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Introducing two new genera, *Paivomyces gen. nov.* and *Pseudoselenophoma gen. nov.*, in *Saccotheciaceae* (*Dothideales*)

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Abstract: Members of the family *Saccotheciaceae* are found in various environments and have different lifestyles. While exploring *Mimosa tenuiflora*-associated endophytic fungi in the Caatinga dry forest in Brazil, the isolates were initially identified as aureobasidium-like fungi. Based on morphological features and phylogenetic analyses using ITS, LSU, *tub2*, *rpb2*, and *tef1* gene sequences, these endophytes were placed within a distinct clade in *Saccotheciaceae*, differing from the genera currently accepted in the family. Here, we describe a new genus, *Paivomyces gen. nov.* (including *Paivomyces mimosae sp. nov.*). Additionally, during our phylogenetic analyses, we observed that *Selenophoma australiensis*, described from leaves of *Eucalyptus mineata* in Australia, could be treated as a unique lineage among the genera in the family *Saccotheciaceae*. Herein, we introduce *Pseudoselenophoma gen. nov.* (including *Pseudoselenophoma australiensis comb. nov.*) to accommodate the species. Our findings improve our understanding of the fungal diversity in the Caatinga dry forest in Brazil and clarify the phylogenetic lineages of *Saccotheciaceae*.

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INTRODUCTION

Bonorden (1864) introduced the family *Saccotheciaceae* (*Dothideales*, *Dothideomycetes*, *Ascomycota*) to accommodate the genus *Saccothecium*. Currently, the genera *Aureobasidium*, *Banningia*, *Columnosphaeria*, *Kabatiella*, *Moringomyces*, *Pseudoseptoria*, *Pseudosydowia*, *Saccothecium*, and *Selenophoma* are included in *Saccotheciaceae* (Hyde *et al.* 2024). However, the genera in *Saccotheciaceae* were previously placed in *Aureobasidiaceae* (Thambugala *et al.* 2014), which was later synonymised under *Saccotheciaceae* because of its morphological features and phylogenetic placement (Liu *et al.* 2015). *Aureobasidium*, *Kabatiella*, and *Selenophoma* represent the genera with the largest number of species according to the Index Fungorum and MycoBank databases (accessed in January 2025). Morphologically, both sexual and asexual reproduction are known for the taxa in this family. In the sexual morph, they may have black ascomata that vary from immersed to erumpent, with globose to subglobose shapes. The asexual morphs are classified as coelomycetes or hyphomycetes, with coelomycetes having dark brown conidiomata, solitary or aggregated, and hyphomycetes with the presence or the absence of hyaline, or slightly pigmented stroma (Hongsanan *et al.* 2020). The family has undergone classification changes owing to phylogenetic relationships (Liu *et al.* 2015), and Calabon *et al.* (2023) recently presented an updated classification of *Saccotheciaceae* showing marine *Aureobasidium* species.

Saccotheciaceae members are mostly found as saprophytes (Pande 2008, Peterson *et al.* 2013) in several environments and on different substrates, such as healthy leaves (Quaedvlieg *et al.* 2013), soil (Wu *et al.* 2023), and have been reported to be human opportunistic pathogens (Chan *et al.* 2011). Studies have also shown that species of this family are endophytes (Saber *et al.* 2023), with *Aureobasidium* being the most common genus (Arzanlou & Khodaei 2012, Saber *et al.* 2023). However, most genera included in *Saccotheciaceae*, except *Aureobasidium* (Silva *et al.* 2024), have not previously been reported as endophytes in the Caatinga (dry forest), an exclusive Brazilian biome

covering approximately 10 % of the country (MMA 2022). Like other biomes in Brazil, the Caatinga is a forest with high anthropogenic influence and unsustainable impact, increasing its degradation and desertification (Aquino *et al.* 2021). In this forest, we have identified several endophytic fungi of native and cultivated plant species (e.g., Bezerra *et al.* 2017a, Barbosa *et al.* 2020, Oliveira *et al.* 2021), and new fungal taxa have been introduced based on Caatinga endophytes. Some examples are *Diaporthe caatingaensis*, isolated from *Tacinga inamoena* (Crous *et al.* 2016), the genus *Bezerromyces* (*Bezerromycetaceae*, *Tubeufiales*) (Bezerra *et al.* 2017a), *Toxicocladosporium* species from cacti (Bezerra *et al.* 2017b), *Quambalaria fabacearum* from *Mimosa tenuiflora* (*Fabaceae*) (Bezerra *et al.* 2018), *Pseudoplagiostoma myracrodruonis* from *Myracrodruon urundeuva* (current name: *Astronium urundeuva*; *Anacardiaceae*) (Bezerra *et al.* 2019), *Leptosillia* species from *M. tenuiflora* (*Fabaceae*) (Silva *et al.* 2021), *Cladophialophora* species from *Tillandsia catimbauensis* (Nascimento *et al.* 2021), and recently *Endophytium* (*Endophytiaceae*, *Endophytiales*, *Dothideomycetes*) was introduced for isolates obtained from cacti (Barreto *et al.* 2024), seven new *Diaporthe* species were described from *Anacardium occidentale* (*Anacardiaceae*), *Miconia* sp. (*Melastomataceae*), and *Brosimum gaudichaudii* (*Moraceae*) (Ferro *et al.* 2024a), and *Aureobasidium caatingaense* and *A. santateresinhaense* from *Anadenanthera colubrina* (*Fabaceae*) (Silva *et al.* 2024).

Our studies describing new taxa showed that the Brazilian Caatinga (dry forest) can be treated as a hotspot for fungal diversity. While studying *M. tenuiflora*-associated endophytic fungi in the Caatinga forest of Brazil, the isolates were morphologically identified as aureobasidium-like. After analysis of the ITS and LSU rDNA, *tub2*, *rpb2*, and *tef1* sequences, these strains were placed in a unique lineage phylogenetically distinct from other genera accepted in *Saccotheciaceae*. Therefore, this study aimed to introduce a new genus based on its morphology, multi-locus phylogeny, and ecology/lifestyle. Furthermore, our phylogenetic analyses revealed that *Selenophoma australiensis* (from type material CBS 124776) could be treated as a unique lineage in the family and is introduced here as a new genus in *Saccotheciaceae*.

MATERIAL AND METHODS

Fungal isolates

Endophytes were isolated from branches of *Mimosa tenuiflora* (*Fabaceae*, *Mimosoideae*) during the dry season of April 2013 and collected in the Fazenda Tamanduá (Tamanduá Farm), a private conservation area (RPPN) of the Brazilian Caatinga (dry forest), in the municipality of Santa Teresinha, state of Paraíba, Brazil (07º02'20"S, 37º26'43"W). Details of the study site, plant processing, and fungal isolation have been described by Bezerra *et al.* (2013) and Oliveira *et al.* (2020). Collections were registered in the Ministério do Meio Ambiente (MMA)/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (number: 40331-1) and the study in the Sistema Nacional de Gestão do Patrimônio Genético (SisGen)/MMA/Conselho de Gestão do Patrimônio Genético (CGen) (number: ACD07BF).

Morphological analyses

Isolates were grown on potato dextrose agar (PDA) (Crous *et al.* 2009), malt extract agar (MEA) (Samson *et al.* 2010), Czapek Yeast Autolysate agar (CYA) (Pitt 1979), Dichloran 18 % glycerol agar (DG18) (Hocking & Pitt 1980), and malt extract yeast extract 40 % glucose (MY40G) (Palacios-Cabrera *et al.* 2005), and incubated in dark at 25 °C. The PDA plates were also incubated at 30 and 35 °C. Colony size and morphological features (e.g., texture, colour, pigmentation, and margin appearance) were visualised after 14 d on PDA, MEA, CYA, DG18, and MY40G. Colony colour was evaluated using Rayner's colour chart (Rayner 1970). Reproductive structures were visualised after 60 d on PDA, and conidiogenous cells and conidia were analysed. Microscopic slides were prepared with lactic acid (85 %). A LEICA® DM500 compound microscope equipped with Flexacam C3 cameras was used to capture digital images using NIS-Elements AR v. 4.20 software. The photos and plates were prepared in Adobe® Photoshop CC 2015.

Isolates are deposited in the URM culture collection (*Micoteca URM Profa. Maria Auxiliadora Cavalcanti*) and slide preparations (holotype) in the HURM herbarium (*Herbário URM Pe. Camille Torrend*), both located at the Universidade Federal de Pernambuco, Recife, Brazil. In addition, isolates are deposited in the working collection FCCUFG (*Coleção de Culturas de Fungos da Universidade Federal de Goiás*) housed at the Laboratório de Micologia (LabMicol) of the Instituto de Patologia Tropical e Saúde Pública (IPTSP), Universidade Federal de Goiás, Goiânia, Brazil.

DNA extraction, PCR amplification, and sequencing

The Wizard® SV Genomic DNA Purification System kit (Promega Corp., Madison, WI, USA) was used for genomic DNA extraction according to the manufacturer's instructions. We analysed the rDNA internal transcription spacer (ITS) and intervening 5.8S nRNA gene, the nuclear ribosomal RNA large subunit (LSU) gene, the β-tubulin (*tub2*) gene, the RNA polymerase II second largest subunit (*rpb2*) gene, and the translation elongation factor 1-α (*tef1*) gene, using primers ITS4/ITS5 (White *et al.* 1990), LR0R/LR5 (Vilgalys & Hester 1990, Rehner & Samuels 1994), Bt2a/Bt2b (Glass & Donaldson 1995), RPB2-5F/RPB2-7cR (Liu *et al.* 1999), and EF-728F/EF2 and EF-983F/EF-2218R (Carbone & Kohn 1999, O'Donnell *et al.* 1998, Rehner & Buckley 2005), respectively. Amplification, sequencing, and sequence editing were performed according to Ferro *et al.* (2024b). The sequences obtained in this study were deposited in GenBank (Table 1).

Phylogenetic analyses

Phylogenetic analyses were performed using the sequences generated in this study and reference sequences of all genera included in *Saccotheciaceae* following recent publications (e.g., Humphries *et al.* 2017, Wijayawardene *et al.* 2020). Alignments were performed individually using the MAFFT v. 7 online interfaces (Katoh & Standley 2013; http://mafft.cbrc.jp/alignment/server) and manually edited using MEGA v. 7.0 (Kumar *et al.* 2016). First, we performed a maximum likelihood (ML) analysis for each gene (ITS and LSU rDNA) and the combined matrix to determine the phylogenetic

Table 1. GenBank accession numbers of sequences used in this study. Sequences in **boldface** were obtained during this study. Ex-type strains are marked with (T).

Species	Strain	Host/substrate	Country	GenBank numbers				
				ITS	LSU	*tub2*	*rpb2*	*tef1*
Aureobasidium iranianum	CCTU 268^{T}	Stems of *Bambusa*	Iran	NR_137598	NG_057049	–	–	–
Aureobasidium leucospermi	CBS 130593^{T}	Leaves of *Leucospermum conocarpodendron*	Indonesia	NR_156246	NG_058566	–	KT693970	–
Aureobasidium lini	CBS 125.21^{T}	Leaves of *Linum usitatissimum*	United Kingdom	MH854694	MH866211	FJ157873	KT693984	–
Aureobasidium namibiae	CBS 147.97	From dolomitic marble	Africa	AJ244231	NG_056961	FJ157863	KT693973	XM_013574385
Aureobasidium proteae	CBS 114273 = CPC 2824^{T}	Leaves of *Protea* sp.	South Africa	JN712491	JN712557	–	–	–
Aureobasidium pullulans	CBS 584.75^{T}	From fruit of *Vitis vinifera*	France	NR_144909	NG_055734	FJ157869	KT693976	–
Aureobasidium thailandense	NRRL 58539^{T}	Leaves of *Cerbera Odollam*	Thailand	NR_147337	–	–	–	–
Aureobasidium tremulum	UN 1^{T}	From Petri dish as contaminant	India	MK503657	MK503660	–	–	–
Banningia maryelizabethiae	BRIP 64084b^{T}	Branch of *Corymbia citriodora*	Australia	NR_191310	–	–	–	–
Columnosphaeria fagi	CBS 171.93	Dead leaves of *Arctostaphylos uva-ursi*	Switzerland	MH861759	MH873458	–	KT693980	–
Dothidea sambuci	AFTOL-ID 274^{T}	Dead corticate twigs of *Sambuci nigrae*	Austria	NR_111220	NG_027611	–	DQ522854	DQ497606
Dothiora agapanthi	CPC 20600^{T}	Leaves of *Agapanthus* sp.	South Africa	NR_155055	NG_059132	KU728617	–	–
Dothiora aloidendri	CBS 146775^{T}	Leaves of *Aloidendron dichotomum*	South Africa	NR_171992	NG_074489	–	–	–
Dothiora cannabinae	CBS 737.71^{T}	Dead branches of *Daphne cannabina*	India	NR_144904	NG_068997	–	–	–
Dothiora prunorum	CBS 933.72^{T}	From fruit of *Prunus domestica*	Great Britain	NR_138366	NG_070590	–	–	–
Dothiora pyrenophora	CBS 142621 = CPC 30632^{T}	Twig of *Sorbus aucuparia*	Germany	KY929146	KY929179	KY929210	–	–
Endoconidioma euphorbiae	CBS 146776 = CPC 38551^{T}	Leaves of *Euphorbia mauritanica*	South Africa	MW175350	MW175390	–	–	–

Table 1. (continued)

Species	Strain	Host/substrate	Country	GenBank numbers				
				ITS	LSU	*tub2*	*rpb2*	*tef1*
Endoconidioma populi	UAMH 10297^{T}	Twigs of *Populus tremuloides*	Canada	NR_121303	NG_059198	–	–	–
Hormonema carpetanum	ATCC 74360	Leaves of *Juniperus communis*	Spain	AF182375	MF611880	–	MF611881	MF611882
Hormonema macrosporum	CBS 536.94^{T}	*Rutilus rutilus*	Russia	NR_145340	NG_064169	–	–	–
Hormonema schizolunatum	CBS 707.95^{T}	Leaves of *Salvia canariensis*	Spain	NR_175111	MH874183	–	–	–
Muellerites juniperi	CBS 339.73	Leaves of *Juniperus nana*	Switzerland	–	MH877745	–	–	–
Neocelosporium corymbiae	CPC 39297 = CBS 147080^{T}	Stems of *Corymbia variegata*	Australia	NR_173062	NG_076748	–	–	–
Neocelosporium eucalypti	CPC 34468 = CBS 145086^{T}	Leaves of *Eucalyptus cyanophylla*	Australia	NR_164293	NG_066297	–	–	–
Paivomyces mimosae sp. nov.	**URM 9011 = FCCUFG 153**	**Endophyte from leaves of *Mimosa tenuiflora***	**Brazil**	**PQ811695**	**PQ826408**	**–**	**–**	**–**
	URM 9012 = FCCUFG 156^{T}	**Endophyte from leaves of *Mimosa tenuiflora***	**Brazil**	**PQ811698**	**PQ826411**	**PQ855593**	**PQ855598**	**PQ855602**
	FCCUFG 154	**Endophyte from leaves of *Mimosa tenuiflora***	**Brazil**	**PQ811696**	**PQ826409**	**PQ855592**	**–**	**–**
	FCCUFG 155	**Endophyte from leaves of *Mimosa tenuiflora***	**Brazil**	**PQ811697**	**PQ826410**	**–**	**PQ855597**	**–**
	FCCUFG 157	**Endophyte from leaves of *Mimosa tenuiflora***	**Brazil**	**PQ811699**	**PQ826412**	**PQ855594**	**PQ855599**	**PQ855603**
Pringsheimia chamaecyparidis	CBS 746.71^{T}	Twig of *Chamaecyparis lawsoniana*	France	MH860328	MH872083	–	–	–
Pringsheimia smilacis	CBS 873.71	Dead branches of *Smilax aspera*	India	AJ244257	FJ150970	–	–	–
Pseudoselenophoma australiensis comb. nov.	CBS 124776 = CPC 14582^{T}	Leaves of *Eucalyptus mineata*	Australia	NR_156527	NG_057833	**PQ855595**	**PQ855600**	**PQ855604**
	CPC 14583	Leaves of *Eucalyptus mineata*	Australia	**PQ811700**	–	**PQ855596**	**PQ855601**	**PQ855605**

Table 1. (continued)

Species	Strain	Host/substrate	Country	GenBank numbers				
				ITS	LSU	*tub2*	*rpb2*	*tef1*
Pseudoseptoria collariana	CBS 135104^{T}	Leaves of bamboo	Iran	NR_156560	KF251721	KF252707	–	–
Pseudoseptoria donacis	CBS 313.68	Leaves of *Phragmites australis*	Netherlands	MH859141	MH877798	–	–	–
Pseudoseptoria obscura	CBS 135103	Leaves of bamboo	Iran	KF251219	KF251722	KF252708	–	–
Pseudosydowia backhousiae	BRIP 28243^{T}	Leaves of *Backhousia citriodora*	Australia	MW443073	–	–	–	–
Pseudosydowia eucalypti	CBS 131832	Leaves of *Eucalyptus* sp.	Australia	MH865934	MH877368	–	–	–
	CPC 14028	Leaves of *Eucalyptus* sp.	Southern Africa	GQ303296	–	–	–	–
Pseudosydowia eucalyptorum	CBS 145546^{T}	Leaves of *Eucalyptus* sp.	Australia	NR_165231	NG_067893	–	–	–
Pseudosydowia indooroopillyensis	BRIP 28248^{T}	Leaves of *Eucalyptus* sp.	Australia	MW443076	MW443081	–	–	–
Pseudosydowia louisecottisiae	BRIP 28159^{T}	Leaves of *Eucalyptus* sp.	Australia	NR_173227	MW443079	–	–	–
Pseudosydowia phantasmae	CBS 146830^{T} = CPC 38883	Leaves of *Moringa ovalifolia*	Africa	NR_171999	NG_074499	–	–	–
Pseudosydowia queenslandica	BRIP 28249^{T}	Leaves of *Eucalyptus* sp.	Australia	NR_173230	MW443082	–	–	–
Saccothecium australianum	BRIP 72385d^{T}	Leaves of *Grevillea decora*	Australia	OR452101	OR452104	–	–	–
Saccothecium rubi	MFLUCC 14-1171^{T}	Dead spines of *Rubus ulmifolius*	Italy	NR_148096	NG_059644	–	–	–
Saccothecium sepincola	MFLU 14-0276	Twigs of *Cornus sanguinea*	Italy	KM388546	KM388554	–	–	–
Saccothecium widdringtoniae	CBS 149071 = CPC 42458^{T}	Twigs of *Widdringtonia wallichii*	South Africa	ON603785	ON603805	–	ON605625	ON605633
Selenophoma juncea	CF285463	Endophytes from leaves of *Salsola oppositifolia*	Spain	KU295578	–	–	–	–
Selenophoma linicola	CBS 468.48^{T}	On *Linum usitatissimum*	Canada	MH856436	MH867982	–	–	–
Selenophoma mahoniae	CBS 388.92	Leaves of *Mahonia repens*	United States	KT693746	FJ150943	–	KT693987	–

Table 1. (continued)

Species	Strain	Host/substrate	Country	GenBank numbers				
				ITS	LSU	*tub2*	*rpb2*	*tef1*
Sydowia japonica	FFPRI 411084	*Cryptomeria japonica*	Japan	JQ814700	–	–	–	–
Sydowia polyspora	CBS 116.29	Branches of *Calluna vulgaris*	Germany	NR_160075	NG_057801	–	–	–
Zalaria alba	DAOMC 250847^{T}	House dust	Canada	NR_153465	NG_060009	KX579117	KX579105	–
Zalaria obscura	DAOMC 250849^{T}	House dust	Canada	NR_153466	NG_060010	KX579118	KX579106	–
Phaeosclera dematioides (outgroup)	CBS 157.81^{T}	Pith of *Pinus contorta*	Canada	MH857756	NG_057860	–	–	GU349047

placement of our isolates among the genera within *Saccotheciaceae*. Furthermore, we constructed a combined dataset (ITS, LSU, *rpb2*, *tub2*, and *tef1*) with only strains/isolates containing sequences of at least one specified protein-coding marker, along with the ITS and LSU nrDNA sequences. The ML analysis was performed using RAxML-HPC BlackBox v. 8.2.12 (Stamatakis 2014) using default system options with 1000 bootstrap replicates in the CIPRES Science Gateway (Miller *et al.* 2010) and IQ-TREE v. 1.6.12 software (Nguyen *et al.* 2015) involving 5000 replications and the ultrafast bootstrap (UFboot2) method to calculate branch support (Hoang *et al.* 2018). ModelFinder (Kalyaanamoorthy *et al.* 2017), included in IQ-TREE v. 1.6.12, was used to determine the partitioning strategy and models based on the Akaike information criterion (AICc). The concatenated data set was also analysed based on Bayesian inference (BI) conducted using MrBayes v. 3.2.7a (Ronquist *et al.* 2012) in the CIPRES Science Gateway (Miller *et al.* 2010, http://www.phylo.org/), using the same models and partitions as in the ML analysis (IQ-TREE). The BI analysis was conducted with 50 M generations and 25 % burn-in value, with chains sampled every 1000 generations. The trees obtained were visualised using FigTree v. 1.4.4 (Rambaut 2012) and subsequently edited. Posterior probability BI (BPP) and bootstrap ML (RAxML-BS and IQ-TREE-BS) ≥ 0.95 and 70 %, respectively, are shown near nodes. The final combined alignments were deposited in Figshare (doi: 10.6084/m9.figshare.28200014).

RESULTS

Phylogeny

The ITS, LSU, *tub2*, *rpb2*, and *tef1* gene sequences of our isolates were compared with the sequence data in GenBank using the BLASTn search tool, which indicated that they were related to genera in *Saccotheciaceae* (e.g., *Aureobasidium*, *Pseudosydowia*, and *Selenophoma*). The combined matrix of ITS and LSU comprised sequences from 56 strains, including the outgroup *Phaeosclera dematioides* (CBS 157.81), and 1592 characters, including gaps (654 characters for ITS and 938 for LSU), of which 1064 were conserved, 501 variable, and 325 parsimony-informative. For the ML analysis, the best tree score and final optimization likelihood value was −ln = −9843.732201 and the estimated base frequency were: A = 0.254699, C = 0.226779, G = 0.278235, and T = 0.240287, with substitution rates of AC = 1.775502, AG = 1.871284, AT = 2.215471, CG = 0.679930, CT = 5.205799, and GT = 1.000000 and the distribution shape parameter gamma: α = 0.430374. For BI, the average standard deviation of the split frequencies was 0.001100 after 50 million generations. The combined matrix of ITS, LSU, *tub2*, *rpb2*, and *tef1* had sequences from 56 strains and 3890 characters including gaps (654 characters for ITS, 938 for LSU, 485 for *tub2*, 664 for *rpb2*, and 1149 for *tef1*), of which 2635 were conserved, 1205 variable, and 844 parsimony-informative. The best-scoring ML tree with a final optimization likelihood value was −ln = −19645.714678 and the estimated base frequency were: A = 0.246000, C = 0.248510, G = 0.272910, and T = 0.232581, with substitution rates of AC = 1.523374, AG = 2.235797, AT = 1.659177, CG = 0.810446, CT = 6.148495, and GT = 1.000000 and the distribution shape parameter gamma: α = 0.478754. For BI,

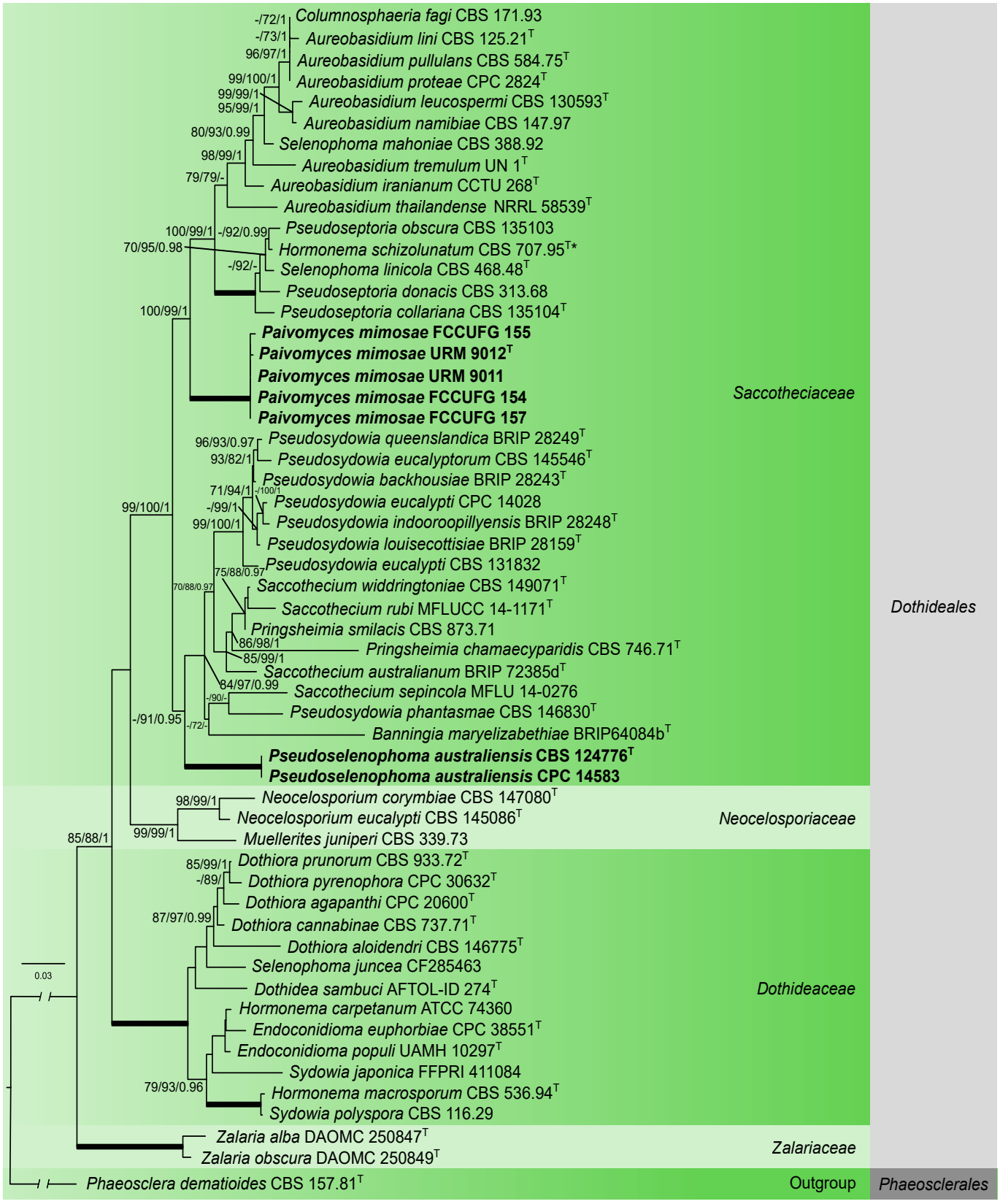

Fig. 1. Maximum Likelihood (ML) phylogenetic tree of the combined ITS and LSU sequences of the new genus *Paivomyces* and related taxa in *Saccotheciaceae* (*Dothideales*). New taxa are in **boldface**. Thickened branches indicate full statistical support in all analyses. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) and BPP ≥ 0.95 are included near the nodes, and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). Species classified in *Dothideaceae* are marked with an asterisk (*). The tree was rooted to *Phaeosclera dematioides* (CBS 157.81) (*Phaeosclerales*, *Dothideomycetes*).

the average standard deviation of the split frequencies was 0.001153 after 50 M generations. The models used for IQ-TREE ML and BI were SYM + I + G for ITS and LSU, GTR + I + G for *rpb2*, and GTR + G for *tub2* and *tef1*. The GTR+I+G model was used for RAxML-HPC.

We conducted combined (ITS–LSU and ITS–LSU–*tub2*–*rpb2*–*tef1*) and individual phylogenetic analyses of each gene; our isolates (URM 9011 = FCCUFG 153, URM 9012 = FCCUFG 156, FCCUFG 154, FCCUFG 155, and FCCUFG 157) and *Pseudoselenophoma* (*P.*) *australiensis comb. nov.* (CBS 124776 = CPC 14582 and CPC 14583) formed unique lineages among the *Saccotheciaceae*. In the combined ITS–LSU matrix (Fig. 1), our sequences formed a unique lineage (ML-BS = 100 %, IQ-TREE-BS = 100 % and BPP = 1) related to a clade having species of *Aureobasidium*, *Selenophoma*, and *Pseudosydowia*. *Pseudoselenophoma australiensis comb. nov.* sequences were also placed in a unique and well-supported lineage (ML-BS = 100 %, IQ-TREE-BS = 100 % and BPP = 1) related to a clade having species of *Pseudosydowia*, *Saccothecium*, *Pringsheimia* and *Banningia*. In the five-gene matrix inference (ITS–LSU–*tub2*–*rpb2*–*tef1*), sequences from our isolates were placed in a unique, well-supported lineage (ML-BS = 100 %, IQ-TREE-BS = 100 % and BPP = 1) near *P. australiensis comb. nov.* (ML-BS = 100 %, IQ-TREE-BS = 100 % and BPP = 1), which were connected by a low-supported node (ML-BS = < 70 %, IQ-TREE-BS = < 70 % and BPP = < 0.95) to sequences from *Aureobasidium*, *Selenophoma*, *Columnosphaeria*, *Pseudoseptoria* and *Hormonema* (ML-BS = 96 %, IQ-TREE-BS = 95 % and BPP = < 0.95) as related taxa in *Saccotheciaceae* (Fig. 2).

In the ML ITS tree (Suppl. Fig. S1), our isolates were phylogenetically placed as a well-supported (ML-BS = 100 % and IQ-TREE-BS=100 %) and unique lineage in *Saccotheciaceae* distant from the other genera of the family, and related to a clade (ML-BS = < 70 % and IQ-TREE-BS = 89 %) with species of *Aureobasidium*, *Selenophoma*, and *Pseudosydowia* (ML-BS = 94 % and IQ-TREE-BS = 97 %). *Pseudoselenophoma australiensis comb. nov.* was also placed as a unique lineage (ML-BS = 100 % and IQ-TREE-BS = 100 %) and related to a clade (ML-BS = < 70 % and IQ-TREE-BS = 86 %) having species of *Pseudosydowia*, *Saccothecium*, *Pringsheimia* and *Banningia* (ML = 73 % and IQ-TREE-BS = 98 %). In the LSU tree (Suppl. Fig. S2), the clade containing our isolates (ML-BS = 100 %, IQ-TREE-BS = 100 %) was phylogenetically related as in the ITS tree. *Pseudoselenophoma australiensis comb. nov.* CBS 124776 has the same phylogenetic placement as described above. In the *tub2* tree (Suppl. Fig. S3), the clade of our isolates (ML-BS = 100 % and IQ-TREE-BS = 100 %) was phylogenetically related (ML = 74 % and IQ-TREE-BS = < 70 %) to the clade of *Pseudoseptoria* species (ML-BS = 100 % and IQ-TREE-BS = 100 %). In the *rpb2* tree (Suppl. Fig. S4), our isolates were well-supported (ML-BS = 100 % and IQ-TREE-BS = 100 %) and phylogenetically related to *Saccothecium widdringtoniae* CBS 149071 (ML = < 70 % and IQ-TREE-BS = < 70 %). *Pseudoselenophoma australiensis comb. nov.* CBS 124776 was well-supported (ML-BS = 100 % and IQ-TREE-BS = 100 %) and placed between *Saccothecium widdringtoniae* CBS 149071 and *Zalaria* species. In the *tef1* tree (Suppl. Fig. S5), our isolates formed a well-supported lineage (ML-BS = 100 % and IQ-TREE-BS = 97 %) related to *Saccothecium widdringtoniae* CBS 149071 (ML = < 70 % and IQ-TREE-BS = < 70 %), and *P. australiensis comb. nov.* CBS 124776 (ML = 100 % and IQ-TREE-BS = 97 %) was placed in a single lineage phylogenetically related to *Aureobasidium namibiae* CBS 14797.

Based on the morphological features and phylogenetic inferences presented above, two new genera, *Paivomyces gen. nov.* (including *Paivomyces mimosae sp. nov.*) and *Pseudoselenophoma gen. nov.* (including *Pseudoselenophoma australiensis comb. nov.*) are here introduced in *Saccotheciaceae*.

Taxonomy

Paivomyces S.S. Nascimento, L.O. Ferro, Souza-Motta & J.D.P. Bezerra, ***gen. nov.*** MycoBank MB 857815.

Etymology: Named in honour of Prof. Dr Laura Mesquita Paiva, a mycologist of the Departamento de Micologia (Universidade Federal de Pernambuco, Recife, Brazil), for her dedication to teaching several students about the mystery of fungal life and kindling our love for fungi.

Hyphae hyaline when young, becoming brown to dark brown with age, smooth, toruloid, and occasionally covered with a mucilage-like sheath. *Conidiogenous cells* enteroblastic, globose to subglobose, apically verrucose, often with an inconspicuous solitary collarette, become dark brown over time. *Conidia* enteroblastic, globose to subglobose, smooth, guttulate, hyaline when young, brown to dark brown with age. *Chlamydospores* occasionally observed, globose to subglobose, intercalary and terminal, and brown to dark brown. *Hyphal coils* occasionally observed. *Hyphopodia-like* structures occasionally observed, elongate, smooth, and brown. *Sexual* morphs not observed.

Type species: *Paivomyces mimosae* S.S. Nascimento *et al.*

Paivomyces mimosae S.S. Nascimento, L.O. Ferro, Souza-Motta & J.D.P. Bezerra, ***sp. nov.*** MycoBank MB 857816. Fig. 3.

Etymology: Named in reference to the host genus *Mimosa*, from which the fungus was first isolated.

Hyphae septate, branched, toluroid, smooth, hyaline when young and becoming brown to dark brown with age, mucilage-like sheath occasionally present, 2.5–6 µm wide. *Conidiogenous cells* enteroblastic, globose to subglobose, apically verrucose, often with an inconspicuous collarette, solitary and grouped in chains, dark brown, (7.5–)10–12.5(–16) × (6–)8–11(–12) µm (av. 11 × 8.5 µm). *Conidia* enteroblastic, globose to subglobose, smooth, guttulate, hyaline when young, brown to dark brown with age, (10–)13–14(–17.5) × (9–)11–14(–17.5) µm (av. 14 × 13 µm). *Chlamydospores* occasionally observed, globose to subglobose, intercalary and terminal, and brown to dark brown. *Hyphal coils* occasionally observed. *Hyphopodia-like* structures occasionally observed, elongate, smooth, and brown. *Sexual morph* not observed.

Culture characteristics: Colonies on PDA measuring 45 mm diam. after 14 d, velvety, slightly furrowed, mostly flat but elevated at the centre, exudates present, olive greenish at the centre and white margins with wavy edges; reverse smoke

grey and white margins. Colonies on MEA, measuring 48 mm diam. after 14 d, glistening with aerial mycelia resembling a black yeast-like fungus, fuscous black to sepia, white wavy margins, and reverse amber to hazel. Colonies on CYA, DG18, and MY40G measuring 25, 20, and 16 mm diam. after 14 d, respectively. Colony growth on PDA was observed at 25 and 30 °C, and no growth was observed at 35 °C.

Typus: **Brazil**, Paraíba state, Santa Teresinha municipality, RPPN Fazenda Tamanduá (07º02'20"S, 37º26'43"W), isolated

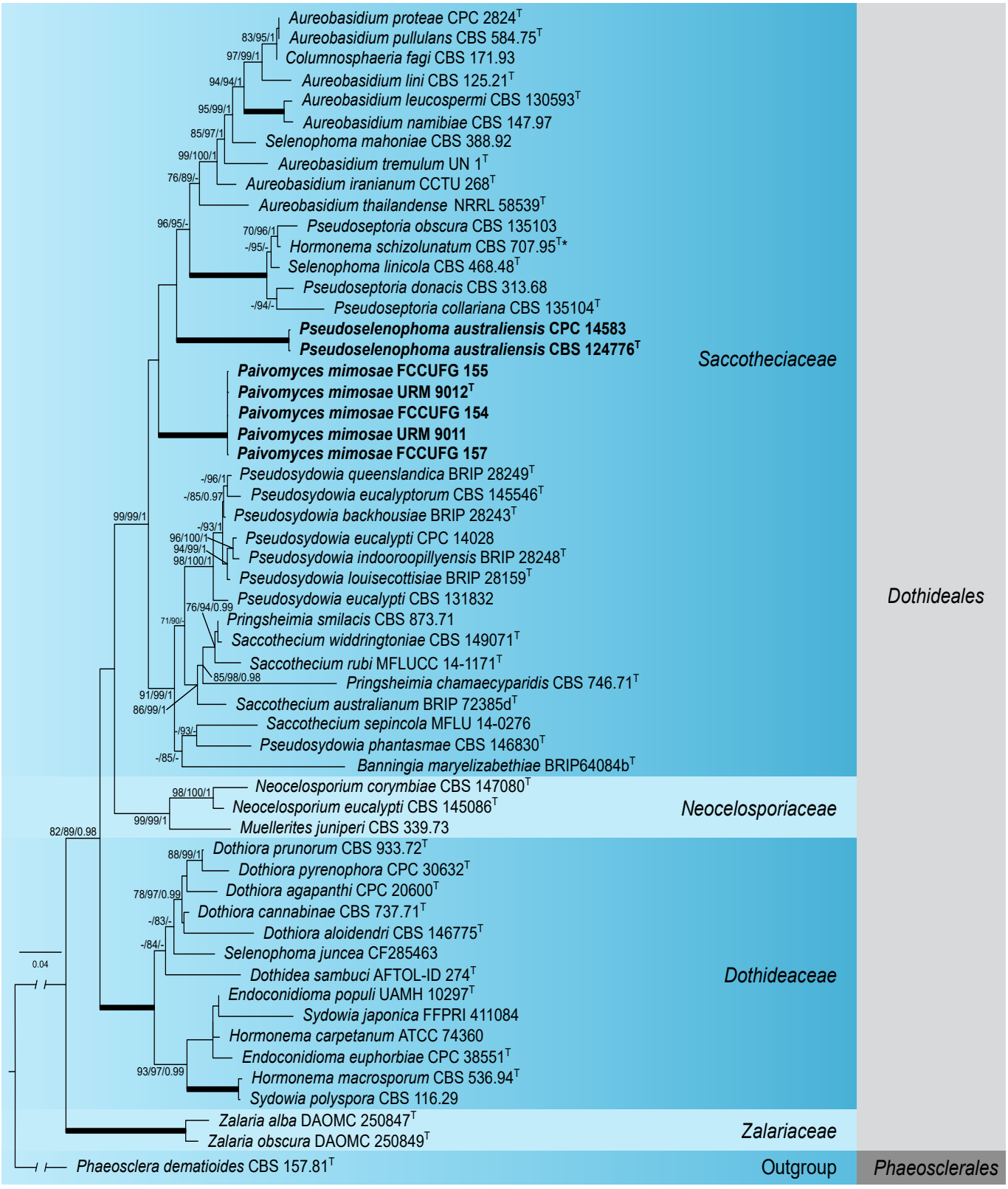

Fig. 2. Maximum Likelihood (ML) phylogenetic tree of the combined ITS, LSU, *tub2*, *rpb2*, and *tef1* sequences of the new genus *Paivomyces* and related taxa in *Saccotheciaceae* (*Dothideales*). New taxa are in **boldface**. Thickened branches indicate full statistical support in all analyses. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) and BPP ≥ 0.95 are included near the nodes, and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). Species classified in *Dothideaceae* are marked with an asterisk (*). The tree was rooted to *Phaeosclera dematioides* (CBS 157.81) (*Phaeosclerales*, *Dothideomycetes*).

Fig. 3. *Paivomyces mimosae* URM 9012. **A.** Colonies on PDA after 14 d at 25 °C in the dark (surface and reverse). **B.** Colonies on MEA after 14 d at 25 °C in the dark (surface and reverse). **C.** Hyphae and conidiogenous cells. **D–F.** Hyphae and conidiogenous cells producing young conidia. **G, H.** Details of old conidia attached to conidiogenous cells. **I.** Hyphae, conidiogenous cells, and hyphopodia-like structures. **J.** Details of hyphal coils. Scale bars = 10 µm.

as an endophyte from branches of *Mimosa tenuiflora* (*Fabaceae*), 4 Apr. 2013, *J.D.P. Bezerra* (**holotype** HURM 95896, **isotypes** HURM 95897 and HURM 95898, culture ex-holotype URM 9012 = FCCUFG 156).

Additional specimens examined: **Brazil**, Paraíba state, Santa Teresinha municipality, Fazenda Tamanduá (07º02'20"S, 37º26'43"W), isolated as endophytes from branches of *Mimosa tenuiflora*, 4 Jun. 2013, *J.D.P. Bezerra* (living cultures URM 9011 = FCCUFG 153, FCCUFG 154, FCCUFG 155, and FCCUFG 157).

Notes: Brazilian isolates exhibited distinct morphological differences from those of other species described in the *Saccotheciaceae*. Morphologically, the main features include enteroblastic conidiogenous cells. Phylogenetically, the new genus is related to a clade that includes members of *Pseudosydowia* (*Pss.*), mostly isolated from leaves (*e.g.*, *Pss. eucalypti*, Thambugala *et al.* 2014), *Pss. eucalyptorum* (Crous *et al.* 2019), *Pss. indooroopillyensis*, *Pss. louisecottisiae*, and *Pss. queenslandica* (Crous *et al.* 2021) isolated from *Eucalyptus* sp. (*Myrtaceae*); *Pss. backhousiae* (Crous *et al.* 2021) isolated from leaves of *Backhousia citriodora* (*Myrtaceae*); *Pss. phantasmae* (Crous *et al.* 2022a) isolated from *Moringa ovalifolia* (*Moringaceae*); *Pringsheimia* (*Pr.*) (e.g., *Pr. chamaecyparidis*, Vu *et al.* 2019) isolated from dead branches of *Chamaecyparis lawsoniana* (*Cupressaceae*) and *Pr. smilacis* (Vu *et al.* 2019) isolated from dead branches of *Smilax parvifolia* (*Smilacaceae*); and *Saccothecium* (*Sa.*) (e.g., *Sa. australianum* (Tan *et al.* 2023) isolated from *Grevillea decora* (*Proteaceae*), *Sa. rubi* (Li *et al.* 2016) isolated from dead spines of *Rubus ulmifolius* (*Rosaceae*), *Sa. sepincola* (Thambugala *et al.* 2014) isolated from the twigs of *Cornus sanguinea* (*Cornaceae*), and *Sa. widdringtoniae* (Crous *et al.* 2022b) isolated from twigs of *Widdringtonia wallichii* (*Cupressaceae*). *Paivomyces* (*Pa.*) can be differentiated from *P. australiensis comb. nov.* by producing pycnidia, endoconidia, and arthroconidia that are absent in *Paivomyces* (Cheewangkoon *et al.* 2009).

Pseudoselenophoma S. S. Nascimento, L. O. Ferro, Souza-Motta & J. D. P. Bezerra, ***gen. nov.*** MycoBank MB 857817.

Etymology: Named in reference to *Selenophoma*.

Two asexual morphotypes, selenophoma-like and hormonema-like. *Selenophoma-like*: *Conidiomata* pycnidial, dark brown, subepidermal to erumpent, and globose. *Pycnidial wall* consists of 2–3 layers of medium to dark brown textura angularis, thick-walled. *Conidiophores* non-uniform, short, barrel-shaped or subovoid, simple, medium brown, thick-walled, composed of 1–3 cells, tapering toward conidiogenous cells, and occasionally reduced to conidiogenous cells. *Conidiogenous cells* subglobose, obpyriform or obovoid, and phialidic, with apical periclinal thickening. *Conidia* aseptate, hyaline, ellipsoidal to obovoid, thin-walled, guttulate. *Hormonema-like*: *Mycelium* immersed and superficial; hyphae hyaline, thin-walled, smooth to slightly verruculose, loosely septate; brown hyphae (type 1) thick-walled, slightly verruculose, densely septate mostly constricted at septa, phialides integrated in hyphal cells, producing hyaline, aseptate conidia; and brown hyphae (type 2), thin-walled, smooth, loosely septate, not constricted at septa, producing endoconidia. *Conidiogenous cells* undifferentiated from creeping hyphae, intercalary or terminal on brown hyphae, producing 1–2 conidia basipetally, with prominent loci and visible collarettes after conidial secession. *Conidia* produced synchronously, along hyphae and on short lateral branches, aseptate, hyaline, ellipsoid to obovoid, smooth, truncate base, slightly thick-walled, turning brown and thick-walled when mature, occasionally becoming 1-medianly septate, slightly constricted at the septum. *Arthroconidia* ellipsoid, medium brown, thick-walled, medially septate, or with slightly longer basal cell, conspicuously constricted at septum, with broadly rounded ends; sometimes producing secondary conidia via microcyclic conidiation. *Endoconidia* produced in thick- and thin-walled hyphae, septate, ellipsoidal, constricted at the septa, and thick-walled. *Chlamydospores* multiseptate, brown, composed of subglobose cells, thick-walled, constricted at the septa, and irregular in shape (based on Cheewangkoon *et al.* 2009).

Type species: *Pseudoselenophoma australiensis* (Cheewangkoon & Crous) S.S. Nascimento *et al.*

Pseudoselenophoma australiensis (Cheewangkoon & Crous) S.S. Nascimento, L.O. Ferro, Souza-Motta & J.D.P. Bezerra, ***comb. nov.*** MycoBank MB 857818.
Basionym: *Selenophoma australiensis* Cheewangkoon & Crous, *Persoonia* **23**: 77. 2009.

Description and illustration: See Cheewangkoon *et al.* (2009).

Typus: **Australia**, Northern Territory, Edith Falls, 14°05'20"S, 14°05'20"E, on *Eucalyptus mineata*, 22 Sep. 2007, coll. *B.A. Summerell*, isol. *P.W. Crous* (**holotype** CBS H-20294, culture ex-type CBS 124776 = CPC 14582).

Additional specimen examined: **Australia**, Northern Territory, Edith Falls, 14°05'20"S, 132°05'12"E, on *Eucalyptus mineata*, 22 Sep. 2007, coll. *B.A. Summerell*, isol. *P.W. Crous* (living culture CPC 14583).

Notes: *Selenophoma australiensis* was originally described from *Eucalyptus mineata* leaves in Australia (Cheewangkoon *et al.* 2009). The authors tentatively included this isolate in *Selenophoma* due to "considerable confusion surrounds the delimitation of *Aureobasidium* and *Hormonema*, complicating species identification in these genera" and because of "a similar yeast synanamorph as observed in *S. eucalypti*" (Crous *et al.* 1995, Cheewangkoon *et al.* 2009). Currently, *S. eucalypti* is placed in *Pseudosydowia* (Thambugala *et al.* 2014), a genus whose morphological characteristics are similar to those of *Aureobasidium* and *Hormonema* species (de Hoog & Yurlova 1994, Crous *et al.* 1995, 2003, Bills *et al.* 2004, Zalar *et al.* 2008). The absence of DNA sequences from the type species of *Selenophoma* (*S. catananches*), along with the replacement of species of this genus with other genera, was also important information for our decision to treat *P. australiensis comb. nov.* as the type species of *Pseudoselenophoma gen. nov.* introduced into *Saccotheciaceae*. Furthermore, our analyses are important for clarifying the phylogenetic position of the taxa in this family.

DISCUSSION

We analysed endophytic fungal isolates from the Caatinga forest in Brazil based on morphological and multi-locus phylogenetic analyses. We introduced a new genus, *Paivomyces* (including *Pa. mimosae sp. nov.*), a unique lineage among the members of *Saccotheciaceae*. During our phylogenetic analyses, we observed that *S. australiensis* was positioned in a clade distinct from the other species treated as *Selenophoma* and differed from the other genera in the family. Based on this analysis and the morphological features, we introduced a new genus, *Pseudoselenophoma* (including *P. australiensis comb. nov.*), to clarify the position of this species in *Saccotheciaceae*. Currently, the family *Saccotheciaceae* has nine accepted genera (Hyde *et al.* 2024), and here, we expand this number to 11 with the descriptions of *Paivomyces gen. nov.* and *Pseudoselenophoma gen. nov.* Our phylogenetic analyses included representative taxa of *Saccotheciaceae*, *Dothideadeae*, *Neocelosporiaceae*, and *Zalariaceae* in *Dothideales* (*Dothideomycetes*). Except for the genus *Aureobasidium*, the species of *Saccotheciaceae* are poorly described; thus, building a robust database for phylogenetic analyses is challenging (Hirooka *et al.* 2013, Quaedvlieg *et al.* 2013, Silva *et al.* 2024). Phylogenetic inferences from our study revealed that sequences identified as *Selenophoma* and *Pseudosydowia* were placed in different clades (e.g., Cheewangkoon *et al.* 2009, Thambugala *et al.* 2014, Crous *et al.* 2022a, b), highlighting the current challenges in consolidating its taxonomy. The description of these two new genera is important for clarifying the phylogenetic relationships among the members of this family, as has been done for *Aureobasidium* and *Hormonema* (Crous *et al.* 2015, Crous *et al.* 2020, Haelewaters *et al.* 2021).

Selenophoma was introduced by Maire (1906); most species of this genus which have been identified before the 2000s are based on morphological differentiation without much access to molecular tools for appropriate phylogenetic analyses (Crous *et al.* 1995, Cheewangkoon *et al.* 2009). In our phylogenetic analyses of *Saccotheciaceae* and related families, *Paivomyces mimosae sp. nov.* and *Pseudoselenophoma australiensis comb. nov.*, are positioned in different clades, reinforcing their separation from other genera within *Saccotheciaceae*. Phylogenetically, in the ITS and LSU matrix, *P. australiensis* is positioned in a unique and distinct clade from *Pa. mimosae*; in the ITS, LSU, *rpb2*, *tub2*, and *tef1* matrices, these species remain in distinct but close clades. Morphologically, both species exhibit hyaline and dematiaceous structures with age, *P. australiensis* presents conidiomata, conidiophores, and conidia, unlike *Pa. mimosae*, which presents hyphae toluroid and enteroblastic conidiogenous cells, often with an inconspicuous collarette.

An example of reclassification in *Saccotheciaceae* is the species *Sphaerulina eucalypti*, isolated from *Eucalyptus* leaves in Southern Africa (Verwoerd & Du Plessis 1931), which was relocated into *Selenophoma eucalypti* (Crous *et al.* 1995) and later to *Sydowia eucalypti* (Crous 2003). Currently, it is classified as *Pseudosydowia eucalypti* (Thambugala *et al.* 2014). This reclassification exemplifies the importance of new taxonomic and phylogenetic analyses, which can provide a precise understanding of evolutionary relationships and enhance our knowledge of the members of *Saccotheciaceae*. Species of this family occur in diverse environments. For example, *Aureobasidium* species are found in various organic materials, demonstrating the importance of studying their ecology in different ecosystems (Wu *et al.* 2023). Similarly, Quaedvlieg *et al.* (2013) described two species of *Pseudoseptoria* from bamboo leaves in Iran, and *Aureobasidium iranianum* was isolated as an endophyte from bamboo stems in Iran (Arzanlou & Khodaei 2012). Recently, two new species of *Aureobasidium* were introduced as endophytes of *A. colubrina* (*Fabaceae*) in Brazil (Silva *et al.* 2024). These findings demonstrate the different lifestyles of related *Saccotheciaceae* genera (Saber *et al.* 2023).

The description of *Paivomyces* and *Pseudoselenophoma* as new genera in *Saccotheciaceae* provides insights into this family's unique lineage and expands the taxonomic information on these understudied taxa in *Dothideales*. Fungal isolates from tropical forests with different lifestyles are important for a broad understanding of fungal diversity and highlighting their contribution to the phylogenetic analyses of taxa in *Saccotheciaceae*.

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Fig. S1. Maximum Likelihood (ML) phylogenetic tree of the representative ITS sequences of the species related to *Paivomyces gen. nov*. New taxa are in **boldface**. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) are included near the nodes, and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). The tree was rooted to *Phaeosclera dematioides* (CBS 157.81) (*Phaeosclerales*, *Dothideomycetes*).

Fig. S2. Maximum Likelihood (ML) phylogenetic tree of the representative LSU sequences of the species related to *Paivomyces gen. nov*. New taxa are in **boldface**. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) are included near the nodes and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). The tree was rooted to *Phaeosclera dematioides* (CBS 157.81) (*Phaeosclerales*, *Dothideomycetes*).

Fig. S3. Maximum Likelihood (ML) phylogenetic tree of the representative *tub2* sequences of the species related to *Paivomyces gen. nov*. New taxa are in **boldface**. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) are included near the nodes and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). The tree was rooted to *Dothiora pyrenophora* (CPC 30632) (*Dothideales*, *Dothideomycetes*).

Fig. S4. Maximum Likelihood (ML) phylogenetic tree of the representative *rpb2* sequences of the species related to *Paivomyces gen. nov*. New taxa are in **boldface**. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) are included near the nodes and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). The tree was rooted to *Dothidea sambuci* (AFTOL-ID 274) (*Dothideales*, *Dothideomycetes*).

Fig. S5. Maximum Likelihood (ML) phylogenetic tree of the representative *tef1* sequences of the species related to *Paivomyces gen. nov*. New taxa are in **boldface**. Confidence values for ML-BS and IQ-TREE-BS ≥ 70 % (UFboot2/RAxML) are included near the nodes and the (-) indicates statistical support below the threshold values. Ex-type strains are marked with (T). The tree was rooted to *Phaeosclera dematioides* (CBS 157.81) (*Phaeosclerales*, *Dothideomycetes*).