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THE JUNCAGINACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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JUNCAGINACEAE L. C. Richard, Démonstr. Bot. ix. 1808, "Juncagines," nom. cons.

(ARROWGRASS FAMILY)

Perennial [or annual], glabrous, typically perfect-flowered [dioecious], scapose herbs, the axis sympodially branched, bulbous or rhizomatous, sometimes with runners, often covered with old leaf bases, the roots fibrous [sometimes tuberiferous]; starch grains of pteridophyte type. Leaves basal, alternate, distichous or spirodistichous, sessile, linear to almost filiform [filiform], terete to semiterete [dorsiventrally or laterally flattened (i.e., ensiform)], ligulate [eligulate]; axillary scales (squamules) present; stomata mostly paracytic. Inflores-

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project currently made possible through the support of National Science Foundation grants BSR-8415769 (Carroll E. Wood, Jr., principal investigator) and BSR-8415637 (Norton G. Miller, principal investigator). The 119th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present.The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on plants of this area, with information about extraregional members of a family or genus in brackets [ ]. References that I have not verified are marked with an asterisk.

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cence of terminal, bractless, pedunculate racemes [spikes] [rarely reduced to a single terminal flower]. Flowers actinomorphic to zygomorphic, hypogynous, perfect to imperfect, anemophilous, proterogynous. Perianth of 6 [4] (or fewer by abortion) distinct and mostly similar tepals in 2 whorls. Androecium usually of 6 [4] subsessile stamens (or fewer by abortion) in 2 whorls, each filament adnate at its base to the base of the subtending tepal; anthers tetrasporangiate, bilocular at anthesis, extrorse, opening by lengthwise slits, the tapetum ameboid, microsporogenesis of the successive type; pollen grains globose to ellipsoid, monocolpate, inaperturate, binucleate (sometimes trinucleate?) when shed. Gynoecium of 6 [4] carpels in 2 whorls (occasional flowers with 3 to 12 carpels), these more or less adnate to the central axis (carpophore) [or central axis lacking], some commonly sterile, the fertile carpels eventually separating from the axis [the carpels connate at least basally, forming a compound ovary in *Maundia* and *Tetroncium*]; styles short to lacking [well developed, subulate, and persistent as beaks on the fruit in *Tetroncium*]; stigmas distinct, plumose to papillose; ovary 1-locular [2–4-locular in *Maundia,* incompletely 4-locular in *Tetroncium*], each locule with a single ovule, this bitegmic, crassinucellar, anatropous [orthotropous], and erect [pendulous in *Maundia*]; megagametophyte (embryo sac) development of the Polygonum (normal) type; endosperm development nuclear; embryogeny of the caryophyllad type. Fruit schizocarpic, the mericarps indehiscent, achenelike [fruit essentially capsular(?) in *Maundia* and *Tetroncium*]; seed linear to ovoid, without endosperm [this present in *Tetroncium*], the embryo straight. (Excluding Lilaeaceae Dumortier, 1829, and Scheuchzeriaceae Rudolphi, 1830, nomina conservanda.) TYPE GENUS: *Juncago* Séguier, nom. illeg. = *Triglochin* L.

A small family of three genera and about 22 species: the monotypic *Maundia* F. Mueller (*M. triglochinoides* F. Mueller), of coastal eastern Australia (New South Wales and Queensland); the likewise monotypic *Tetroncium* Willd. (*T. magellanicum* Willd.), of the Falkland Islands and southern South America (from Tierra del Fuego, northward in the Andes to at least 40°S in Argentina and Chile), unique in the family because it is dioecious; and the widely distributed *Triglochin* L. (including the Australian *Cycnogeton* Endl.), about 20 species, one of which occurs in the southeastern United States.

The circumscription of the Juncaginaceae here accepted (with three genera) has ample precedent in the literature (e.g., by Chant; Cook; Engler & Diels; Hutchinson; Kimura; Mason; Tomlinson, 1982), but the relationships of two additional genera, *Scheuchzeria* L. and *Lilaea* Humb. & Bonpl., remain unsettled. Both (e.g., by Agrawal; Britton; Buchenau, 1903; Buchenau & Hieronymus; Hegi; Johri; Lotsy; Rendle; Suessenguth; Thorne, 1976, 1983; and Wettstein) or either one of these (*Scheuchzeria* only, by authors including Abrams; or *Lilaea* only, by those including Cronquist, 1968, 1981; Dahlgren & Clifford; Dahlgren, Clifford, & Yeo; Markgraf, 1981; Eckardt; Stebbins; and Takhtajan) may be included in an amplified version of the Juncaginaceae.

That *Scheuchzeria* represents a family by itself is accepted by the majority of workers after 1940 (see summary of the various monocot systems in Dahlgren & Clifford). Among the "large" number of important features (Tomlinson,

1982) in which this genus differs from *Triglochin* and *Lilaea* are three- (vs. two-)celled pollen; biovulate (vs. uniovulate) carpels; helobial (vs. free-nuclear) endosperm; the presence (vs. absence) of hypodermal crystals, a leaf apical pore, and floral bracts; and the absence (vs. presence) of squamules (minute scale- or gland-like outgrowths occurring in the axils of leaves; unique in the Helobiae). Floral developmental evidence further confirms the separate familial status of *Scheuchzeria* (Posluszny). A character common to all three genera, however, is the occurrence of the cyanogenic glucoside triglochinin.

The placement of *Lilaea* appears to be less certain. With *Triglochin* it shares two-celled pollen, uniovulate carpels, free-nuclear endosperm, and squamules. Both genera have an unusual type of embryo development in which the "first embryonic root does not originate from the point where the suspensor is attached, but from the lateral position . . . directly from the epidermis of the embryo, therefore not in the manner of adventitious roots, which develop from the deep inner tissue" (Yamashita, p. 205). *Lilaea* differs from *Triglochin* in the number of carpels (one vs. six) and perianth segments (one vs. six) and in the presence of laticifers (also lacking in *Scheuchzeria*). Tomlinson (1982), whose discussion of the three genera is outstanding, concluded that it is better to retain the separate familial status of *Lilaea* until a more extensive study has been made. (See also Posluszny *et al.* and Singh.) It should be noted that knowledge of Juncaginaceae (sensu stricto) is based mostly on Northern Hemisphere representatives of the family; more data are needed on species of *Triglochin* of the Southern Hemisphere, especially those of Australia, most of which are diminutive annuals, as well as on *Tetroncium* and *Maundia.*

Many authors accept a close relationship between the Juncaginaceae and the Potamogetonaceae. Takhtajan suggested that the latter may well be derived from the former (and that the Posidoniaceae probably represent an extreme marine stage of the Juncaginaceae). (Engler & Diels and Skottsberg even included the Juncaginaceae in the Potamogetonaceae.) Such a relationship was postulated over a century ago by Bentham (p. 165): "*Triglochin* . . . appears to me to be much more nearly connected with *Potamogeton* [than with Alismaceae], in the peculiar structure of the flowers, differing chiefly in habit, and even in that respect, the half-floating leaves of *T. procera* show a near approach to that genus." Hutchinson (p. 678) expressed the opinion that "the primitive tribe Helonieae of the Liliaceae has been developed from the same stock as the Juncaginaceae; the general facies of its genera is the same and in both groups the flowers are quite ebracteate." Joseph D. Hooker pointed out that the habit of *Tetroncium* is precisely that of *Narthecium* of the Liliaceae.

Fruit types in the family have been variously, and often questionably, denominated and described. I find, for example, no convincing evidence that the fruits of any of the three genera are indeed "follicles" or that they are "dehiscent." The fruits of *Triglochin* appear to me to be schizocarpic, the mericarps indehiscent (see under *Triglochin* below). Those of the other genera are essentially capsular according to some authors: in *Maundia,* "carpels 2–4, united along the whole length of their inner faces. Fruiting carpels . . . remaining united and together forming a 2- to 4-angled squat cylinder truncate at the summit with 2–4 short spreading beaks" (Aston, p. 241); and in *Tetroncium,* "carpels

4, united at base into incompletely 4-locular ovary. . . . Fruit indehiscent, 4-celled, seed usually single, with three aborted ovules" (Moore, 1968, p. 137). Both genera were included among those with capsular fruits by Dahlgren & Clifford, but three years later Dahlgren, Clifford, & Yeo (p. 312) wrote of them: "carpels . . . more or less fused centrally . . . but becoming separate in the fruit stage." Bentham (p. 169) described the carpels of *Maundia* as being "almost drupaceous, each with a thinly cartilaginous endocarp." According to Thompson (p. 80), the "fruiting carpels [are] joined at the adaxial angle [and have] a spongy covering on the ventral surface." Developmental study of the fruits of both *Maundia* and *Tetroncium* is called for.

Although seeds of the Juncaginaceae are usually described as lacking endosperm, *Tetroncium* is apparently an exception. Of this genus J. D. Hooker (p. 359) wrote "albumen farinaceum." Buchenau (1882, p. 472) acknowledged this exception in a footnote to his assertion that "Der Samen der Juncaginaceen enthält bekanntlich kein Albumen." Later, however, he and Hieronymus (p. 223) were skeptical ("*Tetroncium* mit kleinem Nährgewebe?"). Finally, however, Buchenau (1903, pp. 2, 6), apparently on the basis of his own observation, agreed with J. D. Hooker: "Embryo . . . in *Tetroncio* albuminosus" and "Nur bei *Tetroncium* liegt der . . . Embryo . . . in einem stärkemehlreichen Nährgewebe."

Noteworthy anatomical features of the Juncaginaceae include a single ring of collateral vascular bundles in the inflorescence axis, imparting an "exceedingly dicotyledonous" look (Chrysler, p. 180); the reported occurrence of an "incipient cambium" in the rhizome bundles (Andersson, Hill, Salisbury) (". . . perhaps . . . a case of incipient secondary thickening which is found developed to a much greater extent in Monocotyledons like *Aristea, Dracaena, Yucca,* etc."; Hill, p. 88); the presence of so-called axillary squamules, which are of wide occurrence in the Alismatidae (and one species of Araceae) (Arber [1923] considered them as appendages originating from the abaxial epidermis of the leaf just distal to the leaf in the axil of which they are found); and inflorescence formation by apical bifurcation of the axis (the original terminal meristem forming the inflorescence, the axillary bud of the distalmost leaf continuing further vegetative growth; reported in other Alismatidae).

Adoption of the name Scheuchzeriaceae (e.g., by Kartesz & Kartesz) when *Scheuchzeria* and *Triglochin* are included in the same family is incorrect. The name Juncaginaceae predates Scheuchzeriaceae by 22 years. If the Juncaginaceae are merged with the Potamogetonaceae Dumort. (1829), the latter name must be used (see International Code of Botanical Nomenclature, 1983, Appendix II).

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1. **Triglochin** Linnaeus, Sp. Pl. **1:** 338. 1753; Gen. Pl. ed 5. 157. 1754.[3]

Perennial [annual], perfect-flowered, herbaceous plants of wetlands, axis sympodially branched, somewhat [to strongly] bulbous [rhizomatous], with [without] runners, the roots fibrous [sometimes tuberiferous]; vessels confined to the roots. Leaves basal, distichous, sessile, linear, terete or semiterete [flat], ligulate [eligulate], sheathing, the sheath open. Inflorescence of terminal, bractless, pedunculate racemes [spikes] [rarely reduced to a single terminal flower]. Flowers actinomorphic, perfect to imperfect. Perianth of 6 tepals (or fewer by abortion) in 2 whorls, the upper whorl seemingly distal to the lower whorl of stamens. Androecium of 6 subsessile stamens (or fewer by abortion) in 2 whorls, each filament adnate at its base to the base of the subtending tepal, the stamen and tepal typically deciduous as a unit; pollen inaperturate, spheroidal, reticulate, binucleate (sometimes trinucleate?) when shed. Gynoecium of 6 carpels (occasional flowers with 3 to 12), these more or less adnate to the prolonged central axis (carpophore) [or central axis not prolonged, the carpels free], the lower 3 usually sterile, remaining attached to the axis as wings or ridges, the upper 3 [or all 6] eventually separating from the axis; styles short or lacking; stigmas distinct, plumose to papillose. Fruit schizocarpic, the mericarps indehiscent, achenelike [gynoecium apocarpous, the carpels achenelike in *T. procerum*]. TYPE SPECIES: *T. palustre* L.; see N. L. Britton, N. Am. Fl. **17:** 41. 1909. (Name from Greek *treis,* three, and *glochis,* point, from the pointed carpel bases of *T. palustre,* which spread from the axis at fruit maturity, the gynoecium then slightly recalling a three-barbed spear-point.)—ARROWGRASS.

A genus of about 20 species in two subgenera, widely distributed but best represented in the Southern Hemisphere, especially in Australia. Subgenus CYCNOGETON (Endl.) Buch. (characterized by perennial habit, free carpels, and lack of a carpophore) embraces a single species, *Triglochin procerum* R. Br., which occurs in southern New Guinea and Australia (including Tasmania).

[3]The name *Triglochin* has been—and continues to be—treated as feminine by many authors, either because glochin is a feminine noun or, more likely, because others do it that way. Linnaeus, however, used the name as neuter, and his choice should be followed (ICBN, 1983, Rec. 75A. 3).

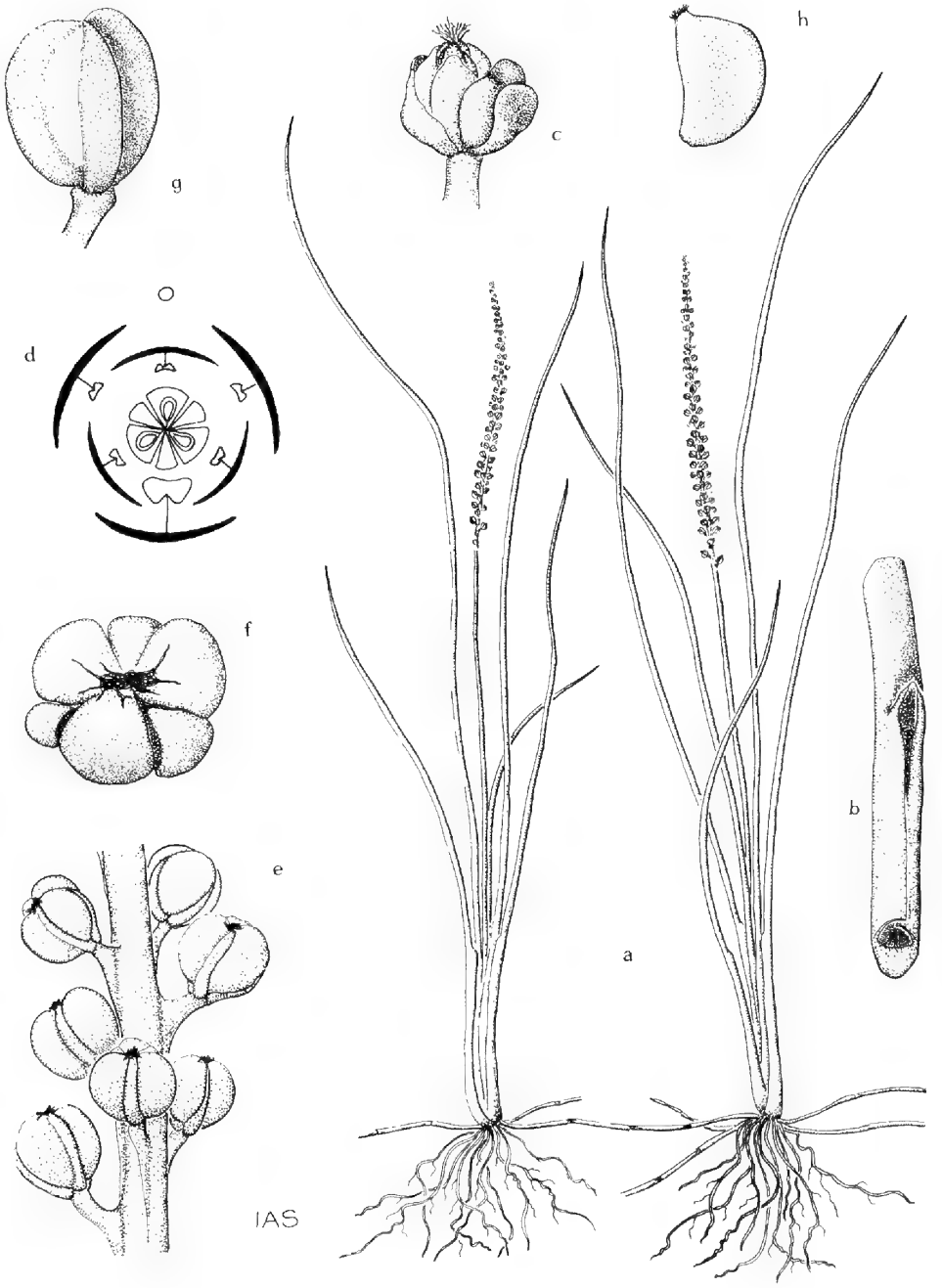

FIGURE 1. **Triglochin.** a–h, *T. striatum:* a, habit, × ½; b, portion of leaf sheath to show ligule, × 4; c, flower, the fertile stamen and its subtending tepal to the right, × 12; d, floral diagram (after Lieu), showing 6 tepals (5 with sterile stamens), 3 sterile and 3 fertile carpels, the latter each with a single 2-integumented ovule; e, portion of infructescence, × 6; f, mature fruit with 3 fertile and 3 sterile carpels, from above, × 12; g, persistent sterile carpels after removal of fertile mericarps, × 12; h, fertile mericarp, × 12.

Triglochin procerum var. *dubium* (R. Br.) Bentham is recognized by some (e.g., Cunningham *et al.*) as a distinct species. *Triglochin procerum,* water-ribbons, is the most aquatic of its congeners, with its leaves up to 2(–3.5) m long (Aston) when the plant grows in deep, flowing water, the distal portion floating or the entire leaf submersed and trailing downstream (in the manner of *Sparganium* L. or *Vallisneria* L.).

Subgenus TRIGLOCHIN (characterized by annual or perennial habit and—except in one annual—the adnation of carpels to a carpophore) is found on all continents except Antarctica. The single species of the southeastern United States, *Triglochin striatum* Ruiz & Pavon (*T. floridanum* Gand., *T. sessile* Gand., *T. triandrum* Michaux) is one of several species (number uncertain; see below) of its genus in North America. In our area it occurs along the coast from Maryland to Louisiana, typically in brackish and saline habitats (marshes, meadows, ditches, swamps), often in shallow water. An impressively wide-ranging plant, it is also distributed in the western United States (Oregon and California), the Valley of Mexico, the Bahamas, Cuba, South America (Peru and southeastern Brazil south to Tierra del Fuego), southern Africa (Cape Peninsula to Angola and Mozambique), and other extratropical regions, mostly coastal Australia (Western Australia to Tasmania and southeastern Queensland), New Zealand, and the Auckland and Chatham islands.

The taxonomy of *Triglochin,* at least in North America, is unsettled; estimates of the number of species here range from three (e.g., Britton) to six (e.g., Kartesz & Kartesz). The circumboreal *T. maritimum* complex, source of most of the uncertainty, is in need of critical study worldwide (see Löve & Löve, 1958a). The North American species of *Triglochin,* all perennials, typically grow in brackish, saline, and alkaline hydric habitats (less frequently in fresh water), especially in the western United States and western Canada, and to the north of our area.

The flowers of *Triglochin* have one or two whorls of three "bractiform perianth-like appendages" (Mason, p. 95), the nature of which has been much discussed. Each appendage subtends and is adnate at its base to a stamen (these reduced in some species), the two typically falling as a unit. The upper whorl of appendages appears to diverge from the axis *above* the lower whorl of stamens; its vascular supply, too, arises *above* that of the lower stamens (Uhl). This morphology led Uhl to interpret the flower of *Triglochin* as a reduced inflorescence of six staminate flowers and one or more naked carpellate flowers, each carpel probably representing a single flower (see also Burger). Such an interpretation has been questioned by Lieu, who found (p. 1418) that both whorls of tepals are initiated in acropetal succession *before* initiation of the stamens, that the anomalous position of the upper tepals results from "differential timing and rates of growth of the inner tepals and outer stamens," and that "the evidence does not support the interpretation of the flower of *Triglochin* as a reduced lateral branch of [an] inflorescence." Lieu did note that emphasis on vasculature would support interpretation of the flower as an inflorescence, but that developmental studies refute such an interpretation and lend support to regarding the flower of *Triglochin* as comparable to the ordinary trimerous monocotyledonous flower.

The flowers of those perennial species for which the floral biology has been studied (*Triglochin maritimum, T. palustre,* and *T. striatum*) are proterogynous, the penicillate stigmas protruding from the perianth two to three days before stamen maturation. Anthers of the lower whorl of stamens dehisce after the stigmas have turned brown, their pollen falling not onto the stigmas of that flower but into the deeply concave tepal below each stamen. The wind finally carries the pollen away or shakes it onto more proximal flowers. The stamens, each often attached to its tepal, eventually drop off. This sequence of events is then repeated for the upper whorl of stamens. Pollen deposition on stigmas of the same flower was reported for the Australian annuals studied by Keighery. These species and at least *T. maritimum, T. palustre,* and *T. striatum* are autogamous and show no significant difference in seed set between open pollination and enforced selfing. In contrast, *T. gaspense* Lieth & Löve, when grown in a greenhouse, did not set seed except when pollinated by hand (Löve & Lieth).

Carpel number in *Triglochin,* although variable, is usually six (but as few as three and as many as 12 have been observed in occasional flowers). In some species (e.g., *T. maritimum*) all six carpels are fertile, eventually falling as achenelike mericarps from the persistent and terete or merely angled carpophore. In others (e.g., *T. palustre, T. striatum*) the three carpels of the outer whorl are sterile (even vestigial) and remain adnate to the thereby winged or ridged carpophore after the inner, fertile carpels have fallen; they often then assume "the appearance of dissepiments of a capsule" (Bailey, 1902, p. 1705). Of the species in subg. TRIGLOCHIN, only *T. turrifera* Ewart, one of the Australian annuals, is said to lack a carpophore.

Chromosome counts, some undocumented, have been published for about ten species of *Triglochin. Triglochin procerum* (subg. CYCNOGETON) has diploid, tetraploid, and octoploid "morphological forms" ($2n$ = 16, 32, 64; Robb & Ladiges).

In subg. TRIGLOCHIN the most counted taxon is *Triglochin maritimum* agg., for which seven out of 12 possible numbers in a polyploid series from diploid (12) to 24-ploid (144) have been noted, some from the Old World, some from the New. (Not fitting into this series are counts of $2n$ = 30 [Bolkhovskikh *et al.*] and 56 [Looman] in *T. maritimum,* or n = 75–77 [Gervais & Cayouette] in *T. elatum* Nutt., a member of the *T. maritimum* aggregate.) According to Löve & Löve (1958a, p. 20), *T. maritimum* is "one of the most collective species known and so heterogeneous that its inclusion in the so-called circumpolar element of distribution is highly misleading." They (1958b, p. 162) further stated that this "supposedly circumpolar [taxon] is in fact an aggregate of at least more than a dozen good species."

Counts for *Triglochin palustre,* which shares with *T. maritimum* a distribution in both the Old and New worlds, are $2n$ = 12, 18, 24, 26, 28, 36, 48; perhaps this taxon, too, is an aggregate (Hess *et al.*).

A strictly North American taxon for which a count is available is *Triglochin gaspense,* $2n$ = 96. Counts for Old World taxa include *T. Barrelieri* Loisel., $2n$ = 30; *T. bulbosum* L., $2n$ = 18; and *T. laxiflorum* Guss., $2n$ = 18. I know of no counts for either *T. striatum* or any of the Australian annuals.

Dispersal of species of *Triglochin* needs further study. Some are certainly hydrochorous. *Triglochin procerum* has been seen to drop its disseminules into the water of a stream, where they were carried away (Keighery). Pojar observed floating seedlings of *T. maritimum,* and mericarps of this species have been collected from drift-line debris (Boorman). However, "seeds" of *T. maritimum* (and of *T. palustre*) float for less than a week in fresh water (perhaps a bit longer in salt water), according to Praeger. Epizoochory in mud and anemochory have been suggested for *T. maritimum* (Pojar).

Disseminules of species of *Triglochin* with mucronate, spurred, or even hooked apices or bases (e.g., *T. palustre* and some of the Australian annuals) have been assumed to be epizoochorous by attachment, an assumption that requires verification. Animal dispersal of the Australian annuals has been questioned by Keighery, who found that in these plants, which occupy shallow, sandy, winter-wet depressions, seed dispersal "has been reduced to a minimum . . . ensuring that the species will occupy the same favourable area next year" (p. 83). It seems possible that in these annuals the structural devices that seem to fit them for animal dispersal serve rather as "anchors" in favorable habitats.

Triglochin maritimum and *T. palustre,* considered in some regions to be "fairly" good forage, may be relished by livestock because of the salt content of the leaves. In the western United States and western Canada, however, both species (but especially *T. maritimum*) are among the major plants poisonous to cattle and sheep, the toxic principle being hydrocyanic acid. Death results from asphyxia or, in severe cases, respiratory failure. *Triglochin striatum* seems not to have been implicated in poisoning; it is grazed by sheep in Chile (Alduante *et al.*) and is considered a good salt-marsh fodder in Australia (Bailey, 1883).

Species of *Triglochin* may be of importance as food for wildlife in some regions. At James Bay, Canada, for example, the perennating bulbs of *T. palustre* were found to be the most strongly selected food item of snow geese (Prevett *et al.*).

The young leaves of *Triglochin maritimum*—their dubious qualities notwithstanding—can be cooked and eaten as a vegetable. They emit an unpleasant odor when cooking ("an Chlor erinnerende"; Suessenguth, 1935, p. 214) and are reputed to be a "blood-purifier." Ashes from this species are rich in sodium carbonate and can be used in making soap (Fedchenko). The fruits were parched and eaten by Oregon's Klamath Indians, who also roasted them as a substitute for coffee (Coville). *Triglochin procerum* produces globose root tubers 2–3 cm across (Van Steenis), of which Mueller (1867–1868, p. 83) said, "tubera edulia nativis avide quaesita."

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REVISION OF CASTANEA SECT. BALANOCASTANON (FAGACEAE)

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Castanea sect. *Balanocastanon* is endemic to the eastern and southeastern United States. It comprises one species, *C. pumila,* of which there are two varieties, *pumila* and *ozarkensis.* Variety *pumila* is the more widespread of the two and is a highly variable shrub or tree. Variety *ozarkensis* is now apparently restricted to the Ozark Plateau due to its extirpation from Alabama by the chestnut blight; it consists mostly of stump sprouts of various sizes. The two varieties differ in reproductive and vegetative characters, as well as in leaf micromorphology and flavonoid constituents. *Castanea* × *neglecta* is a rare hybrid between either variety of *C. pumila* and *C. dentata,* the American chestnut.

Castanea Miller, a genus of limited distribution in two widely separated areas of the Northern Hemisphere, is found in eastern North America and eastern and western Asia (Elias, 1971). Section *Balanocastanon* Dode is endemic to the eastern and southeastern United States from Pennsylvania to Florida, west to eastern Texas, southwestern Missouri, and west-central Kentucky. It includes shrubs and trees that occupy dry, open, usually disturbed sites from near sea level to about 1400 m altitude. Although widely distributed geographically and well represented in herbaria, sect. *Balanocastanon* has not been studied biosystematically and has been without consistent taxonomic treatment (see TABLE 1).

The objectives of this study were to document and describe the patterns of variability within the section, to devise a realistic and consistent taxonomic treatment, to suggest evolutionary relationships among the taxa, and to provide descriptions, synonymy, range maps, and keys for the taxa recognized herein.

TAXONOMIC HISTORY

In 1908 Dode divided *Castanea* into three sections, using both number of nuts per cupule and nut shape as criteria. Section *Castanea* (*Eucastanon* of Dode) included taxa from North America (*C. dentata* (Marshall) Borkh.) as well as eastern and western Asia and was recognized as having three nuts per cupule, each nut being broader than long. Section *Balanocastanon* was delimited by having a solitary elongated nut per cupule. Dode recognized four taxa within this section, one in eastern Asia and three in North America. The Asian *C. vilmoriniana* Dode was reduced by Rehder and Wilson in Sargent (1917)

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to a synonym of *C. henryi* (Skan) Rehder & Wilson, now the only species in sect. *Hypocastanon* Dode (two nuts per cupule, with nut shape intermediate between those of the other sections).

The first species named in sect. *Balanocastanon* was *Fagus pumila* L., which Miller (1768) transferred to *Castanea*. Linnaeus's (1753) description was taken directly from Gronovius's *Flora Virginica* (1739), with the addition of "subtus tomentosus" to distinguish the species from *Fagus dentata* L. (*C. dentata*). Since Linnaeus described *F. pumila*, an additional 28 taxa or new combinations have been proposed, 14 of these by W. W. Ashe (1922, 1923, 1924, 1925, 1926, 1927). The latest changes were proposed by Murray (1982), who elevated *C. alnifolia* Nutt. var. *floridana* Sarg. and *C. pumila* (L.) Miller var. *ashei* Sudw. to subspecies.

The only monograph of *Castanea* was by Camus (1929), who recognized eight species (11 taxa) in sect. *Balanocastanon*. Since this work was published the number of taxa and their level of recognition have differed among authors, although there has been a trend toward a general reduction in the number of taxa (see TABLE 1). After field and herbarium studies in Arkansas, Tucker (1975) reduced *C. ozarkensis* Ashe to a variety of *C. pumila*, in effect reducing almost all taxa and combinations within the section to this species. More recent treatments (Elias, 1980; Little, 1979; Preston, 1976), however, have not followed the concept of a single species.

COMPARATIVE STUDIES

HABIT

The growth form of members of sect. *Balanocastanon* (*Castanea pumila* sensu lato) is highly variable and has been a source of taxonomic confusion. Several taxa have been distinguished by growth form alone—for example *C. alnifolia*, by its stoloniferous habit (Nuttall, 1818), and *C. alnifolia* var. *floridana* Sarg., by its arborescent habit (Sargent, 1919). I consider growth form and other characters to be primarily a result of ecophenic responses to environmental factors such as fire, logging, length of time after disturbance, and—since the early 1900's—the chestnut blight (*Cryphonectria parasitica* (Murrill) Barr). My determination of these ecophenic responses has been based on my experience with natural populations and with plants grown in a common garden situation for several years and on my revisitation (sometimes with the original collector) of populations from which specimens had been taken, sometimes decades before. The latter, especially, gave me the opportunity to compare the plants' response to their environment over an extended period.

Castanea pumila var. *ozarkensis* is normally a large multistemmed shrub or medium-sized tree, up to 20 m in height and never stoloniferous. The canopy is dome shaped, not unlike that of *C. mollissima* Blume, the cultivated Chinese chestnut. Due to the introduction of chestnut blight, most individuals of var. *ozarkensis* now exist only as stump sprouts of variable size and age, as in the case of *C. dentata*, the American chestnut.

The remaining individuals in sect. *Balanocastanon*, herein recognized as

TABLE 1. **Taxa of Castanea sect. Balanocastanon recognized by various authors.**

AUTHOR				
Camus (1929)	**Small** (1933)	**Elias** (1971)	**Tucker** (1975)	**Little** (1979)
C. ozarkensis Ashe	*C. ozarkensis* Ashe	*C. ozarkensis* Ashe	*C. pumila* (L.) Miller var. *ozarkensis* (Ashe) Tucker	*C. ozarkensis* Ashe
var. *arkansana* Ashe	(Syn. of *C. ozarkensis*)	(Not treated)	(Syn. of *C. pumila* var. *ozarkensis*)	(Syn. of *C. ozarkensis*)
C. ×*alabamensis* Ashe	*C. alabamensis* Ashe	*C.* ×*alabamensis* Ashe	(Not treated)	*C.* ×*alabamensis* Ashe
C. pumila Miller	*C. pumila* (L.) Miller	*C. pumila* Miller	*C. pumila* (L.) Miller	*C. pumila* Miller
C. ashei Sudw.	*C. ashei* Sudw.	*C. pumila* Miller var. *ashei* Sudw.	(Syn. of *C. pumila*)	(Syn. of *C. pumila*)
C. alnifolia Nutt.	*C. alnifolia* Nutt.	*C. alnifolia* Nutt.	(Syn. of *C. pumila*)	*C. alnifolia* Nutt.
C. floridana Ashe	*C. floridana* (Sarg.) Ashe	*C. alnifolia* Nutt. var. *floridana* Sarg.	(Syn. of *C. pumila*)	(Syn. of *C. alnifolia*)
var. *margaretta* Ashe	*C. margaretta* Ashe*	(Syn. of *C. alnifolia* Nutt. var. *floridana*)	(Syn. of *C. pumila*)	(Not treated)
var. *arcuata* Ashe	(Not treated)	(Not treated)	(Not treated)	(Not treated)
C. ×*neglecta* Dode	*C.* ×*neglecta* Dode	*C.* ×*neglecta* Dode	(Not treated)	*C.* ×*neglecta* Dode
C. paucispina Ashe	(Not treated)	*C. paucispina* Ashe	(Not treated)	(Not treated)

*Listed under *C. ashei.*

Castanea pumila var. *pumila* sensu lato, may be either a stoloniferous or nonstoloniferous shrub or a tree. The stoloniferous form of var. *pumila* is common in the southeastern United States along roads and railroads and in pine plantations and has been treated as *C. alnifolia*; it develops into the nonstoloniferous or the arborescent form, however, when the disturbance stops. Within a few years no evidence of the stoloniferous form remains. Where the two shrub forms occur together, I have dug them and found that they are often connected below the ground by a stolon or a root sprout.

The nonstoloniferous shrub and arborescent forms of var. *pumila* may attain various sizes, depending on the degree of disturbance in the habitat. Variety *pumila* is found in open or semi-open sites; it is excluded by competition in shaded situations. Most individuals attain a height of 2–5 m, but some may reach 15 m. In previous treatments, the tall individuals have been recognized as *Castanea pumila* sensu stricto or *C. floridana* (Sarg.) Ashe, depending on whether they were collected in the northern or the southern part of the geographic range. The largest individual of *C. pumila* var. *pumila* that I have seen, with a height of 15 m and a d.b.h. of 1.1 m, was in Liberty County, Florida (*G. P. Johnson 1523*, NCSC).

Twigs and Bark

The twigs of *Castanea pumila* are variable in thickness, color, pubescence, and shape; this variability occurs within individuals and populations, as well as over its geographic range, apparently as ecophenic or random genetic variation. However, the twigs of var. *ozarkensis* are more uniform than those of var. *pumila*. Immature twigs of var. *ozarkensis* are slender, dark brown, and puberulent; when mature they are stout (often exceeding 3 mm in diameter), gray-brown, often faintly fluted, and usually essentially glabrous.

The twigs of var. *pumila* may be brown, tan, or yellow-green and range from puberulent to tomentulose (a function of individual variation, as well as of sun/shade position, age of the twig, and vigor of the shoot). Twigs in full sun are often lighter in color and more pubescent than those in full shade. Vigorous shoots may have more vestiture or retain their vestiture longer than slower-growing ones. Twig diameter is usually less than 3 mm.

The twigs of *Castanea pumila* var. *pumila* may be similar to those of shaded individuals of *C. dentata*. Then trichome type and vestiture on the twigs (*C. dentata* has a greater number of bulbous trichomes and nearly no stellate ones) can be used for identification like those on the leaves (Hardin & Johnson, 1985). The twigs of *C. dentata* and *C. pumila* var. *ozarkensis* may be confused due to their sparse pubescence, their stoutness, and their often fluted shape, but the gray-brown color of the twigs and the presence of a few stellate trichomes are diagnostic of var. *ozarkensis*.

Bark characters of the trunk may be useful in distinguishing between the two varieties of *Castanea pumila*. Variety *ozarkensis* has dark-, light-, or reddish-brown bark becoming moderately to deeply fissured between broad, flat ridges that break into loose, platelike scales, while that of var. *pumila* is gray or gray-brown and relatively smooth, becoming at most only slightly fissured and scaly.

These characters may be of little use, however, because the characteristic color and fissuring may not develop before the trunk becomes infected with the chestnut blight (trunks seldom exceed 10–20 cm d.b.h. before the tree succumbs to the blight). Both varieties of *C. pumila* are susceptible, although var. *ozarkensis* is affected more severely.

The bark of *Castanea dentata* is gray and relatively smooth on young trunks, becoming dark brown and deeply fissured between flat ridges on older trees.

Leaves

Leaf characters have been important in the past taxonomy of the chinquapins. Size, shape, vestiture, margin type, number of secondary veins, and apex and base shapes have all been used in the distinction of taxa (Ashe, 1922, 1923, 1924, 1925, 1926, 1927; Sargent, 1919; Sudworth, 1922; Tucker, 1975).

The characters used in this study are derived mainly from Hickey's (1973) system for classification of dicotyledonous leaves, with the addition of criteria provided by scanning electron microscopy. Micromorphological features include trichome types, vestiture, presence or absence of epicuticular wax, and cuticular pattern (Hardin & Johnson, 1985).

Five populations representing the geographic ranges of each of the previously recognized taxa in the section (25 total) were randomly sampled for all comparative studies. In addition, measurements from other personal collections and from herbarium sheets were recorded and compared with the sample populations. Variations within an individual, a population, and a taxon were determined, and comparisons were made between each of the previously recognized taxa. A nonrandom sample was taken from *Castanea dentata.*

Analysis of these data indicated no discontinuities or patterns of variation in the characters examined for any of the previously recognized taxa in the section except for those I call *Castanea pumila* var. *ozarkensis.* Compared to the leaves of the rest of the individuals in the section, those of var. *ozarkensis* tend to be larger (see Table 2), more often lance-elliptic or lanceolate, and more frequently acuminate or long-acuminate. All leaf characters show a wide range of variation, and overlap occurs between them (see Table 2). Shape and size of the leaf, shapes of apex and base, vestiture, and depth of serration are highly plastic, with variability mostly attributable to random variation, plant vigor, and ecophenic responses. Leaves from plants of sunny, xeric sites are smaller, more shallowly serrate, and more pubescent than those from plants of shady, mesic sites. Vigorous branches have leaves that are larger, more deeply serrate, and more often lanceolate than those of slower-growing branches.

The leaves of *Castanea dentata* may be mistaken for those of *C. pumila* var. *pumila* growing in shaded sites. Then a combination of characters must be used for accurate identification. The leaves of *C. dentata* are usually larger, thinner, less pubescent, more deeply serrate, more lanceolate, and with a longer, more acuminate apex than those of *C. pumila* var. *pumila.* The leaves of *C. dentata* and *C. pumila* var. *ozarkensis* are similar in shape, form, and size, which often accounts for collections of *C. pumila* var. *ozarkensis* from Arkansas and Missouri being misidentified as *C. dentata.* These two taxa are only nat-

TABLE 2. **Leaf data from taxa previously recognized in Castanea sect. Balanocastanon.**

Character	Taxon*				
	C. pumila var. pumila	var. ozarkensis	var. ashei	C. alnifolia var. alnifolia	var. floridana
Petiole length (mm)					
Mean	7.4	7.5	6.7	5.5	5.7
SD	2.2	1.4	1.9	1.3	2.0
Range	3–22	4–10	2–13	2–11	2–12
Blade length (cm)					
Mean	11.6	17.2	11.1	9.5	9.6
SD	2.4	3.0	2.2	1.8	2.2
Range	4.9–21.7	4.3–26.6	4.8–17.6	4.1–15.7	4.7–17.1
Blade width (cm)					
Mean	4.1	4.6	3.9	3.8	3.5
SD	.85	.99	.85	.79	.82
Range	2.0–8.0	2.0–9.3	2.2–8.3	1.5–6.6	1.6–6.5
No. of teeth per side of leaf					
Mean	15.0	15.0	13.3	12.3	12.6
SD	2.3	2.7	2.9	2.8	3.1
Range	8–24	5–21	1–22	1–21	1–22
Sinus depth (mm)					
Mean	1.9	2.4	2.0	1.4	1.2
SD	.66	.72	.72	.61	.59
Range	1–5	1–5	1–5	1–4	1–4
No. of secondary veins					
Mean	17.7	17.5	16.3	14.7	15.4
SD	2.2	3.0	2.6	2.5	2.5
Range	9–26	7–26	7–24	7–22	8–24

* For each taxon $n = 250$

urally sympatric in north-central Alabama and can be distinguished by their trichome types and vestiture (Hardin & Johnson, 1985) and by the often glaucous leaves of *C. pumila* var. *ozarkensis.*

Foliar Vestiture

The foliar vestiture of *Castanea pumila* has been fully described elsewhere (Hardin & Johnson, 1985). There are six types of foliar trichomes (simple, bulbous, acicular, solitary, fasciculate, and stellate) and four degrees of vestiture (puberulent, pilose, tomentulose, and tomentose).

The presence of stellate trichomes usually indicates *Castanea pumila* or the hybrid *C.* ×*neglecta* (*C. pumila* × *C. dentata*), although scattered individuals of *C. dentata*—generally located in the area of sympatry with *C. pumila* and mostly restricted to the Appalachian region—also have a few of them. The presence of stellate trichomes in *C. dentata* may indicate introgression with *C. pumila* or may be the result of an incomplete evolutionary loss of this type of trichome. *Castanea sativa* Miller, *C. mollissima,* and *C. crenata* Sieb. & Zucc. belong to the same section as *C. dentata* and also have stellate trichomes.

Leaves of *Castanea pumila* (both varieties) vary greatly in vestiture but not in types of trichomes. Except for a higher frequency of bulbous trichomes on the leaves of *C. pumila* var. *ozarkensis,* this variability does not follow any geographic patterns or correlate with any other characters studied. It is due mostly to leaf age and sun/shade conditions.

Castanea ×*neglecta* cannot be distinguished from *C. pumila* on the basis of vestiture but does have a greater number of bulbous trichomes on its leaves. In frequency of occurrence of this trichome type, the hybrid is intermediate between *C. pumila* and *C. dentata.* The young leaves of *C. dentata* are densely covered with bulbous trichomes that appear as clear or golden resinous dots on the leaf surfaces. Most of these fall as the leaves expand and mature.

Inflorescence

The flowers of *Castanea pumila* are borne on erect, horizontal, or pendent axillary spikes on branches of the current season's growth. There is one inflorescence per leaf axil, and it may be staminate, androgynous, or rarely pistillate. The androgynous spikes are distal to the staminate on a branch, although some branches, especially in shaded situations, may bear only staminate spikes. Androgynous inflorescences are usually shorter than staminate ones.

The spike of *Castanea pumila* is composed of two types of axes. The primary one is a determinate long-shoot, along which are attached cymose short-shoots (dichasia) (Brett, 1964; Kaul & Abbe, 1984). The staminate dichasia are subtended by a single bract and usually have seven florets, although some may have one or three. Pistillate dichasia are subtended by three bracts and typically have one flower. A very unusual inflorescence (Arkansas, Conway County, *G. P. Johnson 1489,* NCSC) had five pistillate florets per dichasium. In comparison, *Castanea dentata* typically has three florets per pistillate dichasium.

The androgynous spikes of *Castanea pumila* have from one to eight pistillate dichasia, and this variability correlates with other characters in distinguishing

var. *ozarkensis* from var. *pumila*. Variety *ozarkensis* usually has five to seven pistillate dichasia per androgynous spike, while var. *pumila* generally has five or fewer. These numbers may vary, however, due to predation, mechanical injury, or plant vigor. *Castanea dentata* usually has one or two pistillate dichasia per androgynous spike.

The length of staminate spikes is not taxonomically significant (Ashe, 1923, 1925; Sudworth, 1922), nor is the number of staminate dichasia per staminate or androgynous spike.

FLOWERS

Staminate flowers were examined for tepal number, shape, and size and for stamen length, arrangement, and number; pistillate flowers for tepal number, shape, and size and for style number, length, and pubescence. Analysis indicated no discontinuities or patterns of variation for characters analyzed for any of the taxa examined. The staminate and pistillate flowers vary only slightly over the geographic range of *Castanea pumila*. In both staminate and pistillate flowers the six tepals are imbricate, pubescent, ovate-triangular, and 1 mm long. Staminate flowers have from six to eighteen stamens (usually 12) that are 2–3 mm long and arranged in one series; the anthers are introrse. A pubescent pistillode is occasionally present. The staminate florets of *C. dentata* are the same as those of *C. pumila*.

The pistillate flowers occasionally have staminodia or stamens that do not elongate or anthers that fail to dehisce. There are four to nine (usually six) styles, basally pubescent and 1–3 mm long. Pistillate flowers of *Castanea dentata* have six to nine styles that are scarcely pubescent at the base.

POLLEN

Pollen from each of the reference populations was examined by scanning electron microscopy for length, diameter, surface ornamentation, and general shape. In all respects it is very uniform, with no observable variation within an individual, population, geographic area, or taxon.

The pollen of *Castanea pumila* is 15–17 μm in length and 9–10 μm in diameter, subprolate, and tricolporate, with the colpi extending most of the distance between the poles (FIGURE 1). The surface is relatively smooth, with a finely rugulose-pitted ectexine; there is no evidence of oils or other substances that would contribute to adhesion of the grains. Harsh treatment of the pollen during fixation or dehydration may cause it to collapse partially or to bulge at the colpi, forming unusually shaped grains that might be regarded as normal.

The pollen of *Castanea dentata* is similar in shape, size, and ornamentation to that of *C. pumila*. Pollen of the genera of the Castaneoideae is uniform in its characters (Crepet & Daghlian, 1980), and fossil pollen of the Castaneoideae is referred to as "*Castanea* type" (Muller, 1981).

CUPULE

The cupule of *Castanea pumila* is composed of two triangular valves that remain fused until maturity, when they split along a suture that appears as a slight furrow flanked by scales. These scales are the ends of the arcs of prickles

FIGURE 1. Pollen of *Castanea pumila* (*G. P. Johnson 1493*), × 6000.

that moderately to densely cover the surface of the valves. At the top of the cupule is an aperture through which the upper portion of the fruit (perianthopodium, *fide* Abbe, 1974) projects. The cupule usually contains a single nut. In contrast, the cupule of *C. dentata* is composed of four valves, which usually enclose three nuts.

The cupule of *Castanea pumila* has probably evolved in a two-step process. The first involved the loss of the lateral flowers of a three-flowered dichasium. The second was the fusion of the lateral valves of a four-valved cupule (Brett, 1964; Forman, 1966). The ancestral type of cupule for *C. pumila* is found in sect. *Castanea*. The occasional presence of more than one flower per cupule may indicate that evolution of the two-valved cupule is incomplete and that reduction in valve number preceded loss of the two lateral flowers.

The use of prickle density[2] as a taxonomic character has been a source of confusion in *Castanea pumila* sensu lato. *Castanea ashei* was segregated from *C. pumila* sensu stricto primarily on the basis of the bur being remotely covered

[2]Density of prickles on the cupules is a function of the number of prickles per area and the amount of branching in the distal portion of the prickle. Attempts to quantify the amount of space between prickles or the amount of cupule body visible through the prickles were unsuccessful. The relative terms "dense," "remote," and "sparse" describe decreasing prickle density.

with prickles in the former, and densely so in the latter (Ashe, 1925, 1926; Camus, 1929; Elias, 1971; Sudworth, 1922). Ashe (1926) also used prickle density to segregate *C. paucispina* from *C. alnifolia.*

Examination of field collections and herbarium specimens from throughout the range of *Castanea pumila* indicates that prickle density is variable within an individual, population, growth form, geographic area, and taxon. The only consistent pattern of variation is a general decrease in density in individuals from the Coastal Plain of the southeastern United States. The prickles of *C. dentata* are thicker and less pubescent than those of *C. pumila*; they always branch distally.

Cupule size varies within an individual, population, growth form, geographic area, and taxon. Information (see TABLE 3) was gathered in the same manner and from the same populations as other comparative data. Analysis indicated no discontinuities or patterns of variation for the characters studied for any of the previously recognized taxa. Cupule size is determined by the width and length of the cupule body and the height to which the distal portions of the prickles rise above the surface. It is not directly correlated with nut size because of the differences in prickle length. The largest cupules seen were on vigorous individuals, or on plants with few cupules.

FRUITS AND SEED GERMINATION

The fruit of *Castanea pumila* is an indehiscent, conical nut formed from an inferior ovary. It is a lustrous, dark, chestnut-brown except for the large tan scar located at the base. The apex is prolonged into a slender, pubescent perianthopodium (Abbe, 1974), which is capped by the shriveled remnants of the styles and tepals. The fruit is minutely pitted with circular or angular depressions that are visible with the aid of a scanning electron microscope.

Nuts were examined for length, diameter, and shape (see TABLE 4). Analysis indicated no discontinuities or patterns of variation for the characters studied for any of the previously recognized taxa. Nuts are largest on vigorous individuals or on plants bearing few fruits. In cross section they are usually circular but may be angular if borne more than one per cupule. In comparison, the nuts of *Castanea dentata* are 18–25 mm long, 18–25 mm in diameter, obovate, and flattened on at least one side.

The fruits of *Castanea pumila* are synzoochorous and dispersed primarily by squirrels and chipmunks, although bluejays and woodpeckers may contribute to distribution as they do with acorns. Animals often open the cupules before the nuts mature. Seeds germinate immediately in the fall, as in the white oaks (*Quercus* L. subg. *Quercus*). Seed viability is short—sometimes only seven days. Stratification requirements are short or nonexistent; some nuts gathered in Florida and mailed to Raleigh, North Carolina, had germinated in transit. Germination is hypogeal, and the root system becomes well developed before the shoot emerges.

REPRODUCTIVE BIOLOGY

There has been debate as to whether pollination in *Castanea* is anemophilous, entomophilous, or a combination of the two. The three different points of view were summarized by Clapper (1954).

Bagging and hand-pollinations similar to Clapper's were conducted at the

TABLE 3. **Cupule data from taxa previously recognized in Castanea sect. Balanocastanon.**

Character	Taxon*				
	C. pumila var. *pumila*	var. *ozarkensis*	var. *ashei*	*C. alnifolia* var. *alnifolia*	var. *floridana*
Length (cm)					
Mean	3.1	3.6	2.8	3.1	2.4
SD	0.6	0.4	0.5	0.4	0.2
Range	1.9–4.2	2.1–4.4	1.5–4.4	2.0–4.6	2.0–2.9
Diameter (cm)					
Mean	2.9	3.4	2.8	3.0	2.3
SD	0.5	0.3	0.5	0.4	0.2
Range	1.6–3.8	2.6–4.2	1.4–4.2	2.0–4.6	1.8–2.8
Prickle length (mm)					
Mean	8.4	10.0	8.5	8.7	6.9
SD	2.2	1.9	1.6	3.0	1.0
Range	4–13	5–14	4–13	6–17	5–11

* For each taxon $n = 250$

Cliffs of Neuse State Park in Wayne County, eastern North Carolina, and near Highlands in Macon County, western North Carolina, to determine the mode of pollination in *Castanea pumila*. Additional observations were made throughout the southeastern United States (Johnson, 1985). From these tests I conclude that *C. pumila* and *C. dentata* are primarily wind pollinated. Any role played by insects is a passive, indirect one. Although insects may dislodge pollen from anthers as they move over the staminate flowers, diurnal and nocturnal observations failed to detect them on pistillate flowers. However, insect exclusion did not inhibit pollination and fertilization. Insects are probably attracted by the odor of the staminate inflorescences and/or by the availability of large numbers of anthers. Crepet and Daghlian (1980) noted that the pollen of the Castaneoideae is the smallest and smoothest of the Fagaceae, consistent with anemophily. The odorous, erect inflorescences of *Castanea* and the stiff, cylindrical styles with punctate stigmas may be remnants from past entomophily. Evolution has not proceeded at the same rate in all floral characters, and unlike some other genera of the Fagaceae, *Castanea* does not exhibit all of the characteristics of the anemophilous syndrome.

TABLE 4. **Nut dimensions for taxa previously recognized in Castanea sect. Balanocastanon.**

Character	Taxon*				
	C. pumila var. *pumila*	var. *ozarkensis*	var. *ashei*	*C. alnifolia* var. *alnifolia*	var. *floridana*
Length (mm)					
Mean	15.6	14.0	12.7	12.7	12.7
SD	1.8	2.1	1.4	1.6	0.6
Range	11.5–20.3	9.6–19.0	7.8–16.9	9.6–18.6	10.7–14.5
Diameter (mm)					
Mean	11.5	10.9	10.3	10.3	9.9
SD	1.3	1.4	1.4	1.2	0.6
Range	7.7–14.7	8.1–13.9	7.7–14.9	7.7–18.6	8.8–11.2

* For each taxon $n = 250$

McKay (1942) and Morris (1914) found evidence of self-compatibility and apomixis, respectively, in *Castanea*. Results from my investigation indicate that these do occur in *C. pumila*, but infrequently. An accurate percentage of cupule formation could not be calculated due to predation, although open-pollinated flowers developed into fertile cupules 86 percent of the time.

CYTOLOGY AND ARTIFICIAL HYBRIDIZATION

Jaynes (1962) examined *Castanea* (including taxa from the three sections of the genus) for chromosome number and morphology. Numbers were obtained from sect. *Balanocastanon* for *C. alnifolia*, *C. ashei*, *C. ozarkensis*, and *C. pumila* sensu stricto. Mitotic figures were taken from root tips of germinating seeds, and meiotic figures from microsporocytes.

In all taxa of *Castanea* except some complex hybrids, the haploid number is $n = 12$, the diploid number $2n = 24$. Although satellites were sometimes present in cells, their significance is unknown. Because of the lack of centromere definition, Jaynes did not construct karyograms, although he noted significant size differences between some chromosomes in a nucleus. He concluded that species differentiation in *Castanea* does not include changes in chromosome number, and that chromosomes retain enough homology to insure normal pairing, as evidenced by the successes of inter- and intrasectional crosses.

Jaynes (1964) effected artificial hybridization within and among the three sections of *Castanea*. Within sect. *Balanocastanon* reciprocal crosses were made among taxa identified as *C. ashei, C. pumila, C. ozarkensis,* and *C. alnifolia*; they were also made between *C. dentata* (sect. *Castanea*) and these taxa with the addition of *C. floridana*. All crosses produced both nuts and seedlings. Jaynes concluded that few if any genetic barriers exist between species of *Castanea,* and that species evolution in the genus has not yet resulted in the development of incompatible genetic systems. However, intersectional crosses result in lower nut set than do intrasectional ones.

I attempted reciprocal crosses between *Castanea dentata* and *C. pumila* var. *pumila* because of the reports of natural hybridization between the two (*C.* ×*neglecta* Dode). The results of these crosses were inconclusive due to destruction by squirrels.

Foliar Flavonoids

I investigated the foliar flavonoids of *Castanea pumila* by standard methods of paper, thin-layer, and column chromatography. *Castanea dentata* and artificially produced *C.* ×*neglecta* were examined because of the reputed hybridization between *C. dentata* and *C. pumila*. Hybrid material was provided by R. A. Jaynes from the collection of the Connecticut Agricultural Experiment Station.

Eleven flavonoids have been detected and characterized at this time. Quercetin is the only flavonoid found in all taxa, and the only one present as an aglycone. The two varieties of *Castanea pumila* recognized in this revision have similar but distinctive flavonoid profiles (44% similarity) (Ellison *et al.,* 1962). In contrast, *C. dentata* has a 25 percent similarity to var. *pumila,* 22 percent to var. *ozarkensis*. When compared with *C. dentata, C. pumila* var. *pumila,* and *C. pumila* var. *ozarkensis, C.* ×*neglecta* had similarities of 25, 50, and 66 percent, respectively. I have no explanation for the greater similarity of *C.* ×*neglecta* to *C. pumila* var. *ozarkensis* than to *C. pumila* var. *pumila*.

TAXONOMIC TREATMENT

This taxonomic treatment is based on my studies in the field, herbarium, and laboratory. Measurements and observations were taken from field collections throughout the southeast and have been supplemented by the examination of approximately 6000 specimens from A, BH, BM, CITA, CLEMS, CU, DUKE, EKY, FARM, FLAS, FSU, FUGR, GA, GH, JSU, L, LAF, LINN, LSU, LYN, MEM, MO, NCSC, NCU, NLU, NY, ODU, P, PH, SMU, TENN, UARK, UNA, US, USCH, VDB, VPI, WIS, WKU, and WVA. Identifications of the exsiccatae and distribution data for both taxa and specimens are available from the author.

My species concept allows for a broad range of variation within a species and calls for distinct morphological discontinuities as well as strong, but not complete, reproductive isolation between species. The variety is considered to be recognizable by a suite of characters, to have a distinct geographic distribution, and to intergrade with other varieties. This treatment reflects these concepts.

TABLE 5. **Comparison of taxa of Castanea from North America.**

CHARACTER	TAXON			
	Castanea pumila var. **pumila**	**Castanea pumila** var. **ozarkensis**	**Castanea dentata**	**Castanea ×neglecta**
Habit	Stoloniferous or nonstoloniferous shrub, or tree (to 15 m)	Large multistemmed shrub or medium-sized tree (to 20 m)	Formerly a large tree, now reduced to sprouts	Formerly a small to medium tree, now reduced to sprouts
Twigs				
Size	Slender	Stout	Stout	Slender to stout
Color	Brown, tan, or yellow-green	Gray-brown	Brown	Brown to tan
Vestiture	Puberulent to tomentulose	Essentially glabrous	Essentially glabrous	Essentially glabrous to tomentulose
Bark				
Color	Gray or gray-brown	Dark-, light-, or reddish-brown	Dark brown	Gray- to dark-brown
Texture	Relatively smooth, slightly fissured and scaly, if at all	Moderately to deeply fissured, flat ridges breaking into loose platelike scales	Deeply fissured between broad, flat ridges	Moderately fissured

Leaf blades				
Shape	Variable; apex usually not acuminate or long-acuminate	Variable, but usually lance-elliptic or lanceolate; apex often acuminate or long-acuminate	Usually lance-elliptic or lanceolate; apex generally acuminate to long-acuminate	Variable, elliptic to lance-elliptic; apex acuminate to long-acuminate
Size (cm)	4.1–21.7 × 1.5–8.3	4.3–26.6 × 2–9.3	9–30.1 × 3.2–10.5	4.1–30.1 × 1.5–10.5
Trichomes	All types; bulbous ones few	All types; bulbous ones more numerous than on var. *pumila*	Stellate usually absent; immature leaves densely covered with bulbous ones	All types
Vestiture	Puberulent to tomentose	Puberulent to tomentose	Essentially glabrous	Essentially glabrous to tomentose
Cupule valves				
Number	2	2	4	2 to 4
Size (cm)	1.5–4.6 × 1.4–4.6	2.1–4.4 × 2.6–4.2	5–7.5 × 5–10	1.5–7.5 × 1.4–10
Prickle density	Remote to dense	Remote to dense	Dense	Dense
Fruits				
No. per cupule	1	1	3	1 or 2
Shape	Conical; circular in cross section	Conical; circular in cross section	Obovate, flattened on at least 1 side	Conical or obovate, depending on number
Size (mm)	7–21 × 7–19	9–19 × 8–14	18–25 × 18–25	7–25 × 7–25

Castanea pumila is widely distributed over eastern and southeastern North America throughout a great range of habitats. The leaves, twigs, and growth forms of the plants reflect this broad distribution in their variability, which is mostly ecophenic and random. These characters have been used in the past to designate taxa of sect. *Balanocastanon.* Examination of living populations and specimens from each of the previously recognized taxa in the section reveals no consistent patterns of variability or discontinuities for any of the characters studied for any of these taxa except *C. pumila* var. *ozarkensis.* These individuals are generally different in leaf, twig, bark, growth-form, and flavonoid characters from individuals of var. *pumila,* and they have a distinct geographic distribution. However, there are numerous instances of intergradation between vars. *ozarkensis* and *pumila.* Because of this intergradation, I treat these individuals at the varietal rather than the specific or subspecific rank. *Castanea dentata,* which differs from sect. *Balanocastanon* in numerous characters indicated in this study, is a species distinct from *C. pumila* and also represents a different section. *Castanea pumila* and *C. dentata* are sympatric over a large portion of their ranges but show only a few signs of possible introgression and relatively rare recognizable F_1(?) hybrids (*C.* ×*neglecta*), even though their flowering phenology is the same. A synopsis of diagnostic characters for the two varieties of *C. pumila, C. dentata,* and *C.* ×*neglecta* is presented in TABLE 5.

KEY TO NORTH AMERICAN SECTIONS, SPECIES, AND VARIETIES OF CASTANEA

1. Cupules 4-valved, enclosing 3 nuts; nuts obovate, flattened on at least 1 side, 18–25 mm long, 18–25 mm in diameter; pistillate dichasia of 3 flowers; leaves usually without stellate trichomes, densely covered with bulbous trichomes when young, puberulent with age. ..... sect. *Castanea* (*C. dentata*).
1. Cupules 2-valved, enclosing 1 nut; nut conical, circular in cross-section, 7–21 mm long, 7–19 mm in diameter; pistillate dichasia of 1 flower; leaves with stellate trichomes, with few bulbous trichomes when young, puberulent, pilose, tomentulose, or tomentose with age. ..... sect. *Balanocastanon* (*C. pumila*).
   2. Cupules usually 1 to 5 per androgynous spike; leaf shape variable, apex seldom long-acuminate; young twigs brown, tan, or yellow-green, puberulent, pilose, or tomentulose, remaining slender; bark of mature trunk light gray or gray-brown, shallowly fissured if at all. ..... *C. pumila* var. *pumila.*
   2. Cupules usually 5 to 8 per androgynous spike; leaves usually lance-elliptic or lanceolate, apex usually acuminate or long-acuminate; young twigs dark brown, puberulent, becoming stout; bark of mature trunk light-, dark-, or reddish-brown, moderately to deeply fissured. ..... *C. pumila* var. *ozarkensis.*

Castanea Miller sect. **Balanocastanon** Dode, Bull. Soc. Dendrol. France **8:** 154. 1908. TYPE SPECIES: *Fagus pumila* L. (= *Castanea pumila* (L.) Miller). Number of species (taxa): 1(2).

Castanea pumila (L.) Miller, Gard. Dict. ed. 8. 1768.

Shrub or tree to 20 m tall. Bark gray, brown, or gray-brown and smooth when young, remaining so or becoming light-, dark-, or reddish-brown and shallowly to deeply fissured with age. Twigs round or slightly fluted, brown,

tan, gray-brown or yellow-green, essentially glabrous to tomentulose, with conspicuous lenticels; pith homogeneous, white, 3- to 5-angled. Buds ovate, 2–4 mm long, essentially glabrous to tomentulose, with 2 to 4 visible scales; terminal buds absent. Leaves simple, alternate, 2-ranked; petiole 2–22 mm long, essentially glabrous to tomentulose; blade ovate, elliptic, lance-elliptic, or lanceolate, 4.1–26.6 by 1.5–9.3 cm, the apex emarginate, rounded, acute, acuminate, or long-acuminate, the margin shallowly to moderately serrate, with 1 serration per secondary vein or major branch of it, sinuses 1–5 mm deep, the venation pinnate, simple craspedodromous, the lower surface puberulent to tomentose, with stellate trichomes. Inflorescences pubescent staminate, androgynous, or rarely pistillate spikes, androgynous and pistillate distal to staminate, axillary on the present season's growth, erect, horizontal, or pendent. Flowers imperfect, incomplete; tepals (5 to) 6 (to 8), imbricate, ovate-triangular, 1–2 mm long; staminate odorous, in dichasial clusters of (1, 3, or) 7 florets in axil of bract, the stamens usually (6 to) 12 (to 18), in 1 series; pistillate usually 1 floret enclosed by bracts; styles (4 to) 6 (to 9), 1–3 mm long, basally pubescent, stigmas punctiform, ovary inferior. Pollen subprolate, 15–17 × 9–10 μm, tricolporate, colpi long, ectexine finely rugulose-pitted. Cupules 2-valved, splitting at maturity, openly to densely covered with branched, pubescent prickles 4–17 mm long, usually enclosing 1 nut; nut conical, 7–21 mm long, 7–19 mm in diameter, chestnut brown, lustrous, apically pubescent. $n = 12$.

PHENOLOGY. Flowering in late spring or early summer after leaves emerge; fruiting in mid-autumn.

Castanea pumila (L.) Miller var. **pumila**

Fagus pumila L. Sp. Pl. **2:** 998. 1753; *Fagus Castanea pumila* Muenchh. Hausvater **5:** 162. 1770. TYPE: U. S. A., without further locality, *Clayton s.n.* (lectotype, here designated, BM!).

Fagus pumila L. var. *praecox* Walter, Fl. Carolin. 233. 1788, *nomen nudum.*[3]

Fagus pumila L. var. *serotina* Walter, *ibid., nomen nudum.*

Fagus pumila L. f. *chinkapin* Bartram, Travels Carolina, 327. 1791, *nomen nudum.*

Castanea nana Muhlenb. Cat. Pl. Amer. Sept. 86. 1813; *Castanea pumila* var. *nana* (Muhlenb.) A. DC. Prodr. **16**(2): 115. 1864. TYPE: U. S. A., Georgia, *Muhlenberg 520* (lectotype, here designated, PH 4773!).

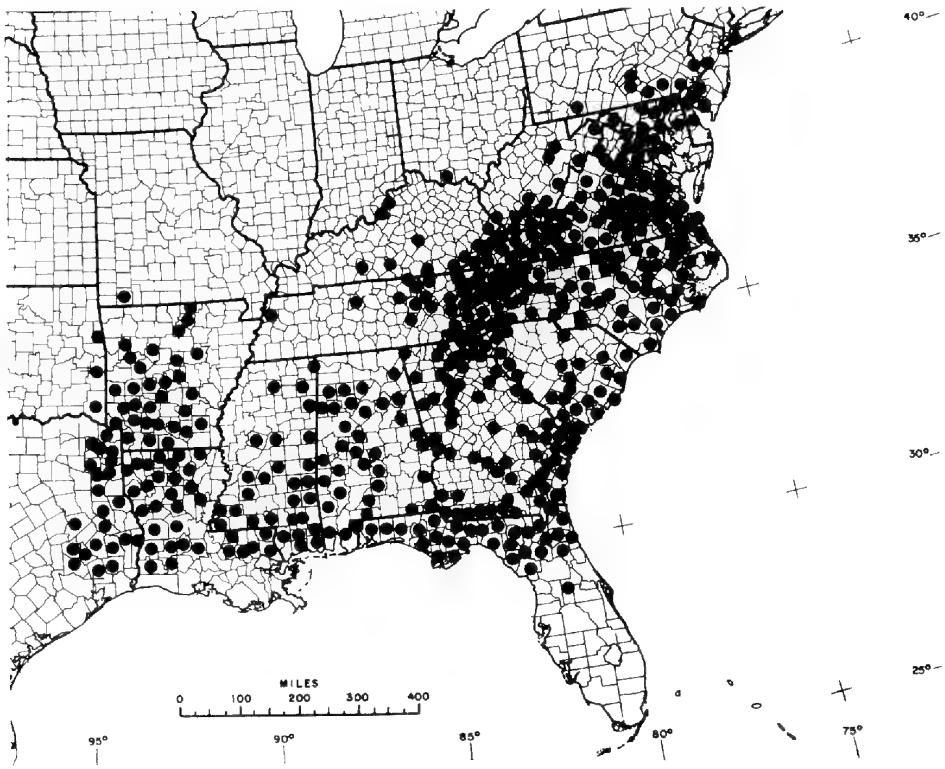
Castanea alnifolia Nutt. Gen. N. Amer. Pl. **2:** 217. 1818. TYPE: U. S. A., South Carolina, near Charleston, 1816, *Nuttall s.n.* (neotype, here designated: U. S. A., Florida, near Tallahassee, 1830, *T. Nuttall s.n.*, BM!).[4]

Castanea alnifolia var. *pubescens* Nutt. N. Amer. Sylv. **1:** 36. 1857, *nomen superfluum.*

Castanea alnifolia var. *floridana* Sarg. Bot. Gaz. (Crawfordsville) **67:** 242. 1919; *Castanea floridana* (Sarg.) Ashe, Bull. Torrey Bot. Club **49:** 266. 1922; *Castanea alnifolia* subsp. *floridana* (Sarg.) E. Murray, Kalmia **12:** 19. 1982. TYPE: U. S. A., Florida, Bay Co., in sandy soil with *Quercus myrtifolia* Willd. on shores of St. Andrew's Bay near Panama City, 28 May 1917, *Harbison 10* (holotype, A!).

[3]Species description was that of Linnaeus (1753), with no varietal description. A Walter specimen at BM is labeled *F. pumila*, but there is no varietal epithet.

[4]Pennell (1936) indicated that Nuttall's early types are located at PH, but no specimen was found. BM does have a specimen, with the label data as "Florida & S Carol." I believe that this specimen represents a collection from Florida in 1830, not from South Carolina in 1816 (Pennell, 1936).



MAP 1. Distribution of *Castanea pumila* var. *pumila,* based on herbarium specimens.

Castanea pumila var. *ashei* Sudw. Amer. Forests **28:** 301. 1922; *Castanea ashei* (Sudw.) Sudw. *in* Ashe, Bull. Torrey Bot. Club **49:** 267. 1922; *Castanea pumila* subsp. *ashei* (Sudw.) E. Murray, Kalmia **12:** 19. 1982. TYPE: U. S. A., North Carolina, Martin Co., Sept. 1909 (fruiting), *Ashe s.n.* (lectotype, here designated, US 1115586!).

Castanea pumila var. *margaretta* Ashe, Bull. Torrey Bot. Club **49:** 265. 1922; *Castanea margaretta* (Ashe) Ashe, *ibid.* **50:** 359. 1923; *Castanea floridana* var. *margaretta* (Ashe) Ashe, Quart. Charleston Mus. **1:** 30. 1925. TYPE: U. S. A., Louisiana, Sabine Parish, Oct. 1921, *Ashe s.n.* (lectotype, here designated, MO 906253!).

Castanea margaretta var. *angustifolia* Ashe, J. Elisha Mitchell Sci. Soc. **40:** 46. 1924; *Castanea floridana* var. *angustifolia* (Ashe) Ashe, Quart. Charleston Mus. **1:** 31. 1925. TYPE: U. S. A., Florida, Leon Co., Sept. 1928, *Ashe s.n.* (neotype, here designated, PH!).

Castanea margaretta var. *arcuata* Ashe, J. Elisha Mitchell Sci. Soc. **40:** 46. 1924; *Castanea floridana* var. *arcuata* (Ashe) Ashe, Quart. Charleston Mus. **1:** 30. 1925. TYPE: U. S. A., Texas, Angelina Co., 5 mi S of Lufkin, 26 Sept. 1920, *Ashe s.n.* (neotype, here designated, NCU 64316!).

Castanea paucispina Ashe, J. Elisha Mitchell Sci. Soc. **41:** 268. 1926. TYPE: U. S. A., Texas, Newton Co., 19 Oct. 1921, *Ashe s.n.* (lectotype, here designated, NCU 24767!).

Stoloniferous or nonstoloniferous shrub or tree 1–15 m tall. Bark light gray or gray-brown, smooth, or scaly and shallowly fissured. Twigs slender, brown, tan, or yellow-green, puberulent to tomentulose. Leaves 4.1–21.7 cm long, apex variable but seldom acuminate or long-acuminate. Cupules usually 1 to 5 at base of androgynous spike, densely to remotely covered with pubescent, branched prickles.

DISTRIBUTION. Southeastern Pennsylvania south to north-central Florida, west to eastern Texas, eastern Oklahoma, southwestern Missouri, and west-central Kentucky (see MAP 1); in open pine, deciduous, or mixed woodlands, in disturbed sites along roads, and along railroads and power lines.

COMMON NAMES. Chinquapin (and several orthographic variations—chincopin, chinkapin, chinkopin, chincapin, chinquepin), bush chestnut.

Variety *pumila* is adapted to early- or mid-successional stages, as evidenced by its ability to recover from fire and other disturbances through rapid suckering and sprouting from the remaining stem at or below ground level, and by its elimination from less disturbed, more mature sites. It suffers from the chestnut blight, but not as severely as *Castanea dentata* and *C. pumila* var. *ozarkensis*; rapid sprouting quickly replaces blight-stricken stems.

Castanea pumila (L.) Miller var. **ozarkensis** (Ashe) Tucker, Proc. Arkansas Acad. Sci. **29:** 68. 1975; *Castanea ozarkensis* Ashe, Bull. Torrey Bot. Club **50:** 360. 1923. TYPE: U. S. A., Arkansas, Searcy Co., 17 Sept. 1923, *Ashe s.n.* (lectotype, designated by Tucker (1975), NCU 64311!).

Castanea arkansana Ashe, *ibid.* 361; *Castanea ozarkensis* var. *arkansana* (Ashe) Ashe, J. Elisha Mitchell Sci. Soc. **40:** 45. 1924. TYPE: U. S. A., Arkansas, Madison Co., near War Eagle Creek, 23 Sept. 1923, *Ashe s.n.* (lectotype, here designated, NCU 64300!).

Castanea alabamensis Ashe, Quart. Charleston Mus. **1:** 30. 1925. TYPE: U. S. A., Alabama, Lawrence Co., hill on east side of branch, south side of Flannigan Creek, 5 Oct. 1921 (fruiting), *Ashe 1180* (lectotype, here designated, NCU 22530!).

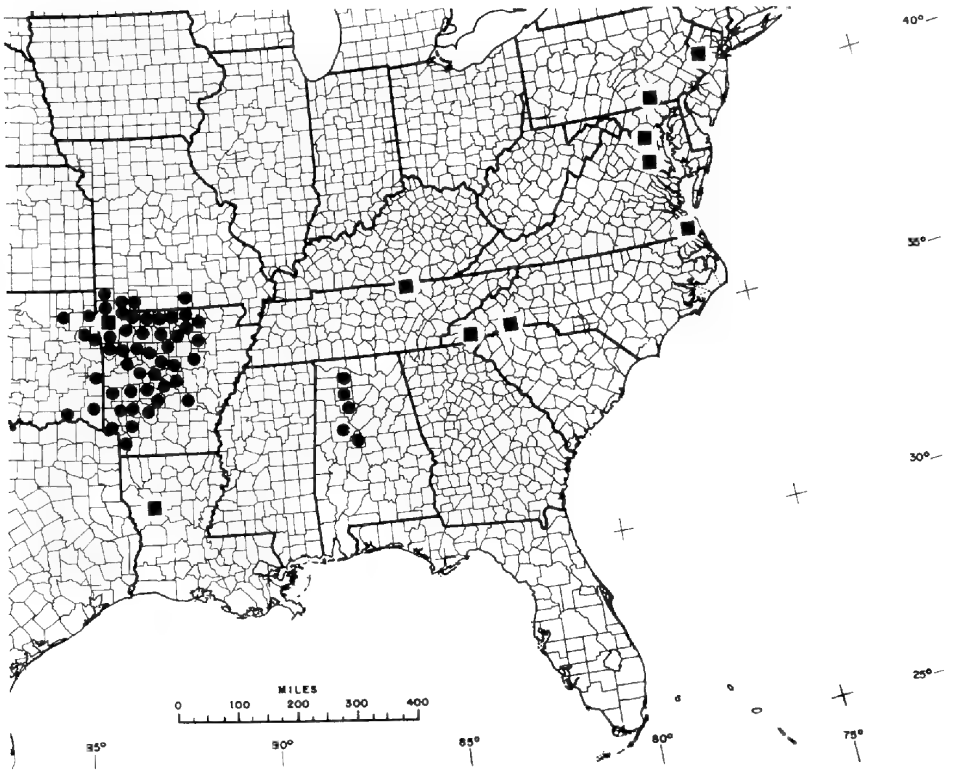
Large shrub or tree formerly to 20 m tall, now mostly reduced to smaller stump sprouts due to chestnut blight. Bark light-, dark-, or reddish-brown at maturity and becoming scaly and moderately to deeply fissured. Twigs slender and dark brown when young, becoming stout (often over 3 mm), gray-brown, essentially glabrous. Leaves 4.3–26.6 cm long, apex variable but usually acuminate or long-acuminate. Bur densely to moderately covered with pubescent, branched prickles. Cupules usually 5 to 7 at base of androgynous spike, with prickles tending to arch over adjacent cupules.

DISTRIBUTION. Ozark Highlands of eastern Oklahoma, southwestern Missouri, Arkansas, and north-central Alabama (Bibb, Lawrence, Tuscaloosa, Walker, and Winston counties) (see MAP 2); in dry deciduous or mixed woodlands, on uplands and cliff margins and ridges, and at base of talus slopes (on sandstone in Alabama, but limestone, sandstone, chert, or a combination of these in Ozarks). Sympatric with *Castanea pumila* var. *pumila* over virtually all of its range and with *C. dentata* in Alabama.

COMMON NAMES. Ozark chinquapin, Ozark chestnut.

Herbarium, laboratory, and field studies indicate that in areas of sympatry of the two varieties of *Castanea pumila,* numerous individuals are intermediate and identification to variety may not always be possible.

Variety *ozarkensis* is severely affected by the chestnut blight and has apparently been extirpated from Alabama. The last sighting was made by G. E.



MAP 2. Distribution of *Castanea pumila* var. *ozarkensis* (dots) and *C.* ×*neglecta* (squares), based on herbarium specimens.

Tucker in the mid 1970's (pers. comm.). My own searches in 1983–1984 in the Bankhead National Forest failed to find any evidence of it.

The disjunct distribution of var. *ozarkensis* between the extreme southwestern Appalachians (southwestern ends of the Ridge and Valley and Cumberland Plateau provinces) and the Ozarks is also matched by other taxa such as *Neviusia alabamensis* Gray (Moore, 1956), which lends support to an Appalachian-Ozarkian floristic relationship as mentioned by Braun (1950). Moore considered *Neviusia* to be a relict species and correlated its distribution with the past position of the Mississippi Embayment and the Gulf Coastal Plain. Fenneman (1938) suggested that the Ozarkian and Appalachian systems may be connected under the sediments of the Embayment. One explanation for the disjunction is the climatic and floristic changes associated with the Pleistocene glaciations. The Ozark and extreme southwestern Appalachian areas may be refugia for var. *ozarkensis* or may represent its limited reestablishment from the southern Mississippi Valley and the Gulf Coast after glacial retreat (Davis, 1983; Delcourt & Delcourt, 1984). Davis has estimated that *Castanea dentata* had a southwest to northeast path of migration at the rate of 100 m per year since the latest glacial maximum 18,000 years B.P. and that it reached New England 2000 years B.P.

The nomenclature for this variety is somewhat confused. Since there was an earlier varietal name already available for this taxon, *Castanea ozarkensis* var.

arkansana (Ashe) Ashe (1924), Tucker (1975) should have transferred it rather than the epithet from *C. ozarkensis* Ashe. This mistake would have required a change from Tucker's var. *ozarkensis,* now established in the literature, to var. *arkansana,* were it not for the recent change in the Code (Article 57.3; Voss *et al.,* 1983) regarding the priority of autonyms (see also Brummitt, 1985, and Reveal, 1983). Under this new ruling, the autonym *C. ozarkensis* var. *ozarkensis* has priority over *C. ozarkensis* var. *arkansana* and Tucker's combination now stands as correct.

Castanea alabamensis Ashe, treated here as a synonym of var. *ozarkensis,* has been considered by some authors (see TABLE 1) to be a hybrid, of various parentages (*C. dentata* × *C. floridana margaretta*(?), *fide* Camus (1929); *C. dentata* × *C. alnifolia* var. *floridana, fide* Elias (1971); *C. dentata* × *C. alnifolia, fide* Little (1979)). Ashe (1925) originally thought that this taxon was the same as *C. arkansana* Ashe (1923) but did not include *C. alabamensis* in the description of *C. arkansana.* Specimens of *C. alabamensis* examined are clearly the same as *C. pumila* var. *ozarkensis* from the Ozarks, indicating that var. *ozarkensis* was not restricted to the Ozark region (as Little, 1977, had believed).

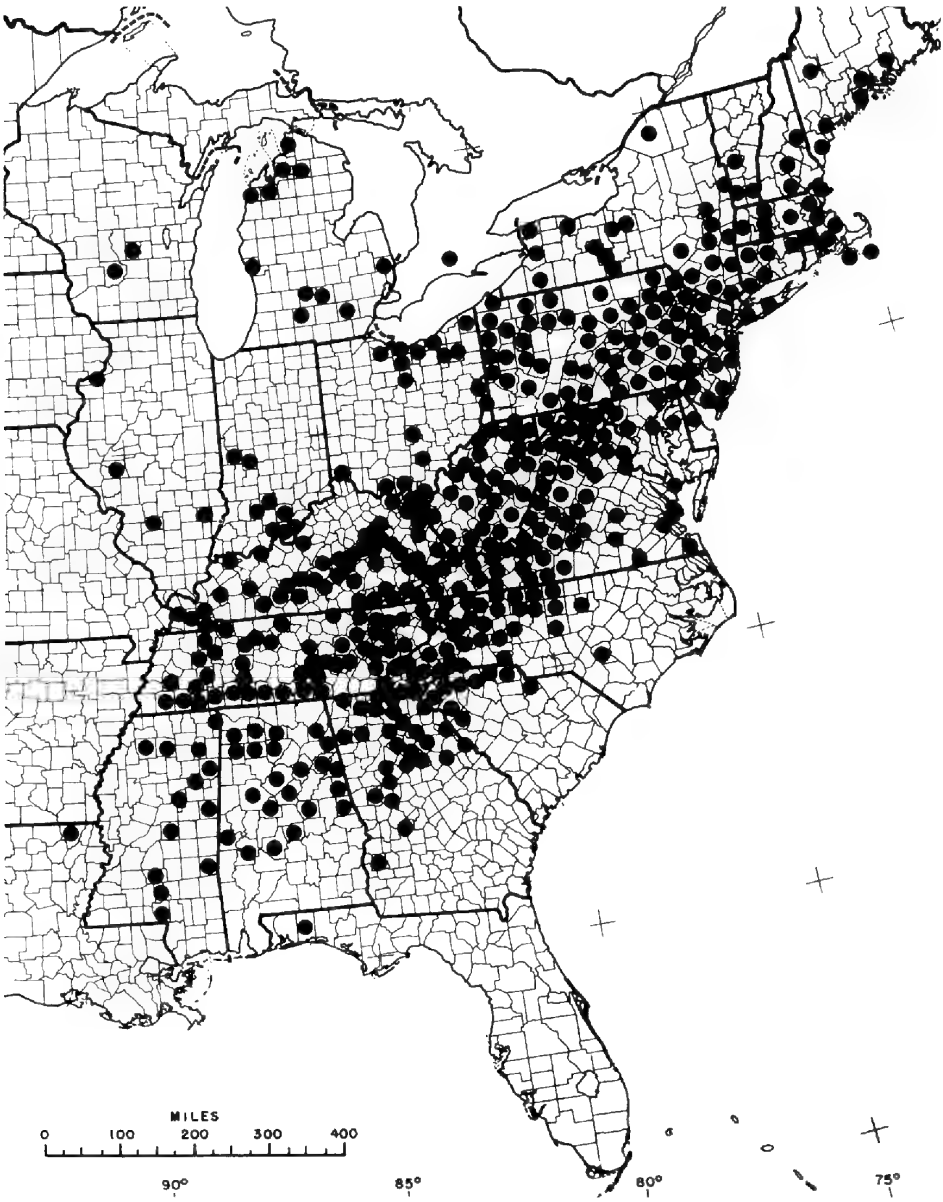
Castanea ×**neglecta** Dode, Bull. Soc. Dendrol. France **8:** 155. 1908 (*C. dentata* × *C. pumila* s.l.). TYPE:[5] U. S. A., North Carolina, Polk Co., Cove and Little Cove Creek, 14 May 1974, *Hardin 13540* (neotype, here designated, NCSC 78380!).

Castanea margaretta f. *dormonae* Ashe, Bull. Torrey Bot. Club **54:** 582. 1927. TYPE: U. S. A., Louisiana, Natchitoches Parish, near Chestnut, 26 Sept. 1926, *Miss C. Dorman 1* (lectotype, here designated, NCU 22526!).

I have seen no living plants of *Castanea* ×*neglecta* and was only able to examine herbarium specimens and specimens from artificial hybridizations made by R. A. Jaynes. The leaves of the hybrid resemble those of *C. dentata* in size and shape but have the vestiture and stellate trichomes of *C. pumila* (Hardin & Johnson, 1985). The twigs, like those of *C. dentata,* are variable in color, ranging from dark brown to tan, and are usually essentially glabrous. The bur is similar in size to or larger than that of *C. pumila* and is composed of two to four valves that are densely covered with pubescent prickles intermediate in form between those of the parents. There is usually one nut per cupule, but two may be found in cupules of three or four valves.

Castanea ×*neglecta* has a scattered distribution (see MAP 2) and occurs in areas of sympatry of the parents (see MAPS 1–3). Its presence in Benton County, Arkansas (*D. M. Moore, 55-477* and *55-476,* both at UARK), is due to hybridization of the native *C. pumila* var. *ozarkensis* with individuals of *C. dentata* in an adjacent plantation, and the specimens from Natchitoches Parish, Louisiana (*Miss C. Dorman 1* and *2,* both at NCU) are probably the result of similar

[5]Dode (1908) failed to list specimens with his description for *C.* ×*neglecta,* although Ashe (1922) cited a list furnished to him by Dode. I have seen two of these specimens (*Small & Heller 152* and *Small & Heller s.n.,* 22 June 1891), and they are not *C.* ×*neglecta.* An inquiry to P failed to locate any of the others.



MAP 3. Distribution of *Castanea dentata,* based on herbarium specimens.

circumstances. Ashe (1927) indicated that if the Louisiana specimens had been within the range of *C. dentata,* he would have considered them to be hybrids. I have seen specimens of cultivated *C. dentata* from Louisiana (*C. A. Brown 5324,* GH, LSU, SMU); another (*R. D. Thomas 35362,* NLU, VDB) may represent native *C. dentata.* A list of plants from the Sicily Island region of Louisiana by C. A. Peck in 1836 (R. D. Thomas, pers. comm.) noted *C. dentata* from Catahoula Parish. The number of herbarium specimens representing the hybrid is small; most so labeled are shade forms of *C. pumila.*

EVOLUTIONARY RELATIONSHIPS

The fossil record offers no indications as to the time or place of origin of sect. *Balanocastanon,* thereby leaving the evolutionary history open to question. The present widespread, disjunct distribution of the genus in the Northern Hemisphere indicates an earlier, broader distribution. Section *Balanocastanon* was obviously derived from the chestnuts by reduction of the number of cupule valves and flowers, but the center of origin is unknown and today the section is restricted to eastern North America. Isozyme similarities between *Castanea dentata* and *C. pumila* (as defined in this paper) may indicate a common ancestor (Santamour *et al.,* 1986). The chinquapins have retained the dense, stellate pubescence found on the leaves of most members of sect. *Castanea,* indicating that the general lack of these in *C. dentata* is probably a derived condition.

The few, subtle characters that distinguish the two varieties of *Castanea pumila,* the fact that evolutionary polarity cannot be determined for some of these characters, and the presence of only two taxa in the section eliminate the possibility of a cladistic analysis. If one considers all of the characters of the two varieties, though, evolutionary relationships can be postulated.

I believe that var. *ozarkensis* is more like the ancestral type and thus less highly evolved than var. *pumila.* The reasons for this belief are the lack of stoloniferous growth in var. *ozarkensis* and its arborescent habit (adaptations to older stages of succession and to areas of higher soil fertility), as well as its larger leaves. The smaller size of var. *pumila* and its capability for stoloniferous growth are considered to be adaptations for survival in early successional stages and areas of low soil fertility. Variety *pumila* is eliminated or severely reduced when the canopy closes and the understory layer is shaded, while var. *ozarkensis* is capable of maintaining itself and reaching the canopy. The smaller leaves of var. *pumila* may be an adaptation to low soil fertility and reduced water availability.

The presence of *Castanea pumila* var. *ozarkensis* in the Ozarks and in northern Alabama may indicate that it once had a much greater range than it does today. The habitats in these two areas are very similar and presumably resemble those occupied by var. *ozarkensis* in the past. Variety *pumila,* on the other hand, grows in differing habitats but is common only in frequently disturbed, open sites. I believe either that var. *pumila* evolved from some element in var. *ozarkensis,* or that the two had a common ancestor and var. *pumila* evolved in response to changing environmental conditions in the southeastern United States some time during or after the Pleistocene glaciations. New areas opened for colonization, and these individuals were capable of rapid and successful dispersal and establishment. Variety *pumila* has been more successful than var. *ozarkensis,* as is evidenced by its greater relative abundance and its broader geographic range.

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THE GENUS HEDYOSMUM (CHLORANTHACEAE) IN THE WEST INDIES[1]

CAROL A. TODZIA[2] AND CARROLL E. WOOD, JR.[3]

This paper presents a revision of the West Indian species of *Hedyosmum* (Chloranthaceae). Five species are recognized: *H. arborescens, H. domingense, H. grisebachii, H. nutans,* and *H. subintegrum*; these range from Cuba, Hispaniola, and Jamaica to Puerto Rico and the Lesser Antilles. A new combination, *H. domingense* var. *cubense* (Urban) Todzia & C. Wood, is made to accommodate the distinctive populations of this species in Cuba. It differs from var. *domingense* (from Hispaniola) in having the upper and lower internodes of flowering stems of unequal (vs. equal) length, longer staminate inflorescences, and longer anthers.

Hedyosmum Sw. consists of about 40 species of Neotropical trees and shrubs, in addition to one herbaceous species, *H. orientale* Merr. & Chun, of southeastern Asia. Members of the genus are readily distinguished by their opposite leaves with connate, sheathing petiole bases and stipular appendages, their staminate catkins of ebracteate stamens, and their racemose pistillate inflorescences of epigynous flowers with a small, three-lobed perianth and subtending floral bracts. The fruit is a drupe with a hard endocarp surrounded by soft, fleshy mesocarp.

Hedyosmum is a conspicuous component of wet montane forests in the West Indies, where there are five species that range variously from Cuba, Hispaniola, and Jamaica, to Puerto Rico and the Lesser Antilles. Cuba has the most species with four, followed by Jamaica and Hispaniola with two; Puerto Rico and the Lesser Antilles have only *H. arborescens* Sw.

The five West Indian species fall into two taxonomic groups. One species, *Hedyosmum arborescens,* belongs to subg. *Tafalla* Solms-Laub., which is characterized by racemose pistillate inflorescences with the flowers usually clustered into cymules and with accrescent, fleshy, usually connate floral bracts, these white or colored at maturity. The four remaining species, *H. nutans* Sw., *H. grisebachii* Solms-Laub., *H. domingense* Urban, and *H. subintegrum* Urban, are members of subg. *Hedyosmum,* which has racemose or spicate pistillate inflorescences with flowers borne singly (i.e., unaggregated) at each node of the axis and with chartaceous floral bracts. In this group it is the pericarp, not the floral bracts, that becomes fleshy and brightly colored (yellow, orange, red,

[1]A full taxonomic treatment of the genus, based on the first author's Ph.D. dissertation, will be published in the *Flora Neotropica* series.

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purple, or black) at maturity. The only other members of this subgenus are the monoecious *H. brenesii* Standley, of Honduras, Nicaragua, Costa Rica, and Panama, and the dioecious *H. orientale,* of southern China, Vietnam, Sumatra, Borneo, and central Celebes.

Hedyosmum was first proposed by Olaf Swartz (1788), who described *H. nutans* and *H. arborescens* from specimens he collected in the West Indies between 1784 and 1786. After a hiatus of over sixty years, Cordemoy (1863), Grisebach (1862, 1864), and Solms (1869) all published on the West Indian taxa, proposing several as new. Three additional species were circumscribed by Urban (1927) from Ekman's Cuban material. Most recently, Marie-Victorin (1948) added *H. leonis* from Cuba. In all, nine species of *Hedyosmum* have been attributed to the West Indies, but the genus has not been comprehensively studied previously in the region as a whole. This paper clarifies the taxonomy of the genus in the area, providing a key for the five West Indian species, along with descriptions and typifications.

Hedyosmum Sw. Prodr. 847. 1788. LECTOTYPE SPECIES: *Hedyosmum nutans* Sw.; see N. L. Britton & P. Wilson, Sci. Survey Porto Rico **5:** 230. 1924.

Tafalla Ruiz Lopez & Pavon, Fl. Peruv. Prodr. **1:** 136. 1794. LECTOTYPE SPECIES (here designated): *Tafalla racemosa* Ruiz Lopez & Pavon.
Tafallaea Kuntze, Revis. Gen. Pl. **2:** 565. 1891.

Monoecious or dioecious aromatic shrubs or trees, rarely herbs, often with prop roots; wood white, usually soft; stems with persistent leaf sheaths or with encircling leaf-sheath scars, nodes swollen. Leaves opposite, simple; leaf sheath with or without stipular appendages on distal margin; petiole grooved above, with base expanded and connate to form sheath around stem; blade fleshy to coriaceous when fresh, margin dentate with hydathode at apex of each tooth, venation pinnate. In dioecious plants, staminate inflorescences axillary or terminal, composed of a solitary spike or of several spikes on racemose or paniculate axes, subtended by pair of leaflike bracts; in monoecious plants, solitary spikes originating on pistillate inflorescence axis or within cymule among pistillate flowers. Staminate spikes with 60 to 300 flowers, each consisting of a solitary, sessile, ebracteate stamen; anthers quadrangular to oblong, 4-locular, longitudinally dehiscent, the connective extended, with apex flat, acute, or acuminate. Pistillate inflorescences axillary or terminal, simple, thyrselike, racemose, or paniculate, often fused above nodes with stem, subtended by leafy bracts. Pistillate flowers solitary on axis or more often clustered into cymules; subtending floral bract cucullate, fully, partially, or not enclosing flower, chartaceous or fleshy; perianth adnate to ovary, with 3 free or partially fused lobes at apex of ovary and often with hole or pore on each ovary face; ovary ellipsoid or trigonous, the stigma sessile or subsessile, papillose. Fruit drupelike with fleshy wall formed by accrescent perianth, or multiple with floral bracts becoming fleshy, colored, and connate, the endocarps surrounded by perianth tissue, embedded in bract matrix; seeds ellipsoid or trigonous, small, brown or black, smooth or minutely papillate.

KEY TO THE SPECIES OF HEDYOSMUM IN THE WEST INDIES

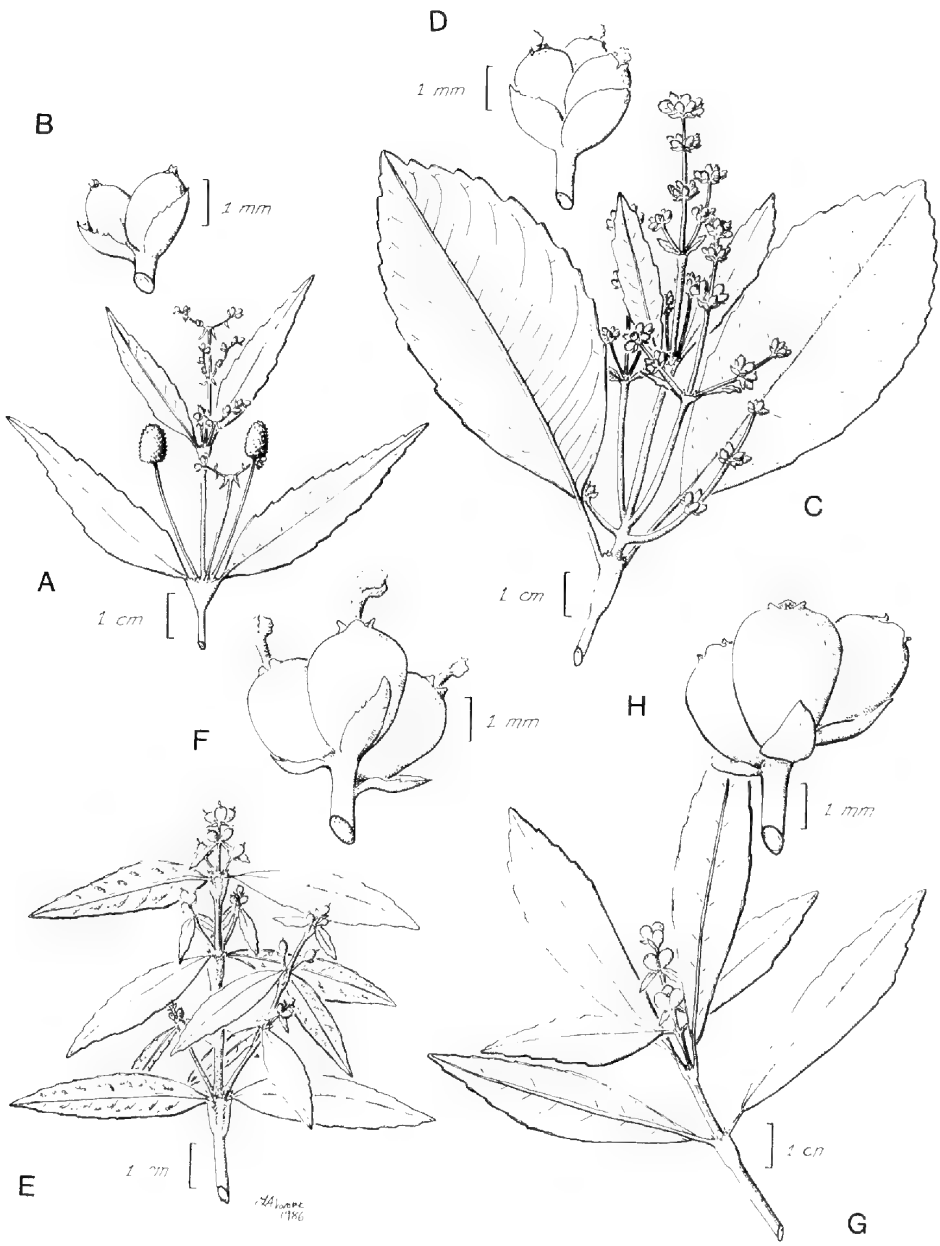
1. Plants monoecious; leaves with tertiary venation slightly impressed, giving upper surface mottled appearance when dry; staminate inflorescences with peduncles 1.4–4 cm long and 18 to 60 stamens; pistillate inflorescences with 13 to 23 flowers, the rachis notably zigzag. ..... 1. *H. nutans.*
1. Plants dioecious; leaves with tertiary venation flush with upper surface, drying to uniform color; staminate inflorescences sessile or on short peduncle 0.1–1 cm long, with ca. 100 to 300 stamens; pistillate inflorescences with 3 to 12 flowers or with 6 to 24 cymules each having 2 to 4 flowers, the rachis more or less straight.
   2. Leaves linear-oblong to lanceolate or narrowly elliptic, without prominent submarginal vein; pistillate flowers solitary at nodes of inflorescence; fruits yellow to red.
      3. Leaves thin, chartaceous to subcoriaceous, the lateral veins raised beneath, always visible, the sheaths 0.6–1.2 cm long, with fimbriate stipular processes; staminate spikes with 100 to 200 stamens.
         4. Leaves 7.1–13.8 cm long, with 10 to 18 pairs of large lateral veins; staminate spikes with ca. 200 stamens; pistillate inflorescences 1.5–3.5 cm long. ..... 2. *H. grisebachii.*
         4. Leaves 3.8–7.8 cm long, with 7 to 9 pairs of large lateral veins; staminate spikes with 100 to 160 stamens; pistillate inflorescences 0.7–1.4 cm long. ..... 3. *H. domingense.*
      3. Leaves thick, coriaceous to subcrassulate, the lateral veins not raised beneath, usually not visible, the sheaths 0.5–0.6 cm long, with entire stipular processes; staminate spikes with ca. 300 stamens. ..... 4. *H. subintegrum.*
   2. Leaves elliptic, with prominent submarginal vein; pistillate flowers in clusters of 1 to 5; fruits green but hidden by bracts, these fleshy and white at maturity. ..... 5. *H. arborescens.*

1. **Hedyosmum nutans** Sw. Prodr. 84. 1788. TYPE: Jamaica, *Swartz s.n.* (lectotype [here designated], s!).[4] FIGURE, A, B.

Tafallaea nutans (Sw.) Kuntze, Revis. Gen. Pl. 2: 566. 1891.

Monoecious shrubs 1–5 m tall; young stems quadrate, older ones terete, with leaf bases disintegrating and leaving circular scars; upper and lower internodes of equal length, 1–4(–6) cm long. Leaves with free portion of petiole 0.1–0.4 cm long, the sheath 4–10 by 4–9 mm, inflated, flared at apex, deciduous, with 2 very small, linear or fimbriate stipular appendages at distal margin; blade lanceolate, 5.3–13.5 by 1–2.4 cm, with acuminate tip 0.5–1 cm long, rounded to cuneate to obliquely cuneate at base, serrate with teeth 2.5–4 mm apart, green to yellowish green, smooth, glabrous, succulent, drying grayish brown above, reddish brown beneath, chartaceous, the midvein impressed above, raised beneath, the lateral veins 6 to 9 on each side, 3.5–5 mm apart, obscure, the tertiary veins drying slightly impressed above, giving upper surface of dry blade a mottled appearance. Staminate inflorescences axillary, simple, originating below pistillate inflorescences, 3.2–4.8 cm long; peduncle pendent, 1.4–4 cm long, slender, emerging from inside leaf sheath; mature spikes 1–3.2 cm long, 0.3–0.6 cm in diameter; stamens 18 to 60, congested along axis, the anther

[4]There are also specimens of *Hedyosmum nutans* annotated by Swartz at C and M, but since they are without locality and collection number, no isolectotypes are designated.



Four West Indian species of *Hedyosmum*. A, B, *H. nutans* (from *Jiménez 1258*): A, branch, showing pistillate inflorescences with solitary flowers borne singly at nodes and staminate spikes; B, 2 pistillate flowers. C, D, *H. arborescens* (*Shafer 2223*): C, branch of pistillate plant; D, cymule with 3 flowers. E, F, *H. domingense* var. *cubense* (*Morton 9338*): E, branch of pistillate plant; F, 3 pistillate flowers. G, H, *H. subintegrum* (*Shafer 4451*): G, branch of pistillate plant; H, 3 pistillate flowers.

sessile, 1.7–2 mm long, ca. 1 mm in diameter, green to yellow, with connective, projecting upward, 0.7–1 mm long, acute. Pistillate inflorescences axillary or terminal, solitary, spicate, 2.3–3.8 cm long, bifurcate or trifurcate with 2 opposite basal lateral branches or 3 or 4 pairs of opposite lateral branches; sterile inflorescence bracts basal, 1–1.5 cm by 1–2 mm, entire or sparsely denticulate; axis notably zigzag, with 13 to 23 sessile flowers borne singly, alternately, or subopppositely at nodes (1–1.5 mm apart); subtending floral bracts 1.5–3 by ca. 1 mm, ciliolate, not enclosing flower, persistent on axis. Pistillate flowers ellipsoid or slightly trigonous, 2–3 mm long, ca. 1.5 mm in diameter, pale green; perianth lobes ca. 0.3 mm long, rounded at tip; stigma linear in outline, 1–2 mm long, papillose. Fruits ellipsoid drupes, 2–3 mm long, ca. 2.5 mm in diameter, orange to red.

DISTRIBUTION AND PHENOLOGY. Eastern Cuba, Hispaniola, and Jamaica; in primary and secondary rainforest, open woodland scrub, pine forest, wet woods, and shady thickets, and along dry roadsides, on dry, gravelly, moist, and swampy soils and limestone, sandstone, and lateritic substrates; 400–1800 m alt. Flowering and fruiting throughout the year.

REPRESENTATIVE SPECIMENS EXAMINED. **Cuba.** ORIENTE: Sierra de Mícara, Mayarí, *Alain & López Figuerras 4645* (GH, US); Sierra de Nipe, Woodfred, *Ekman 9068* (NY, S), *Shafer 3008* (F, NY, US); Sierra de Nipe, San José, *Howard 6200* (GH, NY, S, US), *Léon et al. 19853* (A); Sierra de Nipe, Cayeto de Monte, S of La Mensura, *Léon et al. 19787* (GH); Sierra de Nipe, Loma Mensura, *Léon & Marie-Victorin 19964a* (A, GH), *Marie-Victorin & Clément 22072* (GH); crest of Sierra de Nipe, S of lumber camp, *Morton & Acuña 3160* (GH, K, MO, NY, US); the Pinales, SE of Paso Estancia, *Shafer 1694* (A, F, GH, NY); La Perla to Santa Ana, *Shafer 8617* (A, GH, NY, US); without locality, *Wright 491* (BM, G, GH, MO, S). **Jamaica.** CLARENDON: Bird Cave Rock–Glenwood Springs, Balcarres–Sunbury road, *Morley & Whitefoord 937* (A, BM, MO, S); Glenwood Springs distr., along road between Balcarres and Sunbury, *Proctor 33490* (F). MANCHESTER: along road between Pike and Coleyville, *Proctor 24448* (LL). PORTLAND: Greenhill, *Adams 6645* (BM, MO); trail NW of Silver Hill Gap, *Hespenheide 792* (DUKE, LL, MO, MSU, NY); Blue Mtns., Abraham's ridge, *Morley & Whitefoord 617* (A, BM, MO, S, US); SW of Port Antonio, floodplain of Río Grande near Millbank, *West & Arnold 181* (GH). ST. ANDREW: below and W of Guava Ridge, *Crosby et al. 426* (DUKE, F, GH, LL, MSU, NY). ST. THOMAS: above Bowden Pen, along foot path to Bath via Cuna Cuna Pass, *Crosby & Anderson 1055* (DUKE, F, GH, LL, MSU, NY); vic. of Corn Puss Gap, ca. 3.5 air mi N of Bath, *Gastony 114* (GH); John Crow Mtns., Corn Puss Gap, *Yuncker 18110* (BM, F, S); mountain trail between House Hill and Cuna Cuna Gap, *Maxon 8957* (GH, S, US); Big Level distr., SE end of John Crow Mtns., *Proctor 11809* (GH); John Crow Mtns., Johnston Mtn., *Vuilleumier 78* (A, MO); Red Hills, vic. of Coopers Hill, *Proctor 18261* (A, NY, US). **Haiti:** Massif de la Selle, ridge between Morne Tranchant and Morne Boeuf, *Ekman 1227* (A, GH, S); vic. of St. Louis du Nord, *Leonard & Leonard 14540* (A, GH, NY, US); vic. of Furcy, *Leonard 4494* (GH, NY, US). **Dominican Republic.** LA VEGA: near Jarabacoa, *Fuertes 1672* (A); near Jima, W of Bonao, *Terbough 85* (A); km 12 of hwy. Duarte (Santo Domingo–Santiago) on road to El Río and Constanza, *Zanoni et al. 23069* (JBSD). MONTE CRISTI: Monción, Lagunas de Cenobi, *Ekman 12767* (G, GH, K, S, US); Distr. of Sabaneta, Leonor, *Valeur 508* (F, G, K, MO, NY, S). PACIFICADOR: vic. of San Francisco de Macorís, *Abbott 2183* (G, GH). PUERTO PLATA: Sierra de Yaroa, *Liogier 15687* (GH). SANTIAGO: mouth of Río Leonor, in Río Toma, *Dod s.n.* (JBSD); sides of Pico de Igua, *Jiménez 1258* (US); Los Ramones, Palo Alto, *Marcano 5154* (GH); Distr. of San José de las Matas, Loma Bajita, *Valeur 871* (F, K, LL, MO, NY, US). SANTO DOMINGO: Rancho Arriba, *Liogier & Liogier 19382* (JBSD, NY).

Hedyosmum nutans is distinguished by its pistillate flowers that are borne singly along a zigzag axis; long, narrow leaves; shrubby habit; long-pedunculate, pendent staminate spikes; anthers with pronounced elongate connectives; and red or orange fruits. It is most closely related to *H. brenesii* of Central America, with which it shares a monoecious condition; long, narrow leaves; and numerous pistillate flowers per spike. The two differ in that *H. nutans* has staminate inflorescences on peduncles 1.4–4 cm long arising from the leaf axils at the base of the pistillate inflorescences and has orange to red fruits, while *H. brenesii* has staminate inflorescences on peduncles only 0.3–0.9 cm long arising from the pistillate axis and has purple to black fruits.

2. **Hedyosmum grisebachii** Solms-Laub. *in* DC. Prodr. **16**(1): 479. 1869. TYPE: Cuba, "in Cuba Orientali, prope villam Monte Verde dictam," 1856–57, *Wright 490* (pistillate) (lectotype [here designated], BM!; isolectotypes, G!, GH!, photos from G neg. 33999 at F! and MO).[5,6]

Tafallaea grisebachii (Solms-Laub.) Kuntze, Revis. Gen. Pl. **2**: 566. 1891.
Hedyosmum leonis Marie-Victorin, Contr. Inst. Bot. Univ. Montréal **63**: 8. 1948. TYPE: Cuba, Oriente, "petit bois au sud de la Loma Mensura, Sierra de Nipe," 7 April 1941, *Léon et al. 19964* (staminate) (holotype, MT!; isotypes, HAC(LS), MT!).

Glabrous, dioecious shrubs 1–2 m tall; young stems quadrate, older ones terete, with old leaf bases disintegrating and leaving circular scars; upper and lower internodes of more or less equal length, 2.2–5.4 cm long. Leaves with free portion of petiole 0.2–0.7 cm long, the sheath 0.9–1.2 by 0.7–1 cm, slightly inflated, disintegrating with age, with 2 fimbriate stipular processes ca. 2 mm long on each side of distal margin, these extending down sheath and forming 2 distinct ciliate longitudinal lines (sometimes with a hirsute area along distal margin between them); blade lanceolate to oblanceolate, 7.1–13.8 by 1.9–3.1 cm, with acuminate tip 0.2–1.3 cm long, cuneate to obliquely cuneate at base, serrate with teeth 4–6 mm apart, smooth, glabrous, drying dark brown above, reddish brown beneath, chartaceous to subcoriaceous, the midvein impressed above, raised beneath, the lateral veins 10 to 18 on each side, 4–6 mm apart, narrow, visible above, slightly raised beneath, the tertiary veins obscure. Staminate inflorescences 2.5–4.2 cm long, either solitary spikes in leaf axils (2 per node) or consisting of 3 spikes at stem tip with central one slightly larger and maturing first; subtending bracts paired, linear, 0.5–3 by 0.1–0.9 cm, dentate; peduncle 0.1–0.6 cm long; mature spikes 2.2–3.8(–5) cm long; stamens ca. 200, at first congested but later ca. 1 mm apart on axis (axis less than 0.5 mm in diameter, persisting after stamens have fallen), the anthers ca. 2 mm long, ca. 0.5 mm in diameter, with connective projecting ca. 0.5 mm beyond thecae,

[5]Of the two collections cited by Solms in the protologue, the more distinctive pistillate material was chosen over the staminate (*Wright 1415*, also from Monte Verde).

[6]For the location of Charles Wright's Monte Verde (northeast of Guantánamo and near the Río Toa), as well as other places he visited in eastern Cuba, see R. N. Jervis, "Along the trails of Charles Wright in eastern Cuba" (Asa Gray Bull. II. **1**: 29–40. 1953) and L. J. Underwood's much earlier "A summary of Charles Wright's explorations in Cuba" (Bull. Torrey Bot. Club **32**: 291–300. 1905). Both papers include maps. Underwood's less elaborate than Jervis's.

acute. Pistillate inflorescences 1.5–3.5 cm long, consisting of axillary or terminal, simple or compound spikes, the latter composed of a long center spike with 2 shorter, opposite, basal ones, these each with 3 to 11 sessile flowers borne oppositely or alternately along axis; subtending floral bracts ovate at base, with slender acuminate tip 2–9 mm long. Pistillate flowers ellipsoid to globose, 2–4 mm long, 2–3 mm in diameter; perianth lobes shallowly triangular, ca. 0.5 mm long, acute at tip; stigma lanceolate to oblanceolate, 1–3 mm long, papillose. Fruits ellipsoid to globose drupes, 3–4 mm long, 2.5–3 mm in diameter, yellow; endocarp trigonous, smooth.

DISTRIBUTION AND PHENOLOGY. Central and eastern Cuba; in deciduous woods, moist forests, and dwarf forests, on dry hillsides, and in pine barrens; 450–1200 m alt. Flowering and fruiting apparently throughout the year, but heaviest in December, January, and April through July.

REPRESENTATIVE SPECIMENS EXAMINED. **Cuba.** SANTA CLARA: Lomas de Banao, *Luna 86* (NY); Banao Mtns., woody top of Divisiónes, *Léon & Roca 7868* (NY); Sierra de Gavilones, Sancti-Spiritus Mtns., *Léon et al. 6625* (NY). ORIENTE: Sierra Maestra, Loma del Gato, *Alain 2397* (GH), *Chrysogone & Clément 3183* (US), *León 10456* (NY, US); Sierra Maestra, road from Olimpo to Gran Piedra, *Clément 6475* (GH); Sierra Maestra, near La Gran Piedra, *Ekman 8811* (NY, S); pine barrens, 34 km S of Baracoa, Vía Azul, *Alain & Morton 5045* (GH, US); on Vía Azul between Sabanilla and Cajobabo, km 22 from Sabinilla, *Morton & Alain 8998* (US); Sierra de Nipe, San José, *Howard 6148* (A, DUKE); Sierra de Nipe, Cayo de Las Mujeres, *Léon et al. 19834* (A); Sierra de Nipe, near Woodfred, *Shafer 3406* (NY, US), *3409* (F, NY, US); S slopes of Sierra del Cristal, Mayarí, *Alain et al. 5523* (GH, US); Sierra del Cristal, ponte alta Río Lebisa, *López 170* (US); gulch of Río Lebisa, *Ekman 15952* (NY); prope villam Monte Verde, *Wright 1415* (G, GH, MO, WIS); Moa, Monte La Breña, *Acuña 13070* (US); S of Sierra Moa, Camp La Gloria, *Shafer 8036* (A, NY, US), *8138* (NY); Toa, near summit of Pico Galano, *Alain 3733* (GH).

This species is distinguished by its long, lanceolate leaves, its large pistillate flowers borne singly at the nodes, and its long bracts subtending the pistillate flowers. It is most closely related to *Hedyosmum orientale, H. domingense,* and *H. subintegrum. Hedyosmum grisebachii* has shorter leaves, less congested pistillate inflorescences, and shorter floral bracts than *H. orientale* and can be distinguished from *H. domingense* and *H. subintegrum* by the characters given in the key.

Hedyosmum leonis was described as a new taxon, apparently on the basis of the staminate inflorescences that often have a cluster of three spikes, with the center one much longer than the laterals. This plant was thought to be confined to the Sierra de Nipe, but examination of a large quantity of material from Cuba indicates that this morphological type is characteristic in both Santa Clara and Oriente.

3. **Hedyosmum domingense** Urban, Symb. Antill. 498. 1913. TYPE: Dominican Republic, Barahona, inter brachis rivulorum Cañada Maluca, 1600 m alt., April 1912, *Fuertes 1469* (staminate) (lectotype [here designated], S!; isolectotypes, A!, BM!, F!, G!, GH!, NY!, P!, US!).

Dioecious, sprawling shrubs or small trees 1–5 m tall; young stems quadrate, fragile, with edges ciliate, older ones terete, with leaf bases persisting for some

time but eventually disintegrating and leaving circular scars; internodes 1.6–3(–7) cm long. Leaves with free portion of petiole 1–4 mm long, the sheath 6–10 by 4–7 mm, flared or straight, not inflated, persisting for a short time then disintegrating, distal margin with 2 fimbriate processes 2–4 mm long extending down sheath and forming 2 distinct longitudinal ciliate to fimbriate raised lines; blade lanceolate to narrowly elliptic, 3.8–6.3(–7.8) by 1–1.5 cm, with acute tip 0.1–0.4 cm long, round to oblique at base, serrate with teeth 3–4.5 mm apart, smooth, glabrous, drying light grayish brown above, reddish brown beneath, subcoriaceous to coriaceous, the midvein impressed above, raised beneath, the lateral veins 7 to 9 on each side, ca. 4.5 mm apart, narrow, obscure above, obscure to slightly raised beneath, with or without local clusters of basally fused, brown trichomes ca. ½ distance to leaf margin, the tertiary veins obscure. Staminate inflorescences either solitary axillary spikes or 1 to 3 terminal ones, 1.2–4.4 cm long, light green; subtending bracts 4–10 mm long, acute at tip, entire or dentate; mature spikes 1.2–3.2 cm long; stamens 100 to 160, at first congested but later ca. 1 mm apart on axis (axis 0.5–1 mm wide, persisting or caducous after stamens have fallen), the anthers 1–2 mm long, ca. 0.5 mm in diameter, with connective projecting upward 0.5 mm beyond thecae, acute at tip. Pistillate inflorescences axillary or terminal, simple or compound spikes, the latter comprising long center spike with 2 shorter opposite basal ones; inflorescence bracts basal, leaflike, 1–3.5 cm by 3–8 mm, dentate; spikes 0.7–1.4 cm long, each with 5 to 12 flowers opposite to subopposite along axis; subtending floral bracts ovate, 2–3 mm long, the tip acuminate, 1–6 mm long, the margin ciliate. Pistillate flowers globose to ellipsoid, slightly trigonous, 2–3 mm long, 1.5–2 mm in diameter; perianth lobes triangular, 0.2–0.5 mm long, acute at tip; stigma lanceolate to oblanceolate, 1–2.5 mm long, papillose, caducous. Fruits globose to ellipsoid drupes, 3–4 mm long, 2–3 mm in diameter, yellow to orange; endocarp slightly trigonous, smooth.

KEY TO VARIETIES OF HEDYOSMUM DOMINGENSE

Upper and lower internodes of flowering stems of equal length (generally 1.6–3.1 cm); mature staminate inflorescences 1.2–3.4 cm long, with peduncle 0.1–0.7 cm long, axis ca. 0.5 mm thick, anthers ca. 1 mm long; endemic to Hispaniola. ..... var. *domingense.*

Upper and lower internodes of flowering stems unequal in length (upper internodes 1.6–3.1 cm, lower ones 5.8–6.3 cm); mature staminate inflorescences 3.5–4.4 cm long, with peduncle 0.6–1.1 cm long, axis ca. 1 mm in diameter, anthers ca. 2 mm long; endemic to Sierra Maestra in eastern Cuba. ..... var. *cubense.*

3a. **Hedyosmum domingense** var. **domingense**

Shrubs or small trees 1.5–5 m tall; upper and lower internodes of flowering stems of equal length, 1.6–3.1 cm long. Leaf blades 4–6.3 by 1–1.5 cm. Staminate inflorescences 1.2–3.4 cm long; peduncles 1–7 mm long; mature spikes 1.2–3.2 cm long, 3–4 mm in diameter, the axis ca. 0.5 mm in diameter, caducous; anthers ca. 1 mm long, ca. 0.5 mm in diameter, with connective projecting upward ca. 0.2 mm beyond thecae. Pistillate inflorescences 0.7–1.1 cm long, with 5 to 10 flowers.

DISTRIBUTION AND PHENOLOGY. Hispaniola; in thickets, pine forests, and cloud forests, on lateritic and limestone substrates; 1300–2100 m alt. Flowering apparently February through September; fruiting April to December.

SPECIMENS EXAMINED. **Haiti:** Massif de la Selle, Morne Cabaio, *Ekman 1553* (S); Pétionville, Massif de la Selle, Morne Tranchant, S slope, *Ekman 1883* (S, US); Massif de la Selle, Morne Tranchant, *Ekman 3215* (S); W group, Massif de la Hotte, Torbec, high ridge above La-Mare-Proux, *Ekman 5285* (G, S); Morne de La Hotte, W side of Ma Blanche, *Ekman 607* (S). **Dominican Republic.** BARAHONA: La Tierra Fria, head of Cañada Maluca, NW of Barahona, *Howard 12217* (A, DUKE, NY); trail between Monteada Nueva and Loma Alta, S of Polo, *Howard 12314* (A, BM, BR, S); Monteada Nueva, Caña Brava, S of Cabral, Barahona Mtns., *Liogier 11656* (GH, NY), *Liogier & Liogier 25147* (JBSD, NY). LA VEGA: La Ciénega, N of Constanza, *Jiménez 4019* (US); 4.7 km S of main road of Constanza, 3.3 km W of road to Pinar Parejo, *Zanoni et al. 20234* (JBSD, NY); 4 km W of Culata de Constanza, Loma El Campanario, *Zanoni et al. 23198* (JBSD). MONTE CRISTI: Monción, high ridge between Río Cenobi and Río San Juan, *Ekman 12783* (A, S, US). PERAVIA: El Cañaveral, 24 km NW of Rancho Arriba, near Quita Pena, *Mejia & Pimentel 462* (JBSD); W of Quita Pena, Loma Junumucú, *Zanoni et al. 27357* (GH), *27358* (GH). SAN JUAN: Piedra del Aguacate, *Howard & Howard 9381* (BM, GH, NY, S, US); Piedra del Aguacate, Río del Oro, N of San Juan, *Howard & Howard 9165* (BM, GH, NY, S, US). SANTIAGO: Loma del Valle de Bao, San José de las Matas, *Marcano 5779* (GH).

3b. **Hedyosmum domingense** var. **cubense** (Urban) Todzia & C. Wood, comb. et stat. nov. FIGURE, E, F.

Hedyosmum cubense Urban, Repert. Spec. Nov. Regni Veg. **24:** 1. 1927. TYPE: Cuba, Oriente, "in Sierra Maestra, Pico Turquino," 2400 m alt., 18 April 1915, *Ekman 5535* (pistillate) (lectotype [effectively designated by Marie-Victorin, Contr. Inst. Bot. Univ. Montréal **63:** 10. 1948], S! (photo NY!)).

Shrubs 2–3 m tall; flowering stems with upper internodes 1.6–3.1 cm long, lower ones 5.8–6.3 cm long. Leaf blades 3.8–7.8 by 1.1–1.8 cm. Staminate inflorescences 3.5–4.4 cm long; peduncles 6–10 mm long; mature spikes 2–3.1 cm long, 4–5 mm in diameter, the axis ca. 1 mm in diameter, persisting after stamens have fallen; anthers ca. 2 mm long, 0.5 mm in diameter, with connective projecting upward ca. 0.2 mm beyond thecae. Pistillate inflorescences 0.6–1.4 cm long, with 5 to 12 flowers.

DISTRIBUTION AND PHENOLOGY. Eastern Cuba; Sierra Maestra region; 1250–1800 m alt. Flowering specimens collected in July, August, and October; fruiting collections in January and April.

SPECIMENS EXAMINED. **Cuba.** ORIENTE: Sierra Maestra, summit of Pico Turquino, *Acuña 6742* (A, NY), *Bucher 20* (NY), *62* (NY), *162* (US); Pico Turquino, *Léon 11054* (NY), *11055* (NY); Sierra Maestra, on water divide near Punta de Palma Mocha, *Ekman 5248* (S (photo NY)); Sierra Maestra, La Bayamesa, *Ekman 7225* (S (photo NY)); crest of Sierra Maestra, near summit of La Bayamesa, *Morton 9338* (US), *9360* (US).

Hedyosmum domingense is notable for its short pistillate inflorescences with solitary flowers at the nodes and for its yellow to orange fruits. It is morphologically most similar to *H. grisebachii,* from which it is distinguished by its much smaller leaves and shorter inflorescences.

We recognize *Hedyosmum domingense* var. *cubense* because of its consistent

differences from the populations on Hispaniola as given in the key and because of its disjunct, isolated distribution on the top of the Sierra Maestra in eastern Cuba. In several characters—leaf size and inflorescence length, for example—it is intermediate between *Hedyosmum domingense* var. *domingense* and *H. grisebachii*. In such other characters as stipule shape, presence of clusters of hairs on the underside of the leaf, number of stamens per spike, and size of the pistillate flower, these populations are aligned more closely with *H. domingense* than with *H. grisebachii*.

4. **Hedyosmum subintegrum** Urban, Repert Spec. Nov. Regni Veg. **24:** 1. 1927. TYPE: Cuba, Oriente, "prope Bahia de Taco ad Minas de Iberia," 800 m alt., 7–8 Dec. 1914, *Ekman 3781* (staminate) (lectotype [here designated], s!; isolectotype, NY!). FIGURE, G, H.

Hedyosmum crassifolium Urban, *ibid.* TYPE: Cuba, Oriente, Sierra del Cristal, Río Lebisa, 600 m alt., 15 Dec. 1922, *Ekman 16005* (sterile) (lectotype [here designated], s!).

Glabrous, dioecious, creeping to straggling subshrubs 0.5–1 m tall; young stems quadrate, older ones terete, with persistent leaf bases encircling stem; lower and upper internodes of equal length, 2–6.3 cm long. Leaves with free portion of petiole 0.2–0.5 cm long, the sheath 5–6 by 3–7 mm, slightly inflated, persistent, with 2 raised lines extending down its length and 2 narrowly triangular stipular processes 1.2–2 mm long at distal margin; blade narrowly elliptic to narrowly obovate, (2–)4.5–7.5(–9) by 1–2.2 cm, acute at apex or with acuminate tip 0.3–0.6 cm long, cuneate to obliquely cuneate at base, subentire to obscurely serrate, often revolute, teeth 4–8 mm apart beginning at ⅓ to ½ distance from base of blade, notably coriaceous to subcrassulate, smooth, glabrous, drying dark reddish brown above, medium reddish brown beneath, the midvein impressed above, raised beneath, the lateral veins 5 to 8 on each side, 5–8 mm apart, arcuate, obscure to not visible on both faces, the tertiary veins not visible. Staminate inflorescences solitary terminal or axillary spikes, 2.4–4.3 cm long; subtending bracts linear, 0.3–0.6 cm long; peduncles to 0.2–0.5 cm long; mature spikes 1–3.2 cm long, 4–5 mm in diameter; stamens ca. 300, initially congested but becoming ca. 1 mm apart along 1-mm-thick axis, the anther 1–2 mm long, ca. 0.5 mm in diameter, with acute connective tip projecting ca. 0.5 mm beyond thecae. Pistillate inflorescences axillary spikes 1–1.8 cm long, with 4 to 10 sessile flowers borne oppositely on axis; subtending floral bracts ovate, 2–3 by ca. 2 mm, with linear to spatulate tip 4–6 mm long, entire or slightly ciliate. Pistillate flowers ellipsoid to globose, slightly trigonous, 2.5–3 mm long, 2–3 mm in diameter; perianth with triangular acute lobes 0.3–0.7 mm long; stigma lanceolate in outline, 3-angled, 2–3.5 mm long. Fruits subglobose drupes, ca. 5 mm long, 3–4 mm in diameter, yellow to red; endocarp smooth, trigonous, 3–4 mm long, ca. 2 mm thick.

DISTRIBUTION AND PHENOLOGY. Eastern Cuba; apparently confined to serpentine soils and iron-ore-containing substrates; 650–800 m alt. Flowering and fruiting specimens collected in March, July, and December.

SPECIMENS EXAMINED. **Cuba.** ORIENTE: Moa, Mina Delta, *Clément & Alain 4033* (GH, US); trail Navas to Camp Buena Vista, *Shafer 4451* (NY); S of Sierra Moa, Camp La Gloria, *Shafer 8056* (NY), *8061* (NY, US), *8091* (A, F, NY, US), *8225* (NY).

Hedyosmum subintegrum is distinguished by its creeping or straggling, subshrubby habit, its strongly coriaceous leaves, and its short pistillate inflorescences. It is most closely related to *H. grisebachii,* from which it differs in leaf morphology and in the length of the pistillate inflorescence.

Urban's type specimen of *Hedyosmum subintegrum* consists of staminate and pistillate material of different taxa. Not surprisingly, he (1927) noted that the leaves of the staminate and pistillate plants are a little different! Because the protologue and the specific epithet referring to a subentire leaf margin best conform to the staminate material, that portion is here designated the lectotype. The pistillate material conforms well with *H. grisebachii.* In the same article Urban described *H. crassifolium* from a single sterile specimen. Although the leaves are a little larger and thicker than those of the other specimens studied, this degree of variation is often observed within species of *Hedyosmum*; *H. crassifolium* is therefore considered to be synonymous with *H. subintegrum.* A discrepancy exists between the locality data on the type specimen of *H. crassifolium* and those provided in the description. The former are cited above, while the latter are "in cacumine montis Sierra del Cristal, 1325 m." Since *H. subintegrum* is known only from altitudes of 650 to 800 m, the data cited here are probably incorrect.

5. **Hedyosmum arborescens** Sw. Prodr. 84. 1788. TYPE: Jamaica, *Swartz s.n.* (lectotype [here designated], C!, photos from C neg. 21627 at F!, GH!, and MO!).[7] FIGURE, C, D.

Tafallaea arborescens (Sw.) Kuntze, Revis. Gen. Pl. **2:** 566. 1891.

Hedyosmum elegans Cord. Adansonia **3:** 305. 1862. TYPE: Guadeloupe, Bains Jaunes, Oct. 1845, *Funck & Schlim 89* (pistillate) (lectotype [here designated], P!; isolectotype, G!).

Dioecious shrubs or small trees 2–10 m tall, 2–10 cm d.b.h., with prop roots; young stems quadrate, older ones terete, with leaf bases disintegrating and leaving circular nodal scars; internodes 1–6.8 cm long. Leaves with free portion of petiole 0.5–1.3 cm long, the sheath 10–13 by 3–6 mm, slightly flared at apex, distal margin with 2 narrowly triangular to linear, entire or bifid stipular appendages 1–2 mm long, persistent but disintegrating with age; blade elliptic, (3–)4–12(–17) by 2–6 cm, with acuminate tip 6–12 mm long, cuneate to obliquely cuneate at base, serrate with teeth 4–8 mm apart, green above, light green beneath, succulent to coriaceous, smooth, drying slate gray to light grayish brown above, light reddish brown beneath, stiffly chartaceous, the midvein impressed above, raised beneath, the larger lateral veins 12 to 16 on each side, 3–9 mm apart, slightly arcuate, raised both above and beneath, forming a smoothly curving vein 1–2 mm from blade margin, with an intermediate series

[7]Other sheets of *Hedyosmum arborescens* annotated by Swartz are at BM and LD, but because they are without label data, no isolectotypes are designated.

of lateral veins extending ½ distance to margin, these prominent both above and beneath. Staminate inflorescences simple or cymose spikes borne along a central axis, 1–9 cm long; subtending bracts cymbiform, 3–9 mm long, entire (sometimes dentate); peduncles to 2–3 mm long; mature spikes 1.4–3.1(–3.9) cm long, 0.6–0.7 cm in diameter; stamens ca. 150, congested on axis, the anther (1.2–)2–3 mm long, ca. 0.5 mm in diameter, green, with connective ca. 0.2 mm long, flattened distally, having a minute acute white tip. Pistillate inflorescences axillary or terminal, 3-parted, thyrselike racemes, (2–)4–8 cm long, with 6 to 24 cymules; cymules oppositely arranged 5–20 mm apart on inflorescence axis, sessile, (1- or) 2- or 3- (to 5-)flowered, 3–5 mm long, 3–4 mm in diameter; subtending floral bracts free or connate with adjacent bracts at base, 1.5–3.5 mm long, acuminate at apex, enclosing lower ½ of flower. Pistillate flowers trigonous, 2.5–3.5 mm long, 1.5–2 mm in diameter, green; perianth lobes ca. 0.3 mm long, rounded at apex; stigma linear to clavate in outline, (1.5–)2–3 mm long, white, papillose, elaborated distally, caducous. Fruiting cymules irregularly globose, 6–7 mm in diameter, with white, translucent bracts; fruits trigonous drupes ca. 4 mm long; endocarp 2–3 mm long, brown.

DISTRIBUTION AND PHENOLOGY. Jamaica, Puerto Rico, and the Lesser Antilles; elfin woodlands and wet montane forests; 200–1600 m alt. Flowering and fruiting throughout the year but heaviest January through July.

REPRESENTATIVE SPECIMENS EXAMINED. **Jamaica.** PORTLAND: W slope of Silver Hill, *Anderson & Sternberg 3257* (DUKE, GH, LL, US); trail to Old England, NW of Hardwar Gap, *Hespenheide 705* (DUKE, MO, MSU, NY); St. Andrew–Portland border, at edge of trail in Morse's Gap, *Kapos 1610* (TEX). ST. ANDREW: Morse's Gap, *Nichols 155* (G, GH, MO, NY); trail along leeward slope of Mt. Caledonia, NW of Hardwar Gap, *Anderson & Sternberg 3298* (DUKE, GH, LL, US); trail up Mt. Haub from Hardwar Gap, *Fosberg 4273* (BM, US); Blue Mtns., Port Royal Group, Caledonia Peak and vic., 2 mi NW of Hardwar Gap, *Webster & Wilson 4938* (A, BM). ST. THOMAS: below Portland Gap, *Howard & Proctor 14822* (A, BM). **Puerto Rico:** Caribbean Natl. Forest [Luquillo Mtns.], along El Toro trail, W of Río Blanco Ridge, *Holdridge 112* (A, NY, US); Caribbean Natl. Forest, Luquillo Mtns., Mt. Britton, *Little 13548* (F, US); Caribbean Natl. Forest, Luquillo Mtns., trail from Bella Vista to Pico del Este, *Little 13569* (A, F, NY, US); Luquillo Natl. Forest, along road S of La Mina, *Howard & Nevling 15327* (A); Luquillo Mtns., route 191 S of Molindero road, *Howard 16633* (A); Sierra de Naguabo, Monte el Duque, *Shafer 2223* (F, GH, NY, US); Sierra de Luquillo, Jiménes, *Urban 1364* (BM, G, GH, MSU, NY, S). **St. Kitts:** Mt. Misery, the Gates, *Beard 304* (A, NY); E spur of Mt. Misery, *Proctor 19612* (A); trail to Dos d'Ans (Dodans) Pond, *Howard 11970* (A); ridge leading to Dos d'Ans Pond, *Howard 11974* (A), *11982* (A); trail on Camp Mtn., SE range, *Howard & Nevling 16877* (A); Trinity Palmetto Point Parish, Camp Crater Mtn., *Wadsworth 332* (A, DUKE), *376* (A). **Montserrat:** upper portions of trail to Lang's Soufrière, Paradise Estate, *Howard & Howard 15176* (A); Chance's Mtn., *Shafer 286* (F); Chance's Mtn., near Chance's Pond, *Howard 11910* (A). **Guadeloupe.** BASSE-TERRE: près de l'Étang As de Pique, *Sastre et al. 2629* (A); Massif de la Soufrière, road to Pas du Roi, *Sastre et al. 2848* (A, MO); la Soufrière, above St. Claude, *Webster et al. 9018* (A, DUKE, US); trail Bains Jaunes to Soufrière, *Howard 11810* (A), *11811* (A); Bains Jaunes, *Duss 2960* (F, NY, US). **Dominica:** Morne Diablotins, *Chambers 2649* (TEX), *Hodge & Hodge 2823* (GH); S slope of Morne Macaque (Micotrin) on road to Fresh Water Lake, *Ernst 1718A* (TEX); S slopes of Morne Micotrin, ca. 0.3 mi E of Laudat, St. George, *Webster 13237* (DUKE, TEX); forested slopes of Micotrin along trail from Laudat to Fresh Water Lake, *Wilbur et al. 7391* (DUKE, GH, TEX, US). **Martinique:** Calabasse, Champflore, *Duss 2105* (F, GH, MO, NY); forêt de la

Calabasse, *Hahn 301* (A, G, S); between Fond St. Denis and Balata, *Howard 11703* (BM, NY), *11704* (A, BM, DUKE, NY); Calvaire–Deux Choux road to W of Morne Bellevue, *Kimber 2016* (A, WIS); Gros-Morne aux Deux Choux, *Stehlé 2160* (NY); Fond St. Denis, *Larsen & Larsen 35481* (AAU); Pente du Morne Macouba vers Trou Navet, *Sastre 6862* (A). **St. Lucia:** Quilesse, *Beard 1145* (F, GH, MO, S, US); trail from Quilesse to Morne Troumasse, *Howard 11662* (A); lower elevations to summit of Morne Gimie, *Howard & Weaver 17929* (A). **St. Vincent:** somma of Soufrière volcano, *Howard 11211* (A); summit of Richmond Peak, *Howard et al. 17710* (A); ESE ridge of Mt. Grand Bonhomme, Charlotte, *Proctor 26055* (A, LL).

Hedyosmum arborescens is the only West Indian species that has fleshy floral bracts and numerous-flowered cymules. It appears to be most closely related to *H. costaricense* C. Wood ex W. Burger of Central America, which has very similar inflorescence and leaf morphology, but differs in the higher density of teeth on the leaf margins and in the prominent costal vein 1–2 mm inside the leaf margin. *Hedyosmum gentryi* D'Arcy & Liesner, of Panama, Colombia, and Venezuela, is vegetatively very similar to *H. arborescens* but is easily recognized by its pistillate flowers that are subtended by purple floral bracts and borne singly at each node of the inflorescence.

The disjunct population of *Hedyosmum arborescens* in Jamaica shows two consistent characteristics at variance from those found in contiguous populations in Puerto Rico and the Lesser Antilles: leaf-teeth with rounded sinuses 3–5 mm deep and solitary staminate inflorescences. We do not regard these differences as important enough to warrent taxonomic designation, since morphological variation of this kind has been observed in other *Hedyosmum* species.

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A RECONSIDERATION OF CARDAMINE CURVISILIQUA AND C. GAMBELLII AS SPECIES OF RORIPPA (CRUCIFERAE)

IHSAN A. AL-SHEHBAZ AND REED C. ROLLINS[1]

The generic status of *Nasturtium* is evaluated, and an argument supporting its union with *Rorippa* is presented. The new name *R. floridana* and the new combination *R. gambellii*, based on *Cardamine curvisiliqua* and *C. gambellii*, respectively, are proposed. A key to the white-flowered species of *Rorippa* that grow in North America is given.

One of the most frequently encountered problems in the systematics of the Cruciferae (Brassicaceae) is whether or not generic status should be given to a small group of species that, on the basis of morphology, form a marginal portion of a larger genus. Where sharply defined discontinuities exist, such peripheral groups are usually recognized as independent genera. However, if the differences between the marginal groups and the larger genus break down, whether locally or on a worldwide basis, then the taxonomy of the complex is best treated by not recognizing the smaller species groupings as segregate genera. A case in point involves *Rorippa* Scop. and *Nasturtium* R. Br.

Many authors (e.g., Coode & Cullen, 1965; Fernald, 1950; Stuckey, 1972; Valentine, 1964) who recognize both *Nasturtium* and *Rorippa* distinguish the former by its white petals, its lack of median nectaries, and its coarsely reticulate seeds. *Rorippa* has yellow petals, well-developed median nectaries, and variously sculptured (usually not coarsely reticulate) seeds. However, an examination of many species of *Rorippa* from the Southern Hemisphere reveals that these character sets break down in various combinations, and that none of the other alleged differences between the two genera holds together either. For example, *R. laurentii* Jonsell (Madagascar) has white flowers, median nectaries, and striate seeds (Jonsell, 1979); *R. gigantea* (J. D. Hooker) Garnock-Jones (Australia, New Zealand) has white flowers, median nectaries, and coarsely reticulate seeds (Garnock-Jones, 1978; Hewson, 1982); and almost all of the South American species have white flowers, no median nectaries, and colliculate seeds (Martínez-Laborde, 1985). It is evident that there are no solid grounds to support the maintenance of *Nasturtium* as a genus distinct from *Rorippa*.

Jonsell (1968) followed Schulz (1936) in uniting *Nasturtium* and *Rorippa* and in placing some species of the former in sect. *Cardaminum* (Moench) DC. Schulz, however, adopted *Nasturtium* for the combined genus, instead of the

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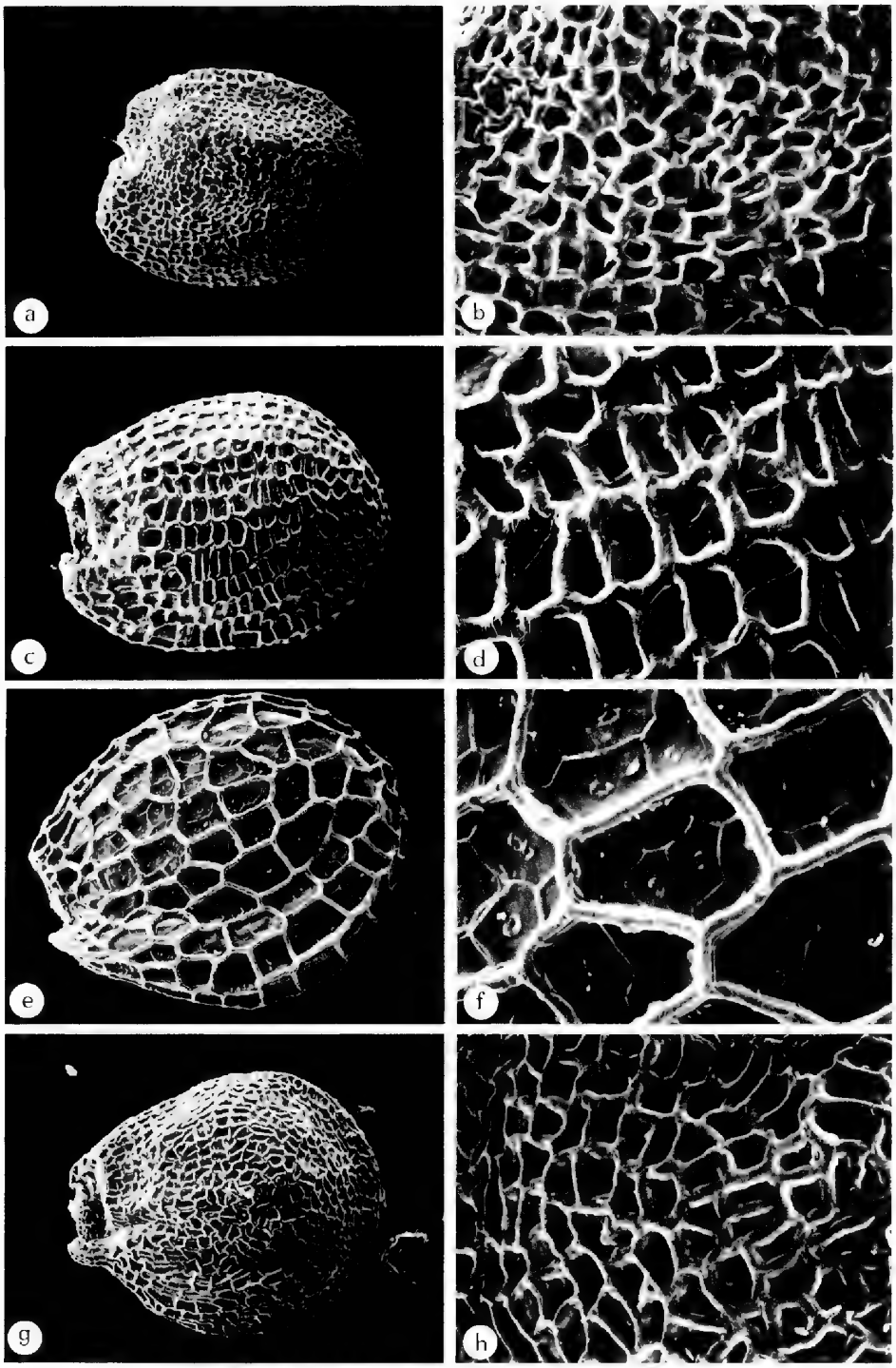

Scanning electron micrographs of seeds of *Rorippa*: a, b, *R. floridana* (*Curtiss 24*, GH); c, d, *R. microphylla* (*Knowlton s.n.*, 25 July 1911, NEBC); e, f, *R. nasturtium-aquaticum* (*Cory 1619*, GH); g, h, *R. gambellii* (*Bingham s.n.*, 1886, GH). a, c, e, g, × 38; b, d, f, h, × 140.

Comparison among Rorippa floridana, R. microphylla, and R. nasturtium-aquaticum.

Character	Taxon		
	R. floridana	**R. microphylla**	**R. nasturtium-aquaticum**
Seeds			
Color	Light or yellowish brown	Reddish brown	Reddish brown
Arrangement in locule	Uniseriate	Uniseriate	Biseriate
Length (mm)	0.65–0.85(–0.9)	(0.8–)1–1.2	(0.8–)0.9–1.1(–1.2)
Width (mm)	0.42–0.65	(0.6–)0.7–0.84(–0.9)	(0.6–)0.7–0.9(–1)
Reticulation size	Minute	Moderate	Coarse
No. of areolae per side	400 to 500	75 to 150 (to 175)	25 to 50 (to 60)
Fruit width (mm)	1–1.5	1–1.5	2–3
Emergent leaves			
Petiole base	Not auriculate	Auriculate	Auriculate
No. of lateral lobes (pairs)	1 or 2 (or 3)	(1 or) 2 to 4 (or 5)	1 to 4 (to 6)
Chromosome number (*n*)	16	32	16

earlier-published *Rorippa*. His sect. *Cardaminum* included the watercress, *R. nasturtium-aquaticum* (L.) Hayek (as *N. officinale* R. Br.), as well as two African and two North American species. Both North American species were originally described in *Cardamine* L. and were treated later in *Nasturtium* (see below). They are transferred in this paper to *Rorippa*, where they are more appropriately placed.

The taxonomic history of both *Cardamine curvisiliqua* Shuttelw. and *C. gambellii* S. Watson, hereafter *Rorippa floridana* Al-Shehbaz & Rollins and *R. gambellii* (S. Watson) Rollins & Al-Shehbaz, respectively, has been discussed previously at some length (Rollins, 1960, 1978) and need not be repeated here. *Rorippa floridana* is endemic to Florida, where it grows in lakes and springs in Brevard, Citrus, Clay, Collier, Columbia, Dade, Duval, Gilchrist, Hillsborough, Lake, Levy, Manatee, Marion, Seminole, Sumter, Taylor, Vollusia, and Wakulla counties. Plants of *R. floridana, R. microphylla* (Boenn. ex Reichb.) Hylander, and *R. nasturtium-aquaticum* produce only simple leaves on deeply submersed stems and pinnate leaves on emergent ones (Michaelis, 1976; Rollins, 1978). The production of simple or pinnate leaves can be controlled by manipulating the depth at which a given plant is grown (Rollins, 1978). These three species are indistinguishable in the submersed state, but they can be identified easily when emergent parts have mature fruits.

Rorippa floridana has previously been recognized as *Cardamine curvisiliqua* (Small, 1933), as "undoubtedly a minor variant" of *C. pensylvanica* Muhlenb. ex Willd. (Patman, 1962, p. 200), and as *R. microphylla* (Clewell, 1985; Godfrey & Wooten, 1981; Rollins, 1978; Wunderlin, 1982). The species does not belong

to *Cardamine* because it does not have the elastically dehiscent fruits, the usually spirally coiled valves, or the narrowly winged replum margin that are unique to that genus. *Rorippa floridana* differs from *R. microphylla* in several features of its seeds (see FIGURE), in its emergent leaves, and in its chromosome number (see TABLE). Consistent chromosome counts of $2n = 64$ have been reported for *R. microphylla* from Canada (Mulligan, 1964), Sweden (Jonsell, 1963), Germany (as *Nasturtium officinale*; Tischler, 1935), England (as *N. uniseriatum* Howard & Manton; Howard & Manton, 1946), and Denmark, England, Holland, Ireland, and Scotland (as *N. officinale*; Manton, 1935). *Rorippa floridana* (as *C. curvisiliqua*) has $2n = 32$ (Rollins & Rüdenberg, 1977).

Seeds of *Rorippa floridana* are smaller in size and have much smaller and far more numerous areolae on each side than those of *R. microphylla* and *R. nasturtium-aquaticum* (see FIGURE). Seeds of the last species are unusual in that their areolae are subdivided by a low understory of reticulum, the units of which contain circular thickenings (see FIGURE, f). These probably correspond to stomata. To our knowledge, such a peculiar pattern of seed sculpture has not been recorded elsewhere in the Cruciferae. The areolae in *R. gambellii* are somewhat intermediate in size and number between those of *R. floridana* and *R. microphylla.*

Perhaps the earliest known collection of *Rorippa microphylla* from the New World was made by W. Boott in 1861 in Waltham, Massachusetts (Green, 1962). The species has not been collected from any of the southeastern states, whereas *R. nasturtium-aquaticum* is naturalized in all of them. Apparently the oldest specimens of *R. floridana* were collected by Leavenworth in 1836 from Tampa Bay (Gray, 1880; McVaugh, 1947; Torrey & Gray, 1840) and by Rugel in 1843 from St. Marks. Evidently the native *R. floridana* was well represented in several herbaria long before *R. microphylla* was recorded for North America.

The following key is provided to aid in the identification of the indigenous and naturalized North American white-flowered species of *Rorippa*:

A. Lateral leaf lobes with 3 to 5 (to 7) teeth; inflorescences bracteate, the bracts toothlike to filiform and to 3 mm long, sometimes much larger, leafy, and pinnate, always adnate to pedicels; fruiting pedicels conspicuously flattened beneath at attachment to rachis. ..... *R. gambellii.*

A. Lateral leaf lobes entire or repand; inflorescences ebracteate; fruiting pedicels not flattened.

B. Petioles of emergent leaves not auriculate at base; seeds yellowish brown, usually < 0.9 mm long and < 0.65 mm wide, minutely reticulate, with 400 to 500 minute areolae on each side. ..... *R. floridana.*

B. Petioles of emergent leaves minutely to coarsely auriculate at base; seeds reddish brown, usually > 0.9 mm long and > 0.65 mm wide, moderately to coarsely reticulate, with 25 to 175 areolae on each side.

C. Mature fruits 1–1.5 mm wide; seeds uniseriately arranged in each locule, moderately reticulate, with 100 to 150 (to 175) areolae on each side. ..... *R. microphylla.*

C. Mature fruits 2–3 mm wide; seeds biseriately arranged, coarsely reticulate-foveolate, with 25 to 50 (to 60) areolae on each side. ..... *R. nasturtium-aquaticum.*

Rorippa floridana Al-Shehbaz & Rollins, nom. nov. Based on *Cardamine curvisiliqua* Shuttelw. ex Chapman, Fl. South. U.S. 605. 1887. LECTOTYPE

(here designated): in uliginosis subsalsis ad fluv. St. Marks, prope St. Marks, Florida, *Rugel s.n.*, April–May, 1843 (isolectotypes, GH!). The specific epithet *curvisiliqua* would become a later homonym if transferred to *Rorippa* because of the existence of *R. curvisiliqua* (W. J. Hooker) Bessey ex Britton, Mem. Torrey Bot. Club **5:** 169. 1894.

Nasturtium stylosum Shuttelw. ex O. E. Schulz *in* Engler & Prantl, Nat. Pflanzenfam. ed. 2. **17B:** 553. 1936; non *N. stylosum* (DC.) O. E. Schulz ex Cheesman, Trans. & Proc. New Zealand Inst. **43:** 179. 1911.[2]

Putative interspecific hybridization between *Rorippa floridana* (as *R. microphylla*) and *R. nasturtium-aquaticum* has been suggested previously (Rollins, 1978). It is likely that the hybrids are more common than is presently known. However, very little can be said about them, and only future field and experimental work can verify these assumptions.

Rorippa gambellii (S. Watson) Rollins & Al-Shehbaz, comb. nov. Based on *Cardamine gambellii* S. Watson, Proc. Amer. Acad. Arts **11:** 147. 1876. TYPE: California, Santa Barbara, *Gambell s.n.* (holotype, GH!; isotype, GH!).

Nasturtium gambellii (S. Watson) O. E. Schulz, Bot. Jahrb. Syst. **66:** 98. 1933.

Specimens of *Rorippa gambellii* in the Gray Herbarium were annotated by one of us (R. C. R.) as early as 1957, but the new combination was never published. Watson (1895) suggested that the spelling of *gambellii* should be changed to *gambelii* because the plant was named after Gambel, not Gambell. However, the original spelling is retained here.

The distribution of *Rorippa gambellii* is based primarily on old collections, the majority of which were made in the nineteenth century. The species apparently occupied marshy or aquatic habitats in southern California (Los Angeles, San Bernardino, and Santa Barbara counties) and occurred disjunctly in the Valley of Mexico. Areas near Santa Barbara and San Bernardino have been searched on two different occasions, but no plants of the species have been found. Likely habitats have mostly been obliterated by urbanization. The same despoiling of habitat seems to have occurred in Mexico. It now appears possible that *R. gambellii* is extinct.

Both glabrous and pubescent forms are known (Rollins, 1960; Watson, 1876), but this variation is apparently insignificant.

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[2]Schulz (1936) had recognized both *Nasturtium stylosum* Shuttelw. and the earlier homonym above as distinct species. The earlier homonym, which was transferred to *Rorippa* (as *R. stylosa* (DC.) Allan, Fl. New Zealand **1:** 188. 1961; non *R. stylosa* (Pers.) Mansf. & Rothm. Repert. Spec. Nov. Regni Veg. **49:** 276. 1940), is now known as *R. gigantea* (J. D. Hooker) Garnock-Jones.

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A NEW SPECIES OF NEONAUCLEA (RUBIACEAE) FROM YUNNAN, CHINA

SHOU-QING ZOU[1]

A large tree of economic importance was found in Xishuangbanna, China. It has proved to be a new species of *Neonauclea*. Its morphology is described; in addition, there is an illustration, a comparison with allied taxa in southern Asia, and a key to the four species of *Neonauclea* known to occur in China.

Four species of *Neonauclea* Merr.—*N. griffithii* (Hooker f.) Merr., *N. sessilifolia* (Roxb.) Merr., *N. reticulata* (Havil.) Merr., and *N. navillei* (Léveillé) Rehder—have been recorded from China. During the 1970's, under the instruction of H. T. Tsai, P. H. Yu and I investigated tropical fast-growing and valuable tree species in Xishuangbanna prefecture, southern Yunnan, China, and discovered several new records in the area. One of them is the giant tree called "mei zhafang" by the local Dai people. It is an important source of timber for many purposes, including construction and furniture. At first, it was identified as *Adina polycephala* Bentham. Because it is extremely tall, only a few people collected specimens of it. In 1935 C. W. Wang gathered two specimens, which were determined to be *Neonauclea navillei* by F. C. How (1946). Ridsdale (1978) placed *N. navillei* in synonymy under *N. griffithii*. However, by comparing specimens from China and southern Asia, I have found that this tree is different from *N. griffithii* and other members of the genus. I am naming the new species in honor of H. T. Tsai, late Director of the Yunnan Institute of Tropical Botany, Academia Sinica, who contributed greatly to the utilization of tropical plant resources in Xishuangbanna.

Neonauclea tsaiana S. Q. Zou, sp. nov. FIGURE.

Neonauclea navillei sensu F. C. How, Sunyatsenia **6**: 250. 1946, non (Léveillé) Rehder.
Neonauclea griffithii sensu Index Fl. Yunnan. **2**: 1266. 1984, non (Hooker f.) Merr.

Species affinis N. griffithii sed petiolis longioribus (ad 1.5–4 cm longis, versus 0.8–1.5 cm longis), foliis ovalibus basibus rotundatis vel late cuneatis (versus attenuatis), subtus in axillis nervorum acarodomatiis tomentellis instructis (versus glabratis), lobis calycis obpyriformibus (versus clavatis), corolla eburnea (versus purpurea) differt.

Tree 30–40 m tall, 1 m d.b.h., with buttresses at base; bole clear, 15–25 m tall, cylindrical, straight. Bark rough; inner bark fibrous, yellow, sometimes with pink. Terminal vegetative bud strongly flattened. Twigs stout, 4–6 mm

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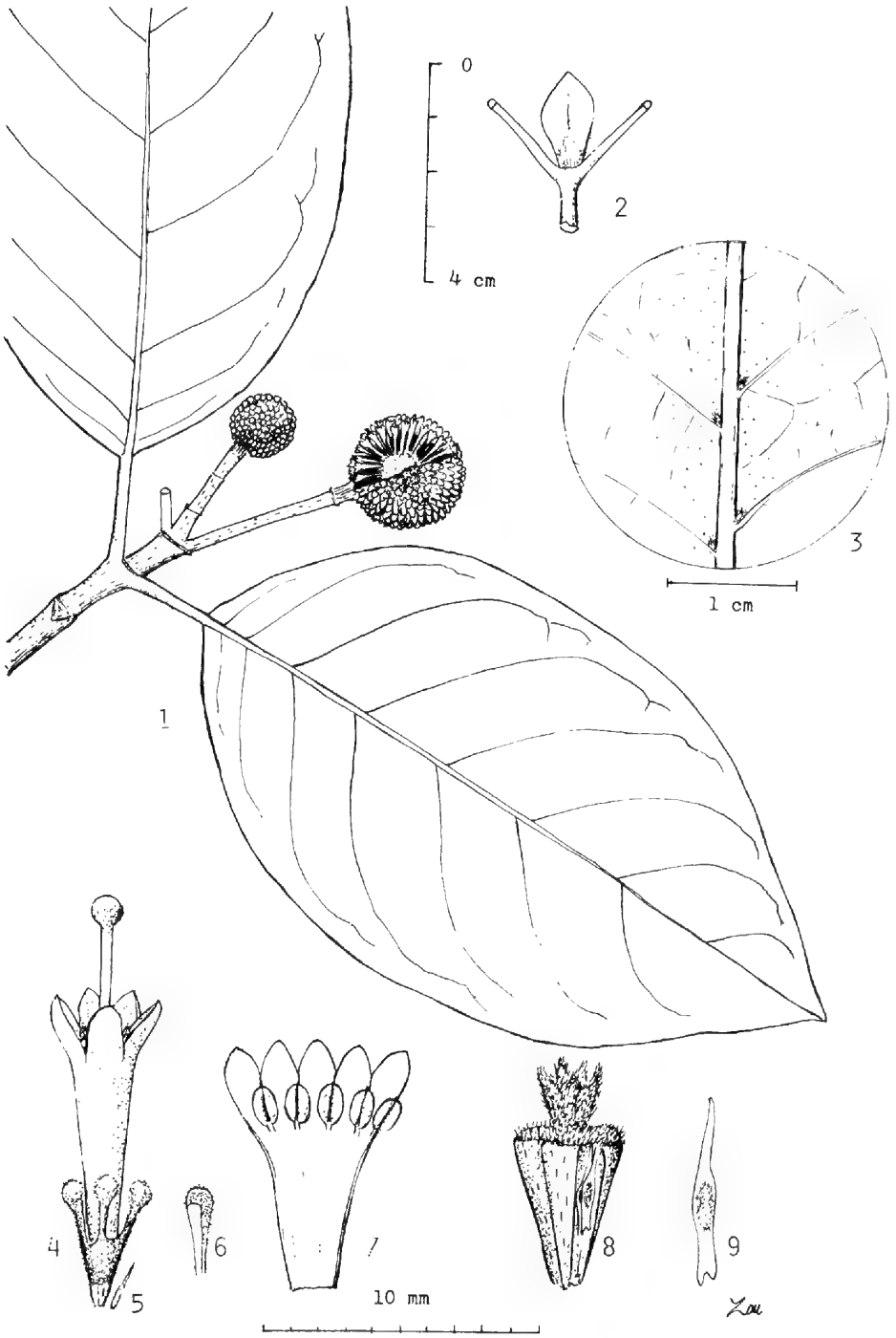

Neonauclea tsaiana: 1, branch with flowering heads and leaves; 2, terminal vegetative bud; 3, axils with domatia; 4, flower; 5, interfloral bracteole; 6, apical portion of calyx lobe; 7, open corolla tube and stamens; 8, fruitlet; 9, seed.

Differences among three species of Neonauclea.

Character	Species		
	N. griffithii	**N. lanceolata**	**N. tsaiana**
Leaves			
Shape	Obovate, sometimes elliptic-oblong	Obovate	Oval or ovate-elliptic
Apex	Mucronate	Short-caudate	Acute to acuminate
Base	Attenuate	Attenuate	Rounded or cuneate
Domatia in nerve axils	Glabrous	Tomentulose	Tomentulose
Petiole	Short and stout, 0.8–1.5 cm long	Slender, 1–2 cm long	Medium thick, 1.5–4 cm long
Flowering axes	1 to 3 (usually 1)	1 to 3	1 to 5 (usually 3)
Flowers			
Apical portion of calyx lobes	Elongate, clavate	Spathulate	Obpyriform
Pubescence on corolla lobes	Absent	On exterior	Absent
Stigma	Fusiform	Globose	Globose
Twigs	Smooth	Smooth	Densely lenticellate
Height of tree (m)	7–20	20–30	30–40
Distribution	India, Burma, China	Java, New Guinea	China (southern Yunnan)

in diameter, densely lenticellate. Leaves with stipules 2, ovate, 12–24 × 8–14 mm, adpressed, glabrous, caducous; petiole 1.5–4 cm long; blade oval or ovate-elliptic, 12–22 × 6–13 cm, rounded or cuneate at base, acute to acuminate at apex, entire, chartaceous, green, glabrous, shiny above, dull beneath, the lateral nerves 7 or 8 pairs, prominent beneath, with tomentulose domatia in axils. Inflorescences terminal, flowering axes 1 to 5; peduncles up to 2–4 cm long, with 2 caducous bracts; flowering heads 10–18 mm in diameter across calyces, 25–30 mm across corollas; interfloral bracteoles conical, 0.7–1 mm long. Flowers with hypanthium 1–1.5 mm long, glabrous below, pubescent above; calyx 0.8–1 mm long, pubescent, the lobes 5, 3–4 mm long, short-pubescent outside, glabrous inside, deciduous apical portion obpyriform; corolla infundibuliform, 7–9 mm long, yellow-white, glabrous, the lobes 5, oblong, 2.5 × 1.2 mm; stamens 5, inserted in upper part of corolla tube, the filaments 0.4 mm long, glabrous, the anthers basifixed, oblong, 1 × 1.4 mm; style 12–15 mm long, exserted 5–6 mm, stigma globose. Fruiting head 15–20 mm in diameter; fruitlets loosely associated, flattened-claviform, 6–7 mm long, glabrous at base, pallid-pubescent at apex, crowned by persistent calyx, septicidally and loculicidally dehiscent. Seeds numerous, ellipsoid, compressed, winged at both ends, base slightly bifid.

Holotype. China, Yunnan, Che-li (Jinghong) Xian, Kuen-ger, 1100 m alt., Oct. 1935, *C. W. Wang 39373* (A).

ADDITIONAL SPECIMENS EXAMINED. **China.** YUNNAN: Che-li, 1000 m alt., *C. W. Wang 81146* (A); Mengla, Menglu, 750 m alt., *G. D. Tao 13656* (YITB[2]), *38578* (YITB).

This species is known only from Mengla and Jinghong Xian, Yunnan, China, from 500 to 1100 m altitude, in tropical, seasonally wet rainforests. It is a canopy tree often growing by streams or at the bottom of valleys, in warm, very humid areas (above 20°C mean temperature and 1500 mm annual precipitation) on latosolic or lateritic soils rich in organic matter. It flowers in September and October and fruits in May and June.

Neonauclea tsaiana was confused with *N. griffithii,* and some herbarium specimens have been annotated as *N. lanceolata* Merr. However, the species are quite different morphologically (see TABLE). They can be separated by the following key:

KEY TO THE GENUS NEONAUCLEA IN CHINA

1. Leaves sessile or subsessile.
   2. Leaf blades elliptic-oblong, with 5 or 6 pairs of lateral nerves. . . *N. sessilifolia.*
   2. Leaf blades obovate, with 7 to 9 pairs of lateral nerves. . . . . *N. reticulata.*
1. Leaves petiolate.
   3. Petioles short, stout, 0.8–1.5 cm long, leaf base attenuate, domatia in vein axils below glabrous. . . . . *N. griffithii.*
   3. Petioles 1.5–4 cm long, leaf base rounded or cuneate, domatia tomentulose. . . . . *N. tsaiana.*

Although the first specimens of this species were collected in 1935, it remained unknown because it is confined to a small area that was visited by few scientists before the 1960's. However, the local Dai people are familiar with it, using the wood widely in their villages.

The sapwood is yellow, and the heartwood is the color of egg yolks, fine textured, heavy, and hard, with interlocked grain; specific gravity of air-dried wood is 0.77 g/cm^3. The wood is strong and durable even under outdoor conditions. It saws easily, turns well, and can be used for a variety of purposes such as pillars, beams, purlins, planks, door and window frames, quality furniture, carvings, decorative paneling, and crafts.

Neonauclea tsaiana is one of the best timber species in Yunnan. However, for the past several years people have cut down most of the mature trees. It is now rare and facing extinction. It should be specially protected and cultivated wherever possible.

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I should like to thank R. A. Howard for his guidance during this study. I should also like to acknowledge P. S. Ashton, S. Y. Hu, and D. Z. Cheng for their suggestions and help.

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[2]Herbarium of the Yunnan Institute of Tropical Botany, China.

NOMENCLATURAL CHANGE FOR AN ECONOMICALLY IMPORTANT PLANT FROM CHINA

SHIU YING HU[1]

A common medicinal plant of southern China has been called *Microcos paniculata* L. in Chinese botanical literature for half a century. Linnaeus proposed this name for a plant sent to Europe from Sri Lanka. To identify some Chinese collections, I compared them with Sri Lankan specimens. This revealed that plants growing in these widely separated regions belong to different species and thus necessitated a nomenclatural transfer. *Microcos nervosa* (Lour.) S. Y. Hu, comb. nov., is proposed.

A shrub or small tree common on the hillsides of southern China, locally called *bu-cha-ye,* has been used for home remedies by the Chinese people since time immemorial. Its medicinal use was first recorded in botanical literature by McClure and Hwang (1934). In this report they observed (p. 17): "An infusion of the leaves is administered internally to relieve indigestion. . .and as a cooling drink. . . ." They identified the plant as *Grewia microcos* L. (Tiliaceae), which is a synonym for *Microcos paniculata* L. During a study of special health-food products available in Chinese groceries in Boston (Hu, in prep.), I observed *bu-cha-ye* on the shelf for herb tea. The botanical identification of this product led to the discovery of a nomenclatural problem and to the necessity of transferring the specific epithet of *Fallopia nervosa* Lour. to the genus *Microcos* L.

The genus *Microcos* was first recorded from material sent to the Netherlands by a Dutch resident of Sri Lanka. In 1737 Johannes Burman described and illustrated a plant received from Sri Lanka called "kleine Cocos" and gave it a Greek name, *Microcos.* Linnaeus (1753), on the basis of Burman's illustration of the inflorescence, named the species *M. paniculata.* Chinese botanists have applied this epithet in their accounts of *bu-cha-ye.*

To identify the imported herb tea in Chinese stores, I carefully examined all Asiatic specimens labeled *Microcos paniculata* in the Harvard University Herbaria, including those from the woods of Sri Lanka, the forests of India (Bombay region), and the open hillsides of Bangladesh, northern Burma, Thailand, Laos, Vietnam, southern China (Yunnan, Guangdong, and Guangxi), and Hong Kong. Specimens from this wide geographic range, grown in varied ecological conditions, involve a complex of several species. The source material of the Chinese *bu-cha-ye* belongs to a species very different from *M. paniculata* L. of Sri Lanka. Recent collections from Sri Lanka, which match Burman's illustration in leaf shape, have leaves uniformly stellate-pubescent on the veins and veinlets

[1]Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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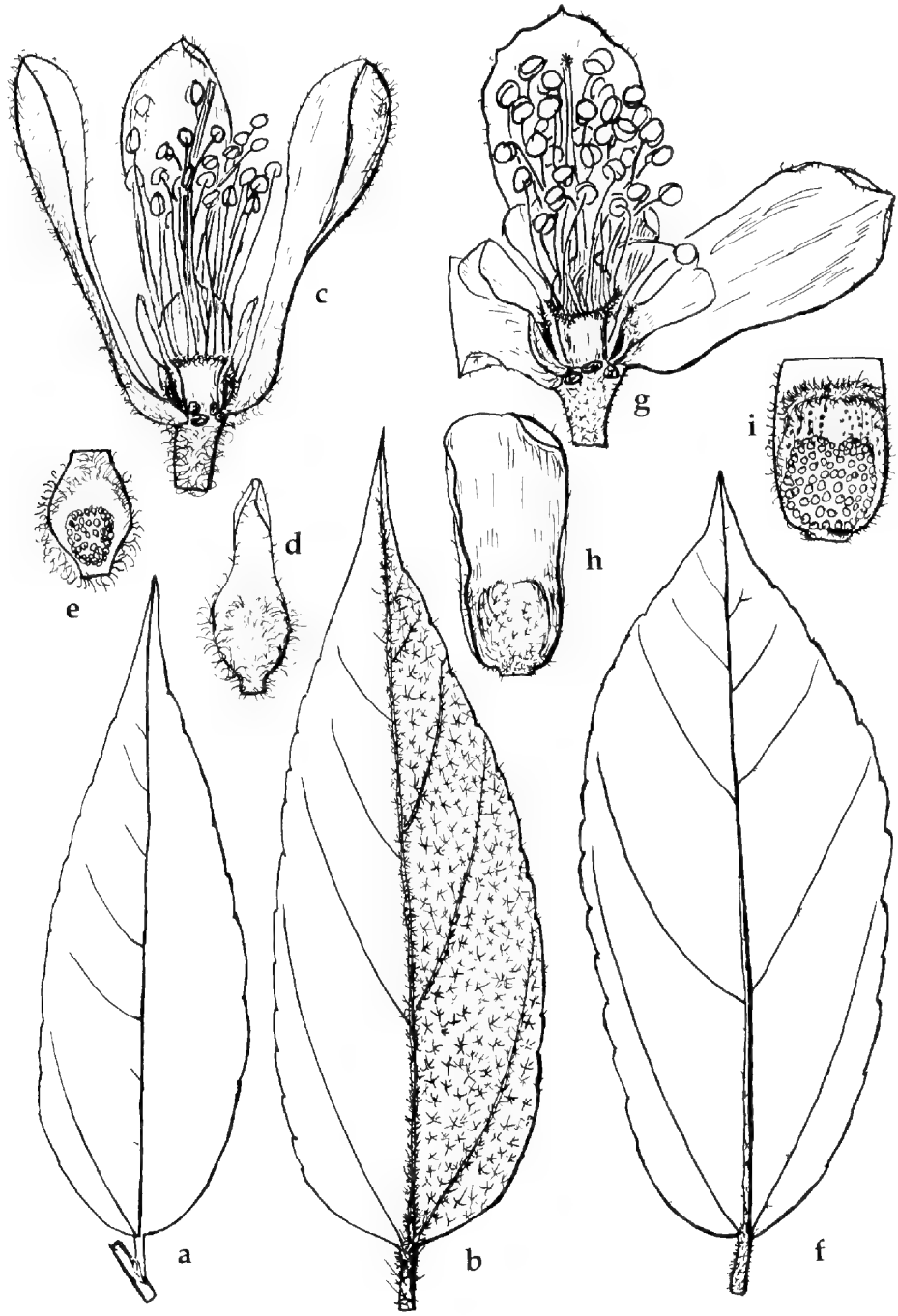

Comparison of leaf and flower characters of 2 species of *Microcos*. a–e, *M. paniculata*, from Sri Lanka (a redrawn from Burman, 1737, *t. 74*; b–e from *J. M. de Silva 41*, A): a, leaf, × 0.6; b, leaf showing portion of uniformly stellate-pubescent lower surface, × 0.6; c, flower from same specimen, 2 sepals and 2 petals removed, showing spathulate sepals, small petals much narrowed and long-villose at base, and stamens and pistil attached to columnar androgynophore with apical hairy annulus, × 6; d, petal, abaxial view, basal half densely long-villose, distal half narrowed, × 9; e, basal portion of same petal, adaxial

beneath, spathulate sepals, and ovate-lanceolate petals with an obovate basal gland on the adaxial surface (see FIGURE, a–e). Specimens from Guangzhou and Hong Kong, which match Loureiro's holotype in leaf shape and the imported herb-tea material of *bu-cha-ye* in texture, color, and trichomes, have leaves often broader above the middle, glabrous except occasionally on the midrib beneath, obovate-oblong sepals, and oblong petals with a large, oblong-orbicular basal gland on the adaxial surface (see FIGURE, f–i). The earliest specific epithet for the Chinese taxon, the source species of *bu-cha-ye,* is *Fallopia nervosa* Lour., which is here transferred to *Microcos.*

Microcos nervosa (Lour.) S. Y. Hu, comb. nov.

Fallopia nervosa Lour. Fl. Cochinch. 336. 1790. TYPE: Canton, *J. de Loureiro s.n.* (holotype, P).

Grewia microcos sensu McClure & Hwang, Lingnan Univ. Sci. Bull. **6:** 17. 1934, non L.

Microcos paniculata sensu How, Fl. Canton, 231. *fig. 110.* 1956, and many Chinese authors after How, non L.

Loureiro obtained the holotype of *Fallopia nervosa* from Canton in the early 1740's. He recorded a Chinese name, *hai pu ip* (provided by his informant but rarely used in China; see How, 1956). His observation of the characteristics of the species was given largely in the generic description. However, some of the terms he used do not have the same meaning as interpreted by current botanists. For example, he called the bracts subtending the ultimate three-flowered branches of the inflorescence "calyx," the sepals "petala," the petals "nectarium," and the androgynophore the "receptaculo." Nevertheless, for a foreign clergyman interested in Chinese plants, his observation was quite good, touching many details. His description of the species was very short, consisting of only 23 words. Since a clear and adequate description of the Chinese species has never been published, one is given below.[2]

Small trees or shrubs 2–8 m high; stems with strong bast fiber; 2-year-old growth glabrous, current year's growth subglabrous or softly covered with very short stellate hairs. Leaves with stipules subulate, coriaceous, striate, densely

[2]The description is based on specimens from Guangzhou (*C. O. Levine 223, 764, 1284,* all at A) and Hong Kong (*C. Wright s.n.,* 1853–1856 (GH), *S. Y. Hu 5229, 5405, 5486, 5525, 5974, 6092, 6672, 6850, 6999, 8065, 9679, 10441, 10634, 11216, 12258, 12949* (all at A), and *Y. Tsiang 621* (A)).

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view, showing obovate basal gland and yoke-shaped hairy zone in middle, × 9. f–i, *M. nervosa,* from southern China (from *S. Y. Hu 10441,* A): f, leaf that matches *bu-cha-ye* purchased from Chinese grocery in Boston, × 0.6; g, flower from same specimen, 2 sepals and 1 petal removed, showing broad oblong sepals, short, broad, retuse petals, stamens and pistil on androgynophore with toothed annulus, × 6; h, petal, abaxial view, showing sparse short, stellate hairs at base, distal half broad, apex retuse, × 9; i, basal portion of petal, adaxial view, showing large, oblong-discoid gland with notch at distal end, hairy ridge in middle, and glossy concave space between, × 9.

pubescent, deciduous; petiole 1 cm long, terete, softly pilose, the apical ⅓ slightly enlarged, glandular, with hairs straight or few stellate; lamina oblong, 9–19 by 4–8 cm, often broadest above middle, oblique-rotund and prominently 3-nerved at base, abruptly short-acuminate at apex with acumen broadly triangular and 5–10 mm long, inconspicuously crenulate-serrulate with each tooth terminated by gland, chartaceous, light yellow-green when fresh, olivaceous when dried, glabrous with pilose hairs on large nerves above, glabrous or occasionally with small stellate hairs on some large nerves and with veinlets prominently reticulate and glabrous beneath. Panicles terminal, sessile, many flowered, the lowest branch often subtended by normal leaves, the major bracts deeply trilobed, caducous, the ultimate branches cymose, 3-flowered. Flowers with pedicel 1–2 mm long, pilose; sepals 5, obovate-oblong, 6 by 3 mm, shortly ciliate; petals oblong, 3 by 1.5 mm, often revolute at margin, shortly pilose and with few soft stellate hairs; androgynophore columnar, glabrous, the terminal annulus 5-toothed, hairy; stamens ca. 40, the filaments in 5 fascicles opposite teeth of annulus, 2–3 mm long, sparsely pilose near base, the anthers globular-oblong; ovary spherical, 1 mm in diameter, 5-celled, glabrous, the style 3 mm long, glabrous, the stigma oblique-punctiform. Drupes globular-obovoid or spherical, 6–8 mm long, 5–7 mm in diameter; exocarp and mesocarp not separable, strongly fibrous, endocarp bony. Seeds oblong-ovoid, 4 mm long, 2 mm in diameter, oily.

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CARDAMINE DISSECTA, A NEW COMBINATION REPLACING DENTARIA MULTIFIDA (CRUCIFERAE)

IHSAN A. AL-SHEHBAZ[1]

The generic status of *Dentaria* is evaluated. A new combination based on *D. dissecta* is proposed in *Cardamine* to replace the later homonym resulting from the transfer of *D. multifida* to *Cardamine*.

The question of whether *Cardamine* L. and *Dentaria* L. should be treated as separate genera or be united has been addressed by many authors. The two genera were simultaneously published by Linnaeus (1753) and were first united by Crantz (1769), who adopted the epithet *Cardamine* for the combined genus. Therefore, this name has priority (see ICBN Article 57.2. 1983). Most North American authors recognize both *Cardamine* and *Dentaria,* while the majority of European systematists reduce the latter to a synonym of the former. For example, Schulz (1903, 1936) reduced *Dentaria* to four poorly defined sections of *Cardamine,* Hooker (1862) and Jones (1964) treated it as a subgenus of the latter, and Torrey and Gray (1838) recognized it as a genus even though they stated (p. 86) that it is "scarcely more than a section of *Cardamine.*"

Dentaria is said to have few cauline leaves, large flowers, petiolate cotyledons, and scaly, usually fleshy rhizomes, while *Cardamine* has several to many cauline leaves, smaller flowers, subsessile cotyledons, and nonscaly to few-scaled, usually nonfleshy rhizomes, or the plants are nonrhizomatous (Detling, 1936; Harriman, 1965). However, study of this complex on a worldwide basis reveals that these alleged differences break down easily. In my opinion, *Dentaria* should be united with *Cardamine* and, at least for the present, should not be recognized as a subgenus or a section. The fruits of *Cardamine* (including *Dentaria*) are unique in the Cruciferae because of their elastic dehiscence, the spiral coiling of their valves, and their narrowly winged replum.

All except one of the North American species previously placed in *Dentaria, D. multifida* Muhlenb. ex Elliott, have validly published, legitimate names in *Cardamine.* When Wood (1870) transferred this species to *Cardamine,* as *C. multifida* (Muhlenb. ex Elliott) Alph. Wood, the name became a later homonym of *C. multifida* Pursh. According to Detling (1939), the latter binomial is a synonym of the widely distributed North American *Descurainia pinnata* (Walter) Britton. Therefore, the specific epithet *multifida* cannot be used for the first species in *Cardamine.* A new combination based on *Dentaria dissecta* Leavenw. is proposed.

[1]Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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Cardamine dissecta (Leavenw.) Al-Shehbaz, comb. nov.; based on *Dentaria dissecta* Leavenw. Amer. J. Sci. Arts **7**: 62. 1824. TYPE: Alabama, Cherokee Country, [*Leavenworth s.n.*], not seen.

Dentaria multifida Muhlenb. Cat. Pl. Amer. Sept. 60. 1813, nomen nudum.

D. multifida Muhlenb. ex Elliott, Sketch Bot. **2**: 142. 1822. TYPE: mountains of Carolina, *Schweinitz s.n.* (CHARL), not seen. See pp. 73 and 77 in Harriman (1965) for typification.

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D. heterophylla Nutt. var. *multifida* (Muhlenb. ex Elliott) Ahles, J. Elisha Mitchell Sci. Soc. **80**: 172. 1964.

C. angustata O. E. Schulz var. *multifida* (Muhlenb. ex Elliott) Ahles, Man. Vasc. Fl. Carolinas, 505. 1968. Invalidly published because neither basionym nor its place of publication was cited.

D. furcata Small, Fl. S.E. U.S. 480, 1331. 1903. TYPE: near Tuscaloosa, Alabama, *Rev. Wm. Johnson s.n.* (holotype, NY!).

Although the types of *Dentaria multifida* and *D. dissecta* were neither seen nor located with certainty, it is evident that the two taxa are conspecific. Leavenworth's original diagnosis (1824, p. 62) ("glabra, erecta. Caule, foliis duobusmultifidis; laciniis linearibus: floribus racemosis") and comments ("leaves many parted; segments three fourths of an inch in length, perfectly linear") are very clearly indicative of *D. multifida*. The type of *D. dissecta* was not located in either NY or YU (Harriman, 1965; R. C. Rollins and R. W. Scott, pers. comm.), the two most likely herbaria where Leavenworth's specimens may be found.

Harriman (1965) reduced *Dentaria furcata* Small to a synonym of *D. laciniata*, but the type of the former has cauline leaves with glabrous, entire, linear segments, which are characteristic of *Cardamine dissecta*. Gleason (1952), on the other hand, considered *D. furcata* and *D. multifida* as conspecific, a view with which I agree. Small (1903) had stated in his original description of *D. furcata* that the three cauline leaves (as bracts) have entire, toothed, or incised margins and that the foliage is sometimes pubescent. These features are generally found in *C. concatenata* (Michaux) Schwarz and not in *C. dissecta*. It is very likely that Small (1903, 1933) had based his descriptions of *D. furcata* on specimens of both *C. concatenata* (*D. laciniata*) and *C. dissecta*.

Although *Cardamine dissecta* occupies a large area in eastern North America, it is not as widely distributed as its three relatives, *C. concatenata*, *C. diphylla* (Michaux) Alph. Wood (*Dentaria diphylla* Michaux), and *C. angustata* (*D. heterophylla*). The range of *C. dissecta* is divided into four discontinuous areas (counties in parentheses): central Alabama (Jefferson, Tuscaloosa, Walker); central North Carolina (Anson, Guilford, Montgomery, Randolph, Rowan); northwestern Georgia (Bartow, Dade, Floyd, Walker), Tennessee (Cheatham, Clay, Davidson, Franklin, Hamilton, Marion, Polk, Putnam, Warren, Williamson), and southern Kentucky (Adair, Edmonson, Muhlenberg, Wayne);

and southeastern Indiana (Jefferson), northeastern Kentucky (Greenup), and southern and central Ohio (Athens, Delaware, Hamilton, Morgan) (Easterly, 1964; Harriman, 1965; Montgomery, 1955, 1957; Radford *et al.,* 1968). As indicated by Harriman (1965), the gaps between the four areas are occupied by the other three species mentioned above, and it is not known why *C. dissecta* does not grow there. Previous records of *C. dissecta* (as var. *multifida*) from West Virginia (Millspaugh, 1913; Radford *et al.,* 1968) were probably based on misidentifications of *C. concatenata* (Strausbaugh & Core, 1978).

The rhizomal and cauline leaves of *Cardamine dissecta* are morphologically very similar, and both have subdivisions highly variable in number, length, and width. The leaves are always glabrous and are divided into three lobes, each of which is once or twice divided dichotomously or ternately into several to many filiform to linear segments (0.5–)1–7 cm long and 0.5–1(–4) mm wide. In a few cases, however, the three initial leaf lobes remain undivided. The leaf margin is almost always entire, and only very rarely does it have a few small teeth. Some plants with coarsely dentate and narrowly linear lobes are wrongly assigned to *C. dissecta*; they may well represent hybrid derivatives of this species with either *C. angustata* or *C. concatenata,* or they may be narrow-leaved forms of the last.

Cardamine dissecta is easily distinguished from its relatives previously placed in *Dentaria* by its glabrous leaves that are divided into filiform to narrowly linear segments. A few authors (e.g., James, 1883; Schulz, 1903; Radford *et al.,* 1968; Smith, 1982) have reduced *C. dissecta* (as *multifida*) to a variety or a subspecies of what is here called *C. angustata* or *C. concatenata.* However, the differences in seeds and seedlings (Harriman, 1965), as well as in leaf morphology and pubescence, clearly support the maintenance of *C. dissecta* as a distinct species.

ACKNOWLEDGMENTS

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CONTENTS OF VOLUME 69, NUMBER 1

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THE GENERA OF ARABIDEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

IHSAN A. AL-SHEHBAZ[3]

Tribe **Arabideae** A. P. de Candolle, Syst. Nat. **2**: 146, 161. 1821.

Annual, biennial, or perennial herbs [rarely subshrubs], glabrous or with simple, furcate, stellate, or dendritic [very rarely malpighiaceous or glandular] trichomes. Inflorescences ebracteate or bracteate, corymbose racemes or rarely panicles, usually elongated in fruit; flowers sometimes solitary on very long

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 120th in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

I am most grateful to Carroll Wood for his advice, continuous support, and help during the preparation of this paper, and especially for his critical review of the manuscript. I am also grateful to Norton G. Miller for reviewing the manuscript, to Richard Simmers, Jr., for specimens of *Cardamine*, and to the late Andrey I. Baranov for translating some of the Russian literature. I am variously indebted to Vernon Bates, William D. Countryman, George K. Rogers, Reed C. and Kathryn W. Rollins, and Randall W. Scott, as well as to Barbara Nimblett, who typed the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

The illustrations in FIGURE 3 (a, b, d–f) were drawn by the late Dorothy H. Marsh (DHM); those in FIGURES 1 (a–e, g–l) and 3 (h, i) by Karen Stoutsenberger (KS) under earlier grants. Carroll Wood prepared the material and supervised the illustrations. The remaining illustrations (FIGURES 1f, m, n; 2; 3c, g) were drawn by me (IAS). The fruits and seeds are from herbarium specimens in the Arnold Arboretum and the Gray Herbarium.

[2]For an account of the family and its tribes, see Al-Shehbaz, The tribes of the Cruciferae (Brassicaceae) in the Southeastern United States. Jour. Arnold Arb. **65**: 343–373. 1984.

[3]Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

peduncles arising from basal rosettes. Sepals erect to spreading, not saccate or strongly saccate at base. Stamens 6, often tetradynamous; filaments free [or very rarely connate], slender [or very rarely broadly winged and/or appendaged]. Fruits dehiscent, linear or sometimes lanceolate, oblong, ovate, or globose, flattened parallel to the septum or sometimes terete; valves glabrous or pubescent, with a prominent or obscure midnerve; septum complete or with a central perforation; styles long to obsolete; stigmas entire to prominently 2-lobed. Seeds several to numerous, uniseriately or biseriately arranged in each locule, mucilaginous or not when wet, winged to marginate or wingless; cotyledons accumbent or very rarely incumbent. (Including Cardamineae Dumort., Selenieae Torrey & A. Gray.) TYPE GENUS: *Arabis* L.

The Arabideae contain some 36 genera and about 615 species, 460 (75 percent) of which belong to three genera: the circumboreal *Arabis* (180 species), the cosmopolitan *Cardamine* L. (200), and *Rorippa* Scop. (80), which form the core of the tribe. Twelve genera are monotypic, and 12 others have two to four species each. About 15 genera of the Arabideae are endemic to central Asia and adjacent Bhutan, China, and Nepal; nine to North America and Mexico; and one each to the Caucasus, southwestern Asia, southern Europe, South America, South Africa, and New Zealand.

Nearly half of the genera included in the Arabideae by earlier authors (e.g., De Candolle (1821, 1824); Bentham & Hooker; Von Hayek) are now assigned to other tribes. Schulz defined the tribe on the basis of its open calyces with ascending or spreading sepals, its long, many-seeded fruits that are usually compressed parallel to the septum, and its embryos with accumbent cotyledons. He relied heavily on the orientation of sepals for the separation of the Arabideae from the Matthioleae O. E. Schulz and on the cotyledonary position for the separation of both of these from the Hesperideae Prantl. Because of the rigid adherence by some authors to these sets of characters, some reasonably well-defined genera were subdivided into several segregates, while other, closely related ones were placed in separate tribes. A case in point involves the genera *Christolea* Camb., *Ermania* Cham., and *Parrya* R. Br., which have been divided into 16 segregates placed in the three tribes above (Botschantzev, 1955, 1972). It is beyond the scope of this flora to evaluate these segregates or to assign them to tribes.

The limits of the Arabideae adopted here follow those of Schulz, except for the reduction of six genera to synonymy and the assignment of nine others, including *Selenia* Nutt. and *Armoracia* Gaertner, Meyer, & Scherb., to this tribe. Although Schulz placed *Selenia* in the Lunarieae O. E. Schulz and *Armoracia* in the Drabeae O. E. Schulz, it is evident that they are closely related respectively to *Leavenworthia* Torrey and *Rorippa*, genera that have been assigned to the Arabideae by many authors, including Schulz.

The Arabideae are represented in the southeastern United States by nine genera and 47 species, all but nine of which are indigenous. Six species and three varieties are endemic, and the ranges of four species and of most taxa of *Leavenworthia* are centered in the Southeast.

Chromosome numbers are known for some 260 species (about 42 percent

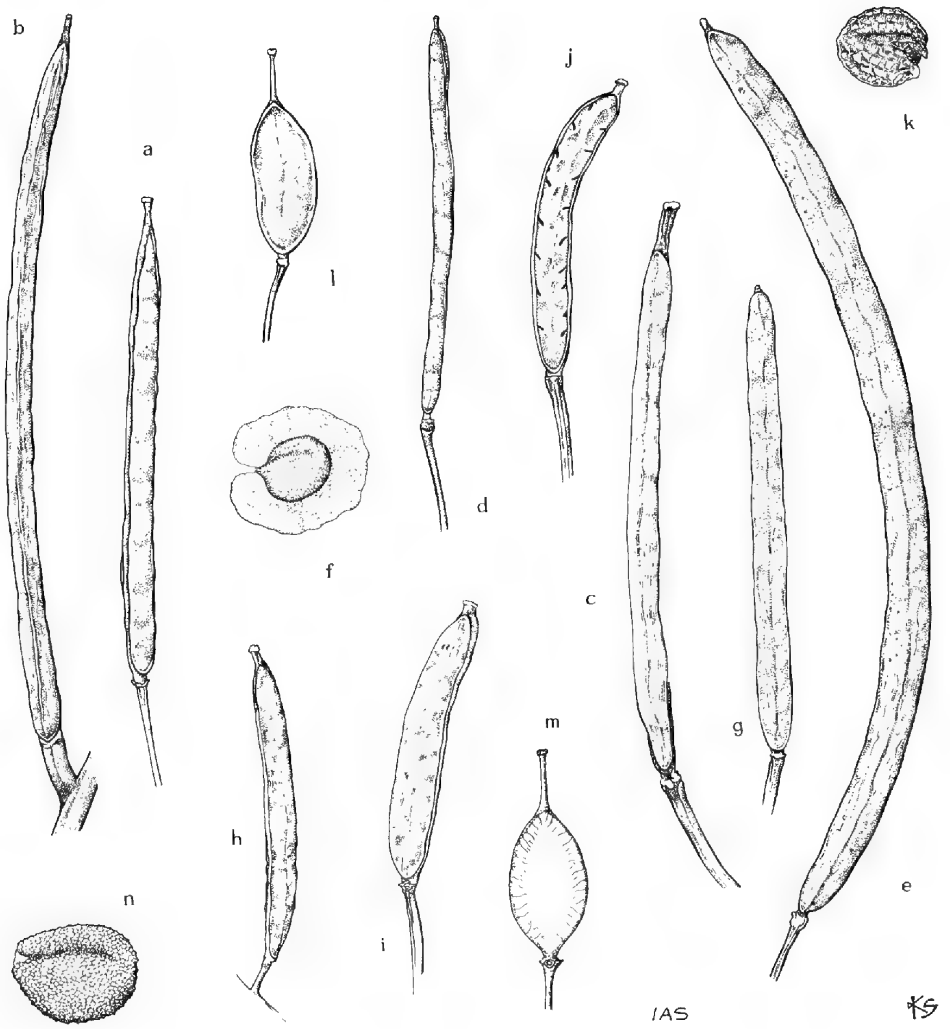

FIGURE 1. Fruits and seeds of Arabideae. a, *Cardamine rhomboidea,* fruit, × 3. b, *Barbarea verna,* fruit, × 2. c, *Iodanthus pinnatifidus,* fruit, × 3. d, *Arabis lyrata,* fruit, × 3. e, f, *A. canadensis:* e, fruit, × 2; f, seed, × 7. g, *Sibara virginica,* fruit, × 3. h, *Rorippa teres,* fruit, × 3. i–k, *R. Nasturtium-aquaticum:* i, fruit, × 3; j, replum and septum, × 3—note funicles of biseriately arranged seeds; k, seed, × 12. l–n, *Armoracia lacustris:* l, fruit, × 3; m, septum and replum, × 3—note central perforation and numerous funicles; n, seed, × 25.

of the tribe) and 18 genera. Nearly 66 percent of the species surveyed have chromosome numbers based on eight, and 20 percent are based on seven. About 52 percent of the species are diploid, while nearly 40 percent are exclusively polyploid (author's compilation). On the basis of the presence of $n = 12$ in a few species of *Rorippa* (as *Nasturtium* R. Br.), Mukherjee concluded that the base chromosome number for the Arabideae is six. His findings, however, are not supported by the data above.

The tribe has been poorly studied for chemical constituents. The seeds of only 40 species, about 30 of which belong to *Arabis,* have been analyzed for fatty acids. The scant data show certain patterns of potential chemotaxonomic value at the generic level. The glucosinolate profiles of about 30 species have been determined. The presence of high methylthioalkyl and methylsulfinylalkyl glucosinolates in *Arabis, Rorippa, Sibara* Greene, and *Drabopsis* C. Koch (monotypic, Southwest Asia) supports the disposition of these genera in the same tribe (MacLeod & MacLeod; Al-Shehbaz & Al-Shammary). However, more species of the first two and of other genera, particularly *Cardamine,* need to be surveyed before any fruitful conclusions can be reached. Several species of *Arabis, Cardamine,* and *Rorippa* have been analyzed for flavonoids, but the data are too fragmentary for meaningful generalizations.

Various members of the Arabideae have dispersal mechanisms similar to those of other tribes. The only exception is *Cardamine,* which has explosive fruits with elastic, spirally coiling valves. Schulz stated that *Loxostemon* J. D. Hooker & Thomson (four species; Bhutan, Sikkim, southern China) resembles *Cardamine* in fruit dehiscence but differs in its winged, spreading or reflexed staminal filaments (slender, wingless, and erect in the latter genus).

Although species of the Arabideae grow in diverse habitats, the majority occupy mesic environments. Several species of *Rorippa* and *Cardamine* are submersed or floating aquatics. The tribe has no xerophytic representatives. Many genera, such as *Anelsonia* Macbride & Payson (monotypic; Idaho, Nevada, California) and *Pegaeophyton* Hayek & Hand.-Mazz. (four species; Himalayas), which are scapigerous, cespitose perennials with thick rootstocks, are exclusively alpine.

Some of the economically important crops of the Arabideae are horseradish (*Armoracia rusticana* Gaertner, Meyer, & Scherb.) and watercress (*Rorippa Nasturtium-aquaticum* (L.) Hayek). Several species of *Arabis* (rockcress) and *Cardamine* (bittercress) are ornamentals, and many of the latter genus and of *Barbarea* R. Br. are widespread weeds.

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KEY TO THE GENERA OF ARABIDEAE IN THE SOUTHEASTERN UNITED STATES[5]

A. Early flowers solitary, borne on scapes 3–10 cm long originating from the center of a basal rosette; radicle straight or slightly curved, much shorter than the cotyledons. ..... 30. *Leavenworthia.*

A. All flowers borne in corymbose racemes, racemes, or panicles; radicle strongly curved, about as long as the incumbent or accumbent cotyledons.

B. Fruits at least 4 times longer (usually much more) than broad, linear or narrowly oblong.

C. Plants with stellate or variously furcate trichomes, sometimes also with unbranched ones. ..... 32. *Arabis.*

C. Plants glabrous or with unbranched trichomes only.

D. Fruits flattened parallel to septum; petals never yellow.

E. Valves of fruits dehiscing suddenly and elastically, coiling spirally or circinately; replums narrowly winged; seeds neither winged nor marginate; plants perennials with tubers or rhizomes, sometimes annuals. ..... 27. *Cardamine.*

E. Valves neither dehiscing elastically nor coiling; replums wingless; seeds winged, marginate, or wingless; plants (ours) biennials or annuals.

F. Cauline leaves entire or toothed; median nectar glands usually present. ..... 32. *Arabis.*

F. Cauline leaves pinnatisect; median nectar glands absent. ..... 33. *Sibara.*

D. Fruits terete or quadrangular, rarely slightly flattened; petals yellow, white, or lavender.

G. Valves of fruits with a prominent midvein; seeds uniseriately arranged in each locule.

H. Flowers yellow; inflorescences corymbose; cauline leaves auriculate to amplexicaul, not cuneate. ..... 28. *Barbarea.*

[5]The genera are numbered as in the treatment of the tribes of the Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986; and genera 20–26 (Alysseae) in *ibid.* **68:** 185–240. 1987.

Nasturtium, genus 34 in my key to the genera of the Cruciferae (Jour. Arnold Arb. **65:** 367. 1984), is united in this treatment with *Rorippa* (genus 35) for reasons given below.

H. Flowers white or lavender; inflorescences elongated racemes; cauline leaves cuneate. ..... 29. *Iodanthus.*

G. Valves nerveless or obscurely nerved; seeds biseriately arranged or, if uniseriate, the plants aquatic. ..... 35. *Rorippa.*

B. Fruits less than 3 times longer than broad, globose, elliptic, or broadly oblong.

I. Inflorescences bracteate throughout; seeds broadly winged; fruits usually compressed parallel to septum. ..... 31. *Selenia.*

I. Inflorescences ebracteate; seeds wingless; fruits somewhat inflated.

J. Flowers yellow; septum complete; plants annual or biennial, rarely perennial. ..... 35. *Rorippa.*

J. Flowers white; septum rudimentary or with a central perforation; plants perennial. ..... 36. *Armoracia.*

27. **Cardamine** Linnaeus, Sp. Pl. **2:** 654. 1753; Gen. Pl. ed. 5. 295. 1754.

Herbaceous annuals, biennials, or rhizomatous or tuberous perennials, glabrous or with unbranched trichomes only. Rhizomes (when present) fleshy or not, scaly or not, continuous or obscurely to conspicuously constricted or moniliform, sometimes readily separated into fusiform to ellipsoid segments, occasionally with clusters of small, stalked or sessile tubers. Stems erect to ascending to decumbent, sometimes rooting from the lower nodes. Basal or rhizomal leaves rarely forming distinct rosettes, petiolate, entire or ternately, palmately, or pinnately lobed or dissected, occasionally resembling compound leaves. Cauline leaves alternate or very rarely opposite or whorled, petiolate or sessile, rarely auriculate at base. Inflorescences bracteate or ebracteate corymbose racemes or panicles, usually greatly elongated in fruit. Sepals erect to spreading, oblong to ovate, often membranaceous at margin, the lateral pair saccate or not saccate at base. Petals white, lavender, rose, purple, or violet, never yellow, erect or spreading, obovate to spatulate, entire to emarginate, clawed or gradually narrowed to a clawlike base, sometimes absent. Lateral nectar glands usually well developed, horseshoe shaped or ringlike, surrounding or subtending the base of single stamens; median glands flat or toothlike, usually 1, rarely 2 or absent. Stamens 6, slightly to strongly tetradynamous, rarely 4; filaments free, erect or spreading, unappendaged; anthers ovate or oblong to linear, usually sagittate at base. Fruits dehiscent, linear to narrowly lanceolate, straight, smooth to torulose, flattened parallel to the septum or rarely subterete, gradually to abruptly narrowed to style; valves glabrous [or very rarely pubescent], dehiscing elastically from the base upward, often circinately or spirally coiled, not veined or sometimes the basal portion with an obscure midnerve; replum broad, persistent, always narrowly winged; septum hyaline, complete; styles long and often beaklike or short to obsolete; stigmas capitate, slightly 2-lobed. Seeds numerous to rarely few, compressed, oblong to ovate, smooth or rugose to reticulate or colliculate, uniseriately arranged in each locule, usually neither winged nor marginate, mucilaginous or nonmucilaginous when wet; cotyledons accumbent or very rarely incumbent, equal or unequal, sessile to petiolate. Base chromosome numbers 6, 7, 8, 10, 12. (Including *Dentaria* L.;[6]

[6]*Dentaria* and *Cardamine* were simultaneously described by Linnaeus (Sp. Pl. **2:** 653, 654, respectively. 1753). Crantz, who was the first to unite the two genera, adopted *Cardamine* for the combined genus, and consequently this name has priority (see ICBN Article 57.2. 1983).

Dracamine Nieuwl.; *Ghinia* Bubani, non Schreber; *Heterocarpus* Phil., non Wight; *Porphyrocodon* J. D. Hooker; *Pteroneurum* DC.) LECTOTYPE SPECIES: *C. pratensis* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 183. 1913. (Name derived from Greek *kardamon,* used by Dioscorides for some cresses.)—BITTERCRESS, CRINKLEROOT, PEPPERROOT, TOOTHWORT.

A natural and well-defined genus of at least 200 species, but Biswas's estimate of 330 species is evidently exaggerated. *Cardamine* is a cosmopolitan genus represented by indigenous species on all continents except Antarctica. It is poorly represented in the Southern Hemisphere, with only about 30 species in South America, ten in New Zealand and Australia, and three each in New Guinea and Africa. The South American species were reduced to only five by Sjöstedt, who adopted a very broad and rather loose species concept, but the actual number may well exceed 30. The center of greatest diversity is the Far East and the Himalayas, where about 70 representatives grow. The genus is also well developed in North and Central America (40 species) and Europe (25). About ten species are widely distributed in Eurasia and/or North America; only four are cosmopolitan weeds. Most taxa grow in wet habitats, alpine areas, and forests; some are aquatic, and none are xerophytes. The great majority are rhizomatous or tuberous perennials, and only about 15 percent of the species are annuals (author's compilation). *Cardamine* is represented in the southeastern United States by 13 indigenous and two naturalized species.

The sectional classification of *Cardamine* is controversial. Schulz (1903, 1936) recognized as many as 13 sections, six of which are monotypic. He overemphasized a few characters of the rhizome (such as shape, fleshiness, pubescence, and scaliness) in defining several of his sections. Careful evaluation of these and the other characters used reveals that Schulz's sections have artificial boundaries and often do not represent natural subdivisions of the genus.

Cardamine and *Dentaria* have been recognized as closely related genera by most North American botanists, who have treated them only for local floras and without critical evaluation of their limits on a worldwide basis. *Dentaria* has been said to differ from *Cardamine* in having larger flowers, fleshier and larger rhizomes, fewer, often palmately divided cauline leaves, and usually petiolate cotyledons (Detling, 1936). On the basis of careful examination of the whole complex, however, it is evident that these alleged differences are neither consistent nor reliable. The taxonomy of *Cardamine* cannot be improved by treating *Dentaria* as a genus on the basis of characters that hold only within a small portion of its geographic range. As indicated earlier (Al-Shehbaz, 1988), *Dentaria* should be united with *Cardamine* and does not have to be formally recognized. The combined genus has fruits with a marginate or narrowly winged replum and elastic dehiscence, accompanied by spiral coiling of the valves. These features, which are also found in the very closely related *Loxostemon,* have not been observed elsewhere in the Cruciferae.

Jones (1964) recognized two subgenera in *Cardamine*: subg. *Cardamine* (rhizomes on the surface of the ground, nonscaly or with only a few scales; cotyledons sessile or subsessile) and subg. *Dentaria* (L.) J. D. Hooker (rhizomes subterranean, scaly; cotyledons petiolate). The former includes all species of the genus except the approximately 17 of subg. *Dentaria.* Although some au-

thors recognize infrageneric subdivisions in *Cardamine,* I prefer not to do so pending a thorough systematic study of the entire genus.

Cardamine rhomboidea (Pers.) DC. (*Arabis rhomboidea* Pers., *A. bulbosa* Schreber ex Muhl. (nomen nudum), *C. bulbosa* (Schreber ex Muhl.) BSP., *C. bulbosa* f. *fontinalis* Palmer & Steyerm.), spring cress, $2n = 64, 80, 96, 112(?)$, is quite common in all of the Southeastern States. It grows in wet, low woodlands, floodplain forests, meadows and pastures, marshy areas, low pinelands, and creek bottoms, as well as along stream banks and moist roadsides. It is distributed from Quebec and New Hampshire south to central Florida, west to Texas, and north through Kansas, eastern South Dakota, Minnesota, and southeastern Manitoba. Forma *fontinalis,* known only from Missouri, is merely an aquatic variant that was said to differ from the rest of the species by its nontuberous roots and its broader leaves with a cordate base.

A very close relative of and often confused with the preceding, *Cardamine Douglassii* (Torrey) Britton (*Arabis Douglassii* Torrey, *Dentaria Douglassii* (Torrey) Greene, *A. rhomboidea* Pers. var. *purpurea* Torrey, *C. purpurea* (Torrey) Britton, *Thlaspi tuberosum* Nutt.), purple cress, pink spring cress, $2n = 64, 96, 144$, is distributed from Connecticut south through the Carolinas into Alabama, west to eastern Missouri, north to Wisconsin, and east through Michigan, Ontario, and New York. It is uncommon in the Southeastern States but is known from North Carolina (Durham, Harnett, Northampton, Orange, and Wake counties), South Carolina (Newberry County), Alabama (Clarke, Colbert, Jackson, Lawrence, Madison, Marengo, and Sumter counties), and Tennessee (Cheatham, Davidson, Knox, and Montgomery counties). It grows in calcareous spring-fed places, rich mesic woods and bottomlands, and floodplain woodlands. In general, it is found in areas drier than those occupied by *C. rhomboidea.* Schulz (1903) treated these species as one, with several varieties and forms. Subsequent authors, however, have recognized two species without any infraspecific taxa.

Cardamine Douglassii is distinguished from *C. rhomboidea* by its pink to dark purple (very rarely white) flowers and its trichomes (0.2–)0.3–0.6(–0.8) mm long. *Cardamine rhomboidea* has white flowers and trichomes 0.02–0.1 (–0.2) mm long. It is also taller (15–45 instead of 7–22 cm) and generally flowers two to four weeks after *C. Douglassii.* Both are easily separated from the other eastern North American species of *Cardamine* by their tuberous bases, erect stems, and simple cauline leaves.

Cardamine rotundifolia Michx. (*Dentaria rotundifolia* (Michx.) Greene), mountain watercress, is a mat-forming, stoloniferous, glabrous perennial with erect to decumbent stems that root from the lower nodes; simple, petiolate, broadly ovate to suborbicular leaves that have an entire to repand margin and an obtuse to cordate base; spreading floral parts and distinct fruiting styles to 5 mm long; and divaricately ascending to widely spreading pedicels to 2.5 cm long. It grows along stream sides and in swamps, low woodlands, and spring-fed places in New York south through Pennsylvania to North Carolina (Ashe, Stokes, and Watauga counties) and Georgia (Walker County), west to Tennessee (Carter and Scott counties), and north to Ohio. It can be confused with *C. rhomboidea,* from which it differs in being totally glabrous and in its nontu-

berous base and spreading floral parts. *Cardamine rotundifolia* is protogynous (pers. obs.) and may be self-incompatible, as is suggested by the lack of fruits among some 40 specimens at the Gray Herbarium.

Cardamine micranthera Rollins, a narrow endemic of North Carolina (Forsyth and Stokes counties), grows in moist woods, seepages, and crevices of outcrops, on moist sandbars, and along stream banks. It is most closely related to *C. rotundifolia,* which it resembles in having spreading floral parts and divaricate fruiting pedicels, but from which it differs in having orbicular anthers ca. 0.5 mm long, narrower petals 1.2–2 mm wide, erect stems without proliferating branches, and smaller fruits 0.8–1.2 cm long. *Cardamine rotundifolia,* on the other hand, has narrowly oblong anthers 1.2–1.6 mm long, lingulate petals 2.5–3.5 mm wide, decumbent stems with proliferating branches, and fruits (1.2–)1.5–2 cm long.

Both *Cardamine flagellifera* O. E. Schulz (*C. Hugeri* Small) and *C. clematitis* Shuttlw. ex A. Gray are endemic to some of the Southeastern States and the adjacent Virginias. A few authors (e.g., Beal, Radford *et al.*) have treated the former (as *C. flagellaris*) as a synonym of the latter, although Schulz (1903) placed them in widely separated sections. In my opinion, the taxa are well-defined, closely related species. They grow in wet woods and spring-fed places, on shady slopes, and along stream banks. *Cardamine clematitis* occurs in Alabama, the Blue Ridge area of Georgia and North Carolina, Tennessee (Blount, Carter, Johnson, Pickett, and Sevier counties), and southwestern Virginia (Grayson, Pulaski, Russell, Smyth, and Washington counties). The range of *C. flagellifera* includes Georgia (Fannin, Rabun, Towns, and White counties), South Carolina (Hog Back Mtn.), North Carolina (Alleghany, Clay, Graham, and Polk counties), Tennessee (Blount, Knox, Polk, and Sevier counties), and West Virginia (Fayette County). Both *C. clematitis* and *C. flagellifera* are rhizomatous perennials with erect stems, reniform or cordate basal leaves, and pinnate cauline leaves with a large, cordate terminal lobe and one or rarely two pairs of smaller, petiolate lateral lobes. *Cardamine flagellifera* is easily distinguished by its stems pubescent on the lower part, its nonauriculate petioles, and its mucronate-crenate leaf lobes. *Cardamine clematitis* has glabrous stems, lanceolate auricles, and entire or obscurely three-angled leaf lobes (FIGURE 2h, i).

Cardamine pensylvanica Muhl. ex Willd. (*C. flexuosa* With. subsp. *pensylvanica* (Muhl. ex Willd.) O. E. Schulz, *C. hirsuta* L. var. *pensylvanica* (Muhl. ex Willd.) Graff, *C. pensylvanica* var. *Brittoniana* Farw.), bittercress, $2n = 32$, 64, is a North American plant widely distributed from Alaska south through British Columbia into northern California, east through Texas to Florida, and north to Newfoundland. It is fairly common throughout the southeastern United States, where it is an aquatic plant of streams, marshes, swamps, ditches, and springs, or a mesophyte of wet grounds along stream banks, in meadows, woodlands, and cultivated fields, and on floodplains. *Cardamine pensylvanica* is quite variable in leaf morphology, particularly in the thickness, width, and number of lateral lobes. In drier habitats it produces many narrow, somewhat fleshy leaf segments, while if submersed or growing in the shade it produces fewer broad, membranaceous ones. Varietas *Brittoniana* is based on aberrant

plants with simple upper cauline leaves. The species is distinguished from the other southeastern members of *Cardamine* that have pinnate leaves by its nonciliate petioles, hispid lower stems (glabrous when submersed), lateral lobes with decurrent and oblique bases, somewhat beaked fruits with styles to 2 mm long, and oblong seeds 1–1.5 mm long.

Although several North American authors have recognized *Cardamine parviflora* L. var. *arenicola* (Britton) O. E. Schulz (*C. arenicola* Britton; *C. virginica* Michx., non L.), $2n = 16$, ca. 48, as a distinct species, many others consider it to be a subordinate of the European *C. parviflora*. According to Fernald (1927), var. *arenicola* differs from var. *parviflora* in having basal leaves with dentate, obovate to suborbicular lobes, cauline leaves with fewer (two to six pairs) lobes, slightly more (26–46) ovules, longer petals (2.5–3.5 mm) and fruits (1.5–3 cm), and shorter (4–8 mm) fruiting pedicels. In var. *parviflora* the basal leaves have entire, oblong lobes, the cauline leaves have five to eight pairs of lobes, there are 22–36 ovules, and the petals, fruiting pedicels, and fruits are 2–2.5 mm, 7–10 mm, and 1–2 cm long, respectively.

Varietas *arenicola* usually grows on sandy soil in habitats that are wet for short periods in winter or spring. It occupies low areas in woods, fallow or cultivated fields, pastures, meadows, floodplains, and clearings and on exposed ledges, as well as drier sites along streams, ditches, and roadsides. It is distributed from British Columbia and Oregon east to Newfoundland, south to Florida, and west to Texas and is widespread throughout the Southeastern States. Rollins (1966) reported $n = 22–24$ (indicating hexaploidy) for var. *arenicola* from plants collected in Morgan County, Alabama. Other counts for this variety from North America and for var. *parviflora* from the Soviet Union and Taiwan are diploid ($2n = 16$). More counts are needed to clarify the distribution of the hexaploid plants in the Southeast.

Cardamine hirsuta L., hoary bittercress, $2n = 16$, is a cosmopolitan Eurasian weed that is sporadic in North America and widespread in all of the Southeastern States. It grows in fields, lawns, waste areas, disturbed sites, and clearings, as well as along roadsides, ditches, and stream banks. It is very closely related to *C. flexuosa* With. (*C. hirsuta* var. *flexuosa* (With.) Forbes & Hemsley, *C. debilis* D. Don), $2n = 32$. The latter is another Eurasian annual that is sporadic in eastern North America and has been reported from Florida (Small, 1933; as *C. debilis*) and North Carolina (Radford *et al.*). They differ from the other annual or biennial species of *Cardamine* with pinnate leaves in having ciliate petioles and lowermost leaves often with suborbicular lobes.

According to Ellis & Jones (1969), *Cardamine flexuosa* is an allopolyploid derived from *C. hirsuta* and *C. impatiens* L. ($2n = 16$). The last, a European weed sporadically naturalized from New Hampshire west to Michigan and south to West Virginia (Rollins, 1981), is easily distinguished by its cauline leaves with sagittate-auriculate bases and five to nine pairs of ciliate, lanceolate to ovate, coarsely dentate to incised lateral lobes. *Cardamine hirsuta* differs from *C. flexuosa* in its usually glabrous (instead of densely pubescent) stems, its fewer (two to four vs. four to ten) cauline leaves, its chromosome number (see above), and its usually four (instead of six) stamens. The differences in pubescence and stamen number, however, are not absolute. Jaspars-Schrader

has demonstrated that in *C. hirsuta* about 89 percent of the stems are glabrous or nearly so and 11 percent are densely pubescent, while in *C. flexuosa* 87 percent of the stems are densely pubescent and 13 percent are sparsely so. Furthermore, he indicated that 80 percent of the flowers of *C. hirsuta* have four stamens, 18 percent have five, and two percent have six, while 97 percent of those of *C. flexuosa* have six stamens and three percent have five. A combination of six stamens and densely pubescent stems would easily distinguish *C. flexuosa* from *C. hirsuta.*

The occurrence of *Cardamine Longii* Fern. in North Carolina has been established only recently (Sutter *et al.*). It is a rare plant of tidal estuaries, mud flats, and sandy or gravelly fresh tidal shores of rivers along the coasts of Maine and Massachusetts south to Chesapeake Bay, Maryland. It is easily distinguished from all other species of *Cardamine* by its apetalous flowers, reniform to suborbicular or oblong leaves with the base obtuse to cordate, lanceolate to linear fruits 5–12(–18) mm long, and fruiting pedicels 0.5–1.5(–5) mm long (FIGURE 2g).

Several authors (e.g., Small (in family references), Patman, Rickett) have recognized *Cardamine curvisiliqua* Shuttlw. ex Chapman as a member of this genus endemic to Florida. As shown below, however, it is a species of *Rorippa.*

The four remaining species of *Cardamine* in the southeastern United States were previously placed in *Dentaria.* They all flower during the spring and usually grow in nonacidic, usually calcareous soils of rocky banks, wooded bottoms, moist rich woods, shaded slopes, and meadows, as well as along stream banks in woods. *Cardamine diphylla* (Michx.) A. Wood (*Dentaria diphylla* Michx.; *D. bifolia* Stokes; *D. incisa* Small, non Eames), crinkleroot, pepperroot, toothwort, is easily distinguished by its long, nonconstricted, conspicuously scaly rhizomes, its two opposite or sometimes approximately alternate, three-foliolate cauline leaves with subappressed marginal trichomes to 0.1 mm long, and its broadly ovate terminal leaflet 7–10 cm long and 2.5–5 cm wide. It is distributed from Minnesota east through Michigan, southern Ontario, Quebec, and Nova Scotia, south to western North Carolina, South Carolina (Pickens County), northern Georgia, and northern Alabama, and north through Tennessee to Wisconsin. It is very rare and possibly introduced in Arkansas (Yell County) and Missouri (Chariton County). *Cardamine diphylla* has rarely been found to produce fully developed fruits. As was suggested by Harriman (1965), it is difficult to interpret how the species could attain such a wide distribution without the regular production of seeds. He suggested that the failure to produce seeds may be caused by both clonal reproduction and self-incompatibility. The species is weakly protogynous (pers. obs.).

Cardamine concatenata (Michx.) Schwarz (*Dentaria concatenata* Michx.; *D. laciniata* Muhl. ex Willd.; *C. laciniata* (Muhl. ex Willd.) A. Wood (1870), non Steudel (1840), non F. Mueller (1855); *D. laciniata* vars. *alterna* Farw., *coalescens* Fern., *integra* (O. E. Schulz) Fern., *lasiocarpa* O. E. Schulz, *latifolia* Farw., *opposita* Farw.; *D. laciniata* f. *albiflora* Louis-Marie, f. *hexifolia* Wolden; *D. anomala* Eames, *pro parte*), pepperroot, is distributed in all the states east of the 95th meridian. It is uncommon in the eastern parts of Texas, Oklahoma, Kansas, and Nebraska and is sporadic in all of the Southeastern States except

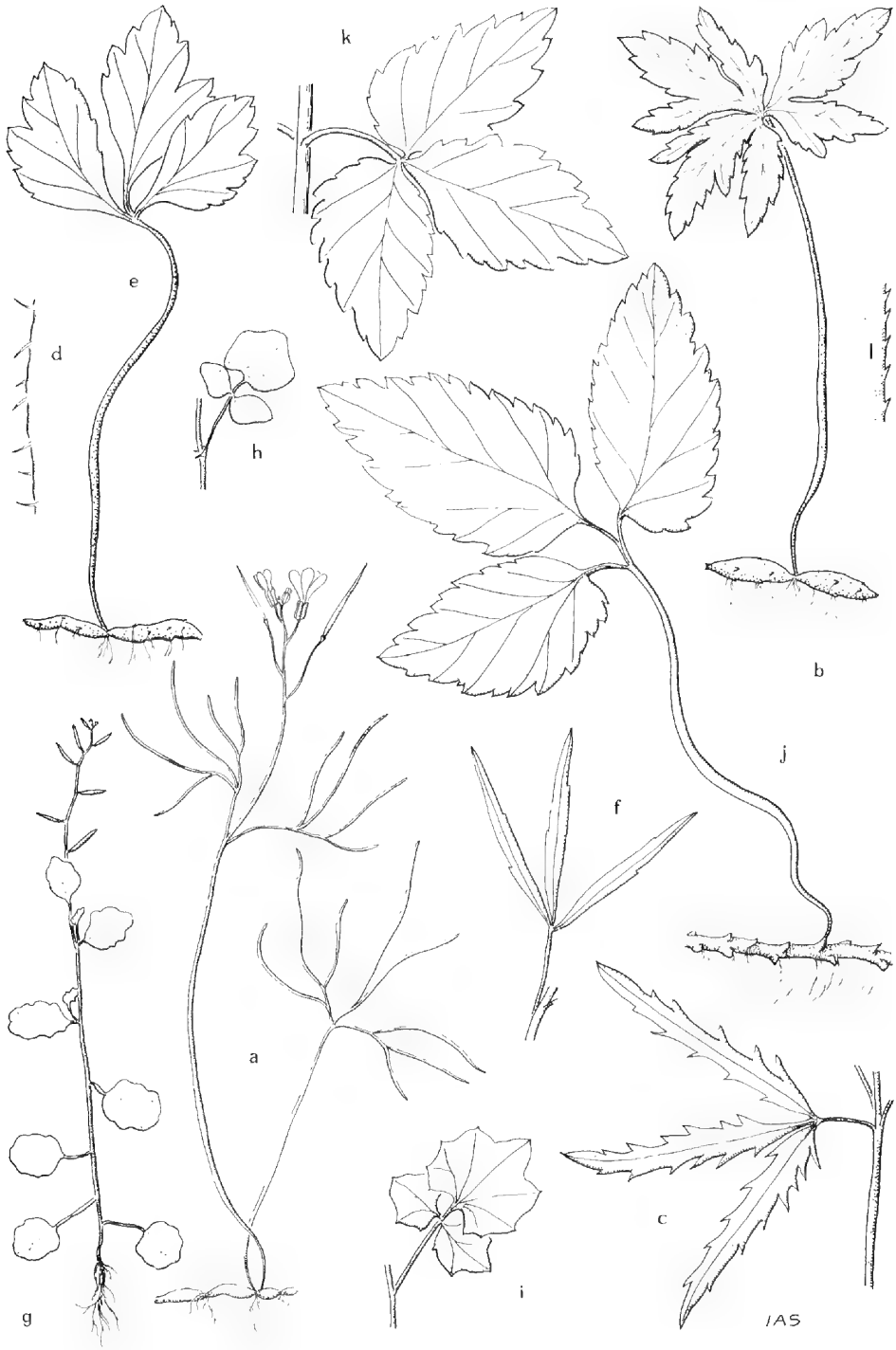

FIGURE 2. **Cardamine.** a, *C. dissecta,* plant, × ½. b–d, *C. concatenata:* b, rhizome and rhizomal leaf, × ½; c, cauline leaf, × ½; d, trichomes of leaf margin, × 15. e, f, *C. angustata:* e, rhizome and rhizomal leaf, × ½; f, cauline leaf, × ½. g, *C. Longii,* plant,

Arkansas, Tennessee, and North Carolina, where it is abundant. In Canada it is restricted to southeastern Ontario and adjacent southern Quebec. *Cardamine concatenata* is easily distinguished by its moniliform rhizomes readily separable into fusiform, fleshy segments, its three (rarely two or more than three) approximate, three-foliolate, sharply toothed to incised (rarely subentire) cauline leaves, its usually hirsute inflorescence rachis, and its nonappressed, leaf-margin trichomes 0.2–0.3 mm long. All infraspecific taxa previously recognized in *Cardamine concatenata* have no geographic continuity, and all are based on minor differences that can be encountered within any sizeable population. The species is highly variable in the number and arrangement of its cauline leaves and in the width and margin of its leaflets.

Cardamine angustata O. E. Schulz (*Dentaria heterophylla* Nutt.; *C. heterophylla* (Nutt.) A. Wood (1870), non Host (1797), Lapeyr (1813), Bory (1820), Hooker (1835), (Forster) O. E. Schulz (1903), Cheo & Fang (1980); *C. angustata* var. *ouachitana* E. B. Smith) is distributed from Indiana south to northeastern Mississippi, east to South Carolina, and north to New Jersey. It is rare in South Carolina (Darlington and McCormick counties), Mississippi (Tishomingo County), and Arkansas (Howard, Montgomery, Polk, Pulaski counties) and has not yet been found in either Florida or Louisiana. Varietas *ouachitana* is said to differ from var. *angustata* in having glabrous instead of pubescent leaf margins (Smith, 1982). However, Harriman (1965) observed both glabrous and variously pubescent leaves in *C. angustata* (as *D. heterophylla*). Because of the continuous variation in the density of leaf-margin trichomes, var. *ouachitana* does not merit recognition. *Cardamine angustata* is recognized by its constricted rhizomes that are readily separable into segments, its rhizomal leaves that are very different morphologically and much broader than the cauline ones, and its leaf trichomes to 0.1 mm long (FIGURE 2e, f).

The final species is *Cardamine dissecta* (Leavenw.) Al-Shehbaz (*Dentaria dissecta* Leavenw.; *D. multifida* Muhl. ex Ell.; *C. multifida* (Muhl. ex Ell.) A. Wood, non Pursh; *C. laciniata* var. *multifida* (Muhl. ex Ell.) J. F. James; *D. laciniata* var. *multifida* (Muhl. ex Ell.) Watson & Coulter; *D. heterophylla* var. *multifida* (Muhl. ex Ell.) Ahles; *D. furcata* Small). It is distributed in Ohio, Indiana, Kentucky, Tennessee, North Carolina, Georgia, and Alabama (see Al-Shehbaz (1988) for further details). It can be recognized easily by its completely glabrous parts, its similar rhizomal and cauline leaves that are finely dissected into filiform to narrowly linear segments, and its moniliform rhizomes that readily separate into segments (FIGURE 2a). Harriman (1965) indicated that *C. angustata, C. concatenata,* and *C. dissecta* (as dentarias) are all self-compatible and have protogynous flowers with extrorse median stamens.

The four eastern North American "dentarias" have highly specialized cotyledons and seedlings. Both *Cardamine diphylla* and *C. concatenata,* as well as their putative hybrid *C.* ×*maxima* (Nutt.) A. Wood, have incumbent cot-

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× ½. h, *C. clematitis,* cauline leaf, × ½. i, *C. flagellifera,* cauline leaf, × ½. j–l, *C. diphylla:* j, rhizome and rhizomal leaf, × ½; k, cauline leaf, × ½; l, trichomes of leaf margin, × 30.

yledons strongly unequal in size. The larger cotyledon partially to completely enfolds the smaller one. When the seed germinates, the larger cotyledon emerges from the ground while the smaller one remains hypogeal within the seed coat (Harriman, 1965). In *C. angustata* and *C. dissecta* the cotyledons are accumbent, subequal, and similar to each other in shape. Seed germination in these two species is hypogeal, as is that of the European *C. pinnata* (Lam.) R. Br. (reported by Schulz, 1903). Hypogeal germination in the Cruciferae is apparently restricted to only a few species of *Cardamine*. In all these North American species the epicotyl enlarges in size and develops into a small rhizome that produces adventitious roots during the degeneration of the primary root.

Cardamine differs from the related *Rorippa* in having flat, elastically dehisced, spirally coiled valves, a narrowly winged replum, and uniseriately arranged seeds. *Rorippa* has convex, neither elastically dehisced nor spirally coiled valves, a wingless replum, and usually biseriately arranged seeds. Many species of *Rorippa* have yellow flowers and/or globose, oval to oblong fruits, neither of which is found in any species of *Cardamine*. *Loxostemon* has fruits similar to those of *Cardamine* but differs in having broadly winged filaments.

The weedy species of *Cardamine* are often autogamous annuals with small flowers and reduced petals. Self-incompatibility is widespread in the genus and has been studied in some detail in *C. pratensis* (Bateman). Protogyny occurs in many species, including *C. flagellifera* and *C. rotundifolia* (pers. obs.), as well as *C. rhomboidea* and *C. Douglassii* (Hart & Eshbaugh). Species of the *C. pratensis* complex are viviparous, capable under moist conditions of producing plantlets on the upper surface of the leaf lobes. The plantlets are derived from adventitious buds that originate exogenously from the hypodermis at the branching of the main veins. *Cardamine bulbifera* (L.) Crantz reproduces primarily by bulbils that are formed in the axils of the upper cauline leaves. The South American *C. chenopodiifolia* Pers. produces both normal flowers on terminal inflorescences and cleistogamous, subterranean, solitary flowers on peduncles that originate from the base of the plant. The latter flowers are apetalous and have a closed calyx, a reduced number of ovules and stamens, and a smaller amount of pollen. They produce indehiscent, one- to three-seeded fruits, while the aerial flowers form dehiscent, many-seeded ones.

Montgomery (1955) reported that the embryo sacs of some species of *Cardamine* (as *Dentaria diphylla, D. laciniata,* and *D. maxima* Nutt.) abort and die shortly after reaching the eight-celled stage. He concluded that these taxa form a sexually sterile polyploid series, members of which reproduce almost exclusively by rhizomes. Braun, however, discovering that *C. concatenata* (as *D. laciniata*) produces viable seeds in Ohio, questioned Montgomery's conclusion about the predominance of apomixis in this complex. Harriman (1965) reached a conclusion similar to Braun's and stated that *C. angustata, C. concatenata, C. diphylla,* and *C. dissecta* (as dentarias) are all sexual when seeds are produced. Spooner demonstrated that both megagametogenesis and megasporogenesis are normal in *C. concatenata* and concluded that the species is sexual. He suggested that sterility of some of the eastern North American dentarias has probably resulted from unbalanced genome combinations in

hybrid populations or, alternatively, from the clonal growth of self-incompatible plants.

Chromosome numbers have been reported for 85 species, 87 percent of which are based on $x = 8$ (author's compilation). About 62 percent of the species are polyploid, and two, *Cardamine concatenata* and *C. diphylla* (both with $2n$ up to 256), have the highest known chromosome numbers in the Cruciferae. The lowest number in the genus ($2n = 12$) has been reported for the Caucasian *C. Seidlitziana* Albov (Goldblatt, 1984). It is evident that polyploidy has played a significant role in the evolution of *Cardamine*.

The eastern North American dentarias are probably the most cytologically variable of any species of Cruciferae. Harriman (1965) discovered that widely divergent chromosome numbers are found in plants of the same population, as well as within single root tips. In a population of *Cardamine diphylla* from Marion County, Tennessee, he observed $2n = 74$–83, 91–93, 96, 97, 100, 108, 113, 115, 130, 133, 134, 147, 148, 150, 151, 157–160, 167, 169, 171–250 (continuous series except 15 unobserved counts), 253, and 256. He also found $2n = 151$, 171, 173, 195, 196, 205, 207, 209–211, 224, and 247 in the same root tip. Harriman concluded that no fruitful generalizations can be made from root-tip chromosome counts of these dentarias and indicated that his attempts to study meiotic material were complicated by multivalent associations, lagging univalents, micronuclei, and high numbers and small sizes of chromosomes.

The *Cardamine pratensis* complex was thoroughly studied by Lövkvist (1956), who observed an exceptional range of chromosome levels from diploid ($2n = 16$) to dodecaploid ($2n = 96$), with many intermediate euploids and aneuploids. The "oscillation" in chromosome numbers depends on the occurrence of two basic numbers ($x = 7$, 8) and on the existence of hybrid swarms originating from parents with different numbers. Several authors have reported a correlation between water content of the soil and chromosome level of the plant. *Cardamine pratensis* sensu stricto ($2n < 56$) occupies drier habitats, while *C. palustris* (Wimmer & Grab.) Peterm. ($2n \geq 56$) is restricted to areas with high moisture content (e.g., bogs, marshes, springs, swamps). These taxa have been recognized either as distinct species (Jones, 1964; Lövkvist, 1956) or as subspecies or varieties of *C. pratensis* (Berg & Segal; Dale & Elkington; Fernald, 1950). Both species occur in eastern North America, but neither has been found in the Southeastern States.

Putative natural hybrids between *Cardamine rhomboidea* and *C. Douglassii* have been found. The species are easy to cross experimentally and are not genetically isolated. A reduction in hybrid fertility occurs when different chromosomal races of the two species are crossed (Hart & Eshbaugh). There is no effective isolating mechanism between the species, and although they generally flower two to four weeks apart, some overlapping occurs. The hybrids have flowering times intermediate between those of the parents.

Despite the lack of experimental evidence, many authors have suggested that natural interspecific hybridization must have occurred among the eastern North American dentarias. *Cardamine* ×*maxima* is intermediate between *C. concatenata* and *C. diphylla* in nearly all morphological characters, particularly

those of the rhizomes and cauline leaves, as well as in its glucosinolate profiles (see below). It is a highly variable hybrid complex treated by Harriman (1965) as a distinct species. *Cardamine* ×*maxima* is almost always completely sterile and has never been found to produce seedlings. Fernald (1950) reported it from Tennessee, but Harriman (1965) did not cite any collections from that state. The latter author also recognized *Dentaria incisifolia* Eames ex Britton (*D. incisa* Eames, non Small), which is known from only one "population" in Fairfield County, Connecticut, as a distinct species said to differ from the other dentarias by the sessile "leaflets" of its cauline leaves. It is a completely sterile plant that can easily be accommodated in the extremely heteromorphic hybrid complex *C.* ×*maxima*. A putative hybrid swarm involving *C. angustata* and *C. dissecta* was found near the banks of Big Marrowbone Creek in Cheatham County, Tennessee (Harriman, 1965).

Jones (1975) listed several interspecific hybrids between various pairs of *Cardamine amara* L., *C. flexuosa, C. hirsuta,* and *C. pratensis.* Most of these hybrids have been recognized in Europe for many decades. Some (e.g., *C. flexuosa* × *C. pratensis* (*C.* ×*Haussknechtiana* O. E. Schulz)) are sterile perennials that reproduce only vegetatively. That this hybrid probably originated a few times independently is suggested by its occurrence in remotely separated areas and its failure to produce viable seeds.

The chemistry of *Cardamine* has not been studied adequately, and only a few species have been surveyed for fatty acids, flavonoids, and glucosinolates. Hart & Eshbaugh found 18 flavonoids in *C. rhomboidea* and *C. Douglassii.* The former is differentiated chemically into three races, of which one is indistinguishable from *C. Douglassii* in flavonoid profile. Of the six species analyzed for seed fatty acids, *C. bellidifolia* L. and *C. pratensis* have the highest content (36 percent) of linoleic acid known for any species of Cruciferae, while *C. graeca* L. contained the highest proportion (54 percent) of nervonic acid so far reported in any seed oil (Jart). The distribution of fatty acids may be chemotaxonomically useful in *Cardamine.*

About ten species of *Cardamine* have been surveyed for glucosinolates. Fresh parts of the western North American *C. cordifolia* A. Gray contain as many as nine compounds, of which one (2-butylglucosinolate) is the major constituent. The species is quite variable in its isothiocyanate-yielding glucosinolates, particularly in relation to plant part, season, and habitat (Rodman & Chew; Rodman & Louda, 1984, 1985; Louda & Rodman, 1983a, 1983b). Feeny & Rosenberry found similar variation in three dentarias and showed that the glucosinolate profile of *C.* ×*maxima* is intermediate between those of *C. diphylla* and of *C. concatenata.* Their findings support the hybrid origin of *C.* ×*maxima* from the last two species. All three contained various amounts of isopropyl, 2-butyl, and 2-methylbutyl glucosinolates, but *C. concatenata* had none or only traces of the last two compounds.

Despite the explosive dehiscence of fruits in *Cardamine,* seed dispersal may not exceed five feet (Kimata). Seeds of some of the weedy species (e.g., *C. hirsuta*) are mucilaginous when wet and can be transported by adhering to animals and equipment. The subterranean fruits of *C. chenopodiifolia* are not

dispersed, and their seeds are buried effectively in the vicinity of the parent plant.

The fleshy underground parts of several species of *Cardamine* are eaten like radishes or used as a substitute for horseradish when grated and mixed with vinegar (Fernald & Kinsey). The young green parts of many species (e.g., *C. pensylvanica* and *C. rotundifolia*) are said to be an excellent substitute for watercress. Certain species are considered to have medicinal properties and are used in Asia as stimulants, diuretics, diaphoretics, and antidysenterics (Caius, Perry). Although a few species are cosmopolitan weeds, only *C. hirsuta* is a noxious garden and greenhouse plant.

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28. **Barbarea** R. Brown in Aiton, Hortus Kew. ed. 2. **4:** 109. 1812, nom. cons.[7]

Biennial or perennial [very rarely annual] herbs, glabrous or sparsely pubescent with unbranched trichomes. Stems erect, angular, usually branched. Basal leaves rosulate, petiolate, lyrately pinnatifid or pinnatisect [or undivided], with 1–10 pairs of lateral lobes, terminal lobe always much larger than the lateral ones. Cauline leaves sessile, usually amplexicaul or auriculate, entire or dentate to pinnatifid, glabrous or ciliate at base. Inflorescence a densely flowered, ebracteate [or bracteate], corymbose raceme, greatly [or not] elongated in fruit; base of flowering pedicels with a minute gland on each side; fruiting pedicels erect and appressed to rachis or spreading, stout and nearly as thick as the fruit or slender, terete or angled. Sepals oblong to linear, ascending [erect or spreading], glabrous [or with subapical trichomes]; outer pair usually cucullate at apex, not saccate at base; inner pair not cucullate, slightly saccate. Petals bright [to pale] yellow, spatulate to oblanceolate, short clawed, about twice as long as [or only slightly longer than] sepals. Nectar glands 4, distinct; lateral pair horseshoe shaped, open to the outside; median pair toothlike or rod shaped. Stamens 6, tetradynamous; filaments free, not appendaged; anthers oblong. Fruits dehiscent, linear, terete to 4-angled or flattened parallel to the septum, torulose to smooth, straight to arcuate, erect or ascending to divaricate; valves with a prominent midnerve and conspicuous or obscure lateral nerves, rarely carinate, glabrous [or very rarely pubescent]; gynophore stout, to 1 mm long; styles persistent, short or long, slender to stout; stigmas capitate, slightly 2-lobed. Seeds dark brown, prominently [or slightly] reticulate, uniseriately arranged in each locule, usually neither winged nor marginate, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Campe* Dulac.) TYPE SPECIES: *Erysimum Barbarea* L. = *B. vulgaris* R. Br.; see ICBN, p. 350. 1983. (Name commemorates St. Barbara, of the fourth century. The seeds of *B. verna* (Miller) Ascherson, a plant called herb of St. Barbara in the Middle Ages, were sown in western Europe in early December near St. Barbara's day. A few authors maintain that the name is derived from the fact that species of *Barbarea* were the only plants available for food on St. Barbara's Day.)—WINTER CRESS, SCURVY GRASS, ROCKET, UPLAND CRESS, CORN MUSTARD (Small).

A well-defined but taxonomically difficult genus of about 20 species distributed primarily in Europe and Asia, particularly the Balkan peninsula (ten species, six endemic), Turkey (ten species, five endemic), and the Caucasus (six species, two endemic). The native range of *Barbarea orthoceras* Ledeb. (*B. americana* Rydb., *B. planisiliqua* C. A. Meyer) includes central and eastern Asia and North America (Alaska to Baja California, east into the Mountain States, Michigan, New York, New Hampshire, and Maine, north throughout most of Canada). Hewson recognized *B. australis* J. D. Hooker and *B. Grayi* Hewson as indigenous to Tasmania and adjacent southeastern Australia, respectively. Both are disjunct from the rest of *Barbarea* and are anomalous in

[7]For conservation of the generic name, see the papers of Eichler, Fuchs, McVaugh, and Rauschert.

that they are annuals with tuberculate, marginate or narrowly winged seeds. It is doubtful whether they should be retained in this genus. The majority of species grow in wet habitats, but at least four are widely distributed weeds of roadsides, fallow and cultivated fields, pastures, waste places, and open woods. The genus is represented in the southeastern United States by two naturalized weeds.

Barbarea vulgaris R. Br. (*Erysimum Barbarea* L., *Sisymbrium Barbarea* (L.) Crantz, *Barbarea Barbarea* (L.) MacM., *Campe Barbarea* (L.) W. F. Wight, *B. taurica* DC., *E. arcuatum* Opiz ex Presl, *B. arcuata* (Opiz ex Presl) Reichenb., *B. vulgaris* var. *arcuata* (Opiz ex Presl) Fries), common winter cress, yellow rocket, bitter cress, rock cress, $2n = 16$, is a Eurasian weed that is naturalized throughout most of North America. It has been reported from all of the Southeastern States except Mississippi and Louisiana, where it is likely to be found. It is one of the most variable species of *Barbarea,* and on the basis of length and orientation of both fruits and fruiting pedicels, a few authors (e.g., Fernald, 1943; Jackson) have recognized several varieties and forms. These characters show continuous variation, and it is highly doubtful that any of the infraspecific taxa of *B. vulgaris* merit recognition. Plants comparable to "vars." *vulgaris* (fruits straight, appressed to rachis) and *arcuata* (fruits spreading, usually arcuate), as well as a wide array of intermediates, grow in the Southeast and throughout the native and naturalized ranges of the species.

Small (1903; 1933, family references) reported the Eurasian *Barbarea stricta* Andrz. from Florida, but it is very likely that his record was based on misidentified plants of *B. vulgaris.* According to Ball, both species have dentate uppermost cauline leaves, but the former has pubescent flower buds and fruiting styles 0.5–1.5 mm long, while the latter has glabrous buds and styles 2–3 mm long. I have not studied enough material of *B. stricta* to evaluate its variation in these characters, but in *B. orthoceras* glabrous or pubescent buds, appressed to spreading fruits and fruiting pedicels, and dentate to pinnatifid upper cauline leaves may be found within the same population. Both *B. stricta* and *B. orthoceras* are distinguished from *B. vulgaris* by their short, stout fruiting styles. *Barbarea orthoceras* is quite variable in North America, and as presently circumscribed, it can easily accommodate the earlier-published *B. stricta.* It is interesting that many earlier North American botanists had passed *B. orthoceras* as *B. stricta.* It is evident that the three species above need careful evaluation of their boundaries and their variation in leaves and fruits. Fernald (1909) recognized plants of *B. orthoceras* with spreading fruits as var. *dolichocarpa* Fern., but as indicated above, forms with appressed or spreading fruits completely intergrade within numerous populations.

Barbarea verna (Miller) Ascherson (*Erysimum vernum* Miller, *Campe verna* (Miller) Heller, *E. praecox* James Sm., *B. praecox* (James Sm.) R. Br.), early winter cress, land cress, scurvy grass, Belle Isle cress, $2n = 16$, is another Eurasian weed that is widely distributed in the United States and is naturalized in all of the Southeastern States. It is easily distinguished from *B. vulgaris* in having basal leaves with six to ten pairs of lateral lobes, pinnatisect uppermost cauline leaves, stout styles 0.5–1(–2) mm long, and ascending fruits 4.5–8 cm

long. *Barbarea vulgaris* has basal leaves with three to five pairs of lateral lobes, dentate to entire uppermost cauline leaves, slender styles 1.5–3 mm long, and appressed to spreading fruits (0.7–)2–3 cm long.

The placement of *Barbarea* in the tribe Arabideae has been accepted by most students of the Cruciferae. The genus is usually associated with *Arabis, Cardamine,* and *Rorippa,* the core genera of the tribe. Von Hayek derived *Barbarea* directly from *Erysimum* L. and considered it to be ancestral to *Rorippa,* while Schulz placed it between the North American *Thelypodium* Endl. (as *Pleurophragma* Rydb.) and *Phoenicaulis* Nutt. ex Torrey & A. Gray. In my opinion, Von Hayek's association of *Barbarea* with *Rorippa,* but not with *Erysimum,* is more acceptable than Schulz's generic disposition. *Barbarea* is distinguished from other genera of the Arabideae by its yellow flowers, uniseriately arranged seeds, strongly nerved valves, and auriculate cauline leaves, as well as by the presence of a pair of glands at the base of each pedicel and by either the lack of indumentum or the presence of simple trichomes only.

As indicated by Fernald (1909, p. 134), species of *Barbarea* are "notoriously difficult of delimitation." Specimens should include mature fruits and basal leaves, and field notes should cover the variation of important diagnostic features, such as the length and orientation of fruits and fruiting pedicels, the number of lateral lobes of the basal leaves, and the margin of the uppermost cauline leaves. Several species are recognized on the basis of minor differences in characters the variation of which is poorly understood. Species boundaries are probably obscured by hybridization, but there is no documentation that this has actually taken place. Careful evaluation of species, particularly of the Caucasus region, Turkey, and the Balkan peninsula, is needed.

Little is known about the reproductive biology of the genus. Both *Barbarea verna* and *B. vulgaris* are self-compatible, and the latter and *B. orthoceras* are often protogynous (pers. obs.). Fertig (in MacDonald & Cavers) estimated that a medium-sized plant of *B. vulgaris* can produce more than 200,000 seeds. The species also reproduces asexually by the formation of adventitious buds from roots (Kott) or by the development of "cauline rosettes" in axils of the uppermost cauline leaves (MacDonald & Cavers; Rich). The latter phenomenon was observed in about one percent of the plants of a given population. If the "cauline rosettes" come in contact with the ground (due to bending of the stem), they may produce adventitious roots and may flower and fruit the next season after overwintering. Factors promoting the formation of "cauline rosettes" are unknown, but hormonal or physiological imbalances following injury have been suggested (Rich). Both *B. verna* and *B. vulgaris* have an obligate cold requirement for flowering.

Chromosome numbers are known for 12 species of *Barbarea,* and all counts except two for *B. vulgaris* indicate that $2n = 16$. Deviating counts of $2n = 18$ have been reported for plants from Czechoslovakia (Dvořák & Dadáková; Dvořák *et al.*). Neither polyploidy nor aneuploidy has played a major role in the evolution of the genus.

Although interspecific hybridization between pairs of closely related species of *Barbarea* has been suggested, none of the alleged cases has been verified experimentally. The putative hybrids *B. stricta* × *B. vulgaris* (*B.* ×*Schulziana*

Hausskn.) and *B. intermedia* Boreau × *B. vulgaris* (*B.* ×*Gradlii* J. Murr) have been recorded from Germany, Czechoslovakia, and Austria (Lange, Markgraf, Stace).

The five species of *Barbarea* that have been surveyed for glucosinolates contain high concentrations of 2-phenylethyl and/or 2-hydroxy-2-phenylethyl glucosinolates. Small amounts of 3-methylthiopropylglucosinolate are found in *B. vulgaris, B. plantaginea* DC., and *B. intermedia,* and traces of isopropylglucosinolate are present in the last and in *B. stricta* (Cole; Al-Shehbaz & Al-Shammary). The seeds of both *B. vulgaris* and *B. stricta* have been analyzed for fatty acids. They contain moderate amounts (21–26 percent) of oleic, linoleic, and erucic acids. Smaller amounts (16 percent) of the last acid were found in *B. orthoceras* (Goering *et al.*).

Barbarea verna and *B. vulgaris* are very similar in seed-coat anatomy. Both have a palisade layer composed of isodiametric cells with thickened radial and inner tangential walls, but cells of the latter species have prismatic crystals. The epidermis in both species has been said to be mucilaginous (Vaughan & Whitehouse), but no mucilage was observed in seeds of these or of several other species of *Barbarea* that I have examined.

Several species of *Barbarea* are cosmopolitan weeds that are among the earliest to flower in the spring. Both *B. verna* and *B. vulgaris* are cultivated in parts of Europe as potherbs and are said to have a flavor similar to that of watercress, *Rorippa Nasturtium-aquaticum. Barbarea vulgaris* was cultivated by the early Egyptians, Greeks, and Romans, and its leaves are eaten in Sweden as a substitute for kale. The plants are not bitter when young but become so as the season progresses. Leaves of older plants are edible only if cooked in two waters. The species is said to be a stimulant, an antiscorbutic, and a vulnerary (Caius), as well as a valuable honey plant in cold regions.

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29. **Iodanthus** Torrey & A. Gray ex Steudel, Nom. Bot. ed. 2. **1**: 812. 1840.[8]

Perennial herbs [or subshrubs]. Stems usually single at base, often branched above, glabrous or sparsely [to densely] pubescent with unbranched trichomes. Leaves petiolate, lanceolate to ovate [or cordate], amplexicaul to auriculate [or not auriculate], glabrous to glabrescent [or hirsute with unbranched or bifurcate trichomes]; lower leaves usually lyrate, with 1–9 pairs of lateral lobes [or undivided]; petioles winged [or wingless]. Inflorescence an ebracteate, elongate [or corymbose] raceme; fruiting pedicels ascending to divaricate, smooth [or striate]. Sepals erect, oblong, glabrous or with a subapical tuft of trichomes [or hirsute on the outside], usually membranaceous at margin. Petals white, lavender, purple, violet [or yellow], spatulate to obovate, much longer than [or about as long as] the sepals. Stamens 6, tetradynamous [or nearly equal in length], slightly exserted [or included]. Nectar glands forming a well-developed ring subtending the bases of median [or all] filaments and surrounding those of lateral ones. Fruits linear, terete [or slightly compressed parallel to the septum], sessile or borne on gynophores less than 1 mm long, glabrous [or sparsely hirsute]; valves conspicuously 1-nerved; styles thick, long [or obsolete]; stigmas entire, capitate. Seeds uniseriately arranged in each locule, wingless, reticulate, oblong; cotyledons accumbent to incumbent. (Including *Chaunanthus* O. E. Schulz, *Oclorosis* Raf.) TYPE SPECIES: *I. pinnatifidus* (Michx.) Steudel. (Name from Greek *iodes,* violet, and *anthos,* flower.)—PURPLE ROCKET, VIOLET ROCKET.

A New World genus of four species, three of which are narrowly endemic to Mexico. Each of the Mexican species has been collected just a few times and from only one area. The fourth is widely distributed in the United States, particularly in the Midwestern States (Ohio, Indiana, Illinois, and Missouri). *Iodanthus pinnatifidus* (Michx.) Steudel (*Hesperis pinnatifida* Michx., *Thelypodium pinnatifidum* (Michx.) S. Watson, *Cheiranthus hesperidoides* Torrey & A. Gray, *I. hesperidoides* (Torrey & A. Gray) A. Gray), purple rocket, violet rocket, occupies an area immediately west of the Appalachian Mountains and east of the 100th meridian. It grows primarily on alluvial soil in moist,wooded ravines and floodplain woods, as well as along stream banks, in southwestern Pennsylvania and adjacent northwestern West Virginia south into Tennessee (Cannon, Cheatham, Davidson, Houston, Knox, Rutherford, Stewart, and Williamson counties) and northwestern Alabama (Colbert, Lauderdale, and Lawrence counties), west into Arkansas (Baxter, Benton, Hempstead, Lawrence, Madison, Marion, and Newton counties) and eastern and central Texas, and north into northeastern Oklahoma, eastern Kansas, central Iowa, and southeastern Minnesota. It was reported by Small (1903, 1933) and Britton & Brown from Louisiana, but I have not seen any specimens from there, and MacRoberts did not include it in his checklist.

Iodanthus pinnatifidus is distinguished from the Mexican species of the genus

[8]Most floras wrongly cite Torrey & Gray (Fl. N. Am. **1**: 72. 1838) as the authors of the genus. As shown by Rollins, however, these authors neither recognized *Iodanthus* as a genus nor assigned a legitimate specific name to it. Steudel should be credited for validating the generic name.

by its herbaceous habit, glabrescent, usually auriculate leaves, petioles with winged margins, and petals usually twice as long as the sepals. *Iodanthus petiolatus* (Hemsley) Rollins (Hidalgo), *I. acuminatus* Rollins (Jalisco), and *I. mexicanus* Rollins (Puebla) are shrubby and have pubescent leaves without auricles, wingless petioles, and petals slightly longer than the sepals.

There is little agreement on the tribal disposition of *Iodanthus*. Von Hayek and Moggi closely associated it with *Hesperis* L. and *Erysimum* (as *Cheiranthus* L.) of the tribe Hesperideae, while Schulz placed one of its species in the Matthioleae and another (as *Chaunanthus*) in the Sisymbrieae DC. The association of *Iodanthus* by these authors with some of the Old World genera was not well founded. On the basis of the cellular pattern of the septum, Dvořák suggested that *Iodanthus* be excluded from the Hesperideae and associated with the Cardamininae as circumscribed by Prantl. Robinson's close association of *Iodanthus* with *Barbarea* in the tribe Arabideae is the most acceptable placement. *Iodanthus* is distinguished from *Barbarea* in having purple or white flowers, undivided, petiolate upper cauline leaves, and nontorulose fruits. The Mexican species of *Iodanthus* have yellow flowers, but they are all subshrubs with undivided, pubescent leaves.

Nothing is known about the floral biology, cytology, embryology, anatomy, chemistry, genetics, or ecology of *Iodanthus*. The genus has no economic value.

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30. **Leavenworthia** Torrey, Ann. Lyc. Nat. Hist. New York **4:** 87. 1837.

Herbaceous, glabrous, taprooted, winter annuals. Leaves petiolate, the earlier ones entire, the later ones progressively more pinnately divided, the mature leaves lyrately pinnatifid, usually forming well-developed rosettes; lateral lobes absent or 1–10, entire to coarsely dentate; terminal lobe entire to prominently angled, markedly or only slightly larger than the adjacent pair of lateral lobes. Early flowers always solitary, borne on scapes 3–15 cm long that originate from center of the rosette; later flowers long pedicellate, borne in lax, ebracteate, few- to many-flowered racemes that arise from the axils of rosette leaves. Sepals narrowly oblong to linear, spreading to erect, glabrous, equal, not saccate or only slightly so at base. Petals much longer than sepals, obovate to oblanceolate, clawed; blades white to lavender or yellow, horizontal to ascending, shallowly to deeply emarginate or sometimes truncate to obtuse; claws erect, much shorter than blades, yellow to orange distally. Nectar glands 4, lobed, the median pair subtending bases of the paired stamens, the lateral pair surrounding those of the single stamens. Stamens 6, strongly tetradynamous; filaments white, erect, linear, unappendaged; anthers oblong, introrse or those of paired stamens sometimes extrorse. Fruits linear to oblong or subglobose, terete or strongly flattened parallel to the septum, torulose or smooth, subsessile to short stipitate; valves glabrous, obscurely veined, thin or thick and somewhat fleshy before drying; replum straight to strongly constricted between seeds; septum membranaceous, usually with an obscure midvein; funicles free from septum; styles slender to stout, persistent; stigmas entire to slightly 2-lobed. Seeds orbicular to slightly longer than broad, flattened, uniseriately arranged, winged to marginate, dark brown, nonmucilaginous when wet, prominently reticulate, the areolae of reticulum nearly uniform in size throughout or those of the embryo region smaller than the rest; radicle much shorter than cotyledons, straight or slightly bent and only obscurely accumbent. LECTOTYPE SPECIES: *L. aurea* Torrey; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 189. 1913. (Name commemorating Melines Conkling Leavenworth, Jan. 15, 1796–Nov. 16, 1862, American physician and amateur botanist who collected plants in Florida, Alabama, Louisiana, Arkansas, and Oklahoma.)

A well-defined genus of eight species confined to limestone glades and distributed primarily in the Southeastern States (Tennessee, Georgia, Alabama, Arkansas). Two of the three species that grow outside this area, *Leavenworthia aurea* (Choctaw and McCurtain counties, Oklahoma) and *L. texana* Mahler (St. Augustine County, Texas), are narrow endemics, while the third, *L. uniflora* (Michx.) Britton, is the most widely distributed member of the genus (see below). In general, the area occupied by *Leavenworthia* can be divided into an eastern and a western part separated by the Mississippi Alluvial Plain, which has no limestone glades. This accounts for the total absence of the genus in southern Illinois, western Tennessee, Mississippi, Louisiana, and all except the northern portion of Arkansas. The eastern part of the range contains all 12 taxa of the genus except *L. aurea* and *L. texana*; *L. uniflora* occurs in both areas.

Leavenworthia uniflora (Michx.) Britton (*Cardamine uniflora* Michx., *L.*

Michauxii Torrey), $2n = 30$, is the most distinctive and the most widely distributed species of the genus. It occurs from southern Ohio and southern Indiana (Clark County) southward into central and southern Kentucky (12 counties), Tennessee (Bedford, Bledsoe, Hamilton, Knox, Marshall, Maury, Rutherford, and Wilson counties), Georgia (Walker County), and Alabama (Jackson, Lawrence, Madison, Marshall, and Morgan counties). It is disjunct and widely distributed in the Ozark region of Arkansas (Baxter, Benton, Carroll, Marion, Randolph, and Sharp counties) and in central and southern Missouri (33 counties). The wide geographic distribution of *L. uniflora* can be attributed to autogamy, weedy tendencies, high seed production, and adaptation to habitats drier than those occupied by the other taxa of the genus (Rollins, 1963, 1981). *Leavenworthia uniflora* is easily distinguished by its highly dissected leaves with coarsely dentate lobes, the terminal one of which is only slightly larger than the adjacent lateral ones, its truncate or rounded petals to 7 mm long, and its subaccumbent radicle.

A close relative and morphologically very distinct, *Leavenworthia torulosa* A. Gray ($2n = 30$) is widespread on limestone barrens of central Tennessee (Bedford, Bradley, Davidson, Giles, Lincoln, Marshall, Maury, Rutherford, Sumner, Williamson, and Wilson counties). It is endangered in Kentucky, where it is known only from a few glades in Logan, Simpson, and Warren counties. Several authors (e.g., Baskin & Baskin, 1984; Freeman *et al.*; Mohr; Small, 1933) have recorded *L. torulosa* from Alabama, but all their reports are apparently based on Mohr's collection from Madison County, which is probably the only known record of the species from that state.

Kotov's report of *Leavenworthia torulosa* from the banks of the Oskol River (Belgord Province, central Russia) and from a swamp near Kuya (Archangel Province, northern Russia) was based on collections made in 1915 and 1912, respectively. Kotov did not discuss the origin of these two collections, but it is highly unlikely that they were made from natural populations in Russia. The species is not weedy nor does it grow outside its native range.

The fruits of *Leavenworthia torulosa* are conspicuously torulose even when young, the seeds are wingless to obscurely winged, and the areolae of the seed coat are nearly uniform throughout. These features should distinguish the species easily from the other leavenworthias.

Leavenworthia stylosa A. Gray ($2n = 30$) is endemic to central Tennessee (Bedford, Davidson, Rutherford, Smith, and Wilson counties). It was said to grow in Williamson County (Sharp *et al.*), but neither Rollins (1963) nor Kral has indicated that it grows there, and I have not seen any material from that county. It is likely that the record was based on misidentified plants of *L. torulosa*. *Leavenworthia stylosa* has the largest flowers and longest styles in the genus and is self-incompatible. In some populations flower color is uniformly yellow, while in others it ranges from white to various shades of lavender. Rollins (1963) observed a gradual mixing of the two major color forms in populations west of Gladeville, Tennessee. In the related *L. torulosa* and *L. uniflora* (both self-compatible) the flowers are smaller and white to lavender. The fruits of *L. stylosa* show a wide range of variation in shape and length. In one collection, *Rollins 59104* (GH!), they are oblong to ovate and only about

0.5 cm long, while in another, *Rollins 53143* (GH!), they are linear and to 4.5 cm long. The variation in fruit morphology, however, is continuous and does not support the division of the species into infraspecific taxa.

Both varieties of *Leavenworthia crassa* Rollins ($2n = 22$) are narrowly endemic to northern Alabama. Varietas *crassa* grows in Lawrence, Marshall, and Morgan counties, while var. *elongata* Rollins is restricted to the last two counties. The fruits in var. *crassa* are 6–10 mm long, the styles are 3–6 mm long, and the petals are 10–13 mm long and white to yellow. Varietas *elongata* has slightly longer (8–12 mm) fruits, shorter (2.5–3.5 mm) styles, and shorter (9–11 mm), yellow petals. Kral (p. 494) has mapped var. *crassa* as occurring in Davidson County, Tennessee. It is possible that this disjunct record is based on plants of *L. stylosa* with very short fruits. The fruits in both *L. stylosa* and *L. crassa* are fleshy when green and have thick valves when dry, but they overlap only slightly in their length, which is rarely less than 1 cm in the former and rarely more than that in the latter. However, the two species differ in chromosome number and in their radicle, which is straight in *L. crassa* and curved in *L. stylosa.*

Another narrow endemic of northern Alabama is *Leavenworthia alabamica* Rollins, $2n = 22$. Rollins (1963) recognized two varieties: var. *alabamica* (Colbert, Franklin, Lawrence, and Morgan counties) and var. *brachystyla* Rollins (Marshall and Morgan counties). The former has styles 2.5–5.5 mm long and fruits acute at apex and base, while the latter has styles 1.5–3 mm long and fruits rounded at both ends. The species is most closely related to *L. crassa* and *L. exigua* Rollins ($2n = 22$). It differs from *L. crassa* in having fruits that are flattened, nonfleshy, and 1.5–3 cm long, with more than 12 nonoverlapping seeds, instead of terete, fleshy, and 0.6–1.2 mm long, with no more than ten overlapping seeds. *Leavenworthia alabamica* is distinguished from *L. exigua* in having deeply emarginate petals 10–14 mm long, slightly longer (1.5–5.5 mm) styles, and fruits 3–4.5 mm wide with more than 12 seeds. In *L. exigua* the petals are shallowly emarginate and 6–9 mm long, the styles are 1–3 mm long, and the fruits are 3.5–5.5 mm wide with only 4–10 seeds.

Leavenworthia exigua consists of three varieties, one of which, var. *laciniata* Rollins, is endemic to northern Kentucky (Bullitt and Jefferson counties). Varietas *exigua* is distributed in Georgia (Catoosa and Walker counties) and Tennessee (Bedford, Davidson, Decatur, Hardin, Marshall, Maury, Rutherford, Williamson, and Wilson counties), whereas var. *lutea* Rollins is endemic to Alabama (Jefferson, Marshall, and St. Clair counties) and Tennessee (Maury County). The flowers are yellow in var. *lutea* and white to light lavender in the other two. Varietas *exigua* has lavender sepals and styles 1–2 mm long, while var. *laciniata* has green sepals and styles 2–3 mm long.

Most records of *Leavenworthia aurea* from Tennessee, Georgia, and Alabama belong to *L. exigua* (Rollins, 1956). The former is so strikingly similar to *L. exigua* var. *lutea* (both with yellow flowers) that the casual observer cannot tell them apart. However, *L. aurea* is a polyploid ($2n = 48$) restricted to portions of southeastern Oklahoma. It is distinguished from *L. exigua* by having thick- (vs. thin-)margined fruits and rounded (vs. angular) terminal leaf lobes. Varietas *lutea* also resembles *L. texana* ($2n = 22$) in flower color, leaf-lobe shape,

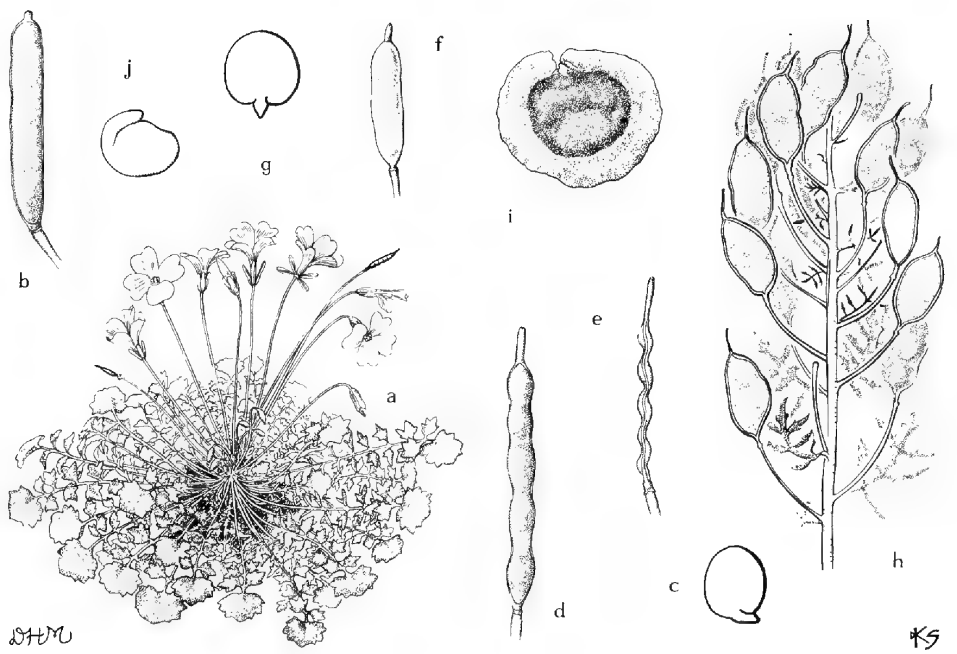

FIGURE 3. **Leavenworthia** and **Selenia.** a, *Leavenworthia stylosa,* plant with flowers, × ½—note single-flowered scapes from center of basal rosette. b, c, *L. uniflora:* b, fruit, × 1; c, embryo, × 10. d, e, *L. torulosa:* d, fruit, valvular view, × 1; e, fruit, lateral view, × 1. f, *L. exigua,* fruit, × 1. g, *L. alabamica,* embryo, × 10—note straight radicle. h–j, *Selenia aurea:* h, infructescence, × 1—note bracts; i, seed, × 6; j, embryo, × 6.

and chromosome number. However, it differs in having shorter styles (1–2 vs. 2–3.5 mm) and thin- (vs. thick-)margined fruits.

Although *Leavenworthia* has no known immediate generic relative, it is probably more closely related to *Selenia* than to any other genus of the Cruciferae (Torrey). Both genera are glabrous annuals with dissected leaves, often yellow flowers, spreading sepals, short gynophores, flattened fruits, somewhat thick valves, winged seeds, and prominently reticulate, thick seed coats. *Leavenworthia* is easily distinguished by its inflorescences and seeds. The early flowers are in solitary scapes that arise from the center of a rosette (FIGURE 3a), while the later ones are in ebracteate racemes. The seeds have straight or slightly curved radicles that are much shorter than the cotyledons (FIGURE 3c, g). *Selenia* has bracteate inflorescences and accumbent cotyledons.

Von Hayek derived *Leavenworthia* directly from *Cardamine* and considered the genus to be ancestral to the monotypic North American *Idahoa* A. Nelson & Macbr. (as *Platyspermum* W. J. Hooker) and the Caucasian *Pseudovesicaria* (Boiss.) Rupr. Schulz also suggested a close association with *Cardamine* and placed *Leavenworthia* between the Asiatic *Loxostemon* and *Pegaeophyton.* In my opinion, *Leavenworthia* is not related to any of these genera, and I agree with Rollins (1963) that it should not be associated with *Cardamine.*

All species of *Leavenworthia* are winter annuals very closely adapted to glades that are usually associated with red cedar, *Juniperus virginiana* L. They grow

primarily on a thin layer of soil overlying flat-bedded outcrops of dolomitic limestone. The glades are often waterlogged from late autumn to early spring, but they become very dry during the summer. As stated by Rollins (1963, p. 6), "this close adaptation to a rather narrow and rigid set of edaphic conditions appears to have been an important factor influencing the direction and extent of evolution within the genus." Seeds of all species of *Leavenworthia* remain dormant during the summer (Baskin & Baskin, 1971). Germination takes place in early fall, and the plants persist through winter as slow-growing rosettes. Blooming may start as early as late February and often continues through April, while seed maturity is usually reached by mid or late May. All species are capable of growing in soils fully saturated with water, and their roots are metabolically adapted to grow under anaerobic conditions (Baskin & Baskin, 1976).

All species except for the widespread *Leavenworthia uniflora* are listed as endangered or threatened (Kral). Man's conversion of the limestone barrens in the Southeast to pastures or industrial and housing developments has altered or destroyed the habitats of *Leavenworthia.* Although a few species are successful in moving onto cornfields, wastelands, and pastures, it is highly unlikely that they will persist in such unstable habitats. During favorable seasons, plants of all species may produce numerous rosette leaves, scapes, and racemes, but under poor edaphic conditions they may produce one to only a few leaves and single-flowered scapes. This aspect of variation in *Leavenworthia* has been well documented by Rollins (1963, *pls. 7–15*).

The reproductive biology of *Leavenworthia* has been thoroughly studied, particularly in relation to breeding systems, population variability, petal-color polymorphism, insect pollination, genetics of self-incompatibility, racial differentiation, interspecific hybridization, and evolution of self-compatibility and autogamy (see Lloyd, Rollins, and Solbrig and references therein). Self-incompatibility was found in all populations of *L. stylosa* tested, but in only one of four races of *L. alabamica* and four of 15 of *L. crassa* (Lloyd, 1965). The remaining species are self-compatible, and only *L. uniflora* is highly autogamous. According to Lloyd (1968a), there is no absolute distinction between self-compatibility and self-incompatibility in either *L. alabamica* or *L. crassa,* and partial unilateral incompatibility has involved quantitative, rather than qualitative, changes in pollen-stigma relationships, which have been gradual, with allele changes at many loci.

Self-compatibility in *Leavenworthia* has arisen independently at least three (Rollins, 1963) or six (Lloyd, 1969) times. The shift from self-incompatibility to self-compatibility is a major trend in the genus and has accompanied the evolution of well-marked varieties in both *L. alabamica* and *L. crassa* (Rollins, 1963). More than 15 evolutionary trends have accompanied this shift in the reproductive system (Lloyd, 1969). The most obvious ones are decrease in length of sepals, petals, anthers, and styles, reduction of petal emargination, and increase in ovule number. Some other changes are from extrorse to introrse anthers of median stamens, from flaring to erect petals, and from odoriferous to nonodoriferous flowers.

All species of *Leavenworthia* are very closely adapted to specific edaphic

conditions (see above), and they usually flower at periods when the pollinating insects are very scarce. The lack of sufficient pollinators and the need for adequate seed set may have been the most important selective forces that favored the shift from self-incompatibility to self-compatibility. The autogamous *L. uniflora* and *L. exigua* var. *exigua* are more widespread than the self-incompatible taxa, and both usually flower a few weeks earlier.

When species of *Leavenworthia* are sympatric, the self-incompatible ones occupy wetter parts of the glade than the self-compatible ones. The self-incompatible taxa can therefore grow for longer periods and can be pollinated before the advent of drought. In the drier glades these plants are under water stress when the pollinators emerge and are therefore unable to produce sufficient seeds to compete with the self-compatible taxa in the next generations (Solbrig & Rollins).

Lloyd (1965, 1969) observed that honey bees, *Apis mellifera* L. (Apidae), were the most frequent visitors to the flowers of *Leavenworthia crassa* and *L. stylosa*; they comprised 57–70 percent of the total insect visitors. Twenty species of solitary bees, particularly of the genera *Andrena* (Andrenidae), *Halictus* and *Dialictus* (Halictidae), and *Ceratina* (Apidae), made up about 15 percent. The remaining insects were flies, butterflies, and beetles. With the exception of *Bombylius major* L. (Bombyliidae), visiting insects did not discriminate among the flower-color morphs. Individuals of this species, however, showed a significant preference for yellow-centered flowers and rarely visited other flower morphs.

Variation in flower color has been thoroughly studied by Rollins (1963) and Lloyd (1969). The number of flower-color morphs is higher in self-incompatible than in self-compatible taxa. Lloyd has suggested that in *Leavenworthia crassa* the difference between the yellow and the yellow-centered flowers is determined by a single locus and that in one race yellow is dominant while in three others it is recessive. In crosses between races, the incomplete dominance of the yellow-centered and yellow forms indicates that the dominant relationships in each population depend on polygenic modifiers.

On the bases of morphology, chromosome numbers, and breeding systems, two major lines of evolution are recognized in *Leavenworthia*. Three species, *L. stylosa, L. torulosa,* and *L. uniflora,* have a diploid number of 30 and have embryos with curved radicles and subaccumbent cotyledons (FIGURE 3c). The first species is self-incompatible and is the most primitive in the group, whereas the last is autogamous and the most advanced. In the second line, four species (*L. alabamica, L. crassa, L. exigua, L. texana*) have $2n = 22$ and embryos with straight radicles (FIGURE 3g). *Leavenworthia aurea* ($2n = 48$), which also has straight radicles, ties in very well with *L. exigua* var. *lutea* and *L. texana.* Embryos with straight radicles are not known elsewhere in the Cruciferae. It is likely, therefore, that the two groups of species have evolved from ancestors with curved radicles. Baldwin stated that species with $2n = 30$ are hexaploid and that *L. exigua* (as *L. aurea*) is an aneuploid derived from ancestral tetraploids with $2n = 20$. These assumptions, however, are unsupported, and all species except *L. aurea* are diploid (Rollins, 1963).

In numerous cedar glades of the Central Basin of Tennessee (Bedford, Da-

vidson, Marshall, Maury, Rutherford, and Wilson counties), various combinations of four species (*Leavenworthia exigua, L. stylosa, L. torulosa,* and *L. uniflora*) grow sympatrically within inches of one another. All are reproductively isolated in nature, and either they cannot be crossed experimentally, or (as in the combination *L. stylosa* × *L. exigua*) their first-generation hybrid is completely sterile. The remaining species of the genus are largely allopatric. Although both *L. alabamica* and *L. crassa* grow in the same general area in northern Alabama, their ranges rarely overlap. However, in Morgan County *L. alabamica* var. *brachystyla* hybridizes with both varieties of *L. crassa,* and their natural interspecific hybrids, which often grow in pastures and cultivated fields, are fully fertile. Meiosis is normal in the artificial hybrids of both species, and only occasional irregularities have been observed (Rollins, 1963).

The chemistry of *Leavenworthia* has not been studied adequately, and only in *L. torulosa* have the seeds been analyzed for fatty acids (Miller *et al.*). The species has a high concentration (53 percent) of eicosenoic acid and lacks erucic acid. In this, *Leavenworthia* resembles the closely related *Selenia* (see below). The same fatty-acid pattern, however, also occurs in the unrelated *Lobularia* Desv. and *Teesdalia* R. Br., of the tribes Alysseae and Lepidieae, respectively.

The seeds of *Leavenworthia* are probably dispersed over short distances by rain-washes, and for longer ones by water in areas where populations grow adjacent to streams. Lloyd (1965) suggested that the seeds lack adaptations for either animal or wind dispersal and that their poor dispersal may have effectively isolated various populations.

The genus has no economic value. The flowers of both *Leavenworthia stylosa* and *L. crassa* are very showy, and both species might well be used as ornamentals.

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31. **Selenia** Nuttall, Jour. Acad. Nat. Sci. Phila. **5:** 132. 1825.

Glabrous, caulescent [or acaulescent with crown usually swollen], spring-flowering annuals. Leaves subsessile [or short to long petiolate], pinnately [or bipinnately] dissected, with numerous entire to dentate or divided lobes, the rachis marginate or winged. Inflorescences bracteate terminal racemes, usually elongated in fruit [or flowers solitary on scapes arising from the axils of rosette leaves in acaulescent taxa]; bracts leafy, pinnately dissected, smaller and less divided upward; rachis of infructescence angled [or terete]; fruiting pedicels slender to stout, spreading to ascending, 1–2.5[–21] cm long. Sepals spreading, slightly unequal and convex at base, caducous [or persistent to fruit maturity], without [or with] a well-developed subapical, hornlike appendage on the exterior, usually membranaceous at margin. Petals yellow, spatulate [to obovate], gradually narrowed to claws, rounded [to emarginate]. Median nectar glands 4 [or 2], lateral gland with [or without] an adaxial lobe and 2 [or 1] abaxial one(s). Stamens 6, tetradynamous; filaments linear, unappendaged; anthers oblong [to ovate or lanceolate], sagittate at base. Fruits dehiscent, narrowly elliptic to broadly oblong [or obovate to globose], compressed parallel to the septum [or inflated], stipitate [or sessile]; valves glabrous [or vesicular], papery [or rather thick], obscurely reticulately veined, the midrib absent; replum flattened to winged [or rounded]; septum complete or incomplete, hyaline, without [or with] a midvein; styles persistent, slender [to stout], strongly flattened [or terete] at base; stigmas capitate, entire [or 2-lobed]. Seeds [3–]6–12[–20], orbicular, flattened, prominently reticulate, broadly winged [or marginate] all around, emarginate at the hilum, biseriately arranged, nonmucilaginous when wet; funicles slender, short, free from septum; cotyledons accumbent, much longer than the radicle. TYPE SPECIES: *S. aurea* Nutt. (Name from Greek *selene,* the moon, in allusion to its superficial resemblance and apparent affinity to *Lunaria.*)

A well-defined genus of four species distributed from central Arkansas and southwestern Missouri west into central New Mexico and south into northeastern Mexico. The genus is represented in the Southeastern States by *Selenia aurea* (*S. aurea* var. *aptera* S. Watson, *S. aptera* (S. Watson) Small), $2n = 46$, which grows on limestone and sandstone barrens and glades, as well as in sandy areas, waste grounds, and cultivated fields. It is widespread in central and western Arkansas (17 counties), southwestern Missouri, southeastern Kansas, and eastern Oklahoma. Although Small and Britton & Brown indicated that it grows in Texas, neither Martin (1940) nor I have seen any specimens from that state. *Selenia aurea* is distinguished from the other selenias by its unappendaged sepals and its pinnate, somewhat reduced leaves that are mostly cauline. In the other species the sepals have a hornlike subapical appendage and the leaves are bipinnate, well developed, and usually basal.

Species of *Selenia* are morphologically very distinct, and they have geographic ranges that rarely overlap. *Selenia dissecta* Torrey & A. Gray (*S. mexicana* Standley), $2n = 14$, is distributed in central New Mexico, the Trans-Pecos region of Texas, and northern Mexico (Coahuila, Nuevo León, and probably Chihuahua). *Selenia Jonesii* Cory occurs mainly in the western part

of the Edwards Plateau, Texas, while *S. grandis* R. F. Martin, $2n = 24$, is known only from the lower valley of the Rio Grande, Texas (Cameron, Dimmit, Hidalgo, and La Salle counties). The last species differs from the other selenias in having vesicular fruit valves, persistent sepals, and stout fruiting pedicels to 21 cm long.

The tribal disposition of *Selenia* has not been established adequately. On the basis of its latiseptate, oblong to elliptic fruits, winged seeds, and accumbent cotyledons, several authors (e.g., Bentham & Hooker; Von Hayek; Schulz; Martin, 1940) have closely associated *Selenia* with the Old World genera *Lunaria* L., *Ricotia* L., *Farsetia* Turra, and *Schlechtera* Bolus, all of which are now placed in the tribe Alysseae DC. In my opinion, *Selenia* is not related to any of these genera and should not be placed in the Alysseae. Robinson's inclusion of *Selenia, Leavenworthia,* and *Idahoa* (as *Platyspermum*) in the Arabideae is evidently more appropriate than the association of *Selenia* with any of the Old World genera. These three genera, however, should be associated with each other only loosely. Torrey & Gray proposed the monotypic tribe Selenieae because they believed that the genus is unique in its inverted embryos. Their conclusion, however, was based on erroneous observation. *Selenia* is easily distinguished by its bracteate inflorescences, pinnate or bipinnate leaves, usually appendaged sepals, short-stipitate fruits, and biseriately arranged seeds.

Selenia dissecta and *S. grandis* are both diploid, with $2n = 14$ and 24, respectively, whereas *S. aurea* is a polyploid, with $2n = 46$ (Rollins, 1966; Rollins & Rüdenberg, 1971, 1977). Chromosome numbers should be helpful in tracing evolution within the genus, but more counts are needed, particularly for *S. Jonesii,* which has not been studied cytologically. Rollins and Rüdenberg (1977) observed univalents and multivalents in *S. aurea* and counted $n = 69$ in one and 23 in three greenhouse-grown plants.

Selenia has not been surveyed adequately for secondary constituents, and only *S. grandis* has been analyzed for glucosinolates (Daxenbichler *et al.*) and fatty acids (Mikolajczak *et al.,* 1963). The species is the richest (58 percent) in eicosenoic acid and among the highest (28 percent) in oleic acid of any source within the Cruciferae. It has, however, very low concentrations of linoleic, linolenic, and erucic acids (4, 2, and 3 percent, respectively).

Nothing is known about the reproductive biology, hybridization, anatomy, or ecology of the genus. *Selenia* has no economic importance, and although Nuttall and Hooker recommended *S. aurea* as an ornamental, the genus has not received the horticultural attention it deserves.

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32. **Arabis** Linnaeus, Sp. Pl. **2:** 664. 1753; Gen. Pl. ed. 5. 298. 1754.

Annual, biennial, or perennial herbs [rarely subshrubs], glabrous or most commonly pubescent with unbranched, furcate, dendritic, or stellate trichomes. Stems erect, leafy [or leafless]. Basal leaves petiolate, usually undivided, entire to variously toothed, rarely lyrate-pinnatifid, often forming a distinct rosette. Cauline leaves sessile or rarely petiolate, amplexicaul or sometimes auriculate at base. Inflorescences ebracteate [or bracteate], terminal, corymbose racemes [or panicles], greatly elongated in fruit; fruiting pedicels erect, spreading, or reflexed. Sepals erect, oblong to ovate, equal or unequal, the lateral pair sometimes saccate at base. Petals white, lilac, or purple, rarely light yellow, spatulate to oblanceolate or oblong, rarely obovate, sharply differentiated into claw and blade, sometimes narrowed to a clawlike base, rounded to emarginate at apex. Lateral nectar glands flat, usually ringlike or horseshoe shaped; median glands flat, conical, or toothlike, free or united with the lateral ones, rarely absent. Stamens 6, tetradynamous; filaments linear, neither appendaged nor winged; anthers ovate or oblong to linear, sometimes sagittate at base. Fruits dehiscent, linear, flattened parallel to the septum, rarely slightly 4-angled or subterete, straight or falcate, sessile or stipitate; valves glabrous or pubescent, usually with a distinct midrib [rarely nerveless]; septum membranaceous, complete, not veined; styles persistent, distinct or obsolete; stigmas capitate, entire or slightly 2-lobed. Seeds numerous, orbicular to oblong, compressed or somewhat plump, winged or marginate to wingless, uniseriately or biseriately arranged, nonmucilaginous when wet; cotyledons accumbent. Base chromosome numbers 6–8. (Including *Arabidium* Spach, *Arabisa* Reichenb., *Boechera* Löve &

Löve, *Fourraea* Greuter & Burdet, *Turrita* Wallr., *Turritis* L.[9]) LECTOTYPE SPECIES: *A. alpina* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2**: 178. 1913. (Name after the Arabian region; see Linnaeus, Philos. Bot. 169. 1751. Fournier's derivation of *Arabis* as a defective form of *Draba* is unlikely.)—WALLCRESS, ROCKCRESS.

A well-defined genus of about 180 species distributed in the temperate areas of the Northern Hemisphere north of the 29th parallel. The only exceptions to this range are the circumpolar *Arabis alpina* and *A. glabra* (L.) Bernh., which appear to be native to the high mountains of tropical East Africa (Jonsell). The genus is most highly diversified in North America, where about 60 of the 75 species are endemic to areas west of the 105th meridian. There are about 44 species (30 endemic) in Europe, 31 (20 endemic) in Southwest Asia and the Caucasus, 19 (10 endemic) in central Asia, 28 (22 endemic) in China and the Far East, and 15 (6 endemic) in northwestern Africa (author's compilation). About 75 percent of the species of *Arabis* are perennial, and only about 17 percent are annual or biennial. The remainder are annuals or biennials that sometimes become perennials (author's compilation). Busch listed four central Asiatic species as shrubs, but these are actually subshrubs that have been transferred to genera allied to *Arabis*. The genus is represented in the southeastern United States by ten species, of which all are indigenous and one is endemic.

Schulz's sectional classification of *Arabis*, which is the latest and most comprehensive, is not satisfactory, nor does it represent natural groupings of species. Sixteen sections (five monotypic) were recognized on the basis of characters (e.g., orientation of fruits, saccation of lateral sepals, length of midnerve of valves) that are now considered to be insignificant. The artificiality of Schulz's sections is immediately recognized if the genus is examined on a worldwide basis. Rollins (1941) was fully justified in concluding (p. 294) that "among the western American species of *Arabis* truly natural subdivisions of the genus other than the species themselves are nonexistent." In my opinion, his conclusion may well apply to the genus as a whole.

Arabis glabra (L.) Bernh. (*Turritis glabra* L.; see Rollins (1941) and Burdet (1969) for nine additional synonyms), tower mustard, $2n = 12$, is a circumpolar species with weedy tendencies. It is widespread in most of the temperate parts of North America, Asia, and Europe, where it grows in meadows, open woods, fields, and disturbed sites, on cliffs, bluffs, canyon walls, and rocky places, and along roadsides, railroad embankments, streams, and lake shores. It is distributed in North America from Quebec to Alaska, south to California, and east

[9]*Arabis* and *Turritis* were simultaneously described by Linnaeus (Sp. Pl. **2**: 664, 666, respectively. 1753). Lamarck (Encycl. Méth. **1**: 218, 219. 1783), who was the first to unite the two genera, adopted *Arabis* for the combined genus, and consequently this name has priority (see ICBN Article 57.2. 1983). Hopkins (p. 64) suggested that Gaudin (Fl. Helvetica **4**: 299. 1829) was the first to unite these genera. However, Lamarck placed the two Linnaean species of *Turritis*, *T. hirsuta* L. and *T. glabra* L., in the synonymy of two species of *Arabis* and specifically stated that he was merging the former genus with the latter. He indicated (p. 218) that, "les genres de l'*Arabis* & du *Turritis* de Linné n'étant nullement distingués entr eux par leur fructification, & n'ayant pas même les caractères qui leur ont été attribués, se trouvent réunis dans cet article."

through Tennessee (Wayne County) and North Carolina (Avery, Madison, and Watauga counties). Hopkins reported *A. glabra* from Little Rock, Arkansas, but E. B. Smith, apparently overlooking this record, excluded it from the state flora. The species is easily distinguished by its creamy-white to yellowish petals, hirsute stems with usually unbranched trichomes near the base, sagittate-amplexicaul cauline leaves, erect, appressed, subterete fruits 4.5–10 cm long, and numerous, usually biseriately arranged seeds.

A few authors have considered *Arabis glabra* to be a European plant wholly naturalized in North America. As shown by Rollins (1981, family references), however, the species is evidently part of the natural vegetation in numerous parts of the United States and is represented in North America by the widespread var. *glabra* and by the indigenous var. *furcatipilis* M. Hopkins. The latter is endemic to a few widely separated localities in California and Utah. A third variety, var. *pseudoturritis* (Boiss. & Heldr.) Fiori (Italy, Sicily, and the Balkan peninsula), has been treated as a distinct species by most European authors, who cite its winged, uniseriately arranged seeds, longer fruits, and shorter fruiting pedicels in separating it from *A. glabra*. Titz & Schnattinger, however, have demonstrated that these alleged differences have little taxonomic value and that the two taxa have no barriers preventing hybridization.

Arabis hirsuta (L.) Scop. (*Turritis hirsuta* L.), $2n = 32$, another circumpolar species, is represented in North America by four indigenous varieties, two of which occur in the Southeastern States. Varietas *pycnocarpa* (M. Hopkins) Rollins (*A. pycnocarpa* M. Hopkins, *A. ovata* sensu Small (1933); see Rollins (1941) for several additional synonyms), $2n = 32$, is widely distributed from Quebec west into British Columbia and Yukon, south to California, and east into Georgia (Floyd County). It grows in calcareous or sandy soils of cliffs, ledges, hillsides, and woods. The range of var. *adpressipilis* (M. Hopkins) Rollins (*A. pycnocarpa* var. *adpressipilis* M. Hopkins) extends from Missouri to Minnesota, east to Ontario, and south to central Tennessee (Rutherford, Wayne, and Wilson counties) and northern Arkansas (Carroll, Marion, and Washington counties). Gattinger's report of *A. hirsuta* from Tennessee (Cumberland Mtn.) probably should be referred to this variety. The type of pubescence on the stem is very important in distinguishing between these varieties. In var. *pycnocarpa* the trichomes are spreading and unbranched, while in var. *adpressipilis* they are appressed and malpighiaceous. Both varieties differ from the western North American ones, vars. *glabrata* Torrey & A. Gray and *Eschscholtziana* (Andrz.) Rollins, in having white to yellowish petals 3–5 mm long and strictly erect fruits. Rickett's report of *A. hirsuta* from Louisiana is doubtful; I have not seen any specimens from that state.

Titz (1972b) suggested that *Arabis hirsuta* is very likely an allotetraploid, the parents of which are *A. sagittata* (Bertol.) DC. and *A. ciliata* Clairv. (both with $2n = 16$). However, he later (1978b) concluded that this origin is unlikely because of the failure of *A. hirsuta* to cross with the synthetic allotetraploid of these species. *Arabis hirsuta* is easily distinguished from the other species of the genus in the Southeast by its erect, torulose, strongly compressed fruits, its winged, uniseriately arranged seeds, its sagittate cauline leaves, and its creamy-white flowers.

The third species, *Arabis lyrata* L. (*Erysimum lyratum* (L.) Kuntze, *Cardaminopsis lyrata* (L.) Hiitonen), sand cress, $2n = 16, 32$, is widely distributed in eastern Asia and in North America north of the 34th parallel. In the southeastern United States it is common in western North Carolina (disjunct in Jones County) and adjacent eastern Tennessee (disjunct in Davidson County) and is rare in northern Georgia and Mississippi (Lafayette County). It is a biennial or short-lived perennial that grows on sand, sandstone, or limestone. It is distinguished by its lyrate to pinnatifid lower leaves, sessile, nonauriculate cauline leaves, and ascending fruits (0.7–)2–4 cm long.

Arabis canadensis L. (*A. falcata* Michx.), sicklepod, $2n = 14$, grows in rich woods and thickets and on bluffs, rocky banks, and wooded dunes from central Maine west through Ontario to Minnesota and Iowa, south through Nebraska to Texas, and east throughout the Southeastern States. It is widespread in Arkansas, Tennessee, and western North and South Carolina and is sporadic in Georgia (Clarke, Early, Randolph, and Wilkes counties), Florida (Jackson, Liberty), Alabama (Lee, Madison, Tuscaloosa), Mississippi (Jefferson, Lee, Lowndes, Marshall, Noxubee), and Louisiana (Bossier Parish). The species is easily identified by its hirsute, oblong-lanceolate, often denticulate leaves attenuate and nonauriculate at the base, its flat, falcate, pendent or recurved fruits to 3.5 mm wide, and its broadly winged, uniseriately arranged seeds.

Arabis laevigata (Muhl. ex Willd.) Poiret (*Turritis laevigata* Muhl. ex Willd.; see Hopkins for six other synonyms), $2n = 14$, is a glaucous and completely glabrous biennial with undivided basal leaves and dentate to entire, auriculate cauline leaves, white petals scarcely exceeding the sepals, and falcate, recurved fruits 6–12 cm long. Of the two varieties generally recognized in the species, var. *laevigata* is widespread and grows in rich woodlands and river-bank thickets and on slopes and floodplains from Quebec west to South Dakota, south through eastern Colorado, Kansas, and Oklahoma, and east to Alabama and Georgia. It has not been recorded from Florida, Louisiana, or Mississippi and is here first reported for South Carolina (based on *Spongberg, Bozeman, & Logue 67–73*, GH, from McCormick County). Varietas *Burkii* Porter (*A. Burkii* (Porter) Small) grows on dry hillsides and bluffs in Pennsylvania, Maryland, West Virginia, Virginia, North Carolina (Swain and Watauga counties), and Tennessee (Knox County). It has been said to grow in Georgia (Radford *et al.*), but I have not seen any material from this state, and Duncan & Kartesz did not include it in their checklist. Varietas *Burkii* differs from var. *laevigata* in having nonauriculate, usually entire, linear-lanceolate cauline leaves instead of auriculate, usually denticulate, lanceolate to oblong-lanceolate ones.

Hopkins reduced *Arabis serotina* Steele (shale barrens of Virginia and West Virginia) to a synonym of *A. laevigata* var. *Burkii*. However, it differs from both varieties of *A. laevigata* in its lax, profusely branched, paniculate inflorescences, pendent flowers, and straight, pendent fruits, as well as in its late (mid-July through August) flowering. *Arabis laevigata* has racemose inflorescences, ascending flowers, and arcuate fruits, and it flowers early (late April to early June). This evidence supports the recognition of *A. serotina* as a distinct species (Wieboldt).

A very close relative of *Arabis laevigata*, with which it is confused, *A. mis-*

souriensis Greene (*A. viridis* Harger, *A. laevigata* var. *missouriensis* (Greene) Ahles), grows on bluffs and ledges, as well as in fields and sandy or rocky woodlands. It is distributed from Maine west to Wisconsin, south to southern Missouri, western and central Arkansas, and adjacent Oklahoma, and east to Georgia (Kenshaw Mtn., Cobb County), South Carolina (Lancaster County), and North Carolina (Anson, Burke, and Stanley counties). It has not been recorded from the other Southeastern States. *Arabis missouriensis* is distinguished from *A. laevigata* in having subappressed, more numerous, nonglaucous cauline leaves, lyrately pinnatifid basal leaves, petals nearly twice as long as the sepals, and fruit valves with a prominent midvein extending at least to the middle. The latter has fewer (to ca. 13), ascending, glaucous cauline leaves, dentate basal leaves, smaller petals hardly exceeding the sepals, and valves prominently veined only at the base. Hopkins recognized the pubescent forms of *A. missouriensis* (Indiana, Missouri, Wisconsin) as var. *Deamii* M. Hopkins. Although I have not seen adequate material of this taxon, it is doubtful that it merits recognition.

The range of *Arabis patens* Sullivan includes Pennsylvania and Indiana south to North Carolina (Madison County), Tennessee (Jefferson and Knox counties), Alabama (Bibb County), and Mississippi (Noxubee County). It grows in rocky places along creeks and rivers and on limestone on wooded slopes. It is distinguished by its hirsute stems with spreading, mostly unbranched trichomes, auriculate cauline leaves that are hirsute on both sides, saccate sepals, white petals (5–)7–10 mm long, divaricately ascending fruits 2.5–4.5 cm long, and winged seeds.

Arabis georgiana Harper, which is most closely related to *A. patens,* is a narrow endemic of the southeastern United States. It occurs on moist rock and rich alluvium along river banks in Georgia (Gordon, Muscogee, and Stewart counties) and Alabama (Bibb and Elmore counties). It differs from *A. patens* in having longer (6–7 vs. 2.5–4.5 cm) fruits and leaves with stalked, furcate or stellate (instead of simple) trichomes.

The two remaining species of *Arabis* in the Southeast are easily distinguished from the previous ones in having nonsaccate sepals, petals 2–4 mm long, pubescent fruits, and wingless seeds. *Arabis perstellata* E. L. Braun grows on clay loam over limestone in the shade of hardwood forests. It consists of two highly localized varieties. Varietas *perstellata* is known only from wooded hillsides at Elkhorn Creek in Franklin County, Kentucky, while var. *ampla* Rollins ($2n = 14$) is restricted to a calcareous bluff above the Stones River at Percy Priest Lake, northeast of Una, in Davidson County, Tennessee. The former is a densely pubescent plant to only 4 dm tall with basal leaves rarely longer than 4 cm, while var. *ampla* is sparsely pubescent, 4–8 dm tall, and with basal leaves 8–16 cm long.

Arabis Shortii (Fern.) Gleason (*A. perstellata* var. *Shortii* Fern.; *Sisymbrium dentatum* Torrey (1833), non Allioni (1785); *A. dentata* (Torrey) Torrey & A. Gray (1838), non Clairville (1811); *Iodanthus dentatus* (Torrey) Greene), $2n = 12$ (F. H. Smith), grows on limestone bluffs, cliffs, and floodplains, in rich woods, and along streams or riverbanks. It is distributed from New York west to Minnesota and South Dakota, south through Nebraska, Kansas, and Okla-

homa, and east to Arkansas (Marion County), Tennessee (Davidson and Montgomery counties), and Alabama (Bibb County). It is very rare and appears to be an endangered species in the Southeast.

All records of *Arabis perstellata* from states other than Kentucky and Tennessee are based on plants of *A. Shortii.* Several authors have recognized glabrous-fruited plants of the latter as *A. Shortii* var. *phalacocarpa* (M. Hopkins) Steyerm. (*A. dentata* var. *phalacocarpa* M. Hopkins, *A. perstellata* var. *phalacocarpa* (M. Hopkins) Fern.). The variety is rare in Iowa and Arkansas (Cleburne, Madison, and Pope counties) but is widespread in Missouri in counties where var. *Shortii* (with pubescent fruits) occurs. It is with some hesitation that I recognize varieties in this species. Field observations may well reveal that both glabrous and pubescent fruits are found in the same population and that no formal subdivisions of the species are needed.

Arabis perstellata is easily distinguished from *A. Shortii* in having pinkish petals 3–4.5 mm long, fruiting pedicels 5–9(–13) mm long, and sessile, stellate trichomes on the leaves. The latter species has creamy-white petals 1.5–2(–3) mm long, fruiting pedicels (1–)1.5–3 mm long, and primarily simple trichomes on the upper leaf surface and short-stalked ones on the lower. A few authors (e.g., Fernald, in family references; Voss) have reduced *A. Shortii* to a variety of *A. perstellata.* However, the morphological differences above are sufficient for recognition of both as distinct species.

Arabis alpina has been reported from Anderson County, Tennessee (Sharp *et al.*), but I have not seen any material from that area, and it is highly unlikely that the species is indigenous to the United States. Hopkins reported *A. alpina* from Greenland, Baffin Island, Labrador, Newfoundland, and Quebec, where it appears to be native.

Arabis is a natural genus characterized by its linear fruits that are almost always flattened parallel to the septum, its accumbent cotyledons, its compressed, usually marginate or winged seeds, its entire to dentate (never pinnatifid) cauline leaves, and its usually branched trichomes. The nearest American relative of *Arabis* is probably *Sibara* Greene, from which it differs in several characters (see *Sibara*). Species of *Arabis* having petiolate cauline leaves and fruit valves with prominent midveins have been transferred to *Cardaminopsis* (C. A. Meyer) Hayek. Although I have not studied this group thoroughly, I concur with Rollins (1941) in retaining the American segregates of *Arabis.*

A few recent European authors (e.g., Burdet, 1967, 1969; Cullen; Dvořák; Hedge) have recently maintained both *Arabis* and *Turritis.* The differences are said to be white to purple flowers, uniseriately arranged seeds, and flattened fruits in *Arabis,* and yellowish flowers, biseriately arranged seeds, and subterete fruits in *Turritis.* These differences, however, readily break down upon careful examination of both genera on a worldwide basis. As was shown by Rollins (1941), all of these differences break down within *A. glabra,* the type species of *Turritis.* Furthermore, *Arabis* and *Turritis* are indistinguishable in seed-coat anatomy, fatty-acid composition, and glucosinolate content. It is quite evident that the latter does not merit recognition.

Löve & Löve have segregated several North American species of *Arabis* as *Boechera* because they have a base chromosome number of seven instead of the eight that is characteristic of the Eurasian species. They and Weber stated that *Boechera* differs from *Arabis* in having entire leaves and clustered caudices, instead of dentate leaves and slender root systems. A casual observation of *Arabis* immediately reveals that these alleged morphological differences are both unrealistic and misleading. I fully agree with Rollins (in Rollins & Rüdenberg, 1977, p. 102) that *Boechera* "has no merit and should not be followed."

Protogyny is apparently more widespread in *Arabis* than was once believed. In addition to the ten protogynous species listed by Al-Shehbaz (1977), there are at least 12 others, of which *A. georgiana, A. laevigata, A. missouriensis, A. patens, A. perstellata,* and *A. Shortii* are reported here for the first time. Earlier observations (e.g., Knuth) of protogyny in *A. glabra* are confirmed by my study of plants growing in Cambridge, Massachusetts. Many species of *Arabis* that are facultatively or predominantly autogamous (e.g., the *A. hirsuta* complex (Titz, 1972b), *A. Holboellii* Hornem. (Johnson)) produce protogynous flowers under favorable conditions.

Böcher's (1951) discovery of agamospermy in diploid and tetraploid plants of *Arabis Holboellii* from Alaska and Greenland was the first record of this type of apomixis for the Cruciferae. He observed several abnormalities in mega- and microsporogenesis (often causing the formation of unreduced nuclei and the development of pollen as monads and dyads), found male nuclei in mature, unfertilized embryo sacs, and reported tetraploid and hexaploid endosperm in diploid and triploid plants, respectively. Johnson did not detect apomixis in *A. Holboellii* from Washington and concluded that his plants were sexual. Apomixis has also been suggested in *A. microphylla* Nutt. and *A. sparsiflora* Nutt. (Böcher, 1969), in *A. divaricarpa* A. Nelson, *A. Drummondii* A. Gray, and *A. Lyallii* S. Watson (Mulligan), and in *A. platysperma* A. Gray var. *platysperma* (Vorobik, 1985). The last author has observed that all of these species have a substantial seed set and very low pollen fertility. Supernumerary chromosomes have been observed in these apomictic species complexes, which are considered to be taxonomically difficult and puzzling. Rollins (1966) suggested that it is very likely that apomixis, hybridization, and polyploidy, whether occurring separately or together, are responsible for creating such highly variable species complexes.

Self-incompatibility has been reported for *Arabis Constancei* Rollins, *A. aculeolata* Greene, *A. modesta* Rollins, and *A. oregana* Rollins (Rollins, 1971; Vorobik, 1985). Polyembryony has been observed in *A. Lyallii* (Lebègue), *A. Halleri* L., and *A. hirsuta* (Miannay). Miannay has suggested that the additional embryos originate from the synergids either by apogamy or by fertilization.

Chromosome numbers have been reported for 84 species. For 44 species (52 percent) the base number is eight, for 34 species (41 percent) seven, and for the remainder six. Burdet (1967) has suggested that the base chromosome number for *Arabis* is four, but as shown by Titz (1968a), his assumption was not well founded. Fifty-five species (65 percent) are diploid, about 16 (ca. 20 percent) are exclusively polyploid, and the remainder have both diploid and

polyploid populations. Unlike *Cardamine,* in which about 62 percent of the species are exclusively polyploid, polyploidy has not played a major role in the evolution of *Arabis.*

Mulligan concluded that all species of *Arabis* indigenous to North America have a base chromosome number of seven, whereas the Asiatic and European species are based on eight. Rollins (1966) suspected that this correlation was based on phylogenetic rather than geographic relationships and suggested that in order to verify Mulligan's hypothesis, several North American species with obvious Asiatic relatives should be studied cytologically. Three such species (*A. aculeolata, A. modesta, A. oregana*) are now known to have $x = 8$ (Rollins & Rüdenberg; Vorobik, 1985). Other exceptions to Mulligan's useful correlation are three Old World species, *A. Turczaninowii* Ledeb. (Far East), *A. conringioides* Ball (Morocco), and *A. Brassica* (Leers) Rauschert (central Europe), all of which have $2n = 14$.

Although interspecific hybridization between many pairs of species has been suggested, only a few cases have been subjected to thorough study. Vorobik (1985) concluded that hybridization is uncommon among species of *Arabis* in Oregon and that complex patterns of variability, which have been attributed to hybridization, may have resulted from agamospermy, autogamy, and the colonizing tendencies of several species. Interspecific hybridization among the European members of the *A. hirsuta* complex is very rare and nearly always produces completely sterile hybrids (Novotná & Czapik, 1971, 1974; Titz, 1968a, 1970). Rollins (1983b) reported several cases of sympatry and putative hybridization between *A. Drummondii* and *A. Holboellii* and between the latter and *A. Williamsii* Rollins. He concluded that, due to the uniformity of the parental species and their intermediates and to the lack of hybrid swarms, apomixis probably dominates the reproductive patterns in these complexes. Rollins also suggested that *A. divaricarpa,* which is widely distributed in northern North America, is most likely derived from hybridization between *A. Drummondii* and *A. Holboellii* and that its present uniformity in many parts of its range may have resulted from facultative apomixis. Braun (1940) collected a supposed hybrid (*Braun 2216,* GH!) and its parents, *A. laevigata* and *A. perstellata,* all growing sympatrically at the type locality of the latter species. No further observations have been made on this or other putative hybrids of *Arabis* in the Southeast.

The glucosinolate profiles of at least 12 species of *Arabis* have been determined. Most species have large quantities of high homologues of methylsulfinylalkyl and methylthioalkyl groups. (Al-Shehbaz & Al-Shammary; Daxenbichler *et al.*; Hasapis *et al.*; Kjaer & Gmelin; Kjaer & Schuster; Rodman & Chew). The seeds of about 29 species show two very distinct patterns of fatty-acid composition, the chemotaxonomic value of which is not fully understood (Appelqvist; Mikolajczak *et al.*; Miller *et al.*; Kerber & Buchloh). Twenty-four species (including *A. alpina, A. caucasica* Willd., and the *A. hirsuta* complex) have high concentrations—(30–)40–67 percent—of linolenic acid and no erucic acid or only a trace (very rarely to 5 percent) of it. The remaining five species (including *A. glabra, A. Holboellii,* and *A. laevigata*) have smaller amounts—

18–30(–37) percent—of linoleic acid and higher concentrations (11–39 percent) of erucic acid.

Several species of *Arabis* are ornamentals, the most widely cultivated of which are *A. alpina* (mountain rockcress) and *A. caucasica* (wall rockcress). Many species have weedy tendencies, but none is a serious weed.

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33. **Sibara** Greene, Pittonia **3:** 10. 1896.

Annual or biennial herbs, usually glaucous above, glabrous or with simple, 2-forked, [or branched] trichomes. Stems erect to decumbent, simple or branched at base. Basal and lowermost cauline leaves petiolate, lyrately pinnatifid [to runcinate or pectinate]; lobes several to many, oblong to ovate [or narrowly linear to filiform], entire or dentate. Upper cauline leaves often similar to the basal ones but usually smaller and less divided, not auriculate [or auriculate to sagittate] at base. Inflorescence an ebracteate, corymbose raceme, greatly elongated in fruit; flowers inconspicuous [or showy]; fruiting pedicels slender [or stout and nearly as wide as the fruit]. Sepals oblong to ovate, purple or green, erect [to spreading], nonsaccate or the inner pair slightly saccate at base, glabrous to sparsely pubescent, membranaceous at margin. Petals white to pinkish [or purple], obtuse [or emarginate] at apex, undifferentiated [or strongly differentiated] into claw and blade. Lateral nectar glands subtending or surrounding the bases of outer stamens; median glands obsolete or absent. Stamens 6, slightly tetradynamous; anthers ovate [to oblong], usually sagittate at base. Fruits linear, torulose [or smooth], flattened parallel to the septum [or terete], subsessile to short stipitate, straight [or arcuate], erect to divaricate [or reflexed]; valves glabrous [or pubescent], obscurely [to prominently] nerved [or nerveless]; septum complete, hyaline; styles obsolete to 1[–5] mm long, conical [cylindrical, or subclavate]; stigmas entire to obscurely 2-lobed. Seeds orbicular [to oblong], compressed [or plump], narrowly winged [or wingless], reticulate, uniseriately arranged, copiously [to only slightly] mucilaginous when wet; cotyledons accumbent [or incumbent]. Base chromosome number 8 [or 7]. (Including *Planodes* Greene.) TYPE SPECIES: *S. angelorum* (S. Watson) Greene. (Name an anagram of *Arabis.*)

A genus of ten species distributed primarily in central Baja California, southeastern California, southwestern Nevada, southern Texas, and central and

northeastern Mexico. *Sibara virginica* (L.) Rollins (*Cardamine virginica* L., *Arabis virginica* (L.) Poiret, *Planodes virginicum* (L.) Greene, *C. hirsuta* L. var. *virginica* (L.) Torrey & A. Gray, *C. parviflora* L. subsp. *virginica* (L.) O. E. Schulz, *C. ludoviciana* W. J. Hooker, *A. ludoviciana* (W. J. Hooker) C. A. Meyer), $2n = 16$, is the most widely distributed member of the genus. It is a weed of open areas, pastures, old fields, clearings, waste places, wet woods, and roadsides from southern and central Texas north through central Oklahoma to southeastern Kansas, eastward into Virginia, and southward throughout the Southeastern States. It is disjunct and rare in central and southern California and adjacent Baja California.

Sibara angelorum, S. pectinata (Greene) Greene, *S. laxa* (S. Watson) Greene, and *S. Brandegeana* (Rose) Greene are narrowly endemic to the lower Sonoran zone of central Baja California, where they grow in sandy or rocky areas among shrubs and trees. *Sibara filifolia* (Greene) Greene is endemic to Santa Cruz Island (California), while both *S. rosulata* Rollins and *S. deserti* (M. E. Jones) Rollins are widespread among creosote-bush scrub in the Death and Saline valleys (California) and in Nye County (Nevada). The remaining species, *S. runcinata* (S. Watson) Rollins (southern Texas south into Puebla, Mexico) and *S. mexicana* (S. Watson) Rollins (Guanajuato, Mexico), together with *S. virginica,* form a well-defined group that differs from the other seven species in its winged, instead of wingless, seeds and its runcinate-pinnatifid, instead of pectinate, leaves.

Species of *Sibara* were previously placed in both *Cardamine* and *Arabis.* As shown by Rollins (1941), however, *Sibara* is easily distinguished from *Arabis* in having petiolate, lyrately pinnatifid to pectinate cauline leaves that resemble the basal ones, no median nectar glands, and fruiting pedicels with unexpanded tips. In *Arabis* the cauline leaves are often morphologically different from the basal ones and are not deeply divided, the median nectar glands are usually well developed, and the fruiting pedicels are expanded below the receptacle. *Sibara virginica* is often confused with *C. hirsuta* and *C. parviflora,* but *Cardamine* has elastic dehiscence of the fruits, spiral coiling of the valves, a narrowly winged replum, and wingless seeds.

Chromosome numbers are known for six species, five of which—*S. angelorum, S. laxa, S. runcinata* (including *S. Viereckii* (O. E. Schulz) Rollins), *S. pectinata,* and *S. deserti*—are tetraploid ($x = 7$). The last species was previously considered to have $2n = 26$, but the most recent count (Rollins & Rüdenberg, 1971) suggests that it has $2n = 28$. Counts for *S. virginica* from material collected in Alabama and Tennessee indicate that it is a diploid, with $2n = 16$. More counts are needed to clarify the chromosomal evolution of *Sibara.*

Only *Sibara virginica* has been surveyed for secondary constituents. The seeds contain high concentrations (44 percent) of erucic acid and smaller amounts (12–17 percent) of eicosenoic, linoleic, and oleic acids (Mikolajczak *et al.*). They also contain three mustard-oil glucosides, 2-hydroxy-2-phenylethyl, 7-methylsulfinylheptyl, and 8-methylsulfinyloctyl glucosinolates (Gmelin *et al.*). It has been suggested that the presence of the last two compounds and of their related nitriles in *Sibara* supports the close association of the genus with both *Rorippa* (as *Nasturtium*) and *Arabis* (MacLeod & MacLeod).

Except for *Sibara virginica,* which is weedy throughout its range, the genus has no economic value.

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Under tribal references see CLEWELL; CORBETT; CORRELL & CORRELL; DUNCAN & KARTESZ; ELLIS *et al.*; GATTINGER; HEBEL; JONES (1975); MACLEOD & MACLEOD; MACROBERTS; MIKOLAJCZAK *et al.*; MOHR; MOORE; PATMAN; ROLLINS *et al.*; SHARP *et al.*; and SMALL. Under references to *Arabis,* see HOPKINS; KERBER & BUCHLOH; and ROLLINS (1941).

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35. **Rorippa** Scopoli, Fl. Carniol. ed. 1. 520. 1760.

Annual, biennial, or rhizomatous perennial herbs, usually of wet or aquatic habitats, glabrous or pubescent, trichomes unbranched, slender or vesicular. Stems erect to prostrate, leafy, sometimes with adventitious roots from the lower nodes. Basal leaves petiolate or rarely subsessile, entire, dentate, sinuate, lyrate, pinnatisect, or pectinate [rarely bi- or tripinnatisect], occasionally auriculate at base, sometimes forming well-developed rosettes; cauline leaves usually resembling the basal ones but progressively smaller upward. Inflorescence an ebracteate [or bracteate], terminal or lateral, few- to many-flowered, corymbose raceme, greatly [or only slightly] elongated in fruit; fruiting pedicels usually with a pair of minute glands at base. Sepals erect to spreading, ovate to oblong or lanceolate, caducous [or persistent], glabrous or pubescent, usually membranaceous at margin; lateral pair not saccate or slightly [to strongly] so at base. Petals pale to bright yellow, sometimes white or lavender, oblong or

oblanceolate to broadly spatulate, undifferentiated to sharply differentiated into blade and claw, longer to shorter than sepals, sometimes vestigial or absent. Lateral nectar glands ringlike or horseshoe shaped; median glands a narrow rim, [toothlike,] or absent, sometimes all glands forming a ring subtending bases of filaments. Stamens 6, tetradynamous [rarely 4 (the lateral pair lacking) and equal in length]; filaments linear, free, unappendaged, usually dilated at base; anthers ovate to oblong, sometimes sagittate at base, obtuse or apiculate at apex. Fruits oblong to linear [or globose], terete, dehiscent [very rarely indehiscent], torulose or smooth; valves 2 [rarely 3–6], thin and papery to coriaceous, glabrous or pubescent, obscurely nerved or nerveless; septum membranaceous, complete, with or without a midvein; styles persistent; stigmas capitate, entire or slightly 2-lobed. Seeds several to numerous, uniseriately or biseriately arranged, oblong to ovoid or cordiform, yellow to reddish brown, colliculate to rugose, tuberculate, foveolate, or reticulate, wingless [or rarely narrowly winged], nonmucilaginous [or mucilaginous] when wet; cotyledons accumbent. Base chromosome numbers 5–8, 11, 12. (Including *Baeumerta* Gaertner, Meyer, & Scherb.,[10] *Brachiolobus* All., *Cardaminum* Moench, *Caroli-Gmelina* Gaertner, Meyer, & Scherb., *Clandestinaria* Spach, *Dictyosperma* Regel, *Kardamoglyphos* Schlecht., *Nasturtium* R. Br., *Pirea* T. Durand, *Radicula* Dill. ex Moench,[11] *Sisymbrianthus* Chev., *Tetrapoma* Turcz. ex Fischer & Meyer.) TYPE SPECIES: *Sisymbrium sylvestre* L. = *R. sylvestris* (L.) Besser.[12] (Name a Latinized form of Old Saxon *rorippen,* used for some mustards.)—YELLOW CRESS.

A well-marked genus of about 80 species distributed on all continents except Antarctica. About 23 species are indigenous to North America, ten to South America, 25 to Europe and Asia, 12 to Africa, five to Australia and New Zealand, four to New Guinea, and one to Polynesia. *Rorippa* is represented in the southeastern United States by eight species, three of which are naturalized weeds. The genus has no xerophytic members, and the great majority of its species grow in open, wet or damp, often disturbed habitats, particularly along streams, rivers, ditches, roadsides, and railroad tracks and in lakes, marshes, and swales.

The sectional classification of *Rorippa* has not been treated adequately on a worldwide basis. De Candolle (1821, 1824) recognized three sections, and Schulz (1936), who united *Nasturtium* and *Rorippa* but wrongly chose the later-

[10]The generic names *Baeumerta, Cardaminum, Dictyosperma,* and *Pirea* are all synonyms of *Nasturtium,* if this is treated as a genus distinct from *Rorippa.* The generic name *Nasturtium* should not be confused with the common English name nasturtium, which is *Tropaeolum majus* L. of the Tropaeolaceae.

[11]*Radicula* was invalidly published when first used by Hill (Brit. Herb. 264. 1756) because "it coincides with the technical term 'radicula' (radicle) and was not accompanied by a specific name in accordance with the binary system of Linnaeus" (ICBN, Article 20.2, Example 2. 1983). Moreover, when the name was later validated by Moench (Meth. 262. 1794), it lacked priority.

[12]Abrams has wrongly designated *Sisymbrium amphibium* L. as the type of *Rorippa.* Scopoli (Fl. Carniol. 520. 1760) recognized a single species (without giving a binomial), cited the exact phraseology of Linnaeus (Sp. Pl. 2: 657. 1753) for *S. sylvestre,* and did not refer to *S. amphibium.* Therefore, *S. sylvestre* is the type species of *Rorippa.*

published *Nasturtium* for the combined genus, recognized six. Two of Schulz's sections are monotypic, and the remaining four are heterogeneous with evidently artificial boundaries. They were defined without a proper consideration of geography. For example, sect. CLANDESTINARIA (Spach) DC. includes several widely disjunct, unrelated species, each of which is indigenous to South America, the West Indies, North America, China, southeastern Asia, or South Africa. As presently delimited, almost all sections of *Rorippa* need careful evaluation of their boundaries, but it is beyond the scope of this flora to do that. Therefore, I am using a few sectional names only to provide a workable framework.

About 50 species of *Rorippa,* including all except two of the North American ones (see below), probably belong to sect. RORIPPA (sect. *Brachylobos* DC., sect. *Sinuatae* Stuckey) (petals yellow; median nectaries usually connate with the larger, lateral ones; fruits linear to oblong or globose; seeds biseriately arranged, reticulate to colliculate). Stuckey (1972) placed six species in sect. SINUATAE, which was said to differ from sect. RORIPPA in having sinuate leaves that form basal rosettes. Differences in these vegetative characters, however, are unreliable, and sect. SINUATAE is an artificial group of doubtful value.

Perhaps the most controversial group is sect. CARDAMINUM (Moench) DC. (*Nasturtium* R. Br.; see footnote 10 for other synonyms) (petals white, median nectaries absent, fruits linear, seeds reticulate, leaves pinnate, lower nodes with adventitious roots). Many European authors recognize the section as a distinct genus, *Nasturtium,* closely related to *Rorippa.* All of the alleged differences that are said to distinguish *Nasturtium* (or sect. CARDAMINUM) from the rest of *Rorippa* break down in various combinations when the latter is carefully studied on a worldwide basis. Numerous species of *Rorippa* indigenous to the Southern Hemisphere, including the South American sect. KARDAMOGLYPHOS (Schlecht.) Martínez-Laborde, have white flowers, median nectaries, and various seed-coat configurations (Al-Shehbaz & Rollins). There are no adequate grounds to support the maintenance of *Nasturtium* as distinct from *Rorippa*; I therefore strongly support its reduction to synonymy.

Two of the five species assigned by Schulz (1936) to sect. CARDAMINUM are North African taxa treated by Maire as subspecies of *Rorippa africana* (J. Br.) Maire. Two others are North American plants now known as *R. Gambellii* (S. Watson) Rollins & Al-Shehbaz (southern California and central Mexico) and *R. floridana* Al-Shehbaz & Rollins (Florida) (see Al-Shehbaz & Rollins for further details). The fifth species, *R. Nasturtium-aquaticum* (L.) Hayek (*Sisymbrium Nasturtium-aquaticum* L., *Nasturtium officinale* R. Br., *Rorippa Nasturtium* (L.) Rusby; see Markgraf and Sprague (1924) for 10 additional synonyms), watercress, sturshum (Small, 1933), $2n = 32$, is a Eurasian cultivated plant and weed naturalized throughout the world. It grows in all of the Southeastern States in quiet or fast-flowing streams, springs, rivers, ditches, brooks, areas of seepage, as well as in swamps, shallow ponds, and pools. Watercress sometimes forms extensive beds, particularly in alkaline waters containing nitrate (Howard, 1976), but only rarely does it grow on wet grounds. All seven of the previously recognized "varieties" of *R. Nasturtium-aquaticum* were based on minor variations in leaf characters, which can be found within the

same population or sometimes even on the same plant (Airy Shaw, 1949; Green, 1962).

Britton & Brown and Small (1933) retained *Rorippa Nasturtium-aquaticum* in *Sisymbrium,* where it was initially placed by Linnaeus (Sp. Pl. **2:** 657. 1753), but they treated the genus as monotypic. As shown by Payson, however, Britton & Brown mishandled the lectotypification of *Sisymbrium* by arbitrarily choosing the first of the 16 Linnaean species listed in *Species Plantarum.*

Rorippa floridana Al-Shehbaz & Rollins (*Cardamine curvisiliqua* Shuttelw., *Nasturtium stylosum* Shuttelw. ex O. E. Schulz), coastal watercress (Small, family references), $2n = 32$, is a submersed or floating plant endemic to Florida (Brevard, Citrus, Clay, Collier, Columbia, Dade, Duval, Gilchrist, Hillsborough, Lake, Levy, Manatee, Marion, Seminole, Sumter, Taylor, Volusia, and Wakulla counties). A few authors (e.g., Clewell; Godfrey & Wooten; Rollins, 1978) have recently reported the European *R. microphylla* (Boenn. ex Reichenb.) Hylander (*N. microphyllum* Boenn. ex Reichenb.; see Airy Shaw (1947) and Markgraf for eight additional synonyms), watercress, $2n = 64$, as naturalized in Florida. Al-Shehbaz & Rollins have shown, however, that all of these records are based on plants of *R. floridana* and that there are no authentic records from the Southeastern States for *R. microphylla,* which is only sporadically distributed in North America.

Deeply submersed plants of *Rorippa floridana, R. microphylla,* and *R. Nasturtium-aquaticum* produce simple (instead of pinnately lobed) leaves, which are characteristic of emergent, floating, or shallowly submersed plants. Rollins (1978) has demonstrated that plants of *R. floridana* (as *R. microphylla*) exhibit high phenotypic plasticity and that leaf morphology can be reversed easily from simple to pinnately lobed, or vice versa, by manipulating the depth at which a given plant is grown. Michaelis has indicated that *R. microphylla* can grow at depths of up to 22 feet (6.5 m).

Rorippa Nasturtium-aquaticum is easily distinguished from both *R. floridana* and *R. microphylla* by its biseriately arranged, coarsely reticulate seeds with 25–50(–60) large areolae on each side and its septum that usually has a distinct midvein. The last two species have uniseriately arranged, moderately to minutely reticulate seeds with more than 100 areolae on each side and have a nerveless septum. The differences among these species are further discussed in Al-Shehbaz & Rollins. *Rorippa floridana* differs from *R. microphylla* in having minutely reticulate seeds with 400–500 areolae on each side and in having emergent leaves with a nonauriculate petiole base and one or two pairs of lateral lobes. On the other hand, *R. microphylla* has moderately reticulate seeds with 100–150(–175) areolae on each side and has emergent leaves with a minutely auriculate petiole base and two to six (rarely one) pair(s) of lateral lobes. They also differ in chromosome number: $2n = 32$ in *R. floridana* (Rollins & Rüdenberg) and $2n = 64$ in *R. microphylla.*

It is often difficult to distinguish between *Rorippa microphylla* and *R. Nasturtium-aquaticum* in material without fruits. Howard & Lyon (1950, 1952) indicated that *R. Nasturtium-aquaticum* has introrse anthers and petals ca. 4 mm long, while *R. microphylla* has extrorse anthers and petals ca. 6 mm long.

On the other hand, Green (1955) and Rowson (in Howard & Manton, 1946) observed smaller pollen and a higher stomatal index (15–18 percent, vs. 10–12 percent) in the former species. These differences, however, are much harder to observe than those of the fruiting material. The two species also differ in their chromosome numbers and, as shown below, produce sterile interspecific hybrids.

The Asian *Rorippa indica* (L.) Hiern (*Sisymbrium indicum* L., *R. indica* (L.) Bailey, *Nasturtium indicum* (L.) DC., *N. montanum* Wall. ex J. D. Hooker, *R. montana* (Wall. ex J. D. Hooker) Small, *S. sinapis* Burman f., *N. sinapis* (Burman f.) O. E. Schulz, *R. sinapis* (Burman f.) Ohwi & Hara, *S. atrovirens* Hornem., *N. atrovirens* (Hornem.) DC., *R. atrovirens* (Hornem.) Ohwi & Hara, *N. heterophyllum* Blume, *R. heterophylla* (Blume) Williams, *Radicula heterophylla* (Blume) Small), $2n = 16, 32, 48, 56$, probably reached North America ca. 1900. Uncommon in the United States (Rollins, 1981), it has been collected from several widely separated localities in Mississippi and Louisiana (Darwin *et al.*, Rickett). *Rorippa indica* is highly variable in petal size, fruit length, leaf margin, and chromosome number, but most of this variation is poorly understood. The taxonomy of this complex is evidently confused, and Schulz (1934) has listed more than 40 synonyms in three species (as *N. indicum, N. sinapis,* and *N. montanum*), all of which probably belong to one polymorphic species. In southeastern Asia, where *R. indica* is indigenous, forms with petals (var. *indica*) and without (var. *apetala* (DC.) Hochr.) are known. These were recognized by Stuckey (1972) as *R. indica* and *R. heterophylla,* respectively. It is evident, however, that the presence or absence of petals was overemphasized and that the two forms are otherwise indistinguishable. Plants of this complex naturalized in North America should be called *R. indica* var. *apetala* (Rollins, 1969). They are easily distinguished from the other annual or biennial rorippas by their small flowers with petals lacking or reduced, their spreading fruiting pedicels 1.5–5 mm long, their linear fruits (1–)1.5–3 cm long, their small, reticulate, uniseriately arranged seeds, and their denticulate, simple or lyrately lobed to pinnatisect, nonauriculate leaves.

Rorippa sylvestris (L.) Besser (*Sisymbrium sylvestre* L., *Nasturtium sylvestre* (L.) R. Br., *Radicula sylvestris* (L.) Druce; see Jonsell (1968) for six additional synonyms), yellow cress, creeping yellow cress, $2n = 32, 40, 48$, is a perennial European and western Asiatic weed that became established in North America as early as 1818 (Stuckey, 1966a). It is common in the northeastern United States and southern Canada and is sporadic elsewhere in North America. It has been reported from all of the Southeastern States except South Carolina, Georgia, and Florida, where it is also likely to be found. *Rorippa sylvestris* grows in a wide range of habitats and as a weed is very difficult to eradicate since it is capable of producing new plants from very small fragments of root. It is highly self-incompatible and rarely sets seeds. The species is distinguished from the other crucifers of the Southeast by its perennial habit with adventitious shoots from root runners, its yellow petals usually 3–5.5 mm long, its spreading fruiting pedicels 4–10(–12) mm long, its often aborted fruits (9–22 mm long when bearing seed), and its deeply pinnatisect leaves with four to six pairs of entire to deeply divided lateral lobes.

The four remaining species of *Rorippa* in the southeastern United States are indigenous. *Rorippa sessiliflora* (Nutt. ex Torrey & A. Gray) Hitchc. (*Nasturtium sessiliflorum* Nutt. ex Torrey & A. Gray, *Radicula sessiliflora* (Nutt. ex Torrey & A. Gray) Greene, *N. limosum* Nutt. ex Torrey & A. Gray, *Radicula limosa* (Nutt. ex Torrey & A. Gray) Greene), yellow cress, marsh cress, $2n = 16$, is distributed throughout all of the Southeastern States, west to central Texas, north to Nebraska, Iowa, and Wisconsin, and east to Virginia. It grows on mud, gravel, or sand along creeks, streams, and rivers, as well as in ponds and wet fields. It is most common in the central United States, particularly in the Mississippi Embayment. *Rorippa sessiliflora* is a glabrous, apetalous annual with small (3–10 × 1.5–3.3 mm), linear fruits borne on pedicels 0.5–1.5 mm long and numerous (ca. 75–100 per locule) foveolate, yellowish brown seeds about 0.5 mm long. Schulz (1936) placed *R. sessiliflora* (as *Nasturtium*) in his highly artificial sect. CLANDESTINARIA, which included no other North American representatives. I support Stuckey's (1972) placement of the species with its relatives of sect. RORIPPA.

Rorippa sinuata (Nutt. ex Torrey & A. Gray) Hitchc. (*Nasturtium sinuatum* Nutt. ex Torrey & A. Gray, *N. trachycarpum* A. Gray, *R. trachycarpa* (A. Gray) Greene, *Radicula sinuata* (Nutt. ex Torrey & A. Gray) Greene, *Radicula trachycarpa* (A. Gray) Rydb.), spreading yellow cress, $2n = 16$, is very rare in the Southeast, where it has been collected from Clay, Crawford, and Pulaski counties, Arkansas (Smith; Stuckey, 1972). It is widely distributed from Missouri north through Illinois to western Wisconsin, and west through all of the Mountain (except Utah), Pacific, and Southwestern states. It is sporadic in Alberta, British Columbia, and Saskatchewan, Canada. *Rorippa sinuata* grows in a wide range of soil types and habitats (see Stuckey, 1972). It is a perennial with vesicular, hemispherical trichomes that become scalelike on pressed specimens. It is easily distinguished from other species with such trichomes by its sinuate to pinnatifid lower leaves, its usually auriculate cauline leaves, its oblong to spatulate petals that are longer (3.5–6 mm long) than the sepals, its divaricate to recurved fruiting pedicels (3.5–)5–12(–15) mm long, and its colliculate seeds. *Rorippa sinuata* is closely related to *R. ramosa* Rollins, from which it differs in several features discussed by Rollins (1961).

Another species with vesicular trichomes is *Rorippa teres* (Michx.) Stuckey (*Cardamine teres* Michx., *Sisymbrium Walteri* Ell., *R. Walteri* (Ell.) Mohr, *N. tanacetifolium* Hooker & Arnott; see Stuckey (1966b) for 14 additional synonyms). Stuckey (1972) recognized two varieties in the species. The first, var. *teres,* is widely distributed on the Atlantic and Gulf Coastal plains from North Carolina to Florida, west to central Texas and is sporadic in scattered localities in Mexico. It has been reported from all of the Southeastern States except Tennessee. Although Mohr stated that it grows in Arkansas and Stuckey (1972) mapped it from the south-central part of the state, I have seen no specimens that support these records. Smith indicated that it is either rare or a waif in Arkansas.

The second variety, var. *Rollinsii* Stuckey, is distributed primarily along the western coast of Mexico and the eastern coast of Honduras and Nicaragua. It differs from var. *teres* in having shallowly foveolate seeds, pubescent fruits,

fruiting pedicels with vesicular trichomes, and glabrous lower stems and upper leaf surfaces. In var. *teres* the seeds are deeply foveolate and the fruits and pedicels are glabrous; the lower stems and upper leaf surfaces bear vesicular trichomes (Stuckey, 1972). *Rorippa teres* is closely related to *R. portoricensis* (Sprengel) Stehlé, from which (in addition to other annual rorippas with vesicular trichomes) it differs in having pinnately lobed leaves with dentate or deeply divided lobes, short (1–2 mm) petals equaling or shorter than the sepals, styles 0.5–1.5 mm long, ascending to divaricate fruiting pedicels 1.5–5 mm long, and foveolate seeds.

Stuckey (1972) suggested that perennial habit, long petals exserted from the calyx, long and apiculate anthers, few and large seeds, and long pedicels, fruits, and styles are primitive, while annual habit, short petals included in the calyx (or absent), short and notched anthers, numerous and smaller seeds, and short pedicels, fruits, and styles are advanced. He considered *Rorippa sinuata, R. teres,* and *R. sessiliflora* to be primitive, intermediate, and advanced, respectively.

Rorippa palustris (L.) Besser (*Sisymbrium amphibium* L. *α palustre* L.; see Jonsell (1968) and Stuckey (1972) for 17 additional synonyms), marsh yellow cress, marsh cress, yellow watercress, $2n = 32$, is the most widely distributed species of the genus. It has an almost complete circumpolar distribution: it is native to North America, Asia, and Europe, apparently introduced in Greenland, Central America, and North Africa, and evidently naturalized in South America, the remainder of Africa, Australia, and New Zealand (Jonsell, 1968). Stuckey (1972) mapped the species as occurring in all of the Southeastern States except Mississippi and Alabama, but Jones (1975) reported it from the former, and it is very likely to be found in the latter.

The infraspecific taxonomy of *Rorippa palustris* is more controversial than that of any other *Rorippa.* Jonsell (1968) recognized four subspecies, of which three are indigenous to North America and the fourth is cosmopolitan, whereas Stuckey (1972) recognized four subspecies and 11 varieties in North America alone. The species contains many morphological extremes that are connected with each other by numerous intermediates that show continuous variation in nearly every character. The lack of sharply defined infraspecific taxa in *R. palustris* makes it rather difficult to identify many of the collected specimens satisfactorily. In this highly variable and widely distributed species, the variation should not be ignored, and some formal groups must be recognized. I am only tentatively accepting Jonsell's (1968) four subspecies, which he described (pp. 158, 159) as "indistinctly delimited." Of these, only one grows in the Southeast.

Subspecies *Fernaldiana* (Butt. & Abbe) Jonsell (*R. islandica* (Oeder ex Murray) Borbás var. *Fernaldiana* Butt. & Abbe, *R. islandica* subsp. *Fernaldiana* (Butt. & Abbe) Hultén, *R. palustris* subsp. *glabra* (O. E. Schulz) Stuckey var. *Fernaldiana* (Butt. & Abbe) Stuckey), $2n = 32$, is widespread in the Southeastern States. It is easily distinguished from the other rorippas by its petals 0.8–2 mm long that are subequal to the sepals, its ovoid to oblong fruits 2.5–7 mm long, its fruiting pedicels subequaling the fruits, and its lack of vesicular trichomes. Records of subsp. *hispida* (Desv.) Jonsell (as a variety or a species)

from Florida and Louisiana (Fernald), Tennessee (Sharp *et al.*), and North Carolina (Small, 1933) are most likely based on plants of subsp. *Fernaldiana.*

Many authors (e.g., Coode & Cullen; Fernald, 1928; Hedge & Rechinger; Radford *et al.*; Valentine) have reduced *Rorippa palustris* to a synonym of *R. islandica.* Jonsell (1968) and Stuckey (1972), however, have demonstrated that these are closely related, very distinct species and that all records of *R. islandica* from North America represent misidentifications of plants of *R. palustris.* According to Jonsell (1968), *R. islandica* consists of two varieties, of which one, var. *islandica,* is restricted to the Alps, Pyrenees, and European North Atlantic region (Greenland, Iceland, Norway, the British Isles), and the other, var. *Dogadovae* (Tzvelev) Jonsell, is confined to certain river systems of eastern Russia and adjacent Siberia. Plants of *R. islandica* are prostrate diploids ($2n = 16$) with nonauriculate cauline leaves, sepals and petals 1–1.5 mm long, finely colliculate seeds, and fruits two or three times longer than the pedicels. On the other hand, *R. palustris* is an erect tetraploid ($2n = 32$) with auriculate cauline leaves, sepals and petals 1.6–2.6 mm long, coarsely colliculate seeds, and fruits less than twice as long as the pedicels (Jonsell, 1968; Stuckey, 1972). Berggren indicated that the diameter of the seed-coat colliculae is about 65 μm in *R. palustris* and 35 μm in *R. islandica.*

Some plants of *Rorippa palustris* produce unusual fruits with three or four valves together with the normal two-valved ones. The production of four (rarely six) valves, however, is a constant feature of *R. barbareifolia* (DC.) Kitagawa (Alaska, Siberia). Such fruits, which are also found in the unrelated western North American *Tropidocarpum* W. J. Hooker, are very rare and must have evolved independently within the Cruciferae. They have little or no taxonomic value in *Rorippa* (Gerber; Stuckey, 1972).

The Eurasian *Rorippa amphibia* (L.) Besser and the European *R. austriaca* (Crantz) Besser are both naturalized in North America, but neither has been reported from the Southeastern States.

Rorippa has traditionally been associated with *Barbarea, Cardamine,* and *Arabis,* from which it is distinguished by its yellow (sometimes white) flowers, its terete, obscurely nerved, nonelastically dehiscent fruits, and its wingless, colliculate or foveolate to reticulate, usually nonmucilaginous, biseriately (rarely uniseriately) arranged seeds. Von Hayek suggested that *Rorippa* was derived from *Barbarea* and was ancestral to both *Armoracia* and *Cardamine,* while Schulz (1936) associated it with *Sisymbrella* Spach (two species; southwestern Europe and North Africa). The last is distinguished from *Rorippa* in having attenuate fruits and mucilaginous seeds.

The reproductive biology of most species of *Rorippa* is poorly studied. *Rorippa amphibia, R. austriaca,* and *R. sylvestris* are highly self-incompatible perennials that rarely set seeds because they often form "pure" clones by vegetative reproduction. Both *R. microphylla* and *R. Nasturtium-aquaticum* are self-compatible (Howard, 1976). Petals of the latter show high ultraviolet reflectance at the claws and high absorbance at the blades (Horovitz & Cohen). *Rorippa palustris* is autogamous (Jonsell, 1968), and I believe that both *R. indica* and *R. sessiliflora* are highly autogamous because of their small, apetalous flowers.

Chromosome numbers are known for about 30 species; all except five are based on $x = 8$ (author's compilation). Polyploidy, which occurs in about 45 percent of the species, probably played an important role in the evolution of *Rorippa*. Aneuploidy is rare in the genus and occurs in both *R. indica* and *R. benghalensis* (DC.) Hara. The lowest chromosome number, $2n = 10$, has been reported for *R. subumbellata* Rollins (Rollins, 1966), while the highest, $2n = 64$, is known for *R. microphylla*. In *R. amphibia* both diploid and tetraploid plants based on eight are known. The diploid race is not as widely distributed as the tetraploid, and their natural triploid hybrid has been verified (Jonsell, 1968). In *R. sylvestris* ($x = 8$) tetraploid and hexaploid plants, as well as their pentaploid hybrid, have been found in numerous parts of Europe and North America. Mulligan & Munro concluded that the tetraploid race of *R. sylvestris* is more common in Europe (68 percent of the sample) than in North America (20 percent), while the reverse is true for the hexaploid race (65 percent in North America and 29 percent in Europe).

Natural interspecific hybridization between pairs of *Rorippa amphibia, R. austriaca, R. palustris,* and *R. sylvestris* has been documented in all six possible combinations. Their hybrids have been formally recognized and are listed by Stace. Mulligan & Munro have reported a sterile pentaploid hybrid between *R. sylvestris* (hexaploid) and *R. palustris* (tetraploid). A sterile, triploid ($2n = 24$), first-generation hybrid between the last species and *R. barbareifolia* has also been found (Mulligan & Porsild, 1968). Tetraploids of *R. amphibia* and *R. sylvestris* produce fertile hybrids that often introgress with both parents. Their hybrid is widely distributed and has been reported from at least 20 European countries (Stace). Hybridization between *R. amphibia, R. austriaca,* and *R. sylvestris,* all of which are strongly outbreeding perennials, has completely obliterated species boundaries along several river systems in eastern and central Europe. These hybrid complexes persist for many years by vegetative reproduction (Jonsell, 1968).

The hybrid *Rorippa Nasturtium-aquaticum* ($2n = 32$) × *R. microphylla* ($2n = 64$), *R.* ×*sterilis* Airy Shaw, brown cress ($2n = 48$), is widespread in Europe (Stace) but rare in the United States, where it has been reported from New Hampshire, Connecticut, Michigan, and Idaho (Green, 1962). A highly sterile plant with 20 percent "good" pollen of variable size, it reproduces only vegetatively. It has been obtained experimentally by using *R. microphylla* as the ovulate parent but not by the reciprocal cross. The production of 16 bivalents and 16 univalents in this hybrid indicates that *R. microphylla* is an allotetraploid and that *R. Nasturtium-aquaticum* is one of its parents (Howard & Manton, 1946). The second parent of *R. microphylla* is unknown, but a species of *Cardamine* with uniseriate seeds and a chromosome number of $2n = 16$ has been suggested (Howard, 1976; Howard & Manton, 1940, 1946). Interspecific hybridization between *R. floridana* and *R. Nasturtium-aquaticum* has been suggested (Al-Shehbaz & Rollins).

Only *Rorippa Nasturtium-aquaticum* has been thoroughly studied for volatile constituents and for fatty acids. It contains large amounts (80 percent) of 2-phenylethylglucosinolate, smaller amounts of 8-methylthiooctyl (7 percent)

and 7-methylthioheptyl (12 percent) glucosinolates, and a trace of benzylglucosinolate (Gil & MacLeod; MacLeod & Islam). Larger and smaller amounts of the first and second compounds, respectively, were also found in *R. microphylla* (Nielsen *et al.*). The occurrence of 7-methylthioheptyl and 8-methylthiooctyl glucosinolates in the genus was said to support its placement in the tribe Arabideae (MacLeod & Islam). A distinct profile of six glucosinolates has been identified in *R. indica* (Hashimoto & Kameoka). Eight South American species that have been surveyed for flavonoids contain only kaempferol and quercetin glycosides. The lack of isorhamnetin in these species is believed to be characteristic of the Arabideae (Carmona & Pero Martínez). The seeds of *R. Nasturtium-aquaticum* contain comparable amounts (20–32 percent) of oleic, linoleic, and erucic acids. The remainder of the genus, however, has not been surveyed for fatty acids.

The presence of calcium-oxalate crystals in the leaves of *Rorippa crystallina* Rollins is unusual. These crystals, which are very rare in the Cruciferae, must have evolved independently since they occur in obviously unrelated genera, such as *Crambe* L., *Sisymbrium* L. (Metcalfe & Chalk), and *Rorippa.*

Small root or stem fragments of *Rorippa amphibia, R. austriaca, R. floridana, R. microphylla, R. Nasturtium-aquaticum,* and *R. sylvestris,* as well as of their hybrids, can easily be transported downstream and are capable of regenerating new plants. Seeds of species that grow on muddy banks can be dispersed over long distances in the mud attached to the feet of birds. The tiny seeds of many species (e.g., *R. sessiliflora*) float on water. The seeds of *R. Nasturtium-aquaticum* sink almost immediately, but a few may float as long as the air film surrounding them is not broken; they germinate readily and do not have any kind of dormancy (Howard & Lyon, 1952).

Watercress, *Rorippa Nasturtium-aquaticum,* is a crop cultivated throughout the world, particularly in Europe and North America; it is used in salads, soups, mixed juices, and casseroles, as well as for a garnish. Correll & Correll stated that the plant is also eaten by deer, ducks, muskrats, and wildfowl. It is rich in vitamin C and has long been valued as an antiscorbutic. Other medicinal uses (e.g., aphrodisiac, depurative, and febrifuge; a remedy for kidney ailments, tuberculosis, asthma, colds, and constipation) that are listed in the old literature are doubtful. *Rorippa indica* is sold in southeastern Asia both as a medicinal plant and as a vegetable (Ochse, Perry). Several species of *Rorippa,* particularly *R. indica, R. palustris,* and *R. sylvestris,* are cosmopolitan weeds. According to Herklots, *R. Nasturtium-aquaticum* has become a noxious weed that chokes some of the waterways in New Zealand. *Rorippa amphibia* is sometimes grown in aquaria (Bailey *et al.*).

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CALFE & CHALK; MUENSCHER; MUKHERJEE; MURLEY; PERRY; RADFORD *et al.*; RICKETT; ROLLINS (1966, 1981); SCHULZ; SMALL; and E. B. SMITH.

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36. **Armoracia** Gaertner, Meyer, & Scherbius, Oek.-Techn. Fl. Wetterau **2:** 426. 1800, nom. cons.

Glabrous, perennial herbs of aquatic, semiaquatic, or somewhat mesic habitats. Roots much branched, usually coarse, woody or somewhat fleshy, sometimes slender and adventitious from rootstocks. Stems usually unbranched at base, up to 2 m high. Basal leaves short or long petiolate, small or to 1 m long, crenate or dentate to serrate; middle cauline leaves short petiolate to subsessile, crenate to laciniate or pinnatisect, or (when submersed) 1–4 times pinnately or dichotomously dissected into numerous capillary to narrowly linear segments; uppermost or emersed cauline leaves serrate to serrulate or crenate to entire. Inflorescence an ebracteate raceme or panicle, greatly elongated in fruit;

fruiting pedicels ascending or divaricate to slightly reflexed. Sepals oblong to ovate, spreading, glabrous, nonsaccate at base, membranaceous at margin. Petals white, oblong or oblanceolate to spatulate [or broadly obovate], short clawed. Nectar glands flat, united into a ring surrounding bases of the lateral stamens and subtending those of the median ones. Stamens 6, slightly tetradynamous; filaments somewhat spreading, slightly dilated at base, not appendaged; anthers linear or oblong to ovate, sagittate at base. Fruits glabrous, oblong to obovoid or subglobose, sessile or short stipitate, flattened parallel or perpendicular to the septum; valves nerveless; septum usually with a central perforation, sometimes reduced to a narrow rim along the interior of replum; styles conspicuous and nearly as long as the fruit or short [to obsolete]; stigmas capitate, entire or slightly 2-lobed, usually much wider than the style. Seeds numerous, turgid, wingless, reticulate, biseriately arranged, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 8. (Including *Raphanis* Moench, nom. rejic.; *Neobeckia* Greene.) TYPE SPECIES: *A. rusticana* Gaertner, Meyer, & Scherb. (*Cochlearia Armoracia* L.). (Generic name is an ancient Greek name for horseradish. However, Courter & Rhodes suggested that the name is derived from Celtic *ar,* near, *mor,* the sea, and *rich,* against, meaning a plant growing near the sea. The word horseradish suggests a coarse or very strong radish, as distinguished from the edible radish, *Raphanus sativus* L. (Rosengarten).)—HORSERADISH.

A genus of four species distributed in eastern and southeastern Europe and Siberia, and disjunctly in the eastern and central United States. *Armoracia* is represented in the southeastern United States by two species, one of which is indigenous.

Armoracia rusticana Gaertner, Meyer, & Scherb.[13] (*Cochlearia Armoracia* L., *Nasturtium Armoracia* (L.) Fries, *Radicula Armoracia* (L.) Robinson, *Rorippa Armoracia* (L.) Hitchc., *Armoracia Armoracia* (L.) Britton, *A. lapathifolia* Gilib., *A. sativa* Bernh., *Cochlearia rusticana* Lam., *Rorippa rusticana* (Lam.) Gren. & Godron), horseradish, $2n = 32$, is a native of temperate eastern Europe from the Caspian Sea north into Russia, Poland, and southern Finland. It is an escape from cultivation and a widely naturalized weed throughout most of Europe and central and northern North America. It usually grows in moist habitats along ditches, riverbanks, and roadsides, as well as in waste grounds, fields, and disturbed sites. Uncommon in the Southeastern States, it has been reported from North Carolina and Tennessee.

Armoracia rusticana is very closely related to *A. macrocarpa* (Waldst. & Kit.) Kit. ex Baumg., a marsh plant of the central Danube Basin (Hungary, Yugoslavia, and probably Rumania), and to *A. sisymbrioides* (DC.) Cajander, a wet-meadow or sometimes aquatic plant of Siberia and Sachalin. From these, *A. rusticana* differs mainly in its smaller flowers and fruits. However, it rarely produces fruits with fully developed seeds. It may have evolved through domestication from ancestors not too different from *A. macrocarpa* and *A. sisymbrioides,* both of which are used occasionally as a substitute for horseradish.

[13]For detailed nomenclature of the species, see Fosberg (1965, 1966), Lawrence (1953, 1971), and McVaugh.

Armoracia rusticana rarely sets seeds in cultivation because it is a self-incompatible crop plant that is propagated by root cuttings originally derived from a few plants. Its high sterility is also caused by several meiotic irregularities, reduced pollen fertility (sometimes as low as 20 percent), abortion of ovules, failure of fertilization, endosperm–maternal tissue incompatibility, or embryo mortality (Stokes). On the basis of these anomalies, several authors (e.g., Lawrence, 1971) have suggested that *A. rusticana* is a hybrid, the ancestral parents of which are unknown. Meiotic irregularities, such as the lagging and partial pairing of chromosomes, may support the hybrid origin of horseradish (Weber), but the evidence is tenuous and more research is needed to confirm such an origin. Dore suspected that *A. rusticana* is a polyploid variant of *A. macrocarpa,* but both are tetraploids based on $x = 8$. Easterly's report of $n = 14$ for the former species is apparently in error.

The North American *Armoracia lacustris* (A. Gray) Al-Shehbaz & V. Bates (*Nasturtium lacustre* A. Gray, *Cochlearia Armoracia* L. var. *aquatica* Eaton, *C. aquatica* (Eaton) Eaton, *N. natans* DC. var. *americanum* A. Gray, *A. americana* (A. Gray) W. J. Hooker, *Rorippa americana* (A. Gray) Britton, *Neobeckia aquatica* (Eaton) Greene, *Radicula aquatica* (Eaton) Robinson, *A. aquatica* (Eaton) Wieg., *Rorippa aquatica* (Eaton) Palmer & Steyerm.), lake cress, river cress, grows in quiet waters in streams, springs, rivers, ponds, and lakes, as well as on muddy shores, mud flats, and floodplains (W. M. Countryman, pers. comm.). It is distributed exclusively east of the 95th meridian from Quebec south into Florida, west into eastern Texas, and north into eastern Oklahoma, Missouri, Iowa, Minnesota, Wisconsin, Michigan, and southern Ontario. *Armoracia lacustris* is sporadic in the Southeast but has been recorded from all of the Southeastern States except the Carolinas (see Al-Shehbaz & Bates for distribution data by county). Beal indicated that the species was reported from North Carolina, but neither he nor I have seen any specimens from this state.

The submersed leaves of *Armoracia lacustris* are pinnately or dichotomously dissected into numerous filiform segments, while the emersed ones have dentate margins. Submersed leaves near the water surface show a gradual transition between these two leaf types. Heterophylly in *A. lacustris,* unlike that in *Proserpinaca palustris* L. (Haloragaceae), is not controlled by photoperiodism and appears to be related to the fluctuation of temperature (C. E. Wood, Jr., pers. comm.). Gray was the first to observe that the submersed leaves of *A. lacustris* fall off readily as the plant is removed from water. Dissected leaves are usually detached in nature during late summer and fall. They float and are transported by water currents; within a week they produce at the petiolar end adventitious roots, a cluster of tiny, undivided leaves, and a small shoot. The new plantlet eventually sinks to the bottom, and the remainder of the leaf degenerates.

Armoracia lacustris is remarkable for its capacity to regenerate plants from tiny fragments of leaves, stems, and roots. According to La Rue, the species (as *Radicula aquatica*) reproduces only vegetatively and has not been found to produce seeds at upper latitudes. In warmer areas, however, the plant occasionally reproduces sexually. It is possible that *A. lacustris* is self-incompatible and that most of the local "populations" are merely clones. Young plants,

plantlets, and stem bases of older plants remain alive during the winter and produce new rosette leaves and shoots in the spring.

Although *Armoracia rusticana* is capable of forming new plants from small root fragments, its capacity for regeneration is apparently confined to the area of lateral-root traces (Lindner). The species produces pinnatifid leaves apparently only during the early and late parts of the growing season (Davis).

Earlier authors (e.g., De Candolle, 1821; Bentham & Hooker) reduced *Armoracia* to a section of *Cochlearia* L., but it is now believed that these genera are unrelated and that the latter belongs to the tribe Lepidieae. With the exception of Schulz, who placed *Armoracia* in the tribe Drabeae, most recent authors follow Von Hayek in associating the genus closely with *Rorippa*. *Armoracia* differs from *Rorippa* in having an incomplete or rudimentary septum (see FIGURE 1m) and flattened fruits. It is distinguished by its white flowers from all rorippas that it resembles by having fruits less than three times longer than broad. It is evident that the boundaries between these closely related genera are not sharply defined, but such a situation is often encountered throughout the Cruciferae.

Whether *Armoracia lacustris* and the *A. rusticana* complex are congeneric or should be placed in different genera is debatable. Rickett (p. 236) believed that they "seem to have nothing in common except that they are both crucifers," and Schulz placed them in different tribes, the former as *Nasturtium* (Arabideae) and the latter as *Armoracia* (Drabeae). The two species share several technical characters that support their placement in one genus (Al-Shehbaz & Bates).

Armoracia rusticana has been extensively surveyed for flavonoids and particularly for root glucosinolates. The hydrolysis products of the latter compounds are the flavoring principles in the commercial horseradish. The pungent taste is attributed to allyl isothiocyanate, which constitutes more than 60 percent of these products. Other important compounds are 2-butyl, 3-butenyl, 4-pentenyl, and 2-phenyl glucosinolates. A total of 30 root glucosinolates (including six new ones and excluding two doubtful compounds reported by Gilbert & Nursten) have been identified by Grob & Matile. This high number of glucosinolates exceeds the number previously isolated in any one species.

The fleshy outer part of the mature root of *Armoracia rusticana* is derived either directly or indirectly from the pericycle. The cork cambium produces a few layers of cork and a broad, spongy phylloderm with axially elongated parenchymatous cells that are mixed with isolated stone cells near the cambium. Roots are capable of regeneration only after the cortex is shed and the periderm is fully developed. Bud primordia are initiated from meristems derived from the cork cambium in areas of the lateral root scars.

Armoracia rusticana has been cultivated for some 2000 years (Rosengarten). The grated root, mixed with vinegar, salt, and oil, is a pungent condiment that is used with roast beef, fish, lamb, and ham. It is one of five "bitter herbs" eaten by Hebrews during Passover (Courter & Rhodes). Several medicinal properties have been attributed to horseradish. It has been used as a stimulant, antiscorbutic, diuretic, aphrodisiac, rubefacient, expectorant, and diaphoretic, as well as a remedy for dropsy, rheumatism, and neuralgia. Horseradish can

be a noxious weed that is extremely difficult to eradicate because small root fragments are capable of regenerating new plants. Kingsbury indicated that poisoning of horses, cattle, and swine has resulted from feeding on the plant. *Armoracia sisymbrioides* is cultivated in Siberia for its roots, which are used as a substitute for horseradish (Busch).

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A REVISION OF SYZYGIUM (MYRTACEAE) IN SAMOA

W. A. WHISTLER[1]

Syzygium is one of the largest genera in Polynesia and the third largest in Samoa. Of the 20 species recognized in Samoa (three herein described as new), 16 are native, and nine of these are endemic. All 20 are distinguished in a key, and complete descriptions are included. Local names and ethnobotanic information are noted for those species recognized and used by the Samoans.

Syzygium Gaertner is one of the largest genera in Polynesia and is represented by 28 native species in Fiji (Smith, 1985), seven in Tonga, four in Wallis and Futuna (St. John & Smith, 1971), two or three on Niue (Sykes, 1970), and four in Hawaii (St. John, 1973). Until now there has been no comprehensive study of *Syzygium* in Samoa, and the most recent publication on the Samoan flora (Christophersen, 1938) did not include a complete enumeration. In the present study 16 native species have been recognized, ranking the genus in size behind only *Cyrtandra* J. R. & G. Forster (Gesneriaceae), with 20 species, and *Psychotria* L. (Rubiaceae), also with 20 (Whistler, 1986). Nine of the species of *Syzygium* are endemic to Samoa; the other seven are also found in Fiji, Niue, Tonga, Wallis, Futuna, and/or Ponape.

In the entire Polynesian region including Fiji, there are 45 native species of *Syzygium*: in addition to the nine endemic to Samoa, there are 22 endemic to Fiji, four to Hawaii, and ten found in two or more islands or archipelagoes. Compared to species in large, widespread genera such as *Psychotria* and *Cyrtandra,* those of *Syzygium* apparently are not as easily dispersed (the genus is even absent from eastern Polynesia except for Hawaii). Speciation does not appear to have occurred as readily in *Syzygium* as in these two genera, which have higher rates of endemism and fewer wide-ranging indigenous species.

TAXONOMIC HISTORY OF THE GENUS IN SAMOA

Twenty-two species of *Syzygium* have been described from or attributed to Samoa since the first records of the Samoan Myrtaceae were published by Asa Gray in 1854. However, since no comprehensive study of the genus in Samoa has been made and no keys have been published, the genus has long been in need of revision.

The first specimens of *Syzygium* recorded from Samoa were collected by the United States Exploring Expedition in 1839. Subsequent collections were made in 1860–1875 by three amateur botanists, Graeffe, Powell, and Whitmee, but their work was never published. Professional botanists followed, and records

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of *Syzygium* specimens are found in Reinecke (1898), Rechinger (1910), Setchell (1924), Christophersen (1938), and Yuncker (1945). The most complete collection of the genus was made by Christophersen, who gathered all but one of the native species. A more detailed account of the botanical collectors in Samoa can be found in Whistler (1986).

During field work in Samoa between 1971 and the present, I have collected over 4500 specimens, including representatives of 13 of the 16 native *Syzygium* species, but no species was collected for the first time. Collections by Bristol in 1968 and Cox over the last several years have likewise failed to include any new species. It thus appears that the available specimens (over 300 collection numbers) represent a fairly complete sampling of the genus, and that very few new species can be expected to turn up in the future. Although the collections seem to be adequate, the study of the genus certainly is not. I have found it necessary to describe three new species and make major corrections in the work of previous botanists.

During my botanical study of Samoa, I visited a number of European and American institutions to study their collections and select specimens that were subsequently to be received on loan. Effort was made to examine and record every specimen gathered in the archipelago. Collections at the following institutions were utilized: Harvard University Herbaria (A and GH), Botanisches Museum of Berlin-Dahlem (B), Bernice P. Bishop Museum (BISH), British Museum (Natural History) (BM), Royal Botanic Garden, Edinburgh (E), Conservatoire Botanique, Geneva (G), Institut für Allgemeine Botanik, Hamburg (HBG), Royal Botanic Gardens, Kew (K), Botanische Staatssammlung, Munich (M), National Herbarium of Victoria (MEL), my own collection at the Pacific Tropical Botanical Garden (PTBG), University of California, Berkeley (UC), U. S. National Herbarium (US), Botanical Institute, Wroclaw (WRSL), and Naturhistorisches Museum, Vienna (W).

Syzygium Gaertner, Fruct. Sem. Pl. **1**: 166. 1788.

Trees up to 25 m tall, glabrous throughout. Stems terete or quadrangular and winged. Leaves opposite, petiolate or rarely sessile; blade chartaceous or coriaceous, glandular-punctate (but sometimes obscurely so), pinnate-nerved, with obvious, straight intramarginal collecting nerve (or this sometimes composed of looping distal ends of primary nerves) and often 1 or 2 outer collecting nerves. Inflorescences terminal or axillary (sometimes cauliflorous), several- to many-flowered panicles or thyrses, the axes with tiny caducous bracts and bracteoles (larger and persistent in 1 species). Flowers sessile or pedicellate, varying in size; hypanthium obovoid, campanulate, cuplike, or turbinate, sometimes tapering into distinct stipe, distally prolonged into rim; calyx lobes 4, sometimes obscure, borne on outer margin of hypanthium rim; petals 4, confluent and imbricate in bud to form fugacious calyptra (sometimes free, imbricate in bud, concave); stamens borne on inner hypanthium rim, numerous (ca. 35 to 450), strongly inflexed in bud, the filaments filamentous, free or proximally fused into many phalanges, the anthers oblong to subglobose, dorsifixed, 2-locular, longitudinally dehiscent; ovary usually 2-locular, placenta-

Distribution of the Samoan species of Syzygium.

Species	Island				
	Savaii	**Upolu**	**Tutuila**	**Manua**	**Other**
S. brevifolium	X	X	X		
S. carolinense	X	X	X	X	X
S. christophersenii	X				
S. clusiifolium	X	X	X	X	X
*S. corynocarpum**	X	X	X	X	X
S. curvistylum	X	X			X
S. dealatum	X		X	X	X
S. effusum	X				X
S. graeffei	X				
S. hebephyllum	X	X			
S. inophylloides	X	X	X	X	X
*S. jambos**	X	X	X?		X
*S. malaccense**	X	X	X	X	X
S. neurocalyx	X	X	X	X	X
S. oligadelphum		X			
S. patentinerve	X	X			
*S. samarangense**	X	X	X	X	X
S. samoense	X	X	X	X	
S. savaiiense	X	X			
S. vaupelii	X				
Total species	19	15	11	9	11
Native species	15	11	7	6	7

*Introduced species.

tion axile, ovules numerous, style slender to stout, stigma small. Fruit baccate, subglobose to ellipsoid, pericarp fleshy or thin, seed usually 1.

The genus in Samoa consists of 16 native species, nine of which are endemic. In addition, there are two aboriginally introduced species in cultivation (rarely escaping), one recent introduction that is thoroughly naturalized in native forests, and one recent introduction in cultivation. The distribution of the species in Samoa is shown in the Table. Savaii, the largest island in the archipelago, has all but one of the native species, Upolu has 11, Tutuila has seven, and Manua has six.

No sections of the genus have been recognized in the region, but in his treatment of *Syzygium* in Fiji, Smith (1985) divided the native species into three "groups" based on the flowers. His first group is distinguished by the presence of large, persistent bracts on the inflorescence and is represented in Samoa by a single species, *Syzygium samoense* (Burkill) Whistler. His second group mainly comprises small-flowered species with the petals fused into a fugacious calyptra; most of the Samoan and the Fijian species fit into this category. The third group consists of large-flowered species with the petals not calyptrate but fugacious singly and is represented in Samoa by only one native species, *S. neurocalyx* (A. Gray) Christoph.

All of the species here are well within the definition of *Syzygium,* and not

Eugenia L. as discussed by Schmid (1972) and Hyland (1983). A single native species of *Eugenia, E. reinwardtiana* (Bl.) DC., is found in Samoa.

Taxonomic Characters of Significance

Stems. Several of the species have distinctly quadrangular and winged stems, which can serve to distinguish them from otherwise similar species with terete stems.

Leaves. The size and shape of the leaves and the length of the petiole are usually sufficient to allow distinction among most of the Samoan species. Also of importance is the degree of glandular punctation on the lower leaf surface. In some species the glands are obscure, in others they are just barely evident, while in still others they are conspicuous. Two species that are very similar in nearly all respects, *Syzygium brevifolium* (A. Gray) C. Mueller and *S. hebephyllum* Melville, can be distinguished from each other by this character even when sterile. Another useful leaf character is venation. In four species the intramarginal collecting nerve is looping and made up from the distal ends of the primary nerves, rather than being distinct and straight.

Inflorescences. The inflorescences vary widely in position, flower number, and structure, and the differences are sometimes useful in distinguishing between otherwise similar species. In most species the inflorescences are axillary or terminal, but in two they are borne on the stem. Many-flowered panicles predominate, but some species have few-flowered panicles and one has nearly capitate inflorescences. The branches are generally terete, although in several species they are flattened or winged. Only one species has conspicuous, persistent bracts, a character that Smith (1985) used to distinguish a separate group of species in Fiji.

Flowers. The flowers differ greatly in size and can be very useful in distinguishing otherwise similar species. Flower size is also partially correlated with the number of stamens in the flowers, which in my counts varied from 35 to several hundred. Nearly all of the species have the petals fused into a calyptra, but the size and shape of the calyx is sometimes useful. The length of the staminal filaments and the style is also of some value in identification.

Fruits. The most important differences are in size and shape. Also significant is the size of the hypanthium (which can indicate flower size in the absence of flowers) and whether or not it is partially surrounded by the fruit.

Key to the Species of Syzygium in Samoa

1. Leaf blades mostly less than 4 cm long.
   2. Young stems terete; leaf blades obovate. ..... 1. *S. vaupelii.*
   2. Young stems quadrangular; leaf blades variously shaped.
      3. Leaf bases acute; hypanthia 2–3 mm long. ..... 2. *S. effusum.*
      3. Leaf bases rounded to subcordate; hypanthia 6–8 mm long.
         4. Lower leaf surfaces conspicuously glandular-punctate. .. 3. *S. brevifolium.*

4. Lower leaf surfaces obscurely (if at all) glandular-punctate. ..... 4. *S. hebephyllum.*

1. Leaf blades mostly 4–30 cm long.
   5. Young stems quadrangular.
      6. Leaves with petiole 1–3 mm long, blade 2–3.5 cm wide; stamens ca. 80, filament up to 12 mm long; montane forest. ..... 5. *S. graeffei.*
      6. Leaves with petiole 7–20 mm long, blade 3–11.5 cm wide; stamens ca. 300, filament up to 20 mm long; lowland and coastal forest. ... 6. *S. dealatum.*
   5. Young stems terete.
      7. Inflorescences on stem; coastal forest. ..... 7. *S. clusiifolium.*
      7. Inflorescences axillary or terminal; various habitats.
         8. Bracts persistent, up to 2.5 mm long. ..... 8. *S. samoense.*
         8. Bracts caducous at anthesis, mostly less than 1 mm long.
            9. Flowers large, hypanthium mostly 9–20 mm long.
               10. Leaves with looping intramarginal collecting nerve formed from distal ends of primary nerves.
                  11. Petioles usually 2–6 mm long; filaments white; forest. ..... 9. *S. samarangense.*
                  11. Petioles 8–20 mm long; filaments red; cultivated. ..... 10. *S. malaccense.*
               10. Leaves with straight, distinct intramarginal collecting nerve.
                  12. Leaves lanceolate to long-elliptic; flowers with calyx lobes 4–10 mm long, style over 3 cm long; mostly cultivated.
                     13. Flowers in capitate umbels, hypanthium strongly longitudinally ribbed; leaves 5–9 cm wide. ..... 11. *S. neurocalyx.*
                     13. Flowers in panicles, hypanthium not ribbed; leaves 2–6 cm wide. ..... 12. *S. jambos.*
                  12. Leaves oblong to elliptic; flowers with calyx lobes 1–4 mm long, style less than 3 cm long; forest.
                     14. Leaves with base subcordate to rounded, sessile or with petiole to 2 mm long. ..... 13. *S. patentinerve.*
                     14. Leaves with base acute to subcuneate, petiole 3–18 mm long.
                        15. Leaf blades 8–24 cm long; inflorescence branches flattened. ..... 14. *S. savaiiense.*
                        15. Leaf blades 5–10 cm long; inflorescence branches terete.
                           16. Lower leaf surfaces conspicuously glandular-punctate; Upolu. ..... 15. *S. oligadelphum.*
                           16. Lower leaf surfaces not conspicuously glandular-punctate; Savaii. ..... 16. *S. christophersenii.*
            9. Flowers small, hypanthium 2.5–8 mm long.
               17. Leaves with blade 2.5–12 cm long, caudate to acuminate at apex, coriaceous, finely pinnately nerved.
                  18. Leaf apexes caudate with blunt tip; fruits 2.5–4 cm long; common, lowlands and foothills. ..... 17. *S. inophylloides.*
                  18. Leaf apexes acuminate with sharp tip; fruits less than 1 cm long; uncommon, montane forest. ..... 18. *S. curvistylum.*
               17. Leaves with blade 6–20 cm long, acute to acuminate at apex, chartaceous, coarsely nerved.
                  19. Hypanthia 2.5–4 mm long; leaf blades 6–20 cm long, usually less than 2.5 times longer than wide, lower surface drying brown; forest. ..... 19. *S. carolinense.*

19. Hypanthia 5–8 mm long; leaf blades 7.5–13 cm long, usually more than 2.5 times longer than wide, lower surface drying light green; cultivated. ..... 20. *S. corynocarpum.*

1. **Syzygium vaupelii** Whistler, sp. nov. FIGURE 1.

Syzygium aff. *effusum* Christoph. Bernice P. Bishop Mus. Bull. **54:** 23. 1938; non C. Mueller.

Syzygio effuso affinis, a qua imprimis differt in foliis obovatis et caulibus teretibus.

Tree, height not recorded. Stems terete. Leaves with petiole 2–6 mm long; blade obovate, 20–35 by 10–18 mm, shortly acuminate at apex, cuneate at base, slightly revolute, coriaceous, glossy above, lighter and conspicuously glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal, paniculate, many flowered, 2–4 cm long. Flowers with pedicel 1–4 mm long; hypanthium cup shaped, 4–6 by 4–5 mm, irregularly and shallowly notched, without distinct calyx lobes; petals confluent, calyptrate; stamens ca. 100, filament up to 12 mm long, anther oblong, 0.5–1 mm long; style 2.5–4.5 mm long. Fruits not known.

TYPE. Samoa, Savaii, S Maugaloa, 1906, *Vaupel 408* (holotype, B!; isotypes, BISH!, K!, PTBG!, US!).

DISTRIBUTION. Endemic to Samoa; uncommon in cloud forest on Savaii, 900–1300 m alt.

PHENOLOGY. Flowering reported in August.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Matavanu, *Christophersen 1997* (A, BISH, K, US).

The measurements in the description are based on one flowering and one sterile specimen and must be considered tentative until more material of this rare species is collected and studied.

2. **Syzygium effusum** (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 838. 1858; A. C. Smith, Fl. Vit. Nova **3:** 334. 1985.

Eugenia effusa A. Gray, Bot. U. S. Expl. Exped., Phan. 524. 1854; Reinecke, Bot. Jahrb. Syst. **25:** 658. 1898. TYPE: Fiji, Mbua Province, near Sandalwood Bay, 1840, *U. S. Expl. Exped. s.n.* (holotype, US *47775*; isotypes, GH!, K!).

Tree, height not recorded. Young stems quadrangular, winged. Leaves with petiole 3–7 mm long; blade elliptic, 2.5–4(–6) by 1–2(–3.2) cm, broadly acute at apex, acute at base, not revolute, coriaceous, dark green above, lighter and obscurely glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal and from upper axils, paniculate, many flowered, 2–7 cm long, the axes quadrangular, winged, bearing deciduous bracts ca. 0.5 mm long. Flowers with pedicel 2–5 mm long; hypanthium 2–3 by 1.5–2 mm, shallowly notched into broadly rounded calyx lobes less than 0.5 mm long; petals confluent,

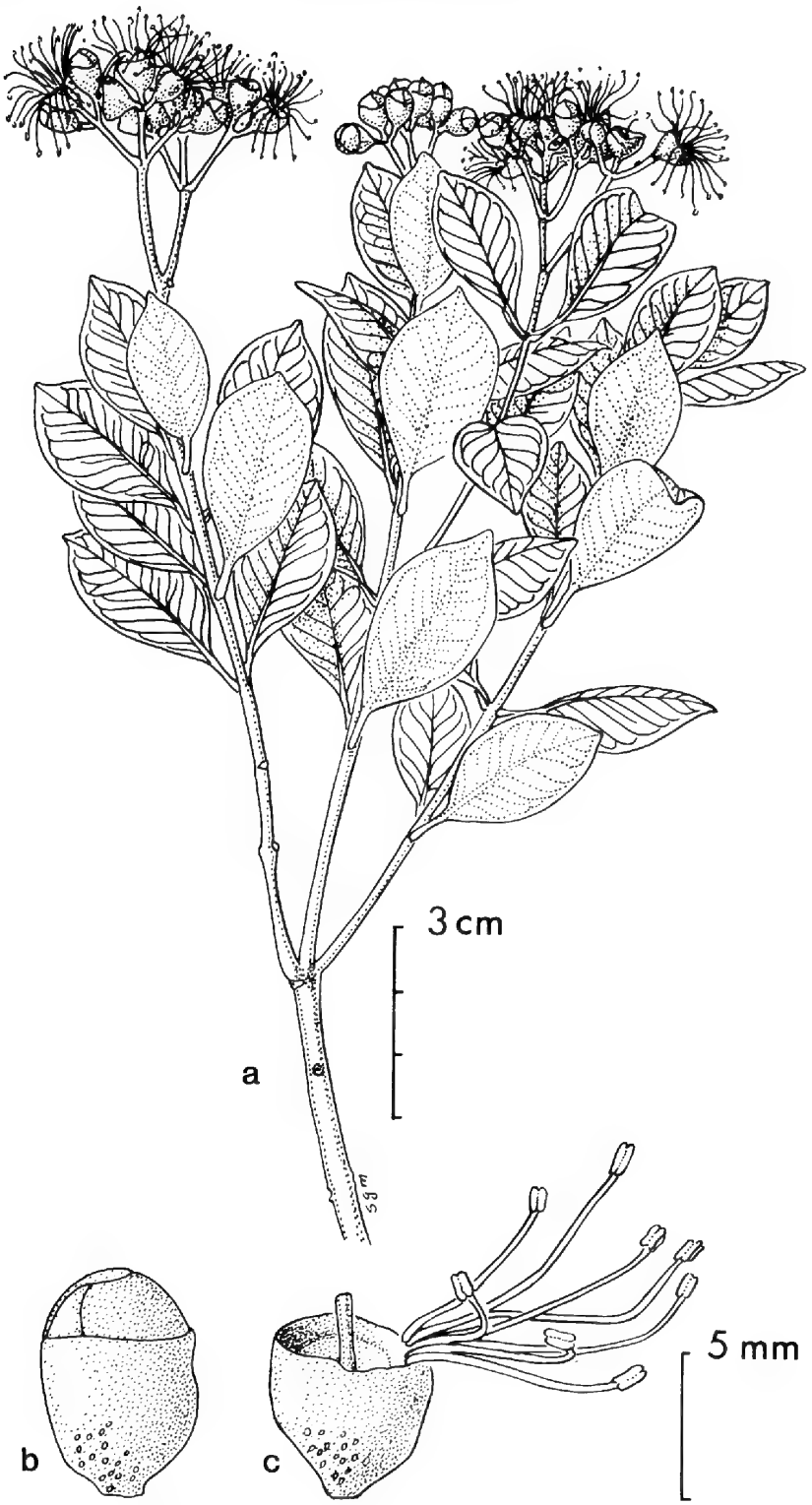

FIGURE 1. **Syzygium vaupelii:** a, flowering branchlets; b, flower bud; c, flower after anthesis.

calyptrate; stamens ca. 35, the filament up to 2 mm long, the anther subglobose, ca. 0.3 mm long; style 1–2 mm long. Fruits not known.

DISTRIBUTION. Indigenous to Samoa; rare in mountain region of Savaii, no altitude reported. Also found from New Guinea to Fiji.

PHENOLOGY. Flowering reported in September.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: mountain region, *Reinecke 485* (G), *487* (G, K). WITHOUT FURTHER LOCALITY: *Reinecke s.n.* (K, WRSL).

Based on specimens cited by Rechinger (1910) and Christophersen (1938), Smith (1985) concluded that this species does not occur in Samoa. However, *Reinecke 485* (cited by Reinecke, 1898) and *487* (not cited), which were not seen by Smith, do belong to this species, although they differ from those collected over the rest of the species' range in having pedicels 2–5 (vs. 0.5–2) mm long.

Two sterile specimens collected from Savaii (above Salailua, 750 m alt., *Christophersen 2900,* BISH; Siuvao-Auala, 600 m alt., *Christophersen 3366,* BISH) may also belong here. Although these specimens have the winged, quadrangular stems typical of *Syzygium effusum,* they differ in having leaf blades up to 10 cm long with the lower surface conspicuously glandular-punctate.

3. **Syzygium brevifolium** (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 839. 1858; Christoph. Bernice P. Bishop Mus. Bull. **154:** 21. 1938; Whistler, Allertonia **2:** 160. 1980.

Eugenia brevifolia A. Gray, Bot. U. S. Expl. Exped., Phan. 531. 1854; Reinecke, Bot. Jahrb. Syst. **25:** 659. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910. TYPE: Samoa, Tutuila, "on the mountains of Tutuila. . .at the elevation of 2,500 feet," 1839, *U. S. Expl. Exped. s.n.* (holotype, US *47772*!; isotype, GH [fragment]!).

Eugenia oreophila Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910; non Diels. TYPE: Samoa, Upolu, mountain region of Lake Lanotoo, 1905, *Rechinger 1811* (lectotype, here designated, W!; isolectotypes, BISH!, BM!, K!, US!).

Tree up to 10 m tall. Stems quadrangular, winged. Leaves decussate and sometimes nearly imbricate on stem, sessile or with petiole up to 2 mm long; blade ovate to elliptic, 1.3–4.2 by 0.8–2.5 cm, acute to subacuminate at apex, rounded to subcordate at base, slightly revolute, coriaceous, glossy above, lighter and conspicuously glandular-punctate beneath, pinnately nerved. Inflorescences terminal and from upper axils, paniculate, many flowered, up to 4 cm long. Flowers sessile or with pedicel less than 1 mm long; hypanthium campanulate, 6–8 by 4.5–6 mm, shallowly notched into broadly rounded calyx lobes ca. 0.5 mm long; petals confluent, calyptrate; stamens ca. 200, the filament up to 15 mm long, probably white, the anther oblong to subglobose, ca. 0.5 mm long; style 5–7 mm long. Fruits ovoid, ca. 14 mm long.

DISTRIBUTION. Endemic to Samoa; in montane to cloud forest on Savaii, Upolu, and Tutuila, 500–1300 m alt.

PHENOLOGY. Flowering reported in August, fruiting in November.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: central mountain region, 1300 m alt., *Reinecke 431* (WRSL). UPOLU: rim of Lanotoo, *Christophersen 118* (A, BISH, K, UC); near Lanotoo, *Rechinger 710* (W), *750* (W), *1811* (BISH [fragment], BM, K, US, W); *sine loco, Rechinger 3346* (W); near Lanoataata, *Whistler 1493* (B, BISH, PTBG). TUTUILA: top of Matafao, *Christophersen 1025* (BISH); Matafao ridge, *Christophersen 1051* (BISH), *1071* (A, BISH); Matafao, *Whistler 3850* (BISH, PTBG). WITHOUT FURTHER LOCALITY (Savaii?): *Reinecke s.n.* (K).

Bristol 2165 (BISH, US), a sterile specimen collected far above Aopo, Savaii, has leaf blades (possibly juvenile) up to 6 cm long but probably belongs here. Another sterile specimen, *Whistler 3911* (PTBG), collected above Tonitoniga, Upolu, may belong to this species as well.

4. **Syzygium hebephyllum** Melville, Kew Bull. **2**: 293. 1955. TYPE: Samoa, Upolu, on lip of canyon at Afiamalu, 1954, *Irwin 5* (lectotype, here designated, K!; isolectotypes, A!, BISH!, K!).

Memecylon sp. Reinecke, Bot. Jahrb. Syst. **25**: 662. 1898.
Eugenia brevifolia sensu Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85**: 145. 1910, *pro parte*; non A. Gray.

Tree up to 18 m tall. Young stems quadrangular, winged. Leaves decussate and often imbricate on stem, sessile or with petiole up to 2 mm long; blade orbicular to lanceolate, 0.6–4(–8 in juvenile leaves) by 0.5–2.5 cm, acuminate to subrounded at apex, round to subcordate at base, slightly revolute, coriaceous, dark green and glossy above, lighter and obscurely glandular-punctate beneath, pinnately nerved. Inflorescences terminal, paniculate, 3- to 11-flowered, 0.8–2 cm long. Flowers with pedicel ca. 1 mm long; hypanthium subglobose, 6–8 by 5–7 mm, shallowly notched into broadly rounded calyx lobes 1–2 mm long; petals confluent, calyptrate; stamens ca. 230, the filament up to 10 mm long, white, the anther oval, 0.5–1 mm long; style 6–8 mm long. Fruits subglobose, 15–24 mm long, hypanthium partially surrounded, pericarp red at maturity.

DISTRIBUTION. Endemic to Samoa; uncommon in cloud forest on Savaii and Upolu, 500–1500 m alt.

PHENOLOGY. Flowering reported in December, fruiting in April.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Patamea, *Bristol 2328* (BISH, K, US); Matavanu lava flow, *Christophersen 1968* (BISH); above Matavanu, *Christophersen 2082* (A, BISH, K, US); central region, 1500 m, *Reinecke 370* (K, US); "Matai," *Vaupel 563* (B, BISH, PTBG). UPOLU: Malololelei ridge, *Christophersen 274* (BISH, W); canyon lip at Afiamalu, *Irwin 1* (K), *2* (A, K), *3* (K), *4* (K); near Lanotoo, *Rechinger 726* (W), *1347* (W), *1954* (W).

The collections made by Irwin are numbered *1* to *5*, and two different dates are involved. Melville listed two type specimens, one with fruit and one with flowers. *Irwin 5*, the specimen in the type collection at Kew, is hereby designated as the lectotype.

5. **Syzygium graeffei** Whistler, sp. nov. FIGURE 2.

Syzygio dealato affinis, a qua imprimis in petiolis brevioribus, foliis angustioribus, filamentis brevioribus, et staminibus paucioribus differt.

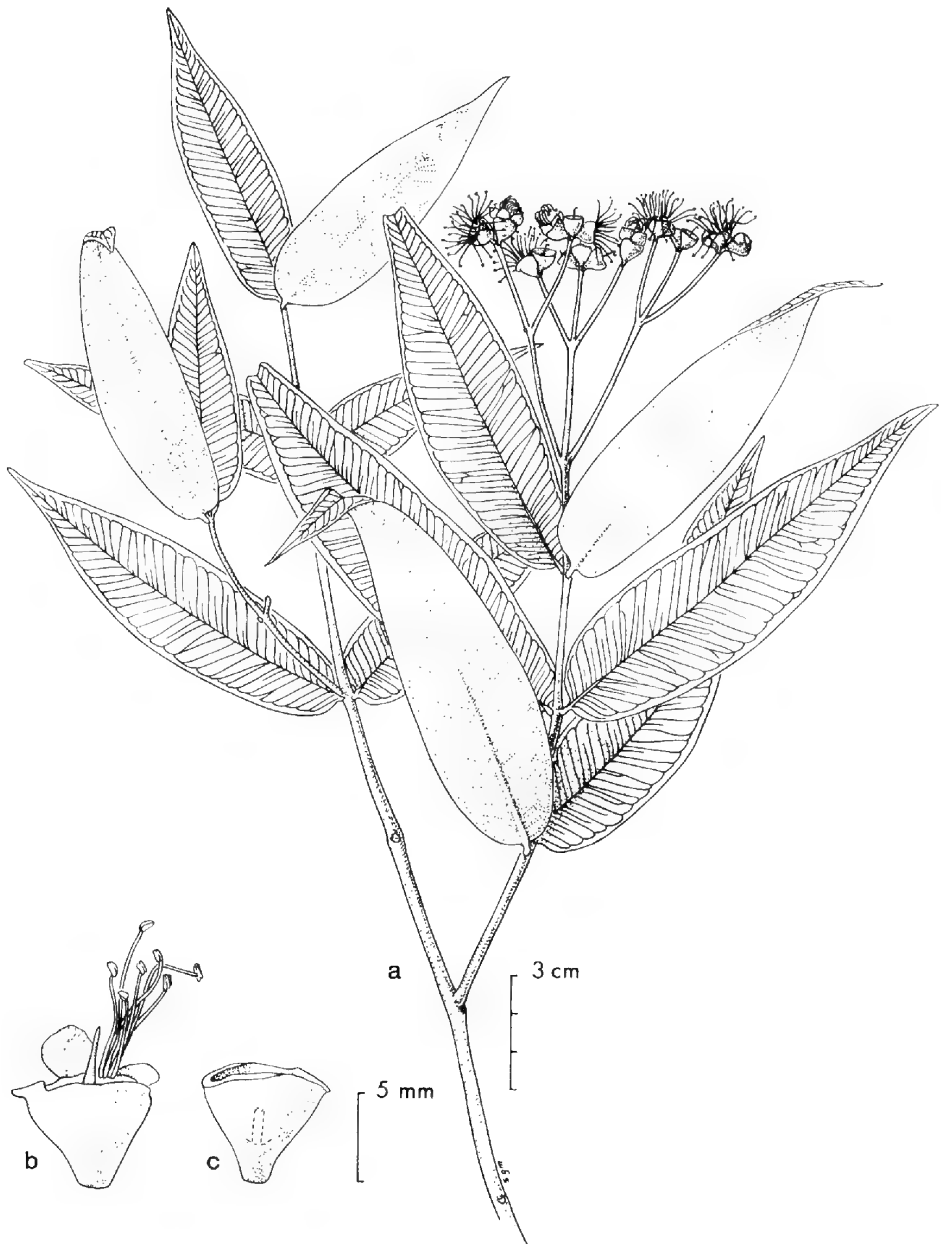

FIGURE 2. **Syzygium graeffei:** a, vegetative and flowering branchlets; b, flower at anthesis; c, flower after anthesis.

Tree, height not recorded. Young stems quadrangular and winged, or sometimes terete. Leaves with petiole ca. 1–3 mm long; blade lanceolate, 8–13 by 2–3.5 cm, acuminate to subacuminate at apex, rounded at base, not revolute, chartaceous, dark above, lighter and sparingly glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal or in upper axils, paniculate, loose, many flowered (up to ca. 27), up to 11 cm long, narrow, the ultimate branches

17–24 mm long, bearing 3 flowers. Flowers subsessile or with pedicel to 3 mm long; hypanthium turbinate, 5–6 by 4–7 mm, divided into suborbicular calyx lobes 2–3 mm long; petals confluent, calyptrate; stamens ca. 80, the filament up to ca. 12 mm long, the anther oblong, 0.4–0.7 mm long; style ca. 4–6 mm long. Fruits not known.

TYPE. Samoa, Savaii, central volcanic region, 1905, *Rechinger 3736* (holotype, W!).

DISTRIBUTION. Endemic to Samoa; presumably rare at high altitudes on Savaii, altitude range not known.

PHENOLOGY. Flowering reported in August.

ADDITIONAL SPECIMEN EXAMINED. **Samoa.** SAVAII: *sine loco, Graeffe 213a* (HBG).

The species is named in honor of Eduard Graeffe, who made extensive collections in the South Pacific during the 1860's and 1870's. He was the first to collect this species, but the holotype is *Rechinger 3736,* a more complete specimen.

6. **Syzygium dealatum** (Burkill) A. C. Smith *in* Yuncker, Bernice P. Bishop Mus. Bull. **220:** 203. 1959; H. St. John & A. C. Smith, Pacific Sci. **25:** 335. 1971; Whistler, Allertonia **2:** 160. 1980.

Eugenia dealata Burkill, J. Linn. Soc., Bot. **35:** 37. 1901. TYPE: Tonga, Eua, 1889, *Lister s.n.* (holotype, K!).
Syzygium clusiifolium sensu Sykes, New Zealand Dept. Sci. & Industr. Res. Bull. **200:** 131. 1970; non C. Mueller.

Tree up to 8 m tall. Stems quadrangular, slightly winged. Leaves with petiole 7–20 mm long; blade oblong to elliptic, 7–16 by 3–11.5 cm, acute to caudate at apex with short somewhat twisted tip (occasionally retuse), rounded to abruptly cuneate at base, slightly revolute, coriaceous, often with 1 to several prominent insect galls, glossy above, dull and glandular-punctate beneath, pinnately nerved. Inflorescences terminal, paniculate, many flowered, 5–9 cm long, widely branching. Flowers sessile; hypanthium campanulate, 4–9 by 4–6 mm, not noticeably ridged when dry, notched into broadly triangular to rounded calyx lobes 1–2 mm long; petals confluent, calyptrate, white and red; stamens ca. 260 to 360, the filament up to 20 mm long, showy white, the anther oblong, ca. 0.5 mm long; style 4–7 mm long. Fruits ovoid to ellipsoid, 18–24 mm long, the hypanthium partially surrounded, the pericarp thin, purple at maturity.

DISTRIBUTION. Indigenous to Samoa; in coastal forest on all main islands except Upolu, near sea level to 150 m alt. Also found on Uvea, Alofi, Tonga (Eua, Tongatapu, Tafahi, Niuafoou, and Niuatoputapu), and Niue.

PHENOLOGY. Flowering reported September–November, fruiting December–January.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Sataua-Papa on coastal bluffs, *Christophersen 3419* (BISH); coast NE of Asau, *Whistler 1015* (G, K, PTBG). TUTUILA: Mt. Tau,

Whistler 2886 (BISH, PTBG); E of Onenoa, *Whistler 3750* (BISH, PTBG). AUNUU: N ridge, *Whistler 3273* (B, BISH, G, K, PTBG, US). OFU: adjacent to air strip, *Whistler 3049* (B, PTBG); Nuutele Is., *Whistler 3780* (BISH, PTBG). TAU: SE side of island, *Whistler 3220* (PTBG); Auauli, *Whistler 3680* (BISH, PTBG). WITHOUT FURTHER LOCALITY: *Whitmee 212* (MEL).

Christophersen (1938) mentioned his specimens in the discussion of *Syzygium clusiifolium* but noted how they differed from this species. The populations outside of Samoa differ in having leaf apexes rounded to obtuse, petioles shorter (2–8 mm long), stems often neither quadrangular nor winged, and fruits with the hypanthium exserted 1.5–4 mm. The only non-Samoan specimen seen with flowers was the holotype; the flowers are 10–12 mm long with calyx lobes up to 2.5 mm long.

7. **Syzygium clusiifolium** (A. Gray) C. Mueller, Ann. Bot. Syst. **4**: 839. 1858; Yuncker, Bernice P. Bishop Mus. Bull. **220**: 202. 1959; Whistler, Allertonia **2**: 160. 1980.

Eugenia clusiaefolia A. Gray, Bot. U. S. Expl. Exped., Phan. 528. 1854; Reinecke, Bot. Jahrb. Syst. **25**: 659. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85**: 144. 1910. TYPE: Samoa, "Tutuila and Savaii: on rocks near the sea," 1839, *U. S. Expl. Exped. s.n.* (holotype, US *47773*!; isotypes, GH [fragment]!, K!).

Tree up to 15 m tall. Stems terete. Leaves with petiole 3–16 mm long; blade obovate to elliptic, 7–16 by 3–9.5 cm, broadly acute or occasionally rounded to retuse at apex, cuneate at base, not revolute, coriaceous, glossy above, dull and glandular-punctate beneath, finely pinnate-nerved. Inflorescences on stem, paniculate, many flowered, 12–30 cm long, widely branching. Flowers sessile; hypanthium campanulate, 5.5–9.5 by 4–6 mm, white at anthesis, longitudinally ridged when dry, shallowly notched into broad, rounded calyx lobes ca. 1 mm long; petals confluent, calyptrate, white; stamens ca. 100, the filament up to 12 mm long, showy white, the anther oblong, ca. 0.5 mm long; style 4–6 mm long. Fruits ovoid, 2–3.3 cm long, hypanthium partially surrounded, pericarp dull purple at maturity.

DISTRIBUTION. Indigenous to Samoa; common to abundant in coastal forest on all main islands, particularly on offshore tuff-cone islets, near sea level to over 100 m alt. Also found in Tonga, Uvea, and Futuna.

PHENOLOGY. Flowering reported August–January, fruiting August–March.

LOCAL NAMES AND USES. *Asi vao,* according to Powell (1868), who noted that he encountered it only on Manono. This name, however, also refers to a number of other species of this genus. The tree is called *asi* on Futuna and *fekika vao* in Tonga. It is sometimes used for timber.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Asau-Aopo, *Christophersen 2546* (BISH); Falealupo, *Christophersen 2784* (BISH); Sataua-Papa, *Christophersen 3415* (A, BISH, K, US, W); near Paia, *Reinecke 376* (G); Paia Mtn., *Reinecke 377* (G, WRSL); Falealupo, *Vaupel 645a* (B); E of Asau, *Whistler 954* (B, BISH, PTBG). UPOLU: Mt. Vaea, *Rechinger 4499* (W); Nuutele Is., *Whistler 470* (B, BISH, PTBG); Fanuatapu Is., *Whistler 1813* (B, BISH, PTBG), *4680* (B, PTBG, US); Namua Is., *Whistler 1888a* (BISH, PTBG). TUTUILA: *sine loco, Long 3024a* (PTBG); Afono–Vatia trail, *Whistler 1280* (G, PTBG); Two-Dollar Beach, *Whistler*

3755 (BISH, PTBG). OFU: Nuutele Is., *Whistler 3779* (BISH, PTBG). OLOSEGA: Alei Ridge, *Whistler 3492* (BISH). TAU: Auauli, *Whistler 3679* (B, BISH, PTBG). WITHOUT FURTHER LOCALITY: *Powell 24* (K), *314* (K); *Whitmee s.n.* (GH, K).

This species is also found in Tonga (Vavau, Eua, Niuafoou, Tafahi, Tongatapu, Niuatoputapu, Kao), Futuna, and Uvea. The populations on Kao and Eua have oblanceolate leaves, and the one on Tongatapu appears to have shorter fruits.

8. **Syzygium samoense** (Burkill) Whistler, Phytologia **38:** 410. 1978, Allertonia **2:** 160. 1980.

Eugenia samoensis Burkill, J. Linn. Soc., Bot. **35:** 38. 1901. TYPE: Samoa, without further locality, ca. 1860's, *Powell 6* (lectotype, here designated, K!).
Eugenia "spec. I" Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910.
Eugenia "spec. II" Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 146. 1910.
"?*Syzygium savaiiense*" sensu Christoph. Bernice P. Bishop Mus. Bull. **154:** 26. 1938, *pro parte*; non C. Mueller.
Syzygium clusiaefolium sensu Christoph. Bernice P. Bishop Mus. Bull. **154:** 22. 1938; non C. Mueller.

Tree up to 17 m tall. Stems terete. Leaves with petiole 7–20 mm long; blade oblanceolate to obovate, 7–23 by 3–11 cm, obtuse to rounded at apex, cuneate to nearly decurrent at base, revolute, coriaceous, dark green and glossy above, lighter and conspicuously glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal, paniculate, many flowered, 5–9 by 5–12 cm, bearing persistent, paired, oblong to triangular bracts 0.5–2.5 mm long. Flowers with pedicel 4–10 mm long, bearing persistent bracts; hypanthium campanulate to cup shaped, 7–10 by 6–8 mm, undulate into broadly rounded lobes ca. 1 mm long; petals confluent, calyptrate; stamens ca. 480, the filament up to 9–12 mm long, white, the anther oblong, ca. 0.8–1.3 mm long; style 5–7 mm long, often persistent on fruit. Fruits ovoid to urceolate, 15–19 mm including partially surrounded, concave hypanthium, pericarp red at maturity.

DISTRIBUTION. Endemic to Samoa; in lowland to cloud forest on all main islands, 100–1200 m alt.

PHENOLOGY. Flowering reported June–July, fruiting in February and July–September but probably year-round.

NATIVE NAMES. Possibly *fena vao,* due to its vague similarity to *fena,* another species of *Syzygium.* This name was not known by my informants, however.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Gataivai, *Bristol 2257* (BISH, GH), *2284* (BISH); above Vaipouli, *Christophersen 1918* (A, BISH, K, UC, US); Manase, *Christophersen 2373* (A, BISH, K); above Salailua, *Christophersen 2888* (BISH, UC, US), *3080* (BISH); Siuvao-Auala, *Christophersen 3368* (BISH); Auala, *Fasavalu 25* (BISH); S Maugaloa, *Vaupel 407* (B, BISH, K, PTBG, US, WRSL), *647* (B); above Asau, *Whistler 7* (BISH, PTBG, US). UPOLU: Mt. Fao, *Christophersen 557* (BISH), *570* (A, BISH, K, M); *sine loco, Graeffe 1315* (HBG); above Utumapu, *Rechinger 32* (W), *980* (W); rim of Lanotoo, *Whistler 1618* (B, BISH, K, PTBG); Mt. Vaea, *Whistler 3992* (PTBG). TUTUILA: Papatele Ridge,

Christophersen 1008 (BISH); top of South Pioa, *Christophersen 1199* (BISH, K, UC); top of Pioa, *Christophersen 3482* (BISH, US), *3498* (A, BISH); Aoloaufou, *Whistler 2688* (B, BISH, G, K, PTBG), *2749* (BISH, K, PTBG); N of Aoloaufou, *Whistler 2957* (B, BISH, PTBG). TAU: Mt. Lata, *Whistler 3731* (BISH, PTBG). WITHOUT FURTHER LOCALITY: *Powell 267* (K), *327* (K); *Whitmee 95* (BM, GH, K, MEL), *96* (MEL), *108* (MEL).

In his description of *Eugenia samoensis,* Burkill noted three specimens, one from Vavau and two from Samoa, as well as a fourth (*Whitmee 95,* from Samoa) that "may well be a form of this species." The specimen from Vavau is conspecific with *Syzygium brackenridgei* (A. Gray) C. Mueller (Smith, 1985), but the other three are distinct from that species, and a lectotype has to be designated from among them.

The persistent inflorescence bracts in *Syzygium samoense* and *S. brackenridgei* distinguish them from other species in the region. *Whistler 7,* collected above Asau, Savaii, probably belongs to *S. samoense* but has leaves with an acuminate apex. Two small-leaved sterile specimens (*Christophersen 2900* and *3366,* both at BISH) from above Salailua, Savaii, probably also belong here.

9. **Syzygium samarangense** (Blume) Merr. & Perry, J. Arnold Arbor. **19:** 115. 1938; Whistler, Allertonia **2:** 160. 1980.

Myrtus samarangensis Blume, Bijdr. Fl. Ned. Ind. 1084. 1826 or 1827.
Eugenia javanica Lam. Encycl. **3:** 200. 1789; non *Syzygium javanicum* Miq. (1855). TYPE: Indonesia, Java, without further locality, *Commerson s.n.* (P-LA).
Syzygium richii sensu Sykes, New Zealand Dept. Sci. & Industr. Res. Bull. **200:** 136. 1970; non Merr. & Perry.

Tree up to 12 m tall. Stems terete. Leaves with petiole 2–6(–10) mm long; blade usually elliptic, 6–21 by 2–10 cm, acute to acuminate (rarely rounded) at apex, rounded to acute at base, not revolute, chartaceous, dark green and glossy above, lighter and glandular-punctate beneath, coarsely nerved, intramarginal collecting nerve composed of looping distal ends of primary nerves. Inflorescences terminal, paniculate or thyrsoid, few- to several-flowered, 9–12 cm long, the apex flattened and bearing 3 flowers, with terminal one on extended rachis. Flowers sessile; hypanthium turbinate, 10–15 by 9–12 mm, notched into rounded calyx lobes 4–6 mm long, these pale yellow, reflexed at anthesis; petals suborbicular, 7–11 mm long, concave, white; stamens ca. 280, the filament up to 22 mm long, white, the anther 0.8–1.3 mm long; style 15–20 mm long. Fruits ovoid to obovoid, 2.5–4 cm long including persistent, inflexed calyx lobes, pericarp fleshy and red at maturity.

DISTRIBUTION. Introduced to Samoa before 1931, now naturalized in lowland to cloud forest on all main islands; 20–740 m alt. Also naturalized on Niue (incorrectly identified as *Syzygium richii*) and occurring in Tonga and Wallis and Futuna.

PHENOLOGY. Flowering reported in August and September, fruiting July–August and December–January.

NATIVE NAME AND USES. Possibly *nonu vao,* literally "Malay apple of the bush." The fruit is edible, according to Smith (1985), but there are no reports of its being eaten in Samoa.

SPECIMENS EXAMINED. **Samoa.** SAVAII: near Saumalaeulu, *Christophersen 2554* (BISH); Le To, above Salailua, *Christophersen 2921* (BISH); Siuvao-Auala, *Christophersen 3292* (BISH); Siuvao-Auala, *Christophersen 3374* (BISH); Papa-Fagatele, *Christophersen 3411* (BISH); near Aopo, *Whistler 1720* (PTBG); below Mata-o-le-Afi, *Whistler 2401* (BISH, PTBG). UPOLU: Tanumalala, *McKee 2998* (BISH); Lanoanea Farm, *Whistler 1078* (G, K, PTBG); W of Mt. Sigaele, *Whistler 2040* (G, PTBG); inside Sigaele crater, *Whistler 2061* (PTBG). TUTUILA: Vaisa Stream, *Kuruc 107* (BISH); Fagaalu Canyon, *Whistler 1461* (PTBG), *2871* (BISH, PTBG). OFU: NE side of island, *Whistler 3013* (PTBG). OLOSEGA: *sine loco, Whistler 3077* (PTBG); atop Piumafua, *Whistler 3824* (PTBG). TAU: N slope of island, *Whistler 3156* (BISH, PTBG), *3210* (B, BISH, K, PTBG).

A sterile specimen (*Vaupel 644,* B) collected in 1906 at "Puapua bush" on Savaii appears to belong to this species. If so, this is by far the earliest record of this species from Samoa, considerably antedating Christophersen's collection of it in 1931.

10. **Syzygium malaccense** (L.) Merr. & Perry, J. Arnold Arbor. **19:** 215. 1938.

Eugenia malaccensis L. Sp. Pl. 470. 1753; A. Gray, Bot. U. S. Expl. Exped., Phan. 510. 1854; Setch. Publ. Carnegie Inst. Wash. **341:** 64. 1924; Christoph. Bernice P. Bishop Mus. Bull. **154:** 19. 1938. TYPE: according to Smith (1985), four references were cited by Linnaeus, but no lectotypification was made.

Jambosa malaccensis (L.) DC. Prodr. **3:** 286. 1828; Reinecke, Bot. Jahrb. Syst. **25:** 658. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 144. 1910.

Tree up to 25 m tall. Stems terete. Leaves with petiole 8–20 mm long; blade elliptic to ovate, 9–26 by 6–13 cm, acute to acuminate at apex, acute to rounded at base, not revolute, coriaceous, glossy above, dull, glandular-punctate, and often marked by large insect galls beneath, the intramarginal collecting nerve formed from looping distal ends of primary nerves. Inflorescences borne on old stems, thyrsoid, few flowered, up to 6 cm long. Flowers with pedicel 2–5 mm long; hypanthium turbinate, 12–18 by 8–12 mm, notched to form broadly rounded calyx lobes 2–4 mm long; petals obovate, 6–9 by 6–8 mm, concave, tuberculate on outside, red, singly fugacious; stamens many, the filament up to 2.5 cm long, red, the anthers oblong, 0.5–1 mm long; style up to 2.5 cm long. Fruits ovoid to obovoid, 3–7 cm long, the pericarp fleshy, red, white, or striped at maturity.

DISTRIBUTION. Aboriginally introduced, common in villages and plantations on all main islands, occasionally persisting in what appears to be primary forest but probably a remnant of past cultivation. Native to the Indo-Malesian region.

PHENOLOGY. Flowering in Samoa reported May–September, fruiting July–December.

NATIVE NAMES AND USES. Commonly *nonu fi'afi'a.* This name has cognates throughout Polynesia: *kavika* (Fiji), *fekika kai* (Tonga), *kafika* (Futuna), *fekakai* (Niue), *ka'ika* (Rarotonga), *'ahi'a* (Tahiti), *kehi'a* or *kehika inana* (the Marquesas), and *'ohi'a 'ai* (Hawaii). The English name is "Malay apple" or, less commonly, "mountain apple." The tree is widely cultivated for its edible fruit and was one of the few fruit trees available to the early Polynesians. Samoans

also use the grated inner bark to make a medicine for mouth and throat infections.

SPECIMENS EXAMINED. **Samoa.** SAVAII: Matautu, *Reinecke 460* (G); Safai, *Vaupel 362* (B, BISH). UPOLU: Savaia (Lefaga), *Bristol 2001* (BISH); above Eva, *Christophersen 529* (A, BISH, UC, US); *sine loco, Graeffe 3a* (HBG); Falefa Falls, *McKee 2867* (BISH, E); Mt. Vaea, *Rechinger 1234* (W); Apia, *Reinecke 403* (BM, BISH, E, G, K, US); near Lanoanea, *Whistler 1095* (PTBG); Nuutele Is., *Whistler 4482* (PTBG). TUTUILA: E side of Alava Ridge, *Christophersen 1120* (A, BISH, K); above Pago Pago, *Setchell 298a* (UC); Pago Pago, *Setchell 352* (UC); Alava Ridge, *Whistler 3635* (PTBG). WITHOUT FURTHER LOCALITY: *Guest 11* (BISH); *Powell 321* (K).

Two specimens listed by Rechinger (1910), *30* from Moamoa, Upolu, and *1749* from Mt. Vaea, Upolu, could not be located at Vienna. Likewise, an unnumbered specimen noted by Pickering (1876) as having been collected by the U. S. Exploring Expedition on Tutuila could not be located at either the U. S. National Herbarium or the Gray Herbarium.

11. **Syzygium neurocalyx** (A. Gray) Christoph. Bernice P. Bishop Mus. Bull. **154:** 27. 1938.

Eugenia neurocalyx A. Gray, Bot. U. S. Expl. Exped., Phan. 512. 1854, U. S. Expl. Exped., Atlas Phan. *pl. 59.* 1856; Reinecke, Bot. Jahrb. Syst. **25:** 658. 1898; Setch. Publ. Carnegie Inst. Wash. **341:** 65. 1924. TYPE: Fiji, Ovalau or Vanua Levu, without further locality, 1840, *U. S. Expl. Exped. s.n.* (holotype, US *47777*!; isotype, GH!).

Jambosa formosa sensu Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 144. 1910; non Niedenzu.

Shrub or small tree up to 4 m tall. Stems terete. Leaves with petiole 1–7 mm long; blade lanceolate to long-elliptic, 12–30 by 5–9 cm, rounded to acute at apex, rounded to subcordate at base, not revolute, chartaceous, often with prominent insect galls, glossy above, lighter, dull, and glandular-punctate beneath, pinnately nerved. Inflorescences terminal, capitate, several flowered. Flowers sessile; hypanthium campanulate to rotate, 15–20 by 15–22 mm, strongly 10- to 14-costate, notched into round to oblong calyx lobes up to 1 cm long, these red to green tinged with red; petals suborbicular, ca. 8–15 by 8–20 mm, white, singly deciduous, sometimes persisting past anthesis; stamens several hundred, the filament up to 2.5 cm long, yellow, the anther linear to oblong, 1–2.5 mm long; style 3–5 cm long. Fruits not seen, but subglobose with urceolate neck and persistent sepals and style, reported (Smith, 1985) to be up to 7.5 by 6 cm in Fiji, fleshy, fragrant.

DISTRIBUTION. Christophersen (1938) and Setchell (1924) believed that this species was aboriginally introduced to Samoa, where it is now rare in cultivation on Savaii, Upolu, and Tutuila. However, two specimens (*Whistler 1907* and *Reinecke 282*) from Upolu were collected in native forest at about 700 m altitude. Additionally, the flowers of the Samoan specimens are smaller than those in Fiji, which may support Smith's (1985) opinion that *Syzygium neurocalyx* is native to Samoa and was brought from the forest and cultivated. Also native to Fiji, and native or aboriginally introduced to Tonga, Rotuma, and Futuna.

PHENOLOGY. Flowering reported April–October, fruiting in April but probably year-round.

NATIVE NAMES AND USES. *Fena,* apparently a strictly Samoan name, and sometimes *'oli,* a cognate of the Tongan and Futunan (*koli*) and the Rotuman (*kori*) names for the plant. According to Powell (1868), it was used only as a perfume, suspended from the neck by a string, but Setchell (1924) noted its use for making an aromatic oil for the hair. It was employed similarly in Tonga (Yuncker, 1959) and Fiji (Smith, 1985).

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: Aopo, *Christophersen 2541* (BISH). UPOLU: *sine loco, Graeffe 27a* (HBG); secondary forest by "Heniger," *Rechinger 490* (W), *492* (W), *1877* (W); above Letogo at 700 m, *Reinecke 282* (E, G); Taitoelau rim, *Whistler 1907* (B, BISH, K, PTBG). TUTUILA: *sine loco, Mitchell 562* (BISH); above Pago Pago, *Setchell 295* (UC), *298b* (UC), *514* (UC). WITHOUT FURTHER LOCALITY: *Powell s.n.* (K); *Whitmee 12* (K), *224* (K).

12. **Syzygium jambos** (L.) Alston *in* Trimen, Handb. Fl. Ceylon **6:** 115. 1931; Christoph. Bernice P. Bishop Mus. Bull. **154:** 27. 1938.

Eugenia jambos L. Sp. Pl. 470. 1753; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 144. 1910. TYPE: four prior references were listed by Linnaeus, but apparently no lectotype has been selected (Smith, 1985).

Tree up to 5 m or more tall. Stems terete, sometimes quadrangular when young. Leaves with petiole 5–13 mm long; blade lanceolate, 9–26 by 2–6 cm, acuminate and sometimes curved at apex, acute at base, not revolute, coriaceous, dark green above, lighter and obscurely glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal or axillary, paniculate, several flowered (up to 10), 5–10 cm long. Flowers with pedicel 8–16 mm long; hypanthium turbinate, 12–17 by 8–13 mm, notched into rounded calyx lobes 4–7 mm long, these tuberculate outside; petals suborbicular, 15–18 mm long, concave, reflexed at anthesis, white, tuberculate outside; stamens 400+, the filament up to 4 cm long, pale yellow, the anther oblong, 1–1.5 mm long; style 3–4 cm long. Fruits globose to ovoid, 2.5–3.7 cm in diameter, the calyx lobes and style persistent, the pericarp fleshy, yellowish to pink.

DISTRIBUTION. Introduced prior to 1860, uncommonly cultivated in villages and plantations. Native to southeastern Asia.

PHENOLOGY. Flowering reported May–September.

NATIVE NAMES AND USES. *Seasea palagi,* literally "European *seasea*" (*Syzygium corynocarpum* (A. Gray) C. Mueller). The English name is "rose apple." The fruit is eaten, but it is not nearly as common or as esteemed as *nonu fi'afi'a,* the Malay apple.

SPECIMENS EXAMINED. **Samoa.** SAVAII: Safotu, *Christophersen 3596* (BISH, UC). UPOLU: Siusega, *Cox 168* (BISH, GH, UC); *sine loco, Graeffe 268* (HBG); near Malifa, *Rechinger 940* (W); near Motootua, *Rechinger 1767* (W); *sine loco, Tiuu s.n.* (PTBG). WITHOUT FURTHER LOCALITY (Tutuila?): *Guest 7* (BISH), *17* (BISH).

13. **Syzygium patentinerve** Christoph. Bernice P. Bishop Mus. Bull. **154:** 24. 1938. TYPE: Samoa, Savaii, forest above Matavanu Crater, 900 m alt., 1931, *Christophersen 2262* (holotype, BISH!).

"*Eugenia* spec. nova," Reinecke, Bot. Jahrb. Syst. **25:** 660. 1898.

Tree up to 10 m tall. Stems terete. Leaves sessile or with petiole to 2 mm long; blade oblong to elliptic, 4–10 (longer in saplings) by 3–7 cm, rounded to obtuse at apex, subcordate to rounded at base, somewhat revolute, coriaceous, glossy above, dull and conspicuously glandular-punctate beneath, pinnately nerved. Inflorescences terminal and in upper axils, paniculate, few- to several-flowered (up to 20), 2.5–6 cm long, broad, with axes and branches somewhat flattened between nodes. Flowers sessile; hypanthium campanulate, 13–18 mm by 8–12 mm, notched into broadly rounded calyx lobes 2–4 mm long; petals imbricate, suborbicular, 6–9 mm across, concave, white, fugacious singly; stamens ca. 300, the filament up to 20 mm long, showy white, the anther oblong, ca. 0.5 mm long; style ca. 18–24 mm long. Fruits ellipsoid to obovoid, 3–4 cm long including hypanthium exserted 2–4 mm or partially surrounded, the pericarp thin, dark purple and glossy at maturity.

DISTRIBUTION. Endemic to Samoa; in cloud forest on Savaii and Upolu, 900–1300 m alt.

PHENOLOGY. Flowering reported September–November, fruiting in May.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Letui, *Christophersen 792* (A, BISH, K); central region at 1200 m, *Reinecke 436* (G); above Asau, *Whistler 1766* (PTBG); below Mata-o-le-afi, *Whistler 2481* (PTBG); above Masamasa, *Whistler 4574a* (PTBG). UPOLU: rim of Mt. Fiamoe, *Whistler 1169* (B, PTBG).

14. **Syzygium savaiiense** (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 839. 1858.

Eugenia savaiiensis A. Gray, Bot. U. S. Expl. Exped., Phan. 530. 1854. TYPE: Samoa, Savaii?, without further locality, 1839, *U. S. Expl. Exped. s.n.* (lectotype, here designated, US *77359*!, *pro parte*; isolectotype, GH [fragment]!).

Syzygium tutuilense (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 839. 1858; Christoph. Bernice P. Bishop Mus. Bull. **154:** 26. 1938.

Eugenia tutuilensis A. Gray, Bot. U. S. Expl. Exped., Phan. 529. 1854. TYPE: Samoa, "Tutuila" (almost certainly Savaii or Upolu), without further locality, 1839, *U. S. Expl. Exped. s.n.* (lectotype, here designated, US *47782*!; isolectotype, GH!).

Eugenia richii sensu Reinecke, Bot. Jahrb. Syst. **25:** 659. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910; non A. Gray.

Tree up to 10 m tall. Stems terete. Leaves with petiole 3–12 mm long; blade oblong to elliptic, 8–24 by 4–9.5 cm, acute to acuminate at apex, acute at base, not revolute, coriaceous, glossy above, dull and obscurely glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal, paniculate, many flowered, 4–15 cm long, broad, with axes and branches flattened between nodes. Flowers sessile; hypanthium campanulate, 11–15 by 7–10 mm, shallowly notched into broadly rounded calyx lobes 1–2 mm long; petals confluent, calyptrate, white(?); stamens ca. 300, the filament up to 25 mm long, showy white, the anther oblong, ca. 0.5 mm long; style 18–30 mm long. Fruits ovoid to ellipsoid

or almost urceolate with distinct neck, 20–33 mm long, pericarp dark purple at maturity.

DISTRIBUTION. Endemic to Samoa; common in lowland to montane forest on Savaii and Upolu, 5–700 m alt.

PHENOLOGY. Flowering reported September–December, fruiting April–June.

NATIVE NAMES. Sometimes *asi* or *asi vai,* but these are not species specific (particularly the former, which is often used indiscriminately for several different species of the genus).

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: near Salailua, *Christophersen 2483* (BISH); Salailua-Latatai, *Christophersen 2629* (A, BISH); near Taga, *Christophersen 2822* (BISH, K, UC, US); above Sili, *Christophersen 3232* (BISH), *3271* (BISH); near Patamea, *Rechinger 1180* (W); Puapua road, *Vaupel 595* (B); E of Asau, *Whistler 981* (B, BISH, PTBG); Puapua-Saumalaeulu, *Whistler 2195* (PTBG). UPOLU: above Lefaga, *Bristol 2457* (BISH), *2459* (BISH, GH, K, US); ridge above Malololelei, *Christophersen 165* (BISH); above Tafatafa, *Cox 366* (BISH, GH, UC); *sine loco, Graeffe 1559* (HBG, K); above Siumu, *Reinecke 203* (E, G, K, US, WRSL); near Utumapu, *Whistler 680* (PTBG); rim of Mt. Mariota, *Whistler 745* (B, G, PTBG), *816* (BISH, PTBG); rim of Mt. Taitoelau, *Whistler 1105* (PTBG); near coast at Saaga, *Whistler 1113* (PTBG); E rim of Lanotoo, *Whistler 1619* (B, BISH, PTBG); crater rim SE of Mt. Mariota, *Whistler 1899* (B, BISH, PTBG); Tanumalala, *Whistler 2034* (BISH, PTBG); E of Lake Lanotoo, *Whistler 3505* (PTBG); NW of Tonitoniga, *Whistler 3911* (PTBG); Mt. Fao, *Whistler 5710* (PTBG). WITHOUT FURTHER LOCALITY: *Whitmee 176* (K).

The type specimens of *Eugenia savaiiensis* and *E. tutuilensis* are conspecific. The former comprises an inflorescence of *E. savaiiensis* and a stem of *Antidesma sphaerocarpum* Muell.-Arg. (Euphorbiaceae) but is noted to have been collected on Savaii; the latter consists of fruits and stems but has the locality listed as "Tutuila," where the species is apparently not found. In order not to belie the distribution of this species, the type specimen of *E. savaiiense* was selected as the lectotype for this species.

15. **Syzygium oligadelphum** (Christoph.) Merr. & Perry, Sargentia **1**: 75. 1942.

Pareugenia oligadelphum Christoph. Bernice P. Bishop Mus. Bull. **154**: 20. 1938. TYPE: Samoa, Upolu, Maugatele Ridge above Saluafata, ca. 550 m alt., 1929, *Christophersen 523* (holotype, BISH!).

Tree up to 7 m tall. Stems terete. Leaves with petiole 3–12 mm long; blade elliptic to obovate, 5–10 by 2.5–4.5 cm, shortly acuminate to caudate at apex with narrow tip somewhat twisted, acute at base, slightly revolute, coriaceous, glossy above, lighter, dull, and finely glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal or in upper axils, paniculate, many flowered, 6–8 cm long, branches terete. Flowers with pedicel 1–2 mm long; hypanthium campanulate to cup shaped, 10–14 by 6–8 mm, shallowly notched into broadly rounded calyx lobes 1–2 mm long; petals confluent, calyptrate; stamens ca. 160, the filament up to 8 mm long, white, the anther oblong, 0.5–1 mm long; style ca. 6 mm long. Fruits subspherical to ovoid, ca. 17–23 mm long including hypanthium exserted 1–2 mm or partially surrounded, the pericarp thin, black and shiny at maturity.

DISTRIBUTION. Endemic to Samoa; in montane to cloud forest on Upolu and possibly Savaii, 400–550 m alt.

PHENOLOGY. Flowering and fruiting reported in September.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** UPOLU: above Utumapu, *Rechinger 1522* (W), *1691* (W); Togitogiga Farm, *Whistler 726* (B, BISH, PTBG).

The only flowering specimen of this species has immature flowers. In addition to the two cited specimens, three other sterile specimens collected above Utumapu, Upolu, and held at W may belong here: *Rechinger 1522* (cited by Rechinger as "*Apocynacea*"), *1543* (incorrectly identified as *Eugenia effusa* A. Gray), and *1691* (cited as *Eugenia* spec. I).

16. **Syzygium christophersenii** Whistler, sp. nov. FIGURE 3.

Syzygio oligadelpho affinis, a qua imprimis differt in foliis infra non conspicuo glandulosis punctatis.

Tall tree. Stems terete. Leaves with petiole 5–18 mm long; blade elliptic to ovate, 5.5–9 by 1.5–4 cm, acuminate to caudate at apex with twisted tip, acute to subcuneate at base, slightly revolute, coriaceous, dull above, lighter, dull, and not appearing glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal, paniculate, many flowered, 4–8 cm long, branches terete. Flowers subsessile; hypanthium campanulate, 7–11 by 7–9 mm, shallowly notched into broadly rounded calyx lobes 1–2 mm long; petals confluent, calyptrate, white; stamens ca. 275, the filament up to 16 mm long, showy white, the anther oblong, ca. 0.8 mm long; style up to 10 mm long. Fruits not known.

TYPE. Samoa, Savaii, above Asau at 450 m, 1974, *Whistler 1671* (holotype, PTBG!; isotypes, B!, BISH!).

DISTRIBUTION: Endemic to Samoa; in montane forest of Savaii, 450–600 m alt.

PHENOLOGY. Flowering reported in March.

ADDITIONAL SPECIMEN EXAMINED. **Samoa.** SAVAII: Siuvao-Auala, *Christophersen 3386* (BISH).

This endemic species from Savaii is superficially very similar to *Syzygium oligadelphum* (endemic to Upolu) but unlike that species lacks obvious glandular punctation on the lower leaf surfaces. The type is the only fertile specimen known, but *Christophersen 3386,* which is sterile, agrees with it vegetatively. Another sterile specimen, *Rechinger 1611* (W), collected at Maugaafi, Savaii, probably belongs here as well. *Whistler 574a,* comprising immature fruits found on the forest floor above Ologogo, Savaii, may belong to this species.

Syzygium christophersenii is named in honor of Erling Christophersen, whose excellent work on Samoan botany is still unequaled.

17. **Syzygium inophylloides** (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 838. 1858; Christoph. Bernice P. Bishop Mus. Bull. **154:** 24. 1938; Whistler, Allertonia **2:** 160. 1980.

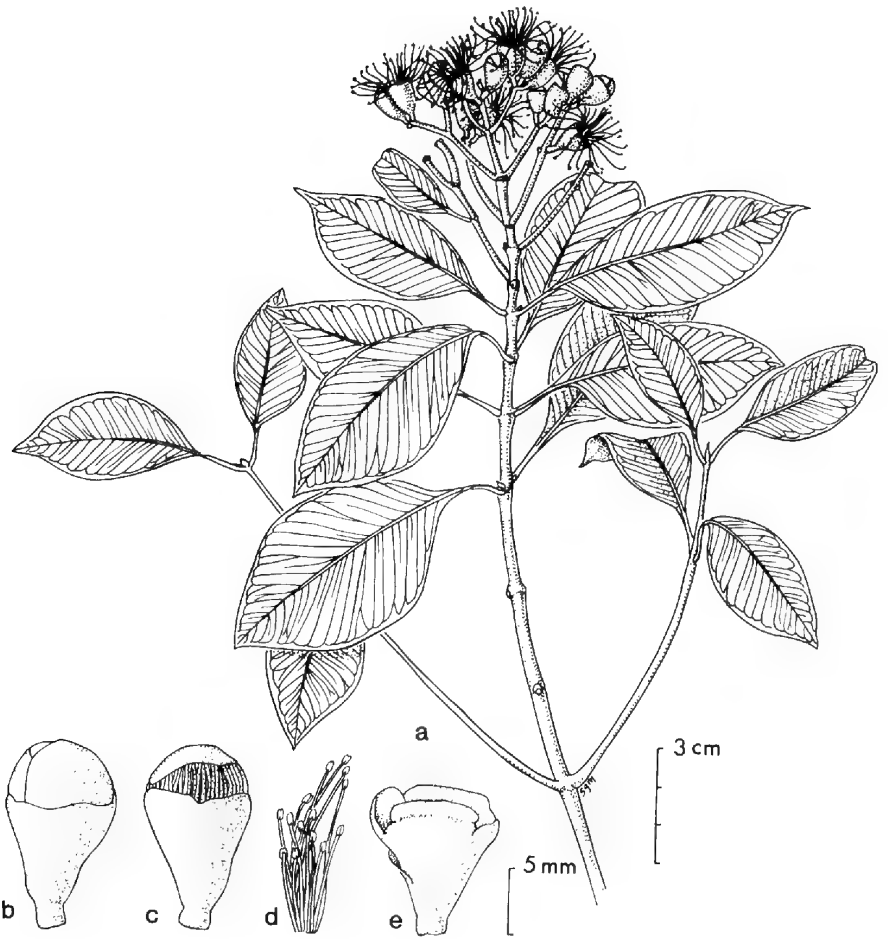

FIGURE 3. **Syzygium christophersenii:** a, vegetative and flowering branchlets; b, flower bud; c, flower at anthesis; d, stamens; e, flower after anthesis.

Eugenia inophylloides A. Gray, Bot. U. S. Expl. Exped., Phan. 521. 1854; Setch. Publ. Carnegie Inst. Wash. **341:** 65. 1924; Yuncker, Bernice P. Bishop Mus. Bull. **184:** 54. 1945. TYPE: Samoa, Tutuila, "common on a wooded ridge, at the elevation of 500 feet," 1839, *U. S. Expl. Exped. s.n.* (holotype, US *47776*!; isotypes, GH!, K!).

Eugenia amicorum sensu Rech. Denkschr. Kaiserl. Akad. Wiss. Math.-Naturwiss. Kl. **85:** 145. 1910, *pro parte*; non A. Gray.

?*Eugenia crosbyi* Burkill, J. Linn. Soc., Bot. **35:** 38. 1901. TYPE: Tonga, Vavau, 1891, *Crosby 61* (holotype, K!).

Tree up to 20 m or more tall. Stems terete. Leaves with petiole 3–10 mm long; blade usually elliptic (ovate to obovate), 2.5–8 (longer in saplings) by 1.5–4.5 cm, caudate at apex with narrow, blunt, somewhat twisted tip 3–12 mm long, acute to rounded at base, slightly revolute, coriaceous, glossy above, dull and usually obscurely glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal and in upper axils, paniculate, many flowered, 2.5–10 cm long. Flowers with pedicel usually less than 1 mm long; hypanthium narrowly campanulate, 5–7 mm by 2–3 mm, shallowly notched into broadly triangular

calyx lobes ca. 0.5 mm long; petals confluent, calyptrate, white; stamens ca. 80–120, the filament up to 7 mm long, white and showy, the anther oblong, ca. 0.5 mm long; style 5–7 mm long. Fruits obovoid to ellipsoid, 2.5–4 cm long, including hypanthium exserted 0.5–1.5 mm, the pericarp thin, yellowish when mature, longitudinally many-ribbed when dry.

DISTRIBUTION. Indigenous to Samoa; common in lowland to montane forest on all main islands, 10–750 m alt. Also indigenous to Alofi (Horne Islands), Tonga, and Niue.

PHENOLOGY. Flowering reported August–December, fruiting February–September so perhaps year-round.

NATIVE NAMES AND USES. Commonly *asi* (on Alofi, as well as in Samoa), which can refer to other species of the genus. It is also called *asi toa, asi vao,* and possibly *asi malo* to distinguish it from most or all of the other species known as *asi.* The tree is one of the major commercial timber trees of Samoa (Whistler, 1984) and is used locally in construction and for house posts.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: above Vaipouli, *Christophersen 1909* (BISH); near Matavanu, *Christophersen 1956* (A, BISH, M, US); Olo, *Christophersen 2292* (A, BISH, W); above Sili, *Christophersen 3225* (BISH); Siuvao-Auala, *Christophersen 3362* (BISH); Papa-Fagatele, *Christophersen 3408* (BISH, K, UC, US); Tapueleele, *Christophersen 3463* (BISH); Auala, *Fasavalu 23* (BISH); Aopo, *Fasavalu 34* (BISH); Aopo-Asau lava flow, *Rechinger 66* (W); above Vaipouli, *Rechinger 4490* (W); above Ologogo, *Vaupel 428* (B, BISH, K, PTBG, US, W, WRSL), *428a* (B); Puapua bush, *Vaupel 594* (B); above Ologogo, *Whistler 519* (BISH, PTBG), *588* (PTBG); above Asau, *Whistler 980* (B, BISH, G, PTBG); NW of Aopo, *Whistler 1712* (B, BISH, K, PTBG). UPOLU: Togitogiga, *Fasavalu 7* (BISH); *sine loco, Funk 208* (WRSL), *Graeffe 36* (HBG); above Luatuanuu, *Whistler 1540* (B, BISH, K, PTBG), *1611* (B, BISH, PTBG). TUTUILA: *sine loco, Bayliss s.n.* (BISH); ridge W of Pago Pago, *Christophersen 1255* (A, BISH, K, US); Pago Pago Harbor, *Diefenderfer 14* (BISH); trail down to Vatia, *Setchell 337* (BISH, UC); above Pago Pago, *Setchell 570* (UC); W of Aoloaufou, *Whistler 2802* (B, BISH, G, K, PTBG); *sine loco, Wilder 93* (BISH). OLOSEGA: Alei Ridge, *Whistler 3493* (PTBG). TAU: Amouli trail, *Garber 637* (A, BISH, K). WITHOUT FURTHER LOCALITY: *Powell 313* (K); *Whitmee 27, pro parte* (K), *50* (K), *212* (K), *s.n., pro parte* (GH), *s.n.* (BM).

Christophersen 2901 (BISH), collected above Salailua, Savaii, is a sterile sapling with long-attenuate leaves and probably belongs here.

The type of *Eugenia crosbyi* Burkill was examined and appears to be conspecific with *Syzygium inophylloides.* It lacks fruits, as does the only other specimen I have seen, *Whistler 6006,* also collected on Vavau, and consequently the reduction to synonymy of *E. crosbyi* is considered to be tentative.

18. **Syzygium curvistylum** (Gillespie) Merr. & Perry, Sargentia **1:** 75. 1942; A. C. Smith, Fl. Viti. Nova **3:** 337. 1985.

Eugenia curvistyla Gillespie, Bernice P. Bishop Mus. Bull. **83:** 21. 1931. TYPE: Fiji, Viti Levu, Mba Province, near Vatuthere, 1927, *Gillespie 4269* (holotype, BISH!; isotypes, BISH!, US).

Tree at least 7 m tall. Stems terete. Leaves with petiole 2–8 mm long; blade lanceolate to elliptic, 4–12 by 1.5–5.5 cm, acuminate (rarely acute) at apex,

acute at base, not revolute, coriaceous, glossy above, lighter, duller, and conspicuously glandular-punctate beneath, finely pinnate-nerved. Inflorescences terminal or rarely axillary, paniculate, several flowered, up to 6 cm long. Flowers with pedicel 1–3 mm long; hypanthium campanulate, 4–6 by 3–4 mm, notched into rounded calyx lobes up to 1.5 mm long; petals confluent, calyptrate; stamens ca. 108, the filament ca. 10 mm long, white, the anther subglobose, ca. 0.5 mm long; style ca. 8 mm long, persistent in fruit. Fruits subspherical, ca. 6 mm long including persistent sepals, pericarp purple at maturity.

DISTRIBUTION. Indigenous to Samoa; uncommon in foothill to cloud forest on Savaii and Upolu, 200–900 m alt. Also found in Fiji.

PHENOLOGY. Flowering reported in June, fruiting in December, both possibly year-round.

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: far above Aopo, *Bristol 2139* (BISH, GH, US). UPOLU: swamp near Tiavi, *Christophersen 171* (BISH); rim of Mt. Fiamoe, *Whistler 2010* (BISH, PTBG); above Saagafou, *Whistler 3921* (PTBG). WITHOUT FURTHER LOCALITY: *Powell 336* (K).

19. **Syzygium carolinense** (Koidz.) Hosok. J. Jap. Bot. **16:** 542. 1940; Whistler, Allertonia **2:** 160. 1980.

Eugenia carolinensis Koidz. Bot. Mag. Tokyo **30:** 402. 1916. TYPE: Ponape, without further locality, 1915, *Koidzumi s.n.* (holotype, TI).
Eugenia ponapensis Merr. ex Kaneh. Trans. Nat. Hist. Soc. Taiwan **6:** 43. 1916.
Syzygium ponapense (Merr.) Diels, Bot. Jahrb. Syst. **56:** 533. 1921; Christoph. Bernice P. Bishop Mus. Bull. **154:** 25. 1938.
Eugenia rubescens sensu Reinecke, Bot. Jahrb. Syst. **25:** 659. 1898; sensu Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910; non A. Gray.
Eugenia richii sensu Yuncker, Bernice P. Bishop Mus. Bull. **185:** 54. 1945; non A. Gray.

Tree up to 10 m tall. Stems terete. Leaves with petiole 3–12 mm long; blade elliptic, 6–20 by 2.5–8.5 cm, acute to acuminate and sometimes twisted at apex, obtuse to acute at base, slightly revolute, coriaceous, dark green and glossy above, lighter and obscurely glandular-punctate beneath, coarsely nerved, intramarginal collecting nerve formed from looping distal ends of primary veins. Inflorescences terminal and in upper axils, paniculate, many flowered, 8–20 cm long, widely branching. Flowers sessile; hypanthium cup shaped to turbinate, 2.5–4 by 2–3 mm including distinct stipe, subentire, lacking distinct calyx lobes; petals confluent, calyptrate, pale green; stamens ca. 100, the filament up to 6 mm long, white, the anther oval, ca. 0.3 mm long; style 2.5–4 mm long. Fruits ellipsoid, 15–25 mm long including exserted necklike hypanthium, sometimes somewhat curved, pericarp red to purple at maturity.

DISTRIBUTION. Indigenous to Samoa; in lowland to cloud forest on all main islands, 100–750 m alt. Also found on Ponape.

PHENOLOGY. Flowering reported June–July and November–January, fruiting March–September so perhaps year-round.

SPECIMENS EXAMINED. **Samoa.** SAVAII: far above Aopo, *Bristol 2163* (BISH); above Gataivai, *Bristol 2251* (BISH); near Matavanu, *Christophersen 1953* (A, BISH, K, UC, US, W); Olo, above Safotu, *Christophersen 2265* (A, BISH, K, US); Salailua, *Christophersen 2614* (BISH); behind Safai, *Vaupel 290* (B, BISH, K, US, WRSL); *sine loco, Vaupel 646* (B, BISH, PTBG). UPOLU: Savaia above Lefaga, *Bristol 2074* (BISH, GH), *2112* (BISH, GH, K, US); Matautu (Lefaga), *Bristol 2475* (BISH, GH, US); ridge to Mt. Vaitou, *Christophersen 272* (BISH); near Lanotoo, *Rechinger 1817* (BM); Lanotoo, *Reinecke 336* (E, G, US, WRSL); E of Lanotoo, *Whistler 2018* (B, BISH, PTBG); ridge W of Lemafa Farm, *Whistler 5138* (PTBG, US); Apia (cult.), *Wilder 415* (A, BISH). TUTUILA: Alava Ridge, *Spence 472* (BISH), *Whistler 2773* (PTBG), *3651* (BISH, PTBG); Aoloaufou, *Whistler 2780* (BISH, G, PTBG), *2796a* (BISH, PTBG); ridge N of Matafao, *Whistler 3543* (BISH, K, PTBG); Aua–Afono trail, *Yuncker 9428* (A, BISH, K). OLOSEGA: top of Piumafua, *Garber 1028* (BISH); Olosegauta-Piumafua Ridge, *Garber 1030* (A, BISH). WITHOUT FURTHER LOCALITY: *Powell 349* (K).

Four specimens (near Lanotoo, *Rechinger 156, 1818, 1850*; near Patamea, *Rechinger 1134*) that probably belong here could not be located. They should be at Vienna but were not found during my visit there in 1974.

20. **Syzygium corynocarpum** (A. Gray) C. Mueller, Ann. Bot. Syst. **4:** 839. 1858; Christoph. Bernice P. Bishop Mus. Bull. **154:** 23. 1938.

Eugenia corynocarpa A. Gray, Bot. U. S. Expl. Exped., Phan. 526. 1854, U. S. Expl. Exped., Atlas Phan. *pl. 64.* 1856; Reinecke, Bot. Jahrb. Syst. **25:** 659. 1898; Setch. Publ. Carnegie Inst. Wash. **341:** 65. 1924; Yuncker, Bernice P. Bishop Mus. Bull. **184:** 54. 1945. TYPE: Samoa or Fiji, without further locality, 1839 or 1840, *U. S. Expl. Exped. s.n.* (holotype, US *62251*!; isotypes, GH!, K!).

Eugenia amicorum sensu Reinecke, Bot. Jahrb. Syst. **25:** 659. 1898; Rech. Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **85:** 145. 1910; non A. Gray.

Tree up to 5 m tall. Stems terete. Leaves with petiole 2–9 mm long; blade lanceolate, elliptic, or oblanceolate, 7.5–13 by 2.5–4.5 cm, acute to acuminate at apex, acute to cuneate at base, not revolute, chartaceous, dark green above, light green and conspicuously glandular-punctate beneath, coarsely nerved, intramarginal collecting nerve composed of looping distal ends of primary nerves. Inflorescences terminal, paniculate, many flowered, 8–16 cm long, widely branching, primary branches perpendicular to rachis. Flowers sessile; hypanthium turbinate, 5–8 by 2–3 mm, entire or shallowly notched into broadly triangular calyx lobes ca. 0.5 mm long; petals confluent, calyptrate, white; stamens ca. 110, the filament up to 5 mm long, white, the anther ovoid to oblong, ca. 0.5 mm long; style 3–6 mm long, persistent on fruit. Fruits fusiform to cylindrical, 2.5–3.5 cm long including necklike hypanthium 4–6 mm in length, the pericarp fibrous inside, fleshy, red, fragrant at maturity.

DISTRIBUTION. Aboriginally introduced to Samoa; uncommon on all main islands in plantations and secondary forest, occasionally cultivated; 25–425 m alt. Probably native to Fiji, aboriginally introduced throughout western Polynesia (Tonga, Uvea, Futuna, and Niue).

PHENOLOGY. Flowering reported in September and November, fruiting in December.

LOCAL NAMES AND USES. *Seasea* (same name used on Futuna; a cognate of *hehea,* its Tongan name). The ripe fruits are suspended with string to form a

fragrant necklace, a use also reported from Fiji (Smith, 1985) and Futuna (St. John & Smith, 1971).

ADDITIONAL SPECIMENS EXAMINED. **Samoa.** SAVAII: behind Safune, *Christophersen 2392* (BISH); Matautu, *Reinecke 396* (BISH, E, G); Vaipouli, *Reinecke 397* (E, G); Safai, *Vaupel 257* (B, BISH, K, US, WRSL). UPOLU: near Vailele, *Christophersen 355* (A, BISH); Sauago, *Christophersen 546* (BISH, US); Vailima, *Eames 82* (BISH); *sine loco, Graeffe 11a* (HBG), *31* (HBG), *558* (HBG); above Moamoa, *Rechinger 38* (W); above Utumapu, *Rechinger 929* (W); Mt. Vaea, *Rechinger 1358* (W); Papaseea Waterfall, *Rechinger 1856* (BM, US, W); "Le Pua," *Reinecke 629* (E, G, WRSL); Faatoia (Apia), *Whistler 2064* (PTBG); Mt. Vaea, *Whistler 4002* (BISH, PTBG). TUTUILA: Aua–Afono trail, *Garber 837* (BISH); *sine loco, Graeffe 274* (HBG); Pago Pago, *Meebold 26574* (BISH); behind Pago Pago, *Setchell 364* (UC); *sine loco, Setchell 451* (UC), *452* (UC). OLOSEGA: SE side of island, *Kuruc 88* (BISH); behind Olosega Village, *Whistler 3828* (PTBG). TAU: plateau behind Luma, *Garber 652* (BISH, K, UC), *658* (A, BISH, UC). WITHOUT FURTHER LOCALITY: *Powell 201* (K), *s.n.* (K); *Reinecke s.n.* (K); *Whitmee 41* (MEL).

Some of the material collected by the U. S. Exploring Expedition has Tahiti given as the locality, but this is almost certainly in error because the natural range of the genus in Polynesia does not extend east of Niue (except for Hawaii). Errors in labeling the specimens from the Expedition are not infrequent.

Two specimens collected on Savaii (Lealatele, *Reinecke 391*; Matautu, *Reinecke 402*) could not be located. These were probably unicates that were destroyed in Berlin during World War II.

ADDITIONAL SPECIES

Two other species of *Syzygium* have been collected in Samoa. *Syzygium cumini* (L.) Skeels, from the government research station at Nafanua, Apia, is represented by *Whistler 2112* (BISH, PTBG) and *2120* (BISH, PTBG). An unidentified species collected in Apia is represented by *Whistler 2065* (PTBG). It has sessile leaves and small, campanulate, edible fruits and was reportedly introduced from Papua New Guinea.

ACKNOWLEDGMENTS

I am greatly indebted to the faculty and staff of the herbaria that I visited and from which I borrowed specimens during the course of my work. I also wish to thank Sue Nakamura for her excellent drawings of the new species.

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JOURNAL OF THE ARNOLD ARBORETUM

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CONTENTS OF VOLUME 69, NUMBER 2

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JOURNAL
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VOLUME 69 JULY 1988 NUMBER 3

DEDICATION

It is with deep esteem, affection, and hearty best wishes that this number of the *Journal of the Arnold Arboretum* is dedicated to Professors Richard Alden Howard and Carroll Emory Wood, Jr., to mark their recent retirements from the Arnold Arboretum and the Department of Organismic and Evolutionary Biology. The careers of both have been full, productive, and intimately associated with Harvard University and the Arnold Arboretum in particular. It will come as no surprise to colleagues and friends when they learn that both Carroll and Dick expect to continue on the job, and that "retirement" from Harvard for them simply marks an anniversary, not the end of their active roles in and contributions to the worldwide botanical community. The vitae given below provide thumbnail outlines of the active years of both.

RICHARD ALDEN HOWARD

Born 1 July 1917, Stamford, Connecticut; B.A., Miami University, 1938; M.A., Ph.D., Harvard University, 1940, 1942; D.Sc. (honorary), Framingham State College, 1977.

Assistant Curator, New York Botanical Garden, 1947, 1948; Assistant Professor, Harvard University, 1948–1953; Professor and Chairman, Department of Botany, University of Connecticut, 1953, 1954; Arnold Professor of Botany and Director, Arnold Arboretum of Harvard University, 1954–1978; Professor of Dendrology, Harvard University, 1954–1988.

CARROLL EMORY WOOD, JR.

Born 13 January 1921, Roanoke, Virginia; B.S., Roanoke College, 1941; M.S., University of Pennsylvania, 1943; M.A., Ph.D., Harvard University, 1947, 1949.

Instructor in Biology, Harvard University, 1949–1951; Assistant and Associate Professor of Botany, University of North Carolina at Chapel Hill, 1951–1955; Associate Curator, Arnold Arboretum, 1954–1970; Curator, Arnold Arboretum, 1970–1988; Editor, *Journal of the Arnold Arboretum,* 1958–1962; Lecturer in Biology, Harvard University, 1964–1969, 1970–1972; Professor of Biology, Harvard University, 1972–1988.

THE GENERA OF ANCHONIEAE (HESPERIDEAE) (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

IHSAN A. AL-SHEHBAZ[3]

Tribe **Anchonieae** A. P. de Candolle, Syst. Nat. **2**: 152. 1821.

Annual, biennial, or perennial herbs [rarely shrubs]; trichomes unicellular, eglandular, simple or furcate, stellate, dendritic, or malpighiaceous, sometimes mixed with multicellular glandular ones. Inflorescences ebracteate [rarely bracteate], corymbose racemes [rarely panicles], usually elongated in fruit. Sepals erect, free or sometimes connivent, usually unequal and slightly to conspicuously saccate at base. Stamens 6, often strongly tetradynamous; median filaments free [rarely connate], unappendaged [or dentate]. Fruits dehiscent or indehiscent and usually lomentaceous, breaking into 1-seeded parts [rarely nutlike], terete, tetragonal, or flattened parallel [or at right angles] to the septum; styles conspicuous [or obsolete]; stigmas strongly 2-lobed [rarely entire], the lobes connivent or spreading, decurrent or not [rarely forming conspicuous horns or appendages]. Seeds few to numerous, uniseriately [or biseriately] arranged in each locule, wingless [or winged], nonmucilaginous [sometimes mucilaginous] when wet; cotyledons accumbent or incumbent. (Including Buniadeae DC., Cheirantheae Webb & Berth., Erysimeae Dumort., Hesperideae Prantl, Matthioleae O. E. Schulz.) TYPE GENUS: *Anchonium* DC.

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 121st in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

I am most grateful to Carroll Wood for his continuous support, advice, and help during the preparation of this paper, and particularly for his critical review of the manuscript. I should also like to thank Norton G. Miller for reviewing the paper, Reed C. Rollins and Robert A. Price for their valuable discussions, and Barbara Nimblett for typing the manuscript. I am grateful to Elizabeth B. Schmidt and Stephen A. Spongberg for their editorial advice.

[2]For an account of the family and its tribes, see Al-Shehbaz, The Tribes of Cruciferae (Brassicaceae) in the Southeastern United States. Jour. Arnold Arb. **65**: 343–373. 1984.

[3]Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

Journal of the Arnold Arboretum **69**: 193–212. July, 1988.

As delimited here, the Anchonieae are a well-defined group of about 27 genera (eight monotypic) and some 240 species that have multicellular glandular trichomes and/or connivent, decurrent stigmatic lobes. *Hesperis* L. (ca. 25 species), *Malcolmia* R. Br. (including *Strigosella* Boiss.; 35 species), and *Matthiola* R. Br. (50 species) are the core genera of the tribe. These and 14 others were placed by Schulz in the Hesperideae and the Matthioleae, while the remainder either were assigned by him to other tribes (e.g., *Bunias* L. in the Euclidieae DC. and *Dontostemon* Andrz. in the Arabideae DC.) or were described after the publication of his monograph. *Atelanthera* J. D. Hooker & Thomson, *Cryptospora* Karelin & Kirilov, *Hesperidanthus* (Robinson) Rydb., *Iodanthus* Torrey & A. Gray ex Steudel, *Maresia* Pomel, *Mathewsia* W. J. Hooker & Arnott, *Notoceras* R. Br., *Pseudocamelina* (Boiss.) Busch, *Tetracme* Bunge, *Thelypodiopsis* Rydb., and *Thelypodium* Endl. have all been excluded from the Hesperideae and the Matthioleae sensu Schulz and assigned to other tribes (Al-Shehbaz, 1973, 1988; Dvořák, 1970, 1972; Miller; Rollins, 1966). *Aubrieta* Adanson (12 species; southwestern Asia, Balkan Peninsula), *Blennodia* R. Br. (two species; Australia), *Pycnoplinthopsis* Jafri (monotypic; Bhutan), *Pycnoplinthus* O. E. Schulz (monotypic; Himalayan region), and *Solms-Laubachia* Muschler (13 species; China), which have been retained in the Hesperideae or the Matthioleae by various workers, should also be excluded from the Anchonieae because they are not related to any of its members and they lack the characteristic stigmas or glands.

Schulz distinguished the Hesperideae from the Matthioleae on the basis of cotyledonary position. However, this distinction is clearly artificial since both accumbent and incumbent cotyledons are found within numerous genera of the Cruciferae. It is evident that this feature is unreliable in tribal delimitation.

The number of genera and species estimated here for the Anchonieae differs markedly from that of Al-Shehbaz (1984) for the Hesperideae because it does not include *Erysimum* L. sensu lato (ca. 200 species) or the genera that I have excluded from the Anchonieae. None of the excluded genera has glandular trichomes, and their stigmatic lobes are neither decurrent nor connivent. They have been assigned to the tribes Erysimeae and Sisymbrieae DC. (Dvořák, 1972), but their proper disposition may be in the latter tribe. In fact, the presence of cardenolides (see below) in both *Erysimum* sensu lato and *Sisymbrium* L. strongly supports their placement in one tribe. I am following my earlier account (Al-Shehbaz, 1984) by retaining *Erysimum* in the Anchonieae, but careful evaluation of the tribal disposition of this and the many excluded genera is needed. It is beyond the scope of this flora to undertake such a task.

Within the Cruciferae multicellular glandular trichomes are apparently unique to the Anchonieae. Unicellular glandular trichomes are found only in *Descurainia* Webb & Berth., which is evidently unrelated to any member of this tribe. The absence of glandular trichomes among some members of the Anchonieae is probably a derived state. The genera *Dontostemon, Hesperis, Matthiola,* and *Parrya* R. Br. include species both with and without glandular structures, while *M. longipetala* (Vent.) DC. and *P. nudicaulis* (L.) Regel have glandular or eglandular plants within the same population.

Anchonieae is the earliest legitimate, validly published name for the tribe that includes *Anchonium.* However, recent students of the Cruciferae place the genus in the tribe Hesperideae even though this name was published 70 years later. All of De Candolle's (1821) tribes of the Cruciferae are perfectly acceptable, and many were recognized by Von Hayek, Hooker (in Bentham & Hooker), Janchen, and Schulz. Avetisian united the Anchonieae (as the Hesperideae) with six other tribes that she placed in the Sisymbrieae. However, this action was inappropriate.

The Anchonieae are distributed primarily in the Old World (Eurasia, northern and tropical Africa); only the range of the *Parrya nudicaulis* complex extends into North America. Dvořák (1972) has considered Pacific North America and northeastern Asia as one evolutionary center for the tribe (as Hesperideae) and central Asia as another. It is very likely, however, that the occurrence of *Parrya* in the New World represents a recent migration.

The Anchonieae sensu lato (43 genera and ca. 500 species; Al-Shehbaz, 1984) are represented in the southeastern United States by three genera and five species, one of which is indigenous.

Chromosome numbers in the Anchonieae sensu stricto (i.e., excluding *Erysimum* and many other somewhat related genera) are known for 18 genera and 88 species (about 37 percent of the tribe). Nearly 77 percent of the species surveyed are diploid, and only about 15 percent are exclusively polyploid. About 45 percent of the species have chromosome numbers based on seven, 30 percent on six, and only 13 percent on eight (author's compilation). The lowest chromosome number ($2n = 10$) has recently been reported for the monotypic *Lonchophora* Durieu (Carrique & Martínez), which is endemic to northwestern Africa. *Diceratella* Boiss. (seven species; tropical eastern Africa, Socotra, southern Iran), *Morettia* DC. (four species; northern Africa, Somalia, Israel, Arabia), and *Parolinia* Webb (five species; Canary Islands) are all diploid with $2n = 22$. They are closely related to *Matthiola,* in which only one species is known to have such a number, and at least 20 others are diploids with $2n = 12$. It is very likely that the base chromosome number for *Matthiola* is six, and that seven and eight, which are rare in the genus, are derived.

The Anchonieae have been poorly studied phytochemically, and the scant data do not provide patterns of potential chemotaxonomic significance. A thorough survey of cardenolides and mustard oils for the many genera that I exclude from the Anchonieae may aid in the adjustment of their tribal placement.

Hooks, spines, wings, hornlike appendages, and sharply pointed beaks on the fruits evidently help in dispersal. These structures are found in *Bunias, Diceratella, Lonchophora, Matthiola, Parolinia,* and *Veselskya* Opiz (= *Pyramidium* Boiss.). Lomentaceous fruits with corky walls are characteristic of most species of *Anchonium, Chorispora* DC., and *Sterigmostemum* Bieb., but the dispersal values of such features are not fully understood. The abundance of glands on the fruits of many species may have defensive rather than dispersal significance.

Except for a few ornamental and several weedy species (see below), the tribe has no economic importance.

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KEY TO THE GENERA OF ANCHONIEAE IN THE SOUTHEASTERN UNITED STATES[4]

A. Multicellular glandular trichomes or papillae usually present; plants without malpighiaceous or 3- to 5-forked, sessile, appressed, medifixed trichomes; stigmatic lobes decurrent, connivent or connate.
  B. Fruits beaked, indehiscent, lomentaceous, often breaking transversely at maturity into 1- or 2-seeded segments; plants with multiseriate, numerous-celled glandular papillae. ..... 37. *Chorispora.*
  B. Fruits beakless, dehiscent, not lomentaceous; plants with uniseriate, few-celled glandular trichomes. ..... 38. *Hesperis.*
A. Multicellular glandular trichomes or papillae absent; plants with malpighiaceous or 3- to 5-forked, sessile, appressed, medifixed trichomes; stigmatic lobes neither decurrent nor connivent, usually divergent. ..... 39. *Erysimum.*

37. **Chorispora** R. Brown ex A. P. de Candolle, Syst. Nat. **2**: 435. 1821, nom. cons.

Annuals [or caespitose perennials with thick, branched or unbranched caudices], almost always with stipitate, multicellular, multiseriate glands, these often mixed with unicellular, unbranched trichomes [rarely glabrous]. Stems simple or most commonly branched at base. Basal leaves petiolate, usually not forming a distinct rosette, dentate, sinuate, runcinate [or pinnatisect]; cauline leaves smaller, less divided [sometimes lacking]. Flowers in ebracteate, corymbose racemes [sometimes solitary on long scapes]; infructescences elongated; fruiting pedicels divaricate [rarely erect or deflexed], stout and nearly as wide as the fruit [or slender and much narrower]. Sepals linear to narrowly oblong [or ovate], erect, somewhat connivent, sparsely [to densely] covered with glandular papillae [or eglandular trichomes], rounded at apex, usually membranaceous at margin, the inner pair strongly saccate at base. Petals purple, rose, lavender [white or yellow], strongly differentiated into blade and claw, 2–3 times longer than the sepals; blades oblong to spatulate [or broadly obovate], rounded [or retuse to emarginate] at apex. Lateral nectar glands horseshoe shaped to ringlike, median glands absent. Stamens 6, tetradynamous; filaments erect, linear, unappendaged; anthers exserted, linear [oblong or ovate], sagittate at base. Fruits linear [oblong or lanceolate], terete, indehiscent, beaked, corky, lomentaceous, smooth to slightly [or strongly] torulose [or moniliform], glabrous or with glandular papillae, breaking into segments; segments 1-seeded, closed, with a

[4]The genera are numbered as in the treatment of the tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. **65**: 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66**: 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* **67**: 265–311. 1986; genera 20–26 (Alysseae) in *ibid.* **68**: 185–240. 1987; and genera 27–36 (Arabideae) in *ibid.* **69**: 85–166. 1988.

thick, corky or woody wall, of which the outer portion is derived from the valve and the inner from the septum; beaks subulate [to filiform], seedless, gradually tapered to the apex, nearly as long as [or much shorter than] the seed-containing part; replums persistent; stigmas with 2 decurrent lobes; septum firm, thick. Seeds uniseriately arranged, oblong, strongly compressed, wingless, embedded in cavities of the septum, nonmucilaginous when wet; cotyledons accumbent. Base chromosome numbers 7, 9. (Including *Chorispermum* R. Br.) TYPE SPECIES: *Raphanus tenellus* Pallas = *C. tenella* (Pallas) DC. (Name from Greek *choris,* asunder, and *spora,* seed, in reference to the fruits that break at the constrictions into one-seeded segments.)

A well-defined genus of about 13 species, all of which are indigenous to southwestern and central Asia. The weedy *Chorispora tenella,* blue mustard, $2n = 14$, is sporadically naturalized throughout most of the Northern Hemisphere, as well as in parts of South America. It is widely distributed in southern Canada and in most of the Mountain and Pacific states. It has been reported from Tennessee, Louisiana, and Arkansas.

Chorispora is easily distinguished by its multicellular glandular papillae, decurrent stigmas, persistent replums, and beaked, indehiscent, corky, lomentaceous fruits that break up at maturity into one-seeded segments. Von Hayek and Schulz both associated *Chorispora* with *Diptychocarpus* Trautv. (monotypic; Afghanistan, Iran, Pakistan, central Asia), which differs in having winged seeds and dimorphic fruits (dehiscent upper ones and indehiscent, lomentaceous, corky lower ones). Dvořák (1972), on the other hand, has suggested that *Chorispora* and *Sterigmostemum* (seven species; central and southwestern Asia) were derived from a common ancestor.

Little is known about reproductive biology in species of *Chorispora,* which vary widely in flower size and color (bright yellow to deep purple). The weedy *C. tenella* has the smallest flowers (petals to 1 by 0.5 cm) and is likely to be self-compatible, while *C. Bungeana* Fischer & Meyer (Afghanistan, Pakistan, central Asia) has the largest flowers (petals to 2.5 by 1 cm). Flowers of all species of *Chorispora* have well-developed lateral nectar glands, and their lateral sepals are strongly saccate at the base. They produce abundant nectar and pollen and are therefore well adapted to cross-pollination.

Chromosome numbers are known for only three species. *Chorispora persica* Boiss. (Iran) and *C. tenella* both have $2n = 14$, whereas *C. iberica* (Bieb.) DC. (Caucasus, Iran, Turkey) has $2n = 18$ (Aryavand, 1975, 1983; Dvořák & Dadáková; Rodman & Bhargava). The closely related *Diptychocarpus* has $2n = 14$.

The chemistry of the genus is poorly surveyed, and only *Chorispora tenella* has been analyzed for leaf glucosinolates. It has high concentrations of allyl-glucosinolate and lower ones of 3-methylthiopropyl and 3-methylsulfinylpropyl glucosinolates (Rodman & Chew). Females of the butterfly *Pieris napi* deposit their eggs on the toxic *C. tenella,* failing to discriminate between it and the nontoxic native North American Cruciferae. Rodman & Chew have suggested that the isothiocyanate derivative of the last compound is probably responsible for the mortality of larvae that feed on this plant.

The seed coat of *Chorispora tenella* consists of flattened epidermal cells and thin-walled palisade cells (Vaughan & Whitehouse).

Except for the weedy *Chorispora tenella,* the genus has no economic value. The fruits of *C. elegans* Camb. (as *C. sabulosa* Camb.) are said to be eaten either raw or cooked by the poorer people in northern Pakistan (Jafri).

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38. **Hesperis** Linnaeus, Sp. Pl. **2.** 663. 1753; Gen. Pl. ed. 5. 297. 1754.

Biennial or perennial herbs with unicellular, eglandular, unbranched or furcate [to stellate] trichomes, these often mixed with multicellular, uniseriate glandular ones. Basal leaves petiolate, dentate [to pinnately lobed]; cauline leaves short-petiolate [or sessile and sometimes auriculate to amplexicaul]. Inflorescences ebracteate [or bracteate], corymbose [or elongated] racemes [or panicles], greatly expanded in fruit; flowers large, showy, fragrant; base of flowering pedicels with a large gland on each side; fruiting pedicels divaricate [to reflexed], slender [or stout and nearly as thick as the fruit]. Sepals erect and somewhat connivent [rarely spreading], oblong, unequal [rarely equal], the lateral (inner) pair strongly saccate at base. Petals white, lavender, pink, purple, violet [yellow, brown, or greenish], often with darker colored veins, about twice as long as the sepals, strongly differentiated into blade and claw; blades obovate [to oblong], rounded at apex; claws erect, flattened. Lateral nectar glands ringlike or horseshoe shaped, median glands absent. Stamens 6, strongly tetradynamous; filaments linear, erect, not appendaged, the median pair usually dilated [or slightly winged] at base; anthers linear [or oblong], strongly sagittate at base. Fruits linear, terete [rarely flattened or 4-angled], torulose, dehiscent [or indehiscent], often attenuate at apex; valves with a prominent midvein, glabrous or pubescent with eglandular [or glandular] trichomes; styles short to obsolete; stigmas strongly 2-lobed, the lobes connivent, sometimes decurrent. Seeds many, oblong, wingless, uniseriately arranged, usually nonmucilaginous when wet; cotyledons incumbent. Base chromosome numbers 6, 7, 8, 10. (Including *Deilosma* Spach, *Kladnia* Schur, *Micrantha* Dvořák.) LECTOTYPE SPECIES: *H. matronalis* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **2:** 175. 1913. (Name from old Greek, *hesperos,* evening, in reference to the time when flowers of certain species are most fragrant.)—DAME'S VIOLET, DAME'S ROCKET.

A well-marked, but taxonomically difficult Old World genus of about 25 species. The higher estimate of 60 species by Dvořák (1980), which I (Al-Shehbaz, 1984) have accepted, is evidently exaggerated. The center of greatest diversity, where about 70 percent of the species of *Hesperis* are endemic, includes the Balkan Peninsula, Turkey, Iran, and the Caucasus. The genus is poorly represented in eastern Asia and northern Africa and is absent from the Southern Hemisphere. A single species, *H. matronalis,* dame's violet, dame's rocket, rocket, $2n = 24$, is a cultivated ornamental plant and a naturalized weed in many parts of the world. It is sporadically distributed in the southeastern United States, where it has been reported from North Carolina, Georgia, Tennessee, and Arkansas. It usually grows along roadsides and in rich, moist woodlands and old gardens.

Hesperis matronalis has been divided into several subspecies on the basis of differences in flower color, petal length, and trichome type (Ball; Cullen). These

taxa are artificially delimited and unsatisfactory because they are based on characters that usually intergrade within many populations. Therefore, I am not recognizing any infraspecific taxa among the North American populations of *H. matronalis*.

The infrageneric classification of *Hesperis* is evidently controversial, for there is a lack of agreement among the several accounts consulted. De Candolle (1821) recognized 22 species, of which two were placed in sect. HESPERIS (as sect. *Hesperidium* DC.) (petal limb linear) and the remainder in sect. DELIOSMA Andrz. ex DC. (petal limb obovate). Tzvelev, on the other hand, placed the 18 species growing in the Soviet Union in three sections and two series, while Dvořák (1968a) assigned the 11 species growing in Iran to two subgenera and two sections. Finally, Dvořák (1973) recognized 31 species in five subgenera that were defined mainly by the presence of bracts and the degree of fruit dehiscence. The infrageneric taxa above are doubtfully practical, and they do not represent natural subdivisions of *Hesperis*.

Hesperis has been variously associated with *Blennodia, Clausia* Trotzky, *Iodanthus, Malcolmia, Parrya,* and *Sterigmostemum.* Contrary to what Von Hayek and Schulz have suggested, the genus is evidently unrelated to either *Blennodia* or *Iodanthus* and is closest to *Clausia* and *Sterigmostemum.* From all these genera, *Hesperis* is easily distinguished in having terete, torulose, dehiscent or indehiscent fruits; incumbent cotyledons; furcate to stellate trichomes usually mixed with glandular ones; free median staminal filaments; and large, odoriferous flowers.

Perhaps one of the most controversial taxonomic problems in *Hesperis* is species delimitation. The majority of the approximately 300 binomials listed in *Index Kewensis* are now assigned to other genera. Many species have been described on the basis of characters with poorly understood variations, while others represent local populations of highly variable species. In the absence of a thorough monographic account for the whole genus, it is advisable to recognize only about 25 species. Although natural interspecific hybridization has been reported a few times (Dvořák, 1965, 1967a), it is highly unlikely that it has played a major role in obscuring the species boundaries.

Chromosome numbers have been reported for about 14 species, four of which are tetraploids ($x = 6, 7$) that belong to the *Hesperis matronalis* complex. The karyotype of this species consists of eight metacentric pairs of chromosomes, two, one, or no submetacentric pairs, and two, three, or four subtelocentric pairs (Bhattacharyya; Dvořák & Dadáková, 1976; Gohil & Raina). Because of associations among four pairs of chromosomes, Gohil & Raina concluded that *H. matronalis* is a segmental allopolyploid and a complex translocation heterozygote. Despite the presence of multivalent associations at metaphase I, meiosis was quite regular and pollen stainability was more than 90 percent. Counts of $2n = 26$ and 28 for *H. matronalis* need careful evaluation; those of $2n = 32$ (e.g., Easterly) are probably erroneous. Furthermore, reports of $2n = 14$ are evidently based on plants of other species. Aneuploidy and tetraploidy ($x = 10$) have been reported for *H. sylvestris* Crantz and *H. ovata* Dvořák, respectively. The eight remaining species are all diploid based on seven or eight.

The reproductive biology of *Hesperis* is poorly understood. Bateman reported self-incompatibility in one species without providing a name. Several species have dull-colored flowers and are apparently pollinated at night by moths, as is *H. tristis* L. (Faegri & Van der Pijl).

Only *Hesperis matronalis* has been surveyed for sterols (Knights & Berrie), fatty acids (Appelqvist, 1971, 1976), and glucosinolates (Christensen & Kjaer; Cole). It contains 4-methylthiobutyl and 6-methylsulfinylhexyl glucosinolates, but allylglucosinolate, reported by Daxenbichler and colleagues, has not been detected by other workers. The seeds contain high concentrations of linolenic, linoleic, and oleic acids (ca. 51–55, 22–24, and 13–14 percent, respectively) but no traces of erucic acid.

The seed coat of *Hesperis matronalis* consists of an epidermis with central swellings that protrude from the outer wall into the lumena of larger cells, a subepidermis with tangentially elongated cells, and a palisade layer with radially elongated cells, the inner tangential walls of which are flattened (Vaughan & Whitehouse).

Except for *Hesperis matronalis,* which is an ornamental and an escape from cultivation, the genus has no economic value.

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39. **Erysimum** Linnaeus, Sp. Pl. **2:** 660. 1753; Gen. Pl. ed. 5. 296. 1754.

Annual, biennial, or perennial herbs [sometimes subshrubs or shrubs]; trichomes always sessile, medifixed, appressed, 2-fid (malpighiaceous) or 3- to 5-(to 7-)fid (stellate). Lower leaves petiolate, entire to dentate, rarely pinnatifid [or pinnatisect]; cauline leaves short-petiolate to sessile [very rarely auriculate]. Inflorescences ebracteate, terminal, corymbose racemes, greatly elongated in fruit. Sepals oblong to linear, erect, densely pubescent, the lateral pair saccate at base. Petals orange to bright yellow [creamy white, lavender, pink, violet,

or purple], strongly differentiated into limb and claw; limbs broadly to narrowly obovate [or oblong]; claws erect, nearly as long as the sepals. Lateral nectar glands ringlike or horseshoe shaped, encircling or subtending the bases of lateral stamens; median glands present [or absent]. Stamens 6, strongly tetradynamous; filaments free, linear, unappendaged, sometimes dilated at base; anthers linear to oblong, sagittate at base. Fruits linear [very rarely oblong], terete, tetragonal [or slightly to strongly compressed parallel, or at right angles, to the septum], smooth [rarely torulose], quickly or tardily dehiscent; valves with a prominent midvein, always pubescent on the outside, very rarely so on the inside; styles obsolete to conspicuous [only rarely subequaling or half as long as the fruit]; stigmas 2-lobed, the lobes neither decurrent nor connivent. Seeds oblong, terete [or flattened], wingless [winged or marginate], uniseriately [rarely subbiseriately] arranged in each locule of the fruit, nonmucilaginous when wet; cotyledons incumbent [to accumbent]. Base chromosome numbers 6–11, 13, 15, 17. (Including *Acachmena* H. P. Fuchs; *Agonolobus* (DC.) Reichenb.; *Cheiranthus* L.;[5] *Cheiri* Ludwig; *Cheirinia* Link; *Cuspidaria* (DC.) Besser (1822) non DC. (1838, nom. cons.); *Dichroanthus* Webb & Berth.; *Erysimastrum* (DC.) Rupr.; *Mitophyllum* O. E. Schulz (1933) non Greene (1904); *Rhammatophyllum* O. E. Schulz; *Strophades* Boiss.; *Stylonema* (DC.) Kuntze (1891) non Reinsch (1874); *Syrenia* Andrz. ex Besser; *Syreniopsis* H. P. Fuchs (1959) non *Syrenopsis* Jaub. & Spach (1842); *Zederbauera* H. P. Fuchs.) LECTOTYPE SPECIES: *E. cheiranthoides* L.[6] (Name probably from old Greek used by Hippocrates, Theophrastus, and others for plants possibly of this genus. Fernald, however, maintained that the generic name is derived from Greek *eryomai,* help or save, from the supposed medicinal properties of certain species.)—BLISTER CRESS, TREACLE MUSTARD, WALLFLOWER.

A well-defined and taxonomically difficult genus of about 200 species (see below for different estimates) restricted to the Northern Hemisphere, with the centers of greatest endemism being the Middle East (Turkey through Iran and Afghanistan; ca. 80 species), southern Europe (ca. 50), and central Asia (20). At least 15 species of *Erysimum* grow in more than one of the areas above; 12 are endemic to North America (Price), four to North Africa, and five to the Canary Islands, Madeira, and the Cape Verde Islands. The genus is represented in the southeastern United States by four species, of which one is indigenous, one is a widely cultivated ornamental, and two are cosmopolitan weeds.

Erysimum capitatum (Douglas ex W. J. Hooker) Greene (*Cheiranthus capitatus* Douglas ex W. J. Hooker), $2n = 36$, is the most variable and widely distributed of all the North American species. Of the nine subspecies recognized

[5]*Erysimum* and *Cheiranthus* were simultaneously described by Linnaeus (Sp. Pl. **2:** 660, 661, respectively. 1753). Wettstein, who was the first to unite the two genera, adopted *Erysimum* for the combined genus; consequently, this name has priority (see ICBN Article 57.2. 1983).

[6]Scopoli (Fl. Carniol. ed. 2. **2:** 27–29. 1772) had effectively lectotypified *Erysimum* by transferring the other original Linnaean species (Sp. Pl. **2:** 660, 661. 1753) to *Sisymbrium* L. while retaining *E. cheiranthoides* in *Erysimum.* Several North American authors (e.g., Britton & Brown; Greene) chose this species as the type of *Cheirinia* and treated *Erysimum* as a small (perhaps monotypic) genus, the type species of which is *E. officinale* (now universally recognized as *S. officinale* (L.) Scop.).

by Price, only subsp. *capitatum* occurs in the Southeastern States (DeKalb, Putnam, and Smith counties, Tennessee; Faulkner and Logan counties, Arkansas). From here the subspecies is distributed westward into the Southwestern and Pacific states and also grows in Idaho (Price). Subspecies *capitatum* is easily distinguished from the other taxa of *Erysimum* that grow in the Southeast by its orange petals to 3 cm long, erect to ascending fruits on thick fruiting pedicels, and fruit valves with the inner surfaces glabrous. Small's (1933) report of *E. asperum* (Nutt.) DC. (as *Cheirinia*) from Tennessee was evidently based on a misidentification of plants of *E. capitatum*.

Erysimum cheiranthoides L. (*Cheirinia cheiranthoides* (L.) Link, *E. parviflorum* Pers.), wormseed mustard, $2n = 16$, is a Eurasian weed widely naturalized in North America. It occurs in North Carolina, Florida, Tennessee, and Arkansas, where it grows in waste grounds, pastures, disturbed sites, grainfields, and hillsides, as well as along roadsides. Ahti and Ball recognized two subspecies in *E. cheiranthoides*; only the type subspecies is naturalized in the United States. *Erysimum cheiranthoides* is readily distinguished from the other North American species of the genus by its fruits 1.5–2.5 mm long, conspicuously pubescent inner valve surfaces, fruiting pedicels much more slender than the fruits, and yellow petals 3.5–5.5 mm long.

Erysimum repandum L. (*Cheirinia repanda* (L.) Link, *E. rigidum* DC.), treacle mustard, $2n = 16$, is another Eurasian weed widely distributed in North America. It has been reported from all of the Southeastern States but South Carolina, Georgia, and Florida, where it is likely to be found. It is an annual with widely spreading, somewhat quadrangular, slightly torulose fruits 4–8 cm long; divaricate, stout fruiting pedicels nearly as thick as the fruit; and yellow petals 6–8 mm long.

Small (1913) listed *Erysimum inconspicuum* (S. Watson) MacM., $2n = 54$, for Arkansas, but the record is highly unlikely because the species is indigenous to western North America and is adventive only in some of the Midwestern States. *Erysimum Cheiri* (L.) Crantz (*Cheiranthus Cheiri* L.), wallflower, $2n = 12$, which is grown as an ornamental throughout the Southeastern States, does not seem to have escaped from cultivation anywhere in North America.

The infrageneric subdivisions of *Erysimum* that were recognized by Busch, De Candolle (1821, 1824), and Wettstein have not been widely accepted. Busch, for example, placed the 51 species growing in the Soviet Union in two sections (one monotypic) divided into 18 series. A close examination of *Erysimum* on a worldwide basis reveals that convergent evolution has probably occurred repeatedly in features such as position of the cotyledons, presence of the seed wing, flattening of the fruit valve, color of the flower, and type of trichomes. Therefore, it is quite difficult, if not impossible, to delimit natural subdivisions within the genus.

Only two of the many generic segregates of *Erysimum* require critical evaluation. *Cheiranthus* has been distinguished from *Erysimum* in several recent floras (e.g., Ball; Townsend) on the basis of having strongly flattened fruits, accumbent cotyledons, subbiseriately arranged seeds, and no median nectaries. *Erysimum*, on the other hand, is said to differ in having terete, quadrangular, or slightly flattened fruits, incumbent cotyledons, uniseriate seeds, and well-

developed median nectaries. As shown by Snogerup (1967a) and Price, however, all of these alleged differences are unreliable; they break down within various species complexes of *Erysimum.*

The systematic position of *Syrenia* is problematic. The genus is distinguished from *Erysimum* in having slender styles that are subequal to the oblong fruits, transversely oriented malpighiaceous trichomes on the fruit valves, and no median nectaries. Long styles are found in several species of *Erysimum* (e.g., *E. cuspidatum* (Bieb.) DC.) that lack the transversely oriented fruit trichomes. Price (p. 6) suggested that *Syrenia* is "apparently either a sister group to or a derivative of *Erysimum.*" I prefer to unite *Syrenia* with *Erysimum,* as has been done by Polatschek (1982).

Erysimum is perhaps the most taxonomically difficult genus in the Cruciferae. It is much in need of a comprehensive treatment. Specimens without a combination of adequate flowers, fruits, and basal leaves are often difficult to identify. Collectors should also make notes on the shape of the cross section of fresh fruits. Many authors (e.g., Busch; Jafri; Schulz; Townsend) have estimated about 80 to 100 species in *Erysimum,* but the actual number is nearly twice that. However, Polatschek (1986) has suggested that the genus contains between 350 and 420 species. Evidently, species delimitation in *Erysimum* is highly controversial. Numerous "species" have been described on the basis of minor variations in populations of previously recognized taxa. Species circumscription can be a nightmare because of the frequent lack of sharply defined discontinuities among the taxa of a given complex. It is not surprising, therefore, to encounter disagreements among systematists on assigning a specific or an infraspecific rank for a given taxon. A case in point is the *E. capitatum* alliance (sensu Price).

Snogerup (1967a) and Price have reported that in several species, including *Erysimum capitatum,* full stigmatic expansion and receptivity take place within a few days after anther dehiscence. These are clear-cut cases of protandry. Protogyny occurs in *E. repandum* and several other species (Al-Shehbaz). The flowers of *E. capitatum* and *E. Cheiri* are sweet scented and are up to 3 cm in diameter. They are among the largest in the Cruciferae. *Erysimum capitatum* is self-incompatible (Mulligan), while *E. Cheiri* has cryptic self-incompatibility (Bateman; Watts). Plants of *E. Cheiri* set seeds and maintain vigor and fertility even after several generations of selfing. However, various cultivars have different levels of self-incompatibility. Bateman has shown that in plants pollinated with a mixture of equal amounts of self and foreign pollen (the latter carrying a dominant allele that produces red flowers) more than 90 percent of their seed set results from cross fertilization.

On the basis of frequent meiotic irregularities, very low pollen fertility, and abundant seed set, both *Erysimum hieraciifolium* L. and *E. inconspicuum* are believed to be agamospermous (Mulligan; Mulligan & Frankton).

Chromosome numbers are known for about 100 species, of which half are diploid and about 40 percent polyploid. There is a continuous series of base chromosome numbers from six to 13, but many species (ca. 39 percent) are based on seven, 20 percent on eight, 15 percent on nine, and 13 percent on six. Both aneuploidy and polyploidy have played major roles in the evolution

of the genus. All members of the North American *Erysimum capitatum* complex are tetraploids based on nine (Price).

Polatschek (1986) has suggested that natural hybrids are not known in *Erysimum.* However, several authors (e.g., Favarger, 1964; Knobloch; Snogerup, 1967a, 1967b; Wettstein) have reported putative hybridization between *E. Cheiri* and four other species. Price, on the other hand, has found a natural hybrid involving *E. capitatum* and *E. insulare* Greene. It is evident that hybridization has been insignificant in obscuring the specific boundaries in the genus. Although species of the *E. capitatum* complex are readily crossed experimentally, they do not hybridize in nature because either they are exclusively allopatric or they occupy different habitats in areas of sympatry (Price).

Numerous species of *Erysimum* have been analyzed for fatty acids, glucosinolates (mustard-oil glucosides), and cardenolides (cardiac glycosides). The glucosinolates in most of the approximately 20 species analyzed are derived from the amino acid methionine. There is a complex array of 3-methylsulfinyl, sulfonyl, or thioalkyl glucosinolates, their higher homologues, or their hydroxylated derivatives that cyclize upon hydrolysis into oxazolidinethiones (Cole; Daxenbichler *et al.*; Kjaer & Schuster, 1970, 1973). Five species have 3-methoxycarbonylpropylglucosinolate, which appears to be unique to *Erysimum* (Al-Shehbaz & Al-Shammary). The glucosinolate profiles may be valuable in solving some of the taxonomic problems in the genus.

The cardenolides have been surveyed for at least 30 species. They are found in every species examined thus far, and it is very likely that they occur throughout *Erysimum,* including *Cheiranthus* and *Syrenia.* Their profiles appear to be useful taxonomically (Kowalewski; Latowski *et al.*; Rodman *et al.*). Because the occurrence of cardenolides in the Cruciferae seems to be restricted to *Erysimum, Sisymbrium* L., and *Conringia* Heister ex Fabr., a few authors (e.g., Latowski *et al.*) have suggested a closer relationship between the first two genera.

Seeds of about 15 species have been studied for fatty acids. The distribution of these compounds shows no patterns of chemotaxonomic significance, except for supporting the union of *Cheiranthus* and *Erysimum.* A similar conclusion is reached from data on sterols (Knights & Berrie), cardenolides (Latowski *et al.*), and glucosinolates (pers. obs.).

Bosbach has suggested that the distribution of rubisco (ribulose 1,5-biphosphate carboxylase-oxygenase, fraction 1 protein) is useful taxonomically in *Erysimum.* These proteins are separated into their polypeptide subunits by using polyacrylamide gel electrophoresis followed by isoelectrofocusing.

Many species of *Erysimum* are grown as ornamentals (Bailey *et al.*), but the one most widely cultivated is *E. Cheiri* (wallflower). Snogerup (1967b) suggested that *E. Cheiri* has probably evolved from hybridization between *E. Senoneri* and *E. cornithum* (Boiss.) Wettst. However, other Aegean taxa of sect. CHEIRANTHUS (L.) Wettst. that also have $2n = 12$ were not excluded. Several species of *Erysimum* are cultivated in eastern Europe, particularly in the Soviet Union, for the pharmacological utilization of their cardiac glycosides (Rodman *et al.*). At least two species, *E. repandum* and *E. cheiranthoides,* are cosmopolitan weeds. The latter is said to cause mortality of swine in Canada (Kingsbury).

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THE GENERA OF SISYMBRIEAE (CRUCIFERAE; BRASSICACEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

IHSAN A. AL-SHEHBAZ[3]

Tribe **Sisymbrieae** A. P. de Candolle, Syst. Nat. **2:** 150, 438. 1821.

Annual, biennial [or perennial] herbs [rarely shrubs]; glabrous or with unbranched, dendritic [furcate, malpighiaceous, or stellate] trichomes, these rarely mixed with unicellular, glandular, subclavate ones. Inflorescences ebracteate [or bracteate], corymbose racemes or panicles, usually elongated in fruit; flowers few to many [sometimes solitary on scapes arising from basal rosettes]. Sepals erect [to widely spreading], usually not conspicuously saccate at base, caducous [or persistent]. Stamens 6, usually tetradynamous; filaments free, not appendaged. Fruits linear, subclavate [oblong or rarely ovate], dehiscent [rarely indehiscent], terete [or conspicuously flattened parallel to the septum]; septum complete [rarely incomplete]; stigmas entire or 2-lobed. Seeds numerous [rarely few], uniseriately or biseriately arranged in each locule, wingless [or rarely winged], mucilaginous or not when wet; cotyledons incumbent. TYPE GENUS: *Sisymbrium* L.

The Sisymbrieae comprise a heterogeneous assemblage of some 70 genera (25 monotypic; about 30 with two to four species each) and approximately 400

[1]Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and currently supported by BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this research was done, and BSR-8415637 (N. G. Miller, principal investigator). This account, the 122nd in the series, follows the format established in the first paper (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

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The figure was drawn by Karen Stoutsenberger under earlier grants. Carroll Wood prepared the material and supervised the illustration. The fruits and seeds are from specimens in the herbaria of the Arnold Arboretum and the Gray Herbarium.

[2]This is the eighth and final account of the Cruciferae. For treatment of the family and its tribes, see Al-Shehbaz, The Tribes of Cruciferae (Brassicaceae) in the Southeastern United States (Jour. Arnold Arb. **65**: 343–373. 1984).

[3]Arnold Arboretum, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138.

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species. It is represented in the Southeastern United States by four genera and seven species, one of which is indigenous. Although the Sisymbrieae are distributed on all continents except Antarctica, the tribe is most highly diversified in southern and western South America, where 24 genera (20 endemic) and ca. 130 species are found. That area is also the center of highest endemism for *Sisymbrium* L. (90 species) and *Descurainia* Webb & Berth. (40 species), the largest genera of the tribe. Nearly half of the species in these genera are South American. Another important center for the tribe comprises the Irano-Turanian (parts of central and southwestern Asia) and Himalayan regions. It has 22 genera (15 endemic) and about 100 species. The tribe is represented in North America by seven genera (none endemic) and approximately 50 species, and in Australia and New Zealand by 11 genera (all endemic) and 26 species.

As delimited by Schulz (1924, 1936), the boundaries of the tribe are highly artificial, and many genera should be associated with those that he placed in other tribes. Schulz overemphasized the importance of cotyledonary position and sepal orientation in defining what he recognized as four tribes. He distinguished the Sisymbrieae from the Arabideae DC. mainly on the basis of incumbent versus accumbent cotyledons, and from the Anchonieae DC. (as Hesperideae Prantl and Matthioleae O. E. Schulz) on open instead of closed calyces. It is evident, however, that these characters can be unreliable, and that there are many genera both in the tribe and elsewhere in the Cruciferae with more than one type of cotyledonary position or sepal orientation. Avetisian is probably justified in uniting the four tribes above in one (as Sisymbrieae), but her inclusion of the Alysseae DC. and the Lepidieae DC. in this tribe is unwarranted. In my opinion, neither Schulz's nor Avetisian's delimitation of the Sisymbrieae is satisfactory, and the complex needs thorough study on a worldwide basis.

Two of the six subtribes that Schulz (1924, 1936) recognized in the Sisymbrieae have somewhat natural boundaries. Subtribes Alliariinae (Prantl) O. E. Schulz (basal leaves undivided, long petiolate, cordate or reniform to orbicular; stigmas entire; petals white; seeds large, oblong) and Descurainiinae O. E. Schulz (leaves highly dissected, trichomes dendritic, seeds mucilaginous) include five and six genera, respectively. The remaining subtribes are artificially delimited because they are based primarily on characters (e.g., presence vs. absence of mucilage on seeds, fruit length in relation to width, separation vs. connation of the median and lateral nectaries) that are not useful at or above the generic level. It is beyond the scope of this flora either to revise the subtribal classification or to delimit the boundaries of the Sisymbrieae.

Chromosome numbers are known for slightly more than 100 species (ca. 25 percent of the tribe) and 25 genera. In about 68 percent of the species surveyed, the numbers are based on seven, while in only 19 percent they are based on eight. Nearly 70 percent of the species are diploid (author's compilation). Although most genera are uniformly based on one chromosome number, a few others (e.g., *Arabidopsis* (DC.) Heynh., *Sisymbrium*) have diploid and polyploid taxa with several base numbers. Polyploidy apparently characterizes most, if not all, species of the South American genus *Weberbauera* Gilg & Muschler (four species) and the circumboreal *Braya* Sternb. & Hoppe (16 species). All

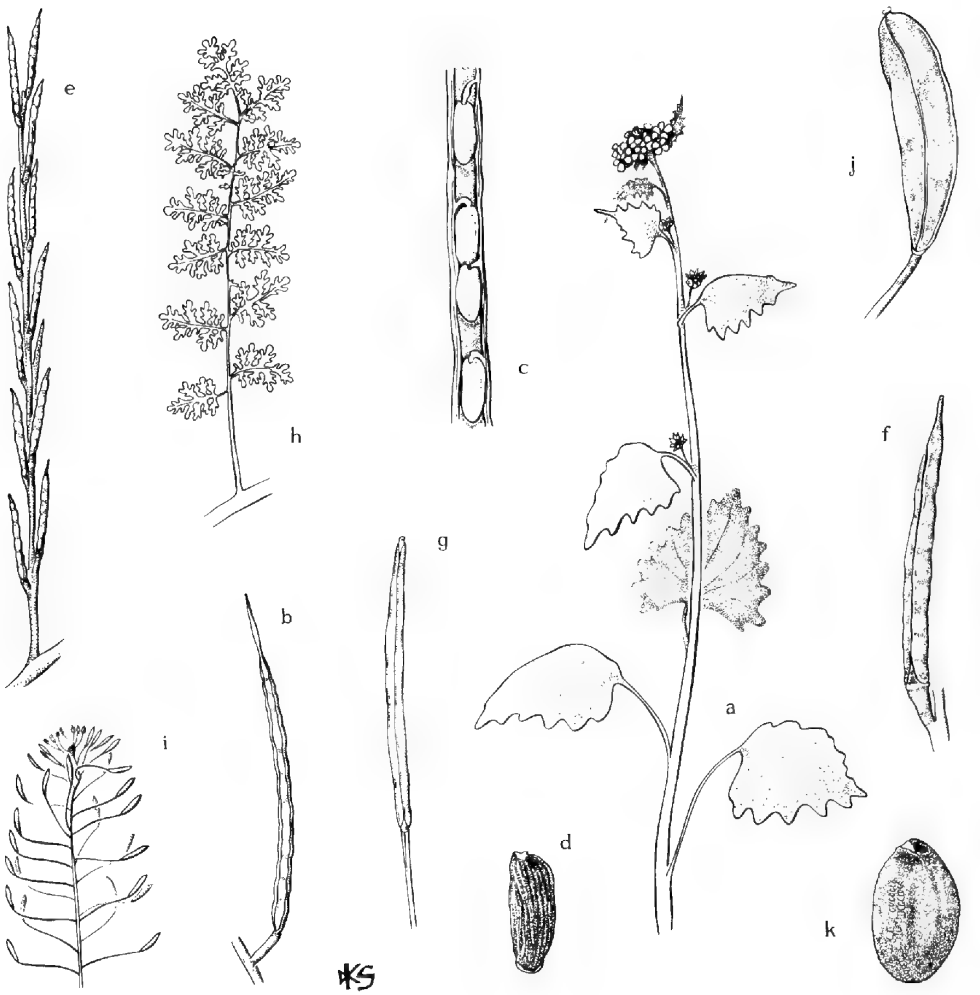

FIGURE 1. Selected representatives of tribe Sisymbrieae. a–d, *Alliaria petiolata:* a, portion of plant with flowers, × ½; b, fruit, × 1; c, portion of fruit after removal of 1 valve, × 3—note uniseriate arrangement of seeds; d, seed, × 6. e, f, *Sisymbrium officinale:* e, portion of infructescence, × 1; f, fruit × 3. g, *Arabidopsis Thaliana,* fruit, × 3. h–k, *Descurainia pinnata:* h, tripinnatisect leaf, × ½; i, portion of infructescence, × 1; j, fruit, × 6; k, seed, × 25.

13 species of the latter that have been surveyed cytologically (Harris) are polyploids based on seven ($2n$ = 28, 42, 56, 70). Numbers in *Smelowskia* C. A. Meyer, which includes 11 alpine species (five in Alaska and the Mountain and Pacific states (Drury & Rollins) and six in central and eastern Asia (Botschantsev)), are apparently based on six. In *S. calycina* (Willd.) C. A. Meyer, diploids ($2n$ = 12), tetraploids ($2n$ = 24), and aneuploid derivatives of tetraploids ($2n$ = 22) characterize the various infraspecific taxa.

The chemical data on the Sisymbrieae are so scant that no meaningful conclusions can be reached. However, the presence of cardenolides (otherwise very rare in the Cruciferae) in both *Erysimum* L. and *Sisymbrium* rather strongly

supports a closer association between the two genera. Schulz (1936) placed the former in tribe Hesperideae, but as was indicated earlier (Al-Shehbaz, 1984, 1988), the status of these tribes needs careful evaluation.

Seed-dispersal mechanisms in the majority of Sisymbrieae are similar to those of other tribes. In *Geococcus* J. Drumm. ex Harvey (monotypic; Australia) the fruiting pedicels almost always become strongly recurved and bury the fruit in the vicinity of the mother plant (Shaw). Geocarpy has evolved independently in the Cruciferae, as is evidenced by its occurrence also in the South American *Cardamine chenopodiifolia* Pers. and in *Morisia monanthos* (Viv.) Ascherson, of Sardinia and Corsica. The strong curvature of fruits into loops or hooks in some species of *Neotorularia* Hedge & Léonard (11 species; southwestern and central Asia) may be an adaptation to dispersal by clinging to the fur of animals.

Except for the many weedy species, particularly of the genera *Alliaria* Scopoli, *Descurainia,* and *Sisymbrium,* the tribe has no economic importance. *Arabidopsis Thaliana* (L.) Heynh. is the most widely used higher plant in biochemistry, genetics, molecular biology, and physiology.

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KEY TO THE GENERA OF SISYMBRIEAE IN THE SOUTHEASTERN UNITED STATES[4]

A. Leaves 2- or 3-pinnatisect, plants with dendritic trichomes. .... 43. *Descurainia.*
A. Leaves entire, toothed, or pinnately lobed, never 2- or 3-pinnatisect; plants glabrous or with unbranched or furcate trichomes.
  B. Lower leaves reniform or cordate, usually dentate; seeds longitudinally striate. ..... 40. *Alliaria.*
  B. Lower leaves oblong to lanceolate or oblanceolate, entire or pinnate; seeds smooth or reticulate.
    C. Plants short, up to 20 cm long; leaves entire; at least some trichomes furcate. ..... 42. *Arabidopsis.*
    C. Plants taller; leaves pinnate; all trichomes unbranched. .. 41. *Sisymbrium.*

40. **Alliaria** Heister ex Fabricius, Enum. Meth. Pl. 161. 1759.[5]

Annual or biennial herbs with unbranched trichomes. Stems simple or branched at base, up to 1.3 m high. Lower leaves long petiolate, not forming rosettes, undivided, reniform, cordate, or rarely deltoid, sinuate-dentate or sometimes crenate to repand; upper leaves short petiolate, cordate, deltoid [oblong or obovate]. Inflorescences corymbose racemes, ebracteate [or bracteate throughout], elongated in fruit; fruiting pedicels divaricately ascending [or subappressed to rachis], nearly as thick as the fruit. Sepals erect-ascending, oblong, equal and not saccate at base, caducous. Petals white, obovate, short clawed. Lateral nectar glands ringlike; median ones connate with the lateral, subtending the bases of paired stamens. Stamens 6, tetradynamous; filaments free, erect, unappendaged; anthers obtuse. Fruits linear, acute [or acuminate], torulose or smooth, subterete or somewhat 4-angled, dehiscent; valves keeled, strongly 3-nerved, glabrous [or scabrous]; septum hyaline, complete; styles slender, 1–3[–6] mm long; stigmas entire or rarely slightly 2-lobed. Seeds numerous [or few], oblong, dark brown to black, longitudinally striate, wingless, uniseriately arranged in each locule, nonmucilaginous when wet; cotyledons accumbent. Base chromosome number 7. (Including *Pallavicinia* Cocconi (1893), non Gray (1821), non De Not. (1847); *Raphanolobus* Rupr.) TYPE SPECIES: *Erysimum Alliaria* L. = *A. petiolata* (Bieb.) Cavara & Grande. (Name from *Allium* L., onion or garlic, referring to the garliclike smell of the plant when crushed.)—GARLIC MUSTARD.

A genus of two species, one of which, *Alliaria brachycarpa* Bieb., is a narrow endemic of the Caucasus and the other is a Eurasian weed now naturalized in many parts of the world. *Alliaria petiolata* (Bieb.) Cavara & Grande (*Arabis*

[4]The genera are numbered as in the treatment of the tribes of Cruciferae in the southeastern United States (Jour. Arnold Arb. **65:** 343–373. 1984). Genera 1 and 2 (Thelypodieae) appeared in *ibid.* **66:** 95–111. 1985; genera 3–13 (Brassiceae) in *ibid.* 279–351; genera 14–19 (Lepidieae) in *ibid.* **67:** 265–311. 1986; genera 20–26 (Alysseae) in *ibid.* **68:** 185–240. 1987; genera 27–36 (Arabideae) in *ibid.* **69:** 85–166. 1988; and genera 37–39 (Anchonieae) in *ibid.* 193–212.

[5]Almost all recent floras cite Scopoli (Fl. Carniol. ed. 1. 515. 1760) as the author of *Alliaria.* As shown by Dandy (Regnum Veg. **51:** 12, 13, 25. 1967), however, the genus should be attributed to Heister ex Fabricius.

petiolata Bieb., *Erysimum Alliaria* L., *Sisymbrium Alliaria* (L.) Scop., *Alliaria Alliaria* (L.) Britton, *Alliaria officinalis* Andrz.), garlic mustard, hedge garlic, $2n = 42$, is a weed of fields, alluvial woods, waste places, roadsides, and riverbanks. It is sporadic in North America (Rollins) and has been reported in our area from North Carolina, Tennessee, and Arkansas.

Schulz (1924) and Markgraf have recognized many varieties and forms in *Alliaria petiolata* on the basis of minor differences in flowers, fruits, and leaves. In my opinion, none of these infraspecific taxa merits recognition.

Schulz (1924, 1936) placed each of the two species of *Alliaria* in its own section. It is doubtful, however, that such sectional classification is useful. *Alliaria* is easily distinguished from all Cruciferae of the Southeastern States by its linear, somewhat quadrangular fruits, three-veined valves, oblong, black or dark brown, striate seeds, and reniform to cordate, sinuate-dentate (rarely crenate or repand) lower leaves with long petioles.

Although Von Hayek, Prantl, and Schulz (1924, 1936) placed *Alliaria* in three different tribes, they all associated the genus closely with *Eutrema* R. Br. (including *Wasabia* Matsum.), *Taphrospermum* C. A. Meyer (two species; central Asia), *Parlatoria* Boiss. (two species; Iran to southeastern Turkey), and *Sobolewskia* Bieb. (four species; Caucasus, Crimea, and Turkey). Von Hayek placed the first three genera in subtribe Arabidinae Hayek and the last two in subtribe Parlatoriinae Hayek, while Prantl and Schulz treated all five in subtribe Alliariinae. I concur with the last two authors. Subtribe Alliariinae has long-petiolate, undivided, reniform to cordate or orbicular basal leaves and usually large, oblong seeds.

The numerous chromosome counts for *Alliaria petiolata* suggest that the species is a hexaploid based on seven. Other counts of $n = 7$ (Naqshi & Javeid), $n = 18$ (Baez Mayor), and $2n = 36$ (Gadella & Kliphuis) have been reported. No chromosome counts are available for *A. brachycarpa*.

Aliaria petiolata is a self-compatible species with small, protogynous flowers that are frequently visited by bees, midges, and flies (Cavers *et al.*). Its seeds have a strong dormancy that can be broken artificially by scarification or by the application of gibberellic acid.

The seeds of *Alliaria petiolata* contain high concentrations of allylglucosinolate and only traces of benzylglucosinolate (Al-Shehbaz & Al-Shammary; Kjaer; Nielsen *et al.*). They are also rich in erucic (47 percent) and linoleic (22 percent) acids and have smaller amounts (four to seven percent each) of eicosenoic, linolenic, oleic, and palmitic acids (Miller *et al.*). *Alliaria brachycarpa* has not been surveyed for any secondary constituents.

The seed coat of *Alliaria petiolata* has flattened, nonmucilaginous epidermal cells with somewhat crystalline granules, and palisade cells with evenly thickened inner tangential walls (Vaughan & Whitehouse).

Alliaria petiolata has been used extensively in Europe and North America as a potherb, a source of fatty oils, a substitute for garlic (Busch), a medicinal plant, and a salad green. The plant has also been employed as a diuretic, a diaphoretic, and an expectorant and has been used in the treatments of asthma and dropsy. It has been said that the leaves of *A. petiolata* have higher amounts of vitamin C per weight than does the orange, and that their levels of vitamin

A are higher than those of spinach, the vegetable richest in this vitamin (Cavers *et al.*). The species is a host for certain mosaic viruses that attack several cultivated plants. Cows that feed on *A. petiolata* produce milk with a disagreeable taste.

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41. **Sisymbrium** Linnaeus, Sp. Pl. **2:** 657. 1753; Gen. Pl. ed. 5. 296. 1754.

Annual, biennial [or perennial] herbs [rarely subshrubs], glabrous or variously pubescent with unbranched [or branched] trichomes. Stems erect [rarely prostrate or decumbent], usually branched above. Basal leaves rosette forming or not, petiolate, lyrate, pinnatifid [runcinate, sinuate, or entire]; cauline leaves usually similar to the basal [sometimes sessile and auriculate to amplexicaul at base]. Inflorescences many-flowered, corymbose racemes, ebracteate [rarely bracteate and the flowers solitary or in fascicles], usually elongated in fruit; fruiting pedicels erect and appressed to rachis or ascending, divaricate [or reflexed], slender or stout and nearly as wide as the fruit. Sepals erect [or spreading], glabrous or pubescent, the inner pair slightly or not saccate at base, the outer pair sometimes cucullate. Petals yellow [white, pink, or purple], oblong to obovate, spatulate [or orbicular], usually differentiated into blades and claws. Nectar glands ringlike, usually surrounding the bases of lateral stamens and subtending those of the median ones. Stamens 6, tetradynamous; filaments free, unappendaged; anthers oblong, usually obtuse at apex. Fruits linear or subulate, terete [rarely flattened parallel to the septum], dehiscent, sessile, many seeded; valves smooth or torulose, glabrous or pubescent, usually with a prominent midvein and 2 less-conspicuous lateral veins; styles cylindrical to subconical [sometimes obsolete]; stigmas capitate or discoid, 2-lobed [rarely subentire]. Seeds numerous, oblong to elliptic, brown, papillose [reticulate or rarely striate], wingless [or marginate], uniseriately arranged in each locule, usually nonmucilaginous when wet; cotyledons incumbent or obliquely so [very rarely folded longitudinally]. Base chromosome numbers 7 [9, 10, 13]. (Including *Chamaeplium* Wallr.; *Chilocardamum* O. E. Schulz; *Coelophragmus* O. E. Schulz (in part); *Dimitria* Ravenna; *Irio* (DC.) Fourr.; *Kibera* Adanson; *Leptocarpa* DC.; *Mostacillastrum* O. E. Schulz; *Norta* Adanson; *Pachypodium* Webb & Berth. (1836), non Lindley (1830), non Nutt. ex Torrey & A. Gray (1838); *Schoenocrambe* Greene; *Tonguea* Endl.; *Tricholobos* Turcz. (1854), non Blume (1850); *Valarum* Schur; *Vandalea* (Fourn.) Fourr.; *Velarum* Reichenb.) LECTOTYPE SPECIES: *S. altissimum* L.; see Payson.[6] (Name Latinized from an

[6]Britton & Brown arbitrarily lectotypified *Sisymbrium* by considering the watercress (*S. Nasturtium-aquaticum* L.), which was the first of 16 species recognized by Linnaeus (Sp. Pl. **2:** 657. 1753), as its type. Payson clearly demonstrated that such lectotypification is unacceptable and appropriately selected *S. altissimum* as the generic type. The watercress is now known as *Rorippa Nasturtium-aquaticum* (L.) Hayek.

ancient Greek name used by Dioscorides and Pliny for various mustards.) —HEDGE MUSTARD, ROCKET.

A heterogeneous genus of about 90 species distributed primarily in temperate areas, with the center of greatest diversity being South America, where ca. 40–45 species grow. In addition, there are 14 species indigenous to Asia, nine to Europe, five to southern Africa, two to northwestern Africa, and about three or four to North America and the West Indies, as well as 11 weedy species of cosmopolitan or wide distribution. *Sisymbrium* is represented in the southeastern United States by three naturalized Eurasian weeds.

Schulz's (1924) sectional classification of *Sisymbrium,* which is the latest and most comprehensive, is controversial and unsatisfactory. Several of his 14 sections are artificially delimited; they include unrelated species and/or elements now believed to belong to other genera. Because of the inadequate infrageneric classification of the genus, I prefer not to recognize any sections here.

Sisymbrium altissimum L. (*Norta altissima* (L.) Britton, *S. sinapistrum* Crantz, *S. pannonicum* Jacq.), tumble mustard, Jim Hill mustard, $2n = 14$, is sporadically distributed in the Southeastern States. It has been reported from North Carolina, Georgia, Florida, Tennessee, Arkansas, and Louisiana, where it grows in fields, waste places, prairies, and disturbed areas, as well as along roadsides and railroad tracks. It is a tall (to 1 m high) annual with sinuate-pinnatifid lower leaves, pinnatisect upper leaves with narrowly linear segments, yellow petals 5–10 mm long, and stout fruiting pedicels nearly as wide as the rigid, terete fruits 4–10 cm long. It produces a very high number of seeds estimated by Muenscher (p. 4) at 511,208 for one plant. *Sisymbrium altissimum* is easily distinguished from the related Eurasian *S. orientale* L. ($2n = 14$), which is sporadic in western North America and adjacent Mexico, by its cucullate outer sepals and its cauline leaves with a linear terminal lobe. In *S. orientale* the outer sepals are not cucullate, and the terminal leaf lobe is ovate to lanceolate, usually with a hastate base.

Sisymbrium officinale (L.) Scop. (*Erysimum officinale* L.), hedge mustard, $2n = 14$, is easily distinguished from other Cruciferae of the Southeast by its pinnatisect lower leaves with large terminal lobes, yellow petals 2–4 mm long, short (1–2 mm), stout fruiting pedicels as wide as the fruits, and short (8–20 mm), subulate fruits closely appressed to the rachis. It is widely distributed in North America and has been reported from all of the Southeastern States. Robinson and most subsequent North American authors (e.g., Fernald; Radford *et al.*) have recognized two varieties in *S. officinale* on the basis of pubescent (var. *officinale*) or glabrous (var. *leiocarpum* DC.) fruits. However, the amount of pubescence on the upper parts of the plant can vary considerably within a given population. Most of the populations of *S. officinale* that I have examined in Southwest Asia, West Europe, and North America include plants with both glabrous and pubescent fruits. Evidently, these varieties do not merit recognition.

The third Eurasian weed is *Sisymbrium Irio* L. (*Norta Irio* (L.) Britton, *Descurainia Irio* (L.) Webb & Berth., *S. erysimastrum* Lam., *S. heteromallum*

Fourn., *S. latifolium* Gray), London rocket, $2n = 14, 28$. Despite its abundance in the southwestern United States and Mexico, *S. Irio* is rare in the Southeast, where it has been reported only from Florida (Long & Lakela) and Louisiana (MacRoberts). Except for a few counts, *S. Irio* is diploid throughout most of its native and naturalized ranges. Amin and Podlech & Dieterle have reported tetraploid counts from Egypt and West Pakistan, respectively, while Khoshoo (1959a) found diploid, triploid, tetraploid, hexaploid, and octoploid plants occurring naturally in India.

The Eurasian *Sisymbrium Loeselii* L., tall hedge mustard, $2n = 14$, and the South African *S. Turczaninowii* Sonder have both been reported from South Carolina (Berkeley and Florence counties) as weeds of waste grounds around wool-combing mills (Al-Shehbaz, 1986). They are not known elsewhere in the Southeast. *Sisymbrium Loeselii* has been recorded only recently from Kentucky (Cranfill & Thieret), but it is widespread in the plains region of the United States and Canada (Rollins, tribal reference).

Schulz's (1924) circumscription of *Sisymbrium* has been followed by most subsequent workers. However, many of the North American species have since been transferred to other genera (Rollins, 1982), while some of his generic segregates are now retained in *Sisymbrium* (Romanczuk, 1982). At least three or four North American species are good members of the genus. Schulz segregated *S. auriculatum* A. Gray and *Dryopetalon runcinatum* A. Gray (as *S. umbrosum* Robinson), both endemic to the Southwestern States and northern Mexico, to *Coelophragmus*. The latter was said to differ from *Sisymbrium* in having slender styles, seeds <0.5 mm long, and deeply pitted septa, instead of stout styles, longer seeds, and nonpitted septa. However, these alleged differences are unrealistic, and many species of *Sisymbrium* have most or all the features said to be unique to *Coelophragmus*. Payson's conclusion (p. 25) that "*Sisymbrium auriculatum* is strikingly reminiscent of certain European members of the genus—notably *S. Irio, S. Loeselii* and even *S. altissimum*" is perfectly valid. In my opinion, *S. auriculatum* and a few other North American species should be retained in the genus. As far as the South American members are concerned, the genus needs a comprehensive study—neither Schulz (1924) nor Romanczuk (1982) adequately solved the problem of its limits.

The generic boundaries of *Sisymbrium* are difficult to define. Although the majority of species have pinnately divided lower leaves, yellow or white flowers, terete, linear fruits, usually three-veined valves, prominently two-lobed stigmas, uniseriately arranged seeds, and incumbent cotyledons, many others do not have this combination of characters. Furthermore, several generic relatives of *Sisymbrium* have the same features and differ only in a few technical characters.

The reproductive biology of the genus is poorly studied. All of the weedy species are self-compatible and predominantly autogamous. In three of these (*S. Irio, S. officinale,* and *S. orientale*), however, the flowers are nearly always protogynous (Al-Shehbaz, 1977; Khoshoo, 1959c).

Chromosome numbers have been reported for 27 species; all but six are diploid. *Sisymbrium elongatum* (O. E. Schulz) Romanczuk (Argentina, Bolivia), *S. luteum* (Maxim.) O. E. Schulz (eastern Asia), *S. polyceratium* L.

(southern Europe and northwestern Africa), and *S. strictissimum* L. (Europe) are all tetraploid ($2n = 28$), while *S. runcinatum* L. (Eurasia) and *S. supinum* L. (Europe) are hexaploid ($2n = 42$). Except for four South American species, the genus is based primarily on seven. Two species, *S. Gilliesii* Romanczuk (Argentina) and *S. littorale* Phil. (Chile), have $2n = 26$, while *S. magellanicum* (Juss. & Pers.) J. D. Hooker (Patagonia) and *S. subscandens* Spegaz. (Argentina) have $2n = 18$ and $2n = 20$, respectively (Carrique & Martínez; Moore; Tschischow).

Due to the presence of the cardenolides helveticoside and corchoroside in *Sisymbrium Loeselii, S. officinale,* and ten species of *Erysimum* L., Latowski and colleagues have suggested that the two genera should be placed in the same tribe. Because of the extreme rarity of these compounds in the Cruciferae, they are potentially useful in assessing generic relationships. However, neither the two genera nor their close relatives have been surveyed adequately for cardenolides. Del Pero de Martínez & Aguinagalde have suggested that the distribution of leaf flavonoids is useful chemotaxonomically, but they studied only four species, and many more need to be surveyed before any meaningful conclusions can be reached.

The seeds of nine species have been analyzed for fatty acids (Appelqvist; Miller *et al.*). All have high concentrations (33–43 percent) of linolenic acid and moderate amounts of erucic (10–23 percent) and linoleic (10–19 percent) acids. *Sisymbrium erysimoides* Desf. has the second highest content (14 percent) of palmitic acid among the 172 species of Cruciferae surveyed thus far (Kumar & Tsunoda).

Glucosinolate profiles are known for at least eight species. In *Sisymbrium Irio* and *S. officinale* high concentrations (86–96 percent) of isopropylglucosinolate and smaller amounts (4–14 percent) of 2-butylglucosinolate have been found (Al-Shehbaz & Al-Shammary). The two compounds are also present in *S. strictissimum* L. In *S. orientale* the major constituent (82 percent) is 3-butenylglucosinolate, and the minor ones are phenylethyl (14 percent) and benzyl (4 percent) glucosinolates (Hasapis *et al.*). A complex chemical profile has been found in *S. austriacum* Jacq.; it has 1-hydroxy-2-propyl and 1-hydroxy-2-butyl glucosinolates, as well as their corresponding benzoate glucosinolates that are very rare in the Cruciferae (Kjaer & Christensen).

Large crystals of calcium oxalate have been found in *Sisymbrium altissimum.* They are seldom found elsewhere in the Cruciferae (Metcalfe & Chalk).

The green parts of certain species of *Sisymbrium* are eaten raw in salads or cooked as a vegetable, while the seeds are used as a condiment (Crisp). Many medicinal properties have been attributed to various species, particularly *S. officinale,* the specific epithet of which means *of the shops,* from its former repute in medicine. This and other sisymbriums were said to be useful as antiscorbutics, diuretics, expectorants, rubefacients, and stimulants, and they were employed in the preparation of remedies for asthma, hoarseness, indurations, and swellings. Some species (e.g., *S. altissimum, S. Irio, S. officinale, S. orientale*) are noxious cosmopolitan weeds that are also hosts for certain viruses of crops.

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42. **Arabidopsis** (DC.) Heynhold in Holl & Heynhold, Fl. Sachsen **1:** 538. 1842.

Annual [biennial or perennial] herbs; trichomes furcate or stellate, usually mixed with unbranched ones, rarely absent. Lower leaves petiolate, entire [dentate or rarely pinnatifid]; upper leaves short petiolate [or sessile and auriculate to amplexicaul]. Inflorescences ebracteate [or bracteate] racemes, greatly elongated in fruit; fruiting pedicels slender, divaricate [to erect-ascending]. Sepals oblong, erect to ascending, equal and not saccate at base. Petals present [rarely absent], white, lilac [or yellow], obovate to spatulate, obtuse to truncate at apex. Nectar glands ringlike, usually subtending the bases of all filaments [sometimes toothlike, separated, 1 on each side of a lateral filament]. Stamens 6 and slightly tetradynamous [rarely 4]; filaments free, unappendaged; anthers ovate to oblong. Fruits linear, terete [or slightly flattened parallel to the septum], dehiscent, smooth [or slightly torulose]; valves 1-nerved, glabrous [or pubescent]; septum hyaline, usually 1-nerved, complete [rarely absent]; styles short, thick or slender; stigmas entire [or slightly 2-lobed]. Seeds ovate, smooth, uniseriately [rarely biseriately] arranged in each locule, wingless, mucilaginous [or nonmucilaginous] when wet; cotyledons incumbent. Base chromosome numbers 5–8. (Including *Hylandra* Å. Löve, *Pilosella* Kostel., *Stenophragma* Čelak., *Thellungiella* O. E. Schulz.) TYPE SPECIES: *Arabis Thaliana* L. = *Ara-*

bidopsis Thaliana (L.) Heynh.[7] (Name from *Arabis*, a genus of the Cruciferae, and the Greek *opsis*, aspect, from a resemblance to *Arabis*.)—MOUSE-EAR CRESS.

A poorly defined genus of 15 to 20 species, the majority of which occur in the Himalayan region and in central and southwestern Asia. *Arabidopsis suecica* (Fries) Norrlin is widespread in subarctic Europe, whereas *A. salsuginea* (Pallas) Busch grows in northern North America (Canada; Colorado, Montana), Siberia, and central Asia. *Arabidopsis Thaliana* (L.) Heynh. (*Arabis Thaliana* L., *Sisymbrium Thalianum* (L.) Gay & Monnard, *Stenophragma Thaliana* (L.) Čelak.), mouse-ear cress, $2n = 10$, is naturalized throughout most of North America and has been reported from all of the Southeastern States. It grows on sandy soil in waste places, gardens, old fields, and river bottoms, as well as along roadsides (Rollins).

The generic limits of *Arabidopsis* are highly artificial, and careful evaluation of these and of the related Asiatic *Drabopsis* C. Koch, *Microsisymbrium* O. E. Schulz, and *Neotorularia*, the European *Cardaminopsis* (C. A. Meyer) Hayek, and the American *Halimolobos* Tausch are needed. Schulz (1924, 1936) and subsequent authors have distinguished *Arabidopsis* from these genera by cotyledonary position (incumbent vs. accumbent), presence or absence of seed mucilage or median nectaries, and nature of the style (slender vs. thick). These characters alone are doubtfully useful in generic delimitation. In my opinion, a few species of *Arabidopsis* can easily be accommodated in *Halimolobos* or the Asiatic relatives above, while a few species of the other genera are more appropriately placed in *Arabidopsis*. *Arabidopsis* includes delicate annuals with undivided, rosette-forming lower leaves, furcate trichomes, narrowly linear, terete fruits, slender fruiting pedicels, uniseriate, mucilaginous seeds, and incumbent cotyledons. A thorough study of the whole complex is needed.

Autogamy is apparently widespread in *Arabidopsis*, as is suggested in *A. parvula* (Schrenk) O. E. Schulz by the lack of petals, in *A. eseptata* Hedge by the reduction of stamen number to four, and in several others by the reduction in flower size. Although *A. Thaliana* is obligately autogamous if grown under

[7]When Heynhold (see above) raised *Sisymbrium* L. sect. *Arabidopsis* DC. to generic rank, he listed a single species, *A. Thaliana*. Many workers have considered this to be the generic type. However, such typification is incorrect because *A. Thaliana* was not one of the original species that De Candolle (1821) placed in sect. *Arabidopsis*. According to Article 7.10 of the Code (ICBN, 1983), the genus must be typified by the type of the basionym sect. *Arabidopsis*. However, none of the seven species originally assigned to this section (De Candolle, 1821) is now retained in *Arabidopsis*. They are placed in *Ammosperma* J. D. Hooker, *Murbeckiella* Rothm., *Neotorularia* Hedge & J. Léonard, *Sisymbrella* Spach, and *Sisymbrium*. Section *Arabidopsis* was first lectotypified by Čelakovsky, who retained only one of its original De Candollean species, *Sisymbrium bursifolium* L. (as *A. bursifolia* (L.) Čelak.) and treated the others in different genera. This species is now recognized as *Sisymbrella dentata* (L.) O. E. Schulz. Acceptance of Čelakovsky's lectotypification would imply that *Arabidopsis* should be reduced to a synonym of the earlier-published *Sisymbrella*. Furthermore, the choice of any of the remaining De Candollean species as the type of *Arabidopsis* would necessitate either the union of this genus with the earlier-published *Sisymbrium* or the reduction of the later-published *Ammosperma* (1862), *Murbeckiella* (1939), or *Neotorularia* (1986) to synonym of *Arabidopsis*. Štěpánek has suggested that the generic name *Arabidopsis* be either conserved or replaced by *Stenophragma*, its earliest generic synonym. I concur with him in conserving *Arabidopsis* because the name is well recognized among biologists.

insect-free conditions, some outcrossing does take place in open habitats. Using genetic markers, Lawrence & Snape have estimated that about 1.2–2.2 percent outcrossing has resulted from insect (e.g., hoverflies, Syrphidae) visitation. Müller's photographic evidence of protogyny in *A. Thaliana* confirms Kerner's (see Al-Shehbaz) original observations that were reported as early as 1895.

Chromosome numbers are known for at least ten species, of which all except *Arabidopsis Korshinskyi* Botsch., which is a hexaploid ($2n = 48$), are diploid. *Arabidopsis pumila* (Stephan) N. Busch (including *A. Griffithiana* (Boiss.) N. Busch) has diploid and tetraploid populations with chromosome numbers based on eight. Six other species are diploids based on eight, while *A. toxophylla* (Bieb.) N. Busch and *A. Thaliana* are diploids based on six and five, respectively. Further studies are needed for *A. Wallichii* (J. D. Hooker & Thomson) N. Busch, which has variously been reported to have $2n = 14$ (Polatschek, 1968), $2n = 16$ (Ginter & Ivanov; Podlech & Bader), and $2n = 18$ (Naqshi & Javeid, 1976). The karyotype of *A. Thaliana* consists of a small pair of subtelocentric chromosomes and four metacentric pairs, one of which has satellites (Ambros & Schweizer).

Several workers have been successful in crossing *Arabidopsis Thaliana* with certain species of *Cardaminopsis.* Although Berger, Hylander, and Löve have suggested that *A. suecica* ($2n = 26$) is an allotetraploid derived from *A. Thaliana* and *C. arenosa* (L.) Hayek ($2n = 32$), Laibach (1958), Měsíček, and Rédei (1974) have demonstrated that the experimental evidence does not support such an origin. Löve has segregated *A. suecica* to the monotypic *Hylandra,* but the overall morphology supports its retention in *Arabidopsis* (Ball).

Arabidopsis has been poorly surveyed for secondary constituents. High concentrations of isopropylglucosinolate and smaller amounts of allylglucosinolate are found in the seedlings of *A. Thaliana* (Cole). The seeds of *A. suecica* and *A. Thaliana* have comparable amounts of oleic (13–18 percent), linoleic (26–32 percent), and linolenic (18–25 percent) acids, but the eicosenoic acid is much higher in *A. Thaliana* (24–26 percent) than in *A. suecica* (11 percent) (Kerber & Buchloh; Miller *et al.*).

Arabidopsis Thaliana is the most widely studied of all flowering plants in biochemistry, molecular genetics, morphogenesis, and physiology. It is an excellent experimental plant because of its small size, brief generation time, low chromosome number ($n = 5$), low DNA content, and predominantly autogamous breeding system (Lawrence; Meyerowitz & Pruitt). Under favorable conditions, certain races flower within three weeks from the date of sowing. The species has the lowest nuclear DNA content reported so far in flowering plants. Its haploid genome, which has about 7×10^7 base pairs (Meyerowitz & Pruitt), is about five times larger than that of the yeast and about 50 times that of *Escherichia coli.*

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The literature on *Arabidopsis* is too voluminous to be surveyed here. The interested reader should consult Rédei (1969) and the annual bibliographies of the journal *Arabidopsis Information Service.*

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43. **Descurainia** Webb & Berthelot, Hist. Nat. Îles Canaries, III. **1:** 72. 1836, nom. cons.

Annual, biennial [or perennial] herbs [or shrubs to 1.5 m high]; stems branched above [or at base], erect to ascending [or prostrate]; trichomes unicellular, dendritically branched or rarely unbranched, usually mixed with clavate [to capitate] glandular ones. Basal leaves petiolate, 2- or 3-pinnatisect [rarely once pinnate], usually forming rosettes early in the season, often withering before fruit maturity, pubescent with dendritic [and/or glandular] trichomes. Cauline leaves resembling the basal ones, progressively smaller and less divided upward. Inflorescences densely flowered, ebracteate [rarely bracteate], corymbose racemes, elongated [or not] in fruit; fruiting pedicels divaricate [rarely erect and

appressed to rachis]. Sepals green [or violet], erect to ascending [rarely spreading], oblong, obtuse at apex, not saccate at base. Petals yellow [rarely white], spatulate, obovate [ovate or oblong], short clawed, usually <3 [or to 6] mm long. Nectar glands ringlike, subtending the bases of all filaments or occasionally surrounding those of the lateral ones. Stamens 6, somewhat tetradynamous, included or slightly exserted; filaments free, not appendaged; anthers oblong, obtuse, yellow [or purplish]. Fruits narrowly linear, subclavate [oblong or elliptic], usually terete, dehiscent from the base upward [or from the apex downward], smooth [rarely torulose]; valves glabrous [or pubescent], with a prominent midvein and usually obscure, somewhat anastomosing lateral veins; septum membranaceous, complete [or reduced to a narrow rim], veinless or 1- to 3-veined; styles obsolete or rarely conspicuous; stigmas discoid to capitate, entire. Seeds oblong to elliptic, reddish brown to yellowish, wingless, uniseriately or biseriately arranged in each locule, usually mucilaginous when wet; cotyledons incumbent. Base chromosome number 7. (Including *Discurea* (C. A. Meyer ex Ledeb.) Schur; *Sophia* Adanson (1763), non Linnaeus (1775).) TYPE SPECIES: *Sisymbrium Sophia* L. = *D. Sophia* (L.) Webb ex Prantl, typ. cons.; see ICBN, p. 351. 1983. (Name commemorating François Déscurain, 1658–1740, pharmacist at Étampes, France.)—TANSY MUSTARD.

A well-defined and taxonomically complex genus of about 40 species distributed primarily in three centers: the Canary Islands (seven species), North America (11), and South America (19). Two of the North American species also grow in South America. One, *Descurainia Kochii* (Petri) O. E. Schulz, is endemic to Turkey, Armenia, and the Caucasus, while *D. sophioides* (Fischer) O. E. Schulz is widespread in arctic North America and Asia. The genus is represented in the southeastern United States by two species, of which one is a Eurasian weed and the other is indigenous.

Schulz (1924) divided *Descurainia* into two well-marked sections. The Canarian sect. SISYMBRIODENDRON (Christ) O. E. Schulz (shrubs; lower leaves with axillary fascicles; petals oblong to ovate, 3–6 mm long; seeds striate-granular, often with a distal wing) has seven species, while the cosmopolitan sect. DESCURAINIA (sect. *Seriphium* O. E. Schulz) (herbs; lower leaves without axillary fascicles; petals spatulate, 0.5–3 mm long; seeds smooth or obscurely reticulate, wingless) includes the remaining species of the genus.

Descurainia pinnata (Walter) Britton (*Erysimum pinnatum* Walter; *Sisymbrium pinnatum* (Walter) Greene; *Sophia pinnata* (Walter) Howell; *Cardamine multifida* Pursh (1814), non *C. multifida* (Muhl. ex Ell.) Wood (1870); *D. multifida* (Pursh) O. E. Schulz; *Sisymbrium canescens* Nutt. (1818), non Bentham (1839), Griseb. (1874); *Sophia myriophylla* Rydb.; *D. multifoliata* Cory), tansy mustard, $2n = 14, 28, 42$, is the most variable species in the genus. Schulz (1924) recognized five species and six varieties in this complex, while Detling accepted a highly polymorphic species with 11 subspecies. Although Detling's account of the *D. pinnata* complex is evidently superior to Schulz's, the species limits were expanded to include elements now believed to belong to other species. Due to the lack of thorough experimental and field studies on the North American taxa, Detling's treatment is closely followed here.

Descurainia pinnata subsp. *pinnata* is widely distributed throughout the Southeastern States, where it grows in fields, prairies, woodlands, desert plains, and waste places, on sandy hummocks, hillsides, and banks, and along streams and roadsides. Because of its sporadic introduction to many parts of North America, the native range of the subspecies has been obscured. However, the subspecies is probably indigenous to most, if not all, of the Southeast. Diploid, tetraploid, and hexaploid counts have been reported, but very little is known about the cytogeography and fertility relationships among the three cytotypes.

The two other subspecies reported by Detling from the Southeastern States are less common. *Descurainia pinnata* subsp. *halictorum* (Cockerell) Detling (*Sophia halictorum* Cockerell, *D. halictorum* (Cockerell) O. E. Schulz, *D. pinnata* var. *halictorum* (Cockerell) M. E. Peck, *S. andrenarum* Cockerell, *D. andrenarum* (Cockerell) Cory, *D. halictorum* var. *andrenarum* (Cockerell) O. E. Schulz), $2n = 14, 28, 42$, has been reported only from Hempstead County, Arkansas. Its range outside the Southeast extends to northern Mexico, the Southwest, and most of the Pacific and Mountain states.

Descurainia pinnata subsp. *brachycarpa* (Richardson) Detling (*Sisymbrium brachycarpum* Richardson, *S. canescens* Nutt. var. *brachycarpum* (Richardson) S. Watson, *D. brachycarpa* (Richardson) O. E. Schulz, *D. pinnata* var. *brachycarpa* (Richardson) Fern.), $2n = 14, 28$, is sporadic in North Carolina, Georgia, and Tennessee, where it may be introduced, and widespread in Arkansas. It is distributed from the Southeastern States north to Quebec, west through subarctic Canada to southwestern Mackenzie District, and south through Washington to Texas.

Descurainia pinnata is easily distinguished from all of the North American species of the genus by its obtuse, clavate to subclavate fruits (4–)5–11(–13) mm long, obsolete styles, biseriately arranged seeds, and divaricate fruiting pedicels. Differences between the three subspecies that grow in the Southeast are not very pronounced. Detling has distinguished subsp. *brachycarpa* from the other two on the basis of its fruiting pedicels spreading at angles of 45 (30–70) (vs. 75 (60–90)) degrees and its noncanescent (vs. canescent) herbage. Subspecies *pinnata* is separated from subsp. *halictorum* by its ovate to oblanceolate (vs. narrowly oblong to linear) leaf segments. It is evident, however, that the boundaries between these subspecies are somewhat artificially delimited, and that the orientation of the fruiting pedicels, the shape of the ultimate leaf segments, and the pubescence of the leaves all show continuous variation.

Small (1903, 1933) reported *Sophia intermedia* Rydb. from the Blue Ridge area of Tennessee. Detling, however, treated this taxon as *Descurainia pinnata* subsp. *intermedia* (Rydb.) Detling and indicated that it is distributed from southern British Columbia and Alberta to southern Colorado, western Nevada, and northeastern California.

The Eurasian *Descurainia Sophia* (L.) Webb ex Prantl (*Sisymbrium Sophia* L., *Sophia Sophia* (L.) Britton, *Hesperis Sophia* (L.) Kuntze, *Sisymbrium parviflorum* Lam., *Sophia parviflora* (Lam.) Standley), flixweed, tansy mustard, $2n = 14, 28$, is a weed of roadsides, waste places, disturbed sites, and fields. It has been reported from North Carolina, Georgia, Tennessee, Arkansas, and Louisiana and is likely to be found in the other Southeastern States. It is easily

distinguished from *D. pinnata* by its narrowly linear fruits, uniseriately arranged seeds, conspicuously two- or three-veined septa, and lack of glandular trichomes. None of the six varieties and eight forms recognized by Schulz (1924) in *D. Sophia* has any taxonomic value.

Descurainia is a sharply defined genus easily distinguished by its fine dendritic trichomes that are often mixed with glandular, subclavate ones, usually bi- or tripinnatisect lower leaves, filiform fruiting pedicels, and small seeds that are often mucilaginous when wet. The nearest relatives of *Descurainia* are *Sophiopsis* O. E. Schulz (four species; central Asia), *Hugueninia* Reichenb. (two species; central Europe and Mallorca, Spain), *Robeshia* Hochst. (monotypic; the Middle East), *Redowskia* Cham. & Schlecht. (monotypic; Siberia), and *Smelowskia*. As was indicated earlier, Schulz (1924, 1936) placed all six genera in subtribe Descurainiinae, a group with somewhat natural boundaries.

The reproductive biology of *Descurainia* has not been studied adequately. The Canarian species, all with large flowers and conspicuous nectaries, are self-incompatible (Bramwell), while the weedy *D. Sophia* is autogamous and protogynous (Al-Shehbaz; Best). Individual plants of the species produce an average of 75,650 seeds that are easily transported by wind because of their light weight (ca. 0.12 mg each) and by animals and farm equipment because of their mucilage (Best).

Chromosome numbers are known for 18 species; all are based on seven or 13 and are exclusively diploid. The Mexican *Descurainia Virletii* (Fourn.) O. E. Schulz is tetraploid, *D. Sophia* and the North American *D. obtusa* (Greene) O. E. Schulz have both diploid and tetraploid populations, and *D. pinnata* and *D. Richardsonii* (Sweet) O. E. Schulz have diploid, tetraploid, and hexaploid plants. The report of $2n = 12$ for *D. Sophia* (Saidabadi & Gorenflot) does not agree with 30 counts of $2n = 14$ and 28 from Asia, Europe, and North America.

Only *Descurainia Richardsonii* and *D. Sophia* have been surveyed thoroughly for glucosinolates. The former, which contains nine compounds in the leaves, has a predominance (89–99 percent) of 3-butenylglucosinolate and traces of allyl, 2-butyl, 4-pentenyl, and benzyl glucosinolates (Rodman & Chew). *Descurainia Sophia* also has 3-butenyl and allyl glucosinolates as the major and minor constituents, respectively, but it has traces of 4-methylthiobutyl and 2-phenylethyl glucosinolates (Lockwood & Afsharypuor). The seeds of *D. Bourgaeana* Webb ex O. E. Schulz, *D. pinnata*, and *D. Sophia* have fatty-acid profiles characterized by moderate amounts (28–37 percent) of linolenic acid, smaller ones (17–20 percent) of linoleic acid, and comparable concentrations (9–14 percent each) of eicosenoic, erucic, and oleic acids (Kumar & Tsunoda).

The seed-coat anatomy of *Descurainia Richardsonii* and *D. Sophia* was studied by Vaughan & Whitehouse. They showed that the epidermal cells contain large, solid columns protruding from the inner tangential walls into the cell lumen. The palisade cells are tangentially elongated, and their radial and inner tangential walls are conspicuously thickened.

Descurainia Sophia was used externally for treating indolent ulcers and internally to eradicate intestinal worms. The plant is said to be antiscorbutic and astringent, and the seeds are reputed to cure fevers, bronchitis, and dysentery. The seeds are also used as a substitute for mustard in the Caucasus (Busch).

Cattle feeding on large quantities of *D. pinnata* become blind and unable to swallow food (Kingsbury).

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THE GENERA OF BAMBUSOIDEAE (GRAMINEAE) IN THE SOUTHEASTERN UNITED STATES[1,2]

GORDON C. TUCKER[3]

Subfamily BAMBUSOIDEAE Ascherson & Graebner, Synop. Mitteleurop. Fl. **2:** 769. 1902.

Perennial or annual herbs or woody plants of tropical or temperate forests and wetlands. Rhizomes present or lacking. Stems erect or decumbent (sometimes rooting at the lower nodes); nodes glabrous, pubescent, or puberulent. Leaves several to many, glabrous to sparsely pubescent (microhairs bicellular); leaf sheaths about as long as the blades, open for over ½ their length, glabrous; ligules wider than long, entire or fimbriate; blades petiolate or sessile, elliptic to linear, acute to acuminate, the primary veins parallel to—or forming an angle of 5–10° with—the midvein, transverse veinlets numerous, usually conspicuous, giving leaf surface a tessellate appearance; chlorenchyma not radiate (i.e., non-kranz; photosynthetic pathway C_3). Inflorescences terminal or terminal and lateral, paniculate, the primary branches nearly horizontal, scabrous and/or hispidulous throughout; secondary branches often (and tertiary branches sometimes) present. Spikelets oblong to lanceolate, subterete to strongly dor-

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[2]For an account of the family, its subfamilies, and tribes, see C. S. Campbell, The subfamilies and tribes of Gramineae (Poaceae) in the southeastern United States. Jour. Arnold Arb. **66:** 123–199. 1985.

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siventrally compressed, 1- to 3- or more flowered. Glumes 0–2, subequal to decidedly unequal, broadly lanceolate, shorter than the lemmas, sometimes aristate, nerveless or weakly 1- or 3-nerved, glabrous. Lemmas narrowly elliptic, aristate or not, margins inrolled around the flower, the abaxial surface glabrous, scabrous, hispid (especially apically), or sometimes densely covered with stiff, clavate to uncinate trichomes. Paleas narrowly elliptic to lanceolate, shorter than lemma (lacking in staminate spikelet). Flowers perfect or imperfect (if imperfect the plants monoecious). Lodicules 0–3 [–12 in *Ochlandra*]. Stamens [1] 2, 3, or 6; filaments filiform, shorter than the lemmas; anthers linear, the apices of the connectives not prolonged. Ovaries narrowly elliptic, glabrous; styles terete basally, stigmas 2 or 3, equaling or longer than the styles, plumose or glandular-stipitate. Fruit a caryopsis or an achene (see *Zizaniopsis* and *Luziola*) [or a berry], ovoid, ellipsoid, or narrowly oblong, often tightly clasped by the indurate lemma and palea. Pericarp adnate to the seed or not; hilum linear; embryo less than ⅓ as long as the caryopsis. Germination epigeal. Base chromosome number 12. (Including Oryzoideae Parodi ex Caro, Dominguezia **4**: 10. 1982.) TYPE GENUS: *Bambusa* Schreber.

The Bambusoideae consist of three large groups: the woody bambusoids, represented in our area by tribe Bambuseae Dumort. (including tribe Arundinarieae Ascherson & Graebner); the herbaceous bambusoids, represented by tribes Phareae Stapf and Brachyelytreae Ohwi; and the oryzoids, represented by the Oryzeae Dumort.

Members of the Phareae are distinguished from all other New World grasses by their leaf blades with divergent, rather than parallel, lateral veins. Species of this tribe (and of the related tribe Streptogyneae C. E. Hubb. ex Calderón & Soderstrom, of the Old World) are the only grasses with resupinate leaf blades. In most bambusoids the greatest density of stomata is on the lower (abaxial) surface, but in the Phareae it is on the adaxial (physically lower) surface. The Phareae comprise three genera. *Scrotochloa* Judziewicz (two species) and *Leptaspis* R. Br. (three species) are widespread in the Old World Tropics. *Pharus* P. Br. (seven species) is widespread in the New World Tropics and is represented in the United States by *P. lappulaceus* Aublet in central and northern Florida. It differs from the other two genera of the tribe in having persistent staminate spikelets and carpellate glumes with the margins free.

The unigeneric tribe Brachyelytreae has often been placed elsewhere than in the Bambusoideae. Bentham (1883) assigned *Brachyelytrum* to the Poöideae, while Honda put it in the Stipeae. Reeder (1957) showed that its embryo was bambusoid, and MacFarlane & Watson showed that it did not belong in the Poöideae. Recently, Campbell and colleagues have summarized previous work and added new data that clearly demonstrate its bambusoid affinities. Similarities shared with the woody and herbaceous bambusoids include stomata on the abaxial leaf surface only (Renvoize) and cross veins in the leaves. Within the Bambusoideae, *Brachyelytrum* is clearly most closely related to the herbaceous bambusoids, but the genus is sufficiently different to warrant its own tribe.

The Bambuseae are the only free-standing, woody-stemmed grasses in North

America.[4] The tribe comprises three (or four) subtribes (Bentham, 1883; Dahlgren *et al.*; Hackel, 1887; Hubbard). It is represented in the Southeast by only two native species of *Arundinaria* (subtribe Arundinariinae Bentham). Subtribes Bambusinae Hackel and Dendrocalaminae Bentham are each represented by one or more cultivated species that persist after cultivation. However, none of these nonnative species is known either to reproduce sexually or to establish new populations by seed, so they are not considered to be naturalized (Soderstrom, pers. comm.).

Plants of the Arundinariinae are generally smaller (usually less than 10 m tall) than other woody bamboos. The flowers have three stamens, and the fruit is a caryopsis. About six genera occur in both the Old World and the New. *Arundinaria* Michx. (ca. 100 species) has two species in the Southeast, *A. gigantea* (Walter) Muhl. and *A. tecta* (Walter) Muhl., and these are the only representatives of this genus indigenous in the New World. Two closely related genera occur in the Neotropics: *Arthrostylidium* Rupr., of the lowlands, and *Chusquea* Kunth (including *Rettbergia* Raddi), of the mountains. In eastern Asia the subtribe is represented by species of *Sasa* Makino & Shibata, *Pleioblastus* Nakai, *Semiarundinaria* Makino, and *Pseudosasa* Nakai. Some of these genera were originally included in *Arundinaria*; their segregation from that genus is by no means generally agreed upon.

Pseudosasa japonica (Sieb. & Zucc.) Makino is cultivated in the eastern United States. It sometimes escapes from cultivation and spreads by rhizomes (specimens seen from central New Jersey, eastern Pennsylvania, eastern Maryland, North and South Carolina, and central Florida). It can be distinguished from other native and nonnative bamboos in the Southeast by its persistent stem-leaf sheaths, glaucous lower internodes, and branches solitary at each node.

Certain genera of the subtribe that have deltoid glumes have been segregated as subtribe Phyllostachyinae Hackel. The genus *Phyllostachys* Sieb. & Zucc., native to China, includes about 80 species. At least 20 species are cultivated in the warmer regions of the United States (McClure, 1957), and at least one of these is hardy as far north as Boston, Massachusetts (C. E. Wood, Jr., pers. comm.). *Phyllostachys aurea* A. & C. Riv., golden bamboo, and *P. Meyeri* McClure have been collected as possible escapes in North and South Carolina, Georgia, and Florida.

Plants of subtribe Bambusinae are tall; several species reach 30 m in height. The flowers generally have six stamens, and the fruit is a caryopsis. The largest genus, *Bambusa,* has about 70 species, all restricted to the Old World. Its New World counterpart, *Guadua* Kunth, with about 30 species, is distinguished by the winged keel of its paleas. McClure (1973), who believed that this difference was not consistent, treated the group as *Bambusa* subg. *Guadua* (Kunth) Hackel. Several species of *Bambusa* are cultivated in the Southeast and on the west

[4]The members of the Neotropical genus *Lasiacis* Hitchc. (subfam. Panicoideae A. Braun), represented by two species in Florida, are indurate to woody-stemmed, weakly clambering plants with subterete spikelets. Southeastern bamboos (both native and nonnative) are free-standing plants bearing dorsiventrally flattened spikelets.

coast from California at least as far north as Portland, Oregon. Individual clones may persist for many years after cultivation. *Bambusa vulgaris* Schrader sometimes continues to grow around old house sites in southern Florida (Long & Lakela). *Bambusa multiplex* (Lour.) Räuschel, hedge-bamboo, a native of southern China, persists after cultivation and sometimes spreads by rhizomes from plantings in central Florida (Judd, pers. comm.).

Members of subtribe Dendrocalaminae Bentham (including subtribe Melocanninae Bentham) are also tall bamboos. In contrast to the Bambusinae, this subtribe has fleshy fruits (drupes). The fruits of the Indian species *Melocanna baccifera* Roxb. are as large as pears and are baked and eaten. Certain species of *Melocanna* Trin. are cultivated in the West Indies.

Classification of bamboos has traditionally stressed vegetative features, and bamboo taxonomy has many terms specific to it. For example, two different kinds of rhizomes characterize bamboos. Leptomorph rhizomes are elongate, slender, and usually horizontal, while pachymorph ones are short, stout, and erect or oblique. The species of *Arundinaria* in the Southeast bear leptomorph rhizomes. Pachymorph species are clump formers, while leptomorph species produce single stems at close or distant intervals. *Arundinaria gigantea* forms close colonies, although the stems are not caespitose. Although bamboo stems elongate by intercalary meristematic activity, the relative lengths of the mature internodes contrast in different genera and species. In *A. Simonii* (Carr.) A. & C. Riv. the tenth internode of the stem is longest, while in *Bambusa multiplex* the fourth is longest. The order in which axillary branching begins falls into three broad patterns (McClure, 1966). In species of *Phyllostachys* and in *A. gigantea,* the direction is acropetal; in other species of *Arundinaria,* basipetal. In *Semiarundinaria viridis* Makino, branch initiation begins in the middle node and spreads upward and downward from there. Certain genera of bamboo produce more than one axillary bud at each node (termed constellate). In *Arundinaria* these buds produce branch complements that are again divided two or three times. Bamboos are the only grasses that have indeterminate inflorescences. The combination of stem elongation and branch initiation imparts the various architectural forms to mature bamboo plants.

The oryzoid grasses (tribe Oryzeae Dumort., including Zizanieae) have been treated as a subfamily, the Oryzoideae Parodi ex Caro. Since their affinities to the bambusoids are strong, they are included here in the Bambusoideae as they were by Campbell (1985), Dahlgren and colleagues, and Clayton & Renvoize. In addition to chromosomal ($x = 12$) and morphological (stamens 6 per flower; cross veins in leaves) similarities, the two groups have strikingly similar suites of amino acids in the endosperm (small amounts of glycine, proline, and phenylalanine and abundant threonine, alanine, valine, methionine, isoleucine, tyrosine, lysine, and arginine in comparison with other grasses; Yeoh & Watson). Oryzoid grasses differ from bambusoids in having stomata about equally distributed on both surfaces of the leaves instead of chiefly or wholly on the abaxial surface. Stomatal distribution of this kind is probably an adaptation to humid, sunny environments.

The Oryzeae, the members of which are herbaceous perennials or annuals, are characterized by one-flowered spikelets and glumes that are greatly reduced

or absent in several of the genera. The genera are clearly divided into three subtribes. The Oryzinae Reichenb. have perfect florets, while the Zizaniinae Honda and Luziolinae Terrell & H. E. Robinson have imperfect ones. The Oryzinae (about eight genera worldwide, pantropic and warm-temperate) are represented in the Southeast by five native species of *Leersia* Sw. and the adventive *Oryza sativa* L.

The Zizaniinae are separated from the Luziolinae by morphological, anatomical, embryological, and chromosomal features. Members of subtribe Zizaniinae have a base chromosome number of 15, laterally exserted stigmas, a typical grass caryopsis (pericarp fused to seed coat), an embryo with a narrow and free epiblast, and aerenchymatous leaf septa. The subtribe is unigeneric: *Zizania* has four species, three in eastern North America and one in eastern Asia. Members of subtribe Luziolinae have a base chromosome number of 12, apically exserted stigmas, an achene (thickened pericarp surrounding but not adnate to seed coat), an embryo with a bilobed fused epiblast, and leaf aerenchyma not forming septa (see Terrell & Robinson for illustrations). *Zizaniopsis* Döll and *Luziola* Gmelin have stellate cells in the midribs (Renvoize). The subtribe includes about 16 species of tropical South America, the Caribbean region, and southeastern North America.

The ecology of members of subfamily Bambusoideae is diverse. There are annuals and perennials and woody and herbaceous species; there are mesic terrestrial and aquatic species but apparently no xeric ones. All genera have non-kranz anatomy and the C_3 photosynthetic pathway, both typical of plants of wet or shaded habitats.

Taxonomically important chemicals of the Bambusoideae are not strikingly different from those of other grass subfamilies; most of our information is derived from investigations of the economically important genus *Oryza* L. Cyanogenesis is reported in several genera (*Bambusa, Dendrocalamus, Leersia* Sw., *Melocanna,* and *Oryza*). Its effect on herbivory is apparently uninvestigated, but cattle have been poisoned by overeating sprouts of bamboos in India. Tannins are rare in the Bambusoideae; only *Phyllostachys aurea* is reported to contain them (Gibbs). Several flavonoids (the anthocyanins cyanidin and malvinidin, the glycosyl flavonoid carlinoside, and the flavones tricin and violanthin) occur in bambusoids, and all are reported from *Oryza sativa. Leersia oryzoides* Sw. (reported as *L. Sayanuka* Ohwi by Kaneta & Sugiyama) produces the flavones isovitexin, iso-orientin, and violanthin. The alkaloidal amine anhaline, the pyrrolidine *dl*-stachydrine, and the sterol satisterol have been reported from *Oryza sativa* (Gibbs).

The cytology of the Bambusoideae is rather uniform. All of our genera have chromosome numbers based on 12, except *Brachyelytrum* (11) and *Zizania* (15). Tetraploidy seems to be common in the Oryzeae, especially in *Oryza,* where it is taxonomically significant. Worldwide, 81 percent of the genera of the woody bambusoids have numbers based on 12, 14 percent are based on 11, and the remainder on 10, 9, or 7 (Hunziker *et al.*). The woody bamboos are overwhelmingly polyploids, while the herbaceous bambusoids are primarily aneuploids. Only four percent of the woody bamboos (vs. 83 percent of herbaceous ones) are diploids. These karyotypic differences may well correlate

with contrasting life histories. Woody bamboos, with their long generation times and rhizomatous habit, have better opportunities for the perpetuation of autopolyploids than do herbaceous ones. Conversely, herbaceous bambusoids have annual flowering and much more chance for meiotic rearrangement leading to aneuploidy.

The reproductive biology of bambusoids has received some attention. Entomophily has been reported in certain tropical herbaceous species. Dioecy is unknown in the subfamily, and apomixis is unreported. Many species of the Oryzeae and Phareae are monoecious, while the Bambuseae have perfect flowers. Self-compatibility, reported in *Pharus latifolius* (Judziewicz, pers. comm.), *Zizania,* and *Oryza,* seems to be more prevalent than in the other subfamilies of grasses. Certain species of *Leersia* (Oryzeae) regularly produce inflorescences containing only cleistogamous spikelets.

The mass flowering and fruiting of many woody bamboos is a puzzling phenomenon, almost a study in itself. Numerous patterns of flowering have been observed; see McClure (1966, pp. 268–279) for a fascinating summary arranged by genus. The flowering cycle of *Bambusa polymorpha* Munro exceeds 80 years; in *B. arundinacea* Willd. it is about 50 (Arber, 1934). In our native southeastern species, colonies of *Arundinaria tecta* flower every four or five years, those of *A. gigantea* every 40–50. Some species remain vegetative for years, and some are not known ever to have flowered either in the wild or in cultivation. Many species (e.g., *Chimonobambusa quadrangularis* (Fenzl) Makino and *Sasa tessellata* (Munro) Makino & Shibata) are monocarpic and die after flowering, while others (e.g., *Bambusa lineata* Munro) flower annually. *Bambusa tuldoides* Munro dies after flowering in its native China, but cultivated plants in Central America flower continuously for years. The number of years until flowering is evidently a genetically controlled character (Janzen), as is suggested by numerous reports of transplanted populations that flower at the same time as clones in geographically distant areas. For example, *Chusquea abietiifolia* Griseb. was introduced to the island of Jamaica, where it was extensively propagated by division. One of these divisions was the source of a cultivated stand in the Botanic Gardens at Kew, England. In 1884–1885 all the plants of this species in Jamaica, as well as those at Kew, flowered and died. Drought and disturbance by cutting have been suggested as causes for local flowering of bamboo populations, but the data are not conclusive. The evolutionary origins and adaptive significance of long generation times in the woody bamboos offer great possibilities for further research.

Several patterns of dispersal are represented in the subfamily. Species of tribe Phareae bear fruits enclosed in lemmas with hooked trichomes that are presumably involved in dispersal by birds and mammals, possibly explaining the pantropic distribution of *Pharus.* In *Zizania palustris* L. the bristly awn of the lemma anchors the enclosed caryopsis to the bottom of the lake or stream, stabilizing it against movement by waves or currents until the root system develops. The fleshy fruits of certain woody bamboos (e.g., *Melocanna*) are as large as pears and fall to the ground beneath the parent. Most are eaten by herbivores, and few survive to germinate. Fruits of *M. bambusoides* Trin. are

viviparous. The hypocotyl and radicle emerge before the small, fleshy caryopsis drops from the parent plant.

The economic importance of certain species of this subfamily is great. Rice is the major food for half the world's population. Woody bamboos provide material for construction in Asia, Africa, and Latin America. Many species of bamboo are cultivated for their edible shoots, a familiar part of Oriental cuisine. Numerous species of woody bamboos are cultivated throughout tropical and warm-temperate regions as ornamentals (see McClure, 1957, 1966, 1973, for an account of those cultivated in the United States, and Lawson for horticultural information). Wild rice (*Zizania*) is extensively gathered for food in North America. Further information on economic importance appears in the generic accounts.

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Key to the Genera of Bambusoideae in the Southeastern United States

General characters: *herbs or shrubs of woods, streambanks, wetlands, and lakes (sometimes submersed or emergent); stems leafy; sheaths open; ligules present, glabrous or hairy; blades sessile or petiolate, the primary veins parallel to or slightly divergent from midvein, secondary veins usually present and perpendicular to main veins, giving the blades a tessellate appearance; inflorescences paniculate; spikelets several to many, 1- to few-flowered; glumes 1 or 2 or lacking; lemmas elliptic to lanceolate; flowers perfect or imperfect; lodicules sometimes present; stamens 2–6; stigmas 2 or 3, usually plumose; fruit a caryopsis or an achene, often firmly clasped by the persistent palea and lemma.*

A. Stems woody, perennial.
  B. Branches solitary at each node of main stem. ..... [*Pseudosasa.*]
  B. Branches 2 to several at each node of main stem.
    C. Stems flattened on one side above each node; leaf scar a distinct line beneath node. ..... [*Phyllostachys.*]
    C. Stems terete; leaf scar on node.
      D. Stems sometimes thorny; lemmas glossy; stamens 6 per flower. ..... [*Bambusa.*]
      D. Stems unarmed; lemmas dull; stamens 3 per flower. .. 1. *Arundinaria.*

A. Stems herbaceous, annual.
  E. Leaf blades petiolate, the primary veins diverging 5–10° from midvein; lemmas densely covered with uncinate to clavate trichomes. ..... 2. *Pharus.*
  E. Leaf blades sessile, the primary veins all parallel to the midvein; lemmas smooth or scabrous.
    F. Rachilla prolonged above base of palea, bristlelike, ½ as long as palea. ..... 3. *Brachyelytrum.*
    F. Rachilla not prolonged above base of palea.
      G. Flowers perfect.
        H. Rhizomes absent, plants annual; spikelets subterete; 2 lower lemmas lanceolate, the fertile one elliptic, commonly awned; stamens 6. ..... 4. *Oryza.*
        H. Rhizomes usually present, plants perennial; spikelets strongly flattened laterally; 2 lower lemmas minute, the fertile one lunate, awnless; stamens 2, 3, or 6. ..... 5. *Leersia.*
      G. Flowers imperfect.
        I. Stems stout; plants tall emergents of shallow waters; carpellate and staminate spikelets on same or different primary branches of the same inflorescence.
          J. Non-rhizomatous annuals; staminate and carpellate flowers on separate inflorescence branches, the carpellate branches distal to the staminate. ..... 6. *Zizania.*
          J. Rhizomatous perennials; staminate and carpellate flowers on same inflorescence branches, the carpellate spikelets distal to the staminate. ..... 7. *Zizaniopsis.*
        I. Stems slender; plants small, submersed or littoral; carpellate and staminate spikelets in separate, few-flowered inflorescences. ..... 8. *Luziola.*

Tribe BAMBUSEAE Dumortier, Anal. Fam. Pl. 63. 1829, "Bambusaceae."

1. **Arundinaria** Michaux, Fl. Bor.-Am. **1:** 73. 1803.

Large, woody perennials of damp thickets, pocosins, brushy pastures, swamp margins, and stream banks. Rhizomes slender (leptomorph), horizontal, extensively creeping, sometimes with air chambers. Stems solitary to caespitose, erect; branches borne in the axils of the leaf sheaths; nodes glabrous. Leaves 10–20; sheaths papery, equaling or shorter than the corresponding internode, closely fitting the stem, persistent or deciduous; ligules bearing several short bristles, deciduous; blades dimorphic, the basal 6–10 leaves bearing linear blades much shorter and narrower than their sheaths, the distal ones bearing narrowly elliptic, petiolate blades with parallel veins and transverse veinlets. Inflorescences open, racemose or paniculate, with first-, second- (and sometimes third-)order branching. Spikelets 4- to 12-flowered, large, dorsiventrally compressed, disarticulating above the glumes. Glumes (1 or) 2 (or 3), unequal, narrowly elliptic, acute, more or less mucronate, shorter than the lowest lemma. Lemmas 4–12, elliptic, [acute, mucronate, or] aristate, 11-nerved. Paleas elliptic, equaling or slightly shorter than the lemmas, acute, 2-nerved, sulcate between the 2 nerves. Lodicules 3 (the adaxial one usually adhering to the palea, easily overlooked), oblong-elliptic, obtuse, 5- to 7-nerved, ciliate abaxially and sometimes marginally also. Flowers perfect. Stamens 3; filaments filiform; anthers linear, the apex of the connective not prolonged. Ovaries broadly obovoid, glabrous. Styles glabrous, much shorter than the stigmas; stigmas 3, aspergilliform (brushlike from long, glandular papillae). Caryopsis narrowly ellipsoid, terete, sometimes with uncinate beak, glabrous. Base chromosome number 12. TYPE SPECIES: *A. macrosperma* Michx. (= *A. gigantea* (Walter) Muhl. subsp. *macrosperma* (Michx.) McClure or *A. gigantea*), the only species treated by Michaux. (Name from Greek *arundo,* reed.)

A genus of some 50 species (Clayton & Renvoize), all confined to the Old World (McClure, 1973) except *Arundinaria gigantea,* $2n = 48$, and *A. tecta* (Walt.) Muhl., which are endemic to southeastern North America. *Arundinaria gigantea* ranges from southern Delaware to southern Ohio, south to Florida and eastern Texas (McClure, 1973). *Arundinaria tecta* occurs chiefly on the Coastal Plain and Piedmont from eastern Virginia to southern Alabama. Both species form thickets called "cane brakes" along streams and in moist woods. *Arundinaria tecta* becomes more abundant in response to frequent fires in pocosins and savannas, and it can become an understory dominant (Wells & Whitford).

Taxonomic variation in the North American representatives has been variously interpreted. At least two taxa are present. McClure (1973) treated these as subspecies of *Arundinaria gigantea,* but it seems justifiable to treat them as species, since they differ by as many features as do Japanese species of the genus in Ohwi's conservative account. The American *A. gigantea* and *A. tecta* differ in several morphological features,[5] have different ranges, and have apparently different phenologies (Fernald & Kinsey) but the same chromosome

number. *Arundinaria gigantea* flowers every 40–50 years, *A. tecta* every 3–4. A third taxon, *A. macrosperma* Michx. (*A. gigantea* subsp. *macrosperma* (Michx.) McClure), was believed by McClure (1973) to be derived from hybridization and introgression of the two preceding species.

Arundinaria japonica Sieb. & Zucc. is "doubtfully escaping" in southern Florida (Long & Lakela).

Arundinaria Simonii (Carr.) A. & C. Riv. (*Pleioblastus Simonii*), $2n = 48$, is widely cultivated in western Europe and also in the southeastern United States. The plants are curious in that the left and right halves of the lower surface of the leaf blades are unlike in the distribution of papillae (Jones & Hermes). The half with more papillae appears darker to the naked eye and is outermost when the leaf is rolled in bud (Clayton & Renvoize).

The stems and leaves of *Arundinaria tecta* are good forage for cattle. The formerly extensive cane brakes of eastern Texas have been greatly reduced by the expansion of cattle ranching.

Stems of *Arundinaria amabilis* McClure, Tonkin cane, are used for making fly-fishing rods. The smaller stems are used for florists' stakes.

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[5]The two species are distinguished as follows, using characters given by McClure (1973, p. 25) checked against specimens examined in this study:

Rhizomes lacking air canals; midstem sheaths shorter than the corresponding internode; leaf blades glabrescent above; lemmas hirsute, greenish, transverse veinlets clearly visible; lodicules translucent, marginally ciliate; ovary and caryopsis without hooked apex. ..... *A. gigantea.*

Rhizomes with longitudinal air canals; midstem sheaths longer than corresponding internode; leaf blades pubescent above; lemmas glabrous, reddish tinted, transverse veinlets inconspicuous; lodicules transparent, entire; ovary and caryopsis with hooked apex. ..... *A. tecta.*

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Tribe PHAREAE Stapf in Thiselton-Dyer, Fl. Capensis 7(2–4): 319. 1898.

2. **Pharus** P. Browne, Civ. Nat. Hist. Jamaica, 344. *tab. 38, fig. 3.* 1756.

Perennials of moist subtropical [tropical] forests and woodlands. Rhizomes lacking; stems decumbent, rooting at the lower nodes, covered (or nearly so) by the overlapping leaf bases. Leaves several; sheaths about as long as the blades, open for over ½ their length, glabrous; ligules wider than long, apically fimbriate; petioles resupinate (abaxial surface of blade uppermost in the third and succeeding leaves); blades elliptic, acuminate [acute], glabrous, the lateral veins forming an angle of 5–10° with the main vein, numerous transverse veinlets connecting the lateral veins, giving the leaf surface a tessellate appearance. Inflorescences terminal, paniculate, the primary branches nearly horizontal, scabrous and/or hispidulous throughout, secondary branches often present. Spikelets 1-flowered, ellipsoid, imperfect, the staminate ones about ½ as long as the carpellate and borne singly on short pedicels from the axils of the carpellate spikelets. Glumes 2, subequal, broadly lanceolate, shorter than the lemmas, nerveless, glabrous. Lemma 1, narrowly elliptic, margins inrolled around the flower, surface densely covered with stiff, clavate to uncinate trichomes. Palea narrowly elliptic to lanceolate, shorter than lemma (lacking in staminate spikelet). Stamens 6; filaments filiform, slightly shorter than the lemmas; anthers linear, the apex of the connective not prolonged. Ovaries narrowly elliptic, glabrous; styles terete basally, becoming flattened distally; stigmas shorter than style, sparsely glandular, exserted at same time as anthers. Caryopsis cylindrical, oblong. Embryo small, basal. Base chromosome number 12. TYPE SPECIES: *P. latifolius* L., the only species treated by Browne (with a polynomial) and named validly (1759) by Linnaeus. (Name from Greek *pharos*, mantle, possibly alluding to the broad leaf blades.)—CREEPING LEAFSTALK GRASS.

A Neotropical genus of seven species (Judziewicz, 1985b), represented in the southeastern United States by *Pharus lappulaceus* Aublet. This species occurs from northern and central Florida and eastern Mexico (San Luis Potosí) south through the West Indies and Central America to Uruguay and Argentina (Prov. Tucumán). It has the widest range of any species of *Pharus*, covering nearly the entire range of the genus. It has not been collected in Florida since 1921 (*Small et al. 10084*, NY, US; *fide* Judziewicz, 1985b) and is probably extirpated in the United States.

Chromosome numbers of $2n = 24$ have been reported for *Pharus glaber* HBK. (Pohl & Davidse) and *P. latifolius* (Reeder).

No economic uses have been reported for the genus, and apparently no species

is a significant weed. In the original description of the genus, Browne noted that the plants were eaten by cattle in Jamaica. Grazing has been suggested as a cause of the disappearance of *Pharus lappulaceus* in Florida.

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Tribe BRACHYELYTREAE Ohwi, Bot. Mag. Tokyo **55:** 361. 1941.

3. **Brachyelytrum** Palisot de Beauvois, Essai Agrost. 39. 1812.

Small perennials of temperate, mesic to wet-mesic forests. Rhizomes short, horizontal, covered with cucullate to lanceolate scales. Stems erect, 1–4; nodes retrorsely hispid. Leaves 2–5; sheaths sparsely retrorsely hispid; ligules broadly oblong, hyaline; blades lanceolate-linear, flat, pilose on the nerves abaxially, scabrous on both surfaces generally, primary veins parallel, secondary veins transverse to slightly oblique. Inflorescences terminal, narrowly paniculate; nodes glabrous; branches erect, scabridulous. Spikelets few, 1-flowered, pedicellate; rachilla bristlelike, about ⅔ as long as the lemma. Glumes 2, unequal, lanceolate (the second sometimes aristate), much shorter than the lemma. Lemma lanceolate, 5-nerved, acute, bearing a long, scabrous, apical awn, the base contracted to a scabrous, indurate callus, the surface scabrous (the nerves sometimes hispid). Palea lanceolate, slightly shorter than the lemma. Stamens 3; filaments filiform, nearly as long as the palea; anthers linear, the connectives not prolonged. Ovaries slenderly conical, bristly; styles very short, glabrous; stigmas 2, stipitate-glandular. Caryopsis firmly enclosed by lemma and palea, oblong, subterete, with bristly apex and spongy beak, the adaxial surface grooved. Base chromosome number 11. TYPE SPECIES: *B. erectum* (Schreber) Beauv. (*Muhlenbergia erecta* Schreber), the only species included in the genus by Palisot de Beauvois. (Name from Greek *brachys,* short, and *elytron,* husk, referring to the minute glumes.)

A genus of three species exhibiting the classic disjunction between eastern North America and temperate eastern Asia. *Brachyelytrum erectum* occurs throughout our area and northward to Massachusetts, central New York, Ohio, southern Michigan, and southern Wisconsin. *Brachyelytrum septentrionale* (Babel) G. Tucker[6] occurs from Newfoundland to Minnesota south to northern

[6]**Brachyelytrum septentrionale** (Babel) G. Tucker, comb. nov., based on *Brachyelytrum erectum* (Michx.) Beauv. var. *septentrionale* Babel, Rhodora **45:** 260. 1943. TYPE: New Hampshire, Strafford County, Durham, *Babel 46* (holotype, WIS; isotypes, F!, GH!). (Not including *B. aristosum* var. *glabratum* Vasey ex Millsp., Bull. W. Virginia Exper. Sta. **24:** 469. 1892. TYPE: West Virginia, Fayette County, Nuttalburg, 1890, *L. W. Nuttall s.n.* (holotype, F, accession no. 100250!), which is a plant of *B. erectum,* not *B. septentrionale* as stated by Koyama & Kawano.)

New Jersey, West Virginia, western North Carolina (Jackson County, below Tuckaseigee Falls, *H. F. Williams s.n.*, 7/6/31, DUKE!, F!), southern Michigan, and central Wisconsin. Stephenson examined the populations of both species in Michigan and found consistent morphological differences. He indicated that further study throughout North America is necessary to confirm that these two taxa are indeed species, as is indicated by their distinctiveness in Michigan. I have examined specimens from throughout eastern North America and find that the two taxa can be easily and consistently separated by his criteria; *B. erectum* has few (5–10(–20) per cm) cilia (macrohairs) on the leaf margins and stiff hairs 0.4–0.6 mm long on the lemmas; *B. septentrionale* has abundant ((30–)40–60 per cm) cilia on the leaf margins and lemma hairs only 0.1–0.2 mm long. There are also differences in the lengths of the palea (10–12 mm in *B. erectum*, vs. 8–10 mm in *B. septentrionale*), the second glume (1.5–2.5 (–4.5) vs. 1–1.5(–2) mm), and the anthers (5–6 mm vs. 2.5–4(–5) mm). The length of the rachilla (6–7 mm vs. 5–6.5 mm) overlaps too much to be used alone. In areas of sympatry (e.g., central New York), about five percent of the collections appear to be intermediates of hybrid origin. Stephenson noted the occurrence of apparent hybrid populations in southern Michigan.

The two species of *Brachyelytrum* are nearly allopatric in Pennsylvania, with *B. septentrionale* occurring in moist woods in the northern half of the state and *B. erectum* in mesic woods in the southeastern third (Pohl). In Wisconsin *B. erectum* has a more southerly distribution than *B. septentrionale* (Fassett). In southern Michigan, where both species are found, *B. septentrionale* flowers about ten days before *B. erectum* (Stephenson). Stephenson reported that anthesis within populations of both taxa was highly synchronous. As far as he could determine, it was confined to the first half of the morning of a single day.

Brachyelytrum japonicum Hackel, $2n = 22$, differs from the North American species in having narrower leaf blades and longer glumes (Koyama & Kawano). It occurs in southern Japan, Korea, and east-central China.

Hackel (1897) also included three tropical species in the genus. These were *Brachyelytrum procumbens* Hackel (northern South America), of subg. *Aphanelytrum* Hackel, and *B. aristatum* (Beauv.) Hackel and *B. silvaticum* (K. Schum.) Hackel (East African mountains), of subg. *Pseudobromus* (K. Schum.) Hackel. Plants of subg. *Aphanelytrum* have 2- or 3-flowered spikelets. Hackel later elevated this taxon to generic status, an opinion shared by Chase (1916), who considered it a member of tribe Festuceae Dumort. (= Poeae). Clayton & Renvoize placed this monotypic genus in tribe Poeae but did not comment on its previous placement in *Brachyelytrum*. They treated *Pseudobromus* K. Schum. as a synonym of *Festuca* L. (tribe Poeae), similarly without mention of its inclusion in *Brachyelytrum* by Hackel.

Plants of *Brachyelytrum* have no reported economic importance. No species are reported as weeds.

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Tribe ORYZEAE Dumortier, Obs. Gram. Belg. 83. 1824.

Subtribe **Oryzinae** Reichenbach, Deutschlands Fl. **5:** 6. 1846, "Oryzeae."

4. **Oryza** Linnaeus, Sp. Pl. **1:** 333. 1753; Gen. Pl. ed. 5. 29. 1754.

Annuals [perennials] of ditches, shores, marshes, and other open freshwater [brackish] wetlands. Rhizomes lacking [present]. Stems erect (sometimes ascendent, rooting at the lower nodes if submersed), single or caespitose by tiller formation; nodes glabrous. Leaves several per culm; sheaths open for much of their length, glabrous; ligules broadly lanceolate, scabrous abaxially; blades linear, flat, surface glabrous, margins scabrous, veins parallel, transverse veinlets lacking, basal auricles sometimes present. Inflorescences terminal, paniculate; branches flexuous and slightly drooping, glabrous generally but axils sometimes pilose. Spikelets 1-flowered, more or less persistent [promptly deciduous]; rachilla not prolonged beyond palea. Glumes 2, greatly reduced, forming a cupulate structure at base of spikelet. Lemmas 3, the 2 basal ones lanceolate [linear], weakly nerved, glabrous, sterile, the fertile one elliptic [ovate], stiffly conduplicate, 5-nerved, acute, mucronate or bearing an awn up to 10 times as long as the body of the lemma, the abaxial surface papillose, glabrous, scabrous, or hirsute. Palea lanceolate, mucronate, 2-nerved submarginally, edges hyaline. Flowers perfect. Stamens 6; filaments filiform; anthers narrowly ellipsoid, the apex of the connectives not prolonged. Ovaries ellipsoid, glabrous, bearing an apiculate appendage adjacent to the style base; styles glabrous; stigmas 2, longer than the styles, aspergilliform, exserted laterally (1 on each side of the lemma), before the anthers. Caryopsis narrowly [to broadly] ellipsoid, cylindrical to compressed, enclosed by the sclerified lemma and palea. Base chromosome number 12. TYPE SPECIES: *O. sativa* L., the only species included by Linnaeus. (Name from Greek *oruza,* rice, derived from Arabic *eruz,* rice.)—RICE.

A pantropic and warm-temperate genus of 18 species (Duistermaat). About 12 species are found in southeastern Asia and Australia, the center of diversity for the genus; six occur in Africa, and three are native to the New World. The genus is well known and economically significant because of *Oryza sativa* L., rice, one of the world's two most important crops.

Oryza is closely related to *Leersia,* but the two genera can easily be distinguished since *Leersia* lacks the two sterile lower lemmas consistently present in species of *Oryza* (see additional comments under *Leersia*). The genus consists of three sections (Tateoka, 1962a, 1962b, 1963) that differ in morphology, embryology, and cytology. Section ORYZA (sect. *Sativae* Roshev.; sect. *Eu-oryza* Baillon) is characterized by embryos in which the epiblasts are laterally fused to the scutellum and lateral outgrowths (auricles) of the lower scutellum fill the space between the epiblast, the coleoptile, and the ventral scale. Such embryos with auricles are not known elsewhere in the Gramineae (Tateoka, 1964). Section ORYZA is composed of two series (Nayar; Sharma & Shastry, 1965). Members of series ORYZA (series *Sativa* Sharma & Shastry) are caespitose annual or perennial plants of wetlands, forming large, gregarious populations. There are five species, all diploids, $2n = 24$, of pantropic distribution (Nayar). They have genome AA, according to the system of Morinaga & Kuriyama. One species, *Oryza sativa,* is cultivated worldwide in tropical and warm-temperate regions. It is adventive in the southern United States (South Carolina to Texas), the Sacramento Valley of California, and various localities in the Neotropics south to northern Argentina. *Oryza glaberrima* Steudel, native to West Africa, is adventive in El Salvador (Adair *et al.*) and in northern South America. Other species of this series are *O. rufipogon* Griff., a pantropic species that is probably the nearest relative of *O. sativa, O. longistaminata* A. Chev. & Roehr., *O. Barthii* A. Chev. (*O. Stapfii* Roshev.), and *O. meridionalis* Ng, an endemic of Australia.

Series LATIFOLIAE Tateoka (sect. *Officinalis* Richharia) includes ten species and has a pantropic distribution. The plants are tall aquatic perennials with large, open panicles. All are tetraploids, $2n = 48$. Seven species, the most widespread of which are *O. minuta* Presl and *O. punctata* Steudel, occur in the Old World. These species have genome BBCC, whereas those from the New World have CCDD. The three remaining species are Neotropical: *O. latifolia* Desv., $2n = 48$, of the West Indies and Central and South America; *O. grandiglumis* (Döll) Prodöhl, $2n = 24, 48$, of the Amazonian region of South America; and *O. alta* Swallen, of Central and South America. These species, similar in habit, differ chiefly in features of the spikelets. All of the New World species were treated as varieties of *O. latifolia* by Chevalier.

Section RIDLEYANAE Tateoka includes two species, *Oryza Ridleyi* J. D. Hooker, of southeastern Asia, and *O. longiglumis* Janzen, of New Guinea. The plants are vigorous rhizomatous perennials, the spikelets have setaceous sterile lemmas, and the keels of the fertile lemmas are hirsute. The caryopsis is oblong and glabrous, the embryo lacks auricles, and the epiblast is laterally free from the scutellum (Tateoka, 1964). The genomic constitution apparently is unknown (Nayar).

Section GRANULATAE Roshev. (*Padia* (Zöll. & Mor.) Baillon) is monotypic. The plants have sparse, contracted panicles with fewer than 20 spikelets, and the lemmas are muticous. Embryologically it is like sect. RIDLEYANAE. The plants are caespitose and grow in woodlands in dry to damp soils. The genomic relations are unknown. The only species, *Oryza Meyeriana* (Steudel) Baillon (including *O. Abromeitiana* Prodöhl), of southern and southeastern Asia, consists of two subspecies, subsp. *Meyeriana* and subsp. *granulata* (Watt) Dui-

stermaat, both $2n = 24$, that differ in the shape of the spikelets. The fossil *O. exasperata* (A. Br.) Heer, of the Miocene strata of Germany, is very similar to *O. Meyeriana* (Duistermaat).

Roshevitz recognized a fourth section, *Coarctatae* Roshev., in his monograph of the genus. On anatomical and embryological grounds, Tateoka (1964) has treated this as *Sclerophyllum* Griff. Its only species, *S. coarctatum* (Roxb.) Griff. (*Oryza coarctata* Roxb.), is endemic to India.

The cultivated forms and varieties of *Oryza sativa,* named and unnamed, number in the thousands. They are generally grouped into three subspecies: subsp. *sativa*[7] (subsp. *indica* Kato), grown primarily in India and Burma; subsp. *japonica* Kato, grown in China and Japan; and subsp. *javanica* Matsuo, of Indonesia. The typical subspecies ("Indica rice") sheds its spikelets most readily; subsp. *javanica* generally has awned spikelets, while both subsp. *sativa* and subsp. *japonica* are awnless. There are chemical and physiological differences as well. Only in subsp. *sativa* does the endosperm react with phenol, giving a reddish color. Subspecies *japonica* has a greater tolerance for anaerobic germination than do the other subspecies, including wild populations. There are thousands of cultivars. Most American cultivars are derivatives of subsp. *javanica* (Adair *et al.*).

Oryza sativa is usually an annual, but some cultivars can be perennial, at least in tropical regions. In wild races of *O. sativa* (by some workers treated as *O. rufipogon*), the mature grains drop into mud or water, but they are internally dormant and do not germinate until the next rainy season (Arber, 1934). The dormancy is not overcome by chilling, but a dry treatment at 40–50°C for one to two weeks produces good germination. Stratification is also effective. Seeds buried in mud for several weeks will germinate when exposed to oxygen. Seeds can remain viable but dormant in damp soil for several years. In certain cultivars dormancy of seeds can be influenced by high temperatures or high moisture affecting the parent plants at the time of pollination.

Cultivars of *Oryza sativa* cross-pollinate with wild or weedy races of the species and perhaps also with plants of *O. rufipogon* in southeastern Asia. Hybrids can be made by simply tying together the panicles of the desired parental plants. Such hybrids introgressed with cultivated strains of *O. sativa,* yielding genetic combinations that have been propagated as new cultivars.

All species reported have chromosome numbers of either $2n = 24$ or $2n = 48$. *Oryza sativa,* $2n = 24, 48$, is well known cytologically and genetically. Four of its 12 chromosomes are sub-metacentric; the others telocentric. The longest chromosome is about twice as long as the shortest. The genes are mapped onto 12 linkage groups corresponding to the 12 chromosomes of the haploid karyotype. Morphologically or chemically related traits are generally not located within the same linkage groups. The loci controlling dormancy are several, and their interaction is complex. The anthocyanin coloration of the apiculus of the lemma is governed by three loci and 20 alleles. An additional locus controls the golden vs. white coloration of the furrows of the lemmas. Additional genes determine the brown or red color of the pericarp. Awn length is governed by

[7]In botanical and agricultural literature this is called subsp. *indica* Kato, "Indica rice." This is, however, a botanical rank, and the autonym rule applies. The type specimen of *O. sativa* came from India and was evidently a cultivated plant of the Indica type.

the interaction of three loci, each located on a different chromosome. The presence or absence of hairs on the lemmas is controlled by a single locus. Two additional ones can lead to lemmas with dense, long hairs. A detailed summary of the genetics of rice with interesting details of inheritance is given by Tsunoda & Takahashi.

As noted above, *Oryza sativa* is most closely related to the pantropic *O. rufipogon*. It is generally believed that cultivated subspecies of *O. sativa* evolved from annual wild progenitors over a broad area from the foothills of northern India to northern Vietnam and southernmost China. This apparently occurred independently and concurrently at a number of sites. "Weed rice" (intermediate between cultivated and wild races) is known from as early as 3500 B.C. from archeological sites in northern Thailand. Carbonized "glumes" (i.e., lemmas) indicate that the plants were gathered or possibly cultivated at that time. Rice was first cultivated in China about 3000 B.C. and in India about 1500 B.C. The Chinese pictograph for rice first appeared about 1500 B.C.; by the first century A.D. several cultivated varieties of rice were mentioned in Chinese literature. Subspecies *sativa* (*indica*) originated in northeastern India and from there was introduced to Malaysia and Taiwan; subsp. *javanica* was developed in Indonesia by 100 B.C. (perhaps earlier) and brought into the Philippines and Japan; and subsp. *japonica* was domesticated in China and introduced to Korea and Japan about the third century B.C. Using electrophoretic data, Second (1986) showed that the distinction between subspecies *sativa* and *japonica* is a natural one, probably a result of allopatric subspeciation between northern and southern populations of wild rice separated by the uplift of the Himalayas.

Oryza glaberrima, the cultivated rice of West Africa, was domesticated from wild populations of the same species (Second, 1986) in swampy areas of the upper Niger Basin of tropical West Africa. Selection began as early as 1500 B.C. *Oryza sativa* was introduced to West Africa in the seventeenth century. In West Africa today *O. glaberrima* and *O. sativa* are customarily grown together in about equal amounts. About 75 percent of West African rice is cultivated in the uplands (while most Asian and American rice is cultivated in inundated soils).

Differences between cultivated and wild strains of rice are similar to those between artificially selected and wild types of other cereal crops, as a result of similar human selection. Cultivated varieties are larger plants and have greater growth rates than wild races. They also have strongly synchronized germination, growth, and seed set within populations. The panicles and spikelets are more persistent and thus do not shatter, a feature that facilitates harvesting. Cultivated plants differ in loss of pubescence on foliage and lemmas and in loss of awns (in certain varieties), and they have shorter anthers and larger, heavier grains. They have less pigmentation, and their karyotypes are more asymmetric at pachytene than those of wild races.

Oryza sativa is a weed in some 30 tropical and warm-temperate countries (Holm *et al.*). The weedy, spontaneous plants are called red rice (because of the reddish spikelets and grains) and are a major weed of American rice fields (Adair *et al.*). Several other species (e.g., *O. rufipogon*) are weeds, particularly in southeastern Asia.

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5. **Leersia** Swartz, Prodr. Veg. Ind. Occ. 21. 1788, nom. cons.

Perennials [annuals] of damp woods, shores, ditches, and rice fields. Rhizomes stiff, horizontal, closely covered with firm, cucullate scales. Stems loosely clustered, erect or decumbent, terete or slightly compressed (sometimes rooting at the lower nodes); nodes glabrous or shortly hirsute. Leaves several, the lowermost sometimes bladeless; sheaths scabrous (sometimes also pubescent), open for much of their length; ligules truncate [broadly lanceolate], 1[–2] times as high as the width of the blades, glabrous, becoming erose with age; petioles short; blades flat to plicate [involute], auriculate, the margins (and sometimes the surfaces) scabrous (the prickles extrorse or retrorse). Inflorescences terminal (smaller axillary ones sometimes present, the lower branches or the entire inflorescence sometimes enclosed within the sheath of the subtending leaf), paniculate; branches 1–4 per node, ascending to spreading, secondary branches frequently present as well. Spikelets 1-flowered, ellipsoid to oblong, strongly flattened. Glumes reduced to a tiny cupulate structure at base of spikelet. Lemma 1, lunate, stiffly conduplicate, acute [contracted into a cauda ("pseudoawn") as long as body of lemma], 5-nerved, glabrous or hispid on the abaxial surface or only on the nerves, the keel scabrellate or ciliate. Palea 1, broadly lanceolate, conduplicate, about as long as lemma, acute, sometimes mucronate, 3-nerved (the middle nerve more conspicuous than the lateral ones, ciliate or scabrellate), the margins straight. Flowers perfect. Lodicules 2, ovate, obtuse

[emarginate], hyaline, 3-nerved. Stamen(s) [1,] 2, 3, or 6; filaments filiform; anthers linear to oblong, the apex of the connectives not prolonged. Ovaries slenderly ellipsoid, glabrous; styles glabrous, very short [absent]; stigmas 2, plumose, exserted with or after the anthers. Caryopses gibbous (adaxial edge straight, abaxial edge broadly convex), flat to subterete. Base chromosome number 12. (*Homalocenchrus* Mieg, Acta Helvetica **4**: 307. 1760, nom. rejic.) TYPE SPECIES: *L. oryzoides* (L.) Sw. (*Phalaris oryzoides* L.), typ. cons. (Named for Johann Daniel Leers, 1727–1774, German botanist and pharmacist.)—CUTGRASS, WHITEGRASS, CATCHFLY GRASS.

A genus of 17 species, worldwide in warm-temperate and tropical regions. The center of diversity is tropical Africa, where eight species (seven of them endemic) occur. *Leersia triandra* is endemic to West Africa, two species are found only in eastern Asia, and two occur in Central and South America. Five species (two of them endemic) grow in North America; all are present in the Southeast.

Launert studied the African species, and Pyrah examined the remaining ones. The genus is, however, in need of a thorough worldwide revision. *Leersia* consistently lacks the two sterile lower lemmas present in all species of *Oryza,* but there has been some confusion of generic limits. Certain African and Asian species of *Leersia* have "awned" lemmas, but these structures are not homologous with the awns of *Oryza* species. The awns of *Leersia* have three vascular bundles, while those of *Oryza* have only one. In *Oryza* the vascular bundles in the lateral nerves of the lemmas end in a pair of mucros at the base of the true awn. In those species of *Leersia* with "awns," the two lateral nerves join the bundle of the midvein and continue into the caudate apex of the lemma (Launert; Pyrah). Confusion about the "awns" of certain *Leersia* species has resulted in their inclusion in *Oryza* by some workers.

The possession of one, two, three, or six stamens by species of a single genus is an uncommon condition noted in few if any other genera of grasses. The studies of Holm (1892, 1895) and Pyrah pointed out two groups in the genus based on concordance of stamen number and leaf anatomy. It seems appropriate to treat these groups as sections. Section HEXANDRAE G. Tucker[8] has six stamens per flower and groups of bulliform cells distributed on both surfaces of the leaf blades. Several African species with caudate ("awned") lemmas form a distinct group within sect. HEXANDRAE. The only New World species of this section is *Leersia hexandra* Sw. (plants rhizomatous, spikelets oblong, keels ciliate), $2n = 48$, a pantropic and warm-temperate species. It is known in North America from southeastern Virginia to Florida and Texas and from central Tennessee.

The four remaining North American species of the genus belong to the more advanced section LEERSIA. They have one to three stamens, and the bulliform cells occur only on the upper surface and in two small patches near the midvein on the lower surface. This section can be divided into two informal groups:

[8]*Leersia* section *Hexandrae* G. Tucker, sect. nov. Leersiae rhizomatosae; cellulae bulliformes in superficiebus ambabus folii; stamines sex.—SPECIES TYPICUS: *L. hexandra* Swartz.

caespitose plants of mesic to dry habitats, and rhizomatous ones of damp soils and shallow water. *Leersia oryzoides* (L.) Sw. (plants rhizomatous, spikelets ellipsoid, stamens 3), $2n = 48$, has the widest range, occurring throughout the United States and southern Canada. It is also reported from western Europe, central Asia, and Japan. *Leersia virginica* Willd. (plants rhizomatous, spikelets ellipsoid, stamens 2), white-grass, $2n = 48$, is widespread in eastern North America from New Hampshire, southern Quebec, and North Dakota south to northern Florida and eastern Texas. *Leersia lenticularis* Michx. (plants rhizomatous, spikelets suborbiculate, keels ciliate, stamens 2), catchfly-grass, $2n = 48$, is endemic to the southeastern Coastal Plain and Mississippi drainage, occurring from eastern Virginia, Illinois, and Minnesota to western Florida and eastern Texas. *Leersia monandra* Sw. (plants lacking rhizomes; spikelets ovate, glabrous; stamens 2), $2n = 48$, a species of the Caribbean basin, is known in the United States only from southern Florida and southern Texas. The nearest relative of *L. monandra* is the Neotropical *L. ligularis* Trin. (see Pyrah). In late Miocene times the now-extinct *L. nebraskensis* (J. Thomasson) G. Tucker,[9] a species most closely resembling *L. ligularis,* occurred in the Great Plains of western Nebraska (Thomasson). This is the earliest record of fossil material of *Leersia,* and indeed of the Oryzeae. *Leersia nebraskensis* grew in a mesic lacustrine community and thus differed ecologically from *L. ligularis* and *L. monandra,* both of which inhabit open rocky woods.

Leersia oryzoides includes plants with either cleistogamous or chasmogamous spikelets (Arber, 1934; Fogg). In the plants bearing cleistogamous spikelets, the panicles remain within the subtending leaf sheath and seed set is high; in the chasmogamous ones the panicles are exserted and seed set is lower. Pyrah noted that in greenhouse-grown plants seed set was high among chasmogamous plants. He suggested that the low seed set reported for wild plants was simply a result of the promptly disarticulating mature spikelets.

A large series of collections of a single species of *Leersia* typically shows a wide range in height from robust to depauperate. Such variation is phenotypic and probably the result of varying combinations of water level, period and depth of inundation, and concentration of nutrients in water or soil.

Nastic movements have been reported for the southeastern Asian species (Monod de Froideville). It is uncertain whether they are present in any New World species.

Leersia hexandra Sw. is a major weed, especially of rice fields, in at least 20 tropical countries in both hemispheres (Holm *et al.*). *Leersia oryzoides* is a minor weed in wet soils and rice fields in some areas of the southern United States.

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Under subfamily references see ARBER (1925, 1934); BENTHAM (1883); CLAYTON; CLAYTON & RENVOIZE; GODFREY & WOOTEN; GOULD & SHAW; HITCHCOCK; HOLM *et al.*;

[9] *Leersia nebraskensis* (J. Thomasson) G. Tucker, comb. nov., based on *Archaeoleersia nebraskensis* J. Thomasson, Am. Jour. Bot. **67**: 877. 1980. Since the fossil species is evidently most closely related to *L. ligularis*, a species of the more advanced sect. LEERSIA, it seems appropriate to treat it as a species of *Leersia*.

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Subtribe **Zizaniinae** Honda, Jour. Fac. Sci. Univ. Tokyo Bot. **3**: 5, 9. 1930, "Zizanieae."

6. **Zizania** Linnaeus, Sp. Pl. **2**: 991. 1753; Gen. Pl. ed. 5. 427. 1754.

Tall, monoecious annuals [perennials] of shallow fresh or brackish waters. Rhizomes lacking [present]. Stems solitary (often producing several tillers) [densely caespitose], unbranched, erect [decumbent, rooting at the nodes]; nodes glabrous. Leaves several, cauline [mostly basal]; sheaths about as long as leaf blades, glabrous (sometimes ciliate on the margins); ligules about as high as the width of the blade; blades flat, linear-lanceolate [linear], both surfaces generally glabrous (but pilose just above sheath), margins hispid. Inflorescences terminal [or both axillary and terminal], paniculate, the staminate branches below the carpellate ones; nodes densely hirsute; branches glabrous. Spikelets 1-flowered, disarticulating below the lemmas, the carpellate lanceolate, appressed-ascendent at anthesis, the staminate ellipsoid, pendulous. Glumes nearly obsolete (reduced to collarlike ridges). Lemmas broadly lanceolate to linear, staminate ones 3-nerved and carpellate ones 5-nerved, acuminate, with awns up to 3 times as long as body of the lemma. Paleas linear-lanceolate, equaling the lemmas, hyaline, 3-nerved, acute. Flowers imperfect. Stamens 6; filaments short, very slender (barely elongating, the palea and lemma spreading, exposing the dehiscent anthers); anthers linear, the apex of the connectives not prolonged. Ovaries slender, glabrous; styles short, glabrous; stigmas 2, longer than styles, aspergilliform, exserted before anthers. Caryopsis narrowly cylindrical, firmly clasped by the indurate carpellate lemma. Base chromosome number 15. LECTOTYPE SPECIES: *Z. aquatica* L.; the other Linnaean species, *Z. terrestris* L., was excluded by Bentham (Gen. Pl. **3**: 1115. 1883). (Name from Greek *ziza-*

nion, a weed of grain fields, the tares of the New Testament parable; cf. Matthew **13:** 24–30.)—WILD-RICE.

A small genus (four species) of eastern North America and eastern Asia. Three species occur in North America (Dore), two of these in the Southeast. *Zizania aquatica* L. (lemmas and paleas scabrous throughout, grains about 12 times longer than wide), northern wild-rice, $2n = 30$, occurs from New Brunswick to Manitoba, south to Florida and Texas. It consists of two varieties: var. *aquatica,* southern wild-rice, grows over the entire range of the species; var. *brevis* Fassett, estuarine wild-rice, only on freshwater tidal shores of the Saint Lawrence River in Quebec (Darbyshire & Aiken; Fassett). The second species, *Z. palustris* L. (*Z. aquatica* var. *angustifolia* Hitchc.) (lemmas and paleas hispidulous apically, otherwise glabrous, grains 6–8 times longer than wide), $2n = 30$, occurs from Nova Scotia to Manitoba (introduced in Saskatchewan), south to Maryland, Missouri, Arkansas, and Kansas. This species also consists of two varieties (Dore): var. *palustris,* northern wild-rice, occurs over the species range, while var. *interior* (Fassett) W. Dore, river wild-rice, is found from southern Ontario to Iowa. Fassett and others have treated *Z. palustris* as a variety of *Z. aquatica.* The two species differ vegetatively and ecologically, as well as in spikelet morphology. *Zizania palustris* generally has narrower leaf blades and grows in deeper water than *Z. aquatica* (Dore). Electrophoretic evidence confirms the separation of *Z. aquatica* and *Z. palustris* at the specific level (Warwick & Aiken).

The third North American species, *Zizania texana* Hitchc., Texas wild-rice, $2n = 30$, is endemic to warm springs in central Texas (Correll & Correll). Unlike *Z. aquatica* and *Z. palustris,* which are annuals, *Z. texana* is a perennial, its prostrate stems rooting at the nodes. It appears to be most closely related to *Z. aquatica,* since plants of both species have scattered prickles on the lemmas. The grains of *Z. texana* are 50–70 percent as long as the palea, while those of *Z. aquatica* are about as long as the palea. *Zizania aquatica* has erect, emergent leaves, while *Z. texana* has submersed, flexible ones. The species is considered endangered; it is known only from the type location in Hays County, Texas, where it grows in calcareous spring waters that have a year-round temperature of 21.5°C.

The fourth species, *Zizania latifolia* (Griseb.) Stapf, Manchurian wild-rice, $2n = 30, 34$, is native to eastern Asia (Korea to northern India). It is a stout, stoloniferous perennial that differs from the three North American species in having apically ciliate pedicels. The awns of the carpellate lemmas are shorter than those of the North American species. It is hardy in the vicinity of Washington, D. C., but in that climate does not flower early enough to set fruit each year. It can be grown outdoors in Ottawa, Canada, but does not flower there. Hybrids of *Z. palustris* and *Z. latifolia* are sterile (Dore).

Because of the economic importance of wild rice, its ecological requirements are well known. The best crops are harvested where there is some movement of water, as in slow rivers or in freshwater coves or bays near the mouths of streams. A stable water table during the summer is necessary; wild rice does

not grow in water deeper than one meter (Dore), nor does it grow in brackish water.

All species are protogynous, the staminate florets of an inflorescence being exserted after the stigmas (Dore), a condition that promotes outcrossing. Greenhouse experiments have shown that pollen from an inflorescence can fertilize carpellate flowers in other inflorescences of the same plant, so *Zizania palustris* is self-compatible (Dore), as is *Z. texana* (Terrell *et al.*). However, stems flowering late in the season sometimes exsert stigmas as the stamens are beginning to shed pollen (e.g., *Tucker 3841,* NYS, Preston, Connecticut). This simultaneous flowering appeared to be characteristic of short stems produced by tillering; earlier stems of the same plant seemed to be strongly protogynous. If pollen is shed when stigmas are receptive, self-pollination appears unlikely because wind would probably not carry it upward to the stigmas of the same plant. Insects gather the pollen of *Z. palustris* and *Z. aquatica* but visit only the stamens and probably do not contribute significantly to pollination. Terrell & Batra reported that individuals of *Bombus vagans* Smith (Bombidae), *Dialictus imitatus* (Smith) (Halictidae), and *Toxomerus politus* (Say) (Syrphidae) visited plants of *Z. aquatica* in Maryland. In an estuarine population of *Z. aquatica* in Preston, Connecticut (*Tucker 3828,* GH, NYS, 12 August 1987), individuals of *Apis mellifera* L., *Bombus impatiens* Cresson, and *Platycheirus quadratus* Say[10] visited staminate flowers only.

Germination has been extensively studied. Caryopses of *Zizania palustris* are dormant when shed and require cold treatment (at or near freezing) for three months to break dormancy. Similar treatment (105 days at 3°C) breaks dormancy in *Z. texana.* Seeds for commercial sowing are mixed with mud, stored in large containers, and frozen over the winter. The seeds of the more southern *Z. aquatica* are less tolerant of freezing than are those of *Z. palustris.* If the seeds are stored dry, their viability rapidly diminishes, reaching one percent after only seven weeks (Fyles). Unlike the buoyant, flotation-dispersed seeds or fruits of most aquatic plants, the ripe grains of wild rice sink rapidly and the awn of the lemma sticks into the mud, anchoring the germinating seedling until adventitious roots are firmly established (Bayly), an adaptation to the flowing waters in which wild rice generally grows.

Northern wild-rice, *Zizania palustris,* is economically important. Hundreds of tons of the grain are gathered each year from lakes and rivers of Wisconsin, Minnesota, western Ontario, eastern Manitoba, and northern Saskatchewan. Much of the harvesting is done by American Indians, using methods employed since pre-Columbian times (Chambliss). Some modern harvesting is accomplished in power boats with attached flails and combines to remove grains from the panicles. Traditionally, the grain is gathered from a canoe. One person propels the canoe from the bow while the other uses two sticks, one to bend the stems over the canoe, the second to strike the panicles and knock the grains loose so they fall into it. Before they are cooked, the grains are parched to

[10]Insects identified by Dr. Timothy L. McCabe, Curator of Entomology, New York State Museum, where voucher specimens are deposited.

loosen the lemmas and paleas, and the chaff is separated by winnowing in a light breeze. Wild rice was a staple grain for the tribes that harvested it. It is an important food for waterfowl and is often planted to attract ducks.

The grains of *Zizania latifolia* are collected and eaten during times of scarcity in China. Shoots infected by the fungus *Ustilago esculenta* Hennings become swollen and are eaten as a vegetable, "kau-sun." The species has been introduced to Indonesia for this purpose by Chinese immigrants (Monod de Froideville). Infected plants do not flower but are propagated by division of the rhizome. *Zizania palustris* is planted for forage in the Soviet Union. It is adventive in New Zealand, where it is weedy in damp pastures.

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Subtribe **Luziolinae** Terrell & H. E. Robinson, Bull. Torrey Bot. Club **101**: 243. 1974.

7. **Zizaniopsis** Döll & Ascherson ex Döll in Martius, Fl. Bras. **2**(2): 13. 1871.

Tall, monoecious perennials [annuals] of fresh or brackish marshes and stream banks. Rhizomes stout, horizontal. Stems 1 or 2 per rhizome node, stout, unbranched; nodes glabrous. Leaves several; sheaths with free margins their entire length, glabrous; ligules deltoid, a little wider than high, sparsely hirsute abaxially; blades linear, slightly auriculate at base, with numerous transverse veinlets, glabrous. Inflorescences terminal, paniculate, with the staminate spikelets borne on the proximal portions of the branches, the carpellate on the distal; nodes pilose; branches hirsute. Spikelets 1-flowered, oblong-lanceolate, disarticulating readily at base of lemma. Glumes lacking. Lemmas broadly lanceolate, acute, mucronate or aristate (the awn up to ½ as long as lemma), 7-nerved, glabrous. Paleas lanceolate, about as long as lemmas, acute, 3-nerved, glabrous. Flowers imperfect. Stamens 6; filaments slender, very short; anthers linear, one theca usually slightly but distinctly longer than the other, connective not prolonged. Ovaries slenderly ellipsoid, obtuse, apiculate, stipitate, glossy; styles glabrous proximally, aspergilliform distally; stigmas 2, about as long as styles, aspergilliform throughout, exserted before anthers. Achene loosely clasped by persistent palea and lemma, ellipsoid, obtuse, apiculate, contracted abruptly to a slender stipe, the surface glossy. Base chromosome number 12. TYPE SPECIES: *Z. microstachya* (Nees) Döll & Ascherson ex Döll (*Zizania microstachya* Nees), the only species included by Döll. (Name from resemblance to *Zizania*.)—GIANT CUTGRASS, SOUTHERN WILD-RICE, MARSH-MILLET.

A genus of five species (Quarín) of tropical and warm-temperate regions of the New World. *Zizaniopsis* is most closely related to *Luziola,* despite its similarity in habit to *Zizania* (Terrell & Robinson). Both genera have achenes, not caryopses, and the base chromosome number 12. The genus has never been revised. Its distinction from *Luziola* is not entirely satisfactory. While most species of *Luziola* have separate staminate and carpellate inflorescences, the only species of *Luziola* sect. CARYOCHLOA (Trin.) Hackel has both mixed in the same inflorescence, as in *Zizaniopsis.* Further study is needed to clarify generic circumscriptions in subtribe Luziolinae.

The single southeastern species, *Zizaniopsis miliacea* (Michx.) Döll, giant cutgrass, water millet, southern wild-rice, $2n = 24$, occurs from eastern Maryland southward and westward along the Coastal Plain to southeastern Oklahoma and Texas, and north along the Mississippi River to western Kentucky and southeastern Missouri. It is also known from western Mexico (McVaugh). It grows in brackish and fresh-water marshes, forming monocultures that provide shelter for waterfowl but are a poor source of food. The total productivity of cutgrass stands is about 1.3 times that of similar grass-dominated vegetation types. The leaf litter is an important contribution to the detrital base of the estuarine ecosystem.

The remaining four species occur in the lowlands of South America. *Zizaniopsis Killipii* Swallen, the only annual species, is known from northwestern

Colombia; *Z. microstachya* (Nees) Döll grows in eastern Brazil; *Z. bonariensis* (Balansa & Poitrasson) Spegaz. occurs in southern Brazil, northern Argentina, and Uruguay; and *Z. villanensis* Quarín, $2n = 24$, espadaña, is endemic to northern Argentina.

Zizaniopsis miliacea is a weed in some parts of the Southeast, where it clogs irrigation ditches and canals (Tarver *et al.*). *Zizaniopsis bonariensis* is a minor weed in temperate South America (Holm *et al.*). The young rhizomes and shoots of *Z. miliacea* can be cooked and eaten as a vegetable (Fernald & Kinsey).

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Under subfamily references see BENTHAM (1883); CLAYTON & RENVOIZE; FERNALD & KINSEY; GODFREY & WOOTEN; GOULD & SHAW; HOLM *et al.*; MCVAUGH; TARVER *et al.*; TERRELL & ROBINSON; and WUNDERLIN.

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8. **Luziola** A. L. de Jussieu [Gen. Pl. 33. 1789] ex J. F. Gmelin, Syst. Nat. ed. 13. **2:** 637. 1791.

Small to medium-sized, monoecious perennials of damp soils or shallow ponds and slow streams (sometimes mostly submersed). Rhizomes soft, producing 1 to several stems per node. Stems branched, slender and erect in terrestrial plants, flexuous in submersed ones; nodes when submersed bearing roots, these with chlorenchymatous cortex. Leaves many, the uppermost floating at water's surface in submersed plants; sheaths shorter than the blades, scabrous, sometimes with transverse veinlets; ligules broadly ovoid, hyaline, basally hispid; blades narrowly lanceolate, barely auriculate, adaxial surface prickly, abaxial smooth. Inflorescences terminal and axillary, small, paniculate, the staminate panicles narrow, terminal, the carpellate ones narrow at anthesis, broadening as the branches spread with maturity; branches glabrous; nodes pilose or glabrous. Spikelets 1-flowered, ovoid to oblong-lanceolate, disarticulating at base of lemma. Glumes lacking. Lemma lanceolate, membranaceous to hyaline, 7- [to 10-]nerved. Palea lance-linear, membranaceous to hyaline, weakly 3- to 7-nerved. Flowers imperfect. Stamens 6; filaments slender; anthers linear, apex of connectives not prolonged. Ovaries ellipsoid; styles glandular; stigmas 2, about as long as styles, aspergilliform, exserted before anther dehiscence. Achene ellipsoid, strongly flattened, apiculate, cuneate at base, loosely surrounded by the persistent lemma and palea. Base chromosome number 12. (*Hydrochloa* Beauv.) TYPE SPECIES: *L. peruviana* J. F. Gmelin, the only species included by Gmelin. (Name a variation of *Luzula*, a genus of Juncaceae.)

A genus of about 12 species of the warm regions of the New World. Three species of *Luziola* are known from the southeastern United States. The others

are chiefly South American, although several extend north to the West Indies and Mexico. The only widespread southeastern species is *L. fluitans* (Michx.) Terrell & H. E. Robinson (*Hydrochloa carolinensis* Beauv., *H. fluitans* Michx.), southern water-grass, which grows in ponds and backwaters of the Coastal Plain from North Carolina (Perquimans County) south to central Florida, and west to eastern Texas. Populations in the United States and eastern Mexico are var. *fluitans,* while those in the uplands of western Mexico are var. *Oconnorii* (Guzmán M.) G. Tucker,[11] which differs in having longer and wider leaf blades, longer spikelets, and longer anthers (Guzmán M.). The differences in dimensions suggest that it may be a tetraploid derivative of the typical variety, but no chromosomal data are available (McVaugh).

Two other species are known in the Southeast from a few collections, although both are more plentiful in the tropics. *Luziola bahiensis* (Steudel) Hitchc. (*L. alabamensis* Chapman) (spikelets oblong-lanceolate; achenes longitudinally striate), $2n = 24$, is known in the United States only from southern Alabama (Conecuh and Mobile counties) and southern Mississippi (Forrest County). *Luziola peruviana* J. F. Gmelin (spikelets ovoid; achenes smooth) is known from western Florida (*fide* Swallen, but not mentioned by Clewell) and from southern Louisiana (Plaquemines Parish).

Most species of this genus grow in damp soils, while *Luziola fluitans* is a submersed plant of ponds and slow streams. It has been placed in a separate genus, *Hydrochloa.* Terrell & Robinson thought it to be an aquatic species of *Luziola* with reduced inflorescences, and their view is accepted here. Swallen did not comment on the status of *Hydrochloa,* although Pohl & Davidse noted that *L. fluitans* is very similar to *L. fragilis* Swallen, of South America, and that *Hydrochloa* should perhaps be included in *Luziola.* Swallen's synopsis of *Luziola* is the only systematic treatment of the genus. Davidse & Pohl (1972a, 1972b) reported several range extensions. There is need for further studies combining field work with extensive herbarium investigations to provide complete descriptions of the species and to confirm the status of *Hydrochloa.*

Chromosome numbers have been reported for several species. *Luziola Pittieri* Luces, $2n = 24$ (Davidse & Pohl, 1972a), and *L. fragilis* Swallen, $2n = 24$ (Pohl & Davidse), are diploids ($x = 12$) like *L. fluitans. Luziola Spruceana* Döll, $2n = 48$ (Davidse & Pohl, 1972a), is apparently tetraploid.

Arber (1928) made a detailed study of the vascularization of the inflorescences and spikelets of *Luziola Spruceana.* She noted that the carpellate florets had six diminutive filaments subtending the ovary, and that the staminate florets had a reduced gynoecium, features overlooked by both Bentham (1883) and Hackel. The six staminal rudiments are clearly not lodicules, two of which are present in both carpellate and staminate florets. Schuster, however, did not detect such reduced gynoecia or stamens in a similar study of *L. peruviana.* Anatomical studies of other species of *Luziola* may turn up interesting details concerning the evolution of monoecy.

Luziola fluitans is economically significant in our area, especially in Florida.

[11] **Luziola fluitans** (Michx.) Terrell & H. Robinson var. **Oconnorii** (Guzmán M.) G. Tucker, comb. nov., based on *Hydrochloa carolinensis* var. *Oconnorii* Guzmán M., Phytologia **48:** 77. 1981, as "*oconneri.*" (Named for Peter O'Connor.)

Its seeds and leaves are a valuable food source for waterfowl. The plants may form dense, matlike populations that interfere with recreational fishing and provide breeding grounds for mosquitoes. The species is able to tolerate prolonged periods of low water ("drawdowns") and is the most difficult aquatic grass species to control with present technology (Tarver *et al.*).

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A NEW SPECIES OF DEGENERIA (DEGENERIACEAE) FROM THE FIJI ARCHIPELAGO

JOHN M. MILLER[1]

The Degeneriaceae have long been of interest to plant systematists, biogeographers, and paleobotanists as "living fossil" magnoliid trees. Recent collections of flowering material from the island of Vanua Levu, in the Fiji Archipelago, South Pacific Ocean, reveal extraordinary departures from the floral morphology of *Degeneria vitiensis*. Self-perpetuating populations of *Degeneria* that bear striking pinkish, rose, and magenta flowers, and fruits half as large as those of *D. vitiensis*, are recognized as a new species of *Degeneria*.

Historically regarded as monotypic, the family Degeneriaceae has long been of interest as a possible "living fossil" group within the angiosperms (Takhtajan, 1969). The only known species at that time was *Degeneria vitiensis* I. Bailey & A. C. Smith, described in 1942. This peculiar plant has been a focus of study by plant morphologists, anatomists, systematists, phylogenists, paleobotanists, and biogeographers in their attempts to understand the origin and history of flowering plants.

The Degeneriaceae combine a number of primitive features that have sparked considerable debate (Thorne, 1974; Cronquist, 1981), including carpels believed to be unsealed, whorled perianths, laminar microsporophylls, multilacunar nodal anatomy, anasulcate pollen, and polycotyledony (Bailey & Swamy, 1951; Takhtajan, 1954, 1969; Dahl & Rowley, 1965; Takhtajan & Meier, 1976; Endress, 1984). Until now, the monotypic *Degeneria vitiensis* has been thought to exhibit only modest variation in floral morphology and coloration (Smith, 1981).

During the course of my studies, flowering material has been collected from the island of Vanua Levu for the first time in January (*J. M. Miller 1075, 1084*). Earlier collections that I have studied from the Wainunu River catchment on this island (*A. C. Smith 1754, DA 15773*) and from trees collected on the island of Taveuni (*A. C. Smith 8200, DA 16937*) are sterile or have only buds or fruits. Therefore, important floral differences with *Degeneria vitiensis* were not seen by Professor Smith or collectors associated with the Fiji Department of Agriculture. This is understandable in view of the seasonality of flowering and the relative inaccessibility of the flowers, which generally occur high in the canopy (Smith, 1981).

The primary purpose of this paper is to describe these heretofore-unknown

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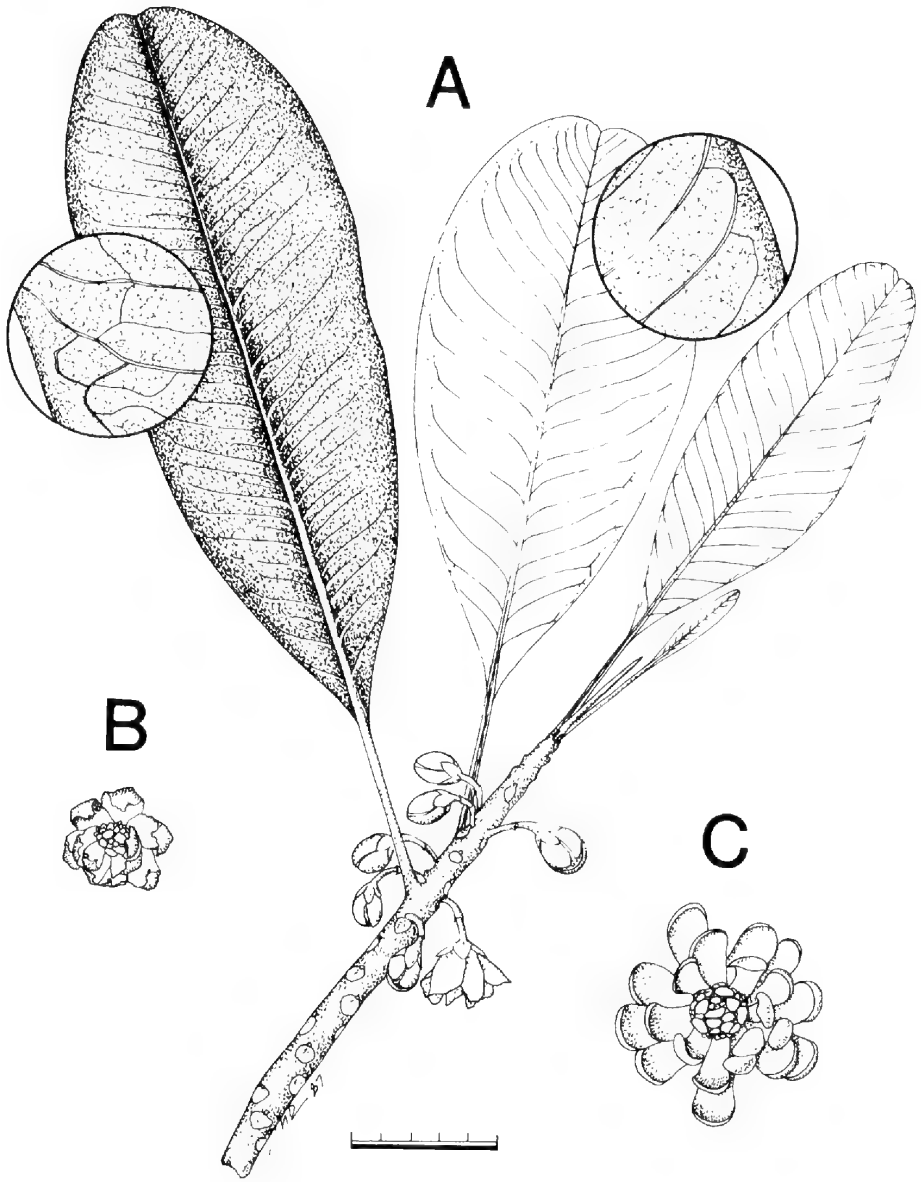


FIGURE 1. *Degeneria roseiflora* and *D. vitiensis*. A, B, *D. roseiflora* (*J. M. Miller 1075*): A, flowering branchlet and leaves; B, detached flower. C, *D. vitiensis* (*J. M. Miller 975*, vic. of Naitaradamu, Viti Levu, RSA), flower. Scale bar = 5 cm.

floral differences of the self-perpetuating *Degeneria* populations on the island of Vanua Levu. A fuller account of past literature, coupled with studies on the morphology, biogeography, and basic biology of *Degeneria*, will appear in a separate work.

NEW SPECIES

Degeneria roseiflora J. M. Miller, sp. nov. FIGURE 1A, B.

A Degeneria vitiense in cortice fulva vel cinnamomea floribus et petalis parvioribus petalis roseis vel purpureis staminodiis 5–11 apice purpureis microsporophyllis atropurpureis differt.

Trees up to 30 m in height, with tan to cinnamon-colored bark; vegetative parts otherwise as in *Degeneria vitiensis*. Flowers 20–40 mm in diameter, pinkish white to rose to magenta, with fragrance similar to that of musty rose. Sepals 3, 5–6 mm long. Outer petals pinkish to magenta; inner ones in several whorls, 16–24 × 5–12 mm, pinkish white to magenta. Microsporophylls purple, 7 × 2 mm. Staminodes 5 to 11, in 2 whorls, 8 × 2 mm, purple distally. Fruits kidney shaped, less than 6 cm long, bearing orange or reddish seeds.

TYPE. Fiji, Vanua Levu, Macuata Province, central spine of island between catchments of Wailevu and Dreketi rivers, *J. M. Miller 1075* (holotype, A; isotypes, K, NSW, RSA, SUVA).

ADDITIONAL SPECIMENS EXAMINED. **Fiji.** VANUA LEVU. Bua Province: lower Wainunu R. valley, *A. C. Smith 1754* (SUVA); N of Cogea, Wainunu R., *DA 15773* (SUVA). Cakaudrove Province: Nacewa Peninsula, in drainage of Navonu R., *J. M. Miller 1158* (SUVA), *1161* (SUVA); Wailevu distr., drainage of Navilagolago R., *J. M. Miller 1167* (SUVA); between Keka and Vatuvonu, *J. M. Miller 1200* (RSA); Yanawai R. region, 41 km W of Transinsular Hwy., *J. M. Miller 1188* (RSA, SUVA). Macuata Province: slopes of Delaikoro, *J. M. Miller 1084* (RSA, SUVA). TAVEUNI: slopes of Mt. Manuka, E of Wairiki, *A. C. Smith 8200* (SUVA); Qacavulo Estate, *DA 16937* (SUVA).

The Vanua Levuan name for *Degeneria roseiflora* is "karawa." The species is a class-III noncommercial timber tree frequently cleared for cattle schemes and as a source of cooking fuel, but individuals seem to persist in logged forest even after preplantation thinning and restocking with *Swietenia* and *Cordia*.

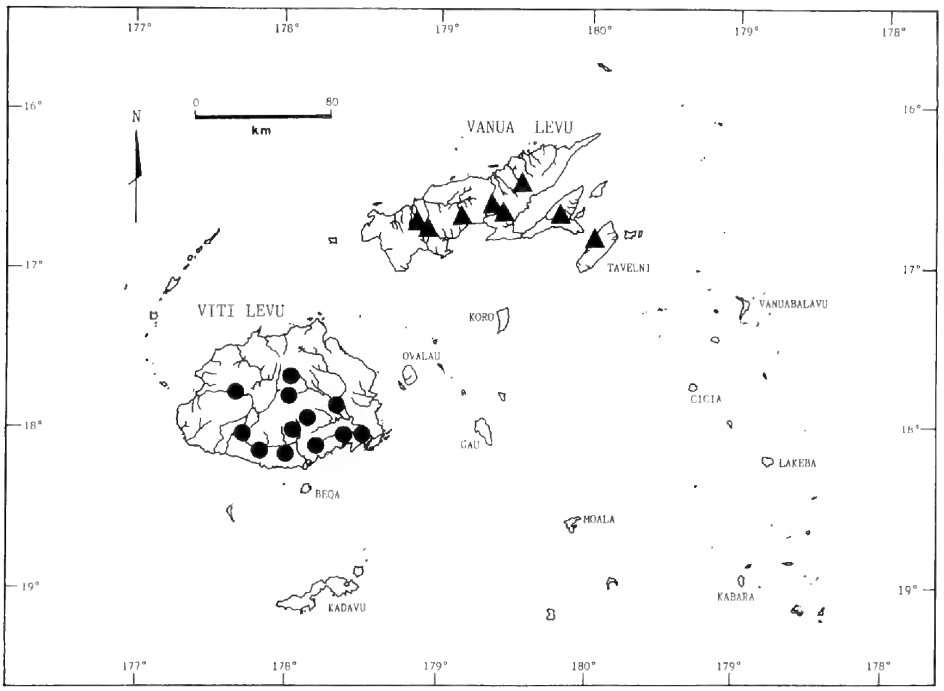
KEY TO THE SPECIES OF DEGENERIA

Flowers pinkish white to magenta, 20–40 mm in diameter; microsporophylls rich purple; staminodes 5 to 11, in 2 whorls, distally purple; fragrance of musty *Rosa*; fruits generally less than 6 cm long; bark cinnamon-brown or light gray; Vanua Levu and Taveuni. ..... *D. roseiflora.*

Flowers white to light beige, 40–80 mm in diameter; microsporophylls white to beige, rarely purple; staminodes 9 to 15, in 2 or more whorls, distally brown and coated with brilliant yellow exudate (rarely streaked with pink); fragrance of *Cananga odorata*; fruits generally 6–12 cm long; bark dark gray to black; mostly on Viti Levu. ..... *D. vitiensis.*

DISCUSSION

The type species of the family, *Degeneria vitiensis*, was described from *Degener 14537* (holotype, A), collected near Nadarivatu, in the interior of the



MAP 1. Distribution of *Degeneria* in Fiji Archipelago: dots = *D. vitiensis,* triangles = *D. roseiflora.*

largest island, Viti Levu. This specimen has flowers with a well-documented morphology (Bailey & Smith, 1942; Smith, 1949). The type material is similar to other flowering collections from Viti Levu, including those illustrated in Smith (1981, *fig. 1*). It cannot be confused with *D. roseiflora,* as the flowers of *D. vitiensis* (see FIGURE 1C) are up to twice as large (see FIGURE 1A, B) and are white to light beige. *Degeneria vitiensis* has beige (rarely purple) microsporophylls, and two or more whorls of staminodes that are sometimes streaked with (rarely wholly) pink and are coated with bright yellow exudate. On the other hand, microsporophylls of *D. roseiflora* are rich purple; the staminodes have purple tissue and are not coated with yellow exudate. The bark of *D. vitiensis* is black or dark gray, while that of *D. roseiflora* is generally cinnamon-brown but sometimes light gray. The fruits of *D. vitiensis* are generally much larger than those of *D. roseiflora* (6–12 vs. 6 cm or less in length). *Degeneria vitiensis* flowers October to January; *D. roseiflora,* January to March.

So far as is presently known, *Degeneria roseiflora* occurs on the islands of Vanua Levu and Taveuni (see MAP 1). It is a common species with a patchy distribution on the central spine and plateau of Vanua Levu, being generally more abundant on the older volcanic formations in the zone of tropical forest.

Many other genera of Fijian plants contain distinct but related endemic species, of which one occurs on Viti Levu and the other on Vanua Levu; examples include *Polyalthia angustifolia* A. C. Smith/*P. amoena* A. C. Smith and *Cyathocalyx insularis* A. C. Smith/*C. stenopetalus* A. C. Smith (Annonaceae), *Elatostema filicoides* (Seemann) Schröter/*E. comptonioides* A. C. Smith

(Urticaceae), *Elaeocarpus subcapitatus* Gillespie/*E. laurifolius* A. Gray (Elaeocarpaceae), *Melochia mollipila* A. C. Smith/*M. grayana* A. C. Smith (Sterculiaceae), *Glochidion gillespiei* Croizat/*G. multilobum* A. C. Smith, and *Macaranga magna* Turrill/*M. membranacea* Muell. Arg. (Euphorbiaceae). In *Endospermum* (Euphorbiaceae) a completely distinct species (*E. robbieanum* A. C. Smith) occurs only on Vanua Levu, being restricted to central and western parts of the island, while the principally Viti Levuan *E. macrophyllum* (Muell. Arg.) Pax & Hoffm. is sparingly sympatric (Smith, 1981). Other examples are well documented (Smith, 1979, 1981, 1985). The two islands are separated by water hundreds of meters deep and may never have been connected, even during the glacial maxima when mean sea levels were much lower than at present. I presume that speciation took place on Vanua Levu among early colonizers of *Degeneria vitiensis,* possibly dispersed over a relatively short distance there from Viti Levu or another, now submerged source, by endemic pigeons, parrots, or fruit doves that eat the seeds. Alternatively, the floral and fruit reductions seen in *D. roseiflora* may be due to long-term reproductive isolation and neotenic evolution, which could have occurred as a result of the original pollinator not being dispersed to the island of Vanua Levu with the colonizing populations of *Degeneria.*

The oldest rocks on Vanua Levu have been dated at 7.5 million years (Rodda & Kroenke, 1984). If this radiometric age is any indication of the actual age of the island, then relatively recent dispersal and subsequent speciation is a possibility. Alternatively, *Degeneria roseiflora* may be the harmonic remnant of a more widespread and ancient species of *Degeneria* that existed in forests of the now-fragmented Vitiaz Island Arc. According to Rodda & Kroenke (1984), portions of the Vanuatuan and Fijian archipelagoes were once part of the Vitiaz Island Arc that existed during the Miocene epoch. If this is true, then relictual *Degeneria* may possibly occur on the older rock formations of Vanuatu, provided that these islands were not ravaged by cataclysmic volcanism in the past.

ACKNOWLEDGMENTS

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STAR MAGNOLIA (MAGNOLIA TOMENTOSA)—AN INDIGENOUS JAPANESE PLANT

KUNIHIKO UEDA[1]

Magnolia tomentosa Thunb. has often been treated as a garden plant originating from *M. praecocissima* Koidz., but it is an endemic Japanese species. Here the natural distribution area and the habitat of *M. tomentosa* are detailed to help clarify its status.

Most Japanese species of *Magnolia* L. have been cultivated as ornamental trees throughout the temperate world and have been described repeatedly in monographic and revisionary treatments (e.g., Rehder & Wilson, 1913; Millais, 1927; Johnstone, 1955; Spongberg, 1976; Treseder, 1978; see also Ueda, 1985, 1986a). The descriptions of the Japanese taxa, however, have almost never been based on field surveys. This has led to various misunderstandings, such as the one pointed out by Ueda (1980) concerning *M. sieboldii* K. Koch subsp. *japonica* Ueda.

Magnolia tomentosa Thunb., star magnolia, which has more commonly been treated as *M. stellata* (Sieb. & Zucc.) Maxim. (see Ueda, 1986b), is an endemic species in Japan. Nevertheless, many botanists have doubted the natural occurrence of this species in Japan and have treated it as being of Chinese origin, as from an unknown locality, or as an ornamental cultivated in gardens.

Iinuma (1865) and Ito (1881), Japanese herbalists who lived within the distribution area of *Magnolia tomentosa,* were the first to mention its natural occurrence. However, later Japanese botanists did not refer to them, and it was not until the mid 1940's that *M. tomentosa* was again recognized as a naturally occurring member of the Japanese flora (Makino, 1947; Inami, 1959). On the other hand, Western botanists (including Maximowicz, 1872; Hooker, 1878; Rehder & Wilson, 1913; Millais, 1927) commonly treated the species as being of Japanese origin until Blackburn (1955) doubted its natural occurrence, although Sargent (1894, p. 2) had pointed out that, "A number of shrubs, familiar in western gardens, and *Magnolia stellata*—usually supposed to be Japanese from the fact that they were first known to Europeans in Japan, or were first sent from that country—are also Chinese or Corean, and in Japan are only found in gardens." Miquel (1866) also suspected the species to be of Chinese origin. The specimens collected by Europeans and cited in the literature, including those of Miquel, were all from plants in cultivation in Japan. Based on our current knowledge of the distribution of the species, it is probable that only the specimens collected by the Japanese collectors Keisuke (= K. Ito; cited

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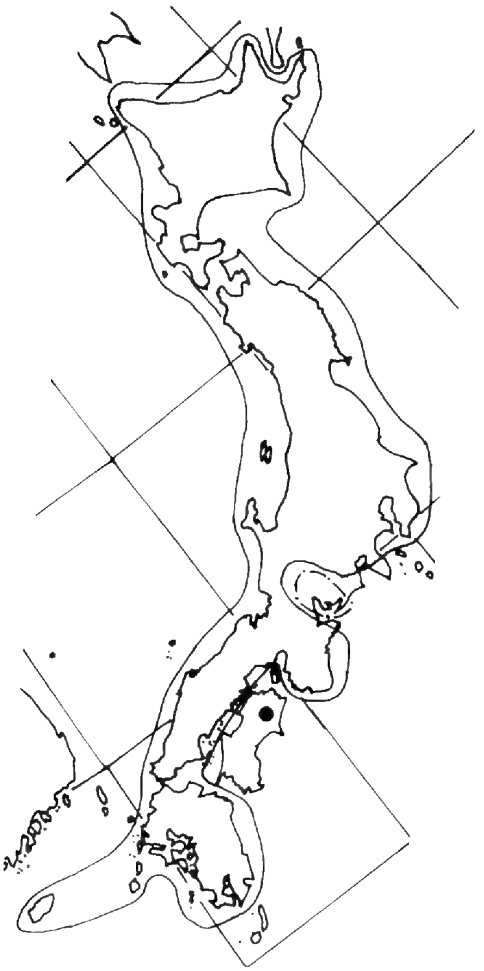
in Miquel, 1866, as "Keiske") and Chônosuke (in Maximowicz, 1872, as "Tschonoski") were from wild collections. Johnstone (1955) correctly cited wild localities, probably from his communication with Makino. Recently, a few horticulturists (Laar, 1981; Jonsson, 1986) briefly reported the natural occurrence of *M. tomentosa* in Japan based on their own field surveys.

Although the star magnolia has generally been considered a distinct species, Blackburn (1954, 1955, 1957) and Spongberg (1976) considered it to be a cultivar or a garden derivative of *Magnolia praecocissima* Koidz. (= *M. kobus* auct. non DC.; see Ueda, 1986b), for they believed that *M. tomentosa* was not a wild species. Inami (1959) published a reply to Blackburn (1955); in support of the natural origin of the species, he referred to the geology, topography, and local floristic characteristics of the distribution area, as well as to the habitat of the plants. He produced a detailed distribution map but did not cite any herbarium specimens. Authors on *Magnolia* (e.g., Treseder, 1972, 1978), however, were strongly influenced by Blackburn and were seriously confused (see, for example, Treseder, 1978, pp. 113, 118). They cited Inami (1959) but did not refer to the details in his paper, instead obtaining information from Japanese correspondents who believed the star magnolia to be a non-Japanese species. They therefore believed the species to be found only in cultivation in gardens and therefore to be of garden origin.

Blackburn (1957) stated that the Japanese name of star magnolia, "shidekobushi," means "kobushi of homes." This interpretation was accepted by Treseder (1978). In Japan, however, it is generally thought that "shidekobushi" means "zigzag-petaled kobushi." "Shide" is Japanese for a cluster of zigzag-folded papers used in Shinto ceremonies; these resemble the petals of *Magnolia tomentosa*. "Kobushi," as is well known in Japan, is the Japanese name of *M. praecocissima*.

In addition, Blackburn (1957) mentioned that many typical plants of *Magnolia praecocissima* were obtained from among seedlings of *M. tomentosa*, and only a small proportion of star magnolia seedlings produced star magnolia. In my experience, though, all of the seedlings of wild star magnolia have produced star magnolia (see also Treseder, 1978).

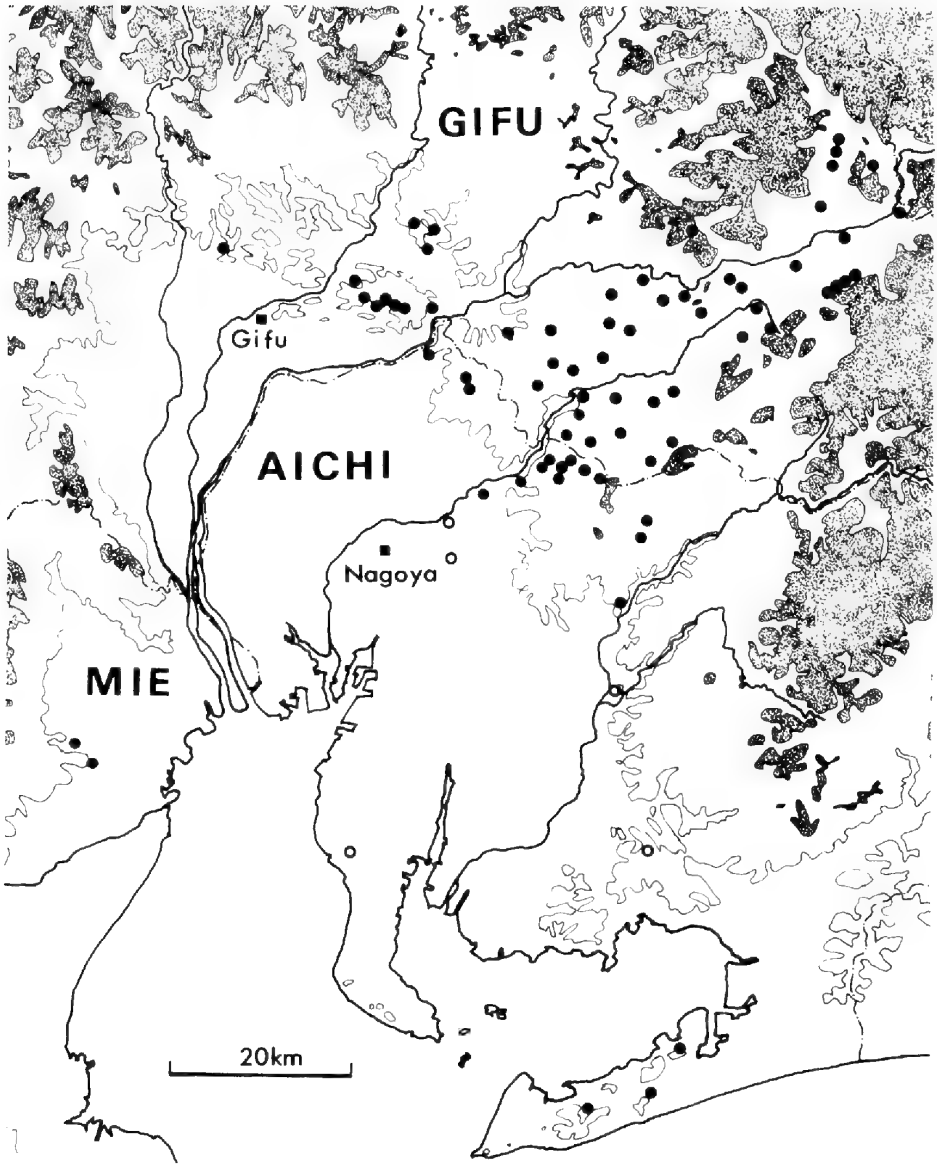
Drawing from Inami (1959) and my own field research, we can summarize the habitat of *Magnolia tomentosa* as follows. As is seen in MAP 1, *M. praecocissima* and *M. tomentosa* clearly show an allopatric distribution pattern. It is noteworthy that no plants of *M. praecocissima* have been reported from Shikoku, where *M. pseudokobus* Abe & Akas. (a species closely related to *M. praecocissima*) occurs (Ueda, 1986c). MAP 2 shows that *M. tomentosa* occurs in hill regions, including Pleistocene to Tertiary uplands and river terraces, in the western part of the Tôkai district from (40–)100 to 500(–650) m altitude. It has never been reported either from Holocene alluvial plains around Nagoya city, or from the mountainous regions shown in MAP 2 (shaded areas). A seed fossil has been recorded from an upper Pliocene *Metasequoia* bed (Miki, 1948). The distribution area is generally warm-temperate, with evergreen forests, while above 600 m alt. the climate is cool-temperate and deciduous forests develop (Inami, 1960). *Magnolia tomentosa* grows without exception along geomorphological boundaries: between the slope of a terrace or hill and a valley plain;



MAP 1. Distributions of *Magnolia praecocissima* (solid line), *M. tomentosa* (broken line; area enlarged in Map 2), and *M. pseudokobus* (dot) based on herbarium specimens and reliable information. Note that distribution areas of these 3 closely allied species do not overlap.

on the gentle slope of a terrace or hill near a river, stream, or pond; in a river bed or a gorge; or along a bank between a river and a terrace. It always occurs in sunny places with a slight water flow, where the ground is usually covered with *Sphagnum* L. (It does not grow in marshes or swamps without water flow.) *Magnolia tomentosa* usually grows rather densely in these habitats, although individual populations are not so large and are rather far from each other. The plants usually reach the canopy layer of thickets 2–10(–15) m tall. Seedlings and immature individuals are few, although each tree produces many layering shoots and sprouts. Naruse and Goto (1985, 1986) reported that the star magnolia thickets fundamentally belong to the *Illici-Alnetum japonicae* association.

It has been well known that in the western Tôkai district where the star magnolia occurs, there are many locally endemic or semiendemic taxa such as *Eriocaulon nudicuspe* Maxim., *Eulalia speciosa* (Debeaux) O. Kuntze, *Acer*



MAP 2. Distribution of *Magnolia tomentosa,* a local endemic species of western Tôkai district, Japan. (Dots, localities based on herbarium specimens; open circles, those based on geographically selected, reliable information; contour lines, 100 m in elevation; shaded areas, over 600 m alt.; broken lines, prefecture borders.)

pycnanthum K. Koch, and *Chionanthus retusus* Lindley & Paxton (Inami, 1956, 1959, 1960). Like *Magnolia tomentosa,* most of these taxa grow in wet to marshy places.

With the evidence at hand, it can now confidently be said that *Magnolia tomentosa* is an indigenous member of the Japanese flora. The plants of wild occurrence are definitely not escapes from cultivation that have become established in a natural habitat.

RECORDS OF OCCURRENCE OF MAGNOLIA TOMENTOSA AS A WILD PLANT

The area of natural distribution is precisely detailed here to help clarify the status of *Magnolia tomentosa*. To record the distribution, comprehensive field surveys were made and specimens at Gifu-higashi High School, Gifu University, KAG, KANA, KYO, MAK, OSA, SHIN, TI, TNS, TOFO, and TUS were examined.

The following are all records of spontaneously occurring individuals and document the natural range of *Magnolia tomentosa*. All specimens are from Mie, Gifu, and Aichi[2] prefectures in central Honshu, Japan (see MAP 2).[3]

SPECIMENS EXAMINED. **Japan. Honshû.** GIFU PREFECTURE. Ena-gun, Sakasita-cho: Nakasode, *Kimura s.n.*, 4/82 (GHHS[4]). Hukuoka-cho: Kichimizawa, Takayama, 310 m alt., *Ishida s.n.*, 1982 (GHHS), *Naruse s.n.*, 4/1/87 (KYO, OSA); Chohne, 340 m alt., *Ishida s.n.*, 1982 (GHHS), *Naruse s.n.*, 4/1/87 (KYO, OSA); Shimono, 380 m alt., *Ishida s.n.*, 4/82 (GHHS), *Naruse s.n.*, 4/1/87 (KYO), *Ueda & Kosuge 1035* (KYO), *Ueda et al. 1001* (KYO). Yamaoka-cho: *Hosono & Tanase s.n.*, 4/6/82 (GHHS). Nakatsugawa-shi: Nakagaito, *Kimura s.n.*, 4/82 (GHHS); N foot of Hoko-yama, E of Nakagaito, Sakamoto, 550 m alt., *S. Fujii 2283* (KYO, OSA); Nishiyama, 340 m alt., *Naruse s.n.*, 4/1/87 (KYO, OSA); Tsudoi, *Kimura s.n.*, 4/82 (GHHS); Ôkute, Ochiai, 320 m alt., *Ueda & Kosuge 1036* (KYO), *Ueda et al. 1002* (KYO), *1003* (KYO), *1004* (KYO), *1005* (KYO), *1006* (KYO). Ena-shi: near Gomoh, Iiji-cho, 650 m alt., *Y. Itô s.n.*, 4/5/81 (GHHS), *Naruse s.n.*, 4/24/83 (GHHS), *H. Takahashi et al. 5226* (KYO), *Ueda & Kosuge 1037* (KYO); Takasa, between Sasaragi and Noi, 400 m alt., *Kuwashima 22353* (OSA); Takeori, Takenami-cho, *Hibino & Kumazaki s.n.*, 4/6/82 (GHHS); Dodogane, *Kimura s.n.*, 4/82 (GHHS); Nakagiri, Higashino, *Kimura s.n.*, 4/82 (GHHS); Shirasaka, Higashino, 380 m alt., *Naruse s.n.*, 4/1/87 (KYO, OSA). Mizunami-shi: between Hosokute and Ôkute, 400 m alt., *Murata et al. 339* (KYO); Ôkute, Ôkute-cho, *Hibino & Kumazaki s.n.*, 4/6/82 (GHHS); Kamado-cho, *Ogata 8902* (TOFO); Ryûgin-fall, Kamado-cho, 260 m alt., *Matsumoto 11011* (OSA); Ryûgin Lake, near Kamado-cho, *Hirano s.n.*, 7/26/75 (OSA (as *OSA18760*)); Rondochi, Kamado-cho, *Hosono & Tanase s.n.*, 4/6/82 (GHHS); Takohdo, Hiyoshi-cho, *Niwa s.n.*, 1981 (GHHS); Hukazawa, Hiyoshi-cho, *Hibino & Kumazaki s.n.*, 4/6/82 (GHHS); Yamada-cho, *Kajita & Inoue s.n.*, 4/6/82 (GHHS); near Matsuno Lake, Kigan, 340 m alt., *Ueda & Naruse 1010* (KYO). Kani-gun, Mitake-cho: Kigan spa, 400 m alt., *Emura s.n.*, 4/9/72 (TI); Obara, *Mizuno s.n.*, 4/30/82 (GHHS); Kukuri, *Kuroda s.n.*, 4/6/82 (GHHS). Kani-shi: Sakuraga-oka, *Tokoro s.n.*, 4/30/82 (GHHS); Yahazama, *Naruse s.n.*, 4/30/82 (GHHS). Kamo-gun, Tomika-cho: vic. of Kawakomaki, 100 m alt., *Naruse s.n.*, 4/6/82 (GHHS, KYO), *Ueda et al. 1341* (KYO); Nagamine-zaka, 90 m alt., *Naruse s.n.*, 4/6/82 (GHHS, KYO), *Ueda et al. 1340* (KYO). Seki-shi: Simo-hazama, *Naruse s.n.*, 4/5/81 (GHHS, KYO); Kakinoki Pass, between Shimouchi and Shizuno, 150 m alt., *Matsuda s.n.*, 4/5/81 (GHHS), *Ueda et al. 1343* (KYO); Kosaka, Shizuno, *Naruse s.n.*, 4/6/82 (GHHS). Kagamihara-shi: Ichitatsu, Sue, 100 m alt., *Naruse s.n.*, 4/2/81 (GHHS), *Ueda et al. 202* (KYO), *682* (KYO); Sue 3, 150 m alt., *Naruse s.n.*, 4/5/81 (GHHS, KYO), *Ueda et al. 673* (KYO); vic. of Kaneba, 100 m alt., *H. Takahashi 6830* (KYO); en route from Ogase-ike to Mitsu-ike, Sue, 100–120 m alt., *Ueda et al. 194*

[2]There are a few reports of *Magnolia tomentosa* from Nagano Prefecture (Shinano Province) and Kobe, Hyogo Prefecture (Settsu Province) but there are no specimens to support these claims.

[3]One of the reasons why recent Western botanists did not believe in the native occurrence of *Magnolia tomentosa* is that the reported localities did not appear to be constant. The following names of administrative units in Japan have been cited in recent Western literature on the star magnolia, but all indicate the same general area (asterisks indicate names used during the Edo period): southern Honshû; central Honshû; western Tôkaidô district*; western Tôkai district; southern Chûbu district; Owari, Mikawa and Mino provinces*; Aichi and Gifu prefectures.

[4]Tentative abbreviation for Gifu-higashi High School.

(KYO), *203* (KYO); Mitsu-ike, Sue, *Naruse s.n.,* 4/5/81 (GHHS); E of Mitsu-ike, Sue, *Ueda & Kosuge 1039* (KYO); Sue 2, *Naruse s.n.,* 4/2/82 (GHHS); near Kanbora-ike, *Naruse s.n.,* 4/5/82 (GHHS). Gifu-shi: Norimatsu, 100 m alt., *Naruse s.n.,* 7/9/82 (GHHS), *s.n.,* 11/9/82 (GHHS), *H. Takahashi 6981* (KYO), *6982* (KYO), *Ueda et al. 1344* (KYO); vic. of Ôboradachi, 100 m alt., *Naruse s.n.,* 4/6/82 (GHHS), *s.n.,* 4/28/82 (GHHS), *H. Takahashi 6829* (KYO); *Ueda et al. 1345* (KYO). Toki-shi: Tsumaki-cho, *Kuroda s.n.,* 4/6/82 (GHHS); Turusato-cho, *Kuroda s.n.,* 4/6/82 (GHHS); Kakino Spa, Tsurusato-cho, 460 m alt., *Ueda et al. 1007* (KYO, OSA); Ôgusa, Sogi-cho, *Kajita s.n.,* 4/6/82 (GHHS); Kitayama, Hida-cho, *Hosono & Tanase s.n.,* 4/6/82 (GHHS); Dachi-cho, *Kuroda s.n.,* 4/6/82 (GHHS); Tokiguchi, Tokitsu-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS); Ôbora, Tokitsu-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS); Gotomaki, Izumi-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS). Toki-gun, Kasahara-cho: Umedaira, *Kuroda s.n.,* 4/6/82 (GHHS). Tajimi-shi: Ôbata, *Z. Tashiro & Shiota s.n.,* 4/20/33 (KYO, MAK (as *MAK153921*), OSA, TI); Hirano, *Z. Tashiro s.n.,* 4/20/33 (TI, TNS (as *TNS-42374* and *-42375*)); Kokei-cho, *Umemura s.n.,* 6/16/01 (MAK (as *MAK153922*)); Kokeizan-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS); Kitaoka-cho, Nemoto, *Naruse s.n.,* 4/2/83 (GHHS); Ichinokura, *Kuroda s.n.,* 4/6/82 (GHHS); Onada-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS); Yamabuki-cho, *Kato & Niimi s.n.,* 4/6/82 (GHHS). AICHI PREFECTURE. Nishi-kamo-gun, Fujioka-cho: between Kize and Ishidatami, 150 m alt., *Ueda et al. 178* (KYO); between Iino and Arata, 200 m alt., *Ueda & Ito 17* (KYO); same locality, 150 m alt., *Ueda & Ito 111* (KYO), *Ueda et al. 167* (KYO), *663* (KYO). Nishi-kamo-gun, Sanage-cho [Toyota-shi]: Mihune, *Soko s.n.,* 4/1/65 (TNS (as *TNS-293615*)). Higashi-kasugai-gun, Mizuno-mura [Seto-shi: Mizuno-cho], *Inayoshi s.n.,* 1933 (KYO); Mizuno-mura [Kutsukake-goryôrin, Mizuno-cho], *Koidzumi s.n.,* 6/25/33 (KYO); between Johkohji and Kohzohji, *Hara 2568* (TI), *2616* (TI); en route from Kutsukake to Miyagari-ike, Johkohji, 150 m alt., *Ueda & Ito 84* (KYO), *125* (KYO); en route from Johkohji station to Miyagari-ike, 200 m alt., *Ito 670* (KYO); Kutsukake, Johkohji, 150 m alt., *Ito 349* (KYO), *Ueda & Ito 18* (KYO), *Ueda et al. 665* (KYO); near Kutsukake, Johkohji, 180 m alt., *Ueda et al. 184* (KYO), same locality, 150 m alt., *Ueda et al. 667* (KYO); Mt. Johkohji, *Hiroe 12175* (KYO); en route from Hironota to Shimo-handagawa, Shinano, 250 m alt., *Ueda & Ito 16* (KYO), *19* (KYO); Hironota, Shinano, 250 m alt., *Ueda et al. 183* (KYO); Shimo-handagawa, *Kuroda s.n.,* 4/6/82 (GHHS); Kami-handagawa, *Kuroda s.n.,* 4/6/82 (GHHS); Tokyo Univ. Forest, *Inokuma 207* (TOFO); Katakusa-cho, *Kuroda s.n.,* 4/6/82 (GHHS). Inuyama-shi: Nakayashiki, Imai, 150 m alt., *Ueda et al. 670* (KYO); Kurama-dera, Iruka, 150 m alt., *Ueda et al. 668* (KYO); near Kurama-dera, between Iruka and Imai, 150 m alt., *Ueda et al. 191* (KYO), *192* (KYO); Inuyama, *Inami s.n.,* 3/29/56 (TNS (as *TNS-286408*)). Moriyama-shi [Nagoya-shi, Moriyama-ku]: Shidami, *Inami s.n.,* 9/58 (TNS (as *TNS-284250*)). Atsumi-gun, Tawara-cho: Kurokawa, *Kurosaki 7129* (KYO); Zaoh-yama, *Torii s.n.,* 7/12/50 (KYO, TI), *s.n.,* 3/21/53 (KYO, MAK (as *MAK63671*), TI), *s.n.,* 6/12/53 (KYO). Atsumi-cho: Ômu-ishi, near Ikawatsu, 50 m alt., *Ueda & Kosuge 1040* (KYO), *Ueda et al. 154* (KYO), *633* (KYO), *658* (KYO). MIE PREFECTURE. Yokkaichi-shi: along Yagoh R., Sakuracho-nishi, 60 m alt., *Ueda et al. 1008* (KYO, OSA); along Kabake R., between Ranpi and Kawashima-cho, 40 m alt., *Ueda & Kosuge 1041* (KYO), *Ueda et al. 1009* (KYO, OSA).

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CONTENTS OF VOLUME 69, NUMBER 3

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TAXONOMIC REVIEW OF ISODON (LABIATAE)[1]

HSI-WEN LI[2,3]

The genus *Isodon* is reviewed taxonomically on a worldwide basis. Tropical and subtropical Asia have many species, while Africa has only a few. Ninety-six species and ten varieties in three sections and ten series are described; among them thirteen species and eight varieties are new combinations. Several keys and figures are included to aid in identification.

Botanical literature contains two opposite interpretations of the generic limits of *Plectranthus* L'Hér.: the inclusive and the restricted. According to the inclusive concept, *Plectranthus* includes taxa having a calyx with one large upper tooth and four small lower ones (as exhibited by the type species of the genus), as well as those having a calyx with five equal or subequal teeth, or three upper teeth and two lower ones (McKean, 1982). Keng (1978) even included *Coleus* Lour. in the genus and interpreted this group as a *Coleus-Plectranthus* complex. The other concept is more strict: only taxa having a calyx with one upper tooth and four small lower ones are included (Kudo, 1929; Hara, 1972; Li, 1975; Murata, 1975). In *Flora Reipublicae Popularis Sinicae,* Wu and I (1977) followed the restricted concept and recognized *Rabdosia* (Blume) Hassk., *Siphocranion* Kudo, and *Skapanthus* C. Y. Wu & H. W. Li, which some taxonomists include in *Plectranthus.* At the same time, I agreed with Wu in putting *P. macranthus* J. D. Hooker into *Siphocranion.* This opinion, however, has not been accepted by other botanists (Hara, 1972; Murata, 1975; McKean, 1982). In 1985 Hara changed the name of the genus *Rabdosia* to *Isodon* (Bentham) Schrader ex Spach because the latter antedates the former. The obvious taxonomic characters of these allied genera are utilized in the following key (see also FIGURE 1), which can be used to distinguish them.

[1]Type specimens have been seen by the author unless otherwise indicated. A full list of specimens examined in this study is on file in the library of the Arnold Arboretum and Gray Herbarium. The majority are also included in the Index to Exsiccatae at the end of the paper.

[2]Xi-wen Li, when transliterated using the Pinyin system.

[3]Kunming Institute of Botany, Academia Sinica, Kunming, Yunnan, China.

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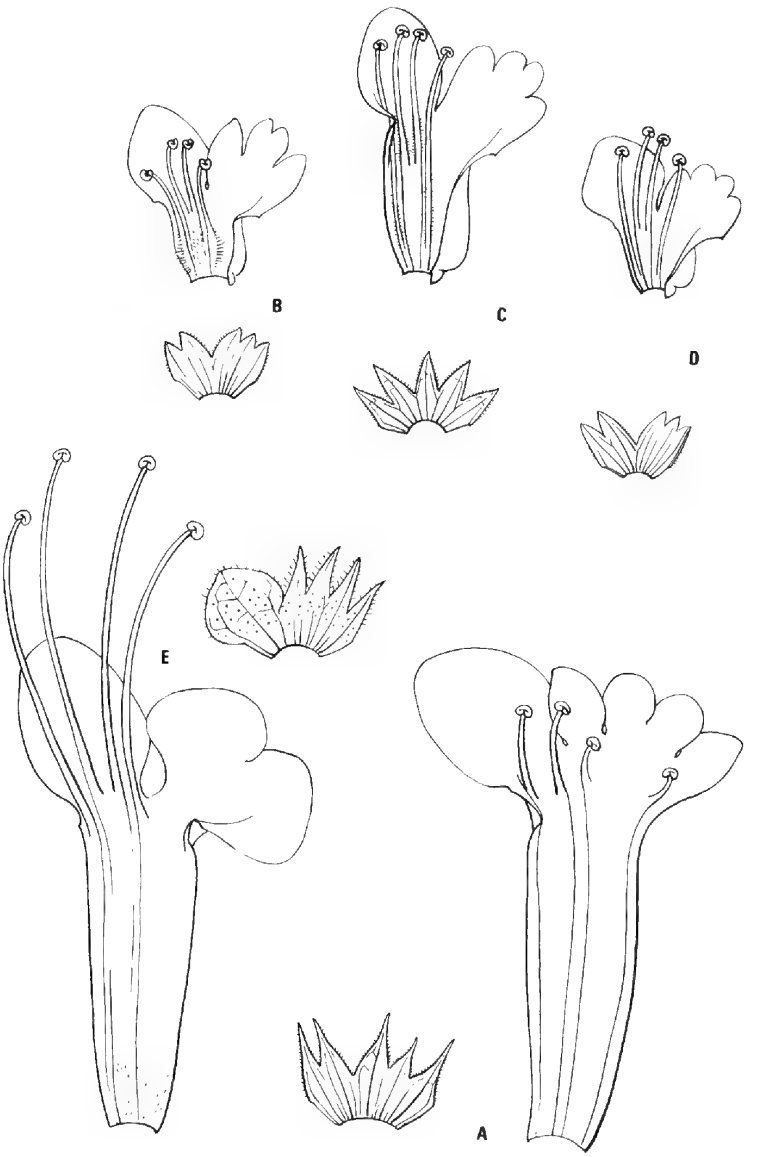

FIGURE 1. Calyces, corollas, and stamens: A, *Siphocranion macranthum* (*W. P. Fang 2804*, PE); B, *Skapanthus oreophilus* (*R. C. Ching 20983*, KUN); C, *Isodon bulleyanus* (*W. S. Liou 51198*, KUN); D, *I. rosthornii* (*W. C. Cheng 6582*, KUN); E, *Plectranthus fruticosus* (*Burchell 6051*, A); all × 3.5. (Drawn by X. L. Zeng.)

1. Flowers with stamens inserted at or near throat of corolla; corolla tube long, straight, neither saccate nor shortly calcarate on upper side above base; calyx 2-lipped (2 species; subtropical regions of China, India, Sikkim, northern Burma, and northern Vietnam). ..... *Siphocranion.*
1. Flowers with stamens inserted on lower part of corolla; corolla tube short or long, declinate or abruptly deflexed, rarely straight, always more or less saccate or shortly calcarate on upper side near base; calyx with 5 equal or subequal teeth or 2-lipped.

2. Calyx with 5 equal or subequal teeth or 2-lipped (in latter case upper lip with 3 teeth and lower one with 2).
   3. Upper lip of corolla limb deeply 3-fid, with middle lobe widened and notched; posterior filaments dilated outside at base (1 species; northwestern Yunnan and southwestern Sichuan). ..... *Skapanthus.*
   3. Upper lip of corolla limb 4-fid; posterior filaments not dilated outside at base (ca. 100 species; tropical and subtropical Asia, few in Africa). ..... *Isodon.*
2. Calyx conspicuously 2-lipped—solitary tooth of upper lip larger than 4 teeth of lower lip (ca. 200 species; tropical and subtropical Africa, southern Asia, few in Philippines and Pacific islands). ..... *Plectranthus.*

Isodon (Bentham) Schrader ex Spach, Hist. Nat. Vég. **9:** 162. 1840; Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 118. 1929; H. Hara, Enum. Spermat. Jap. **1:** 204. 1949, and J. Jap. Bot. **60:** 232. 1985; Farr, Leussink, & Stafleu, Ind. Nom. Gener. **2:** 880. 1979; Codd, Bothalia **15:** 8. 1984. *Plectranthus* L'Hér. sects. *Melissoides* Bentham, *Isodon* Schrader ex Bentham, *Pyramidium* Bentham, and *Amethystoides* Bentham, Labiat. Gen. Spec. 39, 40, 44, 45. 1832, and *in* DC. Prodr. **12:** 55, 61, 62. 1848. *Rabdosia* (Blume) Hassk. Flora **25**(Beibl. 2): 25. 1842; Blake, Contr. Queensland Herb. **9:** 6. 1971; H. Hara, J. Jap. Bot. **47:** 193. 1972, and Enum. Fl. Pl. Nepal **3:** 162. 1982; C. Y. Wu, Fl. Yunnan. **1:** 758. 1977; C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 416. 1977. *Amethystanthus* Nakai, Bot. Mag. Tokyo **48:** 785. 1934. *Homalocheilos* J. K. Morton, J. Linn. Soc., Bot. **58:** 249. *fig. 6.* 1962. *Rabdosiella* Codd, Bothalia **15:** 8. 1984.

Undershrubs, subundershrubs, or perennial herbs; rhizomes always massive and woody. Leaves small to medium-sized, usually petiolate, toothed. Cymes arranged in verticillasters, more or less remote racemes, narrow to open panicles, or rarely dense spikes, (1- to) 3- to many-flowered; lower floral leaves larger, upper ones changed into bracts; bracts and bracteoles small. Flowers usually small, pedicellate. Calyx campanulate, tubular, tubular-campanulate, or ovoid, straight or declinate, often accrescent; limb equally or subequally 5-toothed or 2-lipped (if 2-lipped, upper lip with 3 teeth, lower with 2). Corolla with tube exserted, long or short, declinate or abruptly deflexed, sometimes straight and subequal, always more or less saccate or gibbous and shortly calcarate on upper side near base; limb 2-lipped, the upper lip short, recurved or reflexed, 4-fid, the lower lip concave, boat shaped, entire. Stamens 4, declinate; filament free, edentate, hairy or glabrous; anther cells usually confluent. Disc annulate, subentire or lobed, usually tumid in front; style shortly 2-fid. Nutlets suborbicular or occasionally oblong or ovoid, smooth, granulate, or punctate, glabrous or hairy.

LECTOTYPE SPECIES. *Isodon rugosus* (Wallich) Codd (*Plectranthus rugosus* Wallich).

DISTRIBUTION. Ca. 100 species, mainly in tropical and subtropical Asia, with a few in Africa.

KEY TO THE SECTIONS OF ISODON

1. Fruiting calyces erect, with 5 equal or subequal teeth.
   2. Fruiting calyces tubular or tubular-campanulate to ovoid; inflorescences pyramidally paniculate. ..... I. sect. *Pyramidium.*
   2. Fruiting calyces campanulate or broadly campanulate; inflorescences loosely paniculate. ..... II. sect. *Amethystoides.*
1. Fruiting calyces decurved, with 5 subequal teeth or 2-lipped.
   3. Cymes loosely many flowered, often arranged in panicles, rarely in dense verticillasters; corolla tubes subequal or saccate but never shortly calcarate on upper side near base; fruiting calyces with 5 subequal teeth or 2-lipped. ..... III. sect. *Isodon.*
   3. Cymes few flowered, arranged in remote verticillasters or a terminal spikelike panicle; corolla tubes conspicuously gibbous or even shortly calcarate on upper side near base; fruiting calyces conspicuously 2-lipped. .. IV. sect. *Melissoides.*

I. **Isodon** sect. **Pyramidium** (Bentham) H. W. Li, comb. nov.

Plectranthus sect. *Pyramidium* Bentham, Labiat. Gen. Spec. 44. 1832, and *in* DC. Prodr. **12:** 61. 1848; Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 354. 1897.

Undershrubs, subundershrubs, or perennial herbs. Inflorescences pyramidally paniculate. Fruiting calyx erect, tubular or tubular-campanulate to ovoid, equally or subequally 5-toothed. Corolla tube declinate, saccate on upper side near base.

LECTOTYPE SPECIES. *Isodon ternifolius* (D. Don) Kudo.

KEY TO THE SPECIES OF SECT. PYRAMIDIUM

1. Leaves opposite and/or in whorls of 3 or 4.
   2. Leaves broadly ovate to ovate-oblong; fruiting calyces 3.6–7 mm long, slightly inflated, conspicuously nervate. ..... 1. *I. calycinus.*
   2. Leaves narrowly lanceolate to oblong, rarely ovate-oblong; fruiting calyces ca. 4 mm long, dilated, obscurely nervate. ..... 2. *I. ternifolius.*
1. Leaves consistently opposite.
   3. Stems and inflorescences densely villose with spreading purplish or fulvous, septate hairs, or velutinous with softly fulvous septate ones; leaves all rugose.
      4. Leaves ovate or broadly ovate to triangular-ovate, longer than wide, 1.5–7 by 1–4 cm. ..... 3. *I. enanderianus.*
      4. Leaves triangular-ovate, equally long and wide, 1–2.5 by 1–2.5 cm. ..... 4. *I. brevifolius.*
   3. Stem and inflorescences covered with hairs different from above; leaves not (rarely slightly) rugose.
      5. Leaves long-petiolate, slightly pubescent along midrib and nerves on both surfaces; panicles without floral leaves; calyces gray-lanate, glabrescent and tubular in fruit. ..... 5. *I. eriocalyx.*
      5. Leaves sessile or short-petiolate; inflorescences and calyces different from above.
         6. Leaves ovate, sometimes cordate, 1.5–5 by 0.8–4.5 cm, puberulous above, gray-tomentose beneath; calyces densely pilose. .... 6. *I. phyllostachys.*
         6. Leaves broadly ovate, 7–17 cm long, about half as broad, densely septate-strigose and sparsely glandular above, strigose along nerves and densely glandular beneath; calyces pubescent. ..... 7. *I. pantadenius.*

1. **Isodon calycinus** (Bentham) H. W. Li, comb. nov.

Plectranthus calycinus Bentham *in* E. Meyer, Comm. Pl. Afr. Austr. 230. 1838, and *in* DC. Prodr. **12:** 61. 1848. *Rabdosiella calycina* (Bentham) Codd, Bothalia **15:** 10. 1984. SYNTYPES: in Africa australi inter Morley et Omtata et inter Omsamwubo et Omsamcaba, *Drège* (not seen).

Perennial robust herb or subundershrub. Stems erect, up to 1 m high, much branched, obtusely quadrangular, 4-sulcate and finely striate, densely fulvous- or ferrugineous-tomentose. Leaves in whorls of 3; petiole to 2 mm long, tomentose; blade broadly ovate to ovate-oblong, 2.5–5.5 by 1.3–4 cm, acute at apex, cuneate at base, serrulate, chartaceous, rugose, the upper surface olive-green, sparsely septate-pilose, the lower surface greenish, densely septate-pilose on veins, densely red-glandular, the lateral nerves 3 to 6 per side, ascendent, sunken above but prominent beneath like midrib and veins. Panicles terminal and axillary, compact, together forming complex one 15–35 cm long and up to 4 cm in diameter on top of each branch or stem, composed of many-flowered cymes; cymes 1.5 cm in diameter, the peduncle and pedicels 1–2 mm long, densely tomentose; floral leaves similar to cauline ones, ovate to ovate-lanceolate, always entire; bracteoles linear, 1–2 mm long. Calyx campanulate or tubular-campanulate, ca. 2 mm long, 1.5 mm in diameter, densely tomentose on nerves, otherwise red-glandular, the teeth 5, subulate, equal, 1 mm long; fruiting calyx slightly inflated, ovate-tubular, 3.6–7 mm long, 2–2.5 mm in diameter, conspicuously 10-nerved, with subulate teeth 2 mm long. Corolla ca. 9 mm long, purple, purplish red, or white, puberulous and glandular outside; tube conspicuously saccate on upper side near base, ca. 6 mm long, 1 mm in diameter at base, up to 4 mm where saccate, then abruptly declinate, slightly constricted at throat and there ca. 3 mm in diameter; limb 2-lipped, the upper lip 2.5 mm long, reflexed, 4-fid at apex, the lower lip orbicular-ovate, 3.5 mm long, concave. Stamens and style included. Nutlets ovoid, triquetrous, ca. 1.8 mm long, 1 mm in diameter, costate on ventral side, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. South Africa; in montane grassland, 1000–2000 m alt. Flowering December–January, fruiting January–March.

The species is obviously close to *Isodon ternifolius* (D. Don) Kudo but can be distinguished by its slightly inflated, conspicuously nervate fruiting calyx and its broader leaves.

2. **Isodon ternifolius** (D. Don) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 140. 1929. FIGURE 2A.

Plectranthus ternifolius D. Don, Prodr. Fl. Nepal. 117. 1825. *Rabdosia ternifolia* (D. Don) H. Hara, J. Jap. Bot. **47:** 201. 1972. *Rabdosiella ternifolia* (D. Don) Codd, Bothalia **15:** 10. 1984. TYPE: Nepalia, *Hamilton* (not seen).

P. hosseusii Muschler, Repert. Spec. Nov. Regni Veg. **4:** 268. 1907. TYPE: Thailand, Doi Sutaep, ad viam in formatione graminibus composita, ca. 1580 m, 14 Dec. 1904, *Hosseus 259* (not seen).

Elsholtzia lychnitis Léveillé & Vaniot, Repert. Spec. Nov. Regni Veg. **8:** 425. 1910. SYNTYPES: Kweichou, Tchen-Lin-Tcheou, route de Lo-Pie à Ou-La-Gay, 9 Oct.

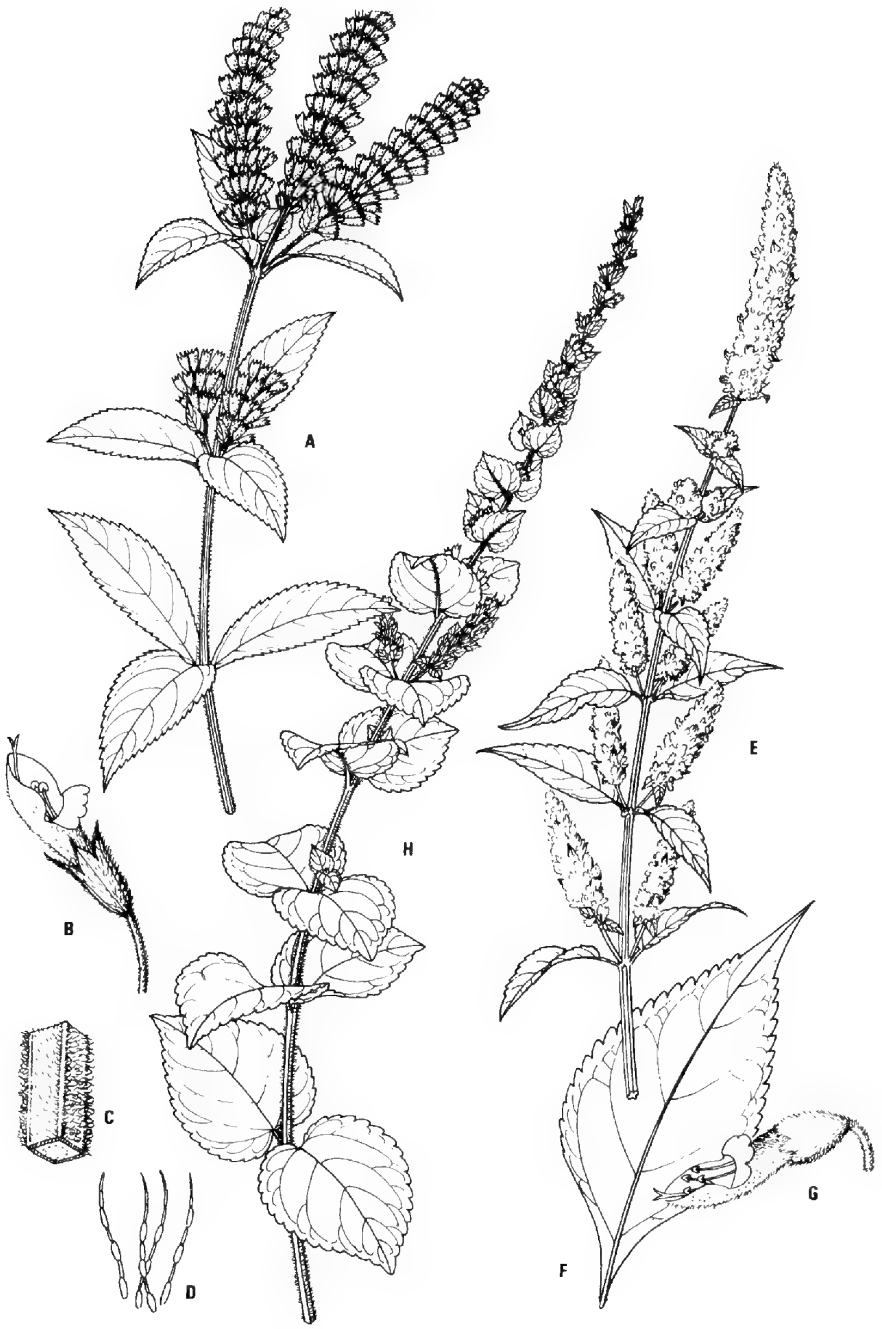

FIGURE 2. A, *Isodon ternifolius* (*Y. H. Li 2144,* KUN), fruiting branch, × 0.6. B–D, *I. enanderianus* (*S. K. Wu 699,* KUN): B, flower, × 3; C, portion of stem, × 3; D, hairs of stem, × 12. E–G, *I. eriocalyx* (*R. C. Ching 24790,* PE): E, flowering branch, × 0.6; F, lower cauline leaf, × 0.6; G, flower, × 3. H, *I. phyllostachys* (*T. N. Liou 21596,* PE), fruiting branch, × 0.6. (Drawn by X. C. Li.)

1897, *Bodinier & L. Martin 1937* (E, not seen); route de Tou-Tchéou à Pien-Yang, Nov. 1905, *Cavalerie 2573* (E, not seen).

Teucrium esquirolii Léveillé, Bull. Acad. Int. Géogr. Bot. **22:** 236. 1912. TYPE: coteaux de Lofou, Kweichow, Nov. 1910, *Esquirol 2576* (holotype, E, not seen).

Perennial robust herb or subundershrub to undershrub. Stems erect, 0.5–2(–7) m high, much branched, obtusely quadrangular, densely tomentose-villose. Leaves opposite and/or in whorls of 3 or 4; petiole 2–3(–10) mm long; blade narrowly lanceolate to narrowly oblong (rarely ovate-oblong), 2–12 by 0.7–5 cm, acute or acuminate (rarely obtuse) at apex, broadly cuneate or cuneate (rarely subrotund) at base, serrulate, chartaceous to subcoriaceous, rugose, the upper surface olive-green, pilose to villose, the lower surface greenish, obviously nervate, densely whitish- or fulvous-tomentose. Spikelike panicles terminal and axillary, very compact, together forming complex one 9–35 cm long and 6–10 cm in diameter on top of each branch or stem, composed of continuous or remote, many-flowered cymes; cymes small, ca. 6 mm in diameter, short-pedunculate; floral leaves similar to cauline ones, lanceolate to ovate, gradually reduced and changed into bracts upward. Calyx campanulate, ca. 2.3 mm long, 2.5 mm in diameter, densely gray- or fulvous-villose; fruiting calyx tubular, dilated, ca. 4 mm long, obscurely nervate, the teeth triangular, equal, 0.5 mm long. Corolla 5–6 mm long, white to purplish, with purple spots on upper lip, villose outside; tube conspicuously saccate on upper side near base, ca. 1–2 mm in diameter; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, 4-fid at apex, the lower lip orbicular-ovate, ca. 3.5 by 2.7 mm, concave. Stamens and style included (sometimes style slightly exserted). Nutlets ovoid, triquetrous, ca. 1.8 mm long, 1 mm in diameter, glabrous.

DISTRIBUTION AND PHENOLOGY. Nepal, Sikkim, India (Assam, Kumaon, Khasia), Bangladesh, northern Burma, Vietnam (Saigon, Hoabinh, Ninbinh), southern China (Guangdong, Guangxi, Guizhou, Yunnan); on open mountain slopes or in sparse forests, 140–2200 m alt. Flowering September–February, fruiting December–April or May.

Due to its leaf arrangement (opposite and/or three or four per whorl) and tubular fruits, *Isodon ternifolius* is quite different from the other species of the genus except *I. calycinus*. It differs from the latter in having narrower leaves and an obscurely nervate but not inflated fruiting calyx.

3. **Isodon enanderianus** (Hand.-Mazz.) H. W. Li, comb. nov. FIGURE 2B–D.

Plectranthus enanderianus Hand.-Mazz. Acta Horti Gothob. **9:** 96. 1934. *Rabdosia enanderiana* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPE: China, Yunnan, ad oppidum Amidschou, 1350 m, 24 Sept. 1926, *S. T. Enander* (holotype, S; isotype, W).

Undershrub 0.6–1.2(–2) m high. Stems erect, quadrangular, finely striate, densely villose with patent purplish or fulvous septate hairs. Leaves opposite; petiole 2–8 mm long (excluding alate portion toward apex), densely puberulous; blade ovate or broadly ovate to triangular-ovate, 1.5–7 by 1–4 cm, acute or shortly acuminate at apex, broadly cuneate and abruptly attenuate at base,

callose-serrate or subcrenate, submembranaceous to chartaceous, rugose, the upper surface green, velutinous especially on veins, the lower surface greenish, very densely velutinous, the lateral nerves ca. 4 on each side, prominent on both surfaces, veins conspicuous beneath. Panicles terminal, spikelike, loose, 5–10 cm long, narrow, composed of 3- to 7-flowered cymes; cymes with peduncle and pedicels up to 5 mm long, slender, these and rachis densely velutinous; floral leaves short-petiolate (upper ones sessile), ovate to suborbicular, gradually reduced upward, almost as long as cymes, caudate at apex; bracteoles linear, 0.5–1 mm long, pilose. Calyx campanulate, 2.5–3 mm long, pilose outside, glabrous inside, the teeth 5, ovate-lanceolate or ovate-triangular, subequal, as long as calyx tube, acute; fruiting calyx tubular-campanulate, slightly dilated, up to 4 mm long, conspicuously nervate. Corolla 5–7 mm long, purple or whitish-blue, sparsely puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 2 mm in diameter at throat; limb 2-lipped, the lower lip ovate, almost as long as corolla tube, concave, the upper lip ca. ½ length of lower one, reflexed, 4-fid at apex. Stamens included; style slightly exserted. Mature nutlets compressed-subspherical, ca. 1 mm long, dark brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (Yunnan and Sichuan); on mountain slopes or in forests and thickets, 700–2500 m alt. Flowering August–September, fruiting in September.

4. **Isodon brevifolius** (Hand.-Mazz.) H. W. Li, comb. nov.

Plectranthus brevifolius Hand.-Mazz. Acta Horti Gothob. **13**: 368. 1939. *Rabdosia brevifolia* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47**: 194. 1972. TYPE: China, Yunnan, declivibus saxosis prope Peyentsin, 18 Oct. 1915, *S. Ten 2* (fragment of holotype, W; isotype, A).

Undershrub. Stems erect, up to 1 m high, much branched, subterete on lower portion, obtusely quadrangular on upper, branches and upper portion of stem densely velutinous with soft, fulvous, adpressed, septate hairs. Cauline leaves opposite; petiole 1.5–2.5 cm long, concave-convex, fulvous-septate-velutinous; blade triangular-ovate, ca. 1–2.5 cm long and broad, acute or slightly obtuse at apex, cuneate at base, serrulate above base, chartaceous, deeply rugose, the upper surface olive-green, very sparsely hispidulous, the lower surface greenish, hispidulous mainly along veins, densely covered with yellowish or white glands, the lateral nerves ca. 3 on each side, these like midrib and veinlets sunken above but conspicuously raised beneath. Panicles terminal, (2–)3–7 cm long, composed of 3- to 5-flowered cymes; cymes with peduncle ca. 3 mm long, pedicels ca. 1 mm long, peduncle, pedicels, and rachis velutinous with adpressed, fulvous, septate hairs; floral leaves similar to cauline ones, ovate, 0.7–1.5 mm long and broad. Calyx campanulate, ca. 1.5 mm long, densely villose, the teeth 5, narrowly triangular, as long as calyx tube, acute. Corolla up to 7 mm long, white, puberulous outside, glabrous inside; tube saccate on upper side near base, ca. 3.5 mm long; limb 2-lipped, the upper lip reflexed, the lower lip oblong-ovate, much longer than upper one, concave. Stamens included. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (Yunnan); on stony slopes, ca. 2000 m alt. Flowering in October.

The leaves of the holotype and the isotype all have a cuneate base, not "basi truncata vel leviter cuneata," as described by Handel-Mazzetti. The species is easily recognized by the shape of its leaves and the indumentum of its leaves and branches. Its affinity with *Isodon enanderianus* is obvious, as was suggested by Handel-Mazzetti.

5. **Isodon eriocalyx** (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 137. 1929. FIGURE 2E–G.

Plectranthus eriocalyx Dunn, Notes Roy. Bot. Gard. Edinburgh **8**: 155. 1913. *Rabdosia eriocalyx* (Dunn) H. Hara, J. Jap. Bot. **47**: 195. 1972. SYNTYPES: China, Szechuan, Mt. Omei, *Wilson 5125*; Yunnan, *Forrest 587, Hancock 73, Henry 9811, Maire 1599, 2024* (all at E, none seen).

Rabdosia eriocalyx (Dunn) H. Hara var. *laxiflora* C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 764. 1976. TYPE: China, Yunnan, Yuo-lo shan, Meng-la, *Y. H. Li 3579* (holotype, KUN).

P. moslifolius auct., non Léveillé: Diels, Notes Roy. Bot. Gard. Edinburgh **7**: 44, 314. 1912.

Perennial herb or undershrub, 0.5–3 m high. Stems obtusely quadrangular, slightly 4-sulcate, always reddish, densely adpressed-pubescent. Leaves opposite; petiole 0.6–5 cm long, pubescent; blade ovate-oblong or ovate-lanceolate, 2.5–18 by 0.8–6.5 cm, acuminate at apex, broadly cuneate or subrotund and abruptly attenuate at base, crenate-serrate or crenate-dentate (sometimes entire), chartaceous, olive-green above, greenish beneath, slightly pubescent along nerves and veinlets on both surfaces. Panicles spikelike, terminal and axillary, 2.5–35 cm long, ca. 1 cm in diameter, densely whitish-floccose-puberulous, composed of compact, many-flowered cymes; cymes with peduncle ca. 2 mm long, pedicels shorter than calyces; floral leaves like cauline ones but smaller, gradually reduced upward; bracteoles minute, linear. Calyx campanulate, 1.5–1.8 mm long, 1.8–2 mm in diameter, gray-lanate at first, glabrescent, the teeth 5, ovate, subequal, ca. ⅓ of calyx length; fruiting calyx erect, tubular, ca. 4 mm long. Corolla 6–7 mm long, purplish or purple, pilose outside; tube slightly saccate on upper side near base. Stamens included; style included (sometimes exserted). Nutlets ovoid, fulvous.

DISTRIBUTION AND PHENOLOGY. South-central China (Sichuan, Yunnan, Guizhou) and northern Thailand; on sunny slopes or in thickets, 750–2600 m alt. Flowering July–November, fruiting November–December.

Isodon eriocalyx can be distinguished by its gray-lanate calyx. It is similar to *I. ternifolius* in its erect tubular fruiting calyx, although in habit it more closely resembles some species in sect. *Isodon* with narrow spikelike panicles. *Rabdosia eriocalyx* var. *laxiflora* differs from the species only in the longer peduncle of the cyme and the sparsity of hairs on the inflorescence. I think this is an insufficient reason for separating it as a variety, so I have reduced it to a synonym of *I. eriocalyx*.

6. **Isodon phyllostachys** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 121. 1929, excl. syn. *Plectranthus rugosiformis* Hand.-Mazz.

FIGURE 2H.

Plectranthus phyllostachys Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 230. 1912. *Rabdosia phyllostachys* (Diels) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: China, Yunnan, Hoching and Lichiang Valley, *Forrest 624* (holotype, E, not seen).

Rabdosia phyllostachys (Diels) H. Hara var. *leptophylla* C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 766. 1977. TYPE: China, Yunnan, Bodo, Zhongdian, *Zhongdian Expedition 1059* (holotype, KUN).

Undershrub or subundershrub, 0.9–3 m high, with erect branches. Branches quadrangular, densely pilose when young, glabrescent. Leaves opposite; petiole 1–6 mm long, pilose; blade ovate, 1.5–5 by 0.8–4.5 cm, obtuse (sometimes acute) at apex, rounded or cordate at base, crenate, rugose, olive-green and puberulous or pilose above, gray-tomentose beneath, venation sunken above and raised beneath. Panicles spikelike, continuous or interrupted, terminal, 4–25 cm long, 1–2 cm in diameter, composed of 4- to 15-flowered cymes; cymes with peduncle 1–10 mm long, pedicels up to 2 mm long; floral leaves reduced upward and gradually changed into bracts, lower ones longer than cymes and upper ones shorter; bracteoles linear, minute. Calyx campanulate, ca. 2 mm long, 2 mm in diameter, densely pilose outside, the teeth 5, ovate-triangular, as long as calyx tube; fruiting calyx ovoid, dilated, teeth ca. ⅓ of calyx length. Corolla ca. 6 mm long, yellowish or white, with purple spots, pilose outside; tube saccate on upper side near base, ca. 3 mm long; limb 2-lipped, the upper lip 4-fid at apex, the lower lip much longer than upper one, concave. Stamens and style included. Nutlets ovoid, brown.

DISTRIBUTION AND PHENOLOGY. South-central China (Sichuan, Yunnan); in thickets or on grassy slopes, 1000–3000 m alt. Flowering August–October, fruiting in October.

This species is close to *Isodon ternifolius* but differs in that the plant is less hairy and the panicle is leafy to the top. Since *Rabdosia phyllostachys* var. *leptophylla* differs from *I. phyllostachys* only in the thinner texture of the leaves, I have placed it in synonymy under the species.

7. **Isodon pantadenius** (Hand.-Mazz.) H. W. Li, comb. nov.

Plectranthus pantadenius Hand.-Mazz. Symb. Sin. **7:** 944. 1936. *Rabdosia pantadenia* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: China, Yünnan bor.-occid., in regionis temperatae ad fluvium Lu-Djiang (Salween) prope Tschamu-tong, *Handel-Mazzetti 8403* (holotype, W).

Perennial herb, covered with small, reddish glands. Stems 70–90 cm long, the lower portion defoliate, glabrate, the upper portion pyramidally branched, 4-sulcate, remotely foliate, pubescent. Leaves opposite, sessile; blade broadly ovate, 7–17 by ca. 3.5–8.5 cm, caudate-acuminate at apex, cuneate-attenuate at base, callose-crenate-dentate, thin-chartaceous, the upper surface green, densely septate-strigose, sparsely glandular, the lower surface greenish, strigose along nerves, densely glandular, the lateral nerves 3 to 5 on each side, arcuate,

like midrib raised beneath, the veinlets conspicuous beneath. Panicles spikelike, terminal, up to 18 cm long, composed of remote, 7- to 9-flowered cymes; cymes shortly pedunculate, densely brown-pubescent; floral leaves broadly or narrowly ovate, shorter than cymes; bracteoles minute. Calyx campanulate, 1–2 mm long, pubescent, the teeth 5, broadly ovate, subequal, shorter than calyx tube. Corolla 4–5 mm long; tube erect, 2.5–3.5 mm long; limb much shorter than tube, densely pilose and glandular outside, the upper lip erect, 4-fid at apex, middle 2 lobes with dark purple spots, the lower lip narrowly ovate, slightly longer than upper one, concave. Stamens and style much exserted. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan); on *Pteridium* grassland, ca. 2800 m alt. Flowering in September.

This species may be only a form of *Isodon eriocalyx,* although it differs from the latter in its smaller leaves and its less hairy calyces with broadly ovate, somewhat acute teeth. More material needs to be examined before a decision can be made.

II. **Isodon** sect. **Amethystoides** (Bentham) H. W. Li, comb. nov.

Plectranthus sect. *Amethystoides* Bentham, Labiat. Gen. Spec. 45. 1832, and *in* DC. Prodr. **12:** 61. 1848; Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 354. 1897.

Perennial herbs. Inflorescences loosely paniculate, composed of patently pedunculate cymes. Fruiting calyx erect, campanulate or broadly campanulate, equally or subequally 5-toothed. Corolla tube declinate, saccate on upper side near base.

LECTOTYPE SPECIES. *Isodon amethystoides* (Bentham) H. Hara.

KEY TO THE SPECIES OF SECT. AMETHYSTOIDES

1. Leaves lanceolate to narrowly lanceolate. ..... 8. *I. nervosus.*
1. Leaves broadly ovate, ovate-orbicular, or ovate-lanceolate.
   2. Fruiting calyces broadly campanulate, as long as or longer than broad; cymes many flowered, with branchlets divaricate and elongate. ...9. *I. amethystoides.*
   2. Fruiting calyces campanulate, longer than broad; cymes few to many flowered, with branchlets divergent and shorter.
      3. Panicles few flowered, ca. 2 cm long. ..... 10. *I. websteri.*
      3. Panicles many flowered, over 6 cm long.
         4. Nutlets whitish-pilose over entire surface. ..... 11. *I. trichocarpus.*
         4. Nutlets glabrous, or whitish-barbate only at apex.
            5. Leaves sparsely septate-puberulous above, whitish-septate-pilose only along midrib and nerves beneath; calyces covered with minute hairs but soon glabrescent. ..... 12. *I. inflexus.*
            5. Leaves with both surfaces sparsely puberulous and glandular, or densely pubescent only on midrib and nerves and dotted with yellowish glands; calyces densely pubescent.
               6. Leaves ovate or ovate-lanceolate, densely pubescent only on midrib and nerves and dotted with yellowish glands on both surfaces, subacuminate at apex, cuneate at base, grossly incurved-serrate; calyces

densely whitish-pubescent and glandular, teeth as long as tube; stamens and style included; nutlets whitish-barbate at apex. ..... 13. *I. serra.*

6. Leaves ovate or broadly ovate, sparsely pubescent and glandular on both surfaces, apical tooth ovate or lanceolate-acuminate, broadly cuneate and abruptly attenuate at base, acutely serrate or crenate-dentate; calyces densely and adpressedly whitish-pubescent, teeth shorter than tube; stamens and style exserted; nutlets verruculose at apex. ..... 14. *I. japonicus.*

8. **Isodon nervosus** (Hemsley) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 123. 1929.

Plectranthus nervosus Hemsley, J. Linn. Soc., Bot. **26:** 272. 1890, *pro parte majore,* excluding *Carles 347, Henry 2725. Rabdosia nervosa* (Hemsley) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 79. 1975. TYPES: Hupeh, Ichang, Patung and neighbourhood, *A. Henry 103* (syntype, K), *995* (syntype, K), *1055* (syntype, K), *2260* (syntype, K; isosyntype, A), *2821* (syntype, K; isosyntype, A); Kwangtung, North River, *Ford's native collector* (syntype, K) (no types at K seen).

P. moslifolius Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 247. 1911. TYPE: Guizhou, Pinfa, *Cavalerie 587* (holotype, E, not seen).

P. angustifolius Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 154. 1913, *pro parte,* quoad *Wilson 2577.*

Amethystanthus stenophyllus Migo, J. Shanghai Sci. Inst., sect. 3, **3:** 231. *t. III.* 1937, non *P. stenophyllus* Baker. *Rabdosia stenophylla* (Migo) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: Zhejiang, Tientaishan, 2 Oct. 1935, *H. Migo s.n.* (holotype, TI, not seen).

P. salicarius Hand.-Mazz. Acta Horti Gothob. **13:** 377. 1939. TYPE: W Hubei, *E. H. Wilson 2577* (holotype, W).

P. stracheyi auct., non Bentham: Hand.-Mazz. Acta Horti Gothob. **9:** 93. 1934.

Perennial herb up to 1 m high. Stems erect, 1 m high, unbranched or slightly branched, quadrangular, conspicuously 4-sulcate, pubescent when young, glabrescent. Leaves opposite; petiole 0.2–1 cm long (upper ones) to nearly absent (lower ones), pubescent; blade lanceolate to narrowly lanceolate, 3.5–13.5 by 1–2 cm, acuminate at apex, cuneate to narrowly cuneate at base, grossly callose-crenate, chartaceous, the upper surface green, pubescent along midrib and nerves, the lower surface greenish, glabrous, the lateral nerves 4 or 5 on each side, raised on both surfaces. Panicles terminal, loose, composed of (3- to) 5- to 9- (to 15-)flowered cymes; cymes with peduncle 5–8 mm long, densely pubescent like pedicels and rachis; bracts foliaceous, narrowly lanceolate, 1–1.5 cm long, densely pubescent; bracteoles linear, 1–2 mm long, densely pubescent. Calyx campanulate, ca. 1.5 mm long, purplish, densely pubescent outside, the teeth 5, lanceolate, subequal, as long as calyx tube, acute; fruiting calyx broadly campanulate, 2.5 mm long, up to 3 mm in diameter, the teeth erect, triangular-lanceolate, as long as calyx tube. Corolla 6–8 mm long, blue or purple, sparsely pilose outside; tube saccate on upper side near base, 3–4 mm long; limb 2-lipped, the upper lip equally 4-fid, with lobes oblong or elliptic, the lower lip elliptic, slightly longer than upper one, ca. 4 mm long, boat shaped. Stamens exserted, filament sparsely pubescent on lower part; style exserted,

equally 2-fid at apex. Nutlets ovoid, 1–1.5 mm long, ca. 1 mm in diameter, pubescent at apex.

DISTRIBUTION AND PHENOLOGY. Widespread in China (Hebei, Shaanxi, Jiangsu, Anhui, Hubei, Sichuan, Zhejiang); on grassy banks, at the edge of forests, shady places in the forest and among shrubs, (60–)300–1000(–1750) m alt. Flowering July–October, fruiting August–November.

This species is very similar in habit to *Isodon angustifolius* (Dunn) Kudo but differs in its erect, broadly campanulate fruiting calyx with five equal teeth.

9. **Isodon amethystoides** (Bentham) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Plectranthus amethystoides Bentham, Labiat. Gen. Spec. 45. 1832, and *in* DC. Prodr. **12:** 61. 1848. *Rabdosia amethystoides* (Bentham) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: China, *Reeves s.n.* (not seen).

P. dubius Vahl ex Bentham, Labiat. Gen. Spec. 711. 1835, and *in* DC. Prodr. **12:** 61. 1848. TYPE: Japan, *Thunberg s.n.* (not seen).

P. pekinensis Maxim. Mém. Acad. Imp. Sci. Saint-Pétersbourg Divers Savans **9:** 213. 1859, *in nota.* TYPE: China, Taithong, Krone (W).

P. sinensis Miq. J. Bot. Néerl. **1:** 115. 1861. TYPE: China, Taithong, Krone (W).

P. daitonensis Hayata, Ic. Pl. Formos. **8:** 107. 1919. *Isodon daitonensis* (Hayata) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 126. 1929. *Rabdosia daitonensis* (Hayata) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: Taiwan, Daitonzan, July 1909, *T. Kawakami s.n.* (holotype, TI).

Isodon koroensis Kudo, J. Soc. Trop. Agric. **3:** 110. 1931. *Rabdosia koroensis* (Kudo) H. Hara, J. Jap. Bot. **47:** 196. 1972. TYPE: Taiwan, inter Koro et Sankyaku, Suogun, Taihoku-shu, 20 Sept. 1930, *S. Suzuki 5910* (holotype, TI, not seen).

Erect perennial herb. Stems 0.3–1.5 m high, quadrangular, 4-sulcate, axillary infertile branchlets always present, densely and adpressedly incurved-pilose or puberulous. Cauline leaves opposite; petiole 0.2–2.5 cm long, alate apically; blade ovate-orbicular or ovate to lanceolate, 0.8–11 by 0.7–3.5 cm (those on lower or middle portion of stem large, those on upper portion of stem and on branchlets smaller), acuminate, acute, or obtuse at apex, abruptly attenuate or broadly cuneate-attenuate at base, crenate except at entire base, thin-chartaceous, the upper surface olive-green, more or less densely hispidulous or sometimes nearly glabrous, the lower surface greenish, pilose, tomentulose, or sometimes nearly glabrous, densely covered with small, white or yellow glands. Panicles terminal, lax, composed of many-flowered cymes; cymes 2–9 cm long, 1.5–8 cm in diameter, peduncle 1–4 cm long, pedicels 3–8 mm long, branchlets divaricate and elongate; floral leaves similar to cauline ones but smaller, generally ovate, gradually reduced and changed into bracts upward; bracts and bracteoles ovate or linear, small to minute but conspicuous. Calyx campanulate, ca. 2.5 mm long and in diameter, sparsely hirtellous or nearly glabrous outside, covered with white or yellow glands everywhere, the teeth 5, triangular, subequal, ca. ⅓ of calyx length; fruiting calyx erect, broadly campanulate, 4–5 mm long, ca. 5 mm in diameter, round at base. Corolla ca. 7 mm long, white, bluish white, or purplish, always purplish blue on upper lip, sparsely puberulous outside, glabrous inside; tube conspicuously saccate on upper side near base,

nearly ½ length of corolla, ca. 2 mm in diameter at throat, slightly curved; limb 2-lipped, upper lip equally 4-fid, lower lip oblate. Stamens and style included. Mature nutlets ovoid, ca. 2 mm long, 1.5 mm in diameter, yellowish brown, with yellow or white glands.

DISTRIBUTION AND PHENOLOGY. Southeastern China (Zhejiang, Guangdong, Guangxi), Taiwan; in forests or wet, grassy areas, 200–920 m alt. Flowering June–October, fruiting September–November.

Although the type specimen of *Plectranthus daitonensis* has no fruits, it does not appear to differ from the specimens of *Isodon amethystoides*. It is best, therefore, to reduce it to a synonym of the latter, which is common in Taiwan. The species seems quite variable in shape and size of the leaves, as well as in hairiness of the stem and leaves, but it always has a loose panicle composed of divaricate cymes and an erect, broadly campanulate fruiting calyx. Thus, it is quite different from all the other species of the genus, although it seems to be related to *I. megathyrsus* (Diels) H. W. Li based on the inflorescence character.

10. **Isodon websteri** (Hemsley) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 130. 1929.

Plectranthus websteri Hemsley, J. Linn. Soc., Bot. **26:** 275. 1890. *Amethystanthus websteri* (Hemsley) Kitagawa, Lin. Fl. Manshur. 353. 1939. *Rabdosia websteri* (Hemsley) H. Hara, J. Jap. Bot. **47:** 202. 1972. TYPE: China, Shingking [Sheng-yang], Peilling, near Moukden, *Webster s.n.* (K, not seen).

Perennial herb. Stems erect, slender, unbranched or branched, quadrangular, shallowly 4-sulcate, sparsely recurved-white-pilose along edges, glabrate on upper portion; internodes shorter than leaves. Cauline leaves opposite; petiole 0.5–3 cm long, slender, triangular-alate on upper part, concave-convex, sparsely white-pilose; blade broadly ovate, 3–6 by 1.5–3.5 cm, acute or nearly acuminate at apex, broadly cuneate at base, regularly crenate-serrate, the upper surface sparsely pilose along midrib and nerves, otherwise nearly glabrous, the lower surface pilose along midrib, otherwise glabrous, dotted with yellowish glands, the lateral nerves 4 or 5 on each side, the veins more or less conspicuous on both surfaces. Panicles terminal, few-flowered, ca. 2 cm long, composed of 3-flowered cymes; cymes with peduncle, pedicels, and rachis all sparsely puberulous; floral leaves ovate-lanceolate, shorter than cymes except lowest 1 or 2; bracts and bracteoles linear, 1–1.5 mm long. Calyx campanulate, 1.5 mm long, pubescent outside, glabrous inside, the teeth 5, triangular, up to ⅓ of calyx length, acute; fruiting calyx dilated, up to 5.5 mm long, rigid, bluish, glabrous. Corolla 4–6 mm long, blue, pilose outside, glabrous inside; tube very short, equal in diameter upward; limb 2-lipped, the upper lip as long as lower one, reflexed, 4-fid at apex, the lower lip concave. Stamens and style exserted. Mature nutlets oblate, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Northeastern China (Liaoning); on roadside along valley, low altitude. Flowering in September.

The species is easily recognized by its short, few-flowered, terminal panicle.

11. **Isodon trichocarpus** (Maxim.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 134. 1929.

Plectranthus trichocarpus Maxim. Bull. Acad. Imp. Sci. Saint-Pétersbourg **22**: 262. 1876, *in indice*. *Rabdosia trichocarpa* (Maxim.) H. Hara, J. Jap. Bot. **47**: 201. 1972. TYPE: Japonia, Hakodate, 1861, *Maximowicz* (holotype, LE, not seen; isotypes, BM, K).

Perennial herb. Stems erect, up to 1.5 m high, much branched in upper portion, woody in lower portion, quadrangular, 4-sulcate and striate, lower portion nearly glabrous, upper portion pubescent; branchlets fertile. Cauline leaves opposite; petiole 1–4 cm long, broadly alate on upper portion, concave-convex, pubescent; blade ovate or broadly ovate, (3.5–)5–13 by 2–6.5 cm, acuminate or long-acuminate at apex, cuneate or broadly cuneate at base, grossly callose-crenate-serrate, chartaceous, the upper surface dark green, sparsely pilose, the lower surface greenish, pubescent, lightly covered with small, yellowish glands, the lateral nerves 2 to 5 per side, ascendent, slightly raised above, strongly so beneath, the veins conspicuous above, slightly raised beneath. Panicles terminal, loose, spreading, composed of (3- to) 5- to 15-flowered cymes; cymes with peduncle 1–6 cm long, lowest one longest, pedicels ca. 3 mm long, peduncle, pedicels, and rachis pubescent; floral leaves similar to cauline ones, broadly to narrowly ovate, longer or shorter than peduncle; bracteoles linear, ca. 1 mm long. Calyx campanulate, ca. 2 mm long, gray-pubescent outside, glabrous inside, the teeth 5, narrowly triangular, almost as long as calyx tube, lower 2 slightly longer, all acuminate; fruiting calyx broadly campanulate, ca. 3 mm long, nervate. Corolla up to 6.5 mm long, dark purple, pubescent outside, glabrous inside; tube saccate on upper side near base, ca. 3 mm long, 1 mm in diameter at base and ca. 2.5 mm at throat; limb 2-lipped, the upper lip reflexed, 4-fid at apex, the lower lip broadly ovate, concave. Stamens and style included. Mature nutlets ovoid, triquetrous, 1.5 mm long, brown, densely whitish-pilose on entire surface.

DISTRIBUTION AND PHENOLOGY. Japan; on grassy slopes, in shady places along valleys in the forest, (200–)400–2040 m alt. Flowering July–August, fruiting September–October.

This species is easily recognized by its large, patent panicles and its densely whitish-pilose nutlets, although it seems to be very close to *Isodon serra* (Maxim.) Kudo and *I. japonicus* (Burman f.) H. Hara.

12. **Isodon inflexus** (Thunb.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 127. 1929.

Ocimum inflexus Thunb. Fl. Jap. 249. 1784. *Plectranthus inflexus* (Thunb.) Vahl ex Bentham, Labiat. Gen. Spec. 711. 1835. *Amethystanthus inflexus* (Thunb.) Nakai, Bot. Mag. Tokyo **48**: 788. 1934. *Rabdosia inflexa* (Thunb.) H. Hara, J. Jap. Bot. **47**: 196. 1972. TYPE: Japonia, *Thunberg s.n.* (not seen).

Plectranthus inconspicuus Miq. Ann. Mus. Bot. Lugduno Batavum **2**: 101. 1865. SYNTYPES: Japonia, *Buerger* and *Textor* (not seen).

P. inflexus (Thunb.) Vahl ex Bentham var. *macrophyllus* Maxim. Bull. Acad. Imp. Sci. Saint-Pétersbourg **20**: 453. 1875. *Rabdosia inflexa* (Thunb.) H. Hara var. *macrophylla* (Maxim.) H. Hara, J. Jap. Bot. **47**: 196. 1972. TYPE: Japan, Hakodate, Yezo, *Maximowicz s.n.* (not seen).

P. coreanus Vaniot, Bull. Acad. Int. Géogr. Bot. **14:** 166. 1904. TYPE: Korea, route de Chemulpo à Seoul, lieux secs et incultes, 13 Sept. 1889, *Bodinier s.n.* (holotype, E, not seen).

Stachys polygonatum Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 449. 1911. TYPE: Korea, Quelpaert in parva insula Mounseum, 9 Aug. 1910, *Taquet 4378* (holotype, E, not seen).

P. inflexus (Thunb.) Vahl ex Bentham var. *microphyllus* Nakai, Bot. Mag. Tokyo **35:** 183. 1921. *Isodon inflexus* (Thunb.) Kudo var. *microphyllus* (Nakai) Kudo, Mém. Fac. Sci. Taihoku Imp. Univ. **2:** 229. 1929. SYNTYPES: Korea, in insula Zetsuedo, *T. Uchiyama*; in monte Kusan, *T. Nakai 3094*; Quelpaert, sine loco speciali, *S. Ichikama*; Quelpaert, in sepibus, *Taquet 5864* (none seen).

P. inflexus (Thunb.) Vahl ex Bentham var. *canescens* Nakai, Bot. Mag. Tokyo **35:** 191. 1921. *Isodon inflexus* (Thunb.) Kudo var. *canescens* (Nakai) Kudo, Mém Fac. Sci. Taihoku Imp. Univ. **2:** 129. 1929. TYPE: Korea, Quelpaert, in sepibus, 600 m, *Taquet 5865* (not seen).

Perennial herb. Stems flexuose-erect, 0.4–1(–1.5) m high, much branched on lower portion, obtusely quadrangular, 4-sulcate, brown, finely striate, edges densely pilose with curved, white, septate hairs. Cauline leaves opposite; petiole 0.5–3.5 cm long, broadly alate on upper portion, concave-convex, densely pilose with white, septate hairs; blade broadly triangular-ovate or ovate, 3–5.5 by 2.5–5 cm, acute or obtuse at apex, broadly cuneate and abruptly attenuate-decurrent at base, grossly callose-crenate-serrate above base, chartaceous, the upper surface olive-green, sparsely septate-puberulous, the lower surface whitish-septate-pilose only along midrib and nerves, the lateral nerves ca. 4 on each side, slightly sunken above and raised beneath like midrib, the veins parallel, conspicuous beneath. Panicles 6–10 cm long, narrow, terminal, also axillary on upper parts of stem and branches, together forming complex one on top of each stem or branch, composed of 3- to 5-flowered cymes; cymes with peduncle up to 5 mm long, this, shorter pedicels, and rachis densely puberulous; floral leaves nearly sessile, ovate, reduced upward, remotely serrate or nearly entire; bracteoles linear or linear-lanceolate, 1–1.5 mm long, ciliate. Calyx campanulate, ca. 2 mm long, pubescent at first but soon glabrescent outside, glabrous inside, the limb slightly 2-lipped, the teeth 5, nearly equal; fruiting calyx slightly dilated, up to 5 mm long, conspicuously nervate. Corolla ca. 8 mm long, reddish to purplish, puberulous and covered with small glands outside, glabrous inside; tube saccate on upper part near base, ca. 3.5 mm long, up to 1.5 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 by up to 4 mm, reflexed, equally 4-fid at apex, the lower lip broadly ovate, 4.5 by 3.5 mm, concave. Stamens included, the filament complanate, barbate below middle; style included, equally 2-fid at apex. Mature nutlets broadly ovoid, 1.5 mm long, rounded at apex, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. Northern China (Liaoning, Hebei, Shandong, Shaanxi), Korea, and Japan; in sparse forests of valleys, on stream sides and hill slopes, in sunny places, 200–1400 m alt. Flowering August–October, fruiting after September.

Although *Isodon inflexus* is easily confused with some species of sect. *Isodon* ser. *Megathyrsi* C. Y. Wu & H. W. Li (e.g., *I. henryi* (Hemsley) Kudo) and ser.

Macrocalyces C. Y. Wu & H. W. Li (e.g., *I. excisoides* (Sun ex C. H. Hu) H. Hara, *I. shikokianus* (Makino) H. Hara, *I. rosthornii* (Diels) Kudo) when in flower, it is quite different from them in having an erect calyx when in fruit. According to the original descriptions, *Plectranthus inflexus* var. *macrophyllus,* var. *microphyllus,* and var. *canescens* differ from the species only in minor characters, so there is not sufficient reason to retain them as distinct varieties.

13. **Isodon serra** (Maxim.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 125. 1929.

Plectranthus serra Maxim. Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg **9:** 426. 1875, and Bull. Acad. Imp. Sci. Saint-Pétersbourg **20:** 454. 1875. *Amethystanthus serra* (Maxim.) Nemoto, Fl. Japan, Suppl. 630. 1936. *Rabdosia serra* (Maxim.) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPES: Mandshuria, ad inferiorem partem fl. Sungari, in prato prope Mongolia, gregarius, et in loco prope Indamo, *Maximowicz* (holotype, LE, not seen).

P. nervosus Hemsley, J. Linn. Soc., Bot. **26:** 272. 1890, *pro parte minore,* quoad *Henry 2725, Carles 347* tantum.

P. lasiocarpus Hayata, J. Coll. Sci. Imp. Univ. Tokyo **30:** 224. 1911. *Isodon lasiocarpus* (Hayata) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 125. 1929. *Amethystanthus lasiocarpus* (Hayata) Nemoto, Fl. Japan, Suppl. 629. 1936. *Rabdosia lasiocarpa* (Hayata) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPE: Taiwan, Taihoku, *Toyen 458* (holotype, TI).

Perennial herb. Stems erect, up to 1.5(–2) m high, much branched on upper portion, woody at base, obtusely quadrangular, slightly 4-sulcate, finely striate, purplish, subglabrescent on lower portion, densely covered with downwardly recurved pubescence on upper portion. Cauline leaves opposite; petiole 0.5–3.5 cm long, broadly alate toward apex, concave-convex, densely pubescent; blade ovate to ovate-lanceolate or lanceolate, 3.5–10 by 1.5–4.5 cm, subacuminate at apex, cuneate at base, grossly incurved-serrate, thin-chartaceous, dark green above, greenish beneath, densely pubescent only on midrib and nerves and dotted with yellowish glands on both surfaces, the lateral nerves 4 or 5 on each side, these and midrib raised on both surfaces, the veins parallel, more or less conspicuous on both surfaces. Panicles terminal, loose, 10–20 cm long, composed of 5- to many-flowered cymes; cymes with peduncle 0.5–1.5 cm long, pedicels 1–3 mm long, both densely pubescent; lower floral leaves similar to cauline ones, shortly petiolate, longer than cymes, the upper floral leaves reduced and changed into bracts upward, lanceolate to linear-lanceolate, almost equal to peduncles; bracteoles 1–3 mm long, pubescent. Calyx campanulate, ca. 1.5 mm long, densely whitish-pubescent and glandular outside, glabrous inside, the teeth 5, erect, narrowly triangular, subequal, as long as calyx tube; fruiting calyx broadly campanulate, dilated, more or less urceolate at base, ca. 3 mm long, conspicuously nervate. Corolla up to 6 mm long, purple, puberulous outside, glabrous inside; tube saccate on upper part near base, ca. 3 mm long, up to 1.2 mm broad at throat; limb 2-lipped, the upper lip ca. 3 mm long, reflexed, equally 4-fid at apex, the lower lip broadly ovate, ca. 3 mm long, concave. Stamens and style included. Mature nutlets broadly ovoid, 1.5 mm long, rounded and whitish-barbate at apex.

DISTRIBUTION AND PHENOLOGY. Southeastern China (Zhejiang, Guangdong), Taiwan, and Korea; on mountain slopes, roadsides, riverbanks, and stream sides, in thickets or forests, frequently on sandy soil, 120–1250 m alt. Flowering August–October, fruiting September–October.

This species is frequently confused with *Isodon japonicus* but is distinct in having nutlets that are whitish-barbate at the apex.

14. **Isodon japonicus** (Burman f.) H. Hara, Enum. Spermat. Jap. **1:** 206. 1949.

Scutellaria? japonica Burman f. Fl. Indica, 130. 1768, quoad specim. ex Japon. *Plectranthus glaucocalyx* Maxim. var. *japonicus* (Burman f.) Maxim. Bull. Acad. Imp. Sci. Saint-Pétersbourg **20:** 454. 1875. *Isodon glaucocalyx* var. *japonicus* (Burman f.) Nakai, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 127. 1929. *P. japonicus* (Burman f.) Koidz. Bot. Mag. Tokyo **42:** 386. 1929. *Amethystanthus japonicus* (Burman f.) Nakai, Bot. Mag. Tokyo **48:** 788. 1934. *Rabdosia japonica* (Burman f.) H. Hara, J. Jap. Bot. **47:** 196. 1972. TYPE: Japonica, *Siebold* (not seen).

P. maximowiczii Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 101. 1865. TYPE: Japonica, *Siebold s.n.* (holotype, LE, not seen; isotype, A).

P. buergeri Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 101. 1865. TYPE: Japan, circa Nagasaki, *Oldham 587* (not seen).

KEY TO THE VARIETIES OF ISODON JAPONICUS

1. Calyx whitish outside; leaves pubescent. ..... 14a. var. *japonicus.*
1. Calyx bluish outside; leaves puberulous. ..... 14b. var. *glaucocalyx.*

14a. **Isodon japonicus** var. **japonicus**

Perennial herb. Stems erect, 0.4–1.5 m high, much branched, woody on lower portion, obtusely quadrangular, 4-sulcate, finely striate, nearly glabrous on lower portion, pubescent and glandular on upper portion. Cauline leaves opposite; petiole 1–3.5 cm long, alate, concave-convex, pubescent; blade ovate or broadly ovate, (4–)6.5–13 by (2.5–)3–7 cm, with ovate or lanceolate and acuminate tooth at apex, broadly cuneate and abruptly attenuate at base, chartaceous, callose- or crenate-serrate, dark green above, greenish beneath, pubescent and glandular on both surfaces, the lateral nerves 5 on each side, ascendent, like midrib slightly raised above and sunken beneath. Panicles terminal, loose and spreading, composed of (3- to) 5- to 7-flowered cymes; cymes with peduncle (3–)6–15 mm long, gradually shorter upward, pedicels ca. 3 mm long, peduncle, pedicels, and rachis pubescent and glandular; lowest floral leaves similar to cauline ones, ovate, the upper ones gradually changed into bracts, bracts sessile, broadly ovate, much shorter than peduncles of cymes; bracteoles linear, ca. 1 mm long. Calyx campanulate, 1.5–2 mm long, with dense adpressed whitish pubescence outside, glabrous inside, the teeth 5, triangular, ca. ⅓ of calyx length, subequal, lower 2 slightly longer and broader, all acute; fruiting calyx tubular-campanulate, up to 4 mm long, slightly curved, conspicuously nervate. Corolla ca. 5 mm long, purplish or purplish blue to blue, with dark spots on upper lip, puberulous outside, glabrous inside; tube saccate on upper side near base, ca. 2.5 mm long, limb 2-lipped, the upper lip

reflexed, 4-fid at apex, the lower lip broadly ovate, concave. Stamens exserted, the filament complanate, barbate below middle; style exserted. Mature nutlets ovoid, triquetrous, 1.5 mm long, brownish, verrucose at apex, glabrous.

DISTRIBUTION AND PHENOLOGY. Eastern China (Hebei, Jiangxi), Korea, Japan, Soviet Union (Far Eastern Region); on roadsides or mountain slopes, or in thickets or valleys, 50–2100 m alt. Flowering July–August, fruiting September–October.

14b. **Isodon japonicus** var. **glaucocalyx** (Maxim.) H. W. Li, comb. nov.

Plectranthus glaucocalyx Maxim. Mém. Acad. Imp. Sci. Saint-Pétersbourg Divers Savans **9:** 212, 475. 1859. *Isodon glaucocalyx* (Maxim.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 126. 1929 (var. *typicus*). *P. japonicus* (Burman f.) Koidz. var. *glaucocalyx* (Maxim.) Koidz. Fl. Symb. Orient.-Asiat. 14. 1930. *Amethystanthus japonicus* (Burman f.) Nakai var. *typicus* (Maxim.) Nakai, Bot. Mag. Tokyo **48:** 789. 1934. *Amethystanthus glaucocalyx* (Maxim.) Nemoto, Fl. Japan, Suppl. 628. 1936. *Rabdosia japonica* (Burman f.) H. Hara var. *glaucocalyx* (Maxim.) H. Hara, J. Jap. Bot. **47:** 196. 1972. SYNTYPES: Mandshuria, *F. Schmidt, Przewalski* (LE, not seen).

This variety differs from var. *japonicus* only in its sparsely puberulous and glandular, obtusely serrate leaves with the apical tooth ovate or lanceolate and acuminate, and in its bluish, densely adpressed-pubescent calyx.

DISTRIBUTION AND PHENOLOGY. Northern China (Heilongjiang, Liaoning, Hebei, Shanxi, Shaanxi, Jiangsu), Japan, Korea, Soviet Union (Far Eastern Region); on roadsides or hill slopes, in grasslands and forests, 50–1800 m alt. Flowering July–August, fruiting September–October.

This species seems to be very close to *Isodon trichocarpus,* differing only in its glabrous nutlets.

III. **Isodon** sect. **Isodon.** *Plectranthus* sect. *Isodon* Schrader ex Bentham, Labiat. Gen. Spec. 40. 1832, and *in* DC. Prodr. **12:** 55. 1848. *Plectranthus* subg. *Isodon* sect. *Euisodon* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 352. 1897, *pro parte majore.*

Undershrubs, subundershrubs, or perennial herbs. Cymes laxly many flowered, often arranged in panicles, rarely in dense verticillasters. Fruiting calyx decurved, with 5 subequal teeth or 2 lips. Corolla large or medium in size, tube subequal in diameter upward or saccate.

KEY TO THE SERIES OF SECT. ISODON

1. Corollas large and stout, 1.2–2 cm long, tube twice as long as limb or nearly so. . . . . A. ser. *Longitubi.*
1. Corollas medium to small, less than 1.2 cm long, stout or slender, if stout tube always less than twice as long as limb.
   2. Fruiting calyces 5-toothed or inconspicuously 2-lipped.
      3. Leaves conspicuously excised at apex. . . . . B. ser. *Excisi.*
      3. Leaves not excised at apex.

4. Fruiting calyces with 5 teeth, these ⅓ length of fruiting calyx tube or less; corolla tubes patent or straight. ..... C. ser. *Gerardiani.*
4. Fruiting calyces with 5 teeth, these greater than ⅓ length of fruiting calyx tube; corolla tubes declinate.
5. Calyces with small teeth ½ their length or less.
6. Branchlets, leaves, and calyces very densely covered with hairs of various kinds; leaves usually rugose. ..... D. ser. *Rugosi.*
6. Branchlets, leaves, and calyces slightly hairy; leaves generally not rugose. ..... E. ser. *Pleiophylli.*
5. Calyces with long, narrow teeth ½ their length or more. .... F. ser. *Setschwanenses.*

2. Fruiting calyces conspicuously 2-lipped.
7. Calyces 2-lipped for ½ their length or less.
8. Cymes arranged into narrow panicles. ..... G. ser. *Coetsae.*
8. Cymes arranged into spreading panicles. ..... H. ser. *Megathyrsi.*
7. Calyces 2-lipped for more than half their length.
9. Cymes arranged into narrow racemose or pseudoracemose panicles. .... I. ser. *Macrocalyces.*
9. Cymes arranged into spreading panicles. ..... J. ser. *Scrophularioidei.*

A. **Isodon** ser. **Longitubi** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Longitubae* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 442, 586. 1977.

Undershrubs or perennial herbs. Cymes arranged in more or less spreading panicles. Calyx campanulate, with 5 subequal teeth or 2 lips; fruiting calyx more or less dilated, sometimes tubular-campanulate, slightly curved. Corolla large and stout, 1.2–2 cm long, the tube at least twice as long as limb, decurved.

TYPE SPECIES. *Isodon longitubus* (Miq.) Kudo.

In this series I put all the species with long corollas together. Although it may be more or less artificial, it is convenient for identification.

KEY TO THE SPECIES OF SER. LONGITUBI

1. Fruiting calyces conspicuously 2-lipped; corolla tubes elongate, ca. 3 times as long as limb.
2. Cymes short; flowers with the peduncle pubescent, less than 1 cm long, the teeth of upper calyx lip triangular, subacute. ..... 15. *I. longitubus.*
2. Cymes diffuse; flowers with the peduncle glabrous, 1–2.5 cm long; the teeth of upper calyx lip lanceolate, acute. ..... 16. *I. effusus.*
1. Fruiting calyces inconspicuously 2-lipped; corolla tubes less than 3 times longer than limb.
3. Plant less than 30 cm tall; cymes 1- to 3-flowered, arranged into narrow panicles. ..... 17. *I. gesneroides.*
3. Plant more than 30 cm tall; cymes 3- to many-flowered, arranged into more or less spreading panicles.
4. Calyces broadly campanulate, always purplish or dark purple-red.
5. Panicles very spreading, up to 30 cm long; bracts small; pedicels 2–7 mm long. ..... 18. *I. forrestii.*
5. Panicles not very spreading, (6–)10–15(–20) cm long; floral leaves large, gradually changed into small bracts upward; pedicels 1–3 mm long. .... 19. *I. irroratus.*

FIGURE 3. A–H, *Isodon rosthornii* (A–F, *W. C. Cheng 6582*, PE; G, H, *C. W. Yao 3197*, PE): A, portion of plant, × 0.6; B, flower, × 3.6; C, calyx, × 3.6; D, corolla and stamens, × 3.6; E, pistil, × 3.6; F, gall, × 3.6; G, fruiting calyx, × 3.6; H, nutlet, × 6. I, *I. longitubus* (*R. C. Ching 2374*, PE), portion of plant, × 0.6. J, *I. macrocalyx* (*M. Chen 2459*, PE), portion of plant, × 0.6. (Drawn by X. L. Zeng.)

4. Calyces campanulate, never tinged with striking color.
   6. Leaves rhombic, grossly crenate-serrate above middle, petiole up to 3.5 cm long. ..... 20. *I. wardii.*
   6. Leaves narrowly ovate, crenate-dentate in apical ⅔, petiole less than 1 cm long. ..... 21. *I. bulleyanus.*

15. **Isodon longitubus** (Miq.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 139. 1929. FIGURE 3I.

Plectranthus longitubus Miq. Ann. Mus. Bot. Lugduno-Batavum **2:** 102. 1865. *Amethystanthus longitubus* (Miq.) Nakai, Bot. Mag. Tokyo **48:** 790. 1934. *Rabdosia longituba* (Miq.) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPE: Japan, *P. F. Siebold s.n.* (possible isotype, A).

P. longitubus Miq. var. *contracta* Maxim. Bull. Acad. Imp. Sci. Saint-Pétersbourg **20:** 451. 1875. *Rabdosia longituba* (Miq.) H. Hara var. *contracta* (Maxim.) H. Hara, J. Jap. Bot. **47:** 197. 1977. TYPES: in Japonia, *Miquel* (syntype, LE, not seen); locis depressus prope oppidum Oakfbu ins. Nippon, *Buerger* (syntype, LE, not seen); prov. Simabara ins. Kiusiu, fine Septembris, *Maximowicz* (syntype, LE, not seen; isosyntype, A).

Perennial herb, up to 1 m high. Stems ascendent, branched from lower part, obtusely quadrangular, slightly sulcate, purplish, densely recurved-pubescent; branches slender. Leaves opposite; petiole (2–)5–20 mm long, concave-convex, densely pubescent; blade lanceolate-ovate to ovate, middle ones 3.5–12 by 2–4 cm, shortly acuminate to acuminate at apex, cuneate or cuneate-decurrent at base, serrate except at entire base, chartaceous, the upper surface olive-green, pubescent along midrib and nerves, otherwise strigillose, the lower surface greenish purplish, densely pubescent on midrib and nerves, dotted with small golden glands, the lateral nerves 3 or 4 on each side, raised on both surfaces like midrib, the veins visible on both surfaces. Panicles terminal and axillary, 10–20 cm long (axillary ones shorter), narrow, all composed of congested 1- to 3- (to 5-)flowered cymes; cymes with peduncles ca. 8 mm long, pedicels up to 5 mm long, peduncle, pedicels, and rachis minutely pubescent; lower floral leaves similar to cauline ones, upper floral leaves gradually changed into bracts upward; bracts subsessile, entire; bracteoles linear, minutely pubescent. Calyx campanulate, up to 4 mm long, 6 mm in diameter, purplish, minutely pubescent along ribs and margin but otherwise glandular outside, glabrous inside, 2-lipped for ½ its length, the upper lip reflexed, with 3 triangular, short, subacute teeth, the lower lip with 2 ovate-triangular, subacute teeth; fruiting calyx up to 6 mm long, conspicuously nervate. Corolla up to 2 cm long, purple-blue, puberulous outside, glabrous inside; tube conspicuously saccate on upper side near base, nearly equal in diameter upward, up to 4 mm in diameter at throat; limb 2-lipped, the upper lip reflexed, ca. 3.5 by 4 mm, equally 4-fid at apex, the lower lip broadly ovate, ca. 4 by 3.5 mm, concave. Stamens and style included. Mature nutlets compressed-spherical, ca. 1.5 mm in diameter, dark brown, glabrous, verruculose.

DISTRIBUTION AND PHENOLOGY. Japan and southeastern China (Zhejiang); on stream sides in forests, 500–1130 m alt. Flowering June–October, fruiting in October.

The long, stout corolla tube of this species is very distinctive.

16. **Isodon effusus** (Maxim.) H. W. Li, comb. nov.

Plectranthus longitubus Miq. var. *effusa* Maxim. Bull. Acad. Imp. Sci. Saint-Pétersbourg **20:** 451. 1875. *P. effusus* (Maxim.) Honda, Bot. Mag. Tokyo **46:** 419. 1932. *Rabdosia effusa* (Maxim.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPE: Nippon jugo Hakone, medio October, *Maximowicz* (holotype, LE, not seen).

Perennial herb, up to 1 m high. Stems ascendent, branched from lower part, quadrangular, 4-sulcate, pubescent; branches slender. Leaves opposite; petiole 0.5–1.5 cm long, concave-convex, densely puberulous; blade lanceolate to ovate-lanceolate, 8–14 by 3–4.2 cm, acuminate at apex, cuneate or cuneate-decurrent at base, grossly crenate-serrate, chartaceous, the upper surface puberulous along midrib and nerves, otherwise sparsely setulose, the lower surface puberulous on nerves, dotted with minute golden glands, the lateral nerves ca. 5 on each side, obliquely patent, like midrib slightly raised above and conspicuously so beneath, the veinlets visible on both surfaces. Panicles terminal and axillary, 10–20 cm long, 5–8 cm in diameter, composed of diffuse, 3- to 7-flowered cymes; cymes with peduncle 1–2.5 cm long, peduncle, pedicels, and rachis glabrous; floral leaves similar to cauline ones, ovate-lanceolate, entire, nearly glabrous; bracts linear, 5 mm long; bracteoles linear, 1–2 mm long, nearly glabrous. Calyx campanulate, 3–4 mm long, nearly glabrous, glandular, 2-lipped for ½ its length, the upper lip reflexed, with 3 lanceolate, acute teeth, the lower lip with 2 triangular-ovate, acute teeth; fruiting calyx up to 6 mm long, conspicuously nervate. Corolla up to 2 cm long, purple-blue, puberulous outside, glabrous inside; tube patent, conspicuously saccate on upper side near base, gradually dilated upward, ca. 5 cm in diameter at throat; limb 2-lipped, the upper lip ca. 3.5 by 4 cm, reflexed, equally 4-fid at apex, the lower lip broadly ovate, ca. 4 by 3.5 mm, concave. Stamens and style included. Nutlets compressed-ovoid, 2 mm long, 1.5 mm in diameter, rounded at apex, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Japan; in light forest, 250–1500 m alt. Flowering August–October, fruiting in October.

Maximowicz considered this species to be a variety of *Isodon longitubus,* but I think it is best to regard it as a distinct species because I have not found intermediate forms linking the two. It is obviously close to *I. longitubus* but differs in its diffuse cymes, glabrous and slender peduncles, and lanceolate teeth of the upper calyx lip.

17. **Isodon gesneroides** (James Sincl.) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Plectranthus gesneroides James Sincl. Notes Roy. Bot. Gard. Edinburgh **20:** 124. 1948. *Rabdosia gesneroides* (James Sincl.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPE: China, Sichuan, Muli, 8 Sept. 1921, *F. Kingdon-Ward 4942* (holotype, E).

Perennial herb, below 30 cm high. Stems ascendent, with fibrous rootlets on lower portion, branched or unbranched, terete, finely striate, dark brown, dense-

ly glandular-pubescent. Cauline leaves few, opposite; petiole 0.8–1.5 cm long, concave-convex, densely glandular-pubescent; blade ovate or orbicular-ovate and 1.5–2.5 by 1–2 cm (lowest pair), or rhombic-ovate and 3–5.5 by 2–3 cm (upper pairs), obtuse to acute at apex, broadly cuneate-attenuate at base, remotely and grossly crenate-serrate, chartaceous, sparsely strigose-hirtellous and yellowish-glandular above, nearly glabrous beneath, the lateral nerves ca. 3 or 4 on each side, like midrib slightly raised above and conspicuously so beneath, the veinlets parallel, visible beneath. Panicles terminal, up to 15 cm long, narrow, few-flowered, composed of 1- to 3-flowered cymes; cymes with peduncle 3–7 mm long, pedicels ca. 5 mm long, peduncle, pedicels, and rachis densely glandular-pubescent; lowest floral leaves similar to cauline ones, others all changed into bracts; bracts sessile, broadly ovate to ovate-lanceolate, acuminate at apex; bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, ca. 3 mm long, puberulent and glandular outside, glabrous inside, the teeth 5, triangular-ovate, subequal, as long as calyx tube. Corolla ca. 1.3 cm long, purple, pilose and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 8 mm long, ca. 3 mm in diameter at throat; limb 2-lipped, the upper lip ca. 4 mm long, reflexed, equally 4-fid at apex, the lower lip nearly orbicular, concave. Stamens and style included. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan); on limestone cliffs in woods, ca. 3000 m alt. Flowering in August.

This is a distinct species, with remotely crenate-serrate leaves, slender unbranched scapes, few-flowered inflorescences, and large flowers.

18. **Isodon forrestii** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 130. 1929.

Plectranthus forrestii Diels, Notes Roy. Bot. Gard. Edinburgh **5**: 229. 1912. *Rabdosia forrestii* (Diels) H. Hara, J. Jap. Bot. **47**: 195. 1972. TYPE: China, Yunnan, eastern flank of Lichiang Range, 27°20′N, August 1906, *G. Forrest 2851* (holotype, E, not seen).

Rabdosia forrestii (Diels) H. Hara var. *intermedia* C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 769. 1977. TYPE: China, Yunnan, Heqing, *R. C. Ching 24680* (holotype, KUN).

Perennial herb. Stems numerous, 0.6–1(–1.8) m high, robust, obtusely quadrangular, pilose. Cauline leaves opposite; gradually changed into floral ones upward; petiole ca. 5 mm long, densely pilose; blade ovate or rhombic-ovate, 5–10 by 4–7 cm (lower and upper ones smaller), obtuse or acute at apex, broadly cuneate-decurrent at base, crenate-dentate except at entire base, chartaceous, olive-green above, greenish beneath, densely pilose and sparsely yellowish-glandular on both surfaces, the veinlets parallel, conspicuous beneath. Panicles terminal, very spreading, up to 30 cm long and 8–9 cm in diameter, composed of 7- to 11-flowered cymes; cymes with peduncle 2–3 cm long, pedicels 2–7 mm long, peduncle, pedicels, and rachis densely glandular-pubescent; bracts ovate, 5–7 cm long, gradually reduced upward; bracteoles spathulate, 2–3 mm long, ciliate. Calyx broadly campanulate, 4–5 mm long, dark purple-red, pubescent on ribs and yellowish-glandular outside, glabrous inside, slightly

2-lipped, the teeth 5, ovate-lanceolate, acuminate at apex; fruiting calyx spreading, very dilated, 7–8 mm long, conspicuously nervate. Corolla up to 16 mm long, dark blue, bluish, or reddish, pilose outside especially on lower part, glabrous inside; tube saccate on upper side near base, almost equal in diameter upward, ca. 10 mm long, ca. 4 mm in diameter near base and 3.5 mm at throat; limb 2-lipped, the upper lip 5–6 mm long, reflexed, equally 4-fid at apex, the lower lip 6 mm long, concave. Stamens and style included. Nutlets ovoid, ca. 1.8 mm long and 1.5 mm in diameter, yellow-brown.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan, southwestern Sichuan); in stony grasslands, at forest edges, in grassy openings in pine forests, 2650–3500 m alt. Flowering July–August, fruiting August–September.

This species is closely related to *Isodon irroratus* (Forrest ex Diels) Kudo but has much larger, more open inflorescences, smaller bracts, longer pedicels, and shorter, broader calyx teeth. *Rabdosia forrestii* var. *intermedia* differs from *Isodon forrestii* only in minor characters. With more material of the species now available, I cannot find any sharp distinctions between them, so I prefer to reduce the variety to synonymy under the species.

19. **Isodon irroratus** (Forrest ex Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 121. 1929. FIGURE 4F, G.

Plectranthus irroratus Forrest ex Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 228. 1912. *Rabdosia irrorata* (Forrest ex Diels) H. Hara, J. Jap. Bot. **47:** 196. 1972. TYPE: China, Yunnan, eastern flank of Lichiang Range, 27°15'N, June 1906, *G. Forrest 2507* (holotype, E, not seen).

Rabdosia irrorata (Forrest ex Diels) H. Hara var. *crenata* C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 770. 1977. TYPE: China, Yunnan, Er-yuan, near He-shan-men, *NW Yunnan Expedition 63-6285* (holotype, KUN).

R. irrorata (Forrest ex Diels) H. Hara var. *longipes* C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 770. 1977. TYPE: China, Yunnan, Heqing, *NW Yunnan Expedition 4797* (holotype, KUN).

R. irrorata (Forrest ex Diels) H. Hara var. *rungshiaensis* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 406, 586. 1977. TYPE: China, Xizang, Rungshia, *Nanking Univ. 697* (holotype, PE).

Erect undershrub, 0.3–1 m high. Stems erect or obliquely ascendent, much branched in upper portion, terete, brown-gray, with lamellate cortex; branches subterete to obtusely quadrangular, purplish, puberulous. Leaves opposite; petiole 1–2 mm long; middle ones with blade ovate to broadly ovate, 1.5–3 by 1.3–2.5 cm, obtuse at apex, broadly cuneate at base, crenate except at entire base, chartaceous, whitish-hispidulous and yellowish-glandular above, sparsely hirtellous along midrib and nerves and dotted with yellowish glands beneath, the lateral nerves 3 or 4 on each side, raised on both surfaces. Panicles terminal, slightly spreading, (6–)10–15(–20) cm long, glandular-pubescent, composed of 3- to 5- (to 7-)flowered cymes; cymes with pedicels 2–3 mm long, glandular-pubescent; lowest floral leaves similar to cauline ones, others all changed into bracts; bracts ovate; bracteoles linear, 1–2 mm long. Calyx broadly campan-

FIGURE 4. A–E, *Isodon bulleyanus* (*W. S. Liou 51198,* KUN): A, flowering branch, × 0.6; B, flower, × 1.8; C, corolla and stamens, × 1.8; D, calyx, × 1.8; E, pistil, × 1.8. F, G, *I. irroratus* (*R. C. Ching 23436,* KUN): F, portion of stem with leaves, × 0.6; G, flower, × 1.8. H, I, *I. calcicolus* var. *calcicolus* (*T. N. Liou 21551,* PE): H, portion of stem with leaves, × 0.6; I, flower, × 1.2. J, K, *I. scoparius* (*Zhongdian Expedition 1268,* KUN): J, cauline leaves, × 0.6; K, flower, × 1.8. L, M, *I. setschwanensis* (*W. C. Wu et al. 12097* (*R.N.7333*, KUN): L, leaf, × 0.6; M, flower, × 2.4. (Drawn by X. C. Li.)

ulate, 4–5 mm long, slightly declinate, purplish, hirtellous on ribs and dotted with yellowish glands outside, glabrous inside, more or less 2-lipped, the teeth 5, lanceolate-ovate, 1–1.5 mm long, with lower 2 slightly broader; fruiting calyx dilated, up to 6–7 mm long, conspicuously 10-nerved. Corolla blue or purple, sparsely pubescent outside, glabrous inside; tube saccate on upper side near base, up to 1 cm long, 3–4 mm in diameter; limb ca. 5 mm long, 2-lipped, the upper lip reflexed, 4-fid at apex, the lower lip boat shaped. Stamens included, filament pilose at base; style included. Nutlets ovoid, 1.5 mm in diameter, dark brown.

DISTRIBUTION AND PHENOLOGY. Southwestern China (northwestern Yunnan and Xizang); dry, shady sites among undershrub in pine, bamboo, and fir forests, 2700–3500 m alt. Flowering June–August, fruiting August–October.

In habit this species is not unlike *Isodon pharicus* (Prain) Murata, but the flowers are much larger and the corolla lips shorter. Since it is variable in leaf form, in pubescence, and in peduncle length, it is best to reduce *Rabdosia irrorata* vars. *crenata, longipes,* and *rungshiaensis* to synonyms of the species.

20. **Isodon wardii** (Marquand & Airy Shaw) H. Hara, J. Jap. Bot. **60:** 237. 1985.

Plectranthus wardii Marquand & Airy Shaw, J. Linn. Soc., Bot. **48:** 216. 1929. *Rabdosia wardii* (Marquand & Airy Shaw) H. Hara, J. Jap. Bot. **47:** 202. 1972. TYPE: China, Tibet [Xizang], Tsangpo Gorge, 19 July 1924, *F. Kingdon-Ward 5957* (holotype, K; isotype, E).

Spreading undershrub, up to 2 m high. Branches quadrangular, slightly 4-sulcate, densely pubescent. Cauline leaves opposite; petiole (1–)1.5–3.5 cm long, slender, plano-convex, pubescent; blade nearly rhombic, (2–)3–6 by (1.5–)2.5–4 cm, with acuminate or nearly obtuse tooth at apex, broadly cuneate at base, grossly crenate-serrate above middle, nearly glabrous or slightly pubescent only on midrib and nerves on both surfaces, the lateral nerves 3 or 4 on each side, slightly raised on both surfaces, the veinlets almost invisible on both surfaces. Panicles terminal, 15–20 cm long, composed of remote 3- to 7-flowered cymes; cymes with peduncle (3–)5–15 mm long, pedicels up to 3 mm long, peduncle, pedicels, and rachis pubescent; lower floral leaves similar to cauline ones, upper floral leaves gradually reduced and changed into entire bracts; bracteoles linear, up to 1.5 mm long. Calyx campanulate, 3.5 mm long, pubescent outside, 2-lipped for almost ½ its length, the teeth 5, triangular-lanceolate, lower 2 slightly longer, all acuminate at apex. Corolla up to 1.2 cm long, pale violet, puberulous outside; tube saccate on upper side near base, equal in diameter upward, ca. 2.5 mm in diameter at throat; limb 2-lipped, the upper lip 4-fid at apex, reflexed, lobes rotund, the lower lip broadly ovate, concave. Stamens and style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. Southwestern China (Xizang); in mixed forests, 2700–3000 m alt. Flowering in July.

This species is allied with *Isodon bulleyanus* (Diels) Kudo but has broader leaf blades that are grossly crenate-serrate above the middle and slender petioles up to 3.5 mm long.

21. **Isodon bulleyanus** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 214. 1929. FIGURE 4A–E.

Plectranthus bulleyanus Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 229. 1912. *Rabdosia bulleyana* (Diels) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: China, Yunnan, eastern flank of Tali Range, 25°40′N, June 1906, *G. Forrest 4554* (holotype, E, not seen).

P. provicarii Léveillé, Cat. Pl. Yun-Nan, 141. 1916. *Rabdosia provicarii* (Léveillé) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: China, Yunnan, pâtures des mont. à Pe long tsin, Nov. 1912, *E. E. Maire s.n.* (holotype, P, not seen; isotype, E).

Rabdosia bulleyana (Diels) H. Hara var. *foliosa* C. Y. Wu, Fl. Yunnan. **1:** 768. 1976. TYPE: China, Yunnan, Teng-chuan, *R. C. Ching 24890* (holotype, KUN; isotype, PE).

Dwarf undershrub, 0.6–0.9 m high, much branched almost from base. Branches slender, obtusely quadrangular, finely striate, purple, densely whitish-hispidulous. Leaves opposite; petiole 1–3 mm long, concave-convex, hispidulous; blade narrowly ovate, (1.5–)4–6 by (1–)2–2.5 cm, acute at apex, cuneate at base, crenate-dentate in upper ⅔ or grossly serrate above entire base, thin-chartaceous, the upper surface sparsely whitish-hirtellous, the lower surface whitish-hispidulous on midrib and nerves, glandular, the lateral nerves ca. 3 on each side, slightly sunken above, raised beneath, the veinlets visible beneath. Panicles terminal, 6–10 cm long, narrow, composed of 1- to 5-flowered cymes; cymes with peduncle 3–10 mm long (lowest longest, gradually shorter upward), pedicels 1.5–3 mm long, peduncle, pedicels, and rachis whitish-pilose; bracts ovate, 0.5–1.3 by 0.3–0.7 cm, entire; bracteoles linear, up to 1 mm long. Calyx campanulate, 2.5 mm long, whitish-pilose, or pubescent and glandular outside, 2-lipped for ½ its length, the teeth 5, ovate-triangular, subequal, acute at apex. Corolla up to 14 mm long, dark blue but pinkish at base, pilose on lower part outside; tube saccate on upper side near base and there ca. 3 mm in diameter, subequal upward, ca. 3.2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 4 mm long, reflexed, equally 4-fid at apex, the lower lip broadly ovate, ca. 5 mm long, concave. Stamens and style included. Mature nutlets ovoid, triquetrous, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (western Yunnan); in dry sites among scrub or in sparse mixed forest, 2450–3200 m alt. Flowering June–September, fruiting in September.

Handel-Mazzetti considered *Plectranthus provicarii* to be very close to *Isodon bulleyanus,* but I think they are identical. Since comparison of the type of *P. provicarii* with the specimens collected from Dali (the type locality of *I. bulleyanus*) reveals only minor differences in leaf serration and in calyx indumentum, I reduce the former to a synonym of the latter. In addition, *Rabdosia bulleyana* var. *foliosa* differs so little from *I. bulleyanus* that it is best to include it in the species. The species is allied to *I. irroratus,* but the calyx is shorter and the corolla tube is longer in relation to the limb.

B. **Isodon** ser. **Excisi** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Excisae* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66**: 490, 589. 1977. *Plectranthus* ser. *Gerardiani* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a**: 353. 1897, *pro parte minore.*

Perennial herbs or subundershrubs, with excised leaves. Cymes arranged into narrow panicles. Calyx campanulate, subequally 5-toothed or slightly 2-lipped in fruit. Corolla medium in size, with declinate tube.

TYPE SPECIES. *Isodon excisus* (Maxim.) Kudo.

KEY TO THE SPECIES OF SER. EXCISI

1. Leaves densely hairy beneath, the apical tooth narrowly lanceolate, 2–2.5 cm long, slightly cuneate, never constricted at its base to midrib of blade, entire; bracts spathulate; flowers 5–6 mm long; cymes 10- to 15-flowered. ..... 22. *I. macrophyllus.*
1. Leaves sparsely hairy or subglabrescent beneath, the apical tooth caudate, 4–6 cm long, cuneate, constricted at its base to midrib of blade, entire or 1- to few-serrate; bracts ovate; flowers up to 9 mm long; cymes (1- to) 3- to 5-flowered. ..... 23. *I. excisus.*

22. **Isodon macrophyllus** (Migo) H. Hara, J. Jap. Bot. **60**: 235. 1985.

Amethystanthus macrophyllus Migo, J. Shanghai Sci. Inst. Sect. 3. **3**: 230. 1937. *Rabdosia macrophylla* (Migo) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 90. 1975. TYPE: China, Jiangsu, prope Chulinssu, Chinkiang, 23 Sept. 1934, *H. Migo* (holotype, TI, not seen).

Perennial herb or subundershrub. Stems numerous, 1–1.5 m high, ca. 5 mm in diameter, sometimes branched in upper portion, woody at base, quadrangular, 4-sulcate, green or sometimes purplish, densely floccose-puberulous. Cauline leaves opposite; petiole (1–)3–5 cm long, broadly alate on upper portion, concave-convex, densely puberulous; blade suborbicular or orbicular-ovate, occasionally broadly lanceolate, (5.5–)10–15 by (4.7–)5–10 cm (smaller in lower leaves), the apex excised (acute and not excised in lower leaves), with apical tooth narrowly lanceolate, 2–2.5 cm long, slightly cuneate at base, the base broadly cuneate or rotund to cuneate and abruptly attenuate, the margin grossly crenate-serrate, the texture chartaceous, the upper surface with midrib and nerves densely puberulous, otherwise sparsely puberulous but glabrescent, the lower surface densely tomentulose, the lateral nerves ca. 4 on each side, inconspicuous above but raised beneath, the veinlets parallel, visible on both surfaces. Panicles terminal or axillary, up to 15 cm long, composed of 10- to 15-flowered cymes; cymes with peduncle 0.5–10 mm long, pedicels 3–5 mm long, peduncle, pedicels, and rachis densely pubescent; floral leaves similar to cauline ones but short-petiolate, smaller, subentire, densely pubescent, gradually changed into spathulate or oblanceolate bracts upward; bracteoles linear, ca. 1 mm long, densely pubescent. Calyx campanulate, 2.2–2.4 mm long, densely pubescent outside, glabrous inside, slightly 2-lipped, the teeth 5, with lower 2 ovate-triangular, 1–1.5 mm long, apiculate at apex, upper 3 smaller; fruiting calyx dilated, obviously nervate, 2-lipped for ca. ⅓ its length, upper 3 teeth

reflexed. Corolla bluish or purplish; tube saccate on upper side near base, ca. 2.5 mm long, 1.5 mm in diameter at throat; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, equally 4-fid at apex, the lower lip broadly ovate, ca. 3.5 by 3 mm, concave. Stamens slightly exserted, filament barbate on lower ½; style exserted. Mature nutlets obovoid, 2.5 mm long, rounded at apex, hairy and glandular.

DISTRIBUTION AND PHENOLOGY. Eastern China (Jiangsu); on mountain slopes or in forests, ca. 120 m alt. Flowering and fruiting September–October.

This species is obviously allied to *Isodon excisus* (Maxim.) Kudo but differs in its cymes that are many flowered and its leaves that are not much excised.

23. **Isodon excisus** (Maxim.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 133. 1929.

Plectranthus excisus Maxim. Mém. Acad. Imp. Sci. Saint-Pétersbourg **9:** 213. 1859. *Amethystanthus excisus* (Maxim.) Nakai, Bot. Mag. Tokyo **48:** 787. 1934. *Rabdosia excisa* (Maxim.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPES: China, Amur, *Maximowicz,* iter secundum 1859 (holotype, LE; isotypes, A, K, W).

Perennial herb. Stems numerous, erect, 0.6–1 m high, unbranched or branched, semiwoody in lower portion, quadrangular, 4-sulcate, finely striate, yellow-brown but sometimes purplish, sparsely pubescent; branches short. Cauline leaves opposite; petiole 0.6–6 cm long, alate on upper portion, concave-convex, sparsely pubescent; blade orbicular or orbicular-ovate, (4–)6–13 by (3–)4–10 cm, apex excised (apical tooth 4–6 cm long, cuneate at base and constricted to midrib of blade, entire or 1- to few-serrate), broadly cuneate or subtruncate and abruptly attenuate-decurrent at base, grossly callose-dentate-serrate except at base, the upper surface densely pubescent on midrib and nerves, otherwise strigose-hispidulous, the lower surface sparsely hairy or subglabrescent, dotted with yellowish glands, the lateral nerves 3 or 4 on each side, raised on both surfaces, the veinlets parallel, conspicuous. Panicles terminal and axillary, 6–15 cm long (terminal one longest), composed of (1- to) 3- to 5-flowered cymes; cymes with peduncle ca. 3 mm long, pedicels 1–2 mm long, peduncle, pedicels, and rachis densely pubescent; floral leaves similar to cauline ones but smaller, shortly petiolate or subsessile; bracts ovate-lanceolate to lanceolate or linear, up to 5 mm long; bracteoles linear, ca. 1 mm long. Calyx campanulate, 3 mm long, pubescent and glandular outside, glabrous inside, 2-lipped for ½–⅔ its length, lower lip slightly longer than upper one (up to 1.8 mm), the teeth narrowly triangular, acute; fruiting calyx slightly dilated, ca. 4 mm long, inconspicuously 2-lipped, teeth subequal. Corolla up to 9 mm long, purplish, purple, or blue, puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 4 mm long, ca. 5 mm in diameter, slightly constricted at throat; limb 2-lipped, the upper lip up to 4 mm long, reflexed, 4-fid at apex, with middle lobes smaller and approximate, the lower lip broadly ovate, up to 5 mm long, concave. Stamens included or slightly exserted. Mature nutlets obovoid, 1.5 mm long, rotund at apex, brown, hairy and glandular.

DISTRIBUTION AND PHENOLOGY. Northern China (Jilin, Hebei, Shanxi, Gansu), Korea, Japan, Soviet Union (Far Eastern Region); on grassland, along roadsides, at forest edges, or in forests, 550–1100 m alt. Flowering July–August, fruiting August–September.

This species is distinct in its very excised leaves and its campanulate calyx that has five subequal teeth or is slightly two-lipped in fruit.

C. **Isodon** ser. **Gerardiani** (Briq.) H. W. Li, comb. nov.

Plectranthus ser. *Gerardiani* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 353. 1897, *pro parte majore.*

Mainly perennial herbs, rarely subundershrubs to undershrubs. Cymes arranged into loose panicles. Calyx with 5 short teeth or 2 inconspicuous lips in fruit. Corolla medium or small, with tube spreading or straight.

LECTOTYPE SPECIES. *Plectranthus gerardianus* Bentham (=*Isodon lophanthoides* (Buch.-Ham. ex D. Don) H. Hara var. *gerardianus* (Bentham) H. Hara).

KEY TO THE SPECIES OF SER. GERARDIANI

1. Corollas usually yellow or yellowish, rarely rose. ..... 24. *I. flavidus.*
1. Corollas purplish, blue, rose, or white, but never yellow or yellowish.
   2. Inflorescences gray-tomentulose. ..... 25. *I. calcicolus.*
   2. Hairs covering inflorescence never gray.
      3. Leaves narrowly lanceolate or lanceolate to elliptic-lanceolate, narrowly cuneate at base. ..... 26. *I. walkeri.*
      3. Leaves broadly ovate, orbicular-ovate to suborbicular or triangular-ovate, or ovate to ovate-lanceolate, rounded to cuneate-attenuate or cordate at base.
         4. Leaves broadly ovate, orbicular-ovate, or suborbicular to triangular-ovate, more or less conspicuously cordate at base.
            5. Leaves conspicuously rugose. ..... 27. *I. nilgherricus.*
            5. Leaves not rugose.
               6. Leaves broadly ovate or orbicular, 3–7 by 2–4.5 cm, subglabrous or more or less pubescent on both surfaces; cymes with short branchlets; corollas ca. 4.5 mm long (less than 2 times length of calyx). ..... 28. *I. wightii.*
               6. Leaves triangular-ovate, 1–5.5 by 0.8–5 cm, whitish septate-villose on both surfaces; cymes with elongate branchlets; corollas up to 6 mm long (more than 2 times length of calyx). ... 29. *I. capillipes.*
         4. Leaves ovate or ovate-lanceolate, rounded to cuneate-attenuate but never cordate at base.
            7. Inflorescences papillose-velutinous. ..... 30. *I. yuennanensis.*
            7. Inflorescences not papillose-velutinous.
               8. Stamens and style included or subincluded.
                  9. Stems villose; leaves rugose, nigrescent when dry. ..... 31. *I. nigrescens.*
                  9. Stems pubescent; leaves not rugose, not nigrescent when dry.
                     10. Fruiting calyces subglabrous or more or less pubescent.
                        11. Leaves ovate to ovate-oblong, truncate or sometimes broadly cuneate at base. ..... 32. *I. hians.*
                        11. Leaves lanceolate or lanceolate-ovate to ovate, cuneate at base.

12. Fruiting calyces ovate-tubular, 5 mm long, up to 3 mm in diameter at mouth, toothed for nearly ⅔ of their length. ..... 33. *I. rivularis.*
12. Fruiting calyces campanulate-tubular or subtubular, 4.5 mm long, 1 mm in diameter at mouth, toothed for ⅕ of their length. ..... 34. *I. dhankutanus.*

10. Fruiting calyces sparingly hirsute. ..... 35. *I. javanicus.*

8. Stamens and style much exserted.
13. Plant much branched; leaves rugose, densely tomentose beneath. ..... 36. *I. ramosissimus.*
13. Plant few branched; leaves not rugose, villose, hirsute, or pubescent beneath.
14. Corollas dark brown-purple. ..... 37. *I. pulchokiensis.*
14. Corollas purplish, white, or pink-lavender.
15. Corolla tubes gibbous near base. .. 38. *I. teysmannii.*
15. Corolla tubes not gibbous near base.
16. Calyces densely septate-villose over entire surface. ..... 39. *I. hispidus.*
16. Calyx sparsely septate-villose only on lower part. ..... 40. *I. lophanthoides.*

24. **Isodon flavidus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 234. 1985.

FIGURE 5A–E.

Plectranthus flavidus Hand.-Mazz. Symb. Sin. 7: 942. 1936. *Rabdosia flavida* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPE: China, Yunnan, ad viam Yünnanfu–Dali (Talifu), in regionis calide temperatae, sepibus supra vic. Hsiaoschao pr. opp. Dschaodschou, 28 Oct. 1915, *Handel-Mazzetti 8563* (holotype, W; isotype, A).

Perennial herb. Stems 40–90 cm high, robust, pyramidally branched from lowest ⅓, quadrangular (angles narrowly alate), glabrous. Cauline leaves sessile, opposite; blade ovate, rhombic, or ovate-oblong, 3.5–15 by 1.2–6.7 cm, acute at apex, broadly cuneate- or subtruncate-attenuate at base, crenate, membranaceous or chartaceous, the upper surface olive-green, furfuraceous-strigillose, glabrescent, the lower surface greenish, glabrous, dotted with brown or dark glands. Panicles terminal, 4.5–35 cm long, 3.2–7(–10) cm in diameter, composed of 3- to 15-flowered cymes; cymes with peduncle patent, 4.5–24 mm long, pedicels 4–10 mm long; lower floral leaves similar to cauline ones, subsessile, upper floral leaves changed into bracts; bracts sessile, lanceolate, ca. 5 mm long; bracteoles linear, much shorter than pedicels. Calyx campanulate, ca. 2.5 mm long, 3 mm in diameter, reddish-brown-gland-dotted and very-short-papillose-velutinous like entire panicle, slightly 2-lipped, the teeth 5, broadly ovate-triangular, almost as long as calyx tube (lower 2 slightly longer), acute at apex; fruiting calyx obliquely tubular-campanulate, 4–4.5 mm long, teeth much shorter than calyx tube. Corolla ca. 7 mm long, usually yellow or yellowish, rarely rose; tube exserted, saccate on upper side near base, ca. 3 mm in diameter; limb dotted with red glands, 2-lipped, the upper lip very reflexed, 4-fid at apex, the lower lip narrowly ovate or oblong, longer, plane, obtuse or acute. Stamens much exserted, the filament complanate, whitish-pilose at base; style exserted, 2-fid at apex. Nutlets ovoid, ca. 1 mm long, greenish, glabrous.

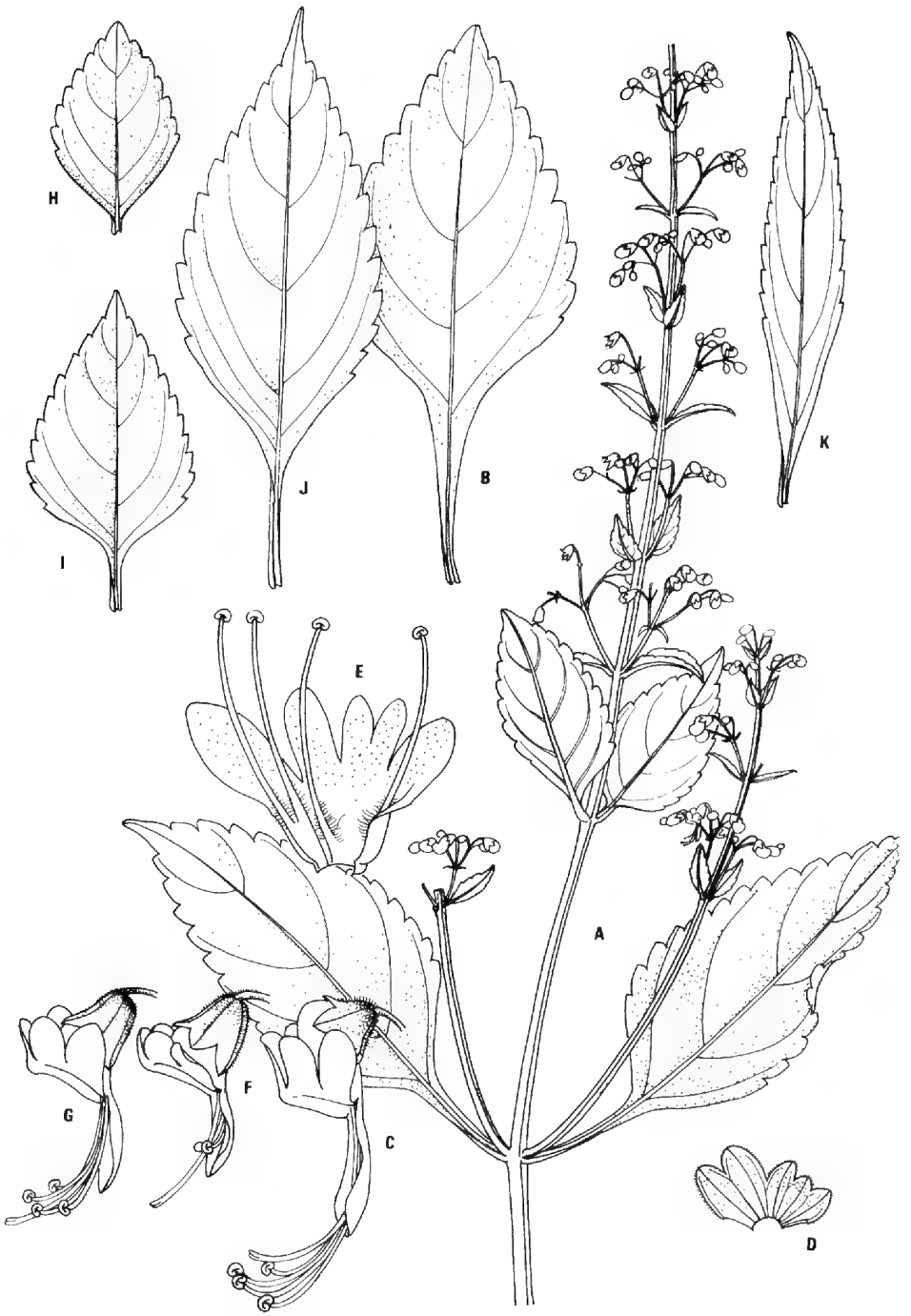

FIGURE 5. A–E, *Isodon flavidus* (*R. C. Ching 25375,* KUN): A, upper portion of plant, × 0.6; B, leaf, × 0.6; C, flower, × 4.2; D, calyx, × 4.2; E, corolla and stamens, × 4.2. F–I, *I. yuennanensis* (*Zhongdian Expedition 2242,* KUN): F, G, flowers, × 4.2; H, I, leaves, × 0.6. J, *I. lophanthoides* var. *graciliflorus* (*W. T. Tsang 16613,* PE), leaf, × 0.6. K, *I. walkeri* (*H. Y. Liang 64068,* PE), leaf, × 0.6. (Drawn by X. L. Zeng.)

DISTRIBUTION AND PHENOLOGY. South-central China (Yunnan and Guizhou); in mixed forests or wet sites at forest edges, 1500–2600 m alt. Flowering and fruiting September–November.

This species is distinctive in its usually yellow or yellowish (rarely rose) corolla and its leaves broadly cuneate- or subtruncate-attenuate at base. It looks much like *Isodon phyllopodus* (Diels) Kudo but differs in its calyx, which is inconspicuously two lipped and in fruit has much shorter teeth, and in its yellow or yellowish (rarely rose) corolla.

25. **Isodon calcicolus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Plectranthus calcicolus Hand.-Mazz. Symb. Sin. **7:** 944. 1936. *Rabdosia calcicola* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 194. 1972. (TYPE: China, Yunnan, inter urbes Dali (Talifu) et Lidjiang (Likiang), in regionis calide temperatae declivibus siccis prope viam Beishan, 26°16'N, 18 Sept. 1915, *Handel-Mazzetti 8537* (holotype, w).

KEY TO THE VARIETIES OF ISODON CALCICOLUS

1. Leaves with lower surface ferrugineous-tomentulose on elevated venation, otherwise gray-tomentose and glandular; corolla white or purple. ..... 25a. var. *calcicolus.*
1. Leaves with lower surface white-tomentulose on elevated venation, otherwise densely papillose–glandular hairy; corolla white or rose. ..... 25b. var. *subcalvus.*

25a. **Isodon calcicolus** var. **calcicolus** FIGURE 4H, I.

Perennial herb. Stems numerous, erect, 40–60 cm high, slender, much branched and woody at apex, obtusely quadrangular, 4-sulcate, sometimes purplish, densely recurved-gray-tomentose. Cauline leaves opposite; petiole very short; blade narrowly lanceolate or obovate-lanceolate, 3–9 by 0.5–1.5(–2.5) cm, acute at apex, narrowly attenuate at base, callose-crenate-serrulate except at base, chartaceous, the upper surface green, densely pilose, the lower surface ferrugineous-tomentulose on elevated midrib and nerves, otherwise gray-tomentose and glandular, the lateral nerves ca. 4 on each side, very oblique, like midrib sunken above but conspicuously raised beneath, the veinlets reticulate, conspicuous beneath. Panicles terminal, loose, 10–30 cm long, composed of 3- to 7-flowered cymes; cymes with peduncle less than 1 cm long, pedicels 1–4 mm long, peduncle, pedicels, and rachis densely gray-tomentose; floral leaves subsessile, more or less lanceolate, gradually reduced upward, upper ones shorter than peduncles of cymes; bracteoles linear, less than 1 mm long, much shorter than pedicels. Calyx campanulate, ca. 2 mm long, densely gray-tomentose outside, glabrous inside, inconspicuously 2-lipped, the teeth 5, ovate-triangular, shorter than calyx tube, subequal; fruiting calyx tubular-campanulate, up to 4 mm long, curved, 10-nerved, slightly 2-lipped, lower 2 teeth larger. Corolla 6–7 mm long, white or purplish, white-pilose and glandular outside, glabrous inside; tube slightly exserted, saccate on upper side near base; limb 2-lipped, the upper lip ca. 2 mm long, reflexed, equally 4-fid at apex, the lower lip broadly ovate, ca. 4 mm long, concave. Stamens and style exserted. Mature nutlets ovoid, triquetrous, ca. 1 mm long, yellow-brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (central and western Yunnan); on grassy slopes or grasslands near forest edges in areas underlain by limestone, (1600–)2300(–2600) m alt. Flowering September–October, fruiting October–November.

25b. **Isodon calcicolus** var. **subcalvus** (Hand.-Mazz.) H. W. Li, comb. nov.

Plectranthus calcicolus Hand.-Mazz. var. *subcalvus* Hand.-Mazz. Acta Horti Gothob. **13:** 378. 1939. *Rabdosia calcicola* (Hand.-Mazz.) H. Hara var. *subcalva* (Hand.-Mazz.) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 90. 1975. *P.* species Hand.-Mazz. Symb. Sin. **7:** 944. 1936, under *P. calcicolus* Hand.-Mazz. TYPE: China, Yunnan, pâtures des mont. à Tong-tchouan, *E. E. Maire s.n.* (holotype, w).

This variety differs from var. *calcicolus* in having the lower surface of the leaves white-tomentulose on the elevated venation, otherwise densely papillose-glandular-hairy, and the corolla white or rose.

DISTRIBUTION AND PHENOLOGY. South-central China (northeastern Yunnan); on grassy slopes, 2600–3000 m alt. Flowering September–October, fruiting October–November.

This species (including both varieties) superficially looks much like *Isodon nervosus* but differs in its decurved, tubular-campanulate fruiting calyx and its leaves that are tomentulose or tomentose beneath.

26. **Isodon walkeri** (Arn.) H. Hara, J. Jap. Bot. **60:** 237. 1985. FIGURE 5K.

Plectranthus walkeri Arn. Pug. Pl. Ind. Or. 36. 1836. *Rabdosia walkeri* (Arn.) H. Hara, J. Jap. Bot. **47:** 202. 1972. TYPE: Ceylon, *Walker s.n.* (not seen).

P. stracheyi Bentham ex Hooker f. Fl. Brit. India **4:** 618. 1885. *Isodon stracheyi* (Bentham ex Hooker f.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 136. 1929. *Rabdosia stracheyi* (Bentham ex Hooker f.) H. Hara, J. Jap. Bot. **47:** 201. 1972. TYPE: Western Himalaya, Kumaon, Surja valley, 4500 ft. alt., *Strachey & Winterbottom s.n.* (not seen).

P. veronicifolius Hance, J. Bot. **23:** 327. 1885. *Isodon stracheyi* (Bentham ex Hooker f.) Kudo var. *veronicifolius* (Hance) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 136. 1929. TYPE: China, Hainan, in praefectura Hung-mo, territori indigenarum Lai dictorum, 21 Nov. 1882, *B. C. Henry Herb. propr. 22298* (not seen).

P. brandisii Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. **59:** 296. 1890. SYNTYPES: Burma, Pegu, *Brandis 813, Kurz 573, 2401, 2405, 2406, 2407* (none seen).

P. striatus auct. non Bentham: Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 158. 1913.

Perennial herb. Stems 40–60 cm high, repent at base, ascendent, unbranched or branched, obtusely quadrangular except subterete lower part, 4-sulcate, septate-puberulous or furfuraceous-pilose; internodes much shorter than leaves. Cauline leaves opposite; petiole 0.2–1.2 cm long, plano-convex, furfuraceous-hispidulous above; blade narrowly lanceolate or lanceolate to elliptic-lanceolate, 2.4–7.5 by 0.6–2.1 cm, shortly acuminate or acuminate at apex, narrowly cuneate at base, more or less remotely serrate just above middle, chartaceous, the upper surface olive-green, furfuraceous-hispidulous on midrib and nerves, otherwise glabrous, the lower surface greenish, subglabrous, dotted with brown glands. Panicles terminal, 4–30 cm long, 2.5–6 cm in diameter, composed of

3- to 15-flowered cymes; cymes with peduncle 0.4–1.4(–2.8) cm long, pedicels 2–5 mm long, peduncle, pedicels, and rachis furfuraceous-pilose; lowest floral leaves similar to cauline ones, upper floral leaves gradually reduced and changed into ovate or lanceolate bracts; bracteoles linear, less than 1 mm long. Calyx campanulate, ca. 2 mm long, 1.6 mm in diameter, subglabrous or furfuraceous-pilose on ribs, dotted with brown glands, conspicuously 10-nerved, slightly 2-lipped, the teeth 5, ovate, lower 2 slightly longer than upper 3; fruiting calyx ca. 3 mm long, 1.1 mm in diameter, lower lip much longer than upper one. Corolla 6–7 mm long, rose or white; tube erect, dilated upward, 3–3.5 mm long, ca. 1 mm in diameter at base and 2 mm at throat; limb 2-lipped, the upper lip purple-maculate, strongly reflexed, 4-fid at apex, the lower lip narrowly ovate, straight, plane. Stamens and style much exserted. Nutlets ovoid, slightly compressed.

DISTRIBUTION AND PHENOLOGY. Sri Lanka, India, Burma, Laos, and southern China (Guangdong, Hainan); along stream banks or in moist sites in shady forests, 300–1300 m alt. Flowering November–January, fruiting December–January.

Although the specimens from Sri Lanka all have narrower, more deeply serrate leaves, I can't find any other differences with those from other localities. I have therefore combined *Isodon stracheyi* with *I. walkeri* and have used the latter name because it has priority. The species is obviously close to *I. lophanthoides* (Buch.-Ham. ex D. Don) H. Hara but differs in having leaves that are narrowly lanceolate or lanceolate to elliptic-lanceolate, narrowly cuneate at the base, and more or less remotely serrate above the base.

27. **Isodon nilgherricus** (Bentham) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Plectranthus nilgherricus Bentham *in* DC. Prodr. **12:** 57. 1848. *Rabdosia nilgherrica* (Bentham) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: in montibus Nilghery peninsulae Indiae Orientalis, *F. Adam* (not seen).

Perennial herb. Stems erect, ca. 60 cm high, obtusely quadrangular, 4-sulcate, finely striate, reddish, densely ferrugineous-septate-villose; internodes shorter than leaves. Cauline leaves opposite; petiole 0.5–3 cm long, plano-convex, densely ferrugineous-villose; blade orbicular-ovate, 4–7 by 3–6.5 cm, acuminate at apex, cordate at base, crenulate, chartaceous, rugose, densely ferrugineous-septate-villose on both surfaces, dotted with reddish brown glands beneath, the lateral nerves ca. 5 on each side, arcuate-ascendent, like midrib and veinlets sunken above but conspicuously raised beneath. Panicles terminal, together forming complex one up to 20 cm long and 14 cm in diameter, composed of spreading, many-flowered cymes; cymes with the peduncle 5–10 mm long, the pedicels 2.5 mm long, slender, the peduncle, pedicels, and rachis densely villose; lowest floral leaves similar to cauline ones, upper floral leaves gradually reduced and changed into bracts; bracts sessile, ovate, 0.5–3 by 0.2–2 mm; bracteoles narrowly ovate to linear, 1.5–3 mm long. Calyx tubular-campanulate, ca. 3 mm long, up to 1.5 mm in diameter, slightly curved, densely

villose, glandular, and conspicuously 10-nerved outside, the teeth 5, ovate-triangular, subequal, ca. 0.5 mm long, obtuse at apex. Corolla ca. 6.5 mm long; tube slightly dilated at throat, ca. 5 mm long, straight, subglabrous; limb ca. 1.5 mm long, villose outside, glabrous but with red spots on lips inside, 2-lipped, the upper lip reflexed, 4-fid at apex, the lower lip suborbicular, patent. Stamens and style exserted. Nutlets compressed-orbicular, ca. 0.7 mm long and in diameter, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. Southern India (Tamil Nadu); on hillsides, ca. 1700 m alt. Flowering and fruiting in October.

This species is distinctive in this series in its conspicuously rugose leaves.

28. **Isodon wightii** (Bentham) H. Hara, J. Jap. Bot. **60:** 237. 1985.

Plectranthus wightii Bentham, Labiat. Gen. Spec. 41. 1832. *Rabdosia wightii* (Bentham) H. Hara, J. Jap. Bot. **47:** 203. 1972. SYNTYPES: in India orientali, in peninsulae montosis circa Madura et Tenivelly, *Wight*; in monte Kedrongon, *Leschenault* (neither seen).

P. nepetaefolius Bentham *in* DC. Prodr. **12:** 57. 1848. TYPE: Peninsula Ind. Orientalis, *Herb. Wight. Propr. 2567* (holotype, K).

P. pulneyensis Hooker f. Fl. Brit. India **4:** 617. 1885. TYPE: India, Pulney Mtns., *Wight s.n.*, Sept. 1836 (holotype, K).

Perennial herb. Stems erect, branched, obtusely quadrangular, slightly 4-sulcate, finely striate, reddish, more or less ferrugineous-pubescent. Cauline leaves opposite; petiole 1–3 cm long, more or less pubescent; blade broadly ovate or orbicular, 3–7 by 2–4.5 cm, acuminate at apex, cordate at base, obtusely serrate, chartaceous, subglabrous or more or less septate-pubescent on both surfaces, dotted with red glands beneath, the lateral nerves ca. 4 on each side, arcuate-ascendent, slightly sunken above but raised beneath like midrib, the veinlets visible on both surfaces. Panicles terminal, together forming large, complex one, composed of spreading, many-flowered cymes; cymes with peduncle 5–10 mm long, pedicels 3–5 mm long, peduncle, pedicels, and rachis pubescent; lowest floral leaves similar to cauline ones, upper floral leaves reduced and changed into bracts upward; bracts subsessile, ovate, 0.5–1.5 by 0.3–1 cm; bracteoles ovate, 2–4 by 1.5–2 mm. Calyx campanulate, ca. 2 mm long, 2 mm in diameter at mouth, more or less pubescent and glandular outside, the teeth 5, ovate-triangular, ⅓ of calyx length; fruiting calyx tubular-campanulate with oblique mouth, up to 4 mm long, subglabrous, conspicuously nervate. Corolla 4.5 mm long, lavender, white, or bright blue, tube slightly saccate on upper side near base, dilated upward, ca. 3 mm long, up to 2.5 mm in diameter at throat, subglabrous outside; limb ca. 1.5 mm long, 2-lipped, the upper lip reflexed, 4-fid at apex, the lower lip suborbicular, straight. Stamens and style included. Nutlets compressed-ovoid, ca. 1 mm long, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. Southern India (Tamil Nadu); along streams, in ravines, or on hillsides, 600–2300 m alt. Flowering and fruiting September–October.

This species is very close to *Isodon nilgherricus* but differs in its leaves that are subglabrous or sometimes less septate-pubescent on both surfaces and that are not rugose when dry.

29. **Isodon capillipes** (Bentham) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Plectranthus capillipes Bentham *in* DC. Prodr. **12:** 57. 1848. *Rabdosia capillipes* (Bentham) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: Ceylonâ, *Walker* (holotype, K; isotypes, A, W).

Perennial herb. Stems ascendent-erect, 30–45 cm high, unbranched or with few branches, obtusely quadrangular, slightly 4-sulcate, yellow-brownish, pubescent and long-septate-strigose. Cauline leaves opposite; petiole 1–2 cm (lower and middle ones) or to 0.5 cm (upper ones) long, pubescent and septate-strigose; blade triangular-ovate, quite variable in size, 1–5.5 by 0.8–4 cm (middle ones largest), acuminate at apex, rotund-truncate or shallowly cordate-truncate at base, grossly crenulate, the upper surface densely septate-strigose, the lower surface strigose on midrib and nerves, dotted with brown glands, the lateral nerves ca. 3 on each side, arcuate-ascendent and anastomosing near margin, slightly sunken above, raised beneath like midrib, the veinlets conspicuously visible beneath. Panicles terminal, 12–15 cm long, up to 5 cm in diameter, together forming large, complex one on top of plant, composed of long, dichotomous 9- to 21-flowered cymes; cymes with the peduncle 0.8–1.5 cm long, the pedicels 4–6 mm long, slender in proportion to calyx length, the peduncle, pedicels, and rachis pubescent; lowest floral leaves similar to cauline ones but smaller, upper floral leaves all changed into bracts; bracts ovate or ovate-oblong, 4–6 by 1–3 mm; bracteoles linear, 0.5–2 mm long. Calyx campanulate, 1.5 mm long, 1.2 mm in diameter, pubescent and glandular outside, glabrous inside, inconspicuously 2-lipped, the teeth 5, ovate-triangular, subequal, ⅓ of calyx length; fruiting calyx urceolate-tubular, 3 mm long, 0.5 mm in diameter, curved, conspicuously nervate, teeth ¼ of calyx length. Corolla up to 6.5 mm long, white, with some purple spots on lips, pubescent only on limb or subglabrous outside; tube subequal in diameter upward, 0.75 mm in diameter at throat; limb ca. 1.5 mm long, 2-lipped, the upper lip reflexed, 4-fid at apex, the lower lip suborbicular. Stamens and style exserted. Nutlets compressed-ovoid, 0.7 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Sri Lanka; in highland forests and on grassy sites near water, ca. 2350 m alt. Flowering in March, fruiting in August.

This species is distinctive in its long, dichotomous, nine- to twenty-one-flowered cymes, its pedicels that are slender in proportion to the length of the calyx, and its slim corolla tube.

30. **Isodon yuennanensis** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 237. 1985. FIGURE 5F–I.

Plectranthus yuennanensis Hand.-Mazz. Symb. Sin. **7:** 943. 1936. *Rabdosia yuennanensis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 203. 1972. TYPE: China, Yunnan, pâtures des mont. à Tong-tchouan, Sept. 1910, *E. E. Maire s.n.* (holotype, W).

Perennial herb. Stems 30–70 cm high, generally unbranched, quadrangular, whitish-puberulous and septate-villose, equally foliate over entire length or more densely so on lower part. Cauline leaves opposite, sessile; blade narrowly or broadly ovate, 2.5–6 by 1.4–3.8 cm, acute or occasionally obtuse at apex, cuneate or attenuate at base, crenate, the upper surface olive-green, strigose, the lower surface greenish, densely purplish-glandular and furfuraceous-hirsute especially on midrib and nerves. Panicles terminal or sometimes axillary, 7–34 cm long, papillose-velutinous, composed of divaricate 5- to 15-flowered cymes; cymes with peduncle 0.6–4.5 cm long, pedicels 3–13 mm long; lowest floral leaves similar to cauline ones, upper floral leaves changed into bracts; bracts triangular or lanceolate, 2–3 mm long, entire; bracteoles narrowly lanceolate or linear, 1–2 mm long. Calyx campanulate, ca. 2.8 mm long, 2.8 mm in diameter at mouth, puberulous and red-glandular outside, the teeth 5, broadly ovate, slightly shorter than calyx tube, lower 2 larger; fruiting calyx nodding, up to 5 mm long, recurved at throat, teeth much shorter than calyx tube. Corolla 4–5 mm long, yellowish or whitish but dark- or red-purple on upper lip and with purple spots on lower one; tube dilated upward, slightly longer than calyx, ca. 1.5 mm in diameter at base and 3 mm at throat; limb 2-lipped, the upper lip as long as corolla tube, reflexed, 4-fid at apex, lobes ovate, the lower lip narrowly ovate, almost equal to upper one, plane. Stamens and style exserted. Nutlets compressed-ovoid, ca. 1.2 mm long, 0.8 mm in diameter, dark brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and southwestern Sichuan); on grassland or in pine forests, 1800–3000 m alt. Flowering and fruiting August–October.

This species looks much like those with narrow leaves (e.g., *Isodon nervosus, I. calcicolus, I. angustifolius*), but it is easily recognized by its rhizome with many red buds, its papillose-velutinous inflorescence, and its leaves that are furfuraceous-hirsute beneath.

31. **Isodon nigrescens** (Bentham) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Plectranthus nigrescens Bentham, Labiat. Gen. Spec. 710. 1832. *Rabdosia nigrescens* (Bentham) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: Ceylon, *Walker s.n.* (lectotype, K, chosen by L. H. Cramer; isolectotype, W).

Perennial herb. Stems flexuose, branched, obtusely quadrangular, shallowly 4-sulcate, dark brown when dry, densely rusty-septate-villose. Cauline leaves opposite, sessile or subsessile; blade ovate, variable in size, 1.5–6 by 1–4 cm, subacuminate at apex, broadly cuneate to rotund at base, crenate, chartaceous, rugose, nigrescent when dry, the upper surface sparsely rusty-hispidulous, the lower surface rusty-septate-villose along midrib and nerves, dotted with red glands, the lateral nerves ca. 4 on each side, arcuate-ascendent, sunken above and raised beneath like midrib, the veinlets visible beneath. Panicles terminal, (3–)7–9 cm long, 1.5–3.5 cm in diameter, composed of remote cymes; cymes with peduncle 2–5 mm long, pedicels ca. 2 mm long, peduncle, pedicels, and rachis densely pubescent; floral leaves similar to cauline ones but smaller. Calyx

campanulate, ca. 2 mm long, 1.75 mm in diameter at mouth, densely puberulous outside, 2-lipped for ⅔ its length, the teeth 5, triangular-ovate, lower 2 slightly longer than others, all obtuse at apex; fruiting calyx tubular-campanulate, dilated, ca. 5 mm long, subglabrous outside, obviously nervate, the upper lip reflexed, with 3 broadly ovate teeth, the lower lip with 2 porrect teeth. Corolla gradually dilated, ca. 4 mm long, up to 2 mm in diameter at throat, white with purple spots on limb; limb 2-lipped, the upper lip ca. 2 by 3 mm, reflexed, 4-fid at apex, the lower lip suborbicular, ca. 1.5 mm long, concave. Stamens and style included or subincluded. Nutlets compressed-ovoid, 1.4 mm long, 1 mm in diameter, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Sri Lanka; on wooded hilltops and upper mountain slopes, or in highland rainforests, 2000–2350 m alt. Flowering March–April, fruiting in October.

This species is very distinctive in its rugose leaves that are nigrescent when dry.

32. **Isodon hians** (Bentham) H. W. Li, comb. nov.

Plectranthus hians Bentham *in* DC. Prodr. **12**: 57. 1848. TYPE: in Ceylonâ, *Walker s.n.* (holotype, K).

Perennial herb. Stems repent-ascendent, slender, branched, obtusely quadrangular, shallowly 4-sulcate, incurved-pubescent. Cauline leaves opposite, sessile or subsessile; blade ovate to ovate-oblong, 1.5–8 by 1–4 cm, subacuminate at apex, truncate or sometimes broadly cuneate at base, grossly crenate, chartaceous, the upper surface hispidulous, the lower surface pubescent along midrib and nerves, dotted with brown glands, the lateral nerves ca. 3 on each side, arcuate-ascendent, slightly sunken above and raised beneath, the veinlets visible beneath. Panicles terminal, (5–)7–15 cm long, 2–4 cm in diameter, composed of remote 7- to 13-flowered cymes; cymes dichotomous and with branches elongate, the peduncle 3–9 mm long, the pedicels 1–2.5 mm long, the peduncle, pedicels, and rachis pubescent; floral leaves and bracts narrowly ovate, 4–8 by 1.5–4 mm, acute at apex; bracteoles linear, 0.75 mm long. Calyx campanulate, ca. 2 mm long, up to 2.5 mm in diameter at mouth, pubescent and glandular outside, 2-lipped nearly to middle of calyx, the teeth 5, broadly triangular, acute at apex; fruiting calyx tubular-campanulate, ca. 4 mm long, glabrescent, 2-lipped for ⅓ of calyx. Corolla ca. 6.5 mm long, white-mauve, slightly pubescent outside; tube dilated upward, ca. 4.5 mm long, up to 2.5 mm in diameter at throat; limb 2-lipped, the upper lip 1.5 mm long, reflexed, 4-fid at apex, lobes oblong, the lower lip broadly ovate, 2 mm long, concave. Stamens and style included. Mature nutlets compressed-ovoid, ca. 1 mm long, 0.75 mm in diameter, dark brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Sri Lanka and southern India (Nilgiri Hills); in medium shade beside paths or in forests, 2000–2350 m alt. Flowering in June.

This species is very close to *Isodon nigrescens* but differs in that the entire plant is pubescent and the leaves are not rugose and are not nigrescent when dry.

33. **Isodon rivularis** (Wight ex Hooker f.) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Plectranthus rivularis Wight ex Hooker f. Fl. Brit. India **4:** 617. 1885. *Rabdosia rivularis* (Wight ex Hooker f.) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: India, Nilgherries, ex *Herb. Wight Propr. s.n.* (holotype, K).

Perennial herb. Stems erect, branched, obtusely quadrangular, shallowly 4-sulcate and finely striate, densely pubescent. Cauline leaves opposite; petiole 0.3–2 cm long, concave-convex, densely pubescent; blade lanceolate or lanceolate-ovate to narrowly ovate, 3.5–6.5 by 1–2.5 cm, subacuminate at apex, cuneate-attenuate at base, crenate, chartaceous, densely pubescent along midrib and nerves on both surfaces, scattered-hispidulous over entire upper surface, the lateral nerves ca. 4 on each side, ascendent, like midrib sunken above and raised beneath, the veinlets slightly raised beneath. Panicles terminal and axillary, 6–15 cm long, together forming complex one on top of each stem, composed of 7- to 13-flowered cymes; cymes with peduncle and rachis 1–1.5 mm long, pedicels 1.5–2.5 mm long, peduncle, pedicels, and rachis densely pubescent; lowest floral leaves similar to cauline ones but smaller, others abruptly changed into bracts upward; bracts narrowly ovate to sublinear, 3–15 mm long, subacute at apex, entire; bracteoles linear, 0.5–1 mm long. Calyx campanulate, ca. 1.5 mm long, 1.5 mm in diameter at mouth, pubescent and glandular outside, 2-lipped for almost ½ length of calyx, the teeth 5, ovate-triangular, lower 2 slightly larger than others, all subacute; fruiting calyx broadly ovate-tubular, 5 mm long, up to 3 mm in diameter at mouth, obviously nervate, 2-lipped for ⅖ its length, upper lip with 3 ovate teeth, lower lip with 2 narrowly triangular ones. Corolla ca. 5 mm long, white(?), subglabrous outside; tube subequal in diameter upward, 2 mm in diameter at throat; limb 2-lipped, the upper lip reflexed, 4-fid at apex, lobes broadly ovate, the lower lip broadly ovate, 1.5 mm long, concave. Stamens and style included. Mature nutlets compressed-ovoid, 1.3 mm long, 0.75 mm in diameter, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Southern India; on stream sides. Flowering and fruiting August–October.

This species is allied to *Isodon nigrescens* but differs in that its leaves are not rugose and are not nigrescent when dry. The narrow leaves of *T. rivularis* look much like those of *I. walkeri* but are crenate, not remotely serrate above the base.

34. **Isodon dhankutanus** Murata, Acta Phytotax. Geobot. **22:** 21. 1966.

Rabdosia dhankutana (Murata) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: East Nepal, Dhankuta, alt. 1200 m, 18 Oct. 1963, *H. Hara et al. 6306467* (holotype, KYO, not seen; isotypes, BM, TI).

Perennial herb. Stems erect, 90–150 cm high, branched on upper part, acutely quadrangular, shallowly 4-sulcate, striate, incurved-pubescent; branches slender. Cauline leaves opposite; petiole 0.5–2 cm long, pubescent-tomentulose; blade ovate-lanceolate, 3–7 by 1–3 cm, acuminate at apex, cuneate-decurrent at base, serrate-dentate above base, the upper surface sparsely and minutely hirtellous, the lower surface greenish, adpressedly puberulous-tomentulose, dotted with very small, yellowish glands. Panicles terminal, up to 25 cm long, together forming complex one on top of stem, composed of 5- to 9-flowered cymes; cymes with peduncle 5–10 mm long, slender, pedicels 2–3 mm long, peduncle, pedicels, and rachis pubescent; floral leaves like cauline ones, gradually reduced and changed into bracts upward; bracts ovate, entire; bracteoles linear, less than 1 mm long. Calyx campanulate, 2–2.5 mm long, pubescent outside, the teeth 5, triangular, nearly equal, 0.5 mm long, acute at apex; fruiting calyx campanulate-tubular or subtubular, very elongate, up to 4.5 mm long, ca. 1 mm in diameter at mouth. Corolla 5–6 mm long, puberulous outside; tube saccate on upper side near base, equal in diameter upward, ca. 1 mm in diameter; limb 2-lipped, the upper lip erect, ca. 1.2 mm long, 4-lobed at apex, the lower lip broadly ovate, as long as upper one, boat shaped. Stamens and style included. Nutlets broadly ellipsoid, 0.9 mm long, 0.5 mm in diameter, brown, smooth.

DISTRIBUTION AND PHENOLOGY. Nepal; dry shady sites in pine forests, 1200 m alt. Flowering and fruiting in October.

This species appears closely allied to *Isodon lophanthoides* when in fruit but is quite different in that the stamens and style are included in the flower. It is also distinctive in its very elongate fruiting calyx.

35. **Isodon javanicus** (Blume) H. W. Li, comb. nov.

Elsholtzia javanica Blume, Bijdr. 825. 1826. *Plectranthus javanicus* (Blume) Bentham, Labiat. Gen. Spec. 145. 1832. *Rabdosia javanica* (Blume) Hassk. Flora **25**(Beibl. 2): 25. 1842. LECTOTYPE: Java, Buitenzorg, *Blume s.n.* (L).

Plectranthus intermedius Zoll. & Moritzi *in* Moritzi, Syst. Verz. 55. 1846. TYPE: Java, *Zollinger 1761* (not seen).

P. rufescens Bentham *in* DC. Prodr. **12**: 59. 1848. TYPE: Java, *Zollinger 1906* (not seen).

P. benthamianus Miq. Fl. Ned. Ind. **2**: 946. 1858. TYPE: Prahoe, *Horsfield s.n.* (not seen).

P. diffusus Merr. Philipp. J. Sci. **1**(Suppl.): 235. 1906. TYPE: Luzon, Lepanto, Mt. Data, *Merrill 4554* (not seen).

P. menthoides auct. non Bentham: Moritzi, Syst. Verz. 55. 1846.

Perennial herb or subundershrub. Stems erect, 0.8–2 m high, slender, often much branched, like branches obtusely quadrangular, shallowly 4-sulcate, striate, pubescent. Cauline leaves opposite; petiole 0.5–1 cm long, plano-convex, pubescent; blade ovate to oblong-ovate or rhomboid, 2–5(–8) by 1–2.5(–5) cm, acuminate at apex, broadly cuneate or rounded at base, prominently serrate except at base, thin-chartaceous, crisped-pubescent on both surfaces, sometimes dotted with red-brown glands beneath, the lateral nerves 3 or 4 on each

side, obliquely ascendent, like midrib slightly sunken above and raised beneath, the veinlets inconspicuous on both surfaces. Panicles terminal or axillary, together forming complex one on top of each stem or branch; composed of dichotomously or duplo-dichotomously branched 3- to 7-flowered cymes; cymes with peduncle 2–8 mm long, gradually reduced upward, pedicels 1–3 mm long, peduncle, pedicels, and rachis pubescent; lower floral leaves similar to cauline ones, others gradually reduced upward and changed into bracts; bracts ovate, 1.5–10 mm long, serrate or entire; bracteoles linear, less than 1 mm long. Calyx campanulate, 1.5–2 mm long, sparingly hirsute and glandular, 2-lipped for ⅓ its length, the teeth 5, triangular, subequal, acute; fruiting calyx broadly tubular-campanulate, 4.5–5 mm long, slightly curved at middle, obviously nervate. Corolla up to 7 mm long, straight, violet- to pale-blue, slightly puberulous outside; tube inconspicuously saccate, up to 3.5 mm long, 2 mm in diameter at throat, straight; limb 2-lipped, the upper lip up to 1.5 mm long, reflexed, 4-fid at apex, lobes semiorbicular, the lower lip broadly ovate, up to 3.5 mm long. Stamens included, filament pubescent below; style included. Nutlets ovoid or ellipsoid, ca. 1 mm long, brown to black, smooth, glabrous.

DISTRIBUTION AND PHENOLOGY. Indonesia (Sumatra (Atjeh), Java, Lombok, Sumbawa) and the Philippines (Luzon); at forest edges, in secondary growth, clearings, grassland, and *Casuarina* forest, and along streams, (850–)1000–2400 m alt. Flowering year-round.

This species appears to be closely allied to *Isodon lophanthoides,* especially var. *gerardianus,* but differs in having the stamens and style included in the lower lip of the corolla. It is also close to *I. dhankutanus,* differing in the calyx being sparingly hirsute and glandular outside.

36. **Isodon ramosissimus** (Hooker f.) Codd, Taxon **17:** 239. 1968.

Plectranthus ramosissimus Hooker f. J. Linn. Soc., Bot. **6:** 17. 1862. *Homalocheilos ramosissimum* (Hooker f.) J. K. Morton, J. Linn. Soc., Bot. **58:** 268. 1962. TYPE: West Trop. Africa, Fernando Po, Clarence Peak, 5000 ft, 1860, *Mann 624* (holotype, K, not seen; isotype, A).

Subundershrub or undershrub. Stems 1.3–2.7 m high, much branched, like branches acutely quadrangular, shallowly sulcate, striate, and densely incurved-septate-pilose mainly along angles. Leaves sessile or subsessile; blade ovate to oblong-ovate, ca. 2 cm by 1 cm (upper ones), acute at apex, rounded at base, crenulate, chartaceous, more or less rugose, densely septate-villose above, very densely whitish-septate-tomentose beneath, the lateral nerves ca. 3 on each side, sunken above and raised beneath like midrib. Panicles terminal, pyramidal, 7–20 cm long, together forming complex one up to 30 cm long and 10 cm in diameter on upper part of each stem, composed of much-branched cymes with up to 21 flowers; cymes with peduncle 0.7–1.8 cm long, pedicels 2–4 cm long, peduncle, pedicels, and rachis densely pilose; lower floral leaves similar to cauline ones, others gradually reduced upward and changed into bracts; bracteoles linear, less than 1 mm long. Calyx urceolate-campanulate, ca. 1.5 mm long, densely villose outside, 2-lipped for ⅕ its length, the teeth 5, trian-

gular, subequal, acute; fruiting calyx urceolate-tubular, 4 mm long, curved, conspicuously nervate, the teeth 5, ca. 0.7 mm long, lower 2 slightly larger than others. Corolla ca. 4.5 mm long, white or rose, slightly pubescent outside; tube gradually dilated upward, ca. 1.5 mm in diameter at throat, straight; limb 2-lipped, the upper lip ca. 1 mm long, reflexed, 4-fid at apex, lower lip broadly ovate, ca. 1.5 mm long. Stamens and style much exserted. Mature nutlets not seen.

DISTRIBUTION AND PHENOLOGY. Western and central Africa (Equatorial Guinea (Macias Nguema), Cameroon, Burundi); mountain slopes, 1000–2300 m alt. Flowering in November.

This species is closely allied to *Isodon lophanthoides* but differs in the much-branched plant, the rugose leaves densely tomentose beneath, and the ample panicle with much-branched cymes that have up to 21 flowers.

37. **Isodon pulchokiensis** (Murata) H. W. Li, comb. nov.

Rabdosia pulchokiensis Murata *in* H. Ohashi, Fl. East. Himal. 3rd Rep. 96. 1975. TYPE: Nepal, Phulchoki, 2400–2700 m, 19 Sept. 1979, *Kanai & Chuma 17* (holotype, TI, not seen).

Perennial herb. Stems 40–100 cm high, few branched, quadrangular, covered with recurved short hairs; internodes 5–6 cm long, 2–3 cm thick. Cauline leaves opposite; petiole 6–20 mm long; blade ovate or ovate-oblong, 3–6 by 2–3.5 cm, acute at apex, broadly cuneate at base, serrate-dentate, hirsute above, glandular and hirsute on midrib and nerves beneath, nerves conspicuous beneath. Panicles terminal and axillary, composed of 5- to 9-flowered cymes; cymes with peduncle 1–2 cm long, slender, hirsute, pedicels 1–5 mm long; floral leaves similar to cauline ones, gradually reduced upward; bracts and bracteoles oblong-lanceolate, minute. Calyx campanulate, 2 mm long (3 mm in fruit), pilose-tomentose and glandular outside, glabrous inside, inconspicuously 2-lipped, the teeth 5, triangular, ca. 0.8 mm long, obtuse or subacute. Corolla 5.5–7 mm long, dark brown-purple; tube short, not gibbous, gradually dilated toward throat, pilose; limb 2-lipped, the upper lip erect, much shorter than lower one, dark purple, 4-fid, the lower lip obovate, 2.5 by 2 mm, rounded at apex, boat shaped. Stamens much exserted, filament pilose at base, anther dark purple; style much exserted. Nutlets smooth.

DISTRIBUTION AND PHENOLOGY. Nepal; on mountain slopes, 2400–2700 m alt. Flowering and fruiting in September.

I have not seen specimens of this species. The above description is translated from the Latin. According to Murata, the species is distinguished from *Isodon lophanthoides* by its dark brownish-purple flowers. More material is needed for further investigation.

38. **Isodon teysmannii** (Miq.) H. W. Li, comb. nov.

Plectranthus teysmannii Miq. Fl. Ned. Ind. **2**: 944. 1858. SYNTYPES: Java, op den Wilis in Madioen, *Teysmann s.n.*, *U37953* and *U37954* (not seen).

P. zollingeri Briq. Annuaire Conserv. Jard. Bot. Genève **2:** 234. 1898. TYPE: Java, *Zollinger 2215* (not seen).

Erect herb or undershrub, 0.5–1.5 m high. Stems and branches slender, quadrangular, 4-sulcate, septate-hispidulous or septate-puberulous. Cauline leaves opposite; petiole 0.2–5 cm long, concave-convex, septate-hispidulous; blade ovate or elliptic-ovate, 2.5–5 by 1.5–3.5 cm, acute or acuminate at apex, truncate or rounded (rarely acute) at base, serrate-dentate except at base, chartaceous, sparsely septate-hispidulous above, pubescent along midrib and nerves and dotted with red glands beneath, the lateral nerves ca. 4 on each side, ascendent, like midrib sunken above and raised beneath, the veinlets conspicuous beneath. Panicles terminal and axillary, 10–15 cm long, together forming complex one 12–15(–20) cm long and 4–5 cm in diameter on top of each stem, composed of 5- to 11-flowered cymes; cymes with peduncle 1–1.5 cm long, pedicels 1.5–4.5 mm long, peduncle, pedicels, and rachis pubescent; lower floral leaves similar to cauline ones, sessile or subsessile, others gradually reduced and changed into bracts upward; bracts ovate to oblong-ovate, 0.4–1 cm long; bracteoles spathulate, 0.5 mm long. Calyx subcampanulate, 1.5–2 mm long, densely glandular-villose, slightly 2-lipped, the teeth 5, deltoid, subequal, ca. ⅓ of calyx length, blunt or rounded at apex. Corolla 5–6 mm long, white with small lilac dots on upper lip; tube gibbous on upper side near base, ca. 1 mm in diameter at throat, straight; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, 4-fid at apex, the lower lip broadly ovate, almost equal to upper one, concave. Stamens and style much exserted. Nutlets ovoid, 0.8–1 mm long.

DISTRIBUTION AND PHENOLOGY. Indonesia (Celebes, Java, Bali, Lombok, Sumbawa, Flores, Timor); in grasslands and thickets, along forest edges, and in *Casuarina* forest, (1000–)1400–2700 m alt. Flowering and fruiting year-round.

Although this species is very close to *Isodon lophanthoides,* it is easily confused with *I. javanicus* in its area. It differs from the latter species in having long-exserted stamens, a white corolla with the tube gibbous on the upper side near the base, and sessile or even amplexicaul upper leaves.

39. **Isodon hispidus** (Bentham) Murata, Acta Phytotax. Geobot. **24:** 82. 1969.

Plectranthus hispidus Bentham *in* Wallich, Pl. Asiat. Rar. **2:** 17. 1831. *Rabdosia hispida* (Bentham) H. Hara, J. Jap. Bot. **47:** 196. 1972. SYNTYPES: India, in montosis prov. Silhet, *Wallich*; Khasiya, *Griffith* (neither seen).

P. chienii Sun ex C. H. Hu, Acta Phytotax. Sin. **11**(1): 52. 1966. TYPE: China, Yunnan, Shangpa, 29 Oct. 1934, *H. T. Tsai 59070* (holotype, PE; isotypes, A, KUN).

Isodon nigropunctata Murata, Acta Phytotax. Geobot. **24:** 108. *figs. 5, 6.* 1979. TYPE: Thailand, Chiang Mai, Doi Chiang Dao, 4 Jan. 1965, *M. Tagawa, K. Iwatsuki, & N. Fukuoka s.n.* (holotype, TI, not seen).

Rabdosia shimizuana Murata, Acta Phytotax. Geobot. **35:** 180. *fig. 1.* 1984. *Isodon shimizuanus* (Murata) H. Hara, J. Jap. Bot. **60:** 236. 1985. TYPE: Thailand, NE Prov. Loei, Phu Kradung National Park, 14 Nov. 1979, *T. Shimizu et al. T-22684* (KYO, not seen).

Perennial herb. Stems repent-ascendent, 33–100 cm high, unbranched or pyramidally branched in upper ⅓ of plant, quadrangular, deeply 4-sulcate,

densely brownish-septate-villose. Cauline leaves opposite, sessile or subsessile; blade ovate to elliptic, 3–11.5 by 1.5–5.5 cm, acute to acuminate at apex, cuneate or rotund and decurrent-attenuate at base, serrate except at base, chartaceous, the upper surface olive-green, septate-hispid above, the lower surface greenish, densely patent-septate-villose on midrib and nerves, dotted with dark brown glands. Panicles terminal and axillary, 4.5–11 cm long, 2.5–4 cm in diameter, densely brownish-septate-villose, composed of 11- to 13-flowered cymes; cymes with peduncle 5–13 mm long; floral leaves and bracts ovate, 7–14 mm long; bracteoles ovate, much shorter than pedicels; pedicels 3–6 mm long, slender. Calyx campanulate, ca. 2 mm long, 2 mm in diameter at mouth, densely septate-villose and reddish-brown-glandular outside, 2-lipped, the teeth 5, broadly triangular, as long as calyx tube, lower 2 slightly larger; fruiting calyx dilated, ca. 3 mm long, 1.5–1.8 mm in diameter. Corolla 5.5–6 mm long, white or pink-lavender, sometimes with purple spots on upper lip, sparsely pubescent outside; tube gradually dilated upward, 3.2 mm long, ca. 0.3 mm in diameter at base and 1.5 mm at throat, straight; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, 4-fid at apex, lobes oblong, the lower lip ovate, ca. 3.2 mm long, straight, plane. Stamens and style much exserted. Nutlets compressed-ovoid, small, with very small points.

DISTRIBUTION AND PHENOLOGY. India (Assam), Burma (Chin), northern Thailand, southern Laos, and south-central China (western Yunnan); in open places or woods, 1300–2000 m alt. Flowering and fruiting October–November.

This species is closely allied to *Isodon lophanthoides,* differing markedly in that all parts of the plant, especially the calyx, are densely septate-villose. *Isodon nigropunctata* is also very close to *I. hispidus*; since it differs only in its larger flowers with long-exserted stamens and its truncate but not decurrent leaf bases, I have reduced it to a synonym of the latter species. Moreover, according to Murata's description of *Rabdosia shimizuana,* this is also identical with *I. hispidus,* so I have likewise reduced it to synonymy.

40. **Isodon lophanthoides** (Buch.-Ham. ex D. Don) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Hyssopus lophanthoides Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 110. 1825. *Rabdosia lophanthoides* (Buch.-Ham. ex D. Don) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPE: in montibus Nepaliae, *Wallich* (not seen).

Plectranthus striatus Bentham *in* Wallich, Pl. Asiat. Rar. **2:** 17. 1831. *Isodon striatus* (Bentham) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 134. 1929. TYPE: India, Silhet, *Wallich* (not seen).

P. stocksii Hooker f. Fl. Brit. India **4:** 618. 1885. SYNTYPES: India, the Concan, *Stocks et al.* (A, W); Bababoodan Hills, *Heyne* (Herb. Rottler, not seen); Belyaum, at Purwar Ghat, *Ritchie* (not seen).

Orthosiphon glabrescens Vaniot, Bull. Acad. Int. Géogr. Bot. **14:** 168. 1904. TYPE: China, Yunnan, environs de Yunnansen, 27 Oct. 1896, *Bodinier s.n.* (not seen).

O. bodinieri Vaniot, Bull. Acad. Int. Géogr. Bot. **14:** 170. 1904. TYPE: China, Kweichow, environs de Kouy-yang, 20 Oct. 1898, *Bodinier 2480* (not seen).

P. esquirolii Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 247. 1911. TYPE: Kouy-Tchéou, Ko-Te-Pang-Kaou, Sept. 1904, *J. Esquirol 214* (not seen).

P. fangii Sun, Ic. Pl. Omei. **1**: *pl. 91.* 1944. *Rabdosia fangii* (Sun) H. Hara, J. Jap. Bot. **47**: 195. 1972. TYPE: Sichuan, Omei, 1 Oct. 1940, *W. P. Fang 14903* (holotype, PE).

P. volkensianus Muschler, Feddes Repert. **4**: 268. 1970. *Isodon volkensianus* (Muschler) Murata, S.E. Asian Stud. **8**: 505. 1971. TYPE: Thailand, Doi Anga-Kette, *C. C. Hosseus 326* (isotypes, E, W).

KEY TO THE VARIETIES OF ISODON LOPHANTHOIDES

1. Plant up to 1.5 m high; leaves acuminate at apex.
   2. Leaves ovate, up to 20 by 8.5 cm. ..... 40b. var. *gerardianus.*
   2. Leaves ovate-lanceolate to lanceolate, 5–8.5 by 1.5–3.5 cm. ..... 40c. var. *graciliflorus.*
1. Plant 0.5–1 m high; leaves obtuse at apex.
   3. Corolla 6–7 mm long. ..... 40a. var. *lophanthoides.*
   3. Corolla 2–3 mm long. ..... 40d. var. *micranthus.*

40a. **Isodon lophanthoides** var. **lophanthoides**

Slender perennial herb. Stems 15–100 cm high, erect or ascendent, quadrangular, 4-sulcate, puberulous or pilose, always very leafy at base. Cauline leaves opposite; petiole shorter than, equal to, or longer than blade; blade ovate, broadly ovate, or oblong-ovate, 1.5–8.8 by 0.5–3.3 cm, obtuse at apex, cuneate, rounded, or broadly cuneate (rarely shallowly cordate) at base, crenate, thin-chartaceous, the upper surface olive-green, densely septate-hirtellous, the lower surface greenish, septate-hirtellous, dotted with brown glands. Panicles terminal and axillary, 7–20 cm long, 3–6 cm in diameter, composed of 11- to 13-flowered cincinnal cymes; cymes with peduncle 5–13 mm long; floral leaves ovate, lower ones similar to cauline leaves but smaller, upper ones gradually changed into sessile bracts; bracteoles linear, 3–5 mm long, slightly longer than pedicels. Calyx campanulate, ca. 2 mm long, 1.7 mm in diameter, sparsely septate-villose on lower part only and dotted with red-brown glands outside, 2-lipped for ⅓ its length, the teeth 5, ovate-triangular, lower 2 slightly larger than upper ones; fruiting calyx elongate, up to 4.5–5 mm long. Corolla 6–7 mm long, white or rose with purple spots on limb; tube 3.7–5 mm long, 0.8–1 mm in diameter at base and 1.5–2 mm at throat, straight; limb 2-lipped, the upper lip 1.6–2 mm long, very reflexed, 4-fid at apex, lobes nearly oblong, the lower lip broadly ovate, slightly longer than upper one, 2–2.8 mm broad, straight, plane. Stamens and style much exserted. Nutlets compressed-ovoid, ca. 1 mm long, 0.75 mm in diameter, brown, smooth, glabrous.

DISTRIBUTION AND PHENOLOGY. India (Tamil Nadu, Mysore, Himachal Pradesh, Uttar Pradesh, Assam), Sikkim, Nepal, Bangladesh, Burma (Kawthule), northern Thailand, northern Vietnam, and southern China (Yunnan, Sichuan, Guizhou, Guangxi, Hubei, Guangdong); on moist slopes or in forests or ravines, 500–3000 m alt. Flowering and fruiting August–December.

The isotypes of *Plectranthus volkensianus* are similar to *Isodon lophanthoides* var. *lophanthoides* except for their somewhat larger cauline leaves, so I reduce it to a synonym of the latter species. *Isodon lophanthoides* is easily recognized by its fruiting calyx with small teeth, its corolla with a long, straight tube, and its exserted stamens and style.

40b. **Isodon lophanthoides** var. **gerardianus** (Bentham) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Plectranthus gerardianus Bentham *in* Wallich, Pl. Asiat. Rar. **2:** 17. 1831. *P. striatus* Bentham var. *gerardianus* (Bentham) Hand.-Mazz. Acta Horti Gothob. **9:** 93. 1934. *Rabdosia lophanthoides* var. *gerardiana* (Bentham) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPE: India orientalis, Kumaon, *Wallich s.n.* (not seen).

P. tatei Hemsley, J. Linn. Soc., Bot. **26:** 274. 1890. TYPE: Kwangtung, Wongyu, in waste ground, *G. R. Tate s.n.* (not seen).

This variety differs from var. *lophanthoides* in that the plant is taller (0.3–1.5 m high) and the leaves are ovate, up to 20 by 8.5 cm, acuminate at the apex, and cuneate at the base.

The habitat, distribution, and phenology of the variety are the same as for var. *lophanthoides.*

40c. **Isodon lophanthoides** var. **graciliflorus** (Bentham) H. Hara, J. Jap. Bot. **60:** 235. 1985. FIGURE 5J.

Plectranthus graciliflorus Bentham *in* DC. Prodr. **12:** 56. 1848. *P. gerardianus* Bentham var. *graciliflorus* (Bentham) Hooker f. Fl. Brit. India **4:** 618. 1885, *excl. syn. P. striatus* Bentham var. *graciliflorus* (Bentham) Hand.-Mazz. Acta Horti Gothob. **13:** 379. 1939. *Rabdosia lophanthoides* var. *graciliflora* (Bentham) H. Hara, J. Jap. Bot. **47:** 197. 1972. SYNTYPES: in montosis prov. Silhet, *Wallich*; Assam, *Griffith* (neither seen).

P. striatus auct. non Bentham: Doan, Lec. Fl. Gén. Indo-Chine **4:** 948. 1936, *pro parte, quoad syn.*

This variety differs from var. *lophanthoides* in that the plant is taller (0.4–1 m high) and the leaves are ovate-lanceolate to lanceolate, 5–8.5 by 1.5–3.5 cm, acuminate at the apex, cuneate at the base, finely scabrous or subglabrescent above, finely scabrous on the nerves and dotted with brown glands on the entire surface beneath, and always reddish brown when dry.

The habitat, distribution, and phenology of the variety are the same as for var. *lophanthoides.*

40d. **Isodon lophanthoides** var. **micranthus** (C. Y. Wu) H. W. Li, comb. nov.

Rabdosia lophanthoides var. *micrantha* C. Y. Wu, Fl. Yunnan. **1:** 775. 1977. TYPE: China, Yunnan, Yan-shan, *C. W. Wang 84114* (holotype, KUN).

This variety differs from var. *lophanthoides* in that the corolla is smaller (only 2–3 mm long), and the leaves are sparsely septate-hirtellous on both surfaces and always purplish beneath.

DISTRIBUTION AND PHENOLOGY. South-central China (southern Yunnan and Guizhou); on stream sides or in forests, 1100–1900 m alt. Flowering September–October, fruiting in November.

D. **Isodon** ser. **Rugosi** (Briq.) H. W. Li, comb. nov.

Plectranthus ser. *Rugosi* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 353. 1897.

Mainly undershrubs or subundershrubs, mostly with rugose leaves; branchlets, leaves, and calyces densely hairy. Cymes arranged into more or less loose panicles or in dense verticillasters. Calyx subequally 5-toothed or slightly 2-lipped, toothed for ½ its length or less. Corolla medium in size, with declinate tube.

LECTOTYPE SPECIES. *Isodon rugosus* (Wallich) Codd.

KEY TO THE SPECIES OF SER. RUGOSI

1. Branchlets, leaves, and calyces densely stellate-tomentose or stellate-lanate.
   2. Calyces toothed for ca. ⅓ their length.
      3. Leaves with single brown gland on top of each tooth beneath.
         4. Panicles 8–24 cm long. ..... 41. *I. leucophyllus.*
         4. Panicles 3–5 cm long. ..... 42. *I. adenolomus.*
      3. Leaves lacking glands on top of teeth. ..... 43. *I. rugosus.*
   2. Calyces with teeth about as long as tube.
      5. Leaves 3–8 cm long. ..... 44. *I. grandifolius.*
      5. Leaves less than 2.5 cm long.
         6. Leaf base rotund or shallowly cordate. ..... 45. *I. oresbius.*
         6. Leaf base cuneate or truncate-cuneate. ..... 46. *I. dawoensis.*
1. Branchlets, leaves, and calyces covered with hairs different from above.
   7. Leaves conspicuously discolor, gray-white beneath.
      8. Calyx teeth narrowly triangular or triangular-lanceolate.
         9. Leaves ovate, 1.5–3.5 by 1–2.8 cm, obtuse at apex, broadly cuneate or truncate-cuneate at base, crenate, dusty-pubescent above, densely whitish-floccose-tomentulose beneath. ..... 47. *I. lihsienensis.*
         9. Leaves elliptic, lanceolate, or oblanceolate, 0.8–1.5 by 0.5–0.7 cm, acute or subrotund at apex, broadly cuneate to rotund or subtruncate and abruptly attenuate at base, entire or sparsely and obscurely few-dentate above middle, densely tomentulose above, densely floccose-tomentose beneath. ..... 48. *I. wikstroemioides.*
      8. Calyx teeth triangular or ovate-triangular.
         10. Leaves 2.5–4.4 cm long. ..... 49. *I. smithianus.*
         10. Leaves less than 2 cm long.
            11. Cymes remote, arranged into verticillasters; leaves oblong-ovate, ovate, or broadly ovate, glandular-pubescent above. ... 50. *I. parvifolius.*
            11. Cymes approximate, arranged into terminal panicles; leaves lanceolate or ovate-lanceolate, densely pilose above. ... 51. *I. tenuifolius.*
   7. Leaves not discolor.
      12. Cymes sessile or with very short peduncle; branchlets, inflorescences, and calyces all densely hirtellous. ..... 52. *I. hirtellus.*
      12. Cymes conspicuously pedunculate; branchlets, inflorescences, and calyces not hirtellous.
         13. Leaves and branchlets reddish, densely tomentose when young, but subglabrescent with age. ..... 53. *I. rubescens.*
         13. Leaves and branchlets not reddish, densely covered with hair even in age.
            14. Leaves 3.5–6(–10) cm long. ..... 54. *I. loxothyrsus.*
            14. Leaves less than 4 cm long.
               15. Branchlets and petioles fulvous-velutinous; leaves ovate-oblong, 1–2.5 by 0.5–1.4 cm, acute at apex, subrotund at base, regularly crenulate above base. ..... 55. *I. xerophilus.*

15. Branchlets and petioles gray-tomentulose; leaves rhombic or triangular-ovate, 1.5–4 by 1–2.5 cm, acute or shortly caudate-acuminate at apex, broadly cuneate to truncate at base, crenate. ..... 56. *I. rugosiformis.*

41. **Isodon leucophyllus** (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 122. 1929. FIGURE 6E–G.

Plectranthus leucophyllus Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 157. 1913. *Rabdosia leucophylla* (Dunn) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPES: China, Sichuan, Tung valley, 1200 m, July 1903, *Wilson 4319* (isosyntype, A); between Tachienlu and Chengtu, October 1904, *Hosie* (syntype, E, not seen).

P. thiothyrsus Hand.-Mazz. Acta Horti Gothob. **9:** 94. 1934. *Rabdosia thiothyrsa* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 201. 1972. TYPE: China, NW Szechuan, Hsu-ting, in declivitate sicca, aprica, 2250 m, *Harry Smith 4798* (isotype, W).

P. pachythyrsus Hand.-Mazz. Symb. Sin. **7:** 937. *Abb. 28, nr. 6.* 1936. *Rabdosia pachythyrsa* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: China, NW Yunnan, Likiang, *Handel-Mazzetti 12993* (holotype, W; isotype, A).

Erect undershrub, 0.5–1.2 m high, much branched, entire plant except corollas densely gray-furfuraceous and stellate-tomentose or stellate-lanate. Young branchlets quadrangular, densely hairy; old branchlets subcylindrical, brown, finely striate, glabrescent, with large, white pith. Cauline leaves opposite; petiole 0.5–1.5 cm long, slightly thickened, plano-convex, densely stellate-tomentose or stellate-lanate; blade ovate or triangular-ovate, 2–6 by 1.3–4 cm, obtuse or somewhat acute at apex, obtuse, subrotund, or subrotund-cuneate at base, chartaceous, rugose, the upper surface green, more or less densely stellate-tomentose or stellate-lanate, the lower surface gray, very densely stellate-tomentose or stellate-lanate, with single brown gland on top of each tooth, the lateral nerves ca. 3 or 4 pairs, very oblique, sunken above but raised beneath like midrib. Panicles terminal, composed of 3- to 9-flowered cymes, sometimes pyramidal and 8 cm long (then compact), sometimes 10–24 cm long (then compact above and loose below); floral leaves similar to cauline ones, longer or shorter than cymes, gradually reduced upward and changed into shortly petiolate or subsessile bracts; bracteoles linear, ca. 1 mm long. Calyx tubular-campanulate, 2.5–3(–4) mm long, straight or slightly curved, very densely tomentulose or lanate outside, glabrous inside, 10-nerved, the teeth 5, triangular-lanceolate, subequal, ¼ length of calyx; fruiting calyx conspicuously tubular, slightly dilated, urceolate at base, slightly curved, glabrous. Corolla 3–5(–7) mm long, rose or purple to dark purple-blue, puberulous on limb outside, glabrous inside; tube abruptly saccate on upper side above base, ca. 1 mm in diameter at throat; limb 2-lipped, the upper lip as long as lower one, ca. 1.5 mm long, reflexed, equally 4-fid at apex, the lower lip ovate, straight, concave. Stamens and style included. Mature nutlets ovoid, 1.5 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and western Sichuan); in thickets on dry slopes, 1400–2900 m alt. Flowering July–October, fruiting October–November.

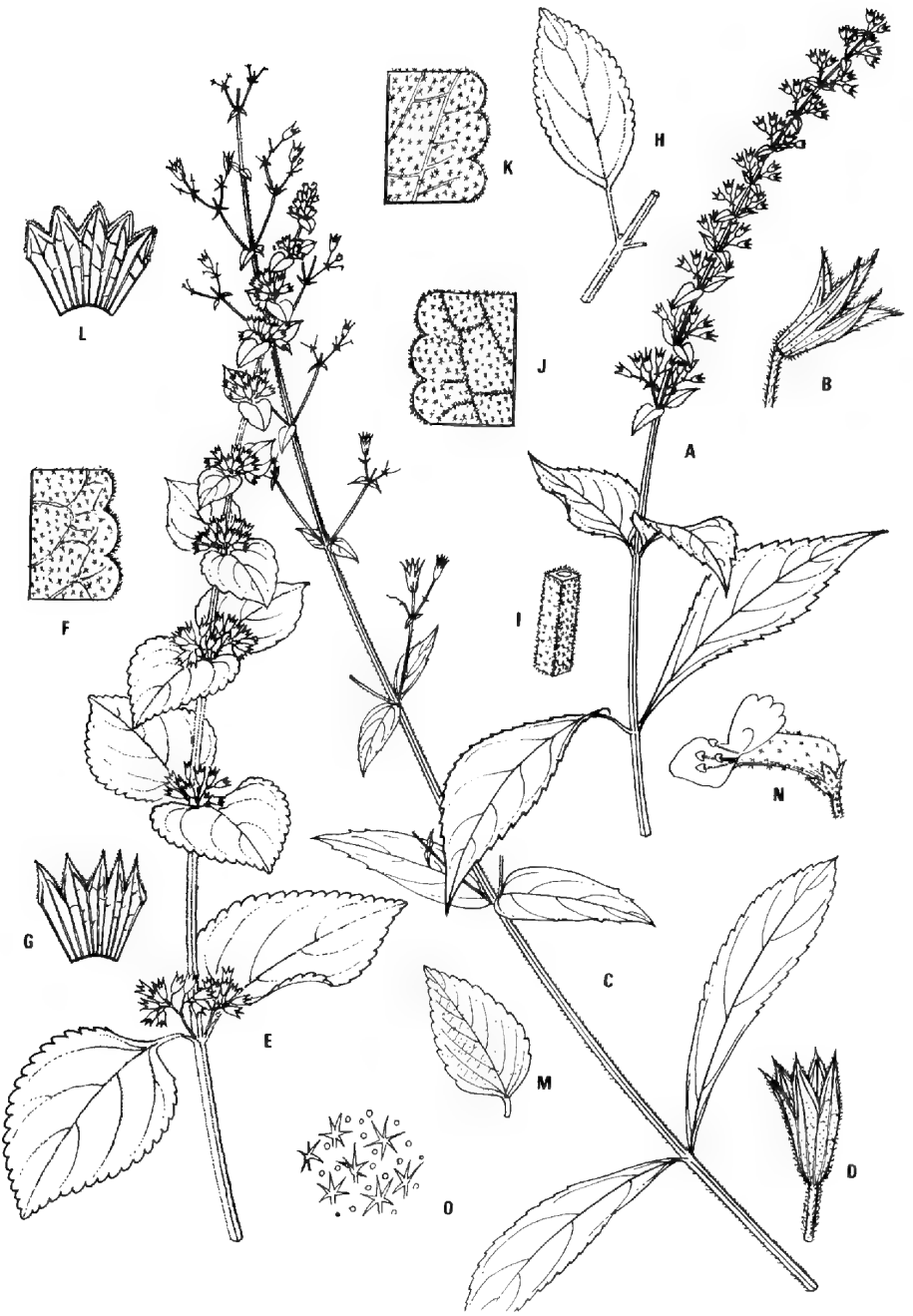

FIGURE 6. A, B, *Isodon setschwanensis* (*S. K. Wu 2618,* KUN): A, fruiting branch, × 0.6; B, calyx, × 4.8. C, D, *I. angustifolius* var. *angustifolius* (*C. W. Wang 84204,* KUN): C, fruiting branch, × 0.6; D, calyx, × 4.8. E–G, *I. leucophyllus* (*H. Smith 13342,* PE): E, fruiting branch, × 0.6; F, lower surface of leaf, × 15; G, calyx, × 6. H–L, *I. adenolomus* (*K. M. Feng 2808,* KUN): H, leaf, × 0.6; I, portion of stem, × 3; J, upper surface of leaf, × 15; K, lower surface of leaf, × 15; L, calyx, × 6. M–O, *I. oresbius* (*Y. W. Tsui 4511,* PE): M, leaf, × 0.6; N, flower, × 3; O, hairs from leaf surface, × 60. (Drawn by X. C. Li.)

After checking specimens of this species, I do not believe the compact pyramidal panicle to be a constant character because both continuous and interrupted cymes occur on the same plant. In addition, the corolla limb is longer than the calyx in perfect flowers but shorter in carpellate ones. Thus, I think *Plectranthus pachythyrsus* and *P. thiothyrsus,* which were established mainly on the above two characters, are identical with *Isodon leucophyllus*; consequently the three species should be treated as one.

Isodon leucophyllus is distinctive in that the entire plant except the corolla is densely gray-furfuraceous and stellate-tomentose or stellate-lanate and the panicle is more or less elongate.

42. **Isodon adenolomus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60**: 233. 1985. FIGURE 6H–L.

Plectranthus adenolomus Hand.-Mazz. Symb. Sin. **7**: 938. 1936. *Rabdosia adenoloma* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47**: 193. 1972. TYPES: China, Yunnan, inter pagos Yungning et Dschungdien, 3100–3200 m alt., 12 Aug. 1915, *Handel-Mazzetti 7597* (syntype, W); Chien-chuan–Mekong divide, 26°40′N, 99°40′E, July 1922, *G. Forrest 21505* (syntype, W; isosyntype, A).

Undershrub. Stems ca. 90 cm high, erect, much branched; branches obtusely quadrangular, decorticate, densely whitish-stellate-tomentose at first, glabrescent in age. Cauline leaves opposite; petiole 0.5–1 cm long, densely gray-stellate-tomentose; blade narrowly ovate to orbicular-ovate, 2–3.5 by 1.2–1.7 cm, obtuse to rotund at apex, broadly cuneate at base, crenate for upper ⅔, with single brown gland on lower surface of each tooth tip, densely gray-stellate-tomentose and with nerves sunken above, densely fulvous-stellate-tomentose and with nerves raised beneath. Panicles terminal, 3–5 cm long, composed of compactly arranged 3- to 5-flowered cymes; cymes with pedicels 2–4 mm long, these like peduncle and rachis densely stellate-tomentose; lowest floral leaves similar to cauline ones but acute at apex, others gradually reduced upward, all longer than cymes. Calyx campanulate, ca. 2 mm long, densely fulvous-stellate-tomentose outside, glabrous inside, the teeth 5, triangular, equal, ⅓ of calyx length. Corolla ca. 7 mm long, purple-red, sparsely pilose outside, glabrous inside; tube slightly exserted, saccate on upper side near base; limb 2-lipped, the upper lip reflexed, equally 4-lobed at apex, the lower lip broadly ovate, concave. Stamens 4, subincluded; style filiform, equally 2-lobed at apex. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and southwestern Sichuan); on open, stony slopes among dwarf scrub and herbage, (2300–)3050–3300 m alt. Flowering in July.

This species is allied to *Isodon leucophyllus* but differs in having the leaves densely fulvous-stellate-tomentose beneath and the panicle only 3–5 cm long.

43. **Isodon rugosus** (Wallich) Codd, Taxon **17**: 239. 1968.

Plectranthus rugosus Wallich, Pl. Asiat. Rar. **2**: 17. 1831. *Isodon rugosus* (Wallich) Murata, Acta Phytotax. Geobot. **24**: 82. 1969. *Rabdosia rugosa* (Wallich) H. Hara,

J. Jap. Bot. **47:** 199. 1972. TYPE: India orientali, ad Choor Royle, in Sirmore Gerard, *Wallich s.n.* (not seen).

Isodon plectranthoides Schrader ex Bentham, Labiat. Gen. Spec. 43. 1832, *pro syn.*

Erect, much-branched undershrub, up to 1.5 m high. Branches subcylindrical, tortuous, irregularly decorticate, gray-brown, with small pith; branchlets slender, obtusely quadrangular, finely striate, brown, very densely stellate-tomentose. Cauline leaves opposite; petiole 0.2–1 cm long, densely tomentose; blade ovate or elliptic, 1–3.5 by 0.5–1.8 cm, obtuse at apex, broadly cuneate to subrotund at base, crenulate above entire base, chartaceous, rugose, olive-green and densely stellate-tomentose above, gray-tomentose beneath, the lateral nerves 4 or 5 pairs, sunken above and raised beneath like midrib. Panicles terminal, composed of axillary cymes; upper cymes with 3 to 5 flowers, lower ones with up to 21, peduncles 2–5 mm long (lower ones sometimes up to 1 cm), pedicels 2–3 mm long, peduncle, pedicels, and rachis stellate-tomentose; floral leaves short-petiolate or subsessile, ovate, lower ones slightly longer than cymes but upper ones much shorter, entire, tomentose like cauline leaves. Calyx campanulate, ca. 2 mm long, very densely stellate-tomentose outside, glabrous inside, the teeth 5, broadly triangular, subequal, ⅓ of calyx tube length; fruiting calyx tubular-campanulate, slightly dilated, ca. 3 mm long, slightly curved, conspicuously 10-nerved. Corolla ca. 7 mm long, white tinged with rose or dark lilac on upper lip, sparsely stellate-tomentose and glandular outside, glabrous inside; tube saccate on upper side above base, ca. 3 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 by 4 mm, reflexed, 4-lobed at apex, the lower lip broadly ovate, ca. 4 by 3 mm, slightly concave. Stamens included, the filament complanate, glabrous; style included, equally 2-lobed at apex. Mature nutlets oblong, triquetrous, ca. 1.5 mm long, dark brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Afghanistan, Pakistan (Northwest Frontier, Punjab), India (Kashmir, Maharashtra, Himachal Pradesh, Uttar Pradesh), Bangladesh, Nepal, Bhutan, and China (Xizang); in thickets on slopes or in valleys, 1000–2700 m alt. Flowering July–September, fruiting August–October.

This species is easily recognized by its leaves that are strongly rugose above and densely tomentose beneath, and its many-flowered cymes with long peduncles.

44. **Isodon grandifolius** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Plectranthus grandifolius Hand.-Mazz. Acta Horti Gothob. **13:** 371. 1939. *Rabdosia grandifolia* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPE: China, Yunnan, Yung-peh mountains, 26°42′N, *G. Forrest 16864* (holotype, W; isotype, A).

P. rugosus auct. non Wallich: W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **17:** 231. 1930.

KEY TO THE VARIETIES OF ISODON GRANDIFOLIUS

1. Leaves ovate-lanceolate, rarely obovate; cymes sessile. .... 44a. var. *grandifolius.*
1. Leaves ovate or triangular-ovate to oblong; cymes pedunculate. ..... 44b. var. *atuntzeensis.*

44a. **Isodon grandifolius** var. **grandifolius**

Much-branched undershrub, 1.2–1.8 m high. Branches striate, with brown cortex, subglabrate, soon defoliate; branchlets subcylindrical, densely stellate-tomentose. Cauline leaves opposite; petiole 1–2.5 cm long, cylindrical, densely yellow-stellate-tomentose; blade ovate-lanceolate, rarely obovate, 3–8 by 1–2.5 cm, acute or obtuse at apex, rotund or truncate-rotund at base, crenulate, chartaceous, rugulose, olive-green and densely stellate-pilose above, densely stellate-tomentose beneath. Panicles terminal or axillary, pyramidal, very compact, composed of sessile cymes; pedicels 1–2 mm long, robust, tomentose; floral leaves lanceolate, longer than cymes, acuminate, entire. Calyx campanulate, 2.5 mm long, the teeth 5, triangular, subequal, as long as calyx tube, acuminate at apex. Corolla saccate on upper side near base, 6–7 mm long, straight, pale blue; limb sparsely stellate-pilose outside, 2-lipped, the upper lip slightly longer than lower one, reflexed, the lower lip porrect. Stamens and style exserted. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan); in thickets and along water courses, 3000–3300 m alt. Flowering in September.

This variety is distinctive in its large leaves (up to 8 by 2.5 cm).

44b. **Isodon grandifolius** var. **atuntzeensis** (C. Y. Wu) H. W. Li, comb. nov.

Rabdosia grandifolia (Hand.-Mazz.) H. Hara var. *atuntzeensis* C. Y. Wu, Fl. Yunnan. **1**: 783. 1977, as "*atuntzensis*." TYPE: China, Yunnan, Atuntze, *C. W. Wang 69865* (holotype, KUN; isotypes, A, PE).

This variety differs from var. *grandifolius* in having ovate or triangular-ovate to oblong leaves and more or less pedunculate cymes.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and western Sichuan); on meadows of mountain slopes, ca. 2700 m alt. Flowering September–October, fruiting in November.

45. **Isodon oresbius** (W. W. Smith) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 120. 1929. FIGURE 6M–O.

Plectranthus oresbius W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **9**: 118. 1916. *Rabdosia oresbia* (W. W. Smith) H. Hara, J. Jap. Bot. **47**: 198. 1972. TYPE: China, Yunnan, on mountain NE of Yangtze bend, 27°45'N lat., Sept. 1913, *G. Forrest 11,154* (holotype, E; fragment of holotype, W).

Small undershrub, up to 60 cm high, much branched. Branches decorticate, subglabrous, soon defoliate; branchlets obtusely quadrangular, densely gray-stellate- and simple-tomentulose. Cauline leaves opposite; petiole ca. 3 mm long, concave-convex, densely stellate- and simple-tomentulose; blade ovate, 0.7–1.5 by 0.5–1.3 cm, obtuse at apex, rotund or shallowly cordate at base, regularly crenate, chartaceous, rugose, olive-green and stellate- and simple-villose above, gray and stellate- and simple-tomentulose beneath, the lateral nerves 3 or 4 pairs, oblique, sunken above and raised beneath like midrib.

Cymes axillary, 3- to 5-flowered, covered with hairs like those of branchlets, peduncle ca. 5 mm long, pedicels ca. 2 mm long; floral leaves similar to cauline ones, gradually reduced upward, entire; bracteoles linear, up to 2 mm long. Calyx campanulate, ca. 4 mm long, 3.5–4 mm in diameter, whitish-stellate-villose and simple-tomentose especially on tube outside, glabrous inside, the teeth 5, narrowly triangular, subequal, ca. 2 mm long, 1 mm broad at base. Corolla purplish or purple-blue, stellate-pilose outside, glabrous inside; tube saccate on upper side above base, slightly longer than calyx, ca. 1.5 mm in diameter at throat; limb 2-lipped, the upper lip almost as long as lower one (ca. 3.5 mm), reflexed, equally 4-lobed at apex, the lower lip broadly ovate. Stamens and style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and western Sichuan); dry, open sites among rocks on mountains or in thickets, 2100–3400 m alt. Flowering July–September.

This species is allied to *Isodon rugosus* but differs in that the plant is much branched, the leaves are smaller, and the corolla is purplish or purplish blue.

46. **Isodon dawoensis** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Plectranthus dawoensis Hand.-Mazz. Acta Horti Gothob. **13:** 371. 1939. *Rabdosia dawoensis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: China, Sichuan, Taofu (Dawo) distr., Taofu, west of river, in declivo, terrae "loess," *Harry Smith 12200* (holotype, w).

Small undershrub, up to 25 cm high, branched. Branches decorticate, defoliate; branchlets gray-stellate-tomentulose, foliate. Cauline leaves opposite; petiole 2–8 mm long, concave-convex, densely whitish-stellate-tomentulose; blade ovate or ovate-triangular, 1–2.5 by 0.6–1.7 cm, acute or obtuse at apex, cuneate or truncate-cuneate at base, grossly crenate except base, with inconspicuous gland on top of each tooth, chartaceous, rugose, densely furfuraceous-pilose above, densely stellate-tomentulose beneath, the lateral nerves 3 or 4 pairs, sunken above and raised beneath like midrib. Panicles terminal, spike-like, 2–7 cm long, whitish- or greenish-stellate-tomentulose, composed of 3- to 5-flowered cymes; cymes with peduncle very short to nearly lacking, the pedicels 1–2 mm long, tomentulose; floral leaves sessile, reduced and changed into bracts upward; bracts ovate-lanceolate to lanceolate; bracteoles linear, minute. Calyx infundibular, 2 mm long, whitish-stellate-tomentose outside, glabrous inside, the teeth 5, triangular, equal, ½ length of calyx, acute at apex. Corolla 7–9 mm long, white, pilose outside, glabrous inside; tube saccate on upper side near base, 3 mm long; limb 2-lipped, the upper lip ca. 3 mm long, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, ca. 4 mm long, concave, boat shaped. Stamens and style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (western Sichuan); on mountain slopes with loess, ca. 3000 m alt. Flowering in September.

This species is allied to *Isodon rugosus* but differs in having short-pedunculate, always few-flowered cymes and calyx teeth that are about as long as the tube.

47. **Isodon lihsienensis** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60**: 235. 1985.

Rabdosia lihsienensis C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66**: 453, 586. 1977. TYPE: China, Sichuan, Li Xian, *T. He 14114* (holotype, Herb. Univ. Sichuan, Chengdu).

Undershrub, ca. 1 m high. Branches subcylindrical, grayish yellow; branchlets subquadrangular, decorticate, brownish yellow, pubescent. Cauline leaves opposite; petiole 0.5–1.3 cm long, pubescent; blade ovate, 1.5–3.5 by 1–2.8 cm (middle and lower ones), obtuse at apex, broadly cuneate or truncate-cuneate at base, crenate, chartaceous, olive-green and dusty-pubescent above, greenish and densely whitish-floccose-tomentulose beneath. Panicles terminal, 1.4–4.5 cm long, composed of puberulous, 1- to 4-flowered cymes; lower floral leaves similar to cauline ones, entire, upper ones changed into bracts; bracts ovate or rhombic, 4–6 by 2.5–5 mm; bracteoles linear, less than 1 mm long. Calyx campanulate, ca. 3.5 mm long, 4 mm in diameter at mouth, floccose-puberulous (especially at base and on margin of teeth) and minutely glandular-hairy outside, 2-lipped, the teeth 5, triangular-lanceolate, slightly longer than calyx tube, acuminate at apex. Corolla ca. 9 mm long, purplish with purple spots, sparsely puberulous outside, glabrous inside; tube saccate on upper side near base, ca. 4.5 mm long, ca. 3 mm in diameter at throat; limb 2-lipped, the upper lip ca. 4.5 mm long, almost as long as lower one, 4-lobed at apex, lobes more or less semiorbicular and concave. Stamens and style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (western Sichuan); in forests or on roadsides, ca. 2540 m alt. Flowering July–September.

Isodon lihsienensis is allied to *I. smithianus* (Hand.-Mazz.) H. Hara but differs in having the upper cauline leaves gradually smaller and changed into floral ones, and all the leaves crenate, dusty-pubescent above, and densely whitish-floccose-tomentulose beneath.

48. **Isodon wikstroemioides** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60**: 237. 1985. FIGURE 7A–C.

Plectranthus wikstroemioides Hand.-Mazz. Acta Horti Gothob. **13**: 369. 1939. *Rabdosia wikstroemioides* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47**: 203. 1972. TYPE: China, Yunnan, Atuntze valley, 28°28′N, *Forrest 13,209* (holotype, w).

Small undershrub, 0.6–1.5 m high, much branched. Branches cylindrical, more or less angulate, with irregularly fissured cortex, gray-brown, glabrous, with small, white pith; branchlets obtusely quadrangular, shallowly sulcate, striate, brown, densely glandular-tomentulose, foliate. Cauline leaves opposite; petiole 1–4 mm long, concave-convex, densely tomentulose and glandular; blade elliptic, lanceolate, or oblanceolate, 0.8–15 by 0.5–0.7 cm, acute or subrotund at apex, broadly cuneate to rotund or subtruncate and abruptly attenuate at base, entire or sparsely and obscurely few-dentate above middle, chartaceous, the upper surface mostly green but yellowish on nerves, densely tomentulose and papillose-glandular, the lower surface gray, densely floccose-tomentose and

FIGURE 7. A–C, *Isodon wikstroemioides* (*C. W. Wang 71776,* PE): A, leaf, × 0.6; B, flower, × 3.6; C, lower surface of leaf, × 15. D, E, *I. loxothyrsus* (*R. C. Ching 24478,* KUN): D, upper portion of plant, × 0.6; E, flower, × 3.6. F–J, *I. xerophilus* (*S. K. Wu 889,* KUN): F, upper portion of plant, × 0.6; G, corolla and stamens, × 3; H, flower, × 3.6; I, calyx, × 4.8; J, nutlet, × 9. K, L, *I. tenuifolius* (*S. K. Wu 3155,* KUN): K, portion of stem with leaves, × 0.6; L, calyx, × 4.8. M, N, *I. glutinosus* (*Zhongdian Expedition 63-3029,* KUN): M, portion of stem with leaves, × 0.6; N, calyx, × 4.8. (Drawn by Y. Xiao.)

yellowish-glandular, the lateral nerves 3 to 5 pairs, spreading, anastomosing near teeth, sunken above and raised beneath like midrib. Cymes 3- to 5-flowered, arising from axils of floral leaves and shorter than them, arranged in dense verticillasters on upper part of branch, the peduncle and pedicels 1–3 mm long, densely glandular-tomentulose; floral leaves gradually smaller upward. Calyx campanulate, ca. 4 mm long, densely glandular-tomentose outside, glabrous inside, 10-nerved, the teeth 5, narrowly triangular, subequal, ca. ⅓ of calyx length, acute at apex; fruiting calyx tubular-campanulate, slightly dilated, ca. 6 mm long, conspicuously nervate. Corolla ca. 7 mm long, light purple or yellowish white, whitish-puberulous outside, glabrous inside; narrowly tubular at base, abruptly dilated upward, ca. 3 mm long, straight; limb 2-lipped, the upper lip ca. 3.5 mm long, reflexed, equally 4-lobed at apex, the lower lip porrect, broadly ovate, ca. 4 mm long, concave. Stamens and style included. Mature nutlets oblong, triquetrous, up to 1.5 mm long, dark brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Southwestern China (northwestern Yunnan, western Sichuan, and Xizang); in dry, open sites among rocks, (2350–)2500–3200 m alt. Flowering and fruiting August–October.

This species seems quite similar to *Isodon tenuifolius* (Batalin) Kudo, but the indumentum is quite different. Its leaves are very much like those of some species of *Wikstroemia* (Thymeleaceae).

49. **Isodon smithianus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 237. 1985.

Plectranthus smithianus Hand.-Mazz. Acta Horti Gothob. **9:** 93. 1934. *Rabdosia smithiana* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: China, Sichuan, reg. bor.-occid., Drogochi, in valle fruticosa, *Harry Smith 4684* (isotype, W).

Undershrub, 0.5–1 m high. Branches subcylindrical, striate, decorticate, gray-brown; branchlets quadrangular, finely striate, yellow-brown, sparsely and minutely pubescent or glabrous. Cauline leaves opposite; petiole 3–24 mm long; blade rhombic-ovate or ovate, 2.5–4 by 0.9–2 cm, obtuse at apex, cuneate, truncate, or broadly truncate-cuneate at base, sparingly grossly crenate or crenate-dentate, thin-chartaceous, the upper surface olive-green, papillose everywhere but sparsely hirtellous especially along margin, glandular, the lower surface gray-green, puberulous, glandular, the lateral nerves 3 or 4 pairs, raised beneath like midrib. Panicles terminal, racemose, composed of 1- to 7-flowered cymes; cymes with peduncle 5–8 mm long or nearly absent, pedicels 2–6 mm long; lower floral leaves similar to cauline ones, upper floral leaves gradually reduced and changed into bracts upward; bracts entire, much shorter than cymes; bracteoles linear, ca. 1 mm long. Calyx campanulate, ca. 3 mm long, 3 mm in diameter at mouth, gray-tomentulose outside, glabrous inside, 2-lipped for nearly ½ of calyx length, the teeth ovate-triangular, subequal (upper lip with 3, middle 1 smaller; lower lip with 2 slightly larger); fruiting calyx dilated, ca. 5 mm long, 5 mm in diameter at mouth, slightly curved, conspicuously nervate. Corolla 7–9 mm long, white on upper lip and purple-red on lower one, pubescent outside; tube saccate on upper side near base, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip erect, as long as lower one (ca. 4 mm),

slightly reflexed, 4-lobed at apex, the lower lip ovate, concave. Stamens slightly exserted, the filament filiform, barbate below middle; style slightly exserted, equally 2-lobed at apex. Mature nutlets ovoid, triquetrous, ca. 1.5 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. China (northwestern Sichuan and southeastern Xizang); in thickets, 2650–3500 m alt. Flowering July–September.

This species is related to *Isodon parvifolius* (Batalin) H. Hara but differs in its leaves that are much larger, papillose everywhere but sparsely hirtellous especially along the margin above, puberulous beneath, and glandular on both surfaces.

50. **Isodon parvifolius** (Batalin) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Caryopteris parvifolia Batalin, Trudy Imp. S.-Petersburgsk. Bot. Sada **13:** 98. 1893. *Plectranthus parvifolius* (Batalin) Pei, Mem. Sci. Soc. China **1:** 183. 1932. *Rabdosia parvifolia* (Batalin) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: Chine borealis, prov. Kansu orientale, Vallis fl. Pei-Shui, 22 Juni 1885, *Potanin* (holotype, LE, not seen).

Plectranthus discolor Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 155. 1913. *Isodon discolor* (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 119. 1929. TYPES: W Szechuan, Min Valley, at 4000–9000 ft, Aug. 1903, *Wilson 4321* (syntype, E; isosyntype, A), *4322* (syntype, E; isosyntype, A); between Tachienlu and Chengtu, Oct. 1904, *Hosie s.n.* (syntype, E, not seen).

Undershrub, 0.5–1 m high, much branched. Branches slender, cylindrical, decorticate, gray-yellow, glabrous; branchlets quadrangular, striate, adpressedly whitish-tomentulose. Cauline leaves opposite; petiole 2–12 mm long; blade oblong-ovate, ovate, or broadly ovate, 0.4–1.5 by 0.4–1.4 cm, rounded at apex, shortly truncate-attenuate at base, entire or grossly crenate, chartaceous, olive-green and minutely glandular-pubescent above, densely and adpressedly gray-tomentulose beneath, lateral nerves and midrib slightly raised beneath, veinlets conspicuous above. Cymes axillary, remote, 1- to 7-flowered, 0.8–2.3 cm long, arranged in verticillasters on upper part of branch, the peduncle 2–12 mm long; floral leaves gradually smaller upward. Calyx campanulate, ca. 3 mm long, 3 mm in diameter at throat, densely whitish-tomentulose outside, slightly 2-lipped, the teeth 5, ovate-triangular, slightly longer than calyx tube, lower 2 slightly longer; fruiting calyx dilated. Corolla ca. 9 mm long, purplish, pilose outside, glabrous inside; tube saccate on upper side near base, ca. 4 mm long, ca. 3 mm in diameter at throat; limb 2-lipped, the upper lip reflexed, 4-lobed at apex, the lower lip porrect, suborbicular, concave. Stamens and style slightly exserted. Nutlets oblong-triquetrous, ca. 1 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Southwestern and central China (western Sichuan, southern Gansu, southwestern Shaanxi, and Xizang); in thickets in dry sites, 1650–2800 m alt. Flowering June–October, fruiting July–November.

This species is allied with *Isodon tenuifolius* but differs in its remote cymes arranged in verticillasters and its smaller leaves that are glandular-pubescent above.

51. **Isodon tenuifolius** (W. W. Smith) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 119. 1929. FIGURE 7K, L.

Plectranthus tenuifolius W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **9**: 118. 1916. *Rabdosia tenuifolia* (W. W. Smith) H. Hara, J. Jap. Bot. **47**: 201. 1972. TYPE: China, Yunnan, Yangtze Valley at Pung-tzu-la, *Forrest 13184* (holotype, E, not seen).

Undershrub up to 1 m high, much branched. Branches subcylindrical, angulate, decorticate lengthwise, yellowish-brown; branchlets elongate, slender, obtusely quadrangular, densely gray-tomentulose. Cauline leaves opposite; petiole 3–5 mm long, concave-convex, densely gray-tomentulose; blade lanceolate or ovate-lanceolate, 0.8–2 by 0.5–1 cm, acute or subacute at apex, cuneate or subrotund at base, remotely crenulate-serrate above middle or entire, chartaceous, green and densely pilose above, very densely gray-tomentulose beneath, the lateral nerves 3 or 4 pairs, oblique, yellowish white above, raised on both surfaces like midrib. Panicles terminal, racemose, up to 20 cm long, composed of 5- to 7-flowered cymes; cymes with peduncle 2–5 mm long, pedicels 1–2 mm long, peduncle and pedicels densely gray-tomentulose; lower floral leaves similar to cauline ones, longer than cymes, upper floral leaves gradually reduced and changed into bracts upward, equal to or slightly longer than cymes, entire; bracteoles linear, ca. 1 mm long, densely gray-tomentulose. Calyx campanulate, up to 3 mm long, densely gray-tomentulose outside, glabrous inside, the teeth 5, triangular, subequal, ⅓ of calyx length, acute at apex. Corolla ca. 7 mm long, whitish purplish, whitish rose, or purplish, pilose outside, glabrous inside; tube abruptly saccate on upper side near base, ca. 3 mm long, up to 1.5 mm broad at throat, straight; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, equally 4-lobed at apex, lower lip porrect, orbicular-ovate, ca. 4 mm long, concave. Stamens included, the filament complanate, barbate below middle; style included, equally 2-fid at apex. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and southwestern Sichuan); in thickets, 1900–3000 m alt. Flowering in September.

Isodon tenuifolius is related to *I. parvifolius* but differs in having the cymes arranged in a long terminal panicle and leaves that are densely pilose above.

52. **Isodon hirtellus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60**: 234. 1985.

Plectranthus hirtellus Hand.-Mazz. Acta Horti Gothob. **13**: 370. 1939. *Rabdosia hirtella* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47**: 196. 1972. TYPE: China, Yunnan boreo-orient., Shi-tsiang-fang, Nov. 1910, *Maire, distr. Bonati s. B6388* (fragment of type, W).

Undershrub or subundershrub, 1–1.5 m high. Stems erect, much branched; branches subcylindrical, striate, yellow-brownish, glabrous; branchlets obtusely quadrangular or subcylindrical, densely and patently hirtellous. Cauline leaves opposite; petiole up to 1 cm long, plano-convex, very densely gray-hirtellous; blade ovate or broadly ovate, 1–3 by 0.7–2.5 cm, acute or obtuse at apex, truncate or broadly cuneate and abruptly attenuate at base, crenulate-serrate

above base, chartaceous, the upper surface olive-green, very densely hirtellous, the lower surface greenish, very densely gray-tomentulose or hirtellous (sometimes glabrescent), glandular. Panicles terminal and/or axillary, 7–15 cm long, narrow, densely gray-hirtellous, composed of remote (lower) and continuous (upper), 3- to 5-flowered cymes; cymes sessile or shortly pedunculate; floral leaves sessile or subsessile, suborbicular, 0.4–1.5 cm broad, gradually reduced and changed into bracts upward, obtuse or rotund at apex, cordate at base; bracteoles linear, ca. 1 mm long, hirtellous. Calyx campanulate, ca. 3 mm long, densely hirtellous outside, glabrous inside, the limb with 5 subequal teeth or slightly 2-lipped, the teeth triangular, about as long as calyx tube, acute; fruiting calyx tubular-campanulate, ca. 4 mm long, conspicuously nervate. Corolla up to 5 mm long, whitish purplish or bluish purple, densely pilose outside, glabrous inside; tube included, saccate on upper side near base, ca. 2.5 mm long, ca. 1.5 mm broad at throat; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, 4-lobed at apex, the lower lip porrect, ca. 2.5 mm long, concave. Stamens included; style slightly exserted, equally 2-lobed at apex. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northeastern Yunnan and southwestern Sichuan); on sunny slopes, 850–1300 m alt. Flowering June–October.

This species is distinctive in its sessile or very-short-pedunculate cymes and its densely hirtellous branchlets, inflorescences, and calyces.

53. **Isodon rubescens** (Hemsley) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Plectranthus rubescens Hemsley, J. Linn. Soc., Bot. **26:** 273. 1890. *Rabdosia rubescens* (Hemsley) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: China, Hupeh, Ichang, *A. Henry 974* (holotype, K, not seen).

P. dichromophyllus Diels, Bot. Jahrb. Syst. **29:** 562. 1900. *I. dichromophyllus* (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 123. 1929. *Rabdosia dichromophylla* (Diels) H. Hara, J. Jap. Bot. **47:** 194. 1972. SYNTYPES: China, S Nanchuan, *BvR 2207*; Wang tien ling, *BvR 1164*; Lung mo-ai, *BvR 861* (none seen).

P. ricinispermus Pampan. Nuovo Giorn. Bot. Ital., n.s. **17:** 707. 1910. *Isodon ricinispermus* (Pampan.) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 132. 1929. *Rabdosia ricinisperma* (Pampan.) H. Hara, J. Jap. Bot. **47:** 199. 1972. SYNTYPES: Hupeh, Yu-koan-tu, *C. Silvestri 2081* (fragment, A); Hupeh, Fan Hsien, Oct. 1906, *C. Silvestri s.n.* (fragment, A).

Undershrub, (0.3–)0.5–1(–1.2) m high. Stems numerous, erect, much branched at apex, subcylindrical at base, decorticate lengthwise, gray-brownish or brownish, glabrous; branches and branchlets like upper part of stem quadrangular, striate, reddish, densely pilose or tomentose when young but subglabrescent with age. Cauline leaves opposite; petiole 1–3.5 cm long (gradually shorter on upper leaves) including pseudopetiole; blade ovate or rhombic-ovate, 2–6 by 1.3–3 cm, acute or acuminate at apex, broadly cuneate and abruptly decurrent, grossly callose-crenate-serrate, membranaceous to chartaceous, the upper surface olive-green, sparsely pilose when young to subglabrescent with age, glandular, the lower surface greenish, densely gray-tomentulose when young to

subglabrescent with age, the lateral nerves 3 or 4 pairs, raised on both surfaces and reddish like midrib. Panicles terminal, 6–15 cm long, narrow, composed of 3- to 5- (to 7-)flowered cymes; cymes with peduncle 2–5 mm long, peduncle, pedicels, and rachis reddish and densely pubescent; floral leaves short-petiolate or subsessile, rhombic or rhombic-ovate to lanceolate, gradually reduced upward, lower ones longer and upper ones shorter than cymes, acute at apex, broadly cuneate at base, remotely serrate or subentire; bracteoles subulate-linear or linear, up to 1.5 mm long, pubescent. Calyx campanulate, 2.5–3 mm long, densely gray-pubescent and glandular and conspicuously reddish outside, glabrous inside, 10-nerved, the limb ½ of calyx length, slightly 2-lipped, the teeth 5, ovate-triangular, subacute, lower 2 porrect and largest, fruiting calyx tubular-campanulate, dilated, 4–5 mm long, slightly curved, conspicuously nervate. Corolla ca. (5–)7(–12) mm long, pubescent and glandular outside, glabrous inside; tube saccate on upper side near base, 3.5–5 mm long, 2–2.5 mm in diameter at throat; limb 2-lipped, the upper lip 2.5–4 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 3.5–7 mm long, concave. Stamens slightly exserted or sometimes included, the filament complanate, barbate below middle; style exserted. Nutlets ovoid, triquetrous, 1.3 mm long, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. China (mainly along Yangtze River but north to Gansu and Hebei and south to Guangxi); in thickets or forests, on roadsides, stony slopes, and dry sites, 100–2800 m alt. Flowering July–October, fruiting August–November.

This species is quite variable in leaf form and in hairiness of leaves and branchlets but is constant in having a narrow panicle, cymes with slender peduncles and pedicels, and campanulate gray-pubescent calyces with ovate-triangular teeth. It is similar in habit to *Isodon amethystoides* but differs in that the plant is reddish in age, the fruiting calyx is slightly curved, and the nutlets are glabrous.

54. **Isodon loxothyrsus** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 235. 1985. FIGURE 7D, E.

Plectranthus loxothyrsus Hand.-Mazz. Acta Horti Gothob. **13:** 372. 1939. *Rabdosia loxothyrsa* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 197. 1972. TYPE: China, Yünnan bor.-occid., in regione subtropica faucium fluvii Djinschadjiang (Yangtse) ad orientem urbis Lidjiang (Likiang), 3 July 1914, *Handel-Mazzetti 3403* (holotype, w).
P. sp. aff. *rugoso* W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **17:** 353. 1930.
P. rugosus auct. non Wallich: Hand.-Mazz. Symb. Sin. **7:** 937. 1936.

Undershrub, 1–1.6 m high, much branched. Branchlets obtusely quadrangular, striate, brown, gray-tomentulose; branches subcylindrical, decorticate, glabrescent. Cauline leaves opposite; petiole 1–2.5 cm long, sometimes narrowly alate on upper portion, concave-convex, gray-tomentulose; blade ovate-lanceolate, 3.5–6(–10) by 1.5–2.5(–4) cm, acuminate at apex, cuneate or rotund-cuneate and abruptly attenuate at base, crenate-dentate above base, chartaceous, the upper surface green or olive-green, rugulose, gray-tomentulose

except along midrib and nerves, the lower surface greenish or gray, more or less tomentulose or pubescent, the lateral nerves ca. 3 pairs, anastomosing at teeth near leaf margin, slightly sunken above, conspicuously raised beneath. Panicles terminal and axillary, terminal ones up to 15 cm long and axillary ones 3–10 cm long, narrow, recurved, composed of 5- to 7-flowered cymes; cymes with peduncle 0.5–1.5 cm long, slender, the pedicels 2–6 mm long, subcapillary, the peduncle, pedicels, and rachis gray-tomentulose; bracts short-petiolate to sessile, ovate-lanceolate, shorter than cymes, 0.5–1 cm long, entire; bracteoles linear, ca. 2 mm long. Calyx campanulate, 2–2.5 mm long, densely gray-tomentulose outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate-triangular, somewhat shorter than calyx tube, lower 3 slightly larger, all obtuse or acute; fruiting calyx tubular-campanulate, 4–5 mm long, slightly incurved, tomentulose along ribs and margin, conspicuously nervate. Corolla 6–10 mm long, pink, or yellowish to white, pilose and glandular outside, glabrous inside; tube saccate on upper side near base, 3–5 mm long, 2–2.5 mm in diameter at throat; limb 2-lipped, the upper lip 2–2.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 3–5 mm long, concave, boat shaped. Stamens included or slightly exserted; style very exserted, equally 2-lobed at apex. Mature nutlets ovoid, ca. 1 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan, southwestern Sichuan, and southeastern Xizang); in thickets or forests, on grassy slopes, and along stream sides, (1450–)1600–3300 m alt. Flowering July–October, fruiting August–November.

In habit this species is like *Isodon rugosus,* but the indumentum is quite different. It seems to be most closely allied with *I. rugosiformis* (Hand.-Mazz.) H. Hara, differing in its loose inflorescence with long peduncle and pedicels and its larger leaves.

55. **Isodon xerophilus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 237. 1985. FIGURE 7F–J.

Rabdosia xerophila C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 787. *pl. 186, figs. 6–10.* 1977. TYPE: China, Yunnan, Shi-ping, *S. K. Wu 889* (holotype, KUN).

Undershrub, ca. 1 m high. Stems much branched; branches slender, virgate, subcylindrical or obtusely quadrangular, decorticate lengthwise, gray-brownish, with white pith; branchlets quadrangular, fulvous but more or less purplish, very densely velutinous with upwardly curved, fulvous hairs. Cauline leaves opposite; petiole 1–3 mm long, purplish, very densely velutinous; blade ovate-oblong, 1–2.5 by 0.5–1.5 cm, acute at apex, subrotund at base, regularly crenulate above base, chartaceous, the upper surface olive-green, rugulose, pubescent, the lower surface gray but purplish along midrib and nerves, very densely velutinous, the lateral nerves ca. 4 pairs, sunken above and raised beneath like midrib. Panicles terminal (sometimes also axillary on upper part of branchlets, then together forming complex, pyramidal ones), 3.5–10 cm long, narrow, composed of 3- to 5-flowered cymes; cymes with peduncle 2–3 mm long, pedicels 3–4 mm long, peduncle, pedicels, and rachis densely pubescent with

upwardly curved hairs; floral leaves narrowly to broadly ovate, shorter than cymes, acuminate at apex, serrulate. Calyx campanulate, ca. 3 mm long, densely pubescent outside, glabrous inside, slightly 2-lipped, the teeth 5, broadly triangular, ca. ⅓ of calyx length, lower 2 always slightly larger than others, all acute at apex; fruiting calyx tubular-campanulate, slightly dilated, ca. 4 mm long, horizontal or slightly curved upward above middle, purplish, conspicuously 10-nerved. Corolla up to 8 mm long, pubescent outside, glabrous inside; tube saccate on upper side near base, ca. 3 mm long, ca. 2 mm broad at throat; limb 2-lipped, the upper lip 3 by 4.5 mm, reflexed, 4-lobed at apex, the lower lip broadly ovate, up to 5 by 4 mm, concave. Stamens included or slightly exserted; style included, equally 2-lobed at apex. Mature nutlets ovoid, ca. 1 mm long, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (southern Yunnan); on roadsides or sunny slopes, 1000–1300 m alt. Flowering October–November, fruiting November–December.

Although allied with *Isodon rugosiformis, I. xerophilus* has velutinous branchlets and petioles, narrowly paniculate inflorescences, and floral leaves the same as the cauline ones.

56. **Isodon rugosiformis** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Plectranthus rugosiformis Hand.-Mazz. Akad. Wiss. Wien, Math.-Naturwiss. Kl., Anz. **62:** 237. 1925. *Rabdosia rugosiformis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPES: China, Yunnan bor.-occid., in regionis siccae subtropicae ad fluvium Land-sang-djiang (Mekong), declivibus infra vicum Lota ubi, 27°50–55′N, *Handel-Mazzetti 10016* (syntype, W; fragment, A); SE Tibet, Tsarong, Salwin-Kiuchiang divide, 28°40′N, 98°15′E, *G. Forrest 19283* (syntype, W).

Subundershrub, 0.8–1.2 m high. Stems erect, much branched; branches decorticate, subglabrescent; branchlets obtusely quadrangular, striate, yellowish brown, densely gray-tomentulose. Cauline leaves opposite; petiole 0.3–1.5 cm long (upper ones gradually shorter), plano-convex, densely gray-tomentulose; blade rhombic or triangular-ovate, 1.5–4 by 1–2.5 cm, gradually reduced upward, acute or shortly caudate-acuminate at apex, broadly cuneate to truncate at base, crenate, thin-chartaceous, dark green and densely gray-puberulous mainly along midrib and nerves above, densely gray-tomentulose beneath, glandular on both surfaces, the lateral nerves ca. 4 pairs, conspicuously arcuate, like midrib slightly sunken above and strongly raised beneath, the veinlets sunken above but conspicuous beneath. Panicles terminal, spikelike, very loose, composed of 3- to 5-flowered cymes; cymes with peduncle 2–7 mm long, pedicels 2–3 mm long, peduncle, pedicels, and rachis densely gray-tomentulose; floral leaves short-petiolate or subsessile, ovate-lanceolate, 0.5–1.5 cm long, gradually reduced upward, subentire. Calyx campanulate, up to nearly 3 mm long, gray-tomentulose outside, glabrous inside, 10-nerved, slightly 2-lipped, the teeth 5, ovate-triangular, almost ½ length of calyx tube, lower 2 slightly longer than others; fruiting calyx slightly dilated, conspicuously nervate. Corolla ca. 7 mm long, purple or purplish blue, puberulous outside, pubescent below

upper lip inside; tube saccate on upper side near base, ca. 3 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 2 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, ca. 4 mm long, boat shaped. Stamens all (or only upper ones) slightly exserted, filament white-barbate below middle; style exserted, equally 2-fid at apex. Mature nutlets ellipsoid, triquetrous, 1.3 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and western Sichuan); in thickets on slopes or in valleys, or in rocky places, 1925–2500 m alt. Flowering and fruiting September–October.

This species is very close to *Isodon rugosus* but differs in its very loose spikelike panicles, elongate pedicels, larger corollas, and slightly exserted stamens.

E. **Isodon** ser. **Pleiophylli** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Pleiophyllae* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66**: 461, 587. 1977.

Mainly undershrubs or subundershrubs, mostly with rugose leaves; branchlets, leaves, and calyces slightly hairy. Cymes axillary or arranged into panicles, with floral leaves reduced to bracts. Calyx campanulate, subequally 5-toothed or slightly 2-lipped, teeth elongate but not exceeding ½ of calyx length. Corolla medium in size, with declinate tube.

TYPE SPECIES. *Isodon pleiophyllus* (Diels) Kudo.

KEY TO THE SPECIES OF SER. PLEIOPHYLLI

1. Stems ascendent; branches elongate; stems, branches, and petioles all densely septate-pilose; cauline leaves triangular-ovate, petiole 1.5–3 cm long. ... 57. *I. flexicaulis.*
1. Stems erect; branches not so elongate; stems, branches, and petioles covered with nonseptate hairs; cauline leaves broadly ovate, suborbicular, ovate, or rhombic-ovate to oblong-lanceolate, petiole less than 1.5 cm long.
   2. Cauline leaves less than 2 cm long.
      3. Cauline leaves broadly truncate-ovate or suborbicular, with glandular hairs on both surfaces. ..... 58. *I. glutinosus.*
      3. Cauline leaves usually ovate or subrhomboid-ovate to oblong-lanceolate, sometimes broadly ovate, lacking glandular hairs.
         4. Flowers with the corolla white, ca. 6 mm long, tube included, the calyx densely white-pilose on teeth inside. ..... 59. *I. medilungensis.*
         4. Flowers with the corolla purplish, ca. 9 mm long, tube exserted, the calyx glabrous inside. ..... 60. *I. pharicus.*
   2. Cauline leaves over 2 cm long.
      5. Stems or branches densely glandular-pubescent; calyx teeth triangular, conspicuously mucronate at apex. ..... 61. *I. mucronatus.*
      5. Stems or branches pubescent or glandular-pubescent; calyx teeth ovate-triangular, never mucronate at apex.
         6. Branchlets and petioles densely gray- (but not glandular-)pubescent.
            7. Cymes 5- to 9-flowered; leaves adpressedly puberulous-tomentose beneath. ..... 62. *I. namikawanus.*

7. Cymes 3-flowered; leaves pubescent only on midrib and nerves beneath. ..... 63. *I. silvaticus.*
6. Branchlets and petioles densely glandular-pubescent. 64. *I. pleiophyllus.*

57. **Isodon flexicaulis** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Rabdosia flexicaulis C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 461, 587. *pl. 96.* 1977. TYPE: China, Sichuan, Muli, *S. K. Wu 3173* (holotype, KUN).

Undershrub, up to 1 m high. Stems ascendent, much branched, slender, subcylindrical, finely striate, yellowish brown, densely glandular and pubescent and sparsely septate-pilose, with large, white pith; branches elongate, slender, flexuous. Cauline leaves opposite; petiole 1.5–3 cm long, slender, plano-convex, densely septate-pilose and pubescent; blade triangular-ovate, 2–4 by 1.3–2.8 cm (always smaller on branchlets), acute at apex, broadly truncate to subtruncate at base, regularly dentate, submembranaceous, the upper surface olive-green, sparsely pilose, yellowish-glandular, the lower surface greenish, pilose along midrib and nerves, gland dotted, the lateral nerves ca. 4 pairs, slightly raised above and conspicuously so beneath like midrib. Panicles terminal, ca. 10 cm long, together forming large, complex one on top of each stem, composed of 3- to 5-flowered cymes; cymes with peduncle 0.5–1.5 cm long, peduncle, pedicels, and rachis densely pubescent and glandular; lower floral leaves like cauline ones, others gradually reduced and changed into bracts upward; bracts petiolate or subsessile, acute at apex, broadly cuneate at base, crenate or subentire. Calyx campanulate, ca. 3 mm long, pubescent and glandular outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate-triangular, ca. 1.5 mm long, lower 2 slightly larger than others, all acute at apex, ciliolate; fruiting calyx tubular-campanulate, dilated, up to 7 mm long, recurved upward, conspicuously nervate. Corolla up to 1.1 cm long, white or pink, sparsely pubescent and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 5 mm long, 2 mm in diameter near base, slightly attenuate upward and ca. 1.5 mm in diameter at throat; limb 2-lipped, the upper lip erect, 4 by up to 6 mm, reflexed, 4-lobed at apex, the lower lip broadly ovate, 6 by 4.5 mm, constricted at base, concave, boat shaped. Stamens included, the filament complanate, barbate on lower part; style included, equally 2-fid at apex. Mature nutlets ellipsoid, triquetrous, ca. 2 mm long, yellowish but with yellow-white markings.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan, Yunnan); in thickets or valleys, 2100–2450 m alt. Flowering and fruiting in September.

This species is quite different from the others of the genus in its slender, ascendent stem, elongate branchlets, and densely septate-pilose branchlets and petioles.

58. **Isodon glutinosus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985. FIGURE 7M, N.

Rabdosia glutinosa C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 788. *pl. 186, figs. 13, 14.* 1977. TYPE: China, Yunnan, Zhongdian, *Zhongdian Expedition 63-3029* (holotype, KUN).

Undershrubs, 0.7–1.5 m high. Stems decorticate lengthwise, gray, subglabrous; branches subcylindrical, purplish, densely puberulous and glandular. Cauline leaves opposite; petiole 2.5–14 mm long; blade broadly truncate-ovate or suborbicular, 0.7–2 by 0.6–2.1 cm, obtuse or acute at apex, rotund at base, crenate-serrate except at base, chartaceous, olive-green above and greenish beneath, glandular-puberulous and glandular on both surfaces. Panicles terminal, together forming complex one on upper part of each stem, composed of loose many-flowered cymes, puberulous and glandular; cymes with pedicels 3–5 mm long; lower floral leaves like cauline ones, the upper floral leaves subsessile, gradually reduced upward, entire; bracteoles ovate-lanceolate or linear, minute, much shorter than pedicels. Calyx campanulate, ca. 3 mm long, 3.5 mm in diameter, densely glandular-puberulous and glandular outside, 10-nerved, slightly 2-lipped, the teeth 5, ovate, subequal, as long as calyx tube, upper 3 slightly reflexed, lower 2 porrect; fruiting calyx dilated, ca. 5 mm long, 3–4 mm in diameter. Corolla ca. 7 mm long, purplish; tube saccate on upper side above base, short, almost as long as calyx; limb 2-lipped, the upper lip ca. 4 by 4 mm, reflexed, 4-lobed at apex, the lower lip horizontal, as long as upper one, concave, boat shaped. Stamens included; style much exserted. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and southwestern Sichuan); in dry thickets or on gravelly slopes of river valleys, 2000–2300 m alt. Flowering in July.

This species is distinctive in that the entire plant is densely covered with both glandular hairs and glands.

59. **Isodon medilungensis** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Rabdosia medilungensis C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 462, 587. 1977. TYPE: China, Sichuan, Medilung, Muli, *NE Yunnan Expedition 4140* (holotype, PE).

Undershrub, 60 cm high, much branched. Branches decorticate, brown, glabrous; branchlets slender, obtusely quadrangular, shallowly sulcate, densely gray-puberulous. Cauline leaves opposite; petiole 3–10 mm long; blade ovate or subrhomboid-ovate, 1–3 by 0.6–1.4 cm, acute at apex, broadly cuneate at base, crenate-serrate or entire, chartaceous, green and rugulose above, greenish beneath, puberulous and glandular on both surfaces, the lateral nerves 4 or 5 pairs, sunken above and raised beneath like midrib. Cymes axillary, 3- to 5-flowered, arranged in verticillasters on upper part of each branch and branch-

let; peduncle ca. 2 mm long, pedicels 1–2 mm long, peduncle and pedicels densely puberulous; floral leaves subsessile, reduced upward, subentire. Calyx campanulate, 4 mm long, densely puberulous outside, densely white-pilose on teeth inside, the teeth 5, lanceolate, subequal, up to 2.5 mm long, spiny-acute at apex, with spine ca. 0.5 mm long. Corolla ca. 6 mm long, white, pilose outside, glabrous inside; tube included, saccate on upper side near base, 2.5 mm long, ca. 1.5 mm in diameter at throat; limb 2-lipped, the upper lip 3 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 3.5 mm broad. Stamens included; style slightly exserted, equally 2-fid at apex. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. China (southwestern Sichuan); in thickets, ca. 2000 m alt. Flowering June–July.

Allied with *Isodon pharicus, I. medilungensis* differs in having the calyx densely white-pilose on the teeth inside.

60. **Isodon pharicus** (Prain) Murata, Acta Phytotax. Geobot. **16:** 15. 1955.

Plectranthus pharicus Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. **59:** 297. 1890. *Rabdosia pharica* (Prain) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: E Himalaya, Phari, 1882, *King's collector 80* (holotype, K).

Rabdosia sinuolata C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 454, 586. 1977. TYPE: China, Xizang, Tsa-ya, *C. W. Wang 66185* (holotype, PE; isotype, A).

R. pseudo-irrorata C. Y. Wu, Fl. Reipubl. Pop. Sin. **66:** 463, 587. *pl. 99.* 1977. *Isodon pseudo-irroratus* (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 236. 1985. TYPE: China, Sichuan, Dao-cheng, *T. T. Yü 12949* (holotype, PE; isotypes, A, KUN).

R. pseudo-irrorata C. Y. Wu var. *centellaefolia* C. Y. Wu, Fl. Reipubl. Pop. Sin. **66:** 463, 587. 1977. TYPE: China, Xizang, Lung-tzi, *G. W. Zhang 1179* (holotype, PE).

Tufted, much-branched undershrub, 30–50 cm high. Branches subcylindrical, decorticate, gray-brownish; branchlets quadrangular, gray-brownish, adpressedly puberulous. Cauline leaves opposite; petiole 1–4 mm long, minutely puberulous; blade oblong-lanceolate, ovate, or broadly ovate, 0.7–2.5 by 0.6–2.2 cm, obtuse at apex, cuneate-attenuate at base, 4- to 6-crenate-serrate on each side above middle, chartaceous, olive-green above, greenish beneath, densely adpressed-puberulous and glandular on both surfaces, the lateral nerves ca. 3 or 4 pairs, oblique, slightly sunken above and raised beneath like midrib. Cymes axillary, 3- to 7-flowered, arranged in verticillasters on upper part of each branch or branchlet; peduncle 0.3–1.5 cm long, pedicels 2–3 mm long, peduncle, pedicels, and rachis adpressedly puberulous; floral leaves gradually reduced upward; bracteoles ovate or linear, 1–3 mm long, always shorter than pedicels. Calyx campanulate, 3 mm long, ca. 3.2 mm in diameter, puberulous and glandular outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate, lower 2 slightly larger than others, all mucronate at apex. Corolla ca. 9 mm long, purplish, puberulous outside, pubescent at middle inside; tube saccate on upper side near base, ca. 4 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 by 4 mm, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, up to 5 by 4 mm, concave, always reflexed. Stamens and style included or slightly exserted. Nutlets ovoid-oblong, ca. 1.6 mm long, 1.1 mm in diameter, gray.

DISTRIBUTION AND PHENOLOGY. Nepal and southwestern China (Xizang and southwestern Sichuan); in thickets, on dry, open, gravelly and rocky slopes, along forest margins, (2300–)3300–4300 m alt. Flowering and fruiting July–September.

I am sure that the types of *Rabdosia sinuolata, R. pseudo-irrorata,* and *R. pseudo-irrorata* var. *centellaefolia* are identical with *I. pharicus,* so I have reduced them to synonyms of the last species. *Isodon pharicus* looks like *I. rugosus* but differs in having smaller, less hairy leaves.

61. **Isodon mucronatus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Rabdosia mucronata C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 464. *pl. 100.* 1977. TYPE: China, Sichuan, Muli, 20 Sept. 1959, *S. K. Wu 3156* (holotype, KUN).

Undershrub or perennial herb, ca. 1 m high. Stems erect, much branched, subcylindrical; branches decorticate, gray-brown, finely striate, with large pith; branchlets yellowish, like stem and branches densely glandular-pubescent. Cauline leaves opposite; petiole 0.5–1.5 cm long, plano-convex, densely glandular-pubescent; blade ovate to orbicular-ovate, 3–5.5 by 2.5–3.5 cm, acute at apex, broadly cuneate to subrotund or shallowly cordate at base, callose-crenate-serrate above base, chartaceous, the upper surface dark green, densely hirtellous, the lower surface greenish, hirtellous along midrib and nerves, dotted with yellowish glands, the lateral nerves ca. 4 pairs, lower 2 pairs always approximate, like midrib slightly raised above and very raised and yellowish white beneath. Panicles terminal, 6–12 cm long, narrow, composed of 5- to 7-flowered cymes; cymes with peduncle up to 1.5 cm long (lower ones) or less than 1 cm long (upper ones), pedicels 1–2 mm long, peduncle, pedicels, and rachis densely glandular-pubescent; floral leaves short-petiolate, suborbicular, the lowest one largest (up to 2.5 cm long), acute at apex, dentate, the others gradually reduced upward, emarginate and caudate at apex, entire; bracteoles subulate, minute. Calyx campanulate, ca. 4 mm long, glandular-pubescent outside, glabrous inside, 10-nerved, slightly 2-lipped, the teeth 5, triangular, ca. 1.5 mm long, lower 2 slightly larger than others, all mucronate at apex. Corolla ca. 8 mm long, pink, sparsely pubescent on lower lip outside, glabrous inside; tube saccate on upper side near base, 3.5 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, ca. 4 mm long, concave. Stamens included; style slightly exserted, filiform, equally 2-fid at apex. Mature nutlets ellipsoid, triquetrous, ca. 2 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan); on sunny grassy slopes, ca. 2150 m alt. Flowering and fruiting September–October.

Isodon mucronatus seems very much like *I. pleiophyllus* but differs in the triangular, conspicuously mucronate calyx teeth. More material is necessary for further investigation.

62. **Isodon namikawanus** Murata, Acta Phytotax. Geobot. **22:** 22. 1966.

Rabdosia namikawana (Murata) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: Nepal, Mu, 3750 m alt., 31 Aug. 1958, *O. Namikawa 50* (holotype, KYO, not seen).

Undershrub, 1–1.6 m high, much branched. Branches obtusely quadrangular, decorticate lengthwise, brown, glabrescent; branchlets quadrangular, finely striate, yellow-brown, pubescent. Cauline leaves opposite; petiole 0.5–1.2 cm long, concave-convex, pubescent, blade ovate, 2–5 by 1.5–3 cm, subacute or obtuse at apex, broadly cuneate at base, chartaceous, serrate-dentate except entire base, the upper surface green, minutely puberulous, the lower surface greenish, adpressedly puberulous-tomentose, minutely glandular, the lateral nerves ca. 3 pairs, arcuate-ascendent, slightly sunken above and raised beneath like midrib, the veinlets visible beneath. Panicles terminal, up to 20 cm long, composed of remote 5- to 9-flowered cymes; cymes with peduncle 1.5–3.5 cm long, pedicels 1.5–2.5 mm long, peduncle, pedicels, and rachis pubescent; lower floral leaves like cauline ones, others gradually reduced and changed into bracts upward; bracts subsessile or sessile, broadly ovate, 1–3 by 1–2 cm, subentire or entire; bracteoles linear-subulate, 1–3 mm long. Calyx campanulate, up to 5 mm long, 5 mm in diameter at mouth, pubescent and minutely glandular outside, slightly 2-lipped, the teeth 5, narrowly triangular, subequal, 2 mm long, acute at apex; fruiting calyx tubular-campanulate, up to 6 mm long, curved upward, conspicuously nervate, teeth ⅓ length of calyx. Corolla ca. 10 mm long, pink, purple, or blue; tube saccate on upper side near base, ca. 3 mm in diameter at throat, subequal upward; limb 2-lipped, the upper lip erect, ca. 3 by 5 mm, 4-lobed at apex, the lower lip broadly ovate, ca. 6 mm long, boat shaped, puberulous outside. Stamens and style included. Nutlets ellipsoid, triquetrous, 1.5 mm long, brown, smooth.

DISTRIBUTION AND PHENOLOGY. Nepal; in shady places, on dry slopes, or in *Cupressus* forests, 3300–4600 m alt. Flowering July–September, fruiting August–October.

This species is similar to *Isodon pleiophyllus* and *I. pharicus,* differing from the former in lacking glandular hairs and from the latter in having long-pedunculate cymes.

63. **Isodon silvaticus** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia silvatica C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 466, 588. 1977. TYPE: China, Xizang [Tibet], Mt. Long-tou-la, in forest, *P. C. Tsoong 5270* (holotype, PE).

Subundershrub. Stems erect, subcylindrical on lower part, obtusely quadrangular on upper part, finely striate, yellow-brown, densely gray-pubescent. Cauline leaves opposite; petiole 0.5–1 cm long, concave-convex, densely pubescent; blade ovate, 3–5 by 1–3 cm, acuminate at apex, broadly cuneate to subrotund at base, grossly crenate-serrate, chartaceous, the upper surface olive-green, sparsely hirtellous, the lower surface greenish, slightly pubescent along midrib and nerves, covered with yellowish glands, lateral nerves ca. 4 pairs.

Panicles terminal and axillary, 5–9 cm long, composed of 3-flowered cymes; cymes with peduncle 0.5–1.4 cm long, pedicels ca. 2 mm long, peduncle, pedicels, and rachis densely pubescent; floral leaves ovate, crenate-serrate or subentire; bracteoles linear or linear-lanceolate, ca. 2 mm long. Calyx campanulate, ca. 4 mm long, 3 mm in diameter at mouth, densely pubescent and glandular outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate-triangular, ca. 2 mm long, uppermost one slightly larger than others, all acute at apex; fruiting calyx tubular-campanulate, dilated, up to 6.5 mm long, slightly curved, conspicuously nervate outside. Corolla ca. 7 mm long, pubescent outside, glabrous inside; tube saccate on upper side near base, ca. 3.5 mm long, ca. 2.5 mm in diameter at throat; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 3.5 mm long, concave. Stamens included, filament glabrous; style exserted, equally 2-fid at apex. Mature nutlets oblong, triquetrous, 1.8 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Southwestern China (Xizang); in forests, ca. 4000 m alt. Flowering and fruiting August–September.

This species is allied to *Isodon namikawanus* but differs in having the cymes always three-flowered and the leaves pubescent only on the midrib, with the nerves not adpressedly puberulous-tomentose beneath.

64. **Isodon pleiophyllus** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 121. 1929.

Plectranthus pleiophyllus Diels, Notes Roy. Bot. Gard. Edinburgh **5**: 228. 1912. *Rabdosia pleiophylla* (Diels) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 87. 1975. TYPE: China, Yunnan, dry, rocky situations amongst scrub in side valleys on eastern flank of the Lichiang Range, 27°12′N lat., 9–10,000 ft alt., June 1906, *G. Forrest 2333* (holotype, E, not seen).

KEY TO THE VARIETIES OF ISODON PLEIOPHYLLUS

1. Calyx teeth ovate-triangular, ca. 2 mm long; corollas 8 mm long. ..... 64a. var. *pleiophyllus.*
1. Calyx teeth narrowly triangular, up to 5 mm long; corollas 10 mm long. ..... 64b. var. *dolichodens.*

64a. **Isodon pleiophyllus** var. **pleiophyllus**

Undershrub, 1–1.5 m high. Stems erect, much branched; branches obtusely quadrangular, striate, decorticate lengthwise, gray-brown, glabrescent, with small, white pith; branchlets more or less quadrangular, shallowly sulcate, brownish, densely glandular-pubescent. Cauline leaves opposite; petiole 1–3 mm long; blade ovate or suborbicular, longer than internodes, 1.5–4.5 by 1.5–3 cm, acute or obtuse to subrotund and mucronate at apex, broadly cuneate to rotund at base, regularly serrate except at base, dark green above and greenish beneath, with minute glandular pubescence and yellowish glands on both surfaces, the lateral nerves 4 or 5 pairs, conspicuous above and raised beneath like midrib, the veinlets visible on both surfaces. Panicles terminal, ca. 10 cm long, com-

posed of axillary, 3- to 7- (to 11-)flowered cymes; cymes with peduncle 2–3(–4) cm long, gradually shorter upward, pedicels 2–3 mm long, peduncle, pedicels, and rachis densely glandular-pubescent; floral leaves gradually reduced and changed into bracts upward; bracts suborbicular, apiculate at apex, entire or remotely serrate; bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, ca. 4 mm long, up to 4 mm broad at mouth, purplish, glandular-pubescent outside, glabrous inside, 2-lipped for less than ½ of calyx length, the teeth 5, ovate-triangular, lower 2 slightly larger than others, all acute at apex; fruiting calyx tubular-campanulate, up to 6 mm long, curved, conspicuously nervate. Corolla bluish, blue-purple, or dark blue, slightly pubescent on limb outside, glabrous inside; tube saccate on upper side near base, ca. 4 mm long, ca. 2.5 mm in diameter from above saccate portion up to throat; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, 4-lobed at apex, the lower lip suborbicular, 4 mm long, concave. Stamens and style included. Mature nutlets ellipsoid, triquetrous, 1.2 mm long, brownish, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan); in thickets on slopes or in pine forests, 2800–3500 m alt. Flowering June–August, fruiting in September.

64b. **Isodon pleiophyllus** var. **dolichodens** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia pleiophylla (Diels) C. Y. Wu & H. W. Li var. *dolichodens* C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 790. 1977. TYPE: China, Yunnan, prope urbem Lidjiang (Likiang), in regionis temperatae dumetis trans rivum Beschui, *Handel-Mazzetti 7014* (holotype, Jiangsu Institute of Botany; isotype, W).

This variety differs from var. *pleiophyllus* in having narrowly triangular calyx teeth up to 5 mm long and a corolla to 10 mm long.

DISTRIBUTION. South-central China (northwestern Yunnan); in thickets on limestone mountains, 2900–3200 m alt.

The species is easily recognized by its densely glandular-pubescent branchlets and petioles, its branchlets that are leafy at the top, and its axillary cymes.

F. **Isodon** ser. **Setschwanenses** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Setschwanenses* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66**: 469, 588. 1977.

Rabdosia ser. *Mulienses* C. Y. Wu & H. W. Li, *ibid.* 467, 588. 1977. TYPE SPECIES: *Isodon muliensis* (W. W. Smith) Kudo.

Perennial herbs, subundershrubs, or undershrubs. Cymes arranged into interrupted or continuous spikelike or narrow panicles; floral leaves or bracts gradually reduced upward. Calyx campanulate, with 5 subequal long, narrow teeth or slightly 2-lipped, toothed for ½ its length or more. Corolla medium in size, with declinate tube.

TYPE SPECIES. *Isodon setschwanensis* (Hand.-Mazz.) H. Hara.

KEY TO THE SPECIES OF SER. SETSCHWANENSES

1. Cymes arranged into interrupted spikelike panicles. ..... 65. *I. interruptus.*
1. Cymes arranged into more or less continuous narrow spikes.
   2. Calyx teeth filiform-acuminate at apex. ..... 66. *I. barbeyanus.*
   2. Calyx teeth never filiform-acuminate at apex.
      3. Leaves 1.2–1.8 cm long, strongly reticulate on both surfaces. ..... 67. *I. scoparius.*
      3. Leaves over 2 cm long, inconspicuously reticulate.
         4. Floral leaves bractlike; calyx teeth ovate-triangular. ....68. *I. muliensis.*
         4. Floral leaves more or less like cauline ones; calyx teeth narrowly lanceolate or lanceolate-triangular.
            5. Panicles terminal, 1.5–13 cm long, composed of cymes with peduncle 2–5 mm long and 3 to 5 flowers (sometimes lower cymes of panicle with peduncle up to 9 mm long and 9 to 11 flowers). ..... 69. *I. setschwanensis.*
            5. Panicles terminal or axillary, up to 20(–34) cm long, composed of cymes with peduncle 0.4–2.5(–4.8) cm long and 3 to 15 (to 23) flowers. .... 70. *I. angustifolius.*

65. **Isodon interruptus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Rabdosia interrupta C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 775. 1977. TYPE: China, Yunnan, Xundian, 28 Aug. 1958, *H. W. Li 31* (holotype, KUN).

R. kunmingensis C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 775. 1977. *Isodon kunmingensis* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985. TYPE: China, Yunnan, Kunming, *C. Y. Wu et al., RN7362* (holotype, KUN).

Erect undershrub, 1.3 m high. Branchlets obtusely quadrangular, brown, densely and retrorsely whitish-septate-pilose. Cauline leaves opposite; petiole 2–10 mm long, densely white-septate-pilose; blade ovate-oblong or broadly obovate to suborbicular, (2.5–)5.5–7.5 by (1.2–)4.5–5 cm, acute, truncate-rotund, or emarginate and mucronate at apex, cuneate or broadly cuneate at base, irregularly and grossly crenate, chartaceous, the upper surface olive-green, sparsely puberulous, glandular, the lower surface greenish, white-septate-pilose along midrib and nerves, the lateral nerves 2 or 3 (to 5) pairs, sunken above but conspicuously raised beneath like midrib. Panicles terminal, more or less interrupted, spikelike, (4–)10–30 cm long, composed of remotely arranged, 4- to 16-flowered cymes; cymes with peduncle 2–3 mm long, pedicels 2–3 mm long, peduncle, pedicels, and rachis densely pilose; lower floral leaves like cauline ones, ovate or ovate-lanceolate, longer than (very rarely subequal to) cymes, entire, others gradually reduced upward. Calyx tubular-campanulate, ca. 2.5 mm long, less than 2 mm in diameter, densely pubescent outside, glabrous inside, 10-nerved, the teeth 5, ovate-lanceolate, subequal, more than ½ calyx length. Corolla conspicuously saccate on upper side near base, ca. 5 mm long, yellowish white, puberulous outside; limb 2-lipped, the upper lip erect, reflexed, 4-lobed at apex, the lower lip suborbicular, slightly longer than corolla tube (up to 3 mm), concave. Stamens and style included. Nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (central Yunnan); on stream sides in *Alnus* forests, ca. 2200 m alt. Flowering August–September.

This species is allied to *Isodon muliensis* (W. W. Smith) Kudo but differs in its somewhat interrupted panicle and its floral leaves more or less like the cauline ones.

66. **Isodon barbeyanus** (Léveillé) H. W. Li, comb. nov.

Leucas barbeyana Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 247. 1911. TYPE: Sichuan, Tonglo, principauté de Kiala, 1893, *Soulié 427* (holotype, E, not seen).

Plectranthus drogotschiensis Hand.-Mazz. Acta Horti Gothob. **9:** 95. 1934. *Rabdosia drogotschiensis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 195. 1972. *Isodon drogotschiensis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 234. 1985. TYPE: China, Sichuan, Drogochi, in colle fruticoso, aprico, ca. 3200 m, 25 Sept. 1922, *Harry Smith 4517* (holotype, W).

Subundershrub, up to 1.5 m high. Stems erect, much branched; branches subcylindrical, decorticate, brown; branchlets slender, obtusely quadrangular, densely gray-substellate-tomentulose. Cauline leaves opposite; petiole 5–14 mm long, gradually shorter upward, densely gray-substellate-tomentulose; blade rhomboid or triangular-ovate, 1.5–3(–6) by 1–2.5(–4.5) cm, acute or slightly obtuse at apex, subtruncate or broadly cuneate (rarely attenuate) at base, crenate or dentate, chartaceous or thin-chartaceous, green, the upper surface rugose, sparsely pilose, the lower surface densely gray-substellate-tomentulose, the lateral nerves 3 or 4 pairs. Panicles terminal or axillary, 4–18 cm long, narrow, interrupted in lower part, composed of 3- to 5- (to 7-)flowered cymes; cymes with peduncle and pedicels 2–3.5 mm long; floral leaves subsessile, the lower ones broadly ovate-triangular, longer than cymes, crenulate, the upper ones ovate-lanceolate to narrowly lanceolate, almost as long as cymes, caudate-acuminate at apex, cuneate-attenuate at base, entire, all densely gray-tomentulose on both surfaces; bracteoles linear, 3–4 mm long. Calyx campanulate, ca. 3 mm long, densely gray-tomentulose outside, glabrous inside, 10-nerved, the teeth 5, narrowly lanceolate, subequal, ca. ½ calyx in length, filiform-acuminate at apex; fruiting calyx broadly campanulate, up to 5 mm long, subglabrous. Corolla 5–6 mm long, purplish, densely pilose and sparsely glandular outside; tube saccate on upper part near base, ca. 3 mm long, slightly longer than calyx, slightly shorter than corolla limb; limb 2-lipped, the upper lip reflexed, 4-lobed at apex, the lower lip broadly ovate or orbicular, slightly longer than upper one, concave. Stamens and style included or slightly exserted. Nutlets ovoid, 1.5 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Sichuan); on roadsides or in thickets on sunny slopes, 2500–3200 m alt. Flowering July–September, fruiting September–October.

This species is easily recognized by its filiform-acuminate calyx teeth.

67. **Isodon scoparius** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 236. 1985. FIGURE 4J, K.

Rabdosia scoparia C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 776. 1977. TYPE: China, Yunnan, Haba, Zhongdian, in pine forest, 22 Aug. 1962, *Zhongdian Expedition 1268* (holotype, KUN).

Undershrub, 0.4–1 m high. Branches upright, slender, decorticate lengthwise, gray-brown; branchlets quadrangular, shallowly sulcate, reddish brown, densely glandular-pubescent. Cauline leaves opposite, subsessile; blade suborbicular to ovate-oblong, 1.2–1.8 by 0.6–1.8 cm, obtuse to acute at apex, rotund at base, callose-serrate except along base, subcoriaceous, olive-green above, greenish below, glabrous, dotted with yellowish glands, strongly reticulate. Cymes axillary on upper ½ of branchlets, 3- to 5-flowered, glandular-pubescent, peduncle 6–10 mm long, pedicels 1.5–3 mm long; floral leaves like cauline ones, ovate, slightly longer than cymes, gradually reduced upward, entire; bracteoles thread-like, ca. 1.5 mm long. Calyx broadly campanulate, ca. 3.5 mm long, up to 5 mm in diameter at mouth, densely glandular-pubescent outside, glabrous inside, slightly 2-lipped, the teeth 5, linear-lanceolate, 2.5–3 mm long, lower 2 slightly longer; fruiting calyx slightly dilated, upper 3 teeth slightly reflexed, lower 2 porrect. Corolla ca. 8 mm long, purplish, sparsely pubescent outside, glabrous inside; tube saccate on upper side near base, nearly equal to calyx, almost equal in diameter (ca. 2 mm) from above saccate portion up to throat; limb 2-lipped, the upper lip 3 mm long, 4-lobed at apex, the lower lip broadly ovate, ca. 5 by 4 mm. Stamens slightly exserted; style exserted, 2-fid at apex. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan); in pine forests on limestone mountains, 2300–2900 m alt. Flowering July–August.

This species is easily recognized by its very slender, upright branches, as well as its strongly reticulate small leaves.

68. **Isodon muliensis** (W. W. Smith) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 122. 1929.

Plectranthus muliensis W. W. Smith, Notes Roy. Bot. Gard. Edinburgh **12:** 218. 1920. *Rabdosia muliensis* (W. W. Smith) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: China, SW Sichuan, Muli, 28°12′N, Sept. 1928, *G. Forrest 17000* (holotype, E, not seen).

Rabdosia brachythyrsa C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 476, 589. 1977. *Isodon brachythyrsus* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 233. 1985. TYPE: China, Sichuan, Muli, *S. K. Wu 3470* (holotype, KUN).

R. chionantha C. Y. Wu, Fl. Reipubl. Pop. Sin. **66:** 475, 589. 1977. *Isodon chionanthus* (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 233. 1985. TYPE: China, Sichuan, Muli, *T. T. Yü 6350* (holotype, PE; isotype, A).

Undershrub, 1.5–3 m high, much branched. Branches subcylindrical, decorticate lengthwise, brown, sparsely gray-pubescent, with large, white pith; branchlets obtusely quadrangular, finely striate, dark brown, densely gray-pu-

bescent. Cauline leaves opposite; petiole 1–5.5 cm long, plano-convex, densely gray-pubescent; blade ovate to ovate-lanceolate, 5–11 by 2–6 cm, subacuminate at apex, broadly cuneate and abruptly attenuate at base, crenate-dentate except at base, chartaceous, rugulose, olive-green, the upper surface gray-pubescent along midrib and nerves, otherwise glabrous, the lower surface greenish, gray-tomentulose especially on midrib and nerves, dotted with yellowish glands, the lateral nerves ca. 5 pairs, sunken above, conspicuously raised beneath like midrib. Panicles terminal and axillary, spikelike, elongate, 2.5–7 cm long in flower, together forming complex ones, composed of (3- to) 6- to 8- (to 11-)flowered cymes; cymes continuous except lowest 1 or 2 more or less remote, densely gray-pubescent; floral leaves very conspicuous, bractlike, the lowest one obovate, largest up to 2.5 by ca. 2 cm, mucronate at apex, shallowly cordate at base, the upper ones lanceolate or ovate-lanceolate, generally 1 by 4 mm, longer than or occasionally subequal to cymes, gradually reduced upward, acuminate at apex. Calyx campanulate, 2–2.5 mm long, densely pilose outside, glabrous inside, 10-nerved, the teeth 5, ovate-triangular, as long as calyx tube, acute at apex, white-ciliate; fruiting calyx campanulate-tubular, dilated, up to 4.5 mm long, slightly curved, conspicuously nervate. Corolla up to 8 mm long, yellow-white tinged with red, or white-bluish, sparsely pubescent outside on upper part of tube and on limb, pubescent below upper lip inside; tube saccate on upper side near base, slightly longer than or equal to limb; limb 2-lipped, the upper lip reflexed, 4-lobed at apex, the lower lip porrect, ovate. Stamens included, the filament complanate, barbate on lower portion; style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan); in thickets on slopes, along margins of thickets or forests, on stream sides, 2350–3300 m alt. Flowering August–September, fruiting in October.

The inflorescence of *Isodon muliensis* looks much like that of *I. phyllostachys* of sect. *Pyramidium,* but the petioles are 1–5.5 cm long and the floral leaves are all bractlike. *Rabdosia brachythyrsa* and *R. chionantha* differ from *I. muliensis* only in minor characters, so I think it best to reduce them to synonyms of that species.

69. **Isodon setschwanensis** (Hand.-Mazz.) H. Hara, J. Jap. Bot. **60:** 236. 1985. FIGURES 4L, M; 6A, B.

Plectranthus umbrosus Hand.-Mazz. *in* Karsten & Schenck, Vegetationsbilder, R. 20, *Taf. 42B.* 1930, nomen nudum, non (Maxim.) Makino, 1922.

P. setschwanensis Hand.-Mazz. Symb. Sin. **7:** 939. *pl. 28, fig. 7.* 1936. *Rabdosia setschwanensis* (Hand.-Mazz.) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: China, Sichuan, ober Sili bei Muli, 25 July 1915, *Handel-Mazzetti 7213* (holotype, W; isotype, A).

Rabdosia taliensis C. Y. Wu, Fl. Yunnan. **1:** 777. *pl. 184, figs. 12, 13.* 1977. *Isodon taliensis* (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 237. 1985. TYPE: Yunnan, Dali, 11 Sept. 1938, *W. C. Wu, T. Y. Yang, & C. Y. Wu 12097* (*RN7333*) (holotype, KUN).

R. setschwanensis (Hand.-Mazz.) H. Hara var. *yungshengensis* C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 778. 1977. TYPE: Yunnan, Yung-sheng, 6 July 1960, *S. Zhang 6213* (holotype, KUN; isotype, PE).

Undershrub, 1–1.5 m high. Branches upright, slender, decorticate, gray; branchlets quadrangular, shallowly sulcate on 2 sides, reddish brown, pubescent. Cauline leaves opposite; petiole very short; blade more or less narrowly rhomboid-ovate or lanceolate, obovate, or ovate, 2.5–10 by 1–3.5 cm, acute or shortly acuminate at apex, cuneate or attenuate at base, serrate, glandular above, greenish brown and yellowish-glandular beneath, the lateral nerves 3 or 4 pairs, obliquely arcuate, sunken above but raised beneath like midrib, the veinlets visible beneath. Panicles terminal, pseudoracemose, 1.5–13 cm long, composed of slightly congested, 3- to 5- (or 9- to 11-)flowered cymes; cymes with peduncle 2–5(–9) mm long, pedicels 2–5 mm long, floral leaves subsessile, lower ones ovate and others lanceolate, equal to or longer than cymes, long-acuminate, entire, adpressedly and minutely puberulous like cymes; bracteoles linear, shorter than pedicels. Calyx campanulate, 3–3.5 mm long, 3.5–4 mm in diameter at mouth, sparsely glandular and adpressedly pilose outside, the teeth 5, narrowly lanceolate, subequal, as long as calyx tube, subulate at apex; fruiting calyx pendent, dilated, 6 mm long, 6 mm in diameter at mouth, slightly curved, upper 3 teeth reflexed, lower 2 porrect. Corolla conspicuously saccate on upper side near base, 8–9 mm long, white with purple spots; tube ca. 5 mm long, pilose and sparsely glandular outside like limb; limb 2-lipped, the upper lip reflexed, 4-lobed at apex, the lower lip orbicular-ovate, almost as long as corolla tube. Stamens and style subincluded. Nutlets ovoid, 1.5 mm long, 1.5 mm in diameter, dark brown, smooth.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan and northwestern Yunnan); in forests or on slopes, 2150–3500 m alt. Flowering in September, fruiting in October.

Rabdosia setschwanensis var. *yungshengensis* was established based only on leaf shape, and I now think it best to include the variety in the species. *Rabdosia taliensis* differs from *I. setschwanensis* only in minor characters (e.g., calyx tube densely white-puberulous outside, leaves densely gray-puberulous), so I reduce it to a synonym of the latter. *Isodon setschwanensis* resembles *I. pleiophyllus,* especially var. *dolichodens,* in calyx characters but is very different in the leaf base and the inflorescence.

70. **Isodon angustifolius** (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 137. 1929.

Plectranthus angustifolius Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 154. 1913, *pro parte,* excl. *Wilson 2577. Rabdosia angustifolia* (Dunn) H. Hara, J. Jap. Bot. **47:** 194. 1972. SYNTYPES: China, Yunnan, *Ducloux 274* (E); Mengtze, *Henry 10069* (E), *10069a* (E); near Yunnan-sen, *Maire 2497* (E), *2600* (E) (none seen).

Rabdosia stenodonta C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 780. 1977. *Isodon stenodontus* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 237. 1985. TYPE: China, Yunnan, Lijiang, *C. Y. Wu & D. Y. Liu 21159* (*RN7394*) (holotype, KUN).

KEY TO THE VARIETIES OF ISODON ANGUSTIFOLIUS

1. Stems puberulous; leaves with both surfaces puberulous (especially on midrib) or subglabrous, dotted with small yellow glands; calyx teeth lanceolate-triangular. . . . . 70a. var. *angustifolius.*

1. Stems glabrous; leaves glabrous on both surfaces, dotted with small yellow glands beneath; calyx teeth ovate-triangular. ..... 70b. var. *glabrescens.*

70a. **Isodon angustifolius** var. **angustifolius** FIGURE 6C, D.

Perennial herb. Stems 0.85–1 m or more high, obtusely quadrangular, shallowly sulcate or not sulcate, puberulous, tufted. Cauline leaves opposite; petiole 1–3 mm long, puberulous; blade linear-oblong, lanceolate, oblanceolate, or sometimes oblong-lanceolate, 2.2–9.5 by 1–2.4 cm, acute or obtuse at apex, narrowly cuneate at base, serrate or obscurely serrate above base (sometimes subentire), chartaceous, olive-green above, greenish beneath, both surfaces puberulous (especially on midrib) or subglabrous, and dotted with small yellow glands, the midrib, lateral nerves, and veinlets conspicuously raised beneath. Panicles terminal and axillary, spreading, up to 20(–34) by ca. 10 cm, glandular-puberulous, composed of 3- to 15- (to 23-)flowered cymes; cymes with peduncle 0.4–2.5(–4.8) cm long; lower floral leaves similar to cauline ones, ovate-lanceolate to lanceolate, the upper floral leaves linear-lanceolate to linear, small; bracteoles linear, minute. Calyx campanulate, ca. 4 mm long, 3.5 mm in diameter, fulvous-hirtellous and dotted with small, yellow glands outside, the teeth 5, lanceolate-triangular, ca. 2 mm long; fruiting calyx tubular-campanulate, ca. 7 mm long, slightly 2-lipped. Corolla ca. 11 mm long, blue; tube saccate on upper side near base, twice as long as calyx, ca. 2 mm in diameter; limb 2-lipped, the upper lip ca. 4.5 mm long, 4-lobed at apex, the lower lip suborbicular, as long as upper one, boat shaped. Stamens and style included. Nutlets compressed-subglobose, ca. 1.8 mm in diameter, purplish brown.

DISTRIBUTION AND PHENOLOGY. South-central China (Yunnan); on grassy slopes or in pine forests, 1200–2600 m alt. Flowering September–October, fruiting October–November.

Rabdosia stenodonta differs from *Isodon angustifolius* only in minor characters (e.g., narrower calyx teeth and glandular-pubescent panicle), so I think it is reasonable to reduce it to a synonym of the latter. The species is undoubtedly close to *I. setschwanensis* (their differences are shown in the key), although in habit it is much like *I. nervosus,* which is quite different in calyx characters.

70b. **Isodon angustifolius** var. **glabrescens** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia angustifolia (Dunn) H. Hara var. *glabrescens* C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 780. 1977. TYPE: China, Yunnan, Zhongdian, 22 Aug. 1962, *Zhongdian Expedition 1280* (holotype, KUN).

This variety differs from var. *angustifolius* in its always purplish and glabrous stems, its elliptic or oblong leaves that are glabrous above and densely covered with small yellow glands beneath, and its ovate-triangular calyx teeth.

DISTRIBUTION. South-central China (northwestern Yunnan); in sparse pine forests or on grassy slopes, 2800–3300 m alt.

G. **Isodon** ser. **Coetsae** (Briq.) H. W. Li, comb. nov.

Plectranthus ser. *Coetsae* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 353. 1897.

Perennial herbs. Cymes arranged into narrow panicles. Calyx conspicuously 2-lipped for ½ or less its length in fruit. Corolla medium in size, declinate, with large lower lip.

LECTOTYPE SPECIES. *Isodon coetsa* (Buch.-Ham. ex D. Don) Kudo.

KEY TO THE SPECIES OF SER. COETSAE

1. Plant dwarf, stems creeping and ascendent at base. ..... 71. *I. repens.*
1. Plant tall; stems erect, not creeping at base.
   2. Leaf blades not cordate.
      3. Stamens included.
         4. Leaves with the upper surface densely strigose along midrib and nerves, otherwise sparsely strigose, the lower surface glabrous; corollas with lower lip shorter than tube. ..... 72. *I. kurzii.*
         4. Leaves densely hirtellous on midrib and nerves, otherwise sparsely strigose or subglabrous on both surfaces, or upper surface densely pilose and lower surface densely floccose-villose; corollas with lower lip generally longer than tube. ..... 73. *I. coetsa.*
      3. Stamens slightly exserted. ..... 74. *I. phyllopodus.*
   2. Leaf blades cordate. ..... 75. *I. secundiflorus.*

71. **Isodon repens** (Wallich ex Bentham) Murata, Acta Phytotax. Geobot. **22:** 21. 1966.

Plectranthus repens Wallich ex Bentham *in* Wallich, Pl. Asiat. Rar. **2:** 17. 1830. *Rabdosia repens* (Wallich ex Bentham) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: in montibus Napaliae, 1821, *Wallich 2746* (holotype, K; isotypes, BM, E, LE, S, W).

Perennial herb, 15–30 cm high. Stems repent and ascendent at base, nearly unbranched, slender, obtusely quadrangular, sulcate, densely ferrugineous-septate-villose; internodes much shorter than leaves. Cauline leaves opposite, approximate at base of stem; petiole 1.5–3.5 cm long, complanate, densely ferrugineous-septate-villose; blade ovate-orbicular, 3.5–6 by 3–4.5 cm, obtuse or subrotund at apex, rounded or shallowly cordate at base, grossly crenate, ferrugineous-septate-villose on both surfaces, dotted with red-brown glands beneath, the lateral nerves 4 to 7 pairs, oblique, anastomosing near margin, like midrib sunken above and slightly raised beneath. Panicles terminal, 6.5–18 cm long, composed of dichotomous 5- to 7-flowered cymes, rachis ferrugineous-septate-villose; cymes with peduncle 0.5–1.5 cm long, pedicels 1.5–3 mm long, peduncle, pedicels, and rachis pubescent or subglabrous; floral leaves similar to cauline ones but much smaller, abruptly reduced upward and changed into bracts; bracts oblong-ovate to oblong, 3–5 by 1–3 mm, serrate or entire; bracteoles subulate to linear, ca. 1 mm long. Calyx campanulate, ca. 1.5 mm long, minutely pubescent and glandular, 2-lipped for ⅓ of calyx length, the teeth 5, triangular-lanceolate, lower 2 slightly longer than others, all acute at apex; fruiting calyx urceolate-tubular, up to 3 mm long, incurved, conspicuously

nervate. Corolla ca. 4 mm long, white, bluish white, pale blue, or blue, subglabrous outside; tube obviously saccate on upper side near base, 2.5 mm long, ca. 1.5 mm in diameter near base, gradually attenuate upward and ca. 1 mm in diameter at throat; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, 4-lobed at apex, the lower lip ovate, as long as upper one. Stamens and style included. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. Sikkim, Nepal, Bhutan, and India (Assam); in shade in moist mixed forests, on rocks in woods, under light forest, 2050–3500 m alt. Flowering August–October, fruiting October–November.

This species is easily recognized by its dwarf plants with slender, repent and ascendent stems.

72. **Isodon kurzii** (Prain) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Plectranthus kurzii Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. **59:** 296. 1890. SYNTYPE: Sikkim, between Ratong and Yoksum, *T. Anderson s.n.* (CAL, not seen; K); *Kurz s.n.* (CAL, not seen; K).

Perennial herb. Stems 30–40 cm high, ascendent, unbranched, acutely quadrangular, finely striate, yellow-brownish, minutely pubescent along angles but otherwise glabrous or subglabrous. Cauline leaves subsessile; blade broadly ovate, (1–)1.2–5.5 by 1.3–4.3 cm, obtuse or sometimes truncate at base, 3- to 7-toothed above middle (terminal tooth largest, blunt), thin-membranaceous, the lateral nerves 3 pairs, ascendent, sunken above and raised beneath like midrib. Panicles terminal and axillary, racemose, 2–10 cm long, composed of 3- to 5-flowered cymes; cymes with peduncle 2–2.5 mm long, pedicels 0.7–1 mm long, peduncle, pedicels, and rachis subglabrous; floral leaves reduced and changed into bracts upward; bracteoles subulate, 0.5 mm long. Calyx campanulate, ca. 2 mm long, subglabrous outside, slightly 2-lipped, the teeth 5, narrowly triangular, subequal, subacute at apex; fruiting calyx slightly dilated. Corolla 5.5 mm long; tube saccate on upper side near base, equal in diameter from above saccate portion upward, ca. 1.2 mm at throat; limb 2-lipped, the upper lip ca. 1.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, ca. 2.5 mm long, concave. Stamens and style included. Nutlets broadly ovoid, small.

DISTRIBUTION. Sikkim; on slopes, 830–1600 m alt.

In his original description of *Plectranthus kurzii,* Prain said, "this species most resembles *Plectranthus excisus* Maxim. from China, but is smaller in all its parts." After checking specimens, I think it is very close to *Isodon coetsa* in its racemose panicles and its corollas with a large lower lip, although it differs in having less hairy leaves and corollas with a shorter lower lip.

73. **Isodon coetsa** (Buch.-Ham. ex D. Don) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 131. 1929.

Plectranthus coetsa Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 117. 1825. *Rabdosia coetsa* (Buch.-Ham. ex D. Don) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: in montibus Napaliae, *Wallich* (not seen).

FIGURE 8. A–G, *Isodon coetsa* var. *coetsa* (A, B, D, E, *W. C. Yin 60-1560,* KUN; C, F, G, *S. Chow 130,* KUN): A, upper portion of plant, × 0.6; B, C, flowers, × 2.4; D, calyx, × 2.4; E, corolla and stamens, × 3.6; F, lower cauline leaf, × 0.6; G, portion of lower surface of leaf, × 1.8. H, I, *I. phyllopodus* (*Zhongdian Expedition 3832,* KUN): H, upper portion of plant, × 0.6; I, flower, × 3. J, K, *I. adenanthus* (*Zhongdian Expedition 60-4062,* KUN): J, upper portion of plant, × 0.6; K, flower, × 1.8. (Drawn by X. C. Li.)

P. menthoides Bentham *in* Wallich, Pl. Asiat. Rar. **2**: 17. 1830. *Rabdosia menthoides* (Bentham) C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 790. 1977. TYPE: Nilghiri and Pulney Mtns., *Wight s.n.* (holotype, K).

P. maddeni Bentham ex Hooker f. Fl. Brit. India **4**: 620. 1885. *Isodon maddeni* (Bentham ex Hooker f.) Murata, Acta Phytotax. Geobot. **22**: 31. 1966. *Rabdosia maddeni* (Bentham ex Hooker f.) H. Hara, J. Jap. Bot. **47**: 198. 1972. TYPES: India, Kumaon, *Strachey & Winterbottom s.n.* (isosyntypes, A, BM, LE), *Duthie* (syntype, not seen); Sikkim, *J. D. Hooker s.n.* (isosyntype, W).

P. leptobotrys Diels, Bot. Jahrb. Syst. **29**: 561. 1900. TYPE: China, Szechuan, S Nanchuan, Hon-ho-kou, *BvR 1135* (not seen).

P. polystachys Sun ex C. H. Hu, Acta Phytotax. Sin. **11**(1): 54. *pl. VII, figs. 36–39.* 1966. *Rabdosia polystachys* (Sun ex C. H. Hu) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 92. 1975. *Isodon polystachys* (Sun ex C. H. Hu) H. Hara, J. Jap. Bot. **60**: 236. 1985. TYPE: China, Sichuan, no further locality, 2 Oct. 1930, *W. P. Fang 5347* (holotype, PE).

Rabdosia coetsoides C. Y. Wu, Fl. Yunnan. **1**: 790. *pl. 187, figs. 1–4.* 1976. *Isodon coetsoides* (C. Y. Wu) H. Hara, J. Jap. Bot. **60**: 233. 1985. TYPE: China, Yunnan, Luxi, *W. C. Yin 60-1560* (holotype, KUN).

R. anisochila C. Y. Wu, Fl. Reipubl. Pop. Sin. **66**: 464, 587. 1977. *Isodon anisochilus* (C. Y. Wu) H. Hara, J. Jap. Bot. **60**: 233. 1985. TYPE: China, Sichuan, Muli, *T. T. Yü 7347* (holotype, PE; isotypes, A, KUN).

R. pluriflora C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 796. *pl. 188, figs. 1, 2.* 1977. *Isodon pluriflorus* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60**: 236. 1985. TYPE: China, Yunnan, NW Likiang, between Tamichung and Tuchi, 25 Oct. 1939, *R. C. Ching 21930* (holotype, KUN; isotype, A).

R. polystachys (Sun ex C. H. Hu) C. Y. Wu & H. W. Li var. *phylloides* C. Y. Wu, Fl. Yunnan. **1**: 796. 1977. TYPE: China, Yunnan, Binchuan, *R. C. Ching 2500* (holotype, KUN).

Rabdosia megathyrsoides H. W. Li, Fl. Xizang. **4**: 221. *pl. 92, fig. 3.* 1985. TYPE: China, Xizang, Cuona, *Qinghai-Xizang Complex Expedition (Supplementary Sect.) 751598* (holotype, KUN).

KEY TO THE VARIETIES OF ISODON COETSA

1. Stems retrorsely pubescent or subglabrous; leaves densely hispidulous along midrib and nerves, otherwise sparsely strigose or subglabrous on both surfaces. ..... 73a. var. *coetsa.*
1. Stems densely puberulous; leaves densely pilose above, floccose-pilose beneath. ..... 73b. var. *cavaleriei.*

73a. **Isodon coetsa** var. **coetsa** FIGURE 8A–G.

Perennial herb or subundershrub. Stems erect, 0.5–2 m high, much branched, obtusely quadrangular, sulcate, retrorsely pubescent or subglabrous. Cauline leaves opposite; petiole 1–5.5 cm long, cuneate-alate, flat, pubescent; blade ovate, 3–9 by 1.5–6 cm, acuminate at apex, broadly cuneate at base, crenate above entire base, densely hispidulous along midrib and nerves, otherwise sparsely strigose or subglabrous and glandular on both surfaces, the lateral nerves ca. 3 pairs, more or less raised on both surfaces like midrib. Panicles terminal and axillary, 5–15 cm long, narrow, composed of 3- to 5-flowered cymes; cymes with peduncle 2–3 mm long, pedicels 1–3 mm long, peduncle, pedicels, and rachis pubescent; lowest floral leaves similar to cauline ones, sessile, ovate, others gradually reduced and changed into bracts; bracts ovate-

lanceolate, shorter than pedicels; bracteoles subulate, less than 1 mm long. Calyx campanulate, ca. 1.5 mm long, 1.5 mm in diameter at mouth, pubescent and glandular outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate-triangular, ca. ⅓ of calyx length, acute at apex; fruiting calyx tubular-campanulate, dilated, ca. 4 mm long, slightly incurved, upper part conspicuously 10-nerved and reticulate. Corolla ca. 6 mm long, purple or purple-blue, pubescent outside; tube conspicuously saccate on upper part near base, ca. 2.5 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, much longer than tube, 3.5 mm long, concave, boat shaped. Style included or exserted, equally 2-fid at apex. Mature nutlets obovoid, ca. 1 mm in diameter, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. India (Tamil Nadu, Uttar Pradesh, Assam), Sri Lanka, Bangladesh, Sikkim, Nepal, Burma (Kachin, Chin, Kawthule), northern Thailand, Laos, northern and southern Vietnam, and southern China (southeastern Xizang, Yunnan, Sichuan, Guizhou, Guangxi, Hunan, Fujian); on grassy slopes, along stream sides, river banks, roadsides, and forest margins, in thickets, pine forests, or evergreen broad-leaved forests, 650–2800 m alt. Flowering and fruiting October–February.

Although this species is variable in leaf shape, inflorescence, and hairiness of different parts of the plant, it is characterized by its corolla with a long, boat-shaped lower lip. Based on this reason, I reduce *Plectranthus menthoides, P. maddeni, Rabdosia pluriflora, R. polystachys* (including var. *phylloides*), *R. anisochila,* and *R. megathyrsoides* to synonyms of *Isodon coetsa.*

73b. **Isodon coetsa** var. **cavaleriei** (Léveillé) H. W. Li, comb. nov.

Plectranthus cavaleriei Léveillé, Repert. Spec. Nov. Regni Veg. **9:** 247. 1911. *Isodon cavaleriei* (Léveillé) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 130. 1929. *Rabdosia coetsa* (Buch.-Ham. ex D. Don) H. Hara var. *cavaleriei* (Léveillé) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 91. 1975. *P. coetsa* Buch.-Ham. ex D. Don var. *cavaleriei* (Léveillé) McKean, Notes Roy. Bot. Gard. Edinburgh **40:** 176. 1982. TYPE: China, Kweichow, without further locality, *Esquirol 834* (holotype, K, not seen).

P. mairei Léveillé, Bull. Soc. Agric. Sarthe **44:** 479. 1914. SYNTYPES: China, Yunnan, Tong-tchouan, *E. E. Maire s.n.* (fragment, A); Tché-hay, *E. E. Maire s.n.* (fragment, A).

P. macraei Bentham, Labiat. Gen. Spec. 42. 1932. TYPE: Ceylon, *Macrae s.n.* (not seen).

This variety differs from var. *coetsa* in having the stems densely puberulous and the leaves densely pilose above and floccose-pilose beneath.

DISTRIBUTION AND PHENOLOGY. India (Mysore, Kerala, Tamil Nadu), Sri Lanka, and south-central China (Yunnan); on grassy slopes, stream sides, roadsides, and forest margins, in thickets or forests, 1630–2300 m alt. Flowering and fruiting October–February.

Plectranthus macraei, according to the original description, is undoubtedly a densely hairy form of *Isodon coetsa,* so I reduce it to the hairy variety (var. *cavaleriei*) of this species.

74. **Isodon phyllopodus** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 135. 1929. FIGURE 8H, I.

Plectranthus phyllopodus Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 227. 1912. *Rabdosia phyllopoda* (Diels) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: China, Yunnan, eastern flank of Tali Range, 25°40′N, July–August 1906, *G. Forrest 4556* (holotype, E, not seen).

P. leucanthus Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 230. 1912. TYPE: China, Yunnan, hills of Yangtse-Mekong divide, Sept. 1904, *G. Forrest 595* (holotype, E, not seen).

P. chenmui Y. Z. Sun ex C. H. Hu, Acta Phytotax. Sin. **11**(1): 51. 1966. TYPE: China, Yunnan, Menghua, 18 Oct. 1934, *M. Chen 3024* (holotype, PE).

Perennial herb, 30–50 cm high. Stems quadrangular, exfoliate at base, pubescent. Cauline leaves with petiole (including alate pseudopetiole) 2–4 cm long; blade triangular-ovate or rhomboid-ovate, 4–6 by 3–4 cm, obtuse at apex, cuneate-decurrent at base, crenulate, thin-chartaceous, very densely gray-septate-pilose on both surfaces, dotted with red glands beneath, the lateral nerves ca. 3 pairs, sunken above and raised beneath like midrib. Panicles terminal, loose, 5–20 cm long, composed of 3- to 7-flowered cymes; cymes with the peduncle 0.3–2 cm long, the pedicels 2–3 mm long, slender, the peduncle, pedicels, and rachis glandular-puberulous; lower floral leaves like cauline ones, others gradually reduced and changed into bracts upward; bracts narrowly ovate or ovate-lanceolate, all longer than peduncles, entire; bracteoles 1–2 mm long, glandular-pubescent. Calyx campanulate, ca. 4 mm long, glandular-pubescent and dotted with dark brown glands everywhere, slightly 2-lipped, the teeth 5, ovate-triangular, lower 2 slightly longer than upper 3, all obtuse or slightly obtuse at apex; fruiting calyx slightly dilated, conspicuously 2-lipped. Corolla white but with purple spots on upper lip, or bluish, slightly pubescent outside, dotted with red-brown glands on limb; tube saccate on upper side near base, ca. 4 mm long and 2 mm in diameter in middle, slightly constricted at throat; limb 2-lipped, the upper lip 3 mm long, reflexed, 4-lobed at apex, the lower lip ca. 3.5 mm long, concave, boat-shaped. Stamens and style slightly exserted. Nutlets ovoid, 1.3 mm long, ca. 0.8 mm in diameter, yellowish white.

DISTRIBUTION AND PHENOLOGY. Southwestern and south-central China (Xizang, Yunnan, Guizhou, and Sichuan); in thickets, on wasteland, or along forest edges, 2100–3000 m alt. Flowering June–September, fruiting August–October.

This species is much like *Isodon flavidus* in foliage but differs in having a conspicuously two-lipped calyx with the teeth slightly shorter than the tube. The species is obviously related to *I. coetsa* but has hairier, less glandular leaves and larger flowers with slightly exserted stamens.

75. **Isodon secundiflorus** (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 236. 1985.

Rabdosia secundiflora C. Y. Wu, Fl. Reipubl. Pop. Sin. **66:** 503, 589. 1977. TYPE: China, Sichuan, Muli, Dongni, 18 Sept. 1939, *K. M. Feng 2933* (holotype, KUN; isotype, A).

Undershrub. Stems erect, cylindrical, finely striate, whitish-glandular-pubescent, with white pith. Cauline leaves opposite; petiole slender, 4.5–5.5 cm

long, slightly sulcate above, finely striate, densely glandular-pubescent; blade cordate, 6.5–10.5 by 5.5–8 cm, acute at apex, cordate at base, regularly callose-crenate, chartaceous, the upper surface olive-green, white-hispidulous along midrib and nerves, otherwise pubescent, the lower surface greenish, pubescent, the lateral nerves ca. 4 pairs, anastomosing near margin, like midrib slightly elevated on both surfaces. Panicles terminal and axillary, up to 25–30 cm long, composed of secund 3-flowered cymes; cymes with peduncle 1.5–4 mm long, pedicels 1–2 mm long, peduncle, pedicels, and rachis densely glandular-pubescent; lowest floral leaves subsessile, orbicular-cordate, ca. 2 cm in diameter, rotund and mucronate at apex, cordate at base, obscurely crenate, others orbicular, gradually reduced upward, less than 4 mm in diameter, mucronate, subentire; bracteoles linear, less than 1 mm long. Calyx campanulate, ca. 2 mm long, 2 mm in diameter at mouth, glandular-pubescent outside, slightly 2-lipped, the teeth 5, ovate-triangular, ca. 1 mm long, lower 2 slightly longer than others; fruiting calyx tubular-campanulate, dilated, up to 5 mm long, spherical at base, patent at mouth, conspicuously 10-nerved. Corolla 6.5 mm long, pink, pubescent outside, glabrous inside; tube abruptly saccate on upper side near base, ca. 2.5 mm in diameter at throat; limb 2-lipped, the upper lip 2 mm long, reflexed, 4-lobed at apex, the lower lip suborbicular, ca. 3 mm long, concave, constricted at base. Stamens included, filament barbate below middle; style included, equally 2-fid at apex. Mature nutlets oblong, triquetrous, ca. 1.2 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (southwestern Sichuan); on slopes, 2000–2300 m alt. Flowering and fruiting September–October.

This species is easily recognized by its cordate leaves and its elongate, secund panicles.

H. **Isodon** ser. **Megathyrsi** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Megathyrsae* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 504, 590. 1977.

Perennial herbs. Cymes arranged into patent panicles. Calyx campanulate or tubular-campanulate in flower, conspicuously 2-lipped for ½ or less its length in fruit. Corolla medium in size, declinate.

TYPE SPECIES. *Isodon megathyrsus* (Diels) H. W. Li.

KEY TO THE SPECIES OF SER. MEGATHYRSI

1. Leaves cordate at base. ..... 76. *I. sculponeatus.*
1. Leaves broadly cuneate or subcuneate at base.
   2. Panicles up to 30 cm long and 20 cm in diameter, composed of 5- to 11-flowered cymes. ..... 77. *I. megathyrsus.*
   2. Panicles 6–10(–15) cm long, ca. 2.5 cm in diameter, composed of 3- to 5-flowered cymes. ..... 78. *I. henryi.*

76. **Isodon sculponeatus** (Vaniot) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 132. 1929, as "sculponiatus."

Plectranthus sculponeatus Vaniot, Bull. Acad. Int. Géogr. Bot. **14:** 167. 1904. *Rabdosia sculponeata* (Vaniot) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: Chine, Kougtcheou [Guizhou], environs de Gan-pin, *L. Martin, Herb. Bodinier 1942* (holotype, P, not seen).

Stachys mairei Léveillé, Bull. Acad. Int. Géogr. Bot. **22:** 236. 1912. TYPE: Yunnan, au tour de Tong-tchouan, Sept. 1911, *E. E. Maire s.n.* (holotype, P; isotype, E; neither seen).

Rabdosia alborubra C. Y. Wu, Fl. Yunnan. **1:** 797. *pl. 188, figs. 6, 7.* 1977. *Isodon alborubrus* (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 233. 1985. TYPE: China, Yunnan, Chu-xiong, 25 Sept. 1939, *M. K. Li 244* (holotype, PE; isotype, KUN).

Erect perennial herb. Stems 0.5–2 m high, branched, quadrangular, sulcate along upper portion, sparsely whitish-patent-strigose and densely puberulous, tufted. Cauline leaves opposite; petiole 1.5–7(–11.5) cm long, covered with same type of hairs as stem; blade broadly ovate-cordate, 3.5–10.5(–19) by 3–9(–15) cm, acute or acuminate at apex, deeply or shallowly cordate at base, crenate or sometimes dentate to entire, thin-chartaceous, olive-green and whitish-floccose-pilose above, whitish-villose and dotted with small, yellow glands beneath, the lateral nerves 4 or 5 pairs, sunken above, raised beneath. Panicles terminal, ca. 2–5 cm in diameter, composed of 9- to 11-flowered cymes; cymes with the peduncle 0.6–1.2(–3) cm long, the pedicels always longer than calyx, slender; floral leaves subsessile, like cauline ones, gradually reduced and changed into bracts upward; bracteoles linear, ca. 1 mm long. Calyx campanulate, ca. 3 mm long, 2.5 mm in diameter at mouth, sparsely white-strigose outside, the teeth 5, triangular-ovate, subequal, almost as long as calyx tube; fruiting calyx tubular-campanulate, saccate-inflated in lower portion, ca. 5 mm long, 3–3.5 mm in diameter, more or less curved, green, conspicuously 2-lipped, teeth as long as calyx tube. Corolla ca. 6 mm long, yellow with purple spots on upper lip inside, rarely reddish, puberulous and glandular outside, glabrous inside; tube subincluded, saccate on upper part near base, ca. 3 mm long; limb 2-lipped, the upper lip 3 by 4 mm, slightly reflexed, the lower lip suborbicular, ca. 3.5 mm broad, concave. Stamens and style included. Nutlets ovoid, triquetrous, ca. 1.8 mm long and 1.2 mm in diameter, castaneous, inconspicuously rusty-verruculose.

DISTRIBUTION AND PHENOLOGY. Sikkim, Nepal, and southwestern China (Xizang, Yunnan, and Sichuan); in open grasslands, thickets, or sparse forests, 500–2800 m alt. Flowering August–October, fruiting October–November.

Rabdosia alborubra differs from *I. sculponeatus* only in minor characters (e.g., leaves subsessile or shortly petiolate, fruiting calyx broader and not very curved, corolla reddish), so I think it is reasonable to reduce it to a synonym of the latter species. *Isodon sculponeatus* is distinctive in that the entire plant is white-septate-strigose and the leaf base is cordate, although the serration of the leaves is often quite variable.

77. **Isodon megathyrsus** (Diels) H. W. Li, comb. nov.

Plectranthus megathyrsus Diels, Notes Roy. Bot. Gard. Edinburgh **5:** 230. 1912. *Isodon forrestii* (Diels) Kudo var. *megathyrsus* (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp.

Univ. **2**: 131. 1929. *Rabdosia megathyrsa* (Diels) H. Hara, J. Jap. Bot. **47**: 198. 1972. TYPE: China, Yunnan, western slope of Tsan shan Range, 25°40′N, Sept. 1903, *G. Forrest 987* (holotype, E, not seen; fragment, W).

KEY TO THE VARIETIES OF ISODON MEGATHYRSUS

1. Entire plant densely pilose or pubescent. ..... 77a. var. *megathyrsus.*
1. Entire plant very densely gray or fulvous-septate-strigose. .....
..... 77b. var. *strigosissimus.*

77a. **Isodon megathyrsus** var. **megathyrsus**

Perennial herb. Stems erect, obtusely quadrangular, sulcate, finely striate, densely pilose. Cauline leaves opposite; petiole 0.5–5 cm long, broadly cuneate-alate on upper part, plano-convex, densely pilose; blade broadly ovate, 3.5–7.5 by 2–4.5 cm, acute at apex, broadly cuneate or subtruncate and abruptly attenuate at base, regularly crenate-dentate, chartaceous, olive-green above, greenish beneath, pilose on both surfaces, the lateral nerves ca. 4 pairs, raised on both surfaces. Panicles terminal, up to 30 cm long and 20 cm in diameter, composed of 5- to 11-flowered cymes; cymes with peduncle 0.5–3.5 cm long, pedicels 0.3–0.5 cm long, peduncle, pedicels, and rachis densely glandular-pubescent and pilose; floral leaves ovate, gradually reduced upward; bracteoles linear or lanceolate-linear, ca. 1.5 mm long. Calyx broadly campanulate, 2.5–3 mm long, up to 4 mm in diameter, densely glandular-pubescent outside but pilose along ribs and margin, glabrous inside, 2-lipped, the teeth 5, narrowly triangular, almost as long as calyx tube, acuminate at apex. Corolla up to 9 mm long, blue or bluish purple, puberulous and glandular outside, glabrous inside; tube gibbous on upper side near base, ca. 5 mm long; limb 2-lipped, the upper lip ca. 3 by 4 mm, reflexed, 4-lobed at apex, the lower lip suborbicular-ovate, ca. 4 by 4 mm, concave, boat shaped. Stamens included, the filament complanate, barbate below middle; style included, equally 2-fid at apex. Mature nutlets ovoid, 1.2 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan and southwestern Sichuan); in *Picea* forests, or mixed *Pinus-Quercus* forests in valleys, 2300–2900(–3500) m alt. Flowering August–September, fruiting in October.

77b. **Isodon megathyrsus** var. **strigosissimus** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia megathyrsa (Diels) H. Hara var. *strigosissima* C. Y. Wu & H. W. Li, Fl. Yunnan. **1**: 799. 1977. TYPE: China, Yunnan, Wei-si(?), *H. T. Tsai 57655* (holotype, KUN; isotype, A).

This variety differs from var. *megathyrsus* in having all parts of the plant very densely gray- or fulvous-septate-strigose.

DISTRIBUTION. South-central China (northwestern Yunnan); in forests.

This species seems to be related to *Isodon amethystoides* based on inflorescence characters but is a much hairier plant that is larger in all its parts. It is also similar to *I. forrestii* but has a smaller calyx with longer, more acute teeth and a considerably smaller corolla.

78. **Isodon henryi** (Hemsley) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 123. 1929, excl. var.

Plectranthus henryi Hemsley, J. Linn. Soc., Bot. **26:** 271. 1890. *Rabdosia henryi* (Hemsley) H. Hara, J. Jap. Bot. **47:** 195. 1972. TYPES: China, Hupeh, Ichang and immediate neighbourhood, *A. Henry 1727* (syntype, K, not seen; isosyntype, GH), *2763* (syntype, K, not seen), *3066* (syntype, K, not seen; isosyntype, BM), *3094* (syntype, K, not seen; isosyntype, GH).

P. ricinispermus auct., non Pampan.: Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 142. 1913, quoad *Wilson 2652.*

P. excisus auct., non Maxim.: Hand.-Mazz. Acta Horti Gothob. **9:** 97. 1934.

Perennial herb. Stems erect, (30–)50–100(–150) cm high, much branched on upper portion, semiwoody on lower, obtusely quadrangular, shallowly sulcate, angles slightly pubescent, lower portion glabrescent; branches slender; internodes shorter than leaves. Cauline leaves opposite; petiole to 4 cm long (upper ones very short to nearly absent), alate, slightly strigillose; blade rhomboid-ovate or lanceolate, ca. 6 by 4 cm (middle ones; upper and lower ones smaller), acuminate at apex, abruptly contracted from middle of blade or subtruncate and decurrent-attenuate at base, callose-crenate-serrate, chartaceous, the upper surface olive-green, densely strigillose, the lower surface greenish, sparsely strigillose along midrib and nerves, otherwise glabrous, the lateral nerves 3 or 4 pairs, raised on both surfaces like transverse veinlets. Panicles terminal, 6–10(–15) cm long, ca. 2.5 cm in diameter, composed of 3- to 5-flowered cymes; cymes with peduncle 1–2 mm long, pedicels up to 5 mm long, peduncle, pedicels, and rachis glandular-pubescent; floral leaves like cauline ones, short-petiolate or subsessile; bracts and bracteoles linear or linear-lanceolate, 1–3 mm long. Calyx broadly campanulate, ca. 3 mm long, purplish, puberulous outside, glabrous inside, 2-lipped, the teeth 5, almost as long as calyx tube, upper 3 slightly smaller than lower 2; fruiting calyx 6 mm long, slightly curved, subglabrous but glandular outside, obviously nervate. Corolla ca. 7 mm long, white or purplish with purple marks, puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 3.5 mm long, ca. 2 mm in diameter at throat; limb 2-lipped, the upper lip 3 mm long, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, ca. 3.5 mm long, concave, boat shaped. Stamens included, the filament complanate, barbate on lower ½; style included. Mature nutlets compressed-oblong, ca. 1.3 mm long, brown, verruculose, glabrous.

DISTRIBUTION AND PHENOLOGY. Central China (Hubei and Sichuan); in valleys, on slopes, or along forest edges, stream sides, or roadsides, (260–)800–2600 m alt. Flowering August–September, fruiting September–October.

This species is very similar to *Isodon rubescens* but differs in its conspicuously two-lipped fruiting calyx.

I. **Isodon** ser. **Macrocalyces** (C. Y. Wu & H. W. Li) H. W. Li, comb. nov.

Rabdosia ser. *Macrocalyces* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 512, 590. 1977.

Perennial herbs. Cymes arranged into racemes, pseudoracemes, or narrow panicles. Calyx campanulate, conspicuously 2-lipped for more than ½ its length, with upper 3 teeth reflexed and lower 2 porrect, especially in fruit. Corolla medium in size, declinate.

TYPE SPECIES. *Isodon macrocalyx* (Dunn) Kudo.

KEY TO THE SPECIES OF SER. MACROCALYCES

1. Leaves regularly or irregularly gross-serrate, dentate, or serrate-dentate.
   2. Inflorescences racemose or pseudoracemose. ..... 79. *I. racemosus.*
   2. Inflorescences more or less conspicuously narrow-paniculate.
      3. Leaves long-acuminate, sometimes more or less excised at apex. ..... 80. *I. excisoides.*
      3. Leaves not long-acuminate or excised at apex.
         4. Leaves cuneate-decurrent at base; all parts of plant pubescent. ..... 81. *I. shikokianus.*
         4. Leaves broadly cuneate to subtruncate and abruptly attenuate-decurrent at base; all parts of plant white-pilose or white-puberulous.
            5. All parts of plant densely white-pilose; leaves callose-dentate-serrate. ..... 82. *I. albopilosus.*
            5. All parts of plant sparsely white-puberulous; leaves grossly serrate. ..... 83. *I. grosseserratus.*
1. Leaves regularly or subregularly crenate-serrate.
   6. Corollas less than 5.5 mm long. ..... 84. *I. rosthornii.*
   6. Corollas more than 5.5 mm long.
      7. Stems densely white-retrorse-puberulous along ridges; corollas gray or reddish, up to 10 mm long. ..... 85. *I. liangshanicus.*
      7. Stems adpressedly pubescent; corollas purplish, purple, or purple-red, ca. 8 mm long. ..... 86. *I. macrocalyx.*

79. **Isodon racemosus** (Hemsley) H. W. Li, comb. nov.

Plectranthus racemosus Hemsley, J. Linn. Soc., Bot. **26:** 273. 1890. *P. excisus* Maxim. var. *racemosus* (Hemsley) Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 156. 1913. *Amethystanthus racemosus* (Hemsley) Nakai, Bot. Mag. Tokyo **48:** 711. 1934, quoad basionym tantum. *Isodon excisus* (Maxim.) Kudo var. *racemosus* (Hemsley) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 133. 1939. *Rabdosia racemosa* (Hemsley) H. Hara, J. Jap. Bot. **47:** 199. 1972. SYNTYPES: China, Hupeh, Ichang, Patung and immediate neighbourhood, *A. Henry 417, 418, 2463, 4855*; Sichuan, south Wushan, *A. Henry s.n.* (all at K, none seen).

P. excisus auct., non Maxim.: Dunn, Notes Roy. Bot. Gard. Edinburgh **6:** 141. 1915, *pro parte.*

Perennial herb. Stems erect, 0.6–1 m high, unbranched or branched, obtusely quadrangular, sulcate, finely striate, purplish red, slightly pubescent; internodes always shorter than leaves. Cauline leaves opposite; petiole 2–10 mm long, concave-convex, puberulous; blade rhomboid-ovate, 3–11 by 1.2–4(–4.5) cm, acuminate at apex, cuneate-decurrent at base, grossly dentate or serrate-dentate,

chartaceous or submembranaceous, the upper surface puberulous along midrib and nerves, otherwise sparsely hispidulous or glabrescent, the lower surface sometimes sparsely puberulous along midrib and nerves, otherwise glabrous, dotted with yellowish glands, the lateral nerves ca. 3 pairs, slightly raised on both surfaces, the veinlets parallel, conspicuous beneath. Inflorescences racemes or pseudoracemes, terminal and axillary, 8–20 cm long, racemes composed of 1-flowered cymes, pseudoracemes of 3-flowered cymes in lower portion and 1-flowered ones in upper; cymes with pedicels 2–3 mm long, pubescent like rachis and peduncle; bracteoles linear, ca. 1 mm long. Calyx campanulate, up to 2.5 mm long, pubescent and glandular outside, glabrous inside, the teeth 5, upper 3 ovate-triangular, lower 2 narrowly triangular and slightly larger, all spinescent at apex; fruiting calyx dilated, up to 7 mm long, slightly curved, obviously nervate. Corolla up to 1 cm long, white or reddish, sparsely puberulous and glandular outside, glabrous inside; tube abruptly saccate on upper side near base, up to 5.5 mm long, up to 3 mm in diameter near base, then gradually contracted upward and ca. 2 mm at throat; limb 2-lipped, the upper lip up to 3.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 4.5 mm long, concave, boat shaped. Stamens and style slightly exserted, style equally 2-fid at apex. Mature nutlets obovoid, ca. 1.5 mm long, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Central China (Hubei and Sichuan); on grasslands or in forests, 700–1500 m alt. Flowering August–September, fruiting September–October.

Isodon racemosus is very close to *I. excisoides* but differs in having racemose or pseudoracemose inflorescences.

80. **Isodon excisoides** (Sun ex C. H. Hu) H. Hara, J. Jap. Bot. **60**: 234. 1985.

Plectranthus excisoides Sun ex C. H. Hu, Acta Phytotax. Sin. **11**(1): 53. *pl. VII, figs. 32–35.* 1966. *Rabdosia excisoides* (Sun ex C. H. Hu) C. Y. Wu & H. W. Li, Acta Phytotax. Sin. **13**(1): 93. 1975. TYPE: China, Sichuan, no further locality, *F. T. Wang 22033* (holotype, PE).

P. excisus auct., non Maxim.: Hemsley, J. Linn. Soc., Bot. **26**: 270. 1890, *pro parte,* quoad specim. Hupeh et Szechuan; Dunn, Notes Roy. Bot. Gard. Edinburgh **61**: 141. 1915, *pro parte.*

Perennial herb. Stems numerous, erect, (0.3–)0.5–1(–1.5) m high, sometimes branched on upper portion, quadrangular, sulcate, glabrescent on lower portion, puberulous on upper. Cauline leaves opposite; petiole 1–5 cm long, broadly alate on upper portion; blade broadly elliptic, ovate, or orbicular-ovate, (2.5–)5–7 by (2–)3.5–5.5 cm, long-caudate and sometimes more or less excised at apex, broadly cuneate or truncate and abruptly attenuate-decurrent at base, irregularly serrate-dentate, chartaceous, the upper surface pubescent along midrib and nerves, otherwise sparsely strigose-hispidulous, the lower surface sparsely puberulous along midrib and nerves, otherwise glabrous, the lateral nerves ca. 3 pairs, sunken above and raised beneath, the veinlets parallel, more or less conspicuous on both surfaces. Panicles terminal or axillary, 6–15 cm long,

composed of 3- to 5-flowered cymes; cymes with peduncle 2–5 mm long, pedicels 2–6 mm long, peduncle, pedicels, and rachis densely pubescent; floral leaves similar to cauline ones, subsessile, gradually reduced upward; bracts and bracteoles linear, 1–3 mm long. Calyx campanulate, up to 3.5 mm long, puberulous outside, glabrous inside, the teeth 5, upper 3 triangular, lower 2 narrowly triangular, all spinescent at apex; fruiting calyx conspicuously dilated, up to 7 mm long, with ribs and margins of teeth obviously elevated, the upper 3 teeth reflexed, the lower 2 porrect. Corolla ca. 10 mm long, white, reddish, or purplish to purple-blue, sparsely puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 6 mm long, up to 3 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 by up to 5 mm, reflexed, equally 4-lobed at apex, the lower lip suborbicular, ca. 4 by 4 mm, concave. Stamens included, the filament complanate, barbate on lower ½; style included or slightly exserted, equally 2-fid at apex. Mature nutlets subspherical, ca. 1.5 mm in diameter, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Central and south-central China (Sichuan, Hubei, and northeastern Yunnan); on grasslands, roadsides, or wastelands, along stream sides, or in sparse forests, (700–)1200–3000 m alt. Flowering July–September, fruiting August–October.

This species is very similar (and perhaps also related) to *Isodon excisus* but differs in having the fruiting calyx conspicuously two-lipped for more than half its length, with the upper three teeth reflexed and the lower two porrect.

81. **Isodon shikokianus** (Makino) H. Hara, Enum. Spermat. Jap. **1:** 208. 1949.

Plectranthus excisus Maxim. var. *shikokianus* Makino, Bot. Mag. Tokyo **6:** 180. 1892. *P. shikokianus* (Makino) Makino, J. Jap. Bot. **2**(6): 24. 1922. *Rabdosia shikokiana* (Makino) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: Japan, Tosa, Mt. Tebako, *T. Makino s.n.* (not seen).

P. longitubus Miq. var. *intermedius* Matsum. & Kudo, Bot. Mag. Tokyo **26:** 302. 1912, *nomen nudum. Isodon longitubus* (Miq.) Kudo var. *intermedius* Matsum. & Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 140. 1929. *I. shikokianus* (Makino) H. Hara var. *intermedius* (Matsum. & Kudo) H. Hara, J. Jap. Bot. **47:** 200. 1972.

Isodon shikokianus (Makino) H. Hara var. *occidentalis* Murata, Acta Phytotax. Geobot. **16:** 45. 1955. *Rabdosia shikokiana* (Makino) H. Hara var. *occidentalis* (Murata) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: Japan, Prov. Yamashiro, Mt. Daihi, Sept. 1932, *Koidzumi* (holotype, KYO, not seen).

Perennial herb, 50–70 cm high. Stems ascendent or suberect, slender, branched on upper part, obtusely quadrangular, sulcate, finely striate, minutely pubescent along angles. Cauline leaves opposite; petiole 1–2.5 cm long, concave-convex, pubescent; blade ovate-lanceolate or rhomboid-lanceolate to lanceolate, (2.5–)3–10 by (1.2–)1.5–3.5(–4) cm, acuminate at apex, cuneate-decurrent at base, grossly serrate, thin-chartaceous or submembranaceous, the upper surface pubescent along midrib and nerves, otherwise sparingly hispidulous, the lower surface sparingly hispidulous along midrib and nerves, otherwise glabrous and dotted with small, yellowish glands. Panicles terminal, 7–15 cm long, 2–3 cm in diameter, composed of 1- to 3- (to 5-)flowered cymes; cymes with peduncle

2–6 mm long, pedicels 1–2 mm long, peduncle, pedicels, and rachis pubescent; lowest floral leaves similar to cauline ones, others abruptly reduced and changed into bracts upward; bracts subsessile, ovate or ovate-lanceolate to linear, 3–10 mm long; bracteoles linear, ca. 0.5 mm long. Calyx campanulate, ca. 3 mm long, up to 4 mm in diameter, pubescent and glandular outside, glabrous inside, 2-lipped for ⅔ of length, the teeth 5, narrowly triangular, acuminate at apex; fruiting calyx dilated, ca. 6 mm long and in diameter, obviously nervate. Corolla ca. 9 mm long, blue-purple, sparsely puberulous and glandular outside; tube abruptly saccate on upper side near base, ca. 5 mm long, ca. 2 mm in diameter near base, abruptly attenuate upward and ca. 1.5 mm in diameter at throat; limb 2-lipped, the upper lip 3 by 4 mm, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, 4 by 5 mm, concave, boat shaped. Stamens and style included. Mature nutlets compressed-ovoid, 1.3 mm long, 1 mm in diameter, rotund at apex, brownish, smooth, glabrous.

DISTRIBUTION AND PHENOLOGY. Japan; in deciduous forests or lightly shaded valleys, by streams, 60–1600 m alt. Flowering August–October, fruiting September–November.

Since *Isodon shikokianus* is quite variable in leaf shape and leaf size, I think it is best not to recognize varieties. It is allied to *I. grosseserratus* but differs in that the entire plant is pubescent and the leaves are cuneate-decurrent at the base.

82. **Isodon albopilosus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Rabdosia albopilosa C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 516, 590. 1977. TYPE: China, Sichuan, Heishui, 24 July 1957, *X. Li & J. X. Zhou 58797* (holotype, PE).

Perennial herb. Stems erect, 0.6–1 m high, branched on upper portion, obtusely quadrangular, sulcate, finely striate, densely white-pilose; internodes always shorter than leaves. Cauline leaves opposite; petiole 0.5–4 cm long (upper ones shorter), narrowly alate on upper part, concave-convex, densely pilose; blade orbicular-ovate to triangular-ovate, 4.5–9 by 3–6 cm, acuminate at apex, broadly cuneate to subtruncate at base, callose-dentate-serrate (terminal tooth lanceolate, large), chartaceous, the upper surface green, densely pilose along midrib and nerves, otherwise white-septate-pilose, the lower surface greenish, white-septate-pilose, both surfaces dotted with yellowish glands, the lateral nerves ca. 4 pairs, ascendent, raised on both surfaces like midrib, the veinlets parallel, obvious on both surfaces. Panicles terminal, those on stem up to 15 cm long, all composed of 3-flowered cymes; pedicels elongate, 5(–8) mm long, densely white-septate-pilose and glandular like peduncles and rachis of cymes; floral leaves similar to cauline ones, gradually reduced and changed into bracts upward; bracts sessile, ovate or ovate-lanceolate, entire, ciliate; bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, ca. 3.5 mm long, densely white-pilose and glandular outside, glabrous inside, 2-lipped for more than ½ its length, upper lip with 3 reflexed teeth, lower lip with 2 porrect ones;

fruiting calyx dilated, up to 6 mm long, obviously nervate. Corolla 8–9 mm long, purplish or reddish, pilose outside, glabrous inside; tube saccate on upper side near base, up to ⅔ of corolla in length, 2.5–3 mm in diameter at throat; limb 2-lipped, the upper lip ca. 3 mm long, reflexed, equally 4-lobed at apex, the lower lip oblate, almost as long as upper one. Stamens included, filament subglabrous; style included, equally 2-fid at apex. Mature nutlets ovoid, 1.2 mm long, yellow-brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (western Sichuan); on slopes or forest edges or in valleys, 2400–3200 m alt. Flowering July–September, fruiting August–October.

This species is allied to *Isodon grosseserratus* (Dunn) Kudo but differs in that the entire plant is densely white-pilose.

83. **Isodon grosseserratus** (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 124. 1929.

Plectranthus grosseserratus Dunn, Notes Roy. Bot. Gard. Edinburgh **8**: 156. 1913. *Rabdosia grosseserrata* (Dunn) H. Hara, J. Jap. Bot. **47**: 195. 1972. TYPE: China, Sichuan, Wushan, *E. H. Wilson 1429* (holotype, E, not seen; fragment, W).

Perennial herb. Stems erect, 0.5–0.8 m high, much branched; stem and branches quadrangular, slightly sulcate, finely striate, sparingly and retrorsely white-puberulous. Cauline leaves opposite; petiole 2–10 mm long, alate, sparsely white-puberulous; blade broadly ovate, 5.5–12 by 3.5–6.5 cm, acuminate at apex, broadly cuneate and abruptly attenuate-decurrent at base, grossly serrate (terminal tooth lanceolate, larger), chartaceous, the upper surface dark green, sparsely pilose along midrib and nerves, otherwise septate-hispidulous, the lower surface greenish, sparsely pilose along midrib and nerves, dotted with small, golden glands, the lateral nerves 3 or 4 pairs, oblique-ascendent, anastomosing near teeth, slightly raised on both surfaces. Panicles terminal and axillary, up to 20 cm long, narrow, composed of remote, generally 3-flowered cymes; cymes with peduncle 0.5–1.5 cm long (lowest longer), pedicels ca. 5 mm long, peduncle, pedicels, and rachis all pubescent; lower floral leaves similar to cauline ones but sessile and remotely serrate or entire, longer than cymes, upper ones changed into bracts; bracts lanceolate, shorter than cymes; bracteoles linear, ca. 2 mm long. Calyx broadly campanulate, ca. 4 mm long, pubescent and glandular outside, glabrous inside, obviously 2-lipped, the teeth 5, upper 3 triangular-lanceolate, lower 2 lanceolate, all acuminate at apex; fruiting calyx up to 8 mm long, obviously nervate, upper lip with 3 reflexed teeth, lower lip with 2 porrect ones, all teeth spinescent at apex. Corolla up to 1 cm long, blue or pink, sparsely pubescent and glandular, glabrous inside; tube abruptly saccate on upper side near base, slightly constricted at throat, ca. 5 mm long and 2.5 mm in diameter; limb 2-lipped, the upper lip ca. 4 mm long, reflexed, equally 4-lobed at apex, the lower lip suborbicular-ovate, ca. 5 mm long. Stamens included, the filament complanate, sparsely barbate on lower ½; style included, equally 2-fid at apex. Mature nutlets ovoid, 1.2 mm long, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (Sichuan); on grassy slopes, along forest edges or valleys, 1600–2600 m alt. Flowering July–October, fruiting September–October.

This species is related to *Isodon excisoides* but differs in its grossly serrate leaves.

84. **Isodon rosthornii** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 135. 1929. FIGURE 3A–H.

Plectranthus rosthornii Diels, Bot. Jahrb. Syst. **29:** 562. 1900. *Rabdosia rosthornii* (Diels) H. Hara, J. Jap. Bot. **47:** 199. 1972. TYPE: China, Sichuan, S Nanchuan, Tien sheng chiao, *BvR 1122* (not seen).

Erect herb. Stems 0.6–1.2 m high, branched on upper portion or unbranched, semiwoody on lower portion, obtusely quadrangular, deeply sulcate, striate, purplish, densely puberulous, with large, white pith. Cauline leaves opposite; petiole 0.5–5 cm long, broadly alate on upper part, plano-convex, densely puberulous; blade broadly ovate or suborbicular, 4–11 by 2.5–7 cm, acuminate at apex, broadly cuneate and abruptly decurrent at base, subregularly crenate-serrate, thin-chartaceous or submembranaceous, the upper surface dark green, densely puberulous along midrib and nerves, sparsely setulose and glandular, the lower surface greenish, the lateral nerves 4 or 5 pairs, raised on both surfaces, the veinlets parallel, visible on both surfaces. Panicles terminal and axillary on upper portion of stem, 5–15 cm long (axillary ones always shorter than leaves), narrow, composed of remote, 3- (to 5-)flowered cymes; cymes with the peduncle 1–2 mm long, the pedicels erect, 2–5 mm long, robust, the peduncle, pedicels, and rachis densely puberulous; bracts linear or linear-lanceolate, shorter than peduncle; bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, up to 2.5 mm long, 3 mm in diameter at mouth, slightly pubescent along ribs and margins of teeth but otherwise dotted with glands outside, glabrous inside, conspicuously 2-lipped for ½ or more its length, the upper lip with 3 shortly triangular, acute, reflexed teeth, the lower lip with 2 narrowly triangular, acute ones; fruiting calyx dilated, up to 6 mm long, obviously nervate, upper lip obviously reflexed, lower lip porrect. Corolla up to 5.5 mm long, purplish white, purplish, or purple to purple-blue, sparsely puberulous and glandular outside, glabrous inside; tube conspicuously saccate on upper side near base (saccate portion never covered by calyx because upper calyx lip reflexed), ca. 2 mm long; limb 2-lipped, the upper lip 2 by 3 mm, 4-lobed at apex, the lower lip suborbicular, ca. 3 mm long, concave, boat shaped. Stamens included or slightly exserted, the filament complanate, barbate on lower ½; style included or slightly exserted, equally 2-fid at apex. Mature nutlets ovoid, 1.3 mm long, yellowish brown, glabrous, glandular.

DISTRIBUTION AND PHENOLOGY. South-central China (central and southern Sichuan, northern Yunnan, and northern Guizhou); on open slopes, 550–2300 m alt. Flowering August–September, fruiting September–October.

The species is distinctive in its corolla tube, which is conspicuously saccate on the upper side near the base. This saccate portion is always exserted because the upper lip of the calyx is reflexed.

85. **Isodon liangshanicus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Rabdosia liangshanica C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 519, 590. 1977. TYPE: China, Sichuan, Pu-ge, 25 Aug. 1959, *Sichuan Economical Plant Expedition 5527* (holotype, PE).

Perennial herb. Stems erect, 0.5–0.8 m high, obtusely quadrangular, shallowly sulcate, finely striate, yellowish brown, densely retrorsely white-puberulous along ridges. Cauline leaves opposite; petiole 1–3 cm long, narrowly alate; blade elliptic to oblong, 6–15 by 2.5–4.5 cm, acuminate at apex, broadly cuneate and abruptly attenuate at base, callose-crenate-serrate, thin-chartaceous, the upper surface green, densely pilose along midrib and nerves, otherwise sparsely pilose, the lower surface greenish, sparsely pubescent along midrib and nerves, otherwise glabrous, dotted with yellowish glands, the lateral veins 4 or 5 pairs, arcuate-ascendent, anastomosing near margin, the veinlets parallel, obvious beneath. Panicles terminal and axillary, 10–20 cm long, composed of 3- to 5-flowered cymes; cymes with peduncle 2–3 mm long, pedicels 3–5 mm long, peduncle, pedicels, and rachis densely gray-puberulous; lower floral leaves similar to cauline ones, sessile, others gradually reduced and changed into bracts upward; bracts linear, up to 5 mm long; bracteoles linear, ca. 2 mm long. Calyx campanulate, up to 4 mm long, pubescent outside, glabrous inside, 2-lipped for more than ½ its length, the upper lip with 3 triangular, acuminate teeth, the lower lip with 2 narrowly triangular, acuminate ones; fruiting calyx ca. 6 mm long, obviously nervate, upper lip with 3 reflexed teeth, lower lip with 2 porrect ones. Corolla up to 10 mm long, gray or reddish, puberulous outside, glabrous inside; tube abruptly saccate on upper side near base (saccate portion always outside calyx), slightly constricted, up to 10 mm long, ca. 2.5 mm in diameter at throat; limb 2-lipped, the upper lip 3 by 5 mm, reflexed, the lower lip oblong, 5 by 3 mm, concave. Stamens slightly exserted, the filament complanate, barbate on lower portion; style exserted, equally 2-fid at apex. Mature nutlets ovoid, ca. 1.5 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (southeastern Sichuan); on sunny, grassy slopes, ca. 2500 m alt. Flowering and fruiting in August.

Allied to *Isodon macrocalyx* (Dunn) Kudo, *I. liangshanicus* differs in its stem that is densely white and retrorse-white-puberulous along the ridges, as well as in its elliptic-oblong leaves.

86. **Isodon macrocalyx** (Dunn) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2:** 138. 1929. FIGURE 3J.

Plectranthus macrocalyx Dunn, Notes Roy. Bot. Gard. Edinburgh **8:** 157. 1913. *Rabdosia macrocalyx* (Dunn) H. Hara, J. Jap. Bot. **47:** 197. 1972. SYNTYPES: China, Chekiang, *Hickin s.n.* (E, not seen; fragment, W); Fukien, Foochow, 7 Nov. 1897, *Carles 734* (E, not seen).

P. bifidocalyx Dunn, Bull. Misc. Inform. **1914:** 238. 1914. *Rabdosia bifidocalyx* (Dunn) H. Hara, J. Jap. Bot. **47:** 194. 1972. *Isodon bifidocalyx* (Dunn) H. Hara, J. Jap. Bot. **60:** 233. 1985. TYPE: China, Kiukiang, Lushan Mtns., 27 Sept. 1891, *Bullock 67* (not seen).

P. drosocarpus Hand.-Mazz. Symb. Sin. **7**: 940. 1936. TYPE: China, SW Hunan, in monte Yun-schan prope urbem Wukang, *Handel-Mazzetti 12316* (holotype, W).

Amethystanthus taiwanensis Masam. Trans. Nat. Hist. Soc. Taiwan **30**: 409. 1940. *Rabdosia taiwanensis* (Masam.) H. Hara, J. Jap. Bot. **47**: 201. 1972. TYPE: Taiwan, Huanlien, *T. Nakamura 5803* (holotype, TI).

Perennial herb. Stems numerous, erect, 0.4–1(–1.5) m high, semiwoody and subcylindrical on lower portion, obtusely quadrangular on upper portion, adpressedly pubescent, with large, white pith. Cauline leaves opposite; petiole (0.5–)2–3(–6.5) cm long, narrowly alate on upper part, concave-convex, densely adpressed-pubescent; blade ovate, (5–)7–10(–15) by (2–)2.5–5(–8.5) cm, long-acuminate at apex, broadly cuneate and abruptly attenuate-decurrent at base, regularly callose-crenate-serrate, chartaceous, olive-green above, greenish beneath, adpressedly pubescent along midrib and nerves but otherwise subglabrous on both surfaces. Panicles terminal and axillary on upper part of stem, 6–10(–15) cm long, ca. 2.5 cm in diameter, together forming pyramidal complex ones, composed of (1- to) 3- to 5-flowered cymes; cymes with peduncle 2–4 mm long, pedicels nearly as long, peduncle, pedicels, and rachis densely adpressed-pubescent; floral leaves subsessile, ovate, gradually reduced upward; bracts and bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, 2.7 mm long, up to 3 mm in diameter, pubescent outside, glabrous inside, 2-lipped, the teeth 5, triangular, lower 2 slightly longer than others, all acute; fruiting calyx dilated, up to 6 mm long, nervate, obviously 2-lipped, upper 3 teeth always reflexed, lower 2 porrect. Corolla ca. 8 mm long, purplish, purple, or purple-red, sparsely puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, ca. 4 mm long, almost equal in diameter (ca. 2 mm) up to throat; limb 2-lipped, the upper lip 2 by 4 mm, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, 4 by 3 mm, concave, boat shaped. Stamens slightly exserted, the filament complanate, barbate on lower ½; style slightly exserted, equally 2-fid at apex. Mature nutlets ovoid, ca. 1.5 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. Southern China (Sichuan, Hunan, and Jiangxi), Taiwan; in thickets or forests, on slopes, 600–1700 m alt. Flowering July–August, fruiting September–October.

This species is easily recognized by its ovate leaves and its deeply two-lipped calyces.

J. **Isodon** ser. **Scrophularioidei** (Briq.) H. W. Li, comb. nov.

Plectranthus ser. *Scrophularioidei* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a**: 352. 1897.

Rabdosia ser. *Kangtingenses* C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66**: 521, 590. 1977. TYPE SPECIES: *Isodon kangtingensis* (C. Y. Wu & H. W. Li) H. Hara (= *I. flabelliformis* (C. Y. Wu) H. Hara).

Perennial herbs. Cymes arranged into spreading panicles. Calyx campanulate, conspicuously 2-lipped for more than ½ its length; fruiting calyx with upper 3 teeth reflexed and lower 2 porrect. Corolla medium in size, declinate.

TYPE SPECIES. *Isodon scrophularioides* (Wallich ex Bentham) Murata.

KEY TO THE SPECIES OF SER. SCROPHULARIOIDEI

1. Leaves more or less shallowly cordate at base.
   2. Teeth of fruiting calyx 1–1.5 mm long, broadly triangular, acute at apex; filaments pilose at base. ..... 87. *I. scrophularioides.*
   2. Teeth of fruiting calyx 3–3.5 mm long, triangular or lanceolate-triangular, acuminate at apex; filaments barbate below middle. ..... 88. *I. flabelliformis.*
1. Leaves never cordate at base.
   3. Stems shallowly sulcate, densely retrorse-puberulous; leaves very broadly ovate or oblate-ovate, rotund at apex, truncate-cuneate or broadly truncate at base, callose-crenate-serrate, with apical tooth lanceolate; corollas reddish purple or white. ..... 89. *I. latifolius.*
   3. Stems deeply sulcate, puberulous only on ridges, otherwise glabrous, dotted with glands; leaves broadly ovate, ovate-orbicular, or suborbicular, acuminate at apex, broadly cuneate or truncate-cuneate and abruptly attenuate-decurrent at base, subregularly and grossly (or sometimes duplo-)callose-serrate, with apical tooth lanceolate-acuminate; corollas white. ..... 90. *I. weisiensis.*

87. **Isodon scrophularioides** (Wallich ex Bentham) Murata, Acta Phytotax. Geobot. **22:** 21. 1966.

Plectranthus scrophularioides Wallich ex Bentham *in* Wallich, Pl. Asiat. Rar. **2:** 16. 1830. *Rabdosia scrophularioides* (Wallich ex Bentham) H. Hara, J. Jap. Bot. **47:** 200. 1972. TYPE: Nepalia, 1829, *Wallich 2738* (holotype, K; isotypes, BM, E, LE, W).
Rabdosia latiflora C. Y. Wu & H. W. Li, Fl. Yunnan. **1:** 802. *pl. 189, figs. 5, 6.* 1976. *Isodon latiflorus* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985. TYPE: China, Yunnan, Lushui, Pian-ma, *S. K. Wu 8429* (holotype, KUN).

Perennial herb. Stems erect, up to 60 cm or more high, branched, quadrangular, sulcate, finely striate, septate-pilose along edges but otherwise subglabrous. Cauline leaves opposite; petiole (1–)3.5–10 cm long, pilose; blade orbicular-ovate to broadly ovate or ovate, (3.2–)5.5–14 by (2–)4–10 cm, acute or shortly acuminate at apex, subtruncate, rotund, shallowly cordate or subcuneate at base, crenate or crenate-dentate, thin-chartaceous, the upper surface olive-green, densely puberulous along midrib and nerves, otherwise sparsely pilose, the lower surface greenish, sparsely pilose along midrib and nerves, dotted with inconspicuous red glands, the lateral nerves 4 or 5 pairs, arcuate-ascendent, like midrib slightly sunken above and raised beneath, the veinlets visible beneath. Panicles terminal and axillary, 8.5–20 cm long, 5.5–6 cm in diameter, glandular-puberulous, composed of 3- to 11-flowered cymes; cymes with peduncle 0.4–3.2 cm long, pedicels 3–5(–7) mm long; lowest floral leaves similar to cauline ones, subsessile, others changed into bracts; bracts ovate, 1–3 mm long; bracteoles linear or scalelike, less than 1 mm long. Calyx broadly campanulate, ca. 3.5 mm long, 5 mm in diameter at mouth, glandular-pubescent outside, obviously 2-lipped, the teeth 5, broadly triangular, upper 3 ca. 1.5 mm long, lower 2 highly connate and only 1 mm long, all acute at apex; fruiting calyx dilated, ca. 6.5 mm long, 6 mm in diameter at mouth. Corolla ca. 9 mm long, whitish, pale yellow, or yellow, always tinged with reddish purple on tip; tube saccate on upper side near base, gradually dilated upward, ca. 6 mm long, ca. 3.5–4 mm in diameter at throat, subglabrous; limb 2-lipped, the upper lip ca. 1.5 mm long, 4-lobed at apex, lobes subequal and reflexed,

the lower lip porrect, ovate, ca. 4 mm long. Stamens long-exserted, filament pilose at base; style long-exserted, 2-fid at apex. Immature nutlets ovoid, ca. 1.5 mm long, 1.1 mm in diameter, yellow, glabrous.

DISTRIBUTION AND PHENOLOGY. Sikkim, Bhutan, Nepal, India (Uttar Pradesh, West Bengal, Assam), Bangladesh, and south-central China (western Yunnan); on damp grassy banks, in shady woods, among secondary shrub growth, and at forest edges, 2000–3500 m alt. Flowering July–October, fruiting September–October.

This species is easily recognized by its wider corolla tube and its filaments that are pilose at the base. The type of *Rabdosia latiflora,* with its wide corolla tube, is obviously identical to *Isodon scrophularioides,* so I reduce it to a synonym of the latter species.

This is the first record of *Isodon scrophularioides* in China. Lushui (Yunnan) is the eastern boundary for this eastern Himalayan species.

88. **Isodon flabelliformis** (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 234. 1985.

Rabdosia flabelliformis C. Y. Wu, Fl. Yunnan. **1:** 801. *pl. 189, figs. 5, 6.* 1977. TYPE: China, Yunnan, Bin-chuan, 17 Oct. 1946, *T. N. Liou 21728* (holotype, PE).

R. kangtingensis C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 521, 591. 1977. *Isodon kangtingensis* (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985. TYPE: China, Sichuan, Kangting (Tachienlu) distr., Chungo valley, prope Chungo, 16 Aug. 1934, *Harry Smith 1116* (holotype, PE; isotype, W).

Perennial herb. Stems ca. 1 m high, unbranched or branched, the lower ½ woody or semiwoody, decorticate, the upper ½ subcylindrical, densely glandular-puberulous. Cauline leaves opposite; petiole 1.7–5.7 cm long, glandular-puberulous; blade broadly ovate to ovate, 3.7–13 by 3–10.5 cm, acute to acuminate at apex, more or less shallowly cordate but sometimes cuneate or subtruncate at base, conspicuously mucronate-crenate or crenate-serrate except along entire base, thin-chartaceous, the upper surface olive-green, densely puberulous and septate-pilose or densely pilose, the lower surface greenish, patently pilose along midrib and nerves, otherwise puberulous, the lateral nerves 1 to 4 pairs, arcuate-ascendent, like midrib sunken above and raised beneath, the veinlets visible beneath. Panicles terminal and axillary, 15–50 cm long, 6–12 cm in diameter, composed of 7- to 15-flowered cymes; cymes with the peduncle 1–3.5 mm long, the pedicels 6–12 mm long, slender, the peduncle, pedicels, and rachis glandular-puberulous; lowest floral leaves similar to cauline ones but subsessile or sessile and smaller, others changed into bracts; bracts oblate, broadly ovate, or ovate, 5–12 by 2.5–12 mm, acuminate at apex, rotund or shallowly cordate at base, generally entire; bracteoles ovate, minute. Calyx campanulate, ca. 4.5 mm long, 4 mm in diameter, purplish, densely and minutely glandular-pubescent, 2-lipped, the teeth 5, subequal, ⅔–¾ of calyx length, upper 3 lanceolate-triangular, lower 2 narrowly triangular, all acuminate at apex; fruiting calyx dilated, ca. 6 mm long, teeth 3–3.5 mm long. Corolla 11 mm long, blue; tube conspicuously saccate on upper side near base, ca. 5–6 mm long, 2.5 mm in diameter; limb 2-lipped, the upper lip 4-lobed at apex, the lower lip orbicular, as long as upper one, boat shaped. Stamens 4, lower 2

slightly exserted, filament barbate below middle; style exserted. Nutlets ovoid-oblong, ca. 1.6 mm long, 1 mm in diameter, yellowish.

DISTRIBUTION AND PHENOLOGY. South-central China (western Yunnan and western Sichuan); in broad-leaved forests, on rocky slopes, along roadsides and forest edges, 2600–3100 m alt. Flowering and fruiting September–October.

Isodon flabelliformis is allied to *I. scrophularioides* but differs in its narrower corolla (ca. 2.5 mm in diameter), its filaments barbate below the middle, and its slightly larger calyx teeth (ca. 2.5–3 mm long).

89. **Isodon latifolius** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Rabdosia latifolia C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 524, 591. *pl. 110.* 1977. TYPE: China, Sichuan, Wuxi, 26 Aug. 1935, *K. L. Chu 2049* (holotype, PE).

Perennial herb. Stems erect, up to 1 m high, obtusely quadrangular, shallowly 4-sulcate, finely striate, purplish, densely and retrorsely puberulous; nodes slightly thickened. Cauline leaves opposite; petiole 1.5–3 cm long; blade very broadly ovate or oblate-ovate, 5.5–10.5 by 6–10 cm, round or acuminate at apex, broadly cuneate or truncate-cuneate and abruptly attenuate-decurrent at base, callose-crenate-serrate (apical tooth lanceolate), thin-chartaceous, the upper surface dark green, densely pubescent along midrib and nerves, otherwise sparsely hispidulous, the lower surface greenish or purplish red, densely puberulous, with small, yellowish glands, the lateral nerves 3 or 4 pairs, raised on both surfaces, the veinlets conspicuous on both surfaces. Panicles terminal and axillary on upper part of stem, together forming complex ones up to 20 cm long, composed of remote 1- to 3-flowered cymes; cymes with the peduncle 1–2 mm long, the pedicels up to 5 mm long, slender, the peduncle, pedicels, and rachis densely glandular-pubescent; lowest floral leaves similar to cauline ones but subsessile and much smaller, others abruptly changed into bracts; bracts ovate to linear; bracteoles linear, less than 1 mm long. Calyx broadly campanulate, up to 4.5 mm long, 4 mm in diameter at mouth, densely pubescent and glandular outside, glabrous inside, conspicuously 2-lipped, the upper lip ca. 2 mm long, with 3 narrowly triangular, shortly acuminate teeth, the lower lip ca. 2.5 mm long, with 2 triangular, acuminate teeth; fruiting calyx slightly dilated, up to 6 mm long, obviously nervate. Corolla 7.5 mm long, reddish purple or white, sparsely puberulous and glandular outside, glabrous inside; tube saccate on upper side near base, 4 mm long, ca. 2.5 mm in diameter at throat; limb 2-lipped, the upper lip 3.5 by 6 mm, reflexed, 4-lobed at apex, the lower lip oblate, 4.5 by 6 mm, concave, boat shaped. Stamens included, filament barbate on lower ½; style included, equally 2-fid at apex. Mature nutlets ovoid, ca. 1.2 mm long, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (Sichuan); in grasslands, 1450–2000 m alt. Flowering and fruiting August–September.

This species is very close to *Isodon weisiensis,* differing mainly in having very broadly ovate leaves. Although I temporarily regard these two geograph-

ically distant species as distinct, more material from Sichuan is needed before a final decision can be made.

90. **Isodon weisiensis** (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 237. 1985.

Rabdosia weisiensis C. Y. Wu, Fl. Yunnan. **1:** 802. *pl. 189, figs. 1, 2.* 1977. TYPE: China, Yunnan, Weixi, *H. T. Tsai 57673* (holotype, PE; isotypes, A, KUN).

Perennial herb. Stems erect, obtusely quadrangular, deeply 4-sulcate, striate, puberulous only on edges, otherwise glabrous, dotted with glands. Cauline leaves opposite; petiole 1–6 cm long, narrowly alate, plano-convex, densely puberulous; blade broadly ovate, ovate-orbicular, or suborbicular, 4.5–11.5 by 3–8 cm, acuminate at apex, broadly cuneate or truncate-cuneate and abruptly attenuate-decurrent at base, subregularly grossly (sometimes duplo-)callose-serrate, thin-chartaceous or submembranaceous, the upper surface olive-green, densely puberulous along midrib and nerves, otherwise sparsely strigose-hispidulous, the lower surface greenish, sparsely white-puberulous everywhere when young but only on midrib and nerves with age, the lateral nerves 4 or 5 pairs, like midrib conspicuous on both surfaces, the parallel veinlets visible beneath. Panicles terminal, up to 15 cm long, narrow, composed of remote 1- to 5-flowered cymes; cymes with the peduncle ca. 2 mm long, the pedicels 2–6 mm long, slender, the peduncle, pedicels, and rachis densely glandular-pubescent; lowest floral leaves short-petiolate, ovate, 1.5–2 cm long, grossly dentate; bracts and bracteoles linear, ca. 1 mm long. Calyx broadly campanulate, ca. 2 mm long, up to 3 mm in diameter, pubescent and glandular outside, glabrous inside, conspicuously 2-lipped for more than ½ its length, the upper lip with 3 narrowly triangular, acuminate teeth, the lower lip with 2 triangular, acuminate ones; fruiting calyx dilated, up to 8 mm long and in diameter, obviously nervate. Corolla ca. 7.5 mm long, white, sparsely pilose outside, glabrous inside; tube saccate on upper side near base, ca. 4 mm long, up to 2 mm in diameter at throat; limb 2-lipped, the upper lip ca. 2.5 mm long, reflexed, 4-lobed at apex, the lower lip broadly ovate, 3.5 mm long, concave, boat shaped. Stamens and style included. Mature nutlets subspherical, ca. 1.5 mm in diameter, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northwestern Yunnan); in valleys, ca. 2600 m alt. Flowering August–September, fruiting September–October.

This species seems very much like *Isodon megathyrsus* but differs in that the plant is less hairy and the calyx is deeply two-lipped.

IV. **Isodon** sect. **Melissoides** (Bentham) H. W. Li, comb. nov.

Plectranthus sect. *Melissoides* Bentham, Labiat. Gen. Spec. 39. 1832, and *in* DC. Prodr. **12:** 62. 1848. *Plectranthus* subg. *Isodon* Bentham sect. *Euisodon* Briq. *in* Engler & Prantl, Nat. Pflanzenfam. IV. **3a:** 353. 1897, *pro parte.*

Perennial herbs. Cymes axillary, few-flowered, arranged into remote verticillasters or into terminal spikelike panicles. Fruiting calyx decurved, conspic-

uously 2-lipped. Corolla medium in size, tube conspicuously gibbous or even shortly calcarate on upper side near base.

LECTOTYPE SPECIES. *Isodon melissoides* (Bentham) H. Hara.

KEY TO THE SPECIES OF SECT. MELISSOIDES

1. Leaves with length/width quotient 3 or more.
   2. Corollas up to 8 mm long, the tube conspicuously gibbous then abruptly declinate, throat smaller in diameter than tube. ..... 91. *I. gibbosus.*
   2. Corollas ca. 7 mm long, the tube gibbous on upper side near base then gradually declinate, throat nearly equaling tube in diameter. ..... 92. *I. lungshengensis.*
1. Leaves with length/width quotient 2 or less.
   3. Inflorescences many remote verticillasters, composed of cymes in axils of middle and upper cauline leaves, these inconspicuously smaller upward. ..... 93. *I. melissoides.*
   3. Inflorescences terminal, spikelike panicles, composed of cymes in axils of floral leaves, these gradually reduced upward on upper part of branchlets.
      4. Leaves with petiole up to 4.5 cm long; corollas with tube abruptly changed into short spur on upper part near base, this approximately twice as wide as throat. ..... 94. *I. brevicalcaratus.*
      4. Leaves with petiole 0.2–1 cm long. Corollas with tube saccate on upper part above base, from here equal in breadth or gradually broader upward.
         5. Leaves broadly ovate, 4–4.5 by 2–2.5 cm, petiole 0.2–0.5 cm long; corolla tubes gradually broader upward, up to 3 mm in diameter at throat. ..... 95. *I. assamicus.*
         5. Leaves rhomboid-ovate to ovate-lanceolate, mostly smaller (middle ones (1.5–)2.5–3.5(–6.5) by (1–)1.5–2.5 cm), petiole 0.2–1 cm long; corolla tubes equal in diameter everywhere, almost 2 mm at throat. ..... 96. *I. adenanthus.*

91. **Isodon gibbosus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 234. 1985. FIGURE 9A–G.

Rabdosia gibbosa C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 532, 592. *pl. 112, figs. 8–13.* 1977. TYPE: China, Sichuan, no further locality, 1932, *West Academy of Sciences 3841* (holotype, PE).

Perennial herb. Stems ascendent, ca. 40 cm high, the lower part repent, rooted, decorticate, the upper part erect, much branched, obtusely quadrangular, profoundly 4-sulcate, densely gray-puberulous; branches very elongate. Cauline leaves opposite; petiole 0.5–1.5 cm long, densely pubescent; blade narrowly lanceolate or oblong, the middle ones 3–7 by 0.8–2.2 cm, gradually smaller upward, acuminate at apex, narrowly cuneate at base, crenate-serrate above base (upper ones entire), chartaceous, the upper surface olive-green, densely pubescent along midrib and nerves, otherwise sparsely hispidulous, the lower surface greenish, sparsely hispidulous on midrib, nerves, and veinlets, dotted with small, yellowish glands, the lateral nerves ca. 4 pairs, like midrib slightly sunken above, raised beneath. Cymes axillary, arranged into many remote verticillasters on upper portions of stem and branches, 0.8–2 cm long, dichotomous, each branch with 1 or 2 (to 4) flowers, peduncle and pedicels 1–3 mm long, these and rachis densely puberulous; bracts and bracteoles linear-

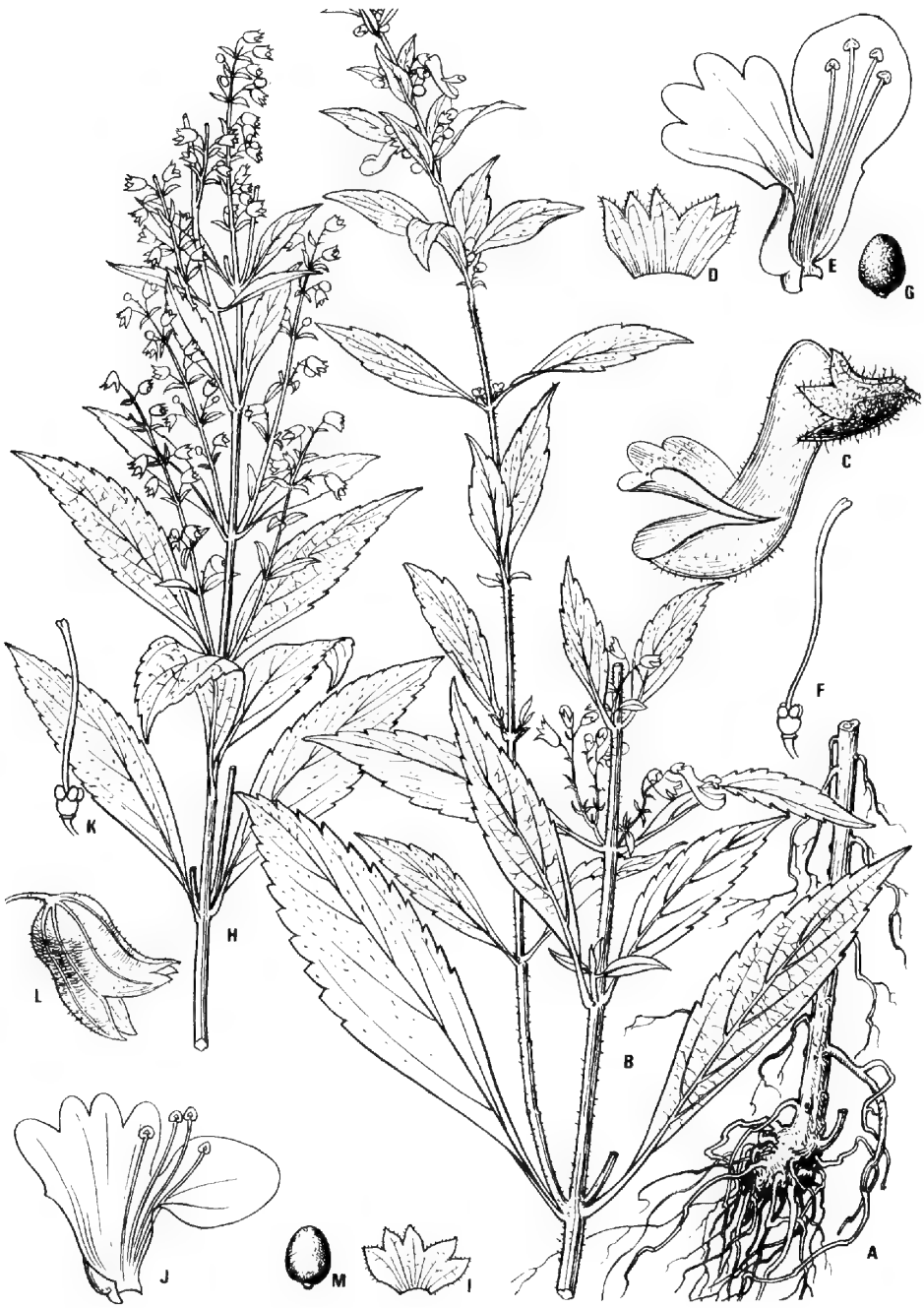

FIGURE 9. A–G, *Isodon gibbosus* (*West Academy of Sciences 3841*, PE): A, lower portion of plant, × 0.6; B, upper portion of plant, × 0.6; C, flower, × 4.2; D, calyx, × 4.2; E, corolla and stamens, × 4.2; F, pistil, × 4.2; G, nutlet, × 6. H–M, *I. lungshengensis* (*Guang-fu Forest Area Expedition 1108*, PE): H, upper portion of plant, × 0.6; I, calyx, × 3.6; J, corolla, × 3.6; K, pistil, × 3.6; L, fruiting calyx, × 4.8; M, nutlet, × 6. (Drawn by X. C. Li.)

lanceolate to linear, 1–2 mm long, entire, ciliolate. Calyx campanulate, ca. 2.5 mm long, up to 2.5 mm in diameter at mouth, puberulous along nerves and margins of teeth but otherwise glandular outside, glabrous inside, 10-nerved, conspicuously 2-lipped, the upper lip with 3 ovate, acute teeth, the lower lip with 2 approximate, narrowly triangular ones; fruiting calyx broadly campanulate, dilated, up to 4.5 mm long, slightly incurved, conspicuously nervate. Corolla up to 8 mm long, sparsely puberulous and glandular outside, glabrous inside; tube conspicuously gibbous on upper side near base (there ca. 2 mm in diameter) then abruptly decurved, slightly constricted and ca. 1.2 mm in diameter at throat; limb 2-lipped, the upper lip 3.5 mm long, reflexed, 4-lobed at apex, the lower lip orbicular-ovate, 4 mm long, slightly concave, entire. Stamens and style included. Mature nutlets subspherical, brown, glabrous.

DISTRIBUTION. South-central China (Sichuan); on slopes.

The species is characterized by its abruptly declinate, conspicuously gibbous corolla tube.

92. **Isodon lungshengensis** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 235. 1985. FIGURE 9H–M.

Rabdosia lungshengensis C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 532, 592. *pl. 112, figs. 8–13.* 1977. TYPE: China, Guangxi, Lung-sheng, 7 Nov. 1955, *Guangfu Forest Area Expedition 1108* (holotype, PE).

Perennial herb. Stems ascendent, repent on lower part, 20–50 cm high, obtusely quadrangular, shallowly 4-sulcate, decorticate, stramineous, very densely puberulous. Cauline leaves opposite, middle ones approximate; petiole 0.5–0.8 cm long, plano-convex, densely puberulous; blade narrowly lanceolate or oblong, 5.5–7.5 by 1.5–2 cm, long-acuminate at apex, narrowly cuneate at base, grossly serrate above middle, chartaceous, the upper surface olive-green, densely puberulous along midrib and nerves, otherwise sparsely hispidulous, the lower surface greenish, sparsely hispidulous along nerves, minutely yellowish-glandular. Panicles terminal, spikelike, ca. 2.5–10 cm long, 2–5 cm in diameter, composed of 1- to 3-flowered axillary cymes; cymes with peduncle 1–1.5 mm long, pedicels 1.5–3 mm long, peduncle, pedicels, and rachis all densely pubescent; floral leaves narrowly lanceolate to linear-lanceolate, 1–2 by 3–4 mm, shallowly serrate or subentire; bracteoles linear, ca. 1 mm long. Calyx campanulate, ca. 2 mm long, purplish green, pubescent and glandular outside, glabrous inside, 10-nerved, 2-lipped, the upper lip with 3 broadly triangular, acute teeth, the lower lip with 2 triangular, acute ones; fruiting calyx urceolate-campanulate, dilated, ca. 4 mm long, conspicuously nervate. Corolla ca. 7 mm long, purplish, sparsely pubescent outside, glabrous inside; tube gibbous on upper side near base, ca. 3.5 mm long; limb 2-lipped, the upper lip ca. 3 mm long, reflexed, 4-lobed at apex, the lower lip suborbicular, ca. 3.5 mm long, concave. Stamens and style included. Mature nutlets ovoid, ca. 1.3 mm long, yellowish brown, glabrous.

DISTRIBUTION AND PHENOLOGY. South-central China (northern Guangxi); shady places along streams in sparse forests, 480–700 m alt. Flowering and fruiting in November.

This species is more or less similar to *Isodon walkeri* but differs in its corolla tube that is gibbous on the upper side near the base and in its included stamens and style.

93. **Isodon melissoides** (Bentham) H. Hara, J. Jap. Bot. **60:** 235. 1985.

Plectranthus melissoides Bentham, Labiat. Gen. Spec. 39. 1832. *Rabdosia melissoides* (Bentham) H. Hara, J. Jap. Bot. **47:** 198. 1972. TYPE: India orientali, in provincia Silhet, *Wallich* (not seen).

Rabdosia melissiformis C. Y. Wu, Fl. Yunnan. **1:** 790. 1976. *Isodon melissiformis* (C. Y. Wu) H. Hara, J. Jap. Bot. **60:** 235. 1985. TYPE: China, Yunnan, Dali, *W. C. Wu, T. T. Yang, & C. Y. Wu 11056* (holotype, KUN).

Perennial herb. Stems quadrangular, sulcate, finely striate, densely retrorse-gray-pubescent and papillose-strigose, with large, white pith; internodes shorter than leaves. Cauline leaves opposite; petiole 0.2–0.7 mm long; blade ovate-triangular or broadly ovate-rhomboid, 2–3 by 1–2.5 cm, gradually reduced upward, acute or shortly acuminate at apex, broadly cuneate-decurrent at base, remotely gross-crenate or crenate-serrate, chartaceous, the upper surface dark green, sparsely hispidulous, the lower surface greenish, sparsely hispidulous along midrib and nerves, otherwise glabrous, the lateral nerves 3 or 4 pairs, ascendent, like midrib slightly raised above and obviously raised beneath. Cymes in axils of middle and upper cauline leaves, arranged into many remote verticillasters, 3- to 5-flowered, peduncle up to 5 mm long, pedicels 1.5–2 mm long, these and rachis pubescent; bracteoles ovate-lanceolate, up to 5 mm long. Calyx campanulate, ca. 3 mm long, pubescent outside, glabrous inside, 2-lipped for less than ½ its length, the upper lip with 3 triangular, acute teeth, the lower lip with 2 ovate-triangular, acute ones; fruiting calyx dilated, up to 5 mm long. Corolla ca. 1 cm long, almost white, sparsely pubescent outside; tube abruptly gibbous near base and then declinate, ca. 5 mm long, slightly constricted at throat; limb 2-lipped, the upper lip 3.5 by up to 5 mm, reflexed, equally 4-lobed at apex, the lower lip broadly ovate, 5 by 5 mm. Stamens and style included. Mature nutlets ovoid, 1.5 mm long, brown, glabrous.

DISTRIBUTION AND PHENOLOGY. India (Assam), Bangladesh, and south-central China (western Yunnan); on slopes, 1300–2000 m alt. Flowering and fruiting August–September.

This species is distinctive in having the cymes arranged into many remote verticillasters. After comparing the type of *Isodon melissiformis* with the specimens collected from India and Bangladesh, I am sure that they are identical. I have therefore reduced *I. melissiformis* to the synonymy of *I. melissoides.*

Dali (Yunnan) is the eastern border of this eastern Himalayan species.

94. **Isodon brevicalcaratus** (C. Y. Wu & H. W. Li) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Rabdosia brevicalcarata C. Y. Wu & H. W. Li, Fl. Reipubl. Pop. Sin. **66:** 529, 591. 1977. TYPE: China, Guangdong, Lien Xian, 11 Oct. 1958, *P. S. Taam 59739* (holotype, KUN).

Perennial herb. Stems erect, 0.9 m high, much branched, obtusely quadrangular, shallowly sulcate, striate, densely retrorse-gray-pubescent along edges. Cauline leaves opposite; petiole up to 4.5 cm long, narrowly alate; blade ovate (middle ones), ca. 4 by 2 cm, shortly acuminate or acute at apex, broadly cuneate or subrotund and abruptly attenuate at base, regularly crenate, thin-chartaceous or submembranaceous, the upper surface dark green, minutely pubescent along midrib and nerves, otherwise sparsely hispidulous, the lower surface greenish tinged with purple, sparsely white-hispidulous. Panicles terminal, 6–8 cm long, narrow, composed of remote 1- to 3-flowered cymes; cymes with peduncle 1–3 mm long, pedicels ca. 3 mm long, peduncle, pedicels, and rachis all densely pubescent; floral leaves gradually reduced and changed into bracts upward, all except lowest 1 or 2 much shorter than cymes; bracteoles linear, less than 1 mm long. Calyx campanulate, ca. 3 mm long, slightly pubescent and glandular outside, glabrous inside, slightly 2-lipped, the teeth 5, ovate-triangular, less than ½ of calyx length, lower 2 slightly larger than others, all acute. Corolla up to 1.1 cm long, purplish blue, pilose and yellowish-glandular outside, glabrous inside; tube tubular, 5 mm long, ca. 1 mm in diameter at base, then abruptly changed into short spur on upper side near base (this conspicuously exserted, ca. 3 mm in diameter), the throat ca. 1.5 mm broad; limb 2-lipped, the upper lip reflexed, up to 4 mm broad, equally 4-lobed at apex, the lower lip broadly ovate, up to 6 mm long, concave, boat shaped. Stamens and style subincluded. Mature nutlets not known.

DISTRIBUTION AND PHENOLOGY. Southeastern China (northern Guangdong); on fertile soil in sparse montane forests, ca. 600 m alt. Flowering in October.

This species is easily recognized by the short spur near the base of its corolla tube.

95. **Isodon assamicus** (Mukerjee) H. Hara, J. Jap. Bot. **60:** 233. 1985.

Plectranthus assamicus Mukerjee, J. Indian Bot. Soc. **19:** 82. *fig. 3.* 1940. *Rabdosia assamica* (Mukerjee) H. Hara, J. Jap. Bot. **47:** 194. 1972. TYPE: India, Assam, Akha Hill, *Bor 1364* (holotype, CAL, not seen).

Erect herb. Stems quadrangular, grooved, minutely adpressedly hairy. Lower leaves not seen, upper ones opposite; petiole 3–5 mm long, slender; blade broadly ovate, 4–4.5 by 2–2.5 cm, acuminate at apex, rounded at base, upper ½ serrate, entire near base, sparsely hairy, glandular-punctate. Racemes terminal, erect, long, slender, composed of lax-flowered, distant cymes; lower cymes axillary, the pedicels as long as or longer than fruiting calyx, slender; floral leaves like cauline ones, shortly petiolate, ovate, 5–12 by 4–8 mm, entire. Calyx campanulate, 2 mm long, puberulous, 2-lipped, the upper lip with 3 acute, slightly recurved teeth, the lower lip longer, with 2 narrow, acute ones; fruiting calyx 4–5 mm long, 3–4 mm in diameter. Corolla 7–8 mm long; tube gibbous at base, short, broad, lower lip 4 mm long, upper lip shorter. Stamens glabrous, the upper pair long, exserted; style included. Nutlets globose, compressed, 1.5 mm in diameter, deep brown, minutely punctate or smooth.

DISTRIBUTION. India (Assam); on hills.

In his original description Mukerjee said: "It bears some similarity to *P. melissoides* Benth. which is also confined to the hills of Assam. The two species resemble in the nature of their inflorescences and calyx but differ from each other in the shape and size of leaves and bracts." Although I have not seen the type of *Isodon assamicus,* I have put it here temporarily; according to the original description it is probably closer to *I. adenanthus* (Diels) Kudo.

96. **Isodon adenanthus** (Diels) Kudo, Mem. Fac. Sci. Taihoku Imp. Univ. **2**: 123. 1929. FIGURE 8J, K.

Plectranthus adenanthus Diels, Notes Roy. Bot. Gard. Edinburgh **5**: 228. 1912. *Rabdosia adenantha* (Diels) H. Hara, J. Jap. Bot. **47**: 193. 1972. TYPE: China, Yunnan, eastern flank of Tali Range, 25°40'N, Aug. 1906, *G. Forrest 4557* (holotype, E, not seen).

Perennial, semiwoody herb. Stems numerous, ascendent, 15–40 cm high, unbranched or with few branches, quadrangular, densely retrorse-gray-pubescent. Cauline leaves opposite, gradually reduced and changed into floral ones upward; petiole 0.2–1 cm long; blade rhomboid-ovate to ovate-lanceolate, (1.5–)2.5–3.5(–6.5) by (1–)1.5–2.5 cm (middle leaves; lower ones smaller), obtuse at apex, broadly cuneate-decurrent at base, subregularly gross-crenate-serrate above entire base, thin-chartaceous, the upper surface dark green, white-septate-pilose, dotted with yellowish glands, the lower surface greenish, densely white-pubescent along midrib and nerves, dotted with yellowish glands. Panicles terminal, spikelike, 10–20 cm long, composed of 3- to 5-flowered cymes; cymes with peduncle ca. 5 mm long, pedicels 2–3 mm long, peduncle, pedicels, and rachis densely pubescent; lowest floral leaves large, similar to cauline ones, others gradually reduced and changed into bracts; bracts lanceolate, subentire to entire; bracteoles linear, ca. 2 mm long. Calyx broadly campanulate, 2–3 mm long, purple, pilose along nerves and dotted with yellowish glands outside, glabrous inside, 2-lipped, the teeth 5, ovate-lanceolate, 1–1.5 cm long, lower 2 slightly larger, all apiculate at apex; fruiting calyx porrect, very dilated, up to 4 mm long, conspicuously 2-lipped, obviously nervate. Corolla blue, purple, pink, or white, densely pubescent and yellowish-glandular outside, glabrous inside; tube gibbous on upper side near base, ca. 4 mm long; limb 2-lipped, the upper lip 4-lobed at apex, reflexed, the lower lip larger, up to 6 mm long, concave, boat shaped. Stamens and style included. Nutlets ovoid, ca. 1.5 mm in diameter, brown.

DISTRIBUTION AND PHENOLOGY. South-central China (Yunnan, Sichuan, and Guizhou); in pine forests or on grasslands, (1150–)1600–2300(–3400) m alt. Flowering June–August, fruiting July–September.

Within the section this species is characterized by its more or less rhomboid leaves and its blue or purple corolla.

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APPENDIX. **Index to exsiccatae.***†

Ajab & Afzal *1546* (43)
Altmann *250* (35)
Anglade *915* (40b)
Anshun Expedition *1087, 1123* (74); *1426* (24)
Auns *8* (38)
Backer *4833* (35)
Bakhuizen van den Brink *2349, 4375, 4722* (35)
Banerji *1495* (71)
Barnes *521* (73a), *522* (28), *560* (73a), *561* (28)
Bayliss *4440* (1)
Bernardi *15799* (31)
Bisset *758, 2270* (14a); *2271* (12)
Biswas *3734* (73a), *4145* (71), *4171* (40c), *5991* (40a), *6488* (2)
Bock–Von Rosthorn *861* (53:T); *1122* (84:T); *1135* (73:T); *1164, 2207* (53:T)
Bodinier *2480* (40:T)
Bodinier & Martin *1937* (2:T)
Bor *1364* (95:T), *6678* (71)
Boufford & Wood *19874* (14a)
Bourne *222, 267, 1176, 1177, 1307, 1487, 1609, 1625, 1628, 1709, 1799, 1800* (28); *4613* (27); *6003* (28)
Bowes *5001* (87)
Brandis *813* (26:T)
Brinkman *271* (35), *608* (38)
Bullock *67* (86:T)

*Specimens lacking a number and most bearing only an institutional number have been omitted.

†The designations in parentheses refer to the corresponding taxa in the text; "T" designates a type specimen.

CRATAEGUS (MALOIDEAE, ROSACEAE) OF THE SOUTHEASTERN UNITED STATES, I. INTRODUCTION AND SERIES AESTIVALES

J. B. PHIPPS[1]

This paper is the first of a series completely revising *Crataegus* for the southeastern United States. The taxonomic history of North American *Crataegus* is outlined, and modern evidence (polyploidy, apomixis, hybridization) for the taxonomic complexity in the genus in North America is summarized. *Crataegus* is described in detail, and its relationship to the other genera of tribe Crataegeae of subfam. Maloideae is discussed. Twenty-one series of *Crataegus* are commonly accepted for the southeastern United States. The revisionary treatment opens with ser. *Aestivales*, a very distinctive group of plants of early anthesis, early fruiting, unusual (seasonally flooded) habitat, and umbellate inflorescences. Two common, almost completely allopatric, polar species and an intermediate, putatively hybrid species are included.

I am preparing the treatment of *Crataegus* L. for *The Vascular Flora of the Southeastern United States*. Since the format of the flora is highly condensed, this series of papers details the revisions underlying that account. Since 1982 I have undertaken fieldwork in all the southeastern states to become familiar with variation in natural populations. The need for a revision, which will be detailed later, has led to the assembly at the University of Western Ontario of nearly all the extant herbarium material of *Crataegus* for the southeastern United States. I have taken advantage of this situation to map (for the first time, in many instances) all the species studied. Discrimination between some taxa—and within several species-groups—has always been difficult, so a morphometric approach to resolving these problems has been incorporated where appropriate. Because typification in this genus in the southeastern United States has generally not been carefully undertaken hitherto, I have given this critical attention wherever appropriate.

Crataegus is a large (about 60 species), ecologically and economically important genus in the southeastern United States, defined here as the area treated by *The Vascular Flora of the Southeastern United States* (Radford *et al.*, 1980)—i.e., east of the Mississippi as far north as Kentucky, West Virginia, Maryland, and Delaware, and also west of the Mississippi to Louisiana and Arkansas. The majority of United States *Crataegus* species (at least, as broadly defined) occur in this region due to the paucity of species in the west of the country and to the fact that most northeastern North American series of *Crataegus* have representatives in the Appalachian area. Of the distinct and reasonably

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common United States and Canadian species, only *C. erythropoda* Ashe (series uncertain; Colorado), *C. douglasii* Lindley sensu lato (ser. *Douglasianae* (Rehder ex Schneider) Rehder; Pacific northwest to Upper Great Lakes area), *C. saligna* Greene (best serial affiliation uncertain; Colorado), and *C. chrysocarpa* Ashe (ser. *Rotundifoliae* (Eggl. ex Eggl.) Rehder; wide-ranging northern) do not occur within the study area. The other moderately distinct taxa not found in the southeastern flora include *C. columbiana* Howell (ser. *Rotundifoliae*; Pacific northwest), members of the series *Brainerdianae* and *Suborbiculatae,* and some Texan endemics like *C. tracyi* Ashe. This revision will therefore be one of the most comprehensive for this genus in North America.

TAXONOMIC PROBLEMS

Some perspective on the taxonomic problems inherent in the genus may be gained from a brief historical overview. Prior to 1895 only some 20 species were recognized from the United States and Canada, many described from plants grown in European botanical gardens. But Ashe, Beadle, and Sargent, between about 1898 and 1912, described some 1500 "species" of North American hawthorn. Brown (1910) provided an interesting discussion of this situation, analyzing the species concepts and the views on hybridization of the cited authors and others. While a good number of names have been placed in synonymy, the proper disposition of many remains uncertain due to lack of study, poor quality of the type material (or, in the case of many Ashe names, its absence), the necessity to lectotypify (mainly ignored until very recently), or simply the intrinsic taxonomic problems of any particular group of *Crataegus.* Consequently, numerous nomenclatural problems exist (see, for example, Phipps, 1988a, 1988b). The number of species to accept is therefore very arguable, and modern limits lie between the 100 or so of Palmer (1952) and the 20 of Gleason and Cronquist (1963). Palmer (e.g., 1946, 1950, 1952, 1956) and Kruschke (1965), both following the tradition of Eggleston (e.g., 1908), attempted to maintain "moderate" species concepts, although Gleason and Cronquist's approach represents an unabashed attempt to reduce the number of entities to a "manageable" level. In the latter case, a substantial number of well-known species were summarily, and without evidence, dismissed as hybrids. The problem remains, therefore, how to treat this complex genus optimally.

In my view (see Phipps & Muniyamma, 1980) a "moderate" approach is generally most useful in *Crataegus.* This is liable to result in 35 to 50 broadly circumscribed species for the Southeast and an as-yet-unknown number of taxa of lower rank or narrower definition. However, as will become clear later, many of the "microspecies" of earlier authors do appear to represent real entities and cannot automatically and cavalierly be disregarded. The "*Crataegus* problem" (Eggleston, 1910; Palmer, 1932; Camp, 1942) requires acknowledging the existence of a multitude of microspecies arising due to apomixis and hybridization, compounded by polyploidy (Phipps, 1983). Some microspecies of earlier workers survive rigorous numerical analysis (e.g., Sinnott & Phipps, 1983), while others do not and their names are clearly synonyms. However, some species

(e.g., *C. punctata* Jacq.) are known to be sexual diploids (Muniyamma & Phipps, 1985) and present no problems.

The Source of Taxonomic Complexity

Generally, a large number of taxonomic synonyms indicates a genuine taxonomic problem. Although some of the synonyms may be due to simple carelessness (redescribing exactly the same entity), this is not always the case. Components of a large and continuous spectrum of variation might, for instance, provisionally warrant new species names. In *Crataegus,* however, the most serious problem arises from discontinuous variation within the limits often accepted for a broad species concept. *Crataegus* has been shown to be apomictic and polyploid in North America and introgressive in Europe (Byatt, 1975, 1976; Christensen, 1982, 1984). Many names given therefore represent major components of geographic variation, while others correspond to fixed hybrids (common or sporadic); some are part of a mosaic of often locally distinguishable apomictic clones. Nowhere is this more clear than in the *C. crus-galli* complex, where a substantial number of reasonably distinct forms can often be found at any one site (e.g., northern Louisiana). Yet for taxonomic recognition of such entities, they must be both globally and locally distinct. Evaluating whether a form is sufficiently and universally distinct is the essence of the *Crataegus* problem.

The Need for a Revision

Chapman (1860) recognized 11 species of *Crataegus* from the southeastern United States, but Beadle (1903) raised this number to 185 in Small's *Flora of the Southeastern United States.* By 1919, 300 species had been described, yet most of these names did not make their way into subsequent floras. Tidestrom (1933), for instance, recognized only 33 species, while Radford, Ahles, and Bell (1964) offered the very conservative approach of only 13 species for two states. Strausbaugh and Core (1953), however, treated 25 species for West Virginia. Correll and Johnston (1970) listed 33 species for Texas (all but the nine endemic or western ones occurring in the Southeast), while Vines (1960; key contributed by E. J. Palmer) gave 69 species for the southwest. Other works (e.g., Clark, 1971) also list the taxa of *Crataegus* that occur in a particular state or area.

All the above works are to some extent defective. Chapman's, of course, is out of date. Beadle's useful treatment contains too many microspecies for a modern flora; Tidestrom's is too succinct and is taxonomically obsolete in some cases; and those of Clark and of Radford and colleagues contain identifiable taxonomic errors. Palmer, the mid-twentieth-century author in the best position to treat southeastern *Crataegus,* unfortunately did not do so comprehensively. Portions of his northeastern treatments are nevertheless pertinent to the southeast, but his contribution to Vines was merely a key. In 1925 he produced a nomenclator, indicating type localities for each species and arranging all species by series. This valuable work is not, however, a revision, since virtually no decisions were made at the species level. In his later works

(1950, 1952, 1956) he moved to moderate species concepts, but unfortunately none of these papers constitutes a complete revision, questions of typification being almost entirely neglected and those of synonymy restricted to a list for the northeastern area (1946). Kruschke's (1965) valuable work can also be partly extrapolated to the southeast, but he did not deal systematically with the species complexes of that area, and his paper does not contain keys or species descriptions, although there are numerous valuable nomenclatural notes. There is, therefore, strong need for a modern revision.

RELATIONSHIP TO OTHER GENERA

Crataegus is a natural genus belonging to the tribe Crataegeae Koehne. It is quite closely related to *Mespilus* L., *Hesperomeles* Lindley, and *Pyracantha* M. Roemer and forms both a graft chimaera and a hybrid with *Mespilus* (Byatt & Ferguson, 1977). *Crataegus* is more distant from *Osteomeles* Lindley, *Cotoneaster* Medikus, *Chamaemeles* Lindley, and *Dichotomanthes* Kurz, if indeed the last-named belongs here. Differences among these genera are shown in TABLE 1 and the key to genera.

KEY TO THE GENERA OF TRIBE CRATAEGEAE

1. Leaves pinnate; inflorescences open, dome-shaped panicles; petals narrow. ..... *Osteomeles.*
1. Leaves entire, although sometimes deeply lobed; neither inflorescences nor petals as above.
   2. Carpels, styles, and pyrenes 1.
      3. Pomes with pyrene ⅓–⅔ extruded. ..... *Dichotomanthes.*
      3. Pomes completely enclosing pyrene, although hypanthial rim perhaps not fully closed.
         4. Inflorescences elongate panicles of flowers < 10 mm in diameter; plant unarmed; pomes cream-yellow. ..... *Chamaemeles.*
         4. Inflorescences flat-topped to somewhat convex corymbs or panicles; flowers generally > 10 mm in diameter; plant thorny; pomes red to black (rarely yellow). ..... *Crataegus,* pro parte.
   2. Carpels, styles, and pyrenes 2 to 5.
      5. Leaves entire, although maybe slightly wavy; stems unarmed.
         6. Inflorescences uniflorous; stamens 30 to 40; pomes 25–45 mm in diameter, brown, with wide hypanthial opening; sepals foliaceous. ..... *Mespilus.*
         6. Inflorescences usually with up to 50 flowers, although uniflorous in several species; stamens 20; pomes < 15 mm in diameter, red or black, hypanthial opening closed; sepals not foliaceous. ..... *Cotoneaster.*
      5. Leaves usually serrate or crenate, also sometimes ± deeply lobed; stems usually thorny.
         7. Plant deciduous; resting buds + globular; leaves thin or less often coriaceous, often lobed, usually serrate; petals white or very rarely pink; hypanthium open in fruit, although not necessarily widely so; pyrenes 2-seeded. ..... *Crataegus,* pro parte.
         7. Plant evergreen; resting buds ± conical; leaves ± coriaceous at maturity, the margin variable, sometimes entire; petals cream-white to pink; hypanthium closed in fruit; pyrenes 1- or 2-seeded.
            8. Usually densely gnarled shrub; leaves variously crenate or dentate to few-lobed; pomes red or purple; petals white or pink; pyrenes 1-seeded; Costa Rica to Bolivia. ..... *Hesperomeles.*

8. Stiff and erect or more laxly branched shrub; leaves ± entire to finely and regularly crenate or serrate, never lobed; pomes orange to red; petals cream-white; pyrenes 2-seeded; Old World. ..... *Pyracantha.*

REVISION OF SOUTHEASTERN UNITED STATES CRATAEGUS

Crataegus L. Sp. Pl. **1:** 475. 1753; Gen. Pl. 213. 1754. TYPE SPECIES:[2] *C. laevigata* (Poiret) DC. (= *C. oxyacantha* L., *pro parte*).

Small trees or shrubs, deciduous (or with leaves persistent through part of winter in some southern taxa), nearly always thorny; branching patterns varied—erect, tabulate, drooping, or irregular, ultimate twigs usually fairly straight but sometimes zigzag at inflexions where thorns occur; thorns 1.5–9 cm long, variously sharp-tipped short shoots, simple shoots of determinate growth, or branched thorns on trunk, if simple then straight to recurved, fine to stout, and usually blackish to reddish-brown when ca. 2 years old; resting buds small, globose, often reddish, showing 6 to 8 bud-scales. Leaves alternate, petiolate (occasionally ± subsessile); petiole occasionally alate; blade generally elliptic or broad-elliptic to ovate or deltoid, sometimes obovate, 2–6(–8) by 0.5–5 cm, shallowly lobed (then with veins only to lobe tips) or deeply so (then with veins to both sinuses and lobe tips), or unlobed, the margin usually serrate (occasionally crenate), the lateral veins 4 to 8, generally increasing in number with narrower leaf types, the surfaces glabrous or pubescent, eglandular or with conspicuous sessile or very short-stalked, black or reddish glands along margin and petiole. Inflorescences paniculate-corymbose or very rarely ± umbellate or uniflorous, (1- to) 6- to 20- (to 50-)flowered, sessile or borne on short, leafy shoots of current season (these always borne on perennial spur shoots), glabrous to very pubescent, bracteolate, sometimes glandular-sticky, flowering in single flush in spring (occasional autumnal flowering known near Gulf Coast). Flowers 5-merous, perigynous; hypanthial bowl ± salverform; calyx lobes triangular, small, entire to pectinate, glandular to eglandular; petals borne on hypanthial rim, usually ± circular in outline with short claw (rarely broadly elliptic), 4–15 mm long, concave, spreading in open bowl at full anthesis; stamens borne on hypanthial rim, generally in approximate multiples of 5 (5 to 8, 9 to 12, 17 to 21), filaments up to length of petals, anthers white, cream, pink, red, or purplish; pistils in center of hypanthial bowl, the styles 1 to 5, corresponding to number of carpels, the ovules 2 per carpel. Fruit a pome, oblate-spheroidal to ellipsoid or pyriform, 5–20 mm long in wild forms to 35 mm long in cultivars, red or reddish (more rarely black, purplish, orange, yellow, or light yellow flushed pink), with filament bases and/or calyx remnants often persistent on hypanthial rim; hypanthial cup in fruit fleshy, floury, succulent and juicy, or dryish, the hypanthial opening almost closed to wide open (3–6 mm) and exposing the pyrenes; pyrenes 1 to 5, corresponding in number to styles, usually grooved dorsally and sometimes erose laterally.

Crataegus comprises about 150 species, approximately 90 North American (ca. 50 in the area of this flora) and 60 Eurasian. The exact number is non-

[2]The question of the type species of *Crataegus* has been discussed by Dandy (1946) and Byatt (1974).

TABLE 1. **Comparison of the genera of tribe Crataegeae.**

Genus	Character				
	DISTRIBUTION; NO. OF SPECIES	HABIT	THORNS	LEAVES	RESTING BUDS
Chamaemeles	Madeira; 1	Evergreen small shrub	Lacking	Medium-sized, simple, ± entire	Small, ± conical, dark, short-pubescent
Cotoneaster	Eurasia; 100 to 200	Evergreen or deciduous small to large shrub	Lacking	Small to large, unlobed, entire	Often larger than those of other genera, ± conical, usually red or brown, densely pubescent
Crataegus	North-Temperate; 150	Deciduous small shrub to small tree	Usually simple thorns, but sometimes thorn-tipped short shoots	Small to large, unlobed to deeply lobed, nearly always serrate	Small, ± globular, deep red, ± glabrous
Dichotomanthes	China; 1	Deciduous medium-sized shrub	Lacking	Medium-sized, unlobed, entire	Small, round, light brown, densely crisped-pubescent
Hesperomeles	Central and South America; 5 to 10	Evergreen shrub or small tree	Short shoots, sometimes thorn tipped	Small, shallowly lobed or not, entire to denticulate or coarsely crenate-serrate	Small, ± conical-pointed, plum red, crinkly-rufous-pubescent
Mespilus	Europe, western Asia; 1	Deciduous large shrub	Short shoots, often thorn tipped	Large, simple, ± entire	Small, narrow-globose to conical, plum red, glabrous, bud scales marginally ciliate
Osteomeles	Eastern Asia to Polynesia (Hawaii); 3	Winter-green small to medium-sized shrub	Lacking	Large, pinnate, entire	Small, conical, brown, ± pubescent
Pyracantha	Eurasia; 9	Evergreen medium-sized shrub, often with arching branches	Short shoots, often thorn tipped	Small, unlobed, serrate	Small, ± conical, color variable, glabrous or pubescent, bud scales marginally ciliate

TABLE 1 (*continued*).

Genus	Character					
	INFLORESCENCES	PETALS	STAMEN NO.	POMES	PYRENE NO.	OVULES PER CARPEL
Chamaemeles	Elongate panicles	Small, round, red and white	20	Small, closed, cream-yellow	1	?
Cotoneaster	Uniflorous, corymbs, or ± flat-topped panicles	Small, ± round, white or reddish	20	Small, closed, red or black	2 to 5	2
Crataegus	Uniflorous, corymbs, or ± flat-topped panicles	Small to medium-sized, ± round, white	5 to 12 or 17 to 21	Small to medium, slightly open, yellow, red, or black	1 to 5	2
Dichotomanthes	± Flat-topped panicles	Small, round, white	20	Small, brownish; nutlet 35% exposed	1	2
Hesperomeles	Corymbs	Small, round, white or pink	20	Small, closed, red or darker	5	1
Mespilus	Uniflorous	Large, round, white	30 to 40	Medium, open, brown	5	2
Osteomeles	Panicles	Small, narrow-elliptic to obovate, white	20	Small, closed, red to black	5	1
Pyracantha	Flat-topped panicles	Small, ± round, white	20	Small, closed, red	5	2

definable due to inconsistent application of species concepts. The breeding system ranges from sexual amphimixis through obligate apomixis, and both introgression and hybridization occur. The base chromosome number (x) is 17, with diploids, triploids, and tetraploids known (Moffett, 1931; Darlington & Wylie, 1955; Gladkova, 1966; Muniyamma & Phipps, 1979a).

Crataegus is common through much of the southeast, although least so in Kentucky, Tennessee (Ulf-Hansen, 1985), Virginia, and North Carolina; it is completely absent from the southern part of Florida. The species range from extreme heliophiles and xeromorphs (e.g., ser. *Flavae,* as conventionally understood) to those with some shade tolerance (sers. *Apiifoliae, Brevispinae, Virides*). Species of some series (for instance, *Aestivales* and *Virides*) flourish in wet ground. However, hawthorns are most common in mesic open woodland (predominantly oak and oak-pine) and open successional sites, including pastures, fence lines, roadsides, and erosion slopes. Most species are strongly browse resistant due to thorniness.

Hawthorns are mass flowering in spring and are open pollinated, mainly by a variety of Hymenoptera and Diptera (Power, 1980). The species exhibit strong phenological rank-order of flowering (Smith, Phipps, & Dickinson, 1980), and the times of flowering of Ontario taxa can be predicted with some accuracy on the basis of summated heat units after an appropriate (specific to species and locality) starting date. Sexual species are self-incompatible, while facultative apomicts are mostly pseudogamous and self-compatible (Dickinson & Phipps, 1986). Apomixis is mainly aposporous (Muniyamma & Phipps, 1979b, 1984).

The fruits ripen in the fall and are dispersed by birds (large and medium-sized passerines and game birds). However, they often persist through the fall and into the winter, or at least until very cold weather. Additionally, the fruits are eaten off the tree by ungulates and off the ground by rodents and ungulates, which are also agents of dispersal (Hoover, 1961). Virtually nothing is known about the relative effectiveness of different dispersing agents.

Infrageneric Groupings

El-Gazzar (1980) divided *Crataegus* into two subgenera—*Crataegus* and *Americanae* El-Gazzar—on inadequate criteria because these subgenera are not fully allopatric nor do they have different base chromosome numbers (Phipps, 1983). Subgenus *Crataegus,* which comprises species often lacking simple thorns and having generally smallish, deeply lobed leaves with veins to the sinuses, is probably a valid grouping, if restricted to sects. *Crataegus* (= *Oxyacanthae*) (western Eurasia) and *Azaroli* (western Eurasia and North Africa) and also perhaps ser. *Apiifoliae* (North America). However, El-Gazzar's subg. *Americanae* is a mélange of quite varied taxa, mainly eastern Asiatic and North American, and may well eventually be broken down into several natural units (see Phipps, 1983; Phipps *et al.,* in prep.).

The most commonly employed infrageneric ranks in *Crataegus*—series and sections—have generally been used alone to provide a direct split of the genus (see, for example, Loudon, 1838; Schneider, 1906; Rehder, 1940; Palmer, 1952;

Rusanov, 1965); therefore, choice of rank does not reflect hierarchy. I utilize series in this work due to the obviously narrow circumscriptions being adopted. More hierarchy is given in Phipps and colleagues (in prep.).

For the 90 or so North American species, some 25 series are generally accepted (Phipps, 1983), all but three of which (*Brainerdianae, Douglasianae,* and *Mexicanae*) are represented in the Southeast. Each series represents a natural group of small taxonomic size and little internal diversity. By contrast, diversity among the North American series of *Crataegus* is substantial. Also, while some series (e.g., *Aestivales, Brevispinae, Microcarpae*) are quite discrete, others (e.g., *Pulcherrimae* and *Virides*) are obscurely differentiated (see Phipps, 1988a), while yet others (e.g., *Crus-galli* and *Punctatae*) intergrade through rare putative hybrids (Wells, 1985). However, the frequency of individuals intermediate between series is generally low, and thus the series can still be construed as representing natural units. Some series (e.g., *Brainerdianae, Dilatatae,* and possibly *Pulcherrimae*), however, themselves appear to be of interserial hybrid origin (Phipps, 1984).

Crataegus sers. *Aestivales, Apiifoliae, Bracteatae, Brevispinae, Coccineae, Cordatae, Crus-galli, Flavae, Intricatae, Macracanthae, Microcarpae, Molles, Oxyacanthae, Pruinosae, Pulcherrimae, Punctatae, Rotundifoliae, Silvicolae, Tenuifoliae, Triflorae,* and *Virides* are generally recognized as occurring in the southeastern United States and will be treated in an order reflecting convenience of work. Note that at this stage this list represents the conventional serial names and circumscriptions developed by Palmer (1952, and *in* Vines, 1960) and Kruschke (1965). In some cases the authorities cited, the names, or the circumscription of the series may have to be changed.

Species Concepts, Synonymy, Typification Practices, and Hybrids

Within-series taxonomy, except for the actual or presumed sexual species, is often extremely difficult, and it is here where the many taxonomic problems reside. In the southeastern United States typical examples of very difficult situations are to be found in sers. *Crus-galli, Flavae* (sensu American authors), *Intricatae,* and probably *Parvifoliae* and *Virides.* In the revision for *The Vascular Flora of the Southeastern United States,* I plan to treat apomictic species complexes as coordinate with sexual species, i.e., to give them a binomial. Apomictic microspecies, where worthy of continued recognition, will be given varietal rank. The wide variety of intermediate forms, however, together with numerous distinctive but rare types, will complicate the picture. Many of the known named forms will undoubtedly prove to be hybrids. However, I do not believe that systematics is served by the bold, but mere, assertion of hybrid origin. Hybrids (or presumed hybrids) of a persistent, distinct nature will be recognized at the species rank. A brief discussion pertinent to each case will give the reasons for the taxonomic decision made or the nomenclatural options presented.

As indicated above, about 300 species of *Crataegus* have been described from the southeastern states (Palmer, 1925), and my preferred disposition will

be indicated for as many of these names as possible. Many will presumably disappear in synonymy. However, at this point it is not possible to estimate what proportion of the remaining 1200 or so names proposed for North American *Crataegus* have application in the Southeast. The enormous synonymy of specific names created by the descriptions of Ashe, Beadle, Sargent, and (to a lesser extent) Murrill can probably not be completely clarified even in this revision. While the synonymy should be better documented than hitherto, it will still not be complete.

Because many species have not been explicitly typified so far, extensive lectotypification will likely be required. There will also be some situations with especially difficult problems of typifying the oldest name (e.g., in sers. *Crus-galli* and *Flavae*, especially if the type is European—but see Phipps, 1988a, 1988b). The potential neotypification of a number of Ashe names has already been alluded to. Nevertheless, so many names exist in the literature that taxonomic novelties, except for rank changes, are expected to be very few.

The ability of *Crataegus* to hybridize, even with species in other maloid genera, is well known (summarized in Phipps, 1984). There are numerous horticultural hybrids reported, and a large number of taxa, some of which occur in our area, have been suspected to be of hybrid origin (Gleason & Cronquist, 1963; Phipps, 1983). There are also many binomials referring to evanescent, apparently hybrid taxa. Actual or presumed, permanent or evanescent hybrids will receive an appropriate comment.

Series I. AESTIVALES (Sarg. ex Schneider) Rehder, Man. Cult. Trees, ed. 2. 366. 1940.

Sect. *Aestivales* Sarg. ex Schneider, Ill. Handb. Laubholzk. **1**: 794. 1906. TYPE SPECIES: *C. aestivalis* (Walter) Torrey & A. Gray.
Aestivales Sarg. Silva (Suppl.) **13**: 35. 1902, *in clavem*, without rank.

Shrubs to 8 m tall, occasionally more; mature bark fibrous; branchlets gray; thorns few to fairly numerous, short (1–2 cm), stout, straight. Leaves not appearing before flowers and often entirely after anthesis, elliptic to broad-elliptic, unlobed or slightly (wavy-)lobed, entire to finely serrate, glossy or matte, ± glabrous to conspicuously rufous-tomentose. Inflorescences umbellate, ± sessile, few-flowered, glabrous to rufous-pubescent. Flowers medium to large (12–28 mm in diameter); calyx lobes ± triangular, ± entire to slightly glandular-serrate; petals white to pale pink; stamens 20, the anthers small or large, usually reddish; styles 5. Fruit 0.8–1.5 cm in diameter, red, succulent, ripening very early (May in south); pyrenes 5, dorsally ribbed.

Three species, one probably deriving from introgression between the other two; Coastal Plain of south-central Texas to North Carolina, south to central Florida, and north through Louisiana to extreme southern Arkansas. Essentially restricted to seasonally inundated sites: sinks, potholes, drainage ditches, low-lying woodlands.

Breeding system unknown, although variation patterns of *Crataegus opaca* and *C. aestivalis* suggest amphimixis with some apomixis. If *C. rufula* is an

TABLE 2. **Characters used in the numerical taxonomic study of Crataegus ser. Aestivales.**

CHARACTER NUMBER	CHARACTER	SCORING
	Branch	
*1.	Tomentum on twigs of current season	None (0) to dense (5)
2.	Length of thorn	In mm
	Leaf size	
*†3.	Length of lamina	In mm
4.	Length of petiole	In mm
5.	Maximum breadth of lamina	In mm
	Leaf shape	
6.	Length/breadth quotient	
*7.	Location of widest part	In tenths from base of blade
*†8.	Tip	Obtuse (0) through acute (3)
*†9.	Lobes	Mean no. per side
*10.	Leaf incision index	Largest lobe (%)
	Leaf margin	
*†11.	Serrations greater than 1 mm deep	Absent (0) or present (1)
12.	Teeth blunt, through sharp	0–1
13.	Percent (from tip) with teeth still at frequent intervals	0–100
14.	Glands	Absent (0) or present (1)
	Leaf venation	
*†15.	Mean no. per side	
*†16.	Mean angle from midrib	In degrees
	Leaf tomentum	
*17.	O⁻ upper surface	Absent (0) through dense (5)
*18.	On lower surface between veins	Absent (0) through dense (5)
*19.	On lower surface on mid-vein	Absent (0) through dense (5)

*Included in 12-character set.
†Included in six-character set.

introgressant, this supports these assumptions. Chromosome number: not counted (probably includes diploids in at least *C. opaca* and *C. aestivalis*).

Series *Aestivales* is among the most distinct of all series of American hawthorns due to its anthesis before leaf expansion, inflorescence form, early fruiting, and habitat. *Crataegus rufula* is quite variable, strikingly so in flower size, and may well be in part apomictic. This would suggest that at least some individuals of *C. opaca* or *C. aestivalis* are also apomictic. The almost perfect allopatry of the last two species, with just slight overlap in southern Alabama, is not easy to explain except by separate southeastern and southwestern Pleistocene refugia, in which case the eastern limits of *C. opaca* and western limits of *C. aestivalis* may still be mobile. Series *Aestivales* is very distinct from other North American *Crataegus* series, and its nearest relatives are unclear. Interserial hybrids are not suspected unless *C. fruticosa* Sarg. (to be treated in a later

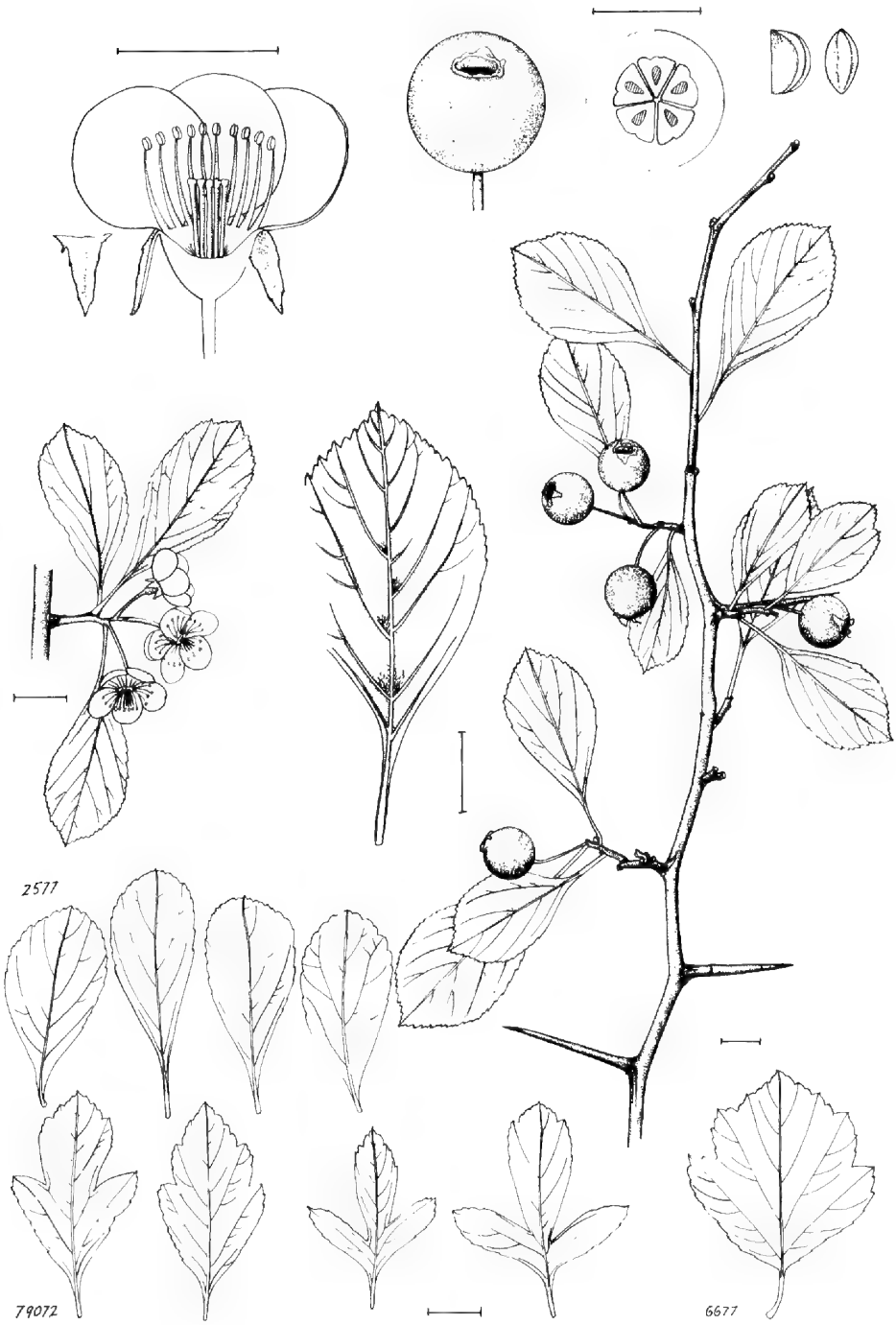


FIGURE 1. *Crataegus aestivalis*. Fruiting branchlet, fruits, seeds, and central leaf based on *Leonard & Davis 7547*; inflorescence and flower on *Duncan 22234*. Note broader and narrower leaf shapes on short-shoot leaves (*Faircloth 2577*) and lobing of vegetative leaves (*Godfrey 79072, Curtiss 6677*). Scales = 1 cm.

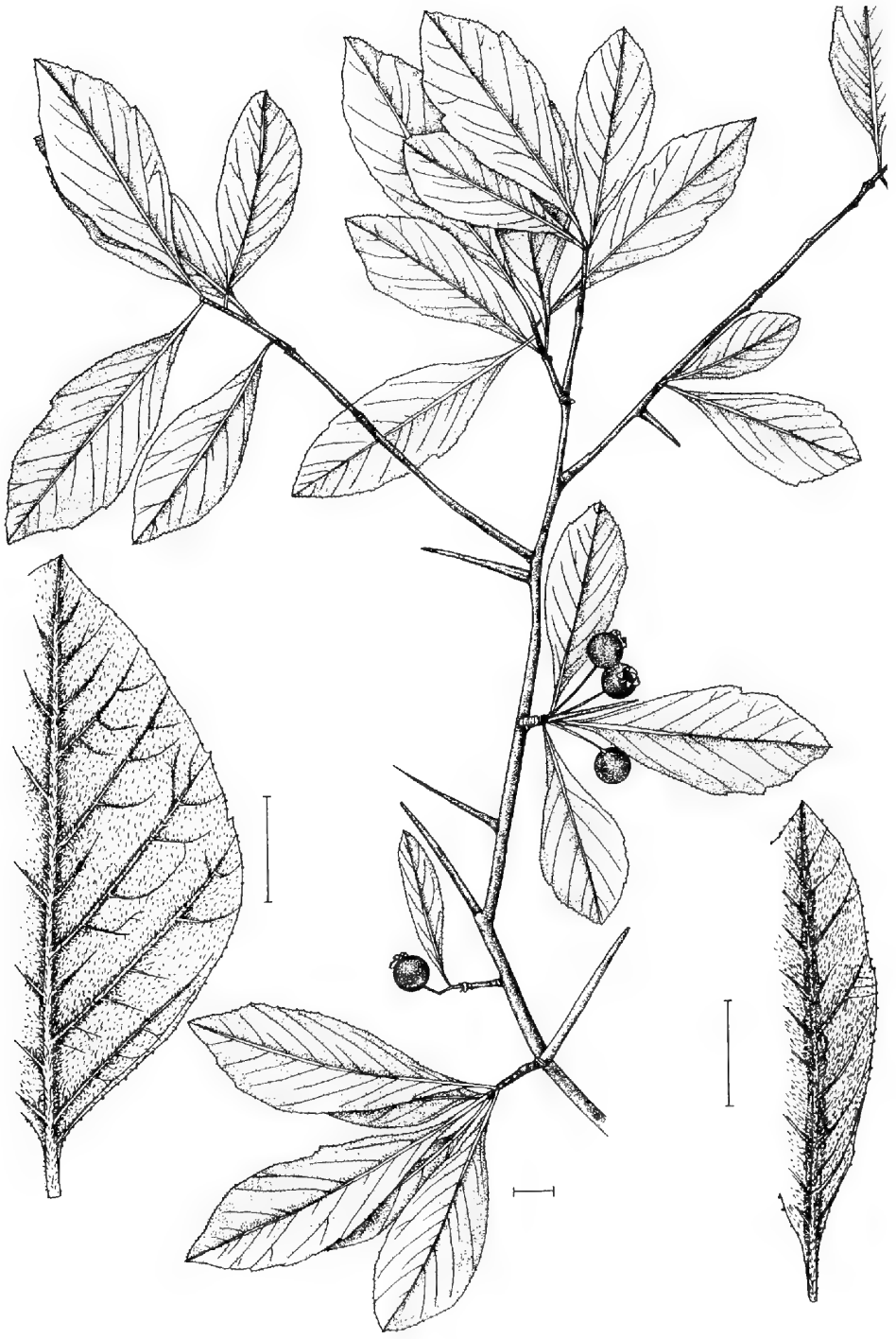


FIGURE 2. *Crataegus opaca,* based on *Rylander 111.* Note tomentose undersurfaces of leaves in enlargements. Scales = 1 cm.

installment) belongs here. Except for the *C. rufula* situation, the two more common species are highly distinct. Therefore, to examine this problem series *Aestivales* was subjected to a small-scale numerical taxonomic study.

NUMERICAL TAXONOMIC STUDY

Forty-five OTUs were initially studied, 22 of "pure" *Crataegus aestivalis,* 13 of "pure" *C. opaca,* and ten from the *C. rufula* complex. Original OTU 25 was rejected as anomalous, and thus the numbering on the diagrams is 1–24 and 26–45. Herbarium specimens were selected from the entire geographic range of the three species. Nineteen characters were scored from vegetative (mostly foliar) characters (see TABLE 2). As can be seen from the illustrations, there is substantial difference between the foliage of *Crataegus aestivalis* (FIGURE 1) and that of *C. opaca* (FIGURES 2, 3), and these two species were considered the polar ones in the hybrid index run; *C. rufula* (FIGURE 4) is intermediate. Flower characters were not used in this analysis because, prior to the numerical taxonomic study, even approximate species assignations could not be made with flowering material. Fruiting characters were likewise not used since no taxonomically meaningful variation could be identified.

This data matrix was subjected to single-link and minimum-variance clustering on the Euclidean distance matrix, principal-components analysis, and character ranking based on variance ratios (Jancey, 1979). A minimum spanning tree was also produced. These results (see FIGURES 5–8) clearly indicate the division *aestivalis*/(*opaca* + *rufula*). The character-ranking algorithm (TABLE 3) demonstrates that characters 19 and 18, in that order, best differentiate *Crataegus aestivalis* from the other two, while—as in the R-PCA—characters 11, 12, and 1 are also important. Inspection of the raw data bears out these interpretations. The Wells Hybrid Index (FIGURE 9) clearly shows the intermediacy of *rufula* OTUs. As in other analyses of the 44-OTU data set, however, *C. opaca* and *C. rufula* are slightly mixed. The Wells Hybrid Index was rerun on a reduced, 12-character matrix, derived by rejecting low-ranking characters determined from R-PCA and variance-ratio tests (see TABLE 3), to obtain better discrimination (see FIGURE 10). However, the results are similar: in both Wells Hybrid indices, all the *rufula* OTUs lie within the inner semicircle, indicating intermediacy of all characters combined.

The *Crataegus opaca* and *C. rufula* data matrix was then reanalyzed using the six characters (19, 18, 12, 1, 11, and 9) that best discriminated between them on the character-ranking algorithm. In the new results there is still some overlap between what had initially been considered C. *rufula* and C. *opaca.* Nevertheless, a somewhat better separation of these two species was thereby achieved (FIGURES 11–13). On the basis of this separation, it was possible to infer (from matched flowering and mature foliage material) that the inflorescence of *C. rufula* is always rufous-tomentose. By contrast, those of both *C. opaca* and *C. aestivalis* are glabrous to subglabrous. In general, the foliage of *C. rufula* is broader than that of *C. opaca* and sometimes lacks the sinuate margins typical of the latter species; it also has fewer lateral nerves, which branch at a wider angle (more like those of *C. aestivalis*). However, *C. aestivalis*

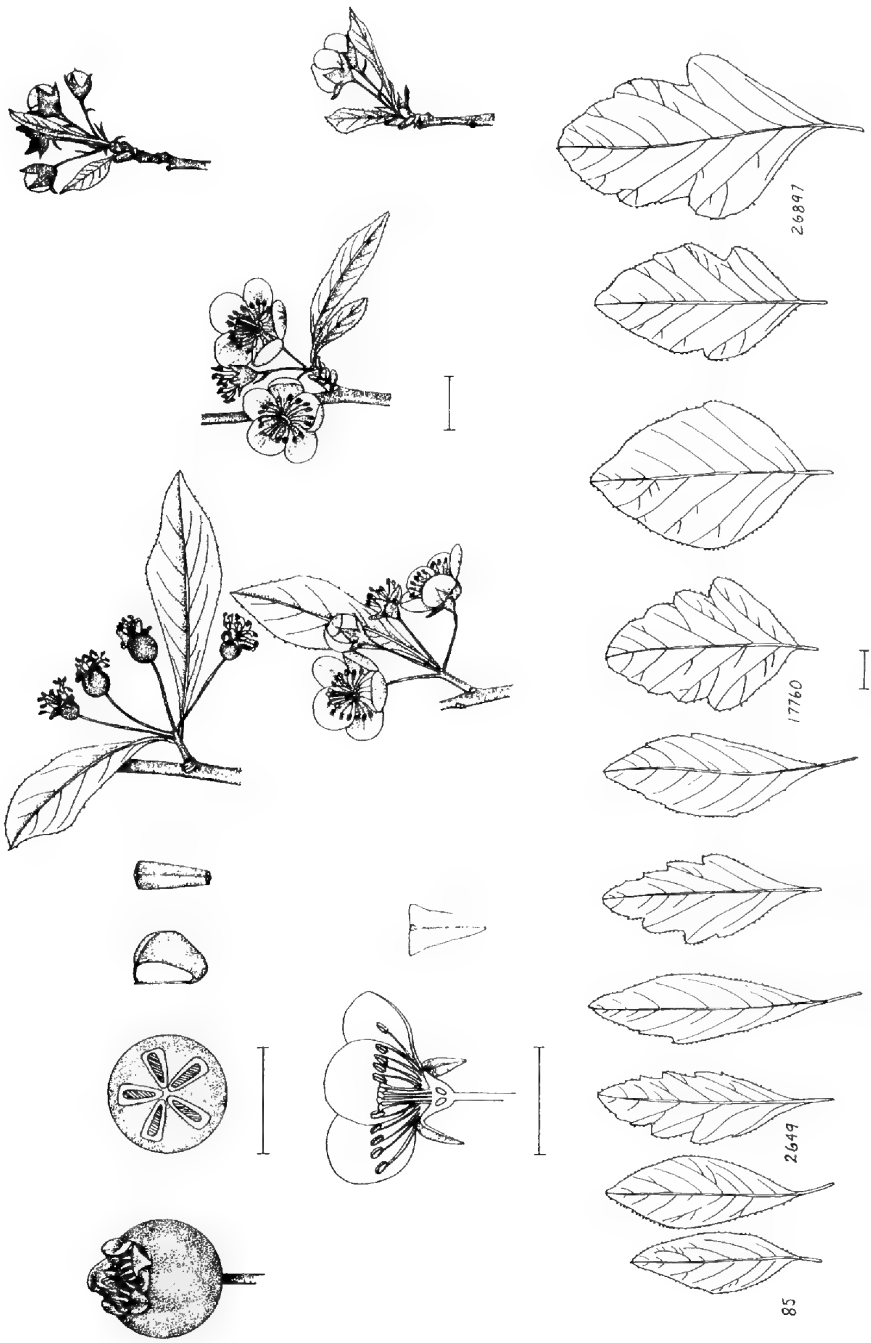


FIGURE 3. *Crataegus opaca*: fruits (*Holmes 2649*), inflorescences and flower (*Allen 6422*), and leaves (*Small 85*, *Holmes 2649*, *Thieret 17760* and *26897*). Scales = 1 cm; sepal × 2.

FIGURE 4. *Crataegus rufula*, based on *Harbison 19*. Scale lines = 1 cm.

FIGURE 5. Sum of squares agglomeration of Euclidean distance of 44 OTUs of *Crataegus* ser. *Aestivales*: squares = *C. aestivalis,* triangles = *C. opaca,* circles = *C. rufula.* Note clear division into *C. aestivalis* and remainder.

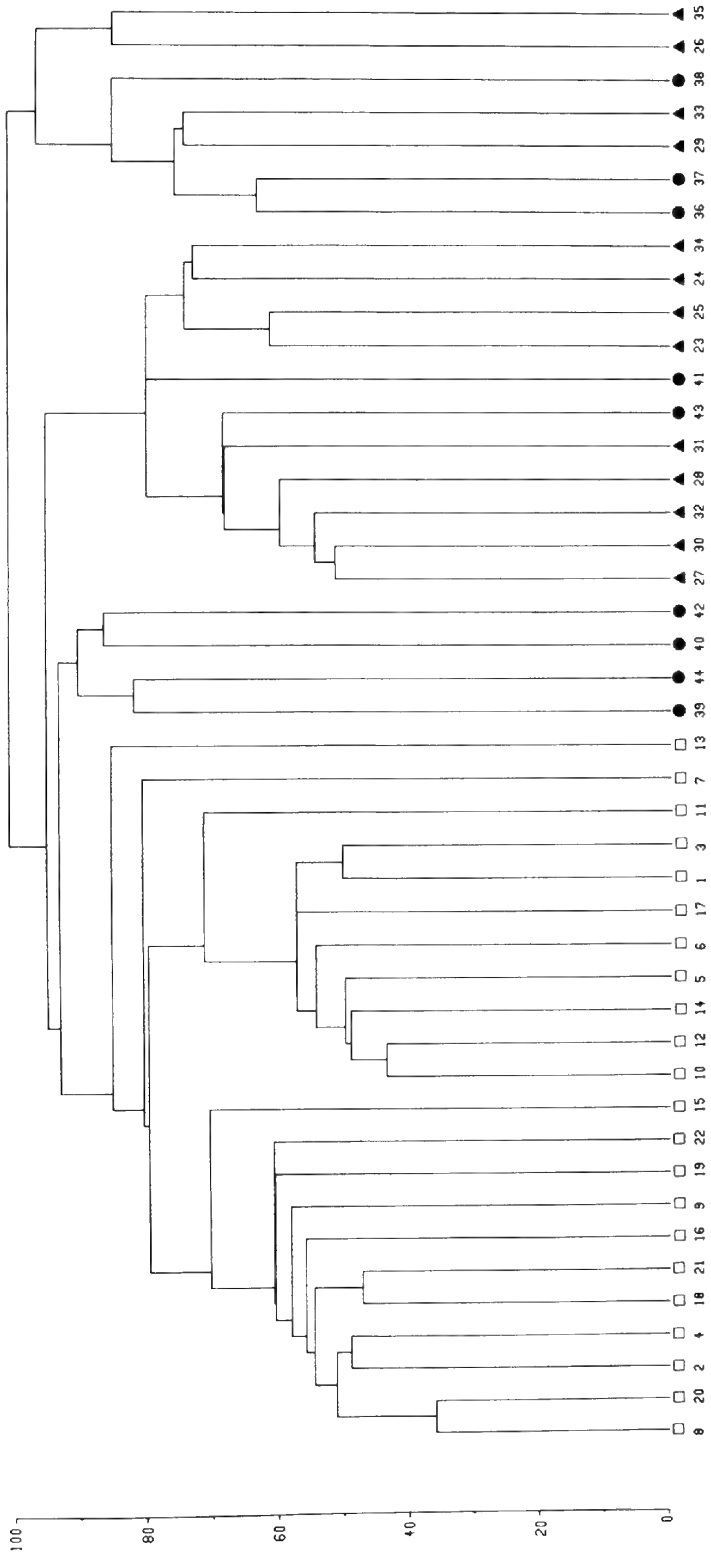


FIGURE 6. Single-link clustering of Euclidean distance of 44 OTUs of *Crataegus* ser. *Aestivales* (symbols as in FIGURE 5).

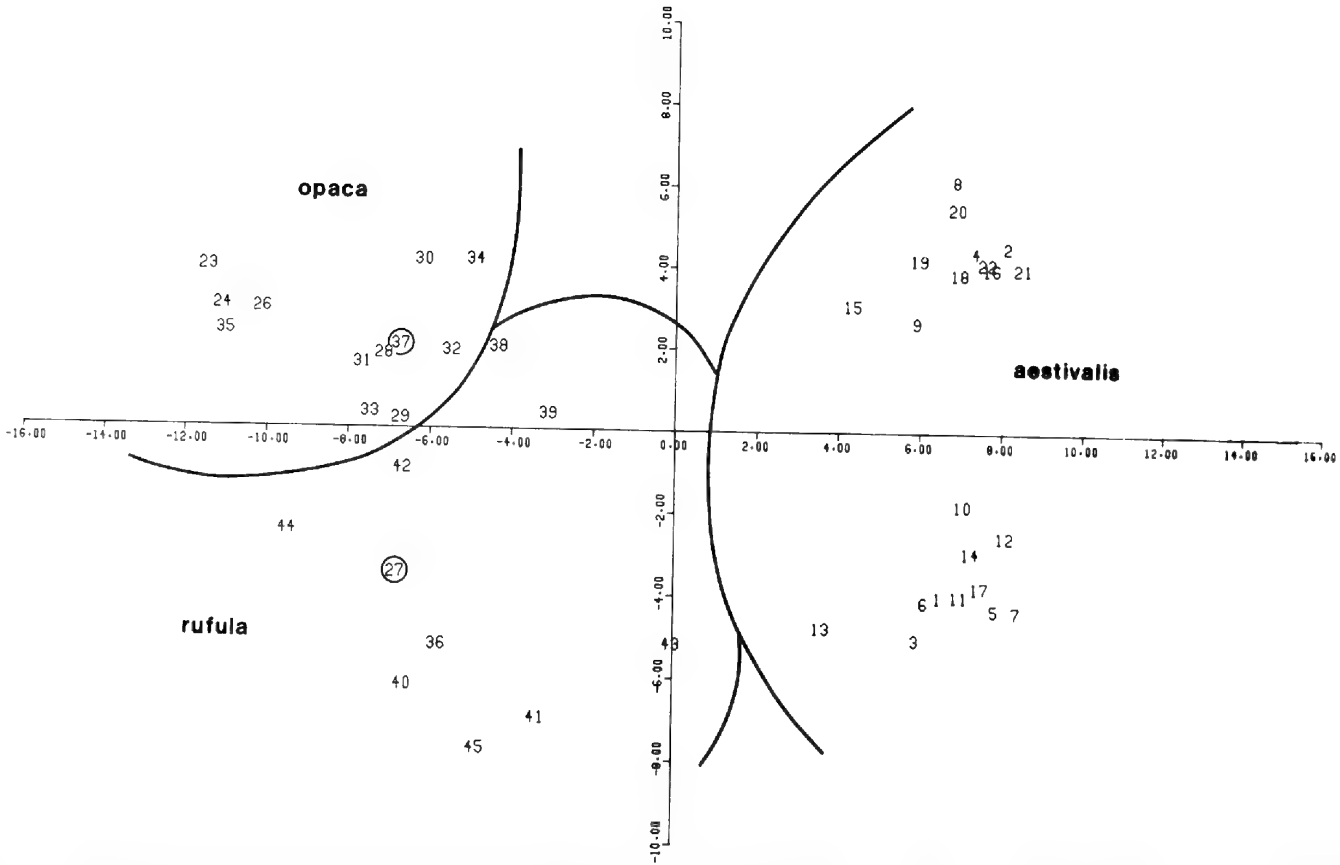


FIGURE 7. Principal-components analysis of 44 OTUs of *Crataegus* ser. *Aestivales*: nos. 1–22 = *C. aestivalis*, 22–35 = *C. opaca*, 36–45 = *C. rufula* (OTU no. 25 not used). Note partial intermediacy of *C. rufula* OTUs.

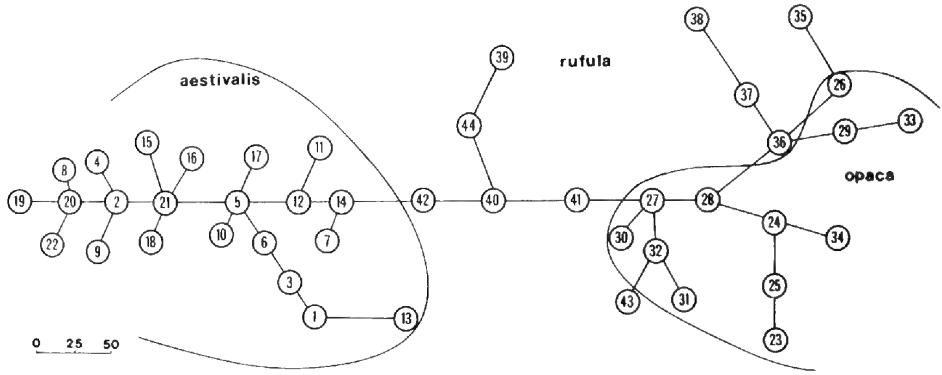


FIGURE 8. Minimum spanning tree of 44 OTUs of *Crataegus* ser. *Aestivales* (scaled to distance units computed by single-link data used for FIGURE 6).

and *C. opaca* are far too different to be treated as a single species in spite of the linkage represented by *C. rufula.* Note also that OTU 43, prior to this study identified as an *aestivalis-rufula* intermediate, sometimes shows up close to the *C. opaca* grouping (see, for example, FIGURE 8).

The intermediacy in foliar characteristics and geographic range, together with local abundance, suggest the hypothesis that *Crataegus rufula* is a variable, relatively new species of hybrid origin. This hypothesis may best be tested with detailed biosystematic studies by workers with easy access to living populations. *Crataegus rufula* is most conveniently treated as a separate species, even though it varies considerably in leaf shape (albeit tending to the broader shape of *C. opaca*), somewhat in foliar tomentum, and greatly in flower size.

KEY TO SERIES AESTIVALES

1. Leaves of short shoots 3–5 cm long, broadly elliptic-obovate, distally clearly serrate or crenate, the margin usually eglandular (glands occasionally present on teeth), unlobed, the surface usually glossy, ± glabrous except for tufts of usually whitish hairs in axils of mid-vein and lateral veins below. ..... 1. *C. aestivalis.*
1. Leaves of short shoots 5–7 cm long, variable in shape, the margin gland-dotted, not regularly and finely serrate-crenate but often sinuous, the surface usually matte, rufous-tomentose below.
   2. Leaves of short shoots elliptic to broad-elliptic, ± sinuate-lobed, lateral veins 5 to 9 (or 10); pedicel ± glabrous. ..... 2. *C. opaca.*
   2. Leaves of short shoots long-obovate to broad-elliptic, rarely ± crenate, lateral veins 3 to 5; pedicel ± rufulous-tomentose. ..... 3. *C. rufula.*

1. **Crataegus aestivalis** (Walter) Torrey & A. Gray, Fl. N. Amer. **1**: 468. 1838. FIGURE 1.

Mespilus aestivalis Walter, Fl. Carol. 148. 1788. Type not seen.

Crataegus cerasoides Sarg. Trees & Shrubs **2**: 237. 1913. TYPE: Florida, Volusia Co., near Seville, *Curtiss 6842* (holotype, A).

C. luculenta Sarg. Trees & Shrubs **1**: 11. *pl. VI.* 1902. TYPE: Florida, Flagler Co., Haw Creek, *Curtiss 6679* (holotype, A; isotype, DOV).

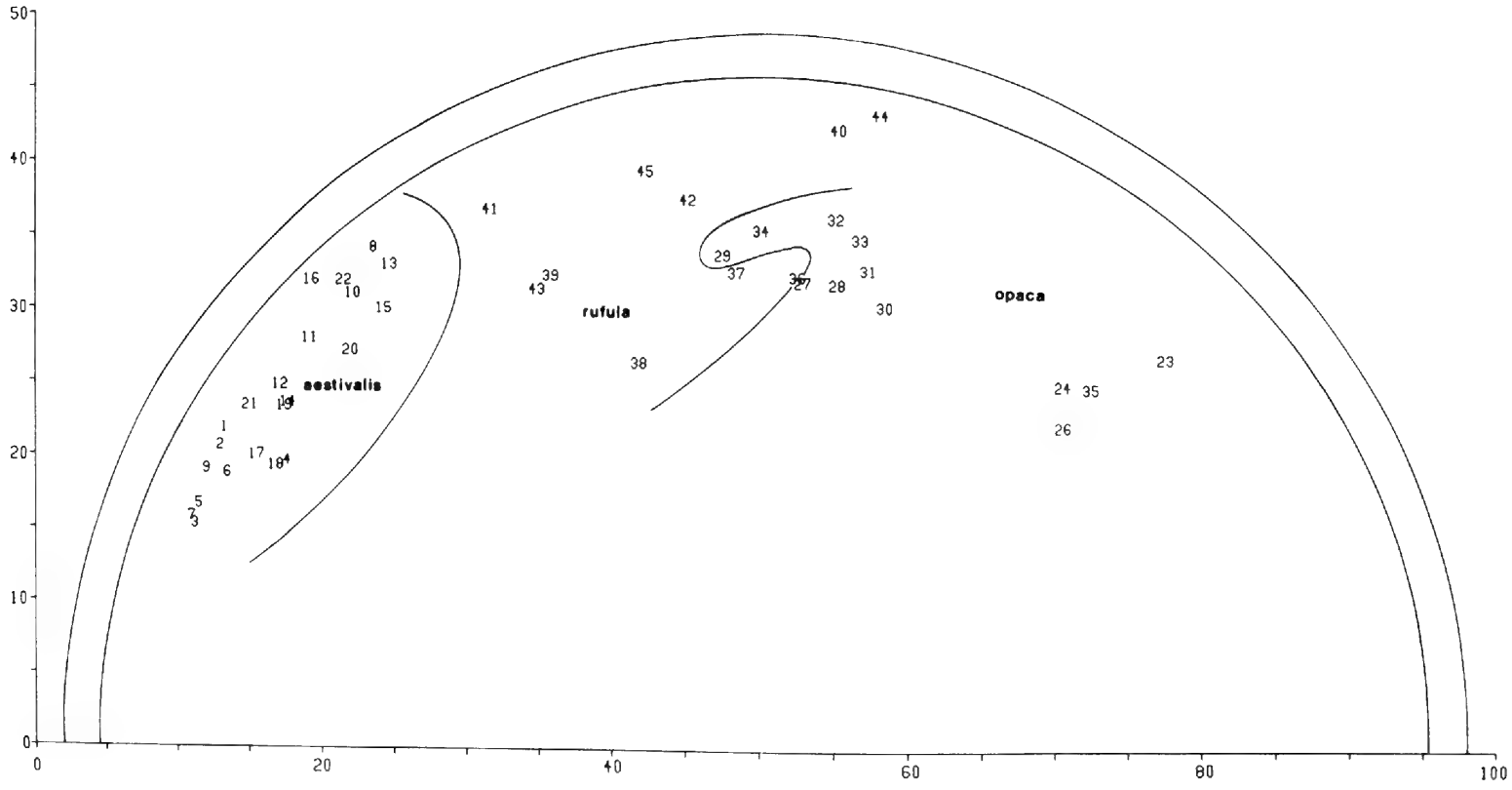


FIGURE 9. Wells Hybrid Index run on 44 *Crataegus* ser. *Aestivales* OTUs with putative hybrid *C. rufula.* Results clearly show intermediacy of *C. rufula.*

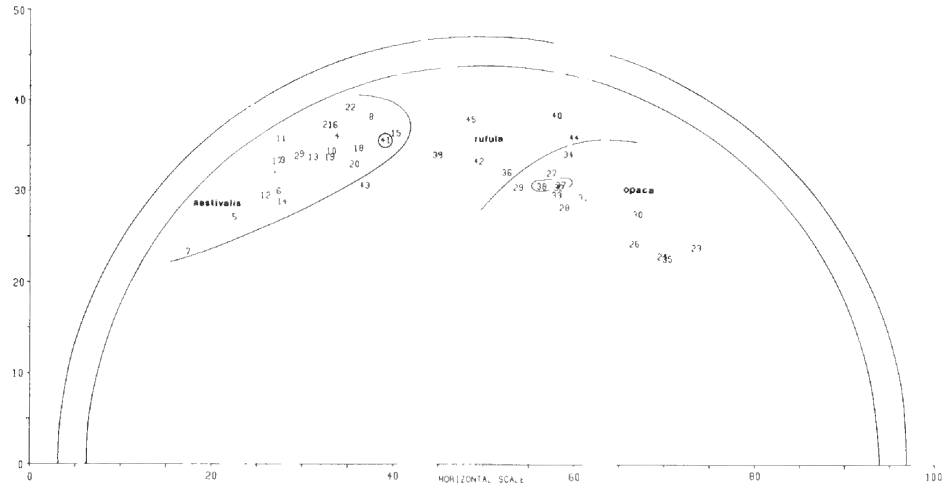


FIGURE 10. Wells Hybrid Index run on 44-OTU, 12-character set. Note results similar to 44-OTU, 19-character set (FIGURE 9).

C. maloides Sarg. Trees & Shrubs **1**: 9. *pl. V.* 1902. TYPE: Florida, Volusia Co., Haw Creek, *Curtiss 6777* (holotype, A).
C. lucida Elliott(?), Sketch Bot. S. Carolina **1**: 548. 1821. Type not seen.
C. elliptica Pursh(?), Fl. Amer. Sept. **1**: 337. 1814. Type not seen.

Shrub to small tree 3–12 m tall; branches gray (those of current season dark brown in late summer), glabrous; thorns less abundant on older shoots, 2–4 cm long when full grown, stout at base, ± straight, transforming ± readily into short shoots; elongating shoots with small, broadly circinate, glandular-margined stipules. Leaves appearing at or after anthesis; petiole 3–8 mm long, alate distally; blade elliptic to oblanceolate or narrowly so, 3–5 by 1.5–2 cm, sometimes much larger on elongating shoots (then sometimes few-lobed, sometimes deeply, even almost tripartite), finely serrate to crenate mainly in distal half,

TABLE 3. **Relative importance of 19 characters used in Crataegus ser. Aestivales study based on percentage of total variance accounted for by each character (R-PCA) and on variance ratio (C. aestivalis vs. others).**

CHARACTER NO.	PERCENT OF TOTAL VARIANCE	VARIANCE RATIO	CHARACTER NO.	PERCENT OF TOTAL VARIANCE	VARIANCE RATIO
1	10.0	196	11	13.9	267
2	2.5	71	12	12.1	238
3	2.2	82	13	3.1	53
4	2.0	71	14	0.7	8
5	2.7	113	15	4.2	101
6	0.7	50	16	1.5	102
7	5.0	58	17	5.5	134
8	5.6	142	18	12.0	755
9	3.8	167	19	10.1	1840
10	2.4	32			

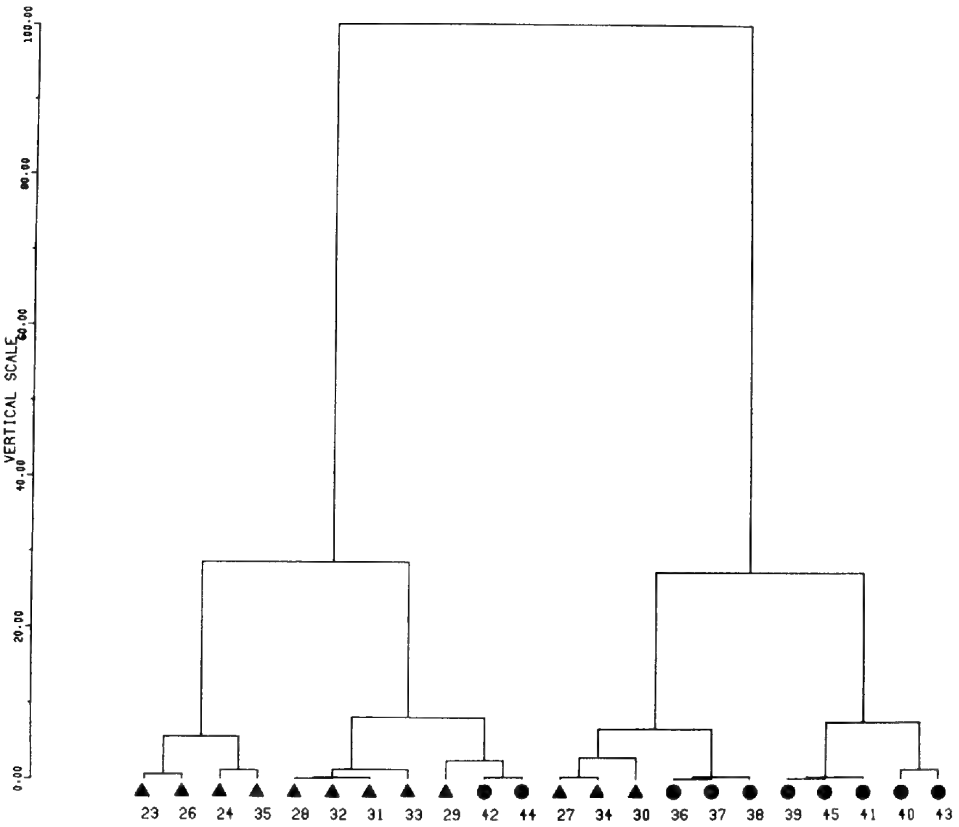


FIGURE 11. Sum of squares agglomeration of Euclidean distance of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters (symbols as in FIGURE 5).

tips of teeth sometimes with small black glands, coriaceous, the upper surface ± dark green, somewhat shiny, scabrous to glabrous, the lower surface glabrous but with tufts of gray (sometimes somewhat rufous) hair in axils of lateral veins and sometimes also along mid-vein. Umbels 2- to 4-flowered, glandular-bracteolate; pedicels glabrous to sparsely long-pilose; anthesis February–March (later northward). Flowers 1.2–1.5 cm in diameter; hypanthia glabrous; calyx lobes ± entire, glabrous; stamens 20, anthers pink(?); styles 4 or 5. Fruit red, fleshy, edible, ripening as early as May in southern part of range and as late as July in North Carolina; pyrenes 4 or 5.

EASTERN MAYHAW.

Common in northern Florida and southern Georgia, continuing up Coastal Plain to about New Bern, North Carolina (see MAP 1). Scarce in northern portion of range. Almost confined to seasonally inundated depressions, including ditches, sink holes, and riversides with fluctuating water levels. Chromosome number and breeding system unknown—possibly a polyploid facultative apomict. See Sargent (1902, *pls. V, VI*), for good illustrations of *Crataegus aestivalis* (as *C. maloides* and *C. luculenta*).

REPRESENTATIVE SPECIMENS EXAMINED. **Alabama.** HOUSTON CO.: 9.8 mi SE of Gordon, *McDaniel 8501* (IBE). **Georgia.** BURKE CO.: in natural pond 7.3 mi W of Waynesboro,

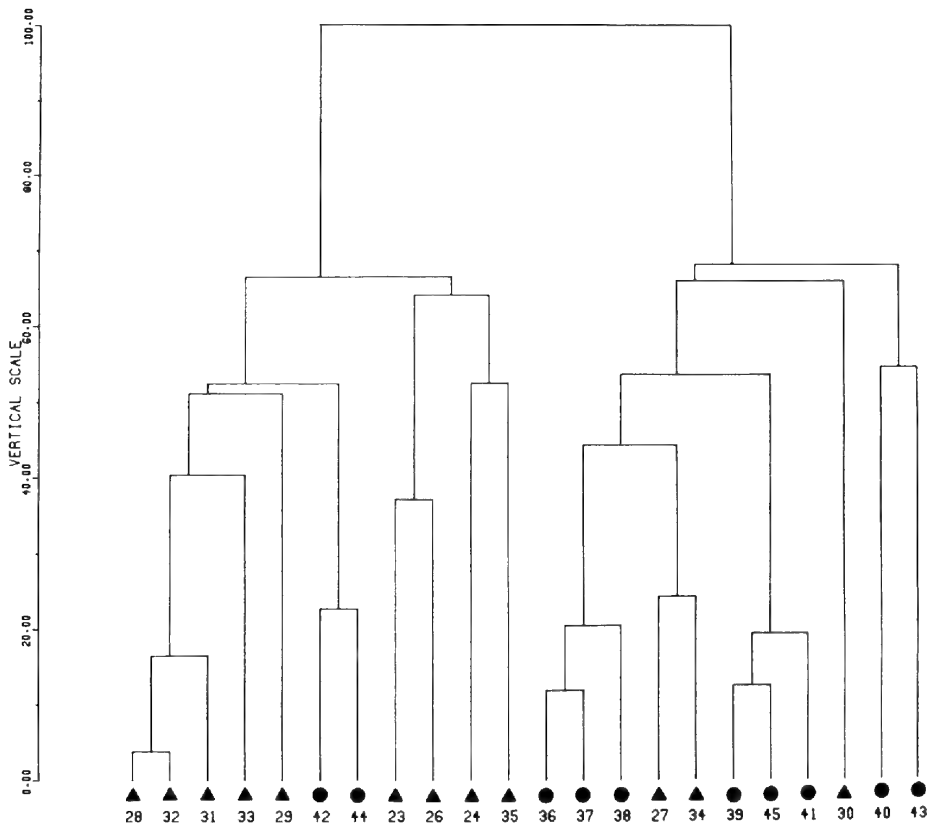


FIGURE 12. Single-link clustering of Euclidean distance of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters (symbols as in FIGURE 5).

W. H. Duncan 22234 (GA, LAF). CHARLTON CO.: Traders Hill, swamp, *Harbison 13963* (TENN); near Folkston, *J. H. Miller 2* (GA); on limestone shelf at edge of Satilla R. in NE part of county, *W. H. Duncan 23298* (GA); on banks of St. Mary's R. just E of St. George, *W. H. Duncan 2066* (GA). TATTNALL CO.: low swampy soil near river, 11 mi, 29 degrees SW of Glennville, *Padgett 262* (GA); THOMAS CO.: ephemeral pond at bottom of slope of pineland, Wade Tract of Tall Timbers, Inc., between Thomasville and Metcalf by Georgia Rte. 122, *Godfrey 80608* (UWO), *80609* (UWO), *80610* (UWO); W side of Georgia Rte. 122, ca. 5 km S of U.S. 319, *J. B. Phipps 5218* (UWO). WARE CO.: low slough area on S side of Satilla R., N of Georgia Power Substation off U.S. hwy. 82, *Faircloth 8164* (GA). **South Carolina.** HORRY CO.: wooded bank of Waccamaw R. at Red Bluff, *C. R. Bell 7738* (USF). **North Carolina.** PENDER CO.: along E channel of Northeast Cape Fear R., ca. 2.5 river mi downstream from Stag Park, *S. W. Leonard & R. J. Davies 7547* (VDB). **Florida.** ALACHUA CO.: near Gainesville, *Murrill s.n.*, 10.iii.1940 (GA, no. *23158*). COLUMBIA CO.: Rice R., *Murrill s.n.*, 9.iii.1940 (FLAS, no. *34598*). FLAGLER CO.: Middle Haw Creek, W of Bunnell, by Florida Rte. 100, *Godfrey 78724* (IBE). GADSDEN CO.: W bank of Ochlocknee R., SE of Havana, *R. J. Wilmont s.n.*, 21.v.1940 (FLAS, no. *35187*). JACKSON CO.: W side of Florida Rte. 271, 16.6 mi N of Sneads (from jct. of U.S. Rte. 90), *Godfrey 80333* (UWO). LEON CO.: W end of Lake Iamonia, *Griscom 21579* (GH); ca. 2 mi S of Talquin Dam, locally common in backwater slough of Ochlocknee R., *McDaniel 7478* (IBE). LIBERTY CO.: *Canby s.n.*, iii.1890 (DOV, no. *4715*). VOLUSIA CO.: low woods bordering Haw Creek, *A. H. Curtiss 6677* (DOV).

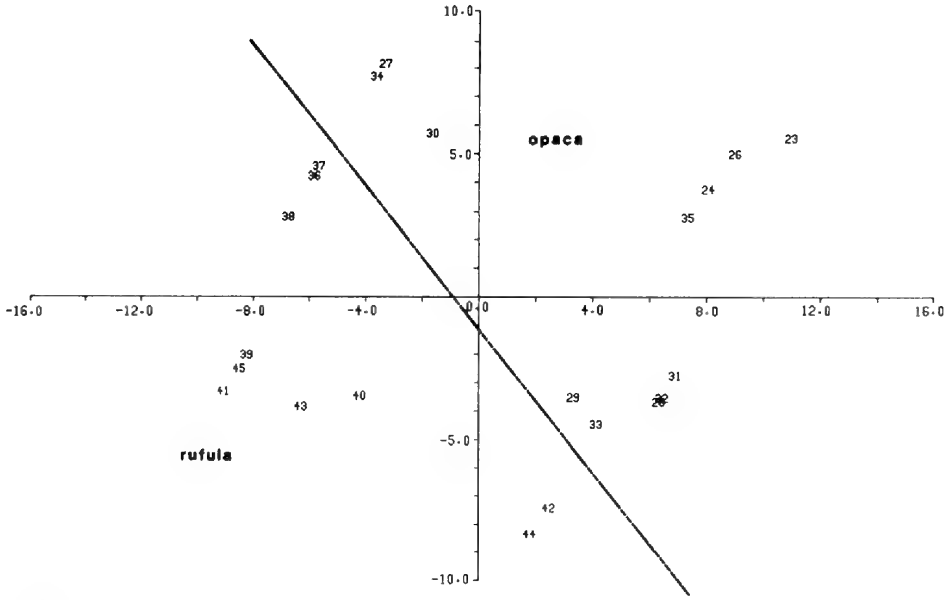
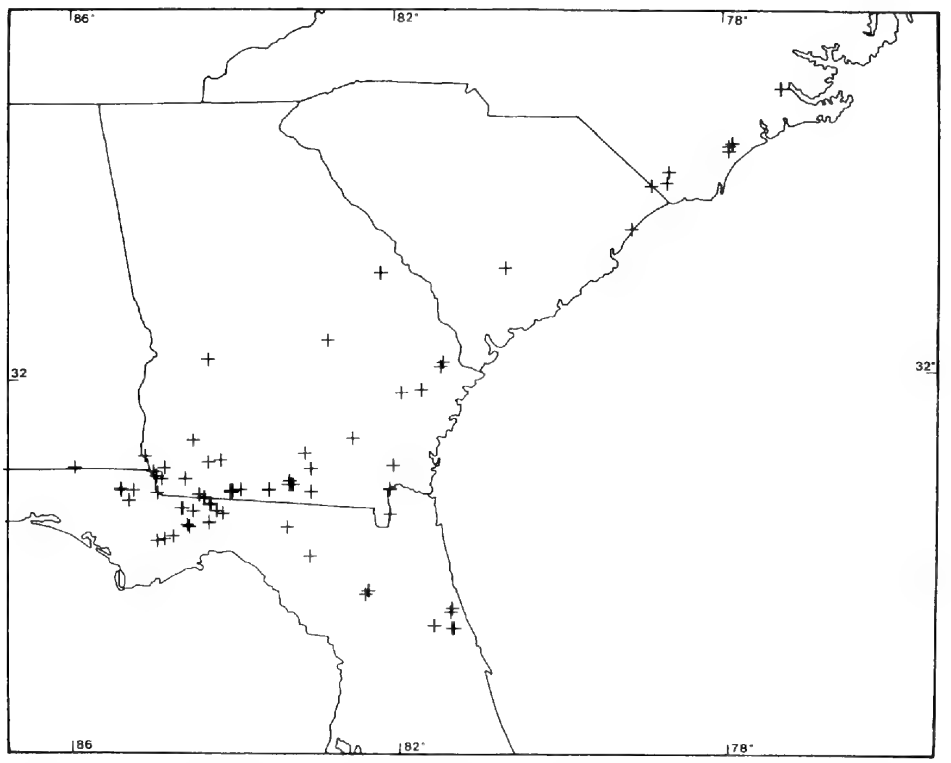


FIGURE 13. PCA of 22 *Crataegus* ser. *Aestivales* OTUs, 6 characters: 23–35 = *C. opaca*, 36–45 = *C. rufula*.



MAP 1. Distribution of *Crataegus aestivalis* based on collated herbarium records.

Torrey and Gray's description of *Crataegus aestivalis,* together with the distribution they ascribed to it, indicates that they included in that species what is now called *C. opaca* Hooker & Arn. Nevertheless, the type location, the original description, and the photograph of a vegetative specimen at BM collected by Walter and possibly *C. aestivalis* (therefore type material) all indicate that the basionym, *Mespilus aestivalis,* must pertain to the plant dealt with here. There is, however, no Walter specimen of *Crataegus aestivalis* in flower or fruit at the British Museum. Likewise, I have been unable to locate Pursh's type of *C. elliptica* (reputedly at BM, OXF) or to access Elliott's material (CHARL) of *C. lucida.* Sargent (1920) thoroughly discussed typification of *C. aestivalis* and presented a convincing argument that these three names represent the same species.

2. **Crataegus opaca** Hooker & Arn. Companion Bot. Mag. **1:** 25. 1835. TYPE: Louisiana, New Orleans, *Drummond 104* (holotype, E[3]). FIGURES 2, 3.

Tree to 8 m or occasionally more; trunk sometimes to 0.3 m in diameter; mature bark flaking; branches medium to dark gray; twigs of current season rufous-tomentose, especially when young; thorns few to moderate in number, 2–4 cm long, stout, straight. Leaves not appearing before flowers and often entirely after anthesis; petiole 4–7 mm long, short rufous-tomentose; blade ± elliptic to lance-elliptic or sometimes broader, 5–7 cm long, gland dotted and unlobed to sinuate lobed at margin (sometimes more deeply and irregularly lobed on vegetative shoots, lobes often broader, margin sometimes obscurely or very shallowly distant-crenate), 5- to 9- (or 10-)nerved, the upper surface scabrate, especially when young, the lower surface rufous-tomentose, especially along veins, occasionally glabrous in old leaves. Umbels 3- to 6-flowered, ± sessile to short stalked, ± glabrous; bracteoles few, oblong-linear, gland-margined, glabrous; anthesis February–March. Flowers 1.25–1.75 cm in diameter; hypanthium glabrous; calyx lobes triangular, 4 mm long, entire to slightly glandular-serrate; petals ca. 7 mm long, white to occasionally pale rose; stamens 20, the anthers 1 mm long, reddish or rose; styles (4 or) 5. Fruit (0.8?–)1.2–1.5 cm in diameter, red, succulent, ripening May–June; pyrenes 4 or 5, shallowly grooved dorsally, with portions of calyx accrescent.

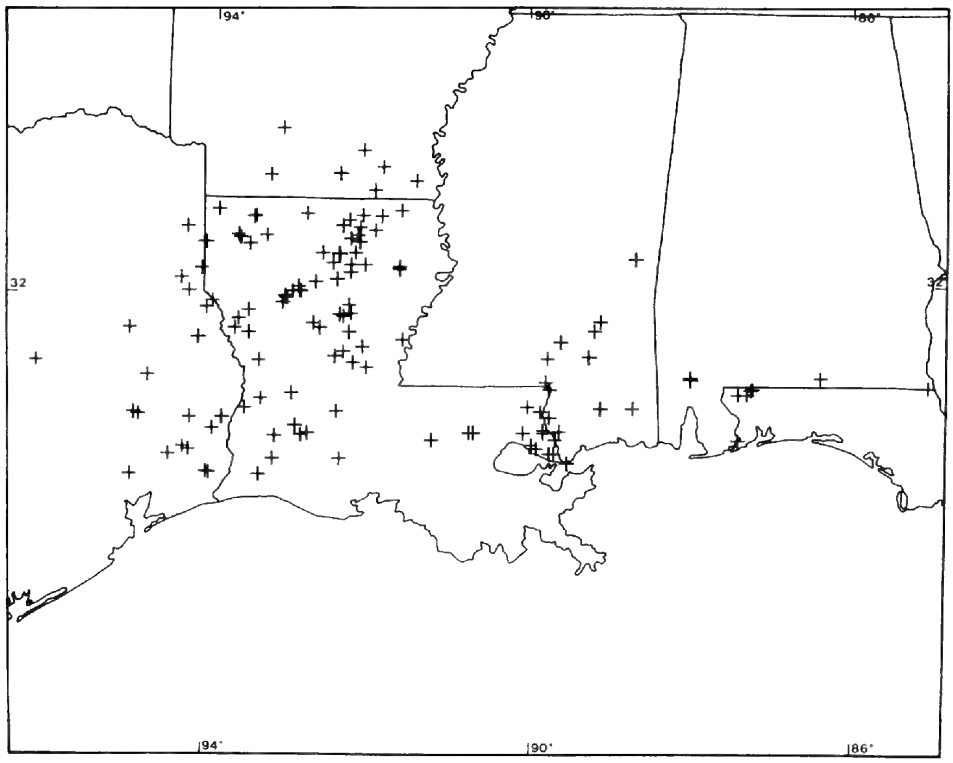
WESTERN MAYHAW.

Eastern Texas to Alabama, most common in Louisiana, apparently rare east of Pearl River (see MAP 2). Chromosome number and breeding system unknown, although possibly a sexual diploid.

Fruit edible and used locally for conserves. Sargent (1890, *pl. CXCII*) illustrated a specimen that is presumably this species under *Crataegus aestivalis.*

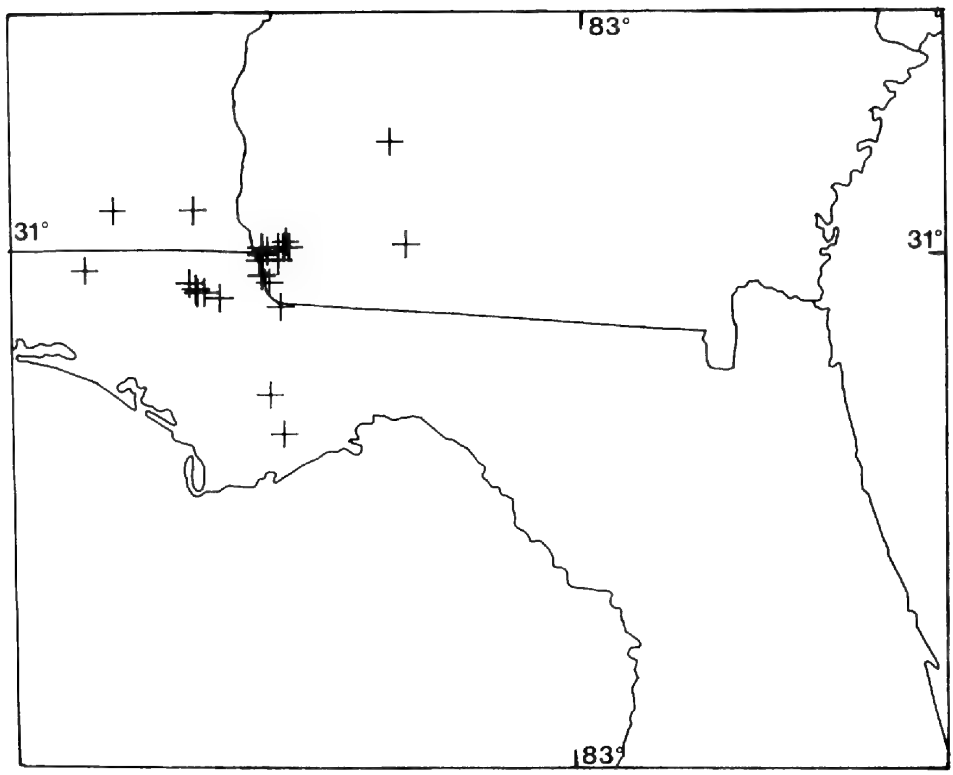
REPRESENTATIVE SPECIMENS EXAMINED. **Texas.** ANGELINA CO.: 2.6 mi SE of Diboll, *Shinners 18200* (SMU). HARRISON CO.: Caddo Lake State Park, W end of park along old abandoned trail, *A. E. Orr 155* (SMU). JASPER CO.: bayou ca. ½ mi E of Neches R., W of Kirbyville, *McVaugh 6834* (SMU). ORANGE CO.: ca. 10 mi E of Beaumont, *C. L. Lundell & A. A. Lundell 10914* (LL, SMU). POLK CO.: in flatwoods ca. 5 mi S of Livingston

[3]The specimen of *Drummond 104* at K is a species of *Prunus.*



MAP 2. Distribution of *Crataegus opaca* based on collated herbarium records.

on Rte. 146, *D. S. Correll 151107* (TEX-LL). TYLER CO.: ca. 1 mi S of Town Bluff, *Whitehouse 22997* (SMU). **Arkansas.** ASHLEY CO.: W of Crossett at Ouachita R. Bridge, water's edge, *D. M. Moore & C. Moore 68141* (UARK). BRADLEY CO.: Johnsonville prairie, 5.9 mi SW of Johnsonville on unnamed county road, *S. Leslie & D. Taylor 94* (UWO). **Louisiana.** ALLEN PARISH: low woods along Barnes Creek, sect. 4, ca. 4 mi SW of Reeve, *Thieret 21896* (DUKE, USLH). BOSSIER PARISH: 3.8–4 mi SE of Benton (by road) from jct. of Louisiana 3 and Bellevue Road, Cypress Black Bayou Reservoir, *Barbour 1109* (LSU). MOREHOUSE PARISH: edge of woods beside Pratt Brake S of Beekman along Louisiana 142, *R. D. Thomas 51378 & P. Pias 734* (NLU); along Morehouse Rd. 2705 just W of Stevenson Fire Tower in Georgia, Pacific Game Management Area, *R. D. Thomas 51380 & P. Pais 736* (NLU). NATCHITOCHES PARISH: Creston, *E. J. Palmer 7024* (NO). OUACHITA PARISH: West Monroe, *Canby et al. 26* (CM, DOV); swampy area beside Louisiana 34 S of Bawcomville, *R. D. Thomas et al. 27538* (NLU); Ark. Road, West Monroe, *Tucker s.n.*, 12.v.1960 (NLU, no. *24968*). ST. TAMMANY PARISH: ca. 2 mi N of Talisheek, *S. Darwin 1320* (IBE, LSU, NO); Honey Is. Swamp, low, wet woods of Carpina, *Sundill 1747* (NO). UNION PARISH: beside Louisiana 2 at DeLoutre Bayou, *Scarbrough s.n.*, 11.v.1969 (NLU, no. *25030*). WASHINGTON PARISH: 5 mi E of Angie, *S. Darwin & Sundill 1255* (NO). WEBSTER PARISH: 2 mi W of Sarepta, *Goldsby s.n.*, 3.v.1971 (NATC, no. *9918*). **Mississippi.** GEORGE CO.: along Red Creek, 5 mi E of Ramsey Springs, *Ray 8119* (USF). JEFFERSON DAVIS CO.: 4 mi NE of Bassfield, *McDaniel 2867* (IBE, UNA). MARION CO.: roadside thicket ca. 7 mi N of Columbia, *M. S. & D. E. Eyles 8319* (DUKE). **Alabama.** COVINGTON CO.: ca. 5 mi N of Florala by U.S. 31, *R. Kral 41875* (VDB). MOBILE CO.: Mount Vernon, *C. Mohr s.n.*, 15.iv (UNA).



MAP 3. Distribution of *Crataegus rufula* based on collated herbarium records.

3. **Crataegus rufula** Sarg. J. Arnold Arbor. **2:** 251. 1920. LECTOTYPE (here designated): Florida, Jackson Co., Cottondale, *Harbison 19* (A).
FIGURE 4.

Shrub to small tree 3–5 m tall, variably thorny; thorns 1–3(–5) cm long, stout at base, tapering, straight. Leaves petiolate; blade elliptic to ovate, 2.5–4.5 cm long, those on rapidly elongating shoots larger, usually proportionately broader than those on short shoots, and sinuate lobed, short-shoot leaves sometimes sinuate lobed, all entire, or barely serrate or crenate in distal ⅓ or ½, glandular-margined, densely white- or rufous-tomentose when young, at maturity scabrous above and densely rufous-tomentose below especially on veins; lateral veins 3 to 5. Umbels 2- to 5-flowered, glabrous to rufous-tomentose, including pedicels, hypanthia, and calyx lobes; anthesis February–March. Flowers 1.5–2.75 mm in diameter; petals to 12 mm long; stamens 20, anthers red; styles (4 or) 5. Fruit a pome, 1 cm in diameter, red, juicy; pyrenes 5, dorsally ribbed.
RUFOUS MAYHAW.

Mainly restricted to the Florida panhandle, adjacent Georgia, and southeastern Alabama (see MAP 3).

REPRESENTATIVE SPECIMENS EXAMINED. **Georgia.** DOUGHERTY CO.: N of R.R. to Milth's just before leaving pasture, Albany, *J.W.G. E3288* (GA). SEMINOLE CO.: 7 mi SW of Donaldsonville by Georgia Rte. 285, just E of jct. with Georgia Rte. 91, *Godfrey 70500* (UWO); in angle formed by jct. of Georgia Rtes. 92 and 285, 7 mi SW of Donaldsonville, *Godfrey 80341* (UWO), *80342* (UWO), *80343* (UWO), *80344* (UWO), *80440* (UWO); 7 mi SW of Donaldsonville, by Georgia Rte. 91 at jct. with road E to Seminole State Park, *Godfrey 80596* (UWO), *80597* (UWO), *80598* (UWO). **Florida.** JACKSON CO.: ponds in pine barrens near Marianna, *A. H. Curtiss 6745* (DOV); to W side of Florida Rte. 271, 16.6 mi N of Sneads (from jct. of U.S. Rte. 90), *Godfrey 80331* (UWO), *80335* (UWO), *80336* (UWO).

Occurring as it does at the exact interface of *Crataegus aestivalis* (more easterly) and *C. opaca* (more westerly), as well as being intermediate in almost all respects between these two species, *C. rufula* represents a presumed hybrid swarm or its descendents, probably with some elements fixed by apomixis. Although in many characters (e.g., the usually sinuate leaf margin) it is more like *C. opaca,* it lacks the characteristic elongate leaves of the latter species. *Crataegus rufula* also tends to intergrade (e.g., in OTU 43) with *C. aestivalis,* with which it is more sympatric. The frequency of *C. aestivalis*–like intermediates could well be accounted for by the fact that pure *C. aestivalis* is reasonably common right up to the *C. rufula* range, while *C. opaca* is very scarce at the interface. Another possibility is that *C. rufula* constitutes a compilospecies in the sense of Harlan and De Wet (1963). Some, but not all, individuals of *C. rufula* have very large flowers.

Crataegus rufula is locally common and is conveniently treated as a species for the purpose of this flora. Detailed cytological, breeding, and morphometric studies are required to clarify its status.

ACKNOWLEDGMENTS

I wish to thank R. K. Godfrey, of Florida State University, Tallahassee, for his generous hospitality and his excellent collections of local ser. *Aestivales* materials, which brought my attention to the dimensions of the *C. rufula* problem. I am also grateful to NSERC of Canada for its operating grant A-1726, under which this work was conducted, and to Susan Laurie-Bourque of Hull, Quebec, for the line drawings.

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INDEX

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Dates of Issue

No. 1 (pp. 1–84) issued 11 January 1988.
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Journal of the Arnold Arboretum *October, 1988*

CONTENTS OF VOLUME 69, NUMBER 4

Volume 69, Number 3, including pages 193–288, was issued 26 July 1988.