



# Phylogenetic analysis of the Brazilian microendemic *Paepalanthus* subgenus *Xeractis* (Eriocaulaceae) inferred from morphology

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*Paepalanthus* subgenus *Xeractis* (Eriocaulaceae) comprises 28 recognized species endemic to the Espinhaço Range, in Minas Gerais state, Brazil. Most species of the subgenus are restricted to small localities and critically endangered, but still in need of systematic study. The monophyly of the subgenus has already been tested, but only with a few species. Our study presents the first phylogenetic hypothesis within the group, based on morphology. A maximum parsimony analysis was conducted on a matrix of 30 characters for 30 terminal taxa, including all species of the subgenus and two outgroups. The biogeographical hypotheses for the subgenus were inferred based on dispersal–vicariance analysis (DIVA). The analysis provided one most-parsimonious hypothesis that supports most of the latest published subdivisions (sections and series). However, some conflicts remain concerning the position of a few species and the relationships between sections. The distribution and origin(s) of microendemism are also discussed, providing the ground for conservation strategies to be developed in the region. © 2011 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2011, **167**, 137–152.

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## INTRODUCTION

The Brazilian Espinhaço Range is characterized by a very rich but endangered endemic flora, including a UNESCO Biosphere Reserve (UNESCO, 2005). It ranges *c.* 1000 km north–south and 10–40 km east–west in Minas Gerais and Bahia states and is located at an intersection between the Atlantic Forest and the Cerrado (Brazilian savanna) biomes. The presence of countless rocky outcrops, associated with altitudes usually > 900 m (e.g. Rapini *et al.*, 2008), forms an ecosystem especially diverse in microhabitats called *campos rupestres*. This ecosystem is one of the richest

in plant diversity and plant endemism in Brazil (Giulietti *et al.*, 1987; Giulietti & Pirani, 1988; Rapini *et al.*, 2008), with a notable diversification of its characteristic families Velloziaceae, Xyridaceae and Eriocaulaceae.

Eriocaulaceae are monocots distinguished by capituliform inflorescences. The family includes 11 genera and *c.* 1110 species (Sano, 2004; Parra *et al.*, 2010; Andrade *et al.*, 2011) and belongs to Poales (APG, 2009). The distribution is pantropical, because of the broad distribution of *Eriocaulon* L., but two main centres of diversity are recognized in the Neotropics: the Brazilian Espinhaço Range (where 35% of the entire family diversity occurs) and the Guyanan, Venezuelan and Brazilian tepuis (Giulietti & Hensold, 1990; Stützel, 1998; Costa, Trovó & Sano, 2008).

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Approximately 96% of Brazilian species of Eriocaulaceae are microendemic (Giulietti *et al.*, 2005). *Paepalanthus* Mart. subgenus *Xeractis* Koern. is as an emblematic group with 28 recognized species (Hensold, 1988, 1996) strictly restricted to the Espinhaço Range in Minas Gerais (ERMG). In addition, several species of the subgenus (e.g. *Paepalanthus nigrescens* (Bong.) Koern.) are frequently overcollected from the wild for craft purposes, providing important resources for many artisan communities (Giulietti *et al.*, 1988). For the management and conservation of such flora and habitats, the systematics of these plants should be investigated in depth.

Previous phylogenetic studies including Eriocaulaceae confirm the monophyly of the family with Xyridaceae as the sister group (Bremer, 2002; Chase *et al.*, 2006; Soltis *et al.*, 2006). At the infrafamilial level, some phylogenetic analyses have been conducted, based on morphology (Giulietti, Amaral & Bittrich, 1995), morphology, anatomy and phytochemistry (Giulietti *et al.*, 2000), molecules (Unwin, 2004; Andrade *et al.*, 2010) or morphology and molecules (Trovó, 2010). The most recent phylogenetic analyses (Unwin, 2004; Andrade *et al.*, 2010; Trovó, 2010) recognized the monophyly of subfamilies Eriocauloideae Ruhland and Paepalanthoideae Ruhland. They also revealed the polyphyly or paraphyly of several genera, which were consequently split, synonymized or recircumscribed (Sano, 2004; Costa, 2005; Giulietti *et al.*, 2009; Parra *et al.*, 2010). *Paepalanthus s.l.* has been known to be polyphyletic since early phylogenetic studies (Giulietti *et al.*, 1995, 2000; Unwin, 2004; Andrade *et al.*, 2010; Trovó, 2010), but many of its infrageneric ranks appear monophyletic. This genus includes c. 380 species occurring in Central and South America and Africa, among which 220 (60%) are reported in the Espinhaço Range (Stützel, 1998; Costa *et al.*, 2008). The infrageneric taxonomy currently used was based upon Ruhland (1903) and six subgenera are currently recognized, including subgenus *Xeractis*. In previous molecular phylogenetic analyses (Unwin, 2004; Andrade *et al.*, 2010), subgenus *Xeractis* was not retrieved as monophyletic, except using *trnL-F* sequences (Andrade *et al.*, 2010). However, adding morphological data, subgenus *Xeractis* appears monophyletic, and putative sister to *Paepalanthus* subgenus *Platycaulon* Mart (Trovó, 2010).

*Paepalanthus* subgenus *Xeractis* was initially recognized by Bongard (1831), but was formally proposed by Koernicke (1863), based on the presence of long involucre bracts surpassing the capitula diameter. Hensold (1988, 1996) provided the latest taxonomic review of the group, recognizing 28 species, classified into four sections and two series. In this taxonomic revision, no phylogenetic analysis was presented, but Hensold (1988) proposed several scenarios for the

evolution of the group, including potential synapomorphies for the subgenus and groups within it. The morphological synapomorphies for the subgenus were tested by Trovó (2010), who proposed as secondary homologies the presence of trichomes on the adaxial surface of the corolla of staminate flowers and the presence of trichomes on the adaxial surface of the involucre bracts. However, the study only included five species of subgenus *Xeractis* and did not investigate evolutionary relationships within the subgenus to any degree. The aim of our study is thus to investigate the phylogeny of *P.* subgenus *Xeractis* using morphological characters, principally to test the monophyly and the potential synapomorphies of the sections and series proposed by Hensold (1988). Furthermore, the resulting cladogram is used as a historical framework for discussing the biogeographical history of the group in the ERMG, providing information that could contribute to conservation strategies.

## MATERIAL AND METHODS

### TAXON SAMPLING

Our ingroup sampling includes all 28 species of subgenus *Xeractis* proposed by Hensold (1988, 1996). We used two species belonging to subgenus *Platycaulon* as the outgroup, identified as sister to *P.* subgenus *Xeractis* by Trovó (2010): *P. hydra* Ruhland and *P. planifolius* Koern. The species coding includes the morphological variation of infraspecific taxa. These were therefore not considered individually as terminals in the phylogenetic analysis. We assume here the monophyly of the ingroup as demonstrated in previous studies.

### MORPHOLOGICAL CHARACTERS

The data were obtained from field observations, herbarium material and the literature (Ruhland, 1903; Silveira, 1928; Hensold, 1988, 1996; Tissot-Squalli, 1997; Stützel, 1998; Giulietti *et al.*, 2000; Rosa & Scatena, 2007). We conducted fieldwork (21 expeditions) during all seasons and throughout the area of occurrence from February 2008 to May 2010, allowing observation in the life of 20 species of subgenus *Xeractis*. Herbarium material studied is housed at B, BHC, P, R, RB and SPF (Thiers, continuously updated), including the types of 25 species. We excluded from the analyses potentially hybrid specimens. Representative specimens examined are listed in Appendix 1.

Primary homology hypotheses were proposed for stem, leaf, inflorescence architecture, floral and anatomical characters (which are partly illustrated in Fig. 1). Thirty selected characters (detailed in Appen-

dix 2) for the 30 taxa were coded in a matrix (Appendix 3). Information sources (fieldwork, herbarium or literature) for each character coding are indicated in Appendix 2.

#### PHYLOGENETIC ANALYSIS

Cladistic analysis with maximum parsimony (MP) was performed using PAUP 4.0b10 (Swofford, 1998) and a heuristic search with 1000 random taxon additions and tree bisection–reconnection (TBR) branch swapping. The resulting MP trees were then rooted on *Paepalanthus hydra*. Characters were optimized on the tree using MacClade 4.06 software (Maddison & Maddison, 2003). We evaluated clade reliability by using the Bremer index (Bremer, 1994) and the presence of secondary homologies. Despite the fact that reversals are primary homologies not retained as secondary homologies, we consider them as synapomorphies, because the synapomorphic and the reversed character state are inherited from the same ancestor. For characters states with ambiguous optimization, ACCTRAN was preferred, because it increases the number of retained homologies (Darlu & Tassy, 1993).

#### BIOGEOGRAPHY

The geographical occurrence of subgenus *Xeractis* was inferred from field observations, from herbarium data and from the literature (Ruhland, 1903; Hensold, 1988, 1996) and is illustrated in Figure 2. An absence/presence matrix was built with the species distribution according to the three areas of endemism of subgenus *Xeractis*, proposed for the ERMG (Echternacht *et al.*, 2011): the Diamantina Plateau, the Serra do Cipó and the Quadrilátero Ferrífero. Thereafter, the ancestral distribution areas were reconstructed on the cladogram obtained by MP, using dispersal–vicariance analysis (DIVA: Ronquist, 1997).

### RESULTS

#### PHYLOGENY

One most parsimonious tree (see Fig. 3) was obtained from MP [length = 62 steps; consistency index (CI) = 0.56; retention index (RI) = 0.86]. Because of graphical issues, only exclusive synapomorphies and reversals and convergences limited to two clades are reported on the tree. The topology is almost completely resolved, with many clades supported by exclusive synapomorphies. All taxonomic sections and series previously proposed for subgenus *Xeractis* are retrieved as monophyletic. The subgenus appears divided in two clades, one grouping sections *Chrysostegis* Hensold and *Gymnostegis* Hensold, the second

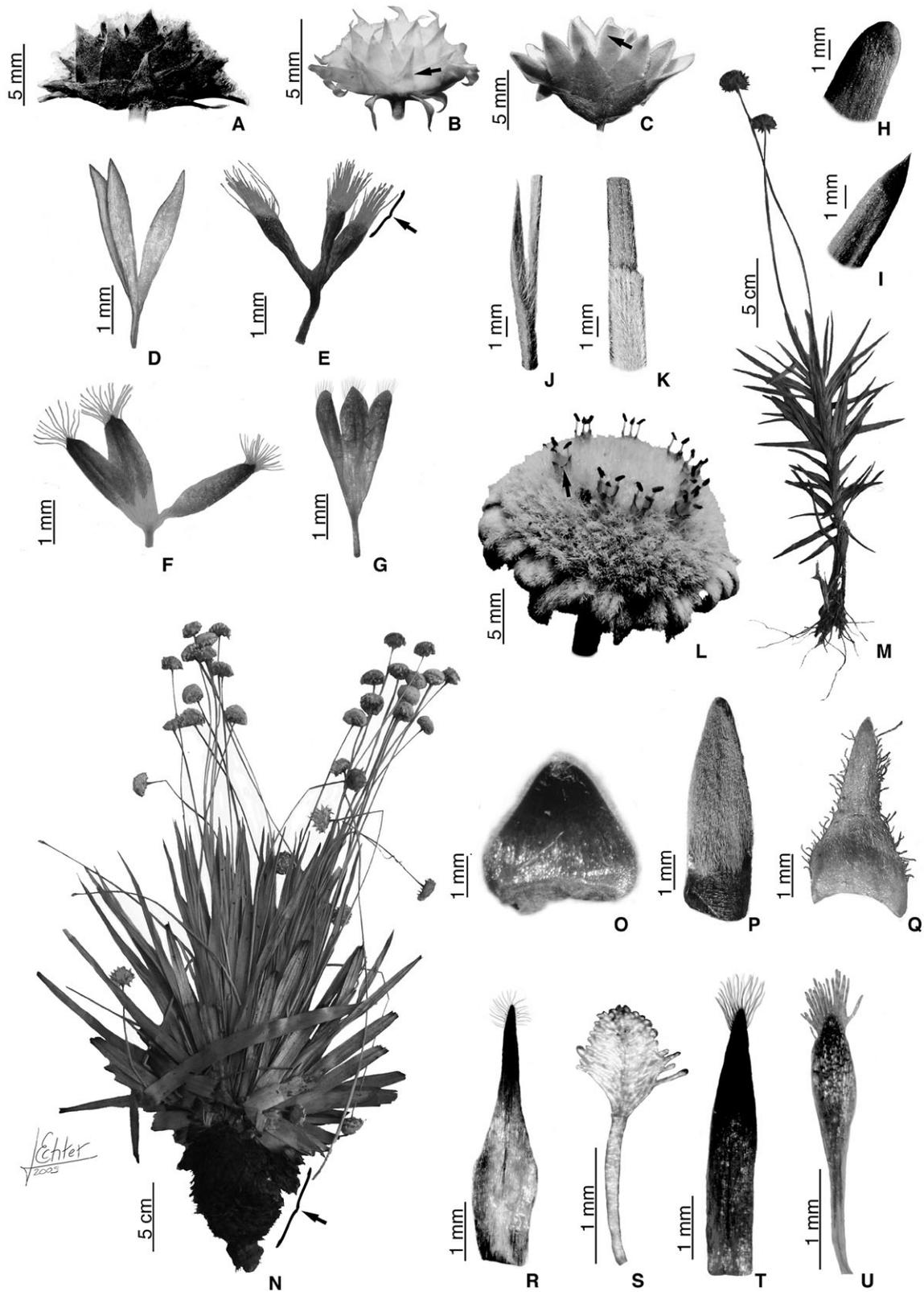
grouping sections *Pleurophyllon* Hensold and *Xeractis*. The clade corresponding to *P.* section *Xeractis* is further divided in two clades corresponding to *P.* series *Albidi* Hensold and *Fuscata* Hensold. The topologies of major clades (sections and series) and their synapomorphies are discussed hereafter. The number of characters and character states (as shown in Appendix 2) are referred to in parentheses, separated by a hyphen and preceded by the uppercase letter ‘C’. Convergences and plesiomorphies are discussed afterwards.

There is no exclusive morphological synapomorphy supporting subgenus *Xeractis*. However, five synapomorphies with one reversal were found: oblique opening of the peduncle sheath (C6-0, Fig. 1J); involucre bracts longer than the flower level (C10-1, Fig. 1A–C) and with the inner series differing in shape from the external series (C11-1, Fig. 1B, C); loss of cilia on the sepals of the staminate flowers (C24-0, Fig. 1D–G); and internal pubescence of the corolla of staminate flowers (C26-1).

#### BIOGEOGRAPHY

All 28 species of subgenus *Xeractis* are endemic to the central and southern portion of the ERMG. Most species are microendemic, only known by a single population, often restricted to a single mountain (see Fig. 2), as already mentioned by Hensold (1988). Other species have a wider distribution, occurring throughout an entire area of endemism. Several species occur in only one of the three regions defined here: *P. chrysolepis* Silveira, *P. comans* Silveira and *P. latifolius* Koern. in the Diamantina Plateau; *P. anamariae* Hensold, *P. ater* Silveira, *P. augustus* Silveira, *P. aureus* Silveira, *P. calvulus* (Ruhland) Hensold, *P. chlorocephalus* Silveira, *P. complanatus* Silveira, *P. digitiformis* Hensold, *P. homomallus* Mart., *P. lepidus* Silveira, *P. parviflorus* (Hensold) Hensold, *P. plumosus* Koern., *P. revolutus* Hensold, *P. senaeanus* Ruhland, *P. stuetzelii* Hensold, *P. superbus* Ruhland and *P. Gardner* in the Serra do Cipó; and *P. clausenii* Hensold, *P. garimpensis* Silveira, *P. langsdorffii* Koern. and *P. xiphophyllus* Ruhland in the Quadrilátero Ferrífero. Two species occur on both the Diamantina Plateau and Serra do Cipó: *P. argenteus* Koern. and *P. nigrescens* Silveira. The Diamantina Plateau and the Quadrilátero Ferrífero also share two species, *P. dianthoides* Mart. and *P. mollis* Kunth, which occurs only in the highest peaks of the ERMG (> 2000 m elevation, in the Serra do Caraça and in the Pico do Itambé, see Fig. 2). No species covers the overall distribution of the subgenus, suggesting a limited capacity for colonization at the specific level.

The distribution areas of hypothetical ancestors (HA) inferred by DIVA were represented on the



**Figure 1.** A–U, edited photographs of selected characters used in the cladistic analysis. The characters and character state numbers are related to Appendix 2 and are given separated by a hyphen and preceded by the letter ‘C’. A–C, capitula showing the colour, shape and length of involucre bracts. A, *P. dianthoides* Mart., homogeneously dark involucre bracts (C9-1) surpassing the flowers (C10-1), all series in a similar shape (C11-0). B, *P. chrysolepis* Silveira, cream involucre bracts (C9-0) surpassing the flowers (C10-1), the inner series in a different shape from the external series (C11-1), the external series caudate, shown by an arrow (C13-1). C, *P. augustus* Silveira, involucre bracts dark in the centre and hyaline at the margins (C9-2), the hyaline margin is shown by an arrow, surpassing the flowers (C10-1), the inner series in a different shape than the external series (C11-1). D–G, sepals of the staminate flowers, showing colour and apical trichome tufts. D, *P. aureus* Silveira, sepals unpigmented (C22-0). E, *P. ater* Silveira, sepals homogeneously dark (C22-3). F, *P. uncinatus* Gardner, sepal pigmentation present at the apex and absent at the base (C22-1). G, *P. complanatus* Silveira, sepal pigmentation present and the apex slightly darker than the basis (C22-2). H–I, leaf apex shape. H, *P. senaeanus* Ruhland, apex rounded (C3-0). I, *P. argenteus* Koern., apex acuminate. J–K, margin and opening of the peduncle sheath. J, *P. uncinatus*, margin entire (C5-0) and oblique opening (C6-0). K, *P. argenteus*, margin lacerate (C5-1) and perpendicular opening (C6-1). L, *P. plumosus* Koern., capitulum showing the involucre bracts densely pilose (C14-1/C15-1/C16-0) and surpassing the flowers (C10-1), the staminate flowers at anthesis with an arrow showing the granular pigmentation at the corolla margin (C25-1). M–N, caulescence and leaf arrangement. M, *P. uncinatus*, caudex absent (C1-0). N, *P. chrysolepis*, the caudex is indicated by an arrow (C1-1). O–Q, inner whorl of the involucre bracts showing the indumentum. O, *P. nigrescens* Silveira, indumentum present at the apex and absent at the limb (C14-1/C15-0/C16-not applicable). P, *P. senaeanus*, indumentum present at the apex and limb, dense at the limb (C14-1/C15-1/C16-1). Q, *P. uncinatus*, indumentum present at the apex and limb, scarce at the limb (C14-1/C15-1/C16-0). R–U, floral bracts showing pigmentation and form. R, *P. uncinatus*, floral bracts pigmented (C17-1) and caudate (C18-2). S, *P. senaeanus*, floral bracts unpigmented (C17-0) and plume-like (C18-3). T, *P. dianthoides*, floral bracts pigmented (C17-1) and triangular to elliptic (C18-0). U, *P. complanatus*, floral bracts pigmented (C17-1) and spatulate (C18-1).

internal branches of the phylogenetic tree (Fig. 3), by different colours corresponding to the areas of endemism. The ambiguous distributions revealed were represented by letters below the branches. The HA of subgenus *Xeractis* is inferred to have occurred in the Serra do Cipó, which appears as its centre of diversification. Then biogeographical process (vicariance, speciation, dispersal and extinction) would have occurred northwards, in the Diamantina Plateau, and southwards, in the Quadrilátero Ferrífero.

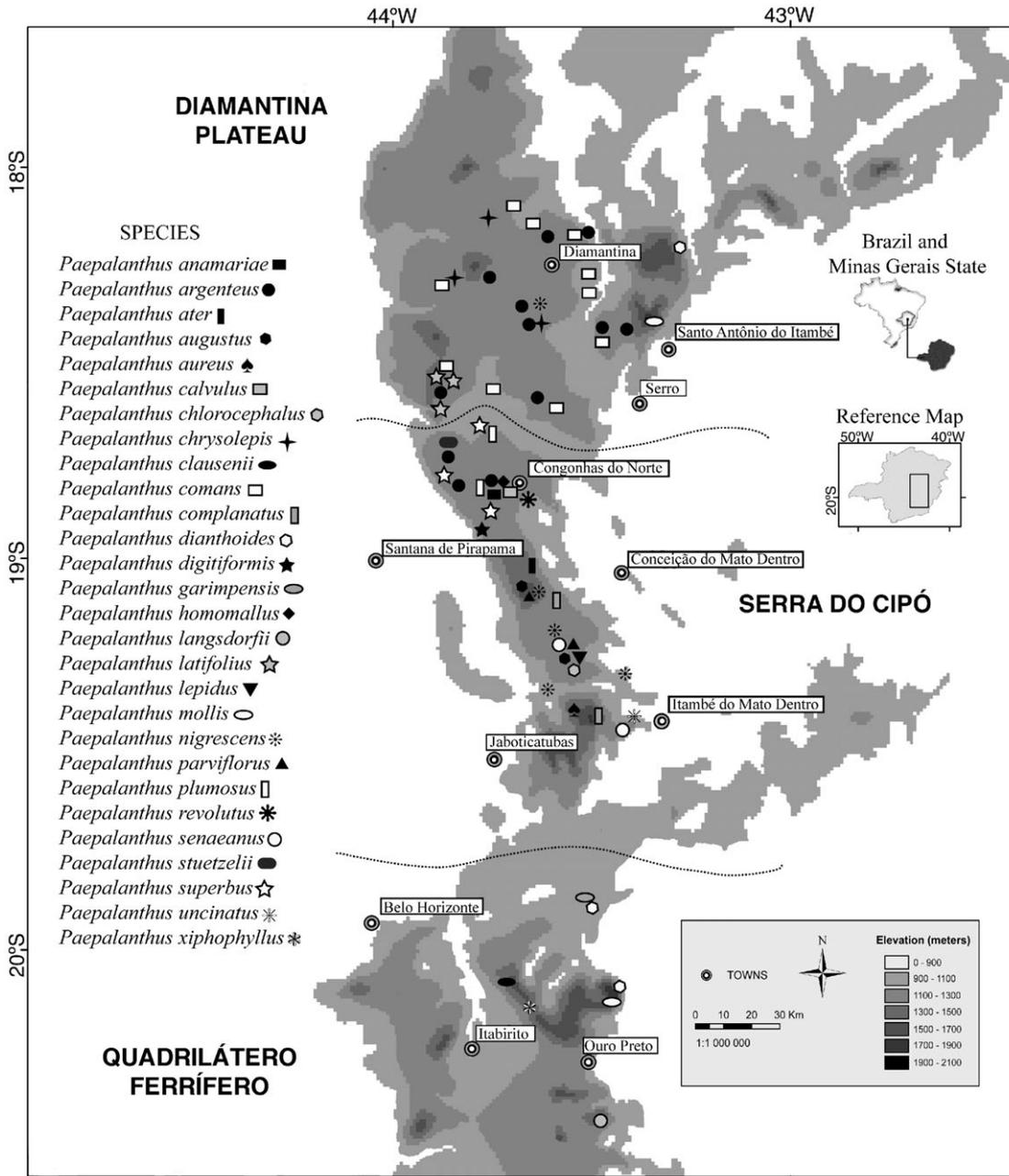
The common ancestors of all sections and series of *P.* subgenus *Xeractis* are also inferred to occur in the Serra do Cipó, except for *P.* series *Albidi*, which has an unclear origin. Colonizations toward the Diamantina Plateau would have occurred five times. One colonization took place in section *Chrystegis*, by the common ancestor of the clade (*P. chrysolepis*, *P. argenteus*, *P. latifolius*), followed by the expansion back to the Serra do Cipó by *P. argenteus*, which only reaches the northern portion of this region. In section *Xeractis*, there have been four independent events in the terminal taxa *P. dianthoides*, *P. nigrescens*, *P. comans* and *P. mollis*. Colonizations toward the Quadrilátero Ferrífero are inferred in three groups: (1) in the clade (*P. clausenii*, *P. mollis*, *P. garimpensis*), (2) in *P. xiphophyllus* and (3) in the clade (*P. langsdorffii*, *P. dianthoides*, *P. uncinatus*, *P. digitiformis*). As this last clade possesses species in the three areas of endemism, DIVA considers all possibilities for the ancestral distribution. As there is no morphological

homology supporting this clade, we will not discuss its possible origins.

## DISCUSSION

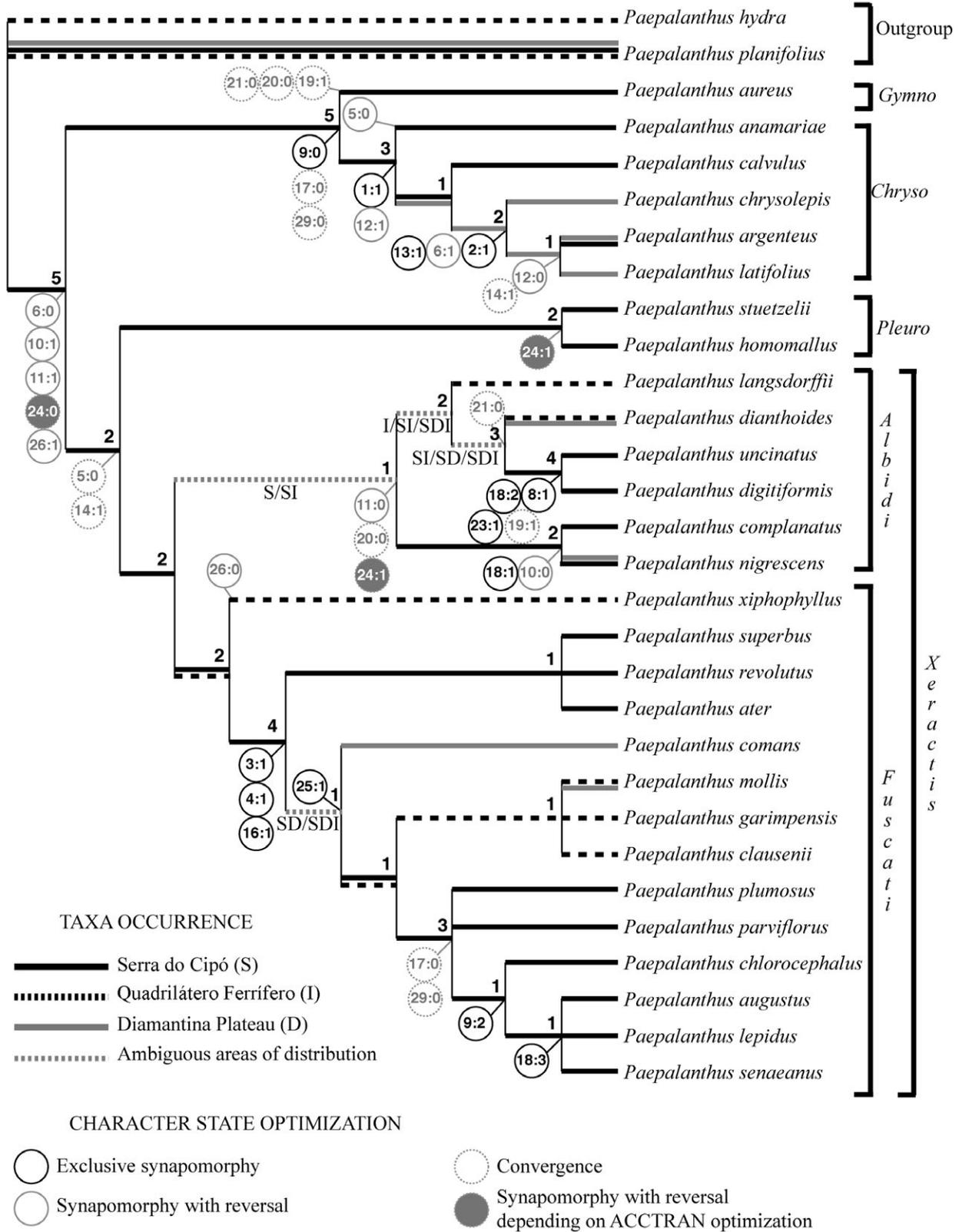
### TAXONOMIC GROUPS AND SYNAPOMORPHIES

*Paepalanthus* subgenus *Xeractis*: Some characters described above as synapomorphies are inferred so, as a consequence of the limited outgroup chosen. The opening of the peduncle sheath (C6-0), for example, is a quite inconstant character within Eriocaulaceae. The involucre bracts surpassing the flowers (C10-1) was the first diagnostic character recognized for subgenus *Xeractis* (Bongard, 1831), but it also occurs in other genera (*Comanthera* L.B.Sm., *Eriocaulon*, *Leiothrix* Ruhland, *Rondonanthus* Herzog and *Syngonanthus* Ruhland) and within *Paepalanthus* in some species outside subgenus *Xeractis* (e.g. *P. elongatus* Koern. and *P. acuminatus* Ruhland). However, the shape differentiation of its internal and external series (C11-1) is rarely found in other *Paepalanthus* spp., although it has been lost in series *Albidi*. The sepal cilia of both staminate (C24-0) and pistillate flowers are also quite variable within *Paepalanthus*. The internal pubescence on the corolla of staminate flowers (C26-1), despite also occurring in *Eriocaulon*, is exclusive in *Paepalanthus* to subgenus *Xeractis*. *Paepalanthus xiphophyllus*, with no pubescence, is an exception, but this species is known only by type material, and



**Figure 2.** Relief map showing the distribution of the species of *Paepalanthus* subgenus *Xeractis* in the Espinhaço Mountain Range at Minas Gerais, Brazil. The species occurrence is represented by symbols. Three areas of endemism are delimited: the Diamantina Plateau, the Serra do Cipó and the Quadrilátero Ferrífero.

**Figure 3.** The most parsimonious tree from the maximum parsimony analysis (length = 62 steps; CI = 0.56; RI = 0.86). Character state optimizations are shown at each node of the cladogram, represented by circles. In each circle, the numbers on the left and right represent the character and character state numbers, respectively (as reported in Appendix 2). Only character states with less than two changes were optimized. The ancestral areas of distribution reconstructed by dispersal-vicariance analysis are represented at the branches by different colours. In the branches with ambiguous results, letters below the branches indicate the combinations of the possible ancestral areas. Taxa names on the right correspond to sections and series of *Paepalanthus* subgenus *Xeractis*: *Gymno*, *P.* section *Gymnostegis*; *Chryso*, *P.* section *Chrysostegis*; *Pleuro*, *P.* section *Pleurophyllon*; *Xeractis*, *P.* section *Xeractis*; *Albidi*, *P.* series *Albidi*; *Fuscati*, *P.* series *Fuscati*.



additional data from other specimens is required to confirm this absence of pilosity.

Another feature identified by Trovó (2010) as a synapomorphy for the subgenus is the presence of adaxial indumentum on the apex and limb of the inner involucre bract whorls (C14-1, Fig. 1L–Q; C15-1, Fig. 1L, P, Q). This indumentum is present in most species, but it is absent in section *Gymnostegis* and in most species of *P.* section *Chrysostegis*. Thus, the character appears as convergence between the clades (section *Pleurophyllon*, section *Xeractis*) and (*P. argenteus*, *P. latifolius*). The results obtained by Trovó (2010) regarding this character were biased by poor taxon sampling (including only five species of the subgenus, all possessing this indumentum). In addition, the involucre bract indumentum was coded in previous studies (Giulietti *et al.*, 2000, who considered the subgenus as a terminal taxon; Trovó, 2010) as a single character. Considering all species of the subgenus, consistent variation of this indumentum can be observed and we found it more appropriate to code it as three independent characters (C14, C15 and C16). Furthermore, we coded only the indumentum of the inner series of bracts, because there is indumentum differentiation between external and internal series.

Giulietti *et al.* (2000) proposed as a further synapomorphy for the subgenus the fusion of the sepals of pistillate flowers. However, this characteristic is found in several subgenera of *Paepalanthus* and is even cited by Ruhland (1903: 121) in his description of the genus.

*Clade (section Chrysostegis, section Gymnostegis):* The exclusive synapomorphy of this clade is the cream to golden colour of the involucre bracts (C9-0, Fig. 1B). Although this feature is also observed outside subgenus *Xeractis*, and in other subgenera of *Paepalanthus* and other genera (e.g. *Leiothrix*, *Syngonanthus* and *Eriocaulon*), it was phylogenetically informative for inferring infrageneric relationships within the subgenus studied.

*Paepalanthus section Gymnostegis:* This section includes only one species, *P. aureus*. It is characterized by exclusive characters, which were excluded from our analysis as being non-informative, so that no autapomorphy is proposed here for this section.

*Paepalanthus section Chrysostegis:* The exclusive synapomorphy found for this section is the presence of a caudex (C1-1, Fig. 1N), the persistent and woody stem of perennial herbs. This character is not rare in *Paepalanthus* spp. and is also found in *Comanthera* subgenus *Comanthera* (e.g. *C. suberosa* (Giul.) L.R.Parra & Giul.). The other synapomorphy is the

involucre bracts recoiling at maturity (C12-1), which reverses in the clade (*P. argenteus*, *P. latifolius*). The clade (*P. chrysolepis*, *P. argenteus*, *P. latifolius*) shows two exclusive synapomorphies: (1) acuminate apex of the leaves (C2-1, Fig. 1I) and the external series of involucre bracts in a caudate form (C13-1, Fig. 1B). Another synapomorphy is the perpendicular opening of the peduncle sheath (C6-0, Fig. 1K), a reversed character state in subgenus *Xeractis*.

*Clade (section Pleurophyllon, section Xeractis):* Only convergent character states support this clade.

*Paepalanthus section Pleurophyllon:* The synapomorphy of this clade is the reacquisition of cilia on the sepals of staminate flowers (C24-1), a reversal that depends on ACCTRAN optimization. Indeed, Hensold (1988) proposed that *P. stuetzelii* and *P. homomallus* were clustered in section *Pleurophyllon* because they are more similar to each other than to other species of the subgenus, despite strong differences. We chose not to select several taxonomic characters suggested by Hensold (1988: 140) because they are too variable, and those selected here were finally revealed as homoplastic. Hensold (1988) suggested that these species could have closer relationships with taxa that do not belong to *P.* subgenus *Xeractis*. Because both species share the synapomorphies of the subgenus, we decided to keep them in the analysis, but further data are required to test the monophyly of this section.

*Paepalanthus section Xeractis:* There is no synapomorphy for this clade. Section *Xeractis* is strongly recognized taxonomically, but no character previously suggested as diagnostic (Hensold, 1988: 58) appears to be synapomorphic.

The first synapomorphy supporting *Paepalanthus* series *Albidi* is the involucre bracts, all similar in shape, which is a reversal to a plesiomorphic character state (C11-1, Fig. 1A). The other synapomorphy depends on ACCTRAN optimization: the absence of ciliated sepals in the staminate flowers (C24-1, Fig. 1R, T, U). Within this series, *P. complanatus* Silveira appears as the sister species of *P. nigrescens* Silveira, based on the involucre bracts not surpassing the flowers (C10-0), which is also a reversal to the plesiomorphic character state, and on spatulate floral bracts (C18-1, Fig. 1U), an exclusive synapomorphy. *Paepalanthus uncinatus* appears as the closest species to *P. digitiformis*, based on three exclusive synapomorphies: (1) the outer involucre bracts whorl green at maturity (C8-1); (2) the floral bract in a caudate form (C18-2, Fig. 2R); and (3) the staminate

flowers with stomata abaxially on the central part of the sepals (C23-1).

*Paepalanthus* series *Fuscata* is supported only by homoplasious characters. *Paepalanthus xiphophyllus* appears as sister species to all the other species and has the loss of the adaxial trichomes of the corolla tube of staminate flowers as an autapomorphy (C26-0). The sister clade of *P. xiphophyllus* is supported by several synapomorphies: the thickened margin of the leaves (C3-1), the presence of a bundle sheath (C4-1) and a dense indumentum on the adaxial limb of the inner whorl of involucral bracts (C16-1, Fig. 1L, P). The clade (*P. superbus*, *P. revolutus*, *P. ater*) is supported by no synapomorphy and its sister clade is supported by the granular pigmentation on the corolla of the staminate flowers (C25-1, Fig. 1L). There are two exclusive synapomorphies supporting the topology [*P. chlorocephalus* (*P. senaeanus*, *P. augustus*, *P. lepidus*)], the most inclusive one being the colour of the inner whorl of involucral bracts, which is darker in the centre and hyaline at margins (C9-2, Fig. 1C). The less inclusive synapomorphy is the plume-like floral bracts (C18-3, Fig. 1S).

#### PHYLOGENETIC INFORMATION OF MORPHOLOGY IN *PAEPALANTHUS* SUBGENUS *XERACTIS*

The taxonomy of Eriocaulaceae is mainly based on floral characters, many of which have been tested in phylogenetic analysis and are considered synapomorphies. Some characters provide phylogenetic information at the generic level and others at infrafamilial level. For example, the synapomorphies of the subfamilies are related to the number of perianth whorls (isostemonous in Paepalanthoideae and diplostemonous in Eriocauloideae), to the presence of glands on the petals in staminate flowers (Eriocauloideae) and to the development of nectariferous portions (Rosa & Scatena, 2007) of the style in the carpel (Paepalanthoideae) (Giulietti *et al.*, 1995; Trovó, 2010). Synapomorphies of the genera, for example, are related to the degree of fusion of the floral parts: pistillate flowers with petals fused in the middle portion in the clade [(*Syngonanthus*, *Philodice* Mart.) *Comanthera*]; lateral carpel appendages free from central carpel appendages at a different level for *Leiothrix* (Trovó, 2010).

All characters retrieved as synapomorphies for subgenus *Xeractis* represent reversals or convergence, if not in the subgenus, in other genera. In other words, there is no true morphological exclusive synapomorphy for subgenus *Xeractis* when considering all Eriocaulaceae. However, there is phylogenetic information in morphological characters, depending on the hierarchical level studied. Some characters that present too much plasticity at the generic level may prove

phylogenetically informative at the infrageneric level. The retrieved exclusive secondary homologies are related to: the presence of a caudex, leaf apex form, leaf margin thickening, presence of a bundle sheath on the leaf, pigmentation, shape and indumentum of the involucral bracts, shape of floral bracts and stomata and indumentum of sepals of staminate flowers. The synapomorphies with reversals are related to the opening of the peduncle sheath, the length of involucral bracts, the differentiation among internal and external series and its recoiling property, the sepal cilia and the corolla indumentum of staminate flowers.

As noted for the entire family, informative phylogenetic characters for subgenus *Xeractis* also focus mainly on reproductive structures (flowers and bracts). In addition, staminate flowers are more informative than pistillate flowers, not only providing more conjunctures of primary homologies but also more retained secondary homologies. It would be interesting to investigate whether these characters would also be informative in inferring relationships in other infrageneric groups of *Paepalanthus* and in other genera.

Some characters evolved in convergence within the ingroup and, despite their influence on the cladogram topology, they are of less relevance to characterize species groups. These homoplastic characters for subgenus *Xeractis* are related to the opening and length of the peduncle sheath, apex indumentum of the involucral bracts, pigmentation, texture, indumentum and apex shape of the floral bracts, pigmentation of sepals, anthers and nectariferous pistillodes of staminate flowers and pigmentation of sepals and petals of the pistillate flowers. The phylogenetic significance of several taxonomically valuable characters (Hensold, 1988) was not assessable because of the great variability found between or within certain species and difficulties in accurately and consistently defining these characters. Some examples of these characters involve the elongation of the stem, the leaf cilia, number of ribs on the peduncle, the apical cell shape of floral trichomes, the position of the insertion of the cilia in the sepals and petals and the presence of crystals at the corolla base.

#### CHARACTER EVOLUTION AND TAXONOMY OF *PAEPLANTHUS* SUBGENUS *XERACTIS*

The phylogenetic tree obtained agrees with many of Hensold's (1988) propositions. Firstly, all sections and series previously proposed appear to be monophyletic and the published hierarchy is also confirmed. Furthermore, many species alliances suggested also appear valid. Nevertheless, some hypotheses about the possible origin of the evolutionary lineage of sub-

genus *Xeractis* and the relationship between sections and series have not been confirmed.

Among these divergences, Hensold (1988: 47) suggested that *P. uncinatus* displays the most plesiomorphic (i.e. ancestral) features, and that it should therefore be placed as sister to all other species of the subgenus. These plesiomorphic features are green floral bracts, deep corolla lobes, stomata on the adaxial surface of the sepals of staminate flowers, pistillate and staminate flowers poorly differentiated, non-specialized leaf anatomy and involucre, non-hygroscopic bracts. By contrast, our results show *P. uncinatus* as sister species to *P. digitiformis* in a clade embedded in the subgenus. Some suggested plesiomorphic characters (green floral bracts and stomata on the adaxial surface of the sepals of staminate flower) are actually revealed as synapomorphies of this pair of species. In addition, Hensold (1988: 47) proposed that series *Albidi* could be non-monophyletic, giving rise to series *Fuscati* and section *Gymnostegis*, whereas sections *Chrysostegis* and section *Pleurophyllon* 'do not have obvious ancestry in *Paepalanthus* section *Xeractis*' (Hensold, 1988: 48). Our work does not confirm the latter hypotheses, probably because they were based on plesiomorphic rather than apomorphic characters, as developed above.

The conflicts between the phylogenetic tree obtained in the present study and Hensold's taxonomic revision (1988) show the need for further phylogenetic studies of the subgenus. Anatomy, phytochemistry and pollen have proved to be useful in the taxonomy of Eriocaulaceae (Ricci *et al.*, 1996; Rosa & Scatena, 2007; Borges, Giulietti & Santos, 2009). New data, including molecular analysis, are expected to reveal new synapomorphies, resolve some conflicts and enhance stability for the phylogeny of subgenus *Xeractis* and its sections. Despite all the research still to be carried out, our results are an important advance in the understanding of the evolution of subgenus *Xeractis* and Eriocaulaceae. It has provided support for several hypotheses proposed by Hensold (1988). The test of morphological characters as synapomorphies and the evaluation of the phylogenetic information may provide the grounds for further studies and new hypotheses to be tested.

#### SPECIES DISTRIBUTION AND ENDEMISM

The high frequency of microendemic species, and the fact that several of them are known from a single location, could initially suggest gaps in the collecting effort. However, botanists have visited the area since the early 19<sup>th</sup> century (e.g. Spix & Martius in 1823; Saint-Hilaire in 1833; Gardner in 1846; and Alvaro da Silveira between 1896 and 1926). Serra do Cipó has

intensively been collected since the early 1970s, with a list of species published in 1987 (Giulietti *et al.*, 1987), and monographies for more than half of angiosperm families occurring in the region have already been published (Rapini *et al.*, 2008), including that for subgenus *Xeractis* (Hensold, 1998). However, many of the species known from a single locality are observed in the Serra do Cipó. During our fieldwork, a large area was covered and most species were not observed outside their already published area of distribution or locality of occurrence. We therefore conclude that the microendemism is real and represents the pattern for all the concerned taxa.

The extensive fieldwork we conducted allowed us to clarify the distribution of the taxa and to improve our knowledge on population variation and distribution. New populations of *P. complanatus* were found at the Serra do Cipó (*L. Echternacht* 1937, SPF, 19°04'37"S 43°34'56"W) and a disjunct population of *P. dianthoides* was found in the Diamantina Plateau (*L. Echternacht* 2153, SPF, 18°13'55"S 43°15'35"W). In addition, we rediscovered taxa that were considered as probably extinct [e.g. *P. stuetzelii* and *P. argenteus* var. *elatus* (Bong.) Hensold, see Echternacht, Trovó & Sano 2010]. We observed important morphological variation within species (e.g. for *P. superbus* and *P. argenteus* in the north-western portion of the Serra do Cipó), but there was no clear evidence of hybrids.

The presence of so many microendemic species is not exclusive to Eriocaulaceae. The microendemism is also high for the entire flora in the Espinhaço Range, raising the question of the biogeographical processes underlying such restricted patterns of distribution. The high frequency of microendemism is probably favoured by regional heterogeneity, implying a mosaic of biotic and abiotic factors such as topography, vegetation, soil and water availability (Vitta, 2002; Conceição & Pirani, 2005; Rapini *et al.*, 2008). This mosaic is frequently associated with highlands, surrounded by lowlands, with different climatic conditions, having an insular effect (Harley, 1995; Simon & Proença, 2000). Isolation and heterogeneity might have favoured the specialization of taxa in microhabitats.

In general, species of Eriocaulaceae appear to be restricted to specific soil types, which may play a central role in the distribution of species and lineages. *Paepalanthus* section *Xeractis* prefers poorly drained, moister soils, whereas sections *Chrysostegis*, *Gymnostegis* and *Pleurophyllon* occur on well-drained, dry soils (Hensold, 1988: 45). In addition, the whole subgenus occurs on quartzitic formations and no species colonized the ferruginous soils of the Quadrilátero Ferrífero. Therefore, the expansion of these narrow endemic species is also probably limited by the availability its specific soil type.

Little is known about the dispersal capacity of Eriocaulaceae. In subgenus *Xeractis*, as in many *Paepalanthus*, it is known that a propulsion mechanism, driving seeds several meters away, provided by the sepals of pistillate flowers, contributes to the dispersal of seeds (Hensold, 1988). However, the efficiency of the dispersal at a populational level is unknown. Indeed, populations of subgenus *Xeractis* are usually composed of a few individuals and not widely distributed, suggesting that the dispersal capacity might be limited, constraining population expansion. Hensold (1988) suggested that some species might have a hybrid origin, such as *P. ater* and *P. garimpensis*. The observation of both of these species in their cited localities during our fieldwork (Pico do Breu, in Santana de Pirapama municipality, and Serra do Garimpo in Caeté municipality, respectively) was unsuccessful. The possibility of hybrid occurrence, that would not be able to produce perennial populations, may explain why some species are so rare (Costa *et al.*, 2008). In our study, we tried to avoid the problem of hybridization by not including possible hybrid specimens in our analyses, because hybrids could be a source of bias in phylogenies. However, further studies should investigate deeper hybridization in Eriocaulaceae and in subgenus *Xeractis*. To explain the numerous cases of microendemism, further investigations at the population level, using population biology approaches, are required, especially to test the real dispersal capacity by evaluating the genetic heterogeneity and gene flow between populations and individuals. It would also be desirable to investigate whether the microendemism observed corresponds to neo- or palaeoendemism.

#### HISTORICAL BIOGEOGRAPHY OF *PAEPALANTHUS* SUBGENUS *XERACTIS*

Vicariance is allopatric speciation after the appearance of a barrier fragmenting the ancestral distribution range of a particular species, and it differs from allopatric speciation by dispersal across a pre-existent barrier (Platnick & Nelson, 1978). It is also important to distinguish between dispersal that leads to the expansion of the species range, hereafter referred as 'range expansion', and the dispersal that leads to speciation.

In spite of the tendency of DIVA to retrieve widespread ancestors toward the base of the cladogram (Ronquist, 1997; Clark *et al.*, 2008), and the outgroup occurring in the whole ERMG, DIVA inferred the occurrence of the HA of subgenus *Xeractis* as restricted to the Serra do Cipó. This is attributable to the fact that all the lineages appearing at the base of the cladogram are exclusive to the Serra do Cipó. Consequently, all the possible vicariance events indicated

by DIVA are preceded by range expansion. Otherwise, allopatric speciation should be explained by dispersal. In addition, clades related to a single area may correspond to microspeciation, rather than illustrate an autochthonous diversification, because sister species are rarely observed sympatrically.

The Espinhaço Range is old and its geological origins are rather complex, dating from 1500 mya (Saadi, 1995; Knauer, 2007). The Espinhaço uplift ended with the collision of the African and American plates during the formation of Pangaea, c. 500–600 mya (Almeida-Abreu, 1995). Therefore, the geological history of the Espinhaço Range is too old and there is no evidence of the history of the areas of endemism to test the vicariant events proposed by DIVA. The hypothetical barriers are probably more related to relatively recent climatic fluctuations and to their impact on the regional vegetation. The presence of several areas of endemism suggests that they have a common evolutionary history in the Espinhaço Range, but currently there is no vicariance hypothesis for the ERMG based on cladistic biogeography.

Low-elevation regions between the Serra do Cipó and the Quadrilátero Ferrífero and the Paraúna River between the Serra do Cipó and the Diamantina Plateau could act as barriers between the areas of endemism (Echternacht *et al.*, 2011). In addition, the southern and eastern ERMG are more influenced by the Atlantic forest, whereas the cerrado predominates northward and westward (Alves & Kolbek, 2010). The influence of both biomes plays a central role in the distribution of the ERMG biodiversity (e.g. Rapini, Mello-Silva & Kawasaki, 2002; Versieux & Wendt, 2007; Kamino, Oliveira-Filho & Stehmann, 2008; Viana & Filgueiras, 2008). *Paepalanthus* subgenus *Xeractis* includes species in both biomes, so that there is no obvious niche conservatism at the subgeneric level. However, the narrow endemic stenotopic species may be exclusive to one biome, resulting in potential barriers to species range expansion.

Vicariance is the most parsimonious explanation for the clades composed by the HA of *P. calvulus*, that might have expanded its range from the Serra do Cipó to the the Diamantina Plateau region and, after the appearance of a barrier, speciated in the Diamantina Plateau, giving rise to *P. chrysolepis*, *P. argenteus* and *P. latifolius*. Vicariance could also be a plausible explanation for the speciation of the clade composed by the HA of *P. comans*. This HA could have occurred in the whole ERMG and the appearance of two barriers might explain the current distribution of the group. A barrier between the Serra do Cipó and the Diamantina Plateau could have promoted the speciation of *P. comans* in the Diamantina Plateau. Another barrier between the Serra do Cipó and the Quadrilátero Ferrífero could have favoured the spe-

ciation and diversification of the HA of *P. mollis* and related species in the Quadrilátero Ferrífero, and of the HA of *P. plumosus* and related species in the Serra do Cipó.

Our results revealed otherwise repeated events of dispersal, followed or not by speciation, as the most parsimonious hypothesis; for example, the disjunct distribution in the Quadrilátero Ferrífero and in the Diamantina Plateau observed for *P. mollis* and *P. dianthoides*. The occurrence of *P. mollis*, restricted to the two highest peaks of the Espinhaço Range, at elevations > 2000 m, may be explained by strong winds usually present at the Pico do Inficionado (Quadrilátero Ferrífero) that may spread the seeds, and this stenotopic species survives only in a similar habitat, in the Pico do Itambé (Diamantina Plateau). In addition, it seems that there is limited or no gene flow between the populations on these peaks, because there is distinct morphological variation and they are consistently considered as distinct varieties. The long dispersal events observed for several species, associated with limited gene flow, may have strongly contributed to diversification in subgenus *Xeractis*. Long dispersal increases the probability of genetic isolation between distant populations, favouring speciation, especially in a mountainous area composed of a mosaic of phytophysionomies where potential barriers are numerous and where microhabitats are favourable to subgenus *Xeractis*. As discussed here above, little is known about the dispersal and colonization abilities of Eriocaulaceae and these hypotheses are still to be tested.

#### CONSERVATION

As the distribution range is restricted for most species of subgenus *Xeractis*, some (29%) are on the list of endangered species of Minas Gerais, and some are also considered as probably extinct (Biodiversitas, 2000). These threatened species are: *P. argenteus* var. *elatus*, *P. ater*, *P. garimpensis*, *P. langsdorffi*, *P. stuetzelii*, *P. lepidus*, *P. uncinatus* var. *uncinatus* and *P. xiphophyllus*. The Espinhaço Range suffers high anthropomorphic impact from urbanization, expansion of agriculture, mining, grazing and annual field burnings. These factors aggravate the endangered situation of the microendemic species. In addition, the conservation units present on the Espinhaço Range do not include more than a half of the species of subgenus *Xeractis*. The results of this study encourage the emergence of more conservation units, in order to preserve Espinhaço Range as a whole. For example, the northern Serra do Cipó, including the mountains between Santana do Pirapama and Congonhas do Norte, is home to several microendemic species that are not protected by conservation units.

Furthermore, our results suggest that the conservation of the three regions, the Diamantina Plateau, the Serra do Cipó and the Quadrilátero Ferrífero, is required to maintain the evolutionary process and diversity in *P.* subgenus *Xeractis*.

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## APPENDIX 1

Representative specimens examined. The writing standardization follows the model: '*Species* Author: Voucher (Herbarium)'. Underlined vouchers refer to type material.

**Ingroup:**

***Paepalanthus anamariae*** Hensold: Hensold 581 (SPF); ***Paepalanthus argenteus*** (Bong.) Koern. var. ***argenteus***: Giulietti 9992 (SPF); Glaziou 19957 (P); Glaziou 19963 (P); L. Echternacht 1881 (SPF); Monteiro-Scanavacca 4303 (P); Saint-Hilaire 2035 (P); Vauthier 68 (P); ***Paepalanthus argenteus*** var. ***elatus*** (Bong) Hensold: Riedel 1037 (B); L. Echternacht 1894 (SPF); ***Paepalanthus ater*** Silveira: Silveira 329 (R); Hensold 472 (SPF); ***Paepalanthus augustus*** Silveira var. ***augustus***: Silveira 373 (R); Borges 114 (SPF); J. R. Pirani CFSC 12940 (SPF); L. Echternacht 1659 (SPF); M. Sazima *et al.* 4066 (SPF); P. T. Sano CFSC 13108 (SPF); ***Paepalanthus augustus*** var. ***picensis*** Hensold: Hensold 489 (SPF); L. Echternacht 1931 (SPF); ***Paepalanthus aureus*** Silveira: Silveira 359 (R); Giulietti 12443 (SPF); Hensold 372 (SPF); Smith 7072 (P); V. L. Scatena s. n. (SPF); V. L. Scatena s. n. (SPF); L. Echternacht 2132 (BHCB); ***Paepalanthus calvulus*** Hensold: Glaziou 199662 (P); Hensold 720 (SPF); L. Echternacht 2121 (BHCB) ***Paepalanthus chlorocephalus*** Silveira: Silveira 372 (R); Albo 4138 (P); L. Echternacht 1606 (SPF); Sazima 3937 (P); ***Paepalanthus chrysolepis*** Silveira: Silveira 691 (R); D.C. Zappi *et al.* 9424 (P); G. Hatschbach 66454 (BHCB); Hensold 307 (SPF); L. Krieger 14019 (BHCB); Mello Barreto 9377 (BHCB); Mello Barreto 9378 (BHCB); L. Echternacht 2169 (BHCB); ***Paepalanthus clausenii*** Hensold: Claussen 50 (P); ***Paepalanthus comans*** Silveira: Silveira 508 (R); Glaziou 19969 (P); Hensold 324 (SPF); Hensold 343 (SPF); T. M. S. Grandi s. n. (BHCB); L. Echternacht 1814 (BHCB); ***Paepalanthus complanatus*** Silveira: Silveira 369 (R); Hensold 418 (SPF); L. Echternacht 1937 (SPF); Mendes Magalhães 2560 (BHCB); ***Paepalanthus dianthoides*** Mart.: Glaziou 15521 (P); Hensold 419 (SPF); Hensold 789 (SPF); Hensold 789 (SPF); L. Echternacht 1954 (SPF); L. Echternacht 2153 (SPF); Saint-Hilaire 446 (P); Saint-Hilaire 545 (P); ***Paepalanthus digitiformis*** Hensold: Hensold 520 (SPF); L. Echternacht 1975 (SPF); ***Paepalanthus homomallus*** Mart.: Hensold 732 (SPF); Hensold 733 (SPF); L. Echternacht 1987 (BHCB); Riedel 1047 (P); ***Paepalanthus garimpen-sis*** Silveira: Silveira 557 (R); ***Paepalanthus langsdorffii*** Koern.: Claussen 1838 (P); Riedel 306 (P); ***Paepalanthus latifolius*** Koern.: Riedel 1067 (B); Mello-Silva 364 (SPF); T. B. Cavalcanti (SPF); T. M. S. Grandi 2256 (BHCB); ***Paepalanthus lepidus*** Silveira: Silveira 374 (BHCB); ***Paepalanthus mollis***

Kunth var. *mollis*: Sellow s.n. (B); Glaziou 15540 (P); Glaziou 15551 (P); L. Echternacht 1617 (SPF); L. Echternacht 1939 (SPF); M. F. Vasconcelos s. n. (BHCB); M. F. Vasconcelos s. n. (BHCB); Anderson 35763 (P); Glaziou 15552 (P); Glaziou 15553 (P); Kawasaki 994 (P); *Paepalanthus mollis* var. *itam-beensis* Hensold: Hensold 613 (SPF); L. Echternacht 1675 (SPF); *Paepalanthus nigrescens* Silveira: Silveira 355 (R); A. M. Giulietti CFSC 9767 (SPF); Hensold 383 (SPF); L. Echternacht 1607 (SPF); L. Echternacht 1936 (SPF); Mello Barreto 2537 (BHCB); Mendes Magalhães 2558 (BHCB); Sano 648 (SPF); *Paepalanthus parviflorus* (Hensold) Hensold: Hensold 438 (SPF); L. Echternacht 1935 (SPF); *Paepalanthus plumosus* (Bong.) Koern.: Glaziou 19969 (P); Hensold 750 (SPF); J. R. Pirani 4143 (SPF); L. Echternacht 1977 (SPF); Vauthier 62 (P); *Paepalanthus revolutus* Hensold: Hensold 518 (SPF); Hensold 705 (SPF); L. Echternacht 1991 (SPF); *Paepalanthus senaeanus* Ruhland: A. B. Joly CFSC 274 (SPF); Guilietti 12500 (SPF); Hensold 815 (SPF); I. Cordeiro CFSC 10520 (SPF); M. B. Horta 160 (BHCB); Mello Barreto 8544 (BHCB); Mello Barreto 2542 (BHCB); Sena s. n. (BHCB); Wanderley 10619 (SPF); *Paepalanthus stuetzelii* Hensold: Glaziou 19956 (P); L. Echternacht 2124 (BHCB); *Paepalanthus superbus* Ruhland var. *superbus*: Glaziou 19972 (P); Hensold 741 (SPF); *Paepalanthus superbus* var. *gracilis* Hensold: Hensold 580 (SPF); L. Echternacht 2045 (SPF); L. Echternacht 2044 (SPF); L. Echternacht 1984 (SPF); *Paepalanthus superbus* var. *niveo-niger* (Silveira) Hensold: Silveira 692 (R); L. Echternacht 1880 (SPF); *Paepalanthus uncinatus* var. *rectus* Hensold: Hensold 425 (SPF); L. Echternacht 1744 (SPF); *Paepalanthus xiphophyllus* Ruhland: Sena Herb. Schwacke 14578 (B).

#### Outgroup:

*Paepalanthus hydra* Ruhland: Schwacke 12040 (B); L. Echternacht 1632 (BHCB); Claussen 266 (P); *Paepalanthus planifolius* Koern.: Sano 807 (SPF); Stützel 11 (SPF).

## APPENDIX 2

Morphological characters and character state coding (primary homology hypothesis). The underlined letters refer to the codage observation source: F, field; H, herbarium; L, literature.

**Vegetative characters.** 1. Caudex: 0 = absent, 1 = present – (F/H/L); 2. Leaves (apex): 0 = round to acute, 1 = acuminate – (F/H/L); 3. Leaves (margin

thickening): 0 = absent, 1 = present – (L); 4. Leaves (bundle sheath): 0 = absent, 1 = present – (L); **Inflorescence characters.** 5. Margin of the peduncle sheath: 0 = entire, 1 = lacerate – (F/H/L); 6. Opening of the peduncle sheath: 0 = oblique to the peduncle, 1 = perpendicular to the peduncle – (F/H/L); 7. Peduncle length: 0 = longer than three times the leaf length, 1 = shorter than twice the leaf length – (F/H/L); 8. Involucral bract (external series green at maturity): 0 = absent, 1 = present – (F/H/L); 9. Involucral bracts (colour): 0 = cream to gold, 1 = homogeneously dark, 2 = dark in the centre and hyaline at margins – (F/H/L); 10. Involucral bract length: 0 = shorter or at the same level as flowers, 1 = longer than the flower level – (F/H/L); 11. Involucral bracts (differentiation): 0 = all similar in shape, 1 = inner series in a different shape to the external series – (F/H/L); 12. Involucral bracts recoiling at maturity: 0 = absent, 1 = present – (F/H/L); 13. Involucral bracts (external series caudate): 0 = absent, 1 = present – (F/H/L); 14. Involucral bracts (inner series – adaxial surface with trichomes at the apex): 0 = absent, 1 = present – (F/H/L); 15. Involucral bracts (inner series – adaxial surface with trichomes at the limb): 0 = absent, 1 = present – (F/H/L); 16. Involucral bracts (inner series – limb trichomes): 0 = scarce, 1 = dense – (F/H/L); 17. Floral bracts (dark pigmentation): 0 = absent, 1 = present – (F/H/L); 18. Floral bracts (form): 0 = triangular to elliptic, 1 = spatulate, 2 = caudate, 3 = plume-like – (H/L); 19. Floral bracts (uncinate apex): 0 = absent, 1 = present – (F/H/L); 20. Floral bracts (cilia): 0 = absent, 1 = present; 21. Floral bract (texture): 0 = firm, 1 = membranaceous – (H/L); **Flower Characters.** 22. Staminate flowers (sepal pigmentation): 0 = absent, 1 = black apex contrasting with the basis, 2 = apex slightly darker than the basis, 3 = homogeneously dark – (H/L); 23. Staminate flowers (stomata abaxially on the central part of the sepals): 0 = absent, 1 = present – (L); 24. Staminate flowers (sepal cilia): 0 = absent, 1 = present – (H/L); 25. Staminate flowers (granular pigmentation at the corolla margin): 0 = absent, 1 = present – (F/H/L); 26. Staminate flowers (trichomes at the adaxial surface of the corolla): 0 = absent, 1 = present – (H/L); 27. Staminate flowers (anther pigmentation): 0 = absent, 1 = present – (F/H/L); 28. Staminate flowers (nectariferous pistillodes homogeneously dark pigmented): 0 = absent, 1 = present – (H/L); 29. Pistillate flowers (sepal pigmentation): 0 = absent, 1 = present – (F/H/L); 30. Pistillate flowers (petal pigmentation): 0 = absent, 1 = present – (H/L).

## APPENDIX 3

Morphological matrix. Characters and coding are detailed in Appendix 2. OG, outgroup taxa.

| Taxa                                 | Characters states |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|--------------------------------------|-------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                      | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 |
|                                      | 1                 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 |
| <i>Paepalanthus planifolius</i> (OG) | 0                 | 0 | 0 | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Paepalanthus hydra</i> (OG)       | 0                 | 0 | 0 | ? | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Paepalanthus uncinatus</i>        | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus dianthoides</i>      | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus digitiformis</i>     | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus langsdorffii</i>     | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| <i>Paepalanthus complanatus</i>      | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Paepalanthus nigrescens</i>       | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| <i>Paepalanthus augustus</i>         | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus lepidus</i>          | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus senaeanus</i>        | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus parviflorus</i>      | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus chlorocephalus</i>   | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus xiphophyllus</i>     | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 |
| <i>Paepalanthus superbus</i>         | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus revolutus</i>        | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus ater</i>             | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus comans</i>           | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus plumosus</i>         | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus mollis</i>           | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus garimpensis</i>      | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus clausenii</i>        | 0                 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus calvulus</i>         | 1                 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus anamariae</i>        | 1                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus argenteus</i>        | 1                 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | ? | 1 | 1 | 0 |
| <i>Paepalanthus chrysolepis</i>      | 1                 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Paepalanthus latifolius</i>       | 1                 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| <i>Paepalanthus aureus</i>           | 0                 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| <i>Paepalanthus stuetzelii</i>       | 0                 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus homomallus</i>       | 0                 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 |

| Taxa                                 | Characters states |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
|--------------------------------------|-------------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|                                      | 1                 | 1 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 |
|                                      | 6                 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 |
| <i>Paepalanthus planifolius</i> (OG) | –                 | 1 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 1 | 1 | 1 | 0 |
| <i>Paepalanthus hydra</i> (OG)       | –                 | 1 | 0 | 0 | 1 | 1 | 1 | ? | 1 | ? | 0 | 0 | 1 | 1 | 0 |
| <i>Paepalanthus uncinatus</i>        | 0                 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus dianthoides</i>      | 0                 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus digitiformis</i>     | 0                 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus langsdorffii</i>     | –                 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus complanatus</i>      | –                 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus nigrescens</i>       | –                 | 1 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 |
| <i>Paepalanthus augustus</i>         | 1                 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus lepidus</i>          | 1                 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus senaeanus</i>        | 1                 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus parviflorus</i>      | 1                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus chlorocephalus</i>   | 1                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus xiphophyllus</i>     | ?                 | 1 | 0 | 0 | ? | 1 | 2 | 0 | ? | 0 | 0 | 1 | 0 | 1 | 1 |
| <i>Paepalanthus superbus</i>         | 1                 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Paepalanthus revolutus</i>        | 1                 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Paepalanthus ater</i>             | 1                 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 |
| <i>Paepalanthus comans</i>           | 1                 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 |
| <i>Paepalanthus plumosus</i>         | 1                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| <i>Paepalanthus mollis</i>           | 1                 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Paepalanthus garimpensis</i>      | 1                 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Paepalanthus clausenii</i>        | 1                 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 |
| <i>Paepalanthus calvulus</i>         | –                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| <i>Paepalanthus anamariae</i>        | –                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>Paepalanthus argenteus</i>        | –                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>Paepalanthus chrysolepis</i>      | –                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Paepalanthus latifolius</i>       | –                 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>Paepalanthus aureus</i>           | –                 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>Paepalanthus stuetzelii</i>       | 0                 | 1 | 0 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | ? | 1 | ? | ? |
| <i>Paepalanthus homomallus</i>       | 0                 | 1 | 1 | 0 | 1 | 1 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 |