

THE GENERA OF BURMANNIACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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BURMANNIACEAE Blume, Enum. Pl. Javae 1: 27. 1827, nom. cons.

(BURMANNIA FAMILY)

Annual (or perennial), autotrophic, partly autotrophic, or achlorophyllous "saprophytic" herbs. Leaves alternate, simple, entire, exstipulate, mostly reduced to scales, the photosynthetic species leafy stemmed, with or without a basal rosette of small, linear leaves. Flowers perfect, regular (actinomorphic) [or zygomorphic or rarely 2-lipped]. Inflorescences mostly monochasia or dichasia, often reduced to a single terminal flower or condensed and headlike. Perianth petaloid, white or colored, of 2 whorls of 3 tepals united to form a tube, the 3 inner usually smaller than the outer in Burmannieae [or the 3 outer smaller, often almost lacking in Thismieae]; perianth tube cylindrical or 3-angled, often 3-winged [or 3- or 6-ribbed]. Anthers 3 and opposite the inner perianth lobes [or in *Haplothismia* and most Thismieae 6], sessile or subsessile in the perianth throat [or with short recurved filaments], 4-loculate, latrorse [or introrse], connective broad, often appendaged at top and/or base; pollen grains single or in tetrads [or dyads], 1- or 2-porate [4-porate or 1-colpate]. Gynoecium 3-carpellate, syncarpous; style single, filiform [or short-cylindrical or conical in Thismieae], tipped with 3 short branches, each with a single stigma [or with 3 sessile or connate stigmas]; ovary inferior, 3-locular with axile placentae or 1-locular with 3 parietal placentae [in some genera with a large, globose gland inside the ovary on each side of the top of each placenta!]; ovules numerous,

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I am indebted to my colleagues Norton G. Miller, George K. Rogers, and Barbara Nimblett for their help with various aspects of the work on this family; to Christopher S. Campbell for Kodachrome pictures and alcohol-preserved material of *Apteris* and of *Burmannia biflora*; and to Walter S. Judd for alcohol-preserved material of *Burmannia capitata* and fruits of *Apteris*. The illustration of *Apteris* was drawn by Margaret van Montfrans from my dissections of the specimens sent by Drs. Campbell and Judd.

minute, anatropous, 2-integumented, tenuinucellar; female gametophyte of the Polygonum or the Allium type. Perianth persistent on the fruit [or the upper part bearing the stamens deciduous, only the lower part persistent, or in *Thismieae* the entire perianth circumscissile, leaving only a basal thickened ring]. Fruit capsular [sometimes fleshy in *Thismieae*], dehiscent irregularly or splitting transversely [or at the top] or sometimes by valves. Seeds numerous, small; embryo minute, undifferentiated, sometimes composed of only a few (3–6) cells; endosperm present, usually consisting of relatively few, large cells. (Including *Thismiaceae* J. G. Agardh, nom. cons.; excluding *Corsiaceae* Beccari, nom. cons.) TYPE GENUS: *Burmannia* L.

A small family of 17 or 18 genera and about 135 species of perennial or annual mycotrophic herbs, varying from leafy-stemmed, green autotrophs to scale-leaved, achlorophyllous "saprophytes." The family occurs primarily in the tropics and subtropics of North and South America, Africa, Asia, and Australia, but with extensions northward to Virginia and Illinois in the United States and to southern Japan, and southward to Brazil and Argentina; Angola, South Africa, and Madagascar; and southeastern Australia, Tasmania, and northern New Zealand. The distribution of *Burmannia* L. (*q.v.*) is nearly that of the family; *Gymnosiphon* Blume occurs in Central and South America, the West Indies, tropical Africa, Madagascar, Malaysia, Indonesia, and New Guinea; and *Thismia* occurs in the Americas, tropical Asia, and Australia–New Zealand. Twelve genera are indigenous in South America, and six of these extend into North America, with *Burmannia* L. and *Apteria* Nutt., of tribe *Burmannieae*, and *Thismia*, of tribe *Thismieae*, reaching the United States. Although most genera are confined to the Americas, to Africa, or to Asia–Australia, there are some truly extraordinary disjunctions. *Glaziocharis* Taub. ex Warm. has two species: *G. macahensis* Taub. ex Warm., known only from Rio de Janeiro, Brazil, and *G. Abei* Akasawa, known from Shikoku and southern Kyushu, Japan. *Thismia* Griff. sect. *RODWAYA* Schlechter includes only two closely related species: *T. Rodwayi* F. Mueller (*Bagnisia Hillii* Cheeseman), of Australia (eastern Victoria and Tasmania) and New Zealand (North Island), and *T. americana* N. E. Pfeiffer, known from only one colony discovered on low prairies near Chicago in 1912 and presumably now extinct. A more familiar pattern is seen in *Burmannia*, in which there are several tropical American–tropical Asian disjunctions.

The family is generally regarded as being composed of two or three groups of genera that have been ranked by various authors as tribes, subfamilies, or families (see Jonker, 1938; Lawrence). Bentham & Hooker, Baillon, and Engler, among others, considered the *Burmanniaceae* to consist of tribes *Burmannieae* (*Euburmannieae*), *Thismieae*, and *Corsiaceae*. Thorne recognized these same groups at the rank of subfamily, while Hutchinson treated them as distinct families. Jonker, Takhtajan, Cronquist, and others have maintained *Corsiaceae* and *Burmanniaceae* (with tribes *Burmannieae* and *Thismieae*) as distinct families. Airy Shaw established a new tribe, *Haplothismieae*, to accommodate *Haplothismia annulata* Airy Shaw (of South India) in *Burmanniaceae*, kept tribes *Burmannieae* and *Thismieae*, and maintained *Corsiaceae* as a separate family.

The Burmanniaceae have been placed variously in relation to other families of monocotyledons. They have often been associated with the Orchidaceae on the basis of their minute seeds that supposedly lack endosperm. Endosperm, although scant, does occur, however, and Jonker (1938, p. 6) wrote, "The presence of endosperm and the construction of the flower makes relationship with the *Liliiflorae* highly probable. Of this order *Amaryllidaceae*, *Iridaceae* and *Taccaceae* seem to be most closely related." Hutchinson (1973, p. 838) placed the Burmanniales (Burmanniaceae, Thismiaceae, Corsiaceae) "next to *Haemodiales*, and especially near *Hypoxidaceae* (*Curculigo*)." He remarked, however, that "the affinity with *Orchidaceae* is probably closer than at first appears, the two groups having developed on parallel lines with regard to certain characters such as saprophytism and minute seeds." At present, most authors seem to favor a position for Burmanniaceae in or near the Liliales, but Cronquist maintains the order Orchidales to include Orchidaceae, Geosiridaceae (removed from Burmanniaceae by Jonker), Burmanniaceae, and Corsiaceae. Melchior, Thorne, and Takhtajan all have favored Liliales (*Liliiflorae*), Melchior placing Burmanniaceae and Corsiaceae in suborder Burmanniineae and Thorne linking Burmanniaceae (with subfamilies Burmannioideae, Thismioideae, and Corsioideae) and Iridaceae (with subfamilies Iridoideae and Geosiridoideae) in suborder Iridineae. Takhtajan thinks the Burmanniaceae to be closely related to Liliales, especially Iridaceae, and evidently derived from them.

Many species of Burmanniaceae are known only from single collections or localities. As a result, although general morphology is the best-known feature of the group, the detailed morphology, mycorrhizal relationships, embryology, and palynology are known for only relatively few species, and the physiological ecology, floral biology, cytology, and chemistry are nearly untouched.

The species of *Burmannia*, the largest genus of the family, range from leafy, green autotrophs to achlorophyllous "saprophytes." The other members of the family appear to be achlorophyllous. Those plants that have been studied are endomycorrhizal, and it has long been assumed that the achlorophyllous Burmanniaceae, most of which "occur almost exclusively on decaying leaves, wood and roots in the deep shade of tropical, wet, primeval forests" (Jonker, 1938, p. 13) are saprophytes. However, in view of research on *Monotropa* (Ericaceae subfam. Monotropoideae) and Orchidaceae (see Furman & Trappe), it seems much more probable that these, along with similar achlorophyllous plants such as *Voyria* (*Leiphaimos*) (Gentianaceae) (see Wood & Weaver), *Sciaphila* (Triuridaceae), and *Epirrhizanthus* (Polygalaceae) that sometimes grow intermixed with them, are instead epiparasites that parasitize the roots of vascular plants, although not directly attached to them, via a shared mycorrhizal fungus. Jonker (1938, p. 12) remarked about *Thismia americana*: "It is hard to believe that Chicago is the normal area for this species, but I cannot give a satisfactory explanation why it occurs there. The habitat, an open prairie among the moss, is very different to the habitats of other *Thismias*, usually growing saprophytically in primeval forests." Epiparasitism of the *Monotropa* type makes such a habitat both quite possible and believable.

The family is of no economic importance.

REFERENCES:

- AIRY SHAW, H. K. A new genus and species of Burmanniaceae. *Kew Bull.* 7: 277–279. 1952. [*Haplothismia exannulata* Airy Shaw from South India, Travancore-Cochin State; new tribe, Haplothismieae, described. Illustrated. “The floral structure of *Haplothismieae* represents the least specialised type found in the Burmanniaceae.”]
- AJILVSGI, G. Wild flowers of the Big Thicket, East Texas, and western Louisiana. xii + 361 pp. College Station, Texas. 1979. [*Burmannia biflora*, 122, 123 (colored illus., 55); *Apteria aphylla*, 123 (colored illus., 56).]
- AKASAWA, Y. A new species of *Glaziocharis* (Burmanniaceae) found in Japan. (In English, Latin, Japanese.) *Jour. Japan. Bot.* 25: 193–196. *pls. 1, 2*. 1950. [*G. Abei*, Awa Prov., Shikoku; genus previously known from one collection from Brazil; see also C. ABE, *ibid.* 197–199, in Japanese.]
- AOYAMA, M., K. KARASAWA, & R. TANAKA. Chromosomes of *Glaziocharis Abei*, a saprophyte. *Chromosome Inform. Serv.* 25: 34, 35. 1978. [$2n = 12$.]
- BAILLON, H. Burmanniacées. *Hist. Pl.* 13: 170–182. 1894.
- BENTHAM, G., & J. D. HOOKER. Burmanniaceae. *Gen. Pl.* 3: 455–460. 1883.
- BOLKHOVSKIKH, Z., V. GRIF, T. MATVEJEVA, & O. ZAKHARYEVA. Chromosome numbers of flowering plants. A. A. FEDEROV, ed. 926 pp. Acad. Sci. USSR. V. L. Komarov Bot. Inst. Leningrad. 1969. [Burmanniaceae, 181.]
- BOWDEN, B. N. Burmanniaceae. Pp. 320, 321 in V. H. HEYWOOD, consultant ed., *Flowering plants of the world*. New York. 1978. [Includes inaccurate distribution map; *Burmannia coelestis*, *Afrothismia* sp., *Haplothismia exannulata* illustrated.]
- BRADÉ, A. C. Sinopse das “Burmanniaceae” da flora do Brasil. *Arq. Jard. Bot. Rio de Janeiro* 7: 11–42. [10 *pls.*, folded map not paged.] 1947 (publ. 1948). [Includes 13 genera; 11 spp. *Burmannia*, 4 spp. *Apteria*.]
- BREWBAKER, J. L. The distribution and phylogenetic significance of binucleate and trinucleate pollen grains in the angiosperms. *Am. Jour. Bot.* 54: 1069–1083. 1967. [Data on 1908 genera, approximately half studied by the author.]
- CHAKRAPANI, P., & B. RAJ. Pollen morphological studies in Burmanniaceae. *Grana* 11: 164–179. 1971. [27 species in 8 genera studied.]
- CHEESEMAM, T. F. *Bagnisia Hillii*, Cheesem. A new species of Burmanniaceae from New Zealand. *Bull. Misc. Inf. Kew* 1908: 419–421. 1908. [= *Thismia Rodwayi* F. Mueller *vide* Jonker.]
- . Notice of the discovery of a species of Burmanniaceae, a family new to the New Zealand flora. *Trans. New Zealand Inst.* 41: 141–143. 1908. [*Bagnisia Hillii*, North Island of New Zealand. = *Thismia Rodwayi*.]
- CIFERRI, R. L. “habitat” e la micorrizia di alcune Burmanniaceae della Repubblica Dominicana. *Atti Ist. Bot. Univ. Pavia*, V. 7: 25–34. 1946.* [Includes key and new formae.]
- COLEMAN, D. G. *Sarcosiphon Rodwayi* in Australia. *Victorian Nat.* 52: 163–166. *pl. 19*. 1936. [*Thismia Rodwayi*.]
- . Further notes on “fairy lanterns.” *Ibid.* 67: 167, 168. *pl. 18*. 1941. [*T. Rodwayi*.]
- CORRELL, D. S., & H. B. CORRELL. Aquatic and wetland plants of southwestern United States. xvi + 1777 pp. Environmental Protection Agency, Washington, D. C. 1972. (Reissued in 2 vols. by Stanford Univ. Press. 1975.) [Burmanniaceae, 686, 688, 689: *Burmannia capitata*, *B. biflora*, *Apteria aphylla*; illustrated. See also D. S. CORRELL & M. C. JOHNSTON, *Manual of the vascular plants of Texas*, 1970: Burmanniaceae, 433, 434.]
- CRONQUIST, A. An integrated system of classification of flowering plants. 1262 pp. New York. 1981. [Orchidales: Geosiridaceae, Burmanniaceae, Corsiaceae; Burmanniaceae, 1236, 1237.]
- DAVIS, G. L. Systematic embryology of the angiosperms. x + 528 pp. New York. 1966. [Burmanniaceae, 63.]
- EICHLER, A. W. Blüthendiagramme. Erster Theil. 348 pp. Leipzig. 1875. [Burmanniaceae, 178, 179.]

- ENGLER, A. Burmanniaceae. Nat. Pflanzenfam. II. 6: 44–51. 1888; Nachträge zu II. 6: 96. 1897.
- ERDTMAN, G. Pollen morphology and plant taxonomy. Angiosperms. 539 pp. Stockholm. 1952. (Corrected reprint with addendum [pp. 541–553]. New York. 1971.) [Burmanniaceae, 84, 85.]
- ERNST, A., & C. BERNARD. Beiträge zur Kenntnis der Saprophyten Javas. I–XV. Ann. Jard. Bot. Buitenzorg 23: 20–61. pls. 9–17. 1910; 24: 55–97. pls. 8–17. 1911; 25: 161–188. pls. 13–17. 1912; 26: 219–257. pls. 17–22. 1912; 28: 99–124. pls. 14–19. 1914. Titles and references to individual papers I–XV follow: [Introduction.] *Ibid.* 23: 20–31. I. Zur Systematik von *Thismia javanica* (by J. J. SMITH). 23: 32–35. pls. 9, 10. II. Äussere und innere Morphologie von *Thismia javanica* J.J.S. 23: 36–47. pls. 11–13. III. Embryologie von *Thismia javanica* J.J.S. 23: 48–61. pls. 14–17. IV. Zur Systematik von *Thismia clandestina* Miq. und *Thismia Versteegii* J. J. Sm. 24: 55–60. pls. 8, 9. V. Anatomie von *Thismia clandestina* Miq. und *Thismia Versteegii* Sm. 24: 61–69. pls. 10–12. VI. Beiträge zur Embryologie von *Thismia clandestina* Miq. und *Thismia Versteegii* Sm. 24: 70–78. pls. 12, 13. VII. Zur Systematik von *Burmanniea candida* Engl. und *Burmanniea Championii* Thw. (by J. J. SMITH). 24: 79–83. pls. 14, 15. VIII. Äussere und innere Morphologie von *Burmanniea candida* Engl. und *Burmanniea Championii* Thw. 24: 84–97. pls. 16, 17. IX. Entwicklungsgeschichte des Embryosackes und des Embryos von *Burmanniea candida* Engl. und *B. Championii* Thw. 25: 161–188. pls. 13–17. X. Zur Systematik von *Burmanniea coelestis* Don (by J. J. SMITH). 26: 219–222. pl. 17. XI. Äussere und innere Morphologie von *Burmanniea coelestis* Don. 26: 223–233. pl. 18. XII. Entwicklungsgeschichte der Embryos und des Endosperme von *Burmanniea coelestis* Don. 26: 234–257. pls. 19–22. XIII. Zur Systematik von *Burmanniea tuberosa* Becc. (by J. J. SMITH). 28: 99–101. pl. 14. XIV. Äussere und innere Morphologie von *Burmanniea tuberosa* Becc. 28: 102–120. pls. 15–18, 18*. XV. Embryologie von *Burmanniea tuberosa* Becc. 28: 121–124. pl. 19.
- ESPINOSA B., M. R. Algunas observaciones sobre la *Arachnites uniflora*. Phil. Revista Chilena Hist. Nat. 30: 299–303. 1926.
- FURMAN, T. E., & J. M. TRAPPE. Phylogeny and ecology of mycotrophic achlorophyllous angiosperms. Quart. Rev. Biol. 46: 219–225. 1971. [*Burmanniea*, *Glaziocharis*, *Gymnosiphon*, *Sarcosiphon*, *Thismia* listed among genera of mycotrophic achlorophyllous members; paper deals primarily with Orchidaceae and Ericaceae subfam. Monotropoideae (as Pyrolaceae).]
- GODFREY, R. K., & J. W. WOOTEN. Aquatic and wetland plants of southeastern United States. Monocotyledons. xi + 712 pp. Athens, Georgia. 1979. [Burmanniaceae, 623–625; illustrations of *Apteria aphylla*, *Burmanniea biflora*, *B. capitata* (from Correll & Correll).]
- GOEBEL, K., & K. SÜSSENGUTH. Beiträge zur Kenntnis der südamerikanischen Burmanniaceen. Flora 117: 55–90. pls. 2, 3. 1924. [Morphology and anatomy; *Thismia Luetzelburgii*, *Cymbocarpa Urbanii* illustrated.]
- GROOM, P. *Thismia Aseroe* (Beccari) and its mycorrhiza. Ann. Bot. 9: 327–361. pls. 13, 14. 1895.
- HATSCHBACH, G., & O. GUIMARÃES. Burmanniaceas do Estado do Paraná. Bol. Mus. Bot. Munic. Curitiba 5: 1–17. pls. 1–4. 1972. [Brazil. Includes *Burmanniea bicolor*, *B. capitata*, *B. alba*, *Cymbocarpa refracta*, *Gymnosiphon tenellus*, *Apteria gentianoides*, *Dictyostega orobanchoides*, *Miersiella umbellata*.]
- HUTCHINSON, J. The families of flowering plants. ed. 3. xx + 968 pp. Oxford. 1973. [Burmanniales, 838–846. As in ed. 1 (1934, 2: 175–179) and ed. 2 (1959, 2: 658–691), the order Burmanniales is composed of Burmanniaceae, Thismiaceae, and Corsiaceae.]
- JOHOW, F. Die chlorophyllfreien Humusbewohner West-Indiens, biologisch-morphologisch dargestellt. Jahrb. Wiss. Bot. 16: 415–449. pls. 16–18. 1885. [Includes *Apteria aphylla* (as *A. setacea*), *Burmanniea capitata*.]

- . Die chlorophyllfreien Humuspflanzen nach ihren biologischen und anatomisch-entwicklungsgeschichtlichen Verhältnissen. *Ibid.* **20**: 475–525. 1889. [Includes *Burmannia capitata*, *Gymnosiphon*, *Dictyostega*.]
- JONES, S. B. Mississippi flora. VI. Miscellaneous families. *Castanea* **41**: 189–212. 1976. [Burmanniaceae, 195, 196; *Apteria aphylla*, *Burmannia biflora*, *B. capitata*; *Apteria* and *B. capitata* mapped, 196.]
- JONKER, F. P. A monograph of the Burmanniaceae. Meded. Bot. Mus. Utrecht **51**: i–v, 1–279. 1938. [Introduction, 1–3; General part, 4–14; Critical part, 15–47; Taxonomic part, 49–273; Index, 275–279. *Burmannia*, 18–26, 57–163; *Apteria*, 35–37, 205–209.]
- . Les Géosiridacées, une nouvelle famille de Madagascar. Rec. Trav. Bot. Néerl. **36**: 473–479. 1939. (Meded. Bot. Mus. Utrecht **60**.) [Geosiridaceae, fam. nov., with *Geosiris aphylla* Baillon, excluded from Burmanniaceae.]
- . Burmanniaceae. In: R. E. WOODSON, JR., & R. W. SCHERY & COLLABORATORS. Fl. Panama III(1). Ann. Missouri Bot. Gard. **32**: 42–47. 1945. [*Apteria aphylla*, *Burmannia capitata*, *Gymnosiphon panamensis*, *G. suaveolens*, *Thismia panamensis*.]
- . Burmanniaceae. In: C. G. G. J. VAN STEENIS, Fl. Malesiana I. **4**: 13–26. 1948; **5**: 553, 554 (corrections). 1958. [15 spp. *Burmannia*, 7 spp. *Gymnosiphon*, 14 spp. *Thismia*, 1 sp. *Geomitra*, 2 spp. *Scaphiophora*.]
- KORES, P., D. A. WHITE, & L. B. THIEN. Chromosomes of *Corsia* (Corsiaceae). Am. Jour. Bot. **65**: 584, 585. 1978. [*C. cornuta*, *C. clypeata*, $2n = 18$.]
- LAWRENCE, G. H. M. Taxonomy of vascular plants. xiii + 823 pp. New York. 1951. [Burmanniaceae, 431, 432; *Burmannia biflora* illustrated.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. Vol. 2. 646 pp. London. 1892. [Burmanniaceae, 561, 562; *Apteria aphylla*, *Burmannia capitata*.]
- MAAS, P. J. M. Neotropical saprophytes. Pp. 365–370 in K. LARSEN & L. B. HOLM-NIELSEN, eds., Tropical botany. London, New York, San Francisco. 1979. [Brief accounts of members of Gentianaceae, Triuridaceae, Burmanniaceae.]
- McLENNAN, E. I. *Thismia Rodwayi* F. Muell. and its endophyte. Austral. Jour. Bot. **6**: 25–37. pls. 1–4. 1958. [Excellent account of morphology, mycorrhizal association.]
- MELCHIOR, H. Unterreihe Burmannineae (Burmanniales). In: H. MELCHIOR, Engler's Syllabus der Pflanzenfamilien, ed. 12. **2**: 538, 539. 1964. [Burmanniaceae, Corsiaceae assigned to suborder Burmannineae of the order Liliiflorae (Liliales).]
- MEYER, K. J. Parthenogenesis bei *Thismia javanica* im Lichte der Haberlandtschen Anschauung. Ber. Deutsch. Bot. Ges. **43**: 193–197. 1925.
- MIERS, J. On some new Brazilian plants allied to the natural order Burmanniaceae. Trans. Linn. Soc. London **18**: 535–556. pls. 37, 38. 1841. [*Gonyanthes*, *Dictyostega*, *Cymbocarpa*, *Apteria*; *A. lilacina* described, *A. aphylla* (as *A. setacea*) discussed.]
- NETOLITZKY, F. Anatomie der Angiospermen-Samen. Handb. Pflanzenanat. II. Archeogon. **10**. vi + 365 pp. 1926. [Burmanniaceae, 91, 92.]
- PFEIFFER, N. E. Morphology of *Thismia americana*. Bot. Gaz. **57**: 122–135. pls. 7–11. 1914.
- . The sporangia of *Thismia americana*. *Ibid.* **66**: 354–363. pl. 16. 1918.
- RAMON DE LA SOTA, E. *Mamorea Singeri*, un nuevo género y especie de Burmanniaceae. Darwiniana **12**: 43–47. 1960. [From Bolivia; related to *Triscyphus*, tribe Thismieae.]
- RAMSBOTTOM, J. Orchid mycorrhiza. Trans. Brit. Mycol. Soc. **8**: 28–61. 6 unnumbered pls. 1922. [Includes Burmanniaceae, Ericaceae, Pyrolaceae, Gentianaceae, and *Lolium* (Gramineae).]
- RAO, V. S. Certain salient features in the floral anatomy of *Burmannia*, *Gymnosiphon* and *Thismia*. Jour. Indian Bot. Soc. **48**: 22–29. 1969. [*B. disticha*, *B. nepalensis*, *G. cymosus*, *G. aphyllus*, *T. Aseroe*.]
- RENDLE, A. B. The classification of flowering plants. Vol. 1. Gymnosperms and monocotyledons. ed. 2. xvi + 412 pp. Cambridge, England. 1930. [Burmanniaceae, 344, 345, 393.]

- RICKETT, H. W. Wildflowers of the United States. Vol. 2. The Southeastern States. Part 1. x + 322 pp. New York. 1966. [Burmanniaceae, 78, 81, color pls. 25, 26. *Burmattia biflora*, *B. capitata*, *Apteria aphylla* illustrated.] Vol. 3. Texas. Part 1. xii + 274 pp. 1969. [Burmanniaceae, 50; *Burmattia capitata*, *Apteria aphylla*, 57 (pl. 13) (illustration same as in Vol. 2.)]
- RIDLEY, H. N. The Burmanniaceae of the Malay Peninsula. Jour. Straits Branch Roy. Asiat. Soc. 22: 331–339. 1890. [*Burmattia longifolia*, *B. disticha*, *B. coelestis*, *B. tuberosa*, *B. gracilis*, *Gymnosiphon borneense*, *Thismia Aseroe*, *T. fumida*; *B. tuberosa*, *B. gracilis* said to be saprophytic.]
- ROYEN, P. VAN. Corsiaceae of New Guinea and surrounding areas. Webbia 27: 223–255. 1972. [23 spp.; Corsiaceae consisting of ca. 25 spp. in New Guinea, 1 in Australia, 2 in the Solomon Islands, and 1 (of *Arachnitis*) in Chile.]
- SCHLECHTER, R. Die Thismieae. Notizbl. Bot. Gart. Berlin 8: 31–45. 1921. [10 genera; 6 later recognized by Jonker (1938), the others combined with *Thismia*.]
- SEUBERT, M. Burmanniaceae. In: C. F. P. VON MARTIUS, Fl. Brasil. 3(1): 53–60. 1847. [Includes *Apteria lilacina*, *Burmattia bicolor*, *B. capitata*, *B. flava*.]
- SHIN, T. Two species of the genus *Glaziocharis* [sic] (Burmanniaceae) from southern Kyushu. (In Japanese.) Jour. Japan. Bot. 49: 3–6. 1974. [*Glaziocharis macahensis* (described from Brazil) and *G. Abei*; generic name spelled *Glaziocharis* throughout.]
- SMITH, J. J.: see ERNST, A., & C. BERNARD, Beiträge zur Kenntnis der Saprophyten Javas, I, VII, X, XIII.
- STONE, B. C. Rediscovery of *Thismia clavigera* (Becc.) F. v. M. (Burmanniaceae). Blumea 26: 419–425. 1980. [*Geomitra clavigera* transferred to *Thismia*; includes key to the nine spp. of *Thismia* known from Malaya.]
- SWAMY, B. G. L., & K. V. KRISHNAMURTHY. The helobial endosperm. A decennial review. Phytomorphology 23: 74–79. 1973 (publ. 1974). [Burmanniaceae, 75; development of endosperm in *Burmattia coelestis* and *B. pusilla* conforms to A-form of helobial ontogeny.]
- TAKHTAJAN, A. L. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. 46: 225–359. 1980. [Burmanniales (Burmanniaceae, Corsiaceae), 313, 358, closely related to Liliales, especially Iridaceae, and evidently derived from them.]
- THORNE, R. F. A phylogenetic classification of the Angiospermae. Evol. Biol. 9: 35–106. 1976. [Order Liliales composed of suborders Liliineae, Iridineae, Orchidineae; Iridineae composed of Iridaceae and Burmanniaceae, 64, 65, 96, 97.]
- WARD, D. B. Checklist of the vascular flora of Florida. Part 1. Univ. Florida Agr. Exper. Sta. Tech. Bull. 726. 76 pp. 1968. [*Apteria aphylla*, *Burmattia biflora*, *B. capitata*, *B. flava*, 57.]
- WILLIAMS, L. O. Notes on the family Corsiaceae. Harvard Univ. Bot. Mus. Leaf. 12: 179–183. pl. 24. 1946. [Includes 2 new spp. of *Corsia*.]
- WILLIS, J. C. A dictionary of the flowering plants and ferns. ed. 7. Revised by H. K. AIRY SHAW. xxii + 1214 pp. + key to families of flowering plants (pp. i–liii). Cambridge, England. 1966. [Burmanniaceae, 166, 167, key ix; Corsiaceae, 286, 287.]
- WOOD, C. E., JR., & R. E. WEAVER, JR. The genera of Gentianaceae in the southeastern United States. Jour. Arnold Arb. 63: 441–487. 1982. [*Voyria*, 483–487.]

KEY TO THE GENERA OF BURMANNIACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Small, erect, green or purplish herbs with solitary or cymose flowers; perianth petaloid, regular, the tepals in 2 whorls of 3, united; anthers 3, nearly sessile on the perianth below the inner whorl of tepals, opening horizontally, the connective appendaged; gynoeceum 3-carpellate, syncarpous, the ovary inferior; fruit a capsule topped*

by the persistent perianth; seeds numerous, minute, the embryo undifferentiated, the endosperm scanty.

Ovary 3-locular, with axile placentae; flowers with or without wings; capsule opening by horizontal fissures or irregular splits; plants green, with or without a basal rosette of linear leaves and with small linear to lanceolate cauline leaves. 1. *Burmannia*.

Ovary 1-locular, with 3 parietal placentae; flowers wingless; capsule opening from base by 3 upward-curling valves (see FIG. 1, k); plants without basal leaves, stem and scalelike leaves purplish or violet. 2. *Apteria*.

Tribe BURMANNIEAE

Subtribe **Burmanniinae**

1. **Burmannia** Linnaeus, Sp. Pl. 287. 1753; Gen. Pl. ed. 5. 139. 1754.

Erect, terrestrial [rarely pendent, epiphytic], annual [or perennial], autotrophic [or "saprophytic" (more probably epiparasitic)], mycorrhizal herbs. Stems 3–60 cm (ours usually less than 25 cm) tall, usually simple (sometimes branched) [in sect. *FOLIOSA* with conspicuous grasslike parallel-veined decurrent leaves to 25 cm long or] with variously reduced, often scalelike leaves and with or without a rosette or a few linear-lanceolate to linear or subulate leaves at the base. Flowers small (in ours 2–12 mm long), blue, pink, white, yellow, or greenish, erect [or rarely pendulous], winged or wingless, usually in the axil of a small bract, basically in bifid cymes (monochasia or dichasia) of 2 to 15 (to many) flowers, but by reduction solitary at the stem tip or in some (e.g., *B. capitata*) the cymes contracted into a head. Perianth with 6 small, erect [rarely spreading] lobes, these often with inrolled margins, the 3 outer lobes smaller than the 3 inner, the tube $\pm$ cylindrical, 3-angled or 3-winged. Anthers 3, nearly sessile on the perianth below the inner perianth lobes, the connective broadly triangular in ours, bearing the 4 locules at its margins and in most species with 2 apical appendages or crests at its apex and in some species (e.g., *B. flava*) also with a median appendage at the base; locules dehiscing horizontally; pollen grains single [or in dyads or tetrads], 1-porate, 1- or 2-porate, [or 2-porate]. Style filiform, divided into 3 short branches at the top, each branch with a funnel-shaped, bowl-shaped, or peltate stigma [or stigmas sessile at top of style]. Ovary 3-angled, with or without wings, 3-locular, the placentae axile, with numerous minute ovules. Perianth persistent and drying atop the winged or wingless capsule; capsule opening by irregular horizontal fissures. Seeds very numerous, minute, oblong to ellipsoid; embryo undifferentiated; endosperm scarce. (*Tripterella* Michaux) TYPE SPECIES: *B. disticha* L., $2n = \text{ca. } 136$; effectively typified by Linnaeus (see below); see also Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. 1: 547. 1913. (Name commemorating the Dutch botanist Johannes Burman, 1706–1779. Linnaeus wrote [in *Critica Botanica*, 1737; transl. Sir Arthur Hort, 1938], "*Burmannia* is a plant of Ceylon [Sri Lanka] with a double spike, seeing that Burman collaborated with Hermann in writing of the plants of that country.")

A genus of pantropical distribution with extensions into cooler areas in the southeastern United States (to southeastern Virginia and southeastern Okla-

homa), southern Brazil (Rio Grande do Sul), Argentina (Corrientes), South Africa (Transvaal and Natal), Madagascar, southeastern Australia, and southern Japan (Honshu). Jonker (1938) recognized 57 species in two sections: FOLIOSA Jonker, including five perennial species with cauline, grasslike, parallel-veined leaves; and BURMANNIA, the remaining species, both chlorophyllous and achlorophyllous, with basal leaves (if present at all) reduced to a few linear leaves and stem leaves scalelike. With the exception of *Burmattia longifolia* Becc., which is widely distributed in Malaya, Indonesia, the Philippine Islands, and New Guinea, the members of sect. FOLIOSA are indigenous to the Western Hemisphere. Jonker recognized 12 species of sect. BURMANNIA in the Americas, 11 in Africa, and 30 in Asia and Australia. Subsequently, two species of sect. FOLIOSA (both leafy epiphytes) and three of sect. BURMANNIA have been described from South America.

Several of the species of *Burmattia* have very wide continental distributions, and Jonker has pointed out, in addition to the geographic disjunction in sect. FOLIOSA, close relationships between the West Indian-South American *B. bicolor* Martius, the African *B. latialata* Hua, and the Asiatic *B. coelestis* G. Don, $2n = \text{ca. } 32$, which are hardly distinguishable, and between *B. tenella* Benth, the only American achlorophyllous species, and *B. lutescens* Becc., of Malaya.

Three chlorophyllous species of sect. BURMANNIA occur in the southeastern United States. *Burmattia biflora* L., characterized by lack of a basal rosette of leaves and by small, bright blue to violet (to white), strongly three-winged flowers either solitary at the tip of the stem or in 1-15-flowered bifid cymes with a central terminal flower, is distributed sporadically in peaty bogs, in savannas, and on grassy pond shores from Collier County, Florida, northward on the Coastal Plain to southeastern Georgia, the Carolinas, and the southeasternmost counties in Virginia, and westward to western Florida, southern Alabama and Mississippi, northern Louisiana (Ouachita Parish), and southeastern Texas (Houston and Hardin counties).

The tropical American *Burmattia capitata* (J. F. Gmelin) Martius (*Tripterella capitata* Michaux), which has small cauline leaves and only a few basal leaves or none at all and small, pinkish, purple (rarely in our area), greenish, or nearly white, wingless flowers in contracted, terminal, headlike inflorescences, occurs in a variety of moist to wet acid habitats, including pinelands, seepage slopes, gravel pits, bogs, and pondshores from Lee and Highlands counties, Florida, northward to the central Piedmont of Georgia, and—on the Coastal Plain—to Lenoir and Harnett counties, North Carolina. It extends westward through Florida, southern Alabama, and southern Mississippi, to central Louisiana and eastern Texas (Smith, Robertson, and Gonzales counties), and it occurs disjunctly in southeastern Oklahoma (Pushmataha County). It is widely distributed southward through the West Indies and Central and South America: Cuba, Hispaniola, Puerto Rico, southern Mexico (Chiapas), Belize, Nicaragua, Panama, Colombia, Venezuela, Guyana, Surinam, French Guiana, Trinidad, Brazil, Bolivia, Paraguay, and Argentina (Corrientes).

Burmattia flava Martius, also of wide distribution, reaches the United States only in southern Florida, where it has been collected only twice (see Ward, 1979): near Fort Myers, Lee County, in 1916, and in the Fakahatchee Strand

in central Collier County, in 1946. It occurs south of our area in Cuba, southern Mexico (Chiapas), Belize, Costa Rica, Colombia, Venezuela, Guyana, Surinam, Brazil, Bolivia, Paraguay, and Argentina (Misiones and Corrientes). It is characterized by linear-subulate rosulate and cauline leaves, and by greenish flowers with narrow yellow wings and yellow perianth lobes.

The anthers of all three species have two apical crests. Anthers of *Burmannia capitata* are unappendaged at the base, while those of *B. biflora* have a short, obtuse median appendage, and those of *B. flava* an acute, pendulous one.

At least *Burmannia biflora* has been found growing with *Apteria* in our area, and there are records of achlorophyllous species of *Burmannia* growing with other burmanniaceous genera (see Jonker, 1938, p. 13), but there seem to be no records of two species of *Burmannia* occurring together.

The wide range of ecophysiological types found in the genus—from leafy-stemmed autotrophic epiphytes, through reduced, scale-leaved but chlorophyllous, terrestrial types, to achlorophyllous “saprophytes”—merits investigation. The range within the single genus is perhaps comparable to that exemplified by the gentianaceous genera *Obolaria-Bartonia-Voyria* (see Wood & Weaver) or by the orchidaceous series *Listera-Goodyera-Myrmechis-Zeuxine* (*Z. purpurascens*)-*Corallorhiza* arranged by Montfort & Küsters (see Furman & Trappe). Although the mycorrhizae and the associated fungus have been described for several species of *Burmannia*, Van der Pijl’s study of the endophytic fungus of *B. candida* Griff. ex J. D. Hooker, $2n = 12$, which he found to be a phycomycete, probably a member of the Peronosporaceae, appears to be the only attempt to identify the fungus associated with a species of *Burmannia* and to determine whether the same fungus is shared by different “saprophytes.”

The floral biology and breeding system do not seem to have been investigated for any species of *Burmannia*; there are only a few recorded chromosome counts; and there seem to have been no investigations of the chemistry.

To judge from the limited liquid-preserved material available, it appears that the flowers of *Burmannia capitata* are self-pollinated, for the pollen seems to be shed before the flower bud opens, and the stigmas are covered with germinating grains. In *B. biflora* the small inner tepals are curved inward above the anthers, hiding them from sight, and the three stigmas protrude between the inner tepals. Whether or not our species actually are annuals is not well established.

Pollen of 19 species of *Burmannia* was studied by Chakrapani & Raj, who found that most species have one-porate grains, while *B. dasyantha* Martius has atreme grains, several species have one- or two-porate grains, and *B. congesta* (Wright) Jonker has two-porate grains. Pollen grains are single (or in tetrahedral tetrads [or dyads] in *B. aprica* (Malme) Jonker). Brewbaker found *Burmannia* to be one of only 10 genera (out of 1908) in which both two- and three-nucleate pollen have been more or less reliably reported. He confirmed the three-nucleate condition of pollen of *B. biflora*, but the two-nucleate pollen reported for *B. Championii* Thw., $2n = 12$, and *B. candida* should be reconfirmed. Both the Polygonum and the Allium types of megagametophyte de-

velopment have been described in *Burmattia*. *Burmattia coelestis* is aposporous, with an unreduced megagametophyte. Embryos are rudimentary and undifferentiated (reportedly four-celled in *B. coelestis* and ten-celled in *B. capitata*). Endosperm ontogeny is A-form helobial in *B. coelestis* and *B. pusilla* (see Swamy & Krishnamurthy).

Burmattia appears to be most closely related to the South American genera *Campylosiphon* Benth (C. *purpurascens* Benth) and *Hexapterella* Urban (H. *gentianoides* Urban).

REFERENCES:

- Under family references see AJILVSGI, BAILLON, BENTHAM & HOOKER, BOWDEN, BRADE, BREWBAKER, BOLKHOVSKIKH *et al.*, CHAKRAPANI & RAJ, CIFERRI, CORRELL & CORRELL, DAVIS, EICHLER, ENGLER, ERDTMAN, ERNST & BERNARD (VII–XV), FURMAN & TRAPPE, GODFREY & WOOTEN, HATSCHBACH & GUIMARÃES, HUTCHINSON (1934, 1959, 1973), JOHOW (1885, 1889), JONES, JONKER (1938, especially pp. 18–26, 57–163; 1945, pp. 43, 44; 1948), LAWRENCE, LUBBOCK, MAAS, MELCHIOR, NETOLITZKY, RAMSBOTTOM, RAO, RENDLE, RICKETT, RIDLEY, SEUBERT, SWAMY & KRISHNAMURTHY, and WARD.
- AREKAL, G. D., & S. N. RAMASWAMY. Embryology of *Burmattia pusilla* (Wall. ex Miers) THW. [*sic*] and its taxonomic status. (In English; German abstract.) Beitr. Biol. Pflanzen 49: 35–45. 1973.
- DUNCAN, W. H., & L. E. FOOTE. Wildflowers of the southeastern United States. vii + 296 pp. Athens, Georgia. 1975. [*B. capitata*, 268, colored illus., 269; *B. biflora* mentioned, 268.]
- ERNST, A. Apogamie bei *Burmattia coelestis* Don. Ber. Deutsch. Bot. Ges. 27: 157–168. pl. 7. 1909.
- JOSEPH, J., R. ANSARI, & C. N. MOHANAN. *Burmattia Championii* Thw.—an addition to the flora of South India. Jour. Bombay Nat. Hist. Soc. 76: 552, 553. 1979 (publ. 1980). [Morphology, distribution, illustration.]
- LARSEN, K. Studies in the flora of Thailand. 14. Cytological studies in vascular plants of Thailand. Dansk Bot. Ark. 20: 211–275. 1963. [*Burmattiaceae*, 262, 263: *Burmattia coelestis*, $2n = ca. 32$; *B. Wallichii*, $n = 16$; *B. disticha*, $2n = ca. 136$.]
- MAAS, P. J. M. Notes on New World saprophytes II. Acta Bot. Neerl. 30: 139–149. 1981. [New species in *Sciaphila* (Triuridaceae); *Burmattia*, *Gymnosiphon*, *Dictyostega* (*Burmattiaceae*); new combinations in *Voyria* (*Gentianaceae*). *Burmattia Jonkeri*, *B. vaupesiana* Van Benthem & Maas, new spp., illustrated.]
- MARTIUS, C. F. P. VON. *Burmattia*. Nov. Gen. Sp. Pl. Brasil. 1: 9–12. pl. 5. 1823. [*B. bicolor*, *B. flava*, *B. dasyantha*.]
- MOLFINO, J. F. Una Burmanniácea interesante para Misiones: “*Apteria lilacina*” Miers. Physis 6: 328–330. pl. 1923. [*B. flava* noted as collected near Paggi, Alto Uruguay, Argentina.]
- PAI, R. M. Studies in the floral morphology and anatomy of the Burmanniaceae. I. Vascular anatomy of the flower of *Burmattia pusilla* (Wall. ex Miers) Thw. Proc. Indian Acad. Sci. B. 63: 304–308. 1966. [Cf. RAO under family references.]
- PIJL, L. VAN DER. Die Mycorrhiza von *Burmattia* und *Epirrhizanthes* und die Fortpflanzung ihres Endophyten. Rec. Trav. Bot. Néerl. 31: 761–779. 1934. [*B. candida* Engler, *B. coelestis* G. Don, *E. elongata* Blume; mycorrhizal fungus of *B. candida* a phycomycete, cf. Peronosporaceae.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1964. [*Burmattiaceae*, 330, 331; *B. biflora*, *B. capitata*; by H. E. AHLES.]
- RAO, V. S. The stamens of *Burmattia*. Jour. Univ. Bombay Sci. 36: 25–27. 1967.*

- . The orientation of the ventral bundles in the ovary of *Burmannia*. *Sci. Cult.* **34**: 253. 1968.*
- SCHININI, A. Notas sobre Burmanniaceas Argentinas. (English summary.) *Bol. Soc. Argent. Bot.* **16**: 349–354. 1975. [*B. flava* recorded from Prov. Misiones and Prov. Corrientes, extending range to 28°20' S lat.; *B. capitata* recorded from Prov. Corrientes, extending range to 28°15' S lat.]
- STEYERMARK, J. A. Una nueva *Burmannia* de seccion *Foliosa* Jonker. *Acta Bot. Venez.* **6**: 89–91. 1971 (publ. 1972). [*B. Carrenoi* Steyermark. described from Estado Bolivar, Venezuela; closest to *B. Wercklei* Schlechter, of Costa Rica. Stems leafy, to 30 cm long, flowers hanging, as in *B. longifolia*, the only Asiatic species assigned to this section by Jonker.]
- TAYLOR, R. J., & C. E. TAYLOR. Additions to the vascular flora of Oklahoma. *Sida* **7**: 361–368. 1978. [*B. capitata*, 364; bog 5.5 mi W of Antlers, Pushmataha Co.]
- THOMAS, R. D. *Burmannia biflora* (Burmanniaceae) and *Bowlesia incana* (Umbelliferae) in Ouachita Parish, Louisiana. *Sida* **3**: 183, 184. 1967.
- WARD, D. B. The genus *Anonymos* and its nomenclatural survivors. *Rhodora* **64**: 87–92. 1962. [*B. capitata* (J. F. Gmelin) Martius, 88; cf. WILBUR.]
- , ed. Rare and endangered biota of Florida (P. C. H. PRITCHARD, series ed.). Vol. 5. Plants. xxix + 175 pp. Gainesville, Florida. [1979.] [Fakahatchee *Burmannia*, *Burmannia flava* Martius, prepared by D. B. WARD, pp. 133, 134; includes account of collection by L. J. Brass, January 14, 1946. Only other collection known from Florida made by J. P. Standley, October 12, 1916.]
- WILBUR, R. L. The identity of Walter's species of *Anonymos*. *Jour. Elisha Mitchell Sci. Soc.* **78**: 125–132. 1962. [*B. capitata* (J. F. Gmelin) Martius the correct name for *Anonymos capitata* Walter; cf. WARD.]

Subtribe **Apteriinae** Jonker

2. **Apteria** Nuttall, *Jour. Acad. Nat. Sci. Philadelphia* **7**: 64. *pl.* 9, *fig.* 2. 1834.

Small, erect, presumably annual mycotrophic herbs lacking chlorophyll. Roots short and thin. Stem simple (sometimes branched above), violet to purple, with 1 to few (to ca. 6, rarely to 10) flowers. Leaves small, scalelike, sessile. Flowers about 1[–2] cm long, the perianth blue, violet, or purplish, rarely white [or blue and white], narrowly campanulate [or salver or funnel shaped]; perianth lobes 6, all the same length, the outer ovate, the inner much narrower, the united part of the perianth more than 3 times the length of the lobes. Stamens adnate to perianth tube below the 3 inner segments, each subtended by a broadly V-shaped, almost saclike, vasculated ridge (cf. FIGURE 1, d–f); filament short and thick, bearing on the abaxial side a large, 2-lobed wing and at the top expanded into a broad horizontal connective; locules borne horizontally and opening latrorsely, exposing the large pollen grains (in tetrads) in 2 masses. Ovary ovoid, abruptly tapering into the filiform style which is expanded into 3 short branches at the top, each branch terminated by a dish-shaped stigma at the level of 2 of the anther locules of 2 adjacent stamens; ovary 1-locular with 3 large parietal placentae bearing numerous minute ovules. Capsule crowned by the persistent perianth, opening from the base by 3 upward-curling valves, the placentae persistent. Seeds minute, very numerous, $\pm$ ellipsoid; embryo undifferentiated; endosperm consisting of 50–80 large cells. TYPE SPECIES: *A. setacea* Nutt., nomen superfluum = *A. aphylla* (Nutt.) Barnh. ex J. K. Small (*Lobelia aphylla* Nutt., 1822). (Name from Greek, *a*, without, and *pteron*,

wing—wingless, in contrast with the three-winged flower of *Burmannia bicolor* L., which Nuttall knew as *Tripterella caerulea* Ell.) — NODDING NIXIE (see J. K. Small, Man. SE. Flora, 1933), a vernacular name of unknown origin, possibly coined, but not very appropriate since the flowers seldom nod.

Three closely related species of the warmer parts of the Western Hemisphere: *A. aphylla*, which ranges from the southern United States to Brazil and Bolivia; *A. lilacina* Miers, known from Colombia, Brazil, and Argentina; and *A. gentianoides* Jonker, of Brazil, Paraguay, and Bolivia. The three differ in the shape and size of the perianth and in the structure of the stamens. Our single species, *A. aphylla* (*A. setacea* Nutt., *A. boliviana* Rusby, *A. hymenantha* Miquel, *A. Ulei* Schlechter), is distributed from northeastern Florida and southwestern Georgia, westward through southern Alabama, Mississippi, and Louisiana, to southeastern Texas, and southward through Florida to Cuba, Hispaniola, Puerto Rico, Jamaica, Dominica, Guadeloupe, and Trinidad, as well as from Mexico and Belize southward through Costa Rica and Panama to Colombia, the Guianas, and Brazil and Bolivia. Jonker reduced *A. hymenantha* to *A. aphylla* var. *hymenantha* (Miquel) Jonker but noted that "intermediate forms occur between the species and its variety especially in the West-Indian Islands." Other workers may well decide on still further reduction.

A confusion that began with Nuttall himself is shown in Jonker's distribution map (1938, p. 37), which shows *Apteria aphylla* as occurring northward in the Mississippi Embayment past St. Louis, Missouri, and in the citation of four collections from the coast of Mississippi (p. 205) as being from Missouri. Nuttall (1834, p. 65) wrote, "Found in the vicinity of St. Louis, Missouri, by Mr. L. C. Beck; in Alabama by Doctor Gates; and discovered in East Florida by Mr. Ware, probably on the margins of shallow grassy ponds, the situations mostly affected by the *Tripterellas*." Whether or not Nuttall confused "St. Louis" with either Bay St. Louis or St. Louis Bay on the coast of Mississippi, or whether a label mistake was involved, *Apteria* occurs only in the southernmost parts of both Mississippi and Louisiana and is not known northward in either Arkansas or Missouri.

Little seems to be recorded about the biology of any of the species of *Apteria*. All are presumed to be annuals and saprophytes via their mycorrhizal association, although the habitats of at least *A. aphylla* (acid, swampy woods, at the edges of bogs and hammocks, and in pine flatwoods, often in the company of *Burmannia*) do not seem to be favorable for a saprophyte. It seems more likely that these are epiparasites (via their mycorrhizae) of the *Galeola* (Orchidaceae) or *Monotropa* (Ericaceae) type. Uphof, who studied *A. aphylla* at Orlando, Florida, did not observe insect visitors to the flowers, and on the basis of the presence in the flowers of pollen-eating mites covered with pollen and crawling over the stigmas, the position of the stigmas (between the pollen masses of adjacent anthers), and the apparent adnation of anther, pollen, and stigma, concluded that the flowers are mostly self pollinated. The essentially smooth pollen is borne in tetrahedral tetrads ca. 47 μ m in diameter (Chakrapani & Raj) and is three-nucleate at the time it is shed (Brewbaker). The megagametophyte is of the *Polygonum* type. The embryo is only four-celled at the time the seed is shed.

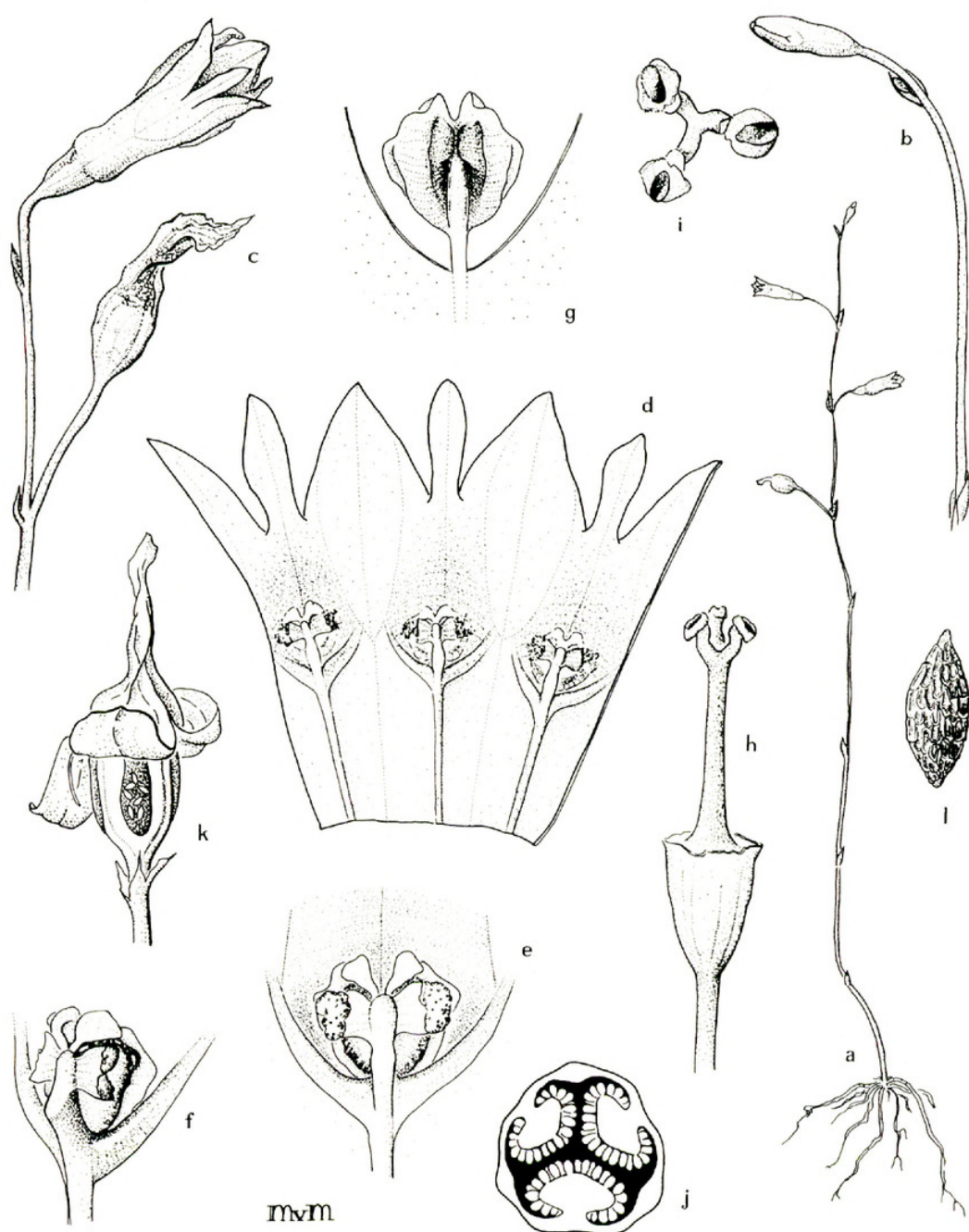


FIGURE 1. **Apteris**. a-l, *A. aphylla*: a, plant with immature fruit, two flowers at anthesis, and flower bud, $\times \frac{3}{4}$; b, flower bud, $\times 3$; c, flower and immature fruit with persistent perianth, $\times 3$; d, perianth laid open to show stamens adnate to perianth, each stamen subtended by a V-shaped, saclike ridge, $\times 6$; e, stamen, adaxial side, with adjoining parts of perianth, showing broad horizontal connective with masses of pollen tetrads at both sides and two-lobed, winglike appendage of filament behind, edges of wing inrolled, apex of wing lobes folded toward sides, $\times 12$; f, same, oblique view, pollen removed to show two of four anther locules, $\times 12$; g, stamen, abaxial side, showing two-lobed, winglike appendage of filament, anther connective and locules invisible behind it, perianth partially cut away to expose stamen, $\times 12$; h, gynoecium, perianth cut away from top of ovary, $\times 6$; i, stigmas and style branches from above, $\times 12$; j, diagrammatic cross section of ovary to show placentation, $\times 12$; k, capsule crowned by persistent perianth, three valves splitting away from placentae and curling upward, a few seeds persistent on placentae, $\times 6$; l, seed, $\times 50$.

The mature fruits are almost never collected and are little known. They should be looked for in localities where the plants have been found in flower. The capsule opens by three upward-curling valves, and the three placentae are persistent as shown in FIGURE 1, k.

REFERENCES:

Under family references see AJILVSGI, BAILLON, BENTHAM & HOOKER, BRADE, BREWBAKER, CHAKRAPANI & RAJ, CIFERRI, CORRELL & CORRELL, DAVIS, ENGLER, ERDTMAN, GODFREY & WOOTEN, HATSCHBACH & GUIMARÃES (*pl.* 3), JOHOW (1885), JONES, JONKER (1938, especially pp. 35-37, 203-211; 1945, pp. 46, 47), LUBBOCK, MAAS, MELCHIOR, MIERS (pp. 545-548), NETOLITZKY, RICKETT, SEUBERT, and WARD.

HOOKER, W. J. *Apteria orobanchoides*. *IC. Pl.* 3: *pl.* 254. 1840. *Apteria setacea*. *Ibid.* 7: *pl.* 660. 1844.

MOLFINO, J. F. Una Burmaniácea interesante para Misiones: *Apteria lilacina* Miers. *Physis* 6: 328-330. *pl.* 1923. [Northeasternmost province of Argentina.]

NUTTALL, T. A description of some of the rarer or little known plants indigenous to the United States, from the dried specimens in the herbarium of the Academy of Natural Sciences in Philadelphia. *Jour. Acad. Nat. Sci. Philadelphia* 7: 61-115. *pls.* 9-12. 1834. [*Apteria*, 61-66, *pl.* 9, *fig.* 2.]

UPHOF, J. C. T. *Apteria aphylla*. Beiträge zur Kenntnis der Burmanniaceae *Apteria aphylla* (Nutt.) Barnhart. *Österr. Bot. Zeitschr.* 78: 71-80. 1929. [Habitat, morphology, pollination, anatomy of stem, leaf, root, and seed.]

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