Two New Species in the *Tillandsia utriculata* Complex (Bromeliaceae) from Mexico

Iván M. Ramírez M. and Germán Carnevali F. C.

Herbarium CICY, Centro de Investigación Científica de Yucatán, A.C., Calle 43 #130, Colonia Chuburná de Hidalgo, Mérida 97200, Yucatán, México. ramirez@cicy.mx; carneval@cicy.mx

Abstract. Two new species in the *Tillandsia utriculata* (L.) L. complex (Bromeliaceae) from Mexico are proposed. Both are herein described and illustrated with their affinities discussed. The first new entity, *T. aesii* I. Ramírez & Carnevali from the states of Jalisco, Guerrero, and Oaxaca, is similar to *T. makoyana* Baker, but the new taxon has an open rosette with leaves that are green adaxially and white lepidote abaxially (vs. a funnelform rosette with gray leaves on both surfaces in *T. makoyana*), actinomorphic flowers with a light apple-green corolla (vs. zygomorphic with a purple to light purple corolla). The second taxon proposed here, *T. pinicola* I. Ramírez & Carnevali, from the state of Oaxaca, is also similar to *T. makoyana*, but is a smaller plant with a more compact growth habit and leaves with proportionally shorter leaf blades that abruptly attenuate from a broad sheath (vs. gradually attenuate into the proportionally longer blade) into a sub-acicular apex. It is also characterized by typically growing on pines, hence the epithet.

Resumen. Dos nuevas especies en el complejo *Tillandsia utriculata* (L.) L. (Bromeliaceae) de México se proponen como nuevas. Ambas se describen, se discuten sus afinidades y se documentan con ilustraciones y fotografías. La primera especie *T. aesii* I. Ramírez & Carnevali de los estados de Jalisco, Guerrerro y Oaxaca, es similar a *T. makoyana* Baker pero la nueva especie tiene rosetas abiertas con hojas verdes adaxialmente y blanco lepidotas abaxialmente (vs. rosetas en forma de embudo con hojas grises en ambas superficies en *T. makoyana*), flores actinomórficas con corola verde manzana claro (vs. flores zigomorfas y con pétalos púrpura o púrpura claro). La segunda especie, *T. pinicola* I. Ramírez & Carnevali, del estado de Oaxaca, es también similar a *T. makoyana* pero es una planta más pequeña con un hábito de crecimiento más compacto y hojas proporcionalmente con láminas foliares más cortas las cuales se atenúan abruptamente en una vaina ancha (vs. vainas atenuándose gradualmente en láminas foliares proporcionalmente más largas) con un ápice acicular. Esta nueva especie también se caracteriza por crecer en pinos, de allí su epíteto.

Key words: Bromeliaceae, Mexico, *Tillandsia*.

The genus *Tillandsia* L. was classified in seven subgenera by Mez (1896) and later supported by Smith and Downs (1977) in their *Flora Neotropica* treatment of the entire Bromeliaceae. The high levels of homoplasy in several morphological characters (such as petal appendages) considered important in traditional classifications (including that of Smith and Downs) have blurred our understanding of the limits of the supraspecific groups within the genus. Some of the subgenera recognized by Mez (1896) and Smith and Downs (1977) have been recently treated as distinct genera, i.e., *Racinaea* M. A. Spencer & L. B. Smith, formerly *Tillandsia* subg. *Pseudocatopsis* Baker (Spencer & Smith, 1993), but without the necessary phylogenetic work to back up the proposals despite their wide acceptance by several taxonomists (e.g., Luther, 1995; Morales, 2003).

Recent novel research and the analysis of new characters (ranging from the re-evaluation of fresh floral material to newly generated DNA nucleotide sequence data) have allowed a better understanding of the relationships within the genus (Gardner, 1986; Terry et al., 1997; Barfuss et al., 2005), but more studies are required before more taxonomic and nomenclatural changes are warranted within the Tillandsioideae. Furthermore, in the most recent phylogenetic study based on DNA sequence data from seven plastid regions, none of the subgenera of *Tillandsia* were found to be monophyletic (Barfuss et al., 2005).

Studies at the population and at the species-complex levels using field data (e.g., habitat and distribution analysis, ecology) and the careful analysis of fresh material either in the field or under cultivation can provide a wealth of new data that are usually unavailable when only working with herbarium material (see Gardner, 1986, for a good example). Within *Tillandsia*, some species complexes, including the relatives of *T. utriculata* (L.) L., can only be understood with this kind of approach because most of the relevant features required to diagnose the taxa in the group become lost upon vouchering, including

plant architecture. In many cases, the taxa that compose these species complexes are allopatric or parapatric, but because herbarium data are scarce, they fail to reveal the often subtle ecological and geographical patterns, which can only be disclosed with extensive fieldwork and an abundant herbarium record.

A brief description of the *Tillandsia utriculata* complex was provided by Ramírez et al. (2004). Described species in the *T. utriculata* complex include *T. makoyana* Baker, *T. limbata* Schlechtendal, *T. dasyliriifolia* Baker, *T. pringlei* S. Watson (treated by Gardner (1984) as *Tillandsia utriculata* subsp. *pringlei* (S. Watson) C. S. Gardner), *T. utriculata*, *T. calcicola* L. B. Smith & Proctor, *T. cucaensis* Wittman, *T. pulvinata* Baker, *T. geniculata* Baker, and a few other related species, some of which are probably still undescribed. A few additional taxa, such as *T. flexuosa* Swartz, *T. karwinskyana* Schultes f., and *T. albida* Mez & Purpus have inflorescences and flowers that recall those of this complex, but the plants are strikingly different. Phylogenetic analyses are required to better ascertain the position of these taxa. *Tillandsia utriculata* is the type species of the genus.

As a result of extensive fieldwork in Mexico, as well as cultivation of plants of the group for several years, the delimitation of taxa in the *Tillandsia utriculata* complex in Mexican populations is now better understood. Species whose identities and circumscriptions have come into focus with the study of this complex include *T. dasyliriifolia* (Ramírez et al., 2004), *T. limbata* Schlechtendal (Espejo et al., 2005), and *T. makoyana*. The type of the latter species is a watercolor painting by Edouard Morren housed in the Kew library without collection data; the name has been applied in herbaria and in the literature (e.g., Smith & Downs, 1977) to several species of the *T. utriculata* complex that display purple corollas. Our interpretation of Morren's plate is that it is conspecific with a species that commonly features a rosette of straight, erect (not twisted nor spreading) gray leaves and purple or light purple corollas that are slightly zygomorphic. *Tillandsia makoyana* has been collected at varying elevations ranging from sea level to ca. 2000 m in central Mexico and is variable in plant size and inflorescence length. However, in most individuals of the species the peduncle of the inflorescence is about as long to slightly longer than the leaves.

As a result of this newly gained understanding of relevant species in the *Tillandsia utriculata* complex, particularly the identity of *T. makoyana*, during the course of this study two distinctive new entities became apparent. The new taxa herein described had been previously collected, but had until now remained misidentified in herbaria variously as *T. limbata*, *T. makoyana*, and/or *T. dasyliriifolia*.

Tillandsia aesii I. Ramírez & Carnevali, sp. nov. TYPE: Mexico. Jalisco: mpio. La Huerta, alrededores de la Est. Biol. Chamela, ca. 19°30′N, 105°03′W, 0–10 m, 12 Mar. 2002, *G. Carnevali & I. M. Ramírez 6973* (holotype, CICY [3]). Figure 1.

Haec species *Tillandsiae makoyanae* affinis est sed rosula aperta, superficie adaxiali foliorum viride non cinerea; inflorescentia breviore, spicis paucioribus ceraciter vestitis; floribus actinomorphis cylindricis cum sepalis petalisque et stigma viridibus differt.

Epiphytic *herb*, 62–100 cm high, with 1 to 4 basal rosettes on the flowering or fruiting plant, or the plants (more commonly) monocarpic; *rosette* with 12 to 18 leaves when flowering, with open aspect, slightly funnelform when young, foliar blades slightly to strongly twisted (curved outward and pointing forward), spreading to reflexed, foliar sheaths barely impounding. *Foliar sheaths* of external leaves almost flat, those of internal leaves forming a funnelform structure, straight and erect, white-lepidote externally, somewhat concave; *foliar blades* widely triangular at base, attenuate and acute, long-caudate, coriaceous, rather stiff, conspicuously nerved abaxially, 30–32 × 2.5–4 cm, light green adaxially, white-lepidote abaxially, margins slightly curving upward into a canaliculate structure. *Inflorescence* pyramidal, a panicle, 32–39 cm, with up to 11 spikes, the new inflorescence developing very slowly and taking up to 3 months before the first flowers open; successively flowering basipetally for several weeks; *peduncle* shorter or as long as the leaves, pink, glaucous, 21–40 cm, ca. 1 cm diam., covered by tubular, acute, imbricate bracts; *internodes* 2–4 cm long; *bracts* of the peduncle almost covering the internodes, green and glaucous, 3.5–4.5 × 2–2.6 cm (longer and wider toward the base), widely triangular, acute, margins hyaline, conspicuously nerved when dry, slightly surpassing the internodes; *inflorescence rachis* red or pinkish flesh-colored, 0.5 cm diam., naked, flexuous, erect; *spikes* 8 to 11, *rachis* green, almost obscured by floral bracts, dorsoventrally flattened with flowers in 2 rows; *bracts of the spikes* widely triangular, obtuse, 2.3 × 1.4 cm, entire, slightly pink, white-lepidote; *floral bracts* narrowly triangular, nerved, acute, margins hyaline, barely covering the rachis, 1.4 × 0.8–0.9 cm, green, shorter than the sepals, white lepidote adaxially. *Flowers* 5–6.5 cm, actinomorphic, erect, 1 to 4 open daily per inflorescence (1 at a time per spike), each flower lasting 1 day, protandrous, odorless, basally geniculate; *sepals* narrowly triangular to wide-elliptic,

Figure 1. *Tillandsia aesii* I. Ramírez & Carnevali. —A. Habit. Scale bar = 10 cm. —B. Upper row, from left to right: flower, flower with floral bract removed, flower without floral bract, sepals, and petals showing the ovary, style, stigma, filaments, and anthers. Bottom row from left to right: floral bract, three sepals, and three petals. Scale bar = 4 cm. Based on the holotype *G. Carnevali & I. M. Ramírez 6973* (CICY). Margins of sepals and floral bracts are somewhat revolute in the figures.

obtusely acute, 1.8–2.5 × 0.7–1.3 cm, 2 sepals basally connate by 6–15 mm, apple green, slightly darker and shinier than petals; *petals* narrowly oblong, apically rounded, 3.2–3.8 × 0.4–0.8 cm, slightly oblique, constricted ca. 1.5 cm distally from base, pale green to cream-green, basally white; *stamens* exserted, in 2 series, filaments concolorous with petals, plicate, lighter at the base, 5–5.5 cm; *anthers* brown, 8 mm, dorsifixed, pollen yellow; *ovary* 15 mm, pyramidal; nectar sweet, abundant, 31° Brix (total concentration of sugars); *stigma* exserted, slightly protruding above the anthers at anthesis, lobes conduplicate, somewhat spiraled, 4.7–4.9 cm, basally light green, apically apple green. *Fruits* and *seeds* not observed.

Habitat, distribution, and phenology. *Tillandsia aesii* is found in low, dry, caducifolious forests, associated with *Cnidoscolus* Pohl, *Plumeria* L., *Pseudosmodingium* Engler, *Agave* L., *Opuntia* (L.) Miller, *Pedilanthus* Necker ex Poiteau, *Cordia elaeagnoides* DC., *Bursera simaruba* Sargent, xeromorphic epiphytes such as *Tillandsia ionantha* Planchon, *T. intermedia* Mez, *T. caput-medusae* E. Morren, *T. concolor* L. B. Smith, *Encyclia adenocarpon* (La Llave & Lexarza) Schlechter, *Myrmecophila galeottiana* (Reichenbach f.) Rolfe, Cactaceae such as *Pachycereus* (A. Berger) Britton & Rose, and thorny leguminous trees and shrubs. It has been collected at 0–600 m of elevation, on the Pacific coast of Mexico. Flowering specimens were collected from March through July, and fruiting specimens were collected from May through September.

Eponymy. The name is based on an acronym of the initials of Dr. Adolfo Espejo Serna, a Mexican botanist associated with herbarium UAMIZ of the Universidad Autónoma Metropolitana in Mexico, D.F., whose work in Bromeliaceae and other monocots has contributed greatly to the knowledge of the Mexican flora.

Tillandsia aesii is phenetically similar and probably phylogenetically closest to *T. makoyana*, a species that commonly features a rosette of straight, erect (not twisted and spreading) leaves. *Tillandsia makoyana*, furthermore, displays purple or light purple flowers and a slightly zygomorphic corolla as opposed to the actinomorphic, green, tubular corolla of *T. aesii*. Both species have been collected at varying elevations ranging from sea level to ca. 2000 m, but *T. aesii* has only been collected at elevations from sea level to ca. 600 m and in dryer environments.

At least three other vegetatively similar taxa in the *Tillandsia utriculata* complex display pale flowers. The widespread *T. utriculata* features longer, thinner (easy to bend) peduncles and branches and the smaller, white corollas are gibbous or somewhat inflated with the petals convergent at apex. *Tillandsia dasyliriifolia* and *T. limbata* are easily distinguished from *T. aesii* by their inflorescences with much longer peduncles bearing flowers with white, slightly zygomorphic corollas. *Tillandsia aesii* is further distinguished from these two taxa by the proportionally smaller rosette of stiff leaves that are slightly twisted. In addition, *T. dasyliriifolia* and *T. limbata* are restricted to the humid lowlands of the Gulf Coast of Mexico (*T. limbata*) or to the Yucatan Peninsula (*T. dasyliriifolia*).

Paratypes. MEXICO. **Guerrero:** mpio. Huitzuco, Amatitlán, 12 km SE del Huitzuco, 4 June 1985, *J. C. Soto Núñez & Aureoles C. 8786* (MEXU). **Jalisco:** mpio. La Huerta, alred. Est. Biol. Chamela, 3 Nov. 1997, *G. Carnevali & G. Salazar 4767* (CICY); camino por la base SE del Cerro de la Tambora, 16 Jan. 1985, *P. Magaña Rueda & E. Lott 10* (MEXU); Chamela Field Stat., 100 km S of Puerto Vallarta, 26 Sep. 1988, *A. Gentry 63981* (MO). **Oaxaca:** mpio. Matías Romero, carr. entre La Ventosa y el entronque a Juchitán, 10 km N de La Ventosa, 4 May 1997, *G. Carnevali, G. Campos, M. Gómez & F. May 4438* (CICY); mpio. Asunción Tlacolulita, dist. Yautepec, ca. 9 km después de Reforma sobre camino a Tehuantepec–Oaxaca, 2 Sep. 2002, *I. Ramírez, A. Espejo, A López, J. Ceja y A. Mendoza 998* (CICY); mpio. Asunción-Ixtaltepec, distrito Juchitán, 1 km después de Santiago de Ixtaltepec, 2 Sep. 2002, *I. Ramírez, A. Espejo, A López, J. Ceja y A. Mendoza 979* (CICY); 28 km NW of La Ventosa, along Trans-Isthmian hwy. (rte. 185), 17 July 1958, *R. M. King 630* (MICH, TEX, US); flat grazed area 5.5 km NE of Juchitán, along Pan-Amer. hwy. (rte. 190), 2 July 1958, *R. M. King 360* (MEXU, MICH, TEX, US); flat grazed area 4 km N-NE of Tehuantepec along the Trans-Isthmian hwy. (rte. 185 & 190), 5 July 1959, *R. M. King 1352* (LL); flat grazed area 16 km N-NE of Tehuantepec, 7 July 1959, *R. M. King 1389* (TEX); mtns. along rte. 190, ca. 74 miles SE of Oaxaca, 22 June 1960, *R. M. King 2975* (TEX, US); Tehuantepec, dry open savannah, 2 Apr. 1957, *M. B. Foster & O. C. Van Hyning 2939* (US [2]); on rte. 185, 6 km N of Union Hidalgo, 10 July 1958, *W. G. Williams Jr. & D. Francoeur 21* (MICH); on rte. 185, 15 km N of Union Hidalgo, at edge of steep drop into a small valley, 11 July 1958, *Walter G. Williams Jr. & Don Francoeur 24* (MICH); mpio. Nejapa de Madero, distrito Yautepec, 2.4 km al N-NE de Río Hondo, brecha a Asunción Lachixonase, 16 May 1995, *A. Salinas T. & E. Martínez-Correa 8155* (MEXU).

Tillandsia pinicola I. Ramírez & Carnevali, sp. nov. TYPE: Mexico. Yucatán: Mérida, floreciendo en cultivo, 13 Jan. 2005, *I. Ramírez & G. Carnevali 1274* (holotype, CICY [2]; isotype, MO) [Oaxaca: mpio. Santa María Chimalapa, Dist. Juchitán, ca. 20 km después de el Mezquite, 7 km después de Lázaro Cárdenas rumbo a Santa María Chimalapa, 16°46′10″N, 94°50′38″W, ca. 385 m, colectada originalmente por I. Ramírez, A. Espejo, A. López-Ferrari, A. Mendoza & J. Ceja el 2 Sep. 2002]. Figure 2.

Haec species *Tillandsiae makoyanae* affinis est sed planta ambito parviore, foliorum vaginis latissimis, foliorum laminis proportione brevioribus, apice acicularibus abrupte attenuatis (vs. paulo apicaliter attenuatis), et habitatio pinicola abhorret.

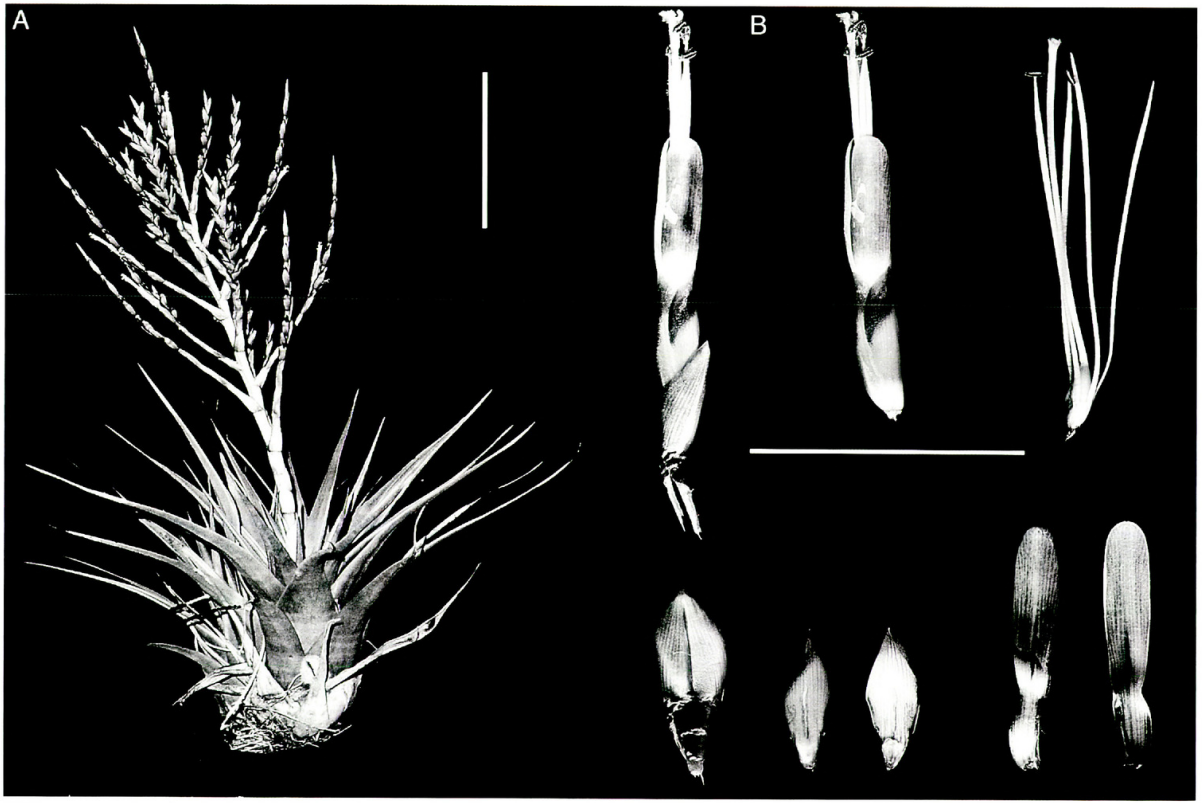

Figure 2. *Tillandsia pinicola* I. Ramírez & Carnevali. —A. Habit. Scale bar = 10 cm —B. Upper row, from left to right: flower, flower with floral bract removed, flower without floral bract, sepals, and petals showing the ovary, style, stigma, filaments, and anthers. Bottom row from left to right: floral bract, two sepals, and two petals. Scale bar = 3 cm. Based on the holotype *I. Ramírez & G. Carnevali 1274* (CICY). Margins of sepals and floral bracts are somewhat revolute in the figures.

Epiphytic *herb*, 50–60 cm high, the rosettes apparently monocarpic; *rosette* with 20 to 30 leaves when flowering, leaves erect with divergent apices, with funnelform rosette, apices erect when young or fruiting and then the rosette shape subcylindrical, foliar sheaths barely impounding. *Foliar sheaths* with incurved margins, 6–10 × 6–8 cm, elliptical, green, adaxially dark castaneous upon drying; *foliar blades* narrowly triangular abruptly attenuating into an acicular apex, margins incurved, coriaceous, rather stiff, conspicuously nerved abaxially, 15–18 cm long, 3.8–4.5 cm wide at the base, concolorous dull green, slightly white-lepidote abaxially. *Inflorescence* an erect panicle, 40–60 cm, ovoid-ellipsoid, some of the lowermost branches 2-pinnate, 50–60 cm long from the base of the rosette, with 11 to 16 spikes, the new inflorescence developing slowly and taking up to 2 months before the first flowers open; successively flowering basipetally and producing new flowers for 2 to 3 weeks; *peduncle* 10–15 cm, shorter or as long as the leaves, bright crimson red, glabrous, ca. 1 cm diam., covered by tubular, acute, imbricating bracts; *internodes* 2–3 cm long; *bracts* of the peduncle slightly shorter than the internodes and not totally enveloping them, crimson with green tinges, glabrous, 3.5–4.5 × 2–2.6 cm (longer and wider toward the base), widely triangular, acute, margins hyaline, conspicuously nerved when dry, slightly surpassing the internodes; *inflorescence rachis* crimson red, of smaller diameter than the peduncle, naked, flexuous, the branches diverging at angles of 45°–60° to the inflorescence rachis; *basal spikes* 15–17 cm, apical ones 9–12 cm, sterile portion of basal ones 6.5–7.5 cm, of the apical ones 1.8–2.5 cm, rachis green with dark red tinges, almost entirely covered by floral bracts, dorsoventrally flat with flowers in 2 rows; (5 to)10 flowers per branch; *bracts of the spikes* 1–1.8 cm (longer ones at base), widely triangular, obtuse, pale crimson with slight greenish tinges, glabrous, similar in shape to the floral bracts; *floral bracts* 1.6–1.8 × 9–10 mm, ovate-elliptic, acute, conspicuously nerved, margin hyaline, shorter than sepals, barely covering the rachis, those subtending mature flowers dull crimson, apple green toward dorsal portion, more immature flowers apple green with crimson confined to the margins and apex, glabrous, shiny. *Flowers* 3.3–3.5 cm, actinomorphic, forming an acute angle with the rachis, up to 7 flowers open daily per inflorescence (1 at a time per spike), each flower lasting 1 day, protandrous, odorless, basally very slightly geniculate; *sepals* spathulate-elliptic, broadly acute, 1.5 cm × 6 mm, the 2 adaxial ones basally connate for 4–6 mm, apple green, apically and marginally dull red-maroon, adaxially sparsely lepidote, more so toward apex; *petals* narrowly oblong, apically rounded, 2.8–3 × 0.5 cm, slightly oblique, constricted about 1.5 cm distally from base, dull purple, paler toward the base, the portion hidden by the sepals hyaline, exserted portion 1.8–2 cm long; *stamens* exserted, in 2 series of unequal length, filaments pale cream-green, plicate upon drying, lighter at the base, 3.7–3.8 cm, flatter toward the base; *anthers* brown or black-brown, 4.5 mm, 8–14 mm thick, dorsifixed, pollen yellow; *ovary* 8 × ca. 3 mm, ellipsoid-pyramidal; nectar sweet, abundant; *stigma* exserted, slightly protruding above the anthers at anthesis, lobes conduplicate, not spiraled; *style* 4.4 cm, basally light green, apically apple green. *Fruits* and *seeds* not observed.

Habitat, distribution, and phenology. *Tillandsia pinicola* grows on pine trees, mostly *Pinus oocarpa* Schiede ex Schlechtendal, and is associated with *Catopsis berteroniana* (Schultes & Schultes f.) Mez, *T. streptophylla* Scheidweiler ex E. Morren, and *T.* aff. *fasciculata* Swartz. It occurs at 300–400 m in elevation and is known only from Mexico (Oaxaca). It has been collected in flower during January and in fruit in September.

Tillandsia pinicola is one of the most distinctive members of the *T. utriculata* complex by its small size, erect, green leaves that are relatively short and with wide sheaths, and its inflorescence with short peduncles and purple flowers. It is very similar to *T. makoyana* and the new species herein described as *T. aesii*, but it differs from them by the overall smaller size, the foliar sheaths wide and abruptly attenuating into a narrow foliar blade that ends in an acicular apex, leaves strongly nerved when alive or dry, leaves dark green on both sides but lightly white-lepidote on the abaxial surface, the inflorescence with a short peduncle that is usually shorter than the leaves, much shorter flowers and floral bracts, and branches that are both fewer in number and shorter.

Paratypes. MEXICO. **Oaxaca:** mpio. Santa María Chimalapa, distrito Juchitán, ca. 20 km después de El Mezquite, 7 km después de Lázaro Cárdenas rumbo a Santa María Chimalapa, 2 Sep. 2002, *I. Ramírez, A. Espejo, A. López-Ferrari, A. Mendoza & J. Ceja 987* (CICY, UAMIZ); mpio. Lázaro Cárdenas, dist. Juchitán, 3.6 km al E de Lázaro Cárdenas, hacia Santa María Chimalapa, entrando por el Mezquite, 22 Jan. 1988, *R. Torres C. & E. Martínez 11225* (IEB, MEXU).

Acknowledgments. To the Elizabeth Bascom Fellowship for Latinoamerican Women and the Missouri Botanical Garden for a scholarship granted to the first author; to the Bromeliad Society for financial support to the first author for field equipment; to the Marie Selby Botanical Gardens for financial support to the first author while working on the Bromeliaceae of Mexico project; to Adolfo Espejo, Ana Rosa López-Ferrari, Aniceto Mendoza, and Jacqueline Ceja for field support in Chiapas, Guerrero, Jalisco, Michoacan, Morelos, and

Oaxaca; to Francisco Chi May, Filogonio May, Silvia Hernández-Aguilar, Lorena Can-Itzá, and José Luis Tapia for herbarium and field assistance in the Yucatan Peninsula when collecting, preparing herbarium specimens, and searching for bibliographical material. To Francisco Lorea-Hernández, Curator of Herbarium XAL and Carlos Durán, for field assistance in Veracruz and Puebla. Our gratitude to Demetria Mondragón for material collected in Chiapas and Oaxaca that allows a better understanding of the species in this complex. To Derek Butcher and Walter Till for useful commentaries and iconographic material of species in this complex. To William Cetzal Ix for his help in elaborating the plates of the two new species. We are grateful to the following herbaria for loans: CIQR, F, GH, LL, MEXU, MICH, MO, TEX, UAMIZ, UCAM, US, and XAL.

Literature Cited

Barfuss, M. H. J., R. Samuel, W. Till & T. F. Stuessy. 2005. Phylogenetic relationships in subfamily Tillandsioideae (Bromeliaceae) based on DNA sequence data from seven plastid regions. Amer. J. Bot. 92: 337–351.

Espejo, S., A., A. R. López-Ferrari & I. Ramírez M. 2005. Bromeliaceae. Pp. 1–305 *in* Flora de Veracruz, Fasc. 136. Instituto de Ecología A. C., Xalapa, Veracruz, México.

Gardner, S. 1984. Natural hybridization in *Tillandsia* subgenus *Tillandsia*. Selbyana 7: 380–393.

———. 1986. Preliminary classification of *Tillandsia* based on floral characters. Selbyana 9: 130–146.

Luther, H. 1995. An annotated checklist of the Bromeliaceae of Costa Rica. Selbyana 16: 230–234.

Mez, C. 1896. Bromeliaceae. *In* C. de Candolle, Mongraphiae Phanerogamarum, Vol. 9. Sumptibus Masson, Paris.

Morales, J. F. 2003. Bromeliaceae. Pp. 297–375 *in* B. E. Hammel, M. H. Grayum, C. Herrera & N. Zamora (editors), Manual de Plantas de Costa Rica. Volumen II. Monogr. Syst. Bot. Missouri Bot. Gard. 92.

Ramírez, I., G. Carnevali & F. Chi. 2004. Portraits of Bromeliaceae from the Mexican Yucatan Peninsula—IV: *Tillandsia dasyliriifolia* Baker: Taxonomy and reproductive biology. J. Bromeliad Soc. 54: 112–121.

Spencer, M. A. & L. B. Smith. 1993. *Racinaea*, a new genus of Bromeliaceae (Tillandsioideae). Phytologia 74: 151–160.

Smith, L. B. & R. J. Downs. 1977. Tillandsioideae (Bromeliaceae). Pp. 663–1492 *in* Flora Neotropica Monograph 14, Part 2. Hafner Press, New York.

Terry, R. G., G. K. Brow & R. G. Olmstead. 1997. Phylogenetic relationships in subfamily Tillandsioideae (Bromeliaceae) using *ndh*F sequences. Syst. Bot. 22: 333–345.