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Phylogenetics and evolution of the *Tillandsia utriculata* complex (Bromeliaceae, Tillandsioideae) inferred from three plastid DNA markers and the ETS of the nuclear ribosomal DNA

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We performed a phylogenetic analysis using maximum parsimony and Bayesian inference of three plastid DNA markers and the external transcribed spacer (ETS) of nuclear ribosomal DNA to assess the species composition of the *Tillandsia utriculata* complex and their phylogenetic relationships, and to reconstruct patterns of character evolution and biogeography. The results showed that species of the *T. utriculata* complex are nested in a clade composed mainly of Mexican and Central American species of *T.* subgenus *Tillandsia* (Mexican Clade), and are organized in two lineages: the *T. utriculata* clade and the *T. limbata* clade. The ancestor of the core Mexican Clade was probably a *T. utriculata*-like epiphyte (Group II-type remote flowers and flexuous rachises). The *T. utriculata* clade is defined morphologically by the presence of acute petals. In this clade, there are two lineages: one of high-elevation, saxicolous, grey-leaved plants from the Mexican Plateau; and one which is more widespread and found from the Gulf of Mexico to Venezuela. The *T. limbata* clade probably arose in western Mesoamerica and is defined by rounded petals. These species are found mainly in tropical dry forests, but one species colonized wet environments of eastern Mesoamerica. Finally, analyses based on the ETS region allowed us to distinguish between *T. utriculata* and *T. pringlei.* © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **181**, 362–390

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INTRODUCTION

Tillandsia L. is the most diverse genus of Bromeliaceae, with > 600 species (Luther, 2012), distributed in tropical and subtropical America, and is one of the most distinctive components of the epiphytic and epilithic flora in that region (Benzing, 2000). The taxonomy of the genus is based mainly on the monograph of subfamily Tillandsioideae (Smith & Downs, 1977) and the subgeneric classification hinges on one or a few floral characters, such as the exsertion of stamens and shape of the sepals. Gardner (1986) challenged the classification of *Tillandsia* subgenus *Tillandsia* of Smith & Downs through a detailed study of floral characters, but that classification remained provisional and has no molecular phylogenetic basis.

For this reason, the phylogenetics of the genus *Tillandsia* need to be elucidated. To deal with such a large and diverse group, two strategies can be followed: (1) a top–down approach, sampling as many species as possible, trying to represent all the

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morphological and ecological variation and the geographical distribution; or (2) a bottom–up approach, sampling all species in a species complex, to deal with a manageable number of taxa with a reduced but representative sampling of the outgroup.

Here, we have chosen to follow the second approach, to answer more fine-scale evolutionary and taxonomic questions than those that could be made for the entire genus. Because *Tillandsia utriculata* L. is the type species of the genus, it is important to correctly assess the relationships and species limits in the species complex, which is composed of morphologically similar taxa, which are difficult to diagnose.

The *T. utriculata* complex, as defined by Ramírez, Carnevali & Chi (2004) (*s.s.*), is represented by a group of species that share vegetative and floral characteristics, including triangular leaves, spicate or paniculate inflorescences with sessile flowers, a flexuous rachis, and exserted stamens and style. The names initially included by Ramírez *et al.* (2004) and Ramírez & Carnevali (2007a,b), in addition to *T. utriculata*, are *T. aesii* I.Ramírez & Carnevali, *T. calcicola* L.B.Sm. & Proctor, *T. cucaensis* Wittm., *T. dasyliriifolia* Baker, *T. geniculata* E.Morren ex Baker, *T. limbata* Schltdl., *T. makoyana* Baker, *T. pinicola* I.Ramírez & Carnevali, *T. pringlei* S.Watson, *T. pulvinata* E.Morren ex Baker, *T. simplexa* Matuda, *T. swartzii* Baker and *T. tehuacana* I.Ramírez & Carnevali. Although not mentioned in the cited references, these species also feature remote floral bracts, which makes the rachis visible, and the flowers are appressed to it.

In addition to the aforementioned taxa, there are two groups of species that, despite sharing the characteristics of the *T. utriculata* complex *s.s.*, were omitted by Ramírez & Carnevali (2007a,b) and Ramírez *et al.* (2004). The first group includes the lithophytic Mexican species *T. albida* Mez & Purpus, *T. fresnilloensis* W.Weber & Ehlers, *T. karwinskyana* Schult. & Schult.f. and *T. socialis* L.B.Sm. The second group comprises *T. extensa* Mez, *T. hildae* Rauh, *T. mima* L.B.Sm., *T. propagulifera* Rauh and *T. secunda* Kunth, which are also lithophytic, but are distributed in north-western South America and are generally larger than the Mexican species. Furthermore, after the publication of the study by Ramírez *et al.* (2004), subsequent studies described additional species that possess characters similar to those in the complex, namely *T. comitanensis* Ehlers, *T. huamelulaensis* Ehlers, *T. nicolasensis* Ehlers (Ehlers, 2006a,b,c), *T. elusiva* Pinzón, I.Ramírez & Carnevali and *T. izabalensis* Pinzón, I.Ramírez & Carnevali (Pinzón, Ramírez-Morillo & Carnevali Fernández-Concha, 2011, 2012).

All of these species (*T. utriculata* complex *s.l.*) possess characteristics that agree with Gardner's (1986) Group II of the classification of *Tillandsia* subgenus *Tillandsia*. That is, they present stamens of unequal length based on cross-sections, erect or recurved petal apices and flowers with an open corolla throat. The only exception is *T. swartzii*, which is a synonym of *Vriesea swartzii* (Baker) Mez, and is characterized by the presence of appendages at the base of the petals and secund spreading flowers (Mez, 1935).

It is important to note that the *T. utriculata* complex *s.l.* is not exactly equivalent to Group II of Gardner (1986), because not all of the species in Group II agree with the characteristics of the *T. utriculata* complex *s.l.* Specifically, *T. andreana* E.Morren ex André and *T. funckiana* Baker have solitary flowers per rosette, *T. argentea* Griseb. and *T. fuchsii* W.Till have filiform leaves and spreading flowers and *T. flagellata* L.B.Sm. (= *T. lehmannii* Rauh), *T. kegeliana* Mez and *T. paraensis* Mez have imbricate floral bracts and the rachis is not regularly flexuous.

Although there are a number of molecular phylogenetic studies that have included *Tillandsia* spp., these were aimed at either addressing taxonomic problems at the family or subfamily levels (Ranker *et al.*, 1990; Terry, Brown & Olmstead, 1997a,b; Horres *et al.*, 2000; Crayn, Winter & Smith, 2004; Givnish *et al.*, 2004, 2011; Barfuss *et al.*, 2005) or focused on understanding the evolution of different species complexes in *Tillandsia* (Granados, 2008; Chew, De Luna & González, 2010). Therefore, such studies include a limited sampling of species belonging to the *T. utriculata* complex. Barfuss *et al.* (2005) provided the most exhaustive sampling of *Tillandsia* conducted to date, including 58 species, but only included one species (*T. utriculata*) from the *T. utriculata* complex.

One of the goals of this study is to assess the phylogenetic relationships of the species that share characteristics of the *T. utriculata* complex. The questions we seek to address are as follows. Do species of the *T. utriculata* complex constitute a monophyletic group? If so, are the Mexican lithophytic species and the South American taxa related to *T. mima* part of the *T. utriculata* complex? Are the South American species with similar characteristics part of this group? Based on these analyses, we also provide a test of monophyly of Group II proposed by Gardner (1986).

By assessing the species composition of the *T. utriculata* complex, of Group II, and the phylogenetic relationships among their constituent species, we are also able to propose probable scenarios of evolution, biogeography and diversification of this group. In addition, the inclusion of specimens from different populations for some of the species analysed (e.g. *Tillandsia karwinskyana*, *T. pringlei* and *T. utriculata*

or *T. makoyana* and *T. tehuacana*) will contribute to resolve taxonomic issues that have remained diffuse and have hindered the delimitation of some of these taxa.

METHODS

Taxon selection

To determine the phylogenetic position of the *T. utriculata* complex *s.l.* in the genus, we conducted independent phylogenetic analyses using the *matK* gene and a section of the 3′ end of the *trnK* intron (*matK-trnK*) and the *rps16* intron (*rps16*), and combined analyses of the two regions (hereafter referred to as 'broad analyses'). We selected these markers as they have been used for the largest number of *Tillandsia* spp. available from public databases. For the analyses of *matK-trnK*, we included 175 accessions which represented 122 *Tillandsia* spp. (169 accessions), two species of *Racinaea* M.A.Spencer & L.B.Sm. (two accessions), one species of *Vriesea* Lindl. (three accessions) and *Catopsis nutans* (Sw.) Griseb. as a functional outgroup (one accession), as the results reported by Barfuss *et al.* (2005) indicate that *Catopsis* Griseb. and *Glomeropitcairnia* Mez form the sister group of the rest of Tillandsioideae. For the analyses using *rps16*, we included 168 accessions representing 113 *Tillandsia* spp. (164 accessions), one *Racinaea* sp. (one accession), one *Vriesea* sp. (two accessions) and *C. nutans* (one accession). The 'broad analyses' combining the two regions (i.e. *matK-trnK* and *rps16*) were performed with 108 *Tillandsia* spp. (145 accessions), one *Racinaea* sp. (one accession), one *Vriesea* sp. (one accession) and *C. nutans* (one accession). Sequences were generated during this study or obtained from GenBank based on studies by Crayn *et al.* (2004), Barfuss *et al.* (2005), Granados (2008), De Castro *et al.* (2009) and Rex *et al.* (2009) (accession numbers: Appendix 1).

A second set of analyses was also performed, hereafter called 'restricted analyses', with more characters, but fewer taxa. Here, we included all the species that exhibited morphological characteristics present in the *T. utriculata* complex *s.l.*, most of the species belonging to Group II (Gardner, 1986) and belonging to the clades that were more closely related to species of the *T. utriculata* complex based on results from the broad analyses. For the 'restricted analyses', we used *matK-trnK*, *rps16* and the *rpl32-trnL* region combined and the external transcribed spacer (ETS) of the nuclear ribosomal (nr) DNA region alone.

Of the names included in the *T. utriculata* complex *s.l.* (see Introduction) and Gardner's Group II, we excluded the following: *T. simplexa* which is a synonym of *T. makoyana*, *T. geniculata* which is a synonym of *T. limbata*, *T. aesii* which is a synonym of *T. cucaensis* (Pinzón *et al.*, 2012), *T. pulvinata* which is a synonym of *T. dasyliriifolia* and *T. lehmannii* which is a synonym of *T. flagellata*. *Tillandsia swartzii* was also excluded, as we had no access to the original material and it belongs to *Vriesea* (Smith & Downs, 1977).

DNA extraction, amplification and sequencing

For the DNA extraction, we used dried (with silica gel) or fresh plant material, obtained from the field or from exchange with the Botanical Garden of the University of Vienna (Austria) or the Marie Selby Botanical Garden (Florida, USA). The herbarium vouchers are listed in Appendix 1. DNA extraction was performed following the cetyltrimethylammonium bromide (CTAB) protocol (Doyle & Doyle, 1987). To amplify the plastid DNA regions, we used the following reagents and final concentrations: buffer (1×), $MgCl_2$ (5 mM), deoxynucleoside triphosphates (dNTPs) (200 μM), 'forward' and 'reverse' primers (0.4 μM), *Taq* DNA polymerase (1 U), 1 μL DNA dilution and the remaining volume of distilled H_2O. For the amplification of *rpl32-trnL*, we modified the $MgCl_2$ concentration to 1.5 mM) and added bovine serum albumin (BSA) (0.2 μg/μL) (Shaw *et al.*, 2007) and, for ETS, we used $MgCl_2$ at 2.25 mM and added dimethylsulphoxide (DMSO) at 2.7%.

The pairs of primers used to amplify the *matK-trnK* region were matK-19F (Molvray, Kores & Chase, 2000) with trnK2R (Johnson & Soltis, 1995) and matK-19F with matK1520R (Whitten, Williams & Chase, 2000), or the pairs matK-19F/matK966r-BRO and matK808fBRO/trnK2R* (Barfuss, 2012). For *rps16*, we used the primers rpsF and rpsR2 (Oxelman, Lidén & Berglund, 1997). For *rpl32-trnL*, we used trnL(UAG) and rpl32-F (Shaw *et al.*, 2007). For ETS, we used the primers Till2 (Chew *et al.*, 2010) and 18S-IGS (Baldwin & Markos, 1998). The PCR conditions for *matK-trnK* and *rps16* were the same as in Barfuss *et al.* (2005) and, for *rpl32-trnL*, we followed Shaw *et al.* (2007). For ETS, we used the following protocol: initial denaturation at 97 °C for 2 min, 15 cycles at 99 °C for 2 min, annealing at 68 °C for 30 s and extension at 72 °C for 1 min, followed by 20 cycles under the same conditions, but with an increment of 5 s/cycle during the extension step; subsequently, a final extension at 72 °C for 7 min and hold at 4 °C.

To verify that DNA extraction and amplification were successful, we performed electrophoresis on 1% agarose gel stained with ethidium bromide. The purification was performed with a QIAquick

(QIAGEN) purification kit following the manufacturer's instructions. Sequencing was performed using the Sanger method with the same primers as used for the amplification on an ABI3730XL (Applied Biosystems) sequencer.

Sequence assembly and alignment and coding of insertions/deletions

Sequences were assembled with Geneious 4.1.4 (Biomatters Ltd., Auckland, New Zealand) and aligned using the algorithm MUSCLE 3.6 (Edgar, 2004) as implemented in the platform eBioTools (www.ebioinformatics.org), through eBioX 1.5.1 (Lagercrantz, 2008), and checked visually. Insertion/deletions (indels) were coded following the simple coding method of Simmons & Ochoterena (2000).

Phylogenetic analyses

We conducted separate analyses with the matrices of *matK-trnK* and *rps16* and with the matrix of both regions combined (broad analysis), including indels. The restricted analyses included the combined analysis of three regions of the plastid DNA (*matK-trnK*, *rps16* and *rpl32-trnL*) and indels, and also the analysis with the ETS nrDNA.

All analyses were performed using the parsimony algorithm of Fitch with equal weight for all characters. The most-parsimonious trees (MPTs) were retrieved from heuristic searches with 10 000 replicates, retaining ten trees per replicate and using tree bisection–reconnection (TBR) as the branch swapping algorithm. The maximum number of trees was fixed at 100 000 (Max. trees). To assess branch support, we performed a bootstrap (BS) analysis with 10 000 iterations employing heuristic searches with ten replicates, and retained ten trees per replicate using the support levels as in Sung *et al.* (2007) for the interpretation of the results. Given that we obtained multiple MPTs in all the analyses, we calculated strict consensus trees. All of these analyses were performed with the program TNT 1.1 (Goloboff, Farris & Nixon, 2003). The consistency index (CI) and retention index (RI) of the MPTs were calculated with the WinClada 1.00.08 platform (Nixon, 2002).

We also conducted Bayesian analyses of all the matrices explained above with MrBayes 3.1 (Ronquist & Huelsenbeck, 2003). The nucleotide substitution model for each DNA partition was selected under the Akaike information criterion (AIC) with three substitution schemes, in program jModelTest 0.1.1 (Posada, 2008). For all analyses, data partitions were set corresponding to each DNA region and indels. For the broad analysis, the nucleotide substitution model used for partitions of *matK* and *rps16* was GTR + I + Γ and the model for *trnK* was GTR + Γ. For the restricted analysis with the three plastid DNA regions combined and the indels, we used the models GTR + I + Γ for the *matK* and *rps16* partitions, GTR + Γ for the *trnK* partition and HKY + Γ for the *rpl32-trnL* partition. Finally, the model used for ETS was HKY + I + Γ. In all cases, the partitions of indels were treated under the binary model, using type of data as 'restriction' and establishing the coding option as 'variable'. For all the analyses, we unlinked the estimation of the parameters of each partition (except for topology and branch length), and the global rate was allowed to vary independently for each partition.

The broad analysis consisted of three simultaneous but independent runs, each consisting of 5 000 000 generations produced by the Metropolis-coupled Markov chain Monte Carlo (MCMCMC), with a sampling every 100 generations using one cold chain and four hot chains with a temperature of 0.17, whereas, for the remaining parameters, we used the default values given by the program MrBayes 3.1. The restricted analyses of the four regions of the plastid DNA plus indels and of the ETS region were performed using the same parameters specified in the previous analyses, but in this case with 10 000 000. Convergence of parameters between runs was considered as reached when the 'average standard deviation of split frequencies' was < 0.01, as recommended by Ronquist, Huelsenbeck & Teslenko (2011), and also by visual examination of the plot of generation vs. log likelihood, considering the convergence achieved when the dots that represented different runs were mixed. For the estimation of parameters and posterior probabilities (PPs), in all cases we discarded 25% of the initial generations.

The clades of interest were labelled with letters in the tree that resulted from the broad analysis with *matK-trnK*, *rsp16* and indels. For the trees produced by the other analyses, we repeated letters for clades that shared species and were congruent with the clades from the first analysis (although tree internal topologies and numbers of species were not necessarily identical between these analyses). To assess the suitability of analysing the plastid DNA and nrDNA (ETS) data together, we performed the incongruence length difference (ILD) test (Farris *et al.*, 1994).

The infrageneric allocation of *Tillandsia* spp. to the trees shown was performed following the circumscription of Smith & Downs (1977), with the exception of *T. tortilis* Klotzsch ex Baker and *T. lepidosepala* L.B.Sm. Although the last two species were considered as part of *T.* subgenus *Tillandsia* by Smith & Downs (1977), subsequent studies found that they belong to *T.* subgenus *Allardtia* (A.Dietrich) Baker (Gardner, 1982; Ehlers (2009).

Character evolution and biogeographical analysis

To explain the evolution of the studied group, we conducted a parsimony-based reconstruction with unordered character states for several morphological and ecological characters with Mesquite 2.75 (Maddison & Maddison, 2011), using the strict consensus tree generated from the parsimony analysis with the three plastid DNA regions and indels.

We reconstructed five groups of morphological characters: (1) the *T. utriculata* complex syndrome, i.e. the combination of characters that define the complex, such as the inflorescence in a spike or panicle, a flexuous rachis, flowers appressed to the rachis, remote floral bracts and exserted stamens and style; (2) the Group II syndrome, i.e. the combination of open corolla throat, filaments in series of two lengths, round and of the same width throughout their entire length; (3) the presence or absence of vegetative reproduction and the position of propagules when present: monocarpic genet, axillary propagules, basal propagules, caespitose growth and propagules originating from the inflorescence; (4) inflorescence colour (including the peduncle), the main axis of a compound inflorescence, the rachis and the floral bracts; and (5) petal colour. The ecological characters that have been reconstructed are the type of substrate in which the species grows as an epiphyte, lithophyte or terrestrial.

We also performed an analysis for the reconstruction of the ancestral distribution areas with maximum parsimony in the same way as for the characters above and with the Bayesian binary MCMC method (BBM) (Ronquist & Huelsenbeck, 2003), as implemented in RASP (Yu *et al.*, 2015) using the default configuration, on one of the 63 MPTs obtained from the restricted analysis of the plastid DNA markers. Both analyses were based on the phytogeographical regions proposed by Gentry (1982): Mexico and Central America; West Indies; northern Venezuela and Colombia; northern Andes; southern Andes; and the Amazon Basin. The region of Mexico and Central America was subdivided into three areas, because most of the studied species are distributed in this region and the use of a finer geographical subdivision was helpful to describe the biogeographical patterns appropriately. This subdivision consisted of: (1) Gulf of Mexico and Caribbean coast; (2) Pacific Ocean coast and mountainous region; and (3) the Mexican Plateau. The subdivision of this phytogeographical region along an east–west (1 and 2) axis, taking, as the division line, the Sierra Madre Oriental and the mountains of northern Oaxaca and Chiapas, was based on the cladistic biogeographical study by Escalante *et al.* (2007), which recognized biogeographical affinities between the combined provinces of the Gulf of Mexico and the Yucatan Peninsula and the combined Pacific coast and the mountains of Oaxaca and Chiapas provinces. The biogeographical province of eastern Central America was included in the Gulf of Mexico coast and the Caribbean. The mountainous zone of Central America (Guatemala, Honduras and Nicaragua) was grouped with the Pacific coast, as both are found in the same province as the mountains of Chiapas (Morrone, 2001). The Mexican Plateau zone was considered as a third subdivision because it has been classified as part of the Nearctic region (Morrone, 2001, 2005) and is limited to the east by the Sierra Madre Oriental, to the west by the Sierra Madre Occidental and to the south by the Trans-Mexican Volcanic Belt. In addition, we included the peninsula of Florida as part of the West Indies region. The areas were assigned to the terminals in a presence/absence scheme, in accordance with the observed distribution of specimens observed in the field, registered in herbaria CICY, WU, MEXU and XAL, or cited in Smith & Downs (1977). When several accessions of the same species were included, the distribution of the whole species was assigned to each accession.

RESULTS

Characterization of DNA regions

Table 1 shows the characteristics of the DNA regions used in the parsimony analyses, such as size and percentage, and number of variable and potentially informative sites. The most variable plastid DNA region with the greatest percentage of potentially parsimony-informative characters was *trnK* (partial) in both the broad and restricted analyses, followed by *matK*. The *rps16* intron was the least informative region. Although *trnK* was the most variable and informative region in terms of percentage of informative sites, *matK* provided a greater absolute number of variable and informative characters. For the restricted analysis of plastid DNA regions, the most variable and informative region was again *trnK*, followed by *rpl32-trnL*, *matK* and, lastly, *rps16*. The level of variability in ETS was more than double that observed for *trnK*, and the percentage of potentially parsimony-informative characters was almost four times greater relative to this region.

Phylogenetic relationships

Broad analyses (Fig. 1)

The parsimony analysis with the *matK-trnK* region yielded 54 MPTs with CI = 0.73 and RI = 0.93, whereas that of the *rps16* region and indels resulted

Table 1. Size, variability and level of information for the parsimony of the DNA markers used for the phylogenetic analyses

Marker	Aligned size (bp)	Variable sites (number, %)	Parsimony-informative characters (number, %)	Matrix	Number of species/ specimens
matK	1438	222, 15.4%	119, 8.3%	*matK*–*trnK*	126/175
matK	1438	205, 14.3%	103, 7.2%	*matK*–*trnK* + *rps16* + indels	111/148
matK	1438	146, 10.2%	53, 3.7%	*matK*–*trnK* + *rps16* + *rpl32*–*trnK* + indels	62/88
trnK intron (partial)	137	38, 27.7%	20, 14.6%	*matK*–*trnK*	126/175
trnK intron (partial)	137	36, 26.3%	19, 13.9%	*matK*–*trnK* + *rps16* + indels	111/148
trnK intron (partial)	137	30, 21.9%	9, 6.6%	*matK*–*trnK* + *rps16* + *rpl32*–*trnK* + indels	62/88
rps16 intron	873	105, 12.0%	47, 5.4%	*rps16* + indels	116/168
rps16 intron	873	105, 12.0%	44, 5.0%	*matK*–*trnK* + *rps16* + indels	111/148
rps16 intron	858	82, 9.6%	25, 2.9%	*matK*–*trnK* + *rps16* + *rpl32*–*trnK* + indels	62/88
rpl32-trnL intergenic spacer	1003	135, 13.5%	52, 5.2%	*matK*–*trnK* + *rps16* + *rpl32*–*trnK* + indels	62/88
External transcribed spacer (partial) (ETS)	440 (423)	255, 58.0% (229, 54.1%)	137, 31.1% (108, 25.5%)	ETS	72/100

in 13 360 MPTs with CI = 0.73 and RI = 0.92. In addition, the parsimony analysis of the combined matrices generated 2196 MPTs with CI = 0.73 and RI = 0.92. The strict consensus tree based on these trees and the majority rule consensus tree from the Bayesian analysis (Fig. 1) did not exhibit incongruence, although the latter had a higher resolution.

The individual analyses of *matK-trnK* and *rps16* (not shown) and the combined analysis yielded a clade composed mainly of taxa of *Tillandsia* subgenus *Tillandsia* (Fig 1, clade A) (BS = 57, PP = 1), which also included the *T. utriculata* complex *s.l.* However, some species inserted in clade A belong to *T.* subgenus *Allardtia* (e.g. *T. guatemalensis* L.B.Sm.) or to *T.* subgenus *Pseudalcantarea* Mez [e.g. *T. paniculata* (L.) L]. Clade A consists of a trichotomy (clades B, C and D). Clade B received high support (BS = 93, PP = 1), whereas clade C had weak support (BS = 73, PP = 1). Within these two clades, some species of the *Tillandsia utriculata* complex *s.l.* were found, such as *T. secunda*, *T. propagulifera* and *T. mima* (clade B) and *T. hildae* (clade C). In clade B, we also found *T. adpressiflora* Mez and *T. marnier-lapostollei* Rauh (*Allardtia*), whereas, for clade C, we had *Vriesea malzinei* E.Morren and *T. paniculata* (subgenus *Pseudalcantarea*).

Clade D (Mexican clade) was also strongly supported (BS = 98, PP = 1) and included a larger number of species (44). The species of the *T. utriculata* complex *s.s.* were placed here and distributed mainly in two clades: clade E, which we named the *T. utriculata* clade, received moderate to high support (BS = 80, PP = 1), and clade F, which we named the *T. limbata* clade, also received moderate to high support (BS = 88, PP = 1). *Tillandsia socialis* also exhibits a morphology similar to species of the *T. utriculata* complex, but its relationship with the clades of the complex remains unclear, as it is part of a polytomy at the base of the clade containing clades E, F, G and H. *Tillandsia tehuacana* and *T. nicolasensis* were grouped with the *T. limbata* clade in the majority rule consensus tree from the Bayesian analysis, albeit without statistical support. This relationship was not observed in the strict consensus tree from the parsimony analysis (Fig. 4).

The internal relationships of the *T. utriculata* clade showed a dichotomy formed by the Mexican Plateau clade (*T. albida*, *T. fresnilloensis* and *T. karwinskyana*) (BS = 62; PP = 1) and the Gulf-Antillean clade (BS = 74; PP = 1), comprising *T. calcicola*, *T. elusiva*, *T. pringlei* and *T. utriculata*. In the *T. limbata* clade, two lineages can be observed, one called here the western Mesoamerican clade (*T. comitanensis*, *T. cucaensis*, *T. huamelulaensis*, *T. pinicola* and *T. makoyana*) and the other named here the eastern Mesoamerican clade (*T. izabalensis*, *T. limbata*, *T. may-patii* and *T. dasyliriifolia*).

In clade D, another lineage can be observed, which is composed of species from subgenus *Allardtia*

Figure 1. Majority rule consensus phylogram resulting from the Bayesian inference analysis of species of the *Tillandsia utriculata* complex *s.l.* and the outgroup, using the plastid DNA regions *matK*, *trnK*, *rps16* and indels for the latter (broad analysis). Above and below each branch, we indicate the bootstrap and posterior probability values, respectively. For a description of the clades labelled with letters, see text.

(clade G) and a clade in which none of the species exhibits the morphology of the *T. utriculata* complex (clade H). Clade G received weak support (BS < 50, PP = 1), whereas clade H had strong support (BS = 93, PP = 1).

Restricted analyses with plastid DNA (Fig. 2)

Parsimony analyses of *matK-trnK*, *rps16* and indels, and *rpl32-trnL* and indels, yielded 63 MPTs with CI = 0.76 and RI = 0.88. Clades A–H (from the broad analyses) were also recovered in strict consensus to the MPTs and the majority rule consensus tree of the Bayesian analysis. There were some incongruences between the topologies of these two trees, but these were only present outside clade A. This clade also received weaker support (BS = 49, PP = 1) in comparison with the same clade in the broad analyses. In contrast, clades B and C received improved support (BS = 97 and 88, respectively) and the latter also showed better resolution. Clade D also received improved support (BS = 99, PP = 1). In clade D, clades G (subgenus *Allardtia*), H and F (*T. limbata* clade) received stronger support with BS values of 71, 99 and 95, respectively (with PP = 0.98 and 1). *Tillandsia nicolasensis* and *T. tehuacana* were not found in sister group position to clade F, whereas clade E (the *T. utriculata* clade) showed a slightly lower support (BS = 78, PP = 1). The internal relationships of clades E and F did not change. Based on the Bayesian analysis, *T. fuchsii* and *T. socialis* were grouped together in a clade (PP = 0.91), whereas, for the parsimony analysis, their relationships in clade D were not resolved.

Restricted analyses with ETS (Fig. 3)

The parsimony analysis produced 19 169 MPTs with CI = 0.60 and RI = 0.77. The strict consensus of this latter analysis (not shown) and the majority rule consensus tree from the Bayesian analysis (Fig. 3) exhibited a few incongruences in the earlier divergent clades, but none of these was well supported (BS < 50, PP < 0.85). For clades A–H resulting from the plastid DNA analysis, only clade G was recovered; all the rest exhibited incongruences. With respect to the phylogenetic relationships of the *T. utriculata* complex *s.s.*, only two clades were recovered: one with weak support (BS = 73, PP = 1), which included *T. calcicola*, *T. elusiva* and *T. utriculata*, and another with moderate support based on the Bayesian analysis (PP = 0.98), which included species of the *T. limbata* clade (according to the plastid DNA data) and all specimens of *T. pringlei*. *Tillandsia fuchsii* and *T. socialis* formed a group with stronger support than in the analyses based on plastid DNA regions (BS = 87, PP = 1).

Test of incongruence

The ILD test showed that the matrices of plastid DNA and ETS are significantly incongruent ($P = 0.0909$).

Character evolution and biogeographical analyses (Fig. 4)

Tillandsia utriculata syndrome

The reconstruction of ancestral states indicated that this set of characters coincided together in clade A at least three times independently. In clade B, they were found together at least once, although it is not clear whether there are two reversions or three gains. All species of this clade have in common many features of the *T. utriculata* complex, with the exception of *T. adpressiflora* and *T. marnier-lapostollei* which have included stamens and *T. spiraliflora* which has polystichous flowers.

In the core Mexican clade (excluding the clade formed by *T. punctulata*, *T. gymnobotrya* and *T. prodigiosa*), these characters are again found together. Most of the species have stamens and style exserted, but clade H has lost the Group II floral morphology and changed to Group I floral morphology, whereas, in clade G, there is a reversion to included stamens.

Floral morphology

The Group II-type floral morphology presumably emerged at least four times: once in clade B, with one reversion; one to three times in clade C; and one to four times in clade D. The reconstruction placed this morphology as ancestral for the clade formed by clades E, F, G and H and *T. fuchsii*, *T. tehuacana* and *T. nicolasensis*. The evolution of violet petal colour is ambiguous for clade A, but ancestral for clades B and D. The ancestral state of clade E is whitish, whereas the ancestral state for clade F is ambiguous. For one subclade of clade F, composed of *T. izabalensis*, *T. limbata*, *T. dasyliriifolia*, *T. comitanensis* and *T. may-patii*, the ancestral petal colour was whitish. Red petal colour evolved independently twice, once in clade C and another in clade D, with *T. nicolasensis*.

Vegetative reproduction

The ancestral form of vegetative reproduction in clade A was the production of axillary propagules. The change to monocarpic plants presumably occurred independently at least seven times. The ancestral state of clade E is ambiguous, although monocarpy evolved at least once in this clade (in *T. utriculata* and *T. elusiva*). In this clade, caespitose growth emerged at least once, in *T. pringlei* and

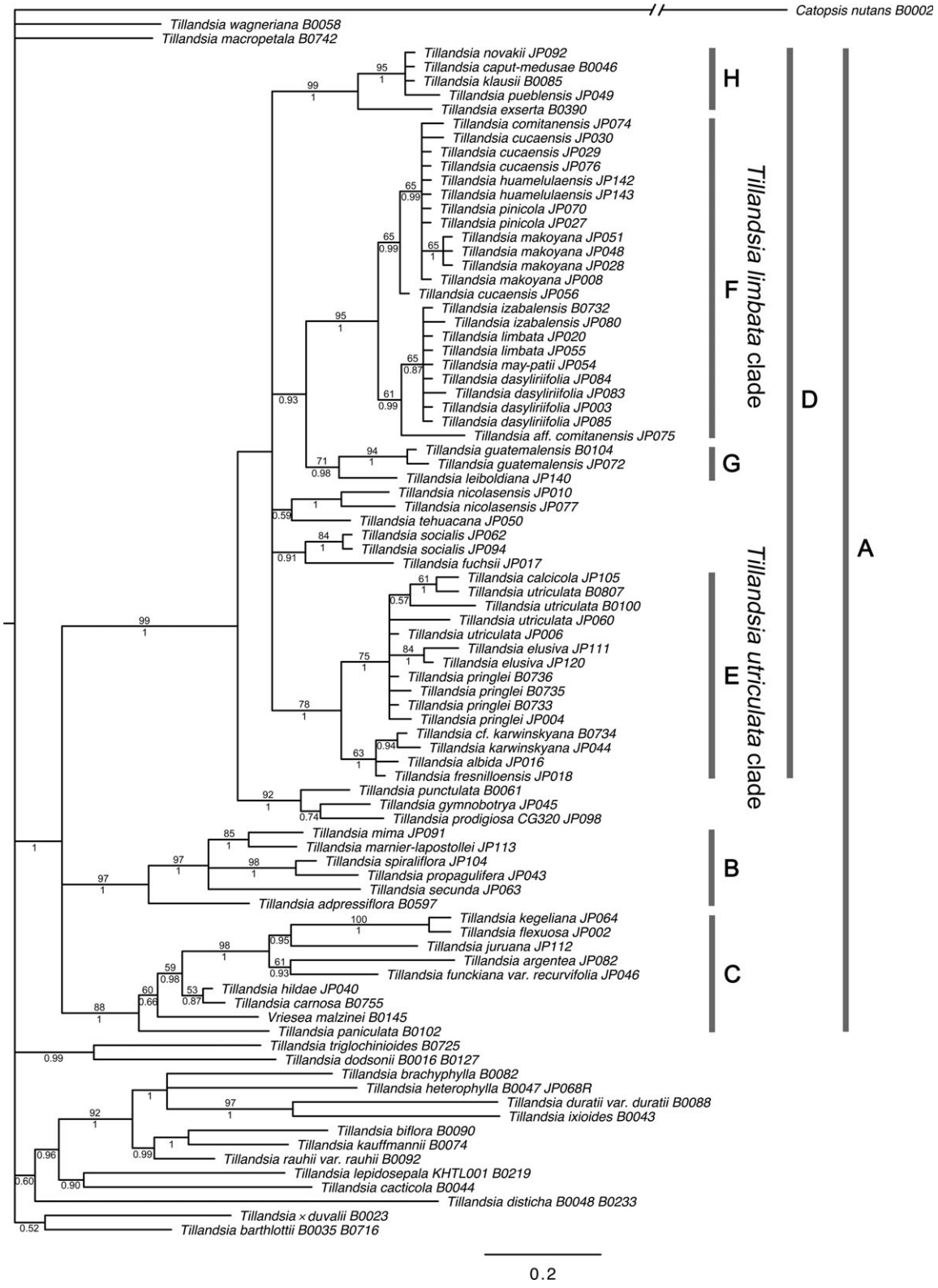


Figure 2. Majority rule consensus phylogram from the Bayesian inference analysis of species of the *Tillandsia utriculata* complex *s.l.* and the outgroup, using the plastid DNA regions *matK*, *trnK*, *rps16*, *rpl32-trnL* and indels from the last two (restricted analysis). Above and below each branch, we indicate the bootstrap and posterior probability values, respectively. For a description of the clades labelled with letters, see text.

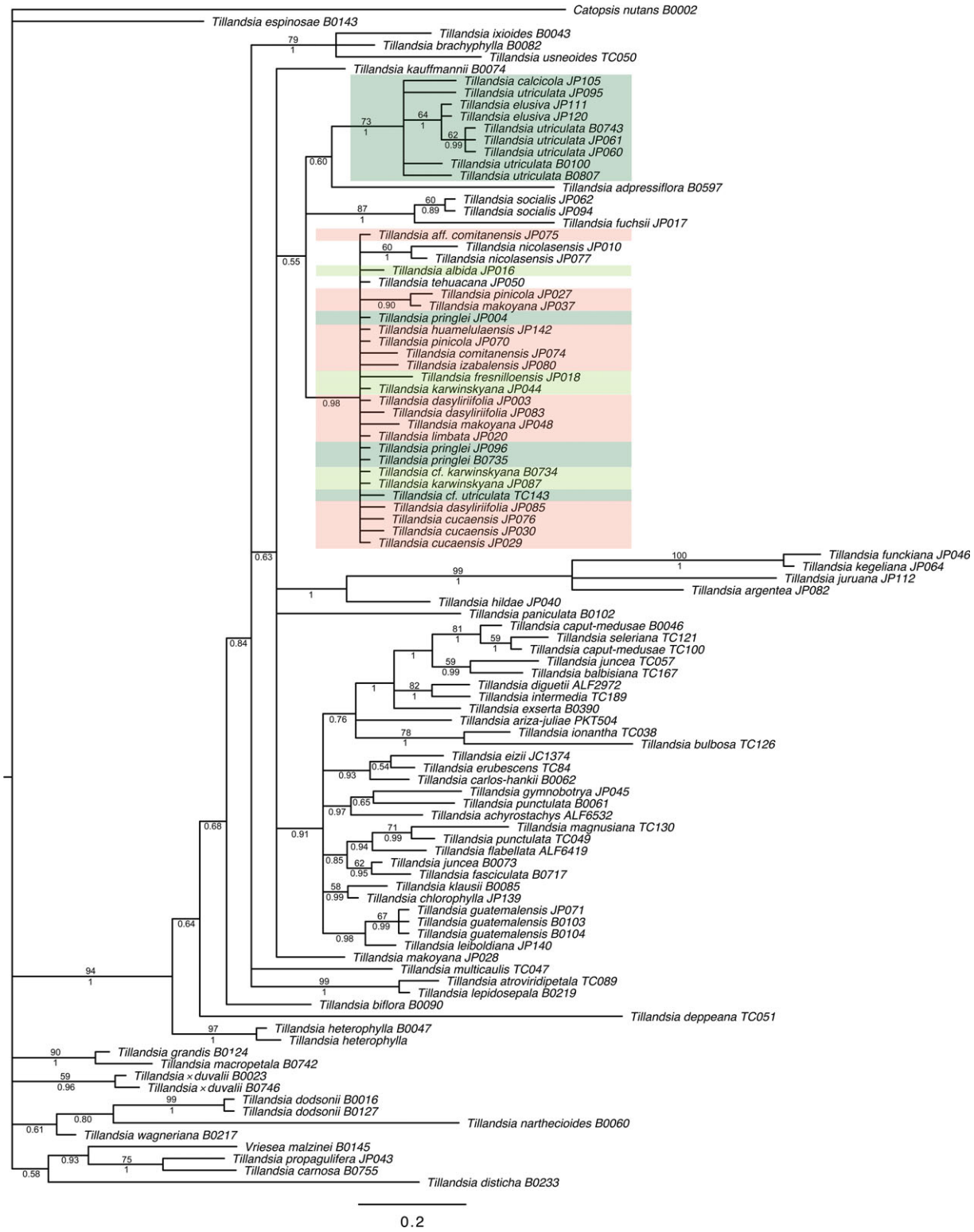


Figure 3. Majority rule consensus phylogram from the Bayesian inference analysis of species of the *Tillandsia utriculata* complex *s.l.* and the outgroup, using the external transcribed spacer (ETS) region from the nuclear ribosomal DNA (restricted analysis). Above and below each branch, we indicate the bootstrap and posterior probability values, respectively. Green: species of the *T. utriculata* clade complex according to results using plastid DNA; dark green, Gulf-Antillean Clade; light green, Mexican Plateau Clade; salmon pink, *T. limbata* clade.

Figure 4. Parsimony-based reconstruction of the ancestral states of five morphological characters, one ecological character and the areas of distribution of the *Tillandsia utriculata* complex and the outgroup. On the branches the series of transformations are indicated by symbols: (1) the solid black rectangular tick indicates the emergence of the *T. utriculata* morphological syndrome, the white rectangular tick indicates its loss; (2) the solid black arrow indicates the emergence of the Group II floral morphology, the white arrow indicates its loss; (3) the ellipse represents the different methods of vegetative reproduction (or absence) indicated by colours: monocarpic genet (white), axillary propagules (green), basal propagules (blue), caespitose growth (red), propagules in the inflorescence (violet); (4) the inflorescence colour is indicated by the colour of the symbol 'flower with stem'; (5) the petal colour is indicated by the colour of the symbol 'corolla'; (6) the growth substrate is represented by a tree and the states indicated by colour: epiphyte (green), lithophyte (grey), terrestrial (orange). The areas of distribution are represented by the colour of the branches and the regions are indicated in the map in the top left corner. These characters were mapped on the strict consensus of 63 most-parsimonious trees (MPTs) from the parsimony analysis of the *T. utriculata* complex *s.l.* and the outgroup, using the plastid DNA regions *matK*, *trnK*, *rps16*, *rpl32-trnL* and indels from the last two (restricted analysis). The pie diagrams show the probabilities of ancestral distribution areas for selected nodes from an analysis of the Bayesian binary Markov chain Monte Carlo (MCMC) method obtained from one of the 63 MPTs from the analysis described above; colour grey indicates an uncertain area or two or more areas. For a description of the clades labelled with letters, see text.

in the clade formed by *T. albida*, *T. karwinskyana* and *T. fresnilloensis*. Propagation via basal propagules, but without caespitose growth, arose at least four times in clade A, once in clade B (*T. mima*), once in clade C (*T. hildae*) and at least five times in clade D. In the *T. limbata* clade (clade F), monocarpy evolved at least three times, in *T. comitanensis*, *T.* aff. *comitanensis*, *T. izabalensis* and *T. huamelulaensis*. In contrast, the production of propagules in the inflorescence arose independently at least three times, once in clade B, once in clade C (*T. flexuosa*) and once in clade F (*T. dasyliriifolia*).

Epiphytism

Epiphytism is the ancestral state in clades A, C, D, F, G and H. The ancestral states of clades B and E are ambiguous. The invasion of the saxicolous habitat occurred at least six times in clade A, once in clade B, three times in clade C, at least once in clade E and at least once in clade H. The invasion of terrestrial habitats occurred only once in clade A, with *T. dasyliriifolia* (clade F).

Biogeographical analysis

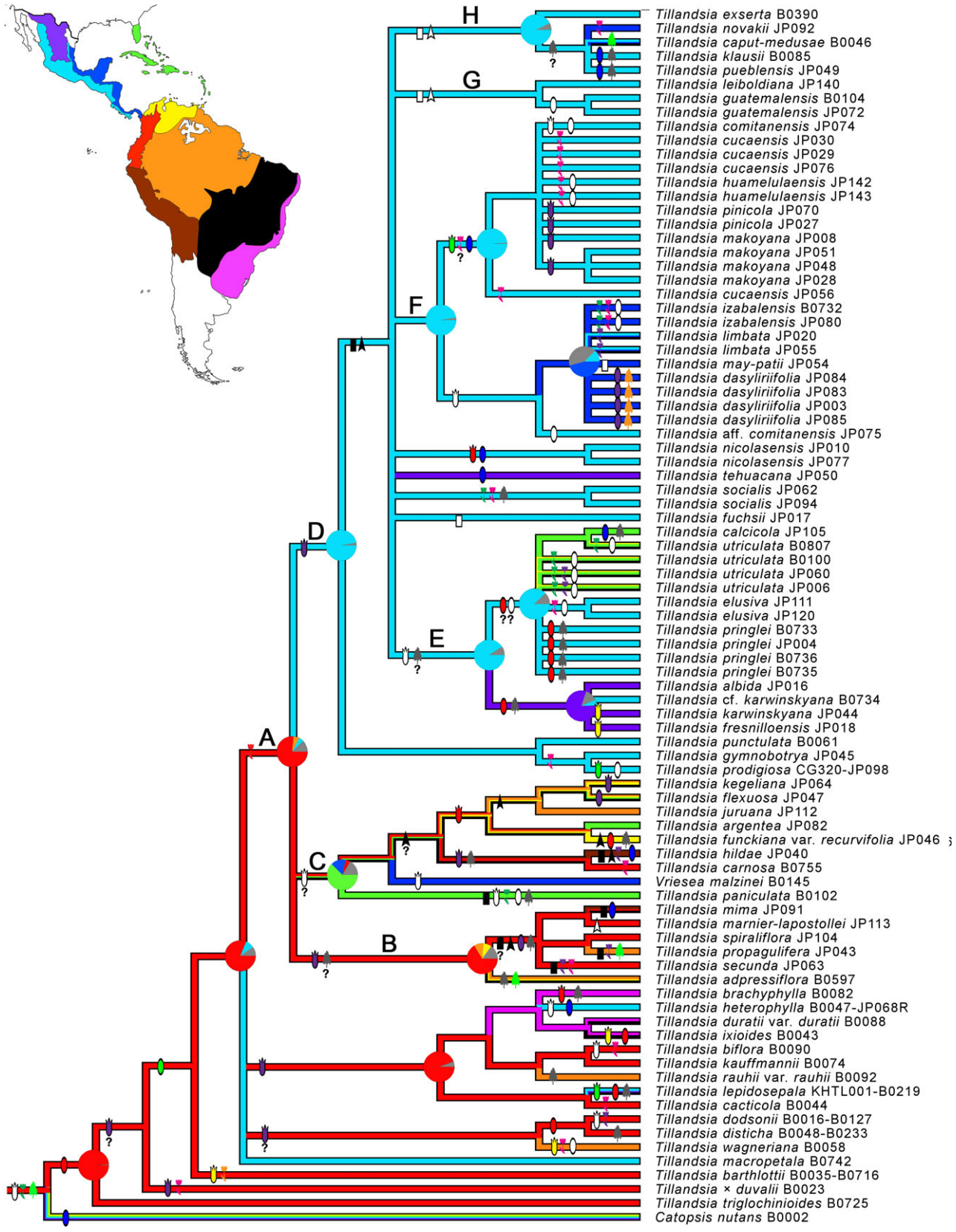
The parsimony-based character state reconstruction indicated that the northern zone of the Andean Region was the ancestral distribution for clades A and B, and this is congruent with the BBM ancestral state reconstruction, which reports a probability of 86.1% and 76.0%, respectively, for the same area. In the latter clade, there was one colonization to the Amazonian region (*T. adpressiflora*). The ancestral distribution area of clade C is ambiguous with parsimony, but BBM analysis showed a probability of 63.9% for the West Indies as the ancestral area for this node. This clade exhibits a broad distribution and is represented in the southern and northern Andes, in northern Venezuela, in the West Indies, in the Amazonian region and in the eastern Mesoamerican Zone. Conversely, the ancestral area of distribution of clade D, according to both parsimony-based reconstruction and BBM, was the western Mesoamerican Zone (97.6%). From this point, there were two colonizations of the Mexican Plateau, one with *T. tehuacana* and another with clade E (the latter at 78.9%), at least two colonizations of the eastern Mesoamerican Zone (one in clade F and one in clade H), and at least one colonization of the West Indies and Florida in clade E (*T. utriculata* and *T. calcicola*).

DISCUSSION

General considerations

To date, the broad analysis presented in our study includes the largest number of *Tillandsia* spp. (108 species of > 620 species in this genus; Luther, 2012). The number of species used in this analysis represented 17.4% of the species of this genus, in contrast with the 58 species (9.3%) analysed by Barfuss *et al.* (2005). It is important to note that the sampling of taxa conducted in our study was designed to assess the phylogenetic position of the species of the *T. utriculata* complex and of species with similar morphology in *Tillandsia*, and to determine the phylogenetic relationships among these species. As a result of the bias in our sampling scheme, any conclusions about the results from phylogenetic analyses at the generic or subgeneric level should be taken with caution. Having said this, we proceed to make observations for some of the most important results from these analyses.

Clade A, or the clade of *Tillandsia* subgenus *Tillandsia s.s.*, is equivalent to clade K plus *T. paniculata* in the study of Barfuss *et al.* (2005). According to our results, this clade presumably originated in


H
G
F
E
D
C
B
A
Tillandsia exserta B0390
Tillandsia novakii JP092
Tillandsia caput-medusae B0046
Tillandsia klausii B0085
Tillandsia pueblensis JP049
Tillandsia leiboldiana JP140
Tillandsia guatemalensis B0104
Tillandsia guatemalensis JP072
Tillandsia comitanensis JP074
Tillandsia cucaensis JP030
Tillandsia cucaensis JP029
Tillandsia cucaensis JP076
Tillandsia huamelulaensis JP142
Tillandsia huamelulaensis JP143
Tillandsia pinicola JP070
Tillandsia pinicola JP027
Tillandsia makoyana JP008
Tillandsia makoyana JP051
Tillandsia makoyana JP048
Tillandsia makoyana JP028
Tillandsia cucaensis JP056
Tillandsia izabalensis B0732
Tillandsia izabalensis JP080
Tillandsia limbata JP020
Tillandsia limbata JP055
Tillandsia may-patii JP054
Tillandsia dasyliriifolia JP084
Tillandsia dasyliriifolia JP083
Tillandsia dasyliriifolia JP003
Tillandsia dasyliriifolia JP085
Tillandsia aff. comitanensis JP075
Tillandsia nicolasensis JP010
Tillandsia nicolasensis JP077
Tillandsia tehuacana JP050
Tillandsia socialis JP062
Tillandsia socialis JP094
Tillandsia fuchsii JP017
Tillandsia calcicola JP105
Tillandsia utriculata B0807
Tillandsia utriculata B0100
Tillandsia utriculata JP060
Tillandsia utriculata JP006
Tillandsia elusiva JP111
Tillandsia elusiva JP120
Tillandsia pringlei B0733
Tillandsia pringlei JP004
Tillandsia pringlei B0736
Tillandsia pringlei B0735
Tillandsia albida JP016
Tillandsia cf. karwinskyana B0734
Tillandsia karwinskyana JP044
Tillandsia fresnilloensis JP018
Tillandsia punctulata B0061
Tillandsia gymnobotrya JP045
Tillandsia prodigiosa CG320-JP098
Tillandsia kegeliana JP064
Tillandsia flexuosa JP047
Tillandsia juruana JP112
Tillandsia argentea JP082
Tillandsia funckiana var. recurvifolia JP046
Tillandsia hildae JP040
Tillandsia carnosa B0755
Vriesea malzinei B0145
Tillandsia paniculata B0102
Tillandsia mima JP091
Tillandsia marnier-lapostollei JP113
Tillandsia spiraliflora JP104
Tillandsia propagulifera JP043
Tillandsia secunda JP063
Tillandsia adpressiflora B0597
Tillandsia brachyphylla B0082
Tillandsia heterophylla B0047-JP068R
Tillandsia duratii var. duratii B0088
Tillandsia ixioides B0043
Tillandsia biflora B0090
Tillandsia kauffmannii B0074
Tillandsia rauhii var. rauhii B0092
Tillandsia lepidosepala KHTL001-B0219
Tillandsia cacticola B0044
Tillandsia dodsonii B0016-B0127
Tillandsia disticha B0048-B0233
Tillandsia wagneriana B0058
Tillandsia macropetala B0742
Tillandsia barthlottii B0035-B0716
Tillandsia × duvalii B0023
Tillandsia triglochinioides B0725
Catopsis nutans B0002

the northern Andes (at 86.1% probability; this and all further probabilities are based on BBM analysis) (Fig. 4) from an epiphytic ancestor with red inflorescences. All the species with the *T. utriculata* complex syndrome are found in clade A, although the ancestor of this clade presumably did not exhibit this morphology (Fig. 4). In clade A, the species with the *T. utriculata* complex syndrome do not form a monophyletic group; rather this combination of characters arose in at least four independent events (Fig. 4).

The *Tillandsia utriculata* complex *s.l.*

Early-diverging clades

Clades B and C are composed mostly of South American species, some of which exhibit the morphology of the *T. utriculata* complex, but were excluded by Ramírez *et al.* (2004) based on their definition of the complex, and have not been associated with these species in any other study. In clade B (clade of *T. secunda*), which originated in the northern Andes, the species that share the *T. utriculata* syndrome are *T. secunda*, *T. propagulifera* and *T. mima* (Fig. 4). The rest of the species are similar, but differ in some characters. For example, *T. adpressiflora* and *T. marnier-lapostollei* differ from this syndrome only in that they have stamens that are included in the corolla (subgenus *Allardtia*), whereas the only character that separates *T. spiraliflora* is the polystichous flowers. Conversely, species of clade C (clade of *T. paniculata*) exhibit morphological variation and a broader geographical distribution. In this clade, we find *Vriesea malzinei*, which is morphologically strikingly dissimilar (mesic species, imbricate floral bracts, appendices in the petals) and a clade that includes species with red petals (*T. funckiana*, *T. argentea*, *T. flexuosa*, *T. kegeliana* and *T. juruana*) (Figs 1, 2, 4). Only *T. hildae* and *T. paniculata* exhibit the *T. utriculata* complex syndrome. *Tillandsia paniculata* is considered to be part of *Tillandsia* subgenus *Pseudalcantarea* because of its stamen and petal morphology (Smith & Downs, 1977), but Beaman & Judd (1996) concluded that this species is more closely related to subgenus *Tillandsia*, and this is consistent with our findings. The ancestral distribution of this clade is uncertain, but the BBM shows a slight preference for the West Indies geographical zone.

Tillandsia socialis, which shows a morphology coherent with the *T. utriculata* complex, is found in the Mexican clade (D). However, it does not group with the *T. utriculata* clade, but with *T. fuchsii*, albeit with relatively low support. These two species share the floral morphology of Group II as a symplesiomorphy. Nonetheless, the presence of scales on the floral bracts represents a synapomorphy of this clade. *Tillandsia fuchsii* has lost some of the typical characteristics of the *T. utriculata* complex, given that the flowers of this species are spreading with respect to the rachis (not appressed) and it has undergone a reduction in size, growing as small, globose rosettes with filiform leaves.

The *Tillandsia utriculata* clade

This lineage is supported by three homoplasious morphological characters, all of which are associated with the petals, namely spathulate shape, acute apex and the loss of violet pigment (petals in these species are whitish or greenish) (Figs 4–6). As a result of the lack of resolution in clade D, the interpretation of the evolution of the ancestral characters is ambiguous in many cases. However, it is possible to infer that the ancestor of this clade already had a morphology similar to the *T. utriculata* complex and exhibited an inflorescence with red tinges and, as mentioned previously, whitish petals. What remains uncertain, however, is whether this ancestor was epiphytic, had vegetative reproduction or was monocarpic. The distribution of this ancestor could have been restricted to the western Mesoamerican Zone, from where some species presumably invaded the eastern Mesoamerican Zone, the Antilles and Florida in one direction and the Mexican Plateau in another direction (Fig. 4).

The Gulf-Antillean clade (*T. utriculata*, *T. calcicola, T. elusiva* and *T. pringlei*) was named because it has a distribution that is limited to the west by the Sierra Madre Oriental and occupies the Gulf of Mexico, the Continental Caribbean shore (except Panama), the Antilles, Florida and northern Venezuela. The Mexican Plateau clade (*T. albida*, *T. karwinskyana* and *T. fresnilloensis*) is restricted to this dry and high area.

The Gulf-Antillean clade is formed by species distributed from eastern Mesoamerica and the Antilles, which share several morphological characteristics: paniculate inflorescences; a zygomorphic corolla with a lateral opening; and warty wing cells of the foliar scales, which have an entire or crenate margin (Fig. 5). The ancestral area analysis indicated that the most probable ancestral distribution area of this clade was the western Mesoamerican Zone. This ancestor presumably colonized warm montane and humid lowland areas with xeric *T. calcicola* in the Antilles and with mesic *T. utriculata*, which has the broadest distribution in this complex, as it is found from arid zones of the Yucatan Peninsula (Mexico) and the Antilles, to warm and humid zones in Mesoamerica, the Gulf of Mexico and the Continental Caribbean slopes and subtropical areas in Florida. *Tillandsia elusiva* occupied a zone restricted to intermediate elevations of warm and subhumid

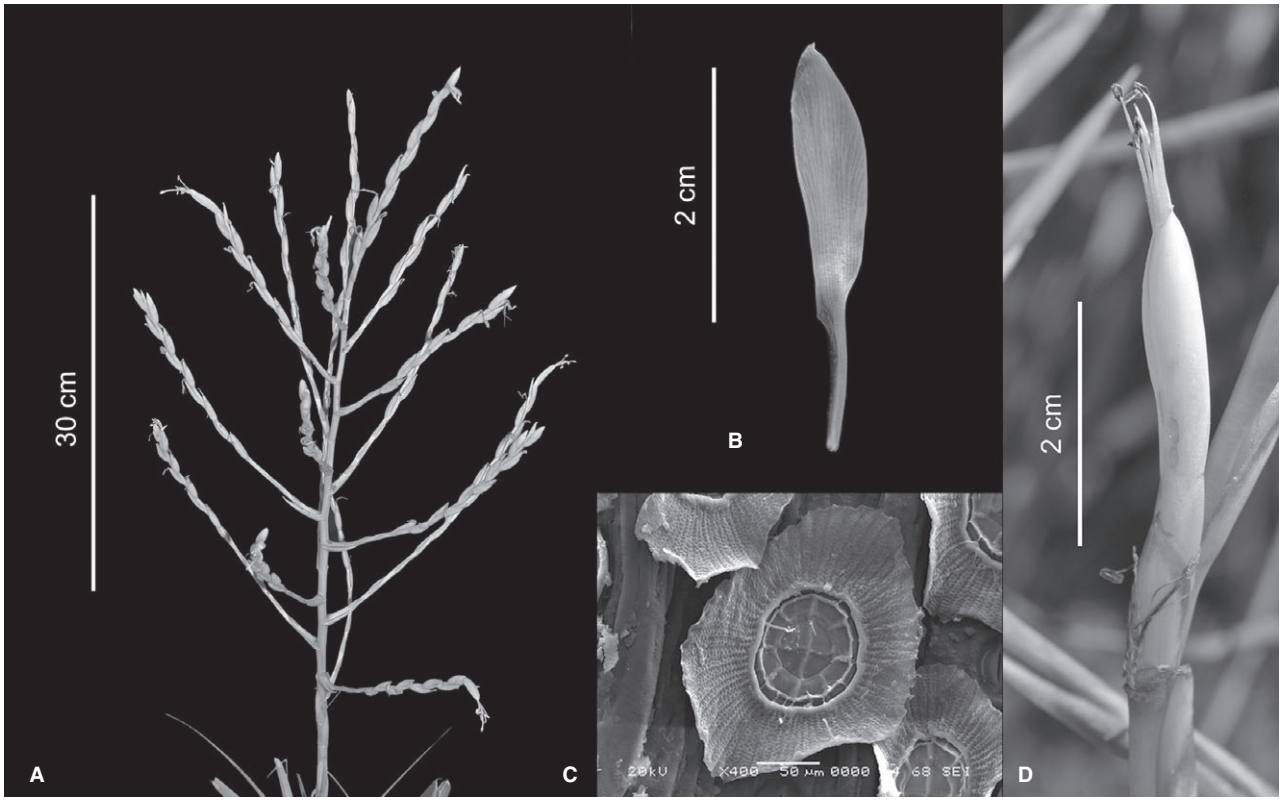


Figure 5. Morphology of the species of the *Tillandsia utriculata* clade, Gulf-Antillean Clade. A, Inflorescence of *T. elusiva*. B, Petal of *T. utriculata* (note acute apex). C, Foliar trichome of *T. utriculata* (note entire margin). D, Flower of *T. pringlei* (note the lateral opening of the corolla).

climatic conditions in western Chiapas, at the limit of the Gulf of Mexico and Pacific provinces (Pinzón *et al.*, 2011). This species is the only one in the *T. utriculata* clade that has a pink inflorescence (Fig. 4).

The species of the Mexican Plateau clade (*T. albida*, *T. fresnilloensis* and *T. karwinskyana*) share simple inflorescences and foliar scales with a dentate margin, in addition to having reddish inflorescences with whitish petals and spreading petal tips (Fig. 6). In this group, *T. albida* (caulescent, with reticulate ornamentation in the wing cells of foliar scales) is the earliest diverging species and subtends the clade formed by *T. fresnilloensis* and *T. karwinskyana* (acaulescent, with smooth wing cells of foliar scales). The ancestor of these three species was probably distributed in the Mexican Plateau, growing on rocks and exhibiting caespitose growth (Fig. 4). The aspect of this ancestor may have been similar to that of *T. albida* but acaulescent, as it presumably had conspicuous foliar sheaths and a dense indumentum, but with scales appressed to the leaf, without the tomentose aspect found in *T. fresnilloensis* and *T. karwinskyana*, which lack conspicuous foliar sheaths. This ancestor presumably was adapted to rocky environments in south-eastern areas of the Mexican Plateau, in the states of Hidalgo, Querétaro and Guanajuato, where it gave rise to *T. albida*, and to more northern areas with gypsum-rich outcrops, where it gave rise to *T. karwinskyana*. Towards the western side of the plateau, this ancestor gave rise to *T. fresnilloensis*, where it adapted to volcanic rocks present in the Sierra de Órganos and related systems in the states of Zacatecas, Durango and Jalisco.

The *Tillandsia limbata* clade

The *T. limbata* clade (F) is composed almost exclusively of species restricted to or including Mexico in their distribution range, the only exception being *T. izabalensis* which is distributed from Honduras to Nicaragua (Pinzón *et al.*, 2012). The inclusion of *T. nicolasensis* and *T. tehuacana* in this complex is weakly supported and only evident in the broad analysis of *matK-trnK* and *rps16* (Fig. 1). Nonetheless, all species of clade F can be differentiated from the *T. utriculata* clade in that the apex of the petal is rounded and they have a constriction of the corolla at the height of the ovary apex (Fig. 7). In any case, *T. nicolasensis* and *T. tehuacana* appear to have

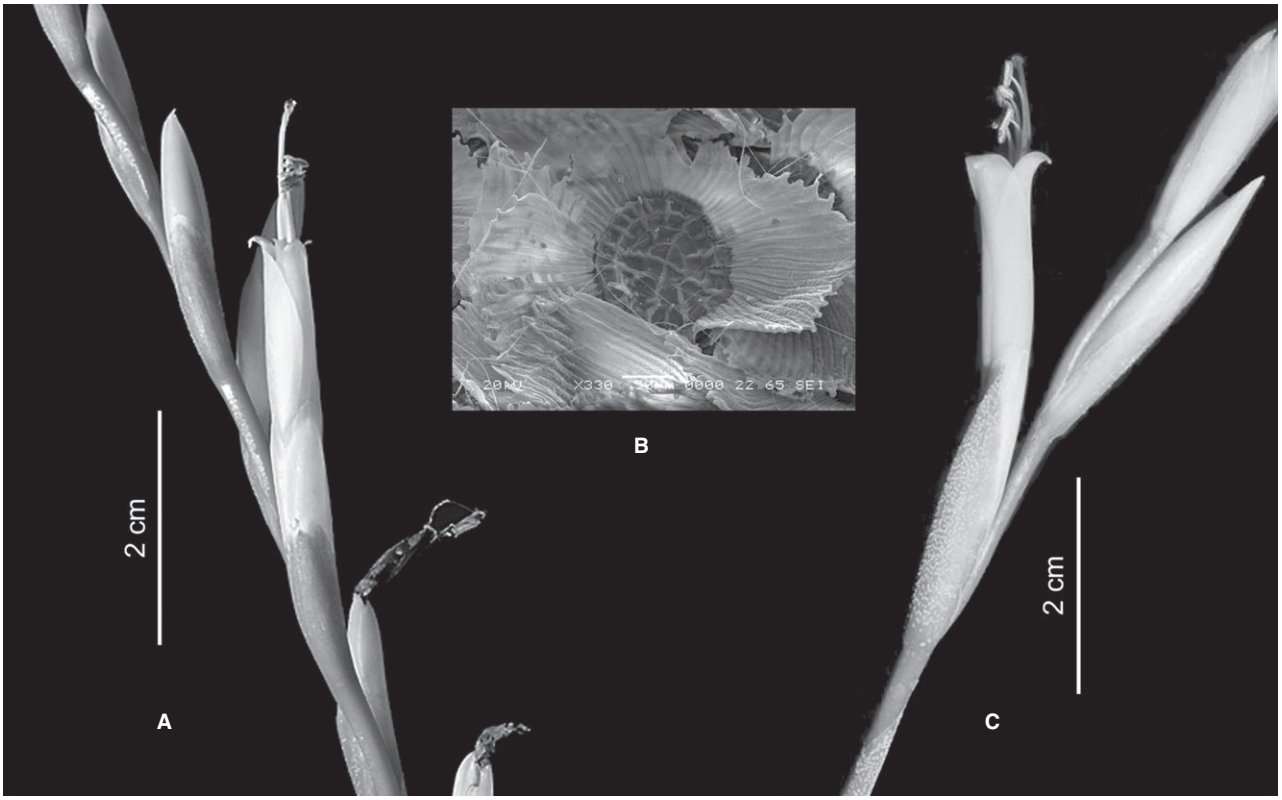


Figure 6. Morphology of the species of the *Tillandsia utriculata* clade, Mexican Plateau Clade. A, Inflorescence of *T. karwinskyana*. B, Foliar trichome of *T. albida* (note the dentate margin). C, Flower of *T. fresnilloensis*.

diverged earlier than the rest of the species belonging to the complex. The ancestor of the *T. limbata* clade, including *T. nicolasensis* and *T. tehuacana*, was presumably distributed in the western Mesoamerican Zone. From there, it migrated and gave rise to *T. tehuacana* in the high-elevation and arid eastern zone of the Trans-Mexican Volcanic Belt Province (Morrone, 2005) and adjacent areas, or in the Valle de Tehuacán-Cuicatlán Province in the phytogeographical scheme of Rzedowski (1978). *Tillandsia nicolasensis* remained in the lowlands and eventually occupied (as at present) coastal areas in southern Mexico. An autapomorphic change that appeared in this species is the red pigment in the petals, which is a unique characteristic in this complex and is rare in the Mexican clade and in *Tillandsia* as a whole (Smith & Downs, 1977) (Fig. 4).

The western Mesoamerican clade (*T. comitanensis*, *T. cucaensis*, *T. huamelulaensis*, *T. pinicola* and *T. makoyana*) is unresolved, except for the position of one early-diverging specimen of *T. cucaensis*, which is separated from the rest of the species, which themselves form a polytomy that includes the remaining specimens of *T. cucaensis*. This early-diverging specimen could represent a cryptic species, but phylogeographical analyses are needed to test this hypothesis.

Although the eastern Mesoamerican clade (*T. izabalensis*, *T. limbata*, *T. may-patii* and *T. dasyliriifolia*) has moderate to low support, it exhibits geographical, morphological and ecological congruence. The inclusion of *T. may-patii* in this clade is remarkable because this taxon does not exhibit the characteristics of the *T. utriculata* complex, instead having a cylindrical and compact paniculate inflorescence and imbricate bracts. *Tillandsia may-patii* is probably a natural hybrid for which *T. dasyliriifolia* is the maternal parent, as this species is the only species in this clade that is sympatric with the former (Ramírez & Carnevali, 1999). The ancestor of the *T. limbata* clade presumably colonized lowlands with a warm subhumid climate present in the Gulf of Mexico and Gulf of Honduras coming from the west, from the other side of the mountains in Mexico and Central America. The invasion of this biogeographical zone presumably occurred once in the *T. limbata* clade, but it is not clear whether the ancestral area of distribution was the actual eastern Mesoamerican Zone (42.68%) or a broader area, including both eastern and western Mesoamerican Zones (42.93%). This ancestor had, according to the parsimony-based reconstruction, reddish inflorescences, whitish petals, was an epiphyte and produced

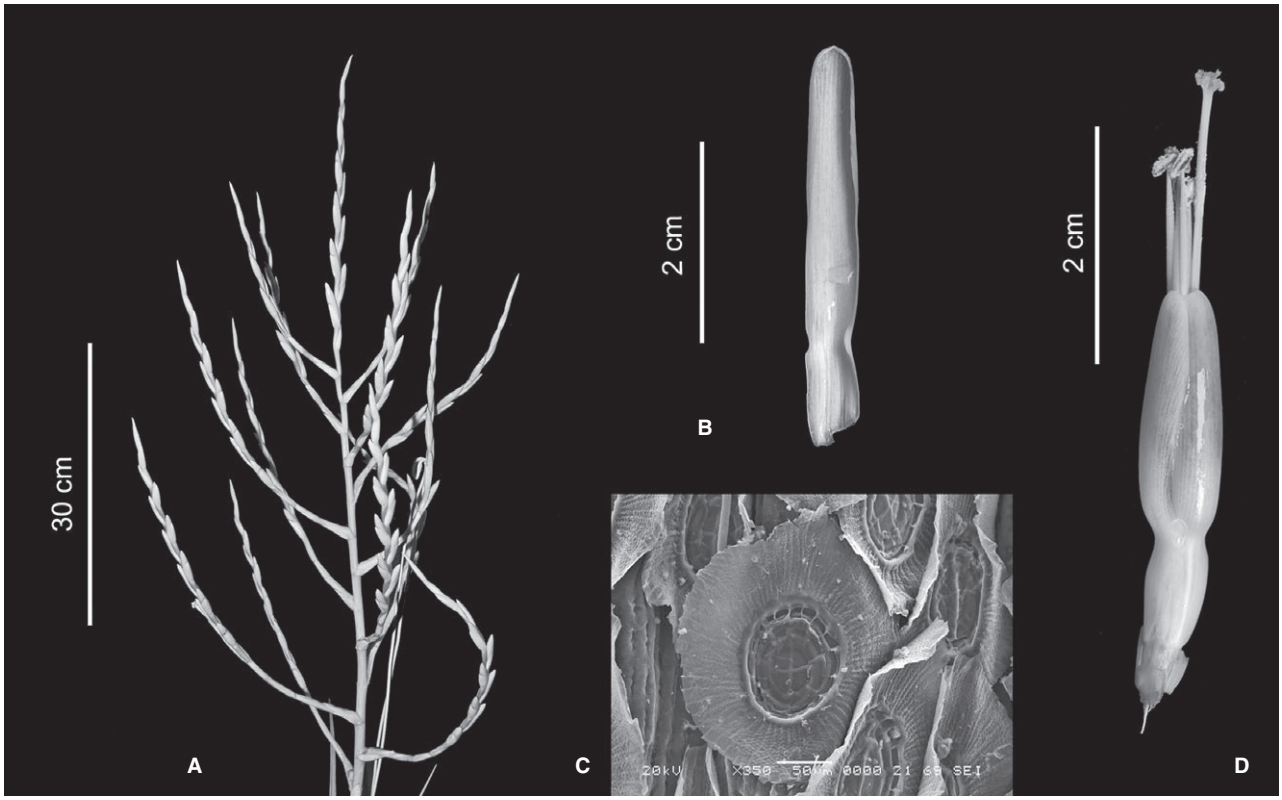


Figure 7. Morphology of the species of the *Tillandsia limbata* clade. A, Inflorescence of *T. cucaensis*. B, Petal of *T. cucaensis* (note the rounded apex). C, Foliar trichome of *T. dasyliriifolia*. D, Corolla, androecium and gynoecium of *T. pinicola* (note the constriction towards the base of the corolla).

axillary propagules (Fig. 4). The three species of the eastern Mesoamerican clade invaded different environments: *T. dasyliriifolia* became established on the Yucatan Peninsula, in warm subhumid environments, and in the arid north-western zone of this region as an epiphytic or terrestrial species with the capacity to produce propagules in the inflorescence (Fig. 4); *T. limbata* occupies the warm and humid region of the Gulf of Mexico and the temperate subhumid mountainous zone of the Sierra Madre Oriental and northern Chiapas (this colonization to mid-elevations was secondary); and *T. izabalensis* occupies the warm humid zone of the Gulf of Honduras, of southern Belize, Guatemala, Honduras and northern Nicaragua. Based on this information, the ancestor of the Gulf-Caribbean clade could have been similar in aspect to *T. izabalensis*.

The ETS nrDNA

The most interesting finding of this analysis is that the Mexican Plateau species of the *T. utriculata* clade and *T. pringlei* are grouped in a lineage together with species of the *T. limbata* clade and not with *T. utriculata*, *T. calcicola* and *T. elusiva* (Fig. 3). This incongruence could have been caused by homoplasious characters (which probably resulted in low support), but could also be indicative of reticulate evolution for which species of the Mexican Plateau clade and *T. pringlei* would have shared a maternal parent of the *T. utriculata* clade and a paternal parent of the *T. limbata* clade. Nonetheless, further exploration using more nuclear molecular markers is needed to reach stronger conclusions in this regard. What is clear is that *T. pringlei* is different from *T. utriculata*, as it is located outside the Gulf-Antillean clade, with up to seven different positions in the alignment.

With regard to the remaining species of the Gulf-Antillean clade, we observed a grouping that included *T. utriculata* specimens from the humid zone of the Gulf and continental Caribbean slopes (Chiapas and Guatemala) and *T. elusiva*, which is found in subhumid and semiarid environments of the transition zone of the Gulf of Mexico Province and the Pacific Province (*sensu* Morrone, 2005). From these results, we did not find evidence that *T. elusiva* is a hybrid between *T. utriculata* and any species of the *T. limbata* clade, as suggested by Gardner (1984). The specimens of *T. utriculata* from the Antilles and *T. calcicola* formed a polytomy at the

base of the Gulf-Antillean clade. Because of the low resolution of the clade, it is not possible to determine whether the populations of the continental tropical area form a species that is different with respect to Antillean populations, as there were insufficient morphological differences to separate them. The only difference we detected was the inflorescence colour, which is dark purple in the continental populations from humid zones and red or green in the populations from the Antilles and the Yucatan Peninsula.

Incongruence of plastid DNA and ETS phylogenetic trees

It is important to mention that results based solely on plastid DNA data, as used primarily in this study, only allow the discussion of maternal-side phylogenetic relationships. In a group with no reticulate evolution, the maternal and paternal phylogenetic history should be identical, but we have evidence that natural hybridization in *Tillandsia* is, if not ubiquitous, at least possible, and there are several reports of putative natural hybrids (Gardner, 1984). Furthermore, there is evidence of reticulate evolution and probably plastid capture in other genera of Bromeliaceae, e.g. in *Puya* Molina, in which plastid data strongly support a Chilean clade, whereas the *PHYC* marker splits Chilean *Puya* into two clades, one of them sister to the core *Puya* clade (Jabaily & Sytsma, 2010). A similar pattern occurs in the *Deuterocohnia* Mez/*Abromeitiella* Mez alliance, which, with nuclear DNA data, forms a monophyletic group, but, with plastid DNA, forms a paraphyletic group, with one of the clades sister to *Dyckia* Schult.f. and *Encholirium* Mart. ex Schult.f. (Schütz, 2012). The author interprets this pattern as plastid capture from a *Dyckia*/*Encholirium* ancestor through hybridization and introgression of a *Deuterocohnia* ancestor through pollination (Schütz, 2012).

Although we found that the matrices with plastid DNA and ETS are not congruent, as the ILD test shows, there are not hard incongruences in the phylogenetic trees, i.e. the incongruent clades in the analysis with ETS have low support. Hence, these incongruences could be a result of plastid capture, but also could be an effect of high homoplasy in the ETS data. To assess this, it is necessary to explore other nuclear DNA markers for comparison with the phylogenetic trees obtained with plastid data.

Comparison with other phylogenetic studies

Previous phylogenetic studies included only a few species of the *T. limbata* and *T. utriculata* clades obtained here. One of the first phylogenetic studies of Bromeliaceae (Terry *et al.*, 1997b) only included *T. utriculata*, which was located in a clade with *T. secunda* and *Vriesea espinosae* (L.B.Sm.) Gilmartin. Excluding *V. espinosae*, this clade would be equivalent to clade A in our study. It seems likely that there was an error in assigning the sequence to *V. espinosae*, as this species is located outside clade A, with other grey-leaved xeric *Vriesea* spp. (Barfuss, 2012). The study of Barfuss *et al.* (2005) only included two accessions of *T. utriculata* which were located in a clade that is equivalent to clades D (clade K in Barfuss *et al.*, 2005) and A (equivalent to clade K plus *T. paniculata* in Barfuss *et al.*, 2005) in our study, and therefore results are consistent. In addition, the phylogenetic study of the *T. macdougallii* L.B.Sm. complex by Granados (2008) included *T. utriculata* and *T. makoyana*. These species formed a polytomy in a clade equivalent to clade D in our study. Also, the phylogenetic analysis with ETS by Chew *et al.* (2010) for species of *T.* subgenus *Tillandsia* with pseudobulbs did not resolve the relationships of *T. utriculata*, which formed a polytomy at the base of their cladogram (excluding *T. deppeana* Steud.); on the other hand, *T. dasyliriifolia* and *T. makoyana* were grouped in a clade with low support (BS = 62), which is consistent with clade F in our study. In the combined analysis of 5.8S, ITS2, ETS nrDNA and coded indels as a fifth state, *T. makoyana* was grouped with *T. filifolia* Schltdl. & Cham., although this relationship is unsupported. However, the coding of indels as a fifth character state is controversial and has not been used often, because it can be redundant in indel-rich markers, giving excessive weight to indels during the phylogenetic reconstruction. This relationship is also not consistent with our analyses, even in the topology obtained here with the ETS nrDNA (Fig. 3).

CONCLUSIONS

Based on our phylogenetic analyses, we conclude that the species that share characteristics of the *T. utriculata* complex do not constitute a monophyletic group, and we instead suggest that this syndrome has been gained and lost repeatedly throughout the evolution of *T.* subgenus *Tillandsia*. However, all the species with this morphology are located in a clade dominated by species of *T.* subgenus *Tillandsia.* The South American species with this morphology are found in two lineages in a trichotomy with the Mexican clade in *T.* subgenus *Tillandsia* and are not closely related to *T. utriculata*. The species originally proposed as part of the complex (*T. utriculata s.l.*) are found in a predominantly Mexican clade, forming two lineages: the *T. utriculata* clade and the *T. limbata* clade. Based on the available information, it is not possible to determine

whether these two complexes represent a monophyletic group. The origin of both lineages appears to be western and central Mesoamerica and the *T. utriculata* complex is symplesiomorphic. In this zone, there were several colonizations of different habitats. The Mexican Plateau clade underwent a diversification in this area and gave rise to lithophytic species with caespitose growth and simple inflorescences; the Gulf-Antillean clade presumably migrated to the Gulf of Mexico region and Antilles, whereas monocarpy arose in *T. utriculata* and *T. elusiva*. Conversely, the western Mesoamerican clade radiated in its ancestral distribution area, where it originally occupied an epiphytic niche and was distributed in tropical and subtropical zones, and, lastly, the eastern Mesoamerican clade colonized lower, warm and humid or subhumid areas in the eastern Mesoamerican zone, adapting to mesic conditions. The analysis with ETS resulted in low resolution, but allowed us to distinguish *T. utriculata* and *T. pringlei*, which were previously considered to be subspecies of the same species.

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Appendix 1

List of taxa, code, GenBank accession number, voucher and locality of the samples used for this study (NS, not sequenced).

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
Catopsis nutans (Sw.) Griseb. var. *nutans*	B0002	AY614392†	AY614148†	KU848418	KU848264	*E. Trauner s.n.* (WU)	Costa Rica
Racinaea fraseri (Baker) M.A.Spencer & L.B.Sm.	GB2910	AF539977*,§	AF537914§	NS	NS	*G. Brown 2910* (RM)	–
R. fraseri	FRP90	EU681906‡‡	EF643192‡‡	NS	NS	*G. Zizka 1582* (FRP)	–
T. achyrostachys E.Morren ex Baker	DTA1	FM210787**	FM211650**	NS	NS	*Dotterer TA1* (NAP)	Mexico
T. achyrostachys	LTA2	FM210788**	FM211653**	NS	NS	*Larson TA2* (NAP)	Mexico
T. achyrostachys	ALF6532	NS	NS	NS	FJ666937‡	*A. Espejo et al. 6532* (UAMIZ)	–
T. adpressiflora Mez	B0597	KU848347	KU848508	KU848440	KU848284	*W. Till 21158* (WU)	Ecuador: Napo
T. aeranthos (Loisel.) L.B.Sm.	B0111	AY614131†	AY614253†	NS	NS	*Coll. M.H.J. Barfuss s.n.* (WU)	–
T. albertiana Verv.	B0033	AY614117†	AY614239†	NS	NS	*HBV B387/90* (WU)	Argentina: Salta
T. albida Mez & Purpus	JP016	KU848380	KU848509	KU848458	KU848321	*I. Ramírez & S. Zamudio 1414* (CICY)	Mexico: Querétaro
T. andrieuxii (Mez) L.B.Sm.	B0063	AY614088†	AY614210†	NS	NS	*HBV B 256/95* (WU)	Mexico
T. atroviridipetala Matuda	TC089	NS	NS	NS	FJ666932‡	*T. Chew 89* (XAL)	Mexico
T. argentea Griseb.	JP082	KU848359	KU848568	KU848431	KU848289	*K. Willinger s.n.* (SEL)	Cuba: Oriente
T. argentina C.H.Wright	B0087	AY614124†	AY614246†	NS	NS	*H. Till 88-45* (WU)	Argentina: Catamarca
T. ariza-juliae L.B.Sm. & J.Jiménez. Alm.	PKT504	NS	NS	NS	Fj666939‡	*Bird Rock Tropical Koide T504*	–
T. balbisiana Schult.f.	TC167	NS	NS	NS	EU126833‡	*T. Chew 167* (XAL)	–
T. baliophylla Harms	B0101	AY614114†	AY614236†	NS	NS	*W. Till 17025* (WU)	Dominican Republic: La Vega
T. barclayana Baker	B0028	AY614079†	AY614201†	NS	NS	*HBV B518/96* (WU)	Ecuador
T. barthlottii Rauh	B0035	AY614076†	AY614198†	NS	NS	*H. & L. Hromadnik 4078* (WU)	Ecuador: Loja
T. barthlotti	B0716	NS	NS	KU848427	NS	*H. & L. Hromadnik 4078* (WU)	Ecuador: Loja
T. bergeri Mez	B0097	AY614134†	AY614256†	NS	NS	*W. Papsch & G. Hold 89-060/074*	Argentina: Buenos Aires
T. bergeri	B0110	AY614133†	AY614255†	NS	NS	*Coll. M.H.J. Barfuss s.n.* (WU)	–

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. bermejoensis L. Hrom.	B0034	AY614123†	AY614245†	NS	NS	*W. Till 144* (WU)	Bolivia: Santa Cruz
T. biflora Ruiz & Pav.	B0090	AY614123†	AY614245†	NS	KU848281	*F.-G. Gruber s.n.*	Venezuela: Lara
T. brachyphylla Baker	B0082	AY614105†	AY614227†	NS	KU848280	*HBV B99B16-1* (WU)	Brazil: Rio de Janeiro
T. brevilingua Mez ex Harms	B0056	AY614113†	AY614235†	NS	NS	*W. & S. Till 2097* (WU)	Peru: San Martin
T. bulbosa Hook.	TC126	NS	NS	NS	FJ666933‡	*T. Chew 126* (XAL)	–
T. cacticola L.B.Sm.	B0044	AY614070†	AY614192†	KU848426	NS	*W. Till 2133* (WU)	Peru: Piura
T. calcicola L.B.Sm. & Proctor	JP105	KU848367	KU848539	KU848445	KU848308	*Rutschmann s.n.* (WU)	Jamaica
T. califanii Rauh	WR36219	FM210789**	FM211651**	NS	NS	*W.Rauh 36219* (HEID)	Mexico: Puebla
T. califanii	WTC5	FM210790**	FM211652**	NS	NS	*Wrinkle TC5* (NAP)	Mexico
T. caput-medusae E. Morren	B0046	AY614098†	AY614220†	KU848500	KU848307	*W. Till 7117* (WU)	Costa Rica: Puntarenas
T. caput-medusae	TC100	NS	NS	NS	FJ666934‡	T. Chew 100 (XAL)	–
T. carlos-hankii Matuda	B0062	AY614089†	AY614211†	NS	KU848296	*L. Hromadnik 15169* (WU)	Mexico: Oaxaca
T. carnosa L.B.Sm.	B0755	KU848356	KU848572	KU848430	KU848269	*W. Till 2066* (WU)	Peru: Amazonas
T. caulescens Brong. ex Baker	B0071	AY614126†	AY614248†	NS	NS	*E. Vitek 820812/72-1* (WU)	Peru: Apurimac
T. chlorophylla L.B. Sm.	JP139	NS	KU848564	KU848498	KU848299	*J.P. Pinzón et al. 119* (CICY)	Mexico: Chiapas
T. coinaensis Ehlers	B0091	AY614102†	AY614224†	NS	NS	*E. Zecher 21/76* (WU)	Peru: Cajamarca
T. comitanensis Ehlers	JP074	KU848387	KU848513	KU848467	KU848327	*J.P. Pinzón et al. 97* (CICY)	Mexico: Chiapas
T. aff. comitanensis	JP075	KU848386	KU848514	KU848468	KU848317	*J.P. Pinzón et al. 98* (CICY)	Mexico: Chiapas
T. cucaensis Wittm.	JP029	KU848388	KU848532	KU848471	KU848342	*J.P. Pinzón et al. 1* (CICY)	Mexico: Oaxaca
T. cucaensis	JP030	KU848389	KU848530	KU848469	KU848341	*J.P. Pinzón & G. Carnevali 77* (CICY)	Mexico: Oaxaca
T. cucaensis	JP056	KU848390	KU848524	KU848470	NS	*J.P. Pinzón et al. 67* (CICY)	Mexico: Chiapas
T. cucaensis	JP076	KU848392	KU848526	KU848472	KU848340	*J.P. Pinzón et al. 99* (CICY)	Mexico: Chiapas
T. dasyliriifolia Baker	JP001	KU848405	KU848534	NS	NS	*I. Ramírez et al. 785* (CICY)	Mexico: Yucatán
T. dasyliriifolia	JP003	KU848406	KU848503	KU848488	KU848331	*G. Carnevali s.n.* (CICY)	Mexico: Campeche

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. dasyliriifolia	JP083	KU848407	KU848521	KU848487	KU848332	*W. Berg s.n.* (SEL)	Belize
T. dasyliriifolia	JP084	KU848408	KU848517	KU848486	NS	*Berg & Cathcart s.n.* (SEL)	Belize
T. dasyliriifolia	JP085	KU848409	KU848519	KU848489	KU848339	*Carnevali et al. s.n.* (SEL)	Mexico: Quintana Roo
T. demissa L.B.Sm.	B0075	AY614115†	AY614237†	NS	NS	*K.-D. & R. Ehlers EE84 s.n.* (WU)	Ecuador: Loja
T. deppeana Steud.	TC051	NS	NS	NS	FJ666926‡	*T. Chew 51* (XAL)	–
T. didisticha (E.Morren) Baker	B0038	AY614127†	AY614249†	NS	NS	*W. Till 10130* (WU)	Argentina: Jujuy
T. diguetii Mez & Rol.-Goss.	ALF2972	NS	NS	NS	FJ666923‡	*Lopez-Ferrari et al. 2972* (UAMIZ)	–
T. disticha Kunth	B0048	AY614068†	AY614190†	NS	NS	*K. Oppitz s.n.* (WU)	Ecuador: Azuay
T. disticha	B0233	KU848346	NS	KU848422	KU848265	*H. & L. Hromadnik 17063* (WU)	Ecuador
T. dodsonii L.B.Sm.	B0016	AY614072†	AY614194†	NS	KU848273	*W. Rauh 34183* (WU)	Ecuador
T. dodsonii	B0127	KU848344	NS	KU848505	KU848282	*C. H. Doson 5225* (WU)	Ecuador: Pichincha
Tillandsia duratii Vis. var. *duratii*	B0088	AY614119†	AY614241†	NS	NS	*W. Till 5072* (WU)	Argentina: La Rioja
T. eizii L.B.Sm.	JC1374	NS	NS	NS	EU126830‡	*Ceja et al. 1374* (MEXU)	–
T. elusiva Pinzón, I.Ramírez & Carnevali	JP111	KU848373	KU848540	KU848451	KU848310	*J.P. Pinzón et al. 104* (CICY)	Mexico: Chiapas
T. elusiva	JP120	KU848374	KU848541	KU848452	KU848311	*J.P. Pinzón et al. 105* (CICY)	Mexico: Chiapas
T. erubescens Schltdl.	TC84	NS	NS	NS	EU126831‡	*T. Chew 84* (XAL)	–
T. espinosae L.B.Sm.	B0143	NS	NS	NS	KU848266	BGBM Berlin-Dahlem 021-03-74-83 16926 (B)	–
T. esseriana Rauh & L.B.Sm.	B0069	AY614120†	AY614242†	NS	NS	*HBV B342/90* (WU)	Paraguay: Amambay
T. exserta Fernald	LTE2	FM210791**	FM211654**	NS	NS	*Larson TE2* (NAP)	Mexico
T. exserta	B0390	KU848414	KU848562	KU848497	KU848306	*Schatzl 51/77* (WU)	Mexico: Nayarit
T. fasciculata Sw. var. *fasciculata*	B0076 B0717	AY614100†	AY614222†	NS	KU848305	*W. & S. Till 7050* (WU)	Costa Rica: San José
T. fasciculata	WTF2	FM210792**	FM211655**	NS	NS	Wrinkle TF2 (NAP)	Mexico
T. fendleri Griseb. var. *fendleri*	B0009	AY614116†	AY614238†	NS	NS	H. & L. Hromadnik 2082 (WU)	Peru: La Libertad
T. flabellata Baker	JP069N	KU848416	KU848559	NS	NS	*J.P. Pinzón et al. 64* (CICY)	Mexico: Chiapas

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. flabellata	ALF6419	NS	NS	NS	FJ666928‡	*A. Espejo et al. 6419* (UAMIZ)	–
T. flexuosa Sw.	JP002	KU848361	KU848569	KU848434	NS	*J.P. Pinzón & G. Carnevali 230* (CICY)	Venezuela: Aragua
T. fresnilloensis W.Weber & Ehlers	JP018	KU848381	KU848537	KU848460	KU848329	*I. Ramírez 1310* (CICY)	Mexico: Zacatecas
T. fuchsii W.Till	JP017	KU848366	KU848556	KU848461	KU848285	*J.P. Pinzón & G. Carnevali 231* (CICY)	Mexico: Chiapas
T. funckiana Baker var. *recurvifolia* Blass ex Rauh	JP046	KU848357	KU848565	KU848432	KU848286	*M. Speckmaier s.n.* (WU)	Venezuela: Carabobo
T. funebris A.Cast.	B0089	AY614118†	AY614240†	NS	NS	*HBV B35/94* (WU)	Bolivia: Cochabamba
T. gardneri Lindl. var. *gardneri*	B0041	AY614104†	AY614226†	NS	NS	*W. Till 11134* (WU)	Brazil: Rio de Janeiro
T. grandis Schltdl.	B0124	NS	NS	NS	KU848271	*E. Zecher s.n.* (WU)	Mexico: Veracruz
T. guatemalensis L.B.Sm.	JP071	NS	NS	NS	KU848300	*J.P. Pinzón et al. 89* (CICY)	Mexico: Chiapas
T. guatemalensis	JP072	KU848363	KU848563	KU848491	NS	*J.P. Pinzón et al. 390* (CICY)	Mexico: Chiapas
T. guatemalensis	B0008	AY614092†	AY614214†	NS	NS	HBV B 260/96 (WU)	Mexico
T. guatemalensis	B0103	AY614094†	AY614216†	NS	KU848301	*H. & L. Hromadnik 14257* (WU)	Mexico: Chiapas
T. guatemalensis	B0104	AY614093†	AY614215†	KU848490	KU848302	*L. Hromadnik 15127* (WU)	Mexico: Chiapas
T. gymnobotrya Baker	JP045	KU848363	KU848551	KU848494	KU848295	*R. Ehlers EM031403* (WU)	Mexico
T. heterophylla E.Morren	B0047	AY614111†	AY614233†	NS	KU848276	*L. Hromadnik 15191* (WU)	Mexico: Veracruz
T. heterophylla	TC052	NS	NS	NS	FJ666927‡	*T. Chew 52* (XAL)	–
T. heterophylla	JP068R	NS	NS	KU848428	KU848277	*J.P. Pinzón & V. Rebolledo 73* (CICY)	Mexico: Veracruz
T. eubergeri Ehlers	B0042	AY614106†	AY614228†	NS	NS	*F. Fuchs. s.n.* (WU)	Brazil: Bahia
T. hildae Rauh	JP040	KU848355	KU848571	KU848429	KU848292	*HBV B148/82* (WU)	Peru: Cajamarca
T. huamelulaensis Ehlers	JP142	KU848393	KU848520	KU848474	KU848325	*J.P. Pinzón et al. 227* (CICY)	Mexico: Oaxaca
T. huamelulaensis	JP143	KU848394	KU848518	KU848473	NS	*J.P. Pinzón et al. 228* (CICY)	Mexico: Oaxaca
T. intermedia Mez	TC189	NS	NS	NS	FJ666935‡	*T. Chew 189* (XAL)	–

Appendix 1. *Continued*

Species	Code	*matK-trnK 3′*	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. ionantha Planch. var. *ionantha*	B0084	AY614099†	AY614221†	NS	NS	*H. & L. Hromadnik s.n.* (WU)	Mexico: Puebla
T. ionantha	TC038	NS	NS	NS	FJ666931‡	*T. Chew 38* (XAL)	–
T. ixioides Griseb.	B0043	AY614129†	AY614251†	NS	KU848275	*G. Neuhuber GN 96-936/3084* (WU)	Argentina: Catamarca
T. izabalensis Pinzón, I.Ramírez & Carnevali	JP080	KU848401	KU848515	KU848482	KU848328	*R. Foster s.n.* (SEL)	Honduras: Cayos
T. izabalensis	B0732	KU848402	KU848522	KU848481	NS	*W. Rauh 70802* (HEID)	Guatemala: Izabal
T. juncea (Ruiz & Pav.) Poir	B0073	AY614097†	AY614219†	NS	KU848304	*W. & S. Till 7033* (WU)	Costa Rica: Limon
T. juncea	TC057	NS	NS	NS	EU126832‡	*T. Chew 57* (XAL)	–
T. juruana Ule	JP112	KU848358	KU848567	KU848435	KU848288	*Hromadnik 23176* (HBV)	Peru: Junin
T. karwinskyana Schult. & Schult.f.	JP044	KU848382	KU848538	KU848459	KU848330	*Schatzl 76/77* (WU)	Mexico: Hidalgo
T. cf. *karwinsyana*	B0734	KU848379	NS	NS	NS	*R. Ehlers & L. Köhres s.n.* (HEID)	Mexico: Tamaulipas
T. kauffmannii Ehlers	B0074	AY614103†	AY614225†	NS	KU848279	*E. Trauner s.n.* (WU)	Peru: La Libertad
T. kegeliana Mez	JP064	KU848360	KU848570	KU848433	KU848287	*M. Speckmaier s.n.* (WU)	Panama
T. klausii Ehlers	B0085	AY614096†	AY614218†	KU848501	KU848298	*K.-D. & R. Ehlers* EM851801	Mexico: Chiapas
T. latifolia Meyen var. *divaricata* (Benth.) Mez	B0068	AY614108†	AY614230†	NS	NS	*W. Till 13069* (WU, QCA)	Ecuador: Chimborazo
T. leiboldiana Schltdl.	JP140	KU848411	KU848553	KU848492	KU848303	*J.P. Pinzón et al. 120* (CICY)	Mexico: Chiapas
T. lepidosepala L.B.Sm.	KHTL001	FM210793**	FM211656**	NS	NS	*Kak.Haa TL001* (NAP)	Mexico
T. lepidosepala	B0219	NS	NS	KU848423	KU848293	*L. Hromadnik 15195* (WU)	Mexico: Puebla
T. limbata Schltdl.	JP020	KU848403	KU848504	KU848483	KU848334	*I. Ramírez et al. 1464* (CICY)	Mexico: Veracruz
T. limbata	JP055	KU848404	KU848528	KU848484	NS	*J.P. Pinzón et al. 70* (CICY)	Mexico: Chiapas
T. × *duvalii* L. Duval	B0023	AY614080†	AY614202†	KU848419	KU848274	*HBV B91/80* (WU)	–
T. × *duvalii*	B0746	NS	NS	NS	KU848283	Göttingen s.n. (WU)	–
T. macbrideana L.B.Sm. var. *macbrideana*	B0070	AY614109†	AY614231†	NS	NS	*HBV B249/87* (WU)	Peru: Lima
T. macdougallii L.B.Sm.	HSSN	FM956440††	NS	NS	NS	*S.H. Salas s.n.* (MEXU)	Mexico: Oaxaca

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. macdougallii	JP100	NS	KU848550	KU848496	NS	*D. Mondragón 28* (CICY)	Mexico: Oaxaca
T. macropetala Wawra	B0742	NS	KU848573	KU848425	KU848272	*J. Lautner 05/17* (GOET, WU)	Mexico: Oaxaca
T. magnusiana Wittm.	TC130	NC	NC	NC	FJ666941‡	*T. Chew 130* (XAL)	–
T. makoyana Baker	JP008	KU848397	KU848533	KU848479	NS	*J.P. Pinzón et al. 28* (CICY)	Mexico: Guerrero
T. makoyana	JP028	KU848398	KU848529	KU848480	NS	*I. Ramírez et al. 1519* (CICY)	Mexico: Mexico
T. makoyana	JP048	KU848399	KU848531	KU848478	KU848333	*J.P. Pinzón et al. 109* (CICY)	Mexico: Oaxaca
T. makoyana	JP051	KU848400	KU848527	KU848477	NS	*J.P. Pinzón et al. 110* (CICY)	Mexico: Oaxaca
T. marconae W.Till & Vitek	B0098	AY614069†	AY614191†	NS	NS	*W. Till 234* (WU)	Peru: Ica
T. marnier-lapostollei Rauh	JP113	KU848352	KU848511	KU848442	NS	*Hromadnik 4125* (WU)	Ecuador: Azuay
T. matudae L.B.Sm.	KHTM001	FM210794**	FM211657**	NS	NS	*Kak.Haa TM001* (NAP)	Mexico
T. may-patii I.Ramírez & Carnevali	JP054	KU848410	KU848536	KU848485	NS	*J.P. Pinzón et al. 76* (CICY)	Mexico: Quintana Roo
T. mima L.B.Sm.	JP091	KU848351	KU848574	KU848438	NS	*Cathcart & Berg s.n.* (SEL)	Ecuador: Azuay
T. multicaulis Steud.	B0107	AY614112†	AY614234†	NS	NS	*H. & L. Hromadnik 1087* (WU)	Mexico: Veracruz
T. multicaulis	TC047	NS	NS	NS	EU126829‡	*T. Chew 47* (XAL)	–
T. narthecioides C.Presl	B0060	AY614071†	AY614193†	NS	KU848278	*HBV B8/90* (WU)	Ecuador
T. nicolasensis Ehlers	JP010	KU848384	KU848554	KU848465	KU848319	*J.P. Pinzón et al. 51* (CICY)	Mexico: Jalisco
T. nicolasensis	JP077	KU848385	KU848516	KU848466	KU848320	*I. Ramírez et. al 1108* (CICY)	Mexico: Guerrero
T. novakii H.Luther	JP092	KU848415	KU848561	KU848499	NS	*A.J. Novak s.n.* (SEL)	Mexico: Veracruz
T. paniculata (L.) L.	B0102	AY614086†	AY614208†	KU848444	KU848294	*W. Till 17057* (WU)	Dominican Republic: Distrito Nacional
T. paucifolia Baker	DL0109	FN550871**	FN550873**	NS	NS	*De Luca & Vazquez-Torres 01.2009* (NAP, HEID)	Mexico: Veracruz
T. pinicola I.Ramírez & Carnevali	JP027	KU848395	KU848535	KU848476	KU848323	*G. Carnevali et al. 7353* (CICY)	Mexico: Oaxaca

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. pinicola	JP070	KU848396	KU848525	KU848475	KU848326	*J.P. Pinzón & G. Carnevali 136* (CICY)	Mexico: Oaxaca
T. plumosa Baker	B0086	AY614075†	AY614197†	NS	NS	*K.-D. & R. Ehlers EM 881905* (WU)	Mexico: Oaxaca
T. pohliana Mez	B0080	AY614128†	AY614250†	NS	NS	*W. Till 11004* (WU)	Brazil: São Paulo
T. pringlei S.Watson	JP004	KU848375	KU848548	KU848457	KU848324	*I. Ramírez & S. Zamudio 1435* (CICY)	Mexico: Querétaro
T. pringlei	JP096	NS	KU848543	KU848455	KU848335	*G. Newhouse s.n.* (SEL)	Mexico: Tamaulipas
T. pringlei	B0733	KU848376	KU848545	KU848456	NS	*W. Rauh 21345* (HEID)	Mexico: San Luis Potosí
T. pringlei	B0735	KU848377	KU848542	KU848454	KU848336	*A. Lau s.n.* (HEID)	Mexico: Querétaro
T. pringlei	B0736	KU848378	KU848544	KU848453	NS	*W. Rauh 21340* (HEID)	Mexico: San Luis Potosí
T. prodigiosa (Lem.) Baker	CG320	FM956437††	NS	NS	NS	*C. Granados 320* (MEXU)	Mexico: Oaxaca
T. prodigiosa	JP098	NS	KU848552	KU848495	NS	*A.R. López-Ferrari et al. 3069* (CICY)	Mexico: Oaxaca
T. propagulifera Rauh	JP043	KU848350	KU848575	KU848443	KU848268	*H. & L. Hromadnik 2139* (WU)	Peru: Amazonas
T. pseudomacbrideana Rauh	B0036	AY614110†	AY614232†	NS	NS	*W. Rauh 53774* (WU)	Peru: Cajamarca
T. pueblensis L.B.Sm.	JP049	KU848417	KU848560	KU848502	NS	*Zecher s.n.* (WU)	Mexico
T. punctulata Schltdl. & Cham.	B0061	AY614087†	AY614209†	KU848493	KU848297	*H.-H. Deissl s.n.* (WU)	Costa Rica
T. punctulata	TC049	NS	NS	NS	FJ666930‡	*T. Chew 49* (XAL)	–
T. rauhii L.B.Sm. var. *rauhii*	B0092	AY614101†	AY614223†	NS	NS	*W. Rauh 69417* (WU)	Peru: Cajamarca
T. remota Wittm.	B0072	AY614095†	AY614217†	NS	NS	*H. & I. Seethaler s.n.* (WU)	Honduras: Copán
T. secunda Kunth	JP063	KU848348	KU848577	KU848441	KU848318	*W. Till 21022* (WU)	Ecuador: Imbabura
T. seleriana Mez	TC121	NS	NS	NS	FJ666929‡	*T. Chew 121* (XAL)	–
T. singularis Mez & Wercklé	B0064	AY614039†	AY614161†	NS	NS	*W. Till 15023* (WU)	Costa Rica: Alajuela
T. socialis L.B.Sm.	JP062	KU848365	KU848557	KU848462	KU848290	*HBV B271/96* (WU)	Mexico
T. socialis	JP094	KU848364	KU848558	KU848463	KU848291	*D. Cathcart s.n.* (SEL)	Mexico: Chiapas
T. spiraliflora Rauh	JP104	KU848349	KU848576	KU848439	NS	*L. Hromadnik 2114* (WU)	Peru: Amazonas
T. stricta Sol. ex Sims var. *stricta*	B0081	AY614130†	AY614252†	NS	NS	*E. Markus s.n.* (WU)	Brazil: Minas Gerais

Appendix 1. *Continued*

Species	Code	*matK-trnK 3′*	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. rupicola Baker	B0039	AY614073†	AY614195†	NS	NS	*W. Till 13081* (WU, QCA)	Ecuador: Azuay
T. tehuacana I.Ramírez & Carnevali	JP050	KU848383	KU848555	KU848464	KU848322	*J.P. Pinzón et al. 47* (CICY)	Mexico: Puebla
T. tenuifolia L. var. *tenuifolia*	B0026	AY614132†	AY614254†	NS	NS	*W. Till 131* (WU)	Bolivia: Santa Cruz
T. tomasellii De Luca, Sabato & Balduzzi	PA3777	FM210795**	FM211658**	NS	NS	*P. de Luca et al. 3777* (PAV)	Mexico: Oaxaca
T. tortilis Klotzsch ex Baker ssp. *tortilis*	B0049	AY614074†	AY614196†	NS	NS	*HBV B218A/88* (WU)	Mexico: Oaxaca
T. triglochinioides C.Presl	B0725	KU848345	KU848506	KU848420	NS	*W. Rauh 34378* (HEID)	Ecuador: Manabi
T. usneoides (L.) L.	B0083	AY614122†	AY614244†	NS	NS	*G. Palim s.n.* (WU)	Venezuela
T. usneoides	B0109	AY614121†	AY614243†	NS	NS	*Coll. M.H.J. Barfuss s.n.* (WU)	–
T. usneoides	TC050	NS	NS	NS	FJ666938‡	*T. Chew 50* (XAL)	–
T. utriculata L.	JP006	KU848370	KU848547	KU848450	NS	*J.P. Pinzón et al. 233* (CICY)	Mexico: Yucatán
T. utriculata	JP060	KU848372	KU848549	KU848449	KU848314	*J.P. Pinzón et al. 56* (CICY)	Mexico: Tabasco
T. utriculata	JP061	NS	KU848507	KU848448	KU848313	*J.P. Pinzón et al. 206* (CICY)	Mexico: Chiapas
T. utriculata	JP095	NS	NS	KU848447	KU848309	*H.B. Rinker s.n.* (SEL)	USA: Puerto Rico
T. utriculata	B0027	AY614091†	AY614213†	NS	NS	*G. Neuhuber 98-982/3296* (WU)	USA: Florida
T. utriculata	B0100	AY614090†	AY614212†	NS	KU848315	*W. Till 17007* (WU)	Dominican Republic: Espaillat
T. utriculata	B0807	KU848368	KU848546	KU848446	KU848316	*W. Janetzky 22* (WU)	Jamaica: Middlesex
T. cf. *utriculata*	TC143	NS	NS	NS	FJ666940‡	*T. Chew 143* (XAL)	–
T. venusta Mez & Wercklé	B0007	AY614081†	AY614203†	NS	NS	*HBV B98B136-1* (WU)	–
T. viridiflora (Beer) Baker	B0006	AY614066†	AY614188†	NS	NS	*HBV B87/80* (WU)	–
T. wagneriana L.B.Sm.	B0058	AY614067†	AY614189†	KU848421	NS	*HBV B222/93* (WU)	Peru: Amazonas
T. wagneriana L.B.Sm.	B0217	KU848343	KU848579	NS	KU848270	*H. Prinsler s.n., 1990-09* (WU)	Peru: Amazonas
T. werneriana J.R.Grant	B0067	AY614078†	AY614200†	NS	NS	*H. & L. Hromadnik 2142* (WU)	Peru: Amazonas

Appendix 1. *Continued*

Species	Code	*matK-trnK* 3′	*rps16* intron	*rpl32-trnL*	ETS	Voucher	Locality
T. xerographica Rohweder	LOSN	FM210797**	FM211660**	NS	NS	*Lozada s.n.* (NAP)	Mexico
T. xiphioides Ker Gawl. var. *xiphioides*	B0040	AY614125†	AY614247†	NS	NS	*F. Strigl FO 275* (WU)	Argentina: Santiago del Estero
Vriesea malzinei E.Morren	B0145	KU848353	KU848510	KU848437	KU848267	*BGBM 109-37-74-83* (B)	Mexico

*Partial *matK* sequence, without non-coding part of 3′ end of *trnK* intron.
†Barfuss *et al.* (2005).
‡Chew *et al.* (2010).
§Crayn *et al.* (2004).
**De Castro *et al.* (2009).
††Granados (2008).
‡‡Rex *et al.* (2009).