Morphological Variation in the *Vriesea procera* complex (Bromeliaceae, Tillandsioideae) in the Brazilian Atlantic Rainforest, with Recognition of New Taxa

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**Abstract**—The family Bromeliaceae is essentially Neotropical, with high endemism and diversity in the Atlantic Rainforest Domain. Species circumscription is a major problem in the family systematics, especially in the most diverse genera. Species of the *Vriesea procera* complex, which occur in forests and restinga (coastal vegetation) along the South American Atlantic coast from Venezuela to southern Brazil, share the same basic vegetative and reproductive morphological patterns. However, they vary widely in the number and position of inflorescence branches as well as in the dimensions, position, and shape of the leaves and flowers in different populations. Here we aimed 1) to evaluate the morphological variation in the *V. procera* complex, through morphometric analyses of natural populations along the Brazilian Atlantic Rainforest; and 2) to determine the taxonomic relationships among these species, establishing the validity and the limits of variation of the taxa through taxonomic treatment. Fourteen natural populations, 271 individuals, and 36 morphometric variables were analyzed. Kruskal-Wallis tests and discriminant analyses were conducted to test statistical differences between previously established groups. Of an original three species and three varieties, our data allowed us to recognize six species, including three new taxa (*Vriesea aureoramosa*, *V. magna*, *V. rubroviolacea*) and one new name and status (*V. flexuosa*). The resulting taxa are distinguished by the inflorescence and leaf sizes and especially by floral characteristics such as the length of bracts, sepals, petals, stamens, and pistils, besides the petal apex posture and relative position of the stamens during anthesis. Recognition of cryptic species under the names *V. procera* and *V. neoglutinata* is an important step toward a better understanding of the biodiversity of the Brazilian Atlantic Rainforest.

**Keywords**—Morphometry, multivariate analyses, taxonomy.

Bromeliaceae Juss. is one of the most morphologically and ecologically diverse Neotropical angiosperm families (Givnish et al. 2011). Studies on diversity have shown that increases in the number of bromeliad species may be related to greater environmental heterogeneity and the consequent structural diversity of the forest (Nadkarni and Matelson 1989). Tillandsioideae ranges more widely across the Neotropics than the other seven subfamilies (Smith and Downs 1977; Barfuss et al. 2016). It is also the richest and morphologically diverse, with 22 newly recircumscribed genera (Barfuss et al. 2016; Leme et al. 2017). Among them, *Vriesea* Lindl. has about 200 species, occurring in different phytosociologicals of Atlantic Rainforest and Cerrado domains, its main center of diversity (Martinelli et al. 2008; Costa et al. 2014; Gomes-da-Silva and Souza-Chies 2017) and richness (Steinhann et al. 2009). The genus distribution extends to western Caribbean, Colombia, Peru, Venezuela, and the Greater Antilles (Barfuss et al. 2016). The genus is especially diverse in floral morphology (petal shape, corolla type, and position of the stamens in relation to the corolla) and in the color of inflorescence bracts (Costa et al. 2014). These features characterize the two traditional sections, *V. sect. Vriesea* and *V. sect. Xiphion* E.Morren (Smith and Downs 1977; Costa et al. 2014), whose monophyly was not corroborated in any phylogeny performed on the genus to date (Gomes-da-Silva et al. 2012; Costa et al. 2015; Barfuss et al. 2016; Gomes-da-Silva and Souza-Chies 2017). On the other hand, different groups of morphologically related species were recovered and are recognized as natural (Costa et al. 2015; Gomes-da-Silva and Souza-Chies 2017). However, some of them have species with difficult delimitations, and conflicting nomenclatural and taxonomic histories (Costa et al. 2014). Recently, some of these species groups or complexes have been studied in order to enable a taxonomic revision of *Vriesea* (Costa et al. 2009; Gomes-da-Silva and Costa 2011; Versieux 2011; Moura and Costa 2014; Neves et al. 2018).

The complex related to *Vriesea procera* (Mart. ex Schlott. f.) Wittm. is part of the *V. sect. Vriesea*, and is composed of taxa that have the same basic pattern in rosette and inflorescence morphology, and encompasses three species and four varieties (Table 1). *Tillandsia procera* (its basionym) was collected by Carl Friedrich Philipp von Martius in the forests of the Itapé River, in the south of the state of Bahia, in a Brazilian Atlantic Rainforest area, in the early 19th century. Later, the monographers of Bromeliaceae, especially Mez (1896) and Smith and Downs (1977), included in the circumscription of the species records from a wide geographic area including the north of South America, greatly extending its morphological and geographic limits. Moreover, the description of new related taxa (including varieties and species) also contributed to the misunderstanding about their limits. This way, the taxa of the complex vary enormously in: 1) dimensions, posture, and shape of the leaves, and 2) number and position of the inflorescence branches, apex posture and shape of the petals, and the position of the stamens and pistil in relation to the corolla from anthesis (Costa et al. 2007; Moura et al. 2007). These variations, together with the imprecise delimitations in the original descriptions, led to conflicts in determinations, as reflected in herbarium collections, especially around the names *V. procera* and *V. neoglutinata* Mez (Moura et al. 2007; Costa et al. 2014; Moura and Costa 2014). Throughout the area of occurrence of this species complex, especially in lowland forests and restingas, distinguishing between these taxa is difficult (Smith and Downs 1977; Reitz 1983; Araújo 2000; Moura et al. 2007).

Considering the huge morphological variation throughout the wide geographic distribution of the complex, we performed morphometric analyses in natural populations along the Atlantic Rainforest Domain due to the occurrence of large populations, and the type locality of *Vriesea procera* at south Bahia, as a first attempt to the understanding of its morphological variation.
Morphometric analyses have been used in families with groups of species that are difficult to delimit (Brusselliacae, Orozco 1991; Brassicaceae, Marhold 1996; Dipsacaceae, Caputo et al. 1996; Berberidaceae, Bottini et al. 1998; Compositae, Hodalová and Marhold 1998), including Bromeliaceae (Costa et al. 2009; Faria et al. 2010; Castello and Galetto 2013; Guarçoni et al. 2017; Neves et al. 2018). Here we aimed 1) to evaluate the morphological variation in the V. procera complex, through morphometric analyses of natural populations along the Atlantic Rainforest domain; and 2) to determine the taxonomic relationships between these species, establishing the validity and the limits of variation of the taxa through taxonomic treatment. Recognition of cryptic species presently under the names V. procera and V. neoglutinosa is an important step toward a better understanding of the biodiversity of the Brazilian Atlantic Rainforest.

## Materials and Methods

**Morphometric Analysis—Populations and Localities**—For morphometric study, vegetative and reproductive structures of natural populations were analyzed. To select populations, specific literature and collections of the herbaria R, RB, GUA, HB, SP, and MBM (see acronyms in Thiens 2017) were consulted. We analyzed 14 natural populations morphologically related to V. procera (Table 2), along the Atlantic coast from southern Bahia (BA) to northeast Paraná (PR) (Fig. 1). The individuals were randomly sampled; the size of the samples varied according to their availability and accessibility. Voucher specimens were deposited in the Herbarium of the National Museum of Rio de Janeiro (R). During the field work, the locations indicated in the herbarium collections for the states of Paraíba, Pernambuco, Alagoas, Sergipe, Minas Gerais, Santa Catarina, and Rio Grande do Sul were visited. However, flowering individuals were observed in none of the populations, hampering their inclusion in morphometric analyses.

**Morphological Characters**—Thirty-six quantitative variables were analyzed: four vegetative and 32 reproductive (Table 3).

**Data Analyses**—The analyses were performed using STATISTICA 8.0 (StatSoft Inc. 2007) and PAST v. 2.16 (Hammer 2010). The normality and homoscedasticity of the data variances were tested using the Shapiro-Wilk (Shapiro and Wilk 1965) and Levene (Levene 1960) tests, respectively. The Kruskal-Wallis test (KW) was also performed to determine statistical differences.

A discriminant analysis (DA) were performed to test for statistical differences between groups that were previously established, to assess the adherence among individuals from each group, and to indicate the characteristics that contributed most to the discrimination (Hair et al. 2009). The groups were composed of individuals from the 14 natural populations. Data available from Dryad (Uribbe et al. 2020).

### Table 1. List of taxa, locality of the type collection, and occurrence, according to the literature, of the members of the *Vriesea procera* complex.

| Taxon | Type collection | Occurrence (BFG 2015) |
|-------|----------------|-----------------------|
| *Vriesea graciliscapa* Weber | Brazil. Bahia: Ilhéus, Seidel 939 (HAL). | Brazil (Bahia) |
| *Vriesea neoglutinosa* Mez | Brazil. Rio de Janeiro: Botafogo, Martius s.n. (M). | Brazil (Bahia) |
| *Vriesea procera* (Mart. ex Schult. & Schult f.) Wittm. var. *procera* | Brazil. Bahia: Rio Taipé, Martius s.n. (M). | Brazil (Bahia) |
| *Vriesea procera* var. *rubra* L.B.Sm. | Brazil, ES, Itapemirim, 8-VII-1939, Foster & Foster 166 (US). | Brazil (Espírito Santo) |
| *Vriesea procera* var. *tenuis* L.B.Sm. | Brazil, São Paulo: Pirajussara, A. Gehrt & L.B. Sm. 1820 (GH). | Brazil (Espírito Santo) |
| *Vriesea procera* var. *debilis* Mez | Brazil. Rio de Janeiro: Rio de Janeiro, Mikan s.n. (W). | Brazil (Espírito Santo) |

### Table 2: Population codes, locations, voucher material, and number of individuals sampled in each natural population used for the morphometric analysis of the *Vriesea procera* complex.

| Population codes | Location | Voucher | Number of individuals |
|------------------|----------|---------|----------------------|
| BA1 | BA, Caraíva, Reserva Indígena de Barra Velha, S 16°50’14.2” W 03°09’59.6” | Uribbe 183 | 20 |
| BA2 | BA, Itamaraju, Parque Nacional do Monte Pascoal, S 16°53’39.2” W 03°09’24.35’ | Uribbe 184 | 11 |
| ES1 | ES, Cariacica, Pau Amarelo, Reserva Biológica de Duas Bocas, S 20°16’46.4” W 040°32’43.7” | Uribbe 189 | 20 |
| ES2 | ES, Linhares, Restinga de Agua Viva, S 19°13’46.1” W 03°49’42.9” | Uribbe 187 | 19 |
| ES3 | ES, Itaguaçu, Pedra do Pontal, S 19°35’48.7” W 040°48’57.0” | Uribbe 188 | 13 |
| RJ1 | RJ, Teresópolis, Canoas, S 22°24’05.4” W 042°53’09.5” | Uribbe 181 | 20 |
| RJ2 | RJ, Teresópolis, Canoas, S 22°24’05.4” W 042°53’09.5” | Uribbe 182 | 20 |
| RJ3 | RJ, Saquarema, Restinga de Jacarepá S 22°55’27.4” W 042°26’09.5” | Uribbe 185 | 11 |
| RJ4 | RJ, Saquarema, Restinga de Jacarepá, S 22°55’27.6” W 042°26’08.8” | Uribbe 186 | 6 |
| RJ5 | RJ, Angra dos Reis, Ilha Grande, Parque Estadual da Ilha Grande, Restinga de Lopes Mendes, S 23°09’56.9” W 044°08’20.1” | Uribbe 190 | 19 |
| RJ6 | RJ, Maricá, APA Maricá, S 22°57’49.3” W 042°53’40.4” | Uribbe 238 | 20 |
| SP1 | SP, Cananeia, Ilha do Cardoso, Parque Estadual da Ilha do Cardoso, S 25°04’29.3” W 047°55’29.3” | Uribbe 229 | 20 |
| SP2 | SP, Ubatuba, Picinguaba, Parque Estadual da Serra do Mar, S 23°20’20.2” W 044°50’15.4” | Uribbe 230 | 20 |
| PR | PR, Paranaguá, Ilha do Mel, Parque Estadual da Ilha do Mel, S 25°34’12.4” W 048°18’37.7” | Uribbe 228 | 20 |
The variables were considered significant for DA based on the distance of each variable from the center of the axis: \( d = \sqrt{2} / n \), where \( n \) is the number of variables (Legendre and Legendre 1998), corresponding to \( d = 0.39 \) in this case.

**Taxonomic Treatment**—For the taxonomic analysis, the main reference works on Bromeliaceae (Mez 1894, 1896, 1934–1935; Harms 1930; Smith and Downs 1977; Luther and Sieff 1994, 1997a, 1997b; Luther 2001; Luther and Rabinowitz 2010; Luther 2012) were consulted for information on protologues and taxonomic history. The collections of the herbaria CEPEC, HB, HST, IPA, MBML, R, RB, SP, TEPB, UFPB, and VIES were consulted and images from the K herbarium were analyzed through the website http://apps.kew.org/herbcat/navigator.do (abbreviations according to Thiers 2017). The descriptions are based on analyses of herbarium material, collections, field observations, and the results of the morphometric analyses. The general terminology used in the morphological description follows Stearn (1973), Smith and Downs (1977), Radford (1986), and Scharf and Gouda (2008). The material examined is listed in a sequence from north to south, followed by the chronological order and collector number.

**Results**

We visited 25 different localities. We constructed a spreadsheet of 575 individuals analyzed, together with the herbarium materials and field collections.

**Morphological Analysis**—Twenty-five areas were visited, totaling 32 days of fieldwork, which provided better observations of the differences among populations and individuals. We analyzed 239 individuals, with a minimum of six and a maximum of 20 per population sampled. For all variables, the Shapiro-Wilk and Levene tests showed absence of normality and homoscedasticity, respectively (Supplemental Tables S1, S2; Uribbe et al. 2020).

**Kruskal-Wallis H Test**—The results of the KW H test for the 36 variables analyzed and the most important variables selected are shown in Table S3 (Uribbe et al. 2020) and Figs. 2 and 3, respectively. The Ilha Grande population (RJ5) was distinguished from the others by the widest sheath (Fig. 2A), and the Itaguaçu (ES3), Canoas (RJ1), and Água Viva (ES2) populations by the narrowest sheaths. The RJ5 population had the longest sheath while the RJ1 population had the shortest one (Table S3; Uribbe et al. 2020). Characters of the leaf blade also separated the populations. Caraíva (BA1) and RJ5 had the widest blades and RJ1 and ES3 the narrowest ones (Fig. 2B). RJ5 had the longest blades, while Canoas (RJ1) had the shortest ones (Table S3; Uribbe et al. 2020).

Regarding the inflorescence, Ilha Grande (RJ5) was distinguished from the other populations by the largest total length (Fig. 2C), the longest peduncle, and the largest peduncle diameter, while RJ1 (Canoas) had the shortest peduncle (Table S3; Uribbe et al. 2020). Regarding the length of the peduncle median internode, the Canoas (RJ1) and Maricá (RJ6) populations had the lowest values, although with some overlap, contrasting with the Ilha do Mel (PR) population which showed the highest values (Table S3; Uribbe et al. 2020). RJ1 and RJ5 stand out from the other populations in having the
The RJ5 population represented the fourth group, which encompassed the populations BA1, BA2, ES1, ES2, RJ2, RJ3, RJ4, RJ5, RJ6, and RJ6. In this analysis the first two axes explained 51.3% of the total variance (26.6% and 24.7%, respectively) (Table 5). Again we rejected the null hypothesis and accepted the type I error, with separation of three groups (Fig. 5). The first was formed by RJ6, which was separated on Axis 2 due to the number of branches, length of the median branch, and pistil length. The second group was formed by RJ5, which was discriminated on Axis 2, even with some overlapping, through the total length of the inflorescence, peduncle length of the distal branch, and petal length. The third group was formed by the remaining populations.

Additionally, aiming to obtain a better resolution, an additional DA was performed only sampling individuals of that fourth group, which encompassed the populations BA1, BA2, ES1, ES2, RJ2, RJ3, RJ4, RJ5, RJ6, and RJ6. In this analysis the first two axes explained 51.3% of the total variance (26.6% and 24.7%, respectively) (Table 5). Again we rejected the null hypothesis and accepted the type I error, with separation of three groups (Fig. 5). The first was formed by RJ6, which was separated on Axis 2 due to the number of branches, length of the median branch, and pistil length. The second group was formed by RJ5, which was discriminated on Axis 2, even with some overlapping, through the total length of the inflorescence, peduncle length of the distal branch, and petal length. The third group was formed by the remaining populations.

Summary of the Results of the Different Analyses—The morphometric analyses, added to the analyses of herbaria collections, including the nomenclatural types, allowed us to distinguish six taxa, including a new status and three new species.

Canoas (RJ1) was distinguished from the others mainly by the sepal length and width and number of branches (DA and KW), as well as by the width and length of the sheath, width and length of the leaf blade, length of the peduncle of the inflorescence, length and width of the floral bracts, length and width of petals, and lengths of stamens and pistil (KW test). This population represents V. procera var. tenuis. The statistical analyses, along with the taxonomic treatment, led us to elevate this taxon to species rank.

The populations SP1, SP2, and PR together formed the second group, which was characterized by sepal length and width, and number of branches (DA and KW test), median peduncle internode length, median branch internode length, distal branch, rachis diameter, petal, sepal, stamen, and pistil length (KW test). This group represents a new species.

For the ES3 population, the variables number of branches, proximal branch length, and sepal width (DA), along with petal length and width, and stamen and pistil length (KW test) contributed to characterize this population as a second new species.

The RJ5 population was determined by number of branches, median branch and pistil length (DA), together with sheath width and length, leaf blade width and length, total length of the inflorescence, and peduncle of the inflorescence length (KW test), is interpreted as the third new species.

The RJ6 population represents V. neoglutinosus. This population stands out from the others by total length of the inflorescence, peduncle length of the distal branch, and petal length (DA), along with length of the median peduncle internode length, sepal width, and pistil length (KW test).

The remaining populations constitute the V. procera species (sensu stricto).

### Table 3. Quantitative characters used in the morphometric analysis of natural populations of the Vriesea procera complex, with their respective codes.

| Characters Codes | Characters Codes |
|------------------|------------------|
| Sheath, width (cm) | SHW |
| Sheath, length (cm) | SHL |
| Blade, width (cm) | BLW |
| Blade, length (cm) | BLL |
| Inflorescence, total length (cm) | ITL |
| Peduncle, diameter (cm) | PDD |
| Peduncle, length (cm) | PDL |
| Median peduncle bract, length (cm) | MPL |
| Median peduncle internode, length (cm) | MIL |
| Number of branches | NMB |
| Proximal branch, length (cm) | 1BL |
| Proximal branch, peduncle length (cm) | 1PB |
| Proximal branch, rachis diameter (cm) | 1BD |
| Proximal branch, primary bract length (cm) | 1PB |
| Proximal branch, internode length (cm) | 1IL |
| Proximal branch, flower number | 1FN |
| Median branch, length (cm) | 2BL |
| Median branch, peduncle length (cm) | 2PB |
| Median branch, rachis diameter (cm) | 2BD |
| Median branch, primary bract length (cm) | 2PB |
| Median branch, internode length (cm) | 2IL |
| Median branch, flower number | 2FN |
| Distal branch, peduncle length (cm) | 3BL |
| Distal branch, rachis diameter (cm) | 3PB |
| Distal branch, primary bract length (cm) | 3BD |
| Distal branch, internode length (cm) | 3PB |
| Distal branch, flower number | 3IL |
| Distal branch, peduncle length (cm) | 3FN |
| Floral bract, length (cm) | FBL |
| Floral bract, width (cm) | FBW |
| Sepal, length (cm) | SPL |
| Sepal, width (cm) | SPW |
| Petal, length (cm) | PTL |
| Petal, width (cm) | PTL |
| Stamens, length (cm) | STL |
| Pistil, length (cm) | PSL |

The largest number of branches (Fig. 2D). Considering the length of the inflorescence median branch, RJ5 had the longest ones with the largest number of flowers, and BA1, the longest internodes (Table S3; Uribbe et al. 2020). In relation to the inflorescence distal branch, RJ5 also had the longest branch with the largest number of flowers (Table S3; Uribbe et al. 2020). The Ilha do Cardoso (SP1) and Caraíva (BA1) populations had the longest distal-branch internodes. Populations SP1 and PR had the longest distal-branch peduncle (Table S3; Uribbe et al. 2020).

All variables of the flowers differed significantly among populations. The Canoas (RJ1) population had the shortest and narrowest floral bracts (Fig. 2E, F) and the shortest sepals (Fig. 3A). Maricá (RJ6) had the widest sepals. Picinguaba (SP2), RJ1, Ilha do Cardoso (SP1), and Ilha do Mel (PR) had the shortest petals, while the Itaguará (ES3) population showed the longest ones (Fig. 3B). RJ1 had the narrowest petals. RJ1, SP1, SP2, and PR had the shortest stamens and pistil, while RJ6 and ES3 had the longest ones (Fig. 3C, D).

**Discriminant Analysis**—In the DA performed with all natural populations studied, the first two axes explained 64.6% of the variation between groups (46.71% and 17.9% respectively) (Table 4). Analysis of all populations combined showed that the null hypothesis must be rejected, and the type I error was accepted, with a separation into four distinct groups (Fig. 4). On Axis 1, the population at Canoas (RJ1) was clearly separate, with the most important variables being the number of branches, sepal length, and sepal width. Also on Axis 1, and segregated by the same variables that separated RJ1, was a second group, formed by the Ilha do Cardoso (SP1), Picinguaba (SP2), and Ilha do Mel (PR) populations.

The third group was formed by the Itaguará population (ES3), which differed in the number of branches, length of the proximal branch, and sepal width. The fourth group was formed by the remaining populations.
Fig. 2. Box-plots show the medians (small square), first and third quartiles (larger box), and minimum and maximum values of each variable. The H-value of the KW test of each variable and the value of p are given. A. Sheath width (SHW). B. Leaf-blade width (BLW). C. Total length of inflorescence (ITL). D. Number of branches (NMB). E. Floral-bract length (FBL). F. Floral-bract width (FBW).
Vriesea aureoramosa F.P.Uribbe & A.F.Costa, sp. nov. TYPE: Brazil, Espírito Santo, Itaguaçu, Pedra do Pontal, S 19°35’48” W 040°48’57”, 9 Mar 2013, F.P.Uribbe 188 (holotype: R!).

Vriesea aureoramosa is distinguished from V. procera (Mart. ex Schult. & Schult. f.) Wittm. by the yellow branches (vs. red), the petals strongly recurved (vs. suberect), and the stamens long-exserted (vs. short-exserted).
Table 4. Canonical coefficients derived from discriminant analysis, including all 14 populations of the Vriesea procera complex. Variables that most influenced the separation of groups are in bold. *Values that are outside the circle of contribution of variables (\(\sqrt{2} / n\) variables). Variable codes and names as in Table 3.

| Variables | Axis 1 | Axis 2 | Variables | Axis 1 | Axis 2 |
|-----------|--------|--------|-----------|--------|--------|
| SHW       | -0.13041 | -0.157745 | 2IL       | 0.11992 | 0.179017 |
| SFL       | 0.23033  | 0.151243 | 2FN       | 0.03312* | 0.127084 |
| BLW       | 0.21556  | 0.606514 | 3BL       | -0.23870 | -0.053898 |
| BLL       | 0.09763  | 0.071567 | 3PB       | -0.28369 | 0.048478 |
| ITL       | -0.20170 | 0.179514 | 3BD       | -0.08976 | 0.041629 |
| PDD       | 0.25592  | 0.507066 | 3IL       | 0.086758 | 0.040709 |
| PDL       | 0.09548  | -0.063000 | 3FN       | 0.31061 | 0.196961 |
| MIL       | -0.01322* | 0.160413 | FBL       | 0.39217 | 0.315632 |
| NMB       | -0.34079 | -0.985169 | FBW       | -0.13999 | 0.113006 |
| 1BL       | 0.13554  | -0.225125 | SPL       | -0.39814 | 0.000002* |
| 1PB       | 0.11484  | -0.033256* | SPW       | -0.30710 | -0.395401 |
| 1BD       | -0.07710 | -0.013512* | PTL       | 0.15774 | 0.032640 |
| 1IL       | -0.14797 | 0.120116 | PTW       | -0.03313* | 0.23496 |
| 1FN       | -0.20239 | 0.053190 | STL       | 0.63879 | 0.196891 |
| 2BL       | -0.06940 | -0.150547 | PSL       | 0.589838 | -0.623210 |
| 2PB       | 0.07254  | 0.167456 | Eigenvalues | 16.96108 | 6.508696 |
| 2BD       | -0.29563 | -0.027257* | Cum. Prop. | 0.46711 | 0.646354 |

Herb epiphytic or terrestrial. Rosette forming a tank, infundibuliflorum. Leaves recurved; sheath 9–17 × 5–7 cm, ovate, entirely pale brown or pale brown at base and green near the blade, densely lepidote on both surfaces; blade 17.8–30 × 5.5–8 cm, narrowly elliptic, apex obtuse, with acuminate projection, green, lepidote on both surfaces. Inflorescence 84–162 cm long, erect to suberect, with 5–14 branches, flowers lax; peduncle 38–74 × 0.3–0.7 cm, red, sparsely lepidote; peduncle bracts 11–18 cm long, narrowly elliptic, apex acute with acuminate projection, not leaf-like, lower bracts imbricate, red with green apex, the upper bracts longer or shorter than the internodes, imbricate or not, red, lepidote; branches 6.5–33.5 × 0.1–0.3 cm, suberect, bearing sterile bract on peduncle, yellow; rachis 46–88 cm long, straight, red, sparsely lepidote; primary bracts 2.4–8.5 cm long, longer or shorter than the peduncle of branches, ovate, apex acute with acuminate projection, red, lepidote; floral bracts 2.7–3.9 × 1.4–2.4 cm, shorter than the sepal, ovate, striate, slightly carinate, yellow, with a transparent and odorless mucilaginous substance inside. Flowers with anthesis diurnal, odorless, distichous, not secund; sepal 1.8–2.4 × 0.7–1 cm, oblong, apex obtuse, straight, carinate, free, pale yellow colored and sometimes slightly greenish, lepidote; petals 2.4–2.9 × 0.3–0.4 cm, linear, straight with apex obtuse or slightly recurved, pale yellow colored and sometimes lightly greenish, glabrous, basal appendages with free portion spatulate and apex entire; stamens 2–2.5 cm long, included, filaments filiform, anthers basifixed; ovary 0.4–0.6 cm long, pyramidal, green, smooth; stigma convolute-blade type. Fruits capsule brown. Figures 6, 7C, D.

Distribution and Habitat—Plant endemic to Espírito Santo State, occurring as an epiphyte on inselbergs at altitudes between 300 and 650 m a.s.l. Vriesea auroramosa has a restricted distribution and is presently known from two inselbergs in the state. The first of these, Morro da Torre de TV in the municipality of Itaúquacu, is the type locality. The other is the Pedra Lisa inselberg, district of Burarama, in the municipality of Cachoeiro do Itapemirim. The species blooms from January to March.

Individuals of V. auroramosa were abundant and frequent in the above-mentioned localities. The ES3 population (Table 2) represents the taxon in the morphometric analyses.

Eymology—The epithet “auroramosa” refers to the yellow color of the branches.

Notes—This species has a striking feature, the presence of yellow branches (red or green in other species of the complex), besides strongly recurved petals with long-exserted stamens (recurved petals with stamens included or short-exserted in the other species of the complex) (Figs. 6A, 7L, M).

Paratypes—Brazil. —Espírito Sán: Burarama, Pedro Lima, trilha da Via Sacra, 14 Mar 2013 (F), F.P.Uribbe et al. 198 (R); Itaúquacu: Pedra do Pontal, 19°35’48”S 40’48”57”W, 9 Mar 2013 (F), F.P.Uribbe 242, 243, 244 (R).

Vriesea flexuosa F.P.Uribbe & A.F.Costa, nom. nov., sta. nov. Replaced: Name: Vriesea procera var. tenuis L.B.Sm., Arq. Bot. Estado Sào Paulo 11. 1: 121.1943. Type: Brazil. São Paulo, Pirajussara, A.Gehrt & L.B.Smith 1820 (holotype: GH!, isotype: SP!).

Herb epiphytic or terrestrial. Rosette forming tank, infundibuliform. Leaves recurved; sheath 8.7–15 × 6–8.2 cm, elliptic, pale or brown at base and green near blade, sometimes with purple macules on both surfaces, lepidote; blade 11–25 × 2.5–4 cm, narrowly elliptic, apex obtuse with acuminate projection, green, sometimes with purple macules, densely lepidote on abaxial surface and sparsely on adaxial one. Inflorescence 76.2–132.8 cm long, suberect, with 8–18 branches, flowers lax; peduncle 30.4–45 × 0.4–0.7 cm, green, sparsely lepidote; peduncle bracts leaf-like, upper bracts 5–13.2 cm long, narrowly elliptic, longer or shorter than the internodes, imbricate or not, apex attenuate with acuminate projection; branches 7–34 × 0.1–0.4 cm, flexuous, patent or pendulous, bearing 1 to 3 sterile bracts on peduncle, green; rachis 45.8–87.8 cm long, straight, green; primary bracts 3.2–9.7 cm long, longer or shorter than the peduncle of branches, narrowly elliptic to ovate, apex attenuate with acuminate projection, green, lepidote; floral bracts 1.6–2.2 × 1–1.6 cm, shorter than the sepals, ovate, striate, slightly carinate, green, with a transparent and odorless mucilaginous substance inside. Flowers with anthesis diurnal, odorless, distichous, not secund; sepal 1.8–2.4 × 0.7–1 cm, oblong, apex obtuse, straight, carinate, free, pale yellow colored and sometimes slightly greenish, lepidote; petals 2.4–2.9 × 0.3–0.4 cm, linear, straight with apex obtuse or slightly recurved, pale yellow colored and sometimes slightly greenish, glabrous, basal appendages with free portion spatulate and apex entire; stamens 2–2.5 cm long, included, filaments filiform, anthers basifixed; ovary 0.4–0.6 cm long, pyramidal, green, smooth; stigma convolute-blade type.

Fruits capsule brown. Figures 6, 7C, D.

Distribution and Habitat—Plant endemic to the Atlantic Rainforest in the states of Bahia, Espírito Santo, Rio de Janeiro, and São Paulo. Vriesea flexuosa is found in low-montane and montane forests, and blooms from January to March.

The population of Canoas (RJ1) (Table 2) represents the taxon in the morphometric analyses.

Eymology—The epithet “flexuosa” refers to the delicate flexuous branches.

Notes—Vriesea flexuosa was described as V. procera var. tenuis but has a very particular combination of floral characteristics. The sepals (1.8–2.4 × 0.7–1 cm) and petals (2.4–2.9 × 0.3–0.4 cm) are much smaller than in V. procera (2.3–3.3 × 1.3–2.4 cm and 3.4–4.3 × 0.4–0.6 cm, respectively) (Figs. 3A, B, 6C, D, 7B, D). The petals are pale yellow colored and sometimes slightly greenish (vs. yellow) and linear with a suberect and obtuse apex (vs. linear with a
slightly curved and rounded apex) (Fig. 7B, D). In addition, it has a green peduncle, rachis, and bracts (vs. red, reddish, or yellow in the other taxa of the complex) and pale yellow colored and sometimes slightly greenish flowers (vs. yellow in other taxa of the complex) (Fig. 7A, C). This set of characteristics supports raising *V. flexuosa* to species rank. The name *Vriesea tenuis* Mez was previously described (Mez 1934–1935), so the epithet "tenuis" cannot be used at the species level.

Representative Specimens—Brazil. —BAHIA: Uruçucu: Cabrucu, 6 Feb 2000 (fl), Costa et al. 757 (R). —ESPIRITO SANTO: Castelo: Trilha para o mirante, Floresta Ombrófila Densa altamontana, inselberges, S 20°31’00” W 041°05’15”, 8 Apr 2009 (fl), Kollmann 11502 (MBML). —RIO DE JANEIRO: Estrada Rio-Itaipava, 600 msm, 20 Jan 1963 (fr), Pabst 7239 (HB). Nova Friburgo: Macaé de Cima, fazenda Ouro Verde, 18 Jul 1993 (fr), Vieira 312 (RB). Rio de Janeiro: Serra da Estrela, 12 Feb 1980 (fl), Penna 1981 (HB); Serra da Estrela-Araras, 29 Jan 1968 (fl), Perina 10672 (HB). Teresópolis: Canoas, área degradada, 17 Feb 1997 (fl), Costa et al. 693 (R); Canoas, área degradada, 10 Feb 1997 (fl), Costa et al. 692 (R). Canoas, propriedade particular, 22°24’05”S 42°53’10”W, 5 Jan 2012 (fl), Uribbe et al. 25 (R); Canoas, propriedade particular, 22°24’05”S 42°53’10”W, 5 Jan 2012 (fl), Uribbe et al. 34 (R). Canoas, propriedade particular, 22°24’05”S 042°53’10”W, 18 Mar 2013 (fl), Uribbe et al. 181 (R). —SÃO PAULO: at Estacion Florestal, 15 Aug 1939 (fr), Foster 352 (R). Pirajuízara: sobre Iaranjera, 3 Feb 1929 (fr), Gehrt s.n. (SP 24580).

*Vriesea magna* F.P. Uribbe & A.F. Costa, sp. nov. **Type**: BRAZIL. Rio de Janeiro: Angra dos Reis, Ilha Grande, Parque Estadual da Ilha Grande, Restinga de Lopes Mendes, 23°09’56”S 44°08’20”W, 16 Apr 2013, F.P. Uribbe 190 & B. Neves (holotype: R!).

*Vriesea magna* is distinguished from *Vriesea procera* (Mart. ex Schult. & Schult. f.) Wittm. by the longer (12.8–31.7 cm vs. 12.8–67.5 cm) and wider (6.3–12.8 cm vs. 3–6.5 cm) leaf blades; the longer inflorescence (137–247 cm vs. 70–210 cm); more numerous (7–22 vs. 3–17) and longer branches (13.5–52.4 cm vs. 8–54 cm); floral bracts entirely yellow (vs. red); stamens short-exserted and petals straight with suberect apex (vs. slightly recurved).

*Herb* epiphytic or terrestrial. **Rosette** forming a tank, infundibuliform. **Leaves** recurved; sheath 12.8–31.7 × 6.3–12.8 cm, ovate, pale brown or brown at base and green near the blade, lepidote on both surfaces; blade 17.8–30 × 5.5–8 cm, narrowly elliptic, apex obtuse with acuminate projection, green, sparsely lepidote on the abaxial surface and dense on the adaxial one. **Inflorescence** 137–247 cm long, suberect, with 7–22 branches, flowers lax; peduncle 71–145 × 0.8–1.5 cm, red, glabrous; lower peduncle bracts leaf-like and the upper ones 5–23 cm long, ovate, acuminate apex, red with greenish apex, longer or shorter than the internode, imbricate or not, sparsely lepidote on the abaxial surface and dense on the adaxial one; branches 13.5–52.4 × 0.2–0.3 cm, suberect to pendulous, bearing sterile bracts on the peduncle, red, sparsely lepidote, peduncle with sterile bracts; rachis 66–102 cm long, straight, red, glabrous; primary bracts 2.7–14 cm long, shorter than the branch peduncles, ovate to narrowly elliptic, attenuate apex, red, sparsely lepidote on the abaxial surface and dense on the adaxial one; floral bracts 2.7–3.9 × 1.5–2.6 cm, shorter than the sepals, ovate, striate, carinate, involute, yellow, with a transparent, slightly curved and rounded apex) (Fig. 7B, D). In addition, it has a green peduncle, rachis, and bracts (vs. red, reddish, or yellow in the other taxa of the complex) and pale yellow colored and sometimes slightly greenish flowers (vs. yellow in other taxa of the complex) (Fig. 7A, C). This set of characteristics supports raising *V. flexuosa* to species rank. The name *Vriesea tenuis* Mez was previously described (Mez 1934–1935), so the epithet “tenuis” cannot be used at the species level.

**Representative Specimens**—Brazil. —BAHIA: Uruçucu: Cabrucu, 6 Feb 2000 (fl), Costa et al. 757 (R). —BAHIA: Uruçucu: Cabrucu, 6 Feb 2000 (fl), Costa et al. 757 (R). —ESPIRITO SANTO: Castelo: Trilha para o mirante, Floresta Ombrófila Densa altamontana, inselberges, S 20°31’00” W 041°05’15”, 8 Apr 2009 (fl), Kollmann 11502 (MBML). — RIO DE JANEIRO: Estrada Rio-Itaipava, 600 msm, 20 Jan 1963 (fr), Pabst 7239 (HB). Nova Friburgo: Macaé de Cima, fazenda Ouro Verde, 18 Jul 1993 (fr), Vieira 312 (RB). Rio de Janeiro: Serra da Estrela, 12 Feb 1980 (fl), Penna 1981 (HB); Serra da Estrela-Araras, 29 Jan 1968 (fl), Perina 10672 (HB). Teresópolis: Canoas, área degradada, 17 Feb 1997 (fl), Costa et al. 693 (R); Canoas, área degradada, 10 Feb 1997 (fl), Costa et al. 692 (R). Canoas, propriedade particular, 22°24’05”S 42°53’10”W, 5 Jan 2012 (fl), Uribbe et al. 25 (R); Canoas, propriedade particular, 22°24’05”S 42°53’10”W, 5 Jan 2012 (fl), Uribbe et al. 34 (R). Canoas, propriedade particular, 22°24’05”S 042°53’10”W, 18 Mar 2013 (fl), Uribbe et al. 181 (R). —SÃO PAULO: at Estacion Florestal, 15 Aug 1939 (fr), Foster 352 (R). Pirajuízara: sobre Iaranjera, 3 Feb 1929 (fr), Gehrt s.n. (SP 24580).
Variables that most influenced the separation of groups are in bold. ∗Values that are outside the contribution circle of the variables (y/2 / n variables). Codes and names of variables as in Table 3.

| Variables | Axis 1 | Axis 2 | Variables | Axis 1 | Axis 2 |
|-----------|--------|--------|-----------|--------|--------|
| SHW       | 0.316841 | 0.164437 | 2IL       | 0.055480 | -0.002771* |
| SHL       | 0.226501 | -0.106949 | 2FN       | -0.056179 | -0.094110 |
| BLW       | 0.631962 | -0.347409 | 3BL       | -0.095550 | -0.463086 |
| BLL       | -0.002699* | -0.029587* | 3PB       | 0.217598 | 0.052318 |
| ITL       | -0.360372 | -0.661068 | 3BD       | -0.276085 | -0.004353* |
| PDD       | 0.533713 | -0.283312 | 3IL       | -0.166053 | 0.033231* |
| PDL       | 0.398334 | 0.196546 | 3FN       | 0.138775 | 0.043128 |
| MIL       | -0.584642 | 0.142812 | FBL       | -0.028527* | -0.023086* |
| NMB       | 0.130745 | 0.611956 | FBW       | 0.050640 | -0.194421 |
| 1BL       | 0.839514 | 0.313034 | SPL       | 0.053645 | -0.137122 |
| 1PB       | -0.477458 | 0.078271 | SPW       | -0.121808 | 0.409319 |
| 1BD       | 0.050724 | -0.043791 | PTL       | -0.336673 | -0.605247 |
| 1IL       | -0.048464 | -0.245761 | PTW       | 0.062199 | -0.002521* |
| 1FN       | -0.730277 | -0.057955 | STL       | 0.094163 | 0.070296 |
| 2BL       | 0.579912 | 0.452156 | PSL       | 0.471143 | 0.948885 |
| 2PB       | -0.435531 | -0.114582 | Eigenvalues | 5.347232 | 4.941954 |
| 2BD       | 0.121225 | 0.014731* | Cum. Prop. | 0.266830 | 0.513436 |

odorless and mucilaginous substance inside. Flowers with diurnal anthesis, odorless, distichous, not secund; sepalas 1.9–3.1 × 0.7–1. cm, narrowly elliptic, apex obtuse, straight, carinate, free, yellow, lepidote; petals 3–4 × 0.5–0.6 cm, ob lanceolate, straight with suberect apex, yellow, glabrous, basal appendages with free portion spatulate and entire apex; stamens 3.3–3.8 cm long, short-exserted, filaments filiform, anthers basified; ovary 0.9–1. cm long, pyramidal, yellow; stigma convolute-blade type. Fruits capsule, brown. Figures 6, 7G, H.

**Distribution and Habitat**—Plant endemic to Rio de Janeiro State. In some restinga areas, it occurs in sympatry with populations of *V. procera*, preferentially in open shrubby vegetation, blooming from October to January, and fruiting all year round.

**Etymology**—The epithet “magna” refers to the large dimensions of the plant.

**Notes**—*Vriesea magna* is closely related to *V. procera*, but the former differs mainly by inflorescence size (longer in *V. magna*; Fig. 2C) and by floral bracts color (yellow vs. red). In addition, the position of the stamens during the anthesis (very little exerted vs. exerted) and longitudinal posture of the petal (suberect vs. slightly recurved) also distinguish the two taxa (Fig. 7B, H). In relation to vegetative characters, *V. magna* has leaves much longer and broader than *V. procera* (Fig. 7A, G).

**Paratypes**—Brazil. —RIO DE JANEIRO: Angra dos Reis, Ilha Grande, Parque Estadual da Ilha Grande, Restinga de Lopes Mendes, 23°09’S 44°08’W, 16 Apr 2013, fl., F.P. Urribbe et al. 240, 241 (R); Ilha Grande, Vila Dois Rios. 17 May 1996, fr., A.F.Costa 641 (R).

**Vriesea neoglutinosa** Mez Engler, Pflanzenz. IV. Fam. 32: 636.1935; *Tillanádia glutinosa* Mart. ex Schult. & Schult. f. in Roemer & Schultes, Syst. Veg. 7(2): 1225. 1890; *Vriesea glutinosa* (Mart. ex Schult. & Schult. f.) Wawra, It. Sax.-Cob. 167. 1883; non Lindley, 1856. Type: BRAZIL. Guanabara, Rio de Janeiro, Botafogo, Martius s.n. (holotype: M, GH [photo]).

**Herb** epiphytic, terrestrial or rupiculous. **Rosette** forming a tank, infundibuliform. **Leaves** suberect; sheath 12.5–17.8 × 7.7–10.6 cm, elliptic, pale brown at base and green near the blade, densely lepidote on both surfaces; blade 19.5–39.7 × 4.3–5.7 cm, triangular, apex acute, with acuminate projection, membranous, green, densely lepidote on the abaxial surface and sparsely on the adaxial one. **Inflorescence** 77.6–178.7 cm long, suberect to pendulous, with 5–14 branches, flowers lax; peduncle 71–145 × 0.8–1.5 cm, red, glabrous; lower peduncle bracts leaf-like, median and upper ones 5.9–13.1 cm long, lanceolate, apex attenuate with acuminate projection, red with apex green, upper ones red, longer or shorter than the internode, lower ones imbricate, upper ones imbricate or not, sparsely lepidote; branches 11.8–46.6 × 0.2–0.3 cm, suberect, bearing sterile bracts on the peduncle, red, sparsely lepidote; rachis 41.9–91.7 cm long, straight, red, sparsely lepidote; primary bracts 2.9–8.5 cm, shorter than the peduncle of branch, narrowly elliptic to ovate, apex attenuate, red, lepidote sparsely; floral bract 2.8–3.6 × 1.4–2.6 cm, shorter than the sepals, ovate, striate, slightly carinate, red sometimes with yellow apex, with a transparent andodorless mucilaginous substance inside.

**Flowers** with anthesis diurnal, odorless, distichous, not secund; sepalas 2–3 × 0.6–1.3 cm, ovate, apex acuminate, straight, entire, carinate, free, yellow, sparsely lepidote; petals 3.2–3.8 × 0.4–0.7 cm, ob lanceolate, straight with apex acute strongly recurvate, yellow, glabrous, basal appendages with free portion spatulate and entire apex; stamens 3.6–4.9 cm long, exerted, filaments filiform, anthers basified; ovary pyramidal; stigma convolute-blade type. **Fruits** capsule brown. Figures 6, 7E, F.

**Distribution and Habitat**—Initially, according to BFG (2015), the *V. neoglutinosa* geographic distribution extends from the states of Bahia to Santa Catarina. Our study showed that *V. neoglutinosa* is endemic to the restingas and inselbergs near the sea, in Rio de Janeiro State. In some restinga areas, it occurs in sympathy with populations of *V. procera*, preferentially in open shrubby vegetation, blooming from October to January, and fruiting all year round.

The individuals of the species were abundant and frequent in all the localities visited. The taxon is represented in the morphometric analyses as the RJ6 population (Table 2).
Etymology—Vriesea neoglutinosa is a new name given by Mez (1894) when he transferred Tillandsia glutinosa Mart. to Vriesea. The new name was necessary because the epithet “glutinosa” already in use for in Vriesea glutinosa Lindl., a species from Trinidad (Smith and Downs 1977).

Notes—Vriesea neoglutinosa was described from a specimen collected by Martius in Botafogo, city of Rio de Janeiro, probably on an inselberg or in a restinga area. It was found with only pre-anthesis flower buds, a stage when all the morphologically related species are very similar, resulting in an unclear circumscription. Our description is based on individuals observed in the field, whose characteristics were similar to those observed in individuals from the type locality. This species is very close to V. procera and is often confused with it. Its main differences are the position of the leaves (suberect vs. recurved, Fig. 7E, A, respectively), posture of the petals (strongly recurved vs. slightly recurved), and position of the stamens during the anthesis (more exserted in V. neoglutinosa) (Figs. 6A, 7B, F). Differentiation of the two species is especially difficult in herbarium material, since the main differences are lost. Therefore, it is essential to provide detailed characterization on the specimen labels.

Representative Specimens—Brazil.—RIO DE JANEIRO: (Araruama); Restinga entre a lagoa de Araruama e a Praia de Massambaba de 0 a 10 msnm, 11 Jul 1979 (fl), Barbosa et al. 2 (RB). (Arraial do Cabo), Reserva Ecológica de Massambaba, restinga arbustiva aberta, cordão interno de restinga, próximo a Lagoa Salgada, 25 Oct 1993 (fl), Fontella et al. 3104 (SP). (Maricá), Restinga de Maricá, APA Maricá 22°57’55”S 42°53’40”W, nível do mar, 1 Feb 2012 (fl), Uribe 238 (R). (São José), Restinga da Jacarepiá, 10 Mar 2013 (fl), Uribe 185 (R).

VRIESEA PROCERA (Mart. ex Schult. & Schult. f.) Wittm., Bot. Jahrb. 13 (Beibl. 29): 21. 1891. Tillandsia procera Mart. ex Schult. & Schult. f. in Roemer & Schultes, Syst. Veg. 7(2): 1224. 1830. TYPE: BRAZIL. Bahia, Rio Itaipé, Martius s.n. (holotype: M!; fragment: B!).

Tillandsia gracilis Gaudich., Atl. Voy. Bonite pl. 67. 1843; Tillandsia gracilis (Gaudich.) Griseb., Nachr. Ges. Wiss. Gött."1864"; 17. 1865; Vriesea procera var. gracilis (Gaudich.) Mez in Mart., Eichl. & Urban, Fl. bras. 3(3): 540. 1894. TYPE: BRAZIL. Rio de Janeiro, Guanabara, Gaudichaud 365 (holotype: P!, GH [photo]), 1831–33.

Tillandsia erectiflora Baker, Jour. Bot. London 25: 346. 1887. TYPE: BRAZIL. Boog s.n. (holotype: K!, GH [photo]).

Tillandsia viscidula Britton, Bull. Torrey Club 48: 328. 1894. TYPE: TRINIDAD. Moruga, Britton & Broadway 2430 (holotype: NY, isotypes: K, TRIN!).

Vriesea procera var. debilis Mez in Mart., Eichl. & Urban, Fl. bras. 3(3): 540.1894. TYPE: BRAZIL. Rio de Janeiro: Rio de Janeiro, Mikan s.n. (holotype: W!), syn. nov.
Vriesea procera var. rubra L.B.Sm., Arq. Bot. Estado São Paulo II.2: 197. 1952. TYPE: BRAZIL. Espírito Santo, Itapemirim, 08 Jul 1939, Foster & Foster 166 (holotype: US!, isotype: GH!), syn. nov.

Vriesea graciliscapa Weber, Feddes Repert. Sp. Nov. Regni Veg. 97(3–4): 104. 1986. TYPE: BRAZIL. Bahia: Ilhéus, Seidel 939 (holotype: HAL!). syn. nov.

**Herb** epiphytic or terrestrial. **Rosette** forming a tank, infundibuliform. **Leaves** recurved; sheath 8–21 × 5–16 cm, elliptic, pale brown or brown at base and green near the blade, may have purple macules on both surfaces, lepidote; blade 12.8–67.5 × 3–6.5 cm, narrowly elliptic, apex obtuse with acuminate projection, green, sometimes yellowish, densely lepidote on abaxial surface and sparsely on adaxial one.

Fig. 6. Floral details of species of the *V. procera* complex. A. Flower with floral bract. B. Floral bracts. C. Sepals. D. Petals and stamens. E. Petal appendages. F. Stigma.
Inflorescence 70–210 cm long, suberect, with 3–17 branches, flowers lax; peduncle 33–110 × 0.4–1 cm, red, sparsely lepidote; lower peduncle bracts leaf-like and upper ones 3.9–18.9 cm long, ovate, apex obtuse with acuminate projection, longer or shorter than the internodes, imbricate or not, red, sometimes with green apex, lepidote; branches 8–54 × 0.1–0.4 cm, pendulous, bearing sterile bract on peduncle, red; rachis 37–100 cm long, straight, red, sparsely lepidote; primary bracts 2.3–6.9 cm long, longer than branches of peduncles, elliptic or ovate, apex obtuse with acuminate projection, red, lepidote; floral bracts 2.2–4.1 × 1.3–2.4 cm, shorter than the sepal, ovate, striate, slightly carinate, red with yellow apex or entirely red, with a transparent and odorless mucilaginous substance inside. Flowers with anthesis diurnal, odorless, distichous, not secund; sepals 2–3.3 × 0.5–1.1 cm, oblong, apex obtuse, straight, entire, slightly carinate, free, yellow, lepidote; petals 3–4.3 × 0.4–0.6 cm, linear, straight with apex rounded and slightly recurved, yellow, glabrous, basal appendages with free portion spatulate and apex entire; stamens 3.1–4.4 cm long, exserted, filaments filiform, anthers basifixed; ovary 0.6–0.7 cm long, pyramidal, red; stigma convolute-blade type. Fruits capsule brown.

**Distribution and Habitat**—Venezuela, Guyana, Suriname, Trinidad, Argentina, and Brazil (Smith and Downs 1977; Martinelli et al. 2008). Initially, according to BFG (2015), the geographic distribution of *V. procera* in Brazil was given as from the states of Piauí to Rio Grande do Sul. After our study, it was evident that *V. procera* is found in restingas and lower montane and montane forests in the states of Bahia, Espirito Santo, Rio de Janeiro, and Minas Gerais. Although the occurrence of *V. procera* for the states of Piauí and Ceará is indicated in the literature (Smith and Downs 1977; BFG 2015), no record was found in the herbaria visited nor during the field work. Its blooming period is from January to March and fruiting year-round. In the restingas of Rio de Janeiro State, the species occurs in sympathy with *V. neoglutinosa*, preferentially in shaded areas. In the restinga of Maricá, its flowering period begins shortly after the

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**Fig. 7.** Habits of the species of the *Vriesea procera* complex in their natural habitats. A–B. *V. procera*. A. Habit. B. Flower. C–D. *V. flexuosa*. C. Habit. D. Flower. E–F. *V. neoglutinosa*. E. Habit. F. Flower. G–H. *V. magna*. G. Habit. H. Flower. J–I. *V. rubrovidis*. I. Habit. J. Flower. L–M. *V. aureoramosa*. L. Habit. M. Flower. Photographs: F. P. Uribbe.
flowering period of *V. neoglutinosa*, and no hybrid was detected (Suizani 2014).

Individuals of the species were abundant and frequent in all the localities visited during the present collections. The populations of Caraiva (BA1), Ilamaraju (BA2), Fau Amarelo (ES1), Água Viva (ES2), and Jacarepá (RJ3 and RJ4) (Table 2) represent the taxon in the morphometric analyses performed here. The population of Ilamaraju is the most morphologically and geographically close to the type population (Fig. 1; Tables 1, 2).

*Vriesea procera* may have a terrestrial habit but is more commonly found as an epiphyte.

**Etymology**—The epithet “procera” from the Latin adjective “procerus” meaning very tall (Steam 1973), refers to the length of the inflorescence.

**Notes**—*Vriesea procera* was described from a fruiting specimen, making its circumscription complex and unclear. *Vriesea procera* is a very polymorphic species, usually with branched inflorescences of varying sizes. However, individuals with simple inflorescences were frequently observed in the populations visited. The specimens of *V. graciliscapa* and *V. procera* var. rubra and *V. procera* var. debilis show a pattern of variation matching that of *V. procera*, so all three taxa should be better regarded as belonging to a single biological entity and should be included in synonymy.

The morphologically closest species is *V. neoglutinosa*, which is often confused with this taxon. Its main differences are the position of the leaves (recurved vs. suberect, Figs. 7A, E, respectively), the posture of the petals (slightly recurved vs. strongly recurved) and stamens during anthesis (little exerted vs. long-exserted) (Figs. 3C, D, 6A, 7B, F).

**Representative Specimens**—Brazil.—BAHIA: (Ilhéus), Ceplac, Quadra “D” [39.228883, -14.778489], 13 Aug 2012 (F), Uribbe et al. 55 (R). (Porto Seguro), Parque Nacional Histórico do Monte Pascoal, 16°53′39″S 39°24′35″W, 9 Aug 2012 (F), Uribbe et al. 49 (R).—ESPERITO SANTO: (Cariacica), Pau Amarelo, Reserva Biológica de Duas Bocas, 20°16′46″S, 46°32′43″W, 10 Mar 2013 (F), Uribbe 184 (R). (Linhares), Restinga de Água Viva, 19°13′46″S 39°42′50″W, 6 Mar 2013 (F), Uribbe 187 (R).—RIO DE JANEIRO: (Maricá), Área de Proteção Ambiental de Maricá, 22°57′87″S 42°53′79″W, 1 Feb 2012 (F), Uribbe et al. 29 (R) .(Área de Proteção Ambiental de Maricá, 22°57′87″S 42°53′79″W, 1 Feb 2012 (F), Uribbe et al. 30 (R). (Teresópolis), Canoas, 22°24′05″S 42°53′10″W, 18 Mar 2013 (F), Uribbe et al. 182 (R).

*Vriesea rubroviridis* F.P.Uribbe & A.F.Costa, sp. nov. **Type** Brazil. Paraná, Paranaguaná, Ilha do Mel, Parque Estadual da Ilha do Mel, 25°34′12″S 48°18′37″W, 21 Feb 2014, F.P.Uribbe 228 & S.S.A.Jacques (holotype: R!)

*Vriesea rubroviridis* is distinguished from *V. flexuosa* F.P.Uribbe & A.F.Costa by the erect to suberect branches (vs. patent or pendulous), peduncle and branches green and sometimes reddish (vs. green), primary and floral bracts reddish with green apex (vs. green), sepalts and petals longer (2.2–2.8 cm and 2.7–3.4 cm, respectively) and yellowish green (vs. pale yellow colored and sometimes slightly greenish). **Herb** epiphytic or terrestrial. **Rosette** forming a tank, infundibuliform. **Leaves** recurved; sheath 8.5–18.8 × 6.5–10.5 cm, elliptic to ovate, pale at base and green near the blade, densely lepidote on both surfaces; blade 13–42.8 × 3.3–4.8 cm, narrowly elliptic, apex obtuse with acuminate projection, green, densely lepidote on abaxial surface and sparsely on adaxial one. **Inflorescence** 63.3–183 cm long, erect to suberect, with 3–12 branches, flowers lax; peduncle 39.5–106 × 0.4–0.9 cm, green and sometimes reddish blurred, glabrous; lower peduncle bracts leaf-like and upper ones 3.8–12.3 cm long, ovate, apex acuminate, slightly reddish with green apex, longer than the internodes or not, imbricate or not, sparsely lepidote on abaxial surface and densely on adaxial one; branches 9–39.5 × 0.1–0.3 cm, suberect, bearing 1 to 3 sterile bracts on peduncle, green; rachis 23.8–77 cm long, straight, green or slightly reddish, glabrous; primary bracts 2.5–6.5 cm long, shorter than the peduncle of branches, narrowly ovate, apex obtuse with acuminate projection, green, lepidote; floral bracts 2.5–3.3 × 1.3–1.7 cm, shorter than the sepalts, ovate, striate, membranous, carinate, reddish with green apex, with a transparent and odorless mucilaginous substance inside. **Flowers** with anthesis diurnal, odorless, distichous, secund; sepalts 2.2–2.8 × 0.6–0.9 cm, obovate, apex acuminate, straight, carinate, free, yellowish green, sparsely lepidote; petals 2.7–3.4 × 0.4–0.6 cm, narrowly elliptic, straight with suberect rounded apex, yellowish green, glabrous, basal appendages with free portion spatulate and apex entire; stamens 2.4–3.1 cm long, included, filaments filiform, anthers basifixed; ovary pyramidal, green, smooth; stigma convolute-blade type. **Fruits** capsule brown. Figures 6, 7J.

**Distribution and Habitat**—Plant endemic to the Atlantic Rainforest in the states of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul. Found in restingas and lower montane and montane forests, the species blooms from January to March and fruits year-round. Individuals of *V. rubroviridis* were abundant and frequent in all the localities visited. The SP2, SP1, and PR populations (Table 2) represent the taxon in the morphometric analyses. The population from Torres, state of Rio Grande do Sul, was not included in the morphometric analyses due the presence of only few flowering individuals found during the field work.

**Etymology**—The epithet “rubroviridis” refers to the green to pale-red blured peduncle and rachis, and the base of the peduncle bracts, primary bracts, and floral bracts.

**Notes**—*Vriesea rubroviridis* is distinguished from the remaining taxa of the complex by its smaller flowers, almost erect petals, and stamens clearly included (Figs. 6A, D, 7J). It has a pale-red blurred peduncle and bracts (vs. green in *V. flexuosa*), branches suberect (vs. patent to pendulous in *V. flexuosa*) (Figs. 7I, C, respectively), and yellow sepalts and petals (vs. sepalts and pale yellow colored and sometimes slightly greenish petals in *V. flexuosa*) (Fig. 7J, D, respectively).

**Paratypes**—Brazil.—SÃO PAULO: Cananéia: Ilha do Cardoso, Parque Estadual da Ilha do Cardoso, 23 Feb 2014 (F), F.P.Uribbe et al. 248 (R). Ubatuha: Picinguaba, Parque Estadual da Serra do Mar, Estrada da Casa da Farinha, 26 Feb 2014 (F), F.P.Uribbe et al. 230 (R).—PARANÁ: Paranaguaná: Ilha do Mel, Parque Estadual da Ilha do Mel, 25°34′12″S 48°18′37″W, 21 Feb 2014 (F), F.P.Uribbe et al. 245 (R).—RS: Torres, Parque Estadual de Itapeva, Triilha do Morro de Itapeva, 19 Feb 2014 (F), F.P.Uribbe et al. 222 (R).

**Excluded Name**—*Vriesea catharinensis* F. Müller, Gartenflora 42:738. 1893. **Type**: BRAZIL: Santa Catarina, Blumenau, F. Müller s.n.

*Vriesea catharinensis* F. Müller was for a long time assigned as a synonym of *V. procera* (Mez 1934–1935; Smith 1955; Smith and Downs 1977). However, no original material was found and no illustration is available. In the protologue, Müller (1893) described a plant with several stolons, which is the only information on its morphology. As this structure is absent in *V. procera*, we inferred that *V. catharinensis* is likely a plant related to *V. vagans* (L.B.Sm.) L.B.Sm., a very common species in the Atlantic Rainforest remnants in southern Brazil.

**Discussion**

The distinction between *V. neoglutinosa* and *V. procera* has long been doubtful, and consequently erroneous determinations and citations are common in the literature (Smith and
The present morphometric analyses performed with natural populations allowed us to recognize six species: *V. procera*, *V. neoglutinosa*, *V. magna*, *V. aureoramosa*, *V. flexuosa*, and *V. rubroviridis*. The new species emerged from the morphological variation in taxa that have existed under the names *V. procera* and *V. neoglutinosa*. The resulting taxa are distinguished by their inflorescences and leaf sizes, and especially by floral characters such as the length of bracts, sepals, petals, stamens, and pistils, besides the petal apex posture and the relative position of the stamens during anthesis. Recognition of cryptic species under the names *V. procera* and *V. neoglutinosa* is an important step toward a better understanding of the biodiversity of the Brazilian Atlantic Rainforest.

The morphometric analyses provided clear geographical distributions for most species of the complex. The results indicated a separation of the populations into two large groups along the Atlantic Rainforest: the first one from the latitude S 25° towards the south, between the states of São Paulo to Rio Grande do Sul (*V. rubroviridis* and *V. flexuosa*), and the second one from the latitude S 22° towards the north between the states of Rio de Janeiro and Bahia (*V. procera*, *V. flexuosa*, *V. neoglutinosa*, *V. magna*, and *V. aureoramosa*). Populations of other *Vriesea* species showed a north-south genetic discontinuity in the Atlantic Rainforest (*V. carinata*, Zanella 2013; and *V. gigantea*, Palma-Silva et al. 2009), as do other groups of plants and animals (Harris et al. 2005; Pellegrino et al. 2005; Grazziotin et al. 2006; Cabanne et al. 2007; Carnaval et al. 2009; Fitzpatrick et al. 2009; Pinheiro et al. 2011; Ribeiro et al. 2011). This phytogeographic division is explained by the hypothesis of Pleistocene refugia, where species survived isolated in favorable environments along the coast. In the Quaternary, climate oscillations during the Pleistocene caused changes in sea levels and expansions and contractions in forest areas, influencing the vegetation type and distribution of the species in the coastal region of Brazil. After the Last Glacial Maximum, with the increases in temperature and precipitation, the Atlantic Rainforest expanded toward the south. The northern-most areas appear to have remained stable during the climate oscillations; the present-day northern populations are older and the southern populations more recent (Haffer 1969; Vanzolini and Williams 1981; Rull 2006; Carnaval et al. 2009).

Phylogenetic and biogeographical hypotheses on Tillandsioideae showed the monophyly of the Brazilian lineage of *Vriesae* (Barfuss et al. 2016; Gomes-da-Silva and Souza-Chies 2017; Kessous et al. 2019), encompassing about 90% of the species of the genus. The Amazonian, Caribbean, and Central American species were poorly sampled and their relationships with the Brazilian lineage remain unknown. The occurrence of widely distributed species (e.g. *V. procera*, *V. simplex* (Vell.) Beer, *V. tectorum* Antoine) suggests the importance of the inclusion of extra-Brazilian accessions in phylogenies with molecular data in order to infer if these species were dispersed from the Atlantic Rainforest and Cerrado domains, or if they are the result of morphological convergence. Besides, the phylogenies proposed so far for *Vriesae* have failed to delineate natural infrageneric groups (Costa et al. 2015; Gomes-da-Silva and Souza-Chies 2017). On the other hand, some small groups of morphologically similar species were recovered, especially among species with simple inflorescences (e.g. Gomes-da-Silva and Souza-Chies 2017). The compound inflorescence species complexes like those related to *V. procera*, *V. friburgenensis* Mez, and *V. morrenii* Wawra, to mention just a few examples, are poorly sampled in the phylogenies, and lack studies that address their processes of diversification and speciation. Therefore, the species morphologically circumscribed in the present study are interesting hypotheses to be tested in the future from a phylogenetic, phylogeographic, and reproductive perspective.

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**Author Contributions**

FPU and AFC conceived the ideas. FPU, BN, and SSAJ collected the data. FPU, BN, SSAJ, and AFC analyzed data. FPU and AFC provided the taxonomic treatment. All the authors contributed to the discussion and writing.

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