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ORIGINAL ARTICLE

Phylogenetic relationships within *Tillandsia* subgenus *Diaphoranthema* (Bromeliaceae, Tillandsioideae) based on a comprehensive morphological dataset

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Abstract *Tillandsia* subgenus *Diaphoranthema* (Tillandsioideae, Bromeliaceae) includes 29 epiphytic species distributed widely from southern North America to central Argentina and Chile. The species of *Diaphoranthema* are characterized by few small flowers, and most species are differentiated by phyllotaxy, leaf shape, flower number, and by the morphology and number of bracts. In addition to the highly variable vegetative characters, most species of subgenus *Diaphoranthema* possesses polyembryonic seeds (rare in Bromeliaceae) and an autogamous breeding system with a few number of species having cleistogamous flowers. In order to clarify relationships within *Diaphoranthema* and to understand the evolution of polyembryony, the breeding system, and diagnostic characters, a cladistic analysis of all known species using 85 morphological characters was conducted. Phylogenetic results suggest that *Diaphoranthema* is monophyletic if some species from the closely related subgenus *Phytarrhiza* are included. These two subgenera can only be distinguished from each other by the shape and size of their petals. A complete sampling of *Phytarrhiza* is still needed to test these hypotheses. None of the six informal groups as previously recognized are monophyletic. Vegetative characters such as phyllotaxy and the shape, length, and width of leaves were the most useful for distinguishing four major clades within *Diaphoranthema*. Flower number, scape development, exocarp and endocarp fusion at fruit ripening, and absence of endosperm in mature seeds were also used to distinguish some clades. Evolutionary trends favour a distichous phyllotaxy, linear shape leaf blades, and a reduction in flower number and bracts per inflorescence. In addition, capsules with disaggregating exocarp and endocarp at ripening, and polyembryonic seeds are also derived states within subgenus *Diaphoranthema*.

Keywords Phylogeny · *Tillandsia* · *Diaphoranthema* · Morphology

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Introduction

Tillandsia L. is the largest American genus of the family Bromeliaceae and subfamily Tillandsioideae with 540 terrestrial or more frequently epiphytic species. The genus is widely distributed from southern North America to central Argentina and Chile (Smith and Downs 1977; Smith and Till 1998). Among Bromeliads, *Tillandsia* is one of the most commonly found genera in cultivation with several species grown as ornamental plants for their remarkable versatility, their interesting plant forms and for the infinite variety of colour combinations in their inflorescences. Some species have medical properties and are useful as bioindicators of atmospheric pollution (Graciano et al. 2003; Barboza et al. 2006; Wannaz et al. 2006). Although they are not parasites, they are considered epiphytic weeds that can sometimes cause serious damage to their host plants (Benzing and Seemann 1978; Bártoli et al. 1993; Caldiz et al. 1993; Caldiz and Fernandez 1995; Aguilar-Rodríguez et al. 2007).

First described by Linnaeus to include *Tillandsia utriculata* L., *Tillandsia* is currently classified into six subgenera: *Allardtia* (A. Dietrich) Baker, *Anoplophytum* (Beer) Baker, *Diaphoranthema* (Beer) Baker, *Phytarrhiza* (Visiani) Baker, *Pseudalcantarea* Mez, and *Tillandsia*. These groups are mainly distinguished by floral characters such as inserted versus exserted stamens, style length, and the

Table 1 Informal subgeneric classification ("aggregates") of *Tillandsia* subgenus *Diaphoranthema* as proposed by Till (1992b)

Species of *Tillandsia* subgen. *Diaphoranthema*	Aggregate	Phyllotaxy	Floral bracts	Petal colour
T. caliginosa	Caliginosa	Distichous	Lepidote	Brown to violet brown
T. cotagaitensis				
*T. porongoensis**				
T. tenebra				
T. andicola	Myosura	Distichous	Lepidote	Yellowish to brownish, rarely dark violet
T. angulosa				
T. gilliesii subsp. gilliesii				
T. gilliesii subsp. polysticha				
T. hirta				
T. mandonii				
T. myosura				
T. retorta				
T. copynii	Loliacea	Polystichous	Mostly lepidote	Yellow, rarely dark brown
T. loliacea				
T. minutiflora				
T. spiralipetala				
T. tricholepis				
T. aizoides	Rectangula	Polystichous	Mostly glabrous	Brownish to dark violet, rarely yellowish or light violet
T. brealitoensis				
T. erecta				
T. funebris				
T. pedicellata				
T. rectangula				
T. capillaris	Capillaris	Distichous	Glabrous to lepidote	Yellow to brown, rarely Light to dark violet
T. castellanii				
T. kuehhasii				
T. virescens				
T. landbeckii subsp. andina	Recurvata	Rarely polystichous	Lepidote, rarely glabrous, with a scape bract ± beyond the floral bract	Violet, white, brownish, green or yellow
T. landbeckii subsp. landbeckii				
T. mollis				
T. recurvata				
T. usneoides				

The species name marked with an asterisk (*) was originally described by Hromadnik and Schneider (1988) as belonging to *Tillandsia* subgenus *Phytarrhiza* although it was considered in subgenus *Diaphoranthema* by Till (1992b)

shape of petals and leaves (Smith and Downs 1977; Smith and Till 1998; Benzing 2000).

Diaphoranthema was first proposed as a monotypic genus for *Tillandsia recurvata* L. by Beer (1854), but its species number was soon increased to eight by the same author (Beer 1857). However, in a synopsis of fourteen species, Baker (1878) decided to treat *Diaphoranthema* as a subgenus within *Tillandsia*, and the taxon has remained within this genus and at the same rank ever since. During the last three decades, several new species have been described within *Diaphoranthema*, bringing the total number of recognized species to 29 (Till and Hromadnik 1983, 1984; Gouda 1986, 1988; Hromadnik and Till 1991; Till 1992b, 1995; Donadío 2011, 2013).

Most recently, Till (1992b) divided *Tillandsia* subgen. *Diaphoranthema* into six informal groups (here after called "aggregates") based on the phyllotaxy, pubescence of floral bracts, and colour of petals as described in Table 1. He treated the 29 species of *Diaphoranthema* and one species of the related subgen. *Phytarrhiza*: *T. porongoensis* L. Hrom. & P. Schneid. The latter species was suggested as a natural hybrid between *T. gilliesii* Baker (subgen. *Diaphoranthema*) and *T. duratii* Vis. (subgen. *Phytarrhiza*) by Hromadnik and Schneider (1988).

According to keys for subgeneric classification (Smith and Downs 1977; Benzing 2000), both subgenera *Diaphoranthema* and *Phytarrhiza* differ mainly by the shape and size of petals. As *Diaphoranthema* and the xerophytic species of *Phytarrhiza* are closely related (Bhöme 1988; Brown and Gilmartin 1984, 1989; Gortan 1991; Gross 1988; Halbritter 1992), the limits of these two subgenera are unclear and in need of revision (Gilmartin and Brown 1986; Till 1992b; Benzing 2000).

Tillandsia subgenus *Diaphoranthema* is widely distributed from southern North America to central Argentina and Chile with well-known representatives like the "Spanish moss" *T. usneoides* (L.) L. and the "ball moss" *T. recurvata* (L.) L. (Smith and Downs 1977). However, its centre of distribution is much narrower with most species being confined to central to northwest Argentina and Bolivia (Till 1992b). *Diaphoranthema* species are characterized by few (ca. 1-10), reduced flowers and they occupy mostly arid and semiarid environments, growing on trees, bushes, or rocks from the sea level to 4,300 m high (Castellanos 1945; Till 1984, 1989a; Schinini et al. 2008; Subils 2009). Although characterization of flowers has been relevant to recognize subgeneric groups, *Diaphoranthema* species are not defined by floral features, instead, phyllotaxy, the shape and size of leaves, flower number, and the number and morphology of bracts are used to discriminate species and groups. Floral morphology is similar among species, by having narrow petals, included stamens, and a short, stout style (Smith and Downs 1977; Till 1984; Benzing 2000). Only the colour of flowers is highly variable (from white, green, to violet or black) and used to recognize a few species (Smith and Downs 1977; Till 1989b, 1991a, 1992a; Hromadnik and Till 1991; Donadío 2011, 2013). In addition, the group is also of evolutionary interest due to the presence of autogamous or even cleistogamous flowers (Billings 1904; Birge 1911; Gilmartin and Brown 1985; Till 1989a, 1992b; Kromer et al. 2006), and the presence of polyembryony, which, apart from *Tillandsia juncea* (Ruiz & Pav.) Poir. (Suessenguth 1921), is only present in species of subgenus *Diaphoranthema* (Subils 1973; Gross 1988).

Previous molecular analyses of Bromeliaceae that have included *Tillandsia* have generally found very poor resolution within the genus and its near relatives (Terry et al. 1997; Horres et al. 2000; Barfuss et al. 2005; Givnish et al. 2011, 2014). Moreover, according to Barfuss et al. (2013), the low variation in plastid sequences, the poor taxonomic sampling, and partially resolved trees in Tillandsioideae have yet prevented an internal classification for the subfamily, but some clades still need further attention in species sampling. In contrast, some morphological analyses have been more successful at reconstructing relationships. An analysis of the closely related subgenus *Phytarrhiza* produced highly resolved trees suggesting that subgen. *Diaphoranthema* was monophyletic, and some of its species might be best treated in *Phytarrhiza* (Gilmartin and Brown 1986). Within Bromeliaceae, morphology has also produced highly resolved trees that have been useful for testing the monophyly of *Puya* (Hornung-Leoni and Sosa 2008) and *Quesnelia* (Almeida et al. 2009) subgenera and other infrageneric groups. Given that there is low molecular divergence within Bromeliaceae subfamily Tillandsioideae (Horres et al. 2000; Barfuss et al. 2005, 2013; Givnish et al. 2011, 2014), especially within the "Tillandsioid core" to which subgen. *Diaphoranthema* belongs (Barfuss et al. 2005), and that morphology has often been successful at resolving relationships at and below the subgeneric level, this study focuses on the morphology of *Diaphoranthema* in order to determine homologies and to test the monophyly of the subgenus and its "aggregates." Moreover, optimization of characters was used to reveal patterns in the evolution of vegetative and reproductive characters within the subgenus. Inferences on the evolution of the breeding systems in subgenus *Diaphoranthema* are also discussed.

Materials and methods

Taxonomic sampling

All species of *Tillandsia* subgen. *Diaphoranthema* (29) were considered as in-group taxa for the morphological study, including both subspecies of *T. gilliesii* Baker (*T. gilliesii* subsp. *gilliesii* and *T. gilliesii* subsp. *polysticha* W. Till & L. Hrom), both subspecies of *T. landbeckii* Phil. (*T. landbeckii* subsp. *landbeckii* and *T. landbeckii* subsp. *andina* W. Till), and both varieties of *T. landbeckii* Phil. subsp. *andina* W. Till (var. *andina* and var. *rigidior* W. Till). Based on bromeliad phylogenies (Gilmartin and Brown 1986; Terry et al. 1997; Barfuss et al. 2005), we considered as out-group taxa: two species of *Tillandsia* subgen. *Phytarrhiza* (*T. crocata* (E. Morren) N.E. Br. and *T. porongoensis*), one species of *Tillandsia* subgen. *Anoplophytum* (*T. aëranthos* (Loisel.) L.B. Sm.), one species of *Tillandsia* subgen. *Allardtia* (*T. australis* Mez), and one species of the genus *Vriesea* (*V. friburgensis* Mez var. *tucumanensis* (Mez) L.B. Sm.). *Vriesea* was then chosen to root the trees ("Appendix 1").

Plant material

Sixteen of the 29 species (57 %) of *Diaphoranthema* were collected in central and NW Argentina and kept in culture for morphological and anatomical studies. Herbarium specimens, including type material, completed the sampling of *Diaphoranthema* and out-group taxa. A total of approximately 700 herbarium specimens from BHCB, CORD, CTES, LIL, LPB, MCNS, SI, SGO, and WU

(Thiers 2013) and 800 living individuals were examined. The list of examined material is shown in "Appendix 1".

Morphological dataset

Eighty-four morphological and one ecological characters were chosen to characterize morphological variation among species. Twenty-three vegetative characters (17 binary and 6 multistate) and sixty-two reproductive characters (45 binary and 17 multistate) were used. Characters were selected following previous taxonomic publications (Castellanos 1945; Smith and Downs 1977; Till and Hromadnik 1983, 1984; Gouda 1986, 1988; Hromadnik and Till 1991; Till 1989a, b, 1991a, b, 1992a, 1995) and personal observations (Donadío 2013).

Exomorphological characters were studied using stereoscopic binocular Nikon SMZ2800 and a Zeiss Standart 28 microscope. Seeds were cleared with lactic acid and polyvinylic alcohol following Ruzin (1999) and then mounted with polyvinylic alcohol for light microscopy. Mature seeds showing the typical radicular constriction of *Tillandsia* seeds (Cecchi Fiordi et al. 1996; Magalhães and Mariath 2012) were selected for analysis. Polyembryos were identified both by light microscope (63X) and by seed dissections (Subils 1973) when possible. The presence of polyembryony was scored for a species when at least one seed with more than one embryo was found. For all other species, information on polyembryony was taken from the literature (Subils 1973; Gross 1985, 1988). Endostome type was taken from Gross (1988). Crystals in sepals and petals were identified by polarizing microscopy.

Living plants were used to infer selfing in species of the subgenus *Diaphoranthema*. For this purpose, individual plants were covered with a bag before anthesis avoiding any possible pollinators (Jones and Little 1983). Information on autogamic species was also revised and completed from the literature (Billings 1904; Birge 1911; Garth 1964; Mc Williams 1974; Gilmartin and Brown 1985; Gouda 1988; Till 1989a, 1992b).

Data for stigma types were also obtained from the literature (Brown and Gilmartin 1989). Only two of the five stigma types described by Brown and Gilmartin (1989) in Bromeliaceae were coded (conduplicate-spiral and simple-erect) as the other three stigma types (convolute-blade, cupulate and coralliform) are not represented in the sampling. Similarly, only three out of ten *Tillandsia* endostome types, as described in Gross (1988), were coded (*Bryoides*, *Cotagaitensis*, and *Incarnata* types) as occurring in our sampling.

Phylogenetic analysis

The morphological dataset was analysed under a parsimony algorithm using TNT version 1.1 (Goloboff et al. 2008). Uninformative characters were removed prior to all analyses, and informative characters were considered unordered and equally weighted. Parsimony analyses consisted of a series of heuristic searches using 1,000 random addition sequences (RAS), swapping the initial tree with bisection reconnection (TBR), and saving ten trees per replicate. Then, all optimal trees were branch-swapped by TBR until completion, and the strict consensus of all most parsimonious trees were calculated. The jackknife test was used to estimate support for individual nodes. Jackknife resampling was conducted using 1,000 replicates, a removal probability of 30 % and starting each replica with 4 RAS and TBR swapped holding three optimal trees. To finally infer evolutionary trends and to determine the taxonomic value of diagnostic features, morphological characters were unambiguously optimized onto one of the most parsimonious trees.

Results

The final matrix consisted of 77 informative characters and 37 taxa. Only eight out of the 85 characters analysed were uninformative. Characters and coding are listed in Table 2 with the data matrix provided in "Appendix 2."

Heuristic searches yielded only four equally parsimonious trees of 329 steps. The strict consensus tree is shown in Fig. 1, with jackknife values below branches.

Tillandsia subgen. *Diaphoranthema* is a paraphyletic group (*Diaphoranthema* clade) that includes one species of subgen. *Phytarrhiza* (*T. crocata*) (jackknife = JK = 90). *Tillandsia porongoensis*, originally included in *Phytarrhiza*, is sister to the *Diaphoranthema* clade, with a strong support value (JK = 98) (Fig. 1).

The six "aggregates" are resolved as poly or paraphyletic. The Rectangula and Recurvata aggregates are paraphyletic groups as they include one species from Loliacea (*T. minutiflora* Donadío) and one species of Capillaris (*T. kuehhasii* W. Till), respectively. The Caliginosa, Capillaris, Loliacea, and Myosura aggregates appear as polyphyletic groups (Fig. 1).

The clade including *T. porongoensis* and *Diaphoranthema* is characterized by three synapomorphic states: adaxially glabrous scape bracts, adaxially glabrous floral bracts, and flowers distically arranged on the inflorescence rachis. This clade is also supported by one homoplastic synapomorphy: the sepals are abaxially lepidote (Fig. 2).

The *Diaphoranthema* clade is supported by the number of flowers per inflorescence, the number of nerves in sepals, petal colour, and anther position with respect to the pistil (anthers just above the stigma) (Fig. 2). Although optimization of petal colour showed a transition from a plesiomorphic blue to a derived ochre tone in the

Table 2 Characters and character states for the cladistic analysis of *Tillandsia* subgenus *Diaphoranthema*

1. Habitat: 0, terrestrial; 1, epiphytic; 2, epilythic (plants growing on rocks)
2*. Radicular system: 0, basal (roots only at the base of the stem); 1, extended (roots along the stem)
3. Stem development: 0, acaulescent; 1, caulescent
4. Stem length: 0, short (<3 cm); 1, medium (3–15 cm); 2, long (>15 cm)
5. Branches: 0, none or <2; 1, ≥2
6. Stem internodes: 0, non-visible; 1, visible
7. Phyllotaxy: 0, polystichous (in more than two ranks); 1, distichous
8. Orientation of the leaf blade: 0, appressed, erect; 1, spreading, curved or "S" shaped; 2, spreading and spirally recurved (circinate)
9. Indument of the leaf blade (both surfaces): 0, inconspicuous (diminute and sparse trichomes); 1, conspicuous (dense, large and imbricate overlapping trichomes)
10. Leaf blade shape: 0, linear; 1, triangular (Lindley 1848)
11. Leaf tip: 0, pungent; 1, non-pungent (Lindley 1848)
12. Apical keel in the leaf: 0, absent; 1, present (Lindley 1848)
13. Leaf blade cross section (in the middle portion of the blade): 0, flat; 1, canaliculated (longitudinally grooved); 2, circular (blades terete) (Lindley 1848)
14. Leaf blade with a knee joint (see Smith and Downs 1977): 0, absent; 1, present
15. Abaxial keel in the leaf blade (Lindley 1848): 0, absent; 1, present
16. Leaf blade length: 0, >2 cm; 1, ≤2 cm
17. Leaf blade width (measurements from herbarium material): 0, >2 mm; 1, ≤2 mm
18. Leaf differentiation between sheath and blade (as seen on the stem): 0, indistinct; 1, distinct
19. Leaf sheath: 0, open; 1, close, tubular
20. Indument of the leaf sheath margins: 0, glabrous; 1, lepidote with trichomes morphologically identical to leaf blade trichomes (not ciliated); 2, lepidote with trichomes morphologically different to leaf blade trichomes (ciliated)
21. Indument of the leaf sheath (abaxial surface): 0, glabrous; 1, lepidote with trichomes morphologically equal to leaf blade trichomes
22. Number of nerves in the leaf sheath: 0, >25 nerves; 1, 16–25 nerves; 2, 12–15 nerves; 3, 8–11 nerves; 4, 5–7 nerves; 5, 3-nerves
23. Distribution of nerves in leaf sheath: 0, centrally distributed (winged margins without nerves); 1, evenly distributed across the sheath.
24. Scape development (at fruit ripening): 0, non-evident, very short, sunk among the terminal leaves; 1, evident, elongated
25. Scape length (at anthesis): 0, same length as scape at fruit ripening; 1, shorter than scape at fruit ripening
26. Density of the scape indument: 0, few, sparse trichomes; 1, abundant, dense, contiguous and overlapping trichomes
27. Indument of the scape internodes: 0, entirely glabrous; 1, entirely lepidote; 2, glabrous at the basal portion and lepidote at the distal portion of the internode
28. Number of scape bracts: 0, No bracts; 1, one; 2, two; 3, three; 4, four; 5, five; 6, six; 7, seven; 8, eight; 9, nine
29. Scape bracts morphology (along the peduncle): 0, leafy; 1, partially differentiated from leaves; 2, completely differentiated from leaves
30. Relative development of the scape internodes: 0, several internodes equally developed, of similar length, bracts evenly spaced along the peduncle; 1, two or more internodes unequally developed, basal and/or distal and/or intermediate bracts; 2, only one internodes, no bracts along the peduncle
31 Number of nerves in the distal most scape bract (scape bract below floral bract): 0, >nineteen; 1, nineteen; 2, thirteen or fifteen; 3, eleven; 4, nine; 5, seven; 6, five, 7, one or three
32* Indument of the scape bracts (abaxial surface): 0, all bracts glabrous; 1, all bracts lepidote; 2, basal bracts lepidote, distal bracts glabrous
33 Distribution of the scape bracts indument (abaxial surface): 0, even along entire bract; 1, present only at bract apex
34 Quantity of scape bract trichomes (abaxial surface): 0, few to some (<10 trichomes); 1, abundant (≥10 trichomes)
35 Disposition of scape bract trichomes (abaxial surface): 0, sparse, separated from each other, not contiguous; 1, contiguous, imbricate, overlapping
36 Indument of the scape bracts (adaxial surface): 0, glabrous; 1, lepidote
37 Foliaceous apex in the scape bracts: 0, absent; 1, present
38 Long paraclades: 0, absent, 1, present
39 Number of flowers per inflorescence: 0, >fifteen; 1, one; 2, two, 3, three; 4, four; 5, five; 5, five, 6, six to twelve
40 Disposition of flowers on the inflorescence rachis: 0, polystichous (in more than two ranks); 1, distichous
41 Branching pattern of the inflorescence rachis (according to Endress 2010): 0, racemose (limitation of axial orders to two); 1, cymose (limitation of lateral axes of each order to two)
42 Rachis of the inflorescence: 0, straight; 1, flexuous
43 Rachis indument: 0, glabrous; 1, lepidote
44 Density of the rachis indument: 0, few and sparse trichomes; 1, dense, contiguous, overlapping trichomes
45 Keel in floral bract: 0, absent; 1, present
46* Appearance of the floral bract nerves: 0, prominent; 1, not prominent
47 Number of nerves in floral bract (basal flower): 0, ≥twenty-three; 1, one; 2, three; 3, five; 4; seven; 5, nine; 6, eleven; 7, thirteen; 8, fifteen; 9, nineteen or twenty-one
48 Floral bract indument (abaxial surface): 0, glabrous; 1, lepidote
49 Distribution of the floral bract indument (abaxial surface): 0, even along the entire bract surface; 1, only at the apex; 2, over the middle nerves
50 Quantity of floral bract trichomes (abaxial surface): 0, few; 1, abundant
51 Disposition of floral bract trichomes (abaxial surface): 0, sparse, not contiguous; 1, contiguous, imbricate, overlapping
52 Floral bract indument (adaxial surface): 0, glabrous; 1, lepidote
53 Foliaceous apex in the floral bract: 0, absent; 1, present
54* Floral bract length in relation to internode length between basal flowers: 0, longer than the internode; 1, same length as the internode

55 Floral bract length in relation to sepal length: 0, getting shorter along rachis; 1, of equal length all along

56 Number of nerves in sepals (basal flower): 0, ≥twelve; 1, one; 2, two; 3, three; 4, four; 5, five; 6; six; 7, seven; 8, eight; 9, nine; 10; eleven

57 Sepal indument (abaxial surface): 0, glabrous; 1, lepidote

58 Distribution of sepal indument (abaxial surface): 0, even along entire sepal (trichomes present in the apical half of the sepals or more); 1, at the apex (trichomes present in the apical one-third of the sepals); 2, at the apex and over the middle nerves of the sepals

59 Quantity of sepal trichomes (abaxial surface): 0, few; 1, abundant

60 Disposition of sepal trichomes (abaxial surface): 0, sparse, not contiguous; 1, contiguous, imbricate, overlapping

61 Sepal indument (adaxial surface): 0, glabrous; 1, lepidote

62 Sepal fusion: 0, sepals free or connate at the base; 1, posterior sepals (adaxial) connate for 50 % or more of their length, and anterior sepal (abaxial) free or basally connate to the posterior sepals

63 Keel in posterior sepals: 0, absent; 1, present

64 Keel in anterior sepal (abaxial sepal): 0, absent; 1, present

65 Appearance of sepal nerves: 0, prominent; 1, not prominent

66 Sepals with raphides: 0, absent; 1, present

67* Petals with scales in the inner part of the claw: 0, absent; 1, present

68 Petal colour: 0, white; 1, pale yellow; 2, yellow; 3, ochre; 4, brown; 5, greenish; 6, pale violet; 7, dark violet; 8, dark blue; 9, pink; 10, black; 11; orange

69 Petal blade shape: 0, narrowly elliptic, tongue-shaped; 1, suborbicular (Lindley 1848)

70 Petal disposition during anthesis: 0, erect; 1, recurved; 2, spirally recurved

71 Petal disposition after anthesis: 0, same disposition as during anthesis; 1, petals closed by a constriction of the corolla just above the calyx; 2, petals closed and spirally recurved along the longitudinal axis; 3, rolled over

72 Petals with raphides: 0, absent; 1, present

73* Stamen length in relation to petal length: 0, stamens exerted, exceeding the petals; 1, stamens included, not exceeding the petals

74* Stamen filaments: 0, straight; 1, plicate

75 Anther position with respect to pistil: 0, anthers above stigma; 1, anthers overlapping stigma, 2, anthers just below stigma

76 Style length in relation to ovary length: 0, style longer than ovary; 1, style the same length as ovary; 2, style shorter than ovary

77* Protuberances in the superior part of ovary: 0, absent; 1, present

78 Fusion of the external (exocarp) and internal (endocarp) valves of the fruit at maturity (open capsule): 0, present (external and internal valves fused together); 1, absent (external and internal valves separated from each other)

79 Maximum degree of curvature of fruit valves at maturity (in open capsules): 0, arched valves (extended); 1, spirally recurved valves (twisted once or more times)

80 Intercellular forked junctions at the chalazal tuft of hairs (in mature seed): 0, absent; 1, present

81 Endosperm (in mature seed): 0, absent; 1, present

82 Polyembryony in mature seed: 0, absent; 1, present

83 Endostome type (from Gross 1988 seed classification): 0, *Incarnata* type (h type); 1, *Cotagaitensis* type (m type); 2, *Bryoides* type (n type)

84 Selfing: 0, absent; 1, present

85 Stigma type (from Brown and Gilmartin 1989): 0, conduplicate-spiral (cs); 1, simple-erect (se)

Uninformative characters are marked with an asterisk (*)

Diaphoranthema clade, this character was highly variable and homoplastic within *Diaphoranthema*, including polymorphisms in several species (Table 2; "Appendix 2"; Fig. 2).

The strict consensus tree is highly resolved within the *Diaphoranthema* clade although few groups were supported by jackknife resampling test (Fig. 1). The *Diaphoranthema* clade is divided in two major clades: clade 1 includes four species of the Loliacea aggregate (*T. copynii* E. Gouda, *T. loliacea* Mart. ex Schult. f., *T. spiralipetala* E. Gouda and *T. tricholepis* Baker), while clade 2, which is divided into two subgroups (2A and 2B, JK = 59, Fig. 1), includes all remaining *Diaphoranthema* species and one species of subgen. *Phytarrhiza* (*T. crocata*).

Clade 1 is characterized by leaf blades ≤2 mm wide, sheath margins with trichomes morphologically identical to leaf blade trichomes (being glabrous in *T. tricholepis* and *T. loliacea*), and a "*Bryoides* type" endostome (Fig. 2).

Clade 2 is characterized by many branched stems (a reversal supporting *T. mandonii* Mez and *T. crocata* clade), scapes with two or more internodes unequally developed, showing basal, apical, and/or intermediate bracts (with the exception of *T. minutiflora* that has sunk inflorescences, and *T. capillaris* Ruiz & Pav., *T. retorta* Griseb. ex Baker, *T. usneoides* and *T. virescens* Ruiz & Pav. that present scapes with only one internode and no scape bracts at all), fruits with endocarp and exocarp valves separated from each other at ripening, and polyembryonic seeds. Within this group, there is one reversion to fruits with the endocarp and exocarp fused together at ripening, and four reversions to non-polyembryonic seeds (Fig. 2).

Subclade 2A includes eight species of subgen. *Diaphoranthema*: *T. angulosa* Mez, *T. minutiflora* and all the species belonging to the Rectangula aggregate (*T. aizoides* Mez, *T. brealitoensis* L. Hrom., *T. erecta* Gillies ex Baker, *T. funebris* A. Cast., *T. pedicellata* (Mez) A. Cast., and *T. rectangula* Baker) (Fig. 1). All these species share a leaf blade ≤2 cm long and 1-flowered inflorescences (only three species with up to 2-flowered inflorescences: *T. brealitoensis*, *T. rectangula*, and *T. funebris*) (Fig. 2).

Subclade 2B (JK = 59) includes 17 species of *Diaphoranthema* belonging to the Caliginosa, Capillaris, Myosura, and Recurvata "aggregates" and one species of

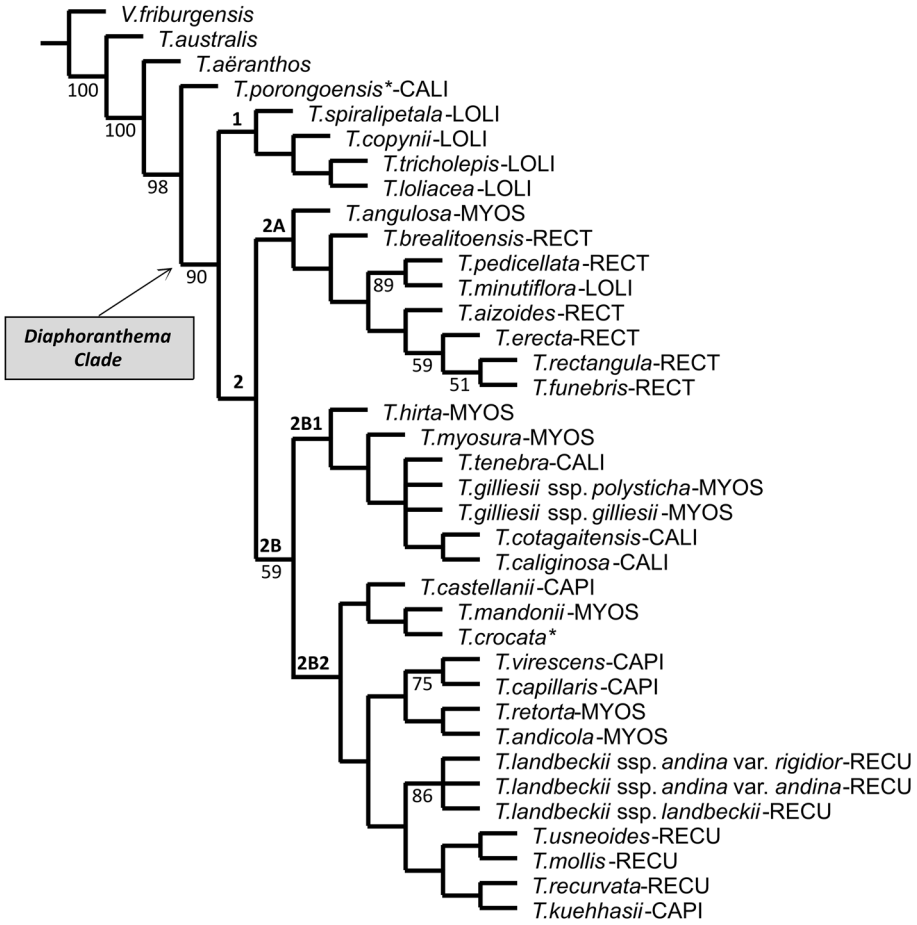


Fig. 1 Strict consensus tree obtained from the 4 most parsimonious trees found during parsimony analysis. *Jackknife values* are shown below branches and numbers in *bold* above branches refer to clades as discussed in the text. The two species of *Tillandsia* subgenus *Phytarrhiza* are marked with an *asterisk* (*) and the *four capital letters* after the species names indicate "aggregates" of *Tillandsia* subgenus *Diaphoranthema*: CALI (Caliginosa), CAPI (Capillaris), LOLI (Loliacea), MYOS (Myosura), RECT (Rectangula), and RECU (Recurvata)

subgen. *Phytarrhiza* (Fig. 1). This clade is supported by distichous phyllotaxy, visible stems internodes, lepidote scape internodes (except for *T. capillaris*, *T. castellanii* L.B. Sm. and *T. usneoides*) and pale yellow petals with some changes to white, yellow, dark violet, brown and polymorphisms in few species (Fig. 2).

Subclade 2B is divided in two groups as well: 2B1 and 2B2 (Fig. 1). Subclade 2B1 includes six species belonging to the Caliginosa and Myosura "aggregates," grouped by having seeds without endosperm and erect petals during anthesis with a reversion to spreading petals in *T. caliginosa* W. Till, *T. cotagaitensis* L.Hrom., and *T. tenebra* L. Hrom. & W. Till (Fig. 2).

Subclade 2B2 comprises species of the Capillaris (3), Myosura (3), Recurvata (4) "aggregates" and one species of subgen. *Phytarrhiza* (*T. crocata*) which are supported by linear leaves and floral bracts with a foliaceous apex (Fig. 2).

Evolutionary trends

Character optimization on a randomly chosen tree showed some interesting trends in the evolution of vegetative and reproductive characters (Fig. 2).

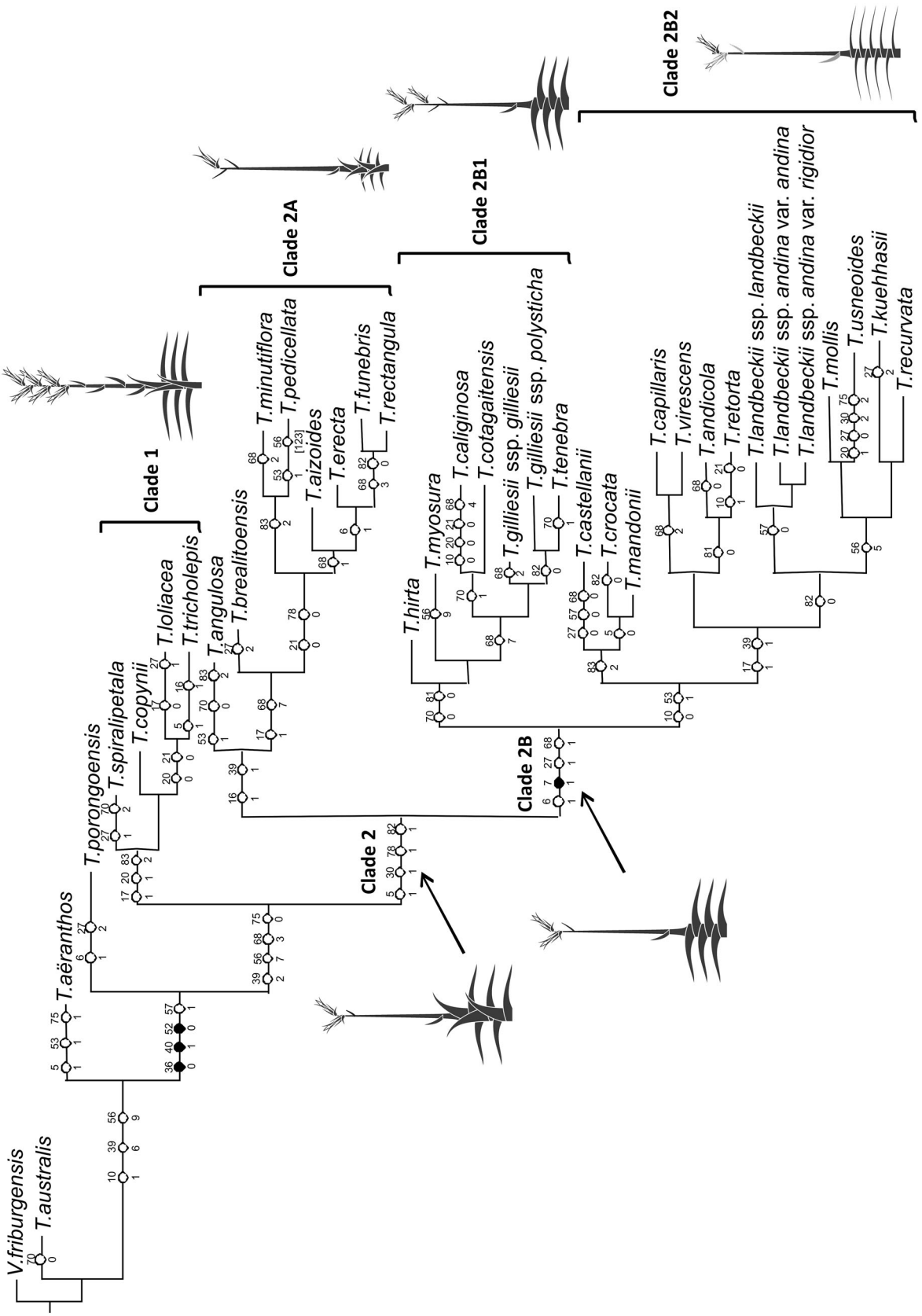
Vegetative characters

Phyllotaxy is the most significant synapomorphy that defines subclade 2B (Fig. 2). The trend within *Diaphoranthema* shows a plesiomorphic polystichous phyllotaxy with distichous phyllotaxy as a derived state. Within *Diaphoranthema*, there is a trend towards an increase in the branch number (clade 2), with stem internodes becoming evident (subclade 2B and some terminal species of subclade 2A), and with leaf blades assuming a linear shape (subclade 2B2) (Fig. 2). In addition, a reduction in the length and width of leaf blades is apparent, being $\leq$2 cm long (subclade 2A) and $\leq$2 mm wide (independently reached in clade 1, part of subclade 2A and part of subclade 2B2) (Fig. 2). Sheaths become glabrous along the margin and abaxial surface (part of clade 1, part of subclade 2A and few species of clade 2) (Fig. 2), with nerves decreasing in number during evolution.

Reproductive characters

Inflorescence

Based on the optimization of characters on one of the most parsimonious trees, a 2-flowered inflorescence is ancestral


V.friburgensis
T.australis
T.aëranthos
T.porongoensis
T.spiralipetala
T.copynii
T.loliacea
T.tricholepis
T.angulosa
T.brealitoensis
T.minutiflora
T.pedicellata
T.aizoides
T.erecta
T.funebris
T.rectangula
T.hirta
T.myosura
T.caligiosa
T.cotagaitensis
T.gilliesii ssp. gilliesii
T.gilliesii ssp. polysticha
T.tenebra
T.castellanii
T.crocata
T.mandonii
T.capillaris
T.virescens
T.andicola
T.retorta
T.landbeckii ssp. landbeckii
T.landbeckii ssp. andina var. andina
T.landbeckii ssp. andina var. rigidior
T.mollis
T.usneoides
T.kuehhasii
T.recurvata
Clade 1
Clade 2
Clade 2A
Clade 2B
Clade 2B1
Clade 2B2

◀ **Fig. 2** Selected common synapomorphies on one of the most parsimonious trees as discussed in the text. *Black circles* represent synapomorphies and *white circles* correspond to homoplastic characters. *Numbers* shown above branches correspond to characters as cited in Table 2, while numbers below branches represent state changes accordingly ("Appendix 2"). Drawings refer to evolutionary trends within *Tillandsia* subgen. *Diaphoranthema* such as changes in phyllotaxy, shape, length and width of leaf blades, and the reduction in flower number and bracts per inflorescence as discussed in the text. *Shaded flower* and *bracts* indicate the variability found in few species

for the *Diaphoranthema* clade (Fig. 2, see character 39). Although flower number is highly variable in most species, subclades 2A and the main subclade within 2B2 are defined by 1-flowered inflorescences. The 1-flowered inflorescence is a homoplastic synapomorphy appearing twice during the evolution of the group (Fig. 2).

Equally developed scape internodes are plesiomorphic, with internodes of similar length and scape bracts evenly spaced along the main axis of the inflorescence. The homologous derived state, only present in clade 2, is having two or more internodes unequally developed and bracts distributed along the scape basally and/or distally and/or intermediate (Fig. 2). An extreme condition of inflorescences having only one scape internode, without scape bracts, has appeared in a few species of the terminal subclade 2B2 (*T. capillaris*, *T. retorta*, *T. usneoides*, and *T. virescens*). Although homoplastic, the petal colour showed a plesiomorphic ochre tone in the *Diaphoranthema* clade, changing to pale yellow petals in subclade 2B, with some changes to white, yellow, dark violet, brown and polymorphisms in few species (Fig. 2, see character 68).

Fruits and seeds

Fruit with the exocarp and the endocarp fused together is plesiomorphic while disaggregation of the external and internal valves of the fruit at ripening appeared once as a novelty for clade 2. A reversion to the ancestral state is only present in a minor subclade within subclade 2A (Fig. 2, see character 78).

Absence of endosperm in mature seeds is a derived character that appeared independently thrice during the evolution of the group. Absence of endosperm at the time of seed dispersal is synapomorphic for subclade 2B1 and for some species of subclade 2B2 (*T. recurvata* and *T. retorta—T. andicola* Gillies ex Baker subclade), (Fig. 2).

Polyembryony and the type of endostome as described by Gross (1988) were also evaluated on the tree. These results showed that polyembryony appeared once in clade 2 with four reversions to the plesiomorphic state of seeds with a single embryo (Fig. 2, see character 82). The type of endostome in *Diaphoranthema* species was homoplastic, and the optimization of this character indicated that the ancestral type for the subgenus is the "*Cotagaitensis* type," while the derived type of endostome would be the "*Bryoides* type," achieved at least five times in the evolution of the group. The "*Bryoides* type" is a synapomorphy for clade 1 and occurs in minor subclades and species of subclade 2A (Fig. 2).

Finally, optimization of selfing in the group showed an unresolved or ambiguous origin within *Diaphoranthema*. However, the presence of selfing is present in the common ancestor of clade 2.

Discussion

A comprehensive phylogenetic hypothesis based on the morphological study revealed *Tillandsia* subgen. *Diaphoranthema* as a paraphyletic group due to the inclusion of at least one species (*T. crocata*) of subgen. *Phytarryza*, rejecting the monophyly suggested by Gilmartin and Brown (1986). However, *Diaphoranthema* might still become a natural group if some species of *Phytarrhiza* are considered within *Diaphoranthema*. In fact, *Tillandsia porongoensis* is placed sister to the *Diaphoranthema* clade in the phylogeny, and Till (1992b), when classifying the subgenus, has already included this species in one of the *Diaphoranthema* "aggregates" (previously in *Phytarrhiza* by Hromadnik and Schneider 1988).

None of Till's six "aggregates" of *Diaphoranthema* resolved as monophyletic in this analysis. Two aggregates resolved as paraphyletic (Rectangula and Recurvata), while four other aggregates (Caliginosa, Capillaris, Loliacea, and Myosura) were polyphyletic. From the optimization of the three morphological diagnostic characters used by Till, phyllotaxy is useful to separate species with polystichous phyllotaxy (plesiomorphic) against species with distichous phyllotaxy (derived) (subclade 2B). Floral bract pubescence and petal colour are homoplastic characters, not conclusive enough to define relationships among species of *Diaphoranthema*. Although ochre and yellowish tones are the most common tones in the group, the colour is very variable and polymorphic within *Diaphoranthema*. Till (1984, 1992b) proposed that the loss of the attractive function of petals and the increasing independence from pollinators are adaptations to extreme habitats where *Diaphoranthema* species grow. In addition, there is a tendency to inconspicuous size of petals which could be related to autogamy during the evolution of *Diaphoranthema*. Except for phyllotaxy, the analysis of morphology revealed characters with relatively high levels of homoplasy; however, phylogenetically useful, homoplastic synapomorphies let us infer patterns of evolution of vegetative and reproductive structures. *Diaphoranthema* is divided into two major clades (clades 1 and 2), and four significant

groups (subclades 2A, 2B, 2B1, and 2B2) supported mainly by vegetative characters and features of the inflorescence related to fruit and seed. Phylogenetically informative vegetative characters mostly reside in the length and general shape of leaf blades and in the nervation and margin indument of leaf sheaths.

As seen from the analysis of character evolution, there is a trend in the reduction of reproductive characters such as flower number per inflorescence, the development and number of scape internodes, and consequently, also in the number and placement of scape bracts. The ability to develop polyembryonic seeds appeared once during the evolution of *Diaphoranthema*, in one of the major clades (clade 2), whereas the sister clade 1 includes species expressing the plesiomorphic condition of a single embryo per seed. Within clade 2, there are reversions to the plesiomorphic state; although we need to search deeper for the presence of polyembryos as they could be present in low frequencies per capsule. Another adaptative strategy in colonizing extreme habitats is the evolution of fruits (capsules) from fused to a derived disaggregated exocarp and endocarp at ripening, which can be seen as an adaptation to dispersion of plumose seeds. The absence of endosperm in mature seeds (subclade 2B1) might indicate that at the moment of seed dispersal, the embryo is well developed and prepared for germination, regardless of whether the seed is polyembryonic or not.

Information about the reproductive system of *Diaphoranthema* species is still fragmentary. As suggested by Culley and Klooster (2007), efforts to analyse their breeding systems should be made by monitoring the flowering phenology and floral production within and among populations over several seasons. Mechanisms, conditions, frequencies of autogamous/cleistogamous flowers, and asexual embryos deserve further studies in *Diaphoranthema*; species of this group should be considered promising models to explore.

Finally, the present study is in agreement with the close relationship found between *Tillandsia* subgenus *Diaphoranthema* and xeric species of subgenus *Phytarrhiza*, and the need of a subgeneric reclassification (Brown and Gilmartin 1984, 1989; Gilmartin and Brown 1986; Bhöme 1988; Gross 1988; Gortan 1991; Halbritter 1992). However, at this moment, taxonomic changes would be premature as good support is still lacking for the majority of clades, and species of *Phytarrhiza*, especially the xeric members, should be included in further analyses to determine whether they may be best placed in subgen. *Diaphoranthema*. Although our preliminary molecular data, based on an incomplete sampling, do not contradict these results, it is still necessary to explore variable molecular markers to build a robust combined phylogenetic hypothesis as the basis of a natural classification for *Diaphoranthema* and related subgenera.

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Appendix 1

List of examined herbarium specimens

Tillandsia aëranthos (Loisel.) L.B. Sm. var. *aëranthos*

ARGENTINA. BUENOS AIRES. Isla Martín García, 06/10/2003, *Hurrell 5330* (SI); Isla Martín García, camino de los Álamos, 08/11/2006, *Hurrell 6467* (SI); Barrancas al Sud, 11/1902, *Venturi 237* (SI); Dpto. Punta Indio. Ruta Prov. 11, entre Punta Piedras y empalme a Ruta Prov. 36, 18/10/2010, *Zuloaga 12154* (SI); CHACO. Dpto. General Güemes. El Colchón, 19/07/2005, *Martínez, G. J. 379* (CORD); CORDOBA. Dpto. Río Segundo. Pilar, 26/10/1986, *Subils 3985* (CORD). BRASIL. SANTA CATARINA. Dpto. Laguna. 28/07/1909, *Dusén 8412* (US). URUGUAY. LAVALLEJA. Cerro Arequita, 03/10/1937, *Legrand 1137* (MVM); MALDONADO. Sierra Animas, 09/1929, *Herter 628 b* (SI); SAN JOSÉ. Ruta 23 km 131, 02/12/2001, *Seijo 2665 b* (CTES).

Tillandsia aizoides Mez

ARGENTINA. CORDOBA. Dpto. Calamuchita. Yacanto, 01/1922, *Vattuone s.n. SI 31918* (SI); Dpto. Ischilín. Unos 10 km al E de Villa Quilino, rumbo a San Pedro Norte, 10/11/1972, *Hunziker 22025* (CORD); Dpto. Punilla. Sierra Grande (Falda E): Ruta Nacional N° 20: Cerro Blanco, 07/04/1973, *Subils 1677* (CORD); Dpto. San Alberto. Mina Clavero, 03/02/1948, *Meyer 13392* (LIL); LA RIOJA. Río Miranda, 26/02/1941, *Burkart 12281* (SI); Dpto. Chilecito. 15/02/1941, *Burkart 12274* (SI); Dpto. General San Martín. E Chepes, km 7 de Ruta Nac. 141, NE Dv. Santa Cruz, 20/04/1986, *Leuenberger 3605* (SI, B); SAN JUAN. Dpto. Valle Fértil. Alrededores del dique del Valle Fértil, 21/04/1995, *Biurrun 4114 a* (SI); 21/04/1995 *Biurrun 4115* (SI); Sierra de Chávez, (40 km al SO de la ciudad de V.Fértil) entre parajes Puesto de la Cumbre y La Rinconada, 30/06/1989, *Biurrun 2883* (SI, IZAC); Río Las Tumanas, 13/04/

1989, *Guaglianone 2452* (SI); San Agustín de Valle Fértil, cerro al borde del lago, 14/12/1987, *Múlgura 698* (SI); SAN LUIS. Dpto. Belgrano. Sierra de las Quijadas, Potrero de la Aguada, 8 km al O de Hualtarán, 06/09/1990, *Haene 1010* (SI); TUCUMÁN. Río Julipao cerca de Timoteo Díaz, 27/05/1949, *Morello 1029* (SI).

Tillandsia andicola Gillies ex Baker

ARGENTINA. CATAMARCA. Cresta de La Chilca (Agua de La Chilca), 03/11/1930, *Schreiter 6415* (LIL); Dpto. Tinogasta. 08/1981, *Hromadnik, H. 7246* (WU); CORDOBA. Capilla del Monte, La Toma, 08/1981, *Hromadnik, H. 7346 (bis)* (WU); LA RIOJA. Dpto. Famatina. 20 km NNW of Famatina along the Ruta Provincial No 11 towards Angulos, 07/02/1990, *Till, W. 5100* (WU); MENDOZA. *Carette s.n. SI 31920* (SI); 01/1926, *Negrete s.n. SI 32184* (SI); Puntilla, 09/11/1913, *Sanzin 110* (SI); Dpto. Capital. Parque Aborigen, 1940, *Minoprio s.n. LIL 113865* (LIL); Dpto. Las Heras. 32 km from Uspallata on new Ruta 7 along Río Mendoza towards Mendoza, 2 km W (above) Guido, 08/01/1995, *Leuenberger 4444* (WU, B, CORD, ZSS); Quebrada de la mina Atala, 08/02/1937, *Ruiz Leal 4448* (LIL); 11/08/1937, *Ruiz Leal 4667* (LIL, CTES); Dpto. Tupungato. 10/1933, *Ragonese, A. E. 10042* (WU, MCNS, CTES).

Tillandsia angulosa Mez

ARGENTINA. LA RIOJA. Dpto. Chilecito. 1981, *Hromadnik, H. 7263* (WU); A la salida de Chilecito (Ruta 40, hacia el N), apenas pasando el Río Los Sarmientos, 13/07/1974, *Hunziker 22575* (CORD); 2 km E Sañogasta, 07/02/1990, *Till, W. 5077* (WU); Dpto. Famatina. Famatina, 1981, *Hromadnik, H. 7252* (WU).

Tillandsia australis Mez

ARGENTINA. BUENOS AIRES (cultivated, unknown locality). Dpto. San Isidro. San Isidro, 04/10/2010, *Donadío 238* (SI); JUJUY. Dpto. Santa Bárbara. Sierra del Centinela, Ojo de Agua, Las Cuevas, 22/04/1975, *Cabrera 26286* (SI); SALTA. Dpto. Candelaria. Camino desde El Tala rumbo a Pampa Grande: a 1 km de Potrerillos, 13/11/1984, *Subils 3603* (CORD, SI); Dpto. Orán. Río Seco, cerca de Río Blanco, bajo de San Andrés, 09/1873, *Lorentz 287* (CORD 2231); Finca San Andrés, Río Seco, 30/10/1997, *Schinini 33091* (CTES); Dpto. Santa Victoria. Parque Nacional Baritú, Lipeo, 04/10/1996, *Hilgert 1523* (MCNS, CORD). TUCUMÁN. Dpto. Tafí. Quebrada de Lules, 02/1920, *Venturi 784* (SI).

Tillandsia brealitoensis L. Hrom.

TIPO. *Hromadnik, H. 7152 b* (WU), ARGENTINA. SALTA. Dpto. Molinos. Valles Calchaquíes, via ad pagum Brealito, 21/07/1981.

Tillandsia caliginosa W. Till

ARGENTINA. N-Argentinien, S-Bolivien, *Rausch 41* (WU); JUJUY. *Muhr s.n. HEID 30925* (HEID); Dpto. Tilcara. Huacalera, 05/02/1959, *Cabrera 13244* (US); Arroyo Queta Cara Chico, 11/03/1957, *Cristóbal 110* (LIL); Pucará, 09/04/1986, *Palací 538 b* (MCNS); Dpto. Tumbaya. Volcán, 1 km N of Tumbaya along the Ruta 9 to Humahuaca, 08/02/1993, *Till, W. 10092* (LIL, WU); SALTA. Seclantás a Brealito, 20/07/1945, *Meyer 9154* (LIL); Dpto. Cafayate. Inter Cafayate et Tolambón, Km 8, 1981, *Irnstorfer 122-124* (WU); TUCUMÁN. Dpto. Tafí. Quebrada de Amaicha, 12/1931, *Schreiter 7663* (NY, LIL); BOLIVIA. COCHABAMBA. Vinto, 11/06/1957, *Jiménez, A. 22* (US); Cochabamba, Plaza Colón, 07/07/1982, *Till, W. 1* (WU); POTOSÍ. 45 km NE Cotagaita, 12/07/1982, *Till, W. 42 a* (WU); TARIJA. San Agustín, cerca de Tarija, 10/06/1873, *Lorentz 969* (GOET, NY, CORD); Cotagaita, Bresadolia, 14/05/1927, *Troll 3369* (B).

Tillandsia capillaris Ruiz & Pav.

ARGENTINA. CATAMARCA. Dpto. Andalgalá. El Alamito, 1600 m s.m., 01/11/2008, *Zuloaga 10563* (SI); Dpto. Ambato. El Rodeo, Ruta Provincial 4, en la entrada al circuito, pasando El Rodeo hacia el N, 1537 m s.m., 14/01/2009, *Donadío 204* (SI, CTES); El Rodeo, Ruta Provincial 4, en la entrada al circuito, pasando El Rodeo hacia el N, 1537 m s.m., 14/01/2009, *Donadío 206* (SI); CÓRDOBA. Dpto. Punilla. Camino a El Cuadrado, 06/10/2009, *Deginani 2053* (SI); JUJUY. Santa Bárbara, De Palma Sola a El Fuerte, ca. 5 km de El Fuerte, 22/02/1985, *Kiesling 5534* (SI); LA RIOJA. Dpto. Famatina. Camino desde la mina La Mejicana hacia Alto Carrizal, 2195 m s.m., 11/01/2009, *Donadío. 168* (SI); Dpto. General Juan Facundo Quiroga. Ruta Prov. 28, desde El Portezuelo hacia Malanzán, 1 km antes de El Salado, 5 km antes de la entrada a Malanzán, 805 m s.m., 12/01/2009, *Donadío 175* (SI); *Donadío 178* (SI); Malanzán, Ruta Provincial 28, saliendo de Malanzán hacia El Portezuelo, sobre vera del arroyo seco, 897 m s.m., 13/01/2009, *Donadío 190* (SI, CTES); SALTA. Dpto. Guachipas. El Guayacán, km 1230, Ruta 38, 8 km N de Alemania, 20/09/1985, *Krapovickas 40276* (CTES). TUCUMÁN. Dpto. Trancas. de Ruta Nac. 9 a Ticucho, 2 km de Ruta 9, 640 m s.m., 30/10/2008, *Zuloaga 10468* (SI).

Tillandsia castellanii L.B. Sm.

ARGENTINA. CATAMARCA. Südlichster Teil der Provinz, 23 km nach Casa de Piedra an der Strabe Recreo-Sierra Brava, 11/10/1987, *Till, H. 87* (WU); Dpto. Andalgalá. 14 km NW of Andalgalá, 4 km N of Choya along the road to Capillitas, 19/02/1993, *Till, W. 10305* (LIL, WU); LA RIOJA. Dpto. General Juan Facundo Quiroga. Northern foot of the Sierra de Porongo, 2 km W of Malanzán, 13/02/1990 *Till, W. 5196* (SI, WU, MO); Along the street from Solca to Malanzán, near the cross to Casangate, 14/02/1990, *Till, W. 5203* (WU); SALTA. Dpto. Cafayate. Taking turnoff 5 km S of Tolombón (plaza). 13 km from Ruta 4 on the road Lara-Hualinchay, 01/12/2003, *Leuenberger 4893* (LIL, B, ZSS).

Tillandsia copynii E. Gouda

TIPO. *Copijn s.n. WU 2796* (WU), BRASIL. MINAS GERAIS. 5 km NE of Paracatú, 12/09/1981.

BRASIL. RIO DE JANEIRO. Dpto. Sao Fidelis. *Leme s.n. WU 1846* (WU); Prope Sao Fidalis, 1989, *Leme s.n. WU 1884* (WU).

Tillandsia cotagaitensis L. Hrom.

TIPO. *Hromadnik, H. 5093* (WU), BOLIVIA. POTOSÍ. Dpto. Nor Chichas. Berge bei Cotagaita, NE of Cotagaita, 20/07/1979.

PARATIPO. *Till, W. 42* (WU), BOLIVIA. POTOSÍ. Dpto. Nor Chichas. 45 km NE Cotagaita and Strabe Camargo-Cotagaita, 12/07/1982.

Tillandsia crocata (E. Morren) N.E. Br.

ARGENTINA. SALTA. Cornissa, 1981, *Markus s.n. WU 3072* (WU); BOLIVIA. TARIJA. 14 km E of Entre Ríos, 15/07/1982, *Till, W. 73* (WU); 27 km Palos Blancos, 16/07/1982, *Till, W. 79 a* (WU); BRASIL. PARANÁ. Just east of the Parque estadual da Vilha Velha, 28/01/1985, *Lewis 1381* (CTES 158514); RIO GRANDE DO SUL. Dpto. São Leopoldo. 15/09/1935, *Rambo s.n. LIL 193425* (LIL); Dpto. Viamão. Morro da grota, acesso pelo Leprosário, 10/06/1980, *Bueno 2614* (HAS, CTES).

Tillandsia erecta Gillies ex Baker

ARGENTINA. LA RIOJA. Cuesta de Miranda, Villa Unión, 1981, *Hromadnik, H. 7260* (WU); Dpto. General Lavalle. 8 km NE of Piedra Pintada along the street from the Cuesta de Miranda to Villa Unión, 08/02/1990, *Till, W. 5112* (SI, WU); MENDOZA. Mendoza, 02/1981, *Irnstorfer s.n. WU 876* (WU); Dpto. Las Heras. 32 km from Uspallata on new Ruta 7 along Río Mendoza towards Mendoza, 2 km W (above) Guido, 08/01/1995, *Leuenberger 4443* (WU); Quebrada de la Mina Atala, 11/08/1937, *Ruiz Leal 4665* (CTES); 08/02/1937, *Ruiz Leal 4449* (LIL); 01/11/1938, *Ruiz Leal 5337* (LIL); Dpto. Luján de Cuyo. Entre Cacheuta y Potrerillos, 19/11/1939, *Ruiz Leal 6435* (LIL).

Tillandsia funebris A. Cast.

ARGENTINA. CATAMARCA. Dpto. Capital. Alrededores de la ciudad de Catamarca: camino a la gruta de la Virgen del Valle, 04/10/1973, *Hunziker 22332* (CORD); SALTA. Dpto. Anta. A 65 km de Las Lajitas, camino a Rivadavia, 22/08/1974, *Saravia Toledo 10367 c* (LIL); Dpto. Cafayate. Abra El Sunchal, Ruta de Cafayate a Salta, 28/07/1990, *Palací 1180* (WU); Dpto. Metán. Cabra Corral, Peñas Azules, 24/10/1986, *Palaú 796* (WU); Dpto. San Carlos. Abra el Sunchal, 08/04/1986, *Palací 548* (MCNS); SAN JUAN. Dpto. Rivadavia. Banda Sur. Cañada Honda, 28/03/1986, *Palací 584* (MCNS); TUCUMÁN. Dpto. Trancas. Vipos, 06/09/1923, *Schreiter 1689* (BA, LIL, B, GH); 30/07/1922, *Schreiter 2362* (WU); BOLIVIA. CHUQUISACA. Dpto. Oropeza. Sucre, Puente Arce, Río Grande, 07/1979, *Hromadnik, H. 5032* (WU); POTOSÍ. Dpto. Linares. 3 km al N de Oron'kota, 22/05/1995, *Kessler 4710* (WU).

Tillandsia gilliesii Baker subsp. *gilliesii*

ARGENTINA. LA PAMPA. Dpto. Lihuel Calel. Sierra de Lihuel Calel, cerro "de la Sociedad," 16/10/1979, *de Azkue 130* (SI, BAB); LA RIOJA. Río Miranda, 26/02/1941, *Burkart 12282* (SI); Dpto. Capital. Ruta Provincial N° 7: Aledaños del barrial de Arauco, 03/10/1995, *Biurrun 4177* (CORD); Ruta 60 (km 1150–1151), unos 11 km antes del cruce con la ruta a Pomán (yendo hacia el oeste), 24/01/1975, *Hunziker 22712* (CORD); MENDOZA. Dpto. Las Heras. En los cerros vecinos a La Ripiera, 22/09/1939, *Ruiz Leal 6256* (LIL); Dpto. San Rafael. Ruta Prov. 179, entre Pto. Agua del Capataz y Punta de Agua, 13/12/2004, *Prina 2694* (CTES); SALTA. Dpto. Cachi. Recta de Tin Tín, cerca del cruce a Tonco, 13/07/1987, *Palací 962* (MCNS); Dpto. Rosario de Lerma. Santa Rosa de Tastil, borde Ruta Nacional 51, km 100, a 40 m. del cementerio, 27/12/1991, *Tolaba 305* (MCNS); SAN JUAN. Dpto. Valle Fértil. Alrededores del dique de Valle Fértil, 21/04/1995, *Biurrun 4119* (SI); San Agustín de Valle Fértil, 23/11/1986, *Haene 467* (SI); SAN LUIS. Dpto. Belgrano. Sierra de las Quijadas, Potrero de la Aguada, 8 km al O de Hualtarán, 06/09/1990, *Haene 999* (SI).

Tillandsia gilliesii Baker subsp. *polysticha* W. Till & L. Hrom.

TIPO. *Hromadnik, H. 7113* (WU), ARGENTINA. JUJUY. Dpto. Humahuaca. Quebrada de Humahuaca, 08/1981.

ARGENTINA. CATAMARCA. Campo del Arenal, 03/1916, *Jörgensen 1772* (SI); Dpto. Andalgalá. Choya, 10 km de Andalgalá, 08/1981, *Hromadnik, H. 7224* (WU); JUJUY. Dpto. Humahuaca. Purmamarca, 10/04/1986, *Palací 539* (MCNS); Dpto. Tilcara. Tilcara, 1981, *Hromadnik, H. 7097* (WU); 10/03/1935, *Schreiter 10049* (LIL, GH); LA RIOJA. Dpto. Chilecito. Chilecito, 1981, *Hromadnik, H. 7265* (WU); SALTA. Dpto. Cachi. Recta de Tintín, 05/04/1987, *Palací 924* (MCNS); Dpto. Cafayate. Valle de Lerma, Cuesta de Cafayate, Obelisk, 24/09/1988, *Till, H. 88* (WU); Dpto. Molinos. Tacuil, 02/03/1988, *Palací 1065* (MCNS); TUCUMÁN. Dpto. Tafí. Amaicha a Tiopunco, 12/1931, *Schreiter 7340* (LIL, GH).

Tillandsia hirta W. Till & L. Hrom.

TIPO. *Hromadnik, H. 5001* (WU), BOLIVIA. COCHABAMBA. Dpto. Punata. Punata near Cochabamba, 08/1979.

ARGENTINA. SALTA. Dpto. Cachi. Recta de Tintín, 05/04/1987, *Palací 923* (WU); BOLIVIA. COCHABAMBA. Dpto. Arani. Above of Arani, 14/03/1999, *Ehlers 991403* (WU); POTOSÍ. Felsen linter Otavi, 02/02/1995, *Hromadnik, L. 19013* (WU); Above of Río Vitichi, 02/02/1995, *Hromadnik, L. 19015 b* (WU).

Tillandsia kuehhasii W. Till

BOLIVIA. Sucre, in via Sucre-Ravelo, prope montem "Cerro Chatajilla," 01/06/1995, *Ehlers 950601* (WU); Chuquisaca/Potosí, in via Sucre-Ravelo, prope montem "Cerro Chatajilla," 1986, *Kühhas s.n. WU 6472* (WU).

Tillandsia landbeckii Philippi subsp. *andina* W. Till var. *andina*

TIPO. *Till, W. 169* (WU), PERÚ. AYACUCHO. Dpto. Lucanas. Tal des Rio San José, 8 km westl. von Lucanas, 10/08/1982.

PERÚ. ANCASH. Dpto. Huaraz. An der Strabe von Huaraz nach Casma, S von Chuchuajirca, 26/07/1982, *Vitek 19-4(2)* (WU); APURIMAC. Dpto. Aymaraes. An der Strabe Chalhuanca-Abancay, 20 km NW von Chalhuanca, 12/08/1982, *Till, W. 176* (WU); CUZCO. Dpto. Calca. Pisac, 02/1949, *Marin 1334* (LIL); Dpto. Quispicanchi. Tal des Rio Vilcanota bei Huancarpay, 13 km N von Andayhuaylillas, 17/08/1982, *Till, W. 200* (WU); LIMA. Dpto. Lima. Coastal desert between La Molina and Cieneguilla, 08/1978, *Hromadnik, H. 4249* (WU).

Tillandsia landbeckii Philippi subsp. *andina* W. Till var. *rigidior*

TIPO. *Till, W. 200* (WU), PERÚ. CUZCO. Dpto. Quispicanchi. Tal des Rio Vilcanota bei Huancarpay, 13 km N von Andayhuaylillas, 17/08/1982.

PARATIPO. *Ehlers s.n. WU 1966* (WU), PERÚ. LIMA. Dpto. Lima. Tal des Río Huaura, "Churin Tal," 1978.

Tillandsia landbeckii Phil. subsp. *landbeckii*

CHILE. I REGIÓN DE TARAPACÁ. Alto Chipana (La Paiquina), 1° a 3° faldeo ladera SW, 31/01/1998, *Pinto s.n. SGO 143010* (SGO); Dpto. Iquique. Cerro Guanacos, 19/08/2001, *Pinto s.n. WU 10991* (WU); Cerros al SO, más o menos 20 km al S de Alto Hospicio, 13/05/1995, *Teillier s.n. SGO 134650* (SGO); III REGIÓN DE ATACAMA. Dpto. Copiapó. Cumbre cuesta La Chicharra, a 25 km de Copiapó, 23/09/1941, *Muñoz-Pizarro 2019* (SGO); Dpto. Huasco. Mpio. Vallenar, 31 km SW of the Panamericana on the gravel road to Mina Algarrobo (=2 km below end of road at entrance to the mine), 07/12/1994, *Eggli 2589* (SGO, B, CONC, ZSS, WU); IV REGIÓN DE COQUIMBO. Ovalle, Las Cardas, 24/09/1950, *Jiles 1870* (LIL); Divide to immediate S of Las Cardas on La Serena. Ovalle road, steep hillside, 03/05/1985, *Wallace 347/85* (SGO); Dpto. Choapa. Illapel, *sin colector s.n. WU 1214* (WU); Dpto. Limarí. Ovalle, Las Cardas, 08/1983, *Hromadnik, H. 11002* (WU); PERÚ. MOQUEGUA. Dpto. Mariscal Nieto. An der Panamericana (km 1192) am SE-Rand des Höhenrückens "Cerro Chupallas" bei der Abzweigung nach llo, 22/08/1982, *Till, W. 224* (WU).

Tillandsia loliacea Mart. ex Schult. f.

ARGENTINA. CORRIENTES. Dpto. San Cosme. Paso de la Patria: Costa Toledo, 25/05/1945, *Meyer 8842* (LIL); FORMOSA. Guaycolec, 08/1919, *Jörgensen 3396 a* (SI); SALTA. Pque. Nac. El Rey. Selva de Mirtaceas, arroyo Los Nobles, 28/01/1981, *Chalukian 1810* (MCNS); Dpto. Anta. J.V. González, Campos del Norte Bañadero de San Francisco, 07/02/1987, *Palací 884* (MCNS); Salta Forestal, 12/08/1985, *Palací 258* (MCNS); A 65 km de Las Lajitas, camino a Rivadavia, 22/08/1974, *Saravia Toledo 10369 c* (LIL); Dpto. Orán. 12/05/1942, *Hunziker 2021* (CORD); Ruta 34, km 1290, 3 km al S del arroyo de los Monos, 11/05/1989, *Novara 8892* (MCNS); Dpto. Rivadavia. Misión La Paz (sobre río Pilcomayo), 01/01/2003, *Scarpa 535* (SI); Dpto. Santa Victoria. Río Lipeo, Parque Nacional Baritú, 19/10/1980, *Zuloaga 1105* (SI); PARAGUAY.

PARAGUARÍ. Cerro Santo Thomas, 02/04/1885, *Kurtz 163 a* (CORD); SAN PEDRO. Primavera, 21/07/1958, *Woolston 1007* (SI).

Tillandsia mandonii Mez

ARGENTINA. SALTA. Cornissa, Cultum in HBV 09/07/1991, *Marcus, E. s.n.* (WU).

BOLIVIA. TARIJA. 14 km E of Entre Ríos, 1500 m epiphytic on tree, 15/07/1982, Cultum in HBV 9.7.91, *Till, W. 73* (WU); 27 km W Palos Blancos, 1430 m s.m. epilythic, 16/07/1982, Cultum in HBV 08/1992, *Till, W. 79* (WU).

Tillandsia minutiflora Donadío

TIPO: *Múlgura, M. E., C. Antuña & E. A. Ulibarri 704* (SI), ARGENTINA, SAN JUAN, Depto. Valle Fértil, San Agustín de Valle Fértil, ladera del cerro, frente camping ACA, 850 m s.m., sobre *Acacia*, 14/XII/1987.

ARGENTINA. BUENOS AIRES. Dpto. Tornquist. Sierra de la Ventana, *Hicken, s.n. SI 31944* (SI); CATAMARCA. Dpto. Ambato. Rodeo-Quebrada del Nogal Marcado, 15/02/1959, *Carenzo 896* (LIL); Dpto. Santa María. 8 km from Santa María towards Tafí del Valle (Tucumán), 23/02/1994, *Leuenberger 4326* (CORD, B, ZSS); La Hoyada, 25/01/1908, *sin colector s.n. SI 31951* (SI); CHACO. Dpto. General Güemes. A 22 km del cruce de la ruta Juana Azurduy en dirección N hacia Nueva Pompeya, 16/11/1990, *Fortunato 1368* (BAB, SI); CORDOBA. Cerro de Totoral, General Mitre, 26/02/1936, *Giardelli 285* (SI). *Kurtz 11990* (SI); Dpto. Calamuchita. Valle de los Reartes, *Castellanos 46* (SI); Dpto. Colón. Jesús María, eastern side of the Sierra Chica, 11 km W of Ascochinga along the street to La Cumbre, below Las Tres Cascadas, 04/02/1990, *Till, W. 5014* (SI); Dpto. Ischilín. Unos 10 km al E de Villa Quilino, rumbo a San Pedro Norte, 10/11/1972, *Hunziker 22017* (CORD); Los Tártagos, 31/03/1944, *O'Donell 667* (LIL); Dpto. Punilla. Cerca de la orilla del Lago San Roque, 09/09/1945, *Hunziker 6079* (CORD); Sierra Chica (Falda O): Cavalango, 25/06/1950, *Hunziker 8410* (CORD); En quebrada vecina al Lago San Roque, 02/09/1945, *Hunziker 6065* (CORD, LIL); Dpto. San Alberto. Villa Cura Brochero, along the street from Mina Clavero to the Cumbre de Achala, 13 km above Niña Paula towards Piedra La Tortuga, 4 km before Pje. Río los Sauces, 16/02/1990, *Till, W. 5220* (SI); Dpto. San Javier, Yacanto, 1925, *Vattuone 1* (SI); LA RIOJA. Dpto. General Juan Facundo Quiroga. Malanzán, subiendo al cerro que se ubica al E del cerro "El Elefante," 12/01/2009, *Donadío 185* (SI); Dpto. San Blas de los Sauces. Quebrada de los Sauces, frente de la casa Ochoa-Huasi, 09/1931, *Hicken s.n. SI 31958* (SI); SALTA. Dpto. Anta. J.V. González. Campos del Norte, 07/02/1987, *Palací 882* (MCNS); Dpto. Cafayate. Cerro Amarillo, en granito al E de Cafayate, 02/06/1987, *Palací 954* (MCNS); Depto. Capital, Parque San Martín, 28/11/1985, *Palací 256* (MCNS); Dpto. Rivadavia. Rivadavia banda sur. Cañada Honda, 28/03/1986, *Palací 551* (MCNS); Misión La Paz (sobre Río Pilcomayo), 01/01/2003, *Scarpa 536* (SI); SAN JUAN. Dpto. Valle Fértil. Alrededores del dique del Valle Fértil, 21/04/1995, *Biurrun 4114* (SI); San Agustín de Valle Fértil, 23/11/1986, *Haene 468* (SI); 20/01/1989, *Haene 788* (SI); SANTIAGO DEL ESTERO. Dpto. Guasayán. De Santa Catalina a Guampacha, 14/04/1979, *Rotman 207* (SI); TUCUMAN. Dpto. Tafí del Valle. Rincón de Quilmes (Valle Calchaquíes), 17/02/1996, *Isasmendi s.n. LIL 600299* (LIL); Dpto. Trancas. Vipos, 08/12/1921, *Schreiter 2029* (LIL); 03/12/1922, *Venturi 1978* (SI); BOLIVIA. CHUQUISACA. Entre Sucre y La Palma, 02/1979, *Ceballos 352* (SI); TARIJA. Cercado. Barrancas, 09/11/1977, *Coro 258/77* (LIL); PARAGUAY. ALTO PARAGUAY. Dpto. Mayor Pedro Lagerenza, Mayor Pedro Lagerenza, 10/04/1978, *Schinini 15008* (CTES, SI).

Tillandsia mollis H. Hrom. & W. Till

TIPO. *Hromadnik, H. 9088* (WU, B, NY, W), BOLIVIA. TARIJA. Near the pass "Cumbre del Cóndor," between Tarija and Narvaez, ca. 25 km W of Narvaez, 15/07/1982.

BOLIVIA. TARIJA. Cumbre del Cóndor, *Till, W. 62* (WU).

Tillandsia myosura Griseb. ex Baker

ARGENTINA. BUENOS AIRES. Delta, Paraná de las Palmas, isla Pflüger, 14/08/1949, *Burkart 17887* (SI); CATAMARCA. Dpto. Andalgalá. Near Villa Vil, 20/02/1993, *Till, W. 10324* (LIL); CORDOBA. Sierra Chica, Agua de Oro, 03/02/1955, *Castellanos 3100* (LIL); Valle de Reartes, 08/02/1919, *Castellanos 105* (SI); Dpto. Capital. Alrededores de la Ciudad de CORDOBA: Hacia el E, camino a Santa Fe, frente a Chacra de la Merced, 29/04/1972, *Hunziker 21988* (CORD); Dpto. Colón. Sierra Chica (falda E): El Diquecito, Piedras Blancas, 09/10/1983, *Di Fulvio 750* (CORD); Dpto. Ischilín. Unos 10 km al E de Villa Quilino, rumbo a San Pedro Norte, 10/11/1972, *Hunziker 22022* (CORD); Dpto. Punilla. Sierra Grande, faldeos orientales: Cuesta blanca, hacia el oeste, 10/07/1966, *Hunziker 18847* (CORD); LA RIOJA. Dpto. Famatina. Guanchín, 24/12/1928, *Venturi 8096* (SI); SALTA. Dpto. Caldera. Cuesta del Gallinato, 16 km N de Salta, 20/03/1977, *Krapovickas 30301* (SI); Dpto. Guachipas. La Viña, Ruta 68, km 103, 20/09/1985, *Palací 246* (MCNS); SAN JUAN. Dpto. Valle Fértil. Alrededores del dique de Valle Fértil, 21/04/1995, *Biurrun 4117* (SI); SAN LUIS.

San Luis a cañada El Balde, 01/10/1968, *Burkart 27142* (SI); TUCUMÁN. Dpto. Trancas. Vipos, 22/10/1921, *Venturi 1371* (SI); Sierra de la Candelaria, 06/08/1924, *Venturi 3520* (SI); Tapia, 22/11/1920, *Venturi 1178* (SI); De Ruta Nac. 9 a Ticucho, 2 km de Ruta 9, 30/10/2008, *Zuloaga 10472* (SI).

Tillandsia pedicellata (Mez) A. Cast.

ARGENTINA. BUENOS AIRES. Depto. Tornquist, El Coral, 20-III-1948, *Fabris 27* (SI). CATAMARCA. Depto. Ambato, Ruta Prov. 1, de Buena Vista a Singuil, 02-XI-2008, *Zuloaga, 10580* (SI); Depto. Andalgalá, Cuesta de la Chilca, 10-XI-2008, *Slanis 49 11-2008* (SI); Depto. Tinogasta, La Mesada 73,5 km N of Fiambalá on Ruta Provincial 43, 14-XII-1998, *Leuenberger 4695* (CORD, B, ZSS). CORDOBA. II/1925, *Lossen 189* (SI); Achala, Sierra Grande, 28-I-1920, *Castellanos s.n. SI 31959* (SI); Depto. Punilla, San Esteban, 09-I-1938, *Nicora 1697* (SI); Depto. San Alberto, Villa Cura Brochero, along the street from Mina Clavero to the Cumbre de Achala, 13 km above Niña Paula towards Piedra La Tortuga, 4 km before Pje. Río Los Sauces, 16-II-1990, *Till 5217* (SI); Depto. San Javier, Yacanto, 1925, *Vattuone 1a* (SI). JUJUY. El Volcán, 10-VII-1922, *Castellanos s.n. SI 31955* (SI); Depto. Humahuaca, N de Humahuaca, 03-I-1992, *Kiesling 8129* (SI); Depto. Tilcara, Maimará, Ruta 9, 30-III-1993, *Deginani 320* (SI); Pucará, 10-IV-1986, *Palací 545* (MCNS); Tilcara, 20-IX-1985, *Palací 188* (MCNS); Tilcara, Cerros a 1 km al W de la Ruta No 9, 28-XII-1989, *Novara 9226* (MCNS); Depto. Tumbaya, Quebrada de Humahuaca, Laguna de Volcán, 07-XI-1974, *Subils 2030* (CORD). LA PAMPA. Depto. Lihuel Calel, Sierra de Lihuel Calel, Cerro "de la Sociedad," ladera N, 16-X-1979, *de Azkue s.n. BAB 91263* (SI). LA RIOJA. Pelagio B. Luna, Sierra Velazco, rancho La Esperanza., 15-IV-1951, *Sparre 8689* (LIL); Depto. Capital, Estribación oriental de la Sierra de Velasco, La Lancha, camino a El Cantadero, 04-III-1944, *A. T. Hunziker 5031* (CORD); Depto. Coronel Felipe Varela, Cuesta de Miranda, Ruta Nac. 40, de Villa Unión a Chilecito, 09-I-2009, *Donadío 79* (SI); Río Miranda, 26-II-1941, *Burkart 12278* (SI); Ruta Nacional 40, de Guandacol a Chilecito, Cuesta de Miranda, 12-II-2011, *Zuloaga 12817* (SI); Depto. General Belgrano, Cumbre de la Sierra de Olta, 08-II-1940, *Castellanos 33503* (LIL); Depto. General Juan Facundo Quiroga, Northern foot of the Sierra de Porongo, ca. 4 km E of Malanzán, 13-II-1990, *Till 5181* (SI); Ruta Prov. 28, desde El Portezuelo hacia Malanzán, 12-I-2009, *Donadío 176* (SI). MENDOZA. *Carette s.n. SI 31946* (SI); Depto. Luján de Cuyo, Crucecita, XII-1906, *Carette s.n. SI 31947* (SI); Lunlunta, 24-II-1936, *Ruiz Leal 3820* (LIL); Potrerillos, XI-1912, *Sanzin 30* (SI); Depto. San Rafael, 31 km W de 25 de Mayo, 03-III-1989, *Leuenberger 3958* (SI, B). RÍO NEGRO. Dpto. San Antonio, Sierra Grande about 100 km S of San Antonio, 20-XII-1938, *Eyerdam 23534* (SI). SALTA. Depto. Cachi, Recta de Tintín, 05-IV-1987, *Palací 925* (MCNS); Depto. Cafayate, Cerro Amarillo, al E de Cafayate, 02-IV-1987, *Palací 955* (MCNS); Depto. Capital, Quebrada de San Lorenzo, 20-IX-1972, *Subils 1450* (CORD); Depto. La Poma, Ruta Nac. 40, El Cajón, *Zuloaga 11243* (SI); Depto. Los Andes, San Antonio de los Cobres, 18-II-1986, *Palací 387* (MCNS); Depto. Molinos, Tacuil, 02-IV-1988, *Palací 1112* (MCNS); Tacuil, 02-IV-1988, *Palací 1113* (MCNS); Depto. Rosario de Lerma, a 3 km de el Gólgota, rumbo a Chorrillos, Quebrada del Toro, 11-III-1984, *Toledo 947* (MCNS); Santa Rosa de Tastil, Quebrada del Toro, km 97, 04-I-1990, *Palací 1129* (MCNS). SAN JUAN. Depto. Angaco, Sierra de Pie de Palo, subiendo por el camino al Mogote Los Corralitos, en la Quebrada del Molle, 28-XI-1980, *A. T. Hunziker 23694* (CORD); Depto. Jáchal, La Ciénaga. Ruta Provincial 491, de Rodeo hacia Huaco, 06-I-2009, *Donadío 52* (SI); Depto. Valle Fértil, alrededores del dique del Valle Fértil, 21-IV-1995, *Biurrun 4114 b* (SI); Astica, 14-XI-1986, *Haene 175* (SI); Cerro Morado, 28-V-1959, *Cuezzo 2966* (LIL); Laderas de cerros Sa. de Elizondo, 16-XII-1987, *Múlgura 801* (SI); Depto. Zonda, El Palque, O de Pachaco, 14-I-987, *Kiesling 6767* (SI). BOLIVIA. LA PAZ. Murillo, Hacienda Huajchilla, 18 km SE of La Paz (La Florida), along the Río La Paz, 07-IX-1986, *Solomon 15577* (SI, MO).

Tillandsia porongoensis L. Hrom. & P. Schneid.

TIPO. *Hromadnik, H. 7321 a* (WU), ARGENTINA. LA RIOJA. Dpto. General Juan Facundo Quiroga. Sierra de Porongo prope Malanzán, 07/08/1981.

Tillandsia rectangula Baker

Localidad dudosa, *Kurtz 11989* (SI); ARGENTINA. CATAMARCA. Dpto. Santa María. 8 km from Santa María towards Tafí del Valle (Tucumán), 23/02/1994, *Leuenberger 4325* (CORD, B, ZSS, WU); CORDOBA. 1919, *Castellanos 634* (SI); 02/1925, *Lossen 190* (SI); Salinas Grandes, km 907, 21/11/1944, *Soriano 758* (SI); Dpto. Pocho. Sierra de Pocho: En la base de la falda oeste, Ruta 20 (km 881–882), 21/01/1974, *Hunziker 22491* (CORD); Dpto. Tulumba. Ruta Nacional N° 9: Entre San José de la Dormida y Rayo Cortado, 10/02/1955, *Hunziker 10659* (CORD); Cerro Colorado, 02/11/1977, *Subils 2389* (CORD); LA RIOJA. Dpto. General Belgrano. Ruta Nac. 38, entre Chamical y Chañar, campo experimental Las Vizcacheras, 05/01/1981, *Biurrun 1702* (SI); Dpto. General San Martín. E Chepes, km 7 de Ruta Nac. 141, NE Dv. Santa Cruz, 20/04/1986, *Leuenberger 3607* (SI, B); 20/04/

1986, *Leuenberger 3602* (SI, B); SALTA. Entre San Tadeo y V. del Norte, 29/08/1957, *Cuezzo 668* (LIL); Dpto. Anta, J. V. González, Campos del Norte, Bañadero de San Francisco, 07/02/1987, *Palací 883* (MCNS); SAN LUIS. Dpto. Belgrano. Sierra de las Quijadas, Potrero de la Aguada, 8 km al Oeste de Hualtarán, 06/09/1990, *Haene 996* (SI); 06/09/1990, *Haene 998* (SI); Dpto. Junín. Bajo de Velis, 23/01/1895, *Kurtz 8472* (SI).

Tillandsia recurvata (L.) L.

ARGENTINA. BUENOS AIRES. Las Palmas, 02/09/1952, *Boelcke 6353* (SI); Delta, Paraná de las Palmas, isla Pflüger, 14/08/1949, *Burkart 17888* (SI); Delta. Río Barca Grande, 01/1931, *Burkart 3727* (SI); Paraná Miní, 11/08/1956, *Burkart 20064* (SI); Arroyo Paycarabí, entre Paraná de las Palmas y Durazno, Delta, 16/04/1954, *Calderón 465* (SI). Delta Paraná, 02/1936, *Troncoso 186* (SI); Dpto. San Isidro. San Isidro, 22/03/1940, *Cabrera 9780* (SI); Dpto. Tigre. Pueblo, 20/09/1931, *Burkart 3864* (SI); Dpto. Zárate. Puerto Terminal Las Palmas; Paraná de las Palmas km 123, 13/09/2003, *Hurrell 5193* (SI); CHACO. *Asp 28* (SI); *Meyer 3* (SI); CORRIENTES. Dpto. Curuzú Cuatiá. Ruta 126, Río Mocoretá, monte marginal, 21/10/1971, *Burkart 28541* (SI); Dpto. Ituzaingó, Ruta 12, aprox. 45 km E de Ituzaingó, Prefectura, 13/12/1976, *Giberti 6 (*SI); Dpto. Mburucuyá. Estancia Santa Teresa, 24/07/1976, *Krapovickas 29589* (SI); Dpto. Monte Caseros. Estancia La Polota, cerca de la estación Libertad, orillas del Timboi, 01/09/1957, *Nicora 5916* (SI); FORMOSA. 08/1919, *Jörgensen 3395* (SI); Dpto. Guaycolec, 08/1919, *Jörgensen 3396 b* (SI); JUJUY. Dpto. Dr. Manuel Belgrano. Camino al Cucho: río Los Blancos, 19/03/1979, *Cabrera 30213* (SI); Dpto. Santa Bárbara. De Palma Sola a El Fuerte, ca. 5 km de El Fuerte, 22/02/1985, *Kiesling 5534* (SI); SALTA. Dpto. Anta. Parque Nacional El Rey: Arroyo El Arenal, 17/09/1984, *Ezcurra 461* (SI); Dpto. La Caldera. Estancia La Despensa, a 25 km de La Caldera, 16/04/1942, *Hunziker 1591* (SI); TUCUMÁN. Dpto. Capital. El Duraznito, 06/01/1924, *Venturi 2797* (SI); BOLIVIA. TARIJA. Dpto. Chaco, 2 km W de Saladillo (cabeceras del río Carapari), 08/04/1977, *Krapovickas 31049* (SI); UNITED STATES OF AMERICA. TEXAS. Hays Co., junction of Hwys. 12 and 226, NW side of San Marcos, 09/10/1993, *Nee 44051 a* (SI).

Tillandsia retorta Griseb. ex Baker

ARGENTINA. CORDOBA. *Castellanos 45* (SI 32121); Dpto. Calamuchita. Sierra de Los Cóndores, entre Embalse de Río Tercero y Berrotarán, 01/11/1981, *Hunziker 24107* (CORD); Yacanto, *Vattuone 75* (SI 32194); Dpto. Colón. Lomas entre la Estancia La Paz y Ascohinga, a ± 3 km de Ascochinga, 25/10/1981, *Subils 2966* (CORD); Dpto. Punilla. Sierra Chica (Falda O): Cavalango, al sudeste de Tanti, 25/06/1950, *Hunziker 8406* (CORD); Dpto. Río Seco. Ruta Prov. No 10: Eufrasio Loza, próximo a las vías del ferrocarril, 20/10/1984, *Subils 3319* (CORD); LA RIOJA. Dpto. General Belgrano. Sierra de los Quiroga: La Huerta, 30/11/1984, *Subils 4346 a* (CORD); Dpto. General Juan Facundo Quiroga. Northern foot of the Sierra de Porongo, c. 1 km W of Loma Larga, 13/02/1990, *Till, W. 5187* (SI); Dpto. General Ortiz de Ocampo. Sierra de Abajo, paraje llamado "Río Grande," entre El Quemado y las cortaderas, 09/05/1995, *Biurrun 4128* (SI); SAN JUAN. Dpto. Valle Fértil. Sierra de Chávez, (40 km al SO de la ciudad de V.Fértil) entre parajes "Puesto de la Cumbre" y "La Rinconada," sobre la quebrada que conduce al último, 30/06/1989, *Biurrun 2882* (SI); SAN LUIS. Dpto. Chacabuco. 7 km al S de Tilisarao, 12/12/1987, *Múlgura 649* (SI); Dpto. Junín. Pie de la Sierra de Comechingones, al E de Carpintería, 18/12/2000, *Leuenberger 4765* (SI, B); TUCUMAN. Dpto. Trancas. Tapia, 12/10/1920, *Venturi 1029* (SI); Camino Nacional frente a Vipos, 20/08/1923, *Venturi 2492* (SI); Tapia, 22/11/1920, *Venturi 1178 a* (SI); Sierra de la Candelaria, 26/09/1924, *Venturi 3522* (SI).

Tillandsia spiralipetala E. Gouda

BOLIVIA. CHUQUISACA. Dpto. Hernando Siles. 48 km de Monteagudo a Padilla, 28/06/1995, *Kessler 4886* (WU); LA PAZ. Dpto. Bautista Saavedra. De Camata 3 km hacia Charazani, 27/06/1997, *Kessler 10374* (WU); PERÚ. AMAZONAS. Tal des Río Utcubamba, 07/1976, *Hromadnik, H. 2141* (WU); JUNIN. Dpto. Tarma. San Ramón, 07/1976, *Hromadnik, H. 2046* (WU).

Tillandsia tenebra L. Hrom. & W. Till

TIPO. *Hromadnik, H. 7275* (WU), ARGENTINA. LA RIOJA. Dpto. Chilecito. Ad pedem montium Sierras Pampeanas prope Chilecito, 28/07/1981.

ARGENTINA. CATAMARCA. Dpto. Belén. 6 km from Belén on Ruta 40 towards Hualfin into the Quebrada de Belén, 21/02/1994, *Leuenberger 4304* (CORD, B, ZSS, WU); LA RIOJA. Sierra de Malanzán, Loma Larga, *Neuhuber 1-1117/4152* (WU); Dpto. Chilecito. Near Chilecito, 01/08/1981, *Hromadnik, H. 7274* (WU); Dpto. Coronel Felipe Varela. East of Villa Unión, 31/07/1981, *Hromadnik, H. 7261* (WU).

Tillandsia tricholepis Baker

ARGENTINA. CATAMARCA. Depto. Ancasti, Alrededores del dique de Ipizca, 17-XI-1984, *Subils 3682* (CORD); Depto. Paclin, El Saltón, en el Arroyito de los

Ovejeros, frente al Lago Sumampa (sobre el camino entre Ruta 67 y La Viña), 20-IX-1970, *A. T. Hunziker 20665* (CORD); 11 km from La Merced on road over the Cuesta del Totoral towards La Viña, on the La Viña side of pass, 24-II-1994, *Leuenberger 4341* (CORD). CHACO. *Meyer 2* (SI); Depto. San Fernando, Isla Soto, 18-XII-1974, *Burkart 30778* (SI). CORDOBA. CORDOBA, 1919, *Castellanos 670* (SI); Depto. Colón, Jesús María, en muros de la Iglesia Colonial, 21-VII-1942, *Burkart 12916* (SI); Jesús María, muro de la Iglesia San Isidro, II-1936, *Giardelli 284* (SI); La Calera, El Diquecito, 12-X-1960, *Ariza Espinar 981* (CORD);, Depto. Río Primero, Laguna de los Ludueña, entre Río Primero y Santa Rosa, 20-IV-1985, *Subils 3806* (CORD); Depto. Río Seco, Ruta Provincial 10, Sebastián Elcano, 20-X-1984, *Subils 3313* (CORD). CORRIENTES. Depto. Capital, Corrientes, 11-XI-1934, *Burkart 6897* (SI), Depto. Mburucuyá, Lomas de Vallejo, 06-X-1954, *Burkart 19312* (SI). FORMOSA. Formosa, XII-1918, *Jörgensen 2800* (SI). JUJUY. Depto. Dr. Manuel Belgrano, Abra de Las Lajitas, 14-II-1995, *Deginani 811* (SI); Camino al Cucho, Río Los Blancos, 19-III-1979, *Cabrera 30212* (SI); Depto. Ledesma, Camino de Fraile pintado a El Aibal, 12-XI-1992, *Kiesling 8178* (SI); Ledesma, 23-II-1940, *Burkart 11431* (SI); "Picada al Arroyo Negrito" Puesto, Parque Nacional Calilegua, 19-VIII-1985, *Iudica 36* (SI); Depto. San Pedro, Moralito, 12-VII-1922, *Castellanos s.n. SI 32228* (SI); Ruta Prov. 56, 2 km de la Villa Turística de Palpalá camino a La Mendieta, 13-XII-1998, *Morrone 3318* (SI); Depto. Santa Bárbara, Alrededores de Finca La Campana, 12-XII-1998, *Ahumada 8953* (SI); De Santa Clara a Abra de los Morteros, 21-XI-1980, *Cabrera 32194* (SI). MISIONES. Depto. General Manuel Belgrano, Deseado, Chacra de Carlos Macoviak, antigua Ruta 19, ca. 2000 m de la Ruta 101, 16-XII-1997, *Múlgura de Romero 1917* (SI). SALTA. Mojotoro, 17-XI-1942, *Burkart 13012* (SI); Parque Nacional El Rey, 10-VII-1979, *Chalukian 871* (MCNS); Selva basal, 10-VI-1981, *Chalukian 1405* (MCNS); Embalse, 25-I-1979, *Rumiz 489 b* (MCNS); Depto. Anta, Coronel Olleros, 21-IX-1957, *Meyer 21177* (LIL); Ruta provincial no 20: Parque Nacional El Rey, proximidades de Finca del Rey, 25-IX-1972, *Subils 1459* (CORD); Dpto. Capital. Ciudad de Salta, 18-V-2003, *Novara 11964* (MCNS); Depto. Guachipas, Alemania, camino a Cafayate, km 80, 07-I-1990, *Palací 1138* (MCNS); Depto. La Viña, Dique Puerta de Díaz, 5 km al oeste de Coronel Moldes, 04-XII-1983, *Novara 4149* (CORD); Depto. Orán, Orán viejo, 16-I-1957, *Burkart 20310* (SI); Pichanal, 14-XI-1913, *Rodriguez 1119* (SI); Ruta Prov. 132, 29 km de la Ruta Nac. 50 camino a Santa María, pasando 6 km la Finca Totó, 16-XII-1998, *Morrone 3435* (SI); Ruta 34, km 1290, 3 km al S del arroyo de los Monos, 11-V-1989, *Novara 8893* (MCNS); Urundel, 13-II-1944, *Soriano 718* (SI); Depto. Rivadavia, Rivadavia banda sur, Cañada Honda, 28-III-1986, *Palací 550* (MCNS); Depto. Rosario de la Frontera, La Hollada, 06-XI-1985, *Palací 201* (MCNS); Termas VI-1931, *Hicken s.n. SI 32243* (SI). SAN JUAN. Depto. Capital, Capital, III-1931, *Correa* s.*n. SI 32240* (SI). SANTA FE. Depto. Castellanos, Colonia Margarita, I-1905, *Wolfhügel s.n. SI 32230* (SI). SANTIAGO DEL ESTERO. Depto. Choya, Sierra de Guasayán, Quebrada de Moquijata, 12-X-1989, *Ulibarri 1690* (SI); Depto. Guasayán, De Santa Catalina a Guampacha, 14-IV-1979, *Rotman, 207 a* (SI); Sierra de Guasayán, Quebrada de Conzo, 21-III-1989, *Ulibarri 1648* (SI); TUCUMAN. Depto. Capital, El Duraznito, 06-I-1924, *Venturi 2799* (SI); Depto. Leales, Chañar Pozo, XII-1919, *Venturi 738* (SI); Depto. Lules, 15-VII-1911, *Lizer 20* (SI); Depto. Trancas, De Ruta Nac. 9 a Ticucho, 2 km de Ruta 9, 30-X-2008, *Zuloaga 10475* (SI). BOLIVIA. SANTA CRUZ. Florida, easternmost rocky foothills of the Andes, abobe narrowest point at La Angostura on highway from Santa Cruz to Samaipata, 9-I-1998, *Nee 47868-a* (SI); Vallegrande, Vallegrande, Estrada Mataral-Vallegrande, 6 km S de Mataral, 10-XII-2002, *Forzza 2319* (SI, RB, CTES, LPB, MBM); TARIJA. Gran Chaco, 30 km N de Yacuiba, Campo de la Tapia, cerca de Caiza, 2 km E de la ruta a Villa Montes, 7-IV-1977, *Krapovickas 30975* (SI). BRASIL. *s.c. s.n. SI 32224* (SI); MATTO GROSSO, Corumbá, 18-III-1906, *Etchichury 52* (SI).

Tillandsia usneoides (L.) L.

ARGENTINA. BUENOS AIRES. Delta del Paraná: Puerto de las Palmas y Carabelas, 03/1941, *Repetto s.n. SI 63051* (SI); CORDOBA. Pampa de Achala, 02/04/1944, *Rentzell 15190* (SI); JUJUY. Dpto. Valle Grande. Camino a Alto Calilegua, 03/01/1978, *Kiesling 1533* (SI); SALTA. Dpto. Santa Victoria. Margen derecha del Río Lipeo, camino a Campo Grande, 30/09/1998, *Ahumada 8322* (SI); TUCUMÁN. *Lorentz s.n. SI 32248* (SI); Dpto. Tafí. Quebrada de Lules, 05/1920, *Venturi 858* (SI); Dpto. Tafí del Valle. El Churqui, 12/1914, *Castillón 3712* (LIL); 12/1914, *Castillón s.n. LIL 36864* (LIL); BRASIL. RIO GRANDE DO SUL. Dpto. São Francisco de Paula. Brasilia, Tainhas, 08/01/1951, *Rambo 9727* (SI, PACA); CHILE. V REGIÓN DE VALPARAÍSO. Dpto. Petorca. Zapallar, Higuera, 25/03/1917, *Behn s.n. SI 32271* (SI); COLOMBIA. BOYACA. Chuquinquira, 07/1909, *Apollinaire 68* (SI); UNITED STATES OF AMERICA. ARKANSAS. Portland, Ashley County, 16/10/1937, *Palmer 44272* (SI); FLORIDA. Near Jacksonville, *Curtiss 2850* (SI); Duval Co., 24/05/1902, *Fredholm 5231* (SI); Altamonte Springs, 18/03/1959, *Schaller 1818* (SI); TEXAS. Hays Co., junction of Hwys. 12 and 226, NW side of San Marcos, 09/10/1993, *Nee 44051* (SI); MEXICO. VERACRUZ. Mun. Ozuluama, along hwy. Mex. 180, 5 km (by air) NE of Ozuluama, 18/08/1986, *Nee 32763* (SI, NY).

Tillandsia virescens Ruiz & Pav.

ARGENTINA. CATAMARCA. Dpto. Ambato. El Rodeo, Ruta Provincial 4, en la entrada al circuito, pasando El Rodeo hacia el N, 1537 m s.m., 14/01/2009, *Donadío 200* (SI, CTES); CÓRDOBA. Dpto. Punilla. Huerta Grande, subida a Sierras Chicas, 07/10/2009, *Zuloaga 11288* (SI); Ruta Prov. 28, Pampa de San Luís, de Los Gigantes a Taninga, 2000 m s.m., 08/10/2009, *Zuloaga 11343* (SI); LA RIOJA. Dpto. Famatina, Camino a la mina La Mejicana, 1223 m s.m., 11/01/2009, *Donadío 130* (SI); Camino desde la mina La Mejicana hacia Alto Carrizal, 2195 m s.m., 11/01/2009, *Donadío 167* (SI).

BOLIVIA. LA PAZ. Manco Kapac, Lago Titicaca, Isla del Sol, Templo del Sol, sobre las paredes de rocas, 3860 m s.m., 10/04/2011, *Nicola 175* (SI); Copacabana, sobre rocas al costado de la escalinata hacia la Horca del Inca, 4130 m s.m., 11/04/2011, *Nicola 176* (SI).

Vriesea friburgensis Mez var. *tucumanensis* (Mez) L.B. Sm.

ARGENTINA. MISIONES. Dpto. Guaraní. Orillas del Arroyo Yabotí, ca. puente, ruta proyectada 102, 08/05/1999, *Deginani 1200* (SI); Dpto. Iguazú. Parque Nacional Iguazú, sector Cataratas, pasarela superior, 08/04/2008, *Múlgura 4425* (SI), Dpto. San Pedro. Cruzando 2 km el puente sobre el Arroyo Yabotí hacia los obrajes, ruta proyectada 102, 10/05/1999, *Deginani 1233* (SI); SALTA. Dpto. Orán. Ruta Prov. 18, 55 km del desvío de la Ruta Nac. 50 camino a San Andrés, Sierra Baja de Orán, Río Maroma, 15/12/1998, *Morrone 3419* (SI); Cortaderia, a 15 km del desvío de la Ruta Prov. 18 camino a Isla de Cañas, 22/11/2001, *Morrone 3949* (SI); Finca San Andrés, Casavindo, Río San Andrés, 29/10/1997, *Schinini 32959* (CTES); Dpto. Santa Victoria. Camino de Los Toldos a Lipeo, desvío hacia aguas termales, 29/09/1998, *Ahumada 8225* (SI); Margen derecha del Río Lipeo, camino a Campo Grande, 30/09/1998, *Ahumada 8295* (SI); TUCUMÁN. Dpto. Monteros. Quebrada de Los Sosa, camino a Tafí del Valle, Ruta Provincial 307, 02/02/2005, *Zuloaga 8427* (SI); Dpto. Yerba Buena. Horco Molle, Ciudad Universitaria, Parque Sierra de San Javier, 27/02/2008, *Pensiero 7590* (SF, SI).

Appendix 2

See Table 3.

Table 3 Morphological data matrix with 37 taxons and 85 total characters

	1	2*	3	4	5	6	7	8	9	10	11	12	13	14	15
V. friburgensis	1	0	0	1	0	0	0	1	0	0	1	1	0	0	0
T. aëranthos	1	0	1	1	1	0	0	1	1	1	1	0	1	0	0
T. aizoides	1	0	1	1	1	0	0	[01]	1	1	0	0	1	0	0
T. andicola	1	0	1	[12]	1	1	1	1	1	0	1	0	2	0	0
T. angulosa	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0
T. australis	[12]	0	0	1	0	0	0	1	0	0	1	1	0	0	0
T. brealitoensis	1	0	1	1	?	0	0	0	1	1	0	0	1	0	0
T. caliginosa	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0
T. capillaris	[12]	0	1	[01]	1	1	1	[01]	1	0	[01]	0	2	0	0
T. castellanii	1	0	1	1	1	1	1	1	1	0	1	0	2	0	0
T. copynii	1	0	1	1	?	0	0	1	1	1	1	0	1	0	0
T. cotagaitensis	1	0	1	1	?	1	1	1	1	1	1	0	1	0	0
T. crocata	2	0	1	1	0	1	1	1	1	0	1	0	1	0	0
T. erecta	[12]	0	1	1	1	1	0	[01]	1	1	0	0	1	0	1
T. funebris	[12]	0	1	1	1	1	0	1	1	1	1	0	1	0	1
T. gilliesii ssp. *gilliesii*	1	0	1	[01]	1	1	1	1	1	1	0	0	1	0	0
T. gilliesii ssp. *polysticha*	1	0	1	1	1	1	[01]	1	1	1	0	0	1	0	0
T. hirta	1	0	1	1	1	1	1	1	1	1	1	0	2	0	0
T. kuehhasii	2	0	1	2	1	1	1	0	1	0	1	0	1	0	0
T. landbeckii ssp. *landbeckii*	[01]	0	1	[12]	1	1	[01]	1	1	0	1	0	1	1	0
T. landbeckii ssp. *andina* var. *andina*	[12]	0	1	1	1	1	1	1	1	0	1	0	1	1	0
T. landbeckii ssp. *andina* var. *rigidior*	[12]	?	1	1	1	1	1	1	1	0	1	0	1	1	0
T. loliacea	[12]	0	1	1	0	0	0	[01]	1	1	1	0	1	0	0
T. mandonii	[12]	0	1	1	0	1	1	1	1	0	1	0	1	0	0

Table 3 continued

	1	2*	3	4	5	6	7	8	9	10	11	12	13	14	15
T. minutiflora	[12]	[01]	1	0	1	0	0	0	1	1	1	0	1	0	0
T. mollis	2	1	1	2	1	1	1	1	1	0	1	0	2	0	0
T. myosura	1	0	1	1	1	1	1	1	1	1	1	0	1	0	0
T. pedicellata	1	[01]	1	[01]	1	0	0	0	1	1	0	0	1	0	1
T. porongoensis	2	0	1	1	0	1	0	[12]	1	1	0	0	1	0	0
T. rectangula	1	0	1	[01]	1	1	0	1	1	1	1	0	1	0	1
T. recurvata	1	0	1	0	1	1	1	1	1	0	1	0	1	1	0
T. retorta	1	0	1	1	1	1	1	1	1	1	0	0	2	0	0
T. spiralipetala	1	0	1	0	0	0	0	1	1	1	1	0	1	0	0
T. tenebra	2	0	1	1	1	1	1	1	1	1	0	0	2	0	0
T. tricholepis	[12]	0	1	1	1	0	0	[01]	1	1	1	0	2	0	0
T. usneoides	1	0	1	2	1	1	1	1	1	0	1	0	2	0	0
T. virescens	[12]	[01]	1	[01]	1	1	1	[01]	1	0	1	0	2	0	0

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
V. friburgensis	0	0	0	0	?	?	0	1	1	0	_	0	9	0	0
T. aëranthos	0	0	0	0	2	1	1	1	1	0	_	0	[34]	1	0
T. aizoides	1	1	0	0	0	0	4	0	1	0	_	0	3	2	1
T. andicola	0	1	0	1	2	1	3	1	1	0	1	1	[01]	2	1
T. angulosa	1	0	0	0	2	1	2	1	0	0	_	0	1	2	1
T. australis	0	0	0	0	?	?	0	1	1	0	_	0	?	0	0
T. brealitoensis	1	1	0	0	1	1	3	0	1	?	[01]	2	1	2	1
T. caliginosa	0	0	1	1	0	0	2	0	1	0	1	1	[01]	2	1
T. capillaris	1	1	0	1	2	1	4	0	1	1	_	0	0	_	2
T. castellanii	0	0	0	1	2	1	2	1	1	0	_	0	[01]	2	1
T. copynii	[01]	1	0	0	1	1	3	0	1	0	_	0	[4567]	2	0
T. cotagaitensis	0	0	0	0	2	1	4	0	1	?	1	1	[012]	1	1
T. crocata	0	0	0	1	2	1	2	1	1	0	1	1	[01]	2	1
T. erecta	0	0	0	0	0	0	3	0	1	0	_	0	[12]	2	1
T. funebris	0	0	0	0	0	0	3	0	1	0	_	0	[23]	2	1
T. gilliesii ssp. *gilliesii*	0	0	0	1	2	1	2	0	[01]	0	1	1	[01]	2	
T. gilliesii ssp. *polysticha*	0	0	0	1	2	1	1	1	1	0	1	1	[01]	2	1
T. hirta	0	0	0	0	2	1	2	1	1	0	[01]	[12]	1	2	1
T. kuehhasii	0	1	0	1	2	1	4	0	1	1	0	2	1	2	1
T. landbeckii ssp. *landbeckii*	0	1	1	1	2	1	?	?	1	0	1	1	[234]	1	1
T. landbeckii ssp. *andina* var. *andina*	0	1	1	1	2	1	?	0	1	0	1	1	[123]	1	1
T. landbeckii ssp. *andina* var. *rigidior*	0	1	1	1	2	1	3	0	1	0	1	1	[23]	1	1
T. loliacea	0	0	0	0	0	0	1	0	1	0	1	1	[456789]2	0	
T. mandonii	0	0	0	?	2	1	2	?	1	0	1	1	[01]	2	1
T. minutiflora	1	1	0	0	0	0	5	0	0	0	_	0	2	2	0
T. mollis	0	1	1	1	2	1	3	1	0	0	1	1	1	2	1
T. myosura	0	0	0	1	2	[01]	2	1	1	0	1	[12]	[01]	2	1
T. pedicellata	1	1	0	0	0	0	5	0	[01]	[01]	_	0	2	1	[01]
T. porongoensis	0	0	0	0	2	1	1	0	1	?	1	2	3	2	0
T. rectangula	1	1	0	0	0	0	4	0	1	0	_	0	[234]	2	1
T. recurvata	0	1	1	0	2	1	4	1	1	0	0	1	1	2	1
T. retorta	0	1	0	1	2	0	3	1	[01]	0	1	1	0	_	2
T. spiralipetala	0	1	0	0	1	1	2	1	1	0	[01]	1	[234]	2	0
T. tenebra	0	0	0	1	2	1	2	0	1	0	1	[12]	[12]	2	1

Table 3 continued

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
T. tricholepis	1	1	0	0	0	0	4	0	1	0	_	0	[23456]	2	0
T. usneoides	[01]	1	0	1	1	1	5	1	0	0	_	0	0	_	2
T. virescens	[01]	1	0	1	2	[01]	4	0	[01]	[01]	1	2	0	_	2

	31	32*	33	34	35	36	37	38	39	40	41	42	43	44	45
V. friburgensis	0	1	0	1	0	1	_	1	0	0	0	0	0	_	1
T. aëranthos	1	1	1	1	1	1	1	0	6	0	0	0	0	_	0
T. aizoides	[46]	0	_	_	_	0	[01]	0	1	_	1	_	_	_	0
T. andicola	4	1	0	1	1	0	1	0	[123]	1	[01]	0	1	1	0
T. angulosa	4	1	0	1	1	0	1	0	1	_	1	_	_	_	0
T. australis	0	1	0	1	0	1	_	1	0	0	0	0	0	_	[01]
T. brealitoensis	6	1	0	1	1	0	[01]	0	[12]	1	1	0	0	_	0
T. caliginosa	1	1	0	1	1	0	1	0	[2345]	1	[01]	[01]	1	1	0
T. capillaris	_	_	_	_	_	_	_	0	1	_	1	_	_	_	0
T. castellanii	4	1	1	[01]	[01]	0	1	0	[12]	_	1	_	_	_	0
T. copynii	[56]	1	0	[01]	[01]	0	1	0	[23456]	1	[01]	0	[01]	0	0
T. cotagaitensis	5	1	0	1	1	0	1	0	[1234]	1	[01]	0	1	1	0
T. crocata	3	1	0	1	1	0	1	0	[23456]	1	[01]	0	1	1	0
T. erecta	6	1	1	0	1	[01]	[01]	0	1	_	1	_	_	_	1
T. funebris	[34]	2	[01]	[01]	1	0	[01]	0	[12]	1	1	_	0	_	0
T. gilliesii ssp. *gilliesii*	[35]	1	0	1	1	0	[01]	0	[123]	1	[01]	0	1	1	[01]
T. gilliesii ssp. *polysticha*	[35]	1	0	1	1	0	[01]	0	[1234]	1	[01]	0	1	1	0
T. hirta	4	1	0	1	1	0	1	0	[123]	1	[01]	0	1	1	0
T. kuehhasii	?	1	0	1	1	0	0	0	1	_	1	_	_	_	1
T. landbeckii ssp. *landbeckii*	[345]	1	0	1	1	0	1	0	[12]	_	1	0	1	1	0
T. landbeckii ssp. *andina* var. *andina*	[23]	1	0	1	1	0	1	0	1	1	1	0	_	_	[01]
T. landbeckii ssp. *andina* var. *rigidior*	[23]	1	0	1	1	0	1	0	[12]	1	1	0	1	1	[01]
T. loliacea	3	1	0	1	1	0	[01]	0	[23456]	1	[01]	1	1	1	0
T. mandonii	?	1	0	1	1	0	1	0	[123]	1	[01]	0	1	1	0
T. minutiflora	7	1	1	0	[01]	0	0	0	1	_	1	_	_	_	0
T. mollis	3	1	0	1	1	0	1	0	1	_	1	_	_	_	0
T. myosura	5	1	0	1	1	0	1	0	[123456]1	[01]	[01]	1	1	0	
T. pedicellata	7	1	1	1	1	0	1	0	1	_	1	_	_	_	0
T. porongoensis	4	1	0	1	1	0	[01]	0	6	1	0	1	0	_	0
T. rectangula	[56]	[12]	[01]	0	[01]	0	[01]	0	[12]	1	1	_	0	_	1
T. recurvata	6	1	0	1	1	0	1	0	[12]	1	1	_	1	0	1
T. retorta	_	_	_	_	_	_	_	0	[12]	1	1	_	1	1	0
T. spiralipetala	4	1	0	1	1	0	[01]	0	[123]	1	[01]	0	1	[01]	0
T. tenebra	[45]	1	0	1	1	0	1	0	[123]	1	[01]	0	1	1	0
T. tricholepis	6	1	0	1	1	0	[01]	0	[12345]	1	[01]	0	0	_	0
T. usneoides	_	_	_	_	_	_	_	0	1	_	1	_	_	_	0
T. virescens	_	_	_	_	_	_	_	0	1	_	1	_	_	_	0

	46*	47	48	49	50	51	52	53	54*	55	56	57	58	59	60
V. friburgensis	0	0	1	1	0	0	1	0	0	1	0	0	_	_	_
T. aëranthos	0	[89]	1	1	1	1	1	1	0	0	[59]	0	_	_	_
T. aizoides	[01]	[45]	0	_	_	_	0	0	_	_	[57]	0	_	_	_
T. andicola	0	7	1	0	1	1	0	1	0	0	7	1	[02]	1	1
T. angulosa	0	5	1	0	1	1	0	1	_	_	7	1	2	1	[01]

Table 3 continued

	46*	47	48	49	50	51	52	53	54*	55	56	57	58	59	60
T. australis	0	0	1	0	1	0	1	0	0	1	0	0	_	_	_
T. brealitoensis	0	[56]	1	0	1	1	0	0	0	0	[678]	1	0	1	1
T. caliginosa	0	7	1	0	1	1	0	[01]	[01]	0	[79]	1	[02]	1	1
T. capillaris	0	[34]	0	_	_	_	0	1	_	_	5	0	_	_	_
T. castellanii	0	[67]	0	_	_	_	0	[01]	0	0	7	0	_	_	_
T. copynii	0	[45]	1	0	1	1	0	0	0	0	[678]	1	1	0	0
T. cotagaitensis	0	6	1	0	1	1	0	[01]	0	0	[57]	1	1	0	0
T. crocata	0	7	1	0	1	1	0	1	0	0	7	1	[02]	1	1
T. erecta	0	5	1	1	0	1	0	0	_	_	[579]	0	_	_	_
T. funebris	1	[56]	0	_	_	_	0	0	0	0	[57]	0	_	_	_
T. gilliesii ssp. *gilliesii*	0	[5678]	1	0	1	1	0	[01]	0	0	[79]	1	0	1	1
T. gilliesii ssp. *polysticha*	0	[5678]	1	0	1	1	0	[01]	[01]	0	[789]	1	0	1	1
T. hirta	0	[467]	1	0	1	1	0	[01]	0	0	7	1	0	1	1
T. kuehhasii	0	4	1	0	1	1	0	1	_	_	5	1	0	0	0
T. landbeckii ssp. *landbeckii*	0	[45]	1	0	1	1	0	[01]	0	0	[79]	0	_	_	_
T. landbeckii ssp. *andina* var. *andina*	0	[67]	1	0	1	1	0	[01]	_	_	[710]	0	_	_	_
T. landbeckii ssp. *andina* var. *rigidior*	0	[56]	1	0	1	1	0	1	0	0	7	[01]	0	0	0
T. loliacea	0	7	1	0	1	1	0	0	0	0	[78]	1	1	0	0
T. mandonii	0	7	1	0	1	1	0	1	0	0	7	[01]	[01]	[01]	1
T. minutiflora	0	1	[01]	1	0	0	0	0	_	_	[457]	1	0	1	1
T. mollis	0	?	1	0	1	1	0	1	_	_	[345]	1	0	1	1
T. myosura	0	[79]	1	0	1	1	0	0	0	0	9	[01]	2	0	0
T. pedicellata	0	[12]	1	1	0	1	0	1	_	_	[123]	0	_	_	_
T. porongoensis	6	1	0	1	1	0	0	0	0	9	1	0	1	1	
T. rectangula	[01]	[345]	[01]	2	0	0	0	0	0	0	[579]	[01]	1	0	0
T. recurvata	0	[345]	1	0	1	1	0	1	0	0	5	[01]	1	0	0
T. retorta	0	[456]	1	0	1	1	0	[01]	0	0	[57]	[01]	2	[01]	1
T. spiralipetala	0	6	1	0	1	1	0	0	0	0	7	1	2	1	1
T. tenebra	0	[67]	1	0	1	1	0	0	0	0	[789]	1	0	[01]	[01]
T. tricholepis	0	4	1	0	1	[01]	0	0	0	0	[57]	1	1	[01]	0
T. usneoides	0	[34]	1	0	1	1	0	1	_	_	[35]	[01]	2	0	0
T. virescens	0	3	1	[01]	[01]	1	0	1	_	_	3	[01]	[02]	1	1

	61	62	63	64	65	66	67*	68	69	70	71	72	73*	74*	75
V. friburgensis	1	0	1	1	0	?	1	2	?	1	?	?	0	0	2
T. aëranthos	0	1	1	0	0	1	0	8	0	1	0	1	1	1	1
T. aizoides	0	0	0	0	[01]	0	0	1	0	1	0	1	1	0	0
T. andicola	0	1	0	0	0	?	0	0	0	1	?	?	1	?	0
T. angulosa	0	0	0	0	0	?	0	3	0	0	0	?	1	?	?
T. australis	1	0	0	0	0	1	0	7	0	0	1	1	1	0	2
T. brealitoensis	0	0	0	0	0	?	0	[67]	0	1	?	?	1	?	0
T. caliginosa	0	1	1	0	0	?	0	4	0	1	[02]	0	1	?	0
T. capillaris	0	1	0	0	0	?	0	[02]	0	1	0	?	1	?	0
T. castellanii	0	0	0	0	0	0	0	0	0	_	_	1	1	0	1
T. copynii	0	1	?	?	0	?	0	3	0	1	?	?	1	0	0
T. cotagaitensis	0	1	?	?	0	?	0	7	0	1	?	?	1	?	0
T. crocata	0	0	1	0	0	?	0	[211]	1	1	?	0	1	?	?
T. erecta	0	0	[01]	[01]	0	?	0	1	0	1	?	1	1	?	0

Table 3 continued

	61	62	63	64	65	66	67*	68	69	70	71	72	73*	74*	75
T. funebris	0	0	0	0	1	?	0	3	0	[12]	2	0	1	?	0
T. gilliesii ssp. *gilliesii*	0	0	[01]	0	0	?	0	2	0	0	0	1	1	?	0
T. gilliesii ssp. *polysticha*	0	0	1	0	0	?	0	7	0	0	?	?	1	?	0
T. hirta	0	0	?	?	0	?	0	1	0	0	?	?	1	?	0
T. kuehhasii	0	1	1	0	0	?	0	2	0	1	3	?	1	?	?
T. landbeckii ssp. *landbeckii*	0	0	1	?	0	?	0	1	0	1	?	?	1	0	?
T. landbeckii ssp. *andina* var. *andina*	0	[01]	0	0	0	?	0	[34]	0	1	?	?	1	?	0
T. landbeckii ssp. *andina* var. *rigidior*	0	0	0	0	0	?	0	?	0	?	?	?	1	0	?
T. loliacea	0	0	0	0	0	?	0	1	0	1	0	1	1	?	0
T. mandonii	0	0	0	0	0	?	0	?	?	?	?	1	1	?	?
T. minutiflora	0	0	1	0	0	0	0	2	0	1	?	1	1	0	0
T. mollis	0	0	0	0	0	?	0	[13]	0	1	?	1	1	0	0
T. myosura	0	0	0	0	0	0	0	[12]	0	0	0	1	1	0	0
T. pedicellata	0	[01]	1	0	0	0	0	7	0	1	0	1	1	0	0
T. porongoensis	0	0	1	1	0	?	0	8	1	1	?	1	1	0	2
T. rectangula	0	0	0	0	1	0	0	3	0	1	2	[01]	1	0	0
T. recurvata	0	0	0	0	0	1	0	[06]	0	1	1	1	1	0	0
T. retorta	0	1	1	0	0	0	0	1	0	1	1	1	1	0	0
T. spiralipetala	0	0	1	0	0	?	0	[34]	0	2	0	1	1	0	0
T. tenebra	0	[01]	?	?	0	?	0	[710]	0	1	?	?	1	?	0
T. tricholepis	0	0	0	0	0	1	0	2	0	[01]	0	1	1	0	0
T. usneoides	0	0	0	0	0	1	0	[15]	0	1	0	1	1	0	2
T. virescens	0	1	0	0	0	0	0	[27]	0	[01]	0	1	1	0	0

	76	77*	78	79	80	81	82	83	84	85
V. friburgensis	?	0	0	1	0	1	0	?	0	?
T. aëranthos	0	0	0	0	0	1	0	1	0	?
T. aizoides	2	0	0	1	0	1	1	1	1	?
T. andicola	?	0	1	0	1	0	1	1	0	?
T. angulosa	?	0	1	0	0	1	1	2	1	?
T. australis	0	0	0	0	0	?	0	0	0	0
T. brealitoensis	2	0	1	0	0	1	1	1	?	?
T. caliginosa	1	0	1	0	0	0	1	1	?	?
T. capillaris	2	0	1	1	0	1	1	1	1	1
T. castellanii	2	0	1	0	0	?	1	2	1	1
T. copynii	2	0	0	0	0	?	?	?	0	?
T. cotagaitensis	2	0	?	?	?	?	1	1	?	?
T. crocata	?	0	1	0	0	?	0	2	?	0
T. erecta	2	0	0	0	0	1	1	1	?	?
T. funebris	2	0	0	0	0	1	0	?	?	?
T. gilliesii ssp. *gilliesii*	2	0	1	0	0	0	1	1	1	?
T. gilliesii ssp. *polysticha*	2	0	1	0	1	0	0	1	?	?
T. hirta	2	0	1	0	0	0	1	1	?	?
T. kuehhasii	?	0	?	?	?	?	?	?	?	?
T. landbeckii ssp. *landbeckii*	?	0	1	0	0	1	0	?	1	?
T. landbeckii ssp. *andina* var. *andina*	?	0	1	0	?	?	?	?	?	?
T. landbeckii ssp. *andina* var. *rigidior*	?	0	1	0	0	1	0	?	?	?
T. loliacea	2	[01]	0	0	0	1	0	2	?	1

Table 3 continued

	76	77*	78	79	80	81	82	83	84	85
T. mandonii	?	0	1	0	0	1	1	?	?	?
T. minutiflora	1	[01]	0	0	0	1	1	2	1	?
T. mollis	0	0	?	?	?	?	?	?	?	?
T. myosura	1	0	1	0	1	0	1	1	1	1
T. pedicellata	2	0	0	0	0	1	1	2	1	?
T. porongoensis	0	?	?	?	?	?	?	?	?	
T. rectangula	2	0	0	0	0	1	0	1	1	?
T. recurvata	2	0	1	1	1	0	0	2	1	1
T. retorta	2	0	1	0	1	0	1	?	1	?
T. spiralipetala	1	?	0	0	0	1	0	2	?	?
T. tenebra	2	0	1	0	0	0	0	?	?	?
T. tricholepis	2	[01]	0	0	0	1	0	2	1	1
T. usneoides	[01]	0	1	1	0	1	0	1	1	1
T. virescens	2	0	1	1	0	1	1	1	1	1

Uninformative characteres are marked with (*)

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