

# ALZATEACEAE, A NEW FAMILY OF MYRTALES IN THE AMERICAN TROPICS<sup>1</sup>

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## ABSTRACT

The suggested affinities of the New World tropical genus *Alzatea* have included eight families in five orders since its discovery in the eighteenth century. Until recently, knowledge of the genus has been superficial, primarily limited to macromorphological features. Now evidence assembled from recently published and current research in anatomy, embryology, morphology, palynology, and cladistics of *Alzatea* and closely related genera allows a more accurate assessment of its relationships. Presence of internal phloem and vested pitting place the genus in the order Myrtales, while stem and nodal anatomy suggest no close affinities to any one family of the order. Embryologically, *Alzatea* is unique in Myrtales in having a bisporic *Allium*-type embryo sac, and shares only with the related genus *Rhynchocalyx* micropylar development by the inner integument. Pollen features are very generalized, relegating the genus to an ancestral position with respect to the pollen of close associates. Parietal placentation and transeptal vascular supply of the ovary and anatomically simple seed relate *Alzatea* to *Rhynchocalyx* (Rhynchocalycaceae) and genera of the Crypteroniaceae sensu stricto, *Crypteronia*, *Axinandra*, and *Dactylocladus*. *Alzatea* is most similar to *Rhynchocalyx*, sharing 27 of 43 selected attributes, followed by *Crypteronia* with which it shares 18 of 43 listed features. Differences between *Alzatea* and *Rhynchocalyx* are deemed sufficient to justify establishment of the family **Alzateaceae**. Plants of *Alzatea* with large, sessile leaves from Central America are recognized as *A. verticillata* subsp. *amplifolia* S. A. Graham, subsp. nov.

*Alzatea* is an enigmatic genus of Central and South America whose suggested affinities, since its discovery in the eighteenth century, have included eight families in five orders. The genus is represented by the single species, *Alzatea verticillata* Ruiz & Pavón. It is a small tree of tropical cloud forests, distinguished by broad, oblong, coriaceous leaves and multi-flowered compound inflorescences of small, apetalous, leathery flowers. These produce compressed, conspicuously veined, bilocular capsules with many thin, winged seeds. A history of the systematic placement of *Alzatea* has been presented by Lourteig (1965), who succinctly reflected that most studies on the genus were as much justification for its exclusion from particular families as arguments for certainty of relationships. The past several years have seen no diminution in shuffling of *Alzatea* from one family to another (Table 1).

Most recently, there has been an increased interest in the genus stimulated by the collaborative reassessment of the Myrtales, the order to which *Alzatea* most certainly belongs. New ob-

servations and data of diverse types for *Alzatea* and related families now allow an evaluation of the phylogenetic and taxonomic position of the genus in the Dicotyledoneae in a more complete way than was possible previously. The evidence for *Alzatea*'s position as a monotypic family of the order Myrtales is assembled from personal observations and the extensive studies of several specialists, with much of the information generated since the Myrtales symposium of the XIII Botanical Congress in 1981. This paper summarizes the most pertinent contributions of macromorphology, palynology, embryology, anatomy, and cladistics as the basis for recognizing the new family Alzateaceae.

## CHARACTERIZATION OF *ALZATEA*

*Macromorphology.* Hemi-epiphytic shrubs or small trees, 2–20 m tall, with stout, gray, roughened trunks or sometimes trunks slender and reaching the forest upper story supported by adjacent trees; branches glabrous, opposite or

<sup>1</sup> The following individuals are gratefully acknowledged for information shared: Peter Raven, Hiroshi Tobe, Thomas Croat, Alwyn Gentry, Sandra Knapp, James Solomon, Alan Graham, and Barbara Timmerman. John Kress kindly provided photographs of *Alzatea* in Panama, H. B. Nicholson and Tony Abbott provided photographs of *Rhynchocalyx* in Natal, and Joan Nowicke provided the scanning electron micrograph of *Alzatea* pollen. I am also indebted to the curators of CR, MO, and F for loan of herbarium collections of *Alzatea* and *Rhynchocalyx* for study.

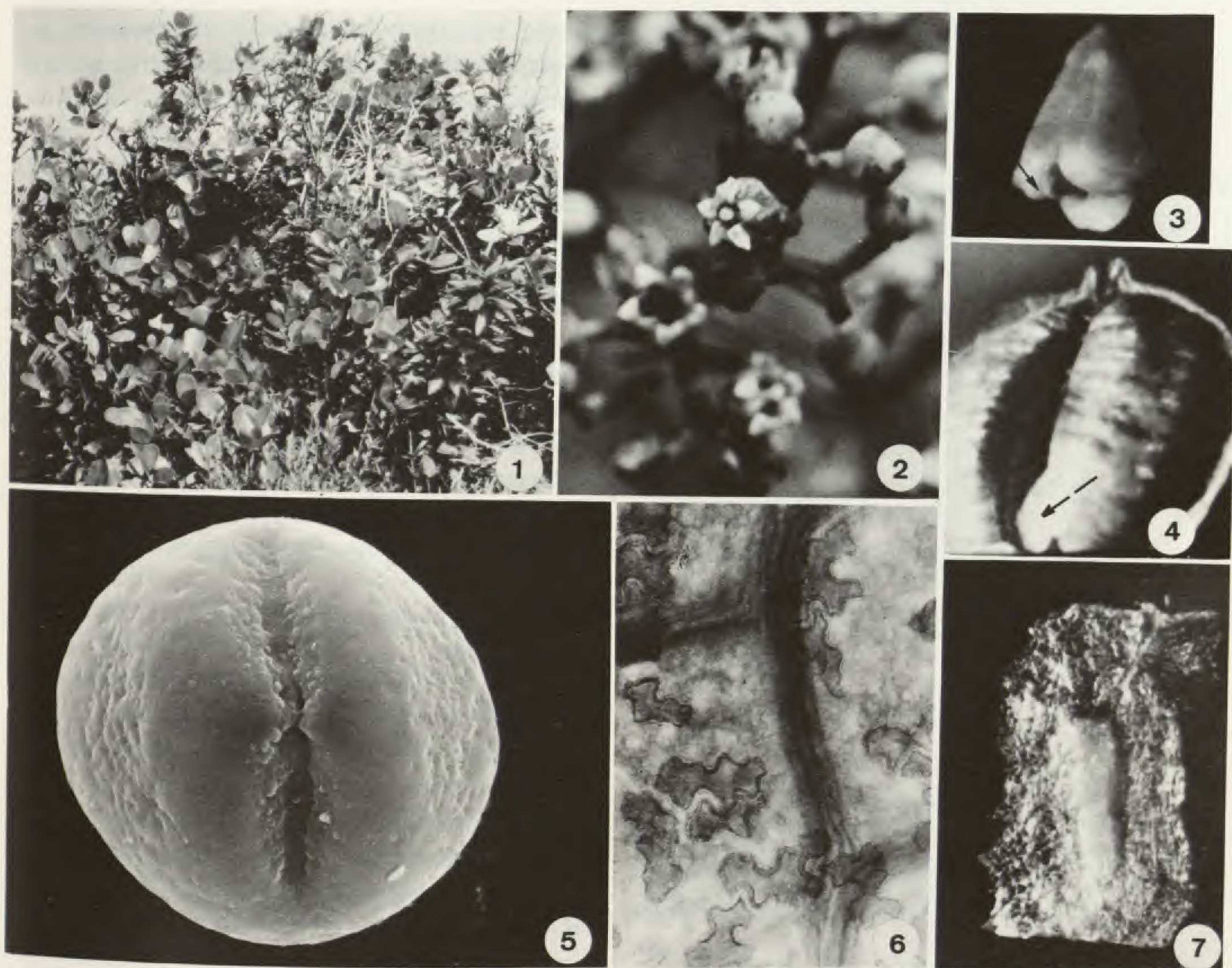
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TABLE 1. Systematic placement of *Alzatea* by selected authors.

Year	Author	Classification
1794	Ruiz & Pavón	Santalaceae (Between genera of)
1825	Candolle, A. P. de	Celastraceae
1826	Blume	Celastraceae, near
1845	Planchon	Lythraceae
1862	Bentham & Hooker	Celastraceae
1868	Candolle, A. L. P. P. de	Crypteroniaceae
1872	Miers	Rhamnaceae
1892	Loesener	Celastraceae, doubtfully
1911	Hallier	Lythraceae sensu lato
1918	Hallier	Melastomataceae sensu lato
1942	Loesener	Flacourtiaceae
1955	Willis	Celastraceae
1956	MacBride	Rhamnaceae (or Clusiaceae or Icacinaceae)
1965	Lourteig	Lythraceae
1966	Airy Shaw	Lythraceae
1967	Hutchinson	Flacourtiaceae
1975	van Beusekom-Osinga & van Beusekom	Crypteroniaceae
1981	Cronquist	Lythraceae, questionably

verticillate, distinctively purple-red, peeling, becoming red-brown with age; stems of the inflorescence distinctly 4-angled to narrowly winged, the young branches scarcely 4-angled, the mature branches round in cross section; nodes enlarged, especially knobby when branches are verticillate; leaf scars half-round to nearly circular, the base slightly raised, the bundles forming a crescent, U-shaped, or nearly closed-circular scar. *Leaves* mostly clustered at the ends of the branches, opposite, less often verticillate, simple, entire, stipulate, the stipules axillary, 2 to a few in the axils at the base of the petiole, the stem wings of the inflorescence also extended at the nodes into stipule-like projections; petioles none or short, thick, deep purple-red, to 13 mm long; blades oblong-obovate, elliptical, or oblong-oval, thick, leathery, lustrous above, 50–145 mm long, 25–100 mm wide, with blades of terminal leaves smallest and mostly about 70 mm long, 40 mm wide, the bases variable, attenuate to acute or rounding, commonly acute, the apices rounding, occasionally retuse, the venation brochidodromous, the secondary vein pairs 16–22, parallel, oriented at 45° to the prominent midvein. *Inflorescences* anthotelic, basically paniculate (sensu Briggs & Johnson, 1979, traditionally termed cymose) with each axis terminating in a flower, axillary at the ends of branches, 10–30 flowered, the pedicels 1.5–2 mm long, lacking bracteoles (prophylls), articulated at the base, the lateral flowers of a

cyme subtended at the base by small fugaceous fertile bracts, i.e., the bracts themselves subtending buds. *Flowers* actinomorphic, 5(–6)-merous, apetalous, bisexual, hemi-epigynous; floral tube leathery, green to yellow, conical in bud, open-campanulate at anthesis, 4–6 mm long, 4–7 mm wide, the thick, persistent, valvate lobes 3 mm long, extending nearly to the base of the floral tube, the interior surface of the lobes irregularly thickened and fleshy; nectary-disc 1 mm wide, lobed, extending from the ovary to the sinuses of the calyx lobes. *Stamens* 5, situated in the floral tube at the sinuses of the lobes, outside the nectary, alternating with the lobes; filaments green, stout, short, as long as the anthers; anthers dorsifixed, introrse, the connective broadly expanded, heart-shaped, pink with white edges, fleshy, at anthesis held at right angles to the filament with the distal apiculate apex extending out of the calyx between the lobes, thus simulating petals, the bisporangia positioned horizontally along the broad terminal end of the anther on each half of the connective, dehiscing longitudinally. *Gynoecium* slightly bilaterally flattened, with a capitate stigma and stout, short style 1 mm long; ovary bicarpellate, bilocular, placentation parietal, the placentae terminating shortly below the style on the inner ovary wall and septum; septum divided into 2 half-septa, the lower fourth provided with a circular opening; ovules horizontally imbricate in staggered



FIGURES 1-7. *Alzatea verticillata*. — 1. Short-shrub (2-3 m) habit of *A. verticillata* subsp. *amplifolia*, Knapp & Kress 4336, on Cerro Tute, Panama. Leafy branch in the lower right foreground belongs to the vegetatively similar *Clusia*. — 2. Closeup of flower at anthesis displaying five petal-like fleshy anthers. Actual flower diameter, 5 mm. — 3. Single stamen; line of microsporangial dehiscence indicated by arrow. Actual length, 1.75 mm. — 4. Interior view of one valve of the bivalved capsule, with septal hole apparent at the base of the septum (arrow) and style remnants visible above the septum. Actual length, 8 mm. — 5. Pollen of *A. verticillata* subsp. *verticillata*, Woytkowski 8331 (F). Actual diameter, 22  $\mu$ m. — 6. Branched sclereids of the leaf palisade tissue. Actual lengths, 92-155  $\mu$ m. — 7. Fertile seed with central embryo. Actual length, 2 mm.

vertical rows. *Fruit* an indurated, loculicidally dehiscent, reddish brown capsule, obcordate, 2-valved, compressed-flattened, to 8 mm long, 9 mm wide, with raised horizontal venation extending outward from the central septal vein on each side, subtended by the persistent, erect to spreading calyx lobes; remnants of the style persistent at the apex of each valve above the central vein. Seeds numerous, crowded in the capsule, ca. 20-30 per locule, thin, flat, the sterile seeds reddish brown with roughened surface, the fertile seeds yellow-brown, obliquely oblong to lunate, 2-3 mm long, 1-1.5 mm wide, the embryo central in the fertile seed, straight, encircled by the membranous wing, the cotyledons oblong to slightly spatulate, the stalk conical, directed to-

ward the micropyle; endosperm not apparent. Figures 1-7; see also Dahlgren and Thorne (1984, Fig. 11), for general habit and floral and fruit morphology.

*Ovary morphology and anatomy.* Ovary bicarpellate, bilocular, and bilateral, at anthesis 3 mm long, 1 mm wide, with suggestion of venation apparent on outer walls, particularly in the center of each slightly compressed side. Venation consisting of a dorsal and ventral supply; dorsal bundle one per carpel, with a few short branches only and independent of the ventral supply; ventral bundles of opposing carpels distinct, positioned laterally in the septum, two on each side of center in each half septum; ventral bundle branches traveling  $\pm$  horizontally through the

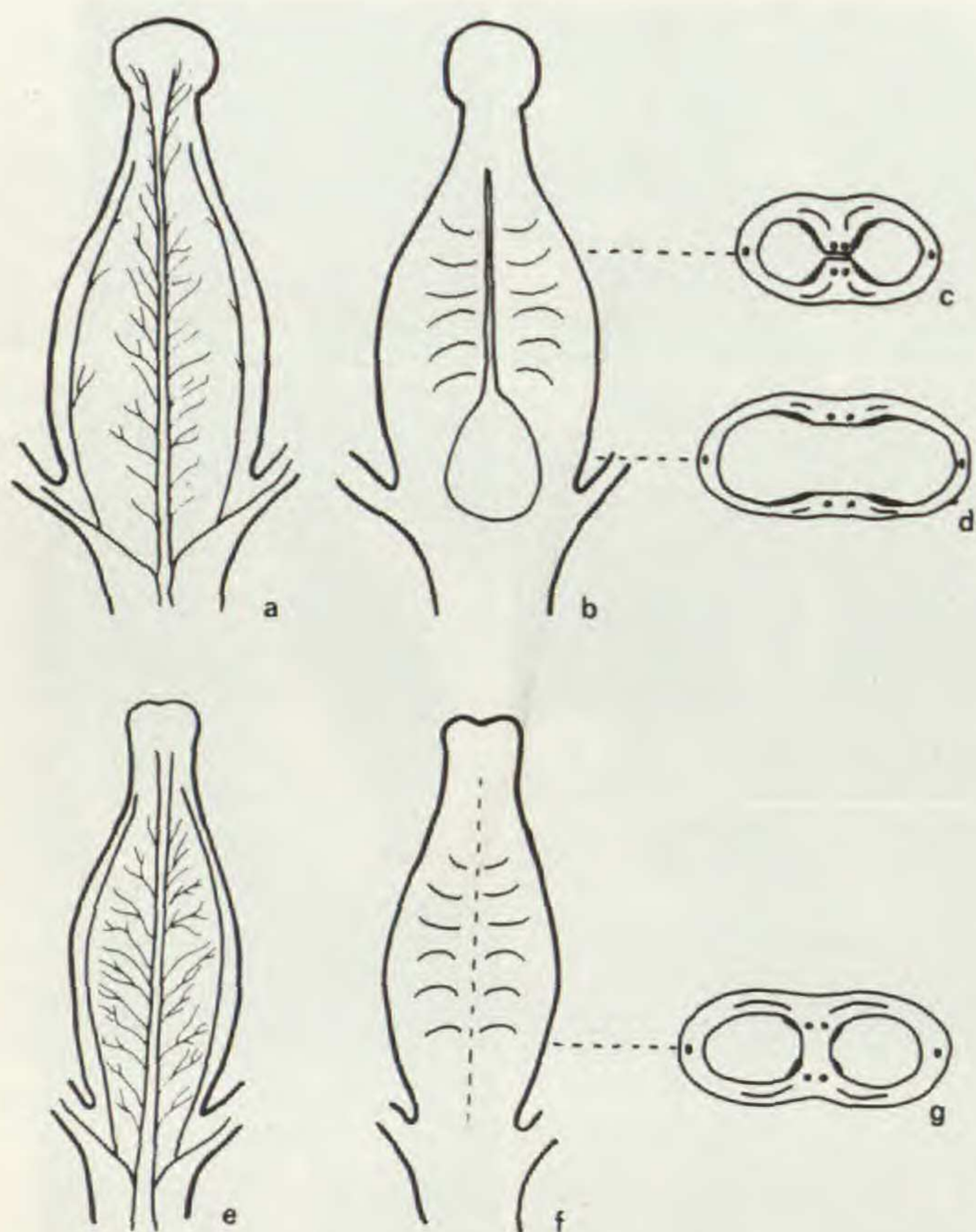


FIGURE 8. a-d. Diagrammatic ovary of *Alzatea verticillata*.—a. Loculicidal plane, with paired ventrals flanked by single dorsal veins.—b. Septal plane, with split septum and basal septal hole.—c. Cross-section at mid to upper ovary level; paired ventral veins and dorsals represented by dark circles, placental regions accentuated to indicate position on inner carpel walls.—d. Cross-section at level of basal opening. e-g. Diagrammatic ovary of *Rhynchocalyx lawsonioides*.—e. Loculicidal plane.—f. Septal plane with complete septum.—g. Cross-section; paired ventral veins and dorsals represented by dark circles, placental regions accentuated to indicate position on inner carpel walls.

septum to supply the ovules and carpel walls. Septum incomplete at the base due to the presence of a central opening in the basal fourth of the septum, septal margins meeting above the opening, but free, not fused at anthesis. Placental region spreading laterally on the carpellary walls, broad, to 1.5 mm wide, terminating ca. 1 mm from the apex of the ovary. Ovules stacked horizontally in vertically staggered rows and superposed in the locules. Figure 8a-d.

The capsule of *Alzatea* has been described elsewhere as unilocular with a false septum developing from the walls of the capsule inward as the fruit matures (Lourteig, 1965). The half septa with basal opening are, in fact, present in the young ovary, their free margins parallel and touching. They separate with dehiscence and subsequent opening of the capsule.

*Seed morphology.* Seeds bilaterally com-

pressed, horizontally layered in the capsule. Fertile seeds yellowish brown when dry, irregularly rectangular to lunate, frequently with a tail at the chalazal end, 2-3 mm long, 1-1.5 mm wide; embryo central in the seed and winged all around, straight with plane, oblong to spatulate cotyledons, the stalk conical, 0.25-0.33 the length of the embryo, the raphe bundle ending at the chalaza. Outer integument (testa) two-layered, the cells reticulate-scalariform, the outermost layer of cells elongate with thin, undulating walls, composing most of the seed wing, the inner layer crushed. Inner integument (tegmen) two-layered, both layers crushed at seed maturity. Sterile seed (ca.  $\frac{1}{3}$  of total seed) reddish brown when dry, primarily crescent-shaped with curved tail, 2-3 mm long, 1-1.5 mm wide, 0.5-1 mm thick on the convex side; raphe bundle on concave side, ending at the chalaza. Testa of densely packed, radially elongate palisade cells with straight walls on the convex side, the remainder of seed coat composed of irregularly arranged, crowded, short, cuboidal or irregularly shaped cells. Central cavity present, no embryo development apparent. Figure 7.

*Pollen morphology.* Pollen prolate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 14  $\mu\text{m}$  long, extending within 4-5  $\mu\text{m}$  of pole (PI 0.22), P/E 1.1, margins invaginated and slightly diffuse, tapering to acute apex with some sexine modification (granulations) extending to poles, ectexine bridge over pore, pore circular, diam. 3-4  $\mu\text{m}$ , situated at midpoint of colpus; wall 1.5-2  $\mu\text{m}$  thick, psilate bordering colpi, verrucate-areolate in elongated mesocolpal region suggesting faint subsidiary colpi; tectate; 18-22  $\mu\text{m}$  by 16-20  $\mu\text{m}$ . This description was provided by Alan Graham, Department of Biological Sciences, Kent State University, Kent, Ohio. Figure 5.

The above description is based on *Klug 3349* (F) and *Woytkowski 8331* (F), both of South American origin with fully developed pollen from functionally bisexual flowers. Pollen fertility in both collections is 97%, based on a count of 200 grains stained in cotton blue in lacto-phenol. In Central American plants pollen fertility is very low and few grains are well-formed. Pollen fertility does not exceed 36% in the Costa Rican collections examined by Tobe (unpubl. data). No fertile pollen has been observed in the Panama collection of *Knapp & Kress 4336* (MO).

Pollen of *Alzatea* has also been described and

illustrated by Muller (1975) as part of a survey of the pollen of the Crypteroniaceae.

*Anatomy.* The following account is condensed from the detailed investigations of van Vliet (1975), Baas (1979), and Keating (1984). *Leaf:* Stomata abaxial only, anomocytic to nearly cyclocytic with subsidiary cells slightly submerged below guard cells. In transverse section, blade dorsio-ventral, 380–440  $\mu\text{m}$  thick. Adaxial epidermal cells mainly square, larger than the abaxial ones. Adaxial, 1–2 layered hypodermis present, limited to each side of midrib or extending over midrib. Palisade tissue 2-layered with abundant large, short-branched astroscleroids. Spongy mesophyll compact, mostly sclerified. Midrib a flattened cylinder with abaxial and adaxial plates and a central lacuna, secondary veins circular in outline, collateral. Scattered druses present in lower mesophyll and near the veins. *Figure 6. Node:* Trilacunar with three traces. *Stem:* Epidermal cells square. Cortex of parenchyma interspersed with stone cells and 1–4 more or less centric cortical bundles in each corner of the 4-angled twig. Cork arising next to perivascular sclerenchyma, the phellem cells in late stages forming alternating layers of flat, thin-walled cells and square cells with unilateral wall thickenings. Primary phloem mostly sclerified in older material. Secondary phloem of sieve tubes, companion cells, chambered parenchyma and infrequent phloem fibers. Secondary xylem with faint growth rings. Vessels diffuse, 36/ $\text{mm}^2$ , solitary and in radial multiples of 2–4. Vessel members (330–)530 and 570(–750)  $\mu\text{m}$  long, mostly with long tails. Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, with vesturing abundant, spreading onto vessel walls to form diagonal bands. Vessel-ray pits large, simple, reticulate to scalariform. Thin-walled tyloses present in some vessels. Fibers (540–)960(–1240)  $\mu\text{m}$  long, walls thin, minutely bordered to simple pits, septate and/or gelatinous. Gelatinous fibers in tangential bands in young material. Parenchyma very scanty paratracheal. Rays heterogeneous I–II type, 1–3 seriate, usually with central portion of procumbent cells. Primary xylem and internal phloem in a continuous ring. Pith of lignified parenchyma. Druses abundant in chambered phloem parenchyma.

*Chemistry.* Leaves of *Alzatea* contain ellagic acid and flavonoid mono- and di-glycosides, including 3-OH flavonols. [Leaves of *Hammel 6247* (MO) were extracted using standard methods

outlined by Bate-Smith (1962). A chromatographic  $R_f$  value of 0.32 was obtained in Forestal solvent, after ethyl acetate extraction. Additional leaf material extracted in 80% methanol was spotted on cellulose TLC plates. Plates were developed in two dimensions, (1) TBA (t-BuOH-HOAc-H<sub>2</sub>O; 3:1:1) and (2) 15% HOAc. The TLC patterns suggest the presence of flavonoid mono- and di-glycosides. Two-dimensional plates, developed for the hydrolyzed material, showed the presence of 3-OL flavonoids. Contributed by B. Timmerman, Institute of Arid Land Studies, University of Arizona, Tucson, Arizona.] The chemistry is consistent with its position in the Myrtales, an order especially characterized by the presence of ellagic acid and tannins (Bate-Smith, 1962; Hegnauer, 1969).

#### PROPOSED RELATIONSHIPS

The relationships suggested for *Alzatea* encompass eight families in five orders of two subclasses (Table 2). Obviously this problematic genus displays a number of floral and vegetative characteristics widespread within the dicotyledons, especially in the subclass Rosidae. Such a diverse assortment of suggested affinities has been based primarily on either shared ancestral features which supply limited or no useful information about its near relationships, or have focused on one or two parallel or convergent specializations while ignoring a preponderance of dissimilarities. Most proposals of relationship were made prior to the availability of data from anatomical, palynological, embryological, and chemical information about *Alzatea*. When all current evidence is assembled, few taxa are serious contenders as close relatives of the genus.

#### DISTANT RELATIONSHIPS AND NON-RELATED FAMILIES

Placement of *Alzatea* in the Flacourtiaceae as a separate tribe or subfamily was first suggested by Loesener (1942), who excluded the genus from his monograph of the Celastraceae. Loesener's suggestion was followed by Hutchinson (1967) who established the monotypic tribe Alzateeae in the Flacourtiaceae to accommodate it. The Flacourtiaceae are generally considered ancestral in the Violales and are highly diversified (Cronquist, 1981), so that several *Alzatea* features can be found within this diversity. However, these are attributes of wide occurrence in flowering plants and even collectively are useless as indi-

TABLE 2. Summary of family placement previously suggested for *Alzatea*, following Cronquist's (1981) classification.

Subclass Dillenidae	
Violales—Flacourtiaceae	
Theales—Clusiaceae	
Subclass Rosidae	
Celastrales—Celastraceae, Icacinaceae	
Rhamnales—Rhamnaceae	
Myrtales—Crypteroniaceae, Lythraceae, Melastomataceae	

cators of close relationship. For example, in *Alzatea* and the Flacourtiaceae there are trilacunar nodes, vessel elements with simple perforation plates, tricolporate pollen, parietal placentation (probably the character most influencing Hutchinson's placement of *Alzatea* in the Flacourtiaceae), and bitegmic, crassinucellate ovules. On the other hand, the family lacks such important Alzatean (and Myrtalean) features as internal phloem, presence of ellagic acid and flavonols in the leaves, and in contrast to *Alzatea* primarily displays alternate leaves with paracytic stomates, imbricate sepals and petals, free styles and stigmas, and seeds with abundant fleshy endosperm. No alliance of *Alzatea* and the Flacourtiaceae is acceptable by reason of these major morphological, anatomical, and chemical differences.

Affinity to the Clusiaceae was postulated only because of similar vegetative morphology. Where *Alzatea* and *Clusia* grow side by side, as in Panama, the similarity in leaf form and general habit is striking (S. Knapp, pers. comm.). The family Clusiaceae differs from *Alzatea*, however, in an overwhelming number of characteristics of all types. Among them are lack of internal phloem and vestured pitting, presence of unilacunar nodes, leaves with resin cavities and paracytic stomates, numerous stamens, gynoeceum of 3–5 carpels, mostly axile placentation, and tenuinucellar ovules.

The relationship of *Alzatea* to the hemi-parasitic Santalaceae was suggested by the placement of the protologue between two genera of the family. Links to the Santalaceae beyond the initial position in publication have not been proposed. As with the Clusiaceae, the Santalaceae lack internal phloem, have unilacunar nodes, and do not produce ellagic acid (Cronquist, 1981). They commonly have a 3-carpellate, unilocular ovary

with few unitegmic, tenuinucellar ovules, and a solitary seed with abundant endosperm, features absent from *Alzatea*.

*Alzatea* was first associated with the Celastraceae by A. P. de Candolle (1825), followed by Bentham in Bentham and Hooker (1862), who chose to ignore Planchon's view (1845) that the genus ought to be in the Lythraceae, not the Celastraceae. In a later volume of the "Prodromous" (1868), A. L. P. de Candolle removed *Alzatea* to the Crypteroniaceae following Blume (1826–1827). Loesener (1892), regarded *Alzatea* of doubtful membership in the Celastraceae. In his later treatment of this family (1942), after reading Hallier's (1911) more extensive descriptions of the genus, he excluded *Alzatea* altogether, suggesting instead that it be accommodated in the Flacourtiaceae, as a new subfamily or tribe. Besides lack of internal phloem, the Celastraceae have axile placentation, a major reason Loesener excluded *Alzatea* from the family. In addition, the sepals and petals are mostly imbricate, and the seeds are often arillate with abundant endosperm. Anatomically, the family differs from *Alzatea* in the presence of unilacunar nodes and secretory canals in the phloem. Even though the Celastraceae is a rather diversified family with several highly distinctive genera, it diverges from *Alzatea* in too many major characters to be considered the appropriate family for the genus.

Possible association of *Alzatea* with the Icacinaceae was suggested by MacBride (1956), but no specific reason was given to support this view. As with the Celastraceae, the number of morphological and anatomical differences are too great for the family to merit serious consideration.

The family Rhamnaceae was thought a suitable, if perhaps temporary, repository for the genus by Miers (1872) by virtue of its antepetalous stamen condition. Miers regarded *Alzatea*, together with *Crypteronia*, and possibly also *Tetrataxis* (Lythraceae) as a "peculiar group" which could be positioned in the Rhamnaceae as a new tribe, the Crypteronieae. Floral morphology in the family exhibits some similarities to that of *Alzatea*, e.g., 5-merous flowers in axillary cymes, stamens alternating with sepals, the sepals often with a raised, fleshy, interior surface as occurs in *Alzatea*, a well-developed infrastaminal nectary disc adnate to the floral tube, and seeds lacking endosperm. There are, however, equally as many specialized features in which the family differs from *Alzatea*. Most distinctive of these are the

Rhamnaceous ovary with its single, basal, erect ovule in each locule; drupaceous fruits; and wingless seeds with stony, multiplicative walls. The family also lacks internal phloem and vested pitting and produces no ellagic acid (Cronquist, 1981). Similarities may be attributed to their common distant ancestry in the Rosidae and parallel development of like structures in different lines of the subclass. Total evidence excludes *Alzatea* from the Rhamnaceae.

COMPARATIVE EVIDENCE FOR ORDINAL,  
FAMILY, AND GENERIC RELATIONSHIPS

Among the several orders suggested for *Alzatea*, the Myrtales offer the only comfortable fit. Two anatomical apomorphies of *Alzatea*, internal phloem and vested pitting, are major definitive features of the Myrtales (Dahlgren & Thorne, 1984). Other characteristics of *Alzatea* prevail in the order. These include vessel elements with simple perforation plates, opposite and verticillate, simple, entire leaves with brochidromous secondary venation, ellagic acid and flavonol glycoside leaf constituents, rudimentary axillary stipules (Weberling, 1968), anomocytic stomata, basically determinate inflorescences, floral tube with floral parts on the rim, bitegmic crassinucellar ovules, as well as several embryological features (Dahlgren & Thorne, 1984).

At the familial level, Myrtalean families to which *Alzatea* has been referred have been subject themselves to numerous interpretations, so that the varying familial placement of *Alzatea* in the order has depended in part on how the families were defined. Hallier (1911), for example, initially considered *Alzatea* a member of the Lythraceae. His concept of the family included *Sonneratia* and *Duabanga* (Sonneratiaceae, traditionally), *Crypteronia* (Crypteroniaceae), *Rhynchoalix* (Rhynchoalixaceae), and *Punica* (Punicaceae, traditionally). After an "angry" letter from the monographer of the Lythraceae, Emil Koehne, disputing Hallier's delineation of Lythraceae, Hallier decided the same genera, questionably excluding *Punica*, were members of the Memecyloideae-Melastomataceae (Hallier, 1918). The change was due, not as much to Koehne's objection, since Hallier dismissed Koehne's argument as "pre-Darwinian," as to his new awareness of the genera *Dactylocladus* and *Axinandra*, which he found overwhelmingly similar to *Crypteronia* and *Alzatea* and which were considered Melastomataceous by their au-

thors. Lourteig (1965), who regarded *Alzatea* as Lythraceous, extended her definition of Lythraceae to include *Crypteronia*. It has also been argued since that *Alzatea*, *Rhynchoalix*, *Dactylocladus*, and *Axinandra*, with *Crypteronia* constitute a redefined Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975). Most recently, *Alzatea* has been removed from that coalition of genera, with the latter three genera repositioned as a new subfamily of the Melastomataceae (van Vliet, 1981) and *Rhynchoalix* comprising the monotypic Rhynchoalixaceae (Johnson & Briggs, 1984).

Several Alzatean characteristics occur repeatedly throughout the order in more than one family and must be regarded as having originated early in the evolution of the group or as instances of convergent or parallel evolution. Examples of the latter include foliar sclereids scattered throughout several families (Rao & Das, 1979); hemi-epigynous flowers seen also in the Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975), Melastomataceae, and Myrtaceae (Dahlgren & Thorne, 1984); expanded fleshy anther connectives in the Crypteroniaceae; and transeptal vascular supply, which occurs in some Onagraceae, Myrtaceae, Oliniaceae, Punicaceae, and in *Rhynchoalix* (Schmid, 1984). Combinations of these characteristics, together with the widely occurring plesiomorphic features of the order, have been used to infer relationship to the families Lythraceae and Crypteroniaceae (and the Melastomataceae via inclusion of Crypteroniaceae in that family).

The most recent arguments for the disposition of *Alzatea* in the Lythraceae have rested on such common Myrtalean characteristics as quadrat branches, subcoriaceous decussate leaves, 5–6-merous flowers, and capsular, bilocular fruit with loculicidal dehiscence (Lourteig, 1965). Apomorphic Alzatean features cited to support placement in the family, e.g., obhaplostemonous stamens with enlarged connective and apetalous are now believed to have evolved more than once in the order (Johnson & Briggs, 1984). Although the parietal placentation of *Ammannia microcarpa* DC. in Lythraceae has been cited in support of *Alzatea*'s placement in the family, the placentation is not homologous in these taxa. *Ammannia microcarpa* is a highly derived herbaceous species whose parietal placentation is unique in the Lythraceae. The species bears no other resemblance to *Alzatea*. Citation of this species as supporting evidence for inclusion of

TABLE 3. Comparison of *Alzatea* and associated genera.

Character	<i>Alzatea</i>	<i>Rhynchocalyx</i>	<i>Crypteronia</i>	<i>Dactylocladus</i>	<i>Axinandra</i>
No. of species	1	1	4	1	4
Habit	Small tree or shrub, hemi-epiphyte	Small tree	Tree	Tree	Tree
Habitat	Wet, submontane tropical forest	Moist, wooded, subtropical ravines	Wet, submontane tropical forests	Lowland peat swamps	Wet, submontane tropical forests
Distribution	Bolivia, Peru, Panama, Costa Rica	Natal & Transkei, South Africa	SE Asia, Phillipines, Malay Peninsula to New Guinea, esp. Borneo	Borneo	Malay Peninsula, Borneo, Sri Lanka
Branches					
Arrangement	Opposite or whorled	Opposite or whorled	Opposite	Opposite	Opposite
X-sect., young	Quadrangular	Terete to flattened	Terete to quadrangular	Flattened	Quadrangular ±
Leaves					
Phyllotaxy	Opposite or whorled	Opposite or whorled	Opposite	Opposite	Opposite
Stipules	Axillary, divided	Axillary, divided	Lateral, rudimentary	?	?
Venation	Brochidodromous	Eucamptodromous	Brochidodromous	Brochidodromous, indistinct	Brochidodromous
Inflorescence					
Type	Anthotelic, paniculate	Anthotelic, paniculate	Blastotelic, racemose	Blastotelic, racemose	Blastotelic, racemose
Position	Axillary, terminal	Axillary, terminal	Axillary, terminal	Axillary, terminal	Axillary, terminal
Flowers					
Sex	Bisexual (& func. unisexual?)	Bisexual	Bisexual & unisexual	Bisexual	Bisexual
Insertion	Hemi-epigynous, barely	Hemi-epigynous, barely	Perigynous	Hemi-epigynous, strongly	Epigynous
Nectary-disc	Present, broad	Absent	Absent	Absent	Absent
Merosity	5(-6)-merous	6-merous	4-5(-6)-merous	5(-4)-merous	5(-4)-merous
Floral bracts	Minute, fugaceous	Minute, fugaceous	Solitary, persistent (?)	Solitary, caducous	Three, persistent (?)
Calyx					
Lobes	Thick, adaxial surface raised, fleshy	Thin, membranous	Thin, membranous	Thin, membranous	Thin, membranous
Duration	Persistent	Persistent	Persistent	Persistent	Evanescent in fruit
Aestivation	Valvate	Valvate	Valvate	Valvate	Valvate



TABLE 3. Continued.

Character	<i>Alzatea</i>	<i>Rhynchocalyx</i>	<i>Crypteronia</i>	<i>Dactylocladus</i>	<i>Axinandra</i>
<b>Petals</b>					
Number	0	6	0	5	5
Shape	—	Hood-like, covering stamens in bud, clawed	—	Hood-like, covering stamens in bud, clawed	± Connate, broad-based
Deciduousness	—	Individually	—	Individually	As cone-shaped unit
<b>Stamens</b>					
Number	5	6	4–5	5	10
Position	Alternisepalous	Alternisepalous	Alternisepalous	Alternisepalous	Episepalous & epipetalous
Filaments	Thick, short, flattened	Thin, long, ± flattened	Thin, long, terete	? ± flattened	Thick, short, ± flattened
Connective	Conduplicate	Elliptical	Orbicular or nearly conduplicate	Orbicular	Conduplicate
Sporangia position	Terminal	Lateral	Lateral to subterminal	Lateral	Terminal
<b>Pollen</b>					
Aperatures	Tricolporate	Tricolporate	Bisyncolporate	Tricolporate	Tricolporate
Shape	Prolate-spheroidal	Prolate-spheroidal	Bilaterally flattened	Prolate-spheroidal	Prolate-spheroidal
Subsidiary colpi	3, indistinct	3, distinct	2, indistinct	3, distinct	3, distinct
Exine	Faintly verrucate to psilate	Faintly verrucate to psilate	Psilate	Psilate to irregularly verrucate	Psilate to finely verrucate
Nuclei at shedding	2	2	2	2	2
<b>Style</b>					
Length	Shorter than ovary, stout	Shorter than ovary, stout	Longer than ovary, filiform	Longer than ovary, filiform	Longer than ovary
In fruit	Base persistent	Base persistent	Entire style & stigma persistent	Entire style & stigma persistent	Non-persistent
Stigma	Capitate	Capitate, narrow	Punctate or capitate	Capitate	Punctate, minute
<b>Ovary</b>					
Shape	Bilateral, compressed	Bilateral, compressed	Bilateral & compressed or globose	Globose	Globose
Carpel No.	2	2	2 (3 or 4)	(3) 4 or 5	3 (2)
Locule No.	2	2	2 (3 or 4)	(3) 4 or 5	6 (4)

TABLE 3. Continued.

Character	<i>Alzatea</i>	<i>Rhynchocalyx</i>	<i>Crypteronia</i>	<i>Dactylocladus</i>	<i>Axinandra</i>
Placentation	Parietal	Axile	Parietal or basal	Basal	Basal
Septal Fusion	Not fused	Fused entirely	Not fused or fused basally (?)	Not fused	Fused slightly basally (?)
Ovule No./Capsule	Ca. 40-60	Ca. 40	Many 6(-12)	12-15	6-12
Ovule Position	Horizontal in staggered vertical rows	Horizontal in single vertical rows	Horizontal in staggered vertical rows or $\pm$ vertical & basal	Vertical & basal	Vertical & basal
Fruit	Indurated capsule	Indurated capsule	Indurated capsule	Indurated capsule	Woody, greatly enlarged capsule
Seed					
Shape	Irregularly oblong to lunate, flattened	Obliquely ovate, flattened	Ovoid-ellipsoid, flattened	Narrowly ellipsoid, flattened	Oblong, ellipsoid, flattened
Embryo Position	Central	Apical	Central	Central	Basal
Seed Wing	Encircling embryo	At micropylar end	At micropylar or chalazal end	?	At chalazal end
Seed Coat Cells	Specialized cell types absent	Specialized cell types absent	?	?	Specialized cell types absent
Testa Layers	2	2	?	?	2
Tegmen Layers	2	2	?	?	2 initially, becoming 3
Embryology					
Anther Wall Formation	Dicot Type	Basic Type	?	?	Dicot Type
Anther Endothecium	Ephemeral	Ephemeral	?	?	Ephemeral
Microsporangial Septum	Non-persistent	Persistent	?	?	Non-persistent
Ovule Archeporium	Multi-celled	Multi-celled	?	?	One-celled
Ovule Endothelium	Absent	Absent	?	?	Present
Micropyle Formation	Inner integument only	Inner integument only	?	?	Inner & Outer integuments
Embryo Sac Formation	Bisporic, <i>Allium</i> -type	Monosporic, <i>Polygonum</i> -type	?	?	Monosporic, <i>Polygonum</i> -type

TABLE 3. Continued.

Character	<i>Alzatea</i>	<i>Rhynchocalyx</i>	<i>Crypteronia</i>	<i>Dactylocladus</i>	<i>Axinandra</i>
<b>Leaf Anatomy</b>					
Cuticle	Granular	Smooth	Granular	Smooth	Granular
Stomate	Anomocytic	Anomocytic	Paracytic	Anomocytic	Paracytic
Petiole Bundle	Cylinder, ab- & adaxial portions with middle lacuna	Curved arc	Cylinder, ab- & adaxial portions with middle lacuna	Cylinder, ab- & adaxial portions with middle lacuna	Curved arc
Sclereids	Present, branched	Present, unbranched	Present, unbranched	Present, unbranched	Absent
Nodes	Trilacunar, 3 traces	Unilacunar, 1 trace	Common gap, 1 median bundle	Common gap, 1 median bundle	Complete girdling trace, 1 median bundle
<b>Stem Anatomy</b>					
Cork Origin	Pericycle	Cortex	Pericycle	Subepidermal	Pericycle
Vessel Aggregation	Mainly radial multiples	Mainly solitary	Mainly radial multiples	Mainly solitary	Mainly solitary
Vessel Member Length	530 & 570 $\mu\text{m}$	460 & 520 $\mu\text{m}$	650-900 $\mu\text{m}$	950-1120 $\mu\text{m}$	390-440 $\mu\text{m}$
Vessel-Ray Pits	Reticulate-scalariform, large	Alternate, small	Alternate, small	Reticulate-scalariform, large	Alternate, small
Vesturing	Spreading, forming bands on vessel wall	Spreading, forming bands on vessel wall	Within pit chamber & on pit margins	Within pit chamber only	Within pit chamber only
Septate Fibers	Present	Present	Absent	Absent	Absent
Fiber Pitting	Simple-minutely bordered	Simple-minutely bordered	Distinctly bordered	Distinctly bordered	Distinctly bordered
Axial Parenchyma	Very scanty paratracheal	Scanty paratracheal to vasicentric	Diffuse or scanty paratracheal to vasicentric	Aliform to confluent	Aliform to confluent
Rays	Heterogeneous I	Heterogeneous I	Heterogeneous I	Heterogeneous III	Heterogeneous I
Phloem Crystals	Clustered in chambered parenchyma	Solitary, prismatic in chambered parenchyma	Styloids in parenchyma	Crystal sand & druses in parenchyma	Styloids in parenchyma

*Alzatea* in Lythraceae (Lourteig, 1965) is an instructive example of how one or a few phenetic similarities can be emphasized to justify relationships of only remotely related or totally unrelated taxa. The relationship of *Alzatea* to the Lythraceae is clearly of a general nature, based on characteristics widely dispersed in the family. No Lythraceous genus shares a sufficient suite of characteristics to be considered directly or closely related to *Alzatea*.

*Alzatea's* closest relationships appear to center around the genera of the Crypteroniaceae, *Crypteronia*, *Dactylocladus*, and *Axinandra*, and the genus *Rhynchocalyx*, by virtue of their possession of more of the distinctive features which define *Alzatea*. Major similarities and differences among these genera, selected from recently published studies and personal observations of herbarium and fixed plant material, are compared in Table 3. Evidence of relationship based on these attributes is discussed in the following pages. In instances where variability occurs within the genus, as among the species of *Crypteronia*, the most common situation is recorded. The table is not meant to be all-inclusive; more complete characterizations may be found in the individual papers cited in the text. The reader is referred to these for further details not presented here.

*Macromorphological evidence.* Among the most strikingly similar, advanced characteristics uniting *Alzatea* with *Rhynchocalyx* and *Crypteronia* pro parte are those of ovule and seed morphology. The three taxa display hemi-epigynous, bilaterally compressed, bicarpellate ovaries in which numerous ovules are borne horizontally in one or more vertical rows. Placentation is parietal in *Alzatea* and *Crypteronia* (van Beusekom-Osinga & van Beusekom, 1975) and axile in *Rhynchocalyx* (Sprague & Metcalfe, 1937; Strey & Leistner, 1968) but the solid central axis in *Rhynchocalyx* (Fig. 8e-g) is only slightly less evolved than the divided septum of *Alzatea* (Fig. 8a-d) and *Crypteronia*. Additional ovarian features in *Rhynchocalyx*, the narrow (ca. 0.5 mm wide) placental region and uniseriate ovules, are similar to those of *Alzatea* but are regarded as evolutionarily somewhat more primitive (Puri, 1952). The shared characteristic of transeptal ovarian vascular supply enhances the similarity of *Alzatea* and *Rhynchocalyx*. The ovarian vascular system in *Crypteronia* is undescribed. However, free-hand sections of limited flower material of *C. paniculata* Planch. indicate that each fleshy half septum is free to the base and

has its own ventral vascular system which supplies the ovules and adjacent carpel wall as in *Alzatea* and *Rhynchocalyx*, although probably differs from them in the major ventral vascular supply of each half septum consisting of a single, rather than double, major bundle. The remaining Crypteroniaceae display quite different features, such as a 4-locular ovary with central conical placenta (other spp. of *Crypteronia*) or a nearly inferior, 4-6-locular ovary with ovules basal between the septa (*Dactylocladus* and *Axinandra*).

Transeptal bundles have been described for other members of the Myrtales and occur infrequently in assorted families of other orders, e.g., in Cornaceae, Rubiaceae, Araceae, Umbelliferae, and Oleaceae (Schmid, 1972, 1984; Eyde, 1967, 1981; Puri, 1952). The condition is considered derived from the common axile system and appears most frequently in families with inferior ovaries (Schmid, 1972; Eyde, 1981). In Myrtales, transeptal bundles are recorded in one or more genera of the Myrtaceae, Oliniaceae, Punicaceae, Onagraceae, and Trapaceae, as well as in *Alzatea* and *Rhynchocalyx* (Schmid, 1984). The condition has most certainly arisen several times in the Myrtales and is not necessarily indicative of close phylogenetic relationship, although in *Alzatea* and *Rhynchocalyx* it is most parsimoniously considered to have been gained from their most recent common ancestor rather than independently evolved.

Fruit type in *Alzatea*, *Rhynchocalyx*, and *Crypteronia* pro parte is basically a dry, bilocular capsule in which the valves are crowned by the persistent base of the style. *Crypteronia* differs in retaining the entire style and stigma after dehiscence of the capsule. A persistent style characterizes *Dactylocladus* as well as *Alzatea* and *Crypteronia* pro parte, but the fruit of the first differs in shape, placentation, and seed number. *Axinandra* is even further differentiated from *Alzatea* by the epigynous, 6(-4)-locular ovary and large, globose capsule with basal, erect ovules. Compressed capsules and transeptal vascular supply are unknown in the Lythraceae.

In seed morphology, *Alzatea* appears to share a simple, anatomically much reduced, thin-winged seed type with *Rhynchocalyx* and Crypteroniaceae sensu stricto. Although the seeds are superficially similar, developmental sequences differ in *Alzatea*, *Rhynchocalyx*, and *Axinandra*, the only genera studied to date, and thus cannot be used to support a close relationship of the genera (Tobe & Raven, 1983, 1984a, 1984b).

The occurrence of a simplified seed in the Sonneratiaceae in *Duabanga*, but not in *Sonneratia*, indicates reduction in seed anatomy has occurred more than once within the Myrtales. The simple seed morphology of *Alzatea* is in marked contrast to the multiple-layered seed coats of core families of the Myrtales which are further specialized by the presence of fibrous and/or sclerotic cell layers (Corner, 1976). Simplicity of seed structure in *Alzatea* is regarded as derived for reasons that the more complex seed coat is the common condition both in the Myrtales and in the Rosiflorae generally, and the simple seed is associated with advanced ovary characteristics of parietal placentation, transeptal vascular bundles, and bilateral symmetry. According to Corner (1976), the main direction of seed evolution in Angiosperms has been toward reduction in complexity and size.

Few other derived macromorphological states are shared by *Alzatea* and any of the other four genera. The unusual anther connectives with terminal or apically placed sporangia (Fig. 3) appear in similar (homologous?) form in *Axinandra* but otherwise the genera hold no features in common other than those widespread in the order. The expanded connective of *Crypteronia* anthers could be taken as an evolutionary intermediate step toward the *Alzatea-Axinandra* type from the merely broadened form seen in *Rhyncho-calyx* and *Dactylocladus*. The inflorescences of *Alzatea* and *Rhyncho-calyx* are fundamentally the same, i.e., anthotelic, with the axes ending in a flower (Figs. 9, 11) but those of *Crypteronia*, *Dactylo-cladus*, and *Axinandra* are blastotelic, an evolutionarily more advanced type in which the inflorescence axes are not terminated by a flower (Briggs & Johnson, 1979; Johnson & Briggs, 1984). The well-developed nectary disc of *Alzatea* is an apomorphy not noted in these other genera.

*Alzatea* displays a total macromorphology which places it at a distance from even those genera considered most closely related or phenetically most similar. The isolation is probably more pronounced than even macromorphology suggests when one takes into account the likelihood that at least some of the phenetic similarities have independent phylogenetic origins.

**Pollen morphological evidence.** Pollen morphological differences among the putative generic relatives of *Alzatea* are considerable. *Alzatea* pollen has very generalized features, being binucleate, prolate-spheroidal, and tricolporate,

with nearly psilate exine. Under the scanning electron microscope (SEM), mesocolpal depressions are apparent and have been interpreted as "incipient" subsidiary colpi (Muller, 1975, 1981). The presence of subsidiary colpi is a typical, although not constant, feature of Myrtalean pollen. It is the only pollen character of *Alzatea* which indicates relationship to the order, since other *Alzatea* pollen features appear in the dicotyledons in a number of unrelated families. There is no pollen characteristic of *Alzatea* which can be used to convincingly align *Alzatea* to any one Myrtalean family. It has been suggested that the pollen is comparable to that of *Physocalymma* in Lythraceae (van Campo in Lourteig, 1965). The characters they share, however, are generalized ones of shape, size, and possession of colporate apertures. They differ in sculpture pattern, *Physocalymma* having a rugulate-striate exine, *Alzatea* a psilate one. No case can be made for a close relationship to *Physocalymma* or any other Lythraceae based on pollen (Graham et al., unpubl. data). In contrast to pollen of *Alzatea*, pollen of *Rhyncho-calyx*, *Dactylocladus*, and *Axinandra* is tricolporate and distinctly 3-heterocolpate, falling within the range of Melastomataceous and Lythraceous pollen types. *Crypteronia* pollen, on the other hand, stands totally apart from both *Alzatea* and the preceding taxa by its unusual bisyncolpate, bilateral condition. Although a hypothetical scheme for transition from *Alzatea* to *Crypteronia* pollen has been postulated, no transitional pollen type is known (Muller, 1975). The generalized features of *Alzatea* pollen relegate the genus to an ancestral position with respect to the pollen of other genera discussed but indicate no special relationship to any one of the families or specific genera in the Myrtales with which it has been aligned.

**Embryological evidence.** Embryological comparisons confirm the Myrtalean position of *Alzatea* (Schmid, 1984; Tobe & Raven, 1984a). A comprehensive report of the embryology of the genus, from which this discussion is excerpted, is presented by Tobe and Raven (1984a). Of the seven ordinal distinctions listed by them, *Alzatea* differs only in one, having a micropyle formed by the inner integument alone, rather than by both inner and outer integuments. The formation of an inner integument micropyle is known elsewhere in Myrtales only in *Rhyncho-calyx* (Tobe & Raven, 1984b). The micropyle in *Axinandra* and all embryologically known Lythraceous and Melastomataceous genera is

MISSOURI BOTANICAL GARDEN  
2155898  
HERBARIUM



PLANTS OF PERU

*Alzatea verticillata* Woytk. 8331  
1972. 42. 1. 1972. 10. 1972.  
Summit of Cerro Tute, above Escuela Agrícola Alto de Piedra, just W of Santa Fé. Windswept elfin forest, 8° 37'N, 87° 07'W, 1410 m.  
Shrub or small tree to 5 dm. Flowers with petals pink, edged white, calyx green. Fruit reddish. Bark red, peeling.  
S. Knapp & W. J. Kress 4336 20 Mar. 1982  
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

9



TYPE LYTHRACEAE  
*Alzatea verticillata* R. & P.  
subsp. *amplifolia* S. A. Graham  
subsp. nov.  
Det. Shirley A. Graham 10 Nov 1982

PANAMA  
Provincia of Veraguas

Family  
Lythraceae

Summit of Cerro Tute, above Escuela Agrícola Alto de Piedra, just W of Santa Fé. Windswept elfin forest, 8° 37'N, 87° 07'W, 1410 m.

Shrub or small tree to 5 dm. Flowers with petals pink, edged white, calyx green. Fruit reddish. Bark red, peeling.

S. Knapp & W. J. Kress 4336 20 Mar. 1982  
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

10

FIGURE 9. *Alzatea verticillata* subsp. *verticillata*, Woytkowski 8331 (MO) from Peru. FIGURE 10. *Alzatea verticillata* subsp. *amplifolia* S. A. Graham, Knapp & Kress 4336 (MO) from Cerro Tute, Panama.

formed from both outer and inner integuments (Tobe & Raven, 1983). Unfortunately, comparisons cannot be made with *Crypteronia* and *Dactylocladus*, which are unstudied embryologically.

The most striking embryological feature of *Alzatea* is the bisporic *Allium*-type embryo sac, a type reported for no other Myrtalean taxa. The characteristic embryo sac type for the order is the monosporic *Polygonum*-type. Two exceptions, besides *Alzatea*, are known, however, in Peneaceae and Onagraceae, each of which has its own peculiar embryo sac type. *Rhynchocalyx* conforms to the general Myrtalean condition.

*Alzatea* is similar to *Rhynchocalyx* by virtue of the same micropylar formation and in having a multicelled ovule archesporium, ephemeral endothelium development, and binucleate pollen. It differs in several ways, in addition to the embryo sac character. In *Alzatea*, anther wall formation is of the Dicotyledonous type with the wall four cell layers thick and the epidermal outer cell walls of the anther flat. The septum between microsporangia is non-persistent. Cells of the nucellus develop normally. In the seed, the embryo is centrally positioned with straight cotyledons and the seed wing forms from the funiculus and outer integument. In *Rhynchocalyx*, anther wall formation is of the Basic type with wall layers five cells thick and epidermal outer cell walls of the anther papillate. The microsporangial septa persist after sporangial dehiscence. In the nucellus, subdermal cells elongate radially. In the seed the embryo is basally positioned with folded cotyledons and the seed wing develops from the funiculus only.

*Axinandra*, the only other putative close relative investigated embryologically, is more distantly separated from *Alzatea* than *Rhynchocalyx* by possession of two important distinctions: a one-celled ovule archesporium with endothelium present and the micropyle formed by outer and inner integuments.

*Alzatea* shares some generalized embryological features with Lythraceae, but differs in many. It can be excluded from the family foremost by the distinctive *Allium* embryo sac. Similarities to Melastomataceae are restricted to anther wall features only. Tobe and Raven have concluded that, embryologically, *Alzatea* takes an isolated position in Myrtales. The limited embryological similarities to *Rhynchocalyx* are attributed to parallel descendency from a common ancestor, from which Lythraceae are also derived.

*Anatomical evidence.* The recent series of an-

atomical studies in Myrtales offers a wealth of new information about *Alzatea* and associated taxa, as well as thorough assessments of relationships based on anatomical data (van Vliet, 1975, 1981; Baas & Zweypfennig, 1979; van Vliet & Baas, 1975, 1984; van Vliet et al., 1981; Keating, 1984). Major anatomical distinctions of *Alzatea* and the genera under discussion are extracted from these works and listed in Table 3 to facilitate comparison.

Anatomical evidence clearly places *Alzatea* in the Myrtales. Familial and generic affinities, however, are not clearly indicated by anatomical characters. *Alzatea*'s leaf anatomy is particularly distinctive in the order. The combination of anomocytic-cyclocytic stomates, midvein vascular system divided by a lacuna into abaxial and adaxial portions, abundant sclereids of two types, and small epidermal cells which are square in cross section, are unlike any other genus investigated in Myrtales (Keating, 1984). Other than the similar stomate condition shared by *Rhynchocalyx* and *Dactylocladus*, this synapomorphy isolates the genus in the order.

Nodal anatomy additionally supports the exclusiveness of *Alzatea* in Myrtales. The trilacunar node with three traces is presently unknown elsewhere in Myrtales, where the unilacunar condition prevails. Trilacunar nodes, regarded as primitive in Angiosperms, may be ancestral in the Myrtales and ancestral to the common gap-median trace seen in some Melastomataceae and Crypteroniaceae (van Vliet & Baas, 1975). Alternatively, the possibility has been raised that the trilacunar node in *Alzatea* is a neotenus condition (Johnson & Briggs, 1984). In either case, the genus is unique within the order for this attribute.

Wood anatomical details indicate *Alzatea* is linked in a general way to several Myrtalean families but is not a close fit to any of them. Within the order there is a wide range of wood anatomical diversity and much overlap in the families tentatively associated with *Alzatea*, i.e., Crypteroniaceae sensu stricto, Lythraceae, and Melastomataceae. This heterogeneity restricts use of the anatomical data as an indicator of family placement for *Alzatea*. At the generic level, there are major anatomical distinctions between *Alzatea* on the one hand and *Crypteronia*, *Dactylocladus*, *Axinandra*, and *Rhynchocalyx* on the other. *Alzatea* has branched foliar sclereids, trilacunar nodes with three traces, and clustered crystals in chambered phloem cells, character-

TABLE 4. Distribution of similar (homologous?) characteristics in genera and family associated with *Alzatea*. Key: + = shared with *Alzatea*; - = not occurring in the genus or family; ( ) = rarely, occasionally, or in part occurring in the genus or family; ? = unknown; \* = evolutionarily advanced feature in *Alzatea*.

Selected <i>Alzatea</i> Characteristic	Presence of a Similar State in:				
	<i>Rhyncho- calyx</i>	<i>Crypte- ronia</i>	<i>Dactylo- cladus</i>	<i>Axin- andra</i>	Lythra- ceae
Leaves opposite and whorled	+	+	-	+	(+)
*Stipules axillary and divided	+	-	-	-	+
Inflorescence antheral (axes terminated by a flower)	+	-	-	-	+
*Flowers hemi-epigynous	+	+	+	-	-
*Nectary disc present	-	-	-	-	(+)
Flowers 5-merous	-	+	+	+	(+)
*Petals absent	-	+	-	-	(+)
*Calyx lobe thick, fleshy within	-	-	-	-	-
*Calyx lobes persistent	+	+	+	-	+
Stamen number five	-	+	+	-	(+)
*Filaments short, thick	-	-	-	+	-
*Connective expanded with terminal sporangia	-	+	-	+	-
Pollen tricolporate	+	-	+	+	(+)
*Subsidiary colpi indistinct, not prominent	-	+	-	-	(+)
Pollen bi-nucleate	+	+	+	+	+
*Style stout	+	-	-	-	(+)
Style base persistent	+	+	+	-	(+)
*Ovary bilateral, compressed	+	(+)	-	-	-
*Carpel number two	+	(+)	-	-	(+)
*Ovary vascular supply transeptal, lateral	+	(+)	?	?	-
*Placentation parietal	-	(+)	-	-	-
*Ovules numerous, ca. 40	+	(+)	-	-	(+)
Ovule position horizontal	+	(+)	-	-	(+)
Ovule archesporium multi-celled	+	?	?	-	+
Ovule endothelium absent	+	?	?	-	?
*Micropyle formed from inner integument only	+	?	?	-	-
*Embryo sac bisporic, <i>Allium</i> -type	-	?	?	-	-
*Seed wing present	+	+	+	+	(+)
*Seed testa 2-layered, unspecialized	+	+	+	+	-
*Seed tegmen 2-layered, unspecialized	+	+	+	+	-
Nodes trilacunar with three traces	-	-	-	-	-
Leaf stomates mainly anomocytic	+	-	+	-	+
Petiole bundle a closed ring	-	+	+	-	-
*Leaf sclereids present	+	+	+	-	-
*Branched leaf sclereids present	-	-	-	-	-
*Wood vessels mainly in radial multiples	-	+	-	-	+
*Vesturing forming surface bands	+	-	-	-	-
*Vessel-Ray pits coarse, large	-	-	+	-	-
*Septate fibers present	+	-	-	-	+
*Fiber pitting simple to minutely bordered	+	-	-	-	+
*Axial parenchyma scanty paratracheal	+	(+)	-	-	+
Rays heterogeneous I	+	+	-	+	(+)
*Clustered crystals in chambered phloem parenchyma	-	-	-	-	(+)

istics absent from the other genera. From *Crypterionia* and *Axinandra*, it also differs in having anomocytic rather than paracytic stomata and septate fibers with simple pits rather than non-septate fibers with distinctly bordered pits. From

*Dactylocladus*, in addition, it has pericyclic origin of cork and less advanced heterogeneous I-II ray types, while *Dactylocladus* has a subepidermal cork origin and heterogeneous III ray type. There are extensive differences from *Rhyncho-*



TABLE 5. Numerical summary of Table 4 listing of 43 characteristics of *Alzatea* shared with associates.

Genus	No. Shared Ancestral	No. Shared Derived	No. Shared in Part	Unknown	Total Wholly Shared	% Shared With <i>Alzatea</i>
<i>Rhynchocalyx</i>	10	17	0	0	27	63
<i>Crypteronia</i>	7	11	1—Ancestral 6—Derived	4	18	45
<i>Dactylocladus</i>	7	7	0	5	14	33
<i>Axinandra</i>	5	5	0	1	10	25
Lythraceae	4	6	7—Ancestral 8—Derived	1	10	25

*calyx* in cuticle texture, mechanical support of the veins, petiole anatomy, and vessel-ray pitting. The coarse, large, reticulate-scalariform vessel-ray pitting contrasts particularly with the small alternate pitting in *Rhynchocalyx*. The two genera are alike in having septate fibers with simple fiber pits, scanty paratracheal parenchyma, and peculiar vesturing of inter-vessel pits which extends beyond the pits in superficial bands. However, only the vesture condition can be considered highly derived; the other two features are typical of unspecialized "protolythraceous" wood (Baas, 1979).

Although there are similarities with Lythraceous anatomy, the trilacunar nodal condition, arrangement of vascular tissue of the petiole and midrib, and banded vesture type are not found in the Lythraceae. Three major features of *Alzatea* wood anatomy, scanty paratracheal parenchyma, heterogeneous rays, and septate fibers with simple pits recall unspecialized wood in Lythraceae. There are also wood anatomical agreements of *Alzatea* with Melastomataceae (e.g., coarse, simple vessel-ray pits), Sonneratiaceae and Oliniaceae, but no particularly close affinities to any one of them and no member of any of these families has most of the characters of *Alzatea*. Anatomical studies have led to the conclusion that *Alzatea* is an isolated remnant of the ancestral stock which gave rise to Lythraceae and Melastomataceae (van Vliet et al., 1981).

#### TAXONOMIC AND PHYLOGENETIC RELATIONSHIPS

Most recent taxonomic classifications associate *Alzatea* with the genus *Rhynchocalyx* and families Crypteroniaceae or Lythraceae, based on phenetic similarities. The extent of features shared with these associates is demonstrated by Table 4 where 43 selected characteristics of *Alzatea* are listed and their presence or absence in these associates is indicated. Twenty-nine char-

acteristics are derived, 14 are regarded as ancestral. The list underlines the dispersed nature of *Alzatea* attributes in putative relatives and the heterogeneity of the Crypteroniaceae sensu lato. Among the associated genera, *Rhynchocalyx*, with 27 similarities, shares the greatest number of features (Table 5; Figs. 11–14). *Crypteronia*, with a maximum of 24 shared features in *C. paniculata*, but only 18 shared with other species of the genus, is less similar. Knowledge of the embryology of *Crypteronia* should contribute significantly to a more accurate assessment of relationships among the genera *Alzatea*, *Rhynchocalyx*, and *Crypteronia*. *Dactylocladus* and *Axinandra* are more distant, sharing, respectively, only 14 and ten of the 43 characteristics. Crypteroniaceae, as construed by van Beusekom-Osinga and van Beusekom (1975), thus groups a diverse assemblage of genera, with *Alzatea* and *Rhynchocalyx* especially separated by significant gaps from the others. At least 25 characteristics of *Alzatea* can be found in one or more genera of the Lythraceae, but no single genus has many and hence none approach *Alzatea* phenetically. With respect to the relationship of *Alzatea* to its most similar associate, *Rhynchocalyx*, *Alzatea* differs from that genus in 16 of the 43 character states listed. At least four of these are apomorphies unique to *Alzatea*. It is this prominent degree of divergence of *Alzatea* from even its nearest taxonomic neighbor which supports establishment of a new family to accommodate this distinctive taxon. On the same basis, *Rhynchocalyx* is also isolated by a substantial suite of specialized characters and is best treated as a separate family. I earlier stated in personal communications with Dahlgren, 1981 and Briggs, 1982 that the genus belonged to the Lythraceae based on evidence then available. It had been regarded, since first described, as most similar to *Lawsonia* in Lythraceae, primarily due to their superficially similar,

2225121



NATAL HERBARIUM DURBAN

Grav. No. Burrivall	Page Natal
H.B. Nicholson	21/3/74
Leaf & No.	Ar.
<i>Rhynchosia laywenii</i> Oliv.	
Ottawa's herbarium kloor (untreated)	

11



14

floriferous, paniculate inflorescences of small white flowers (Strey & Leistner, 1968; Sprague & Metcalfe, 1937). Characters tying it to Lythraceae are now rightly regarded as ancestral ones shared by Melastomataceae and Lythraceae evolutionary lines. New contributions to our knowledge of the genus lead to the conclusion that *Rhynchocalyx* is another relic genus in the Myrtales, without close living relatives. This isolated position is best acknowledged by recognition of the monotypic Rhynchocalycaceae (Johnson & Briggs, 1984).

A phylogenetic study of Myrtales (Johnson & Briggs, 1984), including *Alzatea*, has recently been completed using cladistic methods based on many of the same characters cited in Table 4. In the phylogeny preferred by the authors (their Fig. 3), three major evolutionary groups emerge, the Lythraceae sensu lato—Onagraceae—Trapaceae line, the Myrtaceae—*Heteropyxis*—*Psiloxylon* line, and an assemblage now recognized as members of the Melastomataceae, Crypteroniaceae, Peneaceae, Oliniaceae, and *Rhynchocalyx* and *Alzatea*. Phylogenetic relationships among the members of this last group are uncertain and several alternative evolutionary schemes are proposed. However, in all phylograms of Johnson and Briggs, *Alzatea* and *Rhynchocalyx* share a common ancestral stem which is, in turn, related to Crypteroniaceae, Peneaceae, and Oliniaceae. Evolutionary relationships of *Alzatea* to modern Lythraceae in their preferred phylogram are seen as distant through ancient common ancestors.

*Alzatea* appears to have evolved along an independent course over a long period of time, retaining some generalized ancestral features, as in stem anatomy and pollen, while acquiring many specialized attributes. Ultimately, it has come to occupy an isolated position in the order, well separated from its nearest living relative, *Rhynchocalyx*. Its distribution in the wet forests of tropic Andean South America and in Central America further supports an early separation from the ancestral line which produced the East African *Rhynchocalyx* and the East Asian Cryp-

teroniaceae. Homoplasy in taxa of shared ancestral lineage, especially with respect to macromorphological characters, has obscured the extensive divergence of *Alzatea* and is partly responsible, together with the incorrectly placed emphasis on synplesiomorphy, for misdirected ideas of relationship and questionable taxonomic placement. Carefully considered phenetic comparisons and phylogenetic studies concur that *Alzatea* is an isolated genus within the Myrtales, derived from the same ancestral pool which gave rise to the modern Lythraceae, Crypteroniaceae, and Rhynchocalycaceae, but now distinctly separated from them and consequently best treated as a monotypic family.

#### TAXONOMIC TREATMENT

**ALZATEACEAE** S. Graham, fam. nov. TYPE: *Alzatea* Ruiz & Pavón.

Arbor glaberrima, ramis verticillatis purpurascens. Folia integerrima, coriacea, opposita et verticillata. Inflorescentia paniculata, terminalia, multiflora. Flores bisexuales, 5-meri, apetala, hemi-epigyni. Discus conspicuus, lobatus. Stamina 5, antepetala, margini disci inserta, filamentis brevissimis; antherae cordatae connectivo late expansa ad basi et angustata usque ad apicem; pollinis grana oblata-sphaeroidea, tricolporata, sine colpiis subsidiariis, exinio fere psilato. Ovarium biloculare; dissepimentum incompletum, basi foramene; ovulis in quoque loculo multis, horizontalis, imbricatis. Fructus capsula indurata, lateraliter compressa, nervaturis conspicuis munitus. Semina oblonga ad lunata, plana, circumcirca ala tenui cincta.

This monotypic family of the New World tropics, represented by *Alzatea verticillata*, is distributed along the lower slopes of the Andean Cordillera in Peru and Bolivia in humid forests of the upper Amazonian basin and disjunctly in cloud forests of Costa Rica and Panama. Figure 15.

*Alzatea verticillata* Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 1: 72. 1798. Fl. Peruv. 3: 20, pl. 141, fig. a. 1802. TYPE: Peru. Huanaco: nemoribus ad Chinchao praeruptum prope Mesapata praeditum (holotype, MA, pho-

FIGURES 11–14. *Rhynchocalyx lawsonioides* Oliv., Natal, South Africa, closest living relative of *Alzatea*.— 11. Flowering specimen, H.B. Nicholson s.n. (MO).— 12. Tree in bloom, edge of forest adjoining Table Mountain, Uvongo Nature Reserve.— 13. Typical small tree habit with erect trunk to 6 m in height; bark pale gray, Uvongo Nature Reserve.— 14. Inflorescence, flowers primarily in bud, actual bud length, 3–4 mm; actual leaf length, 25–75 mm.

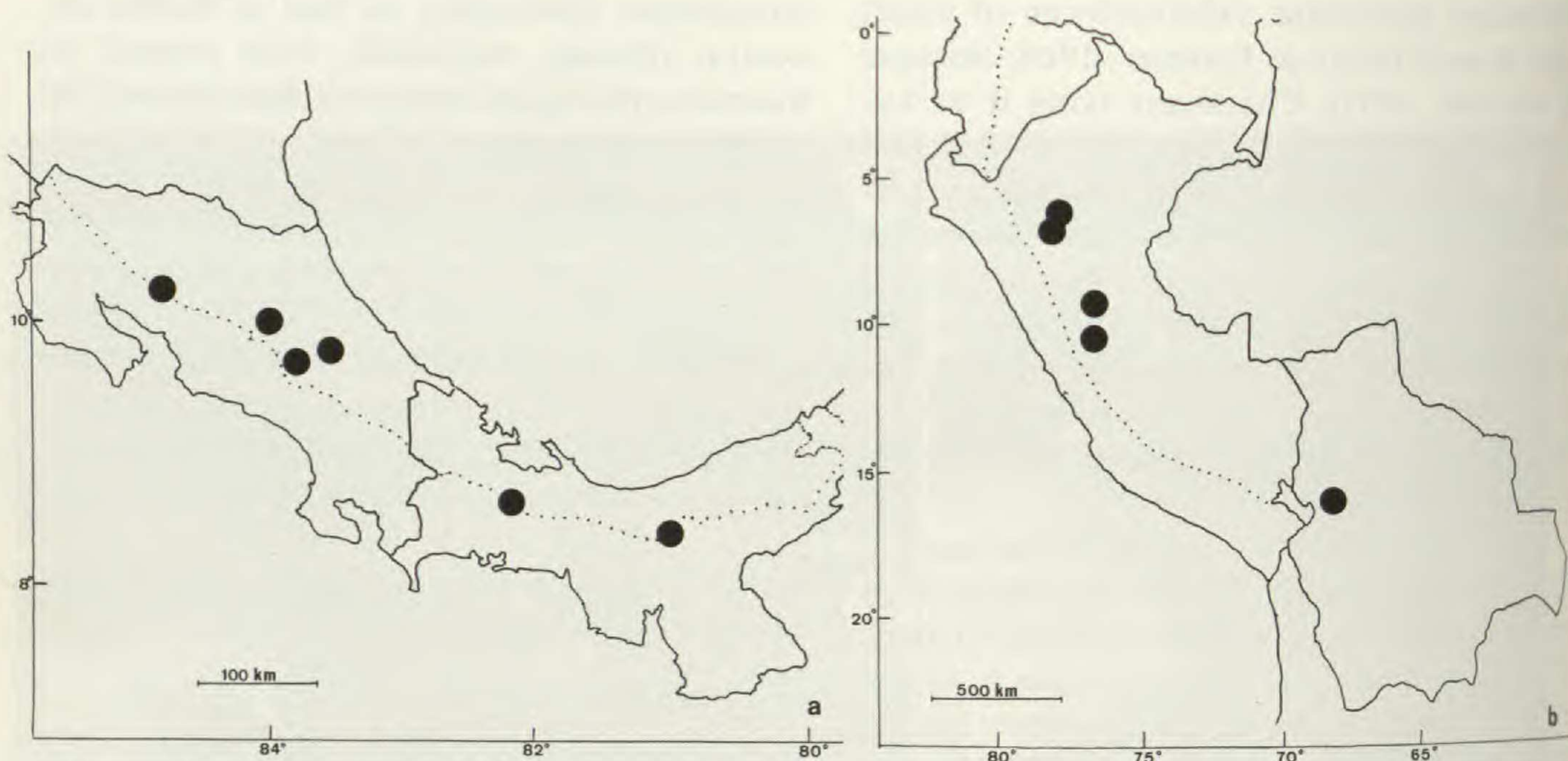


FIGURE 15. Distribution of *Alzatea verticillata*.—a. Subsp. *amplifolia* in Costa Rica and Panama.—b. Subsp. *verticillata* in Peru and Bolivia. Dotted line represents the continental divide.

tograph at F no. 91664!; isotypes, F no. 1573979!, F no. 843533!).

*Alzalia mexicana* F. G. Dietrich, Vollst. Lex. Gärtn. 1: 299. 1802. Nachtr. Vollst. Lex. Gärtn. 1: 199. 1815. Neu. Nachtrg. Vollst. Lex. Gärtn. 1: 187. 1825. TYPE: Based on *A. verticillata* Ruiz & Pavón.

**1a. *Alzatea verticillata* subsp. *verticillata*.**

Leaves elliptical or oblong-obovate, averaging 66 mm long, 35 mm wide, basally attenuate; petioles 2–13 mm long. Peru and Bolivia. Figures 9, 15a.

*Additional specimens* (those not mapped in Fig. 14 due to insufficient locality data are marked with an asterisk). BOLIVIA. Songo (= Zongo Valley), Nov. 1890, *Bang* 829 (K, MO!, NY, US); PERU. AMAZONAS: \*Cerro de Escalero, 1,300 m, Feb. 1903, *Ule* 6750 (K); Mendoza, 1,600 m, 15 Aug. 1963, *Woytkowski* 8331 (F!, MO!). PASCO: Oxapampa Alto Vaquería, 2,200 m, 11 Aug. 1967, *Vasquez A.* 114 (F!), 21 Nov. 1967, *Vasquez A.* 136 (F!). SAN MARTÍN: Zepelacio, near Moyobamba, 1,100–1,200 m, Oct.–Nov. 1933, *Klug* 3349 (GH, F!, K, MO!, S). UNKNOWN: \*Santa Ana, Pitabamba, Nov. 1866, *Pearce s.n.* (K); \*Río Negro, in the forest, 1,000 m, 15 Jan. 1961, *Woytkowski* 6196 (MO!, P).

**1b. *Alzatea verticillata* subsp. *amplifolia* S. A. Graham, subsp. nov. TYPE: Panama. Veraguas: Cerro Túte, 20 Mar. 1982, *Knapp & Kress* 4336 (MO).**

Folia oblonga-ovalia, ad 145 mm longa, 100 mm lata, saepe ca. 90 mm longa, 65 mm lata, basi pleraque

rotundata, sessilia vel subsessilia, petioli 0–2 mm longi. Costa Rica et Panama. Figures 10, 15b.

*Additional specimens* (those not mapped in Fig. 14 due to insufficient locality data are marked with an asterisk). COSTA RICA. CARTAGO: 0.5 km W of Tapantí, 1,200 m, 14 May 1967, *Lent* 966 (CR!, F!), 28 Jan. 1982, *Poveda et al.* 3264 (CR!), Oct. 1982, *Gomez* 18728 (CR!); Moravia de Chirripó, 28 Jan. 1977, *Poveda & Sieng* 1523 (CR!). PUNTARENAS: Flora de Monteverde, cerro N of Pantano Chomogo, 1,620–1,690 m, 15 Jan. 1977, *Dryer* 1133 (CR!, F!). SAN JOSÉ: Bajo La Hondura, above Río Hondura, 1,400 m, 22 Oct. 1967, *Lent* 1443 (CR!, F!), 20 June 1973, *Poveda* 566 (CR!), 24 Mar. 1977, *Poveda* 1564 (CR!). UNKNOWN: \*La Palma, 1,500 m, 31 July 1936, *Valerio* 1403 (F!); \*Quebrada Cuecha, 1,540–1,600 m, *Dryer* 941 (CR!). PANAMA. CHIRIQUÍ: 15 km N of Hornito, 17 Feb. 1979, *Hammel* 6247 (MO!), 12 km N of Hornito, 17 June 1982, *Knapp & Vodicka* 5532 (MO!). VERAGUAS, N of Santa Fe, slopes and peaks of Cerro Arizona (= Cerro Túte), 11 Sept. 1978, *Hammel* 4726 (MO!); Summit of Cerro Túte, 1,410 m, 5 June 1982, *Knapp & Dressler* 5392 (MO!).

Comparison of the South American and Central American collections reveals two character differences consistent with geographical source and significant enough to deserve formal taxonomic recognition. Costa Rican and Panamanian plants have ample, broad, generally oblong to oval, sessile leaves and those of South America have smaller, narrower, generally more elliptic, petiolate ones. The mean size of Central American leaf specimens is 89 mm by 63 mm; leaves are sessile or subsessile with petioles 2 mm long or less. The mean size of South American leaves

is 66 mm by 35 mm; leaves are basally attenuate, petiolate to subsessile with petioles varying from (0-)2-13 mm long, averaging 6 mm. Leaves of the type collection from Peru average 91 mm by 59 mm with petioles 10-12 mm long. On the Bolivian collection examined, leaves average only 57 mm by 33 mm and are mostly sessile. No floral morphological differences separate the Central and South American collections and Baas (1979) found no striking anatomical differences between Peruvian and Costa Rican samples. As more collections of the genus are gathered, perhaps even from the intervening areas of Ecuador, Colombia, and the Darien, it may well become more difficult to apply subspecific names. Based on present collections, however, recognition of subspecies *amplifolia* serves to point up the genetic divergence now expressed in the disjunctly distributed Central and South American plants.

It is possible that a discriminatory biological difference exists between Central and South American *Alzatea*. South American plants surveyed produce heterosexual flowers with pollen viability greater than 95%. In contrast, Central American plants appear to bear only functionally unisexual flowers. No fertile pollen has been found in flowers from Cerro Túte, Panama collections, although approximately 50% of the seed in each capsule appears fully formed. In Costa Rican collections studied, no more than 36% of the pollen appeared normal (Tobe, pers. comm.; Graham, unpubl. data). Investigations are in progress to determine the nature of reproduction in the Panama population (Raven, pers. comm.).

Description of the habit and habitat of the genus are known primarily from collectors' brief notations, mostly on herbarium labels. New observations, however, are rapidly accumulating on Central American *Alzatea* as a result of active research by members of the Missouri Botanical Garden currently working on the Central American flora. *Alzatea* is described in Ruiz's journal (1940) as a tall leafy tree with "a trunk divided into six thick props that formed an arbor underneath." Disparately, it is described as a slender, climbing epiphyte reaching the crowns of the largest trees of the lower montane rain forest in Costa Rica (R. Lawton, pers. comm.) or as isolated, small (ca. 7 m tall), much-branched trees (Poveda, pers. comm. to Raven). In Panama it occurs as a 2-3 m shrub of windswept elfin cloud forest in Veraguas Province (Knapp & Kress 4336, MO), as a stream-side epiphytic shrub in Chiriquí Province (Hammel 6247, MO), and has

been observed also in Chiriquí Province growing epiphytically in tall trees of the forest (Knapp, pers. comm.). Height records vary from 2 m to 20 m and it is apparent that habit varies considerably with site conditions. The typical form is probably a much-branched hemi-epiphytic tree of 6-12 m which is capable of climbing to greater heights with support of surrounding trees when it occurs in tall tree forests. Trunk diameter ranges from 5 cm in high-climbing specimens to 20 cm (to 80 cm in Costa Rica, fide Poveda) on free-standing trees.

It occurs typically on steep slopes of the low montane rain forest at elevations of 1,000-2,200 m either as isolated individuals or, in at least two instances, at Cerro Túte, Panama and Tapantí, Costa Rica, as a locally common component of the flora. In South America the genus appears on the eastern escarpment of the Andean Mountains. In both Central and South America it occurs with and is easily mistaken for *Clusia*. The striking vegetative similarity between *Alzatea* and *Clusia* has led curators to file the unfamiliar *Alzatea* with the Clusiaceae (Guttiferae); curators of Latin American collections are advised to check that family as well as the Celastraceae for undetected specimens of *Alzatea*.

Flowering of the genus in Peru occurs from August to October; mature capsules occur from November onward. The single collection from Bolivia was in bud in November. Collections indicate that in Costa Rica, flowering begins in July and mature fruits are present from January to May, while in Panama buds have been collected in March and in August, suggesting less seasonally restricted flowering.

Production of nectar has not been observed (Knapp, pers. comm.) nor have insect visitors been reported. In the absence of petals, the showy pinkish white anthers may function to attract insects. The anthers are positioned, as petals would be, between the calyx lobes at anthesis and are sometimes mistaken by collectors for petals. The most recent observations of living plants have been on the Cerro Túte, Panama, a windy site with frequent cloud cover where conditions are not often conducive to insect visitation.

Seed containing embryos generally constitute less than half the seed produced. Lack of pollination may partially account for this, but in the Central American populations low pollen fertility is certainly a factor. Studies of the reproductive biology should lead to a better understanding

of how *Alzatea* has managed to retain its place in the flora of the New World tropics.

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