

THE GENERA OF MYRICACEAE IN THE SOUTHEASTERN UNITED STATES <sup>1</sup>

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MYRICACEAE Blume, Fl. Jav. Myric. 3. 1829, nom. cons.

(WAX-MYRTLE FAMILY)

Shrubs or small trees, usually aromatic and resinous, frequently of swampy, acid soils; branches terete, occasionally prostrate; roots fibrous, with numerous nitrogen-fixing nodules. Leaves with revolute vernation, alternate, simple, petiolate, entire, serrate to irregularly dentate, rarely pinnatifid, reticulately veined, generally with aromatic oil or resin glands, persistent or persisting until the next year's growth or deciduous, the leaf scars usually elevated, semiorbicular with three vascular trace scars; stipules usually absent, present only in *Comptonia* and there deciduous. Plants dioecious or occasionally monoecious. Flowers imperfect or rarely perfect, vernal, borne in usually dense unisexual aments, occasionally with aments androgynous or with functionally perfect proterogynous flowers. Staminate flowers subtended by a primary bract, the bract usually ovate to ovate-lanceolate and completely inclosing the stamens; perianth absent; stamens 2-8(-20), the filaments filiform, free or fused near the base; anthers dorsifixed, 2-locular, erect, introrse, with longitudinal dehiscence; pollen grains usually 3-porate,  $\pm$  suboblate to subspheroidal. Carpellate flowers subtended by a usually ovate primary bract, secondary bracts present or absent, linear to lanceolate, usually 2 to 4, rarely more, the bracts persisting and elongating in fruit; perianth absent. Gynoecium bicarpellate, rarely tricarpellate, the ovary superior, 1-locular, the ovule solitary, basal, erect, orthotropous, with a single integument, style very short, divided into two, rarely three, stigmas which exceed the primary bract. Fruit drupaceous or nutlike,  $\pm$  dry, often covered with variously

<sup>1</sup>Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his continuing help and editorial suggestions. Professor Ernst C. Abbe has kindly examined the illustrations and has offered valuable suggestions concerning the interpretation of the inflorescences found in the Myricaceae. The illustrations, the work of Miss Virginia Savage, were prepared from materials collected by R. J. Eaton, N. G. Miller, C. E. Wood, Jr., and the author. Mrs. Nancy Dunkly has helped greatly with the preparation of the manuscript.



shaped protuberances, smooth, lustrous to glandular, frequently with a waxlike coating, inclosed or not by persistent bracts. Seed erect; seed coat thin; endosperm a single layer of cells; embryo straight, the cotyledons  $\pm$  fleshy, plano-convex, the radicle superior, short. Base chromosome number 8. (Galeaceae Bubani.) TYPE GENUS: *Myrica* L.

A small family of one, two, or three genera including approximately 40 to 50 species, mainly in mild-temperate to subtropical regions of the world, including southern Africa. The number of genera comprising the Myricaceae remains in question. If *Myrica* is treated in the broad sense, the family consists only of the one genus (Gray, Lessons Man. Bot., 1887; Engler, Nat. Pflanzenfam. III. 1: 27. 1894; Rendle, 1925). Some workers (Rehder, Man. Cult. Trees Shrubs, ed. 2. 1940; Bailey, Man. Cult. Pl., 1949; Fernald, Gray's Man. Bot. ed. 8. 1950; Melchior, 1964; Hutchinson, 1967) have preferred to recognize the monotypic genus *Comptonia* as distinct from *Myrica*, mainly because of the presence of stipules and of secondary bracts that elongate and persist in the nutlike fruit. Still other workers (e.g., Chevalier, 1901; Radford, Ahles & Bell, Man. Vasc. Fl. Carolinas, 1968) have preferred to recognize the two subgenera of *Myrica* as distinct genera. The difficulty of generic delimitation within the family is not in the recognition of the three taxa but in the rank to be assigned to each. The poorly known *Canacomyrica* Guill. is attributed to the Myricaceae but differs in having a pendulous ovule and bifid stigmas, characters which suggest that it belongs to another family.

Members of the Myricaceae are shrubs or small trees with fragrant, often glandular-dotted leaves, and generally with unisexual aments and a one-locular ovary with a single, erect, orthotropous ovule. The monotypic *Comptonia* and *Myrica*, with four species of subg. *Morella* and a single species of subg. *Myrica*, occur in our range. Two species of *Myrica* (one of each subgenus) are restricted to the Pacific Coast of the United States. Several species described from Central America and the West Indies warrant further study, since some may ultimately prove to be conspecific with those of the United States.

The Myricaceae are presently considered by most workers to be the only family of the order Myricales, although Hjelmqvist (1948) placed the family in the Juglandales. The order Myricales is characterized by the unilocular ovary, the single orthotropous ovule, and the short style with two stigmas. On the basis of vegetative, floral, and fruiting similarities the Myricales are most closely allied with the Garryales and Leitneriales. Cronquist (1968), however, places the Myricales peripheral to the Fagales and Juglandales, while Takhtajan (1969) considers the Myricales to have much in common with the Casuarinales and Betulaceae as well as with the Juglandales.

Initial studies of the staminate inflorescences in the Myricaceae by E. C. Abbe have shown them to be panicles (*Myrica*) or by reduction a lax primary axis bearing primary bracts with four or fewer stamens in the axils (*Comptonia*, *M. Gale*). The most complex panicles are found



in *M. javanica* Blume, of Asia, while New World species have more reduced panicles indicative of their greater specialization. A progressive reduction was observed in the complexity of branching and in an often accompanying reduction in the number of bracts and stamens. Concomitant studies of the xylem anatomy of the Myricaceae by L. B. Abbe confirmed the advanced status of *Comptonia* within the family. In *Comptonia* the single-pore condition in a large number of the secondary vessel elements contrasts with the less specialized many-perforate end walls of those of *M. Gale*.

The Myricaceae is an old family with a fossil record from the Upper Cretaceous to the present. Members of this family apparently were much more numerous and widespread than the distribution of the extant species indicates. During the Tertiary the Myricaceae were apparently more abundant in Europe than in the United States.

Of little primary economic importance, the Myricaceae because of their relative abundance in swampy areas serve as a food source for certain wildlife. Most members of the family have nitrogen-fixing root nodules that not only enrich the soil in which they are growing, but give them a competitive advantage over other plants in areas low in combined nitrogen.

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#### KEY TO THE GENERA OF MYRICACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Shrubs or trees, dioecious or occasionally monoecious; leaves simple, usually lacking stipules, often resinous dotted and fragrant; aments usually unisexual; flowers bracteate; fruit drupaceous or nutlike, frequently with a waxlike coating.*

Leaves entire, dentate, serrate or slightly incised, lacking stipules; fruits with or without a waxlike covering or resinous dotted, bracts 2 to 4, not longer than the fruit or absent. . . . . 1. *Myrica*.

Leaves pinnatifid, with semicordate stipules; fruits glabrous, nutlike, bracts 6 to 8, linear-subulate, persistent, longer than the fruit. . . . . 2. *Comptonia*.

#### 1. *Myrica* Linnaeus, Sp. Pl. 2: 1024. 1753; Gen. Pl. ed. 5. 449. 1754.

Shrubs or small trees of dry or swampy areas; branches terete, usually glandular dotted, slender, the lower ones occasionally prostrate; buds small, scaly. Leaves persisting until the following year's growth or deciduous, entire, serrate, sparingly dentate near the apex [pinnately lobed], glandular dotted, aromatic when crushed, membranaceous to coriaceous; stipules lacking. Plants usually dioecious, infrequently monoecious. Flowers usually imperfect, borne in aments. Staminate aments ellipsoid to cylindric, more or less erect, sometimes appearing spikelike; flowers solitary in the axils of bracts, the primary bract generally ovate; stamens 2-20; filaments free or often united near the base; rudimentary gynoecium occasionally present. Carpellate flowers in ovoid to cylindric,



sometimes interrupted aments; stigmas two, exceeding the ovate primary bract; style short; ovary sessile, subtended by 2 to 4 secondary bracts, these sometimes absent, persisting and enlarging in fruit in *M. Gale*. Fruit drupaceous,  $\pm$  dry, globose to ovoid, often covered with variously shaped protuberances, usually with a waxy coating that becomes white in drying, infrequently glandular dotted. (*Gale* Duham., nom. superfluum; *Morella* Lour.; *Faya* Webb & Berthel.). LECTOTYPE SPECIES: *M. Gale* L.<sup>2</sup>; see Britton, N. Am. Trees, 209. 1908; Britton & Brown, Illus. Fl. No. U.S. ed. 2. 1: 584. 1913; Abrams, Illus. Fl. Pacific States 1: 508. 1923; Hitchcock & Green, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 191. 1929. (Name Latin, adopted from Greek *myrike*, the name of tamarisk.) — WAX MYRTLE, BAYBERRY, SWEET GALE.

Subgenus MORELLA (Lour.) Engler (*Cerophora* Raf.; *Fayana* Raf.; *Faya* Webb & Berthel.; *Cerothamnus* Tidestrom; *Myrica* sect. *Morella* (Lour.) Benth. & Hooker; *Myrica* sect. *Cerophora* (Raf.) Chevalier), with perhaps 25 to 30 species distributed mainly in temperate regions of the world but also extending into Latin America and Africa, is represented in our area by four species in two sections. Plants in this subgenus have the aments borne on old wood, mainly below the leaves; the bracts of the staminate flowers are shorter than the stamens; and the ovary and fruit are globose at maturity with numerous protuberances which usually have heavy waxy coating that frequently dries white. In his revision of the Myricaceae, Chevalier divided *Myrica*, *sensu* Chev., into sect. MORELLA, of eastern and southern Asia and the Malayan Archipelago; sect. FAYA, of western and southern coastal United States and the Canary Islands, Madeira, and the Açores; and sect. CEROPHORA, of Africa and temperate to tropical America. Four species of subg. MORELLA are found in our range: *M. inodora* of sect. FAYA and *M. pensylvanica*, *M. cerifera*, and *M. heterophylla* of sect. CEROPHORA.

Section CEROPHORA,<sup>3</sup> distinguished by simple catkins, spikelets reduced to a single flower, solitary or in threes in the axil of a bract, and fruits 1–5 mm. in diameter, usually with a waxy covering and not fleshy, consists of 25–30 species of both the Old and New Worlds. Found mainly near the coast or on the Coastal Plain, *Myrica pensylvanica* Loisel.,  $2n = 16$ , northern bayberry, is distributed from Newfoundland and Nova Scotia south to North Carolina and locally to Ohio. A low shrub or small tree, this species is distinguished by whitish-gray or drab branches; deciduous to subpersistent, membranaceous, elliptic, oblanceolate or obovate leaves, mostly lacking resin glands on the upper surface; and dense-

<sup>2</sup> Most authors have followed the selection of *M. Gale* as the lectotype of *Myrica*, although Hylander (1945) designated *M. cerifera* L. as the lectotype in place of *M. Gale*, on the mistaken assumption that *Gale* Duhamel (attributed by Chevalier, 1901, to Adanson) was a legitimate name and that *M. Gale* had thus been removed from *Myrica*.

<sup>3</sup> Chevalier divided sect. CEROPHORA into two subsectional categories, Americanae and Africanæ, but without indication of rank, and they apparently have not been assigned one by a subsequent author (cf. ICBN, 1966, Art. 35).



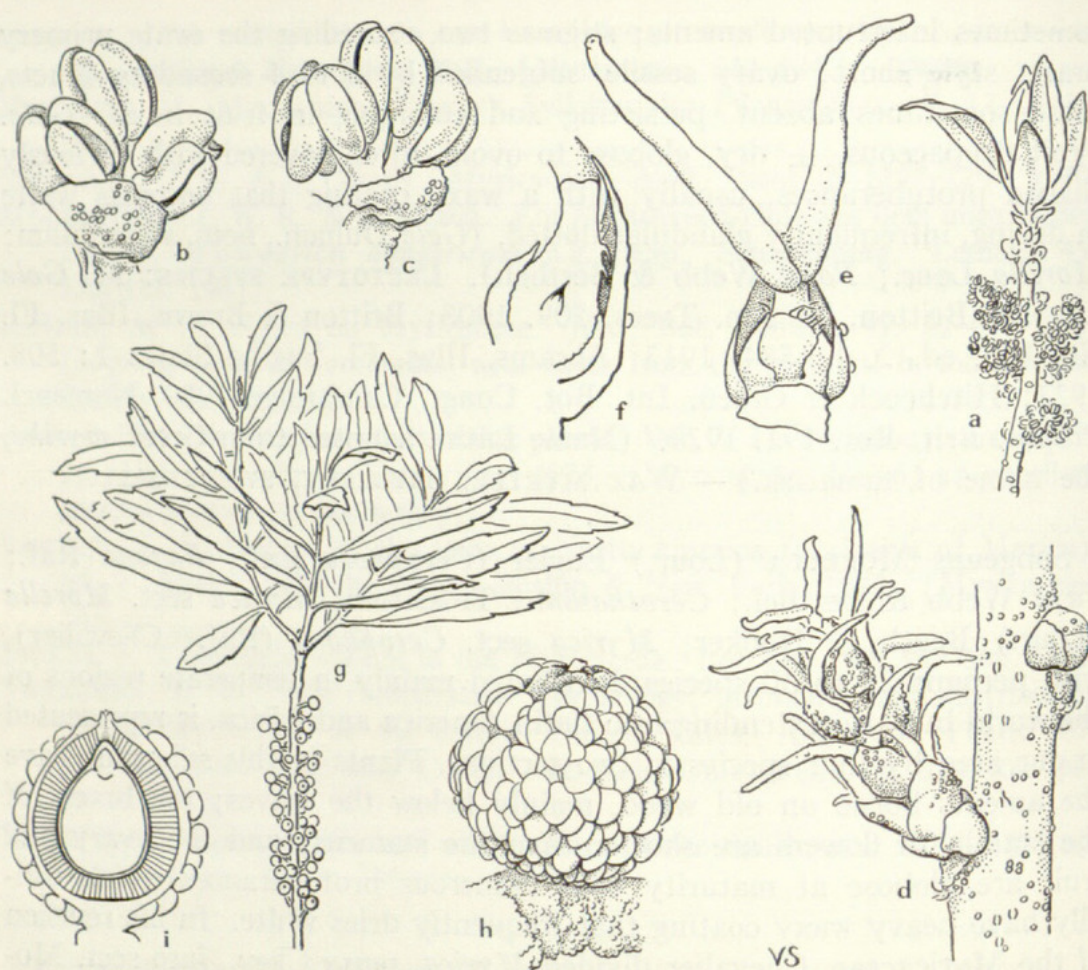


FIGURE 1. *Myrica* subg. *Morella*. a-f, *M. pensylvanica*: a, branchlet with staminate inflorescences,  $\times 1$ ; b, staminate flower,  $\times 10$ ; c, staminate flower, lateral view, showing filaments,  $\times 10$ ; d, carpellate inflorescence,  $\times 6$ ; e, carpellate flower with bracts,  $\times 15$ ; f, semidiagrammatic longitudinal section of carpellate flower to show ovule,  $\times 20$ . g-i, *M. cerifera*: g, fruiting branchlet,  $\times 1/2$ ; h, fruit,  $\times 8$ ; i, semidiagrammatic longitudinal section of fruit, showing endocarp and embryo,  $\times 8$ .

ly pubescent young fruits. It reportedly hybridizes with *M. cerifera* to produce *M.  $\times$  Macfarlanei* Youngken.

A large shrub or small tree, *Myrica heterophylla* Raf., myrtle, evergreen bayberry, or wax myrtle, occurs along the Coastal Plain in thickets and woods from southern New Jersey to Florida and west to Louisiana. The features used to identify this species include its blackish branches; pilose leafy branchlets; coriaceous, evergreen, elliptic to obovate leaves; and glabrous young fruits. On the basis of its nearly glabrous branchlets Fernald (1938) recognized var. *Curtissii* (Chev.) Fern. (*M. Curtissii* Chev.), but later workers (Little, 1953) have not accepted it as distinct. Gleason & Cronquist (Man. Vasc. Pl., 1963) question the recognition of this taxon and suggest that it may be a hybrid of *M. pensylvanica* and *M. cerifera*, a hypothesis that should be investigated.

The southern bayberry, *Myrica cerifera* L. (*Morella cerifera* (L.) Small, *Cerothamnus ceriferus* (L.) Small, *Myrica carolinensis* Mill., *C.*



*carolinensis* (Mill.) Tidestrom),  $2n = 16$ , occurs in swampy or sandy soils in low, acid prairies, thickets and woods, principally along the Coastal Plain from southern New Jersey to southern Florida, west to eastern Texas and southeastern Oklahoma, and north to Arkansas. It also occurs in Bermuda, the Greater Antilles, Mexico, and Central America. Taxonomically important characters are the heavily resinous-glandular glabrescent branchlets; narrowly oblanceolate, coriaceous, persistent leaves, abundantly resinous-glandular on the upper surface; and glabrous fruit. The fruit is eaten by numerous coastal birds, including quail and apparently wild turkey in some areas.

Although *Myrica pusilla* Raf. (*Cerothamnus pumilus* (Michx.) Small),  $2n = 16$ , was recognized as a distinct species by both Fernald (Gray's Man. Bot. ed. 8, 1950) and Gleason (New Britton & Brown Illus. Fl. Northeast. U.S. Vol. 2, 1963), Radford, Ahles, & Bell (Man. Vasc. Fl. Carolinas, 1967) treated it as *M. cerifera* var. *pumila* Michx. It appears that *M. pusilla* is merely a smaller xeric form of *M. cerifera* that does not merit specific status (Thieret, 1966). Varietas *pumila* occurs on dry, sandy pinelands and prairies from eastern Texas and Louisiana, east to Florida and north to North Carolina. The status of this questionable variety should be investigated more thoroughly.

Section FAYA, characterized by simple or branched aments, carpellate spikelets with several flowers, of which only some develop, and fruits 4–6 mm. in diameter, includes only three species. *Myrica inodora* Bartr. occurs in our range; *M. californica* Cham. occurs only along the west coast of the United States from Washington south to California; and *M. Faya* Ait. is restricted to Madeira, the Canary Islands, the Açores, and Portugal (where it is naturalized or possibly indigenous). This type of distribution of closely related species is further evidence of the relict nature of the genus.

Lacking the almost characteristic myricaceous scent, *Myrica inodora* Bartr. (*Morella inodora* (Bartr.) Small; *Cerothamnus inodorus* (Bartr.) Small), odorless bayberry, occurs sparingly in the Gulf Coast pineland swamps from southeastern Louisiana to northwestern Florida. This evergreen shrub is recognized by its smooth, reddish-brown branchlets that are scurfy tomentose when young but later pubescent to glabrous; by its oblong-obovate to ovate coriaceous more or less glandular leaves with the margin usually entire, rarely with a few serrations apically; and by its glabrous fruit.

Subgenus MYRICA (subg. *Gale* [Duham.] Engler; *Gale* Duham.; *Cerophora* subg. *Galestis* Raf.; *Angeia* Tidestrom) includes *M. Gale* L. (*Gale palustris* (Lam.) Chev.),  $2n = 48$ , ca. 96, sweet gale, of northwestern Europe, northern North America, and northeastern Asia, and *M. Hartwegii* S. Wats., of the Sierra Nevada in California. Found principally in swampy areas, *M. Gale* is distributed in North America from Labrador to Alaska, south to Newfoundland, Long Island and Pennsylvania, west to Michigan, Minnesota, Wisconsin, and Washington and Oregon. It reaches our range in Tennessee and in bogs, now largely drained, in Henderson



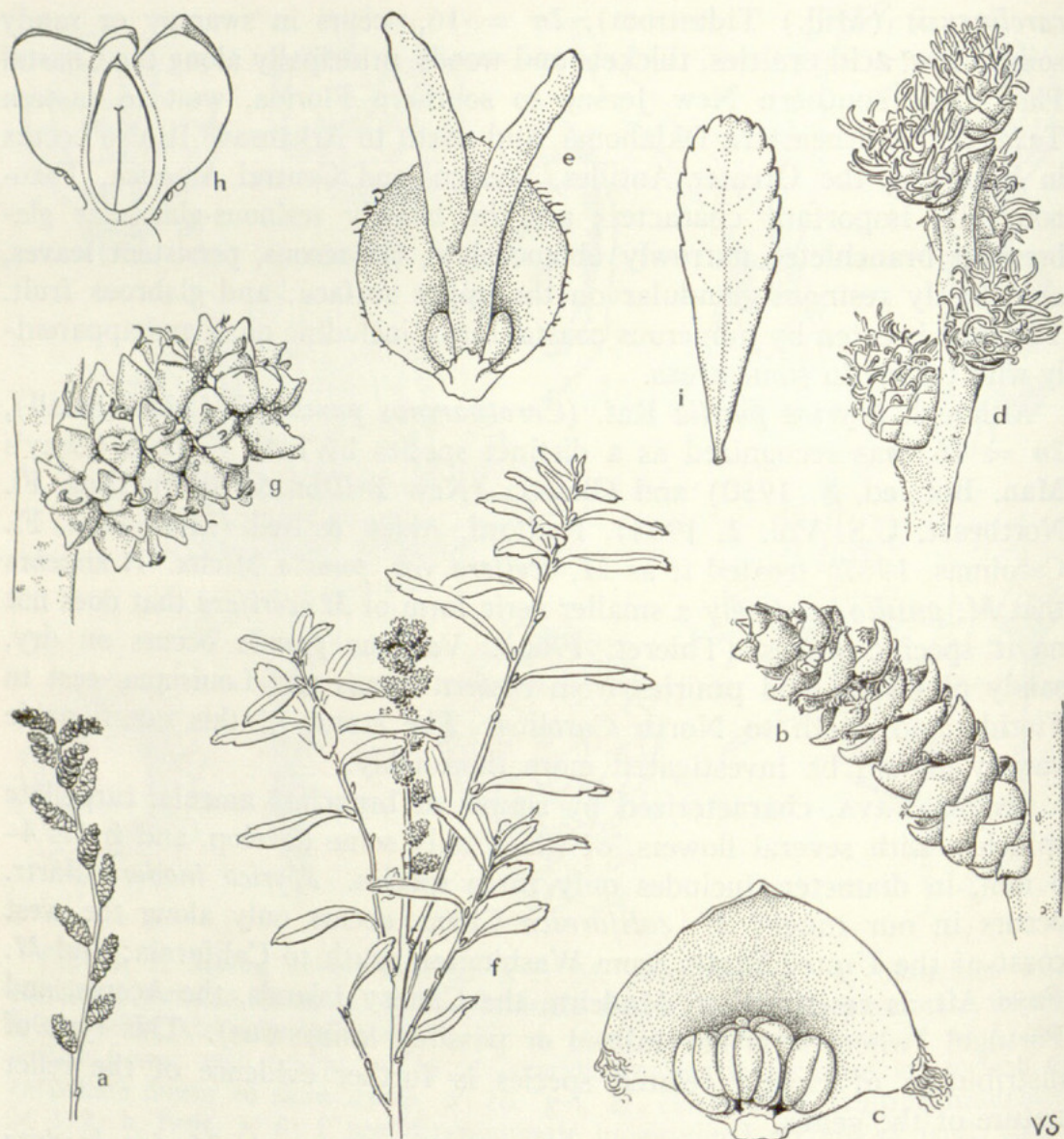


FIGURE 2. *Myrica* subg. *Myrica*. *M. Gale*: a, branchlet with staminate inflorescences,  $\times 1/2$ ; b, staminate inflorescence,  $\times 3$ ; c, staminate flower with bract,  $\times 10$ ; d, branchlet with carpellate inflorescences,  $\times 4$ ; e, carpellate flower with bract and two lateral secondary bracts,  $\times 25$ ; f, habit with mature fruits,  $\times 1/2$ ; g, mature fruits of a single carpellate inflorescence,  $\times 4$ ; h, semidiagrammatic longitudinal section of fruit, showing fleshy secondary bracts and embryo,  $\times 12$ .

County, North Carolina. The species, as well as the subgenus, is characterized by aments borne near the summit of the branchlets of the preceding year; by the bract of the staminate flower longer than the stamens; by the smooth fruit each flanked by two accrescent, more or less fleshy secondary bracts; and by the lack of a heavy wax deposit on the surface of the fruits. The considerable variation in the amount of pubescence has led to the recognition of var. *subglabra* (Chev.) Fern. in eastern and var. *tomentosa* C. DC. in Pacific North America and Eurasia.

The few chromosome counts suggest that European populations of *M. Gale* are hexaploids ( $2n = 48$ ), while those from western North America



are apparently dodecaploids ( $2n = \text{ca. } 96$  in plants from the Queen Charlotte Islands). Further counts are needed throughout the range of the species to determine the extent and levels of polyploidy and its significance.

An interesting phenomenon in *M. Gale* is the great plasticity in the sexes of individual flowers as well as individual plants. Three types of monoecious plants occur (Davy & Gibson, 1917): both staminate and separate carpellate aments may occur on the branchlets of a single plant; the branchlets may produce androgynous aments with staminate flowers on the lower part of the ament; or in some aments perfect proterogynous flowers capable of producing fruit can be found. In addition, the sex of a plant of *M. Gale* may vary from one year to the next, from undetermined causes.

Most, if not all, species of *Myrica* have numerous nodules on the roots, including the adventitious ones arising from prostrate stems or rhizomes. Recent investigations by Bond have clearly demonstrated that the nodules, especially those of *M. Gale*, are accumulators of nitrogen. Bond (1958) postulated that the nitrogen fixing nodules of *Myrica* species may have been the original and principal source of symbiotic nitrogen in temperate regions following the Pleistocene.

Known best to the nonbotanist for their role in candle making, *Myrica cerifera*, *M. pensylvanica*, *M. heterophylla*, and to a lesser extent, *M. inodora* were sought by early settlers of the eastern United States. The fruits were gathered in the fall and placed in boiling water, the waxlike coating (a fat composed mainly of palmitin or palmitic acid) then melting and rising to the surface was skimmed off for use in candle making. Today most bayberry candle fat is imported into the United States from South America. In the eastern United States the making of bayberry candles with locally gathered fat has become a novelty or tourist attraction. In Europe bayberry fat is used in the manufacture of soap, probably for its pleasant scent.

Of limited economic importance, the buds and mainly the fruits serve as a food source for wildlife, especially birds. Muskrats have been observed feeding upon the fruits of *M. Gale*, and the buds and aments are eaten by sharp-tailed deer. The bark of *Myrica cerifera* and *M. pensylvanica* were once used in moderate amounts as an astringent and in larger amounts as an emetic. The bark in the form of a powder or in a decoction was also used to treat inflammations, ulcers, and many other internal problems. It has been reported that the leaves can be used as a substitute for bay leaves (*Laurus nobilis* L.) in flavoring stews and soups. Because of their habit of growth various species are effective in controlling erosion. Several species are attractive ornamental shrubs in cultivation.

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## 2. *Comptonia* L'Heritier ex W. Aiton, Hort. Kew. 3: 334. 1789.

Low-growing shrubs; branches terete, brown, villous to minutely puberulent, fragrant. Leaves appearing after flowering, pinnatifid with rounded lobes, membranaceous, linear-lanceolate, deciduous or persisting until the following spring, glabrous to densely pubescent, short-petiolate; stipules present, semicordate becoming subfoliaceous, deciduous. Plants monoecious or dioecious; flowers usually imperfect, borne in axillary aments. Staminate flowers in cylindrical, flexuous aments near the apex of the branchlets; primary bract cordate, reniform; stamens 3-8; filaments free. Carpellate flowers generally in erect globose-ovoid aments,



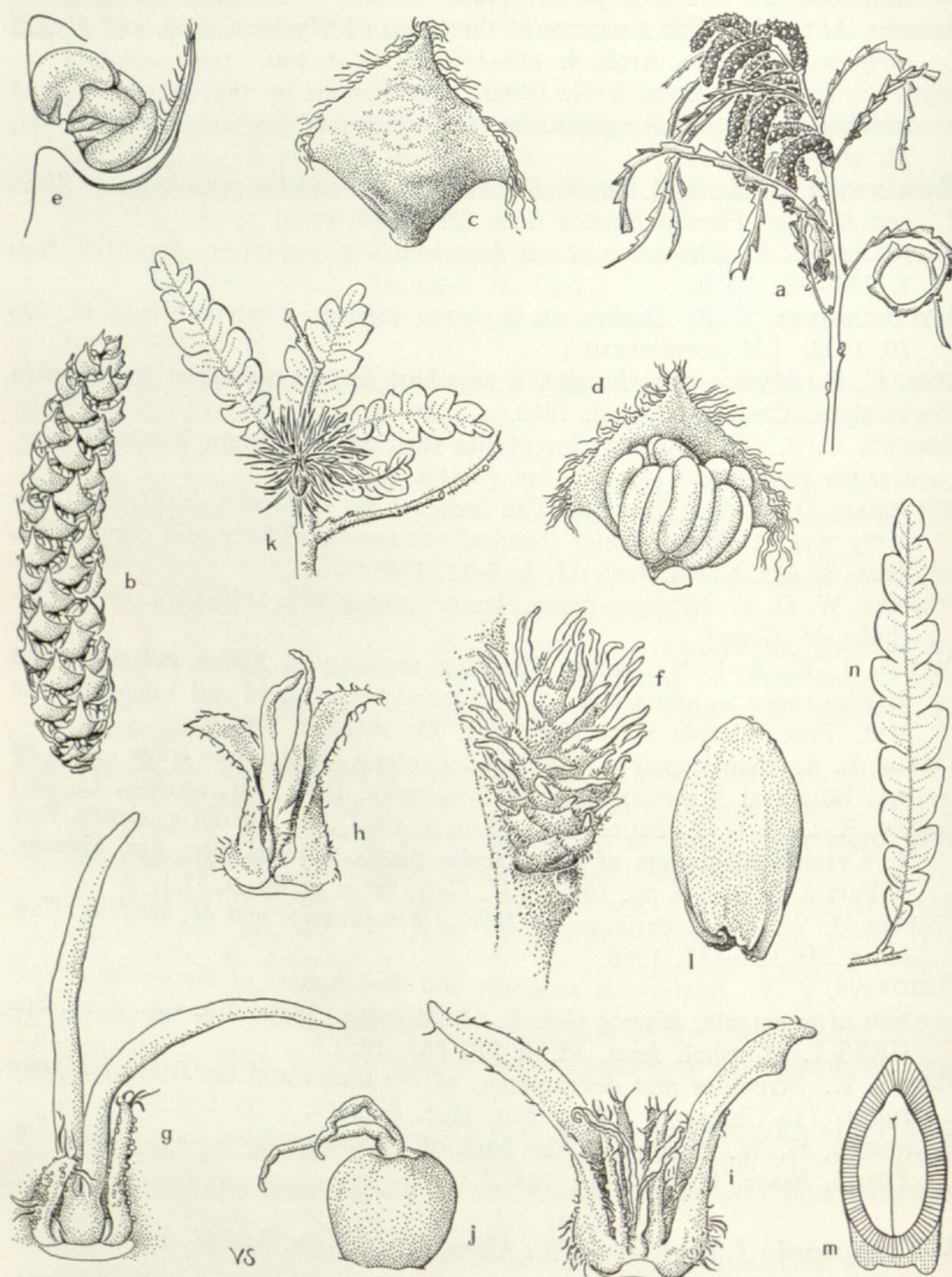


FIGURE 3. *Comptonia*. *C. peregrina*: a, branchlet with staminate inflorescences,  $\times 1/2$ ; b, staminate inflorescence,  $\times 3$ ; c, bract of staminate flower,  $\times 12$ ; d, staminate flower with bract,  $\times 12$ ; e, lateral view of staminate flower in partial section,  $\times 12$ ; f, carpellate inflorescence,  $\times 6$ ; g, carpellate flower at time of pollination,  $\times 25$ ; h, carpellate flower following fertilization showing development of primary bracts,  $\times 12$ ; i, carpellate flower after fertilization showing development of both primary and secondary bracts,  $\times 12$ ; j, young fruit with semipersistent styles,  $\times 6$ ; k, branchlet with mature fruit and accessory bracts,  $\times 1$ ; l, mature fruit,  $\times 6$ ; m, semidiagrammatic longitudinal section of mature fruit to show embryo,  $\times 6$ ; n, mature leaf,  $\times 1$ .



usually on older wood, the primary bract usually ovate, pubescent, at least near the base; each flower subtended by 6–8 minute linear to acicular secondary bracts that persist and elongate in fruit (see FIGURE 3, g–i, k). Fruit a small ovoid-oblong, smooth, shining nut. TYPE SPECIES: *C. asplenifolia* (L.) L'Her. ex W. Ait. = *C. peregrina* (L.) Coult. (Name commemorating H. Compton, 1632–1713, an amateur horticulturist and supporter of botany, who also served as Bishop of London.) — SWEET FERN.

A single extant species, *Comptonia peregrina* (L.) Coult.,  $2n = 32$ , sweet fern, found on poor, often rather dry soils in woodlands, clearings, pastures, and pine barrens from Nova Scotia to Saskatchewan, south to Virginia, western North Carolina (but also in four counties in the lower Piedmont), extreme western South Carolina, and locally in northern Georgia and Tennessee, Ohio, northwestern Indiana, Illinois and Minnesota. The rather attractive low shrub with its fragrant aroma when crushed has been separated into two varieties. The questionably distinct var. *asplenifolia* (L.) Fern., of the Coastal Plain pinelands or pine barrens from Long Island, New York, to Virginia, is characterized by the minutely puberulent branchlets, sparsely short-puberulent or glabrous leaves, and fruits 3–4 mm. long. The more northern and inland var. *peregrina* has more or less pilose branchlets, pilose leaves, and fruits 4–5 mm. long.

The six to eight secondary bracts associated with a single pistillate flower suggest that the solitary flower is derived by reduction from a few-flowered cyme. The inner secondary bracts would be the only grossly observable remnants of the cyme. A second possibility is that the inner secondary bracts are actually modified perianth parts that are completely lacking in *Myrica*. A careful anatomical study of the flowers and aments is needed.

*Comptonia peregrina* is the only survivor of a genus that had perhaps a dozen species in the Eocene and Oligocene. Berry (1906) postulated that *Comptonia* developed in the Upper Cretaceous as a branch from *Myrica* stock, but supporting evidence is lacking. Numerous Tertiary fossils of *Comptonia* clearly demonstrate that several species once occupied regions throughout much of the temperate world. In European Tertiary deposits, *C. difformis* (Sternh.) Berry is the most common fossil species of the genus (Kotlaba, 1967).

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<https://doi.org/10.5962/bhl.part.9115>.

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