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Natural and Cultural History of the Golfo Dulce Region, Costa Rica

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HRSG.: Biologiezentrum der Oberösterreichischen Landesmuseen

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Due to the orographic formation of its interior and its humid climate, the Golfo Dulce Region is rich with biodiversity, containing very dense flora and fauna. After HOLDRIDGE (1971), the region was subdivided into different zones, including the tropical rainforest, the tropical wetland forest, and tropical premontane rainforest. The biogeographical situation in this area shows many similarities to the flora and fauna in the Amazon and the Colombian Chocó Region and serves as a land bridge with a valuable genetic base between North and South America. After unregulated seizure of land by agricultural settlers, lumberjacks, and large landowners in the 1940s and 1950s, regulated, state-subsidised settlement reform intended to support agricultural exports in the 1960s, and intensification of the livestock industry in the 1970s, primary and secondary forest reserves have shrunk to a minimum. The constant expansion of monocultures on new land has far-reaching consequences for the local ecosystem.

The conservation and sustainable use of tropical forests is established in the Forest Declaration, Convention on Climate Protection, and Convention on the Protection of Species, which demonstrate worldwide concern for these issues. As a regional example, in the 4,304.80 km^2 drainage basin, the ACOSA (Área de Conservación OSA), which covers an area spanning the Cantons Osa, Golfito und Corredores, aims to protect species diversity within the 17 game preserves, which are 44.7% covered by forest, through integration and an alliance with the Parques Nacionales, Vida Silvestres y Forestales (Fig. 2). The main sector of the Corcovado National Park on the Osa Peninsula covers 424 km^2 and the Piedras Blancas National Park covers 148 km^2. The altitude ranges from sea level to 745 m on the Osa Peninsula (Cerro Rincón and Cerro Mueller in the Fila Matajambre) and to 579 m in the Esquinas forest (Cerro Nicuesa). The Golfo Dulce Forest Reserve (592 km^2) was established between the two parks, thereby forming a natural forest corridor.

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Diversity and ecology of fungi in the Golfo Dulce region

Diversidad y ecología de hongos en la región del Golfo Dulce

Meike PIEPENBRING & Armando RUIZ-BOYER

Abstract: Fungi play many roles in complex systems of organismic interactions in tropical forests. They provide water and minerals to plants as mycorrhizal fungi, others decompose dead organic material, mainly wood, into compounds which are made available for other organisms. As parasites of insects, they perform a natural biological control of insect populations. As parasites of plants, they contribute to the development and maintenance of plant diversity. Other fungi cause diseases in vertebrates, like chytridiomycosis in frogs, dermatomycosis or systemic mycoses in humans. Fungi live in mutualistic symbiosis with vascular plants as mycorrhizal fungi or endophytes, with algae as mycobionts of lichens, with leaf-cutting ants as fungal garden, and with scale insects. Although fungi are very important in tropical ecosystems and offer many possibilities to be used by humans for food, medicine, and other purposes, there are relatively few mycologists working in the tropics. Our knowledge of tropical fungal diversity is still in the pioneer phase. Estimates suggest that we know less than 4% of the existing tropical fungal diversity. Much research remains to be done in tropical rainforests like those of the Golfo Dulce region.

Key words: mushrooms, lichens, mycorrhiza, plant parasitic fungi, insect parasitic fungi.

Resumen: Los hongos desempeñan muchos papeles en los complejos sistemas de inter-relaciones de los organismos en los bosques tropicales. Como hongos micorrízicos abastecen de agua y minerales a las plantas, otros descomponen materia orgánica muerta, principalmente madera, en compuestos que serán aprovechados por otros organismos. Como parásitos de insectos, realizan el control biológico natural de las poblaciones de insectos. Como parásitos de plantas, contribuyen al desarrollo y mantenimiento de la diversidad de las plantas. Otros hongos causan enfermedades en vertebrados, como quitridiomicosis en ranas, dermatomicosis o micosis sistémica en humanos. Los hongos viven en mutualismo con plantas vasculares como hongos micorrízicos o endófitos, con algas como micobiontes en líquenes, en las hojas cortadas por hormigas y en los denominados insectos escama. Aunque los hongos son muy importantes en los ecosistemas tropicales y ofrecen muchas posibilidades para el ser humano como alimento, medicina, y otros propósitos, hay relativamente pocos micólogos trabajando en los trópicos. Nuestro conocimiento sobre la diversidad de los hongos tropicales todavía se encuentra en una fase inicial. Estimaciones sugieren que conocemos menos del 4% de la diversidad de hongos que existen en los trópicos. Muchas investigaciones faltan por realizar en los bosques lluviosos tropicales como los presentes en la región del Golfo Dulce.

Palabras clave: setas, líquenes, micorriza, hongos patógenos de plantas, hongos patógenos de insectos.

Introduction

Ecology

The Golfo Dulce rainforests, with their high diversity of plants and animals, high humidity, and elevated temperatures all year round, offer numerous niches and good living conditions for a high diversity of fungi. Fungi and fungus-like organisms (certain protozoans, heterotrophic algae, Myxomycota) are omnipresent in tropical ecosystems, with their estimated species diversity being second only to insects. They are easily overlooked, however, because most of them live as microscopic hyphae or yeast cells in the soil, or within and upon plants and animals. Mycelia of relatively few species of fungi form conspicuous fruiting bodies from time to time.

Any organic material placed in this environment is immediately colonised by fungi. In order to grow, and for the development of macroscopically visible fruiting bodies, fungi need energy. As heterotrophic organisms, however, fungi cannot use the energy of the sun like autotrophic plants can. They have to find organic compounds like sugars and carbohydrates which they incorporate by absorption. What are the nutrient sources for a fungus in a tropical environment?

Dead organic material, like dead parts of plants and dead animals, are important substrates for saprophytic

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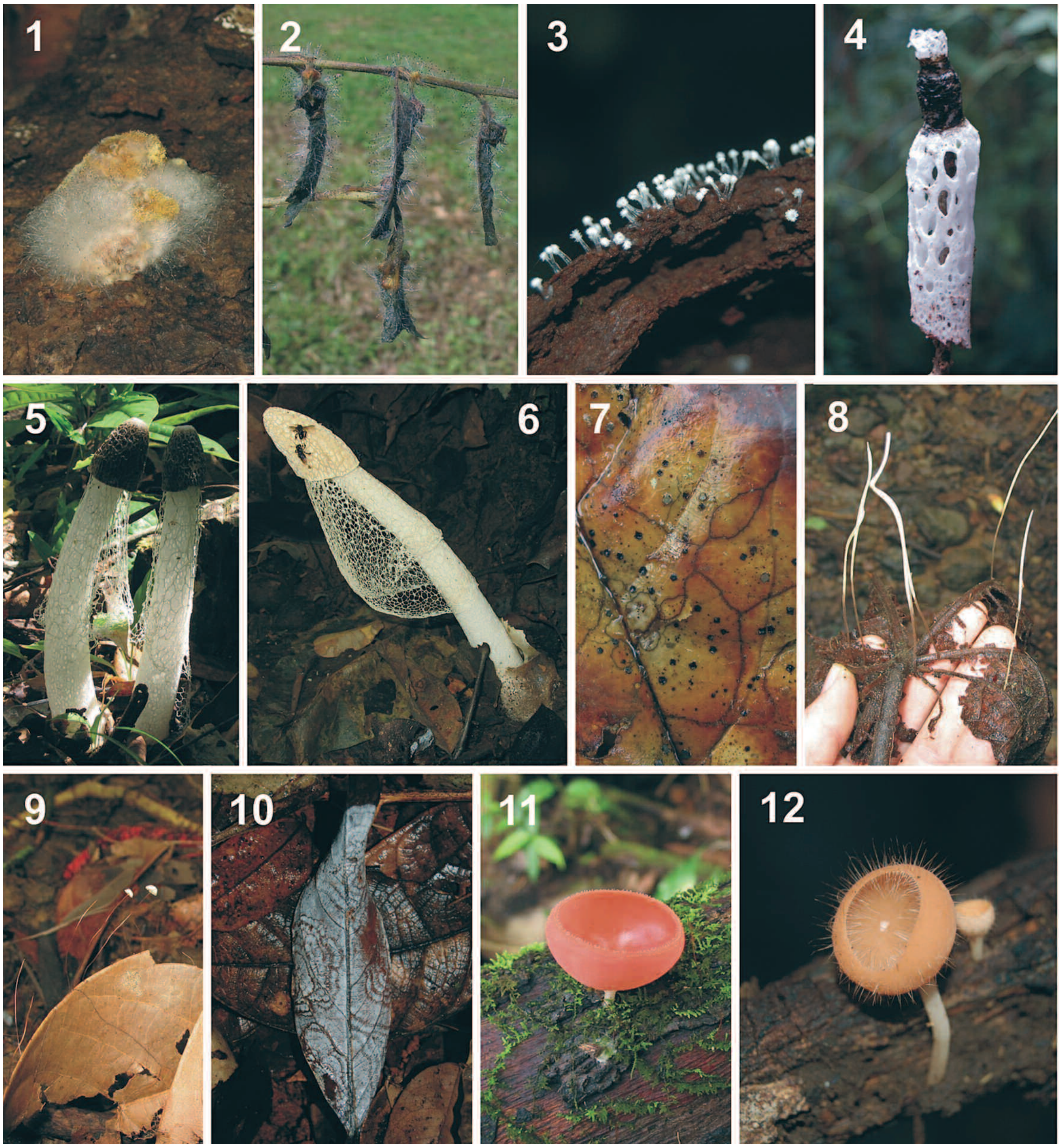


Figs. 1-2: Moulds belonging to the Zygomycota. (**1**) Growing on dung. (**2**) Growing on recently cut leaves.
Fig. 3: A slime mould (Ceratiomyxales, Myxomycota) forming tiny fruiting bodies with white spores.
Figs. 4-6: Phallales. (**4**) *Staheliomyces cinctus* exposes a wet mass of stinking basidiospores on a complex stipe. (**5-6**) *Phallus* (formerly *Dictyophora*) sp. enhances the attractiveness of its fruiting body with a white veil. (**5**) *Phallus* sp. exposing the stinky mass of basidiospores. (**6**) Insects are attracted by the mass of basidiospores, feed and disperse them. At the base of the fruiting body the remains of the envelope of the young fruiting body are evident. **Fig. 7**: *Coccomyces* sp. (Rhytismatales) on a dead leaf. **Fig. 8**: Slender fruiting bodies of *Macrotyphula* sp. (Basidiomycota) on a dead leaf. **Fig. 9**: Tiny gill fungi (*Marasmius* sp.) on a dead leaf.
Fig. 10: Fungal mycelium on a dead leaf. **Fig. 11**: *Cookeina speciosa*. **Fig. 12**: *Cookeina tricholoma*.
Photos 1-2, 5, 7-8, 11: M. Piepenbring; 3-4, 6, 9-10, 12: A. Weber.

fungi. Due to temperatures favourable for growth of any living being all over the year, easily degradable organic material is scarce in tropical lowland forests like those of the Golfo Dulce area and has to be shared with other fungi, bacteria, and animals.

Any living organism is formed by organic compounds on which the fungus might live as well, but is not easily accessible to the fungus. Plants defend themselves with thick, hardly penetrable surfaces, tannins, and complex physiological reactions upon infection. Animals protect themselves by their immune system and other complex defence strategies. Fungi protect themselves against other fungi by complex secondary compounds. Parasitic fungi, however, are able to overcome the defences of certain plants, other fungi, and animals and live on them causing diseases.

During evolution, plants, fungi, and animals have developed sophisticated ways to defend themselves against most parasites. For a stable relationship, the fungus should therefore try to be in some way beneficial to the host organism and assure long term survival of both. Mutualistic fungi have found a way of receiving organic compounds from other organisms by supporting them in some vital aspect.

In a tropical ecosystem with enormous species richness, interactions between species are particularly diverse and far from being well known or understood.

Diversity and importance to humans

Fungi are ecologically, morphologically, and physiologically very diverse and therefore present numerous possibilities to be utilised by people. Some fungi are edible, others can be used for pharmaceuticals, enzymes, food technology, or bioremediation. Some fungi are exploited for biological control of weeds, of plant pathogenic fungi, insects, and nematodes. Other fungi are harmful to man as agents of diseases, poisonous fungi, by destroying human artefacts, or by causing losses of cultivated plants and domestic animals. Moulds grow in any moist place with some organic material and form numerous spores which can cause allergy or even intoxication.

Classification and systematics

In the field, simple classifications are useful, like the distinction of macro- and microfungi. **Macrofungi** develop conspicuous fruiting bodies from fungal hyphae (filiform strands of cells) which grow in the soil, wood or other substrates. To identify Costa Rican macrofungi (Basidio- and Ascomycota) field-guides published by MATA (2003), MATA et al. (2003), and HALLING & MUELLER (2005) as well as the internet page by HALLING & MUELLER (2006) and a database on collections of Costa Rican macrofungi (Anonymous 2006) are available.

Microfungi are fungi growing as yeasts and fungal hyphae which can be visible as moulds. Other microfungi form tiny fruiting bodies or small masses of spores (on plants: sori), visible to the naked eye as tiny dots. Efforts to inventory macro- and microfungi in Costa Rica are presented by MUELLER et al. (2001). An illustrated list of fungi in Costa Rica is found at http://www.inbio.ac.cr/papers/hongos/aclap.htm.

In the past, macrofungi were grouped systematically according to the macromorphology of their fruiting bodies. Nowadays, we try to form systematical groups based on phylogenetic (evolutionary) relationships with the help of microscopical, ultrastructural, and molecular data. Unfortunately, the macromorphology of the fruiting bodies is not a good indicator for evolutionary relationships. For fieldwork and the identification with literature, however, old morphological groups are still very helpful, so we use some of them in the present document. They are enclosed by single quotes ('…') in order to distinguish form systematic groups supported by modern results.

Most fungi belong to two major groups, the Ascomycota and Basidiomycota. These are so-called "true" fungi (Fungi or Eumycota), characterised by the presence of chitin in their cell walls. **Ascomycota** form sexual spores, the ascospores (endospores), usually eight within a special cell called an ascus. The ascus is usually able to eject the spores forcibly into the air. Asci develop in flask-shaped fruiting bodies (perithecia), cup-shaped fruiting bodies (apothecia), or other fruiting structures. Sexual spores of **Basidiomycota** are exospores because they develop on the surface of a special cell called a basidium. The basidium usually carries four basidiospores on outgrowths called sterigmata, which have special structures at their tips to expel the basidiospores forcibly into the air.

Hyphae of many Ascomycota and some Basidiomycota form asexual spores, called conidia. The spores can be carried on exposed hyphae or can be enclosed in small cup-shaped fruiting bodies (acervuli) or small bottle-shaped fruiting bodies (pycnidia). If a fungus only shows asexual development, it is called an **imperfect fungus** belonging to the traditional group of 'Fungi Imperfecti' ('Deuteromycota'). The sexual stage corresponds to the "perfect" fungus. As both stages can be observed independently from each other, the same fungus can have two different names, one to designate the perfect stage and one for the imperfect stage. Further groups belonging to the Fungi are Zygomycota (Figs. 1-2), Glomeromycota, and Chytridiomycota.

Myxomycota and Oomycota, so-called fungus-like organisms, are traditionally studied by mycologists but do not belong to the Fungi. **Myxomycota**, the slime moulds, should better be called Mycetozoa, because they are more closely related to Protozoa than to other fungi. As large, brightly-coloured plasmodia (giant cells with numerous nuclei) they feed on mostly unicellular organisms which they ingest by phagocytosis. When the plasmodium attains a certain size, it migrates to an exposed place and transforms into small fruiting bodies which develop spores for dispersal (Fig. 3).

Oomycota correspond to algae without plastids. Oophyta might therefore be a more adequate name for this group. They can be observed in the field as parasites of plants or as water moulds.

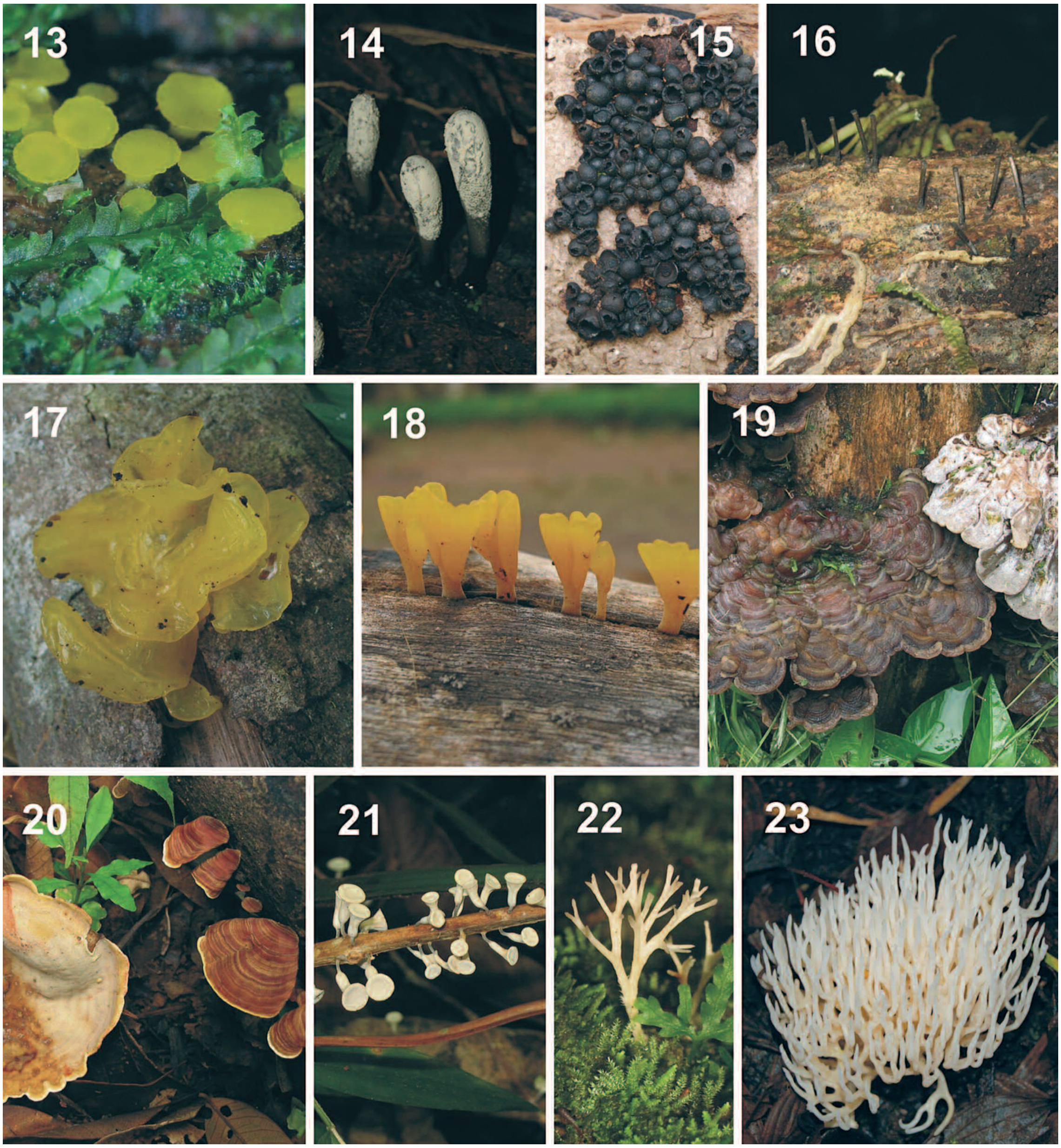


Fig. 13: Small apothecia growing among mosses (Helotiales, Ascomycota). **Figs. 14-16**: Xylariales. (**14**) Fruiting bodies of *Xylaria* sp. covered by white asexual spores. (**15**) Old fruiting bodies of *Phylacia sagraeana*. (**16**) *Leprieuria bacillum*. **Figs. 17-19**: Jelly fungi. (**17**) *Tremella* sp. (Tremellales). (**18**) *Dacryopinax spathularia* (Dacrymycetales). (**19**) *Auricularia mesenterica* (Auriculariales). **Fig. 20**: The fan-shaped fruiting bodies carry a smooth hymenium on the lower side (Stereales, Basidiomycota). **Fig. 21**: *Caripia montagnei* (Basidiomycota). **Figs. 22-23**: Coralloid fungi (Basidiomycota). (**22**) Cf. *Ramariopsis* sp. (**23**) *Ramaria* sp. Photos 13, 17-19, 21-22: M. Piepenbring; 14-16, 20, 23: A. Weber.

Saprophytic fungi

Fungi on soil

Except for some local small niches, like animal excrements (Fig. 1), concentrated, easily accessible dead organic compounds are rare in tropical forests. Tropical soils are mostly poor in nutrients, so fruiting bodies of saprophytic fungi growing on bare soil are not often found. Therefore, when walking through the rainforests of the Golfo Dulce area, fungi appear to be rare or absent. With the help of their hyphae, however, the fungi can make contact with some organic material buried in the ground.

Fungi belonging to the **Phallales** (Basidiomycota) accumulate nutrients in so-called eggs, which grow close to the surface of the soil during a relatively long period of time. In this primordium, the fungus prepares every cell for the entire fruiting body. After heavy rain, water is pumped into the cells and the fruiting body is quickly unfolded. On elegant, conspicuously coloured structures, the fungus exposes a slimy mass of basidiospores (Figs. 4-5). A smell of excrement emanates from this dark mass and attracts flies and other insects (Fig. 6). These feed on the spores, which stick to the insects or pass through their digestive tract and are thereby dispersed.

Fungi on dead organic material

Dead organic material is mainly produced by trees. Dead flowers and small thin leaves are easily decomposed by microscopical fungi like moulds belonging to Ascomycota or Zygomycota (Fig. 2). The degradation of coriaceous leaves requires more time and can involve the development of small but macroscopically visible fruiting bodies. Small immersed cup-shaped fruiting bodies (apothecia) containing asci can be formed by **Rhytismatales** (Ascomycota; Fig. 7). Basidiomycota can be observed as thin, stalk-shaped fruiting bodies (Fig. 8) or small gill fungi ('**Agaricales**'), especially *Marasmius* spp. (Fig. 9). In addition to these fungi, a huge diversity of microscopical filamentous fungi participate in litter decay (Fig. 10), as has been shown for litter samples from the Golfo Dulce forest (BILLS & POLISHOOK 1994).

The decomposition of thick branches, woody fruits, and trunks is a more tedious process and yields energy for many different fungi.

Ascomycota on woody debris

With their distinctive shape and scarlet colour, the stalked apothecia of *Cookeina* spp. (**Pezizales**) are among the most beautiful fungal fruiting bodies in the tropics, both in the Old and in the New World (Figs. 11-12). In our area, *C. tricholoma* (MONT.) KUNTZE and *C. speciosa* (FR.) DENNIS can be found. Apothecia of other fungi are less conspicuous at first sight but reveal their beauty when magnified (Fig. 13).

Hard, perennial, black fruiting bodies on wood mostly belong to species of **Xylariales**. They can also be turned white by the mass of conidia produced during asexual development (Fig. 14). The morphology of the fruiting bodies varies from crusts covering the surface of the wood to cushions, spheres, pedunculate clubs, and slender branch-like forms (Figs. 14-16). Species of Xylariales form dark ascospores in asci packed in bottle-shaped perithecia. Numerous perithecia are located close to the surface of a fruiting body. Ascospores are liberated through a small opening of the perithecium (ostiole) on the surface of the fruiting body. Ostioles can be observed in the field with a hand lens as small dots. In the case of some *Leprieuria* species, perithecia are located only at the top of rod-shaped fruiting bodies which resemble small black cigarettes (Fig. 16).

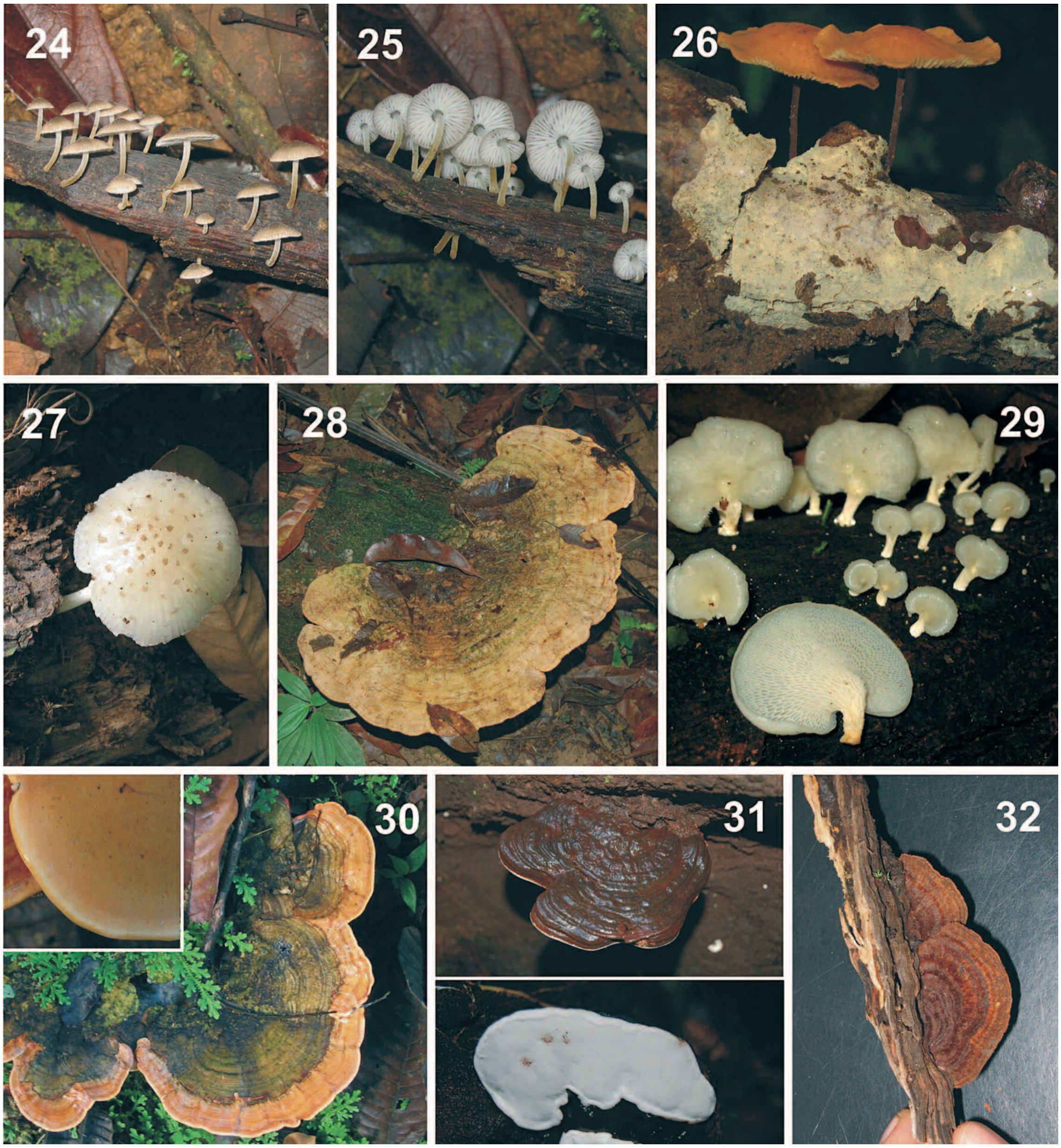
Basidiomycota on woody debris

Wood decomposing Basidiomycota belong to many different groups. The most simple ones morphologically are the so-called **corticioid** Basidiomycota which mostly form white crusts on the surface of wood. This white layer is formed by hyphae carrying basidia in a superficial layer called hymenium. The hymenium of corticioid fungi is smooth, folded, or provided with tooth-like outgrowths, pores, or other structures, which increase the surface area of the hymenium (OBERWINKLER 1992).

Members of **Tremellales** have delicate, gelatinous, often conspicuously coloured fruiting bodies (Fig. 17), **Dacrymycetales** less gelatinous, stalk-shaped, vividly coloured fruiting bodies (Fig. 18), and **Auriculariales** form brown fruiting bodies with the consistency of human ears (Fig. 19). These groups can be difficult to distinguish in the field. Their basidia have to be analysed with the light microscope to assure the correct systematic placement. These jelly fungi are visible only after rain and become almost invisible when dry. Costa Rican jelly fungi have been studied by KISIMOVA-HOROVITZ et al. (2000, and citations therein).

More persistent fruiting bodies are formed by so-called **stereoid fungi** with smooth hymenia (Figs. 20-21) and **clavarioid fungi** with coral-like fruiting bodies (Figs. 22-23). Gill-fungi ('**Agaricales**', Figs. 24-27) and 'Polyporales' (Figs. 28-32) can also grow on dead wood.

The '**Polyporales**' (Figs. 28-32) are conspicuous fungi on wood with large, console-shaped fruiting bodies laterally attached to tree trunks. Their hyphae grow inside dead trees decomposing the secondary xylem (wood), i.e. causing rot, and can kill living, weak plants by destroying their cambium. Fruiting bodies of 'Polyporales' are characterised by the presence of pores on the lower side of the fruiting body which is more or less broadly attached to the substrate without or with stipe (Fig. 29). Most fruiting bodies of 'Polyporales' are formed by different kinds of hyphae, thin-walled living hyphae responsible for reproduction and thick-walled, dead skeletal hyphae. Because of the skeletal hyphae, the fruiting bodies are hard and can survive for long periods of time (several years). From time to time during the life span of a fruiting body, the reproductive hyphae cover the inner surfaces of pores with hymenia formed by basidia. These develop basidiospores for dispersal. Systematically, 'Polyporales' belong to many different systematic groups, including Polyporaceae (Figs. 28-30), Ganodermataceae (Fig. 31) and Hymenochaetaceae (Fig. 32). They differ microscopically in cellular details of the hymenia, the morphology of basidiospores, and by the fact that some of them cause white rot and others brown rot. Species causing white rot are able to decom-

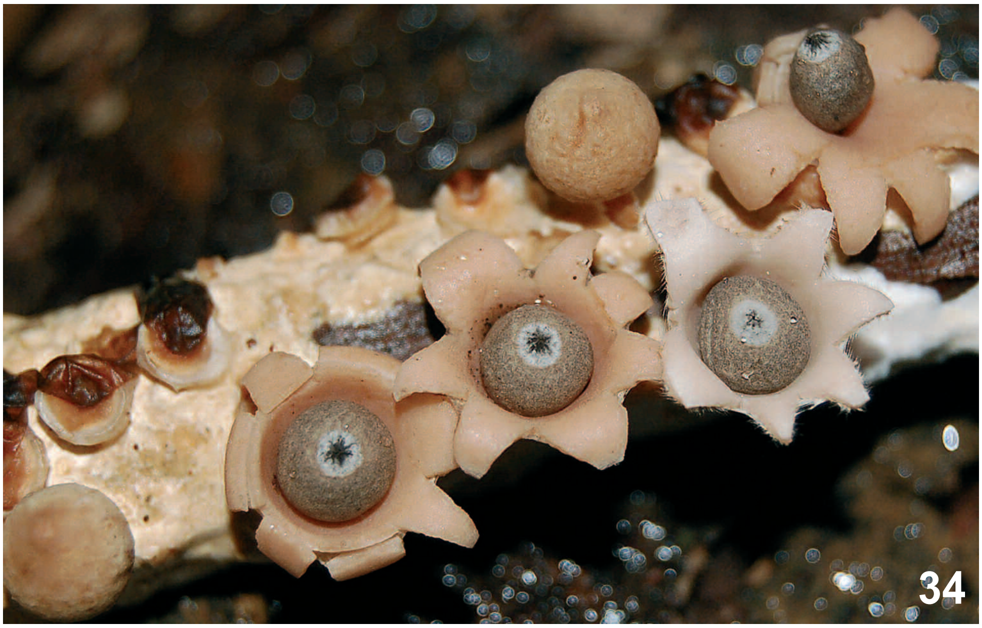


Figs. 24-27: Agaricales. **Figs. 24-25**: *Mycena* sp. **Fig. 26**: Hyphae of *Marasmius* cf. *princeps* cover the woody substrate to retain humidity. **Fig. 27**: *Oudemansiella canarii*. **Figs. 28-30**: Polyporaceae. (**28**) *Laetiporus* sp. (**29**) Stipitate fruiting bodies of *Polyporus tenuiculus*. One fruiting body has been turned around so the pores are visible. (**30**) *Trametes cubensis*. The insert shows tiny pores on the lower side of a fruiting body. **Fig. 31**: A fruiting body of *Ganoderma* sp. (Ganodermataceae) seen from above and from below. **Fig. 32**: *Phellinus gilvus* (Hymenochaetaceae). Photos 24-25, 28, 31: A. Weber; 26-27, 29-30, 32: M. Piepenbring.

pose cellulose and lignin, while those causing brown rot only decompose cellulose.

In Costa Rica, this group has been studied intensively, with 314 species being known for the country to date (Carranza & Ruiz-Boyer 2005, Ryvarden 2005, Ruiz-Boyer 2006). Some species have been reported for the area of the Golfo Dulce: *Echinochaete brachiporus*, *Polyporus leprieurii*, and *Trichaptum sector* (Mata et al. 2003). Some other species are illustrated here, many more will can be found in future by field work carried out in this area.

While most fungi cited above form their basidiospores on the surface of the fruiting bodies, "stomach" fungi (**'Gasteromycetes'**, Figs. 33-34) produce their basidiospores in closed fruiting bodies. Only when the pigmented basidiospores are mature do the fruiting bodies of most species open, and the spores are dispersed for example by rain drops falling onto the puffballs. Fruiting bodies of other species do not open by themselves but rely on fragmentation and dispersal of the spores by animals.



Figs. 33-34: Earth stars (*Geastrum* spp., ´Gasteromycetes´). The outer layer of the envelope has ruptured and become star-shaped, while the inner layer has a central opening through which the basidiospores are liberated. Photo 33: M. Piepenbring; 34: A. Weber.

Even in a rainforest growing in a constantly wet climate, humidity values may change drastically over short periods of time due to intense radiation by the sun. Therefore, some fungi have developed morphological structures to store humidity. Some 'Gasteromycetes' (Fig. 34) as well as some Agaricales growing on rotting wood enclose their substrate in mycelial chambers, so the humidity in the substrate is not lost so quickly (pers. com. G. Kost; Fig. 26).

Saprophytic microfungi

Saprophytic microfungi can be found as yeasts in soil, in the nectar of flowers, in the guts of animals, and in plant resins. Any surface and material with some nutrients can be colonised by yeasts and filamentous microfungi, which can also live on exudates of leaves and roots.

Parasitic fungi

To obtain organic compounds from living organisms, fungi of many different systematic groups have become parasites.

Fungi parasitic on plants

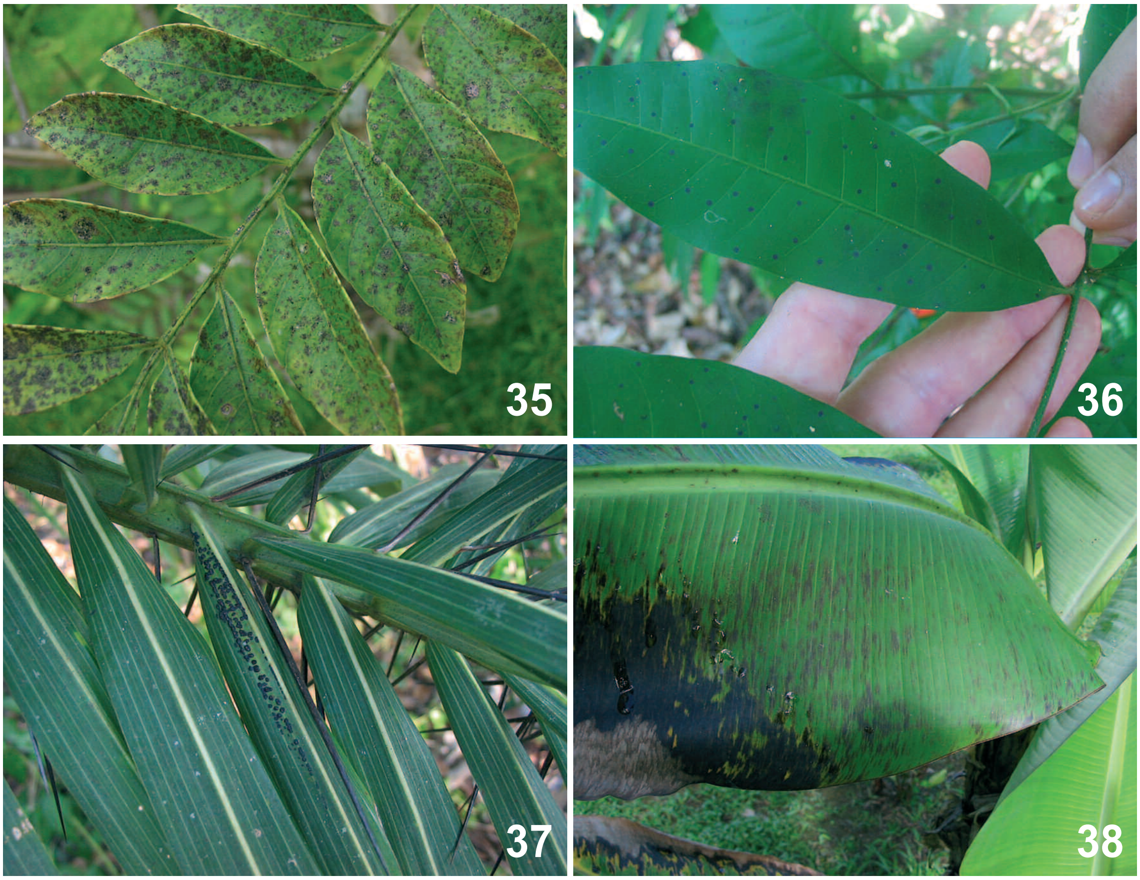
To overcome the defence systems of plants, parasitic fungi have had to adapt closely to their host species. Narrow host ranges can be observed especially for fungi interacting with living plant cells to obtain nutrients. Other plant parasitic fungi kill parts of the plants and live on the dead tissue saprophytically. Few fungi kill entire plants – a lifestyle only possible with many host plants available. During evolution, some fungi of most major systematic groups opted for the plant parasitic lifestyle, with only the most important ones being cited in the following text. Any autotrophic organism can be attacked, including algae, mosses, and vascular plants.

Ascomycota

While in regions with temperate climate, powdery mildews (Erysiphales) are common, tropical plants are more frequently attacked by **black mildews** (Meliolales). Black mildews develop dark-coloured hyphae on the surface of the leaves of host plants (Fig. 35). Dark-coloured, few-celled ascospores develop in globose fruiting bodies (perithecia) which are visible with a hand lens as dark dots on the surface of the leaf. In addition to black mildews, many other Ascomycota and their imperfect stages grow as black mycelia on the surface of leaves. **Fly speck fungi** (Asterinaceae and other groups) protect their asci by dark coloured shield-shaped fruiting bodies called thyriothecia (Fig. 36). These minute fruiting bodies can be mistaken for the excrements of flies in the field. The fruiting bodies of **tropical tarspot fungi** (Phyllachorales) are perithecia surrounded by more or less abundant, dark fungal hyphae (stroma) embedded in host tissue or on the surface of plant organs (Fig. 37).

Fungi Imperfecti

For tropical America, the most important plant parasitic imperfect fungus is probably ***Pseudocercospora fijiensis*** which causes the **Black Sigatoka** disease on leaves of banana (*Musa* species and hybrids, Musaceae; Fig. 38). Infected leaves present elongated striae of brown to lilac colour, on which the fungus develops elongated conidia. These are dispersed and germinate to infect other leaves. Infected leaves die earlier than healthy ones, and the infection affects the process of ripening of the fruit which has to be predictable and



Figs. 35-38: Plant parasitic Ascomycota. (**35**) A black mildew, *Asteridiella* sp. (Meliolales), on *Spondias purpurea* (Sapindaceae). (**36**) A fly speck fungus (Microthyriales) on *Trichilia tuberculata* (Meliaceae). (**37**) A tropical tarspot fungus, *Camarotella costaricensis* (Phyllachorales) on *Acrocomia aculeata* (Arecaceae). (**38**) A leaf of a banana plant (*Musa* sp.) showing symptoms of the Black Sigatoka disease caused by *Pseudocercospora fijiensis* (Fungi Imperfecti).

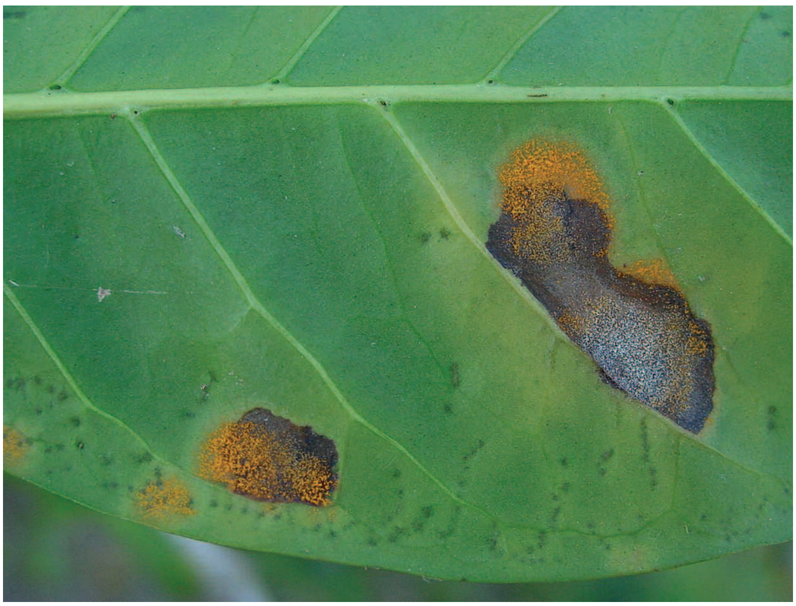


Fig. 39: The Coffee Rust, *Hemileia vastatrix* (Uredinales) on a coffee leaf.

Fig. 40: The Corn Smut, *Ustilago maydis* on corn (*Zea mays*, Poaceae).
Photos: M. Piepenbring

Fig. 41: *Ustilago schroeteriana* on *Paspalum virgatum* (Poaceae) with a healthy host plant on the right hand side.Photo: M. Piepenbring

Figs. 42-43: Fungi parasitic on insects. (**42**) *Isaria tenuipes* (Fungi Imperfecti) growing on the larva of an insect. (**43**) *Cordyceps* sp. (Hypocreales, Ascomycota) growing on a killed ant. The fruiting body at the head of the ant carries perithecia. Photos 33, 35-43: M. Piepenbring; 34: A. Weber.

uniform in large-scale banana plantations. Although fungicides are applied continuously to plantations, they only reduce the infection by the fungus. When an infected leaf is allowed to decompose on the ground, the fungus forms perithecia with ascospores for sexual reproduction and dispersal. The perfect stage is called *Mycosphaerella fijiensis* (Mycosphaerellales, Ascomycota).

Basidiomycota

Among Basidiomycota, the **rust fungi** (Pucciniales, formerly Uredinales) are the most species-rich group of plant parasitic fungi (Fig. 39). Shivas & Hyde (1997) suggest that, in addition to the approx. 7.000 species known world-wide, about 270.000 further species might be discovered in the tropics. This hyperdiversity can be explained by the fact that rusts interact in a highly complex way with specific host plants. A high species richness of plants therefore is a precondition for a high species richness of parasites. Berndt (2005) cites 292 species in his checklist of rust fungi in Costa Rica.

The economically most important species of rust is the **Coffee Rust**, *Hemileia vastatrix* (Fig. 39). It causes devastation in coffee plantations by destroying leaves. On the lower side of the leaf, groups of orange-coloured uredospores can be observed. These can be mixed with teliospores. As in the case of the agent of black sigatoka, control measurements only help to reduce the amount of infection, which cannot be eradicated.

The second most important group of plant parasitic fungi among Basidiomycota are the **‘smut fungi‘** (Figs. 40-41). They mostly form dusty, dark masses of teliospores on their host plants. For Costa Rica, 54 species of smut fungi are known (Piepenbring 1996, 2003).

The most famous smut in tropical America is the corn smut, *Ustilago maydis* on *Zea mays* (Poaceae) (Fig. 40). This fungus provokes hypertropic growth of ovaries and other parts of the corn plant. Within the galls, the fungus forms its brown teliospores for dispersal. When the galls are still white (young) they can be eaten like a vegetable. People in Mexico consume it as huitlacoche (“crow excrement” in nahuatl). Most other smut fungi grow on wild plants, mostly weeds, like those growing in deforested areas close to the Biological Station La Gamba (Fig. 41).

Fungi parasitic on animals

Insects and spiders are highly diverse and numerous in tropical lowland rainforest. The larger the population of a given species of arthropods is, the more frequently the individuals are infected and killed by parasitic fungi. In this way, **fungi parasitic on arthropods** achieve a natural control of the populations of insects and spiders in natural ecosystems. Dead insects and spiders covered by fungi can be found attached to plants. After infecting and killing the animals by hyphae within the bodies, the fungus grows onto the surface of the arthropod and forms spores which can be asexual conidia (Fungi Imperfecti, Fig. 42) or ascospores enclosed in asci in perithecia (Ascomycota, Fig. 43). We can isolate and multiply these fungi to use them for biological control measures against arthropod pests on cultivated plants.

Fig. 44: A human nail destroyed by *Fusarium* sp. (Fungi Imperfecti).

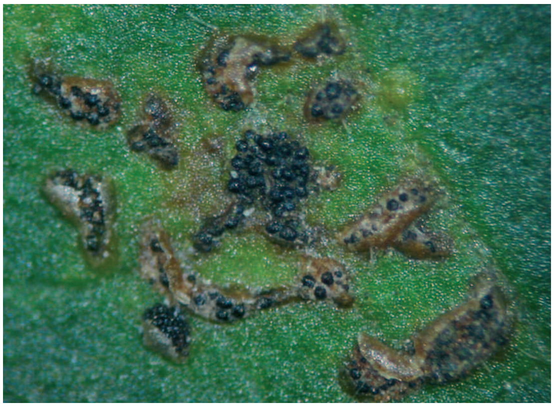
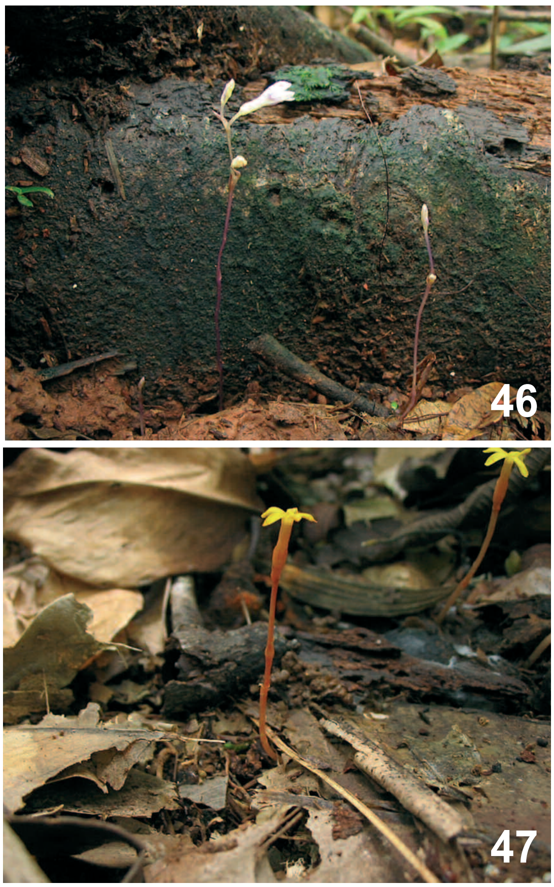


Fig. 45: The black dots correspond to fruiting bodies of *Sphaerellopsis filum* (Fungi Imperfecti) growing in sori of a rust.



Figs. 46-47: Plants parasitic on mycorrhiza. (**46**) *Gymnosiphon* sp. (Burmanniaceae). (**47**) *Voyria* sp. (Gentianaceae).

Other filamentous microfungi are able to trap and to digest **nematodes**. They can be technically used for biological control and reduction of nematodes causing damage to roots of plants or living as parasites in cattle.

Since several years, the populations of certain species of **frogs** like the colourful poison-arrow frogs of tropical America decreased alarmingly in different parts of the world, due to a disease called chytridiomycosis (WELDON et al. 2004 and citations therein). The agent of this disease is a microscopic fungus which was discovered in this context as a species new to science in a new genus, *Batrachochytrium dendrobatidis*, in the Chytridiomycota. We do not know for certain why this fungus suddenly kills many frogs so quickly. Maybe the resistance of frogs against diseases is diminished by pesticide contamination and changing climate.

Other fungi are less harmful to animals. Microscopic Laboulbeniales (Ascomycota) live attached to the exoskeleton of living arthropods. Trichomycetes (Zygomycota) can be found in guts of living arthropods.

Fungi parasitic on humans

Human beings do not usually provide substrates for parasitic fungi, because they are protected by their immune system and a healthy flora including bacteria on the surface of their skin. By wearing tight shoes and excessive sweating, for example in boots in the tropics, however, the environmental conditions for fungal growth on skin and nails can be excellent for dermatophytic and other imperfect fungi (Fig. 44).

When the human immune system is weakened due to disease or immunosuppressive medication, fungi can also develop inside our body, causing systemic mycoses. Histoplasmosis is a serious lung disease caused by *Histoplasma capsulatum* (asexual Onygenales, Ascomycota). Spores of this fungus develop on excrement of bats, especially in caves in tropical regions like Costa Rica.

Further effects of fungi on humans are caused by consumption of poisonous fruiting bodies, by mycotoxins produced by certain moulds (Fungi Imperfecti), and by allergenic spores.

Fungi parasitic on fungi

Some mainly microscopic fungi have opted for the mycoparasitic life style, and they live as parasites on other fungi. The host fungi are macro- or microfungi, saprophytic or parasites of plants. In the latter case, the mycoparasitic fungi are called hyperparasites. A common hyperparasite of rusts is *Sphaerellopsis filum*, an imperfect fungus which develops pycnidia in sori of rust fungi (Fig. 45).

Fungi in mutualistic symbiosis

Mutualistic symbiosis with plants

Mycorrhiza

Although not easily visible, the mycorrhizal mutualistic symbiosis between plants and fungi in the soil is the most important interaction in any terrestrial ecosystem. Without fungi, plants would be significantly less efficient in the uptake of water and minerals, they would grow less vigorously, and they would be more susceptible to agents of diseases than they are in association with fungi. The interaction takes place at the tips of the fine roots where fungal hyphae penetrate into the cortical tissue of the root. The fungus absorbs water and minerals with its hyphae in the surrounding soil, while the plant shares its photosynthetic products with the fungus. In addition to this, the fungus protects the plant against diseases.

Many different fungi are able to interact with plants as mycorrhizal partners. Hyphae of some fungi penetrate between the cortical cells of the root but do not grow into the cells of the plant. This type of mycorrhiza is the **ectomycorrhiza**, which is the dominant mycorrhiza on roots of trees in temperate forests and montane tropical oak forests.

The most widely distributed type of mycorrhiza, which is dominant on roots of herbs and trees in tropical lowland forests, is the **arbuscular mycorrhiza** (AM). AM fungi are species of Glomeromycota, microscopical fungi which are able to grow not only into the cortical host tissue, but also into the cells of the plant (**endomycorrhiza**). To interact with the plant cytoplasm, they develop ramified haustoria called arbuscules, some also form vesicles. Hyphae in the soil form spherical, thick-walled cells for long term survival.

Further kinds of mycorrhizae are known, for example with species of Ericaceae and Orchidaceae. In the case of orchid mycorrhizae, hyphae in the inner cortical cell layers of roots of orchids are digested by the plant while hyphae in outer layers survive.

Mycoheterotrophism

Instead of sharing its sugars with their mycorrhizal fungi, some plants have lost the capacity to perform photosynthesis and depend entirely on the fungus for survival (Figs. 46-47). These heterotrophic plants are not green because they do not develop chloroplasts. They live as parasites on saprophytic fungi, or the fungus itself interacts as mycorrhizal fungus with a green plant, so the heterotrophous plant is a parasite of the mycorrhiza. In tropical forests, small herbs lacking chlorophyll can be found in shadowy places on the soil, like species of Burmanniaceae (Fig. 46) or *Voyria*, a group of gentians (Gentianaceae, Fig. 47) which are fairly common in the Golfo Dulce forests.

Lichens

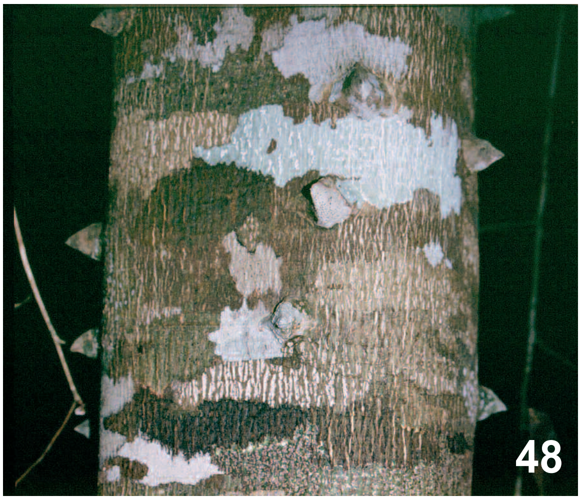
Since the very beginning of evolution, fungi have captured autotrophic cyanobacteria or algae (photobionts) by their mycelium, offering shelter to them and receiving sugars in exchange. Subsequently, the fungi (mycobionts), which belong chiefly to the Ascomycota and more rarely to the Basidiomycota, became completely dependent on the photobionts while the algae can survive without the fungus. The thalli of lichens can be crustose, foliose, or fruticose. In tropical lowland forests, the crustose (to foliose) habit is dominant on the bark of trees (Figs. 48-49) and on long-living leaves (Fig. 50), where numerous different species of lichens form complex communities together with free-living algae, fungi, and mosses. The thalli of most species of lichens are formed by fungal hyphae with algal cells scattered in between. The fan shape of the fruiting-bodies of species of *Coenogonium*, however, is determined by the filamentous algal partner. Thin fungal hyphae grow around the thick filaments of the alga. Small cups evident on many thalli of lichens correspond to apothecia formed by mycobionts belonging to the Ascomycota. For lichens in Costa Rica see UMAÑA & SIPMAN (2002). Lichens themselves may be utilised as substrate by other fungi, so-called lichenicolous fungi.

Endophytic fungi

In any organism, fungal hyphae or yeasts may live without causing symptoms of disease. Similar fungi in plants are called endophytic fungi. In large perennial leaves of tropical plants, these fungi can be very diverse (ARNOLD et al. 2000). Many endophytic and plant parasitic fungi on and in leaves keep growing in their substrate when leaves are shed. They are able to survive as saprophytes and have the advantage to be the first in place as decomposers. Plant parasitic fungi give access into the tissue of dead leaves to bacteria and other fungi by breaking the outer cell layers (epidermis and hypodermal layers) of the leaves which can be rather hard.

Fungi in mutualistic symbiosis with animals

Leaf-cutting ants (Spanish “zompopas” or “arrieras”), mainly species of *Atta* and *Acromyrmex* (Higher Attini, Formicidae, Hymenoptera), are a common sight in and around the rainforests of the Golfo Dulce area. They live entirely on fungi (asexual Agaricales, Basidiomycota) which they cultivate in their nests. To provide a substrate for the fungi, the ants cut leaf segments of living plants in such a quantity that they cause serious losses to crops cultivated by man. The plant fragments are carried to the nest, cleaned, chewed, and pre-



Figs. 48-51: Lichens. (**48**) Different species of crustose lichens cover the bark of *Zanthoxylum* sp. (Rutaceae). (**49**) Reddish thalli of *Cryptothecia rubrocincta*. (**50**) Different epiphyllous lichens and mosses on a single leaf. (**51**) *Coenogonium* sp. growing on a tree trunk. Photos: M. Piepenbring

pared as a substrate for the fungus which is inoculated onto it. A class of very small workers care for the garden protecting it from "weeds", i.e. contamination by other fungi. They use antibiotics against bacteria. For the alimentation of the larvae and themselves the ants harvest so-called gongylidia from the fungus garden – small balls formed by hyphae which are swollen at their tips. Certain termites are also able to cultivate fungi, but their occurrence is restricted to the palaeotropics.

Fungi belonging to the **Septobasidiales** (Basidiomycota) form flat fruiting bodies on the surface of stems, twigs, and leaves of plants (Fig. 52). At first sight they look like lichens. An anatomical investigation, however, shows that they are not usually associated with algae, and form basidia on their surface. The fruiting body is not closely attached to the substrate, but presents a complex system of chambers on its lower surface. This space is used by scale insects for shelter. They are protected by the fungus against predation by other animals. The fungus, however, kills some individuals for its own nutrition, but does not seriously affect a proliferating population of scale insects.

Conclusions

Comparison of tropical and temperate fungi

Fungi generally occupy similar niches in temperate and tropical ecosystems, but some differences can be observed, for example concerning epiphyllous fungi, i.e. fungi living on leaves. Leaves of evergreen tropical trees have a coarser texture and are more persistent than most leaves in temperate climate. They are exposed over a much longer period of time and, therefore, are more densely colonised by fungi (Fig. 50). In addition, high levels of humidity in the air promote fungal growth on leaves and on any other substrate above the ground. Some species of *Marasmius* form long black strands of hyphae, so-called rhizomorphs, which can grow close to the substrate or hang down from the canopy of trees (Fig. 53). The tiny, ephemerous, gilled fruiting bodies grow out of them only when humidity in the air is close to 100%.

Temperature in tropical lowlands is optimal for fungal growth throughout the year. High humidity also is beneficial for fungal growth, but only to a certain degree. Excessive rain, which is rather common during the rainy season in Central America, destroys fruiting bodies, might prevent spore dispersal by wind, favours the growth of moulds on the fungal fruiting bodies, and the proliferation of insects. Together with the fact, that generally few nutrients are available in tropical soils, we can explain why fruiting bodies of fungi in tropical lowlands are generally smaller and less numerous than in temperate regions. The longer a fruiting body needs to develop, to produce and disseminate its spores, the more likely it is to be colonised by insects which reproduce with the help of fungal fruiting bodies providing food for the larvae.

Outlook

Due to the high diversity of plants in tropical regions and the therefore increased number of niches, we can assume that the number of species of fungi is higher in the tropics than in temperate regions. This has been shown for selected groups of fungi (HAWKSWORTH 2001), but our knowledge on tropical fungi is still too limited to generally confirm this hypothesis. Numbers of species of fungi known per unit area in the neotropics are generally lower than numbers of fungal species in regions with numerous mycologists, like Europe. Currently we recognise about 72.000 different species of fungi world-wide. Especially in the tropics, mycologists often make new records, gather new ecological data, and discover new species, so the number of existing fungi is certainly much higher. The estimate of about 1.5 million existing fungal species is widely accepted (HAWKSWORTH 2001). Based on this assumption, we only know about 5% of the existing diversity of fungi world-wide.

For many tropical countries, mycological investigation is still in a pioneer phase. We probably know less than 4% of the existing fungal diversity in neotropical countries, as has been shown by analyses of checklists of fungi known for Mexico (GUZMÁN 1998) and Panama (PIEPENBRING 2006, 2007). The level of knowledge of fungi in Costa Rica is considered low by curators of local herbaria (BERMÚDEZ & SÁNCHEZ 2000), and this certainly applies to the rainforests of the Golfo Dulce region.

Tropical fungi are among the most diverse and the most poorly known organisms of our world. In addition to new scientific data, future investigation will reveal numerous new possibilities to utilise fungi. The number of mycologists performing fieldwork in the tropics is, however, still very small in comparison to the huge task ahead of us. At the same time, tropical primary forests are destroyed and altered by human activities to a frightening degree. Fire and the application of pesticides contaminate the air with ash and chemicals which are carried into the forests by wind. Many organisms in tropical forests will not be able to adapt to the rapidly changing soil and climate conditions. Numerous fungi will lose their habitat and become extinct without being known by us.

Fig. 52: Fruiting body of *Septobasidium* sp.

Fig. 53: Rhizomorphae formed by *Marasmius* sp. hanging down from trees and carrying tiny fruiting bodies when the humidity in the air is close to 100%.
Photos: M. Piepenbring

Hopefully, the present publication contributes to rise our interest and respect for fungi in tropical ecosystems and stimulates biologists to explore the fascinating world of fungi.

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