Phaeoacremonium species diversity on woody hosts in the Western Cape Province of South Africa

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Key words

brown wood streaking decline disease phylogeny systematics Togninia

Abstract Nineteen Phaeoacremonium species are currently known in South Africa. These have been reported from grapevines, fruit trees, fynbos twig litter and arthropods. In other countries some of these Phaeoacremonium species are also known from hosts such as European olive, quince and willow that commonly occur in the Western Cape Province of South Africa, where most South African records of Phaeoacremonium have been made. The aim of this study was to investigate the species diversity and host-range of Phaeoacremonium in the Western Cape Province of South Africa by characterising 156 isolates collected from 29 woody hosts. Phylogenetic analyses of combined actin and beta-tubulin datasets allowed for the identification of 31 species among the 156 isolates, including 13 new species and 3 known species that had not been recorded in South Africa previously. The new Phaeoacremonium species include P. album, P. aureum, P. bibendum, P. gamsii, P. geminum, P. junior, P. longicollarum, P. meliae, P. oleae, P. paululum, P. proliferatum, P. rosicola and P. spadicum. All previous records of P. alvesii in South Africa were re-identified as P. italicum, but both species were recovered during this survey. A total of 35 described Phaeoacremonium species are now known from South Africa, more than double the number reported from any other country. This high diversity reflects the high diversity of indigenous flora of the Cape Floral Region, a biodiversity hotspot mainly situated in the Western Cape Province. Paraphyly and incongruence between individual phylogenies of the actin and beta-tubulin regions complicated species delimitation in some cases indicating that additional phylogenetic markers should be investigated for use in Phaeoacremonium phylogenies to prevent misidentifications and the introduction of vague species boundaries.

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INTRODUCTION

The genus Phaeoacremonium (Togniniales, Togniniaceae) was originally described in 1996 during a re-evaluation of isolates similar to what was considered at that stage to be Phialophora parasitica (Crous et al. 1996). The newly described genus contained six species: Phaeoacremonium angustius, P. chlamydosporum (≡ Phaeomoniella chlamydospora), P. inflatipes, P. aleophilum (= P. minimum), P. parasiticum (type species) and P. rubrigenum (Crous et al. 1996). Some landmark publications regarding the taxonomy of the genus include the identification of Togninia as the sexual morph of Phaeoacremonium (Mostert et al. 2003), the monograph by Mostert et al. (2006) that standardised the taxonomy of 22 Phaeoacremonium and 10 Togninia species known at the time, and the recent review by Gramaje et al. (2015) in which Togninia species are formally included in Phaeoacremonium according to the change to single nomenclature for fungi (Hawksworth et al. 2011). Gramaje et al. (2015) included a total of 46 species in Phaeoacremonium, but failed to consider the synonymy of P. novae-zealandiae with P. leptorrhynchum (Réblová 2011) so the actual total taxa known at that time should have been 45. With the recently described P. tectonae (Ariyawansa et al. 2015), P. pseudopanacis (Crous et al. 2016) and P. nordesticola (Da Silva et al. 2017), the total number of species in Phaeoacremonium currently stands at 48.

Phaeoacremonium has a global distribution, with species being reported from South, Central and North America, Europe,

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Scandinavia, Ukraine, the Middle East, Far East, Oceania and Africa (Gramaje et al. 2015). Most Phaeoacremonium species are associated with wood diseases of plants, e.g., Petri and esca diseases of grapevines (Crous et al. 1996, Essakhi et al. 2008, Gramaje et al. 2009a, b, White et al. 2011, Raimondo et al. 2014) and dieback and cankers on other fruit trees and woody hosts (Damm et al. 2008b, Gramaje et al. 2012, Mohammadi et al. 2014, Sami et al. 2014, Carlucci et al. 2015, Hashemi & Mohammadi 2016, Kazemzadeh Chakusary et al. 2017). Eleven Phaeoacremonium species are also known from human infections (Mostert et al. 2005, Gramaje et al. 2015). Other hosts and substrates have also been reported, including non-woody plants such as Lactuca canadensis and Dactylis glomerata (Sánchez Márquez et al. 2007), arthropods (Kubátová et al. 2004, Mostert et al. 2006, Moyo et al. 2014), soil and once from another fungus (Mostert et al. 2005). Several Phaeoacremonium species are known only from grapevine, and more Phaeoacremonium species have been reported from this host than any other host (Gramaje et al. 2015). This is likely to reflect the higher priority given to trunk disease research on grapevines than to fungi from comparable sites on other hosts. It does not imply host preference or specificity. In fact, species like P. minimum and P. parasiticum have been recorded from more than 10 hosts each, and most species that have been reported from more than one country have also been reported from more than one host (Gramaje et al. 2015).

A total of 19 Phaeoacremonium species are currently known in South Africa. Twelve species have been reported on grapevines; two of these have not been associated with other hosts in South Africa (Groenewald et al. 2001, Mostert et al. 2005, 2006, White et al. 2011). The remaining 10 species known from grapevines and seven species not known from grapevines have

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been reported from fruit trees (Diospyros kaki, Malus domestica, Prunus spp. and Pyrus communis), fynbos twig litter (Brabejum stellatifolium and Leucadendron sp.) and arthropods (Damm et al. 2008b, Marincowitz et al. 2008, Cloete et al. 2011, Moyo et al. 2014, 2016). In other parts of the world, some of these Phaeoacremonium species, such as P. alvesii, P. iranianum and P. minimum, are also known from hosts such as European olive (Olea europaea subsp. europaea), quince (Cydonia oblonga) and willow (Salix spp.) (Crous & Gams 2000, Nigro et al. 2013, Sami et al. 2014, Carlucci et al. 2015, Hashemi & Mohammadi 2016, Kazemzadeh Chakusary et al. 2017). These hosts also occur in the Western Cape Province of South Africa where viticulture is one of the main agricultural enterprises. Other woody plants that might harbour Phaeoacremonium infections are often found growing near vineyards including not just commercial crops or trees and shrubs cultivated for diverse purposes in gardens, but also naturally occurring trees. Many of these plants have not been reported as hosts for Phaeoacremonium species anywhere else in the world. The aim of the present study was to assess the species diversity and host range of Phaeoacremonium in the Western Cape Province of South Africa by characterising isolates obtained from 29 different woody hosts often found in close proximity to vineyards.

MATERIALS AND METHODS

Isolates

Samples of 29 woody hosts exhibiting dieback or decline symptoms were collected in the Western Cape (South Africa). Two additional samples of 10-yr-old grapevines from Limpopo that exhibited symptoms of slow dieback were also included. Isolations were made from various internal wood symptoms (including wedge-shaped or irregular black/brown discolouration, vascular streaking and white rot) as described by Moyo et al. (2016). All isolates were stored as colonised potato dextrose agar (PDA; Biolab) plugs in sterile water at 4 °C or in 10 % glycerol at -80 °C at the Plant Protection Division of the ARC Infruitec-Nietvoorbij in Stellenbosch, South Africa. Isolates of new species were also deposited in the fungal collection of the University of Stellenbosch Department Plant Pathology (STE-U) and in the Westerdijk Fungal Biodiversity Institute (CBS), in Utrecht, the Netherlands.

DNA extraction, PCR and sequencing

DNA was extracted using a CTAB protocol as described by Damm et al. (2008b) and quantified using a NanoDrop ND-1000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). DNA samples were diluted to a range of 5-15 ng/µL prior to PCR amplification.

The beta-tubulin region was amplified in 10 µL reactions with 1× KAPA Taq ReadyMix, primers T1 (O'Donnell & Cigelnik 1997) and Bt2b (Glass & Donaldson 1995) at 0.08 µM each, and 1 µL DNA under cycling conditions entailing initial denaturation for 3 min at 94 °C, 30 cycles of denaturation at 94 °C for 30 s, annealing for 30 s at 58 °C, and extension for 30 s at 72 °C, and a final extension for 7 min at 72 °C. The actin region was amplified using the primers ACT-512F and ACT-783R from Carbone & Kohn (1999) with conditions as described for betatubulin, but annealing at 52 °C. In some cases where these conditions failed to produce usable PCR product for sequencing DNA samples were re-amplified in 20 µL reactions containing primers at 0.8 µM each, and 2 µL DNA with other reagents and conditions as above. A touch-down PCR entailing annealing temperatures decreasing with 2 °C every 5 cycles from 66 °C to 58 °C and a final set of 20 cycles annealing at 55 °C was also used for some actin amplifications.

All PCR products were visualised on 1 % agarose gels and successful amplifications were sequenced in both directions. Successful amplifications from 10 μ L reactions were sequenced directly, but those performed in 20 μ L volumes were purified using a MSB® Spin PCRapace kit (Invitek, Germany) prior to sequencing using the BigDye Terminator v. 3.1 Cycle Sequencing Kit (PE Biosystems, Foster City, CA, USA). Sequencing product was analysed on an ABI PRISM 3130XL DNA sequencer (Perkin-Elmer, Norwalk, CT, USA) at the Central Analytical Facility of Stellenbosch University.

Sequence editing and preliminary species identification

Sequences were trimmed and edited using Geneious R8 (Kearse et al. 2012). Preliminary identifications were obtained by BLAST analyses of single strand beta-tubulin or actin sequences against a curated database containing only sequences used by Gramaje et al. (2015) and those of *P. tectonae* that was described later in the same year (Ariyawansa et al. 2015). Putative novel species identified in these analyses were also subjected to a BLAST search against the NCBI nucleotide database. BLAST identifications were confirmed and refined with preliminary maximum likelihood phylogenies inferred under the GTR+I+G model using PhyML (Guindon et al. 2010) in Geneious R8 without calculation of bootstrap support. Based on these preliminary identifications, strains representing putative new species, first reports for various hosts in South Africa, and intraspecific phylogenetic variants of known species were selected. For these strains both forward and reverse sequences of the beta-tubulin and actin regions were generated, edited and assembled in Geneious R8 and double strand consensus sequences were extracted for alignment and phylogenetic analyses.

Phylogenetic analyses

Sequences used by Gramaje et al. (2015), sequences from the published descriptions of *P. nordesticola*, *P. pseudopanacis* and *P. tectonae*, and representative sequences from previous reports of *Phaeoacremonium* species in South Africa were included as reference sequences (Appendix 1). *Calosphaeria africana* STE-U 6182, *Jattaea algeriensis* STE-U 6201 and *Pleurostoma richardsiae* CBS 270.33 were included as outgroups. Reference and *de novo*-generated sequences of the two gene regions were aligned separately using the E-INS-i algorithm in the MAFFT plugin of Geneious R9 (Katoh & Standley 2013), visually inspected for obvious alignment errors, and concatenated in Geneious R9. Both maximum likelihood and Bayesian analyses were performed on the concatenated alignment, while individual gene alignments were only subjected to maximum likelihood analyses.

Maximum likelihood analysis was performed in PhyML-mpi (Guindon et al. 2010) under the best fit model (HKY+I+G) as estimated with the Bayesian information criterion in jModeltest2 (Darriba et al. 2012). Branch support was calculated from 100 bootstrap replicates for the concatenated dataset only. Bayesian analyses were performed using PhyloBayes-MPI v. 1.7 (Lartillot et al. 2013) under CAT-GTR settings. Two independent chains were run for 20 000 cycles of which every 10th point was saved. Of the 2 000 saved points, the first 100 were discarded as burn-in prior to assessing convergence using the bpcomp and tracecomp commands. The effective population sizes after running these commands were larger than 300 and maxdiff values were less than 0.3, indicating sufficient convergence as per the guidelines set out in the PhyloBayes-MPI manual. Table 1 Host data and GenBank accession numbers of actin (ACT) and beta-tubulin (TUB2) sequences for 156 South African strains of Phaeoacremonium reported in this study.

Species	Strain ^a	Host	ACT	TUB2
Phaeoacremonium africanum	CSN871	Eriobotrya japonica	KY906754	KY906755
	CSN946	Olea europaea subsp. europaea	KY906772	KY906773
	PMM2276	Cydonia oblonga	KY906926	KY906927
Phaeoacremonium album	CBS 142688 [⊤] = STE-U 8379 = PMM1938	Pyrus communis	KY906884	KY906885
	CBS 142689 = STE-U 8378 = PMM2275	Cydonia oblonga	KY906924	KY906925
	CBS 142716 = STE-U 8380 = CSN1256	Vitis vinifera	KY906794	KY906795
	STE-U 8377 = CSN660	Cydonia oblonga	KY906736	KY906737
Phaeoacremonium alvesii	CSN1239	Prunus persica	KY906784	KY906785
	CSN1335	Psidium guajava	KY906800	KY906801
	PMM744	Ficus carica	KY906822	KY906823
	PMM1817	Rosa sp.	KY906844	KY906845
	PMM2222	Melia azedarach	KY906898	KY906899
Phaeoacremonium aureum	CBS 142690 = STE-U 8374 = CSN1322	Psidium guajava	KY906798	KY906799
	CBS 142691 [⊤] = STE-U 8372 = CSN23	Melia azedarach	KY906656	KY906657
	CBS 142692 = STE-U 8375 = PMM1019	Psidium guajava	KY906832	KY906833
	CBS 142693 = STE-U 8376 = PMM2252	Rosa sp.	KY906916	KY906917
	STE-U 8371 = CSN20	Melia azedarach	KY906654	KY90665
	STE-U 8373 = CSN124	Melia azedarach	KY906692	KY90669
Phaeoacremonium australiense	CSN490	Psidium guajava	KY906728	KY90672
	CSN657	Cydonia oblonga	KY906734	KY90673
	CSN904	Punica granatum	KY906760	KY90676
	CSN914	Psidium guajava	KY906764	KY90676
	CSN1024	Ficus carica	KY906774	KY90677
	CSN1244	Eriobotrya japonica	KY906792	KY90679
	PMM1826	5 5 1	KY906848	
		Vitis vinifera		KY90684
	PMM1843	Rosa sp.	KY906856	KY90685
	PMM2277	Cydonia oblonga	KY906928	KY90692
	PMM2439	Malus domestica	KY906934	KY90693
haeoacremonium bibendum	CBS 142694 [⊤] = STE-U 8365 = CSN894	Schinus molle	KY906758	KY90675
haeoacremonium fraxinopennsylvanicum	CSN66	Malus domestica	KY906680	KY90668
haeoacremonium gamsii	CBS 142712 [⊤] = STE-U 8366 = CSN670	Callistemon sp.	KY906740	KY90674
haeoacremonium geminum	CBS 142713 [⊤] = STE-U 8402 = C741 = CSN1944	Malus domestica	KY906648	KY90664
	CBS 142717 = STE-U 8367 = C631 = CSN1945	Malus domestica	KY906646	KY90664
haeoacremonium globosum	CSN471	Cydonia oblonga	KY906724	KY90672
	CSN1258	Vitis vinifera	KY906796	KY90679
haeoacremonium griseo-olivaceum	PMM1829	Vitis vinifera	KY906852	KY90685
haeoacremonium griseorubrum	PMM1828	Vitis vinifera	KY906850	KY90685
	PMM1895	Psidium guajava	KY906874	KY90687
	PMM2220	Melia azedarach	KY906896	KY90689
	PMM2267	Rosa sp.	KY906920	KY90692
	PMM2444	Prunus persica	KY906940	KY90694
Phaeoacremonium inflatipes	CSN47	Morus sp.	KY906664	KY90666
naeederennennenn maapee	CSN57	Prunus armeniaca	KY906674	KY90667
	CSN247	Prunus persica	KY906700	KY90670
	CSN389	Cydonia oblonga	KY906714	KY90671
	PMM739	Psidium guajava	KY906820	KY90682
	PMM1849	Ficus carica	KY906858	KY90685
	PMM1864 PMM1866	Eriobotrya japonica	KY906864 KY906866	KY90686
		Salix sp.		KY90686
	PMM1987	Cinnamomum camphora	KY906892	KY90689
	PMM2230	Malus domestica	KY906900	KY90690
	PMM2608	Quercus robur	KY906956	KY90695
haeoacremonium iranianum	CSN170	Prunus persica var. nucipersica	KY906694	KY90669
	CSN267	Cydonia oblonga	KY906706	KY90670
	CSN689	Cinnamomum camphora	KY906746	KY90674
	PMM2248	Prunus salicina	KY906912	KY90691
haeoacremonium italicum	CSN59	Melia azedarach	KY906676	KY90667
	CSN119	Morus sp.	KY906690	KY90669
	CSN206	Ficus carica	KY906696	KY90669
	CSN254	Punica granatum	KY906702	KY90670
	CSN277	Prunus persica	KY906710	KY90671
	PMM731	Psidium guajava	KY906818	KY90681
	PMM2238	Malus domestica	KY906908	KY90690
	PMM2291	Cydonia oblonga	KY906930	KY90693
haeoacremonium junior	CBS 142695 = STE-U 8398 = CSN13	Vitis vinifera	KY906650	KY90665
,	CBS 142696 = STE-U 8399 = CSN16	Vitis vinifera	KY906652	KY90665
	CBS 142697 ^T = STE-U 8397 = CSN273	Schinus molle	KY906708	KY90670
	CBS 142698 = STE-U 8396 = PMM2445	Prunus armeniaca	KY906942	KY90694
haeoacremonium longicollarum	CBS 142699 ^T = STE-U 8393 = CSN84	Prunus armeniaca Prunus armeniaca	KY906688	KY90668
naooaoremonium iongicolidium	$CBS 142099^\circ = STE-0.8393 = CSN84$ CBS 142700 = STE-U 8395 = PMM1900	Prunus armeniaca Psidium guajava	KY906878	KY90687
haaaaramanium maliaa	STE-U 8394 = CSN655	Psidium guajava Molio ozodoroch	KY906732	KY90673
haeoacremonium meliae	CBS 142709 = STE-U 8391 = CSN256	Melia azedarach	KY906704	KY90670
, ,	CBS 142710 ^T = STE-U 8392 = PMM975	Melia azedarach	KY906824	KY90682
haeoacremonium minimum	CSN668	Cydonia oblonga	KY906738	KY90673
	CSN893	Schinus molle	KY906756	KY90675
	CSN1910	Prunus dulcis	KY906812	KY90681
	PMM1305	Punica granatum	KY906836	KY90683
	PMM1323	Morus sp.	KY906842	KY90684
	FIVIULI 523			
	PMM1822	Rosa sp.	KY906846	KY90684

Table 1 (cont.)

Phatescare Phatesc	Species	Strain ^a	Host	ACT	TUB2
Phaseacaramonium olase Phaseacaramonium olase<	Phaeoacremonium minimum (cont.)	PMM2073	Olea europaea subsp. europaea	KY906894	KY906895
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^a CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands; CSN, collection of Chris Spies at ARC-Nietvoorbij, Stellenbosch, South Africa; ID, collection of Ihan du Plessis at ARC-Nietvoorbij; PMM, collection of Providence Moyo at the University of Stellenbosch Department of Plant Pathology, Stellenbosch, South Africa; STE-U, fungal collection of the University of Stellenbosch Department of Plant Pathology, Stellenbosch, South Africa; STE-U, fungal collection of the University of Stellenbosch Department of Plant Pathology.
 ^T Ex-type strain.

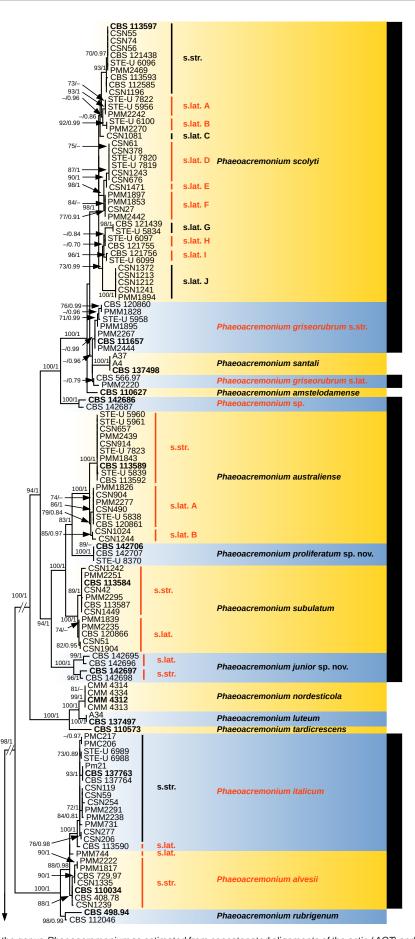
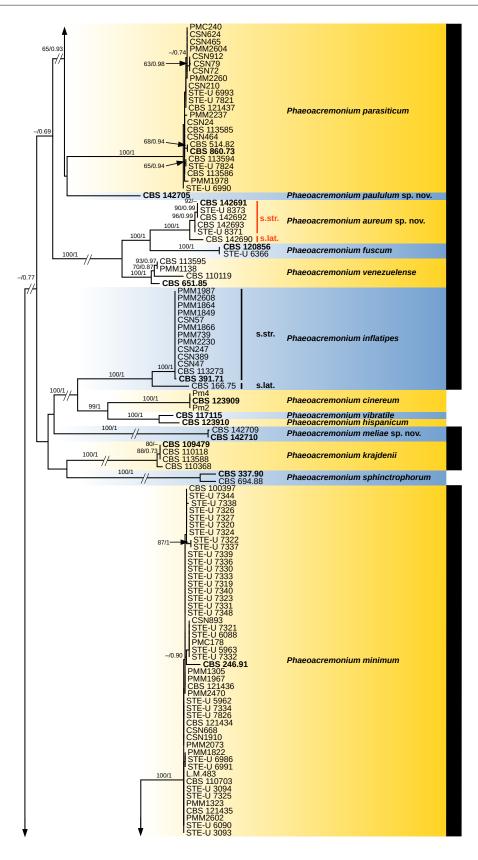


Fig. 1 Maximum likelihood phylogeny of the genus *Phaeoacremonium* as estimated from concatenated alignments of the actin (*ACT*) and beta-tubulin (*TUB2*) regions. Maximum likelihood bootstrap percentages and Bayesian posterior probability values are indicated at the nodes. Support values less than 70 % bootstrap or 0.80 posterior probability are omitted or indicated with '--'. Ex-type strains are indicated in **bold** typeface. In species where considerable intraspecific variation was observed sub-clades that included the ex-type strain were designated *sensu stricto* (s.str.) while the remaining sub-clade(s) were designated *sensu lato* (s.lat.). Clade and sub-clade designations in orange indicate paraphyletic species or incongruence between the combined *ACT-TUB2* phylogeny and individual *ACT/TUB2* phylogenies (see Appendix 2). Vertical black bars on the right of the figure indicate species that have been reported in South Africa.





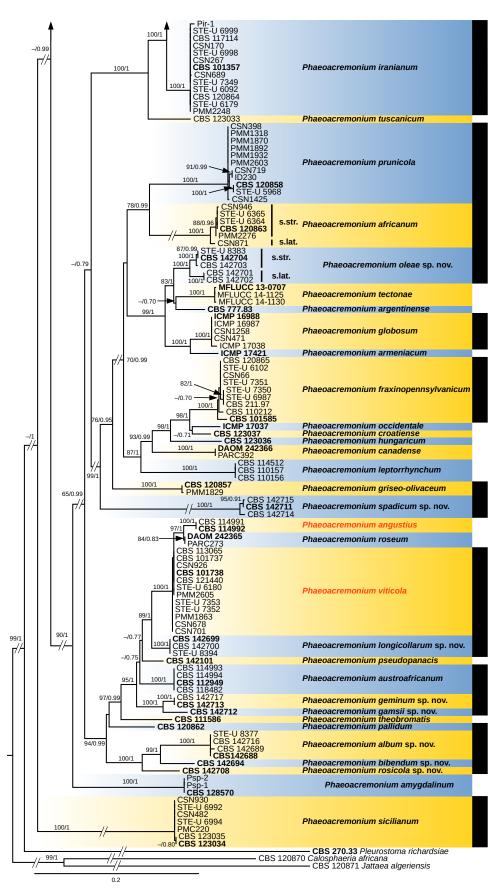
Morphological characterisation

Slide cultures for micromorphologcial characterisation were prepared following a similar protocol as Arzanlou et al. (2007). Isolates of new species were grown on malt extract agar (MEA; Oxoid) for two weeks. Agar blocks (~1 cm × 1 cm) from actively growing regions of the cultures were placed on autoclaved microscope slides in 9 cm Petri dishes containing two autoclaved discs of filter paper that had been moistened with 1.5 mL sterile water. An autoclaved cover slip was placed on each agar block, Petri dishes were sealed with cling wrap and

incubated at 25 °C. After 5 d, both colonised cover slips and colonised microscope slides were used to prepare slides by transferring colonised cover slips to clean microscope slides with 70 % lactic acid, and by placing 70 % lactic acid and clean cover slips on colonised parts of the microscope slides after removing the agar blocks. Slides were pressed under stacks of heavy books for times ranging from several hours to overnight, and sealed with nail polish.

Fungal growth on slides were inspected using a light microscope (Nikon Y-TV55). Images of vegetative hyphae, conidia,





phialides (types I, II and III), collarettes, and conidiophores were captured at 1000× magnification using a Nikon DS-Ri2 camera on a Nikon Eclipse N*i* light microscope. Except where noted otherwise, thirty individual structures of each type were viewed and measured using the NIS-Elements Viewer software (Nikon Instruments Inc.).

Colony morphology was evaluated on MEA, PDA and oatmeal agar (OA; Biolab) after 16 d. Plates of the different media were

inoculated with 4 mm diam plugs taken from actively growing PDA cultures and incubated at 25 °C in the dark for 16 d. Colony colours were evaluated using the colour charts of Rayner (1970). Cardinal temperatures for growth were determined by incubating MEA plates in the dark at temperatures ranging from 5-40 °C in intervals of 5 °C, as well as 37 °C and measuring radial growth after 8 d.

RESULTS

Isolates

Isolates of *Phaeoacremonium* were recovered from 29 different woody hosts. Based on preliminary identifications 156 isolates representing putative new species, phylogenetic variants of known species or first reports for various hosts in South Africa were selected for inclusion in this study. A full list of these strains with host information is given in Table 1.

Phylogenetic analyses

Maximum likelihood and Bayesian analyses of the combined ACT-TUB2 regions yielded a phylogeny with high support (98-100 % maximum likelihood bootstrap and 1.00 Bayesian posterior probability) for all species-level clades except P. alvesii (paraphyletic, 88 % bootstrap support and 1.00 posterior probability for P. alvesii s.str.), P. griseorubrum (paraphyletic, 61 % bootstrap support and 0.99 posterior probability for P. griseorubrum s.str.), P. roseum (84 % bootstrap support and 0.83 posterior probability) and P. viticola (paraphyletic with regards to P. angustius and P. roseum) (Fig. 1). The 267 South African strains clustered in 33 clades and 5 unique or unresolved positions representing 36 Phaeoacremonium species. Of the 156 strains reported here for the first time, 152 strains clustered in 28 clades, and 4 additional strains occupied unique or unresolved positions. In total, these 156 strains represent 31 species, 13 of which are new species described below. Phaeoacremonium alvesii strain CBS 113590 and four South African strains (PMC206, PMC217, STE-U 6988, STE-U 6989) previously reported as P. alvesii (White et al. 2011, Moyo et al. 2014) clustered in the P. italicum clade with good support (100 % bootstrap, 1.00 posterior probability). The phylogenetic positions of all other previously reported South African Phaeoacremonium strains confirmed their reported identifications.

The combined ACT-TUB2 phylogeny revealed sub-clades suggestive of significant intraspecific genetic variation within several species-level clades, including *P. africanum*, *P. aureum* sp. nov., *P. australiense*, *P. inflatipes*, *P. junior* sp. nov., *P. oleae* sp. nov., *P. scolyti* and *P. subulatum*. For each of these species, the sub-clade containing the ex-type strain has been designated the sensu stricto (s.str.) clade and the remaining sensu *lato* (s.lat.) sub-clades have been numbered alphabetically where more than one is present (Fig. 1). Individual gene maximum likelihood phylogenies of ACT and TUB2 (no support calculated) resolved identical sub-clades within *P. africanum*, *P. inflatipes*, and *P. oleae* sp. nov., but suggested conflicting or unresolved placement of some isolates within *P. aureum* sp. nov., *P. australiense*, *P. junior* sp. nov., *P. scolyti* and *P. subulatum* (Appendix 2).

The combined phylogeny (Fig. 1) and individual gene phylo⁻ genies (Appendix 2) revealed paraphyly, incongruence or a lack of resolution for some species. In the P. alvesii/P. italicum group the phylogenetic positions of strains PMM744 (P. alvesii s.lat.) and CBS 113590 (P. italicum s.lat.) were incongruent between the combined and individual phylogenies. The combined and TUB2 phylogenies suggest that P. italicum s.lat. strain CBS 113590 should be included in P. italicum; however, in the ACT phylogeny this strain clustered with P. alvesii. Similarly, P. alvesii s.lat. strain PMM744 held unique positions in the combined and TUB2 phylogenies, but in the ACT phylogeny this strain clustered in the clade otherwise consisting of P. alvesii s.str. and P. italicum s.lat. CBS 113590. Phaeoacremonium griseorubrum was paraphyletic in both the TUB2 and combined phylogenies, with P. griseorubrum s.lat. containing strains CBS 566.97 and PMM2220, and P. griseorubrum s.str. containing all other strains of this species, including the ex-type (CBS 111657). In the ACT phylogeny, however, this species was monophyletic, although

strain CBS 566.97 clustered separately from the remaining strains. Strain PMM2220, on the other hand, clustered within the *P. griseorubrum* s.str. clade. Paraphyly and a lack of resolution was also observed in the *P. angustius/P. roseum/P. viticola* group. In the combined and *TUB2* phylogenies *P. viticola* was paraphyletic with regards to *P. angustius* or *P. roseum*. In the *ACT* phylogeny this species was monophyletic; however, *P. angustius* was paraphyletic with regards to *P. roseum*.

TAXONOMY

Phaeoacremonium album C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB820852; Fig. 2

Etymology. Latin, *album*, meaning white. In reference to the white colour of colonies on MEA, PDA and OA.

Type specimen. SOUTH AFRICA, Western Cape, Durbanville, from internal wood necrosis of pear (*Pyrus communis*), 6 May 2014, *P. Moyo* (holotype CBS-H 23159, culture ex-type CBS 142688 = STE-U 8379 = PMM1938).

MEA slide culture micromorphology — Mycelium septate, hyaline to very pale brown, smooth to coarsely verruculose, 1.5-2.5 (av. 2) µm wide, in bundles of up to 5 strands; no warts observed. Conidiophores (only 9 characterised) smooth to verruculose, mainly branched, hyaline, with up to 5 septa, $16-52 \times 2-2.5$ (av. 25 × 2.5) µm; basal cells sometimes inflated. Phialides terminal or lateral, monophialidic, predominantly type I, smooth, hyaline; collarettes usually short $0.5-1.5 \times 0.5-2(-2.5)$ (av. 1 × 1) µm. Type I phialides subcylindrical to elongate-ampulliform, sometimes very short $(0.5-)1-11(-16) \times 1-2(-2.5)$ (av. 4.5 × 1) µm; type II elongate-ampulliform to navicular, sometimes subcylindrical with tapering apex, $(7.5-)8-13(-13.5) \times 1.5-3$ (av. 10.5 × 2.5) µm; type III elongate-ampulliform to navicular to subcylindrical with tapering apex, sometimes subulate, 13-21.5 $(-22) \times (1-)1.5-2$ (av. 15.5×2) µm. Conidia allantoid to subcylindrical or oblong-ellipsoidal, $3.5-5(-5.5) \times 1-1.5$ (av. 4 × 1.5) µm.

Colony morphology — Colonies reaching a radius of 9–10 mm in 8 d at 25 °C. Minimum temperature for growth 10 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA and PDA smooth, flat, with entire edge; after 16 d white above, white to pale buff in reverse. Colonies on OA woolly, with entire edge; after 16 d white.

Markers used for identification — *TUB2* = KY906885, *ACT* = KY906884.

Additional strains examined. SOUTH AFRICA, Western Cape, Stellenbosch, from internal wood necrosis of quince (*Cydonia oblonga*), 19 June 2014, *P. Moyo* (CBS 142689 = STE-U 8378 = PMM2275).

Notes — *Phaeoacremonium album* is related to *P. bibendum* and *P. rosicola* within the larger clade that also includes *P. angustius*, *P. austroafricanum*, *P. geminum*, *P. gamsii*, *P. longicollarum*, *P. pallidum*, *P. roseum*, *P. theobromatis* and *P. viticola*. Very little or no phylogenetic variation was observed among the four isolates included in the *ACT-TUB2* phylogeny. In addition to the ex-type, only strain CBS 142689 was characterised morphologically. The type I phialides of the ex-type strain were generally shorter than those observed for strain CBS 142689, which had type I phialides 2.5–12.5(–15.5) (av. 6.5) µm in length. Other measured characters as well as colony morphology were similar for these two isolates.

Phaeoacremonium aureum C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821005; Fig. 3

Etymology. Latin, *aureum* (from *aurea*), meaning golden. In reference to the golden pigmentation of some hyphae.

Type specimen. SOUTH AFRICA, Western Cape, Wellington, from internal wood necrosis of syringa (*Melia azedarach*), 6 Oct. 2014, *P. Moyo* (holotype CBS-H 23160, culture ex-type CBS 142691 = STE-U 8372 = CSN23).

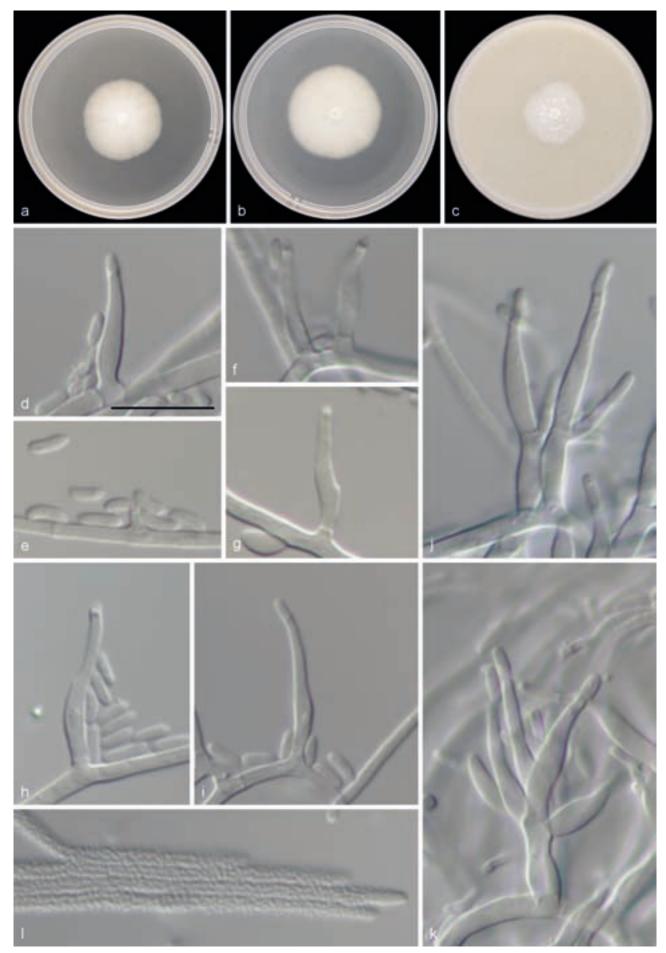


Fig. 2 *Phaeoacremonium album* (CBS 142688 – ex-type culture STE-U 8379 = PMM1938). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. type I phialides, elongate ampulliform (d) and short, subcylindrical, with allantoid conidia (e); f–g. subcylindrical (f) and elongate ampulliform (g) type II phialides; h–i. elongate ampulliform type III phialides; j–k. branched conidiophores; I. bundle of four verruculose hyphal strands. — Scale bar: d = 10 μ m, applies to e–I.

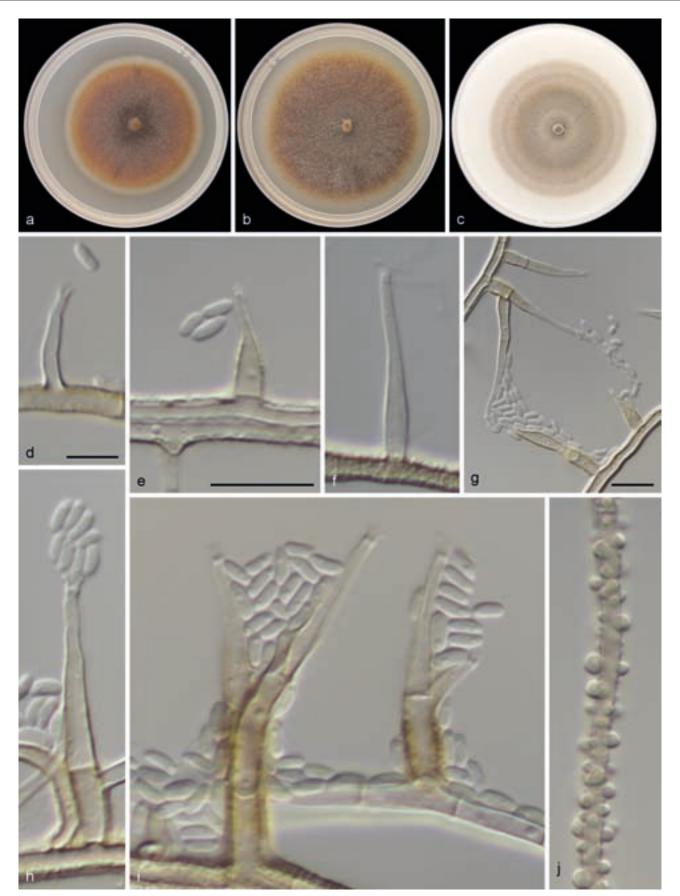


Fig. 3 *Phaeoacremonium aureum* (CBS 142691 – ex-type culture STE-U 8372 = CSN23). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d. subcylindrical type I phialide; e. basally pigmented elongate ampulliform type II phialide; f. elongate ampulliform type III phialide; g. branched conidiophores and a type II phialide showing terminal and lateral vegetative proliferation; h–i. branched conidiophores with a slimy head of conidia (h) and golden-brown vertuculose texture on basal parts (i); j. hyphal exudate observed as warts. — Scale bars: d = 5 μ m, applies to h, j; e, g = 10 μ m, e applies to f, i.

MEA slide culture micromorphology — *Mycelium* hyaline to golden brown, smooth to tuberculate, 1.5-2.5(-3.5) (av. 2) µm wide, in bundles of up to 5 strands, with warts up to 8 µm. *Conidiophores* smooth to verruculose, branched or unbranched, hyaline to golden brown, with up to 4 septa, $(18-)18.5-38(-45) \times 2.5-4(-4.5)$ (av. 27.5 × 3) µm. *Phialides* terminal or lateral, monophialidic, with types II and III dominant, generally smooth to verruculose, hyaline to pale brown; with collarettes $0.5-2 \times 1-2.5$ (av. 1.5×1.5) µm; and with lateral and terminal pro-

liferation occurring frequently. Type I phialides subcylindrical to elongate-ampulliform, (3–)4–17(–18.5) × 1–2.5(–3) (av. 8.5 × 2) µm; type II elongate-ampulliform to subcylindrical with tapering apex, (8–)9–13.5 × 2–3(–3.5) (av. 11.5 × 2.5) µm; type III subcylindrical with tapering apex, sometimes elongate-ampulliform or navicular, (14–)14.5–21.5(–23) × 2–2.5(–3) (av. 17 × 2.5) µm. *Conidia* borne in slimy heads, oblong ellipsoidal to subcylindrical, $3-5(-5.5) \times 1.5-2(-2.5)$ (av. 4 × 1.5) µm.

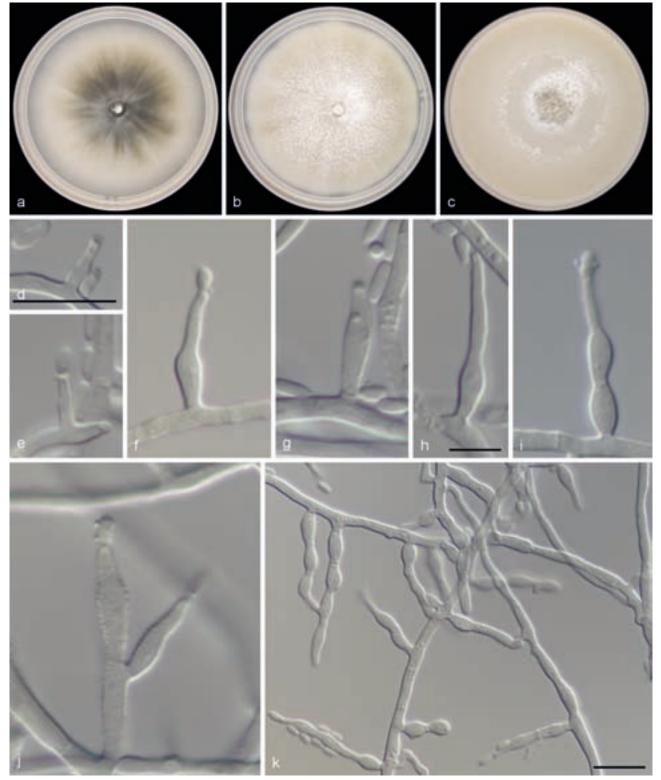


Fig. 4 *Phaeoacremonium bibendum* (CBS 142694 – ex-type culture STE-U 8365 = CSN894). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. subcylindrical type I phialides; f–g. elongate ampulliform (f) and navicular (g) type II phialides; h. elongate ampulliform type III phialide with slightly inflated neck; i–j. conidiophores, unbranched with inflated basal cell and basally inflated conidiogenous cell (i) and branched (j); k. vegetative hyphae, conidiophores and phialides with inflated segments. — Scale bars: d, k = 10 μ m, d applies to e–g, i–j; h = 5 μ m.

Colony morphology — Colonies reaching a radius of 13–14 mm in 8 d at 25 °C. Minimum temperature for growth 15 °C, optimum 30 °C, maximum 37 °C. Colonies on MEA flat, felty, with entire edge; after 16 d luteous sienna with dark brick centre and white margin above, luteous umber with dark brick centre and ochreous buff margin in reverse. Colonies on PDA flat, felty, with entire edge; after 16 d dark brick fading to luteous sienna at the margins above, dark brick fading to luteous umber at the margins in reverse. Colonies on OA flat, felty, with entire edge; after 16 d dark brick fading to luteous umber at the margins in reverse. Colonies on OA flat, felty, with entire edge; after 16 d dark mouse grey to greyish sepia.

Markers used for identification — TUB2 = KY906657, ACT = KY906656.

Additional strains examined. SOUTH AFRICA, Western Cape, Franschhoek, from internal wood necrosis of syringa (*Melia azedarach*), 25 Sept. 2014, *P. Moyo* (STE-U 8371 = CSN20); Western Cape, Calitzdorp, from internal wood necrosis of syringa (*Melia azedarach*), 31 Oct. 2014, *P. Moyo* (STE-U 8373 = CSN124); Western Cape, Porterville, from internal wood necrosis of guava (*Psidium guajava*), 19 Aug. 2015, *C.F.J. Spies* (CBS 142690 = STE-U 8374 = CSN1322); Western Cape, Klawer, from internal wood necrosis of guava (*Psidium guajava*), 12 Aug. 2013, *P. Moyo* (CBS 142692 = STE-U 8375 = PMM1019); Western Cape, Stellenbosch, from internal wood necrosis of rose (*Rosa* sp.), 11 Apr. 2014, *P. Moyo* (CBS 142693 = STE-U 8376 = PMM2252).

Notes — *Phaeoacremonium aureum* is phylogenetically related to *P. fuscum* and *P. venezuelense*. Some intraspecific phylogenetic variation is apparent in this species. With the exception of strain CBS 142690, all strains had identical *TUB2* sequences, while in the *ACT* region, strains STE-U 8371 and CBS 142693 differed from strains CBS 142691 (ex-type), STE-U 8373 and CBS 142692 at two nucleotide positions. In strain CBS 142690, the *TUB2* sequence showed 13 SNPs and one six-nucleotide indel distinct from the other sequences, while, contrastingly, the *ACT* sequence was identical to that of strains STE-U 8371 and CBS 142693. All isolates exhibited similar morphological characteristics. Microcyclic conidiation was observed in strain CBS 142690. This strain did not have hyphal warts and its phialides did not proliferate as in other strains.

Phaeoacremonium bibendum C.F.J. Spies, Moyo, Halleen & L. Mostert, *sp. nov.* — MycoBank MB821006; Fig. 4

Etymology. In reference to the inflated segments frequently observed in the hyphae and conidiophores calling to mind Bibendum (also known as the Michelin Man) who consists of inflated segments.

Type specimen. SOUTH AFRICA, Western Cape, Durbanville, from internal wood necrosis of Peruvian pepper (*Schinus molle*), 27 Feb. 2015, *P. Moyo* (holotype CBS-H 23161, culture ex-type CBS 142694 = STE-U 8365 = CSN894).

MEA slide culture micromorphology — Dense growth on slide culture. Mycelium with individual segments sometimes inflated, hyaline to very pale brown, smooth to finely verruculose, 1.5-2.5 (av. 2) µm wide, in bundles of up to 6 strands, with individual strands in bundles often forming direct hyphal connections. Conidiophores smooth, often unbranched, hyaline, with up to 6 septa, constricted at septa; individual segments often prominently inflated, (10-)11.5-34(-43.5) × (2-)2.5-3.5 (av. 20.5 × 3) µm. Phialides solitary, terminal; monophialidic, with type II dominant, generally smooth to finely verruculose, hyaline; with short collarettes $0.5-1 \times 0.5-1.5(-2)$ (av. $0.5 \times$ 1) µm. Type I phialides subcylindrical to elongate-ampulliform, $(1-)2-9(-10) \times 1-2.5(-3)$ (av. 4.5 × 1.5) µm; type II mainly elongate-ampulliform and constricted at the base as well as often constricted below the neck; in some cases, lageniform with subcylindrical or tapering neck, navicular, with neck sometimes slightly inflated, (6–)7–13 × 2–3 (av. 10 × 2.5) µm; type III (only 14 characterised) subcylindrical with tapering apex to elongateampulliform, lageniform or navicular, $13-19.5 \times 1.5-2.5$ (av. 16 × 2) µm. *Conidia* oblong ellipsoidal, $3-4.5(-5) \times (1-)1.5-2$ (av. 3.5×1.5) µm.

Colony morphology — Colonies reaching a radius of 8 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 20 °C, maximum 30 °C. Colonies on MEA flat, smooth, with entire edge; after 16 d greenish black with white to pale buff margin above and in reverse. Colonies on PDA felty to woolly, with entire edge; after 16 d white to dark olivaceous buff above, pale buff to dark olivaceous buff with olivaceous grey specks at centre on the reverse. Colonies on OA felty to woolly, with entire edge; after 16 d white with smoky grey centre.

Markers used for identification — *TUB*2 = KY906759, *ACT* = KY906758.

Notes — *Phaeoacremonium bibendum* is phylogenetically related to two new species, *P. album* and *P. rosicola*. The inflated segments of hyphae and conidiophores for which *P. bibendum* is named bear some similarity to the swollen phialide bases and conidiophore segments of *P. globosum* (Graham et al. 2009); however, such swollen segments were not reported in vegetative hyphae of *P. globosum*, as is the case for *P. bibendum*, and the two species are clearly phylogenetically distinct.

Phaeoacremonium gamsii C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821008; Fig. 5

Etymology. In honour of Walter Gams, one of the co-authors of the genus *Phaeoacremonium.*

Type specimen. SOUTH AFRICA, Western Cape, Constantia, from internal wood necrosis of bottlebrush tree (*Callistemon* sp.), 25 Nov. 2014, *P. Moyo* (holotype CBS-H 23170, culture ex-type CBS 142712 = STE-U 8366 = CSN670).

MEA slide culture micromorphology — Mycelium hyaline, smooth, 1.5-3 (av. 2.5) µm wide, in bundles of up to 10. Conidiophores uncommon (only 12 characterised), smooth, branched or unbranched, hyaline, with up to 3 septa, $17.5-45.5 \times 2-4$ (av. 31×3) µm. *Phialides* terminal or lateral, monophialidic, with types I and III dominant; generally smooth, hyaline; with collarettes cylindrical to slightly flaring $(0.5-)1-2 \times 1-2(-2.5)$ (av. 1.5×1.5) µm. Type I phialides cylindrical to subcylindrical, sometimes tapering toward the apex, (0.5-)1.5-7.5(-9) \times 1–2(–2.5) (av. 3 \times 1.5) µm; type II uncommon (only 10 characterised), elongate-ampulliform, sometimes subcylindrical tapering toward the apex, $8-13 \times 2-3$ (av. 11×2.5) µm; type III elongate-ampulliform to subcylindrical tapering toward the apex, sometimes navicular, $(13.5-)14.5-23.5(-28.5) \times 2-3(-3.5)$ (av. 18.5 × 2.5) µm. Conidia oblong-ellipsoidal to reniform, obovoid or subcylindrical, $4-6.5(-7) \times 1.5-2(-2.5)$ (av. 5×1.5) µm; microcyclic conidiation frequently observed.

Colony morphology — Colonies reaching a radius of 10 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA smooth, flat, with entire edge; after 16 d white with honey centre above and in reverse. Colonies on PDA flat, felty to woolly, with entire edge; after 16 d fulvous to ochreous with fuscous black centre and buff margin above, umber to pale orange with fuscous black centre and buff margin in reverse. Colonies on OA woolly, with entire edge; after 16 d white with dull green centre.

Markers used for identification — TUB2 = KY906741, ACT = KY906740.

Notes — *Phaeoacremonium gamsii* is currently only known from a single isolate that is phylogenetically closely related to *P. geminum*. It differs from *P. geminum* in several aspects that are outlined in the notes under *P. geminum* below.

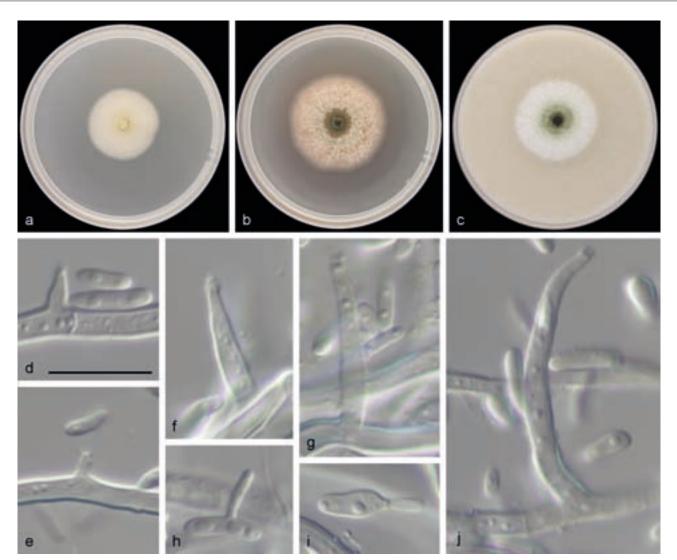


Fig. 5 Phaeoacremonium gamsii (CBS 142712 – ex-type culture STE-U 8366 = CSN670). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. conical (d) and sub-cylindrical (e) type I phialides; f. elongate ampulliform type II phialide; g. type III phialide; h–i. microcyclic conidiation; j. unbranched conidiophore. — Scale bar: d = 10 µm, applies to e–j.

Phaeoacremonium geminum C.F.J. Spies, Havenga & L. Mostert, sp. nov. — MycoBank MB821007; Fig. 6

Etymology. Latin, *geminum*, meaning twins. Referring to the two morphologically similar isolates examined for the description.

Type specimen. SOUTH AFRICA, Western Cape, Riviersonderend, from pruning wound of nursery apple tree (*Malus domestica*), 17 Aug. 2015, *M. Havenga* (holotype CBS-H 23171, culture ex-type CBS 142713 = STE-U 8402 = C741 = CSN1944).

MEA slide culture micromorphology — Mycelium hyaline to pale brown, smooth to vertuculose, 1.5-2.5(-3) (av. 2) μ m wide, in bundles of up to 12, with individual segments occasionally swollen. Conidiophores uncommon (only 14 characterised), smooth to verruculose, branched or unbranched, hyaline to pale brown, with up to 4 septa, $12.5-43.5 \times 2-4$ (av. 28×2.5) µm. Phialides terminal or lateral, monophialidic, predominantly type I, smooth to finely verruculose, hyaline to pale brown; with collarettes cylindrical to slightly flaring $(0.5-)1-1.5 \times 1-2$ (av. 1 × 1.5) µm. Type I phialides cylindrical to subcylindrical, tapering, or elongate-ampulliform, often reduced to an almost sessile lateral collarette on a hyphal segment, $(0-)0.5-8.5(-11.5) \times$ 1-2 (av. 3 × 1.5) µm; type II elongate-ampulliform to navicular, sometimes subcylindrical, $(6-)6.5-13 \times 1.5-3$ (av. 10×2) µm; type III subulate to elongate-ampulliform or subcylindrical, (12.5-)13.5-32(-35.5) × 1.5-2.5(-3) (av. 18.5 × 2) µm. Conidia reniform to allantoid, oblong-ellipsoidal, (3-)4-5 × 1-1.5 (av. 4.5×1) µm; microcyclic conidiation frequently observed.

Colony morphology — Colonies reaching a radius of 8–9 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA smooth, flat, with entire edge; after 16 d buff above and in reverse. Colonies on PDA felty, with entire edge; after 16 d white to pale hazel with umber centre above and in reverse. Colonies on OA woolly, with entire edge; after 16 d white. Yellow pigment produced on OA.

Markers used for identification — *TUB*2 = KY906649, *ACT* = KY906648.

Additional strains examined. SOUTH AFRICA, Western Cape, Ceres, from graft union of a nursery apple tree (*Malus domestica* cv. Gale Gala grafted on CG4204), 15 Aug. 2015, *M. Havenga* (CBS 142717 = STE-U 8367 = C631 = CSN1945).

Notes — The two strains of *P. geminum* that were evaluated here exhibited very similar morphological characteristics. Strain C631 had slightly longer type I phialides and also equally predominant type I and II phialides; however, the short, almost sessile type I phialides are inconspicuous. It is possible that some of these were overlooked during the characterisation of strain C631, and that if more had been measured, higher type I phialide lengths would have been observed. *Phaeoacremonium geminum* differed from the closely related *P. gamsii* in the occurrence of reduced, almost sessile type I phialides and occasional swollen hyphal segments, as well as in the abundance of type II phialides, and in its colony pigmentation on MEA, PDA and OA. Similar, extremely reduced type I phialides were also

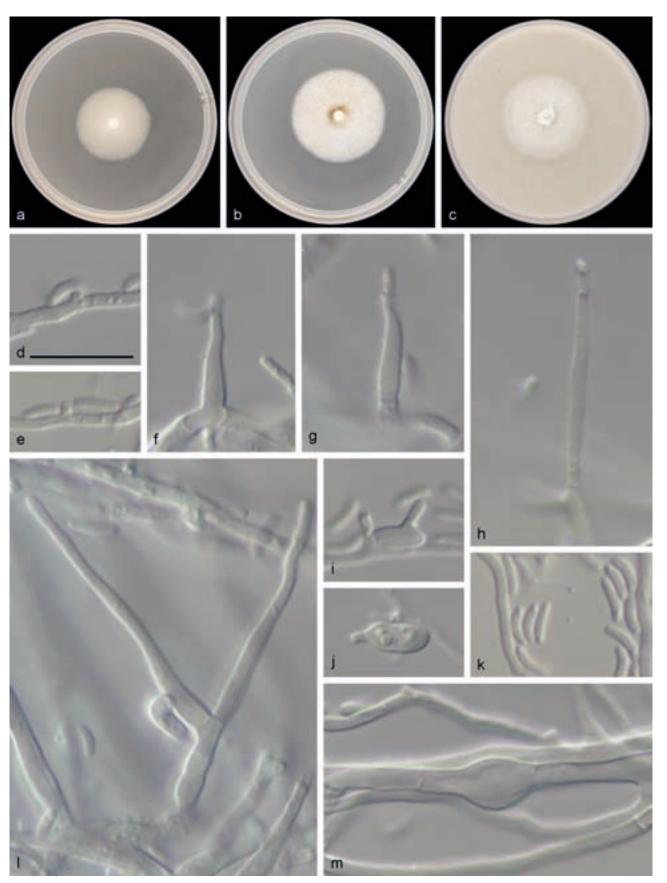


Fig. 6 *Phaeoacremonium geminum* (CBS 142713 – ex-type culture STE-U 8402 = C741 = CSN1944). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–f. reduced (d–e) and elongate ampulliform (f) type I phialides; g. type II phialide; h. type III phialide; i–j. microcyclic conidiation; k. conidia; I. branched conidiophore; m. swollen hyphal segment. — Scale bar: d = 10 μ m, applies to e–m.



Fig. 7 *Phaeoacremonium junior* (CBS 142697 – ex-type culture STE-U 8397 = CSN273). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. type I phialides, subcylindrical widening at the bases (d), and elongate ampulliform (e); f–g. elongate ampulliform type II phialides; h–i. subcylindrical (h) and slender navicular (i) type III phialides; j–k. branched (j) and unbranched (k) conidiophores; I. oblong ellipsoidal and allantoid conidia. — Scale bars: d = 10 μ m, applies to f, h–l; e = 5 μ m, applies to g.

observed in *P. paululum*; however, the two species are clearly phylogenetically distinct.

Phaeoacremonium junior C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821009; Fig. 7

Etymology. 'Junior' was the most common name given to baby boys in South Africa in 2014, the year when this species was recovered from two provinces in this country.

Type specimen. SouTH AFRICA, Western Cape, Robinson Pass, from internal wood necrosis of Peruvian pepper (*Schinus molle*), 7 Nov. 2014, *P. Moyo* (holotype CBS-H 23162, culture ex-type CBS 142697 = STE-U 8397 = CSN273).

MEA slide culture micromorphology — Mycelium hyaline to pale brown, smooth, 1.5-2.5 (av. 2) µm wide, in bundles of up to 6 strands. Conidiophores smooth to verruculose or sparsely tuberculate, branched or unbranched, hyaline to pale brown, with up to 5 septa, $(14-)15.5-59.5(-62) \times 1.5-2.5(-3)$ (av. 33.5×2) µm. *Phialides* terminal or lateral, monophialidic, all three types equally prevalent, smooth to verruculose, hyaline to pale brown; collarettes (only 15 characterised) short, often inconspicuous $0.5-1.5 \times 0.5-2$ (av. 1 × 1) µm. Type I phialides subcylindrical, sometimes elongate-ampulliform or subulate, $(2-)3.5-13(-25) \times 1-2.5$ (av. 9 × 1.5) µm; type II elongate-ampulliform to subulate, rarely subcylindrical, (9-)9.5-15(-15.5) \times 1.5–2.5 (av. 12.5 \times 2) µm; type III subulate or navicular to subcylindrical, (14-)14.5-26(-28.5) × 1.5-2 (av. 19 × 1.5) µm. Conidia borne in slimy heads, oblong ellipsoidal to reniform, $(3-)3.5-5.5(-6) \times 1-1.5(-2)$ (av. 4 × 1.5) µm.

Colony morphology — Colonies reaching a radius of 10–11 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 25 °C, maximum 37 °C. Colonies on MEA flat, smooth, with entire edge; after 16 d white to pale buff above and in reverse. Colonies on PDA flat, smooth, with entire edge; after 16 d white to pale buff with pale luteous buff centre above and in reverse. Colonies on OA felty, with entire edge; after 16 d white to pale buff.

Markers used for identification — *TUB2* = KY906709, *ACT* = KY906708.

Additional strains examined. SOUTH AFRICA, Western Cape, Bonnievale, from internal wood necrosis of apricot (*Prunus armeniaca*) associated with an old wound, 24 June 2014, *P. Moyo* (CBS 142698 = STE-U 8396 = PMM2445); Limpopo, Marble Hall, from cordon of grapevine cv. Early Sweet (*Vitis vinifera*), 18 Sept. 2014, *A. Bredell* (CBS 142695 = STE-U 8398 = CSN13); Limpopo, Marble Hall, from cordon of grapevine cv. Crimson (*Vitis vinifera*), 18 Sept. 2014, *A. Bredell* (CBS 142696 = STE-U 8399 = CSN16).

Notes - Phaeoacremonium junior is related to P. australiense, P. subulatum and the new species P. proliferatum that is described below. Phylogenetically, P. junior comprises two well-supported clades. This sub-clade clustering reflects 10 nucleotide substitutions and one indel along a 602 bp length of the TUB2 region that consistently distinguish the isolates of the two clades. Ten nucleotide substitutions and one indel were also observed along a 208 bp length of the ACT region in these four isolates; however, none of these differences corresponded to the sub-clades observed in the concatenated phylogeny. Colonies of the four isolates had generally similar characteristics on MEA, PDA and OA, although strains CBS 142695 and CBS 142696 had some mouse-grey pigmentation on OA that was not observed for the two strains from the sub-clade containing the ex-type strain. Some variation was observed in the micromorphological characteristics, but these differences were not conspicuous enough to be deemed relevant, nor did they support the phylogenetic sub-clade clustering of this species in the combined ACT-TUB2 tree.

Phaeoacremonium longicollarum C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821010; Fig. 8

Etymology. Latin, *longi-*, meaning long, and *collarum* (from *collare*), meaning collar. In reference to the long collarettes.

Type specimen. SOUTH AFRICA, Western Cape, Kruispad, from internal wood necrosis of apricot (*Prunus armeniaca*), 30 Oct. 2014, *P. Moyo* (holotype CBS-H 23163, culture ex-type CBS 142699 = STE-U 8393 = CSN84).

MEA slide culture micromorphology — Mycelium hyaline, 1.5–3 (av. 2) µm wide, smooth to verruculose, in bundles of up to 13 or more strands, no warts observed. Conidiophores smooth to finely verruculose, branched or unbranched, often associated with mycelial bundles or hyphal whorls; basal cells sometimes slightly inflated, hyaline to pale brown, with up to 3 septa, (21.5-)22.5-41.5(-71) × 2.5-3.5(-4) (av. 30.5 × 3) µm. Phialides terminal or lateral, monophialidic, type I and III dominant, smooth to vertuculose, hyaline; collarettes quite long $1-2 \times 1-3$ (av. 1.5×1.5) µm. Type I phialides subcylindrical to elongateampulliform to subulate, $(1.5-)2-12(-17) \times 1-2(-2.5)$ (av. 7×1.5) µm; type II mainly elongate-ampulliform, sometimes subcylindrical, navicular, or subulate $9.5-14 \times (1.5-)2-3.5$ (av. 12×2.5) µm; type III mainly subulate to elongate-ampulliform or navicular, (14.5-)16-27.5(-28) × (1.5-)2-3(-3.5) (av. 20.5 × 2.5) µm. Conidia shape variable, mostly oblong-ellipsoidal, $3.5-7 \times 1.5-2(-2.5)$ (av. 4.5×2) µm.

Colony morphology — Colonies reaching a radius of 9–10 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA sparsely felty, with entire edge; after 16 d white to pale buff above and in reverse. Colonies on PDA felty to short woolly, with entire edge; after 16 d white to pale buff with ochreous amber centre above and in reverse. Colonies on OA woolly, with entire edge; after 16 d olivaceous grey with white margins.

Markers used for identification — *TUB2* = KY906689, *ACT* = KY906688.

Additional strains examined. SOUTH AFRICA, Western Cape, Wellington, from internal wood necrosis of guava (*Psidium guajava*), 30 Oct. 2014, *F. Halleen* (STE-U 8394 = CSN655); Western Cape, Constantia, from internal wood necrosis of guava (*Psidium guajava*) associated with an old pruning wound, 23 Apr. 2014, *P. Moyo* (CBS 142700 = STE-U 8395 = PMM1900).

Notes — Phylogenetically, *P. longicollarum* occupies a distinct position in the larger clade containing *P. angustius*, *P. austroafricanum*, *P. pallidum*, *P. roseum*, *P. santali*, *P. viticola*, and the five other new species described in this study. The three strains of *P. longicollarum* included in the phylogeny had identical *TUB2* and *ACT* sequences, but morphologically there were some differences. In terms of size, almost all measured structures of strain STE-U 8394 were on average longer than those of the ex-type, while those of CBS 142700 were shorter. CBS 142700 also had noticeably more subcylindrical type II and III phialides, while this shape was scarcer among type II and III phialides of the ex-type and strain STE-U 8394.

Phaeoacremonium meliae C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821016; Fig. 9

Etymology. In reference to the host (*Melia azedarach*) from which both strains of this species have been recovered.

Type specimen. SOUTH AFRICA, Western Cape, Vredendal, from internal wood necrosis of syringa (*Melia azedarach*), 12 Aug. 2013, *P. Moyo* (holotype CBS-H 23168, culture ex-type CBS 142710 = STE-U 8392 = PMM975).

MEA slide culture micromorphology — *Mycelium* hyaline to pale brown, smooth to finely verruculose, 2-3(-3.5) (av. 2) µm wide, in bundles of up to 4 strands. *Conidiophores* smooth, usually branched, hyaline to pale brown, with up to 6 septa, (21.5-)23- $59.5(-64) \times 2-3$ (av. 35×2.5) µm. *Phialides* terminal or lateral, monophialidic with occasional polyphialides, smooth, hyaline to

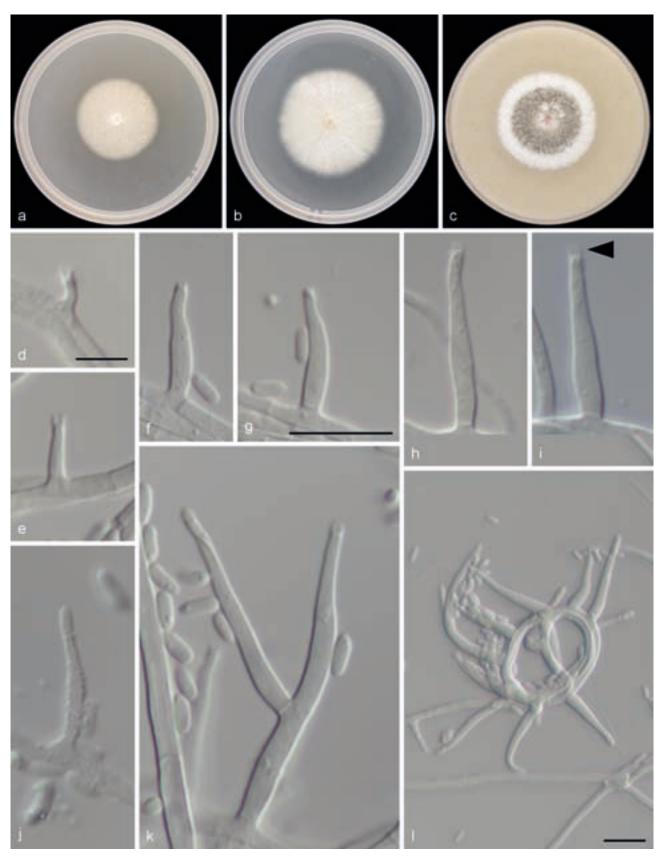


Fig. 8 *Phaeoacremonium longicollarum* (CBS 142699 – ex-type culture STE-U 8398 = CSN84). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–f. sub-cylindrical (d–e) and elongate ampulliform (f) type I phialides; g. elongate ampulliform type II phialide; h–i. elongate ampulliform type III phialides, long collarette indicated with a black arrowhead in i; j. verruculose phialide; k. branched conidiophore; I. hyphal whorl with conidiophores and phialides. — Scale bars: d = 5 μ m, applies to e–f, h–j; g, I = 10 μ m, g applies to k.

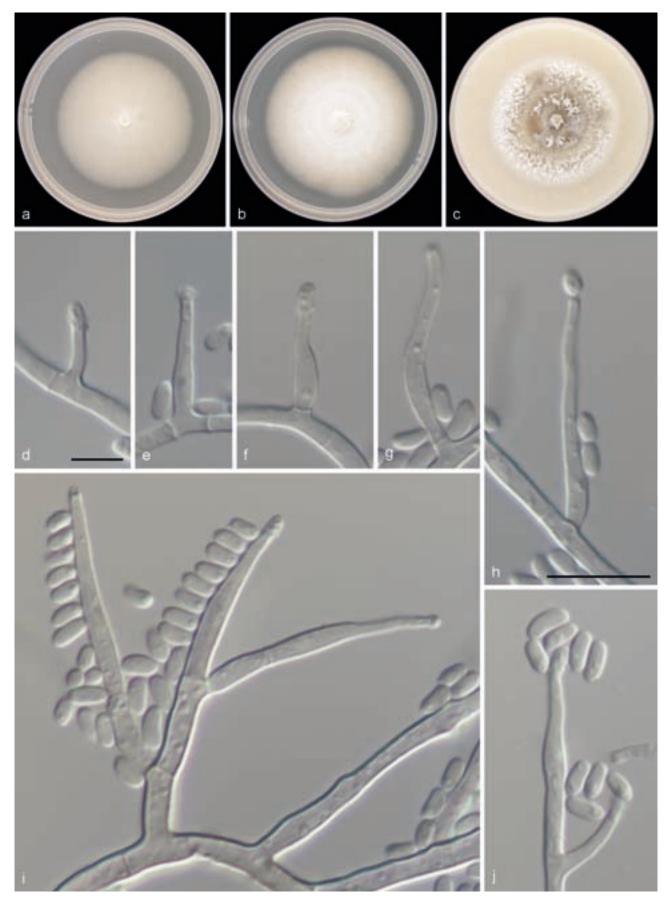


Fig. 9 *Phaeoacremonium meliae* (CBS 142710 – ex-type culture STE-U 8392 = PMM975). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. subcylindrical (d) and elongate ampulliform (e) type I phialides; f. elongate ampulliform type II phialide; g–h. elongate ampulliform type III phialides; i. branched conidiophore with oblong-ellipsoidal conidia; j. oblong-ellipsoidal conidia borne in a slimy head. — Scale bars: d = 5 μ m, applies to e–g; h = 10 μ m, applies to i–j.

sub-hyaline; with collarettes usually prominent $0.5-2 \times 0.5-2$ (av. 1 × 1.5) µm, type III phialides dominant, and with occasional lateral proliferation occurring. Type I phialides subcylindrical, sometimes tapering at the apex to elongate-ampulliform, (4–) $4.5-17(-21) \times 1-2$ (av. 8.5×1.5) µm; type II elongate-ampulliform, sometimes lageniform, navicular or subcylindrical tapering towards the apex, $(7.5-)9.5-13.5 \times 1.5-3$ (av. 11.5×2.5) µm; type III elongate-ampulliform to navicular to subcylindrical taper

ing towards the apex, (14–)15–24.5(–25.5) × (1.5–)2–2.5 (av. 19.5 × 2) µm. Conidia borne in slimy heads, oblong-ellipsoidal to reniform, $3-4(-4.5) \times 1.5-2$ (av. 3.5×1.5) µm.

Colony morphology — Colonies reaching a radius of 15 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 30 °C, maximum 37 °C. Colonies on MEA flat, smooth, with entire edge; after 16 d white to buff above and in reverse. Colonies on PDA flat, felty with woolly centre, with entire edge; after 16 d

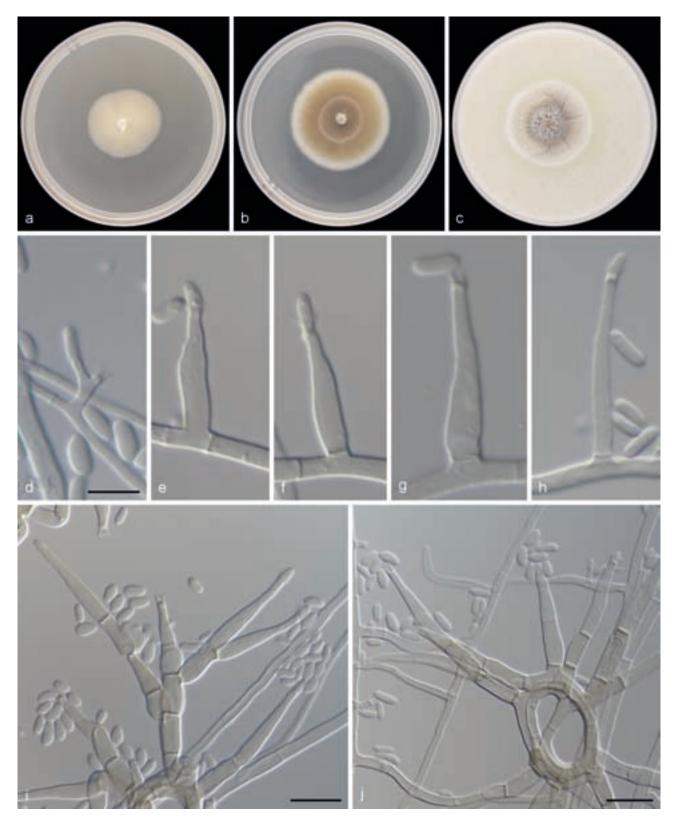


Fig. 10 *Phaeoacremonium oleae* (CBS 142704 – ex-type culture STE-U 8385 = PMM2440). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. type I phialides, subcylindrical polyphialide (d) and elongate ampulliform (e); f. elongate ampulliform type II phialide; g–h. type III phialides, elongate ampulliform (g) and subcylindrical with a tapering apex (h); i. branched conidiophore showing percurrent rejuvenation; j. hyphal whorl with basally pigmented conidiophores and a type III phialide bearing conidia in a slimy head. — Scale bars: d = 5 µm, applies to e–h; i, j = 10 µm.

white to buff above, buff to ochreous in reverse. Colonies on OA woolly with sparsely woolly centre, with entire edge; after 16 d pale mouse grey with white woolly sections.

Markers used for identification — *TUB2* = KY906825, *ACT* = KY906824.

Additional strains examined. SOUTH AFRICA, Western Cape, Calitzdorp, from internal wood necrosis of chinaberry (*Melia azedarach*; also called syringa), 31 Oct. 2014, *P. Moyo* (CBS 142709 = STE-U 8391 = CSN256).

Notes — The two strains examined were highly similar with regards to colony morphology and micromorphology, with the exception of type I and type III phialides, which were slightly shorter in strain CBS 142709 (av. 6.30 μ m and 17.26 μ m, respectively) than those observed in the ex-type strain.

Phaeoacremonium oleae C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821011; Fig. 10

Etymology. In reference to the host (Olea europaea subsp. cuspidata) it was isolated from.

Type specimen. SOUTH AFRICA, Western Cape, Bonnievale, Merwespont, from internal wood necrosis of wild olive (*Olea europaea* subsp. *cuspidata*), 24 June 2014, *P. Moyo* (holotype CBS-H 23264, culture ex-type CBS 142704 = STE-U 8385 = PMM2440).

MEA slide culture micromorphology — Mycelium hyaline to pale brown, smooth to verruculose, (1-)1.5-3 (av. 2) µm wide, in bundles of up to 4 strands. Conidiophores smooth to verruculose, branched or unbranched, hyaline to medium brown especially near base, with up to 6 septa, sometimes slightly constricted at septa, (19.5-)22.5-56.5(-66.5) × (3-)3.5-4.5(-5) (av. 39 × 4) µm. Phialides terminal or lateral, monophialidic with occasional polyphialides, with type III dominant, smooth to verruculose, hyaline to pale brown; collarettes quite long 1–2 \times (1-)1.5-3 (av. 1.5×2) µm; percurrent rejuvenation observed. Type I phialides subcylindrical, sometimes with tapering apex, or elongate-ampulliform, $(1.5-)2-12(-16.5) \times 1-2.5(-3)$ (av. 7 × 1.5) µm; type II elongate-ampulliform, sometimes navicular, subcylindrical, or tapering toward the apex, $(6-)8.5-14.5 \times$ (1.5-)2-4(-4.5) (av. 11.5×3) μ m; type III elongate-ampulliform or subcylindrical with tapering apex, sometimes navicular, (13.5-)15-21(-22) × 2.5-3.5 (av. 17.5 × 3) µm. Conidia borne in slimy heads, oblong-ellipsoidal to obovoid or subcylindrical, $(3.5-)4-5(-5.5) \times 1.5-2.5$ (av. 4.5×2) µm.

Colony morphology — Colonies reaching a radius of 8 mm in 8 d at 25 °C. Minimum temperature for growth 5 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA smooth, flat, with entire margin; after 16 d honey to buff with white margin above and in reverse. Colonies on PDA smooth, flat, with entire edge; after 16 d dark umber fading to amber with white margin above and in reverse. Colonies on OA felty to woolly, creased, with entire edge; after 16 d pale purplish grey or pale amber with white and mouse grey centre. Yellow pigment produced on OA.

Markers used for identification — *TUB2* = KY906937, *ACT* = KY906936.

Additional strains examined. SOUTH AFRICA, Western Cape, Paarl, from internal wood necrosis of wild olive (*Olea europaea* subsp. *cuspidata*), 4 Feb. 2015, *C.F.J. Spies* (CBS 142701 = STE-U 8381 = CSN403); Western Cape, Durbanville, from internal wood necrosis of wild olive (*Olea europaea* subsp. *cuspidata*) associated with a branch canker, 3 Mar. 2015, *W.J. van Jaarsveld* (CBS 142702 = STE-U 8382 = CSN945); Western Cape, Stellenbosch, from internal wood necrosis of wild olive (*Olea europaea* subsp. *cuspidata*), 12 Feb. 2015, *C.F.J. Spies* (STE-U 8383 = CSN703); ditto, from internal wood necrosis of wild olive (*Olea europaea* subsp. *cuspidata*) associated with dieback, 30 Apr. 2015, *P. Moyo* (CBS 142703 = STEU 8384 = PMM1981).

Notes — This species is related to *P. argentinense*, *P. armeniacum*, *P. globosum* and the more recently described *P. tectonae*. Phylogenetically, *P. oleae* can be divided into two subclades (s.str. and s.lat.) with good support (100 % bootstrap, 1.00 posterior probability). This clustering reflects 9 SNPs and a single nucleotide indel over 578 bp of the TUB2 region and 5 SNPs over 204 bp of the ACT region that consistently differentiate between the two sub-clades. The TUB2 sequence of strain CBS 142703 (s.str. sub-clade) had one unique SNP and corresponded to strains from the s.lat. sub-clade in an additional SNP that is not mentioned above. Some variation was observed among phialides and conidia of the five isolates characterised, but these differences did not reflect the sub-clade clustering. Strains CBS 142701, CBS 142703 and STE-U 8383 sometimes produced lageniform type II phialides. Cardinal temperatures and growth rate was only determined for strain CBS 142702 in addition to the ex-type strain. This strain had optimum and maximum growth temperatures of 20 °C and 35 °C, respectively, and exhibited slightly slower growth than the ex-type at 25 °C, reaching a radius of 7 mm on MEA after 8 d.

Phaeoacremonium paululum C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821012; Fig. 11

Etymology. Latin, *paululum*, meaning tiny. In reference to the short type I phialides.

Type specimen. SOUTH AFRICA, Western Cape, Constantia, from internal wood necrosis of guava (*Psidium guajava*), 23 Apr. 2014, *P. Moyo* (holotype CBS-H 23165, culture ex-type CBS 142705 = STE-U 8389 = PMM1914).

MEA slide culture micromorphology — *Mycelium* sometimes slightly constricted at septa, hyaline to pale brown, smooth to finely verruculose, 1.5-3 (av. 2) µm wide, in bundles of up to 7 strands. Conidiophores smooth to finely verruculose, branched or unbranched, hyaline to pale brown, with up to 4 septa, sometimes constricted at septa, (18.5–)19.5–46(–48) \times 2-3.5(-4) (av. 31 \times 2.5) µm. *Phialides* terminal or lateral, monophialidic with occasional polyphialides, with type I dominant, smooth to finely verruculose, hyaline to pale brown; collarettes $0.5-2(-2.5) \times 1-2.5$ (av. 1.5×1.5) µm. Type I phialides subcylindrical, sometimes reduced to almost sessile lateral collarettes on hyphal segments, $0.5-11(-13) \times 1-1.5(-2)$ (av. 4×1) µm; type II elongate-ampulliform, sometimes subcylindrical or navicular, $(7-)9-13.5 \times (1.5-)2-3.5(-4)$ (av. 11.5×2.5) µm; type III elongate-ampulliform to navicular or subcylindrical tapering toward the apex to subulate, sometimes constricted at the base, $14-22.5(-23) \times 1.5-3(-3.5)$ (av. 17.5×2.5) µm. Conidia reniform to oblong-ellipsoidal, $(2.5-)3-4 \times 1-1.5$ (av. 3 × 1.5) µm.

Colony morphology — Colonies reaching a radius of 9–10 mm in 8 d at 25 °C. Minimum temperature for growth 10 °C, optimum 25 °C, maximum 35 °C. Colonies on MEA smooth, flat, with entire edge; after 16 d white with stellate umber pigmentation above and in reverse. Colonies on PDA sparsely woolly, with entire edge; after 16 d pale buff with radial streaks of honey above, white to pale buff with radial streaks of honey in reverse. Colonies on OA felty, creased centrally, with entire edge; after 16 d hazel to dark greyish sepia with white margin.

Markers used for identification — *TUB*2 = KY906881, *ACT* = KY906880.

Note — *Phaeoacremonium paululum* occupies a unique phylogenetic position within the larger *Phaeoacremonium* clade including species such as *P. inflatipes*, *P. parasiticum* and *P. scolyti*.

Phaeoacremonium proliferatum C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821013; Fig. 12

Etymology. In reference to the frequent phialidic and vegetative proliferation of phialides observed in the type strain.

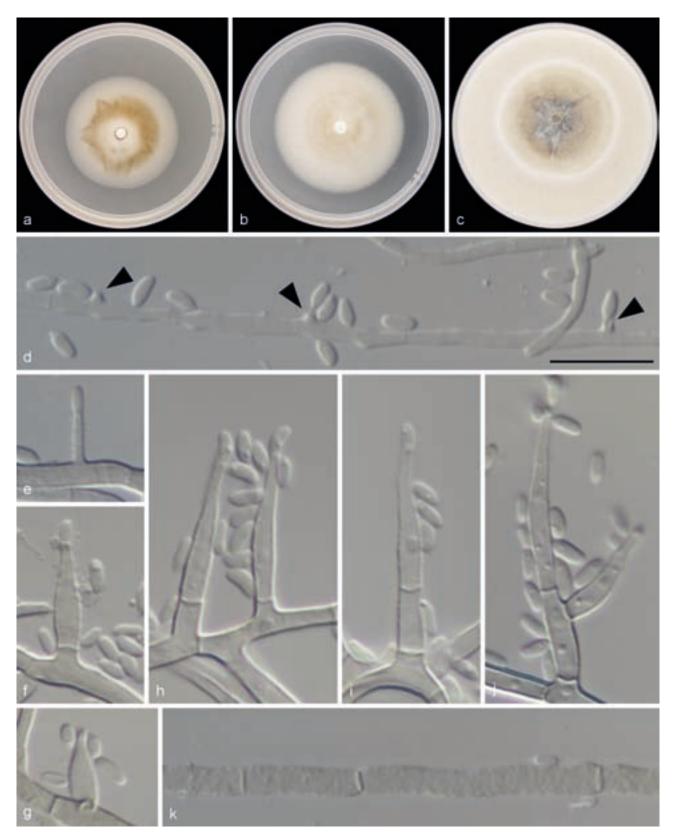


Fig. 11 *Phaeoacremonium paululum* (CBS 142705 – ex-type culture STE-U 8389 = PMM1914). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. reduced (d, indicated with black arrowheads) and subcylindrical (e) type I phialides with oblong-ellipsoidal conidia; f–g. elongate ampulliform type II phialides; h. elongate ampulliform type III phialides; i–j. unbranched (i) and branched (j) conidiophores; k. finely verruculose hypha with constrictions at septa. — Scale bar: d = 10 μ m, applies to e–k.

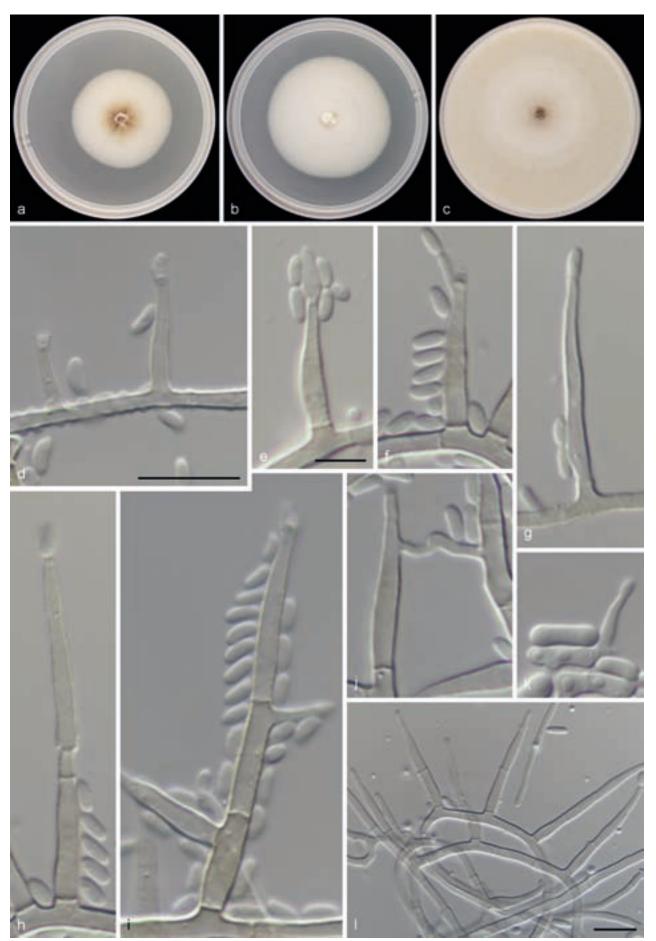


Fig. 12 *Phaeoacremonium proliferatum* (CBS 142706 – ex-type culture STE-U 8368 = PMM2231). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d. subcylindrical to slightly tapering type I phialides on a tuberculate hypha; e. elongate ampulliform type II phialide with a verruculose base and slimy head of conidia; f. subcylindrical type II polyphialide with tapering apex; g. elongate ampulliform type III phialide; h. unbranched conidiophore; j. lateral vegetative proliferation of a type III phialide; k. microcyclic conidiation; I. hyphal whorl with unbranched conidiophores. — Scale bars: d, I = 10 μ m, d applies to f–g, i–k; e = 5 μ m, applies to h.

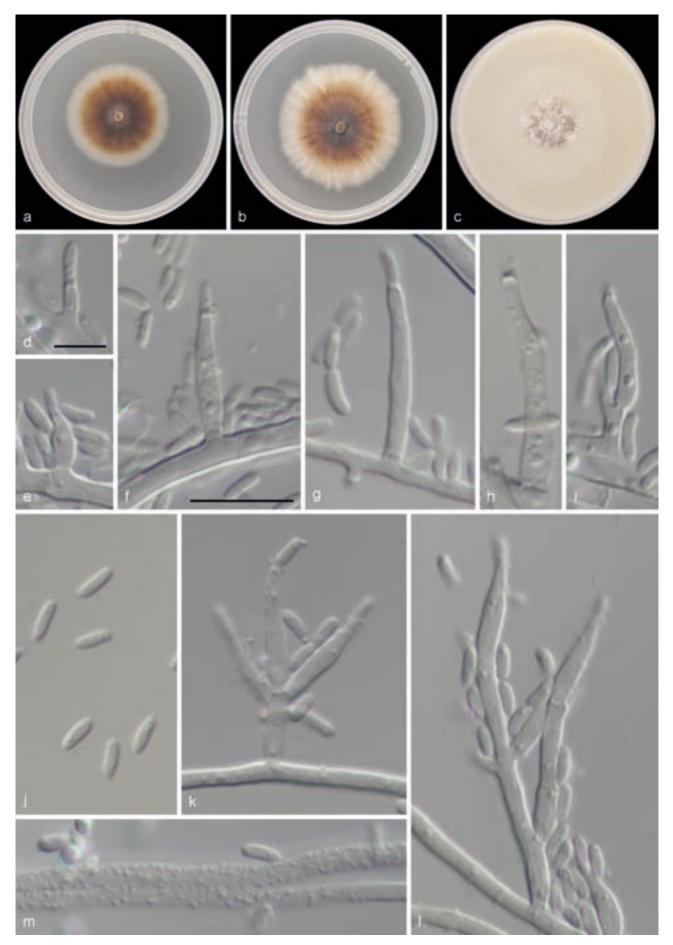


Fig. 13 *Phaeoacremonium rosicola* (CBS 142708 – ex-type culture STE-U 8390 = PMM1002). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d. subcylindrical type I phialide; e–f. elongate ampulliform (e) and navicular (f) type II phialides; g–h. subcylindrical (g) and elongate ampulliform (h) type III phialides; i. percurrent rejuvenation; j. oblong-ellipsoidal conidia; k–l. branched conidiophores; m. verruculose hyphae. — Scale bar: d = 5 μ m, applies to e, h–i; f = 10 μ m, applies to g, j–m.

Type specimen. SOUTH AFRICA, Western Cape, Durbanville, from internal wood necrosis of apple (*Malus domestica*), 17 June 2014, *P. Moyo* (holotype CBS-H 23166, culture ex-type CBS 142706 = STE-U 8368 = PMM2231).

MEA slide culture micromorphology — Mycelium hyaline, smooth to tuberculate, 1.5-2.5(-3) (av. 2) µm wide with warts up to 3 µm, in bundles of up to 7 strands. Conidiophores smooth to roughly verruculose, usually branched, hyaline to pale brown, with up to 4 septa, $22-42.5(-57.5) \times 2-3$ (av. 31.5×2.5) µm. *Phialides* terminal or lateral, commonly becoming polyphialides, smooth to roughly verruculose, hyaline to pale brown, with types II and III dominant; with collarettes $0.5-2 \times 1-2(-2.5)$ (av. 1 × 1.5) µm; percurrent rejuvenation and lateral proliferation observed occasionally. Type I phialides tapering or subcylindrical, occasionally elongate-ampulliform, $3.5-13.5(-17.5) \times 1-2.5(-3)$ (av. 7 × 1.5) µm; type II mainly elongate-ampulliform to navicular, occasionally subcylindrical with tapering apex, $(7.5-)9-14 \times (1.5-)2-2.5(-3)$ (av. 12×2.5) µm; type III subcylindrical to elongate-ampulliform to navicular, 14.5-22.5(-26.5) × 2-2.5(-3) (av. 17.5 × 2) µm. Conidia borne in slimy heads, oblong-ellipsoidal to reniform, $3-5(-5.5) \times$ (1-)1.5(-2) (av. 4 × 1.5) µm, microcyclic conidiation observed.

Colony morphology — Colonies reaching a radius of 9–10 mm in 8 d at 25 °C. Minimum temperature for growth 10 °C, optimum 25 °C, maximum 37 °C. Colonies on MEA smooth, flat, with entire edge; after 16 d white with umber centre. Colonies on PDA smooth to felty, with entire edge; after 16 d white to pale buff with central hazel patches above and in reverse. Colonies on OA flat, felty, with entire edge; after 16 d white to buff.

Markers used for identification — *TUB2* = KY906903, *ACT* = KY906902.

Additional strains examined. SOUTH AFRICA, Western Cape, Vredendal, from internal wood necrosis of rose (*Rosa* sp.) associated with an old pruning wound, 13 Aug. 2013, *P. Moyo* (CBS 142707 = STE-U 8369 = PMM990); ditto, from internal wood necrosis of rose (*Rosa* sp.) associated with an old pruning wound, 13 Aug. 2013, *P. Moyo* (STE-U 8370 = PMM991).

Notes — *Phaeoacremonium proliferatum* is phylogenetically related to *P. australiense* and *P. subulatum. ACT* and *TUB2* sequences of the three isolates included in the phylogeny were identical. Micromorphological characteristics of the three strains were also very similar with only minor variations in the size of hyphae, conidiophores, phialides, collarettes and conidia. On PDA and OA strain CBS 142707 tended toward more woolly growth than CBS 142706 (ex-type), and the umber pigmentation on MEA had a more stellate pattern. Colony morphology of STE-U 8370 was not determined.

Phaeoacremonium rosicola C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821014; Fig. 13

Etymology. In reference to the host (*Rosa* sp.) from which the type strain was recovered.

Type specimen. SOUTH AFRICA, Western Cape, Vredendal, from internal wood necrosis of rose (*Rosa* sp.) associated with an old pruning wound, 13 Aug. 2013, *P. Moyo* (holotype CBS-H 23167, culture ex-type CBS 142708 = STE-U 8390 = PMM1002).

MEA slide culture micromorphology — *Mycelium* hyaline to pale brown, smooth to tuberculate, 1.5-3 (av. 2) µm wide, warts not observed, in bundles of up to 5 strands. *Conidiophores* uncommon (only 9 characterised), smooth to verruculose, branched, hyaline, with up to 5 septa, $13.5-34.5 \times 2-3.5$ (av. 23×2.5) µm. *Phialides* lateral or terminal, monophialidic, sometimes percurrently rejuvenating, with type I dominant, smooth to verruculose, hyaline; collarettes (only 24 characterised) usually short $0.5-1.5 \times 0.5-2(-2.5)$ (av. 1×1.5) µm. Type I phialides subcylindrical, sometimes tapering toward the apex or elongateampulliform, $(1-)1.5-8(-12.5) \times 1-2.5$ (av. 3.5×1.5) µm; type II Colony morphology — Colonies reaching a radius of 10–11 mm in 8 d at 25 °C. Minimum temperature for growth 10 °C, optimum 25 °C, maximum 30 °C. Colonies on MEA flat, smooth, with entire edge; after 16 d dark brick fading to buff margin above and in reverse. Colonies on PDA flat, smooth, with entire edge; after 16 d dark brick fading to buff margin above and in reverse. Colonies on OA felty with central woolly patches, with entire edge; after 16 d buff to white with rosy buff to vinaceous buff central patches.

Markers used for identification — *TUB2* = KY906831, *ACT* = KY906830.

Notes — Phaeoacremonium rosicola is related to P. bibendum and P. album in the larger clade also containing P. angustius, P. austroafricanum, P. longicollarum, P. pallidum, P. roseum, P. theobromatis and P. viticola. Several Phaeoacremonium species produce colonies with various shades of brown pigmentation on MEA, including P. aureum (described above); however, the dark brick pigmentation observed in P. rosicola has not been recorded for other species. Additional strains of this species would need to be examined to determine if this trait has diagnostic value.

Phaeoacremonium spadicum C.F.J. Spies, Moyo, Halleen & L. Mostert, sp. nov. — MycoBank MB821017; Fig. 14

Etymology. Latin, spadicum (from spadix), meaning brown, chestnut. In reference to the colony colour on PDA and, for some strains, also on MEA.

Type specimen. South AFRICA, Western Cape, Darling, from internal wood necrosis of loquat (*Eriobotrya japonica*) associated with a branch canker, 23 Oct. 2013, *P. Moyo* (holotype CBS-H 23169, culture ex-type CBS 142711 = STE-U 8386 = PMM1315).

MEA slide culture micromorphology - Mycelium hyaline to medium brown, smooth to verruculose or finely tuberculate, (1-)1.5-2.5 (av. 2) μ m wide, in bundles of up to 13 or more strands. Conidiophores smooth to verruculose, branched or unbranched, hyaline to pale brown, with up to 5 septa, (13.5-) 14.5-42(-71.5) × 2-3.5 (av. 29 × 3) µm. *Phialides* terminal or lateral, monophialidic, sometimes percurrently rejuvenating, with type III dominant, smooth to verruculose, hyaline to medium brown; collarettes usually small or inconspicuous 0.5-1.5 × 0.5-2 (av. 1 × 1) µm. Type I phialides subcylindrical to elongate-ampulliform, $2.5-16(-16.5) \times 1-3$ (av. 8×1.5) µm; type II elongate-ampulliform to navicular, sometimes subcylindrical tapering toward apex, $7.5-13.5(-14) \times (1.5-)2-3(-4)$ (av. 11×2.5) µm; type III subcylindrical tapering toward the apex, or elongate-ampulliform, sometimes navicular or subulate, (14.5–)15.5–30 × 1.5–3 (av. 22.5 × 2.5) µm. Conidia borne in slimy heads, oblong-ellipsoidal to reniform, obovoid or subcylindrical, $3-4(-5) \times 1.5-2$ (av. 3.5×1.5) µm; microcyclic conidiation observed.

Colony morphology — Colonies reaching a radius of 10 mm in 8 d at 25 °C. Minimum temperature for growth 10 °C, optimum 20–25 °C, maximum 30 °C. Colonies on MEA flat, smooth, with entire edge; after 16 d white to pale buff with central honey patches above, buff with central isabelline patches in reverse. Colonies on PDA flat, smooth, with entire edge; after 16 d buff deepening through luteous to a chestnut centre above, pale luteous with chestnut centre in reverse. Colonies on OA woolly, with entire edge; after 16 d white with olivaceous grey centre.

Markers used for identification — *TUB2* = KY906839, *ACT* = KY906838.

Notes — Phaeoacremonium spadicum occupies a basal phylogenetic position within the larger clade containing *P. africanum, P. argentinense, P. armeniacum, P. canadense, P. croatiense, P. fraxinopennsylvanicum, P. globosum, P. griseo-olivaceum, P. hungaricum, P. novae-zealandiae, P. occidentale, P. oleae, <i>P. prunicola* and *P. tectonae.* Two additional strains of *P. spadicum* included in the phylogeny (CBS 142714 and CBS 142715) were not characterised with regards to micromorphology; however, strain ID208 also produced colonies pigmented in shades of brown varying from dark umber to chestnut on PDA and MEA, and had similar growth rates and cardinal temperatures when compared to the ex-type.

DISCUSSION

South Africa currently has the highest reported diversity of *Phaeoacremonium* species with 35 species, followed by Italy with 15, Spain with 15 and the USA with 13, seven of which have only been reported from human infections (Gramaje et al. 2015; Appendix 3). Most records of *Phaeoacremonium* in South Africa are from the Western Cape, which comprises a large part of the floristically diverse Cape Floristic Region (CFR; Myers et al. 2000). The CFR consists mainly of fynbos, a vegetation type that is dominated by plant species from the *Ericaceae, Proteaceae* and *Restionaceae*. It is possible

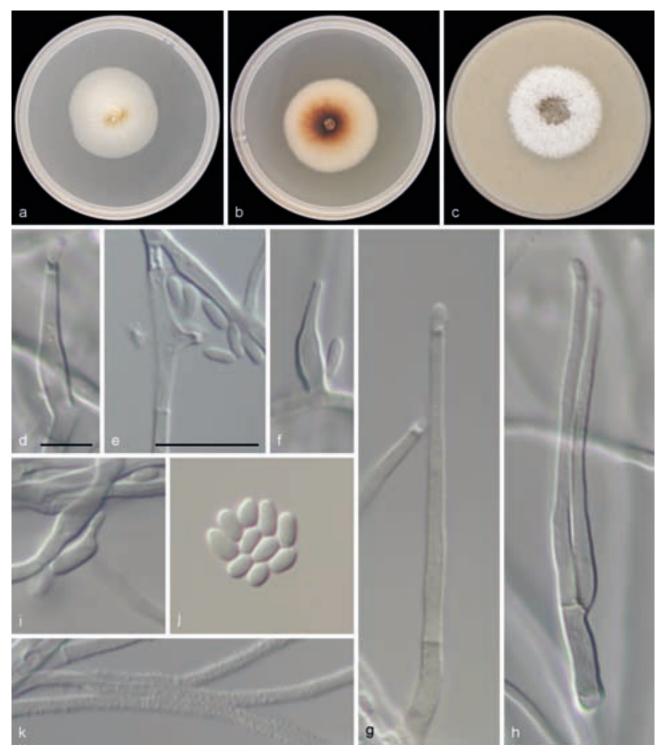


Fig. 14 *Phaeoacremonium spadicum* (CBS 142711 – ex-type culture STE-U 8386 = PMM1315). a–c. Sixteen-day-old colonies incubated at 25 °C on MEA (a), PDA (b) and OA (c); d–e. type I phialides, elongate ampulliform (d) and short with widening base (e); f. elongate ampulliform type II phialide; g–h. unbranched (g) and branched (h) conidiophores with subcylindrical (g) and subulate (h) type III phialides; i. microcyclic conidiation; j. oblong-ellipsoidal conidia; k. verruculose hyphae. — Scale bars: d = 5 μ m, applies to f; e = 10 μ m, applies to g–k.

that the high diversity of possible hosts has generated the high diversity of Phaeoacremonium species in this region. Unfortunately, the Ericaceae, Proteaceae and Restionaceae were not represented among the hosts covered in the current survey. The only records of Phaeoacremonium associated with these plant families in South Africa are of perithecia of P. austroafricanum, P. minimum and P. parasiticum that were found on twig litter of two Proteaceae species collected in the Western Cape (Marincowitz et al. 2008). The same study also reported a putative new species as 'Togninia sp.' from fynbos twig litter; however, BLAST searches of the ITS sequences of this taxon (EU552159 and EU552160) suggest that it is a species of Jattaea (95-98 % similarity to ITS sequences of J. aphanospora, J. discreta and J. taediosa). Dieback or canker disease symptoms observed in fynbos have not been linked to Phaeoacremonium infections (Taylor & Crous 2000, Crous et al. 2013) and the association and interaction of this genus with living fynbos still needs to be elucidated. Only four of the hosts in the current investigation are indigenous to South Africa including coral tree, wild grape, wild olive and yellowwood. It is interesting to note that two of the new species described in this study were recovered from two of the indigenous hosts: P. oleae was recovered only from wild olive (Olea europaea subsp. cuspidata) and P. spadicum was recovered from wild grape (Rhoicissus tomentosa) and wild olive in addition to loquat (Eriobotrya japonica, not indigenous to South Africa).

Damm et al. (2008b) analysed stone fruit samples from the Limpopo Province (a region with summer rainfall) as well as the Western Cape Province (a region with winter rainfall) and, upon finding three new species from Limpopo, but none from the Western Cape, she proposed a lack of previous sampling in Limpopo or the different climate as reasons for this. In the current survey we showed that two of the three species described by Damm et al. (2008b) are also present in the Western Cape, namely, P. griseo-olivaceum and P. prunicola. An additional new species described by us, P. junior, was also recovered both in Limpopo and in the Western Cape. Other species that have been reported from both regions include P. parasiticum and P. scolyti (Damm et al. 2008b, Spies unpubl. data). This suggests that climatological variation does not have a direct impact on the distribution of these Phaeoacremonium species in South Africa. In addition, climatological factors may not directly explain the high diversity of Phaeoacremonium species in this country.

The general perception that Phaeoacremonium species have broad host ranges and lack host specificity were confirmed by this study. Species known to have broad host ranges such as P. minimum, P. parasiticum and P. scolyti (Gramaje et al. 2015) are now respectively known from 19, 17 and 20 hosts in South Africa (Groenewald et al. 2001, Mostert et al. 2005, Damm et al. 2008b, Maricowitz et al. 2008, Cloete et al. 2011, Moyo et al. 2014, 2016; Appendix 3). Other species were thought to have more restricted host ranges; for example, P. prunicola had only been reported from plums (Damm et al. 2008b). The present survey, however, reports an additional nine hosts for this species. Similarly, the recovery of P. africanum, P. globosum and P. griseo-olivaceum from three, two and one additional hosts, respectively, excludes the possibility of hostspecificity in these species, each of which had previously only been reported from single hosts (Damm et al. 2008b, Graham et al. 2009). Eight of the 10 Phaeoacremonium species in South Africa that are currently known globally only from single plant hosts are only known from less than three strains, suggesting that insufficient data is available to draw conclusions regarding the host range of these. The remaining two species in South Africa that are only known from single plant hosts are P. krajdenii and P. oleae. Phaeoacremonium krajdenii has only been recorded on grapevines in South Africa and Spain, but human infections by this species have been reported from Africa, Asia, Europe, the USA and Scandinavia (Gramaje et al. 2015). Phaeoacremonium oleae, on the other hand, has been recovered from eight wild olive samples in four different regions in the Western Cape Province (data not shown). The fact that this species has a wide distribution in the Western Cape, but was not recovered from any other host, not even from European olive, a closely related taxon that was sampled in the same regions, stands in contrast to the lack of host specificity generally observed in Phaeoacremonium species. Seventeen other Phaeoacremonium species not reported in South Africa are only known from single plant hosts or substrates (Appendix 3); however, of these, only P. amygdalinum, P. cinereum, P. luteum, P. nordesticola, P. santali and P. tectonae are known from more than three strains and only P. cinereum, P. hispanicum and P. tuscanicum have been recovered from more than one country (Crous & Gams 2000, Essakhi et al. 2008, Graham et al. 2009, Gramaje et al. 2009b, 2012, 2014, 2015, Berraf-Tebbal et al. 2011, Hu et al. 2012, Úrbez-Torres et al. 2014, Ariyawansa et al. 2015; Appendix 3).

An emerging problem in Phaeoacremonium species-level taxonomy is the lack of distinction between some species using ACT-TUB2 phylogenies. Specific issues have been observed with the resolution of and support for P. griseorubrum, the distinction between P. alvesii and P. italicum, and resolution within the P. angustius/P. roseum/P. viticola group (Gramaje et al. 2015; this study). Incongruence between the ACT and TUB2 regions make these issues difficult to address using currently available molecular data. Although morphological differences between some closely related species have been reported, the use of such data to resolve species requires prior validation of putative distinctive characteristics in a collection of strains that are sufficiently representative of all species in question. In the case of P. italicum and P. alvesii, Raimondo et al. (2014) considered the production of yellow pigment on MEA, PDA and OA one of the features distinguishing the species; however, Mostert et al. (2006) reported yellow pigment production only in P. alvesii strains CBS 110034 (ex-type) and CBS 408.78, but not in CBS 729.97 (phylogenetically P. alvesii s.str.) and CBS 113590 (here classified as P. italicum s.lat.). Other morphological differences between these species were also highlighted, e.g., differences in the number of hyphae in bundles, the number of septa in conidiophores, the predominant phialide types, and minimum, optimum and maximum growth temperatures (Raimondo et al. 2014). In the current investigation, such traits were found to vary among isolates of some species and the variation observed did not correspond to intraspecific phylogenetic variation. This suggests that these morphological differences are not reliable in distinguishing phylogenetically closely related species and can therefore not be used to clarify the species identity of strains that have an unresolved phylogenetic identity, such as PMM744. In light of these shortcomings of morphological data and the available molecular data, a more inclusive approach was followed in the taxonomic treatment of species that exhibited considerable intraspecific phylogenetic variation possibly suggestive of species boundaries, i.e., P. africanum, P. aureum, P. australiense, P. inflatipes, P. junior, P. oleae, P. scolyti and P. subulatum. Species boundaries within such clades need to be investigated using multi-locus sequence data of sufficiently representative collections of strains and applying techniques such as genealogical concordance phylogenetic species recognition (GCPSR) and coalescent-based species delimitation (Taylor et al. 2000, Fujita et al. 2012, Rintoul et al. 2012). Other gene regions previously used for phylogenetic analyses of Phaeoacremonium that could be included in such analyses include translation elongation factor 1-alpha (TEF1-a) and calmodulin (Mostert

et al. 2005, Úrbez-Torres et al. 2014). Although the internal transcribed spacer (ITS) region has been used in Phaeoacremonium phylogenies (Groenewald et al. 2001, Úrbez-Torres et al. 2014), it has proven insufficiently variable to distinguish among several Phaeoacremonium species (Groenewald et al. 2001). Indeed the ITS region is identical in P. angustius and P. viticola (over 517 nucleotides) and 99 % similar in P. fraxinopennsylvanicum and P. occidentale (504/506 with 1 gap), P. minimum and P. iranianum (518/520 with 2 gaps), P. griseorubrum and P. amstelodamense (470/471 with 1 gap) and P. alvesii and P. rubrigenum (527/528 with one C to G transversion). Mostert et al. (2005) sequenced the calmodulin region for a subset of isolates to elucidate the relationships among taxa related to P. rubrigenum. These included species that were paraphyletic or exhibited considerable levels of intraspecific variation in our ACT-TUB phylogeny, such as P. alvesii, P. australiense, P. griseorubrum, P. scolyti and P. subulatum. Unfortunately, calmodulin sequences for only 19 strains representing 11 Phaeoacremonium spp. are currently available on GenBank. For the TEF1- α region, on the other hand, sequences are available for ex-type strains of 31 Phaeoacremonium species (Úrbez-Torres et al. 2014). Other alternatives that could be considered include new markers such as FG1093 and MS204 that were recently introduced by Walker et al. (2012a) for species-level systematics in the Sordariomycetes. These regions have been used in phylogenetic analyses of the genera Ceratocystis, Juglanconis and Ophiognomonia (Walker et al. 2012b, Fourie et al. 2015, Voglmayr et al. 2017). They have not as yet been sequenced for any Phaeoacremonium species.

Thorough taxonomic treatment including phylogenetic analyses of the genus Phaeoacremonium by Mostert et al. (2006), relatively soon after its introduction in 1996 (Crous et al. 1996), provided a good foundation for the identification and description of species within the genus. Sound taxonomic practice has mostly been upheld during the expansion of the genus over the next decade, bringing us to the current 61 species included in Phaeoacremonium. Actin and beta-tubulin data generated from type material are publicly available for 59 species, the only exceptions being P. aquaticum (only ITS data available) and P. inconspicuum (no sequence data or strains available). If the current study is to be taken as an indication, a considerable number of Phaeoacremonium species remain to be discovered when samples from additional hosts and regions are analysed. Care is needed to prevent misidentifications and the introduction of vague species boundaries as the number of species in this genus increases. In light of the shortcomings of the ACT-TUB2 phylogeny highlighted above, the identification of additional phylogenetic markers or techniques to improve phylogenetic resolution of species should be a priority.

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Appendix 1 Reference strain data (host and country of origin) and GenBank accession numbers of actin (ACT) and beta-tubulin (TUB2) sequences included in the phylogeny.

CBS 110212Fraxinus pennsylvanicaUSADQ173136DQ173109Mostert et al. 2006CBS 120865Prunus salicinaSouth AfricaEU128121EU128079Damm et al. 2008bCBS 211.97Fraxinus excelsiorSwedenDQ173184RF246810Groenewald et al. 2001, Mostert et al. 200STE-U 6102Prunus salicinaSouth AfricaEU128122EU12800Damm et al. 2008bSTE-U 6987Vitis viniferaSouth AfricaJQ038913White et al. 2011STE-U 7350Pyrus communisSouth African/aJF934951Cloete et al. 2011STE-U 7351Pyrus communisSouth African/aJF934952Cloete et al. 2011Phaeoacremonium fuscumCBS 1208567Prunus salicinaSouth AfricaEU128141EU12808Damm et al. 2008bPhaeoacremonium globosumICMP16987Vitis berlandieri × Vitis ripariaNew ZealandEU595459EU596527Graham et al. 2009Phaeoacremonium giseo-olivaceumCBS 1208571Prunus armeniacaSouth AfricaEU128139EU596526Graham et al. 2009Phaeoacremonium giseo-olivaceumCBS 1208571Prunus armeniacaSouth AfricaEU128139EU596527Graham et al. 2008Phaeoacremonium giseo-olivaceumCBS 1208571Prunus armeniacaSouth AfricaEU128139EU128079Damm et al. 2008Phaeoacremonium giseo-olivaceumCBS 1208571Prunus aralicinaSouth AfricaEU128117EU128079Damm et al. 2008Phaeoacremonium giseo-olivaceumCBS 1208571 <td< th=""><th>Organism</th><th>Strain</th><th>Host</th><th>Country</th><th>ACT</th><th>TUB2</th><th>References</th></td<>	Organism	Strain	Host	Country	ACT	TUB2	References
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PMC217bArthropodsSouth African/aMF352205Moyo et al. 2014STE-U 6988bVitis viniferaSouth AfricaJQ038925JQ038914White et al. 2011STE-U 6989bVitis viniferaSouth AfricaJQ038926JQ038915White et al. 2011Phaeoacremonium krajdeniiCBS 109479 ^T Homo sapiensCanadaAY579267AY579330Mostert et al. 2005CBS 110118Vitis viniferaSouth AfricaAY579261AY579324Mostert et al. 2005CBS 110368Homo sapiensUSAAY579269AY579332Mostert et al. 2005		Pm21	Vitis vinifera	Italy	KJ534048	KJ534076	Raimondo et al. 2014
PMC217bArthropodsSouth African/aMF352205Moyo et al. 2014STE-U 6988bVitis viniferaSouth AfricaJQ038925JQ038914White et al. 2011STE-U 6989bVitis viniferaSouth AfricaJQ038926JQ038915White et al. 2011Phaeoacremonium krajdeniiCBS 109479 ^T Homo sapiensCanadaAY579267AY579330Mostert et al. 2005CBS 110118Vitis viniferaSouth AfricaAY579261AY579324Mostert et al. 2005CBS 110368Homo sapiensUSAAY579269AY579332Mostert et al. 2005		PMC206 ^b	Arthropods	South Africa	n/a	MF352204	Moyo et al. 2014
STE-U 6988bVitis viniferaSouth AfricaJQ038925JQ038914White et al. 2011STE-U 6989bVitis viniferaSouth AfricaJQ038926JQ038915White et al. 2011Phaeoacremonium krajdeniiCBS 109479THomo sapiensCanadaAY579267AY579330Mostert et al. 2005CBS 110118Vitis viniferaSouth AfricaAY579261AY579324Mostert et al. 2005CBS 110368Homo sapiensUSAAY579269AY579332Mostert et al. 2005			•				•
STE-U 6989 ^b Vitis vinifera South Africa JQ038926 JQ038915 White et al. 2011 Phaeoacremonium krajdenii CBS 109479 ^T Homo sapiens Canada AY579267 AY579330 Mostert et al. 2005 CBS 110118 Vitis vinifera South Africa AY579261 AY579324 Mostert et al. 2005 CBS 110368 Homo sapiens USA AY579269 AY579322 Mostert et al. 2005			•				•
Phaeoacremonium krajdenii CBS 109479 ^T Homo sapiens Canada AY579267 AY579330 Mostert et al. 2005 CBS 110118 Vitis vinifera South Africa AY579261 AY579324 Mostert et al. 2005 CBS 110368 Homo sapiens USA AY579269 AY579332 Mostert et al. 2005							
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CBS 113588 Vitts vinitera South Africa AY579262 AY579325 Mostert et al. 2005							
		000 113588	vius virmera	South Africa	AT3/9262	AT0/9325	wosten et al. 2005

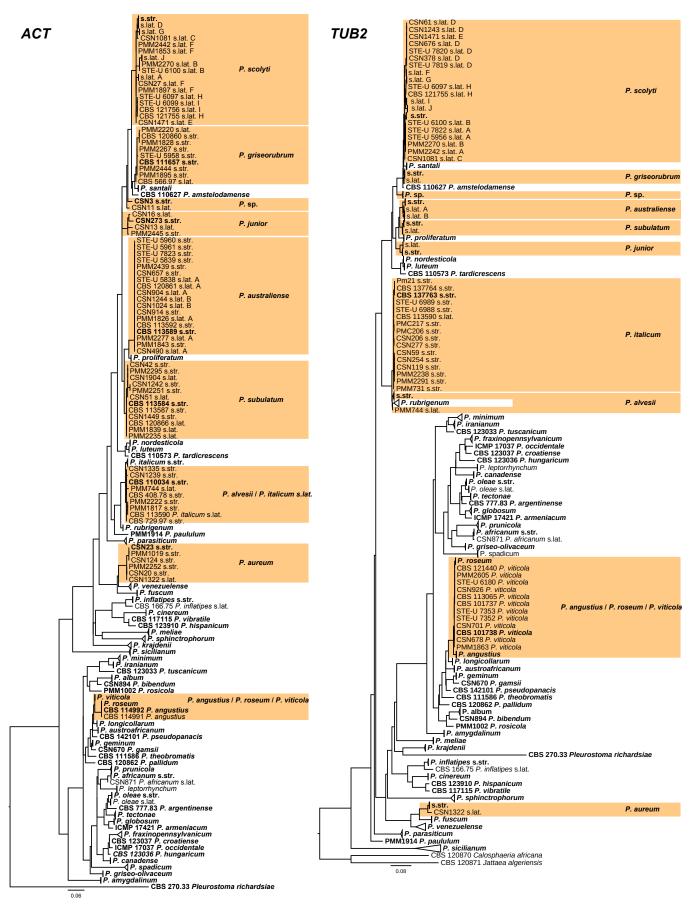
Appendix 1 (cont.)

Organism	Strain	Host	Country	ACT	TUB2	References
Phaeoacremonium leptorrhynchum	CBS 110156°	Cupressus macrocarpa	New Zealand	DQ173139	DQ173110	Mostert et al. 2006
	CBS 110157	Pinus radiata	New Zealand	DQ173140	DQ173111	Mostert et al. 2006
	CBS 114512	Ficinia spiralis	New Zealand	DQ173141	DQ173112	Mostert et al. 2006
Phaeoacremonium luteum	A34	Santalum album	Australia	KJ533543	KJ533541	Gramaje et al. 2014
	CBS 137497 [⊤]	Santalum album	Australia	KF835406	KF823800	Gramaje et al. 2014
Phaeoacremonium minimum	CBS 100397	Vitis vinifera	Italy	AY735498	AF246806	Groenewald et al. 2001, Mostert et al. 200
	CBS 110703	Vitis vinifera	South Africa	DQ173115	DQ173094	Mostert et al. 2006
	CBS 121434	Prunus armeniaca	South Africa	EU128105	EU128063	Damm et al. 2008b
	CBS 121435	Prunus salicina	South Africa	EU128107	EU128065	Damm et al. 2008b
	CBS 121436	Prunus persica	South Africa	EU128110	EU128068	Damm et al. 2008b
	CBS 246.91 ⁺	Vitis vinifera	Yugoslavia	AY735497	AF246811	Groenewald et al. 2001, Mostert et al. 200
	L.M.483	Prunus armeniaca	South Africa	DQ173116	DQ173095	Mostert et al. 2006
	PMC178	Arthropods	South Africa	n/a	MF352202	Moyo et al. 2014
	STE-U 3093	Vitis vinifera Vitis vinifera	South Africa South Africa	n/a	AF246813	Groenewald et al. 2001 Groenewald et al. 2001
	STE-U 3094 STE-U 5962	Prunus salicina	South Africa	n/a EU128108	AF246812 EU128066	Damm et al. 2008b
	STE-U 5963	Prunus salicina Prunus salicina	South Africa	EU128108	EU128067	Damm et al. 2008b
	STE-U 6088	Prunus armeniaca	South Africa	EU128109	EU128067	Damm et al. 2008b
	STE-U 6090	Prunus armeniaca	South Africa	EU128104	EU128064	Damm et al. 2008b
	STE-U 6986	Vitis vinifera	South Africa	JQ038920	JQ038909	White et al. 2011
	STE-U 6991	Vitis vinifera	South Africa	JQ038921	JQ038910	White et al. 2011
	STE-U 7319	Pyrus communis	South Africa	n/a	JE934931	Cloete et al. 2011
	STE-U 7320	Pyrus communis	South Africa	n/a	JF934932	Cloete et al. 2011
	STE-U 7321	Pyrus communis	South Africa	n/a	JF934932	Cloete et al. 2011
	STE-U 7322	Pyrus communis	South Africa	n/a	JF934943	Cloete et al. 2011
	STE-U 7323	Pyrus communis	South Africa	n/a	JF934939	Cloete et al. 2011
	STE-U 7323	Pyrus communis	South Africa	n/a	JF934940	Cloete et al. 2011
	STE-U 7325	Pyrus communis	South Africa	n/a	JF934947	Cloete et al. 2011
	STE-U 7326	Pyrus communis	South Africa	n/a	JF934941	Cloete et al. 2011
	STE-U 7327	Malus domestica	South Africa	n/a	JF934934	Cloete et al. 2011
	STE-U 7330	Malus domestica	South Africa	n/a	JF934935	Cloete et al. 2011
	STE-U 7331	Malus domestica	South Africa	n/a	JF934936	Cloete et al. 2011
	STE-U 7332	Malus domestica	South Africa	n/a	JF934937	Cloete et al. 2011
	STE-U 7333	Malus domestica	South Africa	n/a	JF934938	Cloete et al. 2011
	STE-U 7334	Malus domestica	South Africa	n/a	JF934946	Cloete et al. 2011
	STE-U 7336	Malus domestica	South Africa	n/a	JF934942	Cloete et al. 2011
	STE-U 7337	Pyrus communis	South Africa	n/a	JF934944	Cloete et al. 2011
	STE-U 7338	Pyrus communis	South Africa	n/a	JF934945	Cloete et al. 2011
	STE-U 7339	Pyrus communis	South Africa	n/a	JF934928	Cloete et al. 2011
	STE-U 7340	Pyrus communis	South Africa	n/a	JF934930	Cloete et al. 2011
	STE-U 7344	Pyrus communis	South Africa	n/a	JF934927	Cloete et al. 2011
	STE-U 7348	Malus domestica	South Africa	n/a	JF934929	Cloete et al. 2011
	STE-U 7826	Diospyros kaki	South Africa	MF352200	MF352203	Moyo et al. 2016
Phaeoacremonium nordesticola	CMM 4312 [⊤]	Vitis vinifera	Brazil	KY030803	KY030807	Da Silva et al. 2017
	CMM 4313	Vitis vinifera	Brazil	KY030806	KY030808	Da Silva et al. 2017
	CMM 4314	Vitis vinifera	Brazil	KY030804	KY030809	Da Silva et al. 2017
	CMM 4334	Vitis vinifera	Brazil	KY030805	KY030810	Da Silva et al. 2017
Phaeoacremonium occidentale	ICMP17037 [™]	Vitis berlandieri × Vitis riparia	New Zealand	EU595460	EU596524	Graham et al. 2009
Phaeoacremonium pallidum	CBS 120862 [⊤]	Prunus armeniaca	South Africa	EU128144	EU128103	Damm et al. 2008b
Phaeoacremonium parasiticum	CBS 113585	Vitis vinifera	South Africa	AY579241	AY579307	Mostert et al. 2005
	CBS 113586	Vitis vinifera	South Africa	AY579242	AY579308	Mostert et al. 2005
	CBS 113594	Vitis vinifera	South Africa	AY579244	AY579310	Mostert et al. 2005
	CBS 121437	Prunus armeniaca	South Africa	EU128123	EU128081	Damm et al. 2008b
	CBS 514.82	Homo sapiens	Finland	AY579240	AY579306	Mostert et al. 2005
	CBS 860.73 ^T	Homo sapiens	USA	AY579253	AF246803	Groenewald et al. 2001
	PMC240	Arthropods	South Africa	n/a	MF352212	Moyo et al. 2014
	STE-U 6990	Vitis vinifera	South Africa	JQ038928	JQ038917	White et al. 2011
	STE-U 6993	Vitis vinifera	South Africa	JQ038927	JQ038916	White et al. 2011
	STE-U 7821	Diospyros kaki	South Africa	MF352197	MF352210	Moyo et al. 2016
	STE-U 7824	Diospyros kaki	South Africa	MF352199	MF352211	Moyo et al. 2016
Phaeoacremonium prunicola	CBS 120858 ^T	Prunus salicina	South Africa	EU128137	EU128095	Damm et al. 2008b
	STE-U 5968	Prunus salicina	South Africa	EU128138	EU128096	Damm et al. 2008b
Phaeoacremonium pseudopanacis	CBS 142101	Pseudopanax crassifolius	New Zealand	KY173569	KY173609	Crous et al. 2016
Phaeoacremonium roseum	DAOM 242365 ^T	Vitis vinifera	Canada	KF764507	KF764659	Úrbez-Torres et al. 2014
	PARC273	Vitis vinifera	Canada	KF764506	KF764658	Úrbez-Torres et al. 2014
Phaeoacremonium rubrigenum	CBS 112046	Homo sapiens	USA	AY579239	AY579305	Mostert et al. 2005
	CBS 498.94 ^T	Homo sapiens	USA	AY579238	AF246802	Groenewald et al. 2001, Mostert et al. 200
Phaeoacremonium santali	A4	Santalum album	Australia	KF835397	KF823791	Gramaje et al. 2014
	A37	Santalum album	Australia	KJ533538	KJ533534	Gramaje et al. 2014
	CBS 137498 [⊤]	Santalum album	Australia	KF835403	KF823797	Gramaje et al. 2014
Phaeoacremonium scolyti	CBS 112585	Larvae of Scolytus intricatus	Czech Republic	AY579223	AY579292	Mostert et al. 2005
-	CBS 113593	Vitis vinifera	France	AY579225	AY579293	Mostert et al. 2005
	CBS 113597 [⊤]	Vitis vinifera	South Africa	AY579224	AF246800	Groenewald et al. 2001, Mostert et al. 200
	CBS 121438	Prunus armeniaca	South Africa	EU128125	EU128083	Damm et al. 2008b
	CBS 121439	Prunus salicina	South Africa	EU128132	EU128090	Damm et al. 2008b
	CBS 121755	Prunus persica var. nucipersica		EU128124	EU128082	Damm et al. 2008b
	CBS 121756	Prunus persica	South Africa	EU128128	EU128086	Damm et al. 2008b
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Appendix 1 (cont.)

Organism	Strain	Host	Country	ACT	TUB2	References
Phaeoacremonium scolyti (cont.)	STE-U 5956	Prunus salicina	South Africa	EU128133	EU128091	Damm et al. 2008b
	STE-U 6096	Prunus armeniaca	South Africa	EU128126	EU128084	Damm et al. 2008b
	STE-U 6097	Prunus persica	South Africa	EU128127	EU128085	Damm et al. 2008b
	STE-U 6099	Prunus persica	South Africa	EU128129	EU128087	Damm et al. 2008b
	STE-U 6100	Prunus persica	South Africa	EU128130	EU128088	Damm et al. 2008b
	STE-U 7819	Diospyros kaki	South Africa	MF352195	MF352206	Moyo et al. 2016
	STE-U 7820	Diospyros kaki	South Africa	MF352196	MF352207	Moyo et al. 2016
	STE-U 7822	Diospyros kaki	South Africa	MF352198	MF352208	Moyo et al. 2016
Phaeoacremonium sicilianum	CBS 123034 [⊤]	Vitis vinifera	Italy	EU863520	EU863488	Essakhi et al. 2008
	CBS 123035	Vitis vinifera	Italy	EU863521	EU863489	Essakhi et al. 2008
	PMC220	Arthropods	South Africa	n/a	MF352209	Moyo et al. 2014
	STE-U 6992	Vitis vinifera	South Africa	JQ038929	JQ038918	White et al. 2011
	STE-U 6994	Vitis vinifera	South Africa	JQ038930	JQ038919	White et al. 2011
Phaeoacremonium sp.	CBS 142686	Vitis berlandieri × Vitis rupestris	South Africa	KY084248	KY084246	Spies unpublished
	CBS 142687	Vitis vinifera	South Africa	KY084247	KY084245	Spies unpublished
Phaeoacremonium sphinctrophorum	CBS 337.90 ⁺	Homo sapiens	Laos	DQ173142	DQ173113	Mostert et al. 2006
	CBS 694.88	Homo sapiens	USA	DQ173143	DQ173114	Mostert et al. 2006
Phaeoacremonium subulatum	CBS 113584 ^T	Vitis vinifera	South Africa	AY579231	AY579298	Mostert et al. 2005
	CBS 113587	Vitis vinifera	South Africa	AY579232	AY579299	Mostert et al. 2005
	CBS 120866	Prunus armeniaca	South Africa	EU128134	EU128092	Damm et al. 2008b
Phaeoacremonium tardicrescens	CBS 110573 ^T	Homo sapiens	USA	AY579233	AY579300	Mostert et al. 2005
Phaeoacremonium tectonae	MFLUCC 13-0707 ^T	Tectona grandis	Thailand	KT285555	KT285563	Ariyawansa et al. 2015
	MFLUCC 14-1125	Tectona grandis	Thailand	KT285557	KT285565	Ariyawansa et al. 2015
	MFLUCC 14-1130	Tectona grandis	Thailand	KT285561	KT285569	Ariyawansa et al. 2015
Phaeoacremonium theobromatis	CBS 111586 ^T	Theobroma gileri	Ecuador	DQ173132	DQ173106	Mostert et al. 2006
Phaeoacremonium tuscanicum	CBS 123033 ^T	Vitis vinifera	Italy	EU863490	EU863458	Essakhi et al. 2008
Phaeoacremonium venezuelense	CBS 110119	Vitis vinifera	South Africa	AY579254	AY579318	Mostert et al. 2005
	CBS 113595	Homo sapiens	Canada	AY579255	AY579319	Mostert et al. 2005
	CBS 651.85 [⊤]	Homo sapiens	Venezuela	AY579256	AY579320	Mostert et al. 2005
Phaeoacremonium vibratile	CBS 117115 [⊤]	Fagus sylvatica	France	DQ649064	DQ649063	Réblova & Mostert 2007
Phaeoacremonium viticola	CBS 101737	Vitis vinifera	France	DQ173129	AF246817	Groenewald et al. 2001, Mostert et al. 2006
	CBS 101738 [⊤]	Vitis vinifera	France	DQ173131	AF192391	Groenewald et al. 2001, Mostert et al. 2006
	CBS 113065	Vitis vinifera	South Africa	DQ173128	DQ173105	Mostert et al. 2006
	CBS 121440	Prunus salicina	South Africa	EU128135	EU128093	Damm et al. 2008b
	STE-U 6180	Prunus salicina	South Africa	EU128136	EU128094	Damm et al. 2008b
	STE-U 7352	Pyrus communis	South Africa	n/a	JF934949	Cloete et al. 2011
	STE-U 7353	Pyrus communis	South Africa	n/a	JF934950	Cloete et al. 2011
Pleurostoma richardsiae	CBS 270.33 ^T	Unknown	Sweden	AY579271	AY579334	Mostert et al. 2005

a n/a - Data not available.
 b Previously reported as *P. alvesii.* c Ex-type strain of *P. novae-zealandiae*, which was synonymised with *P. leptorrhynchum* by Réblova (2011).
 T Ex-type strain.



Appendix 2 Maximum likelihood phylogenies of the individual actin (*ACT*) and beta-tubulin (*TUB2*) regions. Species-level clades and sub-clades corresponding to those designated in Fig. 1 have been collapsed. Sensu stricto (s.str.) and sensu lato (s.lat.) designations corresponding to those provided in Fig. 1 are indicated next to collapsed clades or individual strain numbers. Paraphyletic species and clades that are incongruent between these individual phylogenies and/or the combined phylogeny (Fig. 1) are highlighted in orange. Ex-type strains or collapsed clades containing ex-type strains are indicated in **bold** typeface.

Appendix 3 List of known plant-associated *Phaeoacremonium* species, their plant host/substrate range and worldwide distribution.

Phaeoacremonium species	Host/Substrate	Country (Reference)
? africanum	Cydonia oblonga	South Africa (this study)
	Eriobotrya japonica	South Africa (this study)
	Olea europaea subsp. europaea	South Africa (this study)
	Prunus armeniaca	South Africa (Damm et al. 2008b)
album	Cydonia oblonga	South Africa (this study)
album	Pyrus communis	South Africa (this study)
	-	
	Vitis vinifera	South Africa (this study)
alvesii	Dodonaea viscosa	Australia (Mostert et al. 2005)
	Ficus carica	South Africa (this study)
	Fraxinus excelsior	Iran (Kazemzadeh Chakusary et al. 2017)
	Melia azedarach	South Africa (this study)
	Olea europaea subsp. europaea	Italy (Nigro et al. 2013)
	Pinus eldarica	Iran (Kazemzadeh Chakusary et al. 2017)
	Prunus persica	South Africa (this study)
	Psidium guajava	South Africa (this study)
	Pterocarya fraxinifolia	Iran (Kazemzadeh Chakusary et al. 2017)
	Rosa sp.	South Africa (this study)
	Vitis vinifera	Turkey (Essakhi et al. 2008)
amygdalinum	Prunus dulcis	Spain (Gramaje et al. 2012)
angustius	Malus sp.	USA (Rooney-Latham et al. 2006)
	Vitis vinifera	France and Italy (Dupont et al. 1998); Portugal (Chicau et al. 2000);
		Spain (García-Benavides et al. 2013); USA (Groenewald et al. 2001)
aquaticum	Submerged wood	China (Hu et al. 2012)
argentinense	Soil	Argentina (Crous & Gams 2000)
•		
armeniacum	Vitis vinifera Malia ana dana da	New Zealand (Graham et al. 2009)
aureum	Melia azedarach	South Africa (this study)
	Psidium guajava	South Africa (this study)
	Rosa sp.	South Africa (this study)
australiense	Cydonia oblonga	South Africa (this study)
	Diospyros kaki	South Africa (Moyo et al. 2016)
	Eriobotrya japonica	South Africa (this study)
	Ficus carica	South Africa (this study)
	Malus domestica	South Africa (this study)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Psidium guajava	South Africa (this study)
	Punica granatum	South Africa (this study)
	Rosa sp.	South Africa (this study)
	Vitis vinifera	Australia (Mostert et al. 2005); South Africa (this study); Uruguay (Abreo et al. 2011)
austroafricanum	Leucadendron sp. (twig litter)	South Africa (Marincowitz et al. 2008)
austroanian	Vitis vinifera	South Africa (Mathematical al. 2006)
bibendum		
	Schinus molle	South Africa (this study)
canadense	Vitis vinifera	Canada (Úrbez-Torres et al. 2014)
cinereum	Vitis vinifera	Iran and Spain (Gramaje et al. 2009b)
croatiense	Alnus glutinosa	Iran (Kazemzadeh Chakusary et al. 2017)
	Quercus castaneifolia	Iran (Kazemzadeh Chakusary et al. 2017)
	Vitis vinifera	Croatia (Essakhi et al. 2008)
fraxinopennsylvanicum	Actinidia deliciosa	Italy (Prodi et al. 2008)
n ann iop on nog i van ioann		Iran (Kazemzadeh Chakusary et al. 2017)
	Alnus glutinosa	
	Fraxinus excelsior	Sweden (Groenewald et al. 2001)
	Fraxinus latifolia	USA (Eskalen et al. 2005)
	Fraxinus pennsylvanica	USA (Hausner et al. 1992)
	Malus domestica	Iran (Sami et al. 2014); South Africa (this study)
	Malus sp.	USA (Rooney-Latham et al. 2006)
	Mespilus germanica	Iran (Kazemzadeh Chakusary et al. 2017)
	Parrotia persica	Iran (Kazemzadeh Chakusary et al. 2017)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Pyrus communis	
	,	South Africa (Cloete et al. 2011)
	Quercus agrifolia	USA (Lynch et al. 2013)
	Vitis vinifera	Canada (Úrbez-Torres et al. 2014); Croatia and Hungary (Essakhi et al. 2008);
		Iran (Mohammadi 2011); South Africa (White et al. 2011); Spain (Gramaje et al. 2007);
		USA (Groenewald et al. 2001)
fuscum	Prunus salicina	South Africa (Damm et al. 2008b)
gamsii	Callistemon sp.	South Africa (this study)
geminum	Malus domestica	South Africa (this study)
globosum	Cydonia oblonga	South Africa (this study)
9.02000111		
	Vitis vinifera	New Zealand (Graham et al. 2009); South Africa (this study)
griseo-olivaceum	Prunus armeniaca	South Africa (Damm et al. 2008b)
	Vitis vinifera	South Africa (this study)
griseorubrum	Melia azedarach	South Africa (this study)
	Prunus persica	South Africa (this study)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Psidium guajava	South Africa (this study)
	Rosa sp.	South Africa (this study)
	Vitis vinifera	Italy (Essakhi et al. 2008); South Africa (this study)
		Algeria (Devret Tehbal et al. 2011): Chain (Crampia et al. 2000h)
hispanicum	Vitis vinifera	Algeria (Berraf-Tebbal et al. 2011); Spain (Gramaje et al. 2009b)
hungaricum	Vitis vinifera	Hungary (Essakhi et al. 2008)
hungaricum	Vitis vinifera Bambusa vulgaris	Hungary (Essakhi et al. 2008) Phillipines (Eriksson & Yue 1990)
hispanicum hungaricum inconspicuum inflatipes	Vitis vinifera	Hungary (Essakhi et al. 2008)

Appendix 3 (cont.)

haeoacremonium species	Host/Substrate	Country (Reference)
inflatipes (cont.)	Cydonia oblonga	South Africa (this study)
	Eriobotrya japonica	South Africa (this study)
	Ficus carica	South Africa (this study)
	Hypoxylon truncatum	USA (Mostert et al. 2005)
	Malus domestica	South Africa (this study)
	Morus sp.	South Africa (this study)
	Nectandra sp.	Costa Rica (Groenewald et al. 2001)
	Prunus armeniaca	South Africa (this study)
	Prunus persica	South Africa (this study)
	Psidium guajava	South Africa (this study)
	Quercus robur	South Africa (this study)
	Quercus virginiana	USA (Groenewald et al. 2001)
	Salix sp.	South Africa (this study)
	Soil	USA (Rooney et al. 2001)
	Vitis vinifera	Chile (Mostert et al. 2006); Iran (Mohammadi et al. 2013); Spain (Gramaje et al. 2009a)
iranianum	Actinidia chinensis	Italy (Mostert et al. 2006)
	Alnus glutinosa	Iran (Kazemzadeh Chakusary et al. 2017)
	Cinnamomum camphora	South Africa (this study)
	Crataegus rhipidophylla	Iran (Sami et al. 2014)
	Cydonia oblonga	Iran (Sami et al. 2014); South Africa (this study)
	Malus domestica	Iran (Arzanlou et al. 2014, Sami et al. 2014)
	Prunus armeniaca	South Africa (Damm et al. 2008b)
	Prunus dulcis	Spain (Gramaje et al. 2012)
	Prunus persica var. nucipersica	South Africa (this study)
	Prunus salicina	South Africa (this study)
	Punica granatum	Iran (Kazemzadeh Chakusary et al. 2017)
	Pyrus communis	South Africa (Cloete et al. 2011)
	Vitis vinifera	Canada (Úrbez-Torres et al. 2014); Iran (Mostert et al. 2006); Italy (Essakhi et al. 2008);
		South Africa (White et al. 2011); Spain (Gramaje et al. 2009a)
	Zelkova carpinifolia	Iran (Kazemzadeh Chakusary et al. 2017)
italicum	Arthropods	South Africa (Moyo et al. 2014; reported as P. alvesii)
	Cydonia oblonga	South Africa (this study)
	Ficus carica	South Africa (this study)
	Malus domestica	
		South Africa (this study)
	Melia azedarach	South Africa (this study)
	Morus sp.	South Africa (this study)
	Olea europaea subsp. europaea	Italy (Carlucci et al. 2015)
	Prunus persica	South Africa (this study)
	Psidium guajava	South Africa (this study)
	Punica granatum	South Africa (this study)
	Vitis vinifera	Italy (Raimondo et al. 2014); South Africa (White et al. 2011; reported as P. alvesii)
junior	Prunus armeniaca	South Africa (this study)
	Schinus molle	South Africa (this study)
	Vitis vinifera	South Africa (this study)
krajdenii	Vitis vinifera	South Africa (Mostert et al. 2005); Spain (Gramaje et al. 2011)
leptorrhynchum	Acer saccharum	USA (Réblová 2011)
loptomynonam		USA (Réblová 2011)
	Acer spicatum	
	Castanaea sativa	Italy (Réblová 2011)
	Chamaerops humilis	Algeria (Réblová 2011)
	Cupressus macrocarpa	New Zealand (Hausner et al. 1992; reported as <i>P. novae-zealandiae</i>)
	Fagus sylvatica	Ukraine (Réblová 2011)
	Ficinia spiralis	New Zealand (Hausner et al. 1992; reported as P. novae-zealandiae)
	Lactuca canadensis	USA (Réblová 2011)
	Pinus radiata	New Zealand (Hausner et al. 1992; reported as P. novae-zealandiae)
longicollarum	Prunus armeniaca	South Africa (this study)
	Psidium guajava	South Africa (this study)
luteum	Santalum album	Australia (Gramaje et al. 2014)
meliae	Melia azedarach	South Africa (this study)
	Actinidia chinensis	Italy (Crous & Gams 2000)
minimum		
minimum		
minimum	Actinidia deliciosa	Italy (Prodi et al. 2008)
minimum	Actinidia deliciosa Alnus glutinosa	Iran (Kazemzadeh Chakusary et al. 2017)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014)
ninimum	Actinidia deliciosa Alnus glutinosa	Iran (Kazemzadeh Chakusary et al. 2017)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014)
ninimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter)	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008)
ninimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016)
ninimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp.	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (Moyo et al. 2016) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (Moyo et al. 2016) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Kazenzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp.	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (Moyo et al. 2016) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (Moyo et al. 2016) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Kazenzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea Parrotia persica	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014) South Africa (Moyo et al. 2016) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013) Iran (Kazemzadeh Chakusary et al. 2017)
ninimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea Parrotia persica Phoenix dactylifera	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Mohammadi 2014)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea Parrotia persica Phoenix dactylifera Prunus armeniaca Prunus dulcis	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Kazemzadeh Chakusary et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Mohammadi 2014) Iran (Arzanlou et al. 2014); South Africa (Damm et al. 2008b) South Africa (this study)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea Parrotia persica Phoenix dactylifera Prunus armeniaca Prunus dulcis Prunus pennsylvanica	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Arzanlou et al. 2014, Sami et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Mohammadi 2014) Iran (Arzanlou et al. 2014); South Africa (Damm et al. 2008b) South Africa (this study) USA (Hausner et al. 1992)
minimum	Actinidia deliciosa Alnus glutinosa Arthropods Brabejum stellatifolium (twig litter) Cupressus sempervirens Cydonia oblonga Diospyros kaki Eriobotrya japonica Gleditsia caspica Malus domestica Morus sp. Olea europaea subsp. europaea Parrotia persica Phoenix dactylifera Prunus armeniaca Prunus dulcis	Iran (Kazemzadeh Chakusary et al. 2017) South Africa (Moyo et al. 2014) South Africa (Marincowitz et al. 2008) Iran (Mohammadi et al. 2014) Iran (Sami et al. 2014); South Africa (this study) South Africa (Moyo et al. 2016) South Africa (this study) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Kazemzadeh Chakusary et al. 2014); South Africa (Cloete et al. 2011) South Africa (this study) Italy (Crous & Gams 2000);South Africa (this study); USA (Úrbez-Torres et al. 2013) Iran (Kazemzadeh Chakusary et al. 2017) Iran (Mohammadi 2014) Iran (Arzanlou et al. 2014); South Africa (Damm et al. 2008b) South Africa (this study)

Appendix 3 (cont.)

Olea europaea subsp. europaea

Pyrus communis

Salix alba

Vitis vinifera

Phaeoacremonium species	Host/Substrate	Country (Reference)
P. minimum (cont.)	Punica granatum	South Africa (this study)
	Pyrus communis	Iran (Sami et al. 2014); South Africa (Cloete et al. 2011)
	Rosa sp.	South Africa (this study)
	Salix alba	Iran (Hashemi & Mohammadi 2016)
	Salix sp.	South Africa (this study); USA (Hausner et al. 1992)
	Schinus molle	South Africa (this study)
	Soil	Spain (Agustí-Brisach et al. 2013); USA (Rooney et al. 2001)
	Vitis vinifera	Algeria (Berraf-Tebbal et al. 2011); Argentina (Gatica et al. 2001); Australia (Pascoe & Cottral 2000);
		Austria (Reisenzein et al. 2000); Brasil (Correia et al. 2013); Canada (Úrbez-Torres et al. 2014);
		Chile (Auger et al. 2005); France (Larignon & Dubos 1997); Germany (Fischer & Kassemeyer 2003);
		Greece and Hungary (Essakhi et al. 2008); Iran (Mostert et al. 2006); Israel (Essakhi et al. 2008);
		Italy (Crous et al. 1996); Portugal (Rego et al. 2000); South Africa (Crous et al. 1996);
		Spain (Armengol et al. 2001); Turkey (Ari 2000); Uruguay (Abreo et al. 2011); USA (Crous et al. 1996
		Yugoslavia (Crous et al. 1996)
P. nordesticola	Vitis vinifera	Brazil (Da Silva et al. 2017)
? occidentale	Vitis vinifera	New Zealand (Graham et al. 2009)
? oleae	Olea europaea subsp. cuspidata	South Africa (this study)
2 pallidum	Prunus armeniaca	South Africa (Damm et al. 2008b)
parasiticum	Actinidia chinensis	Italy (Di Marco et al. 2004)
	Afrocarpus falcatus	South Africa (this study)
	Aquilaria agallocha	No data (Mostert et al. 2006)
	Arthropods	South Africa (Moyo et al. 2014)
	Carpinus betulus	Iran (Kazemzadeh Chakusary et al. 2017)
	Cupressus sempervirens	Iran (Mohammadi et al. 2014)
	Cupressus sp.	No data (Mostert et al. 2006)
	Cydonia oblonga	Iran (Sami et al. 2014); South Africa (this study)
	Diospyros kaki	South Africa (Moyo et al. 2016)
	Eriobotrya japonica	South Africa (this study)
	Erythrina sp.	South Africa (this study)
	Ficus carica	South Africa (this study)
	Leucadendron sp. (twig litter)	South Africa (Marincowitz et al. 2008)
	Malus domestica	Iran (Sami et al. 2014); South Africa (this study)
	Melia azedarach	South Africa (this study)
	Nectandra sp.	Costa Rica (Hawksworth et al. 1976)
	Olea europaea subsp. europaea	Italy (Nigro et al. 2013); South Africa (this study)
	Parrotia persica	Iran (Kazemzadeh Chakusary et al. 2017)
	Phoenix dactylifera	Iran (Mohammadi 2014); Iraq (Hawksworth et al. 1976)
	Populus caspica	Iran (Kazemzadeh Chakusary et al. 2017)
	Populus nigra	Iran (Hashemi & Mohammadi 2016)
	Prunus armeniaca	South Africa (Damm et al. 2008b); Tunisia (Hawksworth et al. 1976)
	Prunus avium	Greece (Rumbos 1986)
	Psidium guajava	South Africa (this study)
	Punica granatum	South Africa (this study)
	Pyrus communis	Iran (Sami et al. 2014)
	Quercus virginiana	USA (Halliwell 1966)
	Rosa sp.	South Africa (this study)
	Salix alba	
	odini diba	Iran (Hashemi & Mohammadi 2016) South Africa (this study)
	Salix sp.	
	Soil	Tahiti (Dupont et al. 2002); Spain (Agustí-Brisach et al. 2013)
	Ulmus carpinifolia	Iran (Kazemzadeh Chakusary et al. 2017)
	Vitis vinifera	Algeria (Berraf-Tebbal et al. 2011); Argentina (Gatica et al. 2001); Australia (Pascoe & Cottral 2000);
		Brasil (Correia et al. 2013); Chile (Auger et al. 2005); Iran (Mostert et al. 2006);
		Italy (Essakhi et al. 2008); Peru (Romero-Rivas et al. 2009); South Africa (Mostert et al. 2005);
		Spain (Aroca et al. 2006); USA (Mostert et al. 2006)
	Zelkova carpinifolia	Iran (Kazemzadeh Chakusary et al. 2017)
paululum	Psidium guajava	South Africa (this study)
proliferatum	Malus domestica	South Africa (this study)
	Rosa sp.	South Africa (this study)
prunicola	Afrocarpus falcatus	South Africa (this study)
	Cinnamomum camphora	South Africa (this study)
	1	
	Cydonia oblonga	South Africa (this study)
	Eriobotrya japonica	South Africa (this study)
	Olea europaea subsp. cuspidata	South Africa (this study)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Psidium guajava	South Africa (this study)
	Pyrus communis	South Africa (this study)
	Schinus molle	South Africa (this study)
	Vitis vinifera	South Africa (this study)
pseudopanacis	Pseudopanax crassifolius	New Zealand (Crous et al. 2016)
roseum	Vitis vinifera	Canada (Úrbez-Torres et al. 2014)
rosicola		
	Rosa sp. Cydonia oblonga	South Africa (this study)
rubrigenum	Cydonia oblonga	Iran (Sami et al. 2014)
	Dactylis glomerata	Spain (Sánchez-Márquez et al. 2007)
	Diospyros kaki	Iran (Jamali & Banihashemi 2012)
	Alea europaea subsp. europaea	Italy (Nigro et al. 2013)

Italy (Nigro et al. 2013)

Iran (Sami et al. 2014)

Iran (Hashemi & Mohammadi 2016)

Chile (Auger et al. 2005); Croatia (Essakhi et al. 2008); New Zealand (Manning & Munday 2009)

Appendix 3 (cont.)

Phaeoacremonium species	Host/Substrate	Country (Reference)
? santali	Santalum album	Australia (Gramaje et al. 2014)
scolyti	Cydonia oblonga	Iran (Sami et al. 2014); South Africa (this study)
	Diospyros kaki	South Africa (Moyo et al. 2016)
	Eriobotrya japonica	South Africa (this study)
	Larvae of Scolytus intricatus	Czech Republic (Kubátova et al. 2004)
	Malus domestica	South Africa (this study)
	Melia azedarach	South Africa (this study)
	Olea europaea subsp. cuspidata	South Africa (this study)
	Olea europaea subsp. europaea	Italy (Carlucci et al. 2015); South Africa (this study)
	Parrotia persica	Iran (Kazemzadeh Chakusary et al. 2017)
	Prunus armeniaca	South Africa (Damm et al. 2008b)
	Prunus domestica	South Africa (this study)
	Prunus dulcis	South Africa (this study)
	Prunus persica	South Africa (Damm et al. 2008b)
	Prunus persica var. nucipersica	South Africa (Damm et al. 2008b)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Psidium guajava	South Africa (this study)
	Punica granatum	Iran (Kazemzadeh Chakusary et al. 2017); South Africa (this study)
scolyti (cont.)	Pyrus communis	Iran (Sami et al. 2014); South Africa (this study)
555.5 ii (00111.)	Quercus suber	South Africa (this study)
	Rosa sp.	South Africa (this study)
	Salix sp.	South Africa (this study)
	Vitis vinifera	France (Mostert et al. 2005); Italy (Essakhi et al. 2008); South Africa (Mostert et al. 2005);
	vius virmera	Spain (Gramaje et al. 2003); Turkey (Özben et al. 2003).
aiailianum	Arthropodo	
sicilianum	Arthropods	South Africa (Moyo et al. 2014)
	Ficus carica	South Africa (this study)
	Juglans sp.	South Africa (this study)
	Olea europaea subsp. europaea	Italy (Carlucci et al. 2015)
	Vitis vinifera	Italy (Essakhi et al. 2008); South Africa (White et al. 2011); Spain (Gramaje et al. 2009a)
spadicum	Eriobotrya japonica	South Africa (this study)
	Olea europaea subsp. cuspidata	South Africa (this study)
	Rhoicissus tomentosa	South Africa (this study)
subulatum	Cydonia oblonga	South Africa (this study)
	Malus domestica	South Africa (this study)
	Prunus armeniaca	South Africa (Damm et al. 2008b)
	Prunus salicina	South Africa (this study)
	Psidium guajava	South Africa (this study)
	Punica granatum	South Africa (this study)
	Pyrus communis	South Africa (this study)
	Rosa sp.	South Africa (this study)
	Schinus molle	South Africa (this study)
	Vitis vinifera	South Africa (Mostert et al. 2006)
tectonae	Tectona grandis	Thailand (Ariyawansa et al. 2015)
theobromatis	Theobroma gileri	Equador (Mostert et al. 2006)
tuscanicum	Vitis vinifera	Iran (Mohammadi 2012); Italy (Essakhi et al. 2008)
venezuelense	Prunus armeniaca	Spain (Olmo et al. 2014)
	Rosa sp.	South Africa (this study)
venezuelense (cont.)	Vitis vinifera	Algeria (Berraf-Tebbal et al. 2011); South Africa (Mostert et al. 2005)
vibratile	Fagus sylvatica	France and Hungary (Réblová & Mostert 2007)
	Prunus padus	Sweden (Réblová & Mostert 2007)
	Sorbus sp.	Italy (Réblová & Mostert 2007)
viticola	Actinidia chinensis	France (Hennion et al. 2001)
	Cydonia oblonga	South Africa (this study)
	Eriobotrya japonica	South Africa (this study)
	Prunus salicina	South Africa (Damm et al. 2008b)
	Psidium guajava	South Africa (this study)
	Pyrus communis	South Africa (Cloete et al. 2011)
	Quercus robur	South Africa (this study)
	Salix sp.	South Africa (this study)
	Sanx sp. Sorbus intermedia	Germany (Mostert et al. 2006)
	Vitis vinifera	France (Dupont et al. 2000) France (Dupont et al. 2000); Iran (Mostert et al. 2006); Italy (Dupont et al. 2000);
		r rance (Dupont et al. 2000), that (initiate that 2000), that (Dupont et al. 2000),