

TAXONOMIC AND NOMENCLATURAL STATUS OF THE
MEXICAN SPECIES IN THE *TILLANDSIA VIRIDIFLORA* COMPLEX
(BROMELIACEAE)

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ABSTRACT

Based on a systematic study of the Mexican species in the *Tillandsia viridiflora* complex, the taxonomic and nomenclatural status of these species is clarified. The former synonym *T. macropetala* is reestablished as a species. An identification key for the complex species (*T. grandis*, *T. macropetala* and *T. viridiflora*), as well as a complete synonymy and detailed descriptions of the taxa are included.

Key words: Bromeliaceae, Mexico, taxonomy, *Tillandsia grandis*, *T. heterophylla*, *T. macropetala*, *T. viridiflora*.

RESUMEN

Con base en un estudio sistemático de las especies mexicanas del complejo *Tillandsia viridiflora*, se clarifica su situación taxonómica y nomenclatural. Se reestablece como especie a *T. macropetala*, antes considerada como sinónimo. Se incluye una clave de identificación

para los componentes del complejo (*T. viridiflora*, *T. grandis* y *T. macropetala*), así como la sinonimia completa y las descripciones detalladas de cada uno de los taxa.

Palabras clave: Bromeliaceae, México, taxonomía, *Tillandsia grandis*, *T. heterophylla*, *T. macropetala*, *T. viridiflora*.

During the course of two botanical field trips through the state of Oaxaca in the years 2005 and 2006, the late Jürgen Lautner, Renate Ehlers and collaborators collected several plants of a species of *Tillandsia* L. in the Sierra Mixe, which were provisionally identified as *T. viridiflora* (Beer) Baker. Additionally in 2006, Thorsten Krömer and Elisabeth Otto collected one specimen of the same *Tillandsia* species on the slopes of the Santa Marta volcano, located in the southeastern region of Los Tuxtlas, in the state of Veracruz. In order to confirm the identity of these plants, we studied cultivated and herbarium material, and also the related taxonomic literature. After a careful study of literature relating to these plants (Baker, 1889; Smith & Downs, 1977; Weber, 1984; Utley & Burt-Utley, 1994; Beaman & Judd, 1996), an analysis of the original descriptions and plates of the names related to *Tillandsia viridiflora* and its putative synonyms *T. macropetala* Wawra, *T. orizabensis* Baker, *T. longiflora* Sessé & Moç. and *T. billbergiae* (Lem.) Baker (Schlechtendal, 1845; Beer, 1856; Lemaire, 1869; Morren, 1873, 1880; Wawra, 1887; Baker, 1888; Sessé & Moçifio, 1887, 1894; Mez, 1935), and study of all relevant specimens and types deposited in the main Mexican (CHAP, ENCB, FCME, IBUG, IEB, MEXU, OAX, UAMIZ, XAL) and foreign (GH, K, LL, MA, MICH, MO, OXF, P, SEL, TEX, UC, US, WU) herbaria, we come to the conclusion that the plants collected at both localities mentioned above, and also some herbarium material formerly identified as *T. viridiflora*, *T. grandis* and/or *T. heterophylla* E. Morren must be assigned to *T. macropetala*, a name previously considered by some authors as a taxonomic synonym of *T. grandis* (Mez, 1935) or *T. viridiflora* (Smith & Downs, 1977; Espejo & López-Ferrari, 1994; Espejo et al., 2004). We believe that each of these three species constitutes a phenetically distinctive entity, following a morphological-taxonomic species concept. However, besides their differences in habit and the appearance of leaves and peduncle bracts, especially obvious in living plants (Fig. 1, 2 C-D), *T. macropetala* seems most closely related to *T. viridiflora*, as both species are more similar in size and epiphytic, whereas *T. grandis* is much bigger and lithophytic (Fig. 2A; Table 1).

With the reestablishment of *Tillandsia macropetala* as a valid species, the number of taxa of the *T. viridiflora* complex present in Mexico reaches three. Addi-

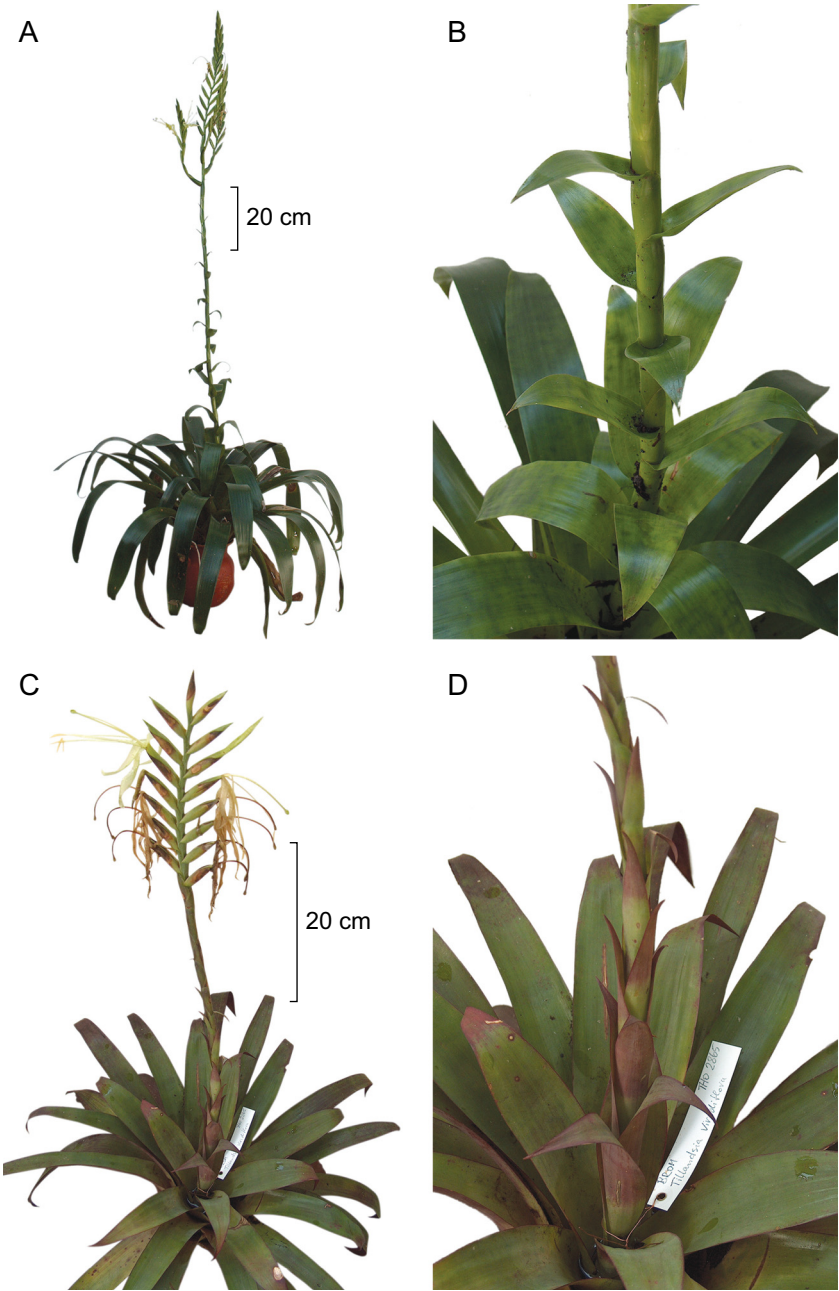


Fig. 1. A, B. *Tillandsia macropetala* (voucher T. Krömer & E. Otto 2866); C, D. *Tillandsia viridiflora* (voucher T. Krömer & E. Otto 2865) (photos by T. Krömer).



Fig. 2. A. *Tillandsia grandis*; B. *Tillandsia heterophylla*; C. *Tillandsia macropetala*; D. *Tillandsia viridiflora* (photos A, B by A. Espejo and C, D by T. Krömer).

Table 1. Comparison of selected morphological characters to distinguish the Mexican species of the *Tillandsia viridiflora* complex.

	<i>Tillandsia grandis</i>	<i>Tillandsia macropetala</i>	<i>Tillandsia viridiflora</i>
Plants	2-4 m high	1.3-1.75 m high	0.65-1 m high
Leaf blades	strap shaped, 60-120 cm x 8-15 cm	strap shaped, 17-45 cm x 3.5-7 cm	narrowly triangular, 25-50 cm x 3-4 cm
Inflorescence	once branched, 15-30 spikes	once branched, 3-7 spikes, rarely simple	simple
Peduncle	to 1 m long	55-83 cm long	45-50 cm long
Peduncle bracts	not imbricate, foliaceous	imbricate, foliaceous, only the distal ones vaginiform	imbricate, vaginiform, only the basal ones foliaceous
Petals	10.3-10.5 cm x 9-10 mm	10.7-12.3 cm x 14-17 mm	9 cm x 10 mm

tionally, because of its close morphological similarity, this species complex probably includes the Caribbean *T. paniculata* (L.) L. and *T. baliophylla* Harms. Following the classification of Smith & Downs (1977), all these belong to *Tillandsia* subgenus *Pseudalcantarea* Mez. However, Beaman & Judd (1996) suggested that this subgenus is paraphyletic, and transferred *T. grandis* and *T. paniculata* to subgenus *Tillandsia*. Furthermore, Barfuss et al. (2005) in a phylogenetic analysis of subfamily Tillandsioideae suggested that *T. baliophylla* and *T. viridiflora* also do not form a clade. Therefore, although we have clarified species limits in this complex, it is clear that much more phylogenetic work is necessary before we can be confident as to their phylogenetic relationships. Below we include an identification key for the three Mexican taxa, their correct names, complete synonymy, descriptions, and a distribution map.

Key to the Mexican species of the *Tillandsia viridiflora* complex

- 1 Inflorescence simple; leaves narrowly triangular, 25-50 cm long; petals ca. 9 cm long; plants 0.65-1 m high *T. viridiflora*
- 1 Inflorescence once branched, very rarely simple in *T. macropetala* but then the leaves strap-shaped; plants 1.3-4 m high.

- 2 Plants 2-4 m high, usually lithophytic; inflorescence branches (7)15-30, with a stipe 15-36 cm long, strongly curved; leaves 60-120 cm long; peduncle bracts not imbricate; petals 10.3-10.5 cm long *T. grandis*
- 2 Plants 1.3-1.75 m high, usually epiphytic; inflorescence branches 3-7, with a stipe 5-11 cm long, straight to slightly curved; leaves 17-45 cm long; peduncle bracts imbricate; petals 10.7-12.3 cm long *T. macropetala*

Tillandsia grandis Schldl., *Linnaea* 18: 424-426. 1845 "1844". TYPE: Veracruz, in praeruptis, hacienda de la Laguna, Aug. fruct., VIII.1829, *C. Schiede s.n.* (Lectotype [W. Weber, 1984] B photo!; Isolectotypes: B photo!, BM, HAL 45629 photo!, LE, OXF). Fig. 2 A.

Rosulate stemless lithophytic or very rarely epiphytic herbs, flowering 2-4 m tall, with solitary tank rosettes to 1.7 m in diameter. Leaves numerous; sheaths brown to light brown on the adaxial surface, dark brown on the abaxial surface, widely elliptic to widely ovate, 10-25 cm long, 10-16 cm wide, densely brown punctulate-lepidote on both surfaces; blades green, paler beneath, strap-shaped, 60-120 cm long, 8-15 cm wide at the base, punctulate-lepidote on both surfaces, acuminate, erect to ascending. Inflorescence terminal, erect, compound, once branched, with 15 to 30 spikes, peduncle terete, to 1 m long, 2.5-3 cm in diameter, partially covered by the bract sheaths; peduncle bracts not imbricate, green, foliaceous, similar to the basal leaves; sheaths 5-6 cm long, blades 5-7 cm long; spikes compressed, oblong, 14-25 cm long, 5-7 cm wide, long stipitate, stipes strongly curved, 15-36 cm long, 8-10 mm in diameter, bracteate, slightly compressed; primary bracts vaginiform, ovate-triangular, 5.5-7 cm long, 4.5-5 cm wide, acuminate; floral bracts dark green, widely elliptic, 3.5-4 cm long, 1.6-2 cm wide, imbricate but the rachis visible after anthesis, nervate, ecarinate, glabrous outside, brown punctulate-lepidote inside, margin erose, apex obtuse to rounded; flowers distichous, erect, 15-20 per spike, actinomorphic, corolla helicoiform, subsessile, pedicels strong, to 1 mm long; sepals free, green, ovate to triangular, 3.4-4 cm long, 1.4-1.6 cm wide, ecarinate, glabrous outside, brown-punctulate lepidote inside, margin erose, apex rounded to acute; petals light green with brown-purple dots, oblong, strap shaped, twisted, 10.3-10.5 cm long, 9-10 mm wide, rounded at the apex; stamens subequal, filaments free, light green to white, filiform, 10-11 cm long, anthers green to green-whithish, linear, curved, 9-12 mm long; ovary green, ovoid, 9-11 mm long, ca. 6 mm in diameter, style green, filiform, 10-11 cm long, stigma green. Capsule green, fusiform, rostrate, 4-6.5 cm long, 6-7 mm in diameter; seeds dark brown, fusiform, ca. 5 mm long, with a white coma ca. 4 cm long.

Specimens examined: Mexico, **Guanajuato**, municipio de Atarjea, arroyo del río Blanco, 1300 m, 7.III.1991, *E. Ventura & E. López 9153* (IEB, MEXU, XAL). **Hidalgo**, municipio de Zimapán, 10 km al NW de Zimapán, 1000 m, 30.IV.1965, *L. González Q. 2376* (ENCB, MICH); municipio de Zimapán, aproximadamente 800 m al sur de las Adjuntas, 16.I.1991, *V. M. Huerta 1176* (IEB); municipio de Zimapán, barranca de Tolimán, 1520 m, 4.V.1954, *E. Matuda 32204* (MEXU, US); municipio de Zimapán, between Zimapán and barranca de Tolimán, on road to mine Loma del Toro, 1200 m, 25.IV.1947, *H. E. Moore jr. 2602* (GH, UC, US). **Oaxaca**, municipio de Huautla de Jiménez, cerca de cascada de Chochotla, Huautla, 1700 m, 7.IV.1974, *E. Matuda 38623* (LL, MEXU); municipio de Huautla de Jiménez, aproximadamente 1.5 km de Aguacatitla, por la terracería a Santa Cruz de Juárez, 1589 m, 12.V.2001, *X. Munn & T. Kasey 1182* (MEXU); municipio de San Juan Bautista Cuicatlán, a 33 km al SE de Cuicatlán, camino a Oaxaca, 1524 m, 8.I.2001, *E. Martínez & V. Torres 33479* (MEXU); municipio de San Juan Bautista Cuicatlán, Santa María Almoloyas - Santa Catarina Tlaxila, 1600 m, 10.XII.1991, *A. Salinas et al. 6671* (MEXU); municipio de Santiago Nacaltepec, a 49 km al NE de San Francisco Telixtlahuaca, camino a Santiago Dominguillo, 6.II.1966, *C. Delgadillo 217* (MEXU, MO, XAL); municipio de Santiago Nacaltepec, El Mirador, headwaters of río Quiotepec, between Santiago Nacaltepec and Santiago Dominguillo, 6.II.1966, *W. R. Ernst 2487* (MEXU, US); municipio de Tepelmeme Villa de Morelos, cerro paraje Ladrón (subiendo por Pasto Chino y barranca Copalillo), 1750 m, 14.IX.1994, *A. Salinas & E. L. Cruz 7836* (MEXU). **Puebla**, municipio de Caltepec, mogote León, lado NE del cerro Grande, 2000 m, 10.II.1984, *P. Tenorio 5434* (MEXU, OAX, TEX); municipio de San José Miahuatlán, Agua los Granados, ca. 20 km al W de San José Axusco, 1100 m, 24.IX.1990, *A. Salinas et al. 5793* (MEXU); municipio de Tehuacán, near Tehuacán, 840 m, 30.VIII.1905, *J. N. Rose et al. 10124* (US). **Querétaro**, municipio de Landa de Matamoros, Tangojón, a la orilla del río Moctezuma, 400 m, 15.IV.1988, *S. Zamudio 6318* (IEB, MEXU, MICH, MO, UAMIZ); municipio de San Joaquín, cañada La Culebra, 1 km al NE de la Tinaja, 1600 m, 27.VIII.1978, *S. Zamudio 3234* (IEB). **Veracruz**, municipio de Coatepec, cerro de Achichuca, entre Tuzamapan y Jalcomulco, 900 m, 21.III.1979, *G. Castillo & R. Ortega 489* (ENCB, XAL); municipio de Fortín, Fortín de las Flores (cultivated at posada Loma), 850 m, 20.VII.1967, *L. I. Nevling & A. Gómez-Pompa 197* (MEXU); municipio de Fortín, between Fortín de las Flores and Orizaba, above the Moctezuma brewery hydroelectric plant, 11.VII.1982, *J. Uitley & K. Burt-Utley 7052* (MEXU); municipio de Nogales, cerros calizos al sur y suroeste de Orizaba, 1200 m, *R. Hernández & R. Dirzo 2087* (ENCB, MEXU); municipio de Nogales, 1-2 km después de Nogales, sobre la carretera de

cuota Orizaba - Puebla, 1350 m, 23.III.1997, *A. R. López-Ferrari et al.* 2446 (IEB, MEXU, UAMIZ, XAL); municipio de Nogales, a 2 km al E de Nogales, autopista a Córdoba, 900 m, 28.IV.1988, *E. Martínez & C. Ramos* 22647 (CHAP, IEB, MEXU, MO); municipio de Orizaba, near Orizaba, 1938, *M. B. Foster VI* (GH); municipio de Orizaba, cerro de San Miguel, Orizaba, 1200 m, 9.III.1971, *R. Hernández & R. Cedillo* 1136 (GH, MEXU); municipio de Orizaba, límite N de la ciudad de Orizaba, cerro de calizas junto a Tugrablok S. A., 1300-1500 m, 25.III.1986, *D. Lorence* 5000 (MEXU); municipio de Puente Nacional, barranca de Panoaya, 790 m, 25.IV.2004, *A. R. López-Ferrari et al.* 3118 (IEB, UAMIZ); municipio de Puente Nacional, barranca situada 2 km al SE de Palmillas, 550 m, 22.V.1985, *M. E. Medina & S. A. Contreras* 104 (ENCB, MEXU, XAL); municipio de Totutla, barranca de Tlalpalan, 1100 m, I.1982, *M. Cházaro & T. Mejía* 2067 (MEXU, XAL).

Tillandsia macropetala Wawra, Wiener III. Gart.-Zeitung 12: 241-244, Fig. 50. 1887. TYPE: *E. Morren in Liège hortus s.n.* (not located). Lectotype, here designated: Figure 50 in Wiener Illustrierte Garten-Zeitung 12. 1887 (Fig. 3). Epitype, here designated: municipio de Soteapan, faldas del volcán Santa Marta, 18°19' N, 94°50' W, 1300 m, 19.VIII.2006, *T. Krömer & E. Otto* 2866 (MEXU, SEL, UAMIZ, XAL). Figs. 1A-B, 2 C.

Rosulate stemless epiphytic or very rarely lithophytic herbs, flowering 1.3-1.75 m tall, with solitary tank rosettes to 1.2 m in diameter. Leaves numerous; sheaths brown to light brown on both surfaces, widely elliptic, 13-15 cm long, 8-8.5 cm wide, densely brown punctulate-lepidote on both surfaces; blades green, paler beneath, strap shaped, 17-45 cm long, 3.5-7 cm wide at the base, punctulate-lepidote on both surfaces, acuminate, erect to ascending. Inflorescence terminal, erect, compound, once branched, with 3 to 7 spikes, very rarely simple, peduncle terete, 55-83 cm long, 5-8 mm in diameter; peduncle bracts imbricate, green, foliaceous only the distal vaginiform ones; sheaths 3.5-4.2 cm long, blades 7-14 cm long; spikes compressed, oblong, 9-23.5 cm long, 3-6 cm wide, stipitate, stipes straight to slightly curved, 5-11 cm long, 3.5-5 cm in diameter; primary bracts vaginiform, ovate-triangular, 5.5-7 cm long, 4.5-5.3 cm wide, acuminate; floral bracts green, glaucous, widely elliptic, 3.3-4.3 cm long, 1.4-2.4 cm wide, imbricate but the rachis visible after anthesis, nervate, ecarinate, glabrous outside, brown punctulate-lepidote inside, margin erose, apex rounded to acute; flowers distichous, erect, (5)15-20 per spike, actinomorphic, corolla helicoiform, subsessile; sepals free, green, oblong, 3-3.4 cm long, 1.3-1.5 cm wide, nervate, ecarinate, glabrous outside, brown-punctulate lepidote inside, margin



Fig. 3. Lectotype of *Tillandsia macropetala*. Figure 50 in Wiener Illustrierte Garten-Zeitung 12. 1887.

erose, apex rounded to acute; petals light green, strap shaped, twisted, 10.7-12.3 cm long, 14-17 mm wide, rounded at the apex; stamens subequal, filaments free, light green to white, filiform, 10.4-11.7 cm long, anthers green to green-whitish, linear, curved, 7.5-8 mm long; ovary green, ovoid, 9-12 mm long, ca. 6 mm in diameter, style green, filiform, 10.7-11.4 cm long, stigma green. Capsule green, fusiform, rostrate, 5.3-6 cm long, ca. 1 cm in diameter; seeds dark brown, fusiform, ca. 4.5 mm long, with a white coma ca. 3 cm long.

Specimens examined: Mexico, **Chiapas**, municipio de Cintalapa, southeast of Cerro Baúl on the border with state of Oaxaca, 16 km northwest of Rizo de Oro, along a logging road to colonia Figueroa, 1600 m, 21.IV.1972, *D. E. Breedlove* 24770 (ENCB, MEXU); municipio de Cintalapa, cerro Baúl, 1600 m, 2.V.1999, *M. A. Pérez Farrera* 1954 (UAMIZ); municipio de Tenejapa, near paraje Yashanal, 2460 m, 28.I.1981, *D. E. Breedlove* 49664 (MEXU); municipio de Villaflores, on the southeast side of cerro Tres Picos and the ridges near summit, 2100-2500 m, 28.III.1973, *D. E. Breedlove* 34445 (ENCB, MEXU, MICH, MO, TEX); municipio de Villaflores, zona núcleo Tres Picos, 1350 m, 21.III.2004, *A. Reyes et al.* 6495 (UAMIZ). **Oaxaca**, municipio de Guevea de Humboldt, recorrido hacia el cerro de la Peña Blanca, al SW de la Cumbre, la cual está a 13.5 km al N de Guevea de Humboldt, 1300 m, 30.III.1991, *A. Campos & R. Torres* 3614 (CHAP, IEB, MEXU); municipio de Guevea de Humboldt, sierra Mixe, between Santa María Guienagati and Santiago Lachiguirí, 1500-1550 m, 20.II.2005, *J. Lautner et al.* EM051104 (MEXU, SEL, WU); *ibíd.*, 1500-1550 m, 9.II.2006, *J. Lautner et al.* EM060602 (UAMIZ); municipio de Guevea de Humboldt, camino a Peña Blanca, entrando por la Cumbre, la cual está a 11 km al N de Guevea de Humboldt, 1230 m, 30.III.1994, *R. Torres & L. Cortés* 14360 (GH, IEB, MEXU); municipio de Ixtlán de Juárez, 39 km al S de Valle Nacional, sobre la carretera a Oaxaca, 1800 m, 26.VI.1975, *J. Rzedowski* 33348 (ENCB); municipio de Ixtlán de Juárez, 39 km al S de Valle Nacional, sobre la carretera a Oaxaca, 1800 m, 27.XII.1975, *J. Rzedowski* 33826 (ENCB); municipio de Ixtlán de Juárez, 10 km al S de Esperanza, carretera Valle Nacional - Oaxaca, 2260 m, 7.VIII.2002, *J. Santana & L. Pacheco* 907A (UAMIZ); municipio de San Andrés Yaá, a 7 km de la desviación a San Andrés Yaá, al S de Villa Alta, camino a Oaxaca, 2030 m, 16.III.1982, *R. Cedillo & R. Torres* 1201 (ENCB, MEXU, MO); municipio de San Felipe Usila, 5.6 km en línea recta al S (172°) de Santa Cruz Tepetotula, 1970 m, 25.II.1994, *C. Gallardo et al.* 919 (MEXU); municipio de San Felipe Usila, vereda Monte Pan hacia el campamento del tramo de la carretera, 1650 m, 12.XI.2007, *G. Ibarra et al.* 3965 (MEXU); municipio de San Felipe Usila, 5.6 km

en línea recta al S (172°) de Santa Cruz Tepetotutla, 2000 m, 22.XII.1993, *A. Rincón et al.* 242 (MEXU); municipio de San Juan Juquila Vijanos, 700 m del entronque Talea - Juquila, sobre la terracería Maravillas - Talea, 1930-1975 m, 7.III.1977, *X. Munn et al.* 275 (MEXU); municipio de San Miguel Chimalapa, arroyo Rana, Cerro Azul, 16.III.1948, *T. MacDougall s.n.* (GH, US); municipio de San Pedro Yólox, 11.5 km después de la Esperanza, rumbo a Ixtlán, carretera Oaxaca - Tuxtepec, 2068 m, 20.XI.2003, *A. Espejo et al.* 6700 (UAMIZ); municipio de Santiago Comaltepec, 5 km al W de la Esperanza, carretera Tuxtepec - Oaxaca, 2000 m, 22.XII.1993, *R. Torres & E. Martínez* 11331 (MEXU); municipio de Santiago Comaltepec, 5 km al W de la Esperanza, carretera Tuxtepec - Oaxaca, 1760 m, 26.I.1988, *R. Torres & E. Martínez* 11344 (MEXU); municipio de Santiago Comaltepec, 5.7 miles S of Vista Hermosa or 24 miles S of Valle Nacional along hwy 175, 6.VIII.1981, *J. Utley & K. Burt-Utley* 6728 (MEXU); municipio de Santiago Comaltepec, Vista Hermosa, 20 miles SW of Valle Nacional, NE Oaxaca (Chinantecas Mountains), 1220 m, *O. C. van Hynning* 5959 (US); municipio de Totontepec Villa de Morelos, rumbo Villa Alta, 16 km al W de Totontepec, 1860 m, 14.IX.1986, *E. Ramírez & P. Ramírez* 552 (IBUG, IEB, MEXU). **Puebla**, municipio de Ahuacatlán, desviación a Amixtlán 3.6 km al S de Ahuacatlán, 1150 m, 14.IV.1985, *P. Tenorio et al.* 8774 (MEXU); municipio de Ahuacatlán, Agua Dulce, 4 km al SE de Ahuacatlán, brecha a Zapotitlán, 1180 m, 17.V.1987, *G. Toriz et al.* 414 (MEXU); municipio de Teziutlán, Agua de Obispo, 1450 m, 9.V.1970, *F. Ventura* 1061 (ENCB, IEB, MEXU); municipio de Xicotepec, 3 km al W de Xicotepec de Juárez (Villa de Juárez), 1100 m, 26.III.1968, *L. Gutiérrez* 168 (ENCB); municipio de Xicotepec, cerca Villa Juárez, al NW, 8.IV.1944, *F. Miranda* 3205 (MEXU); municipio de Zacapoaxtla, Apulco, cerca de Zacapoaxtla, 1300 m, 10.III.1973, *W. Boege* 2744 (MEXU); municipio de Zacapoaxtla, cascada de la Gloria, cerca de Apulco, 850 m, 1400 m, 12.IV.1974, *J. Rzedowski* 31850 (ENCB). **Veracruz**, municipio de Alto Lucero de Gutiérrez Barrios, cerro de la Cima, entre la Sombra y Tierra Blanca, 1700 m, 10.IV.1981, *G. Castillo & F. Vázquez* 1598 (XAL); municipio de Atzalan, Alseseca, 6.XII.1969, *F. Ventura* 187 (ENCB); municipio de Chiconquiaco, los Baúles, al E de parada Paredes, 1650 m, 9.III.1988, *C. Gutiérrez* 3066 (XAL); municipio de Coatepec, Cinco Palos, 3 km al NW, 1700 m, 21.XI.1993, *V. E. Luna et al.* 721 (XAL); municipio de Coatepec, Loma Alta, 4 km al E de Cinco Palos, 1900 m, 13.III.1994, *V. E. Luna et al.* 1423 (XAL); municipio de Coatepec, near Coatepec, 11.IV.1957, *M. B. Foster & O. C. van Hynning* 3002 (US); municipio de Huatusco, 50 m al este de Dos Puentes, carretera Huatusco - Totutla, 1300 m, 29.VIII.1979, *S. Avendaño & G. Castillo* 486 (XAL); municipio de Jilotepec, Jilotepec, on moist cliffs, 500 ft, 30.III.1959, *O. C. van Hynning* 598 (US); municipio

de Juchique de Ferrer, cerro de Villa Rica, cerca de la hacienda de la Flor, 1280 m, *G. Castillo et al.* 1779 (XAL); municipio de Orizaba, Orizaba, *M. Botteri* 65 (GH); municipio de Orizaba, Orizaba, 2550-3000 ft, V.1961, *F. Kubisch* 14 (US); municipio de Perote, barranca de Patula (cerca de Perote) [barranca de las Minas, Perote], 1400 m, 5.VII.1976, *E. Matuda* 38720 (CHAP, ENCB, MEXU, MO, XAL); municipio de Perote, barranca de planta mina, Perote, 1400 m, 5.VII.1976, *E. Matuda et al.* 38734 (MEXU); municipio de Soteapan, cerro Platanillo, ejido de Santa Marta, sierra de Santa Marta, 1500 m, 21.XII.1978, *I. Calzada* 5094 (XAL); municipio de Soteapan, volcán de Santa Marta, 1720 m, 20.XII.1978, *R. V. Ortega* 1121 (XAL); municipio de Tatahuicapan de Juárez, faldas del volcán Santa Marta, 1300 m, 19.VIII.2006, *T. Krömer & E. Otto* 2866 (MEXU, SEL, UAMIZ, XAL); municipio de Tatahuicapan de Juárez, faldas del volcán Santa Marta, 1450 m, 28.VIII.2008, *T. Krömer et al.* 3713 (CITRO, MEXU); municipio de Tlalnelhuayocan, entre Los Capulines y Rancho Viejo, 1500 m, 24.XI.1990, *P. Zamora* 2796 (XAL); municipio de Xalapa, Sedeño - Rancho Servín, 6.VI.1993, *G. Carmona* 50 (XAL); municipio de Yecuatla, Los Capulines, near Paz de Enríquez, ca. 8 km (by air) N of Chiconquiaco, 1400 m, 13.I.1984, *K. Taylor et al.* 139 (XAL); municipio de Yecuatla, 6 km al NW de Santa Rita, 22.II.1975, *M. Vázquez* V-1878 (ENCB, MEXU); municipio de Yecuatla, el Haya, 1300 m, 11.II.1971, *F. Ventura* 3095 (ENCB, MICH).

Smith & Downs (1977) cited *Vriesea macropetala* hort. (Rev. Hort. 69: 336. 1897) as synonym of *Tillandsia viridiflora*. However, this name is only mentioned in a publication of the Société National d'Horticulture de France without any description or mention of a basionym. Probably, Smith & Downs (1977) supposed that the name could be a transfer from *Tillandsia macropetala* Wawra, because of the same epithet, although we think that there is no clear evidence and it might be a *nomen nudum*.

Tillandsia viridiflora (Beer) Baker, J. Bot. 26: 81. 1888. *Platystachys viridiflora* Beer, Fam. Bromel. 81. 1856 "1857". TYPE: Mexico, "diese Pflanze wurde in der Gärtnerei des Grafen Attems zu Graz aus Samen gezogen, welchen Herr *C. Heller* aus Mexico sendete. Sie blühte das erste Mal im November 1854 und ist jetzt in meinem Besitze" (not located). Figs. 1 C-D, 2 D.

Tillandsia orizabensis Baker, J. Bot. 26: 105. 1888. TYPE: Veracruz, Orizaba, region d'Orizaba au Borrego, *E. Bourgeau* 3055 (Lectotype (Smith & Downs, 1977): K!; Isolectotypes: P!, P!); without precise locality, *L. Hahn* s.n. (Syntype: K!).

Tillandsia longiflora Sessé & Moç., Fl. mexic. 88-89. 1894 “1887”; Fl. mexic. ed. 2: 81. 1894. TYPE: Hidalgo, habitat supra arbores montium Huehuetlae. Floret Octobri. Totonaci Tacongxnexanat adpellant, *M. Sessé & J. Moçiño s n.* [No. Cuatrecasas 5459; 196-PB] (Holotype: MA 600161!, MA 606715!) (Blanco Fernández de Caleyá et al., 2010; Stafleu & Cowan, 1985).

Rosulate stemless epiphytic herbs, flowering 0.65-1 m tall, with solitary tank rosettes to 40 cm in diameter. Leaves numerous; sheaths brown to light brown, elliptic to oblong, 10-14 cm long, 5.5-6.5 cm wide, densely but inconspicuously punctulate-lepidote on both surfaces; blades green, slightly glaucous, paler beneath, narrowly triangular, 25-50 cm long, 3-4 cm wide at the base, glabrous on the adaxial surface, sparsely punctulate-lepidote on the abaxial surface, acuminate, erect to ascending. Inflorescence terminal, erect, simple, peduncle terete, 45-50 cm long, 5-7 mm in diameter, totally covered by the bract sheaths; basal peduncle bracts green to reddish, imbricate, vaginiform, only the basal ones foliaceous; sheaths 3.5-4.5 cm long, blades 1-30 cm long; spike compressed, oblong to lanceolate, 17-30 cm long, 6-7 cm wide; floral bracts dark green, glaucous, widely elliptic, 3.2-4 cm long, 2-2.4 cm wide, imbricate but the rachis visible after anthesis, smooth to nervate, ecarinate, glabrous outside, sparsely brown punctulate-lepidote inside, apex rounded; flowers distichous, ascendent, 13-22 per spike, actinomorphic, corolla helicoiform, subsessile; sepals free, green, oblanceolate, 3-3.4 cm long, ca. 1 cm wide, nervate, ecarinate, glabrous outside, sparsely brown-punctulate lepidote inside, margin hyaline and erose, apex acute; petals light green, narrowly oblong, strap shaped, twisted, ca. 9 cm long, ca. 1 cm wide, rounded to acute at the apex; stamens subequal, longer than petals, filaments free, light green to white, filiform, 10-10.5 cm long, anthers green to green-whithish, linear, curved, 9-11 mm long; ovary green, ovoid, ca. 14 mm long, ca. 5 mm in diameter, style green, filiform, 10-11 cm long, stigma green. Capsule green, fusiform, rostrate, 5.7-6 cm long, ca. 9 mm in diameter; seeds dark brown, fusiform, ca. 4 mm long, with a white coma 2.2-2.8 cm long.

Specimens examined: Mexico, **Chiapas**, municipio de Berriozábal, 13 km north of Berriozábal, near pozo Turipache and finca el Suspiro, 900 m, 12.I.1973, *D. E. Breedlove & A. R. Smith 31519* (ENCB); municipio de Berriozábal, Berriozábal - las Vistas, 15.X.1950, *F. Miranda 6708* (MEXU); municipio de La Trinitaria, 15 km east northeast of Dos Lagos above Santa Elena, 1000 m, 29.XII.1981, *D. E. Breedlove 56607* (MEXU); municipio de La Trinitaria, 15 km east northeast of Dos

Lagos above Santa Elena, 1170 m, 19.I.1982, *D. E. Breedlove & F. Almeda* 57551 (MEXU); municipio de La Triniatria, 13 km al E de Tziscaco, 1000 m, 9.VIII.1985, *T. Chehaibar et al.* 202 (UAMIZ); municipio de Ocosingo, en la comunidad lacandona de Nahá, 27 km al sureste de Palenque, por la carretera fronteriza al cruceo Chancalá, después 55.6 km por el camino de terracería hacia Monte Líbano, 950 m, 20.XII.1993, *A. Durán & S. Levy* 55 (MEXU); municipio de Ocosingo, en laguna Ocotolito, a 12 km al N de Monte Líbano, camino a Chancalá, 980 m, 2.II.1986, *E. Martínez* 17008 (MEXU); municipio de Ocosingo, laguna Ocotolito, 12 km al N de Monte Líbano, camino a Najá, 950 m, 12.IV.1986, *E. Martínez & A. García-Mendoza* 17980 (MEXU, MO); municipio de Ocosingo, a 10 km al NE de Monte Líbano, camino a Chancalá, 980 m, 17.VI.1986, *E. Martínez & M. A. Soto* 18835 (MEXU); municipio de Ocosingo, en laguna Ocotolito a 12 km al N de Monte Líbano, camino a Najá, 950 m, 23.V.1987, *E. Martínez* M-21248 (MEXU); municipio de Ocosingo, alrededor del ex poblado del Chamizal, 830 m, 3.XII.1976, *P. Valdivia* 2422 (XAL); municipio de Oxchuc, la Cascada, el río Corralito, 1250 m, 10.IV.1983, *A. Méndez Ton (Shilom Ton)* 5820 (IEB, MEXU); municipio de Yajalón, arroyo de Grava, 800 m, 16.III.1983, *A. Méndez Ton (Shilom Ton)* 5684 (MEXU); without precise locality, VI.1981, *R. W. Read & P. E. Desautles* 84-103 (US). **Hidalgo**, municipio de Chapulhuacán, 3 km al N de Chapulhuacán, 850 m, 15.III.1960, *J. Rzedowski* 12322 (ENCB); municipio de Huehuetla, Huehuetla, X, *M. Sessé & J. Mociño s.n.* (MA); municipio de Lolotla, a 1.55 km al S de Chalma, 1230 m, 27.X.2001, *A. Ponce* 230 (FCME). **Oaxaca**, municipio de San Lucas Zoquiapam, Cerro del Fraile, near Huautla de Jiménez, 1830 m, 2.VIII.1938, *R. E. Schultes & B. P. Reko* 410 (GH); municipio de San Pedro Teutila, el Faro, paraje torre 130 de la L. T. Temascal II - Oaxaca Potencia, 1263 m, 20.I. 2005, *G. Juárez & C. A. Cruz* 1111 (MEXU); municipio de San Pedro Teutila, el Faro, paraje torre 125 de la L. T. Temascal II Oaxaca Potencia, 670 m, 19.I.2005 *C. A. Cruz & G. Juárez* 2481 (MEXU); municipio de Santiago Lachiguiri, recorrido de cruceo Guadalupe a las cuevas, 12.5 km al NE de Santiago Lachiguiri, 1200 m, 10.V.1991, *A. Campos & R. Torres* 3679 (MEXU). **Puebla**, municipio de Xicotepec, Villa Juárez, 1200 m, 3.VII.1969, *C. Beutelspacher s.n.* (MEXU); municipio de Xicotepec, Loma Linda, 6 km al SE de Xicotepec, carretera a la Unión, 1130 m, 11.VI.1985, *P. Tenorio & C. Romero de T.* 8963 (ENCB, MEXU); municipio de Xicotepec, 5 km al NE de Xicotepec, carretera a La Ceiba, 1200 m, 24.II.1987, *P. Tenorio et al.* 12603 (MEXU); municipio de Xicotepec, 5 km al NE de Xicotepec, carretera a La Ceiba, 1200 m, 24.II.1987, *G. Toriz et al.* 288 (MEXU); municipio de Zongozotla, Zongozotla, 0.5 km camino a Huitzila, 840 m, 4.IX.1985, *J. L. Martínez & F. Vázquez* 735 (XAL).

Querétaro, municipio de Jalpan de Serra, 1-1.5 km al E de El Saucito, 1070 m, 7.XII.1989, *E. Carranza 2249* (IEB); municipio de Jalpan de Serra, 2-3 km al N de La Parada (Valle Verde), 1150-1200 m, 31.X.1990, *B. Servín 639* (IEB); municipio de Landa de Matamoros, km 6 de la brecha de Agua Zarca a Neblinas, 850-1100 m, 24.VIII.1988, *S. Zamudio 6716* (IEB); municipio de Pinal de Amoles, ca. 4 km al SE de Santa Águeda, 1190 m, 18.IV.1989, *E. Carranza 1640* (IEB). **San Luis Potosí**, municipio de Rayón, Las Canoas, 17.X.1891, *C. G. Pringle 5100* (GH); municipio de Tamazunchale, cerro de San Francisco, Tamazunchale, 1020 m, *P. Maury 6258* (GH). **Tamaulipas**, municipio de Gómez Farías, reserva de la biosfera Rancho del Cielo, in the vicinity of the station, 1170 m, 2.V.1995, *P. Hietz 107* (XAL). **Veracruz**, municipio de Alto Lucero de Gutiérrez Barrios, Rancho Nuevo, al W de Plan de las Hayas, 1300 m, 6.IV.1981, *G. Castillo & F. Vázquez 1291* (XAL); municipio de Alto Lucero de Gutiérrez Barrios, la Piedra Cuata, entre Plan de las Hayas y Rancho Nuevo, 1400 m, 7.IV.1981, *G. Castillo & F. Vázquez 1352* (XAL); municipio de Atoyac, montagnes d'Atoyac, XI.1903, *A. Dugès 20* (GH); municipio de Atoyac, mountains of Atoyac, X.1899, *A. Dugès s.n.* (US); municipio de Atzalan, Comunidad Cruz Gorda, congregación San Salvador, 990 m, 17.VI.2008, *T. Krömer et al. 3320* (CITRO, MEXU, XAL, XALU); municipio de Chiconquiaco, Santa Rita Chiconquiaco, 1500 m, 28.II.1975, *V. Sosa 88* (XAL); municipio de Córdoba, Vallée de Cordoba, 18.XII.1865, *E. Bourgeau s.n.* (P); municipio de Huatusco, puente antiguo, ca. 5.6 km antes de llegar a Huatusco, viniendo de Totutla, 1290 m, 20.VII. 2007, *A. Espejo et al. 7054* (UAMIZ); municipio de Jilotepec, El Esquilón, cerro del Cuajilote, 26.XII.1978, *G. Castillo 411* (XAL); municipio de Jilotepec, 2.5 km NE of Jilotepec, along road to Naolinco, 1350 m, 10.VII.1982, *G. Diggs & M. Nee 2776* (GH, MO, XAL); municipio de Mecayapan, Santa Marta, al N de Ocotál, 1450 m, 17.VIII.1980, *F. Ramírez 1186* (XAL); municipio de Mecayapan cráter del volcán Santa Marta, por Ocotál Chico, 900 m, 12.III.1981, *F. Ramírez & F. Vázquez 1535* (XAL); municipio de Mecayapan, faldas del volcán Santa Marta, 1090 m, 19.VIII.2006, *T. Krömer & E. Otto 2865* (MEXU); municipio de Misantla, Misantla, VI.1866, *L. Hahn s.n.* (P); municipio de Naolinco, cascada de Naolinco, 1530 m, 3.VII.2003, *A. Mendoza et al. 704* (UAMIZ); municipio de San Andrés Tuxtla, dentro del cráter del volcán San Martín Tuxtla, lado S, 1450 m, 31.V.1984, *I. Calzada 10666* (XAL); municipio de San Andrés Tuxtla, cerro Coyolar al N de Catemaco, 29.V.1985, *I. Calzada 11805* (XAL); municipio de San Andrés Tuxtla, cima del cerro Mastagaga, al N del ejido Ruiz Cortines, sierra de los Tuxtlas, 30.V.1985, *I. Calzada 11825* (XAL); municipio de San Andrés Tuxtla, falda del volcán San Martín, 1300 m, 14.IV.2005, *T. Krömer et al. 1956* (MEXU, XAL);

municipio de San Andrés Tuxtla, ejido Ruiz Cortines, falda del volcán San Martín Tuxtla, 1000 m, 1.VII.2005, *T. Krömer & A. Acebey* 2299 (MEXU); municipio de Soteapan, cráter del volcán Santa Marta, SE del río Xochiapán, 670 m, 15.V.1985, *I. Calzada* 11434 (XAL); municipio de Soteapan, Santa Marta, ladera W del volcán Santa Marta, *F. Ramírez* 969 (XAL); municipio de Tatahuicapan de Juárez, faldas del volcán Santa Marta, 1350 m, 28.VIII.2008, *T. Krömer et al.* 3714 (MEXU); municipio de Tepetzintla, en la Sierra de Otontepec, al NE de Tepetzintla, 1200 m, 27.VIII.1981, *G. Castillo & A. Benavides* 2249 (XAL); municipio de Tepetzintla, sierra de San Juan Otontepec, 900 m, 13.XII.1981, *G. Castillo & A. Benavides* 2384 (XAL); municipio de Tepetzintla, sierra de Otontepec, 1250 m, 14.XII.1981, *G. Castillo & A. Benavides* 2542 (XAL); municipio de Tepetzintla, Sierra de Otontepec, al NE de Tepetzintla, 1170 m, 25.VIII.1981, *F. Vázquez & L. Tapia* 208 (XAL); municipio de Tepetzintla, sierra de la Peña Blanca, sierra de Tantima, 21.IX.1989, *P. Zamora et al.* 1226 (XAL); municipio de Totutla, el Mirador, 21 km E of Huatusco, at km 45 along hwy to Puente Nacional, 23.VIII.1977, *T. Croat* 43973 (MEXU, MO); municipio de Totutla, Mirador, 1841-43 m, *F. Liebmann* 7 (UC); municipio de Totutla, Mirador, VIII.1930, *C. A. Purpus* 15763 (UC); municipio de Xalapa, près de Jalapa, 4.IX.1866, *L. Hahn* 594 (P); municipio de Xico, gorge at puente Acabaloya, ca. 1 km SE of Xico Viejo and 5 km NW of Xico, along trail between the two, 1600 m, 31.III.1983, *M. Nee & K. Taylor* 26268 (XAL); municipio de Zongolica, reserva ecológica La Quinta, Amatitla, 1250 m, 6.III.2008, *T. Krömer et al.* 3131 (CITRO, MEXU, XAL).

It is also important to mention that sometimes plants of *Tillandsia heterophylla* (Fig. 2 B) are confused in herbarium material with *T. viridiflora* and/or *T. macropetala* because of the branched inflorescences and overall morphology of the floral bracts. However, in living plants, the flowers of *T. heterophylla* have infundibuliform and slightly zygomorphic white corollas with included stamens, while the flowers of *T. viridiflora* and *T. macropetala* have helicoiform actinomorphic green corollas, spirally twisted petals, and the stamens are exposed. In addition the plants of *T. heterophylla* are conspicuously glaucous and pruinose.

Finally, we suggest that the name *Vriesea billbergiae* Lem. (*Tillandsia billbergiae* (Lem.) Baker) should probably be excluded from the synonymy of *T. viridiflora* because the original description of the former mentioned the presence of a “gland” at the base of petals: “... [segmentis] internis basi ima glandula maxima rotundato-biloba tenuissima instructis ...”. This character is not present in any species of *Tillandsia* and we think that this name eventually will be assigned to some

species of *Vriesea* Lindl., as this genus in its current circumscription is separated from *Tillandsia* solely on floral characters (Till, 2000). However, as the description could be wrong, it will be necessary to study the type specimen (Type: *Ghiesbreght* in Verschaffelt Hortus, Ghent, no date, Mexico) in order to confidently exclude the name.

All three species of the *Tillandsia viridiflora* complex show a wide distribution in the central and southern states of Mexico (Fig. 4), where they principally occur in or near montane rain or moist pine-oak forests along the slopes of the Sierra Madre Oriental, Sierra de Juarez, and Sierra de Chiapas. However, they can also be found in humid to moderately dry lowland forests. *T. grandis* occurs at 400 m to 2000 m elevation and grows primarily lithophytically on very steep, inaccessible limestone cliffs, but it is very occasionally epiphytic. *T. macropetala* can be found at elevations of (150)1100 m to 2500 m, whereas *T. viridiflora* occurs from 670 m to 1830 m elevation, both species usually occur as epiphytes and only rarely are found terrestrially. Since the distributions of *T. grandis* and *T. viridiflora* range from Mexico to Nicaragua (Beaman & Judd, 1996), it is very likely that a future review of herbarium material in combination with the characters used in our identification key also will demonstrate the existence of *T. macropetala* in Central America, as the latter species is widespread in the southern states of Mexico, and thus probably not endemic to the country.

Their flowering periods are only slightly different, with *Tillandsia grandis* producing flowers between March and July, whereas *T. macropetala* and *T. viridiflora* start blooming in January and last until August (Espejo et al., 2005). In addition to their similar flower morphology and phenology, all three species show inconspicuous greenish inflorescences and a nocturnal anthesis, in contrast to most *Tillandsia* species that have brightly colored bracts with contrasting flowers which are pollinated by hummingbirds (Gardner, 1986; Benzing, 2000; Kessler & Krömer, 2000). Hietz & Hietz-Seifert (1994) suggest sphingid moths as the most likely visitors, because of their long spreading stamina and pistil exerted from an open actinomorphic flower. However, personal observations by the senior author, combined with the identification of hexose-rich nectar in *T. viridiflora* by Krömer et al. (2008), suggest bat-pollination, although the plants in the complex do not show the typical chiropterophilous floral syndrome with bell-shaped, large zygomorphic flowers, characteristic of the bat-pollinated *Werauhia* species (Krömer et al., 2007). Furthermore, since the flowers of *T. macropetala* and *T. viridiflora* are still open during the next morning, they might also be visited by hummingbirds and show a bimodal pollination system.

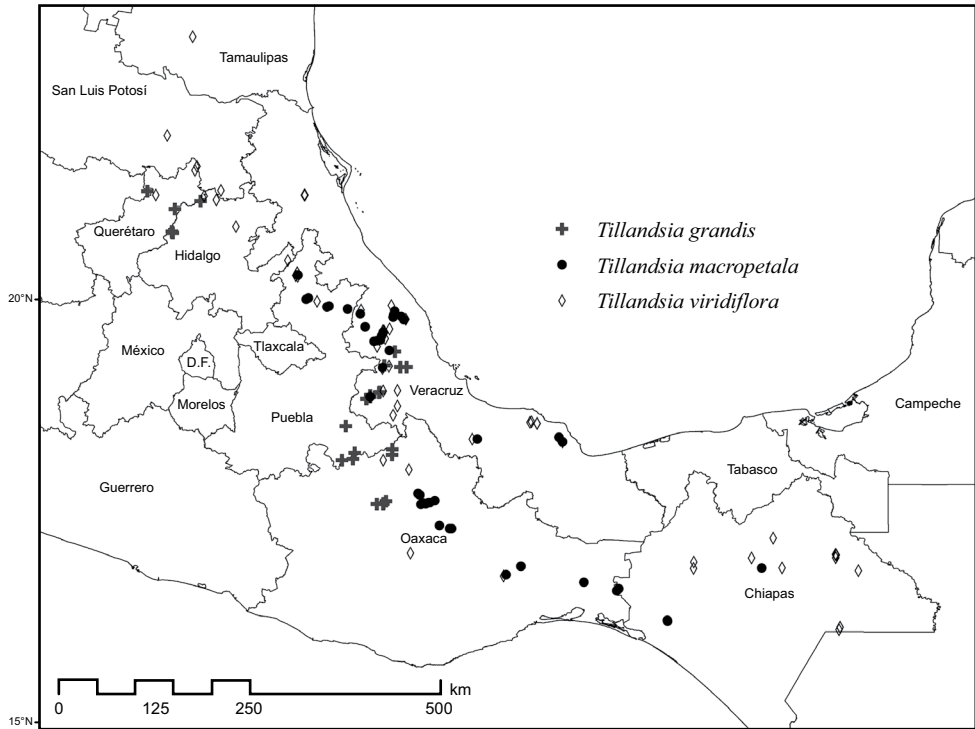


Fig. 4. Distribution of *Tillandsia grandis*, *T. macropetala* and *T. viridiflora* in Mexico.

ACKNOWLEDGMENTS

We thank Amparo Acebey, Manfred Kretz, Ulrich Lautner, Günther Noller, Elisabeth Otto, and Wolfgang Schindhelm for fieldwork assistance, Walter Till, Bruce K. Holst, and two anonymous reviewers for valuable comments on the manuscript, Lilia Ruiz-Ruiz for preparing the figures 1-3, Nancy Martínez-Correa for preparing the distribution map and the curators of CHAP, ENCB, FCME, GH, IBUG, IEB, K, LL, MA, MEXU, MICH, MO, OAX, OXF, P, SEL, TEX, UAMIZ, UC, US, WU and XAL for providing the facilities to consult specimens and data. Sergio Zamudio sent us images of *T. viridiflora* deposited at IEB. To Elizabeth Bascom Scholarship from the Missouri Botanical Garden granted to A. R. López-Ferrari to study the Mexican Bromeliaceae collections deposited at the main U.S. herbaria. The study of T. Krömer was supported by a postdoctoral grant from the

Universidad Nacional Autónoma de México and a research grant from the Bromeliad Society International.

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Recibido en marzo de 2011.

Aceptado en noviembre de 2011.