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THE GENERA OF BROMELIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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BROMELIACEAE A. L. de Jussieu, Gen. Pl. 49. 1789, "Bromeliae," nom. cons.
(BROMELIA FAMILY)

Perennial, stemless or sometimes caulescent herbs, [terrestrial to] optimally or even obligately epiphytic. Roots usually present, but often serving only as holdfasts in the epiphytic species. Leaves alternate, spirally arranged, in numerous ranks (polystichous) or rarely in two ranks (distichous), rosulate or distributed along and almost always concealing more elongate stems, more or less dilated below into a sheath, the blade varying from narrowly and regularly triangular (with a dense indument) to

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In this collaborative effort the senior author has brought to bear his monographic interest and experience in the Bromeliaceae and the junior author has added observations applicable especially to the southeastern United States. The literature references are intended to sample both the taxonomic and general biological literature, as well as some of the pertinent horticultural references on this fascinating family. We are indebted to Julien Marnier-Lapostille for preserved material of *Guzmania*; to Richard A. Howard for living material of *Catopsis, Guzmania,* and *Tillandsia*; to Loren W. Smoyer for living plants of *Catopsis*; to Daniel B. Ward for information on the blight of Spanish moss in Florida; and to Frank C. Craighead and George Avery for their generosity in sharing their field knowledge of Florida bromeliads at various times. A number of the plants used in the illustrations, all of which were prepared from living material, were grown to flower or fruit in Boston, Massachusetts, in the greenhouse of Theodore J. Schultz. The illustrations were drawn by Dorothy H. Marsh, Virginia Savage, Karen S. Velmure, and Sydney B. DeVore under the direction of the junior author, who prepared the dissections.

liguliform (with an inconspicuous indument), the indument consisting of peltate scales, the leaf margin entire or spinose-serrate. Inflorescence terminal or lateral or pseudolateral by the elongation of the stem (sympodial), usually scapose, indeterminate, branched or simple, rarely one-flowered, usually bearing brightly colored conspicuous distichous or polystichous bracts, each with an axillary flower. Flowers perfect, 3-merous, regular. Perianth of 2 differentiated whorls, the sepals and petals free or connate. Stamens 6, in 2 series of 3; filaments free or agglutinated or adnate to the petals; anthers basifixed or dorsifixed, introrse, dehiscing by vertical slits; pollen ellipsoid or globose, 1-sulcate or 2- [3- or 4-]porate [or polyporate]. Gynoecium 3-carpellate, syncarpous; style 3-parted; stigmas 3, often spirally twisted; ovary superior or inferior, 3-locular; placentae axile, extending the length of the locule or variously reduced (e.g., apical in *Ananas*); ovules usually numerous, anatropous, the 2 integuments nearly equal. Fruit a capsule [or berry]. Seeds plumose [or winged or naked]. Embryo small, situated at the base of the abundant mealy endosperm. TYPE GENUS: *Bromelia* L.

An almost exclusively neotropical family of about 45 genera with some 2000 species, but including two genera of temperate latitudes in Chile and one species (*Pitcairnia Feliciana* (A. Chev.) Harms & Milbraed) native to westernmost Africa. Three native genera and one introduced genus occur in our area.

The family is delimited by its mealy endosperm, regular (actinomorphic) or subregular trimerous flowers with contrasting sepals and petals (heterochlamydeous), and trilocular ovary usually with numerous ovules. However, Bromeliaceae are identifiable even when sterile, by the curious indument of peltate scales. The flowers are relatively simple, showing scarcely any reduction of parts in the direction of the Eriocaulaceae or any tendency toward zygomorphy in the direction of the higher Commelinaceae and Pontederiaceae. In fact, the Bromeliaceae would seem to be the most primitive family of the order Farinosae, and some recent authors have emphasized this by placing the family in an order of its own.

Division into three nearly equal subfamilies is primarily on the basis of fruit and seed characters, along with some good vegetative correlations. In the Pitcairnioideae [2] the fruit is dry and usually dehiscent, with the

[2] At the rank of subfamily, the name Navioideae Harms (1929) has priority over Pitcairnioideae Harms (1930) when both *Navia* and *Pitcairnia* are included in the same subfamily, as in the present classification. The first use of the rank subfamily in the Bromeliaceae appears to have been by Harms, who in 1930 raised the conventional tribes Pitcairnieae Meisner (1842), Tillandsieae Dumortier (1829), and Bromelieae Dumortier (1829) to subfamilial rank and recognized Navioideae Harms (1929) as a fourth subfamily. In his treatment in *Das Pflanzenreich* (1934), however, Mez used only three subfamilies, Pitcairnioideae, Tillandsioideae, and Bromelioideae, in his classification, reducing Navioideae to the rank of tribe under Pitcairnioideae. These three subfamilial names, which have been used in all of the subsequent literature, tie in with and continue the use of the tribal names that had been previously applied to the same three basic taxa in the Bromeliaceae. Since the introduction of the name Navioideae for the subfamily that includes both *Navia* and *Pit-*

carpels always distinguishable and the seed with entire appendages or rarely with none. The leaves are almost always spinose-serrate, and the arrangement of cells in their scales is quite irregular. With rare exceptions the plants are terrestrial or saxicolous. The Pitcairnioideae do not occur in our area but approach it closely in Cuba and in Texas.

The Tillandsioideae resemble the Pitcairnioideae in the always dry, dehiscent fruit, but the seeds have plumose appendages, and the leaves are invariably entire. The cells of the leaf scales are arranged in a regular geometric pattern with four equal ones in the center (cf. FIGURE 2, 1). The plants generally are epiphytic. All three of our indigenous genera belong to this subfamily.

The Bromelioideae are unique in the family in their baccate fruit with wholly united carpels and are almost unique in their unappendaged seeds. The leaves with their marginal spines and unorganized scales are very similar to those of the Pitcairnioideae and have led some students to consider these subfamilies to be much more closely related to each other than to the Tillandsioideae. The trend toward epiphytism in the Bromelioideae is about midway between the two other subfamilies. *Ananas*, which has some record of persistence in southern Florida but which is included here only tentatively as naturalized, is strictly terrestrial.

The leaf in the Bromeliaceae is considered by some to be a phyllode, but the evidence is not wholly convincing and must be adjusted to the formation of a new sheath, blade, and petiole in the case of a number of species. There is always some distinction between sheath and blade, and usually it is quite marked. The blade usually varies from narrowly triangular to liguliform, with no contraction at base in either form, but occasionally it can be broadly elliptic, with a slender petiole.

In at least the Tillandsioideae and Bromelioideae, the leaf scales have evolved into very effective organs for absorbing water and transmitting it to the interior of the leaf. In the epiphytic species the scales have taken over the function of the roots and absorb organic compounds as well. Their distribution on the leaf surface correlates with the habit and habitat of the two common epiphytic types. In the more or less caulescent xerophytic type with narrow leaf blades, the scales completely cover the blades, protecting them from the sun and giving an even supply of water that is wholly taken up by the leaf tissue. In the rosette mesophytic type, the broad leaf blades carry the water to the tanks formed by the sheaths, and the scales of the blades are reduced, while those of the sheaths become more important in the absorption of both organic and inorganic compounds.

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cairnia would cause needless confusion, it is proposed that the provisions of Article 11 of the *International Code of Botanical Nomenclature* (1972), which allows for the conservation of names from "family to genus inclusive," be invoked, and that Pitcairnioideae be conserved over Navioideae:

Subfam. Pitcairnioideae Harms in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **15a**: 102. 1930, nom. cons. prop. TYPE: *Pitcairnia* L'Heritier.

Subfam. Navioideae Harms, Notizbl. Bot. Gart. Mus. Berlin-Dahlem **10**: 575. 1929, nom. rejic. prop. TYPE: *Navia* Martius ex Schultes f.

This second type of habit, with water stored in the rosette, allows a symbiotic relationship with many more or less aquatic species of plants and animals, furnishing shelter and receiving materials from waste products. In our area this relationship is confined to southern Florida and, to date, has not involved any insects that are carriers of disease, although in a few more tropical areas bromeliads have harbored malaria-carrying mosquitoes, to the detriment of public health. The possibility of the host plant's being directly insectivorous has been explored and disproved.

The primitive type of inflorescence appears to be a many-flowered terminal panicle, which has evolved by reduction to such extremes as the one-flowered pseudolateral (actually terminal) inflorescences of *Tillandsia usneoides* and the spicate compound fruit of *Ananas*. The family is almost unique in its flowering response to chemical stimuli such as carbide, rocket fuel, and even ripening apples.

Pollination is by insects and birds, especially hummingbirds, and by bats in the case of some night-blooming species. Erdtman & Praglowski divide the family into two groups on the basis of pollen morphology (ca. 125 spp. in ca. 40 genera), the first with 1-colpate pollen grains, the second with 2-, 3-, 4-porate to polyporate grains. The pollen of all of the Pitcairnioideae and Tillandsioideae is of the 1-colpate type, but in the Bromelioideae both types occur and both are found in the genus *Aechmea*.

Chromosome counts made for 21 genera and about six per cent of the known species are $2n = 32, 34, 36, 42, 46, 48, 50, 52, 54, 56, 57, 64, 72, 75, 96, 98, 100, 108, 126$, and 150. These counts show little relation to subfamily grouping, except in the Pitcairnioideae, where the base number appears to be 25, and they vary within genera so that little can as yet be inferred from them. In addition, the identification of the plants from which many of these counts were obtained is suspect, and four of six principal papers on chromosome numbers apparently are not backed by voucher specimens. (See McWilliams in Smith & Downs for a review.)

Economically, the family is most noted for the pineapple, *Ananas comosus*, but *Tillandsia usneoides* has been used for pillow and mattress stuffing, especially in our area, and several species furnish strong fibers for cordage. Horticulturally, the Bromeliaceae are enjoying considerable popularity, and some exotic species have been recorded as spontaneous in Florida, although it remains to be seen if they will persist.

For a fuller summary of general information about the family see Bromeliales in *Encyclopedia Britannica*, ed. 15, 1974, and Smith & Downs (1974, introduction).

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KEY TO THE GENERA OF BROMELIACEAE IN THE SOUTHEASTERN UNITED STATES

A. Fruit dry, capsular; seeds plumose; ovary usually superior; leaves always entire. Subfam. TILLANDSIOIDEAE.
  B. Principal seed appendage basal, not outgrowing the capsule and therefore straight; stamens usually equal or nearly so.
    C. Petals free; flowers arranged distichously (in two rows) or solitary [rarely polystichous in a single spike, but the plant then with narrowly triangular leaf blades.] ..... 1. *Tillandsia.*
    C. Petals closely agglutinated in a tube at least to the height of the sepals (when weakly so, the inflorescence simple and the leaf blades liguliform); flowers always arranged polystichously. .. 2. *Guzmania.*
  B. Principal seed appendage apical, growing faster than the capsule and therefore folded over; stamens strongly unequal. ..... 3. *Catopsis.*
A. Fruit fleshy, baccate; seeds naked at maturity (although the ovules often appendaged); ovary inferior or nearly so; leaves nearly always spinose-serrate. Subfam. BROMELIOIDEAE. ..... 4. *Ananas.*

Subfam. TILLANDSIOIDEAE Harms

1. **Tillandsia** Linnaeus, Sp. Pl. 1: 286. 1753; Gen. Pl. ed. 5. 138. 1754.

Mostly epiphytic, caulescent or acaulescent plants of very diverse habit; roots reduced to wirelike holdfasts or completely lost. Leaves rosulate or fasciculate or distributed along a stem, polystichous or distichous, entire; blades liguliform or triangular or filiform. Scape usually distinct. Inflorescence terminal or rarely lateral or pseudolateral by the elongation of the stem, usually of distichous-flowered spikes [or sometimes a single polystichous-flowered spike formed by the reduction of the spikes to single flowers], or rarely the whole inflorescence reduced to a single flower. Sepals usually symmetrical, free or equally joined or only the two posterior ones joined. Petals free, naked. Stamens mostly equal or subequal, of various lengths relative to the petals and gynoecium; pollen 1-sulcate. Ovary superior, glabrous; ovules usually many, apically caudate. Capsule septicidal. Seeds erect, narrowly cylindric or fusiform; the short apical appendage undivided, the large plumose basal appendage straight, white. (*Renealmia* L., 1753, not *Renealmia* L. f., 1781, nom. cons.; *Caraguata* [Plumier] Adanson, 1763; *Dendropogon* Raf., 1825; *Strepsia* Nutt. ex Steudel, 1841; *Diaphoranthema* Beer, 1854; *Phytarrhiza* Vis., 1855.) LECTOTYPE SPECIES: *T. utriculata* L.; see Britton &

FIGURE 1. **Tillandsia** subgenus **Tillandsia.** a–j, *T. utriculata*: a, plant with flowers and fruit, × 1/20; b, cross section of flower — note three sepals, three free petals, six staminal filaments free from petals, three-loculate ovary with axile placentation, × 6; c, anther, adaxial side, × 6; d, upper part of style with stigmata, × 12; e, ovule at time of anthesis, the apex caudate, the micropyle below (at right), × 25; f, part of inflorescence branch with three nearly mature fruits, × ½; g, partly mature seed oriented as in "e," × 6; h, mature seed with basal appendage of hairs, oriented as in "e" and "g," × 1; i, tip of hair from seed appendage, × 25; j, embryo, oriented as in seed (h), × 12. k, *T. Balbisiana*: plant with developing fruit, × ¼. l–n, *T. Bartramii* (*T. simulata*): l, flowering plant, × ¼; m, inflorescence with open flower, × 1; n, flower, showing tubular corolla and imbricate sepals, × 1 ½.

Millspaugh, Bahama Fl. 64. 1920. (Name in honor of Elias Tillands, professor in Åbo [Turku], Finland, 1640–1693; also a play on words, since the name means "by land," in reference to the professor's abhorrence of travel by water and Linnaeus's mistaken idea that the scales of *Tillandsia* served to shed water.) — WILD PINE.

A genus of over 400 species in seven subgenera, ranging from coastal Virginia, through the West Indies and Mexico, to central Argentina and Chile; represented in our area by 12 native species in two subgenera and a single introduced species in a third subgenus.

The three subgenera of *Tillandsia* in our flora are all widely divergent from the ancestral type of the northern Andes, subg. ALLARDTIA, and presumably have arrived by different routes. Subgenus TILLANDSIA expanded northward, but subg. PHYTARRHIZA moved south to the central Andes and was brought here by man, while its descendant, subg. DIAPHORANTHEMA, developed still farther south but rebounded northward, thanks to the most effective means of dispersal in the Bromeliaceae. Small's *Manual of the Southeastern Flora*, disregarding the complete picture, divides *Tillandsia* into three separate genera. While there may be some grounds for separating *Dendropogon* and *Diaphoranthema* from *Tillandsia* on the floral characters, to take *Diaphoranthema* from *Dendropogon* on a purely habital basis would logically require a genus for each species of *Tillandsia*.

Subgenus TILLANDSIA, with petals erect and forming a long tube, stamens exserted, and style elongate, includes over 100 species distributed from southern Georgia and southern Texas to central Brazil and Bolivia, with the greatest concentration in Mexico. The subgenus is represented in our area by ten species that range in size from *Tillandsia utriculata* L., which may form rosettes 1.2 m. across and paniculate inflorescences 2 m. tall, to *T. pruinosa* Sw., which may be only 7.5–15 cm. tall, with the inflorescence reduced to a 2–5-flowered spike. Other representatives are *T. flexuosa* Sw. (*T. aloifolia* Hooker), *T. Balbisiana* Schult. f., *T. Valenzuelana* A. Rich., *T. circinnata* Schlecht., *T. polystachia* (L.) L., *T. fasciculata* Sw. (*T. hystricina* Small), *T. setacea* Sw. (*T. tenuifolia* of authors, not L.; see Smith, 1962), and *T. Bartramii* Ell. (*T. juncea* of authors, not (Ruiz & Pavon) Poiret, *T. myriophylla* Small, *T. simulata* Small; see Smith, 1966). All except the last species are well known in the West Indies, and some have more extensive distributions.

Tillandsia Bartramii is the most northern species of the subgenus, its range extending from midpeninsular Florida northward well into Georgia (Ben Hill and Liberty counties) and apparently at least formerly into southeastern South Carolina (cf. *Leavenworth* [GH]). *Tillandsia utriculata* reaches southern Georgia, but all of the others, with the possible exception of *T. fasciculata* (see Brooks), are limited to Florida.

At the southern edge of its range in central Florida (e.g., in Polk County), *Tillandsia Bartramii* can be found growing on the same tree with *T. setacea*, there near its northern limit. Although the two are frequently

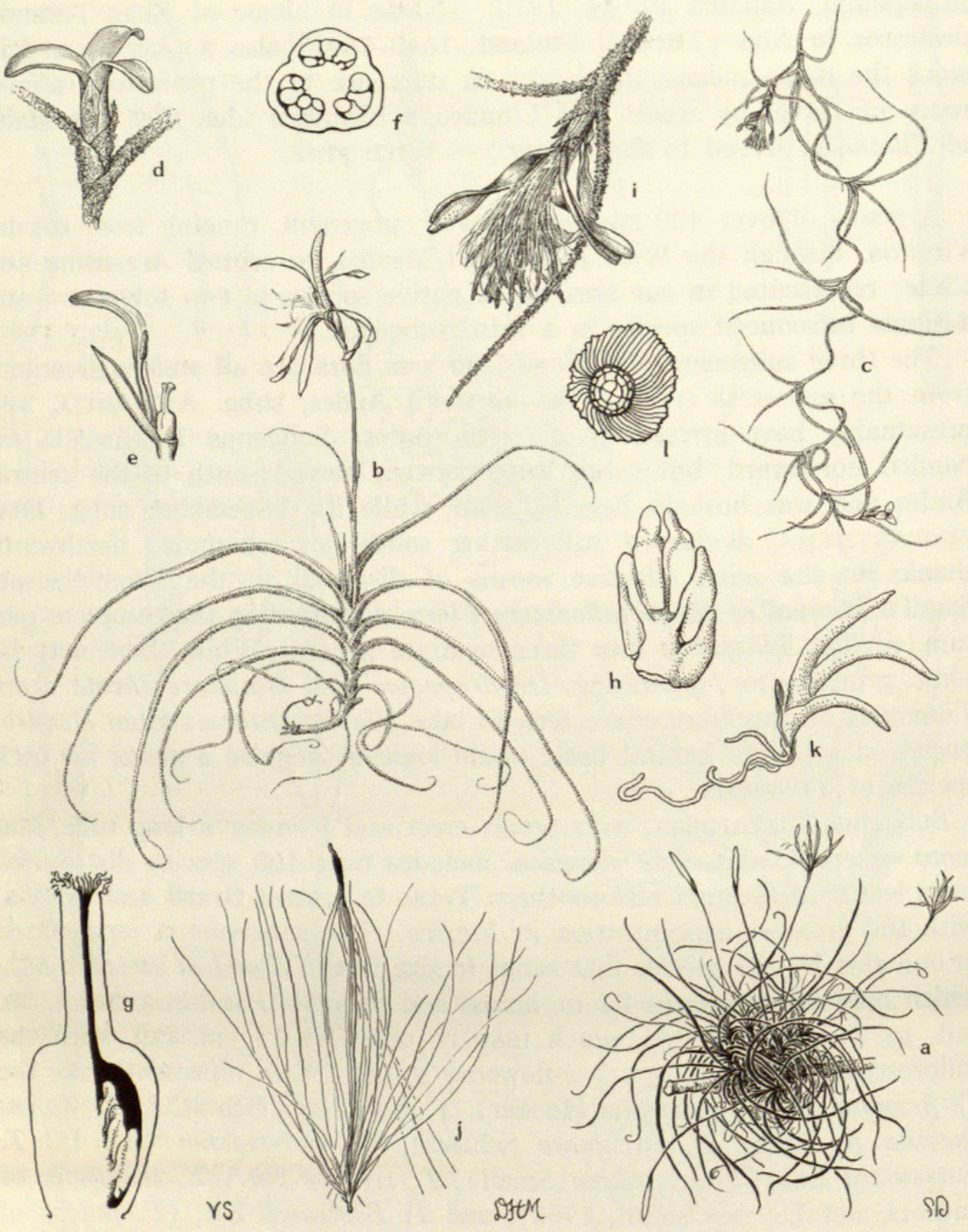

FIGURE 2. **Tillandsia** subgenus **Diaphoranthema.** a, b, *T. recurvata*: a, fruiting plant on branchlet, × ¼; b, single stem with open capsule and seeds — note sympodial growth by axillary shoot at left, × ½. c–l, *T. usneoides*: c, stem with flower and open fruit, × ½; d, flower, × 2; e, flower with 2 sepals, 2 petals, and 5 stamens removed to show gynoecium, × 2; f, cross section of ovary, diagrammatic, × 15; g, gynoecium in vertical section to show placentation and stylar canal, diagrammatic, × 15; h, placenta and ovules from one locule, × 20; i, open capsule with seeds, × 2; j, seed with basal appendage of hairs, × 2; k, seedling, × 4; l, small scale from leaf, × 50.

confused, they are quite distinct (see Smith, 1966), and hybrids between them are unlikely, since *T. Bartramii* flowers in spring, while *T. setacea* flowers in August and September. Another spring flowering species, *T.*

fasciculata, in the northern part of its range in Florida, occurs with *T. Bartramii*, which is extremely variable in this area, strongly suggesting a hybrid swarm. The chromosome number of *T. Bartramii* has not yet been reported, but counts of $2n = 64$ and $2n = 56$ have been recorded for *T. fasciculata* and *T. setacea*, respectively.

Subgenus PHYTARRHIZA (Vis.) Baker, members of which have large and showy, broadly elliptic to orbicular petal blades and stamens that are deeply included but exceed the very short style, comprises 35 species native from Uruguay and northern Argentina to Trinidad and Central America. *Tillandsia Lindenii* Regel, $2n = 64$, of Peru, is widely cultivated and is apparently established in Florida in the Tampa region.

Subgenus DIAPHORANTHEMA (Beer) Baker includes some 26 species of relatively small plants with simple inflorescences; small, narrow, inconspicuous petal blades; and stamens that are deeply included but exceed the very short style. Its species cover the whole American range of the family, and the two in our area, *T. recurvata* (L.) L. (*Diaphoranthema recurvata* (L.) Beer) and *T. usneoides* (L.) L. (*Dendropogon usneoides* (L.) Raf.), are the most widely distributed members of the family. *Tillandsia usneoides*, Spanish moss, long moss, Florida-moss, wood-crape, or crape-moss, $2n = 16$, extends along the Coastal Plain from Virginia to Florida and Texas (rarely entering the Piedmont southward), on into Mexico, and is scattered southward through Central America and the West Indies to central Argentina and Chile, always in relatively humid habitats. Growing on trees in weird-looking, long, gray festoons and often very abundant, it attracts attention in the southeastern United States in a way no other plant does. In 1969 a mysterious blight was reported to be destroying Spanish moss in ten counties in Florida and later on more extensively in Florida, as well as in southeastern Georgia, South Carolina, and Mississippi. Insects, viruses, and air pollution were suspected variously, but Roberts, Jensen, & Weber showed that the blight was caused by a fungus, *Fusarium solani* (Mart.) Appel & Wr. The plant now appears to be recovering in most areas. For details of the structure, life history, and ecology of *T. usneoides*, see especially Billings; Garth; Guard & Henry; Penfound & Deiler; and Tomlinson.

Tillandsia recurvata, ball moss, occurs in more xeric habitats than those of *T. usneoides* in Florida, Louisiana, and Texas, and is the only bromeliad in Arizona. It is widely distributed through the West Indies, Mexico, and Central America to northern Argentina and Chile. Considerable ecotypic differentiation must be involved, since it occupies a variety of habitats from tropical lowland to upland semidesert areas.

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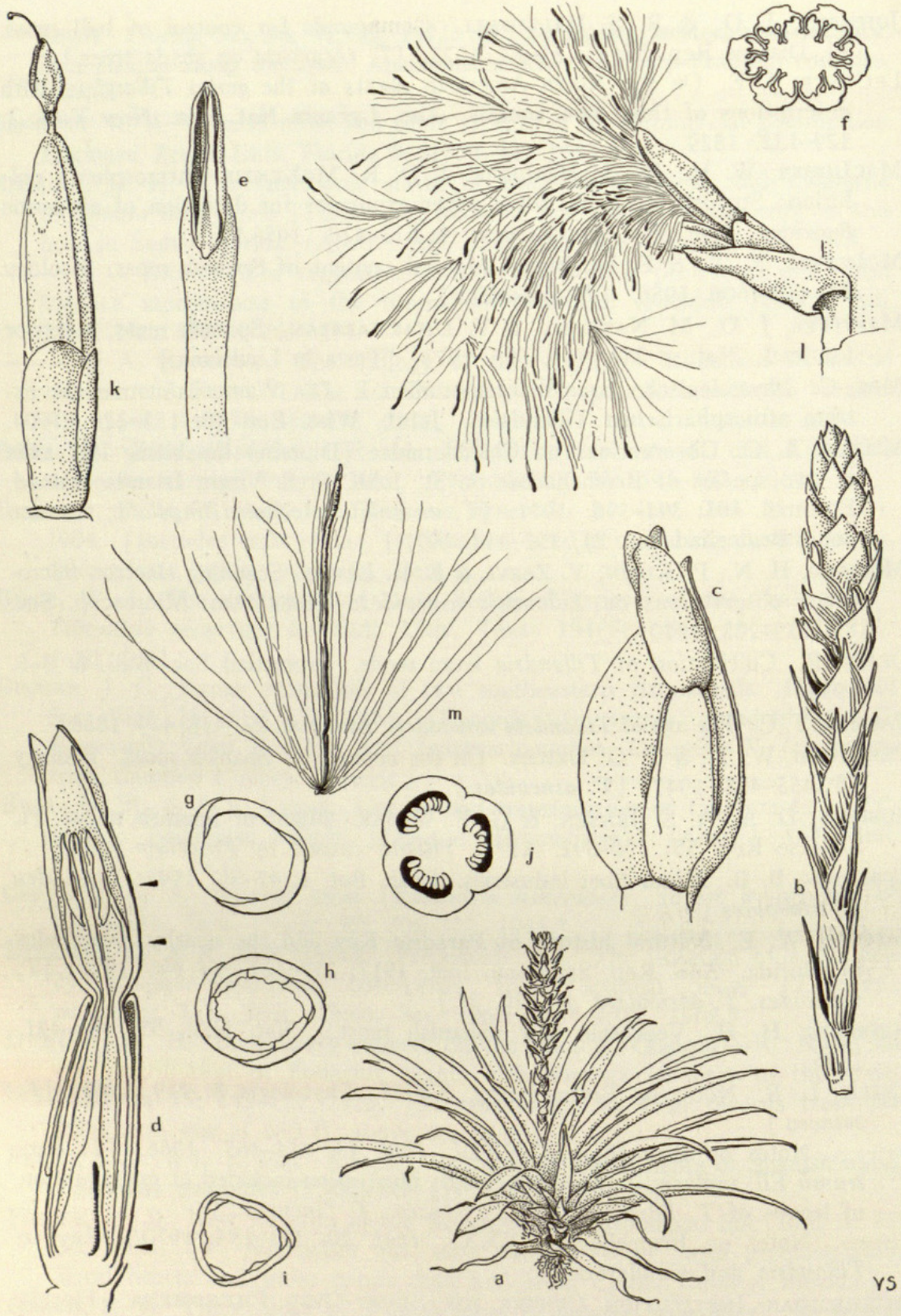

FIGURE 3. **Guzmania.** a–m, *G. monostachia*: a, plant with mature fruit — note new shoot from near base, × ⅙; b, inflorescence, × ½; c, flower with subtending bract seen from adaxial side, × 2; d, flower in vertical section, × 3; e, anther (pollen shed) and upper part of filament, × 5; f, anthers in cross section after anthesis, anthers agglutinated but not connate, × 8; g–i, petals and staminal filaments (h, i) in cross section at levels indicated on "d" — note agglutination of petal margins to each other and of stamens to petals, vascular

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2. Guzmania Ruiz & Pavon, Fl. Peru. Chile. 3: 37. 1802.

Acaulescent [or rarely long-caulescent] mostly epiphytic plants. Leaves polystichous, entire; sheaths usually conspicuous; blades mostly ligulate in shape, with inconspicuous scales. Inflorescence simple [or compound], the bracts usually conspicuous and often brightly colored; flowers always polystichously arranged. Sepals usually somewhat connate. Petals with edges overlapping and closely agglutinated, but not truly connate (see FIGURE 3, g–i), naked, white [or yellow]. Stamens usually included; filaments more or less agglutinated to the petals but not truly adnate (see FIGURE 3, g–i); pollen 1-sulcate. Ovary wholly superior, pyramidal, ellipsoid, or ovoid, glabrous; ovules many, densely glomerate. Capsule septicidal; seeds with a long, straight, usually brownish basal coma. (*Caraguata* Lindley, 1827, not Adanson, 1763; *Massangea* E. Morren, 1877; *Sodiroa* André, 1877; *Schlumbergera* E. Morren, 1883, not Lem., 1858.) TYPE SPECIES: *G. tricolor* Ruiz & Pavon = *G. monostachia* (L.) Rusby ex Mez. (Named in honor of Anastasio Guzman, 18th-century Spanish naturalist and apothecary.)

A genus of more than 120 species extending from southern Florida and southern Mexico to central Brazil and Bolivia, with its main con-

bundles not shown, × 4; j, diagrammatic cross section of ovary to show placentation, × 8; k, nearly mature capsule capped by marcescent corolla and persistent style, × 1 ½; l, opening capsule with seed being extruded by drying and expanding basal appendages, × 1; m, seed with partially expanded basal appendage, × 3.

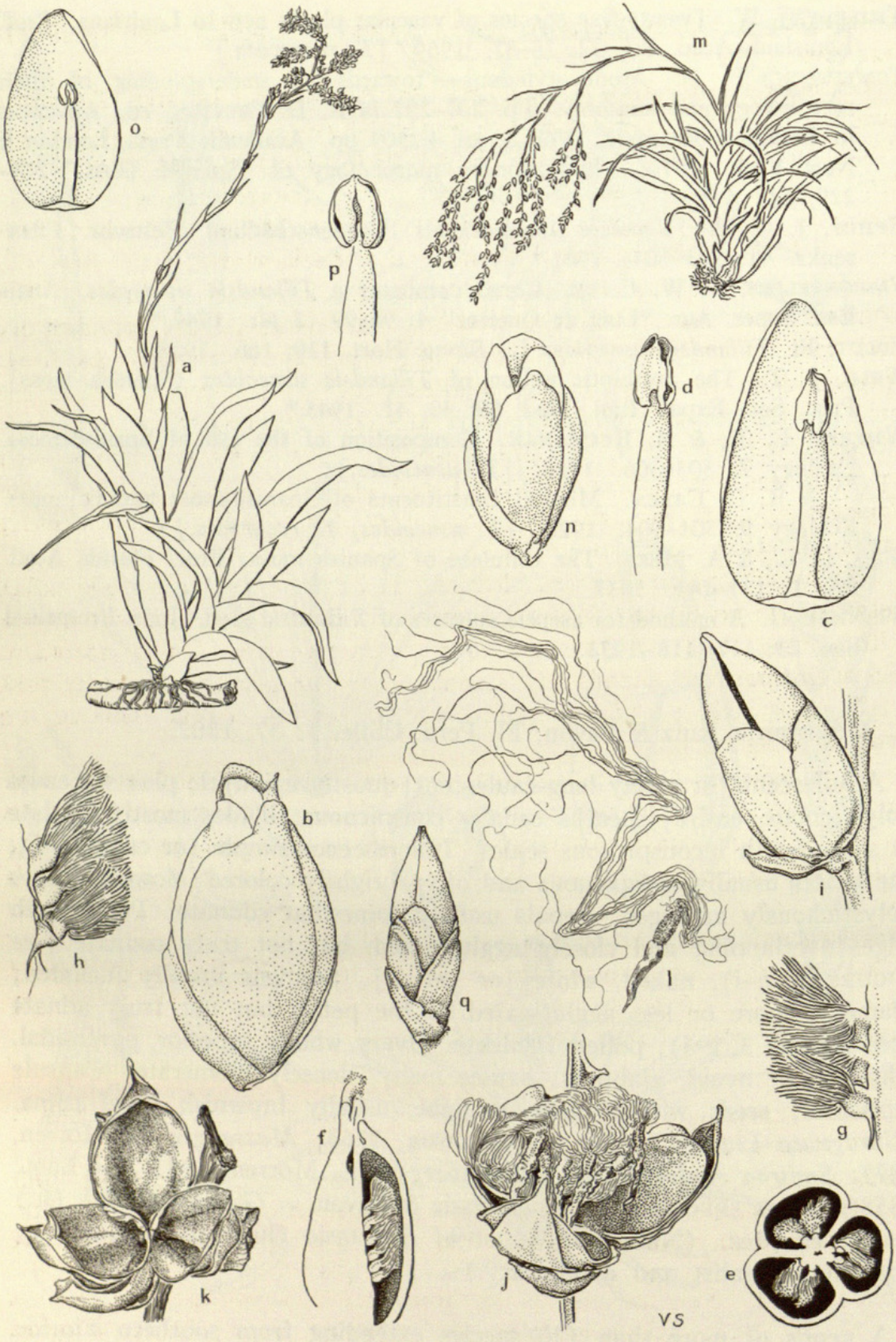

FIGURE 4. **Catopsis.** a–l, *C. Berteroniana*: a, plant in fruit — note new shoot at base, × ⅛; b, flower with subtending bract, × 3; c, petal with stamen adnate at base, × 4; d, antesepalous stamen with dehisced anther, × 4; e, cross section of ovary, showing two rows of ovules in each locule, semidiagrammatic, × 5; f, gynoecium in vertical section, showing one row of ovules in locule at right, × 4; g, h, two views of three ovules, showing elongated integument below and distal tuft of hairs that grows into terminal appendage of seed (l), × 12;

centration in the northern Andes and Central America; one species in our area.

Guzmania monostachia is native to the hammocks and *Taxodium* swamps of southern Florida, extending thence to the West Indies and Nicaragua, northern Brazil, and Peru. In Florida the plant flowers from late May through July (Craighead). The inflorescence is very conspicuous, the upper bracts being pink to salmon [or red], the lower ones pale with dark stripes (see FIGURE 3, b). Each white-petaled flower is open for a single day and, in cultivation at least, is self-pollinated. The plumose seeds are an effective means of dispersal. As the capsules dry and open at maturity, the filamentous basal appendages of the seeds spread out as they dry, and the whole cloudlike mass expands out of the capsule, the inside walls of which are dark brown, shiny, and very smooth (see FIGURE 3, l). The incredibly light seeds are carried even by very weak air currents in the forest interior. The filaments of the appendage catch on almost anything they touch, effectively anchoring the seed. (Obs. C. E. W.).

The most important generic character in *Guzmania* is the pseudo-fusion between the petals and filaments, which simulates a sympetalous corolla with adnate stamens. Although there is no real connation or adnation, the agglutination of petals and stamens is by an adhesive so strong that fresh petals will rupture irregularly under tension, rather than at the lines of meeting.

Harms divided *Guzmania* into five genera and Mez split it into two, largely on the basis of habital characters. These, although striking in the extremes, have so much intergradation that they are quite unusable. The only floral character is the degree of fusion of the sepals, but again there is no firm line of demarcation. In any event, *G. monostachia*, being the type species, would be unaffected.

The chromosome number of *Guzmania monostachia* has been reported as n = ca. 25 and $2n$ = 48. Other counts in the genus are $2n$ = 48, 50, and 56 (see McWilliams in Smith & Downs, 1974).

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Under family references see especially BENZING & RENFROW, CRAIGHEAD, GRAF, HARMS, MEZ, PADILLA, RAUH, RICKETT, and SMITH (1947).

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FOSTER, M. B. New varieties in the Bromeliaceae. Bromeliad Soc. Bull. 3: 29, 30. 1953. [*G. monostachia* var. *variegata* M. B. Foster described from Big Cypress Swamp near Deep Lake, Collier County, Florida.]

i, mature capsule beginning to open, × 2; j, same after dehiscence, seeds being released, × 2; k, empty capsule, × 2; l, seed with long terminal appendage of hairs, × 3. m–q, *C. floribunda*: m, plant with fruit, × ⅛; n, flower with subtending bract, × 3; o, petal with stamen adnate at base, × 4; p, anther and upper part of filament of antesepalous stamen, × 12; q, mature unopened fruit, × 2.

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SMITH, L. B. Notes on Bromeliaceae, XXXII. Phytologia **21**: 73–96. 1971. [Key to *Guzmania* and simulators, 73–90; most recent revision of the genus.]

3. **Catopsis** Grisebach, Fl. Brit. W. Indian Islands 599. 1864.

Epiphytic acaulescent herbs. Leaves densely rosulate, entire, minutely appressed-lepidote, often cretaceous-coated, green; sheath large; blade narrowly triangular or liguliform. Scape conspicuous, the paniculate inflorescence usually bipinnate, rarely simple (cf. *C. nutans*) or tripinnate, equaling or exceeding the leaves. Flowers always polystichously arranged, small or minute, mostly sessile or subsessile, uniform and perfect [or dimorphic with some functionally staminate plants]. Sepals free, usually rounded and strongly asymmetric, glabrous. Petals free, naked. Stamens included; filaments unequal; anthers ovate or elliptic. Ovary superior, broadly ovoid or ellipsoid; style shorter than the ovary or lacking; ovules few to several, with an apical tuft of hairs and a potential but normally undivided coma appearing as a spur on the laterally attached funiculus (FIGURE 4, g, h). Capsule septicidal; seeds with principal coma apical and folded over (FIGURE 4, l). LECTOTYPE SPECIES: *C. nutans* (Sw.) Griseb.; see Britton & Millspaugh, Bahama Fl. 66. 1920. (Name from Greek *katoptos*, a view or a place from which a view may be obtained, not explained, but probably in reference to the epiphytism of the plant.)

A genus of some 19 species extending from southern Florida and southern Mexico to Peru and eastern Brazil; three species in our area.

Catopsis Berteroniana (Schult. f.) Mez, distinctive in its chalky-coated yellowish-green leaves, is locally abundant in hammocks in subtropical Florida, where it grows high up in the trees in full or nearly full sunlight. It occurs through the Greater Antilles and Central America to Brazil. *Catopsis floribunda* L. B. Smith (*C. nutans* of authors, including Small) and true *C. nutans* (Sw.) Griseb. (*C. fulgens* Griseb.) are both plants of shadier habitats. The former occurs in scattered hammock locations in southern Florida, southward through the West Indies and Central America to Venezuela. The latter, notable for its slender, usually decurved simple inflorescence, in contrast with the paniculate inflorescences of the preceding two, is found sparingly in the Big Cypress Swamp area of Collier County, Florida, and it occurs in the Greater Antilles, Mexico, and Central America, southward to Venezuela and Ecuador.

Catopsis floribunda flowers in early summer in Florida, while both *C. Berteroniana* and *C. nutans* are fall-flowering (September, October) (see

Craighead). The conspicuous liguliform, bright yellow petals of *C. nutans* contrast strongly with the inconspicuous white petals (hardly longer than the sepals) that characterize most other members of the genus, including the two other species of our area. Because of its conspicuous petals, *C. nutans* can be presumed to be outcrossing, but *C. Berteroniana* and *C. floribunda* are both self-compatible and self-pollinated, at least under greenhouse conditions (obs. C. E. W.). *Catopsis nutans* has dimorphic flowers (staminate-flowered plants and either perfect [?] or functionally carpellate-flowered ones [?]) in Mexico and Central America, but only perfect flowers elsewhere.

The geographical limits of floral dimorphism in *Catopsis* are one of the most interesting features of the genus. The species that are normally dimorphic are limited to Mexico and Central America, but the species that are both perfect-flowered and dimorphic are dimorphic only within that same area. The northern part of this area overlaps that of *Hechtia*, which is the only completely dimorphic genus in the family. So far no explanation of this situation has been found.

An unusual character for many species is a chalky coating on the leaves that is easily brushed off (cf. *C. Berteroniana*). Its exact nature is not understood, but it may be an epidermal excretion similar to the waxy coat in some other families.

In contrast with the large basal appendage of the seeds of *Tillandsia* and *Guzmania*, which is derived from the splitting of the outer layer of the outer seed coat, the principal one of *Catopsis* is composed of apical hairs that increase greatly in length as the ovule matures into seed, while the basal one appears as a spur on the funicle (see FIGURE 4, e–g, l).

Chromosome counts of $2n = 50$ have been recorded for two species of the genus.

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Subfam. BROMELIOIDEAE [Harms]

4. **Ananas** Miller, Gard. Dict. Abr. ed. 4. ord. alph. 1754.

Coarse acaulescent herbs, not producing stolons but short upright shoots or slips. Leaves densely rosulate, scarcely enlarged at base; blades usually spinose-serrate. Scape evident, mostly erect. Inflorescence densely strobiliform, usually terminated by a series of sterile foliaceous

bracts, often producing slips at the base. Flowers sessile. Calyx lobes free above the epigynous tube, obtuse, slightly asymmetric. Petals free, erect, violet or red, each bearing two slenderly funnelform scales. Stamens included; pollen grains ellipsoid, with two pores. Ovaries coalescing with each other and with the bracts and axis to form a fleshy compound fruit; epigynous tube short; placentae apical; ovules caudate. Seeds naked, completely aborted in the cultivated species. LECTOTYPE SPECIES: *Bromelia Ananas* L. = *A. comosus* (L.) Merrill (*Ananas Ananas* (L.) Voss). (Name from that used by the Indians of the Antilles.) — PINEAPPLE.

A genus of some eight species and numerous varieties and forms, probably native to interior South America from the Amazon Basin to Paraguay but now pantropical in cultivation. *Ananas comosus* (*A. sativus* Schult. f.), $2n = 50, 75$, the commonly cultivated species, is reportedly persistent and may possibly be spontaneous in southern Florida. It is included here tentatively.

Like many other cultivated plants, the pineapple is of obscure and controversial origin. There is good evidence that the Indians brought it to the Antilles before the arrival of Columbus, and probably the Portuguese introduced it into the East Indies, although some authors believe it to be native there.

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