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

A.M. Minnis\(^1\), A.H. Kennedy\(^2\), D.B. Grenier\(^2\), M.E. Palm\(^3\), A.Y. Rossman\(^4\)

**Key words**

Agavaceae
Ascomycota
Anamorphs
Botryosphaeraceae
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Septoplastic
taxonomy

**Abstract**

The core species of the family Planistromellaceae are included in the teleomorph 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 rnSSU, 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 Botryosphaeriales. 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 classificatory system. Alpakesa, Kellermania, Piptarthron, Planistroma, and Planistromella are herein recognised as belonging to the single genus *Kellermania*. The following new combinations are proposed: *Kellermania crassisspora*, *K. dasylinonis*, *K. macrospora*, *K. plurilocularis*, and *K. unilocularis*. Five new species are described, namely *K. con- fusa*, *K. dasylinonicola*, *K. micranthae*, *K. ramaleyea*, and *K. rostratea*. Descriptions of species in vitro and a key to species known from culture are provided.

**Article info**

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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). Höhn (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 conidio- mata, 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 *Septoplastic* 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 ascii 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...
suggested placement in Piptarthron while the presence of unilocular conidial support placed support in Kellermania. Ramaley (1993) circumscribed Planistroma, the sexual state of Kellermania, and noted that it was similar to Planisporium but distinct in having septate ascospores. The genus originally included two new species that were correlated with one new species having septate ascospores. The genus originally did not embrace synonymising the asexual and sexual states. Ramaley (1993) circumscribed it as having two new species with both asexual and sexual states and provided a key to the species of Kellermania and Piptarthron. Most notably among the new species was Planistroma torsiiflorum, 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 Piptarthron and Planistroma states. Planistroma kellermaniae, which has asceptate 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 Planistromellaceae to accommodate “taxa having ascostroma, interthelial tissues, and schizogenously formed, periphyseal ostioles”. Planistromella and Planisporium 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 *Laratospora*, *Euplotia*, *Microcylus*, and *Mycosphaerellopsis* were also classified in *Planistromellaceae*. 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 *Planistromellaceae* and the *Dothideomycetes*? 2) Are the *Planistromellaceae* and its genera monophyletic? 3) Does morphology of conidial appendages or ascospore septation correlate with phylogeny? and 4) Are slight morphogenetic 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=, W=, and Q=, 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 regime. 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 Komerup & 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 *Planistromellaceae* among the *Dothideomycetes*, sequences of the SSU and LSU from the type species of *Kellermania*, *Piptarthron*, *Planistroma*, and *Planistromella* 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 GTR+GAMMA 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 *Planistromellaceae* 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 *Planistromellaceae* 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 Croust et al. (2006), Phillips & Alves (2009), and Schoch et al. (2009); plus type species of genera of *Kellermania*, *Piptarthron*, *Planistroma*, and *Planistromella* as well as at least one representative of each major clade of core *Planistromellaceae* 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.

<table>
<thead>
<tr>
<th></th>
<th>Dothideomycetes alignment</th>
<th>Botryosphaeriaceae alignment</th>
<th>Kellermania alignment</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSU</td>
<td>283</td>
<td>1027</td>
<td>473 (46%)</td>
</tr>
<tr>
<td>ITS</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
</tr>
<tr>
<td>LSU</td>
<td>327</td>
<td>1853</td>
<td>669 (37%)</td>
</tr>
<tr>
<td>RPB1</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
</tr>
<tr>
<td>Combined</td>
<td>342</td>
<td>2880</td>
<td>1162 (40%)</td>
</tr>
</tbody>
</table>

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 monophony 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. pluriocularis* AR 3467, *K. ramalayae* 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
the exception of a well-supported clade (bs = 99 %) containing the type species of the genera Kellermania, Piptarthron, Plani-
stroma, and Planistromellaceae (phylogram not shown). Bayesian inference of the Botryosphaeriaceae
alignment suggested that Planistromellaceae is one of five monophyletic members of Botryosphaeriaceae s.l. (see Dis-
cussion); i) Bagnisella examinans; ii) Saccharata proteae; iii) Melanops (pp = 1.0); iv) Planistromellaceae (pp = 1.0); and v) the remaining members of the family including the core mem-
bers 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. dasylirionicoila 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. uni-
septata AR 3476, K. yuccifoliorum AR 3472, and K. yuccigena AR 3470, and another containing K. anomal a 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 Planistromellaceae 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 line-
ages: i) Kellermania macrospora AR 3468, K. confusa AR 3469, K. ramale yae MEP 1260, and K. rostratae JBS.16.11-01 (pp = 0.89); ii) K. yuccig ena 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. da-
sylirionicoila AR 3465, and K. plu ilocularis 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 Da-
sylirionis (subfamily Nolinoideae) with the exception of K. plu-ilocularis AR 3467 on Yucca (Fig. 2). Lineages i–iii possess septate ascospores and lineages iv–v possess aseptate as-
cospores, 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,
and bear 0–multiple apical appendages. A less useful character included the presence of a frill at the base of conidia. Conidia, often germinate quickly and, in some cases, were exuded from conidiomata in whitish, mucilaginous masses, which developed within weeks or sometimes only after months, e.g., *Planistromella yuccifoliorum* A.W. Ramaley. = A.W. Ramaley as 'Planistroma yuccigenum'. Type species *Petr.*

### 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 macrosporum* (Durieu & Mont.) Höhn.


**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 (Lm = 52.3 μm, Wm = 7.3 μm, Qm = 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 microfungi.

Habitat & Distribution — Dead leaves of *Yucca* spp. (Morgan-Jones et al. 1972b, Nag Raj 1993, Farr & Rossman 2012). The type was found on *Y. dracaonis* (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 Germ 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. anomalata* 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. — Myco-Bank 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 margin uncoloured. *Conidia* 38.5–64 × 6.5–9.5 μm, Q = 4.8–8 (Lm = 49.9 μm, Wm = 8.3 μm, Qm = 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


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).


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

Etymology. This species is named for its occurrence on Dasylirion leiosphyllum.

Culture characteristics — Colonies on PDA 22–25 mm after 2 wk at 24 °C with a 12 h light/dark regime; 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 (Lₐ = 39.4 µm, Wₐ = 4.5 µm, Qₐ = 9.0), more or less cylindrical with irregularly curved shape, flexuose, 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 leiosphyllum. It is known only from the type locality in the USA: TX.


Notes — Although similar to Kellermania dasylirionis, this second species on Dasylirion is distinguished by its asceptate conidia with irregular, curved shapes and slower growth on PDA. Ramaley (in litt.) noted asceptate, 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


Culture characteristics — Colonies on PDA 45–52 mm after 2 wk at 24 °C with a 12 h light/dark regime; surface near greenish grey (30C1), with scattered low, hyphae between 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 (Lₐ = 57.1 µm, Wₐ = 7.2 µm, Qₐ = 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 leiosphyllum, 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 leiosphyllum, 1903, 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 MB801100; Fig. 5, 6


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

Hendersonia piptarthica 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.) Höhnel, Hedwigia 60: 203. 1918.

Culture characteristics — Colonies on PDA 52 mm after 2 wk at 24 °C with a 12 h light/dark regime; 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 (Lₐ = 72.2 µm, Wₐ = 9.0 µm, Qₐ = 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) (Höhnel 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, 110 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 multi-septata, 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 regime; 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 (Lₐ = 49.2 µm, Wₐ = 8.6 µm, Qₐ = 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.


Notes — This species is distinguished from the others known from Nolina by the combination of its asceptate 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 zotoli. 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. nolinifolium (AR 3473); e. K. plurilocularis (AR 3467).
(Ramaley 1998) with aseptate, Planistroma-type asexual spores, which was found on the type specimen of P. kellermaniae on Nolina erumpens in Texas, has an anamorph that is similar to K. micranthae 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


**Culture characteristics** — Colonies on PDA 20–22 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 = 40.5 µm, W = 8.8 µm, Q = 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, NM, 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 AWG 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


**Culture characteristics** — Colonies on PDA23–26 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 × 5–9.5 µm, Q = 5.6–9.3 (L = 49.1 µm, W = 7.1 µm, Q = 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 AWG 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


= 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 = 41.5 µm, W = 6.0 µm, Q = 7.2), slightly curved, falcate, to strongly curved narrowing 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 AWG 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 ramaleyaee** 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 Planistromellaceae and coelomycetous anamorphs.

On host (holotype): Folicilicious, 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 × 11–16 µm, Q = 4.3–5.3 (L = 58.8 µm, W = 12.6 µm, Q = 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 = 42.7 µm, W = 12.3 µm, Q = 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).
Notes — This species is distinguished from the others that occur on Yucca by its conidia in culture with 2–4 septa, $Q = 2.6–4.6$, and appendages lacking. Some differences were observed in dimensions of conidia produced on the host vs in culture. A loculoascomycete 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): **Folicolous**, 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, multicellular. **Conidiophores** absent. **Conidigenous cells** lining the basal and lateral, locular walls, more or less doliform to slightly cylindrical. **Conidia** $30.5–48 \times 5–6.5 \mu m$, $Q = 6.3–9.3$ ($L_{m} = 41.3 \mu m$, $W_{m} = 5.3 \mu m$, $Q_{m} = 7.8$), 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 $33.5–62.5 \times 5–9.5 \mu m$, $Q = 4.2–9$ ($L_{m} = 44.1 \mu m$, $W_{m} = 7.1 \mu m$, $Q_{m} = 6.3$), 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. Mexco, 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. 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 MB001104; Fig. 8


On host (isotype of Piptarthron uniloculare): Conidia 48–72 x 8–9.5 µm, Q = 5–7.6 (L = 56.4 µm, W = 9.0 µm, Q = 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, and 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 9816 (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 ascu (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 stroma. Its asceptate ascospores distinguish it from both lineages. This is the only species in or closely related to lineages i–iii (Fig. 2) with asceptate 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


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, cottytony hyphae; margin uneven, whitish; reverse off white to nearly concolourous with upper surface. Conidia 27–45 x 8–17.5 µm, Q = 2–4.2 (L = 35.8 µm, W = 12.4 µm, Q = 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).


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


Basionym. Neottioceras yuccifolia J.G. Hall, Phytopathology 5: 57. 1915 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 records (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


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, cottytony to velutinous hyphae; margin uneven, whitish; reverse grey to black. Conidia 40–65.5 x 8–11 µm, Q = 3.9–7.4 (L = 52.6 µm, W = 9.8 µm, Q = 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

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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 ‘yucaegenae’. — Fig. 7, 8

= Planistromella 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 even, white; reverse greyish with black conidiomata visible. Conidia 37–56 × 8–13 μm, Q = 3.3–6.2 (L = 48.2 μm, W = 10.1 μm, Q = 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. medially 1(–2)-septate; walls smooth, thin and hyaline, and not or slightly constricted at septa; contents hyaline; appendages present, 5–35 μm (L = 19.6 μm) 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).


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.

= Planistromella 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 *Stigmina* 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.

= Planistromella 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.


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 *Planistromella parryi* (Barr 1996).


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*.


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 macrosorum* by Sutton (1980), this seems to be a distinct species on *Yucca*.


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, asperate. 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 asperate 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*.


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 *Planistromellula parryi* and *Plowrightia agaves* (Barr 1996).


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 asperate 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 asperate. 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 asperate with septate conidia.

**KEY TO KELLERMANIA SPECIES IN CULTURE**

1. Colony distinctly pink ................................ 8. Conidia 2–3-septate, Q = 3.9–7.4, middle cell longer than end cells .................. *K. yucciflorum*
2. Colony not pink ........................................ 9. Conidia asperate ........................................ 4. Conidia 2–3-septate, Q = 5.0–14.3, middle cell shorter than end cells ........ *K. anomala*
4. Conidia 1-septate ....................................... 11. Conidia slightly curved, falcate, to strongly curved, nearly U-shaped .................. *K. plurioculata*
5. Some conidia more than 1 septate .................. 12. Conidia mostly 0–1-septate .......................... *K. rostrata*
6. Conidia with 4 or more septa ........................ 13. Conidia typically with some degree of curvature .................. *K. dasylinonis*
7. Some conidia with 1 apical appendage ............... 14. Conidia 1–3 (mostly 2)-septate ...................... *K. confusa*
8. Some conidia with no apical appendage ............. 15. Some conidia with more than 5 septa, Q = 4.9–13 ....... *K. macrospora*
9. Conidia typically cylindrical to obclavate . *K. ramalaeae*
10. Conidia typically with more than 5 septa, Q = 4.9–13 ....... *K. macrospora*
11. Conidia mostly with 2 or more septa ................ 16. Conidia 2–4-septate, Q = 2.6–4.6 .................... *K. yuccifolia*
12. Conidia mostly with 2 or more septa ................ 17. Conidia 2–4-septate, Q = 5–7.6 ..................... *K. unilocularis†
13. Conidia typically cylindrical to obclavate . *K. rostrata*
14. Conidia typically with some degree of curvature .................. *K. dasylinonis*
15. Some conidia with more than 5 septa, Q = 4.9–13 ....... *K. macrospora*
16. Conidia 2–4-septate, Q = 2.6–4.6 .................... *K. ramalaeae*
17. Conidia 2–4-septate, Q = 5–7.6 ..................... *K. unilocularis†

**DISCUSSION**

Phylogenetic analyses support the placement and monophyly of the core *Planistromellaceae* in the order *Botryosphaeriales* of class *Dothideomycetes* where the *Planistromellaceae* represent a well-supported clade comprised of the coelomycetous genera *Alpakesa*, *Kellermania*, and *Piptarthron* with associated teleomorphic genera *Planistroma* and *Planistromella*. Within *Botryosphaeriales*, it is positioned in a polytomy with four other lineages of *Botryosphaeraceae* 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 *Botryosphaeraceae* (Fig. 1). This core *Botryosphaeraceae* 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 *Botryosphaeraceae* has been recognised with a broad circumscription, i.e. sensu lato (Philips & Alves 2009), and *Planistromellaceae* could well be treated as a later synonym, we prefer to maintain the family *Planistromellaceae* as distinct from *Botryosphaeraceae* s.str. and suggest that further sampling is needed to clarify familial classification within the *Botryosphaerales*. The *Planistromellaceae* is significantly phylogenetically distinct from the *Botryosphaeraceae*. All genera of core *Planistromellaceae* are here considered to constitute one genus, namely *Kellermania*. Four other genera classified in *Planistromellaceae* (Barr 1996) are redescribed as follows: *Eruptio* has been shown to be a member of *Mycosphaerellaceae* (Verkley et al. 2004); *Loratospora* has been shown to be a member of the *Phaeosphaeriaceae* (Schoch et al. 2009); and none of the species of *Mycosphaerellaceae* including the type species, *M. mycriciae* (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 *Botryosphaeriales*. The closest hits resulting from the BLAST searches are members of the *Mycosphaerellaceae*, but its familial classification is uncertain.
Among the Planistromellaceae (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 Planistromellaceae (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 (≡ P. 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 Planistromella for which DNA sequence data exist including the type species, Planistromella yucciformis (≡ K. yucciformis). 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 asceptate 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. crassispisorum (≡ K. crassispora), belong to lineage iv and Planistroma kelleriana, linked to Kellermania nolinae, represents lineage v. Thus, Planistroma and Planistromella 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, ii–iii, and iv (Fig. 2) are largely correlated with plant hosts from different host clades in the Asparagaceae, subfamilies Agavoideae and Nolinioideae 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 Botryosphaeriales are known to inhabit multiple hosts (van Niekerk et al. 2004, Gienke et al. 2011).

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REFERENCES
