

THE GENERA OF HAEMODORACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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HAEMODORACEAE R. Brown, Prodr. Fl. Nov. Holland 1:
299. 1810, nom. cons.
(BLOODWORT FAMILY)

Perennial [or rarely annual], rhizomatous and often stoloniferous herbs; above-ground stem simple, terminating in an inflorescence; roots fibrous; sap often red or orange. Stems, inflorescence branches, and floral tubes often covered with simple [branched or glandular] trichomes. Leaves alternate, mostly basal, *Iris*-like, linear [or narrowly elliptical], flattened [or subcylindrical], 2-ranked, sheathing below, folded lengthwise above, with the folded portions becoming fused together (see FIGURE 2, b-e). Inflorescences much-branched, many-flowered, loose or condensed cymes or corymbs [panicles or racemes, rarely solitary flowers] terminating the aerial stem and exceeding the leaves; bracts present, often conspicuous and persistent. Flowers regularly [or irregularly] symmetrical, 3-merous, the insertion of the perianth and androecium epigynous, perigynous [or hypogynous]. Tepals 6 in 2 whorls [or 1 whorl], \pm equal to unequal, free to level of insertion on the ovary [or united into a tube that may be split along one side], valvate in aestivation, persistent in fruit. Androecium of 6 or 3 stamens [or some reduced to staminodes]; filaments elongate [or very short], free to level of insertion on ovary [or adnate to perianth tube]; anthers 2-loculate, basifixed, dehiscing introrsely by longitudinal slits, often basally sagittate [sometimes also apiculate]; tape-tum amoeboid; pollen grains produced successively. Gynoecium of 3 united carpels; ovary inferior or half-inferior [or superior], 3-locular with

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The illustration of *Lachnanthes* was drawn by Virginia Savage under the supervision of C. E. Wood, Jr., who also collected the material on which it is based. Karen S. Velmure drew the plate of *Lophiola* under my direction from material collected by R. E. Umber and me.

I want to thank Professor Wood for his continuing advice and suggestions and for information about the correct name of *Lachnanthes carolina*. The manuscript was typed by Beverly Vincent.

axile placentae or 1-locular with parietal placentae above and 3-locular with axile placentae below; style 1, undivided [or 3-parted above], elongate [to short]; stigmatic area terminal, very small; ovules orthotropous or anatropous, crassinucellar, few [or 1] or numerous in each locule, arranged in vertical rows or around the margin of a peltate placenta [or covering it]. Fruit a loculicidal [or septicidal or septifragal] capsule [or rarely indehiscent]. Seeds discoid and peltate or elongate and variously curved [or ovoid or flattened]; endosperm present, helobial in development. Embryo sac development of the *Polygonum* type. TYPE GENUS: *Haemodorum* J. E. Smith.

The subfamilial classification and the number of genera included in the family vary considerably with different authors. In the recent worldwide review by Geerinck, two tribes, 13 genera, and about 76 species were recognized. Six genera are monotypic, and only three have more than ten species. Five genera are restricted to Oceania (particularly Australia), three to South Africa, two to eastern North America, and two to South America; one is widespread from Bolivia and Brazil to Cuba and Mexico. *Lachnanthes* and *Lophiola*, both probably monotypic, occur in the southeastern United States.

The nomenclatural history of the family is too involved to give in detail,² but the following account is relevant to the discussion of the genera in the southeastern United States. The family was established by Robert Brown, who divided it into three unnamed sections, with *Haemodorum* in the first, *Conostylis* R. Br. and *Anigozanthos* Labill. in the second, and *Phlebocarya* R. Br. in the third. Bentham, in Volume 6 of the *Flora Australiensis* (1873), placed the genera previously assigned to the Haemodoraceae in tribes Haemodoreae and Conostylideae ("Conostyleae") of the Amaryllidaceae. In the *Genera Plantarum*, however, Bentham & Hooker recognized the Haemodoraceae, considering the family to be composed of 26 genera in four tribes, Euhaemodoreae, Conostylideae, Ophiopogoneae, and Conanthereae. As delimited by Bentham & Hooker, the family was not a natural assemblage. Pax (and Pax & Hoffmann), in both editions of Engler & Prantl's *Pflanzenfamilien*, restricted the Haemodoraceae largely to the genera previously referred to tribe Haemodoreae, placing tribes Conostylideae and Conanthereae in the Amaryllidaceae and tribe Ophiopogoneae in the Liliaceae. Hutchinson (1973) disagreed with Pax, saying, "After a careful examination of all the genera of both families I cannot agree with this treatment, and I am firmly of the opinion that the two tribes [Haemodoreae and Conostylideae] should be again associated to form the Haemodoraceae. Thus constituted, but with the genus *Aletris* L. removed to the Liliaceae, the family is natural and homogeneous, not only in its facies but in its general distribution."

² See table in Geerinck (1969) for an extremely useful outline of the genera that have been included in the Haemodoraceae and Hypoxidaceae, with the taxonomic disposition of each genus by family, subfamily, and tribe from seventeen different works.

Conanthera and related genera were placed by Hutchinson in the segregate family Tecophilaeaceae (Liliales). Geerinck's concept of the family is essentially the same as Hutchinson's, except that Geerinck questionably excludes *Lanaria* Aiton from the Haemodoraceae and places *Lophiola* in tribe Haemodoreae instead of tribe Conostylideae. Melchior returns to the broad concept of the family and recognizes three tribes, Haemodoreae, Conostylideae, and Conanthereae.

Lachnanthes clearly belongs to tribe Haemodoreae and, on morphological grounds, seems to be most closely related to *Haemodorum* (20 species of Oceania) and *Dilatris* Berg. (five species of South Africa). The relationships of *Lophiola*, however, are not clear; it has often been included in tribe Conostylideae. The other members of this tribe are confined to southwestern Australia, and *Lophiola* really does not have much in common with them. Geerinck places *Lophiola* next to *Lachnanthes* in tribe Haemodoreae. While these two genera are superficially quite similar, the morphological differences between them are numerous, and it seems doubtful that they are closely related. De Vos (1963) has recently pointed out numerous similarities between *Lophiola* and *Lanaria*, a monotypic genus of South Africa that has been placed in the tribe Haemodoreae, the tribe Conanthereae, or the family Tecophilaeaceae. As far as is presently known, the two genera of Haemodoraceae in eastern North America do not seem to have any close relatives in the West Indies, Central America, or South America.

As mentioned above, *Aletris* (perhaps 25 species of eastern North America and eastern Asia) was included in the Haemodoraceae by Benthams & Hooker. It is commonly recognized today, however, that this genus is best included in the Liliaceae. *Sansevieria* Thunb. (about 60 species of the Old World), also included in the Haemodoraceae by Benthams & Hooker, is now usually placed in the Liliaceae or Agavaceae; *S. thyrsiflora* Thunb. is naturalized in southern Florida.

The Haemodoraceae, as delimited by Geerinck, contain two pollen types (see Erdtman). The pollen of tribe Haemodoreae is 1-sulcate, while that of tribe Conostylideae is 2-8-aperturate (often 3-aperturate). Erdtman comments that "the occurrence of 3-aperturate grains in Hypoxidoideae-Conostylideae [= Haemodoraceae tribe Conostylideae of this paper] excludes the possibility of assigning 3-aperturate pollen grains to Dicotyledoneae merely on the basis of aperture number." Other monocotyledonous families in which 3-aperturate pollen occurs are the Alismataceae, Araceae, and Bromeliaceae. Erdtman noted that *Lanaria* and *Lophiola* are palynologically more similar to tribe Conanthereae (perhaps best treated as the Tecophilaeaceae) than to the Haemodoraceae *sensu* Pax.

Little is known about breeding systems or pollination and dispersal mechanisms in the family. Some South African Haemodoraceae exhibit a type of enantiostyly, with morphologically different "left-" and "right-handed" flowers (see Barker, Ornduff, and Wilson). The flowers of *Anigozanthos* often have bright, contrasting colors, such as red, yellow, vivid green, blue, and black (an unusual color in flowers), and are

mostly pollinated by birds (honeyeaters, family Meliphagidae). The strange, discoid seeds of *Lachnanthes* and *Haemodorum* are probably dispersed by wind. In *Dilatrís corymbosa* Berg. and *D. Pillansii* Barker, the persistent perianth atop the indehiscent fruit acts as a parachute (see Barker). Reported sporophytic chromosome numbers are: *Anigozanthos* (including *Macropidia* Harv.), 12 (6 species), and *Conostylis* R. Br. (including *Blancoa* Lindl.), 8, 10, 14, 16, and 28 (a total of 17 species examined). *Lachnanthes* and *Lophiola* are cytologically unknown.

Annotations of specimens in the combined herbaria of the Arnold Arboretum and the Gray Herbarium of Harvard University indicate that A. Stoel, of Utrecht, is preparing a revision of the New World Haemodora-ceae.

Except for the occasional cultivation of some species (especially of *Anigozanthos*) as curiosities, the family is of little economic importance. A tincture of the roots of *Lachnanthes caroliana* was used by American Indians as an invigorating tonic and as an herb remedy.

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KEY TO THE GENERA OF HAEMODORACEAE IN THE SOUTHEASTERN UNITED STATES

- A. Stamens 3, exserted; ovary inferior, insertion of tepals and stamens epigynous; tepals glabrous adaxially; seeds few in each locule, reddish brown, peltate, orbicular in outline, strongly flattened. 1. *Lachnanthes*.
- A. Stamens 6, about equalling tepals; ovary half-inferior, insertion of tepals and stamens perigynous; tepals with an adaxial crest of yellow, uniseriate multicellular trichomes; seeds numerous in each locule, whitish, tiny, elongate, variously curved, the hilum basal. 2. *Lophiola*.

1. *Lachnanthes* S. Elliott, Sketch Bot. S. Carolina Georgia 1: 47. 1816. ('1821'), nom. cons.

Stout perennial herbs with reddish rhizomes and fibrous roots; sap red. Upper portions of stem, inflorescence branches, and outer parts of flowers whitish villous-tomentose when young, becoming tawny hoary. Leaves mostly basal, sword-shaped, the cauline ones few and reduced in size. Inflorescences terminal on stem, many-flowered, initially compact and rounded, becoming open and corymbose after anthesis, with each branch resembling a helicoid cyme; bracts conspicuous, subtending each flower. Flowers regularly symmetrical, the insertion of the tepals and stamens epigynous. Tepals 6 in 2 whorls of 3, free to level of insertion, pale yellow, erect-spreading at anthesis, inserted around the top of the ovary, densely pubescent abaxially, glabrous adaxially, valvate in aestivation, the outer 3 narrower and slightly shorter than the inner 3. Stamens 3, exserted, erect-spreading at anthesis; filaments inserted on the top of the ovary opposite the inner whorl of tepals, persistent in fruit and then enclosed by the inrolled margins of the inner tepals; anthers yellow, introrse, basifixed, very slightly sagittate below, curving outward after dehiscence. Ovary inferior, 3-locular; style slightly exceeding the anthers, persistent in fruit; stigmatic area faintly 3-lobed; ovules about 6 per locule, inserted around the margin of a peltate, stipitate, axile placenta. Capsule globose or oblate, capped by the persistent tepals, dehiscent by 3 loculicidal valves, the style not attached to the fruit valves but remaining on the columella or breaking off. Seeds discoid, peltate, reddish brown, few per locule, attached around the placenta; seed coat faintly wrinkled. (Including *Heritiera* J. F. Gmelin, 1791, neither Aiton, 1789, nor Retzius, 1791, nor *Heriteria* Schrank, 1789; *Gyrotheca* Salisb.; *Camderia* Dumortier.) TYPE SPECIES: *L. tinctoria* S. Elliott = *L. caroliana* (Lam.) Dandy. (Name from Greek *lachne*, wool, and *anthos*, flower, in reference to the pubescent flowers.) — REDROOT.

One species of scattered distribution in eastern North America, occurring in southern Nova Scotia; Rhode Island and southeastern Massachusetts; the pine barrens of New Jersey and Delaware; southeastern Virginia; Augusta County, Virginia; Coffee County, Tennessee; and on the Atlantic and Gulf coastal plains from North Carolina south to southern Florida, westward through the panhandle of Florida to Saint Tammany

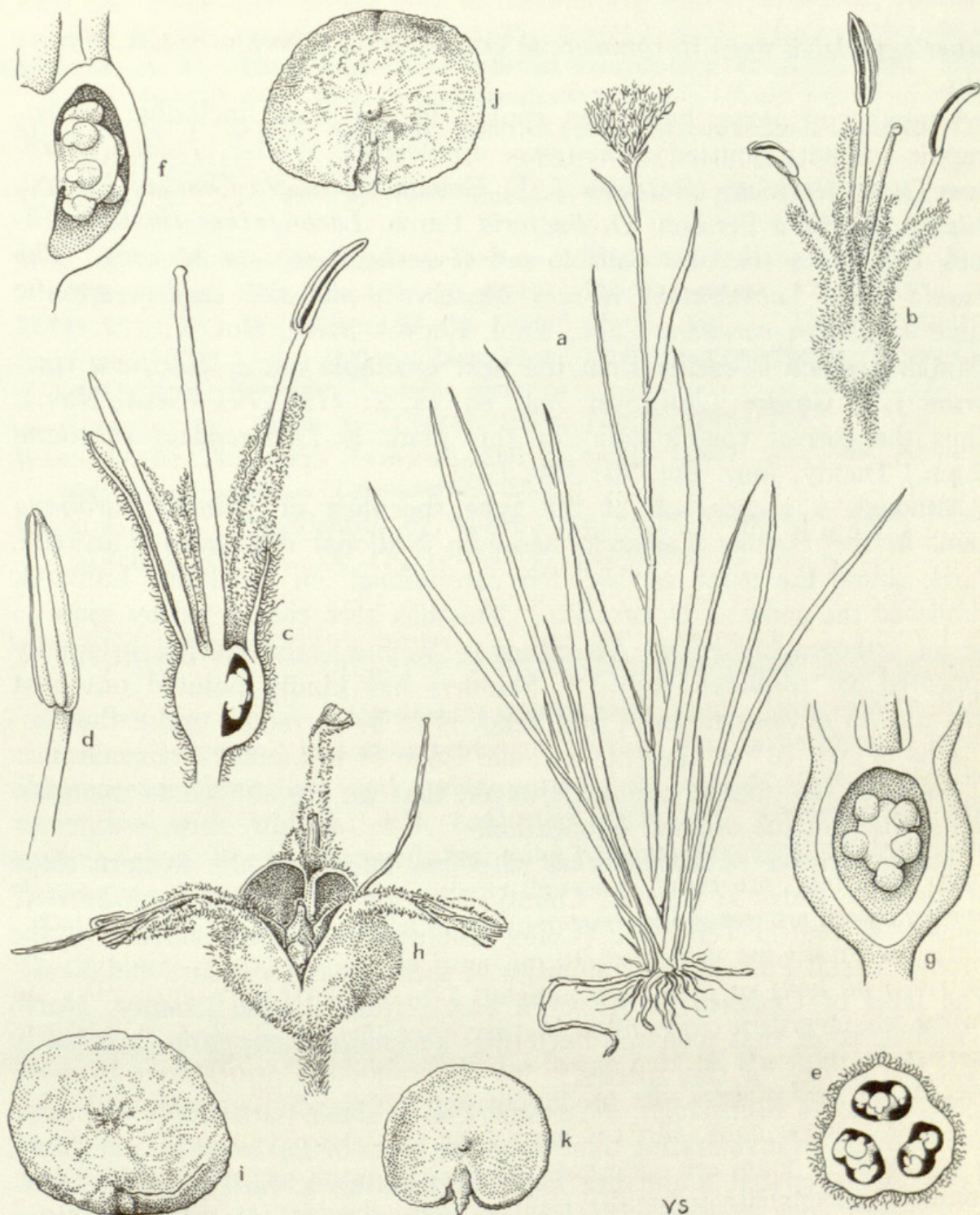


FIGURE 1. *Lachnanthes*. a-k, *L. caroliniana*: a, habit, $\times 1/4$; b, flower, $\times 3$; c, same in vertical section — note placenta, $\times 4$; d, anther before dehiscence, $\times 6$; e, cross section of ovary to show placentation, $\times 10$; f, ovary locule in partial vertical section to show placenta and ovules (trichomes omitted), $\times 10$; g, in vertical section perpendicular to preceding, showing 5 ovules (trichomes omitted), $\times 10$; h, dehiscent capsule, $\times 5$; i, seed, abaxial surface, $\times 12$; j, same, adaxial surface, the hilum in center, $\times 12$; k, seed with wing removed, embryo lies beneath hilum, with radicle pointing downward into projecting portion, $\times 12$.

Parish, Louisiana; also in Pinar del Río Province, Cuba. *Lachnanthes caroliniana* is usually found in acid soils in wet habitats, e.g., in bogs, swamps, and ditches, in low areas in savannahs and pinelands, and along the margins of hammocks and pocosins. The species is sometimes a

rather aggressive weed in commercial cranberry (*Vaccinium macrocarpon*) bogs.

A number of names have been applied to this plant, including (orthographic variants omitted) *Anonymos tinctori*[a] Walter, *Dilatriis caroliniana* Lam., *Heritiera tinctorum* J. F. Gmelin, *Heritiera Gmelini* Michx., *Dilatriis Heritiera* Persoon, *D. tinctoria* Pursh, *Lachnanthes tinctoria* Elliott, *Gyrotheca tinctoria* Salisb., and *Gyrotheca capiata* Morong. The generic name *Lachnanthes* is now conserved, and the earliest specific name is *Dilatriis caroliniana* Lam., Tabl. Encycl. Méth. Bot. 1: 127. 1791 (March), which is earlier than the next available name, *Heritiera tinctorum* J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2: 113. 1791 (Sept./Nov.). Thus the correct combination for this plant is *Lachnanthes caroliniana* (Lam.) Dandy, Jour. Bot. 70: 329. 1932.

Although a photograph of the type specimen of *Dilatriis caroliniana* Lam. in the Herbarium Lamarck, Muséum National d'Histoire Naturelle, Paris, shows the name as "*Dilatriis caroliniana*" on the label, Lamarck published the name as *D. caroliniana*. This has been considered by some to be an orthographic error. According to Wilbur, "the epithet originally appeared as '*caroliniana*,' but Dr. Shinnars has kindly pointed out that this was an obvious misprint and hence is to be corrected under the provisions of Art. 73" of the International Code of Botanical Nomenclature. It seems to the present author, however, that we are obliged to maintain the spelling of the original publication.

The occurrence of *Lachnanthes caroliniana* inland on the western slope of the Blue Ridge in Augusta County, Virginia, and in the "oak-barren" country of central Tennessee (Coffee County) is further evidence of the strong Coastal Plain floristic affinities of these areas (see Carr and Kral). The label of *Channell & Rock 79* (GH), from Bladen County, North Carolina, notes that monarch butterflies (*Danaus plexippus*) abundantly visit the flowers of this species.

According to Millspaugh, some American Indians, particularly the Seminoles, made an invigorating tonic from the roots of *Lachnanthes caroliniana*. They also prepared a tincture used for treating a variety of maladies. Millspaugh gives directions for making a whole-plant infusion and records a number of physiological reactions that it produces.

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Under family references see ASCHERSON, BAILLON, BENTHAM & HOOKER, DUNCAN & FOOTE, GEERINCK (1968, 1969), HUTCHINSON, MELCHIOR, PAX, ROLAND, and WARD.

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2. *Lophiola* Ker-Gawler, *Bot. Mag.* 39: *pl.* 1596. 1813.

Slender, perennial, stoloniferous herbs with erect, leafy stems from rhizomes; roots and rhizomes brown to whitish. Upper portions of stem, inflorescence branches, and outer portions of flowers densely woolly-tomentose with whitish, soft, contorted trichomes. Leaves basal and cauline, erect, linear, flattened, becoming progressively smaller above. Inflorescence a much-branched, many-flowered, bracteate, open [or compact] corymb terminating the erect stem and exceeding the leaves. Flowers regularly symmetrical, the insertion of the tepals and stamens perigynous. Tepals 6 in 2 whorls of 3, nearly equal, free to level of insertion, reflexed at anthesis, brownish or maroon at the tips, with a bright yellow crest of moniliform trichomes on the lower half of the adaxial surface, densely tomentose abaxially, inserted about the middle [or toward the base] of the ovary, persistent and erect in fruit, each whorl valvate in aestivation, with the outer 3 partially enclosing the inner 3. Stamens 6, erect-spreading at anthesis, shorter than the tepals; filaments glabrous, persistent, inserted opposite the tepals on the ovary; anthers yellow, introrse, basifixed, scarcely auriculate at the base. Ovary half-inferior [or nearly superior], 1-locular with 3 parietal placentae above and 3-locular with axile placentae below; style 1, terminal on the ovary, slender, about equalling the stamens, persistent in fruit; stigmatic area slightly 3-lobed; ovules numerous in several vertical rows, evidently anatropous. Capsule \pm globose or ovoid, the valves beaked by persistent style segments, the fruit enclosed before dehiscence by the persistent tepals. Seeds numerous, tiny, elongate, variously curved, whitish; seed coat finely open-reticulate. TYPE SPECIES: *L. aurea* Ker-Gawler. (Name from Greek *lophia*, a mane or crest, evidently in reference to the pubescence on the adaxial side of the tepals.) — GOLDEN-CREST.

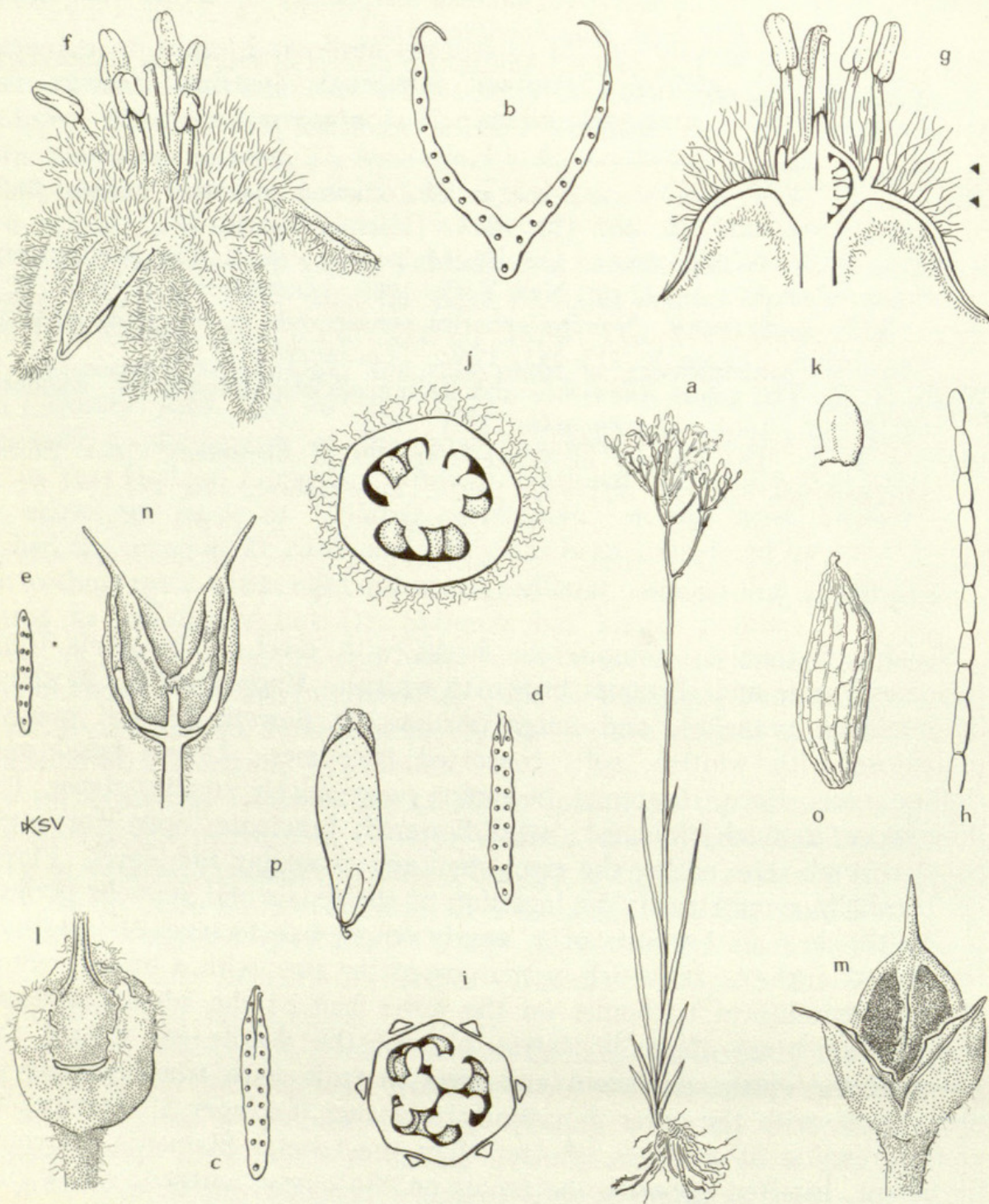


FIGURE 2. *Lophiola*. a-p, *L. aurea*: a, habit, $\times 1/4$; b-e, series of cross sections of leaf from base to tip to show folding and progressive fusion of adaxial surfaces (black area in vascular bundles represents xylem and white is phloem), all $\times 6$; f, open flower—note crest of trichomes on upper surface of tepals, $\times 6$; g, flower in vertical section, ovary half-inferior, placentation parietal above, axile below, $\times 6$; h, moniliform trichome from crest of tepal, $\times 150$; i, cross section of ovary at level of upper arrow in "g," triangles represent filaments, $\times 12$; j, cross section of ovary at level of lower arrow in "g," $\times 12$; k, anatropous ovule, $\times 25$; l, fruit just beginning to dehisce, one tepal removed—note style separating into 3 parts, $\times 6$; m, dehiscent capsule, $\times 6$; n, same, one valve removed, $\times 6$; o, mature seed, $\times 25$; p, seed in vertical section, oriented as seed in "o," endosperm even-stippled, embryo unshaded, $\times 25$.

One (or more ?) species occurring disjunctly along the Atlantic Coastal Plain of North America in western Nova Scotia; in the pine barrens of New Jersey (and formerly Delaware); in southeastern North Carolina; in south-central Georgia; and from the panhandle of Florida to southern Mississippi. The genus apparently occurs infrequently within each of the geographical regions, although individual populations may be composed of many individuals and may cover large areas. Plants of the genus are nearly always found in bogs and low, wet areas in savannahs and pine barrens.

Lophiola has not been studied in detail morphologically, developmentally, anatomically, cytologically, or ecologically, and its reproductive biology is unknown. Because of this general lack of information, the taxonomy and familial affinities of the genus are uncertain (see family discussion).

Fernald (1921, pp. 162, 163, 243, 244) noted apparent differences in the habit, indumentum, leaf size, compactness of the inflorescences, number of flowers, level of insertion of the tepals on the ovary, fruit color, and shape of the base of the seeds that occur between plants from Nova Scotia, New Jersey, and the southeastern United States. He described the plants from Nova Scotia as a new species, *Lophiola septentrionalis*, applied the name *L. americana* (Pursh) Wood to the plants of New Jersey, and used the name *L. aurea* Ker-Gawler for the plants of North Carolina, Georgia, Florida, and Mississippi. However, herbarium specimens and observations on living plants in North Carolina suggest that at least some of this variation may be due to ecological conditions. It is also to be expected that widely disjunct populations, even of the same species, would differ somewhat from each other. Thus, until more detailed studies reveal information to the contrary, it seems best to recognize only one species of *Lophiola*.

There has been considerable debate about whether the name *Lophiola aurea* Ker-Gawler (Bot. Mag. pl. 1596) was published before or after *Conostylis americana* Pursh (Flora Americae Septentrionalis 1: 224), which is the basionym of *Lophiola americana* (Pursh) Wood (Class Book 697. 1861). It appears that Pursh's *Flora* could not have been published before the middle of December, 1813. Graustein relates that the printing of this work was scheduled to be completed during the week of December 7, 1813, and that Pursh presented a copy to the Linnean Society of London on December 21, 1813. The plate of *L. aurea* in the *Botanical Magazine* bears the date "1 Nov. 1813." Plates of this period were dated to comply with British print copyright acts. Stearn (1943b) says that "the dates on these prints were intended to be those of their first publishing, . . . and in the absence of evidence to the contrary, the dates engraved on its [the *Botanical Magazine's*] plates, though possibly not always correct to the exact day, must be accepted as correct as to the month." Thus it seems clear that *L. aurea* was published before *C. americana*. The citation in the *Botanical Magazine* of Pursh's name for this plant and the

exact page number of its description in Pursh's *Flora* can be attributed to the supposed availability of the proofs of the *Flora* to the editor of the *Botanical Magazine* (see Stearn, 1943a).

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