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Morphological phylogenetics of *Puya* subgenus *Puya* (Bromeliaceae)

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Puya, a large genus mostly from South America, has been taxonomically divided into two subgenera: *Puyopsis* and *Puya*. The latter includes only eight species distributed mainly in Chile, extending to Argentina, Bolivia, and Peru. The species of subgenus *Puya* are recognized by the presence of a sterile apex of the inflorescence branches, whereas those of subgenus *Puyopsis* have fertile flowers all along the branches. The objectives of this article were to determine whether this diagnostic character was synapomorphic for subgenus *Puya*, and to explore the relationships between its species. Parsimony analyses were performed for 43 taxa and 93 morphological characters, 87 of which were discrete and six continuous. In the analysis that included all characters, a single most parsimonious tree was found that supported subgenus *Puya* by two synapomorphic character states, including the diagnostic character of a sterile inflorescence branch apex and a blooming pattern in which flowers open gradually from base to apex. The trees were better supported when the continuous characters were included. Further studies are suggested to resolve the infrageneric classification of *Puya* and the relationships of the species belonging to subgenus *Puya*. *Botanical Journal of the Linnean Society*, 2008, **156**, 93–110.

ADDITIONAL KEYWORDS: continuous characters – morphology – *Puya* subgenus *Puyopsis*.

INTRODUCTION

Puya Molina is a genus of Bromeliaceae that is almost exclusive to South America – only two taxa are found in Costa Rica – and includes approximately 199 species (Smith & Downs, 1974; Luther, 2002). The description of *Puya* is based on diagnostic attributes, such as petals spiralled and persistent after anthesis (Smith & Downs, 1974). The genus was previously divided into a number of subgenera, including *Chagualia*, *Pitcairniopsis*, and *Pourretia* (Mez, 1896; Smith & Looser, 1935). However, only two subgenera are currently recognized: *Puya* and *Puyopsis* (Smith, 1970). Subgenus *Puyopsis* (Baker) L.B. Sm. has fertile flowers along the branches of inflorescences, whereas subgenus *Puya* lacks fertile flowers at the apex of the branches of inflorescences (Smith, 1970; Smith & Downs, 1974).

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The majority of the species belong to subgenus *Puyopsis*, and only nine have been included in subgenus *Puya*. Smith & Downs (1974) initially included seven species in subgenus *Puya*: *Puya chilensis* Molina (the type species of *Puya*), *Puya boliviensis* Baker, *Puya castellanosii* L.B.Sm., *Puya alpestris* (Poepp.) Gay, *Puya berteroniana* Mez., *Puya weddelliana* Mez, and *Puya raimondii* Harms. Subsequently, *Puya quillotana* W. Weber (1984) and *Puya gilmartiniae* G.S. Varadarajan & A.R. Flores (1990) were described. However, the only differentiating character between *P. quillotana* and *P. chilensis* was the pubescence of the leaves recorded from a single incomplete specimen. Therefore, here it is considered as a synonym of *P. chilensis*, and only eight species are included in subgenus *Puya*.

The morphological variation in *Puya* is remarkable, mainly in the size of plants and floral parts, the branching patterns of the inflorescence, and the arrangement of the flowers in the inflorescence.

Some of these variable characters are found amongst species of subgenus *Puya*. For example, the largest bromeliad in the world, *P. raimondii*, reaches approximately 12 m in height, in comparison with *P. alpestris* that only grows to approximately 1.5 m. Plants of *P. boliviensis* lack a stem, whereas the plants of the rest of the species of subgenus *Puya* have a well-developed stem, which may be simple, as in *P. raimondii*, or branched, as in *P. chilensis*.

The position of *Puya* has posed a problem in the phylogenetic analyses of Bromeliaceae. It has been included in Pitcairnioideae, related to *Pitcairnia* by morphological characters and chloroplast DNA restriction site variation (Varadarajan & Gilmartin, 1988; Ranker *et al*., 1990). However, current molecular approaches that have considered one or a few species of *Puya* have indicated that the Bromelioideae is the sister group of the genus (Terry, Brown & Olmstead, 1997; Crayn *et al*., 2000, Crayn, Winter & Smith, 2004; Givnish *et al*., 2004; Barfuss *et al*., 2005). The traditional classification of the Bromeliaceae has recognized three subfamilies: Pitcairnioideae, Bromelioideae, and Tillandsioideae (Smith & Downs, 1974). Recent phylogenetic studies have not agreed on the composition or position of these groups; contradictory results are mainly related to which groups emerged first (Clark & Clegg, 1990; Ranker *et al*., 1990; Terry *et al*., 1997; Crayn *et al*., 2000; Horres *et al*., 2000; Givnish *et al*., 2004; Barfuss *et al*., 2005). The monophyly of the Pitcairnioideae has been questioned, and therefore both new subfamilies and tribes could be defined in the future (Ranker *et al*., 1990; Terry *et al*., 1997; Givnish *et al*., 2004). By the way of an example, a new tribe – *Puyeae* – has been suggested (Terry *et al*., 1997; Benzing, 2000).

Phylogenetic analyses of *Puya* are still lacking. The only study that evaluated morphological data included only nine species (Varadarajan & Gilmartin, 1988), not sufficient to understand this varied and complex group. Current molecular phylogenetic approaches in the Bromeliaceae have included only one or a few species of *Puya* (Terry *et al*., 1997; Crayn *et al*., 2000, 2004; Givnish *et al*., 2004; Barfuss *et al*., 2005).

The aims of this study were to carry out phylogenetic analyses based on morphological characters to determine the characters that support subgenus *Puya*, and to investigate the relationships between the species of this subgenus. Molecular approaches in Bromeliaceae have found very little variation in a number of chloroplast DNA regions, such as *trnK*, *rps16*, *trnL*, *trnL-trnF atpB-rbcL*, *rbcL*, and *matK* (Terry *et al*., 1997; Crayn *et al*., 2000, 2004; Givnish *et al*., 2004; Barfuss *et al*., 2005), and nuclear regions, such as internal transcribed spacer (ITS), are only just beginning to be explored (Horres *et al*., 2000). Therefore, this study provides an initial estimate of the phylogenetic relationships of the species of subgenus *Puya* until variable molecular characters are found.

In addition to discrete morphological attributes, continuous characters were considered in the analyses. There is controversy over the use of these characters for cladistic analysis. Arguments against the use of these characters are threefold: (1) those related to the concept of homology; (2) those against the way in which continuous characters are broken down; and (3) those against the concept that characters are classes and not individuals (Archie, 1985; Pimentel & Riggins, 1987; Cranton & Humphries, 1988; Chappill, 1989; Stevens, 1991; Thiele, 1993; Rae, 1998; Kluge, 2003; Grant & Kluge, 2004). In this study, six continuous characters were coded according to their range of measurement, utilizing the computer program TNT (Goloboff, Farris & Nixon, 2003). TNT deals with continuous characters as such, avoiding the use of *ad hoc* methods that have been proposed to discretize continuous distribution in phylogenetic analysis (gap-coding, Thiele's method, etc.) (Goloboff, Mattoni & Quinteros, 2006). The inclusion of continuous characters will allow for an understanding of the evolution of the size of several floral and vegetative elements in subgenus *Puya*.

MATERIAL AND METHODS

Taxon sampling

In addition to the eight species of subgenus *Puya*, 20 taxa of subgenus *Puyopsis* were included on the basis of the following criteria: (1) species representative of the entire range of distribution; and (2) species representative of different morphological patterns, well represented in herbaria. For the outgroups, 15 taxa representative of the three traditional subfamilies were selected: Pitcairnioideae, Bromelioideae, and Tillandsioideae (Baker, 1889; Smith & Downs, 1974). These taxa correspond to the different clades identified by molecular phylogenetic studies (Clark & Clegg, 1990; Ranker *et al*., 1990; Terry *et al*., 1997; Crayn *et al*., 2000; Horres *et al*., 2000; Givnish *et al*., 2004; Barfuss *et al*., 2005). Forty-three terminal taxa were included (see Appendix 1). From these, *Brocchinia* was used to root the tree, as it is the most distantly related genus.

Morphological dataset

The data matrix (Appendix 2) consists of 93 characters: 87 discrete and six continuous characters. Vegetative as well as floral and micromorphological characters were included. Some of these characters are shown in Figures 1 and 2. Micromorphological

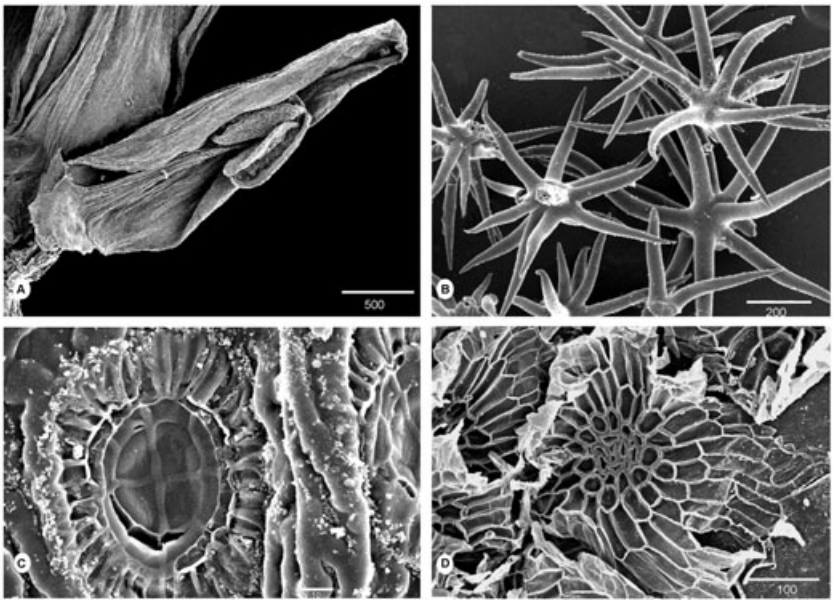

Figure 1. Floral and epidermal characters: A, stamens adnate to petals; B, stellate hairs; C, trichomes with central disc cells and wings; D, trichomes without a central disc but with wings.

characters were observed with either an optical microscope or a JEOL JSM-5600 LV scanning electron microscope. Four hundred and sixty-six herbarium specimens were examined, some of which were collected for this project. They are listed in Appendix 1. The characters and their states are given in Table 1. For characters 25 and 26, the percentage of hairs on both abaxial and adaxial surfaces was estimated by dividing the microscope field into four.

Continuous characters (Table 2) were divided into character states with TNT. The program considers measurements as a range (minimum/maximum) of the character for each species with values from 0 to 65, using up to three decimals. The characters were optimized using Farris' method for additive characters (Farris, 1970). During the optimization of a given node, if the ranges of the descendant nodes overlapped, the method counted no steps; if the ranges did not overlap, it counted the minimum distance from one range to the other (i.e. the numeric difference between the two closest values of the two descendant ranges) (Goloboff *et al*., 2006). Measurements were standardized by a $\log(x + 1)$ transformation, because of differences in scale (Table 2). There were up to 32 states for some of these characters, as implemented in TNT (Goloboff *et al*., 2003).

Phylogenetic analysis

The data matrix was constructed using WINCLADA (Nixon, 2002). Cladistic analyses under parsimony criteria were performed using the program TNT (Goloboff *et al*., 2003). Separate analyses were performed: the first dataset included only the discrete characters, and the second included the discrete and continuous characters. Parsimony analyses were performed with 1000 starting trees with tree bisection–reconnection (TBR), saving 50 trees per replication. Support was estimated by jackknife by resampling 1000 times with the TBR set with a removal probability of 30%. Bremer support (Bremer, 1994) was calculated only for the combined dataset as implemented in TNT (Goloboff *et al*., 2003).

RESULTS

Cladistic analyses

The analysis with discrete characters retrieved nine most parsimonious trees (MPTs) [$L = 505$ steps; consistency index (CI), 0.250; retention index (RI), 0.522]. The strict consensus is shown in Figure 3. In the analysis with discrete and continuous characters, a single MPT was retrieved (Fig. 4) (L = 530 steps; CI, 0.250; RI, 0.515). In the data matrix with discrete characters, the 87 characters were parsimony informative. In the data matrix with continuous + discrete characters, 93 characters were parsimony informative. Autapomorphic characters were scored but not taken into account in the analyses.

Phylogenetic relationships

In the discrete character analysis, only a clade that included two *Pitcairnia* species was well supported

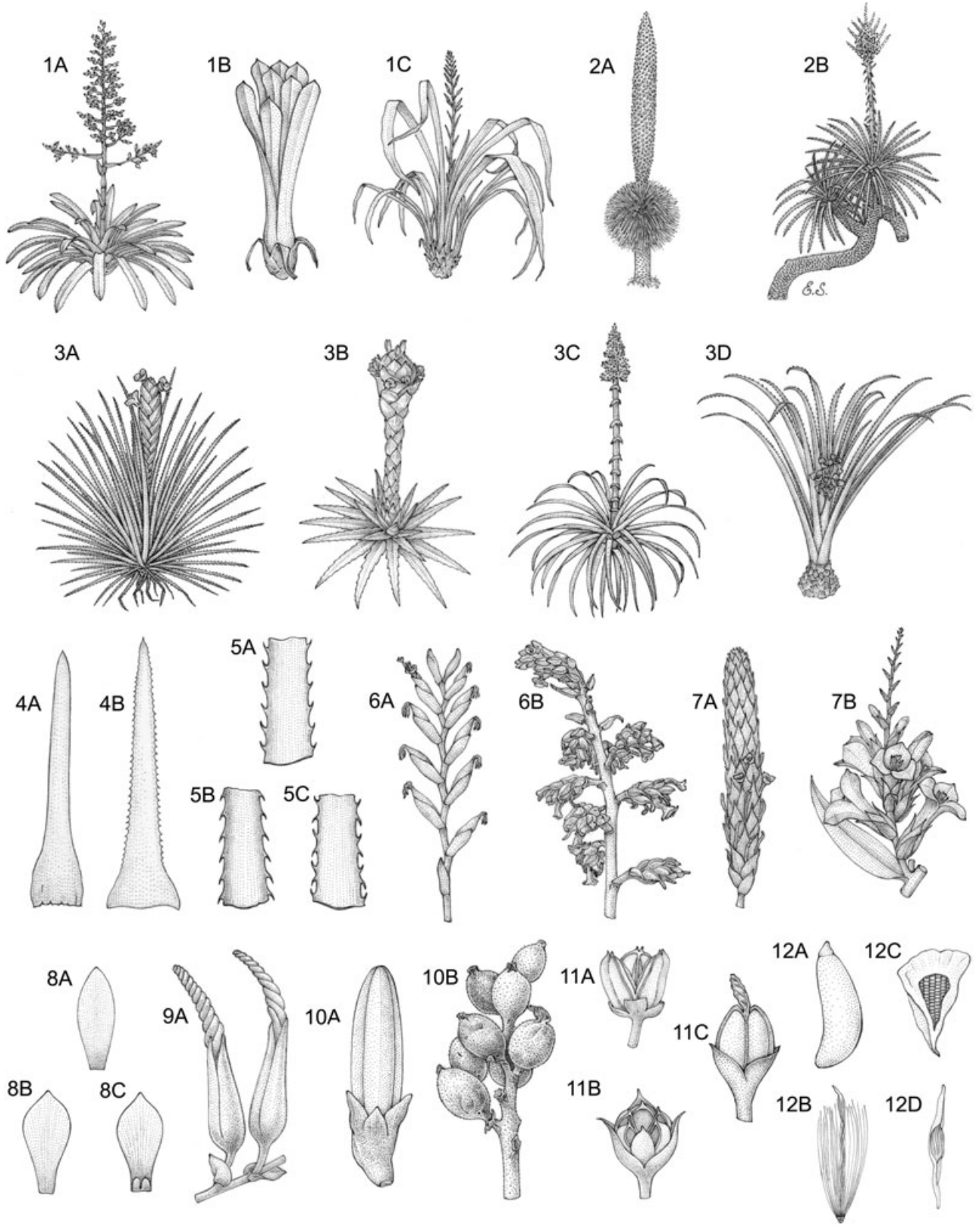
1A
1B
1C
2A
2B
E.S.
3A
3B
3C
3D
4A
4B
5A
5B
5C
6A
6B
7A
7B
8A
8B
8C
9A
10A
10B
11A
11B
11C
12A
12B
12C
12D

Figure 2. Vegetative and floral characters. Rosette type: 1A, tank; 1B, cistern; 1C, tufted. Stem: 1A, acaulescent; 2A, caulescent. Stem type: 2A, erect; 2B, prostrate. Stem branching: 2A, simple; 2B, branched. Inflorescence/rosette relative length: 3A, same; 3B, once the length; 3C, twice the length; 3D, smaller. Leaf margin: 4A, entire; 4B, serrate. Thorn orientation: 5A, antrorse; 5B, retrorse; 5C, antrorse and retrorse. Peduncle: 3D, included; 3B, emerging; 3A, equalling. Peduncle covered with bracts: 3B, totally; 3C, partially. Inflorescence branching: 6A, simple; 6B, branched. Inflorescence strobiliform: 6B, absent; 3B, present. Flower density: 6A, lax; 7A, dense. Inflorescence branch arrangement: 7B, polystichous; 6A, distichous. Sterile apex of inflorescence branch: 6B, absent; 7B, present. Petal shape: 8A, oblong-elliptic; 8B, obovate. Petals spiralled and twisted: 9A, present. Petaloid appendices at base of petals: 8B, absent; 8C, present. Fruit type: 10A, capsule; 10B, berry. Fruit dehiscence: 11A, septicidal; 11B, loculicidal and septicidal. Petals persistent at apex of fruit: 11C, present. Seed: 12A, naked; 12B, plumose; 12C winged; 12D appendiculate.

(jackknife 93%; Bremer support value, > 2) (Fig. 3). The species of *Puya* were grouped in a clade (Bremer support value, > 1). The species in subgenus *Puya* were grouped in a subclade without support within a larger clade together with *Puya goudotiana* and *Puya retrorsa* (Bremer support value, > 1). In the discrete + continuous character analysis, more clades received support (Fig. 4). The *Puya* clade received a jackknife value of 51% and a Bremer support value of > 3. The single MPT retrieved by this analysis shows species of *Puya* in two clades without support. The first is the *Puya laxa* clade and the second has two subclades: the subgenus *Puya* subclade and the *Puya aristeguietae* subclade. The subgenus *Puya* clade received a jackknife value of 52% and a Bremer support value of > 2 (Fig. 4).

Synapomorphic characters

In the discrete character analysis, the genus *Puya* was supported by six synapomorphic character states, two of which were unambiguous: petals spiralled and twisted together after anthesis (77:1; CI, 100) and petals spiralled persistent at the apex of fruit (91:1; CI, 100) (Fig. 3). Subgenus *Puya* was supported by two character states: presence of a sterile inflorescence branch apex (44:1; CI, 100) and flowers opening sequentially from inflorescence branch base to apex (47:0, CI, 100). In the analysis that included the discrete + continuous characters, the genus *Puya* and the subgenus *Puya* were supported by the same synapomorphic states as in the discrete character analysis (Fig. 4).

DISCUSSION

In this study, the species classified in subgenus *Puya* were recovered in a clade supported by two synapomorphic character states. It was confirmed that the diagnostic character for the subgenus (presence of a sterile inflorescence branch apex) is a synapomorphy that supports this clade. The other character state that was synapomorphic was the blooming pattern, in which the flowers open gradually from base to apex. Johow (1898) suggested that a sterile apex on the branches of the inflorescence is an adaptation that provides support for perching birds. We have observed in the field that, in *P. raimondii*, both hummingbirds and passerine birds visit the flowers, and so the sterile apex of branches in this species is not specifically for perching birds. However, more information on the pollination system of the species in subgenus *Puya* will clarify the importance of the sterile apex in relation to pollinators.

Our results imply that subgenus *Puyopsis* is paraphyletic. The studied species of this subgenus are grouped into two clades, one of which is the sister group of the species of subgenus *Puya*. Several other subgenera have been proposed in the past, including *Chagualia* Smith & Looser, *Pourretia* Mez, and *Pitcairniopsis* Mez (Smith & Looser, 1935; Smith, 1970), and, most probably, some will have to be resurrected. Thus, further analyses with more taxa and a larger number of characters are needed to recover trees that are better resolved, and to determine the infrageneric classification of *Puya* and the relationships of its species. Such analyses will also clarify the status of the group formed by northern South American species represented by the *P. aristeguietae* clade that is closely related to subgenus *Puya*.

The topology of the cladograms was better supported when continuous characters were included. None was synapomorphic. This coincides with the results of previous analyses in which these characters were taken into account (for example, Lehtonen, 2006). We did not break up the range of measurements of the characters, as normally carried out (see Garcia-Cruz & Sosa, 2006). Instead, we used TNT, which analyses continuous characters as such. Our results indicate that continuous characters contain phylogenetic information, and justifies that they are homologous.

When the continuous characters are visualized in the single MPT (Fig. 4) retrieved by the discrete + continuous character data matrix, the general pattern of species of subgenus *Puya* is that of an increase in plant, inflorescence, sepal, and petal size. The species of subgenus *Puya* are in a grade, with the

Table 1. Characters and character states for the cladistic analysis of subgenus *Puya*

1. Plant length
2. Leaf length
3. Inflorescence length
4. Floral bract length
5. Sepal length
6. Petal length
7. Rosette type: 0, tank; 1, cistern (tubular cylindrical); 2, tufted (graminoid). In the tank type, the leaves are at an angle of 45° and water is retained; in the cylindrical or tubular type, the leaves overlap and they are erect and form a container; the tufted type is similar to the habit of grasses
8. Stem: 0, acaulescent; 1, caulescent
9. Stem type: 0, erect; 1, prostrate
10. Stem branching: 0, simple; 1, branched
11. Reproduction: 0, monocarpic; 1, polycarpic
12. Inflorescence/rosette relative length: 0, same; 1, inflorescence once the length of rosette; 2, inflorescence twice the length of rosette; 3, inflorescence smaller than rosette
13. Leaf position in the rosette during blooming: 0, erect; 1, recurved-reflexed; 2, ascendent
14. Leaf margin: 0, parallel; 1, convergent
15. Leaf blade apex: 0, acute or attenuate; 1, rounded; 2, mucronate or acuminate
16. Leaf capacity of leaves to retain water: 0, absent; 1, present
17. Leaf margin: 0, entire; 1, serrate
18. Leaf margin: thorn orientation: 0, one way, antrorse; 1, one way, retrorse; 2, with both orientations, antrorse and retrorse
19. Leaf margin: thorn colour: 0, black-brownish; 1, brown-reddish or greenish; 2, yellow to red
20. Leaf nervation: 0, without a prominent median nerve; 1, with a prominent median nerve
21. Leaf petiole: 0, absent; 1, present
22. Leaf pubescence of adaxial surface: 0, glabrous; 1, with scales; 2, with hairs (pubescent)
23. Leaf pubescence of abaxial surface: 0, glabrous; 1, with scales; 2, with hairs (pubescent)
24. Leaf adaxial and abaxial surfaces: trichomes: 0, with central disc cells and wings; 1, without a central disc but with wings; 2, irregular cells with neither central disc nor wings
25. Leaf adaxial surface: percentage of pubescence: 0, 25%; 1, 50–75%; 2, 100%
26. Leaf abaxial surface: percentage of pubescence: 0, 25%; 1, 50–75%; 2, 100%
27. Inflorescence: peduncle: 0, included in rosette; 1, emerging rosette; 2, equalling rosette
28. Inflorescence: 0, erect; 1, pendule or nutant
29. Inflorescence: peduncle diameter: 0, less than 2 cm; 1, 2–10 cm; 2, more than 10 cm
30. Inflorescence reddish coloration: 0, absent; 1, present
31. Inflorescence: peduncle covered with bracts: 0, totally; 1, partially
32. Inflorescence: peduncle bracts shape: 0, oblong-elliptic; 1, ovate
33. Inflorescence: bract margin: 0, entire; 1, serrate or serrulate
34. Inflorescence: bract pubescence: 0, glabrous; 1, with scales; 2, with hairs
35. Inflorescence: branching: 0, simple; 1, branched
36. Inflorescence position: 0, apical; 1, lateral
37. Inflorescence: consistency of the rachis of inflorescence: 0, nonfleshy; 1, fleshy
38. Inflorescence: strobiliform: 0, absent; 1, present
39. Inflorescence: flower disposition type: 0, spikes; 1, racemes
40. Inflorescence: flower density in the entire inflorescence: 0, lax; 1, dense
41. Inflorescence: branch arrangement: 0, polystichous; 1, distichous
42. Inflorescence: branch shape: 0, globose; 1, oblong-elliptic
43. Inflorescence: branch position: 0, alternate; 1, verticillate
44. Inflorescence: sterile apex of branches: 0, absent; 1, present
45. Inflorescence: density of flowers along branches: 0, lax; 1, dense
46. Inflorescence: shape: 0, triangular; 1, oblong
47. Inflorescence: blooming pattern: 0, flowers opening sequentially from inflorescence branch base to apex; 1, flowers opening in any position
48. Inflorescence: bract/branch length: 0, bracts smaller or equalling branches; 1, bracts larger
49. Inflorescence: bract length: 0, larger than the axil of an inflorescence's branch; 1, smaller than or equal to the axil of an inflorescence's branch

Table 1. *Continued*

50.	Inflorescence: bract shape: 0, oblong-elliptic; 1, ovate
51.	Inflorescence: apical zone of the inflorescence bracts apex: 0, acute-attenuate; 1, rounded; 2, mucronate-apiculate
52.	Inflorescence: margin of bract: 0, entire; 1, serrate or serrulate
53.	Inflorescence: blade of bracts: 0, absent; 1, present
54.	Inflorescence rachis pubescent: 0, absent; 1, present
55.	Inflorescence: ferrugineous pubescence: 0, absent; 1, present
56.	Inflorescence: bract apex: 0, acute-attenuate; 2, rounded or obtuse; 2, mucronate or apiculate
57.	Floral bract: margin: 0, entire; 1, serrate or serrulate
58.	Floral bract: carinate: 0, absent; 1, present
59.	Floral bract shape: 0, oblong-elliptic; 1, ovate
60.	Floral bract colour (fresh material): 0, greenish; 1, brownish; 2, red–orange
61.	Floral sterile bracts among flowers: 0, absent; 1, present
62.	Flower disposition: 0, distichous; 1, polystichous
63.	Flower phyllotaxis: 0, opposite; 1, alternate; 2, verticillate
64.	Flower: pedicel: 0, absent; 1, short (< 2 mm); 2, medium (2–6 cm); 3, large (> 6 cm)
65.	Flower: length with regard to bracts: 0, larger; 1, smaller; 2, equal size
66.	Flower: bract pubescence: 0, absent; 1, present
67.	Flower: sepal length with regard to bracts: 0, larger; 1, smaller; 2, equal size
68.	Flower: sepal symmetry: 0, symmetrical; 1, strongly asymmetrical
69.	Flower: sepals carinate: 0, absent; 1, present
70.	Flower: sepal union: 0, free; 1, sepals connate at least at half; 2, connate only at the base
71.	Flower: sepal apex: 0, acute-attenuate; 1, rounded-obtuse; 2, mucronate-acuminate
72.	Flower: sepal length with regard to petal: 0, 1/3 smaller; 1, 1/2 smaller or less; 2, equal size
73.	Flower: sepal colour: 0, yellowish; 1, reddish or coloured; 2, greenish-white–cream; 3, brownish
74.	Flower: sepal pubescence: 0, absent; 1, present
75.	Flower: petal colour: 0, white–cream; 1, blue–violet; 2, dark green–blue; 3, red–rose; 4, yellow-greenish
76.	Flower: petal shape: 0, oblong-elliptic; 1, obovate
77.	Flower: petals spiralled and twisted together after anthesis: 0, absent; 1, present
78.	Flower: petal apex: 0, acute-attenuate; 1, rounded-obtuse; 2, mucronate-acuminate
79.	Flower: petal symmetry: 0, asymmetric; 1, symmetric
80.	Flower: petaloid appendices at base of petals: 0, absent; 1, present
81.	Flower: relative size of stamen with respect to the flowers: 0, inserted; 1, exerted
82.	Flower: stamens adnate to petals: 0, absent; 1, present
83.	Flower: stamens in a column: 0, absent; 1, present
84.	Flower: anthers: 0, basifixed; 1, dorsifixed
85.	Flower: stamen length with regard to style: 0, larger or equal size; 1, smaller
86.	Flower: anther shape: 0, sagittate; 1, oblong-elliptic
87.	Flower: ovary: 0, superior; 1, semi-inferior; 2, inferior
88.	Flower: style size with regard to ovary: 0, larger; 1, smaller or equal
89.	Fruit: type: 0, capsule; 1, berry; 2, drupe; 3, multiple fruit
90.	Fruit: dehiscence of capsules: 0, septicidal; 1, loculicidal; 2, both
91.	Fruit: petals persistent at apex of fruit: 0, absent; 1, present
92.	Seed: 0, naked; 1, plumose; 2, winged; 3, appendiculate
93.	Roots: wide radicular system: 0, absent; 1, present

exception of a small terminal clade formed by *P. castellanosii* and *P. raimondii*. Plants of the former are medium sized, but the latter is the largest bromeliad in the world, with a very large inflorescence (Foster, 1950; Varadarajan & Gilmartin, 1988). In addition, *P. raimondii*'s flowers have larger petals in comparison with those of the other species of the subgenus, but the inflorescence is gigantic, and thus holds several thousands of flowers. Of all the species in Bromeliaceae, *P. raimondii* produces the largest number of flowers per inflorescence (Foster, 1950; Varadarajan & Gilmartin, 1988). *Puya raimondii* does not show clonal growth; it only reproduces by seeds (Hornung-Leoni & Sosa, 2004). Therefore, it is suggested that the reproductive strategy of this species is to produce more flowers to increase seed set. The results of a previous study have shown that there is an allometric pattern in *Puya* in which plant size is

Table 2. Continuous characters and their logarithmic transformation

Species	0		1		2		3		4		5	
	Plant length (cm)	Log (height + 1)	Leaf length (cm)	Log (leaf + 1)	Infl. length (cm)	Log (infl. + 1)	Floral br. length (cm)	Log (fl. br. + 1)	Sepal length (cm)	Log (sep. + 1)	Petal length (cm)	Log (pet. + 1)
Brocchinia reducta	99–100	2.00	159–161	2.21	14.5–15.0	1.19–1.20	1.5–2.0	0.40–0.48	0.65–0.7	0.22–0.23	1.3–1.7	0.36–0.43
Ananas ananasioides	99–101	2.00	160.0	2.21	14.5–15.0	1.19–1.20	1.5–2.0	0.40–0.48	0.65–0.7	0.22–0.23	1.3–1.7	0.36–0.43
Bromelia penguin	100–200	2.00–2.30	30.0–200.0	1.49–2.30	30.0–60.0	1.49–1.79	1.6–3.0	0.41–0.60	1.2–3.0	0.34–0.60	1.5–3.0	0.40–0.60
Broemlia chrysantha	70–150	1.85–2.18	80.0–150.0	1.91–2.18	79.0–81.0	1.90–1.91	1.0–1.5	0.30–0.40	0.9–1.7	0.28–0.43	0.9–1.5	0.28–0.40
Aechmea spectabilis	99–101	2.00–2.01	100.0–140.0	2.00–2.15	60.0–100.0	1.79–2.00	0.1–0.2	0.04–0.04	0.9–2.0	0.28–0.48	2.4–2.5	0.53–0.54
Billbergia macrolepis	98–102	2.00–2.01	119–120	2.08	39.5–40.0	161.00	3.45–3.5	0.65	0.99–1.0	0.30	4.2–4.3	0.72
Cottendorfia florida	200–400	2.30–2.60	99–100	2.00	100.0–300.0	2.00–2.48	0.19–0.2	0.08	0.28–0.3	0.11	0.6–1.0	0.20–0.30
Guzmania monostachia	20–40	1.32–1.61	16.0–24.0	1.23–1.40	8.0–15.0	0.95–1.20	2.3–2.9	0.52–0.59	1.75–1.80	0.44–0.45	3.0–3.3	0.60–0.63
Tillandsia multicaulis	25–40	1.41–1.61	30.0–40.0	1.49–1.61	14.0–14.5	1.18–1.19	4.9–5.0	0.77–0.78	3.5–3.6	0.65–0.66	6.9–7.0	0.90
Tillandsia flexuosa	20–150	1.32–2.18	20.0–50.0	1.32–1.71	50–61	1.78–1.79	2.0–3.0	0.48–0.60	2.0–3.0	0.48–0.60	3.9–4	0.69–0.70
Vriesea espinosae	15–16	1.20–1.23	?	?	6.9–7	0.90	2.4–2.5	0.53–0.54	1.19–1.2	0.34	2.9–3.0	0.59–0.60
Navia ignesicola	16.5–17	1.25–1.26	39–41	1.60–1.62	4.9–5.0	0.77–0.78	2.6–2.7	0.56–0.57	4.4–4.5	0.73–0.74	?	?
Pitcairnia maidifolia	128–131	2.11–2.12	119–120	2.08	44–45	1.65–1.66	0.39–0.40	0.14–0.15	2.6–3.0	0.56–0.60	4.9–5.0	0.77–0.78
Pitcairnia meridensis	50–60	1.71–1.79	70.0–130.0	1.85–2.12	14.9–15	1.20	0.7–1.1	0.23–0.32	3.1–3.2	0.61–0.62	6.35–6.40	0.87
Dyckia ferox	58–62	1.77–1.79	20–60	1.32–1.79	?	?	0.2–0.3	0.08–0.11	0.5–0.9	0.18–0.28	1.2–1.4	0.34–0.38
Puya alpestris	120–150	2.08–2.18	60–70	1.79–1.85	99–100	2.00	2.6–3.3	0.56–0.63	2.2–2.9	0.51–0.59	4.8–5.0	0.76–0.78
Puya berteroniana	495–505	2.70	99–100	2.00	99–100	2.00	4.4–4.8	0.73–0.76	2.2–2.3	0.51–0.52	5.0–5.6	0.78–0.82
Puya weddelliana	?	?	?	?	?	?	1.49–1.5	0.40	1.79–1.80	0.45	3.45–3.50	0.65
Puya chilensis	499–500	2.70	99–100	2.00	99–100	2.00	3.4–5.0	0.64–0.78	3.5–5.8	0.65–0.83	4.9–5.0	0.77–0.78
Puya gilmartiniae	149–151	2.18	10.0–20.0	1.04–1.32	50.0–60.0	1.71–1.79	1.5–2.5	0.40–0.54	1.7–2.4	0.43–0.53	3.0–4.8	0.60–0.76
Puya boliviensis	199–200	2.30	100.0	2.00	99–100	2.00	2.1–3.3	0.49–0.63	3.19–3.20	0.62	4.9–5.0	0.77–0.78
Puya castellanosii	100–300	2.00–2.48	39–40	1.60–1.61	39–40	1.60–1.61	3.2–3.5	0.62–0.65	2.9–3.0	0.59–0.60	3.9–4.0	0.69–0.70
Puya raimondii	950–1200	2.98–3.08	123–125	2.09–2.10	430–500	2.63–2.70	3.1–6.0	0.61–0.85	4.0–4.1	0.70–0.71	7.9–8.0	0.95
Puya retrorsa	200–300	2.30–2.48	40.0–60.0	1.61–1.79	40.0–80.0	1.61–1.69	3.0–3.5	0.60–0.65	1.99–2.0	0.48	3.7–4.0	0.67–0.70
Puya venusta	90–100	1.96–2.00	30.0–35.0	1.49–1.56	30.0–35.0	1.49–1.56	0.39–0.4	0.14–0.15	1.5–2.0	0.40–0.48	3.4–3.5	0.64–0.65
Puya spathacea	99–100	2.00	60.0–100.0	1.79–2.00	40.0–60.0	1.61–1.79	1.3–2.2	0.36–0.51	1.5–2.2	0.40–0.51	2.5–3.3	0.54–0.63
Puya pygmea	20–30	1.32	15.0–22.0	1.20–1.36	3.0–5.0	0.60–0.78	2.9–3.0	0.59–0.60	1.5–1.8	0.40–0.45	1.5–2.0	0.40–0.48
Puya coerulea	199–200	2.30	59–61	1.78–1.79	98–101	2.00–2.01	1.69–1.7	0.43	2.39–2.40	0.53	3.7–5.0	0.67–0.78
Puya aequatorialis	199–200	2.30	99–100	2.00	98–101	2.00–2.01	1.79–1.8	0.45	2.0–2.3	0.48–0.52	2.9–3.0	0.59–0.60
Puya laxa	79–81	1.90–1.91	27–28	1.45–1.46	70.0–80.0	1.85–1.91	1.3–2.0	0.36–0.48	1.69–1.70	0.43	2.9–3.0	0.59–0.60
Puya medica	20–37	1.32–1.58	20–20.5	1.32–1.33	10.0–20.0	1.04–1.32	1.5–1.6	0.40–0.41	1.8–2.0	0.45–0.48	3.4–4.0	0.64–0.70
Puya floccosa	50–200	1.71–2.30	100.0–110.0	2.00–2.05	30.0–100.0	1.49–2.00	1.3–1.7	0.36–0.43	2.5–3.3	0.54–0.63	3.9–4.0	0.69–0.70
Puya venezuelana	59–60	1.78–1.79	25.0–34.0	1.41–1.54	18.0–22.0	1.28–1.36	4.45–4.5	0.74	1.8–2.0	0.45–0.48	3.0–3.5	0.60–0.65
Puya aristeguietae	299–300	2.48	99–100	2.00	100.0–110.0	2.00–2.05	1.6–1.8	0.41–0.45	2.5–3.3	0.54–0.63	5.0–6.0	0.78–0.85
Puya trianae	40–200	1.61–2.30	24.0–28.0	1.40–1.46	15.0–30.0	1.20–1.49	5.0–6.0	0.78–0.85	2.0–2.5	0.48–0.54	3.10–3.20	0.61–0.62
Puya goudotiana	499–500	2.70	100.0–170.0	2.00–2.23	100.0–200.0	2.00–2.30	2.0–3.7	0.48–0.67	2.0–3.0	0.48–0.60	5.0–6.0	0.78–0.85
Puya ferruginea	250–400	2.40–2.60	99–100	2.00	199–200	2.30	4.45–4.5	0.74	1.2–4.5	0.34–0.74	8.0–14.0	0.95–1.18
Puya ferreyrae	150–200	2.18–2.30	55.0–100.0	1.75–2.00	60.0–75.0	1.79–1.88	5.0–7.0	0.78–0.90	3.2–3.7	0.62–0.67	3.9–4.0	0.69–0.70
Puya nitida	170–200	2.23–2.30	35.0–60.0	1.56–1.79	58.0–62.0	1.77–1.80	3.4–3.8	0.64–0.68	2.9–3.0	0.59–0.60	6.9–7.0	0.90
Puya westii	249–250	2.40	99–100	2.00	49–50	1.70–1.71	0.8–1.0	0.26–0.30	1.99–2.0	0.48	3.9–4.0	0.69–0.70
Puya nutans	55–70	1.75–1.85	15.0–23.5	1.20–1.39	29–30	1.48–1.49	1.99–2.0	0.48	1.79–1.80	0.45	3.9–4.0	0.69–0.70
Puya santosii	80–200	1.91–2.30	31.0–37.0	1.51–1.58	32.0–50.0	1.52–1.71	3.2–3.3	0.62–0.63	1.3–2.0	0.36–0.48	3.0–3.6	0.60–0.66
Puya cuatrecasasii	99–100	2.00	25–27	1.43	?	?	2.59–2.6	0.56	2.35–2.4	0.53	4.90–5.0	0.77–0.78

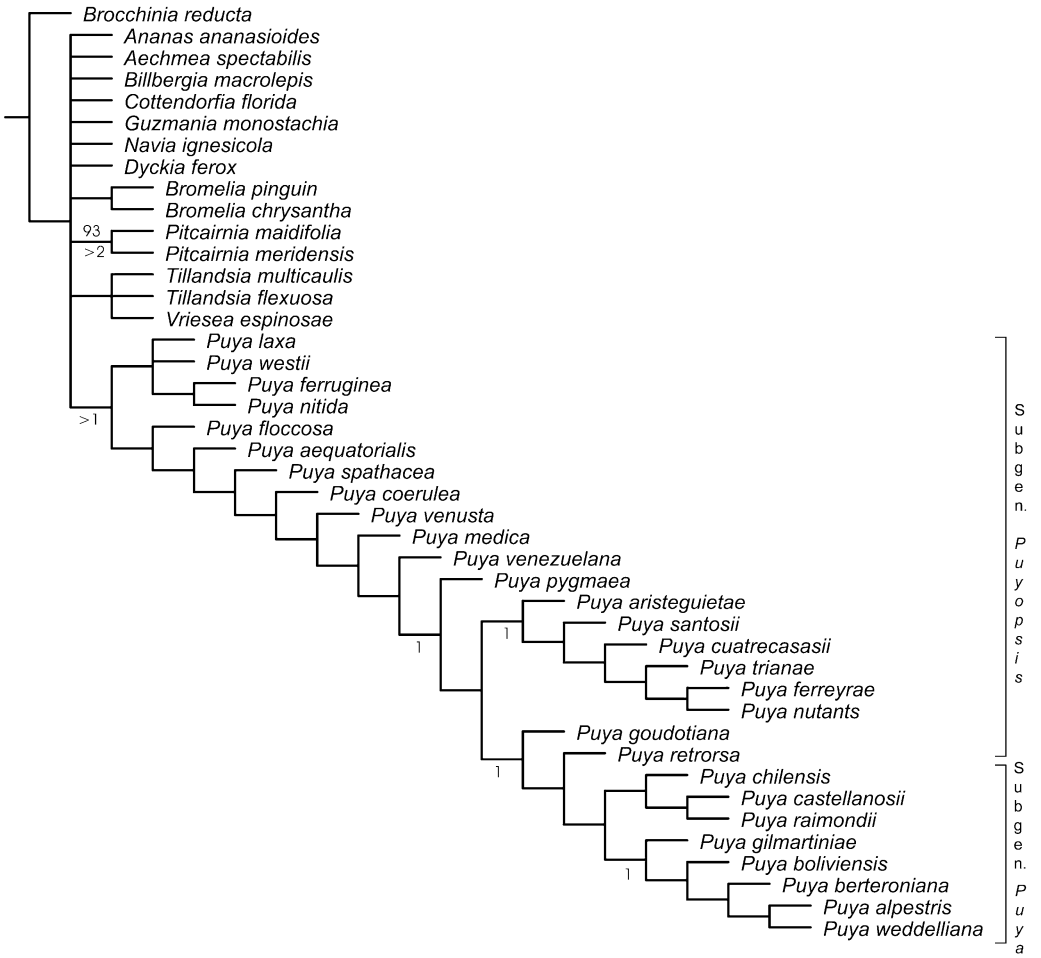

Figure 3. Strict consensus tree of the nine most parsimonious trees based on discrete characters. Numbers above the branches indicate jackknife support. Numbers below the branches indicate Bremer support [L = 505 steps; consistency index (CI), 0.250; retention index (RI), 0.522].

correlated with petal length (Hornung-Leoni & Sosa, 2005). It is suggested that, in subgenus *Puya*, large and giant plants have large inflorescences; this is advantageous because, if the flowers are medium-sized, there is an increase in flower number and a larger seed set can be produced. Furthermore, it has been demonstrated that large plants with a large number of flowers are more attractive to pollinators (Kawasaki & Hori, 1999).

In the clade of subgenus *Puya*, the flowers are covered by small to large bracts. It is interesting that *P. alpestris* and *P. berteroniana*, species that can be confused, are differentiated by the size of their floral bracts (in the latter species they are larger). *Puya chilensis*, *P. castellanosii*, and *P. raimondii* have flowers with large bracts. More information is needed on the pollination system of the species in this group to understand the evolution of this floral character.

It is concluded that, in order to corroborate the infrageneric classification of *Puya*, an extended sampling of the species is needed. Our results clearly show that the species classified in subgenus *Puya* are retrieved in a group; however, the results do not conclusively determine the taxonomic status of these species. More informative characters would also be useful to resolve the relationships of the species belonging to this large genus. Molecular datasets will undoubtedly provide these variable characters.

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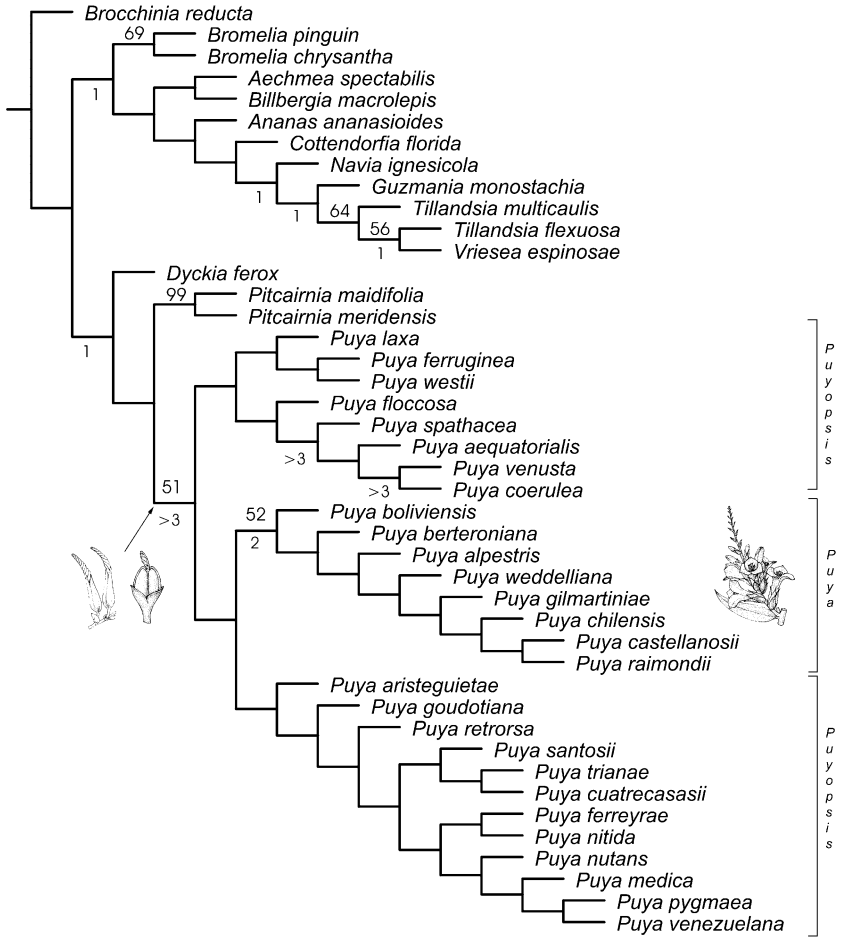

Figure 4. Single most parsimonious tree based on discrete + continuous characters. Numbers above the branches indicate jackknife support. Numbers below the branches indicate Bremer support [L = 530 steps; consistency index (CI), 0.250; retention index (RI), 0.515]. Synapomorphic characters for genus *Puya* and subgenus *Puya* are illustrated.

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APPENDIX 1

HERBARIUM SPECIMENS USED FOR THIS STUDY

Aechmea spectabilis Brongn. ex Houllet. VENEZUELA: Edo. Trujillo, Entre Trujillo y Boconó, *E. Graf* s.n. (F). Edo. Mérida, Mpio. Tovar, *C. Hornung* 209 (MERC). Edo. Mérida, *C. Hornung* 219 (MERC). Edo. Mérida, Mpio Justo Briceño, *P. López* 3472 (MERF). COLOMBIA: Dpto. Magdalena, about 11 km south-east of Molino, *O. Haught* 4051 (F).

Ananas ananassoides (Baker) L.B. Sm. BOLIVIA: Santa Cruz, Nuflo de Chavez, Rancho Zapoco, 90 km de Concepcion, *T. Killleen* 1479 (NY). GUYANE FRANCAISE: Roche Touatou – Basin d'inselberg, *J.J. Granville* 12988 (NY). BRAZIL: Edo. Amazonia, Municipality if Humaitá, Rio Madeira, road to Humaitá to Labrea, km 20, Savana margin, *G.T. Prance* 3407 (F). Minas Gerais, Br 153, 20 km S de Frutal, *A. Krapocickas* 33048 (F). In Cerrado, along Anhuma Creek, 300 km past Cuiaba en route to Goiania, Mato Grosso, *B. Maguire* (F1769731). Mato Grosso, Pantanal de Paiaguas, Fazenda Buriti, 65–70 km de estrada Cuiaba-Campo Grande, *A. Krapovickas* 29916 (F).

3–4 km SW of Mutumparaná on railroad to Abuna, *G.T.Prance* 5453 (F). VENEZUELA: Edo. Bolívar, Basin of Río Parguaza, *Croizat* 40 (F).

Billbergia macrolepis L.B.Sm. BRAZIL: T.F. Do Rondonia, Mpio. De Ariquemes, Mineracao Mibrasa, Setor Alto Candeias, km 128, Sudoeste de Ariquemes, *L.O.A.Teixeira* 611 (NY). VENEZUELA: Edo. Amazonas, Cerro Sipapo (Paráque), *B. Maguire* 28053 (NY). Bajo el Río Guaramacal, *R. Liesner* 10610 (VEN).

Brocchinia acuminata L.B.Sm. VENEZUELA: Edo. Territorio Federal Amazonas, Summint to cerro Duida, on high moist ridge top, *J.A. Steyermark* 58363 (F). Edo. Bolívar, Chimantá Massif, moist forest along quebrada, vicinity of camp 4, south-western edge of Apacará–Tepuí, *J. A. Steyermark* 75007 (F). Edo. Bolívar, Cerro Guanacoco, cumbre, porción nor-oeste cerca del borde riscoso, *J.A. Steyermark* 109715 (F). Amazonas, Dpto. Río Negro, Cerro de la Neblina, Camp XI, 6.2 km NNE of Pico Phelps (= Neblina), *M. Nee* 31098 (NY). Edo. Bolivar, Dto. Piar, summit of Amaruay-tepui, SE quarter of tepui, *R. Liesner* 20869 (NY). Territorio Federal Amazonas, Sierra Parima, *J. Steyermark* 107507 (US).

Brocchinia reducta Baker. VENEZUELA: Edo. Bolívar, Gran Sabana, Roraima, *J. Pruski* 1413 (NY). Edo. Bolívar, Dto. Roscio: Valle del Río Aponguao, *O. Huber* 14.vi.1985 (NY). Edo. Bolívar, Qda. Pacheco, approx. 70 km N de Sta. Elena, *N. Xena* 313 (NY).

Bromelia crysantha Jacq. VENEZUELA: Edo. Mérida, Mpio. Sucre, vía Las Coloradas, *C. Hornung* 89 (MERC). Edo. Mérida, Mpio. Sucre, San Juna-Las Gonzalez, *R. Rico* 335 (MERC).

Bromelia pinguin L. HONDURAS: Dpto. El Paraíso, Río Choluteca near bridge of Ojo de Agua, *L.O. Williams* 42888 (NY). MÉXICO: Veracruz, Mozomboa, Mun. Actopan, *J. Dorantes* 837 (XAL). Veracruz, Chavarillo, 1.5 km delante de la estación de Chavarillo, Mpio. Emiliano Zapata, *G. Castillo-Campos* 12413 (XAL). Veracruz, La Mancha, Mpio. Actopan, *G. Castillo-Campos* 12339 (XAL). Veracruz, 3 km ak E de Santa Fe, Mpio. Veracruz, *V.E. Luna* 305 (XAL). Veracruz, Estación biológica El Morro de La Mancha, Mpio. Actopan, *B. Guerrero C.* 1673 (XAL). Veracruz, 5 km al NO de Panuco, *L.I. Nevling* 401 (XAL). Veracruz, Carro Topila ejido 'Benito Juarez', Mpio. Panuco, *C. Gutierrez* 1999 (XAL). Veracruz, Ocozotepec, Mpio. Soteapan, *H. Cruz Ramírez* 11 (XAL). Yucatán, km 4 del crucero rumbo a San Felipe, Mpio. Río Lagartos, *E. Ucan* 789 (XAL). Yucatán, a 90 km del Crucero, rumbo a Tizimin, Mpio. Río Lagartos, *E. Ucan* 1155 (XAL), *G. Castillo* 5762 (XAL). Bahia de Banderas, Mpio. Bahia de Banderas, Nayarit (XAL 16364). México, Islas Marietas, Mpio. Bahia de Banderas, Nayarit, *G. Castillo* 5914 (XAL). PANAMÁ: Prov. Los Santos, between Limon and Punta Mala, *T.B. Croat* 9746 (NY).

Cottendorfia florida Schult. f. BRAZIL: Mpio. De Macujê, 10–17 km ao NW de Mucujê, na estrada para Andaraí, *S.A. Mori* (US 2854490); Mpio. De Macujê, 10–17 km ao NW de Mucujê, na estrada para Andaraí, *S.A. Mori* (US 2854493). Bahia, Mun. Rio de Contas Pico das Almas, Vertente leste, Na parte norte do vale abaixo do pico, *R.M. Harley* 26196 (F). South of Andarí, along road to Mucugé near small town of Xique-Xique, *R.M. Harley* 18687 (NY). Río Apiaba (mun. Mucugê), Bahia, *G. Hatschbach* 47534 (NY).

Dyckia ferox Mez. ARGENTINA: Dpto. Capital, Prov. Corrientes, Procedente de San Roque, *A. Schinini* 13850 (F). Dpto. Capital, Ruta 12 y Ayo, Richuelo, *A. Schinini* 12439 (F).

Guzmania monostachya Rusby ex Mez. COSTA RICA: *H.E. Stork* 2933 (F). NICARAGUA: *G.S. Bunting* 352 (F). La Selva, *U. Rowlatt* 1851 (F). ECUADOR: Prov. Carchi, environs of Chical, 12 km below Maldonado on the río San Juan, *M.T. Madison* 4484 (F). Dpto. Tumbez, Prov. Tumbez, mts E of Hacienda Chicama, *A. Weberbauer* 7643 (F). PERÚ: Dpto. Cajamarca, Prov. Santa Cruz, alrededores de Monteseco, *A. Sagástegui* 12362 (F). Dpto Cajamarca, Prov. Santa Cruz, Distr. Catache, Upper Río Zaña valley, *M. Dillon* 4371 (F). (L.Rusby) ex Mez; Dpto. San Martin, San Roque, *L. Williams* 7238 (F). VENEZUELA: Edo. Mérida, Mpio. Libertador, *C. Hornung* 210 (MERC). Edo. Mérida, Mpio. Libertador, *C. Hornung* 236 (MERC). Edo. Mérida, Mpio Libertador, Campo de Oro, *T. Ruiz* 14662 (MERF). Edo. Mérida, Mpio. Libertador, Campo de Oro, *T. Ruiz* 14656 (MERF). USA: Florida, s.c, s.n (F 167005). Prov. De Heredia, Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, *T. McDowell* 353 (F). USA: Subtropical Florida, *N.L. Buten* 257 (F).

Navia igneosicola L.B.Sm., Steyerm. & H.Rob. VENEZUELA: Territorio Federal Amazonas, Dpto. Atures: forested areas and igneous outcrops along Río Coromoto, at Tobogán de la Selva, *J. Steyermark* 122478 (US).

Pitcairnia maidifolia Decne. ex Planch. COLOMBIA: Dpto Antioquia, Mpio. De Cocorná (Ant.), camino entre 'la Piñuela' y 'La Vega', margen izquierda del Río Santo Domingo, *R. Fonnegra* s.n. (F 2181034); Mpio. Amalfi, Verede El Oso, Cordillera Central, *J. Betancur* 916 (F). COSTA RICA: San José, Dota, Zona Protectora Cerro Nara, Faldas del Cerro Nara,

O. Valverde 515 (F). Prov. San José, *F. Montgomery G.* 5052 (F). GUIANAS: Region Cuyuni-Mazaruni, Mt. Holitipu, below peak, *T. McDowell* 3027 (F). HONDURAS: Dpto. Morazán, Agua Amarilla, *L.O. Williams* 10814 (F). Dpto. Morazán, Region of Agua Amarilla, above El Zamorano, *P.C. Standley* 5061 (F). Dpto. Morazán, north-west of El Zamorano, *P.C. Standley* 22890 (F). Dpto. Morazán, along and near Río Agua Amarilla, above El Zamorano, *P.C. Standley* 12813 (F). El Paraiso, 3 km north of Las Manos, *L.O.Williams* 42265 (F). Dpto. Morazán, Region of Agua Amarilla, above El Zamorano in pine–oak forest, *P.C. Standley* 10 (F). VENEZUELA: Edo. Bolivar, Massif of Chimantá, *J.A. Steyermark* 75475 (F). Territorio Federal Amazonas, Sierra Parima, *J.A. Steyermark* 105910 (F). Territorio Federal Amazonas, Cero Duida. *J.A. Steyermark* 57969 (F). Edo. Mérida, between El Molino and ridge above San Isidro, *J.A. Steyermark* 56519 (F). Edo. Mérida, Mpio. Libertador, *C. Hornung* (MERC). Edo. Mérida, Mpio. Cardenal Quintero, *C. Hornung* 136 (MERC). Edo. Mérida, Mpio.Tovar, *C. Hornung* 174 (MERC). Edo. Mérida, Mpio. Tovar, *C. Hornung* 175 (MERC). Edo. Mérida, Mpio. Tovar, *C. Hornung* 176 (MERC). Edo. Mérida, Mpio. Tovar, via Zea, *C. Hornung* 177 (MERC). Edo. Mérida, Mpio. Arzobispo Chacón, *C. Hornung* 196 (MERC). Edo. Mérida, *C. Hornung* 221 (MERC). Edo. Mérida, Mpio. Tovar, Zea, *P. López* 1236 (MERF). Edo. Mérida, Dtto. Justo Briceño, *López* 3513 (MER, MERF).

Pitcairnia meridensis Klotzsch ex Mez. VENEZUELA: Edo. Mérida, between El Molino and ridge above San Isidro, *J.A. Steyermark* 56519 (F). Edo. Mérida, Mpio. Campo Elías, *L. Aristeguieta* 2485 (VEN); Edo. Mérida, Ca. Jají, *F. Oliva* 263 (VEN). Edo. Mérida, Mpio. Rivas Dávila, *B. Marcano* 1743 (VEN). Edo. Mérida, Mpio. Rivas Dávila, *C. Benitez* 2072 (VEN). Edo. Mérida, *J.A. Steyermark* 56519 (VEN). Edo. Mérida, Mpio. Campo Elías, *F. Oliva* 228 (VEN). Edo. Mérida, Carbonera-Azulita, *J. de Brujin* 1131 (VEN). Mpio. Dávila, *B. Marcano* 1743 (MER). Edo. Mérida, Estación teleférico La Montaña, *D.L. Kelly* 9099 (MER). Edo. Mérida, Mpio. Rivas Dávila, *P.S. López* 10 (MERF). Edo. Mérida, Mpio. Libertador, *T. Ruiz* 8741 (MERF). Edo. Mérida, Mpio. Sucre, *T. Ruiz* 811 (MERF). Edo. Mérida, Mpio. Libertador, *C. Hornung* 74 (MERC). Edo. Mérida, Minas de Bailadores, *C. Hornung* 107 (MERC). Edo. Mérida, Mpio. Andrés Bello, *C. Hornung* 143 (MERC). Edo. Mérida, Mpio. Arzobisco Chacón, *C. Hornung* 194 (MERC). Edo. Mérida, Mpio. Arzobispo Chacón, *C. Hornung* 198 (MERC). Edo. Mérida, *C. Hornung* 216 (MERC).

Puya aequatorialis Ed. André. ECUADOR: Azuay, Prov. Azuay, between ríos Azogues and Gualaceo, valley of the río Paute, between Puate and Cuenca, *W.H. Camp* 2322 (US). A 15 km de Quito, Otavalvo-70 m terreno volcanico, *A. J. Gilmartin* 1084 (US). *André* 3594 (F). Loja, Cuenca-Ona-Zaraguro, *M.B. Foster* 2608 (F). Azuay, valley of the río Paute, between Paute and Cuenca, *W.H. Camp* 3222 (US). Vicinity of Cumbe, *J.N. Rose* 22954 (NY). Prov. Azuay, valley of the río Paute, between Paute and Cuenca, *W.H. Camp* 2322 (NY).

Puya alpestris (Poepp.) Gay. CHILE: 1877. SGO (046422); *J. West* 4981 (US); F (739422); F (1670523). *N. Floy Bracelin* 2802 (F). *N. Floy Bracelin* 2766 (F). La Hermida, cerca de Santiago, *G. Looser* 2104 (F). Cordillera de Colchagua (SGO 046423). Cerro Sur Baños Flaco, *M. L. Espinosa* (leg) s.n. xii.1937 (SGO). Coordillera de Colchagua, s.n. (SGO 046425). *Reiche* s.n. dic/91 (SGO 061082). Fundo Fray Jorge, SGO (060188); s.n. V/1884 (US photo). Prov. Concepción, Hills north to Concepción, *J. West* 4981 (US). Cerro San Cristóbal, *Germain* s.n., 1854 (SGO). Coquimbo, *M. Muñoz* 909 (SGO). Coquimbo, *C. Muñoz* 1552 (SGO). Coquimbo, *C. Muñoz* 1302 (SGO). Cerro Fray Jorge, *Philippi* s.n. (SGO). Fray Jorge, Ovalle, *Philippi* s.n., I/1883 (SGO). Cordillera de La Dehesa, *Philippi* s.n., XI/1861 (SGO). Región metropolitana, Carr. Santiago-Farellones, *C. Hornung* 1109 (HDCV).

Puya aristeguietae L.B.Sm. VENEZUELA: Edo. Trujillo, Dto. Boconó, Páramo de Guaramacal, *L.J. Dorr* 5000 (NY). Edo. Trujillo, Alrededores de Guirigay, *L. Aristeguieta* 3539 (NY). Edo. Trujillo, Dto. Boconó, Páramo de Guaramacal, SE of Boconó, *L.J. Dorr* 7326 (NY). Edo. Mérida, Bosque exp. 'San Eusebio', Dpto. Campo Elías, *J.P. Schulz* 388 (NY). Edo. Mérida, Dtto. Rangel, Quebrada 'Puya' (unnamed Qba.) *c.* 3–4 km S of the mouth of the Rio Los Granates, Parque Nacional Sierra Nevada, *L.J. Dorr* 5598 (NY). Edo. Trujillo, Páramo de Guirigay, *L. Aristeguieta* 3539 (US). Edo. Mérida, Mpio. Rangel, *C. Hornung* 161 (MERC). Edo. Mérida, Mpio. Páramo Gaviria, *C. Hornung* 208 (MERC). Edo. Mérida, Mpio. Rangel, *T. Ruiz* 7310 (MERF). Edo. Mérida, Mpio. Miranda, *T. Ruiz* 12267 (MERF). Edo. Mérida, Mpio. Miranda, *T. Ruiz* 12268 (MERF). Edo. Mérida, Parque Nacional Sierra Nevada, *A.P. Yañez* 1719 (MER). Edo. Trujillo, Páramo Guirigay, *L. Aristeguieta* 3539 (VEN).

Puya berteroniana Mez. BOLIVIA(?): near La Paz (probably the label is an error), *Rusby* 2850 (US). CHILE: Prov. Curicó, Hacienda Monte Grande, *E. Wedermann* 563 (F). IIX Región, Prov. Santiago, Peñaflor cerro, *G. Montero* 768 (F). CHILE: Limache, *Belen* s.n. 10.ii.1917 (F). Rancagua, *Bertero* 115 (F photo). Viña del Mar, 16.xii.1923 (F). Cuesta de La Dorminda, *L. Gonzalez* s.n. 26.v.1983 (HDCV). Cuesta La Dormida, bajando del Roble, *C. Hornung* 1111 (HDCV). Haci-

enda Rinconada La Cesda, Maipu, Qda La Plata, *F. Schlegel* 1664 (SGO). Prov. Santiago, Región Metropolitana, Reserva Forestal Río Clarillo, *J. Yañez* s.n. 3.viii.1993 (SGO). Prov. Valparaiso, four km southwest of Valparaiso, *P.C. Hutchison* 22 (SGO). Prov. Coquimbo, IV Región, Coquimbo, *M. Muñoz S.* 908 (SGO). IV Región, Playa Las Tacas, 20 km al Sur de Coquimbo, *A.R. Flores* s.n. 15.viii.1986 (SGO). Rancagua, *Bertero* 115 (US). Valparaiso, *Weber* 3252 (US). Concón, *Miers* 347 (US).

Puya boliviensis Baker. BOLIVIA (now Chile): Cobija, Gaudichau, *Julliet* s.n. 1836–1837 (F 1435100). Cobija, *Gaudichaud* s.n. (F 741178). *Gaudichaud* s.n. (US 2144992). *Gaudichau* s.n. (F1435081). CHILE: Antofagasta región II, Prov. Antofagasta, Cero Perales, *c*. 5 km E of Taltal, *M.O. Dillon* 5377 (F). Quebrada Paposo, *c*. 5–7 km E of Caleta, *M.O. Dillon* 5242 (F). CHILE: Antofagasta región II, Prov. Antofagasta, Cerro Perales, *c*. 5 km E of Taltal, *M.O. Dillon* 5377 (F). II Región, Qda. Rinconada de Paposo, *A. Hoffmann* s.n. 2.xii.1988 (SGO). CHILE: II Región, Mirador de Paposo, subiendo por quebrada Los Yales, *A. Hoffmann* s.n. 1.xii.1988 (SGO). II Región, qda. en camino a Cifuncho, *A. Hoffmann* s.n. 1.xii.1988 (SGO). II Región, Qda. Matancilla, *A. Hoffmann* s.n. 3.xii.1988 (SGO). II Región, Taltal, Qda. Matancilla, *A. Hoffmann* s.n. 3.xii.1988 (SGO). Morro de Caldera (SGO), Paposo, *Reich* 360 (SGO). *Gaudichaud* s.n. (US 21449992). Region II, Antofagasta, Prov. Antofagasta, Cerro Perales, *c*. 5 km E of Taltal, *M.O. Dillon* 5377 (F).

Puya castellanosii L.B.Sm. ARGENTINA: Cachi, Prov. Salta, Dpto. Chachi: Brealito, *G.S. Varadarajan* 1476 (US). Dpto. Cachi, Prov. Salta, Brealito, *G.S. Varadarajan* 1476 (US). Prov. Salta, *Catellanos* s.n. [type], 1897 (US). Dpto. Molinos, Prov. Salta, Brealito, *T. Meyer* 9164 (US). Salta, Laguna del Brealito (Valle Calchaqui), *Castellanos* 45819 (US).

Puya chilensis Molina. BOLIVIA (now CHILE): *Gaudichaud*, s.n. (F 1370754). CHILE: Limache, Frisco (F 633928). 1837 (F 1435147). Viña del Mar, 7.ix.1922 (F). Viña del Mar, 7.ix.1922 (F). Prov. Elqui, *T.G. Lammers*, *C.M. Baeza P. & P. Peñalillo B*. 7653 (F). Angol, *Philippi* s.n., i.1877 (SGO). Constitución, *K. Reiche* s.n., xii.1891 (SGO). Fundo Fray Jorge, *C. Carrizo* s.n., 10.iii.1947 (SGO). Cordillera de Colchagua, *L. Landbeck* s.n., xii.1860 (SGO). Cordillera de Colchagua, Philippi s.n. (SGO 6425). Cerro, Sur Baños Flacos, *M. Espinosa* s.n., xii.1937 (SGO). Zapallar, *Philippi* s.n., ix.1875 (SGO). Aconcagua: Zapallar, *Philippi* s.n., ix.1865 (SGO). Paposo, *K. Reiche* s.n., ix.1909 (SGO). Cordillera de Cauquenes, *K. Reiche* s.n., x.1907 (SGO). Angol, *Philippi* s.n., 1877 (SGO). Constitución, *K. Reiche* s.n., xii.1891 (SGO). Chillan, *Philippi* s.n., xii.1869 (SGO). Llico, *Philippi* s.n., xii.1861 (SGO).

Puya coerulea Miers. CHILE: Angostura de Praine, *G. Looser* s.n., 4.xii.1932 (F). s.n. (F1668607), Angostura de Praine, *G. Looser* 2553 (F). Angostura de Praine, *Looser* 2550 (F). Angostura de Praine, *G. Looser* 2549 (F). Angostura de Praine, *G. Looser* 2551 (F). Prov. Santiago, *P.C. Hutchinson* 202 (F). *Phillipii* s.n. (F 741265). Prov. Curicó: Hacienda Monte Grande, *E. Wedermann* 539 (F). s.n. (F 835815). Río Clarillo, s.n. (HDCV 949), Vía El Roble, *C. Hornung* 1110 (HDCV). Baños de Cauquenes, *Philippi* s.n., iii.1875 (SGO). Llico, *Philippi* s.n., xii.1861 (SGO). Inter Poblacion El Cueva, *Philippi* s.n. (SGO 46407). Chillan, *Philippi* s.n., xii.1869 (SGO). Cordillera de Popeta, *Philippi* s.n., i.1884 (SGO 46413). Angol, *Philippi* s.n., i.1877 (SGO). Complejo Turistico La Leonera, *M. Muñoz* & *S. Moreira* 2393 (SGO). Complejo Turistico La Leonera, *M. Muñoz* & *S. Moreira* 2394 (SGO). Las Tacas, *A. Flores* s.n., 15.viii.1986 (SGO). Taltal, *A. Hoffmann* & *A. Flores* s.n., 3.xii.1988 (SGO). Quebrada Camino a Cifuncho, *A. Hoffmann* & *A. Flores* s.n., 1.xii.1988 (SGO).

Puya cuatrecasasii L.B.Sm. COLOMBIA: Dpto. Valle, Cordillera Central: entre Pan de Azúcar, *J. Cuatrecasas* 27573 (COL). Cordillera Central, vertiente occidental, *J. Cuatrecasas* 18962 (COL). Dpto. Cauca, Macizo Colombiano, Páramo de las Papas, *J. Idrobo* 4062 (COL). Dpto. del Cauca, Cordillera Central, vertiente occidental, Cabeceras del Río Palo. *J. Cuatrecasas* 18962 (F). Tolima, above 'Ampilio', Cabeceras río Ereje, *E. L. Core* s.n. 21.xi.1944 (F).

Puya ferreyrae L.B.Sm. ECUADOR: Prov. Loja: Las Chinchas, Reg. Central, *M. Acosta S.* 7803 (F). PERU: Dpto. La Libertad, Prov. Otuzco, road to Huamachuco, 11 km above Samne, *P. C. Hutchinson* 6124 (F). Dpto Cajamarca, Sangal (San Pablo), Prov. San Pablo, *A. Sagástegui* 15367 (F). PERU: Dpto. Cajamarca, *c*. 7 km E of Magdalena, *M.O. Dillon* 6206 (F). Dpto. Cajamarca, Prov. Cajamarca. Entre Magdalena – Chilete, en la parte alta de la hacienda la Viña, *I. Sanchez V.* 3574 (F). Dpto. Cajamarca, Prov. Cajamarca, Dist. Jesús, a 1 km de la localidad de Jesús, siguiendo la carretera, *I. Sanchez V.* 6153 (F). Dpto. La Libertad, Prov. Otuzco, Casmiche (Ssmne-Otuzco). *A. Sagastegui* 11515 (F). Road to Huamachuco, 11 km above Samne, *J. Kenneth* 6124 (F).

Puya ferruginea (Ruiz & Pav.) L.B.Sm. BOLIVIA: Nequejahuira, *SC* 634, 15.v.1926 (NY). Dpto. La Paz, Prov. Murillo, 1 km SW of Mallasilla Golf Course, 9 km SSE of centre of La Paz, *M. Nee* 34161 (NY). Dpto. La Paz, Province of Murillo, *J.C. Solomon* 6668

(NY). Dpto. La Paz, Prov. Murillo, *c*. 0.4 km NE of Alto Irpavi, *Solomon J.C.* 6093 (NY). *O. Kuntze* s.n. 13–21.iv.1892 (NY). La Paz, s.n. 152, 1890 (NY). *H.H. Rusby* 2845, iv.1885 (NY). Yungas, *H.H. Rusby* 2847, 1885 (NY). Dpto. La Paz, Prov. Nor Yungas, 3.6 km NE of (below) Chupipata on road to Yolosa, *J.J. Solomon* 15642 (NY). Dpto. La Paz, Prov. Nor Yungas, 4.7 km al NE (abajo) de Chuspipata, *J.C. Solomon* 17336 (NY). Dpto. La Paz, Prov. Murillo, *M. Nee* 34161 (NY). Nequejahuira, *G.H. Tate* 634, 15.v.1926 (NY). Yungas, *H.H. Rusby* 2847 (F). Dpto. La Paz, *O. Buchtien* s.n. iii.1913 (F). Dpto. La Paz, *O. Buchtien*, iii.1923 (F). Dpto. La Paz, 1890 (F 162549). Dpto. La Paz, *O. Buchtien* s.n. iii.1913 (NY). Prov. Huaura, Lomas de Lachay, *A. Cano* 7081 (USM). ECUADOR: Prov. Loja, Valle Seco de Playas, Catacocha, *M. Costa Solís* 7998 (F). E. Andre 4019 (NY). PERU: Dpto. Junin, Tarma, *E.P. Killip* 21806 (NY). *G. Mandon* 1173 (NY). Yungas, *H.H. Rusby* 2847 (NY). La Paz, *R.S. Williams* 2355 (NY). Cordillera Real, Nequejahuira, *H.H. Tate* 634 (NY). Dpto. Cusco, Prov. Calca, Pisaq ruins, *J.D. Boeke* 1532 (NY). Dpto. Lima, Prov. Huarochiri, Rio Blanco, *P.C. Hutchinson* 573 (NY). Dpto. Cusco, Prov. Calca, Lares Valley above Mantoc, *A. Weberbauer* 7915 (NY). Cordillera Yanachaga, *A. Gentry* 35919 (NY). Dpto Ancash, Prov. Huaylas, Pueblo Libre, *A. Cano* 8882 (USM). Dpto. Lima, Prov. Huarochirí, Sangallaya, *E. Cerrate* 1775 (USM). Dpto. Lima, Prov. Huarochirí, Sangallaya, *R. Ferreyra* 9200 (USM). Pasco, Cordillera Yanachaga, *A. Gentry* 35919 (USM). Prov. Huaura, Lomas de Lachay, *A. Cano* 7081 (USM). Dpto. Cuzco, Prov. Urubamba, *E.W. Davis* 1774 (USM). Dpto. Cuzco, Prov. Urubamba, *W. Davis* 1488 (USM). Cuzco, Prov. Urubamba, Sist. Huayllabamba, *A.Tupayachi* 931 (NY). Dpto. La Libertad, Prov. Trujillo, Cerro Campana. *A. Sagástegui* 12957 (F). Dpto Lima, Prov. Huarochiri, Río Blanco, Canyon of the Río Rimac, *P.C. Hutchinson* 573 (F). Dpto. La Libertad, Prov. Trujillo, *A. Sagástegui* 10980a (F); *J. Francis Macbride* 3148 (F); Dpto. Yucay, *J. Soukup*, xii.1937 (F); Dpto. Cuzco, Prov. Urubamba, Chicon Canyon, on rocky slopes, *C. Vargas* 11091 (F); Cuzco, Colinas de Sacsahuaman, *J. Soukup* 42 (F). Río Blanco, *J.F. Macbridge* 3005 (F). Dpto. Lima, Prov. Huarochiri, Infiernillo, *T.H. Goodspeed* 110601 (F). Dpto. Cuzco, Prov. Urubamba, Chincheros, *E.W. Davis* 1774 (F). Yanano, *J. Francis Macbride* 3812 (F). Río Blanco, *J. Francis Macbride* 711 (F). Dpto. La Libertad, Prov. Otuzco, Cascasday (Collambay-Sinsicap), *A. Sagástegui* 15638 (F). Lima, Prov. Huarochiri, Río Blanco, canyon of the río Rimac, *P.C. Hutchinson* 573 (F). Cusco, Prov. Paucartambo, valle del Pilcopata, road from Patria to Pillahuata, *R. Foster* & *T. Watcher* 7482 (F). Prov. Yanachaga, *A. Gentry* 35919 (F). Dto. Huayllabamba, Cuzco: Prov. Urubamba, *A. Tupayachi* 931 (NY). Prov. Huarochiri, Río Blanco, canyon of the río Rimac, *P.C. Hutchinson* 573 (F).

Puya floccosa E. Morren. BRAZIL: Amazonia, Territorio do Roraima, *G.T. Prance* 4532 (NY). Serra Tepequem, terr. Do Rio Branco, *B. Maguire* 40039 (NY). COLOMBIA: Dpto. Cundinamarca, Cordillera Oriental, Chuneca Creek, 5 km from Ubalá, *M.L. Grant* 10189 (NY). Dpto. Huila, Cordillera Oriental, east of Neiva, *H.H. Rusby* 1122 (NY). Dpto. Santander, northern slope of Mesa de los Santos, Eastern Cordillera, *E.P. Killip* 15002 (NY). Dpto. Cundinamarca, Cordillera Oriental, vertiente Magdalenense, *J. Betancur* 3975 (COL). VENEZUELA: Edo. Barinas, San Isidro, 27 km de Barinitas, Dtto Bolivar, *G. Aymard* 2190 (NY). Edo. Bolívar, Dtto. Roscio, sabanas en el valle del Río Kukenán inferior, en la región de Campo Alegre, a aprox. 14 km al SW de S. Ignacio de Yuruaní, *O. Hubber* 7592 (NY). Edo. Táchira, Dtto. Uribante, S base of Cerro El Morro, *J.L. Dorr* 7086 (NY). Edo. Bolívar, 17 km E of Canaima, *G.T. Prance* 28461 (NY). Edo. Bolívar, 3 km S of El Paují, *R.L. Liesner* 19875 (NY). Edo. Bolivar, Uaipan-tepui, plateau at SE foot of the peak of Uaipan, exposed sandstone shield, *T. Koyama* 7371 (NY). Edo. Bolívar, Dtto. Rosci, *O. Huber* 9201 (NY). Edo. Mérida, *C. Hornung* 206 (MERC). Edo. Mérida, *C. Hornung* 81 (MERC).

Puya gilmartiniae G.S.Varadarajan & A.R.Flores. CHILE: Region IV, Coquimbo, Prov. Elqui, Punta Arrayán, *c*. 20 km N of La Serena, *M.O. Dillon* 5449 (F). Region IV, El Olivar, N de La Serena, *A. Flores* s.n. 16.viii.1986 (SGO).

Puya goudotiana Mez. COLOMBIA: Dpto. Cundinamarca, Macizo de Bogotá, cerro Diego Largo, vert. E., *J. Cuatrecasas* 5162 (F). Dpto. Cundinamarca, Eastern Cordillera, municipality of Calera, Hacienda La Siberia, Páramo de Palacio, *R. Merril K.* 6039 (F). Dpto. Cundinamarca, Cordillera Oriental, Chocontá, *J. Cuatrecasas* 9660 (F). Dpto. Cundinamarca, Cordillera Oriental, Páramo de Guasca, *J. Cuatrecasas* 13547 (F). Dpto. Norte de Santander, Cordillera Oriental, *J. Cuatrecasas* 10039 (F). Dpto. Cundinamarca, Cordillera Oriental, Macizo de Bogotá, *J. Cuatrecasas* 7969 (F). Dpto. Cundinamarca, Eastern Cordillera, Municipality of Calera, Hacienda La Siberia, Páramo de Palacio, *R. Merrill K.* 6039 (F). Dpto. Cundinamarca, Cordillera Oriental, vertiente oriental, Páramo de Guasca, *J. Cuatrecasas* 9506 (F). Dpto. Cundinamarca, Cordillera Oriental, Páramo de Guasca, vertiente oriental, *J. Cuatrecasas* 13547 (F). Dpto. Cundinamarca, Cordillera Oriental, Páramo de Chocontá, *J. Cuatrecasas* 9660 (COL). Dpto. Amazonas, Páramo de Guasca, *A. Fernández P.* 5760

(COL). Dpto. Cundinamarca, Mpio. La Calera, *C. García R.* 85 (COL). Dpto. Cundinamarca, Eastern Cordillera, Municipality of Calera, Hacienda La Siberia, Páramo de Palacio, *R. Merrill K.* 6039 (NY). *G. Gutierrez* 247 (NY). Bogotá 26.xi.1852 (NY). Dpto. Santander, Vicinity of Charta, *E.P. Killip* 18930 (NY).

Puya laxa L.B.Sm. BOLIVIA: About Pulquina, Santa Cruz, *M. Cardenas* 5092 (US). About Pulquina, Santa Cruz, *M. Cardenas* 5092 (US).

Puya medica L.B.Sm. PERU: Shorey, Prov. Santiago de Chuco, Sagástegui, Aldave, *Fernandez* & *Fukushima* 6175 (XAL).

Puya nitida Mez. COLOMBIA: Dpto. Cundinamarca, Cordillera Oriental, Páramo de Guasca, *J. Cuatrecasas* 13539 (F). Macizo de Bogotá, Cerro entre quebrada de Las Delicias y la de Las Ninfas, *J. Cuatrecasas* 5629 (F). Dpto. Cundinamarca, Coodillera Oriental, Páramo de Zipaquirá, *J. Cuatrecasas* 9529 (F). Macizo de Bogotá: Cerro de Guadalupe, *J. Cuatrecasas* 7958 (F). Dpto. Cundinamarca, Mpio. Guatavita, Laguna de Guatavita, Páramo de Guatavita, *J. Betancur* 2713 (COL, NY). Dpto. Cundinamarca, Páramo de Cruz Verde, Cordillera Oriental, vertiente occidental, *G. Gutierrez V.* 366 (F). Boyaca, Paramo de Guina, Sta. Rosita, *A.M. Cleff* 9740 (NY). *M.J. Goudot*, 1844 (NY). Cundinamarca, Macizo de Bogotá, Mpio. De Calera, Páramo del Palacio, *R.E. Schultes* 18727 (NY). Dpto. Boyacá, Páramo de Guina, Sta. Rosita, *A. M. Cleef* 9740 (COL).

Puya nutans L.B.Sm. ECUADOR*:* Azuay, Campo, *W.H. E.* 2291 (NY, US). PERU*:* Cuzco, *Cano, A.* 4324 (F).

Puya pygmaea L.B.Sm. BOLIVIA: Lchmamb 589 (F). ECUADOR: Prov. Azuay, Páramo de Tinajillas, *W.H. Camp* 2236 (F, US). Prov. Morona-Santiago, Páramo de Castillo, *G.S. Varadarajan* 1433 (US). Prov. Azuay, Páramo de Tinajillas, *S.E. Clemants* 2199 (US). PERU: Dpto. Cusco, Prov. Paucartambo, Tres Cruces, Parque Nacional Manu, *A. Cano* 4563 (F). Prov. Paucartambo, Dpto. Cusco, Tres Cruces P.N.M, *A. Cano* 3455 (USM). Dpto. Cusco, Prov. Paucartambo, Altura de Teleban P.N.M., *A. Cano* 3782 (USM). Dpto. Cusco, Prov. Paucartambo, Tres Cruces P.N.Manu, *A. Cano* 4563 (USM). Dpto. Cusco, Prov. Paucartambo, Acjanaco, PN Manu, *A. Cano* 3393 (USM). In this study, we extend the distribution of this species to Bolivia and Peru, following the determination from H. Luther, A. Cano, and L. B. Smith, and confirm the characteristics specific to this species (Manzanares, 2005) as the presence of floral bracts erect (vs. reflexes), amongst others.

Puya raimondii Harms. BOLIVIA: Huacanqui, *M. Cárdenas* 4380 (US). Comanche, *M.B. Foster* 2566 (US). Cochabamba, *M.B. Foster* 2546 (US). Dpto. Cochabamba, Prov. Arani, *G. Schmitt* & *D. Schmitt* 84 (US). La Paz, Prov. Pacajes, Comanche, *J.N. Rose* & *Mrs Rose* 18875 (US). La Paz, Pacajes, Comanche, *J. Luteyn, L. Dorr, D. Smith* & *M. Buddensick* 13840 (US). Dpto. La Paz, Prov. Pacajes, Comanche, *St.G. Beck* 2353 (US). PERÚ: La Libertad, Prov. Otuzco, *A. Sagástegui*, *S. Leiva* & *C. Tellez* 14510 (F). *Weberbauer* 2955 (F). La Libertad, Prov. Otuzco, *S. Leiva*, *P. Leiva* & *E. Zavaleta* 292 (F). Estation 30 miles from Huaraz, Pomopampa, *Macbride* & *Featherstone* s.n, 4.xii.1922 (F). Dpto. Puno, Prov. Melgar, *H. Ilties* & *Don Ugent* 1288 (US). Prov. Bolognesi, Huishcashpampa, *E. Cerrate* 2072 (USM). Prov. Huaylas, Dpto. Ancash, *A. Cano* 6405 (USM). 1/2 km SE of Hacienda Santa Rosa de Achaco, s.n. (USM 159980). Dpto. Huancavelica, carretera Castrovirreyna-Ayacucho, s.n. (USM 159979). Dpto. Ancash, P.N. Huascarán, *C. Hornung* 1118 (USM). Dpto. Ancash, Canchayllo, *C. Hornung* 1120 (USM). Dpto. Ancash, P.N. Huascarán, *C. Hornung* 1121 (USM). Dpto. Ancash, P.N. Huascarán, *C. Hornung* 1122 (USM). Dpto. Ancash, P.N. Huascarán, Pumapashimin, *C. Hornung* 1123 (USM). Dpto. Ancash, Cordillera Negra, *C. Hornung* 1124 (USM). Dpto. Ancash, *C. Hornung* 1126 (USM).

Puya retrorsa A.J.Gilmartin. ECUADOR: Prov. Chimborazo, between Cajabamba and Pallatanga, *G.S. Varadarajan* 1440 (US). Prov. Pichincha, Paramo de Huamani, *G.S. Varadarajan* 1420 (US). Tunguragua, *A.J. Gilmartin* 1103 (US).

Puya santosii Cuatrec. COLOMBIA: Dpto. Cundinamarca, Cordillera Oriental, Páramo de Cruz Verde, *J. Cuatrecasas* 9518 (F). Dpto. de Cundinamarca, Macizo de Bogotá, Páramo de Usaquén, *J. Cuatrecasas* 9441 (F). Dpto de Cundinamarca, Páramo de Usaquén, *J. Cuatrecasas* 7996 (F). Dpto. de Cundinamarca, Páramo de Cruz Verde, Cordillera Oriental, *J. Cuatrecasas* 10468 (F). Dpto. Cundinamarca, Macizo de Bogotá, Páramo de Uraquén, *J. Cuatrecasas* 9441 (COL). Meta: Páramo de Sumapáz, Hoya El Nevado, *A. Cleef* 1503 (COL). Dpto. Cundinamarca, Cordillera Oriental, Páramo de Cruz Verde, *J. Cuatrecasas* 10468 (COL). Dpto. Cundinamarca, Cordillera Oriental, extremo sudeste de la Sabana de Bogotá, en San Miguel, *J. Cuatrecasas* 12042 (F). Dpto. Cundinamarca, Cordillera Oriental, Páramo de Cruz Verde, *G. Gutierrez* 386 (F). Dpto. Cundinamarca, Cordillera Oriental, *J. Cuatrecasas* 9518 (F).

Puya spathacea (Griseb.) Mez. ARGENTINA: Prov. De Cordoba, Sierra Grande, *A.P. Rodrigo* 458 (NY).

Jujuy, *O. Kuntze* s.n. x.1892 (NY). Prov. de Córdoba, Sierra chica, *G. Hieronymus*, s.n. 9.viii.1876 (NY). *O. Kuntze*, s.n. x.1892 (F). Prov. Córdoba, La Cumbre, *A. Haurteig* 203 (F). Jujuy, *O. Kuntze* x.1892 (NY). La Rioja, Guanchín, *Castellanos* 27/1902 (NY). Prov. Cordoba, Las Cumbres, *A. Haurteig* 263 (F). BOLIVIA: *Troll* 661 (F). ARGENTINA: Jujuy, *O. Kuntze* s.n. x.1892 (F). *Hieronymus* s.n. (F). Prov. de Cordoba, Loc. La Falda, Cerro El Chorrito, *M.M. Job* 453 (F). Jujuy, *O. Kuntze* s.n. ix.1892 (NY).

Puya trianae Baker. COLOMBIA: Dpto. Cundinamarca, Macizo de Bogotá, Páramo de Chisacá, Laguna Negra, *J. Cuatrecasas* 25924 (COL, F). Dpto. Cundinamarca, Páramo de Chisacá, *T.R. Soderstrom* 1286 (F). Dpto. Cundinamarca, Andes de Bogotá, Páramo de Cruz Verde, s.n. (COL). Dpto. Cundinamarca, Páramo de Chisacá, *T.R. Soderstrom* 1286 (F). Dpto. Cundinamarca, Páramo de Cruz Verde, Cordillera Oriental. *J. Cuatrecasas* 10474 (F). Dpto. Antioquia, Mpio. Urrao, Páramo de Frontino, *J. Betancur* 1166 (F). Dpto. Cundinamarca, Páramo de Chisacá, en pendientes y colinas, *J.M. Idrobo* 6525 (F). Cundinamarca, *Triana* 1314 (F). Dpto. Cundinamarca, Macizo de Bogotá, Páramo de Chisacá, *J. Cuatrecasas* 25745 (NY). Dpto. Cundinamarca, Macizo de Sumapaz, *J. Cuatrecasas* 27030 (NY). Dpto. Boyacá, Páramo de la Rusia, Serranía Peña Negra, *A.M. Cleef* 7430 (COL). VENEZUELA: Edo. Mérida, Mpio. Campo Elías, *T. Ruiz* 8000 (MERF).

Puya venezuelana L.B.Sm. COLOMBIA: Dpto. del Arauca, Sierra Nevada del Cocuy, Quebrada el Playón, Casa Piedra, *A.M. Cleef* 10124 (COL). Línea divisoria entre Dpto. Santander del Norte y Cesar, *H. García-Barriga* 19737 (COL). VENEZUELA: Edo. Mérida, Páramo de Pozo Negro, between San José and Beguilla, *J. Steyermark* 56285 (F); Edo. Trujillo, *L. Aristeguieta* 3538 (US). Edo. Mérida, Páramo de Pozo Negro, between San José and Beguilla, *J.A. Steyermark* 56285 (F). Edo. Mérida, Páramo Gaviria, *C. Hornung* 204 (MERC). Edo. Mérida, Páramo Gaviria, *C. Hornung* 205 (MERC). Edo. Mérida, Mpio Sucre, *T. Ruiz* 44 (MERF). Edo. Mérida, Mpio. Sucre, *T. Ruiz* 1708 (MERF). Edo. Mérida, Mpio. Libertador, *T. Ruiz* 8476 (MERF).

Puya venusta Phil. ex Baker. CHILE: Gaudichau s.n. (F 741180). Gaudichau s.n. (F 835821). *Quilliman* 8/9/9 (HDCV). Huentelauquén, poco al sur de la desembocadura del río Choapa, *H. González Villalón* s.n. 5.xi.1966 (F). *Philipii* s.n. (F 741266). Prov. Aconcagua, Zapallar, *G. Looser* 2542 (F). Prov. Aconcagua, Zapallar, *G. Looser* 2548 (F).

Puya weddelliana Mez. BOLIVIA: Dpto. Chuquisaca, *D.S. Correll* 644 (US). Tarija, *Weddell* 4001 (US photo).

Puya westii L.B.Sm. PERÚ: Dpto. La Libertad, Prov. Huamachuco, road to Quiruvilca, 18 km above and west of Huamachuco, *P.C. Hutchison* 6146 (NY). La libertad, near Huamachuco, *J. West* 8353 (US). Dpto. La Libertad, Prov. Huamachucho, road to Quiruvilca, *P. C.* Hutchinson 6146 (F).

Tillandsia flexuosa Sw. COLOMBIA: Vaupes, Río Kuduyarí, Yapobodá, sandstone savannah near headwaters, *R.E. Shultes* 18487 (F). PANAMÁ: Prov. Cocle, s.n. (F 1693109). Prov. Panamá, Las Sabanas, s.n. (F 686341). VENEZUELA: Mpio Sucre, Edo. Mérida, *C. Hornung* 48 (MERC). Mpio Livertador, *C. Hornung* 84 (MERC). Mpio Sucre, Edo. Mérida, *C. Hornung* 150 (MERC). Edo. Mérida, Mpio. Libertador, *E. Arellano* s.n. (MERC). Edo. Mérida, Mpio. Sucre, *R. Rico* 275 (MERC). Edo. Mérida, Mpio. Sucre, *R. Rico* 399 (MERC). Edo. Mérida, Laguna de Caparú, *A. Rondón* 202 (MER).

Tillandsia multicaulis Steud. MÉXICO: Edo. Veracruz, Loma Alta. Mpio. Coatepec, *V.E. Luna* 1006 (XAL). Edo. Veracruz, Ahuihuixtla, Mpio. Calcahualco, *J.L. Martínez* 704 (XAL). Edo. Veracruz, Camino Xico a Tonalaco, Mpio Xico, *M. Xhazaro* 1504 (XAL). Edo. Veracruz, Naolinco, Mpio. Naolinco, *F. Ventura* 13214 (XAL). Edo. Veracruz, a 2 km de Ahuihutle, camino a tres Aguas (Coscomatepec), Mpio Calcahualco s.n. (XAL). Edo. Veracruz, Alrededores de la represa Xocollolapa, *A. Flores-Palacios* 941 (XAL). Edo. Veracruz, Jardín Botánico Francisco Javier Clavijero, *K. Fabian* 346 (XAL). Edo. Veracruz, El Esquilon, Mpio. Jilotepec, *R. Ortega* 526 (XAL). Veracruz, Tenejapa, *S. Avendaño R.* 260 (XAL). Edo. Veracruz, *J. Martínes G.* 187 (XAL). Edo. Veracruz, Etlantepec-Tlacolulan, *I. García-Orta* 159 (XAL). El Esquilón, Mpio. Jilopetec, *M.G. Zola* 669 (XAL). Edo. Veracruz, Mpio. Coatepec, *V.E. Luna* 717 (XAL). Edo. Veracruz, 5 Palos, *V.E. Luna M.* 840 (XAL). Edo. Veracruz, Cañada río Ayohuxtla, *A. Rincón G.* 2733 (XAL). Edo. Naranjillos, Mpio. San Andres Tlanehuayocan, Naranjillos, *C. Gutierrez* 2737 (XAL). Edo. Veracruz, rancho grande, 3 km de Xalapa, *J.I. Calzada* 1900 (XAL). Edo. Veracruz, along Río Grande, Mun. Las Choapas, *M. Nee* 29877 (F).

Vriesea espinosae (L.B.Sm.) Gilmartin. PERU: Lambayeque, 17 km E of Olmos on road to Pucara, premontane dry forest, *A. Gentry* 22562 (F).

APPENDIX 2

DATA MATRIX USED FOR CLADISTIC ANALYSIS (CHARACTER NUMBERS CORRESPOND TO THOSE GIVEN IN TABLE 1)

	1 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 87
Brocchinia reducta	10--?100210--00111221000110110001101100010012001000010012101000102210000100101112200-031
Ananas ananasioides	00--1001001020011201101111111001201------1------1001112012001117?01121100111010111212-001
Bromelia pinguin	00--13010010100012-1101101111010110010011010011100001001210100010021000010000011201-001
Bromelia chrysantha	00--13010010100022-2001011121010100010011O-00111001010012201001021014001100110012O1-001
Aechmea spectabilis	00--1210011000011211100110111000000100001011010102111201100101012021310001010111201-000
Billbergia macrolepis	10--1100211010011222110011010000000------1-------02001?00202110010121210011110O?0201?000
Cottendorfia florida	?0--1211000-00111221000110110000101000110110110000O2?012000000011200001100101010100031
Guzmania monostachia	00--1310010--00010-020001100000000------1------102001$012000100211200001100101$10000010
Tillandsia multicaulis	00--1310010--00110010000000-010001------1------0000102000000101001101000l?000110000?010
Tillandsia flexuosa	00--1211010--001102210011001*000000100011010000100000210100100001111030001000011100O2010
Vriesea espinosae	00--1111010--00110221001000100000l------1-------000002001001100O?1101?0?1?0?0?1?000?010
Navia ignesicola	010103100110200--1--000?0---000001------1-------001---01-00?1???0?0???0????10??1000?0?1
Pitcairnia maidifolia	20--1110000--11011-0100?1000000011------1------102001201220001121100000110000000000O2031
Pitcairnia meridensis	20--1110000--11001--20001000000010------1------100001101230101020210310011000020000O2031
Dyckia ferox	00--?1110012100011-11000110-*100010?100110010001000010012001000211214100100111010010$021
Puya alpestris	011112110010100111021010101110101110111010001000100000001220020020121201010000011000$121
Puya berteroniana	011*12110012100011-210101---10101101110100110001020000122$110020021201010000111000?121
Puya weddelliana	011?120100101O0??1??10101?1?10101101111100O??00?000?0001220?000?112120111000O?11000?121
Puya chilensis	011112010012000011-2101011121010110111110001010100001001220120020121401010000011000l121
Puya gilmartiniae	011112210012100111121010111210101101111100100100020001012201000201014010100000110O0?121
Puya boliviensis	00--12110012100011-110101010100011011101000000010000011122010002212140101000001100O2121
Puya castellanosii	0???12010012?00111111101011?2101011011111000101111000O?01220*000200?14?1?1?000???0002121
Puya raimondii	010002010012000$1111102001121011110111110000011100000001220110020021001010000000000l121
Puya retrorsa	011112010012000011-21010111$10110100101110000101121011012201000211315$11?10000???000?121
Puya venusta	00--1121001010011122101101111*000110010011011010102000201225$110121111111111110101010001121
Puya spathacea	00--1211001010010120100*111110001001100110010111001012012201001201111110100000010001l121
Puya pygmea	00--0111001010011112100000121011110010111100010100010101211110O?1121211010000??1000?121
Puya coerulea	010012110101001112210011111100010011001121110000120011010002022111121010010001000l121
Puya aequatorialis	011112110011200111221001111100001O------1------100101$012201001211$1$110100000010O0?121
Puya laxa	00--1211001020022122101011121000101100O?10110011000011002301001201211110100O0???000?121
Puya medica	01??10110010100011-210000011*000110010111000010102100?012211101201?121101000001000O?121
Puya floccosa	010012110012100111221001111110001001100121110000120011010002022111121010010001000l121
Puya venezuelana	00--1211001110001l-211000012001111------1------100100101221110020021111010000011000O121
Puya aristeguietae	00--11210010000011-11010011$1011110?100111010101000000012201000201210111100000000002121
Puya trianae	00--?101001000011101101001120011l1------1------110000101211110020131411010000101000l121
Puya goudotiana	00--12000011000011-2101000121011110?10111000000100000101220100020031$110100001110001121
Puya ferruginea	01***2110012$00$11$210011112*000101100011010000112000100130100022111$011100000$01002121
Puya ferreyrae	0???12?1001$000111021000001100001l------1------100100?012121101200010110100001010001?121
Puya nitida	00--1221001200011112100010l$000010------1------110100101210111020131201000000010100212l
Puya westii	00--12?10012000011-110?0????100010?1?00?101101011210110122010002214121100100100100012l
Puya nutans	00--?101001010O?11?211000011000111------1------110100101220110021031411010000001000l121
Puya santosii	00--?2010010000011-110100011101111001011110001111010010122111002113121111000O?0?0001121
Puya cuatrecasasii	01?112110010100011-010100012101111001011110001111000010121011002003101111?000101000?121

*, polymorphism (0 and 1); $, polymorphism (1 and 2, or 0 and 2); ?, character unknown; –, not applicable.