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A monograph of the entomopathogenic genera *Hypocrella*, *Moelleriella*, and *Samuelsia* gen. nov. (*Ascomycota*, *Hypocreales*, *Clavicipitaceae*), and their aschersonia-like anamorphs in the Neotropics

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Abstract: The present taxonomic revision deals with Neotropical species of three entomopathogenic genera that were once included in *Hypocrella s. l.*: *Hypocrella s. str.* (anamorph *Aschersonia*), *Moelleriella* (anamorph aschersonia-like), and *Samuelsia* gen. nov (anamorph aschersonia-like). Species of *Hypocrella, Moelleriella,* and *Samuelsia* are pathogens of scale insects (Coccidae and Lecaniidae, Homoptera) and whiteflies (Aleyrodidae, Homoptera) and are common in tropical regions. Phylogenetic analyses of DNA sequences from nuclear ribosomal large subunit (28S), translation elongation factor 1-α (TEF 1-α), and RNA polymerase II subunit 1 (RPB1) and analyses of multiple morphological characters demonstrate that the three segregated genera can be distinguished by the disarticulation of the ascospores and shape and size of conidia. *Moelleriella* has filiform multi-septate ascospores that disarticulate at the septa within the ascus and aschersonia-like anamorphs with fusoid conidia. *Hypocrella s. str.* has filiform to long-fusiform ascospores that do not disarticulate and *Aschersonia s. str.* anamorphs with fusoid conidia. The new genus proposed here, *Samuelsia,* has filiform to long-fusiform ascospores that do not disarticulate and aschersonia-like anamorphs with small allantoid conidia. In addition, the present study presents and discusses the evolution of species, morphology, and ecology in *Hypocrella, Moelleriella*, and *Samuelsia* based on multigene phylogenetic analyses.

Key words: multilocus phylogenetics, polyphasic taxonomy, species identification, species recognition.
Taxonomic novelties: New genus: *Samuelsia*. New species: *Hypocrella disciformis*, *H. hirsuta*, *Moelleriella basicystis*, *M. boliviensis*, *M. cornuta*, *M. evansii*, *M. madidiensis*, *M. umbospora*, *S. chalalensis*, *S. geonomis*, *S. intermedia*, *S. rufobrunnea*, and *S. sheikhii*. New combinations: *M. castanea*, *M. colliculosa*, *M. disjuncta*, *M. epiphylla*, *M. gaertneriana*, *M. globosa*, *M. guaranitica*, *M. javanica*, *M. libera*, *M. macrostroma*, *M. ochracea*, *M. palmae*, *M. phyllogena*, *M. rhombispora*, *M. sloaneae*, *M. turbinata*, and *M. zhongdongii*.

INTRODUCTION

Species in the genus *Hypocrella* Sacc. *s. l.* (anamorph *Aschersonia* Mont. *s. l.*) are insect pathogens characterised by their brightly-coloured stromata, filiform ascospores, and pycnidial to acervular anamorphs. They are common in tropical regions, particularly in moist old-growth forests, where they often cause epizootics of disease in their hosts, scale insects (Coccidae and Lecaniidae, Homoptera) and whiteflies (Aleyrodidae, Homoptera). The majority of the species are tropical, but a few are also found in the subtropics (Petch 1921, Mains 1959a, b, Evans & Hywel-Jones 1990, Hywel-Jones & Evans 1993). Other genera, including *Ascopolyporus* A. Möller, *Cosmospora* Rabenh., *Hyperdermium* J.F. White *et al.*, *Podonectria* Petch, *Regiocrella* Chaverri & K.T. Hodge, *Septobasidium* Pat., and *Torrubiella* Boud., among others, are also found as hyperparasites of whiteflies and scale insects, but generally not as frequently as *Hypocrella, Moelleriella,* and *Samuelsia*.

Molecular and morphological characters support the recognition of three well-defined genera within the broad concept of *Hypocrella*: *Hypocrella s. str.*, *Moelleriella* Bres., and *Samuelsia* gen. nov. (*Clavicipitaceae*, *Hypocreales*, *Hypocreomycetidae*, *Sordariomycetes*, *Pezizomycotina*, *Ascomycota*). These new genera and their anamorphs are presented here. *Hypocrella s. str.* has an *Aschersonia* anamorph. The anamorphs of *Moelleriella* and *Samuelsia* are aschersonia-like and thus hereafter will be denoted in quotes (*e.g.* "*Aschersonia*") to avoid confusion.

Until 1897, *Hypocrella s. l.* species were described as phyllogenous and thought to be either parasitic or superficial colonisers of living leaves (Evans & Hywel-Jones 1990). Their parasitic association with scale insects and whiteflies was not recognised until Webber (1897) concluded that several *Moelleriella* species (then identified as "*Aschersonia" aleyrodis* Webber) were important factors in the biological control of whitefly pests in citrus plantations. Indeed, the first biocontrol applications in the U.S.A. were done with "*A." aleyrodis* (teleom. *Moelleriella libera*) to control citrus whitefly (*Dialeurodes citri* Ashmead) in Florida (Berger 1921). Since then, the biocontrol potential and ubiquity of *Hypocrella s. l.* has been widely recognised (Parkin 1906, Morrill & Back 1912, Petch 1921, Fawcett 1936, Ferron 1978, Barua 1983, Brady 1984, Ramakers & Samson 1984, Fransen 1987, Rombach & Gillespie 1988, Gerling 1992, Osborne & Landa 1992, Meekes *et al.* 1994, Samson 1995, Meekes *et al.* 1996, Lourencao *et al.* 1999, Meekes *et al.* 2000, Faria & Wraight 2001, Meekes 2001).

Despite the potential of these species in insect biocontrol, few taxonomic treatments have been written after Petch's (1921) monograph of *Hypocrella s. l.* Approximately 115 names in *Hypocrella* and 79 names in *Aschersonia* have been validly published; however, only about 50 and 44 species, respectively, are currently accepted (Petch 1921, Dingley 1954, Mains 1959b, a, Hywel-Jones & Evans 1993). The present taxonomic treatment deals with *Hypocrella s. str.* (anamorphs *Aschersonia s. str.*) and its newly segregated sister genera *Moelleriella* and *Samuelsia* that are encountered in the Neotropics. Hundreds of freshly collected and herbarium specimens, including types were examined, and multi-gene phylogenetic analyses were conducted. Even though this is a comprehensive study, fungal biodiversity surveys in other poorly explored regions will probably reveal more undescribed species.

THE GENERA *HYPOCRELLA*/*ASCHERSONIA*, *MOELLERIELLA*, AND *SAMUELSIA*

Morphology and Taxonomy

The genera *Hypocrella, Moelleriella,* and *Samuelsia* are recognised by their brightly coloured stromata that form on scale insects or whiteflies. As will be shown in this study, *Hypocrella s. str.* includes species with ascospores that do not disarticulate and fusiform conidia; *Moelleriella* includes species with ascospores that disarticulate inside the ascus and fusiform conidia; and *Samuelsia* species have non-disarticulating ascospores and small allantoid conidia.

The genus *Hypocrella* was erected by Saccardo (1878) to accommodate four species previously assigned to *Hypocrea* Fr. (*Hypocreaceae*, *Hypocreales*): *Hypocrea atramentosa* Berk. & M.A. Curtis (= *Myriogenospora atramentosa* (Berk. & M.A. Curtis) Diehl); *Hypocrea discoidea* Berk. & Broome; *Hypocrea semiamplexa* Berk. (a *Balansia* species according to Petch 1921); and *Hypocrea bambusae* Berk. & Broome (= *Balansia bambusae* (Berk. & Broome) Petch). Only *Hypocrella discoidea* (Berk. & Broome) Sacc. (type of the genus) remains in *Hypocrella*. *Moelleriella* was erected in 1896 to accommodate *Moelleriella sulphurea* Bres. (= *M. phyllogena*). In Bresadola's original diagnosis, *M. sulphurea* has a pulvinate stroma and filiform ascospores that disarticulate into numerous cylindrical part-spores.

The genus *Hypocrella* was originally distinguished from *Hypocrea* by the formation of eight, filiform ascospores in each ascus (Saccardo 1878). Petch (1921) reported that the filiform ascospores in *H. discoidea* disarticulated at the septa while still in the asci and speculated that if whole ascospores were seen in asci, it was an indication of immaturity. Later, Petch (1939) described a new genus, *Stereocrea* H. Sydow & P. Sydow, where he placed species with non-disarticulating ascospores. At that time, Petch did not realise that *H. discoidea* also had non-disarticulating ascospores. Later, Mains (1959b) concluded that the presence of non-disarticulating ascospores in *H. aurantiaca* (Petch) Mains (= *Stereocrea aurantiaca*) was not enough evidence to separate it from *Hypocrella*. Until now, it had been accepted that *Hypocrella* species include those with disarticulating and non-disarticulating ascospores (Petch 1939, Mains 1959a, b, Hywel-Jones & Evans 1993). However, evidence presented in this study supports speculations by Hywel-Jones and Evans (1993) and Petch (1939) that species with disarticulating ascospores form a monophyletic group that should be segregated from *Hypocrella*. In the present monograph, species with disarticulating ascospores are placed in *Moelleriella*.

Anamorphs of *Hypocrella* have been classified in the genus *Aschersonia*, which was erected by Montagne (1848) based on *A. tahitensis* Mont. *Aschersonia s. str.* is characterised by pycnidium-like conidiomata, phialides, paraphyses, and unicellular, fusiform, hyaline conidia that are brightly coloured in mass and produced in copious slime. *Moelleriella, Hypocrella* and *Samuelsia* species may or may not have paraphyses. The presence of paraphyses (sterile, hypha-like elements in the hymenium) has sometimes been used as a character to distinguish *Aschersonia* subgenera. *Moelleriella* and *Samuelsia* also have aschersonia-like anamorphs that are similar to *Aschersonia s. str.* but can be distinguished by conidial size and shape. *Hypocrella s. str.* has fusiform conidia that are larger than those of *Moelleriella* and *Samuelsia*. *Samuelsia* has allantoid and smaller conidia. The anamorphic states of *Hypocrella, Moelleriella*, and *Samuelsia* are more commonly collected than the teleomorphs, and are rarely associated with the teleomorph in the same stroma.

As discussed in Chaverri *et al.* (2005a), within the *Clavicipitaceae*, pycnidial to acervular anamorphic forms have been assigned to one of three anamorph genera: *Aschersonia, Ephelis* Fr., or *Sphacelia* Lév. These types of anamorphs are known only for the plant-associated teleomorph genera *Atkinsonella* Diehl, *Balansia* Speg., *Claviceps* Tul., *Epichloë* (Fr.) Tul. & C. Tul., *Myriogenospora* G.F. Atk. and *Neoclaviceps* J.F. White *et al.*, and the scale-insect and whitefly parasites *Hypocrella*, *Moelleriella*, *Samuelsia*, and *Regiocrella*. Some studies have shown evidence of a single evolutionary origin of the pycnidial-acervular morphology in the *Clavicipitaceae* (Kuldau *et al.* 1997, Sullivan *et al.* 2001, Chaverri *et al.* 2005a). *Regiocrella* was recently described and although similar to *Hypocrella, Moelleriella,* and *Samuelsia* in its pycnidial-acervular conidiomata, brightly coloured ascomata, and its parasitism on scale insects, *Regiocrella* differs from those three genera by its short-fusiform and unicellular ascospores (Chaverri *et al.* 2005a). Within the group of genera with pycnidial-acervular conidiomata, *Hypocrella, Moelleriella,* and *Samuelsia* are easily distinguished by the shapes of their conidia and ascospores.

The first suggestion that *Aschersonia* was the anamorph of *Hypocrella* was made by Massee (1896) in an account of *Aschersonia oxyspora* Berk. (= *Moelleriella phyllogena* = *H. phyllogena* (Mont.) Petch). Later, Möller (1901) reported on the occurrence of both the perithecial and pycnidial states in the same stromata of *H. cavernosa* A. Möller (= *M. cavernosa* = *M. palmae* Berk. & M.A. Curtis), and identified the pycnidial state as aschersonia-like. Although it is not common to find both states in the same stroma, several species of *Hypocrella, Moelleriella,* and *Samuelsia* possess this characteristic (*e.g. M. libera, M. mollii, M. ochracea, M. reineckiana, M. sloaneae, M. turbinata, H. disciformis, H. discoidea, H. viridans,* and *S. rufobrunnea*, among others). It is now widely accepted that *Aschersonia* is the anamorph of *Hypocrella*. However, the whole life cycles of many of the 40–50 species of *Hypocrella, Moelleriella,* and *Samuelsia* are not yet known. Only about 15 species of *Aschersonia s. l.* have been linked to their teleomorphs (Petch 1921, Dingley 1954, Mains 1959b, a, Hywel-Jones & Evans 1993). In the present study, previously unknown life cycles of *Hypocrella*, *Moelleriella,* and *Samuelsia* are described and illustrated (see Table 1 for teleomorph-anamorph connections).

Table 1. Teleomorph-anamorph connections to accepted species of *Moelleriella*, *Hypocrella* and *Samuelsia*. Old World: OW; New World: NW.

Teleomorph[1]	Anamorph[1,2]	Source	Distribution
Hypocrella aurantiaca	*A. aurantiaca*	Petch 1939, Mains 1959a	NW
H. citrina	*A. blumenaviensis*	Mains 1959b	NW
H. disciformis[3]	*A. disciformis*		NW
H. discoidea	*A. samoensis*	Hywel-Jones & Evans 1993	OW
H. hirsuta[3]	Not named		NW
H. hypocreoidea	*A. hypocreoidea*	Petch 1924	OW
H. viridans	*A. viridans*	Petch 1921	NW
Moelleriella africana	Not known	Hywel-Jones & Samuels 1998	OW
M. amomi	*"A." caespiticia*	Petch 1921, Mains 1959a	OW
M. basicystis[3]	*"A." basicystis*		NW
M. bispora	Not known		OW
M. boliviensis	Not known		NW
M. botryosa	Not known		OW
M. castanea	Not named	Mains 1959a, Petch 1932	NW
M. ceramichroa	Not named	Petch 1921	OW
M. colliculosa	Not known		NW
M. convexa	Not known	Petch 1921	OW
M. cornuta	Not known		NW
M. disjuncta[3]	Not named		NW
M. duplex	*"A." duplex*	Petch 1921	OW
M. epiphylla	*"A." cubensis*	Mains 1959a, b	NW
M. evansii[3]	Not named		NW
M. gaertneriana	Not known		NW
M. globosa[3]	Not named		NW
M. guaranitica[3]	*"A." caapi*		NW
M. javanica	*"A." coffeae*	Petch 1921	OW
M. libera	*"A." aleyrodis*	Petch 1924	NW
M. macrostroma	Not named	Chaverri *et al.* 2005	NW
M. madidiensis[4]	Not named		NW
M. mollii	*"A." confluens*	Petch 1921	OW
M. murrayae	Not named	Kobayashi 1973	OW
M. ochracea	*"A." andropogonis*	Petch 1921, Liu *et al.* 2006	NW
M. olivacea	Not named	Petch 1921	OW
M. oxystoma	*"A." oxystoma*	Petch 1921	OW
M. palmae	Not known	Petch 1921	NW
M. palmicola	Not named	Petch 1921	OW
M. phyllogena[3]	*"A." juruensis*		NW
M. raciborskii	*"A." placenta*	Liu *et al.* 2006	OW
M. reineckiana	*"A." marginata*	Petch 1921	OW
M. rhombispora	Not named	Liu *et al.* 2006	NW
M. schizostachyi	Not named	Hywel-Jones & Samuels 1998	OW
M. scutata	Not known		OW
M. sloaneae	Not named	Mains 1959b	NW
M. tubulata	Not named	Petch 1921	OW
M. turbinata	*"A." turbinata*	Petch 1921	NW
M. umbospora[3]	Not named		
M. zhongdongii	*"A." incrassata*	Liu & Hodge 2005	NW
Moelleriella sp.[4]	*"A." insperata*		OW
Samuelsia chalalensis[4]	Not named		NW
S. geonomis	Not known		NW

Table 1. (Continued).

Teleomorph[1]	Anamorph[1,2]	Source	Distribution
S. intermedia[4]	*"A." intermedia*		NW
S. rufobrunnea[3]	Not named		NW
S. sheikhii[4]	Not named		NW
Not known	*A. acutispora*		OW
Not known	*A. australiensis*		OW
Not known	*A. badia*		OW
Not known	*A. crenulata*		OW
Not known	*A. flava*		OW
Not known	*A. papillata*		OW
Not known	*A. tahitensis*		OW
Not known	*A. tamurai*		OW

[1] "Not named" refers to the anamorph or teleomorph that has been described but no name was given; or "not known" when the anamorph has not been documented in the literature.

[2] *Aschersonia* names in quotes (*e.g.* "*Aschersonia*") denotes taxa that are not in *Aschersonia sensu stricto*.

[3] Indicates connections made in the present study.

[4] Based on anamorph; no mature perithecia observed.

Taxonomic Background: Subdividing *Hypocrella/ Aschersonia s. l.*

Few studies have comprehensively dealt with the taxonomy of *Hypocrella* and related genera or have included more than a few species (Petch 1921, Mains 1959a, b, Liu *et al.* 2006). The first taxonomic treatment of the genus was made by Parkin (1906) who considered extensive collections from Sri Lanka. The seminal monograph of Petch (1921) treated 57 species of *Hypocrella*, including anamorphs and teleomorphs from the New and Old Worlds. Mains (1959a, 1959b) dealt with 24 species of *Hypocrella* and 15 species of *Aschersonia*.

Petch (1921) proposed *Hypocrella* subgenus *Fleischeria* for species of *Hypocrella* in which the *Aschersonia* state lacks paraphyses (and *Aschersonia* subg. *Leprieuria* for the corresponding anamorphs). He considered that most of these species attack scale insects (Coccidae; Lecaniidae according to Petch 1921). In that same work, Petch proposed *Hypocrella* subg. *Hypocrella (as "Euhypocrella"* see Art. 21 ICBN) for species on *Aleyrodidae* and with paraphyses in the conidiomata of their *Aschersonia* subg. *Aschersonia* (as *"Euaschersonia"* see Art. 21 ICBN) anamorphs. Recent evidence reveals that, although sometimes diagnostic for individual species, the presence of paraphyses in the conidioma is not phylogenetically informative (Liu & Hodge 2005, Liu *et al.* 2006). Dingley (1954) also questioned this division since "*A." duplex* Berk., with paraphyses in the conidioma, is consistently associated with *Coccidae*. In addition, other studies showed that cultures of *Aschersonia* may lack paraphyses whereas these were present in the conidioma on the host, further indicating that the presence of paraphyses is not a stable taxonomic character (Hywel-Jones 1993, Hywel-Jones & Evans 1993, Meekes 2001).

Petch (1921) also discussed the possibility of splitting *Hypocrella* into groups characterised by the form of the stroma. However, he mentioned that these forms "…grade into one another to such an extent that this character cannot be relied on." In the original diagnosis of the genus, *Fleischeria* was distinguished from *Hypocrella* by its harder stroma (Penzig & Saccardo 1901). Petch (1921) synonymised the two genera because species of *Hypocrella* can vary in hardness, from hard in *H. schizostachyi* Henn. (= *M. schizostachyi*) to soft in *H. convexa* Racib. (= *M. convexa*). Chaverri *et al.* (2005b) demonstrated the presence of three natural groups (*i.e.* clades) in *Hypocrella s. l.* based on DNA sequence data that correlated with stromatal morphology. The Effuse group has flat, effuse stromata of loose hyphal tissue, broad hypothalli, and whitish colouration (*e.g. M. evansii, M. libera, M. madidiensis*, *M. ochracea, M. raciborskii, M. rhombispora,* and *M. zhongdongii*), except pale yellow to orange in the *M. basicystis* species complex; the Globose group includes species that have globose stromata that are generally darker in colour (yellow to brownish), large, compact tissue, hard or coriaceous, moderately to strongly tuberculate, and without hypothalli (*e.g. M. africana, M. boliviensis, M. cornuta, M. epiphylla, M. gaertneriana, M. insperata, M. macrostroma, M. turbinata,* and *M. schizostachyi)*; and the Pulvinate group (now *Hypocrella* and *Samuelsia*) comprises species that have pulvinate or cushion-like stromata, somewhat compact and flattened, yellowish or green, sometimes brownish, with or without hypothalli, generally changing colour in 3 % KOH (*e.g. H. aurantiaca, H. disciformis, H. viridans, H. discoidea*, *H. hirsuta*, *S. geonomis, S. chalalensis, S. rufobrunnea*, and *S. sheikhii*). The groups defined by Chaverri *et al.* (2005b) correlate roughly with some of the groupings that Petch (1921) discussed. Although there are distinct phenotypic characteristics that distinguish each of the three major groups defined in Chaverri *et al.* (2005b), a formal generic or subgeneric revision of the taxonomy to distinguish the Effuse, Globose, and Pulvinate groups was not proposed.

Geographical Distribution

Hypocrella, Moelleriella, and *Samuelsia* are mainly distributed in the Tropics, with a few species found in the Subtropics (*e.g.M. colliculosa*, *M. duplex*, *M. guaranitica*, *S. intermedia, H. aurantiaca,* and *H. citrina*) (Table 1). This pattern of distribution and evolutionary dynamics have been observed in many other organisms where taxa preferentially originate in the Tropics and expand toward the poles without losing their tropical presence (Jablonski *et al.* 2006). This might explain the higher biodiversity of fungi in the tropics compared to that in temperate or arctic regions. Therefore, a tropical diversity crisis would have profound evolutionary effects at all latitudes.

In *Hypocrella* and *Moelleriella* but not *Samuelsia*, taxa with a disjunct distribution are apparent (Lee *et al.* 1996, Taylor *et al.* 1999, Wen 1999, Wu *et al.* 2000). A disjunct distribution is one in which two closely related taxa (*i.e.* morphologically similar) are widely separated geographically. In *Hypocrella* and *Moelleriella*, an Old World (OW) / New World (NW) disjunction is sometimes observed (Petch 1921, Evans 1982, Evans & Hywel-Jones 1990). Disjunctions have been observed in *M. palmae* (NW) vs. *M. sclerotioides* Höhn. (OW); *M. epiphylla* (NW) vs. *M. reineckiana* (OW); *M. libera* (NW) vs. *M. raciborskii* (OW); *M. ochracea* (NW) vs. *M. mollii* (OW); *M. macrostroma* (NW) vs. *M. africana* (OW); *M. castanea* Petch (NW) vs. *M. palmicola* Henn. (OW); and *M. gaertneriana* (NW) vs. *M. schizostachyi* (OW) (Petch 1921, Evans 1982, Evans & Hywel-Jones 1990, Chaverri *et al.* 2005b). It is possible that disjunct geographical distributions are common in *Hypocrella* and *Moelleriella*, but, because this monograph focuses on New World species, this issue is beyond the scope of the study.

Individual species of *Hypocrella, Samuelsia,* and *Moelleriella* may be distributed over a large region or may be endemic to smaller areas. The presumably short dispersal distances of spores, the distributions limited to the Tropics, and the relatively low intraspecific genetic variability suggests the majority of the species form geographically conserved populations (Obornik *et al.* 2000). For example, in the New World Tropics, *M. epiphylla*, *M. libera, M. ochracea, M. rhombispora*, *M. turbinata,* and *M. zhongdongii* are widespread and ubiquitous. In contrast, *M. gaertneriana* and *M. cornuta* have been found only in the Amazon basin (*i.e.* Brazil, French Guiana, Venezuela) and are rare. *Moelleriella evansii* and *S. chalalensis, S. geonomis,* and *S. rufobrunnea* have been found only in Ecuador, Bolivia, and Peru, respectively. The phenomenon of geographically restricted species is also observed in the *M. basicystis* species complex: *M. basicystis s. str.*, *M. phyllogena*, *M. disjuncta*, and *M. umbospora*. The present monograph demonstrates that *M. basicystis* has been found in Panama and Costa Rica (probably southern Central America); *M. phyllogena* in Panama, Brazil, Ecuador, Bolivia, and Peru (probably Panama and Amazon basin); *M. umbospora* in Mexico, Honduras, Guatemala (probably northern Central America); and *M. disjuncta* in Panama and Guyana.

Increased collecting in poorly explored regions will very likely discover new and rare species of *Hypocrella, Samuelsia,* and *Moelleriella*. However, many species are apparently restricted to undisturbed old growth tropical forests. The increased destruction of these sensitive habitats due to deforestation, forest fires, urban sprawl, and other factors, will result in the disappearance of fungal species, some with potential beneficial value to human societies (*e.g.* as biocontrols and sources of novel metabolites) (Evans 1982, Samson & Evans 1985, Evans 1988, Samson 1995, Chaverri & Vílchez 2006).

Habitat

Microclimate

Although *Hypocrella, Samuelsia,* and *Moelleriella* are widespread throughout the Tropics, they do not occur in all types of climates and habitats within the Tropics. Few publications report on the climate or habitat characteristics that *Hypocrella* or *Moelleriella* species prefer, and there is no published information on *Samuelsia* species. Based on studies done for other fungi, ultraviolet light and direct solar radiation may be one important factor affecting the survival of entomopathogenic fungal spores (Fargues *et al.* 1996, Moore *et al.* 1996), as well as scale insects and whiteflies. This explains in part why species of *Hypocrella, Samuelsia,* and *Moelleriella* are found mostly on the abaxial surface of leaves, where the insect and the fungus are protected from direct solar radiation. For example, during the survey of *Hypocrella, Samuelsia,* and *Moelleriella* done for the present study, no specimens were found in open highly sun-exposed areas lacking a tree/shrub canopy.

Temperature may also affect survival of *Hypocrella, Samuelsia,* and *Moelleriella*. Some studies have shown that temperature may affect conidial germination and nymphal mortality by *M. libera* (anam. "*A.*" *aleyrodis*) (Fransen *et al.* 1987, Fransen 1995). In contrast, Meekes *et al.* (2000) considered that temperature did not greatly affect infection ability by *M. libera*, but found a slightly higher conidial germination rate at 25 °C compared to 20 °C. In the present study, it was observed that habitats with a combination of suboptimum temperatures (*ca.* 28–38 °C or below 18 °C) and extreme continuous relative humidity conditions (*e.g.* dry forests, very humid forests) did not produce many fungal collections. For example, six weeks of surveying a lowland very wet tropical forest in Costa Rica yielded only eight species of *Hypocrella s. l.* (Chaverri & Vilchez 2006). Similarly, Hywel-Jones and Evans (1993) in Thailand, did not find specimens of *Hypocrella s. l.* during the driest months of the year (February, March, and April). However, high relative humidity (*ca.* 80 %) may be necessary for increased conidial germination and whitefly mortality by *M. libera* and *M. raciborskii* (Meekes 2001). The environment immediately surrounding the conidia may also influence their survival. Chemicals on the leaf surface may influence the viability of spores, but also they can have an effect on the pest and its susceptibility to pathogens (Hare & Andreadis 1983, Cooke & Rayner 1984, Ramoska & Todd 1985).

Host specificity, co-evolution, and adaptation

Species of *Hypocrella, Samuelsia,* and *Moelleriella* are scale-insect and whitefly pathogens. The insect host is almost always completely consumed by the fungus before the stroma and fruiting structures become evident (Evans 1988, Evans & Hywel-Jones 1990, Meekes *et al.* 1994), at which point it is almost impossible to identify the insect. Therefore, there is scarce information about host specificity in *Hypocrella, Samuelsia,* or *Moelleriella*. Petch (1921) stated that species of *Hypocrella* could parasitise either whiteflies (*Aleyrodidae*) or scale insects (*Coccidae* and *Lecaniidae*). In some cases, it may be possible to hypothesise the identity of the insect host based on neighboring individuals that are not completely consumed by the fungus or not infected. However, this approach can be misleading, because in many cases several species of scale insects or whiteflies are found on the same leaf (Petch 1921). Some species such as *M. libera/"A." aleyrodis, M. raciborskii/"A." placenta,* and *M. ochracea/"A." andropogonis* appear to be generalists and have been found to infect at least five scale-insect and whitefly species (Petch 1921, Meekes *et al.* 2000, Meekes 2001, Meekes *et al.* 2002). In most species of *Hypocrella s. l.* the degree of host specificity is completely unknown.

Characteristics of the plant upon which the host insect is feeding may also be important. A single strain of *M. libera* showed differences in persistence as a consequence of chemical and/or morphological differences between plants (Hare & Andreadis 1983, Cooke & Rayner 1984, Ramoska & Todd 1985, Meekes *et al.* 2000). The co-evolution of fungi and their insect hosts may reflect co-evolution between the insects and their plant hosts. In tropical forests, the spatial separation between conspecific plant individuals may have given rise to spatially separated insect populations that, in turn, coevolved with their fungal parasites (Evans 1988). Successful horizontal dispersal of the pathogens between coccid and whitefly colonies would have decreased proportionally with increasing adaptation and restriction of their hosts to certain trees (Evans 1988).

Epizootics caused by *Hypocrella, Samuelsia,* and *Moelleriella* on coccids and whiteflies in the Tropics are so prominent that several authors have wondered how these insects survived (Petch 1925, Evans 1974, 1982, 1988). As mentioned before, dispersal of the fungus probably played an important role in the co-evolution with its insect host, and the co-evolution of the insect with its plant host. The anamorphic forms of *Hypocrella, Samuelsia,* and *Moelleriella* produce slimy masses of conidia that are well adapted for short-distance, water-borne movement over leaf surfaces (Parkin 1906, Chaverri & Samuels 2003, Hodge 2003). The mucilage that covers the conidia is high in sugar content making the conidia more hygroscopic (Meekes 2001) and attractive to insects. This mode of short-distance dispersal is apparently so efficient that once a colony of insects becomes infected by the fungus, it is difficult to find healthy individuals (Evans 1988).

Evans (1988) speculated about insect adaptation to the threat from entomopathogenic fungi. The short-distance dispersal of conidia that contributes to epizootics may select for discontinuous patterns of insect distribution. On the other hand, the teleomorphic forms of *Hypocrella, Samuelsia,* and *Moelleriella* are less commonly encountered and have dry, discharged ascospores that are probably wind-dispersed and so better adapted for medium to long distance dispersal (Evans 1988, 1989). However, the above hypothesis could be refuted because in related genera, such as *Sphacelia, Ephelis* and *Neotyphodium*, the discharge of conidia in slime appears to aid dispersal by insects (Loveless 1964, Mower *et al.* 1973, Mower & Hancock 1975, Samways 1983, Butler *et al.* 2001, Hodge 2003).

Scale insects and whiteflies often secrete sticky honeydew that is attractive to wasps and ants, so it is also possible that *Hypocrella, Samuelsia,* and *Moelleriella* evolved to produce slimy conidia that adhere to non-host insect vectors. Infected coccid or whitefly alates may further transport the fungus, as shown for some aphid-*Entomophthorales* interactions (Wilding & Perry 1980, Evans 1989). Insect vectors and infected alates could disperse the spores across long distances; water, such as rain splash and run-off, could disperse across short distances (Chaverri *et al.* 2005a).

Plant-insect-fungus specificity is suspected but not well known in *Hypocrella, Samuelsia,* and *Moelleriella*, and further experimental evidence will be important in developing these fungi as biological controls. Based on observations made for the present study, the majority of the specimens were found on shrubs, trees, palms, and *Musaceae* leaves, with a few species (*e.g. M. libera, M. ochracea, H. disciformis,* and *H. viridans*) found on small herbaceous plants. The plant-specificity of the host insects may be important in determining where the fungi are found; scale insects and whiteflies are themselves poorly understood, with the exception of a handful of species that are crop pests. *Samuelsia geonomis, S. chalalensis, S. rufobrunnea*, *M. gaertneriana* and *M. schizostachyi* have been found only on monocotyledonous plants, such as bamboo culms and palm leaves; and the related species *M. africana* and *M. macrostroma* have been found only on stems of dicotyledonous plants (Hywel-Jones & Samuels 1998, Chaverri *et al.* 2005b). Although most species of *Hypocrella, Samuelsia,* and *Moelleriella* are found on leaves, other species such as *M. epiphylla* and *M. turbinata* are found both on leaves and stems (Petch 1921, Mains 1959a, b). A few other species that are more widespread can be found both on monocot and dicot leaves (*e.g. M. basicystis, M. libera, M. ochracea,* and *M. phyllogena*). The great majority of the species of *Hypocrella, Samuelsia,* and *Moelleriella* are found on leaves, with a larger portion occurring on the abaxial surface of leaves and a smaller percentage on the adaxial surface (*e.g. M. epiphylla, M. turbinata, M. reineckiana*) (Petch 1921, Hywel-Jones 1998). Whitefly and scale-insect nymphs are mainly present on the abaxial surface of leaves.

Nutrition

The mechanisms by which *Hypocrella, Samuelsia,* and *Moelleriella* species obtain enough nutrients from the host to support the relatively large size of the stromata are not well studied. In *Moelleriella*, several species have especially large stromata: *M. gaertneriana, M. africana, M. schizostachyi*, and *M. macrostroma*. Other genera in the *Clavicipitaceae*, including *Ascopolyporus* A. Möller, *Dussiella* Pat. and *Hyperdermium*, also parasitise scale insects and have relatively large stromata. In these genera, the stromatal mass greatly exceeds that of the scale-insect host. Sullivan *et al.* (2000) hypothesised that the large size of the stromata results from a kind of secondary plant parasitism. Once the fungus has consumed the scale-insect body, the fungus may continue to access plant nutrients through the insect's stylet. Another hypothesis suggests that the mechanism of nutrient acquisition in fungal species parasitic on scale insects and whiteflies is through the living insect that forms a bridge between the fungus and the plant (Couch 1938, Hywel-Jones & Samuels 1998). Koroch *et al.* (2006) studied host nutrient adaptation in *Balansia henningsiana* (a plant pathogen) and *M. phyllogena* (a scale-insect pathogen). They observed that both fungi exhibit a restricted range of similar nutrient sources that may support growth and that those nutrients (such as sucrose) are most likely from plant sources. This same study suggests that the scale-insect pathogen *M. phyllogena* obtains some of its nutrients from the host plant rather than exclusively from the insect. In terms of its nutrition, *M. phyllogena* is more similar to the plant biotrophs than to entomopathogenic fungi in the same family (Koroch *et al*. 2006). Its close evolutionary relationship with plant pathogens has been supported by previous studies (Bischoff *et al.* 2004, Chaverri *et al.* 2005a).

Hypocrella, Samuelsia, and *Moelleriella* species can usually be grown in culture on most standard laboratory media. Growth rates are relatively slow, but most species will produce conidia in culture. Typical stromata are not formed in culture, and sexual fruiting bodies have not been observed.

Life cycle and epidemiology

Host and conidia may meet in two different ways: (1) direct contact, when conidia are released/introduced upon the insect host (dispersed by water, air, or other insects), or (2) indirect contact, when hatching or moulting nymphs (larvae) settle on or near conidia already present on the leaf surface (Meekes 2001). The sticky mucilage that covers the conidia permits them to adhere to hydrophobic surfaces, such as the insect cuticle in the presence of water (St.-Leger 1991, Meekes 2001). The whitefly or scale insect is infected when germinating spores penetrate the insect cuticle. Germination and appressorium formation in several aschersonia-like species does not seem to be affected by the specific binding site on the insect nor by a specific instar (Meekes 2001). The ideal temperature for germination seems to be *ca.* 25 °C, but as low as *ca.* 20 °C and as high as *ca.* 30 °C; germination and germ-tube length is severely limited at 15 °C and 35 °C (Ibrahim *et al.* 1993). Studies also show that exposure of conidia to extended periods of time at 25 °C or higher reduce their viability after *ca.* 15 d (Fransen 1995, Meekes *et al.* 2000, Meekes *et al.* 2002). The ability of *Hypocrella, Samuelsia,* and *Moelleriella* conidia to remain viable in a potential habitat of the host insect may be influenced by temperature, relative humidity, solar radiation, characteristics of the leaf surface (chemical and/or morphological differences between the plants), canopy characteristics, and the presence of other microorganisms on the leaf. Conidial germination capacity can remain high for at least one month. With respect to ascospores, there is no known information on the factors that influence their germination and viability. Conidia of most species of *Hypocrella, Samuelsia,* and *Moelleriella* germinate in favorable conditions after 24–48 h (Ibrahim *et al.* 1993, Fransen 1995, Meekes *et al.* 2000, Meekes *et al.* 2002).

Under greenhouse conditions, most infections occur during the night following the release of conidia. In *M. libera*, the first sign of infection is a discolouration of the first instar larvae 4–10(–14) d after inoculation (Samson & Rombach 1985, Meekes *et al.* 2000, Meekes *et al.* 2002). The rate of infection declines with increased age of the insect; the fourth instar, prepupae, and pupae are less susceptible. Eggs are not infected. After infection, the fungus proliferates inside the host by first forming hyphal bodies, a yeast-like stage. Once the mycelium has fully colonised the body cavity, it emerges from the insect and forms a fringe around the insect's body, apparently adhering it to the plant host.

Sporulation occurs early in the infection process, soon after the hyphae rupture the dorsal cuticle and produce mat-like pustules of white mycelia on the host surface (Samson & Rombach 1985, Meekes *et al.* 2000, Meekes *et al.* 2002). Pycnidia appear to form first. This is supported by observations of Hywel-Jones and Evans (1993), who found the anamorph in the first months of the wet season and the teleomorph in the last months of the wet season, right before the dry season started. In a few cases, pycnidia and perithecia may be present in the same stroma at the time of collection. Many of the teleomorph collections for the present monograph were made from fallen leaves that were on the forest floor.

In culture, conidia and ascospores of several species of *Hypocrella* and *Moelleriella* (*H. discoidea*, *M. epiphylla, M. turbinata*) germinate to produce long and slender conidiogenous cells, and then secondary conidia (capilliconidia) (Hywel-Jones & Evans 1993, Evans 1994, Meekes 2001). This may be a mechanism to ensure secondary dispersal if the primary spores (*i.e.* ascospores or conidia) do not reach the target insect. This phenomenon has been observed in some entomophthoralean fungi (King & Humber 1981, Keller 1991, Hywel-Jones & Evans 1993). It is thought that these capilliconidia are formed in response to the absence of a suitable host (King & Humber 1981, Humber 1984, Evans 1994) or as a mechanism to increase the chances of transmission to mobile host insects (Glare *et al.* 1985b, a). Other types of anamorphs (*i.e.* synnematous or mononematous synanamorphs) have also been observed in *Hypocrella* and *Moelleriella*: hirsutella-like in *M. insperata* Rombach *et al.* (Liu *et al.* 2005), *M. turbinata*, *M. schizostachyi* (Hywel-Jones & Samuels 1998), and *Hypocrella hirsuta*. This type of synanamorph is usually produced in culture at an early stage in the development of the stroma, and is followed later by the aschersonia-like form (Liu *et al.* 2005).

Species of *Hypocrella, Samuelsia,* and *Moelleriella* are not known to produce resting spores, chlamydospores, or other structures that persist during unfavorable environmental conditions. Carotenoids or similar pigments in their stromata and conidia may contribute to long-term survival—most species are brightly coloured, mostly orange, due to these pigments (Eijk *et al.* 1986). Pigments may enhance the ability of the spores to withstand short periods of exposure to solar radiation.

Although sexual fruiting bodies of *Hypocrella, Samuelsia,* and *Moelleriella* are found in nature, nothing is known of the stimuli or requirements for sexual reproduction. Based on observations made for the present study, no perithecia form in culture. It is possible that the genera are heterothallic or the environmental conditions are not conducive for the formation of perithecia and ascospores. This is also the case for most other clavicipitaceous fungi, among which the development of teleomorphs in culture is rare. Only a few insect pathogens have been reported to fruit in culture after artificial manipulations. For example, *Cordyceps militaris* (L.) Link, *Torrubiella* spp., and *Romanoa* Thirum. have been observed to produce perithecia in semisynthetic media (Thirumalachar 1954, Basith & Madelin 1968, Hodge 2003). Sung (1996) induced the formation of stromata and perithecia in several *Cordyceps* species using media composed of sterilised brown rice with chopped silkworm pupae.

Secondary metabolites produced by *Hypocrella/ Aschersonia* and *Moelleriella*

The death of insects invaded by ascomycetous fungi is thought to be caused by toxins released by the fungus (Roberts 1981, Evans 1988). Evans (1988) hypothesised that toxins probably build up in the haemocoel of the insect as the yeast-like parasitic cells colonise the circulatory system. There is little information regarding secondary metabolites or toxins produced by *Hypocrella, Samuelsia,* and *Moelleriella*, mostly because of the lack of available cultures for studies (Isaka *et al.* 2003). Watts *et al.* (2003) demonstrated that the anthraquinone dimers, rugulosin and skyrin, extracted from *H. discoidea* were cytotoxic to some insect cells (*i.e. Spodoptera frugiperda*). Watts *et al.* (2003) reported that most of the isolates positive against insect cells were from "…*Hypocrella* with whole ascospores…". Destruxins (cyclohexadepsipeptides), which exhibit insecticidal, phytotoxic, antiviral, cytotoxic, and immunodepressance activities, have been found in various entomopathogenic fungi, including *Moelleriella* and *Hypocrella* (Krasnoff *et al.* 1996). These few studies support the hypothesis that secondary metabolites may be involved in insect pathogenicity.

The compounds hypocrellin A and B have been erroneously linked to *Hypocrella* (Zhang *et al.* 1989, Hudson *et al.* 1994, Diwu 1995, Zhang *et al.* 1998, Fei *et al.* 2006). This compound is only known from *"Hypocrella" bambusae*, which is actually a *Balansia* (Petch 1921). A few other secondary metabolites that have been identified but not linked to a function *in vivo* are triterpenes 3β, 15α, 22-trihydroxyhopane from *M. libera* (Eijk *et al.* 1986) and an analog from *M. tubulata* (Boonphong *et al.* 2001). These compounds exhibit activity against *Mycobacterium tuberculosis*. Zeorin (6α, 22-dihydroxyhopane), another triterpene, has been found in several other species of *Hypocrella* and *Moelleriella* (Isaka *et al.* 2003). Interestingly, these triterpenes have been found in *Hypocrella* and *Moelleriella* but not in other entomopathogenic fungi (Isaka *et al.* 2003).

Hypocrella/*Aschersonia*, *Samuelsia*, and *Moelleriella* in biological control of insects

The ability of *Hypocrella, Samuelsia,* and *Moelleriella* to cause epizootics on whitefly and scale-insect populations makes these three genera potentially useful agents of biological control. The first biocontrol applications were done with *Moelleriella libera* (anam. *"A." aleyrodis*) to control citrus whitefly in Florida, U.S.A. (Berger 1921). In some regions, whiteflies are still effectively controlled by epizootics following these original applications (Samson & Rombach 1985). Rolfs and Fawcett (1908) included two *Moelleriella* species (then classified in *Aschersonia*) among the so-called "friendly" fungi. Their "red fungus" is *M. libera*. Their "yellow fungus" was thought to be *Aschersonia flavocitrina*; however Petch (1921) reported that it was *A. goldiana* Sacc. & Ellis. *Aschersonia goldiana* is now considered a synonym of *M. libera,* and modern collections from Florida have also been shown to be a yellow-spored form of *M. libera* (Liu *et al.* 2006).

Interest in the use of *Aschersonia* species as biocontrol agents started to decline around the 1920s, following doubts about their efficacy and the increasing popularity of chemical insecticides (Evans & Hywel-Jones 1990). In the 1960s and 1970s, biological control research on *Aschersonia s. l.* species was revived, especially in Eastern Europe and Asia (Evans & Hywel-Jones 1990). Since then, many studies have shown that aschersonia-like species can been successful biocontrol agents against several species of whiteflies and scale insects (Uchida 1970, Ferron 1978, Ramakers 1983, Ramakers & Samson 1984, Hall 1985, Gerling 1986, Fransen 1987, Gerling 1992, Meekes *et al.* 1996, Faria & Wraight 2001, Meekes 2001, Sengonca *et al.* 2006, among others). Meekes (2001) presented an extensive list of *Aschersonia s. l.* species and susceptible insect hosts (Table 1.1., p. 5, in Meekes 2001). Because *Samuelsia* is a small genus with few known collections, no information on its biocontrol potential exists.

Hypocrella and *Moelleriella* meet some of the important criteria for the development of a mycoinsecticide: ease of production in artificial medium, high spore yield, and high virulence against the target insect. In general, *Hypocrella* and *Moelleriella* species readily produce conidia in artificial media. Light may enhance conidial production (Hirte *et al.* 1989, Ibrahim *et al.* 1993, Lacey *et al.* 1996, Meekes 2001). However, the fact that most species of these two genera do not sporulate in liquid culture, or, if so, only at its surface, is an impediment to mass production for biocontrol (Ibrahim *et al.* 1993). In addition, the lack of dispersing agents in greenhouses (*e.g.* wind and rain) makes repeated applications necessary to maintain high levels of the pathogen in the insect population (Samson & Rombach 1985).

MATERIALS AND METHODS

Isolates and herbarium specimens

Herbarium specimens were obtained from various herbaria: U.S. National Fungus Collection (BPI); Cornell University Plant Pathology Herbarium (CUP); Instituto Agronômico de Campinas (IAC); Botanischer Garten und Botanisches Museum Berlin (B); Royal Botanic Gardens, Kew (K); Farlow Reference Library and Herbarium of Cryptogamic Botany (FH); Erbario Patavinum (PAD); Herbarium of the Botany Department, Swedish Museum of Natural History (S); Instituto de Botánica Carlos Spegazzini (LPS); William and Lynda Steere Herbarium (NY); Herbier Cryptogamique, Dépt. Systématique et Évolution, Muséum National d'Histoire Naturelle (PC); Museum of Evolution, Botany Section (Fytoteket), Uppsala University (UPS); Herbario del Departamento de Botánica, Instituto Nacional de Biodiversidad (INB); Herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN); Herbarium of the Department of Plant Systematics, Polish Academy of Sciences (KRAM); National Herbarium, Department of Agriculture Royal Botanic Gardens, Peradeniya (PDA); Herbarium of Forest Mycology and Pathology, Japan (TFM); Mycological Herbarium, Institute of Microbiology, Academia Sinica (HMAS); Herbarium of the University of Michigan (MICH); and Herbarium, Department of Botany, Naturhistorisches Museum Wien (W). Additional specimens examined were collected by the authors during field expeditions to Florida (U.S.A.), Costa Rica, Honduras, Mexico, Peru, Puerto Rico, and Bolivia, and others provided by collaborators: J.F. Bischoff (JB; Panama), R.O. Gazis (Peru), J. Hernandez (Puerto Rico), M.C. Aime (M.C.A.; Guyana), G.F. Bills (Mexico, Panama), G.J. Samuels (GS; Ecuador, Cameroon, Ghana), and especially H. C. Evans who contributed hundreds of specimens from all over the world; all these specimens are deposited at the Cornell University Plant Pathology Herbarium (CUP).

Cultures were obtained by isolating asci containing ascospores or conidial masses, and placing them on Difco potato dextrose agar (PDA) with a 1 % antibiotic solution (0.2 % Sigma Streptomycin Sulfate + 0.2 % Sigma Neomycin Sulfate). Additional cultures were obtained from ARS Collection of Entomopathogenic Fungal Cultures, New York, U.S.A. (ARSEF); Biotec Culture Collection, Bangkok, Thailand (BCC); and Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands (CBS).

Morphological characterisation

For morphological characterisation, the macromorphology of the stroma was observed: location of the stromata on the plant (*i.e.* abaxial or adaxial surface of leaves, stems, leaf veins), stroma size, colour, shape, hardness, presence/absence of hypothallus, texture of the stroma surface, distribution of perithecia and conidiomata in the stroma, presence of perithecia and conidiomata in the same stroma, presence of projecting or embedded perithecia, colour of ostiole openings, colour of conidiomatal cavities or openings, and colour of conidial masses. Colour terminology is from Kornerup and Wansher (1967). The reaction of the stromatal tissue in 3 % potassium hydroxide (KOH) was noted. If a change in colour was observed then it is noted as KOH+. To observe internal characteristics of the stromata, such as tissue type, diameter of stromal hyphae, and shape of perithecia, the stromata were rehydrated briefly in distilled water with a trace of Tween® 80 (J.T. Baker Chemical Co., Phillipsburg, New Jersey, U.S.A.). Then, the rehydrated stromata were supported by Tissue-Tek O.C.T. Compound 4583 (Miles Inc., Elkhart, Indiana, U.S.A.) and sectioned at a thickness of *ca.* 15 µm with a freezing microtome. Characteristics of the asci, ascospores, phialides, paraphyses, and conidia were observed by rehydrating the stroma in 3 % KOH or water containing Tween® and removing part of the centrum with a fine glass needle and placing it on a glass slide. Terminology applying to stromal tissue types (*i.e. textura angularis, intricata, oblita, epidermoidea*) is used in the sense of Korf (1958). Morphological observations of the colonies and anamorphs in culture were based on cultures grown on PDA for *ca.* 3 wk in an incubator at 25 ºC with alternating 12 h fluorescent light and 12 h darkness. Based on Liu & Hodge (2005), growth rate over 3 wk has been categorised as: fast-growing 30–35 mm diam, moderate growth 20–30 mm diam, and slow-growing <20 mm diam.

Measurements of continuous characters such as length and width were made using the beta 4.0.2 version of Scion Image software (Scion Corporation, Frederick, Maryland, U.S.A.). Confidence intervals (α = 0.05), minimum and maximum values for 10–30 anamorph and teleomorph measurements (except where indicated) were calculated using Systat 8.0 (SPSS, Inc., Chicago, Illinois, U.S.A.).

DNA extraction, PCR and sequencing

Cultures of *Hypocrella, Samuelsia,* and *Moelleriella* species used in the phylogenetic analyses (Table 2) were grown on potato-dextrose broth in a 6-cm-diam Petri plate for about 1 wk. The mycelial mat was harvested in a laminar flow hood and then dried using clean, absorbent paper towels. DNA was extracted with Ultra Clean™ Plant DNA Isolation Kit (MO BIO Laboratories, Inc., Solana Beach, California, U.S.A.). To extract DNA from herbarium specimens, the surface of the stroma was first cleaned briefly with sterilised distilled water, then rehydrated by placing the stroma in a small Petri plate with sterilised distilled water and letting it stand for a few minutes until the stroma became softer. Subsequently, a very thin layer of the surface of the stroma was shaved off using a scalpel and then discarded. Pieces of the clean inner stroma, including centri, were cut out and then placed in a 1.5-mL Eppendorf tube for immediate DNA extraction with Ultra Clean™ Plant DNA Isolation Kit.

Three partial gene regions were amplified, *i.e.*, large subunit nuclear ribosomal DNA (LSU), translation elongation factor 1-α (EF1-α), and RNA polymerase II subunit one (RPB1). The primers used were LSU: LRORf (5'-GTACCCGCTGAACTTAAGC- 3') and LR5r (5'- ATCCTGAGGGAAACTTC- 3') (Vilgalys & Hester 1990); EF1-α: 983f (5'-GCYCCYGGHCAYCGTGAYTTYAT-3') (Carbone & Kohn 1999) and 2218r (5'-ATGACACCRACRGCRACRGTYTG-3') (Rehner 2001); RPB1: cRPB1Af (5'-CAYCCWGGYTTYATCAAGAA-3') and RPB1Cr (5'-CCNGCDATNTCRTTRTCCATRTA-3') (Castlebury *et al.* 2004). Each 50 µL-PCR reaction contained 25 µL of Promega 2X PCR Master Mix (Promega Corporation, Madison, Wisconsin, U.S.A.), 2.5 µL of each forward and reverse primers (10 mM), 1 µL DMSO (dimethyl sulfoxide), *ca.* 25 ng of genomic DNA, and sterile distilled water. The PCR reactions were placed in an Eppendorf Mastercycler thermocycler (Eppendorf, Westbury, New York, U.S.A.) under the following conditions: for LSU (1) 5 min at 94 °C, (2) 35 cycles of denaturation at 94 °C for 30 s, annealing at 50 °C for 45 s, and extension at 72 °C for 1 min, (3) and 7 min at 72 °C; for EF1-α (1) 10 min at 95 °C, (2) 40 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 1 min, (3) and 72 °C for 10 min; and for RPB1 (1) 5 min at 95 °C, (2) 40 cycles of denaturation at 95 °C for 1 min, annealing at 50 °C for 2 min, and extension at 72 °C for 2 min, (3) and 72 °C for 10 min. The resulting PCR products were purified with the QIAquick™ PCR Purification Kit (Qiagen, Inc., Valencia, California, U.S.A.). Sequencing of forward and reverse strands was performed at the DNA Sequencing Facility (Center for Agricultural Biotechnology, University of Maryland, College Park, Maryland, U.S.A.). Sequences were assembled and edited with Sequencher 4.2 (Gene Codes, Madison, Wisconsin, U.S.A.). Sequences have been deposited in GenBank (Table 2).

Phylogenetic analyses

The sequences produced were aligned with Clustal X 1.81 (Thompson *et al.* 1997) and the alignment was refined by hand with GeneDoc 2.6.002 (Nicholas *et al.* 1997). Maximum Parsimony (MP), Neighbor Joining (NJ), and Bayesian Inference (BI) analyses were carried out with all sequences. The MP analysis was done in PAUP v. b10 (Swofford 2002) using a heuristic search, with a starting tree obtained via 1000 random stepwise addition sequences, tree-bisection-reconnection as the branch-swapping algorithm, and MULTREES off. Neighbour-Joining analyses were done using the Kimura 2-parameter model. Bootstrap values (BP) from 1000 replicates were calculated for both MP and NJ. MrBayes 3.0 b4 (Huelsenbeck 2000, Huelsenbeck *et al.* 2001) was used to reconstruct phylogenetic trees based on the Bayesian approach (Rannala & Yang 1996, Mau *et al.* 1999). The Bayesian analysis used a different model of evolution for each of the three partitions (LSU, TEF, RPB1). The models of DNA substitution were estimated using Modeltest 3.6 (Posada & Crandall 1998) and are detailed in Chaverri *et al.* (2005a). Four chains and 5,000,000 Markov Chain Montecarlo generations were run and the current tree was saved to a file every 100 generations. Stability of likelihood scores was confirmed using the software TRACER version 1.2.1 (Rambaut & Drummond 2007), which traces the parameter against the generation number. Once stability was reached both in terms of likelihood scores and parameter estimation, the first 5,000 trees were discarded ("burn in"). The remaining trees ("post-burn in") were pooled and a 50 % majority-rule consensus tree was obtained with PAUP*. *Epichloë elymi* Schardl & Leuchtm.*, Balansia henningsiana* (A. Möller) Diehl, and *Regiocrella sinensis* Chaverri & K.T. Hodge were used as outgroup species. The close relationship of the selected outgroup species to *Hypocrella*, *Moelleriella,* and *Samuelsia* was shown in Chaverri *et al.* (2005a).

Topological incongruence was examined using a reciprocal 70 % bootstrap (BP) or a 95 % posterior probability (PP) threshold (Mason-Gamer & Kellogg 1996, Reeb *et al.* 2004) in order to determine whether the sequences from the three genes should be combined in a single analysis. Bootstrap values were generated using NJ with 1000 replicates and a maximum likelihood distance. Posterior probabilities were calculated using Bayesian analysis in MrBayes. A conflict was assumed to be significant if two different relationships for the same taxa, one being monophyletic and the other non-monophyletic, both with BP ≥70 % and PP ≥95 %, were observed on each LSU, EF1-α, and RPB1 majority-rule consensus trees. The three partitions could be combined if no significant conflicts were detected.

Table 2. Species, isolates, vouchers, geographic origin, and GenBank numbers used in the phylogenetic analyses.

			GenBank Accession Numbers		
Species	**Voucher/Isolate**	**Origin**	**LSU**	**EF-1a**	**RPB1**
Hypocrella citrina	P.C. 597 = CUP 067825	Bolivia	AY986905	AY986930	DQ000331
H. citrina	P.C. 598 = CUP 067826	Bolivia	EU392555		
H. citrina	P.C. 606 = CUP 067827	Bolivia	EU392656	EU392640	EU392694
H. disciformis	M.L. 202i = ARSEF 7695	Puerto Rico	AY986913	AY986939	DQ000340
H. disciformis	P.C. 575 = CUP 067831	Bolivia	EU392557	EU392641	EU392695
H. disciformis	P.C. 589 = CUP 067833	Bolivia	EU392559		
H. disciformis	P.C. 585 = CUP 067832	Bolivia	EU392558	EU392642	EU392696
H. disciformis	P.C. 659 = CUP 067835	Honduras	EU392561	EU392644	EU392698
H. disciformis	P.C. 663.1 = CUP 067837	Honduras	EU392563		
H. disciformis	P.C. 661.1 = CUP 067836	Honduras	EU392562		
H. disciformis	P.C. 655 = CUP 067861	Honduras	EU392560	EU392643	EU392697
H. disciformis	P.C. 676 = CUP 067840	Honduras	EU392566	EU392645	EU392699
H. disciformis	P.C. 667 = CUP 067838	Honduras	EU392564		
H. disciformis	P.C. 673 = CUP 067839	Honduras	EU392565		
H. cf. *discoidea*	P.C. 737 = Afr 55 = ARSEF 7697	Ghana	AY986910	AY986936	DQ000337
H. cf. *discoidea*	I93-901d = ARSEF 7663	Côte D'Ivoire	EU392567	EU392646	EU392700
H. cf. *discoidea*	I95-901d = ARSEF 7668	Côte D'Ivoire	EU392568	EU392647	EU392701
H. cf. *discoidea*	4093	Thailand	AF327381		
H. cf. *discoidea*	2630	Thailand	AF327387		
H. cf. *discoidea*	BCC 2097	Thailand	AF327381	AY986945	DQ000346
H. hirsuta	P.C. 543 = CUP 067841	Bolivia	EU392569	EU392648	EU392702
H. hirsuta	P.C. 436.2 = CUP 067848	Mexico	AY986922	AY986949	DQ000350
H. viridans	P.C. 671 = CUP 067853	Honduras	EU392575		
H. viridans	P.C. 635 = CUP 067850	Honduras	EU392572	EU392651	EU392705
H. viridans	P.C. 670 = CUP 067852	Honduras	EU392574	EU392652	EU392706
H. viridans	P.C. 695 = CUP 067854	Honduras	EU392576		
H. viridans	P.C. 632 = CUP 067849	Honduras	EU392571	EU392650	EU392704
H. viridans	P.C. 637 = CUP 067851	Honduras	EU392573		
H. viridans	I89-490 = IMI 346739	Mexico	EU392570	EU392649	EU392703
Moelleriella africana	P.C. 736 = Afr 33 = ARSEF 7696	Ghana	AY986917	AY986943	DQ000344
M. basicystis	P.C. 374 = CUP 067745	Costa Rica	AY986903	AY986928	DQ000329
M. basicystis	F183147 = CUP 067746	Panama	EU392577	EU392653	
M. boliviensis	P.C. 603 = CUP 067747	Bolivia	AY986923	AY986950	DQ000351
M. disjuncta	M.C.A. 2331 = CUP 067864	Guiana	EU392579		
M. disjuncta	M.C.A. 2445 = CUP 067865	Guiana	EU392580	EU392655	
M. disjuncta	J.B. 205 = CUP 067751	Panama	EU392578	EU392654	
M. epiphylla	M.L. 159	Puerto Rico	EU392584	EU392658	EU392709
M. epiphylla	I95-958 = ARSEF 7671	Ecuador	EU392581	EU392657	EU392708
M. epiphylla	P.C. 545 = CUP 067866	Bolivia	EU392585	EU392660	EU392711
M. epiphylla	P.C. 552 = CUP 067752	Bolivia	EU392586	EU392661	EU392712
M. epiphylla	P.C. 386 = CUP 067755	Costa Rica	EU392582	EU392659	EU392710
M. epiphylla	P.C. 375 = CUP 067754	Costa Rica	AY986906	AY986931	DQ000332
M. epiphylla	I93-813 = IMI 362282	Guiana	EU392583	EU392656	EU392707
M. epiphylla	P.C. 440 = CUP 067763	Mexico	AY986907	AY986932	DQ000333
M. evansii	P.C. 627 = CUP 067764	Ecuador	AY986916	AY986942	DQ000343
M. insperata	ARSEF 2396	Philippines	AY518374	DQ070029	EU392713
M. libera	P.C. 550 = CUP 067769	Bolivia	EU392593	EU392664	EU392716

Table 2. (Continued).

			GenBank Accession Numbers		
Species	**Voucher/Isolate**	**Origin**	**LSU**	**EF-1a**	**RPB1**
M. libera	P.C. 502 = CUP 067867	Costa Rica	EU392592		
M. libera	P.C. 321 = ARSEF 7617	Costa Rica	DQ070121		
M. libera	I93-807 = CUP 067772	Guiana	EU392587		
M. libera	M.C.A. 2335 = CUP 067870	Guiana	EU392590		
M. libera	P.C.672 = CUP 067773	Honduras	EU392594	EU392665	EU392717
M. libera	P.C. 445 = CUP 067869 = ARSEF 7707	Mexico	AY986900	AY986925	DQ000326
M. libera	P.C. 444 = CUP 067868	Mexico	EU392591	EU392662	EU392714
M. libera	I93-815 = IMI 362284 = ARSEF 7654	Trinidad	EU392588		
M. libera	I94-908 = CUP 067774	Venezuela	EU392589		
M. macrostroma	P.C. 605 = CUP 067508	Bolivia	AY986919	AY986946	DQ000347
M. macrostroma	J.B. 115 = CUP 067509 = ARSEF 7748	Costa Rica	AY986920	AY986947	DQ000348
M. madidiensis	P.C. 569 = CUP 067776	Bolivia	AY986915	AY986941	DQ000342
M. madidiensis	P.C. 594 = CUP 067775	Bolivia	EU392595	EU392666	EU392718
M. mollii	Afr 64 = ARSEF 7698	Ghana	EU392596		
M. mollii	Afr 70 = ARSEF 7638	Ghana	EU392597		
M. mollii	I93-901a = ARSEF 7660	Côte D'Ivoire	EU392599	EU392667	EU392719
M. mollii	I93-901c = ARSEF 7667	Côte D'Ivoire	EU392600	EU392668	EU392720
M. ochracea	P.C. 535 = CUP 067777	Bolivia	AY986901	AY986926	DQ000327
M. ochracea	P.C. 384 = CUP 067515	Costa Rica	EU392603		
M. ochracea	P.C. 626 = CUP 067778	Ecuador	EU392604	EU392670	EU392722
M. ochracea	P.C. 661.2 = CUP 067780	Honduras	EU392606		
M. ochracea	P.C. 648 = CUP 067779	Honduras	EU392605	EU392671	EU392723
M. ochracea	P.C. 685 = CUP 067781	Honduras	EU392607		
M. ochracea	IMI 317421 = ARSEF 7672	Jamaica	EU392602		
M. ochracea	IE 1308 = P.C. 726	Mexico	EU392601	EU392669	EU392721
M. ochracea	I85-165 = CUP 067782	Trinidad	EU392698		
M. phyllogena	P.C. 554 = CUP 067784	Bolivia	EU392609	EU392673	EU392725
M. phyllogena	P.C. 555 = CUP 067785	Bolivia	EU392610	EU392674	EU392726
M. phyllogena	P.C. 628 = CUP 067790	Ecuador	AY986902	AY986927	DQ000328
M. phyllogena	J.B. 130 = CUP 067793	Panama	EU392608	EU392672	EU392724
M. raciborskii	Afr 28 = ARSEF 7637	Ghana	DQ070113	EU392675	EU392727
M. raciborskii	P.C. 533	Vietnam	AY986911	AY986937	DQ000338
M. raciborskii	I93-901b = ARSEF 7661	Côte D'Ivoire	EU392611	EU392676	EU392728
M. rhombispora	P.C. 467 = CUP 067538	Costa Rica	AY986908	AY986933	DQ000334
M. rhombispora	CUP 067494	Guatemala	EU392612	EU392677	EU392729
M. rhombispora	P.C. 675 = CUP 067547	Honduras	EU392615		
M. rhombispora	P.C. 691 = CUP 067548	Honduras	EU392616		
M. rhombispora	P.C. 693 = CUP 067549	Honduras	EU392617		
M. rhombispora	P.C. 696 = CUP 067550	Honduras	EU392618	EU392680	EU392732
M. rhombispora	P.C. 698 = CUP 067551	Honduras	EU392619		
M. rhombispora	P.C. 458 = CUP 067795	Mexico	EU392613	EU392678	EU392730
M. rhombispora	P.C. 460 = CUP 067534	Mexico	EU392614	EU392679	EU392731
M. schizostachyi	CBS 100067	Thailand	AY986921	AY986948	DQ000349
M. sloaneae	I94-922c = CUP 067796	Belize	EU392622	EU392683	EU392735
M. sloaneae	I94-920 = CUP 067802	Guatemala	EU392621	EU392682	EU392734
M. sloaneae	I93-805 = CUP 067803	Guiana	EU392620	EU392681	EU392733
M. sloaneae	P.C. 658 = CUP 067804	Honduras	EU392623	EU392684	EU392736

Table 2. (Continued).

Species	Voucher/Isolate	Origin	GenBank Accession Numbers		
			LSU	**EF-1a**	**RPB1**
M. sloaneae	P.C. 665 = CUP 067805	Honduras	EU392624		
M. turbinata	M.C.A. 2432 = CUP 067860	Guiana	AY986912	AY986938	DQ000339
M. turbinata	P.C. 639 = CUP 067808	Honduras	EU392626	EU392686	EU392738
M. turbinata	P.C. 678 = CUP 067863	Honduras	EU392627	EU392687	EU392739
M. turbinata	IMI 352838	Mexico	EU392625	EU392685	EU392737
M. umbospora	P.C. 684 = CUP 067812	Honduras	EU392629		
M. umbospora	P.C. 457 = CUP 067816	Mexico	AY986904	AY986929	DQ000330
M. umbospora	P.C. 461 = CUP 067817	Mexico	EU392628	EU392688	EU392740
M. zhongdongii	I95-954 = CUP 067871 = ARSEF 7670	Bolivia	EU392630		
M. zhongdongii	P.C. 581 = CUP 067821	Bolivia	EU392635		
M. zhongdongii	P.C. 595 = CUP 067823	Bolivia	AY986909	AY986934	DQ000335
M. zhongdongii	P.C. 561 = CUP 067820	Bolivia	EU392634		
M. zhongdongii	P.C. 549 = CUP 067818	Bolivia	EU392632	EU392690	EU392742
M. zhongdongii	P.C. 557 = CUP 067819	Bolivia	EU392633		
M. zhongdongii	P.C. 591 = CUP 067822	Bolivia	EU392636		
M. zhongdongii	P.C. 504 = CUP 067544	Costa Rica	EU392631	EU392689	EU392741
Samuelsia chalalensis	P.C. 560 = CUP 067856	Bolivia	EU392637	EU392691	EU392743
S. geonomis	P.C. 614 = CUP 067857	Bolivia	EU392638	EU392692	EU392744
S. rufobrunnea	P.C. 613 = CUP 067858	Bolivia	AY986918	AY986944	DQ000345
S. sheikhii	P.C. 686 = CUP 067859	Honduras	EU392639	EU392693	EU392745
Regiocrella sinensis	CUP CH-2640	China	DQ118736	DQ118744	DQ127235
Epichloë elymi	C. Schardl 760	U.S.A.	AY986924	AY986951	DQ000352
Balansia henningsiana	GAM 16112	U.S.A.	AY489715	AY489610	AY489643

RESULTS

Phylogenetic analyses

The total number of characters included in the phylogenetic analyses was 2584 bp. Of those, 901 were from LSU, 942 from EF1-α, and 741 from RPB1 (Table 3). RPB1 contributed more polymorphic sites (46 %), than EF1-α (36 %) and LSU (25 %). The amount of homoplasious characters (*i.e.* parallel, convergent, reversed, or superimposed changes) was relatively high, especially in EF1-α and RPB1 data (Table 3). Whelan *et al.* (2001) reported that as homoplasy levels increase the likelihood of finding the correct evolutionary tree using MP is progressively reduced. This was noticed in the individual LSU (Fig. 1) and EF1-α trees where BP values for MP analyses were low, especially at the backbone of the tree, and fewer clades were supported by BP values >75 % (EF1-α and RPB1 trees not shown; BP data indicated in Fig. 2). The high homoplasy especially affects the EF1-α MP tree where low BP values support the internal nodes, thus reducing the effective resolution. Therefore, NJ and BI trees will add confidence to the resulting phylogeny. RPB1 sequence data produced a well-resolved tree with high BP values at internal and external nodes. LSU, EF1-α, RPB1, and combined data trees, show high BP support for the species treated in this study. However, only EF1-α and RPB1 data were able to distinguish between the disjunct sister species *M. ochracea* (New World) and *M. mollii* (Old World).

Hypocrella/Aschersonia, Samuelsia, and Moelleriella

The results of the phylogenetic analyses illustrate three major clades: one that includes species with non-disarticulating ascospores and fusiform conidia (*i.e. Hypocrella*), a second one that includes species with non-disarticulating ascospores and allantoid small conidia (*i.e. Samuelsia*), and a third one that includes species with disarticulating ascospores and fusiform conidia (*i.e. Moelleriella*) (Figs 1–2). The MP and NJ analyses of LSU sequence data supports *Moelleriella* with MP BP of <50 % and NJ BP of 74 %; *Samuelsia* with MP BP of 64 % and NJ BP of 71 %; and *Hypocrella* with MP BP of 89 % and NJ BP of 96 %. Similarly, MP and NJ analyses of RPB1 also support these three major clades/genera: *Moelleriella* is supported by MP BP of 61 % and NJ BP of 97 %, *Samuelsia* by MP BP of <50 % and NJ BP of 61 %, and *Hypocrella* by MP BP of 93 % and NJ BP of 100 %. The low bootstrap values at the internal nodes in EF1-α MP and NJ trees do not support these groups. In the combined analyses (Fig. 2), *Moelleriella* is supported by MP BP 63 %, NJ BP 98 %, and Bayesian Inference (BI) posterior probability (PP) of 100 %; *Samuelsia* by MP BP 67 %, NJ BP 86 %, and PP of 100 %; and *Hypocrella* by MP BP 100 %, NJ BP 100 %, and BI PP of 100 %.

RPB1 and the combined phylogenetic trees show high BP and PP support for the three subclades of *Hypocrella s. l.* that were reported by Chaverri *et al.* (2005b): Pulvinate, Globose, and Effuse (Fig. 2). *Moelleriella* can be divided into the Effuse and Globose clades. The Effuse clade includes *M. basicystis, M. disjuncta,*

Table 3. Results from LSU, EF1-α, and RPB1 sequence analyses.

Locus	LSU	EF1-α	RPB1	Combined
Number of taxa included in analyses	120	98	80	82
Total number of bp included	901	942	741	2584
Number of polymorphic sites (%)	224 (25)	334 (36)	340 (46)	889 (34)
Number of unique polymorphisms	57	34	22	111
Number of informative polymorphic sites (%)	167 (19)	300 (32)	318 (43)	778 (30)
Consistency Index	0.513	0.290	0.337	0.338
Homoplasy Index	0.487	0.710	0.663	0.662
Retention Index	0.903	0.790	0.828	0.802
Number of clades supported by >75% bootstrap in MP and NJ analyses	29, 46	50, 59	45, 62	60, 64

M. evansii, M. libera, M. madidiensis, M. mollii, M. ochracea, M. rhombispora, M. phyllogena, M. raciborskii, M. umbospora, and *M. zhongdongii*. The Globose clade includes *M. africana, M. boliviensis, M. epiphylla, M. insperata, M. macrostroma*, *M. schizostachyi, M. sloaneae,* and *M. turbinata*. The Pulvinate clade (*i.e. Hypocrella s. str.* and *Samuelsia*) includes two groups: Pulvinate A and Pulvinate B. Pulvinate A is *Hypocrella s. str.* and contains *H. citrina, H. hirsuta, H. disciformis, H. viridans,* and *H. discoidea;* and Pulvinate B is *Samuelsia* and includes *S. chalalensis, S. geonomis, S. rufobrunnea,* and *S. sheikhii*. EF1-α data do not support those three groups and LSU data show relatively weak support only for the Pulvinate clade. The *Hypocrella s. str.* clade, and the nodes nested within, have better resolution, BP and PP support, than the Effuse and Globose clades and nodes within *Moelleriella*. Some polytomies are observed within the Effuse clade.

Moelleriella

In the combined analyses (Fig. 2), the close relationship between the disjunct sister taxa *M. ochracea* (NW) vs. *M. mollii* (OW) and *M. libera* (NW) vs. *M. raciborskii* (OW) is clear. The *M. libera* clade is supported by MP BP of 90 %, NJ BP of 100 %, and PP of 61 %. The *M. raciborskii* clade is supported by MP BP of 99 %, NJ BP of 100 %, and PP of 100 %. The node that supports these two taxa has a MP and NJ BP, and PP of 100 %. *Moelleriella evansii*, which is morphologically similar to *M. libera*, is basal to a robust clade that includes *M. libera* and *M. raciborskii* (Figs 1–2). Likewise, the *M. ochracea* clade is supported by high MP BP, NJ BP, and PP values (91, 99, and 100 %, respectively). A *M. mollii* clade is supported by 100 % BP and PP values. The node that includes *M. mollii* and *M. ochracea* is supported by 100 % BP and PP values. *Moelleriella mollii* and *M. ochracea* are within a clade that includes two other morphologically similar taxa: *M. zhongdongii* and *M. madidiensis*. This clade is supported by BP of 78 %, NJ BP of 100 %, and PP of 100 %.

Moelleriella phyllogena (type species of *Moelleriella*), *M. umbospora, M. basicystis*, and *M. disjuncta* are morphologically similar species that belong to a clade supported by high BP and PP values (Fig. 2). The structure of this clade correlates with geographic origin: *M. basicystis* in Panama and Costa Rica (probably southern Central America); *M. phyllogena* in Panama, Brazil, Ecuador, Bolivia, and Peru (probably Panama and Amazon basin); *M. umbospora* in Mexico, Honduras, Guatemala (probably northern Central America); and *M. disjuncta* in Panama and Guyana. Recognition of each of these species is supported by high BP and PP values. *Moelleriella disjuncta* is basal within this clade. Although *M. rhombispora* shares some morphological similarities to the *M. phyllogena* species complex, DNA sequence data do not support their close relationship.

Combined DNA sequence analyses show significant support for most nodes (internal and external) within the Globose clade (Fig. 2). *Moelleriella epiphylla* and *M. turbinata* are morphologically similar species and their close relationship is supported by MP BP of 78 %, NJ BP of 95 %, and PP of 100 %. The *M. epiphylla and M. turbinata* clades are closely related to a group that contains mostly species with relatively large, globose and hard stromata (except *M. insperata*): *M. boliviensis, M. africana, M. schizostachyi*, and *M. macrostroma*. Species with large stromata are closely related (MP BP 78 %, NJ BP 96 %, and PP 100 %). *Moelleriella sloaneae* is basal in the Globose clade and is morphologically different from other species in the group. The inclusion of *M. sloaneae* in the Globose group is weakly supported in the combined phylogenetic analyses: MP BP <50 %, NJ BP 75 %, and PP 100 %. Only RPB1 data shows some support for this relationship (MP BP of 53 %, NJ BP of 88 %).

Hypocrella/Aschersonia s. str.

This clade includes species with non-disarticulating ascospores and fusiform conidia, thus *Hypocrella s. str.* All nodes in this group are strongly supported by BP and PP values (Fig. 2). *Hypocrella citrina, H. disciformis, H. hirsuta*, and *H. viridans* are morphologically similar species, are widespread in the Neotropics, and belong to a robustly supported clade (MP BP 78 %, MP NJ 100 %, PP 100 %). The *Hypocrella discoidea* (type species of *Hypocrella*) species complex is common throughout the Old World, is closely related and morphologically similar to *Hypocrella citrina, H. disciformis, H. hirsuta*, and *H. viridans.*

Samuelsia

This clade includes species with non-disarticulating ascospores and small allantoid conidia. The species contained in this clade are rare and probably endemic, *i.e. S. rufobrunnea* (type species of *Samuelsia*)(Bolivia, Peru), *S. chalalensis* (Bolivia), *S. geonomis* (Bolivia), and *S. sheikhii* (Honduras). The three Bolivian species are morphologically similar and belong in the same monophyletic group (BP and PP of 100 %).

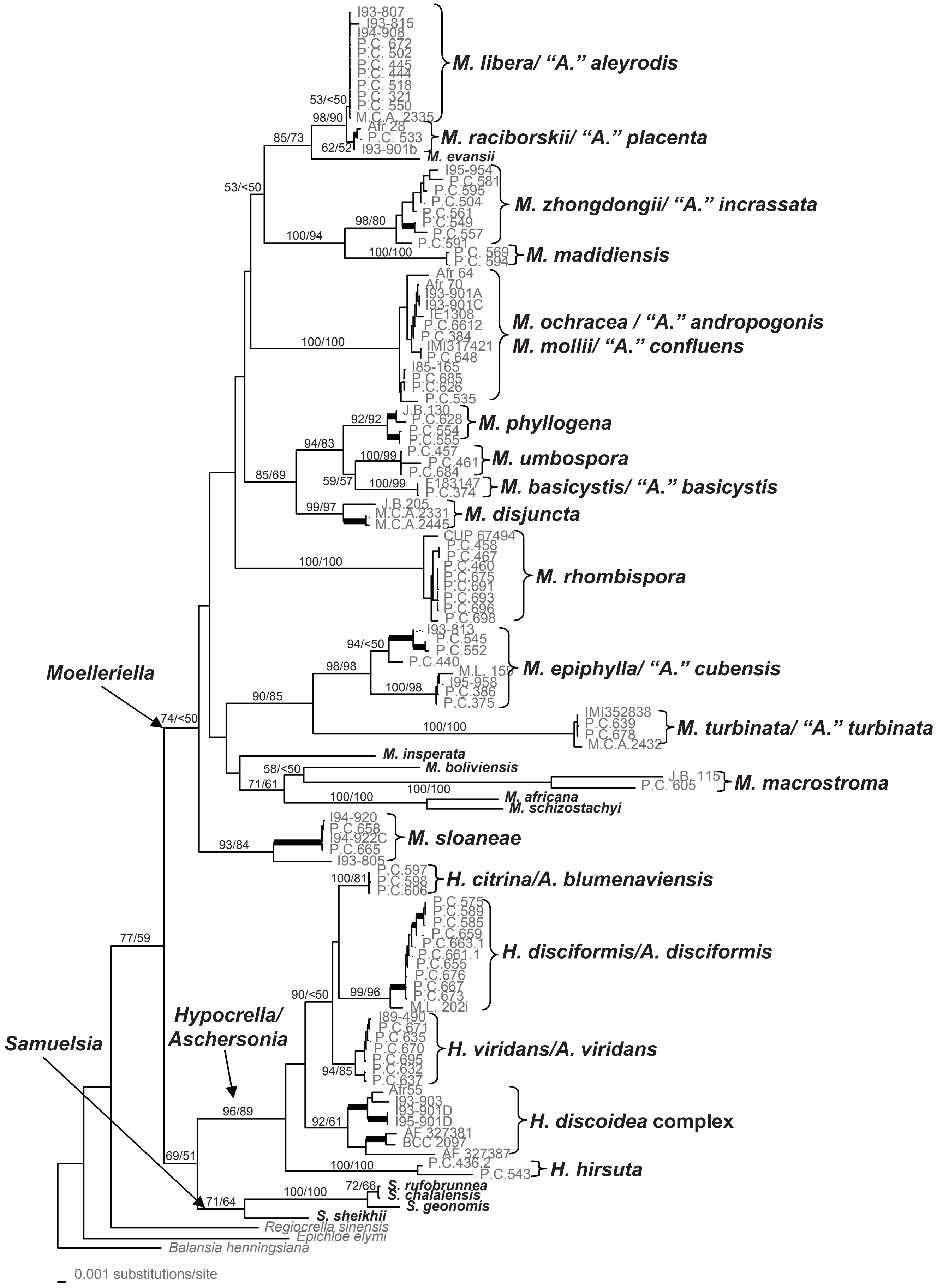

Fig. 1. LSU nrDNA neighbour-joining tree. Bootstrap (BP) values for neighbour-joining/maximum parsimony indicated at branches (1 000 replicates). Only BP values for species are listed. Other BP values >75 % are represented by thicker lines.

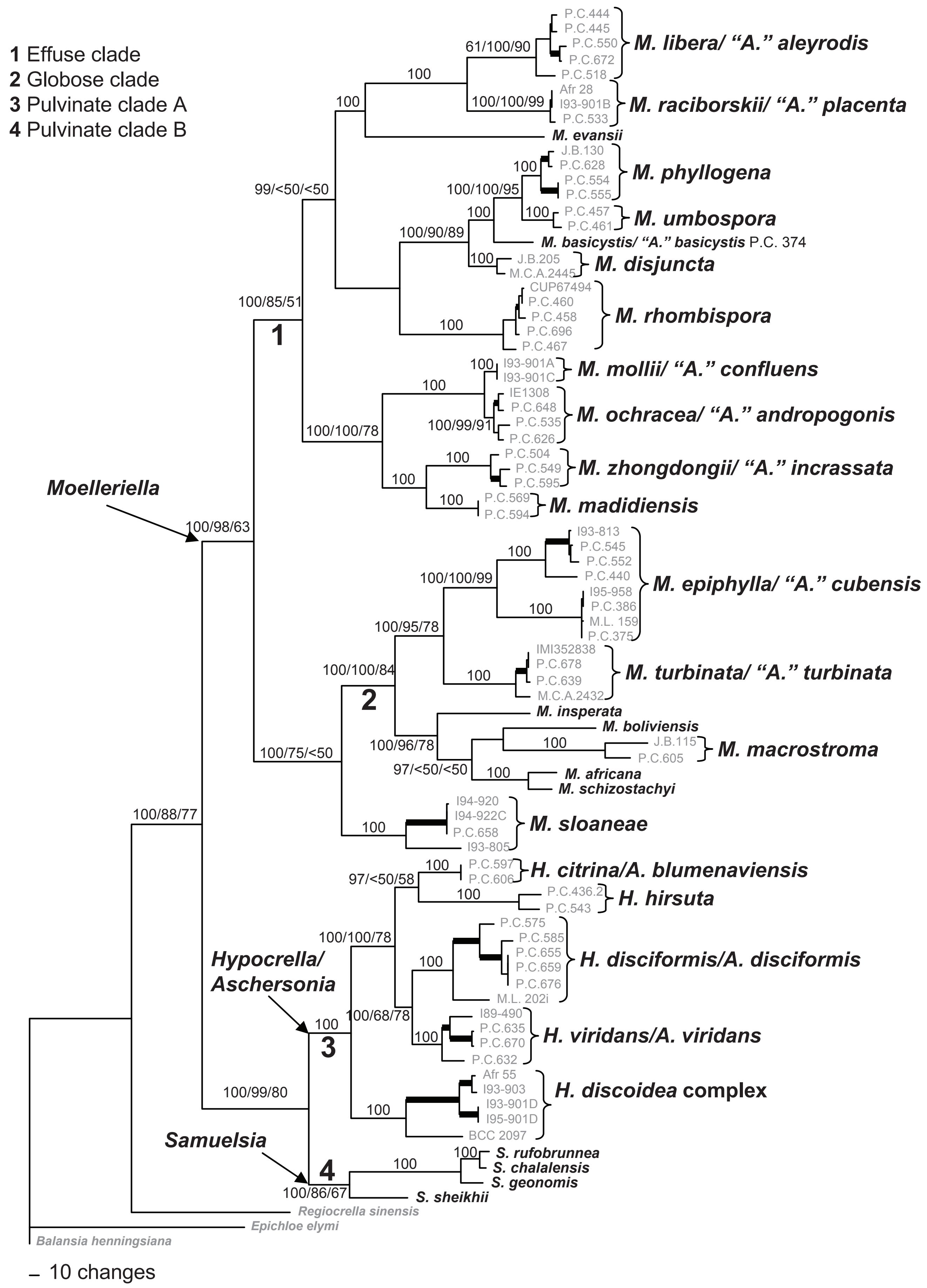

Fig. 2. Combined LSU, RPB1 and EF-1α cladogram based on Bayesian inference. The tree with the best log likelihood is presented (-Ln 22,746.4). Values at branches indicate Bayesian inference posterior probability/neighbour-joining boostrap/maximum parsimony bootstrap (1 000 replicates). Only values for species clades are listed. Other branch-support values >7 5% are indicated by thicker lines. If only one value of 100 % is shown, bootstrap values and posterior probabilities are all 100 %. Globose, Effuse, and Pulvinate clades described in Chaverri *et al.* (2005b) are indicated at nodes 1–4.

Morphological analyses and geographical distribution

Moelleriella, Samuelsia, and Hypocrella/Aschersonia

The distributions of the species presented here are generally poorly known. Based on the specimens collected for this study, *Moelleriella* is most diverse and common in the Neotropics (22 known species), followed by *Hypocrella* (5 known species), and *Samuelsia* (5 known species). *Moelleriella* and *Hypocrella* species are also more abundant that *Samuelsia*. Field collections and additional specimens from collaborators and herbaria yielded hundreds of specimens of *Moelleriella* and *Hypocrella* from many different countries. On the other hand, *Samuelsia* species are only known from one collection each. *Samuelsia rufobrunnea, S. chalalensis*, and *S. geonomis* are known from Bolivia and Peru; *S. sheikhii* from Honduras; and *S. intermedia* from Chile.

Examination of multiple morphological characters shows that segmentation of ascospores and conidial size and shape are the main characters that distinguish *Moelleriella, Samuelsia,* and *Hypocrella*. All known species of *Moelleriella* have filiform multiseptate ascospores that disarticulate at maturity inside the ascus and fusiform conidia < 15 µm long. *Hypocrella* species have filiform to long-fusiform multiseptate ascospores that do not disarticulate and fusiform conidia > 15 µm long. *Samuelsia* species have long-fusiform, non-disarticulating ascospores and small allantoid conidia < 10 µm long. Another character common to most species of *Hypocrella* and *Samuelsia* is a reddish colour reaction of the stroma when 3 % KOH is applied. However, *H. citrina* does not change colour. All studied species of *Moelleriella* lack a reaction to 3 % KOH. *Moelleriella gaertneriana* and *M. cornuta* release brownish pigments when 3 % KOH is added, but the tissue of the stromata does not change colour. Stromal anatomy is somewhat conserved in *Hypocrella*. The *Hypocrella* species examined have pulvinate stromata, with or without hypothalli. On the other hand, stromata in *Moelleriella* are highly variable: from flat or effuse with loose hyphal tissue (*e.g. M. libera*), to somewhat pulvinate (*e.g. M. madidiensis*) or knob-shaped (*e.g. M. phyllogena, M. basicystis, M. umbospora, M. disjuncta*), to large, globose and hard stromatal tissue (*e.g. M. macrostroma, M. gaertneriana*).

Characters of the anamorph are somewhat useful in distinguishing between *Hypocrella, Samuelsia*, and *Moelleriella*. The three genera have pycnidial-acervular conidiomata, slender flask-shaped to cylindrical phialides arranged in a compact hymenium, with or without paraphyses, brightly coloured and slimy conidial masses, and fusoid, unicellular conidia. Only conidial shape and size are useful characters.

Moelleriella morphology

The **stromatal size** of *Moelleriella* species treated in this study ranges from 0.5–30 mm diam. *Moelleriella macrostroma, M. gaertneriana*, and *M. cornuta* have large stromata that range from 2–30 mm diam. The smallest stromata are those of *M. umbospora, M. basicystis, M. turbinata, M. castanea,* and *M. colliculosa*, which range between 0.5 and *ca.* 2 mm in diam. The size of the stroma is generally correlated with the number of perithecia or pycnidia per stroma. The **colours of the stromata** of the species studied are in shades of white, yellow, orange, brown, or black. White and orange are the most common colours. A few species, *i.e. M. cornuta, M. turbinata, M. palmae, M. guaranitica, M. globosa,* and *M. castanea*, have brown to almost black stromata; these species are phylogenetically related in the Globose clade (Figs 1–2). Most of the examined species in the Effuse clade have stromata in shades of white or orange. The **shapes of the stromata** are highly variable. They can range from effuse or flat, to somewhat pulvinate, globose, cerebriform, tubular, conical, or knob-like. *Moelleriella libera, M. ochracea, M. sloaneae,* and *M. evansii* have effuse or thin, pulvinate stromata. *Moelleriella zhongdongii, M. madidiensis, M. rhombispora, M. guaranitica, M. castanea*, and *M. epiphylla*, have pulvinate to convex stromata. The **surface of the stroma** can be shiny or dull/matt, opaque, glabrous or scurfy, and tomentose or roughened. Most species of *Moelleriella* have a stromatal surface that is opaque and pruinose; however, there are many exceptions. *Moelleriella libera, M. evansii, M. zhongdongii, M. madidiensis, M. ochracea, M. rhombispora*, *M. sloaneae*, and some forms of *M. basicystis, M. disjuncta, M. phyllogena*, and *M. umbospora*, have tomentose stroma surfaces. Teleomorph stromata of *M. basicystis, M. disjuncta, M. phyllogena*, and *M. umbospora*, and stromata of *M. macrostroma, M. gaertneriana, M. boliviensis, M. turbinata, M. epiphylla, M. cornuta, M. palmae, M. globosa, M. guaranitica, M. castanea*, and *M. colliculosa* have almost glabrous surfaces. Stromata of *M. macrostroma, M. gaertneriana,* and *M. cornuta*, have somewhat shiny stromata. **Hypothalli** are present in some species, except *M. epiphylla, M. turbinata, M. boliviensis, M. macrostroma, and M. gaertneriana, M. castanea, M. colliculosa, M. globosa*, and *M. guaraniti*ca. There is no **reaction to 3 % KOH** on the tissue of the stromata; only *M. gaertneriana* and *M. cornuta* release brownish pigments when KOH is added. The **tissue structure of the stroma surface** is highly conserved among the examined species. All species studied have the tissue type referred to as *textura intricata* or *epidermoidea*. Some differences are found in the thickness of the cell walls. Darkly pigmented hard stromata are composed of hyphae with thick cell walls (*ca.* 2–6 µm). Lightly pigmented stromata with loose hyphal tissues have thin-walled hyphae (*ca.* 1 µm). The **inner tissue below the outermost layer of the stroma** is generally of *textura oblita*, *intricata*, *epidermoidea* or a condition intergrading between these tissue types.

Perithecia in some species of *Moelleriella* can be formed in well-separated or gregarious tubercles, or they can be completely embedded in the stroma. *Moelleriella libera, M. ochracea, M. rhombispora, M. zhongdongii, M. evansii*, and *M. sloaneae* form perithecial tubercles. When the stroma contains perithecia and pycnidia, the perithecia are either towards the edges of the stroma or scattered, with pycnidia either clustered in the centre or interspersed among the perithecia, respectively. The **ostioles** can range in colour from yellow to orange yellow, to reddish brown or brownish yellow. In longitudinal section, perithecia are generally elongated to subglobose, sometimes globose, with walls composed of 3–4 layers of highly compacted, thin-walled cells.

The **asci** are cylindrical and sometimes swollen in the middle when ascospores have disarticulated and accumulated towards the middle. Generally the ascus cap is thickened (*ca.* 2–5 µm) and capitate. *Moelleriella boliviensis, M. epiphylla, M. globosa, M. guaranitica, M. colliculosa*, and *M. castanea* have thin ascus tips (< *ca.* 1.5 µm). Because the multiseptate filiform ascospores disarticulate at the septum inside the ascus upon mounting, it is difficult to know exactly the length of intact ascospores. The **part-ascospores** are always hyaline and smooth. They can vary in shape, from cylindrical, to fusoid, ventricose, or almost ovoid. *Moelleriella basicystis, M. phyllogena, M. umbospora*, and *M. disjuncta* have a swollen protuberance on one side of the part-spore. In *M. rhombispora*, the part-spores have similar protuberances in the middle (*i.e.* ventricose shape). For the most part, the species studied have part-spores *ca.* 9–14 µm long. *Moelleriella gaertneriana, M. boliviensis, M. guaranitica, M. castanea, M. globosa,* and *M. disjuncta* have small part-spores (ca. 5–8 µm long); and *M. phyllogena, M. umbospora*, and *M. basicystis* have large part-spores (*ca.* 17–25 µm long). *Moelleriella castanea* has the smallest part-spores and *M. umbospora* has the largest.

The **shape of the anamorphic stromata** is highly variable, sometimes even within species. Anamorphic stromata may be pulvinate with pezizoid projections; tuberculate; hemiglobose; scutate; thin pulvinate, almost effuse; or thin pulvinate/effuse with pronounced erect or embedded tubercles. **Conidiomata** of *Moelleriella* are pycnidial to acervular, with one to several locules per stroma. The conidiomata are more commonly found than the perithecia, but sometimes both can be found in the same stroma (*e.g. M. turbinata, M. evansii, M. libera, M. sloaneae,* and *M. ochracea*, among others). The **pycnidial locules** can be simple depressions of the surface with or without distinct rims, or wide-open locules that resemble half-embedded bowls (*e.g. M. turbinata*). The arrangement of the pycnidia in the stroma can be scattered (*e.g.* most species), circular (*e.g. M. libera* and *M. phyllogena* and related species), or central (*e.g. M. epiphylla, M. evansii, and M. globosa*). Filiform **paraphyses** are present in some species, but are not a reliable character because sometimes they are not produced in culture. **Conidiophores** are formed in a compact layer, which sometimes makes it difficult to separate phialides and characterise them. **Phialides** are formed from short conidiophores that are sometimes indistinct, branching once monochasial, twice monochasial, monoverticillate, or two level monochasial (Seifert 1985). In most cases, the same species might have more than one type of conidiophore branching. Phialides are generally flask-shaped to slender and cylindrical (*ca.* 10–15 × 2.5–3 µm). **Conidial masses** are in bright colours ranging from reddish brown to orange to deep or pale yellow. Conidia are hyaline, unicellular, and generally fusoid, *ca.* 9–13 × 2.5–4 µm, with a length/width ratio (l/w) *ca.* 3–4.5. Some species, such as *M. epiphylla, M. turbinata*, and *M. globosa* have ovoid conidia with acute ends (l/w 2–2.5).

The extent of variation in appearance of **colonies** on **PDA at 25 ºC** after *ca.* 3 wk of growth is somewhat significant at the species level. Most of the species studied produce slow-growing spreading colonies, minutely tomentose or compact and leathery. The colonies are initially white and then may turn greyish white, yellowish, or orange. The fastest growing species do not reach more than 35 mm in 3 wks. Generally, **phialides in PDA at 25 °C** are smaller than phialides from stromata. However, *M. epiphylla* has slightly larger phialides in PDA at 25 °C. **Conidia in PDA at 25 °C** after three wk are also generally smaller than conidia from stromata. However, *M. macrostroma* has significantly larger conidia in PDA at 25 °C. A hirsutella-like **synanamorph** was observed in cultures of *M. turbinata* and *M. epiphylla*. This type of synanamorph has also been observed in *M. insperata* (Liu *et al.* 2005). Capilliconidiophores and capilliconidia have been also observed developing from asci and conidia on PDA at 25 °C. Production of **diffusing pigment** was not observed in the cultures examined.

Hypocrella/Aschersonia morphology

Stroma morphology in *Hypocrella* is significantly more conserved than in *Moelleriella*. The **stromatal size** of *Hypocrella* species treated in this study does not vary greatly and ranges from 1.5–2 mm diam. The **colour of the stromata** of the species studied is in shades of yellow, orange, or green. Pale yellow is the most common colour. *Hypocrella disciformis* and *H. viridans* have green stromata; these species are phylogenetically related (Figs 1–2). The **shape of the stromata** is generally pulvinate with a narrow base. The **surface of the stroma** can be dull/matt, opaque, glabrous, or roughened. *Hypocrella hirsuta* has synnematous projections on the surface of the stroma. These projections correspond to a hirsutella-like synanamorph. **Hypothalli** are present in some of the examined species, *i.e. H. hirsuta,* and sometimes in *H. viridans* and *H. disciformis* (but are lacking in culture). The majority of the species examined have a **reaction to 3 % KOH** on the tissue of the stromata. Most of the species turn brown when KOH is added, except *H. citrina*. *Hypocrella discoidea* becomes reddish when KOH is added. The **tissue structure of the stroma surface** is highly conserved among the examined species. All species studied have the tissue type referred to as *textura intricata* or *epidermoidea*. The cell walls of the stromatal hyphae are *ca.* 2 µm thick. The **inner tissue below the outermost layer of the stroma** is also *textura epidermoidea* to *intricata*.

Perithecia in *Hypocrella* are generally completely embedded in the stroma or, sometimes half-embedded. When the stroma contains perithecia and pycnidia, the perithecia are towards the edges of the stroma, with pycnidia towards the centre. The **ostioles** are in shades of orange or brown. In longitudinal section, **perithecia** are elongated to subglobose, sometimes globose, with walls composed of 3–4 layers of highly compacted, thin-walled cells.

The **asci** are cylindrical and sometimes swollen in the middle. The ascus cap is thickened (*ca.* 1–6 µm) and with a conspicuous ring. *Hypocrella viridans* and *H. citrina* have thin ascus caps (*ca.* 1–1.5 µm); and *H. hirsuta* and *H. aurantiaca* have thick ascus caps (*ca.* 4–6 µm). The **ascospores** are always filiform or long fusiform, hyaline and smooth. For the most part, the species studied have ascospores *ca.* 75–140 × 2–5 µm. *Hypocrella citrina* has short ascospores (*ca.* 110–115 µm long); and *H. aurantiaca,* and *H. hirsuta* have long ascospores (*ca.* 120–140 µm).

The **shape of the anamorphic stromata** is pulvinate, sometimes almost discoid, like that of the stromata containing the teleomorph. **Conidiomata** of *Hypocrella* are pycnidial, with one to few (*ca.* 2–5) locules per stroma. The conidiomata are more commonly found than the perithecia, but sometimes both can be found in the same stroma (*e.g. H. viridans* and *H. disciformis*). The **pycnidial locules** are flask-shaped with narrow openings. The arrangement of the pycnidia in the stroma is circular. **Paraphyses** were present in all the species studied. **Conidiophores** are formed in a compact layer, which sometimes makes it difficult to separate phialides and characterise them. **Phialides** are formed from short conidiophores that can be indistinct, branching once monochasial, twice monochasial, monoverticillate, or two level monochasial (Seifert 1985). In most cases, the same species might have more than one type of conidiophore branching. The phialides are flask-shaped to slender and cylindrical (*ca.* 12–20 × 2–2.5 µm). Exuded **conidial masses** are less common, but when present they are in shades of greyish yellow. Conidia are hyaline, unicellular, and fusoid, *ca.* 13–30 × 2–6 µm, with a length/width ratio (l/w) *ca.* 5–6. *Hypocrella aurantiaca*, *H. hirsuta*, and *H. citrina* have the largest conidia (*ca.* 20–30 µm long).

The extent of variation in appearance of **colonies** on **PDA at 25 ºC** after *ca.* 3 wk of growth is somewhat significant at the species level. However, many of the cultures examined did not survive storage at 8 °C and many did not produce conidia in culture. Of the few colonies that grew, the growth rate is slow and the colonies are tomentose compact and leathery. The colonies are initially white and then may turn greyish brown or light brown. Generally, **phialides in PDA at 25 °C** are smaller than phialides from stromata. **Conidia in PDA at 25 °C** after three wk are also generally smaller than conidia from stromata. *Hypocrella hirsuta* did not produce a pycnidial anamorph in culture, but did produce a hirsutella-like **synanamorph**. Production of **diffusing pigment** was not observed in the cultures examined.

Samuelsia morphology

The **stroma** morphology in *Samuelsia* is somewhat conserved. The **stromatal size** of *Samuelsia* species treated in this study does not vary greatly and ranges from *ca.* 2–3 mm diam. The **colours of the stromata** are in shades of yellowish brown. The **shape of the stromata** is generally pulvinate with a wide base, becoming convex. The **surface of the stroma** can be dull/matt, opaque, glabrous, or roughened. A **hypothallus** is present only in *S. sheikhii*. The species examined have a **reaction to 3 % KOH** on the tissue of the stromata. The stromata turn brown when KOH is added; *S. sheikhii* becomes dark reddish. The **tissue structure of the stroma surface** is highly conserved among the examined species. All species studied have the tissue type referred to as *textura epidermoidea*. The cell-walls of the stromatal hyphae are *ca.* 2 µm thick. The **inner tissue below the outermost layer of the stroma** is also *textura epidermoidea*.

Perithecia in *Samuelsia* are completely embedded in the stroma. When the stroma contains perithecia and pycnidia, the perithecia are towards the edges of the stroma, with pycnidia towards the centre. The **ostioles** are in shades of orange or brown. In longitudinal section, perithecia are elongated to subglobose, sometimes globose, with walls composed of 3–4 layers of highly compacted thin-walled cells.

The **asci** are cylindrical and sometimes swollen in the middle. The ascus cap is thickened (*ca.* 1.5–3 µm) and with a conspicuous ring. *Samuelsia geonomis* has a thin ascus cap (*ca.* 1–1.5 µm). The **ascospores** are always filiform or long fusiform, hyaline and smooth. The species studied have ascospores *ca.* 45–50 × 2 µm.

The **shape of the anamorphic stromata** is also pulvinate, like that of the stromata containing the teleomorph. **Conidiomata** of *Samuelsia* are pycnidium-like, with one to few (*ca.* 2–5) locules per stroma. The **pycnidial locules** are simple depressions of the surface with narrow openings, sometimes slit-like. Sometimes the locules merge to form a ring, *e.g. S. rufobrunnea*. The conidiomata are more commonly found than the perithecia, but sometimes both can occur in the same stroma (*e.g. S. rufobrunnea*). The arrangement of the pycnidia in the stroma can be scattered (*e.g.* most species) or circular. **Paraphyses** are somewhat circinate. **Conidiophores** are formed in a compact layer. **Phialides** are formed from short conidiophores that are sometimes indistinct, branching once monochasial, twice monochasial, monoverticillate, or two level monochasial (Seifert 1985). In most cases, the same species may have more than one type of conidiophore branching. The phialides are flask-shaped to slender and cylindrical (*ca.* 10–17 × 1.5–1.8 µm). Exuded **conidial masses** were not observed. Conidia are hyaline, unicellular, and allantoid, *ca.* 4.5–6 × 1.5–2 µm, with a length/width ratio (l/w) *ca.* 3–4. **Cultures** did not survive storage at 8 °C and thus cultural observations were not made.

DISCUSSION

Generic concept

A key purpose of systematics is to identify taxa in a hierarchical system (*i.e.* genera) that reflects the evolution of the organisms. The present taxonomic treatment defines genera based on a combination of phylogenetic and morphological characters. Unlike many other genera in the *Hypocreales*, teleomorph phenotype in *Moelleriella, Samuelsia,* and *Hypocrella* is as diagnostic at the genus and species levels as is anamorph morphology. Results from the present study demonstrate that *Hypocrella s. l.* comprises three distinct and well-supported clades: species with ascospores that disarticulate within the ascus (*Moelleriella*); species with non-disarticulating ascospores and fusiform conidia (*Hypocrella*); and species with non-disarticulating ascospores and allantoid small conidia (*Samuelsia*). Previous authors have speculated that the species of *Hypocrella s. l.* with disarticulating ascospores should be considered a distinct genus (Hywel-Jones & Evans 1993; Petch 1939). In addition to ascospores and conidia, stroma shape and 3 % KOH reaction are synapomorphies for the three genera. *Moelleriella* species have highly variable stromata, but are mostly effuse, pulvinate with wide base (almost convex), or globose, and the tissue is KOH-. *Hypocrella* species almost always have pulvinate stromata with a narrow base and generally KOH+ tissue. *Samuelsia* species have brown pulvinate stromata with a wide base and KOH+ tissue. *Samuelsia* is described here as new.

Petch (1921) proposed subgenera of *Hypocrella s. l.* based on the insect-host and presence of paraphyses in the conidiomata. Based on the results of this study, and others previously published works (Hywel-Jones & Evans 1993, Liu *et al.* 2005, Liu *et al.* 2006), neither host nor paraphyses are phylogenetically informative characters. Therefore, Petch's subgenera (*Hypocrella* subg. *Fleischeria,* anam. *Aschersonia* subg. *Leprieuria* and (*Hypocrella* subg. *Hypocrella,* anam. *Aschersonia* subg. *Aschersonia*) (Petch 1921) are rejected.

Two clades are present within *Moelleriella* that could potentially be classified as subgeneric taxa (*e.g.* section, subgenus). The Effuse and Globose clades of *Moelleriella* were first recognised by Chaverri *et al.* (2005b); each has some phylogenetically informative morphological characters. The Effuse clade includes species with effuse to thin pulvinate stromata that are generally whitish in colour (orangish in a few species), somewhat smaller part-ascospores, and slightly larger conidia. The Globose clade includes species with harder and more globose stromata in darker shades, slightly larger part-ascospores, and smaller conidia. However, these characters are not unique for each clade and may overlap between clades. Therefore, a classification below the genus level is not proposed.

The Pulvinate clade (Chaverri *et al.* 2005b) corresponds to *Hypocrella s. str.* (Pulvinate A) and *Samuelsia* gen. nov. (Pulvinate B). *Hypocrella s. str.* includes *Hypocrella discoidea, H. citrina, H. hirsuta, H. disciformis*, and *H. viridans*, which have species with longer ascospores and longer slightly fusoid conidia than *Samuelsia* species.

Species concept

Over the course of scientific history, taxonomists and evolutionary biologists have attempted to define species concepts using several approaches. The best-known species concepts include the morphological (MSC) (Hawksworth *et al.* 1995, John & Maggs 1997), Biological (BSC) (Mayr 1940), Phylogenetic (PSC) (Cracraft 1983), and the Genealogical Concordance Phylogenetic Species Recognition (GCPSR) (Taylor *et al.* 2000) [see more discussion about this topic in Chaverri & Samuels (2003)]. In the present monograph, a species concept similar to that followed by Chaverri & Samuels (2003) was used. This concept is a combination of the GCPSR and MSC, which can be defined as the smallest diagnosable phylogenetic lineage (clade) that can be distinguished by discrete phenotypic character or characters. The strength of GCPSR lies in its comparison of more than one gene genealogy. The species concept used in the present taxonomic treatment attempts to reflect true evolutionary relationships and make species diagnosis practical to biologists, plant pathologists, and mycologists who do not have access to molecular tools.

In *Hypocrella, Samuelsia*, and *Moelleriella*, phylogenetically informative morphological characters can easily be assigned to each species. Even in the closely related groups of *M. phyllogena, M. basicystis, M. disjuncta,* and *M. umbospora*; or *H. disciformis* and *H. viridans*, discrete conidial and part-ascospore characteristics can reliably be used to distinguish species. In the case of disjunct species pairs, the two species may be almost indistinguishable, but the disjunct distribution (*i.e.* Neotropics vs. Paleotropics) may be used to separate species. For example, *M. palmae* vs. *M. sclerotioides*; *M. epiphylla* vs. *M. reineckiana*; *M. libera* vs. *M. raciborskii*; *M. ochracea* vs. *M. mollii*; *M. macrostroma* vs. *M. africana*; *M. castanea* vs. *M. palmicola*; and *M. gaertneriana* vs. *M. schizostachyi*. Further sampling in Paleotropics may well yield further examples.

Evolutionary hypotheses in *Moelleriella*, *Hypocrella*/*Aschersonia*, and *Samuelsia*

Speciation begins with genetic isolation, then a loss of shared polymorphisms as the loci become fixed, and lastly the locus may become fixed in both daughter species (Taylor *et al.* 2000). Therefore, ancestral lineages are expected to have more phylogenetically informative polymorphisms and better branch/node resolution (*i.e.* stronger bootstrap or posterior probability support) because more polymorphisms have become fixed in each putative species. This can be observed in the phylogeny of *Moelleriella, Hypocrella*, and *Samuelsia*, in which more basal clades (*e.g. Samuelsia*, then *Hypocrella*) have higher bootstrap and posterior probability support at almost every node (Fig. 2, clades 3 and 4). On the other hand, *Moelleriella*, which appears to be more recently derived, has lower bootstrap and posterior probability values for the deeper nodes. We hypothesise that lineage sorting is still occurring among recently diverged *Moelleriella* species (Chaverri *et al.* 2003b). This can be especially noticed in individual gene trees in which *Moelleriella* internal nodes are weakly supported in LSU and EF 1-α trees.

In defining species based on the GCPSR, several uncertainties about its applicability have arisen (Harrington & Rizzo 1999, Taylor *et al.* 2000). One is that species should exhibit a unique phenotype, preferably one that is related to the role of the species in nature. However, if speciation theories are followed, genetic isolation precedes the divergence of character states, whether due to drift or selection. So, it is not expected that recently genetically isolated species will show immediate phenotypic differences, although over time they should. In those cases it might be difficult to place phylogenetic species into formal classification systems if no phenotypic characters can be used to describe them in a practical or usable way. For these reasons, even though some phylogenetic structure (*i.e.* sublineages below species level) was observed in species of *Moelleriella* and *Hypocrella* (*i.e. M. phyllogena, M. disjuncta, M. epiphylla, M. sloaneae, M. zhongdongii, H. disciformis*, and *H. viridans),* no distinct phenotype was correlated to those sublineages. Therefore, no taxonomy was proposed for those sublineages.

It is possible that the limited mobility of the conidia in *Moelleriella, Hypocrella*, and *Samuelsia* may have affected the evolution and geographical distribution of lineages/species. Oborník *et al.* (2000) hypothesised that geographically restricted lineages in *Hypocrella s. l.* might have arisen due to the limited dispersal of spores, its distribution limited to the tropics, and the conservation of host specificity. These factors may have been important in determining endemism in some of the species studied here. Some examples of species with restricted geographic distributions are: *M. madidiensis* (Bolivia), *M. gaertneriana* (Brazil, French Guiana, Venezuela), *M. cornuta* (Brazil), *M. evansii* (Ecuador), *M. basicystis* (probably southern Central America), *M. phyllogena* (probably Panama and Amazon basin), *M. umbospora* (probably northern Central America), *M. disjuncta* in (Panama, Guyana), *S. chalalensis* (Bolivia), *S. geonomis* (Bolivia), *S. intermedia* (Chile), and *S. rufobrunnea* (Bolivia, Peru). Additional collections from Old World and poorly explored areas may provide more insights into the evolution of endemism in these genera and species.

Evolution of anamorph characters

A previous study of *Hypocrella s. l.* (Liu *et al.* 2006) revealed many apomorphies that can be used to define species: *e.g.*, morphology of the stroma, and shape and size of conidia. The anamorph characters that define the more recently derived genera *Hypocrella s. str.* and *Moelleriella* are the shape of the stroma and the fusiform conidia. On the other hand, in *Samuelsia*, which appears to be basal to *Hypocrella* and *Moelleriella*, conidial shape and size resemble anamorphs of related genera such as *Epichloë*, *Claviceps*, and *Regiocrella* (Chaverri *et al.* 2005a). The most parsimonious explanation for the evolution of conidial morphology is that small allantoid conidia is a plesiomorphic character within this group (*i.e. Moelleriella/Hypocrella/Samuelsia* clade), as seen by the basal position of *Samuelsia*. In general, taxa with small, allantoid conidia (*i.e. Samuelsia*) form a monophyletic group, as do species with large, fusiform conidia (*i.e. Hypocrella*), and species with medium-sized, fusiform conidia (*i.e. Moelleriella*).

The presence of paraphyses in the conidiomata seems to be a recently derived character in the *Clavicipitaceae* that is only known in *Moelleriella, Samuelsia,* and *Hypocrella* (Hodge 2003). Although Petch (1921) thought the presence of paraphyses was diagnostic at the subgeneric level in *Hypocrella s. l.*, results from this study show that paraphyses are not phylogenetically informative, and that conspecific individuals may or may not have paraphyses. When present, the paraphyses may aid in the dispersal of conidia extruded from the conidiomata.

Within the *Clavicipitaceae*, pycnidial to acervular anamorphic forms have been assigned to a few genera. These anamorphs are known only for plant-associated genera *Atkinsonella, Balansia, Claviceps, Epichloë, Myriogenospora* and *Neoclaviceps* and the scale-insect and whitefly parasites *Moelleriella, Hypocrella, Samuelsia*, and *Regiocrella*. We hypothesise that this pycnidial-acervular form has a single evolutionary origin in the *Clavicipitaceae* (Chaverri *et al.* 2005a). This conclusion is supported by previous studies (Kuldau *et al*. 1997, Sullivan *et al*. 2001). In the

Hypocreales, in addition to the clavicipitaceous genera mentioned above, a few species in the *Nectriaceae* have pycnidial anamorphs (*i.e. Nectria* spp.: anam. *Zythiostroma* Höhn. and *Gyrostroma* Namouv; and *Cosmospora kurdica* (Petrak) Rossman & Samuels: anam. *Botryocrea* = pycnidial *Fusarium*) (Samuels & Seifert 1987, Rossman *et al.* 1999). The evolution of pycnidial-acervular anamorphs and glioconidia (conidia borne in slime) is widely thought to be associated with spore dispersal by insects (Loveless 1964, Mower *et al.* 1973, Mower & Hancock 1975, Samways 1983, Butler *et al.* 2001, Hodge 2003) or water (*i.e.* rain splash and run-off) (Parkin 1906, Chaverri *et al.* 2003a, Hodge 2003).

The presence of hirsutella-like synanamorphs in *Moelleriella* and *Hypocrella* is a character that has evolved or been lost multiple times. It is only known in a few species that are not phylogenetically related to each other (*e.g. M. turbinata, M. schizostachyi, M. insperata*, and *H. hirsuta*) nor to *Hirsutella s. str.* hirsutella-like states are mainly formed in culture; only *H. hirsuta* produces a synnematous hirsutella-like synanamorph on the surface of the stroma. The roles of synanamorphs and why they evolved in fungi are not well-known, but various studies have proposed that they are an adaptation to insect dispersal (Glare *et al.* 1985b, a, Evans 1994, Hodge 2003). The pycnidial anamorph produces spores that may be more efficient for infecting insects within high-density host populations. On the other hand, the hirsutella-like synanamorphs and capilliconidia may increase the chances of the fungus being transmitted between mobile host insects that occur as dispersed, low-density populations. Another hypothesis is that these synanamorphs, especially the capilliconidiophores and capilliconidia, evolved in response to conditions unsuitable for vegetative growth, presumably in the absence of suitable hosts (see example for *Entomophthorales* in King & Humber 1981). Synanamorphs are also present in many other genera in the *Hypocreales* (Rossman *et al.* 1999, Hodge 2003).

Evolution of teleomorph characters

Several teleomorph characters are phylogenetically informative: stroma morphology, reaction to 3 % KOH, and ascospore morphology. Two clades within *Moelleriella* that correlate with stroma morphology have been described: the Effuse and Globose clades (Chaverri *et al.* 2005b). Each has stroma morphologies that are diagnostic of monophyletic groups. One exception is *M. sloaneae*, which seems to form a separate lineage from Globose and Effuse clades (although closer to Globose clade). *Moelleriella sloaneae* forms flat stromata with perithecial tubercles, similar to *M. libera*. It is possible to hypothesise that *M. sloaneae* is the ancestor to the Effuse clade because it has stromatal characteristics that are also present in species in the Effuse clade; yet it retains some characters from the Globose clade (*e.g.* smaller conidia).

Ascospore morphology is phylogenetically informative and was used in this study to segregate *Samuelsia* and *Moelleriella* from *Hypocrella s. l.* Disarticulation of ascospores in *Moelleriella* is the main diagnostic character. The differences between *Hypocrella* and *Samuelsia* are in ascospore size and conidial size and shape. Most genera in the *Clavicipitaceae* have filiform ascospores that do not disarticulate within the ascus; only *Moelleriella* is known to have filiform ascospores that disarticulate within the ascus. Thus, disarticulation of ascospores is a derived character within the *Clavicipitaceae*, yet it is present in many other ascomycetous fungi. Disarticulation of ascospores may be a mechanism to ensure an increased number of propagules and thus better dispersal (Evans 1988).

Reaction of the stroma tissue to 3 % KOH is another character that is phylogenetically informative, especially at the species level. *Moelleriella* species are KOH-, and a few *Hypocrella* and *Samuelsia* species are KOH-. A change in colour when KOH is added is a characteristic present in many other Hypocrealean genera, especially *Nectriaceae* (Rossman *et al.* 1999). It has also been observed in the clavicipitaceous genus *Regiocrella* (Chaverri *et al.* 2005a). However, because traditionally the KOH reaction has not been evaluated in the *Clavicipitaceae*, assumptions about the evolution of this character cannot be made.

KEY TO GENERA TREATED

1\. Filiform to long-fusiform multiseptate ascospores disarticulating at the septum within the ascus into multiple part-ascospores; stromata KOH- .... *Moelleriella*

1’. Filiform to long-fusiform multiseptate ascospores that do not disarticulate; stromata generally KOH+ 2

2\. Ascospores (50–)75–120(–170) µm long; conidia (10–)12–25(–30) µm long, fusoid .... *Hypocrella/Aschersonia*

2’. Ascospores (90–)100–120(–130) µm long; conidia (4–)1.5–6(–7) µm long, almost allantoid .... *Samuelsia*

SYNOPTIC KEYS

Moelleriella (anamorphs aschersonia-like)

1. *Moelleriella basicystis/“Aschersonia” basicystis*
2. *Moelleriella boliviensis*
3. *Moelleriella castanea*
4. *Moelleriella colliculosa*
5. *Moelleriella cornuta*
6. *Moelleriella disjuncta*
7. *Moelleriella epiphylla/“Aschersonia” cubensis*

8. *Moelleriella evansii*
9. *Moelleriella gaertneriana*
10. *Moelleriella globosa*
11. *Moelleriella guaranitica/“Aschersonia” caapi*
12. *Moelleriella libera/“Aschersonia” aleyrodis*
13. *Moelleriella macrostroma*
14. *Moelleriella madidiensis*
15. *Moelleriella ochracea/“Aschersonia” andropogonis*
16. *Moelleriella palmae*
17. *Moelleriella phyllogena/“Aschersonia” juruensis*
18. *Moelleriella rhombispora*
19. *Moelleriella sloaneae*
20. *Moelleriella turbinata/“Aschersonia” turbinata*
21. *Moelleriella umbospora*
22. *Moelleriella zhongdongii/“Aschersonia” incrassata*

Teleomorph characters

Stromata

1. Size (diam)
    a. 1–2 mm: 1–4, 6, 7, 11, 12, 14, 19–22
    b. >2–3 mm: 5, 10, 15, 17, 18
    c. >3–4 mm: 16
    d. >4 mm: 8, 9, 13

2. Colour
    a. Yellowish white to white, pale yellow 1, 2, 6, 8, 12, 14, 15, 17–22
    b. Yellow 13, 17
    c. Greyish yellow 2, 6, 7, 19, 20
    d. Pale orange 6, 19, 20
    e. Greyish orange 4, 6, 17
    f. Brownish orange 10
    g. Brown 3
    h. Reddish brown 7
    i. Buff to pale greenish 9
    j. Greyish brown 10
    k. Dark brown almost black 5, 10, 11, 16

3. Shape
    a. Globose with head markedly constricted at base (stud-shaped) 1, 2, 6, 17, 21
    b. Globose 9, 11, 13, 16
    c. Subglobose 2–4, 7, 9, 10, 14
    d. Pulvinate, base slightly constricted 3, 4, 7, 14, 15, 18, 22
    e. Pulvinate with sloping sides, ovoid or globose tubercles half-embedded 15, 19
    f. Thin pulvinate with pronounced cylindrical or ovoid tubercles 8, 12, 19, 20
    g. Obconical 5

4. Hypothallus
    a. Present 1, 6, 12, 15, 17, 18, 21, 22
    b. Absent 2–11, 13, 14, 16, 18–20, 22

5. Surface texture
    a. Tomentose 15
    b. Pruinose 8, 12, 15, 18–22
    c. Smooth 1, 2, 4–7, 9–11, 13, 16–18, 20–22
    d. Roughened 3

Perithecia

1. Position in stroma
    a. In gregarious but well-separated tubercles 8, 12, 15, 20

b. In crowded, gregarious tubercles 9, 15, 18, 22
c. Embedded in stroma, scattered 1–7, 13, 19–21
d. Embedded in top/central part of stroma 10, 11,16, 17

Part-ascospores

1. Shape
   a. Cylindrical with rounded or blunt ends 2–5, 7–13, 15, 16, 19, 22
   b. Fusoid 8, 12, 13, 20
   c. Ventricose with rounded or acute ends 1, 6, 17, 18, 21

2. Average length
   a. 5–10 µm 2, 3, 5–7, 9–11, 16, 20, 22
   b. >10–15 µm 4, 8, 12, 13, 15, 18, 19
   c. >15–20 µm 1, 17
   d. >20 µm 21

3.Average width
   a. 1.5–2.5 µm 2, 3, 5, 9, 11, 15, 22
   b. >2.5–3.5 µm 6, 8, 10, 12, 13, 16, 18, 19
   c. >3.5–4.5 µm 1, 4, 7, 17, 20
   d. >4.5 µm 21

Anamorph characters

Stromata

1. Colour
   a. Yellowish white to white, pale yellow 1, 6–8, 12, 14, 15, 17–22
   b. Yellow 13
   c. Greyish yellow 7, 20
   d. Pale orange 20
   e. Greyish 7
   f. Greyish brown 10
   g. Brown 3
   h. Dark brown, black 10, 11

2. Shape
   a. Pulvinate base with pezizoid projections 20
   b. Tuberculate 7, 20, 22
   c. Cylindrical 7, 12, 20
   d. Globose 13
   e. Hemiglobose, subglobose 7, 10, 11, 18
   f. Scutate (a hemisphaerical central region abruptly attenuating and extending to the edge) 1, 6, 8, 11, 14, 15, 17, 18, 21
   g. Thick pulvinate, obconical pulvinate 3, 7, 14, 15, 18, 22
   h. Thin pulvinate, almost effuse 12, 15, 19

Conidiomata

1. Approximate number of locules
   a. Fewer than ten 3, 7, 11, 12, 14, 15, 18, 20, 22
   b. More than ten 1, 6, 8, 10, 12, 13, 15, 17–19, 21, 22

2. Shape of locules
   a. Simple depressions of surface without distinct rims 1, 3, 6–8, 10–13, 15, 17–19, 21, 22
   b. With distinct rims, like half-embedded bowls 14, 15, 22
   c. Pezizoid 20

3. Arrangement of conidiomata on stroma
   a. Scattered 3, 7,10–15, 18–20, 22
   b. Circular 1, 6, 12, 17, 21
   c. Central 8

4. Paraphyses in conidioma
    a. Present 12, 15, 19, 22
    b. Absent 1, 3, 6–8, 10–15, 17, 18, 20–22

Conidia

1. Colour of conidial masses
    a. Pale yellow 13, 15, 18, 22
    b. Yellow 1, 6, 7, 14, 17, 19, 21
    c. Deep yellow 18
    d. Greyish yellow 7, 20
    e. Orange 6, 7, 12, 20
    f. Reddish orange 12
    g. Yellowish orange 20
    h. Reddish brown 7
    i. Brownish orange 7, 20
    j. Yellowish brown 8, 19
    k. Brown 3, 8

2. Average length of conidium
    a. 5–10 µm 3, 6, 19
    b. >10–15 µm 1, 7, 8, 10–15, 17, 18, 20, 22
    c. >15 µm 21

3. Average width of conidium
    a. 1.5–3 µm 3, 6, 8, 12, 13, 15, 18, 19, 22
    b. >3–4.5 µm 1, 11, 14, 17
    c. 4.5 µm 7, 10, 20, 21

4. Average length/width ratio of conidium
    a. 2–3.5 µm 1, 3, 6, 7, 10, 11, 14, 20
    b. >3.5–5 µm 8, 17–19, 21
    c. >5 µm 12, 13, 15, 22

5. Shape of conidium
    a. Fusoid 3, 6, 8, 11–15, 19, 22
    b. Ventricose 1, 17, 18, 21
    c. Ovoid 7, 10, 20

Cultural characteristics on PDA

1. Growth rate on PDA at 25 °C at 3 wk
    a. Relatively rapid (>30 mm diam) 12, 7, 20
    b. Moderate (20–30 mm diam) 1, 17–19
    c. Slow (<20 mm diam) 13, 15, 22

2. Appearance and texture of growing colony
    a. Spreading 7, 12, 20
    b. Compact, leathery 1, 15, 17, 18, 19
    c. Compact, floccose/tomentose 13, 22

3. Synanamorph
    a. Present, capilliconidiophores and capilliconidia 7, 20

Known geographical distribution

1. North America 7, 12, 15, 18, 20, 21
    a. Florida, U.S.A. 12, 15
    b. Mexico 7, 12, 15, 18, 20, 21
2. Central America 1, 6, 7, 13, 15, 17–22
    a. Belize 19
    b. Costa Rica 1, 7, 12, 13, 15, 18, 20, 22

- c. Honduras........7, 12, 15, 18–21
- d. Guatemala........12, 19
- e. Nicaragua........20
- f. Panama........1, 6, 12, 17

3. South America........2, 4–17, 19, 20, 22
   - a. Argentina........17
   - b. Bolivia........2, 7, 12–15, 17, 19, 22
   - c. Brazil........2, 4, 5, 9–12, 16, 17, 19
   - d. Colombia........7, 17, 20
   - e. Ecuador........7, 8, 15, 17, 19
   - f. French Guiana........6, 9, 17
   - g. Guyana........6, 7, 12, 19, 20
   - h. Paraguay........11, 15
   - i. Peru........7, 16, 17, 19, 20
   - j. Surinam........16
   - k. Venezuela........9, 12, 17, 19
4. Caribbean Islands........1, 3, 6, 7, 15, 18–20, 22
   - a. Cuba........1, 7
   - b. Grenada........20
   - c. Guadeloupe........19
   - d. Puerto Rico........6, 12, 15, 18, 22
   - e. Trinidad........3, 6, 10, 12, 15
   - f. Saint Vincent........7

Hypocrella (anamorph *Aschersonia s. str.*)

1. *Hypocrella aurantiaca/Aschersonia aurantiaca*
2. *Hypocrella citrina/Aschersonia blumenaviensis*
3. *Hypocrella disciformis/Aschersonia disciformis*
4. *Hypocrella hirsuta*
5. *Hypocrella viridans/Aschersonia viridans*

Teleomorph characters

Stromata

1. Size (diam)
   - a. 1–1.5 mm........1, 5
   - b.> 1.5–2 mm........2–4

2. Colour
   - a. Yellowish white to white........2
   - b. Pale yellow........2
   - c. Yellow........2, 4
   - d. Greyish yellow........2
   - e. Pale orange........1
   - f. Orange........1
   - g. Greyish orange........2
   - h. Brown........5
   - i. Greenish........3, 5

3. Shape
   - a. Pulvinate, base slightly constricted........1–5
   - b. Discoid........3–5

4. Reaction to 3 % KOH
   - a. KOH+ (changing colour)........1, 3–5
   - b. KOH- (not changing colour)........2

5. Hypothallus
   - a. Present........2–5
   - b. Absent........1–3

6. Surface texture
    a. Pruinose 2–5
    b. Smooth 2
    c. Roughened 1

Perithecia

1. Position in stroma
    a. Gregarious but well-separated half-embedded tubercles 3
    b. In crowded, gregarious tubercles 2–4
    c. Embedded in stroma, scattered 1, 5
    d. Embedded in stroma, in somewhat circular fashion towards the periphery 1, 2, 4, 5

Ascospores

1. Shape
    a. Almost filiform 3–5
    b. Long fusiform 1–5

2. Average length
    a. 70–100 µm 3, 5
    b. >100–130 µm 2
    c. >130 µm 1, 4

3. Average width
    a. <3.5 µm 2, 3, 5
    b. >3.5–5 µm 1
    c. >5 µm 4

Anamorph characters

Stromata

1. Colour
    a. Yellowish white to white 2
    b. Yellow 2, 4
    c. Greyish yellow 2
    d. Pale orange 1
    e. Orange 1
    f. Greyish orange 2
    g. Greenish 3, 5
    h. Greyish brown 5
    i. Brown 5

2. Shape
    a. Subglobose 1
    b. Pulvinate 1–3, 5
    c. Pulvinate, almost discoid 3, 4

Conidia

1. Average length of conidium
    a. <20 µm 3, 5
    b. ≥20 µm 1, 2, 4

2. Average width of conidium
    a. <4.5 µm 2, 3, 5
    b. ≥ 4.5 µm 1, 4

Cultural characteristics on PDA

1. Appearance and texture of growing colony

a. Compact, leathery	3–5
b. Compact, floccose/tomentose	4–5

2. Synanamorph

a. Present, hirsutella-like or capilliconidiophores and capilliconidia	4

Known geographical distribution

1. North America	1, 3–5
a. Florida, U.S.A.	1
b. Mexico	1, 3–5
2. Central America	2, 3, 5
a. Costa Rica	2
b. Honduras	3, 5
3. South America	2–5
a. Bolivia	2–4
b. Brazil	2, 4, 5
c. Colombia	3
d. Ecuador	3, 4
4. Caribbean Islands	5
a. Cuba	5

Samuelsia (anamorphs aschersonia-like)

1. *Samuelsia chalalensis*
2. *Samuelsia geonomis*
3. *Samuelsia intermedia/"Aschersonia" intermedia*
4. *Samuelsia rufobrunnea*
5. *Samuelsia sheikhii*

Teleomorph characters

Stromata

1. Colour

a. Pale yellow	2, 4
b. Brownish yellow	2, 4
c. Reddish brown	4

2. Shape

a. Pulvinate with a wide base, convex, not extending	4
b. Pulvinate to cylindrical, with a wide base, extending	2

3. Reaction to 3 % KOH

a. KOH+ (changing colour)	2, 4
b. KOH- (not changing colour)	1, 3, 5

Anamorph characters

Stromata

1. Size (diam)

a. <2.5 mm	1, 3, 5
b. ≥2.5 mm	4

2. Colour

a. Pale yellow	4
b. Greyish yellow	3
c. Pale orange	1
d. Brownish yellow	4, 5
e. Reddish brown	4
f. Brown	3, 5

3. Shape
    a. Pulvinate with a wide base, convex 1, 4
    b. Pulvinate with a narrow base 3, 5

4. Reaction to 3 % KOH
    a. KOH+ (changing colour) 1, 4, 5
    b. KOH- (not changing colour) 3

5. Hypothallus
    a. Present 3, 5
    b. Absent 1, 3, 4

6. Surface texture
    a. Slightly pruinose 1, 5
    b. Smooth 1, 3, 5

Conidiomata

1. Shape of locules
    a. Simple depressions of stroma, irregular, shallow 1
    b. Simple depressions of stroma, elongated, slit-like, or irregular, deep 3–5

2. Arrangement of conidiomata in stroma
    a. Scattered 1, 3
    b. Arranged in a circular fashion 4, 5

3. Paraphyses
    a. Present 3, 4, 5
    b. Absent 1

Conidia

1. Average length of conidium
    a. <5.5 µm 5
    b. ≥5.5 µm 1, 3, 4

2. Average width of conidium
    a. <1.7 µm 1, 5
    b. ≥1.7 µm 3, 4

3. Average length/width ratio
    a. <3.5 µm 3, 5
    b. ≥3.5 µm 1, 4

Known geographical distribution

1. Central America 5
    a. Honduras 5
2. South America 1, 3, 4
    a. Bolivia 1, 4
    b. Chile 3
    c. Peru.......... 4

DICHOTOMOUS KEYS

Moelleriella key based on teleomorph characters

1\. Part-ascospores >16 µm long, inflated in the middle, stromata stud-shaped 2
1'. Part-ascospores <16 µm long, generally not inflated in the middle, stromata in various shapes 4

2\. Part-ascospores 16–20 µm long; conidia ventricose with acute ends 3

2'. Part-ascospores >20 µm long (24–27 µm); conidia ventricose almost rhomboid .... 21. *M. umbospora*

3. Part-ascospores 16–18 µm long; conidia 13–14 × 4–4.2 µm; distributed mostly in Southern Central America and Caribbean Islands (Costa Rica, Panama, Cuba) .... 1. *M. basicystis/"A." basicystis*
3'. Part-ascospores 18–20 µm; conidia 14–15 × 3.8–4 µm; distributed mostly in South America (Panama through Argentina) .... 17. *M. phyllogena/ "A." juruensis*

4. Part-ascospores <6.5 µm long; stromata globose and hard 5
4'. Part-ascospores >6.5 µm long; stromata in various shapes and textures 8

5. Stromata large, 6–30 mm diam, buff to pale greenish, tuberculate; part-ascospores 4–6.5 × 1.5–2 µm .... 9. *M. gaertneriana*
5'. Stromata small, 1–2 mm diam, in darker colours, smooth 6

6. Part-ascospores 5–5.7 × 1.7–2 µm; stromata brown; conidia fusoid almost allantoid 5.5–6 × 1.8–2 µm; known only from Trinidad .... 3. *Moelleriella castanea*
6'. Part-ascospores > 5.8 µm long; stromata in various colours; conidia fusoid; known from tropical and subtropical South America 7

7. Stromata dark brown, almost black; part-ascospores 6–6.5 × 2.3–2.5 µm; known only from subtropical South America (S. Brazil, Paraguay) .... 11. *M. guaranitica/ "A." caapi*
7'. Stromata greyish yellow to dull yellow; part-ascospores 5.8–6.4 × 2.3–2.5 µm; known only from Bolivia .... 2. *M. boliviensis*

8. Stromata almost black, hard, globose or obconical with 1–3 cone-like projections; part-ascospores cylindrical 8–10 µm long 9
8'. Stromata in various shapes and colours, not black; part-ascospores not as above 10

9. Stromata globose; part-ascospores 8.5–10 × 2.5–2.7 µm .... 16. *M. palmae*
9'. Stromata obconical with cone-like projections; part-ascospores 9–9.5 × 2.2–2.5 µm .... 5. *M. cornuta*

10. Stromata whitish, generally pulvinate with pronounced tubercles, each tubercle corresponding to one perithecium 11
10'. Stromata not in the above combination 15

11. Stromata whitish to yellowish white, thick pulvinate, somewhat constricted at the base, slightly tuberculate; part-ascospores 5–10 × 1–2 µm .... 22. *M. zhongdongii/ "A." incrassata*
11'. Part-ascospores >10 µm long 12

12. Stromata 7–10 mm diam, thin pulvinate almost effuse, with perithecia generally arranged near the periphery of the stroma, tuberculate; part-ascospores 10–12 × 2.7–3 µm; known only from Ecuador .... 8. *M. evansii*
12'. Teleomorph characteristics not as above 13

13. Stromata pulvinate, tuberculate; part-ascospores 10–14 × 2–3 µm; conidia ventricose almost rhomboidal, 9–14 × 2.5–3 µm .... 18. *M. rhombispora*
13'. Stromata pulvinate or thin pulvinate; part-ascospores 12–15 × 1.5–3 µm; conidia fusiform, 8–14 × 1.5–2.5 µm 14

14. Stromata thin pulvinate to pulvinate with wide base, tuberculate, whitish, greyish yellow, pale orange; ascus caps thick 4.5–5.5 µm; conidia 8–10 × 2–2.3 µm .... 19. *M. sloaneae*
14'. Stromata thin pulvinate, tuberculate, whitish (sometimes orange white), ascus caps 3–3.5 µm; 8–14 × 1.5–2 µm .... 15. *M. ochracea/ "A." andropogonis*

15. Part-ascospores <10 µm long 16
15'. Part-ascospores >10 µm long 18

16. Part-ascospores <8.5 µm long 17
16'. Part-ascospores 8.5–10 µm long, teleomorph stromata subglobose to pulvinate, greyish yellow to brown (sometimes brownish red to greyish red) .... 7. *M. epiphylla/ "A." cubensis*

17. Stromata pulvinate with constricted base, stud-shaped, pale greyish orange, pale orange, pale greyish yellow or pale yellow; perithecia completely immersed in stroma; part-ascospores 8–8.5 × 3 µm, curved or cylindrical inflated in the middle .... 6. *M. disjuncta*
17'. Stromata subglobose, brownish orange, greyish brown, dark brown, hard; part-ascospores 7–8.2 × 2.3–2.5 µm; conidia ovoid .... 10. *M. globosa*

18. Stromata yellowish, large (3–22 mm diam), globose, tuberculate, cerebriform; part-ascospores 10.5–11.5 × 2.5–2.7 µm .... 13. *M. macrostroma*

18’. Stromata small, *ca.* 1–2 mm diam, in various shapes; part-ascospores 11–16 × 2.5–4.5 µm 19

19. Stromata pulvinate with constricted base, orangish; part-ascospores 11–12 × 4–4.5 µm; known only from southern Brazil .... 4. *M. colliculosa*
19’. Stromata in various shapes; part-ascospores 13–16 µm long 20

20. Stromata pale orange or greyish yellow, generally with 1–2 pezizoid conidiomata present; part-ascospores 14.5–16 × 3.3–3.5 µm; conidia ovoid .... 20. *M. turbinata/ “A.” turbinata*
20’. Stromata in various colours, without pezizoid conidiomata; part-ascospores 13–16 × 2.5–3 µm; conidia fusiform 21

21. Stromata thin pulvinate to pulvinate with wide base, tuberculate, whitish, greyish yellow, pale orange; conidia 8–10 × 2–2.3 µm .... 19. *M. sloaneae*
21’. Stromata thin pulvinate, sometimes almost effuse, strongly tuberculate, whitish, sometimes yellowish to orange-white; conidia 10–16 × 1.5–2 µm .... 12. *M. libera/ “A.” aleyrodis*

Moelleriella key based on anamorph characters

1. Conidia 20–24 × 5.3–6 µm, ventricose almost rhomboid .... 21. *M. umbospora*
1’. Conidia <20 µm long, in various shapes 2

2. Conidia 5.5–6 × 2 µm; stromata brown .... 3. *M. castanea*
2’. Conidia >6 µm long; stromata in various colours 3

3. Stromata almost black, sometimes greyish brown, hard 4
3’. Stromata not as above 5

4. Conidia 10–11.5 × 3.5–3.5 µm, fusoid; known only from southern Brazil and Argentina (subtropical) .... 11. *M. guaranitica/ “A.” caapi*
4’. Conidia 12–13 × 5–5.5 µm, ovoid; known only from Brazil and Trinidad (tropical) .... 10. *M. globosa*

5. Conidia ovoid, width >4.5 µm 6
5’. Conidia mostly fusoid, width <4.5 µm 7

6. Conidia 11.5–12 × 5 µm; stromata pulvinate to convex with a wide base; conidiomata as simple shallow depressions of stromata .... 7. *M. epiphylla/ “A.” cubensis*
6’. Conidia 10.5–11.2 × 4.5–4.8 µm; stromata subglobose to pulvinate generally with 1 or 2 pezizoid conidiomata .... 20. *M. turbinata/ “A.” turbinata*

7. Conidial width >3.8 µm; stromata thick pulvinate, obconical pulvinate, sometimes stud-shaped 8
7’. Conidial width <3.8 µm; stromata in various shapes 9

8. Conidia 14–15 × 3.5–4 µm; distributed from Panama through Argentina .... 17. *M. phyllogena/ “A.” juruensis*
8’. Conidia 13–13.5 × 4–4.2 µm; distributed mostly southern Central America and Caribbean Islands (Costa Rica, Panama, Cuba) .... 1. *M. basicystis/ “A.” basicystis*

9. Conidia width 1.5–2 µm; stromata generally thin pulvinate to effuse, whitish 10
9’. Conidia width >2 µm; stromata in various shapes 12

10. Conidial masses generally orange; conidia 10–16 × 1.5–20 µm; stromata short cylindrical, thin pulvinate almost effuse; part-ascospores 13–16 × 2.5–3 µm .... 12. *M. libera/ “A.” aleyrodis*
10’. Conidial masses generally pale yellow to yellow; stromata and part-ascospores not as above 11

11. Stromata tuberculate or thick pulvinate (obconical/convex); conidia 10–18 × 1.5–2 µm; part-ascospores 5–10 × 1–2 µm .... 22. *M. zhongdongii/ “A.” incrassata*
11’. Stromata thick pulvinate, scutate or thin pulvinate; conidia 8–14 × 1.5–2 µm; part-ascospores 12–15 × 1.5–2 µm .... 15. *M. ochracea/ “A.” andropogonis*

12. Conidia 7.2–8.2 × 2.5–2.8 µm; stromata stud-shaped .... 6. *M. disjuncta*
12’. Conidia >8.2 µm long; stromata not stud-shaped 13

13. Stromata large, 3–22 mm diam, yellowish, globose, cerebriform, tuberculate; conidia 11.7–13 × 2.3–2.7 µm .... 13. *M. macrostroma*
13’. Stromata smaller, in various colours (mostly whitish); conidia not as above 14

14. Stromata effuse, 7–10 mm diam, with perithecia towards the periphery of the stroma and conidiomata in the centre forming a convex/scutate bulge, whitish; conidial masses yellowish brown to brown; conidia 13–14 × 2.7–3 µm .... 8. *M. evansii*
14'. Stromata generally pulvinate, small (<3 mm diam), sometimes effuse; conidiomata scattered; conidial masses generally yellowish 15

15. Stromata effuse, whitish, with shallow conidiomata, sometimes with short finger-like or cylindrical projections; conidia 8.2–10 × 2–2.3 µm .... 19. *M. sloaneae*
15'. Stromata thick pulvinate, scutate, or subglobose; conidia >2.5 µm wide 16

16. Conidia 8.5–11.3 × 2.8–3 µm, fusiform; known only from Bolivia .... 14. *M. madidiensis*
16'. Conidia 9–14 × 2.5–3 µm, ventricose almost rhomboid; known only from Costa Rica, Honduras, Mexico, and Puerto Rico .... 18. *M. rhombispora*

Hypocrella/Aschersonia key based on teleomorph characters

1. Stromata greenish, sometimes brown when old or over-mature; ascospores ≤105 µm long 2
1'. Stromata in shades of yellow or orange; ascospores >105 µm long 3

2. Stromata 1–1.5 mm diam; conidia 14.5–17 × 3–3.5 µm .... 5. *H. viridans/ A. viridans*
2'. Stromata 1.5–2 mm. diam; conidia 12.5–13.2 × 2.8–3 µm .... 3. *H. disciformis/A. disciformis*

3. Stromata 1–1.5 mm diam, pale orange to orange; ascospores 120–180 × 4.5 µm; conidia 27–30 × 5.3–6 µm .... 1. *H. aurantiaca/A. aurantiaca*
3'. Stromata 1.5–2 mm diam, in shades of yellow; ascospores 110–150 × 2–6.5 µm; conidia 20–31 × 3.5–5.7 µm 4

4. Stromata KOH-, yellowish white to white, pale yellow, yellow, or greyish yellow; ascospores 110–115 × 2–3.5 µm; conidia 20–22 × 3.5–3.7 µm .... 2. *H. citrina/A. blumenaviensis*
4'. Stromata KOH+, yellow, with synnematous projections on the surface of the stroma; ascospores 135–150 × 6–6.5 µm; conidia 30–31 × 5.5–5.7 µm4. .... *H. hirsuta*

Hypocrella/Aschersonia key based on anamorph characters

1. Conidia >25 µm long and >5 µm wide 2
1'. Conidia <25 µm long and <5 µm wide 3

2. Stromata yellow, with synnematous projections on the surface of the stroma; conidia 30–31 × 5.5–5.7 µm .... 4. *H. hirsuta*
2'. Stromata pale orange to orange, glabrous; conidia 27–30 × 5.3–6 µm .... 1. *H. aurantiaca/A. aurantiaca*

3. Stromata greenish; conidia 12–17 × 2.8–3.5 µm 4
3'. Stromata in shades of yellow; conidia 20–22 × 3.5–3.7 µm .... 2. *H. citrina/A. blumenaviensis*

4. Conidia 12.5–13.2 × 2.8–3 µm .... 3. *H. disciformis/A. disciformis*
4'. Conidia 14.5–17 × 3–3.5 µm .... 5. *H. viridans/A. viridans*

Samuelsia key based on teleomorph characters

1. Stromata pulvinate almost cylindrical, elevated at central part and then tapering towards base, base wide, with a sunken circular area in centre of top part of stroma; 3.2–3.5 mm diam; ascospores 40–51 × 2–2.5 µm; no anamorph seen .... 2. *S. geonomis*
1'. Stromata pulvinate with a wide base, with conidiomata arranged in a circular fashion; 2.2–3.3 mm diam; ascospores 48–55 × 1.5–2.5 µm; anamorph pycnidium-like .... 4. *S. rufobrunnea*

Samuelsia key based on anamorph characters

1. Conidia 4.2–4.5 × 1.5 µm .... 5. *S. sheikhii*
1'. Conidia >5 µm long 2

2. Conidia 5.5–5.7 × 1.5 µm; stromata pulvinate, pale orange .... 1. *S. chalalensis*
2'. Conidia >6 µm long; stromata in various colours, not pale orange 3

3. Stromata 1.5–2 mm diam, KOH-; only known from Chile (subtropical) .... 3. *S. intermedia/ "A." intermedia*
3'. Stromata 2.2–3.3 mm diam, KOH+; only known from Bolivia and Peru (tropical) .... 4. *S. rufobrunnea*

GENERA AND SPECIES DESCRIPTIONS

MOELLERIELLA Bres., Hedwigia 35: 298. 1896.

= *Fleischeria* Penz. & Sacc., Malpighia 15: 230. 1902.
Anamorph: aschersonia-like.

Type species: *Moelleriella sulphurea* Bres. now considered a synonym of *Moelleriella phyllogena* (Mont.) Chaverri & K.T. Hodge (basionym *Hypocrella phyllogena* Mont., Ann. Sci. Nat. Ser. II 13: 340. 1840).

Stromata mostly globose, thick pulvinate, convex, tuberculate, scutate, thin pulvinate almost effuse, (0.5–)1.5–2(–30) mm diam; whitish, yellowish, orange, brown, and black; stromatal surface glabrous, tomentose, pruinose, or roughened; stromatic tissue not changing colour in 3 % KOH; perithecia completely embedded in stroma, half-embedded, or forming strong tubercles; stromatal outer tissue of *textura angularis*, *epidermoidea* or *intricata*, cell walls (1–)2–2.3(–5) µm thick; stromatal internal tissue generally of *textura epidermoidea* or *intricata*, cell walls (0.8–)2.2–2.7(–4.7) µm thick. Perithecia, obpyriform to subglobose, (265–)325–375(–450) × (115–)135–200(–450) µm. Asci mostly cylindrical, (120–)180–200(–325) × (5.2–)9.5–11(–18) µm, capitate, cap thickness (0.8–)3.5–4.5(–6.5) µm. Ascospores hyaline, smooth, filiform, multiseptate, disarticulating at septa, part-ascospores fusoid, cylindrical, subcylindrical, or ventricose, (4.5–)11.5–12.5(–30) × (1.5–)3(–5.5) µm.

Conidiomata from original substrate on host aschersonia-like; pycnidium-like conidiomata irregularly shaped; phialides formed in a thick compact palisade, in short conidiophores, sometimes indistinct, branching once monochasial, twice monochasial, monoverticillate, or two level monochasial; phialides flask-shaped to slender, (5.2–)11–12.5(–24.5) × (1.3–)2.2–2.5(–6.3) µm; conidia hyaline, smooth, unicellular, fusoid, ventricose or ovoid, generally with acute ends, (5–)12–12.7(–25.5) × (1.5–)4–4.2(–7.8) µm, length/width ratio (2–)3.1–3.2(–7.7). Paraphyses sometimes present.

Habitat: Parasitic on scale-insects (Lecaniidae and Coccidae, Homoptera) and whiteflies (Aleyrodidae, Homoptera).

Distribution: Pantropical, and a few species in the subtropics.

Notes: *Moelleriella* is considered to include hypocrella-like species with multiseptate ascospores that disarticulate within the ascus. Species with non-disarticulating ascospores are included in *Hypocrella s. str.* and *Samuelsia* gen. nov.

Bresadola erected *Moelleriella* based on his observation that the asci contained many spores from earliest development, thus differing from *Hypocrella* in which the ascospores were initially filiform and later break up. Later Petch (1921) examined the type material and observed that the tight spiraling of the ascospores from early stages gave the illusion of many spores. This spiraling is typical of *M. phyllogena*, an earlier synonym of *M. sulphurea*. Although the concept upon which Bresadola based *Moelleriella* appears faulty, *Moelleriella* is the oldest name available for the clade of phylogenetically related species with disarticulating ascospores and fusoid conidia, which is distinct from *Hypocrella s. str.* and from *Samuelsia*. For the purpose of nomenclatural stability, teleomorph names will be used. Therefore, a new genus for the anamorph of *Moelleriella* will not be used.

Moelleriella was described based on M. *sulphurea*, now considered a synonym of *M. phyllogena* (≡ *H. phyllogena*); thus, the type species of the genus is *M. phyllogena*. The type specimen of *Moelleriella* (*M. sulphurea*) was deposited in herbarium Berlin (B), but the specimen was lost in a fire during World War II; *M. sulphurea* is neotypified herein. A specimen from Brazil was selected as the neotype of *M. sulphurea*.

The name *Moelleriella* has been erroneously used for species in the *Elsinoaceae*. However, based on observations and measurements Petch (1921) made of the type specimen in B, it is undoubtedly in the *Clavicipitaceae*.

The genus *Fleischeria* was described in 1902 and is considered a synonym of *Moelleriella*. In the original description of the genus, based on *F. javanica*, Penzig and Saccardo (1902) distinguished *Fleischeria* from *Hypocrella* by the harder stroma of *Fleischeria*. Only two species have been placed in *Fleischeria*: *F. javanica* and *F. paulensis* Höhn (= *M. palmae*). Species with hard and coriaceous stromata on living branches are in the Globose clade, probably closely related to *M. epiphylla, M. turbinata, M. africana*, or *M. schizostachyi*. The original diagnosis of *F. javanica* also clearly mentions the disarticulating ascospores. Examination of type material of *F. javanica* confirms it is congeneric with *Moelleriella*. *Fleischeria javanica* is transferred to *Moelleriella* herein.

Moelleriella javanica (Penz. & Sacc.) Chaverri & K.T. Hodge, **comb. nov.** [≡ *Fleischeria javanica* Penz. & Sacc., Malpighia 15: 230. 1901 ≡ *Hypocrella javanica* (Penz. & Sacc.) Petch, Ann. Perad. 4: 231. 1910].

1. ***Moelleriella basicystis*** Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511361. Fig. 3A–I.
Anamorph: *"Aschersonia" basicystis* Berk. & M.A. Curtis, J. Linn. Soc. 10: 352.1869.

Teleomorphosis: Stromatibus globosis, 1–1.5(–2) mm diam, flavidus; ascosporae multicellulares, ad septum disarticulatae, incolora, partis subcylindrici vel fusiformes, ventricosus ad medium, (11.5–)16–18(–26) × (2.7–)3.5–4(–4.5) µm. Holotypus: CUP 067746. Anamorphosis: *"Aschersonia" basicystis.*

Teleomorphic stromata with a subglobose head and a markedly constricted base (stud-shaped), whitish when immature becoming pale yellow when mature, 1–1.5(–2) mm diam, surface smooth, opaque, with hypothallus (0.5–)0.7–1 mm. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded and on top part of stroma, numerous perithecia per stroma (>20), perithecia flask-shaped, 300–450 ×160–250 µm. Asci cylindrical, (190–)210–298 × (9.3–)11–18 µm, caps (3.2–)4–5(–5.3) µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical or curved with rounded ends and usually inflated in the middle, (11.5–)16–18(–26) × (2.7–)3.5–4(–4.5) µm.

Teleomorph and anamorph present or not in same stromata; anamorphic conidiomata on natural substrata only on constricted part of stroma when teleomorph present. Exclusively anamorphic stromata pulvinate with sloping sides (convex), whitish to pale yellow, conidiomata simple depressions of surface without distinct rims, numerous conidiomata per stroma (>20), fusing with neighboring ones, widely open. Conidial masses yellow. In section, conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; phialides flask-shaped, generally straight, sometimes curved, (5.5–)8.2–9.5 (–13.5) × (2–)2.3–2.5(–3) µm. Conidia hyaline, unicellular, ventricose, with acute ends, (11–)13–

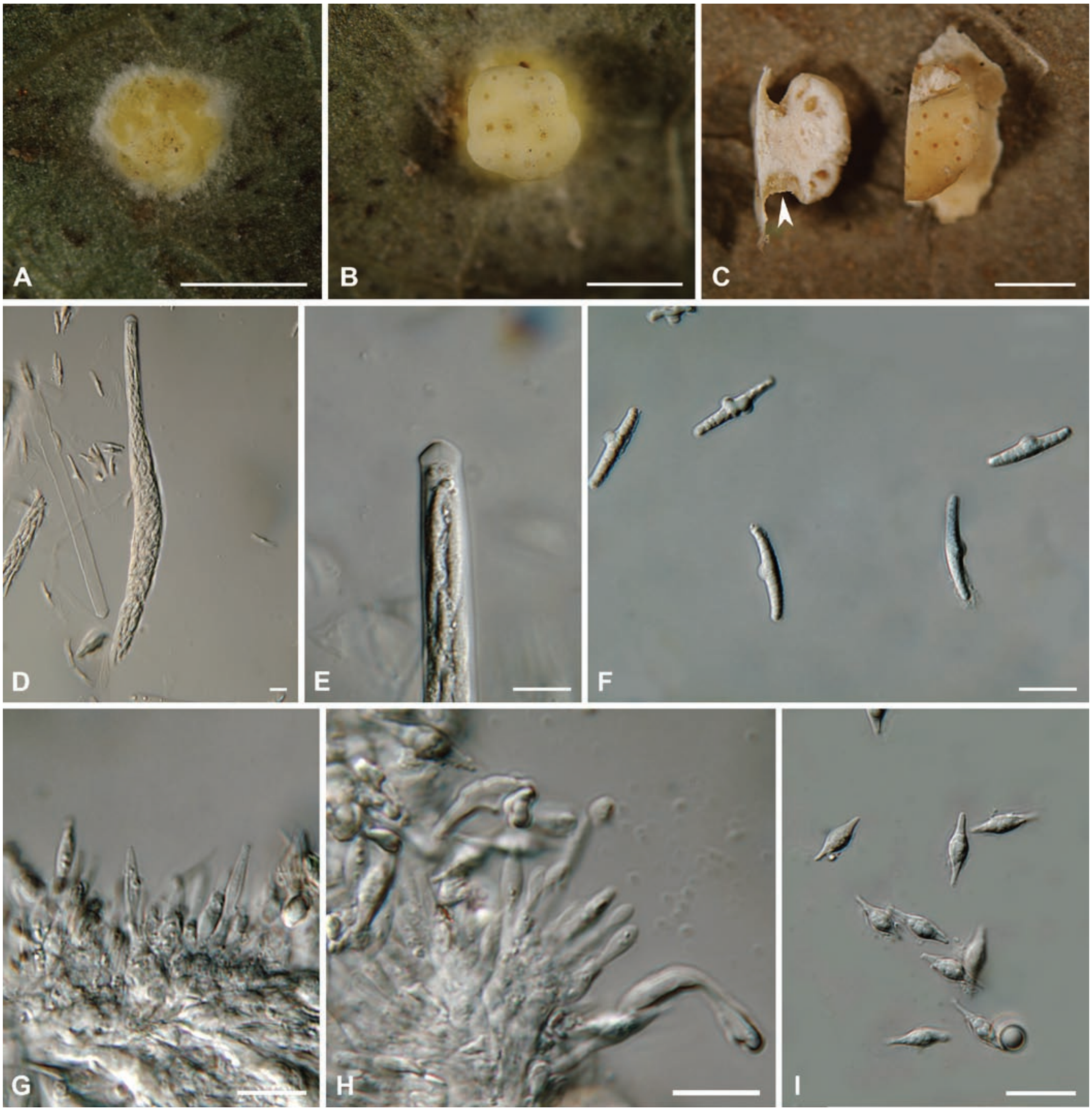

Fig. 3. A–I. ***Moelleriella basicystis.*** A–C. Stromata. A. Young stroma containing only the anamorph. B. Top view of mature stroma showing ostioles. C. Sectioned stroma showing perithecia and anamorph (arrow). D–E. Ascus containing part-ascospores. F. Part-ascospores. G–H. Phialides. I. Conidia. A–B, D–I: CUP 067746 (holotype of *M. basicystis*); C: CUP 67340. Bars: A–C = 1 mm; D–I = 100 µm.

13.5(–15.5) × (3–)4–4.2(–5) µm, l/w (2.5–)3–3.3(–4.2), produced in copious slime. No paraphyses observed.

Colonies on PDA at 25 °C with moderate growth. Colonies whitish, compact, forming a thick stroma, surface minutely velvety. Conidial masses usually not abundant, pale yellow to yellow. Phialides (5–)7.5–8(–12.2) × (2–)2.5(–3) µm. Conidia (10–)12–13(–14.2) × (3–)4(–4.3) µm, l/w *ca.* 3. No paraphyses observed.

Habitat: On scale insects and whiteflies on leaves of *Citrus, Dendropanax*, or unidentified.

Known distribution: Costa Rica, Cuba, and Panama *i.e.* southern Central America and the Caribbean Islands.

Specimens examined: **Costa Rica**, Guanacaste, Guanacaste Conservation Area, Rincon de la Vieja National Park, Las Pailas, on leaf, 30 Nov. 2003, P. Chaverri (*P.C. 374*), J. Hernandez (CUP 067745); Heredia, La Selva Biological Station, Sendero Oriental, on leaf of *Citrus* sp., 20 Jun. 2002, M. Liu (CR 17) (CUP 067340). **Cuba**, C. Wright 776 (**lectotype** of *A. basicystis* designated here K(M) 130013!). **Panama**, Chiriqui, Quebrada Hacha, San Juan Oriente, Besiko, on leaf of *Dendropanax arboreus*, 29 Sep. 2003, G. F. Bills (*F-183.147*) (**holotype** of *M. basicystis P.C. 740* = CUP 067746).

Notes: *Moelleriella basicystis* is similar to *M. disjunta, M. phyllogena*, and *M. umbospora*. The differences are in the size and shape of the part-spores and conidia, and the geographical distribution. *Moelleriella basicystis* belongs in the Effuse clade. In K and FH there are three collections labeled as types of *Aschersonia basicystis* (C. Wright 766); K(M) 130013 is designated here as the lectotype. The specimen K(M) 130014 bears no stromata. Cultures did not survive storage at 8 °C.

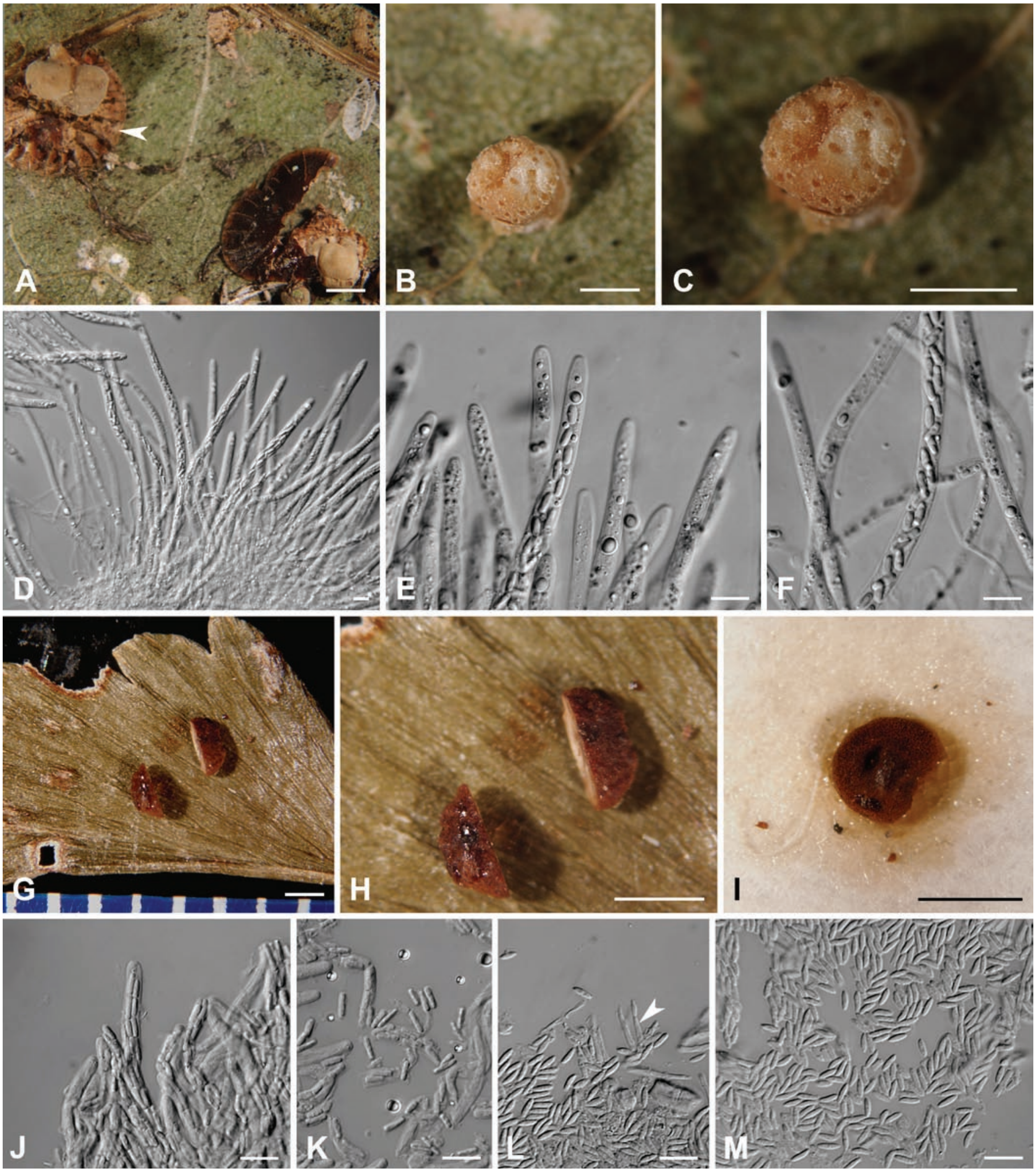

Fig. 4. A–F. *Moelleriella boliviensis*. A–C. Stromata. A. Immature stromata over scale-insects (scale-insect indicated by the arrow). B–C. Stroma showing ostioles. D–F. Asci with ascospores. **G–M. *Moelleriella castanea*.** G–I. Stromata. G–H. Stromata containing the teleomorph. I. Stroma containing the anamorph. J. Asci. K. Part-ascospores. L. Phialides (arrow) and conidia. M. Conidia. A–F: CUP 067747 (holotype of *M. boliviensis*); G–M: K(M)120353 (type of *M. castanea*). Bars: A–C, G–I = 1 mm; D–F, J–M = 10 µm.

2. *Moelleriella boliviensis* Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511362. Fig. 4A–F.
Anamorph: Not known.

Teleomorphosis: Stromatibus subglobosus, 1.2–2 mm diam, cinereoflavidus; ascosporae multicellulares, ad septum disarticulatae, incolora, partis cylindrici, (4.5–)6–6.5(–7.5) × (2–)2.3–2.5 µm. Holotypus: CUP 067747.

Teleomorphic stromata irregularly subglobose to cylindrical, narrowing towards base and then widening slightly, almost knob-shaped, greyish yellow to dull yellow, sometimes pale yellowish, (0.8–)1.2–2(–3) mm diam, surface smooth, opaque. Hyphae of stromata forming compact *textura epidermoidea*. Perithecia fully embedded, numerous perithecia per stroma (>20), ostioles greyish orange, perithecia subglobose to ovoid, 300–400 × 250–300 µm. Asci cylindrical, (134–)138–147(–150) × 8–8.5 µm, caps (0.8–)1–1.5(–1.7) µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are short-cylindrical with rounded or blunt ends, (4.5–)6–6.5(–7.5) × (2–)2.3–2.5 µm.

Habitat: On scale insects on leaves.

Known distribution: Bolivia, Brazil.

Specimens examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, on trail up the mountain along Eslabon River ("Senda RAP"), elev. 400–600 m, on scale-insects on leaves, 12 Jun. 2004, P. Chaverri (*P.C. 603*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067747). **Brazil**, Manaus, Amazon River, Boa Vista, INPA f.r., on leaves, 4 Oct. 1992, H.C. Evans (*I92-785*) (CUP 067748).

Notes: *Moelleriella boliviensis* is similar to *M. globosa* and *M. palmae*. *Moelleriella boliviensis* can be distinguished by the morphology and size of the stromata and smaller part-ascospores. *Moelleriella boliviensis* belongs in the Globose clade. Cultures did not survive storage at 8 °C.

3. ***Moelleriella castanea*** (Petch) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511363. Fig. 4G–M.

≡ *Hypocrella castanea* Petch, Trans. Br. Mycol. Soc. 16: 224. 1931.

Anamorph: aschersonia-like.

Teleomorphic stromata pulvinate to subglobose, hard, brown, 1–1.5(–2) mm diam, surface smooth to scurfy, opaque, without hypothallus. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded in the stroma, numerous perithecia per stroma (>30), perithecia flask-shaped, *ca.* 200–250 × 110–130 µm. Asci cylindrical, with a thin ascus cap. Ascospores filiform, multi-septate, disarticulating into cylindrical with rounded ends part-ascospores, (4.5–)5–5.7(–6.3) × (1.5–)1.7–2(–2.2) µm.

Teleomorph and anamorph not present in same stroma. Anamorphic conidiomata on natural substrata pulvinate with a wide base (*i.e.* convex), brown, conidiomata simple depressions of surface without distinct rims, few conidiomata per stroma (*ca.* 2), conidial masses in dry herbarium specimen dark brown. In section, conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; phialides flask-shaped, slender, generally straight, (7–)11.5–17(–17.5) × 1.5–2 µm. Conidia hyaline, unicellular, fusoid, straight or slightly curved, (5–)5.5–6(–6.7) × 1.5–2 µm, l/w (2.5–)3–3.3(–4.2). No paraphyses observed.

Habitat: On whiteflies on leaves of *Adiantum*.

Known distribution: Trinidad (type locality).

Specimen examined: **Trinidad,** Port of Spain, St. Ann's, on an aleyrodid on *Adiantum* sp., 1939(?), R. Thaxter *9* (**holotype** K(M) 120353!).

Notes: Petch (1921) originally treated *M. castanea* as a synonym of *Hypocrella palmicola* Henn., but later (1931) recognised them as two distinct species. *Moelleriella palmicola* is distributed in the Old World Tropics. Because genetic evidence suggests that other morphologically similar disjunct taxa are distinct (*M. ochracea* vs. *M. mollii*, *M. libera* vs. *M. raciborskii*), in the present study *M. castanea* is kept distinct from *M. palmicola*. *Moelleriella castanea* probably belongs in the Globose clade, based on the characteristics of the stroma.

4. ***Moelleriella colliculosa*** (Speg.) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511364. Fig. 5A–C.

≡ *Hypocrella colliculosa* Speg., Bol. Acad. Nac. Cien. Córdoba 11: 533. 1889.

Anamorph: Not known.

Teleomorphic stromata pulvinate to subglobose, somewhat tuberculate, (1.5–)1.7–2 mm diam, greyish orange, ostioles pale brown, surface smooth, opaque, without hypothallus. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded in stroma, few perithecia per stroma (*ca.* 4–10), perithecia flask-shaped to subglobose, *ca.* 250–300 × 150 µm. Asci cylindrical, caps 1.5–2 µm thick. Ascospores filiform, multiseptate, disarticulating into cylindrical almost ellipsoidal with rounded ends part-ascospores, (10.2–)11–12(–13.7) × (3.5–)4–4.5(–5) µm.

Habitat: On scale insects or whiteflies on living leaves of *Rubiaceae*.

Known distribution: Brazil (type locality). Subtropical.

Specimen examined: **Brazil,** Sao Paolo, Apiahy, on insects on living leaves of *Rubiaceae*, Apr. 1888, C. Spegazzini *301* (**holotype** LPS No. 902!).

Notes: *Moelleriella colliculosa* is one of the few species that occurs in subtropical regions. Based on the characteristics of the stroma, this species probably belongs in the Globose clade.

5. ***Moelleriella cornuta*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB 511365. Fig. 5D–M.

≡ *Hypocrella cornuta* H.P. Krug in Viegas, nom. nud., Bragantia 4: 93. 1944.

Anamorph: Not known.

Teleomorphosis: Stromatibus obconicus, cornutus, fuscus vel nigricans, durus, 1–3 mm diam, 2–9 mm altus; ascosporae multicellulares, ad septum disarticulatae, incolora, partis subcylindrici vel fusiformes, (7.8–)9–9.5(–10.5) × (2–)2.2(–2.5) µm. Holotypus: CUP 067749.

Teleomorphic stromata obconical, sometimes with two cone-like projections, 1–3 mm diam at base, 2–9 mm high, dark brown to black, hard, surface smooth, glossy, without hypothallus; yellow-brown pigment released when 3 % KOH added. Hyphae of stromata forming compact *textura epidermoidea*. Perithecia completely embedded in stroma, numerous perithecia per stroma (>30), perithecia flask-shaped, (275–)297–362(–430) × (135–)145–165(–180) µm. Asci cylindrical, (175–)183–193(–196) × (8.5–)8.8–10.3(–12.2) µm, caps (4.5–)5–5.5(–6) µm thick. Ascospores filiform, multi-septate, disarticulating into cylindrical with rounded ends part-ascospores, (7.8–)9–9.5(–10.5) × (2–)2.3(–2.5) µm.

Habitat: On scale insects or whiteflies on leaves of palms, *Guarea*, and unidentified.

Known distribution: Brazil.

Specimens examined: **Brazil,** Ilha do Tatú, Amazon river basin, on insect on living leaves, 7 Oct. 1992, H.C. Evans (*P.C. 744*) (**holotype** CUP 067749); Sao Paolo, S. Vicente, next to main bridge, on aleyrodid (?) on palm leaves, 20 Feb. 1941, H.P. Krug (IAC 3692!); road to Pariguera, Assú, on *Eucalymnatus* sp. coccid (?) on leaves of *Guarea tuberculata*, 16 Jun. 1939, H.P. Krug (IAC 2900); Chara Morrinhos, Capital, on insect on leaves, 1 Sep. 1942, D.B. Pickel (IAC 5129).

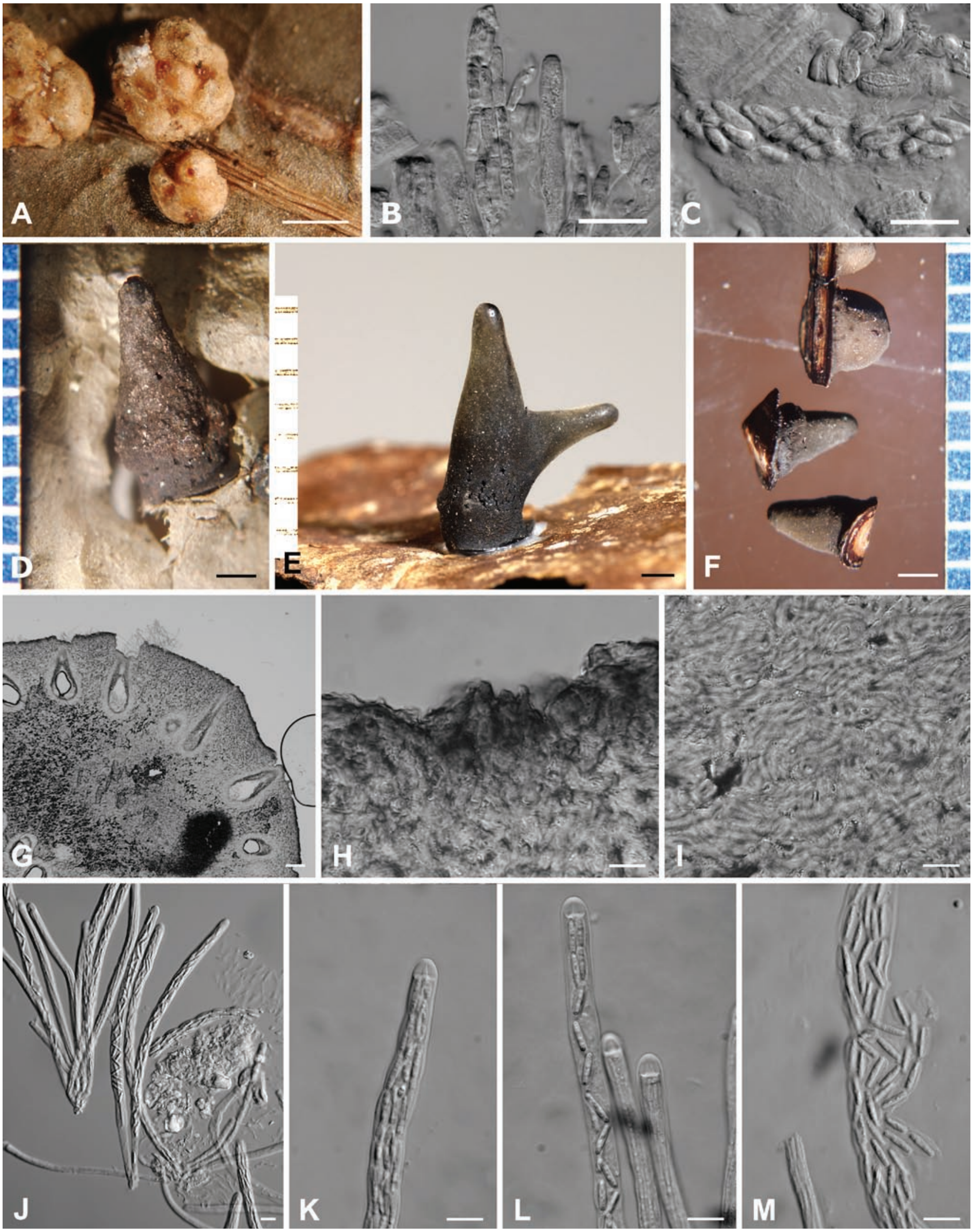

Fig. 5. A–C. *Moelleriella colliculosa*. A. Stromata showing ostioles. B–C. Asci and part-ascospores. **D–M. *Moelleriella cornuta*.** D–F. Stromata. G. Section of stroma. H. Section showing outermost layer of stroma. I. Section showing inner layer of stroma. J–L. Asci and part-ascospores. M. Part-ascospores. A–C: LPS 902 (type of *M. colliculosa*); D: IAC 2900; E, G–M: CUP 067749 (holotype of *M. cornuta*); F: IAC 3692. Bars: A, D–F = 1 mm; G = 100 µm; B–C, H–M = 10 µm.

Notes: Two specimens of *H. cornuta* were included by Viégas (1944) in a listing of Brazilian fungi but the species was never formally described. The original specimens have few stromata, and therefore a collection made by H.C. Evans with many stromata is designated as the holotype. Mains (1959b) considered *M. cornuta* to be conspecific with *H. palmae*, but it differs in its conoid stromata. The collections made by H.P. Krug and D.B. Pickel deposited in IAC are from the State of Sao Paolo, Brazil, which is subtropical. Based on the characteristics of the stroma, this species probably belongs in the Globose clade.

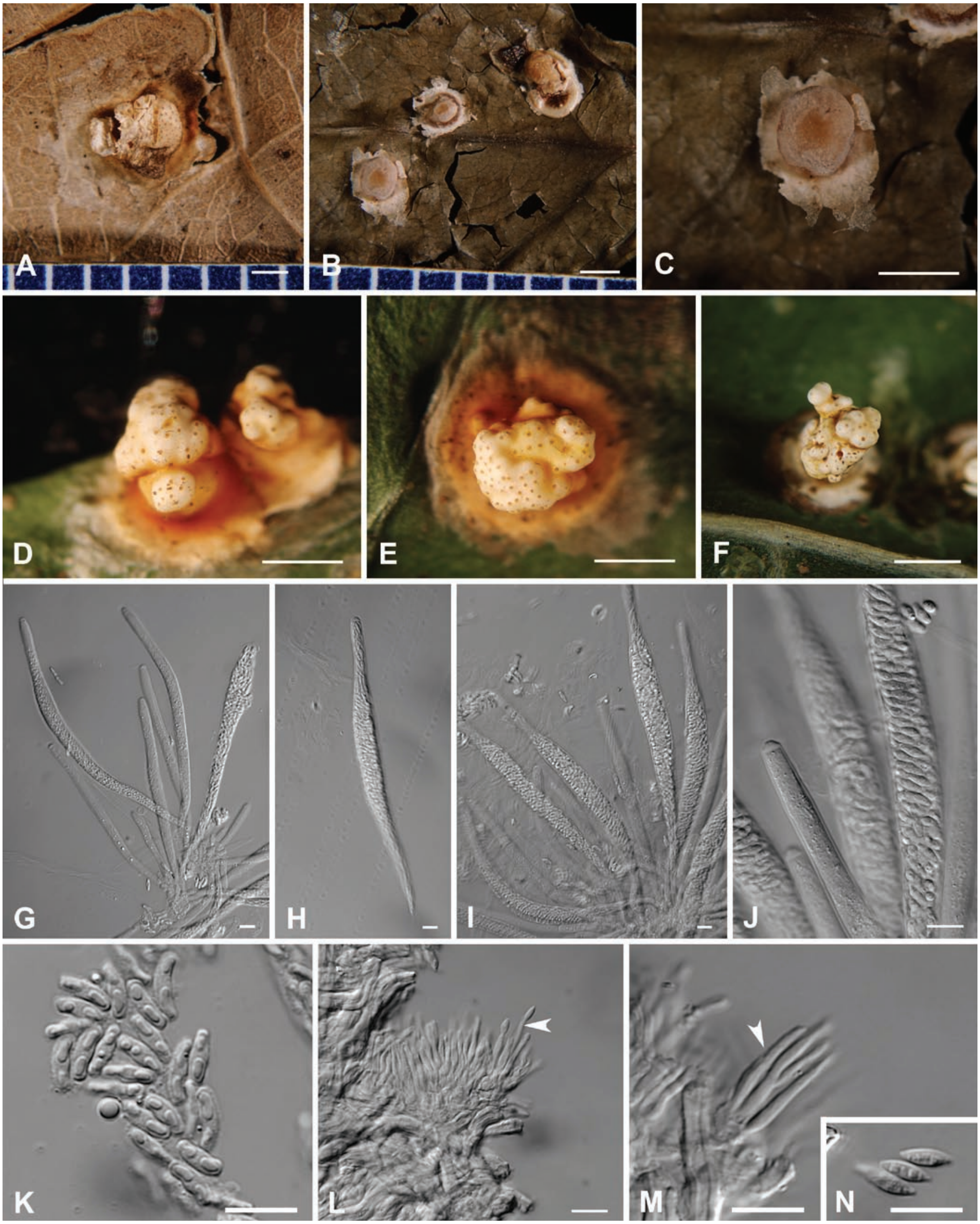

Fig. 6. A–N. ***Moelleriella disjuncta.*** A–F. Stromata. A, D–F. Stromata containing perithecia. B–C. Young stromata containing only anamorph. G–J. Asci and part-ascospores. K. Part-ascospores. L–M. Phialides (arrows). N. Conidia. A, H–J: NY 3370 (epitype); B–C, L–N: NY 1640 (type); D–E: CUP 067864; F–G, K: CUP 067865. Bars: A–F = 1 mm; G–N = 10 µm.

6. *Moelleriella disjuncta* (Seaver) Chaverri & K.T. Hodge, comb. nov. MycoBank MB511366. Fig. 6A–N.

≡ *Hypocrella disjuncta* Seaver, Mycologia 12: 97. 1920.

Anamorph: aschersonia-like.

Teleomorphic stromata with irregularly globose head and markedly constricted base (stud-shaped), sometimes tuberculate, whitish when immature becoming pale greyish orange to pale orange, or pale greyish yellow to pale yellow when mature, (1–)1.5–2(–3) mm diam, surface smooth, opaque, with hypothallus (0.5–)1(–1.5)

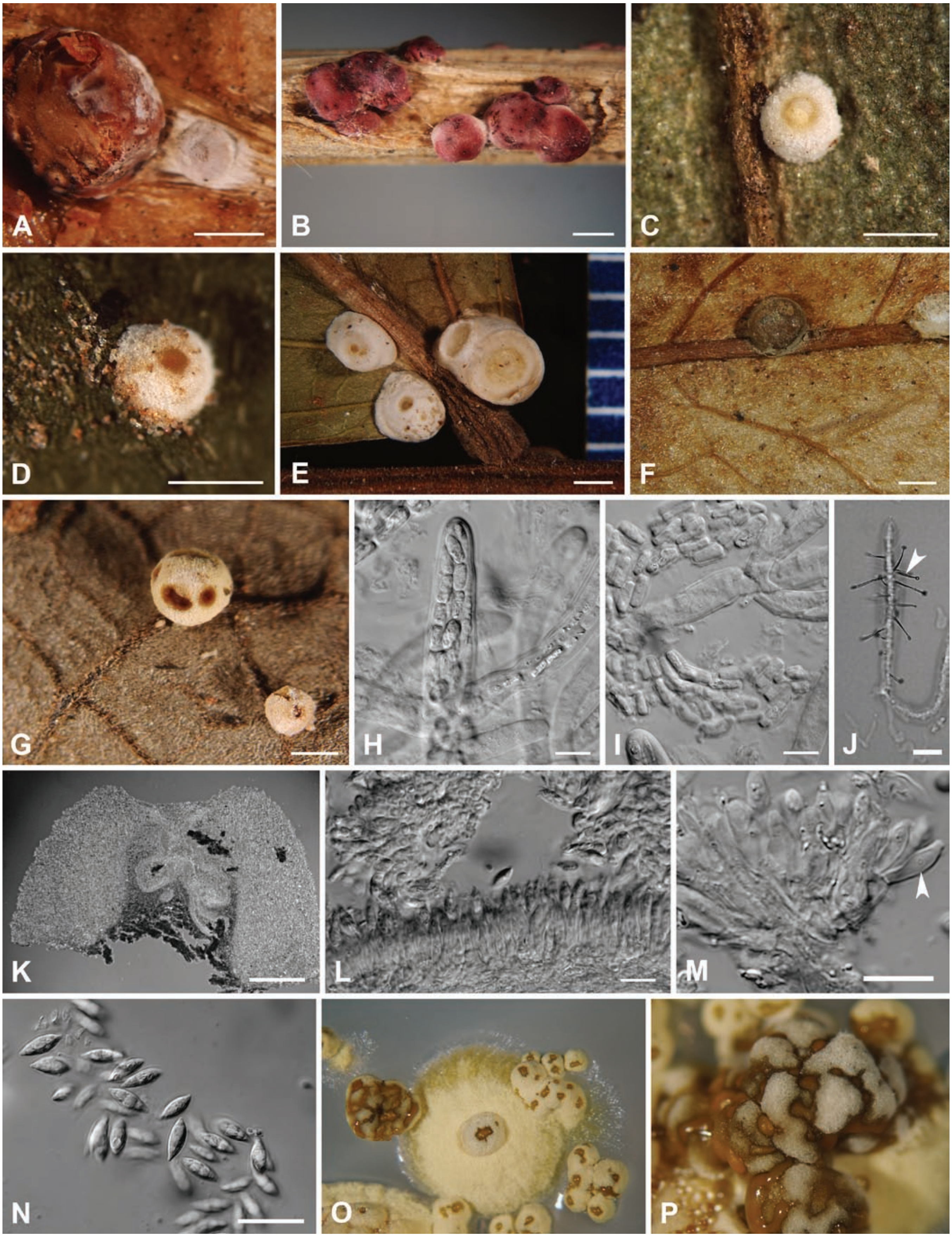

Fig. 7. A–P. *Moelleriella epiphylla*. A–G. Stromata. A–B. Stromata containing perithecia. C–G. Stromata containing only the anamorph. H. Ascus with part-ascospores. I. Part-ascospores. J. Part-ascospores germinating within the ascus and forming capilliconidiophores and capilliconidia (arrow) on PDA. K. Section showing irregularly-shaped conidioma in the center of the stroma. L–M. Phialides. L. Compact palisade of conidiophores with phialides. M. Phialides (arrow). N. Conidia. O–P. Colonies on PDA at 25 °C after *ca.* 3 wk. A, H, I: K(M)120332 (type of *M. epiphylla*); B: CUP 067757; C: CUP 067755; D: CUP 067752; E, K–N: IMI 362282; F: S-F22397; G, J, O–P: CUP 067754. Bars: A–G = 1 mm; H–J, L–N: 10 µm; K: 100 µm.

mm. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded and on top part of stroma, ostioles deep yellow to pale orange, numerous perithecia per stroma (>30), perithecia flask-shaped, 350–400 × 200–250 µm. Asci cylindrical, (145–)212–188(–231) × (9.5–)11.5–14.5(–18.3) µm, caps (1.8–)2.2–3(–3.3) µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical or curved with rounded ends and usually inflated in middle, ventricose, (6.8–)8–8.5(–11.5) × (2.5–)3(–3.5) µm.

Teleomorph and anamorph generally present in same stromata. Anamorphic conidiomata on natural substrata only on constricted part of stroma when teleomorph present. Conidiomata as simple depressions of surface without distinct rims, numerous conidiomata per stroma (>20), but difficult to count due to fusion with neighboring ones, widely open. Conidial masses orange. In section, conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; phialides flask-shaped, generally straight, (9.5–)10.7–14(–16) × (1.5–)2–2.2(–2.5) µm. Conidia hyaline, unicellular, fusoid, with acute ends, (6.8–)7.2–8.2(–9.3) × (2.3–)2.5–2.8(–3) µm, l/w (2.5–)2.8–3(–3.3), produced in copious slime. No paraphyses observed.

Conidia from one dry culture (I93-806 = CUP 067750) (5–)5.8–6(–7) × 2.5–2.7(–3) µm, l/w (1.8–)2.2(–2.5); conidial masses yellow to greyish orange. No paraphyses observed.

Habitat: On scale insects and whiteflies on leaves of *Bignonia* and unidentified.

Known distribution: French Guiana, Guyana, Panama, Puerto Rico, and Trinidad.

Specimens examined: **French Guiana**, Cayenne, on insect on leaves, Leprieur (# 1121) (PC!); Esequibo River, on leaf, 27 Feb. 1993, H.C. Evans (*I93-806*) (CUP 067750). **Guyana**. Pakaraima Mountains, Upper Potaro River, on leaf, 6 Jul. 2003, M.C. Aime (*M.C.A. 2331, M.C.A. 2445*) (CUP 067864, CUP 067865). **Panama**, Fortuna, along trail 1 km West of STRI Biological Station, on dicot leaf, 14 Jul. 2002, J.F. Bischoff (*J.B. 205*) (*P.C. 739* = CUP 067751). **Puerto Rico**, Naguabo, on whiteflies on *Bignonia unguis*, 9 Mar. 1914, J.R. Johnston & J.A. Stevenson (**holotype** NY 1640!). **Trinidad**, Vicinity of Tabaquite, on insect on dead leaf, 26 Mar. 1921, F.J. Seaver (**epitype** designated here NY 3370!).

Notes: *Moelleriella disjuncta* is similar to *M. phyllogena*, *M. umbospora*, and *M. basicystis*. The differences are in the size and shape of the part-spores and conidia, and the geographical distribution. The holotype of *M. disjuncta* (NY 1640) has immature perithecia. A specimen from Trinidad (NY 3370), which has mature perithecia and ascospores, is designated here as the epitype. No cultures survived storage at 8 °C. *Moelleriella disjuncta* belongs in the Effuse clade.

7. ***Moelleriella epiphylla*** (Massee) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511367. Fig. 7A–P.

≡ *Hypocrea epiphylla* Massee, J. Bot. 333: 164. 1892.
≡ *Hypocrella epiphylla* (Massee) Sacc., Sylloge Fungorum 11: 368. 1895.

Anamorph: "*Aschersonia*" *cubensis* Berk. & M.A. Curtis, J. Linn. Soc. 10: 351. 1869.

= *Aschersonia chaetospora* Sacc., Bol. Soc. Broter. Coimbra 11: 69. 1893, *fide* Petch 1921.
= *Aschersonia amazonica* Henn., Hedwigia 43: 338. 1904.
= *Aschersonia consociata* Henn., Hedwigia 43: 338. 1904, *fide* Petch 1921.

Teleomorphic stromata when young subglobose to pulvinate, with slightly constricted base, yellowish gray with a whitish tomentum, stromata when mature subglobose, slightly tuberculate, greyish yellow, becoming brown when old, sometimes brownish red to greyish red, (0.8–)1.3–2(–3) mm diam, surface smooth, opaque, without hypothallus. Hyphae of stromata forming compact *textura epidermoidea*. Perithecia completely embedded in stroma, ostioles brownish orange, dark brown, or reddish brown, numerous perithecia per stroma (>20), perithecia flask-shaped, *ca.* 400–550 × 200 µm. Asci cylindrical, caps thin. Ascospores filiform, multi-septate, disarticulating into part-spores that are short-cylindrical with rounded or blunt ends, (7.8–)8.3–9.5(–12) × (3.5–)3.8–4.2(–4.5) µm.

Teleomorph and anamorph usually not present in same stroma. Anamorphic stromata subglobose, subconoid (convex), or subcylindrical, greyish, greyish yellow, or pale yellow, conidiomata simple depressions of surface without distinct rims, few conidiomata per stroma (<10). Conidial masses yellow, greyish yellow, yellowish brown, orange, to brownish orange. In section, conidioma U-, V-shaped, or irregular, deep. Conidioma with hymenium lining inner surface; conidiophores in a compact palisade, phialides flask-shaped, straight, (8–)9.5–12.5(–12.7) × (2.5–)3–3.5 µm. Conidia hyaline, unicellular, ovoid, with acute ends, (9–)11.5–12(–13.5) × (3.5–)5(–6.5) µm, l/w (1.5–)2.3–2.5(–3.2), produced in copious slime. No paraphyses observed.

Germinating ascospores forming capilliconidiophores and capilliconidia. Colonies on PDA at 25 °C after 3 wk fast-growing. Colony stromatic, pale yellow, spreading, forming a somewhat thin pulvinate structure, surface minutely velvety, wrinkled. Conidial masses abundant, orange or greyish yellow. Phialides in a compact palisade, phialides short, flask-shaped, (6.8–)10–11(–14.7) × (2.5–)3–3.5(–4.2) µm. Conidia ovoid, with acute ends, (9.2–)10.5–11(–13) × (3.3–)4–4.5(–5) µm, l/w (2–)2.5(–3.3). No paraphyses observed.

Habitat: On scale insects and whiteflies generally on the abaxial and adaxial surface of leaves, and sometimes on twigs, of various plants (*e.g. Inga*, *Bignoniaceae*, and unidentified).

Known distribution: Bolivia, Colombia, Costa Rica, Cuba, Ecuador, Guyana, Honduras, Mexico, Saint Vincent; probably widespread throughout the Neotropics.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail Tapacare, on leaf, 10 Jun. 2004, P. Chaverri (*P.C. 552*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067752 = culture ARSEF 7648); Chalalan, near Chalalan lodge, on leaf, 9 Jun. 2004, P. Chaverri (*P.C. 545*), D. Quintana, M. Sogonov, A. Alvarez (CUP 67866). **Colombia**, Choco, Rio Jobi-Coqui, forest, on leaf, 29 May 1993, H.C. Evans (*I93-857*) (CUP 067753). **Costa Rica,** Guanacaste, Guanacaste Conservation Area, Rincon de la Vieja National Park, Las Pailas, on leaf, 30 Nov. 2003, P. Chaverri (*P.C. 375*, *P.C. 386*), J. Hernandez (CUP 067754 = culture ARSEF 7704; CUP 067755 = culture ARSEF 7702); Heredia. La Selva Biological Station, Lindero El Peje, on leaf, 19 Aug. 2003, P. Chaverri (*P.C. 305)* (CUP 067756). CUBA. Santa Paulina, on insect on ferns, C. Wright (427) (**type** of *A. cubensis* S-F22397!; **isotype** of *A. cubensis* K(M) 120358!). **Ecuador**, Guadualupe, Esmeraldas, on twig, 5 May 2000, H.C. Evans (*I00-1203*) (CUP 067757); Manabi: Y de la Laguna, Reserva Bilsa, primary forest, 00°24'N, 79°49'E, elev. 500-600 m, May 2004, G.J. Samuels (*GS 9507, GS 9500, GS 9509*), H.C. Evans, M.C. Aime (CUP 067758, CUP 067759, CUP 067760). **Guyana**, Matthew's Ridge, on leaf of forest shrub, 5 Mar. 1993, H.C. Evans (*I93-813*) (IMI 362282 = culture ARSEF 7676). **Honduras**, Alamikamba, gallery forest, on leaf of small shrub, 16 Jun. 1986, H.C. Evans (*P.C. 750* = CUP 067762). **Mexico**, Veracruz, Catemaco, town of Ejido Lopez-Mateo, project "Cielo, Tierra y Selva", trail to the mountain, elev. 200-300 m, on leaf of *Inga* sp., 13 Dec. 2003, P. Chaverri (*P.C. 440*), J. Garcia-Alvarado, C. Mena-Jiles (CUP 067763). **Peru**, Iquitos, Amazon River, on insect on leaves of *Bignoniaceae*, Jul. 1902, E. Ule *3208* (isotype of *Aschersonia amazonica* S-F22383!). **Saint Vincent**, Morne Cochon, elev. 1200 m., on insect on leaves of *Dieffenbachia* sp., 7 Mar. 1892, W.R. Elliot *364* (**type** of *H. epiphylla* K(M) 120332!).

Notes: The *Moelleriella epiphylla* clade appears to include more than one phylogenetic species (Figs 1–2). However, no discrete morphological characters or geography separate the lineages and thus no names were given to those phylogenetic species. This species belongs in the Globose clade. Evans and Samson (1982) reported this fungus from the Galapagos, although they found only anamorphic specimens.

8. ***Moelleriella evansii*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511368. Fig. 8A–G.

Anamorph: aschersonia-like.

Etymology: In honour of Harry C. Evans, who donated hundreds of specimens of *Hypocrella s. l.* to Herbarium CUP and who has contributed immensely to the knowledge of entomopathogenic fungi.

Teleomorphosis: Stromatibus effusus, planus, tuberculatus, ca. 7–10 mm diam, albidus vel flavidus; ascosporae multicellulares, ad septum disarticulatae, incolora, partis subcylindrici vel fusiformes, (6–)10.3–12(–17.2) × (2–)2.7–3(–4.2) µm. Anamorphosis: *Aschersonia* similis. Phialide 10–17 × 1.5–2 µm; conidii fusiforme, incolora, eseptatus, (11.2–)13–14(–15) × (2.5–)2.7–3(–3.2) µm, longitudo/crassitudo (4–)4.5–5(–6); paraphysis absens. Holotypus: CUP 067764.

Teleomorphic stromata effuse to thin pulvinate with pronounced cylindrical or ovoid tubercles on periphery of stroma, whitish to pale yellow, *ca.* 7–10 mm diam, surface pruinose, opaque. Hyphae of stromata forming loose *textura intricata* to *epidermoidea*. Perithecia fully embedded, one perithecium per tubercle, ostioles yellow, numerous perithecia per stroma (>20), perithecia subglobose to ovoid, *ca.* 300–400 × 300-500 µm. Asci cylindrical, (121–)126–200(–325) × (8.5–)9–11(–13.7) µm, caps thick *ca.* 4.5 µm. Ascospores filiform, multi-septate, disarticulating into part-spores that are short-cylindrical to fusoid with rounded ends, (6–)10.3–12(–17.2) × (1.8–)2.7–3(–4.2) µm.

Teleomorph and anamorph usually not present in same stroma; teleomorph stroma more common. When anamorph present, conidiomata aggregated in centre of stroma, forming a pulvinate bulge with sloping edges, conidiomata simple depressions of the surface without distinct rims, numerous conidiomata per stroma (>20). Conidial masses yellowish brown to brown. In section, conidioma generally U-shaped or irregular, shallow. Conidioma with hymenium lining inner surface; conidiophores in a compact palisade, phialides flask-shaped, slender, straight, 10–17 × 1.5–2 µm. Conidia hyaline, unicellular, fusoid, with acute ends, (11.2–)13–14(–15) × (2.5–)2.7–3(–3.2) µm, l/w (4–)4.5–5(–6), produced in copious slime. No paraphyses were observed.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Ecuador.

Specimens examined: **Ecuador**, Manabi. Y de la Laguna, Reserva Bilsa, primary forest, 00°24'N, 79° 49'E, elev. 500-600 m, on leaf, 2 May 2004, G.J. Samuels (*GS 9504*), H.C. Evans, M.C. Aime (**holotype** P.C. 627 = CUP 067764); Napo, Cuyabeno, on leaves of forest shrubs, 24 Jul. 1993, H.C. Evans (*I93-877*) (CUP 067765); Napo River, Panacocha, on leaf, 26 Mar. 1999, H.C. Evans (*I99-1164*) (CUP 067766); Quito, Puerto Quito, Km 106.5, on leaf, 13 Apr. 2002, H.C. Evans (*P.C. 743* = CUP 067767).

Notes: *Moelleriella evansii* is similar to *M. libera* and the two are phylogenetically related. They can be distinguished by the shapes of the stroma and the conidia. *Moelleriella libera* generally has perithecia and conidiomata scattered throughout the stroma with reddish orange conidial masses. On the other hand, *M. evansii* has perithecia arranged on the periphery of the white to pale yellow stroma and conidiomata in a pulvinate bulge in the centre of the stroma. The stromata of *M. libera* are significantly smaller than those of *M. evansii*. *Moelleriella libera* has more slender conidia (l/w *ca.* 7) than *M. evansii* (l/w 4.5–5). Ascospores and conidia did not germinate. *Moelleriella evansii* belongs in the Effuse clade.

9. ***Moelleriella gaertneriana*** (A. Möller) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511369. Fig. 8H–I.

≡ *Hypocrella gaertneriana* A. Möller, Phycom. & Ascomyc., p. 299. 1901.

Anamorph: Not known.

Teleomorphic stromata large, globose to subglobose, 6–30 × 6–20 mm, buff to pale greenish, surface smooth, shiny, composed of sterile base from which many closely aggregated tubercles arise. Stroma releases a red-orange pigment when 3 % KOH added. Hyphae of stromata forming compact *textura epidermoidea* to *intricata*. Perithecia completely embedded in stroma, ostioles golden yellow, numerous perithecia per stroma (>50), perithecia flask-shaped, (247–)290–358(–378) × (142–)175–221(–378) µm. Asci cylindrical, (120–)139–175(–178) × (4–)5–6(–6.5) µm, caps 3.3–4 thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are oblong to cylindrical with rounded or blunt ends, (4–)4.3–6.5(–8) × 1.5–2 µm.

Habitat: On scale insects on bamboos.

Known distribution: Brazil, French Guiana, Venezuela.

Specimen examined: **French Guiana,** Saül, *ca.* 20 km SW of Saul toward Mt. Galbao, Camp 3, elev. 650 m, on living bamboo culm (?*Guadua*), 22 Jan. 1986, G.J. Samuels and J. Boise *3255* (NY). **Venezuela**, Río Negro Department, Cerro de la Neblina, along Río Mawarinuma, just outside Cañon Grande, near Neblina Base Camp, *ca.* 140 m elev., N 00º 50', W 66º 10', on bamboo culms, Apr.–May 1984, G.J. Samuels *1776* (**epitype** designated here, NY!).

Notes: The type specimen of *H. gaertneriana* was deposited in the Berlin Botany Museum herbarium (B), but was lost in a fire in 1943. For that reason the illustrations in Möller (1901), which were based on a specimen from Brazil on bamboo culms were designated as lectotype by Chaverri *et al.* (2005b). The specimen of *M. gaertneriana* GS 1776 deposited in NY is designated here as the epitype. Based on the characteristics of the stroma, this species probably belongs in the Globose clade.

Additional illustrations: Möller (1901): Taf. III: fig. 51, Taf. IV: fig. 62; Hywel-Jones & Samuels (1998): figs 8–14.

10. ***Moelleriella globosa*** (Syd.) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511370. Fig. 8J–O.

≡ *Hypocrella globosa* Syd., Ann. Mycol. 5: 359. 1907.

Anamorph: aschersonia-like.

Teleomorphic stromata sub-globose, brownish orange, greyish brown, dark brown, (1–)1.5–2.5(–5.5) mm diam, hard, surface smooth to slightly pruinose, opaque. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia fully embedded, mostly on top part of stroma, numerous perithecia per stroma (>20), ostioles pale brown, perithecia flask-shaped, 300–

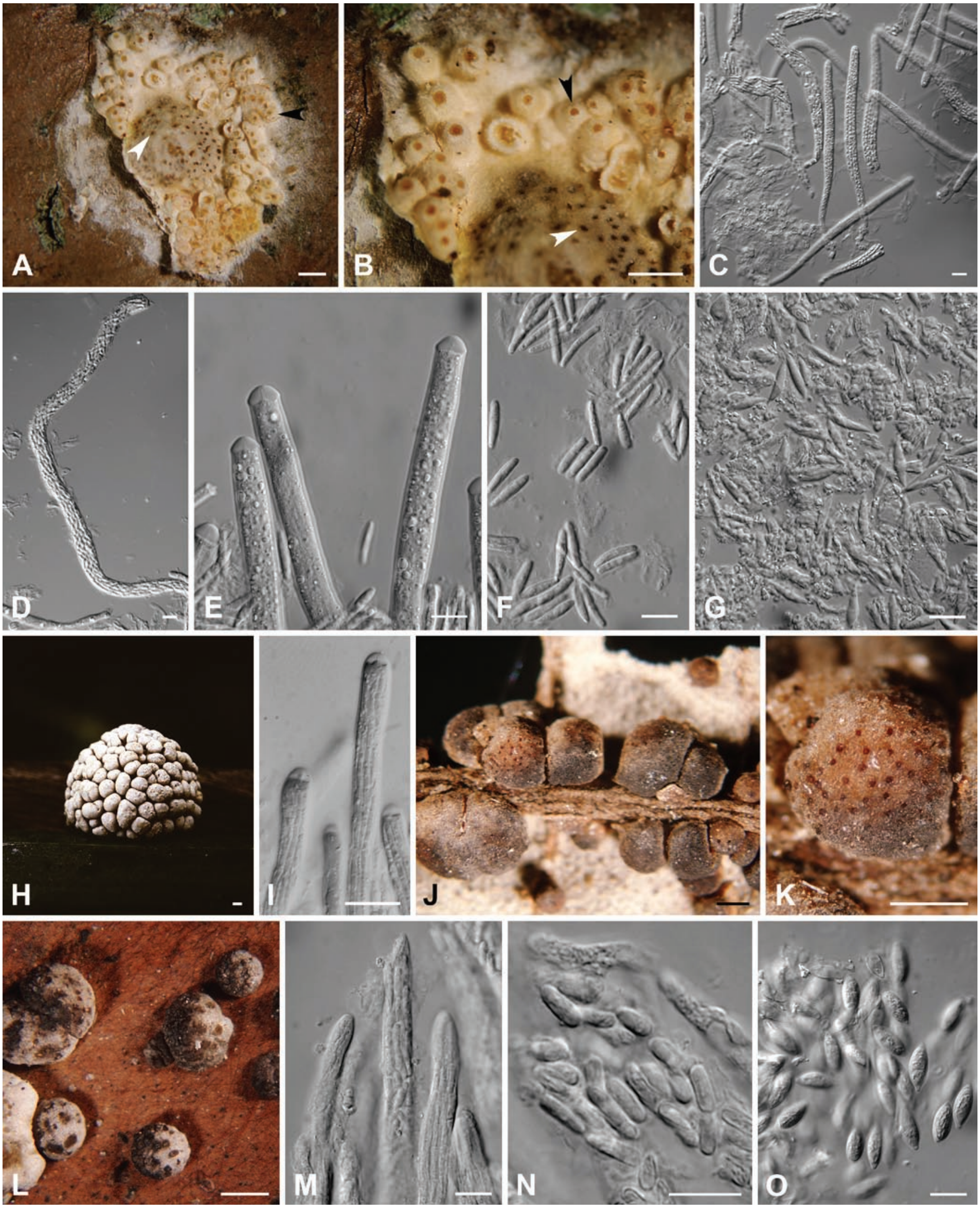

Fig. 8. A–G. ***Moelleriella evansii.*** A–B. Stroma showing perithecia (black arrow) and conidiomata (white arrow). C–E. Asci with part-ascospores. F. Part-ascospores. G. Conidia. **H–I.** ***Moelleriella gaertneriana.*** H. Stroma. I. Asci. **J–O.** ***Moelleriella globosa.*** J–L. Stromata. J–K. Stromata containing only perithecia. L. Stromata containing only conidiomata. M. Asci. N. Part-ascospores. O. Conidia. A–B, D–G: CUP 067764; C: CUP 067766; H–I: NY specimen from French Guiana; J–K, M–N: W 00435; L, O: FH 4241. Bars: A–B, H, J–L = 1 mm; C–G, I, M–O = 10 µm.

400 × 200–250 µm. Asci cylindrical, 150–160 × 8–10 µm, caps thin. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical with rounded ends, (6.5–)7–8.2(–9) × (2–)2.3–2.5(–3) µm.

Teleomorph and anamorph usually not observed in same stroma. Anamorphic stromata sub-globose, greyish brown to dark brown, conidiomata simple depressions of surface without distinct rims, embedded in stroma, openings narrow, numerous conidiomata per stroma (>20), pycnidial openings olive brown to greyish yellow. Conidial masses not visible. In section, the conidioma generally U-, or V-shaped or irregular, deep. Conidioma with hymenium lining inner surface; phialides not seen, probably degraded due to age of specimen. Conidia hyaline, unicellular, ovoid, with pointed ends, (11.5–)12–13(–14.3) × (4.5–)5–5.5(–6) µm, l/w (2–)2.2–2.5(–3). No paraphyses were observed.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Brazil, Trinidad.

Specimens examined: **Brazil**, Brasilia, San Francisco dos Campos, on insects on leaves of *Melastomaceae*, Jan. 1897 (**type** W 00435!; **isotype** S-F10588!); Rio Grande do Sul, Cascata de Caracol, on twig, 19 May 1994, H.C. Evans (*I94-928*) (CUP 067768). **Trinidad**, Aripo Savanna, on insects on leaves, 1912–13, R. Thaxter (as "*Aschersonia*" *cavernosa*, FH 4241!, FH 4242!; as *Hypocrella cavernosa* FH 4102!).

Notes: *Moelleriella globosa* resembles *M. palmae* and *M. guaranitic*a. *Moelleriella guaranitica* has smaller ascospores and conidia than *M. globosa*. *Moelleriella palmae* has larger ascospores than *M. globosa*. Based on the characteristics of the stroma, this species probably belongs in the Globose clade.

The specimens in FH labeled "*Hypocrella cavernosa*" and "*Aschersonia cavernosa*," are not *Hypocrella cavernosa* A. Möller *s. str.* Based on the morphology of their stromata, these FH specimens are considered to be *M. globosa*.

11. ***Moelleriella guaranitica*** (Speg.) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511371. Fig. 9A–J.

≡ *Hypocrella guaranitica* Speg., An. Soc. Cient. Argent. 19: 47. 1885.
= *Hypocrella spegazzini* Sacc. Syll. Fung. 2: 579. 1888.
= *Hypocrella phyllophila* Theiss., Ann. Mycol. 9: 66. 1911, *fide* Petch 1921.

Anamorph: "*Aschersonia" caapi* Viégas, Bragantia 5: 721. 1945.

Teleomorphic stromata globose to pulvinate, with a wide base, dark brown almost black (1–)1.5–2(–4) mm diam, hard, surface smooth, generally shiny. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia fully embedded, mostly on central portion of top part of stroma, numerous perithecia per stroma (>15), perithecia flask-shaped, 400–450 × 200–250 µm. Asci cylindrical, 150–200 × 7.5–10 µm, caps thin. Ascospores filiform, multi-septate, disarticulating into part-spores that are short-cylindrical with rounded or blunt ends, (5.5–)6–6.5(–8.2) × (2–)2.3–2.5(–3) µm.

Teleomorph and anamorph usually not observed in same stroma. Anamorphic stromata sub-globose to pulvinate with sloping edges (convex), dark brown to black, conidiomata simple depressions of surface without distinct rims, few conidiomata per stroma (1–5), pycnidial openings dark brown to black. Conidial masses not visible. In section, the conidioma generally U-, or V-shaped, deep. Conidioma with hymenium lining inner surface, phialides in a compact palisade. Phialides flask-shaped, slender, straight, (14.2–)15–24.5(–25.2) × (2–)2.3–3 µm. Conidia hyaline, unicellular, fusoid, with pointed ends, (9–)10.2–11.5(–13.5) × (3–)3.5(–4) µm, l/w (2.5–)3–3.5(–4). No paraphyses were observed.

Habitat: On insects on monocot stems and dicot leaf veins.

Known distribution: Southern Brazil, Paraguay. Probably subtropical.

Specimens examined: **Brazil**, Sao Paolo, Apiahy, on insects on leaf veins of *Coutarea mollis*, May 1881, C. Spegazzini? (J. Puiggari No. 1483) (type of *H. spegazzini* LPS 903!). Minas Gerais, Falcao Ouro Preto, on insects on stems of a Graminae, 29 Jun. 1941, A.P. Viegas (holotype of *A. caapi* IAC 1977!). **Paraguay,** Santa Barbara, foot of Villa Rica, on leaf veins of *Euphorbiaceae*, Feb. 1882, C. Spegazzini? (**lectotype** of *H. guaranitica* designated here: PAD 3546!; **isotype** in NY!).

Notes: *Moelleriella guaranitica* resembles *M. palmae* and *M. globosa*. The part-spores and conidia of *M. guaranitica* are smaller than those of *M. palmae* and *M. globosa*. *Moelleriella guaranitica* is mostly found in subtropical South America (Paraguay and southern Brazil). Based on the characteristics of the stroma, this species probably belongs in the Globose clade.

12. ***Moelleriella libera*** (Syd.) Chaverri & M. Liu, **comb. nov.** MycoBank MB511372. Fig. 10A–G.

≡ *Hypocrella libera* Syd., Ann. Mycol. 14: 85. 1916.
= *Hypocrella nectrioides* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 225. 1921.

Anamorph: ***"****Aschersonia" aleyrodis* Webber, Bull. USDA Div. Veg. Phy. Path. 13: 21. 1897.

= *Aschersonia goldiana* Sacc. & Ellis, Syll. Fung. 14: 990. 1899.
= *Aschersonia paraensis* Henn., Hedwigia 41: 17. 1902.
= *Aschersonia columnifera* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 258. 1921.

Stroma white, yellowish to orange white, composed of few to numerous gregarious tubercles arising from pulvinate to hemispherical base; sometimes surrounded by thin hypothallus 0.7–2 mm wide; surface of tubercles and base pruinose due to loosely woven, thick-walled hyphae that form stroma. Tubercles strongly projecting and aggregated, hemispherical, cylindrical or slightly narrowing apically, 0.3–0.5 mm diam, 0.3–0.7 mm in height; ostioles reddish orange in fresh specimens, fading to yellow when dry. Perithecia fully embedded, one perithecium per tubercle, perithecia nearly globose to ovoid, 300–400 × 300–600 µm; stromatal tissue around perithecium *textura intricata*. Asci cylindrical, with a cap *ca.* 5 µm thick. Ascospores filiform, slightly shorter than perithecia, septate, sometimes helically twisted in ascus, disarticulating into oblong oval or cylindrical spores, slightly tapering towards ends, with somewhat rounded ends, 13–16 × 2.5–3 µm.

Separate from sexual stroma, anamorphic stroma thin pulvinate or scutate, 1–2(–3) mm diam, white, minutely tomentose; hypothallus usually present in pulvinate stromata, 0.3–1 mm in width, present or absent in scutate stromata; centre of stromata usually covered with conidial masses reddish orange or pale yellow. Conidiomata generally scattered, sometimes circularly arranged; 3–20 per stroma; shape of conidiomatal ostioles circular, or irregular due to fusion of adjacent ostioles; widely open, appearing as simple depressions of stromatic surface without a differentiated rim; conidioma shape in section globose or irregular. Phialides flask-shaped to cylindrical, 10–20 × 1–1.5 µm. Conidia fusiform, unicellular, hyaline, ends acute but not prolonged, (9–)10–16(–18) × 1.5–2(–2.5) µm, produced in copious slime. Paraphyses abundant in the hymenium, especially in thick stromata, hyaline, filiform, 50–90(–113) × 1–1.5 µm.

Colonies on PDA fast-growing, tomentose, white to yellowish white. Conidial masses pale orange, deep orange to reddish orange, abundant, confluent. Most conidiogenous cells, 10–19 × 1–1.5 µm, some phialides elongated to the length of paraphyses. Conidia fusoid, 9–13 × 1.5–2 µm, paraphyses not ordinarily observed in all isolates, 40–123 µm when present.

Habitat: On scale insects and whiteflies on leaves of various plants.

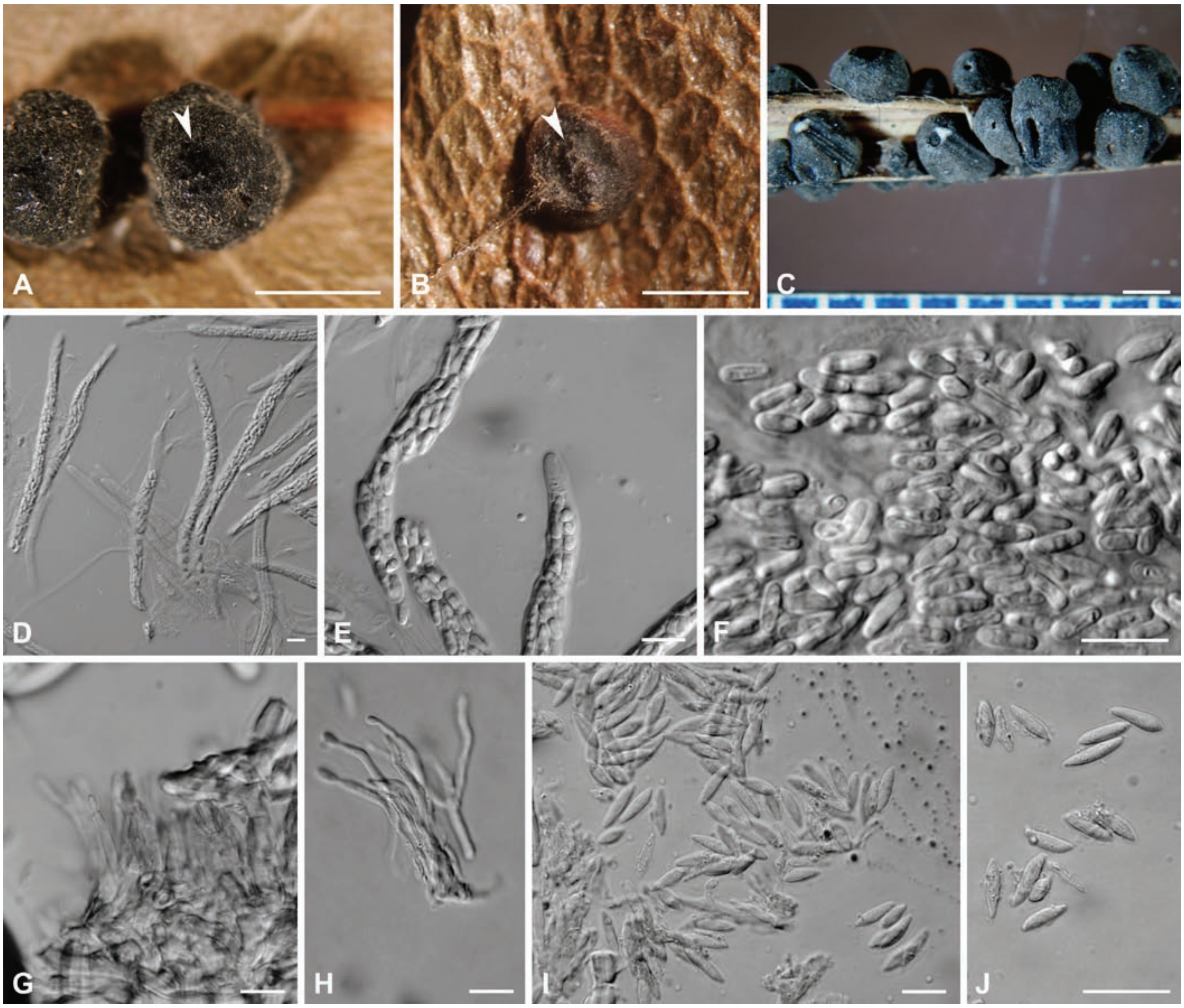

Fig. 9. A–J. *Moelleriella guaranitica*. A–C. Stromata. A–B. Stromata containing only perithecia (perithecia location shown by the arrow). C. Stromata containing conidiomata only. D–E. Asci and part-ascospores. F. Part-ascospores. G–H. Phialides. I–J. Conidia. A–B, D–F: NY 3546 (type of *M. guaranitica*); C, G–J: IAC 1977. Bars: A–C = 1 mm; D–J = 10 µm.

Known distribution: Neotropical, widespread.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, trail Tapacare, on insects on leaves, 10 Jun. 2004, P. Chaverri (*P.C. 550*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067769). Cobija, Rio Acre, on coccids on fallen leaves, Jan. 1912, E. Ule 3413 (**type** of *H. libera*, W 00939). **Brazil**, Para, on leaves of *Psidium pomiferum*, May 1901, J. Huber 50 (S F22444, as *A. paraensis*); Manaus, River Solimoes, on leaf, 30 Jul. 1991, H.C. Evans (*P.C. 745* = CUP 067770). **Costa Rica**, Heredia: OTS La Selva Biological Station, laboratory area, 17 Jun. 2002, M. Liu (culture CR01 = CUP 067280); Camino Cantarrana, 19 Jun. 2002, M. Liu (CUP 067298, CUP 067303 = ARSEF 7512, culture CR11 = CUP 067310); plantation beside entrance RCC, 20 Jun. 2002, M. Liu (culture CR19 = CUP 067341, culture CR20 = CUP 067342); Sendero Oriental 450 m, 20 Jun. 2002, M. Liu (CUP 067325); succession plots, 20 Aug. 2003, P. Chaverri (*P.C. 321*) (culture ARSEF 7617); Lindero El Peje, on leaf, 8–13 Jan. 2004, P. Chaverri (*P.C. 502, P.C. 518*) (CUP 067867, CUP). **Guatemala**, Lake Peten, on leaf of fern, 28 Apr. 1994, H.C. Evans (*I94-919*) (CUP 067771). **Guyana**, Esequibo River, Sharklands, on insect on leaves, 27 Feb. 1993, H.C. Evans (*I93-807*) (CUP 067772). Kamarang, on line to old Ayanganna Airstrip, west Pakaraima mountains, upper Potaro river, 20 km east of Mount Ayangana, near confluence of Potaro and Alukyadongbaru Creek, general area N5°160', W59°540', *ca.* 650 m elev., 8 Jan. 2004, M.C. Aime (*M.C.A. 2465*) (CUP 067565, culture ARSEF 7642). Pakaraima Mountains, Upper Potaro River, on leaf, 6 Jul. 2003, M. C. Aime (*M.C.A. 2335*) (CUP 067870). **Honduras**, Dpto. Copan, Santa Rita, Rio Amarillo, Peña Quemada Reserve, elev. 800 m, on insects on leaves, 9 Sep. 2004, P.A. Sheikh, P. Chaverri (*P.C. 672*) (CUP 067773). **Mexico**, Veracruz, Catemaco, Ejido Lopez Mateo town, project 'Cielo, Tierra y Selva', trail to mountain, 200–300 m elev., 13 Dec. 2003, P. Chaverri (*P.C. 434, P.C. 439*), J. Garcia-Alvarado, C. Mena-Jiles, (CUP 067525, culture ARSEF 7706; and CUP 067528); on leaf of *Piper*, 13 Dec. 2003, P. Chaverri (*P.C. 444*, *P.C. 445*), J. Garcia-Alvarado, C. Mena-Jiles (CUP 067868, CUP 067869 = ARSEF 7707). **Panama**, Fortuna, behind field station, 14 Jul. 2002, J. F. Bischoff (*J.B. 133*) (culture ARSEF 7641). **Puerto Rico**, Guillarte, RD 388 trail, 16 Dec. 2003, M. Liu & Z. D. Wang (cultures ML175-1; ML175-2; ML175-3; ML175-4 = CUP-PR 4421 = ARSEF 7393; ARSEF 7394); On *Psidium guajaba*, 1912, (FH 360 as *A. goldiana*). **Trinidad**, Hollis Reserve, N. Range., on insects on leaves, 10 Mar. 1993, H.C. Evans (*I93-815*) (IMI 362284 = ARSEF 7654). Port of Spain, St. Ann's Valley, on scale insect on *Pentaclethra* sp., R. Thaxter (K(M)120325 as *H. nectrioides*); Maraval Valley, 1912–1913, R Thaxter (FH); Anne's valley, on leaves of *Adiantum*, Feb. 1913, R. Thaxter, (FH). **U.S.A.**, Florida, Manatee County, on whitefly on *Citrus*, Dec. 1896, H. J. Webber (**lectotype** of *A. aleyrodis*, BPI 0389438); H.J. Webber (BPI 0389440); Mar. 1896, H. J. Webber (BPI 0389439); Micanopy, Cross Creek, Majorie Kinnan Rowlings' residence, on *Citrus*, 22 Aug. 2003, M. Liu & Z.D. Wang (CUP 067435 = ARSEF 7339; ARSEF 7340; ARSEF 7343; ARSEF 7344); Lake Alfred, on citrus leaves, 9 Jan. 1980, R.S. Soper (culture ARSEF 430); on scale insects on citrus leaves, M.A. Wolf, (M.H. gift from M.A. Wolf); Inverness, 14 Feb. 1923, E.W. Berger *34* (FH 6298); Gainesville, 1923, E.W. Berger (FH 6301); on *Aleyrodes* on leaves of *Ilex dahoon*, H.S. Fawcett, Apr. 1910 (holotype of *A. columnifera* FH 3966!). **Venezuela**, Bolivar, Canaima, on insects on leaves, 23 Jan. 1994, H.C. Evans (*I94-908*) (CUP 067774).

Notes: *Moelleriella libera* (anam. *"A." aleyrodis*) was extensively discussed in Liu *et al.* (2006). *Moelleriella libera* is distinct in having

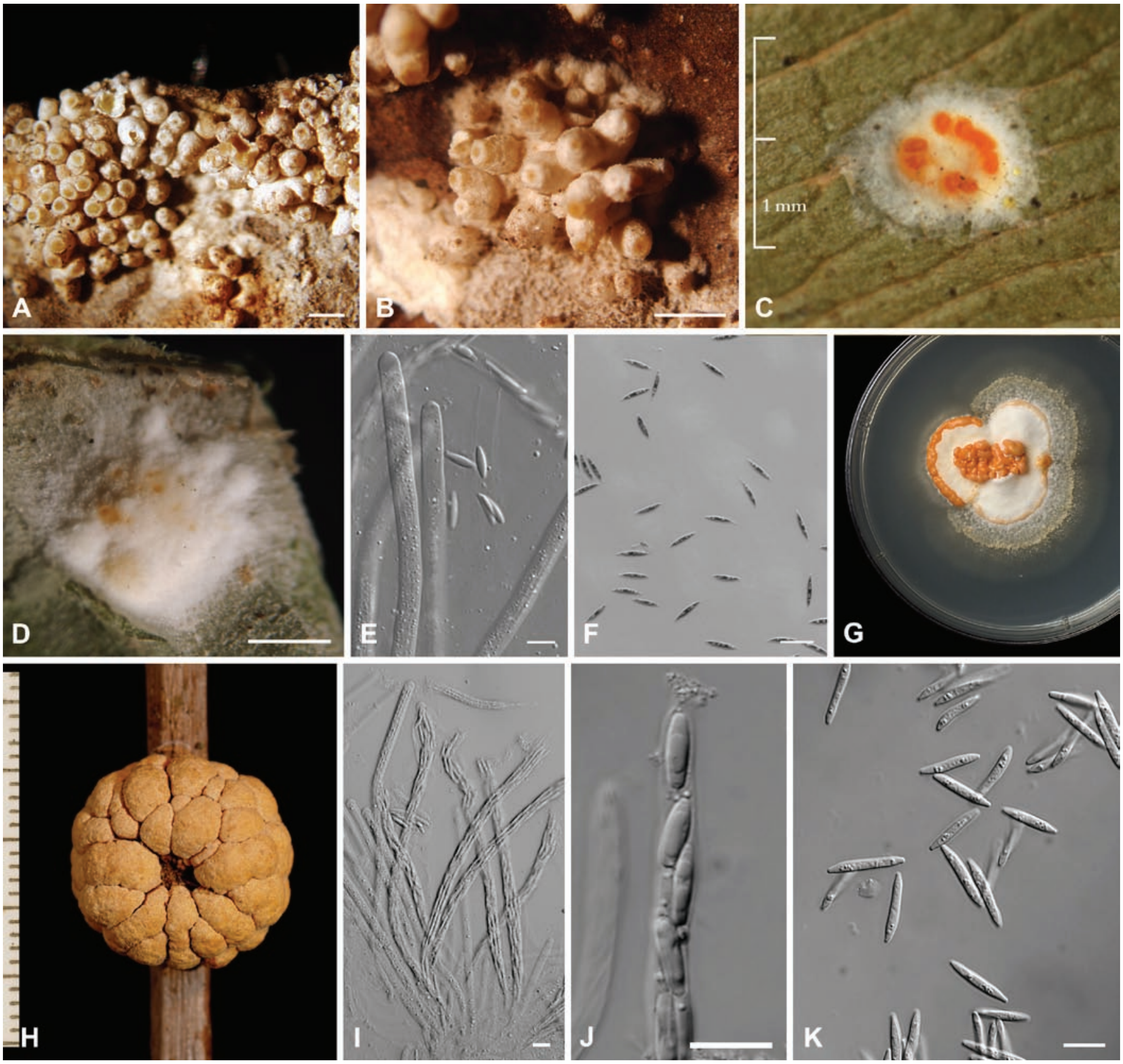

Fig. 10. A–G. *Moelleriella libera*. A–D. Stromata. A–B. Stromata containing perithecia. C–D. Stromata containing conidiomata. E. Asci and part-ascospores. F. Conidia. G. Colony on PDA at 25 °C after *ca.* 3 wk. **H–K. *Moelleriella macrostroma*.** H. Stroma. I. Asci. J. Part-ascospores. K. Conidia. A–B: CUP 067870; C, E: CUP 067341; D: P.C. 321; F–G: CUP-PR 4421; H–J: CUP 67508 (holotype of *M. macrostroma*); K: CUP 67509. Bars: A–B, D = 1 mm; D, F, I–K = 10 µm.

a neotropical and subtropical distribution, orange (or sometimes yellow), narrow fusoid conidia, and a tuberculate teleomorph. As discussed earlier in the introduction, historically, there has been taxonomic confusion regarding the relationship between *M. libera*, commonly called the 'red fungus,' and the 'yellow fungus' "*A.*" *goldiana*. Petch (1921) and Mains (1959a, b) observed that the two species were only distinguished by the colour of the conidial mass, that of the former being red to reddish orange, and the latter yellow to orange. Based on results from Liu *et al*. (2006) and this study, the morphological characters that were in the past used to distinguish "*A.*" *aleyrodis* from "*A.*" *goldiana* are not useful in distinguishing species. The connection between *M. libera* and *"A." aleyrodis* was first inferred by Petch (1925) based on two specimens from Panama. Mains (1959a) cast doubt on the connection due to the inconsistency of the host: *M. libera* was described on coccids, whereas *"A." aleyrodis* was described on Aleyrodes. Examination of the type specimens demonstrate that *M. libera* is clearly the teleomorph of *"A." aleyrodis*, and that is possible that the hosts was misidentified or that M. libera has a wide host range.

Moelleriella libera resembles *M. raciborskii* and *M. evansii*. *Moelleriella raciborskii* is distributed in the Old World. Many specimens found in the Old World that were identified as *M. libera* (anam. *"A." aleyrodis*) are actually *M. raciborskii* (Liu *et al.* 2006). *Moelleriella libera* is restricted to the New World. *Moelleriella libera* generally has perithecia and conidiomata scattered throughout the stroma with reddish orange conidial masses. On the other hand, *M. evansii* has perithecia arranged on the periphery of the stroma and conidiomata in a pulvinate bulge in the centre of the stroma. The stromata of *M. libera* are significantly smaller than *M. evansii*. *Moelleriella libera* has more slender conidia (l/w *ca.* 7) than *M. evansii* (l/w 4.5–5). This species belongs in the Effuse clade.

Additional illustrations: figs 4D–F, 6A–K, in Liu *et al.* (2006).

13. ***Moelleriella macrostroma*** (Chaverri & K.T. Hodge) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511373. Fig. 10H–K.

≡ *Hypocrella macrostroma* Chaverri & K.T. Hodge, Mycol. Res. 109: 1273. 2005.

Anamorph: aschersonia-like.

Stromata large, 3–22 mm diam, yellow, somewhat globose, cerebriform, surface smooth, somewhat glossy, ostiolar openings visible, flush with surface, brownish-yellow, stromata formed of closely aggregated tubercles, tubercles 1–4 mm diam, stroma tissue compact, of *textura angularis* to *epidermoidea*. Perithecia completely immersed in stroma, obpyriform, (377–)389–441(–451) × (137–)138–149(–152) µm. Asci cylindrical, (140–)146–189(–197) × (5.2–)5.5–6.7(–7) µm, caps 3–4 µm thick. Ascospores hyaline, smooth, filiform, multiseptate, disarticulating at septa, part-ascospores fusiform to subcylindrical, (8.7–)10.5–11.5(–18) × (2.2–)2.5–2.7(–3) µm.

Conidiomata sometimes in same stroma as teleomorph. Conidiomata from original substrata, with pycnidium-like depressions in stroma, lacking well-defined walls, irregular in shape. Phialides not observed, probably degraded. Conidia fusiform, hyaline, smooth, unicellular, (10.7–)11.7–13(–14.5) × (2–)2.3–2.7(–3) µm, l/w (4–)4.5–5.7(–7). Paraphyses not observed.

Colony on PDA at 25 ºC slow-growing, floccose or fluffy, compact, pale yellow, forming irregular pycnidium-like concave depressions or cavities in colony and lacking a differentiated wall; conidial masses pale yellow. Conidiophores aggregated into a compact hymenium-lined cavities. Phialides slender, tapering towards tip, somewhat irregular not straight, (23.7–)25–27(–27.5) × (2.5–)2.7–3(–3.5) µm. Conidia fusiform, hyaline, (13.3–)15.5–17(–19) × (2.2–)2.5–2.7(–3.2) µm, l/w (4.5–)6–6.7(–7.7). Paraphyses not observed.

Habitat: On scale insects on living dicotyledonous plants.

Known distribution: Bolivia, Costa Rica.

Specimens examined: **Bolivia**, La Paz Department, Province Franz Tamayo, San José de Uchipiamonas, Madidi National Park, Chalalán Ecolodge, trail to the top of the mountain, along Eslabón River starting at "Senda RAP" camp, elev. 400–600 m, on insects on living vine of dicotyledonous plant, 12 Jun. 2004, D. De La Quintana, M. Sogonov, A. Alvarez, P. Chaverri (*P.C. 605*) (**holotype** CUP 67508!). **Costa Rica,** Heredia, Sarapiquí, La Selva Biological Station, Oriental Trail at 350 m from the beginning, stromata found on ground, substrate unknown, 26 Jun. 2002, J.F. Bischoff (*J.B. 115*) (CUP 67509 = culture ARSEF 7748).

Notes: *Moelleriella macrostroma* belongs in the Globose clade.

Additional illustrations: Chaverri *et al.* (2005b), figs 2–18.

14. ***Moelleriella madidiensis*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511374. Fig. 11A–F.

Anamorph: aschersonia-like.

Anamorphosis: *Aschersonia* similis. Stromatibus lutescentia vel albidus, pulvinata vel conico-pulvinata, 1–2 mm diam; Phialide 10–20 × 2–2.5 µm; conidii fusiforme, 8.5–10.5 × 2–2.5 µm, longitudo/crassitudo 3.5–4.2; paraphysis absens. Holotypus: CUP 067775.

The stromata containing immature perithecia, subglobose, 1–2 mm diam, whitish to pale yellow, surface tomentose. Strictly anamorphic stroma pulvinate to scutate, 1–2 mm diam, whitish to pale yellow, surface tomentose, with hypothallus *ca.* 1 mm; tissue of stroma of somewhat loose *textura intricata* to *epidermoidea*; few conidiomata per stroma (3–5), scattered, conidiomata irregular, with distinct rims, resembling irregular half-embedded bowls, generally V-shaped, conidial masses yellow; phialides flask-shaped, slender, straight, 10–20 × 2.5–3 µm. Conidia fusiform, with acute ends, 8.5–10.5 × 2–2.5 µm, l/w 3–4. Paraphyses not observed.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Bolivia.

Specimens examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail to mountain along Eslabon River ("Senda RAP"), on insect on leaves, 12–13 Jun. 2004, P. Chaverri (*P.C. 594*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067775); Almendrillo trail, on insect on leaves, 11 Jun. 2004, P. Chaverri (*P.C. 569*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067776).

Notes: Although no teleomorph is known for *M. madidiensis*, the teleomorph name is used for this new species because DNA sequence data and anamorph morphology undoubtedly places it in *Moelleriella*. *Moelleriella madidiensis* is similar to *M. zhongdongii* and *M. rhombispora*. *Moelleriella madidiensis* has smaller conidia than the latter species. This species belongs in the Effuse clade.

15. ***Moelleriella ochracea*** (Massee) M. Liu & Chaverri, **comb. nov.** MycoBank MB511375. Fig. 11G–N.

≡ *Hypocrella ochracea* Massee, J. Bot. 34: 150. 1896.

= *Hypocrella andropogonis* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 247. 1921.

Anamorph: "*Aschersonia andropogonis*" Henn., Hedwigia 39: 139. 1900.

= *Aschersonia parasitica* Henn., Hedwigia 43: 149. 1904.

Teleomorphic stromata flattened pulvinate with subglobose tubercles, some tubercles fused together, but more often discrete, surface minutely tomentose, white or orange-white, 1–3 mm diam, with hypothallus. Perithecia develop singly in tubercles, flask-shaped, 250–450 × 160–300 µm. Asci cylindrical, 138–180 × 5–8 µm, caps 3–3.5 µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical with rounded ends, 12–15 × 1.5–2 µm. Teleomorph and anamorph may or may not be present in same stromata.

Strictly anamorphic stromata on natural substrate usually pulvinate, white to pale yellow, 1–4 mm diam, 0.5–1 mm thick. Hyphae of stromata forming compact *textura intricata*. Conidiomata scattered in stromata, 1–6 per stroma, widely open, orifice circular, 0.1–0.6 mm diam, rim of conidiomata sometimes distinctly elevated, conidioma resembles a half-immersed bowl. Conidial masses yellow, yellowish orange to orange, usually contained in conidioma, but sometimes erumpent or forming a column-like cirrus. In section, the conidioma U- or V-shaped. Conidioma with hymenium lining inner surface; phialides cylindrical, slightly narrower near their truncate ends, unicellular, 7–16 × 1–1.5 µm. Conidia fusoid, apices more or less blunt, 8–14 × 1.5–2 µm, l/w *ca.* 6, produced in copious slime. Paraphyses present in some specimens.

Colonies on PDA at 25 °C slow-growing. Stromatic colonies white to greyish white, compact, forming a thick pulvinate structure, surface minutely velvety, wrinkled. Conidial masses usually not abundant, pale yellow to yellow. Phialides 10–17 × 1.5–2 µm, conidia fusoid, apices acute, 8–12 × 1.5–2 µm, l/w *ca.* 5.6. Paraphyses usually long and abundant, up to 190 µm long.

Habitat: On scale-insects and whiteflies generally on the abaxial surface of leaves of various monocot and dicot plants.

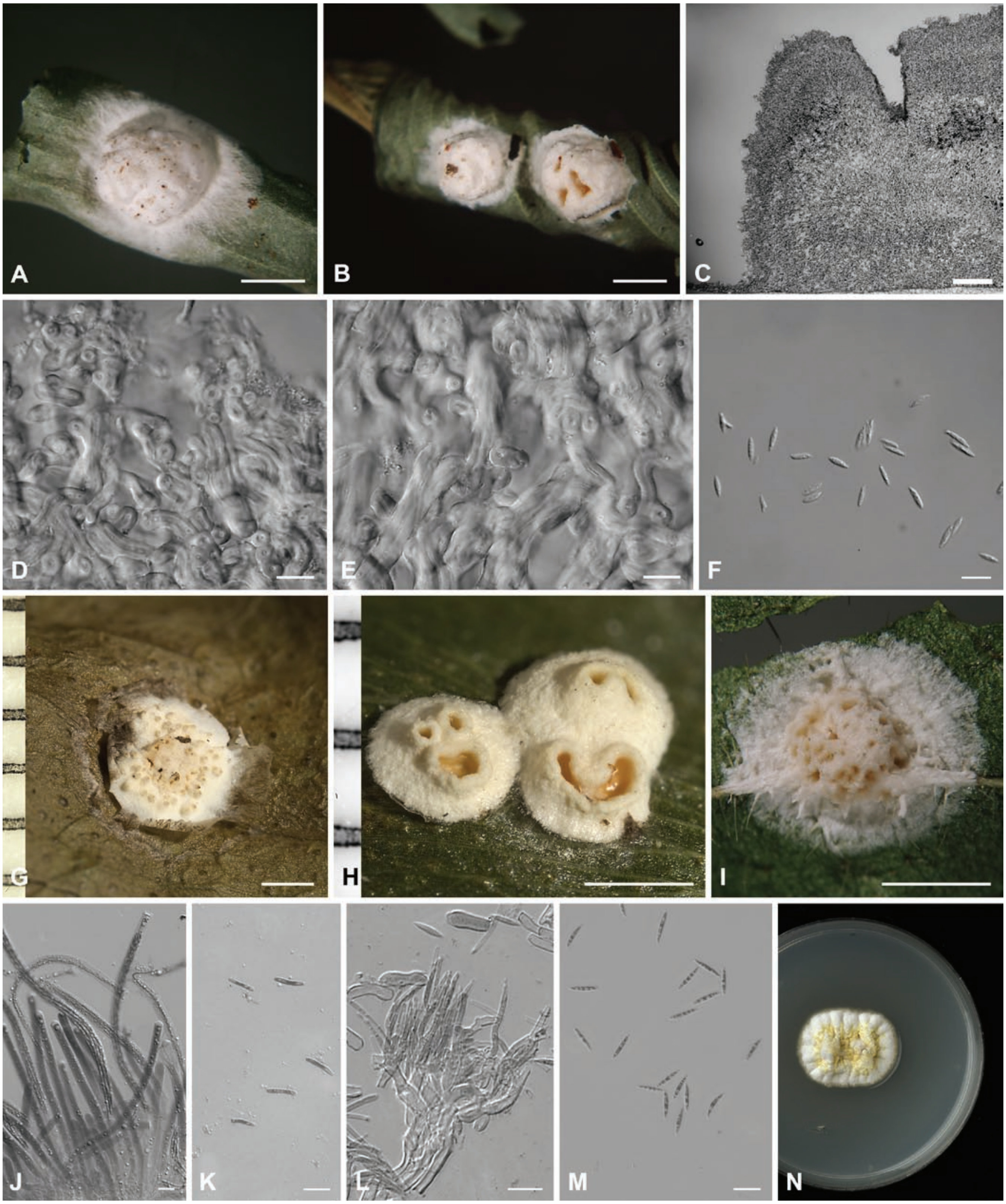

Fig. 11. A–F. *Moelleriella madidiensis.* A–B. Stromata. A. Stroma containing immature perithecia. B. Stromata containing conidiomata. C. Section of conidioma. D. Section showing outermost layer of stroma. E. Section showing inner layer of stroma. F. Conidia. **G–N. *Moelleriella ochracea.*** G. Stroma containing perithecia. H–I. Stromata containing conidiomata. J. Asci. K. Part-ascospores L. Phialides. M. Conidia. N. Colony on PDA at 25 °C after *ca.* 3 wk. A–F: CUP 067775; G: CUP-PR 4438, H: CUP-PR 4407; I: CUP 067781; J–K: K(M) 120354; L, N: CUP 067526; M: CUP 067436. Bars: A–B, G–I = 1 mm; C = 100 µm; D–F, J–M = 10 µm.

Known distribution: Neotropical, widespread.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, near Chalalan lodge, 9 Jun. 2004, P. Chaverri (*P.C. 535*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067777). **Brazil**, On leaves, A. Glaziou *18812* (K(M) 120324!, **isotype** of *H. ochracea*). **Costa Rica**, Heredia. OTS La Selva Biological Station, Sendero Holdridge, 18 Jun. 2002, M. Liu (CUP 067291); Camino Cantarrana, 19 Jun. 2002, M. Liu (CUP 067307); beside entrance to plantation, 20 Jun. 2002, M. Liu (CUP 067343, 067345); Guanacaste, Guanacaste Conservation Area, Rincon de la Vieja National Park, Las Pailas, on insects on ferns, 30 Nov. 2003, P. Chaverri (*P.C. 384*), J. Hernandez (CUP 067515). **Ecuador**, Manabi. Y de la Laguna, Reserva Bilsa, primary forest, 00°24'N, 79°49'E, elev. 500–600 m, on scale-insect on citrus leaf, 2 May 2004, G.J. Samuels (*GS 9474*), H.C. Evans, M.C. Aime (*P.C. 626* = CUP 067778). **Honduras**, Dpto. Atlántida, Tela, Pico Bonito

National Park, loop trail, on insects on leaves, P.A. Sheikh, P. Chaverri (*P.C. 648*) (CUP 067779); Dpto. Copan, Copan Ruinas, Natural trail, elev. 700 m., on insects on leaves, 31 Aug. 2004, P.A. Sheikh, P. Chaverri (*P.C. 661.2*) (CUP 067780); Yojoa, Los Pinos, Cerro Azul/Meambar National Park, elev. 850 m, on insects on leaves, 3 Sep. 2004, P.A. Sheikh, P. Chaverri (*P.C. 685*) (CUP 067781). **Jamaica**, Richmond Vale, St. Thomas, on *Citrus* scale insect, 8 Apr. 1987, C. Prior (IMI 317421). **Mexico**, Veracruz. Municipio Emiliano Zapata, Plan Chico, N19° 26.7350', W 96° 49.865', elev. 900 m, 11 Dec. 2003, P. Chaverri (*P.C. 431*), J. Hernandez, J. Garcia-Alvarado, (CUP 67523); behind Instituto Genetica Forestal Universidad Veracruzana building, 12 Dec. 2003, P. Chaverri (*P.C. 432*), & J. Garcia-Alvarado (CUP 67524); Catemaco, Ejido: Lopez Mateo town, project 'Cielo, Tierra Y Selva,' trail to mountain, 200–300m elev., 13 Dec. 2003, P. Chaverri (*P.C. 436, P.C. 452*), J. Garcia-Alvarado & C. Mena-Jiles (CUP 67526, CUP 67532); culture provided by G.F. Bills IE 1308 (= *P.C. 726*). **Paraguay**, Cerro Coche, on insects on leaves of *Andropogon* sp., K. Fiebrig *770* (type of *A. parasitica*, B 70 0005658). **Puerto Rico**, Guajataca, trail no. 9, on ferns, M Liu & ZD Wang (CUP-PR 4438); Mayaguez, beside Road 105, on ferns, 15 Dec. 2003, M. Liu & Z.D. Wang (CUP-PR 4407 **epitype** of *H. ochracea* designated here). **Trinidad**, Mt. Harris, on insects on leaves of grapefruit tree, 1 Dec. 1985, H.C. Evans (*I85-165*) (CUP 067782); on leaves, R. Thaxter *18* (K(M) 120354, holotype of *H. andropogonis*). **U.S.A.,** Florida: Micanopy, cross creek, Marjorie Kinnan Rawling's residence, on *Citrus*, 22 Aug. 2003, M. Liu & Z.D. Wang (CUP 67436).

Notes: *Hypocrella ochracea* was described based on anamorphic specimens. Other specimens examined here contain both anamorph and teleomorph, and therefore an epitype for this species has been designated here. *Moelleriella mollii* is almost identical to *M. ochracea*. *Moelleriella mollii* has smaller part-spores than *M. ochracea,* and *M. mollii* is distributed in the Old World. Liu *et al.* (2006) discussed *M. ochracea* further. *Moelleriella ochracea* belongs in the Effuse clade.

Additional illustrations: figs 4A–C, 5A–I, in Liu *et al.* (2006). Plate II, fig. 20; plate III, fig. 53, in Petch (1921).

16. ***Moelleriella palmae*** (Berk. & M.A. Curtis) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511376. Fig. 12A–C.

≡ *Hypocrea palmae* Berk. & M.A. Curtis, J. Acad. Nat. Sci. Philad. 2: 285. 1854.
≡ *Hypocrella palmae* (Berk. & M.A. Curtis) Sacc., Syll. Fung. 2: 580. 1883.
= *Hypocrella luteo-olivacea* G. Winter, Grevillea 15: 86. 1988?, *fide* Petch (1921)
= *Hypocrella filicina* Rehm, Hedwigia 37: 200. 1898, *fide* Petch (1921)
= *Hypocrella cavernosa* A. Möller, Phycomyc. & Ascomyc.: 299. 1901., *fide* Petch (1921)
= *Fleischeria paulensis* Höhn., Ergeb. Bot. Exped. K. Akad. Wissensch. Sud Brasilien 2: 21. 1907, *fide* Petch (1921)
= *Hypocrella orbicularis* Syd., Ann. Mycol. 9: 67. 1911, *fide* Petch (1921)
= *Hypocrella ambiens* Theiss., Ann. Mycol. 9: 68. 1911, *fide* Petch (1921), Mains (1959)
= *Hypocrella sydowii* Sacc. & Trott., Syll. Fung. 22: 503. 1913, *fide* Petch (1921)

Anamorph: Not known.

Teleomorphic stromata globose, dark brown almost black (0.6–) 2–5(–6.5) mm diam, hard, surface smooth, generally glossy. Hyphae of stromata forming compact *textura globosa*, *angularis* to *epidermoidea*. Perithecia fully embedded, mostly on top part of stroma, numerous perithecia per stroma (>20), perithecia flask-shaped, 400–450 × 200–250 µm. Asci cylindrical, 160–200 × 7–9.5 µm, caps *ca.* 1 µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are short-cylindrical with rounded or blunt ends, (8–)8.5–10(–11.2) × (2.2–)2.5–2.7(–3) µm. No anamorph seen.

Habitat: On scale insects or whiteflies on leaves and twigs.

Known distribution: Brazil, Peru, Surinam.

Specimens examined: **Peru,** Huanuco Province, Huallaga Valley, Tingo Maria Forest, on leaf, 16 Apr. 1996, H.C. Evans (*I96-971*) (CUP 067783). **Surinam**, on insects on living leaves of palm (**type** of *H. palmae*, K(M) 52653!).

Notes: *Moelleriella palmae* is similar to *M. globosa* and *M. guaranitic*a. They can be distinguished by the morphology of the stroma and ascospores. *Moelleriella palmae* has larger stromata and ascospores than the latter species. Based on observations made by Petch (1921), *H. cavernosa*, *H. orbicularis* and *H. filicina* are conspecific with *M. palmae*. Although type specimens of *H. ambiens, H. sydowii*, and *M. paulensis* were not examined here (they were deposited in Herbarium Berlin (B), where many collections were lost in a fire during World War II), based on Petch's (1921) observations, these species are also conspecific with *M. palmae*. None of the former specimens included the anamorph, according to Petch (1921). The anamorph of *M. palmae* described in Petch (1921) was based on one unidentified collection from Trinidad. Petch's description of the anamorph better fits that of *M. globosa*. *Moelleriella palmae* probably belongs to the Globose clade.

17. ***Moelleriella phyllogena*** (Mont.) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511377. Fig. 12D–K.

≡ *Hypocrea phyllogena* Mont., Ann. Sci. Nat. Ser. II 13: 340. 1840.
≡ *Hypocrella phyllogena* (Mont.) Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 228. 1921.
= *Hypocrella edwalli* Henn., Hedwigia 36: 223. 1897.
= *Hypocrella weberbaueri* Henn., Engler's Bot. Jahrb. 40: 226. 1907.
= *Hypocrella abnormis* Henn., Hedwigia 34: 106. 1895, *fide* Petch (1921)
≡ *Moelleriella sulphurea* Bres., Hedwigia 35: 298. 1896.
= *Hypocrella sulphurea* (Bres.) Arx & E. Müll., Beitr. Kryptogamenfl. Schweiz 11: 393. 1954)

Anamorph: "Aschersonia" juruensis Henn., Hedwigia 47: 388. 1908.

= *Aschersonia lauricola* Speg., An. Mus. Nac. Buenos Aires 20: 457. 1910.
= *?Aschersonia puttemansii* Henn., Hedwigia 48: 1–20. 1908, *fide* Petch (1921)
= *?Aschersonia cheloniae* Speg., An. Mus. Nac. Buenos Aires 20: 456. 1910, *fide* Petch (1921)
= *?Aschersonia jacarandae* Speg., An. Mus. Nac. Buenos Aires 20: 456. 1910, *fide* Petch (1921)

Teleomorphic stromata with a globose head and a markedly constricted base (stud-shaped), sometimes almost cylindrical, whitish to cream-coloured when immature becoming pale yellow, vivid yellow, deep yellow to greyish orange when mature, (1–)2–2.5(–3) mm diam, surface smooth, opaque, with hypothallus (0.5–)0.7–1.2(–0.5) mm. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded and on top part of stroma, numerous perithecia per stroma (>30), perithecia flask-shaped, 300–450 ×160–250 µm. Asci cylindrical, (190–)210–300 × (9.5–)13–20(–21.5) µm, caps (2–)4.5–6.5 µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical or curved with rounded ends and usually inflated in the middle, (13.7–)18.5–20(–25) × (2.5–)3.5–3.7(–4.5) µm.

Teleomorph and anamorph may or may not be present in same stromata. Anamorphic conidiomata on natural substrata only on constricted part of stroma when teleomorph present. Exclusively anamorphic stromata pulvinate with sloping sides (convex), whitish to pale yellow, conidiomata simple depressions of surface without distinct rims, numerous conidiomata per stroma (>20), but difficult to count because they fuse with neighboring ones, widely open. Conidial masses yellow. In section, conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; phialides flask-

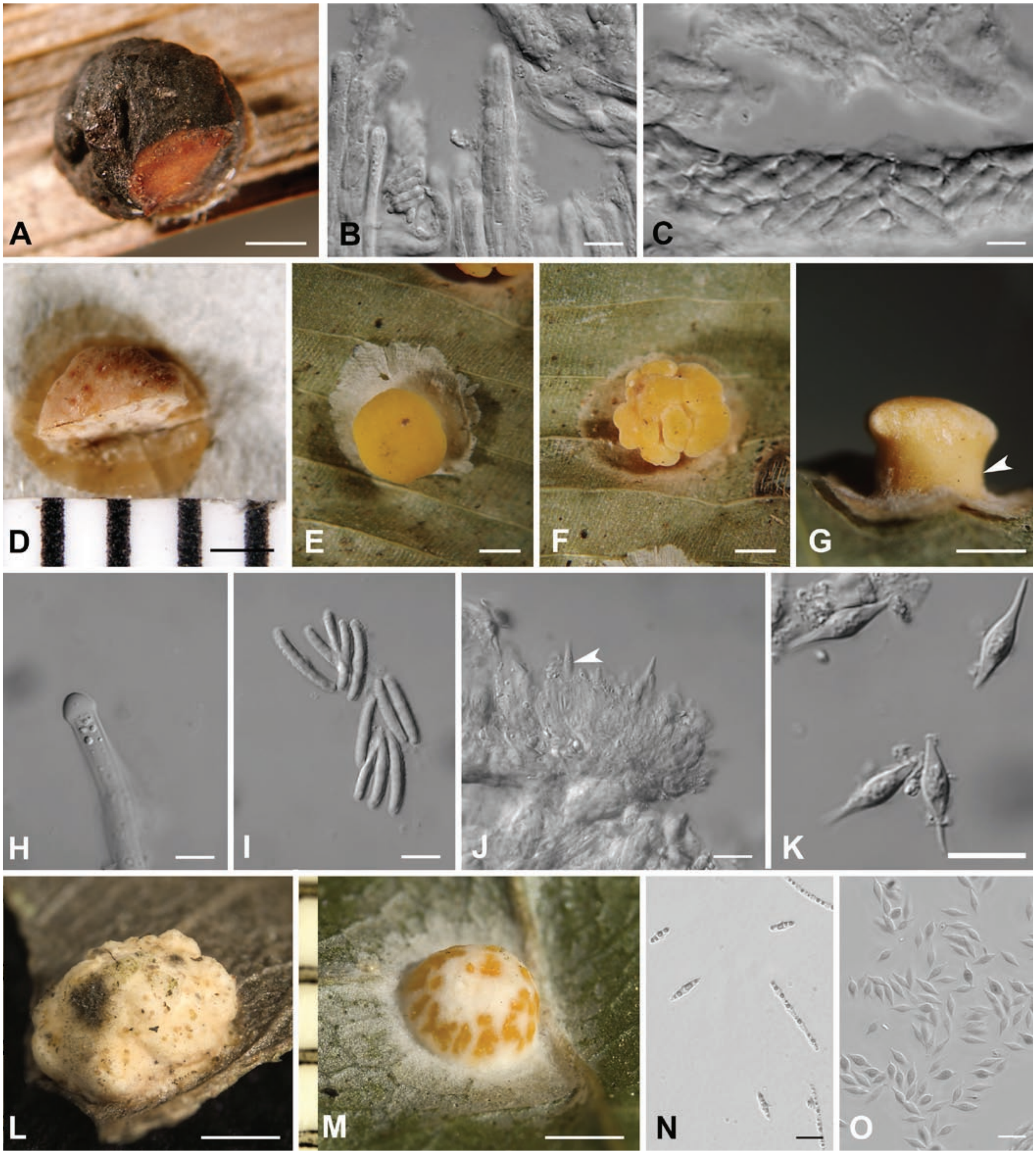

Fig. 12. A–C. *Moelleriella palmae.* A. Stroma. B. Asci. C. Part-ascospores. **D–K. *Moelleriella phyllogena.*** D–G. Stromata. D. Stromata containing perithecia. E–G. Stromata containing conidiomata (arrow indicates where conidiomata are located). H. Ascus showing thickened cap. I. Part-ascospores. J. Palisade of phialides (arrow indicates a phialide). K. Conidia. **L–O. *Moelleriella rhombispora.*** L–M. Stromata. L. Stroma containing perithecia. M. Stroma containing conidiomata. N. Part-ascospores. O. Conidia. A–C: K(M) 52653 (type of *M. palmae*); D: PC No. 580; E–G: CUP 067784; H–I: CUP 067785; J–K: CUP 067793; L, N: CUP 067548 (holotype of *M. rhombispora*); M: CUP 067551; O: CUP-PR 4437. Bars: A, D–F, L–M = 1 mm; B–C, G–K, N–O = 10 µm.

shaped, generally straight, 8–10.5(–10.7) × 2–3 µm. Conidia hyaline, ventricose, with acute ends, (12–)14.5–15.5(–18.5) × (3.2–)3.7–4(–5) µm, l/w (3–)3.7–4(–5), produced in copious slime. No paraphyses observed.

Colonies on PDA at 25 °C with moderate growth. Colonies whitish, compact, forming a thick stroma, surface minutely velvety. Conidial masses usually not abundant, light yellow to yellow. Phialides 6.5–8 × 2.5–3 µm. Conidia (11.2–)13.5–15 × 3.5–4 µm, l/w 3.5–3.8. No paraphyses observed.

Habitat: On scale insects and whiteflies generally on the abaxial surface of leaves of various plants.

Known distribution: Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Panama, Peru, Venezuela; probably widespread in the Neotropics.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail Tapacare, on insect on *Musa* sp. leaf, 10 Jun. 2004, P.

Chaverri (*P.C. 554, P.C. 555*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067784; CUP 067785). **Brazil**, On leaves of *Lauraceae*, Aug. 1895, Edwalli (holotype of *H. edwallii*, S-F10585); Itaimbezinho, on leaf, 22 May 1994, H.C. Evans (*I94-927*) (CUP 067786); Rio de Janeiro, Tijuca National Park, on leaf, 15 Jun. 1989, H.C. Evans (**neotype** of *M. sulphurea P.C. 756* = CUP 067787). **Colombia**, Choco, North of Rio Jobi-Coqui, forest, on leaf, 29–31 May 1993, H.C. Evans (*I93-856* = CUP 067788; *P.C. 753* = CUP 067789). **Ecuador**, Manabi. Y de la Laguna, Reserva Bilsa, primary forest, 00°24'N, 79° 49'E, elev. 500–600 m, 2 May 2004, on insect on leaf, G.J. Samuels (*GS 9513, GS 9508, GS 9516*), H.C. Evans, M.C. Aime (*P.C. 628* = CUP 067790; CUP 067791; CUP 067792). **French Guiana**, Cayenne, on insect on leaf, Mar. 1839, Leprieur *580* (**lectotype** of *H. phyllogena* PC!) **Panama**, Fortuna, on leaf of *Costa*, 14 Jul. 2002, J. F. Bischoff (*J.B. 130 = P.C. 738*) (CUP 067793). **Venezuela**, Bolivar, Canaima, on leaf, 23 Jan. 1994, H.C. Evans (*I94-909*) (CUP 067794).

Notes: *Moelleriella phyllogena* is similar to *M. basicystis*, *M. umbospora*, and *M. disjuncta*. The differences are in the size and shape of the part-spores and conidia, and the geographical distribution. The type of *"A." juruensis* was deposited in herbarium B and was lost in WW II. According to Petch (1921), the type of *A. juruensis* contained only one stroma that was poorly developed and in bad condition. The type of *A. lauricola* in LPS does not include any stromata. However, based on a drawing on the envelope and the original description of the species, this species appears to be a synonym of *M. phyllogena*. The types of *H. weberbauri* and *M. sulphurea* in herbarium B were also lost in WWII. According to Petch's (1921) measurements of these specimens, they seem to be synonyms of *M. phyllogena*. *Moelleriella sulphurea* is neotypified herein with a specimen from Brazil. Cultures did not survive storage at 8 °C. *Moelleriella phyllogena* belongs in the Effuse clade.

18. *Moelleriella rhombispora* (M. Liu & K.T. Hodge) M. Liu & Chaverri, comb. nov. MycoBank MB511378. Fig. 12L–O.

≡ *Hypocrella rhombispora* M. Liu & K.T. Hodge, Mycol. Res. 110: 551. 2006.

Anamorph: aschersonia-like.

Stromata pale yellow to pale orange, pulvinate and slightly tuberculate, 2–2.5 mm diam, slightly constricted at base, sometimes surrounded by hypothallus. Stromatal tissue dense *textura intricata*. If present, hypothallus narrow, 0.6 mm wide, and minutely tomentose. Perithecia densely arranged in stroma, embedded, ostioles not projecting, brownish yellow; 300–450 × 210–300 µm. Asci cylindrical, 148–296 × 6–14 µm, caps 5–8 µm thick. Ascospores initially filiform, dividing into part-spores. Part spores fusoid, acute at both ends, 10–14 × 2–3 µm, or others cylindrical with blunt ends, usually swollen at midpoint, 7–12 × 1.5–2.5 µm.

Anamorphic stromata white, thin pulvinate, hemi-globose or scutate with a hemispheric central region abruptly attenuating and towards edge, 1–3 mm diam; surface minutely pruinose. Hypothallus, if present, 0.2–0.8 mm wide. Conidiomata >4, arranged concentrically, scattered, or forming a reticulum on conical part of stroma. Conidial masses pale yellow, not confluent. Conidiomata U-shaped or convolute in section, hymenium lining inner surface of conidioma. Phialides flask-shaped, slender, tapering near truncate apices, 8–12 × 1.5–2 µm. Conidia 9–14 × 2.5–3 µm, inflated at midpoint and tapering at both ends, l/w *ca.* 3.5–4.5. Paraphyses absent.

Colonies on PDA at 25 °C slow-growing, thick pulvinate, moderately compact, firm and leathery, greyish white to yellowish white, surface minutely tomentose, smooth to radially wrinkled, covered with deep yellow conidial masses. No discrete conidiomata formed, conidial masses directly produced from surface of colony. Phialides 8–12(–15) × 2–2.5 µm. Conidia markedly inflated at the midpoint and tapering at both ends, 8.5–12(–17) × 2–3 µm, l/w *ca.* 4–4.5. No paraphyses observed.

Habitat: On scale insects or whiteflies on leaves of *Cyclanthus, Guarea*, and unidentified.

Distribution: Costa Rica, Guatemala, Honduras, Mexico, and Puerto Rico.

Specimens examined: **Costa Rica,** Heredia, La Selva Biological Station, Camino Cantarrana, on *Cyclanthus bipartitus*, 19 Jun. 2002, M. Liu (CR 07) (CUP 67296 = culture ARSEF 7511); 5 Jan. 2004, P. Chaverri, (*P.C. 466, P.C. 467*) (CUP 067537, CUP 067538); beside entrance to Plantation RCC, 20 Jun. 2002, M. Liu (*ML44-3*), (culture CR32 = CUP 067346); Puntarenas, Las Cruces Biological Reserve, Wilson Botanical Garden, large loop of jungle trail, on *Guarea rhopalocaipa*, 4 Jul. 2002, M. Liu (*ML64*) (culture CR34 = CUP 67369). **Guatemala**, Tikal National Park, on leaf, 26 Jun. 2004, M.G. Milgroom (CUP 067494). **Honduras**, Yojoa, Los Pinos, Parque Nacional Cerro Azul-Meambar, 850 m elev., 3 Sep. 2004, *P. Chaverri* (*P.C. 691, P.C. 693, P.C. 696, P.C. 698*), *P.A. Sheikh*, (**holotype** CUP 067548; CUP 067549, CUP 067550; CUP 067551); Copan, Santa Rita, Reserva Peña Quemada, 9 Sep. 2004, P. Chaverri (*P.C. 675*), P. A. Sheikh (CUP 067547). **Mexico**, Veracruz, Amayaga, Catemaco, 500 m elev., 14 Dec. 2003, P. Chaverri (*P.C. 458, P.C. 460*), J. García-Alvarado (CUP 067795, CUP 067534). **Puerto Rico**, between Mayaguez and Maricao, beside road 105, 15 Dec. 2003, M. Liu & Z.D. Wang, ML164 (CUP-PR 4406; ex-type culture ML164 = ARSEF 7390); Guajataca Forest, trail no. 9, on fern, 18 Dec. 2003, M. Liu (ML201-1, ML201-3, ML201-5a), Z.D. Wang (CUP-PR 4437 = ARSEF 7395, ARSEF 7399, ARSEF 7400).

Notes: The most distinctive characters of this species are the shape of the part-spores and conidia, both of which are distinctly inflated in the middle. These characters are shared by *M. phyllogena, M. basicystis*, and *M. umbospora*. *Moelleriella rhombispora* belongs in the Effuse clade.

Additional illustrations: figs 4J–L, 8A–M, in Liu *et al.* (2006).

19. *Moelleriella sloaneae* (Pat.) Chaverri & K.T. Hodge, comb. nov. MycoBank MB511379. Fig. 13A–I.

≡ *Hypocrella sloaneae* Pat., Enum. Champ. Guadeloupe, p. 80. 1903.
= *Hypocrella amazonica* Henn., Hedwigia 43: 246. 1904.

Anamorph: aschersonia-like

Stromata containing teleomorph, (1.5–)1.7–2(–2.2) mm diam, whitish, greyish yellow, pale orange, thin-pulvinate to pulvinate with wide base, composed of few to numerous gregarious tubercles arising from a pulvinate to hemispherical base; when present, conidiomata scattered throughout; surface of tubercles and base pruinose due to loosely woven, thick-walled hyphae that form stroma. Tubercles projecting and aggregated, hemispherical, cylindrical or slightly narrowing apically; ostioles brownish yellow to brownish orange. Perithecia embedded in stroma, one perithecium per tubercle, perithecia nearly flask-shaped to ovoid, 400–500 × 250–300 µm. Asci cylindrical, (163–)175–240(–248) × 7.2–9.7(–10.5) µm, caps thick, (3.3–)4.7–5.5(–6.3) µm. Ascospores filiform, disarticulating into cylindrical part-spores, with somewhat rounded ends, (9–)13.5–15(–18.3) × (2–)2.8–3(–4) µm.

Teleomorph and anamorph sometimes in same stromata. Exclusively anamorphic stromata when young, effuse, thin, whitish, tomentose, with irregular and shallow conidiomata that may be somewhat circular or irregular and confluent, sometimes forming sterile cylindrical finger-like projections. Conidiomata when mature generally scattered, 2 to numerous per stroma, appearing as simple shallow depressions of stromatic surface without a differentiated

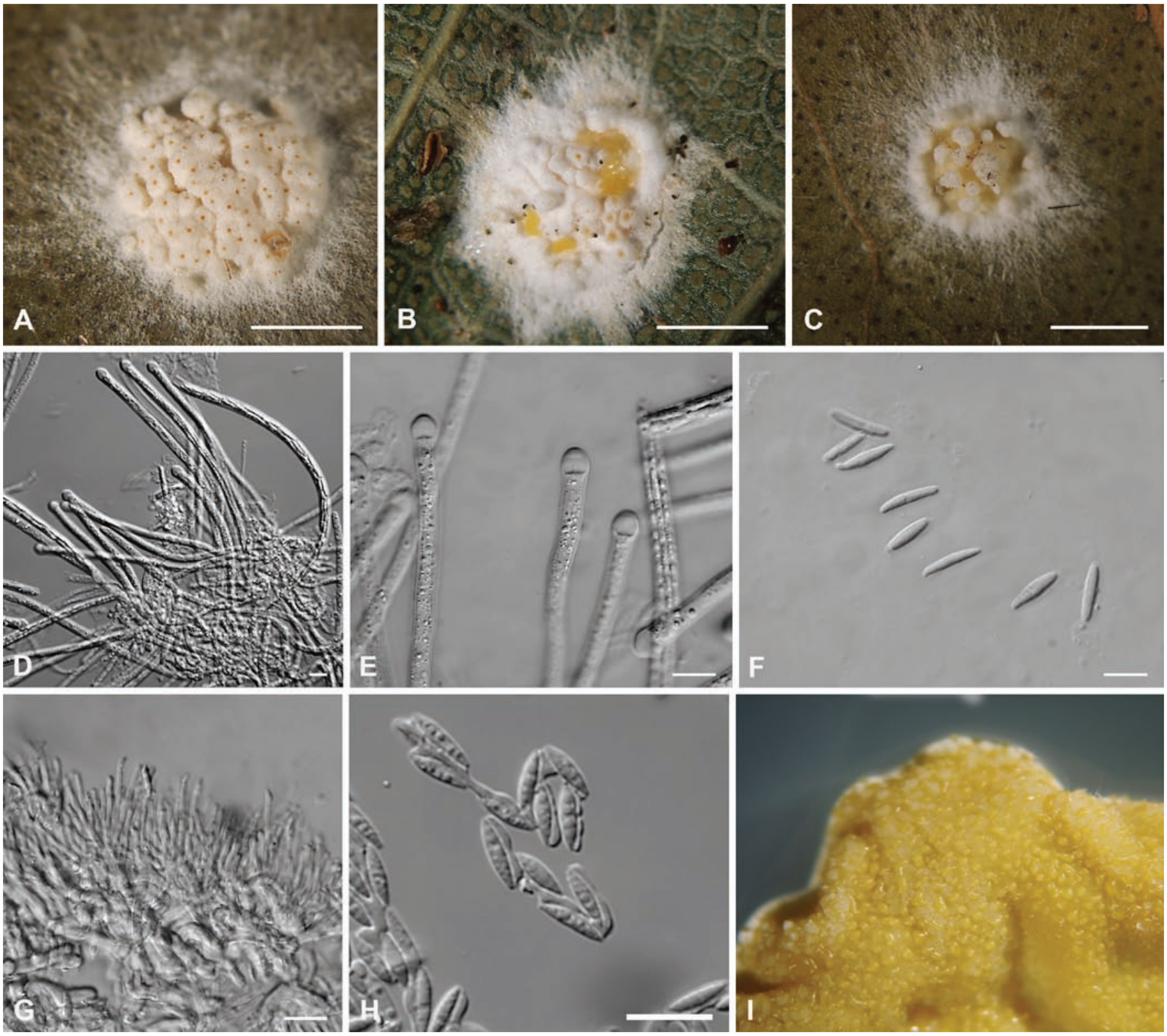

Fig. 13. A–I. *Moelleriella sloaneae*. A–C. Stromata. A. Stroma containing only perithecia. B. Stroma containing perithecia and conidiomata. C. Stroma containing only conidiomata. D–E. Asci. F. Part-ascospores. G. Palisade of phialides. H. Conidia (note that some conidia are still covered with mucilage). I. Colony on PDA at 25 °C after 3 wk. A–E: CUP 067802; F–G: CUP 067796; H–I: CUP 067804. Bars: A–C = 1 mm; D–H = 10 µm.

rim, conidial masses brownish yellow or yellow. Phialides flask-shaped to cylindrical, (5.2–)11.2–14.5(–19.7) × (1.3–)1.7–2(–2.5) µm. Conidia fusiform, unicellular, hyaline, ends acute, (6.3–)8.2–10(–14.7) × (1.8–)2–2.3(–2.8) µm, l/w (3–)3.5–4(–4.5). Paraphyses abundant in the hymenium.

Colonies on PDA at 25 °C, with moderate-growth, compact, elevated, strongly attached to agar, wrinkled, greyish yellow; conidiomata abundant, scattered. Conidial masses yellow, abundant, confluent. Phialides (7.5–)12.3–14.5(–18.2) × (1.3–)1.7–2 µm. Conidia fusiform, (6.5–)7.8–8.3(–9.7) × (1.8–)2–2.2(–2.5) µm, l/w (3–)3.7–4(–4.5). No paraphyses seen in culture.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Belize, Bolivia, Brazil, Ecuador, Guadeloupe, Guatemala, Guyana, Honduras, Peru, Venezuela; probably widespread in the Neotropics.

Specimens examined: **Belize**, Cayo, Rio Frio, on leaf, 26 Apr. 1994, H.C. Evans (*I94-922*) (CUP 067796 = culture ARSEF 7669). **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, Almendrillo Trail, on leaf, 11 Jun. 2004, P. Chaverri (*P.C. 577, P.C. 590, P.C. 592*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067797, CUP 067798, CUP 067799). **Brazil**, Amazonas, Manaus, Ducke Forest Reserve, on leaf, 3 Oct. 1992, H.C. Evans (*I92-784*) (CUP 067800). **Ecuador**, Cuyabeno, Puerto Bolivar, on leaf, 23 Jul. 1993, H.C. Evans (*P.C. 747* = CUP 067801). **Guadeloupe**, Bois des Bains-Jaunes, on leaves of *Sloanea* sp., Feb. 1903 (**type** of *H. sloaneae* FH 6774!). **Guatemala**, Tikal, on leaf, 27 Apr. 1994, H.C. Evans (*I94-920*) (CUP 067802 = culture ARSEF 7667). **Guyana**, Esequibo River, on leaf, 26 Feb. 1993, H.C. Evans (*I93-805*) (CUP 067803 = culture ARSEF 7680). **Honduras**, Dpto. Copan, Copan Ruinas, Natural trail, elev. 700 m, on leaf, 31 Aug. 2004, P. Chaverri (*P.C. 658, P.C. 665*), P.A. Sheikh (CUP 067804, CUP 067805). **Peru**, Iquitos, on leaves of *Sterculiaceae*, Jul. 1902, E. Ule *3198* (type of *H. amazonica* Henn., FH!). **Venezuela**, Isla Margarita, on leaf, 16 Jan. 1994, H.C. Evans (*I94-911*) (CUP 067806).

Notes: Although *M. sloaneae* resembles species in the Effuse clade, phylogenetic analyses place *M. sloaneae* closer to the Globose clade.

20. ***Moelleriella turbinata*** (Petch) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511380. Fig. 14A–N.

≡ *Hypocrella turbinata* Petch, Ann. Roy. Bot. Gard. Peradeniya 5: 535. 1914.

Anamorph: *"Aschersonia" turbinata* Berk., Ann. Nat. Hist. 9: 192. 1852.

= *Aschersonia pittieri* Henn., Hedwigia 41: 104. 1902.

Teleomorph rarely found without anamorph. Conidiomata generally on top of stroma, resembling pezizoid projections, and perithecia below conidiomata and towards base. Stromata 1–2.5(–5) mm diam, subcylindrical, sometimes with 2–3 finger-like projections in strictly anamorphic stromata, pale orange, greyish yellow, when young pulvinate with wide base, whitish to cream-coloured, surface smooth, opaque, slightly pruinose in younger specimens, almost black in some very old specimens, without hypothallus. Hyphae of stromata forming compact *textura epidermoidea*. Perithecia completely embedded in stroma, slightly tuberculate, ostioles brownish orange or brownish yellow, numerous perithecia per stroma (>20), perithecia flask-shaped to obpyriform, (264–)270–320 × 116–127(–130) µm. Asci cylindrical, 210–275 × 8–14 µm, caps thick (2.8–)3.2–4.5 µm. Ascospores filiform, multi-septate, disarticulating into part-spores that are fusoid with rounded ends, (13–)14.5–16(–21) × (2.8–)3.3–3.5(–4.2) µm.

Anamorphic stromata more common. Conidiomata pezizoid, few conidiomata per stroma (1–3). Conidial masses pale greyish yellow, orange yellow, deep orange, or brownish orange. In section, conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; conidiophores in compact palisade, phialides short flask-shaped, (9–)10.7–16.5(–18) × (2.7–)3–5(–6.3) µm. Conidia hyaline, unicellular, ovoid, with acute ends, (8–)10.5–11.2(–13.5) × (3.8–)4.5–5(–6.2) µm, l/w (2–)2.3–2.5(–2.8), produced in copious slime. No paraphyses observed.

Colonies on PDA at 25 °C fast-growing. Stromatic colonies, greyish yellow, with few tinges of green, compact but spreading, surface minutely velvety, wrinkled. Conidiomata scattered. Conidial masses abundant, orange, not confluent. Phialides in a compact palisade. Phialides (5.7–)8.5–10(–11.5) × (2.5–)2.7–3(–3.7) µm. Conidia (8.3–)10–10.5(–12.5) × (3–)3.8–4(–5) µm, l/w (2–)2.5–2.7(–3.5). No paraphyses observed. A hirsutella-like anamorph seen in one culture (M.C.A. 2432 = CUP 067860). Phialides of synanamorph flask-shaped, (17.5–)26.5–46.7(–48) × (3.3–)3.5–4 µm, with a long thin neck (10–)15.5–27.5(–27.5) µm long.

Habitat: On scale insects and whiteflies on twigs and abaxial and adaxial surfaces of leaves of various plants, including *Citrus*.

Known distribution: Widespread throughout the Neotropics.

Specimens examined: **Grenada**, Grand Etang, on leaves, 1912–13, R. Thaxter (**lectotype** of *H. turbinata* FH 4272!). **Colombia**, Choco, Rio Jobi-Coqui, on leaf, 29 May 1993, H.C. Evans (*I93-858*) (CUP 067807). **Costa Rica**, Cocos Island, Wasser Bay, on *Lecanium hesperidum*? on leaves of *Citrus aurantium*, Jan. 1902, Pittier (isotypes of *A. pittieri* S-F22557! and FH 4003!). **Guyana**, Pakaraima Mountains, Upper Potaro River, Jan. 2004, M.C. Aime (*M.C.A. 2432*) (CUP 067860). **Honduras**, Dpto. Atlántida, Tela, Pico Bonito National Park, loop trail, on leaf, 26 Aug. 2004, P. Chaverri (*P.C. 639*), P.A. Sheikh (CUP 067808); Dpto. Copan, Santa Rita, Rio Amarillo, Peña Quemada Reserve, elev. 800 m, on leaf, 9 Sep. 2004, P. Chaverri (*P.C. 677, P.C. 678*), P.A. Sheikh (CUP 067809, CUP 067863). **Mexico**, Estado Veracruz, Xalapa, on Citrus leaves, 22 Feb. 91, H.C. Evans (*I91-598*) (IMI 352838 = culture ARSEF 7675). **Nicaragua**, on leaves, C. Wright *5479* (**isotype** of *A. turbinata* K(M) 120254!); Matagalpa, Selva Negra, 1600 m elev., on leaf, 24 May 1992, H. C. Evans (*P.C. 757* = CUP 067810). **Peru**, San Martin, Tarapoto, Rio Shilcayo, on leaf, 28 Aug. 2002, H.C. Evans (*P.C. 758* = CUP 067811).

Notes: *Moelleriella turbinata* belongs in the Globose clade.

21. ***Moelleriella umbospora*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511381. Fig. 14O–U.

Anamorph: aschersonia-like.

Teleomorphosis: Stromatibus globosis, (0.5–)1–1.5(–2.5) mm diam, flavidus; ascosporae multicellulares, ad septum disarticulatae, incolora, partis subcylindrici vel fusiformes, ventricosus ad medium, (21.5–)24.5–26.2(–30.1) × (4–)4.5–5(–5.5) µm. Anamorphosis: *Aschersonia* similis. Stromatibus lutescentia vel albidus, pulvinata vel subglobosis. Phialide 8.5–10 × 2–2.5 µm; conidii ventricosus, (16.5–)20.2–22(–25.5) × (4.5–)5.3–6(–7.7) µm, longitudo/crassitudo (3–)3.7–4(–4.5); paraphysis absens. Holotypus: CUP 067817.

Teleomorphic stromata with globose head and markedly constricted base (stud-shaped), whitish when immature becoming pale yellow when mature, (0.5–)1–1.5(–2.5) mm diam, surface smooth to slightly pruinose, opaque, with hypothallus (0.1–)0.5–0.7(–1) mm. Hyphae of stromata forming compact *textura intricata* to *epidermoidea*. Perithecia completely embedded and on top part of stroma, numerous perithecia per stroma (>30), ostioles yellowish orange; perithecia flask-shaped, 375–500 ×200–280 µm. Asci cylindrical, (274–)300–330(–340) × (21.2–)25–30(–31.5) µm, caps 3–4 µm thick. Ascospores filiform, multiseptate, disarticulating into part-spores that are cylindrical or curved with rounded ends and strongly inflated in the middle, (21.5–)24.5–26.2(–30.1) × (4–)4.5–5(–5.5) µm.

Teleomorph and anamorph may or may not be present in same stromata. The anamorphic conidiomata on natural substrate only on constricted part of stroma when teleomorph present. Exclusively anamorphic stromata pulvinate with sloping sides (convex), whitish to pale yellow, conidiomata simple depressions of surface without distinct rims, numerous conidiomata per stroma (>20), but difficult to count due to fusion with neighboring ones, widely open. Conidial masses yellow, yellowish orange, or dark pale yellow. In section, the conidioma U-shaped, shallow. Conidioma with hymenium lining inner surface; phialides flask-shaped, generally straight, sometimes curved, 8.5–10 × 2–2.5 µm. Conidia hyaline, unicellular, ventricose almost rhomboid, with acute ends, (11–)13–13.5(–15.5) × (3–)4–4.2(–5) µm, l/w (2.5–)3–3.3(–4.2), produced in copious slime. No paraphyses observed.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Honduras, Mexico.

Specimens examined: **Honduras,** Yojoa, Los Naranjos Eco-Archeological Park, elev. 750 m, on leaf, 2 Sep. 2004, P. Chaverri (*P.C. 684*), P.A. Sheikh (CUP 067812); Yuscaran, Biological Station, elev. 1780 m, on leaf, 4 Sep. 2004, P. Chaverri (*P.C. 703*), P.A. Sheikh, P. Arneson (CUP 067813). **Mexico**, Chiapas, Palenque, on leaf, 24 Apr. 1994, H.C. Evans (*I94-923*) (CUP 067814); Cozumel, Coba, on leaf, 30 Apr. 1994, H.C. Evans (*I94-918*) (CUP 067815); Veracruz, Catemaco, Amayaga, on leaf, 14 Dec. 2003, P. Chaverri (*P.C. 457, P.C. 461*), J. Garcia-Alvarado, A. Ibars-Vera (CUP 067816; **holotype** CUP 067817).

Notes: *Moelleriella umbospora* can be distinguished from the similar species *M. basicystis, M. phyllogena*, and *M. disjuncta* by the significantly larger part-ascospores and conidia of *M. umbospora*. In addition, *M. umbospora* part-spores have a pronounced swelling in the middle, and almost rhomboid conidia. Cultures did not survive storage at 8 °C. *Moelleriella umbospora* belongs in the Effuse clade.

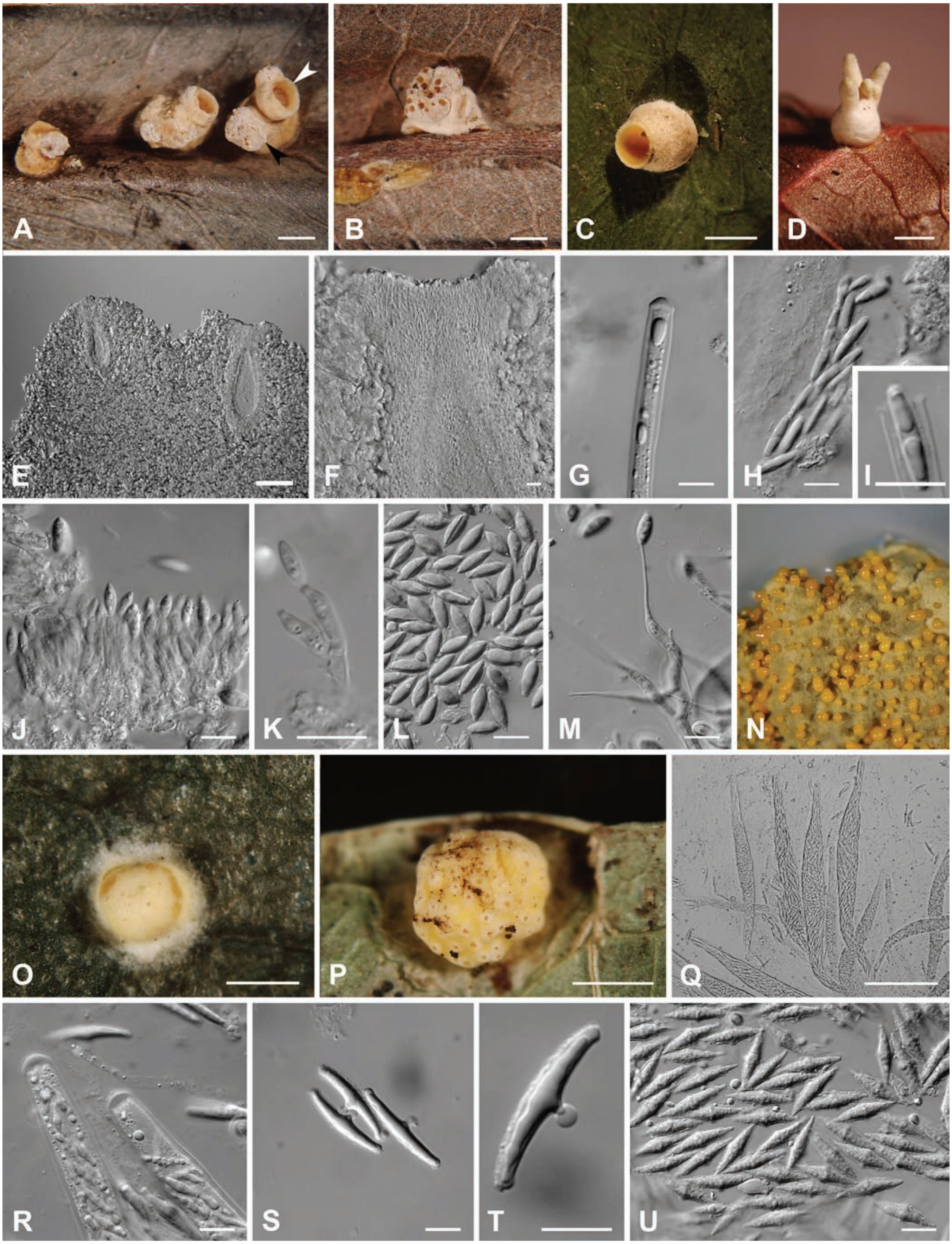

Fig. 14. A–N. *Moelleriella turbinata.* A–D. Stromata. A. Stromata containing perithecia (black arrow) and conidiomata (white arrow). B. Stroma containing perithecia. C–D. Stromata containing conidiomata. E–F. Section of stroma showing perithecia. G. Ascus. H–I. Part-ascospores. J. Palisade of conidiophores and phialides. K. Phialides. L. Conidia. M. Synanamorph formed in PDA at 25 °C. N. Colony on PDA at 25 °C after *ca.* 3 wk. **O–U. *Moelleriella umbospora.*** O–P. Stromata. O. Stroma containing conidiomata. P. Stroma containing perithecia. Q–R. Asci. S–T. Part-ascospores. U. Conidia. A–B: FH 4272 (lectotype of *M. turbinata*); C: CUP 067863; D, J–N: CUP 067860; E–I: P.C. 361; O–T: CUP 067817 (holotype of *M. umbospora*); U: CUP 067816. Bars: A–D, O–P = 1 mm; E, Q = 100 µm; F–M, R–U = 10 µm.

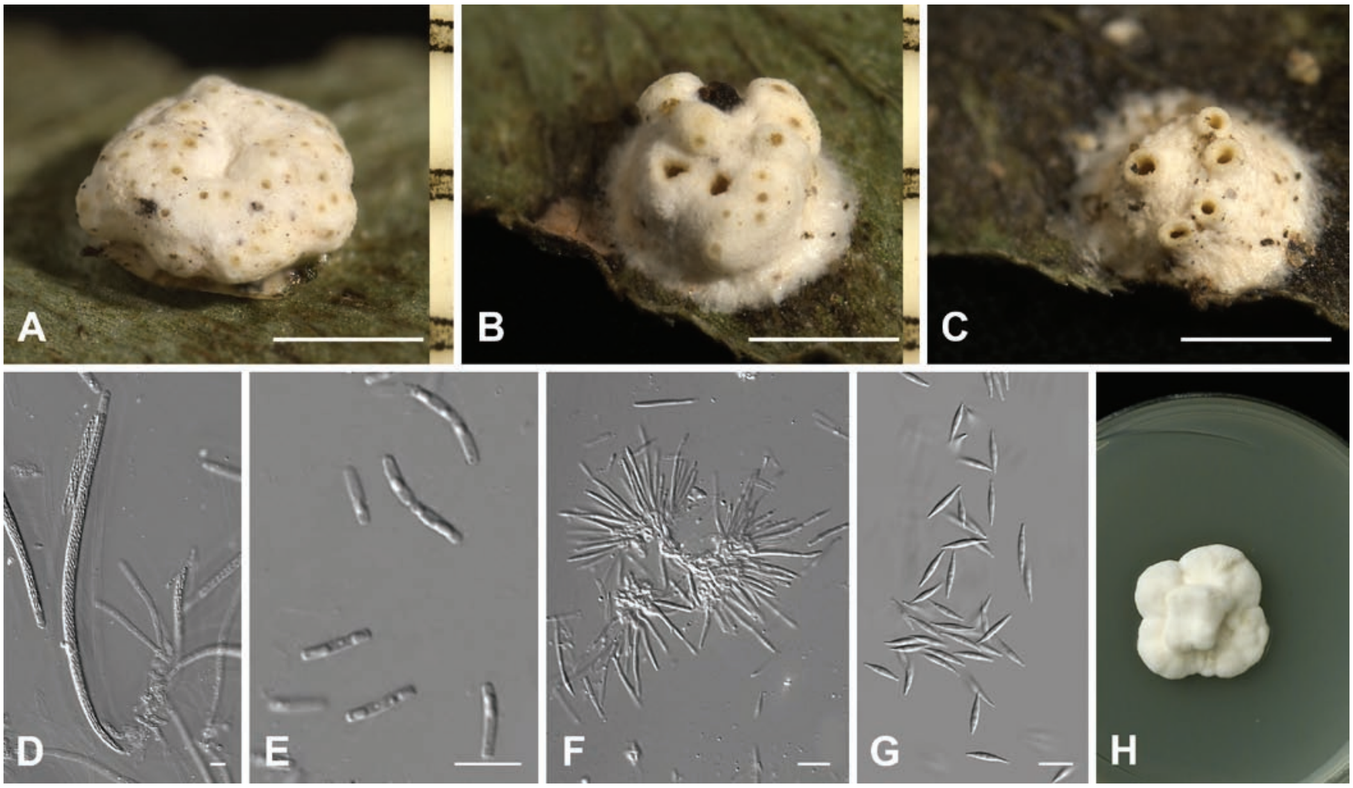

Fig. 15. A–H. ***Moelleriella zhongdongii.*** A–C. Stromata. A. Stroma containing perithecia. B. Stroma containing perithecia and conidiomata. C. Stroma containing conidiomata. D. Ascus. E. Part-ascospores. F. Phialides. G. Conidia. H. Colony on PDA at 25 °C after *ca.* 3 wk. A–H: CUP-PR 4394 (holotype of *M. zhongdongii*). Bars: A–C = 1 mm; D–G = 10 µm.

22. *Moelleriella zhongdongii* (M. Liu & K.T. Hodge) M. Liu & Chaverri, **comb. nov.** MycoBank MB511382. Fig. 15A–H.

≡ *Hypocrella zhongdongii* M. Liu & K.T. Hodge, Mycol. Res. 109: 820. 2005.

Anamorph: *"Aschersonia" incrassata* Mains, J. Insect Pathol. 1: 46. 1959.

Stromata on leaf surfaces, circular in outline, white to yellowish white, thick pulvinate, somewhat constricted at base, 1–2 mm diam Surface slightly tuberculate and minutely tomentose to pruinose. In some specimens stroma surrounded by narrow hypothallus, *ca.* 0.5 mm wide. Perithecia flask-shaped, embedded in slightly bulging tubercles, 350–450 × 125–200 µm. Ostioles pale yellow when fresh, turning yellow brown when dried, not projecting, scattered, 1–40 ostioles per stroma. Asci cylindrical, to 300 × 6–10 µm, caps 4–5 µm thick. Ascospores filiform, part-spores cylindrical to oblong, ends obtuse or truncate 5–10 × 1–2 µm.

Anamorphic conidiomata sometimes present in same stroma as teleomorph. When two stages present in same stroma, conidiomata occur in various positions in stroma; often 1–2 conidiomata present. When teleomorph absent, anamorphic stroma pulvinate, slightly smaller than teleomorphic stromata, white. Conidiomata 1–4 per stroma, usually as simple depressions of surface, cupulate and widely open, sometimes with raised edges. Conidia produced in pale yellow to yellow masses, never confluent. Phialides short or long; short phialides most abundant, 10–20 × 1–1.5 µm, slender, cylindrical; long phialides 40–70 × 1–1.5 µm; long conidiogenous cells at first resemble paraphyses, but careful observation reveals they bear conidia. Conidia fusoid, 10–18 × 1.5–2 µm, l/w *ca.* 7.5. Paraphyses sometimes present.

Stromatic colonies on PDA at 25 °C slow growing, compact, surface minutely tomentose, hyphae congregating sometimes to form numerous tubercle-like tufts. Conidia produced in scanty, pale yellow to yellow masses. Conidia 10–14 × 1.5–2 µm. Colonies liable to die after 2–3 transfers. Paraphyses not observed.

Habitat: On scale insects or whiteflies on leaves of *Synechanthus, Piper, Annonaceae, Doliocarpus,* and unidentified.

Known distribution: Bolivia, Costa Rica, Puerto Rico.

Specimens examined: **Bolivia**, Yungas, on leaf, 3 May 1995, H.C. Evans (*I95-954*) (CUP 067871 = ARSEF 7670); Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, on leaves, 10–13 Jun. 2004, P. Chaverri (*P.C. 549, P.C. 557, P.C. 561, P.C. 581, P.C. 591, P.C. 595*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067818, CUP 067819, CUP 067820, CUP 067821, CUP 067822, CUP 067823). **Costa Rica**, Heredia, La Selva Biological Station, Sendero Cantarrana, on leaves of *Synechanthus warscewiczianus*, 19 Jun. 2002, M. Liu (*ML-25-3*) (CUP 067313); Camino Cantarrana, on leaves of *Piper multiplinervium*, 19 Jun. 2002, M. Liu (*ML-27-1*) (CUP 067316); Sendero Holdridge abandoned plantation, on leaves of *Annonaceae*, 18 Jun. 2002, M. Liu (*ML-6-1*) (CUP 067288); Sendero Oriental, 400 m, on leaves of *Piper holdridgeianum*, 20 Jun. 2002, M. Liu (*ML-32-2*) (CUP 067322); Camino Circular Lejano, on Aleyrodidae larvae on leaves of *Doliocarpus dentatus*, 21 Jun. 2002, M. Liu (*ML-46*) (CUP 067350); Lindero El Peje, on leaf, 8 Jan. 2004, P. Chaverri (*P.C. 504*) (CUP 067544). **Puerto Rico**, Adjuntas, on whitefly on a fern, 13 Mar. 1915, Britton, Cowell & Brown 5250 (**holotype** of *A. incrassata* MICH); El Yunque: Caribbean National Forest, western side of the mountain, on larva of Homoptera on ferns, 5 Jul. 2002, K.T. Hodge (PR-8) (CUP-PR 4314); 12 Dec. 2003, M. Liu (*ML149*) (**holotype** of *M. zhongdongii* CUP-PR 4394 = ARSEF 7369).

Notes: *Moelleriella zhongdongii* belongs in the Effuse clade.

Additional illustrations: figs 2–15 in Liu & Hodge (2005).

HYPOCRELLA Sacc., Michelia 1: 322. 1878.

Anamorph: *Aschersonia* Mont. (type *Aschersonia tahitensis* Mont.)

Type species: *Hypocrella discoidea* (Berk. & Broome) Sacc. (basionym *Hypocrea discoidea* Bark. & Broome, J. Linn. Soc. 14: 113. 1873.

Stromata generally pulvinate, with or without hypothallus, (0.5–) 1–2(–3) mm diam; in various shades of whitish, yellow, orange, and green; stroma surface generally minutely pulverulent or pruinose; stromatic tissue generally changing colour in 3 % KOH, to reddish or brown; perithecia generally embedded in stroma or half-embedded; stroma outer tissue of *textura epidermoidea*, cell walls *ca.* (0.5–)1–2.5(–3) µm thick; stroma internal tissue generally of *textura intricata*, cell walls generally thin, (0.5–)1–2(–3.5) µm. Perithecia, obpyriform to subglobose, 250–350 × 110–200 µm. Asci mostly cylindrical or clavate, 110–180(–250) × 8–12(–20) µm, generally capitate. Ascospores hyaline, multiseptate, smooth, filiform to long fusiform, non-disarticulating, (50–)75–120(–170) × (1–)2–5(–7) µm.

Conidiomata from original substrata pycnidial generally flask-shaped; phialides formed in a thick compact palisade, in short conidiophores sometimes indistinct, branching once monochasial, twice monochasial, monoverticillate, or two level monochasial; phialides cylindrical, slightly tapering towards tip, (9–)12–20(–23) × 2–2.5 µm; conidial masses mucilaginous; conidia hyaline, smooth, unicellular, fusoid, generally with acute ends, (10–)12–25(–30) × (1.5–)2–5(–6) µm, l/w ratio 5–6(–7). Paraphyses generally present.

Habitat: Parasitic on scale insects (Lecaniidae and Coccidae, Homoptera) and whiteflies (Aleyrodidae, Homoptera).

Known distribution: Pantropical.

Notes: *Hypocrella* can be distinguished from *Moelleriella* by the non-disarticulating ascospores in *Hypocrella*. *Hypocrella* can be distinguished from *Samuelsia* by the smaller and allantoid conidia in *Samuelsia*; *Hypocrella* has fusiform conidia with acute ends. The genus *Stereocrea* Syd. & P. Syd. resembles *Hypocrella*. Illustrations and descriptions of the type species, *S. schizostachyi*, in Rossman *et al.* (1999) reveal that the ascospores of *Stereocrea s. str.* are clavate, yellowish green, multiseptate, and slightly constricted at each septum.

Aschersonia tahitensis Mont. is the type of *Aschersonia*. Although we did not examine the type specimen, observations made by Petch (1921) suggest that *A. tahitensis* is close to *H. discoidea*. In addition, Petch states that *A. tahitensis* becomes reddish in "potash"; a characteristic that is only present in *Hypocrella* and *Samuelsia*. Therefore, we conclude that *Aschersonia* is the anamorph of *Hypocrella s. str*.

1. ***Hypocrella aurantiaca*** (Petch) Mains, Mycopathol. & Mycol. Appl. 11: 318. 1959. Fig. 16A–F.

≡ *Stereocrea aurantiaca* Petch, Trans. Br. Mycol. Soc. 23: 135. 1939.

Anamorph: *Aschersonia aurantiaca* Petch, Trans. Br. Mycol. Soc. 23: 135. 1939.

Stromata pulvinate, slightly tuberculate, without hypothallus, 1–2 mm diam; orange, scattered; stroma surface scurfy somewhat glossy; KOH+, perithecia embedded in stroma; stroma outer tissue of *textura epidermoidea*; stroma internal tissue of *textura intricata*. Perithecia, obpyriform to subglobose, 300–350 × 160–200 µm. Asci mostly clavate, 145–180(–250) × (8–)15–20 µm, with a thick ascus cap 3.5–4 µm. Ascospores hyaline, multiseptate, smooth, long fusiform, 120–180 × 4–5 µm.

Teleomorph generally present with anamorph in same stroma. Conidiomata generally circularly arranged towards centre of stroma, and perithecia near periphery of tstroma. Conidiomata pycnidial, generally subglobose, *ca.* 410 × 400, with phialides formed in thick compact palisade. Phialides cylindrical, slightly tapering towards tip, 11–13(–15) × 2–2.5 µm. Conidia hyaline, smooth, unicellular, fusoid, with acute ends, (23.5–)27–30(–32) × (4.5–)5.3–6(–7) µm, l/w (3.8–)4.5–5.7(–6.8). Paraphyses present.

Habitat: On whiteflies on leaves of palms and *Tamala*.

Known distribution: Mexico, U.S.A. (Florida).

Specimens examined: **Mexico,** Veracruz, Catemaco, town of Ejido Lopez-Mateo, project "Cielo, Tierra y Selva", trail to the mountain, elev. 200–300 m, on leaf of palm, 13 Dec. 2003, P. Chaverri (*P.C. 435*), J. Garcia-Alvarado, C. Mena-Jiles (CUP 067824). **U.S.A.**, Florida, Gainesville, Sugarfoot, on whitefly *Paraleyrodes perseae* on *Tamala bortonia*, 7 Oct. 1936, E. West, R.K. Voorhus (no. 11876) (**type** K(M) 120355!).

Notes: Petch originally placed this species in *Stereocrea* for its fusoid asci and ascospores. The conidia of the anamorph are unusually large (28–33 x 4–5 µm), and the anamorph and teleomorph may occur on the same stroma (Petch 1939).

Rossman *et al.* (1999) provided a description of the type, and noted that the spores reported by Mains (1959) as belonging to the anamorph are in fact fusoid part spores that have not formed septa. Hywel-Jones and Evans (1993) considered this species closely related to *H. discoidea*.

Additional illustrations: Plate 54: figs d–j, in Rossman *et al.* (1999).

2. ***Hypocrella citrina*** Speg., Bol. Acad. Nac. Cien. Córdoba 11: 534. 1889. Fig 16G–P.

Anamorph: *Aschersonia blumenaviensis* Henn., Hedwigia 41: 27. 1902.

= *Aschersonia flavocitrina* Henn., Hedwigia 41: 307. 1902.
= *Aschersonia abnormis* Henn., Hedwigia 43: 93. 1904.

Stromata strictly teleomorphic, pulvinate, yellow, pale yellow, greyish yellow, greyish orange, or yellowish white, sometimes with a hypothallus (<1 mm), (0.8–)1.2–2(–3) mm diam, stroma surface smooth to slightly pruinose somewhat glossy; KOH-, tuberculate, each tubercle containing one perithecium; stroma outer tissue of *textura epidermoidea*; stroma internal tissue of *textura intricata*. Perithecia embedded in stroma, sometimes protruding from stroma surface. Perithecia, subglobose, *ca.* 300 × 300 µm. Asci mostly clavate, 118–250(–300) × 8.7–12.7 µm, caps (0.8–)1.5–3 µm. Ascospores hyaline, multiseptate, smooth, long fusiform, (55–) 110–115(–130) × (1–)2–3.5 µm.

Teleomorph sometimes present with anamorph in the same stroma. When anamorph present, stromata pulvinate generally with a flattened top, discoid, conidiomata circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidiomata pycnidial, subglobose, (380–)400–450 × 400–450(–470) µm, with phialides formed in a thick compact palisade. Phialides cylindrical, slightly tapering towards tip, (11–)13.8–17(–

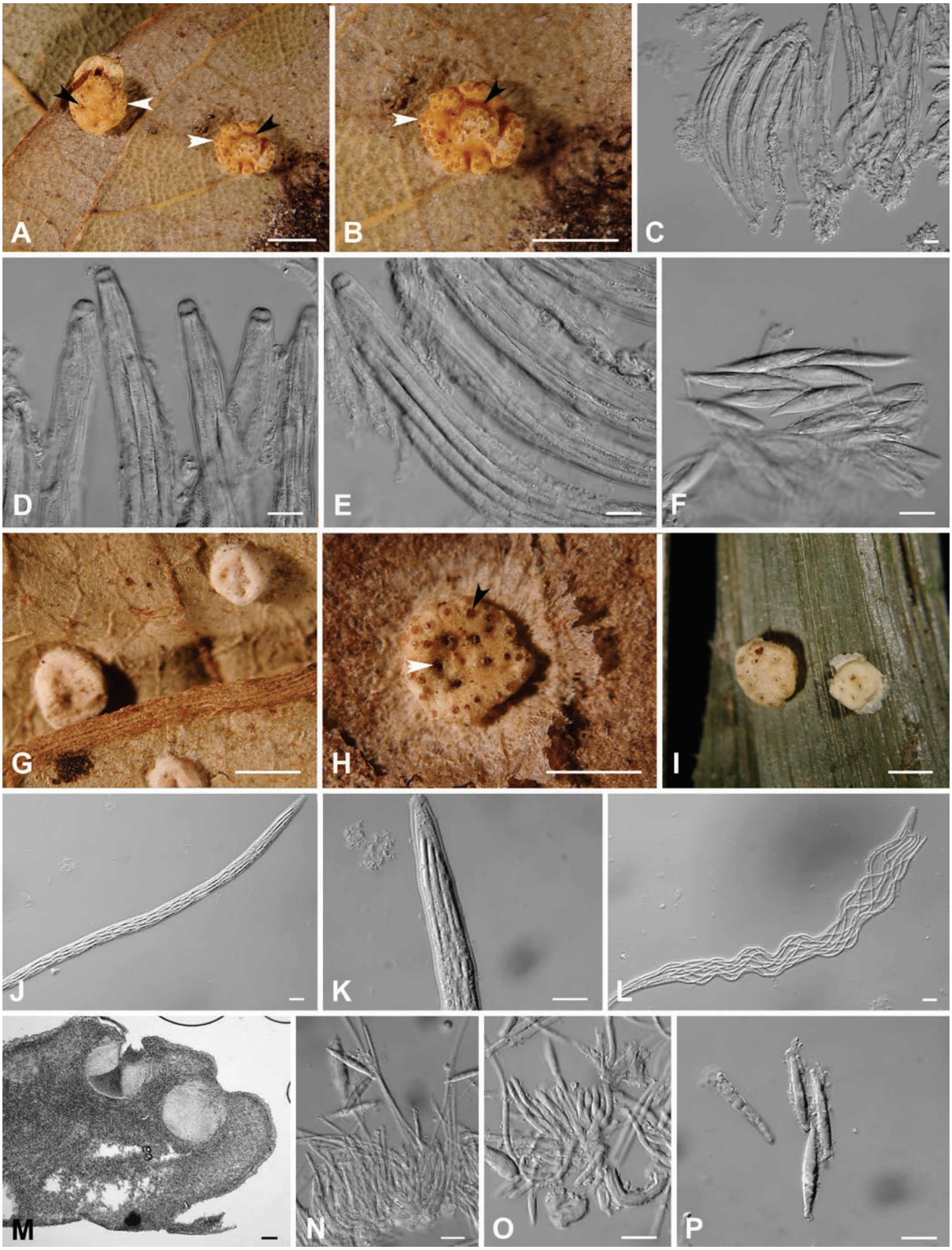

Fig. 16. A–F. *Hypocrella aurantiaca*. A–B. Stromata containing perithecia (white arrow) and conidiomata (black arrow). C–E. Asci containing ascospores. F. Conidia. **G–P. *Hypocrella citrina*.** G–I. Stromata. G, I. Stromata containing conidiomata. H. Stroma containing perithecia (white arrow) and conidiomata (black arrow). J–K. Asci and ascospores. L. Ascospores. M. Section of stroma showing conidiomata. N–O. Phialides and paraphyses. P. Conidia. A–F: K(M)120355 (type of *H. aurantiaca*); G–H: LPS 904 (type of *H. citrina*); I, N–O: CUP 067825; J–M, P: CUP 067827. Bars: A–B, J–I = 1 mm; C–F, J–P = 10 µm.

22) × (2–)2.5(–3) µm. Conidia hyaline, smooth, unicellular, fusoid, with acute ends, (12–)20–22(–29) × (2–)3.5–3.7(–4.5) µm, l/w (4.2–)5.5–6(–7.7). Paraphyses present.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Bolivia, Brazil, Costa Rica.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail to mountain along Eslabon River ("Senda RAP"), on leaf, 12–13 Jun. 2004, P. Chaverri (*P.C. 597, P.C. 598, P.C. 606, P.C. 610*) D. Quintana, M. Sogonov, A. Alvarez (CUP 067825, CUP 067826, CUP 067827, CUP 067828). **Brazil,** Blumenau, Santa Katharina, on leaves, P. Hennings? (Möller *67*) (**type** of *A. blumenaviensis* B 70 0007291); Rio de Janeiro, Macae, on leaf of tree/shrub in Restinga forest, 13 Oct. 1992, H.C. Evans (*I92-786*) (CUP 067829); Rio de Janeiro, Palmiras, on monocot leaf, Apr. 1900, E. Ule *2640* (type of *A. abnormis* S-F22380); Sao Paolo, Apiahy, on leaves of *Myrtaceae* or Zanthoxylea, 1888 (**type** of *H. citrina* LPS 904!); on leaves of *Psidium*, Oct. 1901, No. 362 (type of *A. flavocitrina* S-F22399). **Costa Rica,** Heredia, San Isidro, Calle Zurqui, near P. Chaverri's property, on leaf, May 2004, P. Chaverri (*P.C. 622*) (CUP 067830).

Notes: Cultures did not survive storage at 8 °C.

3. ***Hypocrella disciformis*** Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511383. Fig. 17A–O.
Anamorph: *Aschersonia disciformis* Pat., Bull. Soc. Mycol. France 8: 136. 1892.
= *Aschersonia viridula* Sacc. Ann. Myc. 11: 547. 1913.

Teleomorphosis: Stromatibus pulvinatus vel disciformis (1–)1.2–1.5(–2) mm diam, viridans vel cinereoviridans; ascosporae multicellulares, macrofusiformes, (65–)78–105(–110) × 2.5–3 µm. Holotypus: CUP 067838. Anamorphosis: *Aschersonia disciformis* Pat.

Teleomorph rare. Stromata generally discoid, pulvinate and tuberculate, each tubercle containing one perithecium when teleomorph present, greyish green or olive brown, sometimes with a narrow hypothallus (<1 mm), (1–)1.5(–2) mm diam, stroma surface pruinose; KOH+; stroma outer tissue of *textura epidermoidea*; stroma internal tissue of *textura intricata*. Perithecia embedded in stroma, sometimes protruding from stroma surface. Perithecia flask-shaped, 250–310 × 110–120 µm. Asci mostly cylindrical, (145–)150–168(–175) × (7.5–)8.5–10.2(–10.5) µm, caps 1.5–2.2 µm thick. Ascospores hyaline, multiseptate, smooth, filiform to long fusiform, (65–)78–105(–110) × 2.5–3 µm.

When anamorph present, stromata pulvinate generally with flattened top, conidiomata circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidiomata pycnidial, flask-shaped, (130–)174–230(–270) × (70–)100–150(–170) µm, with phialides formed in a thick compact palisade. Phialides cylindrical, slightly tapering towards tip, 19–25 × (1.5–)2–2.5 µm. Conidia hyaline, smooth, unicellular, fusoid, with acute ends, (17–)18.2–19(–21) × (3.3–)3.5–3.7(–4) µm, l/w (4.5–)5–5.2(–5.8). Paraphyses present.

Colonies on PDA at 25 °C slow-growing, pulvinate, tomentose, hollow underneath, compact, hard, greyish yellow with greenish areas scattered, edge of colony green. Conidiomata scattered; conidial masses pale yellow. Phialides (11–)15.5–17(–20) × (1.7–)2–2.2(–2.5) µm. Conidia (9.7–)12.5–13.2(–15.5) × (2.3–)2.8–3(–3.5) µm, l/w (3.3–)4.5–5(–5.5). Paraphyses present.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Bolivia, Colombia, Ecuador, Honduras, Mexico.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, Almendrillo Trail, on leaf, 11 Jun. 2004, P. Chaverri (*P.C. 575, P.C. 585*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067831 = culture ARSEF 7650; CUP 067832 = culture ARSEF 7652); Jaguar Trail, on leaf, 11 Jun. 2004, P. Chaverri (*P.C. 589*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067833 = culture ARSEF 7653). **Colombia**, Choco, Coqui, forest stream, on leaf of palm, 28 May 1993, H.C. Evans (*I93-862*) (CUP 067834). **Ecuador**, Puente de Chimbo, on leaves, Aug. 1891, Lagerheim? (**lectotype** of *A. disciformis* FH 3980!, **isotype** FH7926!). **Honduras**, Dpto. Copan, Copan Ruinas, Natural trail, elev. 700 m, on leaf, 31 Aug. 2004, P. Chaverri (*P.C. 655, P.C. 659, P.C. 661.1, P.C. 663.1, P.C. 667*), P.A. Sheikh (CUP 067861; CUP 067835; CUP 067836; CUP 067837; **holotype** CUP 067838); Santa Rita, Rio Amarillo, Peña Quemada Reserve, elev. 800 m, on leaf, 9 Sep. 2004, P. Chaverri (*P.C. 673, P.C. 676*), P.A. Sheikh (CUP 067839, CUP 067840). **Mexico**, on leaves, 1913 (type of *A. viridula* FH 4027!; FH 4026!).

Notes: *Hypocrella disciformis* can be distinguished from *H. viridans* by the larger conidia of the former species.

4. ***Hypocrella hirsuta*** Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511384. Fig. 18A–L.
Anamorph: *Aschersonia* sp.

Teleomorphosis: Stromatibus pulvinatus, cum processus (*Hirsutella* similis synanamorph), (1–)1.8–2.3(–3.5) mm diam, luteus; ascosporae multicellulares, macrofusiformes, (120–)135–150(–170) × (5–)6–6.5(–7.2) µm. Anamorphosis: Stromatibus pulvinatus vel disciformis. Phialide (9.5–)12–13.5(–16.5) × (2–)2.2–2.5(–3) µm; conidii fusiformes, (24–)30–31(–36.5) × (4–)5.5–5.7(–6.5) µm, longitudo/crassitudo (4.3–)5.3–5.5(–7); paraphysis prescens. Holotypus: CUP 067841.

Stromata (1–)1.8–2.3(–3.5) mm diam, yellow, KOH+, generally discoid, pulvinate, tuberculate, each tubercle containing one perithecium when teleomorph present, with numerous (>5) synnematous projections that correspond to a hirsutella-like synanamorph, without projections when stroma over-mature, stromata sometimes with hypothallus 0.5–1 mm, stroma surface pruinose; stroma outer tissue of *textura epidermoidea*; stroma internal tissue of *textura intricata*. Perithecia embedded in stroma, sometimes protruding from stroma surface. Perithecia flask-shaped, (305–)315–355(–360) × (110–)113–150(–160) µm. Asci mostly cylindrical, 200–245 × 18–22 µm, caps 5–6.5 µm thick. Ascospores hyaline, multiseptate, smooth, filiform to long fusiform, (120–)135–150(–170) × (5–)6–6.5(–7.2) µm.

When anamorph present, stromata pulvinate generally with a flattened top, conidiomata circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidiomata pycnidial, flask-shaped, 280–310 × 265–270 µm, with phialides formed in a thick compact palisade. Phialides cylindrical, slightly tapering towards tip, (9.5–)12–13.5(–16.5)× (2–)2.2–2.5(–3) µm. Conidia hyaline, smooth, unicellular, fusoid, with acute ends, (24–)30–31(–36.5) × (4–)5.5–5.7(–6.5) µm, l/w (4.3–)5.3–5.5(–7). Paraphyses abundant. The synnematous synanamorph hirsutella-like, indeterminate synnema, sometimes branched, with phialides with a long thin neck, sometimes with more than one neck per phialide.

Germinating conidia forming capilliconidiophores and capilliconidia. Colonies on PDA at 25 °C slow-growing, pulvinate, compact, hard, tomentose, greyish yellow. No pycnidia formed in culture, only a hirsutella-like synanamorph on surface of colony, no synnemata formed. Conidia from synanamorph ellipsoidal to obovoid, unicellular.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Bolivia, Brazil, Ecuador, Mexico.

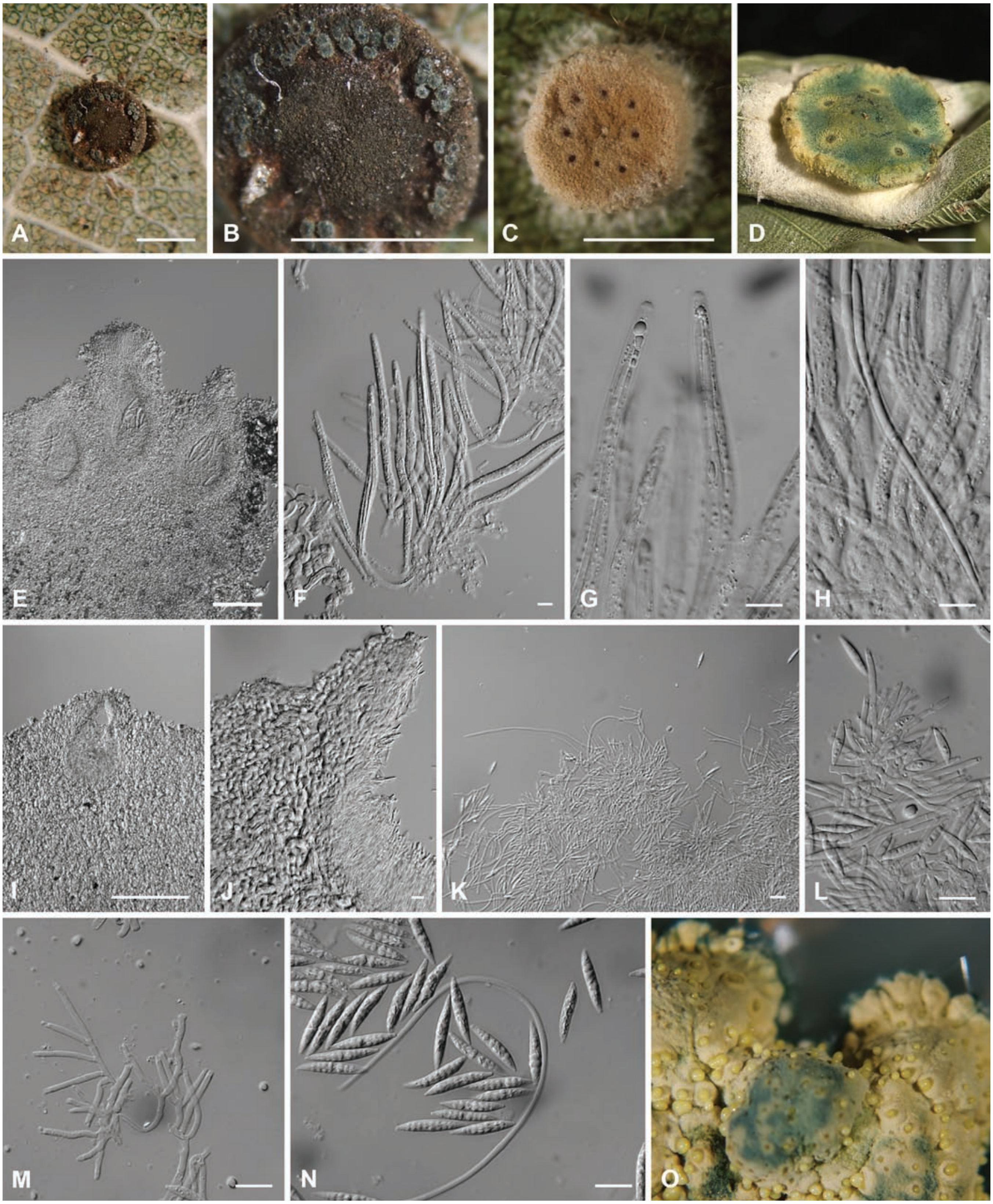

Fig. 17. A–O. ***Hypocrella disciformis***. A–D. Stromata. A–B. Stromata containing perithecia. C–D. Stromata containing conidiomata. E. Section of stroma showing perithecia. F–G. Asci. H. Ascospore. I–J. Section of stroma showing conidioma. K–M. Phialides and paraphyses. N. Conidia. O. Colony on PDA at 25 °C after *ca.* 3 wk. A–B, I–J: CUP 067836; C: CUP 067835; D: CUP 067833; E: CUP 067861; F–H: CUP 067838; K–M, O: CUP 067837; N: FH 7929 (isotype of *A. disciformis*). Bars: A–D = 1 mm; E, I = 100 µm; F–H, J–N = 10 µm.

Specimens examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, near Chalalan lodge, on leaf, 9 Jun. 2004, P. Chaverri (*P.C. 543*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067841); trail Tapacare, on leaf, 10 Jun. 2004, P. Chaverri (*P.C. 559*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067842); Almendrillo trail, on leaf, 11 Jun. 2004, P. Chaverri (*P.C. 574, P.C. 587*), D. Quintana, M. Sogonov, A. Alvarez (CUP 067843, CUP 067844). **Brazil**, Manaus, Ducke Forest Reserve, on leaf, 3 Oct. 1992, H.C. Evans (*P.C. 746* = CUP 067845); Rio Negro, Forest, on leaf, 21 May 1985, H.C. Evans (*P.C. 752* = CUP 067846). **Ecuador**, Cuyabeno, on leaf, 24 Jul. 1993, H.C. Evans (*P.C. 742* = CUP 067847). **Mexico**, Veracruz, Catemaco, town of Ejido Lopez-Mateo, project “Cielo, Tierra y Selva”, trail to the mountain, elev. 200–300 m, on leaf, 13 Dec. 2003, P. Chaverri (*P.C. 436.2*), J. Garcia-Alvarado, C. Mena-Jiles (CUP 067848).

Notes: Cultures did not survive storage at 8 °C.

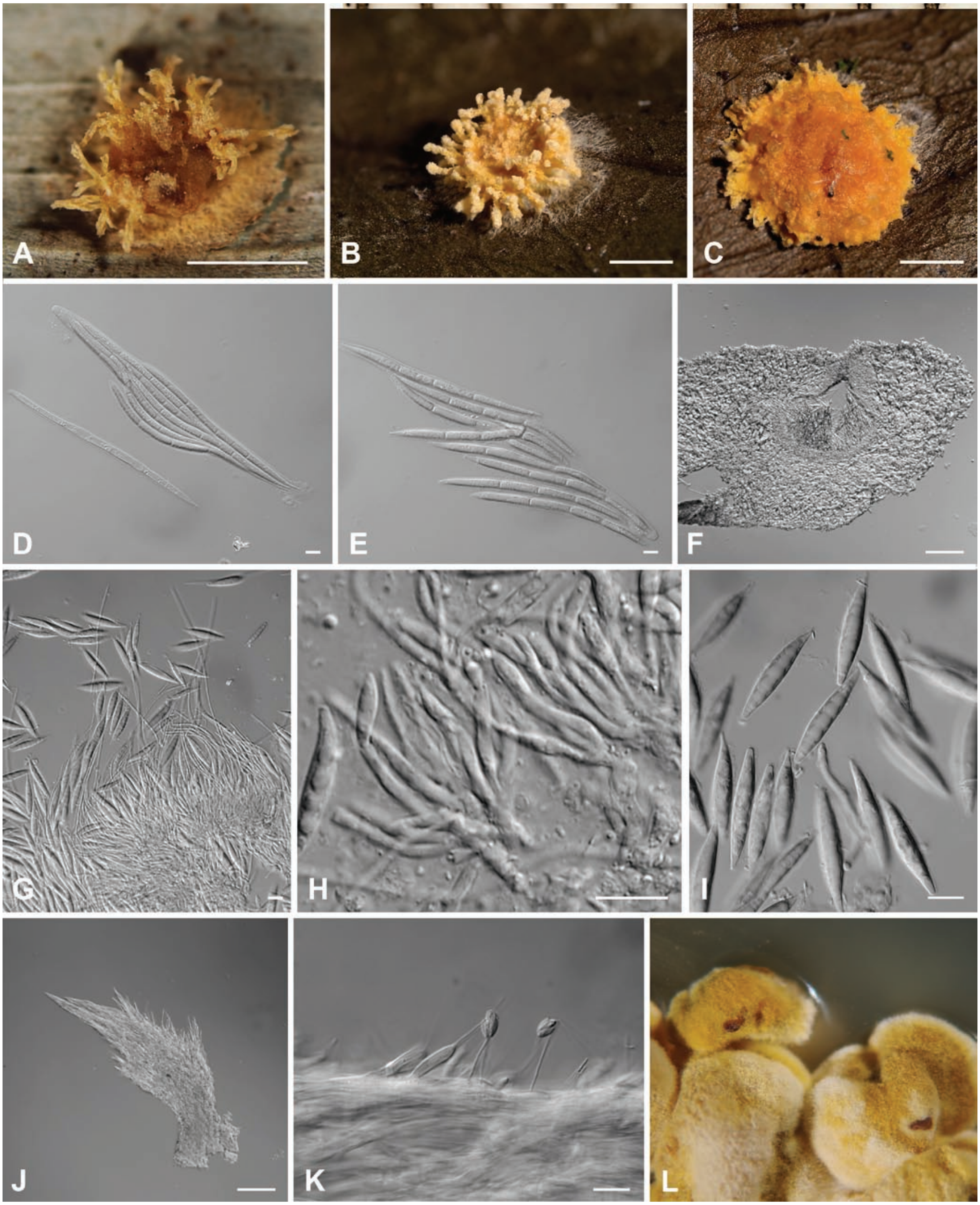

Fig. 18. A–L. *Hypocrella hirsuta*. A–C. Stromata. D–E. Ascus and ascospores. F. Section of stroma showing conidioma. G–H. Phialides and paraphyses. I. Conidia. J. Synnematous synanamorph. K. Synanamorph phialides. L. Colony on PDA at 25 °C after *ca.* 3 wk. A: CUP 067848; B–I: CUP 067841; J–L: CUP 067843. Bars: A–C = 1 mm; D–E, G–K = 10 µm; F = 100 µm.

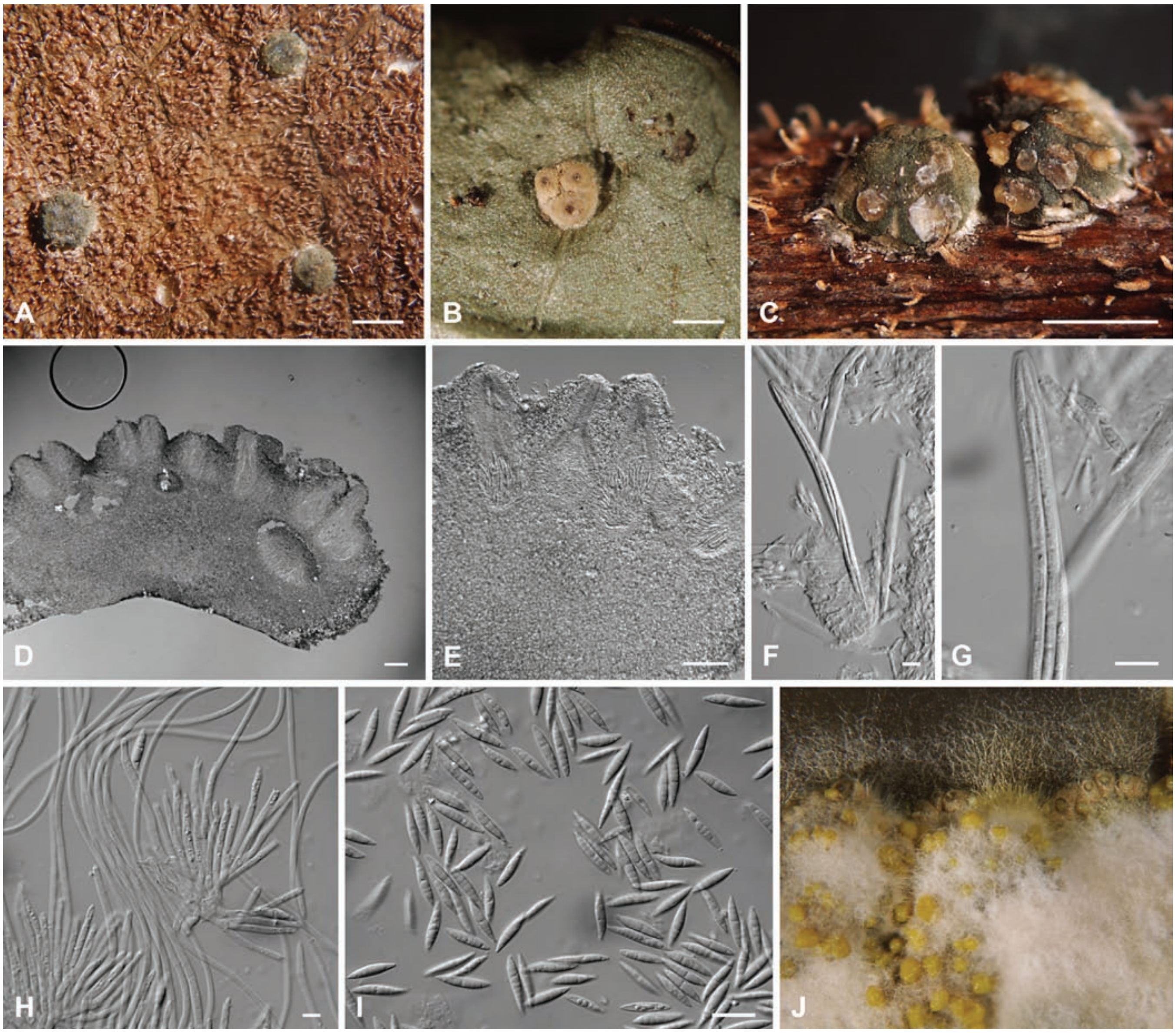

Fig. 19. A–J. *Hypocrella viridans*. A–C. Stromata. A–B. Stromata containing conidiomata. C. Stromata containing perithecia. D–E. Section of stroma showing perithecia. F–G. Asci and ascospores. H. Phialides and paraphyses. I. Conidia. J. Colony on PDA at 25 °C after *ca.* 3 wk. A: K(M)120253 (type); B: CUP 067849; C–G: IMI 346739 (epitype); H–I: CUP 067850, J: CUP 067851. Bars: A–C = 1 mm; D–E = 100 µm; F–I = 10 µm.

5. *Hypocrella viridans* (Berk. & M.A. Curtis) Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 236. 1921. Fig. 19A–J.

≡ *Hypocrea viridans* Berk. & M.A. Curtis in Berkeley, J. Linn. Soc. Bot. 10: 376. 1868.

= *Hypocrella glaziovii* Henn., Engler's Bot. Jahrb. 17: 524. 1893.

Anamorph: *Aschersonia viridans* (Berk. & M.A. Curtis) Pat., Bull. Soc. Myc. France 7: 48. 1891.

= *Aschersonia brunnea* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 251. 1921.

Teleomorph rare. Stromata (0.5–)1.2–1.5(–2.5) mm diam, generally discoid, pulvinate and sometimes tuberculate, each tubercle containing one perithecium when teleomorph present, greyish green or olive brown, dark brown when old, sometimes with a narrow hypothallus (<1 mm), stroma surface pruinose; KOH+; stroma outer tissue of *textura epidermoidea*; stroma internal tissue of *textura intricata*. Perithecia embedded in stroma, sometimes protruding from stroma surface. Perithecia flask-shaped, (235–)265–310(–350) × (100–)115–130(–150) µm. Asci mostly cylindrical, (145–)150–170(–175) × (7.5–)8.5–11 µm, caps 1–1.5 µm thick. Ascospores hyaline, multiseptate, smooth, filiform to long fusiform, 83–89 × 2.5–3.5 µm.

Strictly anamorphic stromata pulvinate, generally with a flattened top, discoid, conidiomata circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidiomata pycnidial, flask-shaped to subglobose, (425–)435–460(–470) × (250–)270–360(–390) µm, with phialides formed in a thick compact palisade. Phialides cylindrical, slightly tapering towards tip, 14.5–16.5 × 1.5–2.5 µm. Conidia hyaline, smooth, unicellular, fusoid, with acute ends, (12.3–)14.5–17(–17.5) × 3–3.5 µm, l/w (4.5–)4.7–5(–5.2). Paraphyses abundant.

Colonies on PDA at 25 °C slow-growing, pulvinate, tomentose, hollow underneath, compact, hard, greyish yellow to cream-coloured with scattered greenish or yellowish areas, edge of colony generally yellow. Conidiomata scattered; conidial masses yellow. Phialides (11.7–)15.5–17.5(–27.6) × (1.5–)2(–2.5) µm. Conidia (9.5–)12.2–13(–15) × (2–)2.5(–3), l/w (3.5–)4.8–5(–6.4). Paraphyses abundant.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Brazil, Cuba, Honduras, Mexico.

Specimens examined: **Brazil**, 1894, Glaziou (type of *H. glaziovii* S!); Para, on leaves, Spruce *528* (type of *A. brunnea*, K(M)130012 in part, under *Hypocrea amazonica* Cooke). **Cuba**, on leaf of *Gesneriaceae*, 1857, Wright *756* (**type** K(M)120253! and isotype FH! of *Hypocrella viridans* and *Aschersonia viridans*). **Honduras**, Dpto. Atlantida, Tela, Lancetilla Natural Reserve, elev. 0 m, on leaf, 24 Aug. 2004, P. Chaverri (*P.C. 632, P.C. 635, P.C. 637*), P.A. Sheikh (CUP 067849, CUP 067850, CUP 067851); Dpto. Copan, Santa Rita, Rio Amarillo, Peña Quemada Reserve, elev. 800 m, on leaf, 9 Sep. 2004, P. Chaverri (*P.C. 670, P.C. 671*), P.A. Sheikh (CUP 067852, CUP 067853); Yojoa, Los Pinos, Cerro Azul/Meambar National Park, elev. 850 m, on leaf, 3 Sep. 2004, P. Chaverri (*P.C. 695*), P.A. Sheikh (CUP 067854). **Mexico**, Guerrero, Cuajimicuilapa, on leaf and rachis of *Mimosa pigra*, 30 Nov. 1989, H.C. Evans (*I89-490*) (**epitype** of *H. viridans* designated here IMI 346739 = culture ARSEF 7674).

Notes: *Hypocrella viridans* can be distinguished from *H. disciformis* by the smaller conidia of the former species. The type of *H. viridans* only contains conidiomata. Therefore, this species is epitypified here with a specimen from Mexico (IMI 346739), which is the only available specimen that contains perithecia. The type of *H. glaziovii* in herbarium S is in bad condition and includes only a half-stroma; however, it resembles an old *H. viridans*. The type of *A. brunnea* in K is in the same packet as the type of *Hypocrea amazonica* Cooke. *Aschersonia brunnea* is an old over-mature specimen of *H. viridans*.

SAMUELSIA Chaverri & K.T. Hodge, **gen. nov.** MycoBank MB511385.

Anamorph: aschersonia-like.

Type: *Samuelsia rufobrunnea* Chaverri & K.T. Hodge.

Etymology: In honour of Gary J. Samuels, for his great contribution to systematics of hypocrealean fungi and for mentoring P. Chaverri.

Teleomorphosis: Stromatibus convexus vel pulvinatus, 1.5–3(–4) mm diam, subaurianticus, brunneus, sub-brunneus, brunneoluteus; ascosporae multicellulares, macrofusiformes, (30–)40–60 × 1.5–2.5 µm. Anamorphosis: Stromatibus pulvinatus, pycnidium. Conidii allantoideus, subelliposideus, (4–)4.5–6(–7) × 1.5–2 µm, longitudo/crassitudo 3–4; paraphysis prescens vel abscens, circinatus aliquando.

Stromata pulvinate, 1.5–3(–4) mm diam, with a wide base, sometimes cylindrical and extending towards base, generally hard, pale yellow, pale orange, brownish orange, brownish yellow, brown, or greyish yellow, no hypothallus, stroma surface generally smooth or slightly pruinose, opaque or glossy; generally KOH+; stroma tissue of compact *textura intricata*, cell walls 1–3 µm thick. Perithecia completely embedded in stroma, scattered. Perithecia, subglobose, 320–380 × 110–120 µm. Asci mostly cylindrical to clavate, (90–)100–120(–130) × 5–7 µm, caps 1–3 µm. Ascospores hyaline, multiseptate, smooth, long fusiform to filiform, (30–)40–60 × 1.5–2.5 µm.

Conidiomata as simple depressions of stroma surface, shallow or deep, U-shaped, from top view elongated and generally fusing with neighboring conidiomata, sometimes arranged in a circular fashion; conidiophores in a compact palisade, short, monoverticillate with 2–5 phialides per verticil, once monochasial, sometimes twice monochasial; phialides cylindrical, long and slender, tapering towards apices, 8–20 × 1–2 µm; conidia small, hyaline, unicellular, smooth, mostly allantoid, (4–)4.5–6(–7) × 1.5–2 µm, l/w 3–4. Paraphyses present or absent, circinate when present. Cultures do not produce conidiomata or conidia in culture; slow-growing.

Habitat: On scale insects and whiteflies on leaves.

Known distribution: Bolivia, Chile, Honduras, Peru.

1. ***Samuelsia chalalensis*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511386. Fig. 20A–D.

Anamorph: aschersonia-like.

Stromatibus convexus vel pulvinatus, (1–)1.5–2.5(–4) mm diam, subaurianticus; phialides (12.3–)13–19.5(–22.7) × 1.3–1.5 µm; conidii allantoideus, (5.3–)5.5–5.7(–6) × (1–)1.5(–2) µm, longitudo/crassitudo (3–)3.5–4.2(–5.2); paraphysis abscens. Holotypus: CUP 067856.

Perithecia not observed. Stromata irregularly pulvinate, highly aggregated, sometimes fusing with neighboring stromata, (1–)1.5–2.5(–4) mm diam, with a wide base, pale orange with yellowish tinges, no hypothallus, stroma surface generally smooth, slightly pruinose; changing to brownish when KOH added; stroma tissue of compact *textura intricata*. Conidiomata as simple depressions of stroma surface, shallow, U-shaped, scattered, conidial masses brown; conidiophores in a compact palisade, short; phialides cylindrical, tapering towards apices, (12.3–)13–19.5(–22.7) × 1.3–1.5 µm; conidia small, hyaline, unicellular, smooth, allantoid, (5.3–)5.5–5.7(–6) × (1–)1.5(–2) µm, l/w (3–)3.5–4.2(–5.2). Paraphyses absent.

Habitat: On whiteflies on bamboo.

Known distribution: Bolivia (type locality).

Specimen examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail Tapacare, on bamboo, 10 Jun. 2004, P. Chaverri (*P.C. 560*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067856).

Notes: Although no perithecia were observed, a teleomorph name is given to this species because the link to *Samuelsia* is proven by DNA sequence data and the morphology of the anamorph. Culture did not survive storage at 8 °C.

2. ***Samuelsia geonomis*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511387. Fig. 20E–I.

Anamorph: Not known.

Teleomorphosis: Stromatibus convexus vel pulvinatus, centralis levatum (3–)3.2–3.5(–4) mm diam, subaurianticus, subbrunneus; asci (107–)112–122(–130) × (5.5–)6–6.7(–7) µm; ascosporae multicellulares, macrofusiformes, (35–)40.5–51(–53) × 2–2.5 µm. Holotypus: CUP 067857.

Stromata pulvinate, elevated at central part and tapering towards base, base wide, with a sunken circular area in centre of top part of stroma, (3–)3.2–3.5(–4) mm diam, hard, pale yellow to brownish yellow, no hypothallus, stroma surface smooth and slightly glossy; generally KOH+ mostly on top central part of stroma; perithecial openings brown; stroma tissue of compact *textura intricata*. Perithecia completely embedded in stroma, scattered. Perithecia, subglobose, 320–350 × 110–120 µm. Asci mostly cylindrical, (107–)112–122(–130) × (5.5–)6–6.7(–7) µm, caps (0.8–)1–1.3(–1.7) µm. Ascospores hyaline, multiseptate, smooth, long fusiform, (35–)40.5–51(–53) × 2–2.5 µm.

Colonies on PDA at 25 °C, slow-growing, pulvinate, compact, brownish yellow, tomentose. No conidiomata or conidia formed.

Habitat: On scale insects or whiteflies on leaves of palm *Geonomis* sp.

Known distribution: Bolivia (type locality).

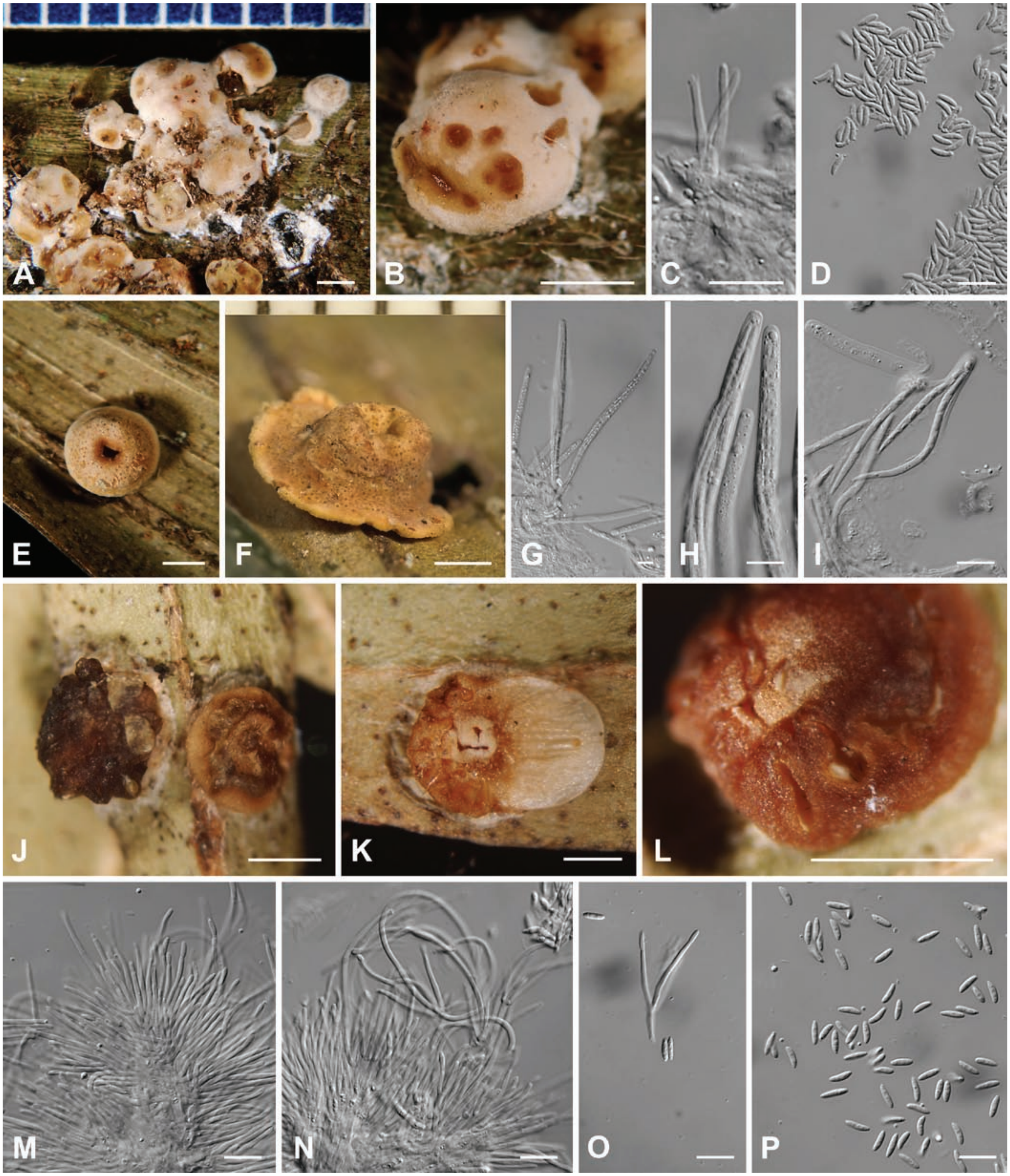

Fig. 20. A–D. *Samuelsia chalalensis.* A–B. Stromata containing conidiomata. D. Phialides. D. Conidia. **E–I. *Samuelsia geonomis.*** E–F. Stromata containing perithecia. G–I. Asci and ascospores. **J–P. *Samuelsia intermedia*.** J–L. Stromata containing conidiomata. M–O. Phialides and paraphyses. P. Conidia. A–D: CUP 067856 (holotype of *S. chalalensis*); E–I: CUP 067857 (holotype of *S. geonomis*); J–L: FH 3990; M–P: FH 3991 (lectotype of *A. intermedia*). Bars: A–B, E–F, J–L = 1 mm; C–D, G–I, M–P = 10 um.

Specimen examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail to mountain along Eslabon River ("Senda RAP"), on leaves of *Geonomis* sp., 12–13 Jun. 2004, P. Chaverri (*P.C. 614*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067857 = ARSEF 7656).

3. *Samuelsia intermedia* Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511388. Fig. 20J–P.

Anamorph: "*Aschersonia*" *intermedia* Petch, Ann. Roy. Bot. Gard. Peradeniya 7: 325. 1922.

Stromatibus pulvinatus, (1–)1.5–2 mm diam, subaurianticus vel sub-brunneus; phialides (13.5–)16–19(–20.3) x (1.3–)1.7–2(–2.2) µm; conidii allantoideus, (5.5–)6–6.5(–7.7) × (1.8–)2(–2.5) µm, longitudo/crassitudo (2.5–)3(–3.8); paraphysis circinatus. Holotypus: FH 3991.

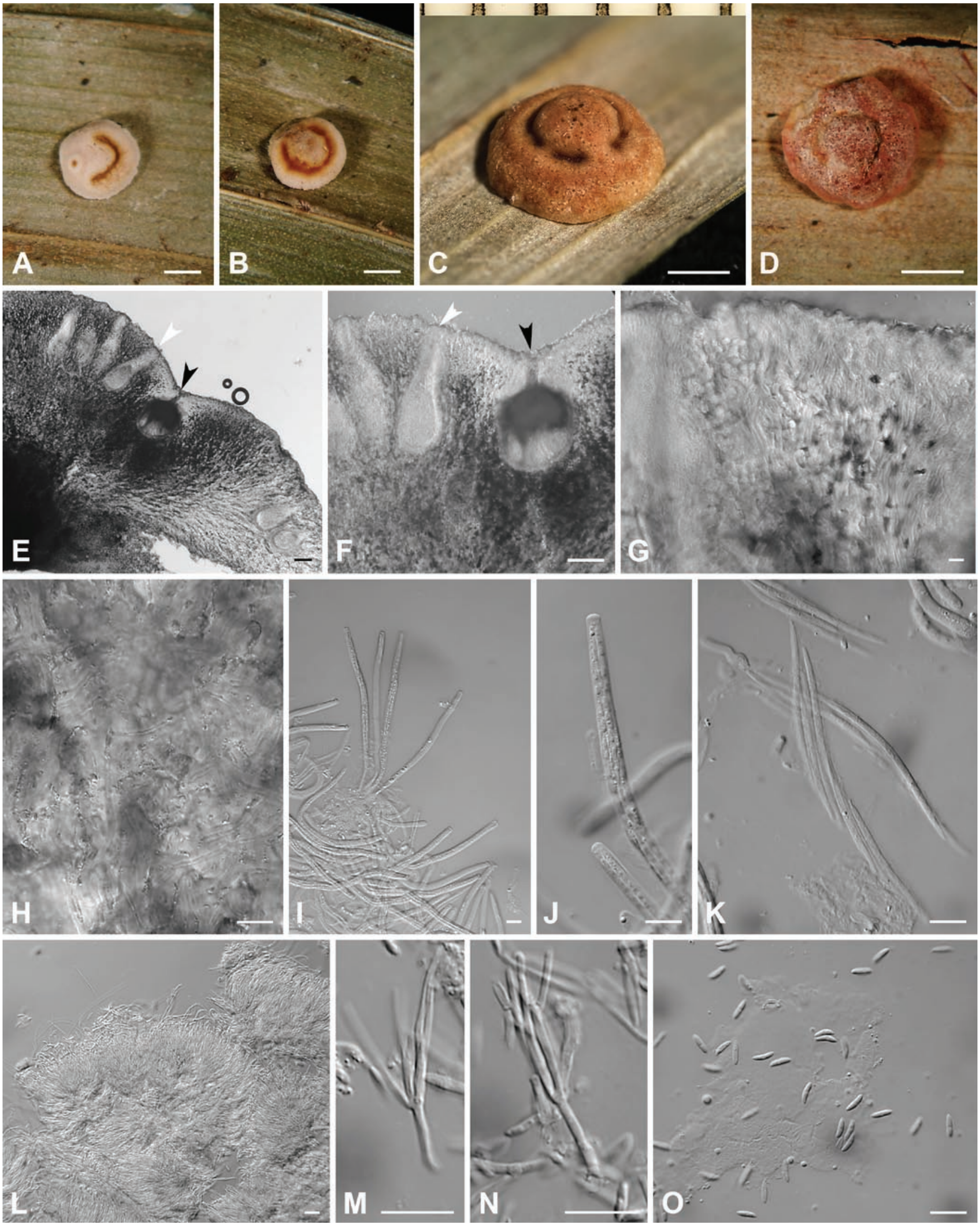

Fig. 21. A–O. *Samuelsia rufobrunnea*. A–D. Stromata at different stages of development. A–B. Young stromata containing conidiomata. C. Stroma containing conidiomata and perithecia. D. Stroma containing perithecia. E–F. Section of stroma showing perithecia (white arrow) and conidiomata (black arrow). G. Section showing outermost layer of stroma. H. Section showing inner layer of stroma. I–J. Asci. K. Ascospores. L. Phialides and paraphyses. M–N. Phialides. O. Conidia. A–O: CUP 067858 (holotype). Bars: A–D = 1 mm; E–F = 100 µm; G–O = 10 µm.

Perithecia not observed. Stromata pulvinate, (1–)1.5–2 mm diam, with a narrow base, greyish yellow to dark brown, no hypothallus or very thin, cream-coloured, stroma surface generally smooth, glossy; KOH-; stroma tissue of compact *textura intricata*. Conidiomata as simple depressions of stroma surface, openings wide and elongated, irregular, deep, U-shaped, scattered, conidial masses not seen; conidiophores in a compact palisade, short; phialides cylindrical, tapering towards apices, (13.5–)16–19(–20.3)

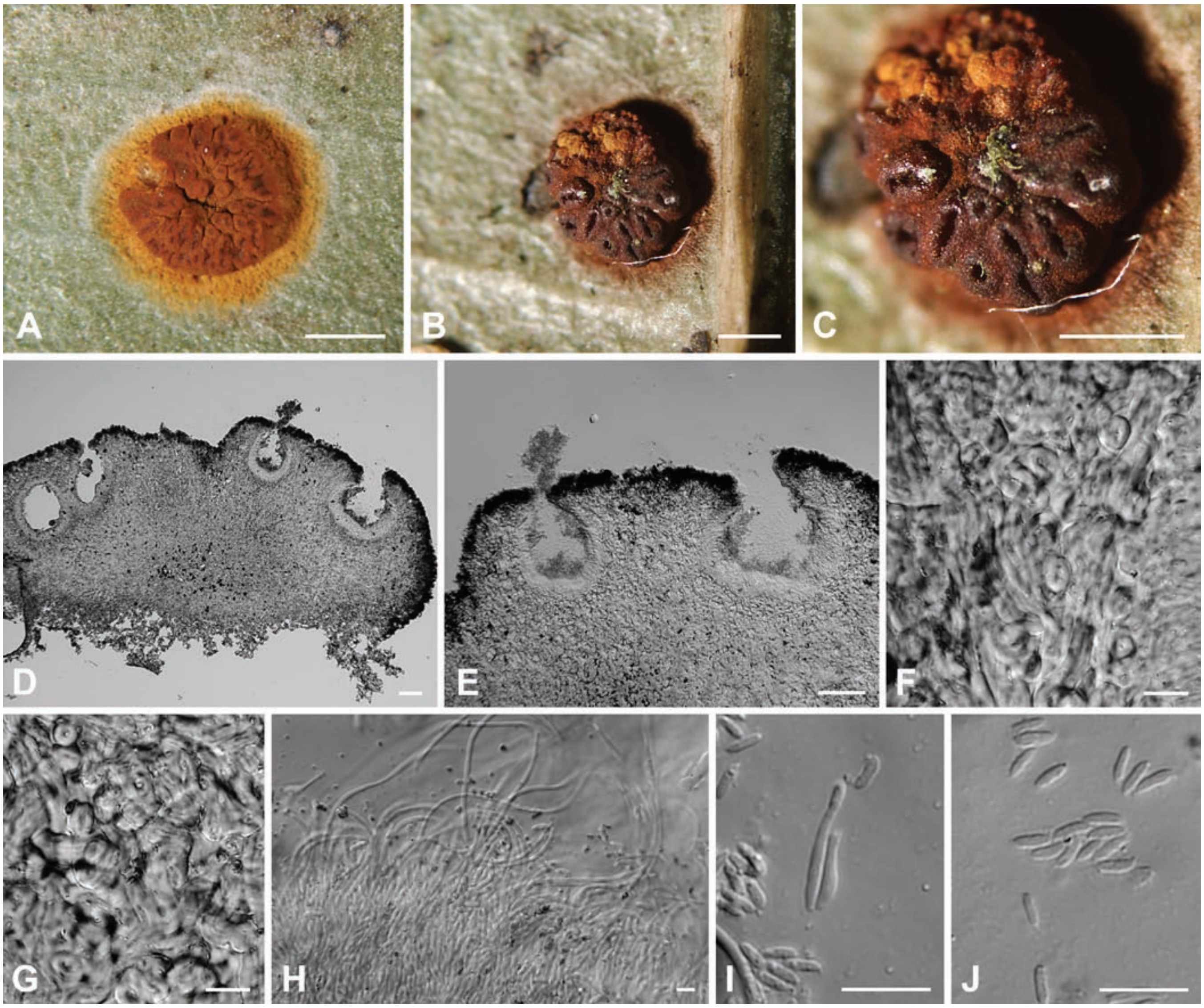

Fig. 22. A–J. *Samuelsia sheikhii.* A–C. Stromata. B–C. Stromata after adding 3 % KOH. D–E. Section of stroma showing conidiomata. F. Section showing outermost layer of stroma. G. Section showing inner layer of stroma. H. Phialides and paraphyses. I. Phialides. J. Conidia. A–J: CUP 067859 (holotype). Bars: A–C = 1 mm; D–E = 100 µm; F–J = 10 µm.

× (1.3–)1.7–2(–2.2) µm; conidia small, hyaline, unicellular, smooth, allantoid, (5.5–)6–6.5(–7.7) × (1.8–)2(–2.5) µm, l/w (2.5–)3(–3.8). Paraphyses present, circinate.

Habitat: On scale-insects on leaves.

Known distribution: Chile (type locality).

Specimens examined: **Chile,** Corral, on scale-insects on leaves, Dec. 1905, R. Thaxter (**lectotype** of *A. intermedia* designated here, and **holotype** of *S. intermedia* FH 3991!); Jan. 1906, R. Thaxter (FH 3990!).

Notes: Micromorphologically, *S. intermedia* is indistinguishable from *S. rufobrunnea*. The species are distinguished by the distinct macromorphologies of the stromata. In addition, *S. rufobrunnea* is tropical (Bolivia and Peru) while *S. intermedia* is subtropical (Chile). There are several specimens in FH labeled as “*A. intermedia*” (Petch 1921), but only one reads “co-type.” Therefore, this species is lectotypified here with FH 3991. Although there are no DNA sequences of S. intermedia, the micro and macro characteristics of the anamorph place this species within *Samuelsia*.

4. *Samuelsia rufobrunnea* Chaverri & K.T. Hodge, **sp. nov.**

MycoBank MB511389. Fig. 21A–O.
Anamorph: aschersonia-like

Teleomorphosis: Stromatibus pulvinatus, (2–)2.2–3.3(–4) mm diam, sub-brunneus vel brunneoluteus; ascosporae multicellulares, macrofusiformes, (42–)48–55(–57) × 1.5–2.5 µm. Anamorphosis: Stromatibus pulvinatus, pycnidium; phialides (14.5–)15.3–19.2(–22.5) × 1.3–1.5 µm; conidii allantoideus vel subelliposideus, (5.5–)6–6.2(–6.7) × (1.3–)1.7–2 µm, longitudo/crassitudo (3–)3.5–3.7(–4.5); paraphysis prescens, circinatus. Holotypus: CUP 067858.

Stromata pulvinate, (2–)2.2–3.3(–4) mm diam, with a wide base, hard, pale yellow when young, then brownish yellow with a reddish tinge when perithecia are fully mature, no hypothallus, stroma surface generally smooth and glossy, KOH+, ostioles brownish orange; stroma tissue of compact *textura intricata*. Perithecia completely embedded in stroma, scattered. Perithecia, subglobose, 320–380 × 110–120 µm. Asci mostly cylindrical to clavate, (98–)100–118(–120) × 5–6.5(–7) µm, caps 2–3 µm. Ascospores hyaline, multiseptate, smooth, long fusiform to filiform, (42–)48–55(–57) × 1.5–2.5 µm.

Conidiomata as deep depressions of stromal surface, from top view elongated and generally fusing with neighboring conidiomata, arranged in circular fashion; in longitudinal section conidiomata subglobose; phialides cylindrical, tapering towards apices, (14.5–)15.3–19.2(–22.5) × 1.3–1.5 µm; conidia allantoid to somewhat ellipsoidal, (5.5–)6–6.2(–6.7) × (1.3–)1.7–2 µm, l/w (3–)3.5–3.7(–4.5). Paraphyses present, circinate. Culture did not survive storage at 8 °C.

Habitat: On insects on leaves of palm *Geonomis* sp.

Known distribution: Bolivia, Peru.

Specimen examined: **Bolivia,** Dpto. La Paz, San Jose de Uchipiamonas, Madidi National Park, Chalalan, trail to mountain along Eslabon River ("Senda RAP"), on leaves of *Geonomis* sp., 12–13 Jun. 2004, P. Chaverri (*P.C. 613*), D. Quintana, M. Sogonov, A. Alvarez (**holotype** CUP 067858). **Peru,** Madre de Dios, Tambopata, Picaflor Research Station, on leaves of *Geonomis* sp., 16 Jun. 2007, R. Gazis, H.C. Evans, P. Chaverri (*P.C. 814*) (CUP 067862).

Notes: Micromorphologically, *S. rufobrunnea* is indistinguishable from *S. intermedia*. The species are distinguished by the distinctive macromorphology of the stromata. In addition, *S. rufobrunnea* is tropical (Bolivia, Peru) and *S. intermedia* is subtropical (Chile).

5. ***Samuelsia sheikhii*** Chaverri & K.T. Hodge, **sp. nov.** MycoBank MB511390. Fig. 22A–J.

Teleomorph: Not known.

Etymology: In honour of P. Chaverri's husband, Pervaze A. Sheikh, who helped the author with collecting in Honduras and who also found this new species.

Stromatibus pulvinatus, subtuberculatus, (1.5–)2–2.2(–2.5) mm diam, brunneus; phialides (8–)9.5–10.5(–12) × (1.3–)1.5–1.7(–2) µm; conidii allantoideus vel subellipsoideus, (3.7–)4.2–4.5(–5) × (1–)1.5(–2) µm, longitudo/crassitudo (2.2–)2.8–3(–4); paraphysis prescens, circinatus. Holotypus: CUP 067859.

Stromata pulvinate, (1.5–)2–2.2(–2.5) mm diam, with a narrow base, brownish yellow or brown, tuberculate, with a thin hypothallus 0.5–0.8 mm, conidiomata arranged in a circular fashion towards periphery of stroma, centre of stroma generally sterile and slightly sunken, stroma surface smooth to slightly pruinose, opaque; becoming dark purple in KOH; stroma tissue of compact *textura intricata*. Conidiomata as simple depressions of stroma surface, openings wide and elongated, slit-like, deep, U-shaped or flask-shaped in longitudinal section, scattered, conidiomatal openings dark brown; conidiophores in a compact palisade, short; phialides cylindrical, tapering towards apices, (8–)9.5–10.5(–12) × (1.3–)1.5–1.7(–2) µm; conidia small, allantoid to somewhat ellipsoidal, (3.7–)4.2–4.5(–5) × (1–)1.5(–2) µm, l/w (2.2–)2.8–3(–4). Paraphyses present, circinate.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Honduras (type locality).

Specimen examined: **Honduras,** Yojoa, Los Pinos, Cerro Azul/Meambar National Park, elev. 850 m, on leaf, 3 Sep. 2004, P. Chaverri (*P.C. 686*), P.A. Sheikh (**holotype** CUP 067859).

Notes: Culture did not survive storage at 8 °C.

EXCLUDED OR DOUBTFUL SPECIES

1. ***Hypocrella abnormis*** P. Henn., Hedwigia: 93.1904.

Notes: The type specimen of *"H." abnormis* from Brazil in Herb. S (S-F 22380) is immature and there is only one stroma. The stroma is *ca.* 4 mm diam, bright yellow, discoid, flat, surface smooth and glossy, KOH-. It is possible that this species belongs in *Moelleriella*, but more and mature collections are necessary.

2. ***Hyperdermium caulium*** (Berk. & M.A. Curtis) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511391.

≡ *Corticium caulium* Berk. & M.A. Curtis, J. Acad. Nat. Sci. Philad. 2: 279. 1854.
≡ *Hypocrella caulium* (Berk. & M.A. Curtis) Pat., Bull. Soc. Mycol. France 30: 346. 1915.
= *Hypocrella camerunensis* Henn., Engler's Bot. Jahrb. 23: 540. 1897.
= *Hypocrella brasiliana* (Henn.) Mains, Mycopath. Myc. Appl. 11: 311. 1959.
≡ *Stigmatea brasiliana* Henn., Hedwigia 36: 230. 1897.
≡ *Hypocrella camerunensis* var. *brasiliana* Henn., Hedwigia 43: 85. 1904.
= *Hyperdermium bertonii* J.F. White, R.F. Sullivan, Bills & Hywel-Jones, Mycologia 92: 910. 2000.
≡ *Epichloë bertonii* Speg., An. Mus. Nac. Hist. Nat. Buenos Aires 31: 416. 1922.

Notes: According to observations made by the authors of type specimens of *Hypocrella caulium, H. brasiliana*, and *H. camerunensis*, all of these are conspecific with a geographically widespread species *Hyperdermium bertonii*. However, because the oldest epithet is *caulium*, a new combination is proposed here.

3. ***Hypocrella chusqueae*** Petrak, Sydowia 2: 334. 1948.

Notes: The type of this species from Ecuador (Herb. W 32179!) is not *Hypocrella, Moelleriella*, or *Samuelsia*. The stromata is flat, extensive, almost subicular. The perithecia are obpyriform and the ascospores are very thin, filiform, resembling more the genus *Hyperdermium*.

4. ***Hypocrella tamoneae*** Earle, Mycologia 2: 87. 1910.

Notes: We did not examine the type of *H. tamoneae*. However, Petch (1921) did examine the specimen and concluded that it is not a *Hypocrella s. l.* because it has paraphyses in the perithecium. Until now, we have not observed paraphyses in the perithecium in any *Hypocrella, Moelleriella*, or *Samuelsia* species.

5. ***Hypocrella tenuispora*** P.G. Liu & Z.Q. Li, Mycotaxon 78:71. 2001.

Notes: We did not examine the type of this species, but based on the original description and illustrations (Liu *et al.* 2001), we conclude that this species belongs in *Balansia*. In addition, Liu *et al.* (2001) mention the similarities with *H. bambusae*, which is also a *Balansia*.

6. ***Moelleriella verruculosa*** (Möller) Chaverri & K.T. Hodge, **comb. nov.** MycoBank MB511392.

≡ *Hypocrella verruculosa* Möller, Phycom. & Ascom., p. 157. 1910.

Notes: Based on descriptions and illustrations in Möller (1910), this species from Brazil seems to be distinct from other described species of *Hypocrella, Moelleriella*, and *Samuelsia*. However, the type that was deposited in Herbarium B was lost during World War II. Illustrations and descriptions of the disarticulating ascospores made by Möller, clearly places this species in *Moelleriella*. A new combination is made herein.

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