Aspen Shale is similar to other early angiosperm floras (e.g., Hickey and Doyle 1977; Crabtree 1987; Wing et al. 1993) in that it suggests that the angiosperms were early successional, weedy to shrubby species that colonized open substrates.

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