

## DIVERSITY PATTERNS OF NEOTROPICAL PLANT PARASITIC MICROFUNGI

M. Piepenbring<sup>1\*</sup>, T.A. Hofmann<sup>1,2</sup>, R. Kirschner<sup>3</sup>, R. Mangelsdorff<sup>1</sup>, O. Perdomo<sup>4</sup>,  
D. Rodríguez Justavino<sup>5</sup> and T. Trampe<sup>1</sup>

<sup>1</sup>Department of Mycology, Institute of Ecology, Evolution and Diversity, Goethe-University of Frankfurt, Siesmayerstr. 71, 60054 Frankfurt am Main, Germany

<sup>2</sup>Facultad de Ciencias Naturales y Exactas, Universidad Autónoma de Chiriquí, 0427, David, Chiriquí, República de Panamá

<sup>3</sup>Department of Life Sciences, National Central University, Jhongda Rd., Jhongli City, Taoyuan County 32001, Taiwan

<sup>4</sup>Sociedad Dominicana de Micología, P. O. Box 151, 10101 Santo Domingo, Dominican Republic

<sup>5</sup>Ministerio de Desarrollo Agropecuario (MIDA), Río Tapia, Tocumen, República de Panamá

**Abstract.** Species richness in different groups of microfungi causing disease symptoms on above-ground plant organs is analyzed based on checklists and databases of five tropical regions in the Americas and two regions outside the tropics in North America. In addition, primary data on plant parasitic microfungi collected in natural habitats in western Panama are considered. According to these data, Asterinaceae, Meliolales, Phyllachorales, and rust fungi are highly species rich groups in the Neotropics, while smut fungi appear to be less diverse in the tropics than in extratropical regions. Species of Albuginales, Erysiphales, Peronosporales, and Taphrinales are rarely found in the tropics, and are especially scarce in tropical forests. Morphologically, many tropical plant parasitic microfungi are characterized by melanized walls of fruiting bodies and spores, apparently an adaptation to tropical conditions with strong solar radiation. Gelatinous substances may slow down the process of drying out. The absence of a winter season in the tropics is probably the reason for the lack of spore dormancy and the dominance of asexual developmental stages in the Erysiphales and rust fungi. *Accepted 9 December 2010.*

**Keywords:** *Albuginales, Asterinaceae, Erysiphales, Meliolales, mycogeography, Peronosporales, Phyllachorales, Pucciniales, Taphrinales, Ustilaginiales.*

### INTRODUCTION

Fungi in tropical countries are more poorly known than in most regions outside the tropics, with numbers of known species equal to 3–4 % of the estimated existing diversity (Guzmán 1998, Piepenbring 2007). Checklists of fungi are available for only a few tropical countries and a single flora exists for Venezuela (Dennis 1970). Monographs are lacking for most groups of fungi in tropical regions (e.g. Nishida 1989, Schmit & Mueller 2007). Many tropical species described one hundred and more years ago have not been re-investigated and therefore are “orphaned” species, according to Hawksworth (2001). In contrast to microfungi on cultivated plants that cause economic losses, pathogenic microfungi on native tropical plants are rarely investigated (e.g. Lodge &

Cantrell 1995, Gilbert & Hubbell 1996, Shivas & Hyde 1997, Chaverri & Vélchez 2006, García-Guzmán & Morales 2007, Hyde *et al.* 2007 and citations therein). However, it is already well documented that plant parasitic microfungi are highly diverse in tropical regions as a result of their adaptation to highly diverse host plants and microhabitats (e.g. Rossman 1997). According to Shivas & Hyde (1997), plant parasitic fungi are more abundant in tropical than in non-tropical regions. However, no comprehensive study has been performed to test this hypothesis.

In this paper, data obtained from checklists and databases on species of plant parasitic microfungi are analyzed and combined with results from extensive fieldwork in Panama, in order to address the mycogeographic question of which groups of plant parasitic microfungi typically occur in the Neotropics as opposed to regions outside the tropics.

\* e-mail: piepenbring@em.uni-frankfurt.de

TABLE 1. Systematic positions of groups of plant parasitic microfungi selected for the present study.

| Division      | Order (family)               | Common name            |
|---------------|------------------------------|------------------------|
| Oomycota      | <b>Albuginales</b>           | white blister rusts    |
|               | <b>Peronosporales</b>        | downy mildews          |
| Ascomycota    | <b>Erysiphales</b>           | powdery mildews        |
|               | <b>Meliolales</b>            | black mildews          |
|               | <b>Phyllachorales</b>        | tropical tarspot fungi |
|               | <b>Asterinaceae</b>          | fly speck fungi p.p.   |
|               | <b>Taphrinales</b>           | -                      |
| Basidiomycota | Pucciniales                  | <b>rust fungi</b>      |
|               | Ustilaginales                | <b>smut fungi</b>      |
|               | Tilletiales and other orders |                        |

Plant parasitic microfungi are harmful to living plants causing leaf, stem, and floral diseases. They are also agents of root diseases, but these are not included in the present analysis. Plant parasitic macrofungi, belonging to Agaricales, “polypores”, Stereales, or Xylariales, are also not considered here.

Ecologically and morphologically well-defined groups of plant parasitic microfungi belonging to Oomycota (Pseudofungi or fungus-like organisms), and sexually reproducing Ascomycota and Basidiomycota (both groups of Fungi), have been selected (Table 1). They represent 63% (about 14600 species) of the estimated 23000 known species of plant parasitic fungi (Shivas & Hyde 1997). Microfungi in most of the selected groups are obligate parasites that do not grow in culture, except for the smut fungi and Taphrinales, which include a saprophytic yeast stage in their life cycle. Asexually reproducing fungi (Fungi Imperfecti) and numerous small groups of plant parasitic Ascomycota, are not included because our knowledge of their diversity and ecology is too limited. For a characterization of the groups considered for the present analysis see the appendix.

## MATERIALS AND METHODS

*Analysis of checklists and databases.* Checklists and databases of fungi for regions of different latitudes in North America and the Neotropics were selected, with preference given to large datasets based on literature covering all groups of fungi. Varieties, subspecies, and forms are not counted. Synonyms have

been checked with the help of the Index Fungorum (<http://www.indexfungorum.org/Names/Names.asp>) and by our taxonomic investigation.

Because collecting has been much more extensive in non-tropical areas, absolute numbers of species are not used to evaluate diversity patterns. Instead, relative species richness has been calculated, based on the number of species known for each group of fungi as a percentage of the total number of species considered in the respective geographic area. Relative species richness for groups of fungi is compared between geographic areas.

The following geographic areas, checklists, and databases have been used in this study:

**State of New York, United States:** BPI fungal databases, Farr *et al.* (n.d.), consulted 6 May 2007.

**State of Florida, United States:** BPI fungal databases, Farr *et al.* (n.d.), consulted 6 May 2007.

**Caribbean:** Minter *et al.* (2001).

**Panama:** Piepenbring (2006a; total number of species 1807) plus records of plant pathogenic microfungi published later (Hofmann & Piepenbring 2006, 2008; Piepenbring 2006b, 2007; Hernández *et al.* 2007, Rodríguez-Justavino & Piepenbring 2007, Trampe & Piepenbring 2007, Perdomo & Piepenbring 2008, Hofmann *et al.* 2010). An updated checklist of fungi known for Panama is available at <http://biogeodb.stri.si.edu/biodiversity>.

**Venezuela:** Dennis (1970) and other publications integrated in the BPI fungal databases Farr *et al.* (n.d.), consulted 7 May 2007. Records of smut fungi are taken from Piepenbring (2003). The total number of fungi was obtained from Iturriaga & Minter (2006) and D. Minter (pers. comm.).

**Ecuador:** <http://www.mycology.com/Ecuador.html> by T. Læssøe & J.H. Petersen, consulted 6 April 2007, and publications integrated in BPI fungal databases, Farr *et al.* (n.d.). Records of smut fungi are based on Piepenbring (2003). For the total number of fungi in Ecuador, see Læssøe & Petersen (2008).

**Brazil:** Sabo-Mendes *et al.* (1998). The lists are complemented by other publications integrated in BPI fungal databases (Farr *et al.* n.d.), data on Oomycota by Milanez *et al.* (2007), records of rust fungi by Hennen *et al.* (2005), and records of smut fungi by Piepenbring (2003). The total number of fungi only refers to fungi on plants in Sabo-Mendes *et al.* (1998).

*Diversity of plant parasitic microfungi in western Panama (ppMP-Project).* Plant parasitic microfungi were collected in 15 different sites in western Panama, southern Central America. The sites correspond to more or less disturbed forests and open disturbed vegetation at altitudes ranging from sea level to almost 3300 m.a.s.l. During 2005-2007, most sites were examined for plant parasitic microfungi a total of four times by three trained mycologists for two hours. Only one specimen was taken during one collecting event for a given species of plant parasitic microfungi. Only data on systematic groups presented above are included in this study. Publications containing the original data on different species are in preparation.

Coauthors focused on systematic groups of plant parasitic microfungi as follows:  
 Peronosporales and related groups – M. Piepenbring  
 Erysiphales – R. Kirschner  
 Meliolales – D. Rodríguez-Justavino, M. Piepenbring (F. Herbst, S. Ix, T. Nozon)  
 Phyllachorales (without Glomerellaceae) – T. Trampe  
 Asterinaceae – T. Hofmann  
 Taphrinales – M. Piepenbring  
 rust fungi – O. Perdomo, R. Mangelsdorff  
 smut fungi – M. Piepenbring

## RESULTS

*Species richness of plant parasitic microfungi in the Americas.* Absolute and relative species richness values of selected groups of plant parasitic microfungi known in regions of North America and the Neotropics are shown in Table 2. The data are plotted in Fig. 1, showing mycogeographical tendencies. According to our data, the relative species richness of the recorded species is lower in the tropics than in regions outside the tropics for the Albuginales, Erysiphales, Peronosporales, Taphrinales, and smut fungi, but higher for the Asterinaceae, Meliolales, and Phyllachorales. Known species of rust fungi are the largest group in all areas except in Panama, where they are topped by Meliolales.

*Diversity of plant parasitic microfungi in western Panama (ppMP-Project).* During 54 two-hour collecting events at 15 different sites by three trained mycologists, a total of almost 1300 specimens of plant parasitic microfungi was collected. No fungal agent of leaf spots could be identified on almost 100 specimens. Only asexually reproducing Ascomycota and Basidiomycota (Fungi imperfecti) were present on approximately 240 specimens and were not considered (except asexual stages of rust fungi). Among

TABLE 2. Numbers (n) of species and percentages (%) relative to the total number of species of plant pathogenic fungi considered for the respective area in selected groups of plant pathogenic fungi (ppf) obtained from checklists and databases for areas in North America and the Neotropics. See Materials and Methods for references. The total numbers of fungi known for the different areas include all systematic groups of fungi, except for Brazil, where the number refers to plant parasitic fungi only.

| latitude       | USA      |     | USA     |     | Caribbean   |     | Panama     |     | Venezuela  |     | Ecuador     |     | Brazil       |     |
|----------------|----------|-----|---------|-----|-------------|-----|------------|-----|------------|-----|-------------|-----|--------------|-----|
|                | New York |     | Florida |     | 10° - 28° N |     | 8° - 10° N |     | 1° - 11° N |     | 2° N - 5° S |     | 5° N - 34° S |     |
|                | n        | %   | n       | %   | n           | %   | n          | %   | n          | %   | n           | %   | n            | %   |
| Albuginales,   |          |     |         |     |             |     |            |     |            |     |             |     |              |     |
| Peronosporales | 31       | 8   | 36      | 6   | 27          | 2   | 10         | 3   | 28         | 4   | 15          | 3   | 30           | 2   |
| Erysiphales    | 44       | 11  | 28      | 5   | 21          | 1   | 3          | 1   | 14         | 2   | 1           | 0   | 37           | 3   |
| Meliolales     | 1        | 0   | 35      | 6   | 455         | 29  | 118        | 35  | 104        | 14  | 74          | 13  | 141          | 11  |
| Phyllachorales | 49       | 12  | 51      | 9   | 239         | 15  | 52         | 15  | 113        | 15  | 64          | 11  | 198          | 15  |
| Asterinaceae   | 1        | 0   | 34      | 6   | 151         | 10  | 14         | 4   | 40         | 5   | 19          | 3   | 42           | 3   |
| Taphrinales    | 14       | 3   | 10      | 2   | 5           | 0   | 1          | 0   | 2          | 0   | 6           | 1   | 1            | 0   |
| rust fungi     | 172      | 43  | 318     | 56  | 577         | 37  | 113        | 33  | 404        | 54  | 346         | 62  | 800          | 60  |
| smut fungi     | 90       | 22  | 56      | 10  | 90          | 6   | 29         | 9   | 43         | 6   | 37          | 7   | 77           | 6   |
| total ppf here | 402      | 100 | 568     | 100 | 1565        | 100 | 340        | 100 | 748        | 100 | 562         | 100 | 1326         | 100 |
| total n fungi  |          |     |         |     | 11260       |     | 1882       |     | 4115       |     | 3766        |     | 4196         |     |

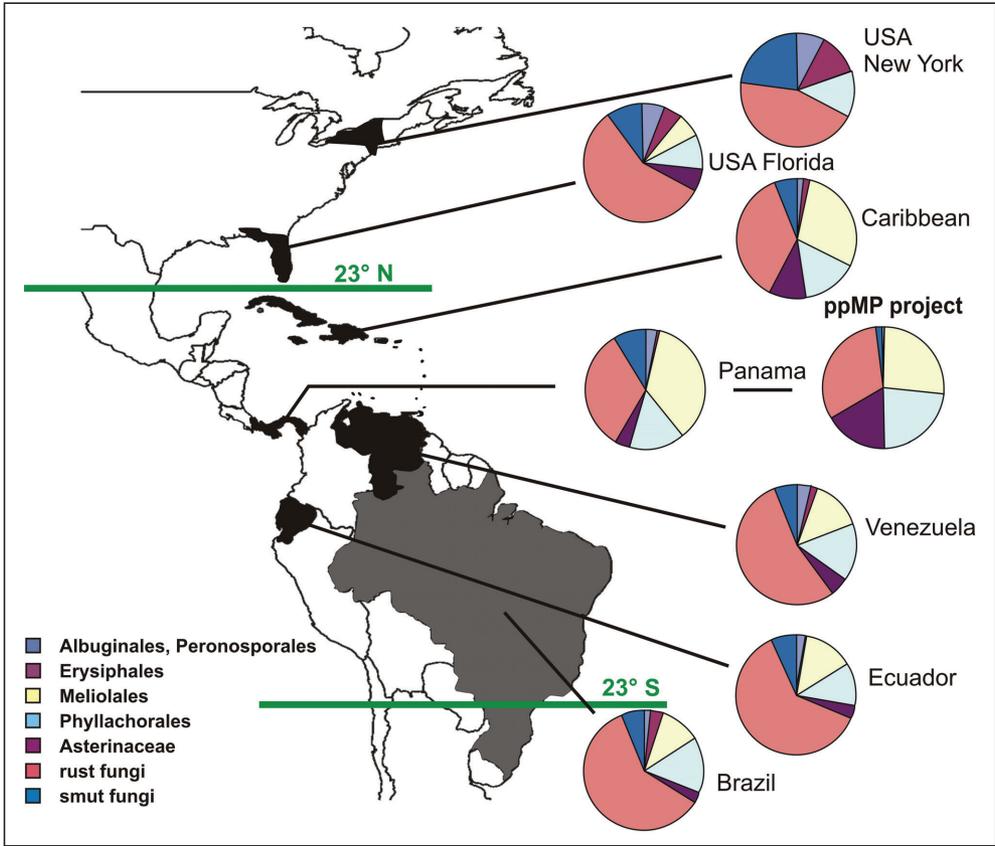


FIG. 1. Diagrams reflecting the relative abundance of species in different groups of plant parasitic microfungi in different areas of the Americas based on checklists, data bases, and results of the ppMP project. The tropics are located between the latitudes 23° N and 23° S (green lines).

TABLE 3. Numbers and percentages of specimens and species of plant pathogenic fungi obtained by ppMP project fieldwork in western Panama.

|                                | specimens | % specimens | species | % species |
|--------------------------------|-----------|-------------|---------|-----------|
| Albuginales/<br>Peronosporales | 5         | 1           | 3       | 1         |
| Erysiphales                    | 0         | 0           | 0       | 0         |
| Meliolales                     | 139       | 19          | 89      | 26        |
| Phyllachorales                 | 180       | 25          | 75      | 22        |
| Asterinaceae                   | 123       | 17          | 60      | 17        |
| Taphrinales                    | 1         | 0           | 1       | 0         |
| rust fungi                     | 262       | 36          | 110     | 32        |
| smut fungi                     | 9         | 1           | 6       | 2         |
| total                          | 719       |             | 344     |           |

the remaining specimens, 719 were identified as members of the groups of fungi analyzed here. Numbers of specimens and numbers of different species are presented in Table 3.

Rust fungi are the most abundant and species-rich group of plant parasitic microfungi in wild vegetation in western Panama with approximately 110 species represented by more than 260 specimens. Rust fungi are most frequently collected in their asexual uredinal spore stage, with orange-colored urediniospores having relatively thin walls. Teliospores were observed on occasion and tended to germinate immediately. Spermogonia and aecidiospores have been found only rarely. All species of rust fungi collected in the ppMP project are most probably autoecious.

Black plant parasitic Ascomycota, represented here by the Asterinaceae, Meliolales, and Phyllachorales, comprised more than half of the specimens and species. Only a few species of Peronosporales, Taphrinales, and Ustilaginales were collected. Only one asexually reproducing species of Erysiphales was found (not counted).

In comparison with data obtained from checklists and databases (Fig. 1), the ppMP project yielded a higher value for Asterinaceae but relatively few collections of Albuginales, Peronosporales, and Ustilaginales.

## DISCUSSION

Although the datasets available are incomplete and many species concepts not yet settled, the analysis of checklist data and results obtained from the ppMP project allow the determination of fungal groups which are typical for temperate or tropical regions.

According to Walker (1983), *downy mildews* are most diverse in temperate regions of the northern hemisphere and mostly live on cultivated and introduced plants. Data presented here support this hypothesis for the Americas. Downy mildews and white blister rusts are apparently absent as parasites of leaves in forests, as shown by the ppMP data and projects in Mexican forests (García-Guzmán & Dirzo 2001, 2004). Species of *Phytophthora* and other species of Oomycota not considered here, however, are certainly present in most forests as pathogens of roots, as saprophytic organisms in the soil, and perhaps as endophytes within the plants.

Most *powdery mildews* are known from temperate areas of the northern hemisphere. However, they also exist in regions with a temperate climate in the

southern hemisphere, for example in southern South America, where they have not been intensively investigated up to now (M. Reychenberg, pers. comm.). According to the hypothesis by Heluta (1992, 1995, translated and summarized in Voytyuk *et al.* 2009), Erysiphales possibly originated in China and migrated via the Bering Bridge to North America and later to South America. While spreading towards tropical regions of the Americas, Erysiphales apparently lost the tendency to develop sexual organs, because a chasmothecium is not necessary as there is no winter in a tropical climate. Powdery mildews are relatively common in their asexual form on cultivated and introduced plants in the tropics, while no species of Erysiphales were found in the forests of Panama according to ppMP data. The hypothesis proposed by Walker (1983), that in tropical regions powdery mildews rarely develop their sexual stage, can be supported for the Neotropics, but several exceptions exist that show a high diversity of life strategies (e.g. Hanlin & Tortolero 1984).

Species of *black mildews* have a higher species richness in the tropics than in non-tropical regions (Dennis 1970, Shivas & Hyde 1997, present data). The relative species richness of this group based on checklists and databases in the Neotropics is similar to that determined in the collecting activities of the ppMP project.

*Tropical tar spot fungi* are most diverse in the tropics, as shown by the data presented here. They are one of the major groups in the ppMP project, as they are relatively common in disturbed and natural, open and forest vegetation throughout western Panama. Within the ppMP project, tropical tar spot fungi are the most abundant Ascomycota but not the most species rich.

Species of *Asterinaceae* are more numerous in the tropics than in temperate regions (Dennis 1970, Hosagoudar & Abraham 2000, present data). Their species richness in the ppMP project is higher than their species richness recorded for other regions, probably because few mycologists investigate these inconspicuous fungi. They were found in every habitat investigated for the ppMP project, with the highest diversity in open vegetation. The Asterinaceae and other small black species of parasitic or epiphyllous Ascomycota, such as Englerulaceae and Parmulariaceae, are highly diverse in tropical vegetation and mostly unstudied.

Species of *Taphrinales* are apparently more diverse at higher latitudes of the northern hemisphere than

in Neotropical regions. They are almost absent in Australia and New Zealand except for some species on introduced plants (Walker 1983). During the ppMP project a single species of this group, *Buerenia myrrhidendri* Döbbeler, was found at high elevations. The synasci of *B. myrrhidendri* germinate immediately upon maturity and liberate a large quantity of yeast cells.

According to the data presented here, it is not possible to decide whether *rust fungi* are more diverse in the tropics than at higher latitudes. However, since rust fungi infect a large range of plants and are generally host-specific, the higher species richness of vascular plants in the tropics should correlate with a higher species richness of rust fungi. Recent observations for South Africa, however, imply that the hypothesis “more host species correlates with more rust species” may give false results, as some species-rich plant families almost completely lack infection by rust fungi (Berndt 2008). In the ppMP project, rust diversity was found to be somewhat low relative to the high number of plant parasitic Ascomycota.

The dominant spore stage observed in tropical ecosystems is the uredinium, sometimes accompanied by telia, while acia and spermatogonia are rarely found (comp. Schmiedeknecht 1986). Apparently, in the tropics some rust fungi successfully reproduce by asexual urediniospores only. The species collected during fieldwork in Panama, and species counted in checklists for tropical regions, all appear to be autoecious, i.e. live on a single host-plant species. This may be due to the absence of a winter season and the availability of green leaves during the entire year in most tropical habitats, but also to the lack of infection studies. As far as we know, a heteroecious life cycle has only been demonstrated by infection studies for two species of rust fungi in the Neotropics, by Thomas (1918).

The present data show a lower relative diversity of *smut fungi* in the tropics than in temperate regions. Smut fungi were rarely collected in the ppMP project, because few habitats with abundant host plants, which are mainly species of Poaceae and Cyperaceae, like savannahs, swamps, and other open habitats, were searched. During the ppMP project, no smut fungus was found in tropical forests.

By comparing fungi that are commoner in temperate regions with those in tropical regions, we can observe differences in morphological and biological characteristics that might correspond to adaptations to the respective environment. The following gen-

eral tendencies of morphological characteristics and life cycle strategies have been noted in groups of tropical plant parasitic fungi:

- Tropical plant parasitic microfungi *protect their spores against intense solar radiation*. Walls of hyphae (Asterinaceae, Meliolales, Figs. 2a,b,d, 4), fruiting bodies (Asterinaceae, Meliolales, Figs. 2a,b, 4), and clypei (Phyllachorales, Figs. 2c, 3) contain melanin pigments in their cell walls which are stable, insoluble, and resistant organic components crucial for cell survival, fungal virulence, and pathogenicity (Parbery & Emmett 1977, Howard & Valent 1996, Jacobson 2000). Peridia or tissue of the host plant (Fig. 2g) surround and protect developing masses of spores of certain species of rusts and smuts. Spores exposed to solar radiation during dispersal may be protected either by thick, dark-colored walls (Meliolales) or carotenoids (rust fungi, Fig. 2f) (e.g. Dickinson 1986 and citations therein). These adaptations are probably important in the tropical climate, but they can also be observed in certain fungi in temperate regions.
- *Dormancy of spores* or other resistance structures (chasmothecia of Erysiphales, synasci of Taphrinales, teliospores of rusts and smuts, sclerotia of Hypocreales etc.) is not necessary in tropical climates because temperatures are favorable and many plants have green leaves throughout the year. Therefore tropical spores mostly germinate immediately, as observed, for example, for *Buerenia myrrhidendri* (Taphrinales, Fig. 2e), rust fungi (e.g. Perdomo & Piepenbring 2008), and species of smut fungi (Piepenbring 1996). The chasmothecia of *Erysiphe malachrae* Seaver (Erysiphales) open as soon as they are ripe in humid conditions to expose their asci and actively liberate their ascospores (pers. obs. M. Piepenbring, specimen from Ecuador).
- Tropical *rust fungi* are apparently mostly *autoecious* which is possible because many tropical plants exhibit green leaves all year. However this apparent tendency may also be due to a lack of knowledge of the life history of tropical rust fungi.
- Numerous species of rust fungi (Fig. 2f), some smut fungi (e.g. *Tilletia ayresii*, Figs. 2g,h), and the majority of Erysiphales species observed in the American tropics *multiply by asexual spores*. Sexuality is apparently not as important as in colder regions, where it is often correlated with dormancy.
- Gelatinous sheaths around spores *slow down desiccation* and speed up rehydration, help adhesion to the substrate, and protect against radiation and

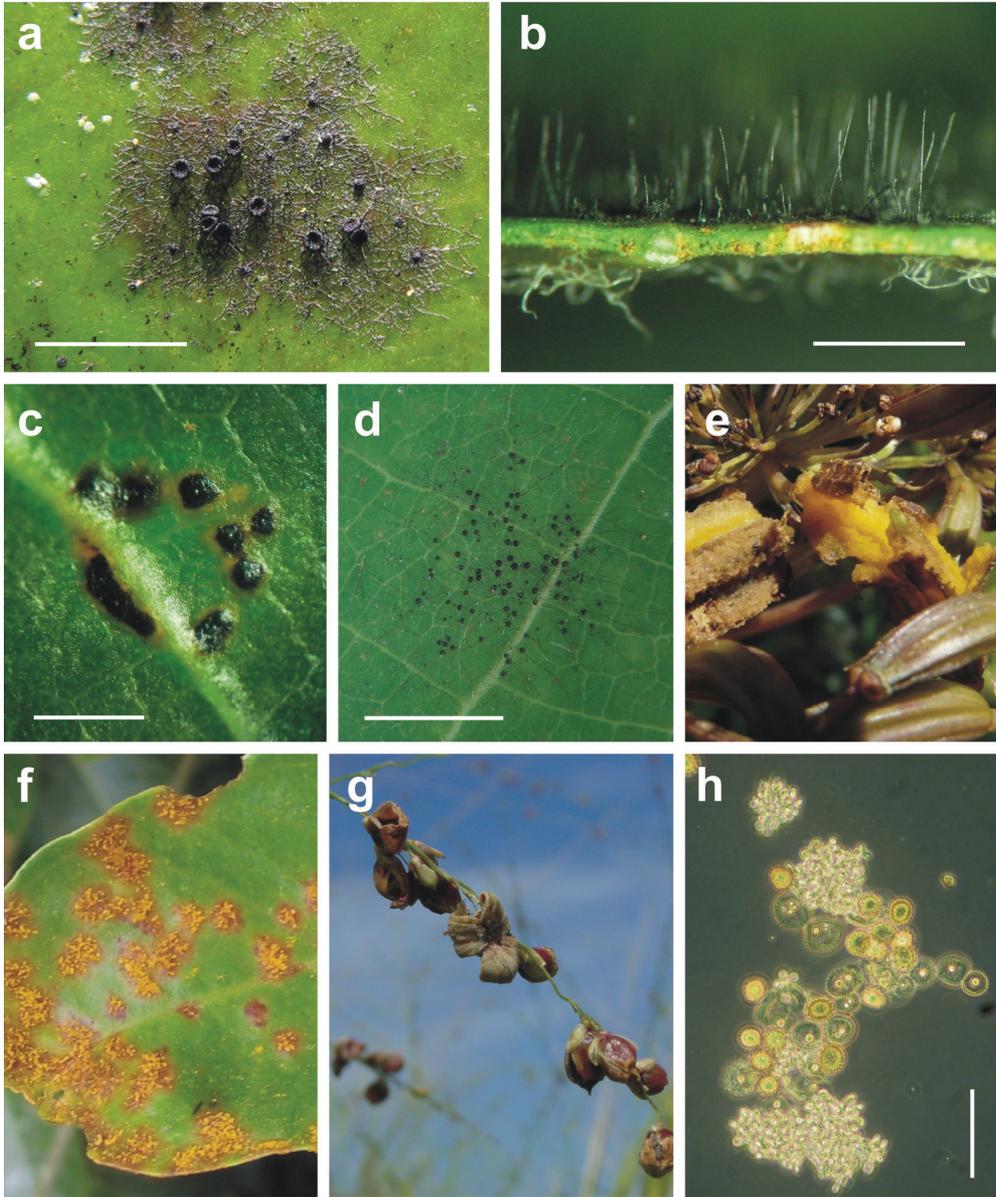


FIG. 2. Tropical plant parasitic microfungi. a-b. Meliolales. (a) A colony of *Meliola bicornis* on *Desmodium* sp. Scale bar = approx. 2 mm. (b) Superficial hyphae, setae, and a perithecium of *Meliola byrsonimicola* on *Byrsonima crassifolia* as seen with a stereomicroscope. Scale bar = 1 mm. (c) Phyllachorales. *Phyllachora ocooteae* on *Ocotea veraguensis*. Scale bar = 1 mm. (d) Asterinaceae. *Asterina manihotis* on *Manihot esculenta*. Scale bar = 1 mm. (e) Taphrinales. *Buerenia myrrhidendri* on *Myrrhidendron donnellsmithii*. Ovaries are transformed to galls, rupture, and expose large orange-colored spores (synasci). (f) Pucciniales. Uredia of *Puccinia psidii* on *Syzygium malaccense*. g-h. Tilletiales. *Tilletia ayresii* on *Panicum maximum*. (g) Ovaries transformed to galls by the smut. (h) Teliospores, sterile cells, and balls of conidia as seen by light microscopy. Scale bar = 50  $\mu$ m.

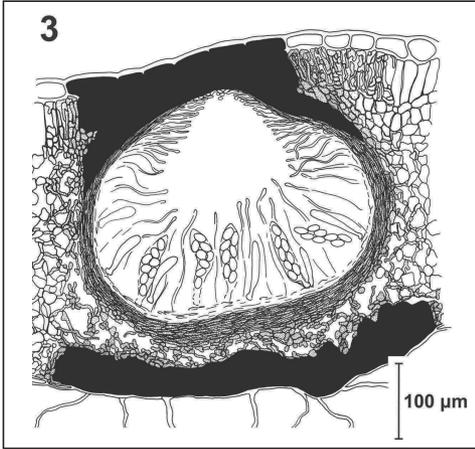


FIG. 3. Phyllachorales. *Phyllachora cecropiae* on *Cecropia* sp. Longitudinal section of a perithecium with amphigenous clypei embedded in leaf tissue.

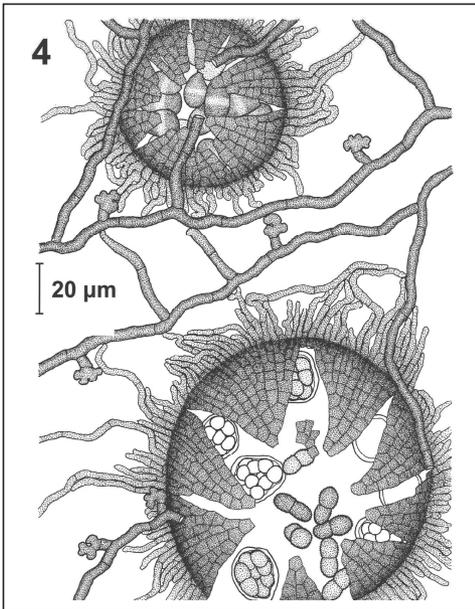


FIG. 4. Asterinaceae. *Asterina radiofissilis* on *Acalypha arvensis*, with a thyriothecium (below) and the asexual form (above) seen from above, together with superficial hyphae with hyphopodia.

parasites (Dickinson 1986). Spores of Phyllachorales have mucilaginous sheaths, which might serve these functions. Mucous substances within fruiting

bodies have been observed in species of Asterinaceae, protecting internal cells against desiccation. All these structures, however, also occur in fungi of temperate regions and have to be interpreted with caution.

Colonies of black mildews are often characterized by long setae located on hyphae or fruiting bodies (Fig. 2b). These setae have a hygrophilous surface and often have tips with branches or other special structures. Thus a water film (dew or rain) is more persistent on a colony of black mildew than on the rest of a leaf (pers. obs. M. Piepenbring). A prolonged period of humidity may enhance the growth of fungal hyphae or may facilitate the movement of spermatia to receptive hyphae, which, however, has never been observed. Humidity also allows the growth of other epiphyllous organisms associated with a colony of black mildew, such as cyanobacteria, algae, and small animals like Tardigrada (M. Piepenbring, pers. obs.). Metabolites excreted by these organisms may serve as a nutritional source for black mildew but also promote the growth of other fungi which inhibit its development.

## CONCLUSIONS AND FUTURE WORK

The data presented here allow speculations about species richness and adaptation of plant parasitic microfungi to tropical climatic conditions, but these conclusions must be submitted to experiment and critical discussion. To improve our knowledge of the diversity and ecology of these microfungi, extensive fieldwork as well as taxonomic, morphological, and phylogenetic research are necessary. In addition to new species, data on the geographical distribution of known and new species, host ranges, and life cycles are needed for a better understanding of plant parasitic microfungi as highly diverse organisms important for our thinking on tropical biodiversity and ecology.

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## APPENDIX:

## CHARACTERIZATION OF SELECTED GROUPS OF PLANT PARASITIC MICROFUNGI

*White blister rusts and downy mildews* (Albuginales and Peronosporales, Oomycota) live as parasites of leaves, stems, or roots (Dick 2001). They form asexual spores ("conidia") or sporangia containing zoospores on coenocytic hyphae growing out of stomata on living leaves (Peronosporales), or produce hyaline sporangia in white sori (Albuginales). Oospores developing within host tissue have dark walls which allow the fungus to survive during adverse environmental conditions. For the present analysis, only species growing as obligate parasites causing symptoms on living shoots are considered. Host plants of these downy mildews and white blister rusts are mostly herbs belonging to various families of dicotyledonous and monocotyledonous plants. Species diversity and molecular phylogeny of white blister rusts and downy mildews are relatively well known (Voglmayr *et al.* 2004, Thines & Spring 2005, Voglmayr & Riethmüller 2006) but sequence data reveal cryptic species (e.g. Choi *et al.* 2008).

*Powdery mildews* (Erysiphales) are morphologically and ecologically somewhat similar to downy mildews, as the fungi in both groups are characterized by the presence of white hyphae and spores on the surface of plant organs. However the Erysiphales are true Fungi (as are all the following groups), they have septate hyphae, form appressoria on the host epidermis, and haustoria in host cells (Braun 1987). Hyaline conidia (asexual spores) are produced during seasons of plant growth. During winter in temperate climates, powdery mildews survive as dark-colored, thick-walled, closed sexual organs (chasmothecia). Chasmothecia contain asci (meiosporangia) with one-celled, not pigmented ascospores, which are liberated under favorable environmental conditions. Powdery mildews infect both dicotyledonous and monocotyledonous herbs and woody plants. For the present analysis, only species of Erysiphales reported by their sexual names are considered. Asexual specimens are difficult to identify and not well recorded for most countries.

In the powdery mildews, DNA analyses contributed considerably to our understanding of the evolution of powdery mildews and their geographical expansions from North to South America (Takamatsu *et al.* 2000, 2006). Several species have expanded

their distribution rapidly due to globalization and climate change (Glawe 2008). Many aspects of host specificity, life cycles, and geographical distribution, however, still await clarification.

*Black mildews* (Meliolales, Figs. 2a,b) grow on the surface of leaves, stems, and sometimes fruits of vascular plants. Black mildews grow superficially on their hosts with dark, thick-walled hyphae and lateral branches with terminal appressoria (Hansford 1961, 1963; Müller & von Arx 1973). The appressorium perforates the wall of the epidermal cell and forms a haustorium inside the host cell for the uptake of nutrients. The hyphae also carry cells with a beak and an opening at the tip from which small spores can be liberated. These spores are rarely observed and they might be conidia formed by phialides for asexual reproduction (Hughes 1981), or spermatia for sexual reproduction. In numerous species of Meliolales, hyphae or fruiting bodies carry numerous long setae. The globose fruiting bodies with openings (perithecia) are located on the surface of the host tissue and contain asci with mostly two to four dark, septate, thick-walled ascospores each.

Host plants are herbs or woody plants, di- or monocotyledones, some species are known on Pteridophyta. Black mildews are apparently mostly host specific, at least at family level, showing morphological variability that is constant on a given host plant (Rodríguez-Hernández 2001).

Our knowledge of species diversity in black mildews in the tropics is still very limited, as well as our knowledge of their ecology, host specificity, and life cycle (Parbery & Brown 1986). Although almost 2000 species of Meliolales are known, DNA sequences are only available for two species (Saenz & Taylor 1999) and for one further species (Rodríguez-Justavino & Piepenbring 2007).

*Tropical tar spot fungi* (Phyllachorales, Figs. 2c, 3) are plant parasitic fungi but mostly do not cause great damage to their hosts. They develop perithecia located on the surface, others break through the epidermis, but most are embedded within the mesophyll of leaves or rarely in stems (e.g. Cannon 1991, Pearce & Hyde 2006). Embedded ascomata are covered by a clypeus, a black and dense shield formed by dark fungal cells. Inside the perithecia, evanescent paraphyses and numerous asci develop. The latter generally contain eight hyaline, aseptate ascospores that may darken at maturity. Freshly released ascospores are usually enclosed by a mucilaginous matrix and may be dispersed by rain splash (Parbery 1963).

Phyllachorales also form small, irregular to flask-shaped fruiting bodies containing mitospores that can be observed either together with the perithecia or independently (Trampe & Piepenbring 2007). We ignore whether the small, hyaline, thin-walled mitospores are able to infect a new host plant or whether they correspond to spermatia – in the latter case the fruiting bodies should be called spermatogonia (Parbery & Langdon 1963, Cannon 1991). Most host plants are woody with long-lived leaves, e.g. species of the families Arecaceae, Cyperaceae, Fabaceae, Melastomataceae, Moraceae, Myrtaceae, and Poaceae (Cannon 1997). As host specificity is unknown and only few molecular sequences are available (Wanderlei-Silva *et al.* 2003), the number of known species is difficult to assess (Cannon 1991).

Species of *Asterinaceae* (Figs. 2d, 4), so-called fly speck fungi, form thin dark hyphae on the surface of host tissue, mainly leaves (Reynolds & Gilbert 2006). They infect the host by forming appressoria with haustoria that penetrate epidermal cells. Other species develop hyphae that grow within the host tissue, between or within host cells. Bitunicate asci containing pigmented, two-celled ascospores are located underneath thyriothecia, small, shield-shaped ascomata on the surface of the leaves (von Arx & Müller 1975, Eriksson 1981). Asexual stages with pigmented conidia on superficial mycelium or underneath flat, shield-shaped pycnidia (pycnothyria) occur with or without their respective sexual forms. Many anamorph-teleomorph connections, however, are still unknown. For the present analysis, only sexual species are considered.

*Asterinaceae* grow mainly on woody evergreen dicotyledonous plants, e.g. on members of Euphorbiaceae, Flacourtiaceae, Lauraceae, Melastomataceae, Myrtaceae, Rubiaceae, and Solanaceae with host specificity assumed to be restricted to single plant genera or families (Rahayu & Parbery 1991, Hofmann & Piepenbring 2008). The host specificity at genus or family level, however, has not yet been analyzed.

The *Asterinaceae* may be as species rich as the black mildews (Hosagoudar & Abraham 2000), but they have been mostly overlooked and less frequently collected than black mildews. DNA sequences are available for five species of *Asterina* and for one asexual species of this family (Hofmann *et al.* 2010), who published the first phylogenetic hypothesis for this group of fungi.

Species of *Taphrinales* (Fig. 2e), some of them agents of leaf-curl disease, differ from the fungi mentioned above by the presence of a saprophytic yeast stage in their life cycle (Kramer 1973, Reddy & Kramer 1975). During their parasitic phase on plants, hyphae which grow in the host tissue can cause hypertrophic growth and distortion of leaves, flowers, or fruits. While species of *Taphrinales* develop thin-walled asci on the surface of hypertrophic host tissue, species of *Protomycetaceae* develop large cells within the host tissue that allow the fungus to survive during winter in regions with a temperate climate. These spores correspond to synasci, i.e. meiosporangia with numerous diploid nuclei that divide by meiosis and are incorporated in numerous ascospores. The ascospores of species of *Taphrinales* form yeast cells which multiply by budding. DNA analyses based on cultures have mostly confirmed the previous taxonomy (Sugiyama *et al.* 2006). Host plants of this small group of host-specific fungi are herbs or woody species of dicotyledonous plants and ferns.

The *rust fungi* (Pucciniales, formerly Uredinales, Fig. 2f) are the most species-rich order of plant parasitic fungi within the Basidiomycota (Cummins & Hiratsuka 2003). The life cycle of rust fungi is generally presented based on *Puccinia graminis* Pers., a species typical of temperate climates. It includes five different generations of spores on two different host plants, so this rust is heteroecious. Spermatia, the first generation of spores, are formed in spermatogonia, small, ephemeral structures, for fecundation of receptive hyphae. Aecidiospores, uredospores, and teliospores are formed in sori called aecidia, uredia, and telia, respectively, mostly on leaves or stems. Sori are usually located within host tissue that breaks open when spores are ready for dispersal, mostly by wind. Aecidiospores and uredospores of most rust species are orange-colored due to the presence of carotenoids in the cytoplasm, while teliospores often have thick, darkly pigmented (melanized) walls. By the elaboration of numerous urediniospores, rusts multiply and are dispersed onto plants of the same host species during summer, while teliospores survive during adverse conditions in winter. Life cycles of many rust species in temperate climates only have some of the generations, a single host plant (autoecious), or other strategies to overcome winter (*cf.* Gäumann 1959).

Species of rust fungi tend to be host-plant specific and infect plants belonging to most systematic groups of plants, including herbs and

woody species, gymnosperms, dicotyledonous and monocotyledonous plants, as well as ferns. Numerous species of rust fungi are known and molecular data are available for an increasing number of species (e.g. Aime 2006), but a great number of unknown rust fungi are estimated to exist, especially in the tropics (e.g. Berndt 2004, Shivas & Hyde 1997).

*Smut fungi* (formerly Ustilaginales, or Ustilaginales and Tilletiales; Figs. 2g,h) today correspond to species in the Doassansiales, Entylomatales, Geogefischeriales, Tilletiales, Urocystales, Ustilaginales (Ustilaginomycotina), Microbotryales (Pucciniomycotina), and the genus *Entorrhiza* of uncertain systematic position (Bauer *et al.* 2001). Here, only “true” smut fungi, species within Ustilaginomycotina forming characteristic teliospores, are considered.

Most smut fungi are characterized by dusty masses of brown to black teliospores formed in sori on the host plant and dispersed mostly by wind (Piepenbring *et al.* 1998, Vánky 2002). Teliospores of smut fungi can survive during cold winters and might need a cold period to germinate. Teliospores germinate forming basidia with basidiospores that can bud, initiating a saprophytic yeast stage which grows in culture. Most species of smut fungi live on species of Asteraceae, Cyperaceae, and Poaceae. Only a few species infect woody plants and ferns.

The taxonomy and systematics of smut fungi is based on the morphology of sexual stages and molecular data are available for many species (e.g. Begeerow *et al.* 2006). Current knowledge of smut fungi in the Neotropics, however, is still far from complete (Piepenbring 2003).