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. Fuscati, 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).
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 mountain-top 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; Louelle & Pirani 2016; Lopes et al. 2016; Mello-Silva 2018; Louelle et al. 2019; Kollmann 2020; Antar et al. 2021), and Sete Sãos 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 magnaﬁca* 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 involucral 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, involucral 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 Sãos 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; MapBiomas...
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 northermmost 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, BHCB, DIAM, F, HUEFS, K, LL, M, MBM, MBML, NY, OUPR, P, R, RB, SPF, UB, and US (acronyms according to Thiers 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.

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, plató 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: BHCB, 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), involucral 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-espiralate, 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 apressed, 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 involucral bracts in 3–5 series, dark brown, hygroscopic, pilose abaxially 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 towards 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 from base to apex; 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 2 – *Paepalanthus oreodoxus* (based on Gonella et al. 1044). A. Habit. B. Capitulum detail, side view. C. Capitulum detail showing hygroscopic involucral bracts. D. Involucral 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. Pistilate flower. I. Petal of pistilate 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 involucral 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 involucral 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.
Andrino & Gonella, A new and disjunct species of Paepalanthus subg. Xeractis

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 Chrysostegis; 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 Ángelo, 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. Louelle & C. Siniscalchi 997; SPF • Serra do Padre Ángelo, Pico do Padre Ángelo, 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 results showed that the species belongs to *P. ser. Fuscati*, 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. Fuscati*, it lacks resolution for the inference of species relationships and biogeography. Recent molecular studies found a monophyletic *P. ser. Fuscati*, but with low support (Andrino et al. 2021). *Paepalanthus oreodoxus* Silveira and another 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 butresses 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. Fuscati*, such as *P. superbus* Ruhland and *P. mollis* var. *tambeensis* Hensold, while in *P. dianthoides* Mart. (*P. ser. Albidii*), 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. Fuscati*. Consequently, the leaf anatomical features further support the placement of *P. oreodoxus* in *P. ser. Fuscati* (fig. 4).

One of the most striking characteristics of *P. oreodoxus* are the long involucral 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

**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 involucral 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. subg. Albidii*, which has species with cream anthers, among other characteristics, and *P. subg. Fuscati*, with brown anthers. Therefore, based solely on anther colour, *P. oreodoxus* would fit in *P. ser. Fuscati* 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. Fuscati*, 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. Fuscati*, it lacks resolution for the inference of species relationships and biogeography. Recent molecular studies found a monophyletic *P. ser. Fuscati*, but with low support (Andrino et al. 2021). *Paepalanthus oreodoxus* Silveira and another 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.
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 Andrinó & Costa (2013), combined with the examination of additional herbarium specimens.

| Character                        | *P. oreodoxus* | *P. dianthoides* | *P. mollis* | *P. superbus* |
|---------------------------------|----------------|------------------|-------------|---------------|
| **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 | Present, short | Sometimes inconspicuously short-ciliate | Absent |
| **Leaf margin thickened**       | Present | Absent | Present or absent | Present |
| **Leaf veins buttresses**       | Only alternate 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) | 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 magnaifica*, 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; Andrin & 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 granite or gneissic massifs covered by highland grasslands (campos de altitude) or are isolated lowland rocky outcrops (inselbergs) with rupeicolous 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 magna* 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 flicifolia* 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 Sorriso; 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 PMG (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.

**REFERENCES**

Alves R.V.J., Cardin L. & Kropf M.F. 2007. Angiosperm disjunction “campos rupestres - restings”: a re-evaluation. *Acta Botanica Brasilia* 21(3): 675–685. https://doi.org/10.1590/S0102-33062007000300014

Alves R.V., Silva N.G., Oliveira J.A. & Medeiros D. 2014. Circumscribing campo rupestre – megadiverse Brazilian rocky montane savannas. *Brazilian Journal of Biology* 74(2): 355–362. https://doi.org/10.1590/1519-6984.23212

Andrino C.O. & Costa F.N. 2013. *Paepalanthus* subgen. *Xeractis* (Eriocaulaceae) na porção central da Cadeia do Espinhaco em Minas Gerais, Brasil. *Rodriguésia* 64(1): 75–89. https://doi.org/10.5915/52175-7860213000100008

Andrino C.O., Trovó M. & Sano P.T. 2016. A field full of green stars: *Paepalanthus multistellaris* (Eriocaulaceae), a new species from Minas Gerais, Brazil. *Phytotaxa* 278(1): 55–61. https://doi.org/10.11646/phytotaxa.278.1.6

Andrino C.O., Sano P.T., Inglis P.W., Hensold N., Costa F.N. & Simon M.F. 2021. Phylogenetics of *Paepalanthus* (Eriocaulaceae), a diverse Neotropical monocot lineage. *Botanical Journal of the Linnean Society* 95(1): 34–52. https://doi.org/10.1093/botlinnean/boaa070

Antar G.M., Harley R.M., Pastore J.F.B., Gonella P.M. & Sano P.T. 2021. *Hyp tidendron pulcherrimm* Antar & Harley, sp. nov. (Hyptidinae, Lamiaceae) a new narrowly endemic species from Minas Gerais, Brazil. *Adansonia, sér. 3* 43(1): 1–8. https://doi.org/10.5252/adansonia2021v43a1

Antonelli A., Verola C.F., Parísod C. & Gustafsson A.L.S. 2010. Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). *Botanical Journal of the Linnean Society* 100(3): 597–607. https://doi.org/10.1111/j.1095-8312.2010.01438.x

Bachman S., Moat J., Hill A.W., de la Torre J. & Scott B. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *ZooKeys* 150: 117–126. https://doi.org/10.3897/zookeys.150.2109
Barbosa N.P.U. & Fernandes G.W. 2016. Rupestrian grassland: past, present and future distribution. In: Fernandes G.W. (ed.) Ecology and conservation of mountaintop grasslands in Brazil: 531–544. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-29808-5_22

Behling H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. Palaeogeography, Palaeoclimatology, Palaeoecology 177(1–2): 19–27. https://doi.org/10.1016/S0031-0182(01)00349-2

Campacci M.A. 2014. Hoffmannseggella alvarenguensis Campacci sp. nov. Coletânea de Orquídeas Brasileiras 10: 382–385.

Campacci M.A. 2015. Dryadella krenakiana Campacci sp. nov. Coletânea de Orquídeas Brasileiras 11: 418.

Colli-Silva M., Vasconcelos T.N.C. & Pirani J.R. 2019. Outstanding plant endemism levels strongly support the recognition of campo rupestre provinces in mountaintops of eastern South America. Journal of Biogeography 46(8): 1723–1733. https://doi.org/10.1111/jbi.13585

Costa F.N., Andrino C.O., Trovó M., Echternacht L. & Sano P.T. 2016. Three new micro-endemic species of Paepalanthus (Paepalanthoideae, Eriocaulaceae) from Serra do Ambrósio, Minas Gerais, Brazil. Phytotaxa 247(2): 118–126. https://doi.org/10.11646/phytotaxa.247.2.3

Costa F.N., Andrino C.O., Sano P.T., Trovó M. & Echternacht L. 2018. Paepalanthus (Eriocaulaceae) in the Central Espinhaço Range in Minas Gerais, Brazil: checklist, endemism, and nomenclatural changes. Phytotaxa 367(2): 133–144. https://doi.org/10.11646/phytotaxa.367.2.3

D’Antonio C.M. & Vitousek P.M. 1992. Biological invasions by alien grasses, the grass/fire cycle and global change. Annual Review of Ecology, Evolution, and Systematics 23: 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Echternacht L., Trovó M. & Sano P.T. 2010. Rediscoveries in Eriocaulaceae: seven narrowly distributed taxa from the Espinhaço Range in Minas Gerais, Brazil. Feddes Repertorium 121(3–4): 117–126. https://doi.org/10.1022/fedr.201000008

Echternacht L., Sano P.T., Trovó M. & Dubuission J.-Y. 2011. Phylogenetic analysis of the Brazilian microendemic Paepalanthus subgenus Xeraxis (Eriocaulaceae) inferred from morphology. Botanical Journal of the Linnean Society 167(2): 137–152. https://doi.org/10.1111/j.1095-8339.2011.01170.x

Echternacht L., Soldevila A. & Beirão M. 2020. Reestablishment and recircumscription of Paepalanthus elatus (Eriocaulaceae, Poales), a threatened micro-endemic species from northern Serra do Cipó, Minas Gerais, Brazil. Phytotaxa 440(2): 171–185. https://doi.org/10.11646/phytotaxa.440.2.6

Fernandes G.W., Barbosa N.P.U., Negreiros D. & Puglia A.P. 2014. Challenges for the conservation of vanishing megadiverse rupestrian grasslands. Natureza & Conservação 12(2): 162–165. https://doi.org/10.1016/j.ncon.2014.08.003

Fernandes G.W., Barbosa N.P.U., Alberton B., et al. 2018. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodiversity and Conservation 27(10): 2587–2603. https://doi.org/10.1007/s10531-018-1556-4

Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available from http://floradobrasil.jbr.jbrj.gov.br/ [accessed 29 Aug. 2019].

Giulietti A.M. & Pirani J.R. 1988. Patterns of geographical distribution of some plant species from the Espinhaço Range, Minas Gerais and Bahia, Brazil. In: Vanzolini P.E. & Heyer W.R. (eds) Proceedings of a workshop on Neotropical distribution patterns: 39–69. Academia Brasileira de Ciências, Rio de Janeiro.

Giulietti A. M., Pirani J.R. & Harley R.M. 1997. Espinhaço Range region, eastern Brazil. In: Davis S.D., Heywood V.H., Herrera- MacBryde O. & Hamilton A.C. (eds) Centres of plant diversity: a guide and strategy for their conservation vol. 3: 397–404. World Wide Fund for Nature/World Conservation Union, Cambridge.

Hensold N. 1988. Morphology and systematics of Paepalanthus subg. Xeraxis (Eriocaulaceae). In: Systematic Botany Monographs 23. The American Society of Plant Taxonomists, Michigan. https://doi.org/10.2307/25027709

Hensold N. 1996. Paepalanthus subg. Xeraxis (Eriocaulaceae): notes and nomenclatural changes. Phytologia 81(1): 24–27.

Hensold N. 1998. Flora da Serra do Cipó, Minas Gerais: Paepalanthus subg. Xeraxis (Eriocaulaceae). Boletim de Botânica da Universidade de São Paulo 17: 207–208. https://doi.org/10.1166/issn.2316-9052.v17i0p207-218

Hueck K. 1953. Distribuição e habitat natural do Pinheiro do Paraná (Araucaria angustifolia). Boletim da Faculdade de Filosofia, Ciências e Letras da Universidade de São Paulo – Botânica 10: 5–24. https://doi.org/10.1166/issn.2318-5988.v10i1p5-24

IBGE 1982. Folha SE-24-Y-C, Colatina, escala 1:250.000. Secretaria de Planejamento da Presidência da República, Instituto Brasileiro de Geografia e Estatística. Available from https://geobases.es.gov.br/cartas-topo-250 [accessed 7 Sep. 2020].

IBGE 1987. Folha SE.24 Rio Doce: geologia, geomorfologia, pedologia, vegetação, uso potencial da terra/Fundação Instituto Brasileiro de Geografia e Estatística. IBGE, Rio de Janeiro.

IBGE 2020. Instituto Brasileiro de Geografia e Estatística. Available from https://mapas.ibge.gov.br/bases-e-referenciais/bases-cartograficas/malhas-digitais [accessed 29 Aug. 2020].

IEF-MG 2019. Parque Estadual de Sete Salões. Instituto Estadual de Florestas de Minas Gerais. Available from http://ief.mg.gov.br/component/content/article/214 [accessed 28 Aug. 2019].

IUCN 2012. IUCN red list categories and criteria version 3.1. Second edition. IUCN Species Survival Commission. IUCN, Gland, Switzerland & Cambridge, UK. Available from https://www.iucn.org/content/iucn-red-list-categories-and-criteria-version-31 [accessed 18 Sep. 2020].

Kollmann L.J.C. 2020. Novelties in Brazilian Begoniaceae II: a new species from Minas Gerais. Phytotaxa 437(3): 156–160. https://doi.org/10.11646/phytotaxa.437.3.4

Leme E.M.C. 2015. Two new species of Orthophytum (Bromeliaceae: Bromelioideae) from Minas Gerais, Brazil. Phytotaxa 205(4): 283–291. https://doi.org/10.11646/phytotaxa.205.4.8

Leme E.M.C. & Kollmann L.J.C. 2013. Miscellaneous new species of Brazilian Bromeliaceae - III. Phytotaxa 177(2): 61–100. https://doi.org/10.11646/phytotaxa.177.2.1
Leme E.M.C., Ribeiro O.B.C., Souza F.V.D., de Souza E.H., Kollmann L.I.C. & Fontana A.P. 2020. Miscellaneous new species in the “Cryptanthoid complex” (Bromeliaceae: Bromelioidae) from eastern Brazil. *Phytotaxa* 430(3): 157–202. https://doi.org/10.11646/phytotaxa.430.3.2

Louveille B. & Pirani J.R. 2016. Two new syncephalous species of *Eremannthus* (Asteraceae: Vernoniae) from southeastern Brazil. *Phytotaxa* 243(2): 128–136. https://doi.org/10.11646/phytotaxa.243.2.2

Louveille B., Semir J. & Pirani J.R. 2019. A synopsis of *Lynchophorinae* (Asteraceae: Vernoniae). *Phytotaxa* 398(1): 1–139. https://doi.org/10.11646/phytotaxa.398.1.1

Lomolino M.V. 2004. Conservation biogeography: introduction. In: Lomolino M.V. & Heaney L.R. (eds) *Frontiers of Biogeography*: 293–296. Sinauer Associates, Sunderland.

Lopes L.E., Marçal B.F. & Chaves A.V. 2016. The patchy distribution of the Pale-throated Serra-Finch *Embernagra longicauda* (Aves: Thraupidae) in the eastern Brazilian mountain tops: the overlooked *campos rupestres* of the Rio Doce valley. *North-Western Journal of Zoology* 12(2): 373–376.

MapBiomas Project 2020. Collection 4.1 of the Annual Land Use and Land Cover Maps of Brazil. Available from http://mapbiomas.org/ [accessed 5 Sep. 2020].

Meira R.M.S.A., Peixoto A.L., Coelho M.A.N., et al. 2016. Brazil’s mining code under attack: giant mining companies impose unprecedented risk to biodiversity. *Biodiversity and Conservation* 25: 407–409. https://doi.org/10.1007/s10531-016-1050-9

Mello Barreto H.L. 1956. Contribuição à ciência geográfica: Regiões Fitogeográficas de Minas Gerais. *Boletim Geográfico* XVI(130): 14–28.

Mello-Silva R. 2018. Land of the Giants: remarkable botanical discoveries highlight a new area for conservation in Brazil. *Rodriguésia* 69(2): 933–937. https://doi.org/10.1590/2175-7860201869245

Mendonça M.P. & Lins L.V. (orgs) 2000. Lista vermelha das espécies e subespécies de campo rupestre: a neglected conservation priority. *Plant and Soil* 403: 129–152. https://doi.org/10.1007/s11104-015-2637-8

Oliveira M.J.R. 2000. Programa Levantamentos Geológicos Básicos do Brasil. Projeto Leste: Folhas Conselheiro Pena/São Gabriel da Palha - SE.24-V-Y-I/USE.24-V-Y-III (parte), escala 1:100.000. SEME/CONAB/PRM, Belo Horizonte.

Oliveira M.J.R. 2000. Programa Levantamentos Geológicos Básicos do Brasil. Projeto Leste: Folhas Conselheiro Pena/São Gabriel da Palha - SE.24-V-Y-I/USE.24-V-Y-III (parte), escala 1:100.000. SEME/CONAB/PRM, Belo Horizonte.

Projeto RADAMBRASIL 1983. Folhas SF 23/24 Rio de Janeiro/ Vitória, geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Ministério de Minas e Energia, Rio de Janeiro.

QGIS Development Team 2019. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from http://qgis.osgeo.org [accessed 20 Nov. 2019].

Reboita M.S., Rodrigues M., Silva L.F. & Alves M.A. 2015. Aspectos climáticos do estado de Minas Gerais. *Revista Brasileira de Climatologia* 11(17): 206–226. https://doi.org/10.5380/abc1ma.v17i10.41493

Silveira F.A.O., Negreiros D., Barbosa N.P.U., et al. 2016. Ecology and evolution of plant diversity in the endangered *campos rupestres*: insights from phylogenetic structure. *New Phytologist* 208(3): 834–846. https://doi.org/10.1111/nph.13876

Thiers B. continuously updated. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. Available from http://sweetgum.nybg.org/ih/ [accessed 25 Jan. 2019].

Vasconcelos M.F. 2011. O que são campos rupestres e campos de altitude nos topos de montanha do leste do Brasil? *Revista Brasileira de Botânica* 34(2): 241–246. https://doi.org/10.1590/S0100-84042011000200012

Vasconcelos T.N.C., Alcantara S., Andrino C.O., et al. 2020. Fast diversification through a mosaic of evolutionary histories characterizes the endemic flora of ancient Neotropical mountains. *Proceedings of the Royal Society B: Biological Sciences* 287: 20192933. https://doi.org/10.1098/rspb.2019.2933

Zappi D.C., Moro M.F., Meagher T.R. & Lughadha E.N. 2017. Plant biodiversity drivers in Brazilian *campos rupestres*: insights from phylogenetic structure. *Frontiers in Plant Science* 8: 2141. https://doi.org/10.3389/fpls.2017.02141

Communicating editor: Isabel Larridon.