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THE GENERA OF CINCHONOIDEAE (RUBIACEAE) IN THE
SOUTHEASTERN UNITED STATES¹

GEORGE K. ROGERS²

The infrafamilial classification of the Rubiaceae is in an unsettled state, with solid answers awaiting accumulation and interpretation of data on some 500 genera. Schumann's system, the only clear, comprehensive one, is followed in the present account. This is not to say that it satisfactorily reflects natural relationships, for it does not—it rests upon heavy-handed application of a few

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Treatments of the first four genera were prepared at the Arnold Arboretum while I held a post-doctoral appointment there. The remainder were prepared at the Missouri Botanical Garden. I owe thanks to the Rubiaceae researchers of St. Louis, who meet occasionally for discussion. This group has broadened my perspective on the family and has been the source of a great deal of factual information. In particular, unpublished documents compiled and distributed by Walter Lewis and Steve Manning were unique references. In addition, John Dwyer's views on *Randia* and information on *Pentodon* from Robert Kral were welcome contributions. Ihsan Al-Shehbaz and Barbara Nimblett helped generously with aspects of the work at the home base in Cambridge, Massachusetts. As always, Carroll Wood supplied information, editorial expertise, guidance, and inspiration. Elizabeth Schmidt and Stephen Spongberg improved the manuscript with their good ideas. The Missouri Botanical Garden provided space and facilities.

The illustrations were drawn by Rachel A. Wheeler (*Cephalanthus*), Dorothy H. Marsh (*Casasia*), and Karen Stoutsenberger (*Hamelia*) from materials prepared by Carroll Wood. The specimens of *Cephalanthus* came from the Arnold Arboretum (Wood) and Louisiana (Joseph Ewan, GH); those of *Casasia* and *Hamelia* from Big Pine Key, Monroe County, Florida (Wood).

²Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166.

characters, and students of the Rubiaceae have since stressed that it breaks apart obvious alliances.

Even Schumann's fundamental division of the Rubiaceae into two subfamilies, the Cinchonoideae and the Rubioideae (Coffeoideae), is based on a single character, the number of ovules in each locule of the ovary (multiple in the former, solitary in the latter). His classification provides, nonetheless, a convenient and useful framework.

The two foremost students of the Rubiaceae since Schumann, Verdcourt (1958 and later works; see especially 1976) and Bremekamp (particularly 1966), have proposed reforms of the infrafamilial classification. Although neither assembled a comprehensive new scheme, both have added new insights, and both have laid out their concepts of the tribes and subfamilies with characterizations and discussion. Further, both have supplied thorough histories of the subject. So that their contributions do not pass ignored, a summary of the various dispositions of our genera in comparison with Schumann's follows.

Bremekamp increased the number of subfamilies from Schumann's two to eight, of which three concern us. He redefined the Rubioideae as members of the Rubiaceae having raphides and generally valvate corollas. With emphasis shifted to these characters (especially the former), the Hedyotideae (including our *Hedyotis* L. sensu lato and *Pentodon* Hochst.) were moved from the Cinchonoideae to the Rubioideae. Also, *Hamelia* Jacq., which has raphides, was transferred along with *Hoffmannia* Sw. from tribe Gardenieae in the Cinchonoideae to the resurrected Hameliaceae DC. in the Rubioideae (see generic treatment).

Bremekamp did not leave the remainder of Schumann's tribe Gardenieae in the Cinchonoideae; instead, he transferred it (containing our *Randia*, *Casasia*, and *Catesbaea*) to the Ixoroideae Raf., a subfamily he composed of tribes showing the "ixoroid" pollination mechanism (pollen deposited on the shaft of the style). My suspicion is that the ixoroid pollination mechanism is too widespread, either by convergence or by persistence from distant common ancestry, to be a reliable character in defining a subfamily of the Rubiaceae. It shows up in *Pentodon*, clearly a member of the Hedyotideae, and in such other families as the Loganiaceae, Campanulaceae, and Compositae. Bremekamp was uncertain of the placement of *Cephalanthus*.

Verdcourt's strong Old World emphasis makes it difficult to apply his ideas to our genera. He recognized three subfamilies, including the Cinchonoideae and the Rubioideae, defined primarily by the presence or absence of raphides. Verdcourt (1958, 1976), like Bremekamp, placed *Hamelia* and our genera of Hedyotideae in the Rubioideae. He departed from Bremekamp and Schumann by merging tribe Condamineeae (containing *Pinckneya*) with the Rondeletieae (DC.) J. D. Hooker & Bentham (Fl. Nigritana, 378. 1849; note earlier authorship than that given by Darwin). Verdcourt agreed with Schumann but disagreed with Bremekamp, placing *Cephalanthus* in the Naucleae and retaining the Gardenieae (minus *Hamelia*) in the Cinchonoideae. Among the authors of interest, he is unique in segregating tribe Catesbaeeae J. D. Hooker from the Gardenieae (see treatment of *Catesbaea*).

To summarize the present state of affairs, in my view the size of the family

Rubiaceae forces botanists concerned with its infrafamilial subunits to subdivide it "from the top down," stressing differences found in a few characters. Much discussion connected with the problem centers around the comparative (not convincingly substantiated) "importance" of various characters for this purpose. Only massive collection of new data and a new, more evolutionary emphasis will eventually allow infrafamilial groups to be built "from the bottom up," buttressed by shared derived similarities.

For those workers interested in determining the correct names of taxa of the Rubiaceae above the rank of genus, S. P. Darwin's thoroughly researched nomenclator for subfamilies, tribes, and subtribes in the family is indispensable.

RUBIACEAE subfam. CINCHONOIDEAE Rafinesque, Ann. Gén. Sci. Phys. 6: 81 (p. 66 in reprint). 1820, "Cinchonaria."

Trees or shrubs (except *Hedyotis* sensu lato and *Pentodon*) with usually opposite, sometimes whorled or fascicled, leaves. Stipules interpetiolar, generally with 1 (sometimes bifid) lobe between adjacent petiole bases (to fimbriate in *Hedyotis* and *Pentodon*, becoming shredded in *Randia*), usually bearing colleters on the adaxial side. Flowers pentamerous or tetramerous, with tubular corollas. Ovary inferior, usually bilocular (but with up to 5 locules in *Hamelia*; *Casasia* unilocular but appearing bi- or trilocular), the locules generally multiovular (uniovular in *Cephalanthus*; *Randia* sometimes with a single seed in the fruit). TYPE GENUS: *Cinchona* L.

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KEY TO THE GENERA OF CINCHONOIDEAE IN THE SOUTHEASTERN UNITED STATES

- A. Plants herbs or infrequently subshrubs; raphides present; placentae peltate; fruits dry and less than 0.5 cm long.

- B. Flowers pentamerous; placentae bilobed apically; plants hygrophilous and fleshy. 3. *Pentodon*.
- B. Flowers tetramerous; placentae entire apically; plants not hygrophilous. 2. *Hedyotis*.
- A. Plants shrubs or trees; raphides absent (except in *Hamelia*); placentae usually axile, sometimes parietal (nearly peltate in *Exostema*), or the ovules pendulous; fruits fleshy and/or over 0.5 cm long.
 - C. Flowers and fruits in globose heads; locules of ovary uniovular. 5. *Cephalanthus*.
 - C. Flowers and fruits not in globose heads; locules of ovary usually multiovular (*Randia* sometimes with only 1 seed in a fruit).
 - D. Plants armed with paired spines; leaves largely in fascicles clustered along stems.
 - E. Flowers mostly tetramerous; aestivation of corolla valvate; stamens inserted at base of corolla; fruit ca. 5 mm long. 9. *Catesbaea*.
 - E. Flowers pentamerous; aestivation of corolla imbricate-contorted; anthers inserted in throat of corolla; fruit ca. 10 mm long. 6. *Randia*.
 - D. Plants unarmed; leaves decussate, whorled, or in terminal clusters.
 - F. Fruits dehiscent; seeds winged; anthers exerted.
 - G. Calyx lobes more or less uniform; seeds vertical or nearly so; flowers solitary. 4. *Exostema*.
 - G. Some calyx lobes expanded into leaflike pink to white "flags"; seeds horizontal or oblique; flowers in compound cymes. ... 1. *Pinckneya*.
 - F. Fruits indehiscent; seeds unwinged; anthers included or partly exerted.
 - H. Flowers perfect; corolla red or orange, lobes a small fraction of length of tube; ovary usually 5-locular; plants pubescent; raphides present. 8. *Hamelia*.
 - H. Flowers imperfect, plants dioecious; corolla white, lobes approximately as long as tube; ovary unilocular (or appearing bilocular); plants mostly glabrous; raphides absent. 7. *Casasia*.

Tribe CONDAMINEAE Bentham & Hooker, Gen. Pl. 2: 8, 12. 1873.

1. *Pinckneya* A. Michaux, Fl. Bor. Am. 1: 103. pl. 13. 1803.

Shrubs to small trees, sometimes in colonies from root suckers. Leaves deciduous, opposite, the blades lanceolate or ovate to usually nearly elliptic, obtuse or rounded to caudate at the base, acuminate or less often acute at the apex, lateral nerves usually rather arcuate-ascending, the petiole and midrib often reddish (color fading in pressed specimens); stipules narrowly deltoid to lanceolate with acuminate apices, acting as bud scales, caducous, bearing col-leters adaxially toward the base; abaxial side of blades of young leaves and the petioles, young stems, inflorescence axes, ovaries, calyces, and corollas usually abundantly provided with variably kinked to straight and spreading or parallel-appressed, tawny to almost white, incompletely septate and nonseptate, uni-seriate trichomes; adaxial side of leaf blades often strigose to glabrate. Inflorescence a pyramidal or hemispheric compound cyme with a straight central axis, the lateral units sometimes repeating the form of the main axis, the branching opposite or distal pedicels alternate; distal bracts linear or greatly expanded to resemble the flaglike sepals, the basal bracts often intergrading with foliage leaves. Flowers fundamentally pentamerous, nearly actinomorphic

(except for the flaglike calyx lobes), fragrant. Calyx lobes briefly connate above the ovary, the nonflaglike lobes ca. $\frac{1}{4}$ – $\frac{3}{4}$ the length of the corolla and subulate or linear, or somewhat broadened toward the base, pink or partly green, in certain flowers 1–3 (or all 5) calyx lobes clawed and with greatly expanded blade(s) much exceeding the corolla in length and breadth, these resembling foliage leaves in shape, but smaller and pink to white, then sometimes with reddish borders. Corolla creamy or greenish yellow to pink, mottled with (pink or) purple or brown, with a long, narrow, cylindrical or slightly flared tube and (4 or) 5 (or 6) ligulate or narrowly elliptic, reflexed lobes about $\frac{1}{4}$ – $\frac{1}{2}$ the length of the tube, the lobes imbricate or some valvate, with particularly coarse trichomes within. Stamens exserted, the filiform filaments inserted near the base of the tube in a pilose ring, anthers dorsifixed, sagittate, elliptic-oblong or broadened below the middle; pollen grains tricolpate and reticulate (*vide* Verdcourt). Ovary surmounted by an epigynous disc, containing numerous ovules arranged more or less in 2 ranks along an axile placenta in each locule; style filiform, the stigma exserted and barely divided into 2 broad lobes. Capsules persistent, slightly longer than broad to slightly broader than long, lightly compressed perpendicular to the septum (this often appearing as a sunken vertical line), predominantly loculicidal, speckled with lenticels, the endocarp made up of light-colored fibrous cells, the apical perianth scar a broad ring around a sunken center. Seeds waferlike, with a broad wing around the embryo (except often at the hilum), wedge or fan shaped, the hilum opposite the broadest edge, the surface area considerably less than cross-sectional area of the locule, stacked horizontally or obliquely along a broadened placenta raised on a ridge running nearly the entire length of the middle of the septum (ridge and placenta T-shaped in transverse aspect, the seeds attached at various points across the head of the T), surface of seeds reticulate from outlines of testa cells, these with reticulate, straplike reinforcements on the outer walls. Embryo in a tough sac (presumably endosperm), spatulate or with cotyledons very slightly auriculate, the radicle about as long as cotyledons or shorter. TYPE SPECIES: *Pinckneya bracteata* (Bartram) Raf. (*P. pubens* Michx.). (Name commemorating General Charles Cotesworth Pinckney, 1746–1825, South Carolinian, veteran of the American Revolutionary War, statesman, presidential candidate, and benefactor of André Michaux and his son François-André.)—GEORGIA BARK, FEVER TREE, POSSUM POD.

A monotypic genus confined to the two southernmost counties of South Carolina, the southern half of Georgia (including the Okefenokee Swamp), and scattered localities in northeastern to northwestern Florida (several counties from Nassau to Volusia, west to Gulf and Jackson), but not in the western portion of the Florida Panhandle (see Little, 1977, for map). The distribution lies mostly, but by no means overwhelmingly, in the Altamaha Grit region of Georgia and is probably largely determined by edaphic factors.

Pinckneya is encountered in low, sandy, wet situations, especially at margins of swamps, stream banks, and low spots in pine barrens. According to Taylor and Uphof (independently?), it thrives best on river hummocks, where its trunk is periodically submerged.

The flowers open sequentially (possibly rarely as early as late April) through May and June (to July).

For explanation of the displacement of the well-known name *Pinckneya pubens* Michx. by *P. bracteata*, consult Merrill and Wilbur.

The most salient characteristic of these shrubs or small trees is that on many flowers one or more calyx lobes are expanded into large pink or sometimes white "flags." This occurs frequently, but sporadically, in the Rubiaceae, although not in any of the other genera indigenous to our area. Kurz & Godfrey remarked that it is "one of the most spectacularly beautiful [trees or shrubs] occurring in northern Florida." The less conspicuous, typically greenish yellow corollas are marked with purple or brown and have reflexed, internally pubescent lobes on the long tubes. The slightly flattened loculicidal capsules persist for long periods on the branches; upon opening they reveal innumerable waferlike seeds stacked horizontally in the two locules. Interpetiolar stipules with abundant colleters on the adaxial side help to distinguish *Pinckneya* from nonrubiaceous genera. The young stems, inflorescence axes, corollas, and sometimes foliage are typically conspicuously pubescent. Midribs of living leaves tend to be reddish.

Most botanists place *Pinckneya* either in the tribe Condamineae or in infrafamilial groups named differently but consistent with the same general circle of affinity. Shared tribal or subfamilial characteristics include absence of raphides, presence of endosperm in the seeds, incompletely septate uniseriate hairs, mostly entire stipules, often "pitted" testa cells, woody habit, and—chiefly—capsular fruits containing numerous horizontal seeds. While most members of the tribe have valvate corolla lobes, an attribute sometimes ascribed to *Pinckneya*, I found the lobes to be imbricate or partly valvate in buds from the one collection available for dissection.

Among the genera of the Condamineae, *Pogonopus* Klotzsch emerges from the literature as likely the closest relative for *Pinckneya*. Bentham & Hooker erected the subtribe "Pinkneyeae" for the pair, and Baillon merged the two genera. Their most conspicuous similarity, expanded flaglike sepals, is too widespread in the Rubiaceae to stand as strong evidence for relationship, yet *Pinckneya* and *Pogonopus* agree further in shape and size of corollas (the lobes are reflexed in *Pinckneya* only), position of anthers and stigmas, shape of capsules (although much smaller in *Pogonopus*), and indument. Their habit and leaves are similar but do not set them apart from other arborescent Rubiaceae. Beyond the differences indicated parenthetically above, *Pogonopus* has smaller seeds less drawn out marginally into wings and has stamens inserted higher in the corolla tube, although the latter difference is hardly appreciable when *Pogonopus speciosus* (Jacq.) K. Schum. is compared with *Pinckneya*. I found the basal portion of the corolla tube of flowers of *Pogonopus speciosus* and *P. tubulosus* (DC.) K. Schum. to be thickened into a woody cylinder, a feature not found in *Pinckneya*. (See Oersted for an illustrated floral dissection of *P. speciosus*, as *P. exsertus*.) In contrast with authors who list internally glabrous corolla lobes in *Pogonopus* as a distinction from *Pinckneya*, I encountered internally pubescent lobes in both genera.

Koek-Noorman & Hogeweg, in an investigation of wood anatomy of the

Condamineae, evidently perceived no particular connection between *Pinckneya* and *Pogonopus*. They called *Pinckneya* "exceptional" among its relatives in having semi-ring-porous wood with tangential pore chains and concentric parenchyma bands. (At least the first of these exceptional features is probably due to the temperate distribution of the genus, which is in itself very unusual among woody Rubiaceae.)

A second possible close relative is the newly described monotypic Brazilian genus *Kerianthera* Kirkbride. Kirkbride held the new genus to be most similar phenetically within the Condamineae to *Pinckneya*. He listed their shared features as foliar calyx lobes, dense pubescence on the inner faces of the corolla lobes, and winged seeds but separated *Kerianthera* from both *Pogonopus* and *Pinckneya* by its "4-merous calyx, 7-8-merous corolla, stamens separating from the apex of the corolla tube, anthers with approximately 300 locelli, septicidal capsules, and seeds irregularly biwinged" (p. 109).

It is doubtful that frequent mention of *Pinckneya* in old botanical-medical literature as a remedy for malaria has any meaningful basis. Cornatzer and colleagues related secondhand that pharmaceutical tests on extracts from *Pinckneya* revealed no antimalarial effects on infected canaries. Application of *Pinckneya* against malaria probably grew out of the perception of its relationship to *Cinchona* L., the source of the familiar antimalarial alkaloid quinine. Whether alkaloids form in *Pinckneya* remains a debatable question: Sumerford and Naudain tried and failed to detect any, but Wall and colleagues indicated the presence of at least one unnamed alkaloid. Further work is desirable.

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- Under subfamily references see BAILLON; BENTHAM & HOOKER; KOEK-NOORMAN & HOGEWEG; LITTLE (1977); SCHUMANN; and VERDCOURT (1958).
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Tribe HEDYOTIDEAE DC. Prodromus **4**: 342, 401. 1830.

2. *Hedyotis* Linnaeus, Sp. Pl. **1**: 101. 1753; Gen. Pl. ed. 5. 44. 1754.

Annual or perennial, delicate to coarse, prostrate to stiffly erect herbs or weak subshrubs [or shrubs], highly variable in habit, sometimes rosette forming,

with 1 or few delicate ascending axes, these (infrequently) unbranched to (frequently) highly branched throughout, or extensively branched at base and scoparioid, axillary growth strongly developed and often overtopping terminal growth, the branching frequently widely divergent and symmetrical. Stems winged or angled, often square, occasionally with adventitious roots when procumbent. Roots thick and woody or fasciculate. Plants usually with conspicuous raphide bundles, and with stems, leaves, and calyces pilose to glabrous. Leaves petiolate or sessile, opposite [or fasciculate or whorled], (frequently) nearly linear to (infrequently) broader than long, commonly more or less narrowly elliptic, entire or scabrous around the margins, infrequently cordate basally; stipules interpetiolar, membranaceous, emarginate or bilobed to deltoid or rounded, or frequently fimbriate, with multicellular glandular heads either adaxial or marginal. Flowers on long, threadlike peduncles or pedicels to sessile, terminal or axillary, solitary or, more often, in fundamentally cymose but highly variable inflorescences, these (usually) compound dichasial, sometimes simple dichasial or partly monochasial, lax and uncrowded to fasciculate, then sometimes tightly clustered into hemispheric heads or pseudoumbellate, flowering axes often between pseudodichotomous branches or forming pseudodichotomies with other axes. Flowers tetramerous, homostylous, heterostylous, or cleistogamous. Calyx lobes separate to top of ovary or briefly connate, usually deltoid or elliptic to subulate, exceptionally with claw and limb. Corolla white or greenish, or blue with a yellow or reddish eye, or pink, or variably purplish, extremely variable in length, usually pubescent within, the tube obsolete or very nearly so to several times longer than calyx, abruptly expanded at the level of the anthers or not expanded; in species with well-developed corolla tubes the corolla most often salverform to funnelform or sometimes obconical, the lobes ca. $\frac{1}{2}$ as long as tube to much longer, spreading or erect, variable in shape. Anthers included or exserted, sessile or on epipetalous filaments, fusiform to orbicular, dorsifixed; pollen grains 3- or 4-colporate, reticulate. Ovary inferior, each of the 2 locules with a peltate placenta bearing numerous reportedly hemianatropous or anatropous ovules; stigmatic lobes 2, included or exserted, long and threadlike to short and stubby, nearly sessile or on a long, filiform style. Fruit a capsule usually compressed perpendicular to the generally sunken septum, much broader than long to cuneiform, often apically emarginate, inferior to almost superior, usually conspicuously belted by calyx sinuses and/or corolla scar, adorned with persistent calyx lobes, primarily loculicidally dehiscent but not rarely also septicidal; dehiscence usually restricted to the apex (but sometimes indehiscent); seeds numerous, minute, rugose to fairly smooth, dark, subglobose to angular or flattened, containing initially nuclear [or exceptionally cellular] endosperm. Megagametophyte (embryo sac) of the *Polygonum* type. (Including *Oldenlandia* L., *Houstonia* L.) LECTOTYPE SPECIES: *H. Auricularia* L. (discussion in text). (Name from Greek, *hedys*, sweet, and *otos*, ear, in reference to habit of plants; see Linnaeus, *Philosophia Bot.* 179. 1751.)

A vaguely circumscribed, polymorphic genus, possibly with 400 species when defined broadly, almost worldwide in warm regions and with extensions into temperate areas, although nearly absent from Europe and the Soviet Union;

present in Australia, Asia (including Japan and the Malay Archipelago), the Middle East (very poorly represented), almost the entire length of Africa, and the Americas from central Argentina to southern Canada. Roughly 60 species occur in the New World, about 50 of them on mainland North America and approximately 30 in the continental United States, with about two-thirds of these reaching the range of the Generic Flora. Most North American species belong to the group often recognized as the genus *Houstonia*, and with a few exceptions, the West Indian and Central and South American species belong to the group often recognized as the genus *Oldenlandia*.

The interrelationships and taxonomic status of *Hedyotis*, *Houstonia*, *Oldenlandia*, and a number of additional extralimital genera have been controversial for centuries and remain inadequately investigated, especially from a worldwide perspective. The disparate circumscriptions and diagnostic characteristics given by different authors cloud the usage of all three names and make it impossible to characterize the segregate genera crisply. The following sketch comes from the literature (see especially Gray, 1860; Lewis, 1961). It must be stressed that the validity of the distinctions changes with the varying concepts of the groups, that much of the variation is continuous, that most of the distinctions rest upon inadequate sampling, and that exceptions and overlap abound.

Oldenlandia sensu stricto is variously estimated to have from 80 to around 300 species, depending on its delimitation when recognized as a genus. Its distribution is almost worldwide in warm regions; it is best represented in the Old World tropics, with a center of diversity in Africa (see Bremekamp, 1952, for a revision of African species; also see Lewis, 1965, under subfamily references). About 15 species are distributed in America from the southern limit given above for *Hedyotis* to New York (*H. uniflora* (L.) Lam.). *Hedyotis corymbosa* (L.) Lam., *H. lancifolia* Schum., and *H. herbacea* L. are Old World species reported as weeds scattered in the American tropics. No fewer than three endemic species have been named from Cuba (see Alain). Five or six species (listed below) are found in the continental United States, all of them reaching the area of the Generic Flora.

Tendencies toward a slender, herbaceous habit, narrow leaf blades, homostylous flowers (for a list of 39 exceptions, see Bahadur, 1963), short corolla tubes, hemispheric placentae partitioned and sessile or inconspicuously stalked from the center of the septum (vs. placentae of irregular shape and stalked from base of septum in other species of *Hedyotis*, according to Hayden), completely inferior ovaries, thin, loculicidal capsules, and numerous tiny, angled or nearly spherical seeds lacking hilar ridges and containing fleshy endosperm have been set forth as distinctive features of *Oldenlandia*. (Hayden (p. 21) rejected the endosperm character as "completely useless.")

Houstonia comprises about 40 species nearly limited to North America; a few of them are rare and possibly introduced in the West Indies, and *H. serpyllacea* Schlecht. thrives in Guatemala. Roughly half the species reach the continental United States, and slightly over half of these occur in the area of the Generic Flora. The others are confined to the Southwestern States. Three species extend from the Southeast as far north as southern Canada, with the

natural northern limit being about 54 degrees north latitude (see Scoggan). North of our range, Carr described from southwestern Virginia *Houstonia setiscaphia*, which Terrell (1959; also see Uttal) reduced to synonymy with *Houstonia canadensis* Willd. ex Roemer & Schultes (*Hedyotis canadensis* (Willd. ex Roemer & Schultes) Fosb.).

Species of *Houstonia* tend to have an herbaceous habit, comparatively wide leaf blades, heterostylous flowers, long corolla tubes, partly superior, fairly thin, loculicidal capsules, and relatively few, large seeds flattened parallel to the placenta, these concave toward their peltate attachments, often with hilar ridges, and containing corneous endosperm. Fosberg (1941, 1954), Fosberg & Terrell, Greenman, Lewis (most papers cited here), Lewis & Terrell, Shinnars (1949), Standley (1918), Terrell (most cited papers), Terrell and colleagues, and Yelton, among others, have studied the taxonomy and related aspects of *Houstonia*.

Potentially of interest in connection with the relationship between *Houstonia* and *Oldenlandia*, the two studied species of *Houstonia* have "naked" or "undifferentiated" ovules not showing an obvious integument separated from a nucellus. Homologies of the exposed layer are not certain (cf. Lloyd; Fagerlind; Roth & Lindorf). Numerous sources (Fagerlind; Siddiqui & Siddiqui; Farooq, 1953, 1958; Farooq & Inamuddin; Raghavan & Rangaswamy; Rao & Babu; Shivaramaiah & Rajan; Shivaramaiah & Rao), on the other hand, agree that species of *Oldenlandia* have ovules with one integument and a reduced nucellus of one or a few cells. More study in *Houstonia* is needed before the difference can be given much taxonomic weight.

Hedyotis sensu stricto, comprising over a hundred species restricted to warm Asia, is ordinarily more woody and shrubby than the two preceding "potential" genera. Additional characteristics are fimbriate stipular lobes, axillary inflorescences, short corollas, sometimes hard, thick, indehiscent or septicidal fruits, and variably shaped (but not concave) seeds. Sinuses between the persistent calyx lobes on the capsules have been said to be narrower than in *Oldenlandia*.

The principal proponent of maintaining all three genera as distinct is Terrell, whose conclusions (1975b) are given credence by his study of a broad spectrum of herbarium specimens, mostly from the New World. He pointed out that *Oldenlandia* and *Houstonia* differ in base chromosome numbers, except in morphologically divergent species. His comparison of type species of the three groups does demonstrate a level of variation consistent with the recognition of three genera but leaves the question of intermediates untouched. (Note, as explained below, that Terrell and I accept different lectotype species for *Hedyotis*.) Subdividing the assemblage into three or more genera requires a willingness to draw rather arbitrary lines to break up a large, awkward, heterogeneous assemblage. Verdcourt (1976) indicated that the cumbersome nature of the complex and its heterogeneity justified partitioning it into multiple genera.

With some trepidation I interpret the case for a broad view of *Hedyotis* as slightly more convincing. In 1961 Lewis (p. 221) concluded with detailed documentation that "no character currently in use" distinguishes *Houstonia* from *Oldenlandia* and added that admittedly incomplete cytological evidence favors the union. His efforts focused chiefly on American species, and he

appears to have had mixed feelings about the status of species from the Old World (see pp. 217 and 221 (footnote)). By incorporating the lectotype species of *Oldenlandia*, *Hedyotis corymbosa*, under *Hedyotis*, he made it necessary to regard *Oldenlandia* as a name in synonymy, although later (1964) he separated *O. corymbosa* from *Hedyotis* and recognized *Oldenlandia* as a genus. Along with Terrell and others, he coauthored a paper in 1986 explicitly holding *Oldenlandia* to be distinct (but see p. 113 for doubts).

Lewis cited palynological evidence in 1965 to support joining *Houstonia* with *Hedyotis*. Further, Fosberg (1937, 1941, 1943b, 1954; Fosberg & Terrell), stressing that the differences are weak and/or break down, followed by Shinnars (1949), has maintained that *Oldenlandia*, *Houstonia*, and *Hedyotis* are insufficiently distinct to stand separately, a position that I find especially convincing in view of the geographic breadth of the sampling that stands behind it. McVaugh (p. 160) dismissed the differences between *Hedyotis* and *Houstonia* as evidently "largely traditional rather than morphological."

Since all three generic names have equal priority, the name to be adopted for the genus encompassing the trio depends on the choices made by the earliest authors to unite them. Lamarck selected *Hedyotis* over *Oldenlandia* in 1792, and Kunth likewise chose *Hedyotis* in 1820 upon placing *Houstonia* in synonymy.

Encircled by a crowd of potentially separate genera, mostly from the Old World, *Hedyotis* is not a sharply defined unit, even containing both of our potential segregates, and cannot be readily characterized in a universally acceptable manner. Fosberg (1943b) listed the attributes of the genus taken broadly. The following enumeration of characters is based mostly upon Fosberg's. *Hedyotis sensu lato* has tetramerous flowers with valvate corollas and equal calyx lobes; stigmatic lobes or branches receptive ventrally; expanded, fleshy, peltate placentae; and capsular or dry indehiscent fruits moderately flattened and with sclerified endocarps. The numerous seeds are often inserted peltately or are taller than broad and are neither imbricate nor horizontal. They lack lateral wings, except for thin edges at the angles. For a discussion of the position of *Oldenlandia* among its African relatives, see Bremekamp (1952).

Hedyotis and *Pentodon* are our representatives of the sizable tribe Hedyotideae (for comparison see *Pentodon*). Bremekamp (1966) and Verdcourt (1976) differed in their characterizations of the tribe, although they agreed that members usually have bilocular ovaries containing numerous ovules. Bremekamp further characterized the tribe as having valvate corolla lobes, peltate placentae inserted at the middle of the septum (Verdcourt said at the base), relatively thin testa cells, and nonconnivant anthers opening by slits. Verdcourt included capsular fruits. (See introduction for remarks on the position of the Hedyotideae.)

A handful of species in our area and several others from outside of it have been included in *Anotis* DC. (or *Anotis* auct.), which Lewis (1966b) determined to be an unnatural assemblage containing American species better placed in *Hedyotis*.

In 1962 and 1965 Lewis developed a phylogenetic hypothesis for five informal subgroups of subg. *HOUSTONIA* in North America, taking into consid-

eration chromosome numbers, apertural fine structure in pollen grains, distributions, and relative levels of advancement as judged from morphological characters. Soon thereafter, Hayden added characters from seed coats. The trunk of Lewis's phylogenetic tree (1965, p. 263) culminates in "Group 2," having the base chromosome number of $x = 11$, a widespread number among Rubiaceae, and thus thought likely to have remained unchanged from the original stock of the subgenus. "Group 2" is confined to southwestern North America, the most likely port of entry and hub of radiation from the American tropics.

Lewis (1962) attributed the level of morphological specialization lower than that of "Group 2" to "Group 1," hypothetically isolated by ancient climatic changes to Baja California, an area possibly "not requiring major adaptations" (1962, p. 864). He went on in 1965 to interpret the pollen of "Group 1" as likewise least specialized and probably relictually similar to pollen in other subgenera of *Hedyotis* and other genera of Hedyotideae. If Lewis is correct, the base chromosome number of $x = 13$ in "Group 1" reflects an aneuploid climb from the ancestral $x = 11$.

An apparent descending aneuploid series along with presumed morphological and palynological specialization in the species toward the end of the series led Lewis to derive "Group 3" ($x = 11-9$), found in the United States and Mexico, from the stem of "Group 2," and "Group 5" ($x = 7, 8$) from the stem of "Group 3." At first glance, the eastern North American "Group 4" might be assumed to be closely related to "Group 5" since the base chromosome number of $x = 6$ (as counted by Lewis) in "Group 4" suggests the next step of the descending aneuploid sequence, but the seemingly unspecialized gross morphology, seeds, and comparatively large chromosomes observed in "Group 4" contradict such a position. In 1965, Lewis used pollen structure to link "Group 4" to "Group 3," and I infer support for this from Hayden.

In 1986 Terrell, Lewis, Robinson, & Nowicke reevaluated species relationships within *Houstonia*, using mostly characters from seed morphology, chromosome numbers, and pollen (with special attention to ora). They set up a dozen "species-groups," seven of which consist of only one or two species. The others correspond roughly to Lewis's groups 1-5, although there were several differences in membership, and the authors of the 1986 paper did not formally connect the new groups with the old. They did conclude that the new groups, except for the intermediate "*H. nigricans* group," fall into two "basic series." To paraphrase their summary, one series (not a formal nomenclatural series) has a haploid chromosome number of $n = 13$ or more (vs. $n = 11$ or less), ellipsoid or sublenticular noncrateriform (vs. crateriform) seeds, and colpate pollen with the nexine merely thin in the equatorial portion of the aperture (vs. grains colpate or the ora with thickened margins). They deferred making taxonomic changes until more data were gathered.

Examining 116 collections from the *Hedyotis purpurea* and *H. caerulea* "groups," Lewis & Terrell came across frequent intraspecific euploid variation in ploidy level but very little intraspecific aneuploidy. In two species the polyploids were separated geographically from the diploids and appeared to be colonizers—no marked geographic separation between the ploidy levels was

detected in the remaining species. The authors could not distinguish individuals with different ploidy levels morphologically, which led them to attribute multiplication of chromosome sets to autopolyploidy rather than allopolyploidy, even though meiosis was mostly normal. Variability in chromosome number seemed to be connected with heterostyly and a perennial habit.

Divergent generic concepts have contributed to the profusion of names of species and infraspecific taxa recorded as occurring in the range of the Generic Flora. Beyond the problem of species and their varieties appearing under multiple generic names, botanists have achieved so little agreement concerning ranks, definitions, and names of taxa in our area that the most recent revision covering our species (by Standley, 1918) is obsolete, and subsequent sources disconcertingly contradictory. Therefore, a complete list of the species in the Southeast is currently impossible. The summary that follows rests heavily on the work of Fosberg, Lewis, and Terrell. (It is based entirely on literature—I have conducted no comparative study at the species level.) Full synonymy and consideration of questionable species lie beyond the scope of the present effort.

Subgenus OLDENLANDIA (L.) Fosb. (not accepted here as validly published by Torrey & Gray) includes in our area *Hedyotis Boscii* DC., $n = 18$; *H. callitrichoides* (Griseb.) Lewis, $n = 11$, also in Africa, probably as an introduction from the New World tropics; *H. corymbosa*, $n = 9, 18, 27$; *H. Salzmannii* (DC.) Steudel (*Oldenlandia thesiifolia* (St.-Hil.) K. Schum., introduced from South America; see Fosberg & Terrell), $n = 15$; and *H. uniflora* (including *H. fasciculata* Bertol. or not), $n = 18, 36$.

Subgenus HOUSTONIA (L.) A. Gray (Man. ed. 1. 180. 1848, see Brizicky) (subg. *Edrisia* (Raf.) Lewis³) corresponds to *Houstonia*, if recognized at the generic level, and as discussed above, has been broken down into informal subgroups.

“Group 3” in subg. *Houstonia* is represented by *H. nigricans* (Lam.) Fosb. (*Houstonia angustifolia* Michx.; see Fosberg, 1954, and Long & Lakela), $n = 9$ (10).

Subgenus HOUSTONIA, Group 4, is the *Hedyotis* or *Houstonia purpurea* “group” revised by Terrell (1959), who remarked on a high percentage of intergradation and geographic variation involving every species. Terrell suspected hybridization and introgression to have played significant roles in producing the pattern of variation; pairs of species seemed to interbreed at some places but not at others. In connection with the probable hybridization, it is of interest to note that Lewis (1962) encountered almost uniformly normal meiosis in his cytological survey of the genus in North America, and Fosberg (1943b, p. 15) described hybridization as “little evident” among Hawaiian species, despite “tremendous evolutionary activity.” Most species of the *H. purpurea* group have polyploid races in addition to diploids (Lewis & Terrell). Terrell took a

³Upon publishing subgenera in *Houstonia*, Rafinesque (Ann. Gén. Sci. Phys. 5: 225 (13 in reprint). 1820) automatically created subg. *Houstonia*, which he called *Houstonia* subg. *Edrisia*. By ICBN Article 57.3, the combination in *Hedyotis* formed by merging the original subg. *Houstonia* and Rafinesque’s other subgenera into one subgenus must be called by the generic name, not subg. *Edrisia* (Raf.) Lewis (Am. Jour. Bot. 49: 858. 1962).

relatively narrow view in recognizing four species as opposed to Fosberg's (1954) placement of the entire complex in *H. purpurea* (L.) Torrey & Gray. Whether or not most components of the complex should be treated as varieties of *H. purpurea* or as distinct species, our representatives can be listed as follows: *Hedyotis purpurea* (including or not *Houstonia montana* Small; cf. Yelton; Terrell, 1978; Kral), $n = 6, 12$; *H. longifolia* (Gaertner) Hooker (including or not *Hedyotis Nuttalliana* Fosb. = *Houstonia tenuifolia* Nutt.; see especially Smith; the latter accepted as a species by Terrell in 1959), $n = 6, 12$; *H. canadensis*, $n = 6, 12$; and *H. ouachitana* E. B. Smith (here presumed to belong to "Group 4").

"Group 5" is represented by *Hedyotis australis* Lewis & Moore (*Houstonia micrantha* (Shinners) Terrell; see Terrell, 1975a; Lewis & Moore), $n = 16$; *H. caerulea* (L.) Hooker (including or not *Hedyotis crassifolia* Raf. = *Houstonia pusilla* Schoepf and *Houstonia patens* Ell., according to Lewis & Moore, $n = 8, 9, 16, 24$ (but see Löve & Löve for reservations); *H. Michauxii* Fosb. (*Houstonia serpyllifolia* Michx.), $n = 16, 24$; *H. procumbens* (J. F. Gmelin) Fosb., $n = 14$ (see Gaddy & Rayner); and *H. rosea* Raf., $n = 7$ (see J. E. Moore; Taylor & Taylor; Waterfall).

Seeds of *Hedyotis corymbosa* have been the subject of a series of studies (see Corbineau & Côme for an entry to the literature). While the physiological results are outside the scope of the present paper, a few salient ecological discoveries deserve mention. The seeds are dimorphic in that for germination some are "dormant" and require stratification while others do not. Artificial selection led to two lines of plants, one of which produces seeds showing no need for stratification. The other produces a mix of the two types of seeds, with the percentage of "dormant" seeds increasing as the season progresses. All demand warm temperatures and must be activated by exposure to light, although (at least in those not requiring stratification) the effects of light are variable, with a number of parameters. "Dormant" seeds are strongly inhibited from germination at a concentration of oxygen as high as that in the atmosphere, except after a sufficient period of stratification.

The citation of a lectotype for *Hedyotis* still requires choosing between alternatives. Of three species comprising the genus in Linnaeus's *Species Plantarum*, *H. herbacea* can be eliminated from consideration first. Although it dates back, along with *H. Auricularia* and *H. fruticosa*, to the year Linnaeus first published *Hedyotis*, it is missing from one of the two generic treatments appearing that year (in 1747a but not 1747b). For this reason and also since authors (see Bremekamp, 1939, 1952) have removed it to *Oldenlandia* (see ICBN T.4.e), since it was least known to Linnaeus, and since two different lectotype species have already been proposed, it is unsuitable as a choice. Ruling out *H. herbacea* has never provoked disagreement—the problem lies in settling on one member of the remaining pair.

As background for discussing the conflict, it is worthwhile to note that Linnaeus's description of *Hedyotis* is repeated essentially verbatim in all Linnaean publications cited in the present context, including the nomenclaturally decisive fifth edition of the *Genera Plantarum*.

The best choice for lectotype does not shine forth from recognition of Lin-

naeus's frequent practice of basing generic descriptions on single species. Both potential lectotype species were well known to Linnaeus from literature and specimens when he wrote the generic description, and examination of the works he cited reveals neither species as focal. (The only source I have not examined is "Marlow. obs.," cited more extensively by Dale and probably the "Marloe" discussed by Jackson.)

Nor is a single species revealed as central by Bremekamp's (1939, 1952) selection of *Hedyotis fruticosa* as lectotype, chiefly on the grounds that it, but not *H. Auricularia*, agrees with the generic description in having dehiscent fruits. (He pulled *H. Auricularia* out of *Hedyotis* as type species of his new genus *Exallage* in 1952.) Dehiscence, however, could not have entered the generic description via *H. fruticosa*, about which Linnaeus (1747a, p. 26, no. 63) admitted, "De fructu nulla nobis certitudo."

Fruits of *Hedyotis Auricularia* were described (although with no mention of dehiscence) in works Linnaeus cited (e.g., Burman). Bremekamp (1939) himself suggested quite plausibly that Linnaeus's failure to register fruits of *H. Auricularia* as indehiscent could have resulted from misinterpretation of them as immature, assuming their presence on the original specimens.

That *Hedyotis Auricularia* deviates from the generic description in this possibly minor character does not show the description to rest on *H. fruticosa*: the information in the generic description that is at odds with *H. Auricularia* did not originate with *H. fruticosa*, and Bremekamp did not show *H. fruticosa* to match the generic description better. Bremekamp's case, then, is based mostly on an error and is incomplete. As explained below, I reject his supplementary contention that Blume rendered *H. Auricularia* "illegitimate" as lectotype in 1826 by placing what Bremekamp regarded as a synonym under the generic name *Metabolos* Blume. Bullock and Terrell (1975b) accepted Bremekamp's lectotypification.

The 1983 International Code of Botanical Nomenclature (Art. 8.1) rules that the first lectotype chosen can be unseated only if demonstrated to be "in serious conflict with the protologue." If it is agreed that *Hedyotis Auricularia* has not been thus exposed, it cannot be displaced (even if it was placed in *Metabolos* under a different name), having been cited twice as typifying the genus before Bremekamp's opposing choice. Chamisso & Schlechtendal designated *H. Auricularia* "typus" in 1829 (accepted by Fosberg, 1943b; also see Wight & Walker-Arnott), although it can be objected that the early use of "typus" is not equivalent to the modern designation of a lectotype. That, however, may be a moot objection, since Hitchcock & Green selected *H. Auricularia* as "standard species" a century later but still ahead of Bremekamp.

In the interest of future investigations, it may be useful to stress that the large number of species of *Hedyotis* in the broadly stated type locality for both potential lectotypes, Sri Lanka, intensifies the hazard of working with incorrectly identified specimens. Types are presumably in the Hermann herbarium at BM (see Trimen). Several specimens of *Hedyotis*, including one labeled *H. Auricularia* by Linnaeus and another labeled *H. fruticosa*, are in the Linnean Herbarium. The latter disagrees with the *foliis lanceolatis* Linnaeus attributed to *H. fruticosa* in the *Species Plantarum*, for it has broad, mostly ovate leaf

blades. (According to Stearn (p. 94), Linnaeus applied "lanceolatus" to blades "oblong, but gradually tapering towards each extremity and terminating in a point, the greatest width being at the middle, not below" (also see p. 91, fig. 6).)

Preparations from species of *Hedyotis* sensu lato serve as folk remedies around the world. *Oldenlandia affinis* (Roemer & Schultes) DC. (*Hedyotis affinis* Roemer & Schultes), which is given to hasten childbirth in Africa, contains the oxytocic phenolic amine serotonin and two oxytocic proteins. Practical modern usage is hampered by the toxicity of serotonin and at least one of the proteins, and both compounds are ineffective when administered orally to laboratory animals (Gran, 1973a, b, d). Topical uses for oldenlandias are common and could, at least in some cases, as exemplified by *Hedyotis diffusa* Willd., be related to the presence of antiinflammatory iridoids.

The red dye "Indian madder" or "chay-root" from the commercially cultivated *Oldenlandia umbellata* L. colors turbans and other products in India. Extracts from this species are also used in treating tuberculosis. Roots of *Hedyotis corymbosa* yield the green (after chemical treatment) dye geranine, and bark from roots of *H. herbacea*, as well as leaves from *H. scandens* Roxb., likewise color fabrics. Capsules from *H. scandens* have been used to blacken teeth.

Leaves of *Hedyotis Auricularia*, *H. scandens*, and *H. nitida* Wight & Arnott are eaten in Asia. *Hedyotis fruticosa* is a minor source of wooden rods. For further information on *Hedyotis* as a medicine and on its other uses, see Datta & Sen, Lin *et al.*, Morton, Sastri *et al.*, Simmonds, and Usher.

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3. *Pentodon* Hochstetter in Krauss, Flora **27**: 552. 1844.

Hygrophilous, prostrate or feebly erect, fleshy, glabrate herbs, usually extensively branched, frequently pseudodichotomously so, often tufted with numerous basal branches; branches more or less quadrangular. Raphide bundles conspicuous on surfaces of most organs when dry. Leaves opposite, nearly sessile or on short, winged petioles, the blades (obovate to) lanceolate or ovate, penninerved, usually minutely scabrous adaxially and marginally, rounded to more often acute or acuminate at the apex, the base usually acute to cuneate or sometimes rounded; stipular sheaths continuous with the flanges on the petioles, membranaceous, interpetiolar, usually fimbriate, occasionally entire, sometimes cuspidate in the center. Inflorescences mostly terminal, sometimes axillary, usually between a pair of pseudodichotomous branches, fundamentally dichasial or monochasial, sometimes with only 1 or 2 flowers, lax with long axes, sometimes compound and sometimes paniculate with straight main or branch axes; bracts and bracteoles mostly distinctly reduced [or foliose]. Flowers pedicellate, pentamerous, small and inconspicuous, perfect, homostylous [or heterostylous in *P. laurentioides* and *P. pentandrus* var. *minor*, or "pseudoheterostylous" in some African members of *P. pentandrus* var. *pentandrus* having the anthers in fairly uniform position in the throat of the corolla but the styles varying in length]. Calyx lobes connate basally into a short tube topped with lanceolate or deltoid teeth $\frac{1}{4}$ – $\frac{3}{4}$ the length of the corolla. Corolla nearly cylindrical but slightly [to broadly] flared, white [or reddish or blue], pubescent or (reportedly) glabrous in the throat, the lobes usually about $\frac{1}{4}$ – $\frac{1}{3}$ the length of the corolla. Stamens inserted near the throat of the corolla tube [or low in the tube in heterostylous flowers], uniform in length and included [or exerted in short-styled flowers]; anthers dorsifixed, elliptic-oblong; filaments shorter than anthers; pollen grains prolate or subspheroidal, tricolporate, reticulate. Ovaries bilocular, containing numerous ovules on apically bilobed, peltate placentae inserted on the septum; styles long enough to bear slightly exerted [or included] stigmas, at least sometimes markedly thickened at the level of the anthers beneath the stigmatic lobes, the thickening covered with pollen and, in conjunction with a pilose ring at the same level, occluding the throat of the tube; stigmatic lobes 2, linear. Capsules bilocular, crowned with persistent calyx tube and teeth, thin walled and papery, obconical or obturbinate, somewhat compressed contrary to the septum, bearing 5 longitudinal

keels corresponding to the midlines of the adherent sepals, dehiscing loculicidally across the summit. Seeds numerous, minute, angular, brown, fairly isodiametric, on the surface reticulate from outlines of testa cells, these with irregular thickenings in the lateral walls. TYPE SPECIES: *P. decumbens* Hochst. = *P. pentandrus* (Schum. & Thonn.) Vatke *fide* Bremekamp (1952); this the sole original species. (Name from Greek, *pente*, five, and *-odon*, toothed, presumably in reference to the five toothlike calyx lobes.)

Probably consisting of only two species, *Pentodon laurentioides* Chiov., endemic to Somalia, and *P. pentandrus*, $2n = 18$, distributed in the Old World across much of tropical Africa and on the southern Arabian Peninsula, Madagascar, the Seychelles, and the Cape Verde Islands. The latter, or possibly a third species, *P. Halei* (Torrey & Gray) Gray (*Hedyotis Halei* Torrey & Gray, *Oldenlandia Halei* (Torrey & Gray) Chapman) is scattered across much of Florida and occurs in southern Georgia, Louisiana, Texas, the West Indies (at least Cuba, the Bahamas, and Guadeloupe), and according to Verdcourt (1976), Nicaragua and Brazil. (I have seen no trustworthy documentation of *Pentodon* from either Mississippi or Alabama.)

Opinion is divided as to whether *Pentodon Halei* is conspecific with *P. pentandrus*. Standley (1918) held the latter to differ from *P. Halei* in having pubescence within the corolla, longer peduncles relative to the leaves, racemose (vs. cymose) inflorescences, and more slender (vs. "clavate") pedicels longer relative to the capsules. This list probably exaggerates the differences—corollas from *P. Halei* that I examined are distinctly pubescent within, and Bremekamp (1952, p. 180) found the distinctions to break down so far as to be "of little importance," if the range of variation in African specimens is considered. He attributed differences in the inflorescence characters largely to differences in the vigor of the plants, which he assumed to be reduced in the marginal North American climate. Noting that the American material has small, elliptic leaves and shorter inflorescences than most African specimens, Verdcourt (1976, p. 263) agreed that *P. Halei* "cannot be specifically distinct" from *P. pentandrus* and agreed further with Bremekamp in suspecting introduction from Africa as lying behind the New World populations of *Pentodon*. Its widely scattered stations speak in favor of an appreciable ability to disperse. As Verdcourt has already noted, better data on the distribution of modifications to the style, as described below, could shed some light on the relationships among the widely separated populations.

Pentodon appears to be most closely related to *Hedyotis* (especially subg. *OLDENLANDIA*), in which it has been included, and from which it differs by the pentamery (vs. tetramery) of its flowers and the distinctive thickenings on the lateral walls of testa cells. Additional features that help to characterize *Pentodon* are its apically bilobed placentae; thin, papery pericarps; and seeds not producing mucilage upon moistening. (This paragraph is based largely on Bremekamp, 1952, and Lewis, 1965a, and verified for *Pentodon* through herbarium specimens.)

Pentodon laurentioides and *P. pentandrus* var. *minor* are heterostylous (for an illustration of the two floral morphs in var. *minor*, see Verdcourt, 1976).

The other members of the genus show two curious variations of the breeding system that call for further research. In the simpler case, the two flowers of *P. pentandrus* from our area that I have been able to examine internally (*Duncan* 21650, Georgia, A, and *Thomas et al.* 72765 & 474, Louisiana, GH) have had the style swollen apically and coated with pollen at the level of the anthers just below the stigmatic lobes. The swelling was so positioned that, in conjunction with the pilose ring borne on the tube, it would partly block entrance to the corolla tube. Except for a thickened stylar apex (with stigmas missing) illustrated in Godfrey & Wooten, I have seen no other indication of the thickening or of adherent pollen for either African or American specimens. The functional role of this condition, if any, will be best elucidated by field observations.

The second curiosity comes from Bremekamp (1952; also see Verdcourt, 1976), who described two floral morphs in African plants of *P. pentandrus* var. *pentandrus*. The styles on different individuals are either of two lengths, included or exserted, but the plants are not heterostylous in the conventional sense of the term, since all flowers have included stamens. Bremekamp indicated that the two morphs were geographically separated, although only on a local scale; both are widespread in Africa.

This raises the question of the condition(s) in American populations. By using bright transmitted light, I have consistently seen the anthers to occupy about the same level in the corolla throats in all examinable flowers from our area in the Harvard herbaria; all of the stigmas that I saw projected slightly beyond the anthers. Moreover, the relative positions of stamens and stigmas in the flower from the Bahamas illustrated by Correll & Correll are the same as I observed on the mainland specimens; this seems also to be true of the flowers shown by Small and by Godfrey & Wooten, although the long style is depicted in each as detached, making its exact position relative to the stamens indiscernible. Still, because the sampling so far is scanty, and because short, included styles could be overlooked in an examination by transmitted light, it would be premature to rule out the presence of such styles in the United States.

Pentodon pentandrus flowers in our area from May into October along shores and in periodically flooded spots, swampy woods, and other low, wet sites.

An incidental note potentially useful in the field, pointed out by Dr. Robert Kral (pers. comm.), is that in habit and overall appearance, *Pentodon* looks deceptively like *Lindernia crustacea* (L.) F. Mueller, an introduced scrophulariaceous weed in Florida.

Economic uses for this genus are negligible.

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on an African specimen, this probably also true of mention of exserted anthers in addition to included ones.]

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Tribe CINCHONEAE DC. Ann. Mus. Hist. Nat. Paris **9**: 217. 1807,
“Cinchonacées, Cinchonaceae.”

4. **Exostema** (Persoon) L. C. Richard ex Humboldt et Bonpland, Plantae Aequinoctiales **1**: 131. 1808 [1807].

Vegetatively glabrous to less often hispidulous or hirsute shrubs or small trees, the branches symmetrical, sometimes supported by surrounding vegetation. Leaves opposite, petiolate [or nearly sessile]; stipules interpetiolar [or reportedly intrapetiolar], broadly deltoid to drawn out into attenuate apices, marginally ciliate, keeled when young [sometimes bilobed]. Flowers borne singly on short pedicels in axils of upper leaves [or terminal; in cymes, thyrses, or panicles in some species], pentamerous [or tetramerous], actinomorphic or nearly so, fragrant. Calyx teeth broadly deltoid [to subulate], much shorter than corolla tube. Corolla with slender cylindrical tube [less than 1 cm to] several cm long (ca. 2–5 cm in our species) [20 cm or more in *E. longiflorum* Roemer & Schultes], white, yellowish, or pinkish [red or purplish], said to change from white to darker hues in some species including ours, the 5 [4] linear-ligulate lobes about as long as the tube or a little [or much] shorter, twisted-imbricate in bud. Stamens exserted [rarely included], epipetalous near base of tube [or reportedly inserted on receptacle], the linear, basifixed anthers long (10 mm or more in our species). Style filiform, much exserted [or infrequently included], thickened apically beneath a pair of stubby stigmatic lobes [or stigma reportedly unlobed]. Capsule ellipsoid, truncate apically, crowned with persistent calyx teeth [or teeth deciduous], dark colored, rugulate, septidical (and sometimes splitting loculicidally to varying degrees); placentae large, flat, detached from septum of dry and dehiscent capsule. Seeds numerous, wafer thin, surrounded by a narrow marginal wing, vertically imbricate; endosperm abundant; embryo with radicle longer than the elliptic cotyledons. LECTOTYPE SPECIES: *E. caribaeum* (Jacq.) Roemer & Schultes.⁴ (Name from Greek, *exo*, out, and *stema*, stamen, in reference to the exserted stamens.)—PRINCEWOOD.

A genus of some 35 or more species in tropical and subtropical America, mostly in the West Indies, but also with a poorly studied group of roughly

⁴Britton & Millspaugh's choice of *Exostema parviflorum* A. Rich. as lectotype (in Bahama Fl. 409. 1920) cannot be followed. This species is ruled out by ICBN (1983) Article 7.10, since this was not a member of the group to which Persoon applied the basionym *Cinchona* subg. *Exostema* Persoon (Syn. Pl. **1**: 196. 1805; cited by Richard on p. 135). (See Brizicky for comments on Persoon's infrageneric taxa.) *Exostema caribaeum* is here designated as lectotype—Persoon included it, and it is the most-widespread and best-known species.

seven species on the mainland in southern Florida (see below), Mexico, Central America, and (chiefly western) South America as far south as Peru (four species?) and southern Brazil (one species; see Angely).

Exostema caribaeum ranges along the full length of the Florida Keys, is unusual on the southern tip of mainland Florida (Tomlinson), occurs throughout much of the West Indies, Mexico, and Central America, and has been reported from scattered localities along the northern coast of South America (probably present in Colombia, but doubtfully so in Venezuela and "Guiana").

Features that help with recognition of *Exostema caribaeum* are elliptic leaves pointed at both ends; solitary, axillary flowers; short, stubby calyx teeth (less than 1 mm long); fragrant, white (or pinkish or yellowish) corollas to ca. 8 cm long, including the long, nearly linear lobes, and with slender, cylindrical tubes; long (1 cm or more), basifixed anthers conspicuously exserted; and ellipsoid, apically truncate capsules containing numerous elliptic, waferlike seeds to about 5 mm long completely surrounded by a narrow wing.

Exostema is our only member of the tribe Cinchoneae (woody plants with bilocular capsules containing numerous vertically or nearly vertically arranged, imbricate seeds having pitted testa cell walls). The genus was once included in *Cinchona* L., from which it differs in its exserted stamens and its imbricate (vs. valvate) corolla lobes. Koek-Noorman & Hogeweg found *Exostema* to differ further from *Cinchona* in having fiber tracheids in the wood, rather than fibers transitional between fiber tracheids and libriform fibers, although broadened sampling is needed to bolster the strength of this character. Additional features that help to separate *Exostema* from other members of the Cinchoneae are uniform calyx lobes, five or sometimes four corolla lobes, and slender, round, symmetrical corolla tubes. Koek-Noorman cited personal communication with C. Bremekamp in noting that the relationships of *Exostema* are unclear.

Taxonomic study of *Exostema* is both outdated and fragmentary. The most recent revision of the entire genus dates back to De Candolle, who divided it into three sections that have been ignored by more recent authors. Most of the species are covered in Standley's treatment in the *North American Flora* (1918), a picture that can be rounded out by an examination of some of his later floristic studies in the New World (1926, 1930, 1936, 1938; 1975, with L. O. Williams).

During the eighteenth century, medicinal interest in *Cinchona*, the original source of quinine as a medicine for malaria, extended to numerous species of *Exostema*. I know of no modern study aimed at relating the alleged curative properties of *Exostema* to bona fide pharmacologic effects or to its chemistry. *Exostema caribaeum* and undoubtedly other species yield a hard, strong, heavy wood that polishes well and is used for turning, cabinet work, and applications requiring durability. Because it burns readily, it has been used for torches. Species of *Exostema* with showy flowers are sometimes cultivated in the West Indies.

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LONG & LAKELA; SARGENT; SOUKUP; STANDLEY (1918, 1926, 1930, 1931, 1936, 1938); STANDLEY & WILLIAMS; and TOMLINSON.

BORHIDI, A., & O. MUNIZ. New plants in Cuba II. Acta Bot. Acad. Sci. Hungar. **18**: 29–48. 1973. [*Exostema caribaeum* var. *pubescens*, var. nov., 44.]

——— & M. F. ZEQUEIRA. Studies in Rondeletieae (Rubiaceae) II. A new genus: *Suberanthus*. Acta Bot. Acad. Sci. Hungar. **27**: 313–316. 1981. [*Exostema neriifolium* is type species.]

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Tribe NAUCLEEAE J. D. Hooker, Fl. Nigrit. 377. 1849.

5. **Cephalanthus** Linnaeus, Sp. Pl. **1**: 95. 1753; Gen. Pl. ed. 5. 42. 1754.

Deciduous (or somewhat evergreen in tropical Florida), sympodially branched shrubs (or infrequently small trees) of wet soil. Leaves opposite or in whorls of 3 (or 4), elliptic to ovate or lanceolate, usually acuminate and often cuspidate apically, the bases variable; stipules usually with 1 deltoid or ovate lobe between bases of adjacent petioles, sometimes bifid, or occasionally with 2 separate lobes between pairs of petioles, the lobe(s) with adaxial and frequently marginal colleters; foliage and twigs (especially abaxial surfaces) glabrous to densely pubescent, the indument sometimes storied and sometimes strigose; buds often multiple in leaf axils. Flowers fragrant, usually tetramerous, protandrous, tight-

ly clustered into distinctly globose heads on long peduncles, the heads terminal or axillary, sometimes solitary, more often in racemose (or infrequently paniculate) clusters at ends of branches. Calyx much shorter than corolla, the tube topped with short, blunt teeth persistent in fruit. Corolla white or nearly so, with a narrow, cylindrical or slightly flared tube several times longer than the oblong to deltoid or ovate, imbricate, usually internally bearded lobes, these alternating with exposed glands (colleters?) in the bud and sometimes after expansion. Anthers sagittate, borne at throat of corolla tube on short, epipetalous filaments. Style filiform, about twice the length of the corolla, expanded apically into a scarcely (or not perceptibly) bifid or 4-lobed knob (*vide* Tomlinson); ovary bilocular, containing a pendulous ovule in each locule. Fruits dry, indehiscent, crowded on spherical head, each with 1 or 2 seeds, cuneiform, the halves often separating along the septum, intermixed with long, narrow bractlets, these as long as the fruits and expanded apically into pubescent knobs. Seed matching shape of locule, with a conspicuous corky caruncle (aril). LECTOTYPE SPECIES: *C. occidentalis* L.; see Haviland, Jour. Linn. Soc. Bot. **33**: 2, 3, 37. 1897; Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. **3**: 255. 1913; Merrill, Jour. Wash. Acad. Sci. **5**: 532. 1915. (Name from Greek, *kephale*, head, and *anthos*, flower, in reference to the spherical floral heads.)—BUTTON BUSH.

A genus of six species as circumscribed in Ridsdale's revision: *Cephalanthus natalensis* Oliver (South Africa), *C. tetrandra* (Roxb.) Rids. & Bakh. (India to Taiwan), *C. angustifolius* Lour. (southeastern Asia), *C. glabratus* (Sprengel) K. Schum. (South America), *C. salicifolius* Humb. & Bonpl. (Texas, Mexico, Central America), and our *C. occidentalis* L. (In the revision preceding Ridsdale's, Haviland recognized seven species; Ridsdale transferred two of these to *Ixora* L., changed the name of one, and added one.)

Cephalanthus occidentalis, $2n = 44$, ranges across North America virtually throughout the area defined by New Brunswick (or possibly Prince Edward Island, according to Scoggan), Cuba, Texas, southeastern Nebraska, southern Minnesota, southern Ontario, and southern Quebec. The species is absent or nearly so from the Florida Keys. A spottier distribution farther west excludes the Rocky Mountains but includes New Mexico, Arizona, Utah, California, and northern Mexico. Standley & Williams noted it in Guatemala and Honduras.

Cephalanthus occidentalis is almost exclusively an inhabitant of freshwater shores and low, wet places. It usually grows in full sun but tolerates some shading. The stands can be dense and extensive.

Distinguishing *Cephalanthus* from other shrubs in the Generic Flora area is not difficult; the restriction to wet sites is a useful character in itself. The pointed leaves are opposite or whorled and are associated with interpetiolar stipules that bear adaxial and often marginal colleters. The small, tubular, fragrant, white or nearly white flowers with long, exserted styles are packed into globose heads, a shape that remains unaltered as the fruits mature. Individual fruits are indehiscent (the halves often separate but do not open) and cuneiform; they generally contain a conspicuously carunculate seed in each locule.



FIGURE 1. *Cephalanthus*. a-i, *C. occidentalis*: a, pendent flowering branchlet, $\times \frac{1}{2}$; b, flower at anthesis, style not yet expanded—note squamule between 2 corolla lobes, $\times 6$; c, flower with mature style, the pollen shed—note bractlets at base of ovary, squamule between 2 corolla lobes, $\times 6$; d, corolla laid open to show adnate staminal filaments, $\times 6$; e, ovary in longitudinal section, 1 ovule (at left) in section, $\times 10$; f, mature fruit, $\times 6$; g, fruit splitting into 2 indehiscent 1-seeded parts, $\times 6$; h, seed, abaxial side at left, adaxial side at right—note corky caruncle, $\times 6$; i, embryo, oriented as in seed, $\times 12$.

Western populations that have narrow leaves on short petioles have been set apart as *Cephalanthus occidentalis* var. *californicus* Benth (*C. occidentalis* subsp. *californicus* (Benth) E. Murray), another segregate that Ridsdale placed in synonymy. Fernald recognized plants with lanceolate leaves attenuate at both ends and only 1–3 cm broad as forma *lanceolatus*. Different individuals of *C. occidentalis* range from being more or less glabrous to thickly pubescent on twigs and abaxial leaf surfaces, a condition that has led some authors (e.g., Steyermark, 1963) to recognize *C. occidentalis* var. *pubescens* Raf., which is

found primarily in the southern United States but has been reported from as far north as Quebec. Neither Haviland nor Ridsdale recognized the pubescent taxon at any rank, and Wells & Sharp rejected it with the observation that the two putative varieties grow together in Tennessee. My examination of herbarium specimens at the Missouri Botanical Garden inclines me to agree with these authors.

Curious threadlike structures (called bracteoles by Haviland and Tomlinson, illustrated in FIGURE 1 and in Tomlinson) are borne at the base of each flower. These are roughly as long as the ovary and are expanded apically into pubescent knobs that appear to plug the spaces between the fruits protectively.

The flowers within each head mature simultaneously and are protandrous, the pollen being released in the bud. Some grains catch in the hairs inside the corolla, and others are carried out of the tube on the apical region of the strongly exerted style. Whether all pollen delivery takes place from the style is not clear. Some wind pollination is suspected. (For more on pollination, see Robertson and Tomlinson.)

Ants may possibly play some role(s) in the life cycle of *Cephalanthus occidentalis*. "Squamules" readily interpretable as nectaries (colleters?) are conspicuous in the sinuses between unexpanded corolla lobes in the bud (see FIGURE 1b, c), and the seeds are capped with large, corky caruncles (arils). It is not inconceivable that the adaxial colleters on the stipules, too, provide nourishment for ants.

In their revisions, written in the last century, both Schumann and Haviland placed *Cephalanthus* in the tribe Naucleaeae, where Haviland regarded it as closely related to the African and Asian genus *Adina* Salisb. *Cephalanthus* differs from *Adina* in having only one ovule in each locule of the ovary, indehiscent fruits, and wingless seeds. In 1976 Ridsdale revised *Cephalanthus* and isolated it as the monotypic Cephalantheae Ridsdale.⁵

Ridsdale defended his isolation of *Cephalanthus* by arguing that the tribe Naucleaeae is in part artificially held together by too much emphasis on the conspicuous clustering of flowers into heads. He thought *Cephalanthus* possibly to be most closely related to *Mitragyna* Korth. and *Uncaria* Schreber, two genera he transferred from the Naucleaeae to the Cinchoneae. *Cephalanthus* differs from these two in its indehiscent fruits and its single seed per locule.

In their survey of alkaloids in the Naucleaeae *sensu lato*, Phillipson, Hemingway, & Ridsdale found *Cephalanthus*, along with *Uncaria* and *Mitragyna*, to deviate from the Naucleaeae *sensu stricto* in producing "significant quantities" of nonquaternary nonglycosidic alkaloids of the heteroyohimbine and oxindole types. Aware of the same set of alkaloids in *Cephalanthus*, Kisakurek and colleagues agreed that the data support maintaining all three genera apart from the Naucleaeae. Further, Koek-Noorman interpreted the wood structure of *C. occidentalis* and *C. salicifolius* as anomalous in the tribe, and Bremekamp

⁵He attributed the authorship to Kunth in HBK., where Cephalantheae appeared, as Ridsdale acknowledged, as a "sectio." Although "Cephalantheae" has been used repeatedly as a name for subgroups of the Rubiaceae (see Darwin, Pfeiffer), Ridsdale appears to have been the first to call it a tribe.

(1966) disfavored a place for *Cephalanthus* in his narrowly conceived Naucleaeae.

Cephalanthus is of minimal consequence in human affairs. The plants are amply supplied with alkaloids and, not surprisingly, are bioactive. They are blamed for killing livestock, but Sperry and colleagues noted that losses are negligible in Texas, probably on account of unpalatable constituents. *Cephalanthus occidentalis* has long been used in folk medicine by American Indians, among others, against such complaints as sore eyes, arthritis, toothache, fevers, and diabetes, and it has found use as a laxative. Sometimes *C. occidentalis* is grown ornamentally. According to Fernald, *C. angustifolius* Hort. (non Lour.) may be *C. occidentalis* f. *lanceolatus* Fern. The fruits serve as food for water birds, and the sweet-smelling flowers are valued by beekeepers as sources of nectar.

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Tribe GARDENIEAE A. Richard ex DC. *Prodromus* **4**: 342, 367. 1830,
“Gardeniaceae.”

6. **Randia** Linnaeus, *Sp. Pl.* **2**: 1192. 1753; *Gen. Pl.* ed. 5. 74. 1754.

Spiny [or unarmed] shrubs or small trees bearing opposite branches and short shoots. Spines axillary, paired, sharp, stiff, usually inserted at ca. 45-degree angle, generally shorter than leaves. Bark on twigs breaking up into conspicuous untidy scales or taking the form of longitudinal flanges separated by long fissures. Plants glabrous to strigillose [or more heavily pubescent] on twigs and stipules. Leaves sessile or on short petioles, opposite or fascicled on short shoots, small (not often longer than 3 cm), (infrequently) ovate to (frequently) oblanceolate or obovate [sometimes trilobed], mostly rounded and mucronate apically, the margins usually revolute when dry. Stipules with a single variably shaped (usually deltoid and apiculate) lobe centered between adjacent petiole bases, often split or shredded by growth of twig and/or by weathering. Plants typically dioecious, the flowers subsessile in leaf axils, solitary or occasionally clustered on short shoots among leaves, mostly pentamerous, imperfect, with the nonfunctional organs reduced (or possibly flowers sometimes perfect, *vide* Tomlinson) [or flowers perfect]. Calyx lobes variable in size and shape, deltoid

to obovate [or foliose to suppressed], coalescent basally into a short tube. Corolla white [or yellowish], cylindrical [flared or campanulate], the imbricate-contorted lobes spreading and roughly as long as the tube, thickly pubescent in and near the throat [or internally glabrous]. Stamens on very short filaments in the corolla throat [or included or exerted]. Ovary inferior, usually bilocular; style expanded and cleft apically into a pair of thick, exerted lobes [or undivided]. Berries globose to ellipsoid, crowned with the persistent calyx, variably reported as white or greenish to purple when ripe, the pulp dark toward the inside. Seeds 1 or few, discoid. LECTOTYPE SPECIES: *R. mitis* L. (see Britton, Fl. Bermuda, 361. 1918), this regarded by most modern authors as a synonym of *R. aculeata* L., the only other species of *Randia* in the *Species Plantarum*. (Named for Isaac Rand, ?-1743, British apothecary and botanist, director of the Chelsea Physic Garden; for biographical notes see Trimen & Thiselton-Dyer.)—INDIGO BERRY.

A rather vaguely defined genus usually estimated to have 200–300 species and with a pantropical distribution (see below). *Randia aculeata*, the only species indigenous to the area of the Generic Flora, occurs in South Florida at the northern edge of its range, which extends to Mexico, Central America, northern South America, and the West Indies. Texan populations are interpretable as belonging to *R. aculeata* (for commentary see Vines, who tentatively favored this stance), although Correll & Johnston and F. B. Jones referred them to *R. rhagocarpa* Standley.

In our area *Randia aculeata* inhabits hammocks, shores (sometimes associated with mangroves), oceanside dunes, pinelands, and thickets. The soil is sometimes marly and is sometimes dry. As described by Tomlinson, the flowers, chiefly borne April–June, are for the most part functionally imperfect by abortion, although possibly some perfect ones may form. In 1966 Bremekamp reported staminate flowers in some Gardenieae to have abortive styles that act to hold pollen. The extent of involvement, if any, of the abortive styles in *R. aculeata* in the pollination system is a question worthy of new observations.

Randia aculeata is recognized and differs from other genera of Rubiaceae treated in this paper, except *Catesbaea* (see treatment of this genus for comparison), in being a shrub or small tree armed with paired axillary spines, each of which diverges from the stem at roughly 45 degrees. Further, our *Randia* has small, frequently apiculate leaves most often broadest above the middle and usually fascicled on short shoots. The small flowers are solitary or clustered on the short shoots. They have white, tubular corollas, and the thick stigmatic lobes protrude from the pistillate flowers. The few-seeded, globose to ellipsoid berries are conspicuously topped by calyx remnants.

Defining *Randia* from a global perspective is hard to accomplish. At present the generic boundaries remain unsettled, especially in the Old World. Authors disagree severely in their generic circumscriptions and synonymy. In a treatment fundamental to taxonomic accounts that followed, Bentham & Hooker conceived of *Randia* as polymorphic, pantropical, and made up of about 90 species in six sections. They named a new genus allied to *Randia*, *Basanacantha* J. D. Hooker, which they thought to differ in being dioecious (an invalid

distinction), and in having glumaceous stipules, terminal flowers, membranaceous leaves, and other distinctive characters. Schumann held nearly the same concept of *Randia* but added a seventh section.

Critical of Schumann's treatment, Fagerlind regretted that *Randia* had become a "refuse dump" for Gardenieae of uncertain position. Emphasizing branching relationships and using diverse additional characters, he pruned *Randia* back to Schumann's sect. *Eurandia* (sect. *RANDIA*), emended this, added *Basanacantha*, and limited *Randia* to American species. Even if Fagerlind's work has not been particularly influential, the merger of *Basanacantha* with *Randia* has been supported by a number of later authors (see especially Standley, 1919), and it is more or less in harmony with a tendency among recent authors to transfer Old World species from *Randia* to other genera.

Concentrating on West African species, Keay dismissed Fagerlind's taxonomic conclusions about *Randia* as "not altogether satisfactory," stressed the need (that persists) for a full revision, and recognized as distinct 21 genera, "all of which have at one time or another been included, wholly or partly, in *Randia* or *Gardenia*." Keay listed new or resurrected generic placements for 126 species previously included in *Randia*. More recently, Hepper & Keay attributed no species to *Randia* in the *Flora of West Tropical Africa*. Tirvengadam, after considering "practically all taxa described under *Randia*," likewise confined the genus to America and characterized it as having [paraphrased] unilocular ovaries with parietal placentae, a nonwaxy bluish pericarp, imperfect flowers, pollen grains remaining in tetrads, and distinct testa cells, and as lacking serial bud formation. (In contrast with Tirvengadam, American floristic authors tend to describe the ovary as generally bilocular.) Yamazaki sorted the Asian species out among five other genera, leaving none in *Randia*. However, it must be emphasized that acceptance of such exclusive boundaries is not unanimous.

Authors working on floras in the New World (Standley; Standley & Williams; Steyermark; Dwyer) have regarded *Randia* as pantropical but have avoided assertions about its limits. They have not adopted infrageneric categories, except that Williams and Standley & Williams recognized subgenus *BASANACANTHA* (J. D. Hooker) L. O. Williams, which they distinguished from subg. *RANDIA* by the former's longer corollas, larger fruits, more often imperfect flowers, and terminal quartets of spines (vs. spines paired and scattered). Like Keay, they stressed the need for revisionary work, not only in terms of delimiting the genus, but also of redefining our *R. aculeata*, which they perceived as too inclusive.

Randia aculeata has been used as a folk remedy for dysentery, and the fruit has been the source of a blue dye. Fruits from at least one extraregional species have served as food for humans. *Randia formosa* (Jacq.) K. Schum. is cultivated as an ornamental in tropical regions, and it yields an essential oil used in making perfume (see Prance & Da Silva for an illustrated account of this species).

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7. *Casasia* A. Richard in Sagra, Hist. Fis. Cuba. ed. 2. 11: 9. 1850.

Dioecious shrubs or small trees with thick, glabrous twigs covered with light-colored flaking bark. Leaves clustered toward branch tips, glabrous except for axillary tufts of trichomes abaxially, petiolate, obovate or oblanceolate, truncate or emarginate to obtuse or rounded at the apex, cuneate to caudate at the base; stipules with the single lobe centered between adjacent petioles, oblong to deltoid or ovate, acute or acuminate and sometimes apiculate apically, frequently denticulate along the margins, the adaxial side with colleter. Flowers fragrant, on tapered pedicels, tending to blacken upon drying, imperfect with the nonfunctional organs (gynoecium or stamens) developing and with staminate and carpellate flowers superficially fairly similar. Staminate flowers in terminal, compound, monochasial or partly dichasial inflorescences; bracts scalelike, highly irregular in shape. Carpellate flowers solitary and terminal, often overtopped and thereby left in lateral position. Calyx made up of a cup-shaped tube topped with 5 finger-shaped to filiform [to deltoid] lobes about as long as to twice as long as the tube, the lobes frequently hooked or curled at the tips when dry. Corolla much longer than calyx, white [or yellow], salverform, with 5 lanceolate or narrowly deltoid lobes as long (or nearly as long) as the slender corolla tube, imbricate-contorted in bud, often hispid-serrulate along apical margin. Stamens inserted in throat of corolla on very short filaments; anthers linear. Ovary unilocular, with 2 (or 3) intrusive, parietal placentae; style rising to throat of corolla tube, expanded apically and divided into 2 (or 3) lobes. Fruit ovoid or ellipsoid, roughly the size of a hen's egg or more nearly globose, tapered at base, spotted on the surface, crowned with the thickened calyx tube, the sclerified endocarp covered by a tough exo- and mesocarp, the large internal cavity filled with the fleshy placentae in which are embedded numerous black (dry), compressed seeds stacked horizontally or obliquely in the fleshy matrix and having pebbled testae. TYPE SPECIES: *C. calophylla* A. Richard, the only species known when the genus was established. (Named for Sr. D. Luis de las Casas, Captain General of Cuba.)—SEVEN-YEAR-APPLE.

A genus of perhaps 11 species in Florida, the West Indies, and Mexico: *Casasia Acunae* Fernandez & Borhidi (Cuba); *C. calophylla* A. Rich. (Cuba); *C. chiapensis* Miranda (Chiapas, Mexico); *C. clusiifolia* (Jacq.) Urban (Bermuda, Bahamas, Florida, Cuba); *C. domingensis* Urban (Hispaniola); *C. Ekmanii* Urban (Hispaniola); *C. haitiensis* Urban & Ekman (Hispaniola); *C. jacquinioides* (Griseb.) Standley (Cuba); *C. parviflora* Britton, synonymy *fide* Standley; *C. longipes* Urban (Jamaica); *C. piricarpa* Urban, synonymy *fide* Adams; *C. nigrescens* (Griseb.) C. Wright ex Urban (Cuba); and *C. Samuelsonii* Urban & Ekman (Hispaniola). (It should be noted that this list comes from an uncritical examination of the literature and from the Gray Herbarium Card Index. The only herbarium materials that I have studied, except for the survey of stipules mentioned below and extralimital specimens of *C. clusiifolia*, originated in the area of the Generic Flora.) Our *C. clusiifolia* (*Randia clusiifolia* (Jacq.) Chapman, *Genipa clusiifolia* Jacq.) is by far the most widespread species, occurring in our area mostly in the Florida Keys, but also as far north along the coast as Lee County, Florida.

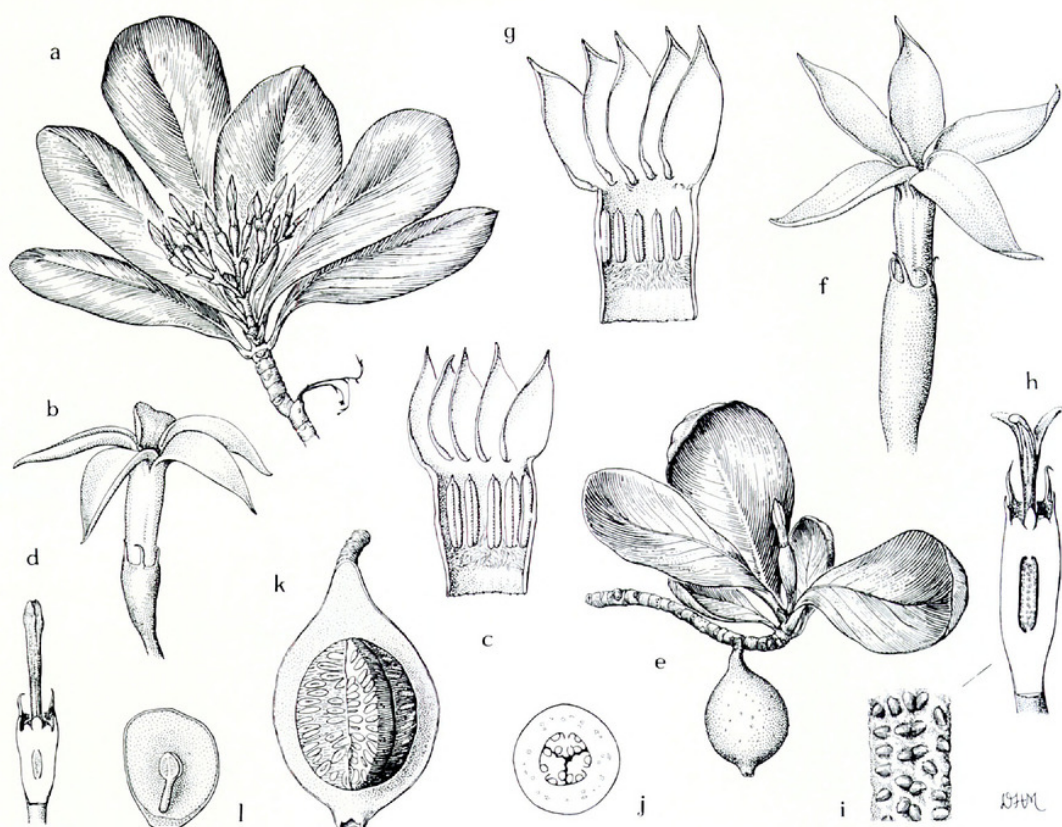


FIGURE 2. *Casasia*. a-l, *C. clusiifolia*: a, branch from staminate plant, showing partially cymose inflorescence, $\times \frac{1}{4}$; b, staminate flower, $\times 1$; c, opened corolla of staminate flower, showing functional stamens adnate to corolla, $\times 1$; d, gynoecium from staminate flower, the ovary in longitudinal section to show rudimentary development of ovary and ovules, $\times 1$; e, branchlet from carpellate plant with single floral bud and fruit, $\times \frac{1}{4}$; f, carpellate flower, $\times 1$; g, opened corolla of carpellate flower with nonfunctional stamens, $\times 1$; h, tricarpellate gynoecium, ovary in longitudinal section to show 1 of 3 placentae, $\times 1$; i, view from axis of portion of spongy placenta showing partially embedded ovules, $\times 5$; j, semidiagrammatic cross section of tricarpellate ovary with 3 parietal placentae, $\times 2$; k, longitudinal section of bicarpellate fruit, 1 placenta sectioned to show embedded seeds, $\times \frac{1}{2}$; l, longitudinal section of seed with embryo embedded in abundant endosperm, $\times 2$.

Casasia clusiifolia tolerates high salinity and lives in coastal scrub and hammocks in our area. Flowers form throughout the year, but mostly during spring and summer. In Florida Tuskes observed that the moth *Aellopos tantalus* uses this species as a larval food plant, evidently along with at least *Annona glabra* L. Almost every plant that he examined showed signs of the moth.

As a whole, the genus *Casasia* is made up of small trees or shrubs with terminal cymose inflorescences (or solitary carpellate flowers), conspicuous white or yellow flowers that blacken upon drying, cupular calyces with subulate to deltoid lobes, salverform corollas with the lobes twisted in bud, stamens on short filaments in the corolla throat, included or nearly included anthers, included stigmas, intrusive parietal placentae bearing numerous embedded ovules, large berries with tough pericarps containing numerous more or less horizontal

seeds in a fleshy matrix, corneous endosperm, and foliaceous cotyledons. Additional useful characters for our species are its usually obovate or oblanceolate, coriaceous leaves clustered toward the tips of thick twigs, staminate flowers in compound monochasia, solitary carpellate flowers, and large, mottled fruits crowned with a much-thickened calyx cup. The parietal placentae filling the ovary make it appear bi- or sometimes trilocular. Most of the published illustrations show either staminate inflorescences or the fruit, seldom the solitary carpellate flowers.

Probably the most closely related genus is *Genipa* L., which throughout the literature is held to differ from *Casasia* in having lateral (vs. terminal or mostly terminal) inflorescences. Urban (1908) further separated *Genipa* by its internally sericeous (vs. glabrous) calyx limb, this entire or with obtuse lobes (vs. lobes filiform to acute), pubescent corolla, exserted anthers and style, and thick (vs. linear) stigmas. A modern reevaluation of these differences is desirable. Despite indications to the contrary in the literature, herbarium material at the Missouri Botanical Garden showed no difference between *Casasia* and *Genipa* in the position of the stipules. One lobe of the interpetiolar stipules is centered between adjacent petiole bases in both, as it is in most Rubiaceae.

The genus needs a full revision. Schumann's treatment in the *Natürlichen Pflanzenfamilien* is based on only one (or perhaps two) species. The principal accounts are those by Standley (*North American Flora*, 1918), Fernandez Zequeira & Borhidi, and Urban (1908, 1927). In addition, Miranda's surprising report of the only continental species should not be overlooked.

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8. *Hamelia* Jacquin, Enum. Syst. Pl. Carib. 2. 1760.

Shrubs with raphide bundles often conspicuous in several organs, pilose to puberulent throughout (except sometimes becoming glabrate with age). Leaves opposite or ternate, petiolate, (oblanceolate to) elliptic (to ovate-lanceolate), with several pairs of pinnate nerves, usually acute or acuminate at both ends;

stipular lobes single between adjacent petioles, narrowly deltoid to subulate. Inflorescence terminal, roughly pyramidal or somewhat flat topped, usually consisting of long, uncrowded cincinni (or occasionally dichasia) in cymose clusters, these not infrequently in thyrsiform arrangements and often with multiple orders of branching. Flowers pentamerous. Calyx lobes low, deltoid, inconspicuous. Corolla red or orange, slender and nearly cylindrical but constricted near the base, the lobes deltoid, only a small fraction of the length of the tube. Stamens inserted on the corolla tube near its base; anthers linear and very long (over half the length of the corolla tube and somewhat longer than the filaments), partly exserted (or sometimes included?), sagittate at base. Style filiform, expanded and papillose in the upper $\frac{1}{2}$ of its length at the mid-level of the anthers. Ovary topped with a conical disc around the base of the style, usually 5-loculate, each locule containing numerous anatropous ovules on axile placentae. Fruit a berry, red before becoming black, ellipsoid, conspicuously crowned with a disc (this sometimes taking the form of a beak) and the persistent calyx. Seeds numerous, small, longer than broad, irregularly shaped, usually angular, coarsely reticulate. LECTOTYPE SPECIES: *Hamelia erecta* Jacq. (= *H. patens* Jacq., the only other species included in the protologue; see Wernham, London Jour. Bot. **49**: 206. 1911; Britton & Millspaugh, Bahama Fl. 411. 1920; and Elias, Mem. New York Bot. Gard. **26**: 112. 1976 for lectotypification and for choice of epithets when the two species are merged). (Named for Henri Louis Duhamel du Monceau, botanist, 1700–1782.)—FIREBUSH.

A genus of about 16 woody species in two sections distributed in tropical and subtropical America and concentrated in Mexico and Central America. A representative of section *HAMELIA*, *Hamelia patens*, $2n = 24$, is the only species indigenous to the continental United States. The range of *H. patens* var. *patens* extends from Lake County, Florida, southward through the West Indies, much of Mexico, Central America, and (mostly western) South America to northern Argentina and Chile. A second variety, *H. patens* var. *glabra* Oersted, is limited to Central America and northern South America.

In Florida *Hamelia patens* var. *patens* most frequently grows in coastal hammocks, although it sometimes occurs inland and has weedy tendencies, turning up in sunny, disturbed places. In tropical America it is common, a pioneer in clearings and a weed, and is cultivated ornamentally. It is also cultivated in the Old World, no doubt escaping there as well. Flowering takes place throughout the year in our area. Bawa & Beach found the flowers to be monomorphic, and they found selfing to yield reduced fruit set, with fruits aborting.

Hamelias are recognized as shrubs or small trees with often secund, red to yellow, frequently angular, tubular flowers with imbricate aestivation and long, linear anthers. The typically five-locular ovary is topped with a persistent, often beaklike disc. The berries contain numerous flattened seeds. *Hamelia patens* var. *patens* is easily separated from all other Rubiaceae in our area by its long, narrow, tubular, orange or red flowers with an inconspicuous calyx and short corolla lobes.

Schumann placed *Hamelia* in his large tribe Gardenieae within subfam.

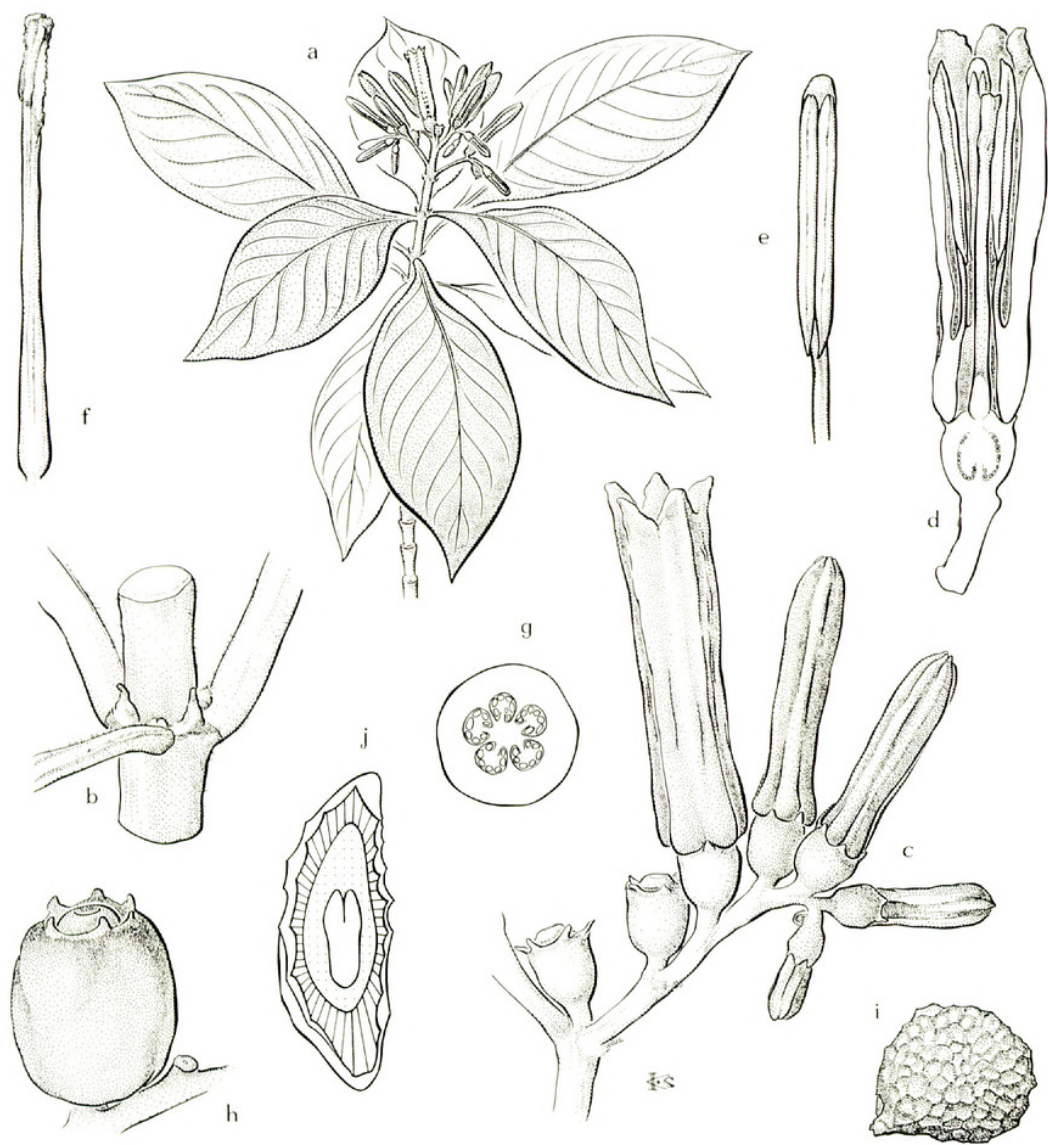


FIGURE 3. *Hamelia*. a-j, *H. patens*: a, flowering shoot—note ternate leaf arrangement, $\times \frac{1}{2}$; b, node with bases of petioles of 3 leaves and interpetiolar stipules, 2 axillary buds visible, $\times 3$; c, portion of inflorescence, $\times 2$; d, flower in longitudinal section—note epipetalous stamens, large anthers, and axile placentation, $\times 3$; e, adaxial side of anther and portion of filament, $\times 4$; f, style with stigmas, $\times 4$; g, diagrammatic cross section of ovary, showing axile placentae with numerous ovules, $\times 6$; h, fruit, a berry, $\times 3$; i, seed, $\times 25$; j, seed in longitudinal section, seed coats unshaded and hatched, endosperm stippled, embryo unshaded, $\times 50$.

Cinchonoideae, a subfamilial and tribal position not generally accepted by subsequent authors. Stressing the presence or absence of raphides in distinguishing the Rubioideae from the Cinchonoideae, Bremekamp (1966), Verdcourt (1958), and Elias positioned *Hamelia* in the Rubioideae, where they all acknowledged, however, that it is anomalous in having imbricate, rather than valvate, aestivation.

At the tribal level, Bremekamp (1966) paired *Hamelia* with *Hoffmannia* Sw.

as the tribe Hamelieae, which Elias adopted in his revision of *Hamelia*, as did Standley & Williams. According to Elias, *Hamelia* and *Hoffmannia* are linked by their woody habit, raphides, imbricate aestivation, ovarian discs, two- to five-locular ovaries, numerous ovules per locule, and baccate fruits. Except for multilocular ovaries, these features are fairly generalized in the Rubiaceae; however, Elias also noted without elaboration similarities in their pollen and seeds. He distinguished *Hamelia* from *Hoffmannia* by the former's occupying lower altitudes and by its having terminal (vs. axillary), usually monopodial, more often paniculate inflorescences generally containing more flowers, usually unribbed and secund corolla tubes, pentamerous (vs. usually tetramerous) flowers, most often 5 (4) locules (vs. usually (4) 3 or 2 locules) in the ovary, stamens inserted lower in the tube, and sagittate anthers. With only a small number of chromosome counts in hand so far, *Hamelia* appears to have $2n = 24$, while only $2n = 48$ is known in *Hoffmannia*.

Steyermark (1974) accepted the tribe Hamelieae but differed from Bremekamp and Elias by including the genus *Bertiera* Aublet, which—unlike *Hoffmannia* and *Hamelia*—has contorted aestivation and lacks raphides. Dwyer, too, associated *Hamelia* and *Hoffmannia* in the Hamelieae but with *Xerococcus* Oersted, which stands apart in having valvate aestivation.

Hamelia has been revised twice in this century. Wernham recognized 28 species in 1911; Elias accepted 12 of these in 1976, changing the name of one, which was a later homonym. Most of the remainder fell into synonymy, a large cluster under the two varieties of *H. patens*. Elias added three species discovered since Wernham's study, bringing the total number in his revision to 16, sorted into two sections of eight species each.

The pollen of *Hamelia patens* is tricolporate, with circular ora and with an areolate, tegillate sexine (Anand & Bhandari).

Beyond being ornamental, *Hamelia patens* has edible berries used in Mexico for preparing a fermented beverage (Standley). Having a high tannin content, the bark has been used in tanning leather (Morton, Standley). As Morton documented, this species has multiple applications in folk remedies, mostly to counter dysentery and to treat skin wounds and irritations.

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9. **Catesbaea** Linnaeus, *Sp. Pl.* **1**: 109. 1753; *Gen. Pl.* ed. 5. 48. 1754.

Spiny shrubs [small trees or scandent shrubs] with puberulous branches often inserted at oblique angles. Leaves opposite or fascicled on short-shoots, glabrous, sessile or on short petioles, small (mostly under 1 cm long in our species) [sometimes virtually absent by reduction]. Spines stiff, sharp, frequently longer than leaves, paired, generally arising at oblique angles. Stipular lobes initially solitary between adjacent petiole bases, quickly cleft into 2 lobes, disappearing during expansion of twig. Flowers borne singly among leaves, on short pedicels, small and inconspicuous [or large and showy], tetramerous. Calyx lobes persistent, subulate, longer than ovary. Corolla white, the tube narrowing toward base, the valvate and deltoid lobes much shorter than tube. Stamens inserted at base of corolla tube, rising to level of lobes. Ovary bilocular, with ovules on faces of septum [or on placentae arising from septum]; stigma bifid. Berries globose, white (or black), containing a small number of compressed seeds with rugose surfaces. TYPE SPECIES: *C. spinosa* L., this the only species in the generic protologue. (Named for Mark Catesby, 1683–1749, British naturalist, known in part for his *The natural history of Carolina, Florida, and the Bahama Islands*.)

A genus of approximately 15 species in the West Indies, one of them reaching the Florida Keys. Most are known from only a single island each, although *Catesbaea spinosa* L., $2n = 24$, *C. melanocarpa* Urban, and *C. parviflora* Sw. occur on a number of islands. Cuba has the greatest number of species—about seven endemics, in addition to two more widespread species. There are about six endemics on Hispaniola. On all other islands where it occurs, *Catesbaea* is limited to one or two species. *Catesbaea parviflora*, the most broadly distributed species, grows on the Florida Keys, the Bahamas, Cuba, Jamaica, Puerto Rico, Antigua, the Cayman Islands, and undoubtedly other islands. In Florida *C. parviflora* is encountered in dry, open areas. Its habitats include pine woods, edges of hammocks, and sand dunes.

With its conspicuous paired thorns and small, clustered leaves widest above

the middle, *Catesbaea* is easily recognized among shrubs in our area, although it might be confused with *Randia*. *Catesbaea* usually has tetramerous flowers (vs. pentamerous ones in *Randia*), valvate (vs. contorted) aestivation, and stamens inserted basally in the corolla (vs. in the throat in *Randia* and *Hoffmannia*). As Proctor pointed out, our species of *Catesbaea* has smaller fruits than our species of *Randia* (4 mm vs. 8–12 mm in diameter). Additional distinguishing features of *Catesbaea* include bilocular ovaries (vs. five-locular in *Hamelia*), perfect flowers (vs. imperfect ones in *Bertiera* and *Randia aculeata*), and solitary, axillary flowers.

Verdcourt diverged from Schumann in placing *Catesbaea* outside of the Gardenieae in the segregate tribe Catesbaeeae J. D. Hooker, which he regarded as close to the Gardenieae. According to him, distinguishing features of the Catesbaeeae are valvate aestivation (vs. contorted or imbricate in the Gardenieae), usually spiny branches, and fleshy fruits containing rugose seeds adhering in a mass.

Catesbaea is in need of revision. The only comprehensive treatment is Standley's (1918). Taxonomy of the genus rests on this, coupled with regional floristic works.

Catesbaea spinosa, which has large, showy flowers, is cultivated as an ornamental shrub.

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