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TAXONOMIC CHANGES IN SUBFAMILY *TILLANDSIOIDEAE*

By Herb Plever

Did you become unhinged a few years ago when I reported a proposal by scientists for a major revision in the number of sub-families in family Bromeliaceae from three to eight? We were used to the three: *Pitcairnioideae*, *Bromelioideae* and *Tillandsioideae*, and now *Pitcairnioideae* has been split into six subfamilies - *Brochinioideae*, *Lindmanioideae*, *Hechtioideae*, *Navioideae*, *Pitcairnioideae* and *Puyoideae*. These changes were made by a group of cooperating molecular biologists and taxonomists from many countries around the world. The molecular biologists are doing phylogenetic DNA sequencing on Bromeliad species to determine their evolutionary and biogeographical history and relationships. The study of the morphology of the Bromeliads has been sharpened with closer looks at their habitats, physical (anatomical) structure and parts: leaves, presence or absence of a central tank, presence or absence of petal appendages (nectar scales), position of the ovary, different shapes of corollas (20), stigmas (18) and pollen (9), ovules and seeds and absence or presence of ovule and seed appendages. (See photos on pages 4 to 8). When conclusions based on DNA sequence data agree with morphological data, it is possible to make more confident proposals that will work taxonomically. Lyman Smith's Monograph



Lutheria splendens (formerly *Vriesea splendens*)

(1974-77) included text and graphics of many of these anatomical characters, but recent morphological studies have resulted in new, more extensive and critical data, particularly the stigma morphology that has been advanced by Gregory Brown.

Now - hold on to your hat - new, important reclassifications have been proposed for subfamily *Tillandsioideae* based on a multi-locus DNA sequence phylogeny and morphology by Michael H. Barfuss, Walter Till, Elton M.C. Leme, Juan P. Pinzón, José M. Manzanares, Heidemarie Halbritter, Rosabelle Samuel & Gregory K. Brown. It was recently published in *PHYTOTAXA* (279-1) P. 1-98. (The phylogeny referred to above is a classification based on DNA clades that indicate the evolutionary relationships between the tribes, genera and species.) The main goals are: "to provide a stable classification based on monophyletic established genera, and new taxa (genera and subgenera) using new synapomorphic combinations of diagnostic morphological characters, provide a key for generic identification, and a comprehensive nomenclature for the accepted genera..."

(A monophyletic genus is a group of species which form a clade of plants that have a recent common ancestor and all its descendants, and thus it

THERE WILL BE NO MEETING IN JANUARY.

BEST WISHES FOR a JOYOUS HOLIDAY and a HAPPY NEW YEAR

will provide a stable classification for taxonomy. Synapomorphic characters are traits that the species in a DNA clade have in common which distinguish the clade from other clades.)

The data from the DNA sequencing shows when and which species have a common ancestor. The genera *Mezobromelia*, *Tillandsia* and *Vriesea* were polyphyletic - (they had common characters, but descended from two or more ancestors); the authors propose to reclassify them to create new monophyletic genera. (Unfortunately, it is necessary for me to use scientific jargon to properly describe and summarize the proposals. If this makes you weary, skip down to paragraph "3." in column 2.)

The authors have succeeded in attaining those stated goals: There is a new, workable key to the genera of subfamily *Tillandsioideae* with many physical characters listed to define each genus. The key will be refined and amended as data from ongoing research becomes available. (There are many species that have not yet been analyzed.) By creating new sub-tribes, genera and sub-genera, and reclassifying species anomalies, a more or less stable classification "based on monophyletic established genera" has been created. The following is a brief summary of the key conclusions and important changes:

1. The heretofore recognized four tribes: *Tillandsieae*, *Vrieseae*, *Pogospermeae* (now called *Catopsidae*), and *Glomeropitcairnieae*, are supported by the data. *Vrieseae* has been split into 2 sub-tribes called *Vriesinae* and *Cipuropsidinae*.

2. Eleven new genera have been created, raising the total of supported genera in sub-family *Tillandsioideae* to Eighteen. (The data suggested the possibility that the species *Vriesea subandina* could be moved to a new, single species genus to be called *Cipuropsis*, but it was too weak to justify such a move at this time.) The genera are: *Racinaea* (78 species), *Tillandsia* (772 species), *Barfussia* (3 species from



Wallisia cyanea (formerly *Tillandsia cyanea*)

Tillandsia), *Lemeltonia* (7 species from *Tillandsia*), *Pseudoalcantarea* (3 species from *Tillandsia*), *Wallisia* (5 species from *Vriesea*), *Guzmania* (219 species), *Gregbrownia* (4 species from *Mezobromelia*), *Mezobromelia* (5 species), *Josemania* (5 species from *Vriesea*), *Werauhia* (92 species), *Goudaea* (2 species from *Vriesea*), *Jagrantia* (1 species from *Vriesea*), *Lutheria* (4 species from *Vriesea*), *Zizkaea* (1 species from *Vriesea*), *Stigmatodon* (18 species from *Vriesea*), *Vriesea* (238 species) and *Alcantarea* (41 species).

3. A new subgenus *Pseudovriesea* has been added to genus *Tillandsia*, (I assume) as a place to transfer the xeromorphic, grey-leaved former *Vrieseas* as proposed by Jason Grant. But only 4 of the 41 species are named in the report.

4. The following is a short list of popularly grown Tillandsioids in which changes have been made.

Some former *Vriesea* species are now:

Tillandsia andreetae, *T. barclayana*, *T. cereicola*, *T. espinosae*, *T. heterandra*, *T. hitchcockiana*, *T. malzinei*, *T. tequendamae*, *T. heliconioides* *T. tillandsioides*.

Some former *Vriesea* species are now:

Goudaea chrysostachys, *G. ospinae*, *G. ospinae* var. *gruberi*, *Jagrantia monstrum*, *Lutheria glutinosa*, *L. splendens*, *Stigmatodon goniorachys*, *Zizkaea tuerckheimii*,

Some former *Tillandsia* species are now:

Barfussia laxissima, *B. platyrhachis*, *B. wagneriana*, *Lemeltonia dodsonii*, *L. monodelpha*, *L. narthecioides*, *L. triglochoides*, *Pseudoalcantarea grandis*, *Ps. viridiflora*, *Racinaea dyeriana*, *R. hamaleana*, *R. venusta*, *Wallisia anceps*, *W. cyanea*, *W. lindeneana* (a new name for former *T. umbellata*), *W. pretiosa*.

Some former *Mezobromelia* species are now: *Gregbrownia hutchisonii*, *Gregbrownia lymansmithii*.

5. Complexes - Some genera are similar in appearance and are closely



Racinaea dyeriana (formerly *Tillandsia dyeriana*)

related biogeographically and/or in their evolution. Similarly, groups of species similar in appearance can be identified as sub-complexes. They may have physical characters in common, but each has its own unique characters to justify retaining a genus or a species rank. These species complexes are a useful taxonomic tool, especially when supported by DNA sequencing.

For example, in his seminar at the Monocots V Conference in 2013 Elton Leme identified and described a *Cryptanthoid Complex* consisting of three related genera: *Cryptanthus*, *Orthophytum* and *Lapanthus*, because they shared habitats and some important physical characters.

The 2016 DNA results support the classification of species complexes, and this report identifies the following: *Tillandsia biflora* (136 species), *T. australis* (4 species), *T. disticha* (2 species), *T. dodsonii*, *T. gardneri* (17 species), *T. lindenii*, *T. purpurea* (6 species), *T. plumosa*, *T. rauhii* 3 species), *T. sphaerocephala* (6 species) and *T. wagneriana*.

6. These many important changes will likely rattle our readers, but just think of the headache the changes have created for Geoff Lawn, our BSI Cultivar Registrar, and his colleagues Eric Gouda and Derek Butcher, who maintain and keep the BCR current. Not only do they have the enormous job of correcting cultivar names to conform to newly created genera and changes in genera, but they have to invent new bigeneric names for cultivars where one or both parents are in changed genera. For example the parents of *x Vrieslandsia* ‘Pink Magic’ (Arden) are former *Tillandsia laxissima* (now *Barfussia laxissima*) and *Vriesea* ‘Redondo Beach’. They will have to create a new bigeneric name from *Barfussia* and *Vriesea*. I am happy to inform you that Geoff, Eric and Derek are already hard at work making those changes.

I have expanded this issue to photos of plants from different habitats and different corollas and stigmas), and to present in its entirety the new key to the genera of subfamily *Tillandsioideae*. (See pages 4-10.) It is too soon to ascertain the assessments of the report by other leading biologists and taxonomists. Some understandable confusion has resulted from the placement of morphologically disparate species in subgenus *Tillandsia*, based apparently on “weakly supported” DNA data. This and other issues will

likely be revisited by the authors. An incomplete, complex system for Tillandsioids cannot be totally neat and tidy.

The bromeliad world owes a debt of gratitude to the authors of this 2016 report and to their colleagues, researchers, lab assistants etc. for this major advance in bromeliad taxonomy. □



Tillandsia biflora - Photo by Hiroyuki Takizawa

NEWS and NOTES

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HABITAT OF SELECTED TILLANDSIOIDEAE



FIGURE 1. Habit of selected Tillandsioideae. Habit (adult): m = mesomorphic, sx = semi-xeromorphic, x = xeromorphic. Central tank (adult): a = absent, p = present. A. *Catopsis hahnii* (Leme 2482; m, p). B. *Barfussia wagneriana* (Takizawa s.n.; m, p). C. *Guzmania kareniae* (Leme 3439; m, p). D. *Josemania singularis* (Leme 2838; m, p). E. *Lemeltonia dodsonii* (Leme 2523; sx, a). F. *Pseudalcantarea viridiflora* (Takizawa s.n.; m, p). G. *Racinaea pugiformis* (Leme 5180; m, a). H. *Tillandsia geminiflora* (Leme s.n.; sx, a). I. *Racinaea hamaleana* (Leme 7319; m, p). J. *Tillandsia fasciculata* s.l. (Leme 4833; x, a). K. *Goudaea chrysostachys* (Leme 2509; m, p). L. *Mezobromelia capituligera* (Leme 5111; m, p). M. *Lutheria glutinosa* (Leme 2525; m, p). N. *Werauhia nephrolepis* (Leme 3955; m, p). O. *Vriesea psittacina* (Leme 7075; m, p). P. *Alcantarea imperialis* (Leme 304; m, p). Q. *Stigmatodon euclidianus* (Leme 5712 sx, p)

COROLLA TYPES IN TILLANDSIOIDEAE



FIGURE 2. Corolla types in Tillandsioideae. A. *Catopsis hahnii* (Leme 2482; urceolate). B. *Catopsis pisiformis* (Leme 2410; urceolate); C. *Gregbrownia lyman-smithii* (Leme 4655; tubular with spreading petal blades); D. *Barfussia laxissima* (Takizawa s.n.; salverform); E. *Guzmania patula* (Leme 4062; tubular with recurved petal blades); F. *Guzmania kareniae* (Leme 3439; tubular with spreading petal blades); G. *Guzmania cylindrica* (Leme 4586; tubular with enlarged, erect, slightly divergent petal blades); H. *Guzmania sanguinea* var. *comosa* (Leme 3253; tubular with cucullate petal tips); I. *Guzmania musaica* (Leme 3538; tubular with cucullate petal tips). J. *Pseudalcantarea viridiflora* (Takizawa s.n.; tubular with spreading, helicoiform petal blades). K. *Racinaea hamaleana* (Leme 7319; salverform); L. *Racinaea crispa* (Leme 2437; urceolate). M. *Tillandsia malzinei* (Leme 361; tubular with recurved petal blades). N. *Tillandsia xiphioides* (Takizawa s.n.; salverform). O. *Tillandsia incurva* (Leme 7299; tubular with divergent petal tips). P. *Tillandsia fasciculata* s.l. (Leme 4833; tubular). Q. *Tillandsia usneoides* (Leme 306; tubular with spreading petal blades). R. *Tillandsia graomogulensis* (Leme 1489; salverform). S. *Tillandsia geminiflora* (Leme s.n.; tubular with spreading petal tips). T. *Tillandsia tectorum* (Takizawa s.n.; tubular).

COROLLA TYPES IN TILLANDSIOIDEAE CONTINUED



FIGURE 3. Corolla types in Tillandsioideae (continued). A. *Lemeltonia dodsonii* (Leme 2523; salverform). B. *Wallisia lindeniana* (Barfuss s.n.; salverform). C. *Alcantarea farneyi* (Leme 1910; tubular with strongly recurved petal blades). D. *Alcantarea robertokautskyi* (Leme 3866; tubular with strongly recurved petal blades). E. *Stigmatodon plurifolius* (Leme 6997; campanulate). F. *Stigmatodon apparicianus* (Leme 7379; campanulate). G. *Stigmatodon amadoi* (Leme 5953; campanulate). H. *Vriesea flammea* (Leme 5471; tubular with spreading petal tips). I. *Vriesea psittacina* (Leme 7075; tubular). J. *Vriesea platynema* (Leme 1670; tubular). K. *Vriesea saxicola* (Leme 5236; campanulate). L. *Vriesea pseudoatra* (Leme 3917; campanulate). M. *Vriesea* ('*Cipuropsis*') *elata* (Leme 743; tubular with recurved petal blades). N. *Vriesea breviscapa* (Leme 8235; tubular). O. *Werauhia nephrolepis* (Leme 3955; cupshaped base and one petal blade spreading, the other two forming a hood). P. *Werauhia gladioliflora* (Leme 3967; campanulate). Q. *Lutheria glutinosa* (Leme 2525; tubular). R. *Mezobromelia capituligera* (Leme 5111; tubular). S. *Goudaea chrysostachys* (Leme 2509; tubular with cucullate petal tips). T. *Zizkaea tuerckheimii* (Gouda s.n.; campanulate).

STIGMA TYPES IN TILLANDSIOIDEAE

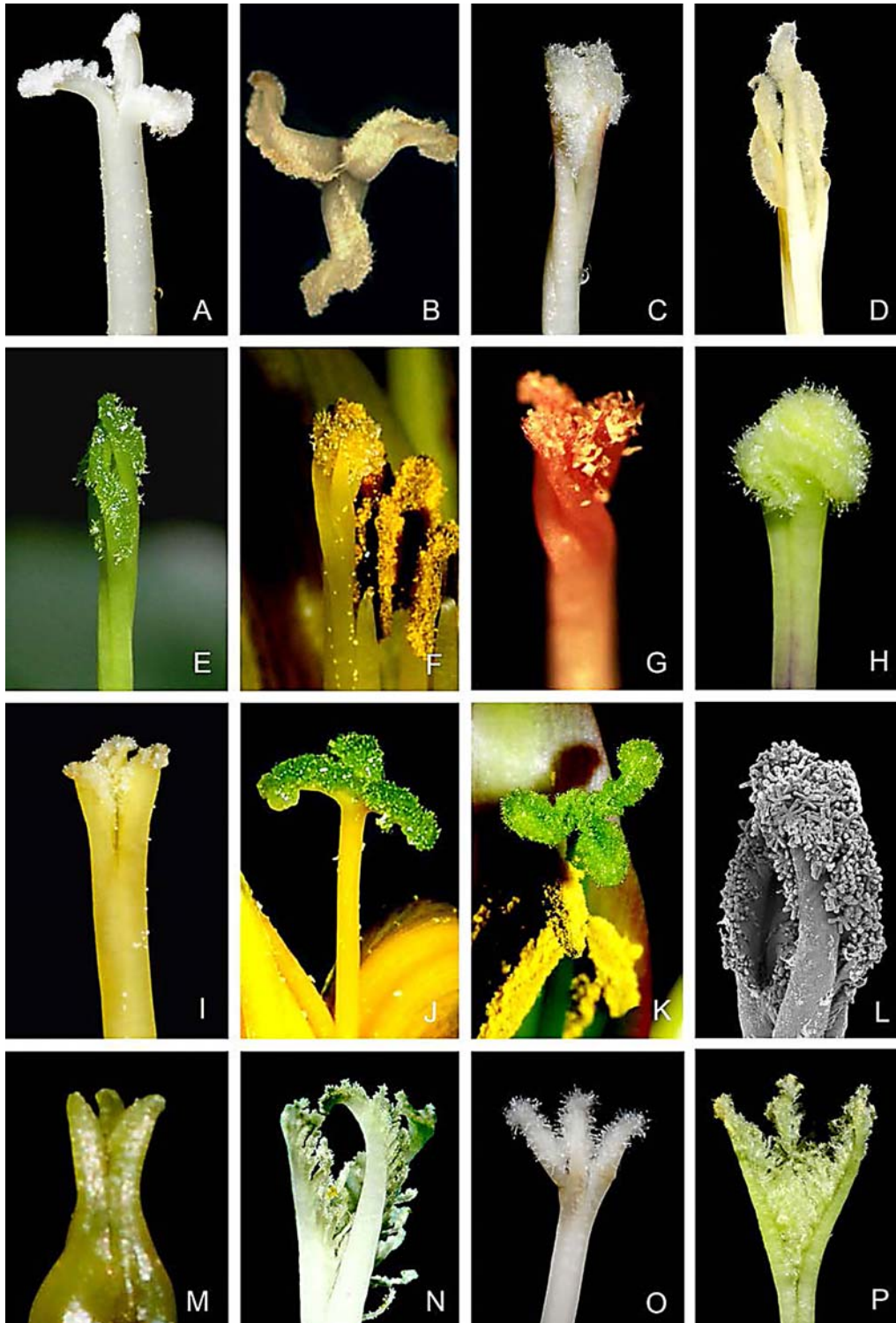


FIGURE 4. Stigma types in Tillandsioideae. Conduplicate and simple types (Table 5). A. *Alcantarea heloisae* (Leme 8055; cp, lateral view). B. *Alcantarea heloisae* (Leme 8055; cp, top view). C. *Alcantarea extensa* (Leme 1942; ce, early anthesis). D. *Alcantarea cerosa* (Leme 8551; ce, late anthesis). E. *Pseudalcantarea viridiflora* (Leme 2835; ce). F. *Gregbrownia lyman-smithii* (Leme 4655; cs). G. *Tillandsia gardneri* (Leme s.n.; cs). H. *Tillandsia fasciculata* s.l. (Leme 4833; cs). I. *Goudaea chrysostachys* (Leme 2509; se). J. *Guzmania sprucei* (Leme 3551; sp). K. *Tillandsia malzinei* (Leme 361; sp). L. *Guzmania musaica* (spi). M. *Catopsis floribunda* (Leme 8101; se). N. *Wallisia anceps* (Till et al. 15046; cpi). O. *Guzmania wittmackii* (Leme 2520; spi). P. *Wallisia lindeniana* (Leme2406;cpi).

STIGMA TYPES IN TILLANDSIOIDEAE CONTINUED

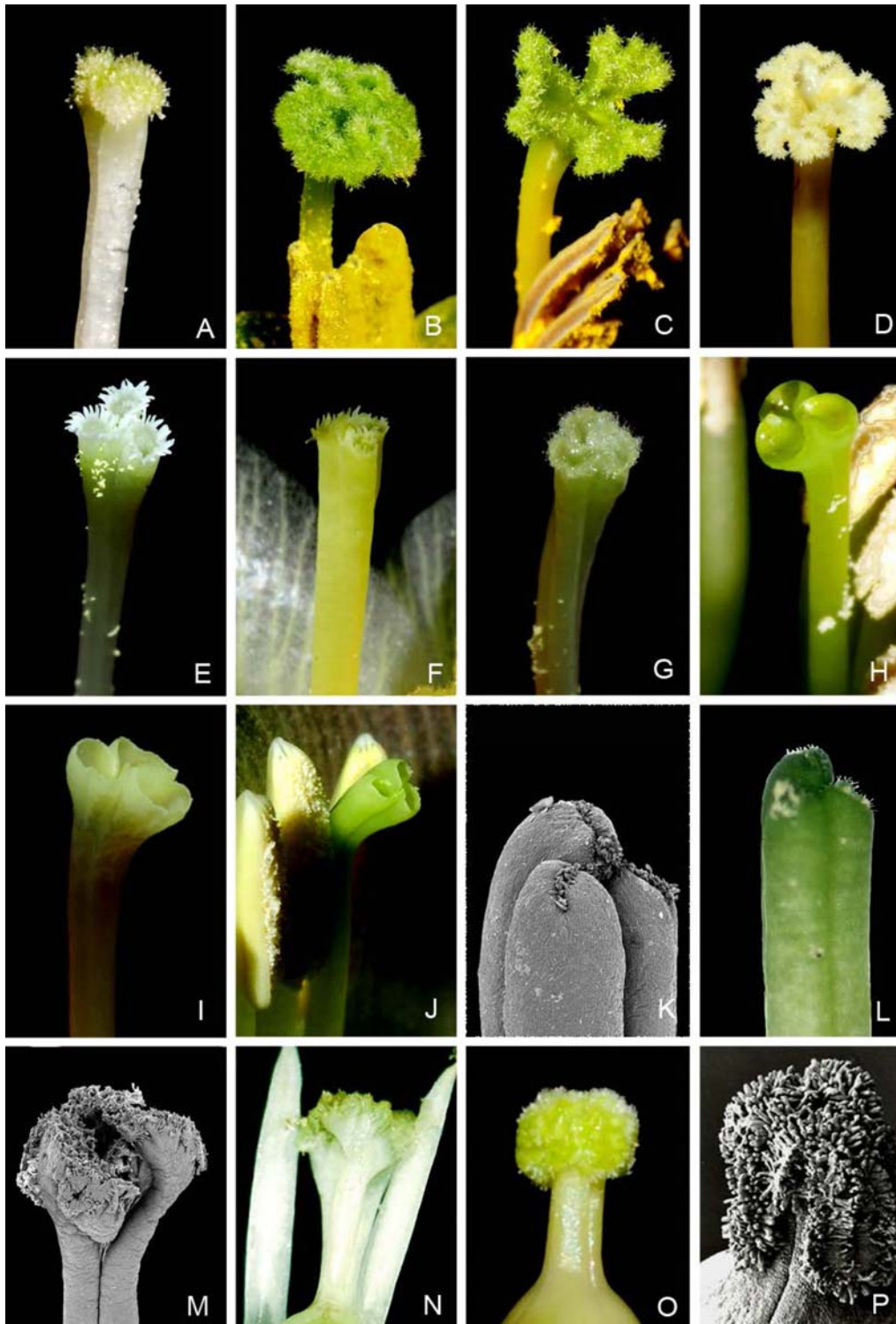


FIGURE 5. Stigma types in Tillandsioideae (continued). Convolute, coralliform, cupulate, tubo-laciniate and urceolate types (Table 5). A. *Guzmania patula* (Leme 4062; cbI). B. *Vriesea gradata* (Leme 5738; cbII). C. *Vriesea psittacina* (Leme 7075; cbII). D. *Vriesea jonghei* (Leme 2189; cbII). E. *Stigmatodon bifidus* (Leme 7368; tl). F. *Stigmatodon funebris* (Leme 7976; tl). G. *Stigmatodon rosulatus* (Leme 8621; tl with papillae). H. *Werauhia pedicellata* (Leme 7320; cup). I. *Werauhia subsecunda* (Leme 2561; cup). J. *Werauhia* sp. (Leme 3987; cup). K. *Zizkaea tuerckheimii* (W. Till 17055 & Hromadnik 25033; urc). L. *Zizkaea tuerckheimii* (W. Till 17055 & Hromadnik 25033; urc). M. *Barfussia platyrhachis* (Belvedere s.n.; co). N. *Barfussia platyrhachis* (Belvedere s.n.; co). O. *Racinaea venusta* (Leme 2590; cf). P. *Lemeltonia dodsonii* (MSBG 1981-0055; cf).

KEY TO THE GENERA IN SUBFAMILY TILLANDSIOIDEAE

1. Ovary about 1/2–2/3 inferior; stigma of the convolute-umbrella type; fruit a partly septical capsule; seeds with appendages of the *Glomeropitcairnia* type, long appendaged on both ends.—Flowers spirally arranged; petals bearing basal appendages *Glomeropitcairnia*
- Ovary less than 1/2 inferior or superior; stigma not of the convolute-umbrella type, if resembling a convolute type, then of the convolute-blade I type (Fig. 5A) or the convolute-blade II type (Figs. 5B–D) or of the convolute-obconic type (Figs. 5M, N); fruit a septical capsule; seeds with appendages of the *Catopsis* type or the Core Tillandsioideae type, usually long appendaged only on one end, but the appendage at the apical end sometimes well developed.—Flowers spirally or distichously arranged; petals bearing or without basal appendages..... 2.
2. Ovary superior to about 1/8 inferior; seeds with appendages of the *Catopsis* type, with a plumose flight apparatus formed at the apical end by multicellular hairs folded at maturity, and a multicellular, undivided plume at the basal end.—Flowers spirally arranged; sepals strongly asymmetric; petals without basal appendages..... *Catopsis*
- Ovary more than 1/8 inferior, but not more than 1/2 inferior; seeds with appendages of the Core Tillandsioideae type, with a plumose flight apparatus formed at the basal end, appendage at the apical end lacking, short and usually undivided, or rarely long and occasionally somewhat divided, not folded at maturity.—Flowers spirally or distichously arranged; sepals usually symmetric or subsymmetric, if occasionally asymmetric, then flowers distichously arranged; petals bearing or without basal appendages..... 3.
3. Petals conglutinated/connate into a tube for more than 1/4 of their entire length; filaments partially agglutinated/adnate to the conglutinated/connate portion of the petals.—Flowers usually spirally, rarely distichously arranged; petals white, yellow, or green (Figs. 2C, E–I); seeds without a distinct appendage at the apical end 4.
- Petals free or sometimes conglutinated/connate into a tube shorter than or equalling about 1/4 of their entire length; filaments free, conglutinated/connate, or short agglutinated/adnate to the petals.—Flowers usually distichously, rarely spirally arranged; petals violet, pink, red, orange, yellow, green, white, and rarely bicolored (Figs. 2D, J–T, 3A–T); seeds usually with a distinct appendage at the apical end usually up to the length of the seed proper, occasionally longer..... 6.
4. Petals without basal appendages.—Stigma of the convolute-blade I type (Fig. 5A) or the simple-erect type, occasionally of the simple-patent type (Fig. 4J) or simple-pinnatisect type (Fig. 4L, O) *Guzmania*
- Petals bearing basal appendages.—Stigma of the simple-erect type or the conduplicate-spiral type (Fig. 4F) 5.
5. Inflorescence compound, once or rarely twice branched, with branches composed of dense flower fascicles (Fig. 1L); petals about 1/3–1/2 of their entire length conglutinate/connate into a tube, tips slightly divergent (Fig. 3R), bearing linear and entire basal appendages, highly adnate to the conglutinated/connate portion of the petals; stamens and style included within the corolla; anthers united into a tube surrounding the stigma, not versatile; stigma of the simple-erect type *Mezobromelia*
- Inflorescence compound, twice or rarely triple branched, a laxly flowered panicle; petals more than 1/2 of their entire length conglutinate/connate into a tube, blades spreading (Fig. 2C), bearing crenulated basal appendages adnate for less than 1/3 of the conglutinated/connate portion of the petals; stamens and style exerted from the corolla; anthers not forming a tube around the stigma, versatile; stigma of the conduplicate-spiral type (weakly spiral) (Fig. 4F) *Gregbrownia*
6. Stigma of the conduplicate-patent type (Figs. 4A, B) or conduplicate-erect type (Figs. 4C–E); petals linear, forming a tubular corolla with strongly recurved and coiled, or spreading and +/- coiled, or spreading and spirally twisted blades.—Stamens and style much exerted from the corolla (Figs. 2J, 3C, D); ovary 1/3–1/2 inferior.....Stigma usually not of the conduplicate-patent type or the conduplicate-erect type, if rarely resembling the conduplicate-patent type, then corolla tubular; petals forming a urceolate, campanulate, salverform or tubular corolla, usually with spreading or recurved blades or tips only (Figs. 2D, 2K–T, 3A–T).—Stamens and style included within or exerted from the corolla; ovary usually up to 1/3, very rarely up to 1/2 inferior 8.
7. Petals light green, spreading and spirally twisted (helicoform; Figs. 1F, 2J), without basal appendages; ovules appendiculate, shorter than or equalling the ovule proper; seeds with an appendage at the basal end distinctly longer than the seed proper, appendage at the apical end short, about half as long as to equalling the seed proper, undivided; stigma green (Fig. 4E)
- Petals white, cream, pale to bright yellow, rarely pale wine-castaneous or dark wine, recurved or coiled (Figs. 3C, D), bearing well-developed basal appendages; ovules distinctly appendiculate, longer than the ovule proper; seeds with an appendage at the basal end rather short, about equalling the seed proper, appendage at the apical end distinctly larger than the seed proper, sometimes somewhat divided; stigma white (Figs. 4A–D) *Alcantarea*
8. Stigma of the cupulate type (Figs. 5H–J) *Werauhia*
- Stigma not of the cupulate type, if occasionally resembling a cupulate type, then of the urceolate type (Figs. 5K, L) or tubo-laciniate type (Figs. 5E–G) 9.
9. Stigma of the urceolate type (Figs. 5K, L)..... *Zizkaea*
- Stigma not of the urceolate type..... 10.
10. Stigma of the tubo-laciniate type (Figs. 5E–G)..... *Stigmatodon*
- Stigma not of the tubo-laciniate type 11.

11. Stigma of the convolute-blade II type (Figs. 5B–D).—Leaves mesomorphic or rarely semi-xeromorphic, usually forming strongly to moderately impounding rosettes (Fig. 1O); petals usually bearing basal appendages *Vriesea*
 - Stigma not of the convolute-blade II type, if rarely resembling a convolute type, then of the convolute-obconic type (Figs. 5M, N) or the convolute-blade I type, the latter with xeromorphic, densely lepidote leaves, not forming impounding rosettes, and petals without basal appendages..... 12
12. Filaments conglutinate/connate at least at the base but sometimes for nearly the whole length, free from the petals; stigma of the coralliform type (Fig. 5P).—Leaves narrowly triangular; inflorescence simple, petals white or rarely yellowish with enlarged, spreading blades (Fig. 1E) *Lemeltonia*
 - Filaments free from each other, but sometimes partially agglutinated/adnate to the petals; stigma usually not of the coralliform type, if rarely resembling the coralliform type (Fig. 5O), then filaments free from each other, leaves lingulate, and inflorescence usually compound (Fig. 1I) 13.
13. Stigma of the conduplicate-pinnatisect type (Figs. 4N, P); leaves mostly conspicuously longitudinally reddish (-brown) striped near the base *Wallisia*
 - Stigma not of the conduplicate-pinnatisect type; leaves not longitudinally reddish striped near the base 14.
14. Stigma of the convolute-obconic type (Figs. 5M, N).—Leaves mesomorphic, lingulate, forming an impounding rosette (Fig. 1B) *Barfussia*
 - Stigma not of the convolute-obconic type, if rarely resembling a convolute type, then of the convolute-blade I type and leaves xeromorphic and narrowly triangular, not forming impounding rosettes 15.
15. Sepals usually distinctly asymmetric, free, and stigma of the simple-erect type or of the conduplicate-spiral type (weakly spiral); rarely sepals subsymmetric and stigma resembling the coralliform type (Fig. 5O) *Racinaea*
 - Sepals usually symmetric or subsymmetric, the adaxial ones often connate (and therefore appearing asymmetric); stigma not of the coralliform type, usually of the simple-erect type (Fig. 4I) or conduplicate-spiral type (Fig. 4G, H), rarely of the simple-truncate type, the simple-patent type (Fig. 4K), the conduplicate-patent type or the convolute-blade I type 16.
16. Floral bracts deciduous along a basal transversal line after anthesis when dry, 3 times the length of the sepals, laterally strongly compressed and sharply carinate..... *Jagrantia*
 - Floral bracts persistent when dry, maximally 2 times the length of the sepals, rounded in transversal section even if carinate *Tillandsia p.p.*
19. Leaves xeromorphic to occasionally semi-xeromorphic, usually densely lepidote; leaf blades narrowly triangular.—Petals usually violet, rarely green (Fig. 2O) or yellowish, often bicolored with contrasting margins, sometimes with crenulated margins; ovules appendiculate, shorter than or equalling the ovule proper *Tillandsia p.p.* (*T. subg. Pseudovriesea p.p.*)
 - Leaves mesomorphic, not densely lepidote; leaf blades lingulate.—Petals white, greenish-white, or yellow, rarely red or deep pink, margins always entire; ovules obtuse or rarely appendiculate 20.
20. Corolla unilaterally bent, slightly zygomorphic (Fig. 2M, 3Q); petals free; stamens and style exerted from the corolla; stigma of the conduplicate-spiral type or simple-patent type..... 21.
 - Corolla actinomorphic (Fig. 3M, S); petals short connate at the base for < 1/4 of their entire length or about 1/4 of their entire length conglutinated/connate into a tube; stamens and style included within the corolla; stigma of the simple-erect type (Fig. 4I)..... 22.
21. Stigma of the conduplicate-spiral type; petals red, deep pink, or yellow, tips straight or slightly divergent (Fig. 3Q)..... *Lutheria*
 - Stigma of the simple-patent type (Fig. 4K); petals white or greenish-white, the adaxial one straight, the two abaxial ones recurved (Fig. 2M) *Tillandsia p.p.* (*'Vriesea' sect. Cylirostachys*)
22. Petals short connate at the base for < 1/4 of their entire length, tips cucullate, forming a hardly opened corolla (Fig. 3S), petal appendages spatulate; anthers free; floral bracts ecarinate..... *Goudaea*
 - Petals about 1/4 of their entire length conglutinated/connate into a tube, tips straight or recurved, petal appendages linear; anthers united into a tube surrounding the stigma, not versatile (Fig. 3M); floral bracts carinate *Cipuropsis and mesomorphic northern Andean 'Vriesea'*