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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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 pycnidal 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 Lecanidae, 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). Other genera, including Ascopolyergus A. Möller, Cosmospora Rabenh., Hyperdermium J.F. White et al., Podoenetria Petch, Regiocrella Chaverri & K.T. Hodge, Septobasidium Pat., and Torrubia 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 phylogenous 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, Lourenco et al. 1999, Meekes et al. 2000, Faria & Wraght 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 Hypocreella, Moelleriella, and Samuelsia are
recognised by their brightly coloured stromata that form on scale
insects or whiteflies. As will be shown in this study, Hypocreella 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 Hypocreella 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 Hypocrea discoidea (Berk. & Broome) Sacc. (type of the
genus) remains in Hypocrea. 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 ascus and speculated that if whole ascospores were seen
in ascii, 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.,
Mynogenospora G.F. Akk. 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 (Kulda 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
pycnidal-acervular conidiomata, brightly coloured ascoma, 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. caverosa A. Möller (= M. caverosa = M.
palmæ 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.
discomiformis, 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,
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                      | Anamorph           | Source                          | Distribution |
|---------------------------------|--------------------|---------------------------------|--------------|
| Hypocrella aurantiaca           | A. aurantiaca      | Petch 1939, Mains 1959a         | NW           |
| H. citrina                      | A. blumenaviensis  | Mains 1959b                     | NW           |
| H. discoidea                    | A. discoidea       | Hywel-Jones & Evans 1993        | OW           |
| H. disciformis                  | A. disciformis     |                                 | NW           |
| H. discoidea                    | A. samoensis       |                                 | OW           |
| H. hirsuta                      | Not named          |                                 | NW           |
| H. hypocreoeidea                | A. hypocreoeidea   | 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                   | “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                    | Not named          |                                 | NW           |
| M. duplex                       | “A.” duplex        | Petch 1921                      | OW           |
| M. epiphylla                    | “A.” cubensis      | Mains 1959a, b                  | NW           |
| M. evansii                      | Not named          |                                 | NW           |
| M. gaethneriana                 | Not known          |                                 | NW           |
| M. globosa                      | Not named          |                                 | NW           |
| M. guartanica                   | “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. maddiensis                   | 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. phydogena                    | “A.” juruensis     |                                 | NW           |
| M. raciborskii                  | “A.” placenta      | Liu et al. 2006                 | OW           |
| M. reinckiana                   | “A.” marginata     | Petch 1921                      | OW           |
| M. rhombispora                  | Not named          | Liu et al. 2006                 | NW           |
| M. schlechtstachyi              | 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                    | Not named          |                                 | NW           |
| M. zhongdongii                  | “A.” incrassata    | Liu & Hodge 2005                | NW           |
| Moelleriella sp.                | “A.” insperata     |                                 | OW           |
| Samuelsia chalalensis           | Not named          |                                 | NW           |
| S. geonomis                     | Not known          |                                 | NW           |
Aschersonia

In that same work, Petch proposed scale insects (Coccidae; Lecaniidae according to Petch 1921). anamorphs). He considered that most of these species attack paraphyses (and for species of Aschersonia sensu lato). In fact, Petch (1921) also discussed the possibility of splitting Hypocrella into groups characterised by the form of the stroma. The seminal taxonomic treatment of the genus was made by Parkin (1906) who considered extensive collections from Sri Lanka. The seminal

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. evansi, M. libera, M. madiidiensis, M. ochracea, M. raciborski, 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. hisruta, 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 were used by 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. guanantica, S. intermedia, H. aurantica, 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

| Teleomorph1 | Anamorph1,2 | Source | Distribution |
|-------------|-------------|--------|--------------|
| S. intermedia4 | “A.” intermedia | NW | |
| S. rufobrunnea3 | Not named | NW | |
| S. sheikhii² | 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. tahitiensis | OW | |
| Not known | A. tamurai | OW | |

1Not 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.
²Aschersonia names in quotes (e.g. “Aschersonia”) denotes taxa that are not in Aschersonia sensu stricto.
3Indicates connections made in the present study.
4Based on anamorph; no mature perithecia observed.

Table 1. (Continued).
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 Samuelisia, 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. sclerotoides 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 Henne. (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, Samuelisia, 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 evansi 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. phylogena, 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. phylogena 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, Samuelisia, 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 & Vilchez 2006).

Habitat

Microclimate

Although Hypocrella, Samuelisia, 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 Samuelisia 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, Samuelisia, 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, Samuelisia, 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, Samuelisia, and Moelleriella. Some studies have shown that temperature may affect conidial germination and mycoplasmal mortality by M. libera (anam. “A.” aleyrodis) (Franssen et al. 1987, Franssen 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 mycoplasmal 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 & Andreasis 1983, Cooke & Rayner 1984, Ramoska & Todd 1985).

Host specificity, co-evolution, and adaptation

Species of Hypocrella, Samuelisia, 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, Samuelisia, or Moelleriella. Petch (1921) stated that species of Hypocrella could parasitise either whiteflies (Aleyrodoidea) 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 & Andreasis 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 Sphaecelia, Ephiola and Neopythodium, 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-Entomothorid interations (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. virdans) 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. chalanensis, 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. macrostoma 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. phylogenata). 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. macrostoma. Other genera in the Clavicipitaceae, including Ascopolyergus 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 stylum. 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. phylogenata (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. phylogenata obtains some of its nutrients from the host plant rather than exclusively from the insect. In terms of its nutrition, M. phylogenata 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
ability of at an early stage in the development of the stroma, and is followed. This type of synanamorph is usually produced in culture hirsuta Meekes et al. Samuelsia, germination and viability. Conidia of most species of there is no known information on the factors that influence their 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. lbera, the first sign of infection is a discoloration 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. discoidae, M. epiphylla, M. turbinata) germinate to produce long and slender conidiogenous cells, and then secondary conidia (capillliconidia) (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 capillliconidia 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 telemorphs 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, Torubiella spp., and Ramona 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 from the fungus (Roberts 1981, Evans 1988). Evans (1988) hypothesised that toxins probably build up in the haemocoele 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 immunodepression 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. lbera (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 species (then classified in 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. i. species was revived, especially in Eastern Europe and Asia (Evans & Hywel-Jones 1990). Since then, many studies have shown that aschersonia-like species can be successful biocontrol agents against several species of whiteflies and scale insects (Uchida 1970, Ferron 1978, Ramakers et al. 1983, Ibrahim et al. 1996, Meekes et al. 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 Agronomico 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 Patavinium (PAD); Herbarium of the Botany Department, Swedish Museum of Natural History (S); Instituto de Botânica Carlos Spazzuzini (LPS); William and Lynda Steere Herbarium (NY); Herbarium Cryptogamique, Dépt. Systémateque 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 Botany, Naturhistorisches Museum Wien (W). Additional specimens examined 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 Kernerup 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, obliqua, 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 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 soft. 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 & Heester 1990); EF1-α: 983f (5'-GCYCCYGGHCAYCGTGAYTTYAT-3') and 2218r (5'-GT breeding for 10 min. The resulting PCR products were purified using 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 & Ronquist 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 elymis 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.
| 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. discoformis   | M.L. 202i = ARSEF 7695 | Puerto Rico | AY986913 | AY986939 | DQ000340 |
| H. discoformis   | P.C. 575 = CUP 067831 | Bolivia  | EU392557 | EU392641 | EU392695 |
| H. discoformis   | P.C. 589 = CUP 067833 | Bolivia  | EU392559 |          |          |
| H. discoformis   | P.C. 585 = CUP 067832 | Bolivia  | EU392558 | EU392642 | EU392696 |
| H. discoformis   | P.C. 659 = CUP 067835 | Honduras | EU392561 | EU392644 | EU392698 |
| H. discoformis   | P.C. 663.1 = CUP 067837 | Honduras | EU392563 |          |          |
| H. discoformis   | P.C. 661.1 = CUP 067836 | Honduras | EU392562 |          |          |
| H. discoformis   | P.C. 655 = CUP 067838 | Honduras | EU392560 | EU392643 | EU392697 |
| H. discoformis   | P.C. 676 = CUP 067839 | Honduras | EU392564 | EU392645 | EU392699 |
| H. discoformis   | P.C. 667 = CUP 067837 | 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 | EU392657 | EU392646 | EU392700 |
| H. cf. discoidea | I95-901d = ARSEF 7668 | Côte D’Ivoire | EU392658 | EU392647 | EU392701 |
| 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 067838 | Honduras | EU392560 | EU392643 | EU392697 |
| H. disciformis   | P.C. 676 = CUP 067839 | Honduras | EU392564 | EU392645 | EU392699 |
| H. disciformis   | P.C. 667 = CUP 067837 | Honduras | EU392565 |          |          |
| H. disciformis   | P.C. 737 = Afr 55 = ARSEF 7697 | Ghana | AY986910 | AY986936 | DQ000337 |
| H. disciformis   | I93-901d = ARSEF 7663 | Côte D’Ivoire | EU392657 | EU392646 | EU392700 |
| H. disciformis   | I95-901d = ARSEF 7668 | Côte D’Ivoire | EU392658 | EU392647 | EU392701 |
| H. disciformis   | 4093 | Thailand | AF327381 |          |          |
| H. disciformis   | 2630 | Thailand | AF327387 |          |          |
| H. disciformis   | BCC 2097 | Thailand | AF327381 | AY986945 | DQ000346 |
| H. hirsuta       | P.C. 543 = CUP 067841 | Bolivia  | EU392569 | EU392646 | 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      | I93-490 | IMI 346739 | EU392650 | 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. bolivensis    | 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     | I93-901d = ARSEF 7697 | 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 | 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 067789 | Bolivia  | EU392593 | EU392664 | EU392716 |
| Species | Voucher/Isolate | Origin       | GenBank Accession Numbers |
|---------|----------------|--------------|---------------------------|
| *M. libera* | P.C. 502 = CUP 067867 | Costa Rica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | P.C. 321 = ARSEF 7617 | Costa Rica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | I93-807 = CUP 067772 | Guiana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | M.C.A. 2335 = CUP 067870 | Guiana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | P.C.672 = CUP 067773 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | P.C. 445 = CUP 067869 = ARSEF 7707 | Mexico | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | P.C. 444 = CUP 067868 | Mexico | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. libera* | I93-815 = IMI 362284 = ARSEF 7654 | Trinidad | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. macrostroma* | P.C. 605 = CUP 067508 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. macrostroma* | J.B. 115 = CUP 067509 = ARSEF 7748 | Costa Rica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. madidiensis* | P.C. 569 = CUP 067776 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. madidiensis* | P.C. 594 = CUP 067775 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. mollii* | Afr 64 = ARSEF 7698 | Ghana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. mollii* | Afr 70 = ARSEF 7636 | Ghana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. mollii* | I93-901a = ARSEF 7660 | Côte D'Ivoire | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 535 = CUP 067777 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 384 = CUP 067515 | Costa Rica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 626 = CUP 067778 | Ecuador | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 61.2 = CUP 067780 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 648 = CUP 067779 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | P.C. 685 = CUP 067811 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | IMI 317421 = ARSEF 7672 | Jamaica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | IE 1308 = P.C. 726 | Mexico | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. ochracea* | I85-165 = CUP 067782 | Trinidad | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. phylogena* | P.C. 554 = CUP 067784 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. phylogena* | P.C. 555 = CUP 067785 | Bolivia | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. phylogena* | P.C. 628 = CUP 067790 | Ecuador | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. phylogena* | J.B. 130 = CUP 067703 | Panama | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. raciborskii* | Afr 28 = ARSEF 7657 | Ghana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. raciborskii* | P.C. 533 | Vietnam | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. raciborskii* | I93-901b = ARSEF 7661 | Côte D'Ivoire | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 467 = CUP 067538 | Costa Rica | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | CUP 067494 | Guatemala | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 675 = CUP 067547 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 691 = CUP 067548 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 693 = CUP 067549 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 696 = CUP 067550 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 698 = CUP 067551 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 458 = CUP 067795 | Mexico | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. rhombispora* | P.C. 460 = CUP 067534 | Mexico | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. schizostachyi* | CBS 100067 | Thailand | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. sloaneae* | I94-922c = CUP 067796 | Belize | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. sloaneae* | I94-920 = CUP 067802 | Guatemala | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. sloaneae* | I93-805 = CUP 067803 | Guiana | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
| *M. sloaneae* | P.C. 658 = CUP 067804 | Honduras | LSU: EU392592, EF-1a: DQ070121, RPBI: EU392590 |
Table 2. (Continued).

| Species                  | Voucher/Isolate | Origin       | LSU    | EF-1α    | RPB1     |
|--------------------------|-----------------|--------------|--------|----------|----------|
| M. sloaneae              | P.C. 665 = CUP 067805 | Honduras     | EU392624 |
| M. turbinata             | M.C.A. 2432 = CUP 067660 | Guiana      | AY986912 AY986938 | DQ000339 |
| M. turbinata             | P.C. 639 = CUP 067808 | Honduras     | EU392626 EU392686 | EU392738 |
| M. turbinata             | P.C. 678 = CUP 067663 | 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. 591 = CUP 067822 | Bolivia      | EU392636 |
| M. zhongdongii           | P.C. 595 = CUP 067823 | Bolivia      | AY986909 AY986934 | DQ000335 |
| M. zhongdongii           | P.C. 581 = CUP 067821 | Bolivia      | EU392635 |
| M. zhongdongii           | P.C. 461 = 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 |
| S. 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. Schardi 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 homoplasic 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. molii (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 69 % 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 of 63 %, NJ BP 98 %, and Bayesian Inference (BI) posterior probability (PP) of 100 %; Samuelsia by MP BP of 67 %, NJ BP 86 %, and PP of 100 %; and Hypocrella by MP BP of 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 Eufus (Fig. 2). Moelleriella can be divided into the Eufus and Globose clades. The Eufus clade includes M. basicystis, M. disjuncta,
M. evansi, M. libera, M. madidiensis, M. mollii, M. ochracea, M. rhombispora, M. phylogena, M. raciborskii, M. umbospora, and M. zhongdiongii. 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. discoidaea; 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 support (Moelleriella evansi, 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. zhongdiongii and M. madidiensis. This clade is supported by BP of 78 %, NJ BP of 100 %, and PP of 100 %.

Moelleriella phylogena (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. phylogena 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. phylogena 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 RP1 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 discoidaea (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 highest posterior probability is presented (-ln 22,746.4). Values at branches indicate Bayesian inference posterior probability/maximum likelihood bootstrapping probability/maximum parsimony bootstrapping probability (1,000 replicates). Only values for species clades are listed. Other branch-support values >75% 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 than 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. georornis 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 or 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 stroma does not change colour. Stromal anatomy is somewhat conserved in Hypocrella. The Hypocrella species examined have pulvinate stromata, or without hypothallii. 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. phylogena, 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 pycnidal-acervular conidiomata, slender flask-shaped to cylindrical phialides arranged in a compact hymenium, with or without paraphyses, brightly coloured and slim 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 stroma 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 stroma 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. phylogena, and M. umbospora, have tomentose stroma surfaces. Teleomorph stromata of M. basicystis, M. disjuncta, M. phylogena, 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. guaranitica. There is no reaction to 3 % KOH on the tissue of the stroma; 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 oblità, intricata, epidermoidà or a condition intergrading between these tissue types.

Perithecia in some species of Moelleriella can be formed in well-separated or gregarious tubercules, or they can be completely embedded in the stroma. Moelleriella libera, M. ochracea, M. rhombispora, M. zhongdongii, M. evansii, and M. sloaneae form perithecial tubercules. When the stoma 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. phylogena, 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.
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 pycnidal 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. evansi, M. libera, M. stoeaneae, 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., Hypocrella). The extent of variation in appearance of the colonies on PDA at 25 ºC was significant at the species level. Generally, 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 diam. in 3 wks. Generally, the colonies are smaller than phialides. However, M. macrostroma has significantly larger conidia in PDA at 25 ºC. A hirsutella-like synanamorph was observed in cultures of M. turbinata and M. evansi. This type of synanamorph has also been observed in M. inesperata (Liu et al. 2005). Capilliconidiofores and capilliconidica have been also observed developing from asci and conidia on PDA at 25 ºC. 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

The shape of the anamorphic stromata is generally pulvinate with a narrow base. The surface of the stroma can be dull/matt, opaque, glabrous, or roughened. Hypocrella hirsuta has symmetrical 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 discoidae 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 hypheae 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 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 pycnidal, 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 are sometimes indistinct, branching once monochaosal, twice monochaosal, monoverchillate, or two level monochaosal (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 × 2.5–3.5 µm). Conidal 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 the 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 ºC are smaller than phialides from stromata. However, M. macrostroma has significantly larger conidia in PDA at 25 ºC. A hirsutella-like synanamorph was observed in cultures of M. turbinata and M. epiphylla. This type of synanamorph has also been observed in M. inesperata (Liu et al. 2005). Capilliconidiofores and capilliconidica have been also observed developing from ascii and conidia on PDA at 25 ºC. Production of diffusing pigment was not observed in the cultures examined.
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 hirtellula-like synanamorph. Production of diffusing pigment was not observed in the cultures examined.

_Samuelia_ morphology

The _stroma_ morphology in _Samuelia_ is somewhat conserved. The _stromatal size_ of _Samuelia_ 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 _Samuelia_ 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. _Samuelia 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 _Samuelia_ 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 cirrinate. _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 (lw) 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_, _Samuelia_, 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 (_Samuelia_). 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. _Samuelia_ species have brown pulvinate stromata with a wide base and KOH+ tissue. _Samuelia_ 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 _Samuelia_ 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 _Samuelia_ 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 (BCS) (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 & Samuelis (2003)]. In the present monograph, a species concept similar to that followed by Chaverri & Samuelis (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, Samuelis, and Moelleriella, phylogenetically informative morphological characters can easily be assigned to each species. Even in the closely related groups of M. phylogena, 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. species pairs, the two species may be almost indistinguishable, can reliably be used to distinguish species. In the case of disjunct evolution of anamorph characters

Evolutionary hypotheses in Moelleriella, Hypocrella/Aschersonia, and Samuelis

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 Samuelis, in which more basal clades (e.g. Samuelis, 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. phylogena, 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 Samuelis may have affected the evolution and geographical distribution of lineages/species. Obornik 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. madidensis (Bolivia), M. gaertneriana (Brazil, French Guiana, Venezuela), M. cornuta (Brazil), M. evansi (Ecuador), M. basicystis (probably southern Central America), M. phylogena (probably Panama and Amazon basin), M. umbospora (probably northern Central America), M. disjuncta in (Panama, Guyana), S. chalensis (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 Samuelis, 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/Samuelis clade), as seen by the basal position of Samuelis. In general, taxa with small, allantoid conidia (i.e. Samuelis) 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, Samuelis, 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, pycnidal 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, Samuelis, 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 (Kulda 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 Namou; 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. 2001, 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 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 (Giare et al. 1985b, a, Evans 1994, Hodge 2003). The pycnidial anamorph produces spores that may be more efficient for infecting insects with 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 Entomothorales 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. 1. 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 comuta
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 macrostoma
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, 16, 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-ascosporas

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. Greysish yellow ............................................................................................................................................................... 7, 20
   d. Pale orange ....................................................................................................................................................................... 20
   e. Greysish ............................................................................................................................................................................... 7
   f. Greysish 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
   a. Florida, U.S.A. .................................................. 12, 15
   b. Mexico .............................................................. 7, 12, 15, 18, 20, 21

2. Central America
   a. Belize ............................................................. 19
   b. Costa Rica .......................................................... 1, 7, 12, 13, 15, 17–22
| Hypocrella | 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

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| Country | Page References |
|---------|-----------------|
| Argentina | 2, 4–17, 19, 20, 22 |
| Bolivia | 2, 7, 12–15, 17, 19, 22 |
| Brazil | 2, 4, 5, 9–12, 16, 17, 19 |
| Colombia | 7, 17, 20 |
| Ecuador | 7, 8, 15, 17, 19 |
| French Guiana | 6, 9, 17 |
| Guyana | 6, 7, 12, 19, 20 |
| Suriname | 7, 16, 17, 19, 20 |
| Venezuela | 9, 12, 17, 19 |
| Cuba | 1, 7 |
| Grenada | 20 |
| Guadeloupe | 19 |
| Puerto Rico | 6, 15, 18, 22 |
| Trinidad | 3, 6, 10, 12, 15 |
| Saint Vincent | 7 |
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
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 chalensis*
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  

DICHTOMOUS 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. phylogena* / "A." juroensis

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 4–6.6 × 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 × 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 >5.6 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 9.9–9.5 × 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 perithecium 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 ......................................................................................................................................8

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. macrostoma*
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 ................................................................. 4. M. macrostroma

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 thick pulvinate, sometimes almost effuse, strongly tuberculate, whitish, sometimes yellowish to orange-white;
    conidia 10–16 × 1.5–2 µm ........................................................................................................... 12. M. libera/“A.” aleurodis

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. phylogenica/“A.” juruensis

8'. Conidia 13–13.5 × 4.4–4.2 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.” aleurodis

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*
Moelleriella was described based on M. sulphurea, now considered a synonym of M. phylogegena (= H. phylogegena); thus, the type species of the genus is M. phylogegena. 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 conicose 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.) Chaverrri & K.T. Hodge, comb. nov. [= Fleischeria javanica Penzig & Sacc., M. phyllogena (Mont.) Chaverrri & K.T. Hodge, Anamorph: “Aschersonia” basicystis Berk. & M.A. Curtis, J. Linn. Soc. 10: 352.1869.

Telemorphosis: 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 subglobous 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. Perithecium completely embedded and on top part of stroma, numerous perithecium per stroma (>20), perithecium flask-shaped, 300–450 × 160–250 µm. Ascii 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 stroma; anamorphic conidiomata on natural substrata only on constricted part of stroma when teleomorph present. Exclusively anamorphic conidiomata on natural substrata only on constricted base of stroma when teleomorph present. In the original description of the genus, Bresadola (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. phylogegena, 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 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, Chiriquí, 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.
2. *Moelleriella boliviensis* Chaverri & K.T. Hodge, sp. nov. MycoBank MB511362. Fig. 4A–F.

Anamorph: Not known.

Teleomorph: Stromatibus subglobosus, 1.2–2 mm diam, cinereoflavidus; ascopora multiloculares, ad septum disarticulatae, incola, 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.

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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.
Habitat: On scale insects on leaves.

Known distribution: Bolivia, Brazil.

Specimens examined: Bolivia, Dpto. La Paz, San Jose de Uchupiamonas, Madidi National Park, on trail up the mountain along Estalbon River (“Senda RAP”), elev. 400–600 m, on scale-insects on leaves, 12 Jun. 2004, P. Chaverri (PC. 603), D. Quintana, M. Sogonov, A. Alvarez (holotype CUP 067747). Brazil, Maruana, Amazon River, Boa Vista, INPA fr., on leaves, 4 Oct. 1982, H.C. Evans (I92-795) (CUP 067748).

Notes: Moelleriella boliensis is similar to M. globosa and M. palmae. Moelleriella boliensis can be distinguished by the morphology and size of the stromata and smaller part-ascospores. Moelleriella boliensis 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: ascensionia-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 epidemoides. Perithecia completely embedded in the stroma, numerous perithecia per stroma (>30), perithecia flask-shaped, ca. 200–250 × 110–130 µm. Ascii 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.

Telemorph 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. mollis, M. libera vs. M. raciborski), 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. Nat. Cien. Córdoba 11: 533. 1889.

Anamorph: Not known.

Teleomorphic stromata pulvinate to subglobose, somewhat tuberculare, (1.5–)1.7–2 mm diam, greyish orange, ostoiates pale brown, surface smooth, opaque, without hypothallus. Hyphae of stromata forming compact textura intricata to epidemoides. Perithecium completely embedded in stroma, few perithecium per stroma (ca. 4–10), perithecium flask-shaped to subglobose, ca. 250–300 × 150 µm. Asci cylindrical, 1.5–2 µm thick. Ascospores filiform, multi-septate, 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, Apiayha, on insects on living leaves of Rubiaceae, Apr. 1888, C. Spegazzini 301 (holotype LPS No. 921).

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.

Teleomorphic: Stromatibus obconicus, cornutus, fuscus vel nigricans, durus, 1–3 mm diam, 2–9 mm altus; ascosporae multicellularae, ad septum disarticulatae, incola, 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 epidemoides. Perithecium completely embedded in stroma, numerous perithecium per stroma (>30), perithecium 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 Eucalytmatus sp. coocid (?) on leaves of Guarea tuberculata, 16 Jun. 1839, H.P. Krug (IAC 2900); Chara Morinhos, Capital, on insect on leaves, 1 Sep. 1942, D.B. Pickel (IAC 5129).

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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.
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. Ascii cylindrical, (145–)212–188–(231) × (9.5–)11.5–14.5–(18.3) µm, caps (1.8–)2.2–3.3(–3.3) µm thick. Ascospores filiform, multiseptate, disarticulating into part-spores that are cylindrical or curved with rounded ends and usually inflated in middle, ventricose, (6.8–)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, conidiomata U-shaped, shallow. Conidiomata with hymenium lining inner surface; phialides flask-shaped, generally straight, (9.5–)(10.7–)14–(16) × (1.5–)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, Lejeune (# 1121) (PC); Esequibo River, on leaf, 27 Feb. 1993, H.C. Evans (CUP 93-800) (CUP 067750).

Guyana: Pakaraima Mountains, Upper Potaro River, on leaf, 6 Jul. 2003, M.C. Aime (M.C. Aime (CUP 067744, 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) (PC: 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 Tabaque, on insect on dead leaf, 26 Mar. 1921, F.J. Seaver (epitope designated here NY 3370).

Notes: Moelleriella disjuncta is similar to M. phylogena, M. umbospora, and M. basicyctis. 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 epitope. No cultures survived storage at 8 °C. Moelleriella disjuncta belongs in the Effuse clade.

7. **Moelleriella epiphylla** (Masseae) Chaverri & K.T. Hodge, comb. nov. MycoBank MB511367. Fig. 7A–P. = Hypocreopsis epiphylla Masseae, J. Bot. 333: 164, 1892. = Hypocreopsis epiphylla (Masseae) Sacc., Sylloge Fungorum 11: 368, 1895. Anamorph: “Aschersonia” cubensis Berk. & M.A. Curtis, J. Linn. Soc. 10: 351. 1869. = Aschersonia chaetospora Sacc., Bol. Soc. Bot. Bucuresti 11: 368, 1893, fide Petch 1921. = Aschersonia amazonica Henn., Hedwigia 43: 338, 1904. = Aschersonia consociata 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. Ascii cylindrical, caps thin. Ascospores filiform, multiseptate, 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 stromata. 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, conidiomata U-, V-shaped, or irregular, deep. Conidiomata 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, (9.1–)10.5–11–(13.5) × (3.5–)(5.6) µm, l/w (1.5–)(2–)3–2(–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–)10–11–13 × (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 067866). Colombia. Choco, Rio Jito-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 Pallis, 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, Linderio El Peje, on leaf, 19 Aug. 2003, P. Chaverri (P.C. 305) (CUP 067756). CUBA. Santa Paulina, on insect on fenns, C. Mena-Jiles (CUP 3208). (Type of a cubensis S-F22297; isotype of a cubensis K(M) 120585). Ecuador. Guadalupe, Esmeraldas, on twig, 5 May 2000, H.C. Evans (CUP 067757). Manabi: Y de la Laguna, Reserva Bilba, 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.A. Curtis, J. Linn. Soc. 10: 351. 1869. = Aschersonia cubensis Berk. & M.A. Curtis, J. Linn. Soc. 10: 351. 1869. = Hypocreopsis epiphylla Masseae, J. Bot. 333: 164, 1892. = Hypocreopsis epiphylla (Masseae) Sacc., Sylloge Fungorum 11: 368, 1895. = Aschersonia chaetospora Sacc., Bol. Soc. Bot. Bucuresti 11: 368, 1893, fide Petch 1921. = Aschersonia amazonica Henn., Hedwigia 43: 338, 1904. = Aschersonia consociata Hedwigia, 43: 338, 1904, fide Petch 1921.
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, lutea, sphaericae vel ovoidales, (6–)10.3–12(–17.2) × (2–)2.7–3(–4.2) µm. Ascii cylindrical, (120–)139–175(–178) × (4–)5–6(–6.5) µm, caps 3.3–4 thick. Conidiose físsiles, multiseptate, disarticulándose en las partes que son a los obrados a cilíndrico con rounded ends, 14–19 × 1.1.5–2(–6). µm, producido en copiosa pluma. No paráfisis fueron observadas.

Habitat: On scale insects on bamboo leaves.

Known distribution: Brazil, French Guiana, Venezuela.

Specimen examined: French Guiana, Saül, ca. 20 km SW of Saül toward Mt. Galbé, Camp 3, elev. 650 m, on living bamboo culm (?Guadua), 21 Jan. 1986, G.J. Samuels and J. Boise 3255 (NY), Venezuela, Rio Negro Department, Cerro de la Neblina, along Río Mawarinuma, just outside Caron 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 (epítipo designado, 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 H. gaertneriana 1776 deposited in NY is designated here as the epítipo. 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.

Anamorph: aschersonia-like.

Teleomorph stroma large, globose to globuliform, 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 e intricata. Perithecio completely embedded in stroma, ostioles golden yellow, numerous perithecios per stroma (>50), perithecios flashe-shaped, (247–290–358(–378) × (142–175–221(–378)) µm. Ascii cylindrical, (120–)139–175(–178) × (4–)5–6(–6.5) µm, caps 3.3–4 thick. Conidios físsiles, multiseptate, disarticulándose en las partes que son a los obrados a cilíndrico con rounded ends, 4–14.3(–6.5(–8) × 1.5–2 µm. 8–14.

Habitat: On scale insects on bamboo leaves.

Known distribution: Ecuador.

Specimens examined: Ecuador, Manabi. Y de la Laguna, Reserva Balsa, 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 (holotipo: P.C. 627 = CUP 067764); Napo, Cuayabeno, on leaves of forest shrubs, 24 Jul. 1993, H.C. Evans (P.C. 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 perithecio and conidiomata scattered throughout the stroma with reddish orange conidial masses. On the other hand, M. evansii has perithecio 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 evansii has more slender conidia (l/w ca. 7) than M. evansii (l/w 4–5). Conidios and conidioma 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.

Teleomorph stroma 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 e intricata. Perithecio completely embedded in stroma, ostioles golden yellow, numerous perithecios per stroma (>50), perithecios flashe-shaped, (247–290–358(–378) × (142–175–221(–378) µm. Ascii cylindrical, (120–)139–175(–178) × (4–)5–6(–6.5) µm, caps 3.3–4 thick. Conidios físsiles, multiseptate, disarticulándose en las partes que son a los obrados a cilíndrico con rounded ends, 4–14.3(–6.5(–8) × 1.5–2 µm. 8–14.

Habitat: On scale insects on bamboo leaves.

Known distribution: Brazil, French Guiana, Venezuela.

Specimen examined: French Guiana, Saül, ca. 20 km SW of Saül toward Mt. Galbé, Camp 3, elev. 650 m, on living bamboo culm (?Guadua), 21 Jan. 1986, G.J. Samuels and J. Boise 3255 (NY), Venezuela, Rio Negro Department, Cerro de la Neblina, along Río Mawarinuma, just outside Caron Grande, near Neblina Base Cam, ca. 140 m elev., N 00º 50’, W 66º 10’, on bamboo culms, Apr.–May 1984, G.J. Samuels 1776 (epítipo designado, 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 H. gaertneriana 1776 deposited in NY is designated here as the epítipo. 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.
400 × 200–250 µm. Asci cylindrical, 150–160 × 8–10 µm, caps thin. Ascospores filiform, multi-septate, disarticulating into part-ascospores 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 Melastomataceae, Jan. 1897 (type W 00435; = Hypocrella glomerata Spez., An. Soc. Cient. Argent. 19: 47. 1885. = Hypocrella hypophyla Theiss., Anm. Mycol. 9: 66. 1911, fide Petch 1921).

**Notes:** Moelleriella globosa resembles M. palmæ and M. guaranitica. Moelleriella guaranitica has smaller ascospores and conidia than M. globosa. Moelleriella palmæ 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** (Spez.) Chaverri & K.T. Hodge, comb. nov. MycoBank MB 511371. Fig. 9A–J.

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 texture intricata to epidermioidea. 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.

Telemorph and anamorph usually not observed in same stroma. Anamorphic stroma 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 conidiomata 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 Paulo, Aparhy, on insects on leaf veins of Cattarea mollis, May 1881, C. Spegazzini? (J. Puggari No. 1483) (type of H. spiegazzini LPS 9031), Minas Gerais, Falcao Ouro Preto, on insects on stems of a Graminae, 29 Jun.

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 peritheciun per tubercle, perithecia nearly globose to ovoid, 300–400 × 300–600 µm; stromatal tissue around peritheciun texture intricata. Ascii cylindrical, with a cap ca. 5 µm thick. Ascospores filiform, slightly shorter than perithecia, separtate, 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 stroma 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 stroma, 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.
Known distribution: Neotropical, widespread.

Specimens examined: Bolivia, Dpto. La Paz, San Jose de Uchupiamonas, 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); Coba, Río Acre, on coccids on fallen leaves, Jan. 1912, E. Ule 3413 (type of H. libera, W00939). Brazil, Para, on leaves of Psidium pomiferum, May 1901, J. Huber 50 (SF22444, as A. paraensis); Manaus, River Solimões, on leaf, 30 Jul. 1991, H.C. Evans (P.C. 745 = CUP 067770, CUP 067771). Costa Rica, Heredia: OTS La Selva Biological Station, laboratory area, 17 Jun. 2002, M. Liu (culture CR01 = CUP 067341, culture CR20 = CUP 067342); plantation beside entrance RRC, 20 Jun. 2002, M. Liu (culture ARSEF 7617); Lindero El Peje, on leaf, 8–13 Jan. 2004, P. Chaverri (P.C. 502, P.C. 518) (CUP 067867, CUP 067868 = ARSEF 7707). 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. 2003, M.C. Aime (M.C.A. 2465) (CUP 067865, culture ARSEF 7642). Holotype of A. columnifera (FH 3966).

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

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: JAC 1977. Bars: A–C = 1 mm; D–J = 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 hosts: *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 scattered throughout the stroma. The stromata of *M. libera* is 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 macrostoma** (Chaverri & K.T. Hodge) Chaverri & K.T. Hodge, *comb. nov*. MycoBank MB511373. Fig. 10H–K. 
≡ Hypocrella macrostoma 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 *epidermidea*. Perithecium completely immersed in stroma, obpyriform, (377–)389–411–(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. Conidial ontogeny from original substrata, with pseudocystid-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)–2.3–2.7–(3) µm, l/w (4–)4.5–5.7–(7–). Paraphyses not observed.

Colony on PDA at 25 °C slow-growing, floccose or fluffy, compact, pale yellow, forming irregular pseudocystid-like concave depressions or cavities in colony and lacking a differentiated wall; conidial masses pale yellow. Conidiophores aggregated into a depression or cavity in colony, lacking a differentiated wall; conidia fusiform, apices acute, 8–12 × 1.5–2 µm, l/w (5.6–)5.9–6.7–(7–). Paraphyses absent. Colony on PDA at 25 °C slow-growing. Stromatic colonies somewhat loose *textura intricata* to *epidermidea*; 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, Chalalán, trail to mountain along Eslabon River (“Senda RAP”), on insects on leaves, 12–15 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 Efluse clade.

15. **Moelleriella ochracea** (M. Liu & Chaverri, *comb. nov.* MycoBank MB511375. Fig. 11G–N. 
≡ Hypocrella ochracea Masse, 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. Perithecium 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, multiseptate, 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.
**Known distribution:** Neotropical, widespread.

Specimens examined: **Bolivia**, Dpto. La Paz, San Jose de Uchupiamonas, 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 Bitia, 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); Yogo, 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 (IM 31741). 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 Universal Veracruzana building, 12 Dec. 2003, P. Chaverri (P.C. 430), J. Garcia-Alvarado (CUP 67524); Catemaco, (CUP 67523) Catemaco, behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado, (CUP 67523); behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado. 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 Universal Veracruzana building, 12 Dec. 2003, P. Chaverri (P.C. 430), J. Garcia-Alvarado (CUP 67524); Catemaco, (CUP 67523) Catemaco, behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado, (CUP 67523); behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado. 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 Universal Veracruzana building, 12 Dec. 2003, P. Chaverri (P.C. 430), J. Garcia-Alvarado (CUP 67524); Catemaco, (CUP 67523) Catemaco, behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado, (CUP 67523); behind Instituto Genetica Forestal Universidad Veracruzana building, J. Hernandez, J. Garcia-Alvarado.

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 MB511377. Fig. 12A-C.

≡ **Hypocrella 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. 1987, fide Petch (1921)
≡ **Hypocrella filicina** Rehm, Hedwigia 37: 200. 1898, fide Petch (1921)
≡ **Hypocrella cavernosa** A. Möller, Phycomyc. & Ascomyc.: 299. 1901., fide Petch (1921)
≡ **Riescheria paulensis** H. ochracea (0.5–)0.7–1.2(–0.5) mm. Hyphae of stromata forming compact textura orbicularis. Perithecia completely embedded and on top part of stroma, numerous perithecia per stroma (>20), perithecia flask-shaped, 300–450 ×160–250 µm. Asci cylindrical, 180–200 × 7–9.5 µm, caps ca. 1 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. No anamorph seen.

Anamorph: Not known.

Teleomorphic stroma with a globose head and a markedly constricted base (stul-dshaped), 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) µm. Hyphae of stromata forming compact textura orbicularis 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.

Teleomorphic and anamorph may or may not be present in same stroma. 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 flasks-

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 living leaves of palm (type of H. palmae, K(M) 52633).

Notes: Moelleriella palmae is similar to M. globosa and M. guanartica. They can be distinguished by the morphology of the stroma and ascosporae. Moelleriella palmae has larger stromata and ascosporae 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.
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 Uchapiamonas, Madidi National Park, Chalalan, trail Tapacare, on insect on Musa sp. leaf, 10 Jun. 2004. P.
Chaverri et al.

Chaverri (P.C. 554, P.C. 555), D. Quintana, M. Sogonov, A. Alvarez (CUP 067784; CUP 067785). Brazil. On leaves of Lauraceae, Aug. 1895, Edwaldi (holotype of H. edwaldi, S-F10585); Itambemirim, 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 Jobo-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 Blasa, primary forest, 0°22′47″, 79°44′48″ 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). French Guiana. Cayenne, on insect on leaf, Mar. 1839, Lepisor 580 (lectotype of M. sulphurea PC) Panama. Fortuna, on leaf of Costa, 14 Jul. 2002, J. F. Bischoff (I.B. 130 = P.C. 738) (CUP 067793). Venezuela. Bolivar, Canaima, on leaf, 23 Jan. 1994, H.C. Evans (I94-909) (CUP 067794).

Notes: Moelleriella philogena is similar to M. basicystis, M. umbrosa, 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. philogena. The types of H. weberbauri and M. sulphurea in herbarium B were also lost in WW II. According to Petch’s (1921) measurements of these specimens, they seem to be synonyms of M. philogena. Moelleriella sulphurea is neotypified herein with a specimen from Brazil. Cultures did not survive storage at 8 °C. Moelleriella philogena 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. Perithecium densely arranged in stroma, embedded, ostioli 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-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 reliculum 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, 1.5–2.5 µm. Conidia markedly inflated at the midpoint and tapering at both ends, 8.5–12–(17) × 2–3 µm, I/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 bifurpatus, 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 CR22 = CUP 067346); Punteranas, Las Cruces Biological Reserve, Wilson Botanical Garden, large loop of jungle trail, on Guarea rhopalocaipa, 4 Jul. 2002, M. Liu (ML49) (culture CR34 = CUP 67366). Guatemala. Tikal National Park, on leaf, 26 Jun. 2004, M.G. Milgroom (CUP 067494). Honduras. Yojca, Los Pinos, Parque Nacional Cerro Azul-Meambar, 850 m elev., 3 Sep. 2004, P. Chaverri (PC. 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 Pesca Quemada, 9 Sep. 2004, P. Chaverri (P.C. 679), R.A. Sheikh (CUP 067547). Mexico. Veracruz, Amayaga, Catemaco, 500 m elev., 14 Dec. 2003, P. Chaverri (PC. 458, PC. 460), J. García-Alvarado (CUP 067795, CUP 067534). Puerto Rico, between Mayaguaz and Maricao, beside road 105, 15 Dec. 2003, M. Liu & Z.D. Wang, ML 164 (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. philogena, M. basicystis, and M. umbrosa. **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–L.

≡ 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 tubercules 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. Tubercules projecting and aggregated, hemispherical, cylindrical or slightly narrowing apically; ostioli brownish yellow to brownish orange. Perithecium embedded in stroma, one perithecium per tubercle, perithecium 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, (3–)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

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, I/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.
neotropical Hypocrellaceae, Moelleriella, and Samuelia

Conidiomata abundant, scattered. Conidial masses yellow, abundant, confluent. Phialides (7.5–)12.3–14.5×(1.3–)1.7–2 µm. Conidia fusiform, (6.5–)7.8–8.3×(9.7–)1.8–2.2–2.5 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, MediP 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.
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 texture epidermoidea. Perithecia completely embedded in stroma, slightly turbinate, ostioles brownish orange or brownish yellow, numerous perithecia per stroma (＞20), perithecia flask-shaped to obpyriform, (264–)270–280 × (21.2–)25–30(–31.5) µm, caps 3–4 µm thick. Ascospores filiform, multi-septate, disarticulating into part-spores that are cylindrical or curved 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, conidia U-shaped, shallow. Conidiomata with hymenium lining inner surface; conidiophores in compact palisade, phialides short flask-shaped, (9–)10.7–16.5(–18) × (2.7–)3–5.6(–6.3) µm. Conidia hyaline, unicellular, ovoid, with acute ends, (8–)10.5–11.2(–13.5) µm (3.8–)4.5–5.6(–6.2) µm, lw (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 greyish yellow, with few tinges of green, compact but spreading, hyaline, unicellular, ovoid, with acute ends, (8–)10.5–11.2(–13.5) × (3.8–)4.5–5.6(–6.2) µm, lw (2–)2.3–2.5(–2.8), produced in copious slime. No paraphyses observed.

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 (93-850) (CUP 067807); Costa Rica, Cocos Island, Wasser Bay, on Lecanemum hesperidum; on leaves of Citrus aurantium, Jan. 1902, Pitiier (isotypes of A. pittier S-F22557 and FH 40031); Guyana, Pakarana Mountains, Upper Potaro River, Jan. 2004, M.C. Alme (M.C.A. 2432) (CUP 067860); Honduras, Dpto. Atlantida, Tela, Pico Bonito National Park, loop trail, on leaf, 26 Aug. 2004, P. Chaverri (PC. 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 (PC. 677, P.C. 678), P.A. Sheikh (CUP 067809, CUP 067863); Mexico, Estado Veracruz, Xalapa, on Citrus leaves, 22 Feb. 91, H.C. Evans (91-598) (IMI 352639 = cultureARSEF 7675); Nicaragua, on leaves, C. Wright 5479 (isotype of A. turbinata K(M) 1205241); Malagasy, Selva Negra, 1600 m elev., on leaf, 24 May 1992, H.C. Evans (PC. 757 = CUP 067810); Peru, San Martin, Tarapoto, Rio Shilcayo, on leaf, 28 Aug. 2002, H.C. Evans (PC. 758 = CUP 067811).

Notes: Moelleriella turbinata belongs in the Globose clade.

Moelleriella umbrosa Chaverri & K.T. Hodge, sp. nov.

Teleomorph: Stromatibus globosis, (0.5–)1–1.5–2.5(–5) mm diam, flavidus; ascospore multicellularis, ad septum disarticulatae, incolorea, partis subcilindricae vel fusiformes, ventricosus ad medium, (21.5–)24.5–26.2(–30.1) × (4–)5.5–(5.5) µm. Anamorphosis: Aschersonia similis. Stromatibus lutescentibus vel albidus, pulvinate vel subglobosis. Phialide 8.5–10 × 2–2.5 µm; conidi venetosus, (16.5–) 20–22(–25) × (4.5–)6–(6.7) µm, longitudo/crassitudo (3–)3.7–4(–4.5); paraphysis absens. Holotypus: CUP 067817.

Teleomorphic stroma with globose head and markedly constricted base (studded-shaped), whitish when immature becoming pale yellow when mature, (0.5–)1–1.5–2.5(–5) mm diam, surface smooth to slightly pruinose, opaque, with hypothallus (0.1–)0.5–0.7(–1) mm. Hyphae of stroma forming compact texture 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. Ascii 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.

Teleomorphic and anamorph may or may not be present in same stroma. 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 yellowish orange, or dark pale yellow. In section, the conidium U-shaped, shallow. Conidiomata 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–)13–15.5(–15.5) × (3–)4–4.2(–5) µm, lw (2–)2.3–3.3(–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-Archaeological Park, elev. 750 m, on leaf, 2 Sep. 2004, P. Chaverri (PC. 684), P.A. Sheikh (CUP 067812); Yucatan, Biologic Station, elev. 1780 m, on leaf, 4 Sep. 2004, P. Chaverri (PC. 703), P.A. Sheikh, P. Ameson (CUP 067813); Mexico, Chiapas, Palenque, on leaf, 24 Apr. 1994, H.C. Evans (94-923) (CUP 067814); Cozumel, Coba, on leaf, 30 Apr. 1994, H.C. Evans (94-916) (CUP 067815); Veracruz, Catemaco, Amayaga, on leaf, 14 Dec. 2003, P. Chaverri (PC. 457, P.C. 461), J. Garcia-Avalar, A. Eiras-Vera (CUP 067816; holotype CUP 067817).

Notes: Moelleriella umbrosa can be distinguished from the similar species M. basicystis, M. phyllogena, and M. disjuncta by the significantly larger part-ascospores and conidia of M. umbrosa. In addition, M. umbrosa part-spores have a pronounced swelling in the middle, and almost rhomboid conidia. Cultures did not survive storage at 8 °C. Moelleriella umbrosa 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. Palmisade 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.
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. Phialidies short or long; short phialidies most abundant, 10–20 × 1–1.5 µm, slender, cylindrical; long phialidies 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 (95-954) (CUP 067871 = ARSEF 7670); Dpto. La Paz, San José de Uchipiamonas, Madidi National Park, Chalaian, on leaves, 10–13 Jun. 2004, P. Chaverri (PC 549, PC 557, PC 561, PC 581, PC 591, PC 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 multilinervium, 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 Aleyrodes larvae on leaves of Doliocarpus dentatus, 21 Jun. 2002, M. Liu (ML-46) (CUP 067350); Puerto Rico, Adjuntas, on whitefly on a fern, 13 Mar. 1915, Britton, Cowell & Brown (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 (ML-149) (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, yellowish, orange, and green; stroma surface generally minutely pulverulent or pruinose; stromatal 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 capitulate. Ascospores hyaline, multiseptate, smooth, filiform to long fusiform, non-disarticulating, (55–)110–150(–180) × (1.5–)2–5(–6) µm, l/w ratio 5–6(–7). Paraphyses generally present.

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

Known distribution: Pantropical.

Notes: Hypocrella can be distinguished from Moellerella 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 anamorph are in fact fusoid part spores that have not formed septa. The species closely related to Hypocrella discoidea; stroma internal 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. Conidomata generally circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidomata pyriform, 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-Axarado, C. Mena-Jiles (CUP 067824); U.S.A., Florida, Gainesville, Sugarfort, on whitefly Paraleurodes perseae on Tamala bortonia, 7 Oct. 1936, E. West, R.K. Voorhus (no. 11876) (type K(M) 12055). Specimens not examined.

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

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

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

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. Ascii mostly clavate, 115–180(–300) × 8.7–12.7 µm, caps (0.8–)1.5–3 µm. Ascospores hyaline, multiseptate, smooth, long fusiform, (55–)110–150(–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, conidomata circularly arranged towards centre of stroma, and perithecia near periphery of stroma. Conidomata 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(–)}

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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 067925; J–M, P: CUP 067927. 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 Uchiquiamonas, 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. blumeniaensis B 70 000729); 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, Palmaris, on monocot leaf, Apr. 1900, E. Ule 2640 (type of A. abnormis S-F22380); Sao Paulo, Apiayi, on leaves of Myrtaceae or Zanthoxylea, 1888 (type of H. citrata LPS 904!) on leaves of Paucidum, Oct. 1901, No. 362 (type of A. flavochirina 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. Annt. Myc. 11: 547. 1913.

Teleomorph: Stromatibus pulvinatus vel disciformis (1–)1.8–2.3(–3.5) mm diam, luteus; ascoparum 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) × (4.5–5.5–5–6.5) µm, l/w (3.5–)4.3–5–5.5–7; paraehysis presences. Holotypus: CUP 067841.

Stromata (1–)1.8–2.3(–3.5) mm diam, yellow, KOH+, generally discoid, conidial, tuberculate, each tubercle containing one periheicum 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 pruinos; stroma outer tissue of texture epidermidea; stroma internal tissue of texture intrica. Perithecia embedded in stroma, sometimes protruding from stroma surface. Perithecia flask-shaped, (305–)315–355(–360) × (110–)113–150(–160) µm. Ascii mostly cylindrical, 200–245 × 18–22 µm, caps 5–6.5 µm thick. Ascospores hyaline, multisepitate, smooth, filiform to long fusiform, (120–)135–150(–170) × (5–6.5–6.5–7.2) 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 pycnidal, flask-shaped, 280–310 × 265–270 µm, with phialides formed in a thick compact palisade. Phialides cylindrical, slightly tapering towards tip, 19–25 × (1.5–)2.5 µm. Conidial hyaline, smooth, unicellular, fusoid, with acute ends. (17–)18.2–19(–21) × (3.3–)3.5–3.7(–4) µm, l/w (4.5–)5.5–6(–7.8). 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.

Known examined: Bolivia, Dpto. La Paz, San Jose de Uchiquiamonas, 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 7660; CUP 067832 = culture ARSEF 7692); Jaguar Trail, on leaf, 11 Jun. 2004, P. Chaverri (P.C. 599, D. Quintana, M. Sogonov, A. Alvarez (CUP 067833 = culture ARSEF 7662). 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 3890!, 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, P.C. 667), P. Sheikh (CUP 067861; CUP 067835; CUP 067836; CUP 067837; holotype CUP 067838; Santa Rita, Amarlo, Peña Quemada Reserve, elev. 800 m, on leaf, 9 Sep. 2004, P. Chaverri (P.C. 673, P.C. 676), P. Sheikh (CUP 067839, CUP 067840). Mexico, on leaves, 1913 (type of A. viridula FH 4027!, FH 4026).
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.
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. Perithecium 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.

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.

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–)4.8–6(–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 SI); Pará, on leaves, Spruce 528 (type of A. brunnea, K(M)130012 in part, under Hypocre a amazonica Cooke). Cuba, on leaf of Gesneriaceae, 1857, Wright 758 (type K(M)120253 and isotype P of Hypocre a viridans and Aschersonia viridans). Honduras, Dpto. Atlántida, Tela, Lancellotta Natural Reserve, elev. 0 m, on leaf, 24 Aug. 2004, P. Chaverri (PC 670, PC 671, PC 672, PC 673, PC 674, PC 675), P.A. Sheikh (CUP 067852, CUP 067853), V Og, Los Pinos, Ceno Azul/Measbar National Park, elev. 850 m, on leaf, 3 Sep. 2004, P. Chaverri (PC 695), P.A. Sheikh (CUP 067854). Mexico, Guerrero, Cuajimalpa, on leaf and rachis of Mimosa pi gra, 30 Nov. 1989, H.C. Evans (epitype of H. viridans designated here IMI 346739 = culture ARSEF 7674).

Notes: Hypocre a 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 Hypocre a 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, subaurantiacus, brunneo, sub-brunneo, bruneoluteus; ascospores multiloculares, macrofusiformes, (35–)40.5–51(–53) × 2–2.5 µm. Anamorphosis: Stromatibus pulvinatus, pyroidium. Conidioides allantoideus, subellipsoides, (4–)4.5–6(–7) × 1.5–2 µm, longitudo/ crassitudo 3–4; paraphysis prescens vel abscens, circlinatus 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 yellow, brown, or greyish yellow, no hypothallus, stroma surface generally smooth or slightly pruinose, opaque or glossy; generally KOH+ mostly on top central part of stroma; perithecial stromata pulvinate, steeped at central part and tapering towards base, 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, subgloboso, 320–380 × 110–120 µm. Asci mostly cylindrical to clavate, (90–)100–120(–130) × 5–7 µm, caps 1–3 µm. Ascospores hyaline, multisepitate, 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, mononerviculate with 2–5 phialides per verticil, once monocha losial, sometimes twice monocha losial; 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, I/w 3–4. Paraphyses present or absent, circlinate 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 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, subaurantiacus; phialides (12.3–)13–19.5(–22.7) × 1.3–1.5 µm; conidia allantoides, (5.3–)5.5–5.7(–6) × (1–)1.5–2 µm, longitudo/ crassitudo (3–)3.5–4.2(–5.2); paraphysis absent. 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, I/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 Uchiquiamonas, Madidi National Park, Chalalan, trail Tapacare, on bamboo, 10 Jun. 2004, P. Chaverri (PC 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 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, subaurantiacus, subbrunneo; asci (107–)112–122(–130) × (5.5–)6–6.7(–7) µm; ascospores multiloculares, 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, subgloboso, 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, multisepitate, 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).
Specimen examined: Bolivia, Dpto. La Paz, San José de Uchupiamonas, Madidi National Park, Chalalan, trail to mountain along Eslabon River (“Senda RAP”), on leaves of Geonomis sp., 12–13 Jun. 2004, P. Chaverri (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, subaurantiaco 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) x (1.8–)2(–2.5) μm, longitudo/crassitudo (2.5–)3(–3.8); paraphysis circinatus. Holotypus: FH 3991.

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. 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 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)
× (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; ascosporeae multicellulares, macrofusiformes, (42–)48–55(–57) × 1.5–2.5 µm. Anamorphosis: Stromatibus pulvinatus, pyxidium; phialides (14.5–)15.3–19.2(–22.5) × 1.3–1.5 µm; conidi allantoides vel subellipsoideus, (5.5–)6–6.2–6.7) × (1.3–)1.7–2 µm, longitudo/crassitudo (3–)3.5–3.7(–4.5); paraphysis prescens, ciricinatus. 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, multisepate, 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–)6.2(–6.7) × (1.3–)1.7–2 μm, l/w (3.5–3.7–4.5). Paraphyses present, circinate. Culture did not survive storage at 8 °C.

Habitat: On scale insects or whiteflies on leaves.

Known distribution: Honduras, Peru.

Specimen examined: **Bolivia**, Dpto. La Paz, San José de Uchíppimamonas, Madidi National Park, Chalalan, trail to mountain along Esabón River ("Senda RAP"), on leaves of Geonomis sp., 12–13 Jun. 2004, P. Chaverri (P.C. 613), D. Quintana, M. Sogonov, A. Álvarez (holotype CUP 067585). **Perú**, Madre de Dios, Tambopata, Picaflores Research Station, on leaves of Geonomis sp., 16 Jun. 2007, R. Gazis, H.C. Evans, P. Chaverri (P.C. 814) (CUP 067582).

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 MBS11390. 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.

Stromata pulvinate, subtuberculatus, (1.5–)2.2(–2.5) mm diam, brunneus; phialides (8–)9.5–10.5(–12) × (1.3–)1.5–1.7(–2) μm; conidia allantoides vel subellipsoideus, (3.7–)4.2(–4.5) × (1–)1.5(–2) μm, longitudo/crassitudo (2.2–)2.8–3(–4); paraphyses prescens, circinatus. Holotypus: CUP 067589.

Stromata pulvinate, (1.5–)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/Meanbar National Park, elev. 850 m, on leaf, 3 Sep. 2004, P. Chaverri (P.C. 686), P.A. Sheikh (holotype CUP 067589).

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.

Notes: According to observations made by the authors of type specimens of **Hypocrella caulium**, *H. brasiliensis*, 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 stroma 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 do 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.

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.

ACKNOWLEDGEMENTS

We thank the following people and institutions for helping us with collecting, permits, and logistics in each country: Bolivia: Emilia Garcia (LPS), Diego De la Quintana (LPS), Costa Rica: Luis D. Gomez (OTS), Giselle Tamayo (INBiO), Loeengun Urquiza (INBiO). Honduras: Phil Ameson (Saman); Peru: Romina O. Gaziz; Mexico: Juventino Garcia-Alvarado (Inst. Ecologia Forestal, U. Veracruzana); Puerto Rico: B. Jean Lodge (USDA), Sharon Cantrell (U. Turabo), Sandra Maldonado (UPRM). We also acknowledge several people who contributed specimens and cultures: Harry C. Evans (CAB), Gary J. Samuels (USDA), Joseph F. Bischoff (NCBI), M. Catherine Aime (LSU), Christopher L. Schardl (U.K.), José Hernández (USDA). We thank the staff at the different herbaria for loaning specimens and the different culture collections (ARCEF, CBS, BCC) for providing cultures. We are grateful to Amy Y. Rosman and M. Catherine Aime for letting the senior author, P. Chaverri, use the lab at the Systematic Botany and Mycology Laboratory (SBML-ARS-USDA, USDA Cooperative State Research, Education, and Extension Service, grant no. 99–35316–12623, and by the National Science Foundation, grant no. 0212719; both to K.T. Hodge.

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