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Standard Paper

Contribution to a modern treatment of *Graphidaceae* biodiversity in South Africa: genera of tribe *Graphideae* with hyaline ascospores

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Abstract

Additions and corrections are provided for the South African species of *Graphidaceae* tribe *Graphideae* with hyaline ascospores. *Allographa oldayana* I. Medeiros sp. nov. is described as new to science based on morphological, chemical and molecular data. The new species is characterized by lirellae with striate labia and a complete thalline margin, a completely carbonized excipulum, large, muriform ascospores, and the presence of hirtifructic acid. *Allographa consanguinea* (Müll. Arg.) Lücking, *A. leptospora* (Vain.) Lücking & Kalb, *Diorygma* aff. *minisporum* Kalb *et al.*, *Graphis crebra* Vain., *Gr. dupaxana* Vain., *Gr. furcata* Fée, *Gr. handelii* Zahlbr., *Gr. longula* Kremp., *Gr. pinicola* Zahlbr., *Gr. proserpens* Vain, *Gr. subhiascens* (Müll. Arg.) Lücking and *Platythecium* sp. are reported as new records for South Africa. *Allographa striatula* (Ach.) Lücking & Kalb, *Graphis analoga* Nyl. and *Gr. scripta* (L.) Ach. are shown to be misapplied names that should be removed from the South African checklist. The new combination *Mangoldia bylii* (Vain.) I. Medeiros comb. nov. (bas. *Graphis bylii* Vain) is made; this represents an earlier name for *M. atronitens* (A. W. Archer) Lücking *et al.* Taxonomic notes are provided for *Graphis bylii* var. *lividula* Vain. and *Gr. denudans* Vain., species that are known only from their South African holotypes. Phylogenetic analyses that include new DNA sequence data from the nrLSU, mtSSU and *RPB2* loci confirm the generic placements of several species for which molecular data were lacking: *Allographa consanguinea*, *Glyphis atrofusca* (Müll. Arg.) Lücking, *Graphis crebra* and *Gr. subhiascens*.

Key words: biodiversity, *Graphis pergracilis* complex, Northern Mistbelt Forest, savannah, Southern Afrotemperate Forest, taxonomy, tropical lichens

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Introduction

The diverse topography, geology, climate and vegetation of South Africa contribute to a rich lichen biota estimated to contain at least 2500–3000 species (Fryday 2015). Approximately 1750 species of lichenized and allied fungi, many of which are endemic to southern Africa, are presently recorded from the country (Crous *et al.* 2006; Fryday 2015; Ahti *et al.* 2016). The majority of the at least 750–1250 undocumented or undiscovered species are expected to be crustose lichens, which have not yet received the taxonomic attention given in South Africa to macrolichen genera such as *Xanthoparmelia* (Fryday 2015).

Graphidaceae is the largest family of crustose lichens worldwide (Staiger 2002; Frisch 2006; Lücking *et al.* 2014, 2017). Research on this family in South Africa has been piecemeal, beginning with the description of *Thelotrema henatomma* Ach. by Acharius (1804). Nylander (1868) published the first taxonomic paper that described new lirelliform *Graphidaceae* from South Africa, based on specimens collected near Pietermaritzburg by Olivia Armstrong and William Mackenzie (Medeiros 2019). His article described one new species in the family and reported several records of previously described species. Additional new species were described by Müller (1886, 1887, 1895), Vainio (1926) and Zahlbruckner (1926, 1932). More recently, Egea & Torrente (1996) described the new saxicolous species *Gymnographopsis latispora* Egea & Torrente from fresh material and Kalb *et al.* (2009) described the new species *Acanthothecis dialeucoides* Kalb & Staiger from a historical specimen. Several species described from South African type material have been revised by modern authors as part of global revisions (Frisch 2006; Lücking *et al.* 2009). The most substantial recent work on *Graphidaceae* in South Africa is a country-level revision of the genus *Diploschistes* (Guderley & Lumbsch 1996), which has an unusual ecology within the family. Whereas most species of *Graphidaceae* occur on bark in shrubby or forest vegetation, *Diploschistes* species occur on rock or soil, often in arid or semi-arid regions (Staiger 2002; Frisch 2006; Lücking *et al.* 2014). Moreover, the only molecular data available for South African *Graphidaceae* is a single nuclear large subunit ribosomal RNA (nrLSU) sequence from *Diploschistes actinostoma* (Ach.) Zahlbr. (Rivas Plata *et al.* 2013).

Throughout this literature, species descriptions and records have accumulated without any synthesis of the systematics of lirelliform *Graphidaceae* in southern Africa. The only attempts at

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summarizing these scattered data have been the lichen checklists compiled by Doidge (1950) and Fryday (2015), which dealt with all lichens and did not make new taxonomic conclusions. Furthermore, no recent publications have dealt with new collections of lirelliform *Graphidaceae* on bark, where we expect a large portion of this family's South African biodiversity. Lücking *et al.* (2014) estimated that the lichen biota of Namibia, Botswana and South Africa includes over 220 species of *Graphidaceae*, with more than 160 species either unreported or undescribed. The method Lücking *et al.* (2014) used to estimate *Graphidaceae* biodiversity excluded strictly extratropical species, but subtropical biodiversity hotspots in South Africa (Mucina & Rutherford 2006) could support substantial biodiversity in this family. The present study is an initial contribution to a modern treatment of *Graphidaceae* biodiversity in South Africa, focusing on the species of the tribe *Graphideae* that have hyaline ascospores, namely species of the lirelliform genera *Allographa*, *Diorygma*, *Glyphis*, *Graphis*, *Mangoldia* and *Platythecium* (Rivas Plata *et al.* 2013; Lumbsch *et al.* 2014*a*). Species of *Graphideae* with pigmented ascospores (i.e. *Phaeographis*, *Platygramme* and related genera) will be treated in a subsequent publication.

Materials and Methods

Specimens were collected in February 2016 and May–June 2019 at forest and savannah sites in Mpumalanga, KwaZulu-Natal and Western Cape provinces (Figs 1 & 2). The forested areas were classified as Northern Mistbelt Forest, Southern Mistbelt Forest, and Southern Afrotemperate Forest (Mucina & Rutherford 2006). Additional relevant specimens were obtained from B, BOL, BM, DBN, LD, NU, PRE, SBBG, TRH, TUR, UPS, US and WIS. These included a large set of *Graphidaceae* from KwaZulu-Natal, collected by Ove Arbo Høeg in the 1920s, that has not previously been studied or discussed in any published work. Approximately 50 new collections and 110 herbarium specimens from South Africa, including four type specimens, were examined for this study.

Morphology and chemistry

Specimens were observed under Leica M60, Olympus SZ61, or Leica MZ6 dissecting microscopes. Photographs were taken with a Canon Rebel XSi camera attached to a Leica MZ125 dissecting microscope or with a Nikon D3200 camera with the VariMag DSLR modular imaging system attached to an Olympus SZ61 dissecting microscope. Hand-cut thin sections of apothecia were mounted in tap water for observation under either a Leica DM1000, Leica DMLB, or Olympus CH30 compound microscope. Morphological characters were documented following Lücking (2009). Recently published keys (Staiger 2002; Lücking *et al.* 2009; Barcenas Peña *et al.* 2014; Joshi *et al.* 2016) and species descriptions from the primary literature were used to assess whether collections represented previously described species.

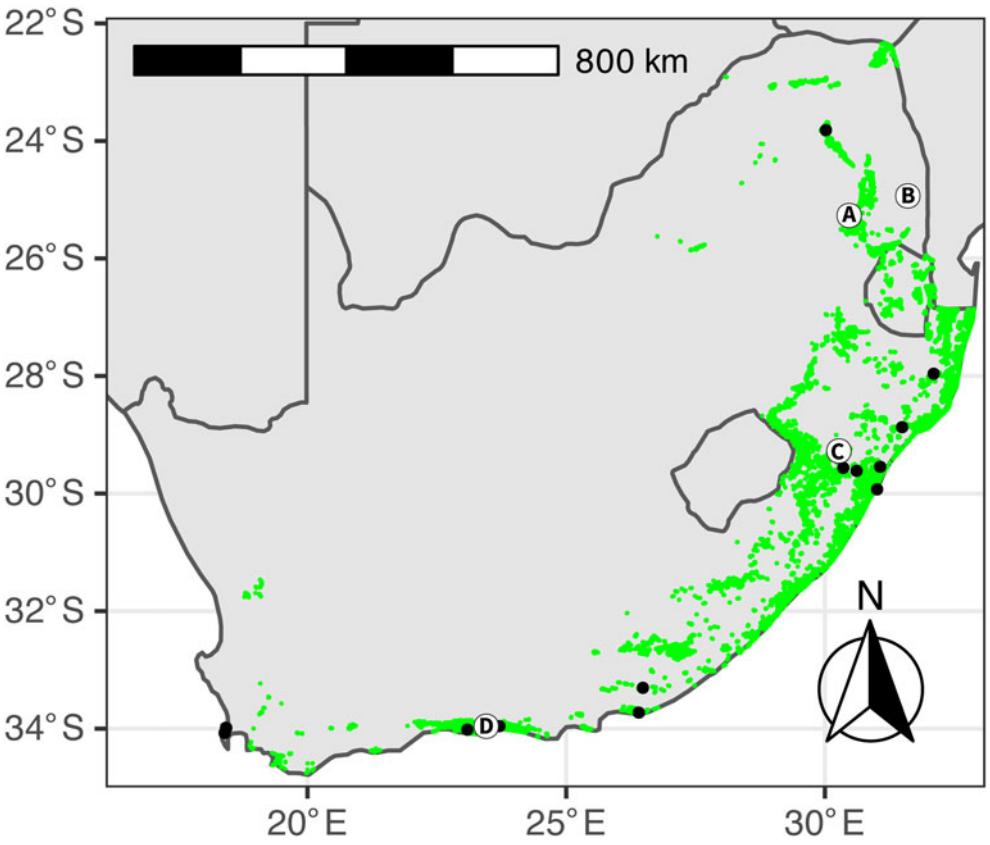

Fig. 1. Map of South Africa showing collection localities for specimens in the present study. Open circles with letters A–D refer to localities depicted in Fig. 2. Filled black circles indicate other collection localities, including historical specimens. Extent of the forest biome in South Africa, Eswatini and Lesotho indicated in green (in colour) or mid grey (South African National Biodiversity Institute 2012). In colour online.

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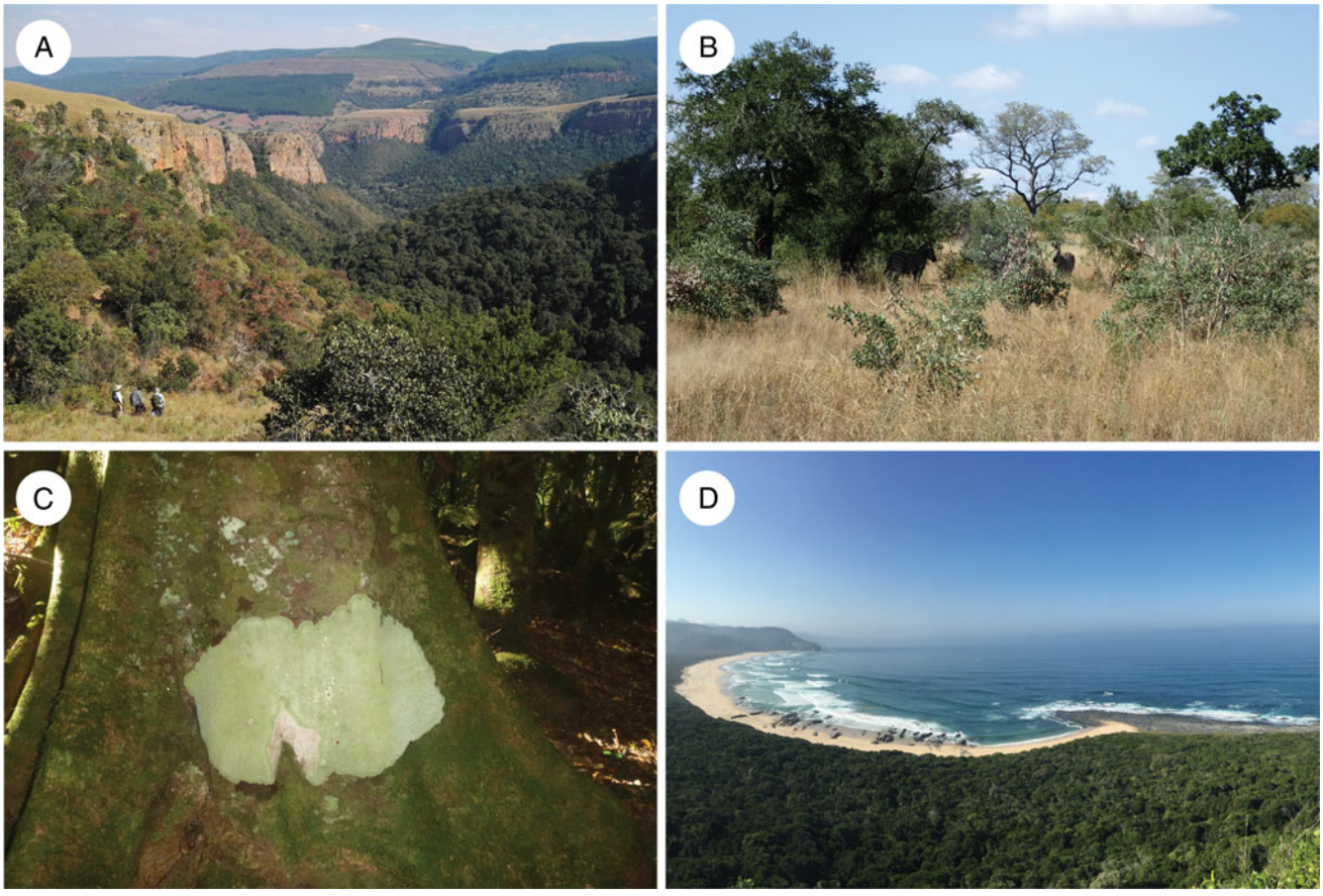

Fig. 2. Example collection sites of South African *Graphidaceae*. A, Northern Mistbelt Forest in a ravine at Buffelskloof Private Nature Reserve. Note planted *Pinus* on former natural grassland in the background. Photograph by József Geml. B, savannah in Kruger National Park. Zebras for scale. Photograph by Shuzo Oita. C, *Diorygma* aff. *minisporum in situ* on a tree trunk in Southern Mistbelt Forest in the Karkloof Nature Reserve. Photograph by Ian D. Medeiros. D, Southern Afrotemperate Forest on the coast at Nature's Valley, Garden Route National Park. Photograph by Betsy Arnold. See Fig. 1 for locations of these sites. In colour online.

Genera and species have been designated as first reports for South Africa if they do not appear in the South African lichen checklist (Fryday 2015; Ahti *et al.* 2016).

Secondary chemistry was assessed with thin-layer chromatography (TLC) using standard methods (Culberson & Kristinsson 1970; Orange *et al.* 2010). Plates were run in solvent systems C (170 toluene: 30 glacial acetic acid) for standard analyses and G (139 toluene: 83 ethyl acetate: 8 formic acid) when necessary to separate stictic acid satellite compounds. Elix (2018) was consulted as an additional reference for identifying TLC spots.

Molecular phylogenetics

All new molecular data are from South African specimens except for one specimen of *Platygramme pachnodes* (Fée) Fée from Florida, USA (LaGreca *et al.* 2021). DNA was isolated either from fresh specimens or from specimens stored at −20 °C in silica gel. Small fragments (*c.* 1–2 mm^2) of thallus or ascomata were excised with a sterile needle. DNA extraction followed the procedure outlined in Hughes *et al.* (2020) using laboratory-made extraction and dilution buffers, except that thallus fragments were frozen in the extraction buffer for 1 h at −20 °C and thawed to room temperature prior to the heating step.

The internal transcribed spacer (ITS) was amplified with primers ITS1F and LR3 (Vilgalys & Hester 1990; Gardes & Bruns 1993). ITS sequences are not widely available for *Graphidaceae* (Cáceres *et al.* 2020) and the few ITS sequences we obtained were not used in subsequent phylogenetic analyses. The nuclear large subunit (nrLSU) was amplified with primer pair AL2R and LR6 (Vilgalys & Hester 1990; Mangold *et al.* 2008), while the mitochondrial small subunit (mtSSU) was amplified with primer pair mrSSU1 and mrSSU3R (Zoller *et al.* 1999). The RNA polymerase II second largest subunit (*RPB2*) was amplified with a nested approach, first using the fungal primers fRPB2-7cF and fRPB2-11aR (Liu *et al.* 1999) and then the internal primers GD-RPB2-7cF and GC-RPB2-11aR, which were designed specifically for *Graphidaceae* (Kraichak *et al.* 2015). Thermal cycler conditions followed Kraichak *et al.* (2015). PCR products were checked on a 1% agarose gel and cleaned with exonuclease I and shrimp alkaline phosphatase (ThermoFisher Scientific, Waltham, MA, USA). Sanger sequencing was performed by Eurofins Genomics (Louisville, KY, USA) using the PCR primers. Forward and reverse reads were assembled and checked for errors in Geneious Prime v. 2022.0.1. GenBank Accession numbers for newly generated sequences are provided in Table 1 (for nrLSU, mtSSU and *RPB2*) or in the remarks under individual species (for ITS). We generated two new ITS sequences, 14 new nrLSU sequences, 21 new mtSSU sequences and 19 new *RPB2* sequences from a total of 21 specimens.

The phylogenetic analyses were based on nrLSU, mtSSU and *RPB2*. We prepared a dataset of reference sequences (Table 1)

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generated in previous studies of *Graphidaceae* and other fungi (Kalb *et al.* 2004; Staiger *et al.* 2006; Mangold *et al.* 2008; Rivas Plata *et al.* 2011, 2013; Cáceres *et al.* 2012; Nelsen *et al.* 2012; McDonald *et al.* 2013; Lumbsch *et al.* 2014*b*; Fazio *et al.* 2018; Vu *et al.* 2019). Species of *Acanthothecis*, *Diploschistes* and *Fissurina*, representing three different *Graphidaceae* clades outside tribe *Graphideae* (Lumbsch *et al.* 2014*a*), were used for the outgroup. The nrLSU and mtSSU sequences were initially aligned in MAFFT with the G-INS-1 option (Katoh *et al.* 2019), while the *RPB2* sequences were aligned by translated amino acids in Mesquite (Maddison & Maddison 2021). Alignments were subsequently corrected and ambiguously aligned regions were delimited in Mesquite. Ambiguous regions were excluded from subsequent analyses. Complete alignments with delimited ambiguous regions are available at FigShare (DOI: 10.6084/m9.figshare.c.6007096).

Model selection and maximum likelihood tree inference were performed using IQ-TREE v. 2.1.2 (Nguyen *et al.* 2015; Chernomor *et al.* 2016) run on the CIPRES server (Miller *et al.* 2010). We first inferred separate trees for each locus. We performed 5000 ultrafast bootstrap pseudoreplicates to calculate bipartition support (Hoang *et al.* 2018) and examined the trees for well-supported conflicts (i.e. ≥ 95% ultrafast bootstrap). There were no well-supported conflicts, so the nrLSU, mtSSU and *RPB2* alignments were concatenated and used as input for a partitioned analysis in IQ-TREE. Our concatenated alignment included 78 specimens, including 15 South African representatives from *Graphidaceae* tribe *Graphideae*. ModelFinder (Kalyaanamoorthy *et al.* 2017) was used to optimize the partitioning scheme and determine the best substitution models (Table 2). We performed 5000 ultrafast bootstrap pseudoreplicates to calculate bipartition support for the concatenated tree topology. The alignments and three-locus phylogeny from this paper have been made available on T-BAS (Carbone *et al.* 2017, 2019) to facilitate access to these alignments and placement of new sequence data from this clade.

Results

The phylogenetic analysis based on the concatenated dataset recovered hyaline-spored samples from South Africa in four highly supported clades, corresponding to the genera *Allographa*, *Diorygma*, *Glyphis* and *Graphis* s. str. (Fig. 3). We also recovered a highly supported clade containing species of the brown-spored genera *Leiorreuma*, *Phaeographis*, *Pallidogramme*, *Platygramme* and *Thecaria*, including three South African specimens. The monophyly of *Graphideae* was highly supported but relationships among genera were not, with the exception that *Mangoldia* was supported as sister to *Allographa* (Fig. 3).

Morphological study of herbarium material and fresh collections yielded one species of *Allographa* new to science, one species based on a South African type that needed to be transferred to *Mangoldia*, and 12 new records for South Africa, all described below. The herbarium material also included a substantial number of *Opegrapha* and *Enterographa* specimens misidentified as *Graphidaceae*; these have been annotated but a complete listing of examined, non-*Graphidaceae* specimens is beyond the scope of this study.

Taxonomy

Note that taxonomic synonyms are provided only when they concern names described from South African material.

Allographa consanguinea (Müll. Arg.) Lücking & Kalb

Herzogia **31**, 549 (2018).—*Graphina consanguinea* Müll. Arg., *Nuov. Giorn. Bot. Ital.* **21**, 362 (1889).—*Graphis consanguinea* (Müll. Arg.) Lücking, *in* Lücking *et al.*, *Fieldiana*, *Bot.* **46**, 67 (2008); type: Brazil, *Glaziou* s. n. (G—holotype, not seen).

(Fig. 4A)

Remarks. *Allographa consanguinea* has not previously been recorded for South Africa; it was reported from Kenya by Kirika *et al.* (2012) and is otherwise known only from the Neotropics (Lücking *et al.* 2009). We provide the first molecular data for *A. consanguinea* and confirm its placement in *Allographa* (Table 1, Fig. 3). This corticolous species co-occurs and shares morphological similarities with *Allographa oldayana*, described below; see the remarks under the new species for characters that separate them. Records of *Allographa acharii* (Fée) Lücking & Kalb from South Africa (Nylander 1868; Doidge 1950; Almborn 1988) may represent *A. consanguinea* or *A. oldayana*. *Allographa acharii* has prominent lirellae and 2–6 large, muriform spores per ascus versus erumpent lirellae and one spore per ascus in *A. consanguinea* (Lücking *et al.* 2009).

Specimens examined. **South Africa:** *Eastern Cape*: 'Grahamstown, natural forest just above Fern Kloof', iii 1961, *H. B. Johnston* s. n. (LD 1948852). *KwaZulu-Natal*: 'distr. Eshowe, on *Eucalyptus* along main road', 26 viii 1919, *O. A. Høeg* s. n. (TRH L-17858, L-17909); 'distr. Eshowe, S of Solheim Miss. St.', 7 ix 1929, *O. A. Høeg* s. n. (TRH L-17921); uMgungundlovu District Municipality, Karkloof Nature Reserve, 29°17′52″S, 30°13′40″E, 2019, *Medeiros* 2095 (BOL). *Limpopo*: De Hoeck Forest, west of Tzaneen, 1953, *R. Kräusel* 4b [with *Allographa oldayana*] (B).

Allographa leptospora (Vain.) Lücking & Kalb

In Kalb *et al.*, *Phytotaxa* **377**, 19 (2018).—*Graphis leptospora* Vain., *Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo* **1**(no. 3), 53 (1921); type: Thailand, *Hosseus* s. n. (TUR-V—holotype, not seen).

(Fig. 4B)

Remarks. This is the first report of this corticolous species for South Africa. It differs from the other species with a striate, completely carbonized excipulum and a complete thalline margin (*A. consanguinea* and *A. oldayana*) in having transversely septate ascospores.

Specimen examined. **South Africa:** *Mpumalanga*: Buffelskloof Private Nature Reserve, 25°15′59″S, 30°31′6″E, 1725 m, 2016, *Medeiros* L449 (BOL).

Allographa oldayana I. Medeiros sp. nov.

MycoBank No.: MB 843785

Differing from *Allographa cerradensis* (Marcelli *et al.*) Lücking & Kalb in the clear hymenium, larger ascospores, and presence of hirtifructic acid.

Type: South Africa, Mpumalanga, Buffelskloof Private Nature Preserve, 2019, *Medeiros* 2078 & *Flakus* (BOL—holotype; DUKE, PRE—isotypes).

(Fig. 4C–E)

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Table 1. Voucher information and GenBank Accession numbers for new sequences of *Graphidaceae* generated for this study (GenBank Accession numbers in bold) and reference taxa used in the phylogenetic analysis. Dashes indicate missing data. Note that the new data include one specimen from outside South Africa (*Platygramme pachnodes* from Florida, USA).

Species	Voucher	Country	nrLSU	mtSSU	*RPB2*
Acanthothecis aurantiaca	33945 hb. Kalb	Australia	DQ431929	DQ431965	—
Acanthothecis sp. 1	*Medeiros* 2096	South Africa	**ON507254**	**ON507276**	**ON492050**
Allographa angustata	*Lücking* 28102	El Salvador	HQ639632	HQ639612	—
A. chlorocarpa	*Lücking* 25522d	Guatemala	—	HQ639595	JF828946
A. chrysocarpa	*Lücking* 00-35	Costa Rica	—	DQ431987	—
A. cinerea	26950 hb. Kalb	Venezuela	DQ431947	DQ431988	—
A. consanguinea	*Medeiros* 2095	South Africa	**ON507250**	**ON507274**	**ON492048**
A. consanguinea	*Medeiros* 2098	South Africa	**ON507249**	**ON507273**	**ON492047**
A. elongata	*Facio & Avanzatto* BAFC39315	Argentina	MG775658	MG775654	—
A. illinata	*Lumbsch* s. n.	Mexico	HQ639634	HQ639614	—
A. oldayana	*Medeiros* 2078	South Africa	**ON507257**	**ON507277**	**ON492051**
A. oldayana	*Medeiros* 2102	South Africa	**ON507248**	**ON507272**	**ON492046**
A. pavoniana	*Lücking* 16100c	Costa Rica	DQ431946	DQ431986	—
A. pseudocinerea	*Lücking* 26537	United States	HQ639639	HQ639620	—
A. rhizocola	*Lücking* 28502	Nicaragua	HQ639643	—	—
A. rimulosa	*Rivas Plata* 1021H	Philippines	—	JX421069	—
A. vestitoides	*Rivas Plata* 2078	Philippines	HQ639648	—	—
Allographa sp. 1	*Medeiros* 2099	South Africa	**ON507244**	**ON507263**	**ON492039**
Diorygma antillarum	*Nelsen* 4037	United States	JX046465	JX046452	—
D. minisporum	*Lumbsch* 19543v	Kenya	HQ639626	HQ639598	KF875520
D. aff. *minisporum*	*Medeiros* 2106	South Africa	**ON507251**	**ON507279**	**ON492053**
D. poitaei	*Lücking* 28538	Nicaragua	HQ639627	HQ639596	JF828942
Diploschistes sp. 1	*Lutzoni* 06.08.19-FL30	South Africa	**ON507247**	**ON507271**	**ON492045**
Fissurina marginata	*Lücking* 24122	Thailand	HQ639629	HQ639613	—
Fissurina sp. 1	*Medeiros* 2126	South Africa	—	**ON507261**	—
Fissurina sp. 2	*Medeiros* 2133	South Africa	**ON507245**	**ON507268**	**ON492043**
Fissurina sp. 3	*Medeiros* 2148	South Africa	**ON507256**	**ON507269**	**ON492044**
Glyphis atrofusca	*Medeiros* 2089a	South Africa	**ON507253**	**ON507275**	**ON492049**
Gl. cicatricosa	*Lücking* 28047	El Salvador	HQ639630	HQ639610	—
Gl. cicatricosa	*Medeiros* 2100	South Africa	—	**ON507260**	**ON492037**
Gl. cicatricosa	*Lumbsch* 19528o	Kenya	JX421503	JX421062	—
Gl. scyphulifera	33140 hb. Kalb	Dominican Republic	AY640027	DQ431956	—
Gl. substriatula	*Lücking* 16532	Costa Rica	AY640026	DQ431982	—
Graphis betulina	*Sohrabi* 16429	China	KF875541	KF875562	KF875524
Gr. caesiella	*Berger* 17247	Cuba	AY640028	DQ431975	—
Gr. aff. *caesiella*	33919 hb. Kalb	Australia	DQ431938	DQ431977	—
Gr. centrifuga	30442 hb. Kalb	Australia	AY640030	—	—
Gr. crebra	*Medeiros* 2088a	South Africa	**ON507255**	**ON507267**	**ON492055**
Gr. dichotoma	*Rivas Plata* 2088	Philippines	HQ639633	—	—
Graphis cf. *gracilescens*	33942B hb. Kalb	Australia	DQ431936	DQ431976	—
Gr. implicata	*Lücking* 16103	Costa Rica	DQ431939	DQ431978	—
Graphis leptoclada	*Lumbsch* 20535b	Fiji	JX421509	JX421068	—
Gr. librata	*Lücking* 28001	El Salvador	HQ639636	HQ639621	JF828945

(*Continued*)

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Table 1. (*Continued*)

Species	Voucher	Country	nrLSU	mtSSU	*RPB2*
Gr. librata	*Medeiros* 2112	South Africa	—	**ON507262**	**ON492038**
Gr. proserpens	*Rivas Plata* 2065	Philippines	—	HQ639619	—
Gr. proserpens	*Medeiros* 2105	South Africa	**ON507252**	**ON507280**	**ON492054**
Gr. pseudoserpens	*Lücking* 28048	El Salvador	HQ639642	—	—
Gr. pulverulenta	*Neuwirth* 11808	Austria	KF875543	KF875564	KF875526
Gr. subhiascens	*Medeiros* 2088b	South Africa	—	**ON507278**	**ON492052**
Gr. tenella	*Rivas Plata* 1007G	Philippines	HQ639647	—	—
Gr. tsunodae	*Lücking* 26096	Venezuela	JX421511	—	—
Graphis sp. 33942A	33942a hb. Kalb	Australia	DQ431941	DQ431980	—
Graphis sp. 33943	33943 hb. Kalb	Australia	DQ431940	DQ431979	—
Leiorreuma hypomelaenum	33916 hb. Kalb	Australia	DQ431933	DQ431971	—
Mangoldia australiana	*Mangold* 27zB	Australia	JX421519	—	—
Pallidogramme chlorocarpoides	*Rivas Plata* 2008b	Philippines	—	JN127362	—
P. chrysenteron	*Rivas Plata* 1157D	Philippines	—	JN127361	—
Phaeographis caesioradians	*Kalb* 33917	Australia	AY640021	DQ431968	—
Ph. elliptica	*Gaya* 16.03.08 EGB12	United States	MH878104	KC592285	—
Ph. intricans	*Kalb* 38864	Thailand	JX421602	JX421254	JX420924
Ph. lecanographa	RLD 071 hb. Kalb	Mexico	DQ431943	DQ431983	—
Ph. leprieurii	*Cáceres* s. n.	Brazil	JN127365	JN127363	—
Ph. lobata	*Berger* 19598	Bermuda	DQ431944	DQ431984	—
Ph. platycarpa	*Mangold* 30za	Australia	JX421604	JX421263	KF875510
Phaeographis sp. 33152	33152 hb. Kalb	Dominican Republic	DQ431926	DQ431959	—
Phaeographis sp. 36885	36885 hb. Kalb	Thailand	JX421606	JX421275	—
Phaeographis sp. F2388	*Lumbsch* F2388	Kenya	KF875533	KF875553	KF875511
cf. *Phaeographis* sp. 1	*Medeiros* 2160	South Africa	—	**ON507264**	**ON492040**
cf. *Phaeographis* sp. 1	*Medeiros* 2137	South Africa	—	**ON507265**	**ON492041**
cf. *Phaeographis* sp. 2	*Medeiros* 2135b	South Africa	—	**ON507266**	**ON492042**
Platygramme australiensis	33930 hb. Kalb	Australia	AY640024	DQ431970	—
Pl. caesiopruinosa	*Mangold* 30eI	Australia	EU075639	EU075593	—
Pl. pachnodes	*LaGreca* 2659	United States	**ON507246**	**ON507270**	—
Schistophoron tenue	*Tehler* 8796	Galapagos Islands	EU544932	EU544933	—
Thalloloma anguinum	*Lumbsch* 19804c	Fiji	—	JX421336	—
T. hypoleptum	*Lücking* 26564	United States	HQ639665	—	JF828954
Thecaria montagnei	*Rivas Plata* 2083	Philippines	HQ639666	JX644422	—
T. quassiicola	*Lücking* 26567	United States	HQ639667	HQ639617	—

Thallus corticolous, epiperidermal, 30–120 µm thick, continuous; surface smooth, pale green; *prothallus* absent. Thallus in section with prosoplectenchymatous cortex 12–30 µm thick, algal layer (*Trentepohlia*) 20–110 µm thick, and irregular clusters of calcium oxalate crystals.

Apothecia lirelliform, unbranched, erumpent to prominent, with thin to thick complete thalline margin, 1.0–7.5 mm long, 0.5–0.6 mm wide, 0.29–0.37 mm high; *disc* concealed; proper margin thick, labia striate, black. *Excipulum* striate, completely carbonized, 60–105 µm wide; *hypothecium* prosoplectenchymatous, 20–30 µm high, colourless to pale yellow; *hymenium* 100–180 µm high, colourless, clear; *paraphyses* unbranched, smooth; *epithecium* granulose, 12–25 µm high, dark olive-brown. *Asci* fusiform, 100–180 × 19–32 µm. *Ascospores* 1–4 per ascus, ellipsoid, muriform, transversely 20–30-septate, longitudinally 2–4-septate, 100–150(–175) × (16–)18–24(–27) µm, 4.5–7 times as long as wide, hyaline, I+ violet.

Conidiomata not seen.

Chemistry. Hirtifructic acid (major), cf. conhirtifructic acid (minor).

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Table 2. Alignment statistics and substitution models. The full concatenated alignment included 78 specimens and 2404 sites. *RPB2* was partitioned by codon position. PI = parsimony-informative sites; Inv = invariant sites.

Partition	Taxa (%)	Length	PI (%)	Inv (%)	Model
nrLSU	64 (82)	883	282 (32)	518 (59)	TIM2 + F + R3
mtSSU	69 (88)	675	200 (30)	424 (63)	GTR + F + I + G4
RPB2: pos. 1–2	29 (37)	564	79 (14)	472 (84)	TVMe + I + G4
RPB2: pos. 3	29 (37)	282	269 (95)	7 (2)	GTR + F + I + G4

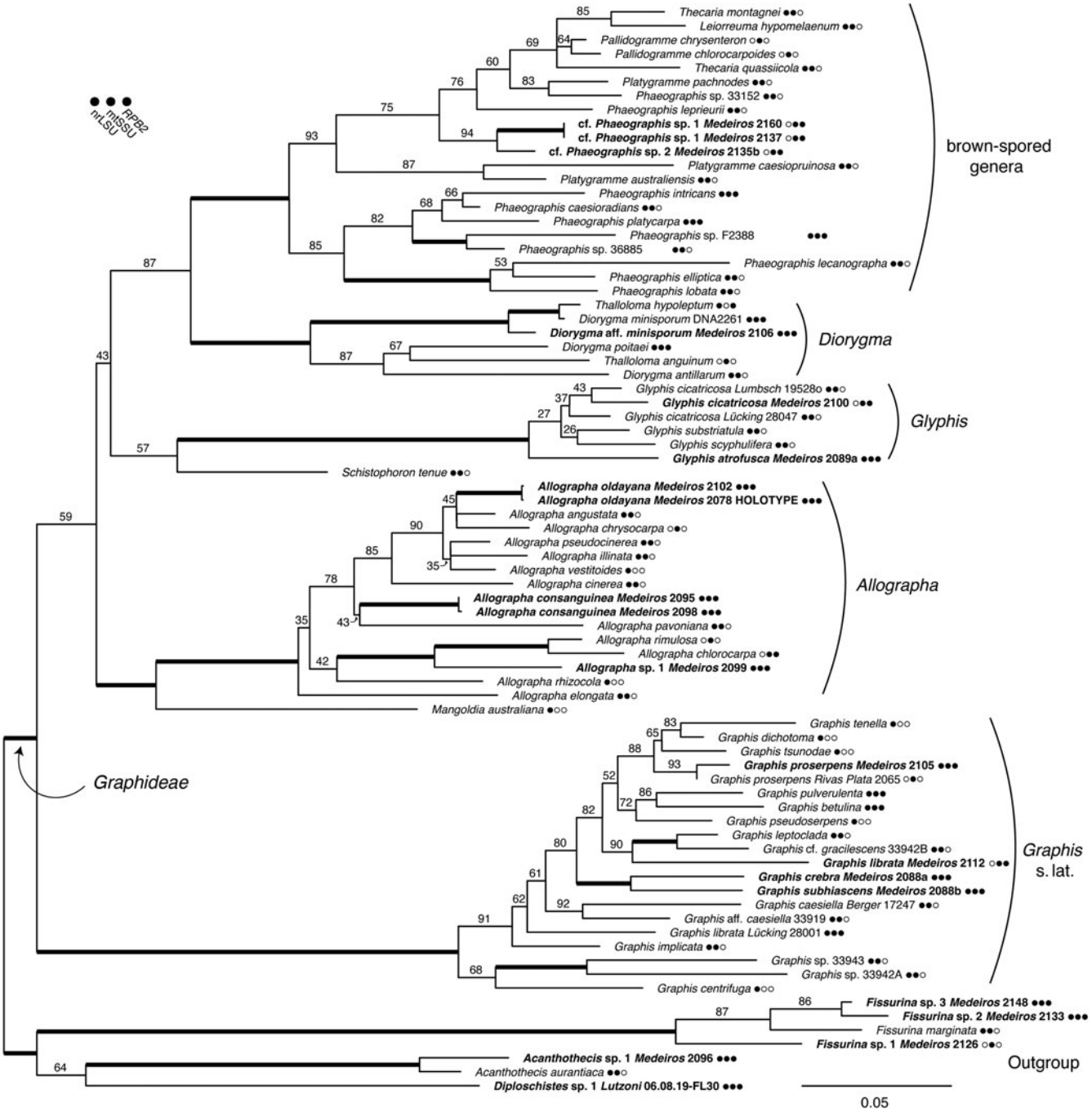

Fig. 3. Maximum likelihood phylogeny of *Graphidaceae* tribe *Graphideae* based on concatenated analysis of nrLSU, mtSSU and *RPB2*. Specimens in bold are from South Africa. Ultrafast bootstrap (UFBoot2; Hoang *et al*., 2018) values ≥ 95 are indicated with thickened branches. Scale indicates substitutions per site. Loci included in the alignment are indicated for each specimen, and their GenBank Accession numbers are shown in Table 1. For information on how *Graphideae* is situated in a wider phylogenetic context within *Graphidaceae*, see Lumbsch *et al*. (2014*a*).

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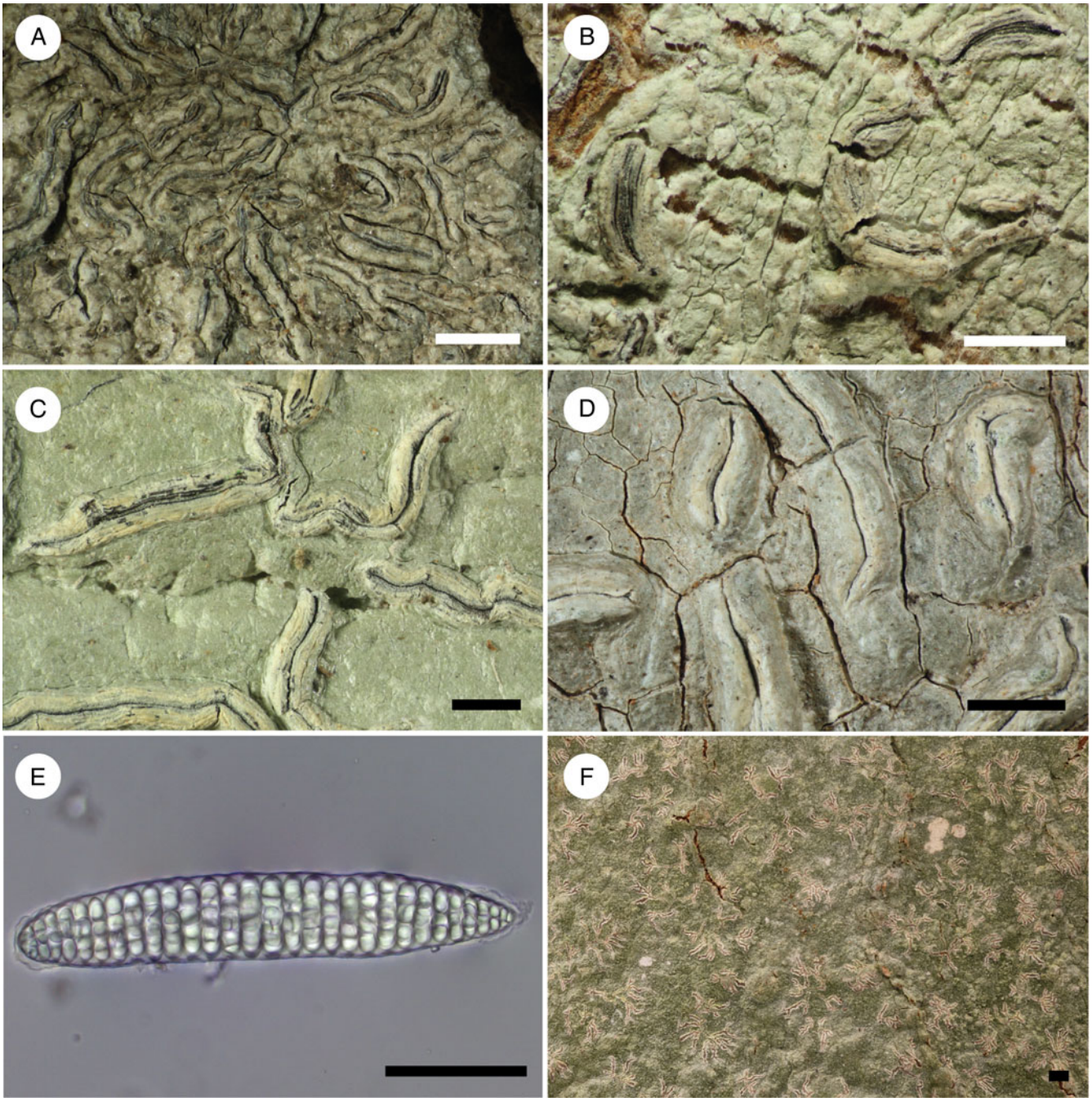

Fig. 4. Images of South African *Graphidaceae*. A, *Allographa consanguinea* (TRH L-17909). B, *A. leptospora* (*Medeiros* L449). C, *A. oldayana* (*Medeiros* L506). D, *A. oldayana* (*Medeiros* 2078—holotype). E, ascospore of *A. oldayana* (*Medeiros* L507). F, *Diorygma* aff. *minisporum* (*Medeiros* 2106). Scales: A–D & F = 1 mm; E = 50 μm. Images by IDM (A–E) and Thomas Barlow (F). In colour online.

Etymology. The specific epithet honours Professor Fred C. Olday (College of the Atlantic, Bar Harbor, Maine, USA), who introduced the first author to the study of lichens.

Distribution and ecology. This species occurs in forested areas of eastern South Africa (e.g. Fig. 2A). Although fresh collections were made only in Northern and Southern Mistbelt Forest at the Buffelskloof and Karkloof reserves, respectively (Mucina & Geldenhuys 2006), one herbarium specimen from near Eshowe suggests that this species occurred in more coastal forest, at least historically (Mucina *et al.* 2006).

Remarks. Molecular data confirm the placement of this species in *Allographa* (Fig. 3). *Allographa elixii* (A. W. Archer) Lücking & Kalb, the only other species in the genus with hirtifructic acid, differs from the new species in having an inspersed hymenium and ascospores which are only terminally muriform (Archer 2001*a*). *Allographa cerradensis* differs in the inspersed hymenium, the presence of stictic acid instead of hirtifructic acid, and the smaller (80–100 × 15–20 μm) ascospores (Lumbsch *et al.* 2011). The North American Appalachian species *Allographa sterlingiana* (E. A. Tripp & Lendemer) Lücking & Kalb lacks lichen substances and has an inspersed hymenium (Lendemer *et al.* 2013).

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The new species and *A. consanguinea* occur in the same habitats and both have a complete thalline margin, striate labia and large, muriform ascospores. They differ in secondary chemistry (no secondary metabolites in *A. consanguinea*), the more prominent lirellae in *A. oldayana*, and ascospore number (*A. consanguinea* has one spore per ascus). Records of *Allographa acharii* from South Africa (Nylander 1868; Steiner 1907; Doidge 1950; Almborn 1988) may represent *A. oldayana* or *A. consanguinea*. *Allographa acharii* has ascospores of similar size and number to the new species but lacks secondary compounds (Lücking *et al.* 2009).

Hirtifructic acid is an uncommon secondary compound in *Graphidaceae*, known from a handful of species in *Allographa* and *Ocellularia* (Lücking *et al.* 2009; Rivas Plata *et al.* 2012). This substance is rare in *Lecanoromycetes* more broadly and its chemical structure is unknown, although it is believed to be related to echinocarpic acid (Elix 2018). In addition to *Graphidaceae*, it is also known in *Parmeliaceae*, where it is found in several species of *Relicina* and one species of *Hypotrachyna* (Elix 1996; Sipman *et al.* 2009). Elix (1996, 2018) does not report an R_f value for this substance in solvent G; we found the R_f value to be 59. Elix (2018) reported that there were no spot test reactions for hirtifructic acid but the new species reacts weakly K+ yellow, best observed when the secondary compounds are eluted with acetone onto filter paper. This is not diagnostic, however, as many *Graphidaceae* species react K+ yellow for more common substances (Lücking *et al.* 2009). TLC is thus required to confirm the presence of hirtifructic acid.

Additional specimens examined (paratypes). **South Africa:** *KwaZulu-Natal*: 'distr. Eshowe, on the trees in open forest along the small stream at Solheim', 3 ix 1929, *O. A. Høeg* s. n. (TRH L-17871); uMgungundlovu District Municipality, Karkloof Nature Reserve, 29°17′52″S, 30°13′40″E, 2019, *Medeiros* 2102 (DUKE, BOL). *Mpumalanga*: Buffelskloof Private Nature Preserve, 25°15′59″S, 30°31′6″E, 1725 m, in ravine forest, on bark, 2016, *Medeiros* L448 (PRE); *ibid.*, 25°17′31″S, 30°30′15″E, 1380 m, wet forest near bottom of ravine, 2016, *Medeiros* L506, L507 (PRE). *Limpopo*: De Hoeck Forest, west of Tzaneen, 1953, *R. Kräusel* 4b [with *Allographa consanguinea*] (B).

Allographa sp. 1

Remarks. Molecular data place the specimen cited below in *Allographa* without a close match to other species for which sequence data are available (Fig. 3). The specimen has a lateral thalline margin, an excipulum that is striate and apically to peripherally carbonized, and a clear hymenium. No ascospores could be found, precluding a species determination.

Specimen examined. **South Africa:** *KwaZulu-Natal*: uMgungundlovu District Municipality, Karkloof Nature Reserve, 2019, *Medeiros* 2099 (BOL).

Diorygma aff. *minisporum* Kalb, Staiger & Elix

Symb. Bot. Upsal. **34**, 161 (2004); type: Guatemala, *Kalb* & *Plöbst* s. n. (WIS, hb. Kalb—holotype, not seen).

(Figs 2C, 4F)

Remarks. Diorygma minisporum was described from Guatemala (Kalb *et al.* 2004) and occurs widely in South America (Medina *et al.* 2012; Aptroot & Cáceres 2018; Pereira *et al.* 2018). Kirika *et al.* (2012) reported this corticolous species from Kenya and cited this as the first record from outside the Americas. Although the specimen cited below fits *Diorygma minisporum* morphologically, the molecular data suggest that our collection may not be conspecific with the neotropical material (Fig. 3).

Specimen examined. **South Africa:** *KwaZulu-Natal*: uMgungundlovu District Municipality, Karkloof Nature Reserve, 29°17′52″S, 30°13′40″E, on bark at base of large tree, 2019, *Medeiros* 2106 (BOL, DUKE).

Glyphis atrofusca (Müll. Arg.) Lücking

In Archer, *Fl. Australia* **57**, 651 (2009).—*Graphina atrofusca* Müll. Arg., *Flora* **70**, 74 (1887).—*Graphis atrofusca* (Müll. Arg.) Stizenb., *Ber. Tätigk. St. Gallischen Naturwiss. Ges.* **1889-1890**, 186 (1891); type: South Africa, *F. Wilms* 70 (G—lectotype, not seen, designated by Lücking in A. W. Archer, *Fl. Australia* **57**, 651 (2009)).

Graphina polycarpa Müll. Arg., *Flora* **70**, 63 (1887); *Graphis polycarpa* (Müll. Arg.) Stizenb., *Ber. Tät. St. Gallisch. Naturw. Gesellsch.* **1889–1890**, 184 (1891); type: South Africa, *F. Wilms* 48 (G—holotype).

(Fig. 5A)

Remarks. We provide molecular data (ITS, ON507259; for other loci see Table 1) for a topotype of *Glyphis atrofusca*, a corticolous species originally described from the general vicinity of modern-day Kruger National Park (Müller 1887) and subsequently reported from Australia and North America (Archer 2001*b*, 2009; Staiger & Kalb 2004; Lücking & Kalb 2018; Guzmán-Guillermo *et al.* 2021). Lücking & Kalb (2018) noted that this species can be mistaken for a species of *Graphis* (its immersed, more or less elongate lirellae can suggest that genus if the presence of brown pruina is missed or indistinct) and that molecular data had not yet confirmed its placement in *Glyphis*. We show that *Gl. atrofusca* falls in *Glyphis* with high support (Fig. 3).

Staiger (2002) established *Glyphis* subgenus *Pallidoglyphis* for two species with a non-carbonized hypothecium: *Glyphis substriatula* (Nyl.) Staiger and *Gl. atrofusca*, the latter under its synonym *Gl. montoensis* (A. W. Archer) Staiger. Recently, Kalb (2020) described a third species from this group, *Gl. frischiana* Kalb. Prior to our study, only *Gl. substriatula* had molecular data. In our phylogenetic analysis, relationships within *Glyphis* were not well supported, and we can neither confirm nor refute the subgeneric classification adopted by Staiger (2002).

We have only seen South African specimens of this species from savannah vegetation (Fig. 2B). It has also been found in dry, well-lit scrubland in other parts of its range (Archer 2001*b*; Staiger & Kalb 2004). The collection by Wilms cited below (which is from the type locality) is the basis for the record of *Graphis sophistica* Nyl. in Stizenberger (1891) and therefore is also one of the records cited for *Gr. platycarpa* (Eschw.) Zahlbr. by Doidge (1950). There are other historical records of *Gr. sophistica* not from the type locality of *Glyphis atrofusca* (Doidge 1950), so for the present we refrain from excluding *Gr. platycarpa* from the South African checklist as a misapplied name.

Specimens examined. **South Africa:** *Mpumalanga*: Kruger National Park, on bark of *Spirostachys africana*, 2019, *Medeiros* 2089a (BOL, DUKE); 'Corticolam prope urbem Lydenburg', s. d., *F. Wilms* s. n., *Lichenotheca Universalis* 90 (UPS L-203515).

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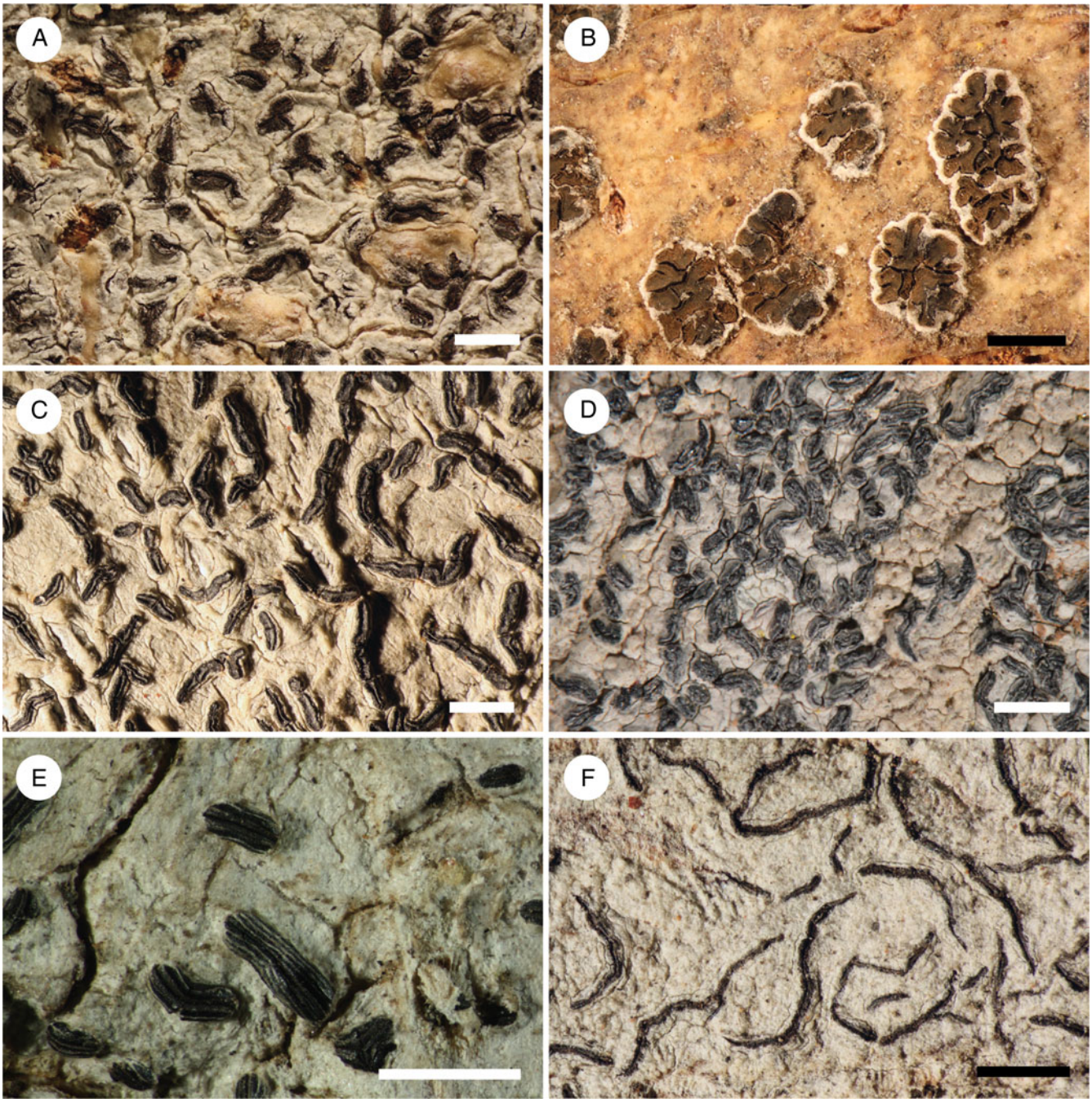

Fig. 5. Images of South African *Graphidaceae*. A, *Glyphis atrofusca* (*Medeiros* 2089a). B, *Gl. cicatricosa* (*Medeiros* 2100). C, *Graphis crebra* (*Medeiros* 2088a). D, *Gr. denudans* (*van der Bijl* 126—holotype). E, *Gr. dupaxana* (*Høeg* s. n.). F, *Gr. furcata* (*Høeg* s. n.). Scales = 1 mm. Images by Willow Torrey (D) and IDM (A–C, E & F). In colour online.

Glyphis cicatricosa Ach.

Syn. Meth. Lich. (Lund), 107 (1814); type: Guinea, s. col. (H-ACH—holotype, not seen).

(Fig. 5B)

Remarks. This distinctive pantropical species has numerous records from KwaZulu-Natal (Nylander 1868; van der Byl 1931; Doidge 1950). There is substantial morphological variation within this species (Staiger 2002) and previous phylogenetic analyses have failed to recover all sequenced individuals in a single, highly supported clade (Rivas Plata *et al.* 2013). In our phylogenetic analysis, specimens from South Africa, Kenya and El Salvador clustered together with poor support (Fig. 3). *Glyphis dictyospora* Staiger, described from Kenya, is externally similar to *Gl. cicatricosa* but has submuriform ascospores (Staiger 2002). It has not been found in South Africa.

Specimens examined. **South Africa:** *Eastern Cape*: 'Alexandria Div., Alexandria State Forest', on *Pinus radiata*, 60 m, *G. Degelius* SA-417 (UPS L-53775, with *Phaeographis* sp.). *KwaZulu-Natal*:

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'distr. Eshowe, Solheim near Eshowe', on loquat trees, 5 ix 1929, *O. A. Høeg* s. n. (TRH L-17867); uMgungundlovu District Municipality, Karkloof Nature Reserve, 29°17′52″S, 30°13′40″E, on bark, 2019, *Medeiros* 2100 & *Flakus* (BOL); Karkloof Region, 1868, *Armstrong* & *Mackenzie* s. n. (DBN); 'Dist. Stanger, Hill north of Umgeni River', 1920, *N. S. Pillans* 10071 (BOL 216555); 'Dist. Nongoma, Umzinene', 18 viii 1929, *O. A. Høeg* s. n. (TRH L-17901).

Graphis bylii var. *lividula* Vain.

Ann. Univ., Fenn. Aboënsis, Ser. A **2**(no. 3), 27 (1926); type: South Africa, Western Cape, Knysna, on *Ficus elastica*, s. d., *P. A. van der Bijl* 277 (TUR-V—holotype!).

Remarks. *Graphis bylii* var. *lividula*, known only from the South African type collection (Vainio 1926), is not closely related to *Gr. bylii* Vain. s. str. (see below) and is morphologically indistinguishable from the northern European species *Gr. inustuloides* Lücking. Both are corticolous species characterized by open, pruinose discs; an apically carbonized, entire excipulum; a clear hymenium; broadly ellipsoid, muriform spores; and the absence of secondary metabolites. The spores of the type of *Gr. bylii* var. *lividula* are 37–49 × 16–22 µm with 9–10 × 4–5 locules, while Lücking & McCune (2012) give measurements of 35–50 × 15–20 µm for *Gr. inustuloides*.

If these are indeed conspecific, their disjunction would be comparable to that of the closely related *Gr. pergracilis*, which is known from South Africa, the Solomon Islands, and the northwestern United States (Archer 2007; Lücking *et al.* 2009; Lücking & McCune 2012). *Graphis bylii* var. *lividula*, *Gr. pergracilis* and *Gr. inustuloides*, together with the Australian species *Gr. coenensis* A. W. Archer and the neotropical *Gr. dimidiata* Vain., form a species complex that requires further study (Lücking & McCune 2012). We have also seen additional specimens from this group that vary slightly from the described species. For example, a South African specimen at PRE (*E. Retief* 551) differs from typical *Gr. pergracilis* in having shorter lirellae, discs that may be partially exposed, and a laterally carbonized excipulum (in some sections carbonized only in the upper two-thirds). Molecular data are not currently available for any species from this group, but such data will be essential for understanding species boundaries in what may represent a complex of cryptic species (Lücking & McCune 2012; van der Pluijm 2014). A precedent for such a pattern can be found in the *Graphis scripta* complex (Neuwirth & Aptroot 2011; Kraichak *et al.* 2015).

Graphis crebra Vain.

Hedwigia **38**, 256 (1899); type: Guadeloupe, *Duss* 541 (TUR-V 27617, not seen).

(Fig. 5C)

Remarks. *Graphis crebra* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species for South Africa, and we provide the first molecular data for the species (Table 1, Fig. 3). *Graphis crebra* and *Gr. handelii* (newly reported from South Africa below) both have open discs, an inspersed hymenium, hyaline, transversely septate ascospores *c.* 25 µm in length, and contain norstictic acid. The hyaline ascospores separate these two taxa from species of *Phaeographis* or *Platygramme* with open discs, whereas these two *Graphis* species can be distinguished from one another by the discs that are white pruinose in *Gr. crebra* and epruinose in *Gr. handelii*. *Glyphis atrofusca* was found at the same savannah site as *Gr. crebra* (Fig. 1B) and also has open discs, but can be readily distinguished by the brown pruina on the discs, clear hymenium, and muriform ascospores. *Graphis pyrrhocheiloides* Zahlbr., which was reported from South Africa by Lücking *et al.* (2009) as an accessory species on the type of *Gr. pergracilis*, is similar to *Gr. crebra* in having open, pruinose discs, a laterally carbonized excipulum, transversely septate ascospores and norstictic acid, but differs in the clear hymenium.

Specimen examined. **South Africa:** *Mpumalanga*: Kruger National Park, on bark of *Euclea divinorum*, 2019, *Medeiros* 2088a (BOL, DUKE).

Graphis denudans Vain.

Ann. Univ., Fenn. Aboënsis, Ser. A **2**(no. 3), 27 (1926); type: South Africa, KwaZulu-Natal, near Durban, s. d., *P. A. van der Bijl* 126 (TUR-V—holotype!).

(Fig. 5D)

Remarks. This corticolous species is characterized by very short (< 1 mm), unbranched to sparsely branched, erumpent lirellae with lateral thalline margin and entire (or weakly striate?) labia, discs that are often partially exposed, a completely carbonized excipulum (sometimes weakly at base) and a clear hymenium; ascospores 8 per ascus, hyaline, transversely 5–6-septate, 17–22 (–25) × 7–8 µm; and the presence of norstictic acid. *Graphis denudans* is known only from the holotype and has not been reported since its original description by Vainio (1926). It may be related to *G. schiffneri* Zahlbr., an eastern palaeotropical species that differs in having longer lirellae, obscurely striate labia and slightly longer ascospores (Lücking *et al.* 2009); additional material might show the two to be conspecific.

Graphis dupaxana Vain.

Ann. Acad. Sci. Fenn., Ser. A **15**(no. 6), 241 (1921); type: Philippines, *McGregor* 14313 (TUR-V—lectotype, not seen).

(Fig. 5E)

Remarks. *Graphis dupaxana* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species for South Africa. It differs from other species of *Graphis* in South Africa by having a completely carbonized, striate excipulum, a combination of characters more associated with *Allographa* (Lücking & Kalb 2018). It differs from South African species of *Allographa* in lacking a thalline margin and having a distinctly white (not greenish) thallus.

Specimen examined. **South Africa:** *KwaZulu-Natal*: 'distr. Eshowe, in a small krantz at Inyezane R., between the Mtunzeni Road and S. Siding', very dense vegetation of small trees, 31 viii 1929, *O. A. Høeg* s. n. (TRH L-17906).

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Graphis furcata Fée

Essai Crypt. Exot. (Paris), 40 (1825); type: South America, s. col. (G—holotype, not seen).

(Fig. 5F)

Remarks. *Graphis furcata* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species for South Africa. See remarks under *Gr. pinicola* for how to differentiate these two species. *Graphis furcata* is known only from a single historical collection and its current status in South Africa is uncertain.

Specimen examined. **South Africa:** *KwaZulu-Natal*: 'distr. Durban, Salisbury Island', small trees in rather dense vegetation outside the mangrove, 20 ix 1929, *O. A. Høeg* s. n. (TRH L-17915).

Graphis handelii Zahlbr.

Symb. Sinic. **3**, 44 (1930); type: China, *Handel-Mazzetti* 12788 (W—lectotype, not seen).

(Fig. 6A)

Remarks. *Graphis handelii* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species for South Africa. It is very close to *Gr. crebra* and in the field could also be mistaken for a species of *Phaeographis*; characters to separate these taxa are provided above in the remarks for *Gr. crebra*. We have seen *Graphis handelii* only in historical specimens from KwaZulu-Natal, where it was found in both coastal and inland forest vegetation. We lack recent collections from the Indian Ocean Coastal Belt vegetation of this province, a threatened vegetation type (Jewitt 2018), so the current status of this species in South Africa is uncertain.

Specimens examined. **South Africa:** *KwaZulu-Natal*: 'distr. Durban, summit of the Bluff, on trees in dense vegetation', 22 ix 1929, *O. A. Høeg* s. n. (TRH L-17922); 'distr. Umgeni, at Petermaritzburg, near Town Bush Road. On small tree (*Solanum*) along small stream', 29 ix 1929, *O. A. Høeg* s. n. (TRH L-17908); 'distr. Eshowe, Solheim near Eshowe', on branches of loquat trees, 5 ix 1929, *O. A. Høeg* s. n. (TRH L-17899, mixed collection with other *Graphis* spp.); 'Pietermaritzburg Division, Table Mountain, epiphloeodal on *Croton sylvaticus* growing along forest margin, 2000 ft', 1948, *D. J. B. Killick* 535 (BOL 207564).

Graphis librata C. Knight

Trans. Proc. New Zeal. Inst. **16**, 404 (1884); type: New Zealand, *Knight* 67:23 (WELT—lectotype, not seen, designated by Hayward, *New Zealand J. Bot.* **15**, 571 (1977)).

Graphis diaphoroides Müll. Arg., *Flora (Regensburg)* **69**(20), 316 (1886); type: South Africa, Mpumalanga, near Lydenburg, 1884, *Wilms* 11 [Lojka *Lichenothecum Universalis* 91] (G—holotype, not seen; BM, M, MICH, NY—isotypes, not seen; US—isotype!).

(Fig. 6B)

Remarks. Lücking *et al.* (2009) synonymized *Graphis diaphoroides*, a corticolous species described from South African material (Müller 1886), with *G. librata*. As currently circumscribed, this species is pantropical; it is one of the most common and widely distributed species of *Graphis* in South Africa. We obtained molecular data from one specimen of *G. librata*. In our phylogenetic analysis, this specimen was recovered distant to *G. librata* from El Salvador but without strong support (Fig. 3). Molecular data for *Graphis librata* from other locations, especially the type locality in New Zealand, will be necessary to understand the delimitation of this species.

Specimens examined. **South Africa:** *KwaZulu-Natal*: Karkloof, on bark, 2019, *Medeiros* 2112 (BOL). *Western Cape*: Kirstenbosch, on *Brabejum*, ii 1946, *S. Garside* s. n. (BOL 207569); Kirstenbosch, on bark, 2019, *Medeiros* 2145 (BOL); Table Mountain National Park, Silver Mine pond, on bark of tree at base of dam, 2019, *Medeiros* 2143 (BOL); 'S. Cape, Zitzikamma forest near Coldstream, on twigs of fruit trees', vii 1944, *J. Pont* s. n. (PRE 766676); Nature's Valley, on vining *Euphorbiaceae*, 2019, *Medeiros* 2134 (BOL).

Graphis longula Kremp.

Flora **59**, 414 (1876); type: Brazil, *Glaziou* 5497 (M—lectotype, not seen).

(Fig. 6C)

Remarks. *Graphis longula* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species from South Africa.

Specimen examined. **South Africa:** *Mpumalanga*: Buffelskloof Private Nature Preserve, 25°17′31″S, 30°30′15″E, 1380 m, wet forest near bottom of ravine, 2016, *Medeiros* L497 (BOL).

Graphis pinicola Zahlbr.

In Handel-Mazzetti, *Symb. Sinic.* **3**, 43 (1930); type: China, *Handel-Mazzetti* 2829 (W—holotype, not seen; US—isotype, not seen).

(Fig. 6D)

Remarks. *Graphis pinicola* has a pantropical distribution (Lücking *et al.* 2009). This is the first report of this corticolous species from South Africa, although it is a widespread species with numerous historical and modern collections. *Graphis pinicola* is similar to *Gr. furcata*; however, the former has a corticate thallus and well-defined thalline margin, while the latter is ecorticate and the thalline margin slopes gradually into the thallus. *Graphis librata* differs from *Gr. pinicola* in producing norstictic acid.

Specimens examined. **South Africa:** *KwaZulu-Natal:* 'distr. Eshowe, S. of Solheim', on trees, 7 ix 1929, *O. A. Høeg* s. n. (TRH L-17911); 'Solheim near Eshowe', on branches of loquat trees, 5 ix 1929, *O. A. Høeg* s. n. (TRH L-17899, mixed collection with other *Graphis* spp.); Karkloof region, *Armstrong* & *Mackenzie* s. n., 1866 (DBN). *Western Cape*: Cape Town, east slope of Table Mtn at Kirstenbosch Botanical Garden, 400 m, 1986, *H. Sipman* 20.181 (B); Garden Route National Park, Nature's Valley, 2019, *Medeiros* 2135a (with *Phaeographis* sp.) (BOL).

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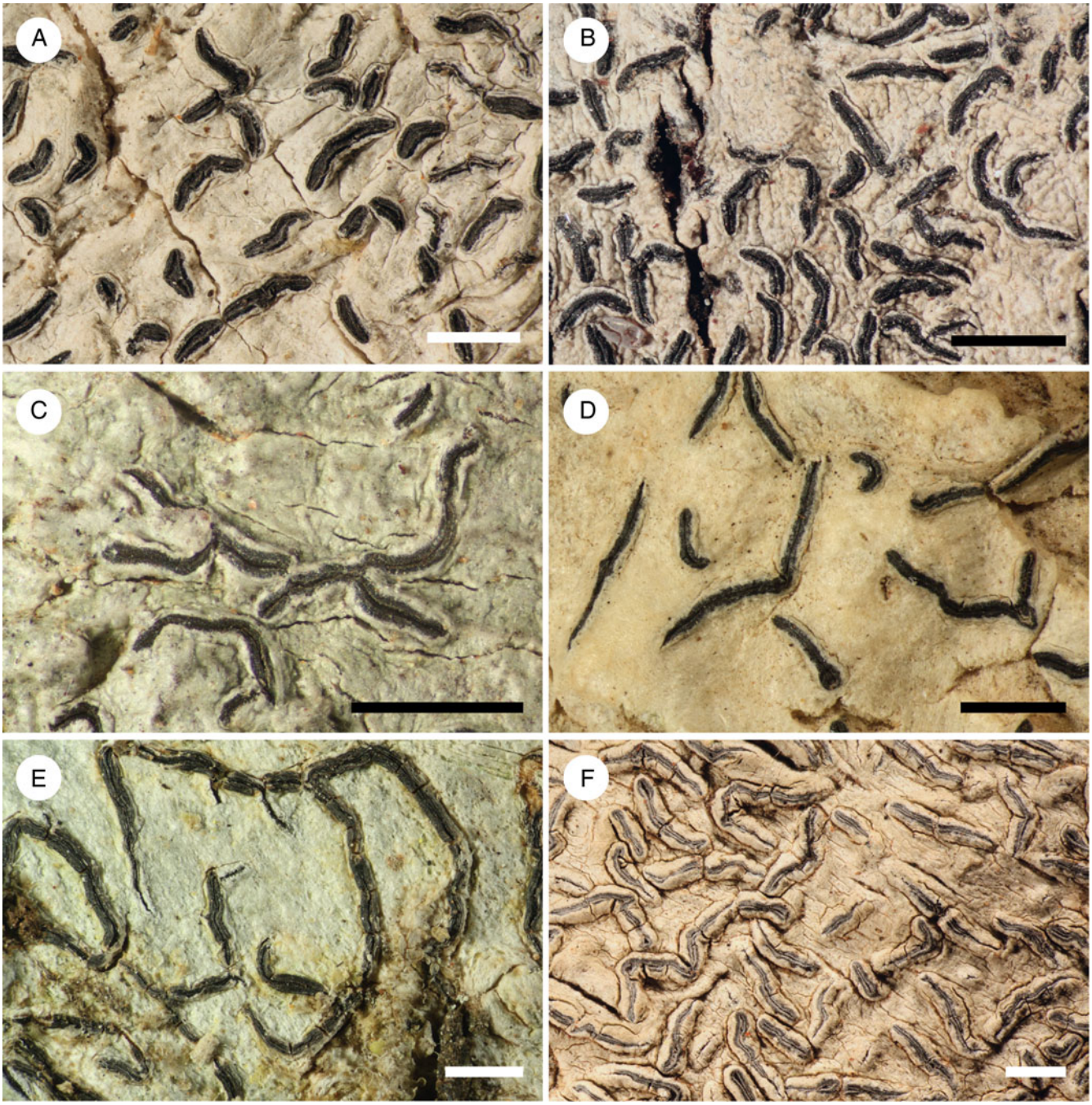

Fig. 6. Images of South African *Graphidaceae*. A, *Graphis handelii* (*Killick* 535). B, *Gr. librata* (*Garside* s. n.). C, *Gr. longula* (*Medeiros* L497). D, *Gr. pinicola* (*Sipman* 20.181). E, *Gr. proserpens* (*Medeiros* L444). F, *Gr. subhiascens* (*Medeiros* 2088b). Scales = 1 mm. All Images by IDM. In colour online.

Graphis proserpens Vain.

Botanisk Tidsskrift **29**, 132 (1909).—*Graphis disserpens* Vain., *Acta Soc. Fauna Flora Fenn.* **7**(2), 123 (1890), nom. illeg. (non *Graphis disserpens* Nyl.); type: Brazil, *Vainio* s. n. (TUR-V—holotype, not seen).

(Fig. 6E)

Remarks. *Graphis proserpens* has not previously been reported from South Africa, although this corticolous species is probably pantropical (Lücking *et al.* 2009). Historical references to *Gr. striatula* Ach. (Nylander 1868) probably represent this species (see discussion of misapplied names, below). Diederich *et al.* (2017) recently reported this species as new to the Seychelles. In our phylogenetic analysis, *Gr. proserpens* from South Africa was recovered as sister to *Gr. proserpens* from the Philippines (Fig. 3). The GenBank Accession number for the ITS sequence of *Medeiros* 2105 is ON507258.

Specimens examined. **South Africa:** *KwaZulu-Natal*: Karkloof, on bark, 2019, *Medeiros* 2105 (BOL, DUKE). *Mpumalanga*: Buffelskloof Private Nature Preserve, 25°15′59″S, 30°31′6″E,

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1725 m, 2016, *Medeiros* L444 (PRE), L447 (BOL); 25°17′31″S, 30° 30′15″E, 1380 m, wet forest near bottom of ravine, 2016, *Medeiros* L498 (PRE).

Graphis subhiascens (Müll. Arg.) Lücking

In Lücking *et al.*, *Fieldiana, Bot.* **46**, 111 (2008).—*Graphina subhiascens* Müll. Arg., *Bot. Jahrb.* **20**, 2811 (1894); type: Tanzania, *Holst* 696 (G—holotype, not seen).

(Fig. 6F)

Remarks. *Graphis subhiascens* has not previously been reported from South Africa, although this corticolous species is pantropical (Lücking *et al.* 2009). We provide the first molecular data for this species (Table 1, Fig. 3). It has medium-sized, muriform ascospores and a complete thalline margin, and can be distinguished from *Allographa consanguinea* and *A. oldayana* on the basis of the larger ascospores and striate, completely carbonized excipulum in those species. Other South African species with an entire, laterally carbonized excipulum (*Gr. crebra*, *Gr. furcata*, *Gr. handelii* and *Gr. pinicola*) have transversely septate ascospores.

Specimen examined. **South Africa:** *Mpumalanga*: Kruger National Park, on bark of *Euclea divinorum*, 2019, *Medeiros* 2088b (BOL).

Mangoldia bylii (Vain.) I. Medeiros comb. nov.

MycoBank No.: MB 843786

Graphis bylii Vain., *Ann. Univ., Fenn. Aboënsis, Ser. A* **2**(no. 3), 27 (1926).—*Graphina bylii* (Vain.) Zahlbr., *Cat. Lich. Univers.* **8**, 604 (1932); type: South Africa, Western Cape, Knysna, on bark of *Ocotea bullata*, 1922, *P. A. van der Byl* 265 (TUR-V—holotype!).

Syn. nov.: *Graphina atronitens* A. W. Archer, *Mycotaxon* **77**, 162 (2001).—*Thalloloma atronitens* (A. W. Archer) A. W. Archer, *Telopea* **11**, 77 (2005).—*Mangoldia atronitens* (A. W. Archer) Lücking *et al.*, *Phytotaxa* **69**, 4 (2012); type: Australia, New South Wales, Black Rock, *c.* 7 km S of Brunswick Heads, 5 November 1998, *A. W. Archer* G292 (NSW—holotype, not seen).

(Fig. 7A)

Remarks. Lücking *et al.* (2012) established the genus *Mangoldia* for two Australian species with *Phaeographis*-like ascomata but *Graphis*-like ascospores. *Mangoldia* is closely related to *Allographa* (Fig. 3). The holotype of *Graphis bylii* closely matches the description of *Graphina atronitens* from Archer (2001*b*); the ascospores of *G. bylii* are slightly larger (41–51 × 12–18 µm versus 30–45 × 10–15 µm) but the difference is not sufficient to treat them as separate species. The previously unrecognized presence of this genus in South Africa highlights biogeographical connections between southern Africa and Australasia (Almborn 1988; Galley & Linder 2006; McCarthy 2006). We have not seen any specimens other than the holotype, and the present status of this species in South Africa is therefore unknown.

Platythecium sp.

(Fig. 7B)

Remarks. The only specimen of *Platythecium* we have seen from South Africa could not be determined to species because mature spores were not seen and none of the TLC spots could be positively identified; secondary chemistry is important for species determination in this genus (Neuwirth *et al.* 2017). We include it here because this genus has not otherwise been reported from South Africa. In South Africa, *Platythecium* is probably restricted to the vegetation of the Indian Ocean Coastal Belt, which is a threatened vegetation type (Jewitt 2018) that lacks recent lichen sampling.

Specimen examined. **South Africa:** *KwaZulu-Natal*: 'distr. Eshowe, rather dense and dark situation in the indigenous forest', 26 viii 1929, *O. A. Høeg* s. n. (TRH L-17910).

Misapplied names

Allographa striatula (Ach.) Lücking & Kalb

In Kalb *et al.*, *Phytotaxa* **377**, 26 (2018).—*Opegrapha striatula* Ach., *Syn. Meth. Lich.* (Lund), 74 (1814).—*Graphis striatula*

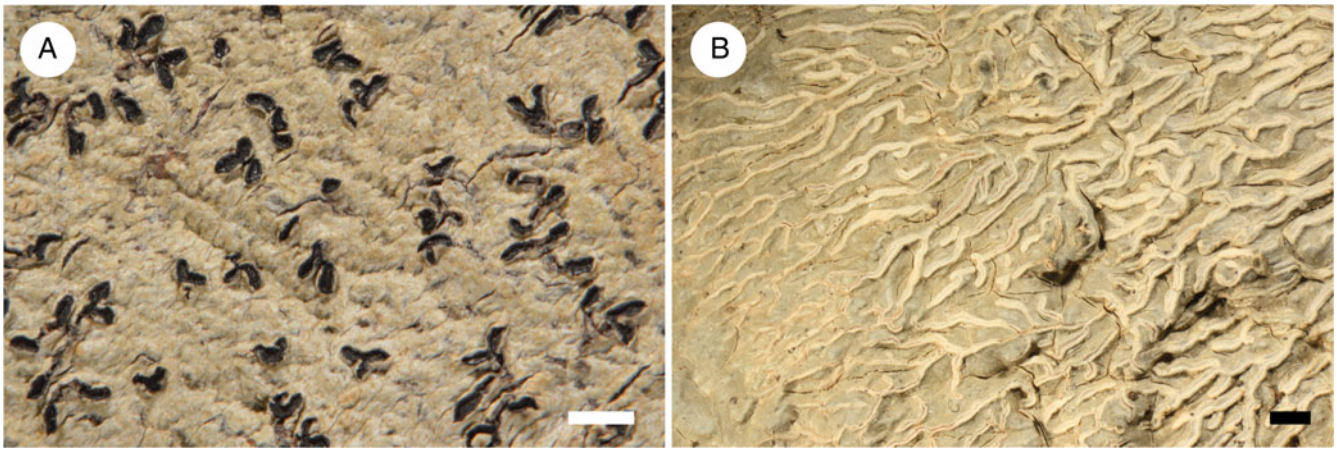

Fig. 7. Images of South African *Graphidaceae*. A, *Mangoldia bylii* (*van der Bijl* 265—holotype). B, *Platythecium* sp. (*Høeg* s. n.). Scales = 1 mm. Images by Willow Torrey (A) and IDM (B). In colour online.

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(Ach.) Spreng., *Syst. Veg., Edn 16* **4**, 250 (1827); type: Guinea, s. col. (H-ACH 629—holotype, not seen).

Remarks. This species is known for South Africa only from Nylander (1868). Several specimens examined by Nylander are in the Armstrong collection at DBN. A small number lack spores and are undeterminable, while several others represent *Graphis proserpens*.

Graphis analoga Nyl.

Annls Sci. Nat., Bot., Sér. 4 **11**, 244 (1859); type: Tahiti, *Viellard & Planchet* G13:8 (H-NYL 7432—holotype, not seen).

Remarks. This species is known for South Africa only from Nylander (1868). The single specimen in the Armstrong collection at DBN is in very poor condition, but the excipulum is striate and completely carbonized. We could not find ascospores, although Nylander's notes on the specimen give spore dimensions of 46–80 µm × 18–30 µm. The excipulum characters and ascospore size contradict the description of this species provided by Lücking *et al.* (2009).

Graphis scripta (L.) Ach.

K. Vetensk-Acad. Nya Handl. **30**, 145 (1809).—*Lichen scriptus* L., *Spec. Plant*. **2**, 1140 (1753); type: Sweden, *Malme* s. n. [*Lich. Suec. Exs*. 47] (UPS—epitype, not seen).

Remarks. This is primarily a temperate, Northern Hemisphere species (Kraichak *et al.* 2015), although there are a small number of confirmed records from the Southern Hemisphere (Neuwirth & Aptroot 2011). Frequent records of this species in older literature (see Doidge (1950) and citations therein) date to an era when *Graphidaceae* biodiversity was poorly known. All South African specimens we have seen identified as *Graphis scripta* are misidentifications of other taxa.

Discussion

The species outlined above consist mostly of pantropical taxa, especially in *Glyphis* and *Graphis* s. str. Conversely, *Allographa oldayana* is a candidate southern African endemic, and *Mangoldia bylii* represents a biogeographical connection between South Africa and Australia. Several species known only from their type specimens (e.g. *Graphis bylii* var. *lividula* and *Gr. denudans*) will require additional study to resolve their taxonomy and biogeography.

The forest habitats preferred by many *Graphidaceae* species are a small proportion of the total land cover in South Africa (Fig. 1; Mucina & Geldenhuys 2006), and their natural patchiness might contribute to both the evolution of endemic species and the susceptibility to disturbance. More than one third of the species we treat in this paper are known from South Africa only from pre-1950s collections. Their current status in the country is uncertain given high levels of forest habitat loss, especially in the Indian Ocean Coastal Belt (Mucina & Geldenhuys 2006; Jewitt 2018).

In addition to the new species and records listed in this paper, we have seen many additional specimens that cannot clearly be assigned to a known species and several putative new species known only from a single specimen. For the time being, we refrain from describing these new species pending the availability of additional specimens and molecular data. The present paper is only a first step towards a modern understanding of lirelliform *Graphidaceae* in South Africa, and we hope it will be a starting point for more researchers to investigate taxonomic problems such as the *Graphis pergracilis* complex and the description of additional new species.

The separation of *Allographa* and *Graphis* s. str. (Lücking & Kalb 2018) resolved one of the broader systematic issues in *Graphideae*: the polyphyly of *Graphis* s. lat. (Berger *et al.* 2011; Rivas Plata *et al.* 2011). Two major problems remain. First, *Thalloloma* is a junior synonym of *Diorygma*, but the two genera have not yet been formally merged. When these genera were resurrected in the modern understanding of *Graphidaceae* (Staiger 2002; Kalb *et al.* 2004), they were recognized as close relatives. Molecular data now strongly support a single genus for this group (Fig. 3) but, to avoid excessive name changes, more molecular data from atypical species of *Thalloloma* are necessary before the genera are formally synonymized. Second, and a greater problem, phylogenetic relationships and generic boundaries among the genera with pigmented ascospores (*Leiorreuma*, *Pallidogramme*, *Phaeographis*, *Platygramme*, *Sarcographa* and *Thecaria*) are unresolved or not well supported (Fig. 3). This group has a complicated nomenclatural and taxonomic history (Staiger 2002; Lücking *et al.* 2007). *Phaeographis* has long been known to be polyphyletic (Rivas Plata *et al.* 2013), and our new data on *Platygramme pachnodes* suggests that *Platygramme* is also polyphyletic (Fig. 3). Genera in this clade have probably been oversplit; for example, there is much more sequence variation within *Graphis* or *Allographa* than there is among *Leiorreuma*, *Pallidogramme* and *Thecaria* (Fig. 3). We will address some of these taxonomic and nomenclatural issues in a subsequent paper on the South African species of *Graphidaceae* tribe *Graphideae* with pigmented ascospores, which will also include a complete key to *Graphideae* in South Africa.

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