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Use of holomorph characters to delimit *Microascus nidicola* and *M. soppii* sp. nov., with notes on the genus *Pithoascus*

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Abstract: Several isolates of a perithecial microascaceous ascomycete having falcate ascospores and a *Scopulariopsis* anamorph were obtained from rotting wood in the boreal forest of Alberta, Canada. Additional isolates appeared conspecific based on anamorphic characters, but failed to produce a teleomorph. These isolates showed similarities to *Microascus nidicola* (type species of the genus *Pithoascus*) and *Scopulariopsis flava*. Sexual compatibility systems were investigated to establish holomorph concepts for these taxa. The teleomorph obtained in mating trials among anamorphic isolates was identical to that of self-fertile isolates. The new heterothallic species *M. soppii* is described. The anamorph is *S. soppii*. Single ascospore isolates derived from *M. nidicola* demonstrated homothallism and lacked an anamorph. *Scopulariopsis flava* (basionym *Acaulium flavum*) is considered a nomen dubium. Generic concepts of *Pithoascus* are evaluated and the genus is treated as a synonym of *Microascus*. *Pithoascus stoveri* is transferred as *M. stoveri* comb. nov.

Key Words: anamorph-teleomorph connections, Ascomycota, hyphomycetes, Microascaceae, *Scopulariopsis*

INTRODUCTION

Studies of rotting wood from the boreal forest in Alberta, Canada (Lumley et al 2000), yielded several isolates of a perithecial ascomycete that formed falcate ascospores and a well-developed anamorph. Several additional isolates from wood appeared to be the same species but failed to produce a teleomorph in culture. The anamorph resembled *Scopulariopsis flava* (Sopp) Morton & G. Smith (Morton and Smith 1963). Ascospores were similar to those of *Microascus nidicola* Massee & E.S. Salmon (Massee and Salmon 1901), but no anamorph has previously been associated with that species (Arx 1973a, Barron et al 1961).

Since its description from dung in England, *M. nidicola* has rarely been reported. The modern concept of the species is based on three living cultures established by C.W. Emmons from rodent dung and soil collected in the desert region of Utah (Barron et al 1961, Morton and Smith 1963, Arx et al 1988). *Microascus nidicola* has falcate to lunate (concavoconvex to planoconvex in face view and fusoidal in edge view) ascospores that are proportionally long and narrow (l:w ca 3:1) (6–8 × 2–2.5 μm). Most other *Microascus* species have broadly reniform ascospores, including the type, *M. longirostris* Zukal (typically 4.5 × 3 μm).

Differences in ascospore shape and other distinctions led Arx (1973a) to establish the genus *Pithoascus* with *M. nidicola* as type. Characters uniting species within the genus included the unique, falcate ascospore morphology, perithecia that were nonostiolate or indistinctly ostiolate and lacking a distinct neck, ascospores without a germ pore, and no anamorph (Arx 1973a, b, 1978). Benny and Kimbrough (1980) erected the family Pithoascaceae, typified by *Pithoascus*, and separated it from the Microascaceae based on the absence of germ pores on the ascospores. More recently, *Pithoascus* has been treated as a valid genus of the Microascaceae (Greuter et al 1993, Eriksson and Hawksworth 1998) containing six species (Arx et al 1988). However, the characters delimiting the genera *Pithoascus* and *Microascus* overlap and the generic separation has not been universally accepted (e.g., Malloch and Hubart 1987). Some species of *Pithoascus* have ascomata that produce, upon aging, a cirrus of ascospores from a prominent ostiole, while others exhibit a 'reduced' *Scopulariopsis* anamorph, i.e., less well developed than most reniform-spored members of the genus *Microascus* (Roberts 1975, Valmaseda et al 1987, Arx et al 1988).

Originally described as *Acaulium flavum* Sopp (1912), *Scopulariopsis flava* was grouped with several anamorphic species in the '*Scopulariopsis brevicaulis*

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Series' by Morton and Smith (1963). Our Alberta isolates were morphologically similar to their concept of *S. flava*, but no type material is extant. Few isolates are available for study and one that was received under this name represented *S. brevicaulis* (Sacc.) Bainier (Abbott and Sigler 2001). Sopp's original description referred to a poorly developed, 'sclerotium-like' sexual stage.

Anamorph characters and compatibility suggested that *M. nidicola* and the Alberta isolates might represent separate species. Since single ascospore isolates and mating trials successfully demonstrated heterothallism and helped to elucidate holomorph concepts for several other species within the '*S. brevicaulis* Series' (Abbott and Sigler 2001), this experimental method was used here to evaluate relationships among isolates thought to represent *S. flava* and *M. nidicola*. Generic concepts for *Pithoascus* are reviewed and arguments in support of its synonymy with *Microascus* are presented.

MATERIALS AND METHODS

Isolation and morphology.—White spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) logs of diameter greater than 15 cm and at various stages of decomposition were sampled from sites in the boreal forest of north-central and northeastern Alberta during the summers of 1996–1998. All samples were surface sterilized by brief flaming, and then plated onto several different media for primary isolation and purification (Lumley et al 2000). Living cultures and holotype herbarium material are maintained in the University of Alberta Microfungus Collection and Herbarium (UAMH). Isotype material is deposited in the Herbarium, Royal Botanic Gardens, Kew (K).

Colonial features were recorded and colony diameters were measured on oatmeal salts agar (OAT; Kane et al 1997) at 25 C after 7, 14, 21, and 28 d. Microscopic mounts were prepared in polyvinyl alcohol or lactofuchsin mounting medium using the slide culture method for observation of conidiogenesis and squash mounts for observation of ascomata (Kane et al 1997). Material for scanning electron microscopy (SEM) was fixed in 2% OsO_4 vapor and critical-point dried for examination with a Hitachi S-2500.

Microascus nidicola *single ascospore isolates.*—Nine single ascospore isolates were obtained from an Emmons collection of *M. nidicola* (UAMH 8979). One perithecium was removed, crushed in 5 mL of sterile water to suspend the ascospores, and 1 mL of the suspension was spread across each of four Takashio agar (Kane et al 1997) plates. These were incubated at 22 C for 3–7 d to promote germination. A hyphal tip was excised from each of 9 colonies resulting from germination of a single ascospore and transferred to individual OAT plates. These isolates were evaluated for expression of anamorph and teleomorph.

Scopulariopsis *species mating tests.*—Eight isolates were included in mating tests. These included five isolated from wood in Alberta and three others tentatively identified as *S. flava* (sensu Morton and Smith 1963). Conidia from each test strain were suspended in semisolid detergent agar (SSD; Pitt 1973) and streaked onto one half of an OAT plate, allowing for a central zone of contact as the isolates grew. Crosses were made in all combinations, including self crosses. Plates were incubated at 22 C and examined after 6 wk and periodically up to 12 mo. Wild-type isolates that yielded a fertile cross were designated as plus (UAMH 9202) or minus (UAMH 9171) mating types. These were back-crossed to a fourth strain (UAMH 9139) that had been received as *S. flava* but later redetermined by mating trials as *S. brevicaulis* (Abbott and Sigler 2001). Perithecia obtained in crosses were compared with those formed by self-fertile wild-type isolates.

TABLE I. Mating reactions among isolates of *Scopulariopsis soppii* on OAT at 12 mo

S. soppii wild-type strains		
	Plus mating type	
Minus mating type	9202	942[a]
9170	+[b]	−
9171	+	I[c]
9172	+	−
9201	+	−

[a] Isolate identified as *S. flava* by Morton and Smith (1963).

[b] +, ascomata with ascospores produced.

[c] I, infertile ascomata produced.

RESULTS

Microascus nidicola.—All single ascospore isolates obtained from the Emmons collection of *M. nidicola* (UAMH 8979) were homothallic and produced abundant, fertile ascomata on OAT within 8 wk. No anamorph was observed in cultures obtained from these single ascospore isolates.

Scopulariopsis *species.*—Five of eight strains demonstrated fertility in matings (TABLE I). Only four pairings, all among isolates from Alberta, produced ascomata with ascospores. One additional strain (UAMH 942), identified as *S. flava* by Morton and Smith (1963), produced infertile perithecia with UAMH 9171 along the contact zone, but no ascospores were produced even after one yr. Two other strains identified as *S. flava* (UAMH 831 and 8895) did not form any sexual structures.

The perithecia, ascospores and conidia of the heterothallic strains were compared with those of self-fertile strains obtained from wood, and found to be identical in all respects. No fertility was expressed in crosses between minus (UAMH 9171) and plus (UAMH 9202) mating strains and the strain (9139)

that had been reidentified as *S. brevicaulis* (Abbott and Sigler 2001). Based on these results, the new species *M. soppii* is described and distinguished from *M. nidicola* by its faster growth in culture, presence of *Scopulariopsis* anamorph and heterothallism.

Microascus soppii S.P. Abbott, sp. nov. FIGS. 2, 4, 7, 9–11

Anamorph: *Scopulariopsis soppii* S.P. Abbott sp. nov.

Perithecia 130–200 × 110–160 μm, globosa vel subglobosa, ostiolata, papillata, nigra; peridia texturae angularis; asci octospori, globosi vel subglobosi, deliquescentes; ascosporae 6–7 × 2.5–3 μm, falcatae vel lunatae, laeves, subhyalinae vel aurantiacae in cumulis; conidiophora annellata; conidia 5.5–9 × 5–8 μm, subglobosa, verrucosa, subhyalina. Heterothallicus. Holotypus UAMH 9169.

Perithecia 130–200 × 110–160 μm, globose to subglobose or pyriform, with a papillate to short-necked (up to 40 μm) ostiolar region, black; peridium of textura angularis, peridial cells typically 6–10 × 4–5 μm, appendages lacking. *Asci* 9–14 × 6–7 μm, irregularly ovoidal, 8-spored, deliquescent at a very early stage and infrequently observed (evanescent). *Ascospores* 6–7 × 2.5–3 μm (typically 6 × 2.5 μm), falcate to lunate (typically plano-convex or infrequently concavo-convex) in face view, fusoidal in dorsal view, orange in mass, appearing subhyaline in transmitted light, smooth, lacking de Bary bubbles and guttules, with single germ pore. *Conidia* 5.5–9 × 5–8 μm diam, globose to subglobose, with truncate, sometimes slightly protruding (lightbulb-shaped) bases, subhyaline to pale yellowish in mass, smooth to finely ornamented or commonly verrucose with prominent, irregular warts at maturity, produced in dry chains from simple or branched annellidic conidiogenous apparati; annellides 3 μm diam at apex, elongate ampulliform, hyaline. *Colonies* mainly conidial, pale yellow-buff, velutinous to fasciculate, shallowly convex, margin entire and white, moderately fast growing, 47–60 mm diam on OAT after 14 d. Heterothallic.

Specimens examined. Microascus soppii. CANADA. ALBERTA: Elk Island National Park, dried colony on OAT at 25 wk ex wood, dry rotted log of aspen (*Populus tremuloides*), 09 Jun 1997, *T. Lumley and S.P. Abbott EI-13-S4G* (HOLOTYPE and ex-type culture UAMH 9169, ISOTYPE K); wood, rotted log of white spruce (*Picea glauca*), 1996/1997, *T. Lumley and S.P. Abbott EI-09- S3D/E/F/G/J* (PARATYPES UAMH 9167, 9168, 9170, 9171, 9172); wood, dry rotted log of aspen (*Populus tremuloides*), 06 Dec 1997, *T. Lumley EI-13-S3G* (PARATYPE UAMH 9492); wood, extremely well-decayed log of white spruce (*Picea glauca*), 26 Nov 1996, *T. Lumley EI-02-S3A* (PARATYPE UAMH 9201); Slave Lake, wood, well-rotted log of aspen (*Populus tremuloides*), 25 Feb 1997, *T. Lumley H681–01-S2F* (PARATYPE UAMH 9202); USA. CALIFORNIA: Pacific Grove, sandy loam soil, *A.L. Cohen* (UAMH 942; =NRRL 1848; =IMI 86923; =LSHB Sc. 68).

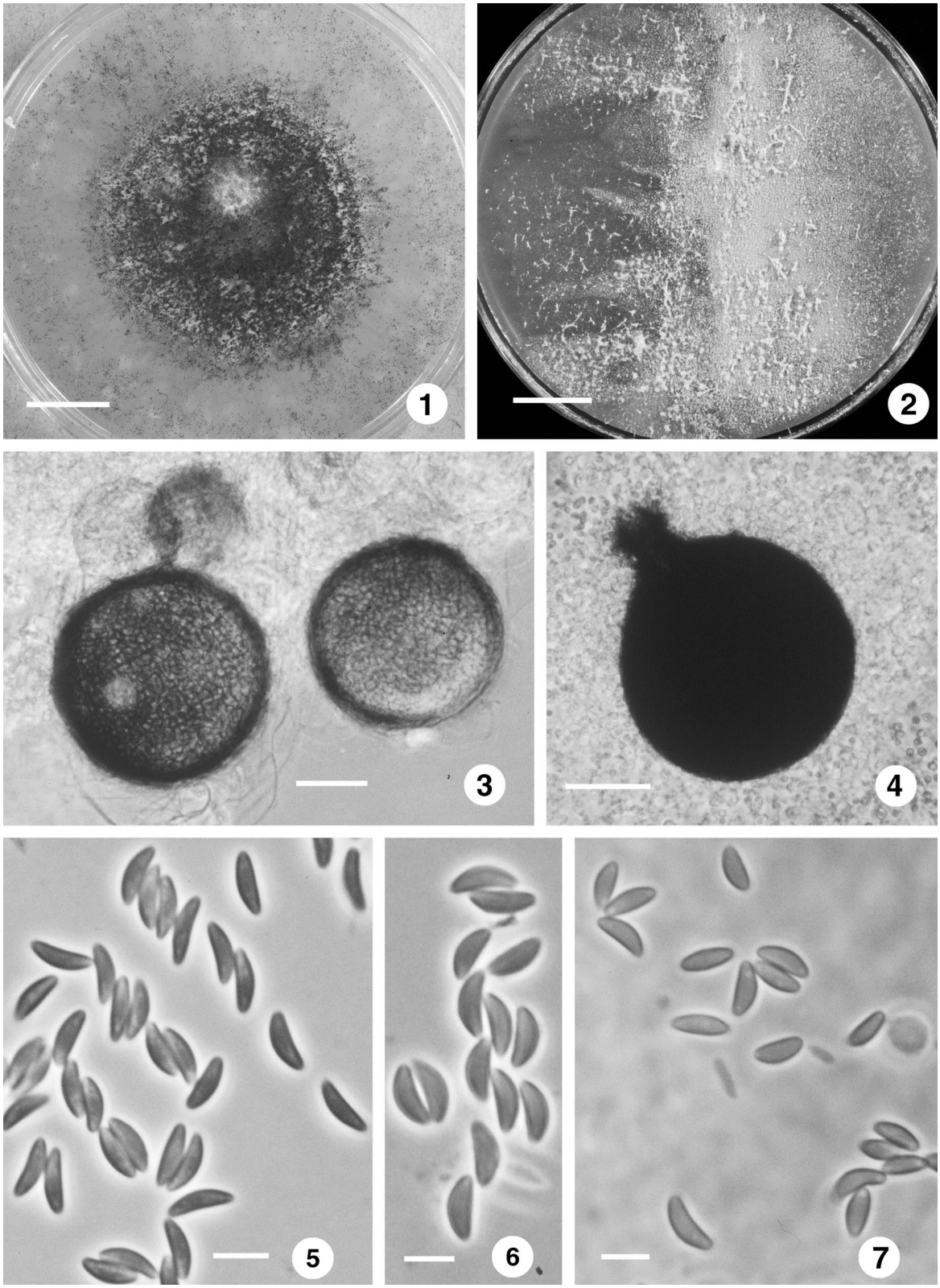
Etymology. after Olav Sopp for his studies of the life histories of species of Microascaceae.

Commentary. The mating behavior of *M. soppii* is consistent with that demonstrated in the heterothallic species *M. brevicaulis* S.P. Abbott, *M. manginii* (Loub.) Curzi, and *M. niger* (Sopp) Curzi (Abbott and Sigler 2001). *Microascus brevicaulis* was described for several self-fertile isolates (Abbott et al 1998), but these were later demonstrated to be heterothallic by single ascospore isolation (Abbott and Sigler 2001). The self-fertile ex-type strain of *M. soppii* produced ascomata on the primary isolation plate and when recovered from lyophilized or cryopreserved stocks. Although germ pores are often difficult to observe, a mount from one isolate (UAMH 9167) revealed a single germ pore in many of the ascospores and these spores exhibited germination morphology typical of other members of the genus.

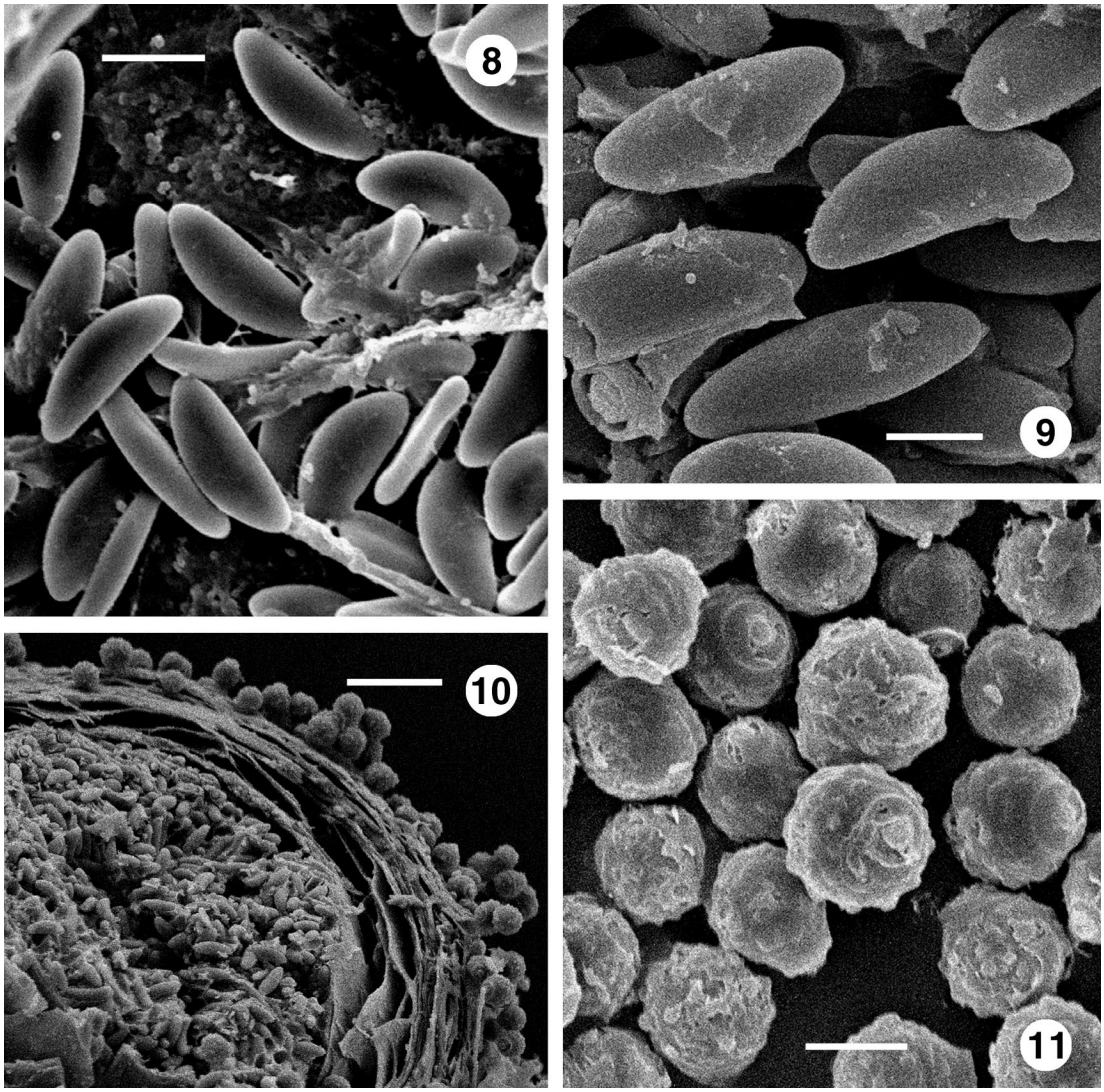
Acaulium flavum was transferred to *Scopulariopsis* by Morton and Smith (1963) for isolates with pallid yellow to buff, ornamented conidia. Although Sopp reported the presence of a poorly developed teleomorphic state and described ascospores within asci as 'oval-round,' he did not illustrate the ascospores or provide measurements in the protologue. Curzi (1931) who transferred several of Sopp's species with teleomorphic stages to the genus *Microascus* [e.g., *M. albonigrescens* (Sopp) Curzi and *M. niger*], did not transfer *A. flavum.* Because a teleomorph was described by Sopp (Sopp 1912), the epithet flava cannot be applied to *Scopulariopsis.* Although the epithet is available for combination in *Microascus*, Sopp's description is too vague to make an accurate diagnosis. Because of the lack of extant type material and the uncertain application of the name by Morton and Smith, *Acaulium flavum* is here considered a *nomen dubium.*

The three strains discussed by Morton and Smith (1963) as *S. flava* represent a heterogenous assemblage. Mating trials proved one strain (UAMH 9139, =LSHB 60) to be *M. brevicaulis* (Abbott and Sigler 2001). A second strain (UAMH 942, =LSHB Sc 68) is identified here as *S. soppii.* This strain, obtained from soil in California, is morphologically identical to the Alberta isolates, and produced infertile ascomata with a single strain in mating trials (TABLE I). Given the length of time required to obtain fully fertile ascomata in matings for this species (results given here after 12 mo) and other species of *Microascus* (12–19 mo, Abbott and Sigler 2001), it is possible that the infertile strain could mate given the appropriate time and conditions.

The identity of the other isolate is uncertain. UAMH 8895 (LSHB Sc. 7), was isolated from cheese in the United States in 1948 and determined origi-



FIGS. 1–7. *Microascus nidicola*, *M. soppii*, and *M. stoveri*. 1. *M. nidicola* perithecia forming on OAT after 14 d at 25 C (UAMH 8979; EPITYPE). 2. Mated strains of *M. soppii* on OAT after 19 mo at 25 C showing central contact zone and confluent growth of *S. soppii* anamorph (UAMH 9170 left × UAMH 9202 right). 3. *M. nidicola* perithecium showing ostiole (UAMH 8979, EPITYPE). 4. *M. soppii* perithecium (UAMH 9169; HOLOTYPE). 5. *M. nidicola* ascospores (UAMH 8980). 6. *M. stoveri* ascospores (UAMH 9138). 7. *M. soppii* ascospores (UAMH 9169; HOLOTYPE). Bars: 1, 2 = 15 mm, 3, 4 = 50 μm, 5 = 6.5 μm, 6 = 5 μm, 7 = 5.5 μm.



FIGS. 8–11. *Microascus nidicola* and *M. soppii* (SEM). 8. *M. nidicola* ascospores (UAMH 9488). 9. *M. soppii* ascospores (UAMH 9169; HOLOTYPE). 10. *M. soppii* perithecium in cross-section showing ascospores inside and conidia outside (UAMH 9169; HOLOTYPE). 11. *M. soppii* globose to subglobose, verrucose conidia with slightly protruding and truncate base (UAMH 9169; HOLOTYPE). Bars: 8 = 4 μm, 9 = 2.2 μm, 10 = 15 μm, 11 = 5 μm.

nally as *S. brevicaulis* var. *alba* Thom. It appeared similar to the ex-type strain (UAMH 831) of *Blastomycoides lanuginosus* Castell., a name of uncertain application. This species was illustrated and discussed by Agostini (1931) as *Glenospora lanuginosa* (Castell.) Agostini, based on a clinical isolate having solitary aleurioconidia, but our examination of the ex-type culture revealed some short chains of smooth to ornamented conidia produced from annellides. These strains failed to mate with isolates of *S. soppii*, and they may represent pale spored variants of *S. brevicaulis*. An authentic isolate of *S. brevicaulis* var. *alba* (UAMH 926) (Thom 1930), originally isolated from cheese, was examined and determined to be a pale variant of *S. brevicaulis*. *Scopulariopsis casei* Loubière, also isolated from cheese, may be considered another potential synonym of *S. brevicaulis*.

Microascus nidicola Massee & E.S. Salmon. 1901. Annals of Botany (London) 15:313. FIGS. 1, 3, 5, 8
≡ *Pithoascus nidicola* (Massee & E.S. Salmon) Arx. 1973. Proc. Kon. Nederl. Akad. Wetenschappen, Ser. C, 76: 292.

Epitype culture selected UAMH 8979 (=NRRL A-6894, =CBS 197.61, =IMI 86918, =LSHB Sc. 44).

Distinguishing morphological characters. Perithecia black, globose to ovoid, papillate; peridium of textura angularis; asci evanescent, irregularly subglobose, 8-spored; ascospores falcate to lunate (concavoconvex to planoconvex in face view and fusoidal in edge view), long and narrow (l:w ca 3:1), 6–8 × 2–

2.5 μm (typically 7 × 2 μm); homothallic. Anamorph absent. Colonies slow growing (20 mm diam in 14 d), mycelium white, developing abundant perithecia producing ascospores in orange droplets or in short cirri at maturity (after 3–4 mo).

Specimens examined. USA. UTAH: Kangaroo rat (*Dipodomys merriami*), Oct 1956, *C.W. Emmons A1671,* (EPITYPE UAMH 8979; =NRRL A-6894; =CBS 197.61; =IMI 86918; =LSHB Sc. 44); soil, Oct 1956, *C.W. Emmons A1836,* (UAMH 8980; =NRRL A-6913). CANADA. ALBERTA: Single ascospore isolates ex UAMH 8979, 10 Jul 1998, *S.P. Abbott Mn-4, Mn-8* (UAMH 9487, 9488).

Commentary. Although it has rarely been reported since its early discovery (Massee and Salmon 1901), *M. nidicola* is readily distinguished from other members of the genus by ascospore size and shape. Although a holotype exists, most modern descriptions have been based on the living strain selected here as epitype (Barron et al 1961, Morton and Smith 1963, Arx et al 1988), that matches the protologue in all respects. The isolate (CBS 103.85, = UAMH 9136) illustrated by Arx et al (1988) as representative of *M.* (*Pithoascus*) *nidicola*, but noted to have an anamorph, was re-examined and found to represent *M. intermedius* Emmons & Dodge. *Microascus intermedius* has smaller ascospores (typically 5.5 × 2.5 μm) and isolates may produce a reduced anamorphic stage. Isolates examined here as typical *M. nidicola* did not produce an anamorph.

DISCUSSION

The discovery of another *Microascus* species with falcate ascospores led to reexamination of the grounds for generic distinction of *Pithoascus*. *Pithoascus*, for which *M. nidicola* is the type, has been separated by longer, narrower and paler ascospores without germ pores, nonostiolate or indistinctly ostiolate ascomata without necks, and generally lacking anamorphs (Arx 1973a, b, 1975, Arx et al 1988). However, these characters vary among the species included in *Pithoascus* and overlap with species retained in *Microascus*.

Ascospore shape demonstrates a gradation from reniform to lunate, rather than a sharp discontinuity, suggesting that this character is not reliable for separating the genera. While there appears to be a clear demarcation between the long and narrow (l:w ca 3:1) ascospores of *M. nidicola*, *M. schumacheri* (Hansen) Curzi, *M. exsertus* Skou, and *P. stoveri* Arx (FIGS. 5, 6, 8) compared with the broadly reniform ascospores (l:w ca 1.5:1) of the type *M. longirostris* Zukal and similar species, ascospores of some species demonstrate intermediate morphology (l:w ca 2:1 or 2.5:1). *Microascus intermedius*, for example, was included in *Pithoascus* (Arx et al 1988), while *M. albonigrescens* with similar ascospore dimensions has not been included in *Pithoascus*.

Ascospore germ pores in *Microascus* species are indistinct and often seen best during the germination process (Malloch 1970, Malloch and Hubart 1987). During germination, the ascospore does not swell and the germ tube begins as a globose bubble at one apex before elongating. In contrast, ascospores lacking germ pores swell noticeably before rupturing to release the germ tube at any point. *Pithoascus* is defined as lacking germ pores (Arx 1975, Benny and Kimbrough 1980). The ascospores of *M. caviariformis* Malloch & Hubart (Malloch and Hubart 1987) and our new taxon, *M. soppii*, resemble those of *Pithoascus* species in shape, but they germinate from a single pore.

Arx (1973a) originally described *Pithoascus* as nonostiolate or with a rudimentary ostiole that remained covered by outer layers of the peridium. Although ascomata of many species of *Pithoascus* lack a prominent ostiolar neck, they demonstrate functional ostioles. *Microascus nidicola* (FIG. 3), *M. schumacheri*, *M. intermedius*, *M. exsertus*, and *P. stoveri* all were observed to exude ascospores in a droplet or cirrus with age. Arx et al (1988) reported that the ex-type culture of *M. exsertus* at the Centraalbureau voor Schimmelcultures was sterile, but a subculture of the same strain held at the Canadian Collection of Fungus Cultures (DAOM 146087, =UAMH 8698) produced abundant perithecia and long, red-brown cirri on OAT after 30 wk.

Conidia are absent in the type of *Pithoascus*, *M. nidicola*, and in *M. exsertus*, but have been recorded in some isolates of *M. intermedius* (Roberts 1975, Arx et al 1988), *M. schumacheri* (Valmaseda et al 1987), and *P. stoveri* (Arx et al 1988). The well developed *Scopulariopsis* anamorphs of both *M. soppii* (FIG. 11) and *M. caviariformis* provide evidence that this character is not correlated with ascospore shape and cannot be used for generic delineation.

Thus, the genus *Pithoascus* cannot be accepted as distinct. Most species of *Pithoascus* already have names in *Microascus*, including *M. exsertus*, *M. intermedius*, and *M. schumacheri*, but *P. stoveri* has not previously been treated and is here transferred. Ascospores of *P. stoveri* (FIG. 6) are very similar to those of *M. nidicola* and *M. soppii*, but differ slightly in median spore size (typically 6.5 × 2.5 μm for *P. stoveri*, 7 × 2 μm for *M. nidicola*, and 6 × 2.5 μm for *M. soppii*). The annellidic anamorph of *P. stoveri* (illustrated in Arx et al 1988) is less well developed than that of *M. soppii* and conidia are ellipsoid or ovoid and smooth. As discussed above, *M. nidicola* lacks an anamorph. Although *P. stoveri* was described as having small (50–110 μm diam) nonostiolate ascomata

(Arx 1973b), perithecia produced in the ex-type culture on OAT after 70 d produced droplets of ascospores from inconspicuous ostioles.

Microascus stoveri (Arx) S.P. Abbott comb. nov.
≡ *Pithoascus stoveri* Arx. 1973. Persoonia 7:373. (basionym)

Two other species that have been placed in *Pithoascus* are not accepted in *Microascus*. *Pithoascus langeroni* Arx (Arx 1978) has been redisposed in *Pithoascina* (Valmaseda et al 1987, Arx et al 1988) and subsequently as *Eremomyces langeronii* (Arx) Malloch and Sigler (Eremomycetaceae) based on the pseudoparenchymatous ascoma initials, cleistothecial ascomata, clavate asci, small, pale ascospores, and arthroconidial *Arthrographis kalrae* (R.P. Tewari & Macph.) Sigler & J.W. Carmich. anamorph (Malloch and Sigler 1988). *Pithoascus platysporus* Arx & Veenbaas-Rijks was described as having broadly ellipsoidal to ovoidal, reddish brown or copper colored ascospores (Arx 1975). Although the ex-type strain proved to be sterile (UAMH 9138, =CBS 419.73, see also Arx et al 1988), it demonstrated resistance to benomyl at 2 μg/mL, a trait consistent among all members of the Microascaceae (Abbott 2000). The ascospore morphology as described suggests a closer affinity to *Kernia* or *Lophotrichus* than to *Microascus*, but no illustrations were provided. A re-examination of the holotype material (CBS 419.73) is required before the disposition of this species can be determined.

The relationship of *M. soppii* to other species of *Microascus* remains unclear. Ascospore morphology, anamorph features, and mating systems suggest different potential intrageneric relationships, and it is uncertain which of these characters provides the best indicator of phylogenetic affinity.

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