Heinz Clémençon
with the assistance of Valerie Emmett and Ernest E. Emmett

Cytology and Plectology of the Hymenomycetes

2nd revised edition

J. Cramer
in der Gebr. Borntraeger Verlagsbuchhandlung

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with the assistance of
Valerie Emmett
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with 636 figures and 12 tables

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front cover: *Armillaria ostoyae*
A member of the „*Armillaria mellea* complex", a group of closely related, economically and ecologically important fungi whose biochemistry, cytology, genetics, ecology, environmental impact, longevity, bioluminescence, rhizomorphs and taxonomy have been studied ever since the early 20th century.

back cover (top-down)
Lenzites betulinus, p. 358. Peripheral hyphae of the basidiome grow around obstacles, incorporating them into the basidiome context.

Russula queletii, p. 325. Artificially stained section through a gill.

Panellus violaceofulvus, p. 296. This gill fungus lacks a stipe and hangs down from a piece of wood. It is attached to the substrate at the centre of its pileus.

Lichenomphalia umbellifera, p. 442. An example of a lichenised Basidiomycete. The green substrate in the lower right is the lichen thallus.

Stromatoscypha fimbriatum, p. 296. Many small cup-shaped basidiomes are united into a bigger complex.

All photos: H. Clémençon

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Foreword to the first edition

When my book “Anatomie der Hymenomyceten” was published in 1997, several colleagues asked for a free review copy, which they obtained; but they never wrote any review. This might have been an act of politeness, and I promised myself not to translate my book into English, and never to write a second edition. My decision was confirmed by a rather unpleasant and often unsubstantiated criticism published in Sydowia, written by an author who did not ask for a free copy, and who never answered my letters.

Things changed in 1999, when two surprisingly good book reviews were published in Mycologia and in Coolia, both written by authors who did not ask for a free copy. This might have been an act of politeness, just as the positive oral remarks I received from various colleagues might have been polite talking, but I promised myself to continue my laboratory work after my retirement from University in August 2000.

Then, in autumn 2000, the British Mycological Society organised a week long foray in Switzerland, an occasion for me to meet good friends and acquaintances. After a long internal fight and quite a lot of hesitation I asked Ernest E. Emmett if he would perhaps consider the possibility to proof-read my manuscript and correct my “continental” English. Without any internal fight and with no hesitation whatsoever he simply said yes and assured me that this would be a pleasure for him. His answer was certainly a pleasure for me, and I decided to start writing. I did not know at that time that Valerie Emmett was going to join Ernest in a truly admirable way and effort to straighten out my wavy expressions.

I kept both my promises, the one about writing and the one about working. This book is not a translation of my German “Anatomie der Hymenomyceten”; and it is not a second edition. It is entirely re-written, and it is considerably shorter. And being freed from Department meetings, Biology meetings, Faculty meetings, University meetings, committee meetings, administration, report writing, teaching, seminars and exams, I could do more collecting and more laboratory work (at home); and so I was able to peacefully build up a collection of microscope slides, and to make many new microphotographs to illustrate the new book.

Valerie and Ernest Emmett did much more than proof-reading and making good English out of mine; they ever so often commented on mycological facts and questions, and pointed out inconsistencies and queer logic. They never admitted my favourite “fibre hyphae,” so its use in this book is entirely of my own responsibility, based on an inborn stubbornness. **Thank you so much, Val and Ern**, and, please, excuse my stubbornness.

After this lengthy attempt to justify the making of this book, let me make some remarks on the book itself. The basic aim is the same as for the “Anatomie der Hymenomyceten”: to bring together in one volume the essentials of the morphological mycology of an important group of fungi. During the past decades, morphology was in steady disfavour and decline, eclipsed by molecular biology. I am not against molecular sciences; I admire them gratefully, since they transformed taxonomy from emotion to science; and I actively contributed to that transformation. But I am against the selfish claim of some molecularists “to have reduced biology to its essentials.” No physicist will ever claim to have reduced

Beethoven to his essentials just by displaying the sound waves of one of his concertos on a screen. Anatomy and morphology are not "quasi sciences for minor minds," an excuse all to often used by taxonomy-starved biologists. This attitude has lead to a reduction or even elimination of morphology and taxonomy from teaching, with the result, that many modern biologists painfully lack adequate information about the organisms they work with.

This book is addressed to biologists and advanced amateur mycologists, in an attempt to promote "organismic biology."

Lausanne, May 2003

Preface to the second edition

It has been said again and again that morphology and anatomy are old fashioned, dead, replaced by the more attractive molecular biology and ecology. But molecular biology and ecology are put to excellent use in the reconstruction of phylogeny and modern taxonomy, not only for animals and plants, but also for fungi. This renewed interest in classification spurred new interest in morphology and anatomy, since taxonomy and systematics cannot live without these sciences. The success the first edition encountered was a pleasant surprise because it showed that interest in morphological mycology is still widespread. This encouraged me to revise, update and enlarge this book.

New publications (from 2003 to 2011) were an important source of new information updating and enlarging the content of this second edition. A few illustrations were replaced or presented in a better way and a few typing errors corrected. The nomenclature of the fungi discussed was updated paying attention to the results of the recent research in molecular taxonomy and systematics.

The first edition was written with the assistance of Valerie and Ernest Emmett; the second edition was not. But since large parts of the text are essentially the same as in the first edition, carrying the work of my friends from the old book to the new one, it is a pleasure to appreciate their help also the second edition and to express my thanks in this edition again.

Lausanne, July 2011

H. Clémençon

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1

BASIC CONCEPTS

In this chapter some essential terms and concepts of the morphology of the Hymenomycetes are introduced. Physiology, biochemistry, genetics, sexuality and ecology are not discussed.

The Hymenomycetes and the Other Fungi

Hymenomycetes are basidiomycetes and thus develop their spores upon **basidia**. In this book only those basidiomycetes are considered to be Hymenomycetes that group their basidia in a more or less continuous layer called a **hymenium** exposed to the open air at full maturity (Persoon 1794, 1801). The basidia are unicellular and only rarely become secondarily septate. The product of the meiosis are 4 naked **haplocytes** located in the apex of the basidium (the haplocytes are thus reduced to their nuclei). Each haplocyte germinates with a single apical **sterigma** producing a single secondary blastospore called a **basidiospore**. In this developmental scheme, which holds in most cases, each basidium comes to bear 4 apical basidiospores, but basidia with other numbers of spores are widespread. At maturity the basidiospores secrete a small droplet at their base (Fayod 1889: 272; Buller 1922) and **actively jump off the basidia** using a droplet displacement mechanism powered by the energy stored in the surface tension of the droplet itself (Webster & Chien 1990; Turner & Webster 1991).

Hymenomycetes in this sense do not include the gasteroid fungi where the hymenium either disappears at maturity or is not exposed, and the spores are not forcibly ejected from the basidia. Also excluded here, are the "Phragmobasidiomycetes," as in these, mostly gelatinous fungi, the haplocytes are thin-walled and occupy almost the complete volume of the basidium, so that the basidium appears septate, by virtue of the walls of the haplocytes, although this is actually not the case. Moreover, the hymenium, if present, is not really exposed to the air.

In this concept, the **traditional Hymenomycetes** embrace the crust fungi, club fungi, chanterelles, spine fungi (hydnums), bracket fungi (polypores), gill fungi (agarics) and boletes, and they represent about 11% of all fungi described (fig. 1.1). Taxonomy, systematics and nomenclature of these fungi cannot be discussed here.

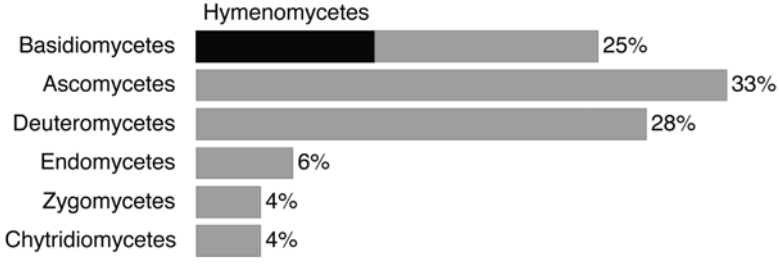

Figure 1.1: Statistics of the major groups of fungi. – From Clémençon 1997.

General Developmental Morphology

Like all higher fungi the Hymenomycetes are composed of fine filaments called **hyphae** (Hook 1665, Willdenow 1810). The vegetative mass of hyphae living in the substrate such as wood, soil or manure, is called a **mycelium** (Trattinnick 1805). It can sometimes be seen when the substrate is broken up, but for precise observation laboratory cultures on nutrient agar in Petri dishes have to be made.

A sexually reproductive mycelium produces **basidiomes** (carpophores, fruit bodies) on the surface of the substrate (fig. 1.2). In addition, some Hymenomycetes may also produce asexual spores among which the arthroconidia and the chlamydospores are the most frequent.

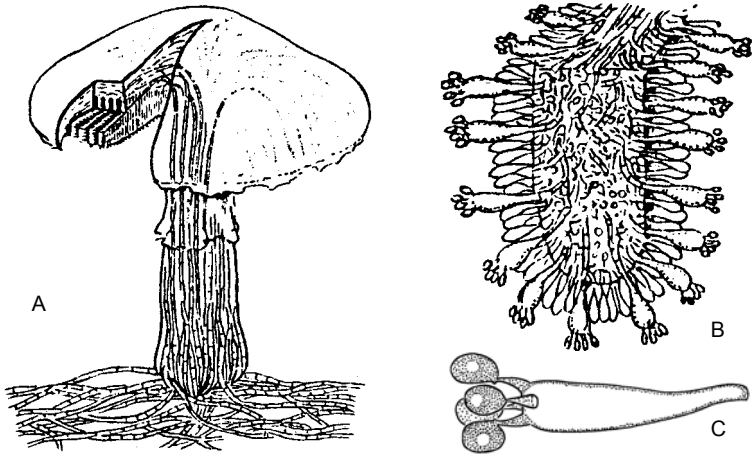

Figure 1.2: Diagrammatic drawings of a basidiome of an agaric. **A**: The basidiome is produced by the mycelium and bears gills with basidia. Like the mycelium, it consists of hyphae. **B**: The gill trama is woven by hyphae and is covered by the hymenium consisting of basidia. **C**: Mature basidium with basidiospores. – A,B from Schmeil-Seybold in Von Frisch 1953. C from Ingold 1971.

The **context** of most basidiomes usually comprises different **plects**, such as specialised surface layers, gill tramas or reinforced supporting structures. The plects correspond to the tissues of the plants but are fundamentally different as they are not produced by meristems but by interweaving of hyphae. Therefore the term tissue should be avoided.

Usually the developmental cycle of the Hymenomycetes is divided into two phases, but these do not correspond to mycelium and basidiome. The two phases are separated by the sexual interaction between two compatible “monokaryotic” mycelia resulting in a single “dikaryotic” mycelium. Monokaryotic mycelia are often called primary or homokaryotic mycelia, and dikaryotic ones secondary or heterokaryotic mycelia. The germ mycelium is equated to the primary mycelium and fruiting body production is said to be limited to the secondary mycelium, but this is an oversimplification. Frequently, the context of basidiomes is called a tertiary mycelium.

This terminology is somewhat misleading or confusing, at least for the student, because the different terms stress different aspects of the life cycle and are thus not equivalent or interchangeable. Monokaryotic and dikaryotic are morphological terms designating the simplest, but frequently wrong, idea of hyphal cells with only one or two nuclei. Heterokaryotic and homokaryotic are genetic terms indicating the presence or absence of genetically different nuclei within a single mycelium. Sometimes a primary mycelium is already heterokaryotic, e.g. when the germinating spore contains two or more genetically compatible nuclei that are passed into the young mycelium. Furthermore, both the primary and the secondary mycelium frequently have multinucleate hyphal cells.

The Hymenomycete life cycle can be divided into four phases: The presomatogamic, - the postsomatogamic, - the diploid - and the post-meiotic phases. Beginning with spore germination, followed by somatogamy between two hyphae, then karyogamy and meiosis respectively (figs. 1.3, 1.7).

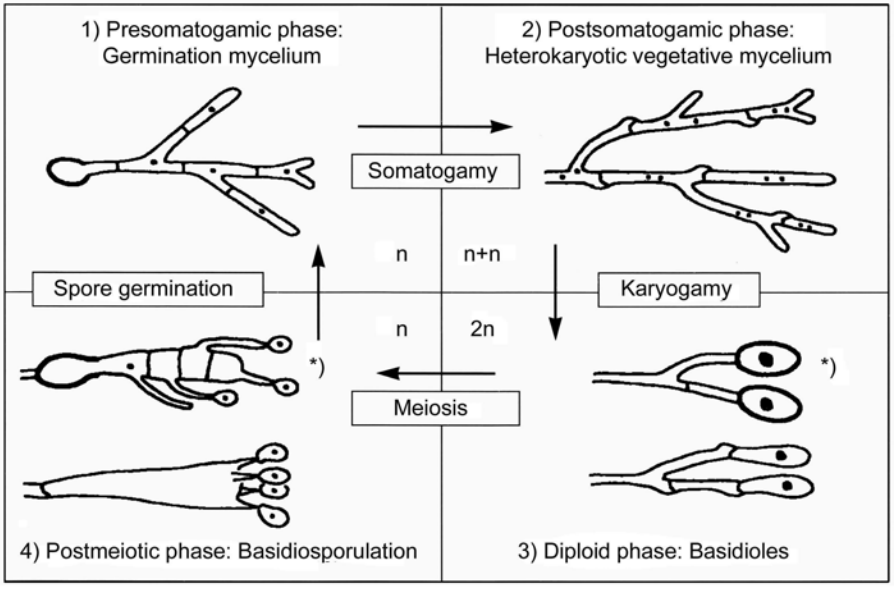

Figure 1.3: The four developmental phases of a basidiomycete.*) for comparison: a fungus with a thick walled diploid phase, the probasidium, and a four-celled postmeiotic phase, the metabasidium, e.g. a *Septobasidium*. – From Clémençon 1997.

1) The **presomatogamic phase** starts with spore germination and ends with hyphal somatogamy. Often this phase contains only one type of nuclei (it is homokaryotic) and only one nucleus per hyphal cell (it is monokaryotic), but very frequently the young mycelium lacks septa and is therefore **coenocytic** (fig. 1.4); or it may be heterokaryotic from the very beginning. In the latter case, the germ mycelium is already a secondary mycelium capable of producing basidiomes.

Some Hymenomycetes are **amphithallic** (Lange 1952: 36; Lamoure 1960; Jacobson & Miller 1994; Calderoni & al. 2003). They produce basidiospores with

different numbers of nuclei so that in one single spore print uninucleate, binucleate, and sometimes multinucleate spores are present. Some of the binucleate or multinucleate spores are heterokaryotic, and the germination mycelium is therefore heterokaryotic and behaves like a postsomatogamic mycelium, but the uninucleate spores produce homokaryotic, presomatogamic mycelia. Examples are *Suillus granulatus, Conocybe pubescens, Agrocybe pediades* and *Mycena filopes* (fig. 1.5).

2) The **postsomatogamic phase** is initiated by the somatogamy between compatible hyphae (fig. 1.6). Unlike plant cells, young compatible mycelia can exchange nuclei, mitochondria and cytoplasm via anastomoses between two hyphae. This is a true plasmogamy and is considered the first step in sexuality. As

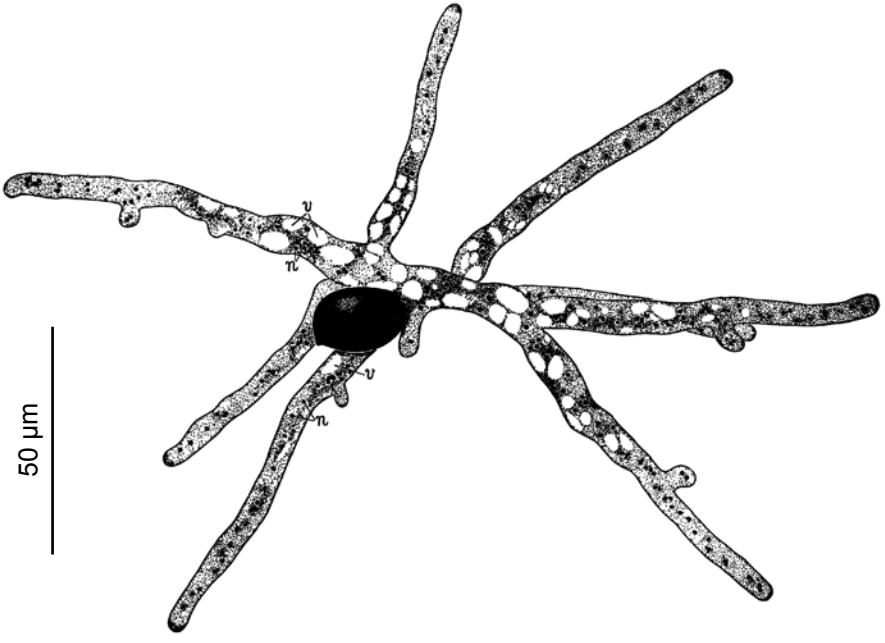

Figure 1.4: Coenocytic germination mycelium of *Coprinus sterquilinus* one day old.
n = nucleoli (mistaken as nuclei by Buller), v = vacuoles. – From Buller 1931, modified.

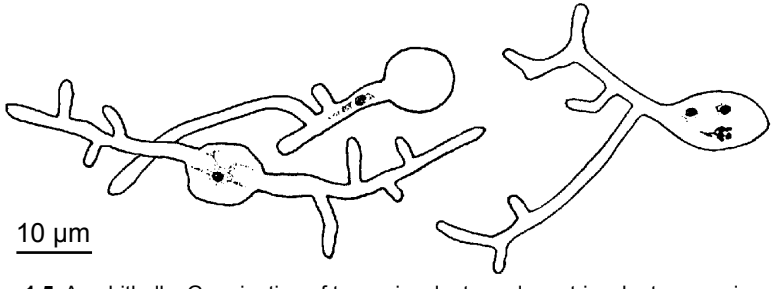

Figure 1.5: Amphithally: Germination of two uninucleate and one trinucleate spore issued from the same fruiting body of *Mycena filopes*. – From Lamoure 1960, modified

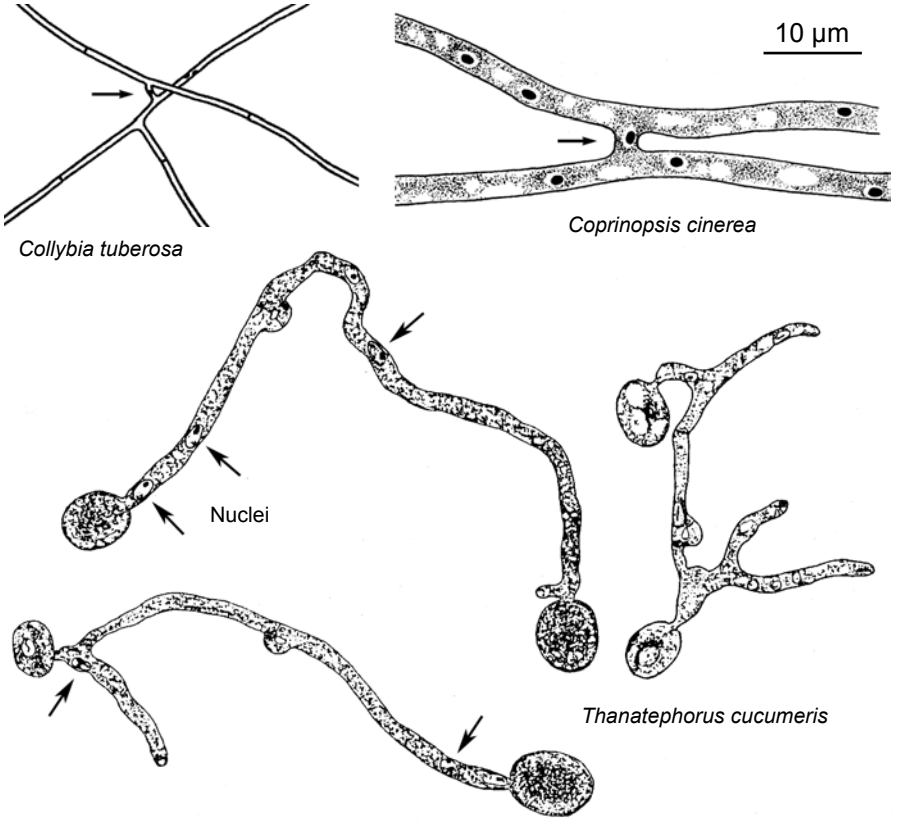

Figure 1.6: Historical drawings: Examples of somatogamy between hyphae. Scale valid for *Coprinopsis* an *Thanatephorus*. – *Collybia* from Harnack 1931; *Coprinopsis* from Chow 1934, as *Coprinus lagopus*; *Thanatephorus* from Lehfeldt 1923, as *Corticium solani*; nuclei difficult to see because of bad fixation, clamp connections already formed.

the nuclei divide and migrate within the recipient hyphae, both mycelia involved become genetically identical and form a single individual.

An essential difference with almost all other organisms, is the fact that the plasmogamy is not limited to the fusion of two cells, and that plasmogamy is not immediately followed by karyogamy. This temporal **separation of somatogamy and karyogamy** results in a very important new state: the heterokaryotic mycelium capable of vigorous growth over a long period of time, sometimes over centuries. It is indeed this phase that is the normal vegetative state of the Hymenomycetes. Repeated somatogamy with young mycelia issued from newly arrived spores leads to a postsomatogamic multikaryotic-haploid phase capable of parasexuality, i.e. rapid genetic engineering by nuclear fusions and genetic segregation within the vegetative mycelium without the necessity to pass through karyogamy and meiosis in a fruiting body.

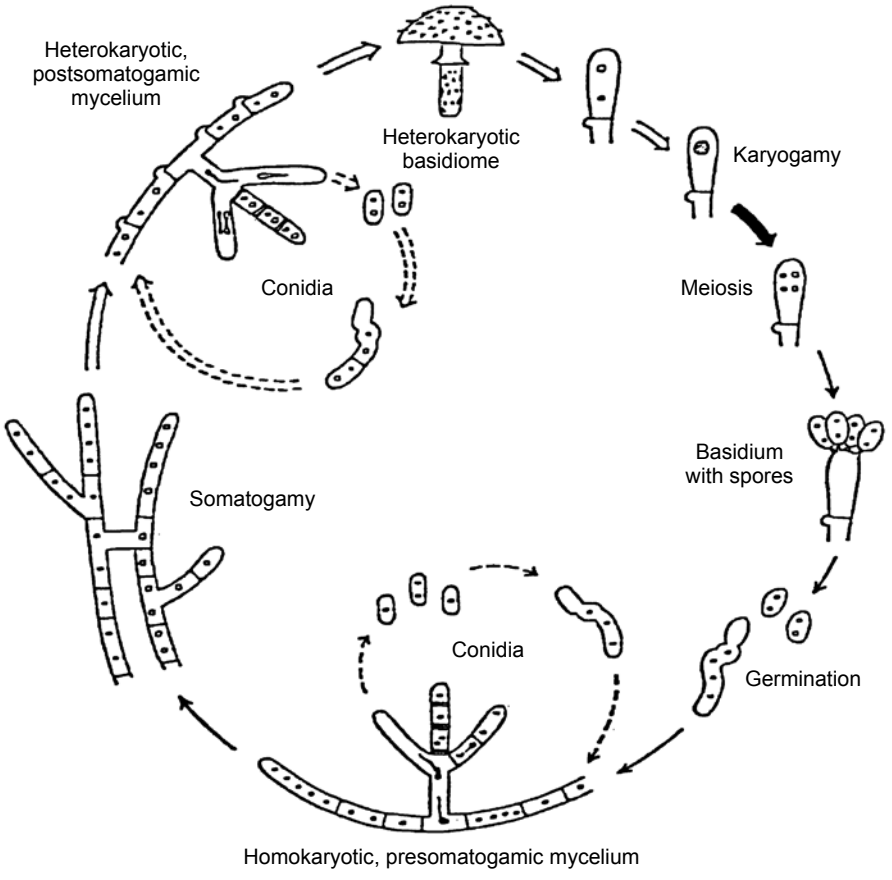

Figure 1.7: A representative life cycle of a hymenomycete *without* a presomatogamic basidiome (*Pholiota adiposa*). **Thin arrows:** postmeiotic and presomatogamic phases. **White arrows:** presomatogamic phase. **Black thick arrow**: diploid phase. **Broken arrows**: formation of mycelial conidia. – From Arita 1979, slightly modified.

Most Hymenomycetes produce basidiomes in the postsomatogamic phase where the two next phases of the life cycle are found.

3) The **diploid phase** is initiated by the karyogamy in the young basidium and is usually very short, mostly lasting only a few hours. But a few Hymenomycetes also produce truly diploid mycelia with just a single diploid nucleus per cell; the best known ones are the species of *Armillaria* (e.g. Ullrich & Anderson, 1978; Korhonen 1980; Anderson & Ullrich, 1982; Lamoure & Guillaumin, 1985; Ota, Fukuda & Suzuki, 1998), but the discovery of polyploid nuclei in many mycelia (Wittmann-Meixner 1989; table 1.1) hints at the possibility of a wider occurrence of diploid mycelia.

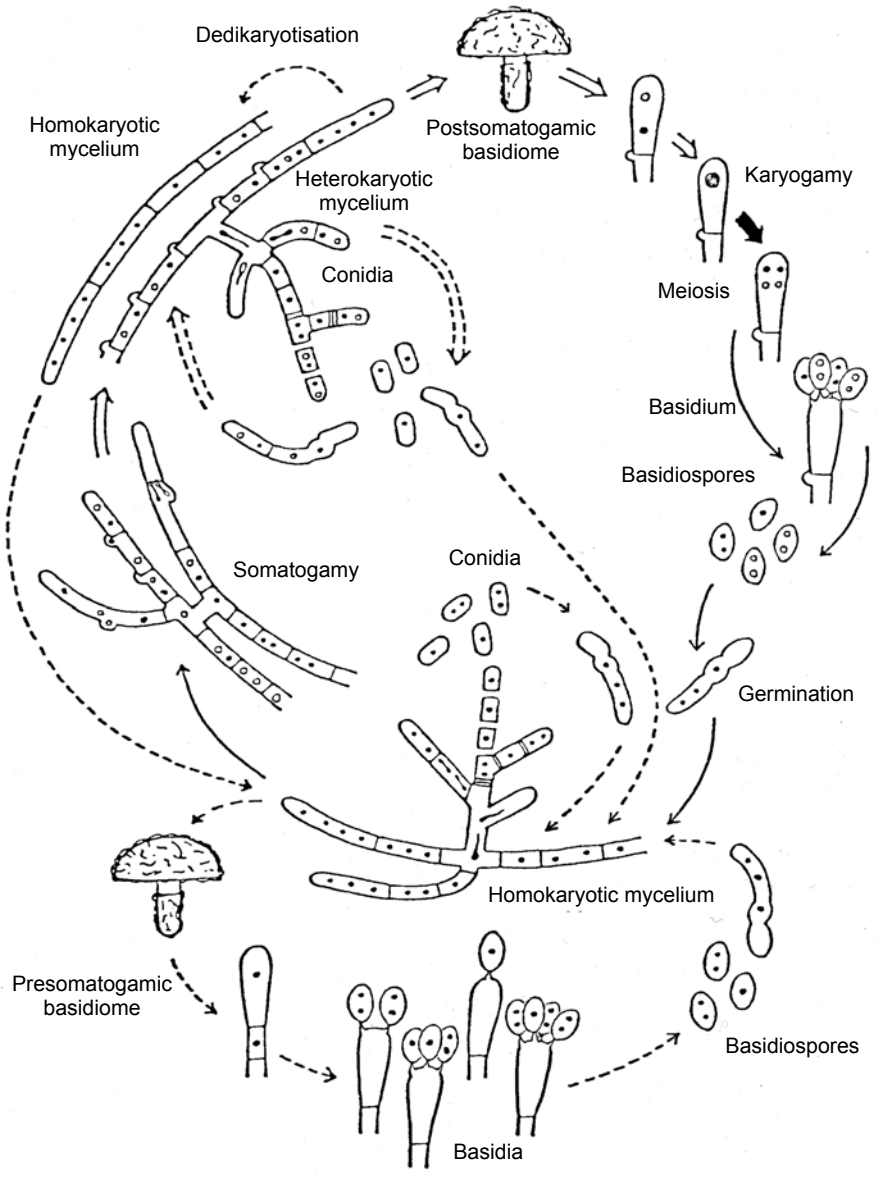

Figure 1.8: Life cycle of an agaric with presomatogamic and postsomatogamic basidiomes and conidia in both phases. Remarkable is the possibility of the postsomatogamic, heterokaryotic mycelium to produce new homokaryotic mycelia through the formation and germination of uninucleate conidia. *Pholiota nameko*. – From Arita 1979, slightly modified.

4) The **postmeiotic phase** is initiated by the meiosis in the young basidium and results in the formation of the basidiospores. These events and the basidiospores are discussed in detail in later chapters.

Two representative life cycles of agaricoid Hymenomycetes are reproduced in figures 1.7 and 1.8. Contrary to many published diagrams the morphology of the somatogamy is correctly drawn as an anastomosis between two hyphae, as already shown in figure 1.6; and the basidiospores are correctly shown to contain two nuclei, as is the case for many basidiomycetes.

Other life cycles do exist in the Hymenomycetes, and their variations may be quite numerous, judging from the fact that only very few species and strains have been studied so far. But these life cycles can hardly be considered Basic Concepts and are therefor not described here. Only the trikaryon formation in *Heterobasidion parviporum* (James & al. 2009) and the three different types of life cycle (pseudohomothallic, heterothallic and homothallic) of *Agaricus bisporus* (Kamzolkina & al. 2006) are mentioned here.

Diploidy and Polyploidy

Using quantitative cytophotometric methods Wittmann-Meixner (1989) and Bresinsky & Wittmann-Bresinsky (1995) found that the "haploid" state of many Hymenomycetes is really a polyploid state (table 1.1). So it seems that the species tagged x = 1 behave in the classical haploid-diploid way, whereas the species of the class x = 2 have a diploid-tetraploid cycle. *Porphyrellus porphyrosporus* has a triploid-hexaploid, and *Gomphidius maculatus* a tetraploid-octoploid rather than a haploid-diploid cycle. The reason and biology of the nuclear conditions "x > 1" remain poorly understood. As Wittmann-Meixner (1989) worked exclusively with Boletales, the nuclear conditions of other Hymenomycetes remain unknown.

In contrast to the diploid *Armillaria* species with a single diploid or triploid nucleus per hyphal cell and no karyogamy in the basidium (e.g. Kim & al., 2000), the species in table 1.1 all have binucleate, heterokaryotic subbasidial cells and basidia showing karyogamy and meiosis. Thus the nuclei of the listed fungi behave like those of normal haploid-diploid species (with x = 1), and only quantitative analysis of their DNA reveals their diploid (x = 2) or polyploid (x > 2) nature.

Table 1.1: Examples of Hymenomycetes (Boletales s.l.) with haploid (x = 1), diploid (x = 2) and polyploid (x > 2) nuclei in the vegetative mycelium.

x = 1:	*Coniophora marmorata, Leucogyrophana mollusca, Paxillus curtisii, Omphalotus japonicus, Suillus acidus, Boletus frostii, Leccinum chromapes.*		
x = 2:	*Boletus calopus, B. luridus, B. queletii, B. impolitus, B. radicans, Chalciporus piperatus, Leccinum holopus, L. rotundifoliae, L. scabrum, Pulveroboletus lignicola, Tylopilus felleus, Strobilomyces strobilaceus, Xerocomus chrysenteron, X. badius, X. parasiticus, X. subtomentosus, Gomphidius glutinosus.*		
x = 3:	*Porphyrellus porphyrosporus*	x = 4:	*Gomphidius maculatus*
x = 6:	*Gomphidius roseus*	x = 10:	*Chroogomphus rutilus*

2

THE HYPHAE OF THE HYMENOMYCETES

All organs of the Hymenomycetes (e.g. mycelia, sclerotia, rhizomorphs and basidiomes) and all their plects are composed of hyphae, and in all organs and plects the hyphae may be morphologically modified by turgescent inflation, wall sclerification or gelification, and by endosecretion or excretion of substances. These modifications may be combined, thus producing several hyphal types, e.g. thick-walled inflated hyphae or gelatinous storage hyphae.

Historical notes

The word "hypha" is of Greek origin and means filament. It has been introduced to mycology by Willdenow (1810), but the filamentous composition of fungi has already been noted by Hook in 1665, Micheli (1729) and Trattinnick (1804-1806), but these authors did not create a term for them. Bonorden (1851: 174-194, 1858) described the hyphae and some of their differentiations in basidiomes, especially of the genera *Amanita, Lactarius* and *Russula;* and Fayod* (1889) distinguished between fundamental and connective hyphae, a terminology still used by some authors.

The secretory hyphae of *Lactarius* have been studied since the early 19th century (Schultz 1833; cited by Saint Hilaire 1837; Corda 1839; Bonorden 1851; Fayod 1889; Istvanffy & Johan-Olsen 1887; Istvanffy 1896a,b; Bambeke 1892-1895), but they have been misinterpreted as conducting hyphae similar to the vascular bundles of plants. Secretory hyphae occur in many types, and Clémençon (1997) proposed a new classification and terminology to try to express this variation, although it seems that we are still far from knowing the full extent of the differentiations of the secretory hyphae.

The thick-walled hyphae have been much neglected by the early authors; only Fayod (1889) and Maire (1902) mentioned them, but without paying much attention to them. Falck (1912) introduced the term "Faserhyphen" for the thick walled hyphae of *Serpula lacrimans*, a term rendered as "fibre hyphae" (e.g. Moore 1998) and preferred in this book, but many mycologists use the term "skeletal hyphae" introduced by Corner (1932a) and promoted by Cunningham (1946), especially when describing basidiomes.

Cytology of the vegetative Hypha

The vegetative hyphae of the mycelium are sometimes called "generative hyphae" because they are identical with the generative hyphae of the basidiome. Unfortunately the term "vegetative hyphae" has been used by some authors to name thick walled hyphae of basidiomes. The term "vegetative hyphae" should be used to name the undifferentiated hyphae of the vegetative mycelium, and the term

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* Contrary to a widespread assumption and sometimes published statement **Victor Fayod** was not a Frenchman, but a Swiss pharmacist from Bex in the Swiss canton of Vaud. His main mycological work has been done as an independent worker associated with the University of Lausanne and the Musée botanique cantonal in Lausanne.

"generative hyphae" should be restricted to designate undifferentiated hyphae of the basidiomes.

Hyphal Walls

At the apex of a vegetative hypha the wall is only about 0.05-0.06 µm thick, compared to 0.1-0.15 µm at the sides. This is just beyond the limit of the resolution of the best light microscope (which is ≈ 0.08 µm when wide angle circular illumination and high contrast are used) but well within the limits of visibility (Françon 1967: see also p. 20). Therefore the wall at the apex appears as a thin featureless line. It can be stained to various degrees with Congo red and alcian blue, indicating the presence of polysaccharides and mucopolysaccharides.

The electron microscope reveals two **wall layers** and a **mucilaginous sheath** (figs. 2.1, 2.4). The inner wall layer is alkali-resistant (resists hot 5M KOH for hours) and contains many chitin fibres. This layer also forms the septa. The outer wall layer is alkali-soluble (dissolves in hot 5M KOH), contains no chitin and does not participate in the formation of the septa. The mucilaginous sheath is easily soluble in hot water (Wessels & al. 1972; Van der Valk & al. 1977).

The mucilage of the sheath contains small proteins called **hydrophobins** secreted by the hypha (Wösten & al. 1999; Wessels 1999, 2000). On surfaces exposed to the air the hydrophobins coalesce into a monomolecular water-repellent layer, rendering aerial mycelia hydrophobic and difficult to moisten. This layer is invisible in the light microscope but can be seen in the electron microscope after immunolocalization (Lugones & al. 1999). The mucilaginous sheaths of closely adjacent hyphae in a basidiome are locally coalescent, even in basidiome contexts that are not noticeably gelatinous (as in *Schizophyllum commune* or in *Agaricus bisporus*), but microscopic air spaces exist between more distant hyphae. Hydrophobins also line these air spaces and "probably ... prevent collapse of air channels allowing efficient gas exchange even under wet conditions" (Lugones & al. 1999; van Wetter & al. 2000).

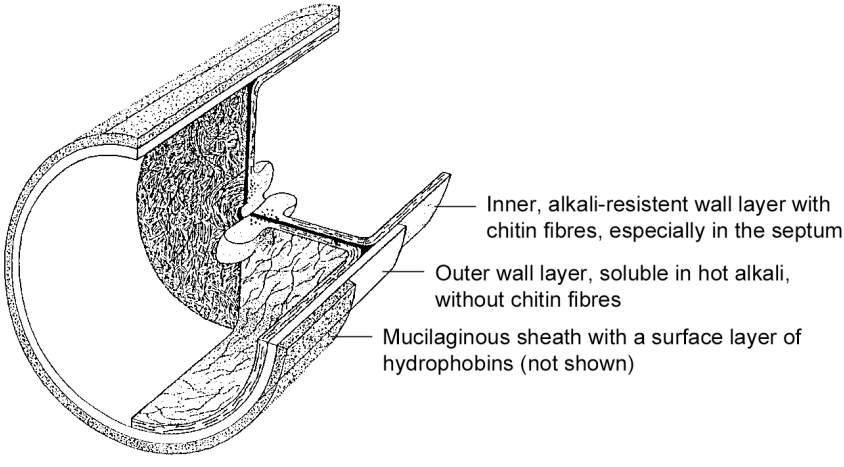


Figure 2.1: Diagrammatic drawing of the hyphal wall and the septum with its dolipore. – Adapted from Wessels 1978,

The pore at the apex of hyphae reported by Strunk (1963, 1968) may be a fixation artefact due to the very small density of chitin fibres and the extreme thinness of the apical wall (Scurfield 1967). Chemical fixation and osmotic shock may result in a rupture of the hyphae at the apex with release of a string of cytoplasm; this phenomenon is called plasmoptysis ("spitting of cytoplasm") and is clearly artificial.

Septa, Dolipores and Hyphal Cells

The mycelia of most Hymenomycetes are septate, but the septa do not delimit autonomous cells comparable to plant cells. Instead, they divide a hypha into communicating compartments connected by a cytoplasmic continuity through a central pore. The cytoplasm, nuclei and mitochondria are allowed to migrate from compartment to compartment along the hypha. The distances between the septa may be quite irregular, and the number of nuclei contained in a compartment may vary greatly. Because the cytoplasm is continuous between hyphal compartments, the plasmalemma lining the hyphal wall and the septa is continuous across the central pore (fig. 2.4). Hyphal compartments in this sense may be called "**hyphal cells**" in order to distinguish them from cells in the more usual sense.

The central pore of the septa of Hymenomycetes is shaped like a doughnut: a thick ring with a central canal (figs. 2.1-2.7). This doughnut is called a **dolipore** (Moore & McAlear 1962; dolium = barrel). In the light microscope it looks like a small central knob, as already noted by early authors (Strasburger 1884: 325; Maire 1902: 181; Kniep 1913). Under favourable conditions even the pore itself can be seen (Strasburger 1884; Wahrlich 1893; Locquin 1943: 76; Clémençon 1998; fig. 2.3). At some distance from the dolipore a dome-like structure surrounds the septal swelling. In sections it looks like a pair of parentheses around the pore, giving rise to the term **parenthesome** (not parenthosome, a wrong spelling used by some authors). It is derived from the endoplasmic reticulum (figs. 2.4-2.6). In most Hymenomycetes it is **fenestrated**, but in *Asterodon*, *Basidioradulum, Botryobasidium, Cantharellus, Coltricia, Cyclomyces, Hyphodontia, Inonotus, Onnia, Paullicorticium, Phellinus, Phylloporia, Ramaria, Schizopora Subulicystidium* and *Trichaptum* **unperforated** parenthesomes do occur (Traquair & McKeen 1978; Moore 1985; Alexander & al. 1989; Langer 1990; Rajchenberg & Bianchinotti 1991, 1992; Langer 199; Keller 1997; Müller & al. 2000). They are considered ancestral to perforated dolipores by Larsson, Larsson & Köljalg (2004). Correlations between taxonomy and pore cap morphology were analysed by Müller & al.

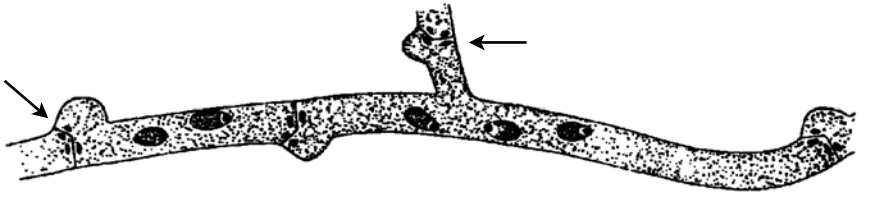


Figure 2.2: Early observation of dolipore structures. The pore itself has not been noted, but the dolipore swellings (**arrows**) have been seen after chrome-osmium fixation and staining with iron haematoxylin. Mycelial culture of *Athelia* spec. – From Kniep 1913, as *Hypochnus terrestris*.

(2000), Bianchinotti & al. (2005) and Van Driel & al. (2009). In some fungi the endoplasmic reticulum produces hemispherical domes at a considerable distance from the parenthesome forming the **outer cap** (Thielke 1972, "Aussenkappe"). Frequently the outer caps around a dolipore are amazingly asymmetrical (figs. 2.3, 2.4).

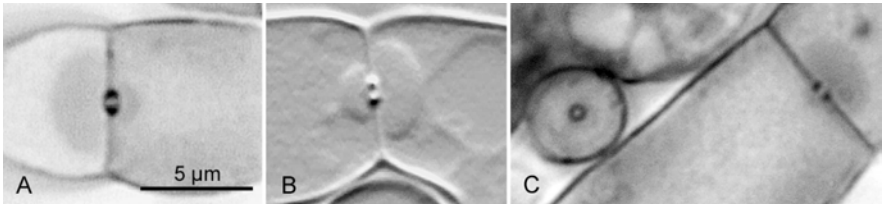


Figure 2.3: The dolipore, the dolipore swelling and the outer cap of a young basidiome of *Agaricus bisporus* as seen with the light microscope in microtome sections stained with aluminium - zirconium - haematoxylin after aldehyde fixation. **A**: Bright field; **B:** Bright field, contrast enhanced with the Emboss function of Adobe Photoshop. **C**: One pore in axial view, the other in median section. Such clear visibility of the pore is exceptional.

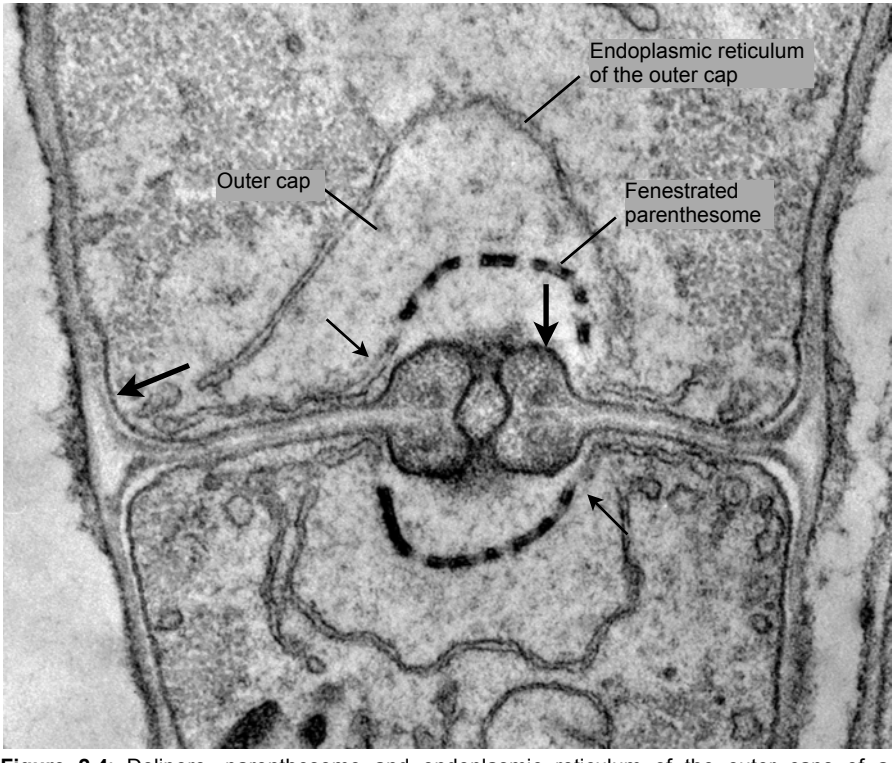


Figure 2.4: Dolipore, parenthesome and endoplasmic reticulum of the outer caps of a subhymenial hyphae of *Rhodocybe mundula*. Permanganate fixation preserves membranes and wall structures but not the other cell organelles. The plasmalemma is continuous around the dolipore swelling (thick arrows), the parenthesome is continuous with the endoplasmic reticulum (thin arrows).

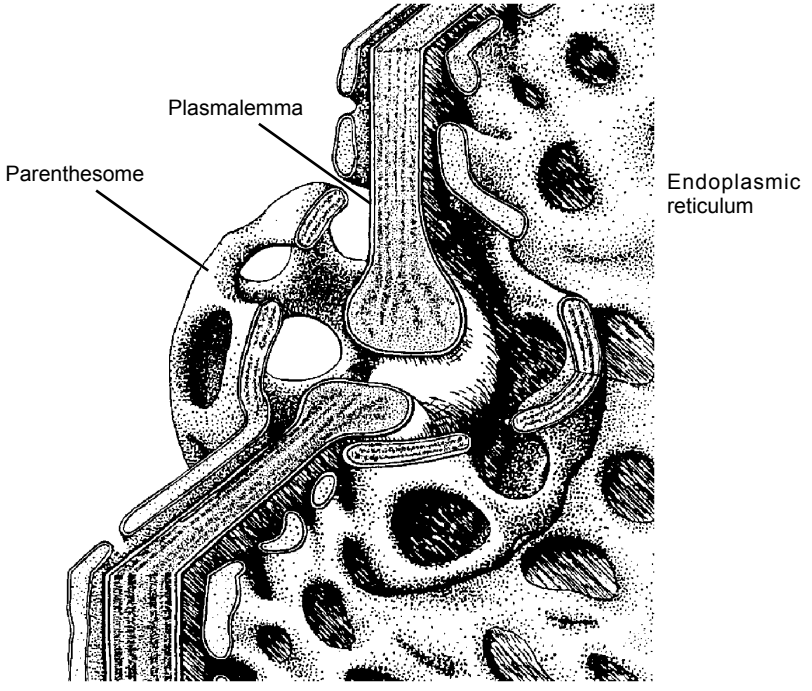


Figure 2.5: Reconstruction of the dolipore and its parenthesome. *Trametes versicolor*. – From Girbardt 1967, slightly modified.

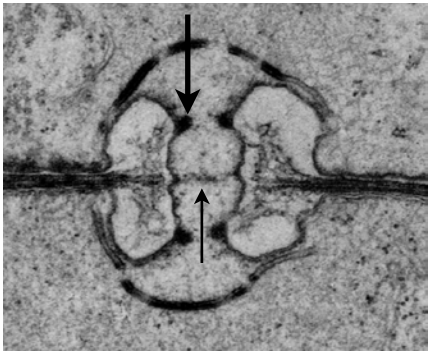


Figure 2.6: Dolipore with occluding proteins partially dissolved (**thick arrow**) and with a membrane-like central valve (**thin arrow**). *Agaricus bisporus*. – From Thielke 1972, modified.

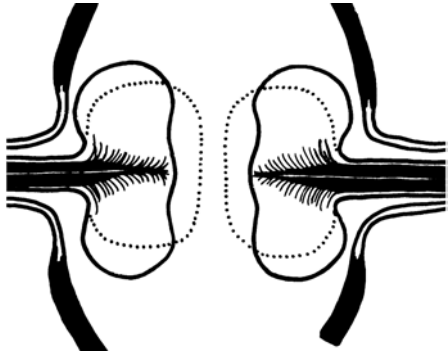


Figure 2.7: Widening of he dolipore swelling during cytoplasmic streaming. Broken line shows the normal shape, the solid line the widened form. *Thanatephorus cucumeris*. From Bracker & Butler 1964.

The pore canal may be partially or completely occluded by electron-dense proteins (Flegler, Hooper & Fields 1976; fig. 2.4); and often a transversal membrane-like middle valve is also present (fig. 2.6), but this is still a matter of controversy.

The dolipore and the occluding proteins are not rigid structures, but they may be temporarily dissolved to make room for nuclear migration (Mayfield 1974; fig. 2.8), or the dolipore ring widens during vigorous cytoplasmic streaming (Bracker & Butler 1964; fig. 2.7).

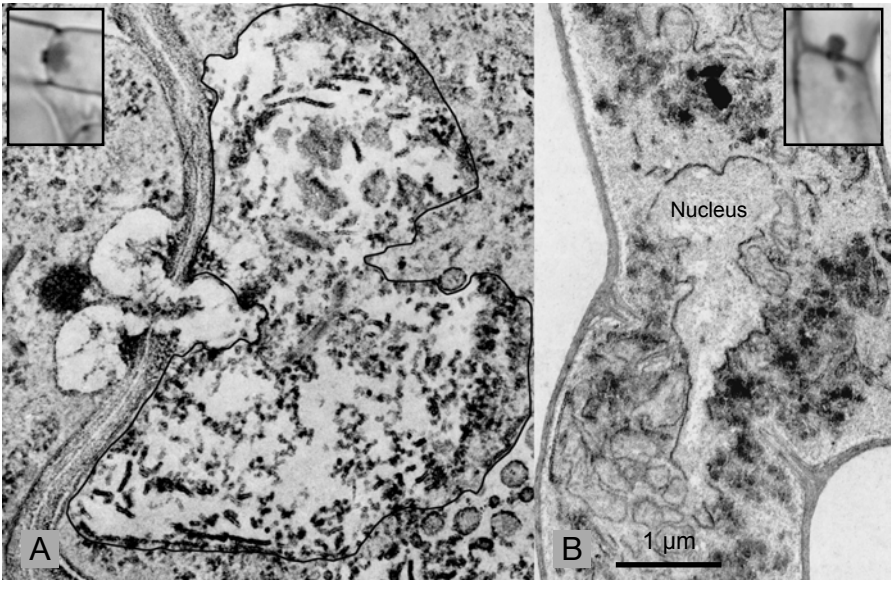


Figure 2.8: A: Dissolution of the dolipore swelling in *Schizophyllum commune* (outlined in the electron micrograph) and *Athelia epiphylla* (inset, light microscopy, SDS-Congo red). **B**: Nuclei migrating through a septum in *Schizophyllum commune* (electron microscopy) and in *Tricholoma columbetta* (inset, light microscopy, gill trama, glutaraldehyde, aluminium zirconium haematoxylin). – *Schizophyllum* from Mayfeld 1974, modified; *Athelia* and *Tricholoma* original photographs.

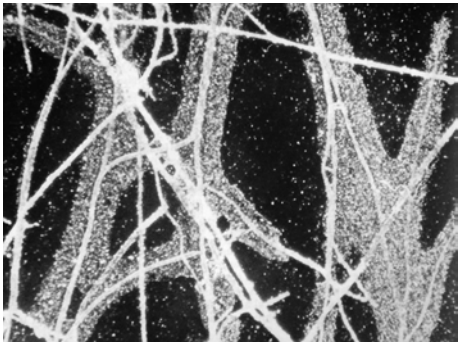


Figure 2.9: Hyphal sheaths of *Xylobolus frustulatus* grown on a solid medium, made visible by reflectance light microscopy. – From Palmer & al. 1983b.

Vegetative hyphae of ligninolytic fungi growing on a solid nutrient surface are frequently surrounded by a mucilaginous **hyphal sheath** about 5-100 µm wide (fig. 2.9; Pechak & Crang 1977; Wheeler & Gantz 1979; Dowsett 1981; Evans & al. 1981; Palmer & al. 1983a,b; Bonfante-Fasolo & al. 1987; Nilsson & al. 1989). They are absent from hyphae growing in liquid media. The mucilage contains microfibres only 10-50 nm wide but up to 25 µm long that are often twisted into thicker strands (Leise & Schmid 1962, 1963). Like the mucus they are made of polysaccharides (Larsen & Green 1992;

Green & al. 1992). The sheaths adhere firmly to the substrate (usually wood) and are rich in enzymes so that the wood can be degraded in an area up to 25-30 µm wide around the hyphae (Ruel & Joseleau 1991; Gardiner & Day 1988).

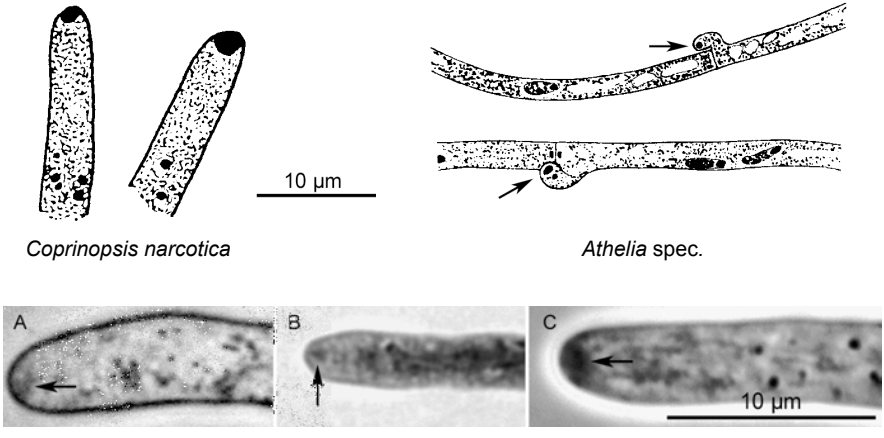
The Cytoplasm

Most of the cytoplasm of the vegetative hyphae is contained in an apical zone that stretches backward for only a few hundred micrometers. This is, physiologically and biochemically, the most active part of the hypha. Vacuoles are absent from the apex and rare and small in the zone below it, but they become larger and more numerous further down the hypha until the cytoplasm is reduced to a thin film adhering to the wall. Older parts of the hypha may even be devoid of cytoplasm, either by rarefaction or by excessive thickening of the wall. The nuclei are not located in the apical zone but usually in the deeper regions already well vacuolated.

The Spitzenkörper and Apical Growth of the Hyphae

Growth of mycelial vegetative hyphae involving synthesis of new wall and cytoplasm occurs mostly in the apical dome; but the older parts of basidiomal hyphae may also grow, sometimes at a considerable distance behind the apex, e.g. during elongation of the stipe or during intercalary growth of rhizomorphs (Vosey 2010).

In the extreme apex of the hyphae a dense zone known as **Spitzenkörper** ("spitzenkorper" or apical body) plays an important role in **apical growth**. Kniep (1913) had already seen it in clamp connections, but it was Brunswik (1924) who named it and who strongly suggested its connection with growth (fig. 2.10).



Coprinopsis narcotica *Athelia* spec.

Coprinopsis cinerea, living *Connopus (Gymnopus) acervatus,* aldehyde fixation

Figure 2.10: Spitzenkörper. **Top**: Historical drawings. Chrome osmium fixation, stained with iron haematoxylin. – *Coprinopsis* from Brunswik 1924, *Athelia* from Kniep 1913.
Bottom: Spitzenkörper in vegetative hyphae from laboratory cultures. **A,C**: Phase contrast, mounted in acacia gum 20% for better observation. **B**: Stained with pyronin B, bright field. – Original photographs.

The Spitzenkörper disappears during strong illumination or when the mycelial culture is mechanically disturbed, e.g. when a cover glass is applied, but it reappears after 20-30 minutes. A new Spitzenkörper is generated during ramification of a hypha, usually far behind the apex, and at the beginning of the formation of the clamp connections, but the mechanism is still unknown. The direction of hyphal growth is controlled by the position of the Spitzenkörper in the apex: displacement to the left or right makes the hypha grow in a the left or right arch, and when the Spitzenkörper oscillates around its central position the hypha shows a wavy growth. Hyphae that have ceased to grow have no Spitzenkörper.

The electron microscope shows the Spitzenkörper as a dense region surrounded by many vesicles that stem from the deeper regions of the hypha and that are transported to the apex. The vesicles contain material and enzymes needed for wall synthesis liberated by the fusion of the vesicles with the plasmalemma. The amount of wall synthesis and wall extension depends directly on the number of vesicles fusing with the plasmalemma. It is thought that the Spitzenkörper somehow controls the direction of the flux of vesicles towards the wall and thus determines the location of maximum wall extension and the direction of apical growth. During vigorous growth several thousand vesicles per minute may fuse with the wall. This mechanism has been studied mathematically and computer models are available to simulate apical growth on screen (Bartnicki-García & al. 1989, 1990; Bartnicki-García 1990; Goriely & Tabor 2008;). Harold (1999), Bartnicki-García (1999), Gierz & Bartnicki-García (2001), Harris & al. (2005), Virag & Harris (2006), Steinberg (2007), Money (2008), Riquelme & Bartnicki-García (2008), Sudbery (2008) and Zhuang & al. (2009) discuss various molecular, cytological and mathematical models of hyphal growth in several model fungi, some not belonging to the Hymenomycetes.

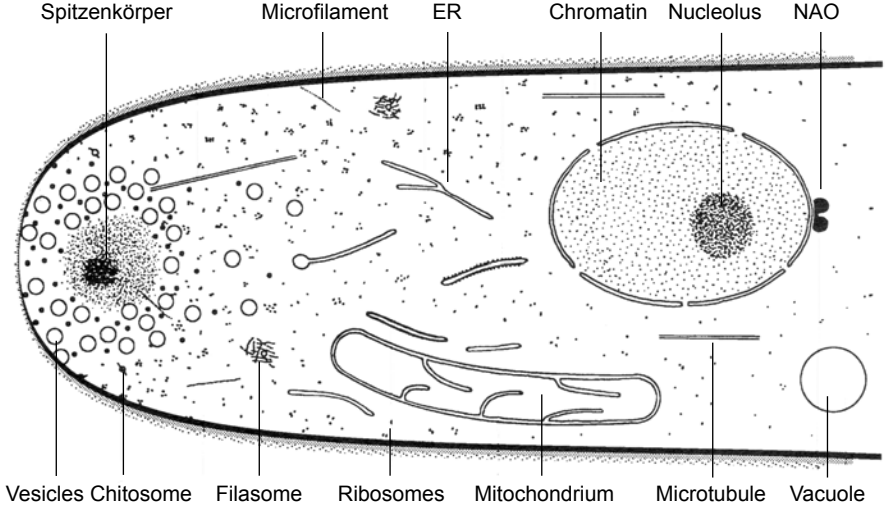


Figure 2.11: Cytology of the vegetative hyphal tip. There are active (ø) and inactive (•) chitosomes. The wall is two-layered and covered with a mucilaginous coating. ER: endoplasmic reticulum. NAO: nucleus associated organelle. – From Clémençon 2004.

Apical growth inserts new wall material at the thin and stretchable apical dome of the hypha. A two-dimensional model based on the action of the Spitzenkörper alone (Bartnicki-García & al. 1989) differs considerably from the three-dimensional one that incorporates turgor pressure as a secondary shape modulator (Bartnicki-García & Gierz 2000; Gierz & Bartnicki-García 2001). Turgor pressure expands the wall in such a way that any point on the wall surface moves outwards in a right angle to the surface. The old hyphal wall "opens" in a way shown in the figure 2.12.

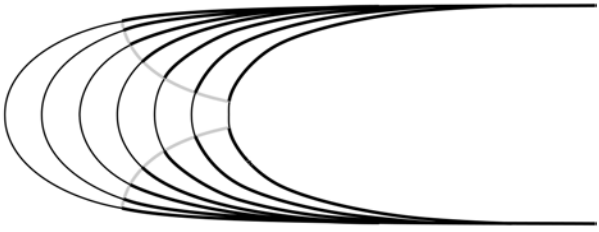


Figure 2.12: Expansion of the apical segment through incorporation of new wall material. The gray lines indicate the paths of a point on the wall. They are always orthogonal to the wall surface. — Adapted from Gierz & Bartnicki-García 2001.

Other Cytoplasmic Organelles

Another major constituent of the hyphal cytoplasm are the **mitochondria**. They can easily be seen with phase contrast microscopy or after suitable fixation and staining. They appear as thin, long filaments in constant, easily observable movement. During plasma streaming they can migrate from one hyphal cell to another, and they are transmitted from one hypha to another during somatogamy (i.e. during the first stage of sexuality). As in other eukaryotic cells they act as energy producing centres and contain their own DNA, thus being part of the genome of the fungi (reviewed by Gray 1989; Barr & al. 2005).

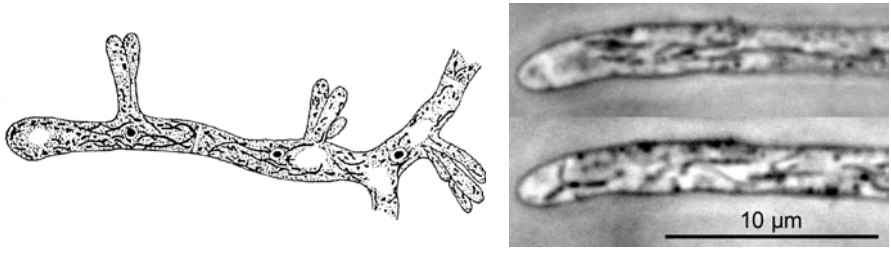
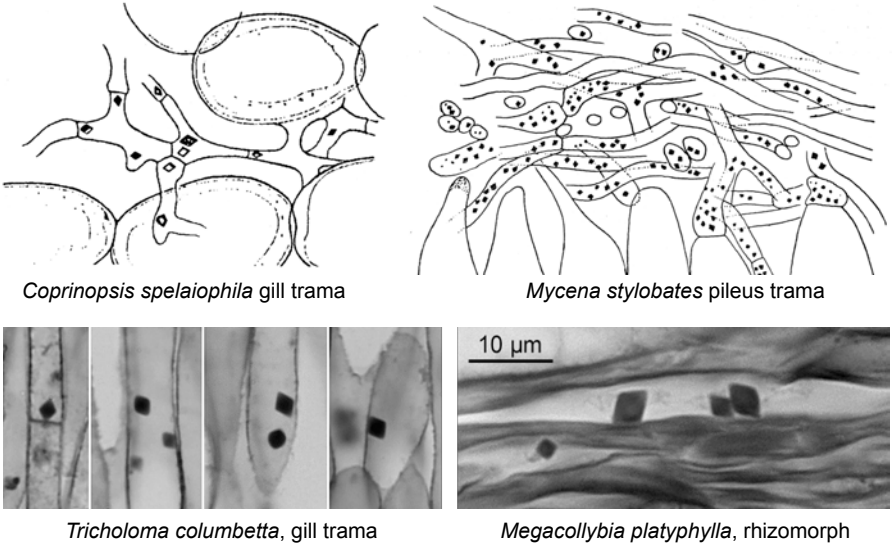


Figure 2.13: Mitochondria of *Coprinopsis cinerea* as seen with the light microscope. The drawing shows a germination hypha with conidial initials after chemical fixation and staining. The photographs show a living hypha observed in phase contrast (in 20% acacia gum) taken in a time interval in order to illustrate their movements. – Drawing from Chow 1934; photographs are originals.

Some hyphae of mycelia, rhizomorphs and basidiomes of many Hymenomycetes contain octahedral, 1-10 µm long **crystals** that stain strongly with most dyes, such as basic fuchsin, safranin, toluidine blue, aniline blue, acid fuchsin and haematoxylin. The crystals dissolve within a few seconds in alkaline solutions and go undetected by many taxonomists who squash their material in KOH or ammonia.

As early as 1892 Rosen described them in the pileus and stipe of young basidiomes of *Coprinopsis spelaiophila* (as *Coprinus extinctorius*) and identified them as protein crystals (fig. 2.14). About one day before onset of spore maturation they are plentiful, but in fully mature basidiomes they become rare. Rosen wrote that such crystals also occur in *Oudemansiella mucida, Agaricus bisporus* and «many other agarics». Bambeke (1902b) thought he was the first author to describe them and noted over 100 agarics with these crystals. Kühner (1938a) found them in many *Mycena* species (fig. 2.14), and Lohwag (1938b) noted protein crystals in *Serpula lacrimans.* Actually they occur in many fungi.



Coprinopsis spelaiophila gill trama

Mycena stylobates pileus trama

Tricholoma columbetta, gill trama

Megacollybia platyphylla, rhizomorph

Figure 2.14: Octahedral crystals (probably proteins) from agarics.
Top: Historical drawings by Rosen (1892; *Coprinopsis*) and Kühner (1938a).
Bottom: Microtome sections stained with acid fuchsin (left) and aluminium zirconium haematoxylin after aldehyde fixation. The left most crystal of *Tricholoma columbetta* is stuck in a dolipore, a situation often seen in basidiomes. It is probably due to cytoplasmic streaming. – Scale valid for both photographs. Originals.

Vacuoles are numerous and often quite big in vegetative, generative and differentiated hyphae of the Hymenomycetes. In most cases they contain a colourless liquid, but pigments may be dissolved in it, e.g. in *Amanita muscaria, Megacollybia platyphylla* and *Mycena rosella*.

In vegetative hyphae they may be spherical or tubular and play an active role in intrahyphal transport and apical growth of the hyphae (fig. 2.15; Watkinson & al. 2005; Darrah & al. 2006; Ashford & Allaway 2007; Riquelme & Bartnicki-García 2008; Veses & al. 2008; Fricker & al. 2008; Zhuang & al. 2009).

In «inflated» thin-walled hyphae of many «fleshy» basidiomes the vacuoles are very voluminous and exert a pressure against the hyphal wall produced by osmotic turgescence. These turgescent hyphae represent one of several systems to keep a basidiome upright and in a position favourable for spore release (Kern & al. 1997).

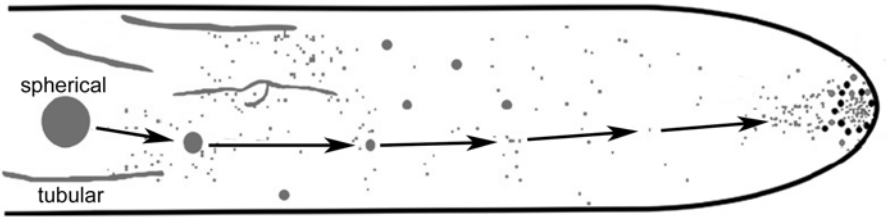


Figure 2.15: Tubular and spherical vacuoles in the hypha of *Neurospora crassa* (a model fungus, Ascomycetes). The arrows indicate the migration of vacuoles that «gradually decrease in size while they move forward until dispersing into very fine vesicles (putative chitosomes) that accumulate at the Spitzenkörper at the hyphal apex.» Adapted from Riquelme & Bartnicki-García 2008.

Chitosomes can be identified in the confocal microscope, but they are to small to be clearly seen in ordinary light microscopy, measuring only about 40-100 nm. They transport enzymes and necessary building molecules from their site of origin behind the hyphal apex to the Spitzenkörper (fig. 2.15) and finally fuse with the plasmalemma, liberating their content that now build new parts of the apical hyphal wall. Chitosomes were isolated from fungal cells and their biochemistry studied (Ruiz-Herrera & Bartnicki-García 1974; Ruiz-Herrera & al. 1975; Bartnicki-García & al. 1979). **Microtubuli** are known since the last quarter of the 19th century, described as spindle fibres that guide chromosomes during nuclear division in animals and plants, but only the transmission electron microscope revealed their construction as fine tubes only about 25 nm wide. Microtubuli are associated with intracellular movements and the **cytoskeleton** (Xiang & Plamann 2003). Their functions and relationships with **microfilaments** and **filasomes** in fungi were investigated by Girbardt (1979a,b), Howard (1981), Runeberg & al. (1986), Raudaskoski & al. (1988), Kaminskyj & al. (1989), Harold & Caldwell (1990) and Kern & al. (1997). Most of our knowledge of these organelles do not stem from work with Hymenomycetes.

The Nucleus and Mitosis

The morphological constituents of the interphase nucleus are the chromatin, the nuclear envelope and the nucleus associated organelle (NAO). During mitosis, the spindle pole body (SPB, derived from the NAO), an intranuclear spindle, a few extra-nuclear microtubules and a small number of chromosomes become visible.

The nuclei are not rigid bodies, but they change their form quite dramatically during nuclear migration, especially when passing from one hyphal cell to another (fig. 2.8) or when migrating through the sterigma into the young basidiospore.

The **chromatin** is a mixture of proteins and DNA and is the site where nuclear genes are located. In living and in carefully aldehyde-fixed fungal nuclei it appears structureless, but coagulating fixation, e.g. Flemming or Bouin, induces coarse artefacts (Girbardt 1961, 1978) that were sometimes interpreted as chromosomes.

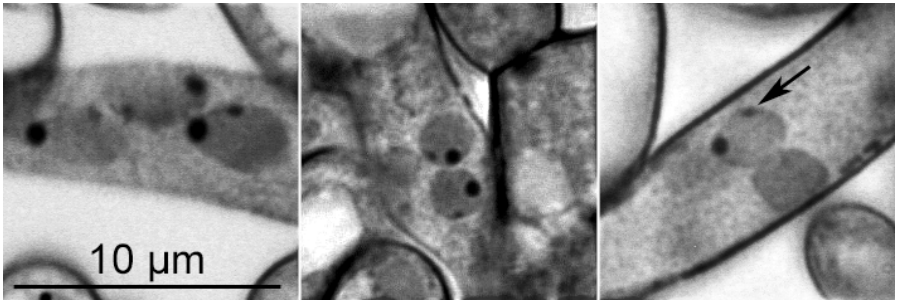


Figure 2.16: Fungal nuclei after aldehyde fixation. The chromatin appears homogeneous, the nucleolus is very prominent, the nucleus associated organelle is visible (one is identified by the arrow). *Agaricus bisporus* primordium about 4 mm high, aluminium zirconium haematoxylin. – Original photographs.

The **nucleolus** is easily visible in the light microscope and survives even strongly coagulating fixations. It behaves like a viscous gel and often becomes deformed during the nuclear cycle. In migrating nuclei, the nucleolus is attached to the nuclear envelope (P. Heim 1954; Girbardt 1955) and is usually shaped like a very long drop with a sharply pointed end, forms that have been misinterpreted as special nuclei called "Komentenkerne" ("comet nuclei") by Ruhland (1901). During the early phases of mitosis the nucleolus disappears, but it reappears towards the end of the nuclear division. The electron microscope reveals a net-like and a granular component (Girbardt 1970, fixation artefact?).

The **nucleus associated organelle** (NAO: Girbardt 1971a,b; Girbardt & Hädrich 1975) is just visible in the light microscope in phase contrast or after staining as an elongated body (fig. 2.16). It is attached to the nuclear envelope at the outside of the nucleus and consists of two globular bodies located at both ends of a middle plate. It is about 0.4-0.5 µm long and 0.15 µm high, and the middle plate is barely 0.025 µm thick. At the beginning of mitosis the two globular bodies separate and migrate to opposite poles of the nucleus where they become the **spindle pole bodies** (SPB) located at the outside of the nuclear envelope. They govern the synthesis of the microtubules of the nuclear spindle during mitosis. Many authors equate NAO and SPB, but it would be better to understand the diglobular structure as being the NAO that generates two uniglobular SPB.

The **nuclear envelope** is homologous with the endoplasmic reticulum, but the connections with the reticulum so frequently reported seem to be an artifact (Girbardt 1970). It is 50-60 Å (= 5-6 nm) thick, and contrary to widespread opinion it is visible in the light microscope, at least after adequate fixation and in phase contrast, since highly contrasted lines are visible even if their thickness is well below the optical resolution of the microscope (for an oil immersion lens with a numerical aperture of 1.32 the limit of visibility (not resolution!) in blue light is 0.0034 µm = 34 Å, in green light 42 Å, using the formula given by Françon 1967: 31; see also Girbardt 1965, 1978).

The nuclear envelope of *Trametes versicolor* is perforated by 40-45 pores per µm^2 (Girbardt 1970), corresponding to 3300-3800 pores for a nucleus 12 µm long and 2.2 µm wide. Each pore consists of a hole 40-50 nm wide, surrounded by a

ring with an outer diameter of about 0.1 µm. The centre is occupied by a small grain, which is connected to the ring by 8-10 radii. The mean surface of a pore measures 0.0016 µm² corresponding to 5-7 µm² for the entire nucleus. This is roughly 7-8% of the total nuclear surface. The pore and the ring together measure about 0.008 µm², so that approximately one third of the entire nuclear envelope is occupied by the ring pores.

Mitosis is the vegetative nuclear division. Its characteristics are the persistence of the nuclear envelope, the narrow, rod-like intranuclear spindle and the absence of a true metaphase plate of chromosomes.

Mitosis in Hymenomycetes is completed in only 5-7 minutes. It begins with the division of the NAO, and the migration of the SPB along the nuclear surface. Frequently the axis defined by the SPBs is oblique or even transversal to the hypha,

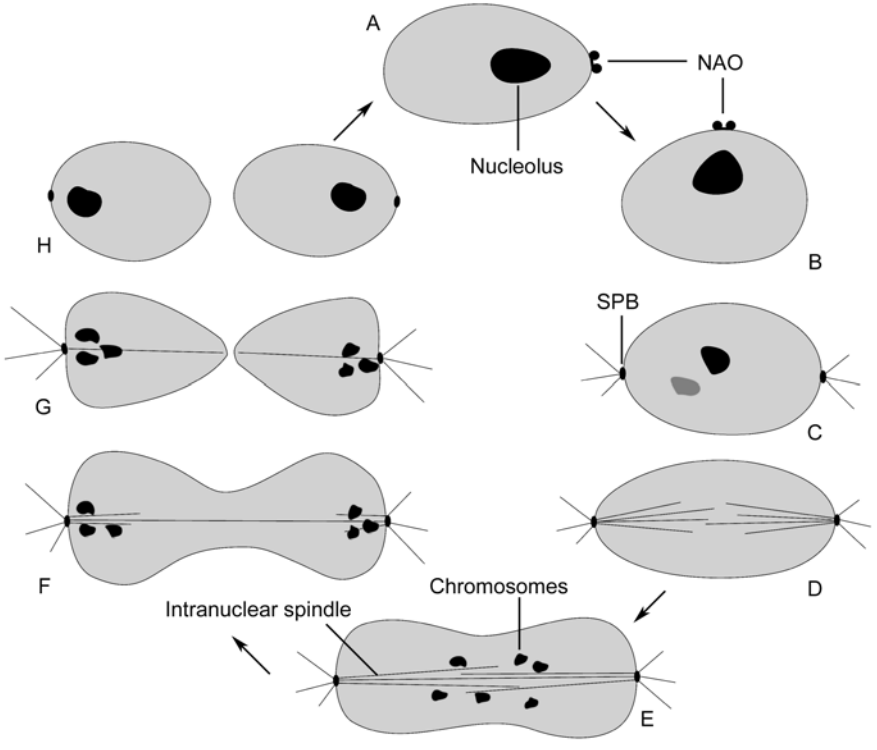


Figure 2.17: Diagram of the mitosis of a Hymenomycete. **A**: Interphase nucleus with homogeneous chromatin and complete NAO. **B**: Nucleus rotated. **C**: The subunits of the NAO separated and migrated to the nuclear poles and become SPB. Nucleolus dissolves and extranuclear microtubules are formed. **D**: The nucleolus has disappeared and intranuclear microtubules form the spindle. **E**: Chromosomes at the periphery of the spindle are in constant movement. The nucleus has been elongated by the action of the spindle. F: The chromosomes have been pulled to the poles. **G**: The nuclear envelope reached the spindle and the daughter nuclei are separated. **H**: The microtubules and the chromosomes have disappeared, the new nucleoli have formed. The SPB are still simple but will form a complete NAO within 30-40 minutes. The nuclear envelope remains intact throughout the entire cycle except under the SPB. – From Clémençon 1997.