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New species and new records of Meliolaceae from Panama

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Abstract Three new species of Meliolaceae, *Appendiculella monsterae* on *Monstera deliciosa* (Araceae), *Asteridiella nitidae* on *Buddleja nitida* (Scrophulariaceae), and *Irenopsis chrysophylli* on *Chrysophyllum* sp. (Sapotaceae), are described based on material collected in Panama. Eighteen species of Meliolaceae are reported for the first time for Panama, which include four first records for the Americas, viz. *Ast. formosensis*, *Meliola indica*, and *M. pisoniae*, previously known only from Asia, and *M. dissotidis* hitherto known only from Africa. Six species of plants are cited as hosts for meliolaceous fungi for the first time. In a phylogenetic hypothesis based on 28S nrDNA sequences, the position of Meliolales, including *Appendiculella*, *Asteridiella*, *Endomeliola*, *Irenopsis*, and *Meliola,* is found to be basal to Sordariomycetidae, Hypocreomycetidae, and Xylariomycetidae within Sordariomycetes. The five genera of Meliolaceae form a strongly supported clade. We suggest adopting the concept of the subclass Meliolomycetidae. The monophyly of *Asteridiella* cannot be confirmed. A hypothetical close relationship between *Asteridiella* and *Appendiculella* is not supported, but *Endomeliola* appears closely related to a species of *Asteridiella*. Two *Meliola* species on the same host family are closely related.

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Introduction

The Meliolaceae (Meliolales, Ascomycota) are a family whose members are obligate plant parasitic fungi. This family contains approximately 2,000 species, classified in 22 genera (Kirk et al. 2008). The members are also known as black mildews because they have a dark, thick-walled, branched, superficial mycelium with capitate hyphopodia and phialides; dark, superficial ascomata containing asci with poorly developed interascal tissue; asci clavate to globose, thin-walled, lacking apical structures and usually containing two to four ascospores; brown ascospores usually divided by four septa, with deep constrictions at the septa. The members of this family are found predominantly in the tropics and subtropics and have been reported from hosts belonging to over 300 different plant families (Hansford 1961; Rodríguez and Piepenbring 2007; Piepenbring et al. 2011; Pinho et al. 2012a, 2013).

Most species of Meliolaceae belong to the genera *Appendiculella* Höhn. (1919), *Asteridiella* McAlpine (1897), *Irenopsis* F. Stevens (1927), and *Meliola* Fr. (1825). The largest genus is *Meliola* with approximately 1,300 species characterized by the presence of mycelial setae. Species of *Asteridiella* (approx. 300 species) lack mycelial and ascomatal setae. *Appendiculella* (approx. 250 species) and *Irenopsis* (approx. 70 species) encompass Meliolaceae with larviform ascomatal appendages and septate ascomatal setae, respectively (Hansford 1961; Kirk et al. 2008).

Describing numerous new taxa and new records, scientists from Asia have made important contributions on Meliolales (Biju et al. 2005; Hu et al. 1996, 1999; Hosagoudar 1996, 2008; Katumoto and Hosagoudar 1989). For example, new

genera such as *Basavamyces* and *Prataprajella* and a new family, Armatellaceae, were added to Meliolales (Biju et al. 2005; Hosagoudar 1992, 2003). On the other hand, Hughes and Pirozynski (1994) described a new genus and a new species of Meliolaceae, *Endomeliola dingleyae* S. Hughes & Piroz. from New Zealand. These systematic studies were based exclusively on morphology.

Although the Meliolales contain numerous species, DNA sequences have been published only for the following species: *Asteridiella lozanellae* Rodr. Just. & M. Piepenbr. (Rodríguez and Piepenbring 2007), *Meliola juddiana* F. Stevens and *M. niessliana* G. Winter (Saenz and Taylor 1999), *Asteridiella obesa* (Speg.) Hansf., *Endomeliola dingleyae* S. Hughes & Piroz., *Irenopsis heveae* Hansf., *Meliola centellae* Pinho & O. L. Pereira and *M. vernaliae* Pinho & O. L. Pereira (Pinho et al. 2012b). Additionally, Pinho et al. (2012b) included our hitherto unpublished sequence data of *Asteridiella* sp. 1 and *Meliola variaseta* F. Stevens. The position of the Meliolales in the Sordariomycetes has not been resolved so far (Hibbett et al. 2007; Lumbsch and Huhndorf 2010; Pinho et al. 2012b) and the phylogenetic relationships of Meliolales with other orders of Sordariomycetes inferred from DNA sequences are still uncertain.

Meliolaceae in Panama have been studied since the beginning of the 20th century and the most relevant investigations of the family were done by Stevens (1927, 1928). Until 2005, only 116 species of the family were known for Panama (Piepenbring 2006, 2007; http://biogeodb.stri.si.edu/fungi). Rodríguez and Piepenbring (2007) published two new species of *Appendiculella* for Panama (*A. lozanellae* Rodr. Just. & M. Piepenbr. and *A. chiriquiensis* Rodr. Just. & M. Piepenbr.) and 22 species with four variaties were recorded as new for this country (Kirschner et al. 2010; Araúz and Piepenbring 2012; Piepenbring et al. 2011, 2012).

In this paper, the new species and new records described for Panama are based on morphology of new collections. The phylogenetic positions of meliolaceous taxa are inferred from 28S rDNA sequence analyses. The position of Meliolales in relationship to other Sordariomycetes, the relationships between genera of Meliolales and in order to evaluate the morphology-based generic concepts, the correlation of clades of these parasitic fungi was compared with known clades of host plants.

Materials and methods

Collection, preservation, and identification of material

Plants with meliolaceous fungi were collected between 2003 and 2006 in Chiriquí province in western Panama. Hyphae and perithecia were mounted in water or 5 % KOH for light microscopy. Semipermanent preparations were made by mounting material in a droplet of following solution: distilled water (60 mL), lactic acid (35 mL), glycerine (10 mL), polyvinyl alcohol (10 g), chloral hydrate (50 g), and cotton blue (0.015 g) (Rodríguez and Piepenbring 2007). The new collections were deposited at the Herbario Nacional of the Universidad de Panamá (PMA). Specimens of Meliolaceae were identified using Hansford (1961, 1963) and by comparison with specimens loaned from the herbaria BPI (Beltsville: U. S. National Fungus Collections, U.S.A.), DAR (Plant Pathology Herbarium, Orange Agricultural Institute, Forest Road Orange, New South Wales, Australia), K (Royal Botanic Gardens, Kew, England, U. K.), M (Botanische Staatssammlung, München, Deutschland), PMA (Herbarium of the University of Panama, Panama), and S (Herbarium, Botany Departments Swedish Museum of Natural History, Stockholm, Schweden).

The unpublished DNA sequence data of *Asteridiella* sp. 1 (ppMP 796, EF094839 from Panama) is designated below as that of *Asteridiella nitidae* Rodr. Just. and that of *Meliola variaseta* (DRJ54, EF094840) was derived from following specimen: PANAMA. CHIRIQUI PROVINCE: Dolega, Los Algarrobos. On leaves of *Cupania* sp. (Sapindaceae), 13 Sep 2005, D. Rodríguez J. 70 (PMA).

Extraction, amplification, and sequencing of DNA

For isolation of nuclear DNA, numerous ascomata were taken from leaves and triturated by shaking in a vibratory mill (Mixer Mill MM301, Retsch, Haan, Germany) for 1.5 min at 30 Hz in a 1.5 mL tube together with one tungsten carbide ball (3 mm diam). Total genomic DNA was extracted from the samples with the PeqLab E.Z.N.A. Fungal DNA kit, following the manufacturer's protocol.

The partial 28S nrDNA was amplified with PCR using the primers, NL1 and NL4 (Kurtzman and Robnett 1997), peqGOLD dNTPs, and peqGOLD Taq DNA polymerase kits according the supplier's protocol. PCR products were cleaned with the PeqLab E.Z.N.A Cycle-Pure kit. PCR products were sequenced by Scientific Research & Development GmbH (Oberursel, Germany). Sequences were edited with CodonCodeAligner version 1.2.2 (2002–2003, CodonCode Corp.) and compared to sequences deposited in GenBank (www.ncbi.nlm.nih.gov/BLAST/) using the BLAST search function.

Alignment and phylogenetic analysis

An alignment with partial DNA sequences of the nuclear large subunit LSU rDNA with 417 positions was obtained. This alignment is represented by 50 species from main orders of Sordariomycetes and Erysiphales as

representatives of Leotiomycetes, with *Saccharomyces cerevisiae* (Saccharomycotina, Saccharomycetales) chosen as outgroup. The sequences were selected according to published phylogenies (Bischoff et al. 2004; Cai et al. 2005, 2006; Campbell et al. 2005; Castlebury et al. 2002, 2004; Fernández et al. 2006; Huhndorf et al. 2001, 2004, 2005; Ito and Takamatsu 2010; Limkaisang et al. 2006; Lumbsch et al. 2002; Miller and Huhndorf 2004a, b; Mori et al. 2000; Morocko and Fatehi 2007; Pinho et al. 2012b; Réblová and Winka 2001; Réblová 2006; Rodríguez and Piepenbring 2007; Rossman et al. 2004; Schoch et al. 2012; Seifert et al. 2003; Smith et al. 2003; Spatafora et al. 1998, 2006; Thongkantha et al. 2009; Witthuhn et al. 1999; Zipfel et al. 2006). Unpublished sequences were not considered in the analysis.

Manual editing was done within the alignment and subsequently deposited in TreeBASE with the following accession number 14648 (Study Accession URL: http://purl.org/phylo/treebase/phylows/study/TB2:S14648). MEGA version 4 was used to perform a neighbor joining (NJ) analysis (all positions containing gaps and missing data were eliminated from the dataset) with a bootstrap analysis with 1,000 replicates (Tamura et al. 2007).

Results

Phylogenetic analysis

The neighbor joining tree (Fig. 1) shows the GenBank accession numbers of the 28S nrDNA sequences of Meliolaceae species obtained by this study (**bold**) and other sequences of Ascomycota included for comparison with *Saccharomyces cerevisiae* (Saccharomycetes) as outgroup in a basal position. A bootstrap value of 100 % supports the Erysiphales (Leotiomycetes) as a clade separate from Sordariomycetes.

The Sordariomycetes including Meliolales are confirmed (89 % bootstrap support). The Meliolales represented by the five genera of Meliolaceae, *Appendiculella*, *Asteridiella*, *Endomeliola*, *Irenopsis,* and *Meliola*, form a well-supported clade (100 %) as sister to all other Sordariomycetes (90 %). In the Meliolales clade, a subclade comprising *Asteridiella nitidae* (on *Buddleja nitida* Benth.) and *Endomeliola dingleyae* (on *Coprosma robusta* Raoul) is supported by 90 %. Both host plants belong to closely related orders, Lamiales and Gentianales, respectively, of the euasterids I (Jansen et al. 2007). Also well-supported (100 %) is a subclade of two *Meliola* species from the same genus of host family Sapindaceae, *Meliola variaseta* (on leaves of *Cupania* sp.) and *M. vernaliae* (on leaves of *Cupania vernalis* Cambess.). Other relationships within the Meliolales on relatively distantly related host plants are not significantly supported.

Morphological data

In the present investigation, 42 species of Meliolaceae were identified on 42 species of plants collected in Panama. Among these, three species of Meliolaceae are described as new, 18 species of Meliolaceae and 30 host plants are reported for Panama for the first time (for details about descriptions, drawings, and photos see Rodríguez 2006). Among the plants, six are new hosts for Meliolaceae.

New species of Meliolaceae from Panama

Appendiculella monsterae Rodr. Just., sp. nov. Fig. 2

MycoBank MB800936

Colonies amphigenous, dense, 2–3 mm diam. Hyphae dark brown, septate, undulating, branching alternate, with cells 24−34×9−10 μm. Appressoria alternate, straight to slightly antrorse, 33−38×21−27 μm; stalk cell cylindrical, straight to bent, 11−19×9−11 μm; head cell lobate, 18−23×21−27 μm. Phialides ampulliform, 17−23×8−9 μm, sparse, alternate, mixed with appressoria. Ascomata sparse, uniformly distributed over the entire colony, black, 180−200×187−200 μm, surface cells conoid, with numerous larviform appendages. Larviform appendages light brown, transversely striate, at the tips slightly bent, 109−144×25−34 μm. Ascospores 2–4, cylindrical, rounded at the tips, 65−67×19−20 μm, smooth, 3-septate, constricted at the septa, dark brown.

Etymology Referring to the host, a species of *Monstera*.

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, Los Quetzales trail, Alto Chiquero, 1,760 m, on leaves of *Monstera deliciosa* Liebm. (Araceae), 27 August 2005, D. Rodríguez J. 65 (holotype, PMA).

Notes: One species of *Asteridiella* and four *Meliola* species are known on Araceae which differ from *A. monsterae* in lacking larviform ascomatal appendages (Hansford 1961, 1963). *A. monsterae* is the first species of the genus *Appendiculella* described on Araceae.

Asteridiella nitidae Rodr. Just., sp. nov. Figs. 3, 4 and 5

MycoBank MB800952

Colonies on the adaxial side of leaves, dense, 0.2–2 mm diam. Hyphae dark brown, septate, straight, branching opposite, mycelial cells 27−40×9−11 μm. Appressoria alternate to unilateral, antrorse, 31−38×17−21 μm; stalk cell bent, 5−12×8−10 μm; head cell slightly lobate, 23−27×17−21 μm. Phialides ampulliform, 19−24×9−11 μm, opposite, not mixed with appressoria. Ascomata sparse, distributed in the centre of the colony, black, 130−270×120−260 μm, surface cells conoid, 21−34×23−34 μm. Ascospores 2–4, cylindrical, rounded at the tips, 56−62×23−26 μm, smooth, 4-septate, constricted at the septa, dark brown.

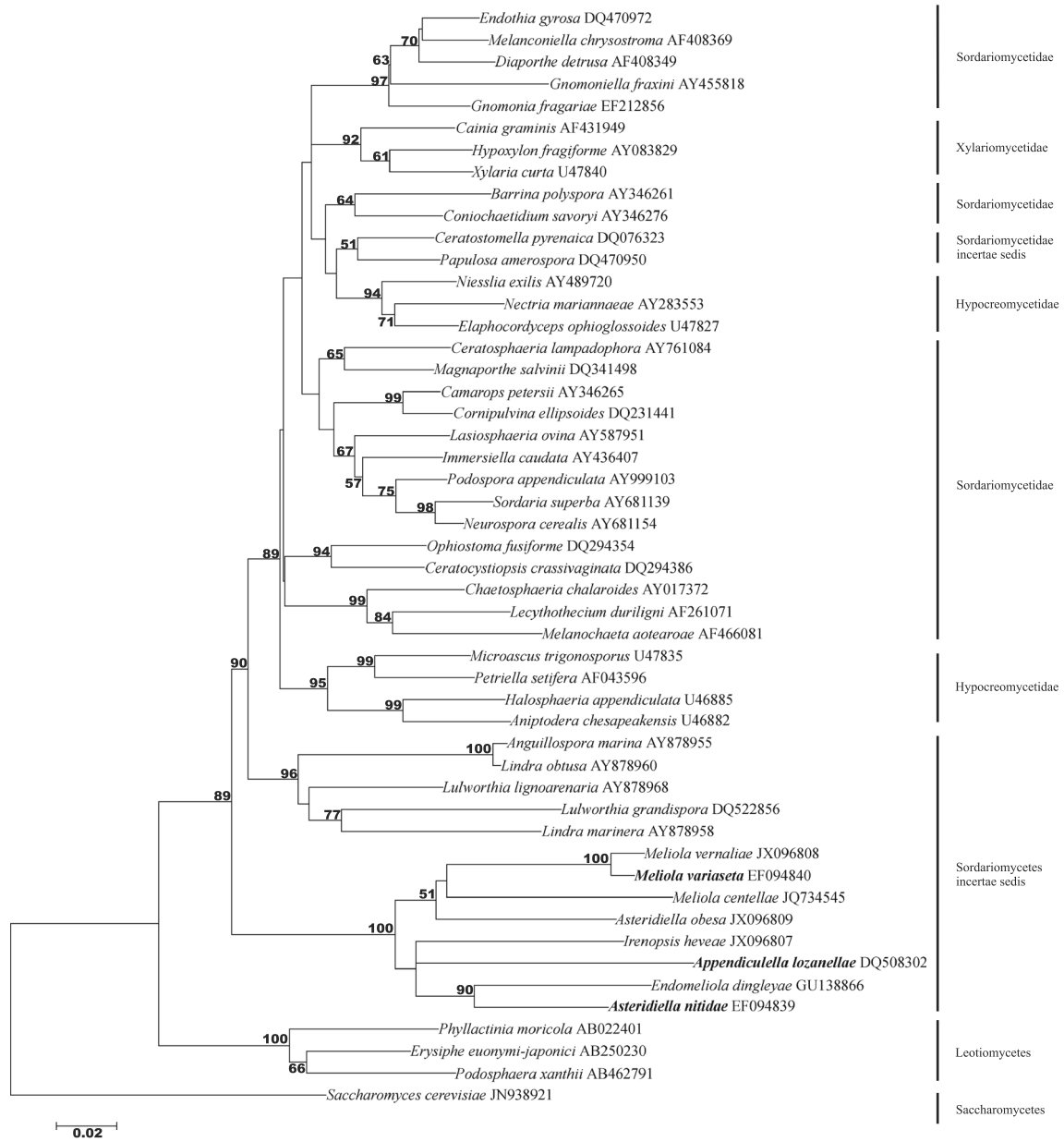

Fig. 1 Phylogram obtained from a neighbor joining analysis of the 28S nrDNA sequences data (50 species) of Ascomycota including three sequences of Meliolaceae from Panama (*boldface*), four from Brazil, and one from New Zealand (*Endomeliola*). The tree was rooted with *Saccharomyces cerevisiae* (Ascomycota)

Etymology Referring to the host species *Buddleja nitida*.

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, Paso Ancho, Volcán, access road to the base of the volcano, 1,760 m, on leaves of *Buddleja nitida* Benth. (Scrophulariaceae), 18 September 2002, D. Rodríguez J. 10 (holotype, PMA). Additional material examined: SOUTH AFRICA, Xumeni Forest, Donnybrook, Natal. *Asteridiella inermis* (Kalchbr. & Cooke) Hansf, on leaves of *Buddleja auriculata* Benth., 9 January 1935, E.M. Doidge 27745 (BPI 697551).

DNA sequence: partial 28S rDNA (GenBank EF094839).

Notes: Seven species of *Asteridiella* are known on Scrophulariaceae and, of these, *A. buddlejae* (Hansf.) Hansf. (China), *A. buddlejicola* (Henn.) Hansf. (Brazil), *A. inermis* (South Africa), and *A. obducens* (Gaillard) Hansf. (Ecuador) are known on species of *Buddleja* (Hansford 1961, 1963). The new species differs from these members of the genus by its larger appressoria and ascospores. For more details on morphological characteristics see Table 1.

Irenopsis chrysophylli Rodr. Just., sp. nov. Fig. 6

MycoBank MB800953

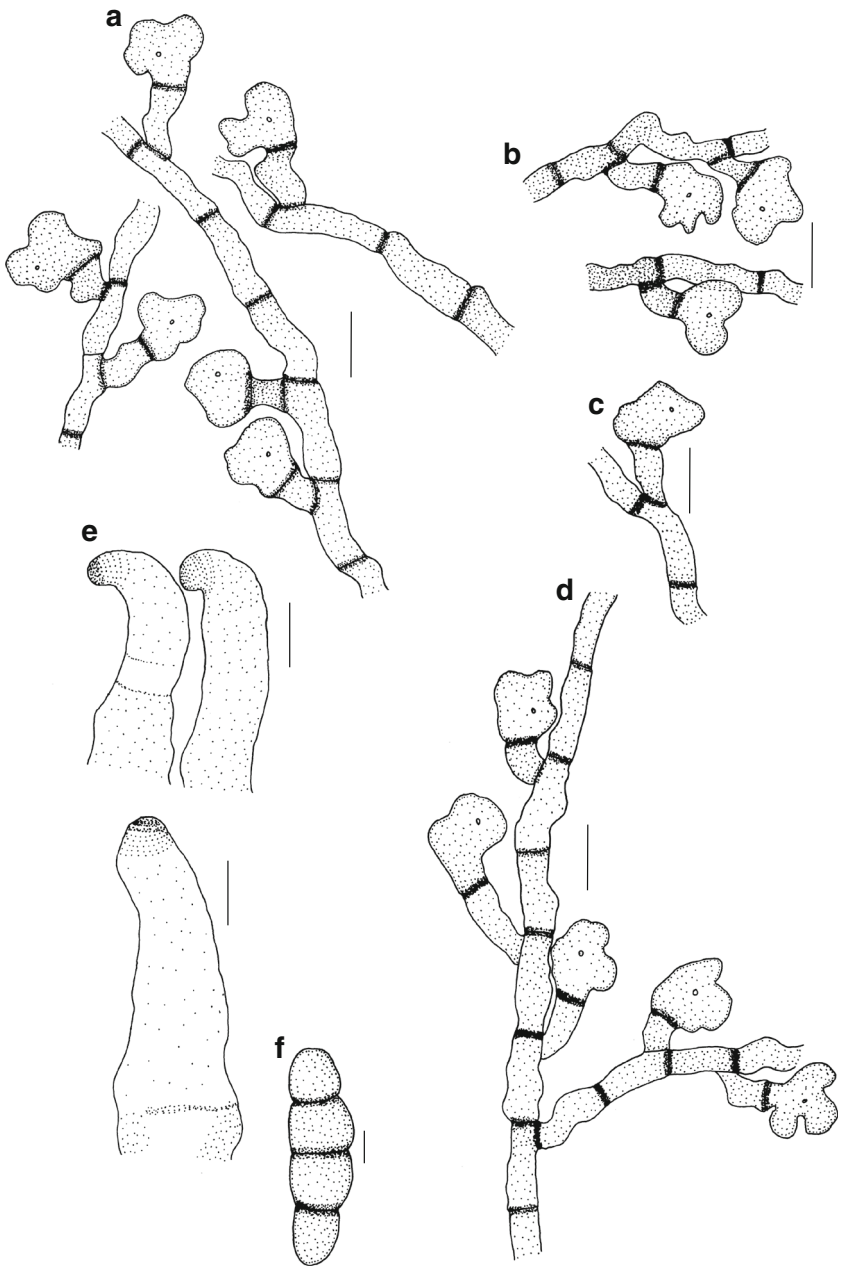

Fig. 2 *Appendiculella monsterae* (holotype). **a**–**d** Hyphae with appressoria. **e** Tips of appendages. **f** Ascospore. Scale bars: **a**–**e**= 20 μm, **f**=10 μm

Colonies on the adaxial surface of leaves, 2–5 mm diam. Hyphae dark brown, septate, straight, branching opposite with angles of 60°–90°, mycelial cells 34−46× 7−8 μm. Appressoria alternate or unilateral, straight to slightly antrorse, 18−29×9−14 mm; stalk cell angular, cylindrical, 3−10×7−8 μm; head cell pyriform, some cylindrical, 12−21×9−14 μm. Phialides ampulliform, 18−23×7−8 μm, opposite to unilateral, mixed with appressoria. Ascomata few, located in the centre of the colony, 170−200×180−200 μm; ascomatal setae 4–5 on each perithecium, 80−103×7−8 μm, dark brown, not septate, at the tips bent to spiral. Ascospores cylindrical, 2–4, rounded at the tips, 38−46×17−22 μm, smooth, 4-septate, constricted at the septa, dark brown.

Etymology Referring to the host, a species of *Chrysophyllum*.

Material examined: PANAMA, Province Chiriqui, Los Algarrobos, on the bank of the river Majagua, 140 m, on leaves of *Chrysophyllum* sp. (Sapotaceae), 13 September 2005, T. Hofmann 349 (holotype, PMA).

Notes: One species of *Amazonia*, three species of *Asteridiella*, and eleven species of *Meliola* are known on Sapotaceae (Hansford 1961, 1963). *Irenopsis chrysophylli* is the only species of the genus *Irenopsis* described growing on

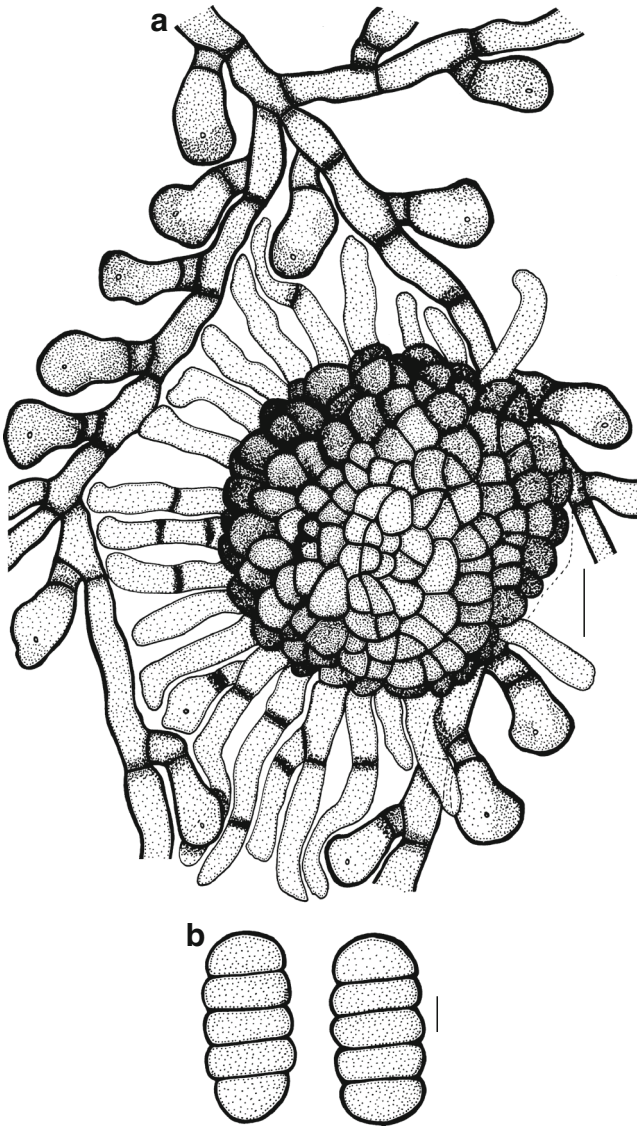

Fig. 3 *Asteridiella nitidae* (holotype). **a** Young ascoma with hyphae and appressoria. **b** Ascospores. Scale bars: **a**=20 μm, **b**=10 μm

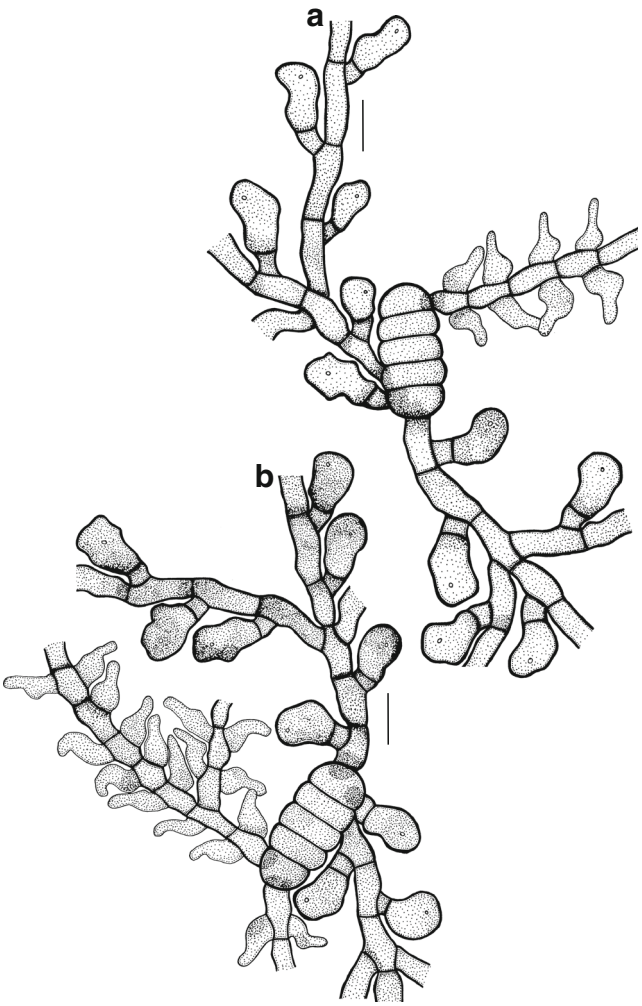

Fig. 4 *Asteridiella nitidae* (holotype). **a**–**b** Germinating ascospores with appressoria and phialides. Scale bars: **a**–**b**=20 μm

Sapotaceae and this differs from other genera by setose ascomata.

New records of Meliolaceae for Panama

Appendiculella calostroma (Desm.) Höhn.

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, Los Quetzales trail, Respingo, 1,000 m, on leaves of *Rubus* sp. (Rosaceae), 15 September 2005, D. Rodríguez J. 77 (PMA). FRANCE, on branches of *Rubus fruticosus* L. (Rosaceae), 1857, Desmazières (holotype, K 368).

Appendiculella calostroma is known from Africa, Asia, Australia, Caribbean Islands, Central America (Costa Rica), Europe, North America, and South America, infecting species of Rosaceae (Hansford 1961; Farr et al. 2013).

Asteridiella formosensis (W. Yamam.) Hansf.

Material examined: PANAMA, Province Veraguas, National Park Isla Coiba, 10 m, on leaves of *Lantana* sp. (Verbenaceae), 17 August 2003, M. Piepenbring 3313 (PMA).

Asteridiella formosensis is up to now known only from Asia (India, Taiwan) and recorded here for the first time for the Americas (Hansford 1961; Farr et al. 2013).

Asteridiella hymenaeicola (Gonz. Frag. & Cif.) Hansf.

Material examined: PANAMA, Province Chiriqui, Dolega, Los Algarrobos, on leaves of *Hymenaea courbaril* L. (Fabaceae), 13 September 2005, D. Rodríguez J. 67 (PMA).

Asteridiella hymenaeicola has been recorded previously only from the Caribbean Islands and South America (Hansford 1961; Farr et al. 2013).

Asteridiella solanacearum Hansf.

Material examined: PANAMA, Province Bocas del Toro, Alto del Valle, Celestine, on leaves of *Solanum* sp. (Solanaceae), 16 March 2003, M. Piepenbring and R. Requena 3248 (PMA).

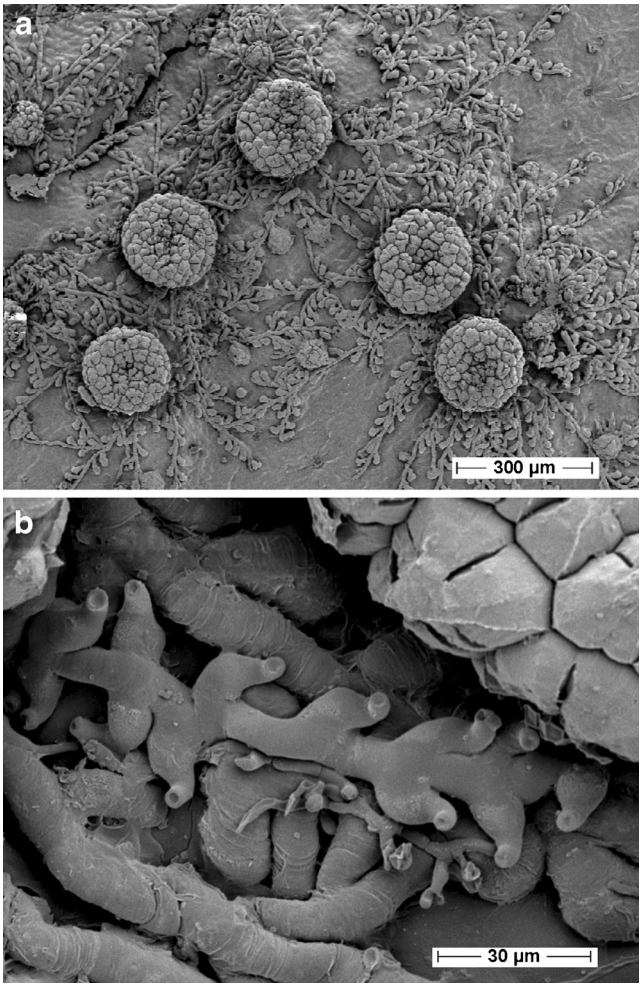

Fig. 5 Scanning electronic photographs of *Asteridiella nitidae* (Rodríguez 10). **a** Colonies on the upper side of a leaf of *Buddleja nitidae* with five ascomata and hyphae with appressoria. **b** Hyphae with phialides. Scale bars: **a**=300 μm, **b**=30 μm

Asteridiella solanacearum has been recorded previously only of the Caribbean Islands and South America (Hansford 1961; Farr et al. 2013).

Asteridiella vegabajensis Hansf.

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, near office of ANAM, 2,500 m, on leaves of *Crusea coccinea* DC. (Rubiaceae), 11 February 2004, M. Piepenbring, R. Rincón, D. Cáceres & M. Vega 3371 (PMA).

Asteridiella vegabajensis is so far known only from Puerto Rico on *Psychotria* sp. (Hansford 1961). It is recorded here for the first time on *Crusea*, a new host genus for Meliolaceae.

Irenopsis miconiicola (F. Stevens) F. Stevens

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, Los Quetzales trail, 1,300 m, on leaves of *Miconia* sp. (Melastomataceae), August 2003, D. Rodríguez J. 27 (PMA).

Irenopsis miconiicola has so far been known only from the Caribbean Islands (Hansford 1961; Farr et al. 2013).

Meliola byrsonimicola F. Stevens & Tehon

Material examined: PANAMA, Province Chiriqui, Divalá, Quebrada Grande, on leaves of *Byrsonima crassifolia* Kunth (Malpighiaceae), 7 August 2005, D. Rodríguez J. 58 (PMA); Divalá, Manchuila, Entrada Las Mendoza, 16 September 2005, D. Rodríguez J. 82 (PMA).

Meliola byrsonimicola is also known from the Caribbean Islands and South America (Hansford 1961; Farr et al. 2013).

Meliola cf. *cucurbitacearum* F. Stevens

Material examined: PANAMA, Province Chiriqui, Nacional Park Volcán Barú, Alto Chiquero, Los Quetzales trail, on leaves of *Rytidostylis gracilis* Hook. & Arn. (Cucurbitaceae), 27 August 2005, D. Rodríguez J. 61 (PMA).

Table 1 Comparison of species of *Asteridiella* on Scrophulariaceae as described by Hansford (1961), based on a herbarium specimen (*A. inermis* BPI 697551) and the type of the new species *A. nitidae* (**bold**)

Asteridiella spp.	Length of the appressoria (μm)	Head cell (μm)	Length of stalk cells (μm)	Ascospores (μm)
A. anthocleistae[a]	14–20	9–13×9–12	4–8	32–39×13–15
A. buddleiae[a]	18–31	13–18×9–15	5–15	33–37×13–16
A. buddleyicola[a]	13–20	9–14×7–11	2–7	28–34×11–13
A. implicata[a]	20–24	10–26×8–20	4–16	50–55×20–24
A. inermis[b]	21–24	14–17×9–14	5–10	39–44×15–17
A. nitidae[c]	31–38	23–27×17–21	5–12	56–62×23–26
A. nuxiae[a]	13–25	9–16×8–13	2–8	39–50×17–22
A. obducens[a]	20–28	13–19×10–12	6–12	38–42×15–17

[a] Species of *Asteridiella* described by Hansford 1961

[b] Specimen of *Asteridiella inermis* of the Herbarium BPI

[c] New species of *Asteridiella* from Panama

BPI Beltsville U. S. National Fungus Collections, U.S.A.

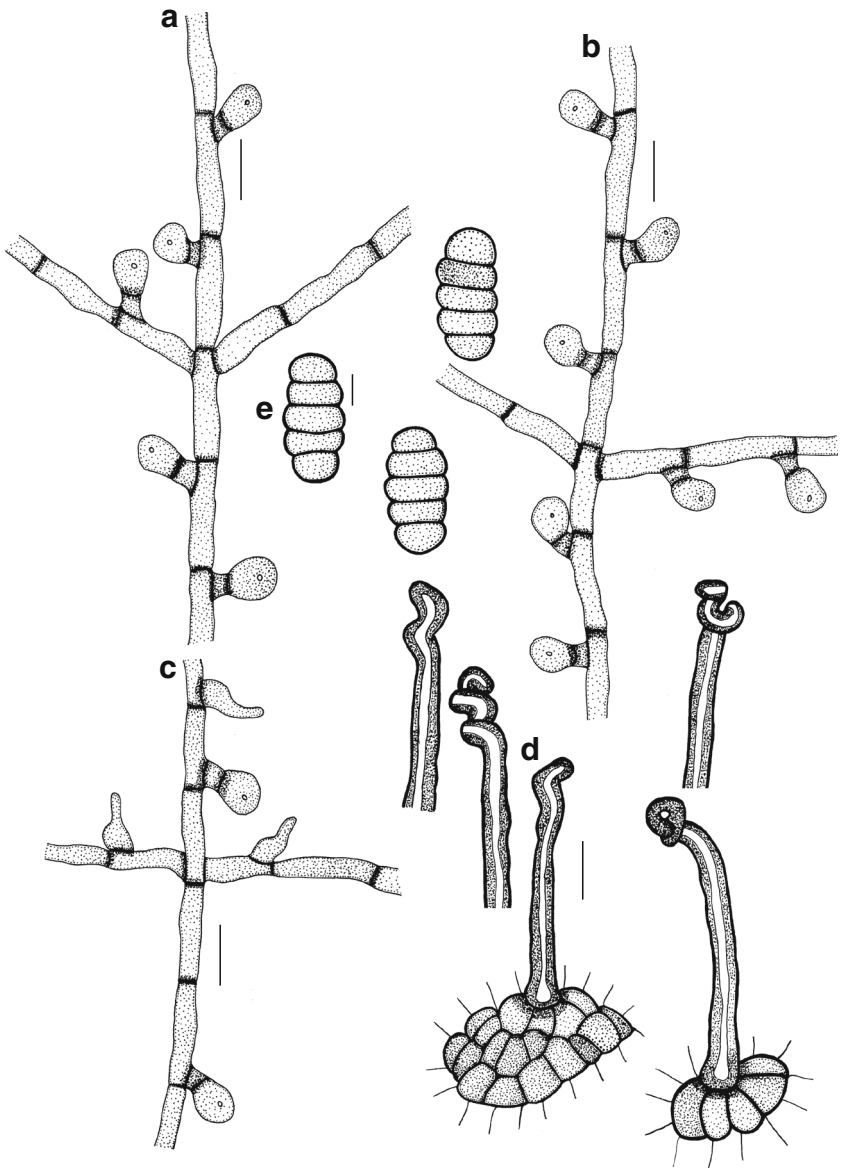

Fig. 6 *Irenopsis chrysophylli* (holotype). **a**–**b** Hyphae with appressoria. **c** Hyphae with conidiogenous cells. **d** Tips of ascomatal seta. **e** Mature ascospores. Scale bars: **a**–**d**= 20 μm, **e**=10 μm

The sample showed undulating hyphae, setae with round tips or double branching; first branching 3–7 μm long; second branching 3–5 μm long while *M. cucurbitacearum* according Hansford (1961) has substraight to slightly undulate hyphae, setae 2-dichotomous, branches wide spread, first branching to 35 μm, second branching to 50 μm long, acute. *Meliola cucurbitacearum* is also known from Asia and the Caribbean Islands (Hansford 1961; Farr et al. 2013).

Meliola dissotidis Hansf. & Deighton

Material examined: PANAMA, Province Chiriqui, Bajo Mono, Los Quetzales trail, on leaves of *Miconia* sp. (Melastomataceae), 7 March 2003, M. Piepenbring et al. 3223 (PMA). SIERRA LEONE, Pelewahun, on leaves of *Dissotis paucistellata* Stapf (Melastomataceae), 9 April 1953, F.C. Deighton s. n. (M 80790).

Meliola dissotidis has so far been known only from Africa (Guinea and Sierra Leone), and is reported here for the first time from Panama and the Americas (Hansford 1961; Farr et al. 2013).

Meliola indica Syd. & P. Syd.

Material examined: PANAMA, Province Chiriqui, International Park La Amistad, close to office of ANAM, 2,270 m, on leaves of *Gustavia* sp. (Lecythidaceae), 5 March 2003, M. Piepenbring et al. 3214 (PMA). BANGLADESH, Dacca, on leaves of *Barringtonia acutangula* (L.) Gaertn. (Lecythidaceae), 20 March 1910, A. Som (E.J. Butler 1036) (type, BPI 694272). PHILIPPINES, San Miguel, Bulacan, on leaves of *B. acutangula* (L.) Gaertn., September 1924, M. S. Clemens 4821 (BPI 694273).

Meliola indica has been known only from Asia (Bangladesh, Java, Philippines) and is recorded for the Americas for the first time (Hansford 1961; Farr et al. 2013).

Meliola lanosa Pat.

Material examined: PANAMA, Comarca Ngöbe Buglé, Hato Pilón, way to La Granja, 600–650 m, on leaves of *Roupala* sp. (Proteaceae), 14 March 2003, M. Piepenbring et al. 3241 (PMA).

Meliola lanosa has been reported from South America (Chile) (Hansford 1961; Farr et al. 2013).

Meliola lundiae F. Stevens

Material examined: PANAMA, Province Chiriqui, Corregimiento de Alanje, Playa La Barqueta, on leaves of *Arrabidaea* sp. (Bignoniaceae), 19 February 2003, M. Piepenbring & R. Kirschner 3176 (PMA). *Meliola dentifera* Syd., BRAZIL, on leaves of *Arrabidaea nicotianiflora* Kraenzl. (Bignoniaceae), April 1911, E.H. Ule Herb. Brasil (type, S 3528).

Meliola lundiae is also known from South America (Ecuador) (Hansford 1961; Farr et al. 2013).

Meliola mammeae Hansf.

Material examined: PANAMA, Province Chiriqui, Divalá, Quebrada Grande, on leaves of *Mammea americana* L. (Clusiaceae), 25 August 2003, D. Rodríguez J. 41 (PMA).

Meliola mammeae has so far been known only from the Caribbean Islands (Hansford 1961; Farr et al. 2013).

Meliola nigra F. Stevens

Material examined: PANAMA, Province Chiriqui, Mangrove area of Remedios, on leaves of *Laguncularia racemosa* C.F. Gaertn. (Combretaceae), 26 February 2004, T. Hofmann 130 (PMA). PUERTO RICO, Guanajibo, on leaves of *L. racemosa* C.F. Gaertn., 19 June 1915, F.L. Stevens 7197 (type, BPI 695629).

Meliola nigra is also known from the Caribbean Islands and Asia (Hansford 1961; Farr et al. 2013).

Meliola ocoteicola F. Stevens

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, on leaves of *Nectandra* sp. (Lauraceae), 15 February 2003, R. Kirschner & M. Piepenbring 1598 (PMA).

Meliola ocoteicola is also known from the Caribbean Islands, and has also been recorded from the Dominican Republic on *Chrysophyllum* (Sapotaceae) (Hansford 1961; Farr et al. 2013).

Meliola cf. *orchidacearum* Cif.

Material examined: PANAMA, Province Chiriqui, National Park Volcán Barú, Los Quetzales trail, Alto Chiquero, on leaves of *Epidendrum* sp. (Orchidaceae), 27 August 2005, D. Rodríguez J. 62 (PMA).

Meliola orchidacearum is also known from the Caribbean Islands (Hansford 1961; Farr et al. 2013). This fungus infects species of the Orchidaceae, *Prosthechea cochleata* (L.) W.E. Higgins, *Encyclia cochleata* (L.) Dressler and an undetermined species of Orchidaceae (Hansford 1961; Schmiedeknecht 1989; Rodriguez and Minter 1998). Setae and ascospores of the sample D. Rodríguez J. 62 measured 210−290×8−11 μm, and 37−42×15−17 μm, respectively. However, Hansford (1961) described setae and ascospores of *M. orchidacearum* with the following measures, 800×8−10 μm, and 47−56×18−20 μm, respectively. The type material of *M. orchidacearum* should be investigated to determine if the morphological characteristics of the Panamanian material agree with the type.

Meliola pisoniae F. Stevens & Roldan ex W. Yamam.

Material examined: PANAMA, Province Panama, National Park Cerro Campana, on leaves of *Neea* sp. (Nyctaginaceae), 19 February 2003, M. Piepenbring & R. Aizprúa 3376 (PMA).

Meliola pisoniae has so far been known only from Asia (China, Philippines, Taiwan) and is recorded here for the first time to the Americas (Hansford 1961; Farr et al. 2013).

Meliola ripogoni Hansf.

Material examined: PANAMA, Province Chiriqui, International Park La Amistad (PILA), 2,300–2,500 m, on leaves of *Smilax* sp. (Smilacaceae), 4 March 2003, R. Kirschner 1718 (PMA). NEW SOUTH WALES, on leaves of *Ripogonum album* R. Br. (Liliaceae), 27 May 1934, Fraser 64 (type, DAR 2276).

M. ripogoni is known from Central America (Honduras) and Oceania (New South Wales, New Zealand). This fungus infects Liliaceae, Luzuriagaceae, and Smilacaceae (Hansford 1961; Farr et al. 2013).

The following two species of *Meliola* were recorded for Panama by Piepenbring et al. (2011) and Araúz and Piepenbring (2012). Here, we cite them again with new data on host species (see Rodríguez 2006).

Meliola crescentiae F. Stevens

Material examined: PANAMA, Province Chiriqui, Divalá, Nuevo México, on leaves of *Crescentia cujete* L. (Bignoniaceae), 18 August 2003, D. Rodríguez J. 24 (PMA). TRINIDAD & TOBAGO, Cumuto, on leaves of *Crescentia* sp., 18 August 1922, F.L. Stevens 940 (type BPI 693618).

Meliola gesneriae F. Stevens

Material examined: PANAMA, Province Chiriqui, International Park La Amistad, Sendero El Retoño, 2,270–2,310 m, on leaves of *Phinaea* sp. (Gesneriaceae), 3 March 2003, M. Piepenbring et al. 3190 (PMA). PUERTO RICO, Mayaguez, Mesa, on leaves of *Gesneria albiflora* Kuntze, 25 June 1915, F.L. Stevens 7431 (type, BPI 694051); 30 December 1913, F.L. Stevens 6590 (BPI 694049). *Meliola epithemae* F. Stevens & Roldan, PHILIPPINES, Naguilion Road, Benguet, on leaves of *Epithema* sp. (Gesneriaceae) 1 July 1931, F.L. Stevens 1394 (type, BPI 693904).

Discussion

Phylogenetic conclusions

In our taxon sampling, Meliolales formed the most basal clade (89 %) in the class Sordariomycetes, followed by the second basal clade of the Lulworthiales (90 %). According to Hibbett et al. (2007), Meliolales, Lulworthiales, Calosphaeriales, Phyllachorales, and Trichosphaeriales were placed in Sordariomycetes incertae sedis, basal to the divergence of the subclasses Hypocreomycetidae and Sordariomycetidae. Lumbsch and Huhndorf (2010) placed Lulworthiales, Meliolales, Phyllachorales, Trichosphaeriales, and Koralionastetales in Sordariomycetes incertae sedis. Pinho et al. (2012b), based on their phylogenetic analysis of the region 28S nrDNA, confirmed that Meliolales represent a monophyletic order of the Sordariomycetes. Members of Erysiphales (powdery mildews), belonging to the class Leotiomycetes are not closely related with Meliolales (black mildews) (Saenz and Taylor 1999). Our findings suggest that the concept of the subclass Meliolomycetidae is justified (Kirk et al. 2001).

Our phylogenetic data (Fig. 1) support the close relationship between *Meliola variaseta* (sample from Panama) and *M. vernaliae* (sample of Brazil), both growing on members of Sapindaceae (Hansford 1961) which belong to Sapindales (Eurosids II, Jansen et al. 2007). Although the relationship between *M. variaseta*, *M. vernaliae,* and *Asteridiella obesa* is weakly supported in our analysis, we hypothesize that these three meliolaceous species share a common ancester because they all grow on members of the order Sapindales. The genetic relationship of *M. centellae* with *M. variaseta* and *M. vernaliae* was weakly supported. In this case, *M. centellae* grows on Apiales and *M. variaseta* and *M. vernaliae* on Sapindales. These two orders belong to Euasterids II and Eurosids II, respectively, and are not closely related, according to Jansen et al. (2007). The mycelial setae of *Meliola* appear to represent a phylogenetically significant morphological marker of a monophyletic genus.

The bootstrap value for the clade of *A. nitidae* (sample from Panama) and *E. dingleyae* (from New Zealand) supported a close relationship between these two fungi. The first one is reported on leaves of *B. nitida* (Scrophulariaceae, Lamiales), while *Endomeliola* grows on leaves of *Coprosma robusta* Raoul (Rubiaceae, Gentianales). These two host plant orders are closely related within the euasterids I (Jansen et al. 2007). *Asteridiella* spp. form exclusively ectophytic hyphae (Hansford 1961), whereas *Endomeliola* is characterized by endophytic hyphae which emerge through the stomata (Hughes and Pirozynski 1994). In spite of this unique characteristic among Meliolales, *Endomeliola* does not appear separated from the other meliolaceous taxa, but is united together with *A. nitidae* in a well-supported subclade. The two well-supported subclades within the Meliolales are each correlated phylogenetically with closely related host plants. This indicates coevolutionary relationships in the speciation of Meliolales on their hosts.

Concluding from the similar morphologies of ascomatal appendages of *Appendiculella* spp. with larviform ascomatal appendages and *Asteridiella* spp. with conical ascomatal projections, we assume that both genera might be closely related, as the larviform appendages formed by single cells of the ascoma wall in species of *Appendiculella* could be homologous to the projecting conical cells of the ascoma wall in species of *Asteridiella*. But our molecular data do not support a close relationship between both genera. The monophyly of *Asteridiella* is not supported by the positions of the sequences of two species. Compared to setae or appendages in other genera, the conical ascomatal projections of *Asteridiella* appear less evolved and might be a plesiomorphic characteristic.

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