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A re-evaluation of *Penicillium* section *Canescentia*, including the description of five new species

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Key words

DNA barcodes
Genealogical Concordance Phylogenetic Species Recognition (GCPSR)
new taxa
secondary metabolites
series *Atroveneta*
series *Canescentia*

Abstract A survey of *Penicillium* in the fynbos biome from South Africa resulted in the isolation of 61 species of which 29 were found to be new. In this study we focus on *Penicillium* section *Canescentia*, providing a phylogenetic re-evaluation based on the analysis of partial beta-tubulin (*BenA*), calmodulin (*CaM*) and RNA polymerase II second largest subunit (*RPB2*) sequence data. Based on phylogenies we show that five fynbos species are new and several previously assigned synonyms of *P. canescens* and *P. janczewskii* should be considered as distinct species. As such, we provide descriptions for the five new species and introduce the new name *P. elizabethiae* for the illegitimate *P. echinatum*. We also update the accepted species list and synonymies of section *Canescentia* species and provide a review of extrolites produced by these species.

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INTRODUCTION

Penicillium section *Canescentia* species are mostly reported from soil and leaf litter (Raper & Thom 1949, Domsch et al. 1980, Pitt 1980, Ramírez 1982) and typically have terminal biverticillate conidiophores with subterminal branching and broad, short swollen phialides (Pitt 1980, Houbraken & Samson 2011). The section is mainly based on *P. canescens* and *P. janczewskii* but includes common species such as *P. antarcticum*, *P. atrovenetum* and *P. novae-zeelandiae*. Past classifications of section *Canescentia* highlight the difficulty of using morphology and more specifically conidiophore branching patterns to define groups in *Penicillium*. *Penicillium canescens* and *P. janczewskii* produce a high proportion of divaricate conidiophores and were therefore respectively placed in sections *Asymmetrica* (Raper & Thom 1949) and *Divaricatum* (Pitt 1980). On the other hand, species such as *P. novae-zeelandiae* and *P. coralligerum* produce symmetrical, biverticillate conidiophores and were classified in sections *Biverticillata-Symmetrica* (Raper & Thom 1949) and *Furcatum* (Pitt 1980), respectively. These past classifications have, however, long been shown to be relatively superficial and are not reflected in phylogenetic classifications (Peterson 2000, Houbraken & Samson 2011). As a result, a phylogenetic approach to subgeneric classifications has become the standard for *Penicillium* (Houbraken & Samson 2011, Visagie et al. 2014b, Houbraken et al. 2020).

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Difficulties in using morphological characters to identify strains of either *P. canescens* and *P. janczewskii* were noted by Pitt (1980). Colonies of these two were found to be similar and were described on Czapek yeast autolysate agar (CYA) as having white to yellow coloured mycelia and reaching diameters between 25–32 mm after 7 d incubation. On malt extract agar (MEA) (Blakeslee 1915), colonies were found to typically be 15–25 mm wide, floccose and producing bluish to greenish grey conidia. As such, Pitt (1980) distinguished between the two based on the rough-walled stipes and smooth-walled conidia of *P. canescens*, in contrast to *P. janczewskii* that was characterised by smooth-walled stipes and rough-walled conidia. However, Pitt (1980) also reported on the existence of strains, such as IMI 149218, that bridge these characters forming roughened stipes and conidia, which he placed in *P. canescens*. As a result of this rather broad concept of both species, Pitt (1980) synonymised several species with *P. canescens* (= *P. raciborskii*, *P. kapuscinksii*, *P. novae-caledoniae* and *P. yarmokense*) and *P. janczewskii* (= *P. echinatum* (*nom. illegit.*), *P. swiecickii*, *P. nigricans* and *P. nigricans* var. *sulphuratum*). However, identification in this group remained problematic. In recent years, phylogenies helped to resolve some of these species. Houbraken & Samson (2011) reclassified *Penicillium* and divided the genus into 25 sections, classifying eight species (*P. antarcticum*, *P. atrovenetum*, *P. canescens*, *P. coralligerum*, *P. janczewskii*, *P. jensenii*, *P. novae-zeelandiae* and *P. yarmokense*) in section *Canescentia*. Since this classification, several new species were introduced in the section while ex-type strains of old names were also sequenced (Visagie et al. 2014a, 2016b, Grijseels et al. 2016, Kirichuk et al. 2016). In a recent *Eurotiales* review, a new series classification was introduced for *Aspergillus* and *Penicillium* and section *Canescentia* was divided into series *Atroveneta* and *Canescentia*, the latter containing species with biverticillate to terverticillate conidiophores and divergent

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Table 1 Strains used for phylogenetic analyses.

Species name	Collection numbers[a]	Source, location	GenBank accession numbers			
			ITS	*BenA*	*CaM*	*RPB2*
Penicillium allsoppiae	CBS:138943, DAOMC:241348, DTO:182-D5, CV:931 (ex-type)	Soil sample, Malmesbury, South Africa	JX140830	JX140992	JX157384	KP016895
	CBS:138945, IBT:31952, DAOMC:241349, DTO:183-C8, CV:1704	Soil sample, Struisbaai, South Africa	JX140822	JX141004	JX157399	KP016910
	CN086C6, S4C2	Soil, Hopefield, South Africa	MW364385	MW357820	MW357831	MW357840
	CN086C7, S4C3	Soil, Hopefield, South Africa	MW364386	MW357821	MW357832	MW357841
	CN086C8, S2E3	Soil, Hopefield, South Africa	MW364387	MW357822	–	MW357842
Penicillium antarcticum	CBS:100492, FRR:4989 (ex-type)	Soil scraping, Ardery Island, Antarctica	KJ834503	MN969371	MN969236	JN406653
	CBS:116938, IBT:3405, IBT:3742, IBT:4599, IBT:6834, DTO:187-D6	Salami, Hillerod, Denmark	KP016845	KP016925	KP016827	KP016848
	CBS:116939, IBT:4017, DTO:187-B7	Beach sand, Rorvig, Denmark	KP016829	KP016921	JX157255	KP016849
	KMM:4668 (ex-type of *P. piltunense*)	Subaqueous soil, Piltun Bay, Sakhalin island, Russia	KU358554	KU358557	KU358560	–
	KMM:4670 (ex-type of *P. ochotense*)	Subaqueous soil, Piltun Bay, Sakhalin island, Russia	KU358553	KU358556	KU358559	–
	KMM:4671 (ex-type of *P. attenuatum*)	Subaqueous soil, Sakhalin Bay, Sakhalin island, Russia	KU358555	KU358558	KU358561	–
Penicillium arizonense	DTO:216-H4	Root tissue of Artemisia tridentata, USA	–	MF974900	–	–
	IBT:12289, CBS:141311 (ex-type)	Dry red soil, South rim of Grand Canyon, Arizona, USA	MH492021	MH492019	MH492020	MH492022
Penicillium atrovenetum	CBS:241.56, ATCC:13352, FRR:2571, IFO:8138, IMI:061837 (ex-type)	Soil, Sussex Downs, England	AF033492	JX140944	KJ867004	JN121467
	CBS:243.56, FRR:1666, IMI:061835	Soil from spinach field, Norfolk, England	KP016835	JX140945	MN969241	KP016854
Penicillium canescens	CBS:300.48, ATCC:10419, FRR:910, IMI:28260, MUCL:29169, NRRL:910 (ex-type)	Soil, England	AF033493	JX140946	KJ867009	JN121485
	EN:1377	Unknown source, Iran	–	KT285862	–	–
	FMR:15028	Dung, Spain	–	LT898237	–	–
	IMI:149218, IBT:5978, DTO:189-A2	Soil sample, Gharyan, Libya	KP016841	JX140951	KP027409	KP016917
	MUT<ITA>:1764	Oil polluted water from the Mediterranean Sea, Italy	–	KU935636	–	–
	MUT<ITA>:1815	Oil polluted water from the Mediterranean Sea, Italy	–	KU935637	–	–
	SQU14069	Unknown	–	MH000349	–	–
Penicillium cf. *murcianum*	CBS:414.68	Unknown source, Helsinki, Finland	KP016842	KP016922	KP016821	KP016859
	CN086C9, S2C3	Soil, Hopefield, South Africa	MW364388	MW357823	MW357833	MW357843
	CN086D1, S1C3	Soil, Hopefield, South Africa	MW364389	MW357824	MW357834	MW357844
	CN086D2, S2B8	Soil, Hopefield, South Africa	MW364390	MW357825	MW357835	MW357845
	CN086D7, S1C1	Soil, Hopefield, South Africa	MW364395	MW357830	MW357839	MW357850
	IBT:31963, DAOMC:241111, DTO:182-A9, CV:816	Air sample, Malmesbury, South Africa	JX140834	JX140949	JX157369	KP016880
	NRRL:35656	Cheek pouch of kangaroo rat, USA	–	DQ658166	–	–
Penicillium coralligerum	CBS:114.69, FRR:1964, IMI:130675	Soil under *Hordeum* sp., Canada	KP016836	KJ866970	KJ866991	KP016847
	CBS:123.65, ATCC:16968, FRR:3465, IFO:9578, IMI:099159, NRRL:3465 (ex-type)	Seed of *Hordeum vulgate*, France	JN617667	MN969378	MN969248	JN406632
Penicillium corvianum	CN086D3, S1G8	Soil, Hopefield, South Africa	MW364391	MW357826	MW357836	MW357846
	CN086D5, S1G1	Soil, Hopefield, South Africa	MW364393	MW357828	MW357838	MW357848
	CN086D6, S1H8	Soil, Hopefield, South Africa	MW364394	MW357829	–	MW357849
	DAOMC:250517, CBS141000 (ex-type)	Soil, Natural Monument Corviano, Tuscany, Italy	KT887875	KT887836	KT887797	MN969170
	DAOMC:250518, CBS141001	Soil, Natural Monument Corviano, Tuscany, Italy	KT887876	KT887837	KT887798	–
	DTO:216-F4	Root tissue of *Psedotsuga menziesii*, USA	–	MF974905	–	–
	DTO:216-F7	Root tissue of *Psedotsuga menziesii*, USA	–	MF974906	–	–
Penicillium doidgeae	CBS:138947, IBT:31950, DAOMC:241107, DTO:183-G7, CV:2189 (ex-type)	Mite from *Protea repens* infructescence, Struisbaai, South Africa	JX140804	JX141006	JX157413	KP016915
	CBS:138948, IBT:31951, DAOMC:241108, DTO:183-G8, CV:2191	Mite from *Protea repens* infructescence, Struisbaai, South Africa	JX140805	JX141007	JX157414	KP016916
Penicillium dunedinense	CBS:138218, DTO:244-G1 (ex-type)	House dust, Dunedin, New Zealand	KJ775678	KJ775171	KJ775405	MN969116
Penicillium eickeri	CBS:138939, IBT:31921, DAOMC:241352, DTO:181-G3, CV:475 (ex-type)	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140824	JX140979	JX157365	KP016876
	CBS:138940, IBT:31956, DAOMC:241350, DTO:181-G5, CV:487	Bract from *Protea repens* infructescence, Stellenbosch, South Africa	JX140825	JX140980	JX157366	KP016877
Penicillium elizabethiae	NRRL:917, MUCL:29170, IBT:21955, DTO:189-B8 (ex-type)	Soil, Scotland	KP016840	KJ866964	KJ867021	KP016918
Penicillium griseoazureum	CBS:162.42, FRR:1361 (ex-type)	Dune sand, France	KC411679	KP016919	KP016823	KP016852
Penicillium janczewskii	CBS:166.81, IMI:253795 (ex-type of *P. granatense*)	Air sample, Madrid, Spain	KC411682	KJ866967	KJ866998	KP016853
	CBS:221.28, FRR:919, IMI:191499, NRRL:919 (ex-type)	Soil under *Pinus* sp., Poland	AY157487	MN969386	MN969267	JN406612
	CBS:279.47, ATCC:9439	Soil, England	KP016837	KJ866968	KJ867008	KP016855
	CBS:413.69, FRR:518, IMI:140344	Unknown source, Helsinki, Finland	KP016838	KJ866969	KJ867014	KP016858
	CBS:744.70, ATCC:18380 (ex-type of *P. nigricans* var. *sulphureum*)	Unknown source, Japan	KP016839	KJ866966	KJ867018	KP016862
	MUT<ITA>:2710	Dysidea fragilis from Atlantic Ocean, Ireland	–	MG832199	–	–
	MUT<ITA>:6182	Contaminated soil, Italy	–	MK521578	–	–

Table 1 (cont.)

Species name	Collection numbers[a]	Source, location	GenBank accession numbers			
			ITS	*BenA*	*CaM*	*RPB2*
Penicillium jensenii	CBS:216.28, ATCC:10456, IFO:5747, IMI:068233, NRRL:3431	Unknown	JN617693	KJ866963	KJ867000	JN606629
	CBS:327.59, ATCC:18317, FRR:909, IFO:5764, IMI:039768, NRRL:909 (ex-type)	Forest soil, Japan	AY443470	JX140954	AY443490	JN406614
Penicillium linzhiense	CCTCC-M2019870	Soil, Linzhi Town, Tibet Autonomous Region, China	MT461156	MT461157	MT461162	–
Penicillium murcianum	CBS:161.81, ATCC:42239, IMI:253800 (ex-type)	Sandy soil, Madrid, Spain	KP016844	MN969419	MN969341	MN969202
	CBS:458.69	Soil, Turkey	KP016843	KP016923	KP016822	KP016860
	CN086D4, S1O1	Soil, Hopefield, South Africa	MW364392	MW357827	MW357837	MW357847
Penicillium nigricans	CBS:354.48, ATCC:10115, IFO:6103, IMI:039767, NRRL:915 (ex-type)	Unknown source, France	KC411755	KJ866965	KJ867012	KP016857
Penicillium novaezeelandiae	CBS:137.41, ATCC:10473, IFO:31748, IMI:040584ii, NRRL:2128 (ex-type)	Apothecium of Sclerotinia sp., Palmerston North, New Zealand	JN617688	MN969390	MN969279	JN406628
	CBS:138936, IBT:31940, DAOMC:241112, DTO:180-G9, CV:42	Air sample, Stellenbosch, South Africa	JX140853	JX140956	JX157352	KP016864
	CBS:138938, IBT:31937, DAOMC:241113, DTO:181-A6, CV:117	Bract from *Protea repens* infructescence, Stellenbosch, South Africa	JX140846	JX140958	JX157356	KP016868
	CBS:138942, IBT:31947, DAOMC:241354, DTO:182-C8, CV:909	Soil sample, Malmesbury, South Africa	JX140854	JX140969	JX157380	KP016891
	CBS:138949, DTO:184-D5, CV:47	Air sample, Stellenbosch, South Africa	JX140835	JX140957	JX157353	KP016865
	CBS:138950, IBT:31931, DTO:185-D6, CV:818	Air sample, Malmesbury, South Africa	JX140843	JX140968	JX157370	KP016881
	CBS:138952, IBT:31949, DTO:185-H9, CV:992	Mite from *Protea repens* infructescence, Malmesbury, South Africa	JX140845	JX140971	JX157393	KP016904
	CBS:138953, IBT:31944, DTO:186-A3, CV:1290	Bract from *Protea repens* infructescence, Malmesbury, South Africa	JX140847	JX140972	JX157395	KP016906
	CBS:138954, IBT:31946, DTO:186-B7, CV:1560	Bract from *Protea repens* infructescence, Malmesbury, South Africa	JX140848	JX140973	JX157398	KP016909
	CBS:138955, IBT:31941, DTO:186-H1, CV:2029	Mite from *Protea repens* infructescence, Struisbaai, South Africa	JX140850	JX140975	JX157401	KP016913
	CBS:138956, IBT:31948, DTO:186-H2, CV:2051	Mite from *Protea repens* infructescence, Struisbaai, South Africa	JX140851	JX140976	JX157402	KP016914
	CBS:546.77	Stem of *Vitis vinifera*, Auckland, New Zealand	KP016846	KP016926	KP016828	KP016861
	CV:0200	Bract from *Protea repens* infructescence, Stellenbosch, South Africa	JX140838	JX140961	JX157360	–
	IBT:31930, DTO:184-I1, CV:406	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140840	JX140964	JX157363	KP016874
	IBT:31932, DTO:186-D9, CV:1812	Mite from *Protea repens* infructescence, Struisbaai, South Africa	JX140849	JX140974	JX157400	KP016912
	IBT:31933, DTO:185-B7, CV:616	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140842	JX140967	JX157368	KP016879
	IBT:31934, DTO:184-F1, CV:129	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140836	JX140959	JX157357	KP016869
	IBT:31935, DTO:185-F3, CV:910	Soil sample, Malmesbury, South Africa	JX140844	JX140970	JX157381	KP016892
	IBT:31936, DTO:185-B4, CV:587	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140841	JX140966	JX157367	KP016878
	IBT:31938, DTO:184-F5, CV:147	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140837	JX140960	JX157358	KP016870
	IBT:31939, DTO:184-I3, CV:452	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	KP016830	JX140965	JX157364	KP016875
	IBT:31942, DTO:184-H7, CV:337	Bract from *Protea repens* infructescence, Stellenbosch, South Africa	JX140839	JX140962	JX157361	KP016872
	IBT:31943, DTO:181-E8, CV:355	Mite from *Protea repens* infructescence, Stellenbosch, South Africa	JX140852	JX140963	JX157362	KP016873
Penicillium nucicola	DAOMC:250521, CBS:140973, KAS:2101, W:109	Fallen nuts of Fagus grandifolia, Milton, Ontario, Canada	KT887846	KT887807	KT887768	–
	DAOMC:250522, CBS:140987, KAS:2203, W:59 (ex-type)	Fallen nuts of Carya ovata, Niagara Falls, Ontario, Canada	KT887860	KT887821	KT887782	MN969171
Penicillium pole-evansii	CBS:138946, IBT:31929, DAOMC:241106, DTO:183-D5, CV:1758 (ex-type)	Bract from *Protea repens* infructescence, Struisbaai, South Africa	JX140831	JX141005	JX157412	KP016911
Penicillium radiatolobatum	CBS:340.79 (ex-type)	Soil, Romania	KC411745	MN969413	MT066183	MN969168
	FMR:15304	Dung, Spain	–	LT898293	–	–
	FMR:15305	Dung, Spain	–	LT898294	–	–
	FMR:15308	Dung, Spain	–	LT898295	–	–
	FMR:15485	Dung, Spain	–	LT898299	–	–
	FMR:15491	Dung, Spain	–	LT898296	–	–
	FMR:15845	Dung, Spain	–	LT898297	–	–
	IBT:31958, DAOMC:241110, DTO:184-G3, CV:198	Bract from *Protea repens* infructescence, Stellenbosch, South Africa	JX140832	JX140948	JX157359	KP016871
	IBT:31959, DAOMC:241109, DTO:180-H5, CV:68	Soil sample, Stellenbosch, South Africa	JX140833	JX140947	JX157354	KP016866
Penicillium sacculum	CBS:231.61, MUCL:51025, IMI:68319	Soil, Canary Islands, Spain	KC411707	KJ834488	KU896849	JN121462
Penicillium scottii	CBS:138935, IBT:31955, DAOMC:241192, DTO:180-G5, CV:30	Air sample, Stellenbosch, South Africa	JX140823	JX140977	JX157351	KP016863
	CBS:138937, IBT:31954, DTO:180-H9, CV:75	Soil sample, Stellenbosch, South Africa	JX140826	JX140978	JX157355	KP016867
	CBS:138941, IBT:31957, DAOMC:241163, DTO:182-B4, CV:864	Air sample, Malmesbury, South Africa	JX140827	JX140981	JX157371	KP016882
	CBS:138944, IBT:31964, DAOMC:241162, DTO:183-B9, CV:1502	Bract from *Protea repens* infructescence, Malmesbury, South Africa	JX140820	JX141002	JX157396	KP016907
	CBS:138951, IBT:31905, DTO:185-F8, CV:930 (ex-type)	Soil sample, Malmesbury, South Africa	JX140812	JX140991	JX157383	KP016894
	DTO:185-G2, CV:939	Soil sample, Malmesbury, South Africa	JX140814	JX140994	JX157386	KP016897
	IBT:31903, DTO:186-B4, CV:1512	Bract from *Protea repens* infructescence, Malmesbury, South Africa	JX140821	JX141003	JX157397	KP016908
	IBT:31904, DTO:185-G6, CV:953	Soil sample, Malmesbury, South Africa	KP016833	JX140995	JX157387	KP016898
	IBT:31906, DTO:185-H1, CV:958	Soil sample, Malmesbury, South Africa	JX140815	JX140996	JX157388	KP016899
	IBT:31907, DTO:185-E7, CV:898	Soil sample, Malmesbury, South Africa	KP016832	JX140988	JX157378	KP016889

Table 1 (cont.)

Species name	Collection numbers[a]	Source, location	GenBank accession numbers			
			ITS	*BenA*	*CaM*	*RPB2*
Penicillium scottii (cont.)	IBT:31908, DTO:185-H3, CV:967	Soil sample, Malmesbury, South Africa	JX140816	JX140997	JX157389	KP016900
	IBT:31909, DTO:185-H4, CV:969	Soil sample, Malmesbury, South Africa	KP016834	JX140998	JX157390	KP016901
	IBT:31910, DTO:185-H7, CV:975	Soil sample, Malmesbury, South Africa	JX140817	JX140999	JX157391	KP016902
	IBT:31911, DTO:185-H8, CV:978	Soil sample, Malmesbury, South Africa	JX140818	JX141000	JX157392	KP016903
	IBT:31912, DTO:185-E3, CV:890	Soil sample, Malmesbury, South Africa	JX140808	JX140984	JX157374	KP016885
	IBT:31913, DTO:185-F7, CV:929	Soil sample, Malmesbury, South Africa	JX140811	JX140990	JX157382	KP016893
	IBT:31914, DTO:185-G1, CV:937	Soil sample, Malmesbury, South Africa	JX140813	JX140993	JX157385	KP016896
	IBT:31915, DTO:185-D8, CV:874	Soil sample, Malmesbury, South Africa	JX140807	JX140982	JX157372	KP016883
	IBT:31916, DTO:185-E4, CV:892	Soil sample, Malmesbury, South Africa	JX140809	JX140985	JX157375	KP016886
	IBT:31917, DTO:185-E6, CV:897	Soil sample, Malmesbury, South Africa	JX140810	JX140987	JX157377	KP016888
	IBT:31918, DAOMC:241164, DTO:182-C2, CV:893	Soil sample, Malmesbury, South Africa	JX140828	JX140986	JX157376	KP016887
	IBT:31919, DTO:185-E1, CV:881	Soil sample, Malmesbury, South Africa	KP016831	JX140983	JX157373	KP016884
	IBT:31922, DAOMC:241353, DTO:182-H4, CV:1163	Mite from *Protea repens* infructescence, Malmesbury, South Africa	JX140819	JX141001	JX157394	KP016905
	IBT:31953, DAOMC:241351, DTO:182-C4, CV:899	Soil sample, Malmesbury, South Africa	JX140829	JX140989	JX157379	KP016890
Penicillium yarmokense	CBS:410.69, FRR:520, IMI:140346 (ex-type)	Soil, Syria	KC411757	MN969407	MN969314	JN406553
	DTO:216-C9	Root tissue of *Pinus ponderosa*, USA	–	MF974897	–	–
	DTO:216-D8	Root tissue of *Pinus monticola*, USA	–	MF974898	–	–
	DTO:216-E4	Root tissue of *Pseudotsuga menziesii*, USA	–	MF974899	–	–

[a] Culture collection designations: ATCC, American Type Culture Collection, Manassas, USA; CBS, Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands; CV, internal culture collection at the Department of Microbiology, University of Stellenbosch, South Africa; DAOM, culture collection and herbarium of the National Mycological Collections, Agriculture & Agri-Food Canada, Ottawa; DTO, internal culture collection of CBS; FRR, Food Science Australia, Ryde, Australia; IBT, culture collection of Center for Microbial Biotechnology (CMB) at Department of Systems Biology, Technical University of Denmark; IFO, Institute for Fermentation, Osaka, Japan; IMI, CABI Genetic Resources Collection, Surrey, UK; MUCL, Mycotheque de l'Universite catholique de Louvain, Belgium; NRRL, Agricultural Research Service Culture Collection, Peoria, Illinois, USA.

branching, while the former have symmetrically biverticillate conidiophores (Houbraken et al. 2020).

A survey of *Penicillium* occurring in the diverse fynbos biome situated in South Africa was initiated in 2009 to characterise *Penicillium* isolated from soil, air, and mites associated with *Protea repens* infructescences. The ± 1 700 strains were found to represent 10 *Penicillium* sections and 61 species, including 29 described as new. The current study follows on from previous papers describing these new species in sections *Aspergilloides* (Houbraken et al. 2014), *Citrina* (Visagie et al. 2014c), *Exilicaulis* (Visagie et al. 2016c), *Lanata-Divaricata* (Visagie et al. 2015a), *Sclerotiora* (Visagie et al. 2013) and *Torulomyces* (Visagie et al. 2016a). The aim of this paper was to provide descriptions for five new *Penicillium* species and compare them with others from section *Canescentia* using phylogenetic inference from three gene regions, morphology and extrolite data. In the process, we review the classification of previously described species in the section, provide reference sequences for these and a review of extrolites produced by this group.

MATERIALS AND METHODS

Isolates

Isolates were obtained from soil, air and *Protea repens* infructescences collected from the fynbos biome as previously described by Visagie et al. (2014c). These strains were accessioned in the collections of the DAOMC (Canadian Collection of Fungal Cultures, Agriculture & Agri-Food Canada, Ottawa, Canada), IBT (the culture collection at the Department of Systems Biology, DTU, Lyngby, Denmark) and CBS (Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands). Reference strains were obtained from IBT, CBS and NRRL (United States Department of Agriculture, Agricultural Research Service, USDA-ARS, Peoria, United States). Table 1 summarises strains, their origin and GenBank accession numbers used for this study.

Morphology

Colony morphologies were recorded from fynbos strains grown on Czapek yeast autolysate agar (CYA), Czapek yeast autolysate agar with 5 % NaCl (CYAS), malt extract agar (MEA; Oxoid), yeast extract sucrose agar (YES), dichloran 18 % glycerol agar (DG18) and creatine sucrose agar (CREA) incubated at 25 °C for 7 d. Additional CYA plates were incubated at 30 and 37 °C for 7 d. Media preparation, inoculation technique, incubation conditions and microscope preparations were standardised according to recommended methods (Visagie et al. 2014b). Colour names and codes used in descriptions follow Kornerup & Wanscher (1967). Microscopic observations and measurements were made using an Olympus SZX12 dissecting and Olympus BX50 compound microscopes. These were equipped with an Evolution MP digital microscope camera and ImagePro v. 6.0 software. Affinity Photo v. 1.7.3 (Serif (Europe) Ltd) was used for creating photographic plates.

Phylogenetic analyses

DNA extractions were made using the ZR Fungal/Bacterial DNA kit (ZymoResearch, California) from 7-d-old colonies grown on MEA. PCR of the internal transcribed spacer rDNA region (ITS), beta-tubulin (*BenA*), calmodulin (*CaM*) and RNA polymerase II second largest subunit (*RPB2*) was carried out using primer pairs and amplification protocols as described in Visagie et al. (2014b), while reagents and master mixes were prepared following Visagie et al. (2013). Sequence contigs were assembled in Geneious Prime v. 2019.2.3 (Biomatters, NZ). GenBank accession numbers for sequences used in this study are summarised in Table 1.

A sequence dataset was compiled containing both ex-type reference sequences and fynbos *Penicillium* of section *Canescentia*. An ITS phylogeny of only ex-type sequences was calculated to determine if the ITS of the rDNA gene cluster distinguish between the species. Subsequently, single-gene trees were calculated for partial *BenA*, *CaM* and *RPB2* genes, as well as trees representing concatenated datasets. All alignments were done using MAFFT v. 1.764b (Katoh & Standley 2013) and selecting the G-INS-i option. Phylogenetic analyses were performed using both Maximum Likelihood (ML) and Bayesian tree inference (BI). The multigene datasets were concatenated in Geneious Prime, with the partitioning scheme and substitution models selected using Partitionfinder v. 2.1.1 (Lanfear et al. 2017) allowing for introns, exons and codon positions to be independent datasets.

Maximum Likelihood trees were calculated using IQtree v. 1.6.12 (Nguyen et al. 2015) and nonparametric bootstrapping done with 1 000 replicates (Felsenstein 1985). Bayesian inference trees were calculated in MrBayes v. 3.2.7a (Ronquist et al. 2012). Analyses were run using two sets of four chains (one cold and three heated) and the stoprule was applied to stop the analyses once the average standard of deviation for split frequencies reached 0.01. Sample frequency was set at 100 with 25 % of the trees removed as burn-in. ML phylograms were

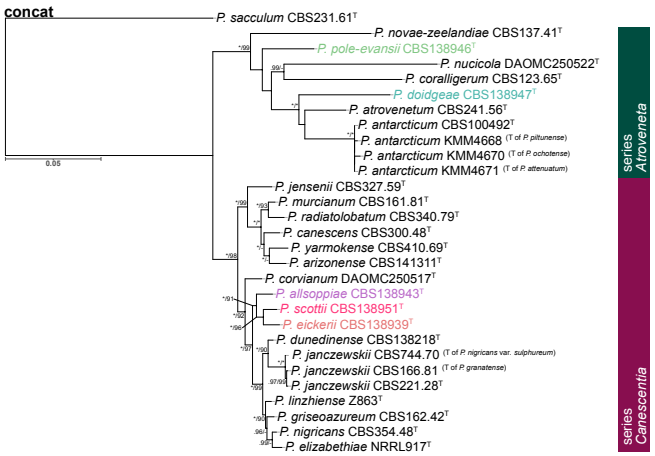

Fig. 1 Phylogenetic tree of *Penicillium* section *Canescentia* ex-type strains using a concatenated dataset of *BenA*, *CaM* and *RPB2*. *Penicillium sacculum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80, respectively, are given above thickened branches. Names in coloured text represent new species, T = ex-type strain.

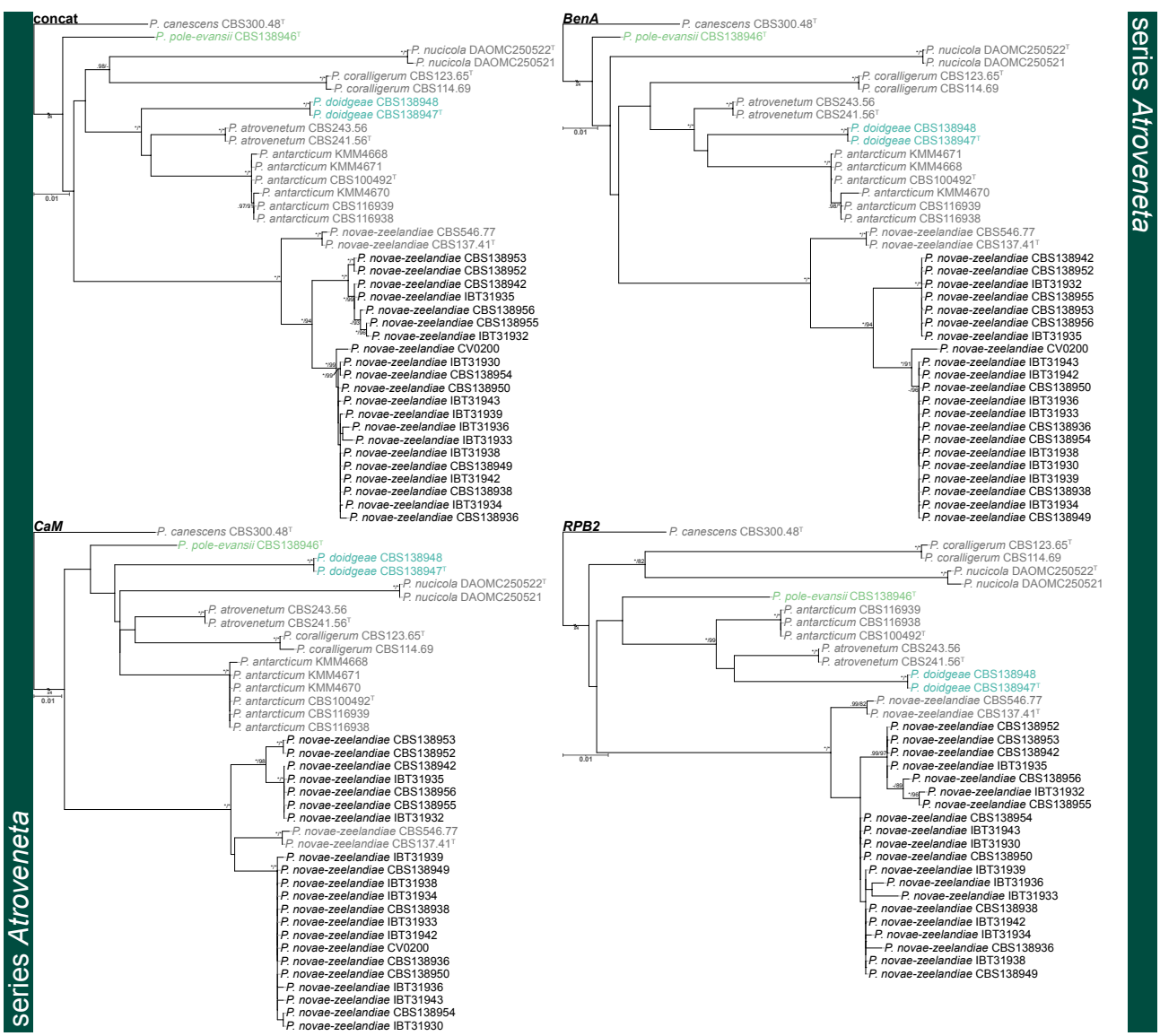

Fig. 2 Phylogenetic trees of *Penicillium* section *Canescentia* series *Atroveneta* based on *BenA*, *CaM*, *RPB2* and concatenated datasets. *Penicillium canescens* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80, respectively, are given above thickened branches. Names in grey text indicate reference strains, black text fynbos strains and coloured text new species, T = ex-type strain.

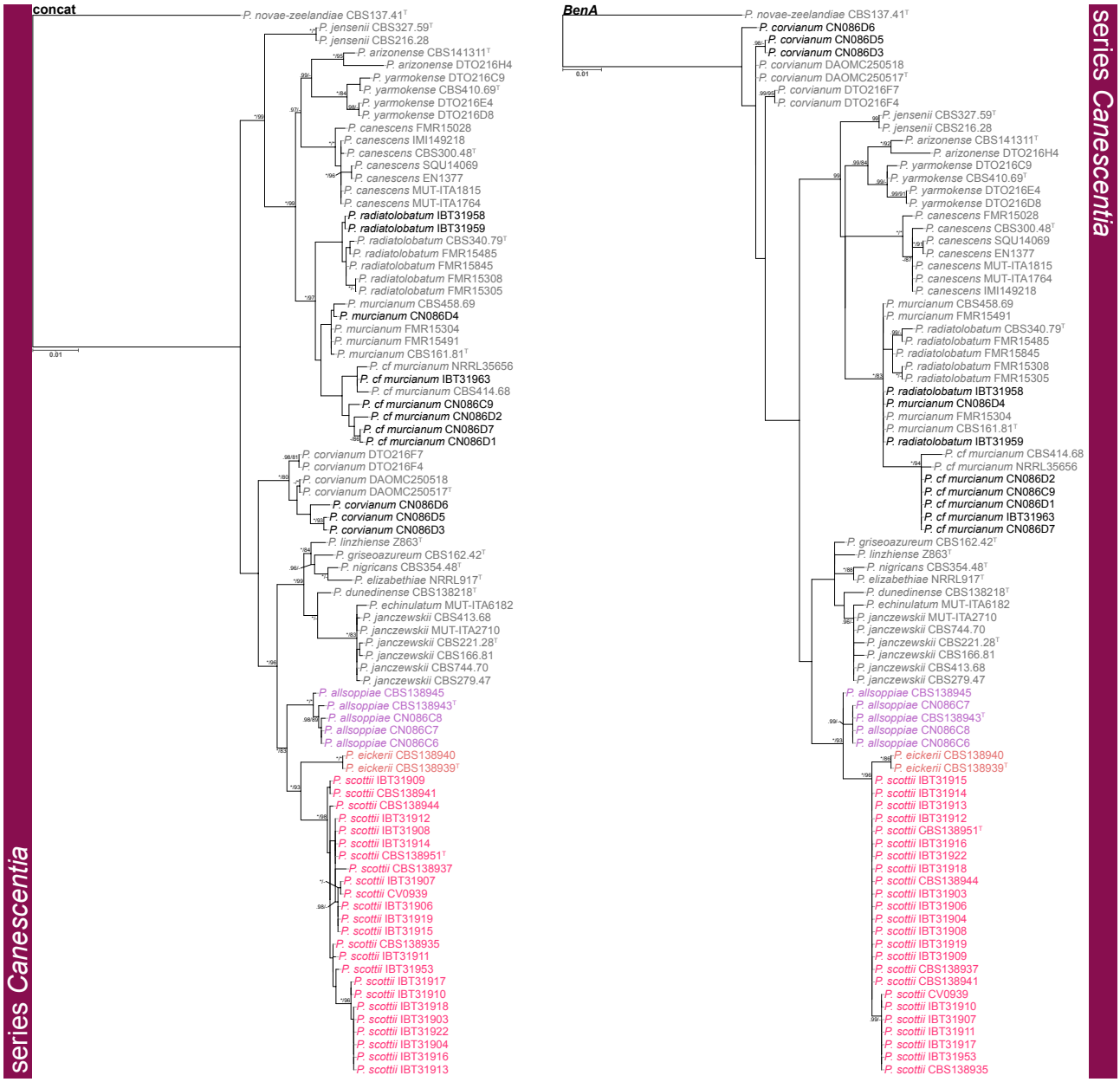

Fig. 3 Phylogenetic trees of *Penicillium* section *Canescentia* series *Canescentia* based on *BenA* and concatenated datasets. *Penicillium novae-zeelandiae* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80, respectively, are given above thickened branches. Names in grey text indicate reference strains, black text fynbos strains and coloured text new species, T = ex-type strain.

used to represent data with both bootstrap values ≥ 80 % and/or posterior probabilities ≥ 0.95 given on thickened branches. Trees were visualised on the Interactive tree of life (iTOL) v. 3 (Letunic & Bork 2016) and edited for publication in Affinity Publisher and Designer v. 1.8.6 (Serif (Europe) Ltd, Nottingham, UK).

Extrolite analysis

Strains were grown on CYA and YES at 25 °C for 7 d with five agar plugs taken from each medium and pooled into one sample. Extractions were made with 0.75 mL ethyl acetate/dichloromethane/methanol (3 : 2 : 1) (v/v/v) with 1 % (v/v) formic acid. Extracts were filtered and analysed by HPLC using alkylphenone retention indices and diode array UV-VIS detection (Frisvad & Thrane 1987, 1993, Nielsen et al. 2011), with minor modifications described in Smedsgaard (1997). A 50 × 2 mm Luna C-18 (II) reversed-phase column (Phenomenex, CA, USA) fitted with a 2 × 2 mm guard column was used for analyses (Nielsen et al. 2011).

RESULTS

Isolates

Isolations resulted in ± 1 700 *Penicillium* isolates obtained from collected fynbos samples. Of these, 155 belonged in section *Canescentia*, which were placed into eight distinct morpho-groups based on colony characters on CYA and MEA. These groupings were later confirmed by sequencing representative strains included here in the phylogenetic analyses. Most strains belonged to two groups, later identified as *P. novae-zeelandiae* (115 strains) and a new species described here as *P. scottii* (30 strains). The largest proportion of *P. novae-zeelandiae* strains were obtained from *Protea repens* infructescence bracts, while most *P. scottii* strains originate from fynbos soil. From each morpho-group, a subset of strains was included for phylogenetic analyses (Fig. 1–4). Additional strains of *P. allsoppiae*, isolated in another fynbos survey from soil obtained from wheat farms, were also included in the phylogenies.

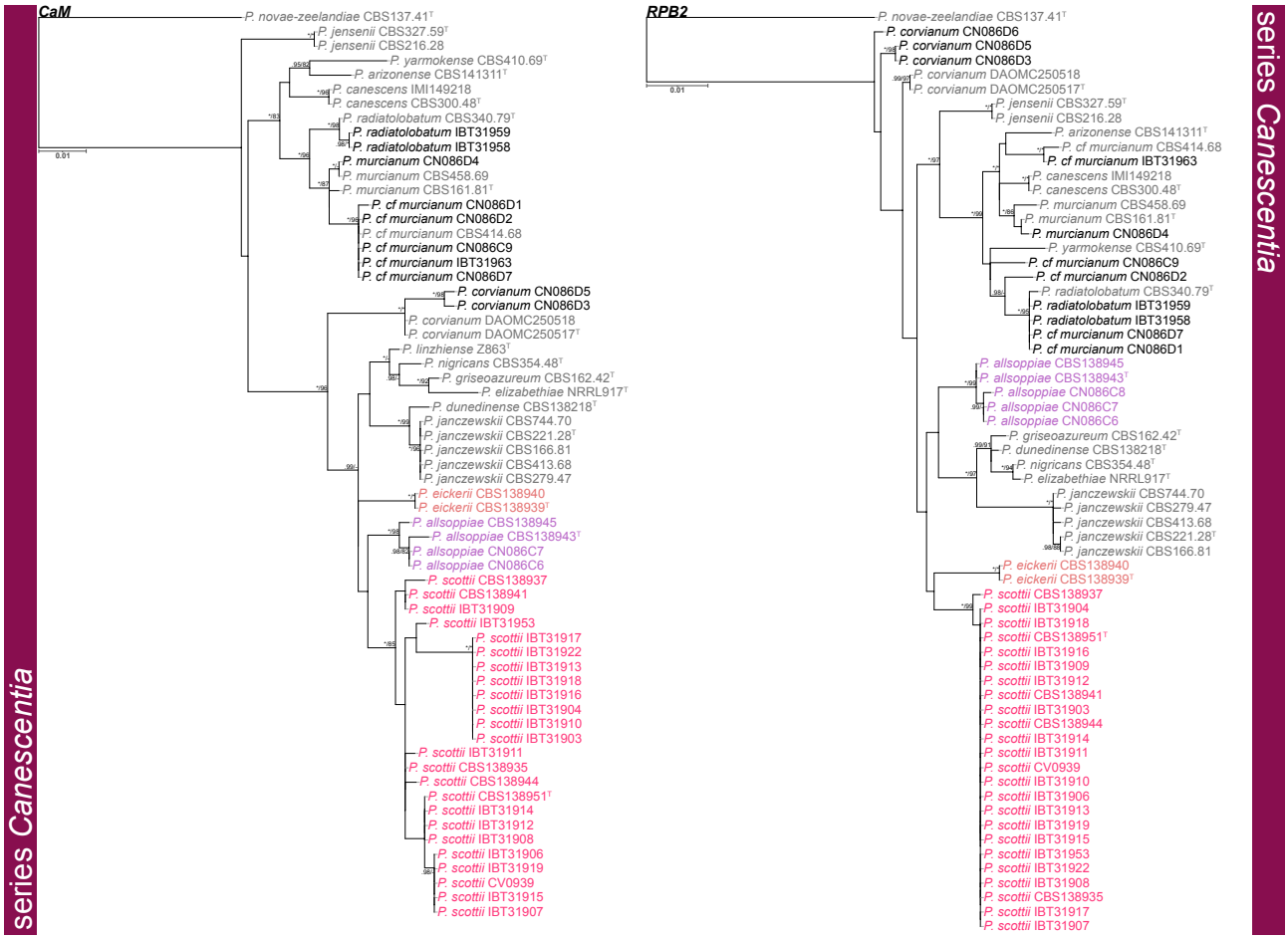

Fig. 4 Phylogenetic trees of *Penicillium* section *Canescentia* series *Canescentia* based on *CaM* and *RPB2*. *Penicillium novae-zeelandiae* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80, respectively, are given above thickened branches. Names in grey text indicate reference strains, black text fynbos strains and coloured text new species, T = ex-type strain.

Phylogenetic analyses

Gene sequence alignments were uploaded to TreeBASE under submission ID 22924. Dataset characteristics, partitioning schemes and substitution models applied during data processing are summarized in Table 2. Phylogenies based on ex-type sequences resolved strains into two main clades: series *Atroveneta* and *Canescentia*. ITS has poor discriminating power between section *Canescentia* members and was omitted from further analyses (Fig. S1).

Series *Atroveneta* — Fig. 2

Phylogenies confirmed two new species, described below as *P. doidgeae* and *P. pole-evansii*. We accept a high degree of infraspecies variation for *P. novae-zeelandiae*. Strains of this species resolved in three main clades with fynbos strains distinct from the ex-type strain (CBS 137.41T). However, as the morphological (Fig. 5) and extrolite data (Table 3, 4) were not consistent between these different clades, we opt to not introduce new species for them until more collections are made from different regions. Kirichuk et al. (2016) recently introduced three new species (*P. attenuatum*, *P. ochotense* and *P. piltunense*) and they considered *P. antarcticum* a close relative. However, alignments of published data (Fig. S2) revealed several frameshift mutations in coding regions at sequence ends, which may imply low-quality sequence reads. Phylogenetic trees (Fig. S3) obtained from untrimmed alignments place all three of these species on long branches within the *P. antarcticum* clade. Trimming of these sequences (Fig. S2) to remove suspected low-quality regions resulted in the long branches collapsing. Reference strains, unfortunately, were not available to study and re-sequence. For this reason, we reduce *P. attenuatum*, *P. ochotense* and *P. piltunense* to synonymy with *P. antarcticum*.

Series *Canescentia* — Fig. 3, 4

Phylogenetic analyses revealed three new species in this clade, noting that the *BenA* phylogeny did not fully resolve the relationship between these clades in contrast to the *CaM* and *RPB2* phylogenies that did. A similar observation was made for *P. murcianum* and *P. radiatolobatum* as discussed below. The largest proportion of strains belonged to the clade described as *P. scottii*, which showed a high degree of infraspecies variation in *CaM*, but less so for *BenA* and *RPB2*. The three new species are introduced in the *P. janczewskii* species complex that contains seven previously described species. The phylogenetic analyses resolved ex-type strains of *P. granatense* (CBS 166.81T) and *P. nigricans* var. *sulphuratum* (CBS 744.70T) with *P. janczewskii* confirming their status as synonyms (Pitt 1980). Also, *P. echinatum nom. inval.* (= *P. janczewskii fide* Pitt 1980), *P. griseoazureum* (= *P. waksmanii fide* Pitt 1980) and *P. nigricans* (= *P. janczewskii fide* Pitt 1980) represent distinct phylogenetic species. The novelty of the more recently described species *P. dunedinense* (Visagie et al. 2014b), *P. corvianum*, *P. nucicola* (Visagie et al. 2016b) and *P. arizonense* (Grijseels et al. 2016) is confirmed. One of Pitt's (1980) morphologically intermediate strains (IMI 149218) is shown here to be *P. canescens*. The relationship between *P. murcianum* and *P. radiatolobatum* is problematic with no coherent clades produced, noting that ex-type strains for these two (CBS 340.79T, CBS 161.81T) are quite distinct. Strains were thus named based on the concatenated multigene phylogeny. Strains identified as *Penicillium* cf. *murcianum* probably represent a new species.

Table 2 Partition-merging results and best substitution model for each partitiion.

Description of dataset	Subset	Parition name	Best Model	# sites
sect. *Canescentia* ex-types (ITS)	1	ITS	K80	509
sect. *Canescentia* ex-types (concat)	1	CaM_codon1, BenA_codon2, CaM_codon3, RPB2_codon1, BenA_codon1	TRN+I	658
	2	CaM_codon2, BenA_codon3	TRN+G	163
	3	CaM_introns, BenA_introns	K80+G	460
	4	RPB2_codon2	JC	327
	5	RPB2_codon3	HKY+G	326
ser. *Atroveneta* (*BenA*)	1	BenA_codon1, BenA_codon2, BenA_codon3,	TRNEF	247
	2	BenA_introns	K80+G	192
ser. *Atroveneta* (*CaM*)	1	CaM_codon1, CaM_codon3	K80+I	179
	2	CaM_codon2	HKY+I	88
	3	CaM_introns	K80+I	239
ser. *Atroveneta* (*RPB2*)	1	RPB2_codon1	TRN+I	284
	2	RPB2_codon2	JC	284
	3	RPB2_codon3	HKY+G	283
ser. *Atroveneta* (concat)	1	CaM_codon1, BenA_codon2, CaM_codon3, BenA_codon1, RPB2_codon1	TRN+G	629
	2	CaM_codon2, BenA_codon3	HKY+G	169
	3	BenA_introns, CaM_introns	K80+I	431
	4	CaM_codon2	JC	284
	5	RPB2_codon3	HKY+G	283
ser. *Canescentia* (*BenA*)	1	BenA_codon1, BenA_codon3	TRNEF	143
	2	BenA_codon2	JC	71
	3	BenA_introns	TRNEF	201
ser. *Canescentia* (*CaM*)	1	CaM_codon1, CaM_codon3	JC	180
	2	CaM_codon2	HKY	89
	3	CaM_introns	K80	231
ser. *Canescentia* (*RPB2*)	1	RPB2_codon1	TRN	284
	2	RPB2_codon2	JC	283
	3	RPB2_codon3	HKY+G	283
ser. *Canescentia* (concat)	1	CaM_codon2, BenA_codon1	TRN+G	161
	2	CaM_codon1, BenA_codon2, RPB2_codon2	JC	445
	3	BenA_codon3, BenA_introns, CaM_introns	K80+G	503
	4	CaM_codon3, RPB2_codon1	TRN	373
	5	RPB2_codon3	HKY+G	28

Table 3 Extrolites produced by section *Canescentia* species (as detected in this study and reported in Visagie et al. 2016b).

Species	Series	Extrolites
Penicillium allsoppiae	*Canescentia*	Penitrem A
Penicillium arizonense	*Canescentia*	Acetylaranotin, austalides, curvulinic acid, fumagillin, pseurotin A, pyripyropenes, tryptoquivalines, xanthoepocin
Penicillium canescens	*Canescentia*	Curvulinic acid, griseofulvin, patulodin, penicillic acid
Penicillium cf. *murcianum*	*Canescentia*	Not examined
Penicillium corvianum	*Canescentia*	Trichodermamide A (= penicillazine), trichodermamide C
Penicillium dunedinense	*Canescentia*	Not examined
Penicillium eickeri	*Canescentia*	Curvulinic acid, xanthoepocin
Penicillium elizabethiae	*Canescentia*	Chrysogine, communesin A & B, griseofulvin, patulodin, xanthoepocin
Penicillium griseoazureum	*Canescentia*	Curvulinic acid, a decaturin/ oxalicin, griseofulvin, pseurotin A, xanthoepocin
Penicillium janczewskii	*Canescentia*	Chrysogine, curvulinic acid, fumagillin, griseofulvin, penitrem A, penitremone A, perinadines, pseurotin A, tryptoquivalines, xanthoepocin
Penicillium jensenii	*Canescentia*	Asperpentyn?, curvulinic acid, griseofulvin, pseurotin A
Penicillium murcianum	*Canescentia*	Asperpentyn?, curvulinic acid, griseofulvin, tryptoquivalines, (apolar alkaloids / indoloterpenes)
Penicillium nigricans	*Canescentia*	Chrysogine, communesin A & B, curvulinic acid, griseofulvin, nigrifortine, patulodin, xanthoepocin
Penicillium radiatolobatum	*Canescentia*	Curvulinic acid, a decaturin / oxalicin, griseofulvin, penitrem A, penitremone A, xanthoepocin
Penicillium scottii	*Canescentia*	Curvulinic acid, dehydrogriseofulvin, griseofulvin, penitrem A, xanthoepocin
Penicillium yarmokense	*Canescentia*	Curvulinic acid, griseofulvin
Penicillium antarcticum	*Atroveneta*	Antarones, atlantinone A, asperentins, chrysogine, deoxyepifructigenine, fischerin, patulin, phyllostin, penitrem A, thomitrem A
Penicillium atrovenetum	*Atroveneta*	Atlantinone A, atrovenetin, communesin B, haenamindole, naphthalic anhydride, 3-nitropropionic acid
Penicillium coralligerum	*Atroveneta*	Austalides, chrysogine, coralligerin, naphthalic anhydride
Penicillium doidgeae	*Atroveneta*	Asperentins, atlantinone A, austalides, fischerin, patulin
Penicillium novae-zeelandiae	*Atroveneta*	Atlantinone A, benzomalvins, citreoviridin, cycloaspeptide A, cyclopiazonic acid in FRR 1905, decaturins / oxalicins, patulin, xanthoepocin in IMI 038496 and IBT 5831
Penicillium nucicola	*Atroveneta*	Andrastin A-D, pulvilloric acid
Penicillium pole-evansii	*Atroveneta*	Atrovenetin, aurantiamine, communesin B, patulin

Table 4 Reported extrolites produced by members of *Penicillium* section *Canescentia*.

Strain	Original identity	Identification method, ITS	Correct identity	Series	Extrolites
CBS 141311	*P. arizonense*	MH492021, culture ex-type of *P. arizonense*	*P. arizonense*	*Canescentia*	Austalide B, J, K, L, curvulinic acid, dechlorogriseofulvin, 6-farnesyl-5,7-dihydroxy-4-methylphthalide, fumagillin, griseofulvin, pseurotin A, pyripyropene A, E, F, O, tryptoquivaline C (or 27-*epi*-tryptoquivaline), tryptoquivaline G (or L), xanthoepocin[1,2]
CGMCC 3.9958	*P. canescens*	Reported to be 100% identical to ex-type of *P. canescens*	*P. canescens*	*Canescentia*	Penicanone, penicanescone A-C, integrastatin B[3]
CGMCC 3.9958	*P. canescens*	Reported to be 100% identical to ex-type of *P. canescens*	*P. canescens*	*Canescentia*	Canescone A-E[4] (Canescone A-C, two stereoisomers each)
PL9A	*P. canescens*	Comparison to culture ex-type of *P. canescens*	*P. canescens*	*Canescentia*	Curvulic acid, dechlorogriseofulvin, griseofulvin, Sch 642305[5]
ATCC 10419	*P. canescens*	Culture ex-type	*P. canescens*	*Canescentia*	Griseofulvin[6], Decaturin A, C, D, F, G, 15-deoxyoxalicine A & B, predecaturin E[7]
4.1.4.6a	*P. canescens*	MH820167	*P. arizonense*, *P. canescens*, *P. janczewskii*, *P. jensenii*, *P. murcianum*, or *P. radiatolobatum* (all in series *Canescentia*). Presence of the bromphilone chromophore in the culture ex-type of *P. canescens* indicates that the fungus is indeed *P. canescens*	*Canescentia*	Bromophilone A & B, citreohybridinol, curvulinic acid, dechlorogriseofulvin, griseofulvin, griseophenone B, C, G, griseoxanthone C, methyl 3-chloro-2-(2,4-dimethoxy-6-methylphenoxy)-6-hydroxy-4-methoxybenzoate, methylcurvulinate, 3-O-methyl curvulinate, norlichexanthone, penicillic acid, piscarinine B, vulculic acid[8]
VKM F-1148, VKM F-1287, VKM F-3108	Unknown identity	Morphology	*P. canescens*	*Canescentia*	Fellutanine A, isorugulosuvine A & B[9]
Sp. 4829	*Penicillium* species	MH465534	*P. rubens* but extrolite data suggest *P. canescens*	*Canescentia*	Citreohybriddione C, citreohybridinol, curvulinic acid, 2,4-dihydroxy-6-(oxopropyl) benzoic acid, (S)-2-(2-hydroxypropanamido) benzamide, griseofulvin, N-(2-hydroxypropanoyl)-2-amino benzoic acid, niacinamide, methyl 2-acetyl-3,5-dihydroxyphenylacetate, 6-O-methylnorlichexanthone, penicamide A & B, peni-isochroman A & B, 2-pyruvamidobenzamide, 2-pyruvoylaminobenzamide, pseurotin A, 3,6,8-trihydroxy-1-methylxanthone[10,11]
MMS 194, MMS 460	*P. canescens*	Morphology	*P.* cf. *canescens*	*Canescentia*	Dechlorogriseofulvin, griseofulvin, maculosin, oxaline, orselllinic acid, penicillic acid, penitremone A-C (tentative id.)[12]
ILF-002	*P. canescens*	FASTA files for ITS and β-tubulin sequences show that this strain is not *P. canescens* s.str., but a new species	New species sister to *Penicillium canescens*	*Canescentia*	Dechlorogriseofulvin, 6-desmethyldechlorogriseofulvin,6-desmethylgriseofulvin, 1,6-dihydroxy-3-methoxy-8-methylxanthone, griseofulvin, orsellinic acid, penicillic acid, pseurotin A, 1,2,3,5,6-pentahydroxy-8-methylxanthone, 1,3,5,6-tetra-hydroxy-8-methylxanthone, vulculic acid[13]
170A/28	*P. canescens*	Morphology	Probably *P. nigricans*	*Canescentia*	Penitrem A[14,15]
CBS 288.53	*P. canescens*	Morphology	New species of *Penicillium*	*Canescentia*	Canescin[16]
BAFC 3291	*P. canescens*	Morphology	Probably *P. aurantiogriseum*	*Canescentia*	Aurantiamine, cyclo(L-Phe-L-Hyp), cyclo(L-Phe-L-Pro), cyclo(D-Phe-L-Val-D-Val-L-Tyr), pseurotin A[17]
No number	*P. canescens*	No data	Unknown	*Canescentia*	Adamantanecarboxanilide, aphthosin, 9,10-anthracenedione, borane, decane, diethylphthalate, di-p-tolylacetylene, dodecane, eicosane, heptadecane, hexa-decane, hexadecanoic acid, 1,3,8-p-menthatriene, nicodicodine, orcinol, oxalic acid, phenanthrene, tetradecane, thioxanthene, tridecane, p-xylene[18] (mostly volatiles)
No number	*P. canescens*	Morphology	Unknown	*Canescentia*	Citrinin[19,20]
No number	*P. canescens* (two strains)	Morphology	*P. cyclopium* or *P. canescens*	*Canescentia*	Penicillic acid[21,22]
ZJQY610	*P. canescens*	GU556971	*P. canescens* or other series *Canescentia* species	*Canescentia*	O-acetylbenzeneamidino-carboxylic acid, griseofulvin, 4-hydroxy-5-methoxy-2-methyl-naphtho[1,2-b]furan-3-carboxylic acid[23]
No number	*P. canescens*	Morphology	Unknown	*Canescentia*	Citrinin, patulin, penicillic acid[24]
SCSIOz053	*P. canescens*	JN585930	*Talaromyces fusiformis*?	*Canescentia*	Canescenin A & B[25]
No number	*P. canescens*	Morphology	*Talaromyces* sp.?	*Canescentia*	Rugulosin[26]

Table 4 (cont.)

Strain	Original identity	Identification method, ITS	Correct identity	Series	Extrolites
No number	*P. canescens*	Morphology	Probably *P. verrucosum*	*Canescentia*	Ochratoxin A[27]
NRRL 2301	*P. janczewskii*	Morphology	*P. janczewskii*	*Canescentia*	Bromogriseofulvin, dechlorogriofulvin, griseofulvin[28,29,30], fungistatic and bacteriostatic red pigment[31]
CBS 141000	*P. corvianum*	KT887875, culture ex-type	*P. corvianum*	*Canescentia*	Compactin (= mevastatin), fiscalin C, trichodermamide C, $C_{11}H_{15}O_3N$, $C_{18}H_{22}O_5$, $C_{29}H_{30}O_7S_2$[32]
VKMF-312	*P. janczewskii*	Morphology	*P. janczewskii*	*Canescentia*	Dechlorogriseofulvin, griseofulvin, patulin[33]
VKMF-2191, VKMF-2378, VKMF-3023	*P. janczewskii*	Morphology	*P. janczewskii*	*Canescentia*	Dechlorogriseofulvin, griseofulvin[33]
VKMF-685	*P. janczewskii*	Morphology	*P. janczewskii* or *P. nigricans*	*Canescentia*	Aurantioclavine, 6-N-ethylaurantioclavine[33]
VKMF-2377	*P. janczewskii*	Morphology	*P. janczewskii*?	*Canescentia*	Epicostaclavine[33]
VKMF-2489	*P. janczewskii*	Morphology	*P. janczewskii*?	*Canescentia*	16-N-ethylroquefortine D, glandicolin B, (E)-3-(1H-imidazol-4-yl-methylene)-6-(1H-indol-3-yl methyl)-2,5-piperazinediol, meleagrin, roquefortine C[33]
DSM 17433 = KMPB H-TW5/869	*P. janczewskii*	Morphology	*P. janczewskii*?	*Canescentia*	3R*,4R*- and 3S*,4R*-Dihydroxy-4-(4'-methoxyphenyl)-3,4-dihydro-2(1H)-quinolinone, 3-methoxy-4-hydroxy-4-(4'-methoxyphenyl)-3,4-dihydro-2(1H)-quinolinone, peniprequinolone[34]
F 2757 & F 2641	*P. janczewskii*	Morphology	*P. janczewskii*?	*Canescentia*	Fumagillin methyl ester, *cis*-fumagillin methyl ester[35,36]
No number	*P. janczewskii*	Morphology	*P. janczewskii*?	*Canescentia*	Cycloaspeptide A, gliovictin, gliovictin acetate, peniprequinolone, pseurotin A[37,38]
IFO 7745 = CBS 744.70 = ATCC 18380	*P. nigricans* var. *sulphuratum*	Morphology	*P. janczewskii*	*Canescentia*	Griseofulvin[39]
IMI 228669 and no number17	*P. janczewskii*	Morphology	*P. janczewskii*	*Canescentia*	19-Deoxypaxillin-16β-ol, nigrifortine (= amauromine), paxilline, penitrem A, penitrem E, pennigritrem[15,40,41,42,43]
SIIA-F3933	*P. janczewskii*	Morphology	Probably *P. corvianum*	*Canescentia*	Compactin (= mevastatin)[44]
NRRL 909	*P. jensenii*	AY443470, culture ex-type	*P. jensenii*	*Canescentia*	Griseofulvin[6]
VKMF-292, VKMF-293	*P. jensenii*	Morphology	*P. jensenii*	*Canescentia*	Meleagrin, roquefortine C & D[9]
F-2813	*P. jensenii*	Morphology	*P. jensenii*	*Canescentia*	Fumagillin, fumagillol[45]
No number	*P. nigricans*	Morphology	*P. nigricans*	*Canescentia*	Griseofulvin[46,47]
No number & LSHTM P38 = BRL 250	*P. nigricans*	Morphology	*P. nigricans*	*Canescentia*	Griseofulvin[48,49]
No number	*P. nigricans*	Morphology	*P. nigricans*?	*Canescentia*	MT81[50]
F-5261	*P. nigricans*	Morphology	*P. nigricans*	*Canescentia*	Fumagillin, fumagillol[45]
IMI 228669	*P. nigricans*	Morphology	*P. janczewskii*	*Canescentia*	19-Deoxypaxillin-16β-ol, nigrifortine (= amauromine), paxilline, penitrem A, penitrem C, penitrem E, PC-M6, pennigritrem[40,41,45,51]
LSHTM P38	*P. nigricans*	Morphology	*P. nigricans*	*Canescentia*	Cyclo(L-Phe-L-Phe)[52]
170/D2 & 170/D4	*P. nigricans*	Morphology	*P. nigricans*? or *P. brasilianum*	*Canescentia*	Verruculogen (as toxin X)[53,54]
No number	*P. nigricans*	Morphology	*P. nigricans*?	*Canescentia*	Albidin[48]
CBS 410.69	*P. yarmokense*	Ex type, KC411757	*P. yarmokense*	*Canescentia*	Griseofulvin[6]
MMS 351 = LCP 99.43.43, MMS 747	section *Canescentia* species	JN676192 (and β-tubulin: JN794530)	*P. yarmokense* (first identified as *P. waksmanii*)[56]	*Canescentia*	Agroclavine, dechlorogriseofulvin, festuclavine, griseofulvin, penicillic acid, ligerin, nortryptoquivaline, orcinol, orsellinic acid[12,55]
FH-14	*P. antarcticum*	Morphology, identified by Westerdijk Fungal Biodiversity Institute (WFBI)	*P. antarcticum*	*Atroveneta*	Antarone A & B[56]

Table 4 (cont.)

Strain	Original identity	Identification method, ITS	Correct identity	Series	Extrolites
MMS 14, MMS 15	*P. antarcticum*	Morphology, ITS	*P. antarcticum*	*Atroveneta*	Antarone A, aurantioclavine, chrysogine, cladosporin (= asperentin), 5-hydroxy-asperentin, patulin, terrestric acid?, violaceic acid[12,57]
AF3-117C	*Penicillium* species	JX967116	*P. antarcticum*	*Atroveneta*	Cladosporin (= asperentin), epiepoformin, patulin, phyllostin[58]
YK-247	*P. coralligerum*	LC2145672	*P. antarcticum*	*Atroveneta*	5'-hydroxyasperentin, cladomarine, cladosporine (= asperentin)[59]
No number	*P. antarcticum*	Polyphasic identification, no data	*P. antarcticum*	*Atroveneta*	*cis*-Cyclo(4R-Hyp, L- Leu), *trans*-cyclo(4R-Hyp, L-Leu), *cis*-cyclo(4R-Hyp, L-Phe), cyclo-(L-Pro, Gly), ethyl 8-hydroxyhexylitaconate, ethyl-9-hydroxyitaconate, (-)-hydroxyhexylitaconate, *cis*-4-hydroxymellein, methyl-8-hydroxyhexylitaconate, methyl-9-hydroxyitaconate, methylitaconate, 2-phenetylalcohol[60]
KMM 4668	*P. piltunense*	Culture ex-type (but synonym of *P. antarcticum*)	*P. antarcticum*	*Atroveneta*	Penigrisacid D, piltunine A-F[61]
No number	Marine-derived *P. atrovenetum*	Morphology	Probably *P. antarcticum*, as *P. atrovenetum* is a soil fungus	*Atroveneta*	Citreohybridinol[62]
9 strains, no numbers	*P. antarcticum*	No data	*P. antarcticum* (?)	*Atroveneta*	Butylphthalate, dibutylphthalate, di-2-ethylhexylphthalate, hydrocarbons, squalene, and fatty acids (the latter are general metabolites)[63]
Strain 68 & 56	*P. atrovenetum* & *P. coralligerum*	MH881491, MH881479	*P. antarcticum*	*Atroveneta*	Aspinonene, atrovenetin, atrovenetinone, brevicompanine E, citreohydridonol, deoxyherquenone, griseofulvin, marcfortine C*, penitrem B, phytosphingosine[64]
Strains 4-7 & 9-13	*P. atrovenetum* & *P. antarcticum*	ITS and morphology	*P. antarcticum* (*P. atrovenetum* is regarded as a soil-borne species)	*Atroveneta*	2-Acetyl-4(3H)-quinazolinone, aflatoxin M1*, andrastin A, andrastin "X" (wrongly identified as (wia) antibiotic UK 88051-9), antarone B (wia purpactin A), antibiotic SMTP8*, arisugacin B*, asperentin (wia (S)-curvularin), atrovenetin, atrovenetinone (wia tetrahydrohalenaquinone A), bionectin B*, (S)-chrysogine, chaetoglobosin 510*, cladosporin-8-methylether (wia antibiotic PO1), cytosporone A*, cytosporone E*, deacetoxyfructigenine A (wia tubingensin A or B), deoxyherquenone (= UP31), dictyosphaeric acid*, hamigeromycin*, hamigerone (wia austalide K), hongoquercin A*, (S)- 5-hydroxyasperentin (wia 11α-hydroxycurvularin), a hydroxyasperentin (wia 7,8-dihydro-7α-hydroxyresorcylide), 4-hydroxy-1-methoxy-5-phenyl-3-(tetrahydro-6-(3-hydroxy-1-methylpropyl)-3,5-dimethyl-2H-pyran-2-yl)-2(1H)-pyridinone*, libertellone B*, 3-O-methylterprenin*, patulin, penitrem A, penitrem E, podosporin A*, sporidesmin D*, stachybosin*, talaroconvolutin B*, territrem C*, 2',2'',3',3''-tetrahydrobisvertinolone*, tropolactone C*, UP10, 11, 12, 15, 9, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 32** [65]
IMI 061837 = CBS 241.56	*P. atrovenetum*	AF033492, culture ex-type, morphology	*P. atrovenetum*	*Atroveneta*	3-nitropropionic acid[66], atrovenetin[67]
HO9-2	*P. atrovenetum*	EMBL no. KC009765	*P. atrovenetum*?	*Atroveneta*	Cyclopiazonic acid[68]
CECT 2886	*P. novae-zeelandiae*	Morphology	*P. novae-zeelandiae*	*Atroveneta*	Gentisylalcohol, 3-hydroxybenzylalcohol, patulin (in 1949 reported as expansine)[6,32,69,70]
IBT 21392 (= IMI 204086), IBT 22457	*P. novae-zeelandiae*	Morphology	*P. novae-zeelandiae*	*Atroveneta*	Atlantinone A[71]
No number	*P. novae-zeelandiae*	Morphology	*P. novae-zeelandiae*?	*Atroveneta*	Penitrem A, verruculogen[15]
No number	*P. novae-zeelandiae*	Morphology	*P. novae-zeelandiae*?	*Atroveneta*	Curvulinic acid[72]
CBS 140987	*P. nucicola*	KT887860, culture ex-type	*P. nucicola*	*Atroveneta*	Andrastin A-D, austin, $C_{20}H_{20}O_6$[32]

* The metabolites tentatively identified may also be other secondary metabolites with the same molecular mass. For example if aflatoxin M1 in *P. antarcticum* would have been correctly identified, one would also expect presence of aflatoxin B1 and B2, which are usually the main biosynthetic products in the aflatoxin secondary metabolite biosynthetic family.

** UP: Unknown secondary metabolites with a known molecular mass.

*** *Penicillium linzhiense* was recently described and thus not examined during this study.

[1]Grijseels et al. 2016; [2]Prigent et al. 2018; [3]Zang et al. 2020; [4]Zang et al. 2019; [5]Nicoletti et al. 2007; [6]Frisvad & Filtenborg 1990; [7]Yaegashi et al. 2015; [8]Frank et al. 2019; [9]Kozlovskii et al. 1997a; [10]Chen et al. 2019; [11]Niaz et al. 2019; [12]Vansteelandt et al. 2012, Vansteelandt et al. 2013; [13]Malik et al. 2020; [14]Shreeve et al. 1978; [15]Di Menna et al. 1986; [16]Brian et al. 1953; [17]Bertinetti et al. 2009; [18]Ghanbari et al. 2014; [19]Bilai 1963; [20]Gedek 1977,[21]Kharchenko 1970; [22]Keromnes & Thouvenot 1985; [23]Wang et al. 2010; [24]Moslem et al. 2013; [25]Dasanayaka et al. 2020; [26]Leistner & Pitt 1977; [27]Ueno et al. 1991; [28]Brian et al. 1949; [29]MacMillan 1951; [30]Grove & Mcgowan 1947; [31]Curtis & Grove 1947; [32]Visagie et al. 2016b; [33]Kozlovskii et al. 1997b; [34]He et al. 2005; [35]Kwon et al. 2000; [36]Bae et al. 1999; [37]Schmeda-Hirschmann et al. 2008; [38]Schmeda-Hirschmann et al. 2005; [39]Udagawa & Abe 1961; [40]Laws & Mantle 1985; [41]Mantle & Penn 1989; [42]Penn et al. 1992; [43]Penn & Mantle 1994; [44]Chu et al. 1999; [45]Goto et al. 1986; [46]Wright 1955; [47]Leistner 1979; [48]Jefferys et al. 1953; [49]Macmillan 1954; [50]Gupta et al. 1984; [51]Mantle et al. 1984; [52]Birkinshaw & Mohammed 1962; [53]Patterson et al. 1981; [54]Patterson et al. 1979; [55]Petit et al. 2004; [56]Shiono et al. 2008; [57]Geiger et al. 2013; [58]Flewelling et al. 2013; [59]Takahashi et al. 2017; [60]Marchese et al. 2020; [61]Afiyatullov et al. 2019; [62]Özkaya et al. 2018; [63]Oleinikova et al. 2018; [64]Fan et al. 2019; [65]Petersen et al. 2019; [66]Raistrick & Stössl 1958; [67]Neill & Raistrick 1957; [68]Alapont et al. 2014; [69]Burton 1949; [70]Alfaro et al. 2003; [71]Dalsgaard et al. 2012; [72]Turner & Aldridge 1983.

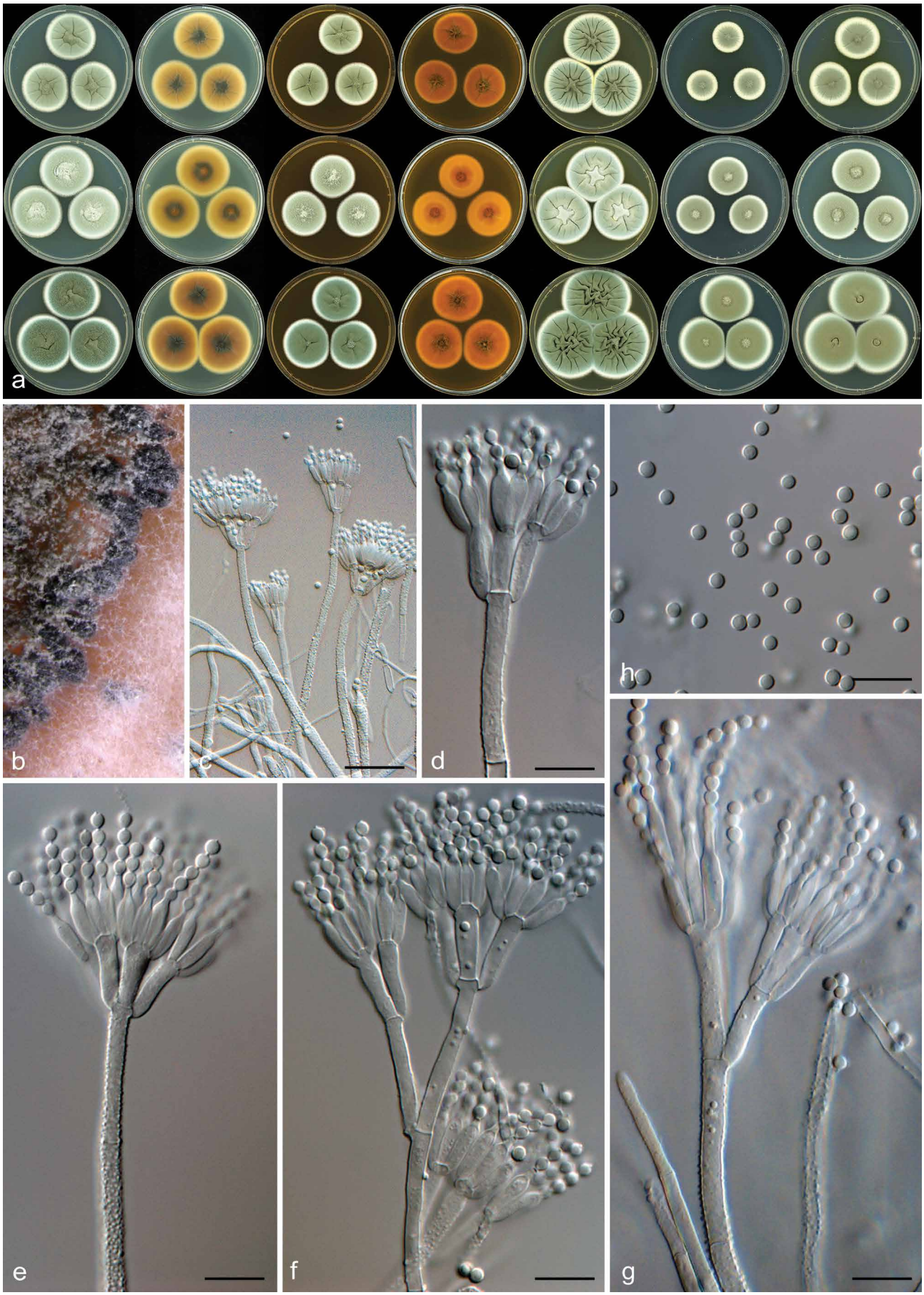

Fig. 5 *Penicillium novae-zeelandiae*. a. Colonies left to right: CYA, CYA reverse, MEA, MEA reverse, YES, DG18, CYAS; top row: CBS 546.77; middle row CBS 138942; bottom row CBS 138949; b. black sclerotia produced on MEA; c–g. conidiophores; h. conidia. — Scale bars: b, c = 50 µm, d–h = 10 µm.

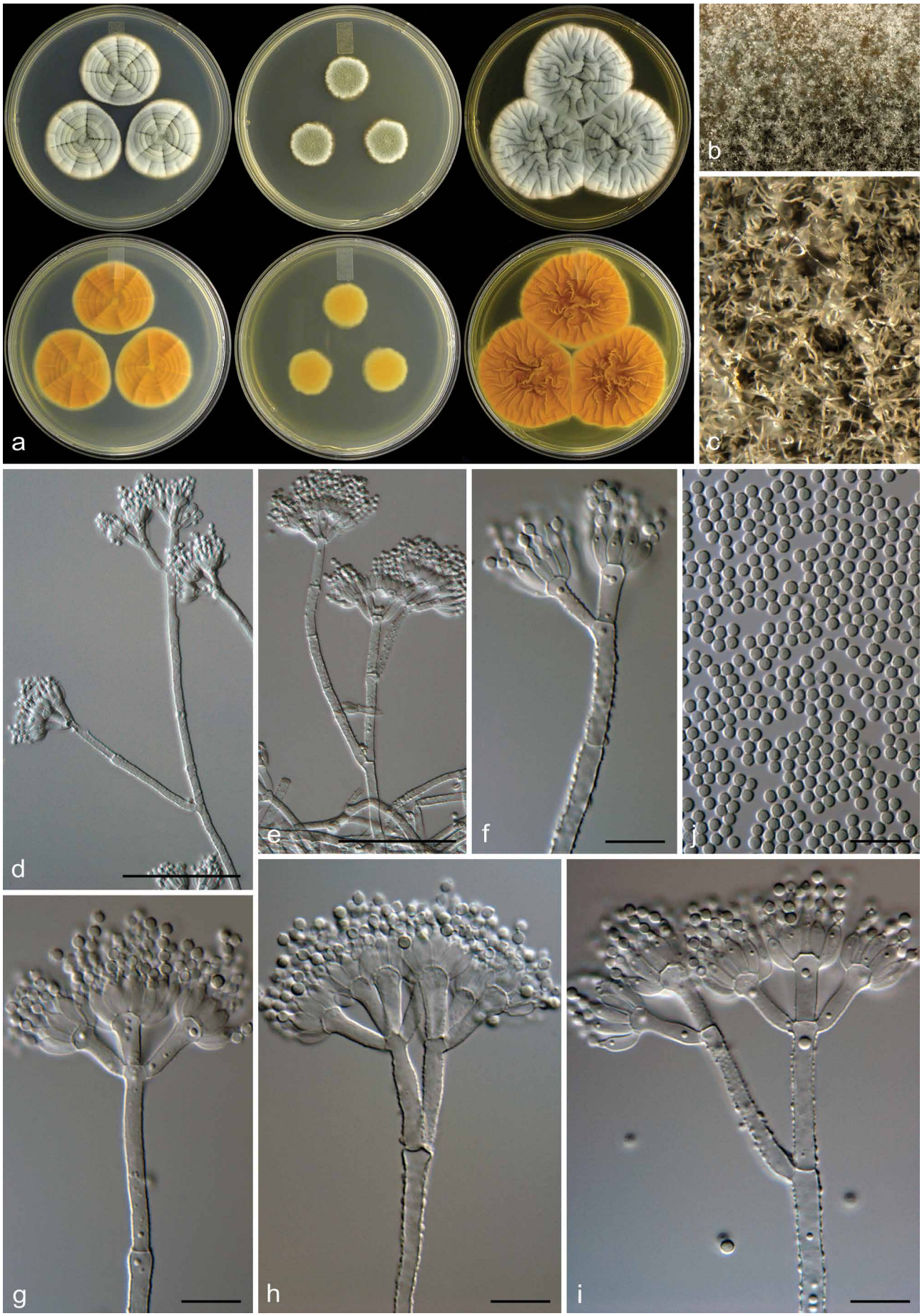

Fig. 6 *Penicillium allsoppiae*. a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse); b, c. colony texture on MEA; d–i. conidiophores; j. conidia. — Scale bars: d = 25 µm, e–j = 10 µm.

However, more strains, sequencing of additional gene regions and extrolite data will be needed to resolve species boundaries in this complex.

Extrolite analysis

Series *Canescentia* is generally characterised by the production of curvulinic acid (11/14 species) and griseofulvin (10/14 species), but xanthoepocin (7/14 species), pseurotins (4/14 species), tryptoquivalines (4/14 species), fumagillin/ligerin (3/14 species) and penicillic acid (2/14 species) are also found in more than one species. In series *Atroveneta*, one or more species produce asperentins (2/7 species), atlantinones/andrastins (4/7 species), patulin (3/7 species), atrovenetins (2/7 species), antarones (1/7 species), aurantiamine (1/7 species), benzomalvins (1/7 species), fischerin (1/7 species) and haenamindole (1/7 species) (Table 3). Many species in section *Canescentia* produce other extrolites (Table 4), and in general this section contain species that produce a broad range of bioactive secondary metabolites. Both clades contain species that produce austalides, chrysogines, communesins, decaturins, and penitrems. The frequency of species producing the extrolites in each series may have been higher, if more media have been used. Likewise genomic analysis may show if the potential of producing these extrolites is larger than expected, and silent gene clusters may be activated by growing the fungi on different substrates and under different conditions.

TAXONOMY

Penicillium allsoppiae Visagie, A. Visagie, Frisvad & K. Jacobs, *sp. nov.* — MycoBank MB 834426; Fig. 6

Etymology. Latin, *allsoppiae*, named after Nicky Allsopp who reported several *Penicillium* species during a survey from the same Malmesbury sampling site we collected samples during our study.

Typus. South Africa, Malmesbury, soil sample, July 2009, coll. *C.M. Visagie* (CBS H-22036 holotype, culture ex-type CBS 138943 = DAOM 241348 = DTO 182-D5 = CV 931).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Canescentia.*

ITS barcode — JX140830. Alternative identification markers: *BenA* = JX140992, *CaM* = JX157384, *RPB2* = KP016895.

Colony diam, 7 d (in mm) — CYA 25–30; CYA 30 °C 30–32; CYA 37 °C 4–6; MEA 20–30; YES 34–38; DG18 20–22; CYAS 25–30; CREA 11–12.

Colony characters — CYA 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white, sometimes pinkish orange; texture floccose; sporulation sparse to moderately dense, conidia *en masse* dull green (25D4–26E4); soluble pigments absent; exudates minute clear droplets; reverse brownish orange to brown (6C6–D6), sometimes pale to light yellow (3A3–4). MEA 25 °C, 7 d: Colonies moderately deep, lightly sulcate; margins low, wide, entire; mycelia white; texture floccose; sporulation sparse to moderately dense, conidia *en masse* greyish to dull green (25C4–D4); soluble pigments absent; exudates clear minute droplets; reverse brownish orange to brown (6C7–E7). YES 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white to pinkish orange; texture floccose; sporulation sparse, conidia *en masse* greenish grey (26B2–C2); soluble pigments absent; exudates absent; reverse brown (7E7), greyish orange (6B6), some light yellow (4A4) areas. DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins low, narrow, entire; mycelia white; texture floccose; sporulation moderately dense, conidia *en masse* dull to greyish green (25D4–5–E5); soluble pigments absent; exudates absent; reverse yellowish brown (5D6) to greyish beige (4C2) to yellowish white (4A2). CREA 25 °C, 7 d: Acid not produced.

Micromorphology — *Conidiophores* mostly biverticillate, terverticillate also present; *stipes* rough walled, smooth also present, 200–800 × 3.5–4 µm; *branches*/*rami* two when present, 13.5–34 × 3.5–4 µm; *metulae* divergent, 2–6 per stipe/branch, 10–18 × 2.5–4 µm, vesicle 4–5 µm; *phialides* ampulliform, 6–7 × 2.5–3.5 µm; average length phialide/metula 0.57; *conidia* finely rough to rough, globose, 2–2.5 × 2–2.5 µm (2.1 ± 0.1 × 2.1 ± 0.1), average width/length = 0.97, n = 40.

Extrolites — Penitrem A.

Distinguishing characters — *Penicillium allsoppiae* is morphologically most similar to *P. dunedinense*, *P. eickeri* and *P. scottii*, all showing relatively fast growth on MEA compared to other series *Canescentia* species. *Penicillium allsoppiae* lacks the dark brownish grey colony reverse on CYA observed in *P. dunedinense*, generally grows more restricted than *P. scottii* and *P. eickeri*, and consistently produces a higher proportion of roughened stipes. This distinguishes it from its closest relatives, but see also distinguishing characters for *P. scottii*.

Penicillium doidgeae Visagie, Frisvad & K. Jacobs, *sp. nov.* — MycoBank MB 834427; Fig. 7

Etymology. Latin, *doidgeae*, named after Ethel Mary Doidge who had a long career as a mycologist/bacteriologist listing, amongst many others, *Penicillium* occurring in South Africa and became the first woman to receive a doctorate in South Africa.

Typus. South Africa, Struisbaai, bract from *Protea repens* infructescence, Aug. 2009, coll. *C.M. Visagie* (CBS H-22038 holotype, culture ex-type CBS 138947 = IBT 31950 = DAOM 241107 = DTO 183-G7 = CV 2189).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Atroveneta.*

ITS barcode — JX140804. Alternative identification markers: *BenA* = JX141006, *CaM* = JX157413, *RPB2* = KP016915.

Colony diam, 7 d (in mm) — CYA 36–41; CYA 5 °C germination; CYA 30 °C 20–27; CYA 37 °C no growth; MEA 34–40; YES 48–52; DG18 40–42; CYAS 41–42; CREA 18–23.

Colony characters — CYA 25 °C, 7 d: Colonies moderately deep, sulcate; margins low, wide, entire; mycelia white, sometimes inconspicuously yellow near centre; texture floccose; sporulation moderately dense, conidia *en masse* greyish green (25C4–D6); soluble pigments absent; exudates absent; reverse brown (5E7–6E7), sometimes greyish yellow to greyish orange to brownish orange (4C5–5B5–C5). MEA 25 °C, 7 d: Colonies moderately deep, plane; margins low, wide, entire; mycelia white; texture floccose; sporulation moderately dense to dense, conidia *en masse* greyish to dull green (25E4–26E4); soluble pigments absent; exudates absent; reverse greenish white to pale yellow (30A2–1A3), sometimes greyish orange (5B4) centrally, brown (6E8) elsewhere. YES 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, wide, entire; mycelia white; texture floccose; sporulation moderately dense to dense, conidia *en masse* greyish to dull green (25C4–E4–5); soluble pigments absent; exudates absent; reverse greyish brown (4B5). DG18 25 °C, 7 d: Colonies low to moderately deep, plane; margins low, wide, entire; mycelia white; texture velutinous and floccose areas; sporulation dense, conidia *en masse* dull green (26E4–27E4); soluble pigments absent; exudates absent; reverse orange (6B7) at centre, fading into dull green (29D4), sometimes centre white. CREA 25 °C, 7 d: Acid very weak only within colony periphery.

Micromorphology — *Conidiophores* mostly biverticillate, terverticillate also present, sometimes a long subterminal branch forms that extends up to 85 µm; *stipes* finely roughened to rough, minor proportion smooth, 85–600 × 3–4 µm; *branches*/*rami* two when present, 23–30(–85) × 3–4 µm; *metulae* appressed

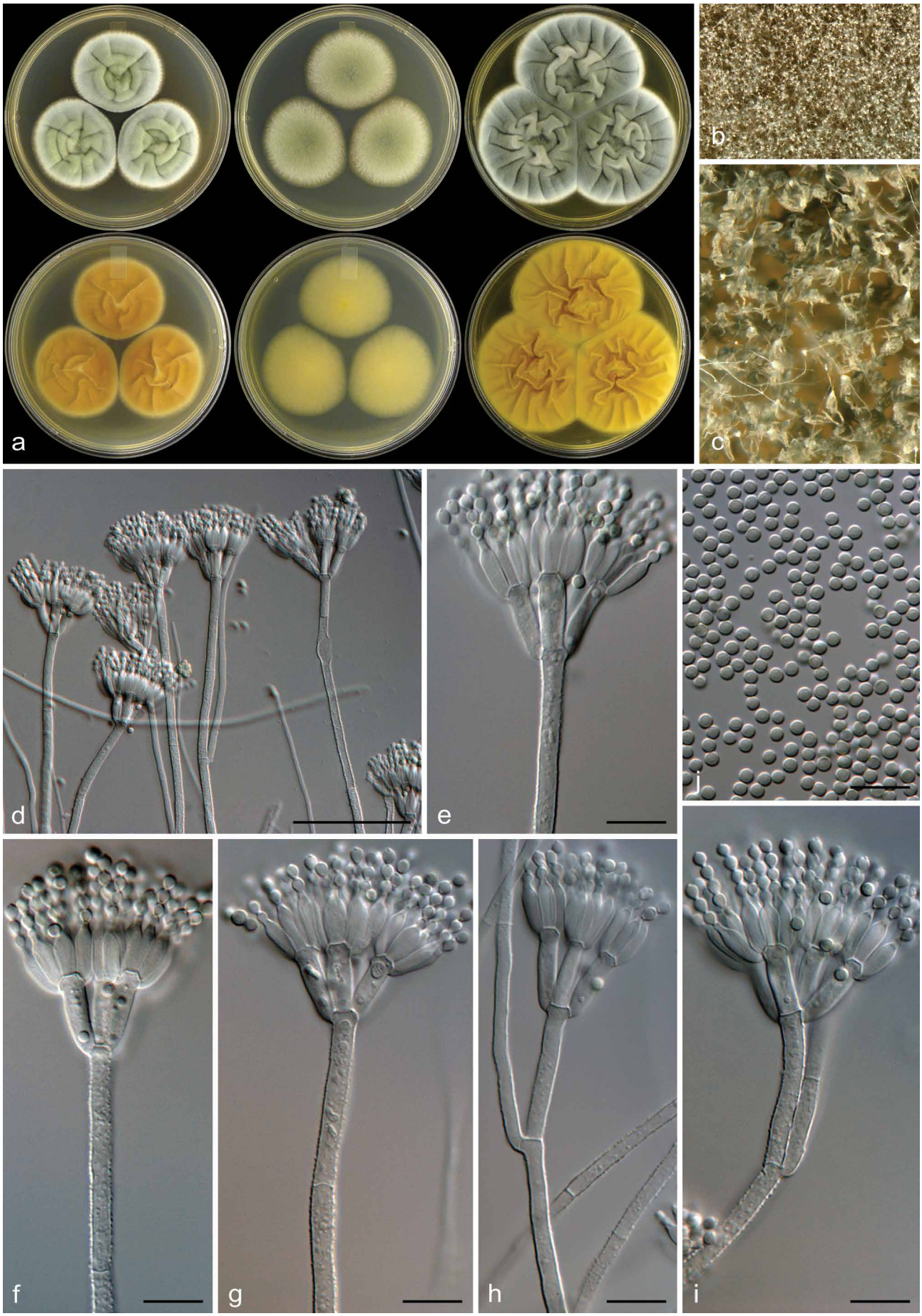

Fig. 7 *Penicillium doidgeae*. a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse); b, c. colony texture on MEA; d–h. conidiophores; i. conidia. — Scale bars: d = 25 µm, e–i = 10 µm.

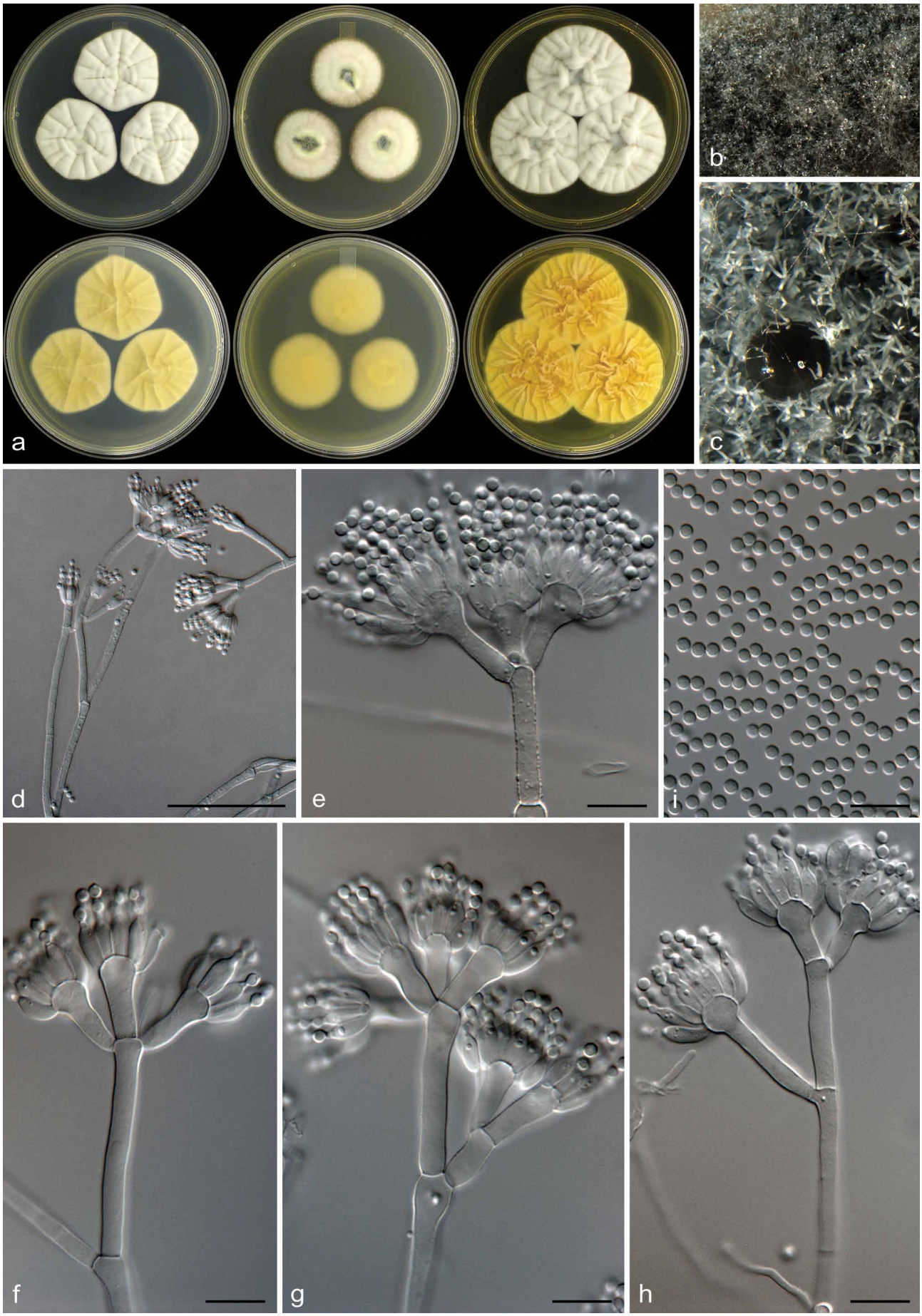

Fig. 8 *Penicillium eickeri*. a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse); b, c. colony texture on MEA; d–h. conidiophores; i. conidia. — Scale bars: d = 25 µm, e–i = 10 µm.

to slightly divergent, 4–6 per stipe/branch, 11–15 × 3–4.5 µm, vesicle 3.5–5 µm; *phialides* ampulliform, 8–10.5 × 2–4 µm; average length phialide/metula 0.74; *conidia* smooth, subglobose, 2–3 × 2–3 µm (2.5 ± 0.1 × 2.4 ± 0.1), average width/length = 0.95, n = 60.

Extrolites — Asperentins, atlantinone A, austalides, fischerin and patulin.

Distinguishing characters — *Penicillium doidgeae* produces fast-growing colonies on most agar media. Conidiophores sometimes are borne subterminally and have mostly roughened stipes and smooth conidia. The observed subterminal conidiophore branch is not borne at an angle to the main stipe, rather the branch leading to the terminal conidiophore is borne at an angle to the main stipe, a character similar to conidiophores of *Penicillium* section *Thysanophora*. The species is morphologically most similar to *P. antarcticum*. However, at cooler temperatures (5 °C) *P. doidgeae* conidia will at most only germinate on CYA, whereas *P. antarcticum* will produce microcolonies. Also, stipes of *P. doidgeae* are mostly finely roughened and generally longer (85–600 µm) compared to the smooth and generally shorter (100–250 µm) stipes of *P. antarcticum* (McRae et al. 1999).

Penicillium eickeri Visagie, Frisvad & K. Jacobs, *sp. nov.* — MycoBank MB 834428; Fig. 8

Etymology. Latin, *eickeri*, named after Albert Eicker who reported several *Penicillium* species isolated from the old Transvaal region in South Africa.

Typus. South Africa, Stellenbosch, mite from *Protea repens* infructescence, Mar. 2009, coll. *C.M. Visagie* (CBS H-22034 holotype, culture ex-type CBS 138939 = IBT 31921 = DAOM 241352 = DTO 181-G3 = CV 475).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Canescentia.*

ITS barcode — JX140824. Alternative identification markers: *BenA* = JX140979, *CaM* = JX157365, *RPB2* = KP016876.

Colony diam, 7 d (in mm) — CYA 38–39; CYA 30 °C 39–42; CYA 37 °C 1–5; MEA 34–38; YES 42–44; DG18 27–28; CYAS 30–31; CREA 15–17.

Colony characters — CYA 25 °C, 7 d: Colonies low, sulcate, raised at centre; margins low, narrow, entire; mycelia white; texture floccose; sporulation absent, conidia *en masse* not determined; soluble pigments absent; exudates clear; reverse greyish yellow (3C3) at centre, yellowish white (2A2–3A2) elsewhere. MEA 25 °C, 7 d: Colonies low to moderately deep, plane to sulcate, raised at centre; margins low, narrow, entire; mycelia white; texture floccose; sporulation sparse to moderately dense only at centre, conidia *en masse* greyish green (26C3); soluble pigments absent; exudates absent to minute clear droplets; reverse brownish orange yellowish brown (5C5–D8), sometimes a darker brown (6E7). YES 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white; texture floccose; sporulation absent, conidia *en masse* not determined; soluble pigments absent; exudates absent; reverse light brown (6D6) at centre, light yellow (3A5) elsewhere. DG18 25 °C, 7 d: Colonies moderately deep, sulcate; margins low, narrow, entire; mycelia white; texture floccose; sporulation moderately dense centrally, conidia *en masse* greyish turquoise to greyish green (24E4–25E4); soluble pigments absent; exudates absent; reverse light brown (5D7) centrally, pale orange (5A3) elsewhere. CREA 25 °C, 7 d: Acid not produced.

Micromorphology — *Conidiophores* mostly biverticillate, terverticillate also present; *stipes* rough walled, smooth also present, 200–820 × 3–4.5 µm; *branches*/*rami* two when present, 11–37 × 3–4.5 µm; *metulae* divergent, 2–6 per stipe/branch, 11–14(–17) × 3–4 µm, vesicle 3–4.5 µm; *phialides* ampulliform, 7–9.5 × 2.5–3 µm; average length phialide/metula 0.60; *conidia* finely rough to rough, globose, 2–2.5 × 2–2.5 µm (2.3 ± 0.03 × 2.3 ± 0.1), average width/length = 0.97, n = 30.

Extrolites — Curvulinic acid and xanthoepocin.

Distinguishing characters — *Penicillium eickeri* is morphologically most similar to *P. dunedinense*, *P. allsoppiae* and *P. scottii*, all showing relatively fast growth on MEA compared to other series *Canescentia* species. *Penicillium eickeri* lacks the dark brownish grey colony reverse on CYA observed in *P. dunedinense*, generally grows faster than *P. scottii* and *P. allsoppiae* and does not sporulate on CYA after 7 d. This distinguishes it from its closest relatives, but see also distinguishing characters for *P. scottii*.

Penicillium elizabethiae Visagie & Frisvad, *nom. nov.* — MycoBank MB 834432

Etymology. Latin, *elizabethiae*, named after Elizabeth Dale who first described this new species but used an illegitimate name.

Basionym. *Penicillium echinatum* E. Dale, Ann. Mycol. 24: 137. 1926 (*nom. illegit.* Art. 53.1; non Rivolta 1873).

Typus. Scotland, soil sample, 1914, coll. unknown (CBS H-22052 holotype, culture ex-type NRRL 917 = MUCL 29170 = IBT 21955 = DTO 189-B8).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Canescentia.*

ITS barcode — KP016840. Alternative identification markers: *BenA* = KJ866964, *CaM* = KJ867021, *RPB2* = KP016918.

Notes — This species was described by Dale (1926) who used an already occupied *P. echinatum* Rivolta (Dei Parassiti Vegetali: 451, 1873; MB263715) currently classified as *Memnoniella echinata* (Riv.) Galloway, Trans. Brit. Mycol. Soc. 18: 165. 1933; MB263706). *Penicillium elizabethiae* is morphologically similar to *P. janczewskii.* However, it is phylogenetically distinct and closely related to *P. nigricans* and *P. griseoazureum*.

Penicillium pole-evansii Visagie, Frisvad & K. Jacobs, *sp. nov.* — MycoBank MB 834429; Fig. 9

Etymology. Latin, *pole-evansii*, named after Illtyd Buller Pole-Evans who recorded the first record of *Penicillium* in South Africa (*P. digitatum* from *Citrus* sp. collected in Kwazulu Natal, 1903).

Typus. South Africa, Struisbaai, bract from *Protea repens* infructescence, Aug. 2009, coll. *C.M. Visagie* (CBS H-22037 holotype, culture ex-type CBS 138946 = IBT 31929 = DAOM 241106 = DTO 183-D5 = CV 1758).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Atroveneta.*

ITS barcode — JX140831. Alternative identification markers: *BenA* = JX141005, *CaM* = JX157412, *RPB2* = KP016911.

Colony diam, 7 d (in mm) — CYA 21–26(–36); CYA 30 °C 18–21; CYA 37 °C no growth; MEA 21–28; YES 36–40; DG18 34–35; CYAS 33–34; CREA 15–21.

Colony characters — CYA 25 °C, 7 d: Colonies moderately deep, sulcate, sometimes shaped as irregular pentagon; margins low, narrow, entire; mycelia white; texture floccose; sporulation moderately dense, conidia *en masse* dull green (25D4–D5–26D4); soluble pigments yellowish brown; exudates yellow and brown droplets; reverse olive brown to brown (4F4–5F4) at centre, fading into olive to yellowish brown (4D6–5D6), with age becoming dark green (25F5–26F5) where colonies meet. MEA 25 °C, 7 d: Colonies moderately deep, lightly sulcate; margins low, narrow, entire; mycelia white; texture floccose; sporulation dense, conidia *en masse* greyish turquoise to dull green (24E4–26E4); soluble pigments absent; exudates absent, sometimes yellowish orange; reverse brown (6E8). YES 25 °C, 7 d: Colonies low to moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white; texture

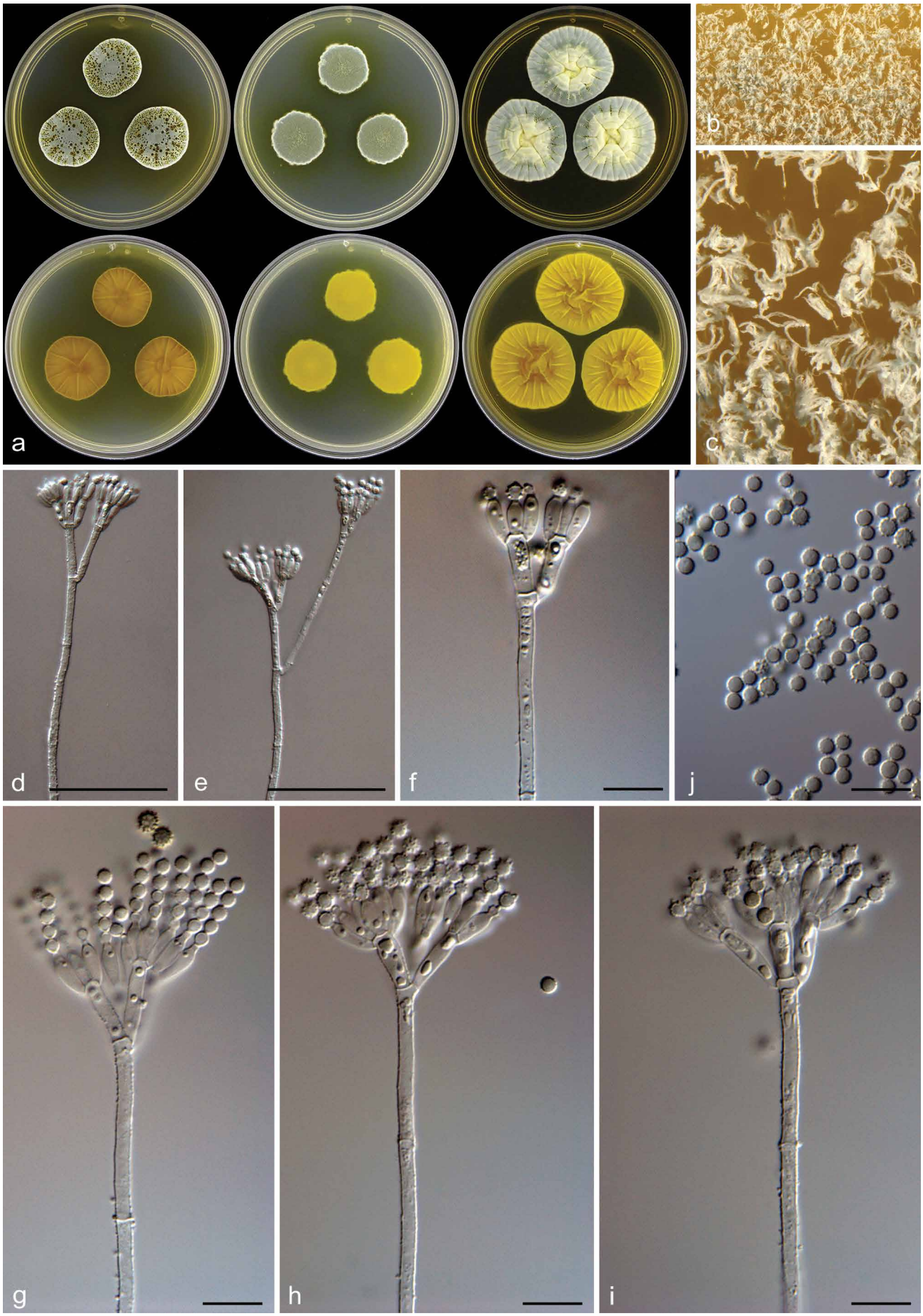

Fig. 9 *Penicillium pole-evansii*. a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse); b, c. colony texture on MEA; d–i. conidiophores; j. conidia. — Scale bars: d, e = 25 µm, f–j = 10 µm.

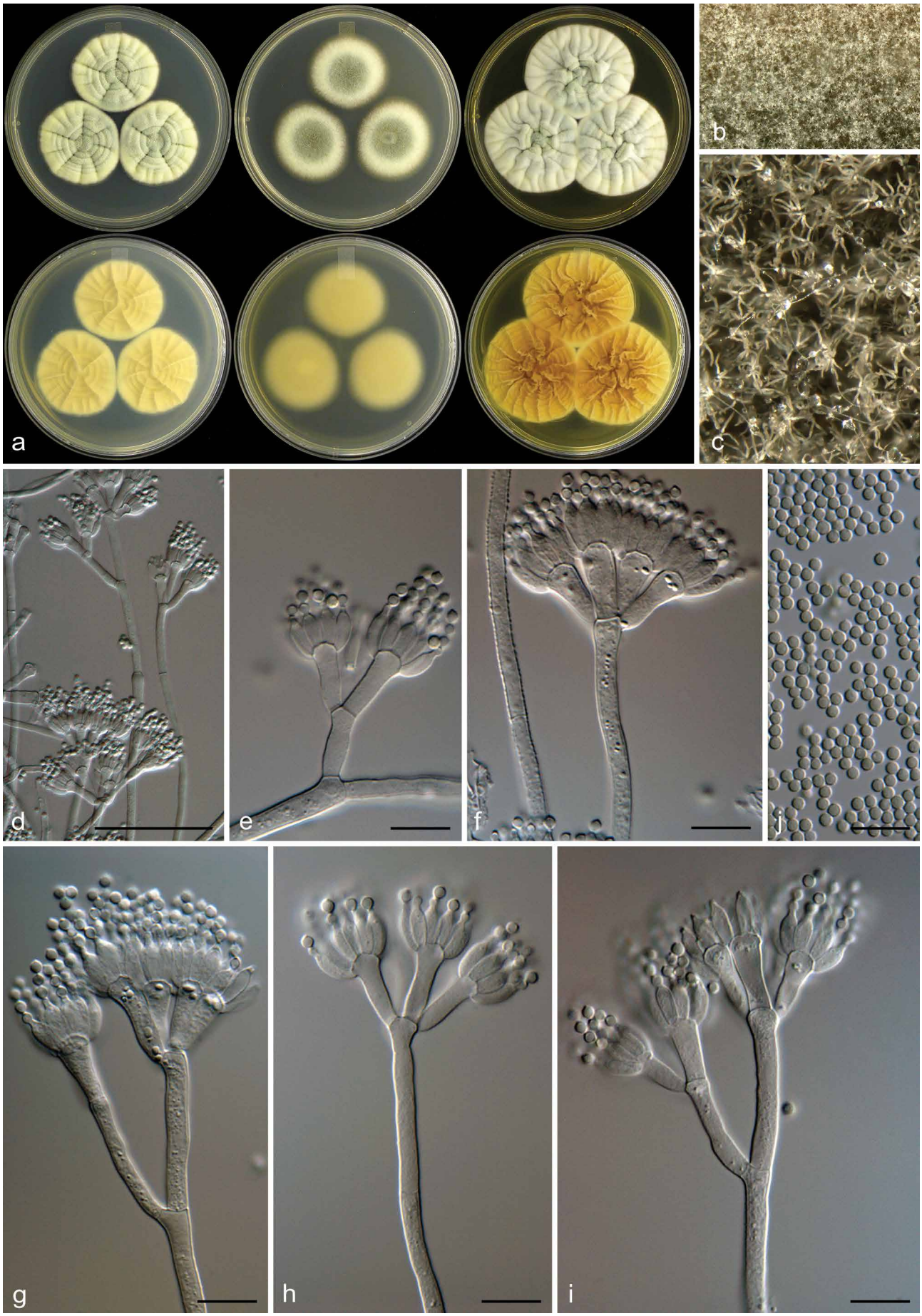

Fig. 10 *Penicillium scottii*. a. Colonies (top row, left to right: CYA, MEA, YES; bottom row, left to right: CYA reverse, MEA reverse, YES reverse); b, c. colony texture on MEA; d–i. conidiophores; j. conidia. — Scale bars: d, e = 25 µm, f–j = 10 µm.

floccose; sporulation sparse to moderately dense, conidia *en masse* greyish turquoise (24B3–C5); soluble pigments absent; exudates minute yellow droplets; reverse dull to greyish yellow (4B4–4C6). DG18 25 °C, 7 d: Colonies low to moderately deep, plane; margins low, narrow, entire; mycelia white; texture velutinous and floccose areas; sporulation dense, conidia *en masse* dull green (25E4); soluble pigments absent; exudates absent; reverse light yellow (2A5) a centre, fading into dull green (29D4). CREA 25 °C, 7 d: Acid not produced.

Micromorphology — *Conidiophores* mostly biverticillate, terverticillate also present, sometimes subterminal branch very long extending up to 65 µm; *stipes* finely rough to rough, 120–475 × 2.5–3.5 µm; *branches*/*rami* two when present, 20–65 × 2.5–3.5 µm; *metulae* divergent, 3–6 per stipe/branch, 9.5–16 × 2.5–4 µm, vesicle 3–4.5 µm; *phialides* ampulliform, 6.5–9 × 2.5–3.5 µm; average length phialide/metula 0.65; *conidia* rough to spiny, globose, 2–3 × 2–3 µm (2.8 ± 0.2 × 2.8 ± 0.2), average width/length = 0.97, n = 64.

Extrolites — Atrovenetin, aurantiamine, communesin B and patulin.

Distinguishing characters — *Penicillium pole-evansii* is distinguished by the copious amounts of yellow exudates and soluble pigments produced on CYA. With age, colony reverses on CYA becomes dark green. *Penicillium pole-evansii* is morphologically similar to *P. atrovenetum*. However, *P. atrovenetum* do not produce the dark green reverses observed after prolonged incubation in *P. pole-evansii*.

Penicillium scottii Visagie, Frisvad & K. Jacobs, *sp. nov.* — MycoBank MB 834430; Fig. 10

Etymology. Latin, *scottii*, named after De Buys Scott who described many new *Penicillium* species isolated from South Africa, all still considered distinct species today (Visagie et al. 2014b).

Typus. South Africa, Malmesbury, soil sample, July 2009, coll. *C.M. Visagie* (CBS H-22040 holotype, culture ex-type CBS 138951 = IBT 31905 = DTO 185-F8 = CV 930).

Subgeneric classification — subgenus *Penicillium*, section *Canescentia*, series *Canescentia*.

ITS barcode — JX140812. Alternative identification markers: *BenA* = JX140991, *CaM* = JX157383, *RPB2* = KP016894.

Colony diam, 7 d (in mm) — CYA (28–)30–40; CYA 30 °C (15–)30–38; CYA 37 °C 0–11; MEA (25–)32–40; YES 38–42; DG18 18–26; CYAS 28–32; CREA 15–20.

Colony characters — CYA 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white to yellow, sometimes pinkish orange; texture floccose; sporulation sparse, sometimes moderately dense, conidia *en masse* greyish green (28B4), dull green (25D4) in denser areas; soluble pigments absent; exudates clear; reverse greyish to brownish orange (5B5–5D6), sometimes yellowish grey to greyish yellow (4B2–3). MEA 25 °C, 7 d: Colonies moderately deep, plane to lightly sulcate, raised at centre; margins low, narrow, entire; mycelia white to yellow to sometimes pinkish orange; texture floccose; sporulation moderately dense, sometimes sparse, conidia *en masse* greyish to dull green (25D4–26D4); soluble pigments absent; exudates absent, sometimes clear; reverse brownish orange to brown (6C8–E8), sometimes olive brown to brown (4D5–5D5). YES 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white to yellow to pinkish orange; texture floccose; sporulation absent, sometimes sparse, conidia *en masse* pale to greyish green (28A3–B3); soluble pigments absent; exudates absent; reverse brown (6E8), greyish orange (6B6), greyish yellow (4B5). DG18 25 °C, 7 d: Colonies moderately deep, sulcate, raised at centre; margins low, narrow, entire; mycelia white to pinkish orange; texture floccose; sporulation moderately dense, conidia *en masse* greyish to dull green (25B4–D4–26E4); soluble pigments absent; exudates absent; reverse light to brownish orange (5A5–6A5–C6), sometimes brown (6E7) at centre, sometimes white. CREA 25 °C, 7 d: Acid not produced.

Micromorphology — *Conidiophores* mostly biverticillate, terverticillate also present; *stipes* smooth to sometimes rough walled, 200–800 × 3–4 µm; *branches*/*rami* two when present, 10–38 × 3–4 µm; *metulae* divergent, 2–6 per stipe/branch, 10–19 × 2–4 µm, vesicle 3–8.5 µm; *phialides* ampulliform, 6.5–9.5 × 2.5–3.5 µm; average length phialide/metula 0.57; *conidia* finely rough to rough, globose, 2–2.5 × 2–2.5 µm (2.2 ± 0.1 × 2.2 ± 0.1), average width/length = 0.98, n = 100.

Extrolites — Curvulinic acid, dehydrogriseofulvin, griseofulvin, penitrem A and xanthoepocin.

Distinguishing characters — *Penicillium scottii* produces biverticillate to terverticillate conidiophores with smooth to rough stipes and roughened conidia. Micromorphologically, it thus resembles other species previously considered to represent *P. janczewskii*. However, colony growth rates on MEA is faster than other species from this group, which generally never reach 20 mm growth in 7 d. The exception is the recently described *P. dunedinense* and *P. arizonense* that phylogenetically is a close relative of *P. janczewskii* but produces colonies up to 36 and 28 mm diam on MEA, respectively (Visagie et al. 2014a, Grijseels et al. 2016). *Penicillium dunedinense* produces an intense and very dark brownish grey reverse, which is not observed in *P. scottii*. *Penicillium eickeri* and *P. allsoppiae*, described in this study, morphologically is most similar to *P. scottii*. However, *P. eickeri* generally grows faster than both these species, while *P. allsoppiae* generally grows more restricted than *P. scottii*. *Penicillium allsoppiae* also consistently produces conidiophores with roughened stipes more regularly than the other two species and *P. eickeri* fails to sporulate on CYA after 7 d incubation.

PENICILLIUM SECTION CANESCENTIA SERIES ATROVENETA ACCEPTED SPECIES AND THEIR SYNONYMS

Penicillium antarcticum A.D. Hocking & C.F. McRae, Polar Biol. 21: 103. 1999 (MB 482749). — Type: DAR 72813 (holotype). Ex-type: CBS 100492 = FRR 4989. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: KJ834503 (alternative markers: *BenA* = MN969371; *CaM* = MN969236; *RPB2* = JN406653).

= *Penicillium attenuatum* Kirichuk & Pivkin, Mycol. Progr. 16: 21. 2016 (2017) (MB 818673). — Type: LE 312279 (holotype). Ex-type: KMM 4671 (PIBOC). ITS barcode: KU358555 (alternative markers: *BenA* = KU358558; *CaM* = KU358561; *RPB2* = n.a.).

= *Penicillium ochotense* Kirichuk & Pivkin, Mycol. Progr. 16: 21. 2016 (2017) (MB 818672). — Type: LE 312278 (holotype). Ex-type: KMM 4670 (PIBOC). ITS barcode: KU358553 (alternative markers: *BenA* = KU358556; *CaM* = KU358559; *RPB2* = n.a.).

= *Penicillium piltunense* Kirichuk & Pivkin, Mycol. Progr. 16: 19. 2016 (2017) (MB 818671). — Type: LE 312276 (holotype). Ex-type: KMM 4668 (PIBOC). ITS barcode: KU358554 (alternative markers: *BenA* = KU358557; *CaM* = KU358560; *RPB2* = n.a.).

Penicillium atrovenetum G. Sm., Trans. Brit. Mycol. Soc. 39: 112. 1956 (MB 302377). — Type: IMI 061837 (neotype, Pitt et al. 2000). Ex-type: CBS 241.56 = ATCC 13352 = FRR 2571 = IFO 8138 = IMI 061837 = LSHBSm683 = QM 6963. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: AF033492 (alternative markers: *BenA* = JX140944; *CaM* = KJ867004; *RPB2* = JN121467).

Penicillium attenuatum: see under *Penicillium antarcticum*.

Penicillium doidgeae Visagie, Frisvad & K. Jacobs, published here (MB 834427). — Type: CBS H-22038 (holotype). Ex-type: CBS 138947 = IBT 31950 = DAOM 241107 = DTO 183-G7 = CV 2189. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: JX140804 (alternative markers: *BenA* = JX141006; *CaM* = JX157413; *RPB2* = KP016915).

Penicillium novae-zeelandiae J.F.H. Beyma, Antonie van Leeuwenhoek 6: 275. 1940 (MB 522253). — Type: IMI 40584ii (neotype, Pitt 1980). Ex-type: CBS 137.41 = ATCC 10473 = IFO 31748 = IMI 040584ii = NRRL 2128 = QM 1934 = VKMF-2886. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: JN617688 (alternative markers: *BenA* = MN969390; *CaM* = MN969279; *RPB2* = JN406628).

Penicillium nucicola Visagie, Malloch & Seifert, Persoonia 36: 259. 2016 (MB 815771). — Type: DAOM 695770 (holotype). Ex-type: DAOMC 250522 = CBS 140987 = W 59 = KAS 2203. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: KT887860 (alternative markers: *BenA* = KT887821; *CaM* = KT887782; *RPB2* = MN969171).

Penicillium ochotense: see under *Penicillium antarcticum.*

Penicillium piltunense: see under *Penicillium antarcticum.*

Penicillium pole-evansii Visagie, Frisvad & K. Jacobs, published here (MB 834429). — Type: CBS H-22037 (holotype). Ex-type: CBS 138946 = IBT 31929 = DAOM 241106 = DTO 183-D5 = CV 1758. Subgenus *Penicillium* section *Canescentia* series *Atroveneta*. ITS barcode: JX140831 (alternative markers: *BenA* = JX141005; *CaM* = JX157412; *RPB2* = KP016911).

PENICILLIUM SECTION CANESCENTIA SERIES CANESCENTIA ACCEPTED SPECIES AND THEIR SYNONYMS

Penicillium allsoppiae Visagie, A. Visagie, Frisvad & K. Jacobs, published here (MB 834426). — Type: CBS H-22036 (holotype). Ex-type: CBS 138943 = DAOM 241348 = DTO 182-D5 = CV 931. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: JX140830 (alternative markers: *BenA* = JX140992; *CaM* = JX157384; *RPB2* = KP016895).

Penicillium arizonense Frisvad, Grijseels & J.C. Nielsen, Sci. Rep. 6: srep35112 p. 8. 2016 (MB 817128). — Type: Herb. C-F-101845 (holotype). Ex-type: IBT 12289 = CBS 141311. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: MH492021 (alternative markers: *BenA* = MH492019; *CaM* = MH492020; *RPB2* = MH492022).

Penicillium canescens Sopp, Skr. Vidensk.-Selsk. Christiana, Math.-Naturvidensk. Kl. 11: 181. 1912 (MB 153765). — Type: IMI 28260 (neotype, Pitt 1980). Ex-type: CBS 300.48 = ATCC 10419 = DSM1215 = FRR 910 = IMI 028260 = MUCL 29169 = NCTC 6607 = NRRL 910 = QM 7550 = VKMF-1148. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: AF033493 (alternative markers: *BenA* = JX140946; *CaM* = MN969241; *RPB2* = JN121485).

Penicillium coralligerum Nicot & Pionnat, Bull. Soc. Mycol. France 78: 245. 1963 (1962) (MB 335721). — Type: IMI 99159 (neotype, Pitt et al. 2000). Ex-type: CBS 123.65 = ATCC 16968 = FRR 3465 = IFO 9578 = IHEM 4511 = IMI 099159 = LCP 58.1674 = NRRL 3465. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: JN617667 (alternative markers: *BenA* = MN969378; *CaM* = MN969248; *RPB2* = JN406632).

Penicillium corvianum Visagie & Seifert, Persoonia 36: 259. 2016 (MB 815770). — Type: DAOM 695764 (holotype). Ex-type: DAOMC 250517 = CBS 141000 = KAS 3618 = IT-2008-4-D. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KT887875 (alternative markers: *BenA* = KT887836; *CaM* = KT887797; *RPB2* = MN969170).

Penicillium dunedinense Visagie, Seifert & Samson, Stud. Mycol. 78: 121. 2014 (MB 809183). — Type: CBS H-21803 (holotype). Ex-type: CBS 138218. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KJ775678 (alternative markers: *BenA* = KJ775171; *CaM* = KJ775405; *RPB2* = MN969116).

Penicillium echinatum: see under *Penicillium elizabethiae.*

Penicillium eickeri Visagie, Frisvad & K. Jacobs, published here (MB 834428). — Type: CBS H-22034 (holotype). Ex-type: CBS 138939 = IBT 31921 = DAOM 241352 = DTO 181-G3 = CV 475. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: JX140824 (alternative markers: *BenA* = JX140979; *CaM* = JX157365; *RPB2* = KP016876).

Penicillium elizabethiae Visagie, Frisvad & K. Jacobs, published here (MB 834432). — Type: CBS H-22052 (holotype). Ex-type: NRRL 917 = MUCL 29170 = IBT 21955 = DTO 189-B8. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KP016840 (alternative markers: *BenA* = KJ866964; *CaM* = KJ867021; *RPB2* = KP016918).

≡ *Penicillium echinatum* E. Dale, Ann. Mycol. 24: 137. 1926 (*nom. illegit.* Art. 53.1; non Rivolta 1873) (MB 505484).

Penicillium granatense: see under *Penicillium janczewskii.*

Penicillium griseoazureum C. Moreau & M. Moreau ex C. Ramírez, Manual and Atlas of the Penicillia: 61. 1982 (MB 115800). — Type: CBS 162.42 (holotype). Ex-type: CBS 162.42 = FRR 1361. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KC411679 (alternative markers: *BenA* = KP016919; *CaM* = KP016823; *RPB2* = KP016852).

≡ *Penicillium griseo-azureum* C. Moreau & M. Moreau, Rev. Mycol. 6: 59. 1941 (*nom. inval.*, Art. 36.1) (MB 289084). — Herb.: CBS 162.42. Ex-type: CBS 162.42 = FRR 1361.

Penicillium janczewskii K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Ser. B., Sci. Nat. 1927: 488. 1927 (MB 120703). — Type: IMI 191499 (neotype, Pitt 1980). Ex-type: CBS 221.28 = FRR 919 = IMI 191499 = NRRL 919. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: AY157487 (alternative markers: *BenA* = MN969386; *CaM* = MN969267; *RPB2* = JN406612).

= *Penicillium granatense* C. Ramírez et al., Mycopathologia 72: 31. 1980 (MB 113023). — Type: IJFM 5965. Ex-type: CBS 166.81 = IJFM 5965 = IMI 253795 = VKMF-2191. ITS barcode: KC411682 (alternative markers: *BenA* = KJ866967; *CaM* = KJ866998; *RPB2* = KP016853).

= *Penicillium nigricans* var. *sulphureum* S. Abe, J. Gen. Appl. Microbiol., Tokyo 2: 83. 1956 (*nom. inval.*, Art. 36) (MB 347374). — Type: unknown. Ex-type: CBS 744.70 = ATCC 18380 = FAT536 = QM 7297. ITS barcode: KP016839 (alternative markers: *BenA* = KJ866966; *CaM* = KJ867018; *RPB2* = KP016862).

Penicillium jensenii K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Ser. B., Sci. Nat. 1927: 494. 1927 (MB 120708). — Type: IMI 39768 (neotype, Pitt 1980). Ex-type: CBS 327.59 = ATCC 18317 = FRR 909 = IFO 5764 = IMI 039768 = LCP 89.1389 = NRRL 909 = QM 7587. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: AY443470 (alternative markers: *BenA* = JX140954; *CaM* = AY443490; *RPB2* = JN406614).

= *Penicillium siemaszkii* K.M. Zaleski, Bull. Int. Acad. Polon. Sci., Cl. Sci. Math., Sér. B., Sci. Nat. 1927: 487. 1927 (Thom 1930, Raper & Thom 1949) (MB 278109). No culture available.

Penicillium linzhiense H.K. Wang & Jeewon, Front. Cell. Infect. Microbiol. 10: e-6045044. 2021 (MB 838576). — Type: CCTCC no: M2019870. Ex-type: CCTCC-M2019870. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: MT461156 (alternative markers: *BenA* = MT461157; *CaM* = MT461162; *RPB2* = n.a.).

Penicillium murcianum C. Ramírez & A.T. Martínez, Mycopathologia 74: 37. 1981 (MB 112524). — Type: IJFM 7031 (holotype). Ex-type: CBS 161.81 = ATCC 42239 = IJFM 7031 = IMI 253800 = VKMF-2196. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KC411678 (alternative markers: *BenA* = MN969419; *CaM* = MN969341; *RPB2* = MN969202).

Penicillium nigricans Bainier in Thom, Penicillia: 351. 1930 (MB 119303). — Type: CBS H-22051 (holotype). Ex-type: CBS 354.48 = ATCC 10115 = IFO 6103 = IMI 039767 = NRRL 915 = QM 1933 = VKMF-313. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KC411755 (alternative markers: *BenA* = KJ866965; *CaM* = KJ867012; *RPB2* =KP016857).

Penicillium nigricans var. *sulphureum*: see under *Penicillium janczewskii.*

Penicillium radiatolobatum Lörinczi, Publ. Soc. Nat. Rom. Pent. Stiinta Sol. 10B: 435. 1972 (MB 114326). — Type: CBS H-7530 (isotype). Ex-type: CBS 340.79. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KC411745 (alternative markers: *BenA* = MN969413; *CaM* = MT066183; *RPB2* = MN969168).

Penicillium scottii Visagie, Frisvad & K. Jacobs, published here (MB 834430). — Type: CBS H-22040 (holotype). Ex-type: CBS 138951 = IBT 31905 = DTO 185-F8 = CV 930. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: JX140812 (alternative markers: *BenA* = JX140991; *CaM* = JX157383; *RPB2* = KP016894).

Penicillium siemaszkii: see under *Penicillium jensenii.*

Penicillium yarmokense Baghd., Novosti Sist. Nizsh. Rast. 5: 99. 1968 (MB 335774). — Type: CBS H-7536 (isotype). Ex-type: CBS 410.69 = FRR 520 = IMI 140346 = VKMF-1076. Subgenus *Penicillium* section *Canescentia* series *Canescentia*. ITS barcode: KC411757 (alternative markers: *BenA* = MN969407; *CaM* = MN969314; *RPB2* = JN406553).

DISCUSSION

Penicillium section *Canescentia* species are often reported in studies, but identifications in this group have remained problematic over the years. One major obstacle was species delineation based solely on morphological characters. Pitt (1980) mentions this difficulty because of, amongst others, the existence of intermediate strains (e.g., IMI 149218) that share characters between *P. canescens* and *P. janczewskii*. Here we show that this particular strain does belong to *P. canescens* which substantiates Pitt's findings or indeed concerns with regards to the group's variable morphologies. In this paper, we provide a sequence dataset for the 19 species previously considered to belong to section *Canescentia* (no culture is available for *P. siemaszkii*). We describe a further five new species *P. allsoppiae*, *P. doidgeae*, *P. eickeri*, *P. pole-evansii* and *P. scottii*. Furthermore, we synonymise *P. granatense* and *P. nigricans* var. *sulphuratum* with *P. janczewskii*, but show that *P. griseoazureum*, *P. murcianum*, *P. nigricans*, *P. radiatolobatum* and *P. yarmokense* should be considered as distinct species. We were unable to obtain a good representative set of strains for *P. canescens* and its close relatives *P. murcianum*, *P. radiatolobatum* and *P. yarmokense*. This particular clade will be subject to a future study to better resolve the group using many more strains and sequencing of additional gene regions. Similarly, *P. novae-zeelandiae* needs further revision with strains from a wider range of sources and locations needed. Even though more work is needed in section *Canescentia*, species identifications using only gene sequences should not present difficulties with the dataset provided in this study. The only concern is using *BenA* sequences to distinguish between *P. murcianum* and *P. radiatolobatum*; however, *CaM* sequences provides sufficient resolution. *Penicillium chrysogenum*, *P. rubens* and *P. allii-sativii* is an example of a similar situation where you may need more than *BenA* sequences for making an identification, both *CaM* and *RPB2* sequences work well (Houbraken et al. 2011, 2012).

Correct species identifications of section *Canescentia* strains is important. Species in this section are often reported as good enzyme producers for biotechnology purposes (Brian et al. 1946, 1949, Pessoni et al. 1999, 2002, Weber et al. 2003, Chávez et al. 2006, Assamoi et al. 2008a, b, Terrasan et al. 2010). For example, JGI undertook whole genome sequencing of *P. canescens* ATCC 10419 with the aim to unravel mechanisms of phosphate solubilisation. In addition, some section *Canescentia* species are producers of antibiotics (Brian et al. 1953, Birch et al. 1965, Shiono et al. 2008), as well as mycotoxins (e.g. beta-nitropropionic acid from *P. atrovenetum*; patulin from *P. antarticum*, *P. doidgeae*, *P. novae-zeelandiae* and *P. pole-evansii*). The possible exploitation of these fungi for human purposes thus makes it very important to resolve the taxonomy of this section, resulting in well-defined species descriptions based on a polyphasic or consilient approach.

Most species from section *Canescentia* produce a diverse range of secondary metabolites that may provide a competitive advantage if produced in the soil environment (Table 3, 4). Fourteen out of 21 species produce known antibacterial compounds (patulin or penicillic acid and/or xanthoepocin) (Igarashi et al. 2000, Rasmussen et al. 2005, Frisvad 2018). Both patulin and penicillic acid are also quorum sensing inhibitors (Rasmussen et al. 2005) and could thus inhibit bacteria in soil and marine environments. Many species in series *Canescentia* also produce antifungal extrolites such as griseofulvin. Apart from the metabolites detected and reported from section *Canescentia*, several further secondary metabolite gene clusters appear to be silent (see for example data for *P. arizonense* (Grijseels et al. 2016)), at least under laboratory conditions. Thus one can anticipate to discover new antibiotics from this section.

Penicillium section *Canescentia* species have a worldwide distribution (Domsch et al. 1980, Houbraken & Samson 2011) and are commonly isolated from the fynbos biome of South Africa, especially from soil. *Penicillium novae-zeelandiae* and *P. scottii* were found to be common at sampling sites across the fynbos. One of our collection sites are situated in the Riverlands

Nature Reserve near Malmesbury. This site also formed part of a previous survey that explored fungal communities associated with *Protea* rhizosphere soil and amongst other species, recovered *P. novae-zeelandiae* and *P. janczewskii* (Allsopp et al. 1987). *Penicillium janczewskii* has not been reported from any other South African surveys and it is our opinion that Allsopp's strains may belong to *P. scottii*. Another survey also found *P. novae-zeelandiae* in *Protea* species (Schutte 1992). It is not often that one has the opportunity to collect samples from the same area as a previous survey, especially ones that identified *Penicillium* to species level. It is quite remarkable that the same species from 1987 were also recorded in our study. This was not only for the section *Canescentia*, but also for *P. corylophilum* classified in section *Exilicaulis* (Visagie et al. 2016c) and section *Torulomyces* (previously the genus *Torulomyces*) (Visagie et al. 2016a). Even though *Penicillium* species are often considered as degraders of dead organic waste, they arguably have additional roles in nature. The fact that the same *Penicillium* species were found almost 20 years later at the same site, might point to stable core fungal communities and suggest that these species either play an important role in this ecosystem or might be associated with specific plant species in the area and thus conidia also occur in soil or litter. Observations from this survey suggest that species might be subjected to vectored dispersal along with common conidia dispersal mechanisms such as air or water dispersal. This has opened a number of questions about the distribution of *Penicillium* species in the fynbos biome and is something that should be studied further. In terms of species diversity, this survey resulted in the recovery of 61 *Penicillium* (29 described as new) and 15 *Talaromyces* species (nine described as new) (Visagie et al. 2009, 2014a, 2015b, Visagie & Jacobs 2012, Yilmaz et al. 2016) with many new DNA reference sequences generated. The large number of species recovered and the high proportion of new species found was not unexpected considering the diversity of endemic plants in the region. However, considering the limited number of sites that were sampled and the diverse vegetation of the fynbos (Mucina & Rutherford 2006), we believe that there are many more new *Penicillium* and *Talaromyces* species waiting to be discovered from this diversity hotspot (Myers et al. 2000).

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Supplementary material

Fig. S1 Phylogenetic tree of *Penicillium* section *Canescentia* ex-type strains using the ITS region. *Penicillium sacculum* was chosen as outgroup. Posterior probabilities (pp) and/or bootstrap values (bs) higher than 0.95 and 80, respectively, are given above thickened branches. Names in grey text indicate reference strains, black text fynbos strains and coloured text new species, ^{T} = ex-type strain.

Fig. S2 Untrimmed ITS, *BenA* and *CaM* alignments of *Penicillium* section *Canescentia*. Annotations: blue = rRNA; green = internal transcribed spacer regions; orange = complete cds; yellow = cds as submitted; red = considered as suspicious base calls (regions trimmed from final alignment).

Fig. S3 Phylogenetic trees of ITS, *BenA* and *CaM* calculated using untrimmed alignments as shown in Fig. S1. *Penicillium brevicompactum* was chosen as outgroup. Posterior probabilities and/or bootstrap values higher than 0.95 and 80, respectively, are given on supported branches. Names in green represent *P. antarcticum*, while red represents species described by Kirichuk et al. (2016).