MASARYK UNIVERSITY, FACULTY OF SCIENCE

DEPARTMENT OF BOTANY AND ZOOLOGY

FUNGAL ECOLOGY

(sometimes with special regard to macromycetes)

Fungi and their environment • Life strategies and interactions of fungi • Ecological groups of fungi, saprotrophs (terrestrial fungi, litter and plant debris, wood substrate, etc.) • Fungal symbioses (ectomycorrhiza, endomycorrhiza, endophytism, lichenism, bacteria, animal relationships) • Parasitism (parasites of animals and fungi, phytopathogenic fungi, types of parasitic relations) • Fungi in various habitats (coniferous forests, broadleaf forests, birch stands and non-forest habitats, fungal communities) • Fungal dispersal and distribution • Threat and protection of fungi

(the study material has not been corrected by native speaker)

SYMBIOTIC RELATIONSHIPS WITH ANIMALS

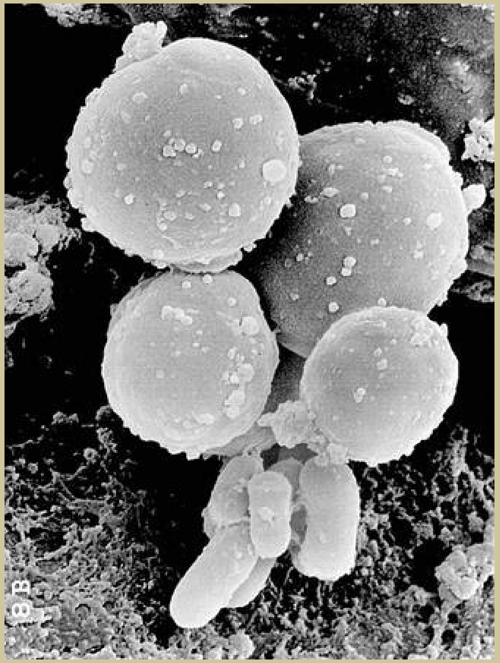
Fungal symbionts of animals can grow on the surface or inside animal bodies. Growth on the surface means colonization of fur, skin, feathers, exoskeleton; the fungus is often limited to dead tissue and does not cause defense reaction of the body, but is exposed to the external environment and there is often low availability of water and nutrients (keratin is very resistant to decomposition).

In contrast, there is usually a stable environment inside the body, plenty of water and freely available nutrients, but fungi have to deal with abundant bacteria, low oxygen content, low pH and strong peristalsis (digestive system) or a strong immune response (blood circulatory system).

A common characteristic of fungi, which can be described as symbiotic (obligatory symbioses or facultative relationships), is not harming the animal partner – seen from a human point of view, the fungus tries to keep its „substrate“ alive and not cause its disease and death. Otherwise there is a risk of loss of this „substrate“ and subsequent competition with necrotrophs.

At first we can mention cases of **endosymbiosis**, where the fungus spends its entire life inside the animal's body – for example, fungi have been found in the cells of amoebae or in the body cavities of annelids.

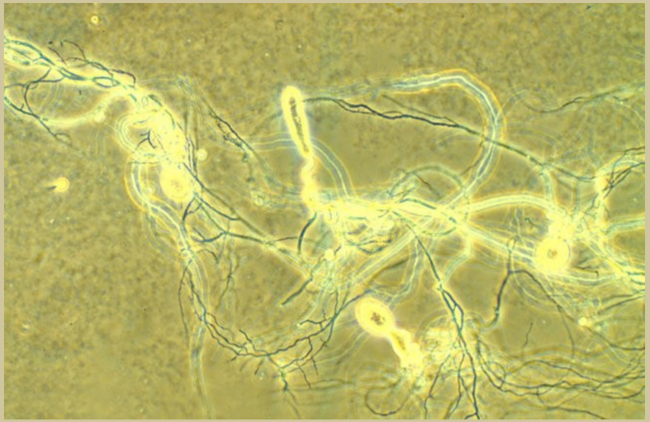
The most common endosymbionts are yeasts or fungi forming yeast-like stages, living in the digestive tract of various animals (e.g. *Spermophthoraceae* are fixed on animals).
The role of *Candida albicans* has not yet been fully elucidated; this fungus is present in humans on the body surface or in the digestive system, where it is a natural inhabitant (cells attached to the intestinal wall). In the case of excessive reproduction it becomes a pathogen that can even cause the death of its host *(see also Parasitism, pathogenic fungi)*.

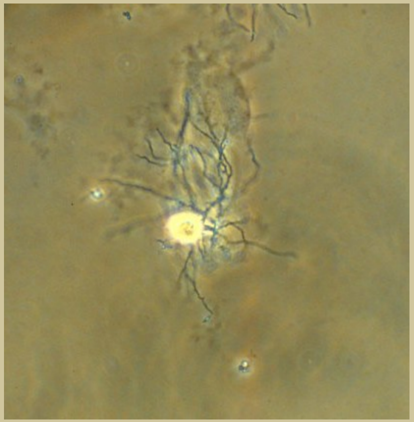


http://medinfo.ufl.edu/year2/mmid/bms5300/images/semyeast.jpg

Fungi also play an important role as part of the microbiota in the **rumen of ruminants** or the **intestines of non-ruminant herbivores**. With the exception of molluscs, animals do not produce cellulases, so they need to „pre-chew“ plant food – especially the obligately anaerobic *Chytridiomycota* (sensu lato), exactly *Neocallimastigomycota* are involved here (carbon dioxide and methane occur in the digestive tract, traces of oxygen are immediately utilised by facultative anaerobes).

Although the question is whether it is a mutalistic relationship or commensalism, it is probably a beneficial interaction of fungi with other microbes, which results in the decomposition of nutrients (these fungi are able to ferment cellulose, xylans, hemicellulose, starch to formic, lactic and acetic acids), the release of vitamins and amino acids (plant food is quite poor of them) and in some cases the detoxification of plant toxins. They are effectively supplemented by rumen bacteria – chytridia mechanically disturb the substrate, bacteria increase the activity of chytrid enzymes and the efficiency of decomposition by producing methane.





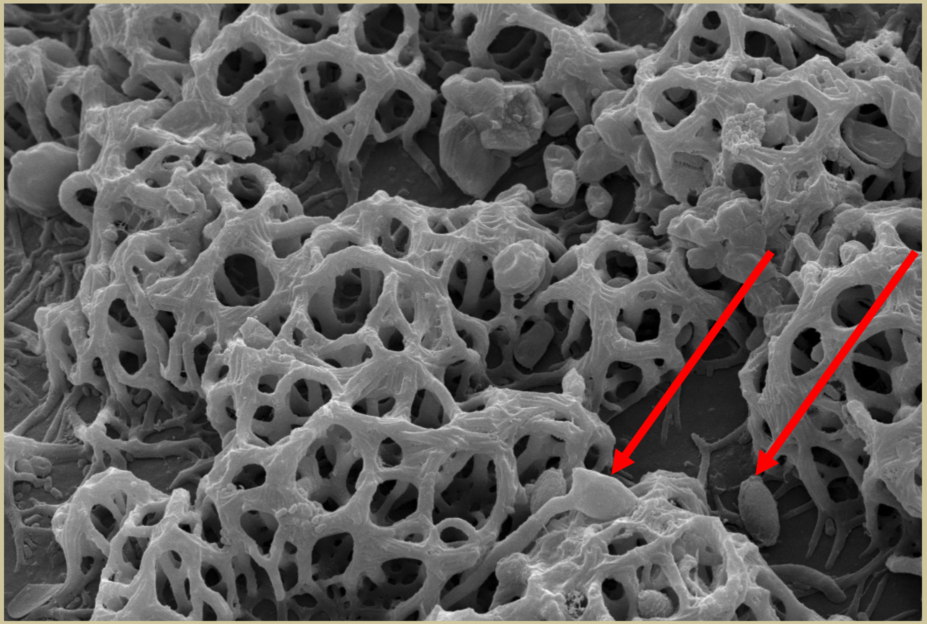
Left and centre: *Neocallimastix frontalis*; right: *Piromyces communis*

http://cgdc3.igmors.u-psud.fr/microbiologie/partie1/chap3_02_eumycota.htm http://www.bsu.edu/classes/ruch/msa/wubah.html (2x)

Most endosymbiotic fungi are associated **with insects** (yeasts, hyphomycetes); they occur in the digestive tract, Malpighian tubules or live in special tissues – mycetomes – or directly in special cells – mycetocytes (bacteria are involved here in addition to fungi). The fungi supply the insects with some amino acids and vitamins, they also help to degrade nitrogenous products of metabolism (urea, uric acid). In order to transfer the fungus to other individuals, it usually passes from the mycetome to the digestive tract, from where it is excreted => then it comes into contact with laid eggs or offspring.

General rule: the more specific structures are evolved, the older (meaning evolutionarily) a given symbiotic relationship usually is.

Springtails and **mites** are common among the organisms which frequently spread spores of fungi (both saprotrophic and mycorrhizal) in the digestive tract and on the body surface,



Surface cerotegument on the dorsal side of the body of the soil oribatid mite *Belba bartosii* with fungal spores (arrows).

Photo Jan Mourek, http://www.rozhlas.cz/leonardo/veda/_galerie/449587?type=image&pozice=1

However, the mutually beneficial effects of these organisms have a broader scope – the hyphae serve as food and the springtails in turn mobilise nutrients in the substrate (urea), maintain the diversity of fungi in the soil and stimulate growth by biting when removing old hyphae (=> compensatory growth). Some ectomycorrhizal fungi are even able to hunt for springtails (of which, however, the „preys“ are probably not very happy...).

Both groups of invertebrates are an important part of edaphon (they feed on strongly decomposed litter, algae, fungi, detritus or are predators).
There are still contradictory opinions, how strong the preferences for the substrate are (phytophagous, mycophagous, herbivorous); probably they are „choosy generalists“ (i.e. they choose what is possible), but we can suppose:
– if the utilise plant debris, it is strongly decomposed (low C:N ratio), i.e. already colonised by fungi;
– if fungi, they prefer dematiaceous (however, the question remains why they feed on them, when melanin is difficult to degrade), not chitinolytic (to avoid the fungus to eat them – but not absolutely, the most common species associated with oribatid mites is chitinolytic (!) *Beauveria bassiana*) and not toxinogenic (except the case of *Aspergillus flavus* on stored grain).

Other cases are symbiotic fungi living **outside the animal bodies** or **on their surface**.

Woodpeckers probably help the spread of lignicolous fungi, whose action in wood, on the contrary, they use in nest formation. Nesting of red-cockaded woodpecker (*Picoides borealis*) is reported in cavities, which it creates in trees with heartwood softened by *Phellinus pini* – the woodpecker does not have to carve so much and at the same time the nest is still protected by hard sapwood.

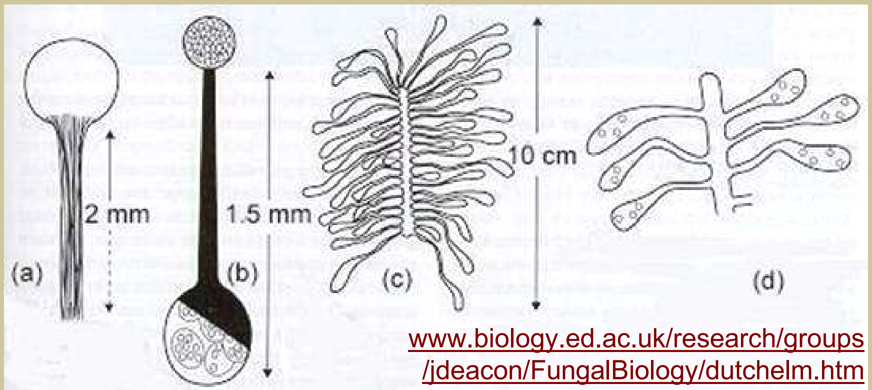
http://www.forestryimages.org/browse/detail.cfm?imgnum=2250085

http://en.wikipedia.org/wiki/Red-cockaded_woodpecker

The use of various habitats created by vertebrates can be described as „free symbiosis“ – bird nests have already been mentioned as a source of nutrients for keratinophilic species, or *Hebeloma radicosum* drawing nutrients from mole „toilets“. Other cases may be crocodile nests with eggs, where thermophilic species occur, or nests where the animals accumulate stocks – e.g. seed stocks of the rodent *Dipodomys spectabilis* (photo), which are colonised by non-toxinogenic species of the genus *Penicillium*.

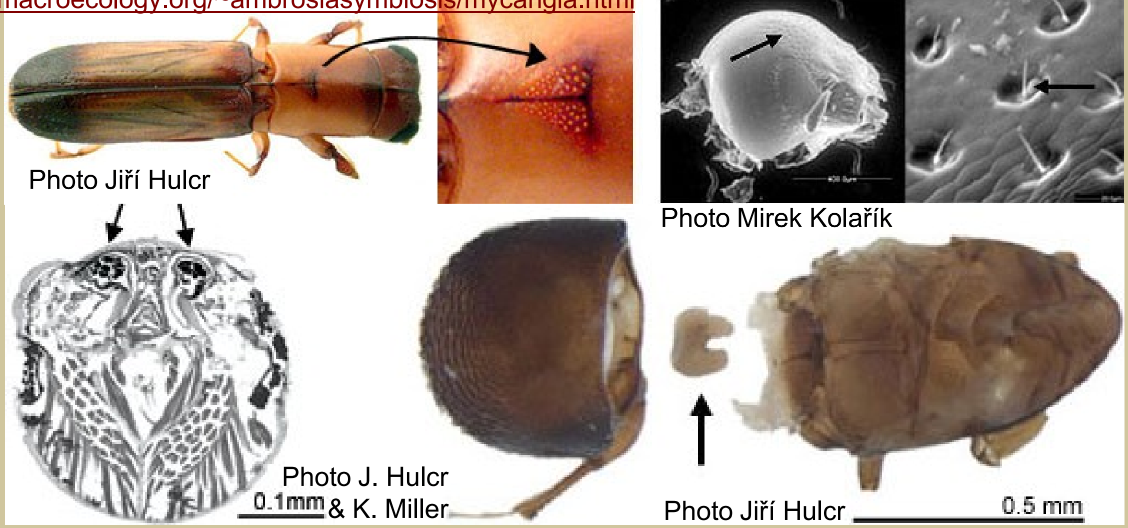
http://www.mnh.si.edu/mna/image_info.cfm?species_id=69

Coexistence of fungi with **bark beetles** (*Scolytidae*) is known – beetle corridors are grown through by *Ophiostoma* spp., which degrade cellulose and lignin, and serve as food for hatched larvae.
Adult beetles then spread the fungus to other trees – not „randomly glued“ fungi (*Ophiostoma* or *Ceratocystis* spores are released from perithecia in sticky mass), but females have „pockets“ on the body surface, below the surface or between the abdominal segments, in which they transfer the mycelium or conidia, so-called mycetangia (mycangia) => when laying eggs, they also „lay“ fungal diaspores.
Weevils form similar symbiosis (transfer of fungal cells in mycetangia) with some yeast species.



www.biology.ed.ac.uk/research/groups/jdeacon/FungalBiology/dutchelm.htm

http://www.antmacroecology.org/~ambrosiasymbiosis/mycangia.html



Top: *Ophiostoma* sp., (a) coremium, (b) perithecium with sticky drop at its top.

Centre: Surface mycangia on the head of *Treptolatypus solidus* (left), *Scolytodes unipunctatus* (right; arrow shows a spore).
Bottom: Internal mycangia of *Xyleborus affinis* (left) and *Xylosandrus germanus* (right).

Similarly, the **sawflies** have mycetangia next to the ovipositor – they spread some stereoid fungi (*Stereum sanguinolentum*, Amylostereum spp.) or polypores (*Cerrena unicolor*). Their larvae do not have to feed directly on the fungus, but wood with degraded lignin and cellulose is better digestible for them. The irony of fate is that the sawfly can carry an unwelcome „companion“ – a nematode that feeds on the same fungi, which can attack the wasp larva, settle in it and in adulthood spread further with laid eggs.

Amylostereum areolatum, Cerrena unicolor

In general, fungi growing through and spread through insect corridors are referred to as **ambrosia fungi** (ambrosia are thin-walled cells forming a continuous layer lining the inner walls of the corridors in the wood).
The narrower concept is that true ambrosia fungi are only those that are carried by insects in specialised organs (mycetomes, mycetangia).

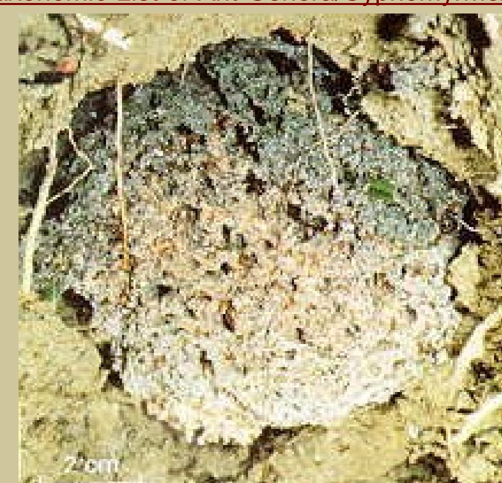
A certain form of the fungus-animal relationship, although it is not an obligatory symbiosis, is also endozoochory or epizoochory, which is common in many animal groups *(more in the chapter Fungal spread and distribution)*.

The **„mushroom growing“** by animals has been found in ants (genera *Atta* and *Acromyrmex* from Latin America), which create „mushroom gardens“ in their ant-hills (up to several hundreds, 20–30 cm in size): they bring leaves and twigs to the anthill and they bite them on the pulp

http://blog.fortumo.com/wp-content/uploads/2009/07/leaf-cutter-ants.jpg

=> they inoculate individual fragments by the fungi (*Agaricaceae*, specifically tribus *Leucocoprinae*; there is a close connection, individual species of ants have „their own“ species of fungi) => the „gardens“ contain chewed pieces of leaves covered with dense mycelium (in species forming underground nests they fill the chambers in the substrate) => hyphae then serve as food for ants, which are obligately mycophagous – workers harvest inflated ends of hyphae and distribute them in bowels to larvae and other adults (larvae are probably fully dependent on this food, in adults it is not such an essential component of nutrition).

Photo Alex Wild, http://www.alexanderwild.com/Ants/Taxonomic-List-of-Ant-Genera/Cyphomyrmex



Left: „farming“ males of *Cyphomyrmex costatus*, Right: „mushroom garden“ of *Acromyrmex* sp.

Fisher et al. 1994; http://www.mycolog.com/chapter16.htm

Inflated terminal cells of hyphae are called gongylidia; they do not grow individually in the „gardens“, but form compact clusters of tangled hyphae called bromatia. No sporulation was found in these fungi and the spread is likely realised through the transfer of mycelium with the queen when a new colony is established.

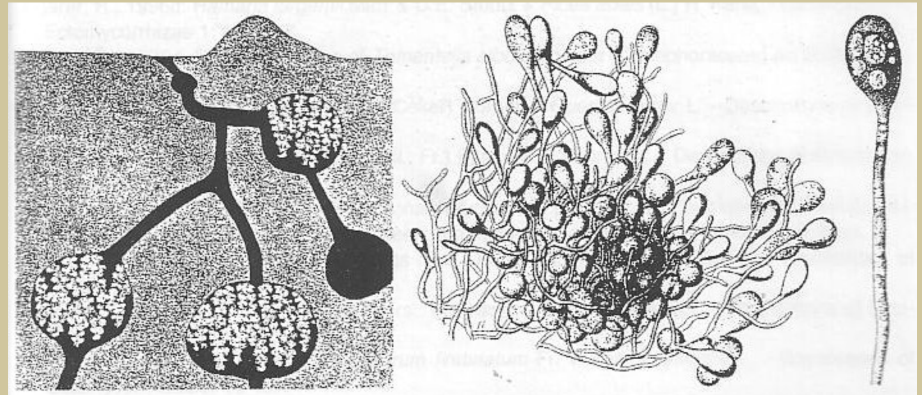


Figure 11.43: Fungus gardens of leaf cutter ants. **Left:** Diagram of the earth-nest of the ant *Trachymyrmex obscurior*. Three chambers with fungus gardens hanging from their ceilings. From Wheeler 1907, modified. **Right:** A bromatium with numerous gongylidia, and a gongylidium on top of a hypha. From Möller 1893, modified.

Clémençon: Cytology & Plectology ..., 2004.

The ants not only „grow their mushrooms“, but also remove other species that contaminate „their culture“ (the mechanism of recognition is still unknown, probably the ants recognise the smell of various species), directly physically, they „weed their gardens“, i.e. they select „the other“ spores from the brought material and take them out of the colony in special pockets (for this purpose, the workers use a separate exit, to minimise the possibility of contamination).

In addition, ants have symbiotic bacteria (genera *Streptomyces* or *Pseudonocardia*) in the holes in the body, which they „feed“ by secretions.
In return, the bacteria produce antibiotics to suppress the growth of „unwanted“ fungi (shape of the holes is species-specific, as well as the symbiont species).

A specific symbiosis is formed by **termites** with fungi of the genus *Termitomyces* (*Basidiomycota*, *Tricholomataceae*, weighing up to 2.5 kg and a pileus diameter of 60 cm) and some xylariaceous fungi: termites in the nests roll „balls“ of wood, herbs, mycelia and fungal conidia, which then they eat together with the wood – the fungal exoenzymes probably allow them to digest the wood => conidia of the fungi are then spread with their droppings.

Various species of termites also form macroscopic formations of sponge-like consistency (using plant remnants and their exudates), containing chambers, which are grown through (and their walls covered) by fungal hyphae.

Termitomyces titanicus

http://panacea.med.uoa.gr/topic.aspx?id=263

Heinz Clémençon: Cytology and Plectology of the Hymenomycetes.

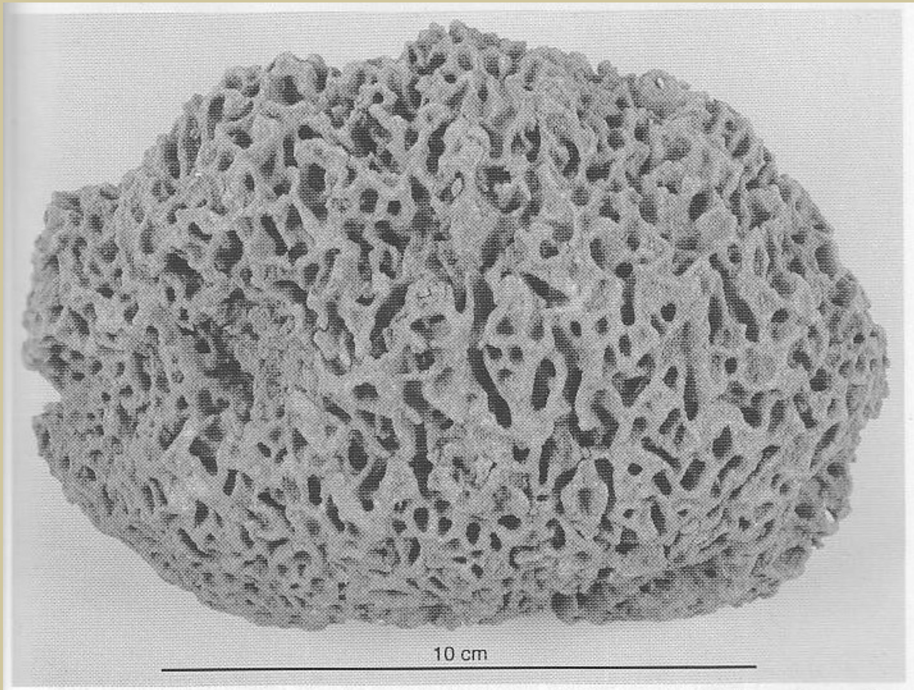


Figure 11.35: A sponge-like substrate prepared by the termite *Macrotermes bellicosus* for growing an unidentified species of *Termitomyces*. The termitospheres are not clearly visible in this picture; see figures 11.36-11.39 for details. – From an experimental termite nest by R. Leuthold, University of Berne, Switzerland. – Original photograph.

Instead of fruitbodies, termitospheres are formed on their surface – tiny structures (analogous to sporodochia), ...

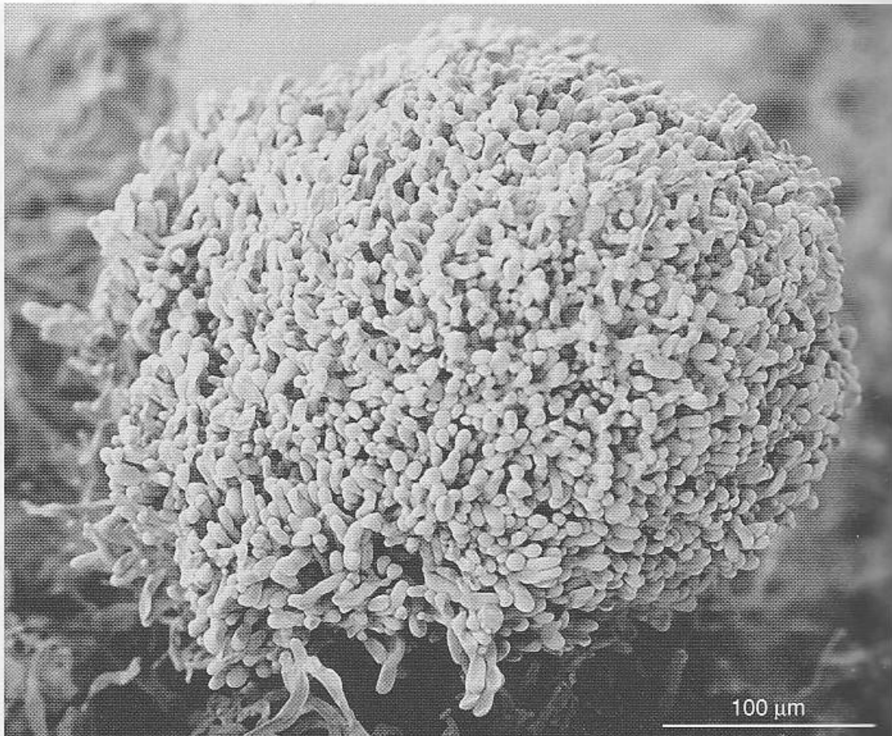


Figure 11.38: Scanning electron micrograph of a termitosphere-nodulus from an experimental nest of *Macrotermes bellicosus* by R. Leuthold, University of Berne, Switzerland. – Photograph by Katia Gindro, University of Lausanne, Switzerland.

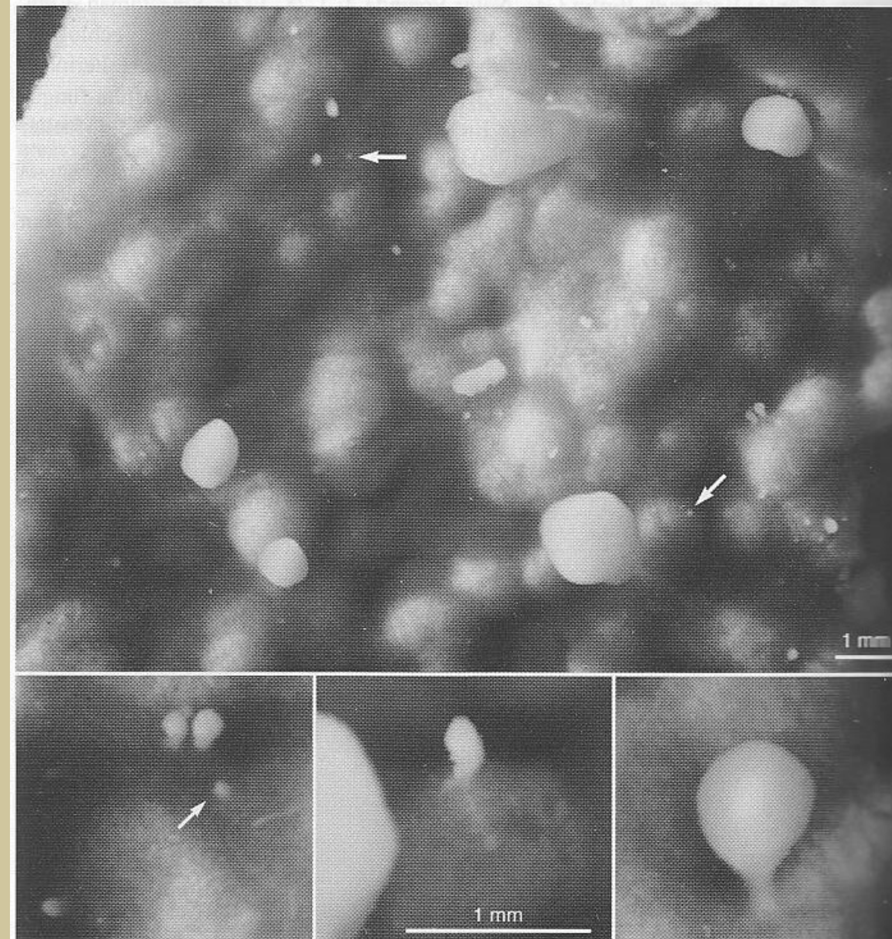


Figure 11.36: Part of the substrate with many young termitospheres of *Termitomyces* spec. in various developmental stages, from tiny spherical noduli (arrows) to pedunculate spheres. – From an experimental nest of *Macrotermes bellicosus* by R. Leuthold, University of Berne, Switzerland. – Original photographs.

Heinz Clémençon: Cytology and Plectology of the Hymenomycetes. Bibliotheca Mycologica 199. J. Cramer, Berlin-Stuttgart, 2004.

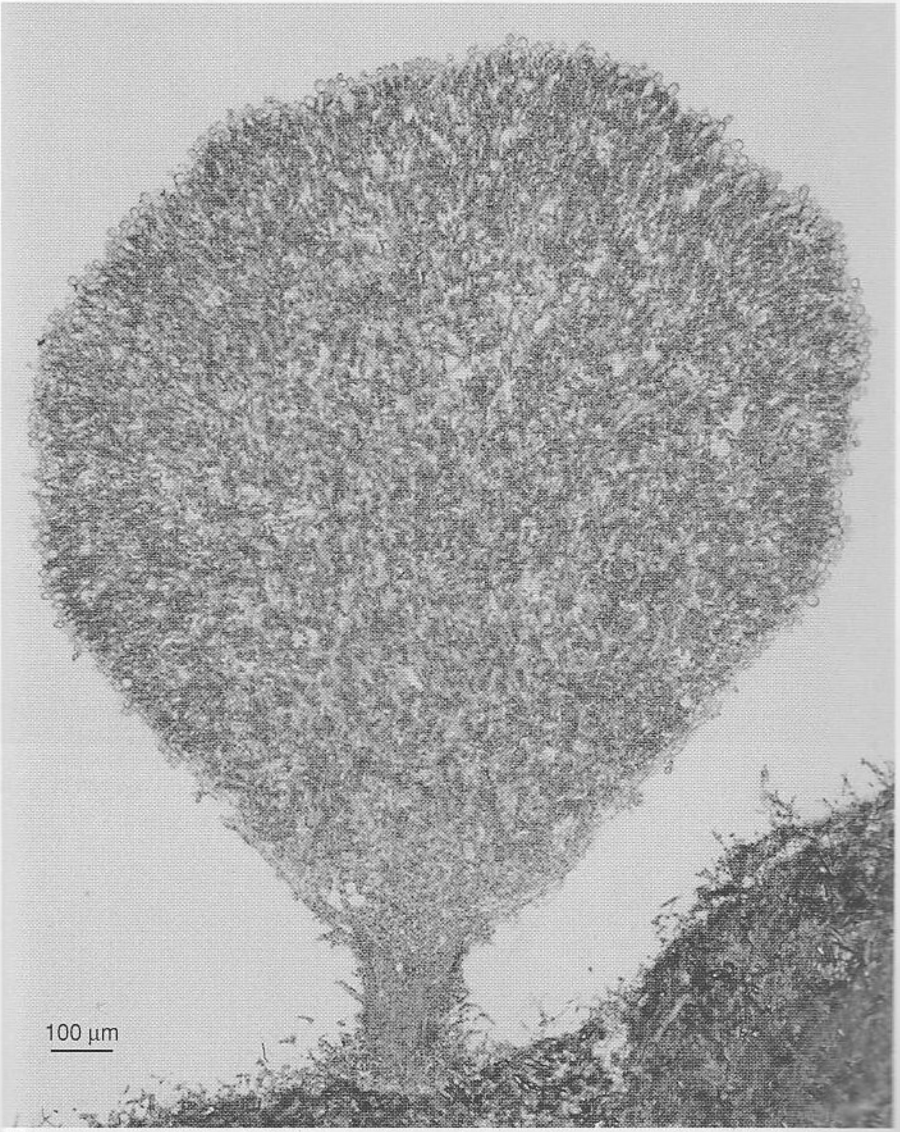


Figure 11.37: Median longitudinal section of a termitosphere. The upper surface is lined with slightly thick-walled aleuria (usually called conidia). The surface of the substrate is covered with a sparse aerial mycelium. – From an experimental nest of *Macrotermes bellicosus* by R. Leuthold, University of Berne, Switzerland. – Microtome section stained with iron haematoxylin. Original photograph. The structure represented in this photograph has been variously named in zoological and mycological publications: Spheren (Rant 1923), mycotêtes (Heim 1977), and sporodochia (Botha & Eicker 1991a,b). Cifferi (1935) treated them as an anamorph state with the generic name *Termitosphaeria*. Sometimes the thick-walled outer cells are called conidia, sometimes the whole termitosphere was called a conidium, an obvious mistake. Since the thick-walled cells are not detached for dissemination, the terms conidium and sporodochium should be avoided. «Termitosphere» (Clémençon 1997: 163) is a morphological term based on Rant's Spheren.

... on the surface of which aleurio-spores (thick-walled conidia) are formed => termitospheres are eaten by termites and aleuriospores spread by faeces (similar to the case of „balls“). If the termitospheres are not eaten, they can later develop into fruitbodies.

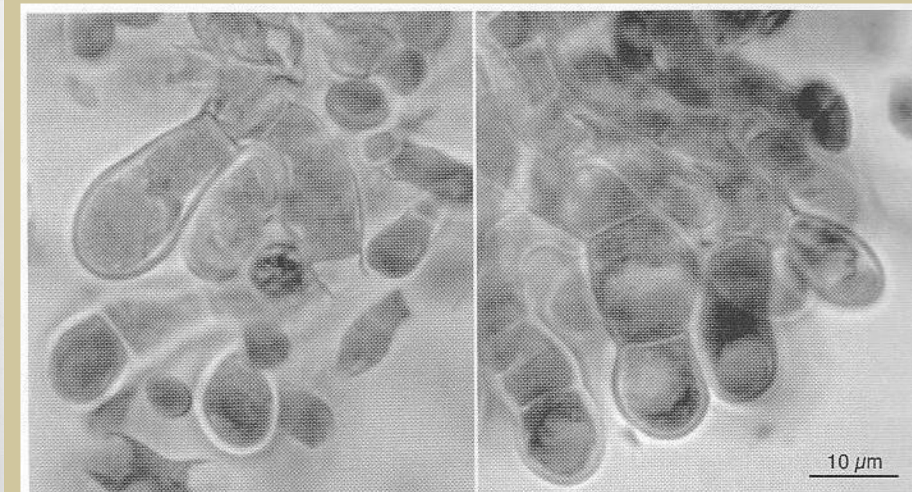


Figure 11.40: Aleuria ("conidia") from a termitosphere from figure 11.36, mounted in cotton blue lactic acid. – Original photographs.

Clémençon: Cytology and Plectology ..., 2004.

„Mushroom growing“ (described for 210 ant species and 330 termite species!) is known only from tropical regions (forests, savannas).

The „triple relationship“ is formed by fungi of the order ***Septobasidiales*** with **plants** and **scale insects**. Wingless insect females live appressed at the leaf from which they suck nutrients (basically it is parasitism) => they are overgrown with fungal hyphae until the fungi form a continuous cover over the insect colony => they immobilise the insects, penetrate haustoria into the blood cavity and suck nutrients from there – in principle the fungus parasitises on parasitic insects (*Septobasidiales* are probably not able to exist independently for a long time).

The relationship is established using chemical attractant secreted by the fungus => insects form a colony in which only some individuals are directly attacked, while others use protection of the fungal cover together with them.

Top: still free individuals of scale insects.
Bottom: *Septobasidium*, which has already covered the colony of these insects.
http://www.morning-earth.org/Graphic-E/SymbiosisCrossKingFungi.html

Individuals of scale insects, into which the haustoria of fungi have penetrated, do not reproduce; reproduction of the species is ensured by other females in the colony, which are not directly attacked by the fungus (insects also ensure spread of the fungus, they transfer basidiospores on their bodies).

To summarise the plus and minus of the relationship, the fungus parasitises on the insects, but on the other hand provides them protection (against predators and pathogens) and a stable environment (limited evaporation) – this is an example of relativity of the meaning of the word symbiosis.

It is therefore appropriate to make a general conclusion at the end of this chapter: **there are no sharp boundaries between mutualistic symbiosis, saprotrophy and parasitism**.