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ROSACEOUS *CHAMAEBATIARIA*-LIKE FOLIAGE FROM THE
PALEOGENE OF WESTERN NORTH AMERICA

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ABSTRACT

Chamaebatiaria and *Chamaebatia*, two characteristic genera of the Californian floristic province, are traditionally placed in different subfamilies of Rosaceae, Spiraeoideae and Rosoideae, respectively. Analysis of the foliar and reproductive characters of the extant species of these genera indicates that the two genera could be closely related and the assignment of *Chamaebatia* to Rosoideae invalid. Fossil leaves of lineages of both genera occur in the Paleogene montane floras of the Rocky Mountain region and provide evidence that the two lineages diverged from a common ancestor in the Eocene. The common ancestor probably was adapted to sunny habitats in mesic coniferous forest, and, during the post-Eocene, the two lineages were able to adapt to progressively drier climates. A third extant genus, the east Asian *Sorbaria*, also appears to be closely related to the California genera and to have been derived from the same common ancestor. New taxa and combinations proposed are: *Stonebergia columbiana*, n. gen. and n. sp.; *Salmonensea prefoliolosa* (R. W. Br.), n. gen. and n. comb.; *Stockeya creedensis* (R. W. Br.), n. gen. and n. comb.; *Stockeya montana*, n. sp.; and *Sorbaria wahrhaftigii*, n. sp.

Key words: Rosaceae, *Chamaebatia*, *Chamaebatiaria*, *Sorbaria*, paleobotany, Paleogene, *Salmonensea*, *Stockeya*, *Stonebergia*.

INTRODUCTION

Similarities in foliage to *Chamaebatia foliolosa* Benth. led Maximowicz to rename *Spiraea millefolium* Torr. as *Chamaebatiaria millefolium* (Torr.) Maxim. Despite the similar aspect of foliage of the two genera (e.g., pinnatisect, markedly viscid and with stipitate glands, and sweetly aromatic), however, the two genera are placed in different subfamilies. The monotypic *Chamaebatiaria* (Porter) Maxim., because of the presence of several ovules that ripen into follicles is placed in the putatively primitive Spiraeoideae, whereas the bitypic *Chamaebatia* Benth., because of the single ovule that ripens in an achene, is placed in the more advanced Rosoideae; within this subfamily, the single pistil places *Chamaebatia* in the Dryadeae. Are, in fact, the two genera subfamilially distinct and thus only distantly related?

Another genus of Spiraeoideae whose species were originally placed in *Spiraea* is the Asian *Sorbaria* (DC.) A. Br., of which approximately 10 species are recognized. Indeed, *Chamaebatia millefolium* was once placed in *Sorbaria* by Foche (1888). Like *Chamaebatiaria* and *Chamaebatia*, *Sorbaria* has foliage that is pubescent and fundamentally pinnatisect (although typically described as com-

pound). *Spiraea* contrasts with these other three genera in having an undissected (although toothed) lamina and in not having stipules.

The oldest previously described fossil leaves of the *Chamaebatiaria-Chamaebatia* type are *Chamaebatia prefoliolosa* R. W. Br., based on material from the late middle Eocene (ca. 37–40 million years or Ma) Salmon flora of Idaho (Brown 1935). This taxon is also reported to occur in the late Eocene (ca. 34.5–37 Ma) to earliest Oligocene (ca. 33–34.5 Ma) Ruby flora of southwestern Montana (Becker 1961) and the latest Miocene (ca. 5–8 Ma) Mulholland flora of west-central California (Axelrod 1944). Brown (1937) also described a second taxon, *Chamaebatiaria creedensis*, from the late Oligocene (ca. 25–27 Ma) Creede flora of southern Colorado, and the same species was determined by Axelrod (1939) from the early Miocene (ca. 18 Ma) Tehachapi flora of southern California. Brown (1935) considered the Salmon and Creede species to be indistinguishable from their extant relatives, and a recent treatment of the Creede taxon (Axelrod 1987) offered no morphologic criteria for separation of the Creede from the extant species. If so, other than establishing a minimal age for their respective genera, the fossil species have no bearing on the phyletic relationships of these genera. However, as discussed below, these fossils have not been critically examined previously; the Eocene and Oligocene fossils cited are unquestionably distinct from any extant species and sufficiently distinct from extant relatives to merit description as extinct, although probably ancestral, genera.

The previous fossil record of *Sorbaria* includes undescribed foliage from the late Eocene of Hokkaido (T. Tanai, written comm., October, 1987). In North America, *S. hopkinsii* (Wolfe) Wolfe & Tanai is known from the Miocene of Alaska (Wolfe and Tanai 1980), although reference has been made to an undescribed, pre-Miocene species (Wahrhaftig, Wolfe, Leopold, and Lanphere 1969).

Recent collecting from the early middle Eocene (ca. 48–50 Ma) One Mile Creek locality of the Princeton flora of southern British Columbia has produced leaves of a markedly pinnatifid to pinnatisect rosaceous taxon, described below as *Stonebergia columbiana* Wolfe & Wehr. Analysis of these leaves indicates that they have strong phenetic similarities to *Chamaebatiaria*, *Chamaebatia*, and *Sorbaria*. Although leaves of the extant species of these two genera have only a few synapomorphic characters, Eocene representatives of the lineages strongly indicate that they diverged from a common ancestor in the Eocene after other putatively related genera in Spiraeoideae and Rosoideae were recognizable.

EXTANT TAXA

The leaves of *Chamaebatia* and *Chamaebatiaria* have been considered by some botanists as pinnately compound, and hence terms such as “bipinnate” and “tripinnate” are applied. We consider that true compound leaves are formed by discrete laminar units that dehisce; thus, true pinnately compound leaves occur in, for example, Leguminosae, Juglandales, and Rutanae. The leaves of both *Chamaebatia* and *Chamaebatiaria*, however, dehisce only at the stem and are thus basically simple. The foliage of *Sorbaria* appears to be truly compound, but again the unit that dehisces is typically the entire “compound” leaf rather than the “leaflets.” Pinnate leaves that are compound in having discrete laminar units that dehisce also typically have lateral leaflets that are arranged opposite to one another, whereas in *Chamaebatiaria*, *Chamaebatia*, and *Sorbaria*, the “leaflets”

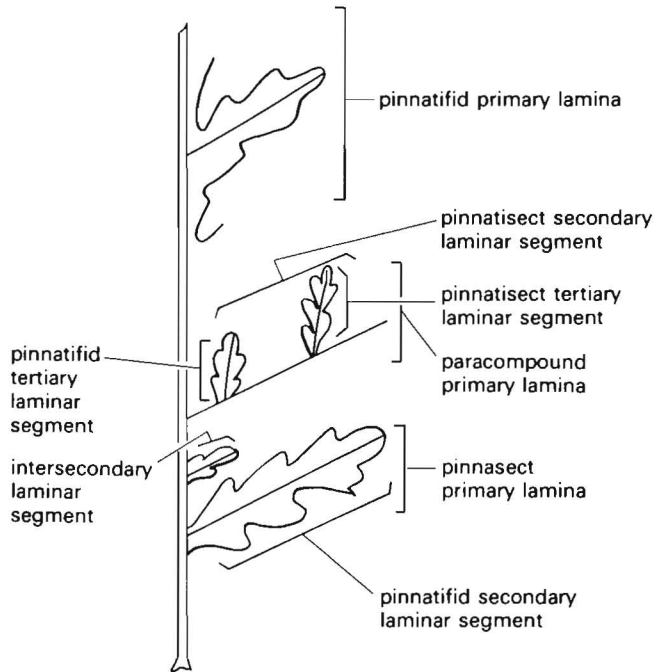


Fig.1. Terminology for foliage of *Chamaebatiaria*, *Chamaebatia*, and other pinnatifid and pinnatisect plants.

are typically subopposite. Terms such as “pinnatifid” (i.e., deeply lobed) and “pinnatisect” (i.e., with lamina or laminar segments completely dissected to primary, secondary, or tertiary veins) are hence appropriate (Fig. 1). We suggest that leaves that have the appearance of compound leaves but that dehisce as entire units be termed *paracompound*. Whereas in pinnatisect leaves (or laminar segments) the dissected segments have a broad base of laminar attachment, in paracompound leaves attachment is only by vasculature.

Whether true pinnately compound leaves occur in Rosaceae is questionable, although some species of *Sorbus* L. may have achieved this state. Because pinnately compound leaves are probably basic for subclass Rosidae (Hickey and Wolfe 1975), the same might be expected to be true for Rosaceae or any rosoid family that appears to have compound foliage. However, saxifragalean families most closely related to Rosaceae (Cronquist 1981; Thorne 1983) and presumably having a sister relationship to the stock from which Rosaceae arose are simple-leaved. Thus, within Rosaceae a reasonable assumption is that the trend is from pinnatifid to pinnatisect to paracompound (and probably to compound) leaves. In this context, the pinnatisect leaves of *Sorbaria* and the bipinnatisect leaves of *Chamaebatiaria* are obviously specialized relative to most other members of Spiraeoideae, as are the paracompound, thrice-divided leaves of *Chamaebatia* relative to other members of Dryadeae.

In the systematics section below, diagnoses for foliage of *Chamaebatiaria*, *Chamaebatia*, and *Sorbaria* are included. Some characters in common between the two genera are probably plesiomorphies, e.g., the basically pinnate venation and

the glandular vestiture, because these characters are found in many genera of Rosaceae and allied families. On the other hand, the totally paracompound primary lamina and pinnatisect secondary laminar segments as in *Chamaebatiaria* and *Chamaebatia* are not found in other genera of Rosaceae; in some instances (e.g., *Poteridium*), secondary laminar segments are deeply pinnatifid but they are not pinnatisect.

In inflorescence, floral structure, and fruit, *Chamaebatiaria* and *Sorbaria* have the characters common in, or defining of, Spiraeoideae and, in particular, the tribe of Sorbarieae. The flowers are arranged in a panicle, which has numerous flowers. The hypanthium is campanulate (or turbinate), the floral formula is $K5/C5/A\infty$, and five pistils are present. Several ovules are present and the fruits are follicles.

The flower and fruit characters just listed are generally considered to be primitive for Rosaceae. From a cladistic standpoint, presence of only plesiomorphic characters should not be taken as evidence of close affinity. Indeed, the foliage of *Chamaebatiaria* and *Sorbaria* is highly specialized and indicates a long divergence from other members of Spiraeoideae.

For a member of Dryadeae, *Chamaebatia* is anomalous in having a many-flowered panicle, which is putatively plesiomorphic for Rosaceae. *Cowania*, *Purshia*, and *Dryas*, for example, typically have solitary flowers. The stamens of *Chamaebatia* are also in several series (a presumably primitive feature), whereas the stamens in other members of Dryadeae are in one to three series. These primitive characters contrast with the advanced foliar characters of *Chamaebatia*.

A single ovule is present in *Chamaebatia*, and primarily this character, plus the achene and single pistil, have been used to place the genus in Rosoideae. Although achenes are, in Rosaceae, generally considered to be restricted to Rosoideae, *Holodiscus* (Spiraeoideae, Holodisceae) also has achenes. An achene has clearly evolved more than once in Rosaceae. Only the single ovule and the single pistil are left as synapomorphic characters shared between *Chamaebatia* and other members of Dryadeae.

Reduction in number of ovules has also clearly occurred more than once in Rosaceae. *Holodiscus*, for example, has two ovules and *Lyonothamnus* four; ovular number is variable in *Physocarpus* (2–4) and *Spiraea* (2–several). The Prunoideae also have a single ovule. Similarly, number of pistils has also been reduced more than once in Rosaceae. Indeed, Prunoideae characteristically have a single pistil, and in Spiraeoideae *Physocarpus* has one to five. We cannot, therefore, find any substantive characters that unquestionably relate *Chamaebatia* to Rosoideae and to Dryadeae in particular. On the other hand, the foliar similarities between *Sorbaria*, *Chamaebatiaria*, and *Chamaebatia*, (and particularly the last two) although few, are fundamental. The advanced floral and fruit characters in *Chamaebatia* are all reductions that could be derived from the plesiomorphic conditions in *Chamaebatiaria* or *Sorbaria*.

FOSSIL TAXA

At least 40 taxa of Rosaceae occur in the early middle Eocene montane assemblages of the Pacific Northwest and adjacent Canada and include members of all four subfamilies. Members of Spiraeoideae include aff. *Physocarpus* (i.e., an extinct genus most closely allied to this extant genus), *Spiraea*, *Sibiraea*, and *Stonebergia*.

Members of Maloideae include *Photinia*, aff. *Sorbus*, aff. *Crataegus*, *Crataegus*, aff. *Malus*, and *Amelanchier*. Rosoideae are represented only by aff. *Kerria* and *Rubus*, while Prunoideae are represented by aff. *Prunus* and *Prunus*. By the later Eocene, other genera of Rosoideae (e.g., *Rosa*, *Cercocarpus*, aff. *Duchesnea*) and more advanced members of Spiraeoideae (*Sorbaria*, *Holodiscus*) and Maloideae (*Heteromeles*, *Sorbus*) appeared. Such a fossil record can be interpreted as reflecting a major, generic-level diversification of Rosaceae during the Eocene.

Stonebergia, which is the oldest known fossil of the *Chamaebatiaria-Chamaebatia* type, has conspicuous, toothed, bilobed stipules; along the margin of the stipule (as well as the petiole) are numerous, simple hairs, a few of which are capped by glands (some other hairs are flat-topped and thus probably were also glandular). On the lamina proper, hairs were simple or stellate. The primary lamina is pinnatifid to pinnatisect, and parts of the primary lamina can be paracompound; the secondary laminae (or primary lobes) are pinnatifid, with large teeth on the lobes (Fig. 2-5). The teeth are obtusely rounded with both apical and basal sides convex (Al of Hickey 1973). In the pinnatisect parts of the lamina, the intersecondary laminar segments can be entire-margined but are typically toothed. The primary lamina has a maximum of nine divisions per side. Venation tends to be obscure (probably related to immersion of the venation in a thick and/or hairy lamina), but the lobes of the secondary laminar segments are entered medially by a strong tertiary vein. The tertiary veins branch close to the point of departure from the secondary vein, with the apical branch extending toward the sinus between lobes. In specimens in which the third-order laminar segments are deeply lobed, the quartary veins have a pattern similar to the tertiary veins (Fig. 2). The tertiary veins are craspedodromous and give off thin quartary veins that form brochidodromous loops.

The stipules of *Stonebergia* (Fig. 48) are similar to, but larger than, the bilobed stipules of *Chamaebatia*, in which the lower part is also fused to the petiole; the stipular lobes in *Stonebergia* are also much more prominent. In *Chamaebatiaria* and *Sorbaria* the stipules are entire-margined. In all three extant genera, as in *Stonebergia*, the foliage is densely stipitate glandular. The hairs of *Stonebergia* are either simple or stellate as in *Sorbaria* and *Chamaebatiaria*; the hairs in *Chamaebatia* are exclusively simple. The primary laminae of *Chamaebatiaria* and *Chamaebatia* are invariably paracompound; the ultimate laminar divisions are always entire-margined in *Chamaebatiaria* (Fig. 17) and *Chamaebatia* (Fig. 9) rather than toothed as in *Stonebergia* (Fig. 2, 15) and *Sorbaria* (Fig. 11). The teeth of *Stonebergia* and the ultimate laminar segments of *Chamaebatiaria* and *Chamaebatia* are rounded, whereas the teeth of *Sorbaria* are sharp. Further, the tertiary and quartary veins are unbranched in *Chamaebatiaria* and *Chamaebatia*, and the fifth-order venation of *Chamaebatia* is open (Fig. 9), rather than forming a closed reticulum. *Stonebergia* is rare but two specimens were deposited together (Fig. 19, 20) suggesting that, like the extant *Sorbaria*, *Chamaebatiaria*, and *Chamaebatia*, the leaves adhered to one another because they were resinous and/or had glandular pubescence. Thus, while sharing certain similarities with leaves of *Chamaebatiaria* and *Chamaebatia*, the leaves of *Stonebergia* are distinguished by what are probably primitive characters for Rosaceae: a less dissected lamina, numerous teeth, and a more elaborate venation pattern. The degree of dissection of the primary lamina is less and the venation pattern is less rigid in *Stonebergia* than in *Sorbaria*, but these two genera have about the same number of teeth.

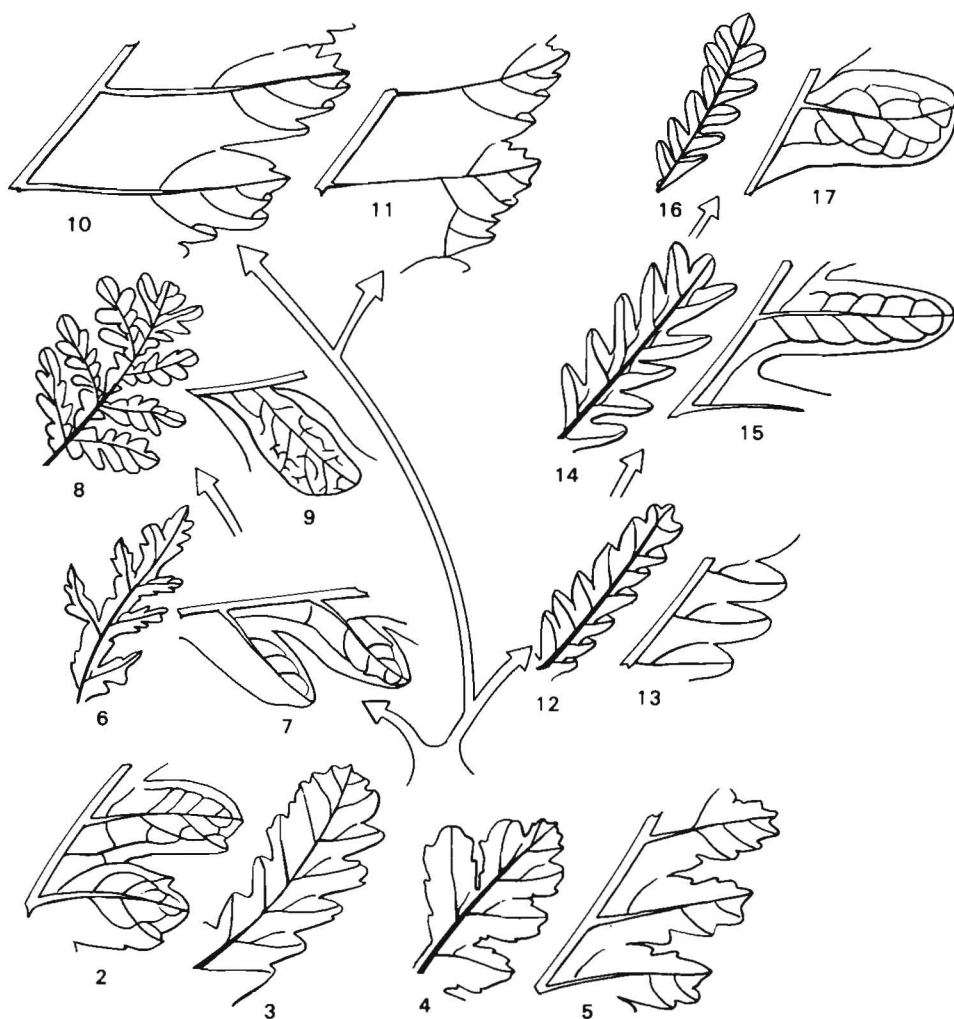


Fig. 2-17. Diagrams of secondary and ultimate laminar segments of some rosaceous taxa.—2-5. *Stonebergia columbiana*.—6, 7. *Salmonensea prefoliolosa*.—8, 9. *Chamaebatia foliolosa*.—10. *Sorbaria pallasii*.—11. *Sorbaria wahraftigii*.—12, 13. *Stockeya montana*.—14, 15. *Stockeya creedensis*.—16, 17. *Chamaebatiaria millefolium*.

In the late Eocene *Salmonensea prefoliolosa* (R. W. Br.) Wolfe & Wehr, which was previously assigned to *Chamaebatia*, the primary lamina is consistently paracompound, and the secondary laminar segments are deeply pinnatifid (Fig. 6). Unlike *Chamaebatia*, in which the tertiary laminar segments can also be pinnatisect (Fig. 8), the tertiary segments in *Salmonensea* are only pinnatifid. *Salmonensea* also has a closed system of fifth-order veins (Fig. 7). The branching of the quartary veins that enter the lobes in *Salmonensea* is similar to the branching of the quartary veins in *Stonebergia*. The stipules in one specimen of *Salmonensea* are represented by a vague outline that has small lobes; apparently the stipule was almost entirely fused to the petiole. *Salmonensea* is specialized relative to

Stonebergia in having a more highly dissected lamina and reduced stipule but is clearly less specialized than *Chamaebatia*.

Except for one fragment, the Ruby leaves previously referred to *Chamaebatia prefoliolosa* represent a genus and species distinct from the Salmon *Salmonensea prefoliolosa*. In the Ruby taxon, which is described below as *Stockeya montana* Wolfe & Wehr, the tertiary laminar segments are totally untoothed, as are the intersecondary laminar segments. The branching tertiary veins in *Stockeya* (Fig. 13) resemble the branching tertiary veins in *Stonebergia*. *Stockeya* shares with *Salmonensea* a consistently paracompound primary lamina. Of the four known specimens of *Stockeya montana*, three were deposited adhering to one another (Fig. 27, 28); as with *Stonebergia*, this suggests foliage that was resinous and had glandular pubescence.

The Creede species formerly assigned to *Chamaebatiaria* is below reassigned to *Stockeya* as *S. creedensis* (R. W. Br.) Wolfe & Wehr; the Ruby and the Creede species have the same degree and order of dissection, both typically lack teeth on the lobes, and both have branching tertiary veins. In *S. montana*, however, the apical branch of a tertiary vein is as thick as the more basal, craspedodromous branch (Fig. 13), and the intersecondary laminar segments are contiguous and numerous (Fig. 51); in *S. creedensis*, the apical tertiary branch is weak (Fig. 15), and the intersecondary laminar segments are widely spaced and few. One specimen of *S. creedensis* (Fig. 50) has some lobes (tertiary laminar segments) that have a few teeth. Although teeth are not known in *S. montana*, obviously this condition was rare in *S. creedensis* and could also have been rare in *S. montana*, which is known from only four specimens.

The two species of *Stockeya* can be viewed as forming a transition from *Stonebergia* to *Chamaebatiaria*. The apical branch of the tertiary vein, strong in *Stonebergia* and *Stockeya montana*, is weak in *S. creedensis* and absent in *Chamaebatiaria*. The tertiary laminar segments are toothed in *Stonebergia* but are typically entire-margined in *Stockeya* and are invariably entire-margined in *Chamaebatiaria*. The intersecondary laminar segments are large and toothed in *Stonebergia*, untoothed but contiguous and numerous in *Stockeya montana*, and untoothed but separated and few in *S. creedensis* and *Chamaebatiaria*.

Foliage of the latest Eocene to earliest Oligocene *Sorbaria wahrhaftigii* Wolfe & Wehr has no characters that separate the species at the generic level from extant species of *Sorbaria*. Although areoles in the latter are typically large, the areoles are small in *S. wahrhaftigii*, as in *Stonebergia*. The tertiary vein that braces the major sinuses between groups of teeth in *Sorbaria wahrhaftigii* (and most extant species of the genus) originates from the apical side of a secondary vein, as in *Stonebergia* (Fig. 10, 11, 15). The extant species of *Sorbaria* examined typically have one subsidiary tooth (a second tooth can be present) on the abmedial side of a primary tooth, but in *Sorbaria wahrhaftigii*, as in *Stonebergia*, up to three subsidiary teeth are present. Of the 23 specimens of *Sorbaria wahrhaftigii* collected, only 5 represent isolated secondary segments, and the other 18 have a total of 53 laminar segments attached. *Sorbaria wahrhaftigii* was clearly paracompound.

However, in some characters, *Sorbaria wahrhaftigii* is specialized relative to some extant species of the genus. In sharpness of the apices of the secondary laminar segments and overall outline of groups of teeth, *S. wahrhaftigii* (Fig. 42)

is unlike *Stonebergia* and thus probably specialized. Less specialized, for example, are the secondary laminar segments of the extant *Sorbaria pallasii* (G. Don.) A. Poj., which tend to have apices and groups of teeth with a rounded outline (Fig. 40); this morphology is particularly similar to one specimen of *Stonebergia* (Fig. 21). *Sorbaria wahrhaftigii*, like most extant species of the genus, has no intersecondary laminar segments, but these are present in the extant *S. sorbifolia*. Except for these last two advanced characters, *S. wahrhaftigii* could be considered as a direct ancestor of all other species of the genus. The presence of these advanced characters indicates that *Sorbaria* had already undergone some diversification by about 35 Ma.

EVOLUTIONARY AND SYSTEMATIC CONSIDERATIONS

Both the *Salmonensea-Chamaebatia* and *Stockeya-Chamaebatiaria* lineages are morphologically transitional back into *Stonebergia*. We do not suggest that *Stonebergia columbiana* is unquestionably the direct and distant ancestor of *Chamaebatia* and *Chamaebatiaria* (as well as of *Sorbaria*), although this could be valid. What we are stating (Fig. 18) is that on morphological grounds, the leaves of the common ancestor of these three extant genera would be assignable to *Stonebergia* and would represent *S. columbiana* or a related species. Further, as conceptualized here, *Stockeya* and *Salmonensea* would contain the ancestors of *Chamaebatiaria* and *Chamaebatia*, respectively, although the described species of these extinct genera may not be in the direct lines of descent. Insofar as known, the described species of *Stockeya* and *Salmonensea* have no specialized characters that would remove these taxa from the direct lines of descent.

Based on known diagnostic features, a strict cladistic viewpoint would place *Stockeya* in *Chamaebatiaria* and *Salmonensea* in *Chamaebatia*, because these fossil genera are segregated from their closest modern relative only on inferred primitive features. We are, however, operating in a classificatory framework based on typology and morphologic similarities when terms such as "Rosaceae" are used. We suggest that were the species of *Stonebergia*, *Stockeya*, and *Salmonensea* still extant, systematists dealing with Rosaceae would, on morphologic distinctiveness, make the same generic separations that we have made.

On the other hand, we emphasize the desirability of making typologic-morphologic categories correspond to monophyletic groups. As currently defined in rather simplistic characters such as pistil/ovule number and general type of fruit, Rosoideae contain more than one lineage that arose from a common ancestor that would not also be a member of Rosoideae; Rosoideae are, therefore, an unnatural or polyphyletic group. The present subfamilial classification of Rosaceae needs to be reexamined, especially using cladistic methodology and the fossil record.

Whether any other extant genera of Rosoideae are closely related to the *Chamaebatiaria-Chamaebatia* group is uncertain. Some species of *Potentilla* also can have a paracompound primary lamina and a pinnatifid secondary lamina; in the species examined, however, intersecondary laminar segments are absent. Further, bracing of the sinus between lobes is typically accomplished by a tertiary vein separate from the tertiary vein that enters the lobes. Such differences, added to the fact that a transition from a pinnatisect to paracompound lamina occurs within *Potentilla*, suggest that the paracompound lamina of *Potentilla* arose separately

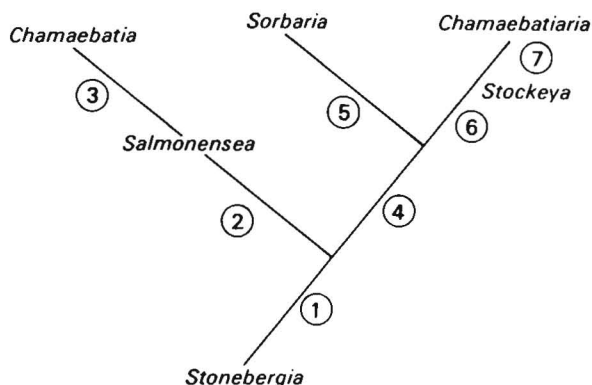


Fig. 18. Inferred phyletic relationships of *Stonebergia* and its descendant genera. 1 Primary lamina only paracompound, secondary laminar segments only pinnatifid. 2 Secondary laminar segments deeply pinnatifid, tertiary laminar segments pinnatifid, stipule size reduced. 3 Secondary laminar segments pinnatisect, tertiary laminar segments pinnatisect, quartary veins freely ending. 4 Intersecondary laminar segments discrete and untoothed, stipule lanceolate. 5 Secondary laminar segments not pinnatifid and strongly serrate. 6 Tertiary laminar segments mostly untoothed. 7 Secondary laminar segments pinnatisect, quartary veins irregularly brochidodromous.

from that of the *Chamaebatia*, i.e., the relationship between *Potentilla* and *Chamaebatia* predates the origin of *Stonebergia*. Capitate glandular hairs also occur in Dryadeae such as *Cowania*, but the presence of such hairs is probably plesiomorphic (e.g., such hairs occur in some species of *Physocarpus* of Spiraeoideae and in Grossulariaceae). Irrespective of the possible relationships of other Rosoideae to *Chamaebatia*, this genus clearly belongs with *Chamaebatiaria* and *Sorbaria* in any classificatory scheme.

Note, however, that one of the suggested synapomorphic foliar characters shared by *Chamaebatiaria* and *Chamaebatia*, namely the pinnatisect secondary laminar segments, was independently achieved in each lineage. *Stonebergia* is uncanalized (cf. Upchurch 1985) in regard to laminar dissection. Some specimens (e.g., Fig. 19b, 20a, 21, 45) have a deeply pinnatifid primary lamina, whereas others (e.g., Fig. 19a, 20b, 21, 23, 49) have a totally pinnatisect primary lamina. The first group also tends to have only moderately pinnatifid secondary laminar segments, whereas the second group tends to have deeply pinnatifid (almost pinnatisect) secondary laminar segments. However, some specimens (e.g., Fig. 19a, 20b, 22) have a pinnatisect primary lamina but only moderately dissected secondary laminar segments. The presumed immediate descendant of *Stonebergia* would have had a totally pinnatisect to paracompound primary lamina and probably uncanalized moderately to deeply pinnatifid secondary laminar segments. In the divergence leading to *Salmonensea*, the secondary laminar segments became only pinnatisect; this occurred within the Eocene. In the divergence leading to *Sorbaria* and *Stockeya*, on the other hand, the secondary laminar segments were first only moderately pinnatifid (*Stockeya montana*), became deeply pinnatifid by the late Oligocene (*Stockeya creedensis*), and subsequently became pinnatisect during the Neogene, when *Chamaebatiaria* is presumed to have evolved. In this regard, what both lineages share is a strong tendency toward laminar dissection, a tendency developed in *Stonebergia* and one perhaps based in genetic structure.

Although *Sorbaria* has the same tendency to dissect the primary lamina, no such tendency has occurred in regard to the secondary laminar segments. Indeed, as we have interpreted the phyletic relationships in this group, the foliage of *Sorbaria* reversed somewhat the trend seen in *Stonebergia*, i.e., the secondary laminar segments of *Sorbaria* are less dissected than those of *Stonebergia*. The less-dissected condition in the secondary laminar segments of *Sorbaria* could represent a more primitive state, but this would necessitate deriving the paracompound primary lamina more than once. Reversal of the trend toward dissection of the secondary laminar segments could be due to the high-latitude environments, which the *Sorbaria* lineage entered during the Eocene. Plants in these environments characteristically, from a variety of factors, have larger leaves than lower-latitude relatives (Wolfe 1985). Assuming that the derivation of *Sorbaria* from a *Stonebergia* descendant that had an already paracompound primary lamina is valid, then expansion of the lamina in response to high-latitude conditions would result in expansion of secondary laminar segments.

BIOGEOGRAPHIC CONSIDERATIONS

As emphasized elsewhere in relation to *Acer* (Wolfe 1987; Wolfe and Tanai 1987), the montane Eocene flora of western North America may have played a, if not the, major role in the origin and diversification of many "arcto-tertiary" taxa. This certainly seems to be valid for Spiraeoideae. The early middle Eocene montane assemblages such as the Republic and Princeton have many representatives of extant woody genera (or related but extinct genera) of Spiraeoideae, including those that are geographically and ecologically now distant from one another, strongly suggesting that the period of 48–50 Ma was geologically a short time after the origin and initial diversification of Spiraeoideae and that the diversification had occurred in this same geographic region.

Further diversification occurred after 48–50 Ma in this same region, as exemplified by *Sorbaria*, *Chamaebatiaria*, and *Chamaebatia*. *Sorbaria* can be considered as an east Asian vicariant of the western American *Stockeya-Chamaebatiaria* lineage, a vicariant relation that probably developed during the post-Eocene as *Stockeya* adapted to progressively drier climates in southwestern North America and became geographically isolated from the northern *Sorbaria*. Note, however, that vicariance in this group did not develop between Asia and North America until after the Miocene, because *Sorbaria* persisted in Alaska into the latest Miocene.

In Raven and Axelrod's (1978) analysis of the California flora, they recognized the basically northern relationships of *Chamaebatiaria*, a relationship confirmed in the present report. Raven and Axelrod, however, included *Chamaebatia* with a group of endemic California genera whose biogeographic relationships were ambiguous. Our analysis indicates that *Chamaebatia*, along with *Chamaebatiaria*, was originally of more northern occurrence and has subsequently entered and become restricted to California. Henrickson (1985) has also suggested that several specialized, dry-adapted genera of Spireae (*Kelseya*, *Luetkea*, *Petrophytum*, *Xerospiraea*) similarly had an origin from a northern lineage of *Spiraea*.

ECOLOGICAL CONSIDERATIONS

The early middle Eocene assemblages from northeastern Washington and adjacent British Columbia represent mesic coniferous forest (Wolfe 1987; Wolfe and

Wehr 1987). The One Mile Creek assemblage, which contains *Stonebergia*, is preserved in lacustrine rocks. Among the dicotyledons, the most abundant leaves are those of *Betula leopoldae* Wolfe & Wehr (a birch of the general *lutea* alliance; cf. Crane and Stockey 1987) and a true *Cercidiphyllum*; many of the birch leaves are >10 cm long. Also common are *Aesculus*, *Prunus* (3 spp.), Ulmoideae, and *Tsukada davidiifolia* Wolfe & Wehr (Davidiaceae). Less common are *Acer* (7 spp.; cf. Wolfe and Tanai 1987), *Spiraea*, *Pterocarya*, and *Fagus*; *Tetracentron*, *Ame-lanchier*, *Rubus*, and *Grossularia* are rare. The leaves of *Aesculus* are large and can occur as complete compound leaves, suggesting little transport. Although some of the leaves display insect damage and biological degradation, little mechanical breakage is evident, again suggesting little transport. The data indicate that the leaves of *Stonebergia* were not transported far and that the plants were in a mesic, summer-wet climate.

However, the presence of foliar pubescence in *Stonebergia* may indicate that the plants occupied sunny habitats (Coley 1983), assuming that the adaptive pattern found in megathermal plants holds for microthermal plants. This inference is consistent with the dissection of the lamina, which probably decreased the effective diameter of the leaf and hence would have lowered temperature in full sunlight. Some other taxa, especially members of Rosaceae, in the Princeton-Republic type assemblages also have a tendency to laminar dissection, although not to the extent of *Stonebergia*.

Salmonensea and *Stockeya montana* from the late middle to late Eocene are also part of lacustrine assemblages that represent mesic coniferous forest (Wolfe 1987). Although Becker (1961) listed a "xeric element" (including "*Chamaebatiaria*" = *Stockeya*) for the Ruby flora, based largely on present ecology of supposed living equivalents, this list included some obvious presently mesic genera, such as *Dipteronia* and *Koelreuteria*. Becker's suggestion that the "xeric element" occupied a woodland climate many kilometers to the south is not consistent with either the lacustrine depositional setting or taphonomic studies (Spicer and Wolfe 1987). The known species of the *Chamaebatiaria-Chamaebatia* group were probably still occupying mesic, summer-wet climate as late as about 33–37 Ma. The greater dissection of the lamina in the later Eocene taxa, however, suggest further adaptation to a sunny/dry habitat.

The late Oligocene Creede assemblage largely represents a montane coniferous forest, but with a large element (including "*Chamaebatiaria*" = *Stockeya creedensis*) interpreted on the basis of supposed living analogs as woodland (Axelrod and Raven 1985; Axelrod 1987). Strong compositional differences occur between some samples and thus may indicate the presence of both forest and woodland (Spicer and Wolfe 1987). However, leaves of *Stockeya* are most common in samples indicative of forest (i.e., high representation of *Abies*) and least common in samples indicative of woodland (i.e., high representation of *Juniperus* and/or *Cercocarpus*). Further, although Axelrod (1987) suggested annual precipitation for the Creede flora of 460–520 mm, the presence of *Picea* probably indicates annual precipitation >1100 mm (Wolfe 1971). Again, we suggest that *Stockeya* was adapted to a relatively mesic climate, although leaf size of the Creede assemblage indicates a drier climate and possibly a more open-canopy forest than do the Ruby and Salmon assemblages.

The extant *Chamaebatiaria millefolium* occupies xeric habitats east of the Sierra-Cascade axis from southern California north to Oregon and occurs in vegetation

ranging from sagebrush scrub to juniper woodland to open bristle-cone pine forest (Munz and Keck 1959; Thorne 1982). The extant *Chamaebatia foliolosa* occurs in open forest in the ponderosa pine and red fir belts along the western slope of the Sierra Nevada, and *C. australis* (Bdg.) Abrams occurs in chaparral in southernmost California and adjacent Baja California (Munz and Keck 1959). Members of both extant genera have vasicentric tracheids, an adaptation to drought survival in the xeric to subhumid environments occupied by these taxa (Carlquist 1985). The ancestry of these taxa, however, is in mesic Eocene vegetation to the north; the respective lineages have morphologically evolved, first adapting to sunny habitats in mesic forest and then to progressively drier climates during the post-Eocene.

Sorbaria has probably changed little ecologically from *Stonebergia*. In China, for example, *Sorbaria* can occur as an understory shrub in coniferous to broad-leaved deciduous forest, although the genus is common in open areas within forested regions (Wang 1961). In the Alaskan Tertiary, the occurrences of *Sorbaria* probably represent similar habitats.

SYSTEMATICS

The specimens examined and cited are in the following institutions: Princeton (B.C.) Museum and District Archive (PMDA), U.S. National Museum (USNM), University of Alberta, Paleobotany Collections (UAPC), University of California Museum of Paleontology (UCMP), University of Colorado Museum, Geology (UCMG), University of Michigan Museum of Paleontology (UMMP), University of Washington Burke Museum (UWBM).

KEY TO CHAMAEBATIA-LIKE FOLIAGE

- Primary lamina pinnatifid to pinnatisect *Stonebergia*
- Primary lamina only paracompound
 - Some intersecondary laminar segments toothed
 - Secondary laminar segments pinnatifid *Salmonensea*
 - Secondary laminar segments pinnatisect *Chamaebatia*
 - No intersecondary laminar segments toothed
 - Secondary laminar segments only toothed *Sorbaria*
 - Secondary laminar segments pinnatifid *Stockeya*
 - Secondary laminar segments pinnatisect *Chamaebatiaria*

Family ROSACEAE

Subfamily SPIRAEOIDEAE

Tribe SORBARIEAE

***Stonebergia* Wolfe & Wehr, gen. nov.**

Diagnosis.—Leaves simple, stipulate; stipules bilobed, lower half fused to petiole; petioles markedly pubescent, hairs simple, both sharp-pointed and stipitate glandular; primary lamina pinnately veined, deeply pinnatifid to pinnatisect to paracompound in part; lamina with many hairs, both simple and stellate; secondary laminar segments pinnatifid and with rounded to broadly acute, nonglandular teeth; lobes of secondary laminar segments furnished with a tertiary vein that branches, the abmedial branch extending toward the lobal sinus, the admedial branch craspedodromous and placed approximately medially in the lobe; quartary veins also forked in a manner similar to the tertiary veins if laminar segments

are deeply pinnatifid; lobes toothed; fifth-order veins forming brochidromous loops; five orders of venation; intersecondary laminar segments toothed, contiguous.

Type species.—*Stonebergia columbiana* Wolfe & Wehr.

Nomenclature.—We take pleasure in naming this genus for Mrs. Margaret Stoneberg of the Princeton (B. C.) Museum and District Archives. Mrs. Stoneberg has supplied both financial support for Wehr's field work and continuing encouragement to both of us.

***Stonebergia columbiana* Wolfe & Wehr, sp. nov.** Fig. 2-5, 19-24, 41, 45, 49

Description.—Leaves simple, pinnately veined, widely elliptic to ovate; 1.7–2.2 cm long, 1.0–3.0 cm wide; apex acute, base cordate; midrib thick; primary lamina deeply pinnatifid to pinnatisect to, in part, paracompound, with toothed, contiguous intersecondary segments; numerous hairs, both simple and stellate; 4–9 pairs of subopposite secondary veins originating at angles of 45–90° (higher near base), thick, straight to slightly curving, craspedodromous; secondary laminar segments moderately to deeply pinnatifid, narrowly elliptic; up to 7 lobes per side of secondary laminar segments and up to 4 teeth per side of lobes; tertiary veins originating at angles of 40–60°, branching, the admedial branch extending medially into lobe and craspedodromous, the abmedial branch extending toward lobal sinus; fourth-order veins as many as teeth, craspedodromous; if teeth deeply dissected (almost pinnatifid), quartary veins forking as in tertiary veins; fifth-order veins forming brochidromous loops; teeth broadly acute to rounded, Al, sinuses angularly acute, apparently nonglandular; petiole 0.8–1.0 cm long; stipule almost half as long as petiole, bilobed, toothed, basal half fused to petiole; petiole and stipule furnished with many simple, straight, pointed hairs and some stipitate glandular hairs.

Holotype.—UWBM 54110A, 54110B.

Paratypes.—UWBM 31509, 31510, 54109, 54111A, 54111B, PMDA-OMC 2, UAPC S50836, S17969A.

Occurrence.—One Mile Creek, British Columbia.

Nomenclature.—Type locality is in British Columbia.

Notes.—Typically the only hairs preserved are the stipular and petiolar hairs, which all appear to be simple. Fourth- and fifth-order venation is not well preserved, suggesting a thick and/or hairy lamina. One specimen (UAPC S17969A) had been infested with probable scale insects (cf. Wolfe and Tanai 1987), which reveals many laminar hair bases and some stellate hairs.

SORBARIA (Ser. ex D.C.) A. Braun

Diagnosis.—Leaves simple, stipulate; stipule lanceolate; petiole markedly pubescent, hairs both simple and stellate; primary lamina pinnately veined, paracompound; secondary laminar segments with teeth in groups; subsidiary teeth almost invariably present on basal sides of major teeth and can be present on apical sides; teeth sharp, basal sides convex, apical sides convex to acuminate; tertiary veins craspedodromous, typically giving off an apical branch that braces the major sinus

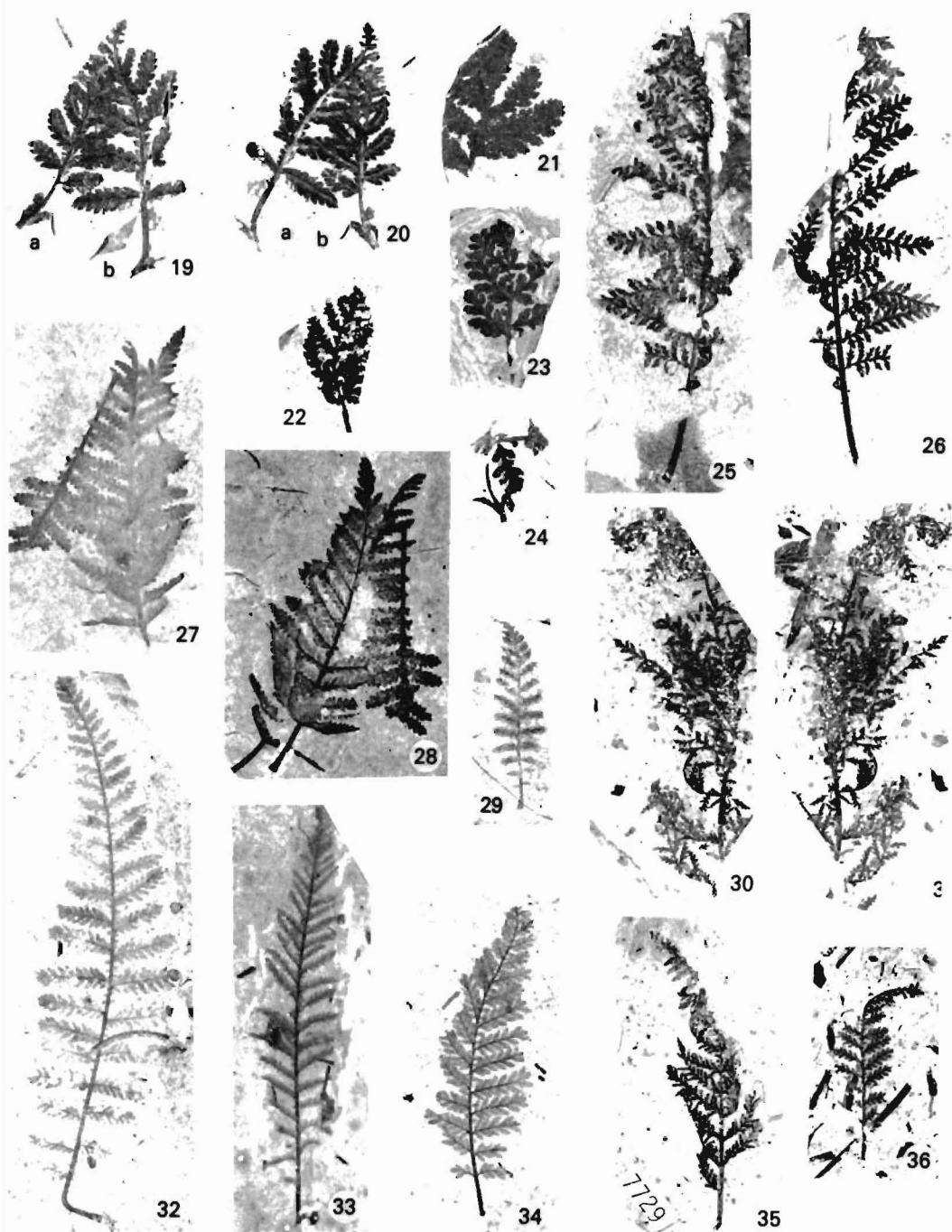


Fig. 19–36. Leaves of fossil taxa allied to *Chamaebatiaria* and *Chamaebatia*, $\times 1$.—19–24. *Stonebergia columbiana*.—19a, 20b, holotype, UWBM 54110A, B.—19b, 20a, 21–24, paratypes, UWBM 54111A, B, 31509, UAPCS50836, UWBM 54109, PMDAOMC-2.—25, 26. *Salmonensea prefoliolosa*, holotype, USNM 39420B, A.—27–29. *Stockeya montana*.—27, 28, holotype, UMMP 33607A, B.—29, paratype, USNM 396066.—30, 31. *Salmonensea prefoliolosa*, hypotype, USNM 396067 A, B.—32–36. *Stockeya creedensis*, hypotypes, UCMG 34057, 18646, 34058, UCMP 7729A, 7715.

above, and giving off basal quartary veins near the margin; these basal quartary veins branching, the apical branch bracing the minor sinus above and the basal branch craspedodromous; intercostal quartary veins widely spaced, AA to RR, percurrent to thinning markedly in the intercostal area; fifth-order veins forming irregularly polygonal areoles; veinlets typically branching at least once; intersecondary laminar segments typically absent, but, if present, as a single, narrow segment between adjacent secondary segments.

Notes.—The above diagnosis is based on cleared specimens of the following species: *Sorbaria aitchisonii* Hemsl., *S. arborea* Schneid. var. *glabrata* Rehd., *S. kirlowii* Maxim., *S. lindleyana* Maxim., *S. pallasii* (G. Don) A. Poj., *S. sorbifolia* (L.) A. Br., and *S. sorbifolia* var. *stellipila* Maxim.

***Sorbaria wahrhaftigii* Wolfe & Wehr, sp. nov.**

Fig. 11, 37–39, 42, 43

Description.—Leaves simple, pinnately veined, widely obovate; 4.5–7.0 cm long, 3.5–6.0 cm wide; apex acute, base cordate; midrib thick; primary lamina paracompound with no intersecondary segments but densely hairy with both simple and stellate hairs; 2–4 pairs of subopposite secondary veins originating at angles of 45–90° (higher near base), typically straight, craspedodromous; lateral secondary laminar segments widely ovate to lanceolate, apex acute, base asymmetrically broadly rounded to acute; apical secondary laminar segment typically with 2 deeply pinnatifid basal segments that resemble lateral secondary segments; 9–12 pairs of subopposite tertiary veins in each secondary segment, straight to typically slightly curving apically, craspedodromous; tertiary veins giving off a strong apical branch that braces major sinus above and strong basal branches; basal branches 2–5, craspedodromous, entering teeth medially; intersecondary quartary veins RR, widely and irregularly spaced, percurrent, branched; fifth-order veins forming with quartaries small (ca. 0.2 mm), irregularly quadrangular areoles; veinlets once-branching, about same thickness as fifth-order veins; groups of teeth as many as tertiary veins, an overall A1 outline; 1–3 subsidiary teeth on apical side of a major tooth and 3–5 on basal side; teeth sharp, B1 or D1; petiole densely hairy, 0.8–>2 cm long.

Holotype.—USNM 396063d.

Paratypes.—USNM 396063a–c, 396064a–e.

Occurrence.—Rex Creek flora, central Alaska Range.

Nomenclature.—Clyde Wahrhaftig has been of invaluable assistance in the collection and stratigraphic placement of the plant assemblages from the Nenana coal field in the Alaska Range.

Notes.—Of the 23 specimens collected of this taxon, 18 are complete or partial specimens of primary laminae, and only five represent isolated “leaflets.” *Sorbaria wahrhaftigii* differs from the Miocene *S. hopkinsii* (Wolfe) Wolfe & Tanai in having (1) fewer tertiary veins per secondary laminar segment (9–12 vs. 17–24), (2) more subsidiary teeth on both apical (1–3 vs. 0–1) and basal (3–5 vs. 1–3) sides of major teeth, and (3) RR and percurrent rather than AA and thinning intercostal quartary veins. An undescribed species from the early Oligocene (but <33 Ma) beds of the Kenai Group at Redoubt Point has tertiary veins intermediate in number between



Fig. 37–39. Leaves of *Sorbaria wahrhaftigii*. —37a–c, 39, paratypes, USNM 396064a–d, 396063a–c, 396064e. —38d, holotype, USNM 396063d.

S. wahrhaftigii and *S. hopkinsii*, but resembles *S. wahrhaftigii* in intercostal quar-
tary veins and *S. hopkinsii* in number of subsidiary teeth.

The Rex Creek flora was recently assigned a latest Eocene age (Wolfe and Tanai
1987). However, this flora could be of earliest Oligocene age but older than 33
Ma (we are accepting an age of 34.5 Ma for the Eocene-Oligocene boundary).

Stockeya Wolfe & Wehr, gen. nov.

Diagnosis. —Leaves simple; petioles markedly hairy, hairs simple, some capitate
glands present; primary lamina pinnately veined, paracompound; secondary lam-

inar segments deeply pinnatifid; lobes typically entire-margined but can have teeth on admedial and abmedial sides; teeth acute, nonglandular; lobes furnished with a tertiary vein that branches, the abmedial branch extending toward the lobal sinus, the admedial branch craspedodromous and placed approximately medially in the lobe; quartary veins forming a single series of brochidodromous loops on either side of admedial tertiary branch; four orders of venation; teeth narrowly rounded, nonglandular, sinuses acute; intersecondary segments typically entire-margined, contiguous or isolated.

Type species.—*Stockeya creedensis* (R. W. Br.) Wolfe & Wehr [*Chamaebatiaria creedensis* R. W. Br.].

Nomenclature.—The Creede species is represented by abundant, well preserved material and is, therefore, selected as the generic type. The second species assigned to this new genus is *Stockeya montana* Wolfe & Wehr, which is based on material from the Ruby flora of southwestern Montana. Prof. Ruth Stockey of the University of Alberta has collected extensively from the Princeton localities and has allowed us free access to these collections.

Stockeya creedensis (R. W. Brown) Wolfe & Wehr, comb. nov.

Fig. 14, 15, 32–36, 50, 52

Synonymy.—*Chamaebatiaria creedensis* Brown, 1937, p. 177, pl. 57, fig. 8, 9. Axelrod, 1987, p. 127, pl. 27, fig. 1–14.

Original description.—“These specimens, which resemble small ferns or mosses, are bipinnate leaves with minute, obovate ultimate divisions. Appendages similar to these divisions appear along the rachis” (Brown 1937, p. 177).

Supplementary description.—Leaves simple, pinnately veined, elliptic to narrowly elliptic or narrowly ovate to lanceolate; primary lamina paracompound 1.5–7.0 cm long, 0.9–2.4 cm wide; apex acute, base cordate; midrib thick; intersecondary segments 0–2, isolated, entire-margined; 11–25 pairs of subopposite secondary veins, originating at angles of 40–90°, straight to typically basally reflexed, craspedodromous; secondary laminar segments narrowly elliptic, deeply pinnatifid; lobes oblanceolate to narrowly oblanceolate, apex narrowly rounded; basal part of lobes elongated admedially along secondary vein; lobes typically entire-margined, but some with as many as 3 teeth along admedial margin and 1 along abmedial margin; teeth acute, Al, nonglandular, sinuses acute; tertiary veins originating at acute angles, branching unequally, the weaker abmedial branch extending into contiguous lobe and the stronger admedial branch craspedodromous and placed medially in lobes; quartary veins forming a single series of brochidodromous loops on either side of admedial tertiary branch; no fifth-order venation; petiole 0.5–1.0 cm long, furnished with many simple hairs and some capitate glandular hairs.

Lectotype.—(here designated) *USNM 39651* (Brown's fig. 9).

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

Occurrence.—Creede, Colorado.

Notes.—The only hairs preserved well are those on the petiole, which, as in *Chamaebatiaria*, are mostly simple and glandular. Whether hairs on the laminar

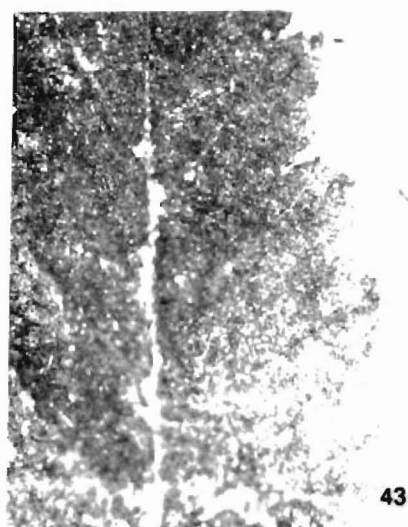


Fig. 40–43. Leaves of *Stonebergia* and *Sorbaria*, $\times 5$.—40. *Sorbaria pallasii*, USGS 8805.—41. *Stonebergia columbiana*, UWBM 31509.—42, 43. *Sorbaria wahrhaftigii*, USNM 396064c, d.

segments are stellate cannot be certainly determined. We reject the assignment to this species of the Tehachapi specimen (Axelrod 1939). Although stated to be part of a "bipinnate" leaf, the specimen has no petiole preserved, and thus the rank of the laminar segments preserved can only be inferred. However, Axelrod correctly observed that the ultimate segments of the fossil are obovate, and this is particularly true of the terminal segments. In *Chamaebatiaria*, the ultimate segments tend to overlap and have a broad area of attachment and thus typically appear as oblong to only slightly obovate as opposed to the markedly obovate ultimate segments in *Chamaebatia*. *Chamaebatia* and *Chamaebatiaria* can be readily separated on venation in the ultimate segments: in *Chamaebatia*, the major vein is placed towards the terminus of the laminar segment that has the ultimate segments and the next order of veins end freely, whereas in *Chamaebatiaria*, the major vein is placed medially and the next order of veins form brochidodromous loops. However, no venation is preserved in the ultimate segments of the fossil, and we consider either generic or specific assignment as highly problematic.

Stockeya montana Wolfe & Wehr, sp. nov.

Fig. 12, 13, 27–29, 51

Synonymy. — *Chamaebatiaria prefoliolasa* auct. non R. W. Brown. Becker, 1961 (part), p. 72, pl. 22, fig. 11, 12.

Description. — Leaves simple, pinnately veined, lanceolate; 2.4–4.0 cm long, 0.7–2.1 cm wide; apex acute, base cordate; midrib thick; primary lamina paracom-pound, with entire-margined, contiguous intersecondary segments; 14–16 pairs of subopposite secondary veins, originating at angles of 50–90°, straight to basally reflexed, craspedodromous; secondary laminar segments deeply pinnatifid; lobes elliptic, entire-margined; basal part of lobes elongated admedially along secondary vein; tertiary veins originating at acute angles, branching equally, the abmedial branch extending toward and apparently terminating at lobal sinus and the ad-medial branch craspedodromous and placed medially in lobes; fourth-order venation not preserved; petiole 0.3–0.8 cm long.

Holotype. — UMMP 33607Aa, 33607Ba.

Paratypes. — UMMP 33607Ab, 33607Bb, 33607Ac, 33607Bc; USNM 396066.

Occurrence. — Becker's Ruby paper-shale flora (upper Ruby River Basin, Montana).

Nomenclature. — Occurs in Paleogene montane vegetation.

Notes. — The poor preservation obscures finer venation and does not allow the determination of presence or absence of foliar hairs. The Ruby taxon differs from *Stockeya creedensis* in having (1) contiguous (and more numerous) rather than isolated intersecondary laminar segments, (2) elliptic rather than oblanceolate lobes, (3) equal rather than unequal branching of the tertiary veins, and (4) the abmedial tertiary branch end at the lobal sinus rather than entering the contiguous lobe.



Fig. 44–48. Foliage of *Chamaebatia* and allied fossil taxa, $\times 8$. —44. *Chamaebatia foliolosa*, USGS 625. —45. *Stonebergia columbiana*, UWBM 54109. —46, 47. *Salmonensea prefoliolosa*, USNM 396067A, UMMP 36912. —48. *Stonebergia columbiana*, PDMA OMC-2.

CHAMAEBATIARIA (Porter) Maximowicz

Diagnosis. —Leaves simple, stipulate; stipule lanceolate, entire-margined, deciduous; petioles markedly pubescent, hairs simple or stellate, both sharp-pointed and glandular-capitate; primary lamina pinnately veined, paracompound; sec-

ondary laminar segments pinnatisect; tertiary laminar segments entire-margined; tertiary veins unbranching and placed abmedially in tertiary laminar segments; quartary veins forming brochidodromous loops; four orders of venation; intersecondary laminar segments isolated, entire-margined.

Salmonensea Wolfe & Wehr, gen. nov.

Diagnosis. — Leaves simple; stipule apparently bilobed and mostly fused to petiole; petiole pubescent, hairs simple, some glandular capitate; primary lamina pinnately veined, paracompound; secondary laminar segments pinnatisect and with rounded to acute, nonglandular teeth; lobes of tertiary laminar segments furnished with a quartary vein that branches, the abmedial branch extending toward the lobal sinus and into the contiguous lobe, the admedial branch craspedodromous and placed approximately medially in the lobe; five orders of venation; intersecondary laminar segments toothed, contiguous.

Type species. — *Salmonensea prefoliolosa* (R. W. Br.) Wolfe & Wehr [*Chamaebatia prefoliolosa* R. W. Br.]

Nomenclature. — Type species is part of flora from vicinity of Salmon, Idaho.

Salmonensea prefoliolosa (R. W. Brown) Wolfe & Wehr, comb. nov.

Fig. 6, 7, 25, 26, 30, 31, 46, 47

Synonymy. — *Chamaebatia prefoliolosa* Brown, 1935, p. 578, pl. 69, fig. 4. Becker, 1961 (part), p. 72, pl. 22, fig. 13.

Original description. — “This fernlike specimen is a tripinnatifid leaf, with minute, bluntly pointed or rounded ultimate divisions; leafy appendages distributed along the rachis; venation not discernable” (Brown 1935, p. 578).

Supplementary description. — Leaves simple, pinnately veined, widely elliptic to ovate; 5–>6 cm long, 3–4 cm wide; apex not preserved, base cordate; midrib thick; primary lamina paracompound, with entire or toothed intersecondary segments; 10–11 (probably more) pairs of subopposite secondary veins, originating at angles of 50–90°, thick, straight to typically curved, craspedodromous; secondary laminar segments pinnatisect, narrowly elliptic; tertiary laminar segments contiguous with a broad area of attachment along secondary vein, pinnatifid with 2–4 lobes on admedial side and 1–2 lobes along abmedial side; lobes narrowly rounded; tertiary veins originating at angles of 40–60°, craspedodromous, placed medially to somewhat abmedially in tertiary segments; quartary veins originating acutely, branching with the abmedial branch extending into contiguous lobe, the admedial branch craspedodromous and placed medially in the lobe; fifth-order veins forming brochidodromous loops; some lobes with a single tooth on basal flank; sinuses acutely angular; stipule indistinct, about ¼ as long as petiole, apparently bilobed; petiole 0.7–1.5 cm long, furnished with many simple hairs and some capitate glands; no stipule preserved.

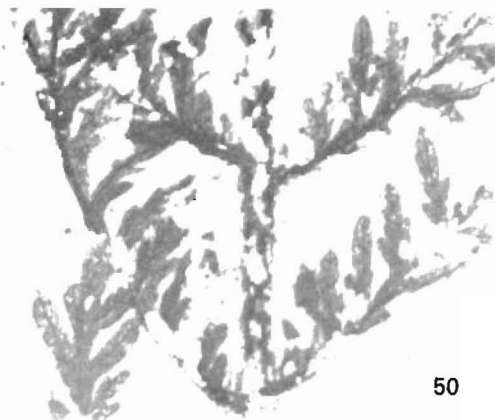
Holotype. — USNM 39240A, B.

Hypotypes. — USNM 396067A, B, 396068A, B (all topotypes), UMMP 36912.

Occurrences. — Oliver coal mine near Salmon, Idaho; Becker's Ruby blocky-shale flora (upper Ruby River Valley, Montana).



49



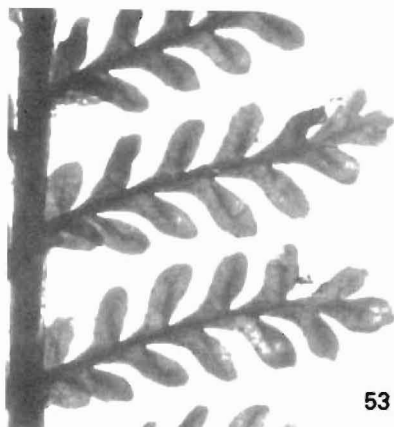
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51



52



53

Fig. 49–53. Foliage of *Chamaebatiaria* and allied fossil taxa, $\times 8$.—49. *Stonebergia columbiana*, UWBM 54110A.—50. *Stockeya creedensis*, UCMP 7729A.—51. *Stockeya montana*, UMMP 33607A.—52. *Stockeya creedensis*, UCMG 34058.—53. *Chamaebatiaria millefolium*, USGS 624.

Notes.—Axelrod's (1944) citation of this species based on a specimen from the Mulholland assemblage of central California must be rejected because, in part, of extremely poor preservation. The specimen has tertiary veins that have an A-A orientation (Hickey 1973). But we cannot determine whether the lamina is continuous between secondary veins or is, as claimed by Axelrod (1944), pinnatisect. The specimen could, if not pinnatisect, represent a leaf similar to *Alnus oregona* Nutt., which has AA tertiary veins that thin markedly midway between the secondary veins. Irrespective of whether the specimen has a pinnatisect primary lamina, the lamina between adjacent tertiary veins is continuous, and therefore the specimen is not twice-divided and cannot represent *Chamaebatia*.

The citation for the Ruby flora is based on a single fragment that apparently represents the ultimate part of a secondary laminar segment. This specimen is in a matrix of blocky shale, which, as noted by Becker (1961), is probably stratigraphically lower than the paper-shale unit, which unit has produced specimens of *Stockeya montana*.

CHAMAEBATIA Bentham

Diagnosis.—Leaves simple, stipulate; stipule bilobed, lower $\frac{2}{3}$ – $\frac{3}{4}$ fused to petiole; petiole markedly stipitate glandular, hairs simple, both sharp-pointed and glandular capitate; primary lamina pinnately veined, pinnatisect; secondary laminar segments pinnatisect; tertiary laminar segments pinnatifid to typically pinnatisect; fourth-order veins unbranching and placed admedially in quartary laminar segments; fifth-order veins branching, most ending freely as sclerids (some anastomosing) and not forming brochidodromous loops; intersecondary laminar segments isolated, entire-margined to toothed and/or pinnatisect.

ACKNOWLEDGMENTS

For discussions of the concepts presented and for critiques of the manuscript we thank James Henrickson and G. R. Upchurch, Jr. Henrickson also shared with us some of his ideas on the relationships of *Sorbaria*, *Chamaebatiaria*, and *Chamaebatia*. Fossil materials for this study were, in part, loaned by C. B. Beck, J. P. Ferrigno, H. E. Schorn, R. A. Stockey, and Margaret Stoneberg. Extant comparative materials were furnished by A, CAS, and UC.

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