



Phylogeny and taxonomic revision of the *Planistromellaceae* including its coelomycetous anamorphs: contributions towards a monograph of the genus *Kellermania*

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Key words

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Abstract The core species of the family *Planistromellaceae* are included in the teleomorphic genera *Planistroma* and *Planistromella* and the connected anamorphic, coelomycetous genera *Alpakesa*, *Kellermania*, and *Piptarthron*. These genera have been defined primarily on the basis of ascospore septation or number of conidial appendages. Due to a lack of DNA sequence data, phylogenetic placement of these genera within the *Dothideomycetes*, evaluation of monophyly, and questions about generic boundaries could not be adequately addressed in the past. Isolates of nearly all of the known species in these genera were studied genetically and morphologically. DNA sequence data were generated for the nSSU, ITS, nLSU, and RPB1 markers and analysed phylogenetically. These results placed the *Planistromellaceae*, herein recognised as a distinct family, in an unresolved position relative to other genera within the order *Botryosphaerales*. Species representing the core genera of the *Planistromellaceae* formed a clade and evaluation of its topology revealed that previous morphology-based definitions of genera resulted in an artificial classification system. *Alpakesa*, *Kellermania*, *Piptarthron*, *Planistroma*, and *Planistromella* are herein recognised as belonging to the single genus *Kellermania*. The following new combinations are proposed: *Kellermania crassispora*, *K. dasylirionis*, *K. macrospora*, *K. plurilocularis*, and *K. unilocularis*. Five new species are described, namely *K. confusa*, *K. dasylirionica*, *K. micrantha*, *K. ramaleyae*, and *K. rostratae*. Descriptions of species in vitro and a key to species known from culture are provided.

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INTRODUCTION

Kellermania was established by Ellis & Everhart (1885) to accommodate an unusual coelomycete, *K. yuccigena*, with large, cylindrical, and septate conidia that were considered stipitate, and it occurred on dead leaves of *Yucca* (Asparagaceae, subfamily Agavoideae sensu APG III (2009) = Agavaceae in earlier classifications). The stipes of the conidia described by Ellis & Everhart (1885) are interpreted as apical appendages (Sutton 1968). Höhnel (1918a) adopted the generic name *Piptarthron* that was provisionally suggested by Montagne for *Septoria macrospora*, a coelomycetous species without appendages that occurred on senescent leaves of *Agave* (Asparagaceae, subfamily Agavoideae = Agavaceae in earlier classifications). He provided a generic diagnosis and comparison to *Kellermania*. Subramanian & Ramakrishnan (1954) established the coelomycetous genus *Alpakesa*, which was characterised in part by conidia with multiple apical appendages, when their study revealed that *Neottiospora yuccifolia*, a species found on dead leaves of *Yucca*, was not congeneric with the type of *Neottiospora*.

Several other studies have added new species to *Alpakesa*, *Kellermania*, and *Piptarthron* and/or provided revised generic

circumscriptions. Sutton (1968) restricted *Kellermania* to species with simple, blastic conidiophores; septate, hyaline, and appendage-bearing conidia; and sclerotoid, pycnidial conidiomata, while discussing segregate genera and excluding many names classified in *Kellermania*. Morgan-Jones et al. (1972a) re-examined the type species of *Alpakesa*, modified the generic circumscription, and added two species. Morgan-Jones et al. (1972b) revised the concepts of the two *Kellermania* species that were accepted by Sutton (1968), added two new species, and included taxa with or without a single apical conidial appendage. Sutton (1977) synonymised the *Yucca*-inhabiting genus *Septoplaca* with *Piptarthron*, but he was unable to determine which species was represented by the type, *S. limbata*. Sutton (1980) later treated *S. limbata* as *Piptarthron limbatum* and subsequently as *P. yuccae* (Sutton 1983). Sutton (1980) maintained *Alpakesa*, *Kellermania*, and *Piptarthron* for genera having multiple, single, or no conidial appendages, respectively. Sutton (1980) also noted the possibility of a broadly expanded *Kellermania* for all species in the complex. Nag Raj (1993) treated *Alpakesa* as a later synonym of *Kellermania* and listed the unexamined or excluded taxa.

Ramaley (1991, 1992, 1993, 1995, 1998) provided the next major advances in the study of this group of fungi by discovering and describing the sexual states of *Kellermania* and *Piptarthron*, adding new species, and reviewing several coelomycetous species. The genus *Planistroma*, the sexual state of *Piptarthron*, was characterised by subepidermal, ostiolate ascomata in multilocular stromata with bitunicate asci and lacking paraphyses (Ramaley 1991). Ramaley (1992) added another species of *Planistroma*, *P. obtusilunatum*, with unilocular conidiomata more typical of *Kellermania*. She noted the intermediate nature of the asexual state in that the lack of apical appendages

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Table 1 Isolates and sequences employed in this study. Taxon names in **bold** indicate newly generated strains and data.

Species	Isolate culture no. ¹	Host	Locality	GenBank accession no. ²			
				SSU	LSU	ITS	RPB1
<i>Bagnisia examinans</i>	CBS 551.66	<i>Lantana camara</i>	India	GU296139	EU167562	GU301803	n/a
<i>Barriopsis fusca</i>	CBS 174.26	<i>Citrus</i> sp.	Cuba	EU673182	EU673330	DQ377857	n/a
<i>Botryosphaeria corticis</i>	ATCC 22927	<i>Vaccinium</i> sp.	USA	EU673176	DQ299247	EU673245	n/a
<i>Botryosphaeria dothidea</i>	CBS 110302	<i>Vitis vinifera</i>	Portugal	EU673174	AY259092	EU673243	n/a
' <i>Botryosphaeria</i> ' <i>tsugae</i>	CBS 418.64	<i>Tsuga heterophylla</i>	Canada	EU673208	DQ458888	DQ377867	n/a
<i>Diplodia corticola</i>	CBS 112546	<i>Quercus ilex</i>	Spain	EU673207	AY259090	EU673262	n/a
<i>Diplodia cupressi</i>	CBS 168.87	<i>Cupressus sempervirens</i>	Israel	EU673209	DQ458893	EU673263	n/a
<i>Diplodia mutila</i>	CBS 112553	<i>Vitis vinifera</i>	Portugal	EU673213	AY259093	AY928049	n/a
<i>Diplodia pinea</i> A	CBS 109727	<i>Pinus radiata</i>	South Africa	EU673220	DQ458897	EU673269	n/a
<i>Diplodia rosulata</i>	CBS 116470	<i>Prunus africana</i>	Ethiopia	EU673211	EU430265	DQ377896	n/a
<i>Diplodia scrobiculata</i>	CBS 109944	<i>Pinus greggii</i>	Mexico	EU673218	DQ458899	EU673268	n/a
<i>Diplodia seriata</i>	CBS 119049	<i>Vitis</i> sp.	Italy	EU673216	DQ458889	EU673266	n/a
<i>Dothiorella iberica</i>	CBS 113188	<i>Quercus suber</i>	Spain	EU673156	AY573198	EU673230	n/a
<i>Dothiorella sarmentorum</i>	CBS 115038	<i>Malus pumila</i>	Netherlands	EU673159	AY573206	DQ377860	n/a
<i>Guignardia bidwellii</i>	CBS 111645	<i>Parthenocissus quinquefolia</i>	USA	EU673223	FJ824766	DQ377876	n/a
<i>Guignardia citricarpa</i>	CBS 102374	<i>Citrus aurantium</i>	Brasil	FJ824759	FJ824767	DQ377877	n/a
<i>Guignardia philoprina</i>	CBS 447.68	<i>Taxus baccata</i>	Netherlands	FJ824760	FJ824768	DQ377878	n/a
<i>Helicomycetes roseus</i>	CBS 283.51	submerged bark, in brook	Switzerland	AY856928	AY916464	AY856881	n/a
<i>Kellermania anomala</i>	AR 3471, CBS 132218	<i>Yucca brevifolia</i>	USA	JX444899	JX444853	JX444869	JX444884
<i>Kellermania confusa</i>	AR 3469, CBS 131723	<i>Yucca thornberi</i>	USA	n/a	JX444854	JX444870	JX444885
<i>Kellermania crassispora</i>	AR 3463, CBS 131714	<i>Nolina micrantha</i>	USA	JX444900	JX444855	JX444871	JX444886
<i>Kellermania dasylirionicola</i>	AR 3465, CBS 131720	<i>Dasylirion leiophyllum</i>	USA	JX444901	JX444856	JX444872	JX444887
<i>Kellermania dasylirionis</i>	AR 3464, CBS 131715	<i>Dasylirion leiophyllum</i>	USA	n/a	JX444857	JX444873	JX444888
<i>Kellermania macrospora</i>	AR 3468, CBS 131716	<i>Agave</i> sp.	USA	JX444902	JX444858	JX444874	JX444889
<i>Kellermania micranthae</i>	AR 3474, CBS 131724	<i>Nolina micrantha</i>	USA	JX444903	JX444859	JX444875	JX444890
<i>Kellermania nolinae</i>	AR 3475, CBS 131717	<i>Nolina erumpens</i>	USA	JX444904	JX444860	JX444876	JX444891
<i>Kellermania nolinifoliorum</i>	AR 3473, CBS 131718	<i>Nolina microcarpa</i>	USA	JX444905	JX444861	JX444877	JX444892
<i>Kellermania plurilocularis</i>	AR 3467, CBS 131719	<i>Yucca baccata</i>	USA	n/a	JX444862	JX444878	JX444893
<i>Kellermania ramaleyae</i>	MEP 1260, CBS 131722	<i>Yucca</i> sp.	Mexico	n/a	JX444863	JX444879	JX444894
<i>Kellermania rostratae</i>	JB 5.16.11-01, CBS 131721	<i>Yucca rostrata</i>	Mexico	n/a	JX444864	JX444880	JX444895
<i>Kellermania unilocularis</i>	AR 3466 (dead)	<i>Yucca baccata</i>	USA	n/a	JX444865	n/a	n/a
<i>Kellermania uniseptata</i>	AR 3476, CBS 131725	<i>Yucca rupicola</i>	USA	JX444906	JX444866	JX444881	JX444896
<i>Kellermania yuccifoliorum</i>	AR 3472, CBS 131726	<i>Yucca brevifolia</i>	USA	JX444907	JX444867	JX444882	JX444897
<i>Kellermania yuccigena</i>	AR 3470, CBS 131727	<i>Yucca filamentosa?</i>	USA	JX444908	JX444868	JX444883	JX444898
<i>Lasiodiplodia crassispora</i>	CBS 110492	unknown	unknown	EU673189	EF622086	EU673251	n/a
<i>Lasiodiplodia gonubiensis</i>	CBS 115812	<i>Syzygium cordatum</i>	South Africa	EU673193	DQ458892	DQ377902	n/a
<i>Lasiodiplodia parva</i>	CBS 356.59	<i>Theobroma cacao</i>	Sri Lanka	EU673200	EF622082	EU673257	n/a
<i>Lasiodiplodia pseudotheobromae</i>	CBS 116459	<i>Gmelina arborea</i>	Costa Rica	EU673199	EF622077	EU673256	n/a
<i>Lasiodiplodia rubropurpurea</i>	CBS 118740	<i>Eucalyptus grandis</i>	Australia	EU673191	DQ103553	DQ377903	n/a
<i>Lasiodiplodia theobromae</i>	CAA 006	<i>Vitis vinifera</i>	USA	EU673197	DQ458891	EU673254	n/a
<i>Lasiodiplodia venezuelensis</i>	CBS 118739	<i>Acacia mangium</i>	Venezuela	EU673192	DQ103547	DQ377904	n/a
<i>Macrophomina phaseolina</i>	AFTOL 1783, CBS 227.33	<i>Zea mays</i>	unknown	DQ678037	n/a	DQ377906	n/a
<i>Melanops</i> sp.	CBS 118.39	<i>Quercus borealis</i>	USA	FJ824763	FJ824771	DQ377856	n/a
<i>Melanops tulasnei</i>	CBS 116805	<i>Quercus robur</i>	Germany	FJ824761	FJ824769	FJ824764	n/a
<i>Neodeightonia phoenicum</i>	CBS 122528	<i>Phoenix dactylifera</i>	Spain	EU673205	EU673340	EU673261	n/a
<i>Neodeightonia subglobosa</i>	CBS 448.91	keratomycosis in human eye	United Kingdom	EU673202	EU673337	DQ377866	n/a
<i>Neofusicoccum luteum</i>	CBS 110299	<i>Vitis vinifera</i>	Portugal	EU673148	AY259091	AY928043	n/a
<i>Neofusicoccum mangiferae</i>	CBS 118531	<i>Mangifera indica</i>	Australia	EU673153	AY615185	DQ377920	n/a
<i>Neofusicoccum parvum</i>	CBS 110301	<i>Vitis vinifera</i>	Portugal	EU673150	AY259098	AY928046	n/a
<i>Phaeobotryon mamane</i>	CPC 12264	<i>Sophora chrysophylla</i>	USA (Hawaii)	EU673183	EU673331	DQ377898	n/a
<i>Phaeobotryosphaeria citrina</i>	ICMP 16812	<i>Citrus sinensis</i>	New Zealand	EU673180	EU673328	EU673246	n/a
<i>Phaeobotryosphaeria porosa</i>	CBS 110496	<i>Vitis vinifera</i>	South Africa	EU673179	AY343379	DQ377894	n/a
<i>Phaeobotryosphaeria visci</i>	CBS 100163	<i>Viscum album</i>	Luxembourg	EU673177	EU673324	DQ377870	n/a
<i>Pseudofusicoccum stromaticum</i>	CBS 117448	<i>Eucalyptus</i> sp.	Venezuela	EU673146	AY693974	DQ377931	n/a
<i>Saccharata proteae</i>	CBS 115206	<i>Protea</i> sp.	Australia	GU296194	n/a	GU301869	n/a
<i>Spencermartinsia viticola</i>	CBS 117006	<i>Vitis vinifera</i>	Spain	EU673166	AY905555	EU673236	n/a

¹ AFTOL: Assembling the Fungal Tree of Life; AR: Culture collection of Amy Rossman, housed at U.S. National Fungus Collections (BPI), Beltsville, MD, USA; ATCC: American Type Culture Collection, Manassas, VA, USA; CBS: CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; CAA: Artur Alves, Universidade de Aveiro, Aveiro, Portugal; ICMP: International Collection of Microorganisms from Plants, Auckland, New Zealand; JB: Joseph Bischoff, cultures housed at BPI; MEP: Mary E. Palm, cultures housed at BPI.

² SSU: partial 18S rRNA gene; LSU: partial 28S rRNA gene; ITS: internal transcribed spacer regions 1 & 2 including 5.8S rRNA gene; RPB1: partial RNA Polymerase II subunit 1 gene.

suggested placement in *Piptarthon* while the presence of unilocular conidiomata supported placement in *Kellermania*. Ramaley (1993) circumscribed *Planstromella*, the sexual state of *Kellermania*, and noted that it was similar to *Planstroma* but distinct in having septate ascospores. The genus originally included two new species that were correlated with one new and one existing species of *Kellermania* (Ramaley 1993). She did not embrace synonymising the asexual and sexual states into a broadly defined *Planstroma* with *Kellermania* anamorphs. Ramaley (1995) added five new species based on both asexual and sexual states and provided a key to the species of *Kellermania* and *Piptarthon*. Most notably among the new species was *Planstromella torsifolium*, the first sexual state having *Alpakesa*-type conidia, which provided further support for the

synonymy of *Alpakesa* and *Kellermania* (Ramaley 1995). Lastly, Ramaley (1998) named two more teleomorphic species connected with known species of *Kellermania* and illustrated another undescribed species with both *Piptarthon* and *Planstroma* states. *Planstroma kellermaniae*, which has aseptate ascospores, was connected to the anamorphic *Kellermania nolinae*, a species with *Alpakesa*-type conidia, providing further confusion in regard to generic boundaries and Ramaley (1998) suggested that a re-evaluation was necessary.

Barr (1996) observed that several genera in the *Dothideales* were not classified easily into any family, and she established the family *Planstromellaceae* to accommodate "taxa having ascostromata, interthelial tissues, and schizogenously formed, periphysate ostioles". *Planstromella* and *Planstroma* were in-

cluded and three species were transferred to the former genus along with circumstantial links to anamorphs for two species (Barr 1996). The genera *Loratospora*, *Eruptio*, *Microcyclus*, and *Mycosphaerellopsis* were also classified in *Planstromellaceae*.

Due to the availability of a number of Ramaley's cultures that represent nearly all of the known species of *Alpakesa*, *Kellermania*, and *Piptarthron* and additional cultures obtained from plant disease interceptions at U.S. ports of entry, a systematic study was made to address the following questions: 1) What are the phylogenetic relationships between members of the *Planstromellaceae* and the *Dothideomycetes*?; 2) are the *Planstromellaceae* and its genera monophyletic?; 3) does morphology of conidial appendages or ascospore septation correlate with phylogeny?; and 4) are slight morphological differences among otherwise similar isolates, which are often obtained from different hosts, indications of distinct phylogenetic species? To answer these questions, nuclear protein-coding DNA and nuclear ribosomal DNA sequence data were generated for several loci and analysed phylogenetically. Additionally, detailed studies were made of these species in culture, including micromorphological characters. Herbarium specimens were examined whenever possible and/or necessary.

MATERIALS AND METHODS

Morphology and herbarium material

Dried herbarium material was rehydrated and viewed in 3 % KOH (Largent et al. 1977), and microscopic observations of cultures were made of material mounted in 3 % KOH or buffered Shear's mounting fluid (Graham 1959). Length to width ratios are given as Q. Mean values for length, width and Q are indicated by L^m, W^m, and Q^m, respectively, based on n = 30. Herbarium acronyms follow Thiers (2012). See Farr & Rossman (2012) for additional information about collections housed at the U.S. National Fungus Collections (BPI). New specimens were deposited at BPI. The Ramaley collections from which many of the cultures utilized in this study were obtained, if extant, are missing.

Cultures

Isolates were grown in plastic Petri plates on Difco potato-dextrose agar (PDA), which was prepared according to the manufacturers' instructions. Growth conditions were 24 °C with a 12 h light/dark regimen. Cultures were measured and photographed after 2 wk. Notes on colour and general appearance were made after 2–3 wk. Terminology for colour includes general terms as well as standard terminology with the sample reference code in parentheses from Kornerup & Wanscher (1967). Cultures that had not sporulated after 3 wk were continuously incubated under the same conditions for up to several months and periodically re-examined. Reference cultures were deposited at the Centraalbureau voor Schimmelcultures (CBS-KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; Table 1).

DNA extraction, PCR amplification, and sequencing

DNA was extracted from fresh mycelium using Qiagen's DNeasy Plant Mini Kit (Germantown, MD). Ribosomal DNA from the nuclear small subunit (SSU), the internal transcribed spacer region (ITS; ITS1, 5.8S, ITS2), and the nuclear large subunit (LSU) were PCR amplified using the primer pairs NS1 and NS4 (White et al. 1990), ITS5 and ITS4 (White et al. 1990), LROR (Moncalvo et al. 2000) and LR7 or LR5 (Vilgalys & Hester 1990), respectively. Additionally, a portion of the largest subunit of the RNA polymerase II (RPB1) was amplified using the primer pair RPB1-Ac and RPB1-Cr (Matheny et al. 2002). Each region was amplified using GoTaq (Promega, Madison,

WI) and associated standard reagents following the manufacturer's recommendations including 2.0 mM MgCl₂ and 1.5 µM of each primer. Thermal cycling conditions for RPB1 and LSU were according to Malkus et al. (2006) and Reeb et al. (2004), respectively. Thermal cycling conditions for the SSU and ITS were: 95 °C for 60 s; 35 cycles at 95 °C for 15 s, 50 °C (55 °C for ITS) for 20 s, and 72 °C for 60 s; and 72 °C for 180 s. Cycle sequencing and fluorescent labelling was conducted with the same corresponding PCR primers that were used for each locus and the BigDye Terminator v. 3.1 Cycle Sequencing kit (Applied Biosystems, Foster City, CA). The purified products were then sequenced on an ABI 3730 automated DNA sequencer. Geneious Pro v. 5 (Drummond et al. 2010) was used to edit electropherograms and to build consensus sequences that were submitted to GenBank (<http://www.ncbi.nlm.nih.gov>; Table 1).

Data matrix and phylogenetic analysis

For the purpose of determining the phylogenetic position of *Planstromellaceae* among the *Dothideomycetes*, sequences of the SSU and LSU from the type species of *Kellermania*, *Piptarthron*, *Planistroma*, and *Planstromella* were manually incorporated into the alignment of Schoch et al. (2009) using the program Geneious Pro v. 5 (Drummond et al. 2010; i.e., *Dothideomycetes* alignment). Identical sequences were removed from this alignment. A Maximum Likelihood (ML) analysis was conducted in RAxML v. 7.3.0 (Stamatakis 2006) using the 'RAxML-HPC2 on XSEDE' tool via the CIPRES Science Gateway (Miller et al. 2010), selecting the GTRGAMMA nucleotide substitution model and *Opegrapha dolomitica* and *Schismatomma decolorans* as outgroups (Schoch et al. 2009). A separate rapid bootstrap (bs) analysis of 1 000 iterations was conducted with identical settings.

Multiple-sequence alignments were conducted for each of the datasets from the *Planstromellaceae* in Geneious Pro v. 5 (Drummond et al. 2010) using MUSCLE v. 3.6 (Edgar 2004), adjusted manually, and then concatenated (i.e., *Kellermania* alignment). Congruence among these four data partitions (SSU, ITS, LSU, RPB1) was evaluated by comparing their topologies in search of well-supported clades (posterior probability > 0.85) with conflicting compositions, and separately with the Incongruence Length Difference test (ILD; Farris et al. 1994). The individual topologies were constructed with Bayesian inference (BI) in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) where best-fitting models for each dataset were determined in MrModeltest v. 2.2 (Nylander 2004) by the Akaike Information Criterion (AIC; Posada & Buckley 2004). All other parameters were left as default. The posterior probability (pp) distribution of trees was estimated from those collected until the standard deviation of split frequencies reached less than 0.01 (1 million generations) minus the burn-in (10 %), which was determined in the program Tracer v. 1.5 (Rambaut & Drummond 2007). The ILD test was implemented in PAUP v. 4.0 b10 (Swofford 2003) as the Partition Homogeneity Test with 1 000 homogeneity replicates. Each replicate searched tree space with 100 random addition sequences (RAS) saving 10 trees per RAS while ignoring uninformative characters.

The monophyly of core *Planstromellaceae* was tested by conducting a phylogenetic analysis of a matrix comprised of SSU, ITS, and LSU from a wide range of *Botryosphaeriaceae* selected from the analyses of Crous et al. (2006), Phillips & Alves (2009), and Schoch et al. (2009); plus type species of genera of *Kellermania*, *Piptarthron*, *Planistroma*, and *Planstromella* as well as at least one representative of each major clade of core *Planstromellaceae*; and *Helicomyces roseus* (CBS 283.51) as outgroup (i.e., *Botryosphaeriaceae* alignment). This matrix was aligned with MUSCLE v. 3.6 (Edgar 2004) and analysed with BI, as described above.

Table 2 A summary of matrix partition statistics (ingroup only) for each alignment which was analyzed phylogenetically in the present study. N = the number of taxonomic units in the alignment, Length = the number of nucleotide characters in the alignment, No. V.C. = the number of variable characters, No. I.C. = the number of phylogenetically informative characters, DNA model = the model of nucleotide substitution used in an analysis for the corresponding partition.

Dothideomycetes alignment					Botryosphaeriaceae alignment					Kellermania alignment				
N	Length	No. V.C.	No. I.C.	DNA Model	N	Length	No. V.C.	No. I.C.	DNA Model	N	Length	No. V.C.	No. I.C.	DNA Model
SSU	283	1027	473 (46%)	295 (29%) N.A.	44	1133	94 (8%)	42 (4%)	GTR+I+G	10	1025	9 (1%)	5 (0.5%)	HKY+I
ITS	N.A.	N.A.	N.A.	N.A.	42	377	130 (34%)	92 (24%)	SYM+I+G	15	351	45 (13%)	27 (8%)	K80+I+G
LSU	327	1853	689 (37%)	542 (29%) N.A.	45	584	134 (23%)	82 (14%)	GTR+I+G	15	883	29 (3%)	18 (2%)	GTR+I+G
RPB1	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	N.A.	15	795	221 (28%)	160 (20%)	GTR+G
Combined	342	2880	1162 (40%)	837 (29%) GTRGAMMA	45	2091	302 (14%)	208 (10%)	Mixed	15	3054	304 (10%)	210 (7%)	Mixed

The major clades of the core *Planistromellaceae* were identified from the results of a mixed-model BI analysis of the *Kellermania* alignment plus *Helicomyces roseus* (CBS 283.51) in MrBayes v. 3.1.2 using the methods outlined above. This phylogeny was also used to i) test the monophyly of generic concepts in *Planistromellaceae*; ii) determine relationships among its species including novel taxa; and iii) evaluate the evolution of key morphological characters and host relationships. All alignments and resulting trees were deposited into TreeBASE (S13234), and nomenclatural novelties in MycoBank (Crous et al. 2004).

RESULTS

Data matrix and phylogenetic analyses

Sequencing was successful for all core *Planistromellaceae* taxa with living cultures except for the SSU of *Kellermania*

confusa AR 3469, *K. dasylirionis* AR 3464, *K. plurilocularis* AR 3467, *K. ramaleyae* MEP 1260, and *K. rostratae* JB 5.16.11-01, which were treated as missing data in all alignments. The *Dothideomycetes* alignment contained 342 ingroup taxa with a total length of 2 880 characters, 837 (29 %) of which were phylogenetically informative (Table 2). The *Botryosphaeriaceae* alignment included 45 ingroup taxa (Table 1) with a total length of 2 091 characters, 208 (10 %) of which were phylogenetically informative (Table 2). The *Kellermania* alignment contained 15 ingroup taxa with a total length of 3 054 characters, 210 (7 %) of which were phylogenetically informative (Table 2).

Phylogenetic relationships of the *Planistromellaceae*

Maximum Likelihood analysis of *Dothideomycetes* revealed high support (bs = 91 %) for a clade comprised strictly of *Botryosphaeriaceae* that was congruent with Schoch et al. (2009) with

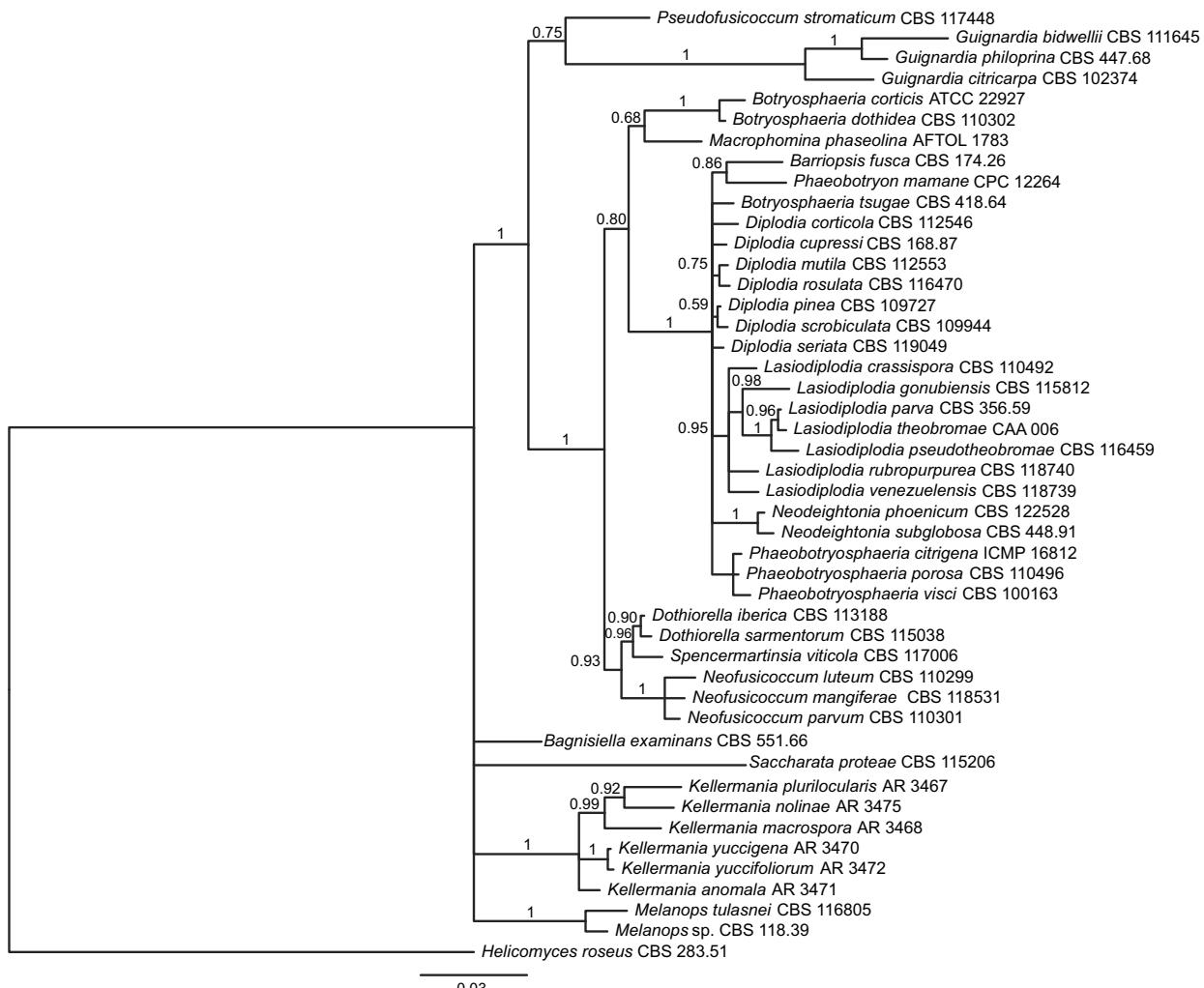


Fig. 1 Bayesian inference 50 % majority-rule phylogram of the *Botryosphaeriaceae* alignment based on analysis of the combined SSU, ITS, and LSU data. This tree reveals a monophyletic *Kellermania* (core *Planistromellaceae*) in an unresolved position among four other major ingroup lineages of *Botryosphaerales*.

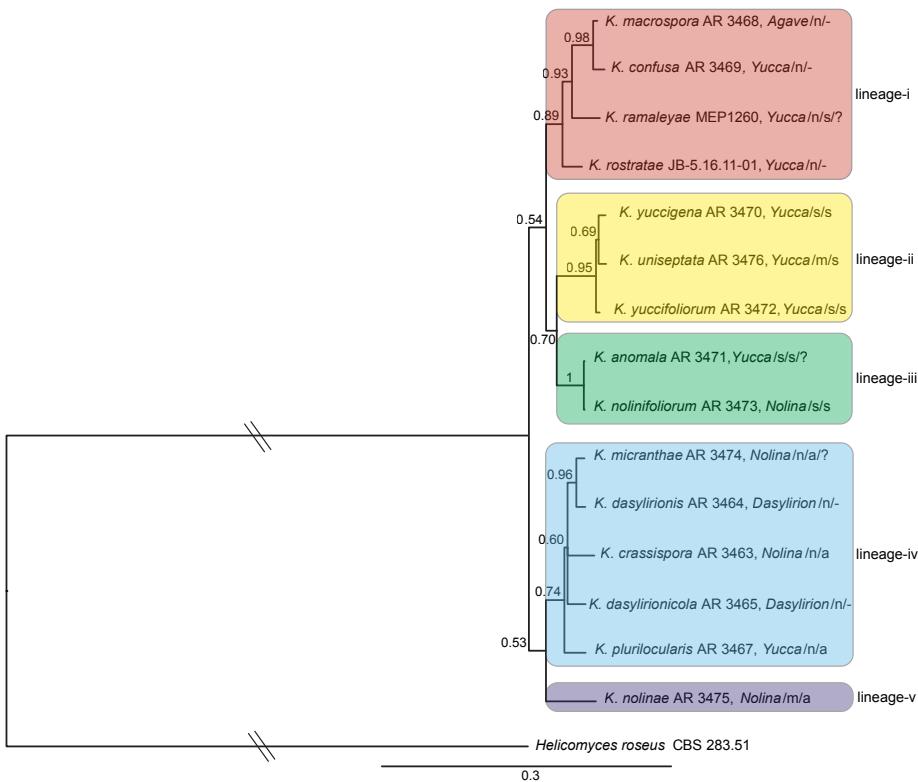


Fig. 2 Bayesian inference 50 % majority-rule phylogram of *Kellermania* (core Planstromellaceae) based on analysis of the combined SSU, ITS, LSU, and RPB1 alignment. Hatch marks indicate that the branch length was shortened by 50 % for presentation purposes. This tree reveals five lineages, i–v. Host genus, numbers of conidial appendages, and ascospore septation are given next to taxon names in that order. For conidial appendages, n = none, s = single, m = multiple. For ascospore septation, a = aseptate, s = septate, - = unknown. A question mark indicates uncertainty in the link of asexual and sexual states.

the exception of a well-supported clade (bs = 99 %) containing the type species of the genera *Kellermania*, *Piptarthron*, *Planistroma*, and *Planstromella* of Planstromellaceae (phylogram not shown). Bayesian inference of the *Botryosphaeriaceae* alignment suggested that Planstromellaceae is one of five monophyletic members of *Botryosphaeriaceae* s.l. (see Discussion): i) *Bagnisella examinans*; ii) *Saccharata proteae*; iii) *Melanops* (pp = 1.0); iv) Planstromellaceae (pp = 1.0); and v) the remaining members of the family including the core members of *Botryosphaeriaceae* (pp = 1.0; Fig. 1).

Phylogenetic diversity and relationships within *Kellermania*

Inspection of the individual phylogenies resulting from BI analyses of SSU, ITS, LSU, and RPB1 revealed a single well-supported incongruence. This incongruence was between the SSU and RPB1 trees where *Kellermania macrospora* AR 3468 was sister with a clade containing *K. crassispora* AR 3463, *K. dasylirionicola* AR 3465, *K. micranthae* AR 3474, and *K. nolinae* AR 3475 in the SSU analysis (pp = 0.94); whereas *K. macrospora* was part of a polytomy (pp = 1.0) in the RPB1 analysis containing two other clades, one comprised of *K. uniseptata* AR 3476, *K. yuccifoliorum* AR 3472, and *K. yuccigena* AR 3470, and another containing *K. anomala* AR 3471 and *K. nolinifoliorum* AR 3473. Results of the ILD test (Farris et al. 1994) suggested that the SSU, ITS, LSU, and RPB1 data from Planstromellaceae were congruent ($P = 0.230$) and thus suitable for combined analysis.

Our BI analysis of the *Kellermania* alignment resulted in a consensus phylogram (Fig. 2) comprised of five major lineages: i) *Kellermania macrospora* AR 3468, *K. confusa* AR 3469, *K. ramaleya* AR 3460, and *K. rostratae* AR 3461 (pp = 0.89); ii) *K. yuccigena* AR 3470, *K. uniseptata* AR 3476, and *K. yuccifoliorum* AR 3472 (pp = 0.95); iii) *K. anomala* AR

3471, *K. nolinifoliorum* AR 3473 (pp = 1.0); iv) *K. micranthae* AR 3474, *K. dasylirionis* AR 3464, *K. crassispora* AR 3463, *K. dasylirionicola* AR 3465, and *K. plurilocularis* AR 3467 (pp = 0.74); and v) *K. nolinae* AR 3475 (Fig. 2). Lineage v, which is based upon a single isolate, is herein labelled as distinct because its position among the other lineages is unresolved and varied in different analyses. The relationships among these five lineages are not well resolved though some major groupings are weakly supported and a sister relationship of lineages ii–iii receives some support (pp = 0.70). Members of lineages i–iii were all isolated from either *Agave* or *Yucca* (Asparagaceae, subfamily Agavoideae), with the exception of *K. nolinifoliorum* AR 3473 on *Nolina* (Asparagaceae, subfamily Nolinoideae). Members of lineages iv–v were isolated from members of *Nolina* or *Dasyliorion* (subfamily Nolinoideae) with the exception of *K. plurilocularis* AR 3467 on *Yucca* (Fig. 2). Lineages i–iii possess septate ascospores and lineages iv–v possess aseptate ascospores, but see *K. unilocularis* below and in Fig. 3. Lineage i possesses conidia without conidial appendages, lineage ii possesses conidia with single or multiple appendages, lineage iii possesses conidia with single appendages, lineage iv possesses conidia without appendages, and lineage v possesses conidia with multiple appendages.

Colony characteristics and micromorphology of *Kellermania*

Colony colour typically ranged from greenish to greyish tones, but *K. crassispora* uniquely remained pink. Differences were observed in growth rates, but in general slight differences in growth rates and overall colony appearances were observed from subculture to subculture. Thus, tendencies toward slower vs faster growth rates are more useful than exact measurements. Conidiomata were produced in culture by all species except *K. crassispora*. They are characterised as: superficial or immersed,

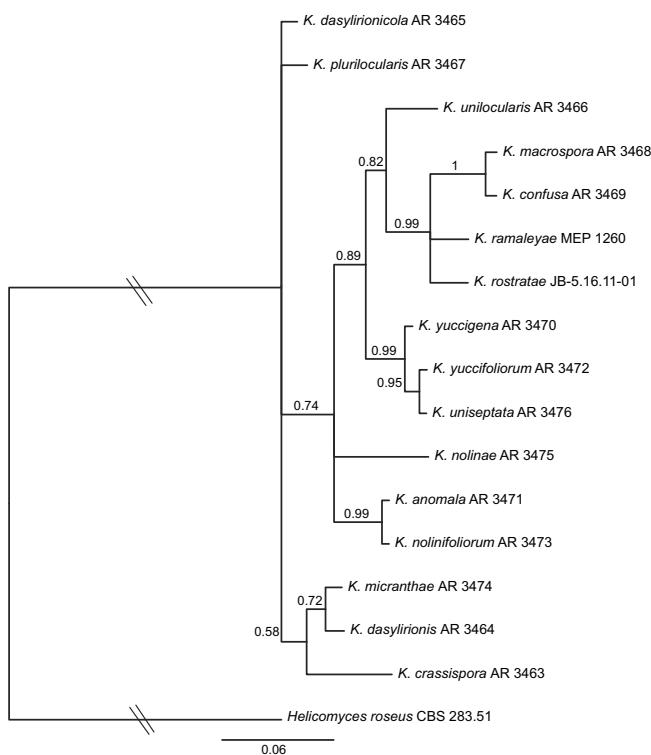


Fig. 3 Bayesian inference 50 % majority-rule phylogram of *Kellermania* based on analysis of the ITS, including *K. unilocularis*. Hatch marks indicate that the branch was shortened by 50 % for presentation purposes.

scattered to densely gregarious, at times confluent becoming fused, discrete or associated with stromatal growths including irregularly column-like and rarely mat-like structures, frequently more or less round in shape, with or without necks, black, at times covered with whitish, greenish, or green grey hyphae. Conidiogenous cells lining the inner conidiomatal walls were holoblastic, determinate, discrete or integrated on short single-celled conidiophores, doliform to cylindrical, hyaline, and smooth. Conidia were variable in size and shape, aseptate, single to multiseptate, and bear 0–multiple apical appendages. A less useful character included the presence of a frill at the base of conidia. Conidia, which developed within weeks or sometimes only after months, were exuded from conidiomata in whitish, mucilaginous masses. Conidia often germinate quickly and, in some several month old cultures, nearly all conidia in the mucilaginous masses had either germinated or desiccated. In the descriptions of cultures, colony appearance, growth rate, and conidia are the most valuable characters for distinguishing species.

TAXONOMY

Planistromellaceae M.E. Barr, Mycotaxon 60: 433. 1996.

Type genus. *Planistromella* A.W. Ramaley.

Kellermania Ellis & Everh., J. Mycol. 1: 153. 1885.

Type species. *Kellermania yuccigena* Ellis & Everh.

= *Piptarthron* Mont. ex Höhn., Hedwigia: 60: 203. 1918.

Type species. *Piptarthron macrosporum* (Durieu & Mont.) Höhn.

= *Alpakesa* Subram. & K. Ramakr., J. Indian Bot. Soc. 33: 204. 1954.

Type species. *Alpakesa yuccifolia* (J.G. Hall) Subram. & K. Ramakr. as 'yuccaeifolia'.

?= *Septoplaca* Petr., Sydowia 17: 271. 1964 '1963'.

Type species. *Septoplaca limbata* Petr.

= *Planistroma* A.W. Ramaley, Mycotaxon 42: 69. 1991.

Type species. *Planistroma yuccigenum* A.W. Ramaley as 'yuccigena'.

= *Planistromella* A.W. Ramaley, Mycotaxon 47: 260. 1993.

Type species. *Planistromella yuccifoliorum* A.W. Ramaley.

Kellermania anomala (Cooke) Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 124: 84. 1915. — Fig. 4, 5

Basionym. *Discella anomala* Cooke, Grevillea 7: 11. 1878.

≡ *Discula anomala* (Cooke) Sacc., Syll. Fung. 3: 677. 1884.

?= *Wettsteinina yuccigena* M.E. Barr, Contr. Univ. Michigan Herb. 9: 547. 1972 as 'yuccaeigena'.

≡ *Planistromella yuccigena* (M.E. Barr) M.E. Barr, Mycotaxon 60: 434. 1996.

Culture characteristics — Colonies on PDA 43–44 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near dull green (30E4), covered with low, cobwebby to velutinous, greenish hyphae; margin uneven, whitish; reverse black with margin uncoloured. Conidia 40–69 × 5–8 µm, Q = 5–14.3 ($L^m = 52.3 \mu\text{m}$, $W^m = 7.3 \mu\text{m}$, $Q^m = 7.4$), cylindrical to fusiform, apices tapering to a relatively acute point, tapering towards and typically truncate at bases that may bear an indistinct frill, 1–2(–3)-septate; walls smooth, thin and hyaline, and not significantly constricted at septa; contents hyaline; appendages absent or present, at times scarcely visible, up to 11 µm long, apical, single, appearing as a short, filiform, hyaline mucro.

Habitat & Distribution — Dead leaves of *Yucca* spp. (Morgan-Jones et al. 1972b, Nag Raj 1993, Farr & Rossman 2012). The type was found on *Y. draconis* (Cooke 1878), probably correctly named *Y. brevifolia*. This fungal species is widely distributed in the western half of the USA (Morgan-Jones et al. 1972b, Farr & Rossman 2012).

Specimen examined. USA, Arizona, Mohave Co., 0.3 miles from Gem Acres Rd., exit mile 20 from U.S. Hwy. 40, on dead leaves of *Yucca brevifolia*, 3 June 1992, coll. A.W. Ramaley, AR 3471 (CBS 132218) isolated by A.W. Ramaley from AWR 9228 (9229 on tube), dried culture on PDA (BPI 882814).

Notes — Ramaley (1993) noted that the appendage may be hard to observe or absent and that the middle cell in conidia with two septa is regularly shorter. We observed that the appendage (when present in culture) was shorter than in previous reports from material in nature (Morgan-Jones et al. 1972b, Nag Raj 1993). Shoemaker & Babcock (1987) redescribed *P. yuccigena* on *Yucca glauca*. Barr (1996) provisionally linked *Planistromella yuccigena* to *K. anomala* based on the circumstantial occurrence of both on the same leaves. This link is indirectly supported by the morphological similarity of the sexual state to that of *K. nolinifoliorum*, a sister species.

Kellermania confusa Minnis & A.H. Kenn., sp. nov. — MycoBank MB801095; Fig. 4, 5

Etymology. The name refers to confusion in regard to the identity of this fungus.

Culture characteristics — Colonies on PDA 35–40 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near pale grey (30B1), covered with low, white cobwebby to velutinous hyphae; margin uneven, whitish; reverse grey with black conidiomata visible. Conidia 38.5–64 × 6.5–9.5 µm, Q = 4.8–8 ($L^m = 49.9 \mu\text{m}$, $W^m = 8.3 \mu\text{m}$, $Q^m = 6.0$), obclavate, at times curved, apices tapering towards and slightly acute, typically truncate at bases, (1–)2(–3)-septate; walls smooth, thin, hyaline, and not constricted at septa; contents hyaline; appendages absent.

Habitat & Distribution — Dead leaves of *Yucca thornberi*. It is known only from the type locality in the USA: AZ.

Specimen examined. USA, Arizona, Santa Cruz Co., Interstate 10, mile 283.6, north side of road, on dead leaves of *Yucca thornberi*, 13 Apr. 1992, coll. A.W. Ramaley, AR 3469 (CBS 131723) isolated by A.W. Ramaley from AWR 9212, dried culture on PDA (holotype, BPI 882824).

Notes — This species is distinguished from the others that occur on *Yucca* by its (1–)2(–3)-septate conidia that lack ap-

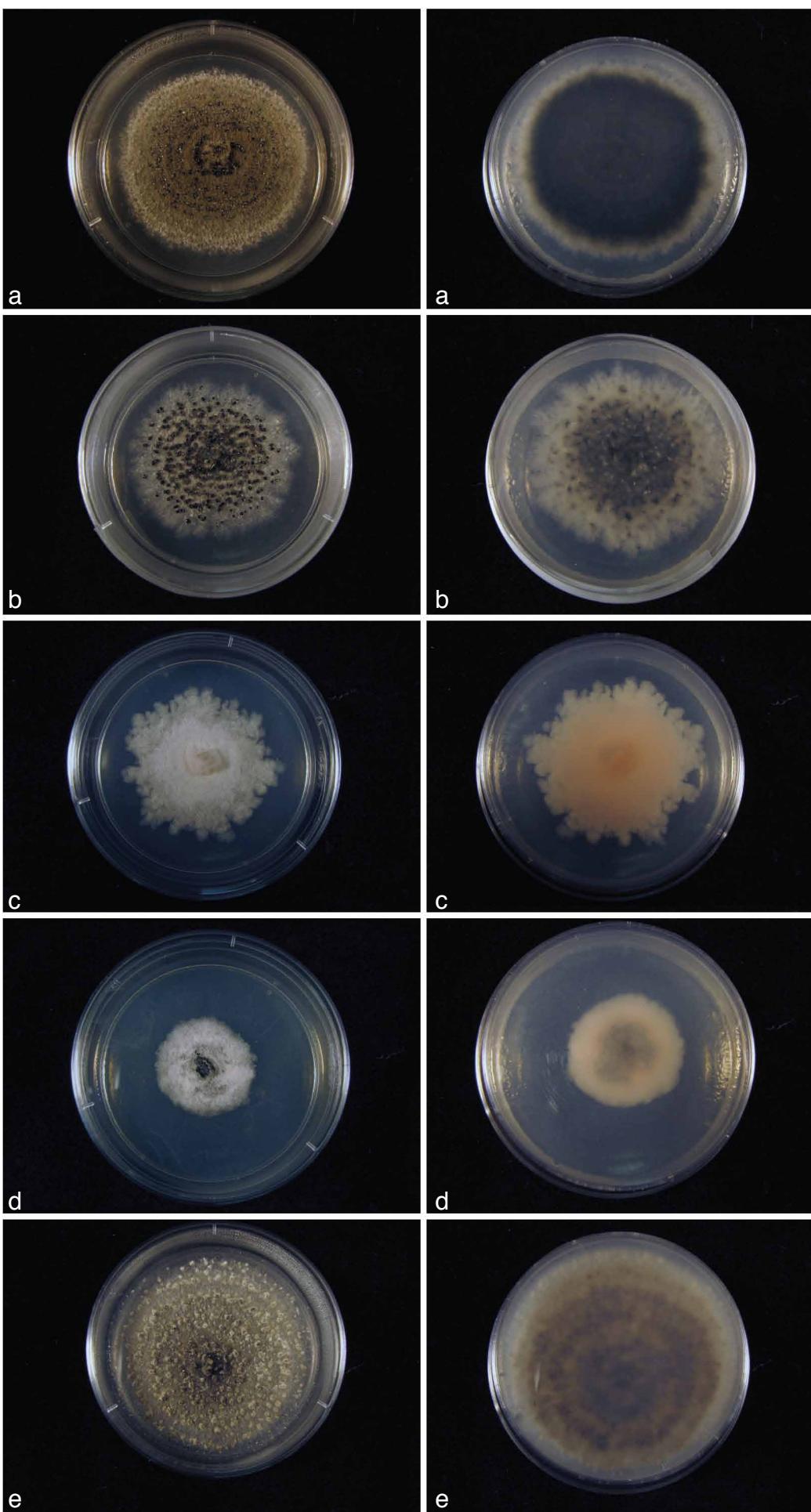


Fig. 4 Cultures of *Kellermania* species. a–e. Cultures (surface and reverse) on PDA at 2 wk after incubation at 24 °C with a 12 h light/dark regime; a. *K. anomala* (AR 3471); b. *K. confusa* (AR 3469); c. *K. crassispora* (AR 3463); d. *K. dasylirionicola* (AR 3465); e. *K. dasylirionis* (AR 3464).

pendages. Ramaley (in litt.) noted that two isolates identified as *Piptarthron macrosporum*, this one from *Yucca* and another from *Agave*, had consistent differences in conidial morphology. Morphological and DNA sequence data support the separation of this species from *Kellermania macrospora* on *Agave*.

***Kellermania crassispora* (A.W. Ramaley) Minnis & A.H. Kenn., comb. nov.** — MycoBank MB801096; Fig. 4

Basionym. *Piptarthron crassisporum* A.W. Ramaley, Mycotaxon 55: 261. 1995.

= *Planistroma nolinae* A.W. Ramaley, Mycotaxon 55: 258. 1995.

Culture characteristics — Colonies on PDA 30–36 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near pinkish white (10A2) to cotton candy-pink, covered with low, velutinous hyphae; margin uneven, whitish to pale pink; reverse near pale red (7A3). No conidiomata observed. No conidia observed.

Habitat & Distribution — Dead leaves of *Nolina micrantha*, *Nolina* sp. (Ramaley 1995, this study). It is known from the USA: NM, TX (Ramaley 1995, this study).

Specimen examined. USA, Texas, Culberson Co., Guadalupe Mtns. National Park, 5.6 miles from highway along Williams Ranch Rd., on dead leaves of *Nolina micrantha*, 23 Oct. 1995, coll. A.W. Ramaley, AR 3463 (CBS 131714) isolated by A.W. Ramaley from AWR 9536, dried culture on PDA (BPI 882815).

Notes — The culture that we studied did not sporulate though Ramaley (1995) observed conidia in culture. Ramaley (1995) stated that conidia on the host were 56.8–78.4 × 12.8–14.4 µm, cylindrical with rounded apices, aseptate, and without appendages. The link between the asexual and sexual states is based on cultural similarities that were noted previously (Ramaley 1995).



Fig. 5 a. Conidia of *Kellermania anomala* from culture (AR 3471); b. conidia of *K. confusa* from culture (AR 3469); c. conidia of *K. dasylirionicola* from culture (AR 3465); d. conidia of *K. dasylirionis* from culture (AR 3464); e. conidia of *K. macrospora* from culture (AR 3468); f. conidia of *K. micranthae* from culture (AR 3474); g. conidia of *K. nolinae* from culture (AR 3475); h. conidia of *K. nolinifoliorum* from culture (AR 3473); i. conidia of *K. plurilocularis* from culture (AR 3467). — Scale bars = 30 µm for all.

***Kellermania dasylirionicola* Minnis & A.H. Kenn., sp. nov. —**
MycoBank MB801097; Fig. 4, 5

Etymology. This species is named for its occurrence on *Dasylirion leiophyllum*.

Culture characteristics — Colonies on PDA 22–25 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface whitish to near pinkish white (10A2), covered with low, tomentose to velutinous hyphae; margin uneven, whitish; reverse near orange white (5A2). **Conidia** 32–45 × 3–5 µm, Q = 6.7–12.5 ($L^m = 39.4 \mu\text{m}$, $W^m = 4.5 \mu\text{m}$, $Q^m = 9.0$), more or less cylindrical with irregularly curved shape, flexuous, apices tapering to a somewhat acute point, typically truncate at bases, aseptate; walls smooth, thin, and hyaline; contents hyaline; appendages absent.

Habitat & Distribution — Dead leaves of *Dasylirion leiophyllum*. It is known only from the type locality in the USA: TX.

Specimen examined. USA, Texas, Pecos Co., 1.2 miles north of T 2400 on U.S. Hwy. 285, roadside plant, on dead leaves of *Dasylirion leiophyllum*, 7 May 1994, coll. A.W. Ramaley, AR 3465 (CBS 131720) isolated by A.W. Ramaley from AWR 9413, dried culture on PDA (holotype, BPI 882821).

Notes — Although similar to *Kellermania dasylirionis*, this second species on *Dasylirion* is distinguished by its aseptate conidia with irregular, curved shapes and slower growth on PDA. Ramaley (in litt.) noted aseptate, curly conidia in material from the host in nature and speculated that the collection may represent an undescribed species. DNA sequence data and associated analyses confirm this as a new species.

***Kellermania dasylirionis* (A.W. Ramaley) Minnis & A.H. Kenn., comb. nov. —** MycoBank MB801098; Fig. 4, 5

Basionym. *Piptarthron dasylirionis* A.W. Ramaley, Mycotaxon 55: 263. 1995.

Culture characteristics — Colonies on PDA 45–52 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near greenish grey (30C2), covered with low, velutinous hyphae that often covers conidiomata; margin uneven, whitish; reverse near brownish grey (7E2) to greyish orange (5B3). **Conidia** 45–64 × 5–9.5 µm, Q = 6.3–12.3 ($L^m = 57.1 \mu\text{m}$, $W^m = 7.2 \mu\text{m}$, $Q^m = 8.1$), cylindrical to narrowly fusiform with some degree of curvature, apices tapering to a relatively acute point, tapering towards and typically truncate at bases, 0–1-septate, septa approx. median when present; walls smooth, thin, hyaline, and not constricted at septa; contents hyaline, at times granular; appendages absent.

Habitat & Distribution — Dead leaves of *Dasylirion leiophyllum*, *D. wheeleri*, *Dasylirion* sp. (Ramaley 1995, this study). This species is known from Mexico and the USA: AZ, TX (Ramaley 1995, this study).

Specimen examined. USA, Texas, Brewster Co., Big Bend National Park, Sotol Vista, on dead leaves of *Dasylirion leiophyllum*, 25 Oct. 1994, coll. A.W. Ramaley, AR 3464 (CBS 131715) isolated by A.W. Ramaley from AWR 9441, dried culture on PDA (BPI 882816).

Notes — Ramaley (1995) noted that conidia in culture were shorter and narrower than those on the host in nature.

***Kellermania macrospora* (Durieu & Mont.) Minnis & A.H. Kenn., comb. nov. —** MycoBank MB801099; Fig. 5, 6

Basionym. *Septoria macrospora* Durieu & Mont., Expl. Sci. Algerie 1: 589. 1849.

≡ *Hendersonia montagnei* Cooke, Nuovo Giorn. Bot. Ital. 10: 19. 1878. Note: This nom. nov. was established since the epithet 'macrospora' was occupied by *H. macrospora* Berk. & Broome 1850.

≡ *Hendersonia piptarthra* Sacc., Michelia 2: 111. 1880. Note: This nom. nov. was established since the epithet 'macrospora' is occupied by *H. macrospora* Berk. & Broome 1850. It is a nom. illeg. via superfluous, ICBN Art. 52

(McNeill et al. 2006), since *H. montagnei* was already published as a replacement name.

≡ *Stagonospora macrospora* (Durieu & Mont.) Sacc., Syll. Fung. 3: 450. 1883.

≡ *Piptarthron macrosporum* (Durieu & Mont.) Höhn., Hedwigia 60: 203. 1918.

Culture characteristics — Colonies on PDA 52 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near light grey (30C1), with scattered low, hyphae between conidiomata; margin uneven, whitish; reverse uncoloured, black, to near greyish brown (6D3). **Conidia** 54.5–93 × 6.5–11 µm, Q = 4.9–13 ($L^m = 72.2 \mu\text{m}$, $W^m = 9.0 \mu\text{m}$, $Q^m = 8.3$), cylindrical to obclavate, at times slightly curved, apices tapering towards and obtuse to slightly acute, typically truncate at bases that frequently bear a marginal frill, 3–5(–7)-septate; walls smooth, thin, hyaline, and not constricted at septa; contents hyaline; appendages absent.

Habitat & Distribution — Dead leaves of *Agave americana*, *Agave* sp. (Sutton 1980, Farr & Rossman 2012). Based on scattered reports, this species is known from Africa (Algeria), Europe, and North America (USA) (Höhn 1918a, Sutton 1980, Farr & Rossman 2012). This species has also been reported from species of *Yucca* from various locations (Sutton 1980, Farr & Rossman 2012), but we have found no specimens on *Yucca*.

Specimen examined. USA, Arizona, Cochise Co., north side of road, I 10 mile 322.5, on dead leaves of *Agave* sp., 13 Apr. 1992, coll. A.W. Ramaley, AR 3468 (CBS 131716) isolated by A.W. Ramaley from AWR 9205, dried culture on PDA (BPI 882817).

Notes — This species was described originally from *Agave*. Collections on *Yucca*, including the type of *Kellermania multisepata*, have been treated as conspecific (e.g. Sutton 1980), but it appears that *K. macrospora* is limited to *Agave*. *Planstromella parryi*, described originally from *Agave shawii* (Cooke 1885), *Plowrightia agaves*, described from *Agave* sp. (Maublanc 1903), and *Plowrightia williamsoniana*, described from *Agave americana* (Kellerman 1906), are potential synonyms (Barr 1996) as well as possibly the sexual state of *K. macrospora*, but these teleomorphs are poorly known.

***Kellermania micranthae* Minnis & A.H. Kenn., sp. nov. —**
MycoBank MB801100; Fig. 5, 6

Etymology. The name is derived from *Nolina micrantha*, the host.

Culture characteristics — Colonies on PDA 38–48 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near greyish green to greenish grey (30B6–30B2) to greyish green to dull green (30E5–30E4), at times portions covered with low, white, cottony hyphae; margin more or less even, whitish; reverse near greyish green to greenish grey (30C3–30C2). **Conidia** 43–61 × 6.5–9.5 µm, Q = 4.5–7.8 ($L^m = 49.2 \mu\text{m}$, $W^m = 8.6 \mu\text{m}$, $Q^m = 5.8$), cylindrical to obclavate, at times curved, apices tapering towards and obtuse, rounded or truncate at bases, aseptate; walls smooth, thin, hyaline; contents hyaline, at times granular; appendages absent.

Habitat & Distribution — Dead leaves of *Nolina micrantha*. This species is known only from the type locality in the USA: TX.

Specimen examined. USA, Texas, Culberson Co., Guadalupe Mtns. National Park, 5.6 miles from highway along Williams Ranch Rd., on dead leaves of *Nolina micrantha*, 23 Oct. 1995, coll. A.W. Ramaley, AR 3474 (CBS 131724) isolated by A.W. Ramaley from AWR 9536, dried culture on PDA (holotype, BPI 882825).

Notes — This species is distinguished from the others known from *Nolina* by the combination of its aseptate conidia that lack appendages and its greenish colouration in culture. Ramaley (in litt.) stated that this was an undescribed species and gave it the provisional name, *Piptarthron sotoli*. An undescribed species

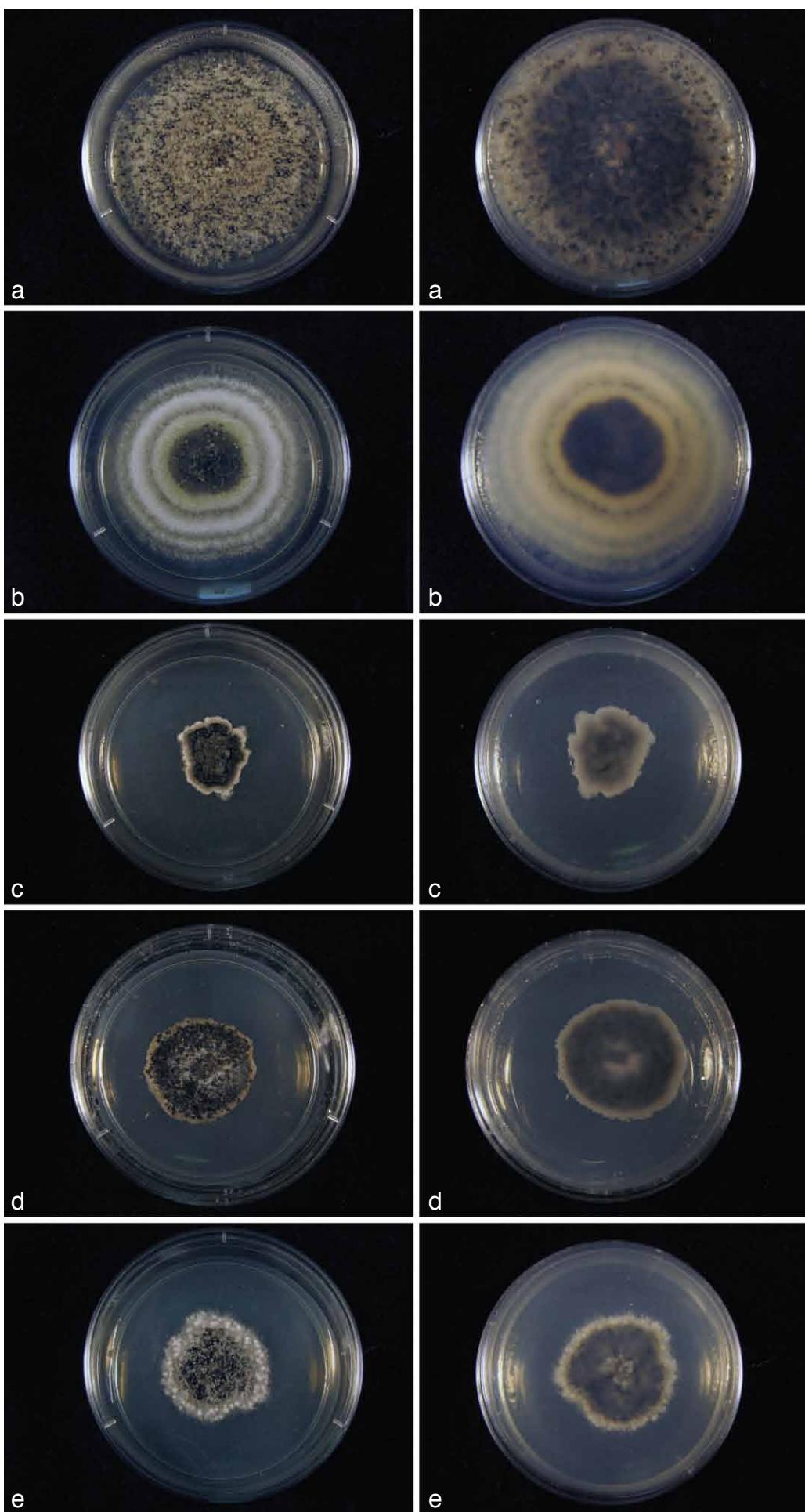


Fig. 6 Cultures of *Kellermania* species. a–e. Cultures (surface and reverse) on PDA at 2 wk after incubation at 24 °C with a 12 h light/dark regime; a. *K. macrospora* (AR 3468); b. *K. micranthae* (AR 3474); c. *K. nolinae* (AR 3475); d. *K. nolinifoliolum* (AR 3473); e. *K. plurilocularis* (AR 3467).

(Ramaley 1998) with aseptate, *Planistroma*-type ascospores, which was found on the type specimen of *P. kellermaniae* on *Nolina erumpens* in Texas, has an anamorph that is similar to *K. micrantha* and the two species may be conspecific.

***Kellermania nolinae* (Pollack) Nag Raj**, in Nag Raj, Coelomycetous anamorphs with appendage-bearing conidia: 442. 1993. — Fig. 5, 6

Basionym. *Bartalinia nolinae* Pollack, Mycologia 39: 620. 1947.

≡ *Alpakesa nolinae* (Pollack) Morgan-Jones, Nag Raj & W.B. Kendr., Canad. J. Bot. 50: 879. 1972.

= *Planistroma kellermaniae* A.W. Ramaley, Mycotaxon 66: 510. 1998.

Culture characteristics — Colonies on PDA 9–20 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near greenish grey (25C2), forming tiers of raised mounds, smooth to grainy, at times portions covered with scattered white, velutinous, aerial hyphae; margin uneven, whitish; reverse near greyish white (25B1). Conidia 35–48 × 8–11 µm, Q = 3.7–6 (L^m = 40.5 µm, W^m = 8.8 µm, Q^m = 4.7), fusiform to obclavate, at times slightly curved, tapering or not towards generally obtuse apices, tapering towards and typically truncate at bases that frequently bear a frill, 2–3-septate; walls smooth, thin and hyaline, and not constricted at septa; contents hyaline; appendages present, 8–24 µm long, apical, 3–5, filiform, unbranched, hyaline.

Habitat & Distribution — Dead leaves of *Nolina erumpens*, *N. microcarpa* (Pollack 1947, Ramaley 1998, this study). It is known from the USA: AZ, TX (Pollack 1947, Ramaley 1998, this study).

Specimen examined. USA, Texas, Brewster Co., Big Bend National Park, 3.75 miles from U.S. Hwy. 385 on road to The Basin, on dead leaves of *Nolina erumpens*, 9 May 1994, coll. A.W. Ramaley, AR 3475 (CBS 131717) isolated by A.W. Ramaley from AWR 9408, dried culture on PDA (BPI 882818).

Notes — The link between the asexual and sexual states is based on the production of characteristic conidia in cultures derived from asci (Ramaley 1998).

***Kellermania nolinifoliorum* A.W. Ramaley**, Mycotaxon 55:

255. 1995. — Fig. 5, 6

= *Planistromella nolinifoliorum* A.W. Ramaley, Mycotaxon 66: 509. 1998.

Culture characteristics — Colonies on PDA 23–26 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near dark grey (28F1), at times portions covered with scattered white, cobwebby, aerial hyphae; margin uneven, whitish, somewhat slimy in appearance; reverse near light grey to dark grey (28D1–28E1) with off white margin. Conidia 37–57.5 × 5–9.5 µm, Q = 5.6–9.3 (L^m = 49.1 µm, W^m = 7.1 µm, Q^m = 7.0), fusiform, straight, slightly curved to somewhat sigmoid, apices tapering to a relatively acute point, tapering towards and typically truncate at bases that may bear mucilaginous material, approx. medianly 1-septate; walls smooth, thin and hyaline, and not significantly constricted at septa; contents hyaline; appendages present or scarcely visible, perhaps absent, up to 5 µm long, apical, single, appearing as a blunt, mucilaginous mucro.

Habitat & Distribution — Dead leaves of *Nolina microcarpa*, *N. micrantha*, *Nolina* sp. (Ramaley 1995, 1998, this study). This fungus is known from the USA: AZ, NM, TX (Ramaley 1995, 1998, this study).

Specimen examined. USA, Arizona, Yarapai Co., 0.1 mile north of Big Creek, west side of Hwy. 17 at mile 262.1, on dead leaves of *Nolina microcarpa*, 19 July 1996, coll. A.W. Ramaley, AR 3473 (CBS 131718) isolated by A.W. Ramaley from AWR 9610, dried culture on PDA (BPI 882819).

Notes — The connection between the asexual and sexual state is based on the production of characteristic conidia in cultures obtained from asci (Ramaley 1998).

***Kellermania plurilocularis* (A.W. Ramaley) Minnis & A.H. Kenn., comb. nov.** — MycoBank MB801101; Fig. 5, 6

Basionym. *Piptarthron pluriloculare* A.W. Ramaley, Mycotaxon 42: 63. 1991.

= *Planistroma yuccigenum* A.W. Ramaley, Mycotaxon 42: 69. 1991 as 'yuccigena'.

Culture characteristics — Colonies on PDA 20–29 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near greenish grey (30D2), at times portions covered with white, cottony hyphae; margin uneven, whitish; reverse near light grey (18D1). Conidia 30.5–56 × 5–8 µm, Q = 4.2–11.7 (L^m = 41.5 µm, W^m = 6.0 µm, Q^m = 7.2), slightly curved, falcate, to strongly curved nearing U-shapes, apices tapering to a relatively acute point, typically truncate at bases, aseptate; walls smooth, thin and hyaline; contents hyaline; appendages absent.

Habitat & Distribution — Dead leaves of *Yucca baccata* (Ramaley 1991, this study). This fungus is known only from the USA: CO (Ramaley 1991, this study).

Specimen examined. USA, Colorado, La Plata Co., Durango, along bike trail between Chapman Hill ski slope and Lion's Den, on dead leaves of *Yucca baccata*, 8 June 2000, coll. A.W. Ramaley, AR 3467 (CBS 131719) isolated by A.W. Ramaley from AWR 2001b, dried culture on PDA (BPI 882820).

Notes — The size range of the conidia of the holotype of *Piptarthron pluriloculare* was reported as (48–)59–76(–98) × (4–)5.5–7(–8) µm (Ramaley 1991). The conidial length of the present isolate (AR 3467) in culture was much shorter, but the overall appearance of the conidia was basically the same as those of the holotype. The link between the asexual and sexual states is based on cultural similarities (Ramaley 1991).

***Kellermania ramaleyae* Minnis, M.E. Palm & Rossman, sp. nov.** — MycoBank MB801102; Fig. 7, 8

Etymology. This species is named in honour of Annette W. Ramaley for her outstanding contributions towards the study of Planstromellaceae and coelomycetous anamorphs.

On host (holotype): *Foliicolous*, stromata approx. 0.5–0.75 mm diam, scattered to gregarious, round in top view, subepidermal, immersed becoming erumpent after peeling back of disc-shaped epidermal tissue, black, multilocular. *Conidiophores* absent. *Conidiogenous cells* lining the basal and lateral, locular walls, more or less doliiform to slightly cylindrical. Conidia 48–70.5 × 11–16 µm, Q = 4.3–5.3 (L^m = 58.8 µm, W^m = 12.6 µm, Q^m = 4.7), cylindrical to slightly clavate or rarely curved, apices obtuse, typically truncate at bases, 2–4(–5)-septate; walls smooth, thin, hyaline, and not significantly constricted at septa; contents hyaline, at times granular; appendages absent.

Culture characteristics — Colonies on PDA 7–21 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near dull green (26D3, 29E4, 30E4,) to dark green (29F4), covered with low, cottony to velutinous hyphae; margin uneven, whitish; reverse multi-coloured: uncoloured, black, near greyish turquoise (24D5), and dull green (27E3). Conidia 35–51 × 9.5–16 µm, Q = 2.6–4.6 (L^m = 42.7 µm, W^m = 12.3 µm, Q^m = 3.5), cylindrical to slightly clavate or rarely curved, apices obtuse, typically truncate at bases, 2–4-septate; walls smooth, thin, hyaline, and not constricted at septa; contents hyaline, at times granular; appendages absent.

Habitat & Distribution — Dead leaves of *Yucca* sp. It is known only from the material from Mexico intercepted at the Laredo Plant Inspection Station.

Specimen examined. Mexico, Intercepted at Laredo, Texas, USA on dead leaves of *Yucca* sp., 2 Dec. 1985, coll. S. Vesper, MEP 1260 (CBS 131722) isolated by M.E. Palm from BPI 525045 (holotype, as '*P. macrosporum*'), dried culture on PDA (BPI 882823).

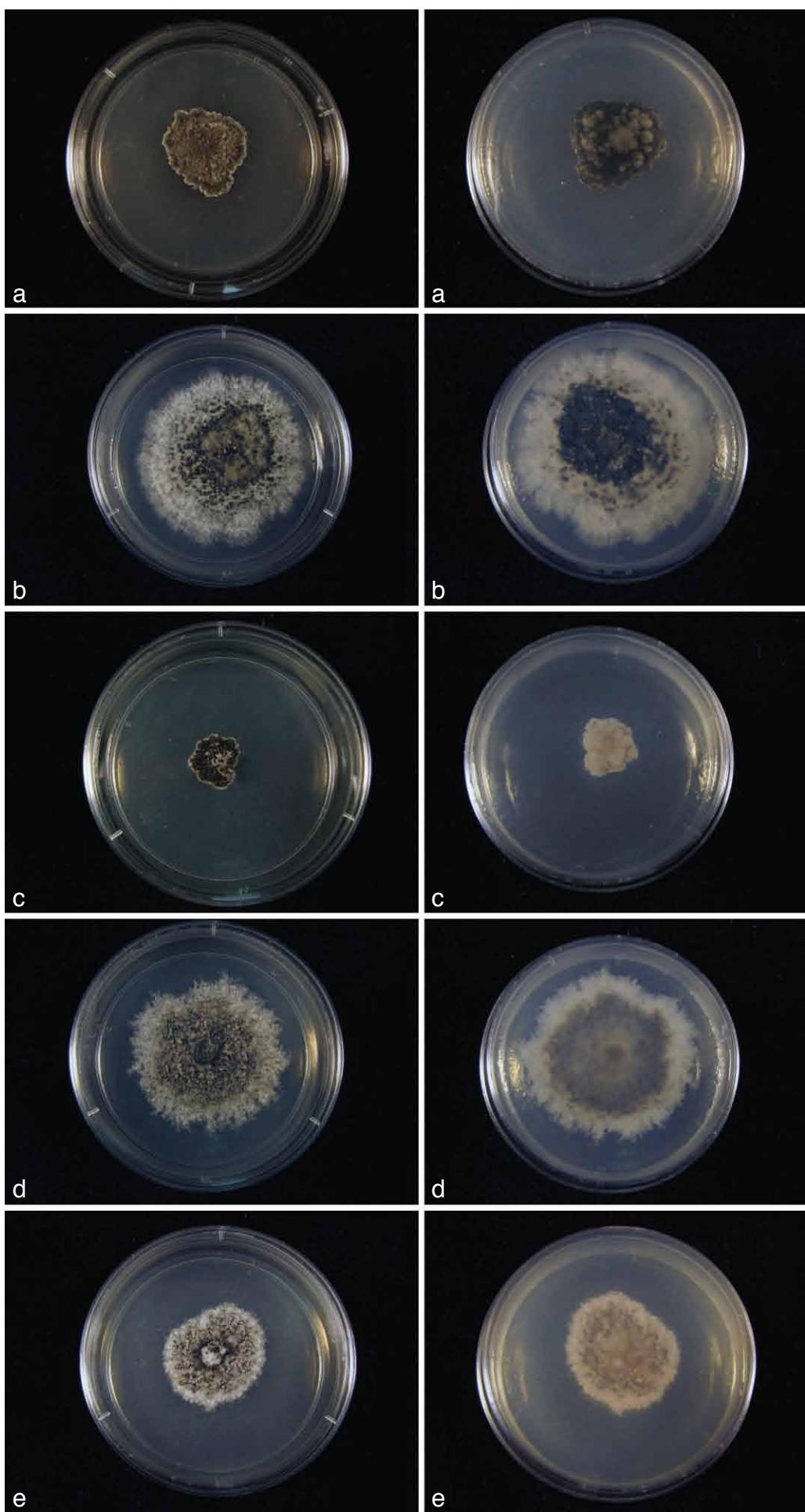


Fig. 7 Cultures of *Kellermania* species. a–e. Cultures (surface and reverse) on PDA at 2 wk after incubation at 24 °C with a 12 h light/dark regime; a. *K. rama-leyae* (MEP 1260); b. *K. rostratae* (JB 5.16.11-01); c. *K. uniseptata* (AR 3476); d. *K. yuccifoliorum* (AR 3472); e. *K. yuccigena* (AR 3470).

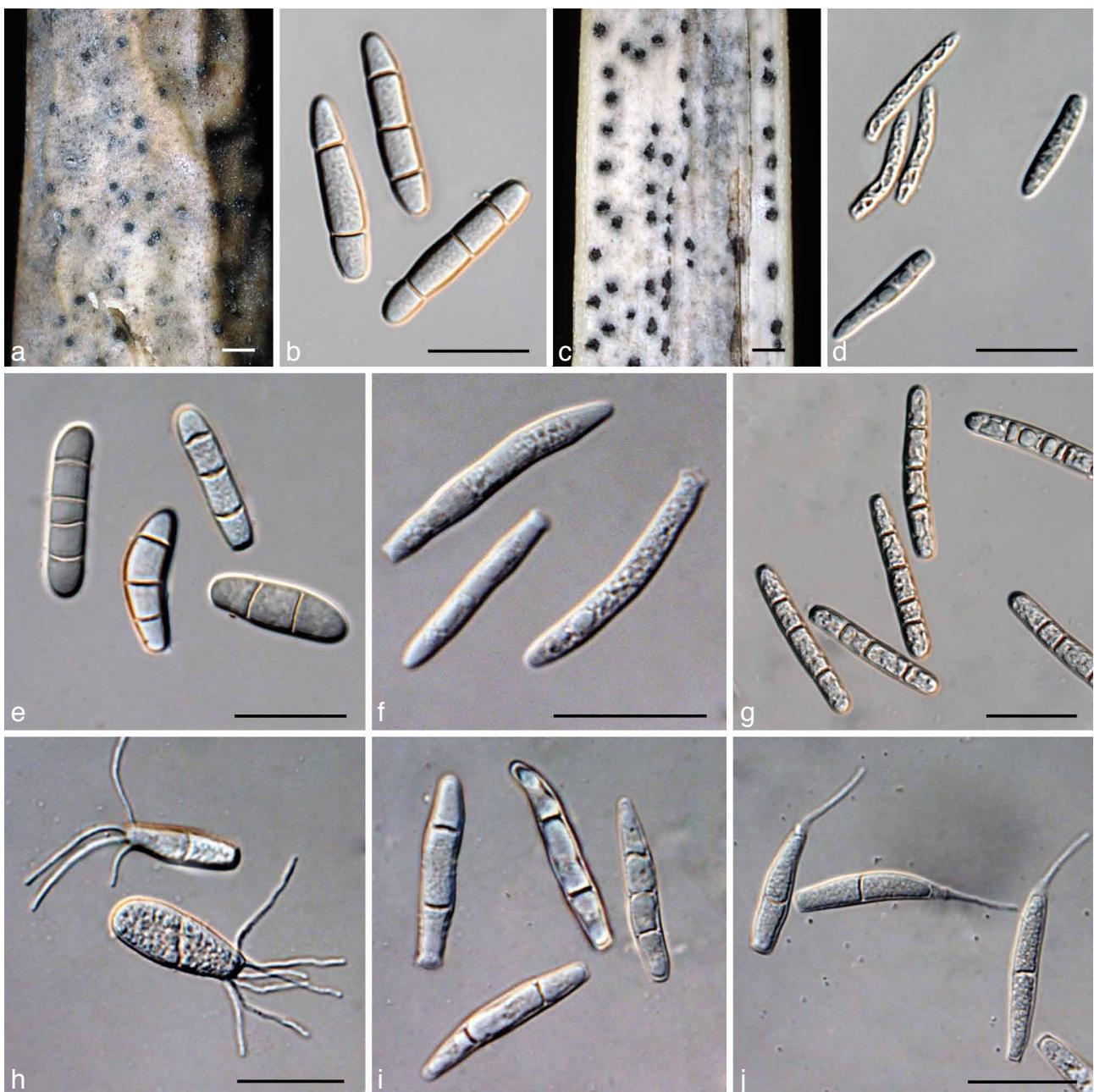


Fig. 8 a. Stromata of *Kellermania ramaleyae* (holotype, BPI 525045) on leaf of *Yucca* sp.; b. conidia of *K. ramaleyae* (holotype, BPI 525045) on leaf of *Yucca* sp.; c. stromata of *K. rostratae* (holotype, BPI 884092) on leaf of *Y. rostrata*; d. conidia of *K. rostratae* (holotype, BPI 884092) on leaf of *Y. rostrata*; e. conidia of *K. ramaleyae* from culture (MEP 1260); f. conidia of *K. rostratae* from culture (JB 5.16.11-01); g. conidia of *K. unilocularis* (isotype of *Piptarthron uniloculare*, BPI 1110167) on leaf of *Y. baccata*; h. conidia of *K. uniseptata* from culture (AR 3476); i. conidia of *K. yuccafoliorum* from culture (AR 3472); j. conidia of *K. yuccigena* from culture (AR 3470). — Scale bars = 1 mm for stromata, = 30 µm for conidia.

Notes — This species is distinguished from the others that occur on *Yucca* by its conidia in culture with 2–4 septa, $Q = 2.6\text{--}4.6$, and appendages lacking. Some differences were observed in dimensions of conidia produced on the host vs in culture. A lculoascomycete producing tardily septate ascospores that was found on the host may be the sexual state of this species.

Kellermania rostratae Minnis, A.H. Kenn. & J.F. Bisch., sp. nov. — MycoBank MB801103; Fig. 7, 8

Etymology. The name is derived from *Yucca rostrata*, the host.

On host (holotype): *Folioicolous*, stromata approx. 0.5–1 mm diam, scattered to gregarious, round to ellipsoid in top view, subepidermal, immersed becoming erumpent after peeling back of disc-shaped epidermal tissue, black, multilocular. *Conidiophores* absent. *Conidiogenous cells* lining the basal and lateral, locular walls, more or less doliform to slightly cy-

lindrical. *Conidia* $30.5\text{--}48 \times 5\text{--}6.5 \mu\text{m}$, $Q = 6.3\text{--}9.3$ ($L^m = 41.3 \mu\text{m}$, $W^m = 5.3 \mu\text{m}$, $Q^m = 7.8$), cylindrical to obclavate, at times curved, apices tapering towards and obtuse to slightly acute, typically truncate at bases, aseptate; walls smooth, thin, and hyaline; contents hyaline, at times granular; appendages absent.

Culture characteristics — Colonies on PDA 52 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface whitish to near greenish grey (30C2), at times portions covered with scattered low, wispy, white hyphae; margin uneven, whitish; reverse uncoloured with conidiomata visible. Conidia $33.5\text{--}62.5 \times 5\text{--}9.5 \mu\text{m}$, $Q = 4.2\text{--}9$ ($L^m = 44.1 \mu\text{m}$, $W^m = 7.1 \mu\text{m}$, $Q^m = 6.3$), cylindrical to obclavate, at times curved, apices tapering towards and obtuse to slightly acute, typically truncate at bases, 0–1(–3)-septate; walls smooth, thin, hyaline, and not constricted at septa; contents hyaline, at times granular; appendages absent.

Habitat & Distribution — Dead leaves of *Yucca rostrata*. This species is known only from an interception of Mexican material.

Specimen examined. Mexico, Intercepted at Los Indios, Texas, USA on dead leaves of *Yucca rostrata*, 12 May 2011, coll. A. Garza, JB 5.16.11-01 (CBS 131721) isolated by J.F. Bischoff from BPI 884092 (holotype), dried culture on PDA (BPI 882822).

Notes — This species is distinguished from the others that occur on *Yucca* by its typically cylindrical to obclavate, 0–1(–3)-septate conidia in culture that lack appendages. Conidia produced on the host were aseptate. In culture, septa were observed on a small percentage of conidia. Some differences in size of conidia were observed between material from host and in culture.

Kellermania unilocularis (A.W. Ramaley) Minnis & A.H. Kenn., comb. nov. — MycoBank MB801104; Fig. 8

Basionym. *Piptarthron uniloculare* A.W. Ramaley, Mycotaxon 45: 451. 1992.

= *Planistroma obtusilunatum* A.W. Ramaley, Mycotaxon 45: 450. 1992.

On host (isotype of *Piptarthron uniloculare*): *Conidia* 48–72 \times 8–9.5 μm , $Q = 5–7.6$ ($L^m = 56.4 \mu\text{m}$, $W^m = 9.0 \mu\text{m}$, $Q^m = 6.3$), cylindrical, at times curved, apices straight, obtuse, less commonly tapering towards, typically rounded to inconspicuously truncate at bases, 2–4(mostly 3)-septate; walls smooth, thin, hyaline, and not significantly constricted at septa; contents hyaline; appendages absent.

Culture characteristics — Only sterile, irregular stromatal growths observed in the dried culture.

Habitat & Distribution — Dead leaves of several *Yucca* spp. (Ramaley 1992). The types of both the asexual and sexual states were found on *Yucca baccata* (Ramaley 1992). This species has been reported from the USA: CO, NV (Ramaley 1992, this study).

Specimens examined. USA, Colorado, La Plata Co., Durango, along bike trail between Chapman Hill ski slope and Lion's Den, on dead leaves of *Yucca baccata*, 8 June 2000, coll. A.W. Ramaley, AR 3466 isolated by A.W. Ramaley from AWR 2001a, dried culture (BPI 883224); Ridge S. of Smelter Mountain, Cactus ridge, on dead leaves of *Yucca baccata*, 10 Feb. 1992, coll. A.W. Ramaley, AWR 9018 (isotype of *Piptarthron uniloculare*, BPI 1110167).

Notes — The conidia of the isotype were observed to be slightly shorter than reported by Ramaley (1992), and no conidia were observed with 5 septa although Ramaley (1992) reported that some had 5 septa. The culture of this species is dead and only a dried culture of this isolate is extant, but Ramaley (1992) reported that typical conidia were formed in culture. The link between the asexual and sexual states is based on the production of typical conidia in cultures obtained from ascii (Ramaley 1992).

An additional analysis was performed as the *Kellermania* analysis above but with the addition of an existing ITS sequence from *K. unilocularis* AR 3466. The results suggested a sister relationship between *K. unilocularis* and lineage i ($pp = 0.82$). This expanded clade with lineage i was member of a larger clade ($pp = 0.89$) also containing lineage ii (Fig. 3). The unilocular stromata of *K. unilocularis* is shared by members of lineage ii having conidia with appendages. Its lack of conidial appendages is shared by members of lineage i having plurilocular stromata. Its aseptate ascospores distinguish it from both lineages. This is the only species in or closely related to lineages i–iii (Fig. 2) with aseptate ascospores. It was excluded from other phylogenetic analyses due to missing data.

Kellermania uniseptata (Morgan-Jones, Nag Raj & W.B. Kendr.) Nag Raj, in Nag Raj, Coelomycetous anamorphs with appendage-bearing conidia: 443. 1993. — Fig. 7, 8

Basionym. *Alpakesa uniseptata* Morgan-Jones, Nag Raj & W.B. Kendr., Canad. J. Bot. 50: 879. 1972.

= *Planstromella torsifoliorum* A.W. Ramaley, Mycotaxon 55: 265. 1995.

Culture characteristics — Colonies on PDA 10–13 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near orange white (6A2), slightly slimy in appearance, at times portions covered with low, cottony hyphae; margin uneven, whitish; reverse off white to nearly colourous with upper surface. *Conidia* 27–45 \times 8–17.5 μm , $Q = 2–4.2$ ($L^m = 35.8 \mu\text{m}$, $W^m = 12.4 \mu\text{m}$, $Q^m = 3.0$), cylindrical, fusiform, obclavate, to ellipsoid, apices tapering or not, obtuse, tapering or not towards and typically truncate at bases bearing indistinct frills, approx. medianly 1-septate; walls smooth, thin and hyaline, and not significantly constricted at septa; contents hyaline, at times granular; appendages present, 13–41.5 μm long, apical, 3–5(–8), filiform, unbranched, flexuous, hyaline.

Habitat & Distribution — Dead leaves of *Yucca rupicola* (Morgan-Jones et al. 1972a, Ramaley 1995, this study). This species is known only from the USA: TX (Morgan-Jones et al. 1972a, Ramaley 1995, this study).

Specimen examined. USA, Texas, Kimble Co., junction of I 10 and U.S. Hwy. 290, on dead leaves of *Yucca rupicola*, 24 Oct. 1994, coll. A.W. Ramaley, AR 3476 (CBS 131725) isolated by A.W. Ramaley from AWR 9432, dried culture on PDA (BPI 882826).

Notes — The connection of the asexual and sexual states is circumstantial (Ramaley 1995).

Kellermania yuccifolia (J.G. Hall) Nag Raj, in Nag Raj, Coelomycetous anamorphs with appendage-bearing conidia: 443. 1993.

Basionym. *Neottiospora yuccifolia* J.G. Hall, Phytopathology 5: 57. 1915 as '*yuccaeafolia*'.

= *Alpakesa yuccifolia* (J.G. Hall) Subram. & K. Ramakr., J. Indian Bot. Soc. 33: 205. 1954 as '*yuccaeafolia*'.

Culture characteristics — This species is not known from culture. It is characterised by its aseptate conidia with multiple appendages (Hall 1915, Morgan-Jones et al. 1972a, Nag Raj 1993).

Habitat & Distribution — Dead leaves of *Yucca filamentosa*, *Y. gloriosa*, and *Yucca* sp. (Morgan-Jones et al. 1972a, Sutton 1980). This species is widespread in the USA based on scattered reports (Morgan-Jones et al. 1972a, Sutton 1980, Farr & Rossman 2012). The type was collected on *Yucca* sp. in the USA: WA (Hall 1915).

Specimen examined — None.

Notes — No DNA sequence data exist for this species, which is the type of the genus *Alpakesa* (Subramanian & Ramakrishnan 1954). Considering that the data presented here for other species of *Kellermania* indicate that conidial septation and appendage number are not important for distinguishing genera, this species belongs in the genus *Kellermania*. The occurrence of this species on *Yucca* and its multiple conidial appendages suggest a probable phylogenetic placement in lineage ii.

Kellermania yuccifoliorum A.W. Ramaley, Mycotaxon 47: 262. 1993. — Fig. 7, 8

= *Planstromella yuccifoliorum* A.W. Ramaley, Mycotaxon 47: 261. 1993.

Culture characteristics — Colonies on PDA 27–40 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface near dark green (30F5–30F3), covered with low, cottony to velutinous hyphae; margin uneven, whitish; reverse grey to black. *Conidia* 40–65.5 \times 8–11 μm , $Q = 3.9–7.4$ ($L^m = 52.6 \mu\text{m}$, $W^m = 9.8 \mu\text{m}$, $Q^m = 5.4$), cylindrical to obclavate, apices tapering towards and obtuse, typically truncate to less commonly somewhat rounded at bases, 2–3-septate; walls smooth, thin and hyaline, and not significantly constricted at septa; contents hyaline; appendages

present, at times scarcely visible, possibly absent, up to 1.5 µm long, apical, single, appearing as a short, dome-like mound.

Habitat & Distribution — Dead leaves of *Yucca baccata*, *Y. brevifolia* (holotypes of both names), *Y. schidigera*, *Y. thornberi* (Ramaley 1993, this study). This species has been reported from the USA: AZ, CA, UT (Ramaley 1993, this study).

Specimen examined. USA, Arizona, Mohave Co., 0.3 miles from Gem Acres Rd., exit mile 20 from U.S. Hwy. 40, on dead leaves of *Yucca brevifolia*, 3 June 1992, coll. A.W. Ramaley, AR 3472 (CBS 131726) isolated by A.W. Ramaley from AWR 9229, dried culture on PDA (BPI 882827).

Notes — Ramaley (1993) reported variation in conidial sizes between specimens found on different hosts and between fresh and dried conidia. Given the diversity found in this study, it is difficult to state with certainty that all specimens from all hosts are conspecific. The conidia from the culture examined here were smaller than those reported from the host in nature (Ramaley 1993). The connection of the asexual and sexual states is circumstantial (Ramaley 1993).

***Kellermania yuccigena* Ellis & Everh., J. Mycol. 1: 154. 1885**
as '*yuccaeigena*'. — Fig. 7, 8

= *Planstromella uniseptata* A.W. Ramaley, Mycotaxon 47: 267. 1993

Culture characteristics — Colonies on PDA 19–25 mm after 2 wk at 24 °C with a 12 h light/dark regimen; surface whitish to near pale grey (30B1), covered with cottony hyphae; margin uneven, whitish; reverse greyish with black conidiomata visible. **Conidia** 37–56 × 8–13 µm, Q = 3.3–6.2 ($L^m = 48.2 \mu m$, $W^m = 10.1 \mu m$, $Q^m = 4.8$), cylindrical to somewhat obclavate, apices tapering towards or not and typically obtuse but sometimes slightly acute, tapering or not, typically truncate at bases, approx. medianly 1(–2)-septate; walls smooth, thin and hyaline, and not or slightly constricted at septa; contents hyaline; appendages present, 5–35 µm ($L^m = 19.6 \mu m$) long, apical, single, filiform, unbranched to rarely branched with a single bifurcation, flexuous, hyaline.

Habitat & Distribution — Dead leaves of several species of *Yucca* (Morgan-Jones et al. 1972b, Nag Raj 1993, Ramaley 1993, Farr & Rossman 2012). The type of the asexual state was found on *Y. glauca* (as *Y. angustifolia*) (Ellis & Everhart 1885) and the type of the sexual state was found on *Y. elata* (Ramaley 1993). This species is widely distributed in the western half of the USA (Morgan-Jones et al. 1972b, Ramaley 1993, Farr & Rossman 2012).

Specimen examined. USA, New Mexico, Chaves Co., mile 302.05 on U.S. Hwy. 380, on dead leaves of *Yucca filamentosa*?, 24 Oct. 1993, coll. A.W. Ramaley, AR 3470 (CBS 131727) isolated by A.W. Ramaley from AWR 9325, dried culture on PDA (BPI 882828).

Notes — The asexual and sexual states were linked through the observation of typical conidia in cultures derived from asci (Ramaley 1993).

EXCLUDED, POORLY KNOWN AND UNCERTAIN TAXA

***Diatrype acervata* Ellis & Everh., J. Mycol. 4: 75. 1888.**

= *Planstromella acervata* (Ellis & Everh.) M.E. Barr, Mycotaxon 60: 434. 1996.

Notes — This species described from *Yucca filamentosa* in New Jersey (Ellis & Everhart 1888) could be the sexual state of a *Kellermania*, but confusion around a species complex as well as a *Stigmella* anamorph have hindered the development of a proper species concept (Barr 1996). Other homotypic synonyms listed in MycoBank are not listed here.

***Endothia parryi* Farl. ex Cooke, Grevillea 13: 102. 1885.**

= *Planstromella parryi* (Farl. ex Cooke) M.E. Barr, Mycotaxon 60: 435. 1996.

Notes — This species found on *Agave shawii* (Cooke 1885) has plurilocular stromata with septate ascospores (Barr 1996). It may represent a distinct species of *Kellermania* or the sexual state of *K. macrospora*. Other homotypic synonyms listed in MycoBank are not listed here.

***Hypocrea agaves* Maubl., Bull. Soc. Mycol. France 19: 292. 1903.**

= *Plowrightia agaves* (Maubl.) Maubl., Bull. Soc. Mycol. France 23: 143. 1907.

Notes — This species based on material from *Agave* sp. in Mexico (Maublanc 1903) may be the sexual state of a *Kellermania*, possibly *K. macrospora*. It has been treated as a synonym of *Planstromella parryi* (Barr 1996).

***Kellermania attenuata* Morgan-Jones, Nag Raj & W.B. Kendr., Canad. J. Bot. 50: 1643. 1972.**

Notes — In the protologue, this species was reported to have conidia 70–85 × 3–5 µm, cylindrical, aseptate, appendages lacking (Morgan-Jones et al. 1972b). The type from Mexico occurs on *Yucca filifera*, but other collections from widespread North American localities occur on other *Yucca* spp. (Morgan-Jones et al. 1972b). Based on the figure of the conidia in the protologue (Morgan-Jones et al. 1972b), the length to width ratio is 12–15. Though treated as a synonym of *Piptarthron limbatum* by Sutton (1980), who later treated both of these as synonyms of *Piptarthron yuccae* (Sutton 1983), this seems to be a distinct species on *Yucca*.

***Kellermania major* Dearn. & Barthol., Mycologia 16: 163. 1924.**

Notes — In the protologue, this species was reported to have conidia 55–75 × 11–14 µm, 2-septate with the middle cell half the size of the end cells with 1–2 appendages, 15–18 × 3–4 µm (Dearness 1924). According to Dearness (1924), the type from the USA: CA occurs on *Hesperoyucca whipplei* (as *Yucca whipplei*; subfam. Agavoideae). There are a few other reports of this species on *Yucca* spp. from the western USA (Farr & Rossman 2012). Though treated as a synonym of *Kellermania anomala* by Morgan-Jones et al. (1972b), Sutton (1980), and Nag Raj (1993), this is almost certainly a distinct species given the importance of host associations since it is the only species described originally from the host genus *Hesperoyucca*.

***Kellermania multiseptata* Morgan-Jones, Nag Raj & W.B. Kendr., Canad. J. Bot. 50: 1644. 1972.**

Notes — In the protologue, this plurilocular species was reported to have conidia 50–68 × 6–7.5 µm, cylindrical to obclavate, aseptate, 3–4-septate, appendages lacking (Morgan-Jones et al. 1972b). The type from the USA: TX occurs on *Yucca macrocarpa* and an additional collection was reported from the USA: AZ on *Yucca brevifolia* (Morgan-Jones et al. 1972b). Based on the figure of the conidia in the protologue (Morgan-Jones et al. 1972b), the length to width ratio is 8.2–12. Though treated as a synonym of *Piptarthron macrosporum* by Sutton (1980), this seems to be a distinct species on *Yucca*.

***Phyllachora yuccae* Ellis & Everh., Bull. Torrey Bot. Club 22: 440. 1895.**

= *Piptarthron yuccae* (Ellis & Everh.) B. Sutton, Trans. Brit. Mycol. Soc. 81: 407. 1983.

Notes — In the protologue, this species was reported to be an immature ascomycete and a question mark was placed next to the genus to indicate uncertainty about its classification (Ellis & Everhart 1895). According to their observations, the immature asci, if interpreted as conidia, are given as 50–60 × 7–8 µm, cylindrical, tapered towards apices, aseptate. The type from Mexico occurs on *Yucca glauca* (as *Y. angustifolia*) (Ellis & Everhart 1895). Based on correspondence with M.E. Barr, Sutton (1983) determined that this species represented a *Piptarthron* and that *P. limbatum* and *K. attenuata* were later synonyms. If the type material is a coelomycete bearing aseptate conidia that lack appendages, this would likely be a distinct species correctly classified in *Kellermania*. However, M.E. Barr's annotation of the type specimen from 1970 (NY) states that the specimen is an immature *K. anomala*.

***Plowrightia williamsoniana* Kellerm., J. Mycol. 12: 186. 1906.**

Notes — Kellerman (1906) described this species from Guatemalan material found on *Agave americana*. The combination of host, plurilocular stromata, and septate ascospores suggests a possible link with *Kellermania macrospora*. It has been treated as a synonym of *Planstromella parryi* and *Plowrightia agaves* (Barr 1996).

***Septoplaca limbata* Petr., Sydowia 17: 272. 1964 '1963'.**

≡ *Piptarthron limbatum* (Petr.) B. Sutton, in Sutton, The coelomycetes: 54. 1980.

Notes — In the protologue, this species was designated as the type of the genus *Septoplaca*, and it was reported to have indistinctly pseudoseptate conidia measuring 35–60(–78) × 3–3.5 (Petrak 1964). The type from the USA: AZ occurs on *Yucca macrocarpa* (Petrak 1964). Sutton (1977) treated *Septoplaca* as a synonym of *Piptarthron*, but he was unable to place the type species. Assuming the conidia may actually be aseptate and after considering conidial measurements, Sutton (1977) suggested that *S. limbata* was an earlier synonym for *Kellermania attenuata*. Later, Sutton (1980) formally transferred *S. limbata* to *Piptarthron*, treated *K. attenuata* as a synonym, and considered the species to be aseptate. Sutton (1983) treated these names as later synonyms of *P. yuccae*. Although Petrak (1964) may have confused pseudoseptate conidia with the euseptate conidia in *Piptarthron*, it seems unlikely that he would confuse aseptate with septate conidia.

KEY TO KELLERMANIA SPECIES IN CULTURE

1. Colony distinctly pink *K. crassispora*
1. Colony not pink 2
2. Conidia with more than one apical appendage 3
2. Conidia with 0–1 apical appendages 5
3. Conidia aseptate *K. yuccifolia**
3. Conidia septate 4
4. Conidia 1-septate *K. uniseptata*
4. Conidia 2–3-septate *K. nolinae*
5. Some conidia with 1 apical appendage 6
5. All conidia with no apical appendages 9
6. Many apical appendages greater than 12 µm long *K. yuccigena*
6. Apical appendages not or rarely greater than 12 µm long 7
7. All conidia 1-septate *K. nolinifoliorum*
7. Some conidia more than 1-septate 8
8. Conidia 1–2(–3)-septate, Q = 5–14.3, middle cell shorter than end cells *K. anomala*

8. Conidia 2–3-septate, Q = 3.9–7.4, middle cell longer than end cells *K. yuccifoliorum*
9. Conidia aseptate 10
9. Some conidia septate 12
10. Conidia typically cylindrical to obclavate *K. micranthae*
10. Conidia typically curved 11
11. Conidia slightly curved, falcate, to strongly curved, nearly U-shaped *K. plurilocularis*
11. Conidia more or less cylindrical with irregularly curved shapes, flexuous *K. dasylirionicola*
12. Conidia mostly 0–1-septate 13
12. Conidia mostly with 2 or more septa 14
13. Conidia typically cylindrical to obclavate *K. rostratae*
13. Conidia typically with some degree of curvature *K. dasylirionis*
14. Conidia 1–3 (mostly 2)-septate *K. confusa*
14. Some conidia with 4 or more septa 15
15. Some conidia with more than 5 septa, Q = 4.9–13 *K. macrospora*
15. Conidia with 5 or less septa, maximum Q = ± 7.6 16
16. Conidia 2–4-septate, Q = 2.6–4.6 *K. ramaleyae*
16. Conidia 2–4-septate, Q = 5–7.6 *K. unilocularis***

*Not known from culture **Based on study of isotype on host (BPI 1110167)

DISCUSSION

Phylogenetic analyses support the placement and monophyly of the core *Planstromellaceae* in the order *Botryosphaeraiales* of class *Dothideomycetes* where the *Planstromellaceae* represent a well-supported clade comprised of the coelomycetous genera *Alpakesa*, *Kellermania*, and *Piptarthron* with associated teleomorphic genera *Planstroma* and *Planstromella*. Within *Botryosphaeraiales*, it is positioned in a polytomy with four other lineages of *Botryosphaeriaceae* s.l., three of which occupy basal positions in previous studies (Philips & Alves 2009, Schoch et al. 2009) relative to the fourth that includes the core diversity of *Botryosphaeriaceae* (Fig. 1). This core *Botryosphaeriaceae* lineage (pp = 1.0) is comprised of two main clades, one with *Botryosphaeria* (pp = 1.0) and another (pp = 0.75) with *Pseudofusicoccum stromaticum* and *Guignardia* (pp = 1.0). The position of *Guignardia* is significant due to its unclear position based on previous studies (Crous et al. 2006, Philips & Alves 2009). Though the family *Botryosphaeriaceae* has been recognised with a broad circumscription, i.e. *sensu lato* (Philips & Alves 2009), and *Planstromellaceae* could well be treated as a later synonym, we prefer to maintain the family *Planstromellaceae* as distinct from *Botryosphaeriaceae* s.str. and suggest that further sampling is needed to clarify familial classification within the *Botryosphaeraiales*. The *Planstromellaceae* is significantly and phylogenetically distinct from the *Botryosphaeriaceae*.

All genera of core *Planstromellaceae* are here considered to constitute one genus, namely *Kellermania*. Four other genera classified in *Planstromellaceae* (Barr 1996) are redispersed as follows: *Eruptio* has been shown to be a member of *Mycosphaerellaceae* (Verleyen et al. 2004); *Loratospora* has been shown to be a member of the *Phaeosphaeriaceae* (Schoch et al. 2009); and none of the species of *Mycosphaerellopsis* including the type species, *M. myricariae* (Höhn 1918b), have been placed phylogenetically; *Microcyclus*, typified by *Microcyclus angolensis* (Sydow & Sydow 1904), is only represented by DNA sequence data of *Microcyclus ulei*, and based on BLAST searches of GenBank using available ITS sequences, it does not belong in the order *Botryosphaeraiales*. The closest hits resulting from the BLAST searches are members of the *Mycosphaerellaceae*, but its familial classification is uncertain.

Among the *Planstromellaceae* (*Kellermania*) are five lineages that, with the exception of lineage iv, are each well supported. Lineage v is treated separately as its position is unresolved. These lineages were recovered in all analyses of individual genes with the exception of the SSU. The lack of resolution in the SSU tree was due to a low level of sequence divergence, and thus a lack of informative characters (Table 2). Overall, the relationships among the five lineages were not strongly supported.

In general, the phylogenetic groupings within the *Planstromellaceae* (*Kellermania*) do not correspond with the presence or absence and numbers of conidial appendages nor with conidial septation (e.g. multiple appendages in lineages ii and v; appendages absent in lineages i and iv). Previous generic circumscriptions of these coelomycetes based on conidial appendages alone are not well supported, a finding which was also recently observed among other genera of appendaged coelomycetes (Barber et al. 2011, Crous et al. 2012). The type species of *Kellermania*, *K. yuccigena*, and *Piptarthron*, *P. macrosporum* (≡ *K. macrospora*), belong to separate lineages ii and i, respectively, that notably form a clade (pp = 0.89) with *K. unilocularis* in the ITS analysis (Fig. 3). Lineage ii, which includes *K. yuccigena*, also includes three well-known species of *Planstromella* for which DNA sequence data exist including the type species, *Planstromella yuccifoliorum* (= *K. yuccifoliorum*). Though lineages i–iii in Fig. 2 contain only species with septate ascospores, *Planistroma obtusilunatum*, linked to *P. uniloculare* (≡ *K. unilocularis*), as mentioned above appears to belong among these lineages (Fig. 3). It has aseptate ascospores (Ramaley 1992). Other species lacking ascospore septation, namely *Planistroma yuccigenum*, the type of the genus and linked to *P. pluriloculare* (≡ *K. plurilocularis*) and *Planistroma nolinae*, linked to *P. crassisporum* (≡ *K. crassispora*), belong to lineage iv and *Planistroma kellermaniae*, linked to *Kellermania nolinae*, represents lineage v. Thus, *Planistroma* and *Planstromella* do not form well-supported clades if circumscribed by ascospore septation alone. Considering the biological and phylogenetic similarities of the species in the five major lineages and the lack of resolution among the lineages, there is little pragmatic value in recognising any subclades or lineages as distinct genera. Thus, the entire clade is herein recognised as a broadly defined genus *Kellermania*, the generic name having priority. In accordance with the changes enacted in the Melbourne Code in regard to Art. 59 (Norvell 2011), we do not recognise separate anamorphic and teleomorphic names.

Morphological variation of conidia among isolates from different hosts or even the same host, especially in regard to appendages, septation, and shape of conidia, is frequently an indicator of the presence of distinct taxa. However, slight differences in size, septation, and appendages of conidia among material from fresh collections, herbarium collections, and culture were frequently observed for a given species (Ramaley 1993, 1995, this study). In spite of these differences, the overall appearance of conidia on the host and in culture is similar for a given species and species differences tend to be obvious when considering within species and among species morphological variation. DNA sequence data are required to distinguish species and to confirm species recognition in ambiguous cases.

From an ecological and evolutionary point of view, it is interesting to note that several lineages including lineages i, sisters ii–iii, and iv (Fig. 2) are largely correlated with plant hosts from different host clades in the *Asparagaceae*, subfamilies *Agavoideae* and *Nolinoideae* sensu APG III (2009). This suggests that host phylogeny is correlated with the phylogeny of these fungi to some degree. However, sampling within these fungi remains limited and it is too early to formulate final conclusions given the lack of resolution among the lineages. Although a number

of *Kellermania* species have been recognised historically as occurring on numerous hosts, we expect that there are few, if any, plurivorous species given the evidence of host specificity and numbers of cryptic taxa found in this study. However, multiple isolates were not available for species of *Kellermania* reported from numerous hosts, thus, this hypothesis needs further study as many members of the *Botryosphaerales* are known to inhabit multiple hosts (van Niekerk et al. 2004, Glienke et al. 2011).

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