Taxonomic Revision of the Spermatopsida of the Oligocene Creede Flora, Southern Colorado

U.S. GEOLOGICAL SURVEY BULLETIN 1923

U.S. DEPARTMENT OF THE INTERIOR
March 3, 1849

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By JACK A. WOLFE and HOWARD E. SCHORN

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DEPARTMENT OF THE INTERIOR
MANUEL LUJAN, JR., Secretary

U.S. GEOLOGICAL SURVEY
Dallas L. Peck, Director

March 3, 1849

UNITED STATES GOVERNMENT PRINTING OFFICE: 1990

First printing 1990
Second printing 1991

For sale by the
Books and Open-File Reports Section
U.S. Geological Survey
Federal Center
Box 25425
Denver, CO 80225

Library of Congress Cataloging-in-Publication Data

Wolfe, Jack A., 1936–
Taxonomic revision of the Spermatopsida of the Oligocene Creede flora, southern Colorado / by Jack A. Wolfe and Howard E. Schorn.

p. cm. — (U.S. Geological Survey bulletin ; 1923)
Includes bibliographical references.
Supt. of Docs. no.: I 19.3:1923
1. Paleobotany—Oligocene. 2. Paleobotany—Colorado. 3. Creede Formation (Colo.) I. Schorn, Howard E. II. Title. III. Title: Spermatopsida of the Oligocene Creede flora, southern Colorado. IV. Series.
QE75.B9 no. 1923
[QE928]
557.3 s—dc20 90-3265
[561′.19788] CIP

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Taxonomic Revision of the Spermatopsida of the Oligocene Creede Flora, Southern Colorado

By Jack A. Wolfe *and* Howard E. Schorn[1]

Abstract

Determination of impressions and compressions of the Oligocene Creede flora of Southern Colorado by two different methods results in markedly different taxonomic results. One method, based on "matching" extant plant organs with fossils, gives little or no consideration to taxonomic significance of the "matching" characters in extant plants. Many "matches," especially of poorly preserved material are based on the present-day association of the "matched" taxon associated with taxa represented in the fossil assemblage by well-preserved material. Some "matching" characters have resulted from different abrasion and (or) degradation stages, and other "matching" characters represent different stages in ontogenetic development. The second method considers all these significant factors, and application of the method to the Creede fossils results in major reduction in numbers of families, genera, and species, as well as reassignment of many fossils to different supraspecific categories.

INTRODUCTION

The Creede flora represents the only documented late Oligocene plant assemblage from the southern Rocky Mountains. Hence, valid determinations of the Creede taxa are critical to understanding biogeographic patterns, phylogeny of clades represented in the Creede flora, and the paleoecologic implications of the Creede assemblage (Wolfe and Schorn, 1989). The geologic setting of the Creede plant-bearing beds, which were deposited in the moat of a calderon, has been discussed elsewhere (Axelrod, 1987; Wolfe and Schorn, 1989). The Creede plant-bearing beds are radiometrically dated at 27.2 million years (Steven and others, 1967; corrected for newer decay constants).

A recent taxonomic treatment of the Creede flora recognized 73 species of Spermatopsida (Axelrod, 1987). Recognized were 2 families, 6 genera, and 19 species of conifers; we recognize 2 families, 4 genera, and 8 species. Also recognized were 21 families, 37 genera, and 53 species of dicotyledons; we recognize 7 families, 18 genera, and 24 species. Many of Axelrod's (1987) species, moreover, are reassigned to different families and (or) genera. How can two systematic treatments of the same material result in such markedly different systematic dispositions of so many taxa?

Axelrod's (1987) systematic treatment of the Creede flora is fundamentally "picture matching" (Wolfe, 1974). In this method, for a given fossil leaf, an extensive search is made of modern comparative collections in herbaria to find the closest "match" for the fossil. The fossil is then assigned to the same genus, family, and order as the modern "match"; these assignments are not made because the fossil has characters that circumscribe the genus, family, or order. The characters that result in the "match" are typically not stated, and, even if they are, no evaluation is made as to whether the characters are taxonomically critical (as opposed to characters that might represent ontogenetic response to environment). If foliar characacters (or characters of other organs) are described and compared, the descriptions and comparisons are typically phrased in undefined terms or terms of uncertain meanings.

Examples of "matches" that are based on uncritical comparisons abound in literature on western American Tertiary floras. Axelrod (1964, p. 127) described samaras assigned to *Acer bolanderi* Lesq. (sect. *Acer*) as having "***a wing that is sharply truncated under the nutlet, and the latter displays a complex network of interlacing prominent veins" versus samaras assigned to *A. columbianum* Chan. & Axelr. (supposedly sect. *Glabra*) as

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Manuscript approved for publication, December 13, 1989.

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"***having a deep sinus under the nutlet owing to constriction of the wing there, and the nutlet does not display a network of veins but has a deep prominent wrinkle." If these fossil samaras are so clearly distinguishable and each is "matched" by different species in different sections of *Acer*, then how was it possible for one specimen (Axelrod, 1964, pl. 15, fig. 9) to be assigned to *A. bolanderi* and the counterpart (Axelrod, 1964, pl. 16, fig. 10) of the same specimen to be assigned to *A. columbianum*?

A method that is frequently employed to narrow the search for a "match" is based on modern associations. Once a few to several taxa (typically the most abundant) are determined in a fossil flora, if the presumed "matches" of these taxa now live in proximity, then search is made among the presently associated taxa, or at least those living in the same general area. Poorly preserved fossil leaves are especially prone to be "identified" in this manner; the "identifications" are difficult, if not impossible, to falsify, but they are seemingly consistent with the modern association. Coming full circle, such "identifications" have been used as evidence for associational stability during the Cenozoic. A classic example of how associational "matches" can deny morphologic data is that of a taxon originally described as *Cinnamomum bendirei* in the Oligocene Bridge Creek flora of Oregon. As discussed by Wolfe (1969, p. 86):

> The "holotype" of the associational method of determination (Cain, 1944, p. 43) is in fact an excellent demonstration of the weakness of the method. Knowlton (1902) originally described *Cinnamomum bendirei* from the Bridge Creek assemblage of Oregon. Chaney (1927), however, interpreted this assemblage as a redwood forest and thus considered *Cinnamomum* an incongruous element. He therefore transferred Knowlton's species to *Philadelphus*, which would be expected in a redwood forest. Brown (1940) pointed out that the leaves morphologically could not be *Philadelphus* but had the diagnostic characters of Lauraceae; he thus transferred the species to *Sassafras*. This transfer was ignored by Chaney (1944b, p. 350), who still considered that *Philadelphus* was a better choice for a redwood forest. After the discovery of the living *Metasequoia* and the realization that the Bridge Creek assemblage contained not *Sequoia* but rather *Metasequoia*, Chaney (1952) accepted Brown's transfer of the species to *Sassafras*. The leaves, however, have the small areoles lacking branched, freely ending veinlets and the continuous marginal [now fimbrial] vein of *Cinnamomum*, *Lindera*, and *Neolitsea*; *Sassafras* has large areoles intruded by branching veinlets and lacks a marginal vein (Wolfe, 1960). Knowlton's determination was more valid than either Chaney's or Brown's.

Both the "picture matching" and "associational" approaches to determinations of fossil leaves, especially those of the dicotyledons, have led to many similar misidentifications.

A second source of error in misidentifications of fossil dicotyledonous leaves is misapplication of the "living equivalent" concept. The worker basically considers the extant species that has foliage (or other organ) most similar to the fossil as the "living equivalent" of the fossil taxon. This concept was originally developed for purposes of inferring paleoecology and paleoclimate by assuming that morphologic similarity indicated physiologic (and hence ecologic) similarity. We will not here discuss ecologic problems inherent in this assumption but will emphasize the taxonomic problems that misapplication of the "living equivalent" concept has caused.

The misapplication is assuming that all fossil leaves (or other organs) that have the same supposed "living equivalent" represent the same fossil species. MacGinitie (1953, p. 79) pointed out the obvious: two fossils can both be closest morphologically to the same living species and yet can differ morphologically from that living species in very different directions. For example, Wolfe (1964) assigned certain *Acer* samaras from the Miocene of Nevada to the extant *A. macrophyllum* Pursh (the sole extant member of section *Macrophylla*) and synonymized with this species the fossil species *A. oregonianum* Knowlt. Detailed morphologic analysis, however, indicates that the Nevada samaras represent an extinct lineage very distinct from that of *A. oregonianum*, which, in turn, represents an extinct lineage distinct from that of its supposed "living equivalent" *A. macrophyllum*, although all three lineages belong to *Macrophylla* (Wolfe and Tanai, 1987).

A second point relevant to the "living equivalent" concept is: a fossil species can have an uncanalized morphology (Upchurch, 1985); that is, a fossil species can have wide morphologic variation, even wider than the variation possessed by extant taxa. If this variable fossil taxon gave rise to several extant taxa by canalizing different characters in different directions, then a number of subsets of the fossil taxon will be most similar to a number of the descendant taxa; misapplication of the "living equivalent" concept will then lead to the partitioning of the fossil taxon into a number of fossil species (see later discussion of *Ribes lacustroides*).

Excessive partitioning of a fossil taxon at the generic level can also result from misapplication of the "living equivalent" concept. In the rosaceous *Chamaebatiaria* group, Wolfe and Wehr (1988) described a middle Eocene taxon, *Stonebergia columbiana*, from one locality in British Columbia. The variation of *S. columbiana* includes characters of *Chamaebatiaria*, *Chamaebatia*, and *Sorbaria*, and *Stonebergia* is considered to be ancestral to all three extant genera. Alternatively, all three extant genera could be considered as "living equivalents" of the most similar fossils. Specimens of *Stonebergia columbiana* that are most similar to *Sorbaria*, for example, might form the basis for a species of *Sorbaria* and the other fossil specimens assigned to two additional species, one placed in *Chamaebatiaria* and the other in *Chamaebatia*. As invalid as this alternative taxonomic partitioning might seem, the same logic has been applied to determinations of numerous Tertiary fossils.

In misapplication of both the "associational" and "living equivalent" methodologies, the extant leaf (or other organ), rather than a fossil, has become the holotype for the morphologic definition of a fossil species. Comparisons then may not be made between two fossils but rather between each fossil and the extant organ, and, if both fossils are similar to the organ(s) of the same extant species, the two fossils are considered to be conspecific. A major result of these approaches has been that morphologic differences between fossil and living taxa or between two fossil taxa are ignored or lost; this morphologic information may be critical in phylogenetic reconstructions and in understanding relationships between extant plants.

For many decades these approaches were the primary methods used for identification of Cretaceous and Tertiary foliage. Since the 1960's and 1970's, however, paleobotanists working with leaves have developed (1) criteria for the recognition of characters that are critical at taxonomic levels above the species and (2) rigorous terminology for descriptions (for example, Hickey, 1973; Dilcher, 1974; Wolfe, 1974, 1989; Hickey and Wolfe, 1975). Our taxonomic revision of the Creede flora reflects this newer approach to the determinations of fossil leaves. Development of this new approach, commonly referred to as leaf architecture, involves detailed comparative morphologic and (or) anatomical analysis of a wide range of foliage of extant plants, typically using chemically cleared specimens. Taxonomically critical foliar characters are those that circumscribe groups of taxa as traditionally recognized on the basis of criteria of morphology of reproductive structures.

Acknowledgments.—We are indebted to Peter Robinson for access to the University of Colorado's Creede collections and to Scott Wing for access to the Smithsonian Institution's Creede collections. The part of the report dealing with conifers was critiqued by C. Millar and the late W.B. Critchfield (U.S. Forest Service) and that dealing with angiosperms by G.R. Upchurch (National Center for Atmospheric Research) and S.L. Wing (Smithsonian Institution). Harvey Scudder (California Academy of Sciences) offered considerable help regarding supposed plant structures that actually represent insect remains. We have also benefited by discussions with James Eckenwalder (University of Toronto) and Patrick Fields (Michigan State University). Baki Kalispagil (University of California, Berkeley) supplied the cone of *Pinus* from the Miocene of Turkey. Modern comparative material was supplied by the following herbaria: A, G, CAS, MO, UC, and US.

SYSTEMATICS OF THE CREEDE FLORA

Many of the Creede species described as new by Axelrod were minimally described, and thus we include thorough descriptions based (for the angiosperms) primarily on Hickey's (1973) terminology. Exceptions and (or) additions are: (1) "abmedial" is used in place of Hickey's "exmedial" (Wolfe and Wehr, 1987), (2) "external secondary vein" (von Ettingshausen, 1861) is used in preference to Hickey's "secondary vein branch," (3) topology of teeth and their associated veins is given (Hickey and Wolfe, 1975), (4) in lobed leaves, topology of lobal sinuses and their associated veins is given (Wolfe and Tanai, 1987), (5) veinlets that branch irregularly from a few to several times are referred to as "dendritically branching," and (6) descriptive terms for deeply cleft laminae follow Wolfe and Wehr (1988).

Comparisons of various conifer organs would be greatly facilitated if all workers adopted a standardized approach for illustration. By convention, objects should be oriented with their upper/distal/apical ends toward the top of a page or plate. Similarly, a standardized terminology for each conifer organ would allow ready comparisons, even in the absence of illustrations. For some organs, terminology exists in the literature, but the winged seeds and cone scales of, for example, *Pinus* have received much less attention. Klaus (1980), however, deals thoroughly with apophysis-umbo-mucro relations for *Pinus* (see fig. 6 later) cone scales, and we propose (see fig. 1 later) a terminology for pinaceous winged seeds.

If standardized morphologic terminologies are not employed and particularly if descriptions are very brief, we urge that illustrations of specimens be adequate for other workers to recognize critical characters of the taxon. In many instances, this should involve photographic enlargements and (or) line drawings at the appropriate magnification to illustrate critical characters.

Some of Axelrod's (1987) new species were also improperly typified according to the International Code of Botanical Nomenclature (ICBN) (Greuter and others, 1988). We have also suggested corrections for some orthographic errors in spelling of specific epithets according to the recommendations of the ICBN.

We have generally excluded from the study most specimens of presumed angiospermous reproductive structures that were determined by Axelrod (1987); most of these specimens are poorly preserved impressions that lack characters critical for identification. The infructescence assigned to *Populus* (Axelrod, 1987, pl. 21, fig. 1), however, has sufficient characters preserved to indicate probable validity of the generic assignment. The specimen thought to represent a pod of the legume *Robinia* (Axelrod, 1987, pl. 32, fig. 6) also has critical characters preserved; this specimen represents a larva of a taxon of the crane-fly family Tipulidae (H.I. Scudder, oral commun., March 1989).

As the last item in each synonymy, the designation used by Wolfe and Schorn (1989) is given. A few taxonomic changes were made after the Wolfe and Schorn (1989) manuscript was accepted for publication. These changes involve recognition of two additional but rare species of *Pinus* and assignment of most fascicles of *Pinus* to *P. crossii*. These changes only minimally alter the sample scores or scores of other species in the multivariate analyses.

The specimens on which our revision of the Creede flora is based include the material deposited in the University of California Museum of Paleontology (UCMP) and the University of Colorado Museum (Geology Department) (UCMG); that is, the same material that formed the basis for Axelrod's (1987) treatment. Material, mostly collected by B.K. Stewart in the 1930's, housed in the U.S. National Museum (USNM) and material in the Harvard University Botanical Museum (HUBM) has also been used. Included in these collections is material of one taxa (Rosoideae gen. indet.) that was apparently overlooked in the prior systematic analysis.

Systematic List

Coniferophyta
  Coniferae
    Coniferidae
      Coniferales
        Cupressaceae
          Juniperus creedensis Axelr.
        Pinaceae
          Abies rigida Knowlt.
          Picea sp.
          Pinus crossii Knowlt.
          Pinus riogrande Axelr.
          Pinus sanjuanensis Axelr.
          Pinus sp. 1
          Pinus sp. 2
Magnoliophyta
  Magnoliatae
    Ranunculidae
      Ranunculanae
        Berberidales
          Berberidaceae
            Berberis coloradensis Axelr.
            Mahonia aceroides (Knowlt.) Schorn & Wolfe
    Dilleniidae
      Dillenianae
        Salicales
          Salicaceae
            Populus larsenii (Knowlt.) Schorn & Wolfe
            Salix sp.
    Rosidae
      Rosanae
        Saxifragales
          Philadelphaceae
            Jamesia caplanii Axelr.
          Grossulariaceae
            Ribes lacustroides Axelr.
            Ribes robinsonii Schorn & Wolfe
            Ribes obovatum Schorn & Wolfe
        Rosales
          Rosaceae
            Eleiosina praeconcinna (Cocker.) Schorn & Wolfe
            Eleopoldia lipmanii (Axelr.) Schorn & Wolfe
            Stockeya creedensis (R. W. Br.) Wolfe & Wehr
            Holodiscus stevenii Schorn & Wolfe
            Crataegus creedensis Axelr.
            Sorbus potentilloides (Knowlt.) Axelr.
            Potentilla creedensis (Axelr.) Schorn & Wolfe
            Cercocarpus henricksonii Schorn & Wolfe
            Cercocarpus nanophyllus Schorn & Wolfe
            Rosoideae, gen. & sp. indet.
            Osmaronia? stewartiae (Axelr.) Schorn & Wolfe
            Prunus creedensis Axelr.
            Prunus sp.
        Fabales
          Leguminosae
            Cercis sp.
            Legume, gen. & sp. indet.
    Asteridae
      Lamianae
        Scrophulariales
          Bignoniaceae
            Catalpa coloradensis (Axelr.) Schorn & Wolfe
  Liliatae
    Incertae Sedis
      Monocotylophyllum sp.

Systematic Descriptions and Discussions

Family CUPRESSACEAE
Genus JUNIPERUS Linnaeus

Juniperus creedensis Axelrod

Plate 1, figures 1, 2

Juniperus creedensis Axelrod, 1987, p. 99, pl. 16, figs. 1–9.
Sabina linguaefolia auct. non (Lesquereux) Cockerell. Knowlton, 1923, p. 187.
Wolfe and Schorn (1989) designation: *Juniperus creedensis*.

Description.—Foliated axis poorly preserved, length about 9 cm, width of basal axis 0.4 cm and of apical parts about 0.15 cm; branching alternately (apparently from all sides of axis).. Leaf shape rhombic, ternate phyllotaxis common, decussate phyllotaxis rare and typically in more apical parts of axis, infrequent poorly expressed glands. Fruit globose, diameter 0.9–1.4 cm, detailed preservation lacking but seed cavities present, stock 0.1–0.2 cm long and with minute leaves.

Discussion.—Juniperus creedensis was described (Axelrod, 1987, p. 99) as "***scale leaves in 2's [decussate], opposite, closely appressed***." Most specimens of *J. creedensis* have ternate rather than decussate phyllotaxis. The poorly preserved holotype of *J. creedensis* shows rare glands and both ternate and decussate phyllotaxis. The ternate phyllotaxis is most prominent in older (proximal) portions of the axis and is particularly evident in specimens that preserve a natural break of the axis. The rare, more flattened decussate phyllotaxis occurs in younger (distal) portions of the foliage. The ternate phyllotaxis excludes the Creede material from the New World group of *Cupressus*, which has exclusively decussate phyllotaxis.

Juniperus creedensis was compared to the extant *J. osteosperma* (Torr.) Little and the extant *J. californica* Carr. (Axelrod, 1987). *Juniperus osteosperma* is both decussate and ternate, and the glands are typically poorly expressed (Edwards, 1983), as in *J. creedensis*; *J. californica* is mostly ternate and has well-developed glands. The Neogene *J. nevadensis* Axelr. has phyllotaxis and degree of glandularity similar to *J. creedensis*, but the axes and ovulate cones of *J. creedensis* are slightly more robust than in *J. nevadensis* (Axelrod, 1987).

A second described species of Creede *Juniperus*, *J. gracillensis* Axelr., is not a gymnosperm. Although described as having closely appressed, scalelike leaves that have two-ranked (decussate) phyllotaxis (Axelrod, 1987, p. 100), the specimens are branching, planar laminae that have medially positioned vascular strands. These specimens represent the rosaceous *Eleopoldia lipmanii* (pl. 13, fig. 3).

Holotype.—7447.

Paratypes.—7448–7475.

Family PINACEAE

Discussion.—The extensive collections available from the Creede area (Axelrod, 1987, tables 1–4) produced 7,628 conifer specimens. Almost half (3,668) are impressions of foliage axes and cones of a single species of juniper. The remaining half (3,955) Axelrod distributed among 10 species of *Pinus*, 3 species of *Picea*, 2 species of *Abies*, and 1 species each of *Pseudotsuga* and *Tsuga*.

The assignment of the Creede material to 5 genera and 17 species of Pinaceae exaggerates the diversity of the family at Creede and partially resulted from failure to exercise caution regarding the identification of poorly preserved material. Identification of the various impression organs must rely on adequate morphological information; that is, in order for any fossil to be assigned to a particular taxonomic level, the fossil must have the set of characters that are necessary to identify the organ to that level. The following discussions of the Creede pinaceous fossils emphasize both preservational states of the fossils and comparative morphology of extant Pinaceae.

Ovulate cones.—The 63 ovulate cone impressions from Creede display all degrees of abrasion and (or) deterioration prior to burial, a major factor not taken into account by Axelrod (1986, 1987). On plate 2 are arranged seven ovulate cones in order of increasing degree of abrasion. We arbitrarily designate these as abrasion stages 1 through 6; stage 1 shows little or no abrasion, but in stage 6 the cone is so seriously abraded that only the sturdy woody axis remains. In our opinion, cones of abrasion stage 4+ or greater are unidentifiable at the generic level. An assignment to a plus (+) designation means we consider the degree of abrasion to be intermediate between the illustrated examples. Using this method, for example, we support our assignment of the holotype of *Picea coloradensis* Axelr. to Pinaceae Genus Indetermined by referring it to abrasion stage 5; the holotype of *P. coloradensis* is chosen to typify abrasion stage 5. Similarly, the holotype of *Tsuga coloradensis* Axelrod is referred to abrasion stage 4+ and is also transferred to the indetermined category (see pl. 2, figs. 5, 8).

Examples of differential cone abrasion and the varying types and quality of fossil preservation are not unique to the Creede material. Illustrated here (pl. 3, figs. 1–3) are two early Pleistocene specimens from Potrero Canyon, California (Axelrod, 1967, 1990), and a Miocene impression from Turkey. Figure 1 is a naturally recovered longitudinal section of a cone that clearly exhibits all "abrasion" stages except the external surface impressions of stages 4 and 5. The specimen illustrated as figures 2 and 3 is a naturally occurring three-dimensional cone broken out of the rock matrix. Figure 2 shows the specimen with 10 attached cone scales that distinguish this as a pine. The outer surface of the cone scales represents approximately abrasion stage 2+. When the small group of identifying cone scales is removed from the specimen (fig. 3), it becomes indetermined to genus; that is, abrasion stage 4+ (fig. 3). The basal part of the Turkish Miocene specimen (pl. 3, fig. 4), which has carbonized cone material present, would be impossible to assign to genus. In the apical area where the carbonized material is absent, the structure of the *Pinus* (*Pinus*) apophysis-umbo-mucro is clearly exposed. The differential preservational states illustrated by these fossils must be recognized in order to evaluate properly the taxonomic significance of the fossil record of Pinaceae. Taphonomic studies directed at understanding the processes and results of biological and (or) mechanical cone abrasion and deterioration are clearly needed in this aspect of paleobotany. An evaluation of the Creede ovulate cones based on abrasion criteria is given in table 1.

Table 1. Abrasion stages of Creede ovulate cones of Pinaceae

[Taxonomic assignment of pinaceous ovulate cones, including partial cones, as recognized by Axelrod (1987), the number censused (and illustrated) by Axelrod (1987), and their abrasion stages. One illustrated specimen of *Pinus sanjuanensis* (Axelrod, 1987, pl. 13, fig. 10) not in collections]

Taxon	Number	Abrasion stage
Picea coloradensis	5 (2)	5 and 6
P. lahontensis	1 (2)	3 and 4+
Pinus coloradensis	2 (2)	2 and 4
P. crossii	35 (2)	1 and 2
P. engelmannoides	1 (1)	4
P. florissantii	0 (1)	2+
P. ponderosoides	2 (3)	2 and 4
P. riogrande	2 (3)	2 and 4
P. sanjuanensis	1 (2)	2 to 2+
Pseudotsuga glaucoides	10 (4)	4+, 5 and 6
Tsuga petranensis	1 (2)	4+ and 5

Winged Seeds.—Seeds that have wings are present in all the least modified members of the Pinaceae. Only certain members of *Pinus*, such as the nut pines (subsection *Cembrae*) and pinyon pines (subsection *Cembroides*), have independently derived wingless seeds. Of the 10 genera in the family, only members of *Pinus* have developed a special condition in which the wing easily separates from the seed without any mechanical tearing of the wing. Such disarticulation of the wing from the seed is accomplished by the hygroscopic tissue of the wing. When the wing is dry a strip of wing tissue clasps firmly on either edge of the seed, holding the wing and seed together. In this condition, the wing and seed are said to be articulated but not adnate or fused. When such winged seeds become wet, the hygroscopic tissue adsorbs water and these cells swell, causing the two strips of wing tissue that clasp the seed to pull away from the seed. Articulated winged seeds have been independently derived in both subgenus *Strobus* and subgenus *Pinus*.

The method of origin of the wing and seed in the Pinaceae is not widely recognized, but this is an extremely important feature because it relates to proper identification and the subsequent interpretation of the fossil record of winged seeds. The wing and seed in Pinaceae are of independent origin, unlike in Cupressaceae and Taxodiaceae, where the wing is derived from the outer coat of the seed. The wing in Pinaceae has its origin with the cone scale and will develop whether or not the ovule is fertilized and (or) matures. This feature has probably been independently recognized a number of times (James Eckenwalder, oral comm., 1985), but we are not aware of a more explicate discussion than the publication on *Pseudotsuga menziesii* (Mirb.) Franco by Allen and Owens (1972, p. 120–123). If, as is typically the situation with the most basal and apical scales in Pinaceae, the scale is sterile or the ovule aborts early in development, the wing is developed without a normal seed and has a very different morphology than its winged seed sibling that has a fully developed wing and seed (pl. 3, fig. 5). In fact, both fully developed and aborted types can be borne on the same cone scale (pl. 3, figs. 5e, g). Recognition of this attribute of Pinaceae wing/seed ontogeny is necessary because very differently appearing structures ensue, and these could be interpreted as different species or even different genera (pl. 2, figs. 10, 11). For example, such undeveloped, atypical winged seeds in the Creede collections were distributed among four genera and seven species (Axelrod, 1987: *Tsuga*, pl. 7, fig. 10; *Picea*, pl. 8, figs. 7–14; *Pinus*, pl. 9, figs. 5–7, pl. 10, figs. 3, 6, and 7, and pl. 12, figs. 2–4; *Pseudotsuga*, pl. 15, figs. 7, 8). When these undeveloped, atypical winged seeds are recognized, they should simply be assigned as atypical winged seeds of the genus, if possible, or otherwise as atypical winged seeds of Pinaceae.

The winged seeds of Pinaceae form a significant part of the fossil record of the family. A literature review and personal observations of 15 paleofloras ranging in age from late Eocene to Pleistocene give the following relative abundance of the different types of detached organs found as Pinaceae impression fossils: defoliated axes, 0.28 percent; foliated axes, 0.85 percent; ovulate cones, 1.14 percent; detached ovulate cone scales, 1.73 percent; detached leaves and (or) fascicles, 36.99 percent; winged seeds, 58.98 percent. Male cones are rare and not commonly recognized or recorded (see pl. 3, figs. 8, 9). The relatively high overall percentage of fossil winged seeds of Pinaceae (55–60 percent) indicates how important this record is to our understanding of the history of the family; however, based on the large number of misidentified winged seeds, the morphology of these organs is apparently the least understood feature in the family. For this reason, we present illustrated keys for generic identification of the winged seeds of Pinaceae (the terminology we use for describing winged seeds is shown in figure 1; the keys are figures 2 and 3). Two keys are presented because single specimens of fossil winged seeds present only one surface of the seed and may not show the resin vesicles, pterostegium, or other features that are necessary for identification. The first key (fig. 2) is usable for living material and those fossils that have the adfacial surface of the winged seed exposed; such fossils should provide a high level of accurate identification, especially if well preserved. If the fossils expose the

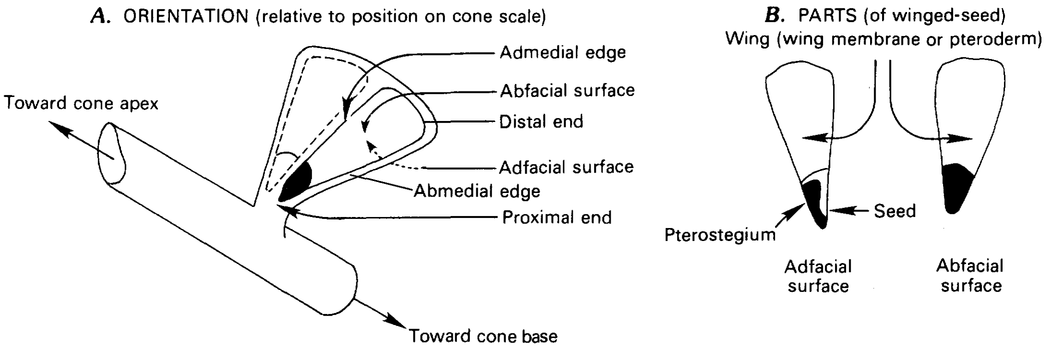

Figure 1. Diagram showing proposed terminology for winged seeds of Pinaceae.

abfacial surface or are of poorer quality preservation, more chance for error of identification exists. The greatest probability is to confuse small *Pinus* and *Picea*, and *Tsuga-Larix-Pseudotsuga*. The indentation on the admedial edge of *Picea* seeds distinguishes them from *Pinus* seeds. If the diagnostic characters of *Tsuga* (resin vesicles and wing cellular pattern), *Larix* (convex adfacial surface of seed and wing cellular pattern) and *Pseudotsuga* (flattened adfacial surface of seed and wing cellular pattern) are poorly preserved or do not show because of orientation in the rock, it would be more realistic and conservative to refer such specimens to Pinaceae cf. *Tsuga-Larix-Pseudotsuga*. These types of fossils can also be compared to other well-preserved specimens from the same fossil flora, giving tentative assignments based on sharing of less critical characters. Whatever course is taken, we suggest that poorly preserved material should not be "overworked" by basing new species on such material.

The winged seeds of Pinaceae from Creede (excluding *Abies*) are keyed out as follows.

A. Wing adnate
  1. Admedial edge of wing 1 cm long or less
    a. Seed small, <3 mm ....atypical *Pinus* 1
    b. Seed large, >3 mm
      1. Admedial edge of proximal end of seed with concave indentation ....*Picea*
      2. Concave indentation absent.........atypical *Pinus* 2
  2. Admedial edge of wing >1 cm long
    a. Seed small, <3 mm long........................atypical *Pinus* 3
    b. Seed intermediate, 3–5 mm long...............*Pinus* type A
    c. Seed large, >5 mm long.............................*Pinus* type B
B. Wing disarticulated
  1. Admedial edge of wing <2 cm long
    a. Vacated seed area <1.5 mm wide.......atypical *Pinus* 4
    b. Vacated seed area 2.5–3.5 mm wide ....*Pinus* type C
  2. Admedial edge of wing >2.5 cm long, vacated seed area >5 mm wide..*Pinus* type D

I. Seeds with resin vesicles; part of abmedial cellular pattern of wing directed toward abmedial edge of wing, intersecting with edge at an angle
  A. Pterostegium well developed on adfacial surface of seed
    1. Wing widest in distal half .... *Abies*
    2. Wing widest in proximal half
      a. Wing 1 1/4-1 1/2 length of seed .... *Keteleeria*
      b. Wing 2 1/2-3 1/4 length of seed .... *Pseudolarix*
  B. Pterostegium little (or not) developed on adfacial surface of seed
    1. Wing widest in distal half ... *Cedrus*
    2. Wing widest in proximal half ... *Tsuga*
II. Seeds without resin vesicles
  A. Cellular pattern of wing undulatory and parallel with long axis of wing; wing typically constricted or wrinkled orthogonal to long axis of wing .... *Pinus*
  B. Cellular pattern of wing not as in A
    1. Wing widest in distal half; seed typically with indentation at proximal end of admedial edge; pterostegium typically not expressed .... *Picea*
    2. Wing widest in proximal half; small area of pterostegium on proximal end of seed
      a. Seed distally rounded, adfacial surface convex .... *Larix*
      b. Seed distally angular, adfacial surface flattened ..... *Pseudotsuga*

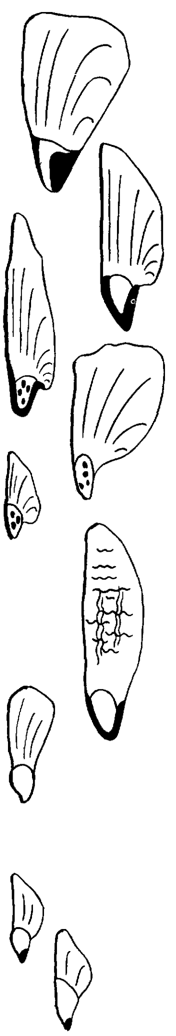

Figure 2. Illustrated key for generic identification of winged seeds of Pinaceae that have adfacial surface exposed. *Cathaya* was not available for study.

The total winged seeds assigned to each species as recognized by Axelrod (1987, tables 1–4) and their keyed equivalents follow.

Abies concoloroides	2 (not in collections, not evaluated)
A. rigida	30 = *Abies rigida* (+ *Picea lahontensis* in part)
Picea coloradensis	10 = atypical *Pinus* 1
P. lahontensis	16 = *Picea* sp. (+ *Abies rigida*, atypical *Pinus* 2, indet. Pinaceae in part)
P. sonomensis	2 = atypical *Pinus* 1 and 3
Pinus alvordensis	6 = atypical *Pinus* 1 and 3
P. coloradensis	3 = atypical *Pinus* 2, 4, and *Pinus* type A
P. crossii	147 = *Pinus* type C
P. macginitiei	1 = *Pinus* type D
P. ponderosoides	22 = *Pinus* type C
P. riogrande	None censused but 3 figured = *Pinus* type A and atypical *Pinus* 4
P. wasonii	At least 3 = *Pinus* type B
Pseudotsuga glaucoidescoides	4 = atypical *Pinus* 2
Tsuga petranensis	2 = atypical *Pinus* 2

The reevaluation just listed, concomitant with our systematic revisions, indicates that pinaceous winged seeds from Creede can be enumerated as follows:

Abies rigida	31
Picea sp.	9
Pinus crossii	172
P. sp. 2	1
P. spp. indet.	33

Fascicles and isolated needles.—Two types of fascicles occur at Creede: a two-needled morphotype that has leaves 2–3 cm long (type 1), and a five-needled morphotype that has leaves varying from slightly more than 2 to about 6 cm long (type 2). Both types have a deciduous sheath and shoot morphology typical of the soft (Haploxylon) pines of subgenus *Strobus*. By shoot morphology we are referring to the shape and structure of the basal "short shoot" axis to which the leaves are attached. In the soft pines, the shoot is circular in outline, and because the sheath is deciduous, the shoot has small scars exposed where the individual sheath elements were attached to the shoot. In the Creede material, the exposed shoot appears as a shortened cylinder that is approximately as wide as tall. The hard pines (subgenus *Pinus*) have a more pronounced, bilaterally symmetrical, slightly bulbous shoot, and the sheath is persistent (except in *Pinus leiophylla* Scheide & Deppe; W. B. Critchfield, oral commun., 1980). Mechanical removal of the persistent sheath very typically results in individual leaves falling off.

I. Cellular pattern of wing undulatory and parallel with long axis of wing; wing constricted or wrinkled orthogonal to long axis of wing .... *Pinus*

II. Cellular pattern of wing not as in I
  A. Part of abmedial cellular pattern of wing directed toward abmedial edge of wing, intersecting edge at angle
    1. Wing widest in distal half
      a. Proximal end of seed blunt; seed oblong, oval, or triangular ... *Abies*
      b. Proximal end of seed not blunt; seed typically oblong .... *Cedrus*
    2. Wing widest in proximal half
      a. Wing + seed typically less than 2 cm long .... *Tsuga*
      b. Wing + seed typically greater than 2 cm long; wing tissue very dense along abmedial edge of seed
        1) Wing 1 1/4-1 1/2 length of seed............... *Keteleeria*
        2) Wing 2 1/2-3 1/4 length of seed............. *Pseudolarix*
  B. All cellular pattern of wing parallel to long axis of wing; no constriction or wrinkling
    1. Wing widest in distal half; seed typically with indentation at proximal end of admedial edge .... *Picea*
    2. Wing widest in proximal half
      a. Seed distally rounded ..... *Larix*
      b. Seed distally angular.. *Pseudotsuga*

Figure 3. Illustrated key for generic identification of winged seeds of Pinaceae that have abfacial surface exposed. *Cathaya* was not available for study.

Variation in needle length of the five-needled type 2 is atypically great for extant pines. A histogram of needle length (fig. 4) indicates that two taxa could be represented, one that has needle length less than 3.5 cm (dominantly 2.0–3.0 cm) and one that has needle length more than 4.0 cm. One shoot (pl. 13, fig. 4) however, has 17 attached fascicles in which needle length varies from 2.4 to 6.0 cm; the long-needled fascicles are both at the basal and at the apical parts of the incomplete shoot, and the short-needled fascicles are in between. These relations could be interpreted as the two groups of long-needled fascicles representing the moister, earlier parts of two growing seasons and the short-needled fascicles representing the drier, later part of the growing season in between. This interpretation is consistent with the dry summers inferred for the Creede assemblage (Wolfe and Schorn, 1989).

The two types of Creede fascicles were distributed among six species, five subsections, and two subgenera (Axelrod, 1987). The absence of a sheath on any of the Creede specimens immediately eliminates their suggested assignment to two of the subsections of subgenus *Pinus*. As determined and censused by Axelrod (1987) and the morphotypes represented, the Creede pine fascicles are:

Pinus alvordensis	17 (type 1)
P. coloradensis	165 (type 2)
P. crossii	703 (type 2)
P. florissantii	535 (type 2)
P. sanjuanensis	38 (type 1)
P. wasonii	16? (type 1)

Based on our systematic revisions and Axelrod's (1987) census data, fascicles of *Pinus crossii* (type 2) are abundant, but fascicles of *P. sanjuanensis* (type 1) are uncommon.

Three isolated needles were assigned to *Pseudotsuga* (Axelrod, 1987, p. 96). Extant *Pseudotsuga* has needles that have a base constricted to form a distinct petiole, have marginal resin canals, and are planar; none of these features are discernible on the Creede specimens. These Creede leaves have a triangular-shaped leaf base and cross section and are approximately 2.5 cm long; they probably represent individual leaves that were separated from fascicles of *Pinus crossii*, although we conservatively relegate such specimens to the indetermined category.

Foliated axes.—Foliated axes, other than those of *Juniperus* and *Pinus*, were assigned to two species of *Abies* and one species of *Pseudotsuga* (Axelrod, 1987). Because none of these axes have leaves that have constricted leaf bases that form a petiole, none can represent *Pseudotsuga*; the specimens assigned to *Pseudotsuga* have circular leaf bases and (or) leaf scars typical of *Abies* (pl. 1, fig. 8).

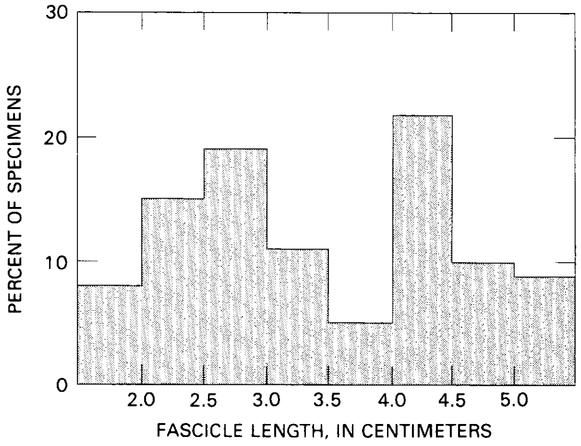

Figure 4. Histogram of needle length for five-needled fascicles of Creede *Pinus*. Based on 79 specimens.

Foliated axes that have longer, more flattened, pseudodistichously arranged leaves were referred to *Abies concoloroides* (except for those referred to *Pseudotsuga*). Foliated axes that have falcate-shaped leaves that appear crowded on the upper sides of the axes were referred to *A. rigida*. Such morphologic differences, however, can occur in branches of the same tree. For example, Sudworth (1908, p. 125) noted that in *A. amabilis* (Loud.) Forbes, "The leaves of lower crown branches are flat***They are about 1¼ inches long, and, by a twist in the bases of those on the lower sides of the branches, they appear massed on the top sides [pseudodistichous]. Branches of the uppermost part of the crown have shorter and stouter leaves, about three-fourths of an inch long***and stand erect in dense masses on the tops of the sprays." Sudworth (1908) and Liu (1971) also described similar conditions for *A. concolor* (Gord.) Parry, *A. procera* Rehd., and *A. magnifica* Murr. The dimorphic condition in the Creede axes of *Abies* is thus similar to that in single species of extant *Abies*, and we consider all these foliated axes to represent *A. rigida*.

Genus ABIES Miller

Abies rigida Knowlton

Plate 1, figures 3–10

Abies rigida Knowlton, 1923, p. 186, pl. 41, figs. 1, 2, 4, 5. Axelrod, 1987, p. 83, pl. 5, figs. 1–8; pl. 6, figs. 1–10.
Abies longirostris Knowlton, 1923, p. 187, pl. 42, figs. 1, 2.
Abies concoloroides auct. non R. W. Brown. Axelrod, 1987 (part), p. 82, pl. 7, figs. 1–3, 6.
Picea lahontensis auct. non MacGinitie. Axelrod, 1987 (part), p. 85, pl. 8, fig. 2.
Pseudotsuga glaucoides Axelrod, 1987 (part, nontypic), p. 96, pl. 15, figs. 1, 3, 9, 10.
Wolfe and Schorn (1989) designation: *Abies rigida*.

Description.—Foliated axis more than 5.6 cm long, 0.5–0.6 cm wide, circular leaf scars slightly less than 0.1 cm wide, almost flush with surface of axis; about 20 leaves preserved, about 1.5 cm long and slightly more narrow than leaf scars; leaf shape falcate, base a circular expansion slightly wider than leaf, apex rounded, leaves twisted so as to appear to be derived from and directed away from one side of axis (presumably adaxial side); other axes have distichously arranged leaves that are about 6 cm long. Ovulate cone scale at least 1–2 cm wide, 1.0–1.5 cm long (scale and stalk); scale-length to stalk-length ratio about 2:1; scale shape cuneate to reniform; bract scale exserted, length relative to cone scale variable, as much as 5.0 cm long; width variable, commonly widest under cone scale (where laminar tissue is expanded but no lobes formed, tapering to a stiff, rigid apex. Winged seeds have wing-length to seed-length ratio of about 1:1; seeds typically ovate to obovate, seed-length to pterostegium-length ratio about 1.25:1.

Discussion.—The detatched cone scales and foliated axes of the Creede fir were originally described as two distinct species (Knowlton, 1923); however, Axelrod (1987) validly recognized their equivalency and combined the two different organs into a single species. Included in *Abies rigida* are ovulate cone scales (attached bract scales are present or absent), winged seeds, axes (foliated or defoliated), and isolated leaves.

The long exserted bract scale is absent from two Creede cone scales assigned to *Abies concoloroides* R. W. Br. (Axelrod, 1987, pl. 7, figs. 2, 3). The size and shape of these cone scales, the ratio of stalk length to scale length, and the shape and relative size of the wing impressions on the scales are all characters shared, however, with cone scales assigned to *A. rigida*.

One winged seed assigned to *Picea lahontensis* (Axelrod, 1987, pl. 8, fig. 2), unlike seeds of extant *Picea*, has no indentation on the proximal end of the admedial edge of the seed. The shape of the seed and the wing, the faint cellular pattern of the wing, and the arrangement of the seed-wing juncture are characters found in winged seeds of *Abies rigida*.

Numerous unfoliated and foliated axes of *Abies* are recognizable by, respectively, the presence of circular leaf scars and the absence of leaf bases constricted into a petiole. Knowlton (1923, p. 187) suggested the possibility that two species of fir were represented by foliated axes in the Creede flora. Axelrod (1987) also recognized two morphotypes of *Abies* axes, assigning the most common type to *A. rigida* and a type that has pseudodistichous leaf arrangement to *A. concoloroides*; however, some axes that have a pseudodistichous leaf arrangement and unconstricted leaf bases (and thus represent the second *Abies* morphotype) were invalidly assigned by Axelrod (1987) to *Pseudotsuga*. As previously discussed, a condition in which leaves are flattened into a pseudodistichous arrangement is common on lower branches of extant firs, even those *Abies* that have leaves of the upper branches twisted and directed toward the upper (adaxial) side of the branch (Sudworth, 1908; Liu, 1971). The variation displayed by extant firs supports assignment of all these foliated axes from Creede to a single entity. Relative to leaf length, the specimens assigned by Axelrod (1987) to *A. concoloroides*, *A. rigida*, and *Pseudotsuga* also overlap (fig. 5).

The cone scales of *Abies rigida* were, because of the highly exserted subtending bracts, originally compared to the extant *A. bracteata* D. Don (Knowlton, 1923). This suggested relationship may be valid. The extant genus most closely related to *Abies* is *Cedrus*, in which the bract is reduced and adnate to the cone scale. This relation could suggest that reduced, inserted subtending bracts, as found in many extant species of *Abies*, represent the plesiomorphic condition. If this suggestion is valid, then the highly exserted bracts of *A. rigida* and *A. bracteata* could represent a synapomorphy and indicate that the two taxa are more closely related to one another than to other species of *Abies*. Until a thorough cladistic analysis of extant *Abies* is undertaken, however, such suggested relationships remain speculative.

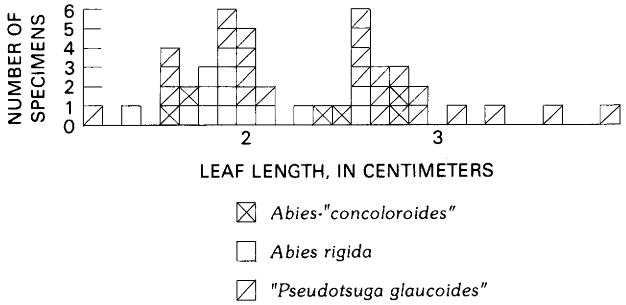

Figure 5. Histogram of leaf length in Creede *Abies*.

That the foliage of *Abies rigida* has little similarity to that of *A. bracteata* (Axelrod, 1987) may not be significant relative to phyletic relationships. The extant *A. bracteata* inhabits far milder climates than the climate inferred for *A. rigida* (Wolfe and Schorn, 1989); foliage of many extant *Abies* that inhabit subalpine environments have, as in *A. rigida*, leaves twisted and directed toward the upper side of the branch.

Two winged seeds from Creede were attributed to *Abies concoloroides* R. W. Br. (Axelrod, 1987, pl. 7, figs. 4, 5). Determination of the taxonomic status of these seeds, which were not placed in the University of California Museum of Paleontology, must await their relocation and examination. *A. concoloroides* is a poorly understood concept, however, and fossil material that appears to be related to the extant *A. concolor* (Gord. & Glend.) Lindl. should not indiscriminately be assigned to *A. concoloroides*. *Abies concoloroides* was founded (Brown, 1940) on an impression of the abaxial surface of an ovulate cone scale that does not have a bract scale and on a foliated axis of a *Picea* (see later discussion of *P. lahontensis*); however, because *A. concoloroides* has never been formally described or diagnosed, the epithet must be considered an illegitimate name. The foliated axes and ovulate cone scales from Creede attributed to *A. concoloroides* (Axelrod, 1987) are reassigned to *A. rigida*.

Lectotype.—USNM 36505.

Syntypes.—USNM 36507–36509.

Hypotypes.—USNM 36517, 36518; UCMP 7248–7263, 7265–7281, 7283–7286, 7308, 7381, 7384, 7410–7416, 7426–7430.

Genus PICEA Dietrich

Picea sp.

Plate 3, figure 6

Picea lahontensis auct. non MacGinitie. Axelrod, 1987 (part), p. 85, pl. 8, figs. 4–6.

Wolfe and Schorn (1989) designation: *Picea* sp.

Discussion.—Of the three species of spruce recognized by Axelrod (1987) in the Creede flora, only one is considered validly to represent *Picea*. The Creede spruce is part of a big-seeded complex that includes *P. lahontensis* Macg. and *P. magna* MacG.; this complex is no longer extant in North America and may represent one or more lineages. From the latest Eocene *P. magna* to the Neogene *P. lahontensis*, morphologic trends are for the winged seed to increase in size and for the wing to become longer relative to the seed. The Creede spruce seeds are most similar to the types of *P. magna* but differ in having shorter and broader wings; these differences are not morphologically intermediate between *P. magna* and *P. lahontensis* and suggest that the Creede *Picea*, in retaining an apparently more primitive morphology, could be a sister lineage to the *P. magna–P.lahontensis* lineage. A complete morphometric analysis of these big-seeded taxa of spruce should further resolve their relationships.

One winged seed assigned to *Picea lahontensis* (Axelrod, 1987, pl. 8, fig. 2) represents *Abies rigida*. Characteristic of spruce seeds relative to other members of Pinaceae is a concave indentation on the proximal end of the admedial edge of the seed, and this indentation is absent in the seed just cited. The fossil also has a cellular pattern on the wing directed outward toward the abmedial edge of the wing; this feature is restricted to, and diagnostic of, the abietoid Pinaceae (*Abies, Cedrus, Keteleeria, Pseudolarix,* and *Tsuga*). Some other supposed spruce seeds (Axelrod, 1987, pl. 8, figs. 7–14) are considered to represent atypical seeds of pine (see later).

None of the Creede ovulate cones assigned to *Picea* (Axelrod, 1987) have characters diagnostic of the genus. Except for one specimen, all these cones are too abraded for generic identification. The taxonomic disposition of these cones follows.

Picea lahontensis (Axelrod, 1987, pl. 8, fig. 1) = Pinaceae genus and species indetermined. This cone (and others of abrasion stage 4+ or greater) exhibits no features that are diagnostic to genus. The presence of spirally arranged, woody, persistent cone scales (or their remnants) indicate that the cone belongs to a genus of Pinaceae that has persistent cone scales (*Cathaya, Larix, Keteleeria, Picea, Pinus, Pseudotsuga, Tsuga*). The size and shape of the cone suggest *Keteleeria, Picea, Pinus,* and perhaps *Pseudotsuga*. Because other, better preserved pinaceous cones in the Creede collections primarily represent *Pinus crossii*, the cone most probably represents that taxon. Other supposed spruce cones (Axelrod, 1987, pl. 8, fig. 15; pl. 8, fig. 16 [holotype of *Picea coloradensis* Axelr.]) represent abrasion stages 6 and 5, respectively; these may also represent *Pinus crossii*.

Picea lahontensis (Axelrod, 1987, pl. 8, fig. 3) = *Pinus* cf. *P. crossii* Knowlt. This cone fragment (a fragment cited as homeotype UCMP 7315 is part of the same cone; see our pl. 2, fig. 3) has the dorsal umbos characteristic of *Pinus*. The cone represents abrasion stage 3.

The single defoliated axis assigned to a spruce probably represents an angiosperm.

Specimens.—UCMP 7302, 7304–7307, 7310, 7313.

Genus PINUS Linnaeus
Subgenus STROBUS Lemmon
Section PARRYA Mayr
?Subsection CEMBROIDES Engelmann

Pinus sanjuanensis Axelrod

Plate 1, figures 11, 12

Pinus sanjuanensis Axelrod, 1986, p. 613, figs. 12–16. Axelrod, 1987 (part), p. 95, pl. 13, figs. 2–8, 10, 11.

Pinus alvordensis auct. non Axelrod, 1944. Axelrod, 1986 (part), p. 627, figs. 79–81.

Wolfe and Schorn (1989) designation: *Pinus* sp.

Description.—Ovulate cone uncertain (specimen misplaced, and detailed description awaits relocation of specimen). Fascicles have two leaves, 1.2–3.1 cm long, mean length of 36 fascicles (including leaf and short shoot) 1.6 cm, about 0.1 cm wide, sheath deciduous.

Discussion.—*Pinus sanjuanensis* was considered (Axelrod, 1986, 1987) to be most similar to the extant pinyon, *P. edulis* Engel. The ovulate cone that is the holotype of the species has not been located. The illustration of the cone lacks details sufficient to make a satisfactory evaluation of the specimen, and the formal description is similarly unsatisfactory. Close affinities of this cone are thus speculative, but we will follow Axelrod (1986, 1987) and consider this cone that of a pinyon.

Had the terminology formulated by Klaus (1980) (fig. 6) been consistently employed, the affinities of *Pinus sanjuanensis* could be deciphered. This species is described, however, as "***apophyses subdued; umbo mucronate, centro in position on scales***" (Axelrod, 1986, p. 613). Klaus (1980, fig. 4) used traditional terminology in reference to either terminal or dorsal position of the umbo relative to the apophysis. In cones that have dorsal umbos, Klaus further differentiated the position of the mucro (spine, thorn, or prickle): (1) mucro positioned on the transverse keel (centromucronate) and (2) mucro positioned distally above the transverse keel in the upper field of the umbo (excentromucronate). Does Axelrod's "centro in position on the scales" refer to the umbo as being centrally positioned on the apophysis (that is, dorsal) or to the mucro being centrally positioned on the umbo (centromucronate)?

Although the affinities of the holotype of *Pinus sanjuanensis* are somewhat uncertain, we have, as did Axelrod (1987), included two-needled fascicles in this

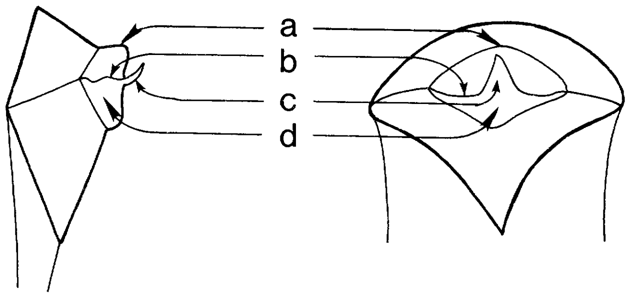

Figure 6. Drawing showing general terminology of apophysis, umbo, and mucro of ovulate cone scale in *Pinus*. *a*, upper umbo field; b, transverse keel; c, mucro (centroerect); d, lower umbo field. Modified from Klaus (1980).

species so as not to proliferate nominal species. We have also included morphologically indistinguishable fascicles assigned by Axelrod (1987) to *P. alvordensis*. Axelrod (1986, p. 627) noted similarities between the fascicles he assigned to *P. sanjuanensis* or to *P. alvordensis* but differentiated fascicles of *P. sanjuanensis* on the basis that "***the fascicle sheath is smaller as compared with those of *P. alvordensis*." None of these two-needled fascicles have sheaths, which were presumably deciduous.

Subsection *Contortae*, to which *Pinus alvordensis* was assigned, has persistent sheaths, and subsection *Cembroides*, to which *P. sanjuanensis* was assigned, has deciduous sheaths. Perhaps Axelrod was referring to the short shoot, upon which the leaves are borne, as the "fascicle sheath," but, if so, the fascicles referred to *P. sanjuanensis* are still inseparable from those referred to *P. alvordensis*.

Pinus sanjuanensis was considered (Axelrod, 1986) to be related to *P. ballii* R. W. Br. from the Eocene Green River flora. Brown (1934) described *P. ballii* on the basis of a single fascicle that he, as well as subsequent authors (MacGinitie, 1969; Axelrod, 1986, 1987), assumed to have three leaves. Four leaves are visible on the specimen, the fourth tip being observable just above the tip of the leaf to the right. This specimen, however, is poorly preserved and is an inadequate basis for the supposed earliest record of pinyon pines. MacGinitie (1969) added a supposed cone to *P. ballii*, an addition accepted by Axelrod (1986, 1987). This open "cone" has "scales" that appear to arise from a common point of origin; the scales are narrow, have no indication of large seed cavities that would be present in a pinyon pine, and have no obvious apophysis-umbo structures at the distal ends. This "cone" certainly does not represent *Pinus* and most probably is an angiosperm fructification.

Holotype.—UCMG 19701.

Paratypes.—UCMP 7239–7244, 7247, 7393, 7400.

Hypotypes.—UCMP 7173–7176, 7236–7238, 7396, 7398, 7399. Note that specimen numbers were reversed on UCMP 7235 and 7174; UCMP 7174 was first illustrated as *Pinus alvordensis* (Axelrod, 1986, fig. 79), and then a second specimen was assigned the same number and also illustrated as *P. alvordensis* (Axelrod, 1987, pl. 3, fig. 3). This second specimen, which is a fascicle of *P. crossii* that has three leaves missing, is now assigned UCMP 7235.

Subsection BALFOURIANAE Shaw

Pinus crossii Knowlton

Plate 2, figures 1, 2; plate 3, figures 7–13; plate 13, figure 4; text figures 7*A*, *B*

Pinus crossii Knowlton, 1923, p. 185, pl. 41, figs. 3, 8–10. Bailey, 1970, p. 239, figs. 34–37. Axelrod, 1986, p. 73, figs. 34–42. Axelrod, 1987, p. 91, pl. 7, figs. 11–16; pl. 9, figs. 10–13; pl. 13, figs. 9, 12.

Pinus coloradensis Knowlton, 1923, p. 186, pl. 41, fig. 6. Axelrod, 1986, p. 615, figs. 43, 48 51, 53. Axelrod, 1987, p. 90, pl. 10, figs. 1, 2. Axelrod, 1986 (part), p. 615, figs. 48, 51, 53.

Pinus similis Knowlton, 1923, p. 186, pl. 41, figs. 11, 12.

Pinus aristata fossilis Cockerell, 1934, p. 573, fig. 1.

Pinus ponderosoides Axelrod, 1986 (part, typic), p. 623, figs. 64–66. Axelrod, 1987 (part), p. 94, pl. 11, figs. 3–7, 9, 10.

Pinus wasonii Axelrod, 1987, p. 96, pl. 14, figs. 6–12.

Pinus alvordensis auct. non Axelrod, 1944. Axelrod, 1987 (part), p. 89, pl. 9, fig. 3.

Pinus florissantii auct. non Lesquereux. Axelrod, 1986 (part), p. 607, fig. 9. Axelrod, 1987, p. 92, pl. 14, figs. 1–5.

?*Pseudotsuga glaucoides* Axelrod, 1987 (part, nontypic), p. 96.

Wolfe and Schorn (1989) designation: *Pinus crossii*.

Description.—Ovulate cone shape oblong to ovate, typically elliptic; as much as 10 cm long, 4.5 cm wide; apophysis in plane or facial view about 1.4 cm wide, 1.0 cm high, width to height ratio about 1.5:1; umbo dorsal; mucro centroerect, as much as 0.8 cm long, shape rhombic, protruding above plane of apophysis. Winged seed disarticulated (rarely found articulated); vacated seed area about 0.3 cm wide (rare seeds 0.7 cm long); line drawn along admedial edge of wing passes through admedial half of vacated seed area; seed wing has admedial edge about 1.2–1.5 cm long, about 0.6 cm wide; abmedial edge tapering distally, distal end typically rounded to obtuse. Fascicles have five (some four) leaves; typically about 2.5–4.5 cm long but ranging from 1.6 to 6.0 cm, 0.1 cm wide; slightly curved; sheath deciduous.

Discussion.—As circumscribed here, *Pinus crossii* Knowlt. is the common pine of the Creede flora. Using Axelrod's (1987) census data and our reassessment of the species, *P. crossii* is represented by approximately 40 ovulate cones, 170 winged seeds, and 1,400 fascicles. Most severely abraded ovulate cone remnants and atypical winged seeds probably also belong to this taxon.

Pinus crossii was originally founded on five-needled fascicles that Knowlton (1923) clearly recognized as a soft pine because of the deciduous sheath. Axelrod (1986) gave a lucid account of our historical understanding of the species and the morphologic evidence that relates this fossil species to the extant *P. aristata* Engelm. of the southern Rocky Mountains of

Colorado and New Mexico. Although Axelrod considered the fossil species to be allied to *P. aristata*, he (1986, p. 615) also recognized that "***there are sufficient differences to indicate that *P. crossii* probably is ancestral to the living bristlecone pine."

Identification of impression fossils of ovulate *Pinus* cones involves some interpretation regarding the three-dimensional reconstruction of the apophysis-umbo-mucro relations. The horizontal pressure during diagenesis of the sediments is minimal and the horizontal outline of the cone is basically the original outline. The vertical pressure, however, significantly distorts original relations, and casts made from natural molds of impressed specimens must be interpreted. The place to observe least distortion of the original relations is along the margins of the cone impression where the cone scale can be seen in profile; care must be taken not to confuse the obliquely oriented apophyses with profiles of the cone scales themselves. Profile and plane view reconstructions of the three types (excluding *P. sanjuanensis*, the sole cone of which is unavailable) of ovulate pine cones from Creede are illustrated in figure 7.

Knowlton originally described *Pinus coloradensis* from a single, incomplete ovulate cone impression. He noted (1923, p. 186) that the "***scales [are] much thickened at the end***" and that the impression was missing "***a few scales at the base***" Axelrod (1986, 1987), in adding two cone impressions to this species, contended (1986, p. 617) that the cone scales were thin rather than thickened. Axelrod's illustrations (1986, figs. 43, 44), including that of a latex cast, of Knowlton's type show, however, that the profile of the scales has a thickened apophysis and protruding umbo (see our fig. 7*B*, which is a specimen referred by Axelrod, 1987, to *P. coloradensis*). Only in plane view do the cone scales appear thin, but this resulted from vertical compression. Thus, the type and one of Axelrod's (1987) unfigured ovulate cones of *P. coloradensis* are referred to *P. crossii*. The third specimen referred to *P. coloradensis* (Axelrod, 1986, fig. 45; 1987, pl. 10, fig. 4) is the apical part of a cone that is abraded to stage 4 and is transferred to *P.* cf. *P. crossii*.

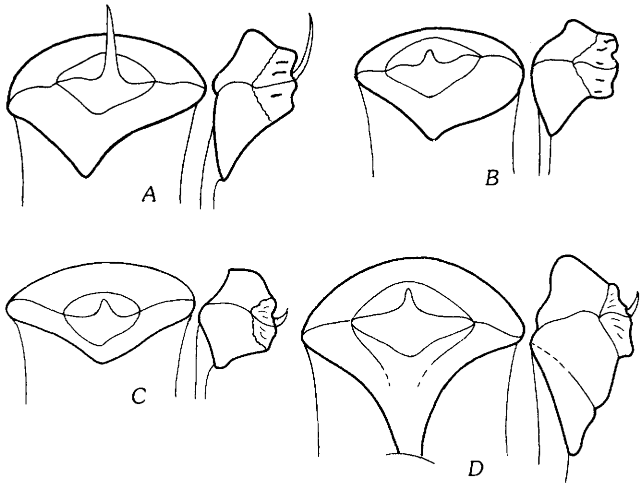

Figure 7. Drawing showing ovulate cones of Creede species of *Pinus*. Plane and profile views. *A*, *B*, *P. crossii* Knowlt. *C*, *P. riogrande* Axelr. *D*, *P.* sp. 1.

The holotype of *Pinus ponderosoides* Axelr. is also placed in *P. crossii*. This specimen is the lateral portion of an ovulate cone that has 16 complete or partially complete apophyses. The apophyses are as high as 1.0–1.2 cm and are slightly wider, giving a length to height ratio of almost 1.5:1. The dorsal umbo protrudes distinctly beyond the plane of the apophysis and is centromucronate; the mucro is erect. The full mucros are missing and are inferred to be abraded; this is the typical situation in *P. crossii* cones.

The disarticulated seed wings and an ovulate cone scale originally included in *Pinus ponderosoides* are also considered to represent *P. crossii*. Two strongly abraded ovulate cones referred to *P. ponderosoides* (Axelrod, 1987) are placed in *P.* cf. *P. crossii*.

The syntypes of *Pinus similis* were synonymized under *P. florissantii*, to which was added a single Creede ovulate cone (Axelrod, 1986, 1987). This cone (pl. 2, fig. 2; abrasion stage 2) has dorsal umbos and represents *P. crossii* of subsection *Balfourianae*, in contrast to the type of *P. florissantii*, which has terminal umbos and thus represents a soft pine of the *P. flexilis* alliance in subsection *Strobi* (Axelrod, 1986).

A few moderately large winged seeds could be assigned to subsection *Strobi* based on their adnate seeds; however, considering the abundance of the typically disarticulated wings of *Pinus crossii*, a few specimens in which seed and wing failed to detach might be expected.

The Creede five-needled fascicles that have deciduous sheaths were segregated by Axelrod (1986, 1987) into four taxa: *Pinus florissantii*, *P. coloradensis*, *P crossii*, and the newly instituted *P. wasonii*. We can see no morphologic basis for such specific distinctions and consider that all these fascicles most probably represent the same biologic entity. Knowlton (1923, p. 186) considered that the leaves of *P. similis* were indistinguishable from *P. hambachii* Kirchn. from Florissant. An enlargement of the negative of the type of *P. hambachii* (illustrated at natural size by MacGinitie, 1953, pl. 19, fig. 1) indicates that the specimen is the frayed end of a reedlike plant.

Some unfigured homeotypes of *Pseudotsuga glaucoides* (Axelrod, 1986, p. 96) probably represent detached leaves of *Pinus crossii*.

Lectotype.—USNM 36514.

Syntypes.—USNM 36511–36513.

Hypotypes.—UCMG 34154; UCMP 7181–7185, 7190–7198, 7200–7202, 7205–7208, 7212–7214, 7216, 7218–7222, 7235 (see UCMP 7174 under *Pinus sanjuanensis*) 7246, 7317, 7326–7328, 7330–7335, 7338, 7437, 7339–7342, 7344–7352, 7354, 7358 (counterpart of 7354), 7362, 7368, 7380, 7387, 7390–7392, 7401–7406, 7408, 7409, ?7431–7433, 7862–7866; USNM 36506, 36516.

Pinus cf. P. crossii Knowlton

Plate 2, figures 3, 4

Pinus engelmannoides Axelrod, 1986, p. 621, fig. 55. Axelrod, 1987, p. 92, pl. 9, fig. 8.

Picea lahontensis auct. non MacGinitie. Axelrod, 1987 (part), p. 85, pl. 8, fig. 3.

Pinus coloradensis auct. non Knowlton. Axelrod, 1986 (part), p. 615, fig. 45. Axelrod, 1987 (part), p. 90, pl. 10, fig. 4.

Pinus florissanti? auct. non Lesquereux. Knowlton, 1923, p. 186, pl. 41, fig. 7.

Pinus ponderosoides auct. non Axelrod, 1986. Axelrod, 1987 (part), p. 94, pl. 11, figs. 1, 2.

Pinus riogrande Axelrod, 1986 (part, nontypic), p. 624. Axelrod, 1987 (part), p. 94.

Wolfe and Scorn (1989) designation: *Pinus crossii.*

Discussion.—All these specimens are ovulate cones of *Pinus*. Most are abraded to approximately stage 4; they cannot be identified to subgeneric level, and none are worthy of standing as holotypes. The material shows the size and general apophysis-umbo shape of *P. crossii* and most probably represents the abundant Creede pine. Some might, if better preserved, prove to represent a different entity than *P. crossii*, but this is speculative. Of the approximately 50 Creede cones of *Pinus* that are determinable to species, almost all represent *P. crossii*, and probably almost all the specimens just cited also represent this taxon.

Specimens.—UCMG 27381; UCMP 7211, 7315, 7316 (= apical third of UCMP 7315), 7230, 7353, 7357; USNM 36510.

Subgenus PINUS
Section PINUS
Subsection PONDEROSAE Loudon

Pinus riogrande Axelrod

Text figure 7C

Pinus riogrande Axelrod, 1986 (part, typic), p. 624, fig. 68.

Pinus sanjuanensis auct. non Axelrod 1986. Axelrod, 1987 (part), p. 95, pl. 13, fig. 1.

Wolfe and Schorn (1989) designation: *Pinus riogrande.*

Description.—Ovulate cone shape narrow ovate (length to width ratio about 2:1); 12 cm long, 4.5 cm wide; apophysis in plane or facial view about 1.5 cm wide and 0.8 cm high, width to height ratio about 2:1; umbo dorsal, not markedly differentiated from apophysis, shape rhombic; mucro centro, straight or erect, about as long as height of umbo field.

Discussion.—Included in this species is an impression of a complete ovulate cone, which is the holotype of *Pinus riogrande*, and a small fragment originally assigned to *P. sanjuanensis*. Both specimens share the features of (1) dorsal umbos that are weakly differentiated from the apophysis and (2) a mucro that is centroerect (situated on the medial keel and directed apically). In his description of the species, Axelrod (1986, p. 624) stated: "***umbo dorsal, centro-reflexed, short mucronate prickles 2–3 mm long, directed distally." This statement is confusing in the context of the terminology defined by Klaus (1980).

Three additional ovulate cone fragments originally assigned to *Pinus riogrande* have well-defined umbos that protrude well above the plane of the apophysis and represent *Pinus* sp. 1. Three winged seeds previously referred to *P. riogrande* (Axelrod, 1987, pl. 12, figs. 2–4) have immature seeds and represent atypical seeds of an indetermined pine.

Holotype.—UCMG 19704.

Hypotype.—UCMP 7393.

Pinus sp. 1

Text figure 7D

Pinus riogrande Axelrod, 1986 (part, nontypic), p. 624, figs. 69, 70. Axelrod, 1987, text (part), p. 94, pl. 12, figs. 5, 6.

Wolfe and Schorn (1989) designation: *Pinus crossii.*

Description.—Ovulate cones incomplete, largest specimen 11 cm long, 5.5 cm wide; apophysis in plane or facial view 1.4 cm wide, about 1.2 cm high, width to height ratio about 1:1; umbo dorsal, distinct, projected above plane of apophysis; apophysis oblate, rhombic; mucro centroerect, about as long as height of upper field of umbo.

Discussion.—Included here in *Pinus* sp. 1 are the apical portions of two ovulate cones originally assigned to *P. riogrande*. The incompleteness of these two specimens dictates against any serving as holotypic material for a named species. These two specimens apparently also represent a species of *Ponderosae*, although they are distinct from *P. riogrande* (compare fig. 7C to 7D).

Specimens.—UCMP 7209, 7210.

Pinus sp. 2

Pinus macginitiei Axelrod, 1986 (part, nontypic), p. 621, fig. 56. Axelrod, 1987 (part), p. 93, pl. 9, fig. 9.

Wolfe and Schorn (1989) designation: *Pinus crossii.*

Discussion.—A single Creede specimen of a disarticulated wing may represent an entity distinct from *Pinus crossii* and other described fossil taxa that are known from winged seeds. The wing is widest immediately distal to the seed area and was probably borne on a cone scale that was expanded near the middle of the scale and narrowed to either end. The wing of *P. macginitiei* from

Florissant is not expanded, and presumably the bearing cone scale was of approximately uniform width; this difference between the Creede and Florissant winged seeds is considered sufficient to exclude the Creede specimen from *P. macginitiei.*

This Creede winged seed has some similarities to seeds of subsection *Ponderosae* but is not sufficiently diagnostic to eliminate from consideration placement in other subsections. Possibly the Creede specimen represents the same entity as our *Pinus* sp. 1, but this suggestion is conjectural.

Nomenclature.—This specimen (UCMG 19701) was cited in figure legends by Axelrod (1986, fig. 56; 1987, pl. 9, fig. 9) as the "holotype" of *Pinus macginitiei.* Axelrod (1986, p. 621), however, designated as the primary type (erroneously called a "lectotype" rather than a holotype) UCMP 3776, which is a long (15 cm), three-needled fascicle (persistent sheath) from Florissant originally attributed by MacGinitie (1953, pl. 20, fig. 1) to *P. florissantii.* In his validating description of *P. macginitiei,* Axelrod (1986, p. 621) first described the Florissant fascicle and then cited UCMG 19703 as a "hypotype" (properly, this is a paratype). Clearly the holotype of *P. macginitiei* is the Florissant fascicle, and the Creede winged seed is a paratype, which is here excluded from *P. macginitiei.*

Specimen.—UCMG 19703.

Subgenus Indetermined

Pinus Species Indetermined (atypical winged seeds and wings)

Plate 1, figures 13, 14; plate 2, figure 10

Picea coloradensis Axelrod, 1987 (part, nontypic), p. 84, pl. 8, figs. 9–14.
Pseudotsuga glaucoides Axelrod, 1987 (part, nontypic), p. 96, pl. 15, figs. 7, 8.
Tsuga petranensis Axelrod, 1987 (part, nontypic), p. 98, pl. 7, fig. 10 (figure legend uses the nomen nudum of *Tsuga coloradensis*).
Picea lahontensis auct. non MacGinitie. Axelrod, 1987 (part), p. 85.
Picea sonomensis auct. non Axelrod 1944. Axelrod, 1987 (part), p. 86, pl. 8, figs. 7, 8.
Pinus alvordensis auct. non Axelrod 1944. Axelrod, 1986 (part), p. 627, figs. 77, 82–84. Axelrod, 1987 (part), p. 89, pl. 9, figs. 5–7.
Pinus coloradensis auct. non Knowlton. Axelrod, 1986 (part), p. 615, figs. 47, 49, 50, 52. Axelrod, 1987, (part), p. 90, pl. 10, figs. 3, 6, 7.
Pinus riogrande auct. non Axelrod 1986. Axelrod, 1987 (part), p. 94, pl. 12, figs. 2–4.
Wolfe and Schorn (1989) designation: *Pinus crossii.*

Discussion.—All the structures listed in the above synonymy are referable to *Pinus.* Attempts to match these to the typically developed winged seeds of various extant pinaceous genera results in unjustified illusions of similarities. As discussed previously, the wings and (or) winged seeds of Pinaceae (especially *Pinus*) are so highly variable that a single cone can produce a variety of atypical wings and (or) winged seeds that can be grossly matched with other species of pine. Such atypical winged seeds should be expected in the fossil record and should be evaluated relative to the more common, recognizably typical, winged seeds in the same fossil assemblage. Most atypical Creede winged seeds of *Pinus* probably represent the abundant *P. crossii* and were thus included in the Wolfe and Schorn (1989) revised census data under that taxon.

Specimens.—UCMG 19706–19708; UCMP 7228–7230, 7232, 7245 (counterpart of UCMP 7228)), 7278, 7296, 7299, 7309, 7318–7324 (7324 = 7319), 7373–7376 (7373 = UCMG 19708), 7378, 7385, 7395, 7397, 7430, 7433, 7434–7437, 7441–7444. Note that UCMP 7232 was figured by Axelrod (1986, fig. 77) as *Pinus alvordensis* and by Axelrod (1987, pl. 8, fig. 14) as *Picea coloradensis.*

Genera and (or) Species Indetermined (cone fragments)

Plate 2, figures 5–9

Picea coloradensis Axelrod, 1987 (part, typic), p. 84, pl. 8, figs. 15, 16.
Tsuga petranensis Axelrod, 1987 (part, typic), p. 98, pl. 7, figs. 7–9.
Pseudotsuga glaucoides Axelrod, 1987 (part, nontypic), p. 96, pl. 15, figs. 2, 5, 6.
Picea lahontensis auct. non MacGinitie. Axelrod, 1987 (part), p. 85, pl. 8, fig. 1.
Pinus coloradensis auct. non Knowlton. Axelrod, 1986 (part), pl. 615). Axelrod, 1987 (part), p. 90.
Pinus crossii auct. non Knowlton. Axelrod, 1987 (part), p. 91.

Discussion.—All the cone remnants included in the above synonymy have been abraded biologically and (or) mechanically. Critical characters needed for generic determination are typically lacking (see previous discussion of abrasion states). A few remnants are probably sufficiently well preserved to indicate inclusion in *Pinus,* but specific assignment is impossible.

The specimen that Axelrod (1987, pl. 7, fig. 9) considered to be an ovulate cone scale of *Tsuga* is a cone scale of *Pinus.* The specimen was figured with the apex pointing toward the bottom of the plate and is incorrectly retouched. The basal end of the cone scale (oriented toward the top of the plate) was eliminated by retouching and is frayed, as if the cone scale had been biologically removed from the parent ovulate cone. The structure that appeared from retouching to be seed cavities is the apophysis of the cone scale.

Specimens.—UCMP 7199 (probably immature cone of *Pinus*), 7287–7294, 7314, 7356 (probably immature cone of *Pinus*), 7417–7424 (7420 is counterpart of 7417), 7438–7440.

Family BERBERIDACEAE
Genus BERBERIS Linnaeus

Berberis coloradensis Axelrod

Plate 4, figures 1–7, 9

Berberis coloradensis Axelrod, 1987, p. 110, pl. 22, figs. 1–3, 6, 7.
Berberis riogrande Axelrod, 1987, p. 110, pl. 21, figs. 8–11.
Fendlera coloradensis Axelrod, 1987 (part, typic), p. 122, pl. 24, figs. 5–8.
Philadelphus creedensis Axelrod, 1987, p. 124, pl. 24, figs. 1–4.
Vaccinium creedensis Axelrod, 1987 (part, typic), p. 147, pl. 33, figs. 3, 4.
Wolfe and Schorn (1989) designation: *Berberis coloradensis.*

Emended description.—Leaves simple; shape symmetric, narrowly elliptic to oblanceolate; base symmetric, cuneate, apex acute to obtuse and mucronate; length 0.8–1.3 cm, width 0.2–0.6 cm; venation perfectly actinodromous to acrodromous; moderate midrib and two lateral primary veins; lateral primary veins typically extending half the distance to apex, where they form angularly brochidodromous loops with secondary veins about half the distance from midrib to margin; two to three pairs of medial secondary veins, originating at angles of 50°–70°, extending straight to form brochidodromous loops that are elongated parallel with midrib; loops abmedial to secondary loops festooned brochidodromous; if teeth present, an external secondary vein from lateral primary vein extends through medial part of tooth to end as spine; intercostal venation formed typically by a composite intersecondary vein that branches into randomly reticulate tertiary veins; fourth-order veins forming quadrangular to pentagonal, well-developed areoles; veinlets mostly once branching; margin has fimbrial vein, typically entire but can have one large spinose tooth on either or both sides; petiole absent.

Discussion.—The five taxa synonymized here share several critical characters: (1) actinodromy, (2) only two lateral primary veins, (3) the lateral primary veins extend typically about half the distance to the apex where they are joined by strong veins that originate from the midrib, (4) festooned brochidodromy, (5) a fimbrial vein, (6) a mucronate (spinose) apex, and (7) absence of a petiole. *Berberis coloradensis* is typically entire-margined. The type suite of *B. coloradensis* comprises leaves that have a pair of spinose teeth and a mucronate (spinose) apex, but the type suite of *B. riogrande* was stated to differ in lacking teeth and in having a rounded rather than an apiculate (mucronate) apex (Axelrod, 1987, p. 111; "mucronate," which specifically refers to an extension of the midrib, is preferred to the more general "apiculate"). The photograph of the holotype of *B. riogrande* (Axelrod, 1987, pl. 21, fig. 11) displays a small projection on the righthand side; cleaning revealed a large, spinose tooth (pl. 4, fig. 3). The apices of the holotype and most other primary types of *B. riogrande* are missing, but one paratype (pl. 4, fig. 2) has a mucronate apex. Similarly, *Fendlera coloradensis* and *Philadelphus creedensis* both have paratypes that, when cleaned, have single spinose teeth (pl. 4, figs. 4, 6) and mucronate apices (pl. 4, figs. 5, 7). The holotype (pl. 4, fig. 9) and one paratype of *Vaccinium creedensis*, although somewhat broader than typical for *B. creedensis* and untoothed, have the seven critical characters listed above, including a mucronate apex; an additional paratype of *V. creedensis* is an undeterminable dicot lamina.

Because *Berberis coloradensis* includes material referred to four different genera in three different families that represent subclasses Ranunculidae, Dilleniidae, and Rosidae, the proper supraspecific assignment of the species is open to question. Festooned brochidodromy is a primitive character in the dicotyledons (Hickey and Doyle, 1977) and is particularly common in Magnoliidae and Ranunculidae. Actinodromy associated with a fimbrial vein is particularly common in Ranunculidae (Lardizabalaceae, Menispermaceae, and Berberidaceae), and spinose teeth occur throughout Berberidaceae. Of the three extant berberidaceous genera that are spinose, *Epimedium* has deeply cordate leaves that have more than one pair of lateral primary veins and numerous teeth, and *Mahonia* has leaves that are pinnately compound, which results in isolated leaflets that are typically asymmetric. The symmetry of the laminae of *B. coloradensis* indicates that the generic reference is valid, and the absence of a well-defined petiole is consistent with this; the laminae of extant *Berberis* are considered to be homologues of the apetiolulate terminal leaflet of *Mahonia* (Ahrendt, 1961).

Extant foliage of *Berberis* varies in venational architecture from actinodromous (and, as in *B. coloradensis*, long and strong lateral primary veins occur) to predominantly pinnately veined; some species have an intermediate stage, in which lateral primary veins are greatly reduced in length and thickness and the medial part of the lamina is dominated by secondary veins that originate near (but not at) the laminar base. Because *Mahonia* appears, as do most ranunculid groups, to be primitively actinodromous, we infer that actinodromy is probably primitive in *Berberis*.

Berberis coloradensis was compared only to *B. candidula* Schneid. (Axelrod, 1987), which is highly dissimilar from the fossil in being pinnately veined and having three or four teeth per laminar side. *Berberis riogrande* was compared to six extant species of *Berberis* (Axelrod, 1987), of which three belong to section *Sinenses* and two belong to section *Asiaticae* (Ahrendt, 1961). Leaves of *Sinenses* represent either the intermediate or pinnately veined conditions, and leaves of *Asiaticae* are pinnately veined. The last supposedly comparable extant species has architecture of the intermediate stage, but section *Angulosae*, to which this species belongs, contains other species that have markedly actinodromous architecture (for example, *B. diaphana* Maxim. and *B. sibirica* Pall.). Laminae of subsections *Diaphanae* and *Sibiricae*, however, typically have four or more teeth (Ahrendt, 1961).

Some members of section *Polyanthae* (for example, *Berberis wilsoniae* Hemsl.) have major venational and marginal architecture similar to *B. coloradensis*, but the secondary and tertiary veins are thick and approximately the same width as the lateral primary veins (the "reticulate venation" of Ahrendt, 1961). In *B. coloradensis*, the tertiary veins are markedly thinner than lower order veins, a condition found in other Ranunculidae and thus probably plesiomorphic.

Relative to minor as well as major venational and marginal architecture, *Berberis coloradensis* is probably most similar to leaves of subsection *Eufranchetianae* of section *Franchetianae*. *Berberis amoena* Dunn, for example, has venation markedly like the Creede species; although *B. amoena* is entire-margined, other related species rarely have one to four teeth per side (Ahrendt, 1961). We question, however, whether *B. coloradensis* should be assigned to *Franchetianae*: (1) marked actinodromy and differentiation of major and minor venation are interpreted as plesiomorphies rather than as synapomorphies, and (2) few to no teeth in *Berberis* appear to be correlative with reduction in laminar size in response to a cold environment. Perhaps significant is that floral and fruit characters that could be assumed to be plesiomorphies in *Berberis* (for example, "subracemose" inflorescences [Ahrendt, 1961] and several or more ovules) are also found in sections *Franchetianae* and *Angulosae*. The inferred plesiomorphies of *B. coloradensis* foliage make problematic assignment of this species to any extant section of the genus.

Holotype.—UCMP 7527.

Paratypes.—UCMP 7525, 7526, 7528, 7529.

Hypotypes.—UCMP 7530, 7534, 7653, 7655–7666, 7745–7753, 7849, 7850.

Genus MAHONIA Nuttall

Mahonia aceroides (Knowlton) Schorn & Wolfe, n. comb.

Plate 4, figures 8, 10, 11; text figure 8

Sterculia aceroides Knowlton, 1923, p. 191, pl. 43, fig. 12.
Mahonia creedensis Axelrod nom. nud., 1956, p. 293. Axelrod, 1987, p. 111, pl. 23, figs. 1–16.
Odostemon hakeaefolia (Lesquereux) Knowlton, 1923 (part, nontypic), p. 190, pl. 43, figs. 1–6.
Odostemon marginata (Lesquereux) Knowlton, 1923 (part, nontypic), p. 188, pl. 43, figs. 7–10.
Mahonia obliqua auct. non MacGinitie. Axelrod, 1987, p. 114, pl. 21, figs. 12–15.
Wolfe and Schorn (1989) designation: *Mahonia* sp.

Description.—Leaves odd-pinnate with at least seven leaflets; leaflet shape ovate to narrowly oblong; base asymmetric, obtuse to broadly rounded, apex acute and spinose; length 1.1–4.0 cm, width 1.1–2.2 cm; some terminal leaflets have basal lateral lobes; venation perfectly actinodromous, three to five primary veins; midrib moderate, typically slightly to markedly curving; most apical pair of lateral primary veins extending one-third or more distance to apex, typically forming a brochidodromous loop with a medial secondary vein and the loop elongated parallel to midrib, rarely craspedodromous and entering teeth medially; most basal pair of lateral primary veins, if present, typically craspedodromous into most basal teeth; veins entering teeth apical to most basal teeth typically originate as either external veins from primary-vein loops or as medial secondary veins or as external veins from secondary-vein loops; intersecondary veins composite, common, some extending to brochidodromous loops; third-order venation randomly reticulate; fourth-order veins forming well-developed, typically quadrangular areoles; veinlets mostly unbranched or once branched; fimbrial vein; two to five large, spinose, C-2 to typically C-3 teeth on each side of lamina, irregularly spaced, typically in basal two-thirds of lamina; sinuses markedly arcuate; apetiolulate.

Discussion.—Odd-pinnate leaves that have actinodromous terminal and lateral leaflets are known only in *Mahonia*. Presence of a few spinose teeth and a fimbrial vein further indicate validity of the generic assignment made by Axelrod (1987).

Mahonia obliqua has an exceedingly narrow lamina, as pointed out by MacGinitie (1953); such laminae were validly determined by Becker (1962) in the Ruby flora. The leaves assigned by Axelrod (1987) to *M. obliqua*, however, are either too broad (his pl. 21, figs. 12, 13), or are folded (his pl. 21, fig. 14), or are a fragment of a larger lamina (his pl. 21, fig. 15). These Creede specimens probably represent *M. aceroides*.

Nomenclature.—Knowlton's type of *Sterculia aceroides* (pl. 4, figs. 8a, 10a) represents the basal part of an actinodromous lamina that appears to have "teeth" atypically large for the Creede *Mahonia*. The "teeth," however, are similar in size and shape to basal lateral lobes that can be found on terminal leaflets of extant species such as the western American *M. nervosa* Pursh; in other characters (for example, areolar venation; fig. 8), the type of *S. aceroides* can be matched by other Creede specimens of *Mahonia*. The specimen of *S. aceroides* has never been completely cleaned because to do so would require partial destruction of an adjacent specimen (pl. 4, figs. 8b, 10b), which is one of Knowlton's (1923) illustrated specimens of *Odostemon hakeaefolia* (a typical lateral leaflet of the Creede *Mahonia*). Because only one species of *Mahonia* is present in the Creede flora, retention of the epithet *aceroides* should not lead to error or confusion; the abundant material of *Mahonia* available from Creede allows full characterization of the foliage of *M. aceroides*..

Although *Mahonia creedensis* was published by Axelrod (1956) as a "new name," the lack of a previously

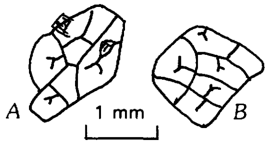

Figure 8. Drawing showing areolar venation of *Mahonia*. *A*, *M. aceroides* (Knowlt.) Schorn & Wolfe, holotype USNM 36537 (same specimen as pl. 4, figs. 8a, 10a). *B*, *M. aceroides* (Knowlt.) Schorn & Wolfe, hypotype USNM 36531 (same specimen as pl. 4, figs, 8b, 10b).

published description and (or) diagnosis clearly, under the ICBN, made this a new species; for a new species, a holotype is selected, not a lectotype. A description and (or) diagnosis of *M. creedensis* was not published by Axelrod (1956, 1987), and therefore this binomial must be rejected as illegitimate. Indeed, the inclusion of *Sterculia aceroides* in Axelrod's (1956) synonymy of *M. creedensis*, although now rejected by him (Axelrod, 1987), made *M. creedensis* a superfluous name at the time of publication. We note also that, in continuing contravention of the ICBN, Axelrod (1987, p. 113) proposes another illegitimate binomial in *Mahonia*: *M. harneyensis* Axelr. is unaccompanied by either a description or a reference to a previously published description.

Holotype.—USNM 36537.

Hypotypes.—USNM 36526–36535; UCMP 7537–7571; UCMG 19749.

Family SALICACEAE
Genus POPULUS Linnaeus

Populus larsenii (Knowlton) Schorn & Wolfe, n. comb.

Plate 5, figures 1, 2, 5; text figure 9

Alnus? larseni Knowlton, 1923, p. 188, pl. 42, fig. 3.
Populus creedensis Axelrod, 1987, p. 103, pl. 18, figs. 1–4; pl. 19, figs. 1–4; pl. 21, fig. 1.
Populus lesquereuxi auct. non Cockerell. Knowlton, 1923, p. 187, pl. 44, fig. 1.
Populus cedrusensis auct. non Wolfe. Axelrod, 1987, p. 101, pl. 19, fig. 5; pl. 20, fig. 3.
Populus pliotremuloides auct. non Axelrod, 1937. Axelrod, 1987, p. 104, pl. 20, fig. 1.
Betula smithiana (Axelrod) Axelrod, 1987 (part, nontypic), p. 106, pl. 21, figs. 7a, 7b.
Wolfe and Schorn (1989) designation: *Populus* sp.

Description.—Leaves simple; shape symmetric, ovate to narrowly ovate; base symmetric, obtuse to broadly rounded, apex acute to attenuate; length 4.0–>10 cm, width 2.5–5.0 cm; venation pinnate, midrib moderate; typically with two pairs of secondary veins originating decurrently close to base and extending about one-fourth to one-half the distance to apex; four to six pairs of more apical secondary veins, originating slightly decurrently at angles of 30°–50°, broadly convex, weakly brochidodromous to eucamptodromous; intersecondary veins simple, common, some extending more than half the distance to margin; tertiary veins A–R to A–O, branching, somewhat sinuous, percurrent; fourth-order veins at variable angles to tertiary veins, forming large, imperfect, irregularly polygonal areoles; veinlets dendritically branching; weak external secondary veins, especially originating from two most basal pairs of secondary veins, typically looping; teeth entered by weak veins that originate either as external secondary veins or typically as branches from loops of external secondary veins; teeth typically at least three to four per secondary vein (more near base), C–1, salicoid; sinuses angular; petiole 1.3–4.1 cm long.

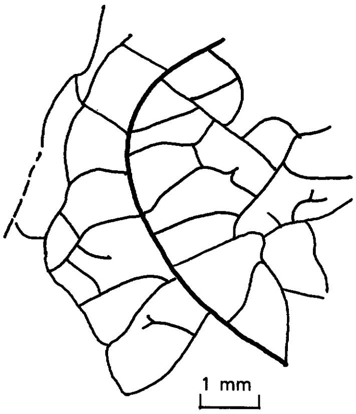

Figure 9. Drawing showing venation of *Populus larsenii* (Knowlt.) Schorn & Wolfe. USNM 36519 (holotype of *Alnus? larseni* Knowlt.).

Discussion.—The Creede *Populus* and many extant species of the genus typically have two pairs of strong, decurrent secondary veins that originate close to the base of the lamina; presumably this architecture is derived from the actinodromous condition found in some *Populus* and the related Flacourtiaceae. Well-preserved specimens of the Creede *Populus* have salicoid teeth (Hickey and Wolfe, 1975), and many specimens also have acropetiolar glands that commonly occur in extant *Populus*.

Within a given species of extant *Populus*, leaves can vary in size, shape, and spacing and size of teeth along a given shoot (S.L. Wing, oral commun., February 1989). Leaves of young plants can differ even more markedly from mature leaves of mature plants. Some suites of leaves can be interpreted as representing mature leaves of mature plants, as in the instance of the suite described and illustrated as *P. creedensis*, but attributing single specimens in the same assemblage to additional species of the genus is very questionable. The Creede specimens attributed to *P. cedrusensis* and *P. pliotremuloides* are considered here probably to be extreme variants of *P. larsenii*.

The specimen assigned to *Populus cedrusensis* differs in several respects from that species, which is known from a large suite of specimens (Wolfe, 1964; Schorn, unpublished data): (1) *P. cedrusensis* is truly actinodromous rather than having one or two pairs of strong suprabasal secondary veins, (2) teeth in *P. cedrusensis* are very reduced and have a basal side 10 to 20 times as long as the apical side, rather than distinct teeth that have a basal side only 2 to 3 times as long as the apical side, (3) teeth in *P. cedrusensis* are only about one or two per secondary vein, rather than two or three, and (4) the lateral primary veins in *P. cedrusensis* typically extend about half the distance to the apex in contrast to suprabasal secondary veins that extend about one-fourth to one-third the distance to the apex.

Axelrod (1987) attributed two fragmentary specimens to *Betula smithiana* (Axelr.) Axelr. Both specimens have brochidodromous rather than craspedodromous secondary veins (and hence cannot represent *Betula*) and have weak external veins that enter small narrowly rounded, closely spaced teeth. A swelling at the top of the petiole of one specimen (UCMP 7512) suggests the acropetiolar glands commonly present in *Populus*.

The leaves of *Populus larsenii* resemble both the extant *P. trichocarpa* Torr. & Gray and *P. balsamifera* L.; however, as noted by Axelrod (1987), the associated two-valved capsules indicate a relationship to *P. balsamifera* rather than to *P. trichocarpa*, which has three-valved capsules.

Nomenclature.—The type of *Alnus? larseni* has strong, decurrent suprabasal secondary veins, ovate shape, and numerous salicoid teeth; venation is preserved to the fourth order (fig. 8) and conforms to venation in *Populus creedensis*. No doubt can exist about the generic affinities of this specimen, and retention of the epithet *larsenii* will not lead to error and (or) confusion.

Holotype.—USNM 36519.

Hypotypes.—UCMP 7476–7494, 7512, 7513; UCMG 34060, 34061.

Genus SALIX Linnaeus

Salix sp.

Salix venosiuscula auct. non H.V. Smith. Axelrod, 1987, p. 106, pl. 20, figs. 7, 8.

Wolfe and Schorn (1989) designation: *Salix* sp.

Discussion.—Salix venosiuscula was founded (Smith, 1941) on leaves that have (1) an elliptic to slightly obovate shape, (2) an acute apex, (3) a length to width ratio of about four to one, (4) about 15 pairs of secondary veins, (5) secondary veins that originate at angles of about 50° from the base to the apex, and (6) a closely and uniformly serrate margin. In contrast, the Creede specimens assigned to this species have (1) a markedly ovate shape, (2) a very attenuated apex, (3) a length to width ratio of more than five to one (the laminae are incomplete), (4) more than 25 pairs of secondary veins, (5) secondary veins that originate at angles of about 40°–60° basally and about 80° apically, and (6) a sparsely and irregularly serrate margin. Although the Creede leaves cannot represent *S. venosiuscula*, their preservation is too poor for valid specific determination or to suggest affinities to extant species.

Specimens.—UCMP 7507–7511.

Family PHILADELPHACEAE
Genus JAMESIA Torrey & Gray

Jamesia caplanii Axelrod

Plate 5, figures 3, 4

Jamesia caplanii Axelrod, 1987, p. 123, pl. 30, figs. 12–16.
Wolfe and Schorn (1989) designation: *Jamesia caplanii.*

Description.—Leaves simple; apparently estipulate; shape symmetric, elliptic to typically slightly ovate; base symmetric, obtuse to rounded, some slightly cordate; apex acute to slightly acuminate; length 1.4–4.2 cm, width 0.9–2.4 cm; venation pinnate; midrib moderate; five to seven pairs of secondary veins, thin, more basal pairs decurrent, originating at angles of as much as 85° near base and decreasing to 20° near apex, broadly convex, some brochidodromous but most craspedodromous, entering teeth medially; tertiary veins A–R to R–R, widely spaced, reticulate; fourth-order veins forming imperfect, irregularly polygonal areoles; veinlets unbranching or typically once branching; zero to two external secondary veins originating at acute angles, broadly convex, craspedodromous; margin with uniformly spaced, large teeth that are one to two per secondary vein, D–1; teeth have lateral accessory veins convergent on an apical foramen; sinuses angular; petiole 0.3–1.5 cm long, with five discrete vascular strands.

Discussion.—Markedly rosoid teeth (Hickey and Wolfe, 1975), as occur in these Creede leaves, are typically associated with actinodromy (see later discussion of *Ribes*). Some pinnately veined, simple leaved Rosaceae can have somewhat weakly developed rosoid teeth, but in those taxa intersecondary veins are common and the tertiary veins are typically not oriented almost orthogonally to the midrib as in *Jamesia caplanii*. Orthogonal orientation of the tertiary veins relative to the midrib, absence of intersecondary veins, a simple leaf, and eucamptodromy are characteristic of many advanced Rosidae (for example, Cornales, Myrtales, Rhamnales, Celastrales, and Santalales) and are found in some basal rosid groups. These basal groups include Iteaceae and Hydrangeaceae, and this architecture is therefore termed iteid. The iteid architecture is typically associated with eucamptodromy, and if the margin has teeth, the teeth are small. Only in *Jamesia* is iteid intercostal venation combined with large, rosoid teeth and craspedodromy of the secondary veins.

Most specimens of *Jamesia caplanii* are markedly similar to the extant *J. americana* Torr. & Gray in all aspects of laminar vasculature and morphology of the teeth; however, even small leaves of *J. caplanii* (pl. 5, fig. 4) have five discrete vascular bundles in the petiole as opposed to three or four in the extant taxon, and the extant taxon typically has a shorter petiole. Laminae and petioles of *J. americana* are densely pubescent; although some specimens of *J. caplanii* are preserved in a fine-

Table 2. Differentiation of Creede species of *Ribes*

Character	*Ribes lacustroides*	*R. robinsonii*	*R. obovatum*
Laminar shape	Orbiculate	Widely ovate	Obovate
Number of lobes	5	5	0
Lobal dissection	(Shallow-)deep	Shallow	None
Lobal apex	Narrowly to broadly obtuse	Narrowly obtuse	None
Lobal shape	Triangular to trapezoidal	Triangular	None
Base shape	Deeply cordate	Shallowly cordate	Acute to obtuse
Stipules	Large	Small	?

grained matrix, no evidence of dense pubescence is preserved. More significantly, some specimens of *J. caplanii* (for example, pl. 5, fig. 3) have small, closely spaced teeth and some secondary veins that are almost eucamptodromous. This morphology is more like that found in Iteaceae and Hydrangeaceae and suggests retention of some primitive characters in foliage of *J. caplanii.*

Excluded from *Jamesia caplanii* is Becker's (1962, pl. 18, fig. 3) Ruby specimen originally referred to *Ulmus paucidentata* H. V. Sm. and included by Axelrod (1987) as a paratype of the Creede *Jamesia.* The Ruby specimen has markedly arcuate dental sinuses and cannot represent *Jamesia*, which has markedly angular dental sinuses.

Holotype.—UCMP 7641.

Paratypes.—UCMP 7642–7651.

Hypotypes.—UCMG 34062, 34063.

Family GROSSULARIACEAE
Genus RIBES Linnaeus

Discussion.—One of the most common dicotyledonous leaf types in the Creede collections is leaves that are actinodromous, palmately lobed, and serrate or crenate. This leaf type accounts for 25 percent of Axelrod's (1987) species of Creede dicotyledons and was split into 13 species representing 5 genera and 4 families: *Ranunculus* (1 species; Ranunculaceae), *Ribes* (8 species; Grossulariaceae), *Physocarpus* (2 species; Rosaceae), *Rubus* (1 species, Rosaceae), and *Acer* (1 species; Aceraceae). A number of morphologic criteria indicate that most of these generic and familial assignments must be erroneous and that far fewer species are represented.

Ranunculaceae have chloranthoid teeth (Hickey and Wolfe, 1975), which are lacking in the single specimen of *Ranunculus creedensis* Axelr. Further, Ranunculaceae are estipulate (Airy Shaw, 1985); cleaning of the specimen of *R. creedensis* revealed a stipulate petiole 1.7 cm long. Similarly, the holotype of *Acer riogrande* as illustrated by Axelrod (1987) appears to be stipulate, whereas all extant *Acer* are estipulate (Airy Shaw, 1985). Indeed, where the base of the petiole is preserved on the Creede actinodromous, lobed leaves, stipules are present. Aside from the two specimens just mentioned, also stipulate are specimens of *Ribes dissecta, R. lacustroides, R. stevenii, R. webbii, R. riogrande, R. birdseyii,* and *Physocarpus petiolaris.* Five of Axelrod's species of *Ribes* were considered to be closely related to extant species that fall into subgenus *Ribes*, a taxon that typically is estipulate. Indeed, stipules are uncommon in extant Grossulariaceae and apparently occur only in some species of subgenus *Grossularia* of *Ribes.* The other two of Axelrod's actinodromous, lobed species in the Creede flora (*R. wasonii* and *P. triloba*) are represented by single specimens that have incomplete petioles.

The rosoid tooth (Hickey and Wolfe, 1975) occurs in three families associated with actinodromous, lobed leaves: Grossulariaceae, Rosaceae, and Vitidaceae. All the Creede lobed, actinodromous leaves have rosoid teeth and thus must represent one or more of these three families. The Creede leaves, moreover, have crenations, and thus Vitidaceae, which typically have broad A–1, D–1, or D–4 serrations, are eliminated from consideration. Further, Vitidaceae typically do not have subsidiary teeth, whereas all the Creede leaves under consideration here have subsidiary teeth.

In Grossulariaceae (as well as Vitidaceae), the rosoid tooth is what could be termed classic, with two strong lateral subsidiary veins approaching and ending at the apical foramen (see pl. 9, fig. 1). In Rosaceae, the lateral subsidiary veins tend to be weak and typically thin conspicuously before reaching the foramen (see pl. 9, fig. 8); in many rosaceous taxa the veins fail to reach the foramen and (or) a foramen is absent. In the better preserved Creede specimens, most have the classic rosoid tooth and thus represent Grossulariaceae. *Ranunculus creedensis* has weakly developed rosoid teeth, however, and is later transferred to *Potentilla* in Rosaceae. Only three, rather than eight, species of *Ribes* are considered to be represented in the Creede flora (table 2), and two of these were assigned by Axelrod (1987) to Rosaceae.

Ribes lacustroides Axelrod

Plate 5, figures 6, 7, 10, 11; plate 6, figures 1–17

Ribes lacustroides Axelrod, 1987, p. 118, pl. 24, figs. 16–18.
Ribes birdseyii Axelrod, 1987, p. 115, pl. 32, figs. 7–9.
Ribes creedensis Axelrod, 1987, p. 116, pl. 28, figs. 12, 13.
Ribes dissecta Axelrod, 1987, p. 117, pl. 24, figs. 14, 15; pl. 25, fig. 10.

Ribes riogrande Axelrod, 1987, p. 119, pl. 25, figs. 11–13.
Ribes stevenii Axelrod, 1987, p. 120, pl. 25, figs. 1–6.
Ribes wasonii Axelrod, 1987, p. 121, pl. 25, fig. 9.
Rubus riogrande Axelrod, 1987, p. 137, pl. 31, fig. 1.
Acer riogrande Axelrod, 1987, p. 141, pl. 32, fig. 10.
Ribes protomelaenum auct. non Cockerell. Knowlton, 1923, p. 188, pl. 42, figs. 5–9.
Vitis florissantella auct. non Cockerell. Knowlton, 1923, p. 189, pl. 42, fig. 4.
Ribes webbii auct. non Wolfe. Axelrod, 1987, p. 121, pl. 25, figs. 7, 8.
Wolfe and Schorn (1989) designation: *Ribes lacustroides*.

Emended description.—Leaves simple; stipulate; shape symmetric, orbiculate; base symmetric, shallowly to typically deeply cordate, apex narrowly to broadly obtuse; length 1.0–3.5 cm, width 1.2–8.0 cm; five lobed, more apical pair of lobes moderately to deeply incised and apices of these typically at widest part of lamina; more basal pair of lobes shallowly incised, typically only slightly larger than compound teeth of suprajacent lobes; lateral lobes broadly triangular to somewhat convex sided to trapezoidal, apices narrowly to broadly obtuse; apical lobe ovate to broadly ovate; venation perfectly actinodromous but most basal pair of lateral primary veins can be palinactinodromous; midrib moderate; five primary veins; lateral primary veins straight to shallowly concave, diverging from medial secondary veins; three to four (rarely as many as six) secondary veins originating from basal sides of lateral primary veins and from both sides of midrib; one to five secondary veins originating from apical sides of lateral primary veins; secondary veins originating at angles of 20°–30°, straight to slightly convex, entering teeth medially, craspedodromous; lobal sinal braces formed by external secondary branches originating from either suprajacent or subjacent secondary vein; tertiary veins A–A, reticulate; fourth-order veins forming imperfect, irregularly polygonal areoles; veinlets dendritically branching; medial lobe and basal sides of most apical pair of lateral lobes have three to four (rarely as many as six) crenate teeth; apical sides of most apical pair of lateral lobes have one to three crenate teeth (rarely as many as five); apical sides of most basal pair of lateral lobes typically have one crenate tooth (rarely as many as three teeth); large teeth may have one to two small crenate subsidiary teeth; large teeth markedly rosoid; sinuses angular; petiole 0.8–3.5 cm long.

Discussion.—Some small leaves of *Ribes lacustroides* have a superficial resemblance to leaves of *R. webbii* and were so referred by Axelrod (1987). Leaves of *R. webbii* are ovate rather than elliptic, however, and the widest part of the lamina is on a line drawn between the apices of the more basal pair of lobes. The medial lobe of *R. webbii* is very shallowly incised, and the lobe narrows from the subjacent lobal sinuses; in these small leaves of *R. lacustroides*, the medial lobe is broadly elliptic, and the lobe first slightly widens apically from the subjacent lobal sinuses.

As conceptualized here, *Ribes lacustroides* is highly variable relative to degree of laminar dissection between lobes and degree of rounding of lobes and teeth. Specimens that we assign to this taxon were assigned by Axelrod (1987) to 10 different species; specific differentiation was, in part, based on characters such as degree of laminar dissection, whether the major teeth have subsidiary teeth, and relative rounding of the lobes and teeth. However, the degree of laminar dissection, for example, represents a normal, if somewhat skewed, distribution for a single species (fig. 10). As defined by Axelrod (1987), *R. lacustroides* was, in part characterized by absence of subsidiary teeth, but examination of the holotype (pl. 6, fig. 2) indicates that some subsidiary teeth are present.

Generally, the greater the dissection between lobes, the sharper the lobes and teeth appear; that is, as the sinuses adjacent to a lobe or tooth become more incised, the lobe or tooth is more elongated and hence appears sharper. On plate 6, a series of specimens form a transition from the deeply dissected and "sharply" lobed and toothed *R. dissecta* to the shallowly lobed and bluntly lobed and toothed *R. webbii* (using Axelrod's, 1987, designations); even if teeth appear sharp, examination shows them to be narrowly rounded. The forms referred to *R. creedensis* (pl. 5, figs. 6, 7) represent a morphotype more extreme in deep dissection than *R. dissecta*. Between these extreme morphotypes called *R. creedensis* and *R. webbii* are specimens referred to *R. dissecta, R. lacustroides, R. stevenii, R. birdseyii,* and *R. riogrande*; the single specimen that forms the basis for *R. wasonii* is aberrant and was damaged (probably by insects) during growth. The central morphotype in this transitional series is *R. stevenii*, which also comprises the most abundant morphotype.

Some of the most aberrant leaves of *Ribes lacustroides* represent the morphotype called *Rubus riogrande* (pl. 5, figs. 10, 11); this is best represented (as are the

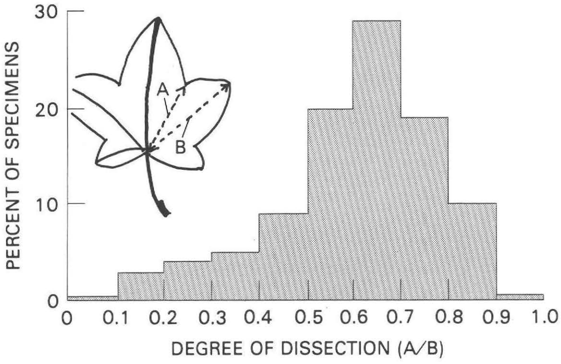

Figure 10. Histogram of laminar dissection in *Ribes lacustroides* Axelr. Horizontal axis is distance from sinus to top of petiole (A) divided by distance from lobe apex to top of petiole (B). The more deeply dissected specimens are to the left. Based on 181 specimens.

more deeply dissected morphotypes of *Ribes creedensis*) at Axelrod's (1987) localities 571–A and 571–B, where *Ribes* leaves are most abundant and the greatest variation might be expected. The morphological intergradations between most of Axelrod's (1987) species of Creede *Ribes* indicate that one species is represented. As discussed earlier (p. 2), a variable taxon such as *R. lacustroides* (as we conceptualize it) could ultimately have given rise by canalization to two or more of the extant species of *Ribes* to which Axelrod (1987) compared different subsets of specimens of *R. lacustroides*.

The single lamina on which *Acer riogrande* was based has not been deposited in the University of California Museum of Paleontology and thus has not been examined by us. The illustration (Axelrod, 1987, pl. 32, fig. 10) appears to indicate a stipulate leaf, which would immediately eliminate Aceraceae. Additionally, one of the most apical lateral primary veins markedly diverges from the medial secondary veins (as in Grossulariaceae and Rosaceae), whereas in *Acer* the most apical lateral primary veins parallel (or slightly converge with) the medial secondary veins (Wolfe and Tanai, 1987). The specimen thus cannot represent *Acer* and probably represents a lamina of *Ribes lacustroides*, in which the margin is poorly preserved.

Nomenclature.—We would have preferred to use the epithet *stevenii* for this taxon; of all the items included in the above synonymy, this is represented by the largest and best preserved suite of primary types. Axelrod (1987, p. 120), however, cited as the "lectotype" for *Ribes stevenii* the same specimen number as the "lectotype" for the previously instituted *R. riogrande*. Thus, being typified by the same specimen, *R. stevenii* immediately became a junior synonym of *R. riogrande*. The suites of primary types of *R. birdseyii, R. creedensis*, and *R. dissecta* are small, and we suggest selection under the ICBN of the epithet *lacustroides*.

Holotype.—UCMP 7594.

Paratypes.—UCMP 7585–7593, 7595, 7596, 7598, 7601, 7606, 7609, 7620, 8599.

Hypotypes.—UCMP 7577–7629, 7631–7638, 7820A, B, 7836–7838, 7860; USNM 36523–36525; UCMG 27388, 27389, 27391, 34065, 34066.

Ribes robinsonii Schorn & Wolfe, n. name

Plate 5, figures 8, 9

Physocarpus petiolaris Axelrod, 1987, p. 133, pl. 31, fig. 10.
Physocarpus triloba Axelrod, 1987, p. 134, pl. 31, fig. 9.
Wolfe and Schorn (1989) designation: *Ribes* sp. 1.

Description.—Leaves simple; stipulate; shape symmetric, widely ovate; shallowly five lobed; most basal pair of lobes about same size as compound teeth of suprajacent lobes; base symmetric, shallowly cordate, apex narrowly obtuse; length 3.2–3.7 cm, width 2.4–2.8 cm; venation perfectly actinodromous; midrib moderate; five primary veins; lateral primary veins straight to slightly concave or convex, diverging from medial secondary veins; three to four secondary veins originating from basal sides of lateral primary veins and from both sides of midrib; two to three secondary veins originating from apical sides of lateral primary veins; secondary veins originating at angles of 30°–40°, straight to slightly concave or typically convex, entering teeth medially, craspedodromous; lobal sinal braces formed by secondary veins originating from subjacent primary vein; tertiary veins R–R, branching; higher order venation not preserved; medial lobe and basal sides of lateral lobes have three to four large crenations; apical sides of most apical pair of lateral lobes have one to two crenations; apical sides of most basal lateral lobes typically have no teeth; large teeth have no subsidiary teeth on apical sides and zero to one on basal sides; sinuses angular; petiole 2.0–2.9 cm long.

Discussion.—In leaves of *Physocarpus* (as well as in many *Ribes*), the most basal lobes are entered by primary veins that originate as external veins from the two lateral primary veins (that is, the lamina is partially palinactinodromous), whereas in *Ribes robinsonii* the lamina is perfectly actinodromous. Foliage that has characters similar to those listed for *R. robinsonii* (table 2) occurs in extant species such as *R. amarum* McClat. The petiole of one specimen of *R. robinsonii* (pl. 5, fig. 9) is densely covered with flat-topped hairs; the tops presumably bore glands.

Nomenclature.—The epithets *petiolaris* and *triloba* (properly *petiolare* and *trilobum* in *Physocarpus*) have both been previously proposed in *Ribes*, and thus a new epithet is necessary. Peter Robinson has been of great assistance to this study by allowing ready access to the University of Colorado's Creede collections.

Holotype.—UCMP 7817.

Hypotypes.—UCMP 7630; UCMG 34064 (counterpart USNM 422591).

Ribes obovatum Schorn & Wolfe, n. sp.

Plate 9, figures 1, 2

Holodiscus hameyensis auct. non Chaney & Axelrod. Axelrod, 1987 (part), p. 130.
Wolfe and Schorn (1989) designation: *Ribes* sp. 2.

Description.—Leaves simple; shape symmetric, narrowly obovate; base symmetric, acute to obtuse; apex narrowly obtuse; length 2.5 cm, width 1.5 cm; venation perfectly actinodromous to acrodromous; midrib moderate; five primary veins; primary veins extending straight, either entering teeth medially and craspedodromous or branching and brochidodromous; all lateral primary veins extending at acute angles to the midrib at least one-half the distance to apex; one pair of medial secondary veins the same thickness as lateral primary veins originating at an angle of 15°, straight, entering teeth medially, craspedodromous; some composite intersecondary veins, extending about one-fourth the distance to margin; tertiary veins A–R, reticulate; fourth-order veins forming well-developed, quadrangular to pentagonal areoles; veinlets branching one to four times; dental sinuses braced by external veins that originate acutely from major suprajacent or subjacent veins; three large A–1 teeth on each side of lamina, crenate to slightly serrate; craspedodromous veins flanked by conspicuous veins that converge on foramen at apex of tooth; a single subsidiary tooth on basal side of most basal tooth on one specimen; sinuses angular; petiole incomplete, >0.2 cm long.

Discussion.—The holotype and one paratype of *Ribes obovatum* were two of Axelrod's (1987) unfigured homeotypes of *Holodiscus harneyensis*. *Ribes obovatum* is clearly actinodromous in contrast to the pinnate venation of *Holodiscus*.

Ribes obovatum is unique in fossil *Ribes* in having a totally unlobed lamina. The leaves of the extant *R. speciosum* Pursh are typically broad and very shallowly three lobed, but some laminae have lobes the same size as teeth. Leaves of *R. speciosum* can also have a single pair of medial secondary veins and three large teeth (counting the reduced lobes as teeth) per laminar side. If *R. speciosum* and *R. obovatum* are closely related, then *R. obovatum* would have to be considered as having the more reduced (specialized) lamina.

Holotype.—UCMP 7788.

Paratypes.—UCMP 7790; UCMG 34067; USNM 422589.

Family ROSACEAE

Discussion.—Foliage of a large family such as Rosaceae is impossible to characterize, although some general characters apply to many, if not most, rosaceous taxa. Typically, teeth are a weakly developed rosoid type, in which the vein enters the teeth medially, but the lateral accessory veins are thin and may not reach the dental apex; a foramen at the dental apex is typically absent, although a small, dark conical gland may be present (especially in Pyroideae). Small, dark conical glands (nectaries) occur on teeth near the base of the lamina in Prunoideae, as well as some laminar glands near the midrib in some *Prunus*. Although the cunonioid tooth (Hickey and Wolfe, 1975) is absent, some Rosaceae have the craspedodromous vein somewhat displaced toward the apical side, and some also have the vein ending at the dental sinus. All Rosaceae that have teeth and (or) have deeply dissected laminae tend to have moderately strong to marked sinal braces, many of which originate from the apical sides of secondary or external secondary veins; this syndrome may be homologous to the apical branch in a typical cunonioid tooth.

The lamina in many rosaceous taxa is deeply dissected and may be totally pinnatisect but apparently rarely, if ever, truly compound (Wolfe and Wehr, 1988). This applies to rosaceous groups that are fundamentally pinnately veined (Spiraeoideae and Pyroideae), as well as to some actinodromous groups (Rosoideae, in part). Whether Rosaceae are primitively pinnately veined or actinodromous is, as yet, unresolved, but the most primitive extant members of Spiraeoideae, as well as of Pyroideae and Prunoideae, are simple-leaved. In at least one instance, evolution of pinnatisect leaves from a pinnatifid ancestor has been inferred (Wolfe and Wehr, 1988).

Somewhat transverse, A–O tertiary veins are typical of many Rosaceae. This architecture could link Rosaceae with the iteid rosids (see discussion of *Jamesia*), but the numerous composite intersecondary veins and typical brochidodromy in Rosaceae are not iteid characters. Finally, most Rosaceae are markedly stipulate, and the stipules tend to be persistent.

Subfamily SPIRAEOIDEAE
Genus ELEIOSINA Rafinesque

Eleiosina praeconcinna (Cockerell) Schorn & Wolfe, n. comb.

Plate 7, figures 1–5

Solidago praeconcinna Cockerell, 1933, p. 72, fig. 1.
Salix creedensis Axelrod, 1987, p. 105, pl. 18, figs. 5, 6; pl. 20, figs. 2, 4–6.
Cercocarpus holmesii auct. non (Lesquereux) Axelrod, 1944. Axelrod, 1987 (part), p. 124.
Peraphyllum septentrionalis auct. non *Daphne septentrionalis* (Lesquerex) MacGinitie. Axelrod, 1987, p. 132, pl. 24, figs. 12, 13.
Wolfe and Schorn (1989) designation: *Eleiosina* sp.

Description.—Leaves alternate, simple; apparently stipulate; shape symmetric, elliptic to narrowly elliptic; base symmetric and acute, apex acute to acuminate and has a short (rarely elongated) mucro; length 2.1–>7.2 cm, width 0.5–1.1 cm; venation pinnate; midrib weak; 7–10 pairs of secondary veins, markedly decurrent (especially basally) then extending at angles of 20°–30° to midrib, thin, straight to typically slightly convex, offset where a major branch originates, weakly brochidodromous to reticulodromous; intersecondary veins simple, common, some joining subjacent secondary vein; tertiary veins thin, R–R, widely spaced, reticulate; fourth-order veins forming imperfect, thin, irregularly polygonal areoles; veinlets thin, dendritically branching; external secondary veins three to four per secondary vein, originating at acute angles, some originating close to midrib, forming loops that are elongated parallel with margin, some reticulodromous; margin entire, thin; petiole absent.

Discussion.—The critical characters of the Creede leaves here grouped under *Eleiosina praeconcinna* are (1) an entire margin that is unthickened and has no fimbrial vein, (2) a glandular, slightly mucronate apex, (3) secondary veins that are markedly decurrent and extend at very low angles relative to the midrib, (4) secondary veins that are thin and are offset at points of origination of major branches, (5) secondary veins that are weakly brochidodromous or that may not loop (that is, some secondary veins are reticulodromous), (6) numerous external secondary veins that originate at low angles, (7) some external secondary veins that originate close to the midrib, (8) external secondary veins that are weakly brochidrodromous or reticulodromous, (9) intersecondary veins that extend over half the distance to the margin and that can merge with a secondary vein so as to isolate a large part of an intercostal area, and (10) widely spaced tertiary veins that form an irregularly branched reticulum. The holotype of *E. praeconcinna*, moreover, has alternate leaves, and stipules appear to be present.

Of the previously listed characters, *Salix* leaves typically lack characters 3, 5, and 7–10. Even in gross characters, the supposed "match" for *Salix creedensis, S. geyeriana* Anderss., markedly differs and has leaves that typically have a few to several salicoid teeth, markedly brochidodromous to eucamptodromous secondary veins, and an acute, non-mucronate apex.

Peraphyllum leaves are perhaps closer than *Salix* leaves to *Eleiosina praeconcinna*, but *Peraphyllum* leaves (pl. 7, fig. 7) typically do not have decurrent secondary veins or a mucronate apex, the secondary veins and external secondary veins are markedly brochidodromous, the secondary veins are not offset at point of origination of major branches, and external secondary veins originate close to the margin.

An entire margin, marked decurrency of secondary veins, and poorly organized venation are generally primitive characters in the dicotyledons and are particularly characteristic of some taxa of Magnoliidae (Hickey and Wolfe, 1975; Hickey and Doyle, 1977). Search has revealed no magnoliid that has a mucronate, apparently glandular apex associated with these other characters, and the fossils show no indication of oil cells characteristic of Magnoliidae. In subclasses other than Magnoliidae, these primitive characters are rarely found in combination. In *Crossosoma* (Crossosomataceae), a putative primitive member of Dilleniidae (but placed by some near Rosaceae), these primitive characters are found but in combination with marked festooned brochidodromy. In *Eleiosina* leaves (pl. 7, fig. 6), however, are the 10 characters, including the 3 primitive characters, listed previously for the fossils, although the Creede leaves typically do not have as pronounced a mucro (but see pl. 7, fig. 3) as the leaves of the four extant species of *Eleiosina* examined and have an elliptic rather than an obovate shape.

The fossils from floras other than Creede that Axelrod (1987) assigned to *Peraphyllum septentrionalis* are here rejected as belonging to *Eleiosina praeconcinna*. These other fossils do not have a mucronate apex or decurrent secondary veins, have markedly brochidodromous secondary and external secondary veins, and have secondary veins that maintain a low origination angle in the apical region (pl. 7, fig. 8). Proper taxonomic disposition of these other fossils awaits more detailed examination and analysis.

Nomenclature.—Axelrod (1987) synonymized *Solidago praeconcinna* under *Cercocarpus holmesii*. Total absence of teeth, thin secondary veins that are widely spaced, and presence of a thin midrib on Cockerell's material readily differentiate *S. praeconcinna* from *C. holmesii* (see later under *C. henricksonii*).

Holotype.—UCMG 18536.

Hypotypes.—UCMP 7496–7506, 7386, 7388, 7389; UCMG 27387A, B.

Genus ELEOPOLDIA Schorn & Wolfe, n. gen.

Diagnosis.—Leaves simple; apparently estipulate; not pubescent; pinnatifid, typically three (some two or four) lobes on either side of lamina, with basal part of lobe decurrent on midrib and including a weakly decurrent vein that enters basal part of lobe; most basal lobes also decurrent to base of petiole; secondary laminar segments pinnatifid, as many as three lobes; some tertiary laminar segments have a tooth on basal side; margin otherwise entire and not revolute; venation pinnate; fourth-order veins forming distinct, irregularly polygonal areoles; branching freely ending veinlets.

Type species.—*Fallugia lipmanii* Axelrod.

Nomenclature.—This genus is named for Estella Leopold, in recognition of her many contributions to the Tertiary palynology, paleobotany, and historical plant geography of the Rocky Mountains.

Eleopoldia lipmanii (Axelrod) Schorn & Wolfe, n. comb.

Plate 8, figures 1, 3, 5, 8, 9; plate 13, figure 3

Fallugia lipmanii Axelrod, 1987 (part, typic), p. 129, pl. 29, figs. 1–9, 11, 12.
Juniperus gracillensis Axelrod, 1987, p. 100, pl. 16, figs. 10–12.
Wolfe and Schorn (1989) designation: aff. *Luetkea* sp.

Description.—Leaves simple; apparently estipulate; glabrous; shape symmetric, orbiculate to oblate, pinnatifid; base symmetric, decurrent, apex acute to narrowly obtuse; length 1.0–4.0 cm, width 1.1–>4.0 cm; venation pinnate; midrib stout; two to five pairs of secondary veins, originating decurrently then extending at angles of

30°–80°, straight to broadly convex or broadly concave, entering lobe along apical side of lobe, craspedodromous; two to three external secondary veins originating at low angles from basal side of secondary veins, one to two from apical side, craspedodromous; sinuses of tertiary laminar segments braced by a minor branch from subjacent external secondary veins, branching at sinus, these branches extending parallel with sides of sinus; veins about same thickness as external secondary branches originating decurrently from midrib, extending into lobe subjacent to secondary vein; fourth-order venation forming somewhat imperfect, irregularly polygonal areoles; veinlets dendritically branching; one to four pairs of secondary laminar segments, decurrent along midrib, narrowly elliptic to obovate, narrowly obtuse to acute apices, pinnatifid; two to three narrow tertiary laminar segments on basal side of secondary laminar segments, one to two on apical side; some tertiary laminar segments with one tooth; sinuses acute to narrowly rounded; petiole 0.2–2.1 cm long.

Discussion.—Leaves that are pinnatifid and have strongly decurrent secondary laminar segments occur in several extant genera of Rosaceae, including *Fallugia* and *Purshia*. Leaves of *Fallugia* (pl. 8, fig. 7), however, are stipulate, strongly pubescent, and strongly revolute and have secondary laminar segments that are rarely lobed (if lobed, teeth are absent on the lobes). Leaves of *Purshia* are shed without stipules (and thus could appear to be estipulate), and some laminae can have a rare lobe on a secondary laminar segment, but the strong pubescence and strongly revolute margin also eliminate this genus from consideration.

Three extant genera of Rosaceae, all herbaceous, appear as the closest extant relatives of *Eleopoldia*: *Luetkea, Geum,* and *Sanguisorba*. *Luetkea* has estipulate, nonpubescent, nonrevolute leaves (pl. 8, fig. 2) that are pinnatifid and that have pinnatisect secondary laminar segments; typically, however, only a single pair of lateral lobes is present, the tertiary laminar segments never have teeth, and the secondary laminar segments have a single pair of lobes. *Geum* has leaves (pl. 8, fig. 6) that have as many as two lobes on the secondary laminar segments and have areolation as in *Eleopoldia*, but these extant leaves are stipulate, pubescent, and pinnatisect. *Sanguisorba* has leaves (pl. 8, fig. 4) that have several lobes on the secondary laminar segments and lack pubescence, but the leaves are stipulate and pinnatisect and the secondary laminar segments lack teeth. We emphasize, however, that absence of stipules on mature leaves that enter the fossil record could also result from the stipules being deciduous.

Eleopoldia was probably a woody plant (Wolfe and Schorn, 1989); leaves of terrestrial dicotyledonous herbs rarely enter the fossil record (they generally do not dehisce from the plant) and then never abundantly. Because *Eleopoldia* has the greatest similarity to leaves of *Luetkea*, we suggest that *Eleopoldia* may have given rise to this extant genus; the differences between leaves of the two genera appear primarily as reductions: fewer secondary laminar segments, fewer tertiary laminar segments, and absence of teeth in *Luetkea*. *Luetkea* also typically has more specialized venation in that the points of origination of the secondary veins and the major branches of these veins are close to sinuses and the secondary veins tend not to be decurrent. We would thus consider *Eleopoldia* to be a member of Spiraeoideae, as is *Luetkea*. The relationship of *Eleopoldia* to *Geum* and *Sanguisorba* is probably more distant; the absence of the plesiomorphic (for Rosaceae) stipulate and pubescent conditions suggests that the *Eleopoldia-Luetkea* line diverged from ancestral stock that could have given rise to these other two extant genera (and possibly other members of Rosoideae).

Nomenclature.—The epithet *lipmanii*, which is based on a large suite of well-preserved specimens, should be selected over *gracillensis*, which is based on a few, poorly preserved specimens.

Holotype.—UCMP 7767.

Paratypes.—UCMP 7761–7765, 7768–7780, 7782–7785.

Hypotypes.—UCMP 7215, 7445, 7446; UCMG 19786, 34068, 34069.

Genus STOCKEYA Wolfe & Wehr

Stockeya creedensis (R.W. Brown) Wolfe & Wehr

Stockeya creedensis (R.W. Brown) Wolfe & Wehr, 1988, p. 193, figs. 14, 15, 32–36, 50–52.

Chamaebatiaria creedensis R. W. Brown, 1937, p. 177, pl. 57, figs. 8, 9. Axelrod, 1987, p. 127, pl. 27, figs. 1–14.

Wolfe and Schorn (1989) designation: *Stockeya creedensis*.

Discussion.—*Stockeya creedensis* was extensively discussed by Wolfe and Wehr (1988). *Stockeya*, of which *S. creedensis* is the genotype, is considered probably to be ancestral to the extant *Chamaebatiaria*.

Lectotype.—USNM 39651.

Hypotypes.—UCMP 7715–7742; UCMG 18646, 34057, 34058.

Genus HOLODISCUS Maximowicz

Holodiscus stevenii Schorn & Wolfe, n. sp.

Plate 9, figures 3, 4, 7, 8

Holodiscus hameyensis auct. non (Arnold) Axelrod, 1950. Axelrod, 1987 (part), p. 130, pl. 30, figs. 1–4.

Holodiscus idahoensis auct. non Chaney & Axelrod nom. nud. Axelrod, 1987, p. 131, pl. 30, figs. 5–11.

Phyllites sp. Knowlton, 1923, p. 191, pl. 43, figs. 13, 15.

Rosa hilliae auct. non Lesquereux. Axelrod, 1987, p. 137, pl. 31, fig. 11.

Wolfe and Schorn (1989) designation: *Holodiscus* sp.

Description.—Leaves simple; apparently estipulate; shape symmetric, elliptic to (in larger specimens only) ovate; base symmetric, decurrent, apex acute to narrowly rounded; length 1.1–>4.0 cm, width 0.5–1.7 cm; venation pinnate; midrib moderate; three to four pairs of secondary veins, originating typically at angles of 20°–30° (rarely greater), straight to slightly convex (rarely concave), extending through medial part of tooth, craspedodromous and flanked on both sides by weak veins that converge on apex of tooth; rarely one to two strong veins originating at higher angles from midrib and basal to most basal secondary veins, brochidrodromous; tertiary veins A–A to R–A, widely spaced, reticulate; fourth-order veins forming small, imperfect, irregularly polygonal areoles; veinlets dendritically branching; external secondary veins originating acutely, few, thinning, brochidrodromous or rarely craspedodromous (if subsidiary tooth present); dental sinuses braced by external veins that originate from both suprajacent and subjacent secondary veins and merge at sinus; margin has as many major teeth as secondary veins, A–1 or D–1 (rarely A–4), typically no subsidiary teeth; subsidiary tooth, if present, on second most basal major tooth; sinuses acute to narrowly rounded.

Discussion.—Both *Holodiscus* and *Cercocarpus* can have teeth that are weakly rosoid and confined to the apical half of the lamina. In *Holodiscus* leaves, the most basal secondary veins are placed away from the margin, brochidodromous external secondary veins are present, and the dental sinuses have conspicuous braces; stipules, if present, are deciduous, and thus fossil foliage will appear estipulate. In *Cercocarpus* leaves, the most basal secondary veins are placed close to the margin, typically no external secondary veins are present, and the dental sinuses have very reduced braces; stipules are present. On these criteria, the leaves referred by Axelrod (1987) to *Holodiscus* represent, in large part, *Holodiscus*.

Extant *Holodiscus* can be separated into two groups based on decurrency of the lamina and number of secondary teeth. In one group, a distinct, naked petiole and numerous secondary teeth are present: *H. discolor* (Pursh) Maxim., to which the larger Creede leaves were compared, *H. dumosus* Nutt., and *H. glabrescens* Greenm. In the second group, the lamina is strongly decurrent along the petiole and secondary teeth are few or absent: *H. boursieri* (Carr.) Rehd. and *H. microphyllus* Rydbg. The smaller Creede leaves were likened to *H. dumosus, H. glabrescens*, and *H. microphyllus*. Both large and small leaves of *H. stevenii* fall into the second group, as do Neogene leaves of *H. fryi* Wolfe. In contrast, the type of *H. harneyensis* (Arnold's, 1937, pl. 4, fig. 3) falls into the first group. The leaf referred to *H. harneyensis* by Axelrod (1966, pl. 16, fig. 10; erroneously synonymized with *Crataegus cuprovallis* by Wolfe, 1977) has the laminar decurrency of the second group, but presence of secondary teeth indicates a relationship to the first group; the Copper Basin taxon may represent an ancestor to both extant groups of *Holodiscus*. Smith's (1941, pl. 12, fig. 1) specimen of *Cercocarpus cuneatus* Dorf (what was to become the type of *H. idahoensis*) has an incomplete base, but the few secondary teeth suggest membership in the second group.

The sole basis for separating the Creede specimens assigned to *Holodiscus harneyensis* from those assigned to *H. idahoensis* was size (minimal length 4 cm versus maximal length 2 cm, respectively (Axelrod, 1987, p. 130–131)), although cited but unfigured specimens of the larger leaved *H. harneyensis* included two only 2.5 cm long. Note that the three localities that produced the five larger leaves of *H. stevenii* are localities that produced samples inferred by Wolfe and Schorn (1989) to represent mesic, closed-canopy forest (Axelrod's localities 571–A, 571–B, and 574–A), whereas the 103 smaller and more typical leaves of *H. stevenii* occur in samples that were inferred to represent the full range of Creede vegetation, from mesic forest to chaparral.

The specimen previously assigned to *Rosa hilliae* (pl. 9, fig. 8) appears at first glance to be different from leaves of *H. stevenii*; however, in details of laminar venation and dental morphology, this specimen is like *H. stevenii*. What gives the specimen assigned to *R. hilliae* a different appearance are the convex sides in the basal part of the lamina, strong veins that originate from the midrib basal to the most basal pair of secondary veins, and the asymmetric base. Some specimens of the Creede *Holodiscus*, however, have convex sides basally (Axelrod, 1987, pl. 30, figs. 3, 6), and some have strong veins basally (Axelrod, 1987, pl. 30, fig. 6). The base of the specimen of *R. hilliae*, moreover, is folded to give a falsely asymmetric appearance.

If, as considered by Axelrod (1987), the Creede *Holodiscus* and *H. fryi* were conspecific, then *H. fryi* would be the oldest validly published name for the Creede material. In *H. fryi*, however, (1) the lamina has a length to width ratio of about one to one in contrast to greater than two to one ratio in *H. stevenii*, (2) the most basal lobes flare abmedially in contrast to their apical orientation in *H. stevenii*, (3) the secondary veins originate at angles of 40°–50° in contrast to less than 30° in *H. stevenii*, and (4) if subsidiary teeth occur, they are on the most basal lobes in contrast to being on the second most basal lobes in *H. stevenii*. The characters that separate leaves of *H. fryi* from leaves of *H. stevenii* are primarily the same characters that separate leaves of *H. boursieri* from leaves of *H. microphyllus*.

Nomenclature.—As just discussed, the holotype of *Holodiscus idahoensis* is incomplete and lacks a character critical in taxonomic partitioning of Holodiscus foliage. More importantly, Smith (1941) presented no description of her specimen of *Cercocarpus cuneatus*, and Chaney and Axelrod (1959) failed to present either description or diagnosis; Axelrod's (1987) cursory description, whether judged adequate, was stated to be based on the Creede leaves only and cannot be construed as validating *H. idahoensis*, which must be considered under the ICBN an illegitimate name. As also just discussed, *H. fryi* represents a taxon distinct from the Creede *Holodiscus*, which thus represents a new species. We take pleasure in naming this distinctive *Holodiscus* for Thomas Steven, who has made numerous contributions to the geology of the Creede area.

Holotype.—UCMG 34070.

Paratypes.—UCMP 7705, 7786–7789, 7791–7816, 7821; UCMG 34071, 34072.

Subfamily PYROIDEAE
Genus SORBUS Linnaeus

Sorbus potentilloides (Knowlton) Axelrod

Plate 9, figure 5

Sorbus potentilloides (Knowlton) Axelrod, 1987, p. 138, pl. 31, figs. 2–6, 8.
Phyllites potentilloides Knowlton, 1923, p. 191, pl. 43, fig. 14.
Wolfe and Schorn (1989) designation: *Sorbus potentilloides*.

Description.—Leaves odd-pinnate; at least nine leaflets; leaflet shape symmetric, lorate; base rounded to acute and some strongly asymmetric, apex acute to narrowly obtuse; length 1.3–3.5 cm, width 0.4–0.8 cm; venation pinnate; midrib moderate; seven to nine pairs of secondary veins, originating at angles of 30°–50°, straight to slightly convex, rarely branching before entering teeth, entering teeth medially, flanked by weak converging veins, craspedodromous; tertiary veins typically R–R, branching, reticulate; fourth-order veins forming well-developed, almost quadrangular areoles; veinlets typically once branching; dental sinuses braced by tertiary veins that originate from either subjacent or suprajacent secondary vein; teeth typically one per secondary vein but some leaflets have no teeth in basal third of lamina; teeth typically B–1, basal side about three times as long as apical side; sinuses angular; apetiolulate or with petiolule <0.1 cm long.

Discussion.—Although Becker's (1962) *Sorbus charcharodonta* was synonymized with *S. potentilloides* by Axelrod, the leaflets of *S. charcharodonta* have rounded A–1 teeth and more numerous secondary veins that originate at high (>60°) angles. The relationships of the various described species of *Sorbus* in the North American Tertiary are poorly known, however, and the fossil material of this genus is in need of thorough revision. The Creede laminae, which have no subsidiary teeth, appear related to the extant *S. aucuparia* L. (Axelrod, 1987, p. 139).

Holotype.—USNM 36539.

Hypotypes.—UCMP 7822–7828; UCMG 19773.

Genus CRATAEGUS Tournefort ex Linnaeus

Crataegus creedensis Axelrod

Plate 9, figure 6

Crataegus creedensis Axelrod, 1987, p. 128, pl. 28, figs. 1–3.
Wolfe and Schorn (1989) designation: *Crataegus creedensis*.

Description.—Leaves simple; apparently estipulate; shape symmetric, ovate to elliptic, pinnatifid to almost pinnatisect; base symmetric, cuneate, apex acute to narrowly rounded; length 1.4–>2.9 cm, width 1.0–2.2 cm; venation pinnate; midrib moderate; three to five pairs of secondary laminar segments, ovate to typically elliptic to obovate, apex acute to narrowly obtuse, base strongly decurrent to subjacent secondary laminar segment; secondary veins originating at angles of 30°–50°, entering laminar segment either medially or toward apical margin of segment, straight to slightly concave, craspedodromous; one to two veins thinner than secondary veins originating basal to secondary veins and extending parallel with secondary vein; tertiary veins in medial (apical) laminar segment R–R to A–R, reticulate; tertiary veins in lateral secondary segments R to A and forming brochidodromous loops or rarely craspedodromous; fourth-order veins forming imperfect, quadrangular to pentagonal areoles; veinlets typically once branched; lobal sinal bracing formed by a weak intersecondary vein that branches at sinus, each branch weak and extending a short distance close to sinal margin; each secondary segment typically has one tooth on basal side near apex of segment; sinuses angular; petiole 0.2–0.6 cm long.

Discussion.—Most leaves of *Crataegus creedensis* are almost pinnatisect, a rare condition that occurs in some leaves of some species of extant *Crataegus*. No extant species of the genus appears closely related to *C. creedensis*. Although compared by Axelrod (1987) to extant species such as *C. azarolus* L., *C. creedensis* has weak lobal sinal braces (in *C. azarolus* the bracing vein and its branches are thick and extend half or more the distance to the apex of the secondary laminar segments) and thin but straight secondary veins (in *C. azarolus*, the thick secondary veins are offset at the points of origination of major branches).

Holotype.—UCMP 7259.

Paratypes.—UCMP 7754–7758, 7760.

Subfamily ROSOIDEAE
Genus POTENTILLA Linnaeus

Potentilla creedensis (Axelrod) Schorn & Wolfe, n. comb.

Plate 10, figure 7; plate 11, figure 1

Ranunculus creedensis Axelrod, 1987, p. 109, pl. 21, fig. 6.
Wolfe and Schorn (1989) designation: *Potentilla* sp.

Description.—Leaves simple; stipulate; tripalmatisect and palmatifid; the three pairs of lateral primary laminar segments doubly palmatifid; shape symmetric, widely ovate; base deeply cordate, apex acute; length 1.5–3.5 cm, width 2.0–3.8 cm; lateral primary laminar segments ovate, palmatifid, base cuneate; venation perfectly actinodromous; midrib moderate; the six lateral primary veins moderate, slightly concave; three to four pairs of secondary veins originating from midrib and from more apical pair of lateral primary veins and one to two pairs from more basal pairs of lateral primary veins at angles of about 30°, typically concave, entering teeth medially, flanked by weak veins, craspedodromous; dental sinal braces formed by external vein that originates from subjacent secondary vein; higher order venation obscure; secondary laminar segment have one to two A–1 teeth on basal side and zero to one on apical side; sinuses angular; petiole 0.9–1.7 cm long.

Discussion.—Ranunculaceae have chloranthoid teeth (Hickey and Wolfe, 1975), whereas the Creede specimen assigned to *Ranunculus* has weakly developed rosoid teeth. Palmatisect to palmatifid foliage in association with weakly developed rosoid teeth is particularly common in *Potentilla.*

Potentilla creedensis is actinodromous and is thus generally related to the many extant species that are palmatisect. Most of these species, however, have laminae that are pentapalmatisect, in contrast to *P. creedensis* laminae, all of which are tripalmatisect and have lateral segments twice palmatifid; this condition has not been observed in extant *Potentilla.* In some Arctic tundra species (for example, *P. norvegica* L. and *P. groenlandica* Malte), laminae are tripalmatisect; the most basal lobes of the lateral segments are entered by veins that originate basally and could thus be regarded as reduced lateral primary veins, but the lobes are about the same size as more apical secondary laminar segments. In *P. subquinata* leaves, the laminae are also typically tripinnatisect as in the Arctic taxa, but some are pentapalmatisect; in the pentapalmatisect laminae, the most basal major veins of the most apical pair of lateral segments are secondary veins, suggesting that indeed the most basal major veins of tripalmatisect leaves are reduced primary veins.

In this context, foliage of the Creede *Potentilla* appears to represent a stable intermediate condition between the exclusively tripalmatisect Arctic species and the exclusively pentapalmatisect species. The Arctic leaves, however, have untoothed, robust secondary laminar segments, in contrast to the toothed, filiform secondary laminar segments of *Potentilla creedensis*. The apparent relationship of the Creede *Potentilla* to the Arctic tundra taxa may indicate that some Arctic tundra lineages originated in middle-latitude, high-altitude regions, a concept held by some plant geographers.

Holotype.—UCMG 19757.

Hypotypes.—USNM 422590; HUBM 62425

Genus CERCOCARPUS Humboldt, Bonpland, & Kunth

Cercocarpus henricksonii Schorn & Wolfe, n. sp.

Plate 10, figures 3–6, 15, 16

Cercocarpus holmesii auct. non (Lesquereux) Axelrod, 1944. Axelrod, 1987 (part), p. 124, pl. 26, figs. 1–14.

Planera myricaefolia auct. non (Lesquereux) Cockerell. Knowlton, 1923, p. 188, pl. 43, figs. 16, 17.

Wolfe and Schorn (1989) designation: *Cercocarpus* sp. 1.

Description.—Leaves simple; stipulate; shape symmetric, very narrowly elliptic or oblanceolate to narrowly oblanceolate; base symmetric, acute to cuneate, apex acute to narrowly obtuse; length 2.7–6.0 cm, width 0.3–1.4 cm; venation pinnate; midrib stout; 6–12 pairs of secondary veins, originating at angles of 10°–20°, typically straight, the basal one to three pairs brochidodromous, the more apical pairs entering teeth medially, flanked by two weak converging veins, craspedodromous; tertiary veins R–R, closely spaced; fourth-order veins forming with tertiary veins small, well-developed, quadrangular areoles; veinlets unbranched; teeth simple, typically confined to apical half of lamina, A–1 or B–2, apical side very short relative to basal side and some teeth are very appressed; sinuses angular; margin revolute; petiole 0.2–0.6 cm long.

Discussion.—The architecture of these leaves is consistent with assignment to *Cercocarpus* (see previous discusssion of *Holodiscus*). Particularly note the stipulate condition (pl. 10, fig. 3).

Cercocarpus bea-anniae Beck., which was synonymized with the Creede material by Axelrod (1987), is based on leaves that have only three to five pairs of secondary veins, a convex curvature to the secondary veins, and a few teeth confined to the most apical part of the lamina. Although conceivably Becker's (1962) leaves could represent extreme variants of the Creede species, none of the Creede leaves of *C. henricksonii* that we have examined combine the characters on which *C. bea-anniae* was founded.

The Florissant *Cercocarpus myricaefolius* (Lesq.) MacG. may be related to *C. henricksonii.* The Florissant leaves, however, typically have large, sharp D–2 or D–3 teeth that occur in the basal half of the lamina.

The presumed achenes assigned to *Cerococarpus holmesii* by Axelrod (1987) present a problem rather than giving confirmatory evidence as to the presence of the genus in the Creede flora. Some specimens have evidence of hairs on the elongated styles, which would indicate *Cercocarpus.* However, the specimen illustrated by Axelrod (1987, pl. 29, fig. 10) as *Fallugia lipmanii* may represent the same taxon as the isolated achenes assigned to *Cercocarpus.* The specimen (pl. 13, figs. 1, 2) has three curved, long styles (preservation is too poor to determine pubescence) that emanate from an apparently striated structure that may represent the hypanthium tube. Two presumably indehiscent structures, also with curved, long styles, cross the hypanthium tube, and the presumed achenes are almost exactly the same length as the hypanthium tube. These other two structures appear as if they were partially removed from the hypanthium tube at the time of deposition; in all preserved characters, these two structures are identical to the achenes assigned to *Cercocarpus* from other Creede localities; the slightly smaller size of the achenes and shorter styles than in the other isolated achenes is probably related to being immature. This specimen was collected at Axelrod's locality 573–A, where 131 leaves of our *C. henricksonii* but only 42 leaves of other angiosperm taxa (including 25 of *Populus*, 7 of *Ribes*, and 3 of *Eleopoldia*) were censused, and this association suggests that this specimen would more probably represent the same taxon as the *Cercocarpus* leaves rather than the *Eleopoldia* (= Axelrod's *Fallugia*) leaves. On the other hand, this pentacarpellary structure cannot represent true *Cercocarpus*, which is exclusively unicarpellate, although it is associated with *Cercocarpus*-like leaves and isolated achenes have been accepted as *Cercocarpus*.

This raises the possibility that, if the leaves and reproductive structures represent the same taxon, *Cercocarpus henricksonii* (and possibly the Florissant *C. myricaefolius*) represents a genus ancestral to *Cercocarpus*, and that five carpels (which are surely primitive in Rosaceae) have been reduced to one. On the other hand, the presence in the Creede of *C. nanophyllus*, which represents the distinct, specialized *C. ledifolius* clade, would indicate *Cercocarpus* had already originated prior to Creede time. "*Cercocarpus*" *henricksonii* would, in this context, not be a species ancestral to any extant true *Cercocarpus* but only a lingering species of the ancestral genus. Additional, better preserved specimens and additional evidence from more associations with the *Cercocarpus*-like foliage would test this hypothesis. The possibility of the validity of the hypothesis suggests that caution should be exercised before attempting to relate *C. henricksonii* to any extant species of *Cercocarpus.*

Although the leaves of *Cercocarpus henricksonii* do not appear to differ in any major architectural features from extant *Cercocarpus.* the stipules are free (pl. 10, fig. 3), whereas in extant *Cercocarpus* (as well as in *C. nanophyllus;* pl. 10, fig. 14), the stipules are adnate to the petiole except at their apices. Additional, detailed architectural comparisons between extant and fossil foliage are needed.

Nomenclature.—The types of Lesquereux' (1887) *Crataegus holmesii*, which form the basis for *Cercocarpus holmesii* (Lesq.) Axelr., are here refigured (pl. 10, figs. 1, 2, 8, 9). These specimens were collected from a locality at Silver Cliff, Colo., and assignment of the Creede leaves of toothed *Cercocarpus* to *C. holmesii* is dubious at best. One of the types of *C. holmesii* (pl. 10, fig. 1) has no indication of secondary veins and is entire-margined; this specimen cannot be generically or familially determined. The margin of the second specimen can be interpreted as either an original margin or one created by tearing along veins; the specimen cannot be determined. The third specimen is a fragment of a lamina that had at least three pairs of secondary veins that originated at very low angles; no teeth and no higher order venation are preserved. The fourth specimen is a fragment of the apical portion of a lamina; the secondary veins originate at very low angles and appear to terminate in very appressed teeth, but greater detail is not preserved. The fourth specimen could well represent the same species as *C. henricksonii* but could equally well represent the same species as *C. bea-anniae* or even some as yet undescribed species. The types of *C. holmesii* are too fragmentary and too poorly preserved to determine their affinities with any degree of certainty.

Axelrod (1987) erred in designating as lectotypes for *Cercocarpus holmesii* two specimens (for a given taxon, only one lectotype can be designated) and also erred in designating USNM 36541 and 36542. These two Creede specimens are those illustrated by Knowlton (1923) as *Planera myricaefolia*; under the ICBN, a lectotype for Lesquereux' (1887) *C. holmesii* must come from the original type suite. We herewith designate as lectotype of *Crataegus holmesii* Lesq. USNM 313299 (pl. 10, fig. 9). We take pleasure in naming this species for James Henrickson, who has contributed greatly to understanding the phylogeny and systematics of extant Rosaceae.

Holotype.—UCMG 34073 (counterpart USNM 422592).

Paratypes.—USNM 36541, 36542; UCMP 7679–7713; UCMG 34074–34077.

Cercocarpus nanophyllus Schorn & Wolfe, n. sp.

Plate 10, figures 12–14

Cercocarpus linearifolius auct. non (Lesquereux) Axelrod, 1950. Axelrod, 1987, p. 126, pl. 28, figs. 5–11.

Wolfe and Schorn (1989) designation: *Cercocarpus* sp. 2.

Description.—Leaves simple; stipulate; shape symmetric, narrowly to very narrowly elliptic, typically falcate; base symmetric, acute to obtuse, apex narrowly obtuse to acute; length 1.0–2.5 cm, width 0.2–0.3 cm; venation pinnate; midrib massive (as much as 15 percent of the width of lamina); 15–30 pairs of closely spaced secondary veins, originating at angles of 50°–(typically) > 70°, straight, forming markedly brochidodromous loops; abmedial segments of loops tending to form an intramarginal vein; numerous composite intersecondary veins, some of which extend to abmedial segment of loop and thus may not be clearly distinguished from secondary veins; tertiary veins typically A–R, forming well-developed, typically quadrangular areoles; veinlets few, unbranched or once branched; margin entire, strongly revolute; petiole <0.1 cm long.

Discussion.—Entire-margined laminae that are reduced in size, such as those just described, typically have reduced venation, which makes their identification difficult. Characters may then have to be employed that are of minor taxonomic significance. For example, the markedly revolute margin of these leaves is not of major taxonomic significance and can be found in *Ledum* in Ericaceae, as well as in *Cercocarpus*. *Ledum* has, however, as do most Ericaceae, reticulodromous venation and, like all Ericaceae, is estipulate. The Creede leaves cannot, therefore, represent Ericaceae.

These Creede leaves also have closely spaced A–R tertiary veins and numerous composite intersecondary veins. This architecture, although not confined to Rosaceae, is particularly common in the family. Combined with the stipulate condition, the assignment by Axelrod (1987) of these leaves to Rosaceae based on resemblance to the extant *Cercocarpus ledifolius* Nutt. appears warranted, although we emphasize the somewhat tenuous nature of the generic and familial assignment.

Although *Cercocarpus nanophyllus* is apparently related to the extant *C. ledifolius*, leaves of the two species are readily distinguished. In *C. ledifolius* leaves the secondary veins typically originate at an angle of less than 45°, and the abmedial segments of the secondary vein loops are aligned to form an intramarginal vein only in the apical region of the lamina.

Nomenclature.—Axelrod (1987) included the Creede material here described as *Cercocarpus nanophyllus* in *C. linearifolius*, which is based on Lesquereux' (1887) *Andromeda linearifolia* from Silver Cliff, Colo. Because *C. linearifolius* has been cited as occurring widely in the Neogene of western North America (Axelrod, 1950, 1956, 1987), as well as in the Creede flora, we reexamined the type material of this taxon.

The extant type suite of *Andromeda linearifolia* includes only two specimens, one represented by part and counterpart. One specimen is a complete lamina but has only vague indications of secondary veins (pl. 10, fig. 11); assignment of this specimen to the angiosperms could be questioned. The second specimen (pl. 10, fig. 10), which lacks base and apex, has a few, widely spaced secondary veins that originate at very low angles (about 20°), an exceedingly thick midrib (the width of the midrib is about 20 percent of the width of the lamina), and a markedly revolute margin (as does the first specimen). When contrasted to the closely spaced secondary veins that originate at high angles in *Cercocarpus nanophyllus*, *A. linearifolia* is clearly distinct. We herewith designate as lectotype of *Andromeda linearifolia* Lesq. USNM 313291 (pl. 10, fig. 10).

Holotype.—UCMG 34078.

Paratypes.—UCMG 34079, 34080; UCMP 7217, 7355A, B, 7359, 7379, 7637A, B (=7638), 7639.

Genus and Species Indetermined

Plate 11, figures 3, 8

Wolfe and Schorn (1989) designation: Not included.

Discussion.—Two poorly preserved specimens have the same dental morphology: very large, almost equal sided, and typically B–3 teeth. One specimen has three laminar segments, and the second specimen has two laminae that are positioned to indicate a similar foliar organization. Because (1) the segments of the first specimen are attached to a rachis, (2) the second specimen appears to have probably had the same organization, and (3) no unattached segments have been found, the lamina is interpreted as tripalmatisect (or possibly pinnatisect) rather than truly compound (Wolfe and Wehr, 1988). In the better preserved specimen, the teeth appear to be weakly rosoid. Several extant genera of Rosoideae (for example, *Potentilla* and allied genera) have this general leaf architecture, and the fossils may represent a tripalmatisect species of *Potentilla*. Until well-preserved specimens are collected, we prefer to leave this fossil taxon unnamed.

Specimens.—UCMG 19766, 34081.

Subfamily PRUNOIDEAE
?Genus OSMARONIA Greene

Osmaronia? stewartiae (Axelrod) Schorn & Wolfe, n. comb.

Plate 11, figures 4, 9; text figure 11*A*

Arbutus stewartii Axelrod, 1987 (part, typic), p. 146, pl. 34, fig. 1.
Wolfe and Schorn (1989) designation: *Osmaronia?* sp.

Description.—Leaf simple; stipulate?; shape symmetric, narrowly elliptic; base symmetric, acute, apex acute and mucronate; length 6.8 cm, width 1.8 cm; venation pinnate; midrib moderate basally, thinning markedly and terminating in the apparently glandular mucro; 11 pairs of secondary veins, originating at angles of 45°–50° (higher apically), decurrent near base of lamina, convex, thin, brochidrodromous to eucamptodromous; intersecondary veins composite, thin, extending about half the distance to margin; tertiary veins R–R to A–O, widely spaced, reticulate; fourth-order veins forming imperfect, irregularly polygonal areoles; veinlets dendritically branching; external secondary veins three to four per secondary vein, originating acutely, forming loops of irregular shape; margin entire, erose; petiole 0.8 cm long.

Discussion.—The two paratypes of *Arbutus stewartii* are excluded from this species. Both specimens lack their original margins and possibly are poorly preserved leaves of *Populus larsenii*.

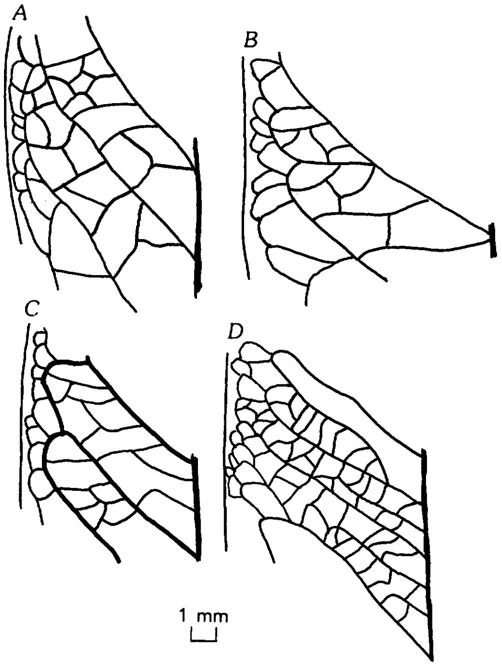

Figure 11. Drawing showing venation of *Osmaronia* and modern comparisons. *A, O.? stewartiae (Axelr.)* Schorn & Wolfe, holotype UCMG 19778 (holotype of *Arbutus stewartii* (Axelr.). *B, O. cerasiformis* (Torr. & Gray) Greene, extant. *C, Dichotomanthes tristaniaecarpa* Kurz, extant. *D, Arbutus arizonica* (Gray) Sarg., extant.

Leaves of *Arbutus arizonica* (Gray) Sarg., which were considered to be closely similar to *A. stewartii*, have closely spaced secondary veins; in a lamina the size of the holotype of *A. stewartii*, about 18, rather than 11, pairs of secondary veins occur. The secondary veins in *A. arizonica*, although some fork and some are angularly crooked, extend approximately straight toward the margin rather than curve. The angle of origination of secondary veins in *A. arizonica* is about 60° in the basal half of the lamina rather than about 45°. No mucro or indication of glandularity occurs on the apex of *A. arizonica* leaves.

On the other hand, the same characters that differentiate the holotype of *Arbutus stewartii* from leaves of *Arbutus* are found in leaves of *Osmaronia*. The one extant species of the west American *Osmaronia, O. cerasiformis* (Torr. & Gray) Greene, has thicker and more strongly brochidodromous secondary veins, stronger external secondary veins, and a longer mucro than does *A. stewartii*. In its thinner secondary veins and weaker loops, the Creede leaf resembles leaves of *Dichotomanthes* and untoothed leaves of *Exochorda*, both extant Chinese genera of Rosaceae. Because only a single specimen of the Creede taxon has been recovered and because it is not as well preserved as desirable, we tentatively and questionably refer it to *Osmaronia*. Citation of a now exclusively Asian genus in the North American Tertiary should, we think, be based on better material than now available. Had a binomial not been based on this specimen, we would not give the specimen any formal designation other than "Rosaceae, genus and species indetermined." The specimen has sufficient characters preserved so that, if better preserved material were found at Creede, this material could with reasonable certainty be considered conspecific and generically determined.

Nomenclature.—Named after Belle Katherine Stewart, the epithet is corrected to *stewartiae*, in accordance with the recommendations of the ICBN.

Holotype.—UCMG 19778.

Genus PRUNUS Linnaeus

Prunus creedensis Axelrod

Plate 11, figures 2, 5–7; plate 12, figure 5; text figure 12*A*, *B*

Prunus creedensis Axelrod, 1987, p. 136, pl. 31, fig. 7.
Sambucus longifolius Axelrod, 1987, p. 150, pl. 34, figs. 5, 6.
Wolfe and Schorn (1989) designation: *Prunus creedensis*.

Description.—Leaves simple; stipulate; shape symmetric, lanceolate, typically slightly falcate; base symmetric, acute to obtuse, apex attenuate; length 3.8–>11.5 cm, width 1.0–2.6 cm; venation pinnate; midrib moderate; 25–>40 pairs of secondary veins, originating at angles of 45°–80°, broadly convex, brochidodromous; numerous composite intersecondary veins, some extending to abmedial segment of secondary loop; tertiary veins A–O to typically R–R, percurrent; fourth-order veins forming quadrangular areas; fifth-order veins forming with fourth-order veins well-developed, polygonal areoles; veinlets branching several times; two to four external veins originating from abmedial side of each secondary vein, entering teeth medially, craspedodromous; teeth about two to four per secondary vein, typically C–1 or D–1; the most basal teeth glandular; sinuses angular; petiole 0.6–1.6 cm long.

Discussion.—The holotype of *Prunus creedensis* has a glandular, most basal tooth but no glands on the more apical teeth. This character is a strong synapomorphy with leaves of extant *Prunus*. Other characters (for example, a closely serrate margin, marked brochidodromy, and craspedodromous external secondary veins) are consistent with the assignment to *Prunus*.

Three additional leaves of *Prunus creedensis* are represented in the University of Colorado's collections and show the holotype to be atypically small. Indeed, although the Florissant *P. gracilis* (Lesq.) MacG. and the Troutdale *P. treasheri* Chan. were differentiated from *P. creedensis* on the basis of their supposedly larger size and (or) greater breadth (Axelrod, 1987), these criteria are no longer valid. *P. creedensis*, however, differs from *P. gracilis* in having many more pairs of secondary veins and from *P. treasheri* in having the secondary loops placed much closer to the margin.

The two large laminae that Axelrod (1987) referred to *Sambucus* are here included in *Prunus creedensis*. One specimen (Axelrod's pl. 34, fig. 5) has a long (1.6 cm), distinct petiole and a gland on the most basal tooth. Although the second specimen (Axelrod's pl. 34, fig. 6, which is the holotype of *Sambucus longifolius* UCMG 19774) lacks a petiole and could thus be interpreted as a leaflet, the base of the lamina is actually missing. Although we cannot demonstrate whether the missing basal teeth were glandular, the intercostal and intramarginal venation and dental morphology of this specimen are the same as in *P. creedensis* (fig. 12).

Prunus creedensis was compared (Axelrod 1987) to the extant Asian *P. davidiana* (Carr.) Franch., but this relationship is distant. Whereas *P. creedensis* has veins that enter the teeth medially, *P. davidiana* has veins that extend to the dental sinuses (fig. 12*D*). The suprabasal teeth in *P. creedensis* are sharp and can have elongated, conical glands, but the teeth in *P. davidiana* are rounded and are eglandular or have short, rounded glands. In addition, the tertiary veins are typically R–R (some are A–O) in *P. creedensis* but are markedly and uniformly A–O in *P. davidiana.* Some teeth are entered medially in *P. pennsylvanica* L. f. and most have elongated, conical glands, but typically veins extend to the sinuses. Leaves of subgenus *Padus,* however, typically have sharp teeth that are entered medially by veins that originate abmedially from brochidodromous loops (for example, *P. pilosiuscula* [Schneid.] Koehne; fig. 12*C*), and these leaves also have marked intersecondary veins and R–R tertiary veins. *Prunus creedensis* appears to represent an extinct member of *Padus* that mimicked the willowlike leaves in some other subgenera of *Prunus.*

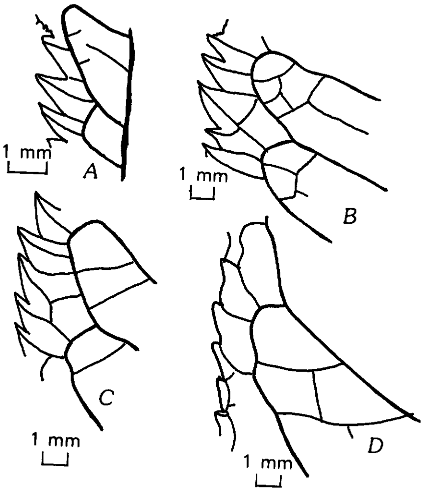

Figure 12. Drawing showing venation of *Prunus. A, P. creedensis* Axelr., holotype UCMP 7819. *B, P. creedensis* Axelr., hypotype UCMG 19774 (holotype of *Sambucus longifolius* Axelr.). *C, P. pilosiuscula* (Schneid.) Koehne, extant. *D, P. davidiana* (Carr.) Franch., extant.

Nomenclature.—Although the type specimens of *Sambucus longifolius* are better preserved and more typical in size than the single primary type of *Prunus creedensis*, the epithet *creedensis* must be accepted as valid.

Holotype.—UCMP 7819.

Hypotypes.—UCMP 7855–7859; UCMG 19774, 34082–34084; USNM 422593.

Prunus sp.

Prunus chaneyii auct. non Condit. Axelrod, 1987, p. 135, pl. 28, fig. 4.
Wolfe and Schorn (1989) designation: *Prunus* sp.

Discussion.—The single Creede leaf referred by Axelrod (1987) to *Prunus chaneyi* validly represents *Prunus*. The most basal teeth on both sides of the lamina have glands, an architecture characteristic of this genus. In having markedly brochidodromous secondary veins and widely spaced, R–R, percurrent tertiary veins, the Creede specimen is a member of subgenus *Padus*, a taxon some systematists consider to be of generic rank. The Creede leaf is similar in gross characters to leaves of *P. virginiana* L., a similarity also suggested by Axelrod (1987).

Nomenclature.—One cotype of *Prunus chaneyi* (Condit's, 1938, pl. 5, fig. 4) has A–0 tertiary veins and salicoid teeth; this specimen is probably an unusually small leaf of the *Salix* that is abundant at many of the Neroly localities. The second cotype has an entire margin and probably represents *Nyssa*. The Creede leaf cannot be assigned to *P. chaneyi*, but this single leaf in which areolar venation is not preserved is insufficient basis for a new species.

Specimen.—UCMP 7818.

Family LEGUMINOSAE
Genus CERCIS Linnaeus

Cercis sp.

Text figure 13*B*

Cercis buchananensis auct. non Condit. Axelrod, 1987, p. 139, pl. 32, fig. 11.
Wolfe and Schorn (1989) designation: *Cercis* sp.

Discussion.—The top of the petiole of the single specimen is swollen and has some vague indications of cross striations, thus indicating the presence of the

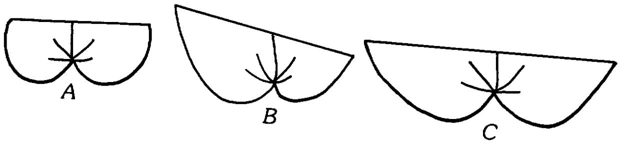

Figure 13. Drawing showing basal configuration of *Cercis. A, C. occidentalis* Torr. & Gray. *B, C.* sp., UCMG 19775, *C, C. chinensis* Bunge.

characteristic pulvinus of Leguminosae. In combination with simple leaf organization and marked actinodromy, assignment to *Cercis* is probably valid.

Cercis buchananensis was validly compared by Condit (1944) to the extant *C. occidentalis* Torr. & Gray. The leaves of both species have cordate bases that extend in a continuously convex curve abmedially and then apically: that is, from the top of the petiole to a point slightly apical of the petiole the margin describes an approximate circle, with the most basal points of the cordate base on lines approximately parallel with the midrib and approximately half the distance from the midrib to the margin (fig. 13). The Creede leaf, however, has a margin that is circular only to the most basal points of the base and then markedly changes to a much flatter curvature; the most basal points of the base on lines parallel to the midrib are closer to the midrib than in *C. occidentalis*. This basal configuration is found in *C. chinensis* Bunge (fig. 13*C*).

Specimen.—UCMG 19775.

Genus and Species Indetermined

Robinia califomica auct. non Axelrod, 1939. Axelrod, 1987 (part), p. 140, pl. 32, figs. 1–5.

Symphoricarpos wassukana auct. non Axelrod, 1956. Axelrod, 1987, p. 149, pl. 33, figs. 1, 2.

Wolfe and Schorn (1989) designation: Legume.

Discussion.—None of these presumed leaflets is well preserved, and, even among the specimens assigned by Axelrod (1987) to *Robinia*, only one shows the cross-striated pulvinus that occurs throughout extant Leguminosae and on even moderately well preserved fossil legume foliage. The fossils lack preservation of venation above the third order. As preserved, these leaflets could be matched by leaflets of a large number of legume genera.

As MacGinitie (1969, 1974) emphasized, even well-preserved legume foliage offers major problems in identification. Although extensive study of leaf architecture in extant and fossil legumes now underway by P.F. Herendeen may provide criteria for differentiating well-preserved fossil legume foliage at the generic level, the preservation of the Creede fossils is too poor for generic or specific determination.

The two specimens of *Symphoricarpos wassukana* illustrated by Axelrod (1987) are probably short, broad variations of the Creede legume leaflet. Although UCMP 7853 has a very rounded apex, the second specimen (UCMP 7851) has an apex no more rounded than one legume leaflet (UCMP 7830). Relative to shape of the base, one *Symphoricarpos* specimen (UCMP 7851) has a base like one legume specimen (UCMP 7833), and the second *Symphoricarpos* specimen (UCMP 7853) has a base like a second legume specimen (UCMP 7835). One unfigured cited hypotype of *S. wassukana* (UCMG 19784) was also cited as a paratype of *Quercus creedensis* (Axelrod, 1987, p. 108).

Specimens.—UCMP 7829, 7830, 7832–7835, 7851, 7853, 7861.

Family BIGNONIACEAE
Genus CATALPA Scopoli

Catalpa coloradensis Schorn & Wolfe, n. comb.

Plate 12, figures 1, 2, 7

Nuphar coloradensis Axelrod, 1987, p. 108, pl. 33, figs. 4, 5.

Wolfe and Schorn (1989) designation: *Catalpa* sp.

Description.—Leaves simple; shape symmetric, widely to very widely ovate; base symmetric, cordate, apex unknown; length unknown but >10 cm, width 10–12 cm; venation perfectly actinodromous; nine primary veins; five primary veins including midrib massive; most apical pair of lateral primary veins convex, extending apically to beyond the same distance as the origination point of the second most basal pair of medial secondary veins, typically slightly convergent with medial secondary veins, brochidodromous or, if lateral lobes present, craspedodromous; four to five secondary veins originating at angles of 30°–40° from basal sides of most apical pair of lateral primary veins, convex, brochidrodromous; second most apical pair of lateral primary veins extending apically to the same (or less) the distance as the origination point of the most basal pair of medial secondary veins, slightly convergent with secondary veins of suprajacent lateral primary vein, convex, brochidodromous; three to five pairs of secondary veins originating at angles of 30°–40° from basal sides of second most apical pair of lateral primary veins, convex, brochidrodromous; third most apical pair of lateral primary veins extending abmedially and away from apex, slightly convergent with secondary veins of suprajacent lateral primary vein, convex, brochidodromous; two to four pairs of secondary veins originating acutely from basal sides of third most apical pair of lateral primary veins, convex, brochidodromous; most basal pair of lateral primary veins about same thickness as secondary veins of suprajacent lateral primary vein, brochidodromous; tertiary veins R–R, percurrent, some branching; higher order venation not preserved; brochidodromous loops formed by an external vein of suprajacent secondary vein that joins subjacent secondary vein; abmedial side of loop extends almost to margin; some external veins originating acutely from apical sides of most apical pair of lateral primary veins, brochidodromous; margin entire, thickened but no fimbrial vein; some leaves have a single lateral lobe that has a rounded apex; petiole very thick, >7 cm long, with broad base.

Discussion.—The distinctive leaves of *Catalpa coloradensis* are highly dissimilar to leaves of *Nuphar*. Leaves of *Nuphar* (1) have an auriculate base, (2) are basically pinnately veined, (3) have major veins that markedly diverge from one another, (4) have secondary veins that fork into branches of approximately equal size (that is, dichotomize) two or three times, with the first forking typically occurring about half the distance (or less) to the margin, and (5) are unlobed. The broad petiolar base (pl. 12, fig. 2) represents the presumed plane of dehiscence. The leaves of Nymphaeaceae die attached to plant and are dissociated by degradation of the petiole. The specimen (UCMP 7523) considered to be a nymphaeaceous "rootscar" (Axelrod, 1987, p. 17) is a poorly preserved impression of unknown affinities.

The specimen illustrated as figure 2 on plate 12 is the most complete lamina of *Catalpa coloradensis* known, although the preserved margin has apparently resulted from degradation of the original margin. One paratype (pl. 12, fig. 7), although a fragment, illustrates the margin and adjacent venation. The holotype (Axelrod, 1987, pl. 22, fig. 5) is perhaps lobed, but the margin is sufficiently decayed to be uncertain about lobing; one paratype (pl. 12, fig. 1), however, is unquestionably lobed.

Deeply cordate leaves that are actinodromous, have as many as nine primary veins, have an entire margin that can be lobed but that does not have a fimbrial vein, and have secondary veins that are markedly brochidodromous close to the margin, occur primarily in the palmate dilleniids (Hickey and Wolfe, 1975). In the palmate dilleniids, however, the venation around the top of the petiole tends to have a spiderweb appearance: the tertiary veins are arranged concentrically around the top of the petiole, and the fourth-order venation is strong and orthogonal to the tertiary veins. On the other hand, the Creede leaves are very similar in primary, secondary, and tertiary venation patterns to leaves of *Catalpa* (Bignoniaceae) and *Paulownia* (Scrophulariaceae), which are considered to be closely related to one another (Airy Shaw, 1985). *Catalpa* especially can have leaves that (1) have a thick petiole and major veins, (2) can be lobed, and (3) have markedly brochidodromous secondary veins. Lobes that have rounded apices are found in leaves of the Asian *C. ovata* D. Don.

Holotype.—UCMP 7520.

Paratypes.—UCMP 7518, 7519, 7521, 7522.

Hypotype.—UCMG 34085.

LILIATAE, Family Indeterminded
Genus MONOCOTYLOPHYLLUM Chandler

Monocotylophyllum sp.

Cyperacites creedensis Axelrod, 1987, p. 100, pl. 17, fig. 1.

Discussion.—In order for leaf impressions-compressions to be placed in Cyperaceae, they should have evidence of a triangular cross section. In fact, the Creede leaves assigned to *Cyperacites* are described as "grass-like." The morphology of many monocotyledonous leaves, including these Creede specimens, is too simple to determine even the family represented. No point is served by giving an epithet to such material.

Specimen.—UCMP 7495.

Names of Dubious Value

Species, as well as citations of previously described species, based on fragmentary and (or) poorly preserved specimens create nomenclatorial as well as taxonomic problems. Although the ICBN allows for formal rejection of such names, the procedure is long. In the previous discussions of systematics of the Creede conifers, we suggested that some formally named species were based on material that is too fragmentary or poorly preserved for valid characterization of the species: *Picea coloradensis* Axelr. and *Tsuga petranensis* Axelr. Following we list and discuss other species based on Creede material that we consider also to be good candidates for rejection; citations based on Creede specimens of species previously described from other floras are also listed and discussed, except for those citations previously included in our formal synonymies.

Quercus creedensis Axelrod, 1987, p. 107, pl. 21, figs. 2–5.

Plate 12, figures 4, 6

Discussion.—These specimens are all entire-margined. Some indications of secondary veins are present, but not even the manner of looping can be determined (pl. 12, figs. 4, 5). Tertiary and higher-order venation is totally lacking; the basis for Axelrod's (1987, p. 107) description of tertiary and higher order venation is unknown. The shortness of the petiole suggests that it could be a petiolule; concomitant with the asymmetry of the laminae, these laminae may represent very poorly preserved specimens of the indetermined legume.

Specimens.—UCMP 7514–7517; UCMG 19784 (note that this cited paratype was also cited (Axelrod, 1987, p. 149) as a hypotype of *Symphoricarpos wassukana*).

Hippurus coloradensis Axelrod, 1987, p. 143, pl. 33, fig. 9.

Discussion.—The specimen on which *Hippurus coloradensis* is based is an axis that has three nodes, to which three smaller axes are attached. One node has a filamentous structure also attached. The three smaller axes also have nodes, to which smaller filamentous structures are attached. Striations on the axes suggest some vascularization. The specimen is not diagnostic as to whether it is even an angiosperm; included in the University of Colorado's Creede collections is a similar specimen (UCMG 19689) that has the nodal sheaths of *Equisetum*.

Specimen.—UCMP 9840.

***Shepherdia creedensis* Axelrod, 1987, p. 145, pl. 34, fig. 3.**

Discussion.—The holotype of *Shepherdia creedensis* lacks preservation of the original margin and of venation above the tertiary level. The broadly ovate shape, truncate base, irregularly spaced secondary veins, and thin, undulatory tertiary veins are characters that are found also in *Populus larsenii*. This may be a poorly preserved specimen of *P. larsenii*, but without the margin we cannot be certain.

Specimens.—UCMP 7844, 7845.

***Chilopsis coloradensis* Axelrod, 1987, p. 150, pl. 34, fig. 7.**

Plate 12, figure 3

Discussion.—Although the leaf of *Chilopsis coloradensis* is linear, the photographic enlargement (pl. 12, fig. 3) indicates much compression by folding. What superficially appears to be strongly decurrent secondary veins that have a very low angle of origination are folds in the lamina. The margin appears to be entire, but folding makes this impossible to determine certainly. The specimen is possibly a folded lamina of *Eleiosina praeconcinna*.

Specimen.—UCMP 7852.

***Fraxinus creedensis* Axelrod, 1987, p. 148, pl. 33, fig. 6.**

Plate 12, figure 8

Discussion.—As shown in the photographic enlargement (pl. 12, fig. 7), the "leaflets" of this specimen have, where not degraded, sharp B–2, closely spaced serrations. The secondary veins originate at angles of about 35° and are brochidodromous; the teeth are entered by external secondary veins, which appear to enter near the apical side of the tooth.

The preserved characters of *Fraxinus creedensis* can be found in several families of Northern Hemisphere Rosidae (as redefined by Wolfe, 1989): Juglandaceae, Rosaceae, Araliaceae, and Oleaceae (which includes *Fraxinus*). An additional, poorly preserved specimen in the University of Colorado's collections appears also to represent *F. creedensis* and has five "leaflets" attached to a rachis. The fact that both specimens have laminae still attached to a rachis suggests that the leaf was not truly compound but was pinnatisect (Wolfe and Wehr, 1988), a condition that commonly occurs in Rosaceae and Sambucaceae. The poor preservation of both specimens prohibits further speculation on affinities.

Specimen.—UCMG 19777.

***Picea lahontensis* auct. non MacGinitie. Axelrod, 1987 (part), p. 85.**

Discussion.—A defoliated axis (UCMP 7295) appears to have irregularly arranged bud and leaf scars and probably represents an angiosperm. A supposed winged seed (UCMP 7301) could be either a floral organ or a fragment of a monocot leaf; the "seed" area of the specimen is an artifact of wrinkling, and the specimen has weak parallel venation (accompanied by transverse veins) the entire length.

Specimens.—UCMP 7295, 7301.

***Pseudotsuga glaucoides* Axelrod, 1987 (part, nontypic), p. 96, pl. 15, fig. 4.**

Discussion.—This supposed ovulate cone scale lacks a bract scale, impression of the seeds or wings or any other character that is diagnostic of a pinaceous cone scale. What taxon or organ this specimen represents is problematic.

Specimen.—UCMP 7425.

***Sapindus coloradensis* auct. non Cockerell. Axelrod, 1987, p. 142, pl. 33, fig. 7.**

Discussion.—The falcate shape and attenuate apex would appear to differentiate this specimen from the legume taxon called *Robinia californica* (our "legume"): however, one "*Robinia*," UCMP 7833, is also somewhat falcate and has an acute apex. UCMP 7833 also has an asymmetrically, broadly rounded base, as does the "*Sapindus*." A second "*Robinia*," UCMP 7829, does not have a complete apex, but the margin changes to a concave curvature, which suggests that an attenuate apex was present. In the "*Sapindus*," however, the secondary veins are "poorly preserved" and "finer nervation [is] not preserved" (Axelrod, 1987, p. 142). Further discussion is pointless.

Specimen.—UCMP 7899.

***Condalia mohavensis* auct. non Axelrod, 1939. Axelrod, 1987, p. 144, pl. 33, fig. 8.**

Discussion.—The specimen is partially covered by a mineral growth (stain), and details of venation and character of the margin are thus uncertain. The specimen has suprabasal secondary veins that are "crowded" at the base as in *Populus*, and two conspicuous, rounded stains are present on either side of the top of the petiole; these stains could represent the acropetiolar glands of *Populus*.

Specimen.—UCMP 7841.

***Zizyphus florissantii* auct. non (Lesquereux) MacGinitie. Axelrod, 1987, p. 144, pl. 34, fig. 4.**

Discussion.—In *Zizyphus florissantii*, the lateral major veins are close to the margin and are connected to the midrib by numerous percurrent veins (MacGinitie, 1953). In this Creede specimen, however, (1) the lateral primary veins have external veins that form elongated brochidrodromous loops between the margin and the lateral primary veins, and (2) strong intersecondary veins extend apically between the lateral primary veins and the midrib, and thus no percurrent veins are present. This Creede specimen cannot represent *Z. florissantii*. In these two characters, concomitant with the actinodromous three primary veins and the linear shape, this specimen is similar to *Berberis coloradensis* and may be nothing more than a large, battered lamina of that species.

Specimen.—UCMP 7843.

Summary of Systematic Revisions

Of the 42 new specific epithets based on Creede material by Axelrod (1956, 1987), we recommend rejection of 10 because the basionyms are poorly preserved and (or) fragmentary and either cannot be distinguished from previously named species of the same genera or lack characters sufficient for familial determination. Eight of Axelrod's (1987) new species and one new combination we accept as valid and properly assigned to their respective genera. Of the remaining species, 5 are transferred to other genera and 19 are synonymized under other species. The following list summarizes our recommended disposition of these epithets.

Picea coloradensis Axelr.: Recommend rejection.
Pinus engelmannoides Axelr.: Recommend rejection.
P. ponderosoides Axelr.: Synonymized under *P. crossii* Knowlt.
P. riogrande Axelr.: Accepted.
P. sanjuanensis Axelr.: Accepted.
P. wasonii Axelr.: Synonymized under *P. crossii* Knowlt.
Tsuga petranensis Axelr.: Recommend rejection.
Juniperus creedensis Axelr.: Accepted.
J. gracillensis Axelr.: Synonymized under *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe.
Cyperacites creedensis Axelr.: Recommend rejection.
Populus creedensis Axelr.: Synonymized under *Populus larsenii* (Knowlt.) Schorn & Wolfe.
Salix creedensis Axelr.: Synonymized under *Eleiosina praeconcinna* (Cocker.) Schorn & Wolfe.
Quercus creedensis Axelr.: Recommend rejection.
Nuphar coloradensis Axelr.: New combination as *Catalpa coloradensis* (Axelr.) Schorn & Wolfe.
Ranunculus creedensis Axelr.: New combination as *Potentilla creedensis* (Axelr.) Schorn & Wolfe.
Berberis coloradensis Axelr.: Accepted.
B. riogrande Axelr.: Synonymized under *B. coloradensis* Axelr.
Mahonia creedensis Axelr. [nom. nud.]: Synonymized under *Mahonia aceroides* (Knowlt.) Schorn & Wolfe.
Ribes birdseyii Axelr.: Synonymized under *R. lacustroides* Axelr.
R. creedensis Axelr.: Synonymized under *R. lacustroides* Axelr.
R. dissecta Axelr.: Synonymized under *R. lacustroides* Axelr.
R. lacustroides Axelr.: Accepted.
R. riogrande Axelr.: Synonymized under *R. lacustroides* Axelr.
R. stevenii Axelr.: An automatic junior synonym of *R. riogrande* Axelr., which is synonymized under *R. lacustroides* Axelr.
R. wasonii Axelr.: Synonymized under *R. lacustroides* Axelr.
Fendlera coloradensis Axelr.: Synonymized under *Berberis coloradensis* Axelr.
Jamesia caplanii Axelr.: Accepted.
Philadelphus creedensis Axelr.: Synonymized under *Berberis coloradensis* Axelr.
Crataegus creedensis Axelr.: Accepted.
Fallugia lipmanii Axelr.: New combination as *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe.
Physocarpus petiolaris Axelr.: Transferred to *Ribes* as *R. robinsonii* Schorn & Wolfe (a new epithet required because of homonomy).
P. triloba Axelr.: Synonymized under *Ribes robinsonii* Schorn & Wolfe. (*triloba* would also be a homonym in *Ribes*).
Prunus creedensis Axelr.: Accepted.
Rubus riogrande Axelr.: Synonymized under *Ribes lacustroides* Axelr.
Sorbus potentilloides (Knowlt.) Axelr.: Accepted.
Acer riogrande Axelr.: Synonymized under *Ribes lacustroides* Axelr.
Hippurus coloradensis Axelr.: Recommend rejection.
Shepherdia creedensis Axelr.: Recommend rejection.
Arbutus stewartii Axelr.: New combination as *Osmaronia? stewartiae* (Axelr.) Schorn & Wolfe.
Vaccinium creedensis Axelr.: Synonymized under *Berberis coloradensis* Axelr.
Fraxinus creedensis Axelr.: Recommend rejection.
Chilopsis coloradensis Axelr.: Recommend rejection.
Sambucus longifolius Axelr.: Synonymized under *Prunus creedensis* Axelr.

Of the 73 species in Axelrod's (1987) Creede flora, 30 represent citations of species previously described from other floras; none of these citations are considered valid. Further, many of the nonbasionymic specimens assigned to species based on Creede material represent other taxa. The following list summarizes the systematic disposition of Axelrod's (1987) Creede flora as made in our current report.

Abies concoloroides R.W. Br.: *A. rigida* Knowlt.
A. rigida Knowlt.: *A. rigida* Knowlt.
Picea coloradensis Axelr.: *Pinus* cf. *P. crossii* Knowlt., *Pinus* spp. indet., Pinaceae gen. indet.
P. lahontensis MacG.: *Abies rigida* Knowlt., *Picea* sp., *Pinus* cf. *P. crossii* Knowlt., *P.* spp. indet., Pinaceae gen. indet., Magnoliophyta gen. indet.
P. sonomensis Axelr.: *Pinus* spp. indet.
Pinus alvordensis Axelr.: *P. sanjuanensis* Axelr., *P. crossii* Knowlt., *P.* spp. indet.
P. coloradensis Knowlt.: *P. crossii* Knowlt., *P.* spp. indet., Pinaceae gen. indet.
P. crossii Knowlt.: *P. crossii* Knowlt., Pinaceae gen. indet.
P. engelmannoides Axelr.: *P.* cf. *P. crossii* Knowlt.
P. florissantii Lesq.: *P. crossii* Knowlt.
P. macginitiei Axelr.: *P.* sp. 2.
P. ponderosoides Axelr.: *P.crossii* Knowlt., *P.* cf. *P. crossii* Knowlt.
P. riogrande Axelr.: *P.* cf. *P. crossii* Knowlt., *P. riogrande* Axelr., *P.* sp. 1, *P.* spp. indet.
P. sanjuanensis Axelr.: *P. sanjuanensis* Axelr., *P. riogrande* Axelr.
P. wasonii Axelr.: *P. crossii* Knowlt.
Pseudotsuga glaucoides Axelr.: *Abies rigida* Knowlt., ?*Pinus crossii* Knowlt., *P.* spp. indet., Pinaceae gen. indet., indet. plant.
Tsuga petranensis Axelr.: *Pinus* spp. indet., Pinaceae gen. indet.
Juniperus creedensis Axelr.: *J. creedensis* Axelr.
J. gracillensis Axelr.: *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe.
Cyperacites creedensis Axelr.: *Monocotylophyllum* sp.
Populus cedrusensis Wolfe: *P. larsenii* (Knowlt.) Schorn & Wolfe.
P. creedensis Axelr.: *P. larsenii* (Knowlt.) Schorn & Wolfe.
P. pliotremuloides Axelr.: *P. larsenii* (Knowlt.) Schorn & Wolfe.
Salix creedensis Axelr.: *Eleiosina praeconcinna* (Cocker.) Schorn & Wolfe.
S. venosiuscula H. V. Sm.: *S.* sp.
Betula smithiana (Axelr.) Axelr.: *Populus larsenii* (Knowlt.) Schorn & Wolfe.
Quercus creedensis Axelr.: Magnoliatae indet. (possibly Leguminosae gen. indet.).

Nuphar coloradensis Axelr.: *Catalpa coloradensis* (Axelr.) Schorn & Wolfe.
Ranunculus creedensis Axelr.: *Potentilla creedensis* (Axelr.) Schorn & Wolfe.
Berberis coloradensis Axelr.: *B. coloradensis* Axelr.
B. riogrande Axelr.: *B. coloradensis* Axelr.
Mahonia creedensis Axelr.: *M. aceroides* (Knowlt.) Schorn & Wolfe.
M. obliqua MacG.: *M. aceroides* (Knowlt.) Schorn & Wolfe.
Ribes birdseyii Axelr.: *R. lacustroides* Axelr.
R. creedensis Axelr.: *R. lacustroides* Axelr.
R. dissecta Axelr.: *R. lacustroides* Axelr.
R. lacustroides Axelr.: *R. lacustroides* Axelr.
R. riogrande Axelr.: *R. lacustroides* Axelr.
R. stevenii Axelr.: *R. lacustroides* Axelr.
R. wasonii Axelr.: *R. lacustroides* Axelr.
R. webbii Wolfe.: *R. lacustroides* Axelr.
Fendlera coloradensis Axelr.: *Berberis coloradensis* Axelr.
Jamesia caplanii Axelr.: *J. caplanii* Axelr.
Philadelphus creedensis Axelr.: *Berberis coloradensis* Axelr.
Cercocarpus holmesii (Lesq.) Axelr.: *Eleiosina praeconcinna* (Cocker.) Schorn & Wolfe, *C. henricksonii* Schorn & Wolfe.
C. linearifolius (Lesq.) Axelr.: *C. nanophyllus* Schorn & Wolfe.
Chamaebatiaria creedensis R.W. Br.: *Stockeya creedensis* (R.W. Br.) Wolfe & Wehr.
Crataegus creedensis Axelr.: *C. creedensis* Axelr.
Fallugia lipmanii Axelr.: *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe.
Holodiscus harneyensis (Arn.) Axelr.: *Ribes obovatum* Schorn & Wolfe, *Holodiscus stevenii* Schorn & Wolfe.
H. idahoensis Chan. & Axelr. [nom. nud.]: *H. stevenii* Schorn & Wolfe.
Peraphyllum septentrionalis (Lesq.) Axelr.: *Eleiosina praeconcinna* (Cocker.) Schorn & Wolfe.
Physocarpus petiolaris Axelr.: *Ribes robinsonii* Schorn & Wolfe.
P. triloba Axelr.: *Ribes robinsonii* Schorn & Wolfe.
Prunus chaneyii Cond.: *P.* sp.
P. creedensis Axelr.: *P. creedensis* Axelr.
Rosa hilliae Lesq.: *Holodiscus stevenii* Schorn & Wolfe.
Rubus riogrande Axelr.: *Ribes lacustroides* Axelr.
Sorbus potentilloides (Knowlt.) Axelr.: *S. potentilloides* (Knowlt.) Axelr.
Cercis buchananensis Cond.: *C.* sp.
Robinia californica Axelr.: Leguminosae gen. indet.
Acer riogrande Axelr.: *Ribes lacustroides* Axelr.
Sapindus coloradensis Cocker.: Magnoliatae gen. indet. (possibly Leguminosae gen. indet.).
Hippurus coloradensis Axelr.: indet. plant (possibly *Equisetum*).
Condalia mohavensis Axelr.: Magnoliatae gen. indet. (possibly *Populus larsenii* [Knowlt.] Schorn & Wolfe.
Zizyphus florissantii (Lesq.) MacG.: Magnoliatae gen. indet. (possibly *Berberis coloradensis* Axelr.).
Shepherdia creedensis Axelr.: Magnoliatae gen. indet. (possibly *Populus larsenii* (Knowlt.) Schorn & Wolfe).
Arbutus stewartii Axelr.: *Osmaronia? stewartiae* (Axelr.) Schorn and Wolfe, Magnoliatae gen. indet. (possibly *Populus larsenii* [Knowlt.] Schorn & Wolfe).
Vaccinium creedensis Axelr.: *Berberis coloradensis*, Magnoliatae gen. indet.
Fraxinus creedensis Axelr.: Magnoliatae gen. indet.
Symphoricarpos wassukana Axelr.: Leguminosae gen. indet.
Chilopsis coloradensis Axelr.: Magnoliatae gen. indet. (possibly *Eleiosina praeconcinna* [Cocker.] Schorn & Wolfe).
Sambucus longifolius Axelr.: *Prunus creedensis* Axelr.

DESCRIPTION AND DISCUSSION OF A NEOGENE SPRUCE

Family PINACEAE
Genus PICEA Dietrich

Picea lahontensis MacGinitie

Picea lahontense MacGinitie, 1933 (part, typic) p. 46, pl. 3, figs. 6, 8 only.
Pseudotsuga masoni MacGinitie, 1933, p. 47, pl. 3, figs. 1–3. Oliver, 1934, p. 14. Dorf, 1938, p. 107, pl. 1, fig. 3.
Pinus harneyana Chaney and Axelrod, 1959 (part, typic), p. 141, pl. 13, figs. 1, 2. Axelrod, 1964 (part), p. 108, pl. 6, figs. 20–22.
Picea magna auct. non MacGinitie. Axelrod, 1956, p. 275, pl. 4, figs. 7–12; pl. 25, figs. 8, 9. Chaney and Axelrod, 1959, p. 140, pl. 12, figs. 10–15. Axelrod, 1964, p. 108, pl. 6, figs. 9–13. Wolfe, 1964, p. 15, pl. 1, figs. 3, 5; pl. 6, figs. 7, 12, 17, 18, 22. Graham, 1965, p. 58, pl. 3, figs. 9, 10.
Pseudotsuga sonomensis auct. non Dorf. Axelrod, 1956 (part), p. 277, pl. 4, fig. 21.
Picea breweriana auct. non S. Watson. Wolfe, 1964 (part), p. 14, pl. 6, figs. 4, 5, 8, 9.
Pinus alvordensis auct. non Axelrod, 1944. Axelrod, 1985, p. 114, pl. 17, figs. 15–19.
Conifer of unknown affinities. Chaney and Axelrod, 1959, p. 144, pl. 14, fig. 9.

Emended description.—Ovulate cone incomplete (small part of apex missing); shape lanceolate, slightly asymmetrical, base obtuse; 11.8 cm long, 3.5 cm wide; stalk 0.2 cm long; cone scales as wide as 1.5 cm, 0.9 cm high, width to height ratio about 1.6:1, apex rounded and with a small notch, margin smooth to incipiently crenulate, weak vertical ribbing, scales appearing woody, no exposed bract scale. Winged seed has cellular pattern parallel with long axis of wing; wing 1.2–1.4 cm long, 0.7–1.0 cm wide, wing-length to wing-width ratio 1.6:1; seed surface convex, indentation at proximal end on admedial edge, proximal end truncate, 0.7 cm long, 0.4–0.5 cm wide, seed-length to seed-width ratio 1.5:1; length of seed and wing 1.8–2.1 cm, wing-length to seed-length ratio 2:1. Foliated axis more than 3.8 cm long, 0.4 cm wide in apical part, furnished with pulvinae about 0.2 cm long that are directed about 70° from vertical plane of main axis; leaf scar shape on adaxial surface rounded and on abaxial surface triangular; leaves at least 3.2 cm long, 0.2 cm wide, base tapers slightly at base, distinct keel on abaxial side.

Discussion.—When MacGinitie (1933) described *Picea lahontensis* (as *P. lahontense*), only one other fossil specimen from conterminous United States had been referred to the genus. Considerable confusion now exists regarding the circumscription of MacGinitie's species, which is related to the Creede spruce.

The holotype of *Picea lahontensis* (MacGinitie, 1933, pl. 3, fig. 8) is a partially foliated axis that has four attached leaves. The figure was retouched and shows the lower righthand leaf as complete. Further preparation shows, however, that the apex of this leaf is missing (as are the apices of the other leaves); however, tapering at the point of the break indicates that the leaf is almost complete. Additional material from the Trout Creek locality and deposited in UCMP has complete leaves, which are, as leaves of the holotype, broad for *Picea* (about 1 mm). The epithet *lahontensis*, which is well entrenched in the literature, can thus be retained by basing an emended description on topotypic material that includes complete leaves, cones, and winged seeds that were originally referred to *Pseudotsuga masoni*.

Three morphotypes of foliated axes of *Picea* occur in the Neogene of western North America: one morphotype is represented by the specimen from a Mascall flora locality originally assigned to *Abies chaneyi* Mason (Mason, 1927) and later transferred by Axelrod (1976) to *Cephalotaxus bonseri* (Knowlt.) Chan. & Axelr.; a second morphotype is represented by the Tipton specimen that was first referred to *A. chaneyi* by Brown (1937; pl. 45, fig. 24) and later transferred by him (Brown, 1940) to *A. concoloroides* R.W. Br.; and a third morphotype is represented by *P. lahontensis*, which occurs at Tipton as well as Trout Creek. All three morphotypes have the pulvinae (peglike structures on the axis) and leaves that are unconstricted or only slightly constricted and thus do not form a petiole; this leaf base is, in Pinaceae, restricted to *Picea* leaves.

The defoliated axis from Tipton that Mason (1927, pl. 3, fig. 2) assigned to *Picea* sp. (Chaney and Axelrod, 1959, reassigned the specimen to *P. sonomensis* Axelr.) is *Abies*. Structures that appear to be the pulvinae characteristic of *Picea* are the persistent bud scales of the male cones characteristic of *Abies* and *Keteleeria*, as are the circular leaf scars of the fossil. Whereas *Keteleeria* typically has two or three male cones per bud, the fossil and extant *Abies* have one male cone per bud.

In the absence of organic connection, the assignment of the large cone (MacGinitie, 1933, pl. 3, fig. 6) to *Picea lahontensis* is uncertain. This *Picea* cone and the *P. lahontensis* foliage are, however, the only morphotypes of their respective organs of *Picea* found at Trout Creek, and both also occur at Tipton (the second morphotype of *Picea* foliage also occurs at Tipton). We tentatively consider the large cone to belong to *P. lahontensis*. The large *Picea* winged seeds that formed the basis for *Pseudotsuga masoni* MacG. (MacGinitie, 1933) would readily be accommodated on the large cone scales of this cone type, and similar large cones occur in association with large winged seeds at both Tipton and Hidden Lake.

The winged seed (MacGinitie, pl. 3, fig. 4) originally included as a paratype of *Picea lahontensis* apparently has a seed that is not fully developed; of the 75 winged seeds of *Picea* known from Trout Creek, all except this single specimen have large seeds such as the specimens assigned to *Pseudotsuga masoni*. This single specimen is similar to seeds borne on basal or apical cone scales, where typically an ovule is absent and only the wing develops or an ovule aborts early in development; as in aborted extant seeds, the Trout Creek specimen represents a flattened, linear seed that is flanked on either side by wing tissue that is as wide as the seed. Most winged seeds referred to *Picea lahontensis* by subsequent authors represent broken or similarly aborted specimens. Winged seeds of *Picea sonomensis* Axelr. consistently differ in having a seed outline that is elongated (length: width >2:1) versus a seed outline that is wide (length: width <2:1) in winged seeds of *P. lahontensis*.

Affinities of *Picea lahontensis* to extant species are uncertain. MacGinitie (1933) considered *P. lahontensis* to be similar to *P. engelmannii* Parry ex Engelm., but this comparison was partly based on the atypically small winged seed. Axelrod (1985) considered *P. lahontensis* to be related to some Asian spruces, for example, *P. polita* (Sieb. & Zucc.) Carr.; these spruces have angular four-sided leaves and thus are very dissimilar. The broad, flattened leaves that have a keel only on the abaxial side of *P. lahontensis* suggest that the fossil is an extinct member of section *Omarika*.

The foliated axis of the conifer of unknown affinities (Chaney and Axelrod, 1959) from the Tipton flora has the stout pulvinae characteristic of *Picea*. The width of the leaves relative to their length is similar to *P. lahontensis*. The supposed cone of the Tipton specimen has features indicative of a spruce gall (H.I. Scudder, oral commun., 1982), such as formed on extant species of *Picea* by the spruce gall aphid *Chermes* (=*Adelges*). A similar gall was thought to represent an aroid spadix (MacGinitie, pl. 7, fig. 4), and an unfigured specimen is present in collections of the Stinking Water flora (UCMP loc. P4120).

Holotype.—UCMP 550.
Paratypes.—UCMP 551, 552.
Hypotypes.—UCMP 553, 554.

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PLATES 1–13

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PLATE 1

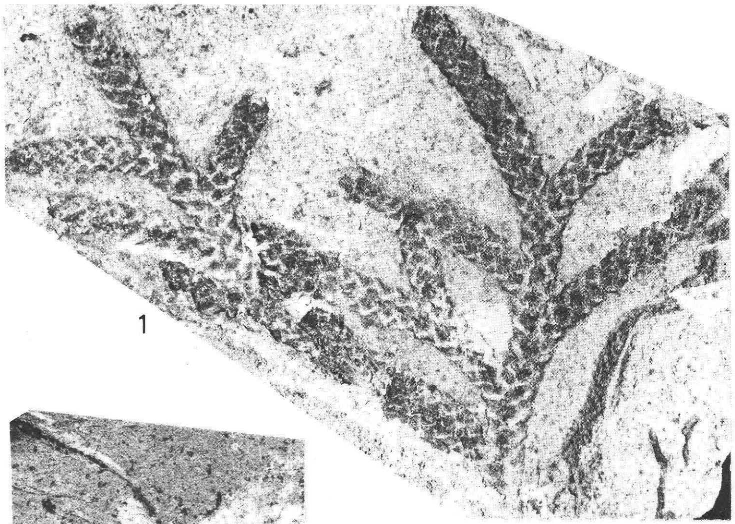
[All figures enlarged]

FIGURE 1, 2. *Juniperus creedensis* Axelr. (p. 4).
- 1. Paratype UCMP 7452, ×2.5.
- 2. Paratype UCMP 7460, ×3.5.

3–10. *Abies rigida* Knowlt. (p. 9).
- 3. Hypotype UCMP 7258, × 2.5.
- 4. Hypotype UCMP 7280, × 2.5.
- 5. Hypotype UCMP 7279, × 2.5.
- 6. Homeotype UCMP 7260, × 2.5.
- 7. Hypotype UCMP 7251, × 2.5.
- 8. Hypotype UCMP 7410 (homeotype of *Pseudotsuga glaucoides* Axelr.), × 3.5 (note circular leaf scars at top).
- 9. Hypotype UCMP 7275, ×9 (lined area is pterostegium).
- 10. Homeotype UCMP 7267, × 3.5.

11, 12. *Pinus sanjuanensis* Axelr. (p. 11).
- 11. Paratype UCMP 7239, × 2.
- 12. Paratype UCMP 7242, × 2.

13, 14. *Pinus* spp., atypical winged seeds (p. 15).
- 13. Specimen UCMP 7229 (homeotype of *P. alvordensis* Axelr.), × 2.
- 14. Specimen UCMP 7230 (homeotype of *P. alvordensis* Axelr.), × 2.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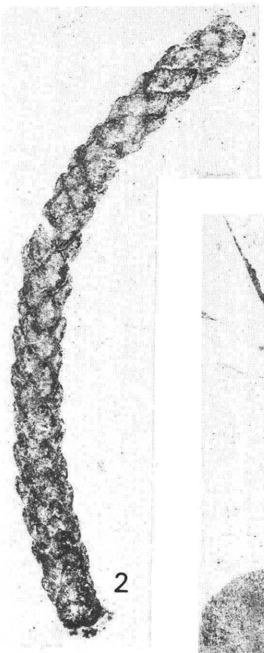
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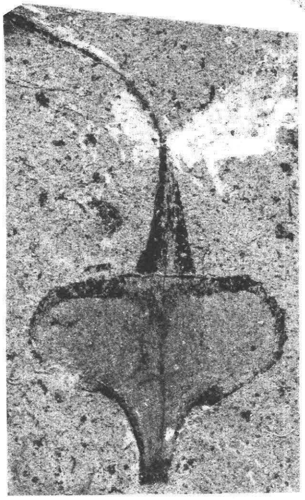
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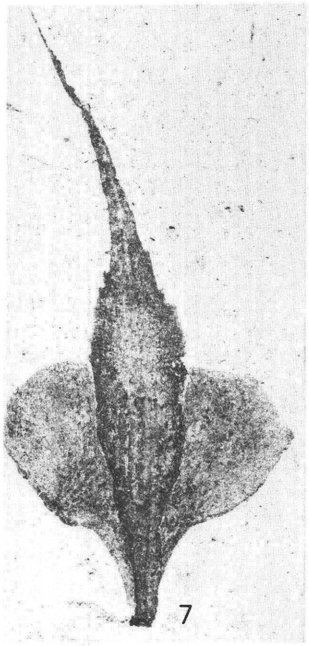
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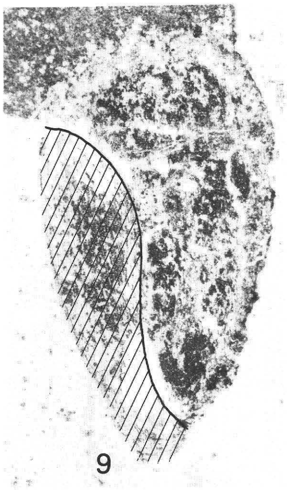
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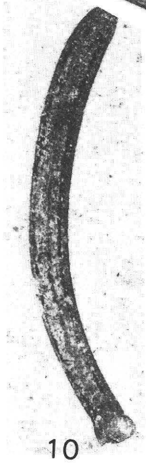
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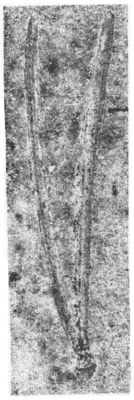
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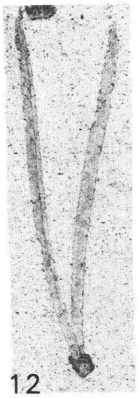
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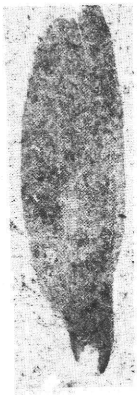
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JUNIPERUS, *ABIES* AND *PINUS*

PLATE 2

[All figures natural size unless otherwise indicated]

FIGURES 1–9. Pinaceae, ovulate cones (p. 5).

Arbitrary abrasion stages of ovulate cones of Pinaceae from least abrasion (stage 1) to high abrasion (stage 6).

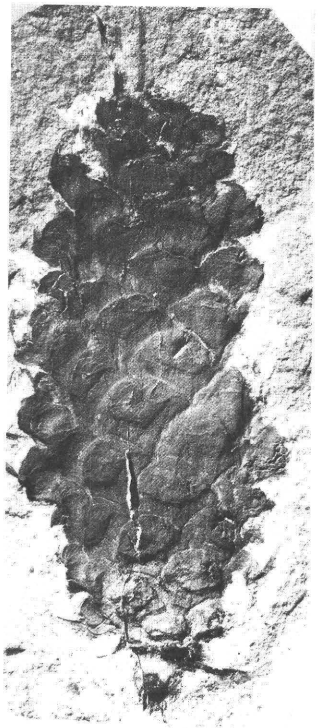
1. Stage 1, *Pinus crossii* Knowlt., hypotype UCMP 7354 (p. 12).
2. Stage 2, *P. crossii* Knowlt., hypotype UCMP 7216 (hypotype of P. florissantii Lesq.) (p. 12).
3. Stage 3, *Pinus* cf. *P. crossii* Knowlt., specimen UCMP 7316 (hypotype of *Picea lahontensis* MacG.) (p. 14).
4. Stage 4, *P.* cf. *P. crossii* Knowlt., specimen UCMP 7353 (paratype of *P. ponderosoides* Axelr.) (p. 15).
5. Stage 5, Pinaceae, gen. indet., specimen UCMP 7287 (holotype of *Picea coloradensis* Axelr.) (p. 15).
6. Stage 6, Pinaceae gen. indet., specimen UCMP 7290 (paratype of *Picea coloradensis* Axelr.) (p. 15).
7. Stage 6, Pinaceae gen. indet., specimen UCMP 7418 (hypotype of *Pseudotsuga glaucoides* Axelr.) (p. 15).
8. Stage 4+, Pinaceae gen. indet., specimen UCMP 7419B (hypotype of *Pseudotsuga glaucoides* Axelr.), ×2 (p. 15).
9. Stage 4+, Pinaceae gen. indet., specimen UCMP 7442 (paratype of *Tsuga petranensis* Axelr.), ×2 (p. 15).

10. *Pinus* sp., atypical winged seed (p. 15).

Atypical winged seed possibly belonging to *P. crossii* Knowlt., specimen UCMP 7299 (paratype of *Picea coloradensis* Axelr.), ×2.

11. *Pinus aristata* Engelm.

Atypical winged seed, × 2. Introduced for comparison with preceding figure.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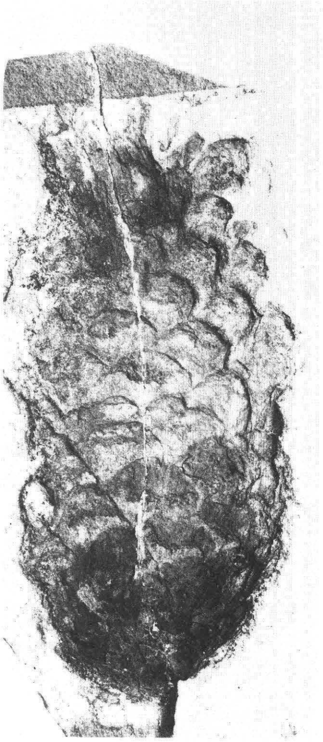
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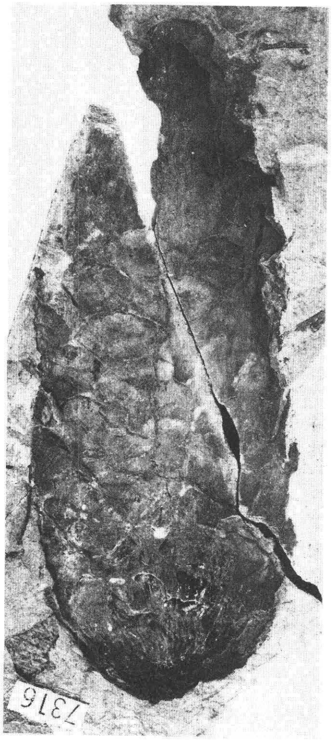

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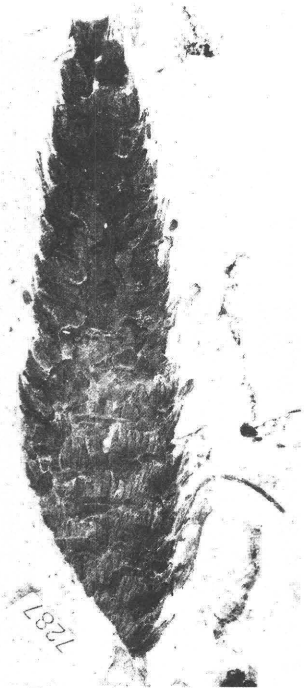

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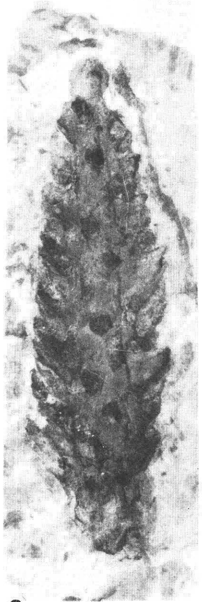
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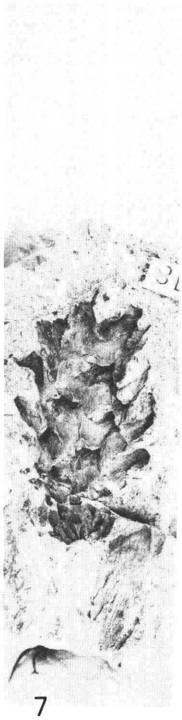

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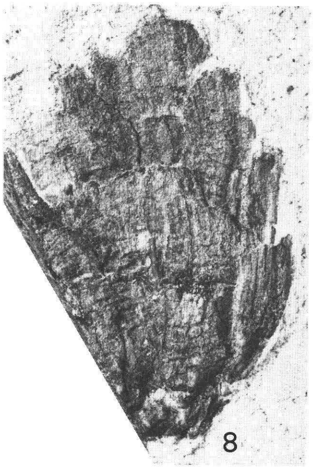
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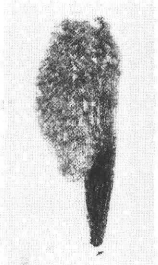
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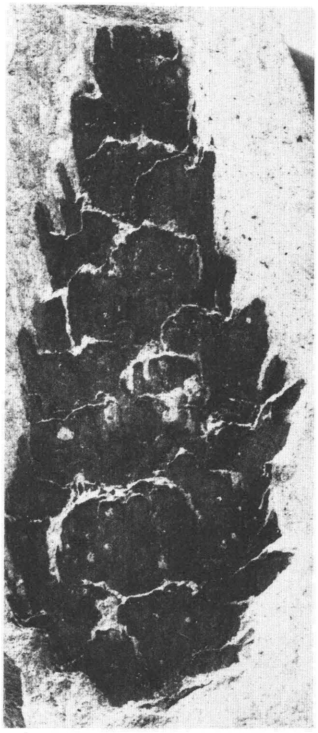
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PINUS AND PINACEAE

PLATE 3

[All figures natural size unless otherwise indicated]

FIGURES 1–3. *Pinus remorata* Mason.

1. Ovulate cone preserved in longitudinal section.
2. Exterior of ovulate cone preserved in three dimensions and with 10 attached cone scales.
3. Same cone as in figure 2 but parts of cone scales removed, which represents abrasion stage 4+. Potrero Canyon, California. Introduced for comparison.

4. *Pinus (Pinus)* sp.

Ovulate cone; basal two-thirds of cone represents abrasion stages 4+ and 5, and cleaned apical one-third of cone represents abrasion stage 1, showing typical apophyses, umbos, and mucros. Miocene, Turkey. Introduced for comparison.

5. *Pinus aristata* Engelm.

Winged seeds taken from a single cone. Introduced for comparison.

5a–f. Winged seeds atypical in development of seed and shape of wing.
5g–5i. Winged seeds typical in development of seed and shape of wing.

6. *Picea sp.* (p. 11).

Specimen UCMP 7373, ×2.5.

7–13. *Pinus crossii* Knowlt. (p. 12).

7. Winged seed, hypotype UCMP 7334, ×2.5.
8, 9a. Staminate cone probably belonging to *P. crossii,* hypotype UCMP 9337b, ×2.5.
9b. Winged seed, hypotype UCMP 9337a, ×2.5.
10. Fascicle, hypotype UCMP 7221 (homeotype of *P. florissantii* Lesq.), × 2.5.
11. Winged seed, hypotype UCMP 7220 (holotype of *P. wasonii* Axelr.), × 2.5.
12. Fascicle, hypotype UCMP 7174 (hypotype of *P. alvordensis* Axelr.), × 2.5.
13. Fascicle, hypotype UCMP 7361, ×2.5.


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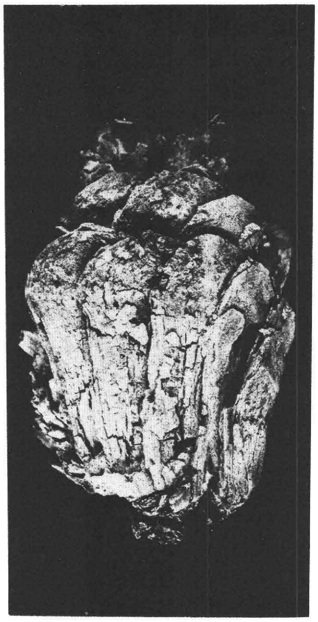
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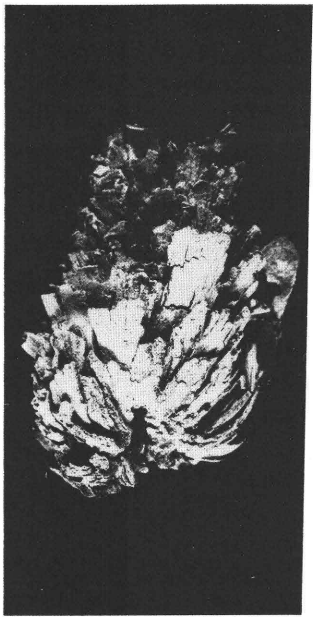
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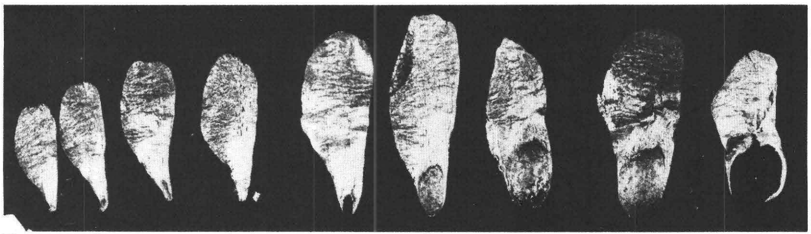

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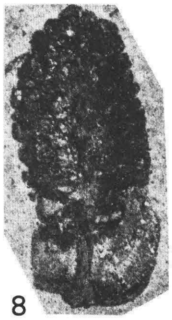
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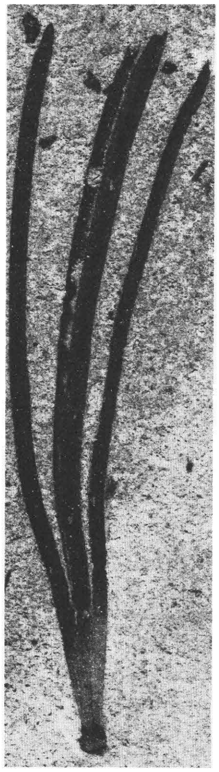
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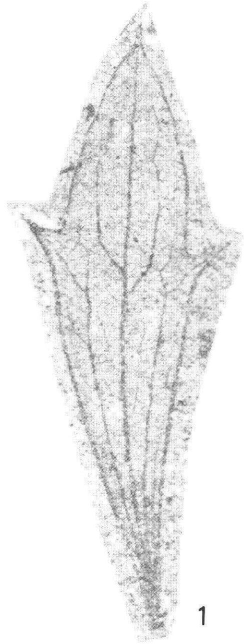
PINUS AND *PICEA*

PLATE 4

[All figures × 4 unless otherwise indicated]

FIGURES 1–7, 9. *Berberis coloradensis* Axelr. (p. 15).
  1. Holotype UCMP 7527.
  2. Hypotype UCMP 7532 (paratype of *B. riogrande* Axelr.).
  3. Hypotype UCMP 7530 (holotype of *B. riogrande* Axelr.).
  4. Hypotype UCMP 7745 (paratype of *Fendlera coloradensis* Axelr.).
  5. Hypotype UCMP 7747 (paratype of *F. coloradensis* Axelr.).
  6. Hypotype UCMP 7665 (paratype of *Philadelphus creedensis* Axelr.).
  7. Hypotype UCMP 7656 (paratype of *P. creedensis* Axelr.).
  9. Hypotype UCMP 7849 (holotype of *Vaccinium creedensis* Axelr.).

8, 10, 11. *Mahonia aceroides* (Knowlt.) Schorn & Wolfe (p. 17).
  8a, 10a. Holotype USNM 36537 (holotype of *Sterculia aceroides* Knowlt.).
  8b, 10b. Hypotype USNM 36531. Fig. 8b, × 1.
  11. Hypotype UCMG 19749, × 1.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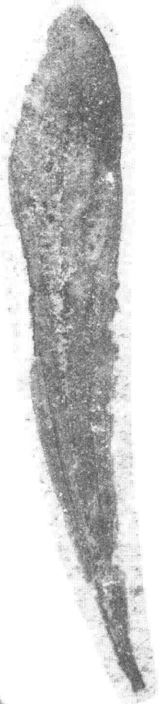
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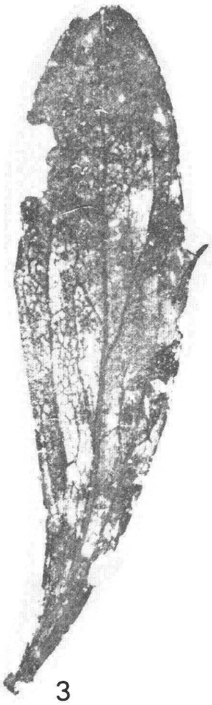
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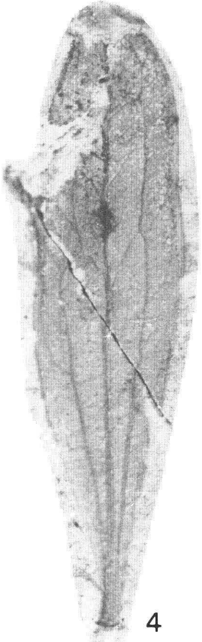
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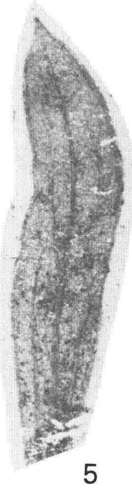
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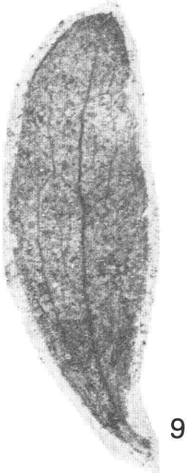
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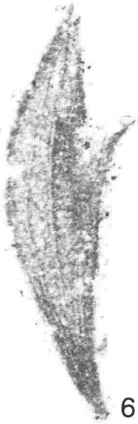
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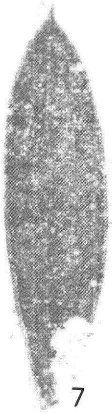
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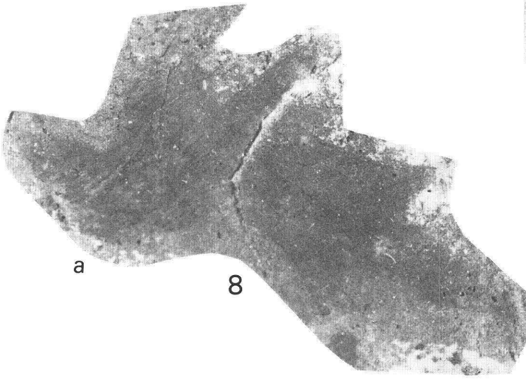

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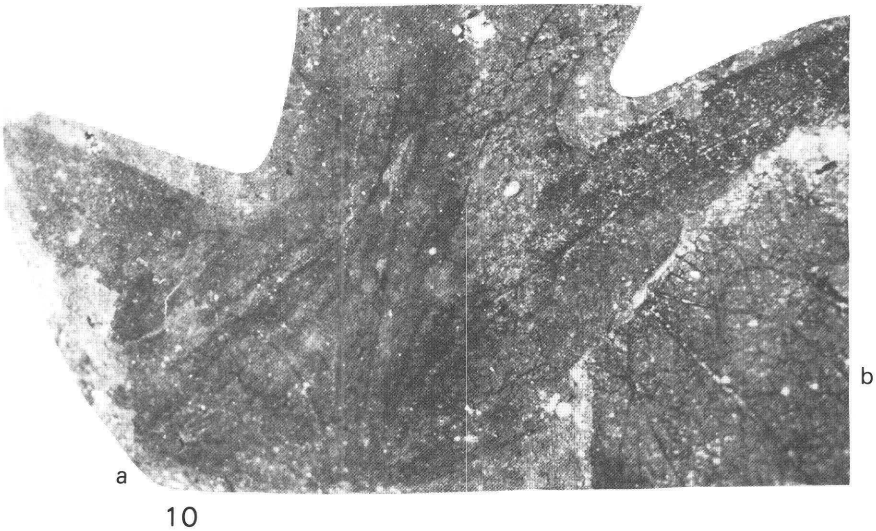

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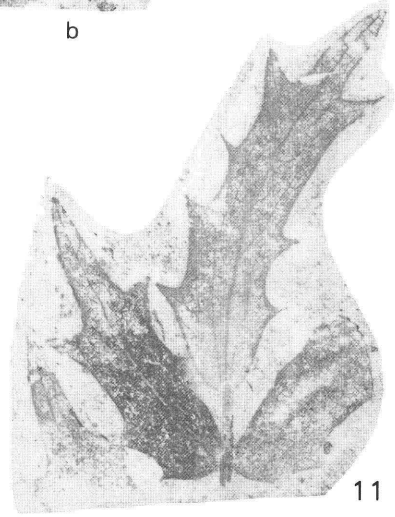
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BERBERIS AND *MAHONIA*

PLATE 5

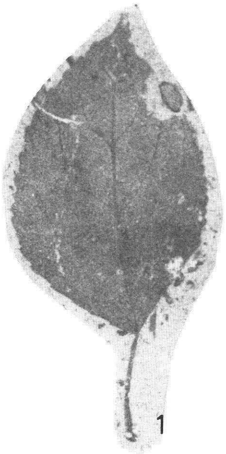
[All figure × 1.3 unless otherwise indicated]

FIGURES 1, 2, 5. *Populus larsenii* (Knowlt.) Schorn & Wolfe (p. 18).
  1. Hypotype UCMG 34060, ×1.
  2. Holotype USNM 36519 (holotype of *Alnus? larseni* Knowlt.).
  5. Hypotypes UCMG 34061.

3, 4. *Jamesia capalanii* Axelr. (p. 19).
  Hypotypes UCMG 34062, 340630.

6, 7, 10, 11. *Ribes lacustroides* Axelr. (p. 20).
  6. Hypotype UCMG 27391 (holotype of *R. creedensis* Axelr.)
  7. Hypotype UCMG 34065.
  10. Hypotype UCMG 34066.

8, 9. *Ribes robinsonii* Schorn & Wolfe (p. 22).
  8. Holotype UCMP 7817 (holotype of *Physocarpus petiolaris* Axelr.).
  9. Hypotype UCMG 34064.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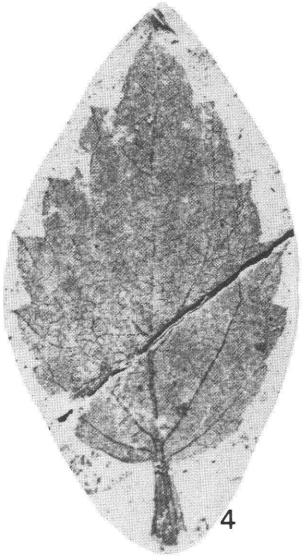
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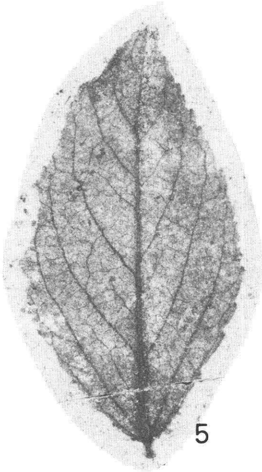
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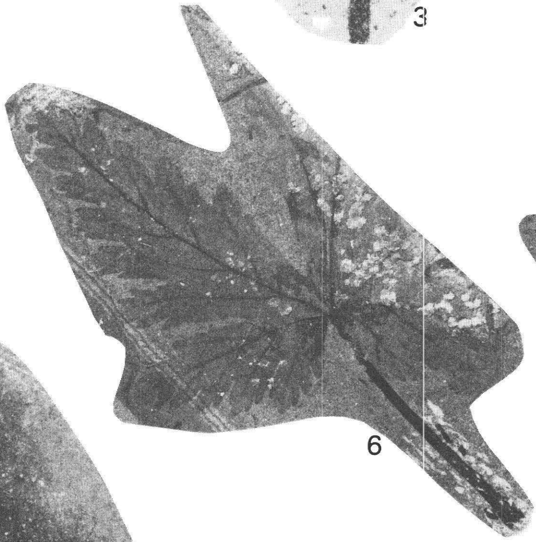
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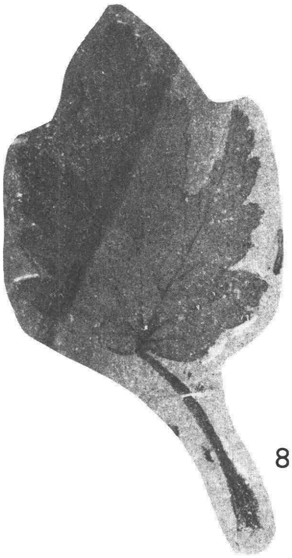
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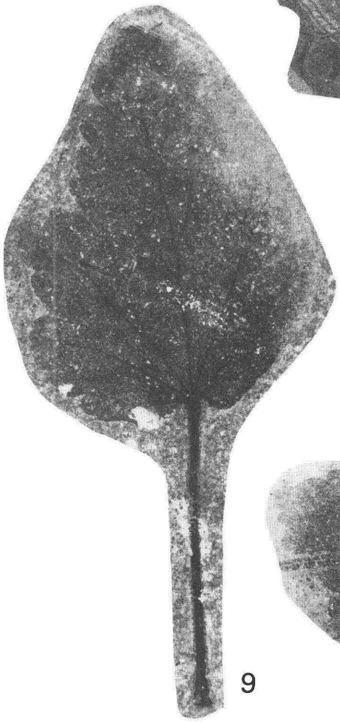
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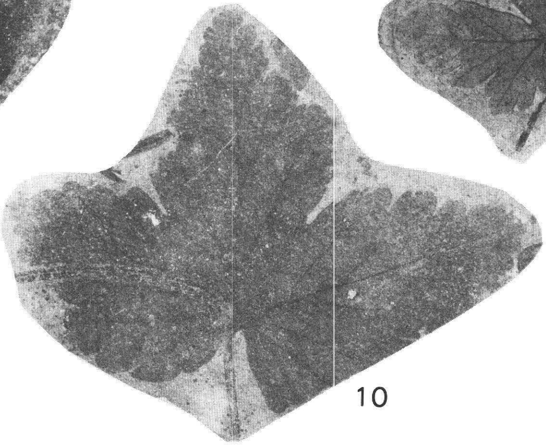
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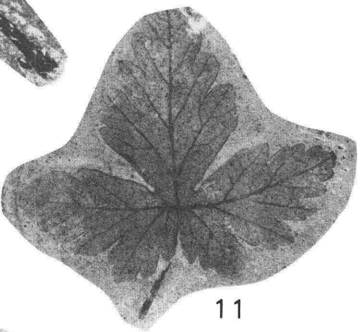

11

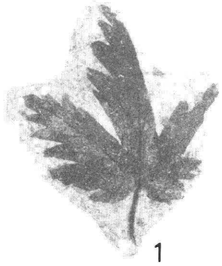
POPULUS, *JAMESIA*, AND *RIBES*

PLATE 6

[All figures × 1.3]

Figures 1–17. *Ribes lacustroides* Axelr. (p. 20).

1. Hypotype UCMP 7581 (holotype of *R. dissecta* Axelr.).
2. Holotype UCMP 7594.
3. Paratype UCMP 7600.
4. Paratype UCMP 7594.
5. Hypotype UCMP 7626 (hypotype of *R. stevenii* Axelr.).
6. Hypotype UCMP 7629 (homeotype of *R. stevenii* Axelr.).
7. Hypotype UCMP 7603 (hypotype of *R. stevenii* Axelr.).
8. Hypotype UCMP 7614 (hypotype of *R. stevenii* Axelr.).
9. Hypotype UCMP 7602 (hypotype of *R. stevenii* Axelr.).
10. Hypotype UCMP 7624 (homeotype of *R. riogrande* Axelr.).
11. Paratype UCMP 7609.
12. Hypotype UCMP 7837 (paratype of *R. birdseyii* Axelr.).
13. Hypotype UCMP 7608 (homeotype of *R. riogrande* Axelr.).
14. Hypotype UCMP 7625 (hypotype of *R. riogrande* Axelr.).
15. Hypotype UCMP 7616 (homeotype of *R. birdseyii* Axelr.).
16. Hypotype UCMP 7608 (homeotype of *R. riogrande* Axelr.).
17. Hypotype UCMP 7632 (hypotype of *R. webbii* Wolfe).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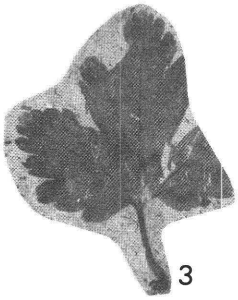
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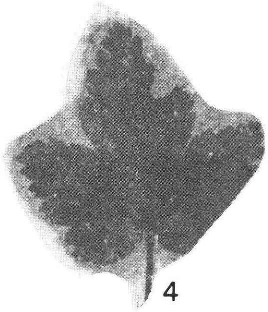
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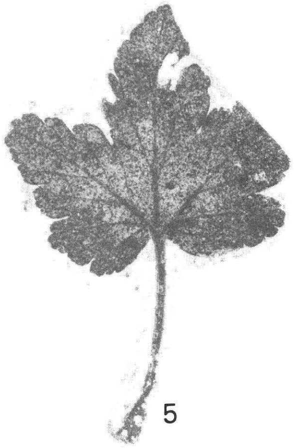
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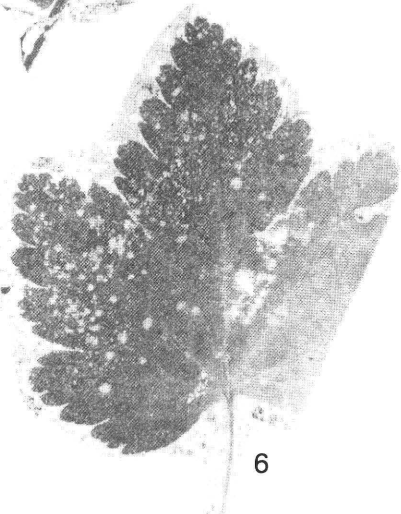
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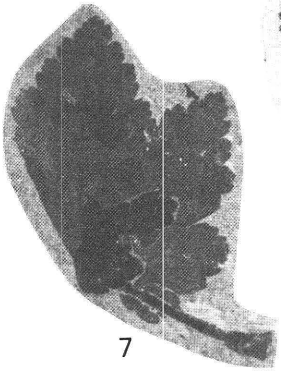
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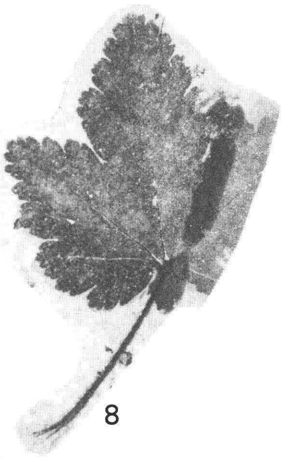
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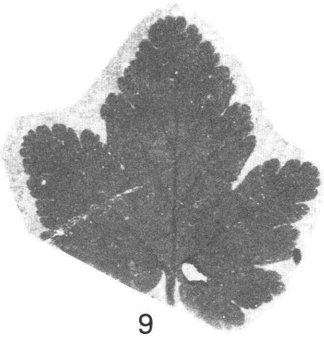
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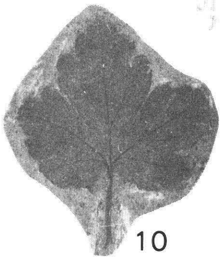
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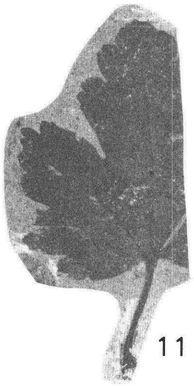
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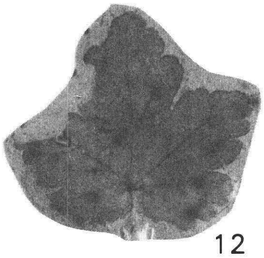
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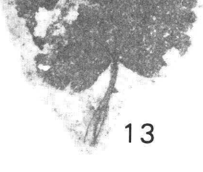
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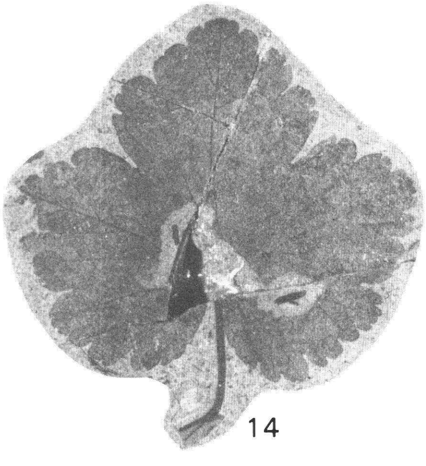
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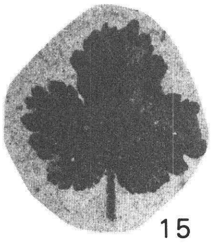
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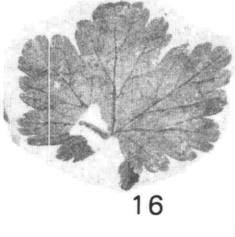
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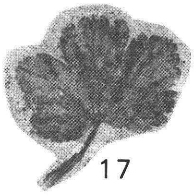

17

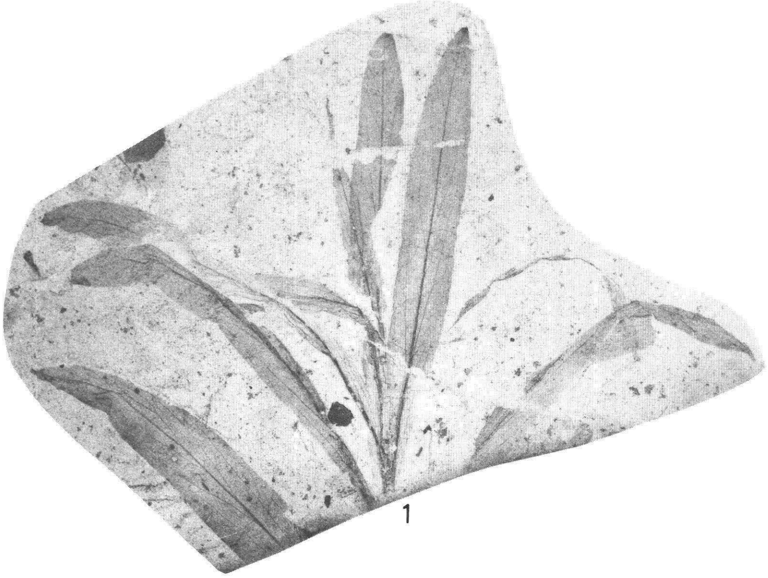
RIBES

PLATE 7

[All figures ×4 unless otherwise indicated]

FIGURES 1–5. *Eleiosina praeconcinna* (Cocker.) Schorn & Wolfe (p. 23).
- 1. Holotype UCMG 18536 (holotype of *Solidago praeconcinna* Cocker.), × 1.
- 2. Hypotype UCMP 7389 (hypotype of *Peraphyllum septentrionale* [Lesq.] Axelr.).
- 3. Hypotype UCMP 7505 (paratype of *Salix creedensis* Axelr.).
- 4, 5. Hypotype UCMG 27387A, B (holotype of *S. creedensis* Axelr.).

6. *Eleiosina laevigata* (L.) Rafin. Extant, *Rock 23760*, Yunnan Prov., China. Introduced for comparison.
7. *Peraphyllum ramosissimum* Nutt. Extant, *Gentry 143*, Nevada, U.S.A. Introduced for comparison.
8. *Daphne septentrionale* (Lesq.) MacG.
   Hypotype UCMP 3876, Florissant flora. Introduced for comparison.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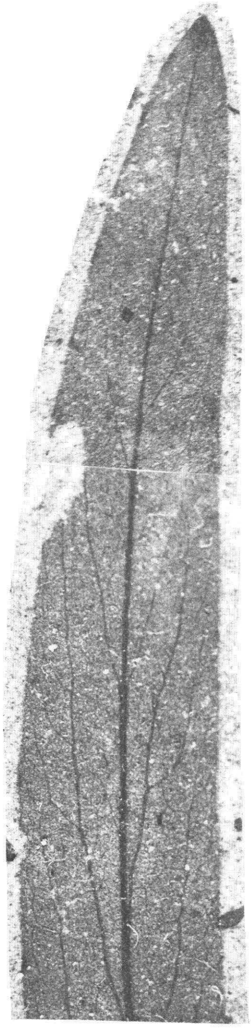
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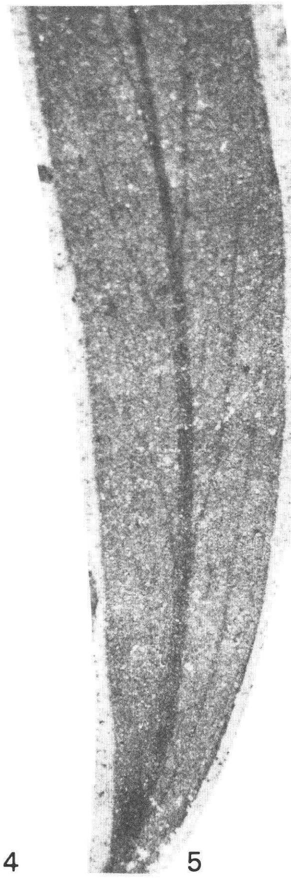
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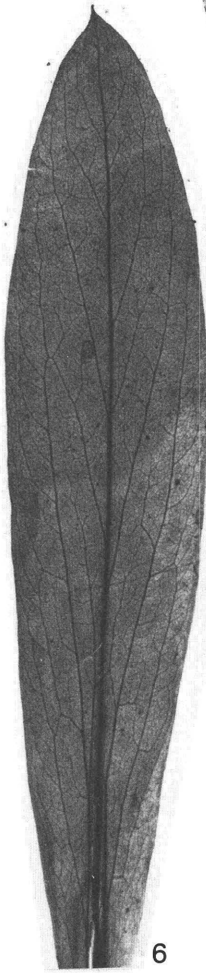
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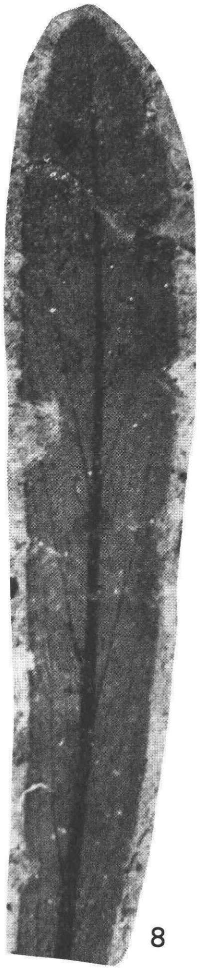
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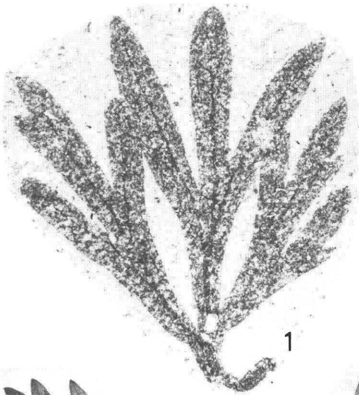
ELEIOSINA

PLATE 8

[All figures × 4 unless otherwise indicated]

FIGURES 1, 3, 5, 8, 9. *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe (p. 24).
1, 3. Hypotype UCMG 34068. Fig. 3, × 1.
5, 8. Hypotype UCMG 19786, Fig. 5, ×1.
9. Hypotype UCMG 34069.
2. *Luetkea pectinata* (Pursh) Kuntze.
Extant, *Thompson 5295,* Washington, U.S.A. Introduced for comparison.
4. *Sanguisorba occidentalis* Nutt.
Extant, *Ferris and Duthie 1254,* Washington, U.S.A. Introduced for comparison.
6. *Geum ciliatum* Pursh.
Extant, *Hitchcock 17993,* Montana, U.S.A. Introduced for comparison.
7. *Fallugia paradoxa* (D. Don) Endl.
Extant, *Fosberg S3434,* New Mexico, U.S.A. Introduced for comparison.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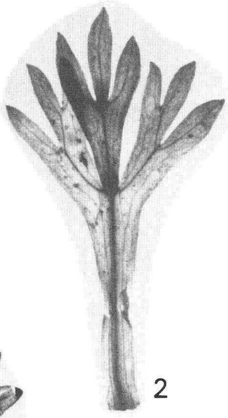
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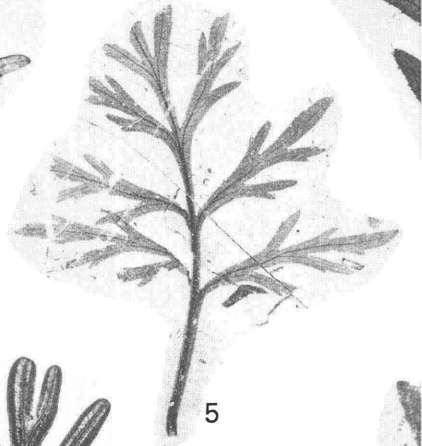
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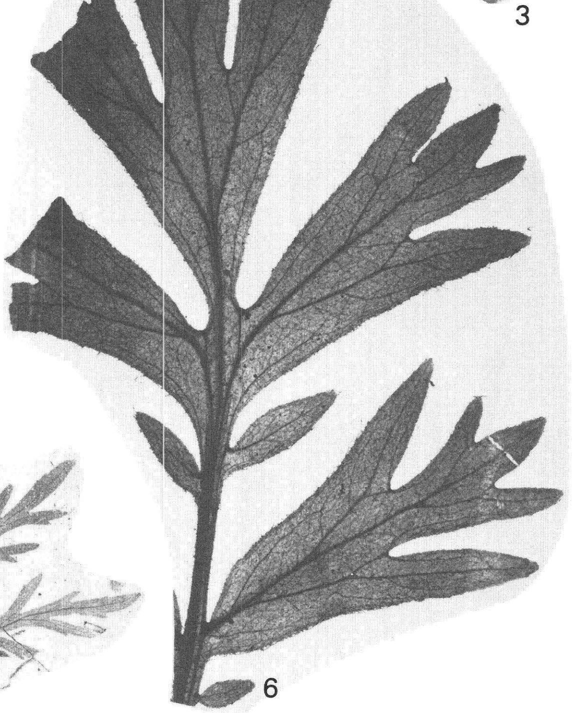
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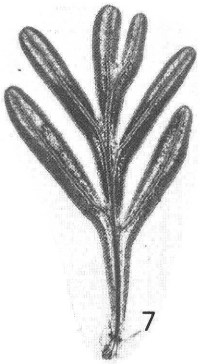
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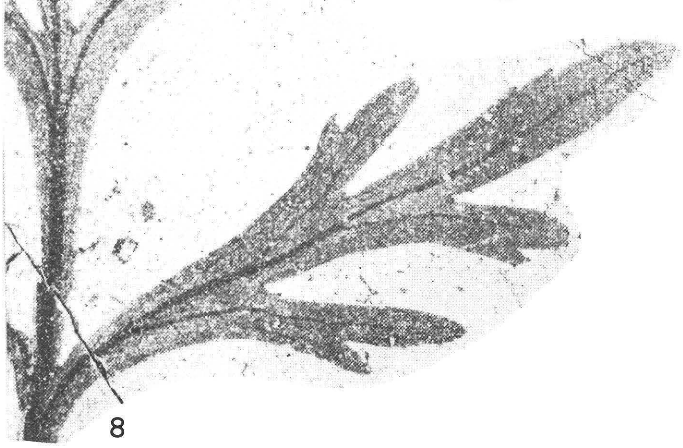
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9

ELEOPOLDIA

PLATE 9

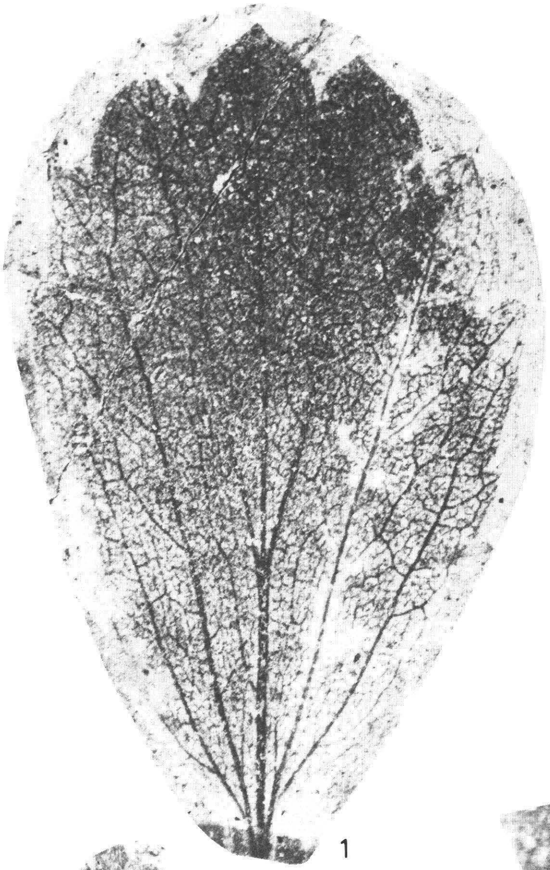
[All figures × 4 unless otherwise indicated]

FIGURES 1, 2. *Ribes obovatum* Schorn & Wolfe (p. 22).
  1. Holotype UCMP 7788 (homeotype of *Holodiscus harneyensis* Chan. & Axelr.).
  2. Paratype UCMG 34067, ×1.3.

3, 4, 7, 8. *Holodiscus stevenii* Schorn & Wolfe (p. 25).
  3. Paratype UCMG 34071.
  4. Holotype UCMG 34070.
  7. Paratype UCMG 34072.
  8. Paratype UCMP7821 (hypotype of *Rosa hilliae* Lesq.).

5. *Sorbus potentilloides* (Knowlt.) Axelr. (p. 27).
  Hypotype UCMG 19773.

6. *Crataegus creedensis* Axelr. (p. 27).
  Holotype UCMP 7259B.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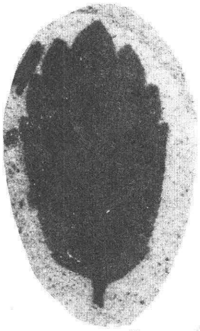
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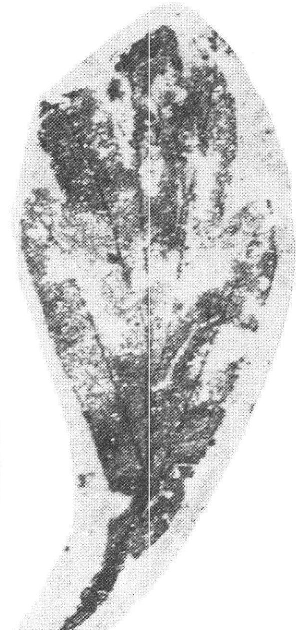
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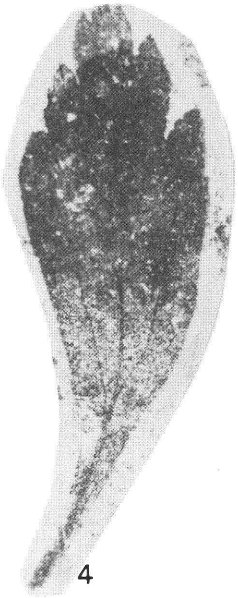
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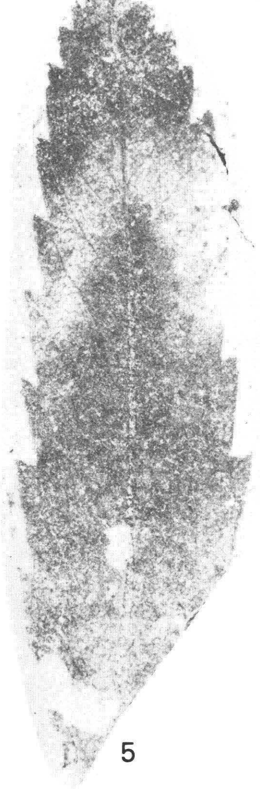
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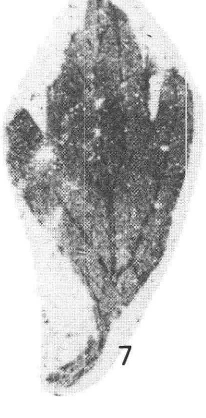
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RIBES, *HOLODISCUS*, *SORBUS*, AND *CRATAEGUS*

PLATE 10

[All figures × 4 unless otherwise indicated]

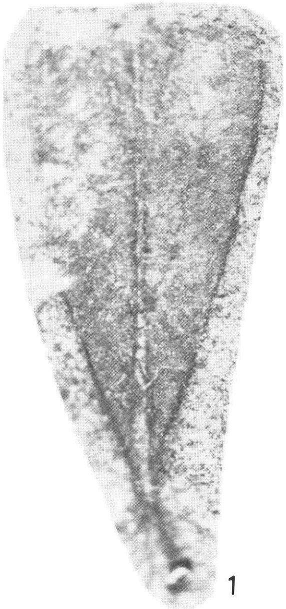
FIGURES 1, 2, 8, 9. *Crataegus holmesii* Lesq. [= *Cercocarpus holmesii* (Lesq.) Axelr.] (p. 29).
Silver Cliff, Colorado. Introduced for comparison.
1. Syntype USNM 313296.
2. Syntype USNM 313294.
8. Syntype USNM 313295.
9. Lectotype USNM 313299.

3–6, 15, 16. *Cercocarpus henricksonii* Schorn & Wolfe (p. 28).
3. Holotype UCMG 34073, × 1.3.
4. Paratype UCMG 34074, × 1.3.
5. Paratype UCMG 34075, × 1.3.
6. Paratype UCMG 34076.
15, 16. Paratype UCMG 34077. Fig. 15, × 1.3.

7. *Potentilla creedensis* (Axelr.) Schorn & Wolfe (p. 27).
Hypotype USNM 422590, × 1.3.

10, 11. *Andromeda linearifolia* Lesq. [= *Cercocarpus linearifolius* (Lesq.) Axelr.] (p. 30).
Silver Cliff, Colorado. Introduced for comparison.
10. Lectotype USNM 313291.
11. Syntype USNM 23528.

12–14. *Cercocarpus nanophyllus* Schorn & Wolfe (p. 29).
12. Holotype UCMG 34078.
13. Paratype UCMG 34079.
14. Paratype UCMG 34080.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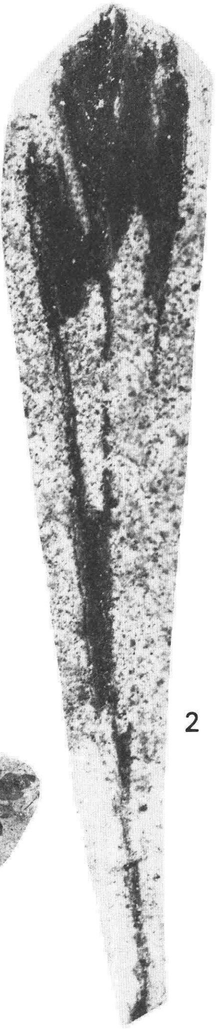
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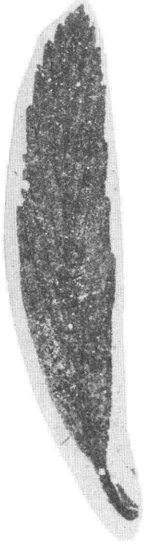
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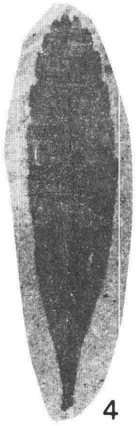
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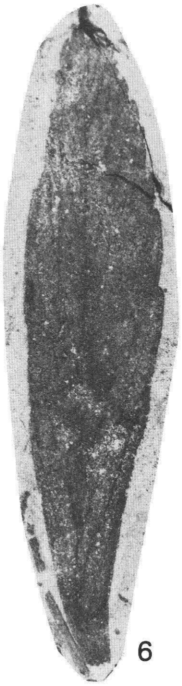
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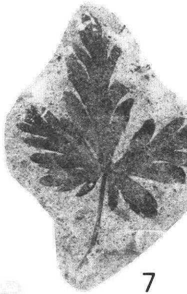
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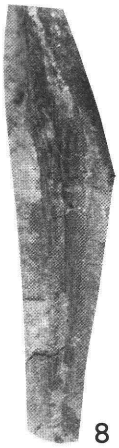
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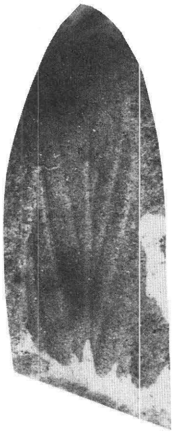
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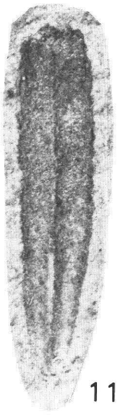
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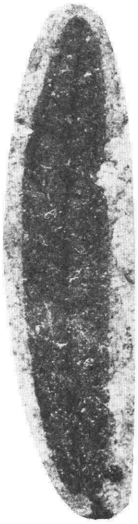
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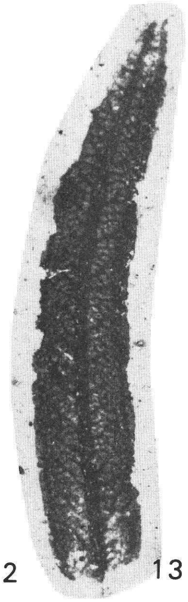
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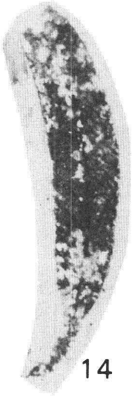
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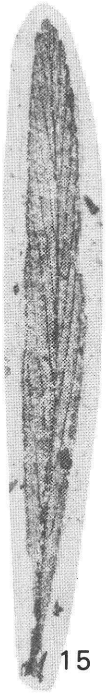
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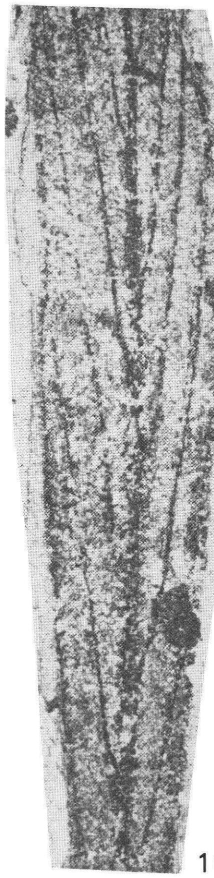
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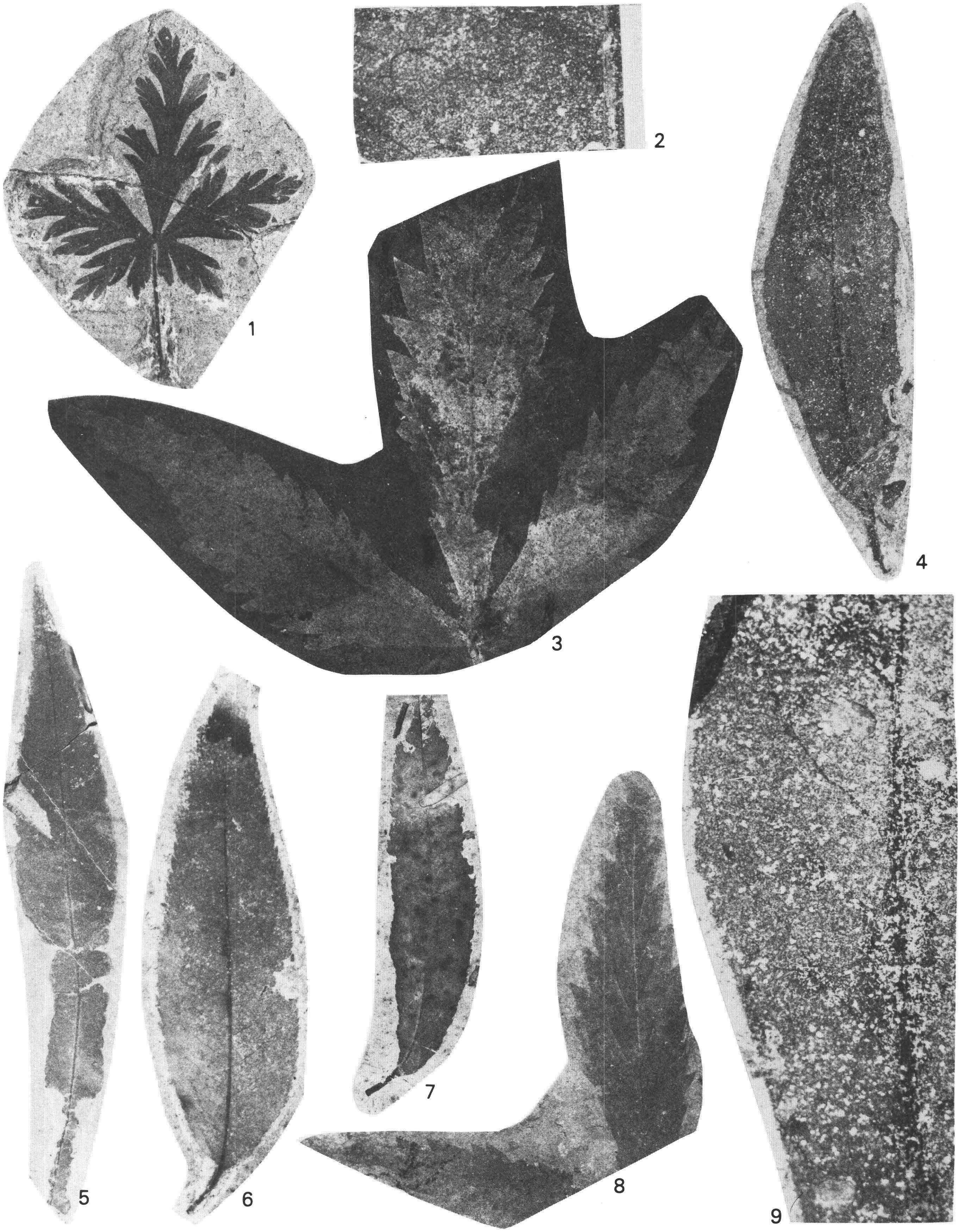
CERCOCARPUS AND *POTENTILLA*

PLATE 11

[All figures × 1.3 unless otherwise stated]

FIGURE 1. *Potentilla creedensis* (Axelr.) Schorn & Wolfe (p. 27).
    Holotype UCMG 19757 (holotype of *Ranunculus creedensis* Axelr.).
2, 5–7. *Prunus creedensis* Axelr. (p. 31).
    2. Hypotype UCMG 19774 (holotype of *Sambucus longifolius* Axelr.), × 4.
    5. Hypotype UCMG 34082.
    6. Hypotype UCMG 34083.
    7. Hypotype UCMG 34084.
3, 8. Rosoideae, genus and species indetermined (p. 30).
    3. Specimen UCMG 19766.
    8. Specimen UCMG 34081.
4, 9. *Osmaronia? stewartiae* (Axelr.) Schorn & Wolfe (p. 30).
    Holotype UCMG 19778 (holotype of *Arbutus stewartii* Axelr.). Fig. 9, × 4.



POTENTILLA, *PRUNUS*, ROSOIDEAE, AND *OSMARONIA?*

PLATE 12

[All figures natural size unless otherwise indicated]

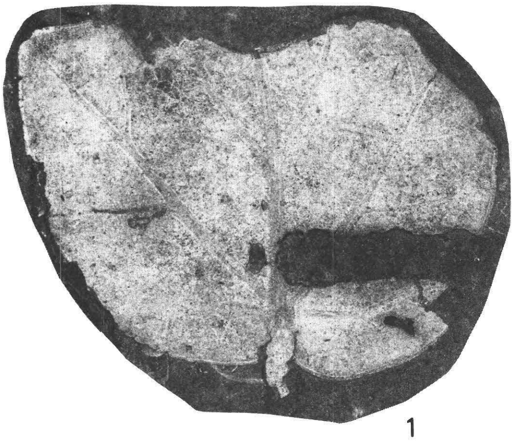
FIGURES 1, 2, 7. *Catalpa coloradensis* (Axelr.) Schorn & Wolfe (p. 33).
  1. Paratype UCMP 7521.
  2. Hypotype UCMG 34085, × 0.6.
  7. Paratype UCMP 7522.

3. "*Chilopsis coloradensis* Axelr." (p. 35).
  Name of dubious value. Holotype UCMP 7852, × 4.

4, 6. "*Quercus creedensis* Axelr." (p. 34).
  Name of dubious value.
  4. Holotype UCMP 7516, × 4.
  6. Paratype UCMP 7515, × 4.

5. *Prunus creedensis* Axelr. (p. 31)
  Hypotype USNM 422593, × 1.3.

8. "*Fraxinus creedensis* Axelr." (p. 35)
  Name of dubious value. Holotype UCMG 19777, × 4.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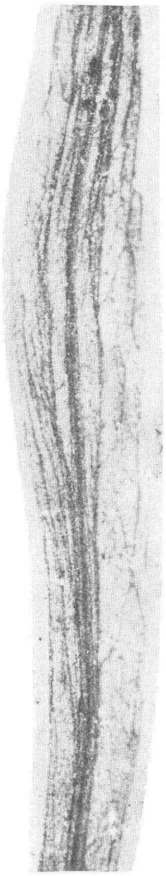
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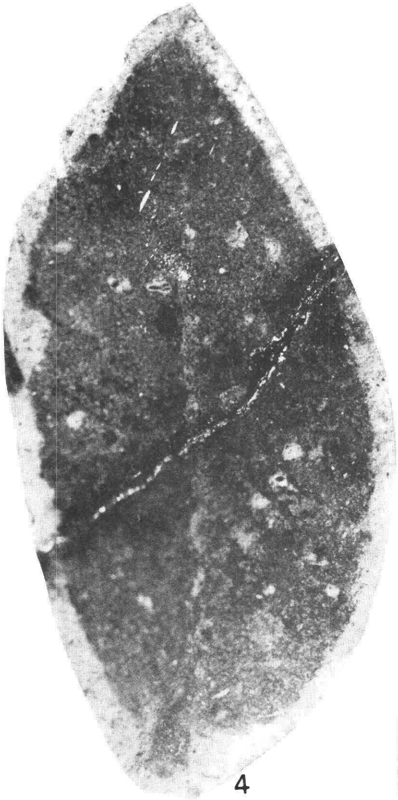
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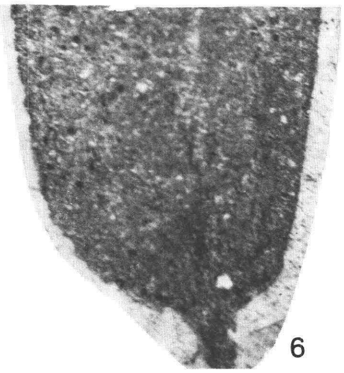
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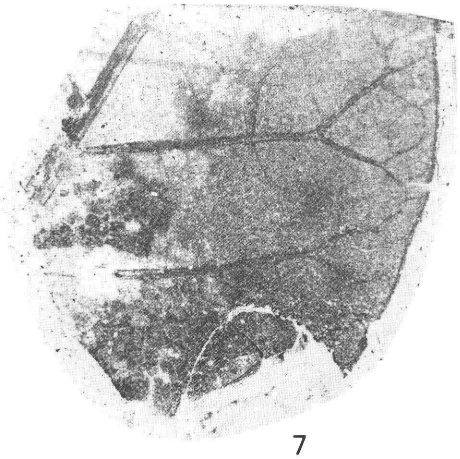
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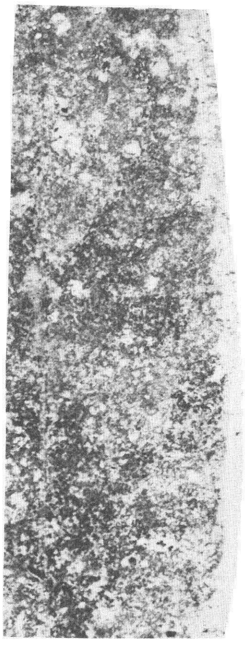
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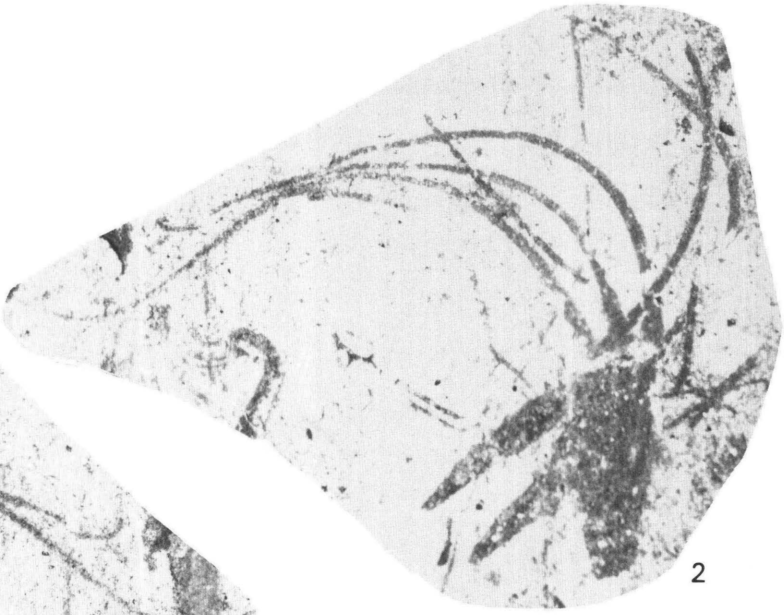
CATALPA AND *PRUNUS*

PLATE 13

[All figures natural size unless otherwise indicated]

FIGURES 1, 2. Group of achenes of uncertain affinity (p. 28).
Specimens UCMP 7781A, B (paratype of *Fallugia lipmanii* Axelr.), ×4.
3. *Eleopoldia lipmanii* (Axelr.) Schorn & Wolfe (p. 24).
Hypotype UCMP 7445 (holotype of *Juniperus gracillensis* Axelr.), ×5.
4. *Pinus crossii* Knowlt. (p. 12).
Hypotype UCMG 34154.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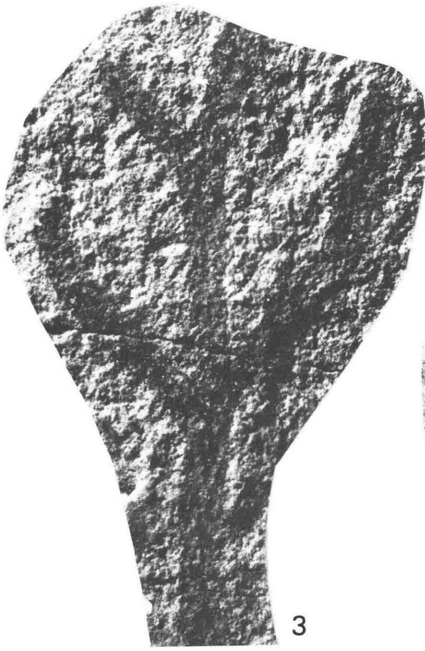
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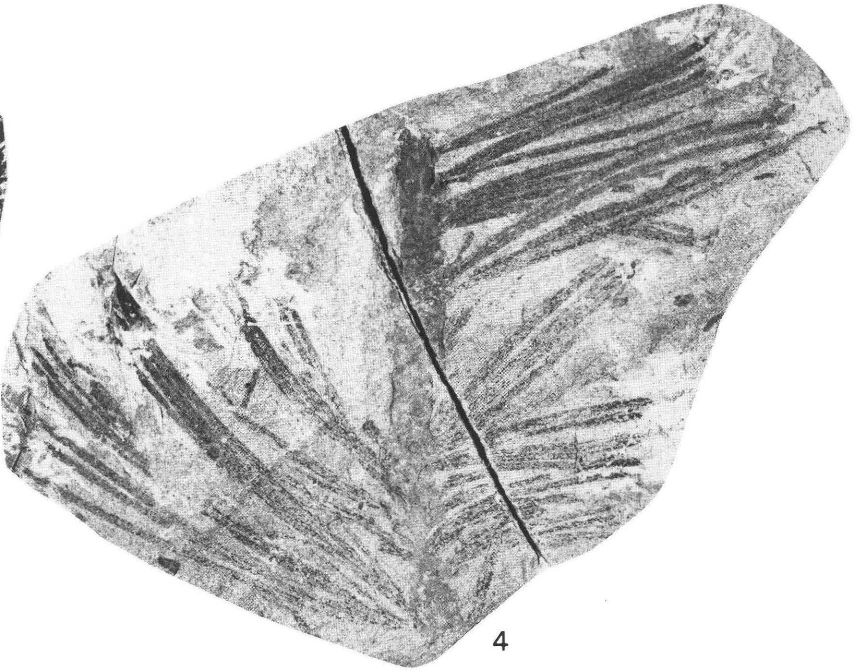
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PINUS, *ELEOPOLDIA*, AND ACHENES

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