Morphological Phylogenetic Analysis of Two Early-Diverging Genera of Bromelioideae (Bromeliaceae)

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Abstract

Bromelia includes 66 species, grouped in three subgenera: *Bromelia, Distiacanthus* and *Karatas.* The genus is one of the earlier divergent groups within Bromelioideae, a subfamily with innumerable problems of generic delimitation. Considering that few phylogenetic studies have included more than one species of *Bromelia*, the objectives of this study were to carry out a phylogenetic analysis for the genus, seeking to evaluate its monophyly as well as its subgenera, and to better understand the interspecific evolutionary relationships within the genus and the intergeneric relationships within Bromelioideae. Also included in the analysis were the two species of *Fernseea,* a genus originally described from a species placed in *Bromelia*. The phylogenetic analysis was conducted with combined micro- and macromorphological data, including 39 taxa with 116 characters. As in other studies on Bromeliaceae, the clades have low statistical support and many questions regarding the relationships of the groups remain. The circumscription of *Bromelia* is still uncertain, due to the position of *B. irwinii*; *Fernseea* seems to emerge within this genus, as the marority-rule consensus suggests, and the infrageneric categories are debatable because they do not constitute monophyletic groups. However, *Bromelia* seems to be paraphyletic and, without *B. irwinii*, the genus can be considered monophyletic. Beginning with the premise that the most recent common ancestor of Bromelioideae appeared first in the southern Andes, *Bromelia* and *Fernseea* seems to have dispersed along three biogeographical routes. The present work is an important contribution to understand the evolution and biogeography of the Bromelioideae.

Key words: *Bromelia*, *Fernseea*, dry diagonal, Brazilian Shield, morphology.

Introduction

The family Bromeliaceae includes about 3,320 species and has been subdivided into eight subfamilies (The Plant List 2013; Givnish *et al.* 2007, 2011). The Bromelioideae is the subfamily that has diverged more recently among Bromeliaceae lineages, and frequently emerges as monophyletic and sister to Puyoideae (Givnish *et al.* 2004, 2007, 2011; Evans *et al.* 2015). About 85% of the more than 860 species of Bromelioideae occur in Brazil, with the major center of diversity in the Atlantic Forest (Martinelli *et al.* 2008; Forzza *et al.* 2014). The importance of this subfamily in the evolutionary history of the bromeliads is represented by the combination of an epiphytic habit, formation of a tank, CAM metabolism, and an extensive recent diversification in the Neotropical region,

mainly in forest formations along the east coast of Brazil (Benzing 2000; Crayn *et al.* 2004). Bromelioideae taxonomy is very complex. Most genera are artificial, circumscribed using particular groups of morphological features rather than synapomorphies, and genera limits are often been redefined, since they are based on symplesiomorphies (Schulte *et al.* 2009).

Several phylogenies (Schulte *et al.* 2005, 2009; Givnish *et al.* 2011) agree that one of the earlier divergent lineages in Bromelioideae comprises five terrestrial genera that lack a leaf tank: *Fascicularia*, *Ochagavia* and *Greigia*, which have C3 metabolism and occur in humid environments; *Deinacanthon*, which presents CAM metabolism and occurs in the Chaco (Schulte *et al.* 2005); and *Bromelia*. The later is the largest genus among this early-diverging lineage and includes species with

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CAM metabolism. Its members are concentrated at low to intermediate altitudes (0 to 1200 m elev.), and occur widely in South and Central America, reaching their greatest diversity in areas with open vegetation and alternate wet and dry seasons; but are also found in more humid environments (Benzing 2000; Crayn *et al.* 2004; Monteiro *et al.* 2011). Another member of this early-branching lineage in Bromelioideae is the genus *Fernseea* (Schulte & Zizka 2008; Schulte *et al.* 2009; Jabaily & Systma 2010).

Bromelia includes 66 species (The Plant List 2013; Forzza *et al.* 2014) robust with curved spines on the leaf margins; showy flowers often covered by trichomes; petals chartaceous and fleshy, helmet-shaped to reflexed, from pink to red or lilac to purple, and smooth; with yellow berries (Mez 1891; Smith & Downs 1979). Mez (1891) proposed a division of the genus into three subgenera: *Bromelia* subg. *Distiacanthus*, *Bromelia* subg. *Bromelia* and *Bromelia* subg. *Karatas*. The first subgenus includes species with petiolate leaves. In the second, species have inflorescences that extend outside the foliar rosette, as well as an ovary with sparse, white indumentum. The third subgenus includes species with inflorescences inside the foliar rosette, and an ovary with tomentose chestnut-brown indumentum (Fig. 1). In spite of Mez' proposal, Smith and Downs (1979) did not accept infrageneric categories in *Bromelia*.

Fernseea has only two species, both of which occur in southeastern Brazil, in montane regions with scrub vegetation ("campos de altitude", Vasconcelos 2011). The type species of the genus, *F. itatiaiae* (Wawra) Baker (Fig. 1), was described in *Bromelia* and some years later it was combined in the new genus *Fernseea* (Baker 1889). Nearly a century later, its congener *F. bocainense* was described by Pereira and Moutinho (1983). *Fernseea* is characterized by narrow leaf blades; bracts with a dense imbricate peduncle; a simple racemose inflorescence; well-developed floral bracts; pedicellate flowers with free, symmetrical sepals; free petals without appendices; stamens free and included; and a long epigynous tube (Smith & Downs 1979).

Fernseea and *Bromelia* have seldom been analyzed simultaneously in the same phylogenetic analysis (Schulte *et al.* 2009; Evans *et al.* 2015). *Fernseea* forms a clade with *Fascicularia* and *Ochagavia* in a polytomy with *Bromelia* (Horres *et al.* 2007), or occurs as a sister to the eu-

bromelioids (Schulte & Zizka 2008). *Bromelia* appears either in a polytomy with *Fascicularia*, *Deinacanthon* and *Ochagavia* (Schulte *et al.* 2005), as a sister to *Greigia* and to *Ochagavia* and *Fascicularia* (Givnish *et al.* 2011), or as a sister to eu-bromelioids (Evans *et al.* 2015) or all other Bromelioideae (Givnish *et al.* 2007; Schulte *et al.* 2009; Sass & Specht 2010).

Even though some morphological characters have been shown to be homoplastic (Hornung-Leoni & Sosa 2008; Almeida *et al.* 2009; Gomes-da-Silva *et al.* 2012; Schulte *et al.* 2009; Donadío *et al.* 2014), many of them continue to be extremely important in the delimitation of taxonomic groups in Bromeliaceae (Hornung-Leoni & Sosa 2008; Almeida *et al.* 2009; Gomes-da-Silva *et al.* 2012), in contrast to the lack of molecular divergence in traditional analyzed fragments of DNA (Clark & Clegg 1990; Horres *et al.* 2000; Schulte *et al.* 2005; Faria *et al.* 2004; Versieux 2009). Although intensive efforts have been made to search for new and informative DNA fragments together with the use of microsatellites (Versieux *et al.* 2012) and amplified fragment length polymorphism (AFLP; Rex *et al.* 2007; Louzada 2012), detailed studies of morphology are also necessary in order to reveal traits of evolution that might not appear in molecular phylogenies, and important for identifying morphological synapomorphies (Assis 2009).

In view of this situation, and using a morphological phylogenetic analysis, our aims were: (1) to test the monophyly of *Bromelia* and *Fernseea*, as well as (2) of the subgenera *Bromelia*, *Distiacanthus* and *Karatas*; (3) to examine the relationships among the species of the two genera; and (4) to discuss the adaptive radiation and geographical diversification of the early-diverging bromelioids during the conquest of the Brazilian Shield.

Materials and Methods
Taxon Sampling
Twenty-five species of *Bromelia* (13 of the subgenus *Bromelia,* 10 of *Karatas*, and 2 of *Distiachanthus*), the two species of *Fernseea*, 11 species from other related genera of Bromelioideae, and one from *Puya* were analyzed, in a total of 39 terminals (Appendix a and b). The species of *Bromelia* were selected on the basis of their occurrence, particularly taxa that are the best delimited taxonomically and also
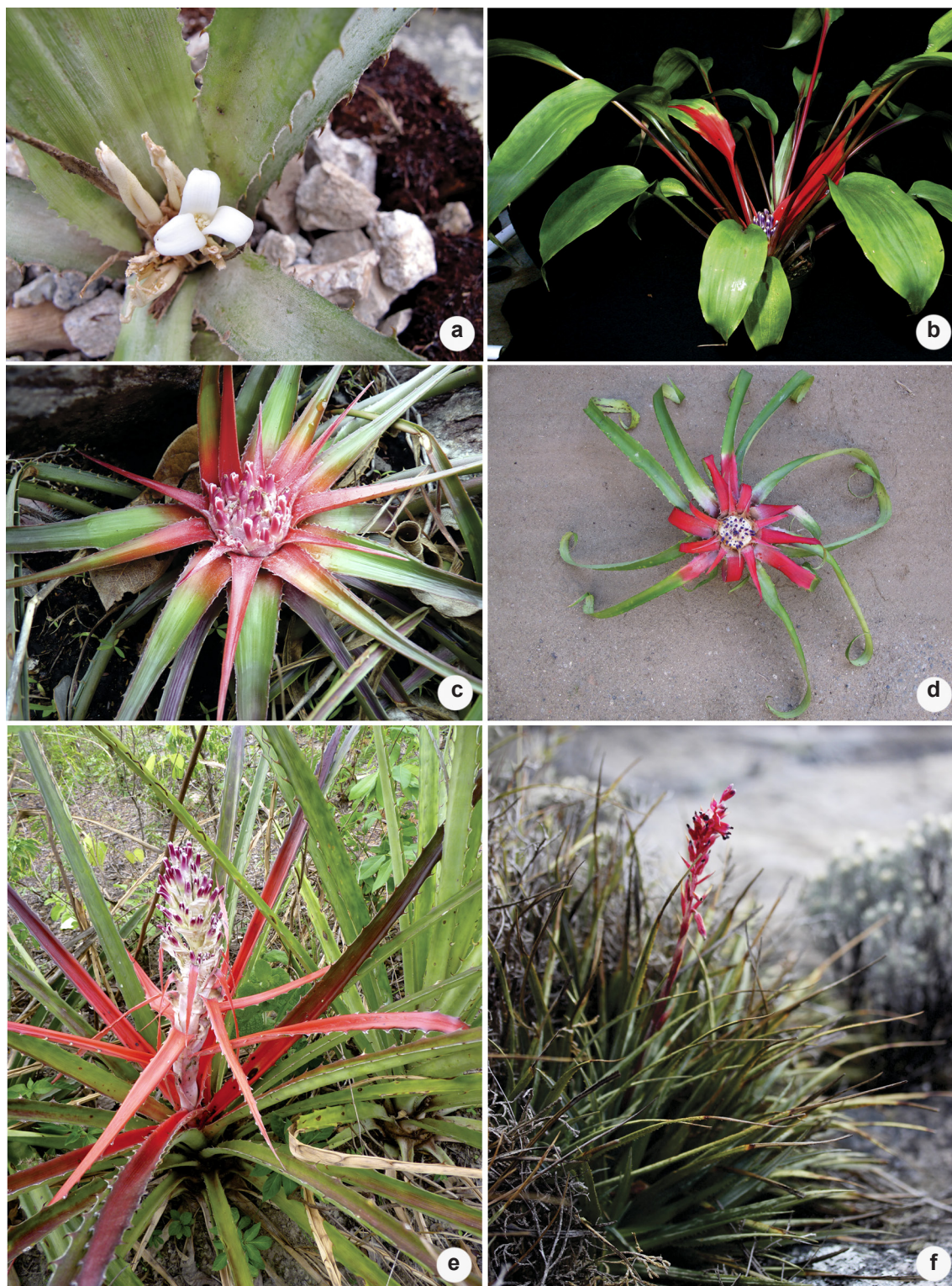
Figure 1 – a-b. *Bromelia* subg. *Distiacanthus*. – a. *B. morreniana*; b. *B. scarlatina* (Photo: B. Holst). c-d. *Bromelia* subg. *Karatas*. – c. *B. macedoi*; d. *B. villosa*. e. *Bromelia* subg. *Bromelia*. – *B. balansae*. f. *Fernseea*. – *F. itatiaiae* (Photo: M. Wolowski Torres).

are well represented in the herbarium collections consulted. The voucher material is listed in Appendix a. We included all the patterns of morphological variation observed in the genera.

Morphological dataset

A data matrix of Species x Characters with 116 discrete characters, including 67 binary and 49 multistate characters (Apendix b), was constructed with the aid of the program Mesquite 2.7 (Maddison & Maddison 2011). The characters list was built following Sereno [2007, (Table 1)]. All the characters were treated as unordered and were equally weighted. All the characters and their states are listed in table 1. The macromorphological characters were analyzed for specimens obtained from field sampling, living collections, or herbarium specimens (Appendices a and b). The majority of the flowers analyzed were fixed in 70% ethanol at the time of collection. Existing published informations on the taxa, such as the color and position of the petals, were also used.

To obtain the micromorphological characters, the leaf anatomy of *Bromelia* was examined from freehand sections observed with a light microscope. The samples used were fixed in 70% ethanol; herbarized leaves were used if fresh leaves were not available. The methodology followed Monteiro *et al.* (2011). Anatomical and macromorphological informations for some non-*Bromelia* species were obtained from published descriptions (Sajo *et al.* 1998; Zizka *et al.* 1999; Forzza 2001; Mantovani & Iglesias 2005; Leme & Siqueira Filho 2006; Mantuano 2008; Mantovani *et al.* 2012). The terminologies adopted follow the definitions of Radford *et al.* (1974) and Weberling (1989) for macromorphology, and Tomlinson (1969) for micromorphology.

Phylogenetic analysis

The cladistics analyses used the criterion of maximum parsimony. We conducted a heuristic search with 1000 repetitions, using 10 trees per replication, by the branch-swapping algorithm of the tree bisection-reconnection (TBR) method, based on the character optimization method ACCTRAN (accelerated transformation optimization; Swofford & Maddison 1992), unordered and unweighted, with retention of multiple most parsimonious trees (MAXTREE), using the program PAUP* 4b10 for Macintosh

(Swofford 2002). *Puya nana* was used to root the tree, as this genus is sister to the Bromelioideae (Givinish *et al.* 2007; Nixon & Carpenter 1993). Each branch support value was evaluated by bootstrap (BS), performed with random addition sequence of taxa, using TBR for two hundred replicates and holding 10 trees by step (Felsenstein 1985). The Bremer (B) support was also calculated increasing the number of the optimal tree steps until the branches have collapsed (Bremer 1994). The program Mesquite 2.7 was used to visualize the cladograms and to reconstruct the ancestral characters states (Maddison & Maddison 2011) and the WinClada 1.00.08 (Nixon 2002) to trace the characters on the trees.

Biogeographical evaluation

The biogeographical evaluation of the species of *Bromelia* and *Fernseea* used in the analysis was based on published data (Smith & Downs 1979; Ramírez-Morillo *et al.* 2004; Forzza *et al.* 2014), original descriptions, field observations, and herbarium data. The maps were made with ESRI® ArcMap™ 9.3 program.

Results

The maximum-parsimony analysis generated 34 equally parsimonious trees with 951 steps, a consistency index (CI) of 0.379, a retention index (RI) of 0.450, and a rescaled consistency index (RC) of 0.170. The strict consensus tree and the majority-rule tree are presented (Figs. 2, 3, 4).

Bromelia is paraphyletic, due to the positioning of *B. irwinii* (Fig. 4). Without this taxon the remaining species of the genus formed a group (Fig. 2, clade B) sustained by nine synapomorphies: rosette position in relation to the central axis during flowering ca. 45°, bracts of peduncle patent during anthesis, floral bracts equaling or exceeding ovary, but not sepals; petal carnose and oblong, fruit yellow, stomata apparatus below the level of the epidermis, vascular bundles of smaller diameter taller than wider and habit terrestrial.

Fernseea did not appear to be monophyletic (Figs. 3a, 4). However, this genus was recovered in the analyses as closely related to *Bromelia*, principally to *B. irwinii*. Although they appeared in a polytomy in the strict consensus (Fig. 2), the positioning of the two species of *Fernseea + B.*
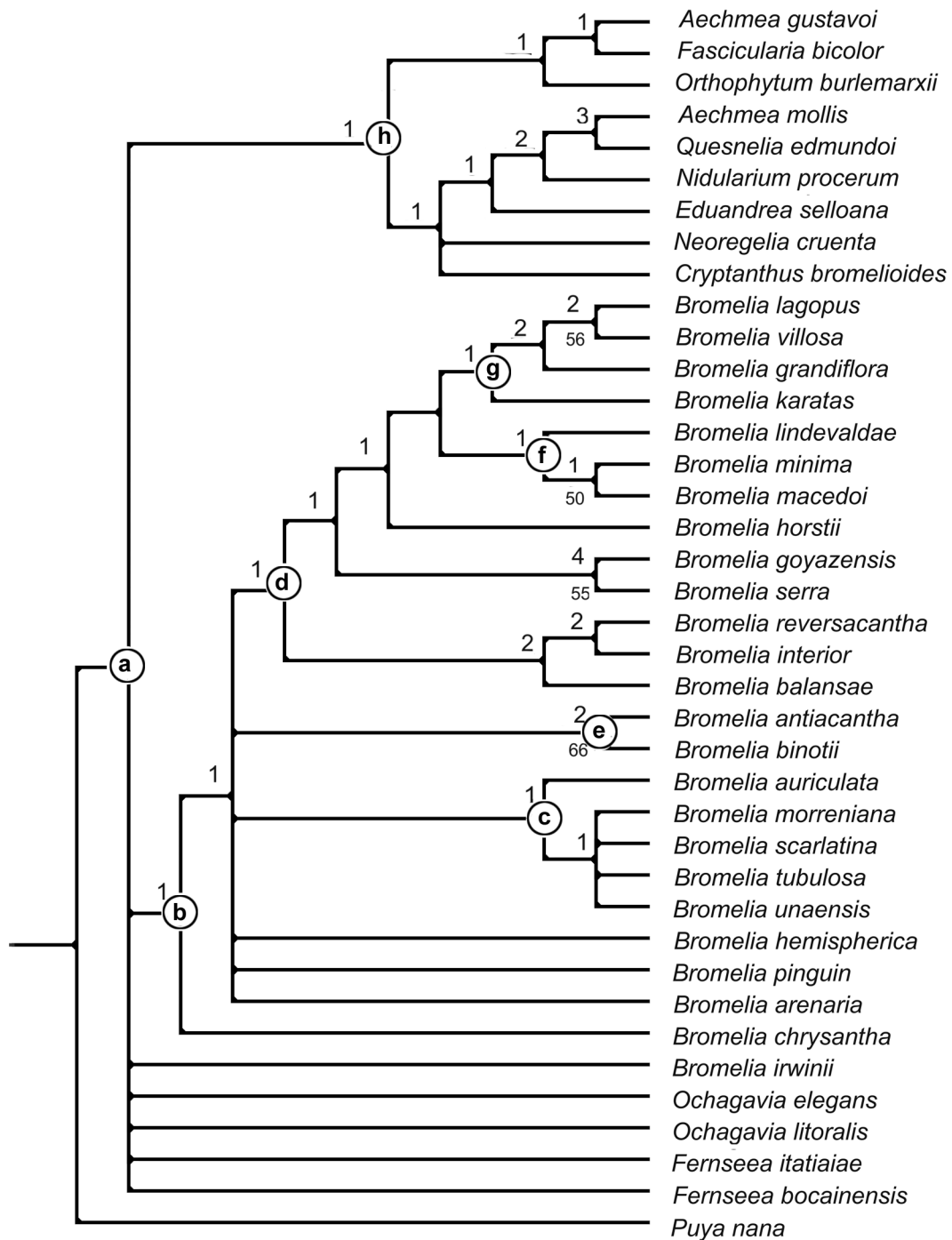
Figure 2 – Strict consensus of 34 most-parsimonious trees based on the analysis of 116 characters. The numbers below the branches correspond to the values of BS (≥50), and numbers above the branches are the values of B. Black stripes represent the subgenus *Karatas*, gray stripes represent the subgenus *Bromelia,* and the white strip represents the subgenus *Distiacanthus.*
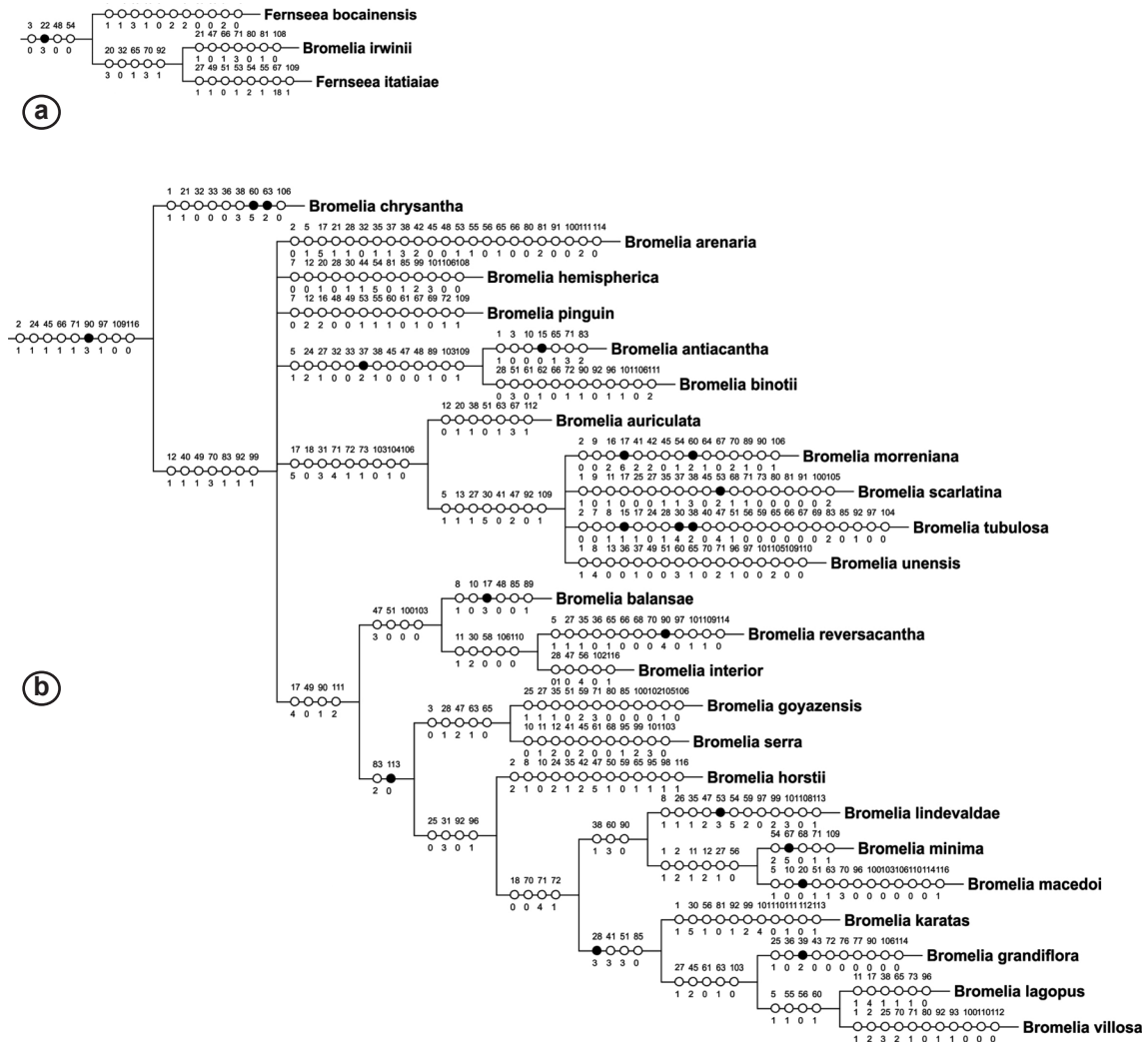
Figure 3 – a. Part of majority rule consensus of 34 most-parsimonious trees based on the analysis of 116 characters highlighting *Fernseea* and *Bromelia irwinii*; b. Part of strict consensus of 34 most-parsimonious trees based on the analysis of 116 characters highlighting *Bromelia* without *Bromelia irwinii*. Black circles represent non-homoplastic synapomosphies and white circles represent homoplastic synapomorphies. Numbers above branches correspond to characters while below branches correspond to character state according to table 1.

irwinii at the base of *Bromelia* was recovered in 82% of the trees. The clade *Bromelia+Fernseea* is supported by four synapomorphies: leaf apex erect, peduncle pink, floral bract entire and sepal ovate (Fig. 3a).

Few of the clades were well supported by the bootstrap analysis. *Bromelia antiacantha + B. binotii* (Fig. 2, clade E) obtained 66% BS and 2 for B, with the synapomorphies of: leaf apex pungent, primary bracts reflex during anthesis, bracts of peduncle apex pungent, flowers lax, branches of inflorescence high developed, primary

bracts completely reflexed and oblong; floral bracts shorter than the ovary, ovate and entire; petals persistent during frutification, water-storage hypodermis adaxial up to 1/3 of the blade thickness and vascular bundles of smaller diameter thickening wider than tall; *Bromelia goyazensis + B. serra* obtained 55% for bootstrap and 4 for Bremer support, with the synapomorphies: leaf apex erect, bracts of peduncle tomentose, floral bracts, sepals aculeate and petal apex cuculate during the anthesis. *Bromelia minima + B. macedoi* obtained 50% support, with the
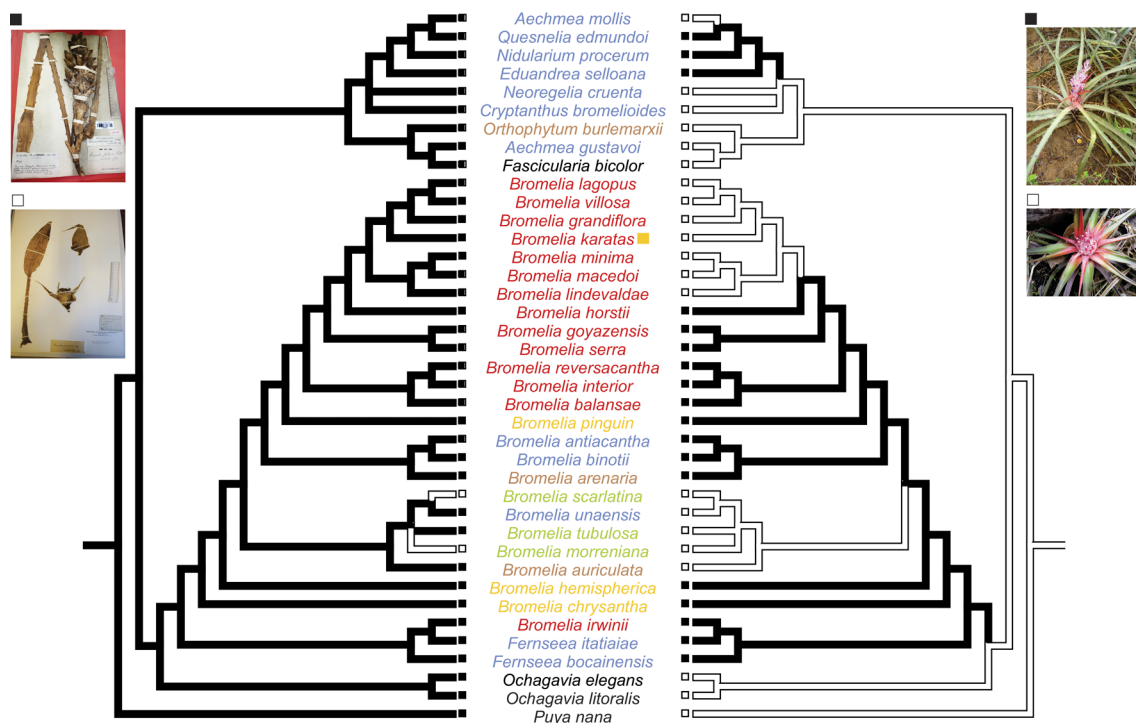
Figure 4 – Majority rule consensus of 34 most-parsimonious trees based on the analysis of 116 characters. Tree on the right: black branches indicate the presence of a peduncle (*Bromelia arenaria*); white branches indicate the absence of a peduncle (*B. macedoi*). Tree on the left: black branches indicate the absence of a petiole (*B. balansae*; Balansa 608, P); white branches indicate the presence of a petiole (*B. scarlatina*; Morren s.n., LG). Distribution of species: blue – Atlantic Forest, green – Amazon Forest, red – Cerrado, brown – Caatinga, yellow – Central America, black – Andes. The yellow square represents the presence of *Bromelia karatas* also in Central America.

synaphomorphies: rosette position in relation to the central axis when sterile ca. 45°, rosette position in relation to the central axis during flowering ca. 90°, leaf-blade color when sterile green to red, leaf-blade color of central leaves of rosette during blooming completely red, bracts of peduncle with apex pungent and sepal white. Finally, the clade *B. lagopus* + *B. villosa* had 56% BS and 2 B support, supported by the leaves without apex pungent, sepals asymmetrical, white, and sepal apex attenuate. The remaining clades of the genus obtained less than 50% BS (Fig. 2).

Our results suggest that *Bromelia* subg. *Karatas* and *Bromelia* subg. *Bromelia* are paraphyletic. Nothing can be concluded about the monophyly of *Bromelia* subg. *Distiacanthus,* which emerged in a polytomy in the strict consensus (Figs. 2, 3b). Eight synapomorphies supported this group: leaves without apex pungent, leaf-blade

chartaceous, bracts of peduncle with apex pungent, bracts of peduncle red, primary bracts lepidote, floral bract oblong, contour of leaf abaxial surface smooth to slightly wavy and vascular bundles of smaller diameter wider than tall.

Bromelia binotii and *B. antiacantha* (Fig. 2, clade E), species with large and lax inflorescence, appeared together in one clade supported by 13 synapomorphies (Figs. 2, 3b). *Bromelia pinguin* emerged just above in the majority-rule consensus, (Fig. 4), also has a large inflorescence. Clade D (Fig. 2) grouped species that occur predominantly in the Brazilian Cerrado and is possible to note the gradually reduction of the inflorescence upward the cladogram. *B. balansae* (Fig. 1), *B. interior* and *B. reversacantha* have a large but congested inflorescence; *B. serra* and *B. goyazensis* have little reduced and congested, but not sunk, inflorescence; and lastly the species of the F and G clades have

a sunk and deeply congested inflorescence. The clade F (*B. minima, B. macedoi* and *B. lindevaldae*) consisted of small-sized species, while the clade G contained larger species (*B. lagopus, B. villosa, B. grandiflora,* and *B. karatas*).

In the majority-rule consensus (Fig. 4), *Ochagavia* emerged as a sister to *Bromelia + Fernseea*, and the remaining species of Bromelioideae were grouped in a single clade. However, in the strict consensus (Fig. 2), the clade *Aechmea gustavoi, Orthophytum, Fascicularia* and *Cryptanthus + Neoregelia + A. mollis + Quesnelia + Nidularuim + Canistropsis* (clade H) emerged in a polytomy with *Bromelia, Fernseea* and *Ochagavia*.

Discussion

All the phylogenies that have included more than one species of *Bromelia* have indicated that the genus is monophyletic (e.g., Schulte & Zizka 2008; Sass & Spech 2010; Silvestro *et al.* 2014; Evans *et al.* 2015). However, the monophyly of *Bromelia* was not confirmed in the present analysis, because of the positioning of *B. irwinii*.

Another novel result revealed in the majority consensus tree was *Ochagavia*, an Andean genus, as a sister-group of *Bromelia + Fernseea*. However, the strict consensus recovered a large polytomy between *Bromelia, Fernseea, Ochagavia* and the clade with the remaining species of Bromelioideae. The difficulty of establishing the relationships of *Bromelia* and *Fernseea* with the remaining members of Bromelioideae is also apparent from the different phylogenies based on molecular characters (e.g., Horres *et al.* 2007; Givnish *et al.* 2007, 2011; Schulte & Zizka 2008; Schulte *et al.* 2009; Evans *et al.* 2015), where these genera emerge in different positions. These results illustrate the need for new studies to develop more conclusive and robust hypotheses, since the branches have low support (Schulte *et al.* 2009) and the schemes for the relationships among the early-diverging groups of Bromelioideae will likely be subject to frequent modification. Similarly, the relationship among *Bromelia, Fernseea* and *Ochagavia* remains unresolved, and further studies are needed in order to reach firm conclusions. The inclusion of other, non-Eubromelioideae taxa such as *Greigia, Disteganthus,* and especially *Deinacanthon urbanianum* (Mez) Mez, which has been included in *Bromelia* in the past (Smith 1967), and is often found in a sister-group position to this genus in molecular studies (Schulte *et al.* 2009; Givnish *et al.* 2011), requires further evaluation.

Bromelia irwinii appears together with *Fernseea itatiaiae* and *F. bocainensis.* Although *Fernseea* did not emerge as a sister of *Bromelia* in other phylogenetic studies, those that included species of *Bromelia* used only one to three species of this genus. The present study, since it included a good part of the species of *Bromelia* and both species of *Fernseea,* allowed us to reach firmer conclusions with respect to the phylogenetic affinity and the naturalness of these genera, even the strict consensus do not shows a good resolution.

The close relationship among *Fernseea, Bromelia* and *Ochgavia* that is apparent from the present results, constitutes an argument against the hypothesis that there was a single migration of the ancestral members of Bromelioideae from the Andes directly to high-altitude regions in southeastern Brazil, the region that is today the great center of diversity of the Bromelioideae (Schulte *et al.* 2005, 2009).

Although our results show weak support, making firm biogeographical conclusions premature, they do provide some insights into the evolution of Bromelioideae. The most recent common ancestor of the subfamily would have established itself first in the southern Andes (Zizka *et al.* 2009; Givnish *et al.* 2011), the locale where part of the present "basal-bromelioids" *sensu* Schulte *et al.* (2009) occur. Beginning with this premise, we can suggest, based on the phylogenetic analysis presented here, that there were three possible biogeographical routes for the clade *Bromelia + Fernseea* (Fig. 5):

Route 1: Southern Andes ⟶ Northern Andes ⟶ Lowlands of the Amazon and Atlantic Forests ⟶ Central America

This route could be represented by the ancestors of the Venezuelan and Colombian species, such as *B. chrysantha*; species of Central America such as *B. hemispherica*; and clade C, which includes species of the Amazon Forest (*B. tubulosa, B. scarlatina* and *B. morreniana*) and the

Atlantic Forest of Brazil, with *B. unaensis,* which is restricted to forests in the lowlands of southern Bahia, and *B. auriculata*, which is restricted to fragments of the Atlantic Forest in Ceará.

The disjunction between the Amazon and Atlantic Forest lineages, principally in the region of the central corridor of the Atlantic Forest, is reported for a multitude of taxa (Amorim *et al.* 2008; Simonelli *et al.* 2008; Cavalcanti & Tabarelli 2004). It is believed that the intense climate variations during the Pleistocene, in which expansions and retractions of forests occurred in glacial and interglacial periods, respectively (Haffer 1969; Prance 1987; Haffer & Prance 2002), reduced the extent of the dry areas between the Atlantic and Amazon Forests and allowed an exchange of species, including bromeliads (Givnish *et al.* 2011). For *Bromelia* this pattern appears in clade C (Fig. 2), and once again corroborates the recent differentiation of the species, as indicated for the entire family (Givnish *et al.* 2011).

Route 2: Southern Andes ⟶ High-altitude areas of the central Brazilian plateau (*B. irwinii*) ⟶ High-altitude fields of the Atlantic Forest domain (*Fernseea*)

This route was referred to as a long, direct route (high road), with dispersal from the Andes to the high-altitude fields of southeastern Brazil (Givnish *et al.* 2011). This type of distribution involves long-distance dispersal across the Brazilian Shield, and is associated with species that are endemic to high-altitude regions (*Bromelia irwinii* from the Chapada dos Veadeiros, rupicolous, 1,400 m elev.; *Fernseea bocainensis* from the Serra da Bocaina, rupicolous, 2,400 m elev.; and *Fernseea itatiaiae* from the Itatiaia Plateau, rupicolous, 2,400 m elev.)

Route 3: Southern Andes ⟶ Chaco ⟶ Central Brazilian Plateau (Cerrado) ⟶ Caatinga

⟶ Lowlands of the Atlantic Forest

This last route follows the dry diagonal (Prado & Gibbs 1993), passing through the Chaco; arriving on the Central Brazilian Plateau, a locale of intense diversification of *Bromelia*; and later reaching the Caatinga, an area of intense hydric stress, and the lowlands of the Brazilian Atlantic coast. However, the species of clade E occurring in the Atlantic Forest domain, in contrast to the species that followed Route 1, are distributed in areas of restinga (*B. antiacanta* and *B. binotii*). The restingas are sandy coastal flatlands of Pleistocene origin (ca. 10,000 years ago), where the species composition and physiognomic structure of the vegetation have a strong relationship to the Cerrado (Pereira & Araujo 2000), and a similar microclimate, which is hotter, dry, and with more intense sunlight than in the adjacent humid forest environments (Mantovani & Iglesias 2005). The Caatinga and dry forests are environments with pronounced hydric seasonality (*B. arenaria*). This relationship to hydric seasonality is also observable in *Bromelia pinguin*, present in the same clade, which occurs in coastal and desert regions in Central America and Mexico.

The results obtained in this study suggest that the species of the Cerrado (except for *B. irwinii*) probably had a single origin, and that some taxa of this clade (*e.g., B. serra* and *B. balansae*) occupied other localities later. This hypothesis agrees with similar proposals for the Fabaceae (Novaes *et al.* 2010), of a single migration event followed by later diversification within the Cerrado biome. We can therefore conclude that the great evolutionary success of *Bromelia* began with the second occupation of the Cerrado (clade D); and that in the future, dated phylogenies may help to determine the time period when this radiation occurred. Therefore, it is possible to conclude that the Atlantic Forest domain was occupied by *Bromelia* through a series of repeated occupancy, as shown for *Pitcairnia* by Saraiva (2013), but differing from that found by Forzza (2001) for *Encholirium*.

Periods of aridification and increased frequency and intensity of fire might have had a more profound impact on species occurring in the already dry biomes (Simon *et al.* 2009), thus causing a higher rate of extinction among

the tankless bromelioids (Silvestro *et al.* 2014). Nevertheless, these factors might have been strong forces driving the speciation and the evolutionary success of *Bromelia* in the Cerrado. Similarly, the repeated expansions and contractions of the Atlantic Rainforest and Cerrado during the Pleistocene (Pennington *et al.* 2004; Antonelli *et al.* 2009; Antonelli & Sanmartin 2011; Silvestro *et al.* 2014) may have affected the occupation of *Bromelia* and its speciation in the Atlantic Rainforest (*Bromelia antiacantha, B. unaensis* and *B. binotii*). Probably it is also the key for the migration of members of Bromelioideae from arid environments to the evergreen forest, the present diversity center for this subfamily (Martinelli *et al.* 2008; Forzza *et al.* 2014).

Although the dry diagonal is the most problematic area for speciation and establishment of Bromelioideae, with a higher extinction rate of the terrestrial tankless lineages because of the harsher conditions (Silvestro *et al.* 2014), in this environment *Bromelia* underwent extensive diversity, making the Cerrado the most important biome in terms of species richness of this genus. The increased speciation rate could be associated with the water saving CAM physiology and the low competition for the niches, since they occupy sites in which plants with no adaptations for dry environments can not be established (Benzing 2000; Givnish *et al.* 2014; Silvestro *et al.* 2014).

The origin of taxa in open areas and subsequent occupation of forest areas, was previously discussed for Bromelioideae (Schulte *et al.* 2009), and can over again be suggested by our results. The most recent common ancestor

of *Bromelia*, *Fernseea* and *Ochagavia* would have occupied open areas of the Andes and then migrated to other open areas, Cerrado, Chaco and high-altitude fields of the Atlantic Forest domain; and afterwards, to forest areas (Amazonia and Atlantic Forest). This same pattern was also found in *Philodendron* subgenus *Meconostigma*, which was originated in "campos rupestres" and Cerrado, followed latter by Amazonia and Atlantic Forest (Calazans *et al.* 2014).

Bromelia subg. *Distiacanthus* emerged unresolved (Fig. 2). The presence of a foliar petiole, uncommon in Bromeliaceae, is a homoplastic character, appearing in other genera such as *Disteganthus*, *Cryptanthus* and *Pitcairnia* (Smith & Downs 1979; Saraiva 2013). This morphological condition, which is restricted to Bromeliaceae from shaded parts of forest environments, especially in species of the Amazon basin, makes it possible to reduce water loss via respiration through decreasing the area and thickness of the leaf, because of the limited photosynthetically active radiation that reaches the soil (Carswell *et al.* 2000). Little is known about the ontogenetic origin of the petiole in leaves of Bromeliaceae, but the sympatric existence of terrestrial bromeliads with petiolate (*B. morreniana, B. scarlatina*) and non-petiolate leaves (*B. tubulosa*), with or without a CAM metabolism (*Pitcairnia*), offers an opportunity to test hypothesis about carbon economy in future studies.

Bromelia tubulosa, B. unaensis and *B. auriculata*, according to Mez' (1891) definition of subgenera, belong in *Karatas* because of the leaf without a petiole and the inflorescence within the rosette. Nevertheless, this latter character
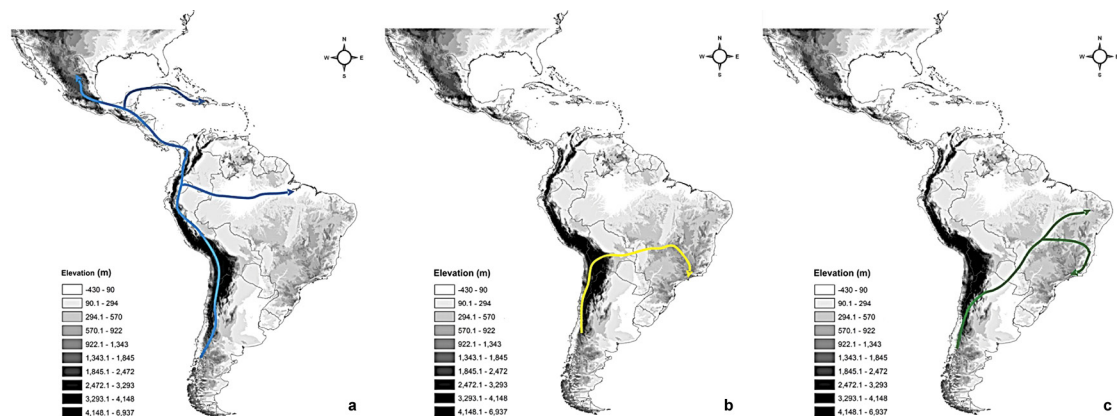

Figure 5 – Biogeographical routes proposed for *Bromelia* and *Fernseea*. a. Route 1; b. Route 2; c. Route 3. ESRI® ArcMap™ 9.3.

Table 1 – Character and character status list.

1	**Leaf,** rosette position in relation to central axis when sterile: 0, 15-30º;1, ca. 45º
2	**Leaf,** rosette position in relation to central axis during flowering: 0, 15-30º; 1, ca. 45º; 2, ca. 90º
3	**Leaf,** apex, orientation: 0, Erect; 1, Reflex
4	**Leaf,** apex, form: 0, Attenuate; 1, Acute; 2, Obtuse; 3, Emarginate; 4, Apiculate
5	**Leaf,** apex, pungent: 0, Present; 1, Absent
6	**Leaf,** margin: 0, Entire; 1, Aculeate
7	**Leaf,** spines, orientation: 0, One orientation, antrorse; 1, One orientation, retrorse; 2, Two orientations, antrorse and retrorse, on same leaf.
8	**Leaf**, spines, color: 0, Brown; 1, Green; 2, Red; 3, Yellow; 4, Wine-colored
9	**Leaf**, petiole: 0, Present; 1, Absent
10	**Leaf**, differentiation between sheath and blade: 0, Abrupt; 1, Tenuous
11	**Leaf**, blade, color when sterile: 0, Completely green; 1, Green to red at apex; 2, Completely red;
12	**Leaf**, blade, color of central leaves of rosette during blooming: 0, Completely green; 1, Green to red at base; 2, Completely red
13	**Leaf**, blade, consistency: 0, Carnose; 1, Chartaceous
14	**Leaf,** sheath, indumentum: 0, Present; 1, Absent
15	**Leaf**, sheath, indumentum position: 0, Only on adaxial face; 1, Only on abaxial face; 2, On both faces
16	**Leaf,** sheath, type of indumentum on adaxial face: 0, Lepidote; 1, Tomentose; 2, Floccose; 3, Villous; 4, Pannose; 5, Sericeous
17	**Leaf**, sheath, type of indumentum on abaxial face: 0, Lepidote; 1, Tomentose; 2, Floccose; 3, Villous; 4, Pannose; 5, Sericeous; 6, Strigose
18	**Inflorescence**, peduncle, size related to the rosette: 0, Inside, peduncle very reduced; 1, Emergent
19	**Inflorescence**, peduncle, indumentum: 0, Present; 1, Absent
20	**Inflorescence**, peduncle, type of indumentum: 0, Velutinous; 1, Tomentose; 2, Floccose; 3, Villous; 4, Lepidote; 5, Sericeous
21	**Inflorescence**, peduncle, cover by bracts: 0, Completely covered, imbricate bracts; 1, Partially covered, lax bracts
22	**Inflorescence**, peduncle, color: 0, Completely white; 1 Red; 2, Green; 3, Pink; 4, Brown
23	**Inflorescence**, bracts of peduncle, size related to the internode: 0, Longer; 1, Shorter
24	**Inflorescence**, bracts of peduncle, position related to the peduncle during anthesis: 0, Erect; 1, Patent, 45º-90º; 2, Completely reflexed
25	**Inflorescence**, bracts of peduncle, form: 0, Ovate; 1, Oblong; 2, Elliptical; 3, Lanceolate; 4, Linear
26	**Inflorescence**, bracts of peduncle, apex form: 0, Attenuate; 1, Acute; 2, Apiculate
27	**Inflorescence**, bracts of peduncle, apex pungent: 0, Present; 1, Absent
28	**Inflorescence**, bracts of peduncle, type of indumentum: 0, Lepidote; 1, Tomentose; 2, Floccose; 3, Villous
29	**Inflorescence**, bracts of peduncle, margin: 0, Entire; 1, Aculeate
30	**Inflorescence**, bracts of peduncle, color: 0, Stramineous with red apex; 1, Green; 2, Pink; 3, Wine-colored; 4, White; 5, Red
31	**Inflorescence**, type: 0, Raceme; 1, Capitulum, 2, Spike, 3, Corymb
32	**Inflorescence**, flowers, disposition: 0, Lax, exposing the branches; 1, Congested, covering the branches
33	**Inflorescence**, branches, development: 0, Highly developed, long; 1, Less developed, short
34	**Inflorescence**, viability of apex: 0, Sterile; 1, Fertile
35	**Inflorescence**, flowers, anthesis of flowers on each branch: 0, Opening upward; 1, Opening disorderly
36	**Inflorescence**, primary bracts, size in relation to branches of inflorescence: 0, Smaller; 1, Larger
37	**Inflorescence**, primary bracts, postion relative to peduncle during anthesis: 0, Erect; 1, Patent, 45º; 2, Completely reflexed
38	**Inflorescence**, primary bracts, form: 0, Ovate; 1, Oblong; 2, Elliptical; 3, Lanceolate
39	**Inflorescence**, primary bracts, apex form: 0, Attenuate; 1, Acute; 2, Obtuse
40	**Inflorescence**, primary bracts, apex pungent: 0, Present; 1, Absent
41	**Inflorescence**, primary bracts, type of indumentum: 0, Lepidote; 1, Tomentose; 2, Floccose;
42	**Inflorescence**, primary bracts, position of indumentum: 0, On apex only; 1, Covering primary bract; 2, On base only

43	**Inflorescence**, primary bracts, margin: 0, Entire; 1, Aculeate
44	**Inflorescence**, primary bracts, color: 0, Red; 1, Green; 2, Pink; 3, Stramineous
45	**Inflorescence**, floral bracts, size: 0, Shorter than ovary 1 Equaling or exceeding ovary, but not sepals, 2, Equaling or exceeding sepals, but not petals, 3, Equaling or exceeding petals
46	**Inflorescence**, floral bracts, color: 0, White; 1, Stramineous; 2, Red; 3, Pink; 4, Brown; 5, Blue; 6, Green
47	**Inflorescence**, floral bracts, form: 0, Ovate; 1, Oblanceolate; 2, Oblong; 3, Lanceolate; 4, Linear; 5, Triangular
48	**Inflorescence**, floral bracts, margin: 0, Entire; 1, Aculeate
49	**Inflorescence**, floral bracts, carin: 0, Present; 1, Absent
50	**Inflorescence**, floral bracts, indumentum: 0, Present; 1, Absent
51	**Inflorescence**, floral bracts, type of indumentum: 0, Lepidote; 1, Tomentose; 2, Floccose, 3, Villous
52	**Inflorescence**, floral bracts, position of indumentum: 0, On apex only; 1, Covering floral bract
53	**Inflorescence**, floral bracts, apex: 0, Acute; 1, Attenuate; 2, Obtuse; 3, Rounded
54	**Flower**, sepal, form: 0, Ovate; 1, Obovate; 2, Oblong; 3, Lanceolate; 4, Linear; 5, Triangular; 6, Elliptical
55	**Flower**, sepal, symmetry: 0, Symmetrical; 1, Asymmetrical
56	**Flower**, sepal, color: 0, White; 1, Brown; 2, Blue; 3, Green; 4, Pink; 5, Stramineous
57	**Flower**, sepal, indumentum: 0, Present; 1, Absent
58	**Flower**, sepal, type of indumentum: 0, Lepidote; 1, Tomentose; 2, Floccose; 3, Villous
59	**Flower**, sepal, position of indumentum: 0, On apex only; 1, Covering sepal; 2, On base only
60	**Flower**, sepal, apex: 0, Acute; 1, Attenuate; 2, Obtuse; 3, Rounded; 4, Retuse; 5, Apiculate
61	**Flower**, sepal, consistency: 0, Membranaceous; 1, Carthaceous; 2, Coriaceous
62	**Flower**, sepal, carena: 0, Present; 1, Absent
63	**Flower**, sepal, margin: 0, Entire; 1, Aculeate; 2, Crenate
64	**Flower**, sepal, concrescence: 0, Free; 1, Conate
65	**Flower**, petal, position of apex during anthesis: 0, Cuculate; 1, Erect; 2, Recurvate
66	**Flower**, petal, consistency: 0, Membranaceous; 1, Carnose
67	**Flower**, petal, color of blade: 0, White; 1, Pink; 2, Red; 3, Lilac; 4, Purple; 5, Wine-colored; 6, Green; 7, Blue; 8, Black; 9, Yellow
68	**Flower**, petal, color of margin: 0, The same as the blade; 1, Different from the blade
69	**Flower**, petal, indumentum: 0, Present; 1, Absent
70	**Flower**, petal, apex: 0, Acute; 1, Attenuate; 2, Obtuse; 3, Rounded
71	**Flower**, petal, form: 0, Oblanceolate; 1, Oblong; 2, Obovate; 3, Elliptical; 4, Linear; 5, Triangular
72	**Flower**, petal, concrescence: 0, Free; 1, Conate
73	**Flower**, petal, kind of concrescence: 0, Up to1/3; 1, More than 1/3
74	**Flower**, petal, appendix: 0, Present; 1, Absent
75	**Flower**, petal, callosity: 0, Present; 1, Absent
76	**Flower**, stamens, length related to the petals: 0, Exceeding; 1, Not exceeding
77	**Flower**, stamens, position related to the petals: 0, Exserted; 1, Included
78	**Flower**, stamens, color of anthers: 0, White; 1, Yellow
79	**Flower**, stamens, concrescence in relation to petals: 0, Adnate; 1, Free
80	**Flower**, stamens, anthers insertion: 0, Basifixed; 1, Dorsifixed
81	**Flower**, stamens, anthers form: 0, Oblong; 1, Sagittate; 2, Elliptical
82	**Flower**, ovary, position: 0, Superior; 1, Inferior
83	**Flower**, ovary, form: 0, Ovate; 1, Elliptical; 2, Oblong; 3, Obovate
84	**Flower**, hypanthium, indumentum: 0, Present; 1, Absent
85	**Flower**, hypanthium, type of indumentum: 0, Villous; 1, Tomentose; 2, Floccose
86	**Flower**, hypanthium, sulcus: 0, Present; 1, Absent
87	**Fruit**, type: 0, Berry; 1, Capsule
88	**Fruit**, concrescence of external walls: 0, Free; 1, Concrescent
89	**Fruit**, petals: 0, Persistent; 1, Not persistent
90	**Fruit**, color: 0, Brown; 1, Green; 2, Orange; 3, Yellow; 4, Wine-colored; 5, Pink; 6, Red; 7, White
91	**Seeds**, appendix: 0, Present; 1, Absent
92	**Leaf anatomy**, abaxial surface, contour: 0, Smooth to slightly wavy; 1, Grooved

93	**Leaf anatomy**, epidermal cells of adaxial surface, thickening type: 0, Strongly thickened inner periclinal wall, reduced lumen; 1, Inner periclinal wall thickened, with a smooth, wide lumen; 2, Strongly thickened outer periclinal wall, reduced lumen
94	**Leaf anatomy**, epidermal cells of abaxial surface, thickening type: 0, Strongly thickened inner periclinal wall, reduced lumen; 1, Inner periclinal wall thickened, with a smooth, wide lumen; 2, Strongly thickened outer periclinal wall, reduced lumen
95	**Leaf anatomy**, trichome, number of pedicle cells: 0, Two; 1, More than two
96	**Leaf anatomy**, trichome on adaxial surface: 0, Present; 1, Absent
97	**Leaf anatomy**, stomatal apparatus, position related to epidermis: 0, Same level; 1, Down, 2, Up
98	**Leaf anatomy**, mechanical hypodermis adaxial, thickening: 0, Present; 1, Absent
99	**Leaf anatomy**, mechanical hypodermis adaxial, number of layers: 0, One; 1, Two; 2, Three; 3, Four; 4, Five
100	**Leaf anatomy**, mechanical hypodermis adaxial, thickening of cell: 0, Slightly thickened; 1, Strongly thickened
101	**Leaf anatomy**, mechanical hypodermis abaxial, number of layers: 0, One; 1, Two; 2, Three; 3, Four; 4, Five
102	**Leaf anatomy**, mechanical hypodermis abaxial, thickening of cell: 0, Slightly thickened; 1, Strongly thickened
103	**Leaf anatomy**, water-storage hypodermis adaxial, size: 0, Up to 1/3 of the blade thickness; 1, More than 1/3 of the blade thickness
104	**Leaf anatomy**, transition between adaxial water-storage hypodermis and chlorenchyma: 0, Abrupt; 1 Tenuous
105	**Leaf anatomy**, adaxial water-storage hypodermis cell shape: 0, Rounded, 1, Elongated in anticlinal direction
106	**Leaf anatomy**, water-storage hypodermis, position: 0, Adaxial face; 1, Abaxial face; 2, Both sides
107	**Leaf anatomy**, brachiform parenchyma, cell shape: 0, With short arms (forming small gaps); 1, With long arms (forming large gaps)
108	**Leaf anatomy**, cell of bundle sheath parenchyma, disposition: 0, Radiate; 1, Not radiate
109	**Leaf anatomy**, vascular bundles of smaller diameter, shape of the thickening (fiber): 0, Taller than wide; 1, Wider than tall
110	**Leaf anatomy**, vascular bundles of larger caliber, thickening of fibers: 0, Calotte; 1, Circling totally
111	**Leaf anatomy**, palisade chlorenchyma, shape: 0, Palisade; 1, Not palisade; 2, Palisade and not palisade
112	**Leaf anatomy**, adaxial epidermis, outer periclinal walls: 0, Smooth; 1, Papillose
113	**Leaf anatomy**, raphides: 0, Present; 1, Absent
114	**Leaf anatomy**, secretory ducts: 0, Present; 1, Absent
115	**Leaf anatomy**, extravascular fibers: 0, Present; 1, Absent
116	**Habit:** 0, Terrestrial; 1, Rupiculous; 2, Epiphytic

seems to be homoplastic, since it appeared twice independently, in clades C and D. The species with pedunculate inflorescences appeared at the base of *Bromelia*, indicating that this character is ancestral in the genus. Interestingly, *Ochagavia, Fascicularia* and *Greigia* possess a sunk inflorescence.

In clade E, species possess a large and lax inflorescence, with the peduncle emerging from the rosette; nevertheless, from clade D, as we proceed in the direction of the branches that diverged more recently, the axes of the inflorescence become reduced, and the flowers are arranged closer together (*B. balansae, B. reversacantha, B. interior, B. serra* and *B. horstii*). Further up clade D, the peduncle of the inflorescence is gradually reduced, such as in *B. serra, B. goyazensis* and *B. horstii,* until the inflorescence is completely included within the foliar rosette in *B. lindevaldae, B. minima, B. macedoi, B. karatas, B. grandiflora, B. villosa* and *B. lagopus.*

The reduction in the size of the inflorescence in Bromelioideae may be an important factor to allow them to occupy xeric environments, optimizing the use of resources in stressful, nutrient-poor environments (Reekie & Bazzaz 2005). Species of the genus *Bromelia* are predominantly terrestrial in habit, and their leaves do not absorb water and nutrients efficiently (Benzing 2000); therefore, they depend on the soil for water and nutrient balance. The environments of the Cerrado (Ratter *et al.* 1997) and restinga (Mantovani & Iglesias 2001, 2008) are notorious for their oligotrophic and rapidly draining soils. The little information available about the cost of producing inflorescences in bromeliads indicates that more biomass is allocated to pedunculate inflorescences (Benzing 2000; Mantovani & Iglesias 2009). At the same time, studies of the nested inflorescence have shown that the input of carbon in this type of

inflorescence is potentially much smaller than that in a peduncular inflorescence (Benzing & Ott 1981).

Finally, *Bromelia minima*, *B. macedoi* and *B. lindevaldae*, the clade F, small-sized species that occur almost sympatrically in the cerrado, emerge as a single group, even when metric data are not included in the analysis. In these species the nutrient-allocation economy is not associated only with sexual reproduction (i.e*.,* the absence of a peduncle), because this would be insufficient for a positive nutrient balance under the conditions in the Cerrado. Therefore, the reduction has extended to the plant body, whose smaller size can improve the heat balance through convection (by reducing the surface/ volume ratio of the leaves) and microclimate protection (a smaller hydric deficit next to the soil), in addition to requiring less carbon and nutrients for its construction (Vieira & Mantovani 1995).

Conclusion

The evolution and diversification of the Bromelioideae remain to be extensively explored, seeing that the basis for their understanding lies in the clades that branched first in this subfamily, which until now have been little studied. For this purpose, it is necessary to carry out a thorough study of these genera (which are also inadequately collected), since they possess a larger number of symplesiomorphies and is one of the closest genera to the most recent common ancestor of the Bromelioideae. The present analysis of *Bromelia* and *Fernseea* is a first step toward this end. It would be desirable to continue proposing new phylogenetic hypotheses for these groups, with the most varied types of characters available, including molecular characters (DNA sequences, AFLPs and microsatellites). This process may lead additional evolutionary inferences, with stronger support.

The present study provides also the necessary foundation to futher elucidate character evolution in *Bromelia,* since some morphological characters may carry strong phylogenetic signals in bromeliads (Louzada *et al.* 2014), and morphological studies of these characters are desirable.

Analyses at the infrageneric level, involving several terminals of the same genus, can change the fine structure of the evolutionary history (Wagner *et al.* 2012), indicating that occupation events (multiple events, versus a single entry), routes, or modes of diversification (e.g., sympatry *versus* allopatry) should be re-evaluated, and should continue.

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