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Rust fungi (Pucciniales, Basidiomycota) of the Brazilian Cerrado: Taxonomic advances and new taxa in a threatened biome

Malte Ebinghaus[a], João M. T. Martins[b], Maria D. M. Santos[c], Dirceu Macagnan[d], Silvino Intra Moreira[e], Erica S. C. Souza[f], Zuleide M. Chaves[g], Denise V. de Rezende[g], José R. Lucas Gomes[c], Anibal A. Carvalho-Junior[h], Danilo B. Pinho[g], and José C. Dianese[b,g]

[a]Institut für Pflanzenwissenschaften und Mikrobiologie, Organismische Botanik und Mykologie, Ohnhorststr. 18, Hamburg 22609, Germany; [b]Departamento de Biologia Celular–Biologia Microbiana, Universidade de Brasília, Brasília 70910-900, Brazil; [c]Departamento de Ecologia, Universidade de Brasília, Brasília 70910-900, Brazil; [d]Instituto Federal de Brasília, Rodovia DF 128 Km 21S/N, Zona Rural, Brasília 73380-900, Brazil; [e]Departamento de Fitopatologia, Universidade Federal de Uberlândia, Campus Santa Mônica, Uberlândia-Minas Gerais 38400-902, Brazil; [f]Embrapa Agroenergia, Parque Estação Biológica, PQEB, sn, Final da Asa Norte, Brasília 70770-901, Brazil; [g]Departamento de Fitopatologia, Universidade de Brasília, Brasília 70910-900, Brazil; [h]Instituto Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão Pacheco 915, Rio de Janeiro, 22460-030, Brazil

ABSTRACT

The Brazilian savanna designated as Cerrado is one of the most biodiverse biomes in the world, yet it has lost nearly 50% of its native vegetation since the mid-20th century, mostly due to agricultural expansion. This rapid degradation makes it one of the most threatened biodiversity hot spots worldwide, highlighting the urgent need for intensified conservation and biodiversity research efforts. The systematic study of rust fungi (Pucciniales) in the Brazilian Cerrado began around 140 years ago with the temporary emigration from Germany of the explorer and collector Ernst Heinrich Georg Ule (*1854–†1915) to Brazil where he was hired as a "visiting naturalist" serving in the National Museum of Rio de Janeiro from 1891 until 1895. Since then, approximately 270 species of rust fungi have been documented in the Cerrado. Historically, taxonomic classifications of rust fungi relied strongly on the interpretation of morphological traits, which are prone to subjective bias that has led to taxonomic instability and is reflected in complex taxonomic histories. Furthermore, recent molecular phylogenetic studies have revealed a high frequency of homoplasious traits in rust fungal morphology, further complicating accurate taxonomic decisions when such traits are considered in isolation. In this study, we conducted morphological and molecular phylogenetic analyses on several rarely collected and studied genera of Cerrado rust fungi, evaluating phylogenetic relationships and discussing their taxonomy. We describe a new *Puccinia* species infecting the genus *Coracoralina* (Eriocaulaceae: Poales), *Puccinia coracoralinae*, sp. nov. along with a new genus *Dietelomyces*, gen. nov. and several new combinations, i.e. *Cerradopsora pouteriae*, nom. nov. *Dietelomyces copaiferae*, comb. nov. besides defining the suprageneric status of *Esalque holwayi, Dietelia duguetiae, Kimuramyces cerradensis*, and *Mimema venturae*. Additionally, we discuss the effects of identified homoplasious traits on rust fungal systematics based on our phylogenetic analyses. Considering published estimates of rust fungal diversity in other regions, we conclude that with approximately 12 356 documented vascular plant species in the Cerrado, at least ca. 2300 rust fungal species can be expected to be present. This suggests that, to date, ca. of 13% of the rust fungi occurring in the Cerrado has been documented. Given the alarming threat status of the Cerrado and its extremely significant biodiversity, we also emphasize and discuss the potential implications of systematic rust fungal research for future conservation policies in this unique ecosystem. By addressing key taxonomic and phylogenetic gaps, this study highlights rust fungi as a critically understudied component of Cerrado biodiversity and reinforces the urgent need to expand field collections and integrate fungal systematics with conservation strategies as habitat loss accelerates.

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INTRODUCTION

The study of Brazilian fungi has a long history and received an important impetus with the temporary immigration of the German botanist and collector Ernst Heinrich Georg Ule (*1854–†1915) to the states of Santa Catarina and Rio de Janeiro, Brazil, from 1883 to 1912. Ule's work provided foundational contributions to the study of Brazil's botanical and fungal diversity (Harms 1916; Stafleu and Cowan 1986), yielding an estimated 750 fungal types (Friederichsen 1973; Borges et al. 2018) and an eponymy list including names of nine fungal and seven plant genera (Stafleu and Cowan 1986). Large fractions of his fungal collections from

CONTACT José C. Dianese jcarmine@gmail.com
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Brazil, specifically collections made between 1883 and 1903, were deposited at Herbarium Berolinense (B), Berlin, and at the Hamburger Botanisches Museum, Hamburg, Germany, with the latter collection now being integrated into the Herbarium Hamburgense (HBG) (Harms 1916; Friederichsen 1973), comprising rust fungi from south (Hennings 1896), east (Hennings 1904a, 1904b), northeast (Hennings 1908) and central (Hennings 1895a, 1895b) Brazil, as well as the Amazonian rain forest (Hennings 1902, 1904a, 1904b, 1904c). Ule's collections also provided Dietel (1897, 1899) with important raw material for his work on rust fungi from Brazil. In addition, Hennings (1896, 1897, 1899) described other rust fungi with the Brazilian exsiccates provided by Ule, also including specimens from Argentina and Paraguay.

Paul Hennings' and Ernst Ule's contributions to the knowledge of Brazilian rust fungi constitute the first nationwide effort during times of largely intact forest and savanna ecosystems (Dutra 2020). Similar work was done by Holway (Jackson 1926, 1927, 1931a, 1931b, 1931c, 1931d, 1932) for South America, about three decades later, followed by Viégas (1945) in Brazil. In the 1970s, the North American mycologist Joe F. Hennen started collections mostly centered in the Brazilian Cerrado with some incursions into the Amazonian and the Brazilian Atlantic Forest biomes (Hennen et al. 2005). Summarizing these efforts, Hennen et al. (2005) listed and annotated almost 800 species of Pucciniales in 65 genera in their monumental review of the Brazilian rust fungi.

Despite the long tradition of biodiversity exploration and the great diversity of Brazilian rust fungi, in the second edition of the classic manual Illustrated Genera of Rust Fungi (Cummins and Hiratsuka 1983), the only genus attributed to a Brazilian mycologist was *Porotenus*, described 23 years earlier (Viégas 1960). This changed in the 2003 edition with the inclusion of two new genera, *Batistopsora*, with type species *B. crucisfilii* (Dianese et al. 1993), and *Kimuramyces*, originally described as *Kimuromyces*, with type species *K. cerradensis* (Dianese et al. 1995), plus the reinstatement of *Mimema* based on *Mimema venturae* (Dianese et al. 1994), all three described from the Cerrado. The growing taxonomic interest in Cerrado rust fungi during the late 20th century emerged at a time when significant environmental degradation of the Cerrado biome was already progressing. A shift in land use policies, particularly initiated around the 1960s, has driven rapid agricultural exploitation of the Cerrado (Klink 2013), leaving profound impacts on its natural vegetation (Lahsen et al. 2016; Alencar et al. 2020). As a result, only about 50% of the original Cerrado, which once spanned approximately 2 million km^2, remains intact today, with a mere 6.5% of its native vegetation formally protected (Colli et al. 2020). Pessimistic projections suggest that by 2030, significant samples of natural vegetation will persist solely within those protected areas due to ongoing agricultural expansion (Machado et al. 2004), whereas others are in apprehension of an ecosystem collapse by the 2050s (Hofmann et al. 2021). Consequently, the Cerrado biome ranks among the most threatened biodiversity hot spots worldwide (Mittermeier et al. 1998; Myers et al. 2000; Myers 2003; Françoso et al. 2020). The precarious status of the Cerrado highlights the urgent need for advancing conservation and biodiversity research, with particular emphasis on the fungi, especially when it comes to rust fungi that are fully dependent on the survival of their host plants. The Cerrado's critical conservation status underscores the pressing need to intensify informed conservation efforts supported by comprehensive biodiversity assessments. Yet fungi, particularly rust fungi, which are strictly dependent on living host plants and thus directly affected by vegetation loss, are largely overlooked and thus remain poorly documented and taxonomically neglected. For instance, despite the historical and ongoing efforts to document Cerrado rust fungi, comprising 112 type species across 27 genera listed by Hennen et al. (2005) and Carvalho-Júnior et al. (2008), as well as the recently erected *Neopuccinia* (Martins-Junior et al. 2019), *Crossopsorella* (Souza et al. 2018), *Pseudocerradoa* (Ebinghaus et al. 2022), *Raveneliopsis* (Ebinghaus et al. 2023a), and *Cerradopsora* (Ebinghaus et al. 2023b), our understanding of the rust fungal diversity in this region remains vague, with only a total of about 268 species documented to date (Dianese et al. 1997; Souza 2016). This scarcity in our knowledge is also illustrated by a survey covering an area of just about 0.1% of the Cerrado, where Carvalho-Júnior et al. (2008) identified 157 species of rust fungi in 36 genera. This serves as an example of the intensive collection effort that would need to be replicated for a more comprehensive understanding of this diversity across the entire biome. Moreover, referring to the abovementioned studies, only a small fraction of Cerrado rust fungi have been analyzed using molecular genetic methods, an effort that only initiated in the last decade (Souza et al. 2015; Souza 2016).

The scarcity of molecular data not only limits our understanding of the actual species richness but also impedes the development of a taxonomic framework that more accurately reflects evolutionary relationships.

In rust fungal taxonomy, the generic and suprageneric classification has traditionally relied on a narrow set of morphological traits (e.g., Cummins and Hiratsuka

2003), an approach that has been proven problematic, as molecular phylogenetics revealed that homoplasy is widespread among those traits (Maier et al. 2003; Aime 2006; Aime and McTaggart 2021). The reliance on such unrecognized homoplasious traits has frequently led to incorrect assumptions about natural relationships, consequently necessitating numerous reclassifications (e.g., Beenken and Wood 2015; Aime and McTaggart 2021; Scholler et al. 2022; Ebinghaus et al. 2023a, 2023b). The continuous validation of morphological features is therefore essential to identify and account for convergent traits in the classification and delimitation of taxa. This is not only essential for understanding the evolutionary history and diversification of rust fungi but also critical for assessing known, emerging, and potential agricultural pathogens (Anderson et al. 2004; Hyde et al. 2024a). These include economically important species such as soybean rust (*Phakopsora pachyrhizi*) and sugarcane rust (*Puccinia kuehnii*), as well as others such as *Austropuccinia* species that may play a significant or potentially significant role as biological invaders and thus in shaping conservation policies (Glen et al. 2007; Ebinghaus et al. 2024).

As part of an ongoing series of studies on the Cerrado rust fungi of Brazil using specimens housed in the Mycological Collection of the Herbarium UB (Universidade de Brasília), we present here the most recent results of morphological and molecular phylogenetic studies on specimens collected during field campaigns in the Brazilian Cerrado from 2015 (Souza et al. 2015; Souza 2016) until 2023 (Martins 2023). The studies resulted in the discovery of the first Neotropical rust fungus on a member of the Eriocaulaceae, i.e., *Coracoralina* (= *Paepalanthus*), confirmed as a novel *Puccinia* species. We will furthermore show phylogenetic allocations of several poorly studied rust fungi and provide taxonomic revisions at both the generic and family levels. Our findings are discussed in the context of taxonomic misclassifications arising from the single use of homoplasious traits and their implications for the evaluation of the diversity of Neotropical rust fungi and on conservation priorities.

MATERIALS AND METHODS

Specimens of rust fungi examined in this study were collected between 2012 and 2022 in different regions of the Brazilian Cerrado. After collecting, specimens were dried in a plant press between paper sheets until they were fully dry and then stored in Herbarium UB until being further processed for light microscopy (LM), scanning electron microscopy (SEM), and DNA extraction with subsequent gene sequencing. Nineteen specimens were successfully sequenced in the present study and are listed in TABLE 1.

DNA extractions, sequencing, and phylogenetic analyses.—For DNA extraction, spores were either scraped from the leaf surface using a scalpel or rust pustules were carefully excised and transferred into 2.0-mL screw-cap tubes along with three steel beads of 3 mm in diameter. The samples were then ground using a Retsch mill (Haan, Germany) through three consecutive freeze-thaw cycles. DNA extraction was performed using the Qiagen DNeasy Blood & Tissue Kit (Valencia, California) following the manufacturer's protocol. Polymerase chain reaction (PCR) was carried out for fragments of the internal transcribed spacer (only ITS2), 28S and 18S rDNA, and cytochrome *c* oxidase subunit III (*CO3*) using the GoTaq G2 Hot Start DNA polymerase kit (Promega, Mannheim, Germany). Primers Rust2INV (Aime 2006) and LR6 (Vilgalys and Hester 1990) were used to amplify a fragment consisting of ITS2 and a fragment of the 28S, and LR0R and LR6 for a fragment of 28S alone (Vilgalys and Hester 1990), and primers NS1 and Rust18SR (White et al. 1990; Aime 2006) and CO3-R1 and CO3-F1 (Vialle et al. 2009) were used for the amplification of fragments of the 18S rDNA and *CO3*, respectively. Amplification of the ITS–28S rDNA was performed as in Ebinghaus et al. (2024); for the 28S rDNA and *CO3*, we applied the conditions of Ebinghaus et al. (2020), and for the 18S rDNA those of Ebinghaus et al. (2022). The PCR products were sequenced in both directions by Macrogen (Seoul, South Korea) and assembled and manually edited using Sequencher 5.0 (Gene Codes, Ann Arbor, Michigan). Sequences were checked for erroneously sequenced contaminants against the BLASTn database (Altschul et al. 1990) of the National Center for Biotechnology Information (NCBI) and to estimate their suprafamilial affiliations. All newly generated sequences, as well as those downloaded from GenBank for analysis, are listed in TABLE 1.

BLASTn searches of the 28S rDNA indicated that the newly sequenced specimens represent members of either the suborder Raveneliineae or Uredinineae. Consequently, we assembled two distinct sets of alignments, each corresponding to one of the suborders. For the suborder Raveneliineae, we prepared taxonomically representative alignments for sequence data of the nuclear ribosomal 28S and 18S gene regions, the internal transcribed spacer 2 (ITS2), and the mitochondrial cytochrome *c* oxidase subunit III *CO3* gene. Additionally, gap positions in the 28S and ITS2 alignments were coded as binary data using FastGap 1.2

Table 1. Specimens used in the phylogenetic analyses.

			GenBank accessions				
Fungus	Host	Specimen	ITS2	28S	18S	*CO3*	Reference
Aecidium guatteriae	*Guatteria anthracina*	ZT-Myc57044	KM217362	KM217362	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria intermedia*	ZT-Myc57045	KM217360	KM217360	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria ouregou*	ZT-Myc57046	KM217359	KM217359	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria ouregou*	ZT-Myc57047	KM217361	KM217361	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria ouregou*	ZT-Myc57052	KM217363	KM217363	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria ouregou*	ZT-Myc57053	KM217357	KM217357	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria punctata*	ZT-Myc57054	KM217358	KM217358	—	—	Beenken (unpublished)
Aecidium guatteriae	*Guatteria schomburgkiana*	ZT-Myc57055	KM217356	KM217356	—	—	Beenken (unpublished)
Aecidium verannonae	*Annona spraguei*	PUR43011	KF528007	KF528007	—	—	Beenken (2014)
Allodus podophylli	*Podophyllum peltatum*	BPI842277/ AWW605	DQ354543	DQ354543	—	MG907270	Aime (2006); Aime et al. (2018)
Allodus podophylli	*Podophyllum peltatum*	U272	JQ423258	JQ423258	—	—	Minnis et al. (2012)
Allodus podophylli	*Podophyllum peltatum*	U273	JQ423259	JQ423259	—	—	Minnis et al. (2012)
Allodus podophylli	*Podophyllum peltatum*	U803	JQ423260	JQ423260	—	—	Minnis et al. (2012)
Aplopsora nyssae	*Nyssa sylvatica*	BPI877823	—	MW049244	—	—	Aime and McTaggart (2021)
Austropuccinia licaniae	*Moquilea tomentosa*	UB23956	OR082911	OR082911	—	OR060914	Ebinghaus et al. (2024)
Austropuccinia licaniae	*Moquilea tomentosa*	UB24360	OR082912	OR082912	—	OR060915	Ebinghaus et al. (2024)
Austropuccinia licaniae	*Moquilea tomentosa*	UB24361	OR082913	OR082913	—	OR060916	Ebinghaus et al. (2024)
Austropuccinia licaniae	*Moquilea tomentosa*	UB24337	OR082914	OR082914	—	OR060917	Ebinghaus et al. (2024)
Austropuccinia psidii	*Syzygium jambos*	UB24098	OR082910	OR082910	—	OR060913	Ebinghaus et al. (2024)
Austropuccinia psidii	*Pimenta dioica*	BPI910266	—	KY764157	—	—	Demers et al. (ubpublished)
Austropuccinia psidii	*Rhodamnia angustifolia*	BRIP57793	—	KF318449	—	KT199419	Pegg et al. (2014); McTaggart et al. (2016a)
Austropuccinia psidii	*Myrtaceae*	U1460	—	MG907209	—	MG907257	Aime et al. (2018)
Batistopsora crucis-filii	*Annona* sp.	UB24134	PX214383	PX214383	—	OQ268262	Ebinghaus et al. (2023a); This study
Batistopsora crucis-filii	*Annona paludosa*	ZT-Myc48990	KF528016	KF528016	KF528041	KF528049	Beenken (2014)
Bibulocystis pulcherrima	*Daviesia latifolia*	BRIP58450	—	MW049247	—	MW036498	Aime and McTaggart (2021)
Catenulopsora flacourtiae	*Flacourtia indica*	PUR-N13865	—	MW049248	MW049293	—	Aime and McTaggart (2021)
Cephalotelium evansii	*Vachellia davyi*	PREM61845	MG945968	MG946000	PX214324	MN095322	Ebinghaus et al. (2018); Ebinghaus et al. (2020); This study
Cephalotelium macowanianum	*Vachellia karroo*	PREM61222	MG945975	MG946007	PX214325	PX215304	Ebinghaus et al. (2018); This study
Cephalotelium xanthophloeae	*Vachellia xanthophloea*	PREM61000	MG945984	MG946016	PX214326	MN095314	Ebinghaus et al. (2018); Ebinghaus et al. (2020); This study
Ceratocoma jacksoniae	*Daviesia* sp.	BRIP57762	—	KT199394	KT199382	KT199405	McTaggart et al. (2016a)
Cerradoa palmaea	*Syagrus comosa*	UB24136	MT734676	MT734676	—	ON456322	Ebinghaus et al. (2022)
Cerradoa palmaea	*Syagrus comosa*	UB24137	MT734677	MT734677	—	ON456323	Ebinghaus et al. (2022)
Cerotelium fici	*Ficus coronulata*	BRIP56890	—	MH047209	—	MH047205	Liberato et al. (unpublished)
Cerotelium fici	*Morus nigra*	MN1	—	OM296992	—	OP797407	Gonçalves et al. (2023); Santos et al. (unpublished)
Cerotelium fici	*Ficus carica*	Cero_001	PP491081	PP491081	—	PP491074	Ha (unpublished)
Cerradopsora pouteriae	*Pouteria ramiflora*	UB24051	—	—	PX214327	PX215305	This study
Cerradopsora pouteriae	*Pouteria ramiflora*	UB22260	—	PX214313	—	PX215306	This study
Cerradopsora pouteriae	*Pouteria* sp.	UB22481	—	PX214314	—	—	This study
Cerradopsora pouteriae	*Pouteria lucuma*	BPI910181	—	KY764060	—	—	Demers et al. (ubpublished)
Cerradopsora hennenii	*Qualea* sp.	UB22895	—	OQ275075	OQ275088	OQ268263	Ebinghaus et al. (2023a, 2023b)
Cerradopsora hennenii	*Qualea parviflora*	UB24152	—	OQ275076	OQ275089	OQ268264	Ebinghaus et al. (2023a, 2023b)
Cerradopsora rossmaniae	*Campomanesia* sp.	UB22354	—	OQ275077	—	OQ268265	Ebinghaus et al. (2023a, 2023b)
Cerradopsora rossmaniae	*Campomanesia* sp.	UB24135	—	OQ275078	OQ275090	OQ268266	Ebinghaus et al. (2023a, 2023b)
Cerradopsora rossmaniae	*Campomanesia* sp.	UB24154	—	OQ275079	OQ275091	OQ268267	Ebinghaus et al. (2023a, 2023b)
Cerradopsora rossmaniae	*Campomanesia* sp.	UB24155	—	OQ275080	OQ275092	OQ268268	Ebinghaus et al. (2023a, 2023b)
Crossopsora antidesmae-dioicae	*Antidesma ghaesembilla*	BRIP56870	—	MW147039	—	MW139652	Aime and McTaggart (2021)
Dasyspora echinata	*Xylopia aromatica*	BPI746651	JF263462	JF263462	JF263497	—	Beenken et al. (2012)
Dasyspora emarginatae	*Xylopia emarginata*	PUR-N6196	NR_132854	JF263465	NG_064971	JF263514	Beenken et al. (2012)
Dasyspora ferrugineae	*Xylopia frutescens* var. *ferruginea*	ZT-Myc3404	JF263467	JF263467	JF263499	JF263515	Beenken et al. (2012)

(*Continued*)

Table 1. (Continued).

Fungus	Host	Specimen	GenBank accessions				Reference
			ITS2	28S	18S	*CO3*	
Dasyspora ferrugineae	*Xylopia frutescens* var. *ferruginea*	ZT-Myc3407	JF263466	JF263466	—	—	Beenken et al. (2012)
Dasyspora frutescentis	*Xylopia frutescens* var. *ferruginea*	ZT-HeRBA141	JF263471	JF263471	JF263501	JF263517	Beenken et al. (2012)
Dasyspora frutescentis	*Xylopia frutescens* var. *frutescens*	ZT-Myc3403	JF263468	JF263468	JF263500	JF263516	Beenken et al. (2012)
Dasyspora gregaria	*Xylopia cayennensis*	ZT-Myc3393	JF263474	JF263474	—	—	Beenken et al. (2012)
Dasyspora gregaria	*Xylopia cayennensis*	ZT-Myc3397	JF263477	JF263477	JF263502	JF263518	Beenken et al. (2012)
Dasyspora guianensis	*Xylopia benthamii*	ZT-Myc 3413	JF263479	JF263479	JF263503	JF263519	Beenken et al. (2012)
Dasyspora mesoamericana	*Xylopia frutescens* var. *frutescens*	BPI US0116379	JF263482	JF263482	—	—	Beenken et al. (2012)
Dasyspora mesoamericana	*Xylopia frutescens* var. *frutescens*	PUR42390	JF263480	JF263480	JF263504	JF263520	Beenken et al. (2012)
Dasyspora mesoamericana	*Xylopia frutescens* var. *frutescens*	PUR64451	JF263483	JF263483	—	—	Beenken et al. (2012)
Dasyspora nitidae	*Xylopia nitida*	ZT-Myc3409	JF263484	JF263484	JF263505	JF263521	Beenken et al. (2012)
Dasyspora nitidae	*Xylopia nitida*	ZT-Myc3412	JF263487	JF263487	NG_064974	JF263522	Beenken et al. (2012)
Dasyspora segregaria	*Xylopia aromatica*	BPI853915	JF263490	JF263490	—	—	Beenken et al. (2012)
Dasyspora segregaria	*Xylopia aromatica*	PMA MP4941	JF263488	JF263488	JF263507	JF263523	Beenken et al. (2012)
Dasyspora winteri	*Xylopia sericea*	S F30078	JF263492	JF263492	JF263508	JF263524	Beenken et al. (2012)
Dietelia codiaei	*Codiaeum variegatum*	PUR-N16488	—	MW049255	—	—	Aime and McTaggart (2021)
Dietelia duguetiae	*Duguetia furfuracea*	PUR87978	KM217365	KM217365	KM217382	—	Beenken (unpublished)
Dietelia duguetiae	*Duguetia furfuracea*	UB22524	PX214384	PX214384	—	PX215307	This study
Dietelia duguetiae	*Duguetia furfuracea*	UB24378	PX214385	PX214385	—	PX215308	This study
Dietelia duguetiae	*Duguetia furfuracea*	UB24480	PX214386	PX214386	—	PX215309	This study
Dietelia mesoamericana	*Mikania micrantha*	BPI871533	—	MW147040	—	—	Aime and McTaggart (2021)
Dietelia mesoamericana	*Mikania micrantha*	IMI393070	—	DQ917691	—	—	Maier et al. (2007)
Dietelia portoricensis	*Mikania micrantha*	BPI844288	DQ354516	DQ354516	—	—	Aime (2006)
Dietelomyces copaiferae	*Copaifera langsdorfii*	UB22385/ UB24053	—	PX214315	—	PX215310	This study
Dietelomyces copaiferae	*Copaifera langsdorfii*	UB24217	—	—	—	PX215311	This study
Diorchidium woodii	*Millettia grandis*	U1241	—	OQ215007	—	—	Wood and Aime (2024)
Diorchidium woodii	*Millettia grandis*	U1353	—	OQ215008	—	—	Wood and Aime (2024)
Diorchidium woodii	*Millettia grandis*	U1475	—	MW111538	MW111533	—	Aime and McTaggart (2021)
Diorchidium woodii	*Millettia grandis*	ZT-Myc582	KM217352	KM217352	—	—	Beenken and Wood (2015)
Endoraecium disparrimum	*Acacia disparrima*	BRIP55626	KJ862358	KJ862304	KJ862403	KJ862437	McTaggart et al. (2015)
Endoraecium falciforme	*Acacia falciformis*	BRIP57583	KJ862360	KJ862306	KJ862405	KJ862439	McTaggart et al. (2015)
Endoraecium maslinii	*Acacia daphnifolia*	BRIP57872	KJ862367	KJ862314	KJ862408	KJ862444	McTaggart et al. (2015)
Endoraecium parvum	*Acacia leiocalyx*	BRIP57524	KJ862369	KJ862316	KJ862409	KJ862445	McTaggart et al. (2015)
Endoraecium podalyriifolium	*Acacia podalyriifolia*	BRIP57576	KJ862387	KJ862334	KJ862414	KJ862449	McTaggart et al. (2015)
Endoraecium tierneyi	*Acacia harpophylla*	BRIP27071	KJ862388	KJ862335	KJ862415	KJ862450	McTaggart et al. (2015)
Endoraecium tropicum	*Acacia tropica*	BRIP56555	KJ862391	KJ862336	KJ862416	KJ862451	McTaggart et al. (2015)
Esalque holwayi	*Caesalpinia leiostachya*	UB24482	—	PX214316	—	PX215315	This study
Esalque holwayi	*Caesalpinia ferrea*	UB24150	—	—	—	PX215313	This study
Esalque holwayi	*Caesalpinia ferrea*	UB22287	—	PX214317	—	PX215312	This study
Esalque holwayi	*Caesalpinia leiostachya*	UB24355	—	—	—	PX215314	This study
Gymnosporangium betheli	Not stated	RSP01-237	KJ720163	KJ720163	—	—	Nowick et al. (unpublished)
Gymnosporangium clavariiforme	*Crataegus* sp.	BRIP59471	—	MW049261	MW049296	MW036499	Aime and McTaggart (2021)
Gymnosporangium juniperi-virginianae	*Juniperus* sp.	MCA3585	—	MG907217	MG917687	MG907268	Aime et al. (2018)
Gymnosporangium juniperi-virginianae	Not stated	RSP98-137	KJ720176	KJ720176	—	—	Nowick et al. (unpublished)
Gymnosporangium miyabei	Not stated	IBA 6650	KJ720178	KJ720178	—	—	Nowick et al. (unpublished)
Gymnosporangium nidus-avis	Not stated	RSP 05-29	KJ720181	KJ720181	—	—	Nowick et al. (unpublished)
Hamaspora acutissima	*Rubus moluccanus*	BRIP55606	KT199409	KT199398	KT199385	—	McTaggart et al. (2016a)
Hamaspora longissima	*Rubus ludwigii*	BPI871506	—	MW049262	MW049297	—	Aime and McTaggart (2021)
Hamaspora rubi-alceifolii	*Rubus alceifolius*	GMB0109	OQ067094	OQ067532	—	—	Wu et al. (2023)

(*Continued*)

Table 1. (Continued).

			GenBank accessions				
Fungus	Host	Specimen	ITS2	28S	18S	*CO3*	Reference
Kimuramyces cerradensis	*Astronium fraxinifolium*	UB23923	PX214387	PX214387	—	PX215316	This study
Kuehneola uredinis	*Rubus argutus*	BPI871104	DQ354551	DQ354551	—	—	Aime (2006)
Kuehneola uredinis	*Rubus* sp.	BPI879274	GU058013	GU058013	—	—	Dixon et al. (2010)
Kuehneola uredinis	*Rubus* sp.	HMUT100479	—	KU059177	—	—	Xu et al. (unpublished)
Mimema venturae	*Dalbergia miscolobii*	UB22323	—	PX214318	—	—	This study
Mimema venturae	*Dalbergia miscolobii*	UB22364	PX214388	PX214388	—	—	This study
Miyagia pseudosphaeria	*Sonchus oleraceus*	PDD97677	KX985753	KX985753	—	—	Padamsee and McKenzie (2014)
Neoolivea tectonae	*Tectona grandis*	PUR-N15331	—	MW049282	MW049307	MW036507	Aime and McTaggart (2021)
Neopuccinia bursa	*Protium heptaphyllum*	RB757071	—	MH047186	—	—	Martins-Junior et al. (2019)
Neopuccinia bursa	*Protium heptaphyllum*	RB75725	MK491188	MK491188	—	—	Junior et al. (2019)
Newinia heterophragmatis	*Kigelia* cf. *africana*	PUR N16505	—	MW049271	—	—	Aime and McTaggart (2021)
Newinia kigeliae	*Kigelia africana*	AW9	—	PX214319	—	PX215317	This study
Nyssopsora cedrelae	*Toona sinensis*	KUSF33693	OR978254	OR964892	—	PP261120	Lee et al. (2024)
Nyssopsora cedrelae	*Toona sinensis*	KUSF33702	OR978215	OR964893	—	PP261121	Lee et al. (2024)
Nyssopsora cedrelae	*Toona sinensis*	TNSF99270	OR978218	OR964896	—	PP261097	Lee et al. (2024)
Nyssopsora cedrelae	*Toona sinensis*	TNSF99272	OR978220	OR964898	—	PP261098	Lee et al. (2024)
Nyssopsora echinata	*Meum athamanticum*	KR0012164	—	MW049272	—	—	Aime and McTaggart (2021)
Nyssopsora sp.	*Ailanthus altissimus*	GMB0103	OQ067089	OQ067529	—	—	Wu et al. (2023)
Nyssopsora thwaitesii	*Schefflera wallichiana*	AMH9528	KF550283	KF550283	—	—	Baiswar et al. (2014)
Nyssopsora toonae	*Toona sinensis*	AMH10124	—	MT712660	—	—	Yadav et al. (2023)
Ochropsora ariae	*Anemone nemorosa*	KR0015027	—	MW049273	—	—	Aime and McTaggart (2021)
Ochropsora ariae	*Anemone nemorosa*	KR-M-42604	KX228773	KX228778	—	—	Scholler et al. (2019)
Ochropsora ariae	*Sorbus aucuparia*	KR-M-43444	KX228772	KX228777	—	—	Scholler et al. (2019)
Ochropsora nambuana	*Elaeagnus multiflora*	IBAR8737	—	LC493090	—	—	Ono et al. (2020)
Ochropsora nambuana	*Elaeagnus multiflora*	IBAR9544	—	LC493091	—	—	Ono et al. (2020)
Ochropsora staphyleae	*Staphylea bumalda*	IBAR7936	LC492076	LC492081	—	—	Ono et al. (2020)
Ochropsora staphyleae	*Staphylea bumalda*	IBAR8587	LC492077	LC492082	—	—	Ono et al. (2020)
Olivea scitula	*Vitex doniana*	BPI871108	—	DQ354541		—	Aime (2006)
Phakopsora cherimoliae	*Annona cherimola*	ZT-RB3096	KF528011	KF528011	KF528040	KF528048	Beenken (2014)
Phakopsora coca	*Erythroxylum coca*	BPI910190	KY764072	KY764072	—	—	Demers et al. (unpublished)
Phakopsora coca	*Erythroxylum* sp.	UB24066	—	OQ275084	—	OQ268271	Ebinghaus et al. (2023a, 2023b)
Phakopsora gossypii	*Gossypium* sp.	BPI910192	—	KY764074	—	—	Demers et al. (unpublished)
Phakopsora gossypii	*Gossypium* sp.	UB24151	—	OQ275086	—	OQ268272	Ebinghaus et al. (2023a, 2023b)
Phakopsora myrtacearum	*Eucalyptus grandis*	PREM61155	KP729468	KP729472	—	KT199414	Maier et al. (2016)
Phakopsora pachyrhizi	*Neonotonia wightii*	BRIP56941	—	KP729475	MW049300	MW036503	Maier et al. (2016); Aime and McTaggart (2021)
Porotenus bisporus	*Adenocalymma validum*	ZT-Myc3414	—	JF263494	—	—	Beenken et al. (2012)
Porotenus concavus	*Adenocalymma pedunculatum*	UB23198	—	PX214320	—	—	This study
Prospodium aculeatum	*Tecoma stans*	BPI910201	KY764086	KY764086	—	—	Demers et al. (unpublished)
Prospodium appendiculatum	*Tecoma stans*	BPI879956	—	MW049276	—	—	Aime and McTaggart (2021)
Prospodium cydistae	*Bignonia neoheterophylla*	BPI871910	—	MW147030	—	—	Aime and McTaggart (2021)
Prospodium gentryi	*Parmentiera aculeata*	APR109	KY800407	KY800407	—	—	Demers and Castlebury (unpublished)
Prospodium lippiae	*Aloysia polystachya*	U00152	—	DQ354555	DQ831024	—	Aime (2006)
Prospodium tuberculatum	*Lantana camara*	BRIP57630	—	KJ396195	KJ396196	MW036504	Pegg et al. (2014); Aime and McTaggart (2021)
Pseudocerradoa lygodii	*Lygodium japonicum*	U1226	—	MG907211	—	MG907260	Aime et al. (2018)
Pseudocerradoa lygodii	*Lygodium volubile*	RB2240	—	—	—	ON456326	Ebinghaus et al. (2022)
Pseudocerradoa paullula	*Monstera deliciosa*	FDACS-DPI PPST 2019-101665	ON887197	ON887197	—	PP112881	Urbina et al. (unpublished)
Pseudocerradoa paullula	*Monstera deliciosa*	CFSZ9998	MK949148	MK949154	—	—	Yang et al. (unpublished)
Pseudocerradoa paullula	*Monstera* sp.	FDACS8840	—	PP116112	—	PP112883	Urbina et al. (unpublished)
Puccinia aff.cyperi	*Cyperus* sp.	DAOM140303	MW009479	MW009479	—	—	Léveillé-Bourret et al. (2021)
Puccinia canaliculata	*Cyperus rotundus*	BRIP40326	—	OL437029	—	—	Tabe et al. (2022)
Puccinia canaliculata	*Cyperus* sp.	BRIP57789	—	MW147046	—	MW139656	Aime and McTaggart (2021)
Puccinia canaliculata	*Cyperus rotundus*	TA427	—	OL437027	—	—	Tabe et al. (2022)
Puccinia canaliculata	*Cyperus rotundus*	U677	HQ412647	HQ412647	—	—	Deadman et al. (2011)
Puccinia canaliculata var. *tenuis*	*Cyperus esculentus*	TA430	OL437018	OL437033	—	—	Tabe et al. (2022)
Puccinia caricina	*Carex appressa*	BRIP57951	—	KX999870	—	KX999912	Marin-Felix et al. (2017)
Puccinia caricis	Not stated	ZP-R227	—	MK518533	—	—	Zhao (unpublished)

(*Continued*)

Table 1. (Continued).

Fungus	Host	Specimen	GenBank accessions				Reference
			ITS2	28S	18S	*CO3*	
Puccinia caricis-atractylodes	Not stated	HMJAU8890	—	MW414421	—	—	Ji (unpublished)
Puccinia coracoralinae	*Coracoralina chiquitensis*	UB24487	—	PX214321	—	PX215318	This study
Puccinia coracoralinae	*Coracoralina chiquitensis*	UB24491	—	PX214322	—	PX215319	This study
Puccinia coronata	*Rhamnus cathartica*	BPI844300	—	DQ354526	—	—	Aime (2006)
Puccinia cyperi	*Cyperus iria*	BRIP60997	KU296885	KU296885	—	—	McTaggart et al. (2016b)
Puccinia dichondrae	*Dichondra repens*	BRIP60027	—	KX999874	—	KX999914	Marin-Felix et al. (2017)
Puccinia geitonoplesii	*Geitonoplesium cymosum*	BRIP55679	KM249860	KM249860	—	KX999916	McTaggart et al. (2016b); Marin-Felix et al. (2017)
Puccinia gnaphaliicola	*Gamochaeta* sp.	BRIP58451	KF690683	KF690703	—	KX999917	McTaggart et al. (2014a); Marin-Felix et al. (2017)
Puccinia graminis	*Glyceria maxima*	BRIP60137	—	KM249852	—	MW036505	McTaggart et al. (2016b); Aime and McTaggart (2021)
Puccinia haemodori	*Anigozanthos* sp.	BRIP56965	KF690674	KF690692	—	KX999919	McTaggart et al. (2014a); Marin-Felix et al. (2017)
Puccinia helianthi	*Helianthus* sp.	BPI910243	—	KY764126	—	—	Demers et al. (unpublished)
Puccinia hemerocallidis	*Hemerocallis* sp.	BRIP53476	KM249855	KM249855	—	KX999920	McTaggart et al. (2016b); Marin-Felix et al. (2017)
Puccinia hieracii	*Taraxacum officinale*	PDD98711	KX985752	KX985752	—	—	Padamsee and McKenzie (2014)
Puccinia junci	*Juncus tenuis*	PDD99243	KX985745	KX985745	—	—	Padamsee and McKenzie (2014)
Puccinia lagenophorae	*Emilia sonchifolia*	BRIP57563	KF690677	KF690696	—	KT199417	McTaggart et al. (2014a, 2016a)
Puccinia liberta	*Eleocharis ochrostachys*	BRIP59686	—	KX999881	—	KX999922	Marin-Felix et al. (2017)
Puccinia menthae	*Cunila origanoides*	BPI871110	DQ354513	DQ354513	—	—	Aime (2006)
Puccinia menthae	*Mentha spicata*	BRIP59667	—	KU296890	—	MW139661	McTaggart et al. (2016b); Aime and McTaggart (2021)
Puccinia merrilliana	*Operculina brownii*	BRIP56913	—	KX999885	—	KX999926	Marin-Felix et al. (2017)
Puccinia muehlenbeckiae	*Muehlenbeckia adpressa*	BRIP57718	—	KX999884	—	KX999925	Marin-Felix et al. (2017)
Puccinia myrsiphylli	*Asparagus asparagoides*	BRIP57782	—	KM249854	—	KT199418	McTaggart et al. (2016a, 2016b)
Puccinia punctiformis	Not stated	ZP-R314	—	MK518598	—	—	Zhao (unpublished)
Puccinia scirpi	*Nymphoides indica*	BRIP61027	KX999892	KX999892	—	KX999929	Marin-Felix et al. (2017)
Puccinia stylidii	*Stylidium armeria*	BRIP60107	KJ622216	KJ622215	—	KT199420	McTaggart et al. (2014a, 2016a)
Puccinia ursiniae	*Ursinia anthemoides*	BRIP57993	KF690684	KF690705	—	KT199421	McTaggart et al. (2014a, 2016a)
Puccorchidium polyalthiae	*Polyalthia longifolia*	MGB101	OQ925894	OQ925894	—	—	Mahadevakumar (unpublished)
Puccorchidium polyalthiae	*Polyalthia longifolia*	MGB102	OQ925895	OQ925895	—	—	Mahadevakumar (unpublished)
Puccorchidium polyalthiae	*Polyalthia longifolia*	ZT-HeRB251	JF263493	JF263493	—	JF263525	Beenken et al. (2012)
Puccorchidium popowiae	*Monanthotaxis caffra*	ZT-Myc1976	JF263495	JF263495	—	JF263526	Beenken et al. (2012)
Ravenelia escharoides	*Senegalia burkei*	KR-M-004360	PX220112	MG954480	—	MN095330	Ebinghaus and Begerow (2018); This study
Ravenelia glabra	*Calpurnia aurea*	KR-M-0006450	—	MN072691	—	MN095333	Ebinghaus et al. (2020)
Ravenelia molopa	*Senegalia galpinii*	PREM61879	PX220113	MN072679	PX214328	MN095323	Ebinghaus et al. (2020); This study
Ravenelia sp.	*Tephrosia* sp.	PUR F19717	—	MW147024	MW168382	MW166322	Aime and McTaggart (2021)
Ravenelia spinifera	*Senegalia mellifera* ssp. *detinens*	PREM61895	PX220114	MN072696	—	MN095336	Ebinghaus et al. (2020); This study
Ravenelia stictica	*Mundulea sericea*	PREM60784	—	MN072663	PX214329	MN095307	Ebinghaus et al. (2020); This study
Raveneliopsis cenostigmatis	*Cenostigma macrophyllum*	UB23957	—	OQ247914	OQ244508	OQ268256	Ebinghaus et al. (2023a)
Raveneliopsis cenostigmatis	*Cenostigma macrophyllum*	UB23959	—	OQ247915	OQ244509	OQ268257	Ebinghaus et al. (2023a)
Raveneliopsis spiralis	*Cenostigma macrophyllum*	UB23929	—	OQ247917	OQ244510	OQ268259	Ebinghaus et al. (2023a)
Raveneliopsis spiralis	*Cenostigma macrophyllum*	UB23930	—	OQ247918	OQ244511	OQ268260	Ebinghaus et al. (2023a)
Schroeteriaster elettariae	*Alpinia caerulea*	BRIP56855	—	MW147052	—	MW139662	Aime and McTaggart (2021)
Sorataea arayatensis	*Derris elliptica*	BRIP57452	—	MW147036	—	—	Aime and McTaggart (2021)
Sorataea arayatensis	*Derris elliptica*	U416	—	MW049280	—	—	Aime and McTaggart (2021)
Sorataea sp.	*Baphia* sp.	PUR N1652	—	MW147037	—	—	Aime and McTaggart (2021)
Sphaerophragmium acaciae	*Albizia lebbeck*	TA432	—	OL437039	—	—	Tabe et al. (2022)
Sphaerophragmium dalbergiae	*Dalbergia armata*	U541	—	OQ215082	—	—	Wood and Aime (2024)
Sphaerophragmium longicorne	*Dalbergia hostilis*	PUR N16513	—	MW147053	MW147077	—	Aime and McTaggart (2021)

(*Continued*)

Table 1. (Continued).

			GenBank accessions				
Fungus	Host	Specimen	ITS2	28S	18S	*CO3*	Reference
Sphaerophragmium sp.	*Albizia* sp.	BRIP56910	—	KJ862350	KJ862429	KJ862462	McTaggart et al. (2015)
Sphaerophragmium sp.	*Senegalia brevispica*	U1761	—	OQ215083	—	—	Wood and Aime (2024)
Sphenorchidium deightonii	*Xylopia aethiopica*	PC0096724	KM217351	KM217351	KM217369	—	Beenken and Wood (2015)
Sphenorchidium deightonii	*Xylopia aethiopica*	PC0096730	KM217350	KM217350	KM217368	—	Beenken and Wood (2015)
Sphenorchidium sp.	*Xylopia* sp.	MCA7071	—	MW147054	MW147078	—	Aime and McTaggart (2021)
Tranzschelia arthurii	*Prunus serotina*	MCA2865	—	—	MG907202	—	Aime et al. (2018)
Tranzschelia arthurii	*Prunus* sp.	MCA4540	—	MG907212	—	—	Aime et al. (2018)
Tranzschelia discolor	*Prunus persica*	BRIP57662	—	KR994891	KR994969	KR995082	Doungsa-ard et al. (2015)
Tranzschelia discolor	*Prunus persica*	RP1	OP611170	OP611170	—	—	Chitta et al. (unpublished)
Tranzschelia discolor	*Prunus persica*	U884	DQ995341	DQ995341	—	—	Deadman et al. (2007)
Tranzschelia fusca	Not stated	BJFCR04644	—	PP468796	PP468800	—	Liu (unpublished)
Uredo baruensis	*Chrysophyllum sparsiflorum*	BPI 863952	DQ021883	DQ021883	—	—	Hernández et al. (2005)
Uredo elephantopodis	*Elephantopus scaber*	BRIP58415	—	MW049283	—	MW036509	Hernández et al. (2005)
Uredo hiulca	*Dioscorea transversa*	BRIP53244	—	MW049284	—	MW036510	Hernández et al. (2005)
Uromyces appendiculatus	*Phaseolus vulgaris*	BRIP60020	—	KM249870	—	KX999933	McTaggart et al. (2014b); Marin-Felix et al. (2017)
Uromyces ari-triphylli	*Arisaema triphyllum*	BPI871111	DQ354529	DQ354529	DQ354528	—	Aime (2006)
Uromyces ciceris-arietini	*Cicer arietinum*	BRIP53857	—	MW147057	—	—	Aime and McTaggart (2021)
Uromyces hawksworthii	*Passovia ovata*	UB24223	PX220115	PX214323	—	—	This study
Uromyces orientalis	*Indigofera linifolia*	BRIP60934	KX999899	KX999899	—	KX999934	Marin-Felix et al. (2017)
Uromyces pisi-sativi	*Genista monspessulana*	BRIP60151	—	KX999900	—	—	Marin-Felix et al. (2017)
Uromyces salsolae	*Kali australe*	BRIP57696	—	KX999901	—	KX999935	Marin-Felix et al. (2017)
Uromyces socius	*Cladocolea* sp.	BPI910299	—	KY764198	—	—	Demers et al. (unpublished)
Uromyces tenuicutis	*Sporobolus africanus*	BRIP60012	—	KX999904	—	KX999937	Marin-Felix et al. (2017)
Uromyces trifolii-repentis	*Trifolium repens*	BRIP57653	—	KX999905	—	KX999938	Marin-Felix et al. (2017)
Uromyces tripogonicola	*Tripogonella loliiformis*	BRIP58112	—	MW147058	—	MW139664	Aime and McTaggart (2021)
Uromyces viciae-fabae	*Vicia faba*	BRIP59246	—	KM249865	—	—	McTaggart et al. (2016b)
Uromycladium falcatarium	*Falcataria moluccana*	BRIP57990	KJ632994	KJ632974	KJ633014	KJ639060	Doungsa-ard et al. (2015)
Uromycladium maslinii	*Acacia acuminata*	BRIP57697	KR994751	KR994700	KR994796	KR995001	Doungsa-ard et al. (2018)
Uromycladium notabile	*Acacia mearnsii*	BRIP59233	KR994844	KR994835	KR994851	KR995044	Doungsa-ard et al. (2018)
Uromycladium tepperianum	*Acacia ligulata*	BRIP59895	KR994775	KR994729	KR994821	KR995029	Doungsa-ard et al. (2018)
Uropyxis daleae	*Dalea pringlei*	BPI910337	KY798364	KY798364	—	—	Demers and Castlebury (unpublished)
Uropyxis daleae	*Dalea pennellii* var. *chilensis*	Socoroma	MG969964	MG969964	—	—	Sepúlveda et al. (2021)
Uropyxis daleae	*Dalea pennellii* var. *chilensis*	Socoroma-2	MN337263	MN337263	—	—	Sepúlveda et al. (2021)
Uropyxis daleae	*Dalea pennellii* var. *chilensis*	Socoroma-3	MN337264	MN337264	—	—	Sepúlveda et al. (2021)
Uropyxis diphysae	*Diphysa americana*	BPI864148	—	MW049288	—	—	Aime and McTaggart (2021)

(Borchsenius 2009) following Simmons and Ochotena (2000). The *CO3* sequence alignment was additionally translated into the corresponding amino acid sequences using MEGA 11 (Tamura et al. 2021), with codon usage based on translation table 4. Alignments were generated with MAFFT 7.154b (Katoh and Standley 2014) using the L-INS-i strategy and visualized and manually edited in MEGA 7.0.26 (Kumar et al. 2016).

The data sets for a taxonomic subset of the suborder Uredinineae were constructed in a similar manner; however, the 18S gene region was excluded as publicly available sequences for these taxa were scarce. Alignments of both groups were used as partitioned data sets for maximum likelihood (ML) analyses in IQ-TREE 2.1.3 (Minh et al. 2020). The analyses were performed with 10 000 ultrafast bootstraps (UFboots; Hoang et al. 2018) and tested with 10 000 replicates of the Shimodaira-Hasegawa approximate likelihood-ratio test (SH-aLRT; Guindon et al. 2010). ModelFinder was used to determine the optimal evolutionary models for the data sets, including FreeRate heterogeneity models (Kalyaanamoorthy et al. 2017). Additionally, a codon

model was selected for the *CO3* partition. All alignments used in this study are available as SUPPLEMENTARY FILES 1 and 2.

RESULTS

Maximum likelihood (ML) analyses of Uredinineae and Raveneliineae largely supported previously established phylogenetic frameworks at the family and genus levels. However, several newly sequenced taxa revealed unexpected placements that diverge from prior morphology-based classifications, as seen in phylogenetic trees shown in FIGS. 1 and 2. The rust fungus collected on *Coracoralina* was resolved within the Pucciniaceae and is described as a new species in the Taxonomy section. Detailed accounts of all revised taxa are presented and discussed below.

TAXONOMY

Uredinineae

Pucciniaceae.—New *Puccinia* species, the first on *Coracoralina* (Eriocaulaceae) from the Cerrado

The plant genus *Coracoralina* was recently segregated from *Paepalanthus* (Eriocaulaceae) and accommodates 22 species (Andrino et al. 2023) and is usually found in rupestrian areas of the Brazilian Cerrado, the so-called "campos rupestres" (Andrade et al. 2010). The genus includes *Coracoralina chiquitensis* and *C. koernickei*, both recently found to be infected by an unknown rust fungus, which is described below as a novel *Puccinia* species based on morphological characteristics and molecular phylogenetic data.

Puccinia coracoralinae Ebinghaus, Z.M. Chaves & Dianese, sp. nov. FIG. 3
Index Fungorum IF902700

Etymology: Epithet designated after the host genus.

Description: Spermogonia and Aecidia were not observed. Aparaphysate uredinia and telia were located within striated linear sori, along the leaf veins, with ferruginous yellow areas containing urediniospores, and dark brown areas where the teliospores are located, measuring 3–4 mm in length × 0.3 mm in width. Urediniospores 15–18 µm diam, globose, subglobose, rarely reniform, subhyaline to ferruginous, echinulate, pedicellate, sessile, 1–2 equatorial germ pores rarely seen. Teliospores 40–45 µm long × 14–18 µm wide, bicellular, with slight constriction at the septum, cylindrical with thickened obtuse apex, rounded base, pedicellate; pedicels 40–50 µm long × 4–8 µm diam.

Typification: BRAZIL. GOIÁS: Alto Paraíso, Parque Nacional Chapada dos Veadeiros, −14.1164S, −47.7465W, in live leaves of *C. chiquitensis*, 28 Jul 2022, *JMT Martins 04* (**holotype** UB (Mycol. Coll.) 24487). GenBank: 28S = PX214321; *CO3* = PX215318.

Other specimens examined: BRAZIL. GOIÁS: Alto Paraíso, Parque Nacional Chapada dos Veadeiros, −14.1166S, −47.7463W, in live leaves of *Coracoralina chiquitensis*, 28 Jul 2022, *JMT Martins 06* (UB (Mycol. Coll.) 24494); Parque Nacional Chapada dos Veadeiros, −14.1165S, −47.7463W, on live leaves of *C. chiquitensis*, 28 Jul 2022, *JMT Martins 05* (UB (Mycol. Coll.) 24491), GenBank: 28S = PX214322, *CO3* = PX215319; −13.9029S, −47.3783W, in live leaves of *C. koernickei*, 29 Jul 2022, *JMT Martins 07* (UB (Mycol. Coll.) 24506).

Diagnosis: Puccinia coracoralinae differs from the only known rust fungus on Eriocaulaceae (*Uredo ruhlandii*), found infecting *Eriocaulon trilobatum* in Madagascar, by showing smaller and generally more globoid urediniospores instead of ovoidal to ellipsoid uediniospores.

Notes: This is the first rust fungus found in Brazil on members of the Eriocaulaceae for which, to our knowledge, only a single other specimen of an Eriocaulaceae rust has ever been collected and described, i.e., *Uredo ruhlandii* (as *Uredo ruhlandi*) on *Eriocaulon trilobatum* in Madagascar (Hennings 1899). The Eriocaulaceae, together with the Cyperaceae and Juncaceae, are members of the order Poales. In our analysis, the new fungus showed the closest relationship to the heterecious Cyperaceae rusts *P. canaliculata* and *P. cyperi*, both host-alternating between aecial hosts in the Asteraceae family and telial hosts in genus *Cyperus*, preferentially found in warmer climates worldwide. Furthermore, the *Coracoralina* rust fungus is phylogenetically linked to other *Puccinia* species with hosts alternating between the Asteraceae and the Cyperaceae or the Juncaceae families, e.g., *P. merrilliana* and *P. liberta* (FIG. 1; Maier et al. 2007; van der Merwe 2007; Aime et al. 2018), and further *Puccinia* species parasitizing the Poales.

Sphaerophragmiaceae.—Establishment of *Dietelomyces*, gen. nov., and reclassification of *Diorchidium copaiferae* to *Die. copaiferae*, comb. nov. (FIGS. 4 and 5)

The genus *Diorchidium* was established by Kalchbrenner (1882) based on a fungus with 2-celled, vertically septate teliospores found in South Africa on *Milletia grandis* (Fabaceae). Soon after, other rust fungi on various host groups were also classified under *Diorchidium*, with Magnus (1891) contributing several species, i.e., *D. insuetum, D. lateripes*, and

Figure 1. Maximum likelihood (ML) reconstruction of representative families of the Uredinineae based on ITS2, 28S, and *CO3* sequence data, including amino acid sequences and indels of ribosomal DNA. The discussed rust fungal taxa are highlighted in red font. Black arrows indicate taxa currently assigned to the polyphyletic genus *Dietelia*.

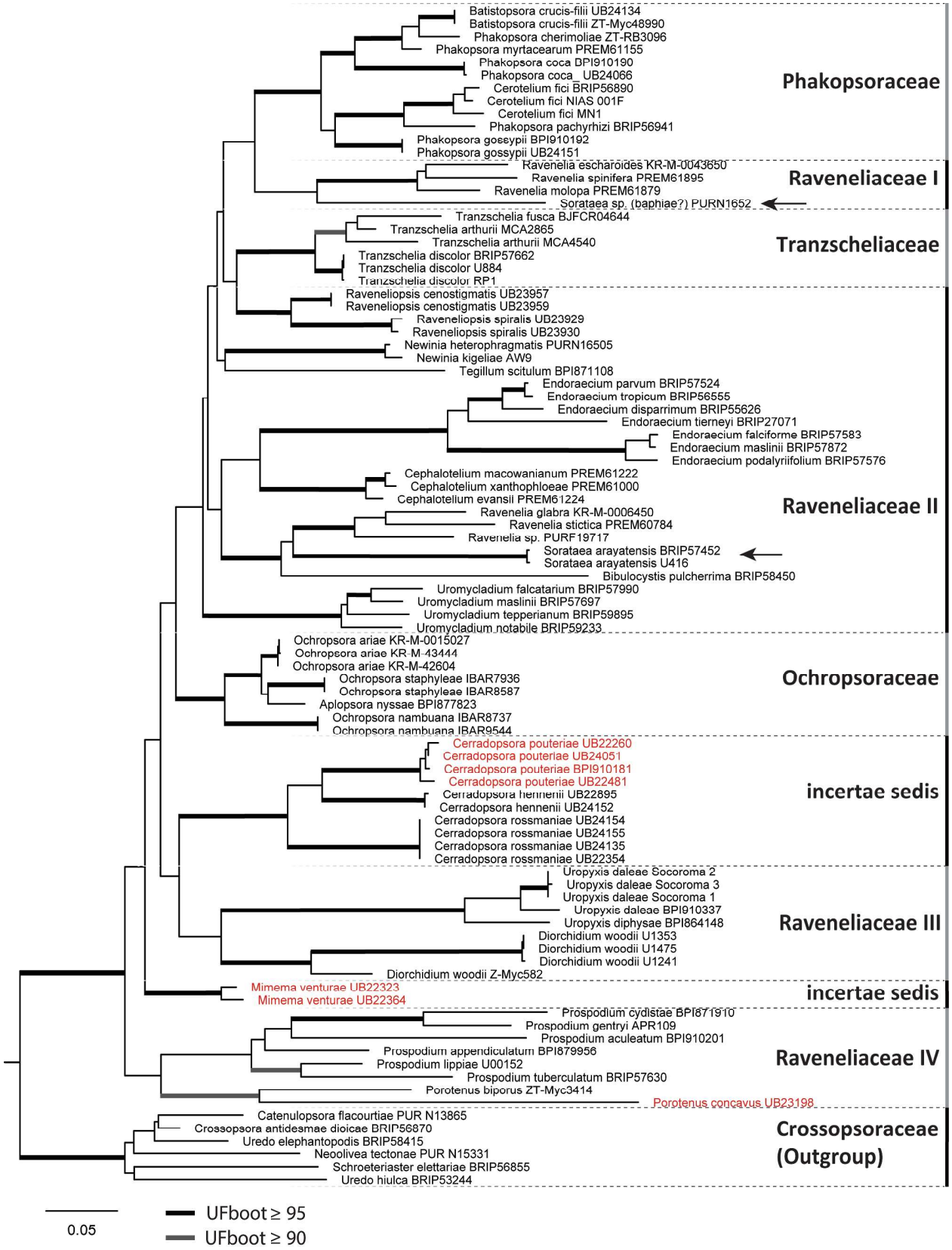

Figure 2. Maximum likelihood (ML) phylogenetic reconstruction of the Raveneliineae based on 28S, ITS, 18S, and *CO3* sequence data, including amino acid data of the *CO3* data set and gap data of the 28S and ITS sequences. The discussed rust fungal taxa are highlighted in red font. Black arrows indicate taxa currently assigned to the polyphyletic genus *Sorataea*.

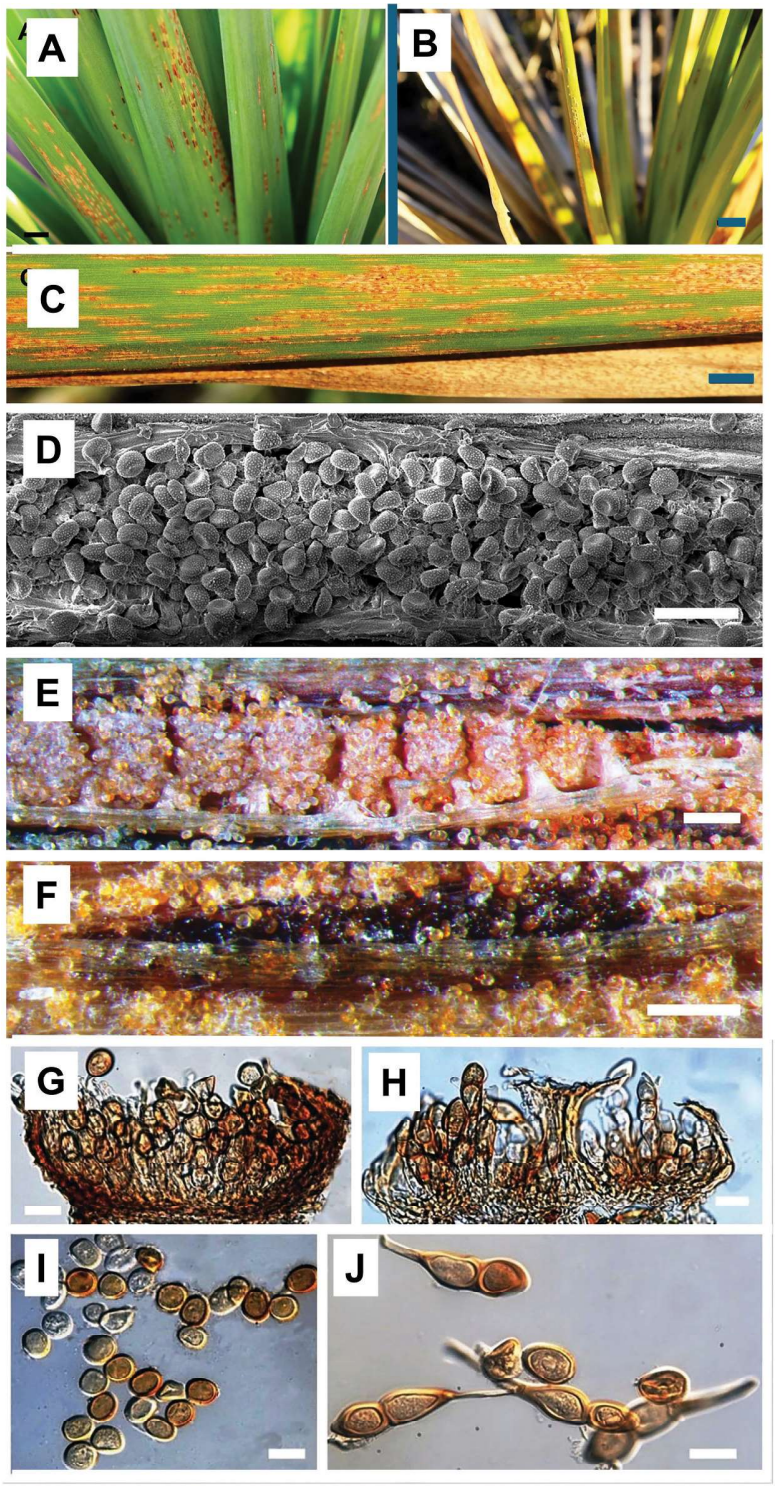

Figure 3. A–J. *Puccinia coracoralinae*, sp. nov., in *Coracoralina chiquitensis*, UB (Mycol. Coll.) 24487, holotype. A–C. Foliar symptoms showing striated pustules with some leaf blight. D. Uredinium seen in SEM. E. Uredinium seen in light microscopy. F. Telium with spores darker and larger than those of the uredinium. G. Uredinium. H. Telium. I. Urediniospores. J. Teliospores. Bars: A = 2 cm; B = 4 cm; C = 2 cm; D = 50 µm; E–F = 100 µm; G–J = 20 µm.

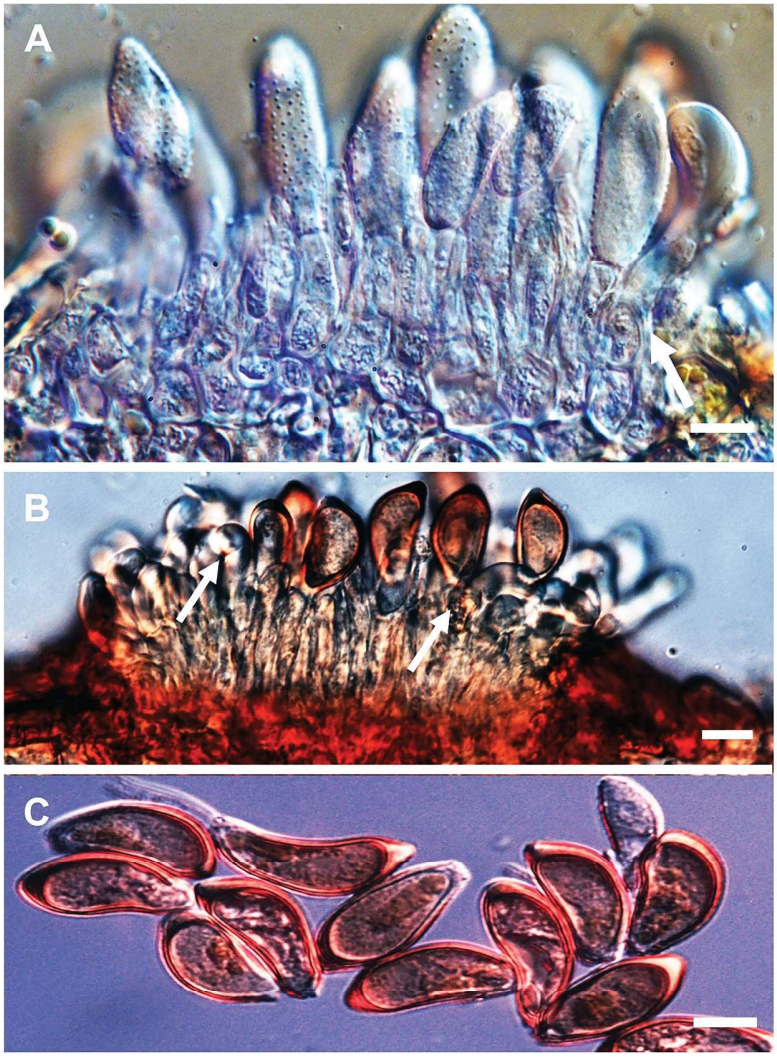

Figure 4. A–C. *Dietelomyces copaiferae*, nom. nov. et comb. nov., on *Copaifera langsdorfii*. A–B. Uredinium, with arrows showing curved paraphyses. C. Urediniospores. Bars: A–C = 10 µm.

D. steudneri, which he distinguished from *Puccinia* based on vertical septation and the "polar" orientation of the germ pores. However, Dietel (1892) reviewed these species and questioned the natural coherence of the genus, as well as Magnus's (1891) criteria for separating *Diorchidium* from *Puccinia* based on germ pore positioning, although he recognized at least two groups within the genus. The first included species parasitic on grasses that, in addition to typical "diorchidioid" teliospores, featured the "puccinioid" type with 2-celled, horizontally septate teliospores, as seen in species such as *Diorchidium leve* (syn. *Puccinia levis*), suggesting that they were closely related to *Puccinia* species, consequently transferring them to *Puccinia*, e.g., *P. lateripes*, *P. wolgensis*, or *P. boutelouae* (Dietel 1897). Dietel's hypothesis for these taxa can now be largely regarded either as being confirmed by molecular phylogenetic studies or as commonly accepted (e.g., Marin-Felix et al. 2017). On the other hand, Dietel (1892) recognized the exclusive presence of diorchidioid teliospores in species such as the type species *D. woodii*, *D. tracyi*, and *D. binatum*, which he proposed as a distinct "series" within *Diorchidium*, closely related to *D. steudneri* (Magnus 1891). Dietel (1892) also identified a separate form, *D. pallidum* on *Dioscorea*, that differed in teliospore development and placed it in the newly created genus *Sphenospora*. Although *D. steudneri* and *D. binatum* have been transferred to *Uropyxis* (Uropyxidaceae) and *Dicheirinia* (Raveneliaceae), respectively, they remain without a modern revision, whereas *Sphenospora* forms a monophyletic group within the Pucciniaceae, restricted to monocot families such as Dioscoreaceae, Orchidaceae, and Smilaceae

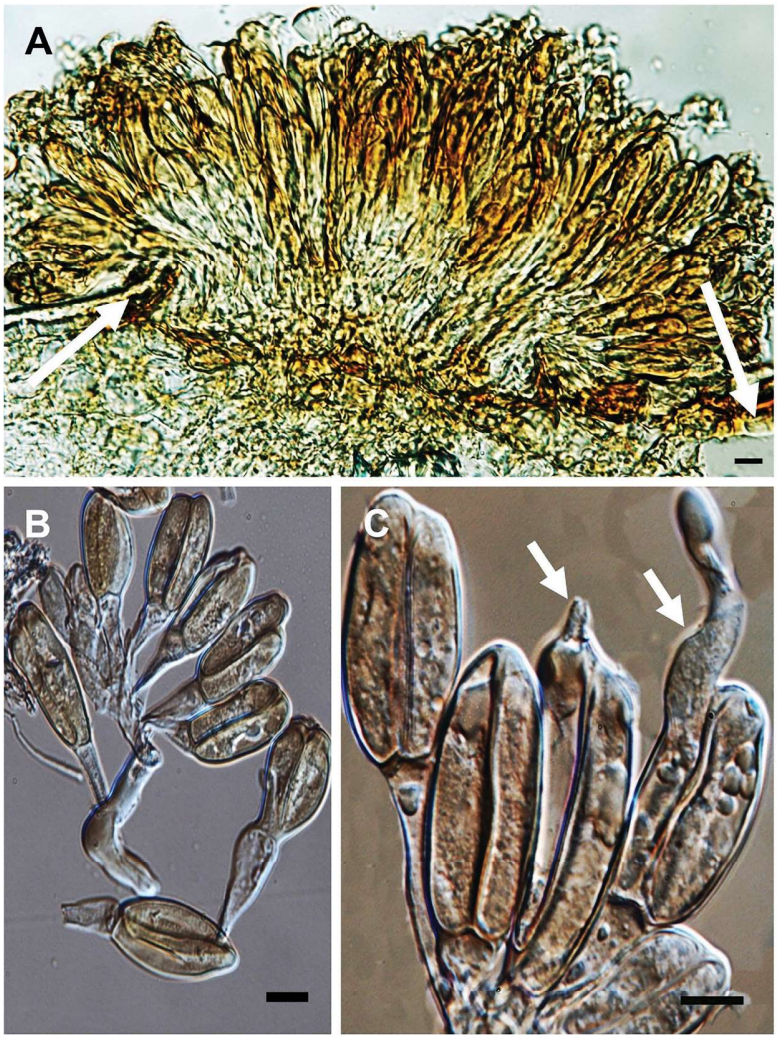

Figure 5. A–C. *Dietelomyces copaiferae*, nom. nov. et comb. nov., on *Copaifera langsdorfii*. A. Telium with germinated teliospores; arrows showing host epidermis. B. Group of pedicellate teliospores originated from one sporogenous cell. C. Teliospores germinating through the apical pore (arrows) of the cells. Bars: A = 20 µm; B–C = 10 µm.

(Beenken and Wood 2015; Aime and McTaggart 2021). Cummins and Hiratsuka (2003) accepted 12 species of *Diorchidium*. However, more recent studies have provided support for the polyphyletic nature of this genus (Beenken and Berndt 2010; Beenken and Wood 2015; Wood and Aime 2024), a pioneer hypothesis adopted by Dietel (1892) as briefly outlined above. For example, *Diorchidium polyalthiae*, known from India and Sri Lanka on *Polyalthia* (Annonaceae), and *D. gerstneri*, infecting *Uvaria* (Annonaceae) in South Africa, have since been reclassified into the genera *Puccorchidium* and *Sphaerophragmium*, respectively (Beenken and Berndt 2010; Beenken and Wood 2015). Despite these advancements, the taxonomy of *Diorchidium* remains insufficiently resolved. Hennings (1909) described the anamorph of a rust fungus on *Copaifera* (Fabaceae) from São Paulo, Brazil, as *Uredo copaiferae*. Sydow and Sydow (1924) suggested that the teliospores in the type material were likely overlooked by Hennings and transferred it to the genus *Sphenospora* due to its similarity with *Sph. pallida*. Later, Cummins and Hiratsuka (1983) moved *Sphenospora copaiferae* to *Diorchidium*, noting the absence of the gelatinous matrix typically associated with the telial stage of other *Sphenospora* species. However, the elongated and often curved urediniospores, along with numerous peripheral inward-curved paraphyses, are characteristic of *D. copaiferae* and distinct from those described for the type species of *Diorchidium, D. woodii*.

Our phylogenetic analyses of *D. copaiferae* from Brazil place the fungus as a distinct lineage within the Sphaerophragmiaceae (FIG. 1), away from the type *D. woodii*. Based on detailed morphological studies

now and previously by Rezende and Dianese (2002), reinforced by the present phylogenetic analyses, we propose the reclassification of *D. copaiferae* into *Dietelomyces*, gen. nov., with type species *Dietelomyces copaiferae* as described below.

Dietelomyces Dianese & Ebinghaus, gen. nov. FIGS. 4–5

Index Fungorum IF903354

= *Diorchidium* Kalchbr., Grevillea 11(57):26. 1882.

Etymology: Honoring the German mycologist Paul Hermann Dietel for his outstanding contribution to the study of Brazilian Pucciniales.

Description: Spermogonia and aecidia not observed. Uredinia hypophyllous, erumpent, brown, paraphysate; paraphyses peripheral. Urediniospores mostly allantoid, ellipsoidal, brown, echinulate. Telia similar to uredinia. Teliospores 2-celled, vertically septate, elongate-ellipsoid, smooth, pedicelate with single apical germ pore per cell.

Type species: ***Dietelomyces copaiferae*** (Henn.) Ebinghaus & Dianese, comb. nov. FIGS. 4–5

Index Fungorum IF9033553

Basionym: Uredo copaiferae Henn., Hedwigia 48:2. 1908 [1909].

= *Diorchidium copaiferae* (Henn.) Cummins & Y. Hirats. [as "*copaifera*"], Illustr Gen Rust Fungi, APS (St Paul):147. 1983.

= *Sphenospora copaiferae* P. Sydow & H. Sydow, Monogr Ured 4:584. 1924.

= *Uredo copaiferae* P. Hennings, Hedwigia 48:2–3. 1908.

Description: Spermogonia and aecidia not observed. Uredinia hypophyllous, subepidermal, erumpent, scattered, powdery, brown, paraphysate; paraphyses 43–65 × 10–12 µm, abundant at the periphery, basally united, incurved, pale brown. Urediniospores 34–44 × 13–18 µm, variable in size and shape, mostly allantoid, ellipsoidal, reniform, cinnamon to chestnut brown, moderately echinulate, with a single germ pore at the base. Telia similar to uredinia, yellowish brown. Teliospores 34–44 × 15–22 µm, 2-celled, vertically septate, elongate-ellipsoid, smooth, pale golden or nearly colorless, a single germ pore in the apical part of each cell, germination occurs without dormancy; pedicel colorless, persistent.

Specimens examined: BRAZIL. DISTRITO FEDERAL: Brasília, Asa Norte SQN 413, Parque Ecológico Olhos D'água, −15.7603S, −47.8813W, in live leaves of *Copaifera langsdorffii* (Fabaceae), 12 Sep 2012, *E.S.C. Souza 145* (UB (Mycol. Coll.) 22385), GenBank: 28S = PX214315; in live leaves of *Copaifera langsdorffii* (Fabaceae), 12 Sep 2012, *E. S.C. Souza 146* (UB (Mycol. Coll.) 22386); MATO GROSSO: Barra do Garça, Parque Estadual da Serra Azul, −15.8399S, −52,2458W, in live leaves of *Copaifera langsdorffii* (Fabaceae), 12 Aug 2014, *Débora C. Guterres 27* (UB (Mycol. Coll.) 22946); DISTRITO FEDERAL: Brasília, Universidade de Brasília, Centro Olímpico, −15.7665S, −47.8565W, 21 Feb 2019, *J.C. Dianese 3757* (UB (Mycol. Coll.) 24053), GenBank: *CO3* = PX215310; GOIÁS: Cristalina, Fazenda Nova Índia, in live leaves of *Copaifera langsdorffii* (Fabaceae), 10 Aug 1993, *J.C. Dianese 254* (UB (Mycol. Coll.) 4169); DISTRITO FEDERAL: Brasília, Campus Darcy Ribeiro, Universidade de Brasília, near Reitoria, 20 Jul 1998, *D.V. Rezende 48* (UB (Mycol. Coll.) 13256).

Diagnosis: Within the Sphaerophragmiaceae, *Die. copaiferae* shares significant similarities in teliospore morphology with *Sphenorchidium xylopiae* (Beenken and Wood 2015). However, besides its distinct phylogenetic position, the rust on *Copaifera* (Fabaceae) can be distinguished from species of *Sphenorchidium* on Annonaceae by the absence of an aecial stage, the presence of allantoid, elongated-ellipsoid urediniospores, which are entirely absent in *Sphenorchidium*, and by its larger teliospores, measuring 34–44 × 13–18 µm, compared with those of *Sph. xylopiae* that measure 28–35 × 12–16 µm (Beenken and Wood 2015). To date, species of *Sphenorchidium* are only known from annonaceous host plants, occurring in the Paleotropics, whereas *Die. copaiferae* is only known from *Copaifera*, a fabaceaeous plant species restricted to the Neotropics.

Notes: For specimens of *Die. copaiferae* examined in this study, we confirm features previously observed (Rezende and Dianese 2002; Cummins and Hiratsuka 2003; Hennen et al. 2005), including the curved paraphyses around the uredinia; the allantoid, reniform, and sometimes curved, brown, lightly echinulate urediniospores; and finally, 2-celled, vertically septate, smooth, nearly colorless teliospores, typically with two apical projections and one germ pore per teliospore cell. These characteristics clearly distinguish this fungus from the *Diorchidium* type species *D. woodii*, which exhibits smaller, oval to ellipsoid, brown, and echinulate teliospores. As paraphyses and urediniospores have not yet been described for *D. woodii*, these traits cannot be used for comparison. However, our phylogenetic analysis groups *Die. copaiferae* within the Sphaerophragmiaceae (suborder Uredinineae), contrasting with the placement of *D. woodii* in Suborder Raveneliineae (Wood and Aime 2024).

Sphaerophragmiaceae.—Taxonomy of *Dietelia duguetiae*, a parasite of *Duguetia furfuracea* (Annonaceae), confirming its familial assignment to the Sphaerophragmiaceae (Uredinineae)

In a phylogenetic study, Zhao et al. (2020) included a specimen of *D. duguetiae*—based on sequences provided by Beenken (2014) (GenBank KM217365 and KM217382), which, alongside *Austropuccinia*, was placed in family Sphaerophragmiaceae—but did not discuss the outcome, as it was not in the scope of their studies. To characterize this fungus in more detail and to provide a reevaluation of its phylogenetic positioning within the Sphaerophragmiaceae, we first sequenced the ITS2, 28S, 18S, and *CO3* gene markers and provided phylogenetic analyses to molecularly characterize our specimens (FIG. 1) and complemented morphological illustrations with an updated description based on collections housed in the Herbarium UB (Mycological Collection), as follows.

Description: Spermogonia dark, adaxial, formed on grayish galls that may cover a large part of the leaf surface. Telia abaxial with firm, orange-yellow peridium, formed by rhomboid to angular cells; cell walls radially striated and inner wall warty, up to 4 µm thick, hyaline. Teliospores catenulated, broadly globoid to polyhedral, with intensely warty wall when seen in SEM; germ pores well developed (FIGS. 6–7)

Specimens examined: BRAZIL. DISTRITO FEDERAL: Brasília, Parque Ecológico Ermida Dom Bosco, Lago Sul, −15.7971S, 47.8079W, in live leaves of *Duguetia furfuracea*, 25 Jul 2013, *ESC Souza 201* (UB (Mycol. Coll.) 22524), GenBank: ITS2-28S = PX214384, *CO3* = PX215307; GOIÁS, Alto Paraíso, Parque Nacional da Chapada dos Veadeiros, −14,14756S, 47.77311W, in live leaves of *Duguetia furfuracea*, 15 Jun 2022, *JMT Martins 02* (UB (Mycol. Coll.) 24378), GenBank: ITS2-28S = PX214384, *CO3* = PX215308; −14.1343 S, −47.7733 W in live leaves of *Duguetia furfuracea*, 18 Jun 2022, *JMT Martins 03*, UB (Mycol. Coll.) 24480), GenBank: ITS2-28S = PX214384, *CO3* = PX215309.

Notes: The genus *Dietelia*, with the type species *Dietelia verruciformis* (syn. *Cronartium verruciforme*), was established by Hennings (1897) based on material collected in Córdoba Province, Argentina, infecting *Krapovickasia flavescens* (syn. *Sida flavescens*) (Malvaceae). Today, the genus comprises 12 species, following the recombination of three species, i.e, *D. canavaliae, D. eupatori*, and *D. vernoniae*, into the genera *Cerotelium, Baeodromus*, and *Puccinia*, respectively, and is classified within the artificial family Pucciniosiraceae (Cummins and Hiratsuka 2003; Hennen et al. 2005; Berndt 2018; Aime and McTaggart 2021).

Buriticá and Hennen (1980) provided a comprehensive review of the species belonging in tribe Pucciniosireae (Dietel 1928) from the Neotropics and revised the known genera based on detailed morphological analyses. They considered the Pucciniosireae to be a polyphyletic tribe within the Pucciniaceae, containing genera with reduced, endocyclic life cycles, presumably derived from macrocyclic species within the *Puccinia-Uromyces* complex. They recognized nine genera in tribe Pucciniosireae: *Alveolaria, Baeodromus, Chardoniella, Cionothrix, Didymopsora, Dietelia, Endophyllum, Pucciniosira*, and *Trichopsora*. Although *Alveolaria, Cionothrix*, and *Baeodromus* were provisionally retained within the tribe due to a lack of understanding of their phylogenetic relationships, *Masseeella* was excluded.

Cummins and Hiratsuka (2003) elevated the tribe to the rank of family, Pucciniosiraceae, and, while incorporating *Ceratocoma*, a genus established by Buriticá (1991), they excluded the endocyclic *Endophyllum*. Nevertheless, this family is dedicated to including autoecious, endocyclic rust fungi. Molecular phylogenetic studies have recently confirmed the hypothesis that the Pucciniosiraceae are derived from within the Pucciniaceae. This has been demonstrated for taxa such as *Baeodromus eupatorii, Chardoniella gynoxidis, Cionothrix praelonga, Didymopsora solani-argentei, Dietelia* (*D. mesomaericana, D. portoricensis, D. codieaei*), *Endophyllum* (*E. berchemiae-floribundae, E. cassiae, E. circumscriptum, E. dichroae, E. elaeagnilatifoliae, E. elytropappi, E. maiense, E. rhamnusii-globosae, E. rhamnellae-franguloidese, E. osteospermi*), and *Pucciniosira* (*P. anthocleistae, P. cornuta, P. dissotidis, P. pallidula, P. solani, P. tuberculata*) (Maier 2002; Maier et al. 2003; Aime 2006; Aime and McTaggart 2021; Sun et al. 2024; Wood and Aime 2024).

Among the 12 species remaining in *Dietelia, D. duguetiae* (syn. *Endophylloides duguetiae* [as "*deguetiae*"]) was described from *Duguetia furfuracea* (Annonaceae) from Uberlândia, Minas Gerais, Brazil. Viégas (1945) described the same fungus from *D. furfuracea* in the Paraíba Valley, São Paulo, and assigned it to the genus *Alveolaria* (Pucciniosiraceae), later synonymized with *D. duguetiae* (Buriticá and Hennen 1980). The fungus is commonly found in the Cerrado and morphologically well documented, especially through the descriptions by Buriticá and Hennen (1980) and complemented by the illustrative drawings in Viégas (1945), which include spermogonia. However, the taxonomic placement of this rust fungus within the genus *Dietelia* remained controversial (Buriticá and Hennen 1980). This is partly due to the artificial classification of endocyclic rust fungi as a distinct phylogenetic group and partly due to errors in the original species description and hence its assignment to *Dietelia* in the first place. As Buriticá and Hennen (1980) pointed out, Thurston

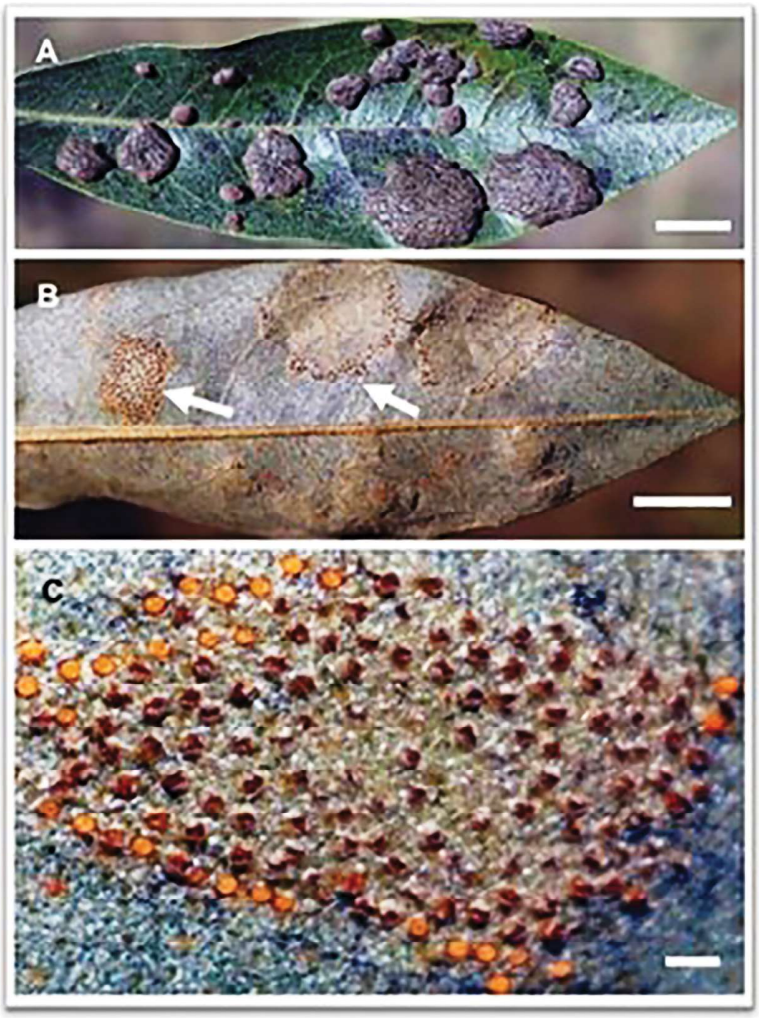

Figure 6. A–C. *Dietelia duguetiae* in *Duguetia furfuracea* (Annonaceae), UB (Mycol. Coll.) 24480, showing foliar symptoms and signs of the fungus. A. Galls on the adaxial surface of the leaf. B. Arrows indicating location of groups of supposedly aecidioid telia opposite to the adaxial galls. C. Telia at different stages of maturation. Bars: A–B = 1 cm; C = 0.5 mm.

(1940)'s original description of *Endophylloides duguetiae* contained several inaccuracies, such as the supposed absence of a peridial wall on the telial columns, waxy texture of the teliospore columns, and incorrect spore size, characteristics supposedly leading Thurston to his interpretation as an endocyclic fungus. Additionally, Buriticá and Hennen (1980) suggested that Viégas (1945) may have confused peridial cells with spores in his description of *Alveolaria duguetiae*, prompting him to mistakenly assign the fungus to *Alveolaria*. Consequently, Buriticá and Hennen (1980) considered the possibility that the fungus represents an aecidial anamorph, supported by the lack of observed basidiospore germination.

In congruence with Zhao et al. (2020), our analyses place *D. duguetiae* within the Sphaerophragmiaceae (FIG. 1), thereby demonstrating the polyphyletic nature of *Dietelia*.

To what extent *D. duguetiae* truly exhibits an endocyclic life cycle remains unresolved, as no basidiospore production has ever been observed. However, we concur with Buriticá and Hennen (1980) in their skepticism about its endocyclic nature. This perspective is supported by molecular phylogenetic studies, which have demonstrated that all confirmed endocyclic species examined to date have emerged within the Pucciniaceae (Aime and McTaggart 2021; Wood and Aime 2024). This contrasts with the fungus under discussion. In previous studies of *D. duguetiae*, germ pores were not documented. However, our SEM imaging revealed multiple, scattered germ pores (FIG. 7G–I), a feature that contrasts with endocyclic species, which typically exhibit only a single germ pore or pores being obscure, which might reflect an adaptation for basidia germination. The numerous germ pores and their scattered distribution in our fungus, on

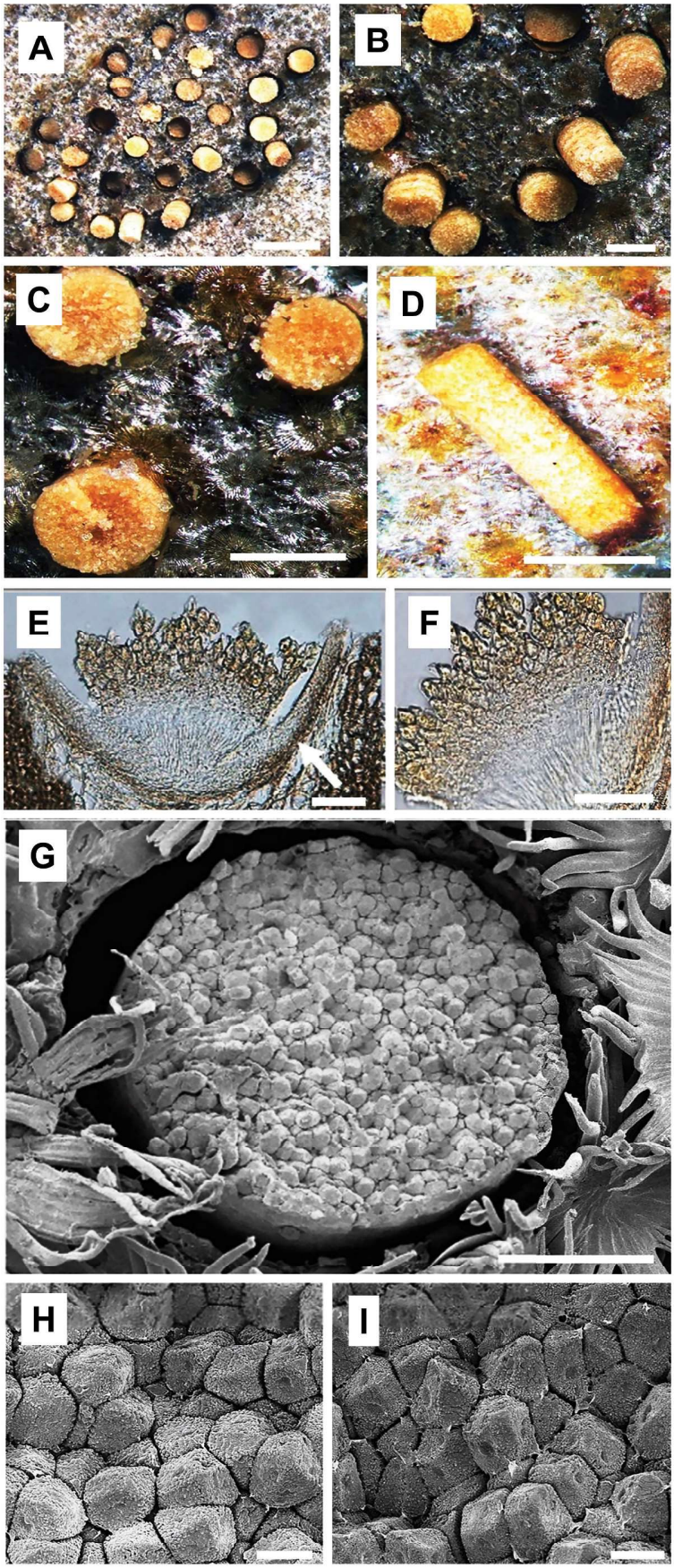

Figure 7. A–I. *Dietelia duguetiae* in *Duguetia furfuracea* (Annonaceae), UB (Mycol. Coll.) 24480. A–D. Details of mature aecia-like telia. E–F. Cryomicroscopic sections, with arrow showing the telial peridium with sporogenous cells originating catenate aeciospore-like teliospores. G–I. SEM images. G. Insertion of a telium in the host tissue. H. Slightly warty surface of teliospores. I. Teliospores showing germ pores. Bars: A = 0.5 mm; B–C = 0.2 mm; D = 0.5 mm; E–F = 50 µm; G = 100 µm; H–I = 10 µm.

the other hand, suggest typical aecidiospores. It should also be noted that this fungus is closely related to *Uredo baruensis*, which was described on *Chrysophyllum* (Sapotaceae) in Guyana (Hernández et al. 2005). This observation reflects the typical host relationships seen within the Sphaerophragmiaceae, as all aecidial morphs known to date in this family are associated with the Annonaceae, whereas species found on plant families other than the Annonaceae entirely lack aecidial morphs (Beenken and Berndt 2010; Beenken et al. 2012; Beenken and Wood 2015; Beenken 2017). When additionally considering the endocyclic type species of *Dietelia*, *D. verruciformis*, forming teliospores of the aecidioid type on *Krapovickasia* (Malvaceae), we can also hypothesize that these two taxa are not closely related. However, we refrain from recombining the *Duguetia* rust here due to the lack of recent collections of *D. verruciformis*.

Incertis sedis.—Taxonomy and phylogenetic allocation of the rare fungus *Esalque holwayi*, a parasite on *Caesalpinia leiostachya*, to the Uredinineae

The genus *Esalque* is monospecific (Hennen et al. 2000), accommodating only the type species *Esalque holwayi* (≡ *Triactella holwayi*)—described by Jackson (1931a) with type on *Caesalpinia* sp. mistakenly identified as *Cassia* sp., according to Hennen et al. (2000), with material collected in Rio de Janeiro, Tijuca, Brazil, on 23 December 1921 by Holway—and treated as a member of the Raveneliaceae (Hennen et al. 2000, 2005). Rezende and Dianese (2002) studied *E. holwayi* infecting *Caesalpinia leiostachya*, collected at the Campus Darcy Ribeiro of the Universidade de Brasília (UB (Mycol. Coll.) 14235), with detailed images using light and scanning electron microscopy.

The morphological description provided by Rezende and Dianese (2002) and Martins (2023) agrees with Hennen et al. (2000), as follows.

Description: Spermogonia and aecidia not observed. Uredinia amphigenous, subepidermal, erumpent, mainly hypophyllous, small 0.1–0.4 × 0.1–0.3 mm, paraphyses abundant, 22–37 × 5–7 µm, short and arched, peripheral, golden-brown walls, 1–1.5 µm thick. Urediniospores obovoid or broadly ellipsoid, 14–23 × 12–14 µm, echinulate; walls, 1.5–2 µm thick; germ pores 2–3 equatorial. Telia similar to the uredinia, often as mixed sori containing both teliospores and urediniospores, dark brown. Teliospores 3-celled, with two cells at the top, one smaller at the base, thickened at the angles, 22–28 × 22–27 µm, tuberculated with conical or cylindrical projections or tubercles; germ pores obscure, pedicellate; walls cinnamon brown, 1–1.5 µm thick; pedicels hyaline, 16–28 µm long, connected to the median portion of the basal cell. This description resulted from a study of the UB (Mycol. Coll.) 14235 specimen collected at Campus Darcy Ribeiro, Universidade de Brasília close to the Concha Acústica, in leaves of *Caesalpinia leiostachya*, on 11 May 1997, by D. V. Rezende.

Specimens examined: BRAZIL. DISTRITO FEDERAL: Brasília, Setor Noroeste, in live leaves of *Caesalpinia leiostachya*, 9 Sep 2022, *DV Rezende* (UB (Mycol. Coll.) 24482), GenBank: 28S = PX214316, *CO3* = PX215315; Campus Darcy Ribeiro, Universidade de Brasília, on live leaves of *Caesalpinia leiostachya*, 9 May 2022, *JMT Martins 01* (UB (Mycol. Coll.) 24355), GenBank: *CO3* = PX215314; Super Quadra Norte 209, in live leaves of *Caesalpinia ferrea*, 7 Oct 2012, *ESC Souza 79* (UB (Mycol. Coll.) 22287), GenBank: 28S = PX214317, *CO3* = PX215312; Super Quadra Norte 402, in live leaves of *Caesalpinia ferrea*, 8 Jun 2019, *Rita Carvalho* (UB (Mycol. Coll.) 24150), GenBank: *CO3* = PX215313.

The specimens studied here (UB (Mycol. Coll.) 24482, UB (Mycol. Coll.) 24355, UB (Mycol. Coll.) 22287, and UB (Mycol. Coll.) 24150) perfectly fit the description by Rezende and Dianese (2002), Hennen et al. (2000), and Hennen et al. (2005).

Notes: All four specimens herein considered were subjected to morphological (FIGS. 8–9) and phylogenetic analyses (FIG. 1). Our study refutes the previous assignment of this genus to the Raveneliaceae (Raveneliineae) (Hennen et al. 2000, 2005). Instead, all specimens grouped with an uncertain familial affiliation but phylogenetically more closely aligned to the Sphaerophragmiaceae (Uredinineae). Specifically, they formed a moderately supported monophyletic clade with *Neopuccinia bursa* (Martins-Junior et al. 2019) (FIG. 1), a monospecific genus also described from the Brazilian Cerrado, and a complex of *Aecidium guatteriae*, known from Minas Gerais, Brazil (Dietel 1897), and more recently from French Guiana (Beenken pers. comm.). Since no aecidia have been described for either *Esalque* or *Neopuccinia*, only teleomorph characteristics can be used for their differentiation. The most distinguishing feature between the two taxa is seen in their teliospores: Those of *E. holwayi* are consistently 3-celled, with one basal and two apical ("triphragmioid") tuberculate cells, whereas *Neopuccinia* exhibits 2-celled "puccinioid" teliospores with distinctive pocket-shaped apical outgrowths (Martins-Junior et al. 2019). Another key difference was found in the uredinia, where *Esalque* produces paraphysate sori and echinulate urediniospores showing 2–3 germ pores, whereas, in contrast, *Neopuccinia* displays aparaphysate uredinia with coarsely verrucose spores lacking visible germ pores. We consider these features to be the primary distinguishing characteristics between these two genera. Unfortunately, no urediniospores or teliospores have been identified from the *Aecidium guatteriae* complex, limiting further

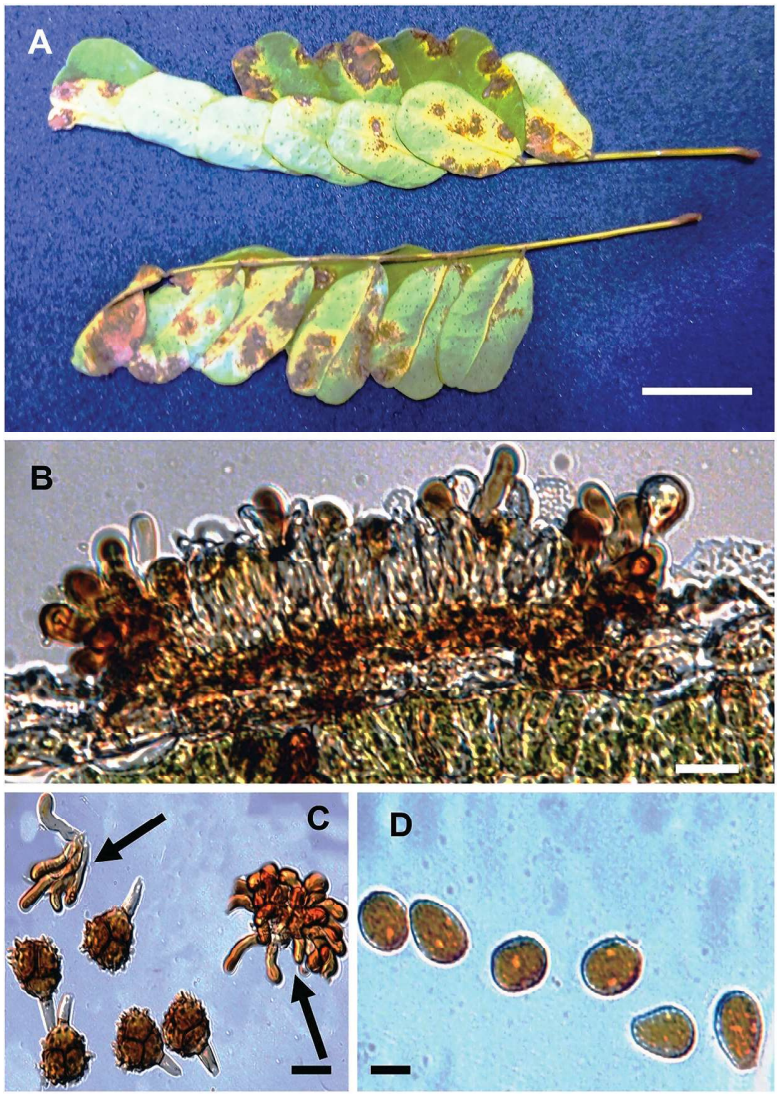

Figure 8. A–D. *Esalque holwayi* (UB (Mycol. Coll.) 24482) on leaves of *Caesalpinia leiostachya*, collected on Campus Darcy Ribeiro, Universidade de Brasília. A. Symptoms shown on host leaflets. B. Section of a highly paraphysated uredinium equipped with peripheral and hymenial paraphyses. C. Highly tuberculate teliospores, showing a basal cell supporting two terminals; curved paraphyses (arrows). D. Group of urediniospores showing mostly 2 equatorial germ pores. Bars: A = 2 cm; B = 50 µm; C = 20 µm; D = 10 µm.

interpretation of their relationships. Another genus warranting mention here is *Hennenia* (Buriticá 1995), which currently has only one known species, *H. ditelia*. However, no type specimen has been deposited for this genus, and the epithet has not been correctly latinized, rendering it a nomen invalidum (Buriticá 1995; Cummins and Hiratsuka 2003). Like *Esalque*, this species exhibits triphragmioid teliospores, although lacking ornamentation as seen in *Esalque*. The occurrence of *H. ditelia* on Annonaceae (*Annona* sp.) and its group VI (type 5) spermogonia suggests a relationship within the Sphaerophragmiaceae sensu Beenken and Wood (2015), or even with *Esalque* (Cummins and Hiratsuka 2003).

Incertae sedis.—Taxonomy and new phylogenetic allocation of the monospecific genus *Kimuramyces* within the Uredinineae, infecting *Astronium fraxinifolium* (Anacardiaceae)

Kimuramyces, originally described as *Kimuromyces*, is a monospecific genus and is represented by the type species *K. cerradensis*, infecting leaves of *Astronium fraxinifolium* (Anacardiaceae) (Dianese et al. 1995), illustrated in FIGS. 10–11, with the genus description summarized as follows.

Description: Spermogonia and aecia not observed. Uredinia mostly on the abaxial side of leaves, subpidermal, erumpent, scattered, powdery, light

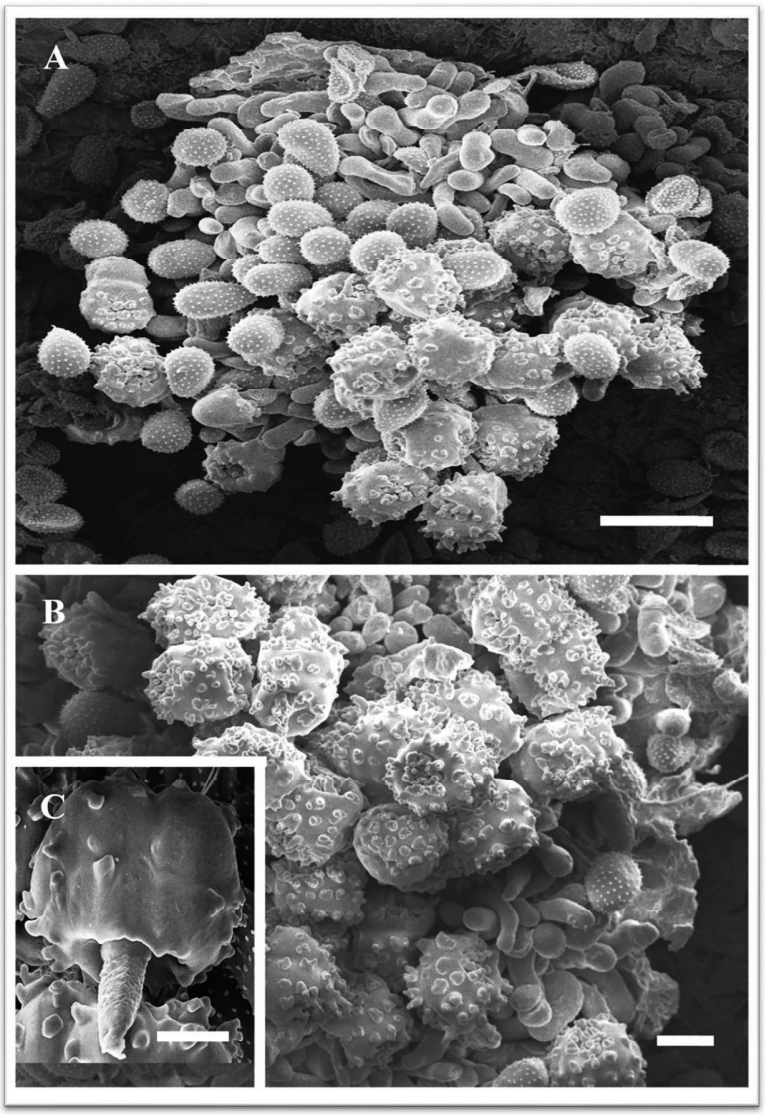

Figure 9. A–C. *Esalque holwayi*, UB (Mycol. Coll.) 24482. SEM images on leaves of *Caesalpinia leiostachya*, collected at the Darcy Ribeiro Campus of the University of Brasília. A. Mixed paraphysate sorus containing both urediniospores and teliospores. B. Paraphysate telium showing strongly tuberculated teliospores. C. Detail of the insertion and shape of the pedicel of a teliospore. Bars: A = 20 µm; B = 10 µm; C = 5 µm.

chestnut brown when paraphyses predominate, 0.1–0.2 mm diam. Paraphyses hyaline, peripheral, numerous, cylindrical to clavate, 25–48 × 8–12 µm, straight or curved with obtuse refractive apex; walls smooth, thin, colorless, light verrucose at top. Urediniospores with a reniform profile when attached to the pedicel, flattened-rhomboid, 22–27 × 18–25 µm in face view, chestnut brown to light brown, echinulate; germ pores 2 equatorial, at the side corners; paraphyses and spores originated from a compact layer of sporogenous cells. Telia similar to uredinia, hypophyllous, subpidermal, erumpent, peripherally paraphysate, flat, with compact layer of sporogenus cells. Teliospores mostly 2- rarely 3-celled, 24–35 × 15–20 µm, obovoid to subclavate, smooth but showing simple, digitate to palmate mini-projections up to 5 µm long, mostly on top and side of the cells; pedicellate, pedicels mostly deciduous; wall irregularly thickened, subhyaline to light brown; germpores not observed.

Notes: Originally, Dianese et al. (1995) assigned *Kimuramyces* to the Uropyxidaceae, a family recently identified as artificial or polyphyletic, with its former genera reclassified into the Pucciniaceae, Sphaerophragmiaceae, and Raveneliaceae s.l. (Aime and McTaggart 2021). In our study, *Kimuramyces* was placed within the

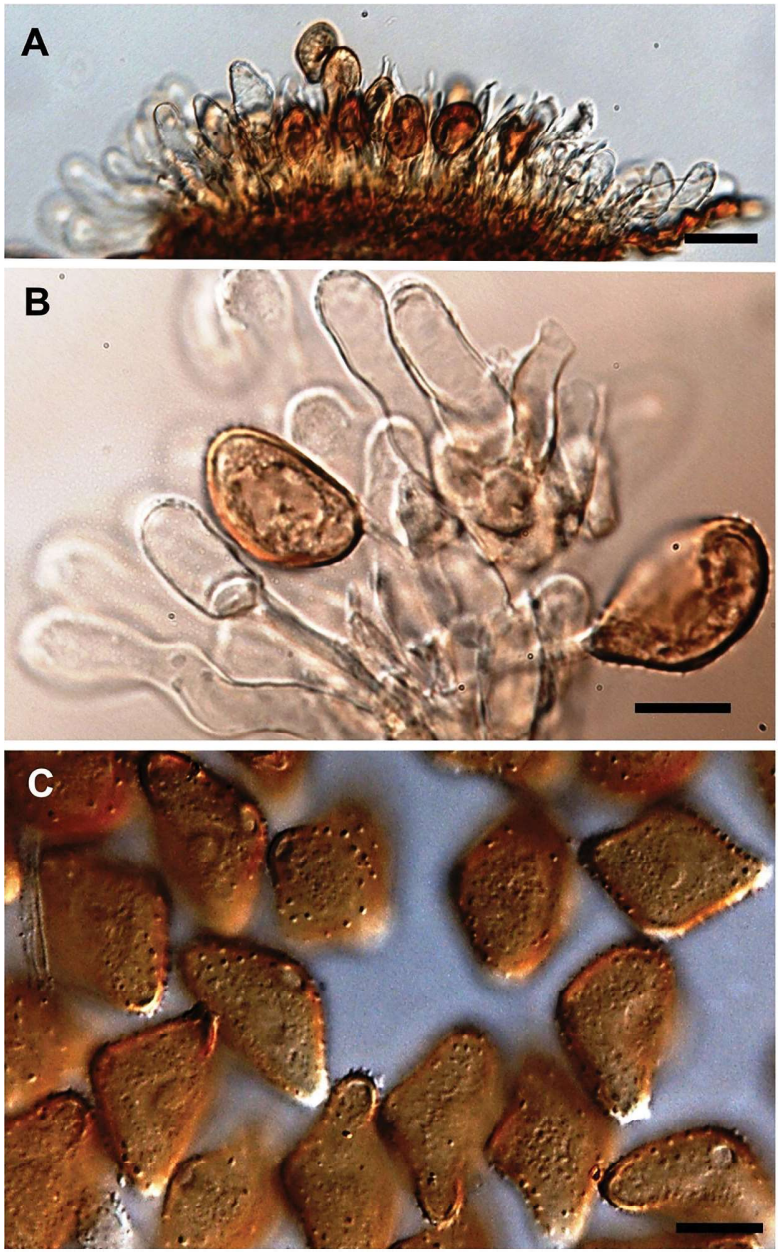

Figure 10. A–C. *Kimuramyces cerradensis* from the type species (UB Mycol. Coll. 4474). A. Cross-section of an uredinium showing pedicellate, brown urediniospores encircled by hyaline, whitish, mostly cylindrical paraphyses. B. Paraphyses and two urediniospores. C. Urediniospores. Bars: A = 20 µm; B = 10 µm; C = 10 µm.

Uredinineae but could not be assigned to any known taxon, although it shows uncertain phylogenetic proximity to the *Annona* rust *Aecidium verannonae*. It is furthermore placed between the Sphaerophragmiaceae and a lineage comprising the *Aecidium guatteriae* species complex, *Esalque* and *Neopuccinia* (FIG. 1). Other rust fungi possibly being closely related to or even being congeneric with *Kimuramyces* include *Uredo rhombica, U. mauriae*, and *U. roupalae*, as suggested by Hennen et al. (2005), based on the highly similar rhombic urediniospores and their anacardiaceous hosts, namely, *Myracrodruon urundeuva* (syn. *Astronium urundeuva*) originally described as *A. juglandifolium* and *Mauria heterophylla* (syn. *M. glauca*, Anacardiaceae). Hennen et al. (2005) listed further records of *Kimuramyces* and *U. rhombica* for various *Astronium* species from Brazil and Paraguay. Whether these rust fungi are conspecific with *K. cerradensis* or represent distinct taxa has to be evaluated in future studies. *Nyssopsora panamensis*, described in Panama on *A. graveolens* (Carvalho-Junior et al. 2014), shares its

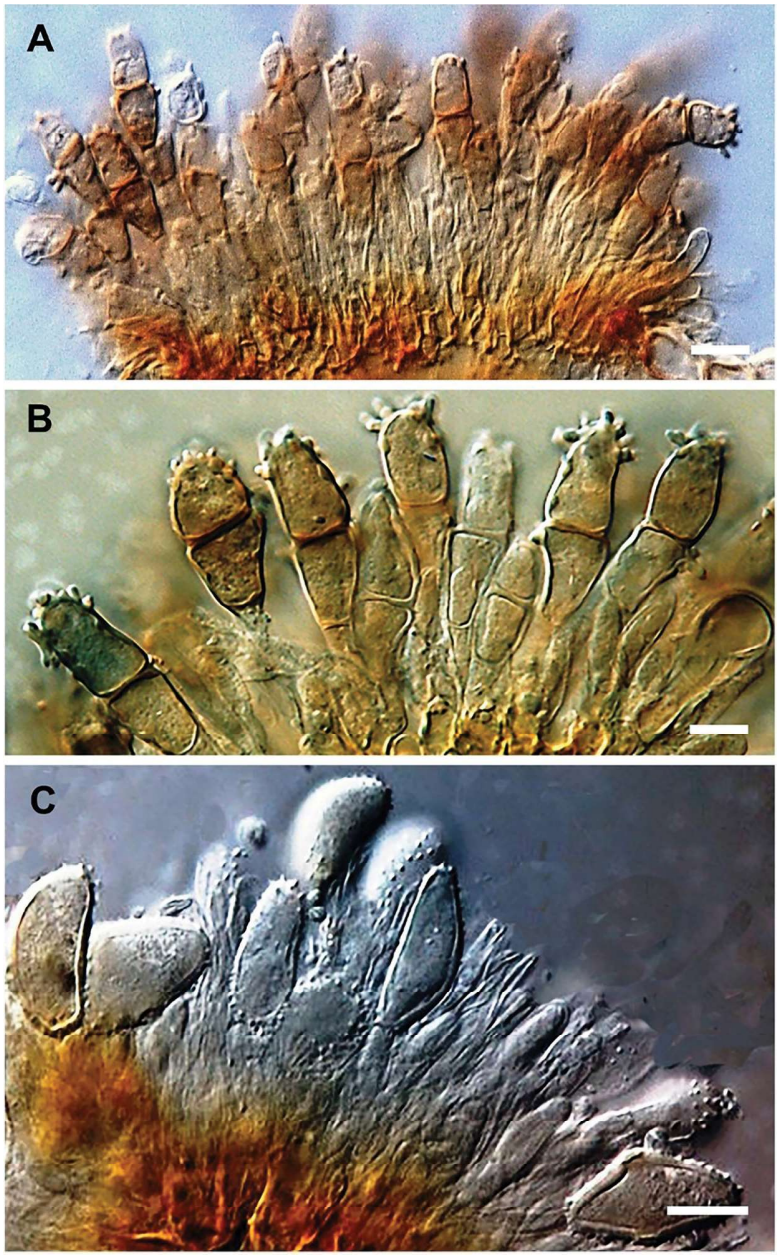

Figure 11. A–C. *Kimuramyces cerradensis* from the type species (UB Mycol. Coll. 4474). A. Telium. B. Teliospores. C. Urediniospores. Bars: A = 20 µm; B = 10 µm; C = 10 µm.

distinctive urediniospore morphology with the aforementioned taxa. Although the authors attributed the Panamanian rust to *Nyssopsora* due to its mostly 3-celled, occasionally 2-celled, heavily ornamented teliospores, it is worth noting that *K. cerradensis* sporadically exhibits 3-celled teliospores in the same arrangement (Hennen et al. 2005). We therefore consider them possibly congeneric; however, in agreement with Carvalho-Junior et al. (2014), we refrain from synonymizing these taxa for now, pending further molecular phylogenetic analysis to ensure taxonomic stability. Cummins and Hiratsuka (2003) mention another taxon, *Leptinia brasiliensis*, on *Astronium* (Anacardiaceae). However, in the original description, the host plant is listed as an unidentified species, with a presumed affiliation to the Meliaceae or Sapotaceae instead of Anacardiaceae (Juel 1897). Irrespective of the host, *K. cerradensis* differs significantly from this fungus, especially in teliospore morphology. Although the teliospores of *Leptinia* are also 2-celled, the individual cells are arranged obliquely and lack ornamentation. Juel (1897) also describes the teliospores as emerging in small groups from a single basal cell, thus appearing

in bundels of one to several stalked teliospores, a characteristic not seen in *Kimuramyces*.

Raveneliineae

Incertae sedis.—*Cerradopsora pouteriae*, sp. nov., replacing *Catenulopsora henneneae* nom. inval.

The genus *Catenulopsora* was established by Mundkur in Mundkur and Thirumalachar (1943), with the type species *C. flacourtiae* from India. Diagnostic features include uredinia bearing pedicellate, obovoid to reniform, echinulate urediniospores with intermixed slightly incurved paraphyses, showing unicellular, catenulate teliospores, which are laterally free and, although may fall loose from the sorus, do not disintegrate at maturity. Teliospore germination occurs without dormancy with metabasidia formed by apical elongation of the teliospore (Mundkur and Thirumalachar 1943). This characteristic, along with the presence of a few basally free peripheral paraphyses, distinguishes this genus from *Cerotelium*, which has basally fused paraphyses and catenulate teliospores that, contrastingly, disintegrate easily at their distal ends upon maturity (Ono et al. 1992). However, due to these features, *Catenulopsora* was later synonymized with *Kuehneola* (Phragmidiaceae) showing similar teliospores (Thirumalachar 1960). However, Buriticá and Hennen (1994) and Buriticá (1999) kept the two genera segregated, whereas Cummins and Hiratsuka (2003) followed Thirumalachar's classification. To further complicate matters, according to Index Fungorum (https://www.indexfungorum.org/Names/Names.asp) citing Arthur (1906), *Catenulopsora* has been synonymized with *Cerotelium* and hence placed in the family Phakopsoraceae. However, phylogenetic analyses by Aime and McTaggart (2021) allocated the *Catenulopsora* type species, *C. flacourtiae*, in family Crossopsoraceae, thus rejecting the synonym with *Kuehneola* (Phragmidiaceae). The taxonomic placement of further taxa within this and similar genera, such as *Phragmidiella*, primarily parasitizing species of Bignoniaceae, remains hindered by a lack of sequenced species and must therefore be considered provisional.

Of the seven species placed in *Catenulopsora* by Mundkur and Thirumalachar (1943), only three (*C. henneneae, C. petreae*, and *C. praelonga*) have not yet been recombined into other genera (Buriticá 1999). These three species were collected in South America, with *C. henneneae* being described from the Brazilian Cerrado on *Pouteria* spp. (Sapotaceae) Buriticá (1999), *C. praelonga* (syn. *Rostrupia praelonga*) from Argentina (Spegazzini 1896) on *Pavonia* sp. (Malvaceae), and *C. petreae* from Colombia on Verbenaceae (Pardo-Cardona 2003).

The specimen described by Buriticá (1999) as *C. henneneae* is housed at the Arthur Fungarium (Purdue University) with the following registration record: "*Catenulopsora henneneae* Buriticá, Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 23: 429. 1999. Host: *Pouteria* sp., Sapotaceae, N. of São Gotardo, Minas Gerais, Brazil, 16.VI.1988, J. F. Hennen & Y. Ono-88-243." However, on the published description, a holotype was not designated (Buriticá 1999), invalidating the name as defined by Art. 40.1 (Melbourne Code), according to Index Fungorum. Thus, we allocated the fungus in *Cerradopsora pouteriae*, sp. nov., based on the description by Buriticá (1999) complemented by our detailed morphological and phylogenetic analyses, as follows.

Cerradopsora pouteriae Ebinghaus & Dianese, sp. nov. FIGS. 12–15

Index Fungorum IF902977

Synonym: Catenulopsora henneneae Buriticá, Acad Col Cien Exactas Fís y Nat 23:271–305. 1999. Nom. inval., Art. 40.1 (Melbourne).

Description and illustrations: Buriticá (1999), Martins-Junior et al. (2022), Hennen et al. (2005).

Diagnosis: The new species differs from the other two *Cerradopsora* species by its catenate teliospores contrasting with the sessile teliospores of *Cr. hennenii*, and spores present in phakopsoroid telia of *Cr. rossmaniae*.

Description: Spermogonia and aecidia not observed. Uredinia 80–150 µm diam, hypophyllous, subepidermal, erumpent, powdery, light brown to brown. Paraphyses 15–34 µm × 5–10 µm, peripheral, numerous, curved, smooth, lightly pigmented, thick walls, ca. 3 µm thick, flexuous when hymenial. Urediniospores 20–33 µm × 19–28 µm, obovoid to reniform, brown, thick wall up to 3 µm thick, echinulate, uniform morphologically and in distribution on the spore surface, germ pores not observed. Teliospores basipetally catenulate, with rectangular front view, individually measuring 10–13 µm wide × 8–15 µm high, forming chains with up to 5–7 teliospores, top spores germinating apically to originate a cylindrical metabasidium, spores in lower positions germinate through lateral pore at the distal wall; chains reaching up to 50 µm long.

Specimens examined: BRAZIL. DISTRITO FEDERAL: Brasília, nearby the Centro Olímpico, Universidade de Brasília, −15.7637S, −47.8606W, on live leaves of *Pouteria ramiflora*, 21 Jun 2012, *Mariza Sanchez 4663* (**holotype** UB (Mycol. Coll.) 22260), GenBank: 28S = PX214313, *CO3* = PX215306; –

PX215306. CO3ll.) 22260, 60, 2012, UB (*Pouteria ramiflora*, 25 Jun 2012, *ESC Souza* (UB (Mycol. Coll.) 22267); −15.7665S, −47.8565W, on live leaves of *Pouteria ramiflora*, 25 Jun 2023, *JC Dianese* (UB (Mycol. Coll.) 24051), GenBank: 18S = PX214327, *CO3* = PX215305; SÃO PAULO: Luiz Antônio, Estação Experimental, −21.6011 −47.7558, on live leaves of *Pouteria* sp., 30 Jan 2017, *A. Martins-Junior*, 22 Jun 2017, *A.A. Carvalho-Junior* (**isotype** RB 757351).

Notes: Morphological characteristics of the uredinial and telial stages of collection by J. F. Hennen and Y. Ono (88-243) at Arthur Fungarium (FIG. 12) are the same as those observed in Brazilian collections from Brasília and São Paulo (FIGS. 13–15). The illustration from Arthur Fungarium (FIG. 12) shows typical catenulate teliospores, as well as uredinia and urediniospores with the same morphological features as those in UB (Mycol. Coll.) 22260 and RB757351, collected at the Darcy Ribeiro Campus of the Universidade de Brasília and Estação Experimental, Luiz Antônio, São Paulo, respectively. It must be noted, however, that the paraphysate telia described by Buriticá (1999) could not be documented in the Brazilian collections, although loose teliospores were found in routinely prepared slides. Specimens collected in Brasília were sequenced for ITS2, 28S and 18S rDNA, and *CO3* and included in the phylogenetic reconstruction (FIG. 2). In this analysis, the rust fungus on *Pouteria* was placed within the well-supported monophyletic genus *Cerradopsora* (*Cr.*), together with the type species *Cr. rossmaniae* and *Cr. hennenii* (Raveneliineae), phylogenetically distinct from the *Catenulopsora* type species *C. flacourtiae* (Uredinineae). Molecular and morphological evidence therefore clearly supports the recognition of the *Pouteria* rust as a distinct *Cerradopsora* species and justifies its reclassification accordingly.

Noteworthily, all three species currently placed in this genus were originally assigned to three different genera in three families, highlighting the challenges of relying on limited morphological features for the systematic classification of rust fungi. As discussed in Ebinghaus et al. (2023b), *Cr. rossmaniae* and *Cr. hennenii* were originally placed in the genera *Phakopsora* and *Aplopsora*, respectively, based on their teliospore

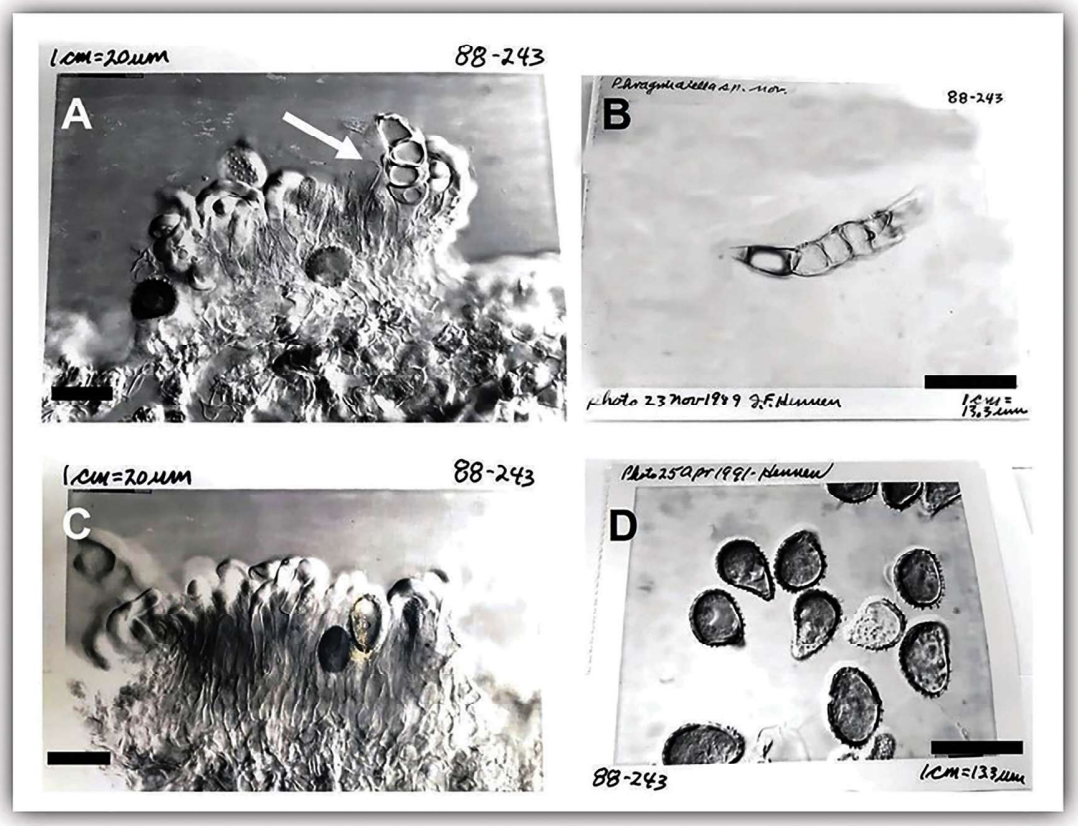

Figure 12. A–D. Images of the holotype of *Cerradopsora pouteriae*, sp. nov., taken by Prof. Joe F. Hennen, deposited in the Arthur Fungarium (collection number 88-243). A. Telium with catenulate teliospores (arrow). B. Catenulated teliospores. C. Uredinium. D. Reniform urediniospores. Bars: A–D = 20 µm.

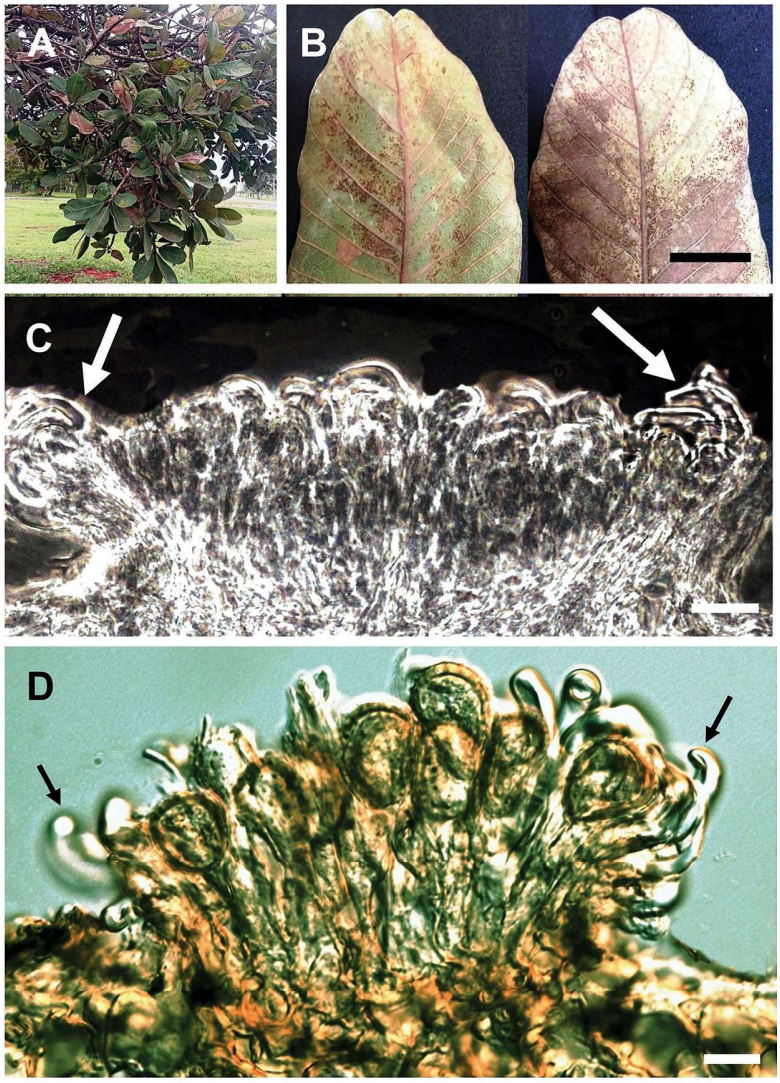

Figure 13. A–D. *Cerradopsora pouteriae* sp. nov. (UB (Mycol. Coll.) 22260), collected at the Campus Darcy Ribeiro, Universidade de Brasília, on leaves of *Pouteria* sp. A. Field symptoms. B. Leaves with two stages of infection on the abaxial surface, on the left partially infected leaf and on the right infection leading to leaf blight. C. Section of a highly paraphysate uredinium with curved peripheral paraphyses (arrows). D. Uredinium showing flexuous hymenial and curved peripheral paraphyses. Bars: B = 3 cm; C = 10 µm; D = 10 µm.

characteristics and the numerous peripherally located and basally fused paraphyses. The multiseriate, single-celled, sessile teliospores formed in crustose sori of *Cr. rossmaniae* resemble telial characteristics of *Phakopsora*. In contrast, the well-documented single-seriate, sessile, hyaline teliospores of *Cr. hennenii* show closer resemblance to those being characteristic of *Aplopsora* species (Ebinghaus et al. 2023b). The anamorphic and teleomorphic characteristics of the fungus discussed here, on the other hand, prompted Buriticá (1999) to place it in the genus *Catenulopsora* in the first place. This again highlights the taxonomic challenges, caused by unrecognized homoplasious traits.

The two remaining species of *Catenulopsora* described in South America, *C. praelonga* and *C. petreae* (Buriticá 1999), lack characteristics that would justify their inclusion in *Cerradopsora* without molecular phylogenetic support. *Catenulopsora praelonga*, parasitizing Malvaceae, possesses emerging catenulate teliospores such as *C. flacourtiae*, but with visible germ pores, unlike the type species, which forms basidia through apical spore elongation (Ono 2015). Furthermore, both the catenulate teliospores and the absence of reniform urediniospores, which are described in *C. praelonga* as "ellipsoid to broadly obovoid or globose" (Hennen et al. 2005), together with a lack of molecular data, argue against its inclusion in *Cerradopsora*.

Besides the morphological traits commonly shared within the genus, all known species of *Cerradopsora*

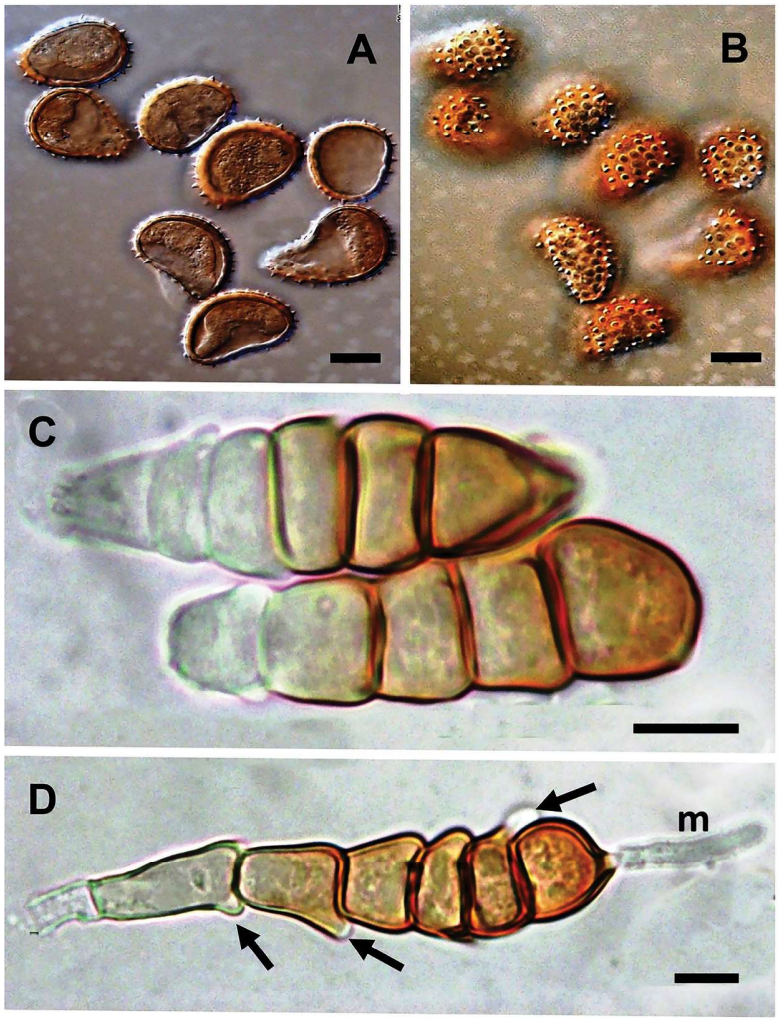

Figure 14. A–D. *Cerradopsora pouteriae*, sp. nov., RB 757351, collected at Estação Experimental, Luiz Antônio, São Paulo, on leaves of *Pouteria* sp. A–B. Urediniospores in medial and superficial focus, respectively. C–D. Chains of teliospores, with D showing metabasidium (m) at top cell and lateral germination pores (arrows). Bars: A–D = 10 µm.

have so far been documented exclusively from the Brazilian Cerrado, suggesting a geographic restriction of their distribution. Even though the hosts of the currently known *Cerradopsora* species are primarily distributed in the Neotropics, few species of *Campomanesia* and *Pouteria* also occur in subtropical and tropical regions of America, Asia, and Africa. Future studies will therefore be needed to determine the worldwide distribution range of *Cerradopsora*.

Incertae sedis.—Phylogenetic reallocation of *Mimema venturae* within the Raveneliineae

Mimema, with type species *Mimema holwayi*, was established by Jackson (1931b) for a rust fungus collected in Bolivia on a *Dalbergia* species (Fabaceae), then misidentified as *Cassia versicolor* (Hennen et al. 2005). Characteristics of *Mimema* include uredinia showing numerous, inwardly curved and basally united peripheral paraphyses (*Calidion*-type) and long-pedicellate, elongated, and transversely multiseptate *Hamaspora*-like teliospores. Jackson (1931a), considering the characteristically multiseptate teliospores, proposed an alternative name, *Hamaspora holwayi*, for this fungus. These teleomorph features are shared completely with *Hamaspora* by *Mimema*, and via intermediate forms with genera such as *Sorataea* and finally *Porotenus* (Viégas 1960; Hennen et al. 2005). Cummins and Hiratsuka (1983), based on Jackson's mere speculation that the spermogonia of *Mimema* probably being subcuticular, synonymized this fungus with *Sorataea* (type species: *S. amiciae*), a genus described on *Amicia lobbiana* (Fabaceae) and named after the type locality, the town of Sorata in Bolivia (Sydow 1930). Eboh and

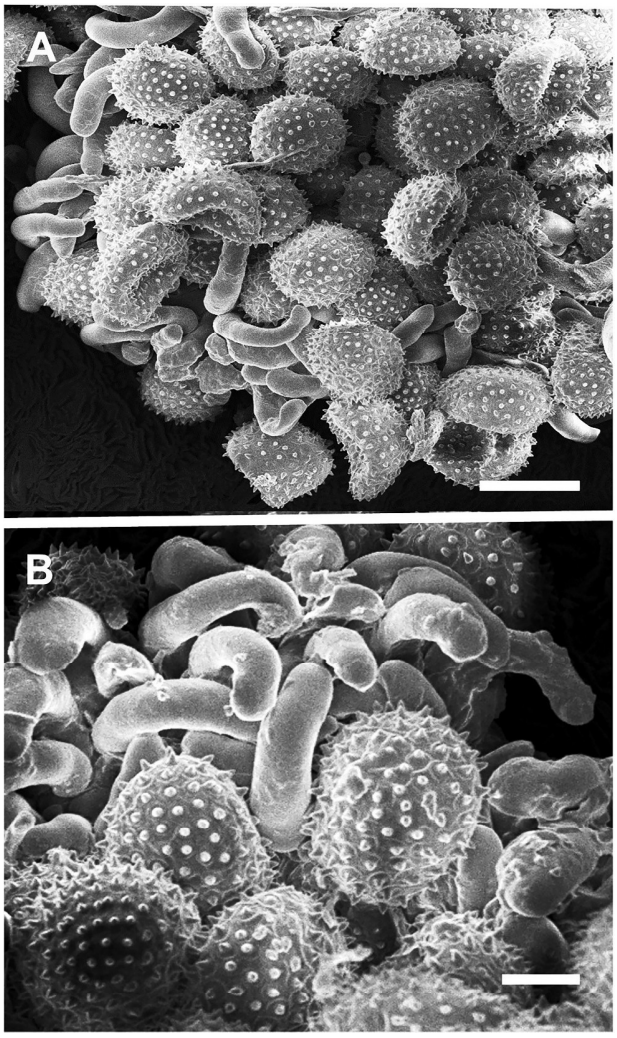

Figure 15. A–B. *Cerradopsora pouteriae*, sp. nov., UB (Mycol. Coll.) 22260, observed in SEM. A. Paraphysate urediniu. B. Details of paraphyses and urediniospores. Bars: A = 20 µm; B = 10 µm.

Cummins (1980) accepted six *Sorataea* species, all on fabaceaous hosts (*S. amiciae, S. arayatensis, S. bafiae, S. nephroidea, S. ostryoderridis*, and *S. periodica*), in addition to *S. acanthophora* recombined from *Puccinia* by Ono (2015), all accommodated in the polyphyletic family Uropyxidaceae.

However, three species from other host families were transferred into *Leucotelium* (Uropyxidaceae) according to Index Fungorum (https://www.indexfungorum.org/Names/Names.asp). Like *Mimema, Sorataea* is characterized by *Calidion*-type uredinia but produces thin-walled, transversely 1- or 2-septate and thus puccinioid teliospores, as illustrated by Prof. G. B. Cummins in 1985 (FIG. 16), instead of multiseptate teliospores. Moreover, these genera differ in their modes of basidial germination: in *M. venturae*, germination occurs directly through apical and lateral germ pores on individual cells of the multiseptate teliospores, whereas in *S. amicina* germination occurs via apical elongation. With this, *Sorataea* shares substantial similarity with *Porotenus* in teliospore characteristics. However, *Porotenus* can be differentiated from *Sorataea* by producing uredinioid aecia, aparaphysate uredinia, and by its distinct host association to *Adenocalymma* (= *Memora*) species (Bignoniaceae) instead of the Fabaceae (FIG. 17). Distinguishing features between *Sorataea* and *Puccinia*, on the other hand, include the type 7 spermogonia as well as its uredinial structure. *Allopuccinia diluta* (≡ *S. amiciae*), established by Jackson in 1931, corresponds to *S. amiciae* and was later synonymized by Eboh and Cummins (1980), despite Sydow (1930) noting the absence of paraphyses in the telia and Jackson (1931b) describing them as paraphysate.

Mimema was reinstated only after the discovery of another fungus with *Calidion*-type uredinia and long-

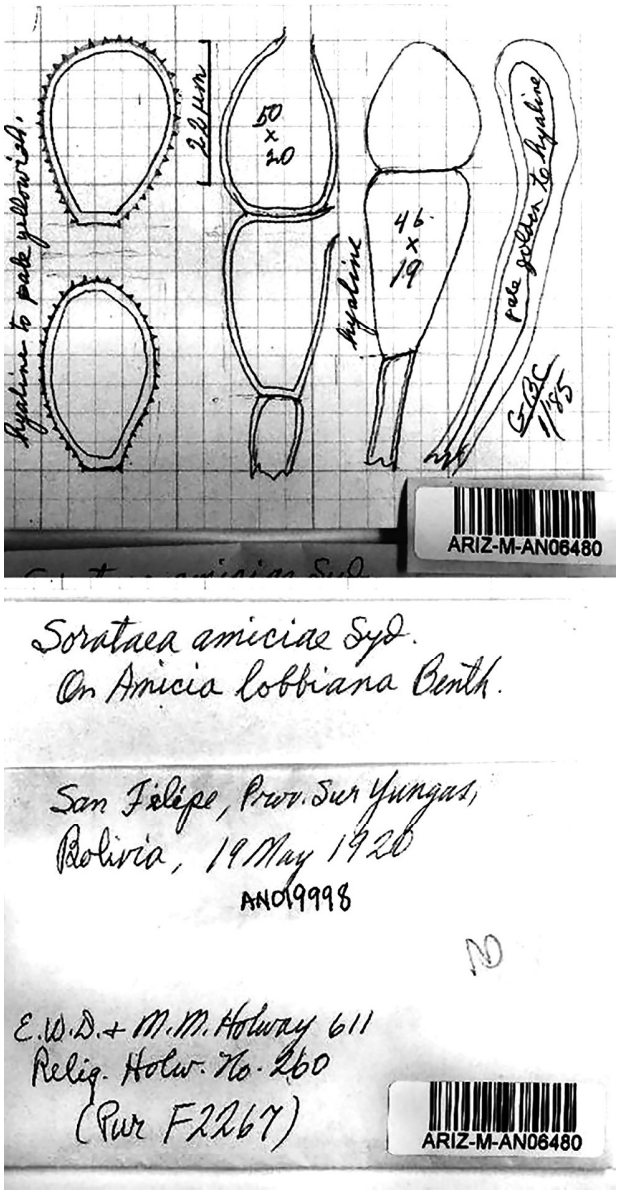

Figure 16. *Sorataea amiciae* (PUR F2267) on *Amicia lobbiana*: drawing by Prof. G. B. Cummins in 1985, illustrating urediniospores, teliospores, and paraphysis; obtained online via the Mycology Collections Portal MyCoPortal (http://www.mycoportal.org/portal/imagelib/search.php) on 28 December 2024.

pedicellate, elongated, transversely multiseptate teliospores (Dianese et al. 1994). This taxon, *M. venturae*, parasitizing *Dalbergia miscolobium* (Fabaceae), produces teliospores with sticky pedicels, allowing for the attachment to one another and to newly developing teliospores, leading to the formation of fragile spore "columnar threads" of up to 1.5 mm in length, as illustrated by Dianese et al. (1994), shown in FIGS. 18–19.

The elongated, transversely septate teliospores of *Mimema* are practically identical to those of the tropical genus *Hamaspora*, parasitizing *Rubus* (Rosaceae) species. As spermogonia are unknown in *Mimema* and cannot be compared with the type 8 and 10 spermogonia of *Hamaspora*, Jackson's rationale for designating *Mimema* as a new genus in the first place drew solely on the principle stated by Dietel (1928), i.e., that rust fungi appear to evolve within closely related host groups, leading to parallel development of similar forms without direct phylogenetic connection.

To determine the phylogenetic placement of *Mimema* and to confirm or refute its phylogenetic distinction from genera such as *Sorataea*, *Hamaspora*, or

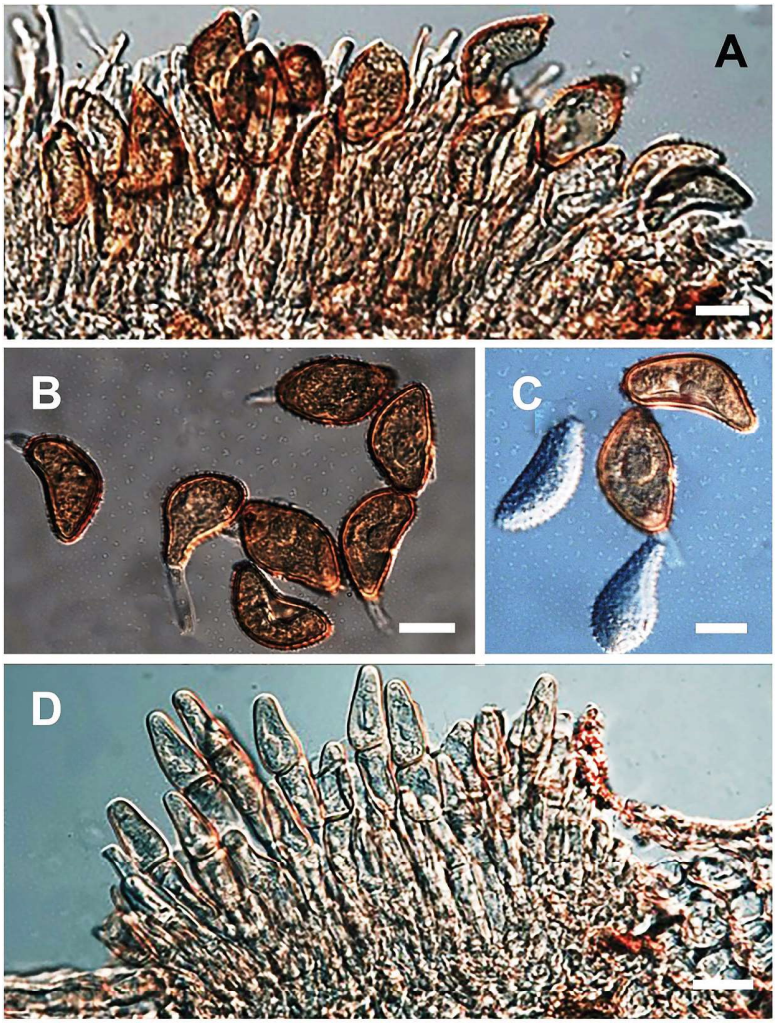

Figure 17. A–D. *Porotenus concavus* on *Adenocalymma penduculatum* (≡ *Memora pedunculata*), UB (Mycol. Coll.). A. Aparaphysate uredinium showing straight pedicels left after urediniospore release. B–C. Urediniospores. D. Aparaphysate telium with 2-celled, pedicellate teliospores. Bars: A–C = 10 µm; D = 20 µm.

even *Porotenus*, we sequenced *Mimema venturae* and Herbarium UB collections of the type species of *Porotenus* (*P. concavus*) used in our molecular phylogenetic analyses.

Based on our 28S and *CO3* sequence data, *Mimema* was classified within the Raveneliineae (FIG. 2) and appears clearly distinct from species of *Sorataea*, i.e., *S.* cf. *baphiae* (found on *Baphia* species in Bolivia) and *S. arayatensis* (on *Derris elliptica*, Philippines), recently shown to be not directly related to each other (Aime and McTaggart 2021), whereas *Hamaspora* has earlier been proven to belong to the Phragmidiaceae (McTaggart et al. 2016a). Our data therefore are reinforcing a morphology- and host-based distinction among these three genera. Unfortunately, more recent collections of the type species, *S. amiciae*, were unavailable to improve the support for our analyses and conclusions. Due to its relative geographic proximity to *Mimema* and the close relationship of its host plants with both *Dalbergia* and *Amicia* residing in the tribe Dalbergieae (Fabaceae), *S. amiciae* remains central to conclusively delineating the boundaries between *Mimema* and *Sorataea*. Nevertheless, we consider the striking differences in teliospore morphology, including metabasidial germination modes, sufficient to justify the separation of both genera.

Collections of *Mimema* are known mostly through the 24 specimens deposited in Herbarium UB, the 1931 type specimen of *M. holwayi*, and another specimen labeled as *Mimema* sp. from Sierra Leone (Deighton 1936). Additionally, Hennen et al. (2005) identified *Uredo dalbergiae* (Goiás, Brazil) and

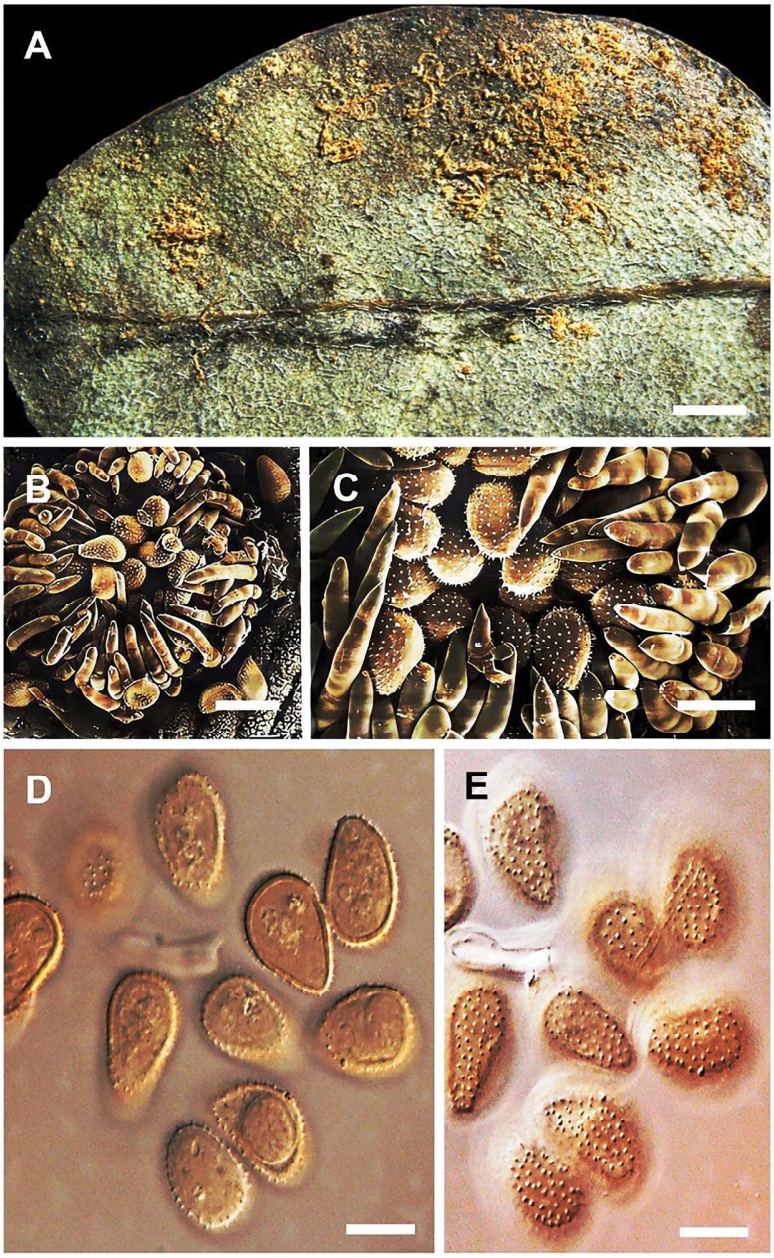

Figure 18. A–E. *Mimema venturae* holotype on *Dalbergia miscolobium*, UB (Mycol. Coll.) 1315. A. Foliole showing abaxial sporulation of the fungus. B–C. SEM images of paraphysate urediniu with echinulate urediniospores. D–E. Urediniospores with median and superficial focus on a light microscope, respectively. Bars: A = 0.2 cm; B–C = 20 µm; D–E = 20 µm.

U. mararyensis (Rio Juruá, Amazonas), both on *Dalbergia* sp., along with *U. nidulans* (Guani-Tipuani, Bolivia) on *Dalbergia foliosa* as possible congenerics with *Mimema* or *Sorataea* based on uredinial morphology. The exact generic affiliation and whether they represent a single or multiple species remain uncertain. Given the estimated 40 *Dalbergia* species in Brazil alone (https://floradobrasil.jbrj.gov.br), we assume that there are further, still unknown species of *Mimema*.

As noted above, *Porotenus* is a genus with a teliospore morphology similar to *Sorataea*, but parasitizing species of *Adenocalymma* (Bignoniaceae) and lacking the peripheral paraphyses characteristic of both *Sorataea* and *Mimema*. In this study, we sequenced a specimen identified as the type species *P. concavus* (FIG. 2), confirming its sister relationship to *Prospodium* as proposed by Aime and McTaggart (2021) in particular, away from *Mimema*, and moreover supporting the artificial nature of the Uropyxidaceae in general.

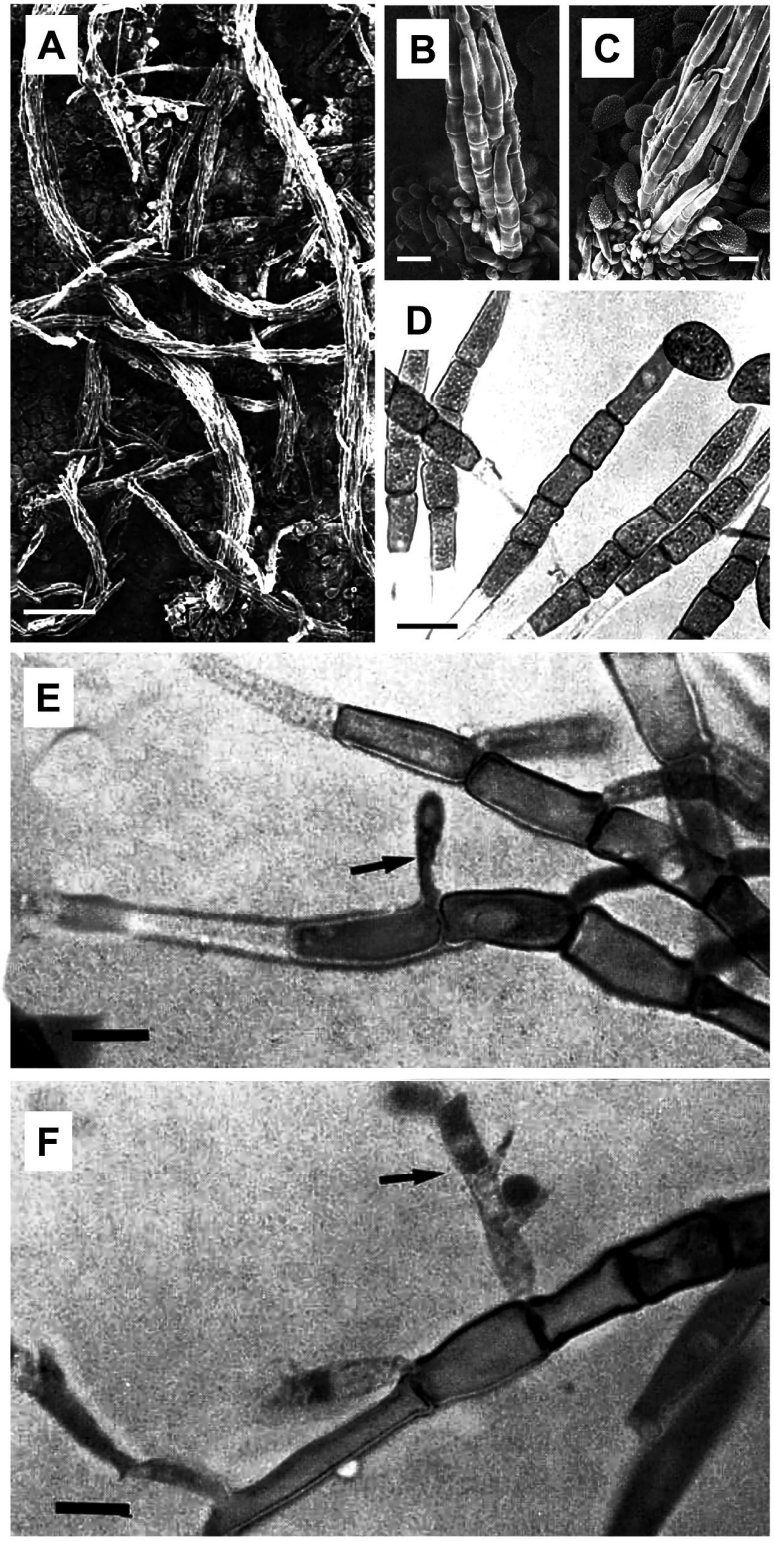

Figure 19. A–F. *Mimema venturae* holotype on *Dalbergia miscolobium*, UB (Mycol. Coll.) 1315 by Dianese et al. (1994). A. Fragile teliospores columns seen in SEM. B–C. SEM images of columnar paraphysate multiseptate teliospores. D. Light microscope image of multiseptate teliospores. E. Arrow showing the positions of the germ pores under the septum at the distal wall of the teliospore cell. F. Germinated teliospore with mature metabasidium (arrow). Bars: A = 100 µm; B–C = 10 µm; D = 20 µm; E–F = 10 µm.

DISCUSSION

The taxonomic advances, including reclassifications and newly described species as presented in this study, are supported by a polyphasic approach using morphological traits, molecular data, and ecological information, refining our understanding of the phylogenetic relationships among rust fungi of the Cerrado biome. Specifically, the findings highlight somewhat unexpected phylogenetic placements within or in proximity to the family Sphaerophragmiaceae in the suborder Uredinineae (FIG. 1). This includes, e.g., *Dietelomyces copaiferae* and *Esalque holwayi*, both formerly assigned to the Raveneliaceae, and *Kimuramyces cerradensis*, formerly assigned to the Uropyxidaceae, and *Dietelia duguetiae*, previously in Pucciniosiraceae (https://www.indexfungorum.org/Names/Names.asp). Conversely, *Mimema venturae* was initially assigned to the Uropyxidaceae but is now confirmed as a distinct lineage within the Raveneliineae, whereas *Catenulopsora hennenae* is reclassified in *Cerradopsora* as *Cer. pouteriae*, within the same suborder of Pucciniales, and the *Adenocalymma* rusts *Porotenus concavus* and *P. bisporus* were revealed as a monophyletic sister genus to *Prospodium*, within Raveneliaceae, not in Uropyxidaceae as stated in Index Fungorum (http://www.indexfungorum.org/Names.asp) (FIG. 2). These reclassifications underscore the value of integrative approaches in rust fungi taxonomy for achieving more accurate classifications and highlight limitations of traditional, morphology-based approaches. To a large extent, generic classifications of rust fungi traditionally relied on the structure of anamorph sori (e.g., *Aecidium, Caeoma*, and *Uredo, Calidion*, or *Malupa*) as well as on teliospore traits such as the general shape, number of cells, and plane of septation in combination with characteristics such as ornamentation, number and position of germ pores, modes of germination, etc. (e.g., Ono and Hennen 1983 and references therein; Cummins and Hiratsuka 1983, 2003; Hennen et al. 2005). However, morphological characters in rust fungi often reflect homoplasy, as shown herein, rather than true phylogenetic relationships, which also has been discussed and shown in various studies (Savile 1971; Petersen 1974, 1978; Aime 2006; Aime and McTaggart 2021). The significance of those traits may fall particularly on subjective interpretations, which leads to taxonomic instability and is reflected in complex taxonomic histories (e.g., Dietel 1928; Ono and Hennen 1983), as herein exemplified and shown by Aime and McTaggart (2021) for a broad range of taxa in various families or by Scholler et al. (2022) in the Melampsorineae genus *Pucciniastrum*. Spermogonial traits (Hiratsuka and Cummins 1963; Cummins and Hiratsuka 2003), on the other hand, have been proven to often provide good indication on higher rank classifications, but which are often absent (Cummins and Hiratsuka 2003; Aime and McTaggart 2021). In the present study, we found various homoplasious traits being particularly relevant in some Cerrado taxa. The recently established genus *Cerradopsora*, for instance, comprises species that were initially classified within *Phakopsora, Aplopsora*, and *Catenulopsora*, respectively, primarily based on teleomorph morphologies. It has since become evident that neither the multicellular, transversely septate, long-pedicellate teliospores of *Cr. pouteriae* (FIG. 14) nor the single-celled, hyaline teliospores of *Cr. rossmaniae* and *Cr. hennenii*, whether in multiple rows as in the former or in single rows as in the latter (Ebinghaus et al. 2023b), serve adequately as generic criteria. However, the *Malupa*-type uredinia and the distinctive reniform urediniospores, common among the three *Cerradopsora* species, appear to link these species at the generic level. The homoplasious nature of vertically septate, 2-celled teliospores of the diorchidioid type has been confirmed in more recent studies on genera such as *Sphenospora, Sphenorchidium*, and *Diorchidium* (Beenken and Berndt 2010; Beenken and Wood 2015; Wood and Aime 2024) and is further emphasized here for *Dietelomyces copaiferae*, now being segregated from *Diorchidium*.

This study lines up with previous findings where molecular phylogenetic analyses identified homoplasious traits that recently led to numerous systematic rearrangements on generic and familial ranks in rust fungi (Aime 2006; Aime and McTaggart 2021; Scholler et al. 2022). It therefore highlights the need for careful evaluation and context-specific interpretation of individual morphological traits, always in conjunction with phylogenetic analyses, to avoid misclassification and achieve accurate taxonomic decisions.

Biodiversity assessment and implications for conservation priorities.—Approximately 268 species of rust fungi are currently known from the Cerrado biome (Dianese et al. 1997; Souza 2016). The extent to which the Cerrado is still underexplored in terms of its rust diversity becomes particularly evident when compared with well-studied regions. For example, Germany hosts 568 rust fungi species with a vascular plant count of 3062 species (Thiel et al. 2023; BfN 2024), thus constituting an approximate ratio of rusts per plant of 1:5.4, which is slightly lower than an estimated ratio of 1:6 for fungi per vascular plants in Great Britain proposed by

Hawksworth (1991) or in Switzerland, Austria (each 1:6), and Japan (1:7) as suggested by Berndt (2012). Applying the same ratio of 1:6 to the Cerrado's rust funga for its approximately 12 356 reported vascular plant species, an estimated 2059 species of rust fungi can be expected. This suggests that only about 13% of the potential rust fungal diversity in the Cerrado has been documented so far (see also Salazar-Yepes and Piepenbring 2022). Observed ratios of 1:3 to 1:4 in the rust funga of the Mogi-Mirim nature reserve suggest that our estimates are likely even more conservative (Hennen and McCain 1993, in: Berndt 2012). Providing additional support, Carvalho-Júnior et al. (2008) recorded 157 rust fungi species across 36 genera in a study covering just 0.1% of the Cerrado area.

Considering these indications, it is likely that some of the genera discussed here, particularly those that are monospecific, represent groups that are more species-rich than current knowledge suggests. For instance, *Pouteria*, the host genus of *Cr. pouteriae*, comprises 155 reported species in Brazil (www.worldfloraonline.org). Applying again the same ratio of rust fungus to host species of 1:5.4, an additional 28 species of rust fungi could be expected and therefore the number of hidden rust species on *Pouteria* might be significant. Additionally, genera such as *Mimema* and *Kimuramyces* are also potentially highly undersampled. *Dalbergia*, the host genus of *Mimema*, is represented by about 43 species in Brazil alone (www.worldfloraonline.org). To our knowledge, three other rust taxa (*Uredo* spp.) from other *Dalbergia* species are known from the Neotropics and may represent potential congenerics of *Mimema* due to morphological similarities (Hennen et al. 2005). *Astronium*, the host genus of *K. cerradensis*, comprises approximately 11 species in Brazil and the broader Neotropics (www.floradobrasil.jbrj.gov.br, www.worldfloraonline.org). As previously mentioned, this host genus is also associated with another anamorphic taxon (*Uredo* sp.) as well as with *Nyssopsora panamensis*. These fungi display characteristics indicative of a close phylogenetic relationship with *K. cerradensis*. These examples show that substantial effort is required to comprehensively document the rust fungal diversity of the Cerrado and beyond in regions that face similar conservation challenges due to the ongoing loss of natural biodiversity (Salazar-Yepes and Piepenbring 2022; Mardones et al. 2024).

Although the revision and accurate taxonomic reassignment of known rust fungi based on an improved understanding of natural relationships cannot fully substitute expansions of collection efforts in the Cerrado, it still holds relevance at various levels. Firstly, efforts in nature conservation typically prioritize regions based on biodiversity richness and uniqueness (Simijaca et al. 2022). By providing a clearer understanding not only of sole species counts but also of the phylogenetic diversity of Cerrado rust fungi, reexamining their taxonomy by phylogenetic means contributes to more precise biodiversity evaluations and helps guiding conservation strategies aimed at preserving unique ecosystems (Vane-Wright et al. 1991; Vellend et al. 2011). Our study furthermore aligns with findings from recent taxonomic efforts across diverse fungal lineages, which have consistently revealed hidden phylogenetic diversity across multiple taxonomic ranks, ranging from species to classes and even subdivisions (e.g., Hyde et al. 2024b). Examples include basidiomycetous yeasts (Li et al. 2020), Ustilaginomycotina (Aime 2006; McTaggart et al. 2020), or members of the Hymenochaetales (Wu et al. 2022), all of which underscore the critical global importance of refining fungal classification for advancing biodiversity research (Niskanen et al. 2023). Secondly, the role of rust fungi in plant ecosystems is significant, as they influence host species fitness, growth, and survival (Dobson and Crawley 1994; Pasailiuk et al. 2022). The correct identification and classification of rust fungi therefore provide the basis for understanding these complex host-pathogen interactions and contribute to an improved understanding of ecosystem functioning, which is increasingly relevant in environmental stress scenarios such as climate change and agricultural exploitation in the Cerrado and elsewhere (Anderson et al. 2004; Nnadi and Carter 2021).

Our taxonomic investigations on the rarely studied rust fungi of the Cerrado demonstrate the need for careful evaluation and context-specific interpretation of individual morphological traits to avoid misclassification and achieve more accurate taxonomic decisions. Furthermore, we emphasize the deficient knowledge currently available on the immense diversity of rust fungi in this unique and highly threatened biome. Expanding our understanding of the Cerrado rust funga is essential to fill key knowledge gaps and integrating fungi into broader biodiversity assessments. Recognizing this, we advocate for increased efforts in fungal conservation, supporting initiatives such as the IUCN SSC Fungal Conservation Committee (FunCC) (www.iucn.org) and the recently introduced "Fungal Conservation Pledge," first raised at COP16 in 2024 in Cali, Colombia (www.cbd.int). This pledge advocates for recognizing fungi as vital components of ecosystems, shifting the traditional focus beyond plants and animals to foster more inclusive conservation strategies (Simijaca etal. 2020; Niskanen et al. 2023). Together,

these developments illustrate how advances in rust fungal taxonomy not only contribute to an enhanced understanding of fungal evolution and diversity but also provide practical value for ecosystem management and informed conservation planning. A comprehensive assessment of the Cerrado rust fungi is therefore not only an academic endeavor but a crucial step toward preserving fungal diversity in one of the most endangered ecosystems worldwide.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

The NEXUS-formatted sequence alignments and the obtained tree files in NEWICK format generated for this study are provided in two supplementary files: "SUPPLEMENTARY FILE 1. Data sets Uredinineae" containing the data for the Uredinineae data set and "SUPPLEMENTARY FILE 2. Data sets Raveneliineae" containing the data for the Raveneliineae data set. These files are publicly available through the Taylor & Francis figshare platform. CNPq: https://www.gov.br/cnpq/pt-br

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ORCID

José C. Dianese http://orcid.org/0000-0002-9100-0545

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