

THE GENERA OF ERICACEAE IN THE SOUTHEASTERN
UNITED STATES ¹

CARROLL E. WOOD, JR.

ERICACEAE Jussieu (HEATH FAMILY)

Trees or shrubs to herbs or fleshy parasites, rarely trailing or scrambling vines [or epiphytes], almost all of acid soils and mostly with mycorrhizal associations. Leaves alternate or sometimes opposite or whorled, simple,

¹Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment (which includes Monotropaceae and Pyrolaceae) follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued through those in volumes 40 and 41. It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area with any supplementary material in brackets. The key (which attempts to avoid switching from flowering to fruiting material) is designed for the species of this area. References which I have not seen are marked by an asterisk.

The preparation of this study of Ericaceae has led into unexpected byways, and the results are somewhat more voluminous than had been anticipated. The group is one which has long attracted attention, and, in addition to the taxonomic difficulties, the literature is formidable. On the other hand, the numerous published studies have begun to provide real bases for an understanding of the complex biological problems, and the many papers have been most gratefully drawn upon. The outlines of the family itself seem clear, but those of the subfamilies and tribes are subject to very different interpretations. At the generic level knotty problems were encountered especially in the Andromedeae, in which *Andromeda* was long used as a catchall; I am satisfied with the generic limits of all of our members of the tribe with the possible exception of *Leucothoe*, in which § *Eubotrys* is still something of a snag. The generic treatment of *Vaccinium* is another thorny question, and on the subgeneric classification of this and *Rhododendron* taxonomic conclusions are anything but unanimous. Difficult problems in variation at the specific level are present especially in *Rhododendron* and *Vaccinium*, both of which I am glad to be able to leave in abeyance.

Many people have contributed generously to this study. In addition to the valued comments of my immediate colleagues and the careful help of Mrs. Gordon W. Dillon in the preparation of the manuscript, I am grateful for their assistance with specimens or information to R. B. Channell, G. R. Cooley, W. H. Duncan, R. J. Eaton, Mrs. J. Norman Henry, J. Kucyniak, Miss Clermont H. Lee, Mrs. E. O. Mellinger, J. D. Ray, L. E. Richardson, H. F. L. Rock, and E. T. Wherry. Henry T. Skinner has kindly read the manuscript on *Rhododendron*, R. A. Howard has generously given me access to his unpublished data on the nodal anatomy of members of the family, and J. L. Thomas has struggled valiantly with some frustrating cytological material. I have also been privileged to check a number of distributions against the mounted materials of the herbarium of the Department of Botany at the University of North Carolina at Chapel Hill. The eight generic illustrations are the continuing and careful work of Dorothy H. Marsh.

exstipulate, often coriaceous and persistent [frequently needle-like]; nodes with one trace from one gap. Flowers bisexual (rarely functionally unisexual and the plants dioecious), characteristically regular, in some irregular (mostly by displacement), most commonly 5(4-7)-merous, typically obdiplostemonous, the insertion hypogynous to epigynous. Inflorescences basically racemose (racemes, panicles or corymbs), the individual flowers in the axils of leaves or bracts, the pedicels typically with 2 lateral bractlets. Perianth usually biseriate (the calyx reduced in *Monotropa*). Calyx 4-7-lobed or sepals distinct, usually persistent, valvate, imbricate or reduplicate in bud. Corolla of 4-7 sometimes distinct but usually united petals, often funnelform, campanulate or urceolate, convolute or imbricated in bud. Stamens usually twice or (less frequently) equal the number of petals, usually inserted at the edge of a nectariferous, variously lobed disc [rarely epipetalous], distinct, the filaments often flattened, dilated, or S-shaped [united in some tropical *Vaccinioideae*]; anthers becoming inverted in development, dehiscing from the base (the apparent apex) by longitudinal slits, clefts, or pores, often with terminal awns or abaxial spurs; pollen grains in tetrads or single. Gynoecium syncarpous, the carpels [2]3-7[-10], typically 4 or 5; stigma simple, often lobed; style single, with a stylar canal with as many rays as locules and continuous with the locules; ovary 1, superior, half-inferior or inferior, typically with as many locules as carpels, the placentation axile, but sometimes loculate below and 1-locular above, the placentation then axile below, parietal above, or with twice as many locules as carpels by the development of additional partitions; ovules anatropous to campylotropous, 1-integumented, numerous to 1. Fruit a loculicidal or septicidal capsule, berry, or drupe, the calyx usually persistent, rarely accrescent and fleshy. Seeds usually small, sometimes winged or tailed; embryo small (in parasitic forms very much reduced), straight, with fleshy endosperm. Base chromosome numbers 6, 8, 12, 13, 19, 23. (Including *Monotropaceae*, *Pyrolaceae*, *Vacciniaceae*.) TYPE GENUS: *Erica* L.

A family of about 75-80 genera and some 2000 species, widely distributed, mostly in acid soils, from sea level to high elevations in the tropics, and throughout the temperate regions of both hemispheres (although largely lacking in Australia where replaced by *Epacridaceae*), some extending into the arctic. About 35 genera occur indigenously in the United States, 20 in our area. *Erica* L. and *Calluna* Salisb. are naturalized to the north of our area.

Ericaceae share the syncarpous gynoecium with single stigma, style, and ovary, the style with a fluted canal continuous with each locule; the flowers generally with sympetalous corolla; the androecium typically obdiplostemonous, the usually distinct stamens from the edge of a nectariferous disc; the anthers inverted either in development or at anthesis, opening by morphologically basal pores or slits or longitudinally; and the pollen usually in tetrads (with the exception of *Monotropoideae* and a few others). Some of the apopetalous genera appear to be primitively so (e.g.,

Befaria, *Elliottia*) but others seem to be derived types (e.g., *Ledum*, *Pyrola*, *Chimaphila*, *Monotropa*). The group is predominantly woody with specialized forms herbaceous (e.g., species of *Gaultheria*, Pyroleae, Monotropoideae).

The family is further characterized by a well-marked combination of embryological features found only in the Ericales: ovules with a single integument and thin, evanescent nucellus, a more or less differentiated endothelium, a lack of parietal cells; embryo sac of the Polygonum type from a single archesporial cell which functions directly as the megaspore mother cell; endosperm cellular, the first two divisions transverse; the formation of endosperm haustoria at both ends of the embryo sac (with a few exceptions); single-layered seed coat formed from the outermost layer of the integument; endosperm fleshy, the embryo straight; anthers lacking a fibrous layer, the tapetum with multinucleate cells; pollen grains 2-celled and (in most instances) adhering in tetrads.

Structurally and embryologically the Ericaceae are clearly related to Clethraceae and Cyrillaceae, on the less specialized side, and to Epacridaceae and Empetraceae, on the more specialized, the five constituting the Ericales.

Subfamilial categories are not well agreed upon, and the limits of the family itself have been variously interpreted, some authors separating Pyrolaceae, Monotropaceae, and Vacciniaceae. However, Pyroleae and Monotropeae appear to be related to Andromedeae and Arbutaeae, and, with the exception of the herbaceous or parasitic habit and attendant modifications, the features are all those of Ericaceae (Henderson, Copeland). The Vaccinioideae differ only in the partially to completely inferior ovary (cf. *Gaultheria*) which becomes baccate or drupaceous in fruit (cf. Arbutaeae, Monotropoideae); separation as a family on the basis of this one character seems hardly justifiable. The Ericaceae are here treated as composed of subfamilies Ericoideae (including Rhododendroideae, Arbutoideae, Pyroloideae), Monotropoideae, and Vaccinioideae; five tribes (by some regarded as eleven) occur in our area.

The family includes both small, isolated, well-marked genera and large, polymorphic complexes with indistinct generic lines. Within genera species may be similarly distinct or complicated. Polyploidy is frequent in some genera.

The flowers of most are showy, those of the temperate areas being adapted for pollination by insects (or those of some tropical species by birds). The stamens of species with campanulate to urceolate pendent flowers are often appendaged in such a way that the disturbance of the anthers by an insect visitor and the sifting out of pollen are insured. In species with horizontal flowers and exserted stamens, on the other hand, the stamens are unappendaged but the pollen tetrads are often linked by viscin strands so that the entire mass is pulled from the anther as a cobwebby net. In Andromedeae the anthers frequently have disintegration tissue which produces powdery white areas (of apparently unknown function) in the connective.

Economically the group is notable chiefly as a source of showy ornamental woody plants, but various species of *Vaccinium* (blueberries, cranberries, mountain cranberries) are of increasing importance for their fruits.

REFERENCES:

- ARTOPOEUS, A. Über den Bau und die Öffnungsweise der Antheren und die Entwicklung der Samen der Ericaceen. *Flora* 92: 309–345. 1903.
- BAILLON, H. Éricacées. *Hist. Pl.* 11: 122–210. 1892. [Includes Epacridaceae, Lennoaceae, Diapensiaceae, Empetraceae, Clethraceae, *et al.*]
- BELL, H. P., and J. BURCHILL. Winter resting stages of certain Ericaceae. *Canad. Jour. Bot.* 33: 547–561. 1955. [Mostly concerned with state of development of ovules and stamens; includes most woody Ericaceae of eastern Canada, many of our genera.]
- BENTHAM, G., and J. D. HOOKER. Vacciniaceae, Ericaceae, Monotropeae. *Gen. Pl.* 2: 564–608. 1876.
- BERGMAN, H. F. Internal stomata in ericaceous and other unrelated fruits. *Bull. Torrey Bot. Club* 47: 213–221. 1920.
- BREITFELD, A. Der anatomische Bau der Blätter der Rhododendroideae in Beziehung zu ihrer systematischen Gruppierung und zur geographischen Verbreitung. *Bot. Jahrb.* 9: 319–379. *pls. 5, 6.* 1888.
- CANDOLLE, A. P. DE. Vaccinieae, Ericaceae. *Prodr.* 7: 552–733; Pyrolaceae. 772–776; Monotropeae. 779–781. 1839.
- COPELAND, H. F. The development of seeds in certain Ericales. *Am. Jour. Bot.* 20: 513–517. 1933. [Stages in development of seeds and ovules observed in *Sarcodes*, *Chimaphila*, *Pyrola*, *Pterospora*, *Pleuricospora*.]
- . A study, anatomical and taxonomic, of the genera of Rhododendroideae. *Am. Midl. Nat.* 30: 533–625. 1943. [Many important data; extensive bibliography.]
- . Observations on the structure and classification of the Pyroleae. *Madroño* 9: 65–102. 1947.
- COX, H. T. Studies in the comparative anatomy of the Ericales. I. Ericaceae — subfamily Rhododendroideae. *Am. Midl. Nat.* 39: 220–245. 1948. II. Ericaceae — subfamily Arbutoideae. *Ibid.* 40: 493–516. 1948. [Wood anatomy.]
- DON, D. An attempt at a new arrangement of the Ericaceae. *Edinburgh New Philos. Jour.* 17: 150–160. 1834. [The basic paper in the taxonomy of the family.]
- DRUDE, O. Pyrolaceae, Ericaceae. *Nat. Pflanzenfam.* IV. 1: 3–11, 15–65. 1889.
- DUFRENOY, J. The biological significance of false witches'-brooms in ericaceous plants. *Jour. Wash. Acad. Sci.* 8: 527–532. 1918. [Fungi on *Arbutus* and *Vaccinium*; no evidence of a symbiotic association comparable to the mycorrhizal one.]
- ERDTMAN, G. Pollen morphology and plant taxonomy. V. On the occurrence of tetrads and dyads. *Sv. Bot. Tidskr.* 39: 286–297. 1945.
- GODLEY, E. J. Unisexual flowers in the Ericales. *Nature* 180: 284, 285. 1957. [In Epacridaceae (*Cyathodes*, *Leucopogon*); also mentions *Gaultheria*, *Epigaea*.]
- GRAY, A. Ericaceae. *Syn. Fl. N. Am.* 2(1): 14–50. 1878. [An important revision.]

- GREVILLIUS, A. Y., and O. KIRCHNER. Ericaceae. In O. KIRCHNER, E. LOEW, & C. SCHRÖTER, *Lebensgeschichte der Blütenpflanzen Mitteleuropas*. 4(1): 1-164. 1923. Monotropaceae. *Ibid.* 181-243. 1925. [Includes extensive bibliography.]
- GRIS, A. Anatomie comparée de la moelle dans les Éricinées. *Bull. Soc. Bot. Fr.* 17: 11-16. 1870.
- HAGERUP, O. Morphological and cytological studies of Bicornes. *Dansk Bot. Ark.* 6(1): 1-27. 1928.
- . Zytoökologische Bicornes-Studien. *Planta* 32: 6-14. 1941. [Ericaceae (including Pyrolaceae), Empetraceae.]
- . The morphology and systematics of the leaves in Ericales. *Phytomorphology* 3: 459-464. 1953.
- HARA, N. Development of the leaf margin in the Ericaceae (a preliminary report). *Bot. Mag. Tokyo* 69: 442-446. *pl.* 12. 1956.
- HENDERSON, M. W. A comparative study of the structure and saprophytism of the Pyrolaceae and Monotropaceae with reference to their derivation from the Ericaceae. *Contr. Bot. Lab. Univ. Penn.* 5: 42-109. 1920.
- IKUSE, M. The presence of the viscid threads among pollen grains in Phyllo-doceae, etc. of Ericaceae. *Jour. Jap. Bot.* 29: 146-148. 1954. [Cf. COPELAND, 1943.]
- KEARNEY, T. H. Report on a botanical survey of the Dismal Swamp Region. *Contr. U. S. Natl. Herb.* 5: 321-550. *pls.* 65-77. 1901. [499-503, leaf anatomy of *Leucothoë axillaris*, *L. racemosa*, *Lyonia lucida*, *L. ligustrina*, *Kalmia angustifolia*, *Vaccinium arboreum*, *V. macrocarpon*.]
- KELLEY, A. P. Mycotrophy in plants. xvi + 223 pp. *Chronica Botanica*, Waltham, Mass. 1950. [Includes a complete review of the literature on mycorrhizae.]
- MATTHEWS, J. R., and E. M. KNOX. The comparative morphology of the stamen in the Ericaceae. *Trans. Proc. Bot. Soc. Edinburgh* 29: 243-281. 1926.
- NIEDENZU, F. Über den anatomischen Bau der Laubblätter der Arbutoideae und Vaccinioideae in Beziehung zu ihrer systematischen Gruppierung und geographische Verbreitung. *Bot. Jahrb.* 11: 134-263. *pls.* 3-6. 1890. [General and systematic account of leaf anatomy.]
- PALSER, B. F. Studies of floral morphology in the Ericales. I. Organography and vascular anatomy in the Andromedeae. *Bot. Gaz.* 112: 447-485. 1951. II. Megasporogenesis and megagametophyte development in the Andromedeae. *Ibid.* 114: 33-52. 1952. III. Organography and vascular anatomy in several species of the Arbuteae. *Phytomorphology* 4: 335-354. 1954.
- PELTRISOT, C. N. Développement et structure de la grain de quelques Éricacées. *Jour. Bot. Morot* 18: 309-367, 386-402. 1904. (Note préliminaire. *Ibid.* 234-242.)
- RECORD, S. J. Woods of the Ericales, with particular reference to *Schizocardia*. *Trop. Woods* 32: 11-14. 1932. [See *Cyrillaceae*.]
- RYDBERG, P. A. Pyrolaceae. *N. Am. Fl.* 29: 21-32. 1914.
- SAMUELSSON, G. Studien über die Entwicklungsgeschichte der Blüte einiger Bicornes-Typen. *Sv. Bot. Tidskr.* 7: 69-188. 1913. [A classical embryological study.]
- SLADKOV, A. N. On morphological characteristics of pollen grains of the heath family (Ericaceae). (In Russian.) *Dokl. Akad. Nauk SSSR.* 92: 1065-1068. 1953.*

- SMALL, J. K. Monotropaceae, Ericaceae. N. Am. Fl. **29**: 11-18, 33-102. 1914.
[Does not include Vaccinioideae.]
- SMITH, A. C. The American species of Thibaudieae. Contr. U. S. Natl. Herb. **28**: 311-547. pls. 1-19. 1932.
- STANLEY, O. B. Fat deposits in certain Ericaceae. Butler Univ. Bot. Stud. **2**: 33-41. 1931. [*Cassandra*, *Arctostaphylos*, *Kalmia*, *Leiophyllum*, *Rhododendron*, *Vaccinium*, *Gaylussacia*.]
- TAKEMOTO, T., and N. YAHAGI. Studies on the constituents of Ericaceae. III. (In Japanese; English summary.) Jour. Pharm. Soc. Japan **78**: 304, 305. 1958.*
- WARMING, E. The structure and biology of arctic flowering plants. I. Ericineae (Ericaceae, Pirolaceae). 1. Morphology and biology. Meddel. Grönl. **36**: 1-71. 1908. [See also H. E. PETERSON. 2. The biological anatomy of the leaves and stems. *Ibid.* 75-138.]
- WHERRY, E. T. Observations on the soil acidity of Ericaceae and associated plants in the Middle Atlantic states. Proc. Acad. Nat. Sci. Philadelphia **72**: 84-111. 1920.
- . Correlation between vegetation and soil acidity in southern New Jersey. *Ibid.* 113-119.
- . Soil tests of Ericaceae and other reaction-sensitive families in northern Vermont and New Hampshire. Rhodora **22**: 33-49. 1920.
- YANG, B. Y. Pollen grain morphology in the Ericaceae. Quart. Jour. Taiwan Mus. **5**: 1-24. 1952. [58 spp. in 20 genera described and figured.]

ARTIFICIAL KEY TO THE GENERA OF ERICACEAE IN THE SOUTHEASTERN UNITED STATES

(Based upon flowering material, with subsidiary characters from the fruit.)

- A. Plants woody or herbaceous, autotrophic, with green leaves; pollen in tetrads.
- B. Petals distinct; ovary superior.
- C. Plants woody, shrubs or small trees; flowers 4-7-merous; ovary 3-7-locular, the placentae axile; capsule septicidal.
- D. Ovary 2-, 3-, or 7-locular; ovules anatropous; seeds not winged; evergreen shrubs.
- E. Ovary 7-locular; petals 7; stamens 12-20 (usually 14); flowers showy, in terminal racemes, producing quantities of sticky nectar. 1. *Befaria*.
- E. Ovary 2- or 3-locular; petals 5; stamens 10; flowers small, in umbel-like inflorescences. 4. *Leiophyllum*.
- D. Ovary 4- or 5-locular on the same plant; ovules flat, sessile on the massive placentae; rarely fruiting; seeds winged all around; deciduous shrub or small tree with racemes or panicles of white flowers with recurved petals. 2. *Elliottia*.
- C. Plants herbaceous, evergreen, with slender subterranean rhizomes; flowers 5-merous; ovary 5-locular below, 1-locular above, the placentae axile below, becoming parietal above; capsule loculicidal.
- F. Inflorescence corymbose; flowers regular; filaments hairy, enlarged at or below the middle; style short, straight; capsule valves with smooth margins. 15. *Chimaphila*.

- F. Inflorescence racemose; flowers more or less irregular; filaments glabrous, not enlarged in the middle; style declined; capsule valves with cobwebby margins. 16. *Pyrola*.
- B. Petals united (usually conspicuously so) or, if appearing distinct, the ovary inferior (some species of *Vaccinium*).
- G. Stamens with disintegration tissue (appearing white, powdery) on the apparent abaxial side at the top of the filament or in the connective or upward on the anther-halves, the anthers or filaments often appendaged (or if stamens aborted or not opening see 14. *Epigaea*); fruit a loculicidal capsule (the calyx fleshy in *Gaultheria*, surrounding the fruit and appearing berry-like).
- H. Plants low, subherbaceous, evergreen, with underground rhizomes; anther-halves with 2 terminal awns; flowers solitary in the axils of leaves, with a pair of bracteoles immediately beneath the calyx; calyx accrescent, fleshy, berry-like; seeds with hard coats. 8. *Gaultheria*.
- H. Plants erect, conspicuously woody, shrubs or trees; calyx not accrescent; seeds with thin, loose coats.
- I. Inflorescence clearly elongate, racemose or paniculate; capsule margins not differentiated.
- J. Anthers appendaged on the abaxial side with 2 stout, reflexed spurs just above junction with filament, these lacking white disintegration tissue; each anther-half with a line of disintegration tissue extending upward above spurs; corolla glabrous; evergreen shrubs with terminal and axillary racemes. 11. *Pieris*.
- J. Anthers not appendaged on abaxial side, with or without terminal awns.
- K. Corolla puberulous without; deciduous trees with terminal panicles; stamens unappendaged, with a small area of disintegration tissue near apex of each anther-half; capsule ovoid-pyramidal. 13. *Oxydendrum*.
- K. Corolla glabrous; deciduous to evergreen shrubs with terminal and axillary racemes; anthers with or without 2 or 4 terminal awns, with white disintegration tissue in angle between awns or this position when lacking awns; capsule depressed-globose. 7. *Leucothoe*.
- I. Inflorescences of corymbose clusters (reduced racemes) in axils of leaves or bracts (sometimes thus a raceme of corymbs) of the same or preceding season.
- L. Stamens with 4 prominent terminal awns; disintegration tissue in a conspicuous patch below awns; shrub with white, broadly campanulate flowers on wood of preceding season. 9. *Zenobia*.
- L. Stamens without terminal awns, with or without reflexed spurlike appendages on upper part of filament (these, when present, with a margin of white disintegration tissue extending upward onto the anther-halves); carpel midrib differentiated (colored or thickened), and to varying degrees splitting away separately from valves in fruit; evergreen

- to deciduous shrubs with globose-urceolate to cylindric corollas. 10. *Lyonia*.
- G. Stamens lacking white disintegration tissue on apparent abaxial side. (If not opening or aborted, see 14. *Epigaea*.)
- M. Ovary superior; stamens unappendaged; fruit a capsule.
- N. Corolla saucer-shaped, with 10 pouches in which the anthers are held in bud. 3. *Kalmia*.
- N. Corolla various, without pouches for the anthers.
- O. Flowers 4-merous; corolla campanulate or urceolate; stamens included; anthers opening by short slits; capsule septical. 5. *Menziesia*.
- O. Flowers 5-merous.
- P. Stamens conspicuously exerted; anthers not tapering, opening by terminal pores; flowers showy, in corymbose inflorescences from buds of the preceding season; capsule septical. 6. *Rhododendron*.
- P. Stamens included; capsule loculicidal.
- Q. Anthers tapering into tubular beaks, opening by terminal pores; flowers bisexual; corolla oblong-urceolate; flowers solitary in the axils of reduced foliage leaves; scurfy-leaved shrub of bogs. 12. *Cassandra*.
- Q. Anthers opening along the entire length; plants functionally dioecious, the stamens aborted or not opening in carpellate flowers; corolla salverform; flowers in the axils of bracts; trailing broad-leaved evergreen subshrub. 14. *Epigaea*.
- M. Ovary inferior or half-inferior; fruit fleshy.
- R. Ovary half-inferior; flowers 4-merous; each anther-half with a bifurcate terminal awn; diminutive creeping subherbaceous plant of cold mountain bogs, the solitary flowers in the leaf axils; fruit white. 8. *Gaultheria*.
- R. Ovary inferior; flowers 4- or 5-merous; anthers without terminal awns but the anther-halves more or less prolonged and tubular; inflorescences various; fruit black, blue, or red (very rarely white).
- S. Ovary 4- or 5-locular, or 10-locular above by the development of partial false partitions; ovules numerous; fruit a many-seeded, fleshy to leathery berry; anthers with or without spurs on the abaxial side. 19. *Vaccinium*.
- S. Ovary 10-locular, 10-ovuled, becoming baccate-drupaceous with 10 hard nutlets; anthers unappendaged. 20. *Gaylussacia*.
- A. Plants herbaceous, parasitic, lacking chlorophyll, with reduced scalelike leaves, variously colored; pollen grains single.
- T. Petals united; calyx of 5 regular sepals; fruit a berry. 17. *Monotropis*.
- T. Petals distinct, saccate at the base; calyx represented by 1-5 scale- or bractlike sepals; fruit a loculicidal capsule. 18. *Monotropa*.

Subfam. ERICOIDEAE Endlicher ('Ericinae')

Tribe RHODOREAE D. Don ²1. *Befaria* Mutis ex Linnaeus, Mantissa Pl. 152, 242. 1771.

Evergreen shrubs [or small trees, rarely to 20 m., but with slender trunks] with alternate, more or less coriaceous, persistent, usually entire, obovate to elliptic [or rarely linear], flat [or revolute-margined], short-petioled leaves. Flowers showy, 7(5-8)-merous, in terminal (and sometimes axillary) racemes [or, by reduction, corymbs]. Calyx campanulate, 7-parted, the lobes persistent. Petals usually 7, free, narrow, linear- to obovate-spatulate, white or pinkish [to red], imbricate in aestivation (the odd petal abaxial). Stamens hypogynous, 12-20 (usually 14), the filaments free, elongate, dilated at the base, pubescent below; anthers dorsifixed, muticous, dehiscing by 2 oblique slits at the apex, without dis-

² According to changes adopted by the IX International Botanical Congress (1959) modifying Article 19 of the International Code of Botanical Nomenclature (to read, in part, "The name of any taxon of a rank below family and above genus which includes the type of the next higher taxon must be based on the same stem as the name of the next higher taxon, but, contrary to Article 46, without citation of an author's name"), the correct name for this tribe is "Rhododendreae" if subfamily Rhododendroideae Endl. is recognized as distinct from Ericoideae. Fortunately, in the Ericaceae only this tribe is likely to have two possible correct names, depending upon the subfamilial classification adopted, for most of the proposed subfamilies (all of later date than the tribes) reflect the name of an included tribe. However, other well-known tribal names (Ericaceae, Monotropeae, Pyroleae, Vaccinieae) of David Don, who first blocked out these basic units of the family in 1834, may have to be cited without an author. Other families may not fare so well. Under the principle of the repetition of generic or subgeneric names for included subgenera and sections, already in use in Article 22 of the Code and now to be embodied in Articles 17 and 19, precisely the same taxon in large and complex orders, families, or genera may have alternative names (and types) depending upon the taxonomic ideas of the author as to the next higher category.

In connection with the effects of Article 22, G. L. Webster has aptly commented (Jour. Arnold Arb. 41: 279. 1960), "This ruling is unfortunate, in my opinion, since it fallaciously assumes a parallel between typification of a genus or species with that of a subgenus. The subgenus does not appear in the name of the species and is a purely intercalary category, as is the section. That the new rule does not really contribute to stability is shown in the present case. If subgenera are recognized in *Phyllanthus*, the epithet of this section must be *Kirganelia*; but if one chooses not to recognize subgenera then the same section must take the epithet *Anisonema*." While it may be useful to have the type family of an order reflected in the subordinal categories, the type genus of a family in the subfamilial categories, the type species of a genus in the subgeneric categories, the extension of this principle to every subordinate taxon between the rank of order and series would seem to lead only to confusion and obfuscation of formerly clear taxa and to work against the interests of nomenclatural stability and taxonomy. This principle seems to the writer to have been considerably overextended. Since, pending formal publication of a new edition of the Code, these changes are not yet binding, the 1956 edition is followed here and authors are cited for subfamilial and tribal names. (For a further example of name switching engendered by Article 22 see the subgeneric categories in *Rhododendron*, and, for an exercise in total confusion, attempt to correlate nomenclaturally and taxonemically the classifications adopted by Rehder, Sleumer, Seithe-von Hoff, and the present author!)

integration tissue; pollen tetrads with viscin strands. Stigma depressed-capitate, 7-grooved; style terete, elongate, bent to one side; ovary superior (or the base slightly immersed in the receptacle), 7-sulcate, 7-locular, with numerous elongate ovules on large axile placentae. Capsule erect, depressed globose, surrounded at the base by the persistent calyx and terminated by the elongate style, 7-valved, septicidal from the apex. Seeds numerous, elongate, narrow, curved, tapered, some angled by compression. (*Bejaria* Vent.) TYPE SPECIES: *B. aestuans* L. (Described from Mutis' manuscript, the name, apparently intended in honor of Mutis' friend José Bejar, professor of botany at Cadiz, misread and written consistently by Linnaeus as *Bejaria*, rather than *Bejaria*.)

Perhaps 10–30 species in two sections: *Bejaria racemosa* Vent. in our area; *B. cubensis* Griseb. in western Cuba; four or more species in Mexico, Guatemala, and Honduras; the remainder in the Andes, from Venezuela to Bolivia, and on the disjunct table-topped mountains eastward to Mt. Roraima. Mansfeld and Sleumer recognized 20 species in South America, whereas Camp has suggested that as few as four basic species may account for the range of variation, the difficulties in delimiting taxa being ascribed to hybridization.

Bejaria racemosa, a shrub 1–2.5 m. tall, with sparsely hispid twigs and conspicuous, fragrant, white flowers in winter, spring, or early summer, occurs in flatwoods and sand-scrubs from Dade, Highlands, and Lee counties, Florida, northward to Camden, Glynn, and Worth counties, Georgia. Nectar is produced copiously from the glandular inner surface of the calyx, hence the name tar-flower or fly-catcher. The species lacks a hypodermis in the leaves, in contrast to all other species, and differs further in the elongate raceme (or panicle) much exceeding the leaves. It is relatively invariable and isolated within the genus and is the sole member of sect. RACEMOSAE Fedtsch. & Basilev. According to Mansfeld and Sleumer its closest relatives are *B. glauca* Humb. & Bonpl., of Colombia, and *B. laevis* Benth., of Mexico, the two later united under the former name by Camp. *Bejaria cubensis*, geographically nearest to *B. racemosa*, is a very different and highly specialized plant, presumably most closely related to *B. ledifolia* Humb. & Bonpl., of Colombia.

Copeland has shown that *Bejaria* shares with *Elliottia* and *Cladanthamnus* viscin strands among the pollen tetrads and resorption tissue in the anthers, a combination found nowhere else, but differs from them in having haustoria at both ends of the endosperm and in the opening of the anthers by a brief slit. It is unique among genera of Rhodoreae in the trilacunar vascular supply to the sepals and in the opening of the anthers by the formation of a cleft between intact cells (rather than by collapse or resorption of cells). On the basis of these features, as well as the gross morphology of the flower, the genus was set apart by Copeland as a tribe and regarded as the most primitive of the Ericaceae. In wood structure, however, "*Bejaria* [5 species of sect. BEFARIA] is more advanced than several of the lower genera of other tribes" (Cox). In a comparison of

Bejaria with *Clethra* Copeland concluded, "The effect of this comparison is to show that while *Clethra* and the Rhododendroideae are descended from a common ancestor, this ancestor and all transitions between it and the groups named have disappeared, leaving the survivors quite isolated."

REFERENCES:

- Under family references see also COPELAND (1943, pp. 548-553), COX (Ericales I, pp. 228, 229).
- CAMP, W. H. Studies in the Ericales. A discussion of the genus *Bejaria* in North America. Bull. Torrey Bot. Club 68: 100-111. 1941. [Recognizes 4 species and 1 variable taxon of hybrid origin.]
- FEDTSCHENKO, B. A., and N. A. BASILEVSKAJA. Revisio generis *Bejaria* Vent. (In English.) Not. Syst. Leningrad 6: 37-45. 1926.
- . Origin and geographical distribution of the genus *Bejaria* Mutis. (In Russian; English summary.) Zhur. Russ. Bot. Obsch. 11: 285-296. 1927.*
- . Revision of the genus *Bejaria* Mutis. Bot. Gaz. 85: 299-322. 1928. [41 spp., 8 new, 36 in South America.]
- MANSFELD, R., and H. SLEUMER. Revision der Gattung *Bejaria* Mutis. Notizbl. Bot. Gart. Berlin 12: 235-276. 1935.
- SMALL, J. K. *Bejaria racemosa*. Addisonia 15: 21-23. pl. 491. 1930.

2. *Elliottia* Muhlenberg ex Elliott, Sketch Bot. S. C. & Ga. 1: 448. 1817.

Deciduous tree to 6 (9) m., or often a shrub to 3 m., with gray bark, the twigs chestnut-brown. Leaves alternate, petiolate, oblong or oblong-elliptic, the apex acute, the base cuneate, membranaceous, pale and pubescent beneath. Inflorescences terminating the growth of the season, elongate panicles or loose racemes 8-25 cm. long, the flowers slightly irregular, slender-pedicel, with deciduous, subulate bracts. Calyx small, 4(5)-lobed, persistent. Petals 4 (or almost as frequently 5 in the same inflorescence), free, oblong-lanceolate, recurving, white. Stamens 8 (10), the filaments flattened, the anthers 2-lobed at the base, the apex apiculate, opening almost from base to apex by 2 V-shaped areas of resorption tissue; pollen tetrads with viscin strands. Stigma discoid-capitate, with 4 (5) grooves; style longer than the petals, thickened and incurved above, soon deciduous; ovary superior, 4(5)-locular, on a 4(5)-lobed disc (gynophore?); placentae large, the ovules 5-8 in each locule, strongly flattened, sessile. Fruit a depressed-globose 4(5)-lobed capsule (8-12 mm. broad), sometimes with a very short gynophore, septicidally dehiscent from above, the valves and enlarged placentae persistent; seeds 1-several in each locule (many ovules aborting), discoid, winged all around, strongly compressed between placenta and ovary wall, 3-4 mm. across, falling from the placenta. TYPE SPECIES: *E. racemosa* Muhl. ex Ell. (Named for Stephen Elliott, 1771-1830, distinguished South Carolina botanist.)

One to three very distinct species, depending upon the generic concept; *Elliottia racemosa* in our area, two others in Japan (see below).

Elliottia racemosa, with numerous showy panicles or racemes of 40-80 white flowers produced in June or early July, is one of the handsomest,

as well as one of the rarest, of our native shrubs. It apparently is largely confined to isolated colonies in mediacid sandy soils (Norfolk sand) of the Coastal Plain in an area roughly bounded by Aiken County, South Carolina (where it is now presumed extinct), and Columbia, Screven, and Coffee counties, Georgia. Although usually seen as a shrub where subjected to burning, in its best development the plant is a small tree to 9 m. tall and grows in moist but always well-drained sands in mixed woods within a few hundred feet of streams. The plant shows a considerable range of tolerance, however, and some colonies are in rather dry locations, on oak ridges, in *Pinus australis* savannas, or in *Pinus-Quercus* woods. (In cultivation, given an acid and well-drained soil and an eastern or southern slope, it is hardy at least as far north as Philadelphia.)

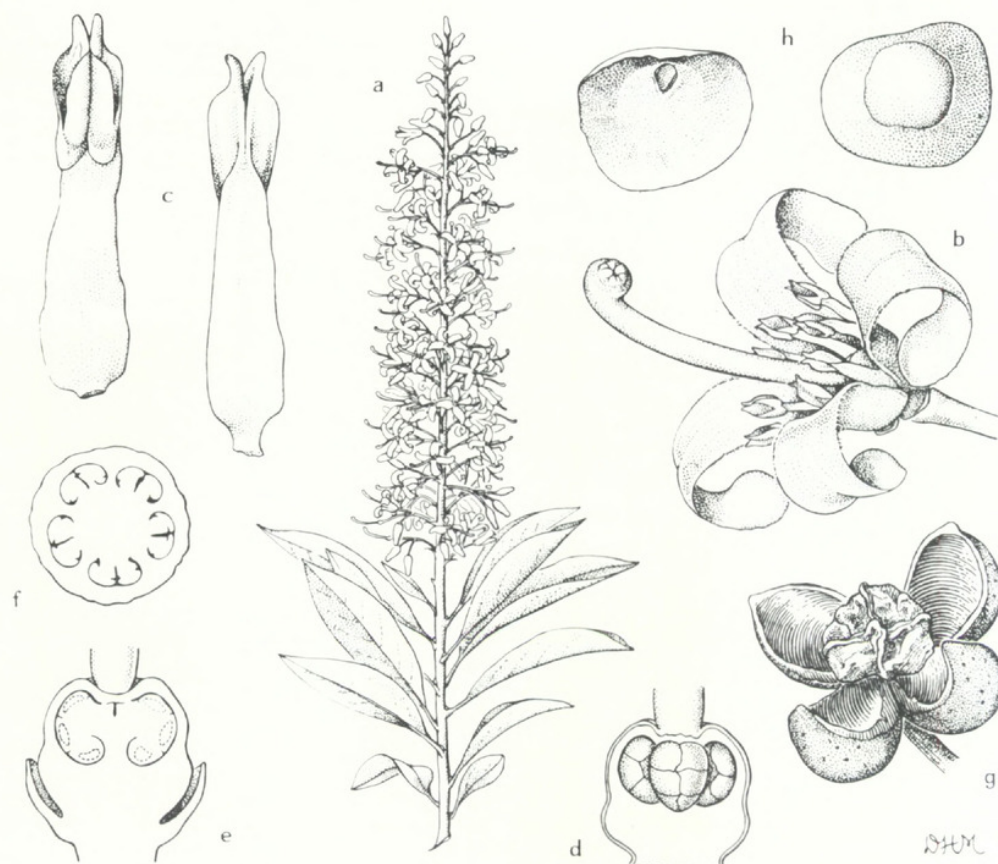


FIG. 1. *Elliottia*. a-h, *E. racemosa*: a, flowering branch, ca. $\times \frac{3}{8}$; b, flower, $\times 3$; c, stamens, inner and outer views, $\times 10$; d, four-locular ovary, half of wall removed to show sessile ovules on placentae in three locules, $\times 10$; e, ovary and calyx in vertical section, showing sessile ovules on massive placentae, semi-diagrammatic, $\times 10$; f, five-locular ovary in cross section, showing divided placentae, sessile ovules, $\times 10$; g, open 4-carpellate capsule after shedding of seeds, $\times 4$; h, inner and outer views of thin-winged seed, $\times 4$.

At a number of the known stations *Elliottia* apparently seldom or never fruits, and a number of misconceptions concerning fruits and seeds have remained in the literature. (See Drude, Copeland; but see Wherry for an accurate description.) In at least two localities fruits are produced, how-

ever, and reproduction by seedlings has been found. (It is perhaps significant that these stations are relatively moist.) The lack of fruiting has led to the supposition that each colony is clonal and self-sterile, but no evidence of root-suckering or clonal connections between plants has been produced. (The plant suckers abundantly from the stem-base after burning or cutting, however.) Chromosome counts, further observations on the pollination mechanism, and artificial crossing experiments are suggestive lines of approach to the problem. Copeland observed in preserved material that the pollen is shed in the pendent bud, falling in four cylindrical masses from each anther and lodging in the apex of the closed corolla beyond the stigma. He supposed that as the style elongates the pollen is pressed against the spoonlike tips of the petals by the stigma, and then exposed as the flower rises to the horizontal and the petals recurve.³

Lack of unanimity has characterized the generic treatment of *Elliottia racemosa* and the two Japanese species, both of which have five sepals, three petals, six stamens, and a three-locular ovary. *Tripetaleia paniculata* Sieb. & Zucc. (*E. paniculata* (Sieb. & Zucc.) Benth. & Hook.), a shrub of Kyushu, Shikoku, Honshu, and Yezo, resembles *E. racemosa* in many respects, but for the smaller, more complex panicles of smaller flowers, the trimerous symmetry, the development of a definite gynophore, and the lack of a well-developed marginal wing on the seed; it may well be included in *Elliottia*. *Tripetaleia bracteata* Maxim. (*E. bracteata* (Maxim.) Benth. & Hook.), a smaller shrub of Honshu and Yezo, is considerably more modified, with comparatively large bracts, reduced, purely racemose inflorescences, subfoliose sepals, an obscure gynophore, and different seeds. Stapf regarded *E. racemosa* and *T. paniculata* as congeneric, but treated the third as *Botryostege bracteata* (Maxim.) Stapf, thinking it closer to *Cladothamnus pyroliflorus* Bong. (distributed from Oregon to Alaska)

³ A number of the ecological data above were corroborated or supplied by Miss Clermont H. Lee, of Savannah, Georgia, who has also very kindly made additional field observations on the flowers and their opening. She has observed that the buds are upright at first, becoming pendent when about 4–4.5 mm. long. At 5–7 mm. the pollen has started to fall from the stamens onto the underside of the stigma. Eventually it works its way under and around the stigma, there being a space between it and the spoonlike petal tips. At the time of opening of the flower, most of the pollen seems to be adherent to the stigma. Although the contents of most fall out, some anthers continue to contain pollen until anthesis. At anthesis the bud (then about 14 mm. long) has assumed a horizontal position. Some pollen may fall from the spoonlike tips of the petals and some from the stigma as the petals reflex. (Open flowers showed no evident pollen on the petals.) The stigma seemed to be moist at the time the petals began to reflex. "Small yellow bees" were observed climbing and flying over opened and unopened flowers, apparently collecting nectar from the slightly fragrant flowers, their wing tips seeming most often to touch the stigmas. Bees were observed flying from one plant to another. A single hummingbird was also seen to visit the flowers. It was also observed that on the lateral branches of the panicle the terminal (or central) flower of the two or three present opens first, and that sometimes the terminal flower of the panicle was open before those just below. An attempt by Dr. Joab Thomas to secure meiotic chromosomal counts from material from this colony kindly fixed by Miss Lee was unsuccessful, for, although the buds were of the proper size, the pollen mother cells, for reasons unknown, showed a complete lack of divisions.

than to *Elliottia*. Copeland and Cox arrived at opposing conclusions regarding *Elliottia* and *Tripetaleia*, but neither was able to study material of *Botryostege*. Whatever the taxonomic treatment followed, all four taxa are clear-cut, relict species of great morphological and phytogeographic interest.

Copeland characterized his tribe Cladothamneae (which included only these plants) by the free petals, by the anthers opening throughout their length by resorption tissue, by viscin strands among the pollen tetrads, by endosperm without chalazal haustoria, and by the characteristic manner of discharging the pollen. *Ledum* L., associated with these genera by Drude, was removed to a position near *Rhododendron*.

REFERENCES:

- See also under family references COPELAND (1943, pp. 533-559), Cox (Ericales I, pp. 230, 231), and IKUSE (1954).
- HARPER, R. M. Notes on *Elliottia racemosa*. Pl. World 5: 87-90. pl. 12. 1902.
- . Two new stations for *Elliottia*. Ibid. 6: 60. 1903.
- . *Elliottia racemosa* again. Torreya 3: 106. 1903.
- . A phytogeographical sketch of the Altamaha Grit Region of the coastal plain of Georgia. Ann. N. Y. Acad. Sci. 17: 1-415. 1906. [*Elliottia*, 187. pl. 19, fig. 2; pl. 20.]
- HENRY, M. G. *Elliottia racemosa*. Natl. Hort. Mag. 20: 223-226. 1941. [Includes photographs of flowering and fruiting plants.]
- KNIGHT, W. A. A rare American shrub. Arnold Arb. Bull. Pop. Inform. IV. 6: 7-13. 1938. [Notes on ecology and details of *Elliottia*.]
- SARGENT, C. S. *Elliottia racemosa*. Gard. Forest 7: 206. fig. 37. 1894.
- . *Elliottia*. Silva N. Am. 14: 29-32. pl. 712. 1902.
- SEALY, J. R. *Elliottia racemosa*. New Fl. Silva 10: 154-164. figs. 49, 50. 1938.
- SMALL, J. K. The rediscovery of *Elliottia*. Jour. N. Y. Bot. Gard. 2: 113, 114. 1901.
- STAPP, O. *Elliottia racemosa*. Bot. Mag. 138: pl. 8413. 1912.
- . *Botryostege*: a new genus of Ericaceae. Kew Bull. 1934: 191-195. 1 pl. 1934. [Includes discussion of relationships of *Elliottia*, *Tripetaleia*, and *Botryostege*.]
- TRUDELL, H. W. "Rescuing *Elliottia*." Bartonica 9: 11-15. 1926.
- . A new colony of *Elliottia*. Ibid. 10: 24-27. 1929.
- WHERRY, E. T. Discovery of *Elliottia* seed. Ibid. 17: 51. 1936.

3. *Kalmia* Linnaeus, Sp. Pl. 1: 391. 1753; Gen. Pl. ed. 5. 185. 1754.

Evergreen or rarely deciduous shrubs or small trees to 12 m. Winter buds with about 2 outer scales. Leaves alternate, opposite or whorled, entire, usually coriaceous, petioled or rarely sessile, glabrous, pubescent, hirsute or glandular. Flowers in terminal or axillary corymbs or solitary in the axils of leaves and forming a loose terminal "raceme"; each flower in the axil of a leaf or (in those species with corymbs) of a small, thick bract, and with a pair of bractlets at the base of the slender pedicel. Flowers 5-merous; base of receptacle impressed. Calyx synsepalous, deeply 5-parted, persistent, or deciduous in fruit. Corolla sympetalous, saucer-shaped, with a short, narrow tube, shallowly 5-lobed, and with 10 pockets

in which the anthers are held. Stamens 10, the filaments slender, the anthers short, unappendaged, opening by apical slits, without white disintegration tissue; anthers lodged in the pockets of the corolla in the bud so that the filaments are strongly recurved and held under tension by the expansion of the corolla and spring up suddenly when the corolla is touched; pollen tetrads with or without viscin strands. Style slender, straight; stigma flat, unexpanded, 5-grooved; ovary superior, 5-locular, with massive placentae and numerous ovules, on a conspicuous disc. Capsule subglobose to globose-ovoid, septicidal, 5-valved, opening from above, the style persistent on the central axis. Seeds numerous, minute, essentially cylindrical, with a loose coat. (Including *Kalmiella* Small.) LECTO-TYPE SPECIES: *K. latifolia* L.; see N. L. Britton, N. Am. Trees 756. 1908. (Dedicated to Pehr Kalm, 1716–1779, student and friend of Linnaeus, who travelled and collected in North America from 1748 to 1751.)

About six species of North America, including *K. polifolia* Wengen. (consisting of vars. *polifolia* and *microphylla* (Hook.) Rehd.), of cold bogs and alpine meadows from Labrador to Alaska, south to Pennsylvania, Minnesota, Colorado, Montana, and California; *K. ericoides* C. Wright ex Griseb. (including *K. aggregata* (Small) H. F. Copel. and *Kalmiella simulata* Britt. & Wilson, based on variations in pubescence and compactness of inflorescence), of Pinar del Río and the Isle of Pines, Cuba; four species in our area.

Kalmia latifolia, mountain laurel, widely distributed in acid soils, largely in deciduous woodland, from western Florida to Louisiana, northward to New England, New York, Ohio, and Indiana, is a shrub, or occasionally a tree to 10–12 m. tall, with elliptic or elliptic-lanceolate, mostly alternate leaves 5–10 cm. long and showy terminal corymbs of white to pink flowers 1.5–3 cm. across, the petioles glandular-pubescent. The plant is a popular horticultural subject and a number of variant forms have been named. (See Rehder, Holmes.) Plants with the pedicels less markedly glandular have been named var. *laevipes* Fern. *Kalmia angustifolia* L. var. *carolina* (Small) Fern. (*K. carolina* Small), a shrub to about 1 m. tall, with short-petioled oblong to lanceolate mostly opposite or ternate leaves, pubescent beneath even at maturity, axillary to terminal corymbs of deep pink or purple flowers about 1 cm. across, ranges from southeastern Virginia southward through eastern North Carolina to eastern South Carolina, and occurs in scattered localities in western Virginia (Carroll County), eastern Tennessee (Johnson County), western North Carolina, and northeastern Georgia (Rabun County). In southeastern Virginia it intergrades with the northern var. *angustifolia* (southeastern Virginia northward through eastern Pennsylvania and New Jersey to Labrador and Hudson Bay and west to northern Michigan) which differs in having the leaves glabrous beneath at maturity. *Kalmia cuneata* Michx. is a distinctive deciduous shrub with oblong-obovate, cuneate leaves, glandular beneath, and almost umbellate corymbs of white flowers about 1.5 across produced from the axils of leaves of the preceding year. One

of the rarest of American shrubs, it is known from wet thickets or shrub bogs in only a few localities in southeastern North Carolina and from an early collection of Nuttall between Camden [Kershaw County], South Carolina, and Statesville [Iredell County], North Carolina.

Kalmia hirsuta Walt. (*Kalmiella hirsuta* (Walt.) Small), a straggly shrub with thin, hirsute, alternate, persistent leaves, of the Coastal Plain from southeastern North Carolina (?) and South Carolina southward to Flagler, Putnam, and Alachua counties, Florida, and west to southernmost Alabama; and *K. ericoides*, a low, revolute-leaved shrub of Cuba, differ from other species in the deciduous calyx (cf. *Lyonia*) and in having the flowers borne singly in the axils of ordinary-sized or somewhat reduced foliage leaves (instead of bracts). The plants are otherwise entirely consistent with *Kalmia* both morphologically and anatomically and there seems to be no real justification for the removal of these species (as *Kalmiella* Small) from *Kalmia*. The six species of *Kalmia* are quite distinct morphological entities which are separated ecologically and/or geographically and perhaps genetically. Artificial hybrids do not seem to have been attempted, and no natural hybrids are known. The chromosomal data reported by Hagerup ($2n = 24$ rather large chromosomes in *K. latifolia* and $2n = 48$ chromosomes about half as large in *K. polifolia*) suggest an interesting pattern of polyploidy which should be investigated further.

The most distinctive generic feature of *Kalmia* is the pollination device. In the flower bud the ten anthers are pushed upward by the growth of the filaments into corresponding pockets in the corolla. As the corolla opens and expands the anthers are held by the pockets and the filaments are bent backward under tension. The weight of a suitably heavy insect displaces the corolla, and frees one or more of the anthers; the filaments snap suddenly upward, showering the visitor with pollen. In *K. latifolia* viscin strands occur in the pollen, which is hurled like a sticky net, while in *K. angustifolia* var. *angustifolia* (and probably *K. polifolia*) the pollen is powdery and dusts the visitor.

The leaves of at least *Kalmia latifolia* and *K. angustifolia* are poisonous to many mammals when eaten. The toxic principle is thought to be andromedo-toxin which is presumably the same as that in other poisonous Ericaceae (including evergreen *Rhododendron* species, *Ledum*, *Leucothoë*, *Lyonia*, and *Andromeda*). A mycorrhizal association, without which growth does not occur, has been demonstrated in *K. latifolia*.

Kalmia, *Leiophyllum*, and seven other small, definitely distinct and rather isolated genera are sometimes segregated as the tribe Phyllodoceae Drude. All are evergreen plants, mostly with ericoid or buxoid leaves; in those with pentamerous flowers the median petal is abaxial; and the seeds generally lack appendages (except in *Kalmia*). As defined by Copeland the tribe is characterized primarily by the presence of resorption tissue involving the epidermis of the anther and by the absence of filaments among the pollen tetrads. The latter characteristic does not hold, however, for viscin filaments have been reported in *Phyllodoce*, *Loiseleuria*, and *Kalmia*. The closest relative of *Kalmia* both morphologically and anatomi-

cally appears to be *Rodothamnus* Reichenb. (including *Kalmiopsis* Rehd.), comprised of two species, *R. Chamaecistus* Reichenb., of the eastern Alps, and *R. Leachianus* (Henderson) H. F. Copel., of the Siskyou Mountains, Oregon. *Rhodothamnus*, *Kalmia*, and *Phyllodoce* Salisb. are regarded as relatively primitive within the group.

REFERENCES:

- Under family references see also BELL & BURCHILL, COPELAND (1943), COX (Ericales I), IKUSE, KEARNEY, MATTHEWS & KNOX, PELTRISOT, and STANLEY. BRITTON, E. G. Wild plants needing protection. 8. "American or mountain laurel" (*Kalmia latifolia* L.). Jour. N. Y. Bot. Gard. 14: 121-123. pl. 117. 1913.
- . A freak of the mountain laurel. *Ibid.* 26: 187-190. 1925. [*K. latifolia* f. *polypetala* (Nicholson) Rehd.]
- BROWN, N. E. *Kalmia cuneata*. Bot. Mag. 136: pl. 8319. 1910.
- BUTTRICK, P. L. Connecticut's state flower, the mountain laurel, a forest plant. Marsh Bot. Gard. Publ. 1. 28 pp. 1924.
- CURTIS, W. *Kalmia hirsuta*. *Ibid.* 4: pl. 138. 1795; *K. latifolia*, 5: pl. 175. *K. glauca* = *K. polifolia*, pl. 177. 1792; *K. angustifolia*, 10: pl. 331. 1796.
- ENLOWS, E. M. A. A leafblight of *Kalmia latifolia*. Jour. Agr. Res. 13: 199-212. pls. 14-17. 1918. [*Phomopsis kalmiae*.]
- FERNALD, M. L. A new southern *Kalmia*. Rhodora 42: 53, 54. 1940. [*K. latifolia* var. *laevipes* Fern.]
- FLEMER, WM., III. The propagation of *Kalmia latifolia* from seed. Bull. Torrey Bot. Club 76: 12-16. 1949. [Mycorrhizal relationships.]
- FORBES, E. B. Mountain laurel and rhododendron as food for the white tailed deer. Ecology 12: 323-333. 1931. [*K. latifolia* and *R. maximum*.]
- HADLEY, W. J., and H. H. HADEN, JR. Alabama's "sheep kill" laurel, *Kalmia latifolia* L. — A preliminary study. Jour. Am. Pharm. Assoc. Sci. Ed. 35: 340-342. 1946.*
- HOLMES, M. L. *Kalmia*, the American laurels. Bailey 4: 89-94. 1956. [Includes cultivars of *K. latifolia* and *K. angustifolia*; *K. ericoides* omitted.]
- LOVELL, J. H. The pollination of *Kalmia angustifolia*. Rhodora 36: 25-28. 1934.
- MARSH, C. D. The poisonous laurel. (Abs.) Jour. Wash. Acad. Sci. 20: 350, 351. 1930. [*K. latifolia* and *K. angustifolia*.]
- and A. B. CLAWSON. Mountain-laurel (*Kalmia latifolia*) and sheep laurel (*Kalmia angustifolia*) as stock-poisoning plants. U. S. Dep. Agr. Tech. Bull. 219: 1-22. 1930.*
- REHDER, A. Note on the forms of *Kalmia latifolia*. Rhodora 12: 1-3. 1910. [Corolla shape and color, leaf shape variants.]
- SARGENT, C. S. *Kalmia*. Silva N. Am. 5: 137-142. pls. 236, 237. 1893.
- . *Kalmia latifolia* var. *myrtifolia*. Gard. Forest 8: 315. fig. 44; *K. cuneata*. 434. fig. 60. 1895.
- TREVETT, M. F. Control of lambkill (*Kalmia angustifolia*) in lowbush blueberry fields. Northeast. Weed Control Conf. Proc. 10: 193-198. 1956.*

4. *Leiophyllum* (Persoon) Hedwig filius, Gen. Pl. 313. 1806.

Evergreen shrubs, prostrate to erect and to about 1 m. tall with crowded, small (to 1.5 cm. long), leathery, alternate to opposite, oblong to orbicular leaves, the petioles short, articulated at the base. Inflorescences ter-

minal umbel-like simple or compound corymbs, the flowers borne singly in the axils of reduced leaves, each with 2 small lateral bracts at the base of the slender pedicel. Flowers 5-merous; base of receptacle impressed. Calyx lobes 5, free nearly to the base, persistent. Corolla of 5 spreading, equal, white or pinkish petals. Stamens 10, conspicuously exserted, equaling or exceeding the petals; filaments filiform, glabrous; anthers small, almost globular, opening by 2 lengthwise slits, unappendaged, blue to purple or pink, without disintegration tissue; pollen tetrads without viscin strands. Stigma not expanded; style filiform, about as long as the stamens, straight, tapering into the more or less glandular 3- or 2 (rarely 4 or 5)-locular, superior ovary which is seated on a conspicuous disc; ovules numerous, axile. Capsule ovoid, 3- or 2 (rarely 4 or 5)-valved from the apex, the central axis persistent, pointed, the valves nearly smooth to sharp-tuberculate on the back, the style adhering to one valve or broken away. Seeds numerous, brown, minute, plump, unappendaged, the seed coat reticulate. (*Ledum* † *Leiophyllum* Pers. Syn. Pl. 1: 477. 1805; *Dendrium* Desv. Jour. Bot. Desvaux II. 1: 36. 1813; *Ammyrsine* Pursh; *Fischeria* Sw.) TYPE SPECIES: *Ledum thymifolium* Lam. = *Leiophyllum buxifolium* (Berg.) Ell. (Name from Greek, *leios*, smooth, and *phyllon*, leaf, in allusion to the shining, leathery leaves.) — SAND-MYRTLE.

A single variable species (sometimes treated as two or three) of open habitats on acid rocks and sands from the higher summits of the Smoky and Blue Ridge mountains of North Carolina, Tennessee, and northernmost Georgia, via several disjunct stations to the coastal plain of southeastern North Carolina and northeastern South Carolina, and of the pine barrens of southern New Jersey.

Most of the characters used by Small (habit, petal shape, disc, style/ovary proportions, capsule valves) in distinguishing three species in the genus do not hold, and even those of glandular pubescence, leaf shape and leaf arrangement adopted by Camp in delimiting two species (one composed of two varieties) are not altogether constant. The course of Rehder, who recognized a single species, *L. buxifolium*, composed of three varieties, seems to be most in line with the information presently available. Varietas *Hugeri* (Small) Schneid. (*L. Hugeri* (Small) K. Schum.), considered by Camp to be the basic entity, is a decumbent to erect shrub to about 1 m. tall, primarily of the Coastal Plain of southern New Jersey and the Carolinas (but with a few disjunct stations inland in the latter states and eastern Kentucky) with glandular hairs on the pedicels and with mostly alternate leaves which tend to be oblong and slightly apiculate. Varietas *prostratum* (Loud.) Gray (*L. Lyonii* (Sweet) Sweet [nomen subnudum] sensu Small, Camp, *et al.*), prostrate to almost 1 m. high depending upon the habitat, and with glandular pedicels but mostly opposite, elongate-oval to orbicular leaves which are rarely apiculate, is confined principally to exposed ledges and summits in the higher mountains of North Carolina, Tennessee, and northernmost Georgia. Varietas *buxifolium*, primarily of southern New Jersey, has the leaves and leaf arrangement of

var. *Hugeri* but has glabrous pedicels. It should be noted that vars. *buxifolium* and *Hugeri* may occur together in New Jersey; that at least some plants with glabrous pedicels occur in the Carolinas with var. *Hugeri*; that one New Jersey collection with glandular pedicels has predominantly opposite leaves; that all of the mountain plants have glandular pedicels but that in herbarium materials leaf arrangement is somewhat variable and there are possible evidences of ecological influences; and that leaf shape is far from a dependable characteristic in this genus.

As Camp has noted, the type of var. *Hugeri*, from Table Mountain, Pickens County, S. C., is, unfortunately, biologically closer to var. *prostratum* than to the glandular-pedicel plant of the Coastal Plain; the name is retained tentatively, however, in the sense of Camp, until further information on variation and geography is obtained. Ecological and population studies are very much in order. Of particular interest in an understanding of the genus is the relationship of alternate *vs.* opposite leaves to genetic and ecological factors. Transplant experiments and observations on sprouting after fire and the effect of rapidity of growth on leaf arrangement should provide pertinent information.

Little seems to have been recorded of the biological features of the genus, except that the numerous small flowers (April to June) are very attractive to insects.

Leiophyllum has been associated with *Ledum* in the past, largely on account of the distinct petals, but the relationships of the latter appear to be instead with *Rhododendron*. In wood anatomy *Leiophyllum* lies between *Ledothamnus* Meissn. and *Loiseleuria* Desv.

REFERENCES:

- Under family references see also COPELAND (1943, pp. 567-569), Cox (Ericales I, p. 233), and STANLEY.
- CAMP, W. H. Studies in the Ericales III. The genus *Leiophyllum*. Bull. Torrey Bot. Club **65**: 99-104. 1938.
- FERNALD, M. L. *Leiophyllum* versus *Dendrium*. Rhodora **29**: 225-227. 1927.
- FOX, W. B., R. K. GODFREY, and H. L. BLOMQUIST. Notes on distribution of North Carolina plants — III. *Ibid.* **54**: 165-182. 1952. [176, var. *Hugeri* reported from Gaston Co., N. C.]
- HOOKE, J. D. *Leiophyllum buxifolium*. Bot. Mag. **110**: pl. 6752. 1884. [See also EDWARDS, Bot. Reg. **7**: pl. 531. 1821.]
- SMALL, J. K. Shrubs and trees of the southern states. — IV. Bull. Torrey Bot. Club **28**: 356-361. 1901. [360, 361, *Dendrium Hugeri* described.]

5. *Menziesia* J. E. Smith, Pl. Icon. Ined. **3**: pl. 56. 1791.

Deciduous shrubs (to about 2 m.) with the general aspect of *Rhododendron* § *Anthodendron*. Branches erect or spreading, the leaves alternate, crowded at the ends, the blades thin, broadly elliptic to obovate, apiculate, often strigose, ciliate, entire, gland-tipped, short-petioled. Winter buds swollen, with several outer scales. Flowers 4[5]-merous, appearing with the leaves, in sub-umbellate (to short-racemose) clusters terminating the branches of the previous year, nodding, the pedicels slender, be-

coming erect in fruit. Calyx small, flat or saucer-shaped, circular or shallowly 4[5]-lobed, glandular-ciliate, persistent. Corolla yellowish white at the base, rose at the tip [or greenish to purplish], campanulate or urceolate [or cylindric and sometimes irregular], the tube stout, [often] swollen, the lobes 4[5], rounded and much shorter than the tube, often erect. Stamens 8 [or 5 or 10], included [or exserted]; filaments subulate, flattened; anthers narrow, linear to linear-sagittate, unappendaged, without disintegration tissue, opening (through collapse tissue) by short slits broadened above; pollen tetrads with viscin strands. Stigma truncate; style columnar, included; ovary 4[5]-locular, superior, obscurely lobed, glandular-hairy [glabrous or pubescent], commonly ovoid; ovules many, axile, elongate; disc 8[10]-lobed. Capsule ovoid, oval or obovoid, firm, rather thick-walled, septicidally 4-valved; the style broken or persistent on the central axis; seeds numerous, linear, abruptly pointed or tailed. TYPE SPECIES: *M. ferruginea* J. E. Sm. (Named in honor of Archibald Menzies, 1754–1842, who served as surgeon-botanist on Vancouver's great expedition of survey, 1790–1795, in the course of which he collected the type species.)

A small genus of disjunct distribution including about five or six species: three or four in Japan and Sakhalin (*Menziesia ciliicalyx* (Miq.) Maxim. vars. *ciliicalyx* and *multiflora* (Maxim.) Makino, *M. purpurea* Maxim., and *M. pentandra* Maxim.); *M. ferruginea* vars. *ferruginea* and *glabella* (Gray) Peck in western North America (Alaska to northern California, Alberta, Idaho, and Wyoming); and *M. pilosa* (Michx.) Juss. in the eastern United States, in rocky upland deciduous woods from Pennsylvania southward to West Virginia, Virginia, North Carolina, northern Georgia, and eastern Tennessee.

Menziesia pilosa is easily recognized by the azalea-like aspect, the terminal clusters of nodding, tetramerous, campanulate, yellowish-white to orange-pink flowers about 6–7 mm. long, and the glandular or glandular-setose, septicidal, ovoid capsule 3–4 mm. long. It is closely related to the western American species, from which it differs primarily in details of pubescence of bud scales, leaves, pedicels, calyx, filaments, and ovary and in shape and size of fruit. Both eastern and western species are far from stable in most of these features and the full range of variation has not been adequately described in either group (e.g., the undersurfaces of the leaves of *M. pilosa* vary from densely pilose with short, nonglandular hairs in much of its range to almost glabrous with scattered glandular hairs along the veins in some high-mountain localities in North Carolina).

The American species are characterized by reduced calyces, regular corollas, and tetramerous symmetry, while the Japanese have more prominent calyces, more or less irregular corollas (some almost cylindric and about 1.5 cm. long), and prevailing pentamerous symmetry (although with a tendency toward tetramery and reduction in the number of stamens). The genus presumably stands nearest *Rhododendron* from which it differs most obviously in the included stamens and the opening of the

anthers by short slits, rather than by pores. In *Tsusiophyllum* Maxim. (monotypic, Japan), in which the stamens are ten, the corolla 5-lobed, and the ovary 3-locular, the anthers open by longer slits, so that in this respect *Menziesia* stands between *Tsusiophyllum* and *Rhododendron*. In wood anatomy, however, *Tsusiophyllum* is more highly specialized than either and is on a level with *Ledum* L. which was placed near *Rhododendron* by Copeland.

REFERENCES:

See also under family references COPELAND (1943, pp. 589–592), Cox (Ericales I, p. 243), and PELTRISOT.

CORMACK, R. G. H., and A. L. GORHAM. Effects of exposure to direct sunlight upon the development of leaf structure of two deciduous shrub species. *Canad. Jour. Bot.* 31: 537–541. 1953. [*M. glabella* and *Lonicera glaucescens*.]

SIMS, J. *Menziesia ferruginea*. *Bot. Mag.* 37: pl. 1571. 1813. [Plant figured is *M. pilosa*.]

6. *Rhododendron* Linnaeus, Sp. Pl. 1: 392. 1753; Gen. Pl. ed. 5. 1754, "*Rhododendrum*."

Evergreen or deciduous shrubs (rarely trees) [sometimes epiphytes], with alternate, entire (rarely ciliate-serrulate), glabrous to tomentose, lepidote, or strigose leaves. Buds with several to many imbricate scales. Flowers pedicellate, usually in terminal corymbs [sometimes solitary or few, rarely from lateral buds]. Calyx 5-parted, various, often very small [rarely 6–10-parted], persistent. Corolla white to yellow, pink, purple or deep red, rotate to campanulate or funnelform [sometimes tubular], usually irregular, with a 5 [rarely 6–10]-lobed limb [rarely some of the lobes divided to the base], the median lobe adaxial; deciduous. Stamens 5–7–10 [–20], usually exserted from the corolla [except in some tropical montane groups], the filaments usually unequal, the anthers unappendaged, muticous, without white disintegration tissue, opening (through collapse tissue) by apical pores; pollen tetrads with viscin strands. Stigma capitate; style slender, curved; ovary 5 [–10–20]-locular, superior, free from the calyx; ovules numerous in each locule. Fruit a septicidal capsule, usually ovoid to oblong; seeds numerous, minute, flat and more or less winged to fusiform [or caudate]. Basic chromosome number 13. (Including *Azalea* L. sensu Desv., *Azaleastrum* Rydb., *Biltia* Small, *Hymenanthus* Blume, *Rhodora* L.) LECTOTYPE SPECIES: *R. ferrugineum* L.; see N. L. Britton, N. Am. Trees 752. 1908. (Name from Greek, *rhodon*, rose, and *dendron*, tree; the ancient Greek name of *Nerium Oleander* L.) — RHODODENDRONS, AZALEAS.

A genus of 800 or more species of the colder and temperate parts of the Northern Hemisphere, centering in eastern and southeastern Asia, and especially the Himalayas, extending southward on the high mountains of Malaysia, the Philippines, and New Guinea to Queensland, and with a

much smaller center of development in eastern North America, a few species in the mountains of Europe, and *R. lapponicum* (L.) Wahlenb. ($2n = 26, 52$) circumboreal. About 21 species occur in continental North America, including 17 species in four sections in the southeastern United States.

Most authors with more than a regional viewpoint have maintained *Rhododendron* as a polymorphic genus difficult to divide into large, well-marked natural units and susceptible of only artificial division into genera of convenience. Both Copeland and Cox have proposed dismemberment of the inclusive genus on anatomical grounds, but very few (including almost none of the taxonomically critical) species have been examined in this respect. The subgeneric classification is still in a state of flux, and from four to eight subgenera and as many as 20 sections or some 43 informal "series" have been recognized. The conservative course of emphasizing morphological and genetic similarities, rather than differences, is followed here and the subgeneric categories are taxonomically those of Rehder. The species of the southeastern United States fall into four well-marked groups which have been placed in three genera (*Rhododendron*, *Biltia*, *Azalea*). The relationships of these are not directly with each other but with species elsewhere, and the much greater diversity of the Asiatic species bridges the discontinuities seen on a purely regional basis.

Subgenus RHODODENDRON (subg. *Eurhododendron* Drude) comprises evergreen [or rarely deciduous] species with flowers produced in terminal umbel-like racemes on shoots of the preceding year, the stamens 5–20. Two sections are represented in our area. Section PONTICUM G. Don (§ *Leiorhodium* Rehd.; *Hymenanthus* Blume) has glabrous to tomentose persistent leaves, [glabrous,] glandular or hairy ovaries, and 10–20 stamens. *Rhododendron catawbiense* Michx. and *R. maximum* L. (both $2n = 26$) occur in the eastern United States, the former largely in the southern Appalachians. Most closely related to *R. ponticum* L. ($2n = 26$), of Europe and Asia Minor, and to *R. macrophyllum* D. Don ex G. Don ($2n = 26$), of California to British Columbia, the two are distinctive morphologically (leaf shape, flower size and color, indument of ovary, etc.), ecologically, and seasonally, hybridizing occasionally (to produce *R. × wellesleyanum* Waterer ex Rehd.) when ecological and seasonal barriers break down. *Rhododendron catawbiense* is interfertile with a number of other species of the section and has been used extensively in the production of hardy ornamental hybrids.

Section RHODODENDRON (§ *Leiphipherum* G. Don), with leaves and ovary lepidote with entire-margined, patelliform scales, and stamens 10, is represented by three closely related magenta- to white-flowered taxa (subsect. *Caroliniana* Sleumer) ranging entirely within our area. *Rhododendron carolinianum* Rehd. ($2n = 26$) occurs mostly at higher altitudes in the mountains of North Carolina, Tennessee, South Carolina, and northeastern Georgia. Although usually with pink or white corollas, a clear yellow form (f. *luteum* Frisbie) has been described from a cultivated plant presumably collected in western North Carolina. *Rhododendron minus*



FIG. 2. *Rhododendron*. a-e, *R. carolinianum*: a, flowering branchlet, $\times \frac{1}{2}$; b, flower, $\times \frac{1}{2}$; c, flower, lateral view, corolla and four stamens removed, $\times 1$; d, ovary, cross section, semidiagrammatic, $\times 10$; e, seed, hilum at lower end, ca. $\times 20$. f-k, *R. Vaseyi*: f, inflorescence, $\times \frac{1}{2}$; g, flower, $\times \frac{1}{2}$; h, flower, lateral view, corolla and three stamens removed, $\times 1$; i, branchlet with fruits of two seasons, flower buds and vegetative bud, $\times \frac{1}{2}$; j, capsule showing dehiscence by septicial slits, $\times 1\frac{1}{2}$; k, seed, hilum at lower end, ca. $\times 20$. l-q, *R. atlanticum*: l, flowering branchlet, $\times \frac{1}{2}$; m, flower, $\times 1$; n, anther, inner view, $\times 5$; o, stigma, $\times 10$; p, capsule, $\times 1\frac{1}{2}$; q, seed, hilum at lower end, ca. $\times 20$.

Michx. (*R. punctatum* Andr., *R. Cuthbertii* Small) ($2n = 26$) is a plant of lower altitudes, primarily in the Piedmont, in scattered localities from central Alabama to southwestern Georgia and northward to North Carolina, while *R. Chapmanii* Gray is of much more restricted distribution, occurring in scattered colonies in pinelands and on bluffs in the Apalachicola region of western Florida and in northeastern Florida. The latter two are similar in conformation of the corolla, while *R. minus* and *R. carolinianum* are similar in leaf shape and habit (although the former is a taller, more straggling and later flowering shrub than the latter). The three apparently are largely separated geographically and ecologically, although the ranges of *R. carolinianum* and *R. minus* seem to approach one another closely in northeastern Georgia and some intergradation may occur.

Subgenus ANTHODENDRON (Reichenb.) Rehd.⁴ includes deciduous to evergreen species with the flowers in leafless corymbs at the ends of shoots of the previous season, the stamens 5–10. Four sections are recognized, two in our area, two entirely Asiatic. Section TSUTSUSI Sweet (§ *Tsutsusi* G. Don) includes many of the commonly cultivated azaleas: *R. indicum* (L.) Sweet, *R. Simsii* Planch., *R. obtusum* (Lindl.) Planch., among others, as well as many artificial hybrids.

Section RHODORA (L.) G. Don, with flowers from a terminal bud, the leafy shoots from separate lateral buds and stamens 10 or 7, includes five species: three of Asia; *R. canadense* (L.) Torr. ($2n = 52$, and unique in the genus in the deeply divided corolla) entirely within the glaciated area to the north of our range; and *R. Vaseyi* Gray (*Biltia Vaseyi* (Gray) Small) ($2n = 26$), restricted to a limited area of western North Carolina at 900–1600 m. altitude. *Rhododendron Vaseyi* is quite distinct in the pale-pink, 2-lipped, rotate-campanulate corolla with very short tube, the uppermost corolla lobe exterior in the bud, and the stamens 7 (5 or 6), but, as Rehder (1926) has shown, *Biltia* Small cannot be maintained on these bases. The species is isolated among the American taxa and is probably most nearly related to the Japanese *R. Albrechtii* Maxim. Both species reportedly have been crossed with *R. Schlippenbachii* Maxim. (very similar in floral structure, but of the Asiatic sect. BRACHYCALYX Sweet

⁴ Seithe-von Hoff (1960, p. 312) adopts subg. *Azalea* (L.) Planchon (Fl. des Serres 9: 75. 1853/54) as the correct name for this taxon, maintaining that Rehder (Jour. Arnold Arb. 2: 156–159. 1921) was incorrect in typifying *Azalea* L. by *A. procumbens* L. (*Loiseleuria procumbens* (L.) Desv.) and that *A. pontica* L. (*Rhododendron luteum* Sweet) should be selected instead as lectotype species. However, Rehder's arguments seem relevant, and, as he pointed out, *Azalea* was effectively typified by Salisbury who removed the other species to *Rhododendron*, leaving only *A. procumbens* in *Azalea*. Since this species is also the type of the conserved name *Loiseleuria*, *Azalea* L. is automatically unavailable. Planchon, moreover, published this combination as a section, rather than a subgenus. It is mentioned only briefly as "un sous-genre auquel nous réservons le nom sous-générique d'*Azalea*." However, sect. *Tsutsia* Planchon, which is clearly indicated on the following page as "*Rhododendron*, sect. *Tsutsia*," receives similar treatment, Planchon noting that it is composed of the "Azalées de l'Inde, encore plus clairement un simple sous-genre du type *Rhododendron* pour lequel nous proposerons le nom de *Tsutsia*." The parallel is clear, and "sous-genre" is to be translated as "sectio" in this instance.

[§ *Sciadorhodium* Rehd. & Wils.] in which the flowers are from terminal buds with leafy shoots from the axils of the lower scales of the same bud).

Section ANTHODENDRON (§ *Pentanthera* G. Don), with the inflorescence from the terminal bud and leaves from lateral buds below, stamens 5, leaves mostly deciduous, and pubescence, if present, setose or the hairs flattened, includes the European *R. luteum* Sweet (*R. flavum* G. Don), the Japanese *R. japonicum* (Gray) Suringar, the Chinese *R. molle* (Blume) G. Don, the western American *R. occidentale* (Torr. & Gray) Gray, and about 13 species centering in the southeastern United States but extending northward to New England, southern Quebec, central New York and westward to Arkansas and eastern Texas. The group includes the red- to yellow-flowered *R. Bakeri* (W. P. Lemmon & McKay) Hume (including *R. cumberlandense* E. L. Braun), *R. flammeum* (Michx.) Sarg. (*R. speciosum* Sweet), *R. calendulaceum* (Michx.) Torr., *R. austrinum* (Small) Rehd., and *R. prunifolium* (Small) Millais; the pink-tubed to pink-flowered *R. roseum* (Loisel.) Rehd., *R. nudiflorum* (L.) Torr., and *R. canescens* (Michx.) Sweet; and the essentially white-flowered *R. alabamense* Rehd., *R. atlanticum* (Ashe) Rehd., *R. viscosum* (L.) Torr., *R. serrulatum* (Small) Millais, *R. oblongifolium* (Small) Millais, and *R. arborescens* (Pursh) Torr. These basic species are distinctive, differing morphologically in characters of bud scales, corollas, leaves, and pubescence, but hybridization in many areas has so blurred the lines between species that precise identification of individual specimens is difficult or impossible. With the exception of *R. calendulaceum* ($2n = 52$), all are diploids ($2n = 26$) which produce largely fertile hybrids. However, considerable hybridization seems to have occurred between *R. calendulaceum* and diploid species; in most instances the hybrids are tetraploid. Differences in geographical distribution, ecology, and flowering time appear to be the chief barriers to hybridization, and wherever these overlap perplexing hybrid swarms, sometimes involving three or more species, may occur. Only the late-flowering and isolated *R. prunifolium*, of southwestern Georgia and adjacent Alabama, is not known to hybridize with other species in the wild, but *R.* × *gladwynense* M. G. Henry, its artificial hybrid with *R. serrulatum*, is fertile and vigorous. Other combinations of allopatric species also produce fertile hybrids, and *R.* × *gandavense* (K. Koch) Rehd. is noteworthy as a showy artificial hybrid swarm involving at least *R. luteum*, *R. calendulaceum*, and *R. nudiflorum* and probably *R. viscosum* and other species.

Chromosome numbers have been reported for about 360 species of *Rhododendron*. The species of subg. RHODODENDRON § PONTICUM, subg. AZALEASTRUM, and subg. ANTHODENDRON appear to be diploids ($2n = 26$), with the two exceptions noted above, but subg. RHODODENDRON § RHODODENDRON includes a number of series with varying degrees of polyploidy (about 44 known tetraploids, 22 hexaploids, 1 octoploid, 1 duodecaploid), apparently correlated with altitude in the high mountains of Asia. A large number of species are in cultivation, especially in the milder

climates of Great Britain and the northwestern United States, and many hybrids have been made both between closely related species and even those of different subgenera (e.g., *RHODODENDRON* \times *ANTHODENDRON* = subg. \times *AZALEODENDRON*). All of the intersubgeneric hybrids appear to be sterile, however, and some are weak or inviable. Self-compatibility to incompatibility have been recorded for various species (e.g., *R. catawbiense*) and hybrids. The genus appears to be proterogynous throughout. The horticultural and technical literature on the genus is enormous.

REFERENCES:

- The vast number of references has been reduced here primarily to those of either general interest or dealing specifically with the southeastern United States. See also *Rhododendron* Yearb. Roy. Hort. Soc. 1-7, 1946-1953, continued as *Rhododendron and Camellia* Yearb. and Quart. Bull. Am. Rhododendron Soc.; Rehder, *Man. Cult. Trees Shrubs*, *Bibl. Cult. Trees Shrubs*, and in Bailey, *Stand. Cyclop. Hort.*; also under family references COPELAND (1943, pp. 592-619), COX (Anatomy of Ericales. I, pp. 239-243), MATTHEWS & KNOX (1926, pp. 245-247), PELTRISOT (1904), STANLEY (1931).
- ALEXANDER, E. J. *Azalea viscosa glauca*. *Addisonia* 11: 35, 36. *pl.* 370. 1926.
Azalea calendulacea. *Ibid.* 13: 17, 18. *pl.* 425. *Azalea arborescens*. *Ibid.* 19: 17, 18. *pl.* 617. 1935.
- BALDSIEFEN, W. Deciduous azaleas from cuttings. *Proc. Pl. Propagators Soc.* 8: 172-175. 1958.
- BOWERS, C. G. *Rhododendrons and azaleas. Their origins, cultivation and development.* i-xv + 549 pp. Macmillan Co., New York. 1936.
- . The development of pollen and viscin strands in *Rhododendron catawbiense*. *Bull. Torrey Bot. Club* 57: 285-314. *pls.* 11-15. 1931.
- BRAUN, E. L. The red azalea of the Cumberlands. *Rhodora* 43: 31-35. 1941. [*R. cumberlandense*.]
- BRITTON, E. G. Wild plants needing protection. 6. "Wild Azalea" (*Azalea nudiflora* L.). *Jour. N. Y. Bot. Gard.* 14: 79-81. *pl.* 114. 1913. 14. Great laurel or rose bay (*Rhododendron maximum* L.). *Ibid.* 23: 137, 138. *pl.* 277. 1922.
- CAIN, S. A., and J. D. O. MILLER. Leaf structure of *Rhododendron catawbiense* Michx. grown in *Picea-Abies* forest and in heath communities. *Am. Midl. Nat.* 14: 69-82. 1933.
- CLARKE, J. H. A selected list of *Rhododendron* literature. *Quart. Bull. Am. Rhododendron Soc.* 10: 163-168. 1956.
- COGGESHALL, R. Rooting Ghent azaleas under plastic. *Am. Nurseryman* 107(11): 7, 8, 29. 1958. (See also *Arnoldia* 20: 1-7. 1960.) [Method applicable to American deciduous species.]
- COKER, W. C. The distribution of *Rhododendron catawbiense* with remarks on a new form. *Jour. Elisha Mitchell Sci. Soc.* 35: 76-82. *pls.* 19-22. 1919. [Stations in the Piedmont of N. C.; also comments on *R. maximum*, *R. minus*.]
- . *Azalea atlantica* Ashe and its variety *luteo-alba* n. var. *Ibid.* 36: 97-99. *pls.* 1, 7. 1920.
- . A remarkable new *Rhododendron*. *Ibid.* 51: 189, 190. *pls.* 53, 54. 1935. [*R. Ashleyi* = form of *R. maximum*.]
- COVILLE, F. V. The effect of aluminum sulphate on rhododendrons and other acid-soil plants. *Rep. Smithson. Inst.* 1926: 369-382. *pls.* 1-13. 1927.

- COWAN, J. M. A survey of the genus *Rhododendron*. *Rhododendron Yearb. Roy. Hort. Soc.* 4: 29–58. *figs.* 3, 6–19. 1949.
- . The *Rhododendron* leaf: a study of the epidermal appendages. xi + 120 pp. Oliver & Boyd, London. 1950.
- CREECH, J. L. An embryological study in the *Rhododendron* subgenus *Anthodendron* Endl. *Bot. Gaz.* 116: 234–243. 1955. [Embryology of *R.* (§ *Anthodendron*) *japonicum*, *R.* (§ *Tsusutsi*) *mucronatum*, and hybrid.]
- DAVIDSON, H., and D. P. WATSON. Teratological effects of photoperiod on *Rhododendron catawbiense* Michx. *Proc. Am. Soc. Hort. Sci.* 73: 490–494. 1959.
- DUNCAN, W. H. Ecological comparison of leaf structures of *Rhododendron punctatum* Andr. and the ontogeny [sic] of the epidermal scales. *Am. Midl. Nat.* 14: 83–96. 1933. [*R. carolinianum* in the Smoky Mts., Tenn.]
- FERNALD, M. L. Some forms of *Rhododendron atlanticum*. In *Another century of additions to the flora of Virginia*. *Rhodora* 43: 619–624. *pl.* 692. 1941.
- FOSTER, A. S. Structure and behavior of the marginal meristem in the bud scales of *Rhododendron*. *Am. Jour. Bot.* 24: 304–316. 1937. [*R. ponticum*, *R.* × *Loderi*, *R. grande*.]
- FOSTER, H. *Rhododendron carolinianum* naturalized in New England. *Rhodora* 49: 116. 1947.
- GORDON, H. D. Mycorrhiza in *Rhododendron*. *Ann. Bot.* II. 1: 593–613. *pl.* 23. 1937.
- GRAY, A. *Rhododendron* (*Azalea*) *Vaseyi*. *Bot. Gaz.* 8: 282. 1883. [Additional notes on the species. See also BOWERS, *Natl. Hort. Mag.* 15: 202, 204, 205. 1936; SARGENT, *Gard. Forest* 1: 377. *fig.* 60. 1888; SKAN, *Bot. Mag.* 132: *pl.* 8081. 1906; SMALL, *Addisonia* 16: 97, 98. *pl.* 525. 1931; SMITH, *Bull. Torrey Bot. Club* 15: 164, 165. 1888.]
- HARDIKAR, S. W. On *Rhododendron* poisoning. *Jour. Pharmacol. Exp. Therap.* 20: 17–44. 1922.* [See also FORBES under *Kalmia*.]
- HARSHBERGER, J. W. Thermotropic movement of the leaves of *Rhododendron maximum* L. *Proc. Acad. Nat. Sci. Philadelphia.* 1899: 219–224. 1899.
- HAYES, S., J. KEENAN, and J. M. COWAN. A survey of the anatomy of the *Rhododendron* leaf in relation to the taxonomy of the genus. *Notes Bot. Gard. Edinburgh* 21: 1–34. 1951.
- HENRY, M. G. A new hybrid deciduous *Rhododendron*. *Rhodora* 55: 205–208. *pl.* 1193. 1953. [*R.* × *gladwynense*.]
- HUME, H. H. *Azaleas: kinds and culture*. ix + 199 pp. Macmillan, New York. 1948.
- HUTCHINSON, J. Evolution and classification of *Rhododendrons*. *Rhododendron Yearb. Roy. Hort. Soc.* 1: 42–47. 1946.
- . The distribution of *Rhododendrons*. *Ibid.* 2: 87–98. 1947.
- ILTIS, H. H. Studies in Virginia plants. II. *Rhododendron maximum* in the Virginia coastal plain and its distribution in North America. *Castanea* 21: 114–124. 1956. [See also *Wild Flower* 32: 57–66. 1956.]
- JANAKI AMMAL, E. K. Polyploidy in the genus *Rhododendron*. *Rhododendron Yearb. Roy. Hort. Soc.* 5: 92–98. 1950.
- , I. C. ENOCH, and M. BRIDGWATER. Chromosome numbers in species of *Rhododendron*. *Ibid.* 78–91. [360 species, total of 550 counts, representatives of 42 “series”; counts mostly undocumented, although source in cultivation given.]

- LAWRENCE, G. H. M. The status of *Rhododendron nudiflorum* and *R. roseum*. *Baileya* 2: 1, 2. 1954.
- LEACH, D. G. The re-creation of a species. *Quart. Bull. Am. Rhododendron Soc.* 12: 188–191. 1958. [*R.* × *Furbishii* W. P. Lemmon pro. sp. = *R. arborescens* × *Bakeri*.] See also *Gard. Jour. N. Y. Bot. Gard.* 9: 3, 4. 1959.
- LEE, F. P. Additional notes on the azaleas and rhododendrons of the Blue Ridge Mountains. *Quart. Bull. Am. Rhododendron Soc.* 12: 74, 75. 1958.
- . The azalea book. xii + 324 pp. Van Nostrand, Princeton, N. J. 1958. [See especially *Luteum* and *Canadense* subseries, pp. 161–171.]
- , F. O. COE, B. Y. MORRISON, M. PERKINS, and F. WEISS. The azalea handbook. *Natl. Hort. Mag.* 31: 1–148 (Index, 293–303). 1952. (Also reprinted separately.)
- LEMMON, W. P. Notes on a study of the southeastern azaleas with description of two new species. *Bartonia* 19: 14–17. 1938. [*A. fastigifolia*, *A. Bakeri*.]
- . A new *Azalea* from the mountains of Georgia. *Ibid.* 21: 5, 6. 1942. [*A. Furbishii*; see LEACH.]
- LI, H. L. Chromosome studies in the azaleas of eastern North America. *Am. Jour. Bot.* 44: 8–14. 1957. [271 plants representing all of the native species of § *Anthodendron* and many hybrids.]
- LOVELL, J. H., and H. B. LOVELL. The pollination of *Rhodora*. *Rhodora* 34: 213, 214. *pl.* 222. 1932. [*R. canadense*.]
- MILLAIS, J. G. Rhododendrons, in which is set forth an account of all species of the genus *Rhododendron* (including azaleas) and the various hybrids. xi + 268 pp. Longmans, Green & Co., London, 1917. Rhododendrons and the various hybrids. 2nd series. xii + 265 pp. 1924.
- MORRISON, B. Y. *Rhododendron Chapmanii* A. Gray. *Natl. Hort. Mag.* 18: 48–50. 1939.
- RAMSEUR, G. S. A natural stand of *Rhododendron* × *wellesleyanum* Waterer ex Rehder in the southern Appalachians. *Jour. Elisha Mitchell Sci. Soc.* 75: 131. 1959. [In the Black Mts., western N. C., alt. ca. 1700 m.]
- REHDER, A. *Rhododendron carolinianum*, a new rhododendron from North Carolina. *Rhodora* 14: 97–102. 1912. [See also G. V. Nash, *Addisonia* 1: 1, 2. *pl.* 1. 1916.]
- . *Azalea* or *Loiseleuria*. *Jour. Arnold Arb.* 2: 156–159. 1921.
- SARGENT, C. S. *Rhododendron*. *Silva N. Am.* 5: 143–150. *pls.* 238, 239. 1893. [*R. maximum*.]
- SAX, K. Chromosome stability in the genus *Rhododendron*. *Am. Jour. Bot.* 17: 247–251. 1930. [Undocumented counts of 16 spp., 9 hybrids.]
- SCHRENK, H. VON. Branch cankers of *Rhododendron*. *Missouri Bot. Gard. Rep.* 18: 77–80. *pls.* 5, 6. 1907. [On *R. maximum*.]
- SEITHE-VON HOFF, A. Die Haarformen der Gattung *Rhododendron* L. und die Möglichkeit ihrer taxonomischen Verwertung. *Bot. Jahrb.* 79: 297–393. *pls.* 6–11. 1960.
- SHAMMARELLO, A. M. The propagation of rhododendrons by stem cuttings. *Proc. Pl. Propagators Soc.* 7: 85–87. 1957.*
- SIMS, J. *Rhododendron calendulaceum*. *Bot. Mag.* 41: *pl.* 1721. 1815. [See also 47: *pl.* 2143. 1820; 62: *pl.* 3439. 1835. *R. catawbiense*, 39: *pl.* 1671. 1814; *R. maximum*, 24: *pl.* 951. 1806; *R. minus*, 49: *pl.* 2285. 1822; *R. speciosum*, 5: *pl.* 180. 1792; *R. Vaseyi*, 132: *pl.* 8081. 1906.]

- SINCLAIR, J. The *Rhododendron* bud and its relation to the taxonomy of the genus. Notes Bot. Gard. Edinburgh 19: 267-271. 1937. [223 spp.; convolute buds in lepidote species, revolute in elepidote.]
- SKINNER, H. T. In search of native azaleas. Morris Arb. Bull. 6: 1-10, 15-22. 1955 (Abridged, *Rhododendron Camellia* Yearb. Roy. Hort. Soc. 11: 9-28. 1956). [A general account of extensive collecting, including many comments on species and hybridization.]
- . An evaluation of our eastern wild azaleas. Arb. Bull. 22: 80, 81, 106. 1959.
- and W. H. CAMP. Luteum subseries. In LEE *et al.*, *Azalea Handb.* pp. 29-36. [§ *Anthodendron*.]
- SLEUMER, H. Ein System der Gattung *Rhododendron* L. Bot. Jahrb. 74: 511-533. 1949. [Eight subg., 20 sects.; see also *Gartenflora* 86: 103-105. 1937.]
- . *Florae Malesianae Precursores XXIII*. The genus *Rhododendron* in Malaysia. *Reinwardtia* 5: 45-231. 1960.
- . The genus *Rhododendron* L. in Indochina and Siam. *Blumea Suppl.* 4: 39-59. 1958.
- SMALL, J. K. A Georgia *Rhododendron*. *Torreyia* 2: 9, 10. 1902. [*R. Cuthbertii* Small = *R. minus*.]
- STEVENSON, J. B., editor. The species of *Rhododendron*. i-viii + 861 pp. *Rhododendron Society*, Edinburgh. 1930. [Species of Malaysia and New Guinea omitted; species arranged in 43 series; no key to series; § *Ponticum* by H. F. Tagg; § *Rhododendron* by J. Hutchinson; subg. *Anthodendron*, *Azaleastrum*, etc., by A. Rehder.]
- TOTTEN, H. R. A station for *Rhododendron Chapmannii* in eastern Florida. *Proc. Fla. Acad. Sci.* 7: 105. 1944 [1945.] [Clay County.]
- VEILLET-BARTOSZEWSKA, M. Éricacées. Développement de l'embryon chez le *Rhododendron ferrugineum* L. *Compt. Rend. Acad. Sci. Paris* 244: 1952-1954. 1957.
- . Développement de l'albumen chez le *Rhododendron ferrugineum* L. *Bull. Soc. Bot. Fr.* 106: 17-20. 1959.
- WARD, F. K. *Rhododendron* seeds, with special reference to their classification. *Jour. Bot.* 73: 241-247. 1935.
- . Observations on the classification of the genus *Rhododendron*. *Rhododendron Yearb. Roy. Hort. Soc.* 2: 99-114. 1947.
- WHERRY, E. T. The American azaleas and their varieties. *Natl. Hort. Mag.* 22: 158-166. 1943.
- WILSON, E. H. The "Indian Azaleas" at Magnolia Gardens. *Jour. Arnold Arb.* 2: 159, 160. 1921. [Charleston, S. C.]
- and A. REHDER. A monograph of azaleas. *Rhododendron* subgenus *Anthodendron*. *Publ. Arnold Arb.* 9: 1-219. 1921. [The basic monograph for subg. *Anthodendron*.]

Tribe ANDROMEDEAE Endlicher

7. *Leucothoë* D. Don, *Edinburgh New Philos. Jour.* 17: 159. 1834.

Evergreen or deciduous shrubs (or small trees), with alternate, short-petioled, serrulate or crenulate to entire leaves; winter buds small, with several outer scales. Inflorescences racemose, from axillary buds on wood

of the preceding season; flowers in the axils of small, persistent bracts [in *L. Grayana* one or more flowers in the axils of leaves, the inflorescence terminating a short leafy branch of the same season from an axillary bud]; pedicels with two opposite bracteoles at the base or beneath the calyx. Calyx of 5 nearly distinct sepals imbricate or quincuncial in bud. Corolla ovoid or cylindric, glabrous, white [to red], with 5 short lobes. Stamens 10, on the base of the corolla; filaments straight or S-shaped, expanded at the base, glabrous to villous, unappendaged; anthers opening by pores, obtuse or 2- or 4-awned at the apex (the awns sometimes minute), with white disintegration tissue in the angle between the awns (or in this position when the awns are lacking); pollen tetrads without viscin strands. Stigma expanded, somewhat peltate and 5-lobed to truncate; style straight, included or exserted from the corolla; ovary superior, 5-locular; placentae undivided, at the top of the axis, with the anatropous to campylotropous ovules mostly pendulous on the outer and/or under side. Fruit a 5-lobed, depressed-globose capsule, 5-valved, loculicidal, without thickened sutures, the calyx and placentae persistent; seeds pendulous, scobiform, angled, with a loose, thin testa, sometimes winged. (Including *Eubotrys* Nutt., *Agarista* D. Don ex G. Don.) TYPE SPECIES: *L. axillaris* (Lam.) D. Don. (A poetic name, for Leucothoë, daughter of Orchamus, King of Babylon, mentioned by Ovid.)

A genus of about 50 species, variously placed in about six genera, two subgenera, or seven sections; about four species in eastern Asia, 35 in South America, one in Central America, one in California and Oregon, and five (in three sections) in the eastern United States.

Section LEUCOTHOË, composed of evergreen species with bracteoles at the base of the pedicels, erect, glabrous to short-pubescent filaments, and anthers with four very short (in ours) to long awns, is represented in the southeastern United States by two closely related species. *Leucothoë axillaris* (*L. Catesbaei* (Walt.) Gray, but not sensu Gray or most authors; *L. platyphylla* Small), with abruptly pointed leaves with petioles to about 1 cm. long and with rather broadly ovate or rounded bracts and sepals broadly ovate (hence still imbricate at anthesis), is confined to low woods on the Coastal Plain from Florida westward to Louisiana and northward to southeastern Virginia. *Leucothoë Fontanesiana* (Steud.) Sleum. (*Andromeda Fontanesiana* Steud., *L. editorum* Fern. & Schub., *L. Catesbaei* sensu most authors), with decidedly long-acuminate leaves, longer petioles, and the bracts lanceolate-acuminate, the sepals ovate-oblong and acutish (hence scarcely imbricate at anthesis), is a plant of cool, moist woods (especially along streams) in the mountains of southwestern Virginia, western North Carolina, eastern Tennessee, and northern Georgia. The two species, which appear to be completely isolated, are in need of further study, for, although the leaf shapes usually are distinctive, those of bracts and sepals appear to be less so. *Leucothoë Fontanesiana* is far hardier than *L. axillaris* and is important horticulturally northward to New England.

The closest relative of these two species is *L. Griffithiana* C. B. Clarke (including *L. tonkinensis* Dop), of Indochina, Burma, Yunnan, and south-eastern Tibet. The placing of this species, which is amazingly similar to ours, in sect. OLIGARISTA Sleum. on the basis of the greater development of the four awns on the anthers unfortunately obscures another of the close relationships between species of Asia and North America. Other related species which fit well into sect. LEUCOTHÖE are *L. Davisiae* Torr. (§ *Acranthes* Sleum.), of California and Oregon, and *L. Keiskei* Miq. (§ *Paraleucothoe* Nakai), of Japan.

Section AGASTIA DC. (*Agarista* D. Don ex G. Don), a distinct section of clearly related species in which the leaves are persistent and entire, the anthers without awns, the filaments S-curved and villose, the stigmas truncate, and the bracts and bractlets narrow, is primarily South American with its center of differentiation in Brazil. *Leucothoe mexicana* (Hemsl.) Small, ranges from Honduras to Mexico, and the similar *L. populifolia* (Lam.) Dippel (*L. acuminata* (Lam.) G. Don), $2n = 24$, occurs in swamps and low hammocks on the Coastal Plain from central Florida northward to South Carolina. Among our species, *L. populifolia* is easily recognized by the entire, lanceolate to ovate-lanceolate, persistent leaves, the loose racemes of long-pediceled white flowers in April or May, as well as by the other characters of the section.

Section EUBOTRYS (Nutt.) Gray (*Eubotrys* Nutt.) includes only two deciduous species of the eastern United States with axillary inflorescences developing the summer before flowering (as in *Cassandra* and *Pieris*), bracteoles on the pedicel just beneath the calyx, and anthers conspicuously 2- or 4-awned at the apex. One, *L. racemosa* (L.) Gray, with 4-awned anthers and wingless seeds, is a plant of the Coastal Plain from Massachusetts to Florida and eastern Texas. Within this species three varieties (*racemosa*, *elongata* (Small) Fern., and *projecta* Fern.) have been proposed on the basis of pubescence of branchlets, development of the inflorescence, and size of corolla. The other, *L. recurva* (Buckley) Gray, with recurved racemes, 2-awned anthers, and winged seeds, is a montane species, mostly of rocky, open woods with other Ericaceae, *Pinus*, and *Quercus*, from western Virginia to eastern Tennessee and northern Georgia. On the basis of floral anatomy and embryology these two species were the most primitive of the 22 of the Andromedeae studied by Palser. The exact relationship of these and *L. Grayana* Maxim. (§ *Eubotryoides* Nakai), of Japan, to the remainder of the genus is in need of thorough study.

Leucothoe is distinguished by the axillary racemes (those of *L. Grayana* terminating short, leafy branches from axillary buds of the preceding season), the imbricate sepals, the stamens with terminal awns (or these lacking), the white areas of disintegration tissue in the connective lobes extending to the base of the awns (or the position they should occupy if present), the lack of spurs on the filaments, the dry capsular fruit lacking thickened margins, and the seeds with loose seed coats, sometimes winged. The genus appears to be most closely related to *Gaultheria* (q.v.); when

awned, the stamens are strikingly like those of both *Gaultheria* and *Zenobia*.

The observations of Palser that "the species of *Leucothoë* have one character in common which separates them from other species studied — the position of the placentae against the outer carpel walls with the ovules borne on the inside surfaces," need to be extended, for other species do not conform. In *L. axillaris*, *L. Fontanesiana*, and *L. Davisiae* the stalked placentae extend along the top of the locule and bend downward, bearing ovules only on the lower, inner surface; and in *L. racemosa* and *L. recurva*, the placentae are like those of *Cassandra*: columnar with the end pressed against the ovary wall, the ovules borne around the margins. However, in *L. populifolia*, *L. Griffithiana*, and *L. Grayana*, the ovules are borne on the outer as well as lateral surfaces of the stalked placentae.

REFERENCES:

- Under family references see also COX (Ericales II), KEARNEY (1901), and PALSER (1951, 1952).
- BAKER, J. G. *Leucothoë Davisiae*. Bot. Mag. 32: pl. 6247. 1876.
- DE WILDEMAN, E. *Leucothoë recurva* A. Gray. Ic. Sel. Horti Thenensis 1: 171–174. pl. 40. 1900. [Detailed illustration.]
- FERNALD, M. L. Last survivors in the flora of tidewater Virginia. Rhodora 41: 465–504, 529–559, 564–574. pls. 570–583. 1939. [Vars. of *L. racemosa*, 553, 554, pl. 578.]
- . Botanical specialties of the Seward Forest and adjacent areas of southeastern Virginia. Ibid. 47: 93–142, 149–182, 191–203. pls. 876–911. 1945. [*L. axillaris* var. *ambigens* Fern. and discussion of *L. axillaris* and *L. Fontanesiana*.]
- and B. G. SCHUBERT. Studies of American types in British herbaria. Ibid. 50: 149–176, 181–208, 217–233. pls. 1097–1117. 1948. [*Andromeda Catesbaei* Walt. is *L. axillaris* (Lam.) D. Don; *L. editorum* Fern. & Schub.]
- HARA, H. Observationes ad plantas Asiae orientalis. Jour. Jap. Bot. 11: 622–633. 1935. [*Eubotryoides* (Nakai) Hara, gen. nov., for *L. Grayana* Maxim.]
- MIYAJIMA, S., and S. TAKEI. Ueber grayanotoxine, die wirksamen Inhaltstoffe von *Leucothoë Grayana*. II. Jour. Agr. Chem. Soc. Japan 12 (Bull.): 73. 1936.*
- SARGENT, C. S. *Leucothoë recurva*. Gard. Forest 9: 224. fig. 33. 1896.
- SIMADA, H. Ein Bestandteil der Blätter von *Leucothoë Keiskei* Miq. (In Japanese; German summary.) Jour. Pharm. Soc. Japan 59: 619, 620. 1939.*
- SIMS, J. *Andromeda Catesbaei*. Bot. Mag. 45: pl. 1955. 1818. [*L. Fontanesiana*.]
- SLEUMER, H. Ericaceae americanae novae vel minus cognitae III. Notizbl. Bot. Gart. Berlin 13: 206–214. 1936. [Key to sects. of *Leucothoë*, 211–213.]
- . Studien über die Gattung *Leucothoë* D. Don. Bot. Jahrb. 78: 435–480. 1959. [Key to sects. and spp.; detailed treatment of Centr. and S. Am. spp. of § *Agastia*.]
- SMALL, J. K. *Leucothoë Catesbaei*. Addisonia 4: 61, 62. pl. 151. 1919.
- YAMASHITO, M. On grayanotoxin, the poisonous constituent of the leaves of *Leucothoë Grayana* Max. I. Sci. Rep. Tôhoku Univ. Ser. Math. Chem. Phys. 21: 537–544. 1932.*

8. *Gaultheria* Linnaeus, Sp. Pl. 1: 395. 1753; Gen. Pl. ed. 5. 187. 1754.

Dwarf, prostrate, evergreen undershrubs [to upright shrubs or rarely small trees] with broad, alternate [rarely opposite], short-petioled, usually serrate leaves; winter buds ovoid, with several outer scales. Flowers bisexual [or rarely both bisexual (?) and carpellate, the latter with much reduced stamens], 5(rarely 4)-merous, [in terminal panicles or axillary racemes or clusters or] in ours solitary in the axils of leaves; pedicels with 2 bractlets [at the base or middle or] immediately beneath the calyx [or the bracteoles several, scattered]. Calyx 5(4)-parted, [usually] accrescent and becoming fleshy. Corolla campanulate to urceolate, white to pink, glabrous or hairy within. Stamens 10 (8), on the base of the corolla; filaments expanded at the base, hairy or glabrous; anthers with white disintegration tissue on the abaxial side at the base of the bifid terminal awn on each anther-half [or in this position when awns are lacking], or disintegration tissue lacking in the most reduced species, the anthers opening by terminal pores; pollen tetrads without viscin strands. Stigma obtuse or truncate; style straight; ovary superior (and free from the calyx) or rarely partly inferior, 5(4)-locular, the axile placentae with 5–10[–many] ovules; disc 10-lobed. Fruit a 5(4)-valved loculicidal capsule inclosed by and rarely united with the usually colored (red, white [to bright blue or black]) and fleshy calyx, appearing berry-like; seeds usually numerous, small, hard, angled, wingless. (Including *Chiogenes* Salisb.) TYPE SPECIES: *G. procumbens* L. (Named in honor of Jean-François Gaultier, ?1708–1756, botanist and court-physician at Quebec.)

A genus of perhaps 150 species, many of high mountains: in Asia ranging from Japan, China, and the Himalayas, southward to New Guinea, Australia, Tasmania (three species), and New Zealand (about six species); in North America from Labrador to British Columbia, southward through Mexico and the West Indies to Patagonia. *Gaultheria* has not been revised as a unit, but Airy-Shaw has placed the species of continental Asia in five sections which include the species of North America. Section GAULTHERIA (§ *Eugaultheria* Airy-Shaw) occurs in America as two widespread species primarily of the East; sects. AMBLYANDRA Airy-Shaw and BROSSAEOPSIS Airy-Shaw are represented in the West by *G. ovatifolia* Gray and *G. humifusa* (Graham) Rydb. and by *G. Shallon* Pursh, respectively. The two species of the West Indies and those of Central America also belong to sect. BROSSAEOPSIS.

Section GAULTHERIA (dwarf undershrubs with mostly small leaves and solitary flowers with two opposite bracteoles immediately beneath the calyx) includes the most reduced species in the genus. Series *Procumbentes* Airy-Shaw comprises only the pentamerous, red-fruited *G. procumbens* ($2n = 24$), nomenclaturally typical but morphologically an isolated type in the genus. Widespread in eastern North America (Newfoundland to Manitoba, south to Minnesota, Georgia and Alabama [in the mountains], and southeastern North Carolina), the species is prob-

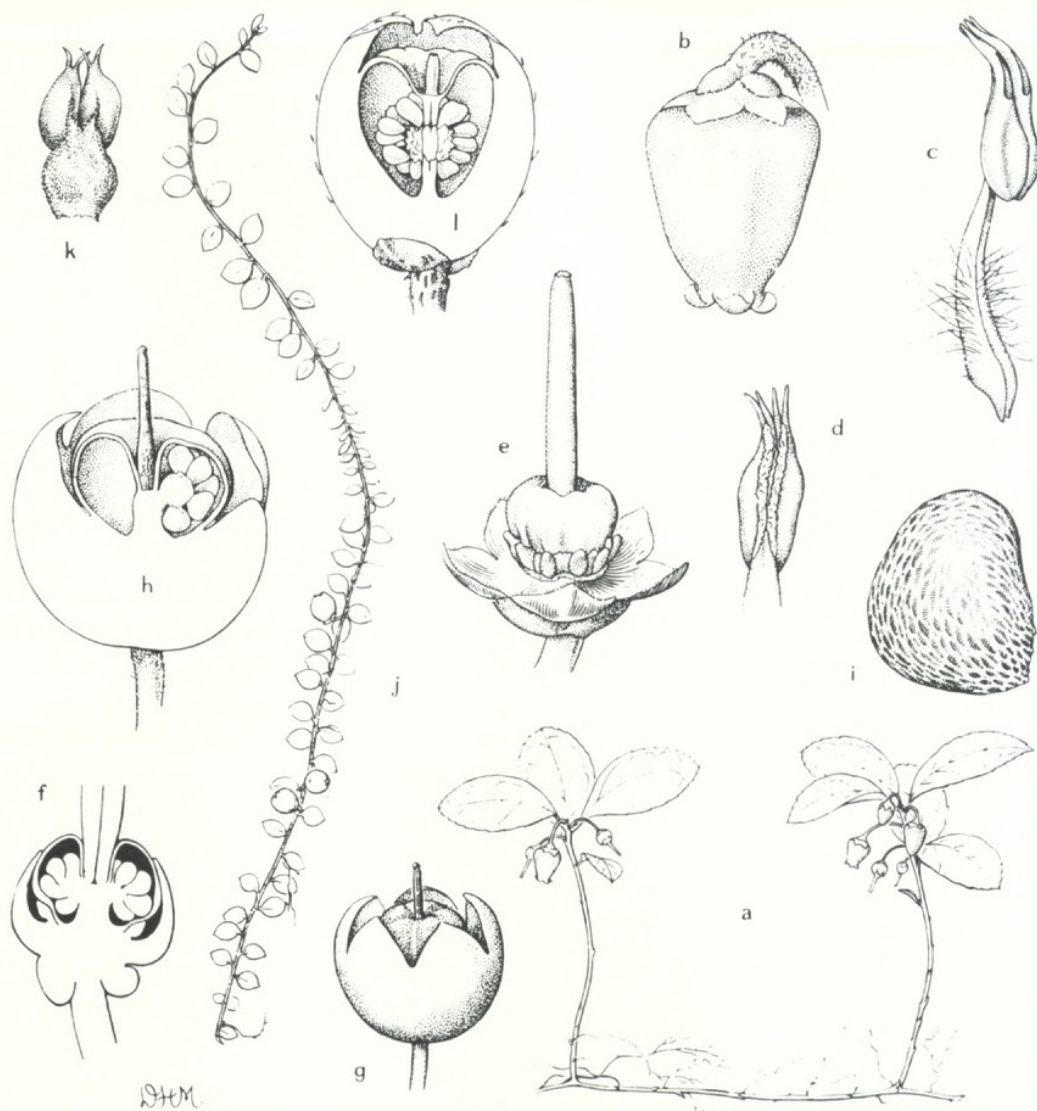


FIG. 3. *Gaultheria*. a-i, *G. procumbens*: a, habit, $\times \frac{1}{2}$; b, flower, $\times 3$; c, stamen, $\times 10$; d, anther, outer view, showing lines of disintegration tissue, awns, $\times 10$; e, calyx, disc, gynoecium, $\times 6$; f, ovary, disc, calyx, vertical section, $\times 6$; g, fruit with accrescent calyx, $\times 2$; h, fruit and calyx in vertical section, $\times 3$; i, seed, $\times 20$. j-l, *G. hispidula*: j, fruiting shoot, from below, $\times \frac{1}{2}$; k, stamen, outer view, showing lack of disintegration tissue, $\times 20$; l, immature fruit in vertical section — note two calyx lobes at top, $\times 4$.

ably most closely related to *G. (§ Leucothoides) pyroloides* Miq., of Japan. Series *Hispidulae* Airy-Shaw (which seems to have little relationship to *Procumbentes*) includes only two tetramerous-flowered, small-leaved, delicate, creeping species which represent "the last word in reduction in the genus." *Gaultheria hispidula* (L.) Muhl. var. *hispidula* (*Chiogenes hispidula* (L.) Torrey & Gray) is a white-fruited plant, mostly of cold woods and bogs to the north of our range (Labrador to New England and Pennsylvania, westward to Minnesota, Idaho, and British Columbia) but extends sporadically southward in cold mountain bogs to western North Carolina. Varietas *japonica* (Gray) Makino, of central and northern

Japan, differs only in the more obovate leaves with more cuneate base and in the shorter and less deeply bifid awns of the anthers. The second species, the awnless, red-fruited *G. suborbicularis* W. W. Sm., occurs in the high mountains of Yunnan. In both, the calyx tube enlarges into a berry-like structure which almost completely surrounds and is united with the capsule, while the calyx lobes persist almost unchanged at the top. The appearance thus given of a berry from an inferior ovary (in flower the ovary is about half-inferior) has led to the erroneous association of *G. hispidula* (as *Chiogenes*) with the Vaccinioideae. A third series, *Trichophyllae* Airy-Shaw, consists of eight or more pentamerous species, of the Sino-Himalayan ranges.

Closely related to (and perhaps congeneric with) *Gaultheria* is *Pernettya* Gaud. (Mexico to Patagonia, New Zealand, and Tasmania) which differs consistently only in the baccate (*vs.* capsular) fruit, although usually, but with exceptions in both genera, in the dry *vs.* fleshy calyx. Natural hybrids (\times *Gaulthetia* Camp) have been found in New Zealand, Mexico, and the Falkland Islands. \times *Gaulthetia wisleyensis* (Marchant) Rehd. (*G. Shallon* Pursh [$2n = 88$] \times *P. mucronata* (L. f.) Spreng. [$2n = 66$]) is a heptaploid ($2n = 77$) which is partially fertile (presumably through pairing within the polyploid parental genomes?) producing aneuploid offspring (e.g., $2n = 70, 71, 79$). Such hybridization was suggested by Callan as a possible method of origin of new species; Camp suggested independently that the Mexican *P. ciliata* (Cham. & Schlecht.) Small and perhaps *P. hirsuta* (Mart. & Gal.) Camp may have resulted from a back-cross between a \times *Gaulthetia* and the *Pernettya* parent or from genetic segregation within the hybrid itself. A number of interspecific hybrids, some fertile, are known in *Gaultheria*. Base chromosome numbers of 11, 12, and 13 have been reported in *Gaultheria* ($2n = 22, 24, 26, 44, 88, 96$), and of 11 in *Pernettya* ($2n = 22, 44, 66$).

Gaultheria shows with other genera reticulate relationships which hardly support the retention of the tribe Gaultherieae as a natural unit apart from the Andromedeae. Airy-Shaw notes *G. codonantha* Airy-Shaw, from Assam, as nearest to the prototype of the genus, and indicates a close agreement "in the morphology of the calyx, corolla, filaments, anthers and seeds," as well as in the inflorescence, between this species and *Zenobia* and *Lyonia* § *Lyonia* and § *Maria*. He further calls attention to the resemblance of *G.* (§ *Leucothoides*) *Griffithiana* Wight to *Leucothoë* *Griffithiana* C. B. Clarke, remarking that the former provides an almost perfect link between *Gaultheria* and *Leucothoë* § *Leucothoë*. He would regard *Gaultheria* as an advanced type "adapted for seed-dispersal by the agency of birds."

REFERENCES:

- Under family references see also ARTOPOEUS, BELL & BURCHILL, BERGMAN, COX (Ericales II), MATTHEWS & KNOX, and PELTRISOT.
 ABRAMS, L. The dwarf gaultherias in California. *Madroño* 2: 121, 122. 1934.
 [*G. humifusa*, *G. ovatifolia*.]
 AIRY-SHAW, H. K. Studies in the Ericales. IV. Classification of the Asiatic

- species of *Gaultheria*. Kew Bull. 1940: 306-330. 1940. [Includes sects., series applicable to N. Am. spp.]; VI. Further notes on *Gaultheria dunicola* W. W. Sm. *Ibid.* 1948: 109, 110. 1948; VII. Illustrations of four scarce Asiatic gaultherias. *Ibid.* 158-161; X. An undescribed Asiatic *Gaultheria*, with a key to the Sino-Himalayan species of section *Leucothoides*. *Ibid.* 1952: 171-174. 1952.
- ALEXANDER, E. J. *Gaultheria procumbens*. Addisonia 12: 53, 54. pl. 411. 1927.
- BESANT, J. W. Gaultherias. New Fl. Silva 11: 211-218. 1939.*
- BRIDEL, M., and S. GRILLON. La glucoside à salicylate de méthyle du *Gaultheria procumbens* L. est le monotropitoside. Jour. Pharm. Chim. VIII. 9: 1-16. 1929.* [See also Compt. Rend. Acad. Sci. Paris 187: 609-611. 1928.]
- BURTT, B. L., and A. W. HILL. The genera *Gaultheria* and *Pernettya* in New Zealand, Tasmania, and Australia. Jour. Linn. Soc. Bot. 49: 611-644. map. 1935. [Important comments on generic lines, hybrids, etc.]
- BROOK, P. J. Mycorrhiza of *Pernettya macrostigma*. New Phytol. 51: 388-397. pl. 9. 1952.
- CALLAN, H. G. The cytology of *Gaulthetia wisleyensis* (Marchant) Rehder, a new mode of species formation. Ann. Bot. II. 5: 579-585. 1941.
- CAMP, W. H. Studies in the Ericales. IV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and adjacent regions. Bull. Torrey Bot. Club 66: 7-28. 1939. [Includes *Gaulthetia*.]
- CHOU, Y. L. Floral morphology of three species of *Gaultheria*. Bot. Gaz. 114: 198-221. 1952. [*G. procumbens*, *G. ovatifolia*, *G. Shallon*; includes embryology.]
- HOLM, T. Medicinal plants of North America. 11. *Gaultheria procumbens* L. Merck Rep. 17: 1-14. 1908.
- LEBEDEV, D. V. Gibridy autoploidov i vidoobrazovanie (Hybrids of autopolyploids and the formation of species). Priroda Leningrad 36(3): 62, 63. 1947.* [\times *Gaulthetia wisleyensis*.]
- MORRISON, T. M. Host-endophyte relationships in mycorrhizas of *Pernettya macrostigma*. New Phytol. 56: 247-257. pl. 6. 1957.
- MULLIGAN, B. O. A probable bigeneric hybrid between *Gaultheria* and *Pernettya*. Jour. Roy. Hort. Soc. 64: 125-127. figs. 14-16(?17). 1939. [*P. mucronata* \times *G. Shallon* = \times *Gaulthetia wisleyensis*.]
- SIMS, J. *Gaultheria procumbens*. Bot. Mag. 45: pl. 1966. 1818.
- SLEUMER, H. Ericaceae americanae novae vel minus cognitae II. Notizbl. Bot. Gart. Berlin 12: 277-294. 1935. [Includes key to *Gaultheria* in Mexico and Guatemala, 285-287.]
- . Revision der Gattung *Pernettya* Gaud. *Ibid.* 626-655.
- . Florae Malesianae praecursores XV. The genus *Gaultheria* in Malaysia. Reinwardtia 4: 163-188. 1957.
- VEILLET-BARTOSZEWSKA, M. Embryogénie des éricacées; développement de l'embryon chez le *Gaultheria Shallon* Pursh. Compt. Rend. Acad. Sci. Paris 248: 720-722. 1959.

9. *Zenobia* D. Don, Edinburgh New Philos. Jour. 17: 158. 1834.

Deciduous to half-evergreen, glabrous, often glaucous shrubs with alternate, short-petioled serrulate-crenulate to entire, veiny, coriaceous leaves; buds ovoid, obtuse, with several outer scales. Flowers showy, nodding, fragrant, in corymbs from axillary buds on the upper part of twigs of the

preceding season; individual flowers in the axil of a short bract, the pedicel with 2 lateral bracteoles at the base. Calyx lobes 5, valvate, thickish, persistent and somewhat accrescent in fruit. Corolla white, broadly campanulate, obtusely 5-lobed. Stamens 10; filaments abruptly enlarged below, flattened; anthers opening by oblong pores, each anther-half surmounted by a pair of slender ascending awns and with a conspicuous area of white disintegration tissue in the connective; pollen tetrads without viscin strands. Stigma truncate, simple; style columnar, about as long as the corolla; ovary superior, 5-locular, 5-lobed, placentae from about the middle of the axis in each locule, with numerous ovules; disc 10-lobed. Fruit an erect depressed-globose loculicidal 5-valved capsule, the valves, axis, and placentae persistent; seeds numerous, angled, not winged. TYPE AND SOLE SPECIES: *Z. speciosa* (Michx.) D. Don = *Z. pulverulenta* (Bartr. ex Willd.) Pollard. (Name fanciful, for Zenobia, queen of Palmyra, 267–272 A. D., who conquered Egypt and most of Asia Minor.)

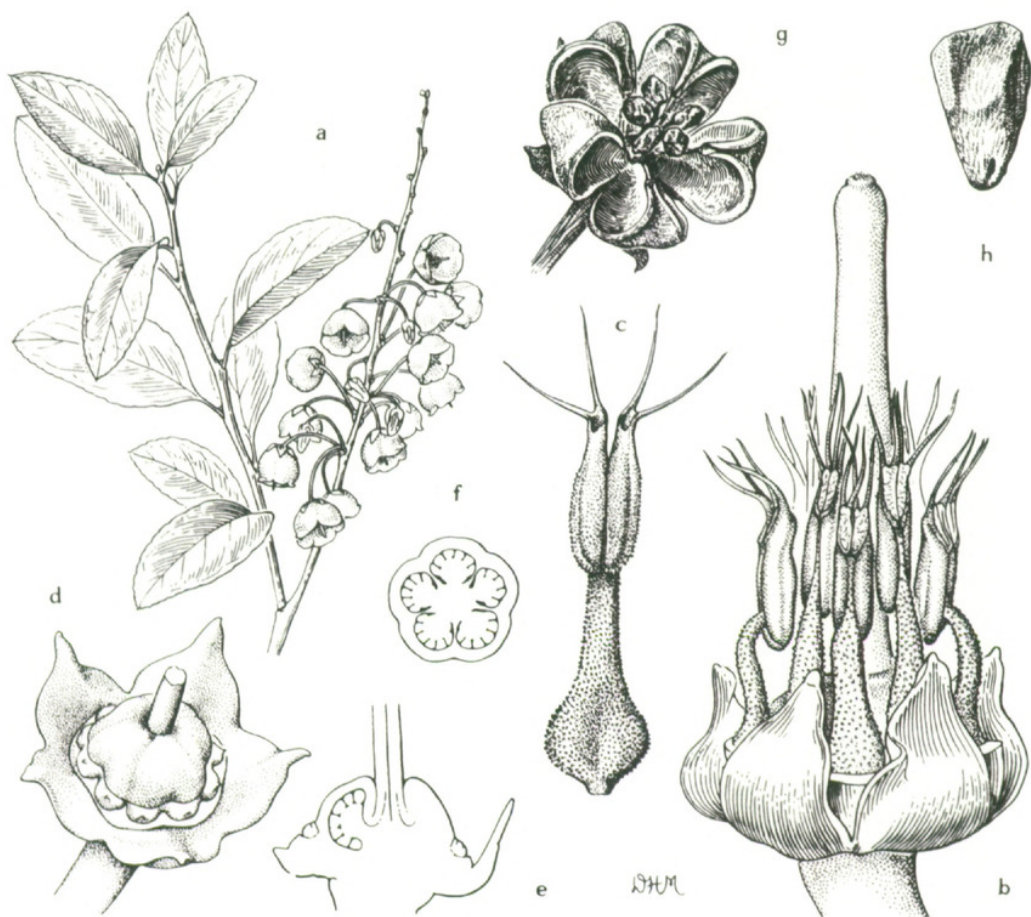


FIG. 4. *Zenobia*. a–h, *Z. pulverulenta*: a, flowering twig and new growth, $\times \frac{1}{2}$; b, flower with most of corolla removed—note white areas of disintegration tissue on back of each anther-half at base of awns, $\times 8$; c, stamen, inner view, $\times 10$; d, calyx, disc, and ovary, $\times 5$; e, ovary and calyx in section, showing placentation and disc, semidiagrammatic, $\times 5$; f, ovary, cross section, semidiagrammatic, $\times 5$; g, open capsule, $\times 4$; h, seed, $\times 15$.

A single isolated species of damp, sandy or peaty, pine savannas, shrub-bogs, or swamp margins on the Coastal Plain from southeastern Virginia to northeastern South Carolina. *Zenobia pulverulenta* is a showy shrub with racemes of (1-)5-10-flowered corymbs of fragrant, campanulate, white flowers about 1.5 cm. across borne from May to mid-June. In f. *pulverulenta* the undersides of the leaves (in addition to stems, pedicels, calyces, and ovaries) are heavily glaucous, while in f. *nitida* (Michx.) Fern. (*Z. cassinefolia* (Vent.) Pollard; *Z. speciosa* (Michx.) D. Don. var. *nitida* (Michx.) Rehd.) the leaves are green beneath. Although the two have been treated as separate species, they occur together, along with intermediates, and there is no question that only a series of forms of a single distinctive species is represented. Both are showy but not often cultivated plants which are quite hardy at least as far north as Massachusetts.

Zenobia is characterized by the combination of inflorescence, 4-awned stamens, relatively large campanulate corollas, capsular fruit, and angled, unwinged seeds. There seem to be no close relatives, but the placentation and inflorescence resemble *Lyonia* § *Maria* while the corolla and stamens are reminiscent of *Gaultheria codonantha*, suggesting interrelationships with these genera. (See *Gaultheria*.) Neither the chromosome number nor observations on the biology of the plant seem to have been recorded.

REFERENCES:

- Under family references see also ARTOPOEUS and PELTRISOT.
 FERNALD, M. L. A century of additions to the flora of Virginia. *Rhodora* 42: 355-416, 419-498, 503-521. pls. 626-649. 1940. [Discussion of forms, nomenclature, and distribution of *Zenobia*, 471-473, map 16; see also 385, 397.]
 LINDLEY, J. *Andromeda dealbata*. Bot. Reg. 12: pl. 1010. 1826. [An aberrant form with deeply lobed corollas.]
 PIERCE, S. A. *Zenobia pulverulenta*. Gard. Chron. III. 119: 148. 1946. [Notes on the plant, its culture and propagation.]
 POLLARD, C. L. The genus *Zenobia* D. Don. Bull. Torrey Bot. Club 22: 231, 232. 1895.
 SIMS, J. *Andromeda pulverulenta*. Bot Mag. 18: pl. 667. 1803; *Andromeda cassinefolia*. Ibid. 25: pl. 970. 1807.

10. *Lyonia* Nuttall, Gen. N. Am. Pl. 1: 266. 1818, nom. cons.

Evergreen or deciduous shrubs [rarely small trees], with terete or angled branches. Leaves alternate, short-petioled, entire or shallowly toothed or serrulate, glabrous, or with hairs or peltate scales; winter buds ovoid, with 2 outer scales. Inflorescences axillary (sometimes appearing to be terminal, but falsely so), corymbose, [racemose] or paniculate, the racemes sometimes contracted into axillary clusters; each flower in the axil of a small leaf or bract and with 2 lateral bracteoles at the base of the pedicel, these sometimes quickly deciduous. Calyx 5 (rarely 4-8)-lobed, the lobes valvate or reduplicate in bud, persistent or rarely deciduous in fruit.

Corolla cylindric-campanulate to urceolate or globose-urceolate, with 5(4–8) short lobes, white to pink, glabrous to hairy or lepidote. Stamens 10 (rarely 8–16); filaments flattened, often S-shaped, glabrous to hairy or roughened, with or without a pair of short, spurlike appendages on the back near the apex; anthers obtuse, the lobes parallel, lacking apical awns, dehiscent by large terminal pores, always with a white line of disintegration tissue on the back of each lobe extending at least along the apex of the filament and along the upper edge of the appendages when present; pollen tetrads without viscin strands. Stigma truncate to capitate; style columnar to fusiform, straight, not exserted; ovary superior, 5-locular, the placentae large, undivided; disc an enlargement of the ovary wall, variously developed. Capsule subglobose to ovoid, 5-angled, loculicidal, with paler, thickened sutures which may separate from the 5 valves in dehiscence; placentae persistent at the top of the columella; seeds scobiform, with a loose, thin testa. (*Xolisma* Raf.; not *Lyonia* Raf., 1808, or *Lyonia* Ell., 1817, nomina rejicienda; including *Arsenococcus* Small, *Desmothamnus* Small, *Neopieris* Britton.) LECTOTYPE SPECIES: *L. ferruginea* (Walt.) Nutt.; see I.C.B.N. 261. 1956, and Rickett & Stafleu, *Taxon* 9: 75. 1960. (In commemoration of John Lyon, 17?–1818, early American botanist and explorer of the southern Appalachians, “who fell victim to a dangerous epidemic amidst those savage and romantic mountains which had so often been the theatre of his labours.”)

A genus of perhaps 40–50 species, in three or four sections, about ten in Asia (Kashmir to Japan, south to Malaya), perhaps 30 or more in the Greater Antilles, one or two in eastern and southern Mexico, and five in the United States. The Asiatic species belong to sect. *PIERIDOPSIS* (Rehd.) Airy-Shaw, with 1-sided, usually elongated racemes, filaments with or without appendages; leaves entire, persistent or deciduous), which might well be merged with sect. *MARIA*. Although the genus has been divided into a number of genera, the distribution of the characters used is so reticulate, when all of the species are considered, that segregates are essentially based on single-character differences. The species of the southeastern United States are distinctive, but the genus as a whole (especially § *LYONIA*) is in need of a thorough monographic study. Section *MARIA* (DC.) C. E. Wood⁵ (*Xolisma* § *Maria* (DC.) Rehd.), as defined here, includes only three isolated species which are placed together on the basis of the filaments appendaged near the summit, the nonlepidote pubescence, and the

⁵ The proper combination under *Lyonia* does not appear to have been made previously for this section. This combination, with additional synonymy is:

***Lyonia* Nutt. sect. *Maria* (DC.), comb. nov.** *Leucothoë* D. Don, sect. *Maria* DC. Prodr. 7(2): 602. 1839; *Andromeda* L. sect. *Maria* (DC.) Gray, Man. Bot. North. U. S. 266. 1848; *Pieris* sect. *Maria* (DC.) Benth. & Hook. Gen. Pl. 2: 588. 1876; *Lyonia* subgen. *Maria* (DC.) Drude, Nat. Pflanzenfam. IV. 1: 44. 1889; *Xolisma* Raf. sect. *Maria* (DC.) Rehd. Jour. Arnold Arb. 5: 55. 1924; *Arsenococcus* Small in Small & Carter, Fl. Lancaster Co. 218. 1913; *Xolisma* Raf. sect. *Arsenococcus* (Small) Rehd. Jour. Arnold Arb. 5: 54. 1924. TYPE SPECIES: *Lyonia mariana* (L.) D. Don.

axillary corymbose (fasciculate) inflorescences. *Lyonia mariana* (L.) D. Don (*Neopieris mariana* (L.) Britton), $2n = 24$, ranging mostly on the Coastal Plain from Florida to Missouri, Arkansas, and eastern Texas, and

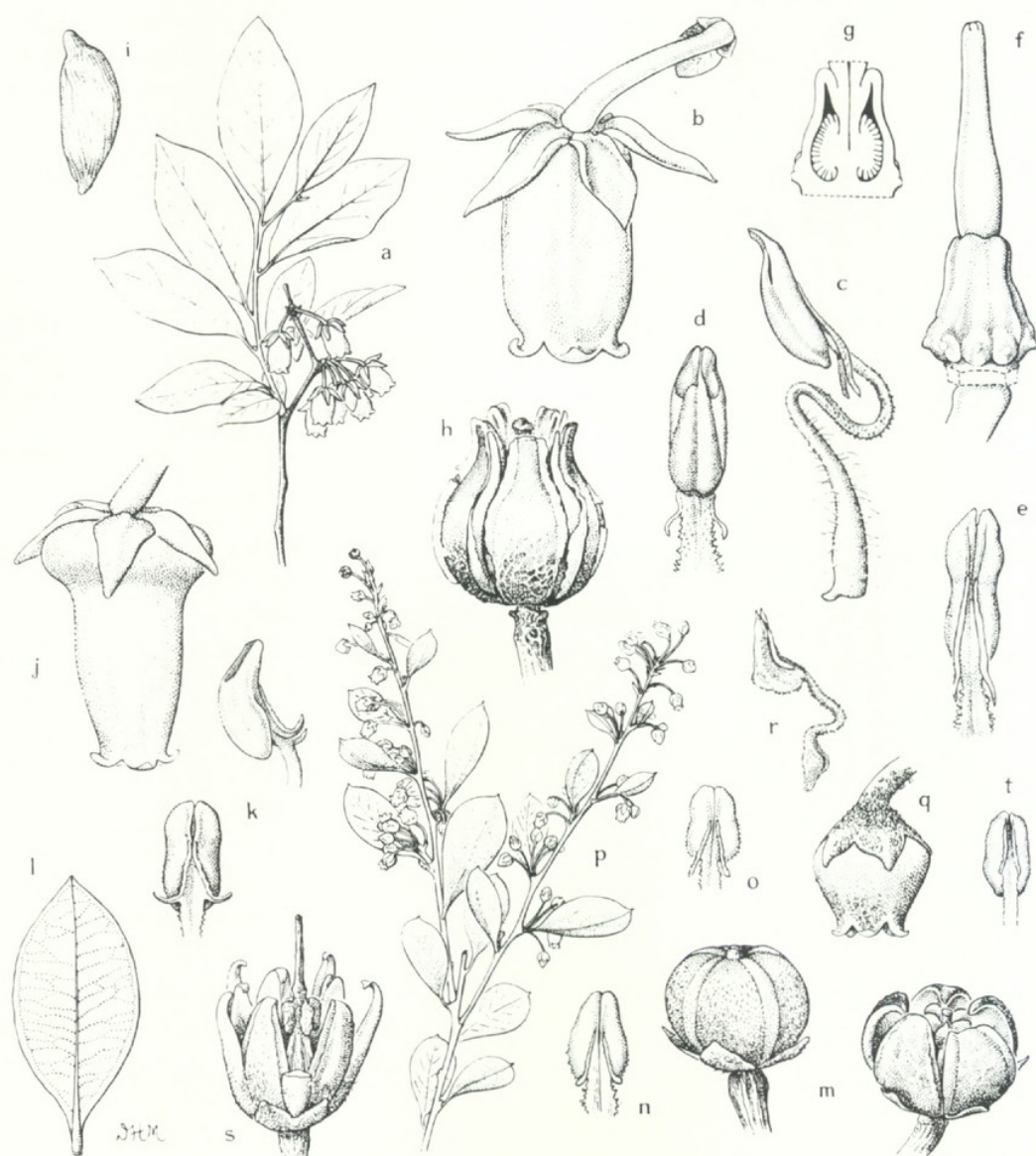


FIG. 5. *Lyonia*. a-i, *L. mariana*: a, branchlet, $\times \frac{1}{2}$; b, flower with bract and bractlets, $\times 3$; c-e, lateral, inner and outer views of stamen and anthers to show filament appendages, disintegration tissue and anther dehiscence, $\times 10$; f, gynoeceum, lateral view — note glandular development of base of ovary, $\times 5$; g, ovary, vertical section, semidiagrammatic, $\times 5$; h, opened capsule — note partial separation of thickened valve-margins (carpel midribs), $\times 4$; i, seed, $\times 20$. j-l, *L. lucida*: j, flower, $\times 3$; k, lateral and outer views of anthers — note appendages with margin of disintegration tissue, $\times 10$; l, leaf, to show marginal vein, $\times \frac{1}{2}$. m-o, *L. ligustrina*: m, immature and opened capsules — note separation of differentiated margins, $\times 4$; n, o, outer view of anthers of two collections to show appendages. p-s, *L. fruticosa*: p, flowering branchlet, $\times \frac{1}{2}$; q, flower, $\times 3$; r, stamen, lateral view, $\times 10$; s, opened capsule, one differentiated midrib (valve-margin) partially removed, $\times 4$. t, *L. ferruginea*: outer view of anther, showing lines of disintegration tissue, $\times 10$.

northward to eastern Pennsylvania, New Jersey, and southern Rhode Island, is notable for the calyx lobes deciduous with the leaves in fall, while *L. lucida* (Lam.) K. Koch (*Desmothamnus lucidus* (Lam.) Small, *Neopieris nitida* (Bartr.) Britton), $2n = 24$, distributed from western Cuba northward on the Coastal Plain to southeastern Virginia and Louisiana, is unique in the shining, persistent, coriaceous leaves with an intramarginal vein. Although *L. ligustrina* (L.) DC. is unique in the genus in the axillary or pseudoterminal inflorescences which are small panicles (racemes of corymbose fascicles) aggregated near the end of the growth of the preceding year, its separation as a monotypic section is doubtfully justifiable.⁶ Within the broad range of this species (New England to New York, West Virginia, Kentucky, Arkansas, Oklahoma, and eastern Texas southeastward to Florida) a number of not very sharply limited geographical varieties in need of further study have been defined: vars. *ligustrina*; *salicifolia* (Wats.) DC.; *capreaefolia* (Wats.) DC.; *foliosiflora* (Michx.) Fern.; and *pubescens* (Gray) Bean (*Arsenococcus frondosus* (Pursh) Small).

Section LYONIA (*Xolisma* Raf.), with the flowers in dense axillary fascicles (as in § MARIA), the filaments unappendaged, the leaves persistent and lepidote, and the thickened part of the sutures separating as a whole from the rest of the capsule (sometimes seen in other sections as well), is primarily of the Greater Antilles, with two species, *L. ferruginea* (Walt.) Nutt. and *L. fruticosa* (Michx.) G. S. Torrey on the Coastal Plain from Florida to South Carolina. *Lyonia ferruginea* also occurs in Mexico along the eastern Sierra Madre from San Luis Potosí south to Oaxaca. The former is a shrub or small tree with leaves much rolled on the margin, while the latter is always a shrub of stricter habit with nonrevolute leaves and flowers as much as two months later.

Matthews and Knox (1926) and Anthony (1927) have doubted that any real distinction exists between appendages on the back of the anthers (spurs) and those at the summit of the filament (used by Rehder [1924] in separating *Pieris* and *Lyonia*). Their contention as to the lack of a real difference in the position of the appendages in these genera may be quite correct, but the appendages are not to be confused, for Palser has shown that those of *Pieris* lack the white disintegration tissue which is always present on the upper margin of the appendages of *Lyonia*.⁷ Some

⁶ The additional difference of a supposed absence of appendages on the filaments of this species does not hold, for short spurs which are comparable with those of *L. lucida* and *L. mariana* are present in this species. (See FIG. 5, *n, o.*) Palser (1951, p. 461) wrote, "Very short downward and laterally projecting spurs formed largely of tissue which disintegrates, arise from the filament below its point of attachment with the anther . . . The disintegrating areas continue upward. These spurs are observable only on young filaments, as they have disintegrated completely on mature ones and only the ragged lateral margins of the filaments remain." These appendages are clearly present in boiled-up flowers of the material which I have examined.

⁷ Even when the filaments of *Lyonia* lack the awnlike appendages near the summit, a line of white disintegration tissue is present on each anther-half, in some species of § LYONIA forming an inverted "V" at the junction of filament and anther. (See also footnote 6.) Confusion of the two types of appendages may have come in

of the other anatomical distinctions made by Palser (e.g., vertically *vs.* horizontally S-shaped filaments) do not hold, but the conspicuously paler, usually thickened sutures of the fruit, exclusively axillary inflorescences from the wood of the preceding season, two bracteoles at the base of the pedicels, and two large outer scales of the winter buds set *Lyonia* off as a natural group of species quite distinct from *Pieris*.

REFERENCES:

- Under family references see also COX (Ericales II), KEARNEY, PALSER (1951, 1952), and PELTRISOT.
- AIRY-SHAW, H. K. *Lyonia macrocalyx*. Bot. Mag. **160**: pl. 9490. 1937. [Includes comments on § *Pieridopsis* and *Pieris bracteata*.]
- ANTHONY, J. A description of some Asiatic phanerogams. Notes Bot. Gard. Edinburgh **15**: 239–246. 1927. [*Pieris macrocalyx*; merges *Pieris* and *Xolisma*.]
- FERNALD, M. L. The varieties of *Lyonia ligustrina*. Rhodora **43**: 624–629. 1941. [In "Another century of additions to the flora of Virginia."]
- GREENE, E. L. A name explained. Torreya **4**: 173, 174. 1904. [Derivation of *Xolisma* Raf.]
- KUCERA, C. L. The genus *Lyonia* in Missouri. Rhodora **55**: 155. 1953. [*L. mariana*.]
- LOVELL, J. H., and H. B. LOVELL. Pollination of the Ericaceae: *Chamaedaphne* and *Xolisma*. Rhodora **37**: 157–161. 1935. [*L. ligustrina*.]
- REHDER, A. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. Jour. Arnold Arb. **5**: 49–59. 1924. [49–55, takes up and defines *Xolisma* Raf., sects., new combinations.] (See also *ibid.* **20**: 425, 426. 1939, for correct name for *L. lucida*.)
- SARGENT, C. S. *Andromeda*. Silva N. Am. **5**: 129–132. pl. 234. 1893. [*L. ferruginea*.]
- SIMS, J. *Andromeda mariana* (α.) *ovalis*. Bot. Mag. **37**: pl. 1579. 1813.
- SLEUMER, H. Neue *Xolisma*-arten von Hispaniola. Repert. Sp. Nov. **36**: 270–273. 1934. [Seven new spp.]
- SMALL, J. K. *Desmothamnus lucidus*. Addisonia **11**: 51, 52. pl. 378. 1927.
- YASUE, M., and Y. KATO. Studies on the constituents of *Lyonia ovalifolia* Sieb. et Zucc. var. *elliptica* Hand.-Mazz. (In Japanese; English summary.) Jour. Pharm. Soc. Japan **79**: 403–405. 1959.*

11. *Pieris* D. Don, Edinburgh New Philos. Jour. **17**: 159. 1834.

Evergreen shrubs [small trees] rarely vines, with alternate [rarely opposite], short-petioled, coriaceous, broad, entire, crenulate, or toothed leaves; winter buds ovoid, with several narrow outer scales. Flowers white, in terminal panicles or axillary racemes produced the preceding summer, or racemes from axillary buds of the preceding growing season; pedicels each in the axil of a bract and with 2 alternate to opposite brac-

part from the stamens of *Pieris bracteata* W. W. Sm. which were used as an example of both awned and appendaged anthers by Matthews & Knox and by Anthony. The plant has been found by Airy-Shaw to be not a *Pieris* but a form of *Vaccinium Forrestii* Diels (or a closely related species) with foliaceous bracts (Bot. Mag. **160**: pl. 9490. 1937).

teoles from above the base to beneath the calyx. Calyx deeply 5-lobed, the firm, thick-edged, ovate lobes valvate in bud, persistent in fruit. Corolla ovoid-urceolate to ovoid, with 5 short lobes. Stamens 10, included; filaments more or less vertically S-shaped and flattened; anthers with a pair of stout, deflexed spurs (without disintegration tissue) on the back just above junction with filament, otherwise unappendaged but with white disintegration tissue on the abaxial side of each of the often divergent anther-halves, each anther-half opening by a large oval to V-shaped pore; pollen tetrads without viscin strands. Stigma flat; style straight, as long as the corolla; ovary superior, 5-lobed, 5-locular, each locule with a short-stalked, pendent placenta on the axis near the top of the locule, the outer, lateral and lower surfaces with pendulous ovules; disc 10-lobed, with nectariferous lobes extending upward between the filaments. Capsule subglobose, loculicidally 5-valved, the sutures not thickened; seeds scobiform, nearly all pendulous, with a loose, cellular coat. (Including *Ampelothamnus* Small, *Arcterica* Coville.) TYPE SPECIES: *P. formosa* (Wall.) D. Don. (Name poetic, for *Pieris*, a Muse.)

A small genus of about eight species, five in eastern Asia, one in western Cuba, and two in the southeastern United States. *Pieris floribunda* (Pursh) Benth. (*Andromeda floribunda* Pursh) is a handsome shrub (to about 1.5 m.) of moist to dry, more or less open, rocky woods and mountain slopes from Virginia and eastern West Virginia to northern Georgia, eastern Tennessee, and Alabama. The inflorescences terminate the growth of the season in June or July; the small white flowers expand the following April or May. Although without any very close relatives, *P. floribunda* appears to be related to *P. japonica* (Thunb.) G. Don ($2n = 24$), *P. formosa* (Wall.) D. Don ($2n = 24$), *P. taiwanensis* Hayata, and *P. Swinhoei* Hemsl., all of Asia. *Pieris floribunda* and *P. japonica* are two of the best of the ornamental Ericaceae for the eastern United States.

Pieris phillyreifolia (Hook.) DC. (*Ampelothamnus phillyreifolia* (Hook.) Small), is a curious plant of cypress ponds, sphagnum bogs, or wet pine-lands from southernmost Georgia to central Florida, western Florida, and southern Alabama, in which the inflorescences are axillary and apparently produced just prior to flowering (January to March). The plant, which may be a shrub to about 1 m. tall, may climb to 10 m. as a vine by growing beneath the outer bark of *Taxodium ascendens* Brongn. and sending out leafy stems at intervals. No rootlets or other organs of support are formed, and the species seems to climb only this *Taxodium*, in which the outer bark is composed of long, parallel, easily separable fibers. Although segregated as *Ampelothamnus* Small, largely on the basis of the axillary racemes and the strongly S-shaped flattish filaments, this species belongs in *Pieris*. The details of floral anatomy and the characteristic anthers are precisely those of *Pieris*, the flattening and curving of the filaments are only a matter of degree, and *P. cubensis* (Griseb.) Small, of Pinar del Río, an undoubted member of the genus, seems also to have

exclusively axillary racemes. The production of a number of deciduous scale-leaves on the lower part of the new growth, although seldom seen in *P. floribunda*, is well developed in *P. phillyreifolia* and is a characteristic pattern in *P. japonica* and its close allies.

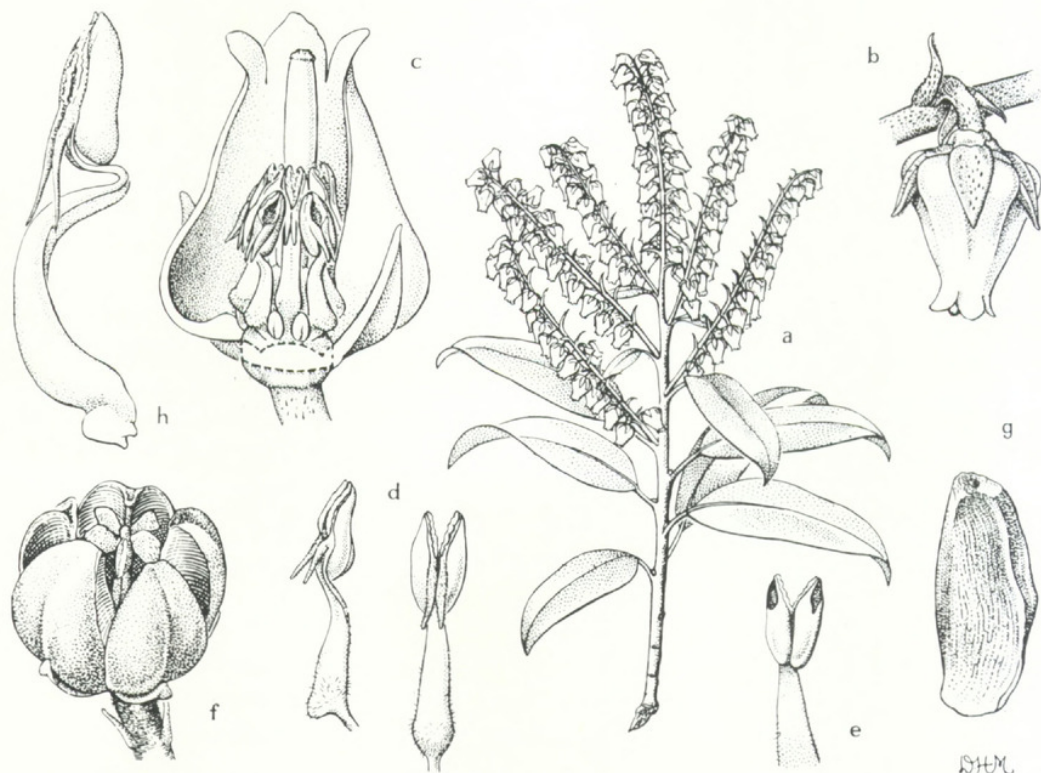


FIG. 6. *Pieris*. a-g, *P. floribunda*: a, flowering branchlet, $\times \frac{1}{2}$; b, flower, $\times 3$; c, flower with half of corolla and calyx removed — note nectariferous lobes of disc between stamens, $\times 6$; d, outer views of stamens from outer (left) and inner staminal whorls — note disintegration tissue along each anther-half above spurs, $\times 10$; e, inner view of stamen from inner staminal whorl to show pores, edge of disintegration tissue on each anther-half, $\times 10$; f, capsule, $\times 4$; g, seed, $\times 10$. h, *P. phillyreifolia*: stamen from outer staminal whorl, $\times 10$.

The limits of *Pieris* have been a source of great confusion (see *Lyonia*), but the genus seems to be a natural unit consisting of evergreen species with persistent, coriaceous, serrulate, undulate, or bristle-margined leaves; winter buds with several narrow outer scales; racemose inflorescences either aggregated into terminal panicles or from the upper leaf axils; pedicels with bracteoles above the base; valvate sepals with fiber strands; anthers with stout deflexed spurs lacking disintegration tissue but with disintegration tissue in the connective above; and capsules without thickened or otherwise differentiated margins. The appendaged anthers are very distinctive and are in no way to be confused with those of *Lyonia*.

REFERENCES:

Under family references see also COX (Ericales II), MATTHEWS & KNOX, PALSER (1951, 1952), and PELTRISOT.

- AIRY-SHAW, H. K. *Pieris formosa* var. *Forrestii*. Bot. Mag. 157: pl. 9371. 1934. [Includes comments on the generic limits of *Pieris*.]
- BRIDEL, M., and A. KRAMER. L'asebotoside et son identité avec le phlorizoside. Bull. Soc. Chim. Biol. 15: 531-551. 1933.* [*P. japonica*.]
- EDWARDS, S. *Andromeda floribunda*. Bot. Reg. 10: pl. 807. 1824.
- HARPER, R. M. A unique climbing plant. Torreya 3: 21, 22. 1903. [*P. phillyreifolia*.]
- HOOKE, W. J. *Andromeda phyllyreifolia*. Hooker Ic. 2: pl. 122. 1837.
- MURAKAMI, S., and M. FUKUDA. Studies on the constituents of *Pieris japonica* D. Don. III. Inconsistency of the occurrence of asebotin. (In Japanese; English summary.) Jour. Pharm. Soc. Japan 75: 603, 604. 1955.*
- SIMS, J. *Andromeda floribunda*. Bot. Mag. 37: pl. 1566. 1813.
- SKAN, S. A. *Pieris formosa*. Bot. Mag. 135: pl. 8283. 1909.
- SMALL, J. K. *Pieris floribunda*. Addisonia 5: 5, 6. pl. 163. 1920.
- STAPF, O. *Pieris taiwanensis*. Bot. Mag. 149: pl. 9016. 1923. [Includes comments on confusion among *Pieris*, *Andromeda*, *Lyonia*, *Cassandra*, etc.]
- TAMURA, K. Studies on the structure of asebotin, a component of *Andromeda japonica* Thunb. Bull. Chem. Soc. Japan 11: 781-785. 1936.*
- WILKIE, D. The genus *Pieris*. Arb. Bull. 11(2): 6, 7, 38. 1948.* [Horticulture.]

12. *Cassandra* D. Don, Edinburgh New Philos. Jour. 17: 158. 1834.

Low, evergreen shrubs of sphagnum bogs, peaty swales, and pond margins. Leaves alternate, elliptic to lanceolate, short-petioled, entire or crenulate, more or less appressed to the stem; buds small, with several outer scales; vegetative parts, pedicels, and calyx (especially underside of leaves) scurfy with peltate scales. Flowers small, white, nodding, short-pedicel, solitary in the axils of the small upper leaves, forming almost horizontal, apparently 1-sided, 10-30-flowered, leafy racemes. Calyx small, 5-lobed, subtended by 2 persistent bractlets, aestivation quincuncial. Corolla oblong-urceolate, with 5 short lobes. Stamens 10, included; filaments flat, tapering upward; anthers terminating in 2 elongated tubes opening by a terminal pore, each sometimes prolonged beyond the pore as a minute triangular awn, otherwise unappendaged, lacking white disintegration tissue; pollen tetrads without viscin strands. Stigma slightly expanded; style straight, exserted from the corolla; ovary superior, 5-lobed, 5-locular, the placentae columnar, undivided, 1 in each locule from the center of the axis, the end flattened against the ovary wall, bearing about 15 campylotropous ovules around the edge; disc dark green, 10-lobed, nectariferous. Capsule depressed-globose, with slightly thickened sutures, loculicidally 5-valved, but the wall splitting into 2 layers, the inner 10-valved; seeds about 10 in each locule, small, somewhat compressed laterally, brown, shining, wingless. (Not *Cassandra* Spach, 1840, = *Leucothoe*; *Chamaedaphne* Moench, Meth. Pl. 457. 1794; not *Chamaedaphne* Mitchell, Diss. Brevis Principiis Bot. Zool. 1769 [= *Mitchella* L.].⁸) TYPE AND SOLE

⁸ *Chamaedaphne* Moench (1794) is clearly a later homonym of *Chamaedaphne* Mitchell, first published in 1748 and taken by Linnaeus as the basis for *Mitchella* L. (1753) but republished validly in 1769. The earliest legitimate name appears to be

SPECIES: *Andromeda calyculata* L. = *Cassandra calyculata* (L.) D. Don. (A poetic name, for Cassandra, a daughter of Priam, King of Troy, and Hecuba.)

Cassandra calyculata (*Chamaedaphne calyculata* (L.) Moench) is of almost circumpolar distribution, ranging from Scandinavia, the Baltic States and northern Poland to northern Russia and northern Asia, Kamchatka, Manchuria, and northern Japan; and from Alaska to Labrador and Newfoundland, southward to British Columbia, Alberta, Minnesota, the northern parts of Illinois, Indiana, and Ohio, New York, Pennsylvania, and New Jersey, and southward in more or less isolated localities, mostly on the Coastal Plain, in Delaware, Maryland, North Carolina (there also inland in Henderson County), and South Carolina. Three geographical varieties have been distinguished: var. *calyculata* in Eurasia; var. *angustifolia* (Ait.) Rehd., the too similar widespread American form; and var. *latifolia* (Ait.) Fern., a dwarfish broad-leaved form of Labrador, Newfoundland, and Nova Scotia, westward in the north to Mackenzie.

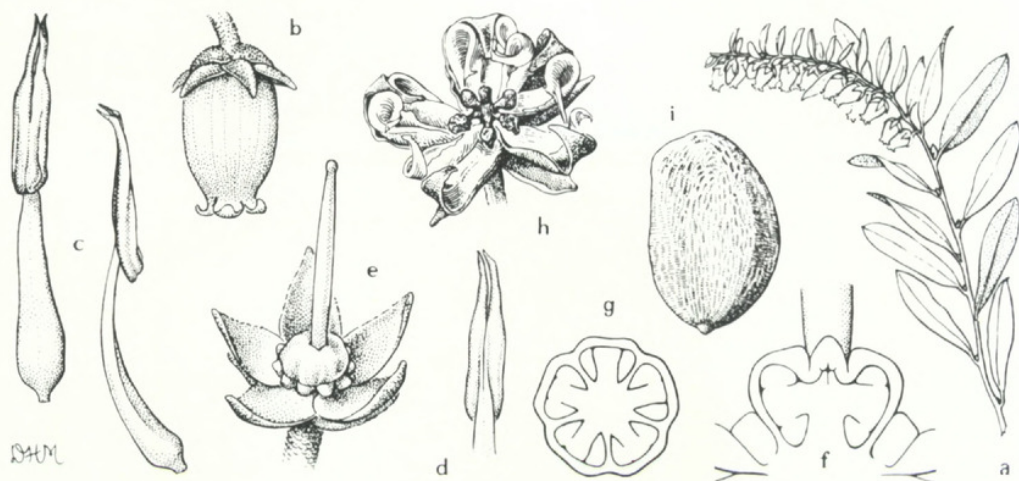


FIG. 7. *Cassandra*. a-i, *C. calyculata*: a, flowering twig, $\times \frac{1}{2}$; b, flower, $\times 3$; c, inner and lateral views of stamens, $\times 10$; d, outer view of anther, $\times 10$; e, calyx and gynoecium with disc, $\times 6$; f, ovary, disc, petals in diagrammatic vertical section — note columnar placentae, peripheral ovules, $\times 15$; g, ovary, diagrammatic cross section, $\times 15$; h, opened capsule — note five outer, ten inner valves, $\times 5$; i, seed, raphe to left, $\times 20$.

A low (exceptionally to 1.5 m.) and much-branched evergreen shrub with coriaceous, scurfy leaves, *Cassandra* is one of the most abundant and characteristic plants of bogs in the glaciated portions of eastern North

Cassandra D. Don (1834) by which this plant was known to botanists of the nineteenth century. Although conservation may be advocated by some, such a course seems hardly justifiable for this single species, the list of *nomina generica conservanda* being already too cluttered with favorite "names my professor taught me," rather than consisting only of those of real consequence. It is not inappropriate, moreover, that *Cassandra* should be returned to the company of *Andromeda*, *Cassiope*, *Leucothoë*, *Phyllodoce*, *Pieris*, and *Zenobia*. See, however, M. L. Fernald's comments on the intrusion of *Harrimanella* upon this classic bevy (pages 28, 29, in "Some Historical Aspects of Plant Taxonomy," *Rhodora* 44: 21-43. 1942).

America. It shows a wide tolerance, being an early invader of bogs, but often persisting long after the establishment of tree species. In some bog areas the plant is completely dominant, forming a closed association with *Sphagnum* and several other mosses. South of the glacial boundary, with the exception of southern New Jersey, the colonies appear to be rare and scattered.

The horizontal inflorescences terminate the growth of the year, and flower buds develop in late summer; the plants flower from March in the South to early July in Labrador; a partial second flowering sometimes occurs in the fall. The reduced leaves of the inflorescence are deciduous after maturity of the fruit (that portion of the shoot then dying) but the larger leaves below persist another year. Growth of the shoot is continued after flowering by one or more axillary buds below the inflorescence. The small, brown seeds have a large raphe of spongy tissue and appear to be capable of floating. The roots have been reported to lack mycorrhizae under bog conditions but to show such an association under drier conditions in cultivation. The leaves are poisonous, containing andromedotoxin.

Cassandra is a well-marked and apparently isolated genus distinctive in the bracteoles beneath the calyx, the stamens, the inflorescence, peltate scales, fruit, and seeds. The closest relationship seems to be with *Andromeda*, *Pieris*, and *Lyonia*.

REFERENCES:

- Under family references see also BELL & BURCHILL, COX (Ericales II), GREVILLIUS & KIRCHNER (pp. 57-62), PALSER (1951, 1952), PELTRISOT and STANLEY.
- FERNALD, M. L. *Chamaedaphne calyculata* (L.) Moench, var. *latifolia* (Ait.), comb. nov. *Rhodora* 47: 390, 391. 1945.
- GATES, F. C. The relation of snow cover to winter killing in *Chamaedaphne calyculata*. *Torreyia* 12: 257-262. 1912.
- . Winter as a factor in the xerophily of certain evergreen ericads. *Bot. Gaz.* 57: 445-487. 1914. [Includes many data on *Cassandra*.]
- . The bogs of northern lower Michigan. *Ecol. Monogr.* 12: 213-254. 1942. [The *Chamaedaphne* association, 238-240.]
- LEMS, K. Ecological study of the peat bogs of eastern North America. III. Notes on the behavior of *Chamaedaphne calyculata*. *Canad. Jour. Bot.* 34: 197-207. 1956.
- LOVELL, J. H., and H. B. LOVELL. Pollination of the Ericaceae: *Chamaedaphne* and *Xolisma*. *Rhodora* 37: 157-161. 1935. [*Cassandra* and *Lyonia ligustrina*.]
- SEGADAS-VIANNA, F. Ecological study of the peat bogs of eastern North America. II. The *Chamaedaphne calyculata* community in Quebec and Ontario. *Canad. Jour. Bot.* 33: 647-684. 1955.
- SIMS, J. *Andromeda calyculata* var. *ventricosa*. *Bot. Mag.* 32: pl. 1286. 1810.

13. *Oxydendrum* A. P. de Candolle, Prodr. 7: 601. 1839.

A deciduous tree to 25 m., with a tall, straight trunk to 25-50 cm. in diameter, the bark deeply fissured. Winter buds small, axillary. Leaves membranaceous, oblong-lanceolate, petiolate, serrulate, pale beneath (remi-

niscent of *Prunus Persica*). Flowers bisexual, 6–8 mm. long, in drooping panicles (terminating the growth of the year) of 6 or more slender, declined racemes, these 1-sided (by the bending of the pedicels); each flower in the axil of a minute, deciduous bract, each pedicel with 2 minute, alternate, persistent bractlets. Calyx deeply divided into 5 separated lobes, valvate in bud. Corolla white, cylindric-ovoid to ovoid, puberulous, with 5 short, spreading or recurved lobes imbricate in bud. Stamens 10, hypogynous, free from the corolla; filaments broad, stout, swollen at the base; anthers appressed to the style, fixed near the base, linear-oblong, opening from the apex to above the middle by slitlike pores, the connective near anther apex with a region of white disintegration tissue; pollen tetrads without viscin strands. Stigma simple, unexpanded; style columnar, straight, slightly exerted; ovary superior, 5-locular, extending upward around the base of the style; ovules numerous on outer, lateral and upper surfaces of the conspicuous placentae, all near bottom of locule and extending upward. Pedicels recurving in fruit, the ovoid-pyramidal capsule erect, ca. 5 mm. long, crowned by the persistent style, loculicidally 5-valved; seeds numerous, elongate, ascending, the seed-coat pointed at the ends; embryo minute. TYPE AND SOLE SPECIES: *O. arboreum* (L.) DC. (*Andromeda arborea* L.). (Name from Greek, *oxys*, sour, and *den-*

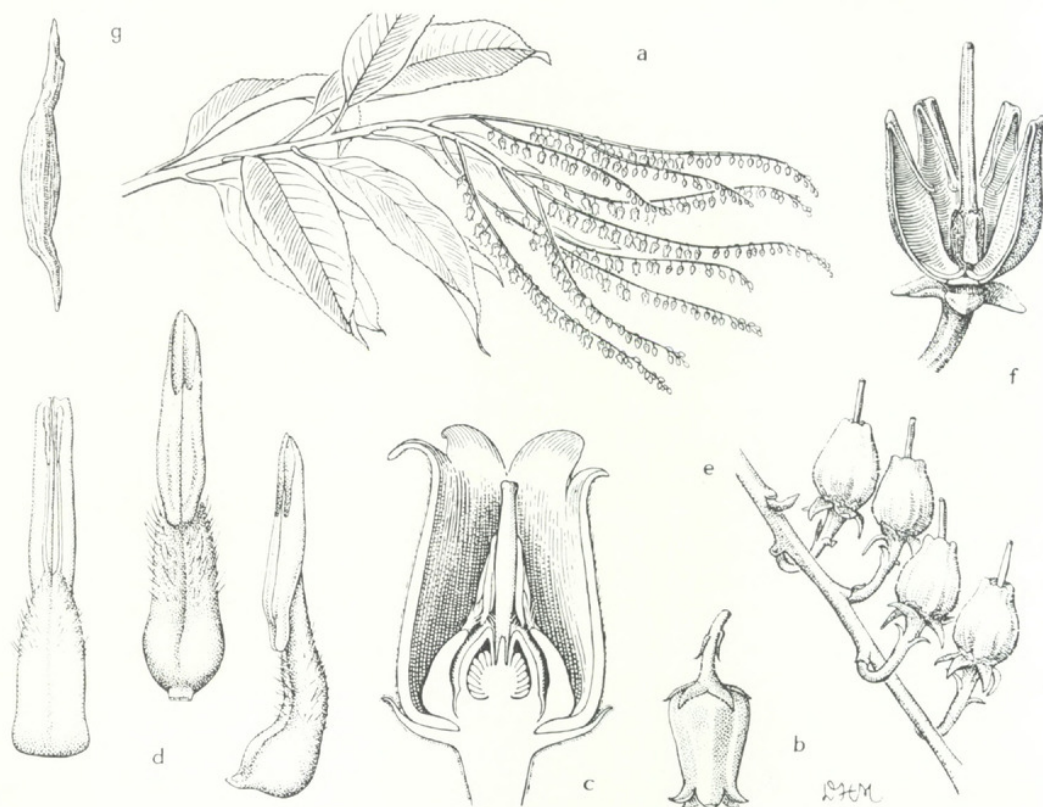


FIG. 8. *Oxydendrum*. a–g. *O. arboreum*: a, flowering branch, $\times \frac{1}{4}$; b, flower, $\times 2$; c, flower, in section, $\times 6$; d, outer, inner, and lateral views of stamens — note area of disintegration tissue on upper part of outer surface of each anther-half. $\times 12$; e, portion of raceme with immature fruits, $\times 2$; f, opened capsule, one valve removed — note deeply immersed style, $\times 4$; g, seed, $\times 10$.

dron, tree, referring to the acid taste of the leaves.) — SOURWOOD, TITI, SORREL-TREE.

Oxydendrum arboreum is of wide distribution in the eastern United States in acid, well-drained soils in dry woods, on bluffs and ridges, in hammocks and creek bottoms, from southern Pennsylvania to northern and western Florida and to southern Ohio, southern Indiana and Illinois, and Mississippi and southeastern Louisiana. One of the largest of the Ericaceae, it is a handsome, slow-growing tree of great ornamental value both for its panicles of small, white flowers in June or July and for the showy red autumn coloration. It reaches its greatest size on the western slopes of the Smoky Mountains of eastern Tennessee. The plant is easily raised from seeds and transplants easily. It is hardy northward at least to eastern Massachusetts.

The species is an isolated one among the Ericaceae, apparently with no close relatives. Largely on the basis of the rather advanced evolutionary level of the wood anatomy in comparison with other members of the Andromedeae, Cox concluded that *Oxydendrum* is "the survivor of a comparatively long evolutionary sequence paralleling that of the other tribes," and placed it in a separate tribe, Oxydendreae. It is anatomically notable for the tapered receptacle with traces to all floral organs completely distinct.

REFERENCES:

- See also under family references COX (Ericales II), PALSER (1951, 1952), and PELTRISOT.
- BALDWIN, J. T. Cytogeography of *Oxydendrum arboreum*. Bull. Torrey Bot. Club 69: 134-136. 1942. [Includes distribution map; 31 collections showed $2n = 24$.]
- CLOVIS, J. F. A note about *Oxydendrum*. Castanea 24: 51-53. 1959. [Calls attention to pendent flowers vs. erect fruit.]
- ESSON, J. G. The sourwood — a neglected tree. Jour. N. Y. Bot. Gard. 51: 12-15. 1950. [Horticultural merits.]
- LEWIS, C. E. Tips for better landscapes; the sorrel tree. Am. Nurseryman 105(4): 14, 15. 1957.*
- NASH, G. V. *Oxydendrum arboreum*. Addisonia 4: 37, 38. pl. 139. 1919.
- SARGENT, C. S. *Oxydendrum*. Silva N. Am. 5: 133-136. pl. 235. 1893.
- SIMS, J. *Andromeda arborea*. Bot. Mag. 13: pl. 905. 1806.

14. *Epigaea* Linnaeus, Sp. Pl. 1: 395. 1753; Gen. Pl. ed. 5. 186. 1754.

Prostrate evergreen shrubs with creeping stems. Leaves alternate, oval to elliptic, petiolate, coriaceous. Plants functionally dioecious (at least in *E. repens*), the flowers in short terminal and axillary bracteate spikes, the pedicels with 2 bractlets at the base. Flowers either carpellate (with rudimentary stamens, usually only filaments) or apparently bisexual, but with unexpanded stigmas and functionally staminate. Sepals 5, imbricate, conspicuous, green. Corolla salverform, with 5 spreading [or recurved] lobes, in staminate flowers about 1/3 larger than in carpellate. Stamens

of staminate flowers 10; filaments adnate to the base of corolla tube, half as long to as long as corolla tube; anthers elongate, the halves joined almost to the tip, lacking white disintegration tissue, opening by longitudinal slits (those of carpellate flowers, when present, not opening); pollen tetrads with viscin strands. Stigma 5-lobed, radiate and glandular in carpellate flowers, the lobes erect and dry in staminate flowers; styles half as long to as long as corolla tube; ovary superior, 5-locular, glandular-hairy; placentae 2 in each locule, axile below but parietal above (cf. *Pyroleae*, *Monotropeae*) with numerous anatropous ovules. Capsule depressed-globose, fleshy, glandular, hirsute, loculicidal, the valves thin; seeds numerous, minute, hard, brown, shining, on white, succulent placentae filling the locules. TYPE SPECIES: *E. repens* L. (Name from Greek, *epi*, on, and *gaca*, earth, in allusion to the creeping habit.) — TRAILING ARBUTUS.

Two species, *Epigaea repens*, of wide distribution in eastern North America (Labrador to northern Florida, Alabama, Tennessee, Indiana, Michigan, Minnesota, and Saskatchewan), and *E. asiatica* Maxim., of Japan to Formosa. Although closely related, *E. asiatica* differs from *E. repens* in the more acute, coriaceous leaves, the longer pedicels (to 1.5 cm. vs. 5 mm.), the greater number to flowers per inflorescence, the broader corolla tube and shorter lobes, and other details. *Epigaea* appears to be most closely related to the monotypic *Orphanidesia* Boiss., of the mountains inland from the southeast corner of the Black Sea, a similar low evergreen with 1–3 flowered racemes and a larger, cup-shaped corolla, but with anthers opening as in *Epigaea*. Within the Andromedeae both genera seem to be isolated, although, on the basis of wood structure, Cox placed *Epigaea*, *Agauria*, *Cassiope*, and *Enkianthus* together as *Cassiopeae* Cox.

Epigaea repens is noteworthy for its functional dioecism, the plants bearing either carpellate flowers with only rudimentary stamens (usually only the filaments developed) or seemingly bisexual but functionally staminate flowers with well-developed stamens and apparently functional embryo sacs, but stigmas which are not receptive to pollen. Although filament and style length vary, pollen grains are of a single size, and experimental evidence is all against any form of heterostyly. *Epigaea asiatica* does not appear to have been studied in this respect, but two artificial hybrids with *E. repens* (one a backcross to *E. repens*), both were of the pistillate type.

The roots do not develop root hairs, and a mycorrhizal association is obligate; as a result, the species transplants with difficulty. Although the plant seems to tolerate a fairly wide range of moisture and soil acidity (pH 7.6–4.5), constant moisture, good drainage, some shade, and acid soil apparently are required for optimum growth. The plant was formerly gathered in large quantities for the fragrant pink to white flowers produced in earliest spring, and has been very nearly exterminated in some areas. The fruit requires 40–55 days to mature, and the seeds presumably are dispersed by ants, which have been observed attacking the fleshy placentas.

REFERENCES:

- Under family references see also BELL & BURCHILL, BERGMAN, COX (Ericales II), IKUSE and PALSER (1951, 1952).
- ANDREWS, M. F. Die Anatomie von *Epigaea repens* L. Beih. Bot. Centr. 19(1): 314-320. pls. 6-8. 1906.
- . The embryo-sac and pollen of *Epigaea repens*. *Ibid.* 44(1): 264-266. 1927.
- ARLAND, F. L. Growing the trailing arbutus. Jour. N. Y. Bot. Gard. 46: 102-109. 1945. [*E. repens*.]
- BARROWS, F. L. Propagation of *Epigaea repens* L. I. Cuttings and seeds. Contr. Boyce Thompson Inst. 8: 81-97. 1936. II. The endophytic fungus. *Ibid.* 11: 431-440. 1941.
- . How to propagate trailing arbutus. Pl. Gard. II. 3: 49-53. 1947.
- BASTIN, E. S. Structure of *Epigaea repens*. Am. Jour. Pharm. 67: 213-236. 1895.*
- COUNCILMAN, W. T. The root system of *Epigaea repens* and its relation to the fungi of the humus. Proc. Natl. Acad. Sci. 9: 279-285. 1923.
- COVILLE, F. V. The use of acid soil for raising seedlings of the mayflower, *Epigaea repens*. Science 33: 711, 712. 1911.
- . The cultivation of the mayflower. Natl. Geogr. Mag. 27: 518, 519. 1915.*
- EDWARDS, S. *Epigaea repens*. Bot. Reg. 3: pl. 201. 1817.
- GRAY, A. Heteromorphism in *Epigaea*. Am. Jour. Sci. III. 12: 74-76. 1876. (Reprinted, Am. Nat. 10: 490-492. 1876.)
- HALSTED, B. D. Notes upon *Epigaea repens*. Bull. Torrey Bot. Club 18: 249, 250. 1891. [Comments on supposed heterostyly.]
- HOLM, T. Medicinal plants of North America. 73. *Epigaea repens* L. Merck Rep. 22: 144-146. 1913.*
- LANGDON, F. E. A study of *Epigaea repens*. Asa Gray Bull. 2: 1-3. 1894. [Observations on dioecism.]
- MULLIGAN, B. O. *Epigaea hybrids*. Jour. Roy. Hort. Soc. 64: 507-510. figs. 114-116. 1939. [*E.* \times *intertexta* Mulligan = *E. asiatica* \times *repens*.]
- STAPP, O. *Epigaea asiatica*. Bot. Mag. 154: pl. 9222. 1930.
- STEVENS, N. E. Dioecism in the trailing arbutus, with notes on the morphology of the seed. Bull. Torrey Bot. Club 38: 531-543. 1912. [Plants functionally dioecious; no evidence of heterostyly; embryo-sac development normal.]
- STOKER, F. *Ophanidesia gaultherioides*. Jour. Roy. Hort. Soc. 65: 210, 211. figs. 55, 56. 1940. [Description from living plants in cultivation.]
- WARD, L. F. Sexual differentiation in *Epigaea repens*. Am. Nat. 14: 198-200. 1880.
- WEED, C. M. The guests of the mayflower. Pop. Sci. Monthly 45: 17-23. 1894.*
- WILSON, K. E. Double flowers of the *Epigaea repens*. Bot. Gaz. 15: 19, 20. 1890.
- WILSON, W. P. Observations on *Epigaea repens*, L. Contr. Bot. Lab. Univ. Penn. 1: 56-63. pl. 8. 1893. [Dioecism; about 1000 plants studied; includes illustration of various types of flowers.]

Tribe PYROLEAE D. Don

15. *Chimaphila* Pursh, Fl. Am. Sept. 1: 279, 300. 1814.

Low, suffrutescent to nearly herbaceous plants with long, scaly, creeping subterranean rhizomes and short, evergreen aerial shoots with alternate to subopposite or almost whorled, coriaceous, often shining, serrate, short-petioled leaves. Rhizomes with distant scale-leaves, each with an axillary bud and an associated root; roots reported to form adventitious buds. Inflorescence a stalked, terminal 1–8-flowered corymb, each flower in the axil of a deciduous [or persistent] bract, the pedicels lacking bracteoles. Flowers 5-merous, regular, fragrant, nodding. Sepals 5, united at the base, persistent. Petals 5, distinct, white to pink, concave, orbicular, forming a saucer-shaped corolla. Stamens 10; filaments enlarged and hairy at or below the middle; anthers extrorse in bud but at anthesis inverted by the inflexion of the apex of the filament, opening by a pore at the apparent apex (the base) of each of the divergent anther-halves (cf. *Arbutus*, *Arctostaphylos*); pollen in tetrads, 3-colpate. Stigma peltate, 5-lobed; style very short, top-shaped, immersed in the summit of the ovary; ovary superior, depressed-globose, 5-locular below, the placentae axile, but 1-locular above, the placentae becoming parietal (cf. *Epigaea*); ovules numerous, anatropous; disc circular, nectariferous, at the base of the ovary. Capsule depressed-globose, erect, 5-lobed, loculicidally 5-valved, the valves smooth on the edges; seeds small, numerous, with a thin cellular coat, an endosperm of a few large cells and a minute, undifferentiated embryo. LECTOTYPE SPECIES: *C. maculata* (L.) Pursh; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 672. 1913. (Name taken from the common name "wintergreen," from Greek, *cheima*, winter, and *philos*, friend.) — WINTERGREEN.

A well-marked boreal genus of about four or five species, including *Chimaphila umbellata* (L.) Bart., of circumboreal distribution with disjunct stations southward in Mexico and Guatemala and a close relative, *C. dominicensis* Blake, in Hispaniola; *C. japonica* Miq., in eastern Asia; *C. Menziesii* (R. Br.) Spreng. ($2n = 26$), from British Columbia to California, Sonora, and Jalisco; and *C. maculata* in eastern North America and Central America.

A number of geographical variants have been recognized in the widespread *C. umbellata*. The plant of eastern North America is var. *cisatlantica* Blake, which occurs from eastern Quebec to western Ontario, southward to Virginia, North Carolina, and Georgia, Ohio, Michigan, northeastern Illinois, and Minnesota; var. *umbellata* ($2n = 26$) is of Eurasian distribution. *Chimaphila maculata* ranges widely in dry woods, from southern New Hampshire westward to Michigan and northeastern Illinois, southward to Georgia, Alabama, and Tennessee, and, as a more robust form (apparently with larger flowers and fruits), from the mountains of Chihuahua and Sonora southward to Guatemala, Honduras, and Costa Rica.

The genus shares many features with *Pyrola*, from which it is readily distinguished by the corymbose inflorescence, enlarged staminal filaments, presence of a disc, and fruit with non-cobwebby valve margins.

REFERENCES:

- BLAKE, S. F. A new *Chimaphila* from San Domingo. Jour. Bot. 52: 169. 1914.
[*C. dominicensis*, closely related to *C. umbellata*.]
———. The varieties of *Chimaphila umbellata*. Rhodora 19: 237–244. 1917.
CAMP, W. H. Studies in the Ericales. IV. Notes on *Chimaphila*, *Gaultheria* and *Pernettya* in Mexico and adjacent regions. Bull. Torrey Bot. Club 66: 7–28. 1939.
COPELAND, H. F. Observations on the structure and classification of the Pyroleae. Madroño 9: 65–102. 1947.
HENDERSON, M. W. A comparative study of the structure and saprophytism of the Pyrolaceae and Monotropaceae with reference to their derivation from the Ericaceae. Contr. Bot. Lab. Univ. Penn. 5: 42–109. 1920.
HOLM, T. Medicinal plants of North America. 28. *Chimaphila umbellata* L. Merck Rep. 18: 143–145. 1909.*
———. The flower of *Chimaphila*. Rhodora 29: 1–6. 1927.
LEMMON, R. S. Propagation of the native species of *Chimaphila*. Jour. N. Y. Bot. Gard. 39: 129, 130. 1938. [Propagation by seeds and runners unsuccessful; success with cuttings with a stub taken just before young leaves reached full size; a summer and winter required before rooting began.]
MEEHAN, T. *Chimaphila umbellata*. Meehans Monthly 7: pl. 9. 1897. *Chimaphila umbellata*. Ibid. 9: 1, 2. pl. 1. 1899.
MOUILLEFARINE, E. Le *Chimaphila maculata* Pursh aux environs de Paris. Bull. Soc. Bot. Fr. 49: 281–284. 1903.
SCHWARTING, A. E., and L. D. HUNER. A histological study of *Chimaphila umbellata*. Jour. Am. Pharm. Soc. Sci. Ed. 32: 182–187. 1943.*
SIMS, J. *Pyrola umbellata*. Bot. Mag. 20: pl. 778. 1804. *Pyrola maculata*. Ibid. 23: pl. 897. 1806.

16. **Pyrola** Linnaeus, Sp. Pl. 1: 396. 1753; Gen. Pl. ed. 5. 188. 1754.

Low, smooth, evergreen perennial herbs, with slender, creeping subterranean rhizomes (as in *Chimaphila*) and erect shoots bearing a cluster of petioled, coriaceous, persistent basal leaves and/or a raceme of [2] 6–20 ascending, spreading or nodding flowers on an upright, more or less scaly-bracted scape; flowers in the axils of bracts, lacking bractlets on the pedicels. Flowers 5-merous, nodding, irregular [or regular]. Calyx 5-parted, persistent. Petals 5, concave, distinct, deciduous, [greenish-]white [to pink], imbricate in aestivation. Stamens 10; filaments glabrous, not enlarged, usually bent, the anthers then clustered on the upper side of the flower; anthers extrorse in the bud but in flower inverted by the inflexion of the apex of the filament, opening by a pore at the apparent apex (base) of each of the anther-halves, constricted [or not] below the pores, sometimes mucronate at the apparent base; pollen in tetrads, 3-colpate. Stigma of 5 narrow, erect lobes extending from the top of the style which forms a rim beneath the lobes; style [short to] long, [straight to] declined with the apex curved upward; ovary 5-locular below and the placentae axile,

but 1-locular above, the placentae becoming parietal; ovules numerous, anatropous; disc lacking. Capsule 5-lobed, loculicidally 5-valved, the valves cobwebby on the edges; seeds minute, as in *Chimaphila*. (Excluding *Ramischia* Opiz.) LECTOTYPE SPECIES: *P. rotundifolia* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 668. 1913. (Name Latin, diminutive of *Pyrus*, pear, from the somewhat similar leaves.)

A circumboreal genus, sometimes overestimated at 40 species, distributed southward along the higher mountains to Central America (Guatemala) and southeastern Asia (Sumatra). About six species occur in northeastern North America. The circumboreal *Pyrola rotundifolia* L. ($2n = 46$) reaches our area as var. *americana* (Sweet) Fern., distributed from Quebec to Ontario, southward to North Carolina, Tennessee, Kentucky, northern Indiana, Michigan, Wisconsin, and Minnesota. A report of *P. elliptica* Nutt. from Tennessee is unconfirmed, the species apparently not being known with certainty south of West Virginia.

The few chromosome numbers thus far determined support the separation of *Ramischia* Opiz (*Pyrola secunda* L., $2n = 38$) and of *Moneses* S. F. Gray (*M. uniflora* (L.) A. Gray, $2n = 26$), but not that of *Erxlebenia* Opiz (*P. minor* L., $2n = 46$), from *Pyrola* in which the diploid numbers are 46 or 92.

Both *Pyrola* and *Chimaphila* show tendencies toward vegetative reduction which culminate in the herbaceous *Moneses uniflora*, in which the rhizome has been eliminated, the aerial shoots arising from adventitious buds on the roots. The four genera of the tribe form a natural group which seems to have its closest affinities with Andromedaeae and Arbuteae, although there can hardly be a direct relationship. Aside from the tendency toward reduction of the plant body and of the size and complexity of the seed and embryo, the group has no combination of features which distinguishes it from the Ericaceae proper.

REFERENCES:

- See also under family references COPELAND (1933, 1947), PELTRISOT, WARMING.
ANDRES, H. Piroleen-Studien. Beiträge zur Kenntnis der Morphologie, Phyto-geographie und allgemeinen Systematik der Pirolaceae. Verh. Bot. Ver. Brandenburg 56: 1-76. 1914.
———. Studien zur speziellen Systematik der Pirolaceae. IV. Revision der Gattung *Ramischia* Opiz. Repert. Sp. Nov. 19: 209-224. 1923.
CAMP, W. H. Aphyllous forms in *Pyrola*. Bull. Torrey Bot. Club 67: 453-465. 1940.
FERNALD, M. L. The American representatives of *Pyrola rotundifolia*. Rhodora 6: 197-202. 1904.
———. The American varieties of *Pyrola chlorantha*. Ibid. 22: 49-53. 1920.
———. *Pyrola rotundifolia* and *P. americana*. Ibid. 121-123.
FÜRTH, P. Zur Biologie und Mikrochemie einiger *Pirola*-Arten. Akad. Wiss. Wien. Sitz-ber. 129: 559-588. pl. 1. 1920.*
HOLM, T. *Pyrola aphylla*: a morphological study. Bot. Gaz. 25: 246-254. pl. 17.

1898. [Notes adventitious buds from roots of several species; also data on *Chimaphila*.]
- HULTÉN, E. The amphi-Atlantic plants and their phytogeographical connections. Sv. Vet-akad. Handl. IV. 7(1): 1-340. 1958. [p. 142, *maps* 123, 124, *P. rotundifolia*, *P. grandiflora*, *P. asarifolia*; p. 268, *map* 250, *P. chlorantha*, *P. renifolia*.]
- INOUE, H., and Y. KANAYA. Studies on the constituents of pirolaceous plants. VII-VIII. (In Japanese; English summary.) Jour. Pharm. Soc. Japan 78: 298-303. 1958.*
- LOVELL, H. B., and J. H. LOVELL. Pollination of the Ericaceae: IV. *Ledum* and *Pyrola*. Rhodora 38: 90-94. 1936. [*P. elliptica*, *P. americana*.]
- SKAN, S. A. *Pyrola uliginosa*, *P. bracteata*. Bot. Mag. 143: *pl.* 8710A, B. 1917.
- SOUÈGES, R. Embryogénie des Éricacées. Développement de l'embryon chez le *Pyrola rotundifolia* L. Compt. Rend. Acad. Sci. Paris 209: 635-637. 1939.
- WILCKE, J. Dissemination of seeds of Indianpipe and *Pyrola*. (In Dutch.) Levende Nat. 57: 9-11. 1954.*

Subfam. MONOTROPOIDEAE Gray ('Monotropeae')

Tribe MONOTROPEAE D. Don

17. **Monotropis** Schweinitz in Elliott, Sketch Bot. S. C. & Ga. 1: 478. 1817.

Low, smooth, reddish to purplish-brown (violet, pink, or white) plants with the aspect of *Monotropa Hypopithys*, lacking chlorophyll, the stem bent, emerging from the ground center part first, the plant hidden beneath fallen leaves, flowering in early spring. Rhizome lacking, erect flowering stems from adventitious buds from the roots, as in *Monotropa*. Stems with spirally arranged obovate, obtuse, scalelike bracts, the flowers 1-16 in a dense terminal raceme, each flower in the axil of a bract and the pedicel with 2 bracteoles. Flowers 5(4-8)-merous, nodding, very fragrant. Calyx of 5 oblong-lanceolate erect, distinct, persistent, scalelike sepals. Corolla campanulate, sympetalous, 5-lobed, slightly 5-gibbous at the base, the lobes ovate, 1/3-1/4 the length of the tube, persistent. Stamens 10; filaments filiform; anthers short, with a conspicuous connective, unappendaged, 4-locular at first but becoming 1-locular, horizontal at first but becoming inverted in flower (as in *Pyrola* and *Chimaphila*) and opening by 2 terminal pores in the apparent apex; pollen grains single, 2-colpate. Stigma large, capitate, not evidently lobed; style short, thick; ovary superior, 5(4)-locular at the base, each locule with a divided axile placenta, becoming 1-locular above, the placental halves then becoming parietal forming 5(4) conspicuous placentae; ovules anatropous, the integument of 2 layers of cells, embryo sac of the Polygonum type; disc 10-lobed, the lobes in pairs, each clasping the base of a petalad stamen. Fruit a subglobose berry remaining inclosed in the persistent corolla, filled by the enlarged placentae and the numerous minute, ovoid, unappendaged, red or orange seeds; seeds with an endosperm of a few cells and a globular (4-celled?) embryo. (*Schweinitzia* Nutt., *Cryptophila*

Wolf.) TYPE SPECIES: *M. odorata* Schwein. in Ell. (Name composed of *Monotropa* plus Greek, *opsis*, appearance, resembling *Monotropa*.) — SWEET PINE-SAP.

A distinctive genus of one or two species of the southeastern United States. *Monotropsis odorata* ranges at least from eastern Maryland and Virginia to central North Carolina, eastern Tennessee, northern Georgia, and northern Alabama. Since the plant flowers and fruits under a cover of leaves it is usually overlooked, and it is possible that its range is much wider, especially southeastward. The cycle of the plant above ground extends from the fall of one year, when the flowering shoots first appear beneath the fallen leaves, through anthesis early the following spring (March–April), to fruiting in July or early August. Baldwin has demonstrated the changing proportions of corolla tube/lobes from bud to anthesis and has effectively disposed of *M. Lehmaniae* Burnham as the immature fall phase of *M. odorata*. The status of *M. Reynoldsiae* Gray, described from scrub-oak thickets near St. Augustine, Florida, and known elsewhere only southward in the Indian River region, is dubious but unsettled. In *M. odorata* the colored corolla is as long as, shorter, or longer than, the oblong sepals, while the white corolla of *M. Reynoldsiae* is about twice as long as the ovate or ovate-lanceolate sepals. Wolfe, in his careful study of *M. odorata* in Alabama, found, however, a wide range in size (4–20 cm.) and color (reddish pink to brownish red, light lavender to darker shades, pink, white with pink vascular bundles, or pure white) of the plant and a wide variation of the length of the sepals (7–13 mm.). As in *Monotropa*, neither size nor color of plant or corolla can be regarded as diagnostic, and corolla/sepal ratio should be treated with the utmost suspicion.

Pollen is shed in bud on the inner surface of the corolla lobes, and pollination is by insects attracted by the strong, spicy fragrance at anthesis. Seed dispersal apparently is by ants which attack the berry with its fleshy, sweetish placentae; the seeds are relatively plump and hard, well adapted to this habit, in contrast to the slender, tailed, wind-dispersed seeds of *Monotropa*. (Compare other baccate-fruited *vs.* dry-fruited Monotropoideae; *Epigaea*; *Gaultheria* and *Leucothoe*.)

Monotropsis is of particular interest for the 2-bracteolate pedicels, the well-developed calyx of five sepals, the sympetalous corolla, and the relatively unspecialized anthers. Its relationships are with *Monotropa*, *Pityopus* Small, *Monotropastrum* Andres, the two last of which also have baccate fruit. All four are more specialized than *Pterospora* Nutt., *Sarcodes* Torr., and *Allotropa* Gray, which constitute the tribe Pterosporeae. *Pterospora* is especially notable for the appendaged anthers which strongly suggest those of Arbutae. Aside from the reductions and specializations to be expected in connection with the parasitic habit, there seems to be no basis for setting the Monotropoideae apart as a separate family, for the details of morphology, anatomy, and embryology fit excellently with those of other Ericaceae.

REFERENCES:

- A number of references pertaining to Monotropoideae other than ours are included here. See also COPELAND (1941) under *Monotropa*.
- BAKSHI, T. S. Ecology and morphology of *Pterospora andromedea*. Bot. Gaz. **120**: 203–217. 1959.
- BALDWIN, J. T., JR. *Monotropis Lehmaniae* not a real species. Rhodora **59**: 259–262. 1957.
- BURNHAM, S. H. A new species of *Monotropis*. Torreya **6**: 234, 235. 1906. [*M. Lehmaniae*.]
- COPELAND, H. F. The structure of the flower of *Newberrya*. Madroño **2**: 137–142. 1934. [*Hemitomes*.]
- . On the genus *Pityopus*. *Ibid.* **3**: 154–168. 1935.
- . The reproductive structures of *Pleuricospora*. *Ibid.* **4**: 1–16. 1937.
- . The structure of *Allotropa*. *Ibid.* 137–153. 1938.
- . The structure of *Monotropis* and the classification of the Monotropoideae. *Ibid.* **5**: 105–119. 1939.
- DOMIN, K. Vergleichende Studien über den Fichtenspargel mit Bemerkungen über Morphologie, Phytogeographie, Phylogenie und systematische Gliederung der Monotropiden. Sitz-ber. Böhm. Ges. Wiss. Math.-Nat. Cl. **1915**: 1–111. 1915.
- DOYEL, B. E., and L. M. GOSS. Some details of the reproductive structures of *Sarcodes*. Madroño **6**: 1–7. 1941.
- GRAY, A. *Chloris boreali-americana*. Mem. Am. Acad. Arts Sci. II. **3**: 1–56. pls. 1–10. 1848. [*M. odorata*, 15–20, pl. 2.]
- HENDERSON, M. W. A comparative study of the structure and saprophytism of the Pyrolaceae and Monotropaceae with reference to their derivation from the Ericaceae. Contr. Bot. Lab. Univ. Penn. **5**: 42–109. 1920.
- HOWELL, J. T. A year with *Pityopus*. Leaflet West. Bot. **6**: 57–61. 1950.
- MCDUGAL, D. T., and F. E. LLOYD. Roots and mycorrhizas of some Monotropaceae. Bull. N. Y. Bot. Gard. **1**: 419–429. pls. 10–12. 1900. [*Pterospora*, *Sarcodes*, *Monotropa*.]
- PLITT, C. D. Notes on *Monotropis odorata*. Rhodora **11**: 153, 154. 1909.
- SMALL, J. K. Monotropaceae. N. Am. Fl. **29**: 11–18. 1914.
- SPAWN, W. Notes on *Monotropis*. Bartonia **20**: 7–10. 1940.
- WOLF, W. Notes on Alabama plants. A new monotropoid plant. Am. Midl. Nat. **8**: 104–129. 1922. [Extensive observations on *M. odorata*, as *Cryptophila pudica*.]

18. *Monotropa* Linnaeus, Sp. Pl. **1**: 387. 1753; Gen. Pl. ed. 5. 183. 1754.

Low, fleshy, tawny to reddish to translucent white herbs, lacking chlorophyll, blackening in drying. Main root thick, horizontal, with a surrounding mass of short, fleshy, intertwined secondary roots, each incased in a mycelial sheath; rhizomes lacking, the stems from adventitious (endogenous) buds from the roots. Flowering stems with scales or bracts, the tip nodding at first (erect in fruit), with 1–15 flowers in the axils of bracts, bractlets absent. Flowers 5-merous or the terminal 5-merous, the others 3- or 4-merous. Calyx(?) of 1–5 lanceolate, deciduous, bractlike scales. Corolla appearing campanulate, of 5 (3 or 4) erect, scalelike, distinct petals

saccate at the base and tardily deciduous. Stamens 10 or 8; filaments subulate, the outer whorl (opposite petals) shorter than the inner; anthers short, kidney-shaped, becoming 1-locular at anthesis, opening transversely through 2 curving slits; pollen grains single, 2- or 3-colpate. Stigma funnel-shaped to discoid, obscurely lobed opposite the petals; style columnar, thick and fleshy; ovary superior, 10-8-lobed, 5- or 4-locular at the base and 1-locular above with 5 or 4 bilobed parietal placentae; ovules anatropous, very numerous; disc 10- or 8-lobed, the lobes in pairs clasping the bases of the petalad stamens. Capsule ovoid, 10-8-grooved, erect, loculicidally 5- or 4-valved, the very thick placentae covered with numerous minute, elongate, tailed seeds with a very loose coat, very few large endosperm cells and a 9-2-celled embryo. (*Hypopitys* Hill.) LECTOTYPE SPECIES: *M. uniflora* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 674. 1913. (Name Greek, *monos*, one, and *tropos*, turn, the summit of the stem nodding, bent to one side.) — INDIAN PIPE, PINE-SAP.

A small, but widely distributed, genus of parasitic herbs of the Northern Hemisphere, including two or more species, both occurring in our area.

Section *HYPOPITYS* Gray (*Hypopitys* of authors), with several-flowered racemes, the terminal one usually 5-merous, the others 3- or 4-merous, the sepals 3-5 (mostly as many as the petals), the anthers opening by a continuous line into two very unequal valves, and the style longer than the ovary, includes *M. Hypopithys* L. (*Hypopitys lanuginosa* (Michx.) Nutt., *H. americana* (DC.) Small), pine-sap, a woodland plant distributed from Newfoundland to British Columbia, southward to Iowa, Louisiana, and Florida in the East and to Arizona in the West, with a wide Eurasian range, as well. The species is quite variable in size of plant, color, pubescence, indentation of margins of bracts, and proportions of ovary and style, on the basis of which a number of species have been erected. Only a single species seems to be represented in North America, but a careful study of variation is needed. Diploid chromosome numbers of European material of *M. Hypopithys* and *M. Hypophegea* Wallr. (*M. Hypopithys* var. *glabra* Roth), which differ in pubescent *vs.* glabrous filaments, styles, and inner surface of the petals, have been reported as 48 and 16 respectively.

Section *MONOTROPA* (§ *Eumonotropa* Gray), differing in the 1-flowered shoots, the more reduced calyx of 1-4 scales, the transverse anthers opening by two short slits, and the short, thick style, includes only *M. uniflora* L. (*M. Brittonii* Small), Indian pipe. A frequent woodland plant of North America from Newfoundland and Quebec to British Columbia, southward to Oregon, Montana, Minnesota, Missouri, Oklahoma, Texas, and Florida, the species is disjunct southward in Central America in the mountains of central Mexico, Guatemala, and Columbia, and occurs in Japan, central China, and the Himalayas, as well. A number of variants in color, size, and other minor characters have been proposed, but only a single wide-ranging species seems to be involved.

Monotropa Hypopithys is segregated by some as *Hypopitys* Hill, on

the basis of the several flowers, the stem anatomy (a flattened cylinder *vs.* a ring of ten bundles), and the number of grooves on the pollen grains (2 *vs.* 3), but the plants are so similar in all other features that they are here maintained in a single genus.⁹

The wide range of habitats from which *Monotropa* has been recorded (moist woods to sand dunes to sphagnum bogs, but always in association with trees) and the tight mycorrhizal underground masses of the plant are more in keeping with a parasitic habit than with the saprophytic mode often assigned to it. In a recent study Björkman found that the same mycorrhizal fungus occurs in *M. Hypopitys* and adjacent trees; that the mycorrhizal masses of *Monotropa* are associated with the roots of trees (although there is no direct connection between *Monotropa* and tree); and, on the basis of trenching and radioactive tracer experiments, that it is probable that "*Monotropa* obtains its energy requirements from the trees via the mycorrhizal fungus common to them both."

There is still some question as to whether the "sepals" of *Monotropa* are bracts or sepals.

REFERENCES:

- Under *Monotropsis* see especially COPELAND (1939), DOMIN, HENDERSON, and McDOUGAL & LLOYD; under family references see BERGMAN and PELTRISOT.
- BJÖRKMAN, E. On the metabolism of *Monotropa Hypopitys* L.: an epiparasite on forest tree roots. (Abs.) Proc. IX Int. Bot. Congr. 2: 35, 36. 1959.
- CAMPBELL, D. H. *Monotropa uniflora* as a subject for demonstrating the embryo-sac. Bot. Gaz. 14: 83. 1889. [Whole mounts of placenta and ovules in 3% sugar solution.]
- COPELAND, H. P. Further studies on Monotropeae. Madroño 6: 97-119. 1941. [Includes details of *M. Hypopitys*, *M. uniflora*, *Pterospora*, *Hemitomes*.]
- DAVIS, J. J. Occurrence of Indian pipe. Torreya 14: 162. 1914. [In sphagnum in a swamp of *Picea mariana* and *Larix*.]
- D'HUBERT, E. Recherches sur le sac embryonnaire des plantes grasses. Ann. Sci. Nat. Bot. VIII. 2: 37-128. pls. 1-3. 1896.
- GRIER, N. M. Preserving Indian pipes without discoloration. Rhodora 24: 225, 226. 1922.
- HERRICK, J. A. The nutrition of Indian pipe. Turtox News 35: 188-190. 1957. [Parasitic on the mycorrhizal fungus.]
- HULL, E. D. Occurrence of the Indian pipe (*Monotropa uniflora*) in a xerophytic habitat. Torreya 14: 101-105. 1914. [Among an open stand of *Quercus velutina* on dunes, Lake Co., Indiana.]
- KAMIENSKI, F. Die Vegetationsorgane der *Monotropa Hypopitys*, L. Bot. Zeit. 39: 457-461. 1881.
- . Les organes végétatifs du *Monotropa Hypopitys* L. Mém. Soc. Natl. Sci. Nat. Math. Cherbourg 24: 5-40. pls. 1-3. 1882.
- KOCH, L. Das Entwicklung des Samens von *Monotropa Hypopitys* L. Jahrb. Wiss. Bot. 13: 202-252. pls. 9-11. 1882.

⁹Those who wish to separate them must find another generic name, for *Hypopitys* Hill is illegitimate, having been proposed as a substitute for *Monotropa*. Hill wrote, "This author [Linnaeus] takes away its received name *hypopitys*, and calls its *monotropa*." Hill's *Hypopitys* includes both Linnaean species.

- MEEHAN, T. *Monotropa uniflora*. Meehans Monthly 12: 133, 134. pl. 9. 1902.
- NIEUWLAND, J. A., and A. D. SLAVIN. Preservation of *Monotropa* and similar plants without discoloration. Proc. Indiana Acad. Sci. 38: 103, 104. 1928. [Saturated solution of sulfur dioxide in alcohol.]
- QUEVA, C. Le *Monotropa Hypopitys* L. Anatomie et biologie. Bull. Soc. Bot. Fr. 57: 639. 1910.
- SHIBATA, K. Die Doppelbefruchtung bei *Monotropa uniflora*. Flora 90: 61-66. 1 pl. 1902 [1901].
- SMALL, J. K. *Monotropa Brittonii*. Addisonia 13: 35, 36. pl. 434. 1928.
- WILCKE, J. Dissemination of seeds of Indianpipe and *Pyrola*. (In Dutch.) Levende Nat. 57: 9-11. 1954.*

Subfam. VACCINIOIDEAE Endlicher ('Vaccineae')

Tribe VACCINIEAE D. Don

19. *Vaccinium* Linnaeus, Sp. Pl. 1: 349. 1753; Gen. Pl. ed. 5. 1754.

Evergreen or deciduous, often stoloniferous shrubs [sometimes epiphytic], rarely trees. Leaves alternate, short-petioled, entire or serrate; winter buds small, ovoid, with 2 or several outer scales. Flowers solitary in the axils of bracts or leaves, the more or less well-defined inflorescences thus racemose; inflorescences from buds of the preceding season, rarely reduced to 1 or 2 flowers; pedicels usually with 2 bracteoles. Calyx adnate to the ovary, the lobes 4 or 5, rarely obsolete. Corolla white or greenish to red, cylindric, urceolate or campanulate, 4- or 5-lobed or sometimes 4-parted to the base. Stamens 8 or 10; anthers with or without spurs on the back, lacking white disintegration tissue in the connective, the halves narrowed upward into tubes, opening by a terminal pore, without awns; pollen tetrads without viscin strands. Stigma small, simple or somewhat capitate; style straight; ovary [partly to] completely inferior, 4- or 5- or falsely 10-locular (then usually 10-locular above, 5-locular below) by the development of ingrowths of the ovary wall which unite with the axile, more or less enlarged and pendulous placentae; ovules usually numerous on the surface of the placenta; disc conspicuous, on the surface of the ovary. Fruit a [5-]many-seeded berry crowned by the persistent calyx lobes; seeds usually small. (Including *Batodendron* Nutt., *Cyanococcus* (Gray) Rdyb., *Herpothamnus* Small, *Hugeria* Small, *Oxycoccus* Hill, *Polycodium* Raf., *Rhodococcus* (Rupr.) Avorin.) LECTOTYPE SPECIES: *V. Myrtillus* L.; see Britton & Brown, Ill. Fl. North. U. S. ed. 2. 2: 698. 1913. (*Vaccinium*, the classical name of *V. Myrtillus*.) — DEERBERRIES, BLUEBERRIES, and CRANBERRIES.

A polymorphic genus of perhaps 150 species, mostly of the Northern Hemisphere, from the mountains of the tropics northward to the Arctic Circle. The genus is composed of a number of more or less well-marked subgenera and sections, these often of restricted geographical distribution; but the classification is not yet well worked out and opinions as to the segregation of sections, subgenera, or genera vary. *Vaccinium* is treated conservatively here (cf. *Rhododendron*), for many reticulate relationships

are evident between the various subgenera. (Note also natural and artificial hybrids between sections and subgenera.) Seven subgenera occur in the United States, subg. *VACCINIUM* (subg. *Euvaccinium* Klotzsch), including sects. *VACCINIUM* (§ *Myrtillus* Koch) and *VITIS-IDAEA* (Moench) Koch, entirely to the north and west of our range.

Vaccinium is taxonomically difficult and much herbarium material is inadequate for study. Collectors should note accurately height of plant, glaucescence of various parts, corolla shape and color, fruit color, habitat, and presence of other species or individuals of varying size in the same or adjacent habitats.

Subgenus *BATODENDRON* (Nutt.) Klotzsch (*Batodendron* Nutt.), in which the flowers are in bracteate racemes, the corolla campanulate and 5-lobed, the stamens included, the anthers spurred on the back, the style exerted from the corolla, the pedicels jointed beneath the flower, the ovary incompletely 10-locular, and the berry black, leathery, and persistent, includes *Vaccinium cubense* Griseb. (and perhaps other species), of Cuba and Hispaniola, *V. arboreum* Marsh., of the southern United States, and *V. leucanthum* Cham. & Schlecht. and *V. stenophyllum* Steud., of Central America. *Vaccinium arboreum* (including var. *glaucescens* (Greene) Sarg.), farkleberry or sparkleberry, is an easily recognized shrub or small tree (to ca. 9 m.) with a wide range from Florida westward to Texas (Edwards Plateau) and northward to southeastern Virginia, Illinois, southern Missouri, and Oklahoma. The common southeastern form has lustrous, persistent leaves; in the western part of the range a glaucescent phase appears and leaf proportions, size of bracts, shape of flower, pubescence, and glandularity change to varying degrees. A careful study of variation is needed. Small observed that this species is tolerant of calcareous soil.

Subgenus *POLYCODIUM* (Raf.) Sleumer (*Polycodium* Raf., *Picrococcus* Nutt.), the deerberries, in which the corolla is campanulate and open in bud, the stamens exerted and spurred on the back, the pedicels not jointed, the flowers in leafy or bracted racemes, the ovary incompletely 10-locular, the fruit greenish to nearly black and insipid, is a well-marked group ranging from Florida to Maine, westward to central Canada and Texas, and in Mexico along the Sierra Madre Oriental from Puebla to Nuevo León. About 27 "species" have been described, but the number is undoubtedly far lower. The taxonomy of the group is chaotic and no practical treatment exists. All of the characters used are variable, including leaf size (note dimorphism between flowering and vegetative shoots), size of plant, pubescence, glaucescence, fruit color, and presence or absence of stipitate glands. The corolla is open in the young bud and continues to enlarge (as in *Halesia*), making size-comparisons difficult. Transplant and crossing experiments, population and cytological studies are an absolute necessity before the biology of this group can possibly be understood. The few chromosome counts ($2n = 24$) suggest that the polyploidy so characteristic of subg. *CYANOCOCCUS* may be lacking here.

Subgenus *HERPOTHAMNUS* (Small) Uphof (*Herpothamnus* Small), in-

cludes a single isolated species in our area, *V. crassifolium* Andr. (*H. crassifolium* (Andr.) Small), $2n = 24$, a creeping or trailing, narrow- and coriaceous-leaved evergreen with condensed 1-5-flowered axillary racemes, the flowers in the axils of small bracts, the pedicels with 2 bracteoles of almost the same size as the bracts, the ovary 5-locular, the stamens 10 with hairy filaments and unspurred anthers with short tubules, the berries black, sweet. The species is localized in moist, sandy habitats on the Coastal Plain from South Carolina to southeastern Virginia. Camp has called attention to the curious nodular enlargement of the roots and has suggested a relationship to a few montane South American pendent epiphytic species in which a similar development occurs, observing further that a species epiphytic at lower altitudes may become terrestrial at higher, with an even greater development of the root enlargements.

Subgenus CYANOCOCCUS (Gray) Klotzsch (*Cyanococcus* (Gray) Rydb.), the blueberries, with flowers in racemes or clusters from axillary buds, corollas urceolate to cylindric or ovoid-campanulate with 5 short lobes, anthers spurless, filaments pubescent, ovary incompletely 10-locular, and berries blue or black and often glaucous, includes about 24 species of eastern North America (about 16 in the Southeast), perhaps 10 of Japan and Korea, and probably *V. Selerianum* (Loesen.) Sleum., of Chiapas, Mexico. Extensive field studies and careful morphological comparisons, along with a series of cytological and hybridization studies, have revealed many of the underlying causes of the taxonomic difficulties encountered in this subgenus in eastern North America. (See especially Camp [1945] and Darrow & Camp [1945] for biology, discussion, keys to North American species and hybrids, chromosome numbers.)

In the United States the subgenus comprises about nine diploids ($2n = 24$), twelve tetraploids (including *V. corymbosum* L., a hybrid complex of varying combinations of about six tetraploids to the north of the glacial boundary), and three hexaploids (including *V. Ashei* Reade, a complex allopolyploid involving about five tetraploids). Interspecific hybridization (often extensive) occurs at the diploid, tetraploid, or hexaploid levels, the principal barriers being geographical and ecological isolation with no interspecific sterility between homoploids. Segregation within allopolyploid complexes adds further complications, for some of the derivatives may simulate the parental species. Autopolyploidy is postulated for six species which appear to be more robust tetraploid counterparts of diploids; three other tetraploids (*V. myrsinites* Lam., *V. marianum* Wats., *V. fuscatum* Ait.) and the hexaploid *V. Constablaei* Gray appear to be of allopolyploid origin. Pentaploid hybrids, but no triploids, have been found in the wild. Individual plants may be self-sterile, but others of the same species may be partly or largely self-fertile.

Vaccinium hirsutum Buckl. ($2n = 48$), of the mountains of eastern Tennessee and western North Carolina, is aberrant in the subgenus in the glandular pubescence of flowers and fruit. Camp has raised the intriguing possibility (based on some early hybrids made by Coville) that this species may have arisen as an allopolyploid between subg. CYANOCOCCUS

and subg. POLYCODIUM and has suggested that a pubescent-leaved, black-fruited *V. vacillans* Torr. and a pubescent-leaved, nonglaucous, gland-bearing form of subg. POLYCODIUM be used in attempting to resynthesize *V. hirsutum*.

Blueberries are a commercial fruit crop of ever-increasing importance, and a number of cultivars including both selections from the wild and a series of artificial hybrids (begun by Coville) have been named. The low, diploid *V. angustifolium* Ait. ($2n = 24$) is the most important commercial species in the Northeast, while commercial plantations of highbush types on the Coastal Plain, from eastern Massachusetts southward to Florida and Louisiana, are largely *V. australe* Small, southeastern highbush blueberry ($2n = 48$), or (especially to the south) *V. Ashei*, rabbit-eye blueberry. *Vaccinium corymbosum* is cultivated to a slight degree.

Subgenus OXYCOCCOIDES (Benth. & Hook.) Sleumer (*Hugeria* Small), shrubs in which the leaves are deciduous, the flowers solitary in the axils of leaves, nodding on slender pedicels, the corolla deeply 4-cleft and the lobes revolute, the anthers with very long terminal tubules and usually spurless, the filaments short, hairy, the ovary 4-locular, and the fruit red to black, insipid to acid and pleasant tasting, comprises only *Vaccinium japonicum* Miq. (including vars. *sinicum* (Nakai) Rehd., of China, *lasio-stemon* Hayata, of Formosa, and *japonicum*, of Japan and Quelpaert Island) and *V. erythrocarpum* Michx., of the southern Appalachians. *Vaccinium erythrocarpum*, mountain cranberry, a shrub to 2 m., is a plant of cool montane habitats from eastern Tennessee, and western North Carolina, to western Virginia and eastern West Virginia. The fruit varies widely in taste from insipid to pleasantly acid, and in color from red to black (f. *nigrum* Allard). Although this subgenus and subg. OXYCOCCUS are similar in many floral details, the two are undoubtedly of quite independent derivation and are not closely related. The anthers are usually spurless, but Hooker figured a plant with short spurs, and in an occasional individual some (but not necessarily all) anthers of a flower may bear (one or) a pair of very short divergent spurs.

Subgenus OXYCOCCUS Drude (*Oxycoccus* Hill), the cranberries, is a well-marked group of about three trailing, small-leaved, evergreen bog species of the Northern Hemisphere with 4-merous flowers, the corolla parted nearly to the base, the lobes linear-oblong and revolute, the ovary 4-locular, the anthers with very short filaments and very long tubules; spurless on the back, the flowers articulated to slender 2-bracteolate pedicels, axillary or in short racemes, the berry bright red and acid. *Vaccinium macrocarpon* Ait. (*O. macrocarpus* (Ait.) Pers.), cranberry, a diploid ($2n = 24$), ranges from Minnesota to Newfoundland and southward on the Coastal Plain to Delaware, southeastern Virginia, and eastern North Carolina, and in the mountains to West Virginia, western Virginia, northeastern Tennessee, and western North Carolina.¹⁰ A second diploid, *V.*

¹⁰ There is also in the Gray Herbarium a small fruiting specimen of *Vaccinium macrocarpon*, labeled in Asa Gray's hand, "Little Rock, Arkansas, Dr. Hasse, 1886," which is presumably the basis for reports of this species from Arkansas.

microcarpum (Turcz.) Schmalhaus. ex Busch (*O. microcarpus* Turcz.) occupies a more northern and western area in North America (Alberta and British Columbia to Alaska) and ranges across Eurasia to Iceland. The tetraploid and relatively variable *V. Oxycoccus* L. (*O. quadripetalus* Gilib.) combines the characters of the diploids and has a virtually circumpolar distribution, overlapping in part that of both diploids. In eastern North America it extends southward in cold bogs in the mountains to Pocahontas County, West Virginia.¹¹ Isolated, sterile, hexaploid plants ($2n = 72$), distinguishable primarily by larger size, have been reported from Europe. Hagerup thought these to have resulted from the hybridization of *V. Oxycoccus* and *V. microcarpum*, while Camp has suggested instead a derivation directly from the tetraploid and has further postulated both the sporadic occurrence of similar hexaploids throughout the range of *V. Oxycoccus* and the possible occurrence of fertile hexaploids. *Vaccinium macrocarpon* is an important commercial plant, the crop of cranberries from Massachusetts, New Jersey, and Wisconsin (and to a lesser extent Oregon, Washington, Maine, and Rhode Island) amounting to 10–20 million dollars annually.

REFERENCES:

Under family references see also BELL & BURCHILL, DUFRENOY, KEARNEY, MATTHEWS & KNOX, PELTRISOT, SMITH, and STANLEY; under *Gaylussacia* see CAIN & POTZGER; for special information on *Vaccinium macrocarpon* see Cranberries, the national cranberry magazine (Wareham, Massachusetts, 1936+).

¹¹ Fernald (Gray. Man. Bot. ed. 8. 1950) records *Vaccinium Oxycoccus* var. *ovalifolium* Michx. from North Carolina. Apparently this record is based on a sheet in the Gray Herbarium which bears two collections, both labeled in Gray's handwriting. To the left is a fruiting specimen of *V. Oxycoccus* with "N. Carolina, Croom" beneath it; to the right are two flowering shoots of *V. macrocarpon* and a characteristic blue label "Herb. Asa Gray" (on which the smaller label "Syn. Fl. N. Amer." has been pasted) with "*Vaccinium macrocarpon*. W. New York," also in Gray's hand. Another sheet bearing five collections of *V. Oxycoccus* has two small fruiting specimens which are associated with a similar label with "*Vaccinium Oxycoccus*. W. New York." Croom's botanizing seems to have been confined mostly to the Coastal Plain, especially around New Bern, North Carolina, and Tallahassee and Aspalaga, Florida, with observations obtained in the course of his travels between these areas. (See Jour. N. Y. Bot. Gard. 21: 164. 1920.) His published botanical notes do not list montane plants (with the exception of *Pinus pungens* which he recorded from Pilot Mountain, Stokes County, North Carolina), and I have been unable to find any evidence that he collected in the high mountains of western North Carolina where *V. Oxycoccus* might possibly be expected. Furthermore, he listed *Oxycoccus macrocarpus* in his *Catalogue of Plants Native or Naturalized in the Vicinity of New Bern, North Carolina* (1837). In view of these circumstances and of the two labels bearing "W. New York," it seems likely that an error in mounting or labeling is involved and that the specimen of *V. macrocarpon* should be attributed to Croom, while that of *V. Oxycoccus* should be assigned to New York. It is also significant that Gray himself (Syn. Fl. N. Am. 2(1): 26. 1886) did not admit *V. Oxycoccus* south of the mountains of Pennsylvania, whereas *V. macrocarpon* was given a range including Newfoundland and North Carolina. Until more convincing evidence is presented, it seems best to regard Pocahontas County, West Virginia, as the approximate southern limit of *V. Oxycoccus* and to exclude this species from the flora of the southeastern United States.

- ADDOMS, R. M., and F. C. MOUNCE. Notes on the nutrient requirements and the histology of the cranberry (*Vaccinium macrocarpon* Ait.) with special reference to mycorrhiza. *Pl. Physiol.* **6**: 653–668. *pls.* 11, 12. 1931. [See also *ibid.* **7**: 643–656. 1932.]
- ALLARD, H. A. *Vaccinium erythrocarpum* — what is the fruit color? *Castanea* **12**: 117, 118. 1947. [See also *ibid.* **13**: 127. 1948.]
- AMMONS, N., and E. L. CORE. Huckleberries, blueberries and cranberries of West Virginia. *Castanea* **10**: 103–109. 1945.
- ASHE, W. W. *Polycodium*. *Jour. Elisha Mitchell Sci. Soc.* **46**: 196–213. 1931. [One of Ashe's numerous contributions to confusion; useful only in showing the range of variability in the subgenus.]
- AVORIN, N. A. On the genus *Rhodococcum* (Rupr.) gen. nov. (Vacciniaceae). (In Russian.) *Bot. Zhur.* **43**: 1719–1724. 1958. [*V. Vitis-Idaea* segregated; \times *Rhodocinium intermedium* (Ruthe) Alava for *V. Myrtillus* \times *Vitis-Idaea*; tribe *Oxycocceae* (previously published by Small, Man. Southeast. Fl. 1006. 1933) maintained.]
- BAIN, H. F. Production of synthetic mycorrhiza in the cultivated cranberry. *Jour. Agr. Res.* **55**: 811–835. *pls.* 1–10. 1937. [Includes critical review of the literature on mycorrhiza in the Ericaceae; bibliography.]
- and H. DERMEN. Sectorial polyploidy and phyllotaxy in the cranberry (*Vaccinium macrocarpon* Ait.). *Am. Jour. Bot.* **31**: 581–587. 1944.
- BELL, H. P. Determinate growth in the blueberry. *Canad. Jour. Res. C.* **28**: 637–644. 1950. [*V. angustifolium*; the same species in other studies by this author.]
- . The growth cycle of the blue-berry and some factors of the environment. *Canad. Jour. Bot.* **31**: 106. 1953.
- . The development of the blueberry seed. *Ibid.* **35**: 139–153. 1957.
- and J. BURCHILL. Flower development in the lowbush blueberry. *Ibid.* **33**: 251–258. 1955.
- and E. C. GIFFIN. The lowbush blueberry: the vascular anatomy of the ovary. *Ibid.* **35**: 667–673. 1957.
- CAMP, W. H. *Hugeria erythrocarpa*. *Addisonia* **21**: 3, 4. *pl.* 674. 1939.
- . On the structure of populations in the genus *Vaccinium*. *Brittonia* **4**: 189–204. 1942.
- . A survey of the American species of *Vaccinium*, subgenus *Euvaccinium*. *Ibid.* 205–247.
- . A preliminary consideration of the biosystematy of *Oxycoccus*. *Bull. Torrey Bot. Club* **71**: 426–437. 1944.
- . The North American blueberries with notes on other groups of Vacciniaceae. *Brittonia* **5**: 203–275. 1945.
- and C. L. GILLY. Polypetalous forms of *Vaccinium*. *Torreyia* **42**: 168–173. 1942 [1943].
- CLARK, J. H., and S. G. GILBERT. Selection of criterion leaves for the identification of blueberry varieties. *Proc. Am. Soc. Hort. Sci.* **40**: 347–351. 1942.*
- COVILLE, F. V. Experiments in blueberry culture. *U. S. Dep. Agr. Pl. Industry Bull.* **193**: 1–100. *pls.* 1–18. 1910.
- . Directions for blueberry culture, 1921. *U. S. Dep. Agr. Bull.* **974**: 1–24. *pls.* 1–29. 1929. [See also **334**: 1–16. 1915; *U. S. Dep. Agr. Pl. Industry Circ.* **122**: 3–11. 1913.]
- . Blueberry chromosomes. *Science* **66**: 565, 566. 1927. [Reports on hybridization experiments.]

- DARROW, G. M. Rest period requirement for blueberries. *Proc. Am. Soc. Hort. Sci.* **41**: 189–194. 1942.*
- . New varieties of blueberry. *Yearb. U. S. Dep. Agr.* **1943/47**: 300–303. 1947.
- . The big six blueberry varieties for northern states. *Natl. Hort. Mag.* **35**: 162–165. 1956.*
- . Blueberry growing. *U. S. Dep. Agr. Farmers Bull.* **1951**: 1–33. 1957.*
- and W. H. CAMP. *Vaccinium* hybrids and the development of new horticultural material. *Bull. Torrey Bot. Club* **72**: 1–21. 1945.
- , ———, H. E. FISCHER, and H. DERMEN. Chromosome numbers in *Vaccinium* and related groups. *Ibid.* **71**: 498–506. 1944.
- , E. B. MORROW, and D. H. SCOTT. An evaluation of inter-specific blueberry crosses. *Proc. Am. Soc. Hort. Sci.* **59**: 277–282. 1952.*
- DERMEN, H. The mechanism of colchicine-induced cytohistological changes in cranberry. *Am. Jour. Bot.* **32**: 387–394. 1945.
- . Periclinal cytochimeras and histogenesis in cranberry. *Ibid.* **34**: 32–43. 1947.
- and H. F. BAIN. Periclinal and total polyploidy in cranberries by colchicine. *Proc. Am. Soc. Hort. Sci.* **38**: 400. 1941.*
- . A general cytohistological study of colchicine polyploidy in cranberry. *Am. Jour. Bot.* **31**: 451–463. 1944.
- EATON, E. L. The spread of blueberry seed through manure and by migrating robins. *Proc. Am. Soc. Hort. Sci.* **69**: 293–295. 1957.*
- EGGERT, F. P. Shoot emergence and flowering habit in the lowbush blueberry (*Vaccinium angustifolium*). *Ibid.* 288–292.
- FERNALD, M. L. The variations and distribution of American cranberries. *Rhodora* **4**: 231–237. 1902.
- FLINT, E. M. Structure of wood in blueberry and huckleberry. *Bot. Gaz.* **65**: 556–559. *pls.* 10, 11. 1918. [*V. corymbosum*, *V. angustifolium*, *Gaylussacia* sp., *Rhododendron* sp.]
- GLEISBERG, W. Systematisch-kritische Vorarbeit für eine Monographie der Spezies *Vaccinium Oxycoccus* L. *Bot. Arch.* **2**: 1–34. 1922.
- . *Vaccinium Oxycoccus* L., ein weiterer Beitrag zur Typenfrage der Art. *Ibid.* 130–139.
- . Vergleichend-anatomische Untersuchung des Blattes der *Vaccinium Oxycoccus*-Typen. *Ber. Deutsch. Bot. Ges.* **40**: 139–147. 1922.
- GOHEEN, A. C. The cultivated highbush blueberry. *Yearb. U. S. Dep. Agr.* **1953**: 784–789. 1953. [Diseases; see also BERGMAN, H. F. Disorders of cranberries. *Ibid.* 789–796.]
- HAGERUP, O. Studies on polyploid ecotypes in *Vaccinium uliginosum* L. *Hereditas* **18**: 122–128. 1933.
- . Studies on the significance of polyploidy. IV. *Oxycoccus*. *Ibid.* **26**: 399–410. 1940.
- HALL, I. V. The botany of the lowbush blueberry. *Nova Scotia Fruit Growers Assoc. Rep.* **94**: 87–89. 1957.*
- . The tap root in lowbush blueberry. *Canad. Jour. Bot.* **35**: 934. *pl.* 1. 1957. [*V. myrtilloides*, *V. angustifolium*, *V. Brittonii*.]
- . Plant populations in blueberry stands developed from abandoned hayfields and woodlots. *Ecology* **40**: 742, 743. 1959. [New Brunswick.]
- HOOKE, J. D. *Vaccinium erythrocarpum*. *Bot. Mag.* **51**: *pl.* 7413. 1895.

- HOOKE, W. J. *Vaccinium corymbosum*, *V. angustifolium*. *Ibid.* 62: pls. 3428, 3434. 1835.
- KARMO, E. A. Pollination of the lowbush blueberry. Nova Scotia Fruit Growers Assoc. Rep. 94: 93-97. 1957.*
- KRAMER, A., and A. L. SCHRADER. Significance of the pH of blueberry leaves. *Pl. Physiol.* 20: 30-36. 1945.
- LONGLEY, A. E. Chromosomes in *Vaccinium*. *Science* 66: 566-568. 1927.
- LOVELL, H. B. Pollination of the Ericaceae: VI. *Vaccinium caespitosum* on Mt. Katahdin. *Rhodora* 44: 187-189. 1942. [By 3 spp. of *Bombus*.]
- and J. H. LOVELL. Pollination of *Vaccinium pennsylvanicum*. *Ibid.* 39: 60-63. pl. 456. 1937. [*V. angustifolium* Ait.]
- MAHLSTEDE, J. P., and D. P. WATSON. An anatomical study of adventitious root development in stems of *Vaccinium corymbosum*. *Bot. Gaz.* 113: 279-285. 1952.
- NEWCOMER, E. H. Chromosome numbers of some species and varieties of *Vaccinium* and related genera. *Proc. Am. Soc. Hort. Sci.* 38: 408-470. 1941.
- PORSILD, A. E. The cranberry in Canada. *Canad. Field-Nat.* 52: 116, 117. 1938.
- RITCHIE, J. C. A natural hybrid in *Vaccinium*. I. The structure, performance and chorology of the cross *Vaccinium intermedium* Ruthe. *New Phytol.* 54: 49-67. 1955. [*V. Myrtillus* × *V. Vitis-Idaea*.] II. Genetic studies in *Vaccinium intermedium* Ruthe. *Ibid.* 320-335. pls. 6, 7. [Fls. homologous in both parental spp.]
- . *Vaccinium Myrtillus* L. *Jour. Ecol.* 44: 291-299. 1956.
- ROBERTS, R. H., and B. E. STRUCKMEYER. Growth and fruiting of the cranberry. *Proc. Am. Soc. Hort. Sci.* 40: 373-379. 1942.*
- . Blossom induction of the cranberry. *Pl. Physiol.* 18: 534-536. 1943.
- ROBINSON, C. B. *Polycodium*. *Bull. Torrey Bot. Club* 39: 549-559. 1912. [Discussion of generic limits; an attempt at delimitation of species.]
- ROZANOVA, M. A. A survey of the literature on the genera *Vaccinium* and *Oxycoccus*. (In Russian; English summary.) *Bull. Appl. Bot. Genet. Pl. Breed.* VIII. 2: 121-186. 1934.*
- SARGENT, C. S. *Vaccinium*. *Silva N. Am.* 5: 115-120. pl. 230. 1893. [*V. arbo-reum*.]
- . *Vaccinium hirsutum*. *Gard. Forest* 2: 364, 365. 1889.
- SAWYER, W. H., Jr. Stomatal apparatus of the cultivated cranberry, *Vaccinium macrocarpon*. *Am. Jour. Bot.* 19: 508-513. pl. 41. 1932.
- SEYMOUR, F. C. *Oxycoccus* as a genus. *Am. Midl. Nat.* 49: 935, 936. 1953.
- SIMS, J. *Vaccinium crassifolium*. *Bot. Mag.* 29: pl. 1152. 1809. [Also *V. myrsinites*, 37: pl. 1550. 1813; *V. arboreum*, 38: pl. 1607. 1814; *V. macrocarpon*, 52: pl. 2586. 1825.]
- SLEUMER, H. Die Arten der Gattung *Vaccinium* L. in Zentral- und Südamerika. *Notizbl. Bot. Gart. Berlin* 13: 111-140. 1936.
- . *Vaccinioideen-Studien*. *Bot. Jahrb.* 71: 375-510. 1941. [*Vaccinium*, 408-493, including key to 33 sects., revision of spp. of India and East Asia.]
- SMALL, J. K. *Polycodium floridanum*. *Addisonia* 17: 35, 36. pl. 562. 1932.
- SMITH, B. E. Notes on *Polycodium* of North and South Carolina. (Abs.) *Am. Jour. Bot.* 36: 803, 804. 1949. [See also *Jour. Tenn. Acad. Sci.* 24: 168. 1949.]
- STEVENS, N. E. The development of the endosperm in *Vaccinium corymbosum*. *Bull. Torrey Bot. Club* 46: 465-468. 1919.

- VEILLET-BARTOSZEWSKA, M. Ericacées; développement de l'embryon chez le *Vaccinium Myrtillus* L. Compt. Rend. Acad. Sci. Paris 246: 824–826. 1958.
- WASSCHER, J. Vergelijkend-anatomische onderzoeken bij eenige *Vaccinium*-soorten. (In Dutch; English summary.) Ned. Dendr. Ver. Jaarb. 15: 65–112. 1947. [Comparative-anatomical studies of 11 spp. of *Vaccinium*.]
- WELCH, W. H. A contribution to the phytoecology of southern Indiana with special reference to certain Ericaceae in a limestone area of the Bloomington Quadrangle. Proc. Indiana Acad. Sci. 38: 65–83. 1929. [Includes data on *Gaylussacia baccata*, *Vaccinium vacillans*, *Epigaea repens*.]

20. **Gaylussacia** Humboldt, Bonpland & Kunth, Nova Gen. Sp. Pl. 3: ed. fol. 215, ed. quart. 275. *pl.* 257. July 1819, nom. cons.¹²

Evergreen or deciduous, branching, often stoloniferous shrubs with the aspect of *Vaccinium*. Leaves alternate, short-petioled, entire or toothed, membranaceous to coriaceous, often with glandular hairs; winter buds ovoid with about 3 outer scales. Flowers in axillary, usually few-flowered and sometimes much condensed racemes from buds of the preceding growing season, bracteate, the bracts persistent to deciduous; pedicels with (1 or) 2 bractlets. Calyx adnate to the ovary, 5-lobed, persistent. Corolla white, greenish to red, ovoid or campanulate, 5-lobed. Stamens 10, inserted on the base of the corolla; filaments short; anthers unappendaged on the back, each half narrowed upward into more or less of a tube and opening by a terminal pore or short slit, awnless, without disintegration tissue; pollen tetrads without viscin strands. Stigma more or less capitate and 5-angled; style straight; ovary inferior, 10-locular, each locule with a single axile, campylotropous ovule; disc conspicuous, on the surface of the ovary. Fruit a berry-like drupe with 10 smooth, 1-seeded lenticular nutlets (pyrenes), crowned by the persistent calyx lobes, black or blue, sometimes glaucous. (Including *Buxella* Small, *Decachaena* Torr. & Gray, *Lasiococcus* Small.) TYPE SPECIES: *G. buxifolia* HBK. (Named in honor of Joseph Louis Gay-Lussac, 1778–1850, eminent French chemist and physicist.) — HUCKLEBERRIES.

A genus of perhaps 50 species of eastern North America and of South America, with the center of diversity in southeastern Brazil; lacking in Central America and the West Indies. Three well-marked sections including six to nine species occur in eastern North America; the application of subgeneric categories to the South American species is not yet well worked out.

Section GAYLUSSACIA (§ *Eulussacia* Benth. & Hook.), includes two species of our area with clavate-stipitate gland hairs in which the glandular portion is usually without a conspicuous secretion pellicle. *Gaylussacia Mosieri* Small (*Lasiococcus Mosieri* (Small) Small), with conspicuously glandular-hirsute hypanthia, is a plant mostly of sandy bogs from western

¹² Conservation superfluous. *Adnaria* [odorata] Raf., 1817, against which *Gaylussacia* was conserved, has been shown by Camp to be *Styrax* [americanum Lam.]. See Castanea 6: 82. 1941 and Taxon 9: 75. 1960.

Florida and southwestern Georgia to eastern Louisiana. The widespread *G. dumosa* (Andr.) Gray (*Lasiococcus* Small), with inconspicuous short-stalked glands on the hypanthium, ranges from southern Florida northward mostly on the Coastal Plain to Newfoundland, and westward to eastern Louisiana, with scattered stations inland across all but northwestern Alabama, in Coffee County, Tennessee, in the mountains of northern Georgia, North Carolina and Virginia and West Virginia, and in Pennsylvania. Southward a plant of drier soils, northward the species usually occurs in bogs. Considerable variation occurs in the length of the hairs on the hypanthium, those of some collections appearing to be almost intermediate in length with *G. Mosieri*; *G. orocola* (Small) Camp, described from a single collection from Flat Rock, Henderson County, North Carolina, may be one of these. The variation and interrelationships of these three taxa need further study.

Section DECAMERIUM (Nutt.) Benth. & Hook. (§ *Decachaena* (Torr. & Gray) Sleumer), including in our area plants with the leaves bearing capitate sessile glands with a conspicuous golden secretion layer, and usually with the inflorescence bracts deciduous, is represented by *G. baccata* (Wangenh.) K. Koch ($2n = 24$), wide-ranging from Newfoundland to Manitoba, southward inland to Iowa, Kentucky, and northern Georgia, in which the leaves are golden-glandular on both leaf surfaces, and by three or four species in which the glands are confined to the lower leaf surface. *Gaylussacia ursina* (M. A. Curtis) Torr. & Gray ex Gray, with pubescent stamen-filaments, is a clear-cut forest species of the mountains of eastern Tennessee, western North Carolina and South Carolina, and northern Georgia. The relationship of *G. frondosa* (L.) Torr. & Gray ex Torr., a shrub to 2 m. high, confined mostly to the Coastal Plain from Florida to Louisiana and northward to southeastern New York, Massachusetts, and southern New Hampshire, to two similar stoloniferous shrubs, the very glaucous *G. nana* (Gray) Small (1–4 dm. high) and the very hairy and nonglaucous *G. tomentosa* (Gray) Small (to 1 m. high), both ranging from southern Georgia and Florida to southern Alabama, is uncertain. Camp tentatively maintained the two latter at the rank of species, suggesting that chromosomal counts might clarify the interrelationships (as in *Vaccinium* § *Cyanococcus*).

Section VITIS-IDAEA Benth. & Hook. includes only *Gaylussacia brachycera* (Michx.) Gray (*Buxella* Small), the box-huckleberry or juniperberry, a low, evergreen species completely lacking glandular hairs, which occurs in scattered localities on the coastal plain of Delaware and Maryland and on mostly north-facing slopes in Pennsylvania, southeastern West Virginia (the area of greatest abundance), eastern Kentucky, and eastern Tennessee. Most colonies seem to consist of single individuals (one in Pennsylvania some eight acres in extent estimated to be 1200 years old) which are largely self-sterile. (*Gaylussacia baccata* has also been observed to be self-sterile. The flowers in this species are homogamous and are cross-pollinated by *Apis* and various andrenid bees.)

Although Small considered the North American species to represent

three genera distinct from South American *Gaylussacia*, Camp has shown numerous interlocking relationships (e.g., the remarkable similarity of *G. Mosieri* and the Brazilian *G. pseudogaultheria* Cham. & Schlecht.). Camp concludes, in part, "Considered alone the North American material consists of three well-marked groups, but when critically examined each of these gives clear indication that it has been rather directly derived from South American material, having counterparts in the common plexus of the genus. . . . It is certainly clear that any separation into subgeneric categories on a geographic basis violates the fundamental phylogeny of the group."

On the basis of the 10-locular, 10-ovulate ovary and the fruit with 10 smooth, 1-seeded nutlets, *Gaylussacia* is sometimes segregated as a separate tribe, Gaylussacieae Small.

REFERENCES:

- Under family references see also BELL & BURCHILL, BERGMAN, and STANLEY; under *Vaccinium* see AMMONS & CORE and WELCH.
- CAIN, S. A., and J. E. POTZGER. A comparison of leaf tissues of *Gaylussacia baccata* (Wang.) C. Koch. and *Vaccinium vacillans* Kalm. grown under different conditions. *Am. Midl. Nat.* **14**: 97-112. 1933.
- . A comparison of leaf tissues of *Gaylussacia baccata* grown under different conditions. *Ibid.* **24**: 444-462. 1940.
- CAMP, W. H. Studies in the Ericales. I. The genus *Gaylussacia* in North America north of Mexico. *Bull. Torrey Bot. Club* **62**: 129-132. 1935.
- . Studies in the Ericales: A review of the North American *Gaylussacieae*; with remarks on the origin and migration of the group. *Ibid.* **68**: 531-551. 1941.
- . Studies in the Ericales: the search for *Adnaria odorata* Raf., and *Arbutus obtusifolius* Raf. *Castanea* **6**: 80-83. 1941. [*Adnaria* = *Styrax americanum* Lam., not *Gaylussacia*; *Arbutus* = *Vaccinium arboreum* Marsh.]
- COVILLE, F. V. The threatened extinction of the box huckleberry, *Gaylussacia brachycera*. *Science* **50**: 30-34. 1919.
- DE WILDEMAN, E. *Gaylussacia resinosa* Torrey et Gray. *Ic. Sel. Horti Thenen-sis* **4**: 139-141. 1903. [*G. baccata*.]
- FERNALD, M. L. The northern variety of *Gaylussacia dumosa*. *Rhodora* **13**: 95-99. 1911. [Var. *Bigeloviana* Fern.]
- GRAY, A. *Chloris boreali-americana*. *Mem. Am. Acad. Arts Sci.* **II. 3**: 1-56. pls. 1-10. 1848. [*G. ursina*, 49-55, pl. 10.]
- GRAY, F. W. Scores of stations for *Gaylussacia brachycera* in West Virginia. *Torrey* **22**: 17, 18. 1922.
- LOVELL, H. B. Pollination of the Ericaceae: V. *Gaylussacia baccata*. *Rhodora* **42**: 352-354. 1940.
- MACKENZIE, K. K. The scientific name of our common huckleberry. *Torrey* **7**: 60. 1907. [*G. baccata* (Wangenh.) K. Koch.]
- ROBINSON, B. L. A blue-fruited huckleberry. *Rhodora* **2**: 81-83. 1900. [*G. resinosa* f. *glaucocarpa* = *G. baccata* f. *glaucocarpa* (Robins.) Mackenz.]
- SIMS, J. *Vaccinium buxifolium*. *Bot. Mag.* **23**: pl. 928. 1806; *Vaccinium dumosum*. **27**: pl. 1106. 1808; *Vaccinium resinsum* (β.). **32**: pl. 1288. 1810. [*G. buxifolia*, *G. dumosa*, *G. baccata*.]

- SLEUMER, H. Vaccinioideen-Studien. Bot. Jahrb. **71**: 375-510. 1941. [*Gaylussacia*, 382-385.]
- SMALL, J. K. A new gopher-berry from the Gulf States. *Torrey* **27**: 35, 36. 1927. [*G. Mosieri*.]
- WHERRY, E. T. The box huckleberry as an illustration of the need for field work. Bull. Torrey Bot. Club **61**: 81-84. 1934. [Summarizes data on distribution, etc.]



Wood, Carroll E. 1961. "The Genera of Ericaceae in the Southeastern United States." *Journal of the Arnold Arboretum* 42(1), 10–80.

<https://doi.org/10.5962/p.324673>.

View This Item Online: <https://www.biodiversitylibrary.org/item/33618>

DOI: <https://doi.org/10.5962/p.324673>

Permalink: <https://www.biodiversitylibrary.org/partpdf/324673>

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Missouri Botanical Garden

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

Rights Holder: Arnold Arboretum of Harvard University

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.