Fungi – Macrofungi

Morphology

Within the fungus kingdom, macrofungi are a group that form visible, often coloured, cup- or cap-like structures (scientifically known as 'fruiting bodies' or 'sporophores') that emerge from the soil. These fruiting bodies are where the spores are formed. The spores are small (1 - 100 μm), usually single-celled, reproductive structures able to tolerate unfavourable growing conditions (e.g. drought). Below the fruiting bodies, each fungus has a mass of hyphae, the typical branching thread-like filaments produced by most fungi. The mycelium is made up of the mass of these hyphae and is responsible for its growth. In the case of soil macrofungi, a large portion of the mycelium is hidden since it grows belowground. When environmental conditions become favourable, the fungus develops the fruiting body and spores that, once released, disperse through the air, or are carried by insects or water. [35, 36]

Taxonomy

Macrofungi, taxonomically belonging to the subkingdom Dikarya, are classified into two main phyla: Ascomycota and Basidiomycota. The Ascomycota, the largest group of macrofungi with more than 64 000 described species, are usually characterised by a cup-like or disc-like fruiting body (technically known as ascoma), where spores are formed within a typical structure, named the 'ascus'. The Basidiomycota (more than 31 000 described species) mostly have a fruiting body (called basidioma) with an umbrella-shaped cap (known as pileus) borne on a stalk (known as a stipe) where the spores are produced. Other phyla that include soil fungi are Glomeromycota, Zygomycota, Chytridiomycota and Blastocladiomycota (see pages 40-41).

Microhabitat

Macrofungi are found in most terrestrial habitats, from woodlands to grasslands, but they are probably most diverse in forests. They need the right climatic conditions to form fruiting bodies; in particular, moisture to allow their spores to develop. Depending on their functions, they can be defined as saprotrophic, parasitic or mycorrhizal. The saprotrophic species play a key role in the degradation of decaying organic matter (i.e. soil, leaf litter and dead wood). The parasitic (see box on page 33) fungi are responsible for several diseases in plants (see box, next page), animals (mostly invertebrates) and other fungi. The mycorrhizal fungi form symbioses with plant roots, a mutualistic association that is beneficial to both partners (see box, page 33).

The Basidiomycota is a group of fungi that comprises the well known, common mushrooms. Their visible part usually has an umbrella-like shape. (**a**) *Hygrocybe* sp.; (**b**) *Hygrocybe graminicolour*; (**c**) *Cyptotrama asprata*; (**d**) *Gymnopilus purpuratus*. (SA)

The Ascomycota is a group of fungi that usually have a visible part, scientifically defined as the fruiting body, with a cup-like shape. (**a**) *Donadinia nigrella*; (**b**) *Sarcoscypha coccinea*; (**c**) *Phillipsia subpurpurea*; (**d**) *Rhodoscypha ovilla*. (SDA, FF, SA, AV)

Fungi: edible, poisonous, bioluminescent and giant

- There are several edible Basidiomycota and Ascomycota. Mushrooms, such as *Boletus edulis* and truffles (*Tuber* spp., see box on page 40), are consumed in many countries.
- Some Basidiomycota produce deadly toxins, such as amatoxin produced by *Amanita phalloides*. Thirty grammes of this fungus may kill a person; others, such as *Ganoderma lucidum*, are considered medicinal fungi.
- Some Basidiomycota (e.g. species belonging to the genus *Mycena*) are bioluminescent.
- In Hainan Island (southern China) a giant specimen of *Fomitiporia ellipsoidea* (belonging to the group of bracket fungi, also included in Basidiomycota) was found to be 20 years old with an estimated volume of 409 000 - 525 000 cm^3 and a weight of 400 - 500 kg. This represents the largest fungal fruiting body (both in volume and in weight) ever found.

Mycena chlorophos is a bioluminescent fungus that can be found in Asia (e.g. Japan and Sri Lanka), Oceania (Australia) and South America (Brazil). The mechanism underlying the bioluminescence has not yet been fully described. (SA)

Diversity, abundance and biomass

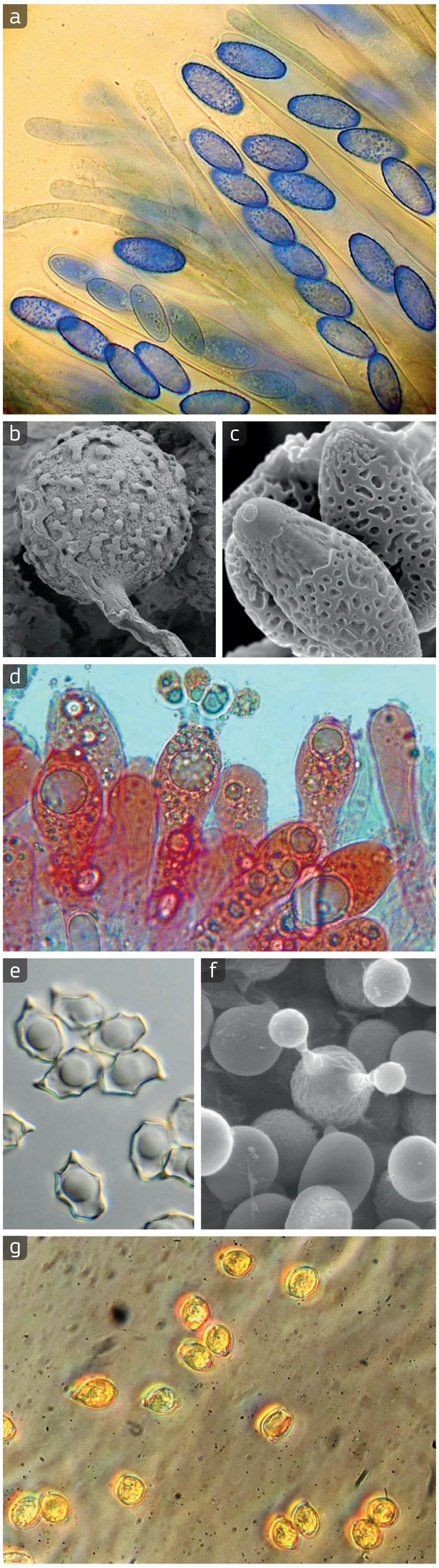
Fungi are extremely abundant. Millions of species have been estimated, but only about 150 000 have been described. Macrofungi have about 90 000 known species. Together with bacteria, fungal hyphae constitute the largest portion of the microbial biomass of soil. Generally, fungal biomass is found to be greater than bacterial biomass in forest soils.

Fungi are very diverse in terms of both shape and colour. Some fungal species showing these aspects are: (**a**) *Leratiomyces* sp.; (**b**) *Geastrum triplex*; (**c**) *Hygrocybe graminicolour*; (**d**) *Cyathus striatus*. (SA)

How a fungus is made

Fungal hyphae have a branching structure that resembles plant roots. They allow the fungus to obtain nutrients from the soil. (SA)

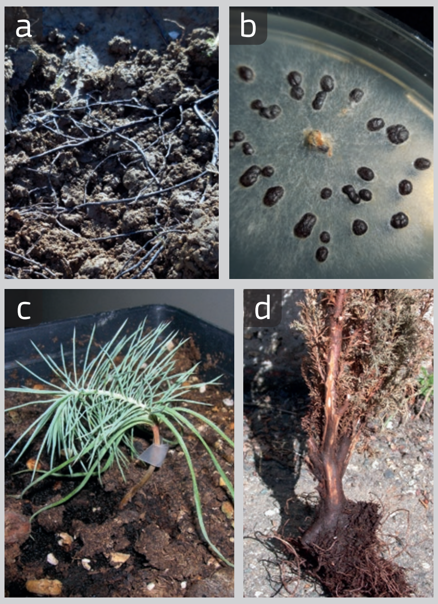
- A hypha is a long, branching filamentous structure. In most fungi, hyphae are the main mode of growth, and collectively form the mycelium.
- Hyphae grow at their tips. They can branch through the bifurcation of a growing tip, or through the emergence of a new tip from an established hypha.
- There are different types of hyphae:
  - septate, which have cross walls (called septa) at fairly regular intervals;
  - aseptate or coenocytic, which do not have septa.
- Hyphae can fuse to one another. This process is known as anastomosis.
- Yeasts are fungi that do not have hyphal structures. They are the only unicellular fungi.



Spores allow fungi to reproduce. Due to their microscopic dimension, they can easily disperse through air or water. They grow into new individuals under suitable conditions of moisture, temperature and food availability. (**a**) Spores of Ascomycota (blue coloured) develop inside structures called asci; (**b**) electron micrograph of spores from the puffball *Calbovista subsculpta*; (**c**) electron micrograph of spores from *Austroboletus mutabilis*; (**d**) spores of Basidiomycota develop inside structures (red coloured) called basidia; (**e**) spores of *Entoloma* sp.; (**f**) electron micrograph of spores from *Agaricus bisporus*; (**g**) spores of *Botryobasidium aureum*. (LP, SJA, RHL, LP, LK, DEMF, JP)

Soil-borne plant pathogenic fungi

- Soil-borne plant pathogenic fungi (SPPF) comprise organisms that are included in the Fungi kingdom and in the group of fungal-like organisms currently assigned to the Stramenopiles (see page 37). As pathogens, they are responsible for several plant diseases. [37]
- Among fungi, both Ascomycota and Basidiomycota are represented. The major species belong to the genera *Fusarium*, *Phoma*, *Sclerotinia* and *Verticillium* within Ascomycota, and to *Armillaria* and *Rhizoctonia* within Basidiomycota.
- SPPF produce survival structures that may be as simple as cells, called chlamydospores, with a thick wall, or may be more complex like the sclerotia, typical of some fungi (e.g. *Sclerotium*, *Sclerotinia* and *Botrytis*).
- In addition to the survival function, aggregation of hyphae, called rhizomorphs since they resemble plant roots, are typical of species belonging to the fungal genus *Armillaria* and may play a crucial role in fungal spread through the soil, host infection and disease transmission.
- Soil type, pH, water content and temperature of the soil are among the major factors affecting the presence of the soil-borne plant pathogenic fungi.
- *Fusarium* species and *Rhizoctonia solani*, although commonly present in moist soils, tolerate lower water content levels. They also prefer warmer soils (25-35 °C).
- SPPF are grouped into two functional categories: soil inhabitants and soil invaders. The first category generally includes unspecialised microbes that infect seedlings and young roots, while the second are disease agents that show a degree of host specificity. Seed decay, damping-off and root rots of seedlings are the most common diseases caused by soil-borne fungi.
- Soil-borne plant pathogenic fungi are reported worldwide in agricultural and forests soils.
- The number of plant pathogenic fungal species on Earth has been estimated to be as high as 270 000; however, the number of SPPF is largely unknown.
- The abundance of SPPF is generally measured as 'inoculum density', which is expressed as the mass, or the number, of spores per gramme of soil. Inoculum density has been reported as ranging from 100 to 10 000 spores per gramme of soil, depending on the species.

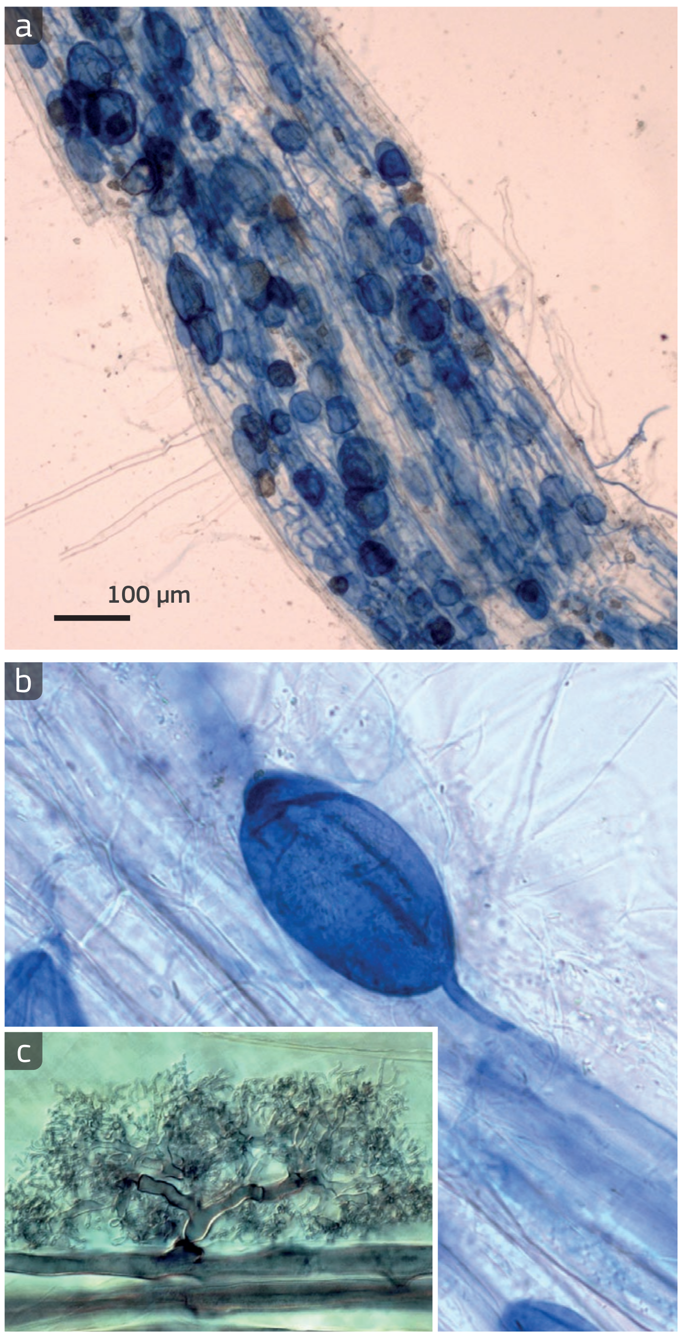


Structures that allow soil-borne plant pathogenic fungi to survive adverse environmental conditions: (**a**) rhizomorphs, as it resembles roots, of the fungus *Armillaria* sp. and (**b**) the black dots are sclerotia of the fungus *Botrytis cinerea*, grown in the laboratory. Diseases caused by soil-borne plant pathogenic fungi: (**c**) damping-off on a stone pine seedling and (**d**) root rot caused by *Phytophthora cinnamomi* on a Port Orford cedar. (LG, PG)

Fungi – Mycorrhizal fungi

Morphology

Mycorrhizas are literally 'fungus-roots' created by symbiotic associations (see box, page 33) between plant roots and fungi. Mycorrhizal fungi help their host plants acquire mineral nutrients from the soil in return for plant sugars. Mycorrhizal fungi form structures outside and inside plant roots. All types form extensive networks of microscopic hyphae that extend outwards from plant roots into the surrounding soil or leaf litter. Arbuscular mycorrhizas (AM), ericaceous mycorrhizas and orchid mycorrhizas are sometimes called 'endomycorrhizas' because the fungi form distinctive structures between and inside the cortical cells of plant roots, but do not generally cause obvious changes in root morphology. By contrast, ectomycorrhizas (EcM) often cause distinct changes to roots that can be observed without a microscope. Reproductive structures also differ among mycorrhizal types. Arbuscular mycorrhizal fungi reproduce with microscopic spores produced in the soil or within plant roots, whereas many ectomycorrhizal fungi reproduce with mushrooms or underground truffles. [38]



Stained roots (**a**) show the colonisation by arbuscular mycorrhizal fungi (AMF). The AMF develop unique structures within root cells: (**b**) vesicles with storage function, and (**c**) arbuscules, the typical brush-like structure which gives the name to this group of fungi. (SLS, MBR)

Diamonds of cuisine

- Mycorrhizas are among the most widespread symbionts in the world. They are found in more than 80 % of all plant species and 92 % of all plant families.
- Mycorrhizas can be managed as biofertilisers as they increase plant nutrient uptake (see pages 98-99).

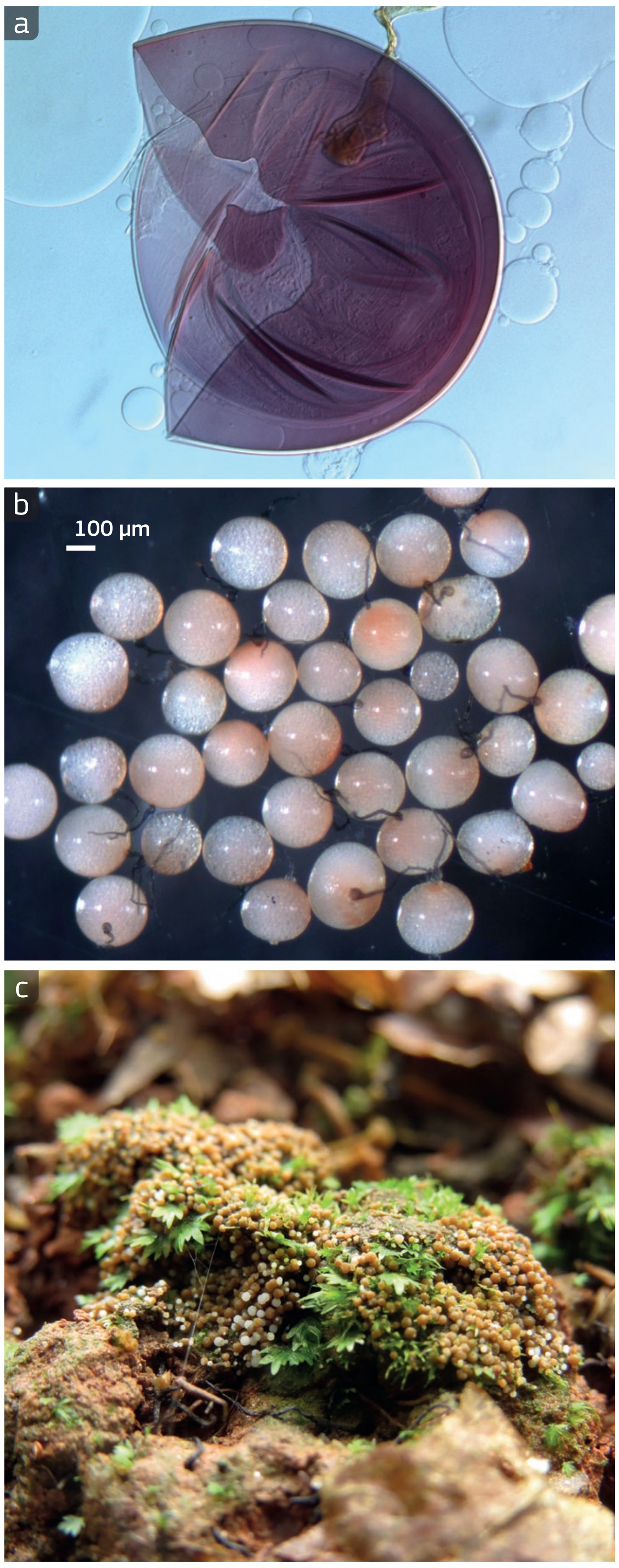
- Many species of ectomycorrhizal fungi are important culinary mushrooms and truffles.

They look like potatoes but are mycorrhizal fungi. The white truffle (*Tuber magnatum*), known as the diamond of cuisine, is a prized ingredient for cooking. (AO)

The significant mutual benefit of mycorrhizal symbioses is evident from their tremendous abundance and diversity. Mycorrhizal fungi are found in all terrestrial biomes and in association with most plant families. They are found with trees, shrubs, forbs, grasses and agricultural crops. Arbuscular mycorrhizas are abundant in tropical forests, grasslands, savannahs, deserts and arable lands, and ectomycorrhizas dominate temperate and boreal forests. Ericaceous mycorrhizas are common in boreal forests and heathlands. Orchid mycorrhizas are essential to the survival of orchids throughout the world.

Glomeromycota

Fungi in the phylum Glomeromycota form arbuscular mycorrhizal symbioses with the majority of plant species, by colonising the root cortex (see box, page 43) and forming an extensive mycelium, vesicles and arbuscules. This phylum contains 17 genera and 240 species distributed in nine families and four orders. Common genera include *Glomus*, *Rhizophagus*, *Sclerocystis*, *Gigaspora*, *Scutellospora*, *Cetraspora* and *Acaulospora*. Glomeromycota produce abundant hyphae and spores in soils. In grasslands and agricultural lands, these fungi comprise an estimated 20-30 % of soil microbial biomass, making arbuscular mycorrhizal fungi among the most abundant organisms in many soils.



Arbuscular mycorrhizal fungi reproduce through spores that can have various dimensions and colours: (**a**) a broken spore of *Cetraspora pellucida*, (**b**) the rosy spores of *Gigaspora rosea*, and (**c**) structures producing spores (sporocarps) of the fungus *Sclerocystis coremioides* associated with mosses. (SLS, KK)

Ectomycorrhizas

Approximately 6 000 fungal species establish ectomycorrhizal associations with many species of trees and woody plants. At least 20 families of Basidiomycota (e.g. Amanitaceae, Russulaceae, Boletaceae) and seven families of Ascomycota (e.g. Pezizaceae, Tuberaceae) are known to establish ectomycorrhizas. The biomass of ectomycorrhizal fungi mycelia has been estimated to range from 700 to 900 kg per hectare, and 20-40 % of an ectomycorrhizal root weight is due to the fungus.

Some of the fungi that are found in woodlands are ectomycorrhizal: (**a**) *Boletus bicolour*, and (**b**) *Scleroderma aurantium*. (MW)

Short lateral roots of a beech tree colonised by a white layer of hyphae of the ectomycorrhizal fungus *Xerocomus pruinatus*. (MB)

Ericaceous and orchid mycorrhizas

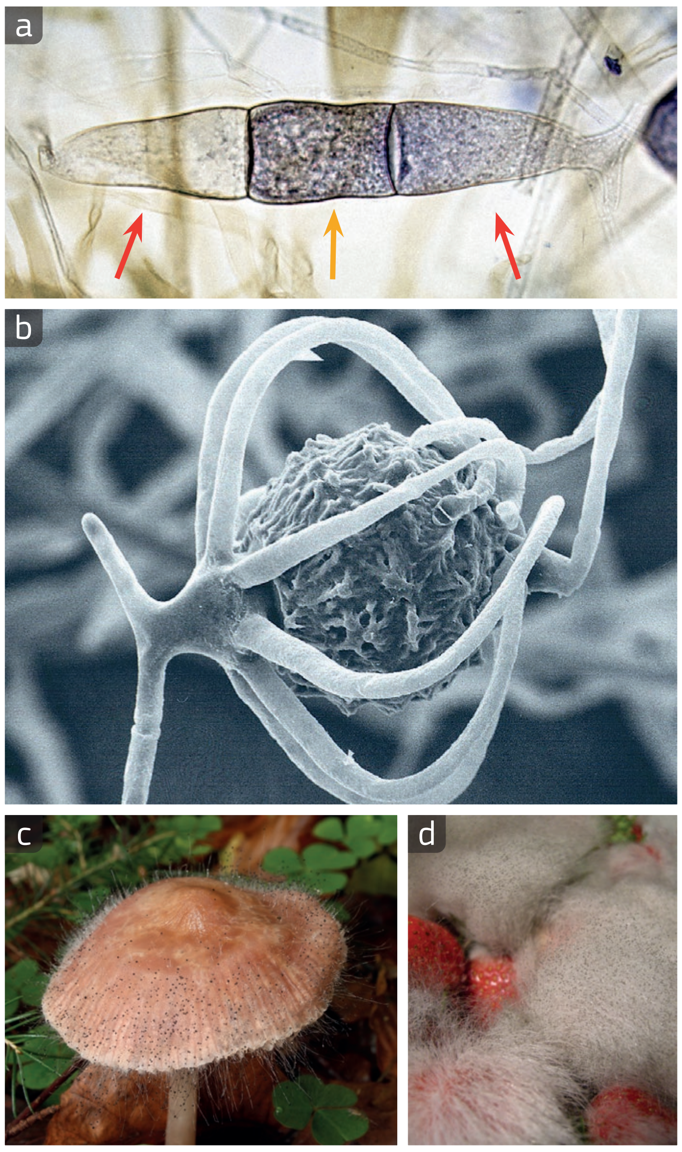
Most plant species belonging to Ericaceae, including the genera *Rhododendron*, *Calluna* and *Vaccinium*, form ericoid mycorrhizas. These plants form delicate roots lacking root hairs and their outermost radical cells become heavily colonised by Ascomycota from the genera *Rhizoscyphus* and *Hymenoscyphus*. Orchid mycorrhizas are established between plant species of the family Orchidaceae (20 000 to 35 000 species) and several groups of fungi in the phylum Basidiomycota, as well as some rare Ascomycota.

Plants belonging to Ericaceae, like heather (*Calluna vulgaris*) and Orchidaceae, may form specific fungal symbioses called ericaceous and orchid mycorrhizas, respectively. (RH)

Fungi – Other fungi

Zygomycota

A unique feature of the Zygomycota is the zygospore, which is formed within a structure called the zygosporangium after the fusion of specialised hyphae called gametangia during sexual reproduction [35, 36]. The mature zygospore is often thick-walled and undergoes a dormant period before germination. Nevertheless, asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae grow over the surface of the material on which the fungus feeds and produce clumps of erect stalks, called sporangiophores. The tips of the sporangiophores form spore-producing structures, the sporangia. Thin-walled spores are produced within the sporangia and are thus shed above the substrate, in a position where they may be dispersed by wind or water, allowing the fungus to spread and colonise new substrates quickly and efficiently. The Zygomycota include two main classes: Zygomycetes (that comprise Mucorales, the most studied order) and Trichomycetes. More than 1 000 species have been described so far. Zygomycetes are commonly decomposers, symbionts or parasites (see box, page 33) in terrestrial habitats. For example, members of the Mucorales are easily isolated from soil, humus and dung. Furthermore, some Mucorales are used to ferment foods and produce important industrial products, such as lactic acid and rennin (used to make cheese). Conversely, some species have a negative economic impact by causing storage rot in fruits. Trichomycetes are obligate associates of arthropods, including insects and millipedes. The host may be an adult or larva, in terrestrial or aquatic habitats. The fungi are usually found attached to the gut lining of the host. The precise relationship is difficult to determine in most cases; however, they often seem to be commensals, doing little or no harm to their hosts, with the fungus gaining nutrients from the gut of the host. Some zygomycota can also be pathogens of animals, plants, amoebae and, especially, other fungi. Of the more than 1 000 species of described Zygomycota, the majority are found in soil, with some genera (*Mucor, Mortierella* and *Rhizopus*) that are extremely common and reported in almost all surveys of soil fungi.



(**a**) Once the hyphae of two opposite mating types (red arrows) have made initial contact, they give rise to a young zygospore (orange arrow). (**b**) A highly ornamented mature zygospore held by hyphae. (**c–d**) Zygomycota can attack other fungi and fruits. (GB, HK, CSI)

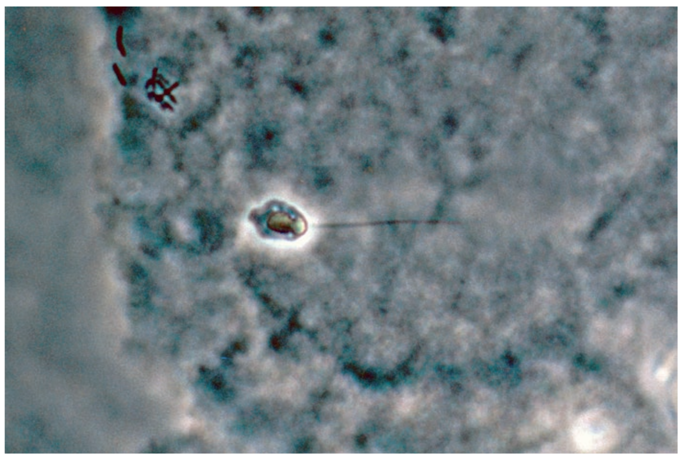
The hat thrower

- A unique spore dispersal strategy for the Zygomycota of the order Mucorales is exhibited by the dung fungus of the genus *Pilobolus*.
- Its name literally means 'the hat thrower'. When spores are ready, the turgor pressure within the vesicle beyond the sporangium (spore-producing structure) builds to a sufficient level that allows the sporangium to be launched. The entire black sporangium is explosively shot off up to distances of several metres.
- For an organism less than 1 cm tall, this involves acceleration from 0 to 20 km/h in only 2 μs, equivalent to a human being launched at 100 times the speed of sound (more than 120 000 km/h).

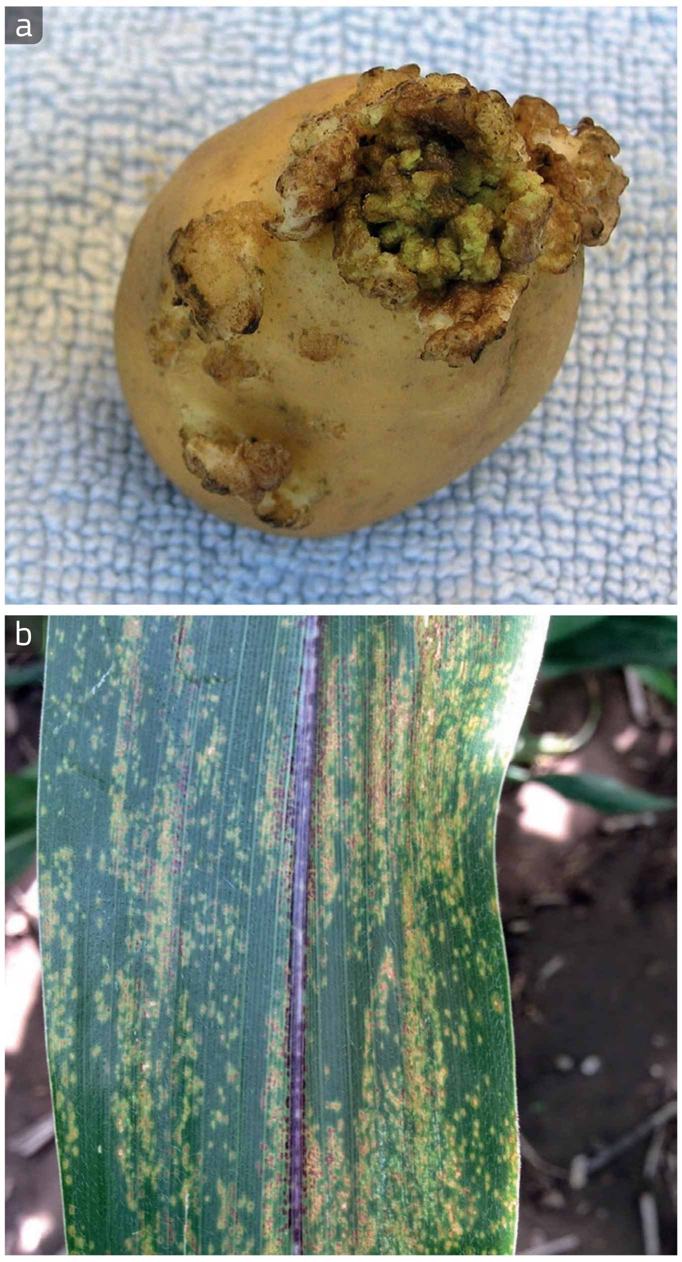
A species of *Pilobolus* showing a black sporangius that will be launched several metres away to disperse the spores. (RK)

Chytridiomycota

Chytridiomycota (chytrids) are characterised by their asexual state, a motile (capable of moving) zoospore with a single whiplash flagellum oriented and located posteriorly [35, 36]. Zoospores are released through an opening in the wall, and their release usually indicates the death of the 'body' of fungus, called thallus. They are the only fungi that form flagellate spores. Chytridiomycota are typically unicellular, with limited hyphal growth in some cases. Chytrids require a water film in which zoospores can swim until a desirable substrate is found. For this reason, chytrids are usually regarded as aquatic fungi, although those that thrive in the capillary network around soil particles are typically considered terrestrial. Approximately 700 species of chytrids have been described, including species living in temperate forest and rainforest soils. Soil chytrids include plant pathogens and vectors of plant viruses such as *Synchytrium endobioticum,* which causes the potato wart disease (black scab) and serious commercial damage. Some chytrids are nematode (see pages 46-47) and algae parasites. As Chytridiomycota often feed on decaying organisms, they are also important decomposers. These organisms are responsible for the decomposition of resistent materials, such as pollen and cellulose. This colonisation of pollen usually occurs during the spring when bodies of water accumulate pollen falling from trees and plants. Estimates of the number of chytrid species occurring in soil are currently unavailable.



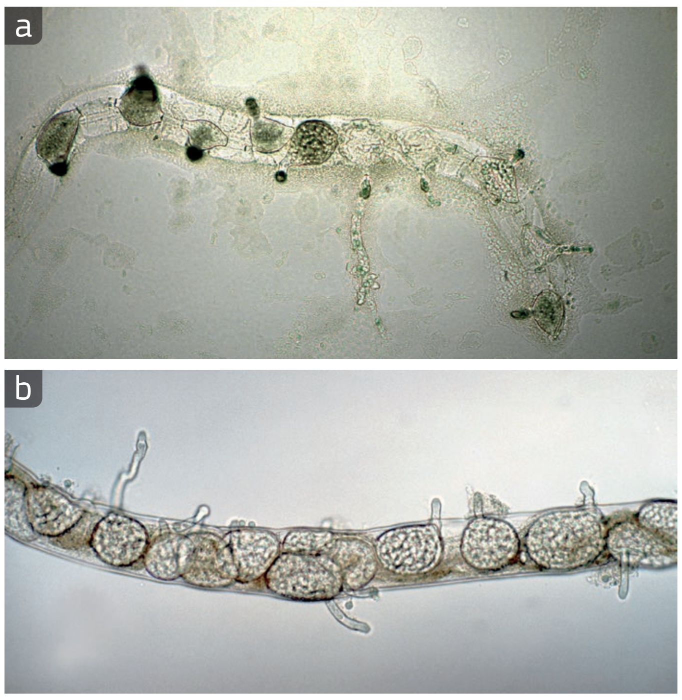
A zoospore with its flagellum (thin dark line) allowing it to move. Chytridiomycota and Blastocladiomycota are the only fungi producing this type of spore. (GB)



Chytridyomycota and Blastocladiomycota are responsible for some plant diseases: (**a**) potato wart disease caused by the chytrid *Synchytrium endobioticum* and (**b**) brown spot disease brought by the blastoclad *Physoderma maydis* on maize. (SK, mm, SPR)

Blastocladiomycota

The Blastocladiomycota (blastoclads) are one of the currently recognised phyla within the Fungi kingdom. Blastoclads were originally the order Blastocladiales within the phylum Chytridiomycota, until molecular and zoospore structural characters were used to demonstrate that it was a group separated from chytrids. Similar to Chytridiomycota, Blastocladiomycota produce zoospores to colonise new substrates. Furthermore, members of Blastocladiomycota are capable of decomposing complex materials, such as cellulose and chitin. Of economic importance is *Physoderma maydis*, a parasite of maize and the causal agent of brown spot disease. There is a blastoclad, *Sorochytrium milnesiophthora*, that is a tardigrade parasite (see page 44). However, the best known species, belonging to the genus *Catenaria*, are nematode parasites. As they are mainly known to be aquatic fungi, a reliable evaluation of their abundance in soil is not available.



(**a**) The blastoclad *Catenaria anguillulae* living inside a nematode, which it has parasitised. (**b**) The spore-producing structures (sporangia) of *Catenaria* emerge from an infected nematode. (EK, GB)