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PRELIMINARY CLASSIFICATION OF TILLANDSIA BASED ON FLORAL CHARACTERS

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ABSTRACT. Previous classifications within subfam. Tillandsioideae Harms (Bromeliaceae) are based primarily on characters determined from dried specimens. Floral characters are seldom well preserved in dried material and no associated suites of characters delimiting groups have been described. Some genera and subgenera are currently distinguished by single "key characters." Taxonomically useful suites of floral traits ascertainable only from fresh or spirit-preserved flowers of 91 species of *Tillandsia* L. subgen. *Tillandsia* are used here to circumscribe five preliminary taxonomic groups. Sixteen species of subgen. *Allardtia* (A. Dietrich) Baker were also examined, and 13 were assigned to three of these groups.

Previous taxonomic treatments of the Bromeliaceae have been based on characters observed on dry herbarium specimens (Baker, 1889; Mez, 1935; Smith & Downs, 1977). Although competent taxonomists have studied the Tillandsioideae satisfactory classifications based on suites of characters have not been produced. Smith and Pittendrigh (1953) noted that there has been an inconsistency among authors regarding the delimitation of genera in this subfamily, and cited a lack of correlation between habit and floral characters as cause for this problem.

Taxonomists working with angiosperms find floral characteristics more likely to be important than vegetative characters (Cronquist, 1968). Smith and Pittendrigh (1953) noted that "virtually all useful phylogenetic characters are limited to the petals, stamens and pistil, yet available material is so frequently inadequate in these parts . . . ." To facilitate the sorting of species into groups, previous taxonomic treatments of the Bromeliaceae have, by default, been based mainly on vegetative characters. The difficulty experienced by workers in finding suitable characters in dry material has resulted in the circumscription of taxa at the generic and subgeneric levels with single or few character distinctions. For example, *Vriesea* is distinguished from *Tillandsia* by the presence of a pair of nectar scales at the base of each petal. Several species of *Tillandsia* have been transferred to *Vriesea* when more complete material revealed scales on the petals. On the other hand, *Tillandsia pabstiana* Pereira is treated by Smith and Downs (1977) as a synonym of *Vriesea drepanocarpa* (Baker) Mez. Pereira (1974) had noted a similarity between the species. Smith and Downs found the lack of petal appendages an inadequate distinction to warrant maintaining *T. pabstiana* as a species even though they used it to distinguish two large genera.

Baker (1889) distinguished subgen. *Tillandsia* (subgen. *Platystachys* Beer at that time) from subgen. *Allardtia* (A. Dietrich) Baker by leaf characteristics. Mez (1935), using a floral characteristic he could determine on many dried specimens, distinguished *Platystachys* from *Allardtia* by exserted stamens of the former. Less than half of the species that Baker placed in *Platystachys* were retained there by Mez or by Smith and Downs (1977). An 80 percent congruence between Mez's treatment and that of Smith and Downs (1977) reflects the conservative approach they took with Mez's characters. Smith and Downs assigned 816 species in subfam. Tillandsioideae to six genera. Of these, 410 species were placed in seven subgenera of *Tillandsia* (including 122 species in subgen. *Tillandsia,* and 147 species in subgen. *Allardtia*). *Vriesea* Lindley (257 species) (Smith & Downs, 1977), is the genus to which *Tillandsia* is most closely related.

The circumscription of genera or subgenera on the basis of a single character is unlikely to produce taxa with predictive value. If the classification of subfam. Tillandsioideae is to be reconsidered, fresh, or at least spirit-preserved flowers, must be examined. The objective of this study was to examine flowering specimens in vivo, and describe floral characteristics of *Tillandsia* subgen. *Tillandsia* that might prove useful for improving the classification of this group of species.

MATERIALS AND METHODS

Herbarium specimens (from US, F, GH, MEXU, SEL) of the 269 species included by Smith and Downs (1977) in subgen. *Tillandsia* and subgen. *Allardtia* were examined. In addition, type specimens of 150 species of these two subgenera were also studied (including 35 type photographs).

Field collected samples from Florida, southern Texas and Mexico (N = 6–8 individuals per

species) representing 79 species of subgen. *Tillandsia* were examined. In many cases, collections were made from the type locality. Plants that were not flowering at the time of collection were grown to maturity in a greenhouse in Texas. No taxonomically significant differences were noticed in plants flowering in the greenhouse as compared to those that flowered in the wild. Fresh or spirit-preserved flowers of 15 additional species were examined from cultivated material or from other collectors, plus cultivated clones of eight types at the University of Heidelberg. Twelve species of subgen. *Allardtia* (Smith & Downs, 1977) were also examined for comparison. Twenty-two other species were assigned to groups on the basis of photographs of fresh flowers, or apparent close relationship to other species for which flowers were examined, on the basis of vegetative characteristics. Voucher specimens are deposited at TAMU and SEL.

Results

Important Floral Characters

Suites of character states that consistently occurred together were detected and employed to circumscribe five preliminary taxonomic groups. The stamens of flowers of *Tillandsia* are rich in useful morphological characteristics. Filaments may be round, slightly flattened, or flat in cross section; even in width throughout their length, broad at the base, or broad near the apex; and equal in length, or in two sets of differing lengths. The anthers may be versatile with median to submedian attachment, or subbasifixed. If versatile, anthers may pivot freely, or appear basifixed by the reflexed locules clasping the filament apex. Two discrete classes of anther lengths occur: 2–3 mm and 6–8 mm. Associations between anther and filament characteristics form the basis for the five taxonomic groups presented here. Petal and sepal characteristics coincide with those of the stamens. Petal shape may be spatulate or ligulate. Sepals may be elliptic to subdeltoid, obovate or spatulate. They may also be carinate or ecarinate, and free or connate. Petals are typically rolled into a tube. The corolla may be open, or closed due to petals constricting about broadened filaments; actinomorphic with spreading petal blades, or zygomorphic by twisting of the petals.

Taxonomic Groups

Tillandsia subgen. *Tillandsia* Smith & Downs are highly heterogeneous in vegetative, inflorescence and floral characteristics. Floral traits form discrete suites of characters, and support the recognition of groups at the subgeneric level. Hybridization occurs among species within the groups, but is not known to occur among the groups (Gardner, 1984). The vast majority of the species examined fall into Group I. These species have been assigned to subgroups that are based primarily on characteristics of the vegetative body and inflorescence. Several species formerly assigned to subgen. *Allardtia* are placed into three of these groups. The synonyms provided are only those first designated in this paper. All synonyms previously recognized are not indicated.

Key to the Groups of Tillandsia

1. Filaments not equal in length.
   2. Filaments flat in cross section for entire length, broadened near apex; petal apices constricted about filaments; corolla throat closed. ..... Group I.
   2. Filaments round in cross section for entire length; petal apices erect or recurved; corolla throat open. ..... Group II.
1. Filaments equal in length.
   3. Filaments round in cross section near apex, flat and broadened at base.
      4. Anthers subbasifixed, more than 4 mm long. ..... Group III.
      4. Anthers versatile, less than 3 mm long. ..... Group IV.
   3. Filaments flat in cross section for entire length. ..... Group V.

Group I (species 1–85) FIGURE 1.

Highly variable group of species in both vegetative and inflorescence characteristics. Epiphytic or saxicolous in bright, exposed habitats, some semimesic shade species. All have xerophytic adaptations. Leaves triangular to linear, coriaceous or rigid. Indumentum lightly scurfy to tomentose. Inflorescence a spike, or panicle with long or short dorsiventrally, or laterally compressed branches longer or shorter than subtending bracts. Floral bracts usually imbricate, concealing the sepals, or nearly so, rarely absent. Flowers protogynous, ascending or descending, distichous, except when inflorescence branches reduced to single flowers, then flowers polystichous. Sepals elliptic to subdeltoid, the posterior pair usually more or less carinate, typically slightly to highly connate. Corolla violet, chartreuse, rarely white, red or yellow. Petals typically spatulate with a distinct claw, 40–67 mm long. Sinus along sides of petal blade in some species. Petal apex often acute, tightly recurved and constricted about the filaments, closing the throat. Stamens in two sets of unequal lengths. Filaments flat, broadened near apex, usually concolorous with corolla, occasionally contrasting. Anthers 2–3 mm

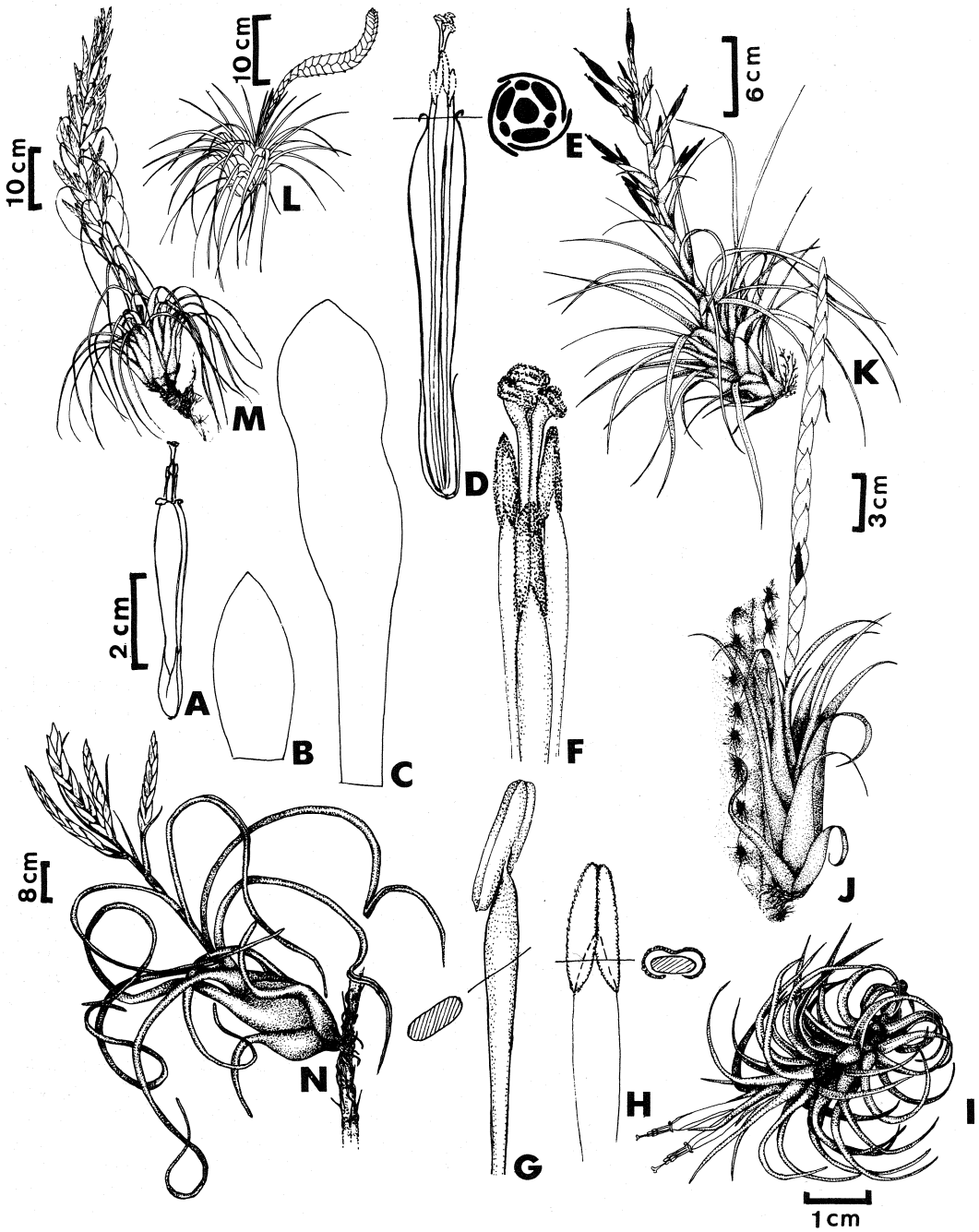

FIGURE 1. *Tillandsia* Group I. A–H, floral characteristics: A, flower; B, sepal; C, petal; D, longitudinal section of flower; E, cross section of flower; F, arrangement of stamen and style apices; G, distal portion of stamen before anther dehiscence; H, distal portion of stamen after anther dehiscence. I–N, habits of representative species: I, *T. ionantha*; J, *T. califani*; K, *T. chlorophylla*; L, *T. jaliscomonticola*; M, *T. dugesii*; N, *T. caput-medusae.*

long, versatile, with median to submedian attachment, often appearing basifixed by reflexed locules clasping broadened filament apex. Style longer than or about equal to stamens.

DISTRIBUTION. In arid to mesic forests and canyons at elevations from sea level to above 3,000 m; from southern Texas and Florida, throughout Mexico, Central America, the Caribbean and into northern South America (FIGURE 2).

Group I corresponds to *Tillandsia* subgen. *Pityrophyllum* (Beer) Baker, Bromel. 17, 79. 1857. TYPE: *Tillandsia erubescens* Schlechtendal.

Due to the large number of species and their heterogeneity in vegetative and inflorescence characteristics, Group I is divided into eight subgroups. The suites of characters used to circumscribe these subgroups are primarily vegetative and inflorescence traits. In some cases the boundaries separating some of the subgroups are still unclear.

Key to Subgroups of Group I

1. Leaves triangular to acuminate.
   2. Inflorescence branches dorsiventrally compressed, reduced to a single flower, or inflorescence simple, lowest sterile bract ecarinate or once carinate.
      3. Lowest primary bract sheath less than ½ the length of the branch, or inflorescence simple.
         4. Floral bracts glabrous, glabrescent or at least not evenly lepidote. Inflorescence simple or compound. . . . . Subgroup 1.
         4. Floral bracts evenly lepidote. Inflorescence usually simple. . . . . Subgroup 7.
      3. Lowest primary bract sheath exceeding ½ the length of inflorescence branch.
         5. More than five flowers on lowest inflorescence branch. . . . . Subgroup 3.
         5. Inflorescence branches reduced to five flowers or fewer.
            6. Primary bracts petaloid and usually broadened. Inflorescence branches often reduced to a single flower. Floral bracts absent, or rarely present in lowest few inflorescence branches. . . . . Subgroup 8.
            6. Primary bracts foliiform. Usually two to five flowers on lowest inflorescence branches, floral bracts present. . . . . Subgroup 6.
   2. Inflorescence branches laterally compressed and well developed, inflorescence rarely simple, lowest sterile bract adjacent to rachis bicarinate. . . . . Subgroup 2.
1. Leaves linear or involute and appearing linear.
   7. Leaf sheath obscure, or short and triangular. . . . . Subgroup 4.
   7. Leaf sheath conspicuous, broad, inflated. . . . . Subgroup 5.

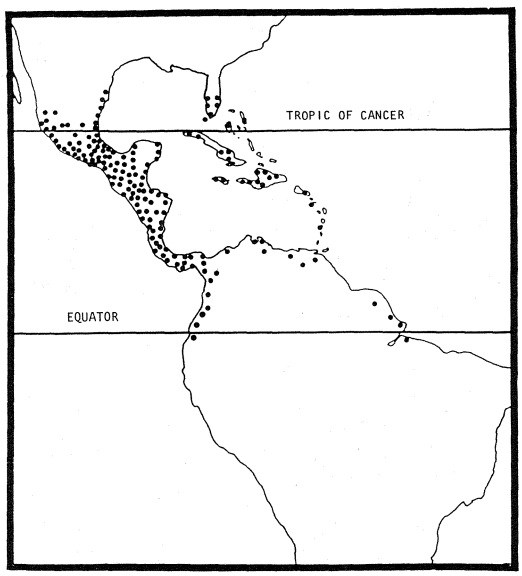

FIGURE 2. Distribution of *Tillandsia* Group I in tropical America.

Subgroup 1 (species 1–32)

Highly variable group of species. Epiphytic or saxicolous from sea level to above 2,000 m. Typically acaulescent herbs. Funnelform water impounding, rarely nonimpounding, rosettes. Leaves narrowly triangular. Leaf blades moderately thin to thick and rigid. Leaf sheath expanded and distinct, occasionally slightly inflated. Inflorescence simple or branched. Scape distinct. Inflorescence branches, when present, dorsiventrally compressed; erect or spreading to 45 degrees from rachis. Primary bract sheath to one-half the length of branch, usually less. Flowers typically ascending or horizontal, rarely descending. Filaments concolorous with corolla, rarely contrasting.

1. *Tillandsia acostae* Mez & Tonduz, Repert. 14: 252. 1916. TYPE: Costa Rica, San Ramon, Tremandal, 1913, *Tonduz 17891* (B, holotype; US!, isotype).
2. *Tillandsia aguascalientensis* C. S. Gardner, Selbyana 7: 361–363. 1984. TYPE: Mexico, Aguascalientes, saxicolous on rock walls and boulders, 2,000–2,200 m elev., 1980, *Gardner 1322* (SEL!, holotype; US!, MEXU!, isotypes).
3. *Tillandsia buchii* Urban, Repert. Sp. Nov. 15: 99. 1917. TYPE: Haiti, Mont Descouflay, 1901, *Buch 581* (B; US!, photo).
4. *Tillandsia calothyrsus* Mez, DC. Monogr. Phan. 9: 704. 1896. TYPE: Mexico, Oaxa-

ca(?), Guayimapo, *Karwinsky s.n.* (M, holotype; GH, isotype, holotype photo!), SYNONYM: *Tillandsia rettigiana* Mez, Repert. Sp. Nov. 14: 249. 1916. TYPE: Mexico, without exact locality, *Hasselmann s.n.* (B, holotype; B, photo 1249/23!).

5. *Tillandsia chlorophylla* L. B. Smith, N. Am. Fl. 19: 145. 1938. FIGURE 1K. TYPE: Guatemala, Petén, Monte Santa Teresa, *Lundell 2649* (GH!, holotype; MICH!, isotype). SYNONYM: *Tillandsia santiago-tuxtlensis* Matuda, Cact. Suc. Mex. 22: 1, figure 11. 1977. TYPE: Mexico, Veracruz, El Vigia, south of Santiago Tuxtla, epiphytic at 840 m elev., 1965, *Sousa 2260* (MEXU, n.v., photo!).
6. *Tillandsia compressa* Betero ex Schultes in Roemer & Schultes, Syst. 7(2): 1210. 1830. FIGURE 1L. TYPE: *Bertero s.n.* (B?, n.v.). SYNONYM: *Tillandsia flavobracteata* Matuda, Cact. Suc. Mex. 20: 4, figures 49, 50. 1975. TYPE: Mexico, Veracruz, Hidalgotitlan, southeast of Venustiano Carranza, *Valdivia Quijano 875* (MEXU, n.v., photo!).
7. *Tillandsia concolor* L. B. Smith, Phytologia 7: 249, plate 1, figures 1, 2. 1960. TYPE: Mexico, Oaxaca, 16 km N-NE of Tehuantepec along the Pan American Highway (Route 185 & 190), 1959, *King 1385* (US!, holotype; MICH!, isotype).
8. *Tillandsia dugesii* J. G. Baker, J. Bot. 25: 278. 1887. FIGURE 1M. TYPE: Mexico, Guanajuato, 1885, *Duges s.n.* (K!, holotype). SYNONYM: *Tillandsia mexicana* L. B. Smith, N. Am. Fl. 19: 140. 1938. TYPE: Mexico, Guanajuato, near Guanajuato city, 1901, *Duges s.n.* (GH, holotype; US!, isotype).
9. *Tillandsia elizabethae* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 31: 5–7, Abb. 1. 1979. TYPE: Mexico, Chihuahua, Barranca del Cobre in *Commiphorae* trees, 1,200 m elev., *Rauh 50 385* (HEID, holotype, living clone!, photo!).
10. *Tillandsia exserta* Fernald, Bot. Gaz. 20: 537. 1895. TYPE: Mexico, Sinaloa, Mazatlan, 1895, *Lamb 381* (GH!, holotype; DS, isotype).
11. *Tillandsia fasciculata* Swartz, Prod. Veg. Ind. Occ. 56. 1788. TYPE: Jamaica, without exact locality, *Swartz s.n.* (S, holotype; GH!, photo).
12. *Tillandsia ferresiana* L. B. Smith, Bromel. Soc. Bull. 10: 92, figures. 1960. TYPE: Mexico, Sinaloa, Labradas, *Ferris & Mexia 5121-A* (DS, holotype; US!, photo).
13. *Tillandsia flabellata* J. G. Baker, J. Bot. 25: 242. 1887. TYPE: Guatemala, Sacatepequez–Chimaltenango boundary, Volcan de Fuego, Barranca Hondo, *Salvin s.n.* (K!, holotype; GH!, photo).
14. *Tillandsia foliosa* Martens & Galeotti, Bull. Acad. Brux. 10(1): 119. 1843. TYPE: Mexico, Veracruz, Jalapa, *Martens & Galeotti 4909* (BR, holotype; US!, photo).
15. *Tillandsia jaliscomonticola* Matuda, Cact. Suc. Mex. 20: 4, figure 51. 1975. TYPE: Mexico, Jalisco, El Tuito, pine & oak forest, 700 m elev., 1974, *Beutelspacher 74* (MEXU, holotype, n.v., photo!).
16. *Tillandsia kolbii* W. Till & Schatzl, Plant Syst. Evol. 138: 259–262, Abb. 1. 1981. TYPE: Mexico, Oaxaca, Copala, Sierra Madre del Sur, in oaks, 1,750–2,000 m elev., *Schatzl s.n.* (WU, holotype, n.v.).
17. *Tillandsia leucolepis* L. B. Smith, Phytologia 8: 497, plate 1, figures 1–3. 1963. TYPE: Mexico, Oaxaca, cultivated, probably of local origin, *MacDougall 280* (US!, holotype).
18. *Tillandsia magnusiana* Wittmack, Bot. Jahrb. 11: 66. 1901; L. B. Smith, Phytologia 19: 287. 1970. TYPE: Guatemala, Baja Verapaz, San Miguel and Rabinal, 1882, *Lehmann 1467* (G-B, holotype; GH!, photo).
19. *Tillandsia matudae* L. B. Smith, Contr. U.S. Natl. Herb. 29: 278, figure 3. 1949. TYPE: Mexico, Chiapas, Comitan and Amatenango del Valle, 2,100 m elev., 1945, *Matuda 5811* (GH!, holotype; US!, isotype). SYNONYM: *Tillandsia veleckiana* L. B. Smith, Phytologia 28: 39, plate 1, figures E, F. 1974. TYPE: cultivated in Los Angeles from material from Guatemala without exact locality, *G. J. Velick s.n.* (US!, holotype).
20. *Tillandsia mazatlanensis* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 33: 105–106, Abb. 2. 1981. TYPE: Mexico, Sinaloa, near Mazatlan, 50 m elev., *Rauh 50 441* (HEID, holotype, living clone!).
21. *Tillandsia palmasolana* Matuda, Cact. Sub. Mex. 18: 51, figure 25. 1973. TYPE: Mexico, Veracruz, Punta Limón, Cerro de Oro, Mun. Alto Lucero, 400 m elev., 1972, *J. Durnates s.n.* (MEXU!, holotype, photo!).
22. *Tillandsia parryi* J. G. Baker, J. Bot. 25: 277. 1887. TYPE: Mexico, region of San Luis Potosi, 1878, *Parry & Palmer 873* (K, holotype; GH!, US!, isotypes).
23. *Tillandsia polystachia* Linnaeus (Linnaeus), Sp. Pl. ed. 2. 410. 1762. TYPE: West Indies, without exact locality, *Plumier s.n.* (P!, holotype).
24. *Tillandsia rodrigueziana* Mez, Repert. Sp.

Nov. 16: 73. 1919. TYPE: Guatemala, without exact locality, 1884, *Rodriguez s.n.* (B!, holotype).

25. *Tillandsia roland-gosselinii* Mez, Repert. Sp. Nov. 14: 249. 1916. TYPE: Mexico, Colima, 400 m elev., *Diguet in Roland-Gosselin Hortus s.n.* (B?, n.v.) [identification made from description and type locality]. SYNONYM: *Tillandsia maritima* Matuda, Cact. Suc. Mex. 16: 90, figure 47. 1971. TYPE: Mexico, Jalisco, Axamala, epiphytic in high woods near coast, *Matuda 38361* (MEXU!, holotype).
26. *Tillandsia schiediana* Steudel, Nom. Bot. ed. 2. 2: 688. 1841. TYPE: Mexico, Veracruz, Hacienda de la Laguna, *Schiede & Deppe 1004* (B!, holotype; BM, isotype).
27. *Tillandsia supermexicana* Matuda, Cact. Suc. Mex. 22: 1, figure 12. 1977. TYPE: Mexico, Guerrero, forest near Yerbabuena in coastal mountains, 1,900 m elev., 1953, *Matuda 38641* (MEXU, holotype!, photo!).
28. *Tillandsia thyrsigera* Morren ex J. G. Baker, Handb. Bromel. 185. 1889. TYPE: Mexico, without exact locality, 1896, *Morren Icon* (K, n.v.), painted from *Kienast s.n.* (LG, n.v.).
29. *Tillandsia tricolor* Schlechtendal & Chamisso, Linnaea 6: 54. 1831. TYPE: Mexico, Veracruz, Jalapa, *Schiede & Deppe 1006* (B, holotype, photo!).
30. *Tillandsia variabilis* Schlechtendal, Linnaea 18: 418. 1845. TYPE: Mexico, Veracruz, Papantla, *Schiede 1003* (HAL, holotype; US, photo, n.v.).
31. *Tillandsia vicentina* Standley, J. Wash. Acad. Sci. 13: 364. 1923. TYPE: El Salvador, San Vicente, Volcán de San Vicente, 1922, *Standley 21588* (US!, holotype).
32. *Tillandsia xerographica* Rohweder, Senckenbergiana 34: 113, figures 8–11, plate 1, figure 1. 1953. TYPE: El Salvador, Sonsonate, Los Cobanos, 1951, *Rohweder 157* (HBG, holotype; US!, photo).

Subgroup 2 (species 33–41)

Intermediate to large, acaulescent herbs. Epiphytic at 1,000 m or above. Leaves broadly triangular to acuminate in funnelform rosette. Leaf blades moderately thin to coriaceous. Leaf sheaths taper evenly into blade or may be distinctly broadened. Inflorescence typically branched, rarely simple. Inflorescence carried on distinct scape. Inflorescence branches laterally compressed and bear a secondary, bicarinate sterile bract adjacent to rachis; spread to 90 degrees from rachis, rarely strict. Primary bract sheaths may exceed and conceal inflorescence branches. Flowers typically horizontal or ascending, occasionally descending.

33. *Tillandsia cretacea* L. B. Smith, Phytologia 28: 31, plate 3, figures A, B. 1974. TYPE: Mexico, Chihuahua, southwest of Creel, *Knobloch 564* (US!, holotype).
34. *Tillandsia eizii* L. B. Smith, Phytologia 28: 33, plate 3, figures C, D. 1974. TYPE: Mexico, Chiapas, Cascada Siltepec on tree in wet forest, *Matuda 21012* (US!, holotype; MEXU!, isotype).
35. *Tillandsia kalmbacheri* Matuda, Cact. Suc. Mex. 19: 1, figure 16. 1974. TYPE: Mexico, Guerrero, on oaks near Rincon de la Via, *Kruse 3119* (MEXU, holotype!, photo!).
36. *Tillandsia kirchoffiana* Wittmack, Gartenflora 38: 107, figure 22. 1889. TYPE: *Kirchoff Icon* (B, n.v.).
37. *Tillandsia langlasseana* Mez, Bull. Herb. Boiss. 11, 3: 142. 1903. TYPE: Mexico, Michoacan, Las Seneguias, 1898, *Langlasse s.n.* (B, holotype; G, GH, P, US!, Field photo 25265). SYNONYM: *Tillandsia intumescens* L. B. Smith, Phytologia 5: 177, plate 1, figures 1–3. 1955. TYPE: Mexico, Mexico, Ixtapantongo to La Junta, 24–25 Apr. 1954, *Matuda 30665* (US!, holotype).
38. *Tillandsia mooreana* L. B. Smith, Phytologia 20: 167. 1970. TYPE: Mexico, without exact locality, 1873, *Roezl s.n.* (LG, holotype; GH!, photo).
39. *Tillandsia orogenes* Standley & L. O. Williams, Ceiba 3: 188. 1953. TYPE: Honduras, Comayagua, south of Siquatepeque, Barranca del Socorro, 1951, *L. O. & R. P. Williams 18461* (EAP, holotype; US!, isotype).
40. *Tillandsia punctulata* Schlechtendal & Chamisso, Linnaea 6: 53. 1831. TYPE: Mexico, Veracruz, Jalapa, *Schiede & Deppe 1006-A* (B, holotype, B, photo, n.v.).
41. *Tillandsia violacea* J. G. Baker, J. Bot. 25: 279. 1887. TYPE: Mexico, Mexico, Toluca, 1834, *Andrieux 60* (K, holotype; GH!, photo; M, isotype). SYNONYM: *Tillandsia sierrajuarezensis* Matuda, Cact. Suc. Mex. 18: 2, figure 24. 1973. TYPE: Mexico, Oaxaca, in humid cloud forest of la cumbre de la Sierra de Juarez at 2,000–2,300 m elev., 1972, *Matuda 38420* (MEXU, holotype!, photo!).

Subgroup 3 (species 42–49)

Typically acaulescent or subcaulescent herbs. Epiphytic at 2,000 m or above. Coriaceous leaves

in funnelform rosettes. Leaf blades triangular to acuminate, densely lepidote, at least abaxially. Leaf sheaths large and distinct. Inflorescence pinnately branched. Inflorescence branches dorsiventrally compressed, erect to spreading, subtended by distinct primary bracts with sheaths at least one-fourth branch length, and often equal or greater. Flowers horizontal or ascending. Filaments concolorous with corolla.

42. *Tillandsia bourgaei* J. G. Baker, J. Bot. 25: 278. 1981. TYPE: 24 Aug. 1865, *Bourgeau 893* (K, holotype; GH!, photo).
43. *Tillandsia carlsoniae* L. B. Smith, Phytologia 7: 1, plate 1, figures 1, 2. 1959. TYPE: Mexico, Chiapas, Las Casas to Comitan, Pan American Highway, *Carlson 1697* (US!, holotype; F, isotype).
44. *Tillandsia carlos-hankii* Matuda, Cact. Succ. J. (Los Angeles) 45: 186, figures 1, 2. 1973. TYPE: Mexico, Oaxaca, Yautepec, Sierra de Santiago Lachevia in mixed pine and oak forest, 2,900 m elev., 1972, *Matuda 38514* (MEXU!, holotype).
45. *Tillandsia cossonii* J. G. Baker, J. Bot. 25: 279. 1887. TYPE: "Mexican Desert," *Bilimek 440* (GH, K, US!, isotypes).
46. *Tillandsia hintoniana* L. B. Smith, Phytologia 28: 34, plate 1, figures I, J. 1974. TYPE: Mexico, Mexico, Temascaltepec, Tejupilco, on oak, *Hinton 7636* (US!, holotype; GH, isotype).
47. *Tillandsia macrochlamys* J. G. Baker, J. Bot. 26: 142. 1888. TYPE: central Mexico, 1865–1866, *Hahn 589* (P, holotype, n.v.).
48. *Tillandsia prodigiosa* (Lemaire) J. G. Baker, Handb. Bromel. 186. 1889. TYPE: *Bhiesbreght in Linden Hortus s.n.* (BR?, n.v.).
49. *Tillandsia roseospicata* Matuda, Cact. Suc. Mex. 20: 9, figure 13. 1975. TYPE: Mexico, Mexico, Zacualpan on oaks, cerro de Tres Coronas, 2,000 m elev., *Matuda 38575* (MEXU!, holotype).

Subgroup 4 (species 50–55)

Epiphytic to saxicolous. Moderately to strongly xerophytic from sea level to 2,500 m elevation. Small, acaulescent, occasionally stoloniferous. Leaves linear, numerous in fascicle. Leaf blades linear, subulate. Leaf sheaths highly reduced. Inflorescence few branched or simple with distinct scape much longer than spike or dorsiventrally compressed branches. Primary bract to one-half length of inflorescence branch, usually less. Branches erect or spreading to 45 degrees. Flowers horizontal to ascending.

50. *Tillandsia bartramii* Elliott, Bot. So. Carol. & Georgia 1: 379. 1817; L. B. Smith, Phytologia 13: 454. 1966. TYPE: United States, Georgia, Liberty County, Mortar Swamp, *LeConte s.n.* (CHARL, holotype; NY, isotype, n.v.).
51. *Tillandsia chaetophylla* Mez, DC. Monogr. Phan. 9: 726. 1896. TYPE: Mexico without exact locality, *Sessé & Mociño s.n. in Herb. Pavon* (BM, n.v.).
52. *Tillandsia festucoides* Brongniart ex Mez, DC. Monogr. Phan. 9: 678. 1896. TYPE: Mexico, without exact locality, *Brongniart in Paris Hortus s.n.* (P, holotype; GH!, photo).
53. *Tillandsia juncea* (Ruiz & Pavon) Poiret, Encyl. Suppl. 5: 309. 1817. TYPE: Peru, Huanuco, Muna, *Ruiz & Pavon s.n.* (MA?, n.v.).
54. *Tillandsia ortgieseana* E. Morren ex Mez, DC. Monogr. Phan. 9: 678. 1896. TYPE: Mexico, without exact locality, 1873, *Roezl s.n.* (LG!, holotype; GH, US!, photo).
55. *Tillandsia setacea* Swartz, Fl. Ind. Occ. 1: 593. 1797; L. B. Smith, Phytologia 8: 219. 1962. TYPE: Jamaica without exact locality, *Swartz s.n.* (S!, holotype; GH, US!, photo).

Subgroup 5 (species 56–67)

Small to medium sized epiphytes. Xeric habitats from sea level to 2,000 m. Leaves few in bulbous rosette. Leaf blades coriaceous, often involute. Leaf sheaths broad, inflated, constricted at union with blade forming partially hollow pseudobulb. Ants often inhabiting. Inflorescence simple to few branched with distinct scape. Inflorescence branches dorsiventrally compressed, erect or spreading. Primary bracts to one-half length of branch, usually less. Flowers typically ascending. Filaments concolorous with corolla.

56. *Tillandsia ariza-juliae* L. B. Smith & Jimenez, Phytologia 6: 433, plate 1, figures 1, 2. 1959. TYPE: Republic Dominicana, La Vega, La Vega to Jarabacoa, 500 m elev., on *Pinus occidentalis,* Apr. 1958, *Ariza Julia s.n.* (US!, holotype; hb. J. J. Jimenez, isotype).
57. *Tillandsia baileyi* Rose ex Small, Fl. Southeast U.S. 246, 1328. 1902. TYPE: United States, Texas, Kennedy County, San Ignacio Ranch, *Bailey 226* (US!, holotype).
58. *Tillandsia balbisiana* Schultes filius in Roemer & Schultes, Syst. 7(2): 1212. 1830. TYPE: Jamaica, *Bertero s.n.* (TO, holotype, n.v.). SYNONYM: *Tillandsia dressleri* L. B. Smith, Phytologia 8: 221, plate 1, figure 7.

1962. TYPE: Mexico, Sinaloa, on trees, 8 miles south of Agua Nueva, *Dressler s.n.* (MO!, holotype).

59. *Tillandsia bulbosa* Hooker, Exoct. Fl. 3: plate 173. 1826. TYPE: Hooker, 1826: plate 173, lectotype selected here.
60. *Tillandsia butzii* Mez, Pflanzenreich IV. Fam. 21: 636. 1935. TYPE: Mexico, Veracruz, Jalapa, *Schiede s.n.* (B, holotype, n.v.).
61. *Tillandsia caput-medusae* E. Morren, Belg. Hortic. 30: 90. 1880. FIGURE 1N. TYPE: *Morren Icon* (K, n.v.).
62. *Tillandsia diguetii* Mez & Roland-Gosselin ex Mez, Repert. Sp. Nov. 14: 250. 1916. TYPE: Mexico, Colima, Manzanillo, *Diguet s.n.* (B, holotype; B, US!, photo).
63. *Tillandsia paucifolia* J. G. Baker, Guard. Chron. II, 10. 1878. TYPE: Cultivated plant of unknown origin, 1878, *Kew Hortus s.n.* (K, holotype; GH, US!, photo).
64. *Tillandsia pruinosa* Swartz, Fl. Ind. Occ. 1: 594. 1797. TYPE: Jamaica, without exact locality, *Swartz s.n.* (S, n.v.).
65. *Tillandsia pseudobaileyi* C. S. Gardner, Selbyana 7: 363–365, figures 2, 4, 5. 1984. TYPE: Mexico, Chiapas, Ocozocoautla, epiphytic in trees of open, seasonally dry forests, growing horizontally or descending, 300–1,000 m elev., 1979, *Gardner 1118* (SEL!, holotype; US!, MEXU!, CAS!, isotypes).
66. *Tillandsia seleriana* Mez in Loesener, Bull. Herb. Boiss. 11, 3: 84. 1903. TYPE: Mexico, without exact locality, *Seler 3439* (B, lectotype, n.v.).
67. *Tillandsia streptophylla* Schiedweiler ex Morren, Hortic. Belig. 3: 252, plate. 1836. TYPE: Mexico, without exact locality, *Institut Gembloux s.n.* (BR, holotype; GH, US!, photo).

Subgroup 6 (species 68–73)

Xerophytic or semixerophytic. Epiphytic or saxicolous from sea level to 1,500 m. Acaulescent or rarely caulescent. Leaf blades triangular to acuminate, thin to coriaceous. Leaf sheaths distinct, or tapering evenly into blade. Inflorescence branches small, obscured by leaflike primary bracts, separated by very short internodes, erect. Flowers ascending. Filaments concolorous with corolla.

68. *Tillandsia abdida* L. B. Smith, Phytologia 8: 10, plate 1, figures 15–17. 1961. TYPE: Costa Rica, San Jose, Cerro de Escau, Aug. 1935, *Solis 314* (F!, holotype).
69. *Tillandsia brachycaulos* Schlechtendal, Linnaea 18: 422. 1844. TYPE: Mexico, Veracruz, Hacienda de la Laguna, *Schiede s.n.* (HAL, holotype, n.v.).
70. *Tillandsia capitata* Grisebach, Cat. Pl. Cub. 255. 1866. TYPE: Cuba, Oriente, Sierra San Andrews, *Wright 3274* (GOET, holotype; GH!, isotype).
71. *Tillandsia hondurensis* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 33: 103–105, Abb. 1981. TYPE: Honduras, Tegucigalpa, Valle de Angel, 1,800 m elev., *Kamm s.n.* (HEID, holotype, living clone!, photo!).
72. *Tillandsia ionantha* Planchon, Fl. Serres 10: 101, plate 1006!. 1855. FIGURE 1I. TYPE: Planchon, 1855: plate 1006, lectotype selected here.
73. *Tillandsia kammii* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 21: 45–48, Abb. 25, 26. 1977. TYPE: Honduras, Catacamas, near Juticalpa, *E. Kamm s.n.* (HEID, holotype, living clone!, photo!).

Subgroup 7 (species 74–79)

Xerophytic from 500 to 2,000 m. Epiphytic or saxicolous. Caulescent or acaulescent. Leaves strict, rarely spreading. Leaf blades triangular, coriaceous, variously lepidote. Leaf sheaths broad, tapering evenly into blade. Inflorescence simple, erect or arching with distinct scape, rarely branched. Inflorescence branches (when present) dorsiventrally compressed, greatly exceeding primary bract. Flowers ascending. Filaments concolorous with corolla.

74. *Tillandsia achyrostachys* E. Morren ex J. G. Baker, Handb. Bromel. 171. 1889. TYPE: *Morren Icon* from a plant received from *Kienast* of Zurich (K; GH, photo, n.v.).
75. *Tillandsia califanii* Rauh, J. Bromel. Soc. 21: 67, figures. 1971. FIGURE 1J. TYPE: Mexico, Puebla, Tehuacan, near Teotitlan, *Rauh RM 15447* (HEID, holotype, living clone!; US!, isotype).
76. *Tillandsia chiapensis* C. S. Gardner, Selbyana 2(4): 338–339. 1978. TYPE: Mexico, Chiapas, Ocozocoautla, saxicolous on canyon walls, 600 m elev., 1977, *Gardner 211* (SEL!, holotype; US!, MEXU!, CAS!, isotypes).
77. *Tillandsia circinnatoides* Matuda, Cact. Succ. J. (Los Angeles) 45: 187, figures 4, 4a, 5. 1973. TYPE: Mexico, Guerrero, dry ravine near Chilpancingo, 1,500 m elev., 1972, *Matuda 38432* (MEXU!, holotype; US!, isotype).
78. *Tillandsia pueblensis* L. B. Smith, Contr. Gray Herb. 104: 81, plate 3, figures 1, 2. 1934. TYPE: Mexico, Puebla, Zapotitlan, 1912, *Purpus 5856* (GH, holotype; BM, F, MO, NY, UC, US!, isotypes).

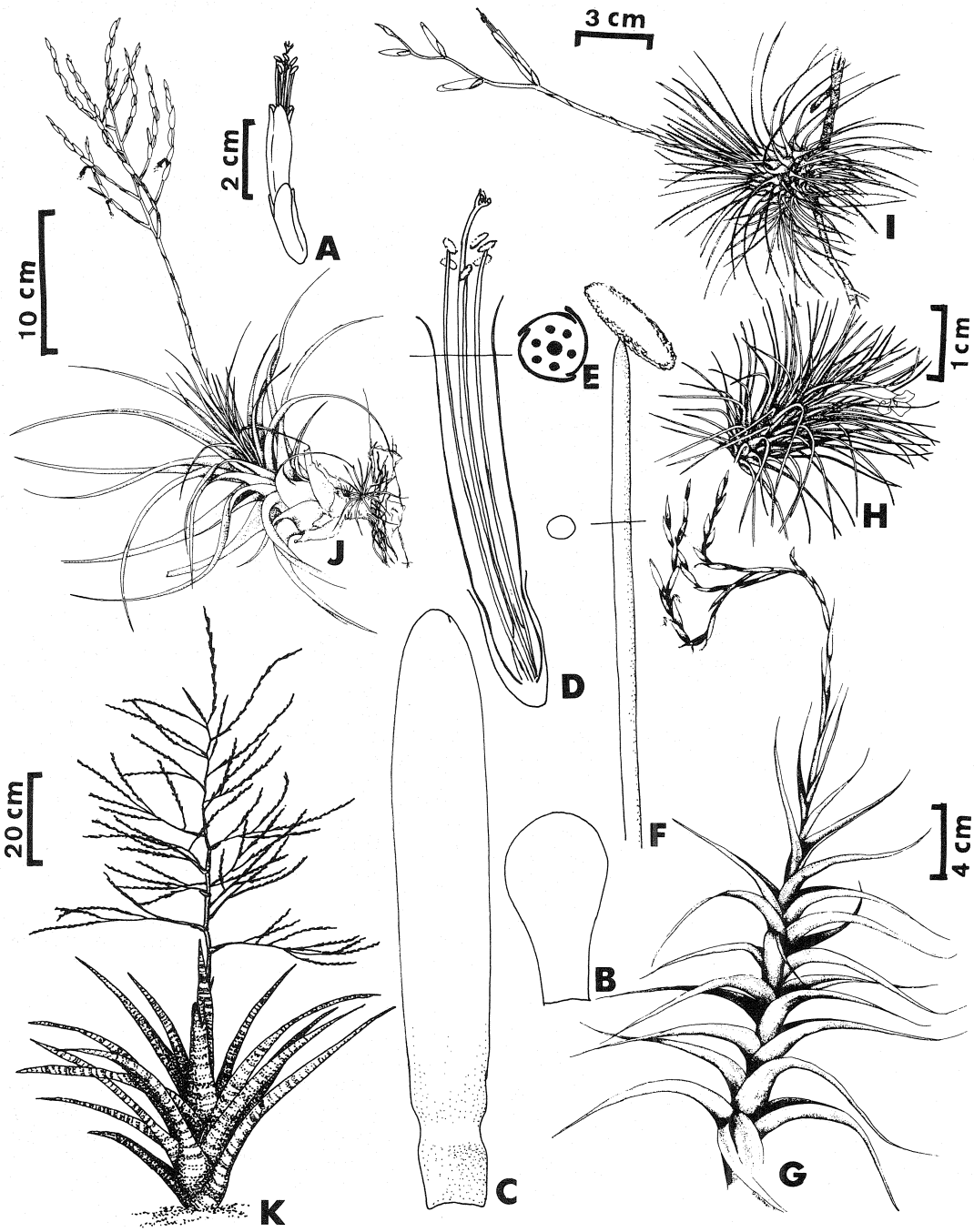

FIGURE 3. *Tillandsia* Group II. A–F, floral characteristics: A, flower; B, sepal; C, petal; D, longitudinal section of flower; E, cross section of flower; F, distal portion of stamen with anther. G–K, habits of representative species: G, *T. albida*; H, *T. andreana*; I, *T. argentea*; J, *T. utriculata*; K, *T. hildae*.

79. *Tillandsia schatzlii* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 27: 426. 1979. TYPE: Mexico, Puebla, steep rock walls between Oaxaca and Tehuacan, *Rutschmann s.n.* (HEID, holotype, living clone!, photo!).

Subgroup 8 (species 80–85)

Small acaulescent epiphytic or saxicolous herbs, in areas of frequent fogs above 2,000 m. Leaf blades triangular, soft, densely lepidote to tomentose. Leaf sheaths broad, somewhat inflated. Inflorescence branches reduced to single flowers with no floral bract; multiple flowers subtended by bracts on dorsiventrally compressed branches rarely occur at inflorescence base. Flowers descending. Filaments concolorous with corolla.

This subgroup corresponds to *Tillandsia* subgen. *Pityrophyllum.*

80. *Tillandsia andrieuxii* (Mez) L. B. Smith, Contr. Gray Herb. 117: 31. 1937. TYPE: Mexico, Mexico, Chalco, 1834, *Andrieux 58* (K, holotype; GH!, photo; P, isotype).
81. *Tillandsia atrococcinia* Matuda, Cact. Suc. Mex. 22(1): 22–23, figure 13. 1977. TYPE: Mexico, Oaxaca, Tonala, in oaks, 1,400 m elev., 1974, *Lau s.n.* (MEXU, holotype!, photo!).
82. *Tillandsia erubescens* Schlechtendal, Linnaea 18: 427–429. ("1844") 1845. TYPE: Mexico, S. Angel, S. Bartolo, *Schiede 101* (HAL, holotype; US!, photo).
83. *Tillandsia macdougallii* L. B. Smith, Contr. U.S. Natl. Herb. 29: 277, figure 2. 1949. TYPE: Mexico, Oaxaca, Lachatao, 1947, *MacDougall s.n.* (US!, holotype).
84. *Tillandsia oaxacana* L. B. Smith, Contr. U.S. Natl. Herb. 29: 279, figure 4. 1949. TYPE: Mexico, Oaxaca, Lachatao, 1947, *MacDougall s.n.* (US!, holotype).
85. *Tillandsia quaquaflorifera* Matuda, Cact. Suc. Mex. 22: 23–24, figure 14. 1977. TYPE: Mexico, Guerrero, mines near Petatlan, in oak forest, 1,500 m elev., *Matuda 38699* (MEXU, holotype, photo!).

Group II (species 86–104) FIGURE 3.

Epiphytic, saxicolous, or rarely terrestrial in bright, exposed, xerophytic or semixerophytic habitats. Leaves triangular to acuminate, moderately thin to coriaceous, appressed lepidote to tomentose. Inflorescence a spike, or panicle with long or short dorsiventrally compressed branches exceeding subtending bracts, or rarely reduced to a single flower. Floral bracts remote, equal to or shorter than sepals, rarely large and imbricate.

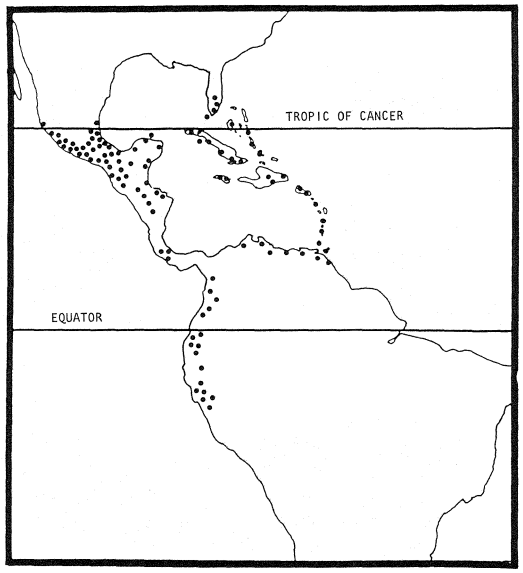

FIGURE 4. Distribution of *Tillandsia* Group II in tropical America.

Flowers distichous, or weakly so, protogynous, horizontal or ascending. Sepals obovate or spatulate, coriaceous, ecarinate, free or equally subfree. Corolla tubular, actinomorphic or rarely zygomorphic, throat open. Petals ligulate or spatulate, 20–53 mm long, often pinched or twisted at union of claw with blade, creamy or greenish white, chartreuse, lavender, rose or red. Stamens in two sets of unequal lengths. Filaments round in cross section, equal in diameter for entire length except ends tapering, usually concolorous with corolla. Anthers 2–3 mm long, versatile, attachment median or submedian. Style longer than or about equal to stamens. No fragrance.

Group II corresponds to *Tillandsia* subgen. *Tillandsia.* TYPE: *Tillandsia utriculata* Linnaeus.

DISTRIBUTION. Southern Florida; throughout the Caribbean; from central Mexico through Central America and along the northern and northwestern coasts of South America (FIGURE 4).

86. *Tillandsia argentea* Grisebach, Cat. Pl. Cub. 254. 1866. FIGURE 3I. TYPE: Cuba, Oriente, Monte Verde, *Wright no. a* (GOET, holotype; GH, isotype, n.v.).
87. *Tillandsia andreana* E. Morren ex Andre, Enum. Bromel. 7. 1888; Revue Hort. 60: 567. 1888. FIGURE 3H. TYPE: Colombia, Cundinamarca, Pandi, Río de la Honda

near Icononzo, *Andre 1762* (K!, holotype; GH!, photo).

88. *Tillandsia albida* Mez & Purpus ex Mez, Repert. Sp. Nov. 14: 248. 1916. FIGURE 3G. TYPE: Mexico, Hidalgo, Ixmiquilpan, *Purpus 38* (B, holotype, n.v.).
89. *Tillandsia calcicola* L. B. Smith & Proctor, Phytologia 16: 77, plate 1, figures 21, 22. 1968. TYPE: Jamaica, Trelawny Parish, Ramgoat Cave, between Albert Town and Kinloss, 450 m elev., *Read 1759* (US!, holotype; IJ, UCWI, isotypes).
90. *Tillandsia dasyliriifolia* J. G. Baker, J. Bot. 25: 304. 1887. TYPE: Mexico, Quintana Roo, Holbox Island, *Gaumer s.n.* (K, holotype; GH, photo, n.v.).
91. *Tillandsia flexuosa* Swartz, Prod. Veg. Ind. Occ. 56. 1788. TYPE: Colombia, Cartagena, based on *Jacquin s.n.* (W, n.v.) [as nomen novum for *Tillandsia tenuifolia* sensu Jacquin].
92. *Tillandsia funkiana* J. G. Baker, Handb. Bromel. 196. 1889. TYPE: *Funck & Schlim 1258* (BM, P!).
93. *Tillandsia hildae* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 3: 19, figures 9–13. 1973. FIGURE 3K. TYPE: Peru, Cajamarca, valley of Río Chamaya, 1,100 m elev., *Rauh 24319* (HEID, holotype, living isotype!; US!, isotype).
94. *Tillandsia karwinskyana* Schultes filius in Roemer & Schultes, Syst. 7(2): 1209. 1830. TYPE: Mexico, without exact locality, *Karwinsky s.n.* (M!, holotype; F, US!, photo).
95. *Tillandsia kegliana* Mez, DC. Monogr. Phan. 9: 725. 1896. TYPE: Surinam, Paramaribo, *Kegel 881* (GOET, lectotype; US!, photo).
96. *Tillandsia lehmanii* Rauh, Bromolienstudien, Trop. Subtrop. Pflan. 8: 15–19, Abb. 5, 6, 6a. 1974. TYPE: Ecuador, Loja, Macara, dry forest, 1970, *Rauh 24195* (HEID, holotype, living clone!; US!, photo).
97. *Tillandsia limbata* Schlechtendal, Linnaea 18: 419. ("1844") 1845. TYPE: Mexico, Veracruz, Hacienda de la Laguna, 1828, *Schiede s.n.* (HAL, holotype; US!, photo).
98. *Tillandsia makoyana* J. G. Baker, Handb. Bromel. 189. 1889. TYPE: from a plant flowered by M. Jacob-Makoy & Co., at Liege, 1879, *Morren Icon* (K?, n.v.).
99. *Tillandsia mima* L. B. Smith, Caldasia 3: 244, figure. 1945. TYPE: Colombia, Valle, Lobo Guerrero, western slope of the Cordillera Occidental, *Cuatrecasas 17816* (GH, holotype; F, US!, VALLE, isotypes).
100. *Tillandsia paraensis* Mez in Martius, Fl. Bras. 3(3): 586, plate 109. 1894. TYPE: Brazil, Para, 1826, *Sieber 68* (BR, holotype; GH!, photo).
101. *Tillandsia propagulifera* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 3: 10, Abb. 4–6. 1973. TYPE: Peru, Libertad, epiphytic on *Prosopis,* bank of Río Utcabamba near Milagro, 450 m elev., *Rauh 24346* (HEID, holotype, living isotype!; US!, isotype).
102. *Tillandsia socialis* L. B. Smith, Phytologia 6: 257, plate 1, figures 1, 2. 1958. TYPE: Mexico, Chiapas, on rocks at bridge of Río Grijalva, 1,200 m elev., *Foster & Vanhyning 2958* (US!, holotype).
103. *Tillandsia spiraliflora* Rauh, Bromelienstudien, Trop. Subtrop. Pflan. 18: 338–342, Abb. 3, 4. 1976. TYPE: Peru, Valle Maronon, 12 km above Balsas toward Leimebamba, 1,700 m elev., *Rauh 38567* (HEID, holotype, photo!).
104. *Tillandsia utriculata* Linnaeus, Sp. Pl. 286. 1753. FIGURE 3J. TYPE: Jamaica, *Sloane s.n.* (BM, holotype; GH, US!, photo).

Group III (species 105–115) FIGURE 5.

Epiphytic, mesic or semimesic. Habitat with bright, filtered light. Leaves triangular, thin to subcoriaceous, often lepidote abaxially, or glabrous on both sides, waxy cuticle covering epidermis, including trichomes. Inflorescence a spike, or panicle, long or short dorsiventrally compressed branches longer or shorter than subtending bracts. Floral bracts large, polished, imbricate. A slimy fluid commonly exuded from within the floral bracts. Flowers protogynous, distichous, ascending. Sepals elliptic, carinate and free. Petals ligulate, 65–85 mm long. Corolla violet, yellow, chartreuse or white, occasionally zygomorphic, throat open or closed. Stamens equal in length. Filaments round in cross section near apex, often broad and flat near base. Filaments white or near white. Anthers subbasifixed, erect, 8–10 mm long. Style longer than stamens or nearly equal.

DISTRIBUTION. Midelevation humid forests of eastern Mexico from below the Tropic of Cancer, through Central America to Costa Rica (FIGURE 6).

105. *Tillandsia deppeana* Steudel, Nom. Bot. ed. 2. 2: 688. 1841; nom. nov. based on *Tillandsia paniculata* Schlechtendal & Chamisso, Linnaea 6: 54. 1831 (non Linnaeus, 1762). TYPE: Mexico, Veracruz, Jalapa, *Shiede & Deppe 1008* (HAL, holotype; LE, G?, isotypes; US!, photo).
106. *Tillandsia heterophylla* A. Morren, Belg. Hortic. 23: 138. 1873. TYPE: Mexico, cul-

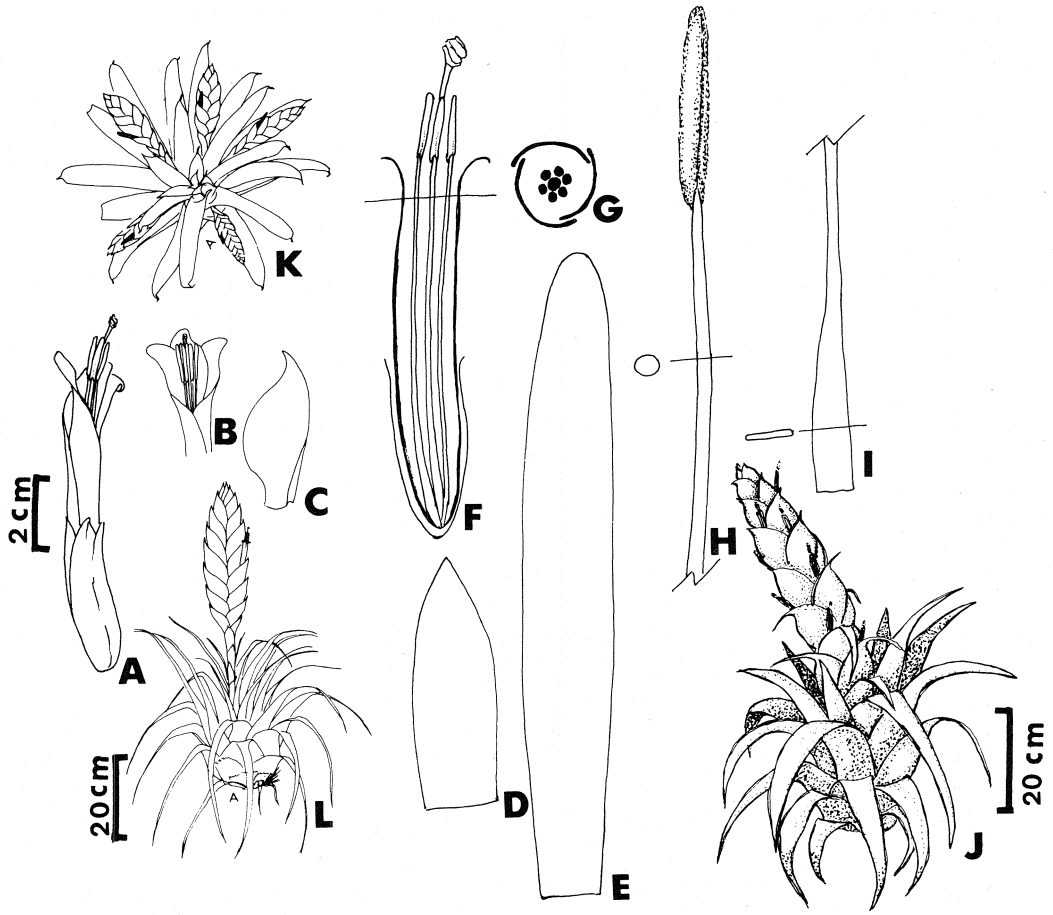

FIGURE 5. *Tillandsia* Group III. A–I, floral characteristics: A, flower, side view; B, distal portion of flower, frontal view; C, floral bract; D, sepal; E, petal; F, longitudinal section of flower; G, cross section of flower; H, distal portion of stamen; I, proximal portion of stamen. J–L, habits of representative species: J, *T. imperialis*; K, *T. multicaulis*; L, *T. lampropoda.*

tivated, 1881, *Malzine in Morren Hortus s.n.* (LG, type clone; GH, photo, n.v.).

107. *Tillandsia hotteana* Urban, Ark. Bot. 17(7): 16. 1921. TYPE: Haiti, Du Sud, Morne La Hotte, Ma Blanche Range, 1917, *Edman 561* (B, holotype; S, isotype; GH, photo, n.v.).
108. *Tillandsia imperialis* E. Morren ex Mez, Pflanzenreich IV. Fam. 32: 482. 1935. FIGURE 5J. TYPE: Mexico, Veracruz, Orizaba, 1866, *Bourgeau 2389* (K, holotype; GH, photo, n.v.).
109. *Tillandsia lampropoda* L. B. Smith in Yuncker, Field Mus. Publ. Bot. 17: 320, plate 9. 1938. FIGURE 5L. TYPE: Honduras, Comayagua, El Achote above Siguatepeque, 1,350 m elev., 1936, *Yuncker, Dawson & Youse 5895* (GH, holotype, n.v.).
110. *Tillandsia laui* Matuda, Cact. Suc. Mex. 20: 96–97, figure 48. 1975. TYPE: Mexico, Oaxaca, Copala, 1,800 m elev., 1974, *Lau s.n.* (MEXU, holotype!, photo!).
111. *Tillandsia multicaulis* Steudel, Nom. Bot. ed. 2. 2: 688. 1841. FIGURE 5K. TYPE: Mexico, Veracruz, Xalapa, *Schiede & Deppe 1007* (B, holotype; BM, isotype; GH, photo, n.v.).
112. *Tillandsia ponderosa* L. B. Smith, Contr. Gray Herb. 154: 37, plate 4, figures 8, 9. 1945. TYPE: Guatemala, Zacapa, Sierra de Las Minas, below Finca Alejandria, 1939, *Steyermark 29797* (F!, holotype).
113. *Tillandsia rauhii* L. B. Smith, Bromel. Soc. Bull. 8: 44, figures. 1958. TYPE: Peru, Piura, below Florida in valley of Río Sana, 700 m elev., 1956, *Rauh P-379* (US!, holotype).
114. *Tillandsia superinsignis* Matuda, Cact.

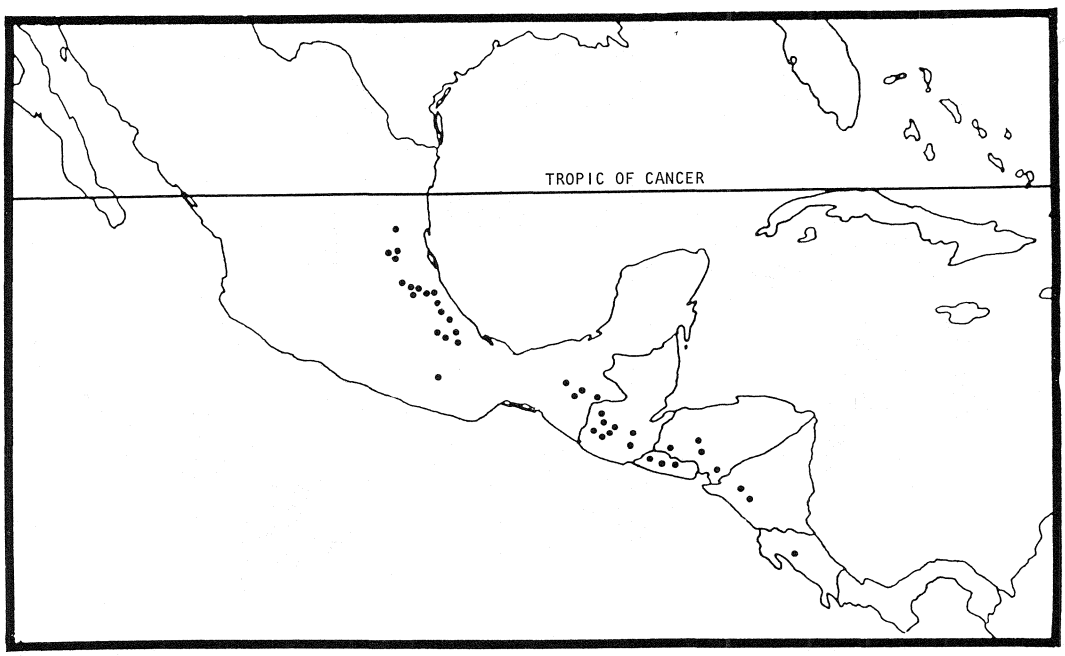

FIGURE 6. Distribution of *Tillandsia* Group III in Mexico and Central America.

Succ. J. (Los Angeles) 45: 189, figure 6. 1973. TYPE: Mexico, Mexico, ravine ridge of El Tequesquite, Divisadero, Canada de Nanchititla, 1,700 m elev., 1973, *Matuda 38531* (MEXU, holotype!, photo!).

115. *Tillandsia yunckeri* L. B. Smith in Yuncker, Field Mus. Publ. Bot. 17: 322, plate 10. 1938. TYPE: Honduras, Comayagua, summit of range above El Achote, above plains of Siguatepeque, *Yuncker, Dawson & Youse 6432* (GH!, holotype).

Group IV (species 116, 117) FIGURE 7.

Epiphytic, mesic to semimesic habitats, filtered light. Leaves filiform, appressed lepidote. Inflorescence a panicle, branches much exceeding subtending bracts. Flowers protogynous, distichous, horizontal or ascending. Sepals elliptic, carinate or ecarinate, free. Petals ligulate, 10–13 mm long, broadly recurved, creamy white, yellow or pale lavender. Corolla throat open. Stamens equal in length. Filaments round in cross section entire length, concolorous with corolla. Anthers versatile, 2 mm long. Style equal or slightly exceeding stamens.

DISTRIBUTION. Midelevation mesic, semimesic or xeric forests from middle gulf coast of Mexico through Central America into northern South America (FIGURE 8).

116. *Tillandsia filifolia* Schlechtendal & Chamisso, Linnaea 6: 53. 1831. FIGURE 7G. TYPE: Mexico, Veracruz, Hacienda de la Laguna, *Schiede & Deppe 1005* (B, holotype; BM, G, isotypes, n.v.).

117. *Tillandsia distichia* Humboldt, Bonpland & Kunth, Nov. Gen. & Sp. 1: 292. 1816. TYPE: Ecuador ("Peru" Smith & Downs, 1977), Loja, Lucarque, *Humboldt & Bonpland 3455* (P, holotype; GH, photo, n.v.).

Group V (species 118–123) FIGURE 9.

Epiphytic or saxicolous in bright semiarid habitats. Leaves narrowly triangular; succulent or filiform. Indumentum lepidote to tomentose. Long asymmetrical trichomes with divergent alae. Inflorescence a spike or reduced panicle appearing digitate. Floral bracts imbricate, membranous, nerved, equal or slightly longer than sepals. Flowers protandrous, distichous, horizontal to descending. Sepals elliptic, membranous, nerved, carinate, free, or posterior slightly connate. Petals moss green, ligulate, weakly recurved, 22–40 mm long. Corolla throat open. Stamens equal in length. Filaments filiform, flat in cross section entire length, white. Anthers subbasifixed, erect, 2–4 mm long. Style shorter than stamens, below anthers at anthesis, subsequently elongating, spreading stigma lobes pushed through anthers.

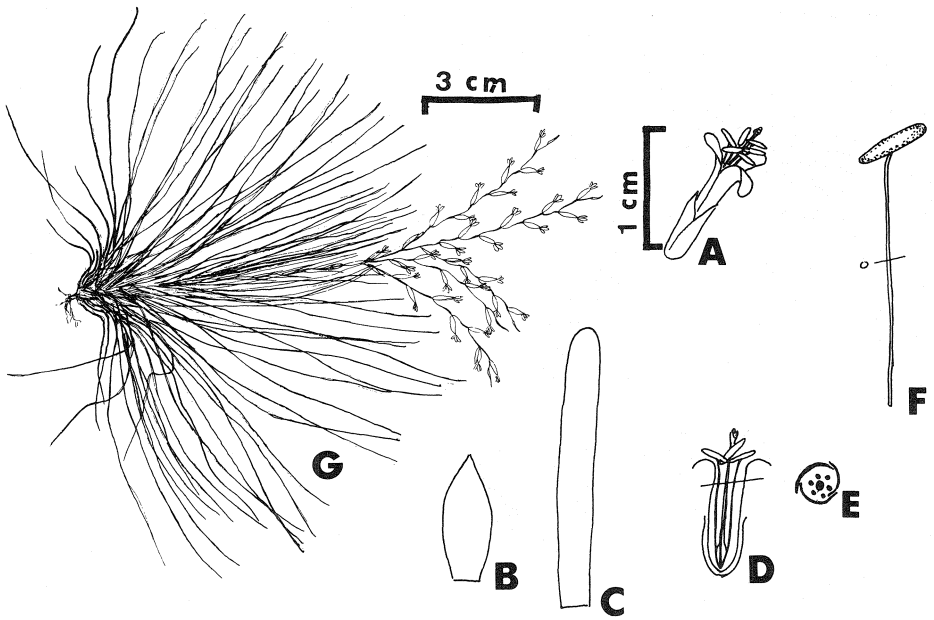

FIGURE 7. *Tillandsia* Group IV. A—F, floral characteristics: A, flower; B, sepal; C, petal; D, longitudinal section of flower; E, cross section of flower; F, stamen. G, habit of representative species: *Tillandsia filifolia.*

DISTRIBUTION. Midelevation forests, deserts and canyons of low rainfall, but frequent fogs on the central plateau and Sierra Madre del Sur of Mexico (FIGURE 10).

118. *Tillandsia atroviridipetala* Matuda, Cact. Suc. Mex. 2: 53, figure 40. 1957. TYPE: Mexico, Mexico, Puente de Calderon, *Matuda 32632* (MEXU!, holotype).

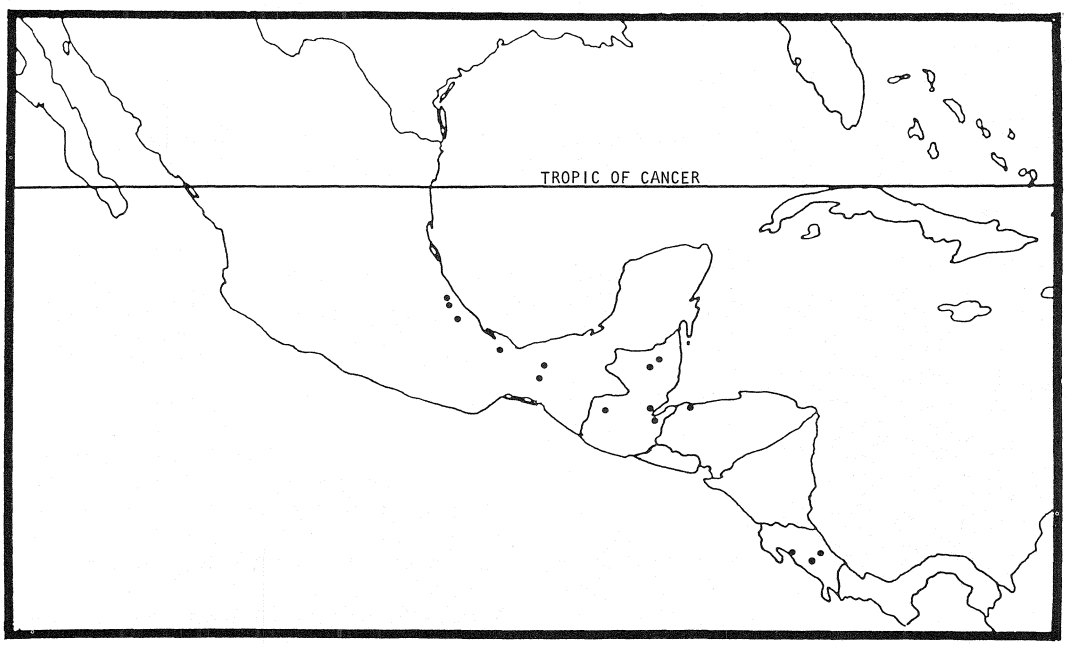

FIGURE 8. Distribution of *Tillandsia* Group IV in tropical America.

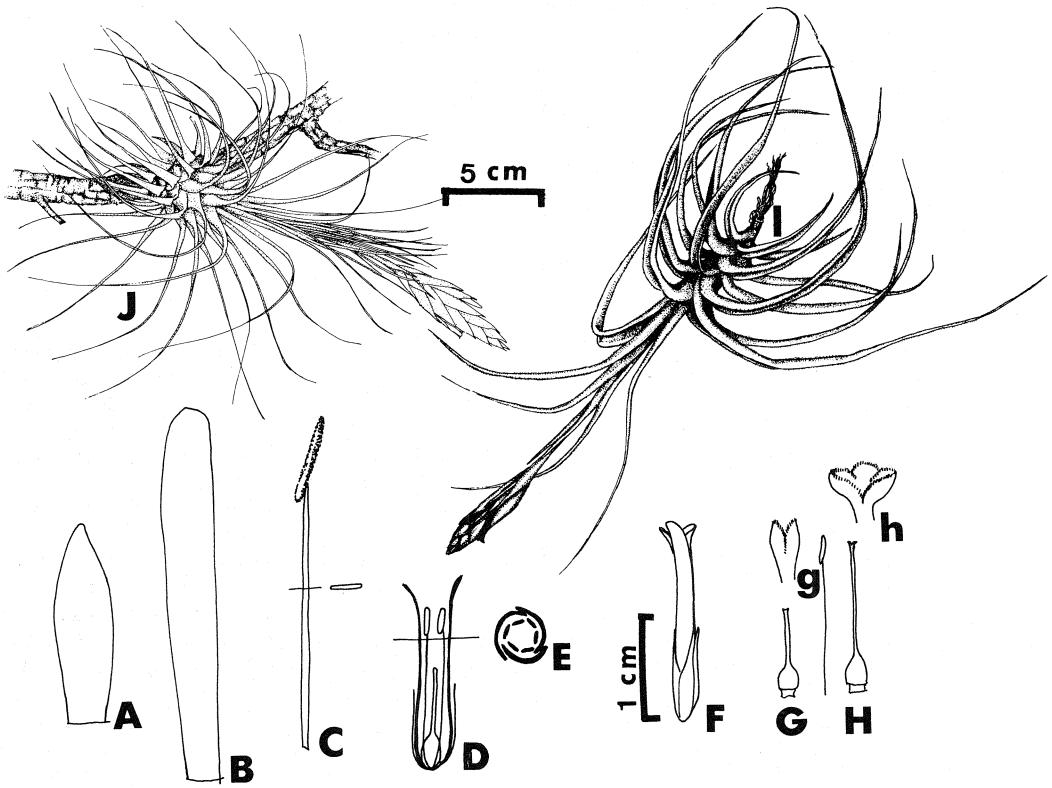

FIGURE 9. *Tillandsia* Group V. A–H, floral characteristics: A, sepal; B, petal; C, stamen; D, longitudinal section of flower; E, cross section of flower; F, flower; G, style at anther dehiscence; g, style tip at anther dehiscence; H, style post anther dehiscence; h, style tip post anther dehiscence. I, J, habit of representative species: I, *Tillandsia ehrenbergii*; J, *T. ignesiae*.

119. *Tillandsia ehrenbergii* (K. Koch) Klotzsch ex Mez, DC. Monogr. Phan. 9: 727. 1896. FIGURE 9I. TYPE: Mexico, *Ehrenberg s.n.* (B!, holotype).
120. *Tillandsia ignesiae* Mez, Bull. Herb. Boiss. II. 3: 143. 1903. FIGURE 9J. TYPE: Mexico, Michoacan, Monte de Santa Ignes, 1908, *Langlasse 93 in part* (B, holotype; G, GH, P, isotypes, n.v.).
121. *Tillandsia lepidosepala* L. B. Smith, Proc. Am. Acad. (Contr. Gray Herb. 106) 70: 155, plate 2, figures 2, 3. 1935. TYPE: Mexico, Michoacan, Lake Cuitzeo, 1892, *Pringle 5323* (GH!, holotype).
122. *Tillandsia mauryana* L. B. Smith, Contr. Gray Herb. 117: 31, plate 2, figures 32, 33. 1937. TYPE: Mexico, Hidalgo, Canada de Metzitlan, 1891, *Maury 5747* (GH, holotype; F, isotype, n.v.).
123. *Tillandsia plumosa* J. G. Baker, J. Bot. 26: 13. 1888. TYPE: Mexico, Puebla, *Andrieux 57* (K, holotype; G, M, isotypes; GH, photo, n.v.).

Incertae sedis

NOTE. Fresh or spirit-preserved flowers of these subgen. *Tillandsia* species have not been examined.

1. *T. adamsii* R. W. Read, Phytologia 28: 21. 1974.
2. *T. brevior* L. B. Smith, Contr. U.S. Natl. Herb. 29: 436. 1951.
3. *T. canescens* Swartz, Prod. Veg. Ind. Occ. 57. 1788.
4. *T. carnosa* L. B. Smith, Phytologia 9: 251. 1963.
5. *T. cryptopoda* L. B. Smith, Ceiba 1: 229. 1951.

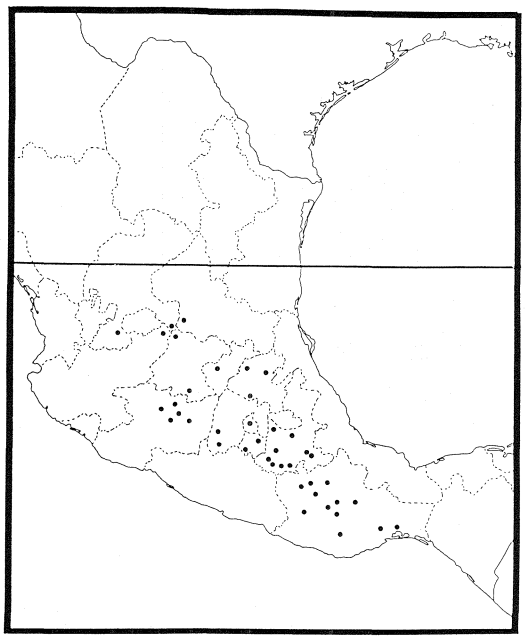

FIGURE 10. Distribution of *Tillandsia* Group V in Mexico.

6. *T. deflexa* L. B. Smith, Contr. Gray Herb. 154: 35. 1945.
7. *T. ecarinata* L. B. Smith, Phytologia 20: 162. 1970.
8. *T. extensa* Mez, Repert. Sp. Nov. 3: 33. 1906; emend. Rauh. Akad. Wiss. & Litt. Mainz 1973(3): 29, 1973.
9. *T. ferreyrae* L. B. Smith, Publ. Mus. Hist. Nat. "Javier Prado" Univ. Nac. Mayor San Marcos Ser. B 16: 5. 1964.
10. *T. gracillema* L. B. Smith, Phytologia 28: 34. 1974.
11. *T. graebeneri* Mez, Repert. Sp. Nov. 14: 253. 1916; known from type specimen only—inflorescence missing!
12. *T. limae* L. B. Smith, Phytologia 20: 166. 1970.
13. *T. lineatispica* Mez, DC. Monogr. Phan. 9: 699. 1896.
14. *T. moscosoi* L. B. Smith, Phytologia 5: 281. 1955.
15. *T. nervata* L. B. Smith, Phytologia 28: 36. 1974.
16. *T. plagiotropica* Rohweder, Senckenbergiana 34: 112. 1953.
17. *T. platyphylla* Mez, Repert. Sp. Nov. 3: 37. 1906.
18. *T. steiropoda* L. B. Smith, Phytologia 6: 257. 1958.
19. *T. subinflata* L. B. Smith, Phytologia 28: 38. 1974.
20. *T. subulifera* Mez, Repert. Sp. Nov. 16: 74. 1919.
21. *T. teres* L. B. Smith, Phytologia 16: 78. 1968; emend. Rauh. Akad. Wiss. & Litt. Mainz 1973(3): 33. 1973.

DISCUSSION AND CONCLUSIONS

The classification of the Tillandsioideae, particularly the remaining *Tillandsia* and *Vriesea,* should be re-examined with a greater emphasis on fertile parts. Suites of character states only available in fresh or spirit-preserved flowers can be used to circumscribe taxonomic groups with a higher predictive value than characters found in dried and pressed specimens.

Exsertion or inclusion of the stamens is a characteristic that can easily be misinterpreted if a flower was immature when dried. Stamens are included during the early stages of anthesis in flowers that exhibit exserted stamens at maturity. An example is *Tillandsia dressleri* L. B. Smith (subgen. *Allardtia*). Smith (1962) noted that it was like *T. balbisiana* Schultes (subgen. *Tillandsia*) in habit, but differed in having stamens shorter than the petals. Fresh specimens collected from the type locality displayed exserted stamens, and were determined to be *T. balbisiana. Tillandsia dressleri,* therefore, is a synonym of *T. balbisiana.* The relative lengths of the petals to the androcium also varies among members of many species. Individuals with stamens about equal to the petals or slightly shorter have been found within populations which typically exhibit exserted stamens. Petal posture has also influenced the interpretation of stamen length relative to that of the petals. For example, *T. deppeana* Steudel and *T. ponderosa* L. B. Smith share numerous floral and habit characteristics, yet the former is classified in subgen. *Allardtia* and the latter in subgen. *Tillandsia. Tillandsia deppeana* typically exhibits at least two erect petals that form a weak hood over the stamens, while the petals of *T. ponderosa* recurve, exposing the anthers. Stamens of *T. filifolia* Schlechtendal & Chamisso (subgen. *Tillandsia*) are exserted only because the petals recurve, exposing the shorter stamens. Of the 12 species examined here that were classified in subgen. *Allardtia* by Smith and Downs (1977), nine can be assigned to three of the new groups described according to floral characters.

Fewer than 25 percent of the known species of *Tillandsia* were examined. The majority were subgen. *Tillandsia,* sensu Smith and Downs

(1977), from Mexico, Florida or southern Texas. Additional fresh or spirit-preserved flowers of subgen. *Allardtia,* centered in northwestern South America, need to be examined. Subgenus *Allardtia,* even larger than subgen. *Tillandsia,* may be equally polyphyletic.

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