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William C. Dickison

*University of North Carolina*

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## STEM AND LEAF ANATOMY OF THE ALSEUOSMIACEAE<sup>1</sup>

WILLIAM C. DICKISON

*Department of Biology, University of North Carolina,  
Chapel Hill, North Carolina 27599*

### ABSTRACT

The stem and leaf anatomy of five species representing all three genera of the small Southwest Pacific dicotyledonous family, Alseuosmiaceae, were studied. Salient anatomical features common to all genera include: a trilacunar, three-trace leaf-node structure in which petioles are supplied with three separate vascular bundles; rosoid teeth bearing hydathodes; anomocytic stomata; unicellular, bicellular, and multicellular, unbranched, living trichomes; a superficial origin of periderm; leaf mesophyll composed of a uniseriate palisade region and a loosely constructed spongy zone; and the presence of a stem and foliar endodermis. Sclerenchyma occurs in stem tissues of species belonging to all three genera and *Crispiloba disperma* contain numerous elongate, filiform or fibrosclereids in the stem, petiole, and leaf mesophyll. Leaves are pinnately veined or, in the case of *Wittsteinia vacciniacea*, with acrodromous venation. Secondary venation is brochidodromous or semicraspidodromous. As presently constituted the family has a distinctive combination of derived wood and stem anatomical characters, and provides an excellent example of the successful application of vegetative anatomical evidence in solving problems of family relationship and generic affinities. The presence of an endodermis in the aerial organs provides additional support to the suggestion that the family evolved from a small, shrubby ancestor, subsequently became semiherbaceous, followed by the development of a secondarily woody body in some taxa. The totality of anatomical characters reinforces the view that the Alseuosmiaceae have their nearest relatives within the rosalean-saxifragalean complex.

Key words: *Alseuosmia*, Alseuosmiaceae, *Crispiloba*, leaf anatomy, nodal anatomy, Rosales, Saxifragales, *Wittsteinia*.

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### INTRODUCTION

The Alseuosmiaceae represent a small Southwest Pacific, dicotyledonous family. The family, as redefined by van Steenis (1984), includes three well-defined genera: *Alseuosmia* Cunn., with about four to eight species from New Zealand; *Wittsteinia* F. Muell., encompassing three species from New South Wales, New Caledonia, and New Guinea; and a new monotypic genus, *Crispiloba disperma* (S. Moore) Steenis from Queensland. Previously, the component taxa were variously treated as having diverse affinities. Van Steenis (loc. cit.) based his realignment upon floral and leaf characters, although the comparative evidences used were often desultory and not always compelling.

It has recently been observed that all three genera brought together by van Steenis are characterized by narrow vessel elements with primitively scalariform perforation plates composed of a high number of bars (Dickison 1986). Since the basic premise of cladistic philosophy holds that such primitive character states are of no value in establishing phylogenetic relationships, these character states, although phenetically useful, do not provide convincing evidence that the three genera form a natural unit, or to what group they are most closely allied. More meaningful in this case is the shared possession by all taxa of the clearly derived wood character states of living septate fibers that store starch at maturity. The scarcity and even absence of axial parenchyma in addition to pores that are distributed as a combination of both solitary elements and radial multiples are

also derived features. Septate fibers, in particular, often tend to be common throughout natural groups and, when coupled with the retention of a living protoplast, form an extremely useful apomorphic index of affinity (Metcalf and Chalk 1983).

A study of the young stem and leaf anatomy of the *Alseuosmiaceae* was undertaken in order to provide additional evidence to clarify problems of family relationships and generic affinity.

#### MATERIALS AND METHODS

Leaves and young stems were prepared by standard methods of paraffin embedding and sectioning. Staining was accomplished with safranin-fast green. Both FAA-preserved and dried specimens were examined. Dried materials were initially reexpanded in dilute NaOH and treated as if preserved in FAA. Nodes were serially sectioned, and petiole vascularization was studied by obtaining sections throughout the length of the petiole. Stomatal patterns were observed in prepared paradermal sections. Stomatal dimensions were based on twenty measurements. Leaf venation was examined using leaves cleared in 5% NaOH at 60 C followed by staining with safranin. Drawings were made from prepared and stained sections with a Wild Heerbrug camera lucida.

*Specimens examined.*—*Alseuosmia banksii* A. Cunn. NEW ZEALAND: coll. unknown s.n. (A).—*A. linariifolia* A. Cunn. NEW ZEALAND: Kirk s.n. (A).—*A. macrophylla* A. Cunn. NEW ZEALAND: Gardner 1021 (AKU); Sampson s.n. (A).—*A. pusilla* Colenso. NEW ZEALAND: Gardner 1032 (AKU); Sampson s.n. (A).—*A. quercifolia* A. Cunn. NEW ZEALAND: Masamer 30 (A).—*Crispiloba disperma* (S. Moore) Steenis. AUSTRALIA, QUEENSLAND: Hyland 6762 (BRJ); Gray 3964 (QRS, NCU).—*Wittsteinia balansae* (Baillon) Steenis. NEW CALEDONIA: McPherson 5963 (MO, NOU); Deplanche 413 (AKU).—*W. papuana* (Steen.) Steenis. NEW GUINEA: (type) s.n. (A).—*W. vacciniacea* F. Muell. AUSTRALIA, Victoria Lake Mtn.: Palsler & McConkie s.n. (MEL, NCU).

#### RESULTS

##### *Axis (Young Stem, 1–3 mm in Diameter)*

Unicellular, bicellular and multicellular, unbranched, and living trichomes are occasionally present in the epidermal layer of *Alseuosmia* and *Wittsteinia vacciniacea*. Hairs are thick walled, with a tapering apex and broad or bulbous base within which the nucleus resides (Fig. 13). All members of the family possess a distinctive hair type in the leaf axils, these hairs are multicellular and uniseriate, and contain dark, reddish pigment. The smooth cuticle is thin or moderately thick. The epidermis is uniseriate, and cells are square or rectangular in transectional outline and have a procumbent or, as in *W. vacciniacea*, erect orientation. Outer walls are flat or sometimes dome shaped or conical, occasionally approaching the papillate condition in *Crispiloba*.

The cortex is differentiated into an outer collenchymatous region, and an inner zone of large, thin-walled parenchyma cells. The inner cortical cells of *Alseuosmia* and *W. vacciniacea* are loosely arranged with abundant intercellular space. Some cortical cells of *Crispiloba* are conspicuously enlarged, and all have dark-staining amorphous contents. Cortical and pith cells may also contain small, dark deposits. Similar appearing contents occur in scattered cells of *Alseuosmia*. Very thick-walled brachysclereids, as well as elongate fibrosclereids, are distributed throughout the cortex of *Crispiloba*.

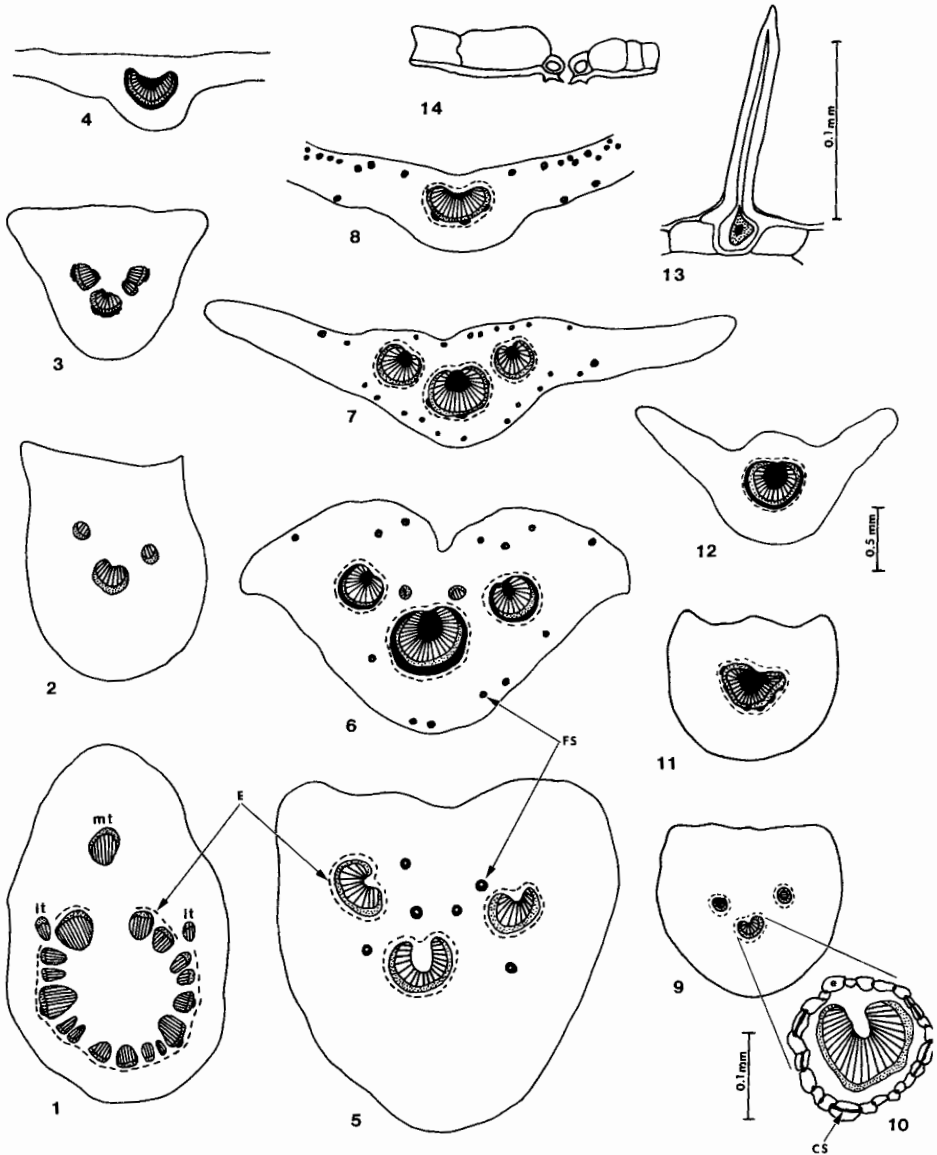


Fig. 1-14. Camera lucida drawings of stem and leaf anatomy Alseuosmiaceae.—1-4. *Wittsteinia balansae*.—1. Transverse section of node showing trilacunar, 3-trace condition and presence of an endodermis (E).—2. Transverse section of proximal region of petiole showing three vascular bundles. Note absence of endodermis.—3. Transverse section of distal end of petiole.—4. Transverse section of midrib illustrating single, arc-shaped vascular strand.—5-8. *Crispiloba disperma*.—5. Transverse section of proximal end of petiole showing fibroclereids (FS).—6. Transverse section thru midlength of petiole.—7. Transverse section of base of lamina.—8. Transverse section of midrib at midlength of lamina.—9-12. *Alseuosmia pusilla*.—9. Transverse section of proximal end of petiole.—10. Enlargement of vascular bundle illustrating surrounding endodermis and casparian strip (CS).—11. Transverse section thru midlength of petiole showing open vascular strand with incurved margins.—12. Transverse section of the base of the lamina.—13-14. *Wittsteinia vacciniacea*.—13. Unicellular, unbranched trichome from stem. Note nucleus in enlarged hair base.—14. Transverse section of stomata from abaxial leaf surface. Note cuticular ridges on guard cells. Xylem, striped; phloem, dotted; sclerenchyma, solid black.

In all species the innermost layer of the cortex is differentiated into a well-defined uniseriate endodermis. Endodermal cells are thin walled, elongate along the tangential axis, and oval or elliptical in transverse view (Fig. 22, 29). Walls are provided with modified areas in the form of casparian strips that extend as bands around the radial and transverse walls (Fig. 21, 29). In sectional view the casparian strips are seen as thickened areas or dots on the radial wall.

Vascular tissue forms a complete cylinder early in development in *Alseuosmia*, *Crispiloba* and *Wittsteinia vacciniacea*, whereas a ring of discrete vascular bundles is present in *W. balansae*. In younger stems a few scattered aggregations of perivascular fibers are present in *W. balansae* and *W. vacciniacea*. The pith is circular and typically heterogeneous. Pith cells of *Alseuosmia*, *Crispiloba*, and *W. vacciniacea* are moderately thick walled and pitted. Thick-walled sclereids occur in the pith of *Crispiloba*. The central pith region of young stems of *W. balansae* is composed of thin-walled parenchyma, whereas peripheral pith cells and those in interfascicular regions develop pitted, secondary walls. As the stem matures, all pith cells become sclerified.

#### *Bark (of Mature Stem)*

The secondary phloem forms a continuous cylinder in *Alseuosmia*, *Crispiloba* and *Wittsteinia balansae*. In *W. vacciniacea* the phloem is located in discrete, hemispheric patches around the perimeter of the xylem, with each phloem region associated with a well-developed fibrous cap. The functional phloem is composed of thin-walled elements without mechanical tissue. Very thick-walled sclereids occur as isolated elements, or as small groups, throughout the older phloem of *Crispiloba*. A discontinuous, one- to three-layered, ring of sclerified parenchyma differentiates in the older, more peripheral phloem of *Alseuosmia*.

The cortex is delimited from the vascular tissue in *Alseuosmia* and *W. vacciniacea* by a darkly-staining endodermal layer, that in older stems is made up of cells, with uniformly thickened walls. An irregular ring of thick-walled, pitted sclerenchymatous cells that show all intergrades from fibers to sclereids separates phloem and cortex in *W. balansae*. Neither a recognizable endodermis nor a perivascular sclerenchymatous ring is present in older stems of *Crispiloba*. The persistent cortex is divided into an inner parenchymatous zone and an outer collenchymatous region. Very infrequent, elongate fibrosclereids occur in the cortex of *Alseuosmia*, whereas large, extremely thick-walled sclereids are scattered throughout the cortical tissue in *Crispiloba*. The entire cortex becomes generally sclerotic in *W. balansae*.

The continuous phellogen arises in the outer layers of the cortex and produces a rather narrow, thin-walled phellem that in transection consists of rectangular-shaped cells. Cork cells of *Crispiloba* are occasionally thick walled and sclerotic.

#### *Node and Petiole*

Nodes are uniformly trilacunar, three-trace. Traces are collateral and the median and lateral strands diverge from the cauline system at approximately the same level (Fig. 1). The median trace is typically larger than the two laterals.

At proximal levels, petioles are always provided with three separate bundles. The bundles vary between collateral, C-shaped or nearly concentric in outline

(Fig. 2, 6, 7, 9). The vasculature of *Alseuosmia* undergoes lateral fusion at medial levels of the petiole, or within slightly more distal levels, and forms a single open vascular strand with incurved margins (Fig. 9–12, 27). In *Crispiloba* and *Wittsteinia* the three bundles extend the length of the petiole unfused, although small concentric subsidiary bundles may interconnect the major veins, (Fig. 2, 3, 5–7, 23).

A single arc-shaped midvein forms at the base of the lamina in *W. balansae* (Fig. 4) and *W. papuana* (Steen.) Steen., whereas the petiole vasculature remains uncombined into the lamina in *Crispiloba* and *W. vacciniacea*.

Except for *W. vacciniacea*, abaxially and adaxially positioned, fibrous bundle caps develop at distal regions in the petiole. In addition, each vascular bundle of the petiole is surrounded by a clearly identifiable endodermis, containing cells that possess a bandlike casparian strip on the transverse and radial walls (Fig. 6, 7, 9–12). A recognizable endodermis is absent only in petioles of *W. balansae* (Fig. 2, 3).

Unicellular and multicellular trichomes are present on the petioles of *W. vacciniacea*. A uniseriate epidermis, consisting of conspicuously erect cells in *W. balansae*, covers a cortical region that is divided into 1–3 layers of subdermal, thick-walled collenchyma and an inner zone of loosely arranged parenchyma. Brachysclereids and rod-shaped macrosclereids occur as isolated idioblasts throughout the cortex, particularly at proximal levels of the petiole, in *Alseuosmia quercifolia*, A. Cunn., *A. linariifolia*, A. Cunn., *A. macrophylla* A. Cunn., *A. pusilla* Col., as well as *Wittsteinia papuana*. The cortex of *Crispiloba disperma* contains numerous elongate fibrosclereids that are oriented parallel to the long axis of the petiole (Fig. 5, 6).

### Lamina

*Epidermis.*—A thin cuticle covers both epidermal surfaces. Both epidermides are uniseriate, and composed of square or rectangular-shaped cells with generally flat outer walls in transectional view (Fig. 15, 19, 20). The exposed outer walls of *W. vacciniacea* are occasionally slightly curved or pointed. Cells of the adaxial epidermis range from distinctly larger to more commonly only slightly larger than those of the lower surface. Epidermal cells over the midrib of *Crispiloba* and *W. balansae* are comparatively small and have dome-shaped outer periclinal walls. Epidermal cells have thickened outer periclinal walls in *Crispiloba* and *Wittsteinia*, whereas walls are uniformly thickened in *Alseuosmia* (Fig. 20). In surface view epidermal cells have curved or more commonly undulate and deeply lobed anticlinal walls (Fig. 18).

Stomata are confined to the abaxial surface and are level with the unspecialized epidermal cells. Guard cells have prominent outer cuticular ledges or rims. In *W. vacciniacea* double outer guard cell ridges are present (Fig. 14). Mature stomata are anomocytic (sensu Metcalfe and Chalk 1950) (Fig. 18), and guard cell pairs range between 25–40  $\mu\text{m}$ , mostly 30–35  $\mu\text{m}$ , in length, and 25–35  $\mu\text{m}$ , mostly 27–33  $\mu\text{m}$ , wide.

*Mesophyll.*—The mesophyll is bifacial in structure, although generally not strongly differentiated into palisade and spongy layers (Fig. 15, 19, 20). The palisade parenchyma is uniformly one layered, and in *Alseuosmia*, *Crispiloba* and *Wittstei-*

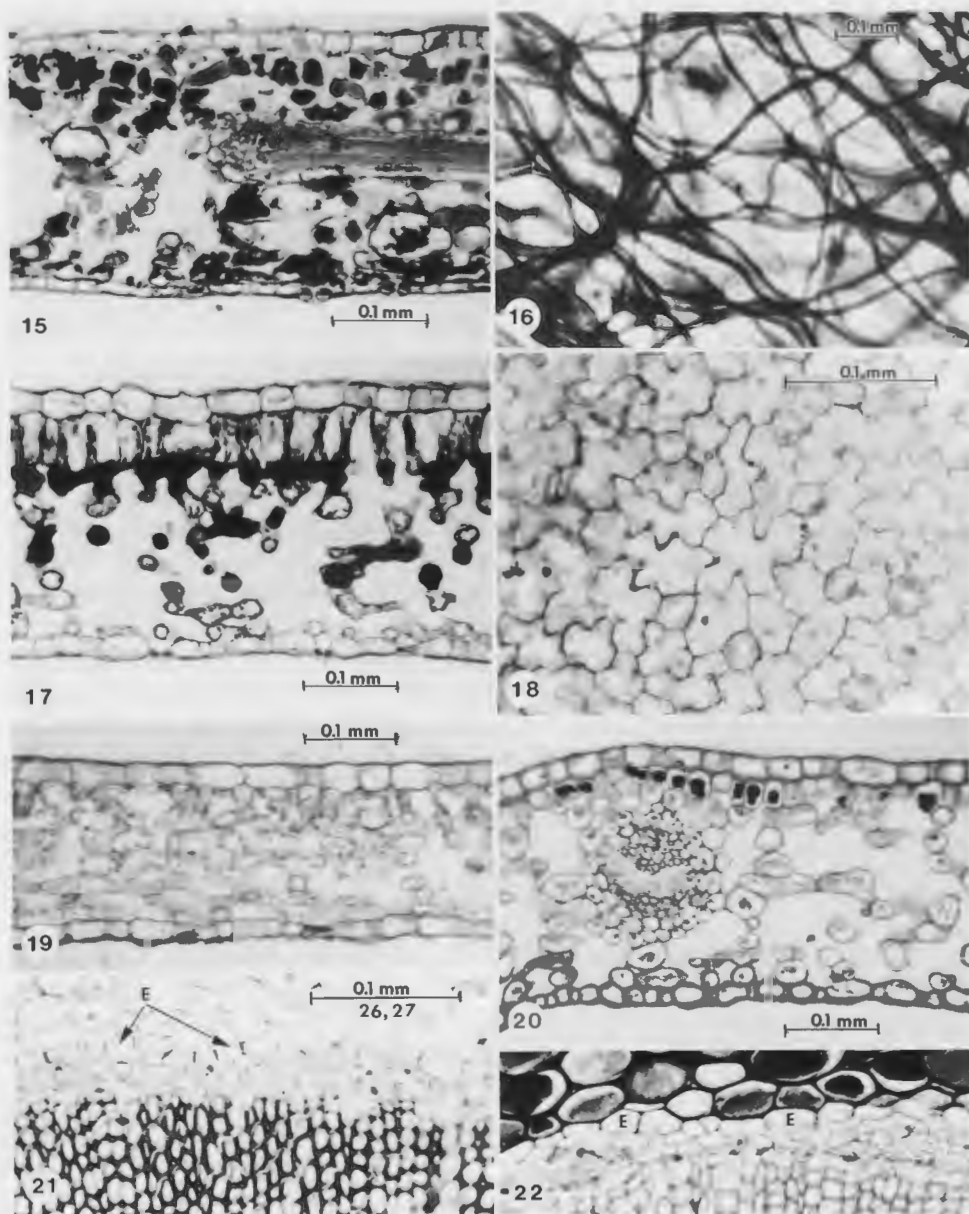


Fig. 15–22. Stem and leaf anatomy of Alseuosmiaceae.—15–16. *Crispiloba disperma*.—15. Transverse section of lamina showing poorly differentiated mesophyll and abundant intercellular space.—16. Cleared leaf illustrating numerous filiform sclereids.—17–18. *Wittsteinia vacciniacea*.—17. Transverse section of lamina. Note uniseriate palisade region and loosely organized spongy tissue.—18. Paradermal section of abaxial epidermis showing anomocytic stomata and epidermal cells with undulate anticlinal walls.—19. *W. balansae*; transverse section of lamina showing weakly differentiated mesophyll.—20. *Alseuosmia banksii*; transverse section of lamina in vicinity of a major vein. Note abaxial fibrous bundle cap and enclosing parenchymatous sheath cells.—21. *Wittsteinia balansae*; transverse section of stem showing endodermal cells (E) with thickenings on the radial walls.—22. *W. vacciniacea*; transverse section of stem showing well-defined endodermis (E).

*nia balansae* is composed of very short cells that are often nearly indistinguishable from spongy mesophyll cells. The palisade cells of *W. vacciniacea* are longer in comparison (Fig. 17). The spongy mesophyll occupies the majority of total mesophyll space and consists of very loosely arranged cells. Mesophyll cells contain a darkly staining substance in *Crispiloba*.

Large numbers of filiform or fibrosclereids are present in the mesophyll of *Crispiloba disperma*, where they are oriented parallel with the surface of the lamina (Fig. 16). The sclereids are particularly concentrated in the palisade region. These slender cells are of great length with tapering ends, and have a very irregular shape. The cells are only rarely branched. Their walls are very thick, lignified, and sparsely pitted. The extensive development of these sclereids results in an interwoven mass of cells that permeates the mesophyll. Numerous diffuse, lobed or armed, more or less rod-shaped sclereids are distributed in the cortex of the midrib along either side of the midvein in some collections of *Wittsteinia balansae* (e.g., McPherson 5963). These cells are moderately elongated with blunt ends, and have only slightly thickened, lignified walls.

*Venation and bundle sheathing.*—Leaves of *Alseuosmia* and *Wittsteinia balansae* are pinnately veined, since the petiole vascular supply emerges as a single primary vein that subsequently serves as the origin for higher order venation (Fig. 23, 27). The midvein of *Alseuosmia* may follow a rather sinuous course toward the leaf apex.

*Wittsteinia vacciniacea* is distinguished by an acrodromous venation pattern in which three bundles emerge from the petiole, and become a strong medial primary vein and two thinner, laterally positioned, basal secondary veins (Fig. 24). The secondaries extend in convergent arches toward the leaf apex. The midrib of *Crispiloba* is initially multistranded, containing three closely spaced, vertically extended primary veins of approximately equal thickness. At a level about midway between leaf apex and base the medial and two lateral primary veins fuse, forming a single midvein (Fig. 26). The resulting midvein, as in all *Alseuosmiaceae*, has the form of a crescent-shaped bundle (Fig. 4, 8).

Secondary venation is brochidodromous or semicraspidodromous. Species with entire leaf margins, such as *Crispiloba disperma* and *Wittsteinia balansae*, have brochidodromous venation (Fig. 31). The presence of marginal teeth is correlated with semicraspidodromous venation, in which the secondaries branch within the leaf margin, one of the branches terminating in a marginal tooth, the other joining the super-adjacent secondary (Fig. 24, 27). Occasionally in *Alseuosmia* the secondary veins may terminate directly at the tooth apex.

Tertiary venation is random reticulate or infrequently weakly percurrent. High order veins form incomplete or imperfectly developed areoles of irregular shape and variable size. Free vein endings are mostly branched, and terminate in narrow veinlets composed of linear tracheids, or as in *Crispiloba*, clusters of tracheary cells.

The glandular teeth of *Alseuosmia* have hydathodal swellings at the tip and are vascularized by either a single veinlet that is broadened or flared at the end, or as can be observed in *A. linariifolia*, by three veins, a large medial vein that usually originates as a branch bundle from the arching secondaries, and two weaker laterals that converge upon the medial vein at its distal end, where the three veins may or may not fuse (Fig. 28). Sometimes only a single lateral vein is present. The



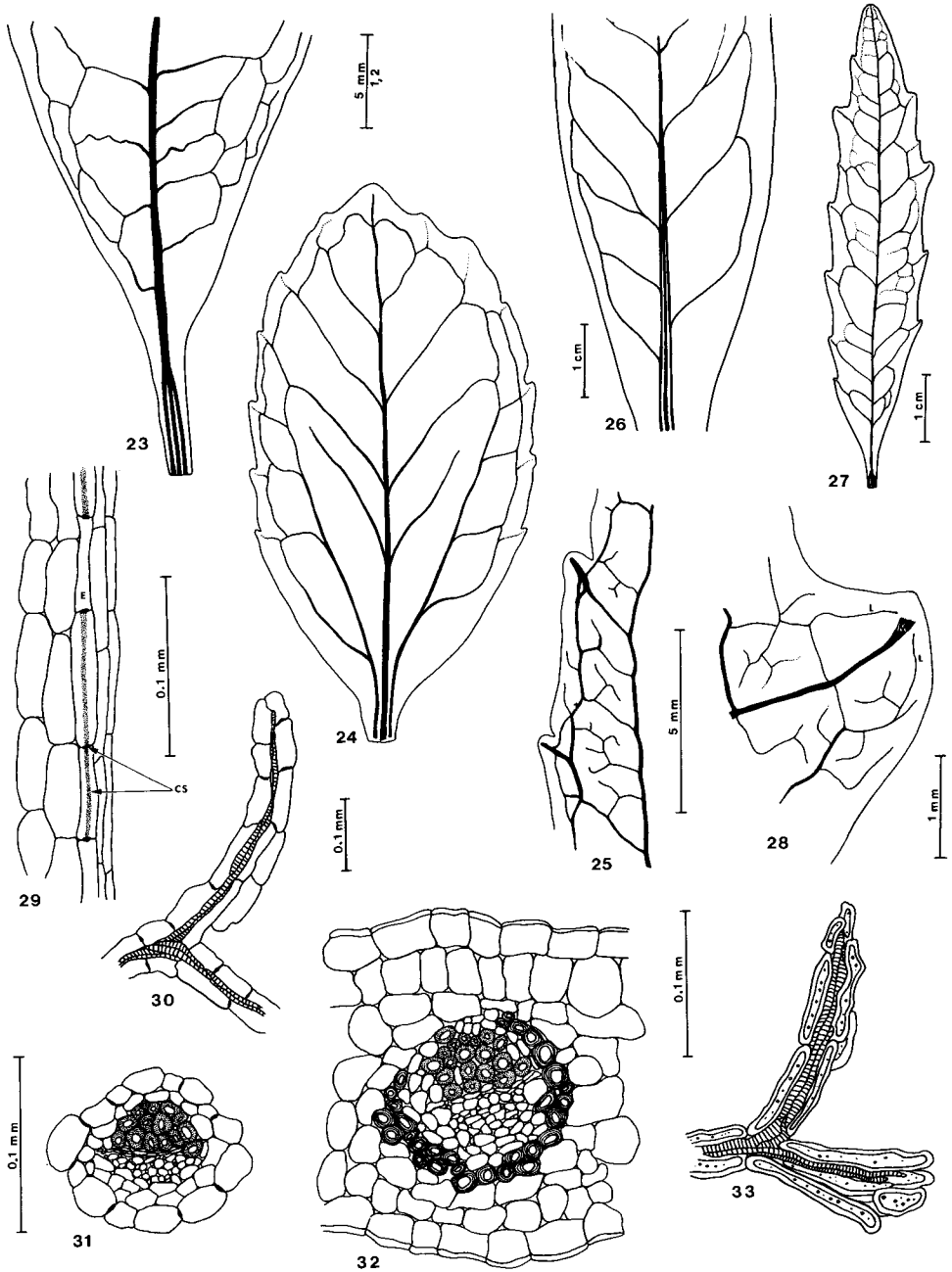


Fig. 23–33. Camera lucida drawings of leaf and stem anatomy of Alseuosmiaceae. — 23. *Wittsteinia balansae*; lower third of cleared leaf showing mature venation pattern. — 24. *W. vacciniacea*; cleared leaf showing acrodromous venation pattern. — 25. *W. vacciniacea*; cleared leaf showing details of tooth vascularization. — 26. *Crispiloba disperma*; portion of lower third of lamina illustrating multistranded primary venation. — 27. *Alseosmia linariifolia*; leaf showing semicraspidodromous venation. — 28. *A. linariifolia*; details of tooth vascularization. Note medial (M) and two lateral (L) tooth veins. — 29. *W. balansae*; longitudinal section of stem endodermis (E) showing the casparian strips (CS) in face view and as radial wall thickenings. — 30. *Alseosmia linariifolia*; leaf veinlets showing sheath composed of

marginal teeth of *Wittsteinia vacciniacea* are also supplied by a median vein that is joined at right angles by two accessory or lateral veins within the tooth base (Fig. 25). The central vein extends into the tooth and terminates at the tooth apex as a plexus of loosely arranged tracheary elements.

Fibers are positioned abaxial to the primary vein, or veins, in all taxa except *Wittsteinia vacciniacea*, in which sclerenchyma is entirely absent from the leaves. Secondary and higher order veins of *Crispiloba* are surrounded by one or two layers of large sheath cells that are thin walled and parenchymatous in appearance, very elongated parallel to the course of the vein, and that are modified by a deposition of lignified or suberized material on the radial walls (Fig. 31). A true casparian strip encircling the cell is not evident.

The major veins of *Alseuosmia* have abaxial sclerenchymatous caps, external to which is a uniseriate or biseriate parenchymatous sheath (Fig. 20). Sclerenchymatous elements may also be present as isolated fibrous cells adjacent to the higher order venation. The thin-walled sheathing cells are continuous around the free vein endings as a one or two-layered sheath of large, elongate, endodermoid cells (Fig. 30, 31).

A foliar endodermis is absent from all specimens now referred to as *Wittsteinia balansae*, and a lignified, sclerenchymatous sheath consisting of elongated, pitted, fibrous elements encircles, or nearly encircles, the major and intermediate-sized veins (Fig. 32). Elongate fibrous elements, as well as some sclerotic cells resembling sclereids, also occur as a continuous or discontinuous sheath, or cluster of cells, next to the ultimate vein endings, sometimes extending beyond the terminal tracheary elements (Fig. 33). The fibrous cells are mostly oriented parallel with the veins, only rarely extending at right angles into the mesophyll. The outer walls of the sheath cells are lobed or wavy in outline.

Only the midvein and major secondaries of *W. papuana* have an abaxial covering of fibers. Sclerenchyma is entirely absent from leaves of *W. vacciniacea*. The major and minor veins of both species are surrounded by clearly differentiated parenchymatous sheath cells that, at least in *W. vacciniacea*, have no specialized wall characteristics. Sheath cells associated with the major veins are typically devoid of chloroplasts, whereas those around minor veins contain numerous plastids.

#### DISCUSSION

Prominent stem and leaf anatomical features of the Alseuosmiaceae include: a trilacunar, three-trace leaf-node structure in which petioles are supplied with three separate vascular bundles; brochidodromous and semicraspidodromous venation; rosoid teeth bearing hydathodes; anomocytic stomata; unicellular, bicellular, and multicellular, unbranched trichomes; a superficial origin of phellogen; and leaf mesophyll composed of a uniseriate palisade region and loosely constructed spongy

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elongate endodermoid cells with thickenings on the radial walls.—31. *Crispiloba disperma*; transverse section of leaf vein showing ensheathing endodermoid cells.—32. *W. balansae*; transverse section of major leaf vein illustrating nearly complete sheath of fibrous elements.—33. *W. balansae*; ultimate leaf veinlets associated with thick-walled, pitted, sclerenchymatous cells.

zone. An aerenchymatous cortex occurs in *Alseuosmia* and *Wittsteinia vacciniacea*. Sclerenchyma occurs in stem tissues of species belonging to all three genera of the family. Brachysclereids, or armed and unarmed, rod-shaped sclereids, are restricted to the petiole or midrib of *Alseuosmia* and species of *Wittsteinia*. *Crispiloba disperma* from Queensland, in contrast, is readily distinguished from other family members by numerous elongate filiform or fibrosclereids distributed in the stem, petiole, and leaf mesophyll. *Wittsteinia vacciniacea* is the only taxon entirely lacking foliar sclerenchyma, either as bundle sheathing or in the form of idioblastic sclereids. Calcium oxalate crystals are absent from all vegetative tissues.

Major variation can be observed in the pattern of foliar vascularization, particularly as related to the degree of union and course of the petiole bundles and type of secondary venation. The New Zealand *Alseuosmia* shows the most extensive fusion of the petiole vasculature, characterized by the union of the three bundles at approximately in the middle of the length of the petiole. An opposite extreme is represented by *Wittsteinia vacciniacea*, in which three separate bundles emerge from the distal end of the petiole and immediately diverge, with the central strand continuing as the midvein of the lamina and the two lateral strands forming arching secondary veins. A structurally intermediate condition is present in *Crispiloba* where the three discrete petiole bundles extend into the midrib as a multistranded primary vein to a level approximately midway between leaf apex and base. The trends of specialization in leaf venation are unclear.

The most interesting anatomical feature of the young stems and leaves of *Alseuosmiaceae* is the occurrence of an endodermis. All members of the family have a morphologically differentiated uniseriate endodermis in the stem that is composed of cells with casparian strips in the form of bands on the radial and transverse walls. The same primary form of endodermis is also continuous around each vascular bundle in the petiole, with the notable exception of *Wittsteinia balansae*.

The lamina is variable with respect to the presence and structure of a vein sheathing endodermis. Major and minor veins of *Alseuosmia* and *Crispiloba* have an encircling layer of enlarged, parenchymatous appearing cells that are elongated along the course of the vein and that possess thickened, lignified or suberized radial wall layers. A true casparian strip is generally not evident and it is probably preferable to refer to these cells as endodermoid cells (Esau 1964). Morphologically similar cells also appear to be present in *Wittsteinia papuana*. Leaf veins of *W. vacciniacea*, however, have a clearly differentiated bundle sheath consisting of cells that resemble endodermal cells in form and arrangement but that lack recognizable wall modifications. The low and high order venation of the New Caledonian *W. balansae* in contrast, is associated with a sclerenchyma sheath. Carlquist (1975) suggested that sclerenchyma can sometimes substitute for a conventional endodermis in regulating water movement under certain climatic conditions. The *Alseuosmiaceae* show such a structural transition.

The presence of a stem and foliar endodermis is a relatively uncommon feature in woody dicotyledons and is additional compelling evidence in support of the generic realignments of van Steenis (1984). As presently constituted the family has a distinctive combination of derived stem and foliar anatomical characters. Woods of most species of *Alseuosmiaceae* show features that can generally be interpreted as arising from an herbaceous ancestry, such as raylessness or very high and wide rays of largely erect cells, although the ancestral habit of the group

remains uncertain since *Crispiloba* has seemingly retained a more primitive xylem structure. It is significant in this regard that the presence of an endodermis in the aerial organs of dicotyledons is largely confined to specialized or basically herbaceous groups (Esau 1964). It seems very likely that the family evolved from a small, shrubby ancestor, subsequently became semiherbaceous, followed by the development of a secondarily woody body in some taxa.

The totality of similarities of vegetative anatomy among several genera of Rosaceae, Saxifragaceae *sensu lato*, and Alseuosmiaceae reinforces the view that the Alseuosmiaceae have their nearest relatives within the rosalean-saxifragalean complex. This opinion agrees with conclusions reached from floral and ovular morphology (Philipson 1977) and has been followed by Cronquist (1981) and Thorne (1983). In addition to a similar xylem structure, rather widespread resemblances include trilacunar, three-trace nodes, unbranched and bulbous-based trichomes, and anomocytic stomata. The assertion by Airy Shaw (1965) and others of a close relationship between Alseuosmiaceae and Escalloniaceae is weakened, however, by the presence of unilacunar nodes in species of *Escallonia* (Stern 1974).

A significant character in relating the Alseuosmiaceae to the Saxifragales is the occurrence of an endodermis in the stem and leaf of some Rosaceae and herbaceous Saxifragaceae. An endodermal layer is well defined in stems of a number of rosaceous genera, including *Alchemilla*, *Fragaria*, *Gillenia*, *Kerria*, *Neviusia*, *Potentilla*, and certain species of *Rubus* (Metcalf and Chalk 1950). Anatomically distinctive petioles with concentric or hemiconcentric bundles, each surrounded by an endodermis, occur in *Alchemilla*. The petioles of many species of *Saxifraga* have three such bundles, each with a separate endodermis, thus markedly resembling the anatomy of Alseuosmiaceae. An endodermis has not been reported for any woody Cunoniaceae (Dickson 1975) nor for the following genera of woody Saxifragaceae: *Deutzia*, *Ribes*, *Hydrangea*, *Philadelphus*, and *Escallonia* (Stern 1974, 1978; Stern, Sweitzer, and Phipps 1970; Styer and Stern 1979*a, b*).

Also of significance is the occurrence in the Alseuosmiaceae of a foliar tooth structure that conforms to the general rosoid type as described by Hickey and Wolfe (1975). The rosoid tooth, with a hydathodal tip and vascularized by a major central vein accompanied by a pair of connivent lateral veins, has developed in a number of taxa in the Saxifragales and Rosales. Keating (1985) has suggested that this is a useful phyletic marker indicative of a Saxifragalean origin. One of the guiding principles of comparative anatomical study is that vegetative anatomy has been most reliable and significant in statements of negation of close relationship rather than positive assertion of relationship. The Alseuosmiaceae provide an example where stem anatomy offers definitive phylogenetic evidences showing that its component taxa are related, and for interpreting the affinities and habit transformations of the group.

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## FOOTNOTE

<sup>1</sup> Based on a presentation given at the XIV International Botanical Congress in Berlin, 22 April 1987, as part of the Rolf Dahlgren Memorial Symposium entitled "Steps toward the natural system of the Dicotyledons," chaired by R. F. Thorne and H. Huber.