THE GENERA OF THE CYRILLACEAE AND CLETHRACEAE OF THE SOUTHEASTERN UNITED STATES [1]

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CYRILLACEAE Lindley (CYRILLA FAMILY)

Deciduous or evergreen shrubs or small trees, leaves simple, alternate, entire, exstipulate, short-petioled [sessile], glabrous. Inflorescences terminal or axillary racemes, each flower in the axil of an obovate, spatulate, or lanceolate, caducous or persistent bract; pedicels with [or without] 2 lanceolate or oblanceolate bracteoles. Sepals 5, rarely 6 or 7, equal [unequal], [quincuncially] imbricate in bud, ovate, lanceolate, or deltoid, persistent. Petals as many as the sepals, spatulate to oblong-elliptic, white or pinkish white [deep pink or violet]. Stamens 5–10, the insertion hypogynous, filaments terete or flattened and petaloid below the middle; anthers versatile, dehiscing through longitudinal slits [or morphologically basal pores]; pollen grains single, tricolporate (or tetracolporate), with wide longitudinal furrows which narrow in polar view to produce a Y-shape. Gynoecium syncarpous, ovary superior, 3–5-locular, each locule containing 1–3 ovules; style short, stigma 2–5-lobed [or not lobed]. Fruit indehiscent, globose or distinctly 3–5-winged, often devoid of seeds. Seeds without seed coats; endosperm cellular; embryo straight, cylindrical.

A small family of three genera and fourteen species, distributed along the Coastal Plain of the southeastern United States, in the West Indies, Central America, and northern South America. *Cyrilla* and *Cliftonia*, each containing but a single species, occur in our area. The third, *Purdiaea* Planch., is composed of 12 species, distributed in Cuba, British Honduras, Guatemala, and northern South America.

Most authors who have attempted a phylogenetic classification of the Cyrillaceae have placed this family either near the Celastrales or the Ericales, with a few suggesting a relationship with both of these groups. The Cyrillaceae have been shifted from one to the other many times, and

[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation, and under the direction of R. C. Rollins and C. E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40, 41.** (See also the Ericaceae in this issue.) The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in descriptions which is inapplicable to species of this area is placed in brackets. References which have not been checked are marked by an asterisk. The figures of *Cyrilla* and *Clethra* were drawn by Dorothy H. Marsh, in part from material collected by R. B. Channell and H. F. L. Rock.

have been treated as a subfamily of both the Celastraceae and the Ericaceae. They were also occasionally changed from one of these groups to the other in later editions by the same author (Endlicher, 1840, 1841; Lindley, 1835, 1847). As the family has been studied in greater detail, however, the evidence has become increasingly strong for a close relationship between the Cyrillaceae and members of the Ericales, particularly the Clethraceae.

The Cyrillaceae have a well-documented fossil record, with cyrillaceous pollen grains occurring as far back as the Upper Cretaceous, thus indicating that the family is a relatively old one. Although these pollen grains cannot be definitely assigned to any of the living members of the Cyrillaceae, they are quite similar to the pollen of *Cyrilla* and *Cliftonia*. The best documented fossil record is in the Brandon Lignite of Vermont. The most abundant wood and the second most abundant pollen in this fossil flora is that of *Cyrilla* (Spackman, Traverse). The wood, and particularly the pollen, from this deposit is very similar to that of living material — remarkably so in view of the age of the deposit, estimated as late Upper Oligocene by Barghoorn.

The Cyrillaceae are distinguished from related families by the outer whorl of stamens opposite the sepals, the dry, indehiscent fruit, the ovary with 1–3 ovules per locule, and seeds without seed coats.

References:

Baillon, H. Ilicacées. Hist. Pl. **11**: 211–220. 1892. [Includes *Cyrilla* and *Cliftonia*.]

Beauvisage, L. Contributions à l'étude anatomique de la famille des Ternstroemiacées. 470 pp. Tours, 1920. [Includes discussion of the anatomy, particularly of the leaves, of *Cyrilla* and *Cliftonia*.]

Bentham, G., and J. D. Hooker. Cyrilleae. Gen. Pl. **2**: 1225, 1226. 1876.

Candolle, A. de. *Cyrilla*. Prodr. **17**: 292. 1873.

Copeland, H. F. Observations on the Cyrillaceae particularly on the reproductive structures of the North American species. Phytomorphology **3**: 405–411. 1953.

Endlicher, S. Gen. Pl. 1413. 1840. [Ericaceis affines. Cyrilleae.]

———. Ilicineae. Enchiridion Bot. 577–579. 1841. [Includes Cyrilleae.]

Gilg, E. Cyrillaceae. Nat. Pflanzenfam. III. **5**: 179–182. 1892.

Grisebach, A. H. Erläuterungen ausgewählter Pflanzen des tropischen Amerikas. Abh. Ges. Wiss. Göttingen **9**: 3–58. 1860. [Cyrileen. 45.]

Heimsch, C., Jr. Comparative anatomy of the secondary xylem in the "Gruniales" and "Terebinthales" of Wettstein with reference to taxonomic grouping. Lilloa **8**: 83–198. 1942. [Includes a discussion of the anatomy and relationships of the Cyrillaceae.]

Lindley, J. Celastraceae. Nat. Syst. Bot. **2**: 119. 1836. [Includes *Cyrilla* and *Cliftonia*.]

———. Cyrillaceae. Veg. Kingdom ed. 2. 445. 1847.

Mohr, C. T. Cyrillaceae. Plant Life of Alabama. Contr. U. S. Natl. Herb. **6**: 601. 1901.

Sargent, C. S. *Cyrilla, Cliftonia*. Silva N. Am. **2**: 1–8. *pls. 51, 52*. 1891.

Spackman, W. The flora of the Brandon Lignite: geological aspects and a com-

parison of the flora with its modern equivalents. Unpublished Ph.D. Thesis, Biology Dept., Harvard University, Cambridge, Mass., 1949.

STEEVES, M. W. Pollen and spores of the Raritan and Magothy (Cretaceous) formations of Long Island. Unpublished Ph.D. Thesis, Biology Dept., Harvard University, Cambridge, Mass., 1959.

THOMAS, J. L. A monographic study of the Cyrillaceae. Contr. Gray Herb. **186:** 1–114. 1960.

TORREY, J., and A. GRAY. Celastraceae. Fl. N. Am. **1:** 256. 1838. [Includes *Cyrilla* and *Cliftonia*.]

TRAVERSE, A. Pollen analysis of the Brandon Lignite of Vermont. U. S. Bur. Mines Rep. Invest. **5151.** 107 pp. 1955.

UPHOF, J. C. Cyrillaceae. Nat. Pflanzenfam. ed. 2. **20:** 1–12. 1942.

KEY TO THE GENERA OF CYRILLACEAE

Stamens 5, filaments terete; fruit globose or subglobose, longitudinally bisulcate or trisulcate. ..... 1. *Cyrilla.*

Stamens 10, filaments broad and petaloid below the middle; fruit distinctly 3–5-winged. ..... 2. *Cliftonia.*

1. **Cyrilla** Garden ex Linnaeus, Mantissa Pl. 5. 1767.

Shrubs or small trees [up to 25 m. tall], usually branching near the base; bark light gray or brown. Roots shallow, usually running horizontally a few inches beneath the surface of the soil. Leaves simple, alternate, entire, exstipulate, short-petioled, subcoriaceous to coriaceous, dark green, shining above, pale beneath, often clustered toward the ends of branches, densely reticulate, the midvein prominent beneath, prominent or depressed above. Flowers in slender, glabrous, erect or pendulous racemes, borne near the ends of branches, in the axils of leaves or leaf scars of the previous growing season; pedicels articulate at the point of attachment to the rachis, persistent; bracts lanceolate, persistent; 2 bracteoles borne above the middle of the pedicel, alternate or opposite, lanceolate, persistent. Sepals 5, rarely 6, free or occasionally coalescent laterally at the extreme base, persistent, ovate-lanceolate to deltoid, imbricate in bud. Petals as many as the sepals, white or pinkish, inserted on a small glandular disc, membranaceous laterally and above the middle, thickened and glandular on the inner surface medially and below the middle. Stamens 5, opposite the sepals; filaments terete, subulate; anthers versatile, attached near the middle on the dorsal side, 2-lobed, the lobes free below the point of attachment to the filament, united above. Ovary sessile, 2- or 3(rarely 4)-locular, ovules pendulous, anatropous, 1–3 in each locule; stigma 2–4-lobed, the lobes equal to the number of locules. Fruit globose to ovoid or obpyriform, dry, indehiscent, often devoid of seeds, not more than 1 seed developing in each locule. Seeds pendulous, elongate; embryo elongate, cylindrical, the cotyledons short, inferior, the radicle superior. TYPE SPECIES: *C. racemiflora* L. (Named in honor of Dominico Cirillo, an Italian physician and professor at Naples.) — LEATHERWOOD, TITI.

A genus of a single species, *Cyrilla racemiflora* L., easily distinguished from other Cyrillaceae by the pair of persistent bracteoles on the pedicel, petals medially thickened and glandular, five stamens opposite the sepals, and three ovules per locule. It is a plant of acid, and usually sandy, soil along the margins of swamps and small streams and in wet pinelands, distributed in our area along the Coastal Plain from Florida to southeastern Virginia and to southeastern Texas. It also occurs in Mexico, British Honduras, the West Indies, and northern South America.

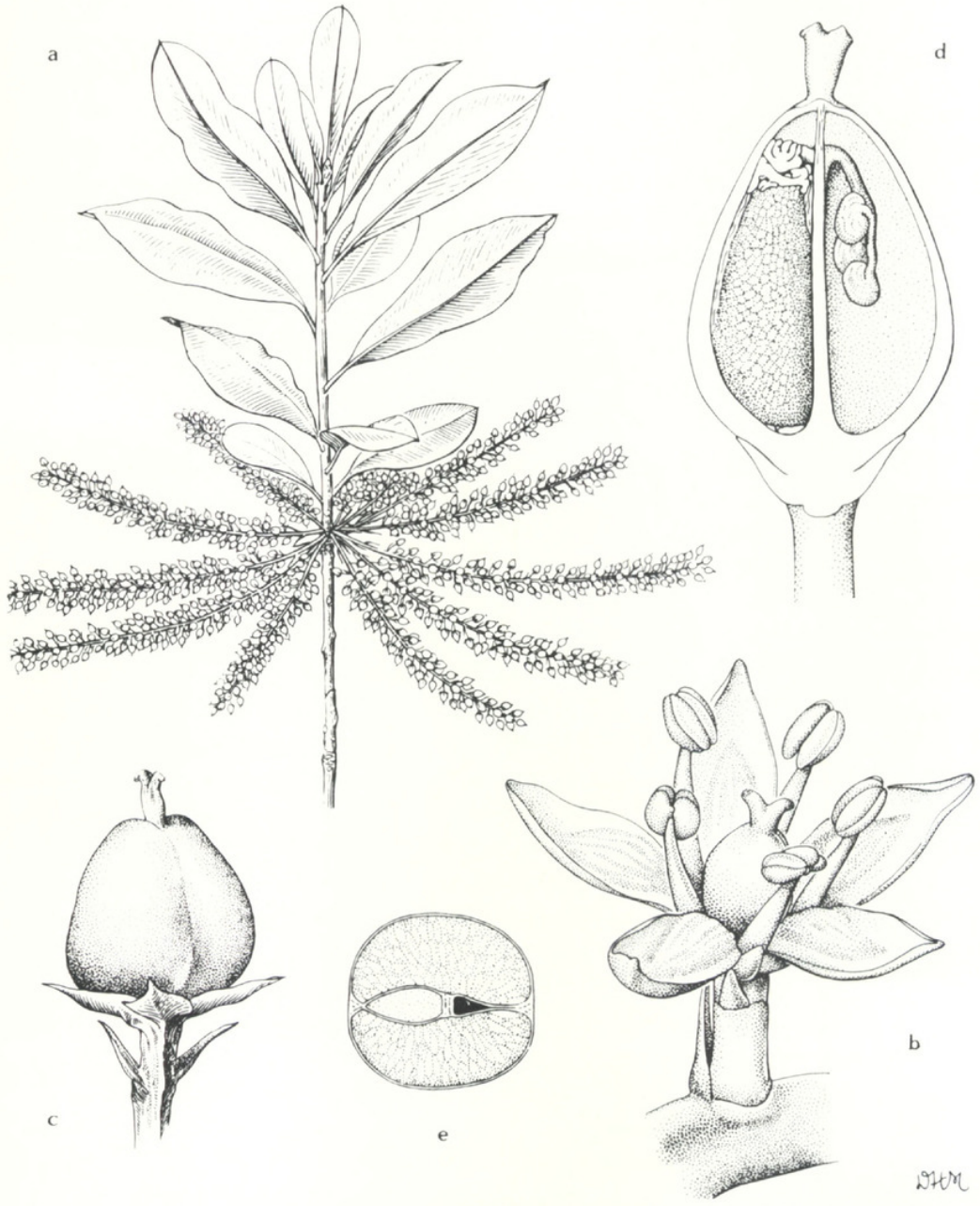

FIG. 1. **Cyrilla.** *C. racemiflora*: a, fruiting branchlet, × ½; b, flower, × 15; c, fruit, × 10; d, nearly mature fruit in vertical section — note large seed (not sectioned) filling left locule, three ovules in right locule, × 15; e, fruit, semi-diagrammatic cross section, position of seed in left locule shown by stippled area, embryo omitted — note parenchymatous development of pericarp, × 10.

This widespread species shows a high degree of local variation in the mountains of northern South America, in Oriente Province, Cuba, and in the southeastern United States, especially in northern Florida. On the basis of this variation, some authors have divided the group into several species, including *C. parvifolia* Raf. and *C. arida* Small in the Southeast. The different variation patterns are graded, however, with intermediate forms connecting the various extremes.

Cyrilla reproduces prolifically by means of adventitious shoots which arise from the roots. These root sprouts spread out radially from an individual, and as they increase in size and become established, they, in turn, give rise to additional sprouts. In some areas, clones of this sort become quite extensive and may cover an acre or more. The buds which give rise to the shoots are exogenous in origin, developing in or near the cork cambium, and apparently do not develop before the initiation of secondary activity. The buds remain in the root for three to four years before emerging as a shoot. During this time the bud establishes vascular connection with the root and increases in size at a rate which is just sufficient to keep pace with the secondary activity of the root.

This sprouting mechanism is the primary means of reproduction in the Cyrillaceae, for the abundant fruits produced each year rarely contain seeds. Parthenocarpic fruits of this type are found, almost without exception, toward the middle of a large clone, thus indicating that *Cyrilla* must have a rather high degree of self-sterility. Apparently self-fertilization provides sufficient stimulus to initiate fruit development, but seeds are developed only when a plant receives pollen from a different individual.

Cyrilla is occasionally cultivated as an ornamental in the southeastern United States and in a few botanical gardens outside that area on the East Coast and in Europe. It is valued for its graceful racemes of white flowers which bloom over a period of a month or more and are followed by small yellow fruits which are also attractive and persist until late autumn. In some areas *Cyrilla* is an important source of nectar for honey known locally as "titi" honey, in reference to one of the colloquial names for *Cyrilla*, and said to have a delicate and very delicious flavor.

REFERENCES:

BARGHOORN, E. S. Geological and botanical study of the Brandon Lignite and its significance in coal petrology. Econ. Geol. **45**: 344–357. 1950.

——— and W. SPACKMAN. A preliminary study of the flora of the Brandon Lignite. Am. Jour. Sci. **247**: 33–39. 1947.

FERNALD, M. L. Overlooked species, transfers and novelties in the flora of eastern North America. Rhodora **46**: 46. 1944. [Notes on *C. racemiflora* var. *subglobosa*.]

LUNDELL, C. L. Cyrillaceae. Fl. Texas **3**: 109–111. 1943.

MASTERS, M. T. *Cyrilla racemiflora*. Gard. Chron. III. **30**: 198. 1901.

SHUTTLEWORTH, R. *Cyrilla parvifolia*. In NASH, Notes on some Florida plants II. Bull. Torrey Bot. Club **23**: 101, 102. 1896.

STOUTEMYER, V. T., and F. L. O'ROURKE. Vegetative propagation of *Cyrilla*. Am. Nurseryman **76**(11): 5, 6. 1942.

2. **Cliftonia** Banks ex Gaertner f. Fruct. et Sem. Pl. 3: 246. 1805.

Evergreen shrubs or small trees, usually branching near the base, rarely becoming up to 12 m. tall; bark reddish brown or gray, thick and spongy on the trunks of older trees; young stems dark red, smooth, becoming gray and scaly after 1–2 years. Leaves simple, alternate, entire, exstipulate, short-petioled, subcoriaceous or coriaceous; light green, shining above, pale, glaucous beneath; oblanceolate-elliptic or rarely obovate-oblanceolate, apex acute or slightly emarginate. Flowers in terminal or axillary racemes, glabrous; rachis attenuate, ridged, each ridge terminating in a small, concave mound at the base of a bract; bracts white or occasionally pinkish, usually turning brown above the middle, membranaceous, obovate-spatulate or spatulate, slightly concave and thickened basally, articulate at the base, caducous well before anthesis; 2 bracteoles borne alternately on the pedicel, usually shedding shortly after anthesis. Sepals 5, rarely 6 or 7, white or pinkish, deltoid, persistent, membranaceous at anthesis, becoming foliaceous at maturity. Petals white or pinkish, imbricate in bud, occasionally weakly clawed near the base, longitudinally 3-veined. Stamens 10 in 2 whorls of 5, the outer opposite the sepals and inserted lower on the receptacle than the inner which is opposite the petals; filaments laterally expanded and petaloid below the middle, narrowing abruptly, becoming terete and subulate above; anthers versatile, attached slightly below the middle. Ovary borne on a small, slightly concave, glandular nectariferous disc, 3–5-locular, each locule with a single, pendulous ovule; stigma massive, subsessile, 2–5-lobed. Fruit 2–5-winged, dry, indehiscent, usually devoid of seed, but sometimes with as many as 5. Seeds consisting of an elongate embryo with short cotyledons, surrounded by a mass of cellular endosperm. TYPE SPECIES: *Cliftonia monophylla* (Lam.) Britton ex Sarg. (Named in honor of D. G. Clifton, Chief Justice of West Florida) — BUCKWHEAT TREES.

A genus of a single species, *Cliftonia monophylla,* distributed along the Coastal Plain of southern Georgia, Alabama, Mississippi, and northern Florida. *Cliftonia* apparently has a very narrow ecological tolerance, as well as geographical range, occurring only in very wet, sandy, acid soils. It is nearly always found growing in association with *Sarracenia* L.

Cliftonia is very distinctive and is easily distinguished from related genera by the winged fruit which resembles that of *Fagopyrum,* the massive, 3–5-lobed, subsessile stigma, and the filaments which are laterally expanded and petaloid below the middle. In spite of its distinctiveness, *Cliftonia* was originally described as a species of *Ptelea* by Lamarck, apparently on the basis of the winged fruits.

The fruits of *Cliftonia,* as of *Cyrilla,* are usually parthenocarpic, and the plants reproduce primarily by root sprouts. In contrast to *Cyrilla,* however, *Cliftonia* shows very little variation throughout its range and has been treated as a monotypic genus by every author who has dealt with this group. The narrow geographic range and the lack of variation indicate that *Cliftonia* is probably a relict form in the present-day flora.

REFERENCES:

BRITTEN, J. Note on the history of *Cliftonia*. Jour. Bot. **43**: 282–284. 1905.

NUTTALL, T. Buckwheat Tree. N. Am. Sylva **2**: 39–44. 1865.

RENDLE, A. B. Notes on Myricaceae. Jour. Bot. **41**: 87. 1903. [Includes notes on the origin of the name *Cliftonia*.]

WATSON, S. A point in nomenclature. Bull. Torrey Bot. Club **14**: 167. 1887. [On the specific name of *Cliftonia*.]

WILLDENOW, K. L. *Mylocaryum* (*Cliftonia*). Enum. Pl. Berol. 454. 1809.

CLETHRACEAE Klotzsch (WHITE ALDER FAMILY)

Deciduous shrubs or small trees with alternate, simple, exstipulate, serrate-margined leaves. Flowers in terminal racemes or panicles, bisexual, regular, the insertion hypogynous. Rachis, bracts and pedicels densely clothed with stellate [simple] trichomes. Sepals 5, persistent, quincuncially imbricate, united at the extreme base, free above. Petals 5, free, alternate with the sepals, deciduous. Stamens 10 [rarely 12], in 2 whorls of 5, the outer whorl opposite the petals, the inner opposite the sepals; filaments glabrous or pubescent, adnate to the corolla at the extreme base; anthers extrorse in bud, becoming inverted and introrse at anthesis by a straightening of the filament, dehiscing by means of apical (morphologically basal) slitlike pores; pollen grains single, tricolporate. Gynoecium syncarpous, the ovary superior, 3-locular, with axile placentation; ovules numerous, small, anatropous; style single, dividing near its apex into a 3-lobed stigma. Fruit a 3-valved, loculicidal capsule. Seeds numerous, small [occasionally winged], with fleshy endosperm and very thin seed coats, the embryo cylindrical. TYPE GENUS: *Clethra* L.

A small family composed of a single genus, *Clethra*, with 30–40 species primarily of tropical or subtropical Asiatic and American distribution. *Schizocardia* Smith & Standley, from Central America, was described in the Clethraceae, but is now known to be a species of *Purdiaea* (Cyrillaceae).

The Clethraceae were first raised to family status by Klotzsch on the basis of the regular flowers with separate petals, anthers with poricidal dehiscence, three-lobed stigma, and loculicidal capsule. Most subsequent authors have agreed with this treatment, and generally the Clethraceae have been considered to be primitive members of the Ericales. However, recent authors have suggested that certain of the characteristics of *Clethra* which are often considered as primitive, may be derived. Among these Copeland (1943) included the tricarpellate ovary with loculicidal dehiscence, and Kavaljian pointed out that the corolla of separate petals may be a derived condition in the Clethraceae, as was previously suggested for this condition in the Pyroleae and Monotropoideae by Copeland (1947). Also, the vascular supply to the sepals in the species of *Clethra* which have been studied show a single trace with a single associated gap, a condition generally considered to be derived, not primitive. The seeds

of *Clethra,* with seed coats only a single cell layer thick, also indicate a reduction.

References:

Baillon, H. Ericacées. Hist. Pl. **11:** 122–210. 1892. [Includes *Clethra* as series Clethreae.]

Britton, N. L. Clethraceae. N. Am. Fl. **29:** 3–9. 1914.

Candolle, A. P. de. *Clethra.* Prodr. **7:** 588–590. 1839. [Under tribe Andromedeae of Ericaceae.]

Copeland, H. F. A study, anatomical and taxonomic of the genera of Rhododendroideae. Am. Midl. Nat. **30:** 533–625. 1943. [Comments on *Clethra* under *"Bejaria."*]

———. Observations on the structure and classification of the Pyroleae. Madroño **9:** 65–102. 1947.

Drude, O. Clethraceae. Nat. Pflanzenfam. IV. **1:** 1, 2. 1897.

Gray, A. Clethraceae. Syn. Fl. N. Am. **2:** 44, 45. 1878.

Kavaljian, L. G. The floral morphology of *Clethra alnifolia* with some notes on *C. acuminata* and *C. arborea.* Bot. Gaz. **113:** 392–413. 1952.

Klotzsch, J. F. Stüdien uber die natürliche Klasse Bicornes Linné. Linnaea **24:** 1–88. 1851.

Lamarck, J. Clethra. Encycl. Méth. Bot. **2:** 45, 46. 1786. [*C. tomentosa,* 46.]

Smith, A. C., and P. C. Standley. *Schizocardia,* a new genus of trees of the family Clethraceae. Trop. Woods **32:** 8–14. 1932.

Thomas, J. L. *Schizocardia belizensis*: a species of *Purdiaea* (*Cyrillaceae*) from Central America. Jour. Arnold Arb. **42:** 110. 111. 1961.

1. **Clethra** Linnaeus, Sp. Pl. **1:** 566. 1753; Gen. Pl. ed. 5. 188. 1754.

Deciduous shrubs or small trees, leaves alternate, simple, obovate, ovate or oblong, with serrate margins. Flowers in terminal racemes or panicles, fragrant. Bracts subtending the flowers, lanceolate, caducous or persistent, usually dropping shortly after anthesis; densely clothed with stellate or simple trichomes or both. Pedicels ridged and somewhat flattened laterally, increasing considerably in length during the maturation of the flower. Sepals 5, equal, quincuncially imbricate (with 2 sepals that are totally external, 2 totally internal, and 1 with 1 edge external and 1 edge internal), united at the extreme base, free above, lanceolate, elliptic, or ovate, the apex acute or obtuse, persistent in fruit. Petals 5, free, arranged in a quincuncial pattern in bud, spreading apart at anthesis, white or occasionally pinkish, alternate with the sepals, glabrous [ciliate margins], obovate or obovate-elliptic. Stamens 10, in 2 whorls of 5, the outer whorl opposite the petals, arising at a slightly lower level and often somewhat shorter than the inner whorl which is opposite the sepals; filaments glabrous or pubescent, somewhat flattened, laterally expanded and adnate to the corolla at the extreme base; anthers extrorse in bud, becoming inverted and introrse at anthesis by a straightening of the filament, 2-lobed, sagittate, the lobes separate above the middle for about one-half their length, but remaining together below the middle, becoming attenuate toward the base, the two thecae of each lobe becoming confluent shortly before the

pollen is shed, dehiscing by means of apical (morphologically basal) pore-like slits; pollen grains single, tricolporate. Gynoecium syncarpous, pubescent to hirsute, ovoid to subglobose, with a small depression at the apex at the point of connection with the style; 3-locular, each locule containing a single, pendent, placental arm which arises from a central column of tissue extending longitudinally from the receptacle to near the apex of the ovary; ovules numerous, small, anatropous, borne on the outer surface of the placental arm; style single, cylindrical, dividing near the apex into 3 lobes which are stigmatic at their tips, shorter than the stamens at anthesis, becoming equal to or longer than the stamens shortly after anthesis. Fruit a globose or subglobose, 3-lobed, 3-valved, loculicidal capsule, more or less inclosed at maturity by the persistent calyx. Seeds numerous, small, irregularly ovoid [occasionally winged], with very thin seed coats. TYPE SPECIES: *C. alnifolia* L. (Name Greek, *Clethra*, alder, alluding to the resemblance of the leaves of the type species to those of an alder.) — SWEET PEPPERBUSHES.

A genus of 30–40 species, represented in our area by only *Clethra alnifolia* L., *C. acuminata* Michx., and *C. tomentosa* Lam. *Clethra tomentosa*, treated by some authors as a variety of *C. alnifolia*, differs from that species in having leaves that are densely tomentose on the lower surface and sepals that are longer and obtuse, rather than acute.

De Candolle divided *Clethra* into two sections: EUCLETHRA (§ *Clethra*) with exserted stamens and styles, and CUELLARIA, with included stamens and styles. Drude described a third section intermediate between these to include a single species, *C. arborea*, with stamens included but with the style exserted. Hu, in a revision of the Chinese species, added still another section, again to include only a single species, and divided sect. CLETHRA (§ *Euclethra* DC.) into four series. According to this scheme, the species in our area belong in sect. CLETHRA, ser. *Alnifoliae*.

In common with a majority of the Ericales, species of *Clethra* are usually found growing in acid soils. *Clethra alnifolia* is distributed in acid swamps and low, moist woods and pinelands along the Coastal Plain from Maine to Texas, with occasional extensions into the Piedmont, particularly in the Carolinas. *Clethra tomentosa* (or *C. alnifolia* var. *tomentosa* Michx.) is more restricted, occurring only on the Coastal Plain from southern North Carolina to Louisiana. The two thus overlap geographically in this area. *Clethra acuminata*, distinguished from the other species in our area in having oval or oblong, acuminate leaves, solitary racemes, and pubescent filaments, is geographically isolated from the other species, occurring on the Appalachian Plateau and inner Piedmont, from southern West Virginia to northern Georgia.

Chromosome numbers have been reported by Hagerup for *C. arborea* ($n = 8$), and *C. alnifolia* ($n = 16$). Other genera of the Ericales for which a base number of 8 has been reported are *Calluna* and *Monotropa* in the Ericaceae (Hagerup, Löve & Löve) and *Melichrus* in the Epacridaceae (Smith-White). Several other genera of the Epacridaceae, however, have

been reported to have a base number of $n = 4$, which could easily be the original base number for the Clethraceae.

FIG. 2. **Clethra.** *C. alnifolia*: a, flowering branchlet, some leaves and racemes removed, × ½; b, flower, × 3; c, d, anthers, inner and outer views, × 15; e, ovary and base of style in vertical section, diagrammatic, stylar canal in black, × 15; f, ovary, diagrammatic cross section, × 15; g, mature capsule, seeds shed — note persistent placentae, × 8.

The unusual structure of the stamens in the Clethraceae has been the subject of considerable discussion, and there is still no universal agreement as to whether the anther is in the normal position in bud and inverted at anthesis or vice versa. A majority of recent authors is of the opinion that the anthers are inverted at anthesis, so that the apparent apex is the morphological base. This interpretation, which is that followed in the present treatment, is based on the pattern of the vascular trace in the anther. At anthesis, the stamen trace bends downward just beyond the point at which it enters the anther. There is, however, a small extension of the trace which continues upward in the connective tissue for a short distance. In the normal pattern of stamen vascularization, in taxa in which the stamens do not undergo a 180° rotation, the stamen trace passes longitudinally through the anther toward the apex. A pattern similar to this is found in the stamens of *Clethra* before anthesis. Thus

the anther is interpreted as being in the normal position in bud and inverted after anthesis. Hu disagrees, stating that the 180° rotation of the anther is merely the result of a straightening of the filament, and only after the filament has straightened is the anther normally oriented. In this connection, she suggests that the anther rotation is comparable to the unfolding or unrolling of a leaf.

Several species of *Clethra,* including the three species in our area, are cultivated as ornamentals in many parts of the world. They are easily propagated either by seeds or by soft-wood cuttings. The cultivated species are prized for the spicy fragrance of their blossoms, and for their mid- or late-summer flowering period — a time when few plants are in flower. *Clethra alnifolia* f. *rosea* Rehd., a pink-flowered form which occurs sporadically in the wild, is commonly found in cultivation.

REFERENCES:

BENTHAM, G., and J. D. HOOKER. *Clethra.* Gen. Pl. **2:** 603, 604. 1876.

BRITTON, E. G. *Clethra alnifolia.* Addisonia **1:** 23. 1916.

FOX, H. M. Three hardy native American shrubs. Gard. Chron. III. **122:** 89. 1947. [*Fothergilla Gardenii, Itea virginica,* and *Clethra alnifolia.*]

FULLING, E. H. Two midsummer flowering shrubs — *Abelia* and *Clethra.* Jour. N. Y. Bot. Gard. **28:** 237–242. 1927.

HAGERUP, O. Morphological and cytological studies of *Bicornes.* Dansk Bot. Ark. **6**(1): 1–27. 1928.

HANDY, L. H. A pink-petaled form of *Clethra alnifolia.* Rhodora **9:** 195, 196. 1907.

HU, S. Y. A revision of the genus *Clethra* in China. Jour. Arnold Arb. **41:** 164–190. 1960.

LECHNER, S. Anatomische Untersuchungen über die Gattungen *Actinidia, Saurauia, Clethra* und *Clematoclethra* mit besonderer Berücksichtigung ihrer Stellung im System. Beih. Bot. Centr. **32**(1): 431–467. 1915.

MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. **36:** 513–660. 1946. [*C. alnifolia,* 585.]

MEISSNER, C. F. *Clethra. In* Martius, Fl. Brasil. **7:** 165–170. 1863.

REHDER, A. Einige neuere oder seltenere Gehölze. Mitt. Deutsch. Dendr. Ges. **1907**(16): 69–76. [1908.] [*C. alnifolia* f. *rosea,* 75.]

SARGENT, C. S. *Clethra alnifolia* var. *tomentosa.* Gard. Forest **4:** 64. 1891.

WILSON, C. L. The phylogeny of the stamen. Am. Jour. Bot. **24:** 686–699. 1937.