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Vriesea (Bromeliaceae, Tillandsioideae): a cladistic analysis of eastern Brazilian species based on morphological characters

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Abstract

Vriesea, with about 280 species distributed in two sections, *Vriesea* and *Xiphion*, is recognized as polyphyletic. We provide the cladistic analysis based on morphological data, with emphasis on species from eastern Brazil, its main center of diversity, which emerged as a monophyletic group in previous molecular and combined analysis. The data matrix contained information of 60 species of *Vriesea*, and two of *Alcantarea*, for a total of 62 terminal taxa and 66 characters. The analysis produced one tree with 652 steps. The classic infrageneric division of the sections was not corroborated. Characters traditionally used to separate the two sections supported clades containing species from both sections. Morphologically related monophyletic groups were recognized. Some characters have been highlighted as potentially important in the circumscription of small groups of species and have not yet been much used in the systematics of *Vriesea*.

Key words: morphology, phylogeny, taxonomy, *Vrieseeae*.

Introduction

Bromeliaceae has been recognized as a natural group since the development of ancient classification systems (e.g., Dahlgren et al. 1985; Cronquist 1988). Recently, their relationship with Poales has been supported by various phylogenetic hypotheses based on plastid sequencing data (e.g., Clark *et al*. 1993, *rbc*L; Givnish *et al*. 2006, *ndh*F; Bouchenak-Khelladi *et al.* 2014, *rbc*L and *ndh*F). Phylogenetic studies have been conducted in the Bromeliaceae based on both molecular and morphological data. The first group of studies used different data sets, with a focus on relationships among the subfamilies (Ranker *et al*. 1990; Terry *et al*. 1997a; Horres *et al*. 2000; Givnish *et al.* 2007, 2011), within the subfamilies (Terry *et al.* 1997b; Crayn *et al.* 2000; Barfuss *et al.* 2005; Horres *et al.* 2007; Schulte *et al.* 2009; Sass & Specht 2010) or within genera and subgenera (Rex *et al.* 2007; Sousa *et al.* 2007; Chew *et al.* 2010; Versieux *et al.* 2012). With the exception of the study of Gilmartin & Brown (1987), which questioned the monophyly of the family, its possible sister-group, and the relationships among the subfamilies, phylogenetic analysis based on morphological data have focused on subfamilies (Varadarajan & Gilmartin 1988), tribes (Forzza 2001), genera (Gilmartin *et al.* 1989; Leme 2000; Faria *et al.* 2004; Hornung-Leoni & Sosa 2008; Almeida *et al.* 2009; Monteiro 2009, Gomes-da-Silva *et al.* 2012; Saraiva 2013) or subgenera (Gilmartin & Brown 1986; Beaman & Judd 1996; Tardivo 2002; Sousa 2004) in all subfamilies. Combined morphological and molecular data were also used to improve the resolution of the analysis (Faria 2006; Sousa *et al.* 2007; Aguirre-Santoro 2009; Gomes-da-Silva 2013).

All the phylogenetic analysis conducted has indicated the monophyly of the subfamily Tillandsioideae, and the isolated position of *Catopsis* Griseb. and *Glomeropitcairnia* (Mez) Mez (Terry *et al.* 1997b; Horres *et al.* 2000; Barfuss *et al.* 2005; Givnish *et al.* 2007, 2011; Gomes-da-Silva 2013). Despite the homogeneity of the plastid and nuclear sequences used in the analysis in Bromeliaceae (Terry *et al.* 1997b; Horres *et al.* 2000; Barfuss *et al.* 2005; Gomes-da-Silva 2013), the "core tillandsioid" shows great morphological

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and ecological diversification in relation to the rest of the family (Gomes-da-Silva 2013).

Vriesea Lindl., the third-largest genus in the Bromeliaceae (Luther 2012), is currently composed of about 280 species (Luther 2012; Forzza *et al.* 2014) in two sections: *Vriesea* and *Xiphion* (E.Morren) E.Morren ex Mez. The genus has two centers of diversity. The first lies in northern South America, Central America, and the Caribbean (Smith & Downs 1977); and the second lies in eastern Brazil, where ca. 74% of the species occur. *Vriesea* is also the richest genus of the family in the Atlantic Domain (Martinelli *et al.* 2008). The species occur primarily in mesophytic environments, but are also common in "campos rupestres", high-altitude fields and inselbergs. The geographic distributions of the species range from very wide, from the north-eastern to southern parts of the Brazilian Atlantic coast, to microendemics (Costa *et al.* 2014).

However, the genus has been recognized as polyphyletic (Terry *et al.* 1997b; Horres *et al.* 2000; Barfuss *et al.* 2005; Givnish *et al.* 2011; Gomes-da-Silva *et al.* 2012) and many taxonomic and nomenclatural changes were made, including transferring of species to *Tillandsia* L. and the segregation of the genera *Alcantarea* (E.Morren ex Mez) Harms and *Werauhia* J.R.Grant (Grant 1993, 1995a, 1995b, 2004; Butcher 2009). Besides its controversial circumscription, there is also difficulties to delimit several species (Costa & Wendt 2007; Costa *et al.* 2007, 2014). Some of these so-called species-complexes were taxonomic revised contributing to the systematics of the genus (Costa *et al.* 2009; Gomes-da-Silva & Costa 2011; Versieux 2011; Moura & Costa 2014; Silva 2014; Uribbe 2014). The taxonomic history and a detailed morphological description of the genus are provided by Costa *et al.* (2014).

The analysis conducted by Barfuss *et al.* (2005), based on seven plastidial regions, suggest the polyphyly of *Vriesea,* since its species emerged into the two main lineages of "core tillandsioids". In one of these lineages, the tribe Vrieseeae, at least four distinct lineages were recognized: two of them formed by Brazilian species of *Vriesea,* with *Alcantarea* as the sister-group; and two others formed by extra-Brazilian species of *Vriesea* and species of *Werauhia*. *Alcantarea* was also recognized as sister-group of *Vriesea* in a molecular analysis based on a low-copy nuclear (*Floricaula/Leafy*) and two plastidial sequences (*trnK-rps16 and trnC-petN*), where ten species of *Vriesea* were included (Versieux *et al*. 2012). In the most inclusive contribution to date, Gomes-da-Silva (2013) conducted the cladistic analysis of *Vriesea* based on both plastidial and morphological data, in which the Brazilian lineage was recuperate as monophyletic, and *Alcantarea* was corroborated as its sister-group. In the present study, we performed a cladistic analysis for the species from eastern Brazil of genus *Vriesea* based on morphological data, focusing especially on the Brazilian center of diversity of the genus, considering the proposed monophyly of this group.

Thus, the aims of this study were: (1) test the monophyly of the sections *Vriesea* and *Xiphion*; (2) recognize monophyletic groups among the Brazilian species of *Vriesea*, to support the taxonomic revisions of small groups; and (3) evaluate potential morphological characters for elucidating phylogenetic hypotheses in the genus.

Material and Methods

Morphology and Taxonomy: The morphology of the Brazilian species of *Vriesea* is described and commented by Costa *et al.* (2014). The morphological study was based on a large set of herbarium specimens, field sampling, and observation of specimens grown in private (A. Costa and E. Leme) and public (Instituto de Pesquisas Jardim Botânico do Rio de Janeiro) collections. The main references used to the morphological analysis were Smith & Downs (1977) modified with Stearn (1973), Radford (1986), Weberling (1989) and Sharf & Gouda (2008). The taxonomy followed the monograph by Smith & Downs (1977); for the taxonomic and nomenclatural changes in the family after them, the series De Rebus Bromeliacearum (Luther & Sieff 1994, 1997 a, b; Luther 2001; Luther & Rabinowitz 2010) and the List of Brazilian Species (Forzza *et al.* 2014) were consulted.

Cladistic analysis:

Selected taxa. Our study included 60 species of *Vriesea* from southeastern Brazil, mainly from the Atlantic Forest domain, which represent a monophyletic group (e.g. Barfuss *et al.* 2005; Versieux *et al.* 2012; Gomes-da-Silva 2013). The ingroup included species of *Vriesea* (Appendix 1) with both simple and compound inflorescences of both sections, in an attempt to cover the widest possible range of morphological variation of the Brazilian species of the genus.

We included two species of *Alcantarea* (*A. farneyi* and *A. glaziouana)* as outgroup since it is the sister group of the Brazilian species of *Vriesea* (Barfuss *et al.* 2005; Versieux *et al.* 2012; Gomes-da-Silva 2013), representing a suitable group for rooting (Nixon & Carpenter 1993).

Selected samples. The criteria for selection of specimens were based on the good condition of the structures analyzed. Live and dried specimens, flowers preserved in 70% ethanol, photographs, and information in the literature to complement the information gathered from examination of specimens were used. It was selected between one and two vouchers to represent each taxa in the following herbaria, in a total of 99 specimens analyzed: ESA, CEPEC, GUA, HB, MBML, R, RB, SP (for acronyms see Thiers, continuously updated) (Appendix 1).

Selected characters. The characters selected for the analysis are listed in Appendix 2. We selected 66 characters (of which 21 are binary and 45 are multi-state). Due to the heterogeneity and diversity of the species, quantitative characters were included in the analysis. The use of quantitative traits in cladistic analysis has been criticized by several authors (see Poe & Wiens 2000). However, their use can also increase the resolution of the analysis in many cases (Thiele 1993, Rae 1998, Wiens 2001) and should not be rejected. But, is important to clarify that we just use discrete characters (though some them are quantitative) in our analysis and measurements were used only to delimit more precisely the character states, which are largely used in taxonomical studies, e.g. small, medium and large.

Data Analysis. Morphological data were tabulated in a matrix of characters per species (Appendix 3) using Nexus Data Editor Software (NDE 0.5.0, Page 2001). Non-applicable data were represented by "-". Missing data were represented by "?". Autapomorphies were included in the data matrix as results of the cladistics investigation (Yeates 1992), but were not included in the computation of ensemble value of the consistency index (CI), as proposed by Bryant (1995).

We performed an analysis of Maximum Parsimony (MP), with Fitch' parsimony approach (Fitch 1971), and polarized after the rooting (Nixon & Carpenter 1993). All procedures were carried out using TNT (Goloboff *et al.* 2008), and WINCLADA version 1.00.08 (Nixon 2002) was used as a complementary tool for characters optimization. For characters in which there is more than one most-parsimonious reconstruction (MPR-sets), the criterion for accelerated transformation (ACCTRAN) was used (Swofford & Maddison 1987) aiming to maximize the initial hypotheses of primary homology (De Pinna 1991).

The characters were analyzed with implied weight (Goloboff 1993), with concavity constant equal to eleven (K = 11). Characters weighting based on their self-consistence improves the decision among the MPT(s) resolving conflicts produced by homoplasies, especially for morphological characters (Goloboff *et al.* 2008).

TNT was performed with New Technology (*cf.* Goloboff 1999; Nixon 1999) heuristic search algorithms, with following commands: hold 100000, collapse 3, qcollapse, condense, unique*, best*, xmult = rss, hits 5 replications 100 drift 100 fuse 5 ratchet 200.

Relative stability of individual branches was evaluated with two indexes: Bootstrap (BS, Felsenstein 1985) and Jackknife (JK, Goloboff *et al.* 2008). All indexes were calculated using implied weighting. Two different measures were chosen to assess the statistical support of each branch, since there are limitations of the indexes (Soltis & Soltis 2003; Müller 2005). Bootstrap (BS) and Jackknife (JK) were obtained with the same parameters listed above, with 10000 each pseudo-replicates.

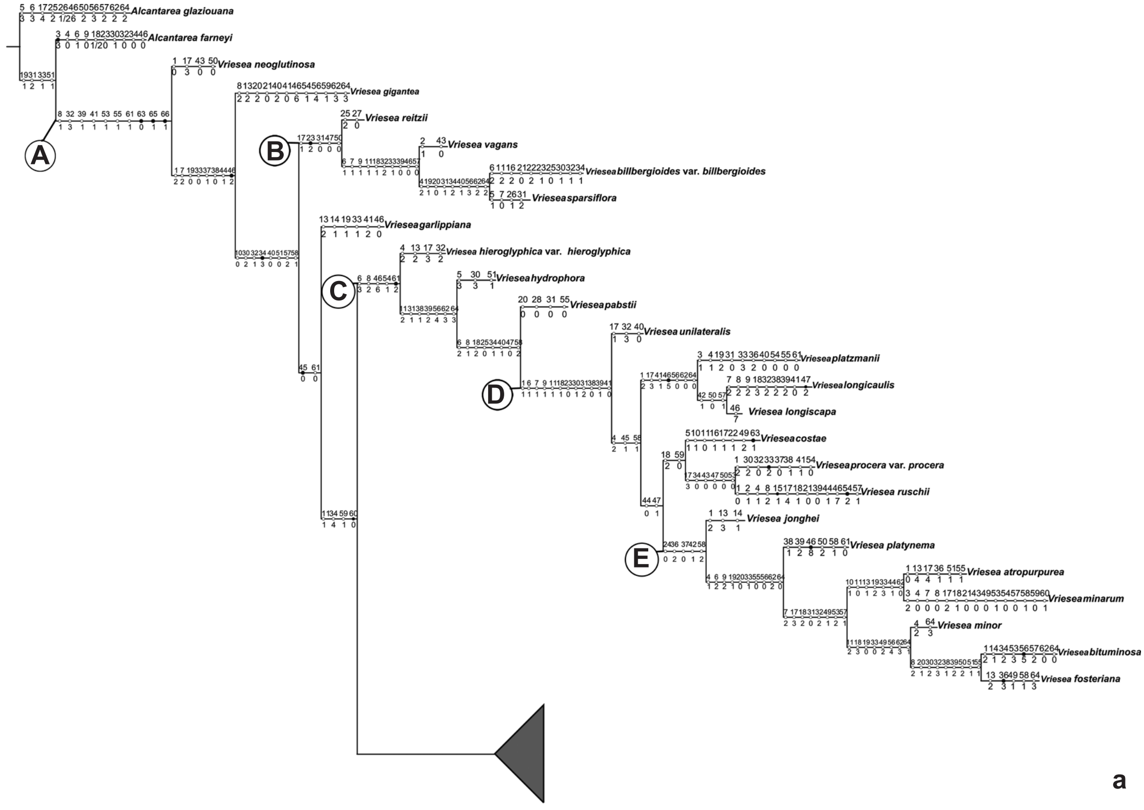
Results and Discussion

Cladistic Analysis: The cladistic analysis produced one tree with 652 steps. The indexes were CI 0.21, RI 0.52 (Fig. 1). Among the 66 characters analyzed, 65 were informative. The two *Alcantarea* species emerged as sister to the Brazilian species of *Vriesea*. In the first infrageneric classification proposed for *Vriesea* (Wawra 1883), the species subsequently classified under *Alcantarea* were included in the group Reginae. In the other monographs for the family (Mez 1894, 1896, 1934-5; Smith 1966; Smith & Downs 1977), the essence of the original classification was maintained even with the addition of new species. Only Baker (1889) and Harms (1930) did not consider *Alcantarea* as a subgenus of *Vriesea*. The former author classified the species of *Alcantarea* under *Tillandsia* subg. *Vriesea*, and the latter proposed a separate genus for them. Currently, *Alcantarea* is considered as a valid genus (sensu Harms 1930; Grant 1995 a, b; Versieux *et al*. 2012) due to the peculiar combination of seeds with a long and erect apical coma, and petals strongly recurvate. Analysis based on molecular and combined data indicate that *Alcantarea* is the sister-group of Brazilian species of *Vriesea* (Barfuss et al. 2005; Versieux *et al*. 2012; Gomes-da-Silva 2013).

The Brazilian species of *Vriesea* (clade A, BS 90, Tab. 1, Fig. 2) was supported by ten synapomorphies among them, the stamens and pistil in gullet blossom position during anthesis (char. 61:1), the stigma convolute-blade type (char. 63:0), superior ovary (char. 65:1), and the seed with short apical coma (char. 66:1), the three later are not homoplastic. The classic infrageneric division into the two sections *Vriesea* and *Xiphion* (Mez, 1894, 1896, 1934–5; Smith & Downs, 1977) was not supported. However, the study identified clades including species belonging to both sections (clades B, G, H, I, J to *V*. sect. *Vriesea*, and C, D, E to *V*. sect. *Xiphion*).

The clade B is supported by the inflorescence triple raceme (char. 23:2, non homoplastic, and except *V. billbergioides* var. *billbergioides*), the floral bracts membranaceous (char. 47:0), and pedicel less than 5 mm long (char. 50:0). *Vriesea billbergioides* var. *billbergioides* and *V. sparsiflora* share the peduncle red (char. 19:1), the white petals (char. 56:3), stamens (char. 62:2), and stigma (char. 64:2), among others. These two species occur in narrow areas of montane forest in Rio de Janeiro and São Paulo States (Costa & Wendt 2007; Costa *et al.* 2007).

The clade C includes species exclusively of *V*. sect. *Xiphion*, with both simple and compound inflorescences, and is supported by the foliar sheath more than 13 cm wide (char. 6:3), blade more than 51 cm long (char. 8:2), floral bracts green (char. 46:6), obovate petals (char. 54:1), stamens and pistil in flag-blossom position (char. 61:2), this last one non homoplastic. The basal lineages of this clade have species with compound inflorescences. This grade includes *V. hieroglyphica* var. *hieroglyphica*, *V. pabstii*, and *V. hydrophora*, all of them with nocturnal and secund flowers, and filaments enlarged toward the apex. These species occur along the Brazilian Atlantic Forest between Espírito Santo and Paraná states forming epiphyte populations. Among them, we highlight the clades *V. longicaulis* + *V. longiscapa* and *V. procera* var. *procera* + *V. ruschi*, which include other morphologically related taxa, two groups that



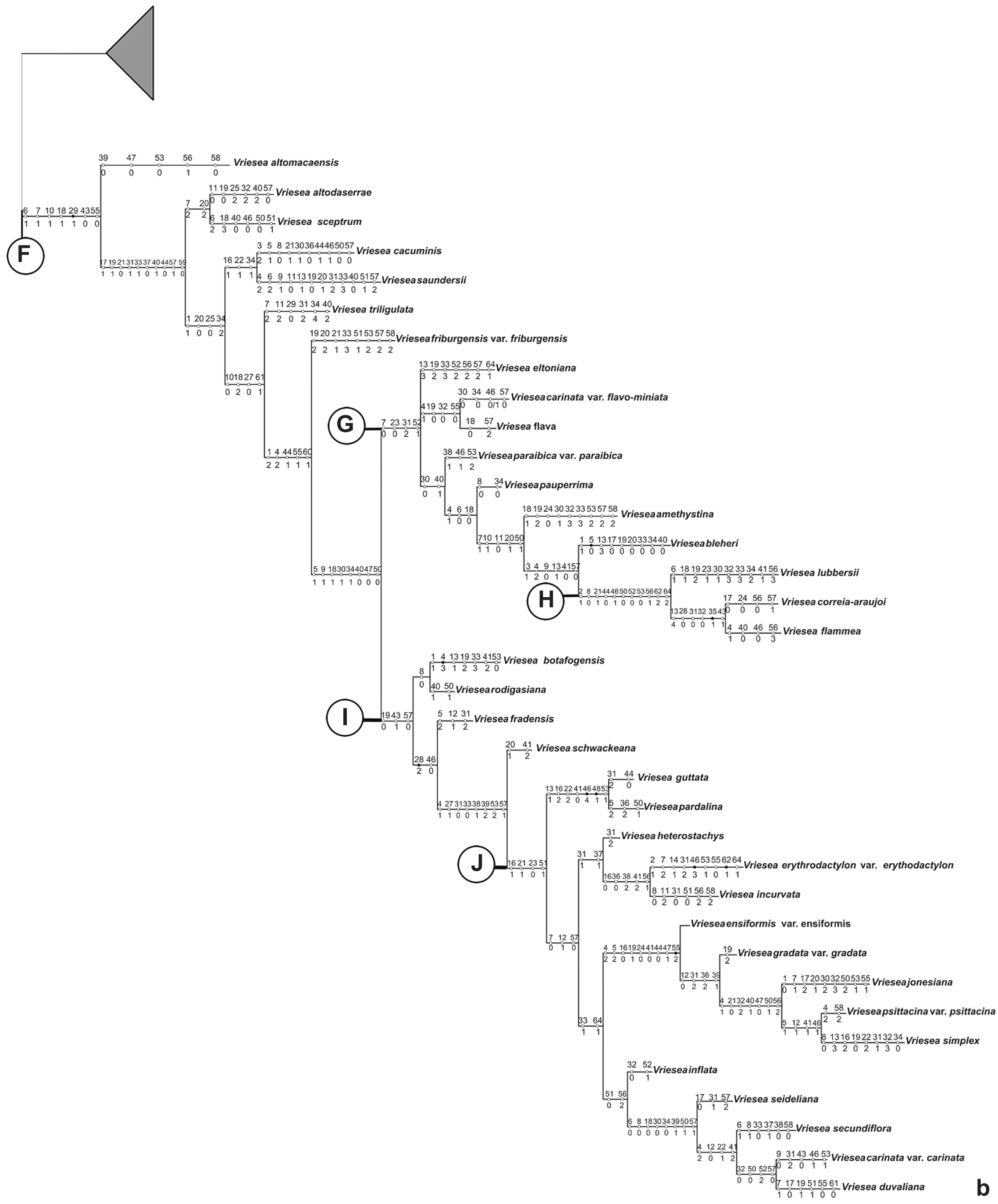


Figure 1 – Resulting tree as a hypothesis of relationships among species of *Vriesea* and *Alcantarea* outgroup. Black circles non homoplastic characters; white squares, characters with homoplastic transformation.

are in need of better taxonomic circumscriptions of the species. The derived lineages of clade C, are formed by species with simple inflorescences (char 23:0), the clade D. This clade is supported by leaf sheaths castaneous to vinaceous (char. 7:1), and floral bracts without keel (char. 41:1), among other nine, including quantitative ones. The species of the basal lineages of this clade have secund flowers. In the clade E occurs the reversion to non-secund flowers (char. 37:0) in *V. jonghei*, the type-species of

Table 1 – Character optimization using ACCTRAN in the resulting tree as a hypothesis of relationships among species of *Vriesea* and *Alcantarea* as outgroup. Discussed clades; exclusive synapomorphies in bold.

Clades	Synapomorphies
A	8:1, 32:3, 39:1, 41:1, 53:1, 55:1, 61:1, **63:0**, **65:1**, **66:1**
B	17:1, 23:2, 31:0, 47:0, 50:0
C	6:3, 8:2, 46:6, **54:1, 61:2**
D	1:1, 6:1, 7:1, 9:1, 11:1, 18:1, 23:0, 30:1, 31::2, 38:0, 39:1, 41:0
E	24:0, 36:2, 37:0, 42:1, 58:2
F	6:1, 7:1, 10:1, 18:1, **29:1**, 43:0, 55:0
G	7:0, 23:0, 31:2, 52:1
H	2:1, 8:0, 21:1, 44:0, 46:1, 50:0, 53:0, 56:1, 62:2, 64:2
I	19:0, 43:1, 57:0
J	16:1, 21:1, 23:0, 51:1

V. sect. *Xiphion*. It is supported by the development of the inflorescence with floral bracts and flowers apressed before anthesis and ascending to patent at anthesis (char. 24:0), flowers patent at anthesis (char. 36:2), base of the floral bracts decurrent (char. 42:1), and petal appendages more than 1.1 cm long (char. 58:2). The species in this clade have always been considered to be closely related (e.g., Mez 1896), and had their identity misunderstood, especially in the major monographs of the family (Mez 1894, 1896, 1934–5; Smith & Downs 1977), probably because of the drying process for herbarium collections of the specimens that fails on preserve structures important to delimitate species, characters such as the color of the floral bracts, the longitudinal posture and the color of the petals, and the position of the stamens and pistil during anthesis. This led to an erroneous interpretation in subsequent works (e.g., Smith and Downs 1977; Reitz 1983; Leme & Marigo 1993; Siqueira-Filho & Leme 2006; Costa *et al.* 2007). This group now comprises 41 species, which were recently revised by Moura (2011; see Moura & Costa 2014). These species have their center of diversity in eastern Brazil, occurring mainly in the Atlantic Forest Domain, but also in the Cerrado and Caatinga, with only two extra-Brazilian species.

Sister to clade C, the clade F includes only species of *V*. sect. *Vriesea*, with simple and compound inflorescences. The basal lineages of this clade include species of compound inflorescence, with primary bract longer than the branch peduncle, narrowly-oblong to linear petals, petals straight with apex apressed, and stamens included, including *V. sceptrum*, *V. saundersii*, *V. triligulata* and also *V. altodaserrae, V. altomacaensis* and *V. cacuminis*. These three first species were classified by Mez (1896, 1934–5), Harms (1930), and Smith & Downs (1977) sometimes in *V.* sect. *Vriesea*, and sometimes in *V*. sect. *Xiphion*. The species belonging to this grade are in need of taxonomic revision, with special attention to floral morphology and geographic distribution (predominantly in forests at higher altitudes and high-altitude fields of the Serra do Mar, Brazil), not only to confirm their position in the genus, but also to improve their circumscriptions.

The clade G includes the species related to *V. paraibica* that were taxonomically treated by Costa *et al.* (2009). It was supported by simple inflorescences (char. 23:0), and keel present in two sepals (char. 52:1), among others. The derived lineage of this clade (clade H**,** BS 82; JK 97) was supported by 11 synapomorphies, among them the presence of stolons (char. 2:1), leaf blades up to 20 cm long (char. 8:0), no keel on the sepals (char. 52:0), stamens (char.62:2) and stigma white (char. 64:2). It includes three species of the so called *V. corcovadensis* group which was taxonomically treated by Gomes-da-Silva & Costa (2011). This group of species, formed by 11 taxa, shares the presence of unusual characters in *Vriesea*, including linear-triangular leaf blades, less than 1.5 cm in width, upper peduncle bracts long-caudate, peduncle bracts differentiated in blade and sheath, and polystichous flowers (in present analysis synapomorphic and non homoplastic to the highly supported BS 89 and JK 93, *V. correia-araujoi* + *V. flammea*), in addition to the utriculiform rosettes. Despite its polyphyletic situation by Gomes-da-Silva *et al.* (2012), this group was recovered as monophyletic by Gomes-da-Silva (2013) and the present study. Though Smith (1966) suggested that the polystichous flowers are only useful in separating species in the genus and do not justify the adoption of an infrageneric category (*sensu* Mez 1894, 1896, 1934–5), a more comprehensive phylogenetic

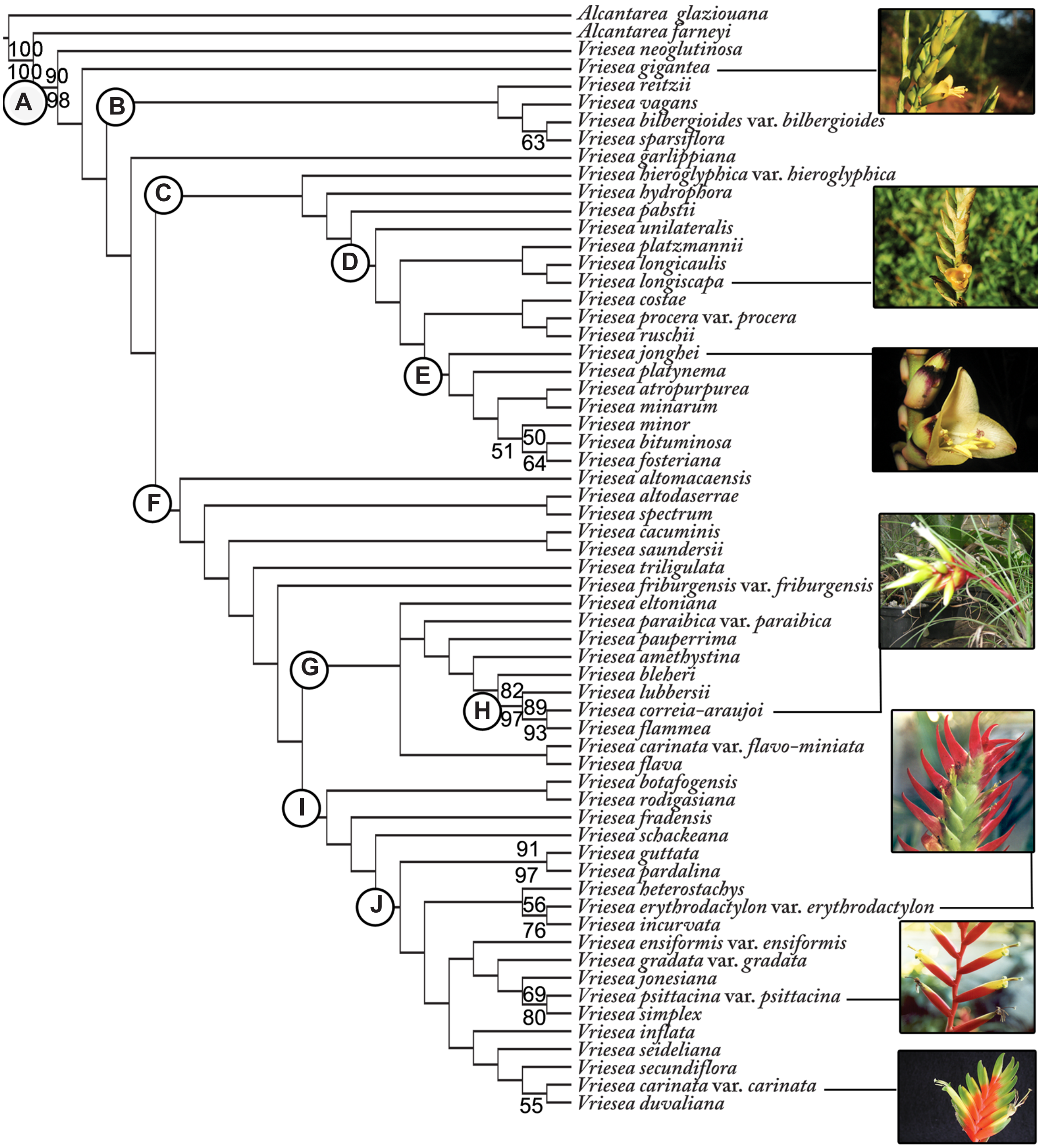


Figure 2 – Resulting tree as a hypothesis of relationships among species of *Vriesea* and *Alcantarea* as outgroup. The numbers above and below each node correspond to the values of Bootstrap (BS) and Jackknife (J) values above 50%, respectively.

analysis in the subfamily will elucidate the evolution of these characters and the relationship of the *V. corcovadensis* group in the tillandsioid complex.

The clade I, sister to G, includes also species from *V.* sect. *Vriesea* with both simple and compound inflorescences, and is supported by the floral bracts inflated (char. 43:1) and the petal appendages obtuse (char. 57:0). The species with compound inflorescences form the basal grade. The species of clade J, represents a group that now includes about 35 species occurring in the Atlantic Domain (Forzza *et al.* 2014), many of which have questionable circumscriptions (Costa & Wendt 2007; Costa *et al.* 2007). These species have always been treated as a closely related group (e.g., Mez 1896; Smith & Downs 1977), and includes only species with suberect peduncle (char. 16:1), bracts of the peduncle similar to the floral bracts (char. 21:1), simple inflorescence (char. 23:0), and sepals with 3 cm long or more (char. 51:1). This clade splitted into four morphologically and narrowly related species clades.

The first of them shows a basal lineage formed by *V. guttata* + *V. pardalina* and form a well-supported clade (BS 91; JK 97) by the floral bracts rose (char. 46:4) covered with white wax (char. 48:1), among others. These species also share the foliar blades spotted, peduncle and fertile part of the inflorescence pendulous, and floral bracts pale rose. Together with *V. capixabae* Leme the three species form a group which boundaries are sometimes difficult to delimit (Gouda 2011). The second lineage includes *V. heterostachys*, *V. incurvata* and *V. erythrodactylon* var. *erythrodactylon*, which share the secund flowers (char. 37:1). Two important contributions were made on the phylogeography (Zanella 2013) and morphological variation (Silva 2014) of *V. incurvata* which helped to improve the species delimitation and its relatives. The lineage formed by *V. ensiformis*, *V. gradata*, *V. psittacina* and their varieties, form a group of species which the boundaries are very difficult to delimit even with live material because of the development of the inflorescence (char. 24:0). The same occurs with *V. simplex* and *V. scalaris* (not included in the present analysis), especially due to the feature used to separate one from the other, the length of the floral bract related to the sepals (Smith & Downs 1977). This clade is supported by the red peduncle (char. 19:1), the floral bract with no keel (char. 41:0), with the longitudinal posture involute (char. 44:0), and petals erect with apex strongly recurvate (char. 55:2). The remaining clade, including *V. inflata*, *V. seideliana*, *V. secundiflora*, *V. carinata* var. *carinata* and *V. duvaliana*, was supported by the sepals less than 3 cm long (char. 51:0), and petals yellow with green apex (char. 56:2). The taxonomic revision of the species of clade J is urgent because they form large populations between south Bahia and Rio Grande do Sul states along the Atlantic Forest, and the difficulty in delimiting these taxa resulted in misapplied names in most Brazilian herbarium collections.

The main morphological characters that traditionally distinguish *Vriesea* from *Alcantarea* species are the presence of the seed with short apical coma and the petals erect at anthesis (Harms 1930; Smith & Downs 1977), both of them were synapomorphic to the genus in the present analysis. The color of the floral bracts and the position of the stamens related to the corolla were homoplastic. These characters were traditionally used to delimit the two sections (Smith & Downs 1977). However, the floral bracts green supported clade C with species of *V.* sect. *Xiphion*. The stamens included are synapomorphic and seems to be ancestral to clades C + F, with species of both sections. On the other hand, the exserted stamens supported the clades I + G + *V. friburgensis* var. *friburgensis*, all of them belonging to *V.* sect. *Vriesea*. Some other characters were adopted by different authors to circumscribe groups of species (Mez 1896; Smith & Downs 1977). The base of the floral bracts decurrent is characteristic of the species of clade E, related to *V. jonghei*; the species of clade J with species of *V.* sect. *Vriesea* have the floral bracts inflated and simple inflorescences; and the development of the inflorescence with the floral bracts and flowers apressed before anthesis and ascending to patent at anthesis are related to species of clades E and *V. ensiformis* clade.

The results of this analysis allowed the selection of some characters that are potentially important in the infrageneric systematics of *Vriesea* as the longitudinal posture of the floral bracts (char. 44, for clade H and *V. ensiformis* clade), presence of keel on the sepals (char. 52, for clade G), shape of the petals (char. 54, for clade C), transverse posture of the petals (char. 55, for clade F and and *V. ensiformis* clade), shape of the apex of the petal appendages (char. 57, for clade I), shape of the filament (char. 59, clades C+F) and position of stamens and pistil during anthesis (char. 61, for clade C). It deserves notice that some characters were already used as diagnostic for groups of species in the genus but never widely adopted as the petal shape (Wawra 1883) and the shape of the filaments (Morren 1874).

Final Remarks

Although the analyses conducted here did not corroborate the monophyly of the sections, some groups of morphological related species were recuperated with clear synapomorphies. Several characters neglected to circumscribe the groups are proposed as potentially important to the systematics of the genus and should be investigated in a more inclusive analysis in the future.

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References

Aguirre-Santoro, J.A. 2009. Filogenia e delimitação do gênero *Ronnbergia* E. Morren & André (Bromelioideae: Bromeliaceae). Master Dissertation, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro. 88p.

Almeida, V.R., Costa, A.F.; Mantovani, A.; Esteves, V.G.L.; Arruda, R.C.O. & Forzza, R.C. 2009. Morphological phylogenetics of *Quesnelia* (Bromeliaceae, Bromelioideae). Systematic Botany 34: 660-672. DOI: 10.1600/036364409790139619.

Baker, J.G. 1889. Handbook of the Bromeliaceae. George Bell & Sons., London. 243p.

Barfuss, M.H.J.; Samuel, R.; Till, W. & Stuessy, T.F. 2005. Phylogenetic relationships in subfamily Tillandsioideae (Bromeliaceae) based on DNA sequence data from seven plastid regions. American Journal of Botany 92: 337-351. DOI: 10.3732/ajb.92.2.337.

Beaman, R.S. & Judd, W.S. 1996. Systematics of *Tillandsia* subgenus *Pseudalcantarea* (Bromeliaceae). Brittonia 48: 1-19.

Bouchenak-Khelladi, Y.; Muasya, A.M. & Linder, H.P. 2014. A revised evolutionary history of Poales: origins and diversification. Botanical Journal of the Linnean Society 175: 4-16. DOI: 10.1111/boj.12160.

Bryant, H.N. 1995. Why autapomorphies should be removed: a reply a Yates. Cladistics 11: 381-384.

Butcher, D. 2009. Names and synonyms. Bromeliaceae 43: 4-5.

Chew, T.; De Luna, E. & González, D. 2010. Phylogenetic relationships of the pseudobulbous *Tillandsia* species (Bromeliaceae) inferred from cladistic analyses of ITS 2, 5.8S ribosomal RNA gene, and ETS sequences. Systematic Botany 35: 86-95. DOI: 10.1600/036364410790862632.

Clark, W.D.; Gaut, B.S.; Duvall, M.R. & Clegg, M.T. 1993. Phylogenetic relationships of the Bromeliiflorae-Commeliniflorae-Zingiberiflorae complex of monocots based on *rbc*L sequence comparisons. Annals of the Missouri Botanical Garden 80: 987-998.

Costa, A.F. & Wendt, T. 2007. Bromeliaceae na região de Macaé de Cima, Nova Friburgo, Rio de Janeiro, Brasil. Rodriguésia 58: 905-939.

Costa, A.F.; Wanderley, M.G.L. & Moura, R.L. 2007. *Vriesea* Lindley (Bromeliaceae). *In*: Wanderley, M.G.L.; Shepherd, G.J.; Melhem, T.S. & Giulietti, A.M. Flora Fanerogâmica do Estado de São Paulo. Instituto de Botânica-FAPESP, São Paulo. Vol. 5, pp.126-155.

Costa, A.F.; Rodrigues, P.J.F.P. & Wanderley, M.G.L. 2009. Morphometric analysis of *Vriesea paraibica* Wawra complex (Bromeliaceae). Botanical Journal of the Linnean Society 159: 163-181. DOI: 10.1111/j.1095-8339.2008.00919.x

Costa, A.F.; Gomes-da-Silva, J. & Wanderley, M.G.L. 2014. *Vriesea* (Bromeliaceae, Tillandsioideae): taxonomic history, and morphology of the Brazilian lineage. Journal of the Torrey Botanical Society 141: 338-352. DOI: 10.3159/TORREY-D-13-00070.1.

Crayn, M.D.; Terry, R.G.; Smith, A.C. & Winter, K. 2000. Molecular systematic investigations in Pitcairnioideae (Bromeliaceae) as a basis for understanding the evolution of crassulacean acid metabolism (CAM). *In:* Wilson, K.L. & Morison, D.A., Monocots: Systematics and Evolution. CSIRO, Melbourne. Pp. 569-579.

Cronquist, A. 1988. The evolution and classification of flowering plants, 2nd ed. The New York Botanical Garden, New York. 555p.

Dahlgren, R.M.T.; Clifford, H.T. & Yeo, P.F. 1985. The families of the Monocotyledons. Structure, evolution and taxonomy. Springer Verlag, Berlin. 520p.

De Pinna, M.C.C. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367-394.

Faria, A.P.G. 2006. Revisão taxonômica e filogenia de *Aechmea* Ruiz & Pav. Subg. *Macrochordion* (De Vriese) Baker, Bromelioideae-Bromeliaceae. Ph.D. Thesis. Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro. 199p.

Faria, A.P.G.; Wendt, T. & Brown, G.K. 2004. Cladistic relationships of *Aechmea* (Bromeliaceae, Bromelioideae) and allied genera. Annals of the Mossouri Botanical Garden 91: 303-319.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783-791.

Fitch, W.M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20: 406-416.

Forzza, R.C. 2001. Filogenia da tribo Puyae Wittm. e revisão taxonômica do gênero *Encholirium* Mart. ex Schult. & Schult. f. (Pitcairnioideae, Bromeliaceae). Ph.D. Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo. 208p.

Forzza, R.C.; Costa, A.; Siqueira Filho, J.A.; Martinelli, G.; Monteiro, R.F.; Santos-Silva, F.; Saraiva, D.P.; Paixão-Souza, B.; Louzada, R.B. & Versieux, L. Bromeliaceae. *In*: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. Available at <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB6414>. Access on 29 September 2014.

Gilmartin, A.J. & Brown, G.K. 1986. Cladistic test of hypoteses concerning evolution of xerophytes and mesophytes within *Tillandsia* subg. *Phytarrhiza* (Bromeliaceae). American Journal of Botany 73: 387-397.

Gilmartin, A.J. & Brown, G.K. 1987. Bromeliales, related Monocots and resolution of relationships among Bromeliaceae subfamilies. Systematic Botany 12: 493-500.

Gilmartin, A.J.; Brown, G.K; Varadarajan, G.S. & Neighbours, M. 1989. Status of *Glomeropitcairnia* within evolutionary history of Bromeliaceae. Systematic Botany 14: 339-348.

Givnish, T.J.; Pires, J.C.; Graham, S.W.; Mcpherson, M.A.; Prince, L.M.; Patterson, T.B.; Rai, H.S.; Roalson, E.H.; Evans, T.M.; Hahn, W.J.; Millan, K.C.; Meerow, A.W.; Molvray, M.; Kores, P.J.; O'Brien, H.E.; Hall, J.C.; Kress, W.J. & Sytsma, K.J. 2006. Phylogenetic relationships of monocots based in the highly informative plastid gene *ndh*F: evidence for widespread concerted convergence. Aliso 22: 28-51.

Givnish, T.J.; Millan, K.C.; Berry, P.E. & Sytsma, K.J. 2006. Phylogeny, adaptive radiation, and historical biogeography of Bromeliaceae inferred from *ndh*F sequence data. *In*: Columbus, J.T., Friar, E.A.J., Porter, M.L., Prince, M. & Simpson, M.G. Monocots: Comparative Biology and Evolution - Poales. Rancho Santa Ana Botanic Garden, Claremont. Pp. 3-26.

Givnish, T.J.; Barfuss, M.H.J.; Ee, B.V.; Riina, R.; Schulte, K.; Horres, R.; Gonsiska, P.A.; Jabaily, R.S.; Crayn, D.M.; Smith, A.C.; Winter, K.; Brown, G.K.; Evans, T.M.; Holst, B.K.; Luther, H.; Till, W.; Zizka, G.; Berry, P.E. & Sytsma, K.J. 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. American Journal of Botany 98: 872–895. DOI: 10.3732/ajb.1000059.

Goloboff, P.A. 1993. Estimating character weights during tree search. Cladistics 9: 83-91.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415-428.

Goloboff, P.A.; Farris, J.S. & Nixon, K. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774-786. DOI: 10.1111/j.1096-0031.2008.00217.x

Gomes-da-Silva, J. 2013. Análise filogenética de *Vriesea* Lindley (Bromeliaceae: Tillandsioideae), baseada em dados morfológicos e moleculares. Ph. D. Thesis. Museu Nacional-Universidade Federal do Rio de Janeiro, Rio de Janeiro. 222p.

Gomes-da-Silva, J. & Costa, A.F. 2011. A taxonomic revision of *Vriesea corcovadensis* group (Bromeliaceae: Tillandsioideae) with description of two new species. Systematic Botany 36: 291-309. DOI: 10.1600/036364411X569499.

Gomes-da-Silva J.; Vargens, F.A.C.; Arruda, R.C.O. & Costa, A.F. 2012. A new evidence of non-monophyly of *Vriesea* (Bromeliaceae: Tillandsiodeae) based in a morphological cladistic analysis of the *Vriesea corcovadensis* group, with an anatomical description. Systematic Botany 37: 641-654. DOI: 10.1600/036364412X648599.

Gouda, E.J. 2011. Introducing *Vriesea pardalina*. Journal of the Bromeliad Society 61: 224-227.

Grant, J.R. 1993. True Tillandsias mispplaced in *Vriesea* (Bromeliaceae: Tillandsioideae). Phytologia 75: 170-175.

Grant, J.R. 1995a. The ressurection of *Alcantarea* and *Werauhia*, a new genus. Tropische und Subtropische Pflanzenwelt 91: 1-59.

Grant, J.R. 1995b. Addendum to "The ressurection of *Alcantarea* and *Werauhia*, a new genus" (Bromeliaceae: Tillandsioideae). Phytologia 78: 119-123.

Grant, J.R. 2004. New combinations and names in Andean *Pitcairnia*, *Tillandsia* and *Werauhia* (Bromeliaceae). Vidalia 2: 23-25.

Harms, H. 1930. Bromeliaceae. *In*: Engler, H.G.A. & Prantl, K.A.E. *Die naturlichen Pflanzenfamilien*... 2ed. Vol. 15a. Wilhem Engelman, Leipzig. Pp. 65-159.

Hornung-Leoni, C.T. & Sosa, V. 2008. Morphological phylogenetics of *Puya* subgenus *Puya* (Bromeliaceae). Botanical Journal of the Linnean Society 156: 93-110. DOI: 10.1111/j.1095-8339.2007.00740.x

Horres, R.; Zizka, G.; Kahl, G. & Weising, K. 2000. Molecular phylogenetics of Bromeliaceae: evidence from *trn*L (UAA) intron sequence of the chloroplast genome. Plant Biololgy 2: 306-315. DOI: 10.1055/s-2000-3700.

Horres, R.; Schulte, K.; Weising, K. & Zizka, G. 2007. Systematics of Bromelioideae (Bromeliaceae) – Evidence from molecular and anatomical studies. Aliso 23: 27-43. DOI: 10.5642/aliso.20072301.05.

Leme, E.M.C. 2000. *Nidularium*. Bromélias da Mata Atlântica. Ed. Sextante, Rio de Janeiro. 263p.

Leme, E.M.C. & Marigo, L.C. 1993. Bromélias na Natureza. Marigo Comunicação Visual, Rio de Janeiro. 183p.

Luther, H.E. 2001. *De Rebus Bromeliacearum* III. Selbyana 22: 34-67.

Luther, H.E. 2012. An alphabetical list of *bromeliad binomials* (13th ed., edited by Bruce Holst and Larry Rabinowitz). Marie Selby Botanical Gardens and Bromeliad Society International, Sarasota. 44p.

Luther, H.E. & Sieff, E. 1994. *De Rebus Bromeliacearum* I. Selbyana 15: 9-93.

Luther, H.E. & Sieff, E. 1997a. *De Rebus Bromeliacearum* II. Selbyana 18: 103-140.

Luther, H.E. & Sieff, E. 1997b. *De Rebus Bromeliacearum*: *Addenda et corrigenda.* Selbyana 18: 215.

Luther, H.E. & Rabinowitz, L. 2010. *De Rebus Bromeliacearum* IV. Selbyana 30: 147-189.

Martinelli, G.; Vieira, C.M.; Gonzalez, M.; Leitman, P.; Piratininga, A.; Costa, A.F. & Forzza, R.C. 2008. Bromeliaceae da Mata Atlântica Brasileira: Lista de espécies, distribuição e conservação. Rodriguésia 59: 209-258.

Mez, C. 1894. Bromeliaceae. *In*: Martius, C.F.P. von; Eichler, A. W. & Urban, I. *Flora brasiliensis*. Munchen, Wien, Leipzig. Vol. 3, pars 3, pp: 173-674.

Mez, C. 1896. Bromeliaceae. *In*: de Candolle, A.L.P.P. & de Candolle, A.C.P. *Monographiae phanerogamarum*. Vol. 9. G. Masson, Paris. 990p.

Mez, C. 1934-5. Bromeliaceae. *In*: Engler, H.G.A. *Das pflanzenreich* IV.32 (Heft 100, 1-4), Wilhem Engelmen, Berlin. 667p.

Monteiro, R.F. 2009. Estudos anatômicos e filogenéticos em *Bromelia* L. (Bromeliaceae, Bromelioideae). Master Dissertation. Instituto de Pesquisas Jardim Botânico do Rio de Janeiron - Escola Nacional de Botânica Tropical, Rio de Janeiro. 84p.

Morren, E. 1874. Notice sur le *Tillandsia* (*Xiphion*) *jonghei*. La Belgique Horticole 34: 291-4, pl. XII, XIII.

Moura, R.L. 2011. Revisão taxonômica do grupo *Vriesea platynema* Gaudich. (Bromeliaceae). Ph.D. Thesis. Museu Nacional - Universidade Federal do Rio de Janeiro, Rio de Janeiro. 192p.

Moura, R.L. & Costa, A.F. 2014. Taxonomic notes on *Vriesea* Sect. *Xiphion* (Bromeliaceae) with descriptions of three new species. Systematic Botany 39: 791-803. DOI: 10.1600/036364414X681536.

Müller, F.K. 2005. The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. BMC Evolutionary Biology 5: 58. DOI:10.1186/1471-2148-5-58.

Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407-414.

Nixon, K.C. 2002. 'Winclada', version 1.00.08. Published by the author, Ithaca.

Nixon, K.C. & Carpenter, J.M. 1993. On outgroups. Cladistics 9: 413-426.

Page, R.D.M. 2001. Nexus data editor 0.5.0. Program distributed by the author, Institute of Biomedical and Life Sciences. University of Glasgow, Glasgow. Available at <http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde. html>. Access on 15 June 2009.

Poe, S. & Wiens, J.J. 2000. Character selection and the methodology of morphological phylogenetics. *In:* Wiens, J.J. Phylogenetic, analysis of morphological data. Smithsonian Institution Press, Washington. Pp: 20-36.

Radford, A.E. 1986. Fundamentals of plant systematics. Harper & Row, Publ. Inc., New York. 498p.

Rae, T.C. 1998. The logical basis for the use of continuous characters in phylogenetic systematics. Cladistics 14: 221-228.

Ranker, T.A.; Soltis, D.E.; Soltis, P.S. & Gilmartin, A.J. 1990. Subfamilial phylogenetic relationships of the Bromeliaceae: evidence from chloroplast DNA restriction site variation. Systematic Botany 15: 424-434.

Reitz, R. 1983. Bromeliáceas e a Malária-Bromélia endêmica. *In*: Reitz, R. Flora Ilustrada Catarinense. Fasc. BROM. Herbário Barbosa Rodrigues, Itajaí. 559p.

Rex, M.; Patzolt, K.; Schulte, K.; Zizka, G.; Vásquez, R.; Ibisch, P.& Weising, K. 2007. AFLP analysis of genetic relationships in the genus *Fosterella* L.B.Smith (Pitcairnioideae, Bromeliaceae). Genome 50: 90-105. DOI: 10.1139/g06-141

Saraiva, D.P. 2013. Filogenia morfológica de *Pitcairnia* L'Hér. (Pitcairnioideae - Bromeliaceae). Master Dissertation. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro - Escola Nacional de Botânica Tropical, Rio de Janeiro. 79p.

Sass, C. & Specht, C.D. 2010. Phylogenetic estimation of the core Bromelioids with an emphasis on the genus *Aechmea* (Bromeliaceae). Molecular Phylogenetics and Evolution 55: 559-571. DOI: 10.1016/j.ympev.2010.01.005.

Scharf, U. & Gouda, E.J. 2008. Bringing Bromeliaceae back to homeland botany. Journal of the Bromeliad Society 58: 123-129.

Schulte, K.: Barfuss, H.J.M. & Zizka, G. 2009. Phylogeny of Bromelioideae (Bromeliaceae) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. Molecular Phylogenetics and Evolution 51: 327-339. DOI: 10.1016/j.ympev.2009.02.003

Silva, B.N.F. 2014. Revisão taxonômica do complexo *Vriesea incurvata* Gaudich. (Tillandsioideae, Bromeliaceae). Master Dissertation. Museu Nacional - Universidade Federal do Rio de Janeiro, Rio de Janeiro. 79p.

Siqueira-Filho, J.A. & Leme, E.M.C. 2006. Fragmentos de Mata Atlântica do Nordeste, biodiversidade, conservação e suas Bromélias. Andrea Jakobsson Estúdio, Rio de Janeiro. 415p.

Smith, L.B. 1966. Notes on Bromeliaceae XXIII. Phytologia 13: 84-161.

Smith, L.B. & Downs, R.J. 1977. Bromeliaceae, subfamily Tillandsioideae. Flora Neotropica. Hafner Press, New York. Monograph 14, part 2, pp. 663-1492, fig. 213-467.

Soltis, P.S. & Soltis, D.E. 2003. Applying the Bootstrap in Phylogeny Reconstruction. Statistical Science18: 256-267. DOI:10.1214/ss/1063994980.

Sousa, G.M. 2004. Revisão taxonômica de *Aechmea* Ruiz & Pavon subg. *Chevaliera* (Gaudich. ex Beer) Baker, Bromelioideae-Bromeliaceae. Ph.D. Thesis. Instituto de Biociências - Universidade de São Paulo, São Paulo.

Sousa, L.O.F.; Wendt, T; Brown, G.K.; Tuthill, D.E. & Evans, T.M. 2007. Monophyly and phylogenetic relationships in *Lymania* (Bromeliaceae: Bromelioideae) based on morphology and chloroplast DNA sequences. Systematic Botany 32: 264-270.

Stearn, W.T. 1973. Botanical Latin. David & Charles, Newton Abbot, London. 566p.

Swofford, D.L. & Maddison, W.P. 1987. Reconstructing ancestral character states under Wagner parsimony. Mathematical Biosciences and Engineering 87: 199-229.

Tardivo, R.C. 2002. Revisão taxonômica de *Tillandsia* L. subgênero *Anoplophytum* (Beer) Baker (Bromeliaceae). Ph.D. Thesis. Instituto de Biociências - Universidade de São Paulo, São Paulo. 244p.

Terry, R.G.; Brown, G.K. & Olmstead, R.G. 1997a. Examination of subfamilial phylogeny in Bromeliaceae using comparative sequencing of the plastid locus *ndh*F. American Journal of Botany 84: 664-670.

Terry, R.G.; Brown, G.K. & Olmstead, R.G. 1997b. Phylogenetic relationships in subfamily Tillandsioideae (Bromeliaceae) using *ndh*F sequences. Systematic Botany 22: 333-345.

Thiele, K. 1993. The Holy Grail of the perfect character: the cladistic treatment of morphometric data. Cladistics 9: 275-304.

Thiers, B. [cont. updated]. *Index Herbariorum:* A global directory of and associated staff. New York Botanical Garden's Virtual Herbarium. Available at <http://sweetgum.nybg.org/ih/>. Access on 29 September 2014.

Uribbe, F.P. 2014. Variação morfológica no complexo *Vriesea procera* (Mart. ex Schult. & Schult. f. (Tillandsioideae, Bromeliaceae). Master Dissertation. Museu Nacional - Universidade Federal do Rio de Janeiro, Rio de Janeiro. 85p.

Varadarajan G.S. & Gilmartin, A.J. 1988. Phylogenetic relationships of groups of genera within the subfamily Pitcairnioideae (Bromeliaceae). Systematic Botany 13: 283-293.

Versieux, L.M. 2011. Brazilian plants urgently needing conservation: the case of *Vriesea minarum* (Bromeliaceae). Phytotaxa 28: 35-49.

Versieux, L.M.; Barbará, T.; Wanderley, M.G.L.; Calvente, A.; Fay, M.F. & Lexer, C. 2012. Molecular phylogenetics of the Brazilian giant bromeliads (*Alcantarea*, Bromeliaceae): implications for morphological evolution and biogeography. Molecular Phylogenetics and Evolution 64: 177-189. DOI: 10.1016/j.ympev.2012.03.015>.

Wawra, H.R. Von F. 1883. *Itinera Principum S. Coburgi. Die Botanische Ausbeute von den Reisen ihrer Hoheiten der Prinzen von Sachsen-Coburg-Gotha. I. Reise der Prinzen Philipp und August um die Welt (1872-1873). II. Reise der Prinzen August und Ferdinand nach Brasilien beschreiben von Dr. Heinrich Ritter Wawra v. Fernsee*. Druk und Commissionsverlag von Carl Gerold's sohn, Wien. 240p.

Weberling, F. 1989. Morphology of flowers and inflorescences. Cambridge University Press, Cambridge. 405p.

Wiens, J.J. 2001. Character analysis in morphological phylogenetics: problems and solutions. Systematic Biology 50: 689-699. DOI: 10.1080/106351501753328811.

Yeates, D. 1992. Why remove autapomorphies? Cladistics 8: 387-389.

Zanella, C.M. 2013. Padrões históricos e processo de hibridação entre duas espécies simpátricas de bromélias da Mata Atlântica: implicações evolutivas e conservacionistas. Ph.D. Thesis. Universidade Federal do Rio Grande do Sul, Porto Alegre. 123p.

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