

An escape from the Espinhaço Range: a new species of *Paepalanthus* subg. *Xeractis* (Eriocaulaceae) from the campos rupestres of Serra do Padre Ângelo, Minas Gerais, Brazil

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Background and aims – Recent botanical discoveries have highlighted the occurrence of campos rupestres in the Serra do Padre Ângelo (SPA), eastern Minas Gerais, Brazil. Here, we introduce the first new species of *Paepalanthus* subg. *Xeractis* to be described in the last three decades. Discovered in the SPA, it belongs to an emblematic lineage endemic to the campos rupestres of Minas Gerais.

Material and methods – The new species is described based on herbarium material and in situ observations. A morphological phylogenetic analysis was carried out by including the new species in a previously published character matrix. Its spatial distribution is discussed based on the obtained topology.

Key results – The new species is endemic to the SPA, but its closest related taxa are endemic to the Espinhaço Range (ER), ca 200 km distant. Its placement in the phylogeny supports the inclusion in *P. ser. Fuscata*, representing an escape from the ER. We present a clear morphological differentiation between the new species and its closest related taxa. Other similar cases of disjunct distribution among these areas of campos rupestres (SPA vs ER) are reviewed and discussed.

Conclusion – Based on the restricted distribution, allied with threats to the habitat, the new species is inserted in the IUCN category of Critically Endangered (CR). This new discovery reinforces the singularity of the SPA and the relevance of biodiversity inventories and conservation studies in the easternmost campos rupestres, and their classification as a priority area for conservation.

Keywords – Atlantic Forest; campos rupestres; Critically Endangered; disjunction; *Paepalanthus oreodoxus*; Serra do Padre Ângelo.

INTRODUCTION

The Brazilian campos rupestres are a vegetation type characterized by an herbaceous-shrubby stratum over shallow, sandy, and oligotrophic soils of ancient, mainly quartzitic mountaintops in eastern South America (Vasconcelos 2011). Despite growing on mountains of ancient orogeny as old as the Precambrian, the floristic elements of campos rupestres have shown recent and rapid radiation around 5 Mya, which could be explained by several

events of expansion and contraction of climatically suitable areas leading to isolation of populations on the complex topography of the campos rupestres, promoting speciation by vicariance, but also hybridization events during range expansions (Vasconcelos et al. 2020). This unique ecosystem therefore harbours an exceptionally rich and endemic flora, which has been the focus of several recent studies that reinforced its fragility and urgency for specific conservation measures (Alves et al. 2014; Fernandes et al. 2014; Silveira et al. 2016; Colli-Silva et al. 2019).

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Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

The campos rupestres are mainly centred in two larger areas in eastern Brazil: the Espinhaço Range (hereafter ER), in the states of Minas Gerais and Bahia, and the Chapada dos Veadeiros, in the state of Goiás. In the state of Minas Gerais, campos rupestres are additionally found in the western Serra da Canastra, and further south from the ER, on smaller mountaintop complexes towards Serra da Mantiqueira (Vasconcelos 2011). Recent botanical and zoological discoveries, however, have highlighted the occurrence of this vegetation 200 km further east of the ER, in Serra do Padre Ângelo and Pico da Aliança (Gonella et al. 2015; Loeuille & Pirani 2016; Lopes et al. 2016; Mello-Silva 2018; Loeuille et al. 2019; Kollmann 2020; Antar et al. 2021), and Sete Salões State Park (Siniscalchi et al. 2016).

The Serra do Padre Ângelo (hereafter SPA) is a quartzitic mountain complex in the Rio Doce valley in the municipality of Conselheiro Pena, in eastern Minas Gerais, that has recently attracted attention due to the discovery of several botanical novelties, most remarkably the emblematic *Drosera magnifica* Rivadavia & Gonella (Droseraceae; Gonella et al. 2015). These works have drawn attention to the up to recently neglected SPA, and also highlighted that this quartzitic Serra harbours a remnant area of campos rupestres vegetation, whose floristic representatives suggest close ties with the vegetation of the ER.

Eriocaulaceae (Poales, monocots) is one of the most species rich families of the campos rupestres in southeastern Brazil (Giulietti et al. 1997; Costa et al. 2018; Colli-Silva et al. 2019), with six genera and 474 species occurring in this vegetation type in the country (Flora do Brasil 2020). The family is easily recognized by the capituliform inflorescence, with *Paepalanthus* Mart. being the largest genus in the Neotropical region. It is also the most taxonomically complex genus in the family, with 26 infrageneric categories and ca 400 species (Costa et al. 2018). One of such infrageneric groups is *Paepalanthus* subg. *Xeractis* Mart., hitherto with 29 species, all endemic to the campos rupestres of Minas Gerais (Hensold 1988, 1996; Echternacht et al. 2020). The subgenus can be diagnosed by the pilose interior of the corolla of staminate flowers and involucrel bracts surpassing the diameter of the capitulum. Its species are grouped into four sections, with *P.* sect. *Xeractis* further divided into *P.* ser. *Albidi* and *P.* ser. *Fuscati*. The sections and series proposed by Hensold (1988) are distinguished based on habit, leaf anatomy, involucrel bract colour, and floral pubescence and pigmentation, and were found to be monophyletic in the morphological phylogenetic study of Echternacht et al. (2011). Nevertheless, the monophyly of the subgenus remains inconclusive in recent molecular phylogenetics hypotheses (Andrino et al. 2021), as the subgenus emerges divided in two groups in a polytomy with *P.* subg. *Platycaulon*.

Twenty-eight of the 29 formerly known species of *P.* subg. *Xeractis* are endemic to the Central and Southern ER in Minas Gerais, with its diversity centred in Serra do Cipó (Hensold 1988; Echternacht et al. 2020). A single variety, *P. mollis* Kunth var. *mollis*, was also recorded in the campos rupestres of highlands connecting the southern ER to the Mantiqueira Range (Hensold 1988; Mourão et al. 2017), an area known as Planalto do Alto Rio Grande (Projeto

RADAMBRASIL 1983). The subgenus is remarkable by its high micro-endemism rate, with most species known from a single locality (Echternacht et al. 2011), and six species known from the type collection only, which led these to be classified as presumably extinct in official Red Lists (Mendonça & Lins 2000). Nevertheless, increased sampling effort might reveal new populations, lead to rediscoveries (Hensold 1996; Echternacht et al. 2010), and even aid in a better understanding of the taxonomy of its species (Echternacht et al. 2020).

Even though an increasing number of new species of *Paepalanthus* have been discovered and described in the past few years (e.g. Andrino et al. 2016; Costa et al. 2016; Tissot-Squali & Sauthier 2017), no novel taxon of *P.* subg. *Xeractis* was published since the comprehensive revision of the subgenus by Hensold (1988). However, during field expeditions for the ongoing floristic inventory of the SPA, a species of *P.* subg. *Xeractis* was found. A thorough study of the specimens' morphology revealed that these represented an unnamed taxon, which is here first described, illustrated, and compared to previously known species.

To discuss its placement in the subgenus, we included the new species in the morphological phylogenetic analysis performed by Echternacht et al. (2011). Complementarily, we discuss the spatial distribution pattern and events that might have led to its isolation in the SPA, reviewing similar cases of disjunction in the recent literature.

MATERIAL AND METHODS

Study area

The Serra do Padre Ângelo is a mountain complex situated in the municipality of Conselheiro Pena, east Minas Gerais. It is located in the Rio Doce valley and belongs to the João Pinto Formation, a geological formation composed by Neoproterozoic quartzites of the Rio Doce Group (Oliveira 2000). Such formation also includes the Serra da Onça (currently protected by the Sete Salões State Park, in the municipalities of Conselheiro Pena, Itueta, Resplendor, and Santa Rita do Itueto; IEF-MG 2019) and the Pico da Aliança (municipality of Alvarenga). The SPA is contiguous with the Serra do Pinhão and the Serra do João Pinto to the north, and the Serra da Palha Branca to the southeast, altogether forming the SPA Complex, with the highest points at the Pico do Sossego (1605 m), Pico do Padre Ângelo (also known locally as Pico da Bela Adormecida, 1547 m), and Pico do Pinhão (ca 1530 m; IBGE 1982, 1987). The municipality of Conselheiro Pena has the Aw climate of the Köppen-Geiger classification (tropical with dry winter; Reboita et al. 2015), but the absence of climate data for the SPA hinder a specific classification for the Serra, which may experience lower average temperatures and higher humidity and precipitation throughout the year due to the higher elevations when compared to the surroundings.

The region is part of the Atlantic Forest phytogeographical domain, and the original surrounding matrix was stationary semideciduous forest, which has been severely suppressed over the last centuries for timber and charcoal and converted into pasture for livestock, as well as coffee and *Eucalyptus* plantations (Moura 1975; MapBiomias

Project 2020). Above 1000 m and up to the summits, the campos rupestres vegetation predominates, occurring on rocky outcrops and open fields with sandy soils. These areas are intercalated with small patches of montane ombrophilous dense forest, some of which, concentrated around the Pico do Pinhão, include the northernmost natural occurrence of the endangered conifer *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae; Hueck 1953; Mello Barreto 1956; Moura 1975). An increasing number of new and endemic species have been described for the SPA in recent years (see Discussion), but the Serra is currently not protected by any sort of conservation unit.

Taxonomy and conservation assessment

Specimens of the new taxon and of other *P.* subg. *Xeractis* species were studied in situ (including the putative closest taxa) and also analysed in the herbaria ALCB, B, BHC, DIAM, F, HUEFS, K, LL, M, MBM, MBML, NY, OUPR, P, R, RB, SPF, UB, and US (acronyms according to Thiers continuously updated). The description was based on living and dry specimens, which were analysed with a stereomicroscope; capitula and flowers were rehydrated from dried specimens.

For the observation of anatomical features, leaves from herborized specimens were rehydrated, hand sectioned, and observed under an optical microscope.

Measurements, description of structures, and terminology standards follow Hensold (1988), the latter with adaptations following recent literature on *Paepalanthus* (Echternacht et al. 2011; Costa et al. 2016). Data for the preparation of the comparative table were obtained from Hensold (1988), Andrino & Costa (2013), and from the study of herborized specimens.

The distribution map (fig. 1) was produced with the software QGIS (QGIS Development Team 2019) using layers available from IBGE (2020). Coordinates were obtained from herbarium specimens or approximated for specimens without precise coordinates.

Conservation status was assessed using the IUCN Red List Categories and Criteria (IUCN 2012). The extent of occurrence (EOO) and area of occupancy (AOO) were estimated using the GeoCAT tool described in Bachman et al. (2011), using the standard IUCN cell size of 4 km² for AOO estimation.

Phylogenetic analysis and spatial distribution patterns

The ingroup sampling included all 30 species of *Paepalanthus* subg. *Xeractis*. The character matrix published by Echternacht et al. (2011) was used, which included data from 28 species of the subgenus, with the further addition of the newly re-established *Paepalanthus elatus* (Bong.) Körn., whose data was gathered from Echternacht et al. (2020). Finally, data from the new species here described were obtained from the specimens cited below. As the outgroup, the same species from Echternacht et al. (2011), *P. hydra* Ruhland and *P. planifolius* Körn., were used. The cladistic analysis and parameters used were the same described by Echternacht et al. (2011).

The spatial distribution patterns of the species were plotted on the tree, using the endemism areas in the ER applied by Echternacht et al. (2011), with the addition of two new areas outside the ER, to encompass the new species and the new occurrence records of *P. mollis* var. *mollis* (Mourão et al. 2017).

TAXONOMIC TREATMENT

Paepalanthus oreodoxus Andrino & Gonella, **sp. nov.** (figs 1–3, table 1) – Type: BRAZIL • Minas Gerais, Conselheiro Pena, Serra do Padre Ângelo, Pico do Padre Ângelo, platô do topo do pico; 19°19'05.04"S, 41°34'42.26"W; 1480 m; 8 Jun. 2020; *P.M. Gonella, R.S. Ribeiro, G.A. da Silva & A.P. Araújo 1245*; holotype: SPF; isotypes: BHC, DIAM, MBML, RB.

Diagnosis – The new species is morphologically most similar to *Paepalanthus mollis* Kunth, but differs in the stem branches loosely arranged (vs densely arranged in compact clumps), well-developed, longer and erect (rarely pendulous) stem 8–40(–230) cm long (vs decumbent and inconspicuous stem, rarely up to 12 cm long), leaves laxly arranged along the stem with conspicuous internodes (vs congested in a rosette with inconspicuous internodes), old stems with persistent dead leaves (vs caducous leaves on plants with elongated stems), scapes 3-costate (vs 4–5-costate), involucre bracts of the internal series narrower (0.7–2.2 mm wide vs 2.1–4.1 mm wide) and surpassing the floral disc in 4 to 6 mm (vs 1.5 to 4.5 mm), anthers dorsally brown and cream-coloured in the ventral portion (vs dark brown to light yellow brown), and floral bracts narrowly spatulate to subulate (vs linear to lance-linear or spatulate).

Description – Perennial herbs up to 40(–230) cm long, caulescent. Stem well developed, 8–40(–230) cm long, green leaves present on the apical 5 to 15 cm, ca 2 mm in diameter, erect, self-supporting or supported by surrounding vegetation, or pendulous in exceptionally long specimens, branched, branching mostly at the base but also occasionally above, branches loosely arranged, covered by persistent leaves. Leaves laxly inserted along the stem (internodes conspicuous), bi-espilate, 2.0–3.5 cm × 0.05–0.40 cm, green, linear to lanceolate, apex acute, margins short-ciliate, thickened, patent to recurved, glabrescent on both surfaces to sparsely pubescent with simple hairs, hairs appressed, caducous with age, sheath with long hairs along the margins (up to 4.5 mm long). Inflorescences solitary and axillary emerging along the stems. Spathes 2.5–3.5 cm long, chartaceous, cylindrical, lax, obliquely opened, apex acute, margin entire and ciliate, indumentum with dense patent capitate hairs and less frequently also simple hairs abaxially, adaxial surface glabrous, ca 0.2–0.4 mm. Scapes erect, 7–23 cm long, green to straw-coloured with age, 3-costate, costae marked by lines of pubescence, trichomes antrorse, shortening towards the apex, caducous in older scapes. Capitula 4–12 mm in diameter, obconic involucre bracts in 3–5 series, dark brown, hygroscopic, pilose adaxially at the apex and ciliated, hairs ca 0.1–0.3 mm long, those of the external series sparsely pilose abaxially, the internal series abaxially glabrous to glabrescent, apex acute; external series

1.0–2.5 × 0.5 mm, triangular to ovate, mostly with clavate hairs; internal series 2.5–8.0 × 0.7–2.2 mm, narrowly lanceolate to lanceolate, with mixed clavate and simple hairs, surpassing the flower disc in 4–6 mm, tips recurved to reflexed. Floral bracts narrowly spatulate to subulate, 2.0–4.0 × 0.5 mm, glabrous on both surfaces, margins ciliate from base to apex or trichomes concentrated on the apical half, cream to golden-coloured, membranaceous. Staminate flowers 2–4 mm long; pedicel 0.6–1.0 mm long, with long trichomes, up to 2 mm long; sepals free, obovate to lanceolate, 1.7 × 0.2 mm, adaxially pilose towards the apex, glabrous abaxially, ciliate toward the acuminate apex; corolla tubular, membranaceous, green with dark pigmentation at the apex in living specimens, cream-coloured with dark apices in dried specimens, internally pilose; stamens 2.0–2.7 mm long, anthers brown dorsally and cream-coloured in the ventral portion; pistillodes 3, papillose. Pistillate flowers 2–6 mm long; pedicel 0.4–0.9 mm long; sepals free, obovate to lanceolate, ca 2 mm long, adaxially pilose towards the apex, glabrous abaxially, ciliate towards the obtuse apex; petals membranaceous, obovate, ca 2 mm long, cream to brown hyaline, pilose on abaxial surface, ciliate towards the acute apex; gynoecium ca 2 mm long, stigmatic branches bifid at the apex, 4 times longer than the nectariferous branches;

staminodes 3, scale-like. Seeds ellipsoidal 0.65–0.95 mm long, 0.45–0.65 mm wide, red- to orange-brown, abundantly ornamented by appendages from cell walls of the testa.

Distribution and habitat – *Paepalanthus oreodoxus* is endemic to SPA, being found at the highest peaks of these highlands, Pico do Padre Ângelo (Bela Adormecida, fig. 3A), and Pico do Sossego (photographic record – 19°14'28.27"S, 41°34'57.99"W – Fernando Rivadavia pers. comm.), occurring in campos rupestres at elevations from 1400 m to 1530 m a.s.l. The species grows on shallow sandy soils with organic matter among grasses and rocks (fig 3B). In Pico do Padre Ângelo, it is abundant at the top plateau, where it is found forming scattered groups of individuals, mostly concentrated on the eastern slope of the plateau and around large rocky outcrops.

Phenology – Individuals were collected or observed with flowers in May, June, July, August, September, November, and December, suggesting a continuous or sub-annual flowering during the study period.

Etymology – From the Greek oreo “pertaining to mountains” and doxa “glory”. This epithet was chosen as this gracious new species is exclusively found on the mountaintops of a recently discovered area of campos rupestres, representing

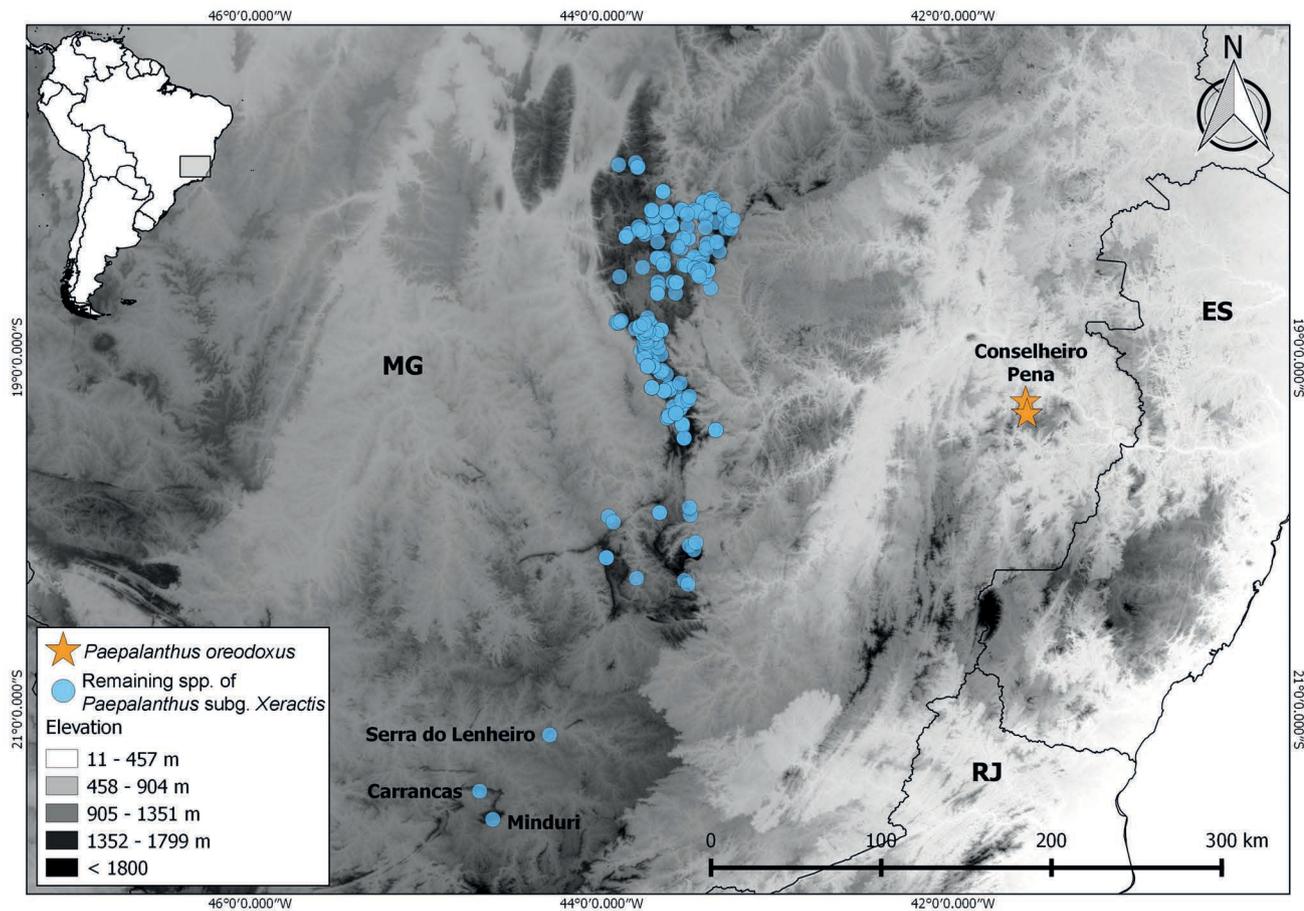


Figure 1 – Occurrence area of *Paepalanthus oreodoxus* (orange stars) and distribution area of the remaining species of *Paepalanthus* subgenus *Xeractis* (blue circles). Map created with QGIS (QGIS Development Team 2019) and layers available from IBGE (2020).

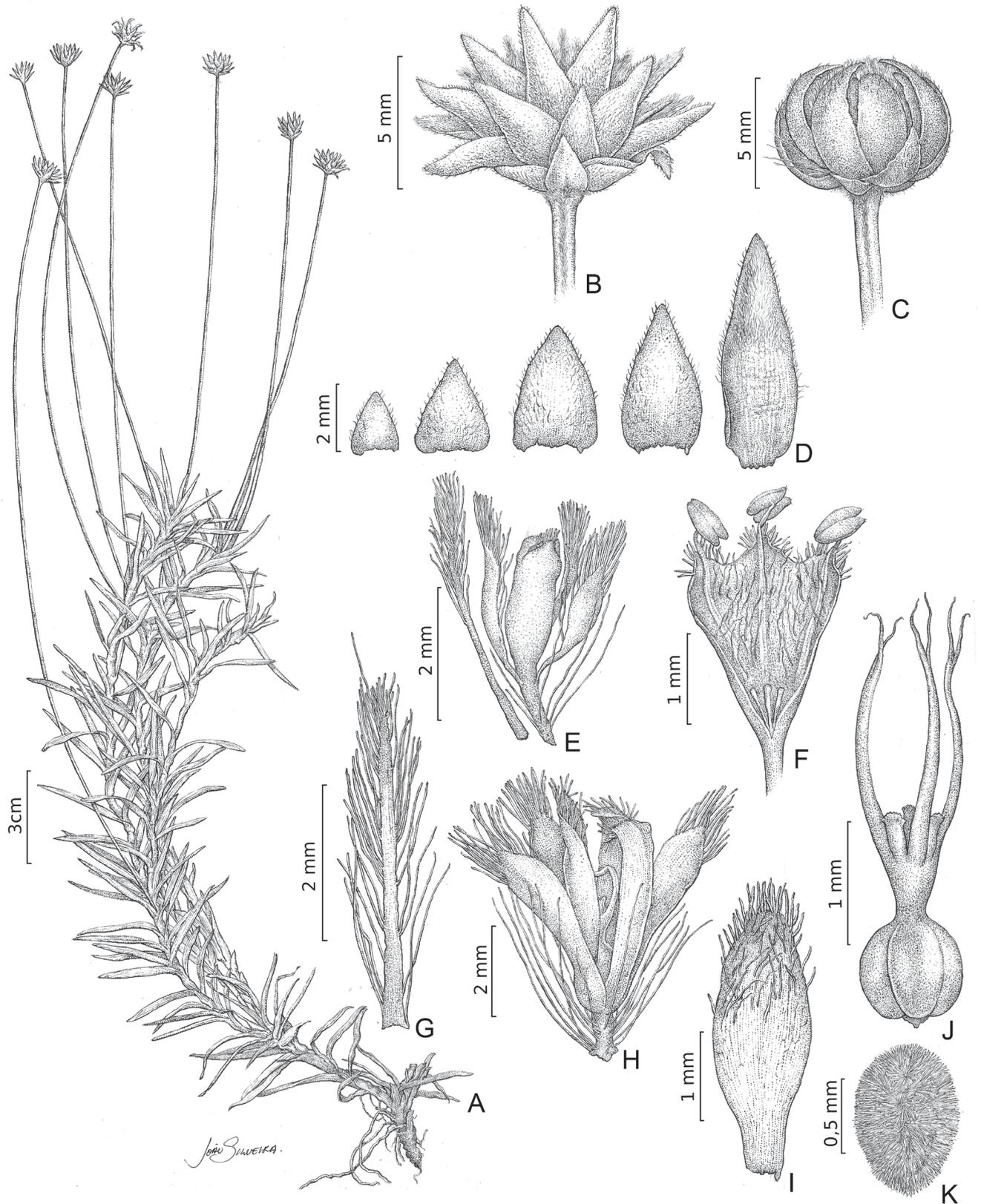


Figure 2 – *Paepalanthus oreodoxus* (based on *Gonella et al. 1044*). **A.** Habit. **B.** Capitulum detail, side view. **C.** Capitulum detail showing hygroscopic involucre bracts. **D.** Involucre bracts, abaxial surface, external series on the left side and internal ones on the right. **E.** Staminate flower with the floral bract. **F.** Staminate flower with sepals removed and open corolla. **G.** Floral bract. **H.** Pistillate flower. **I.** Petal of pistillate flower, adaxial surface. **J.** Gynoecium. **K.** Seed. Illustration by João Silveira.



Figure 3 – A. View of the campos rupestres on the top of Pico do Padre Ângelo, habitat of *Paepalanthus oreodoxus*, with Pico do Sossego and Pico do Pinhão in the background. B. *Paepalanthus oreodoxus* among rocks. C. Exceptionally long specimen of *P. oreodoxus* growing pendulous in a shaded area with one of the authors for scale. D. Immature capitulum in dry weather, showing recurved involucre bracts. E. Side view of the capitulum with bracts opening after a wet night. F. Capitulum with hygroscopically bent bracts over the flower disc in wet weather. G. Capitula with recurved bracts in dry weather. H. Front view of capitula, showing the long involucre bracts characteristic of the species. I. Staminate flower with anthers cream-coloured with dark pigmentation in the dorsal portion. A, D, F–H by Paulo M. Gonella; C by Danilo Pacheco Cordeiro; B, E, I by Andreas Fleischmann.

an outstanding discovery that reinforces the singularity of the SPA flora and the importance of its conservation.

IUCN Conservation assessment – Critically Endangered: CR A1a+B2ab(ii,iii,v). *Paepalanthus oreodoxus* was found in two subpopulations ca 8 km apart (fig. 2), outside any conservation area, and always at elevations above 1400 m and associated with quartzitic rock. Therefore, the suitable area for species occurrence is very limited and fragmented. The Pico da Aliança, at 12 km from the SPA and also not protected, is the only other area of similar elevation and substrate in the region and was also studied but no population of *P. oreodoxus* was found so far. The area of occupancy (AOO) was estimated at 8 km², and several threats could be identified, putting at risk the long term survival of the species. The largest known population, on the summit of Pico do Padre Ângelo, suffered a dramatic reduction in the number of individuals with a recent and intense wildfire in late September 2020 (late dry season) that consumed most of the vegetation of the peak. It is estimated that more than 90% of the adult plants of *P. oreodoxus* were destroyed in this event that also affected several other endemic and

endangered species. Except for the southern slope, which was likely protected by the rocky outcrops and ascending winds from the south, the whole top plateau of Pico do Padre Ângelo was affected. The presence of the invasive grass species *Melinis minutiflora* P.Beauv. (Poaceae) was already identified as a threat to the endemic flora of the SPA (Gonella et al. 2015), and this large fire event can expand the invaded area by this and other alien species, as grasses quickly recover and reproduce after burning (D’Antonio & Vitousek 1992). Limited knowledge is available about the dynamics of Eriocaulaceae and fire (Neves et al. 2011), especially for *Paepalanthus*. Nevertheless, recruitment from the soil seed bank could be expected if the fire was not intense enough to burn the peat layer where seeds are deposited. However, days after the burning of the superficial vegetation, the fire was still observed consuming the peat in the top plateau of the Serra (Paulo M. Gonella pers. obs.). Additionally, the rea is further susceptible to a dramatic reduction of climatic suitability in the coming decades due to climatic changes, which overall threatens to significantly reduce the suitable area for the mountaintop vegetation of campos rupestres (Fernandes et al. 2014; Barbosa & Fernandes 2016). This scenario is

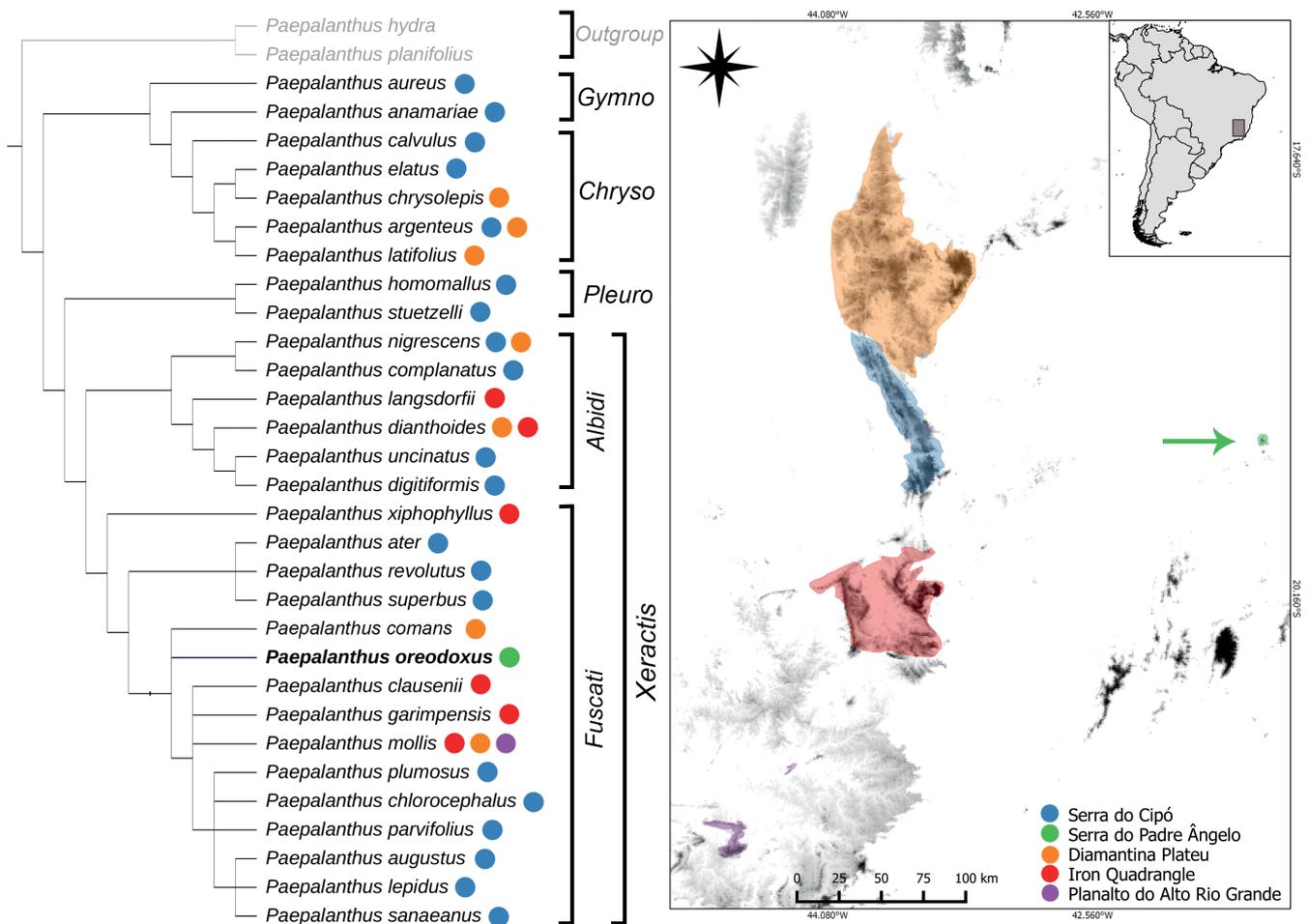


Figure 4 – Strict consensus tree from the maximum parsimony analysis (length = 63 steps; CI = 0.52; RI = 0.85) with the addition of *P. oreodoxus* described here and *P. elatus* in the morphological matrix of Echternacht et al. (2011; see that work for character state optimizations). Taxa names correspond to sections and series of *Paepalanthus* subgenus *Xeractis*: *Gymno*, *P.* section *Gymnostegis*; *Chryso*, *P.* section *Chryso*; *Pleuro*, *P.* section *Pleurophyllon*; *Xeractis*, *P.* section *Xeractis*; *Albidi*, *P.* series *Albidi*; *Fuscati*, *P.* series *Fuscati*. Coloured circles after the species names indicate the spatial distribution of each species (areas of the same colour on the map).

especially concerning for mountaintop endemics such as *P. oreodoxus*, which are unable to migrate to higher elevations to avoid the rising temperatures. Finally, combined with the small population size, the distribution of *P. oreodoxus* is restricted to an unprotected area that is prone to disturbance by human activities, mostly related to agriculture and livestock activities in the surrounding areas, such as the use of herbicides and insecticides, and the common use of fire for pasture renovation, which can escape to the native vegetation and further aggravate the invasion by alien grass species (D'Antonio & Vitousek 1992). Given the listed threats, which can affect all subpopulations of this microendemic species at once, this taxon is considered to occur at a single location, meeting criterion B2a of IUCN (2012). Due to the restricted occurrence, the numerous threats, and the lack of protection, the species is here categorized as Critically Endangered (CR) according to IUCN (2012), requiring urgent action such as habitat protection, and fire and invasive species management.

Additional material examined – BRAZIL – Minas Gerais • Conselheiro Pena, Pico do Padre Ângelo, no cume do pico; 19°19'13.96"S, 41°34'45.14"W; 1500 m; 28 Nov. 2013; *P.M. Gonella* & *F. Rivadavia* 643; SPF • *ibid.*; 19°19'14.2"S, 41°34'43.7"W; 1530 m; 8 Jul. 2014; *P.M. Gonella*, *F. Rivadavia*, *C. Rohrbacher* & *R. Vasconcelos* 683; SPF • *ibid.*; 19°19'15"S, 41°34'43"W; 1500 m; 3 Aug. 2014; *C.T. Oliveira*, *B. Loeuille* & *C. Siniscalchi* 997; SPF • Serra do Padre Ângelo, Pico do Padre Ângelo, no platô do topo do pico; 11 Jun. 2017; *P.M. Gonella*, *L. Medeiros* & *D. Caetano* 770; SPF • *ibid.*; 4 Dec. 2018; *P.M. Gonella*, *A. Fleischmann*, *L. Medeiros*, *L. França* & *D. Silveira* 1044; SPF • *ibid.*, na entrada da gruta; 22 Aug. 2020; *P.M. Gonella*, *E. Ramos*, *D.P. Cordeiro*, *T.H. Condez* & *P.R. Bartolomay* 1661; MBML.

Morphological phylogeny and spatial distribution patterns – The maximum-parsimony analysis generated 36 equally parsimonious trees with 63 steps, a consistency index (CI) of 0.52, a retention index (RI) of 0.85. The strict consensus tree is presented (fig. 4). The topology was generally concordant with the tree presented by Echternacht et al. (2011). *Paepalanthus elatus* was placed as sister of *P. chrysolepis*, in *P.* [subg. *Xeractis*] sect. *Chrysostegis*. *Paepalanthus oreodoxus* was placed in *P.* [subg. *Xeractis*] sect. *Xeractis*] ser. *Fuscata*, appearing in an unresolved clade, with *P. comans*, *P. mollis*, *P. plumosus*, and others (fig. 4).

The spatial distribution pattern shows *P. oreodoxus* in a clade with ambiguous area of distribution, with species occurring in Diamantina Plateau, Iron Quadrangle, and Serra do Cipó (fig. 4). Nevertheless, the distribution of the species of the whole *P.* subg. *Xeractis* already allowed the inference that its common ancestor likely occurred in Serra do Cipó, in the south of the ER (Echternacht et al. 2011).

DISCUSSION

Taxonomy and phylogenetic placement

Paepalanthus oreodoxus is the 30th species of *P.* subg. *Xeractis*, characterized by the elongated stem, which is branched mostly at the base, the scapes laxly inserted along the stems, capitula with long involucre bracts far exceeding

the height of the flowers, petals with dark apices, staminate flower corolla internally hairy, and anthers that are dorsally brown and cream-coloured in the ventral portion. This combination of characters places this species in *P.* [subg. *Xeractis*] sect. *Xeractis* (Hensold 1988).

Paepalanthus sect. *Xeractis* comprises another 16 species, which are divided into two series (fig. 4): *P.* ser. *Albidi*, which has species with cream anthers, among other characteristics, and *P.* ser. *Fuscata*, with brown anthers. Therefore, based solely on anther colour, *P. oreodoxus* would fit in *P.* ser. *Fuscata* because of the presence of pigmentation, although it presents an intermediate anther colouration.

The inclusion of the new species in the morphological phylogeny presented here (fig. 4) was intended to test its inclusion in the sections and series of the current classification of *P.* subg. *Xeractis*. The results showed that the species belongs to *P.* ser. *Fuscata*, which is supported only by homoplasies in the character set used by Echternacht et al. (2011) and here. *Paepalanthus oreodoxus* appears in a polytomy with *P. comans* Silveira and another clade with nine other species, with low internal resolution (fig. 4). Therefore, while the character set was informative enough to support the inclusion of *P. oreodoxus* in *P.* ser. *Fuscata*, it lacks resolution for the inference of species relationships and biogeography. Recent molecular studies found a monophyletic *P.* ser. *Fuscata*, but with low support (Andrino et al. 2021). *Paepalanthus* ser. *Albidi*, on the other hand, was found to be paraphyletic, with *P. digitiformis* Hensold sister to *P.* ser. *Fuscata*, and a clade formed by *P. nigrescens* Silveira and *P. complanatus* Silveira found sister to a monophyletic *P.* sect. *Chrysostegis*. This suggests that the bract colour and how much it exceeds the height of the flower disc in the capitula may have a strong phylogenetic signal, but additional molecular studies with a larger sampling and including morphological data are needed for such conclusions.

The presence and degree of parenchymatous buttresses joining the veins to the upper and lower epidermis of the leaves is an important character for distinguishing between sections and series of *P.* subg. *Xeractis* (Hensold 1988). In *P. oreodoxus*, only alternate major veins are buttressed, similarly to most species of *P.* ser. *Fuscata*, such as *P. superbus* Ruhland and *P. mollis* var. *itambeensis* Hensold, while in *P. dianthoides* Mart. (*P.* ser. *Albidi*), even the minor veins are often buttressed at least to the adaxial surface (table 1). Furthermore, *P. oreodoxus* presents thickened leaf margins, which is a character typical of *P.* ser. *Fuscata*. Consequently, the leaf anatomical features further support the placement of *P. oreodoxus* in *P.* ser. *Fuscata* (fig. 4).

One of the most striking characteristics of *P. oreodoxus* are the long involucre bracts (fig. 3H), which are longer and more conspicuous than those of most species in *P.* subg. *Xeractis*, surpassing the length of the flowers in the capitulum by more than 4 mm. This character is rarely found in other groups outside of *P.* subg. *Xeractis*, and is therefore very useful for field identification. These bracts are usually reflexed and recoil at the tips, showing different degrees of hygroscopicity. In *P. oreodoxus*, these bracts are patent and bend over the capitulum in wet weather (figs 2C, 3F), and

Table 1 – Main morphological differences between *P. oreodoxus*, *P. dianthoides*, *P. mollis*, and *P. superbus*. All measurements for *P. dianthoides*, *P. mollis*, and *P. superbus* are from Hensold (1988) and Andrino & Costa (2013), combined with the examination of additional herbarium specimens.

Character	<i>P. oreodoxus</i>	<i>P. dianthoides</i>	<i>P. mollis</i>	<i>P. superbus</i>
Stem	Erect, elongated, 8–40(230) cm long. Internodes conspicuous	Erect, elongated, up to 50 cm long. Internodes conspicuous	Decumbent, slightly elongated, rarely up to 12 cm long. Internodes inconspicuous	Erect, elongated, 25(–40) cm long. Internodes slightly conspicuous
Leaf margin cilia	Present, short	Present, long	Sometimes inconspicuously short-ciliate	Absent
Leaf margin thickened	Present	Absent	Present or absent	Present
Leaf veins buttresses	Only alternate major veins or fewer are buttressed	Major veins are usually buttressed and minor veins are often buttressed at least to the adaxial surface	Only alternate major veins or fewer are buttressed	Only alternate major veins or fewer are buttressed
Number of costae of peduncle	3-costate	Obscurely 5–7 costate	4–5-costate	(4–)5-costate
Inflorescence arrangement	Lax, solitary along the stem	Lax, 5 or fewer per cohort (up to 10–14)	Lax, 1–3(–6) per cohort	Congested, 5–20(–34) per cohort
Involucral bracts length (internal series)	2.5–8 mm	4.2–6.7 mm	3.5–7.7 mm	2.5–13 mm
Involucral bracts surpassing capitulum by	4–6 mm	up to 2.5 mm	1.5–4.5 mm	0.5–5.5 mm
Anther colour	Brown dorsally and cream in the ventral portion	Cream	Dark brown to light yellow-brown	Cream to dark brown

are revolute in dry weather (fig. 3D, G), which is a common feature in *P.* subg. *Xeractis*.

At first glance, the new species is morphologically most similar to *P. dianthoides* and *P. superbus*, which also have well-developed, elongated stems. However, in *P. dianthoides* the involucral bracts barely surpass the height of the flowers and the anthers are cream, while in *P. superbus*, the scapes are congested and numerous at the apex of the stem (usually 5 to 20 per cohort, up to 34) and the anthers are cream to dark brown (table 1). The stem of *P. oreodoxus* usually reaches up to 40 cm, but an exceptionally long specimen was observed growing in the shade at a cave entrance reaching 230 cm (fig. 3C), setting a new length record for a *P.* subg. *Xeractis* species. Previously, Hensold (1988) reported stems up to 50 cm in *P. dianthoides*.

The species also shares similarities with *P. mollis*, more specifically with *P. mollis* var. *mollis*, such as bract and flower morphology, but also the more or less continuous flowering period throughout the year. *Paepalanthus oreodoxus* can be easily distinguished from this variety by the caulescent habit (vs rosetted), with elongated stems commonly reaching up to 40 cm (up to 230 cm in exceptional specimens vs stem compact, rarely reaching up to 12 cm long), the green leaves laxly arranged on the apical 5 to 15 cm of the stem and the dead leaves persistent (vs green leaves densely arranged in a rosette and dead leaves caducous), erect and laxer stems (vs decumbent and forming dense clumps), the shorter leaves (2–3.5 vs 2–7 cm long), the 3-costate scapes (vs 4–5-costate),

the involucral bracts surpassing the capitulum in 4–6 mm (vs 1.5–3.5 mm), the characteristic anther colouration (vs anthers dark brown to light yellow brown;), and by the floral bracts narrowly spatulate to subulate (vs linear to lance-linear or spatulate; table 1).

Paepalanthus oreodoxus and *P. mollis* share similar habitat preferences, both occurring on mountaintop areas of quartzite peaks. A similar pattern is described for another endemic of the SPA, *Drosera magnifica*, whose closest species, *D. graminifolia* A.St.-Hil., also occurs on the mountaintops of Serra do Caraça (Gonella et al. 2015), therefore also showing a similar biogeographic pattern as *P. oreodoxus* and *P. mollis*. The patterns observed for these pairs of species suggests allopatric speciation with niche conservatism, which is assumed to be a common driver in campos rupestres diversification (Zappi et al. 2017), but requires further investigation. Curiously, *D. magnifica* also presents an elongated stem, which is not observed for *D. graminifolia* (Gonella et al. 2015). The development of elongated stems in the two SPA endemic species (*P. oreodoxus* and *D. magnifica*) could be related to the evolutionary history of their ancestors in a denser vegetation, promoting selection of elongated stems to compete for light. In both species, however, the elongated stem can be observed in plants growing isolated and exposed, suggesting that this trait might have been retained from their ancestors.

Paepalanthus mollis is one of the few species for which Hensold (1988) recognized varieties. While the autonym

variety occurs in the southern range of the species (Iron Quadrangle of the ER and Planalto do Alto Rio Grande), *P. mollis* var. *itambeensis* is restricted to the Pico do Itambé, on the Diamantina Plateau (Hensold 1988; Andriano & Costa 2013), ca 180 km north of the range of *P. mollis* var. *mollis*. *Paepalanthus oreodoxus* is more similar to *P. mollis* var. *mollis*, since *P. mollis* var. *itambeensis* has a more robust habit, with longer and broader leaves, and broader involucral bracts that are abaxially pilose (even the uppermost ones). Similar to other trimerous *Paepalanthus*, species of *P.* subg. *Xeractis* are autochorous, with seeds ejected for short distances by the calyx (Hensold 1988; Trovó & Stützel 2011). However, the understanding of the dispersal capacity of the family is still limited. Long-distance dispersal was evoked by Echternacht et al. (2011) to explain the disjunct distribution of the varieties of *P. mollis* on the mountaintops of the highest peaks of the ER, arguing that the small seeds could be transported by strong winds, common on these mountaintops. Vicariance, with range expansion during cooler past periods followed by isolation with the rise of temperatures, could also explain this pattern (Vasconcelos et al. 2020). These hypotheses should also be further investigated for the isolation of *P. oreodoxus* in the SPA, so distant from all other members of *P.* subg. *Xeractis*.

Both varieties of *P. mollis* are morphologically distinct by a set of characters (Hensold 1988) and occur allopatrically, likely with no gene flow between the populations, which would justify further investigation of their taxonomic status. Hensold (1988) suggests that the differences could also include chromosome numbers, with *P. mollis* var. *itambeensis* being tetraploid in comparison to the autonym variety, but this requires further investigation. As a recent example in *P.* subg. *Xeractis*, the re-evaluation of the taxonomic status of *P. argenteus* Körn. var. *elatus* (Bong.) Hensold justified the segregation and reestablishment of *P. elatus* at the species rank (Echternacht et al. 2020).

The easternmost campos rupestres of Minas Gerais – what do we already know?

Recent botanical and zoological discoveries have brought attention to the occurrence of campos rupestres vegetation and taxonomic singularities in the quartzitic massifs of the João Pinto Formation in eastern Minas Gerais, such as the SPA, the Serra da Onça, and Pico da Aliança.

While the core of the campos rupestres are located in the Espinhaço Range, which is situated in a transition zone between the Cerrado, Atlantic Forest, and Caatinga domains, these easternmost campos rupestres areas are entirely situated in the Atlantic Forest domain, in a region in which quartzitic outcrops are rather uncommon and where the majority of the highland landscape is composed of granitic or gneissic massifs covered by highland grasslands (campos de altitude) or are isolated lowland rocky outcrops (inselbergs) with rupicolous vegetation (Vasconcelos 2011). Such different substrates combined with the rugged terrain create an abundance of micro-habitats, providing the opportunity for multiple speciation events and often giving rise to high levels of endemism (Giulietti & Pirani 1988; Antonelli et al. 2010; Nevado et al. 2018). The geographical proximity

of floristic communities on different bedrocks may provide interesting biogeographical patterns, especially for non-edaphic specialists.

These easternmost campos rupestres areas are situated in the Rio Doce valley and are largely understudied regarding their floristic diversity. *Paepalanthus oreodoxus* is an example of this, as it is the 16th new species described from these mountains in a period of only seven years. In such a short period, many new species and geographic records have been described for these mountains, such as in Droseraceae (Gonella et al. 2015), Asteraceae (Loeuille & Pirani 2016; Siniscalchi et al. 2016; Loeuille et al. 2019), Bromeliaceae (Leme & Kollmann 2013; Leme et al. 2014, 2020; Leme 2015), Orchidaceae (Campacci 2014, 2015; Harding & Bohnke 2015), Velloziaceae (Mello-Silva 2018), Begoniaceae (Kollmann 2020), and Lamiaceae (Antar et al. 2021). These new records also include the easternmost record of a bird species typical from the campos rupestres (Lopes et al. 2016). Therefore, these areas are good laboratories where the “Linnean shortfall” (the discrepancy between the documented species and those still undescribed) and the “Wallacean shortfall” (lack of data on species distribution; Lomolino 2004) are highly evident, meaning that more new species and geographic records are expected to be uncovered as these areas are further investigated. Furthermore, these findings cover a phylogenetically diverse assemblage of lineages, supporting the area as relevant not only for the conservation of threatened and endemic species, but also with a great phylogenetic diversity.

Filling these gaps is key to understanding the biogeography of these disjunct campos rupestres areas. Nevertheless, a recurrent biogeographic pattern is highlighted by this new species of *P.* subg. *Xeractis*. As mentioned before, Gonella et al. (2015) point out that the species more closely related to *Drosera magnifica* are endemic to the ER (Serra do Caraça, Diamantina Plateau, and Grão Mogol mountains). Besides that, *Vellozia gigantea* was previously only known in Serra do Cipó (Mello-Silva 2018). A new *Hyptidendron* Harley (Lamiaceae) species from the SPA also finds its most similar species in the Serra do Cipó (Antar et al. 2021). Two newly described Lychnophorinae species (Asteraceae; Loeuille & Pirani 2016; Loeuille et al. 2019) from Pico da Aliança also show a similar pattern, as does *Chresta filicifolia* Siniscalchi & Loeuille (Asteraceae; Siniscalchi et al. 2016) from Sete Salões State Park, whose closest taxa are from the northern ER in Minas Gerais and from the Chapada Diamantina in Bahia. Similarly, the species morphologically closer to *P. oreodoxus* are endemic to the ER, with the exception of *P. mollis*, which is also found in the Planalto do Alto Rio Grande (fig. 4). Even though the resolution of the morphological phylogeny did not allow for a precise hypothesis of the ancestral biogeographical area of *P. oreodoxus*, it does allow to infer that the ancestor of this species was from the ER, over 200 km from the SPA. This suggests a recent colonization of the SPA by this lineage followed by in situ speciation, resulting in a neo-endemism.

Such distribution patterns without intermediaries in the interjacent areas highlight the specialization to particular environmental conditions of the campos rupestres flora, mostly related to edaphic and climatic conditions, resulting

in a high degree of micro-endemism, a very common pattern in *P.* subg. *Xeractis* (Hensold 1988; Hensold 1998; Andrino & Costa 2013; Echternacht et al. 2011, 2020).

The occurrence of such floristic elements typical of campos rupestres in these disjunct areas in eastern Minas Gerais raises many questions on how, when, and how many times this flora reached the area. Expansion of grasslands during glacial times might have connected or approximated patches of the highland vegetation, allowing these elements to reach these easternmost areas, which were then isolated on the mountaintops when temperatures rose again (Behling 2002; Siniscalchi et al. 2016). Edaphic specialization might also have played an important role in the isolation of these lineages, as these are usually associated with the quartzitic bedrock. Even though no quartzitic mountains connect these easternmost campos rupestres to the ER, lowland patches of white quartz sand could have worked as stepping stones between these regions. Occurrence of typical campos rupestres flora in lowland sandy patches is well documented, including species of Eriocaulaceae (Giulietti & Pirani 1988; Alves et al. 2007). The expansion of elements from colder areas followed by isolation is further supported by the natural occurrence of *Araucaria angustifolia* in the SPA, which is the northernmost area of occurrence for this species (Hueck 1953; Mello Barreto 1956; Moura 1975). Phylogeographic studies focusing on the groups found in these areas in eastern Minas Gerais, including *Paepalanthus*, will help elucidate the history of the colonization of these highlands by elements from the core campos rupestres.

The singular and largely unknown biodiversity of these easternmost campos rupestres, however, is on the brink of extinction. Severe threats, such as the expansion of invasive grasses, are facilitated by the continuing presence of fires and the change of land use in the surroundings, which was aggravated in the last century, confining the last remnants of natural vegetation to these mountaintops. Moura (1975) already describes the severe destruction of the native vegetation around the SPA and the impoverishment of the few remnants by anthropic fires. Furthermore, projections for the impact of climate change on the campos rupestres are fairly pessimistic, with the rise of temperatures threatening to significantly reduce the areas suitable for the occurrence of these species in the next few decades (Fernandes et al. 2018). The Rio Doce valley has experienced an intense human impact, not only on land use with the severe transformation of its forests into pastures during the last two centuries, but also on its water resources, compromised by a recent environmental catastrophe (Meira et al. 2016; Nazareno & Vitule 2016). In this context, the protection and correct conservation management of the SPA and surrounding campos rupestres areas are critical, not only to protect the future of this unique biodiversity but also to safeguard the ecological services provided by these highlands for the human population in the region.

ACKNOWLEDGEMENTS

The authors are grateful to Nancy Hensold, Ana Carolina Loss, Frederic Mendes Hughes, Livia Echternacht, and an anonymous reviewer for valuable suggestions on the

manuscript; to João Silveira for the illustrations; to Rafael Gomes Barbosa-Silva for aid in the preparation of the map and photo plate; to Carolina Siniscalchi for the English proofreading and suggestions to the manuscript; to Guilherme Antar for his aid in data collection; to Andreas Fleischmann and Danilo Pacheco Cordeiro for the photographs of the plant; to Fernando Rivadavia for the photographic record of this species in Pico do Sossego; to Ednilson Caetano Ribeiro, Danúbia Ribeiro Segala, Eva Helena dos Santos, Júlio César Ribeiro, Paulo Ricardo Ribeiro, Lucian Medeiros, Luiz França, and Reginaldo Vasconcelos for the company and guidance during field expeditions and for valuable information about SPA. Permission for fieldwork was granted by the Authorization and Information System in Biodiversity (SisBio), from the Chico Mendes Institute for Biodiversity Conservation (ICMBio). We thank the curators and staff of the visited herbaria. Financial support was provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior-CAPES to COA and by Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq to COA (grant #316014/2018-4) and PMG (grants #140135/2013-8, #302306/2019-6). PMG also thanks the Mohamed bin Zayed Species Conservation Fund (grant #192522325) and IDEA WILD for financial support.

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Communicating editor: Isabel Larridon.

Submission date: 20 Jun. 2020

Acceptance date: 18 Sep. 2020

Publication date: 23 Mar. 2021