

RESEARCH ARTICLE

A microendemic and enigmatic new cactus species from the *campo rupestre* of Minas Gerais, Brazil: *Uebelmannia nuda* (Cactaceae, Cactoideae)

Daniela C. Zappi,¹ Nigel P. Taylor,² Fabiane Nepomuceno Costa,³ Simone Nunes Fonseca,⁴ Paula Leão Ferreira,⁴ Monique Romeiro-Brito,^{2,5} Milena C. Telhe,² Matias Köhler,² Fernando F. Franco² & Evandro M. Moraes²

¹ Programa de Pós-Graduação em Botânica, Instituto de Ciências Biológicas, Universidade de Brasília (UNB), Brasília 70919-970, Brazil

² Departamento de Biologia, Universidade Federal de São Carlos, Sorocaba 18052-780, São Paulo, Brazil

³ Departamento de Ciências Biológicas, Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina 39100-000, Minas Gerais, Brazil

⁴ Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio, Diamantina 39100-000, Minas Gerais, Brazil

⁵ Florida Museum of Natural History, Department of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.

Address for correspondence: Daniela C. Zappi, danielazappi14@gmail.com

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Abstract A phylogenetic study of *Uebelmannia* investigates the relationships of a newly discovered taxon in this enigmatic, early-diverging genus that is sister to all the other c. 460 species of tribe Cereeae. Here we present a coalescent-based phylogenetic tree inferred with nuclear genes captured by the Cactaceae591 probe set encompassing all *Uebelmannia* species. The new taxon *U. nuda* is sister to *U. pectinifera*, while *U. gummifera* and *U. buiningii* form another pair of closely related species. The unusual characteristics of the new cactus (semi-subterranean/geophytic habit, turbinate stem, naked areoles) distinguish it from all other *Uebelmannia* species. The definition of the relationships within this early-derived genus endemic to the *campo rupestre* of Minas Gerais State became more evident, and this new find adds to the importance of this biogeographic province for the evolution of tribe Cereeae. The new species is described, and a preliminary conservation assessment is presented. Additionally, a key for all taxa of the genus is provided.

Keywords Cactaceae; Cereeae; conservation status; target capture sequencing; *Uebelmanniinae*

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The eastern Brazilian, highland rock-dwelling vegetation mosaic known as the *campos rupestres* of the Serra do Espinhaço (Zappi & al., 2017; Colli-Silva & al., 2019; Vasconcelos & al., 2020) has been recognized, due to its outstanding plant diversity (Giulietti & al., 1987; Stannard, 1995; Zappi & al., 2003, 2014; Pirani & al., 2009; Carmo & Jacobi, 2016), as two biogeographic provinces, the Chapada Diamantina province in the state of Bahia and the Southern Espinhaço province in Minas Gerais (Colli-Silva & al., 2019). The latter has been subdivided into the Grão Mogol district, the Diamantina Plateau district, and the Iron Quadrangle district. The Diamantina Plateau is home to the endemic cactus genus *Uebelmannia* (Nyffeler, 1998; Schulz & Machado, 2000).

The small, endemic genus *Uebelmannia* was found to be the early-diverging clade in relation to all c. 460 remaining species of the tribe Cereeae (Romeiro-Brito & al., 2023), which includes widespread genera such as *Melocactus* (c. 40 species

from the Caribbean and Central America to Peru and south-eastern Brazil), *Pilosocereus* (40+ species, from the Florida Keys, Caribbean islands and Mexico to Paraguay, reaching the state of Mato Grosso do Sul in Brazil) and *Echinopsis* (c. 80 species, central/southern Andes to southern Brazil and Uruguay). Most genera of Cereeae, however, are restricted to South America, and subtribe Cereinae has eastern Brazil as its centre of diversity (Romeiro-Brito & al., 2023).

Despite the restricted distribution of the three species then known, *Uebelmannia* populations were found to have moderate to high levels of genetic diversity (Silva & al., 2020). These extremely highly structured populations are found even at small geographic scales, with population clusters exhibiting high inbreeding and genetic signatures of a recent bottleneck. Further concerns regarding diminishing population-sizes to habitat degradation and targeted commercial plant collection were also confirmed during recent fieldwork in the region (Taylor & al., 2023).

During actions to control illegal mining in the Parque Nacional das Sempre Vivas, near Diamantina in northern

Minas Gerais, a surprising *Uebelmannia* was unearthed by S.N. Fonseca and P.L. Ferreira. It grows almost sympatrically with *Uebelmannia pectinifera* Buining (a population geographically and morphologically intermediate between *U. pectinifera* subsp. *horrida* (P.J.Braun) P.J.Braun & Esteves and *U. pectinifera* subsp. *flavispina* (Buining & Brederoo) P.J. Braun & Esteves). The two distinct species, however, colonize different substrates, with the newly discovered taxon growing as a geophyte in quartz gravel and sand, while *U. pectinifera* occupies nearby quartzitic rock outcrops, where it grows in rock crevices.

We decided to investigate the position of this remarkable plant by running a phylogenetic analysis to determine its position prior to its formal naming and description. We also provide a key for all taxa of the genus, and conservation assessments.

■ MATERIALS AND METHODS

Data sampling, genomic sequencing, and data processing.— Seven specimens from the genus *Uebelmannia* were sampled in our phylogenetic inference, including the three recognized species of this genus, as well as two specimens of the potential new species. The outgroup sampling comprised eight species from the tribe Cereeae (Appendix 1). We combined newly generated data and data available on GenBank (National Center for Biotechnology Information, NCBI; <https://www.ncbi.nlm.nih.gov/genbank/>) from previous phylogenetic studies in tribe Cereeae (Romeiro-Brito & al., 2023; here detailed in Appendix 1). Genomic DNA was extracted from root tissues using a high-salt CTAB protocol (detailed in Romeiro-Brito & al., 2023). Nuclear loci were enriched using the Cactaceae591 probe set (Romeiro-Brito & al., 2022). Library preparation and sequencing were performed by RAPiD Genomics (Gainesville, Florida, U.S.A.). Raw reads were trimmed using fastp v.0.23.4 (Chen & al., 2018), where poor-quality reads (phred <20), adapters, and short reads (<60 bp) were removed. The trimmed reads were mapped and assembled using HybPiper v.2.0.3 pipeline (Johnson & al., 2016; <https://github.com/mossmatters/HybPiper>). Reads were mapped against reference sequences for each locus (Romeiro-Brito & al., 2022) with the software BWA (Li & Durbin, 2009) and assembled into contigs using the software SPAdes v.3.15 (Bankevich & al., 2012). We excluded from our analysis the putative paralogs identified by Romeiro-Brito & al. (2022) across the tribe Cereeae. We recovered the ontarget loci and their flanking regions (named here as “supercontig” dataset), using the “retrieve_sequences” command. The dataset was aligned using MAFFT v.7 (Katoh & Standley, 2013) and indel-rich regions trimmed using trimAL v.1.3 (Capella-Gutiérrez & al., 2009) with the –gt command. We also removed poorly aligned and hypervariable sites using the software spruceup (Borowiec, 2019). To minimize the effects of missing data on our phylogenetic analysis, the dataset comprised loci and samples with less than 30% of missing data. The alignment is provided as suppl. Appendix S1. Accession

numbers for raw reads of target sequence capture data are presented in Appendix 1. The raw reads are available on the National Center for Biotechnology Information Sequence Read Archive (NCBI SRA) under the BioProject accession number PRJNA812417.

Phylogenomic analyses.— The phylogenetic inferences using the supercontig dataset were carried out employing the multi-species coalescent model. In contrast to concatenated approaches (e.g., maximum likelihood), which assume that all genes conform to the same topology, this method addresses the discordance between gene trees and species trees, a prevalent phenomenon often observed within phylogenies of the tribe Cereeae (Romeiro-Brito & al., 2023; Taylor & al., 2023). The phylogenetic reconstructions were estimated using the coalescent summary method implemented in Weighted ASTRAL (wASTRAL) and the function *astral-hybrid* (Zhang & Mirarab, 2022). The gene trees used as input were inferred by IQ-TREE v.2.2 (Minh & al., 2020) using the *ModelFinder Plus* and ultrafast bootstrap (Hoang & al., 2018) with 10,000 replicates. The inferred gene trees were summarized by wASTRAL, using local posterior probability (LPP) as branch support.

Morphology and conservation assessments.— Morphological descriptions were prepared according to the methodology and nomenclature from Taylor & Zappi (2004), and the conservation assessments were prepared using GeoCAT software and following IUCN criteria and categories (Bachman & al., 2011; IUCN, 2012).

■ RESULTS

The supercontig dataset recovered 454 nuclear loci, comprising 854,622 bp of both exonic and intronic regions. This dataset contains 125,806 variable sites (14.7%) and 46,208 parsimony-informative sites (5.4%). The genus *Uebelmannia* was recovered as monophyletic and sister to the remaining lineages of tribe Cereeae. The new species was placed sister to *Uebelmannia pectinifera*, and these two species form a pair as the sister to the other species pair in the tree, formed by *U. gummifera* (Backeb. & Voll) Buining and *U. buiningii* Donald (Fig. 1).

The new species is described below, with a conservation assessment, and a new key is presented for the genus.

■ DISCUSSION

The monophyletic genus *Uebelmannia* (Fig. 1) is only known from the Diamantina Plateau of the Southern Espinhaço province in Minas Gerais (Colli-Silva & al., 2019). Previous studies of the genus that we have consulted include Nyffeler (1998), Schulz & Machado (2000) and Taylor & Zappi (2004). Until the present discovery, it was thought that, while *U. gummifera* and *U. buiningii*

occur exclusively in quartz gravel to the east of the Cadeia do Espinhaço mountains, *U. pectinifera* inhabited the western areas, growing in crevices of quartzitic outcrops. The newly discovered species, almost sympatric with *U. pectinifera* and forming a species pair with it, was found growing on quartz sand and gravel, the substrate that is typical for the other two species of the genus. The perceived similarities between *U. nuda* sp. nov. and the *U. buiningii* and *U. gummifera* pair is probably due to shared environmental pressures (plants growing in sand rather than in rock crevices as is the case with *U. pectinifera*). It is interesting to notice that *U. buiningii* shows some putative neotenic characteristics in relation to the *U. gummifera* complex, such as a smaller number of ribs and lack of mucilaginous ducts (Nyffeler, 1998). Both species are geographically restricted and almost sympatric in the Parque Estadual da Serra Negra, whereby *U. buiningii* presents the narrowest range, with an extension of occurrence of about 40 km² (Machado & al., 2013). It is possible that *U. buiningii* “budded off” through peripheral isolate speciation from its close relative *U. gummifera*, but this should be investigated in future studies using a broader phylogenetic sampling.

TAXONOMIC TREATMENT

***Uebelmannia nuda* Zappi & N.P. Taylor, sp. nov.** – Holotype: BRAZIL. Minas Gerais, Parque Nacional das Sempre Vivas, Mun. Bocaiúva, alto da serra, 17°S, 43°W, approx. 1200 m a.s.l., 26 Apr 2023, F.N. Costa, P. Leão & S.N. Fonseca 2293 (UB barcode UB0338137; isotypes: DIAM, RB).

Diagnosis. – Differs from all other species of *Uebelmannia* in its semi-subterranean habit, stem turbinate and flat-topped;

ribs 14–50, closely and evenly spaced, rounded; areoles sunken and devoid of spines. Fig. 2A–H.

Description. – Mature stems <4–11 cm diam., generally solitary, napiform, buried in the substrate, meristematic apex protected by densely white trichomatous young areoles, epidermis roughened/scaly/waxy and in older individuals with sand grains stuck to the surface, dark purplish when young, later dull green to cinereous, rib edge dull yellowish, often remaining purplish between the ribs; ribs 14–50, number directly related to the diameter of the stem, increasing and becoming narrower with age, but sometimes repeatedly dividing then re-coalescing, rib edges bluntly rounded, tissues under the ribs with mucilage cavities formed by single enlarged cells. Areoles 0.5–1.0 mm diam., initially cushion-like then reduced and sunken, pit-like, always spineless, trichomatous when young, glabrescent when mature. Flowers arising from the apical and subapical densely hairy areoles, 1–3 flowers open together, 14–16 × 10–13 mm, anthesis diurnal; pericarpel 2.8–3.0 × 2.0–2.2 mm, smooth, greenish; hypanthial tube 10–12 × 2–2.1 mm at base, flared towards the insertion of perianth segments, to 8.0 mm wide, subcampanulate, pale yellow and densely clad in cream to pale brown hairs in the axils of triangular bract-scales, these sometimes subtending dark brown bristles to 6 mm long; outer perianth-segments to 6.0 × 1.5–2.0 mm, narrowly spatulate to lanceolate, apiculate, yellow, inner segments to 8.0 × 2.5–3.0 mm, oblong, apex apiculate, yellow; stamens 30–40, 3–5 mm long, inserted within the tube and turning inwards, cream; style 10 mm long, stigma 6–7-lobed, cream, ovary with c. 20 ovules. Fruit and seeds not seen.

Etymology. – Named for its completely naked mature vegetative areoles, a unique character in the genus.

Range. – Eastern Brazil: endemic to the *campo rupestre* of the Diamantina Plateau, in Minas Gerais State.

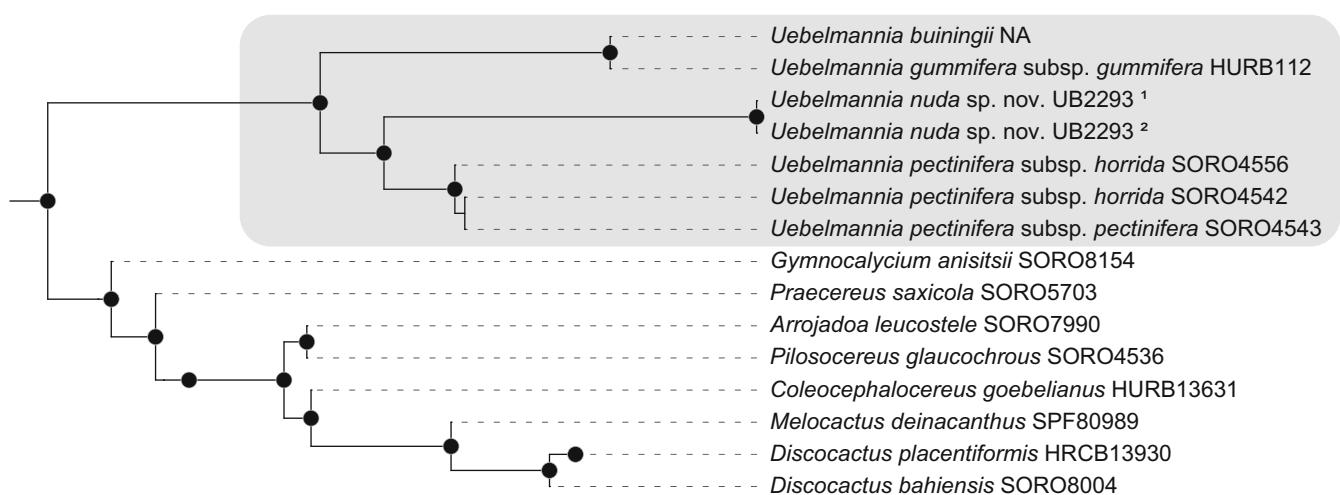


Fig. 1. *Uebelmannia* phylogeny including outgroups. The phylogenetic tree was reconstructed using a coalescent-based inference and the supercontig dataset with 454 nuclear loci from the Cactaceae591 probe set. The *Uebelmannia* clade is highlighted in grey. All nodes present LPP higher than 0.9. Nodes with branches supported equal to 1 are depicted as black circles. Dashed lines were used to align the names of the taxa, solid line in *U. nuda* denotes this species had the shortest branches. The voucher for each accession is provided after the species name.

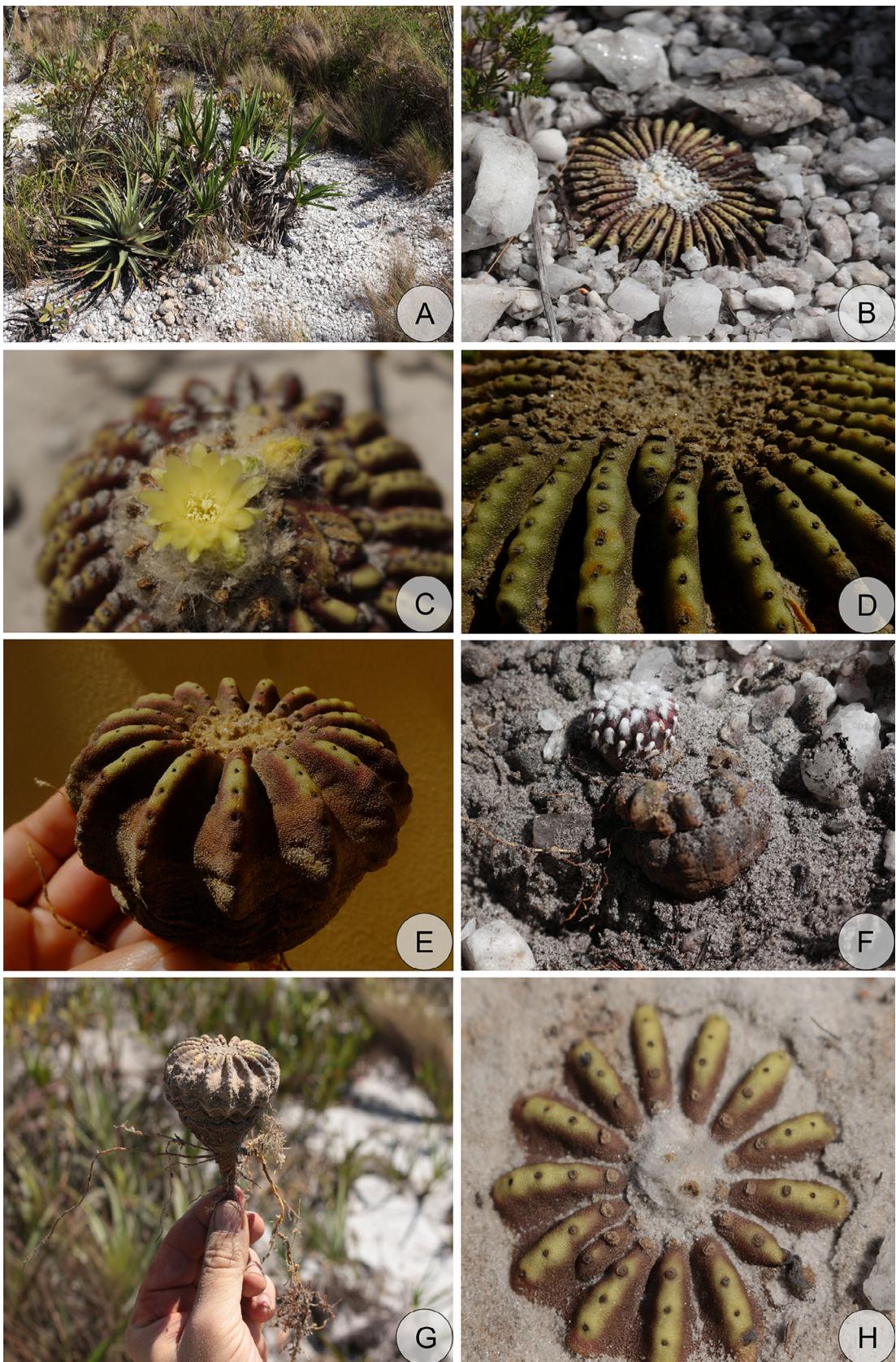


Fig. 2. *Uebelmannia nuda*. **A**, In habitat, growing with *Vellozia* sp. and *Dyckia* sp.; **B**, Habit, growing amongst quartz gravel; **C**, Flowering specimen; **D**, Detail showing naked areoles and papillose epidermis; **E**, Young specimen, showing plant shape; **F**, Plant with dying apex, producing a hairy side-sprout; **G**, Turbinate cactus body; **H**, Geophytic habit. — Photos: A–C & F–H, F.N. Costa; D & E, D.C. Zappi.



Fig. 3. **A**, *Discocactus pseudoinsignis* growing in the same area as *Uebelmannia nuda*; **B**, Disturbance of habitat caused by quartz mining; **C**, Solidified substrate due to digging and trampling in search of quartz; **D & E**, Plants semi-buried in disturbed, solidified substrate; **F**, *Uebelmannia pectinifera* growing on a rock outcrop 300 m from the type locality of *U. nuda*. — Photos: F.N. Costa.

Habitat. – Sandy, quartzitic open vegetation, growing sympatrically with other cactus species (*Cipocereus crassisepalus* (Buining & Brederoo) Zappi & N.P.Taylor, *Discocactus pseudoinsignis* N.P.Taylor & Zappi), as well as many typical *campo rupestre* genera and species, such as *Syagrus glaucescens* Becc., *Anthurium affine* Schott, *Clusia diamantina* Bittrich, *Didymopanax gardneri* Seem., *Chamaecrista* spp., *Vellozia* spp., *Barbacenia* spp., *Calliantha* sp., *Lagenocarpus* sp., and *Dyckia* sp. (Figs. 2A, 3A, 4).

Conservation status. – Known from a single population totalling an AOO (area of occupancy) of 4 km² in the high areas of the Parque Nacional das Sempre Vivas (PNSV) in Minas Gerais at a locality formerly disturbed by illegal quartzitic crystal mining. A specimen count was carried out in the area and less than 100 individuals were found. Therefore, the new species is considered Critically Endangered (CR), fitting criteria B2ab(iii, iv); C2a(i) (IUCN, 2012). It is important to highlight that this vegetation type forms discrete patches, the substrate (sandy and gravelly quartz) being extremely fragile, and that there was evidence of plants becoming buried by disturbance of the sand by illegal quartz

mining using heavy machinery. This illegal operation was stopped by environmental agents from ICMBio in 2009. Another concern is the collectable nature of the species of the genus *Uebelmannia*; therefore we do not disclose the exact coordinates for this plant. Even if theoretically protected within the PNSV (and internationally in Appendix 1 of CITES), the species continues to be at risk due to pressures such as quartz removal, sand movement and trampling (Fig. 3B,C). It is advisable for the managers of the PNSV to frequently monitor and inspect the area where *U. nuda* is found. Brazilian authorities have a good track record for protecting endangered cactus species, with populations of endangered and collectable cacti that were at the verge of extinction being protected in the Parque Estadual de Grão Mogol, which has a policy of extremely restricted entry to the location where Critically Endangered *Discocactus horstii* grows (CNCFlora, 2012).

Observations. – Given the phylogenetic relationship of *Uebelmannia nuda* within the genus *Uebelmannia*, the characteristics that differentiate this species from its congeners are likely to be apomorphic traits that evolved exclusively in the

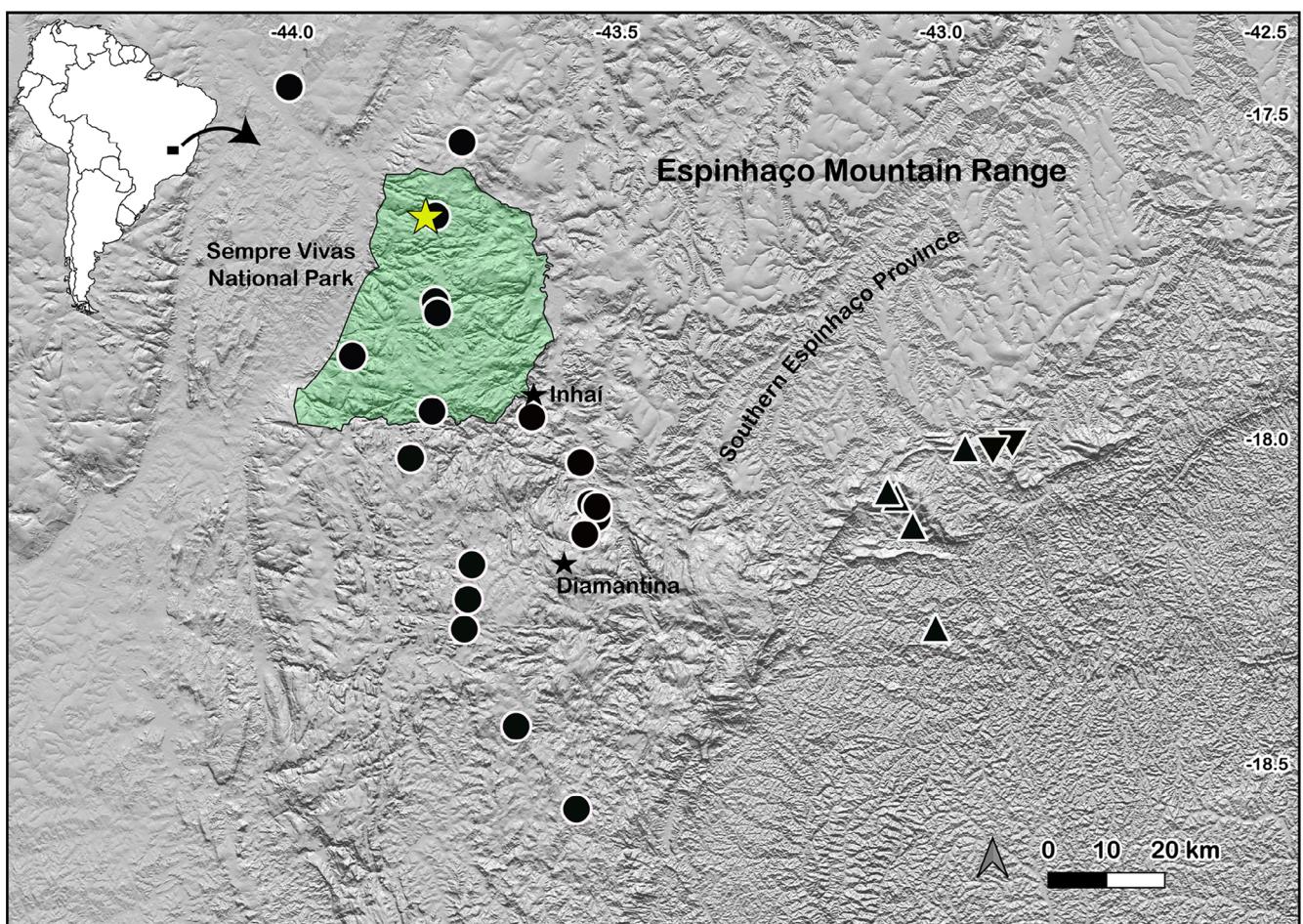


Fig. 4. Distribution map of the genus *Uebelmannia*, restricted to the Espinhaço mountain range in eastern Minas Gerais, Brazil (Southern Espinhaço province). Yellow star, *U. nuda*; circles, *U. pectinifera*; triangles, *U. gummifera*; inverted triangles, *U. buiningii*. Black stars represent nearby towns, and the area of the Parque Nacional das Sempre Vivas (PNSV – Sempre Vivas National Park) is marked in green.

lineage that gave rise to this new species. The remarkable papillose epidermis (Fig. 2D), referred to as “bumps” by Nyffeler (1998) for other species of the genus, and the deep maroon-purplish coloured young plants (Fig. 2F) suggest that, like some species of *Discocactus*, *U. nuda* is a geophyte (Fig. 2) adapted to spend its first years of life under the translucent quartzitic sand and gravel. Even at maturity,

only the flat apex of the turbinate stem is visible at ground level (Fig. 2G,H), with most of the plant remaining underground. This is possibly a strategy for reducing water loss and parallels that seen in certain Mexican cacti, such as *Ariocarpus* Scheidw., and the Chilean *Eriosyce occulta* Katterm.

Specimen examined (paratype). — BRAZIL. Minas Gerais, Mun. Bocaiúva, Parque Nacional das Sempre Vivas,



Fig. 5. Portraits of the other species of *Uebelmannia*. **A**, *Uebelmannia gummifera* subsp. *gummifera*; **B**, *U. buiningii*; **C**, *U. pectinifera* subsp. *flavigaster*; **D**, *U. pectinifera* subsp. *pectinifera*. — Photos: A & D, G. Charles; B, V.D. Teixeira., C, D.C. Zappi.

alto da serra, 1200 m a.s.l., 14 Sep 2023, F.N. Costa, S.N. Fonseca & E.L.M. Machado 2367 (DIAM).

Key to all taxa of *Uebelmannia*

1. Ribs not divided into tubercles, flowers to 13 mm diam. 2
1. Ribs divided into tubercles, flowers 15 mm diam. or wider..... 5
2. Mature areoles completely spineless *U. nuda*
2. Mature areoles always armed... 3 (*U. pectinifera* complex)
3. Epidermis grey-green, with white scales, ribs 13–20(–26) *U. pectinifera* subsp. *pectinifera* (Fig. 5D)
3. Epidermis green, devoid of white scales, ribs (16–) 18–29..... 4
4. Spines yellow when young, ascending, organized in lines running along the ribs, plants mostly not taller than 50 cm..... *U. pectinifera* subsp. *flavispina* (Fig. 5C)
4. Spines grey, divergent, not organized in lines, plants reaching 100 cm..... *U. pectinifera* subsp. *horrida*
5. Ribs 15–22, cortex without mucilaginous ducts *U. buiningii* (Fig. 5B)
5. Ribs 22–42, cortex with vertical mucilaginous ducts..... 6 (*U. gummifera* complex)
6. Areoles not placed at the tip of the tubercles, spines not paired..... *U. gummifera* subsp. *gummifera* (Fig. 5A)
6. Areoles at the tip of the tubercles, armed with a pair of spines each..... *U. gummifera* subsp. *meninensis*

■ AUTHOR CONTRIBUTIONS

DCZ, FNC and NPT were responsible for the initial conception and design of the paper. Data collection was a collective effort by all authors, MK prepared DNA samples for sequencing, MRB and MCT ran phylogenetic analyses under the supervision of FFF and EMM. NPT and DCZ were responsible for taxonomic circumscription and descriptions. Environmental information on habitat and conservation was provided by FNC, PLF and SNF. DCZ prepared the initial manuscript and all authors edited and reviewed the final draft.

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Appendix 1. Specimen sample information for *Uebelmannia* phylogeny, including ingroup and outgroup samples from tribe Cereeae. Sequences newly obtained in this study are marked with an asterisk. NA: not available.

Tribe Cereeae: Subtribe Gymnocalyciinae: *Gymnocalycium anisitsii* (K.Schum.) Britton & Rose, Brazil, Mato Grosso do Sul, Porto Murtinho, G. Olsthoorn s.n. (SORO 8154), SRR24727760. **Subtribe Uebelmanniinae:** *Uebelmannia buiningii* Donald, Brazil, Minas Gerais, Serra Negra State Park, S. Ribeiro-Silva s.n. (NA), SRR24727758; *Uebelmannia gummifera* (Backeb. & Voll) Buining subsp. *gummifera*, Brazil, Minas Gerais, Itamarandiba, L.Y.S. Aona 3575 (HURB 112), SRR18315881; *Uebelmannia pectinifera* Buining subsp. *pectinifera*, Brazil, Minas Gerais, Mendanha, E.M. Moraes s.n. (SORO 4543), SRR18315882; *Uebelmannia pectinifera* subsp. *horrida* (P.J.Braun) P.J.Braun & Esteves, Brazil, Minas Gerais, Diamantina, E.M. Moraes s.n. (SORO 4556), SRR28877996*; *Uebelmannia pectinifera* subsp. *horrida*, Brazil, Minas Gerais, Diamantina, E.M. Moraes s.n. (SORO 4542), SRR28877997*; *Uebelmannia nuda* sp. nov. (indiv. 1), Brazil, Minas Gerais, Bocaiúva, F.N. Costa & al. 2293 (UB0338137), SRR28877994*; *Uebelmannia nuda* sp. nov. (indiv. 2), Brazil, Minas Gerais, Bocaiúva, F.N. Costa & al. 2293 (UB0338137), SRR28877994*, **Subtribe Cereinae:** *Arrojadoa leucostele* (Gürke) Anceschi & Magli, Brazil, Bahia, Jequié, N.P. Taylor s.n. (SORO 7990), SRR24727736; *Coleocephalocereus goebelianus* (Vaupel) Buining, Brazil, Bahia, Urandi, D.B. Mendes 23 (HURB 13631), SRR24727728; *Discocactus bahiensis* Britton & Rose, Brazil, Bahia, Carnaíba do Sertão, N.P. Taylor s.n. (SORO 8004), SRR24727727; *Discocactus placentiformis* K.Schum., Brazil, Minas Gerais, Grão Mogol, N.P. Taylor 1512 (HRCB 13930), SRR24727721; *Melocactus deinacanthus* Buining & Brederoo, Brazil, Bahia, Riacho de Santana, D.C. Zappi 150 (SPF 80989), SRR24727711; *Pilosocereus glaucochrous* (Werderm.) Byles & G.D.Rowley, Brazil, Bahia, Seabra, M.C. Machado s.n. (SORO 4536), SRR24727746; *Praecereus saxicola* (Morong) N.P.Taylor, Brazil, Mato Grosso do Sul, Porto Murtinho, G. Olsthoorn s.n. (SORO 5703), SRR24727715.