



Molecular phylogenetics and biogeography of Neotropical Paepalanthoideae with emphasis on Brazilian *Paepalanthus* (Eriocaulaceae)

MARCELO TROVÓ^{1,2*}, MARIA JOSÉ GOMES DE ANDRADE³, PAULO TAKEO SANO¹, PATRÍCIA LUZ RIBEIRO³ and CÁSSIO VAN DEN BERG³

¹Laboratório de Sistemática Vegetal, Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo, Rua do Matão 277, Cidade Universitária, CEP 05508-900, São Paulo, Brazil

²Evolution and Biodiversity of Plants, Faculty for Biology and Biotechnology, Ruhr University Bochum, D-44780 Bochum, Germany

³Laboratório de Sistemática Molecular de Plantas, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Av. Transnordestina s.n., CEP 44036-900, Feira de Santana, Brazil

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Subfamily Paepalanthoideae encompass the largest generic diversity in Eriocaulaceae. In the present study, the main goals were to infer the phylogeny of this subfamily focusing on *Paepalanthus*, to evaluate recent classifications and morphological characters in a phylogenetic context and to reconstruct the historical biogeography of the group. Sampling involved 94 ingroup species corresponding to all recognized genera and three outgroup species. Two molecular data sets, nuclear ribosomal internal transcribed spacer (nrITS) and plastid *trnL-trnF*, were analysed under parsimony and Bayesian methods. *Rondonanthus* is monophyletic and confirmed as sister to the remaining Paepalanthoideae. *Leiostrix* and *Actinocephalus* are each monophyletic, whereas *Syngonanthus* may be either monophyletic or paraphyletic with the recognition of *Philodice*. Four subgenera of *Paepalanthus* are monophyletic, but *P.* subgenus *Paepalanthus* is polyphyletic. Morphological characters used in previous classifications are assessed as putative synapomorphies for recognized genera. Some of the characters employed in defining *Paepalanthus* subcategories appear to have evolved multiple times, and many clades may be exclusively defined by molecular synapomorphies. Biogeographical reconstructions suggest that the current distribution patterns may be related to vicariance and a few long-distance dispersal events. Furthermore, some clades are restricted to narrow geographical areas, perhaps important as a means of conserving evolutionary processes. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, 171, 225–243.

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INTRODUCTION

Eriocaulaceae comprise c. 1200 species and 11 genera distributed throughout the tropics (Giulietti &

Hensold, 1990; Stützel, 1998; Sano, 2004; Parra *et al.*, 2010; Andrade *et al.*, 2011). The family is historically divided into two subfamilies: Paepalanthoideae and Eriocauloideae (Koernicke, 1863; Ruhland, 1903). The former is characterized as possessing haplostemonous androecia, eglandular corollas and gynoecia with alternating stigmatic and nectariferous branches (Ruhland, 1903; Rosa & Scatena, 2007). All nine genera and c. 800 species of Paepalanthoideae

*Corresponding author. Current address: Departamento de Botânica, Instituto de Biologia, Universidade Federal do Rio de Janeiro, CCS, Bloco A1, Cidade Universitária, Ilha do Fundão, CEP 21941-590, Rio de Janeiro, RJ, Brasil. E-mail: martrovo@gmail.com

(Fig. 1) are predominantly distributed throughout the Neotropics (Giulietti & Hensold, 1990; Stützel, 1998). According to Giulietti *et al.* (2005), c. 95% of the species included in this subfamily are narrow endemics and restricted to a few small populations. Some species are of great economic importance. Every year, large numbers of inflorescences from species of *Syngonanthus* Ruhland, *Comanthera* L.B.Sm. and *Paepalanthus* Mart. are exported to North America and Europe as 'everlasting plants' and, more recently, as 'golden grass' (Giulietti *et al.*, 1988; Schmidt, Figueiredo & Scariot, 2007; Costa, Trovó & Sano, 2008; Parra *et al.*, 2010). These species are not cultivated but simply harvested *in situ*, leading to depletion of the natural populations. Indeed, many species of Paepalanthoideae are highly endangered. For example, 94 species have been cited on the Red List of State of Minas Gerais and 20 on the Red List of Brazil (Biodiversitas, 2008). *Paepalanthus* spp. are also notable for their antioxidant and mutagenic properties (Varanda *et al.*, 2006; Devienne *et al.*, 2007).

In Paepalanthoideae, *Paepalanthus* is the largest genus with c. 380 species (Giulietti & Hensold, 1990; Stützel, 1998). Morphological and species diversity is concentrated in Brazilian campos rupestres in the Espinhaço Range and in the Guayana Shield Highlands (Giulietti & Hensold, 1990; Hensold, 1991, 1999). The genus is characterized by pistillate flowers with free petals and stigmatic/nectariferous branches that are free at the same insertion point. Nevertheless, with the exception of these few floral characters, morphological variation in both floral and vegetative traits is broad. This variation provided the basis for the proposition of > 20 infrageneric categories in previous classifications of the genus (Koernicke, 1863; Ruhland, 1903). Some categories, such as *Paepalanthus* subgenus *Platycaulon* Koern., are morphologically easily recognized, whereas others, such as *Paepalanthus* series *Paepalanthus*, simply represent aggregations of possibly unrelated species (Stützel, 1998). Thus, the extensive morphological variation in *Paepalanthus* may obscure the phylogenetic relationships and explain, at least in part, its complex nomenclatural and taxonomic history.

The first phylogenetic study involving Paepalanthoideae was based entirely on morphological data (Giulietti, Amaral & Bittrich, 1995). In this study, Paepalanthoideae emerged as monophyletic, whereas *Paepalanthus* was polyphyletic. In a later study, Giulietti *et al.* (2000), taking into consideration morphology, anatomy and chemistry, concluded that Paepalanthoideae are paraphyletic, but many of the genera are monophyletic. Polyphyly of *Paepalanthus* was also stated in that study. The outcome of recent molecular phylogenetic analyses (Unwin, 2004;

Andrade, 2007; Andrade *et al.*, 2010) was fairly similar: all confirming the monophyly of both subfamilies and the genera *Leiothrix* Ruhland and *Actinocephalus* (Koern.) Sano *emend.* (F. N. Costa & P. T. Sano, unpubl. data; including *Paepalanthus* subsection *Aphorocaulon* Ruhland) and the polyphyly of *Paepalanthus*. Thus, based on the monophyly of Paepalanthoideae (Giulietti *et al.*, 1995; Unwin, 2004; Andrade, 2007; Andrade *et al.*, 2010), our main goal was to infer phylogenetic relationships in the subfamily, with an emphasis on *Paepalanthus* and its Brazilian subgroups. Evolution of morphological characters and biogeographic history of the Paepalanthoideae were reconstructed in order to clarify the classification and evolution of the group in the Neotropics.

MATERIAL AND METHODS

TAXA SAMPLED

All nine genera of Paepalanthoideae and all infrageneric categories of *Paepalanthus* recognized by Ruhland (1903) were sampled, except for *Paepalanthus* subgenus *Psilandra* Ruhland, known exclusively from the type specimen. Overall, 94 species were sampled as follows: *Actinocephalus* 5/28 (species sampled/species belonging to the genus), *Comanthera* 3/37, *Lachnocaulon* Kunth 1/7, *Leiothrix* 6/64, *Paepalanthus* 73/380, *Philodice* Mart. 1/2, *Rondonanthus* Herzog 2/6, *Syngonanthus* 2/150 and *Tonina* Aubl. 1/1. The sampling in *Paepalanthus* and *Syngonanthus* is limited at a first glance. However, many species of these genera are known only from the type specimen or unknown type localities. Recent taxonomic revisions identified many synonyms in these groups, and the number of species of *Paepalanthus* and *Syngonanthus* may actually be much smaller. Moreover, *Syngonanthus* is monomorphic in relation to the morphological traits evaluated (Koernicke, 1863; Ruhland, 1903). Three species of *Eriocaulon* L. were included as outgroups, based on previous phylogenies (Unwin, 2004; Andrade *et al.*, 2010). The complete list of taxa and voucher specimens is given in Appendix 1.

SEQUENCES AND ALIGNMENT

The nuclear internal transcribed spacer (ITS) region and the plastid *trnL-trnF* region were chosen because of their rate of sequence variation, based on previous studies in the family by Unwin (2004), Andrade (2007) and Andrade *et al.* (2010). Sequences for 59 species were obtained from Andrade *et al.* (2010) and additional sequences for 35 species were obtained for this study. All GenBank accession numbers are listed in Appendix 1.

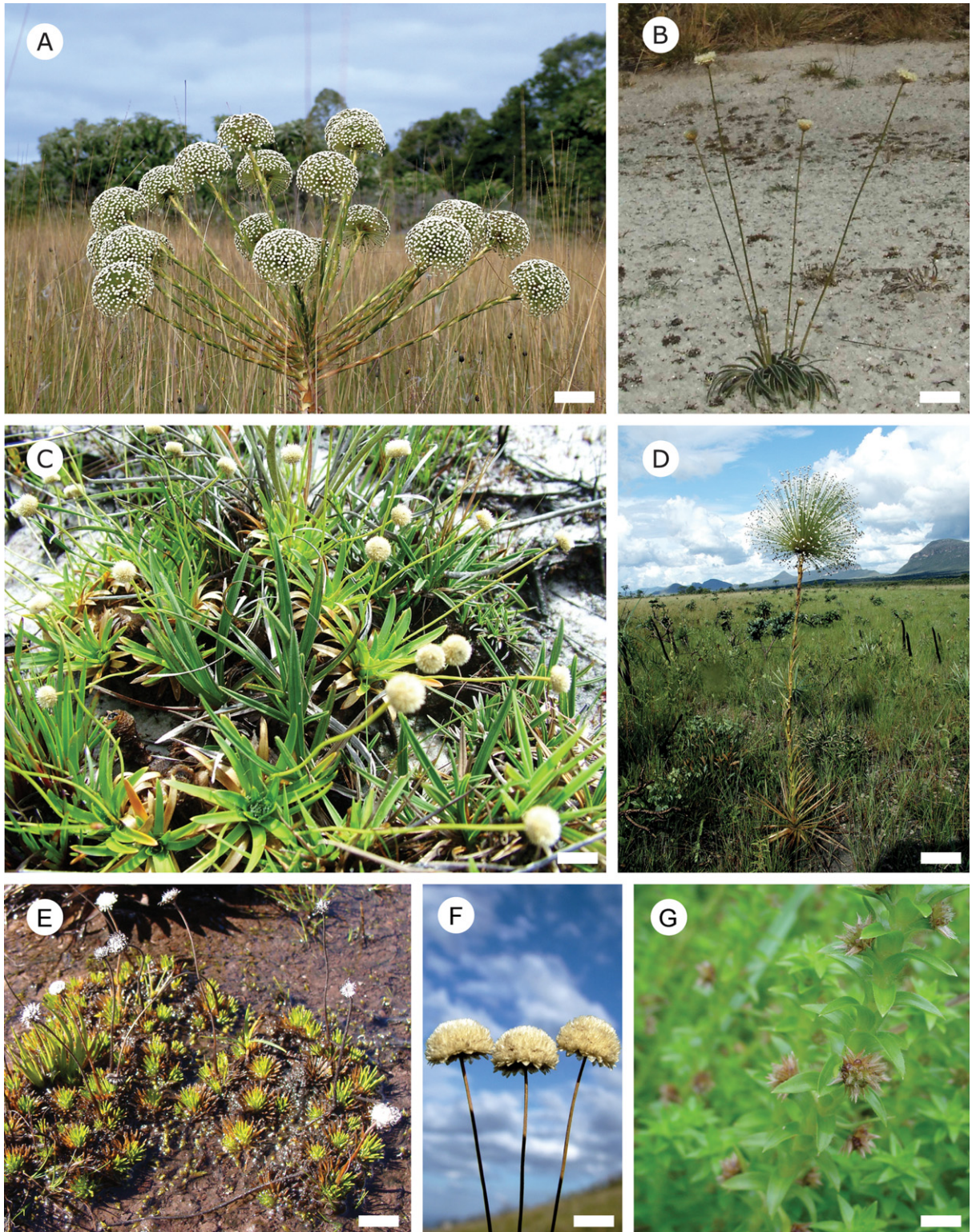


Figure 1. Photographs of Paepalanthoideae representatives in nature. A, *Actinocephalus polyanthus* (Bong.) Sano. B, *Comanthera linearis* (Ruhland) L.R. Parra & Giul. C, *Leiothrix crassifolia* (Bong.) Ruhland. D, *Paepalanthus chiquitensis* Herzog. E, *Rondonanthus roraimae* (Oliver) Herzog. F, *Syngonanthus nitens* (Bong.) Ruhland. G, *Tonina fluviatilis* Aubl. Scale bars, 5 cm (A); 4 cm (B); 0.5 cm (C); 25 cm (D); 7 cm (E); 0.4 cm (F); 0.3 cm (G). [Photographs: M. Trovó (A, C, D and F); L. Echternacht (B and E); S. Martins (G)].

Total DNA was extracted from leaves dried in silica gel, using 5–50 mg and a modified 2 × cetyl trimethylammonium bromide (CTAB) protocol (Doyle & Doyle, 1987). The *trnL-trnF* spacer was amplified and sequenced using the c and f universal primers (Taberlet *et al.*, 1991). Amplification was conducted on 50 µL reaction containing 1 × polymerase chain reaction (PCR) reaction buffer, 2.5 mM magnesium chloride (MgCl₂), 0.2 mM deoxyribonucleotide triphosphates (dNTPs), 0.5 µM each primer, 0.5 µg bovine serum albumin (BSA) and 0.25 units *Taq* DNA polymerase (Phonectria Ltd, Belo Horizonte, Brazil). PCR included an initial denaturing cycle at 94 °C for 3 min, followed by 35 cycles at 94 °C for 1 min, 50–52 °C for 1 min and 72 °C for 2 min, and a final extension of 72 °C for 5 min. The ITS region was amplified and sequenced using primers 75 and 92 for angiosperms (Desfeaux *et al.*, 1996). ITS amplification was with a 50-µL reaction containing 1 × PCR reaction buffer, 2.5 mM MgCl₂, 0.2 mM dNTPs, 0.5 µM each primer, 1 µg BSA, 1.0 M betaine, 2% dimethyl sulphoxide and 0.25 units *Taq* DNA polymerase. PCR included an initial denaturing cycle at 94 °C for 3 min, followed by 35 cycles of 94 °C for 45 s, 56–58 °C for 1 min and 72 °C for 2 min, and a final extension of 72 °C for 5 min.

PCR products were purified by enzymatic treatment using the EXOSAP-IT kit (GE Healthcare, USB, Cleveland, OH, USA). Sequencing reactions were carried out with Big Dye Terminator kit, ver. 3.1 (Applied Biosystems, Foster City, CA, USA). Samples were sequenced in both directions using the same primers in an ABI 3130XL automatic sequencer, according to protocols supplied by the manufacturer.

Sequences were edited using the STADEN package (Staden, Beal & Bonfiel, 1998) and aligned using MUSCLE (Edgar, 2004), with subsequent visual correction. The molecular data sets ITS and *trnL-F* were analysed independently and simultaneously. The combined molecular matrix included only terminals sequenced for both markers. All molecular matrices are available at TreeBase <http://www.treebase.org> (study no. 10836).

PHYLOGENETIC ANALYSES

Parsimony analysis was conducted in PAUP* 4.0b10 (Swofford, 2002). One thousand replicates with random taxon-addition were conducted with tree-bisection-reconnection (TBR). Up to 250 trees were retained for each replicate. For combined analysis, the partition homogeneity test implemented in PAUP 4.0b10 (Swofford, 2002) including both partitions was run with 1000 homogeneity replicates, saving a maximum of 1000 trees. Measurements of clade support were estimated by bootstrap analyses using

the same parameters applied for the initial tree search (Felsenstein, 1985). Gaps were treated as missing data. Multiple equally most-parsimonious trees were summarized as strict consensus trees (Sokal & Rohlf, 1981).

For Bayesian analyses, evolutionary models for the molecular data were chosen with hLRTs using MrModeltest 2.2 (Nylander, 2004). Model selection was conducted for the ITS region split into three parts, corresponding to ITS1, 5.8S and the ITS2 regions, and the *trnL-trnF* region split in two, corresponding to the intron and spacer regions. Analyses were performed on MrBayes 3.1 (Ronquist & Huelsenbeck, 2003), run for 5 000 000 generations using two sets of four chains, sampling one tree every 500 generations. Instead of selecting the burn-in using the graphic approach by plotting the likelihood scores against the number of generations, we discarded the trees obtained before the standard deviations between two sets of chains reached a value < 0.01. We consider this a stricter way of guaranteeing that chains achieved stability. A majority rule consensus of the remaining trees was obtained in PAUP*, with group frequencies representing the posterior probabilities.

CHARACTER AND BIOGEOGRAPHICAL RECONSTRUCTION

All specimens were analysed under a stereomicroscope in order to evaluate the morphological characters, especially those that are taxonomically relevant. Thirteen characters were coded into binary states and mapped onto the consensus tree of the combined molecular data set using ‘Trace Character History’ implemented in Mesquite ver. 2.74 for Macintosh (Maddison & Maddison, 2009). For this, all characters were treated as unordered and optimization with accelerated transformations (ACCTRAN) was used. Tree and character distributions were edited and summarized using Figtree 1.3.1 for Macintosh (Rambaut, 2009), facilitating the visualization of all character state distributions. All characters and their respective states and the morphological matrix encompassing all species in the combined analysis are available in Appendix 2.

Distributions of all species were established according to recent taxonomic revisions and herbarium searches (Appendix 3). They were coded as binary states in a matrix according to the following a priori defined regions (outlined together with the results in Fig. 5): Espinhaço Range in Minas Gerais (A); Espinhaço Range in Bahia (B); cerrado (C); Lowland Guianan savanna (D); restingas (E); tepuis (F); and Caribbean (G). Biogeographical reconstructions were performed using S-DIVA-RASP ver. 1.107 (Ronquist,

Table 1. Statistics for analyses of *trnL-trnF* and internal transcribed spacer (ITS) data sets for Paepalanthoideae

Characteristic	<i>trnL-trnF</i>	ITS	<i>trnL-trnF</i> , ITS
No. of taxa	89	90	82
Aligned length	1372	998	2370
Constant characters	740	397	1142
Variable characters	382	535	909
Informative characters	270	428	690
No. of trees obtained*	2509	165	112
Minimum tree length*	807	1798	2599
Consistency index	0.642	0.531	0.565

*Statistics for parsimony.

1997; Nylander *et al.*, 2008; Yu, Harris & He, 2011) using the last 8000 trees from the post burn-in sample, over the combined Bayesian tree. Polytomies were solved manually but not interpreted in the final reconstruction. Frequencies of ancestral area reconstructions are described for each tree node.

RESULTS

Statistics for analyses of the *trnL-F* and ITS data sets are given in Table 1. The partition homogeneity test indicated no significant disagreement between *trnL-F* and ITS regions ($P = 0.10$). The evolutionary model selected for ITS1, ITS2, the *trnL* intron and the *trnL-trnF* spacer was GTR + I + G; for 5.8S K80 + G was selected. For *trnL-F* the following characters were excluded in the aligned matrix: 1–55, 550–590, 910–940, 1250–1280 and 1280–1372; for ITS 1–40, 507–518, 791–802 and 996–998 were excluded. These regions were excessively variable and, consequently, we were not confident in the alignments achieved. Variation in the ITS region was greater than in *trnL-trnF* (47.3 vs. 25.9%). In addition, a comparison among tree topologies from all the analyses revealed high congruence, with no supported disagreement between the topologies derived from individual or combined data sets. Therefore, the trees derived from individual analyses are presented in the Supporting Information (Appendix S1 and Appendix S2). In either individual or combined trees, the main clades are supported by high bootstrap values and high Bayesian posterior probabilities. The main results of the combined analyses (Fig. 2), the morphological character optimizations (Figs 3, 4) and the biogeographical reconstruction (Fig. 5) are detailed below. In the few cases of discrepancies between tree topologies, Appendix S1 and/or Appendix S2 (see Supporting Information) are also cited.

Rondonanthus is monophyletic (89/95, bootstrap/Bayesian posterior probabilities) (see also Supporting Information, Appendix S1), has linear staminodes (character: state 6:1) and is sister to clade B (100/100). The clade including *Rondonanthus* and the remaining genera is characterized by the absence of glands on the staminate flower (2:1), the haplostemonous androecium (3:1) and absence of leaf fenestration (4:1). The monophyly of clade B (91/97) is supported by the tubular corolla in the staminate flower (5:1). *Leiostrix* (100/100) is sister to clade C (90/99), which contains clade D (100/94) and the core *Paepalanthus* clade (100/100) (Fig. 2; see also Supporting Information, Appendix S2). Clade D consists of *Syngonanthus* spp. sister to *Philodice* (100/100), together forming a monophyletic group with the recently re-established *Comanthera* (100/100). The relationship between these three genera is supported by the median fusion of the pistillate flower (8:1). There are two distinct lineages in the core *Paepalanthus* clade, clades E (95/100) and F (90/95) (Fig. 2; see also Supporting Information, Appendix S2). Clade E is composed of a basal dichotomy with *Tonina/Lachnocaulon* (100/100) (Supporting Information, Appendix S1) and species of *Paepalanthus* and *Actinocephalus* (90/100). The relationships among these species may vary according to the different analyses (Fig. 2; see also Supporting Information, Appendix S1). Both species of *Paepalanthus* subgenus *Thelxinöe* Ruhland form a strongly supported clade (100/100) and emerge in clade G, (85/100). In clade G, *Actinocephalus* emerges as sister to a clade, comprising *Paepalanthus* section *Diphyomene* Ruhland and *Paepalanthus* series *Dimeri* (Ruhland) Giul.

In two analyses (Fig. 2; see also Supporting Information, Appendix S1), *Paepalanthus* subgenus *Mono-sperma* Hensold (100/100) is sister to the remaining species in clade F (90/95) and has only the median locule of the gynoeceum fertile (7:1). In clade H (100/100), clade I (90/97) includes *Paepalanthus erigeron* Mart., the type species of *Paepalanthus*. Clade J (–/95) is split in two main lineages. In clade K (90/100), *P.* subgenus *Platycaulon* is monophyletic (Fig. 2; see also Supporting Information, Appendix S2) (100/100), defined by the fused scapes (11:1), and is sister (98/100) to *P.* subgenus *Xeractis* Mart. (85/91) (Fig. 2; see also Supporting Information, Appendix S1), which is defined by the hairs on the adaxial surface of the staminate flower corolla (9:1). *Paepalanthus* subsection *Dichocladus* is sister (85/91) to species originally placed in the recently synonymized *Blastocaulon* Ruhland. Clade L (92/96) comprises several infrageneric categories of *Paepalanthus*.

Biogeographical reconstruction of Paepalanthoideae is presented in Figure 5. Although *Rondonanthus* is restricted to the tepuis and adjacent

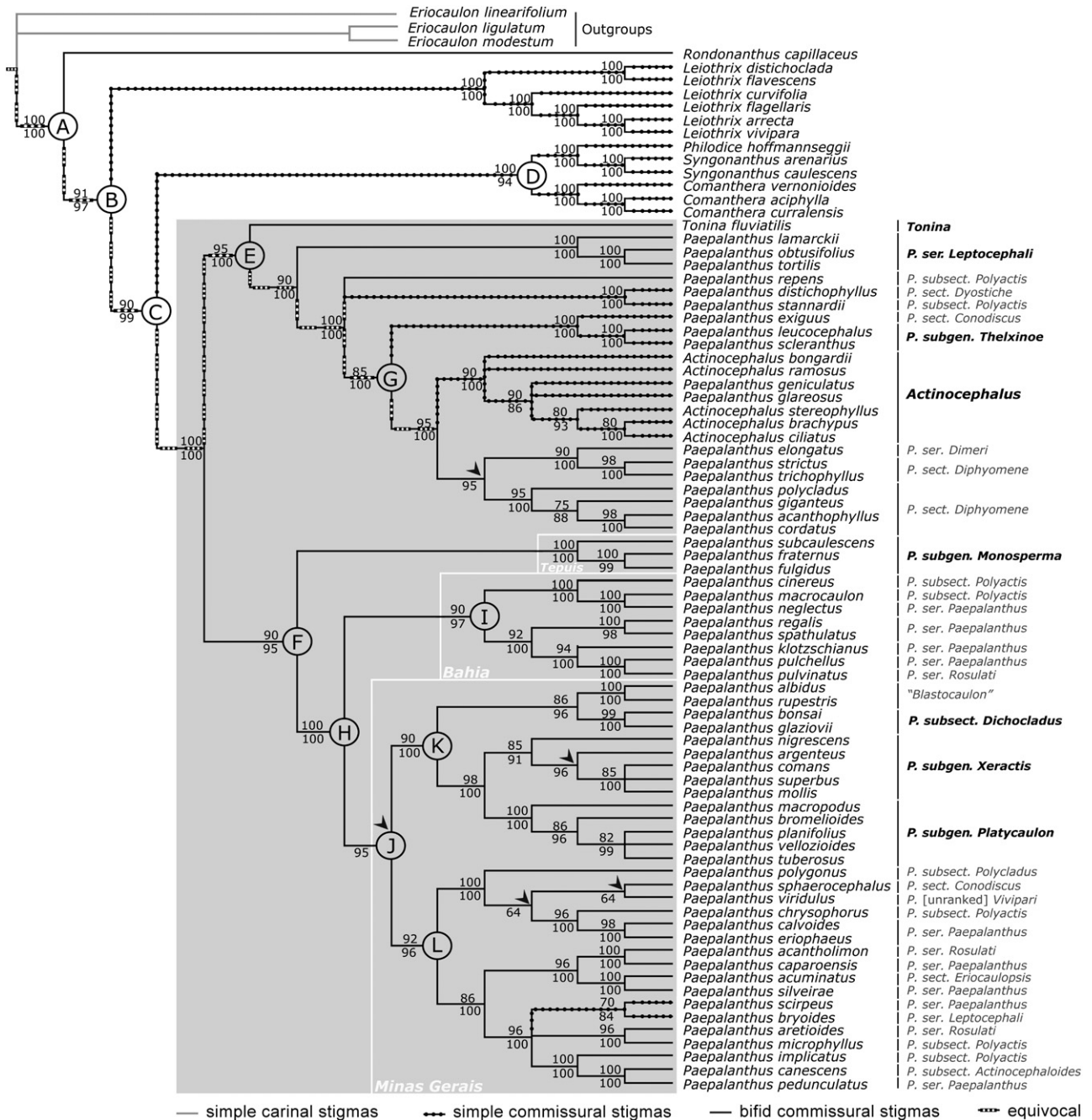


Figure 2. The 50% majority rule consensus tree from the Bayesian analysis of the combined *trnL-trnF* and internal transcribed spacer (ITS) data sets. Numbers above branches indicate bootstrap support and numbers below indicate Bayesian posterior probabilities. Arrowheads indicate clades not recovered in the parsimony analysis. The shaded box indicates the core *Paepalanthus* clade, in which white boxes are correlated with biogeographical patterns. Clade names follow the classification of Ruhland (1903). Branches marked with grey lines have simple carinal stigmas, branches marked with dark dotted lines have simple commissural stigmas, branches marked with dark plain lines have bifid commissural stigmas and branches marked with white dotted lines have an equivocal character state.

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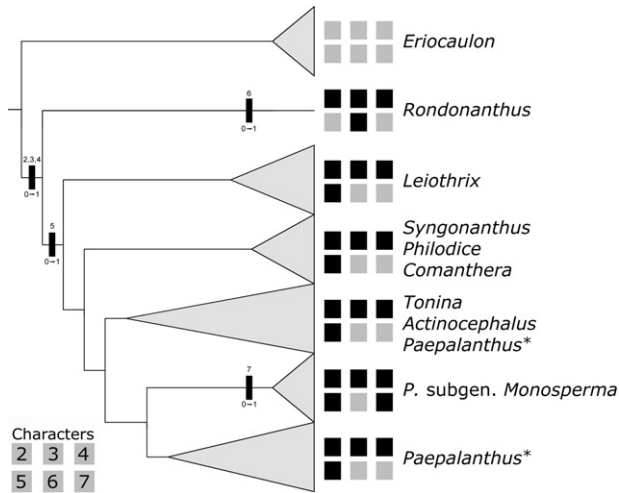


Figure 3. Character distribution of six morphological characters onto the summarized combined molecular phylogenetic tree shown in Figure 2. Characters are: 2, glands on staminate flower; 3, androecium; 4, leaf fenestration; 5, petals of the staminate flower; 6, staminodes on pistillate flower; 7, fertile locules of the gynoecium. Grey squares represent the state 0, black squares represent the state 1. Numbers above the character bars indicate the character on Appendix 2 and numbers below the character bars indicate the character state transition.

lowlands Guianan savannas, the ancestor of clade A is not confidently reconstructed to a specific area. The Espinhaço Range in Minas Gerais, which is the primary centre of diversity, is consistently recovered as ancestor for many clades. In clade E, with uncertain ancestral distribution, emerge species restricted to the Espinhaço Range, mainly in Minas Gerais, and a clade optimized to the savannas. Subclades include one formed by *Actinocephalus*, diversified in the Espinhaço Range, and a clade with dimerous flowers, diversified in the cerrado and lowland Guianan savannas. In clade F, the biogeographical signal is significant. A clade restricted to the tepuis is sister to a clade restricted mainly to the Espinhaço Range (clade H). In the Espinhaço Range clade, two distinct lineages are clearly recognized, one associated with the Espinhaço Range in Bahia (clade I) and one with the Espinhaço Range in Minas Gerais (clade J).

DISCUSSION

PHYLOGENETIC IMPLICATIONS

Based on morphological and chemical data, Giuletta *et al.* (2000) concluded that Paepalanthoideae were paraphyletic, a hypothesis not confirmed here or in previous molecular analyses (Unwin, 2004; Andrade,

2007; Andrade *et al.*, 2010). After re-rooting their tree (Giuletta *et al.*, 2000: 585) between Paepalanthoideae and Eriocauloideae, similarities with our conclusions are evident. The existence of a clade comprising *Paepalanthus*, *Actinocephalus*, *Tonina* and *Lachnocaulon* can be confirmed, with the exception of the sister relationship between *Philodice* and *Tonina*. The existence of a clade including *Actinocephalus* and some species of *Paepalanthus* with dimerous flowers can also be confirmed. Nevertheless, the relationship between *Leiothrix* and *Syngonanthus* needs to be re-evaluated, as it is again not supported here, but only in one of the cladograms of Andrade *et al.* (2010: 382).

Similarities with previous molecular phylogenetic analyses (Unwin, 2004; Andrade, 2007; Andrade *et al.*, 2010) are not surprising, attributable to the previous levels of support of previous studies and the use of the same molecular markers and part of the data set of Andrade (2007) and Andrade *et al.* (2010). The main similarities are the monophyly of *Leiothrix*, the sister-group relationship between *Tonina* and *Lachnocaulon* and the formation of two main lineages in the core *Paepalanthus* clade, one formed by species from *Paepalanthus*, *Actinocephalus*, *Tonina* and *Lachnocaulon* and the other by species recognized as *Paepalanthus*, including the type species.

There are, however, some differences between the present study and results from previous analyses (Andrade, 2007; Andrade *et al.*, 2010). The main differences are that a monophyletic *Rondonanthus* was sister to the remaining Paepalanthoideae and that *Comanthera* and not *Leiothrix* was sister to a clade that includes *Syngonanthus* and *Philodice*. These differences may arise as a result of alignment differences and increased sampling. They are in accordance with morphological evidence, as the included *Rondonanthus* spp. have free petals on the staminate flowers at maturity. However, the remaining species of the genus, which were not sampled, have a typical tubular corolla. The inclusion of such species will be crucial to further evaluate this character and the monophyly of the group itself. *Syngonanthus*, *Philodice* and *Comanthera* share pistillate flowers with petals fused in the middle. The inclusion of more terminals, especially of *Paepalanthus*, may increase the clade support and the resolution in the core *Paepalanthus* clade. In this clade, four of the five subgenera of *Paepalanthus* are monophyletic, but *P.* subgenus *Paepalanthus* is polyphyletic. Clade F comprises *P.* subgenus *Monosperma*, restricted to the tepuis of northern South America, and sister to a clade comprising two subclades, one restricted to the north of the Espinhaço Range and the other restricted to the south of the Espinhaço Range.

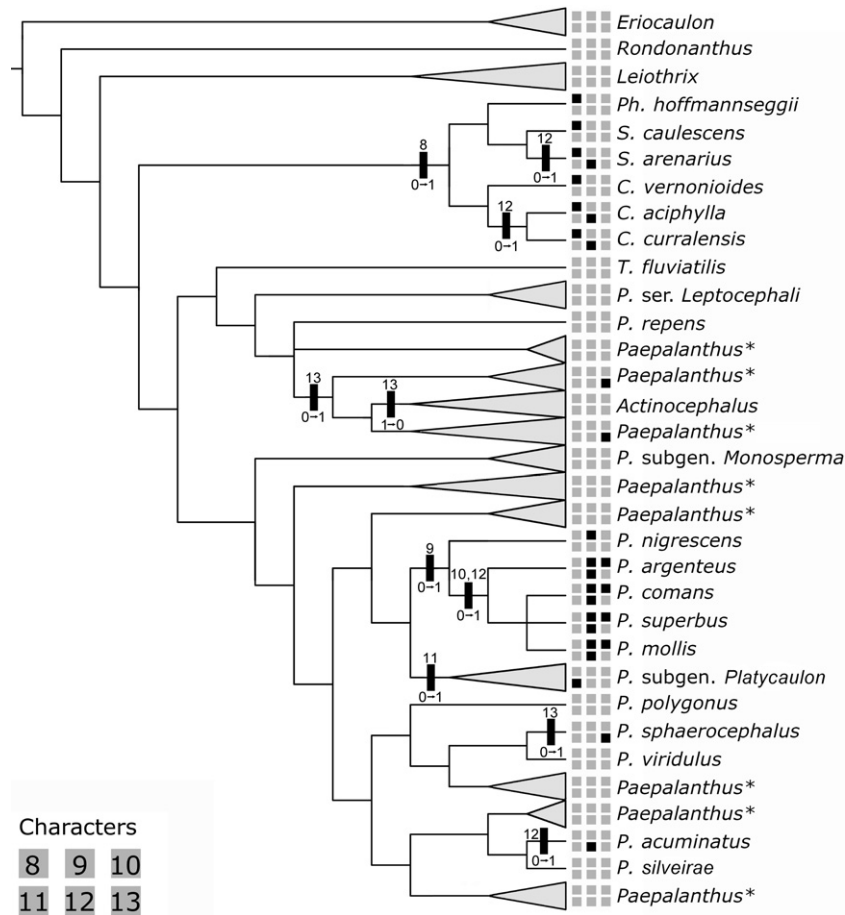


Figure 4. Character distribution of six morphological characters onto the summarized combined molecular phylogenetic tree shown in Figure 2. Characters are: 8, petals of the pistillate flower; 9, trichomes inside the corolla of the staminate flower; 10, involucre bracts adaxial surface; 11, scapes; 12, involucre bracts; 13, floral merism. Grey squares represent state 0, black squares represent state 1. Numbers above the character bars indicate the character on Appendix 2 and numbers below the character bars indicate the character state transition.

MORPHOLOGICAL IMPLICATIONS

The monophyly of Paepalanthoideae suggests several putative synapomorphies for the group, including central projection of the carpels arising on nectariferous branches, lateral projections of the carpels arising on stigmatic branches (Fig. 2), eglandular petals and a haplostemonous androecium (Fig. 3). Most species of this subfamily have unfenestrated leaves (Fig. 3). Based on current sampling, clade B may be defined as having the petals of the staminate flower forming a tubular corolla (Fig. 3). However, this character is shared with *Mesanthemum* Koern., all species of *Rondonanthus* except *Rondonanthus capillaceus* (Koern.) Hensold & Giul. and it is absent in some unsampled species, such as *Leiothrix fluitans* (Mart.) Ruhland.

Several characters commonly used to separate the genera of Eriocaulaceae may be putative synapomor-

phies. *Rondonanthus* is defined by the presence of linear staminodes (Fig. 3). The position of this genus as an early divergent genus in Paepalanthoideae was previously suggested by Hensold & Giulietti (1991). Some characters, such as the linear staminodes in the pistillate flower and the bisexual flower in *R. flabelliformis* (Moldenke) Hensold & Giulietti could be interpreted as plesiomorphies. In Eriocaulaceae, the linear staminodes are best interpreted as a synapomorphy, the first steps in the reduction of one of the two whorls of stamens. In Paepalanthoideae, the presence of the linear staminodes may, however, be regarded as plesiomorphic as they are lost in descendant clades. The inclusion of *R. flabelliformis* (not sampled) will be also crucial in evaluating the evolution of this character, because of its supposedly unique bisexual flowers, with apparently functional stamens. That species will be also important for

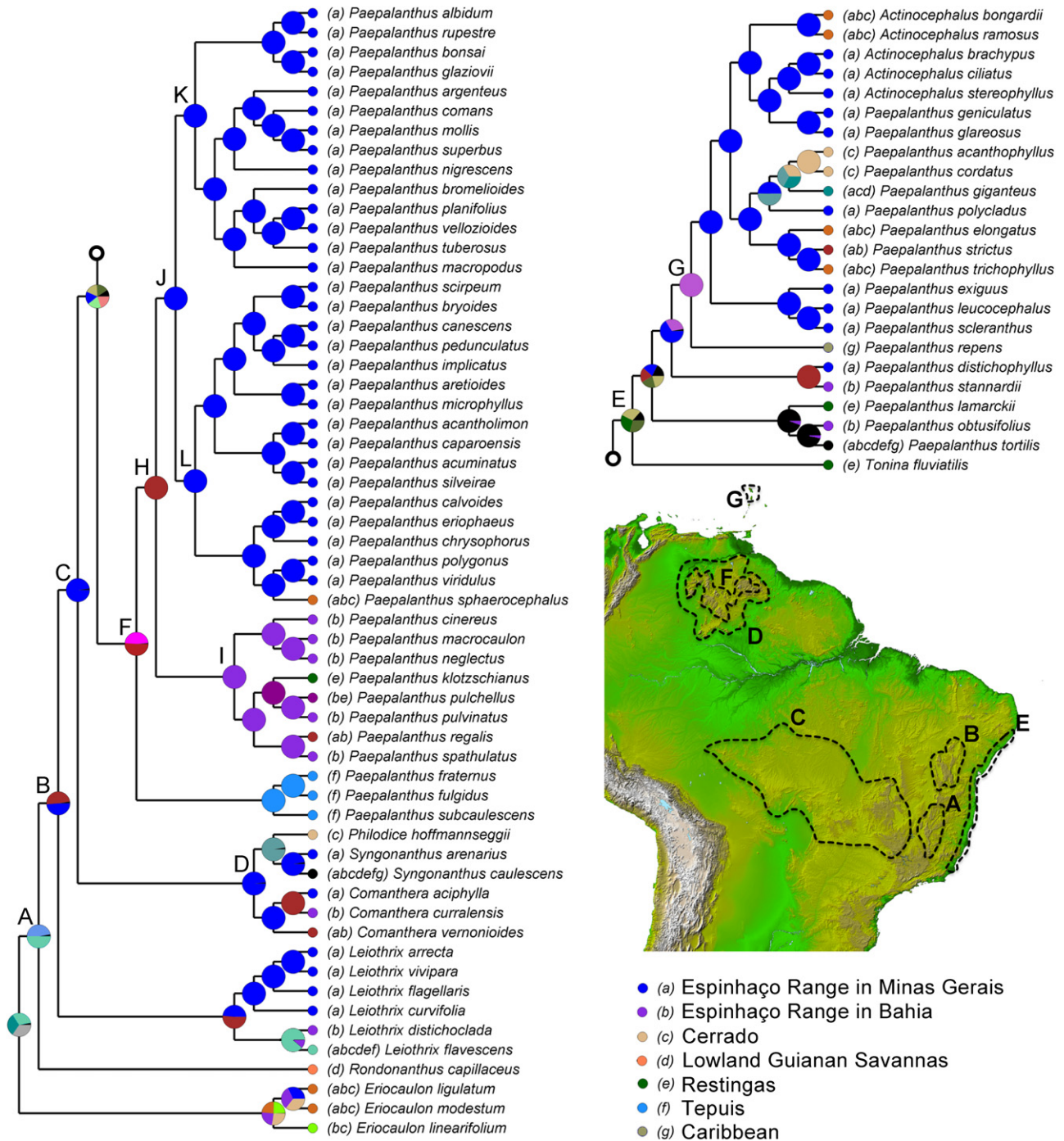


Figure 5. Graphical representation of ancestral distributions reconstructed over the combined Bayesian tree for sub-family Paepalanthoideae. The pie charts on each node show the relative probabilities of ancestral distribution obtained from the last 8000 Bayesian post-burn-in trees. States of extant species and colour correspondence with the respective areas can be assessed directly from the terminals. Biogeographical regions: (1) Espinhaço Range in Minas Gerais; (2) Espinhaço Range in Bahia; (3) cerrado; (4) Lowland Guianan savannas; (5) restingas; (6) tepuis; and (7) Caribbean.

testing the monophyly of the genus itself and to test the validity of the morphological placement of *Wurdackia* Moldenke in *Rondonanthus* (Hensold & Giulietti, 1991).

Leiothrix has nectariferous and stigmatic branches inserted at the style at different levels and the presence of basifixed anthers (shared with *Tonina*) as putative synapomorphies (Andrade *et al.*, 2010).

Fused petals in the mid-region of pistillate flowers, also a feature in *Mesanthemum* (Eriocauloideae) and three unsampled *Rondonanthus* spp., are a synapomorphy for clade D, containing *Comanthera*, *Syngonanthus* and *Philodice* (Fig. 4). In this clade, *Syngonanthus* appears monophyletic and is sister to *Philodice*; however, *Syngonanthus* is poorly sampled so far. The *Tonina/Lachnocaulon* clade may be defined as having smaller petals in pistillate flowers. In *Tonina*, this reduction is only partial, resulting in a small petal with long trichomes, whereas in *Lachnocaulon* the reduction to many trichomes is complete (Ruhland, 1903; Unwin, 2004; Andrade *et al.*, 2010).

In *Paepalanthus*, certain characters used to distinguish infrageneric categories may also constitute clade synapomorphies. *Paepalanthus* subgen. *Xeractis* can be defined by the hairs on the adaxial surface of the corolla in staminate flowers as a putative synapomorphy (Fig. 4). Some *Eriocaulon* spp., such as *Eriocaulon linearifolium* Koern. and *Eriocaulon modestum* Kunth, both included as outgroups, are described as possessing similar trichomes. However, in the specimens analysed, such trichomes are lacking. The inclusion of a few more species, such as the rare *Paepalanthus aureus* Silveira, would be relevant to test the validity of the hairs on the adaxial surface of the bracts (10:1) as a putative synapomorphy (Fig. 4). This species does not display this feature (Hensold, 1988) and, in a recent phylogenetic analysis, Echternacht *et al.* (2011) indicate that this character is not uniform in the group and should be studied in greater depth. *Paepalanthus* subgenus *Platycaulon* is defined by the fusion of scapes at various levels (Fig. 4) (Tissot-Squalli, 1997), and in *P.* subgenus *Monosperma*, the achene-like fruits, as a result of abortion of two locules, are a putative synapomorphy (Fig. 3) (Hensold, 1991). Nevertheless, the relevance of monospermy as a meaningful character would require that the same locule is always fertile in all species belonging to this group, which has to be better investigated.

As shown in Figure 2, the well-supported monophyletic groups have uniform gynoecium composition, with either simple fully congenitally fused (1:1) or bifid, only basally fused stigmas (1:2). Ruhland (1903) already noticed the relevance of this character, constructing his classification system in a pragmatic way, separating the morphologically uniform groups first and reordering the variable species under *Paepalanthus* subgenus *Paepalanthus* (= *P.* subgenus *Paepaloccephalus* Ruhland). In this subgenus, Ruhland (1903) found some other uniform groups, such as *Paepalanthus* section *Actinocephalus* Koern. (now part of *Actinocephalus*), but placed most of the remaining species under *P.* series *Paepalanthus* (= *P.* ser. *Variabiles* Ruhland). Towards a better understanding of

the phylogeny, the focus has to be on key species that now form morphologically heterogeneous clades. In contrast, further sampling in well-supported and morphologically well-defined clades such as *P.* subgenera *Platycaulon* and *Xeractis* and *Actinocephalus* may not be necessary to elucidate further the intergeneric relationships in *Paepalanthus*.

Other important features, such as relative size of involucral bracts and floral merism (characters 12 and 13) seem to have evolved multiple times in the group (Fig. 4) and appear in many clades. The flowers are usually trimerous in most *Paepalanthoideae*, but are dimerous in a few species (Koernicke, 1863; Ruhland, 1903). Dimerous flowers may have evolved at least twice, in *Paepalanthus sphaerocephalus* Ruhland and in clade G. As far as is known from developmental studies (Stützel, 1984, 1985) the precondition for this shift to dimery is the late initiation and subsequent reduction of the median sepal. The parallel shift to dimery in different genera, such as *Paepalanthus*, is therefore not surprising. In clade G, only *Actinocephalus* has trimerous flowers, probably attributable to a reversion. The inclusion of more dimerous species and studies on their floral development would be of interest in determining the evolution of this character. The relative size of the floral bracts was considered an important feature in defining groups such as *P.* subgenus *Xeractis* (Ruhland, 1903). They evolved, however, in different genera and even in *Paepalanthus* appear in unrelated species, as predicted by Hensold (1988) and Echternacht *et al.* (2011).

Various groups in the core *Paepalanthus* clade are defined exclusively by molecular characters. Searching for and testing morphological synapomorphies for these clades will be crucial for their recognition and understanding. Nevertheless, this search requires novel approaches in Eriocaulaceae morphology, which is still grounded on Ruhland's (1903) concepts. Certain clades, such as *P.* subsection *Dichocladus*, represented only by the Brazilian species or the clade comprising *Paepalanthus stannardii* Giul. & L.R.Parra / *Paepalanthus distichophyllus* Mart., possess unusual ramification patterns, which could turn out to be synapomorphies. Detailed studies on inflorescence morphology could also lead to new perspectives in the discovery of novel synapomorphies (Stützel, 1984; Oriani, Scatena & Sano, 2008; Trovó *et al.*, 2010). Two recently reinterpreted, putative morphological synapomorphies for *Paepalanthoideae* were derived from a new developmental framework: the central projection of the carpels giving rise to nectariferous branches, and lateral projections of the carpels to stigmatic branches. In this context, we stress the importance of seeking other unusual and less explored characters, such as embryological and

developmental characters (Coan & Scatena, 2004; 2007; Rosa & Scatena, 2007).

BIOGEOGRAPHICAL IMPLICATIONS

The occurrence of both subfamilies in Africa and South America may suggest a Gondwanan origin of Eriocaulaceae, roughly consistent with its crown node estimated at *c.* 105 Mya (Janssen & Bremer, 2004). The initial split of these lineages may have occurred shortly before the separation of the continents. African species of *Paepalanthus* and *Syngonanthus* may be considered relics of the past distribution, mainly because the favoured habitats of these genera are now rather uncommon in north, north-east and south-west Africa. Alternatively, long-distance dispersal has already been evoked to justify the amphiatlantic distribution of many groups; for example, in Bromeliaceae (Givnish *et al.*, 2004; Renner, 2004) and Sapotaceae (Bartish *et al.*, 2011). In Eriocaulaceae, long-distance dispersal has also been suggested to explain the occurrence of *Eriocaulon aquaticum* (Hill) Druce in North America and in Great Britain (Giulietti & Hensold, 1990).

In Paepalanthoideae, two main biogeographical patterns arose from our combined analysis (Fig. 2) and the biogeographical reconstruction (Fig. 5). As in Rapateaceae and Bromeliaceae (Givnish *et al.*, 2004), in Eriocaulaceae, we infer that species occurring in the Venezuelan–Guayana Highlands are early divergent in their lineages. *Rondonanthus* (all species except *R. capillaceus* are restricted to the Venezuelan–Guayana Highlands) is sister to the remaining Paepalanthoideae and *P.* subgenus *Mono-sperma* is sister to clade H. The explanation of such a pattern might be found in the advanced age of the region and isolation of the populations in the Brazilian and Guiana Shields. Diversity would be autochthonal and derived from isolated ancestries in a heterogeneous habitat (Berry & Riina, 2005). Givnish *et al.* (2004) pointed to the possibility of mutual colonization of both these highlands and the adjacent lowlands, as a result of climate variation. In Eriocaulaceae, species diversity is concentrated in the highlands, although there are a few endemic species in the lowlands. Inclusion of these will be essential for understanding the processes of local occupation and diversification (Hensold, 1991, 1999).

An interesting pattern is revealed in clade H, with the split between a clade formed by plants from the northern region of the Espinhaço Range in Bahia (clade I) and a clade formed by species from the southern Espinhaço Range in Minas Gerais (clade J) and adjacent mountains. Harley (1988) described a similar pattern in Lamiaceae. He suggested that

floristic composition is distinct in the two parts of the Espinhaço Range, despite the similar physiognomies and geological origin.

Most representatives of Paepalanthoideae inhabit rocky dry soils and are usually confined to a single or a few adjacent mountain tops because of limited dispersal ability (Giulietti & Hensold, 1990; Stützel, 1998). Such constraints might explain the great local diversification of Paepalanthoideae and the elevated number of microendemic species. In clade G, groups such as *Paepalanthus* section *Diphyomene* and *Paepalanthus* (unranked) *Dimeri*, have experienced most of their diversification after the dispersal to cerrado and Lowland Guianan savannas, which is an exception in Eriocaulaceae. Simon *et al.* (2009) indicated, based on molecular dating of various plant groups, that diversification in the cerrado may be recent, not older than 10 Mya, and related to fire adaptations. However, without a broader sampling and a dated phylogeny it is still difficult to assess whether the habitat restrictions in Eriocaulaceae and the various adaptations to fire are derived from an ancestor not adapted to fire, as suggested by Simon *et al.* (2009).

Besides the relatively old age of the Brazilian and the Guiana Shields and the invasion of the savannas, a series of events during the Neogene may be responsible for the species diversification in South America (Antonelli *et al.*, 2009; Hoorn *et al.*, 2010). Hoorn *et al.* (2010) correlated Amazonian diversity with the Andean uplift and its consequences for geology, landscape evolution and climate change. The diversity of Eriocaulaceae in Amazonia and the Andes is known to be low in comparison with the Espinhaço Range. However, such diversity is almost certainly underestimated, considering both low collecting and taxonomic efforts (Giulietti & Hensold, 1990). Regarding the dynamics and the examples described by Antonelli *et al.* (2009) and Hoorn *et al.* (2010) for the region, the inclusion of these species in a dated phylogeny would be relevant in evaluating whether they are phylogenetically related or not and in reconstructing the patterns and routes of colonization of these and adjacent regions in South and Central America.

FINAL REMARKS AND PERSPECTIVES FOR THE NEXT DECADE

Although slightly different from previous phylogenetic analyses, our results are strongly supported and consistent with morphology and with part of the historical classifications. The previous changes in nomenclature proposed for solving issues of *Blastocaulon*, *Syngonanthus* and *Philodice* are further supported (Giulietti *et al.*, 2009; Andrade *et al.*, 2011). The segregation of *Comanthera* from *Syngonanthus*

(Parra *et al.*, 2010) is also supported, but not required. Further studies are needed to solve the taxonomic problems in the core *Paepalanthus* clade. With current sampling and resolution it is not clear whether these groups should be split or if they should be merged into *Paepalanthus s.l.*, as suggested by Andrade *et al.* (2010). As it stands, the taxonomic arrangement of *Paepalanthus* remains incongruent with respect to modern taxonomy, but until we have more solid evidence, it may be adequate to avoid premature taxonomic and nomenclatural changes. Despite the relatively low number of species included in this analysis, several large categories are strongly supported as monophyletic groups and are expected to be maintained in further analyses. Therefore, we emphasize the need for including morphologically relevant species and searching for other synapomorphies based on morphology, as a means of defining clades. This search, in a combined morphological and molecular scenario, together with advanced knowledge of ontogeny, should be the basis for establishing a future informative phylogenetic classification of Paepalanthoideae.

Given the relevance of isolation in Paepalanthoideae diversification, the inclusion of species from poorly sampled regions, especially Amazonia, the Caribbean, the Andes and Central America, will be essential for a more thorough reconstruction of the biogeographic history of the clades. This will provide clarification of how the Amazonian, Andean and Caribbean species are related to the remaining groups of Paepalanthoideae and will allow an assessment of the role of South and Central American geology in their diversification. As in other families such as Xyridaceae, some clades occur specifically in the Venezuelan Guayana Highlands or the northern and southern parts of the Espinhaço Range and exhibit the highest species diversity in these areas. It would be relevant to perform a dated biogeographical analysis to correlate it to geology, vegetation and hydrographic basins in order to evaluate the role of vicariance and long-distance dispersal in their present distribution. This may also emphasize the phylogenetic approach to biodiversity conservation, in contrast to an ordinary species-richness approach (Faith, 1996; Ennos, French & Hollingsworth, 2005; Forest *et al.*, 2007).

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APPENDIX 1

Voucher information and GenBank accession numbers for taxa used in this study. An asterisk indicates the number in the HUEFS genetic bank. A dash indicates the molecular region was not sampled.

- Diamantina/MG, *6878, EU924452, EU924299; *Paepalanthus calvoides* Ruhland, *MJG Andrade* 550 HUEFS, Itacambira/MG, *6812, GQ475208, GQ475239; *Paepalanthus canescens* Koern., *MLO Trovó* 351 SPF, Diamantina/MG, *6919, GQ475209, GQ475240; *Paepalanthus caparoensis* Ruhland, *MLO Trovó* 249 SPF, Alto Caparaó/MG, *6925, GQ475210, GQ475241; *Paepalanthus chrysophorus* Silveira, *MM Lopes* 951 SPF, Grão-Mogol/MG, *6958, GQ475211, GQ475242; *Paepalanthus cinereus* Giulietti and Parra, *AM Giulietti s/n* HUEFS, Rio de Contas/BA, *1293, EU924469, EU924316; *Paepalanthus comans* Silveira, *MJG Andrade* 540 HUEFS, Diamantina/MG, *6820, EU924482, EU924329; *Paepalanthus cordatus* Ruhland, *MLO Trovó* 443 SPF, Alto Paraíso de Goiás/GO, *6917, GQ475212, GQ475243; *Paepalanthus cylindraceus* Silveira, *MLO Trovó* 383 SPF, São Roque de Minas/MG, *9262, -, GQ475244; *Paepalanthus distichophyllus* Mart., *MLO Trovó* 218 SPF, Diamantina/MG, *6907, GQ475213, GQ475245; *Paepalanthus elongatus* Bong. Koern., *MJG Andrade* 572 HUEFS, Tiradentes/MG, *6884, EU924467, EU924314; *Paepalanthus erigeron* Mart. ex Koern., *AA Ribeiro-Filho* 107 HUEFS, Lençóis/BA, *6882, -, EU924306; *Paepalanthus eriophaeus* Ruhland, *MJG Andrade* 504 HUEFS, Itacambira/MG, *6811, EU924459, EU924307; *Paepalanthus exiguus* Bong. Koern., *E Guarçoni* 710 HUEFS, Alto Caparaó/MG, *6885, EU924481, EU924328; *Paepalanthus fraternus* N.E. Br., *P Fiaschi* 3202 SPF, Mount Roraima/Venezuela, *6912, GQ475214, GQ475246; *Paepalanthus fulgidus* Moldenke, *P Fiaschi* 3196 SPF, Mount Roraima/Venezuela, *6911, GQ475215, GQ475247; *Paepalanthus geniculatus* Bong. Kunth, *MLO Trovó* 205 SPF, Diamantina/MG, *6921, GQ475216, GQ475248; *Paepalanthus giganteus* Sano, *MJG Andrade* 527 HUEFS, Diamantina/MG, *1943, EU924478, EU924325; *Paepalanthus glareosus* Kunth, *MJG Andrade* 548 HUEFS, Datas/MG, *1959, EU924475, EU924322; *Paepalanthus glaziovii* Ruhland, *Sano* 3851 SPF, Diamantina/MG, *6902, GQ475217, GQ475249; *Paepalanthus henriquei* Ruhland, *MLO Trovó* 179 SPF, Lima Duarte/MG, *6927, GQ475218, -; *Paepalanthus implicatus* Silveira, *MJG Andrade* 550 HUEFS, Datas/MG, *1961, EU924472, EU924319; *Paepalanthus klotzschianus* Koern., *MLO Trovó* 257 SPF, Linhares/ES, *6959, GQ475219, GQ475250; *Paepalanthus lamarckii* Kunth, *DS Carneio-Torres* 461 HUEFS, Lagartos/SE, *6880, EU924456, EU924303; *Paepalanthus leucocephalus* Ruhland, *MJG Andrade* 620 HUEFS, Rio de Contas/BA, *6886, EU924487, EU924334; *Paepalanthus macrocaulon* Silveira, *MJG Andrade* 431 HUEFS, Rio de Contas/BA, *766, EU924470, EU924317; *Paepalanthus macropodus* Ruhland, *MLO Trovó* 214 SPF, Santana do Riacho/MG, *6922, GQ475220, GQ475251; *Paepalanthus microphyllus* Kunth, *MLO Trovó* 225 SPF, Santana do Riacho/MG, *6923, GQ47522, GQ475252; *Paepalanthus mollis* Kunth, *MLO Trovó* 376 SPF, Diamantina/MG, *6961, GQ475222, GQ475253; *Paepalanthus myocephalus* Mart., *MJG Andrade* 613 HUEFS, Feira de Santana/BA, *6879, EU924454, EU924301; *Paepalanthus neglectus* Koern., *BRN Araújo* 85 HUEFS, Rio de Contas/BA, *1805, EU924460, EU924308; *Paepalanthus nigrescens* Silveira, *MLO Trovó* 204 SPF, Santana do Riacho/MG, *6932, GQ475223, GQ475254; *Paepalanthus obtusifolius* Koern., *R Harley* 54802 HUEFS, Rio de Contas/BA, *1321, EU924457, EU924304; *Paepalanthus parviflorus* Hensold Hensold, *MLO Trovó* 202 SPF, Santana do Riacho/MG, *6962, GQ475224, -; *Paepalanthus pedunculatus* Ruhland, *MJG Andrade* 547 HUEFS, Datas/MG, *1958, GQ475225, GQ475255; *Paepalanthus planifolius* Bong. Koern., *MJG Andrade* 526 HUEFS, Diamantina/MG, *1942, EU924485, EU924332; *Paepalanthus polycladus* Silveira, *MLO Trovó* 391 SPF, São Roque de Minas/MG, *6909, GQ475226, GQ475256; *Paepalanthus polygonus* Koern., *MLO Trovó* 413 SPF, Diamantina/MG, *6913, GQ475227, GQ475257; *Paepalanthus pulchellus* Herzog, *AM Giulietti* 2423 HUEFS, Rio de Contas/BA, *1409, EU924461, EU924309; *Paepalanthus pulvinatus* N.E. Br., *R Harley* 54634 HUEFS, Mucugê/BA, *638, EU924465, EU924313; *Paepalanthus regalis* Mart., *R Harley* 54640 HUEFS, Mucugê/BA, *660, EU924462, EU924310; *Paepalanthus repens* Koern., *R. Abbott* 21006 FLAS, Dominican Republic, *7416, EU924474, EU924321; *Paepalanthus rupestris* Gardner, *MJG Andrade* 542 HUEFS, Diamantina/MG, *1954, EU924440, EU924288; *Paepalanthus scirpeus* Mart. ex Koern. Giulietti, *JR Pirani* 4162 HUEFS, Congonhas do Norte/MG, *6876, EU924441, EU924289; *Paepalanthus scleranthus* Ruhland, *MJG Andrade* 537 HUEFS, Diamantina/MG, *1951, EU924410, EU924335; *Paepalanthus sessiliflorus* Mart. ex Koern., *JG Jardim* 2237 HUEFS, Maraú/BA, *6881, EU924458, EU924305; *Paepalanthus silveirae* Ruhland, *MJG Andrade* 568 HUEFS, Tiradentes/MG, *1976, EU924463, EU924311; *Paepalanthus spathulatus* Koern., *R Harley* 55476 HUEFS, Itaberaba/BA, *6883, EU924464, EU924312; *Paepalanthus sphaerocephalus* Ruhland, *MJG Andrade* 456 HUEFS, Rio de Contas/BA, *790, EU924480, EU924327; *Paepalanthus stannardii* Giulietti and Parra, *MJG Andrade* 438 HUEFS, Rio de Contas/BA, *773, EU924473, EU924320; *Paepalanthus strictus* Koern., *MJG Andrade* 491 HUEFS, Grão-Mogol/MG, *1926, EU924471, EU924318; *Paepalanthus subcaulescens* N.E. Br., *P Fiaschi* 3195 SPF, Mount Roraima/Venezuela, *6957, GQ475228, GQ475258; *Paepalanthus superbus* Ruhland, *AM*

Giulietti 2504 HUEFS, Santana do Riacho/MG, *6858, EU924483, EU924330; *Paepalanthus tortilis* Bong. Mart., *MJG Andrade 479* HUEFS, Grão-Mogol/MG, *1914, EU924455, EU924376; *Paepalanthus trichophyllus* Bong. Koern., *MJG Andrade 439* HUEFS, Rio de Contas/BA, *774, EU924479, EU924326; *Paepalanthus tuberosus* Bong. Kunth, *van den Berg 1364* HUEFS, Conceição do Mato Dentro/MG, *1641, EU924486, EU924333; *Paepalanthus urbanianus* Ruhland, *MLO Trovó 435* SPF, Alto Paraíso de Goiás/GO, *6918, –, GQ475259; *Paepalanthus vaginatus* Koern., *MLO Trovó 353* SPF, Diamantina/MG, *6904, –, GQ475260; *Paepalanthus vellozioides* Koern., *MLO Trovó 198* SPF, Santana do Riacho/MG, *6906, GQ475229, GQ475261; *Paepalanthus viridulus* Ruhland, *C Sarquis 12* SPF, Lima Duarte/MG, *6915, GQ475230, GQ475262; *Philodice hoffmannseggii* Mart., *AM Giulietti 2483* HUEFS, Nossa Senhora do Livramento/MT, *6887, EU924411, EU924336; *Ron-*

donanthus capillaceus Koern. Hensold and Giulietti, *van den Berg 1792* HUEFS, Mount Roraima/Venezuela, *6889, GQ478282, EU924338; *Rondonanthus roraimae* Oliver Herzog, *P Fiaschi 3201* SPF, Mount Roraima/Venezuela, *6916, GQ475231, –; *Syngonanthus aciphyllus* Bong. Ruhland, *MJG Andrade 532* HUEFS, Diamantina/MG, *1948, EU924491, EU924339; *Syngonanthus arenarius* Gardner Ruhland, *MJG Andrade 493* HUEFS, Itacambira/MG, *6802, EU924498, EU924342; *Syngonanthus caulescens* Poir. Ruhland, *MJG Andrade 616* HUEFS, Rio de Contas/BA, *786, EU924500, EU924344; *Syngonanthus curralensis* Moldenke, *MJG Andrade 595* HUEFS, Rio de Contas/BA, *6890, EU924492, EU924340; *Syngonanthus vernonioides* Kunth Ruhland, *AM Giulietti 2185* HUEFS, Rio de Contas/BA, *220, EU924499, EU924343; *Tonina fluviatilis* Aubl., *MJG Andrade 616* HUEFS, Recife/PE, *6895, EU924501, EU924345.

APPENDIX 2

MORPHOLOGICAL CHARACTERS WITH THEIR RESPECTIVE STATES AND THE MORPHOLOGICAL MATRIX

(1) Stigmatic branches: 0 carinal single, 1 commissural single, 2 commissural bifid; (2) glands on staminate flower: 0 present, 1 absent; (3) androecium: 0 diplostemonous, 1 haplostemonous; (4) leaf fenestration: 0 present, 1 absent; (5) petals of the staminate flower: 0 free, 1 tubular; (6) linear staminodes on pistillate flower: 0 absent, 1 present; (7) fertile locules of the gynoecium: 0 all, 1 only the median; (8) petals of the pistillate flower: 0 free, 1 fused at the middle; (9) trichomes inside the corolla of the staminate flower: 0 absent, 1 present; (10) involucre bracts adaxial surface: 0 glabrous, 1 hairy; (11) scapes: 0 free, 1 fused; (12) involucre bracts: 0 not surpassing the capitula, 1 surpassing the capitula; (13) floral merism: 0 trimerous, 1 dimerous.

Taxa/character	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Eriocaulon linearifolium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eriocaulon ligulatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eriocaulon modestum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rondonanthus capillaceus</i>	2	1	1	1	0	1	0	0	0	0	0	0	0
<i>Leiothrix distichoclada</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Leiothrix flavescens</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Leiothrix curvifolia</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Leiothrix flagellaris</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Leiothrix arrecta</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Leiothrix vivipara</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Philodice hoffmannseggii</i>	1	1	1	1	1	0	0	1	0	0	0	0	0
<i>Syngonanthus arenarius</i>	1	1	1	1	1	0	0	1	0	0	0	1	0
<i>Syngonanthus caulescens</i>	1	1	1	1	1	0	0	1	0	0	0	0	0
<i>Comanthera vernonioides</i>	1	1	1	1	1	0	0	1	0	0	0	0	0
<i>Comanthera aciphylla</i>	1	1	1	1	1	0	0	1	0	0	0	1	0
<i>Comanthera curralensis</i>	1	1	1	1	1	0	0	1	0	0	0	1	0
<i>Tonina fluviatilis</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus lamarckii</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus obtusifolius</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus tortilis</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus repens</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus distichophyllus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus stannardii</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus exiguus</i>	1	1	1	1	1	0	0	0	0	0	0	0	1

APPENDIX 2 *Continued*

Taxa/character	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Paepalanthus leucocephalus</i>	1	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus scleranthus</i>	1	1	1	1	1	0	0	0	0	0	0	0	1
<i>Actinocephalus bongardii</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Actinocephalus ramosus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus geniculatus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus glareosus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Actinocephalus stereophyllus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Actinocephalus brachypus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Actinocephalus ciliatus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus elongatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus strictus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus trichophyllus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus polycladus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus giganteus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus acanthophyllus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus cordatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus subcaulescens</i>	2	1	1	1	1	0	1	0	0	0	0	0	0
<i>Paepalanthus fraternus</i>	2	1	1	1	1	0	1	0	0	0	0	0	0
<i>Paepalanthus fulgidus</i>	2	1	1	1	1	0	1	0	0	0	0	0	0
<i>Paepalanthus cinereus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus macrocaulon</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus neglectus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus regalis</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus spathulatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus klotzschianus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus pulchellus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus pulvinatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus albidus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus rupestris</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus bonsai</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus glaziovii</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus nigrescens</i>	2	1	1	1	1	0	0	0	1	0	0	0	0
<i>Paepalanthus argenteus</i>	2	1	1	1	1	0	0	0	1	1	0	1	0
<i>Paepalanthus comans</i>	2	1	1	1	1	0	0	0	1	1	0	1	0
<i>Paepalanthus superbus</i>	2	1	1	1	1	0	0	0	1	1	0	1	0
<i>Paepalanthus mollis</i>	2	1	1	1	1	0	0	0	1	1	0	1	0
<i>Paepalanthus macropodus</i>	2	1	1	1	1	0	0	0	0	0	1	0	0
<i>Paepalanthus bromelioides</i>	2	1	1	1	1	0	0	0	0	0	1	0	0
<i>Paepalanthus planifolius</i>	2	1	1	1	1	0	0	0	0	0	1	0	0
<i>Paepalanthus vellozioides</i>	2	1	1	1	1	0	0	0	0	0	1	0	0
<i>Paepalanthus tuberosus</i>	2	1	1	1	1	0	0	0	0	0	1	0	0
<i>Paepalanthus polygonus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus sphaerocephalus</i>	2	1	1	1	1	0	0	0	0	0	0	0	1
<i>Paepalanthus viridulus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus chrysophorus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus calvoides</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus eriophaeus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus acantholimon</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus caparoensis</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus acuminatus</i>	2	1	1	1	1	0	0	0	0	0	0	1	0
<i>Paepalanthus silveirae</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus scirpeus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus bryoides</i>	1	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus aretioides</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus microphyllus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0

APPENDIX 2 *Continued*

Taxa/character	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Paepalanthus implicatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus canescens</i>	2	1	1	1	1	0	0	0	0	0	0	0	0
<i>Paepalanthus pedunculatus</i>	2	1	1	1	1	0	0	0	0	0	0	0	0

APPENDIX 3

Geographical distribution matrix according to the following areas: (A) Espinhaço Range in Minas Gerais; (B) Espinhaço Range in Bahia; (C) cerrado; (D) Lowland Guianan savannas; (E) restingas; (F) tepuis; and (G) Caribbean. 0 = absent; 1 = present.

Taxa/area	A	B	C	D	E	F	G
<i>Eriocaulon linearifolium</i>	0	1	1	0	0	0	0
<i>Eriocaulon ligulatum</i>	1	1	1	0	0	0	0
<i>Eriocaulon modestum</i>	1	1	1	0	0	0	0
<i>Rondonanthus capillaceus</i>	0	0	0	1	0	0	0
<i>Leiothrix distichoclada</i>	0	1	0	0	0	0	0
<i>Leiothrix flavescens</i>	1	1	1	1	1	1	0
<i>Leiothrix curvifolia</i>	1	0	0	0	0	0	0
<i>Leiothrix flagellaris</i>	1	0	0	0	0	0	0
<i>Leiothrix arrecta</i>	1	0	0	0	0	0	0
<i>Leiothrix vivipara</i>	1	0	0	0	0	0	0
<i>Philodice hoffmannseggii</i>	0	0	1	0	0	0	0
<i>Syngonanthus arenarius</i>	1	0	0	0	0	0	0
<i>Syngonanthus caulescens</i>	1	1	1	1	1	1	1
<i>Comanthera vernonioides</i>	1	1	0	0	0	0	0
<i>Comanthera aciphylla</i>	1	0	0	0	0	0	0
<i>Comanthera curralensis</i>	0	1	0	0	0	0	0
<i>Tonina fluviatilis</i>	0	0	0	0	1	0	0
<i>Paepalanthus lamarckii</i>	0	0	0	0	1	0	0
<i>Paepalanthus obtusifolius</i>	0	1	0	0	0	0	0
<i>Paepalanthus tortilis</i>	1	1	1	1	1	1	1
<i>Paepalanthus repens</i>	0	0	0	0	0	0	1
<i>Paepalanthus distichophyllus</i>	1	0	0	0	0	0	0
<i>Paepalanthus stannardii</i>	0	1	0	0	0	0	0
<i>Paepalanthus exiguus</i>	1	0	0	0	0	0	0
<i>Paepalanthus leucocephalus</i>	1	0	0	0	0	0	0
<i>Paepalanthus scleranthus</i>	1	0	0	0	0	0	0
<i>Actinocephalus bongardii</i>	1	1	1	0	0	0	0
<i>Actinocephalus ramosus</i>	1	1	0	0	1	0	0
<i>Paepalanthus geniculatus</i>	1	0	0	0	0	0	0
<i>Paepalanthus glareosus</i>	1	0	0	0	0	0	0
<i>Actinocephalus stereophyllus</i>	1	0	0	0	0	0	0
<i>Actinocephalus brachypus</i>	1	0	0	0	0	0	0
<i>Actinocephalus ciliatus</i>	1	0	0	0	0	0	0
<i>Paepalanthus elongatus</i>	1	1	1	0	0	0	0
<i>Paepalanthus strictus</i>	1	1	0	0	0	0	0
<i>Paepalanthus trichophyllus</i>	1	1	1	0	0	0	0
<i>Paepalanthus polycladus</i>	1	0	0	0	0	0	0
<i>Paepalanthus giganteus</i>	1	0	1	1	0	0	0
<i>Paepalanthus acanthophyllus</i>	0	0	1	0	0	0	0
<i>Paepalanthus cordatus</i>	0	0	1	0	0	0	0
<i>Paepalanthus subcaulescens</i>	0	0	0	0	0	1	0
<i>Paepalanthus fraternus</i>	0	0	0	0	0	1	0

APPENDIX 3 *Continued*

Taxa/area	A	B	C	D	E	F	G
<i>Paepalanthus fulgidus</i>	0	0	0	0	0	1	0
<i>Paepalanthus cinereus</i>	0	1	0	0	0	0	0
<i>Paepalanthus macrocaulon</i>	0	1	0	0	0	0	0
<i>Paepalanthus neglectus</i>	0	1	0	0	0	0	0
<i>Paepalanthus regalis</i>	1	1	0	0	0	0	0
<i>Paepalanthus spathulatus</i>	0	1	0	0	0	0	0
<i>Paepalanthus klotzschianus</i>	0	0	0	0	1	0	0
<i>Paepalanthus pulchellus</i>	0	1	0	0	1	0	0
<i>Paepalanthus pulvinatus</i>	0	1	0	0	0	0	0
<i>Paepalanthus albidus</i>	1	0	0	0	0	0	0
<i>Paepalanthus rupestris</i>	1	0	0	0	0	0	0
<i>Paepalanthus bonsai</i>	1	0	0	0	0	0	0
<i>Paepalanthus glaziovii</i>	1	0	0	0	0	0	0
<i>Paepalanthus nigrescens</i>	1	0	0	0	0	0	0
<i>Paepalanthus argenteus</i>	1	0	0	0	0	0	0
<i>Paepalanthus comans</i>	1	0	0	0	0	0	0
<i>Paepalanthus superbus</i>	1	0	0	0	0	0	0
<i>Paepalanthus mollis</i>	1	0	0	0	0	0	0
<i>Paepalanthus macropodus</i>	1	0	0	0	0	0	0
<i>Paepalanthus bromelioides</i>	1	0	0	0	0	0	0
<i>Paepalanthus planifolius</i>	1	0	0	0	0	0	0
<i>Paepalanthus vellozioides</i>	1	0	0	0	0	0	0
<i>Paepalanthus tuberosus</i>	1	0	0	0	0	0	0
<i>Paepalanthus polygonus</i>	1	0	0	0	0	0	0
<i>Paepalanthus sphaerocephalus</i>	1	1	1	0	0	0	0
<i>Paepalanthus viridulus</i>	1	0	0	0	0	0	0
<i>Paepalanthus chrysophorus</i>	1	0	0	0	0	0	0
<i>Paepalanthus calvoides</i>	1	0	0	0	0	0	0
<i>Paepalanthus eriophaeus</i>	1	0	0	0	0	0	0
<i>Paepalanthus acantholimon</i>	1	0	0	0	0	0	0
<i>Paepalanthus caparoensis</i>	1	0	0	0	0	0	0
<i>Paepalanthus acuminatus</i>	1	0	0	0	0	0	0
<i>Paepalanthus silveirae</i>	1	0	0	0	0	0	0
<i>Paepalanthus scirpeus</i>	1	0	0	0	0	0	0
<i>Paepalanthus bryoides</i>	1	0	0	0	0	0	0
<i>Paepalanthus aretioides</i>	1	0	0	0	0	0	0
<i>Paepalanthus microphyllus</i>	1	0	0	0	0	0	0
<i>Paepalanthus implicatus</i>	1	0	0	0	0	0	0
<i>Paepalanthus canescens</i>	1	0	0	0	0	0	0
<i>Paepalanthus pedunculatus</i>	1	0	0	0	0	0	0

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The 50% majority rule consensus tree of the Bayesian analysis of the *trnL-trnF* data set.

Appendix S2. The 50% majority rule consensus tree of the Bayesian analysis of the ITS data set.