



## *Paepalanthus* (Eriocaulaceae) without scapes and spathes, a survey with the description of a new species

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### Abstract

Eriocaulaceae are mainly characterized by their unisexual flowers arranged in capituliform inflorescences at the apex of scapes surrounded by closed spathes. The lack of the scapes and spathes is a rare condition in the family, restricted to a small number of species in *Eriocaulon*, *Paepalanthus*, and *Syngonanthus*. In this manuscript we explore the species of *Paepalanthus* lacking spathes and scapes based on morphological and molecular data (ITS, *trnL-trnF*, and *psbA-trnH*). The specimens with dimerous flowers form a monophyletic group represented by the only two species of *P.* subg. *Thelxinoë*. The accessions with trimerous flowers cluster with species of the polyphyletic *P.* ser. *Leptocephali*. As expected, the ancestral character reconstruction indicates that the loss of scapes and spathes occurred at least twice in *Paepalanthus*, but probably occurred four to five times in the family. Based on molecular data, SEM images, and morphological analysis, most of the specimens lacking scapes were assigned to previously described species with the exception of the trimerous-flowered specimens treated here as a new species, *P. paganuccii*. Besides the full treatment for this new species, we provide an annotated checklist for all *Paepalanthus* species without scapes, with nomenclatural novelties, a distribution map, illustrations, photos, and a comparative table.

**Keywords:** Bahia, *campo rupestre*, Minas Gerais, *Paepalanthus paganuccii*, phylogenetic analysis, systematics

### Introduction

Eriocaulaceae comprises 1,400 species distributed in 10 genera with mainly pantropical distribution. It has been recovered as monophyletic in all studies thus far, either morphological or phylogenetic. The main synapomorphies of the family are shared by more than 95% of the species, these being the unisexual flowers arranged in capituliform inflorescences at the apex of scapes surrounded by a closed spathe, and the spiroaperturate pollen grains (Stützel 1998, Giulietti *et al.* 2000, 2012a, Borges *et al.* 2009, Andrade *et al.* 2010, Trovó *et al.* 2013, Andrino *et al.* 2021).

The absence of scapes is usually accompanied by the absence of spathes, resulting in sessile capitula that are, more rarely, also accompanied by the absence of involucre bracts. These characters, and even the absence of a defined closed spathe in species with very short scapes are a rare in Eriocaulaceae (Stützel 1998, Giulietti *et al.* 2012a). *Tonina fluviatilis* Aublet (1775: 857) and *Syngonanthus cuyabensis* (Bongard 1831: 634) Giulietti, Hensold & L.R. Parra in Giulietti *et al.* (2012b: 53) are species with short scapes but with open or lacking spathes, respectively (Ruhland 1903), while a few paleotropical species of *Eriocaulon* Linnaeus (1753: 87) and *Syngonanthus acephalus* Hensold (1991:

434) completely lack the scapes, spathes, and involucral bracts (Watanabe *et al.* 2015). The complete absence of spathes and scapes is especially noted in some species of *Paepalanthus* Martius (1834: 28), a polyphyletic group with ca. 400 species mostly distributed in the Neotropical region (Stützel 1998, Giulietti *et al.* 2012a, Andrade *et al.* 2010, Trovó *et al.* 2013, Andrino *et al.* 2021).

Ruhland (1903) included the four known species of *Paepalanthus* without scapes into three infrageneric categories comprising trimerous and dimerous flowered species. The trimerous-flowered species are *P. sessiliflorus* Mart. ex Körnicke (1863: 361) described from Bahia state included in *P. ser. Leptocephali* (Ruhland 1903:152) Giul. in Andrade *et al.* (2010: 387) and *P. guyanensis* Klotzsch ex Körnicke (1863: 347) included in *P. subsect. Dichocladus* Ruhland (1903: 179). *Paepalanthus scleranthus* Ruhland (1903: 199) along with *P. leucocephalus* Ruhland (1903: 200) compose *P. subg. Thelxinöe* Ruhland (1903: 199), a taxon mainly from the Espinhaço Range differentiated not only by the sessile capitula, but by having dimerous flowers. Later, *P. lilliputianus* Moldenke (1949: 115) and *P. sessiliflorus* var. *venezuelensis* Moldenke (1974: 193) were described from Northern South America. Hensold (1991), when analyzing the Eriocaulaceae species from the Guyana Highland, synonymized six taxa under *P. dichotomus* Klotzsch ex Körnicke (1903: 348), including *P. guyanensis*. Later, Hensold (1999) recognized *P. sessiliflorus* var. *sessiliflorus* and *P. sessiliflorus* var. *venezuelensis* as valid distinct varieties, and included *P. lilliputianus* in the synonymy of *P. sessiliflorus* var. *venezuelensis*.

The first molecular phylogenetic study considering this group of species included *Paepalanthus sessiliflorus*, *P. scleranthus*, and *P. leucocephalus* (Andrade *et al.* 2010). In the combined dataset analysis, only *Paepalanthus scleranthus* and *P. leucocephalus* emerged as a monophyletic group in all analyses, corresponding to the unique species in *P. subg. Thelxinoë* (Andrade *et al.* 2010). Subsequent phylogenies focused in *Paepalanthus* confirmed these relationships (Trovó *et al.* 2013, Andrino *et al.* 2021) and suggested the closeness of *P. dichotomus* with some species belonging to *P. ser. Leptocephali* (Andrino *et al.* 2021), but do not discuss in detail the evolution of the relevant characters related to these species.

Aiming to provide a deeper insight on the *Paepalanthus* that lack scapes and spathes, we assess the morphological and phylogenetic framework focusing on such species. This effort is consonant with the increase in the collections of Brazilian Eriocaulaceae in the Espinhaço Range and elsewhere over the past decades. Specimens of *Paepalanthus* recently collected in Bahia, Maranhão, and Tocantins states are noteworthy for lacking scapes and spathes structures. A comparative morphological analysis is also provided to circumscribe these taxa and, as a consequence, we are describing here a new species, *P. paganuccii*.

## Materials and Methods

**Taxon sampling and DNA data:** To establish the phylogenetic position of the *Paepalanthus* taxa lacking scapes and spathes, especially regarding the new species, we included the representatives of the well-supported clades of *Paepalanthus* s.l. considering the taxonomic diversity, geographic distribution, and morphological variation according to Andrade *et al.* (2010, 2011), Trovó *et al.* (2013), and Andrino *et al.* (2021). We included 34 species, those including *Paepalanthus*, *Actinocephalus* (Körnicke 1863: 189) Sano (2004: 99), *Tonina* Aublet (1775: 856), and *Lachnocaulon* Kunth (1841: 497). Rotting point was established based on other genera of Eriocaulaceae: *Eriocaulon* (1), *Comanthera* L.B. Smith (1937:38) (1), *Leiothrix* Ruhland (1903: 225) (1), and *Syngonanthus* Ruhland (1900: 487) (1). The DNA dataset includes the regions: nuclear ITS and plastid *psbA-trnH* and *trnL-F*, including the *trnL* intron, all from previous studies (e.g., Andrade *et al.* 2010, 2011; Trovó *et al.* 2013; Andrino *et al.* 2021) and available in the GenBank (for vouchers and GenBank accessions, see Appendix 1).

**Alignment and phylogenetic analysis:** Both sequence directions for the selected DNA regions were assembled and edited in Geneious 5.3 software (Drummond *et al.* 2010), and automatically aligned in Muscle (Edgar 2004) with posterior manual correction. Substitution models were selected with MrModestest 2.3 (Nylander 2004) for each dataset partition using the Akaike (AIC) information criteria: GTR+I+G for ITS and *psbA-trnH*, and GTR+G for *trnL-F*. Analysis followed Bayesian Inference (BI), Maximum likelihood (ML), and Maximum Parsimony (MP) criteria for three different data arrangements 1) nuclear, 2) plastid, and 3) combined nuclear + plastid.

Bayesian analyses were implemented in MrBayes 3.2.3 (Ronquist *et al.* 2012), with two parallel runs of Metropolis-coupled Markov Chain Monte Carlo (MCMC) for 20 million generations, sampling one tree every 1,000 generations. Output files were evaluated using Tracer 1.7 (Rambaut *et al.* 2018), considering sufficient the effective sample sizes (ESS) >200. Burn-in was defined as discarding the initial 10% of the trees, and the final tree was summarized as a 50% majority-rule consensus. Maximum likelihood analyses were implemented in RAxML 8.1.20 (Stamatakis 2014) with

GTRGAMMA model for all dataset partitions. Clade support was obtained using a 1,000 rapid bootstrap replicated with the algorithm best-scoring ML tree. Maximum Parsimony analysis were implemented in PAUP 4.0b10 (Swofford 2002). An initial heuristic search was implemented with 1,000 replicates using the TBR addition algorithm saving 15 trees per replicate. The trees stored in the initial run were submitted to a second run using the same parameters with maxtrees adjusted to 10,000. Clade support was estimated using a 1,000 non-parametric bootstrap replicated using the same heuristic parameters (Felsenstein 1985). We show the phylogenetic relationships of MP and BI through majority-rule consensus, with better overall clade resolution.

All analyses were run via CIPRES Science Gateway on-line portal (Miller *et al.* 2010). The resultant trees were edited using FigTree 1.4.3 (Rambaut 2012). Incongruences and conflicting clades were considered only when supported by posterior probabilities valued  $> 0.95$  and bootstrap values  $> 80\%$ .

Character reconstruction and taxonomic and morphological notes: We performed a character state reconstruction for the character absence of scapes coded as scapes present (0) and scapes absent (1) in a morphological matrix containing all species. The matrix was imported into Mesquite v.3.02 (Maddison & Maddison 2014) and analyzed using the Parsimony Ancestral State Reconstruction Package (Maddison & Maddison 2005). The character was mapped in a set of 1,000 trees resulting from the da BI of the combined dataset (the last 500 of each parallel run). Reconstruction frequencies were summarized as pie charts over the BI tree for the combined dataset. In the *Paepalanthus* species evaluated, the absence of scapes is always associated with the absence of spathes, while the involucre bracts are always present, therefore only one character was reconstructed.

Taxonomic studies were based on extensive fieldwork in Brazil, including Bahia, Maranhão, Minas Gerais, and Tocantins, where these plants occur, and specimens were collected for herbarium and molecular studies. The specimens were identified by AMG, MJGA, and MT. Some of these samples were used in previous work (Andrade *et al.* 2010, Trovó *et al.* 2013, and Andriano *et al.* 2021). We also analyzed all *Paepalanthus* specimens housed at the following herbaria: ASE, B, BHCB, BM, BR, C, G, HAL, HBG, HUEFS, INPA, K, LE, LL, M, MBM, MO, NY, OUPR, P, R, RB, SPF, U, UB, VEN (acronyms according to Thiers 2021), and the available virtual collections (herbarium barcode number indicated between square brackets).

All taxa in *Paepalanthus* with descriptions mentioning the lack of scapes and spathes or at least with very short scapes with closed spathes absent were evaluated. Nomenclatural changes follow the most recent International Code of Nomenclature for algae, fungi, and plants (Turland *et al.* 2018), and we followed the taxonomic species concept for species circumscription (Stuessy 1990). The morphological terminology is in accordance with Barthlott (1981), Stützel (1998), Giuliatti *et al.* (1988, 2012a), and Stützel & Trovó (2013). For the new species GeoCat methodology was used to estimate Extent of Occurrence (EOO) and Area of Occupancy (AOO) (Bachmann *et al.* 2011). The map was prepared using DIVA-GIS 7.5 (Hijmans *et al.* 2017), based on the analyzed materials.

Seed, flower and capitulum samples from HUEFS herbarium specimens were mounted on stubs using a thin layer of silver glue. Each sample was coated with a layer of 5 nm of gold in Balzers SCD 050 for 3 min, using 25 mA. Samples were analysed using the LEO 1430VP scanning electron microscope of the Universidade Estadual de Feira de Santana, Bahia, Brazil. The morphology drawings were prepared by the authors in HUEFS and K using a stereomicroscope with a light camera attached, inked in by Carla Lima.

## Results

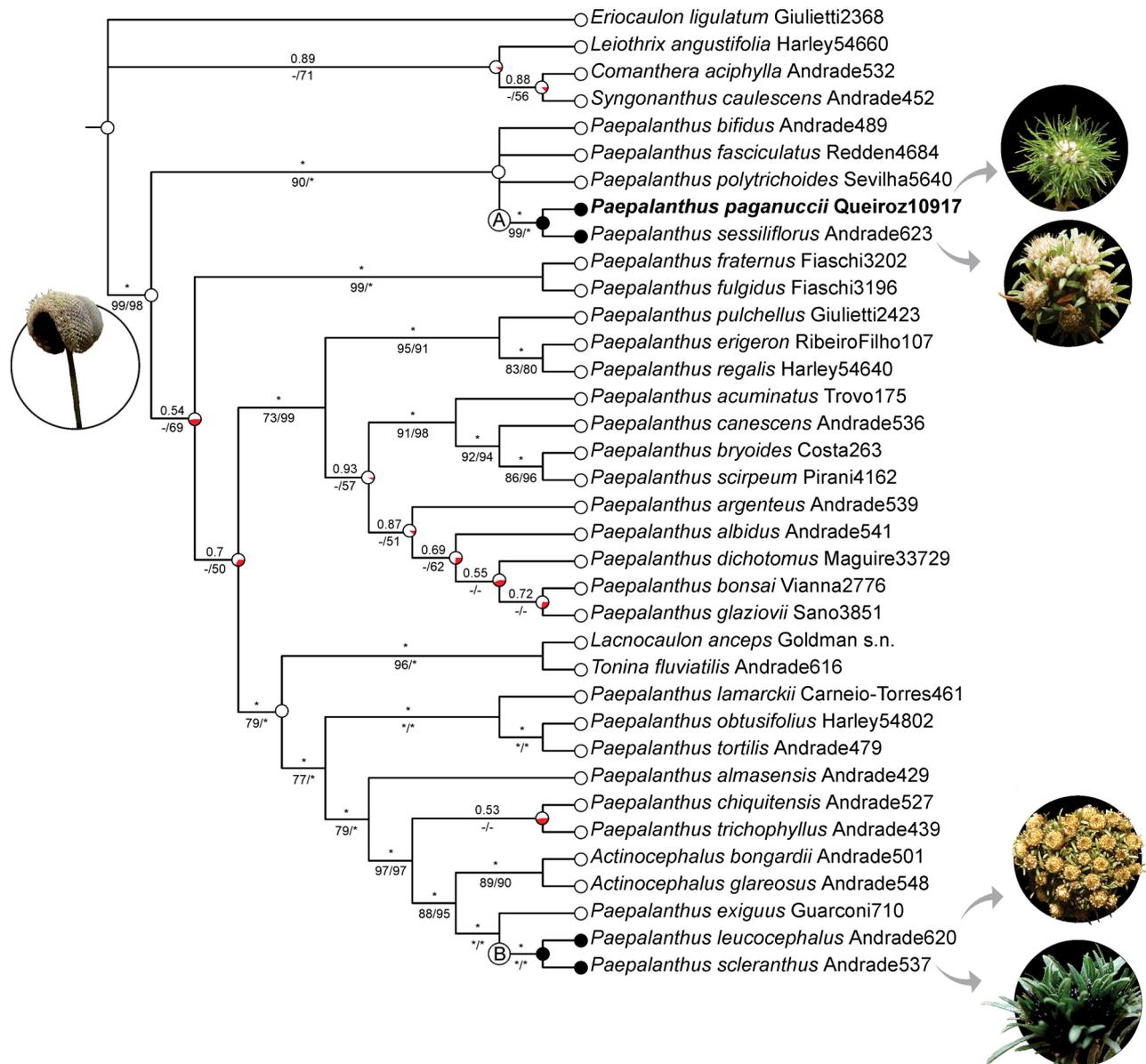
### Phylogenetic position of the *Paepalanthus* species lacking scapes

Analyses with isolated datasets showed that the most parsimonious informative dataset was from ITS analysis and in the plastids the *trnL-F* analysis, and *psbA-trnH* was the least informative. General features and statistics for three DNA markers are summarized in Table 1. The resulting tree from the BI, ML, and MP analysis of the combined dataset are well resolved with high support values and present very similar topologies. Most of the clades are well supported and coherent with the previous studies (Figure 1, see also the supplementary material, Figures S1–9).

The specimens with trimerous flowers lacking scapes and spathes: *P. sessiliflorus* (Andrade 623) *Paepalanthus paganucci* sp.nov. (Queiroz 10917), both from Bahia, form a well-supported clade (Clade A) (PP-BI 1.00/BS-MP 99/BS-ML 100), which emerges from a polytomy formed by *Paepalanthus polytrichoides* Kunth (1841: 504), *P. bifidus* (Schrad. ex Schultes 1824: 468) Kunth (1841: 512) and *P. fasciculatus* (Rottbøll 1778: 271) Kunth (1841: 506). These form a well-supported clade (1.00/90/100). More internally in the tree, a well-supported Clade B (1.00/100/100) diverges, retrieving dimerous-flowered specimens representing *P.* subg. *Thelxinoë*, sister to *P. exiguus* (Bongard 1831: 627) Körnicke (1863: 314). In Clade B, *P. leucocephalus* emerges as sister of *P. scleranthus* (1.00/100/100).

**TABLE 1.** Features of the DNA data sets, parsimony-based tree characteristics, and nucleotide substitution models. N = Number of taxa; Align. = length of the aligned DNA matrix; PI = number of parsimony informative characters; L = length of most parsimonious tree; NTR = Number of trees retained; CI = consistency index; RI, retention index.

DNA marker	N	Align. (bp)	PI (%)	L	NTR	CI	RI	Subst. model
ITS	33	886	370 (41,8%)	1422	12	0.6048	0.7451	GTR+I+G
<i>psbA-trnH</i>	29	734	88 (11,9%)	368	15	0.7310	0.6887	GTR+I+G
<i>trnL-trnF</i>	34	1229	180 (14,6%)	676	15	0.7396	0.7250	GTR+G
Combined plastid	36	1963	268 (13,6%)	1065	15	0.7221	0.6920	Mixed
Combined nuclear+plastid	41	2849	638 (22,3%)	2525	15	0.6451	0.7170	Mixed



**FIGURE 1.** Majority-rule consensus tree from the Bayesian Inference analysis with combined nuclear and plastid data sets. Circles indicate the result of the Ancestral Character reconstruction by parsimony for the escape, indicate the frequency of the states in the last 1,000 post-burn-in trees from IB analysis of nuclear and plastid combined data set: white = scape present; black = scape absent; red = node absent. Above branches are values of posterior probabilities (PP), below are the bootstrap (BS) percentages from maximum parsimony (left) and maximum likelihood analyses (right); \* indicates PP=1.00 and/or BS=100%; - indicates BS < 50%. Figures show species with scape (*P. regalis*, by R.M. Harley) and without scape (*P. paganuccii* and *P. sessiliflorus*, by R.M. Harley; *P. leucocephalus*, by C.N. Fraga; *P. scleranthus*, by M. Trovó).

## Character state reconstruction and morphological analysis

The character state reconstruction is summarized over the majority rule consensus resulting from the BI analysis (Figure 1, see also the supplementary material, Figure S10). In *Paepalanthus*, the scape and spathes were lost at least twice, and may be diagnostic of Clade A and B.

The morphological analysis of *Paepalanthus sessiliflorus* based on *Andrade 623* and other specimens were morphologically compared with the specimen *Queiroz 10917* and other unidentified specimens from several various herbaria. The specimen *Queiroz 10917*, from Bahia, is however too different to be merged within the morphological variation of *P. sessiliflorus* (Table 2). Therefore, this specimen, associated with others with similar morphology, are treated as a new species, *Paepalanthus paganuccii*, described and compared in detail in the taxonomic treatment section.

**TABLE 2.** Comparison of *Paepalanthus paganuccii* and the other species without scapes or spathe.

Characters/Species	<i>P. paganuccii</i>	<i>P. sessiliflorus</i> *	<i>P. leucocephalus</i>	<i>P. scleranthus</i>
<b>Plant height</b>	4.5–7.0 cm	0.6–2.0 (– 3.0) cm	2.0–4.0 cm	2.0–2.5 cm
<b>Leaf: form/sheath</b>	Lanceolate/ Sheath abrupt detached from the limb	Lanceolate/ Sheath ovate, not evident detached from the limb or narrow base	Lanceolate/ Slightly enlarged	Lanceolate/ No or slightly enlarged
<b>Leaf: apex</b>	Acuminate	Obtuse, acute, rarely acuminate	Acute	Acute
<b>Apical Leaf (L) vs Capitulum (C)</b>	L 2x > C	L ½–1x > C	Unknown	Unknown
<b>Capitulum color</b>	White	Whitish	Whitish to light brown (Figure 2)	Blackish
<b>Involucral bract: ranks number/form/apex</b>	2/Lanceolate (external), obovate-elliptic (inner), apex acute	2/Narrowly-oblong, cuspidate apex	Not present	Not present
<b>Floral bract: form/apex</b>	Spathulate/ Rounded	Oblong to linear Obtuse-apiculate	Subcarinate, broadly-obovate, long-acuminate	Subcarinate, broadly-obovate, long-acuminate
<b>Flower 2-or 3-merous</b>	3-merous	3-merous	2-merous	2-merous
<b>♂: floral bract (FB) vs flower (F)</b>	FB slightly < or = F	FB > F rarely FB < F	FB slightly > F	FB < F
<b>♂: sepal form/apex</b>	Spathulate-obovate/Rounded or emarginate	Linear-oblong/ Truncate, rounded, obtuse or acute	Linear-lanceolate/ Obtuse	Oblong/ Truncate
<b>♀: sepal form/apex</b>	Linear-spathulate/ Rounded	Oblong, oblong-elliptic, oblong-linear/ Truncate, rounded or acute	Widely-spatulate to obovate/ Obtuse	Widely-oval/ Obtuse
<b>♀: petal form</b>	Linear-spathulate	Obdeltoid, narrowly-oblong or oblong-linear	Oblong-obovate Widely-elliptical	Elliptic
<b>♀: petal apex</b>	Rounded	Truncate or rounded	Obtuse-truncate to obtuse	Rounded obtuse
<b>♀: sepals (S) vs petals (P) in flower</b>	S = P	S = P	S > or = P	S > P
<b>Seed coat in SEM</b>	Tuberculate-striate	Reticulate	Reticulate	Unknown

\*Including specimens of *P. sessiliflorus* var. *sessiliflorus* and *P. sessiliflorus* var. *venezuelensis*.

## Discussion

*Paepalanthus* species lacking scapes were placed in two major clades recovered are in accordance with the previous phylogenies, mostly coinciding in the use of molecular markers and the sharing a large proportion of the studied specimens (Andrade *et al.* 2010, Trovó *et al.* 2013, Andriano *et al.* 2021). As in *Paepalanthus*, the scapes and spathes may be absent in some species of other Eriocaulaceae genera, such as *Eriocaulon* and *Syngonanthus*, reinforcing the homoplastic condition of this character state. The most extreme situation is reported in *S. acephalus*, an Amazonian species lacking scapes, spathes, and involucral bracts, whose capitula are reduced to a few dimerous and bisexual flowers arising from the stem apex (Hensold 1991). However, these character states are still underexplored and their ontogenetic, ecological mechanisms, and evolutionary implications are poorly understood.

Ruhland (1903) defined *Paepalanthus* subsect. *Dichocladus* mainly by the elongated, dichotomously branched stem, comprising only four species: *P. dichotomus* Klotzsch ex. Körnicke (1863: 348), *P. guyanensis* Klotzsch ex. Körnicke (1863: 347) *P. muscosus* Körnicke (1863: 348), and *P. glaziovii* Ruhland (1903: 181). *Paepalanthus guyanensis* was keyed out by Ruhland's (1903) alongside *P. dichotomus*, because of the almost absent or very short scapes equalling the apical leaves, and further segregated by its "pedunculi vaginaeque subnullae" (Körnicke 1863, Ruhland 1903). The syntypes of *P. dichotomus* from the same locality in Guyana (*Schomburgk 676-K000640008* and *Schomburgk 899-K000640009*) have evident scapes. Meanwhile, at first glance, the three isotype specimens of *P. guyanensis* (*Schomburgk s.n.*) housed at K Herbarium in one sheet [K00064010], seem to lack scapes and spathes. However, removing the terminal leaves of the fertile branches, a pubescent 2 mm long scape surrounded by a delicate spathe equal in size spathe can be observed. In this sense, we follow the synonymization of *P. guyanensis* under *P. dichotomus* proposed and justified by Hensold (1991) citing the "great variation found in pubescence, leaf texture, and peduncle elongation". We thus do not consider this species within the group of taxa consistently lacking scapes.

## Taxonomic Treatment

The specimen *Queiroz 10917* is phylogenetically and morphologically related to *Paepalanthus sessiliflorus* but considered here as a distinct species (Figure 1). In this taxonomic treatment we provide a detailed description of this species along with an annotated checklist of *Paepalanthus* species without scapes and spathes that occur in Brazil, including a distribution map, photos, illustrations and a comparative table (Table 2).

### 1. *Paepalanthus paganuccii* Giul. & M.J.G. Andrade, *sp. nov.* (Figures 2C–E, 3, 4A–K, 5A–I).

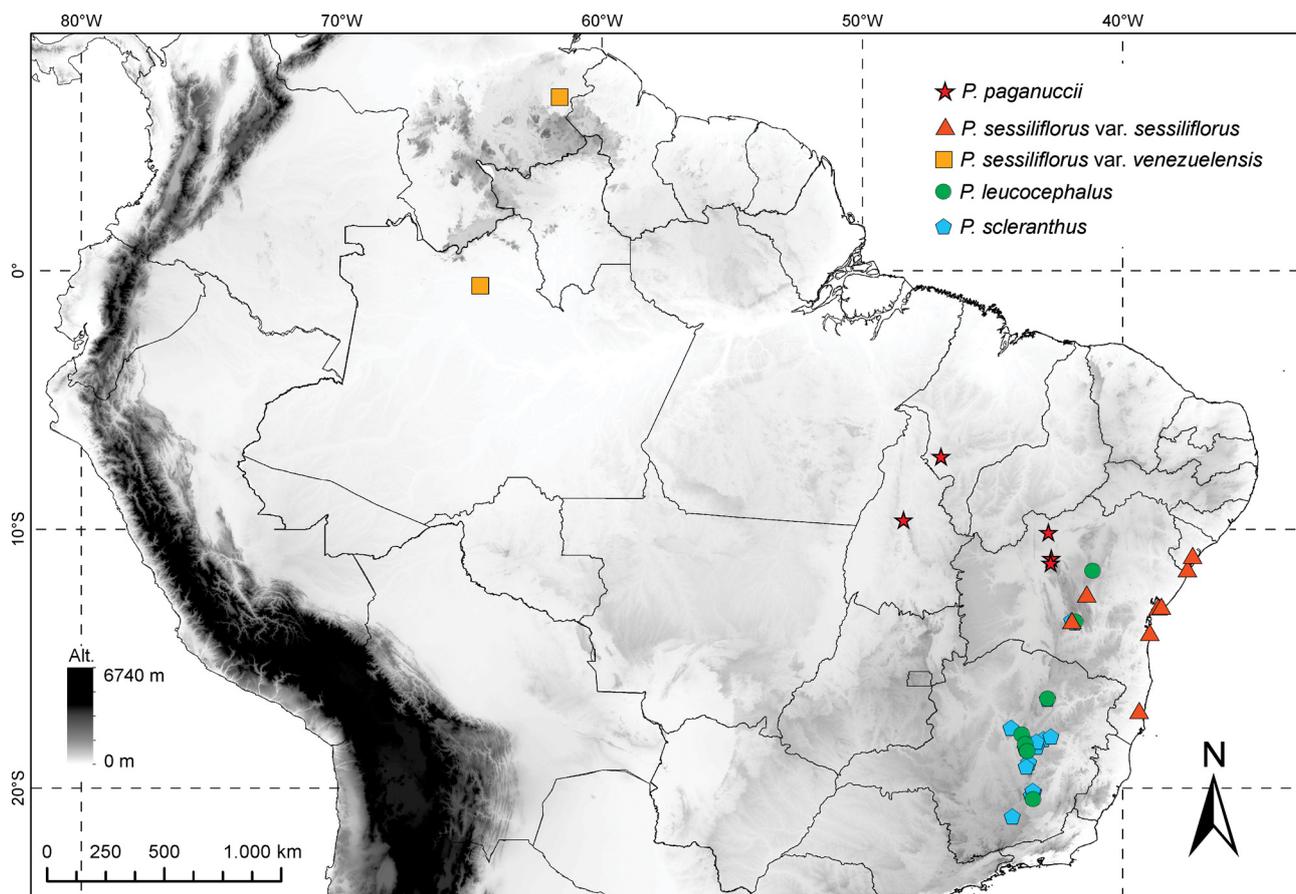
**Type:**—BRAZIL. Bahia: Município de Pilão Arcado, Barra do Iuiu, 10°07'09"S, 42°51'15"W, 436 m alt., 07 September 2005 (fl., fr.), *L.P. Queiroz et al. 10917* (holotype: HUEFS [101058]!).

**Diagnosis:**—*Paepalanthus paganuccii* resembles *P. sessiliflorus*, sharing with it the general habit consisting of an elongated stem, the lack of scapes and spathes, two series of involucre bracts, trimerous flowers, and floral bract pilose at apex. *Paepalanthus paganuccii* is mainly distinguished by its being robust with 4.5–7.0 cm long tall (vs. 0.6–1.6 (–3.0 cm long); leaves usually senescent at the lower parts of the stem with persistent leaf sheaths (vs. persistent leaves along the entire stem), erect to patent, 8–10 mm long, acuminate apex (vs. recurved, 3–5 mm long, acute to obtuse apex), differentiated into sheath and blade (vs. undifferentiated); apical leaves surpassing the flowers by two times or more the floral disc size (vs. apical leaves surpassing the flowers slightly or one time the floral disc); involucre bracts lanceolate (external series) to obovate-elliptic (inner series), apex acute (vs. involucre bracts narrowly-oblong, apex cuspidate); floral bracts spatulate (vs. oblong to linear); seed coat tuberculate-striate (vs. seed coat reticulate).

**Description:**—Annual caulescent herb, 4.5–7.0 cm tall., roots brown. Stem erect, branched at the distal parts, leaves spirally arranged along the stem, persistent from middle to the apex and usually deciduous from the middle to base with persistent sheaths. Leaves lanceolate, erect to patent, membranous to chartaceous, 8–10 × 0.2–0.3 mm, apex acuminate, sheath abruptly detached from the limb, ca. 0.8 mm wide, ciliate along the margin from the middle toward the limb base, trichomes long (ca. 1.2 mm long), filamentous, 3–4-celled, basal and collar cells bulging, distal cells with short tuberculate wall; the uppermost leaves subtending the capitulum, about two times longer than the floral disc. Scape and spathe absent. Each capitulum terminating an abbreviated leafy branch, sessile, hemispherical, ca. 2 mm diam., receptacle densely long-villous with erect white trichomes, ca. 1.3 mm long. Involucre bracts in 2 series, ca. 6 bracts in each series, bracts of the outer series ca. 1.6 × 0.5 mm, lanceolate, apex acute, glabrous, bracts of the inner series ca. 1.4 × 0.8 mm, obovate-elliptic, apex acute, glabrous. Floral bracts spatulate, ca. 1.6 × 0.4 mm, apex round, long-ciliate in the upper part, filamentous trichomes (ca. 0.4 mm long), uniseriate, 4–5-celled, apex acute, slightly shorter than staminate flowers and with the size of the pistillate flowers. Flowers trimerous. Staminate flowers ca. 2 mm long; pedicel ca. 0.6 mm long; sepals spatulate-obovate, concave, fused at base, ca. 0.7 mm long, apex round or emarginate, white-ciliate, with short trichomes; anthophore ca. 0.5 mm long, corolla campanulate, shortly lobed, involute after anthesis, glabrous, overtopping the calyx due to the anthophore; stamens 3, exserted, filaments filiform, adnate to corolla, 2-theous, 4-sporangiate, anthers dorsifixed; carpellodes 3, reduced. Pistillate flowers, ca. 1.4 mm long, pedicel ca. 0.6 mm long; sepals linear-spatulate, concave, free, ca. 0.8 mm long, apex rounded, glabrous, becoming rigid and revolute during the fruit development; petals 3, free, flat, linear-spatulate, ca. 0.8 mm long, loosely ciliate at the rounded apex; gynoecium ca. 1.0 mm long, 3-locular ovary, ca. 0.4 mm long, styles united



**FIGURE 2.** Life-forms and inflorescences in *Paepalanthus* species without scape. **A–B.** *Paepalanthus leucocephalus* growing in the Chapada Diamantina, BA. **C–E.** *P. paganuccii*. **C.** Population growing in Tocantins (Harley 56669) on sandy soil. **D.** Rupicolous individual growing on sandstone. **E.** Detail of the capitulum. **F.** *P. scleranthus*, growing in Diamantina, MG, showing the black capitula. **G.** *P. sessiliflorus* growing in campo rupestre in Pico das Almas, BA. Scale bar: 5 mm. (photo credits: A–B. C.N. Fraga, C–E, G. R.M. Harley, F. M. Trovó).



**FIGURE 3.** Geographical distribution of *Paepalanthus* species without scape. Red-orange symbols = *Paepalanthus* ser. *Leptocephali*; Blue-green symbols = *P.* subg. *Thelxinoë*.

in column ca. 0.6 mm long, stigmatic branches united, short stigmas, caducous during fruiting, nectariferous branches lacking. Fruit a capsule, released from the capitulum with the erect petals still connected at the top by the ciliate margin, through the elevation of the fruit associated with the pression of the rigid and revolute sepals. Seed obovate, ca. 0.4 mm long, seed coat with primary sculpture with a tuberculate-striate pattern, with tubercule organized in rows. This pattern is probably associate to a presence of an almost intact periclinal wall when the seed is liberated.

**Distribution, Habitat, and Conservation:**—The type of *Paepalanthus paganuccii* was collected in the Caatinga of western Bahia, forming a dense population over seasonally humid sandy soils in a temporary lagoon in the São Francisco riverbanks (400 m high). Other disjunct populations were found in sandy areas of the Cerrado in Maranhão, and Tocantins (Figure 3), but further detailed botanical expeditions and careful analysis of herbarium specimens may reveal a more continuous distribution.

*Paepalanthus paganuccii* has EOO = 118,138.378 km<sup>2</sup>, and A00 = 16.000 km<sup>2</sup>. Its populations are threatened by disturbance and change of the water regime near the São Francisco River as well as increasing disturbance and clearing of vast tracts of the Cerrado of Maranhão and Tocantins for agrobusiness. Apart from the population found within the Parque Nacional da Chapada das Mesas (*Silva 903*), the other populations are currently under threat. According IUCN (2019) criteria B1(bii,iv) and B2 (b,iii,iv), we consider the species should be treated as Endangered (EN).

**Etymology:**—The epithet honours Prof. Dr. Luciano Paganucci de Queiroz from the Universidade Estadual de Feira de Santana, Bahia, Brazil, for collecting the holotype and specially for his relevant contributions to the botanical studies of the Brazilian Semiarid region.

**Comments:**—*Paepalanthus paganuccii* differs from the majority of the Eriocaulaceae by lacking one of the family's main diagnostic characters, the presence of scapes and spathes. In this species the sessile capitulum terminates a short leafy branch, resembling the two species of *P.* subg. *Thelxinoë*. The flowers in the new species are however trimerous instead of dimerous, being therefore morphologically more related to *P. sessiliflorus*, its sister species (Figure 1). *Paepalanthus paganuccii* is provisionally placed in *P.* ser. *Leptocephali*, which also comprises *P. sessiliflorus* and *P. polytrichoides*, both also annual herbs, with the seeds with a similar dispersal mechanism (Figures 2–5).

Among the *Paepalanthus* species with trimerous flowers, *P. paganuccii* is morphologically most related to *P. sessiliflorus*, and the differences between both species are detailed in the diagnosis and in Table 2 and illustrated in Figures 4–5. The specimens which have been included as paratypes were not examined in the phylogeny, nor were their seeds examined under SEM. However, they display other morphological characters, which is in accord with those found in *P. paganuccii*, even though some specimens may have leaves that are persistent along the stem, when juvenile (see *Harley 56669* from Tocantins). Another aspect, which distinguishes between the two species in their distribution. While *P. paganuccii* is limited to a few populations within the Caatinga and Cerrado, *P. sessiliflorus* occurs in the Atlantic dunes and *campo rupestre* of the Chapada Diamantina in Bahia, with a heterotypic variety in northern South America (Figure 3).

**Additional material examined:**—BRAZIL. Bahia: Gentio do Ouro, estrada de Gentio do Ouro para Xique-Xique (BA-160/BR-330), ca. 20 km de Xique-Xique, 11°07'04"S, 42°44'14"W, 03 May 2014, *C.M. Siniscalchi et al. 471* (HUEFS, SPF). Maranhão: Carolina, Rodovia MA-010, Serra do Portal da Chapada, solo arenoso na base dos paredões de arenito, em áreas sombreadas, 296 m, 07°11'12"S, 47°25'22"W, 19 May 2012, *C. Silva et al. 903* (HUEFS). Tocantins: Miracema do Tocantins, Rodovia TO-010, para a cidade de Lagedo e Palmas, ca. 9 km da cidade, paredão úmido na beira da estrada, 263 m, 09°37'48"S, 48°25'04"W, 01 February 2012, *R.M. Harley et al. 56669* (HUEFS).

### 2.1. *Paepalanthus sessiliflorus* var. *sessiliflorus* Mart. ex Körn. in Martius, Fl. Bras. 3(1): 361. 1863.

Lectotype (designated by Moldenke 1976b):—[BRAZIL] “Crescit in prov. Bahiensis campis haud procul a mari prope praedium Caballo”, s.d., *Luschnath 33* in Martius Hb. Fl. Bras. 557 (M [0165226]!, isolectotypes B [10 0247672-a]!, B [10 0247672-b]!, BM [000938297]!, BR [0000008619570]!, BR [0000008619587]!, HAL [0109753]!, K [000293242]!, MO [202612]!, NY [00102939]!, NY [00102940]!).

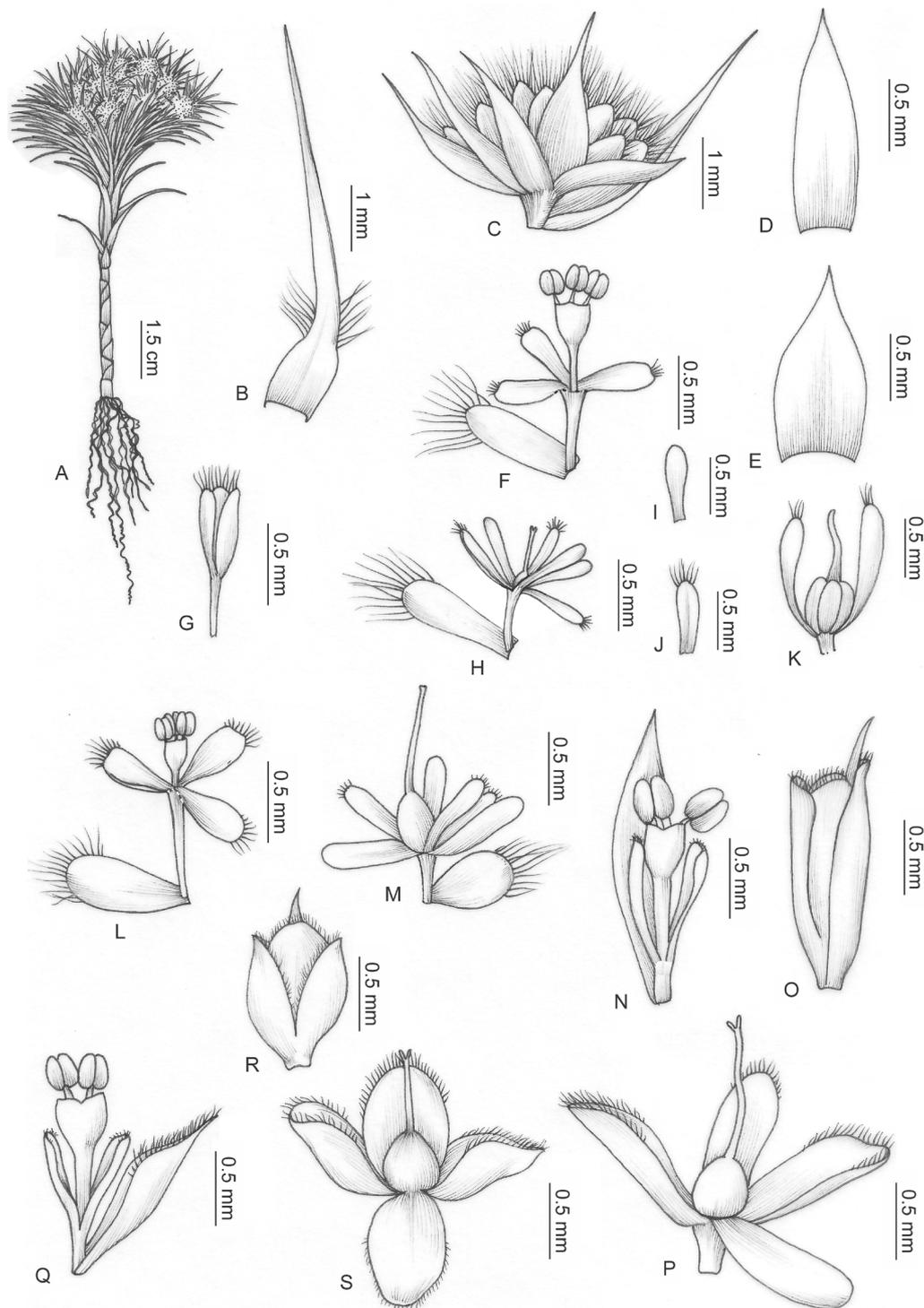
(Figures 2G, 3, 4L–M, 5J–N).

The name *Paepalanthus sessiliflorus* was initially suggested in manuscripts and annotated in specimens by Martius, but was only validly published by Körnicke (1863: 361), who cites two different collection numbers *Luschnath 33* and *Mart. Hb. Fl. Bras. 557*. These numbers are in fact the same collection, as suggested by the specimens at BR. One of the herbarium sheets kept at BR contain both original labels *Luschnath 33* and *Mart. Hb. Fl. Bras. 557*, with the first including the original location description. The other specimen contains one original label *Mart. Hb. Fl. Bras. 557* indicating *Luschnath* as the collector. The label *Mart. Hb. Fl. Bras. 557* represented Martius's personal numbering system. The specimen at B is a single sheet with two labels, but in this case, there is a later attempt to segregate both collections. The remaining material was distributed to various herbaria labelled only as *Mart. Hb. Fl. Bras. 557*. Moldenke (1976b) explicitly refers as type the specimen *Luschnath 33* (distributed as *Martius 557*) housed at M, and as isotypes the specimens at B, and BR (2x). According to the current ICN (Turland *et al.* 2018), Moldenke type citation is to be followed as an inferential lectotype (articles 7.11, 9.10, and 9.23).

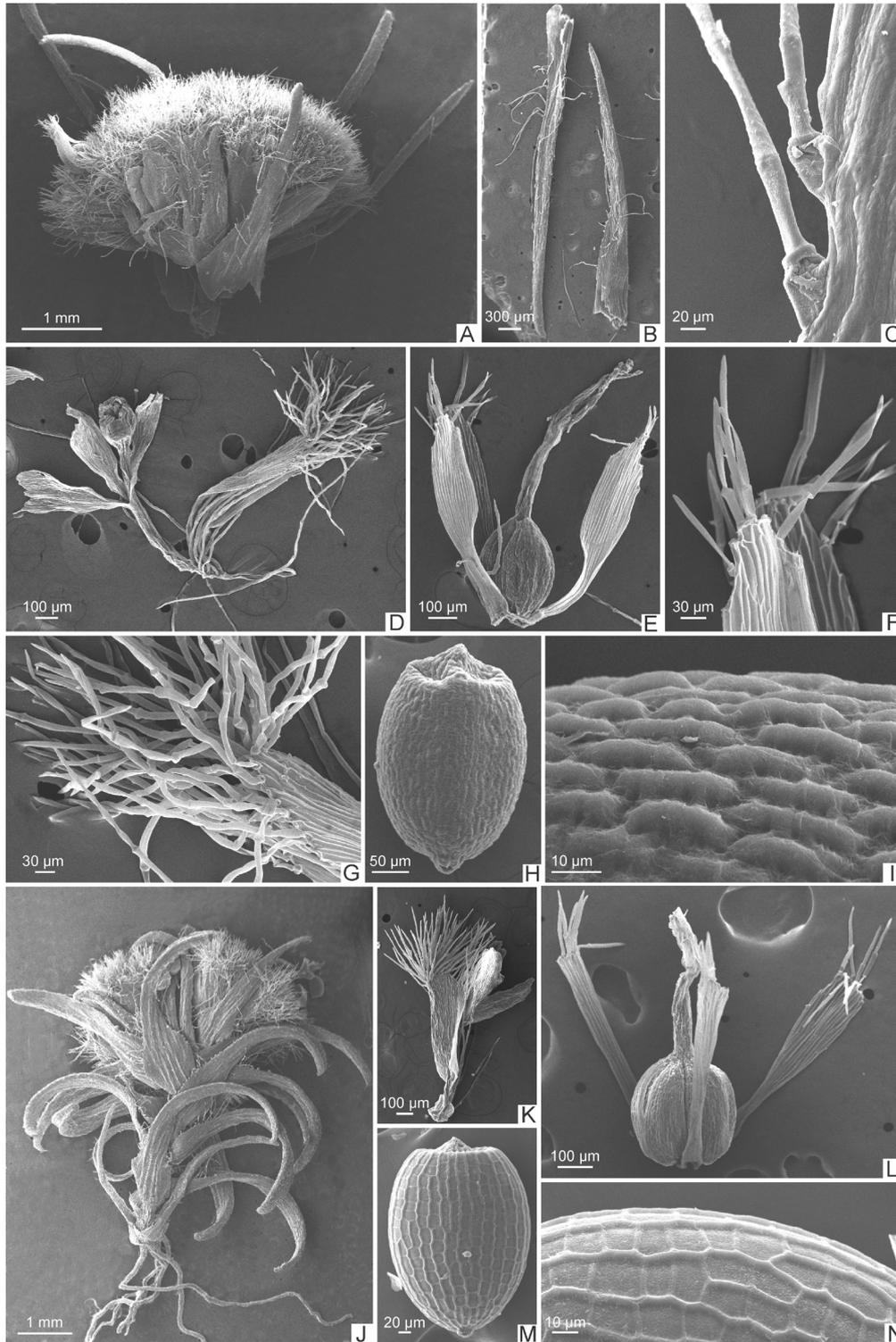
*Paepalanthus sessiliflorus* is mainly distinguished by its annual dwarf 0.6–2.0 cm long habit; erect stem with persistent, recurved, lanceolate, leaves 3.0–5.0 mm long, and blade almost indistinguishable from the sheath, margin ciliate in the basal half, with obtuse to acute apex, the apical leaves slightly to twice as long as the floral disc. These characters are present in both varieties, however there are few differential morphological characters according to Moldenke (1974) and Hensold (1999).

Körnicke (1863) described the seed as subrounded, brown and glabrous. Using SEM, the seeds are obovate, ca. 0.4 mm long, seed coat with primary sculpture with a reticulated pattern, cells 4–5 walled, the longitudinal anticlinal walls more prominent than the transverse walls, giving rise to longitudinal ribs along the seed coat (Figures 5M–N). This seed coat pattern is similar with that of *Paepalanthus perpusillus* Kunth (1841: 503) (see Giulietti *et al.* 1988), but it is different from *P. paganuccii*, all three species included in *Paepalanthus* series *Leptocephali*.

*Paepalanthus sessiliflorus* var. *sessiliflorus* (Figure 2G) is endemic to Brazil, mostly distributed in sandy soils of the *restingas* of Bahia and Sergipe states, with populations occurring also in the northern part of the Espinhaço Range in Bahia (Figure 3). Field observations and the analysis of recent and historical collections of this variety reveal few morphological differences between the populations found in the coastal sand dunes, and the *campo rupestre*. The *campo rupestre* plants are usually larger (1.5–2 cm long), and the inner involucre bracts can be ciliate. In this treatment, this is interpreted as within the range of morphological variation of a single taxon, especially because all specimens seen have the same seed coat pattern.



**FIGURE 4.** Morphology of plant and flowers in *Paepalanthus* without scape. **A–K:** *Paepalanthus paganuccii*. **A.** habit. **B.** leaf. **C.** capitulum. **D.** involucral bract of the outer series. **E.** involucral bract of the inner series. **F.** open staminate flower showing calyx, anthophore, corolla, androecium and floral bract. **G.** closed staminate flower showing pedicel, calyx and corolla trichomes. **H.** open pistillate flower showing calyx, corolla, gynoecium and floral bract. **I.** sepal. **J.** petal. **K.** developing fruit with two petals. **L–M:** *Paepalanthus sessiliflorus* var. *sessiliflorus*. **L.** open staminate flower showing calyx, anthophore, corolla, androecium and floral bract. **M.** open pistillate flower showing calyx, corolla, gynoecium and floral bract. **N–P:** *Paepalanthus leucocephalus*. **N.** open staminate flower showing calyx, anthophore, corolla, androecium and floral bract. **O.** closed pistillate flower showing calyx, corolla and floral bract apex. **P.** open pistillate flower showing calyx, corolla and gynoecium. **Q–S:** *Paepalanthus scleranthus*. **Q.** open staminate flower showing calyx, anthophore, corolla, androecium and floral bract. **R.** closed pistillate flower showing calyx, corolla and floral bract apex. **S.** open pistillate flower showing calyx, corolla and gynoecium [A–K. Queiroz 10917, holotype of *P. paganuccii* (HUEFS), L–M. Andrade 623 (HUEFS), N–P. Andrade 549 (HUEFS), Q–S. Alves 4015 (RB), drawings by AMG inked in by Carla Lima].



**FIGURE 5.** SEM micrographs. **A–I:** *Paepalanthus paganuccii*. **A.** capitulum rounded by the terminal leaves. **B.** leaf with filamentous trichomes. **C.** leaf margin showing tricellular filamentous trichomes with a ring on the apex of the basal cell. **D.** staminate old flower showing bract with trichomes, calyx and involute corolla. **E.** pistillate flower showing three ciliate petals and gynoecium with stigmatic branch, lacking nectariferous branches. **F.** detail of petal apex showing 1-3-celled filamentous trichomes, basal cell with ring. **G.** detail of the floral bract apex showing 4-5-celled filamentous trichomes. **H–I.** mature seed, seed coat with a tuberculate-striate pattern, with the long tubercule organized in rows. **I.** detail of the seed coat showing the elongate tubercules. **J–N:** *Paepalanthus sessiliflorus*. **J.** a complete individual plant. **K.** staminate old flower showing long ciliate floral bract and calyx. **L.** pistillate flower showing three ciliate petals and gynoecium with stigmatic branch, lacking nectariferous branches. **M–N.** mature seed, seed coat with a reticulate pattern. **N.** detail of the seed coat showing cells 4-5-walled, the longitudinal anticlinal walls more prominent than the transverse walls (A–I. *Queiroz 10917*, J. *Queiroz 880*, K. *Harley 53657*, L–N. *Andrade 623*).

**Additional selected material examined:**—BRAZIL. Bahia: Itamaraju, 12 August 1995, *Hatschbach et al. 63034* (MBM); Lençóis, Capitinga, 12°30'S, 41°23', 15 August 2006, *F.F. Rocha 63* (HUEFS); Maraú, povoado de Saquirá, 15 August 1999, *J.G. Jardim 2237* (HUEFS, NY); Rio de Contas, Serra Marsalina, campo cerrado, 16 August 2006, *M.J.G. Andrade et al. 623* (HUEFS); Pico das Almas, campo rupestre, *R.M. Harley et al. 53657* (HUEFS); Salvador, 30 September 1984, *L.P. Queiroz 880* (HUEFS). Sergipe: Indiaroba, 16 August 201, *A.P. Prata et al. 2824* (ASE).

## 2.2. *Paepalanthus sessiliflorus* var. *venezuelensis* Moldenke in *Phytologia* 28: 193. 1974.

Holotype:—VENEZUELA. Bolívar: “carretera El Dorado to Santa Elena de Uairen, 198 km south of El Dorado, at 1200-1400 meters altitude”, 7–10 December 1972, *J. Steyermark et al. 106609* (LL [00374800]!, isotypes MO [202560]!, VEN [99028]!, U [00088400]!).

= *Paepalanthus lilliputianus* Moldenke in *Phytologia* 3: 115. 1949. Holotype:—GUYANA. November 1931, *R. Giglioli s.n.* (FI [005381]!, isotypes K [000587316]!, NY [00102895]!).

Moldenke (1974) described *Paepalanthus sessiliflorus* var. *venezuelensis* based on the specimen *Steyermark et al. 106609*, distinguishing the taxon from the typical variety by the sepals of the staminate flowers with acute apex, rather than truncate nor erose; involucre bracts obtusely cuspidate and more gradually attenuate, and stamens slightly exerted.

Moldenke (1949) had previously described *Paepalanthus lilliputianus* as a very small species of ca. “80 mm” (but the correct measurement is 8 mm, based on the isotypes seen at K and NY), with sessile capitula, lacking scapes, sheaths, and involucre bracts. He comments also that *P. lilliputianus* resembles *P. sessiliflorus* from Bahia, Brazil, differing “in technical characters” (Moldenke 1949). Although described with capitula lacking involucre bracts, the analyses of the isotype at K show the presence of these bracts in two series. Also, another important character observed, was the sepals of the staminate flower with obtuse apex, ciliate with long trichomes, and dorsal face villous with long-trichomes. However, the sepals in *P. sessiliflorus* var. *sessiliflorus* are rounded and simply ciliate.

Hensold (1999) refers *Paepalanthus sessiliflorus* var. *venezuelensis* as occurring in the Brazilian Amazon, and includes *P. lilliputianus* in its synonymy, a position followed here after our own analysis of the historical collections. *Paepalanthus sessiliflorus* var. *venezuelensis* occurs in sandy soils of the savannas to rock outcrops Northern South America, with records in Venezuela and Brazil (Figure 3).

**Additional selected material examined:**—BRAZIL. Amazonas: Santa Isabel do Rio Negro, campina de Temendaru, ca. 40 km below Tapuruvara, 13 October 1978, *M.T. Madison et al. 6226* (NY); Along the Rio Negro, between Manaus and São Gabriel, Temendui Lagoon, 00°35'S, 64°40'W, 29–30 June 1979, *J.M. Poole 1795* (INPA, NY).

## 3. *Paepalanthus leucocephalus* Ruhland in Engler, *Pflanzenr.* IV.30 (Heft 13): 200. 1903.

Lectotype, first-step (designated by Moldenke 1975): at B. **Lectotype, second-step (here designated):** BRAZIL. Minas Gerais: Serra dos Cristaes, 4 April 1892, *C.A.W. Schwacke 8503* (B [10\_0243944]!, isolectotypes B [10\_0243943]!, K [000640071]!). (Figures 2A–B, 3, 4N–P, 6A–H)

Ruhland (1903) described *Paepalanthus leucocephalus* based on the collection *Schwacke 8503*, gathered in Minas Gerais. We found three specimens related to this collection, two deposited at B, where Willy Ruhland mostly worked, and one housed at K. It is also a situation with no holotype being clearly indicated, requiring a lectotype selection (McNeill 2014, Turland *et al.* 2018). Moldenke (1975) indicated that the type of this species is deposited at B with the indication “*Thelxinoë leucocephala*”. The two specimens at B contain the same annotation, therefore we consider Moldenke’s (1975) statement as a first-step lectotype indication according to the article 9.17 of the ICN (Turland *et al.* 2018). One of the specimens housed at B contains Ruhland’s original handwritings and drawings attached, also perfectly matching the description. We designate this specimen [B barcode 10\_0243944] as the second-step lectotype.

*Paepalanthus leucocephalus* is sister of *P. scleranthus* and they are the only species in *Paepalanthus* subg. *Thelxinoë* according to Ruhland (1903). They also share the annual caulescent habit of small plants, with the absence of scapes and spathes, capitulum sessile, involucre bracts not differentiated from the apical leaves, floral bracts acuminate, and dimerous flowers. They are sympatric in the Espinhaço Range in some mountains in Minas Gerais, and also in Rio de Contas, Bahia. There is also a population occurring in sandy soils further north in Morro do Chapéu in Bahia (Figure 3). *P. leucocephalus* is morphologically similar to *P. scleranthus* (Figures 6I–N), sharing also the loss of the nectariferous branches (Silva *et al.* 2016), a condition observed in *P. paganuccii* and *P. sessiliflorus* as well (Figures 4–5). The whitish capitula are a visible character to distinguish *P. leucocephalus* from *P. scleranthus*, along

with the convex leaves clearly distinguished into sheath and blade, and the morphology of the flowers, illustrated for the first time in this paper. However, the segregation of these species is weak and deserve further investigations as previously stated by Moldenke “The species is extremely close to *P. scleranthus* and I am not at all certain that the two are distinct” (Moldenke 1975).

As expected of a widespread species, *Paepalanthus leucocephalus* encompasses a relevant morphological variation and the relationship with *P. scleranthus* is complex (Figures 2, 4, 6). Some populations, as the one represented by the specimen *Andrade 625* from Rio de Contas in Bahia, are composed of individuals noteworthy for being smaller than specimens from other populations, especially from those occurring in the Southern Espinhaço Range. The populations from Minas Gerais, occurring mostly in the Diamantina Plateau, also have more hairy floral structures and a shinier white capitulum. The inclusion of specimens from the whole morphological and geographical range of *P. leucocephalus* and *P. scleranthus* in future studies at the population level is crucial to circumscribe these species more accurately.

**Additional selected material examined:**—BRAZIL. Bahia: Morro do Chapéu, Tabuleiro dos Tigres, 11°36'09"S, 41°09'44"W, 20 July 2005, *M.J.G. Andrade et al. 589* (HUEFS); Rio de Contas, Serra Marsalina, campo cerrado, 16 August 2006, *M.J.G. Andrade et al. 620* (HUEFS); Idem, *M.J.G. Andrade et al. 625* (HUEFS). Minas Gerais: Datas, 04 km da estrada Datas-Milho Verde, 07 April 2004, *M.J.G. Andrade et al. 549* (HUEFS); Diamantina, 05 May 2010, *C. Munhoz et al. 7283* (UB); Grão Mogol, Trilha do Barão, 02 April 2004, *M.J.G. Andrade et al. 481* (HUEFS); Mariana, Parque Estadual do Itacolomi, 06 April 2018, *D. Rodrigues et al. 27* (OUPR).

#### 4. *Paepalanthus scleranthus* Ruhland in Engler, Pflanzenr. IV.30 (Heft 13): 200. tab. 28, 1903.

**Lectotype (here designated):**—BRAZIL. Minas Gerais: Perpetua près Diamantina, entre les rochers, 11 April 1892, *A.F.M. Glaziou 19990* (B [10\_0247678]!, isoelectotypes BR [0000008619495]!, C [10011014]!, G [00192125]!, K [000640072]!, LE [00001220]!, P [00716724]!, P [00716725]!).

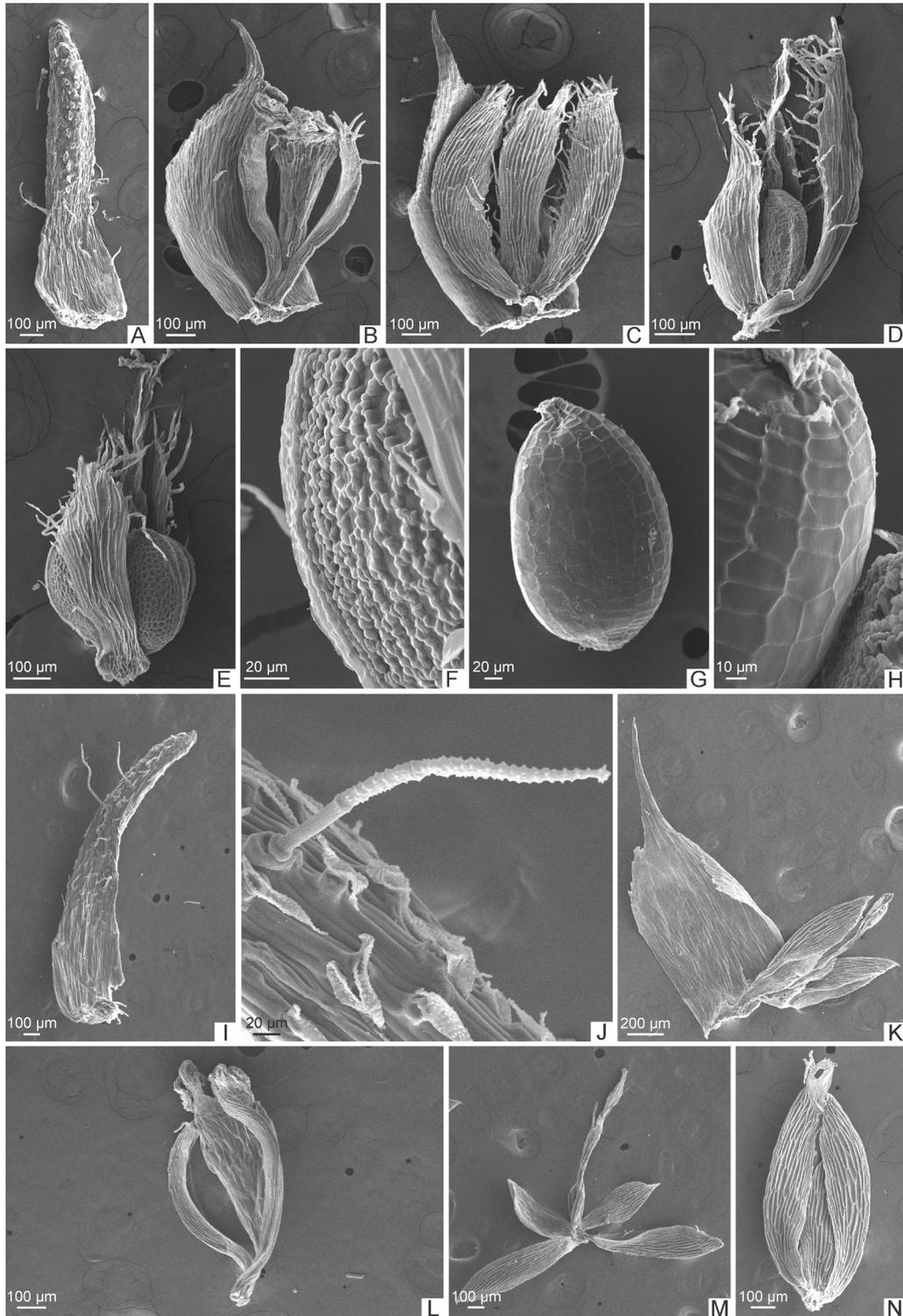
(Figures 2F, 3, 4Q-S, 6I-N).

Ruhland (1903) described *Paepalanthus scleranthus* based on the specimens *Schwacke 11987*, *Ule 2714*, *Ule 2717* and *Glaziou 19990*, collected in Minas Gerais and distributed throughout many herbaria. According to the ICN (Turland *et al.* 2018) and the type clarifications provided by McNeill (2014), a lectotype must be selected. Moldenke (1976a) argued that the specimen *Glaziou 19990* deposited in B was the most relevant specimen used for the species description but referred all specimens as cotypes. We agree with Moldenke's (1976a) interpretation, as among the original material, the specimen *Glaziou 19990* at B perfectly matches the original description and plate and contains the original handwriting and line drawings provided by Willy Ruhland himself. It is therefore designated here as the lectotype.

*Paepalanthus scleranthus* (Figure 2F) is restricted to the sandy soils of the *campo rupestre* from the Espinhaço Range in Bahia and Minas Gerais, and it is sympatric in some areas with *P. leucocephalus* (Figure 3). According to Ruhland (1903), it is mainly differentiated from *P. leucocephalus* by the blackish capitula (vs. whitish), besides a few floral variations explored in Table 2 and Figures 6 A–N. Although in some specimens the capitulum colour is clearly distinctive, in field observations and some herbarium specimens (e.g., the lectotype housed at C) the difference may be misleading. Moldenke (1976a) had previously expressed doubts on maintaining these two taxa segregated, especially regarding the type specimens, gathered in the same area.

Based on our field observation and herbarium analysis, we decided to keep *Paepalanthus scleranthus* and *P. leucocephalus* as distinct units as detailed in the Table 2 and Figures 2, 4, 6. The difficult in differentiating both species is mainly regarding the populations from the Diamantina Plateau (where the types came from), and a few other localities where both species are frequently found growing together. The capitulum colour variation may represent a phenological and/or ecological condition, but yet no individual presenting capitula with intermediate color or with both capitula colors was recorded. Herbarium specimens with some individuals presenting whitish capitula and other presenting blackish capitula may represent problematic field collections (a common situation in small Eriocaulaceae), but not necessarily reflect the species delimitation. We also may keep in mind that hybrids in Eriocaulaceae may be more frequent than we expected, as exemplified in Hensold (1988). *Paepalanthus* being a group of recent diversification (Vasconcelos *et al.* 2020) and with the relevance of the capitulum color to the reproductive biology of Eriocaulaceae (Martins Junior *et al.* 2022), further investigations along the entire species distribution, including population genetics, reproductive biology, and morphology would be of benefit to precisely establish the species circumscription.

**Additional selected material examined:**—BRAZIL. Bahia: Rio de Contas, Serra Marsalina, 6 October 2006, *R.M. Harley et al. 55538a* (HUEFS); Rio de Contas, Serra Marsalina, 6 October 2006, *R.M. Harley et al. 55538b* (HUEFS). Minas Gerais: Catas Altas, Serra do Caraça, *Ule 2717* (B, HBG, NY); Diamantina, Biribiri, 25 March 1984, *A.M. Giuliatti et al. CFCR 4290*; Ouro Preto, *Ule 2714* (B, HBG, R); Serra das Camarinhas, *Schwacke 11987* (B, BHCB); Tiradentes, Serra de São José, 21°05'S, 44°10'W, s.d., *R. Alves 4015* (RB).



**FIGURE 6.** SEM micrographs. **A–H:** *Paepalanthus leucocephalus*. **A.** leaf with two types of trichomes: filamentous and malpighiaceus (2 armed) trichomes. **B.** staminate flower showing bract, calyx, anthophore, corolla and anther. **C.** pistillate flower showing bract, calyx with two concave sepals and one petal and part of ovary. **D.** pistillate flower showing one sepal, one petal and gynoecium with style with stigmatic branch, lacking nectariferous branch. **E.** pistillate flower showing detail of the petal and gynoecium. **F.** detail of the external ovary surface. **G.** mature seed, seed coat with a reticulate pattern. **H.** detail of the seed coat showing the cells 4-5 walled. **I–N:** *Paepalanthus scleranthus*. **I.** leaf with two types of trichomes: filamentous and malpighiaceus (2 armed) trichomes. **J.** adaxial leaf surface showing detail of the filamentous and malpighiaceus trichomes. **K.** pistillate flower showing bract, one sepal, one petal and gynoecium. **L.** staminate flower showing calyx, anthophore, corolla and anther. **M.** pistillate open flower showing two sepals bigger than the two petals and gynoecium with stigmatic branch, lacking nectariferous branches. **N.** pistillate closed flower showing two concave sepals involving the corolla. (A–C. Andrade 589, D–F. Andrade 625, G–H. Andrade 620, I–J, M. Harley 55538a, K–L, N. Harley 55538b).

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**APPENDIX 1. List of vouchers and GenBank accession numbers of samples used in this study. Order of data: Taxon name, voucher, collection location, GenBank accession number for ITS, *psbA-trnH*, *trnL-F*.**

*Actinocephalus bongardii* (A. St.-Hil.) Sano, *M.J.G. Andrade 501*, Itacambira/MG, EU924282, EU924355, EU924434. *Actinocephalus glareosus* (Bong.) Kunth, *M.J.G. Andrade 548*, Datas/MG, EU924322, EU924397, EU924475. *Comanthera aciphylla* (Bong.) L.R. Parra & Giul., *M.J.G. Andrade 532*, Diamantina/MG, EU924339, EU924414, EU924491. *Eriocaulon ligulatum* (Vell.) L.B. Sm., *A.M. Giuliatti 2368*, Mucugê/BA, EU924278, EU924350, EU924430. *Lachnocaulon anceps* Morong, *D. Goldman s/n*; Florida, U.S.A. GU078712, EU924363, EU924442. *Leiothrix angustifolia* Ruhland, *R.M. Harley 54660*, Rio de Contas/BA, EU924290, EU924364, EU924443. *Paepalanthus acuminatus* Ruhland, *M. Trovó 175*, s.l., GQ475234, —, GQ475204. *Paepalanthus albidus* Gardner, *M.J.G. Andrade 541*, Diamantina/MG, EU924287, EU924360, EU924439. *Paepalanthus almasensis* Moldenke, *M.J.G. Andrade 429*, Rio de Contas/BA, EU924315, EU924390, EU924468. *Paepalanthus argenteus* (Bong.) Körn., *M.J.G. Andrade 539*, Diamantina/MG, EU924331, EU924406, EU924484. *Paepalanthus bifidus* (Schrad.) Kunth., *M.J.G. Andrade 489*, Grão Mogol/MG, EU924300, EU924374, EU924453. *Paepalanthus bonsai* Trovo & Sano, *P.L. Vianna 2776*, São Gonçalo do Rio Preto/MG, GQ475237, —, GQ475206. *Paepalanthus bryoides* Kunth, *F.N. Costa 263*, Diamantina/MG, EU924299, EU924373, EU924452. *Paepalanthus canescens* (Bong.) Körn., *M.J.G. Andrade 536*, Diamantina/MG, EU924324, EU924399, EU924477. *Paepalanthus chiquitensis* Herzog, *M.J.G. Andrade 527*, Diamantina/MG, EU924325, EU924400, EU924478. *Paepalanthus dichotomus* Klotzsch ex Körn., *B. Maguire 33729*, Bolívar/Venezuela, —, —, MN860936. *Paepalanthus erigeron* Mart. ex Körn., *A.A. Ribeiro-Filho 107* (ITS, *psbA-trnH*), *C.O. Andrino 337* (*trnL-F*), Lençóis/BA, EU924306, EU924380, MN861016. *Paepalanthus exiguus* (Bong.) Körn., *E. Guarçoni 710*, Caparaó/MG, EU924328, EU924403, EU924481. *Paepalanthus fasciculatus* (Rottb.) Kunth, *K.M. Redden 4684*, s.l., —, MF786090, —. *Paepalanthus fraternus* N.E. Br., *P. Fiaschi 3202*, Bolívar/Venezuela, GQ475246, —, GQ475214. *Paepalanthus fulgidus* Moldenke, *P. Fiaschi 3196*, Venezuela, GQ475247, —, GQ475215. *Paepalanthus glaziovii* Ruhland, *P.T. Sano 3851*, s.l., GQ475249, —, GQ475217. *Paepalanthus lamarckii* Kunth, *D.S. Carneio-Torres 461*, Lagartos/SE, EU924303, EU924377, EU924456. *Paepalanthus leucocephalus* Ruhland, *M.J.G. Andrade 620*, Rio de Contas/BA, EU924334, EU924409, EU924487. *Paepalanthus obtusifolius* (Steud.) Körn., *R.M. Harley 54802*, Rio de Contas/BA, EU924304, EU924378, EU924457. *Paepalanthus paganuccii* M.J.G. Andrade & Giul., *L.P. Queiroz 10917*, Pilão Arcado/BA, HQ843074, HQ843079, HQ843084. *Paepalanthus polytrichoides* Kunth, *A.C. Sevilha 5640*, Carolina/MA, —, —, MN860756/MN860937. *Paepalanthus pulchellus* Herzog, *A.M. Giuliatti 2423*, Rio de Contas/BA, EU924309, EU924383, EU924461. *Paepalanthus regalis* Mart., *R.M. Harley 54640*, Mucugê/BA, EU924310, EU924384, EU924462. *Paepalanthus scirpeus* Mart. ex Körn., *J.R. Pirani 4162*, Congonhas do Norte/MG, EU924289, EU924362, EU924441. *Paepalanthus scleranthus* Ruhland, *M.J.G. Andrade 537*, Diamantina/MG, EU924335, EU924410, EU924488. *Paepalanthus sessiliflorus* var. *sessiliflorus* Mart. ex Körn., *M.J.G. Andrade 623*, Rio de Contas/BA, HQ843075, HQ843080, HQ843085. *Paepalanthus tortilis* (Bong.) Mart., *M.J.G. Andrade 479*, Grão Mogol/MG, EU924302, EU924376, EU924455. *Paepalanthus trichophyllus* (Bong.) Körn., *M.J.G. Andrade 439*, Rio de Contas/BA, EU924326, EU924401, EU924479. *Syngonanthus caulescens* (Poir.) Ruhland, *M.J.G. Andrade 452*, Rio de Contas/BA, EU924344, EU924424, EU924500. *Tonina fluviatilis* Aubl., *M.J.G. Andrade 616*, Recife/PE; EU924345, EU924425, EU924501.