Podospora anserina

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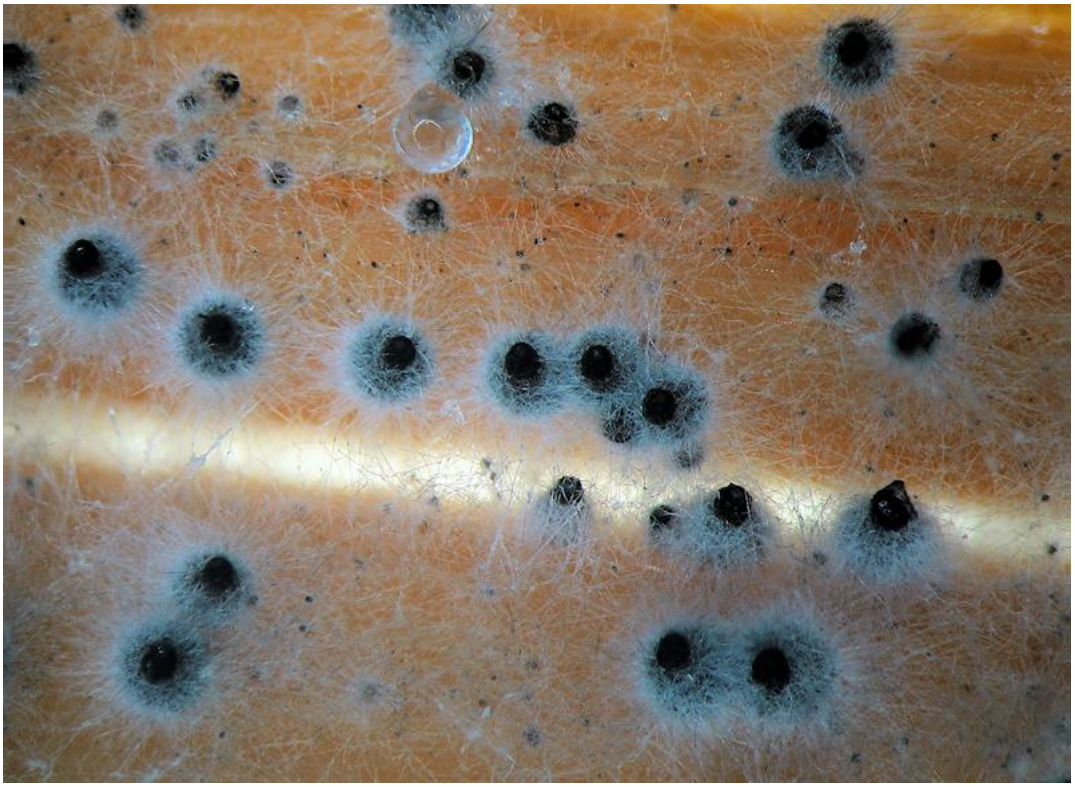

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Foreword

In any good movie, the cast is a large part of its success. Of course, the stars playing the main characters are important. However, a good set of supporting roles is often equally crucial to fully bring to the fore all the qualities of the film. The science of Biology is a little bit like a movie. Indeed, it needs models to decipher the fundamental laws of the living. Some are superstars, such as mouse, drosophila, the bacterium *Escherichia coli* or the baker's yeast *Saccharomyces cerevisiae* and play foremost roles. However, other less-known models are sometime key actors in major discoveries. Examples are numerous: Mendel used peas to decipher laws of heredity and Hämmerling used Acetabularia to show that the cell's nucleus is the location where genetic information is stored…

For the filamentous fungi, the stars of the cast are *Neurospora crassa* and *Aspergillus nidulans*. The former has for example been instrumental in the discovery of the nature of the gene. Indeed, experiments on this model showed that "one gene codes for one enzyme", a paradigm which still holds for the most part. It is currently used in many labs to study many fundamental processes ranging from the circadian clock to epigenetic gene regulation. The second fungus is used to decipher many cellular phenomena ranging from the cell cycle to the role of the cytoskeleton. It has however been particularly important in the discovery of the parasexual cycle in eukaryotes in the 1950's. The supporting cast for filamentous fungi is too numerous to cite them all. *Cryptococcus neoformans* and *Magnaporthe grisea* are instrumental to study pathogenicity; *Coprinopsis cinerea* and *Sordaria macrospora* are used to study reproduction, to cite a few of them. This book will focus on one of the supporting cast, the "friendly mold" *Podospora anserina*. This fungus is used for over a hundred years in the laboratory to study processes as diverse as senescence, prions and sexual reproduction. Few reviews dealing with its biology are available. However, no large monography exists on this species. This book proposes to fill this void.

Podospora anserina: a brief history

Podospora anserina is a filamentous fungus, *i.e.*, a mold, used now for more than a century in several laboratories to study various biological processes ranging from those typical of fungi such as anastomoses and vegetative incompatibility (= heterokaryon incompatibility), hyphal interference, spore germination, mycelium degeneration and fruiting body formation, to those of general importance for eukaryotes such as sexual reproduction, Meiotic Drive Elements that cheat Mendel's laws, mitochondrial and peroxisomal physiology and those of general relevance in biology, *e.g.*, senescence, cell differentiation, degeneration and death, respiratory metabolism, or structural and regulatory inheritance caused by prions and prion-like hereditary units.

Early researchers working with *P. anserina* were mostly concerned with the cytological descriptions of cellular phenomena and structures beyond those used to classify the fungus. Wolf[1] in 1912 and Satina in 1916 dealt mostly with the description of the sexual process from the differentiation of the gametes to the production of ascospores, Ames in 1930, 1932 & 1934, Dowding in 1931 and Dodge in 1936 with the breeding system, finally Buller in 1931 with hyphal anastomoses. Page analyzed the complete cycle of *P. anserina* and related species in 1939. It is however with the work of the French geneticist Georges Rizet (figure 1) that *P. anserina* was extensively used as a model. Rizet and its students gave the complete explanation of the pseudo-homothallic breeding system and complex nuclear behavior during sexual reproduction of the fungus, enabling them to perform elegant genetic analysis. They describe the vegetative incompatibility (the "Barrage"phenomenon), the still mysterious Senescence process and the peculiar behavior of the S/s incompatibility system that we now know is due to a prion. They use the fungus to

Figure 1. Georges Rizet.

[1] All references are given at the end of the book.

study genetic recombination, gene structure, translation and mitochondrial physiology and evolution. Along with Karl Esser, a German mycologist, who visited Rizet's lab during a postdoc in the 1950's, they develop all the tools, which are now routinely used, including the growth and germination media as well as the methods for macromolecule extractions and analyses. This culminated by the development of genetic transformation procedures enabling the entry of *P. anserina* in the era of molecular genetics, by permitting the identification of mutant genes and later on gene deletions and modifications. Finally, it is Rizet's "scientific progeny" who established in 2008 the complete genomic sequence of the fungus.

Presently, the fungus is still studied in a few labs, mostly in France and Germany as expected from its history. However, many publications also originate from the Netherlands, Mexico, Switzerland, Taiwan… showing an ever increasing popularity! It truly deserves its nickname: the friendly mold…

Figure 2. *Podospora anserina*, the friendly mold.
Picture courtesy Pierre Grognet.

Part 1: Biology of *Podospora anserina*

Podospora anserina in the tree of life: classification of the species

When dealing with living organisms, it is always advisable to know their exact position in the tree of life as this greatly help to outline their main characteristics. *P. anserina*, also known as the "friendly mold", is thus a "mold" or a "filamentous fungus" (figure 3). This means that it belongs to the domain *Eukaryota* (figure 4), *i.e.*, the major part of its genetic information is contained inside a nucleus, the remaining part being located inside the mitochondria. It is related to animals in the sense that like animals it belongs to the *Opisthokonta* superphylum (figure 4). Species of this superphylum share many characters, like the capacity to use extensively chitin as a coat material, to store carbon as glycogen and to use UGA as a tryptophan codon in the mitochondrial genetic code. Their name stems from the fact that they differentiate flagellated cells with a single posteriorly-orientated flagellum. However, *P. anserina* is a terrestrial fungus and, as such, it has altogether lost the capacity to differentiate the flagellum. *Opisthokonta* belongs to the subdomain *Amorphea*, which has been defined by molecular

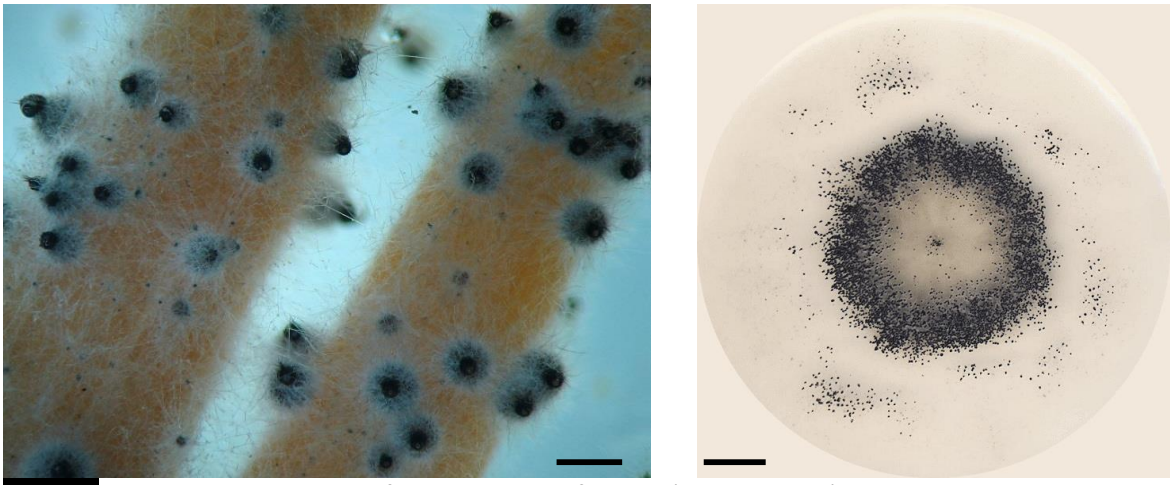


Figure 3 ***Podospora anserina*.** Left at high magnification (bar= 0.3 mm) and grown on toothpicks; Mycelium and fruiting bodies (the pear-shaped perithecia) are visible. Right: the friendly mold at low magnification (bar= 1 cm) and grown on a minimal medium (M2) Petri plate. The black dots are the perithecia.

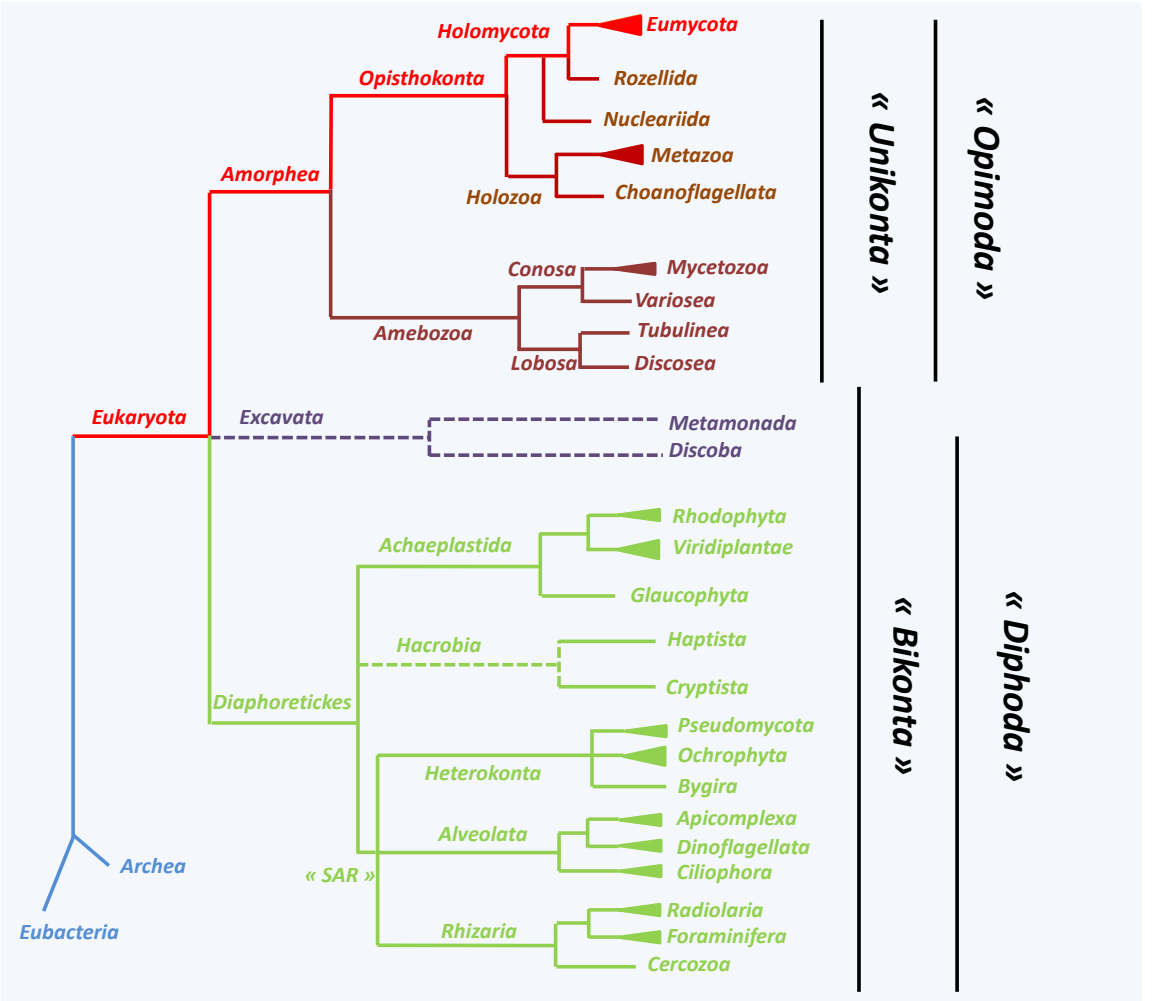


Figure 4 ***P. anserina*** **belongs to the *Eumycota*, or true fungi.** In red, the lineage to which *P. anserina* belongs.

phylogeny. Species from *Amorphea* share little characteristics, hence their name that means “formless”. In *Opisthokonta*, two phylogenetic lineages are presently recognized: *Holozoa* that contains the *Metazoa* or animals, and *Holomycota* that contains the *Eumycota* or true fungi, to which *P. anserina* belongs. Fungi, and hence *P. anserina*, feeds by osmotrophy, *i.e.*, they degrade their food outside the cells by secreting enzymes and then absorb the released molecules through transporters located in their plasma membrane. Species from the *Holozoa* lineage, and also those located at the base of the *Holomycota,* feed by phagotrophy or ingestion, *i.e.*, ingest food as large particles and digest it inside the cells (or digestive

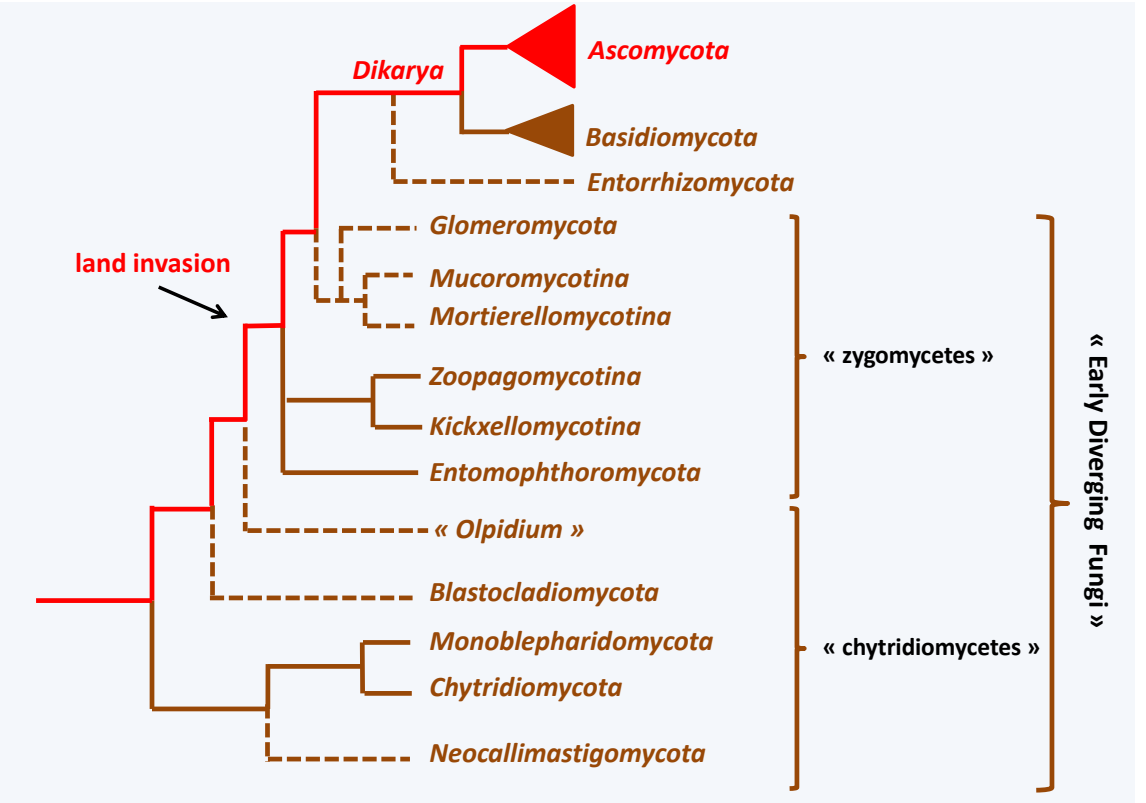


Figure 5 Diversity of the Eumycota. In red, the lineage to which *P. anserina* belongs.

track for animals). Other eukaryotic organisms feed by osmotrophy, the *Pseudomycota*. They look very much like *Eumycota*, but have evolved from completely different ancestors (figure 4).

Eumycota is a highly diverse group containing at least 14 phyla (figure 5). Its basal members, the "chytridiomycetes", are still aquatic organisms that disperse thanks to a flagellum. However most species are terrestrial and have invaded nearly all biotopes. Some have even returned to an aquatic lifestyle, as whales and dolphins did. These terrestrial or formerly-terrestrial species all share the inability to produce a flagellum. The two major phyla that contain over 90% of the species of *Eumycota* are the *Ascomycota* and the *Basidiomycota*. They are related and able to produce dikaryotic cells (cells with two genetically-different nuclei) during an extended period of their life cycle, hence the name of the lineage that contains them; the *Dikarya* (figure 5). For most *Dikarya* species, the major part of their life is completed as a mycelium, a network of interconnected and elongated cells called hyphae. This mycelium is the stage of the life cycle during which the fungus feeds, *i.e.*, the vegetative part of the life cycle. The major difference

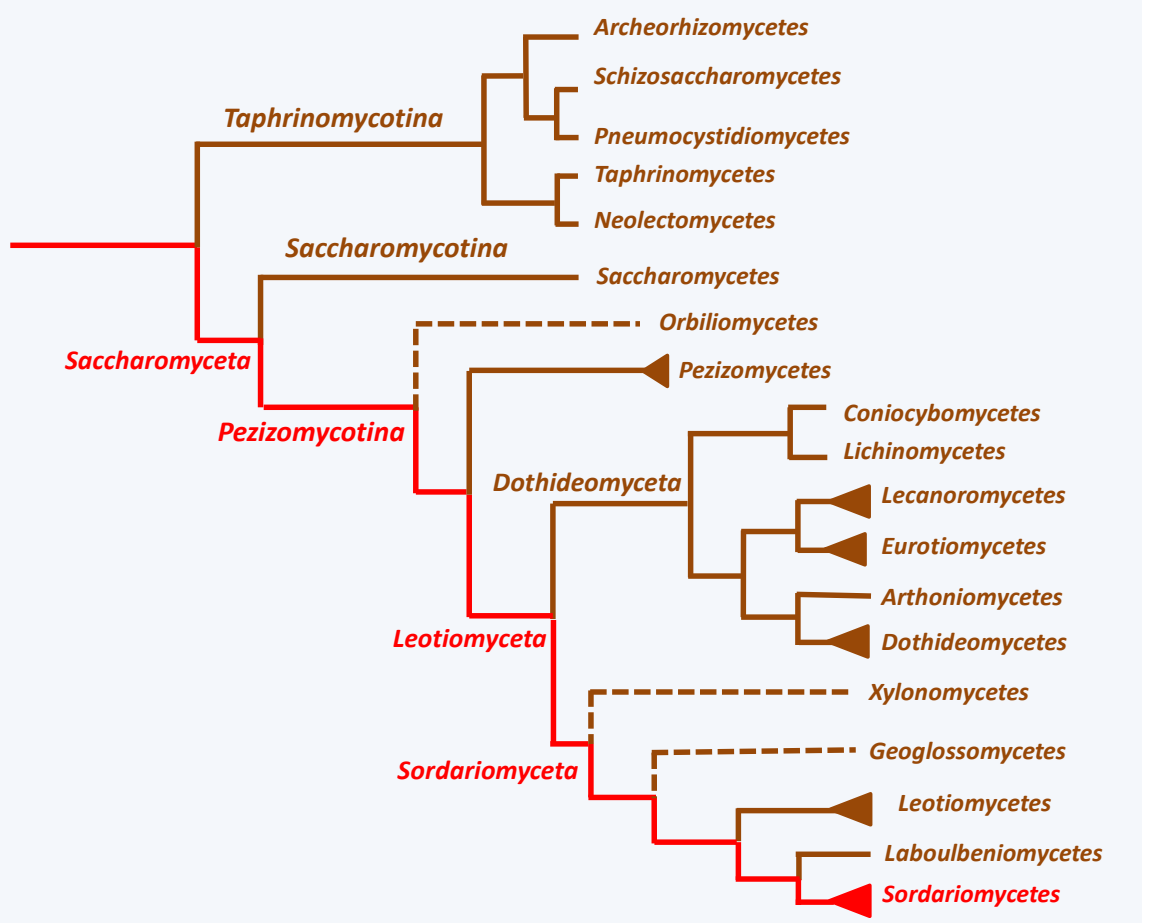


Figure 6 Diversity of the *Ascomycota*. In red, the lineage to which *P. anserina* belongs.

between the *Basidiomycota* and the *Ascomycota* is the way they differentiate their sexual (meiotic) spores during the reproductive part of their lifecycle. In the *Basidiomycota,* spores are produced outside the mother cell or basidium that undergoes meiosis; they are called basidiospores. In the *Ascomycota*, they are formed inside the mother cell or ascus. They are then called ascospores. *P. anserina* belongs to the phylum of the *Ascomycota*, also known as the "ascomycetes" in the vernacular language. *P. anserina* differentiates a typical mycelium during its vegetative phase (figure 3) and produces archetypal asci during sexual reproduction (see those on figure 16).

Ascomycota are further subdivided into three subphyla (figure 6). The basal *Taphrinomycotina* and *Saccharomycotina* contain species unable to differentiate complex multicellular structures. They

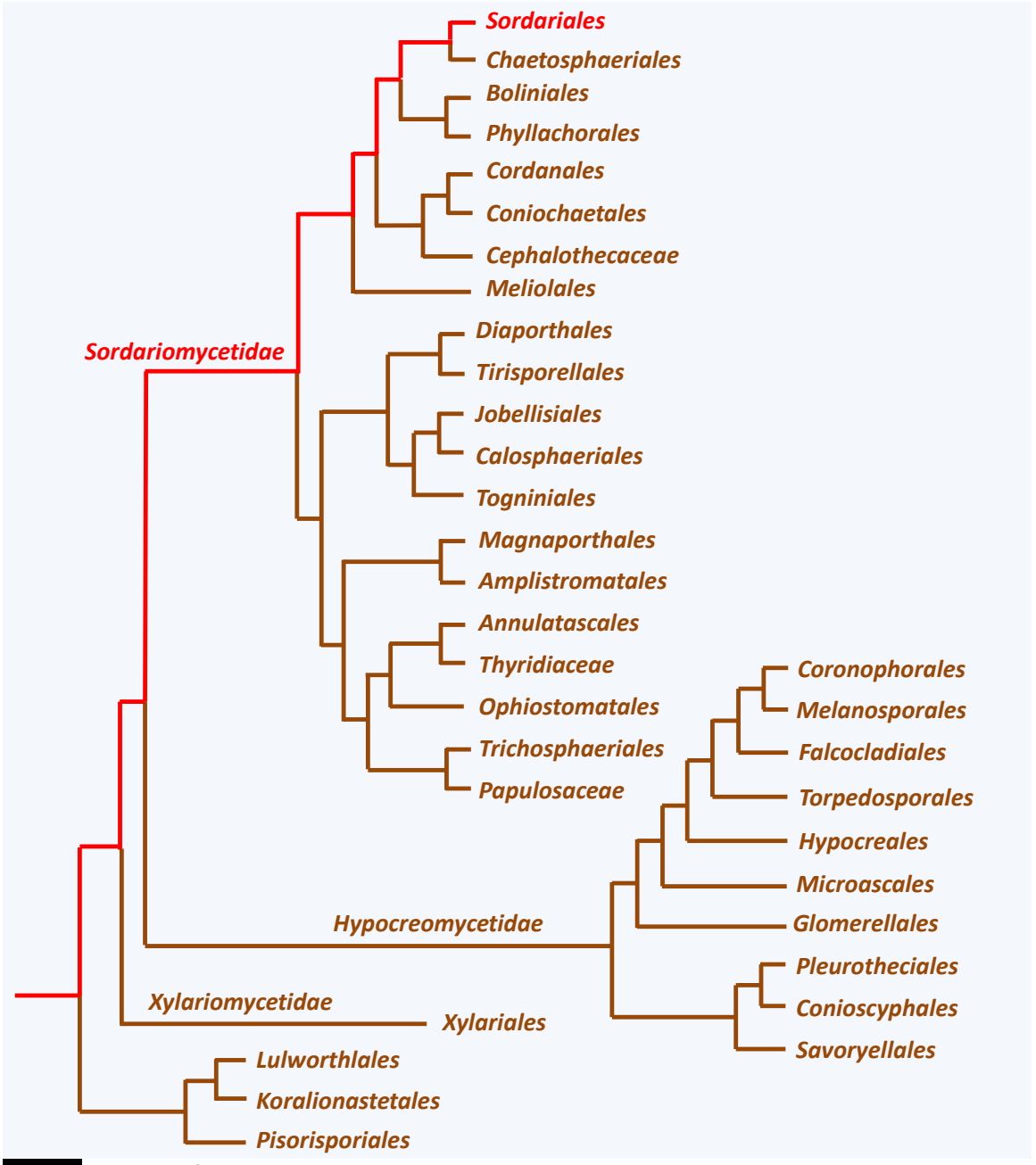


Figure 7 Diversity of the *Sordariomycetes*. In red, the lineage to which *P. anserina* belongs.

often live as yeast or as mycelium in which communications between cells remains simple. *P. anserina* is a member of the third subphylum: *Pezizomycotina*. The species of *Pezizomycotina* often have complex life

cycles and behaviors, as we shall see for *P. anserina*. Their mycelium is highly interconnected, firstly by central pores that exist between two consecutive articles (*i.e.*, the elongated cells that made up the hyphae), and secondly by the ability of hyphae to fuse by a process called anastomosis. Different types of hyphae can also be distinguished, primarily by their diameter. *Pezizomycotina* are often able to differentiate complex multicellular structures, especially during sexual reproduction. For example, *P. anserina* differentiate a fruiting body looking like a tiny pear that is called a perithecium (figure 3). *Pezizomycotina* fungi also disperse through asexual spores, often conidia. *P. anserina* differentiate conidia-looking cells that are used as male gamete for fertilization. They are called spermatia. As yet in the laboratory, germination of *P. anserina* spermatia is achieved with very low efficiency (in the range of one out of 10^6-10^7), questioning their role as asexual dispersal unit. However, it cannot be ruled out that the proper conditions for their germination are still unknown.

Differentiating a perithecium during sexual reproduction is a general characteristic of species in the class *Sordariomycetes* (and also in the related class *Laboulbeniomycetes*) to which *P. anserina* belongs (figure 7). More than 10 000 species of *Sordariomycetes* have been described, but this number is likely largely underestimated. They live as saprobes (*i.e.*, they live freely and feed on dead organic matter) or as parasitic or mutualistic associates of plants and animals. However, none appears to live as lichen or

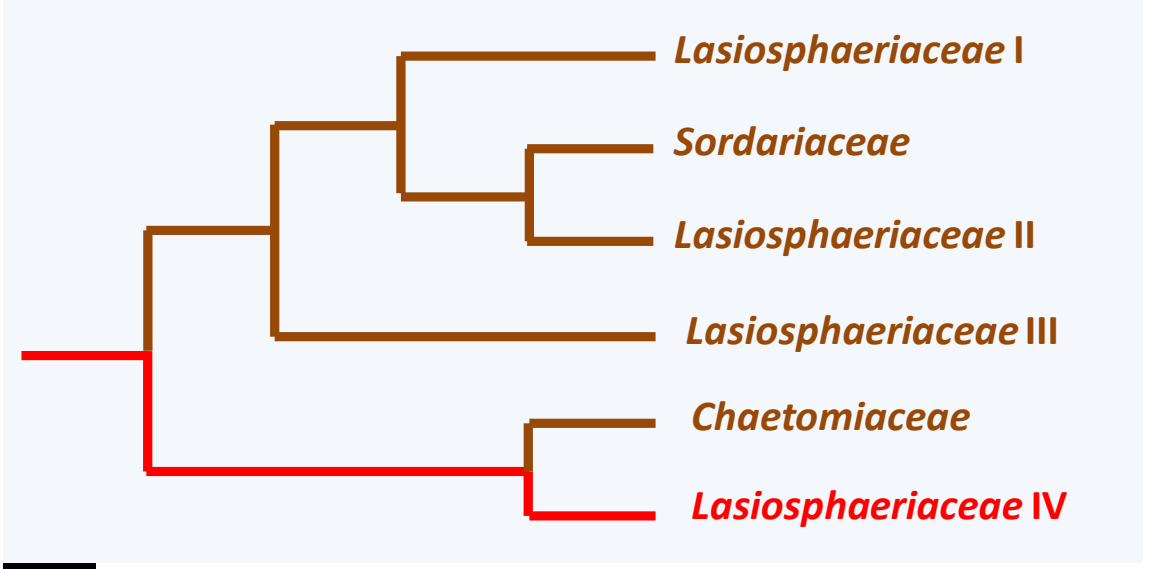
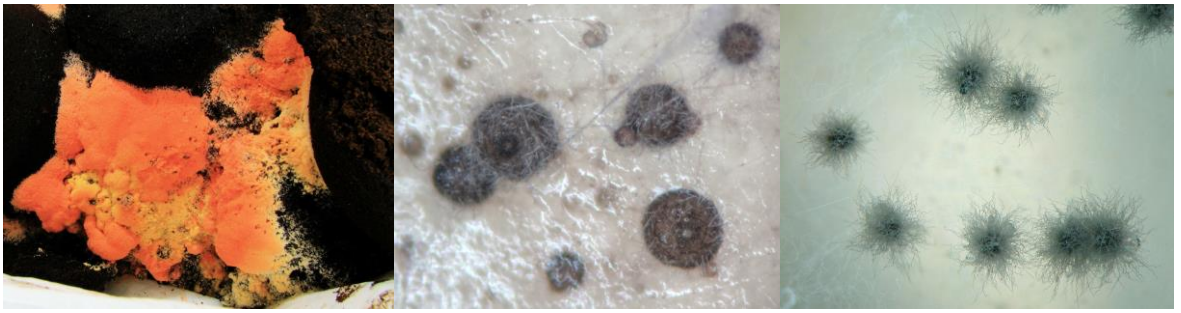


Figure 8 Diversity of *Sordariales*. In red, the lineage to which *P. anserina* belongs. The numbering is based on the one of Kruys *et al.* 2015.

mycorrhiza, two lifestyles largely adopted by fungi. *P. anserina* lives primarily as a saprobe on herbivore dung and less frequently in soil, but it also seems to be able to associate with plants as an endophyte*, i.e.*, it may also live within plants. Molecular phylogeny has recognized three major lineages of *Sordariomycetes*, as well as additional as-yet nameless basal groups (figure 7). Most species of *Xylariomycetidae* produce dark perithecia often embedded collectively within a stroma. Most species of *Hypocreomycetidae* produce brightly-colored perithecia and most species of *Sordariomycetidae*, to which *P. anserina* belongs, produced dark greenish ones. Molecular phylogeny has also helped to refine the classification of the various *Sordariomycetes* species into orders (figure 7). The order containing *P. anserina* is the *Sordariales*. Species of this order produce solitary perithecia that most often contain darkly-pigmented ascospores, as *P. anserina* does. *Sordariales* presently contains three families: *Sordariaceae*, *Chaetomiaceae* and *Lasiosphaeriaceae*. The definition of these families has greatly changed over time and was previously based on the fine structures of the fruiting bodies as well as the shape and ornamentation of the ascospores. The new data generated by the molecular phylogenies have shown that the *Lasiosphaeriaceae* is paraphyletic and four distinct phylogenetic groups can be identified. The monophyletic *Sordariaceae* and *Chaetomiaceae* are nested within these four lineages (figure 8). We are thus waiting for a complete reclassification of the order. This will entail name changes for three of the *Lasiosphaeriaceae* lineages… *P. anserina* is in the *Lasiosphaeriaceae* lineage IV that is more closely related to the *Chaetomiaceae*. Other well-known species of *Sordariales* (figure 9) are those of genera *Neurospora* and *Sordaria* belonging to the *Sordariaceae* and of the genus *Chaetomium* belonging to the



Neurospora crassa ***Sordaria macrospora*** ***Chaetomium globosum***

Figure 9 Relatives of *P. anserina* from the order *Sordariales*. On the left, *Neurospora crassa* is known to produce large amounts of orange conidias. On the center, *Sordaria macrospora* produces typical glabrous perithecium. On the right, *Chaetomium globosum* differentiates very hairy fruiting bodies.

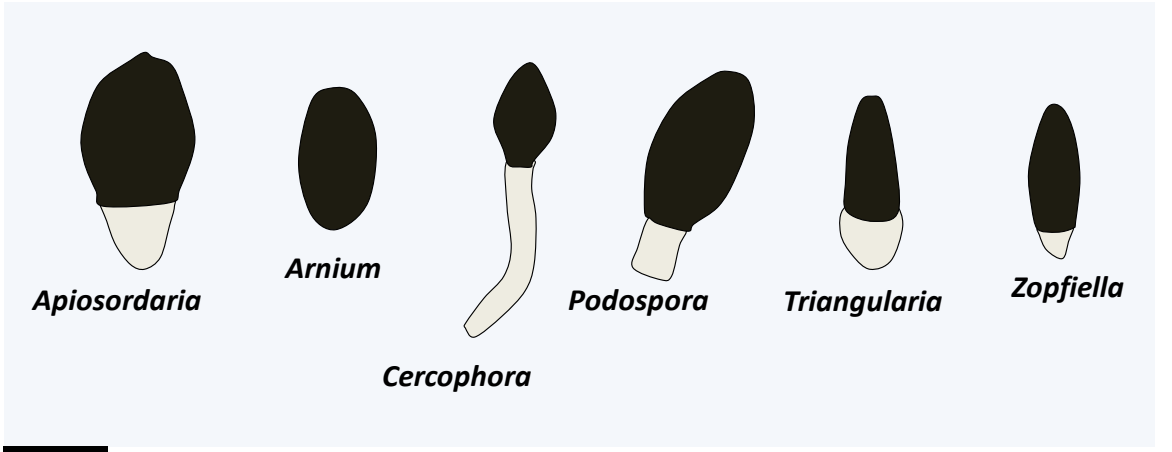


Figure 10 Main ascospore shapes in the *Lasiosphaeriaceae* IV. The size of the ascospores can be very different among the different species. Moreover, some can be decorated with gelatinous appendages not represented here.

Chaetomiaceae. In addition to the famous *Neurospora crassa*, *Neurospora intermedia, Neurospora tetrasperma, Sordaria macrospora* and *Sordaria fimicola* are often used in the laboratories or in classrooms for genetic studies. *Chaetomium species*, especially *Chaetomium globosum*, are well adapted to grow on cellulose and are often responsible for the spoilage of books in humid libraries. Some *Chaetomium* species are responsible of very rare but often fatal mycosis in human. To give an insight into the biodiversity of the *Sordariales*, species in this order are as genetically diverse as the vertebrates. For example, the genetic divergence between *P. anserina* and *N. crassa* is at least as large as that between fishes and humans!

The traditional classification of the *Lasiosphaeriaceae* is based primarily on the form of the ascospores. Figure 10 depicts the shape of the ascospores of the species presently known in *Lasiosphaeriaceae* IV. Alas, this criterion turned out to be highly unreliable to trace the true relationship between species of *Lasiosphaeriaceae*. For example, most ascospores of *Lasiosphariaceae* IV are bicellular with one cell large and melanized and the other smaller and unpigmented. This latter cell may have undergone an apoptosis-like death. Nevertheless, *Arnium* ascospores are unicellular, showing that having bicellular ascospores is not a character shared by all species. Most genera of this family are thus polyphyletic. For instance, *Podospora* species are present in *Lasiosphariaceae* IV, but also in *Lasiosphariaceae* I, *Lasiosphariaceae* II and *Lasiosphariaceae* III! A paper by Miller & Hundorf in 2005 suggested that the peridium of the perithecium (= the envelop of the fruiting body that protects the asci)

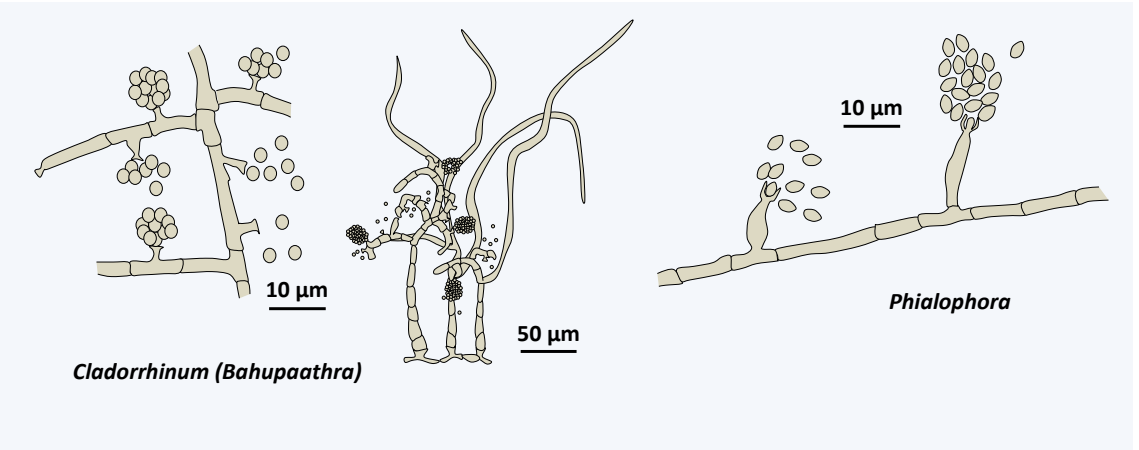


Figure 11 Known anamorphs in the *Lasiosphaeriaceae* IV.

might be a better predictor of the true phylogeny. Unfortunately, too few species have been analyzed with regard to this character to know if it is actually able to predict relationships in the *Lasiosphaeriaceae.*

In addition to the species differentiating sexual structures (or teleomorph), several species of *Lasisopshaeriaceae* clade IV are only known through their asexual forms (or anamorph). These are known as *Cladorrhinum* (= *Bahupaathra*) or *Phialophora* (figure 11). Finally, it is most likely that many species of *Lasiosphaeriaceae* IV are presently unknown and those listed in figure 12 are likely to be only the "tip of the iceberg".

To complicate the matter, few studies are devoted to the deciphering of the true phylogeny of the *Lasiosphaeriaceae*, as this family contains mostly saprobic species with inconspicuous life styles. Note that a fungus responsible for some mycetoma, *Madurella mycetomatis*, is a close relative, but it is not yet known whether this species belongs to *Lasiosphaeriaceae* IV or is more likely closely related to the *Chaetomiaceae*. Mycetomas caused by *M. mycetomatis* are rare but very debilitating and among the most dreadful diseases that one can catch! Presently, molecular phylogeny recognizes three subsets of species in *Lasiosphaeriaceae* IV (figure 12). In figure 12, the species of each subset are listed (mostly) alphabetically because their actual relationships are as yet unknown.

The two *Podospora* species most closely related to *P. anserina* are *P. setosa* and *P. austroamericana*. Both are also coprophilous fungi. *P. setosa* produces asci with 128 ascospores, *P. austroamericana* with eight ascospores, while *P. anserina* asci have four ascospores. *P. setosa* and *P. austroamericana* are homothallic, *i.e.*, spores with a single nucleus will give rise to self-fertile thalli. *P.*

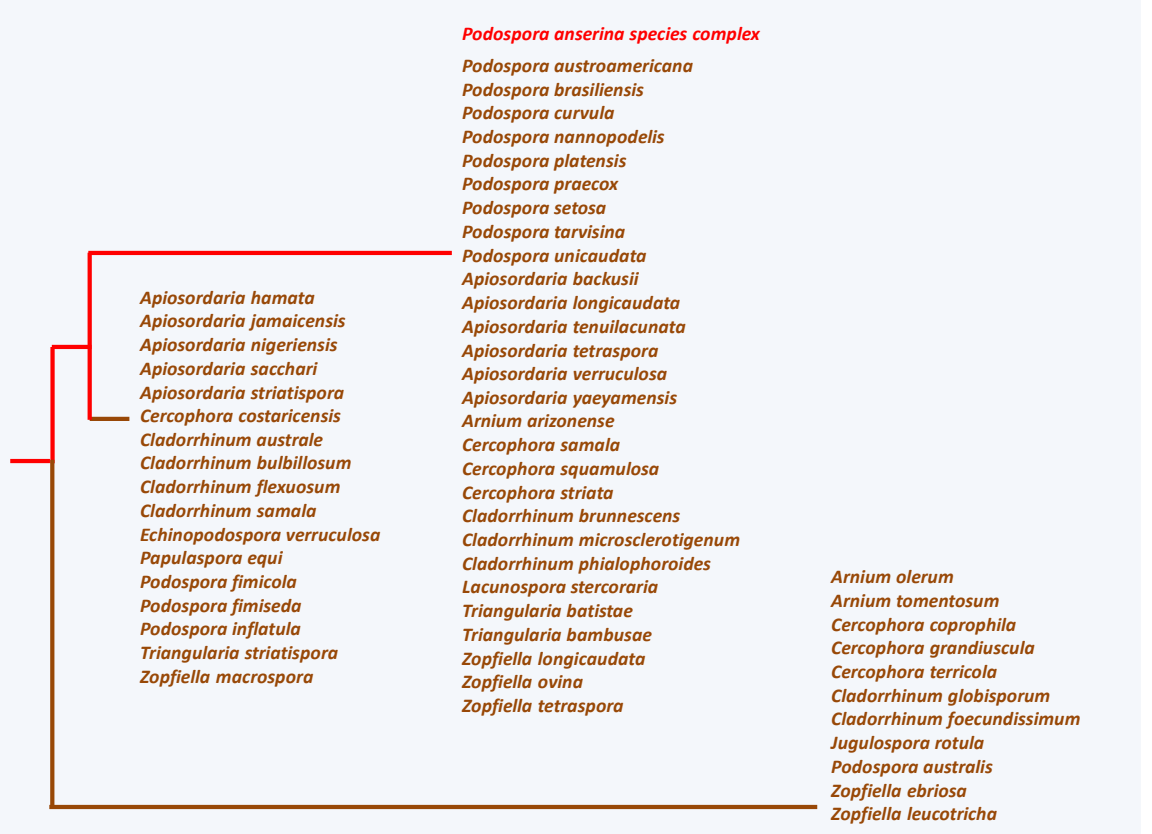


Figure 12 The species most closely related to *P. anserina*. Precise phylogeny of these species is still not known. However, three subsets of species are defined in most analyses. One contains the "*Podospora anserina* species complex". Another contains *Podospora fimiseda*, the type species of the genus *Podospora*. The last one includes *Podospora australis*.

anserina is pseudo-homothallic. Most of its ascospores give rise to self-fertile thalli. They in fact contain two kinds of sexually compatible nuclei and both are required for starting sexual reproduction. We shall come back to this point in the section dealing with *P. anserina* reproduction. It is not known whether these two *Podospora* are the actual closest relatives of *P. anserina*. Indeed, few molecular data are available for most of the species and the published phylogenies are poorly supported or partial (*i.e.*, they only deal with a few species). Nevertheless, the best candidates appear to date to be *Cercophora samala* or *Zopfiella tetraspora*, because these two species have sequences of their Internal Transcribed Spacer (ITS) of the rDNA that are the closest to *P. anserina*. This is supported by their life style or their morphology (Table 1), the former being coprophilous and the latter producing four-spored asci. Note that *Zopfiella tetraspora* (also known as *Tripterospora tetraspora*) usually produces neckless perithecia (also

Table 1 : some species related to *P. anserina*				
Species	**habitat/life style**	**fruiting body**	**mating**	**Asci**
Apiosordaria backusii	**soil**	**perithecium**	**homothallic**	**8-spored**
Apiosordaria longicaudata	**soil**	**perithecium**	**homothallic**	**4-spored**
Apiosordaria tetraspora	**soil and dung**	**perithecium**	**homothallic ?**	**4-spored**
Apiosordaria verruculosa	**soil, dung and endophyte**	**perithecium**	**pseudo-homothallic ?**	**4-spored**
Apiosordaria yaeyamensis	**soil**	**perithecium**	**homothallic ?**	**8-spored**
Arnium arizonense	**dung**	**perithecium**	**apomictic**	**4-spored**
Cercophora samala	**dung**	**perithecium**	**heterothallic**	**8-spored**
Cercophora striata	**decaying stems**	**perithecium**	**homothallic ?**	**8-spored**
Cercophora squamulosa	**aquatic decaying wood**	**perithecium**	**homothallic ?**	**8-spored**
Cladorrhinum microsclerotigenum	**endophyte of *Musa sp.***	**anamorph**	**unknown**	**NA**
Cladorrhinum phialophoroides	**desert soil**	**anamorph**	**unknown**	**NA**
Podospora austro-americana	**dung and endophyte**	**perithecium**	**homothallic**	**8-spored**
Podospora setosa	**dung, soil and endophyte**	**perithecium**	**homothallic**	**128-spored**
Triangularia batistae	**soil and endophyte**	**perithecium**	**homothallic ?**	**8-spored**
Zopfiella longicaudata	**dung and soil**	**« cleistothecium »**	**homothallic ?**	**8-spored**
Zopfiella tetraspora	**dung and soil**	**« cleistothecium »**	**homothallic ?**	**4-spored**

known as ”cleistothecia”, although this term is now reserved for species in the *Eurotiales*); yet an isolate was shown to produce both neck-endowed and neckless fruiting bodies… As seen in Table 1, many other potential applicants are possible. It is striking to see the diversity in the habitat/life style and developmental patterns of these species.

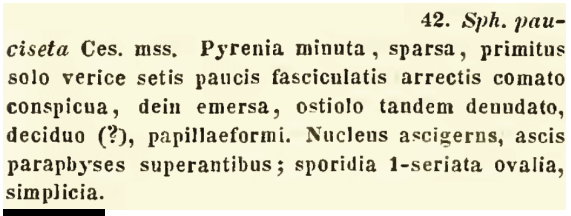
We are now finally reaching the species level in our journey through the classification of *P. anserina*. However, recent analyses of several strains of this “species” has reserved some surprises: *P. anserina* is a morpho-species - meaning that it has been defined by the morphology of its perithecia, asci and ascospores - that encompasses in fact at least seven species that appear to intercross rarely. All these species present different characteristics, including divergent genome sequences. Before going into the detail of each species, we need to go back to the traditional classification of *P. anserina*, which has seen battles of experts at to what is the proper name for this fungus!

Indeed, when one is looking in the fungal culture collections for strains of *P. anserina*, one is surprised to find that in some of them it is labelled as *Podospora pauciseta*. Moreover, in some early

Table 2: The different names of *P. anserina*	
Name	**Reference**
***Sphaeria pauciseta* (Cesati)**	Unknown author (1852) Botanische Zeitung 10: 285-288
***Malinvernia anserina* (Rabhenhorst)**	Rabenhorst, L. (1857) Hedwigia 1: 116 - pl. 15 fig.4
***Sphaeria anserina* (Cesati)**	cited as « in litt. » in Rabenhorst, L. (1857) Hedwigia 1: 116
***Sordaria pauciseta* (Cesati & De Notaris)**	Cesati, V & De Notaris, G (1853) Schema di classificazione degli sferiacei italici aschigeri pp 51-53
***Sordaria anserina* (Rabhenhorst) Winter**	Winter G. (1873)) Botanische Zeitung 31: 481-485
***Hypocopra anserina* (Cesati)**	cited as « in litt. » in Sacchardo P.A. (1882) A Sylloge fungorum omnium hucusque cognitorum. 1: 238
***Hypocopra erecta* (Spegazzini)**	Spegazzini C. (1880) An. Soc. Cient. Argentina 10: 5-33
***Podospora anserina* (Rabhenhorst) Niessl**	Niessl G. (1883) Hedwigia 22: 153-156
***Sordaria Penicillata* (Ellis & Everhart)**	Ellis, J. B. and B. M. Everhart (1888). The Journal of Mycology 4(8): 73-82.
***Pleurage anserina* (Rabhenhorst) Kuntz**	Kuntze, o. (1898). Revisio generum plantarum. 3(2): 504-505.
***Sordaria communis var. tetraspora* (Spegazzini)**	Spegazzini, C. (1899). An. Mus. Nac. Hist. Nat. Buenos Aires Ser. 2 6: 289-365.
***Podospora pauciseta* (Cesati) Traverso**	Traverso, J. B. (1905) Flora Italica Cryptogama ParsI: Podospora pauciseta. 1(2): 431-432
***Bombardia anserina* (Rabhenhorst) Migula**	Migula, W. (1913) Thome's Kryptogamic Flora. 10: 123-129.
***Schizothecium anserinum* (Rabhenhorst) Bessey**	Bessey, E. A. (1950). Morphology and Taxonomy of Fungi. pp 264-265

papers, this fungus was called *Pleurage anserina*. *Pleurage anserina* is only one of the names that this fungus has been designated and a full list is given in Table 2[2]. This proliferation of names stems from the fact that different authors classified the fungus under different names, for taxonomic purposes. Indeed, the genus is supposed to reflects on the relationships between close species. Depending on the characters used to regroup species, as well as the concept of "close" by the mycologist that has first identified the species, a fungus ends up in an already-known genus or in a new one. The "type" for the new fungus should at the same time be deposited in a herbarium or a culture collection for future analyses. This is called an exsiccata in the case of dried specimen kept in herbaria and it has a voucher for further reference. Then, as knowledge progressed, and as new species are identified, another taxonomist may reexamine the fungus and its name may change because new genera are created to accommodate growing numbers of species (or because this new specialist deemed his/her own set of characters to be important for classification!). Normally, during these transfers between genera the species epithet should

[2] Table 2 may be incomplete, as some authors, such as F. Doveri in "Fungi Fimicoli Italici", list more synonyms, but direct consultation of the cited literature does not permit to conclude that the described species is indeed our friendly mold.



42. *Sph. pauciseta* Ces. mss. Pyrenia minuta, sparsa, primitus solo verice setis paucis fasciculatis arrectis comato conspicua, dein emersa, ostiolo tandem denudato, deciduo (?), papillaeformi. Nucleus ascigerus, ascis paraphyses superantibus; sporidia 1-seriata ovalia, simplicia.

42. *Sph. pauciseta* Ces. mss. Perithecium small, sparse, at first like a wart with few coarse upright hair, then emerging, finally with an ostiole naked and deciduous (?), forming a papilla. Formation of asci in the center, asci taking over the paraphyses; spores uniseriate, oval, simple.

Figure 13 First description of *P. anserina* as *Sphaeria pauciseta* in the Botanische Zeitung in 1852 vol. 10 pp 285-288.

not change (although it may be corrected to comply with the Latin terminology). Another source of names is that a species may be identified as new, while it was already known. When this is realized, the two names are synonymized and the first one should be used. All of this participate to a proliferation of names and add to the confusion. Note that this is not restricted to *P. anserina*, but is common for many fungi, especially when they are molds with tiny fruiting bodies…

So why two species epithets for our friendly mold? Well, the proper name being normally the first one given, it should be *P. pauciseta* because the fungus appears to have been first formally described in 1852 as a "*Sphaeria pauciseta*" by an italian botanist called Vincenzo de Cesati (1806-1883). It was deposited in the "Klotsch herbarium mycologicum" under the number n° 1642. However as seen on figure 13, the description given in the Botanische Zeitung of this new species is rather limited (especially, it has no associated iconography) and the description from the herbarium associated with the original exsiccata is identical[3]. Note that in the description the number of ascospores in asci is not given, nor are the sizes of perithecia, asci and ascospores. There is thus no way to know based on this description whether this fungus is actually *P. anserina* with its typical four-spored asci. Many species of *Sordariales* may fit the description of the Botanische Zeitung. There is for example *Podospora australamericana* having asci with eight ascospores that may also fit to the description for "*Sphaeria pauciseta*". This description was nonetheless validated by Giovanni Battista Traverso (1878-1955), an italian mycologist in 1907 in his "Flora Italica Cryptogama", this time with an associated drawing (figure 14). The depicted species seems to be indeed our friendly mold, hence, the name validated by the taxonomists, "*Podospora pauciseta* (Ces.) Trav." that is used in some papers and culture collections.

[3] Pictures of the original exsiccatas, as well as old publications dealing with the fungus, are appended in the annexes at the end of the book.

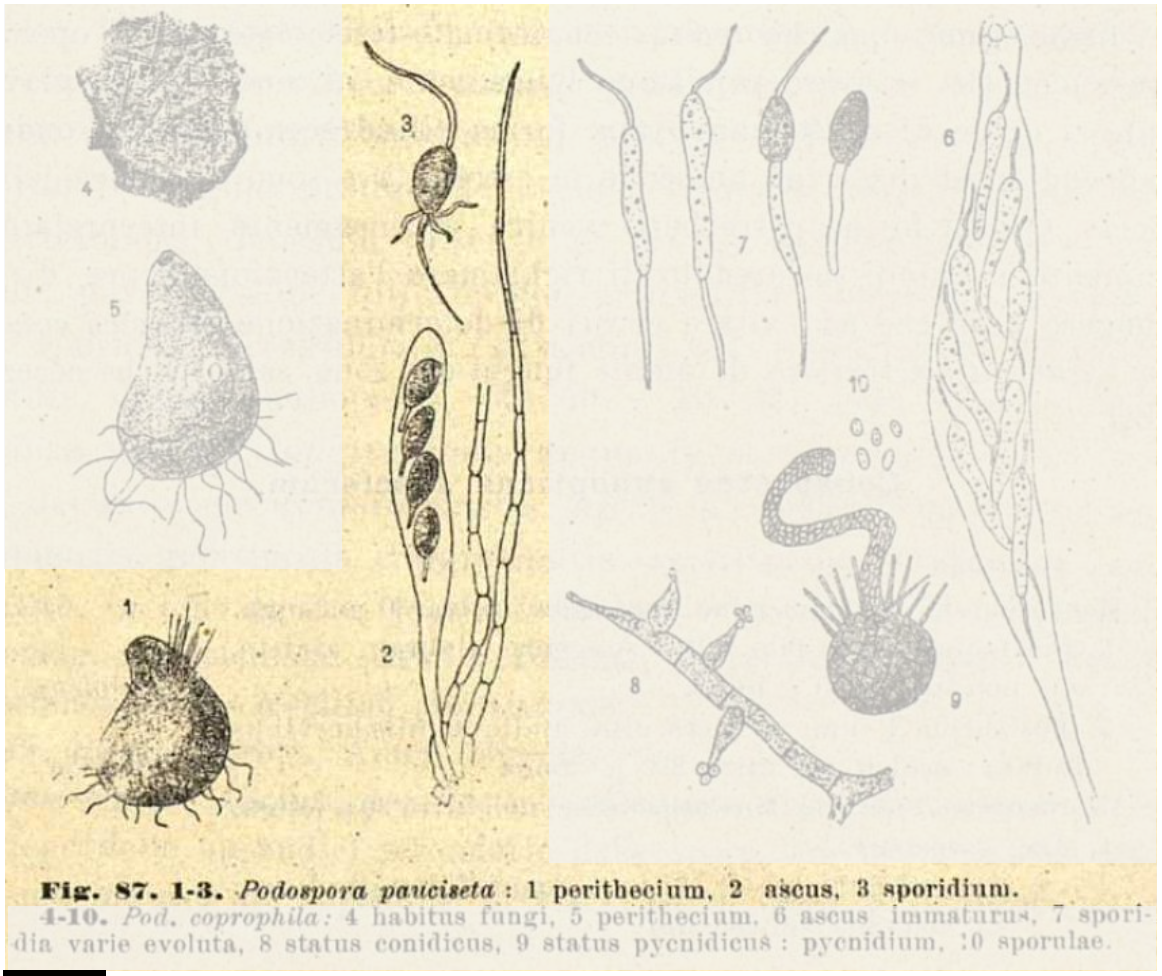
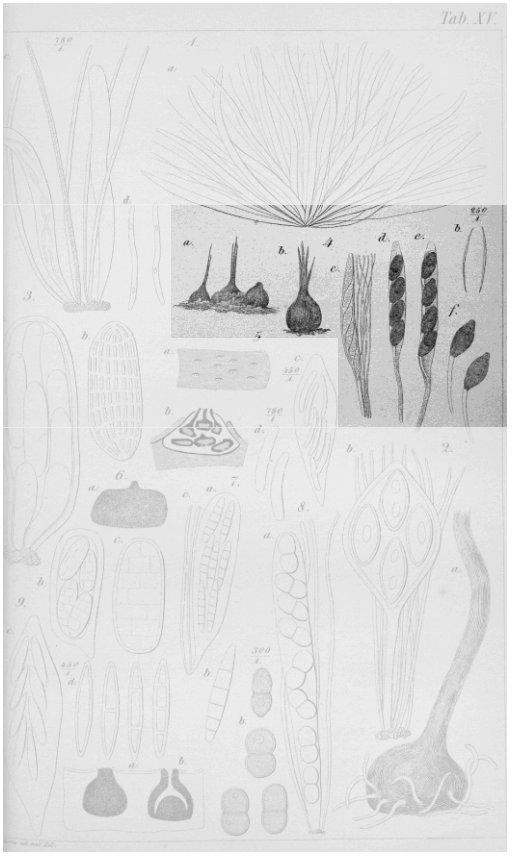


Figure 14 Illustration of *P. pauciseta* by Traverso in his "Flora Italica Cryptogama". Note the similarity of these drawings with those of Griffiths published six years earlier (figure 17)…

The second historical and formal mention of the fungus appears to be by the German mycologist Gottlob Ludwig Rabenhorst (1806-1881) as "*Malinvernia anserina"* in the first issue of the journal Hedwigia. The description is also rather scant (figure 15), but is associated with some drawings, most likely the first ones for our friendly mold. In fact, "*Malinvernia anserina"* is only described in the legend of a figure! The type for this "*Malinvernia anserina"* was deposited under n° 526 in the "*Klotschi herbarium vivum mycologicum sistens fungorum per totem Germaniam crescentum collectionem perfectuam*, ed. II". There, the description is more extensive. Many mycologists consider this to be the first accurate description of *P. anserina* and hence prefer to use *"anserina"* as the species epithet, especially given the



F. 4. **Malinvernia Rabenh.** Mspt.
Sphaeriacearum nov. genus.
M. anserina Rabenh.
Sphaeria anserina Ces. in litt.
a. Perithecium, vario stadio evolutionis, magnopere auctum.
b. Perith. liberatum, adhuc magis auctum.
c. Pars nuclei immaturi.
d., e. Asci, vario maturitatis gradu. Long. = 45/500 mill.
f. Sporae maturae. Long. = 10/500 mill.: lat. = 5—6/500 mill.

F. 4. **Malinvernia Rabenh.** Mspt.
Sphaeriacearum nov. genus
M. anserina Rabenh.
Sphaeria anserina Ces. in Litt.
a. Perithecia at various late stages of maturity
b. Perithecium, isolated, at an even later stage of maturation
c. Part of an immature centrum
d.e. Asci at various stages of maturity. length= 45/500 mm.
f. Mature ascospores length = 10/500 mm.: width = 5-6/500 mm.

Figure 15 Second description of *P. anserina* as *Malinvernia anserina* in the first volume of Hedwigia p 116 Fig. 4 of plate 15.

doubts that shroud the first description as *Sphaeria pauciseta* and the fact that Cesati also described *a* "*Sphaeria anserina*" and a "*Hypocopra anserina*" in earlier letters (see in litt. in Table 2). Unfortunately, I have not been able to find these letters nor their date of writing, to ascertain whether Cesati was indeed referring to the same species.

All this confusion regarding the proper name was already noted by the American mycologist George Francis Atkinson (1854-1918) in a footnote of a paper published in 1912 by another American mycologist, Frederick Adolph Wolf (1885-1975). Atkinson recommended using the name *P. anserina*... In fact, we may never know which description for the fungus is the good one, even if we go back to the herbarium specimens. Indeed, at that time pure cultures were rare and descriptions often relied on samples collected from the wild and not on strains isolated in pure cultures. The original specimens for *P.*

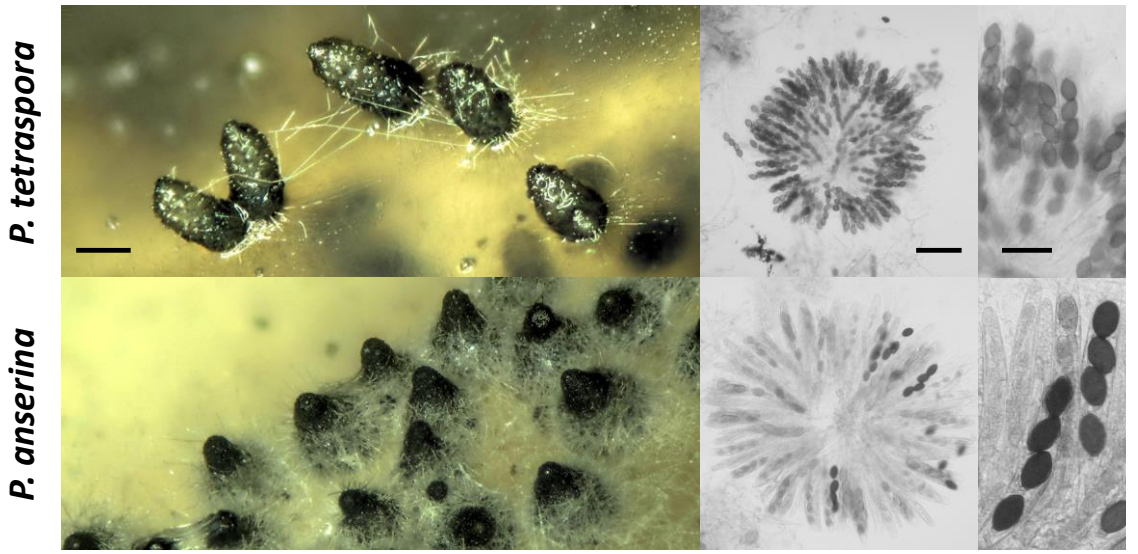


Figure 16 ***Podospora tetraspora.*** This four-spored species may be the one actually described as *Malinvernia anserina*. It produces slender perithecia with a differently-shaped neck, as well as smaller ascospores. The bottom pictures are from *P. anserina* taken at the same magnification for comparison. From left to right, bar= 250 µm, 250 µm & 100 µm.

pauciseta and *P. anserina* consist in dried dung with potentially more than one fungal species on it! Accordingly, in his thesis "Nordic Sordariaceae S. Lat." the Swedish mycologist Nils Lundqvist mentions that he was not able to find *P. pauciseta* in the "authentic" collections he examined. Intriguingly, it seems to me that the dimensions of the spores given by Rabenhorst, the long appendages on the neck of the fruiting bodies as well as the presence of a bubble in the center of the spores (discernible in figure 15), fit more with *P. tetraspora* than with *P. anserina*… This *Podospora* species looks very much like *P. anserina* (figure 16). It has similar-sized and -looking perithecia with four-spored asci, but these are smaller than in *P. anserina*. This species belongs to *Lasiosphaericeae* clade I. This casts strong doubts on the original description of *Malinvernia anserina* being that of our friendly mold. Along this line, some authors such as Mirza & Cain in their "Revision of the Genus *Podospora*" in 1969 even state that it is doubtful that *P. pausiceta* and *P. anserina* are the same species! So it is possible that neither "*pauciseta*" nor "*anserina*" should be the proper species epithet…

The quality of the microscope in the mid-19th century likely prevented a more accurate description of our friendly mold by Rabenhorst (the drawings of figure 15 show many inaccuracies in the appendage of the spore and the neck of the perithecium even if the represented species is *P. tetraspora*

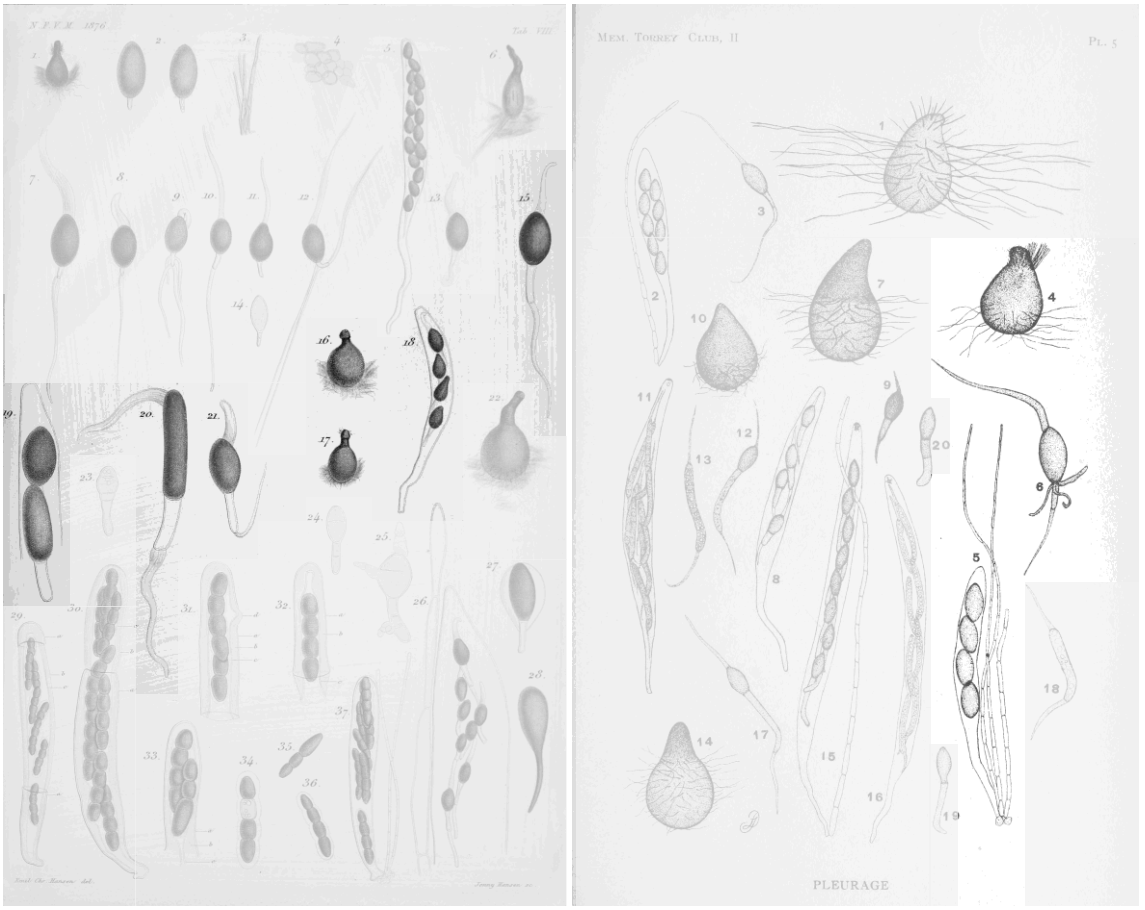


Figure 17 Two early drawings of *P. anserina*. Left (fig. 15-21), by E.C. Hansen in 1876 under the name *Sordaria anserina*; Right (fig. 4-6) by D. Griffiths in 1901 under the name *Pleurage anserina*. Compare the right drawings with those of Traverso (figure 14).

and not *P. anserina*). Though, improvement in microscope quality rapidly permitted to obtain better drawings for the fungus. Figure 17 gives two of them showing the actual *P. anserina*. The first one by the Danish mycologist Emil Christian Hansen (1842-1909) in his "Champignons Stercoraires du Danemark" published in 1876 and the second one by the American mycologist David Griffiths (1867-1935) in his "North American *Sordariaceae*" published in 1901. It is likely that Traverso (figure 14) got some inspiration from the earlier drawings from Griffiths (figure 17)…

At the beginning of the XXth century, confusion was already high regarding *P. anserina*, when in 1937 a Ukrainian mycologist, M. Milovtzova, described a new species closely related to *P. anserina* and

named it *Podospora comata* (figure 18). This species was described as having slightly smaller ascospores and perithecia. On the provided drawing, the neck of the perithecium lacks the small brush of hair at the base of the neck that is characteristic of *P. anserina*. This species was subsequently considered either a true species or only a "minute" form of *P. anserina*, depending on the mycologist…

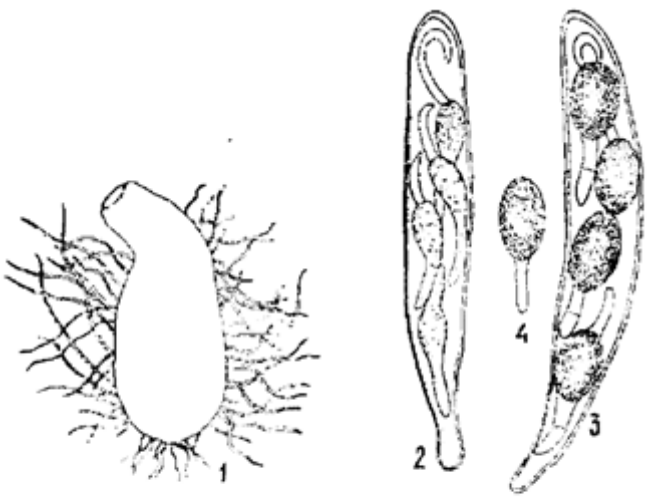


Рис. 2. Podospora comata sp. nova.

1. Перитецій, 2. Сумка з 4 молодими аскоспорами, 3. Сумки з стиглими аскоспорами, 4. Стигла аскоспора.

1. Perithecia. 2—3 development of ascospores. 4. The ripe ascospora.

Figure 18 ***Podospora comata*, a new species described by M. Milovtzova.** This species is described as having smaller ascospores and perithecia. The drawing on the left of the perithecium does not mention the presence of the small brush of erected hair typical of *P. anserina*. This species was considered either as a true species or as a minute form of *P. anserina*.

Owing to the doubts concerning the original descriptions of *P. pauciseta* and *P. anserina*, as well as the uncertain status of *P. comata*, we reexamined in my lab many strains conserved under these names in culture collections. Thanks to the molecular tools now available, we were able to show that the strains stored in the culture collection under the three names belong in fact to seven *bona fide* species, *i.e.*, populations that likely rarely interbreed in the wild, although they can mate with each other in the laboratory. This means that they accumulated throughout evolutionary times many differences or polymorphisms in their genome. Quantification of the differences between the seven species shows that their genomes differ in average by 1-4% at the nucleotide level, a difference similar to the one between the genomes of human and chimpanzee. Moreover, many genes present in one species, may be missing in the others. We identified for example genes encoding a laccase, a histone or a cytochrome P450 as

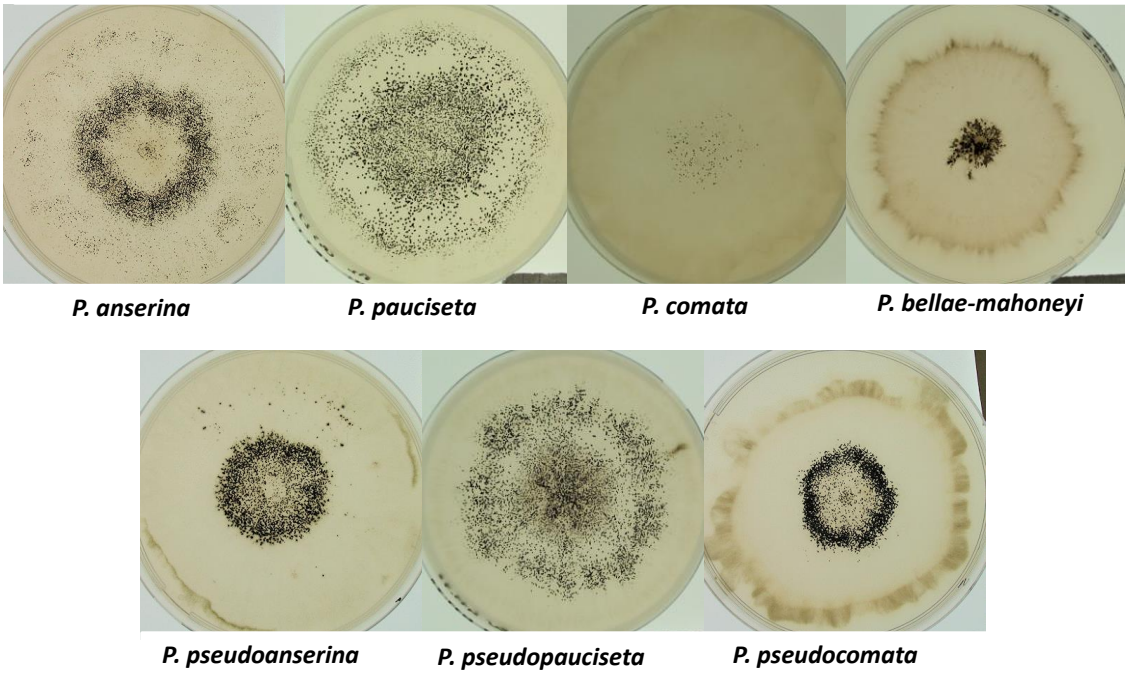


Figure 19 Perithecium production patterns of the species from the *P. anserina* species complex are species-specific. The medium is the minimal M2 medium with 4g/L of potato dextrins. On other media, the strains will exhibit different patterns.

being present in the strain named T and absent in our reference strain named S. Importantly, phenotypic analysis showed that the criteria traditionally used to differentiate *P. comata* from *P. anserina* were not valid. For example, strains belonging to the same species could be labelled under different names in the collections and reciprocally strains having different names could belong to the same species! On the contrary, careful analyses showed that the seven species could be differentiated by the way they produced fruiting bodies on several media differing by the carbon source (figure 19). Some also exhibited typical phenomenon not displayed by the others (Table 3). We were able thus to name these seven species and provided new types for them. We kept the three already used species epithets (*anserina*, *pauciseta* and *comata*) for three species that we formally redefined and proposed four new names (*bellae-mahoneyi*, *pseudoanserina*, *pseudocomata* and *pseudopauciseta*). Of course, we chose to give the name *P. anserina* to the species to which our major working strain belong (strain S or BIG S). Most work on *P. anserina* has been made with this strain or with strain s (small-s), which fortunately also belongs to the *P. anserina* species as newly redefined. We designated as belonging to the redefined *P. comata*, the

Table 3: some features of the species from the *P. anserina* species complex.				
	Hyphal Interference[1]	Crippled Growth[1]	ring of perithecia[1]	Senescence[1]
P. anserina	**efficient**	**yes**	**yes**	**yes**
P. pauciseta	**inefficient**	**no**	**no**	**yes**
P. comata	**inefficient**	**no**	**no**	**yes**
P. bellae-mahoneyi	**inefficient**	**no**	**no**	**yes**
P. pseudoanserina	**inefficient**	**no**	**no**	**yes**
P. pseudocomata	**inefficient**	**no**	**yes**	**yes**
P. pseudopauciseta	**inefficient**	**no**	**no**	**yes**

[1]These phenomena will be described in the chapter "Physiological and molecular analysis: deciphering developmental pathways".

aforementioned strain called T. This strain has previously been used in few molecular studies under this name. It is the only publicly known cultivated isolate for this species. Fortunately, strain T produce smaller ascospores and perithecia, as did the original isolate described by Milovtzova as a new species. We chose *P. pauciseta* for a group of three strains, since this will limit name change in the culture collections. These have not been yet used for genetical or biochemical studies, nor have the strains belonging to the four new species. Nonetheless, the seven species share common features. Their ascospores germinate with the same modalities. Their mycelium grows, differentiates aerial hyphae and

Eukaryota.....*Domain*
Amorphea
Opisthokonta
Holomycota
Eumycota.....Kingdom
Dikarya
Ascomycota.....Phyllum
Saccharomyceta
Pezizomycotina.....subphyllum
Leotiomyceta
Sordariomyceta
Class.....*Sordariomycetes*
Sordariomycetidae
Order.....*Sordariales*
Family .....*Lasiosphaeriaceae* IV
Genus.....*Podospora anserina species complex*
Species.....*Podospora anserina*

Figure 20 Current Identity card of *P. anserina*. This card has been established thanks to molecular phylogenetic analyses. Except for potential modifications in the names of the family and genus, pending a revision of the *Lasiosphaeriaceae*, this identity card should now not change. Prior, *P. anserina* was included in the now defunct *Pyrenomycetes* class, *Sphaeriales* order and *Sordariaceae sensus Lato* family.

accumulates pigment in a similar fashion, even if minor differences between the strains can easily be spotted. They all undergo senescence (Table 3).

P. anserina, as usually known, is thus a species-complex with at least seven members that cannot be distinguished by simple visual inspection. It is likely that several more species belonging to the complex as yet not isolated exist in the wild. The now newly-redefined *P. anserina* is only one of the species of the complex. This book will be focused on this particular one with some references to *P. comata*. Its complete identity card is given in figure 20. To summarize, *P. anserina* is a filamentous fungus from the *Pezizomycotina* subphylum of the *Ascomycota*. As such, it has a lifecycle typical of this group of fungi, including the ability to differentiate a multicellular fruiting body. This fruiting body is a perithecium having a greenish color, typical of the *Sordariales*.

In a turn of fate, as this book was in its final stage of writing, a paper starting to partially revise the phylogeny of *Lasiosphaeriaceae* was published (in august 2019 by Wang et al. in Studies in Mycology) in which the name of *Podospora anserina* was changed into "*Triangularia anserina (Rabenh.) X. Wei Wang & Houbraken"*, and all the species of the complex had accordingly the name of their genus changed to *Triangularia*. A name for the *Lasiosphaeriaceae* Clade IV was also given: *Podosporaceae*. While it is most likely that the name *Podosporaceae* will stick for *Lasiosphaeriaceae* Clade IV, I think it is highly unlikely that the change to *Triangularia* will be adopted. Indeed, although it would be the correct way to name the friendly mold, two reasons militate against its usage. Firstly, researcher working on ageing, prions, sexual development, *etc.*, especially those not working on fungi will not understand the need for a change and will thus not use the new name. This is especially true because several hundreds of papers have already been published on the friendly mold with its *P. anserina* name, and this is not counting the thousands of paper citing studies with this fungus! Changing the name of the fungus will thus only lead to great confusion. Note that very few papers have been published (I am aware of only two) on *Podospora fimiseda* the type species of the genus, apart from the purely taxonomic ones. According to me it would therefore be wise to maintain for all eternity the name of friendly mold as *Podospora anserina.* This can be done only by changing the type species for *Podospora* to *P. anserina*; however this is not an easy task as taxonomist tends to be very very conservative… Note that intense battles other the names of famous fungi (such as *Aspergilli*) have lately been won by changing the International Code of Botanical Nomenclature. Facilitating the change of genus types for fungi such as *Podospora*, whose origin is obscure since the herbarium types for the species although available are not useful would be

appreciated… Ironically, the taxonomic origin of *Podospora fimiseda* is as mysterious as the one of *P. anserina*, if not more!

A second reason for not adopting the name is that it is most likely that, according to the rule of nomenclature, it will change again shortly! Indeed, the genus adopted for the new name is highly diverse. *P. anserina* is in a lineage different from *Triangularia bambusae*, the type species for *Triangularia*. Hence, once additional species are identified of *Podosporaceae* and their phylogeny sorted out, it is most likely that *Triangularia* will be split into many genera! Note that as explained above *P. anserina* has already suffered many battles upon its naming. In the end, it appears that the name *Podospora anserina* has always prevailed…

Therefore, whatever the fate of the new naming to *Triangularia*, I have decided to conserve the name under which the friendly mold is known and that is *Podospora anserina*!!

Podospora anserina in its natural biotopes

Many fungal species have evolved through natural selection life strategies that permit them to use dead plant material as carbon and energy sources. These fungi produce and export outside the cells many enzymes that allow them to degrade plant polymers (like cellulose or lignin). Released nutrients are then transported into the fungal cell by very efficient transport systems. Such nutrition strategy is called saprotrophy and the fungi are said to be saprotrophic, saprophytic or saprobic. *P. anserina* is one such a saprotrophic fungus that has specialized to retrieve its nutrients from materials that have not been completely digested by herbivorous vertebrates, *i.e.*, their dung. About 2000 fungal species are known to inhabit dung including many *Podospora* species. They are called coprophilous, coprophilic or fimicolous.

Coprophilous fungi fructify sequentially in a fashion that recapitulate what we know about fungal evolution. The first ones to be observed are basal fungi such as species from genera *Mucor* or *Pilobolus*, then basal *Ascomycota* from the class *Pezizomycetes* such as species from genera *Ascobolus* and *Saccobolus*. These are followed by species from the class *Sordariomycetes* including those from genera *Sordaria* and *Podospora* that appear just before the final *Basidiomycota* from genera *Coprinopsis*, *Coprinus* or *Cyathus* among others. This succession experiences nonetheless many exceptions and it is not rare for example that fast-growing *Coprinus* or *Coprinopsis* appear early and prevent appearance of other fungi. It is likely that all fungi are inoculated in the dung as spores stuck on the plants ingested by the animals. Spores are triggered to germinate while passing through the digestive track. All the coprophilous fungi likely start thus to grow at about the same time. The observed succession is in fact the complex result of interactions between growth speeds of the mycelia and timing of differentiation of the sporophores. Both are modulated upon the ability of each species to use more or less hard to digest plant remnants and their ability to eliminate the bacterial and fungal competitions.

P. anserina is usually one of the last species to fructify. Although very rapid on synthetic medium or sterile dung (the complete cycle is then completed in one week), when in competition with other microorganisms, *P. anserina* takes more time to fructify (about two to three weeks). Its growth speed of about 7 mm/day is slower for example than that of *Sordaria macrospora* which is of 2-3 cm/day.

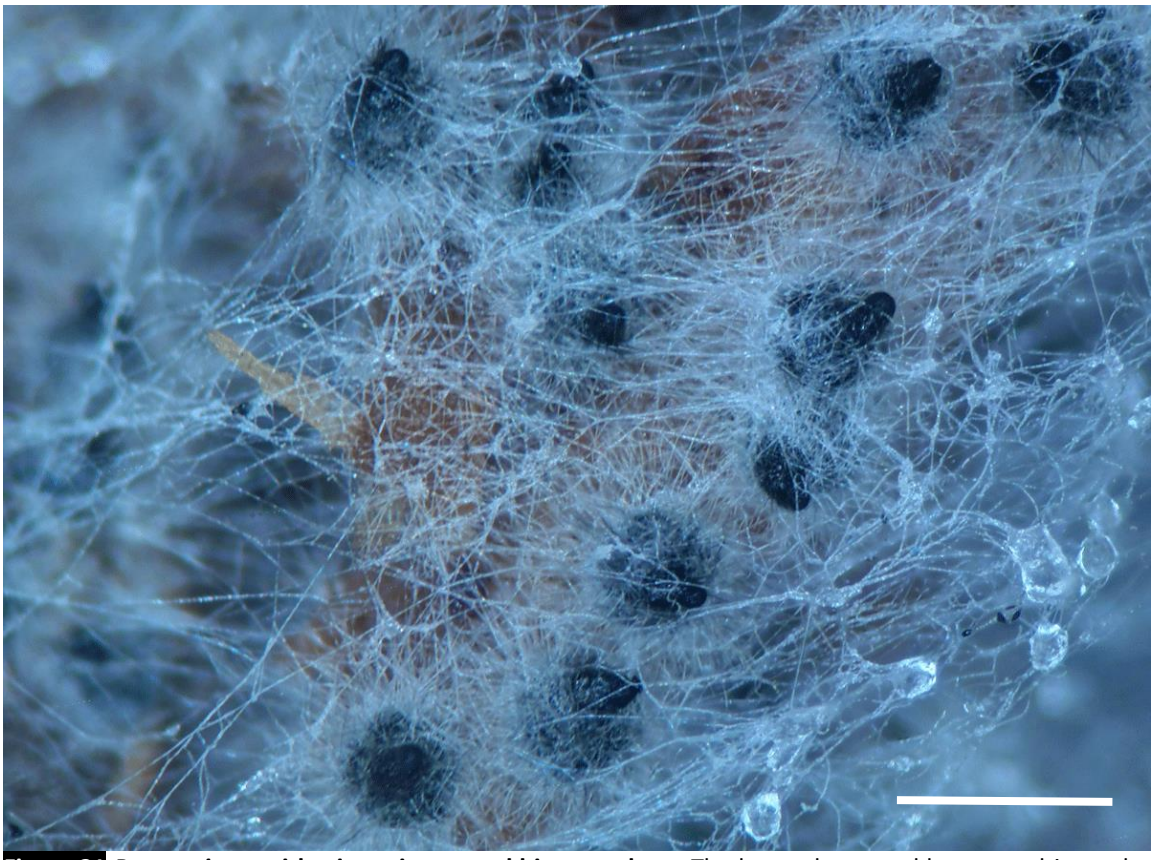


Figure 21 ***P. anserina*** **perithecia on its natural biotope: dung.** The horse dung used here to cultivate the fungus is composed of partially digested plant debris, which can be further broken down thanks to the numerous enzymes encoded in the genome of *P. anserina*. Bar=0.5 mm.

However, the genome of *P. anserina* contains more genes coding for enzymes enabling to cope with lignocellulose and the fungus exhibits hyphal interference towards some fungi, while *S. macrospora* does not. Hyphal interference is a mechanism whereby hyphae are able to kill hyphae from other species upon contacting them. Although the fruiting bodies of the two fungi appear at roughly the same time on dung, to do so *S. macrospora* rely mostly on its fast growth and utilize easy to reach cellulose, while *P. anserina* appears to count on its abilities to extract nutrient from harder to digest plant debris and to kill competition.

Investigation of *P. anserina* in the wild has presently been made only by visual determination of the perithecia (figure 21), with isolation in pure cultures and molecular determination only in few cases. Therefore, there is no way to know whether the observed specimens belonged actually to *P. anserina* or

to one of the others from the complex. Inventories of fungi growing on dung have shown that these are frequently found on many kinds of dung from birds and mammals originating from all regions of the world. The exact geographic distribution of *P. anserina* is unknown. We know that the fungus is commonly found in Western Europe during summer, because all strains of *P. anserina* but one hosted in culture collections come from this region. The only exception originates from Ontario in Canada. The strains from culture collections isolated from other regions of the world often belong to the other species of the complex, tentatively suggesting that there is a geographical structuration of the complex. Each species would have evolved to adapt to the faunas/floras present in each region. This would nicely fit with the fact that they seem to utilize carbons sources differently (see previous chapter, figure 19). *P. anserina* would thus be the one adapted to mild climates. However, most *P. anserina* strains were isolated from domestic horse and cow dung and it is possible that it cohabits with other species more adapted to dung from other herbivores including birds like geese or smaller mammals like hares, rabbits or even mice.

In addition to being collected from dung, species from the *P. anserina* complex have also been isolated from a decaying Chinese mat, soil and living plants. Its presence in soil and as a plant endophyte is confirmed by metagenomic data, since its DNA is sequenced along with that of related species when analyzing various plants and soils. At the present time, it is not clear if these alternate ecological niches are part of the normal cycle of the fungus or are occupied accidentally.

Overall, we know little about *P. anserina* in its natural biotopes, unlike for example *Neurospora spp.* for which extensive data regarding strain variations exist. To better understand *P. anserina*, and the other species from the complex, we now need to investigate its population structure thanks to molecular technologies. Extensive analyses of many isolates collected around the world will permit to identify more species and to understand if there is a geographical structuration of the populations related to the particular faunas and floras present in the ecosystems. Another needed line of investigation is the catalogue of all the natural biotope the fungus is able to invade.

Isolation, culture and preservation

In this section, I will describe how to collect, grow and preserve *P. anserina* and the other species of the complex, since they all behave similarly. The recipes for the media are the optimal ones and I will not in this section examine how modifications of the media impact on the fungus. This will be dealt in the appropriate sections regarding the modalities of germination growth and reproduction. The toolkit required to isolate and cultivate the fungus is rather simple. In addition to a 10-40 X binocular microscope, it should include tools to manipulate ascospores and mycelia (figure 22). The fungus can be grown at room temperature, but a temperature-controlled chamber should ensure reproducible result. Ideally, it should have also controlled humidity and light. Indeed, optimal growth conditions are 27°C, 70-80% humidity (to prevent desiccation of the Petri plates) and constant illumination or 12 hours alternation of light and dark (to allow for perithecium production). There is no need for a sterilized chamber and all manipulation can be performed on the bench.

If you wish to recover *P. anserina* strains from nature in order to grow them in the lab, you need to fetch dung from the fields. Horse dung seems rather efficient, but any kind of herbivore dropping

Figure 22 The basic tool kit to work with *P. anserina*. Pen point holders are used to slice explants of mycelium from jellified growth plates. The ones with replaceable nibs are ideal. Mounted needles or "pique-huile" are used to collect fruiting bodies and ascospores. These tools can be sterilized with an alcohol burner.

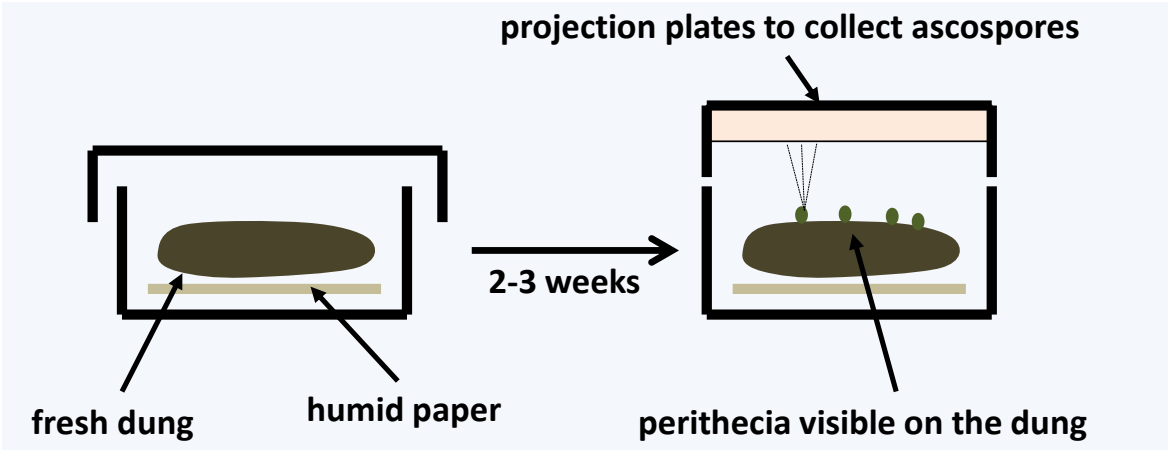


Figure 23 Humid chamber and projection plates are ideal to collect new *P. anserina* strain from the wild.

should do; the fungus has seemingly been first seen on pig and goose dung! Fresh dung is preferable since in old ones it may have already fructified. Incubate the dung in a closed and humid container as to make a humid chamber and let the various fungi grow. Perithecia can be easily spotted on the dung after 10-20 days of incubation and ascospores can be recovered on a projection plate as described in figure 23. Recipe for the projection plate is given in the "projection plate" box. On wild dung, many fungi should grow, some having morphologies quite similar to our friendly mold. I find it easier to recognize the asci of *P. anserina* once expelled on the projection plate than the perithecia on dung; those look quite similar to those of many other species.

Perithecia may be collected with a mounted needle or a "pique-huile" and transported onto a fresh projection plate (see movie n°1). After bursting the perithecium, ascospores may be collected also with a mounted needle and transported onto germination medium. Antibiotics could be added to the germination plates to prevent bacterial contamination. To burst the perithecia, simply squeeze them with a thin tweezer or between two mounted needles or "pique-huiles". Rosettes of asci are liberated. Individual asci can then be gently probed with a mounted needle as to break them apart. Usually the four ascospores stick together thanks to a small rope connecting them. The trick to collect the ascospores is then to break apart this rope. This demands some skill that one usually masters in two or three sessions of ascospore collection (movie n°2). Individual ascospore stick reversibly to the mounted needle and can be deposited at will on fresh media. Note that the needle must be sterile and this is achieved by flaming

Projection plates: Also called “agar covers”, these are used to recover ascospores that are ejected outside the perithecia. Ascospores on these covers can resist for a few weeks at 4°C before dying. Projection plates are made by pouring a thin layer of melted agar (20 g/L) supplemented with NaCl (10 g/L) in a Petri plate. Autoclave for 20 min at 120°C and pour (12 mL for an Ø=8 cm plate) very hot as to make the agar very compact.

the tip. Once flamed, the tip is very sticky and should be re-humidified by cooling it in the jellified medium of the projection plates, otherwise ascospores will stick irreversibly on it. Note that starting directly from the projection plates has three advantages. Firstly *P. anserina* asci are easily recognized, since the four ascospores often stick together until landing on the projection plates. Their morphology is quite distinctive (see next chapter). Secondly, bacterial contamination is less frequent. Finally, breaking apart the rope is somewhat easier, especially if the projection plates were stored at 4°C for a few days.

Once ascospores are recovered, they can be transported onto Germination plates containing G medium. I usually put 12-16 ascospores per plate (figure 24). Germination will proceed overnight at temperature ranging from 18°C to 35°C with nearly 100% efficiency. We routinely use 27°C as it appears to be the optimal growth temperature. One day after collection, the germination thalli are often barely visible to the naked eye, but two days after germination they should have a diameter of over one cm (figure 24). Alternatively, ascospores may be collected on M2 medium. A heat shock is then required to awaken the ascospores (25-30 minutes at 65°C works best). With this procedure up to 90% of the ascospores may germinate. However, lower percentages are often obtained.

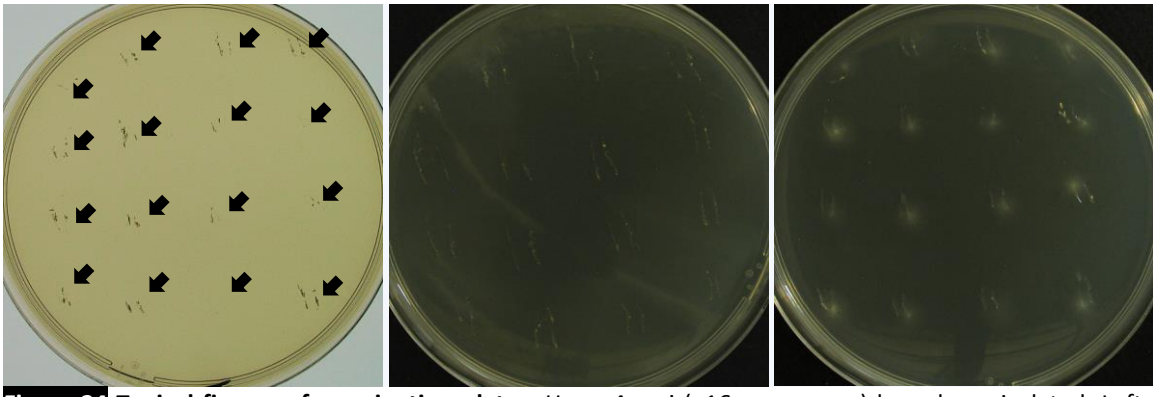


Figure 24 Typical figures of germination plates. Here, 4 asci (=16 ascospores) have been isolated. Left: after ascospore collection, arrows point the locations where the ascospores were placed, middle: one day after coolection, germination thalli are still not visible with the naked eye, right two days after collection.

Germination plates: These plates containing G medium are mainly used for ascospore germination. G medium allows the germination of nearly 100 % of wild-type ascospores. On this medium, the thalli never produce pigment (figure 25). Composition of G medium is ammonium acetate (4.4 g/L or 10 mL from a 440 g/L solution), bactopeptone (15 g/L) and agar (13 g/L). Autoclave (20 min at 120°C) and pour 23 mL per Ø=8 cm plate. Variations in germination efficiency and size of germination thalli are observed depending upon the age and brand of the components used to make G medium, especially water. Fresh bacto-peptone is better; if too old the germination percentage may drop. This can be corrected by adding yeast extract (5 g/L). This product should also be rather fresh as it inhibits growth when too old.

Like all the filamentous fungi, *P. anserina* will produce a mycelium on its growth media. Germination thalli are thus typical mycelia. It is possible to cut them into small pieces (to do so we use a pen point holder whose nib has been sterilized with an alcohol burner). Each piece should regenerate a new thallus when inoculated onto fresh growth medium. At the macroscopic level, the mycelium grows as a disk. However, it can display many different aspects, depending upon the growth medium (figure 25). Some media permit the differentiation of numerous aerial hyphae and the mycelium looks velvety. Others prevent the growth of such hyphae and the mycelium is smooth. Color also may vary. Most of the time it is greenish but it may also be brownish or pigments may be absent.

We routinely use the M2 Medium at 27°C in the presence of light to grow our friendly mold. Crosses, stocks and most phenotypic tests are made on it. It permits the mycelium to grow at about 7mm per day. In stationary phase (figure 25), the mycelium develops aerial hyphae, presents a greenish pigmentation and, if *mat+/mat-* heterokaryotic (see chapter “The sexual cycle and genetical analysis”), it should undergo sexual reproduction in a week with four days between fertilization and ejection of the ascospores out of the perithecium.

Another frequently used medium is Corn Meal medium (that we often call MR). It is a semi-defined medium that we use less and less because M2 is easier to prepare and often satisfy most needs. On this medium, the mycelium develops no or few aerial hyphae (figure 25) and pigmentation is variable, but is often more pronounced that on M2. Fertility is lower than on M2 and the sexual cycle takes longer as it is completed in about ten days. An advantage of this medium is that is contains almost all amino acids, bases, vitamins, *etc.* Hence, most auxotrophic mutants grow on this medium. The mycelium will also not penetrate cellophane and can thus be scraped more easily than when grown on M2. Cellophane

Figure 25 ***P. anserina*** **mycelium morphology on three commonly-used media.** The strains inoculated on the plate are homokaryons that do not differentiate fruiting bodies.

is used to collect biomass directly from Petri plates (see the protocols to extract macromolecules). To this end, sterilized cellophane cut to fit the plate is overlaid onto the medium. Explants are inoculated on it and permitted to grow. On M2, the mycelium will penetrate cellophane after two days of incubation and

M2 medium. M2 medium has the following composition: KH_2PO_4 0.25 g/L, K_2HPO_4 0.3 g/L, $MgSO_4$ 0.25 g/L (if $MgSO_4$ 7 H_2O), dextrin dissolved in warm water 4-6 g/L (this depends on the type of dextrin, we find that potato dextrin at 4g/L works fine, while blond dextrin needs to be added at 5.5 g/L), urea 0.5 g/L, thiamine 0.05 mg/L, biotin 0.05 µg/L and oligo-elements (citric acid 5 mg/L, $ZnSO_4$ 5 mg/L, $CuSO_4$ 0,25 mg/L, $MnSO_4$ 50 µg/L, boric acid (H_3 BO_3) 50 µg/L, sodium molybdate (Na_2 Mo) 50 µg/L, iron alum (Fe $(NH_4)_2$ $(SO_4)^2$) 1 mg/L). Adjust to pH=7 with a KH_2PO_4 solution and autoclave for 20 minutes at 120°C.

We find it easier to have stock solutions and to prepare the medium using these stocks. For 1 L: 5 mL of 50 g/L KH_2PO_4, 5 mL of 60 g/L K_2HPO_4, 5 mL of 50 g/L $MgSO_4$ - 7 H_2O, 5 mL of 100 g/L urea, 0.5 mL of 100 mg/L biotin, 0.5 mL of 100 mg/L thiamine, 1 mL oligo-elements stock solution prepared as follows for 500 mL: 5 g citric acid - 1 H_2O, 5 g Zn SO_4 - 7 H2O, 1 g Fe $(NH_4)_2$ (SO_4)2 - 6 H_2O, 250 mg $CuSO_4$ - 5 H_2O, 50 mg $MnSO_4$ - 1 H2O, 50 mg anhydrous H_3BO_3, 50 mg Na_2MoO_4 - 2 H_2O and one drop of chloroform to avoid precipitation of the chemicals. Dextrin is added after dissolving it in hot water.

For Petri plates, agar is added at 10 g/L. Pour 28 ml per Ø=8 cm Petri plate. For race tubes, double the amount of agar (*i.e.*, add 20 g/L). Race tubes are used to measure longevity of the fungus. Designs of race tubes will be explained in the section dealing with Senescence.

will thus be difficult to scrape as early as three days after inoculation, while penetration will not occur for several days on MR. To collect the mycelium, simply scrape with a sterilized spatula. An additional bonus of the MR medium is that longevity is much higher and strains seldom undergo senescence.

MR (Corn Meal) Medium: MR is produced by dissolving in H_2O 25 g/L of corn flour and 25 g/L of corn cream. Mix and incubate overnight at 58°C (no more and no less). Filter the mix twice with filter papers, then adjust with H_2O again to one liter. Add agar at 12 g/L. Autoclave for 20 minutes at 120°C and pour 28 mL per Ø=8 cm Petri plate.

Other used media are the RG (or M1) medium, an hyperosmotic medium mainly used for protoplasts regeneration (after mutagenesis or transformation), the "Sorbose" medium only used to obtain male gametes (spermatia/microconidia) in high amount and the "Fiole de Roux" medium that is used to produce high quantities of mycelium, especially for protoplast preparation.

RG medium: Same as M2 + 205 g/L of saccharose. Autoclave for 20 minutes at 120°C. Pour 28 mL per Ø=8 cm Petri plate.

Sorbose medium: Yeast Extract 2 g/L, sorbose 2 g/L, glucose 1 g/L, agar 12 g/L. Autoclave for 20 minutes at 120°C. Pour in tilted assay tubes. Utilization is as follows: inoculate numerous explants per tube and incubate for at least four days. The longer the more spermatia will be recovered. Add 2 ml of sterile water, vortex and filter the suspension with sintered glass filter n°4.

"Fiole de Roux" medium: same as M2 + yeast extract 5 g/L. Autoclave for 20 minutes at 120°C. The medium is poured into Roux culture bottles as to obtain about 1 cm at the bottom when laid. It is advisable to add antibiotics in this medium as it is frequently contaminated with bacteria.

Note that dextrin is only one of the food sources that the fungus will eat. Many carbon sources will do. The base is the M0 medium, which is the same as M2, but without dextrin. M3 is M0 + 5.5 g/L of glucose. M4 is M0 + 5.5 g/L of avicel. These can be poured into the Petri plates as the M2 or MR media.

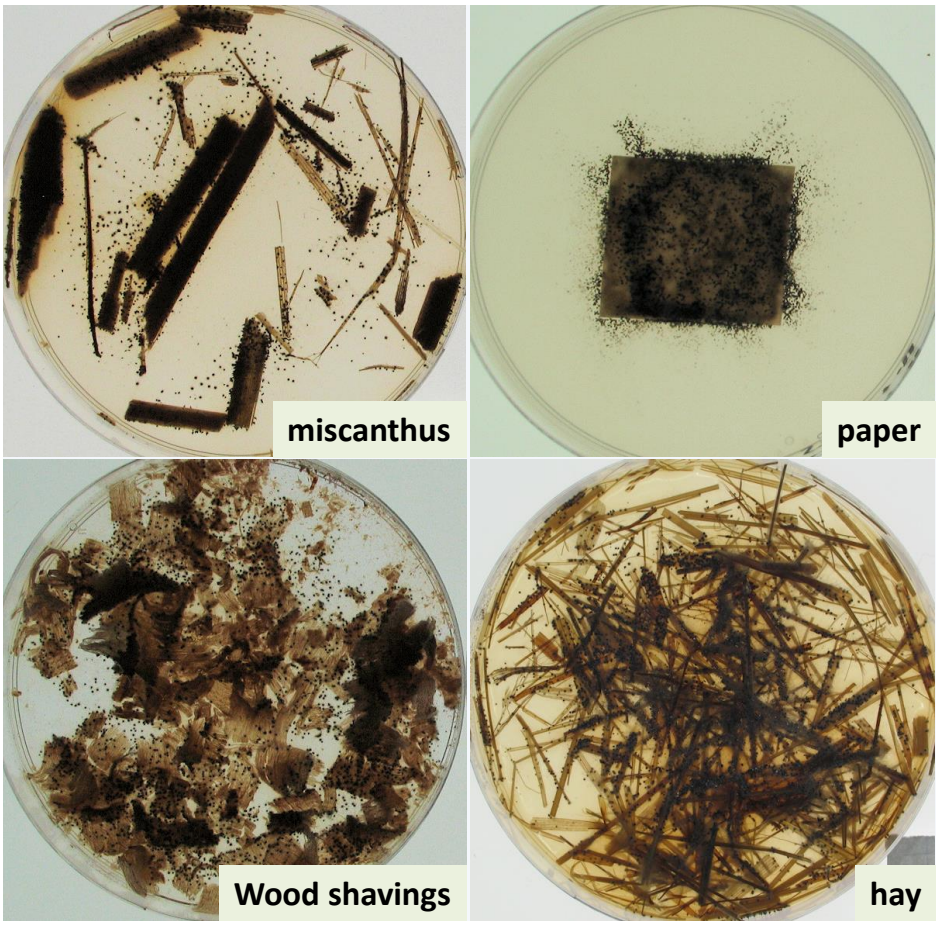


Figure 26 ***P. anserina*** **grows and reproduces on complex carbon sources.** The fructifications are the little black dots.

Solid carbon sources, such as hay, miscanthus, wood shavings, paper… can also be used (figure 26). The sterilized food source is added in the plate (usually we use 0.5 g per plate) and 12 mL of sterilized M0 (with or without 12 g/L of agar depending on the need) is poured on it. Strains reluctant to fructify on M2 or M4 may do so on medium with more complex food sources. Hay seems to be particularly handy for this, because many strains obtained from culture collections and that have accumulated mutations, usually yield perithecia on this medium.

In all these media, it is possible to add various metabolites or antibiotics to select for genetically-transformed strains or to allow auxotrophic strain to grow. The concentration for some of them is given in Table 4.

Table 4: supplements to be added to growth media	
Uridine : 100 µg/mL	**Hygromycin B: 75 µg/mL**
Leucine : 50 µg/mL	**Phleomycin: 10 µg/mL**
Lysine : 100 µg/mL	**Nourseothricin: 40 µg/mL**
Tryptophane : 30 µg/mL	**Geneticin: 500 µg/mL**
Methionine: 30 µg/mL	**Tricyclazol: 1 µg/mL**

Tricyclazol is used to remove melanin; ascospore without melanin will germinate on all media, but are rather fragile.

As a final note, it is worth stating that *P. anserina* will complete its whole cycle on sterilized horse dung: ascospores will readily germinate on it, mycelium will grow efficiently and fruiting body will be obtained in 7/8 days. However, we have observed some variations with various dung batches; some will permit abundant growth and reproduction, while other will only allow for scarce growth and few perithecia.

Strains preservation

Long term conservation of *P. anserina* presents no problem. Culture on M2 plates can be kept at 4°C for about two years. To do this, put several explants of the strain to be conserved on a M2 plate. Incubate until the plate is covered with mycelium (if not, contamination by other fungi may occur more frequently). Conserve the stock at 4°C with a parafilm seal. A temperature of no more of 4°C is important, because otherwise residual growth of the fungus will occur and "*incolore*" mutations will appear at high frequency. These mutations trigger a proliferation of nuclei that carry them to the detriment of wild-type nuclei. Incolore nuclei thus rapidly invade the thalli that become female sterile, lack pigment and produce many spermatia/conidia. For extended conservation, we use cryotubes at -70 to -80°C. To this end, put several explants on a M2 plate. After 2-3 days of growth, take numerous large explants at the growing edge. Store them in a tube containing 1 mL liquid RG (i.e. RG without agar). Place directly the tubes at -80°C. These tubes can be frozen and defrosted numerous times without notable effect on explants regeneration. The strains can be conserved in this way for several years. In my lab, some strains are frozen for nearly 20 years and the explants still regenerate without any problem. Note that some mutant strains may not be stocked as well…

Methods for macromolecules extraction and genetic transformation

Below are described methods for molecular analyses of the fungus that work well. This list is not exhaustive and many variants for each protocol exist. Note that many of these methods can be used for other species of filamentous fungi. The fungal biomass may conveniently be obtained in two different ways: liquid cultures or Petri plate cultures. For the liquid cultures, shaken Erlenmeyer flasks may be used, especially if aeration is needed. I find that 1 liter Roux flask in which 100 mL of medium is added may be preferable because the flasks can be stacked and shaking is not necessary. Inoculation is made with mycelium fragments obtained with a Fastprep or similar instrument. Calibration of the instrument is required as too much shaking will result in mycelium death... For the Petri plate cultures, we recommend to overlay the medium with a cellophane sheet. The mycelium is inoculated as for the liquid cultures or with mycelium plugs. If the plugs are small, it is not necessary to subsequently remove them. The mycelium will grow on the cellophane and can then be easily scraped with a spatula. However, be aware that the fungus may penetrate the cellophane if incubation is too long (see previous chapter). We usually used liquid cultures when large amount of biomass is needed and Petri plates when small amounts are required.

DNA Extraction

Depending on the amount and quality of the DNA necessary two different methods may be used: large scale prep or miniprep. The large scale prep will yield large amounts of high quality DNA that can be used for genomic bank constructions (including cosmid banks), sequencing with PacBio or PCR amplification of large DNA regions (> 3 kb). A few samples may be processed in parallel. Miniprep yield is lower and DNA has a lower quality than large scale prep DNA. This DNA does not store as well as the one from large scale prep. It can be used for routine DNA amplification of small DNA fragment (<3 kb), Southern blot analysis or sequencing by illumina. Up to 24 samples may be processed in parallel, although I recommend to

process by batches of 12. Note that a last "instant" method may be used for PCR amplification of small DNA fragment (< 300 bp). It requires minimum manipulation and many samples can be processed in parallel. However, DNA cannot be stored. This last method is used mostly for microsatellite analyses on many samples, as for example required in some mapping analyses.

For Large scale prep extraction:

- cultivate the mycelium in Roux flasks in M2 supplemented with 10g/l of Difco yeast extract. Filter with sterile gauze to recover the mycelium and weight it
- freeze in liquid nitrogen. The mycelium can then be kept at – 20°C or – 70°C for extended period
- grind the mycelium with a mortar
- for 2 g of mycelium, add 10 ml of ice-cold TES/Sarkosyl (Tris 12.5 mM, EDTA, 12.5 mM, NaCl, 25 mM pH=8 + Sarkosyl 2.5%) made at the last minute from stocks of Sarkosyl 5% and TES 4x
- incubate for 1h30 at 4°C, mix frequently
- centrifuge for 10 min at 6000 rpm, 4°C
- dialyse supernatant against TES 1x at 4°C overnight
- do alpha-amylase treatment for 2 hours at 20°C (500 µl added from a solution at 2.5 mg/ml in NaCl 3.5M and kept at -20°C)
- do proteinase K treatment for 2 hours at 20°C (50 µl added from a solution at 20 mg/ml and kept at -20°C)
- add 2 vol ethanol 100° and 1/10 vol sodium acetate 3M pH=6
- centrifuge for 5 min at 8000 rpm
- recover in sterile water to make a cesium centrifugation (for a 65VTI rotor, add 4ml sterile water, 4.6 g of cesium chloride and 20 ml of DAPI 1mg/ml, centrifuge for 12h at 45000 rpm). This method allows the separation of nuclear (lower band) and mitochondrial (upper band) DNA.

→ Yield of large scale prep is around 1 mg DNA/Roux flask

For miniprep

- inoculate a M2 Petri plate containing a sheet of sterile cellophane. Let grow for 2-3 days
- recover the mycelium with a spatula and put it into a 2 ml eppendorf tube containing 600 µl of TNE/SDS

(Tris 10 mM, EDTA 1 mM, NaCl 100 mM + SDS 2%) to be made from stocks of SDS 10% and TNE 2X
- To break open the mycelium, do 3 cycles of freeze/thaw in liquide nitrogen /water bath at 70°C; vortex between each cycle. Alternatively, if a "Fastprep" or a similar instrument is available, the mycelium may be broken with small glass beads (add ~50 µL of glass beads with Ø= 250-500 µm in the Eppendorf tube). Speed will of course depend upon the used apparatus and must be calibrated beforehand.
- add one volume of phenol pH=8
- centrifuge for 5 min at 4°C 13000 rpm and retrieve the supernatant
- repeat with phenol + chloroform and with only chloroform
- precipitate the supernatant by adding 2 volumes ethanol 100° and 1/10 vol sodium acetate 3M pH=6
- rinse with ethanol 70°, dry and suspend in 40 ml of sterile water

→ Yield of miniprep is a few µg DNA/plate

For Instant extract
- collect half of a 2 cm thallus grown 48 hours on M2.
- add 20 µL of Ø= 250-500 µm glass beads and 20 µL of freshly-made NaOH 0.5 N
- break open with in a calibrated Fastprep
- centrifuge briefly to precipitate the mycelium + beads
- incubate in boiling water for 45 sec – 1 min
- Neutralize with 100 µL of 1:4 Tris 1 M pH= 8.0: TE pH=8.0

→ PCR amplification is done on 1 µL. DNA is very dirty and does not keep more than a few days.

RNA Extraction

Owing to its fragility, RNA extraction are more difficult than DNA ones. Kits dedicated to the extraction of plant RNA usually work well (such as the RNeasy kits from Qiagen), the key point being to break open the mycelium well enough to recover large amounts of nucleic acids. To do so, it is necessary to ground in a Mikro-Dismembrator (Sartorius, Goettingen, Germany) or similar apparatus for 1 min at 2600 rpm in

vessels containing 9 mm chromium steel grinding balls frozen in liquid nitrogen. Note that apparatuses with lower grounding strength will give low yields of RNA. For those that prefer using their own devices, here is a **"hot phenol" extraction** that works well:

- recover the mycelium (from Roux flasks for large scale preps or M2 plates + cellophane for small scale preps)
- freeze in liquid nitrogen
- suspend in 1 or 2 vol of hot phenol made by incubating at 70°C a mix of 1 vol phenol pH=7.5 and 1 vol of tpRNA (NaCl 100 mM, Tris 10 mM pH=7,5, EDTA 1 mM, SDS 0.1%, Sarkosyl 2%), the mix must be homogenous
- incubate at 70°C for 5 min
- centrifuge for 5 min at 14 000 rpm for small scale preps and 8 000 rpm for large scale preps
- recover the supernatant in a new tube
- repeat by adding phenol + chloroform and then only chloroform
- add 2 vol. of LiCl 6 M and let precipitate overnight at -20°C
- centrifuge for 5 min at 14 000 rpm for small scale preps and 8 000 rpm for large scale preps

→ Yield is low (~50 µg/plate). However, the RNA is very clean and can be used for all usage (northern, cDNA, RT-PCR ...)

Protein Extraction

Depending on the intended uses, there are two methods to recover proteins. The first one is intended for Western blotting analyses and the recovered proteins are denatured. The second one is for crude extracts, to measure enzyme activity for example.

Extraction of denatured proteins for Western blotting

- recover the mycelium from one M2 Petri plate overlaid with cellophane in a 2 mL Eppendorf tube

- add 50 µL of Ø= 250-500 µm glass beads and 50-200µL of lysing buffer (Tris-HCl pH=7.5 20 mM, NaCl 100 mM, EDTA 1 mM, Triton X100 : 0.05%)

-incubate on ice, while processing all samples

The following steps must be made very quickly:

- break open with in a calibrated Fastprep for 40 sec
- add 0.25 vol. of Laemmli charge buffer (Tris pH=6.8 0,4M, 1% β-mercaptoethanol or DTT 50 mM, 1% SDS, 30% Glycerol, bromophenol blue)
- incubate 5 min. at 100°C
- centrifuge 5 min. at max speed in a microcentrifuge
- collect supernatant in a new tube and store at -70°C

→ Use 20 µL per lane for Western blot analysis. Depending on the strain volume should be optimized.

Crude extract for enzyme assays

- recover the mycelium from one M2 Petri plate overlaid with cellophane in a 2 mL eppendorf tube
- add 50 µL of Ø= 250-500 µm glass beads and 50-200µL of lysing buffer (Tris-HCl pH=7.5 20 mM, NaCl 100 mM, EDTA 1 mM, Triton X100 : 0.05%

-incubate on ice, while processing all samples

The following steps must be made very quickly:

- break open with in a calibrated Fastprep for 40 sec
- centrifuge 2 min. at max speed in a microcentrifuge at 4°C
- collect supernatant on ice in a new tube and store at -70°C

→ Protein amounts should be assessed before assays are performed.

Protoplasts preparation

Protoplasts are mostly used for genetic transformation. They however may also be used in mutagenesis

experiments (see chapter "The sexual cycle and genetical analysis") or to breakdown heterokaryons into homokaryons. They are prepared according to the following procedure. All steps are performed in sterile conditions.

- Roux flasks are inoculated with mycelia fragmented with a Fastprep or similar instrument.
- Cultures are grown for 36 h at 27° C in the dark in M2 medium supplemented with 2.5 mg/ml yeast extract ("Fiole de Roux" medium).
- Mycelium is harvested on cheesecloth and washed with TPS1 buffer (0.6 M saccharose, 5 mM Na2HPO4, 45 mM KH2PO4).
- Weight the mycelium. For X g of wet mycelium, add X ml of TPS1 containing 40 mg/ml of Glucanex (Novo Nordisk Ferment AG, glucanex amount may vary upon the efficiency of the batch) and digested for 3 to 4 h at 37° C.
- The protoplasts are separated from mycelial debris by filtration through cheesecloth.
- They are concentrated by 10 min centrifugation at 3200 rpm, washed twice with TPS1 and once with TPC buffer (0.6M saccharose, 10 mM CaCl2, 10 mM Tris, pH= 7.5).
- The final pellet is resuspended in TPC buffer and protoplasts concentration is determined by counting under microscope with a hemocytometer. Protoplasts can be transformed immediately or stored at - 70° C. They can be regenerated in liquid RG medium or on RG plates.

Genetic transformation

- Before transformation, the protoplasts are subjected to a 5 min heat shock at 48° C and transferred 30 secondes on ice and then 5 minutes at room temperature.
- The DNA is added (5 µg of DNA for 0.2 ml of protoplasts at a 10^8/ml concentration) and protoplasts are incubated for 10-15 min at room temperature.
- Two ml of a PEG solution (60% polyethylene glycol 4000, 10 mM CaCl2, 10 mM Tris pH 7.5) are added and carefully mixed.
- After a 15 min incubation, The protoplasts are centrifuged 10 min at 3200 rpm and then suspended in 5 mL liquid RG and incubated overnight at 27°C.

- The culture is centrifuged 10 min at 3200 rpm and suspended in 500 µL of liquid RG; 100µl aliquots are spread onto M2 selection plates.

Routinely 10 to 50 transformants are obtained per µg of plasmid DNA. Plasmids carrying different selective markers are available for transforming *P. anserina* protoplasts. The *Leu1* or *Ura5* wild-

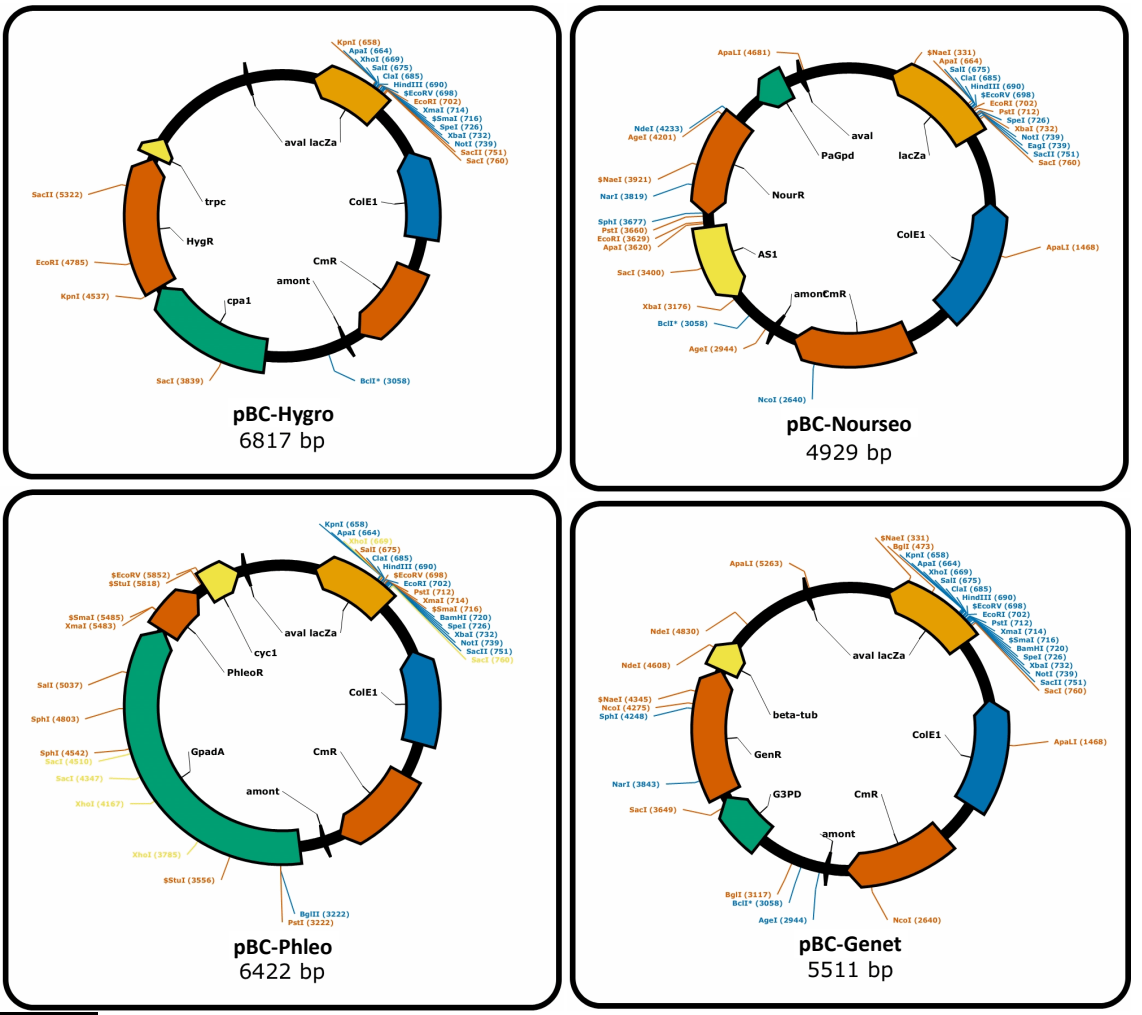


Figure 27 Plasmids routinely used to transform *P. anserina*. The four plasmids derive from pBluescript pBC-SK+ from Stratagene carrying the chloramphenicol resistance marker. Resistance markers for *P. anserina* were inserted at the unique *Xmn1* site located outside the polylinker. The SK+ polylinker is thus intact allowing for the blue/white selection with the α fragment of the lacz gene, for the production of single-stranded DNA with the f1 origin, as well as for RNA production with the T3 and T7 promoters. Enzymes cutting once are indicated in blue. The position of the amont and aval primers used for deletion cassette is indicated by the black triangles.

type genes restore growth on minimal medium when introduced into the *leu1-1* and *ura5-6* mutants auxotrophic for leucine or uridine, respectively. Genes allowing selection of transformants resistant to hygromycin B (75-100 µg/mL), phleomycin (5-10 µg/mL), geneticin (250-500 µg/mL) and nourseothricin (40 µg/mL) are also available. These have been placed into the pBC-Hygro, pBC-Phleo, pBC-Genet and pBC-Nourso plasmids to allow convenient cloning of DNA fragments (figure 27).

Note that, while nuclear transformation is easy, introduction of DNA into the mitochondria has never been successfully achieved, despite several attempts made by biolistic as described in *Saccharomyces cerevisiae*.

Gene deletion, single nucleotide change and at-will modification of the genome

Gene deletion is also fairly straightforward in *P. anserina*. The most convenient way is likely the split cassette method (figure 28). This method starts with two rounds of PCR to construct a two-part deletion cassette. To amplify the selection marker, regions allowing to reproducibly amplify all markers from the pBC vectors were identified (figure 27: amont and aval, Table 5). They can be used to make the fusion primers required to link the flanking regions and resistance markers in the split marker method (the red regions of primers B, C, E and F of figure 28). Noteworthy, they permit to construct deletion cassettes with the four markers using the same set of primers, a feature particularly handy, if one needs the deletion with different markers to construct multiple mutants or combine the deletion with GFP constructs. Once created, the two-part deletion cassette is transformed into *P. anserina*. Inside the fungus, the DNA usually integrates the nuclear genome mostly thanks to the non-homologous end joining pathway. Indeed, only DNA fragments contained in cosmids (hence with a size of about 35 kb) integrate with a frequency of about 80% with the homologous recombination pathway. Fragments even as large as 20 kb integrate with a frequency of 95-99% with the non-homologous pathways. To circumvent this problem, it is advised to use recipients with deletions in the *mus51* and *mus52* genes coding for the Ku70 and Ku80 subunits of the protein complex performing the non-homologous end joining, respectively.

Table 5: amont and aval regions for resistance marker amplification

amont	**5'-CTATTTAACGACCCTGCCCTGAACCG-3'**
aval	**5'-CTTACCGCTGTTGAGATCCAGTTCGATG-3'**

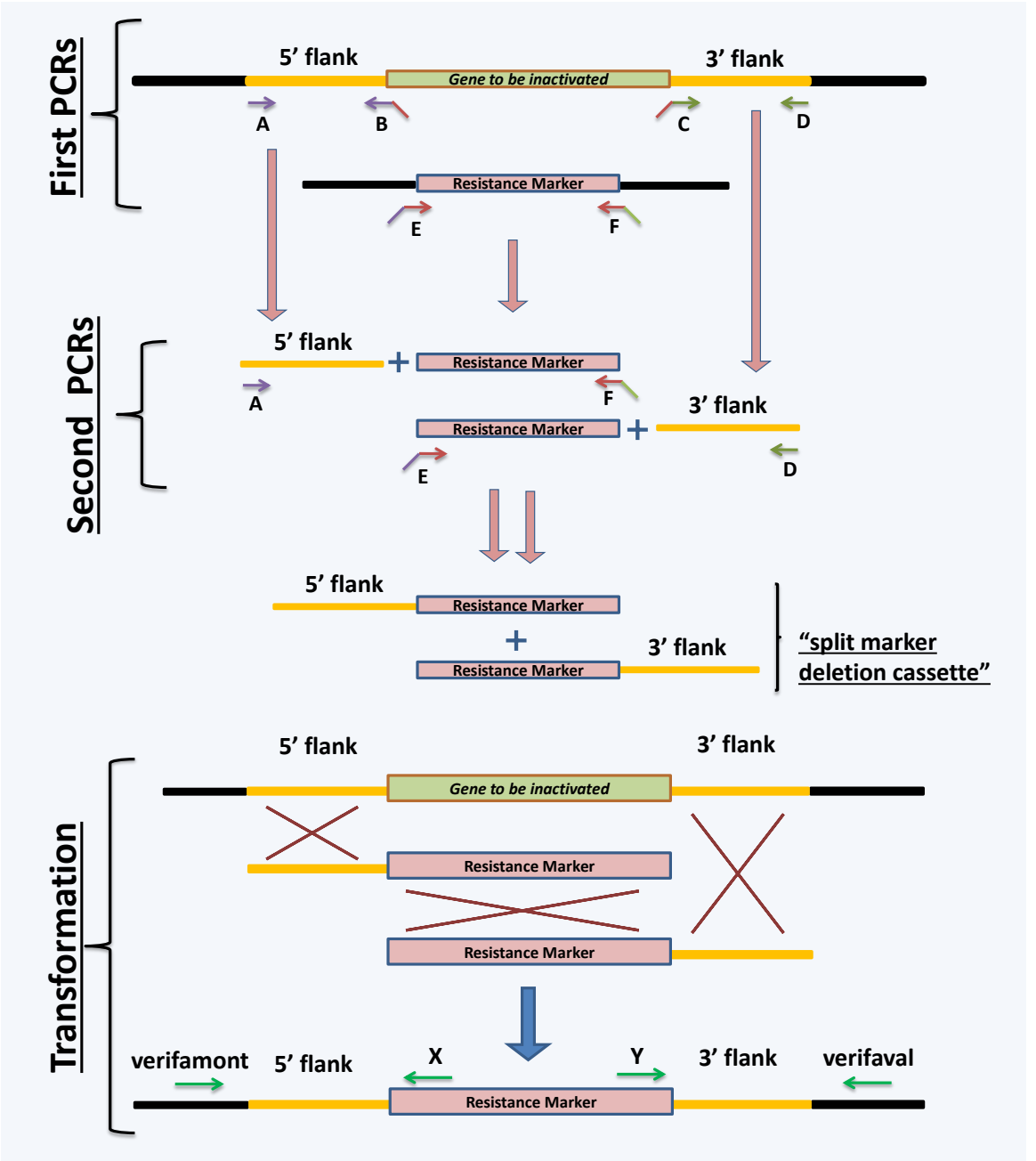


Figure 28 The split marker method for gene deletion. This method is based on two successive rounds of PCRs to construct a two-part deletion cassette, followed by its transformation into *P. anserina*. Three crossing-overs result in the replacement of the gene by the resistance marker. Utilization of recipients deleted for the *mus51* or *mus52* genes coding for the Ku70 and Ku80 subunits that function in the non-homologous end joining of DNA breaks results in a high proportion of *bona fide* replacements.

Deletions for *mus51* and *mus52* are available with all four resistance markers, allowing deletion of any gene with either one of the resistance markers. The *mus51* gene is located on chromosome 6 (CDS number *Pa_5_6180*) and *mus52* on chromosome 7 (CDS number *Pa_7_9250*). Choose carefully which strain to use for deletion of genes on these two chromosomes! After deletion it is strongly recommended to verify the deletion by PCR and Southern blotting analysis, because non-homologous and faulty integration still occurs in the *Δmus51/Δmus52* strains. A good practice is to first select a few potential good candidates by amplifying with PCR the expected function fragments (with the primer pairs "verifamont + X" and "verifaval + Y"). These are crossed with the wild type to clean the strain, *i.e.*, to segregate out the *Δmus51/Δmus52* mutation and any other potential mutations resulting from the transformation procedure. Southern blotting with appropriate probe can then be performed on the F1 progeny.

Interestingly, it is also possible to change a single nucleotide or modify the nuclear genome at

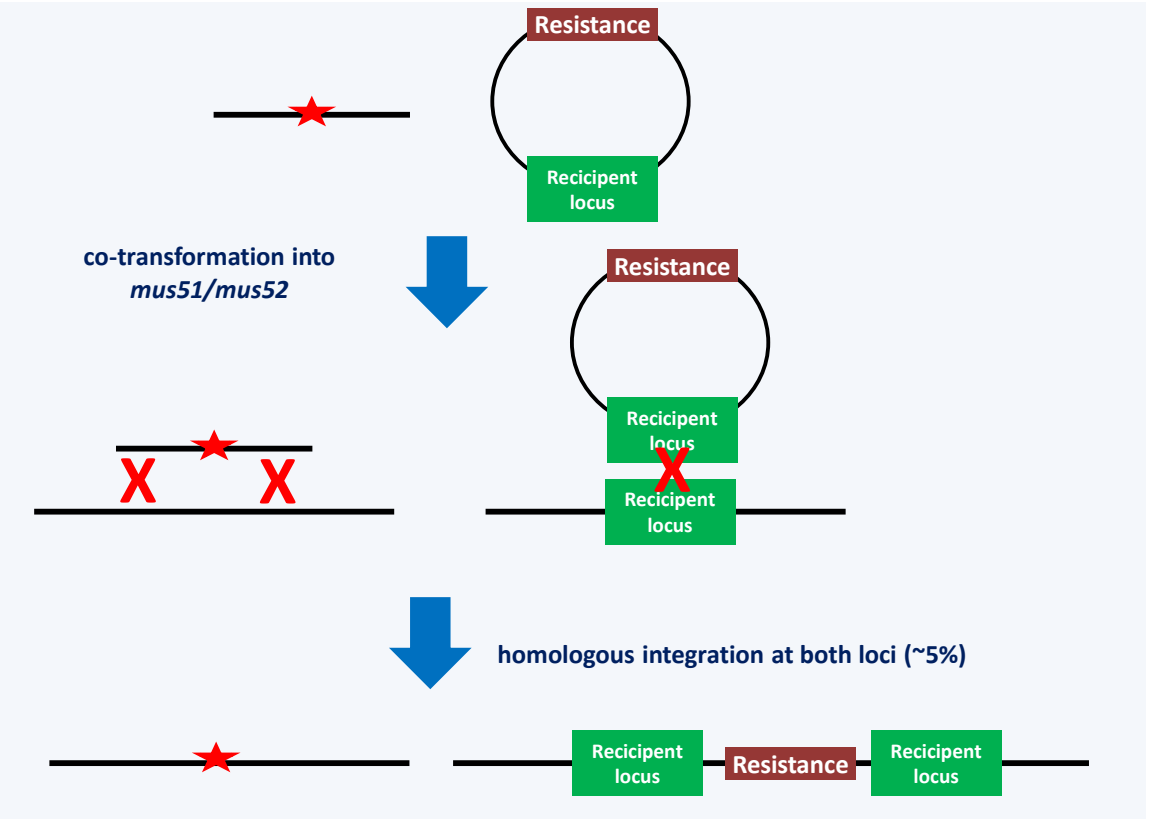


Figure 29 At will modification of the *P. anserina* genome. See text for explanation.

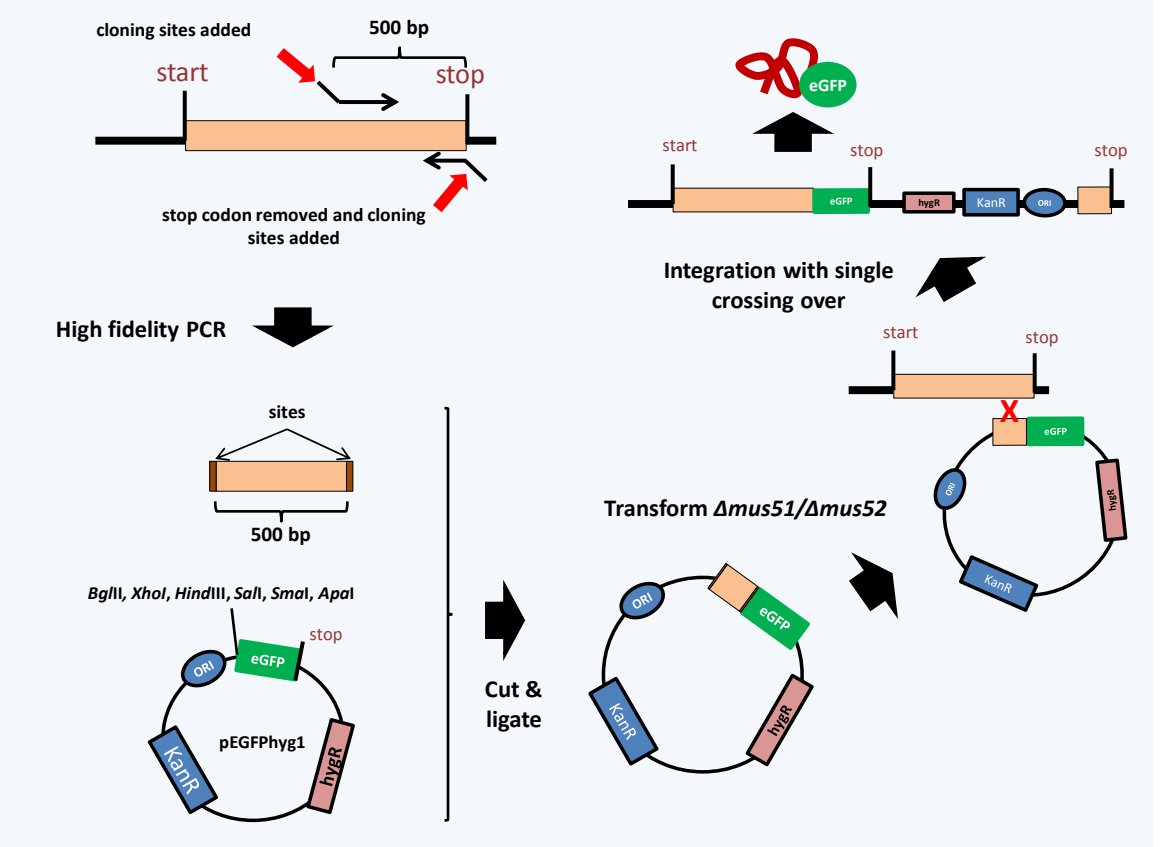


Figure 30 Scheme to tag with fluorescent proteins. A 500 bp DNA fragment from the 3'-end of the gene and lacking the stop codon is amplified by PCR with a high fidelity polymerase and cloned into a plasmid containing the CDS of a fluorescent protein, eGFP or mCherry (here the pEGFPhyg1 vector carrying also an hygromycin B resistance marker). Note that pmCherry-Hyg with the same multi-cloning site and resistance marker carrying the mCherry CDS is also available. Integration after a single crossing-over following transformation in a *Δmus51/Δmus52* strain results in the expression of the tagged protein from the native site.

will by co-transforming two DNA fragments into the *Δmus51/Δmus52* strains (figure 29). Indeed, one circular fragment carrying the selection marker allow to select for potential candidates and in a subset of them the linear fragment carrying the desire change integrates by a double crossing-over and changes the sequence as desired. Usually, integration takes place in 5-10% of the transformants, implying that it is better to have a selection scheme for the correct replacement. A genetic cross with the wild type permits then to segregate out the *Δmus51/Δmus52* mutation as well as the integrated copy of the circular molecule. This method has for example been used to construct PM154, the self-fertile homokaryotic

strain carrying in tandem the two mating type idiomorphs (see chapter "The sexual cycle and genetical analysis"). The final strain differs from the wild type only by the desired modification!

Other genome modifications frequently made are those required for gene overexpression and protein tagging with fluorescent proteins. For overexpression, it is possible to use the constitutive and strong promoters of the *gpd* and *AS4* genes. The *gpd* gene encodes the glyceraldehyde 3-phosphate dehydrogenase, a highly expressed glycolysis enzyme. The *AS4* gene encodes the cytosolic translation elongation factor eEF1A (also known as EF-1α). A region of 300-400 bp upstream of the translation start site from both genes is sufficient to drive high expression. Note that if one wants to express genes from other fungi (for complementation purposes for example), promoters from related *Sordariomycetes* fungi usually work well in *P. anserina*. On the contrary, promoters from the distantly related *Eurotiomycetes* often do not work well. For protein tagging, eGFP and mCherry works fine in *P. anserina* (see figure 34 of the next chapter). Tagging is often made following the strategy depicted in figure 30 that results in the expression of the fusion protein from the native promoter at the endogenous locus. In the wild type, integration occurs randomly in the genome, usually at a single location. However, integration is often

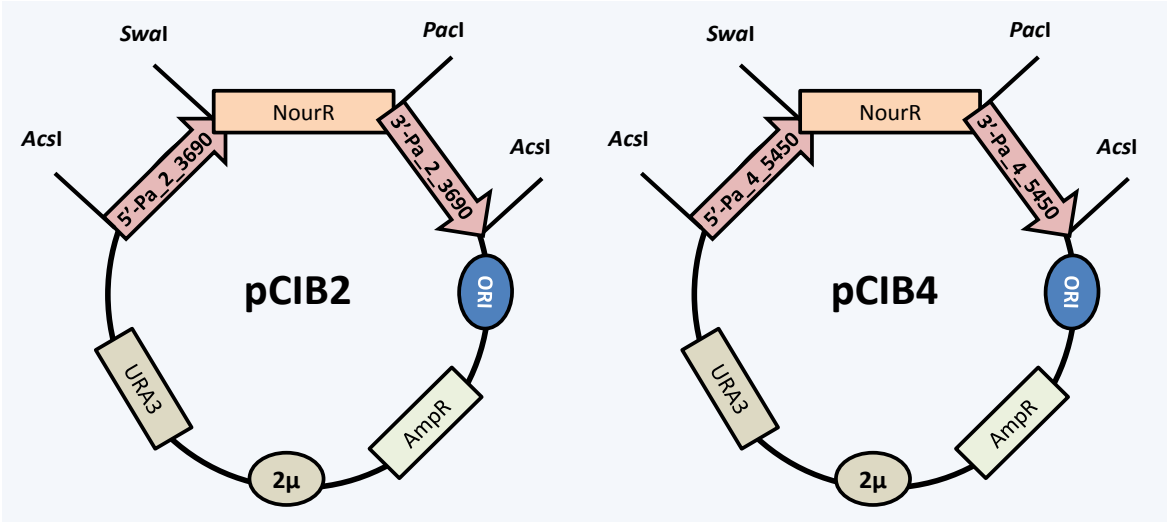


Figure 31 pCIB2 and pCIB4 plasmids for targeted integration in the genome of *P. anserina*. The plasmids carry the nourseothricine resistance marker flanked with the 5' and 3' regions of the *Pa_2_3690* (pCIB2) or *Pa_4_5450* (pCIB4) genes. The *Swa*I and *Pac*I sites can be used to clone the cassette/gene to be expressed. The *Asc*I sites can then be used to cut the plasmids. After transformation in a *mus51/52* strain, the linear fragments carrying the 5' region followed by the expression cassette, the nourseothricine resistance marker and the 3' region will replace by a double crossing-over the *Pa_2_3690* or *Pa_4_5450* genes. The *Swa*I, *Pac*I and *Asc*I enzymes recognize 8-bp sites with 4 bo overhang to facilitate cloning.

is often preceded by concatenation of several molecule of the transforming DNA, followed by internal deletions. Correct expression of the transgenes is thus often variable depending on the modalities of the DNA integration. To ensure a correct expression of transgenes, it is possible to use along with the *mus51/mus52* strains the pCIB2 and pCIB4 plasmids that target integration at the *Pa_2_3690* and *Pa_4_5450* loci, respectively (figure 31). This strategy ensures correct expression and even allow for comparison between transgenes. However, their utilization results in the inactivation of either *Pa_2_3690* or *Pa_4_5450*. So far, no phenotype has been associated with the inactivation of these genes.

Overall, it is possible to extract macromolecules and modify easily and at will the genome of *P. anserina*. Many additional tools generated by the laboratories working on this fungus are available. Only those routinely used in my lab are presented here.

Tools for expression analysis

Although it is still possible to analyze gene expression one gene at a time, tools for transcriptomic analyses have been developed. For example, microarrays of the whole transcriptome are available for strain S. Although, these are based on the first annotation of the *P. anserina* genome, they probe the overwhelming majority of the genes, since few new genes have been discovered since. Transcriptome analyses using these microarrays have been made on *mat+* and *mat-* strains, at various times of ascospores germination, mycelium growth and perithecium development. Most, but not all, of these data are available in public databases. More recently, RNAseq data have been obtained and made public for the following developmental stages: one-day-old and four-day-old mycelia, two-day-old and four-day-old perithecia, non-germinated ascospores and eight-hour-old germinated ascospores. RNAseq data of *P. anserina* grown on two different biomasses are also available. It is likely that additional RNAseq data will be made available in public databases in the near future. All of these data can be searched to have a first idea on the expression pattern of interesting genes.

Morphology and cytology

As stated in the previous chapters, morphological analysis of the sexual reproduction apparatus was the basis for the definition of the species and is still used to differentiate species of the *P. anserina* complex from other fungi. However, it is only a part of the structures that the fungus is able to differentiate during its lifecycle (figure 32). In this section, we will thus examine the morphological features of both the reproductive and vegetative structures elaborated by *P. anserina*.

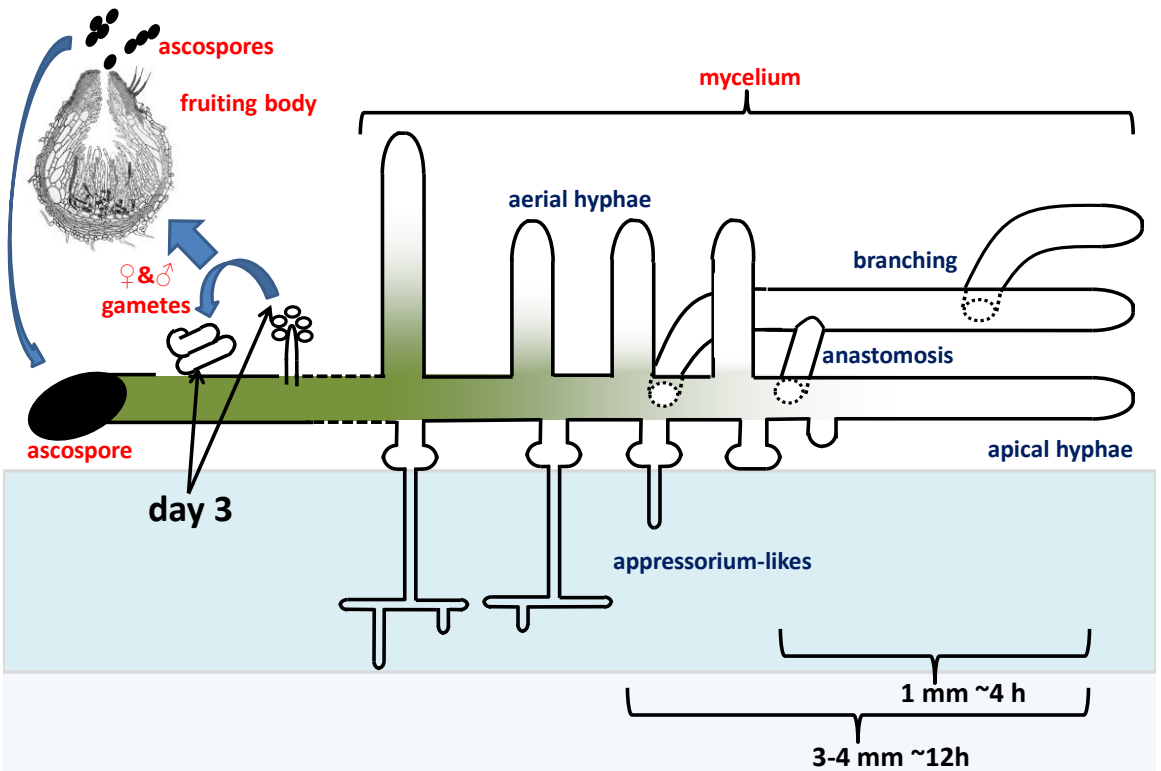


Figure 32 Schematic representations of the major cellular structures differentiated by *P. anserina*. After the germination of ascospore, the fungus differentiates a complex mycelium having different kinds of hyphae. Onto this mycelium, both male and female gametes are differentiated. After fertilization of compatible gametes, the fruiting body or perithecium is formed. In this sexual sporophore, ascospores are produced. They are then expelled to ensure the dispersal of the fungus. The different structures are not to scale.

The mycelium

The mycelium differentiated by *P. anserina* is typical for a *Pezizomycotina*. Apical hyphae from the outer edge of the thallus (figure 33) have a diameter of about 4-6 µm and contain few nuclei (often 2-5). Very quickly, hyphae branch and anastomose (figure 33). Meanwhile septa are deposited (Figure 34). They contain a central pore associated with Woronin bodies, which are modified peroxisomes involved in regulating the flow within the central pore (figure 34). Once mature, the mycelium is thus a complex network of interconnected hyphae (figure 33). These may have different diameters, suggesting different functions; yet nothing is known about the potential roles of these differently shaped-hyphae. All these hyphae have an internal structure typical for *Dikarya* fungi (figure 34). If in contact with the atmosphere,

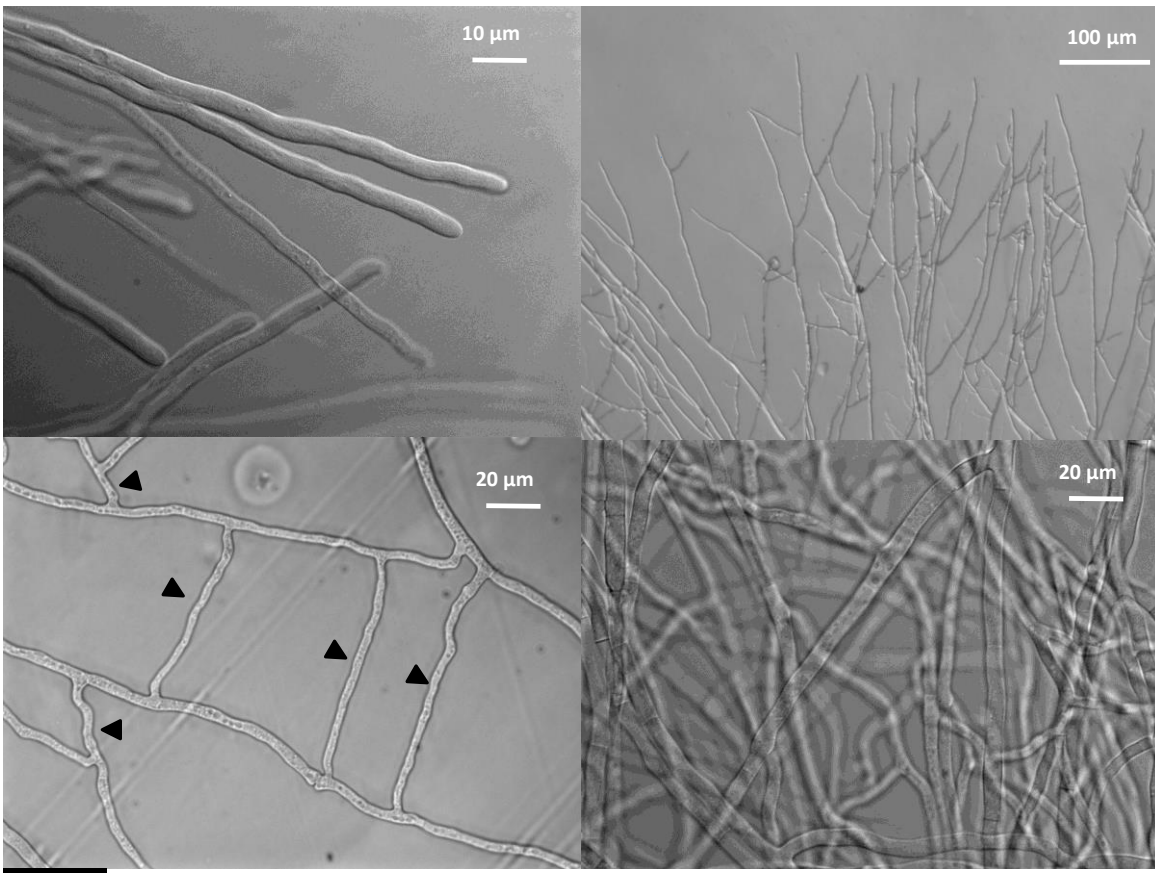


Figure 33 Vegetative hyphae of *P. anserina*. Top left, typical apical hyphae; top right; branching pattern of subapical hyphae; bottom left, anastomoses (arrowheads) showing the typical ladder-like morphology; bottom right, typical hyphae from an internal part of the mycelium showing different diameters

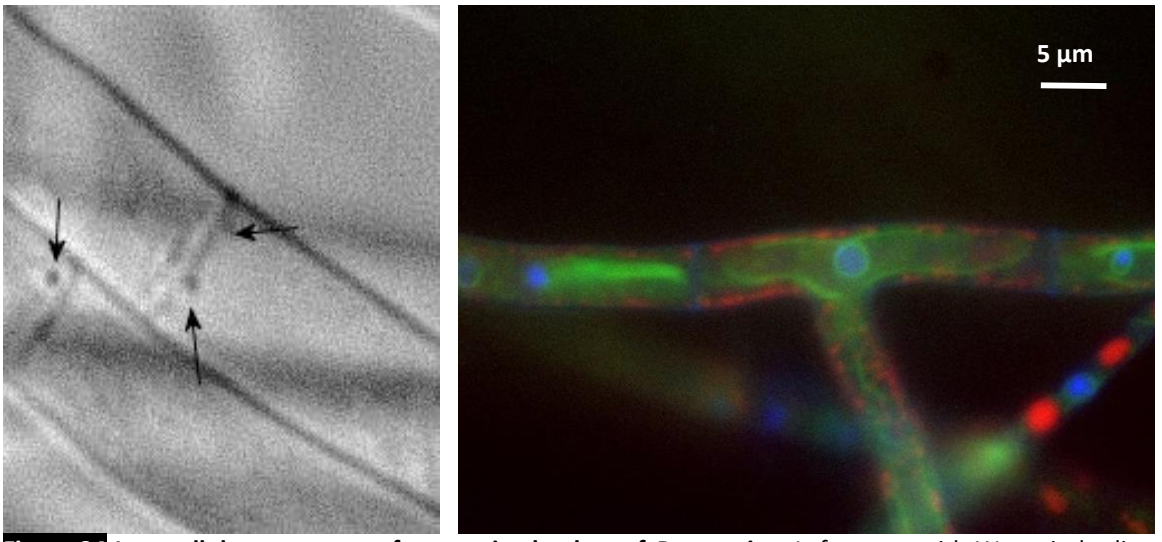


Figure 34 Intracellular structures of vegetative hyphae of *P. anserina*. Left, septa with Woronin bodies (arrows); right, some of the structures of the nucleus/reticulum/vesicular network (nuclei in blue, endoplasmic reticulum in green and vacuoles in red. Pictures by S. Brun.

some hyphae will erect, likely thanks to a coating of hydrophobins (figure 35). Additionally, melanin pigments will accumulate at the center of the colony (figure 35).

At the microscopic level, there is no difference between the mycelia differentiated by the *mat+*, *mat-* and *mat+/mat-* thalli. At the macroscopic level, the presence of fruiting bodies specifically on the *mat+/mat-* thalli appears to modify the behavior of the mycelium with decreased pigmentation and aerial hyphae amounts in the outer edge of the culture (figure 36). Moreover, differences between the *mat+* and *mat-* thalli may be exhibited on some media, especially in interaction with lighting conditions. This is

Figure 35 Aerial hyphae and pigments of 4-day-old *P. anserina* thallus grown on M2. Pigments are partially masked by the aerial hyphae. On M2, these are mostly erected in a ring region located between 1 cm and 2 cm from the center of the culture. This ring region also accumulates more pigment.

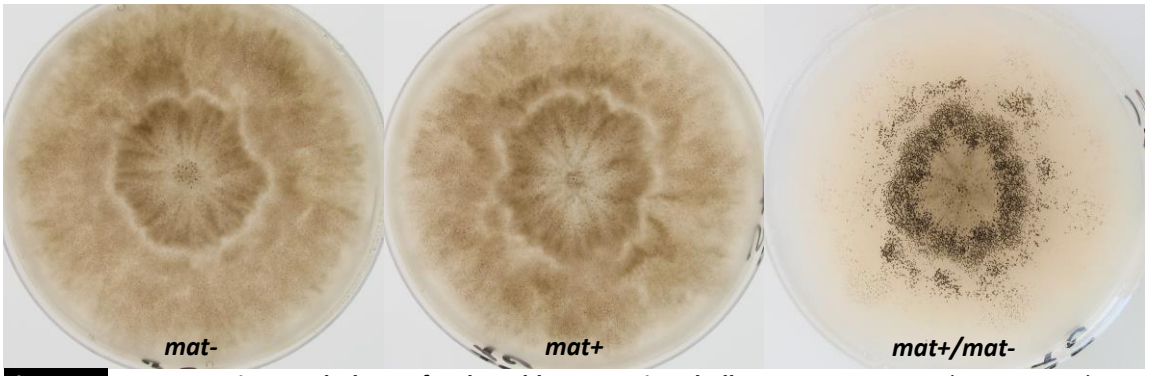


Figure 36 Macroscopic morphology of 7-day-old *P. anserina* thallus grown on M2. The *mat+* and *mat-* cultures are older than the one on figure 31 and many aerial hyphae have collapsed onto the medium. The accumulation of pigment is thus more visible, showing the typical ring region. On the *mat+/mat-* culture, perithecia are mostly located in the ring region. Note that beyond the ring in the outer edge of the culture, pigment are lacking, while they are present in the inner part of the culture inside the ring.

due to the presence of polymorphic genes on chromosome 1 near the mating type, in a region nearly devoid of recombination. One such gene that has been shown to trigger differences between the *mat+* and *mat-* thalli is *rmp1*. In strain S, the *mat+* thalli carry the *rmp1-2*, while the mat- thalli carry the *rmp1-1* allele. Noteworthy, *rmp1-2* confers a slight thermosensitivity. Hence, *mat+* thalli do not produce aerial hyphae when grown at 36°C and grow slightly slower. As seen on figure 31 and 32, there is on M2 a defined ring region with an inner diameter of 1 cm and an outer diameter of 2 cm. It is visible on homokaryotic thalli thanks to melanin and aerial hyphae accumulation and in *mat+/mat-* dikaryons thanks to fruiting bodies. How this ring region is produced is still unknown. It is not present on all media and its size and density is agar and carbon-source dependent. Usually the more digestible and abundant the nutrients, the more pronounced this region. For example on the crystalline-cellulose-containing M4, the ring is only visible in *mat+/mat-* dikaryons (since *P. anserina* does not produce pigments and aerial hyphae on M4). The ring is wider (inner diameter is 2 cm and outer diameter is 4 cm) and perithecia are much sparser.

When in contact with cellophane, *P. anserina* differentiates special hyphae dedicated to penetrate the solid nutrient layer and digest it from the inside: the appressorium-like structures (figures 32 and 37). These are differentiated after about 12 hours of growth on cellophane and are especially abundant in the ring zone with dense aerial hyphae/perithecia. When inoculated on M0 medium with

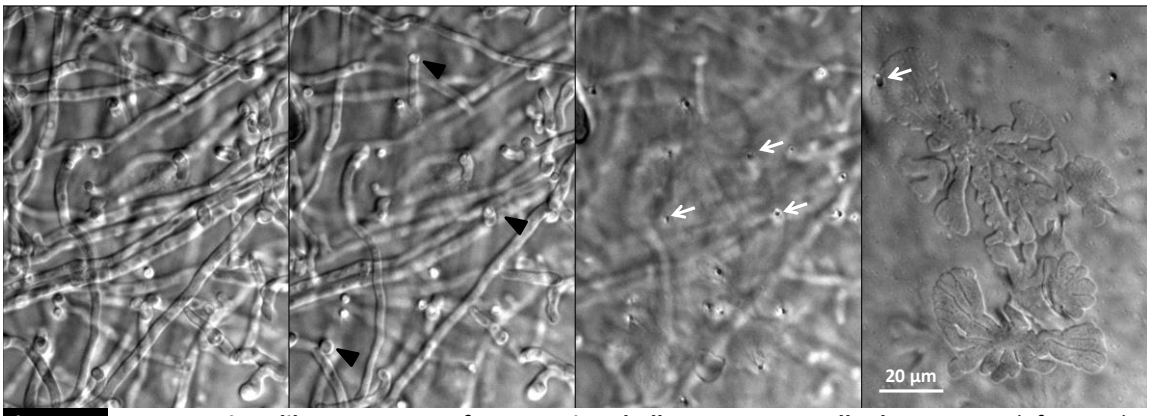


Figure 37 Appressorium-like structures of *P. anserina* thallus grown on cellophane. From left to right, different focuses highlight these structures from top to bottom. There is a distance of about 10 µm, between each picture. First on the left, hyphae grow parallel to cellophane. Then hyphae reorient and differentiate the appressorium-like structures (black arrowhead) that contact the solid layer of cellophane. From these, hyphae with a tiny diameter called penetration pegs (white arrows) penetrate the cellophane. Then on the right, haustorium-like structures develop inside the cellophane. From these, new penetration pegs (white arrow) descend further inside the cellophane layer.

cellophane, the fungus will cross the cellophane layer (about 50-100µm) in about three days. These structures are inhibited by the presence of glucose in the medium. It is presently not known if they are also differentiated when *P. anserina* grows on natural biomass, especially when growing on dung.

In addition, to the hyphal structures described above, the friendly mold is able to differentiate lasso-like hyphae, whose role is unknown (figure 38). The fungus also differentiates in media poor in

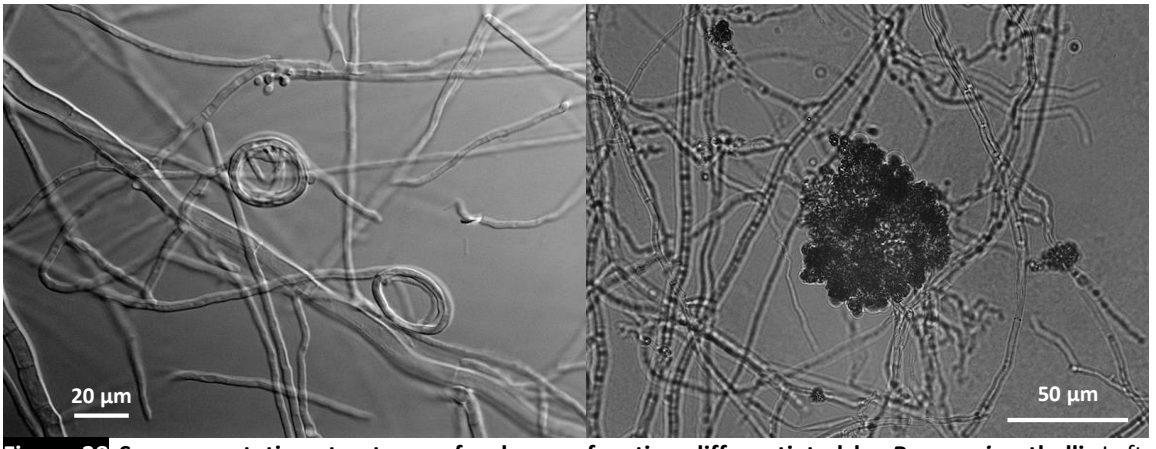


Figure 38 Some vegetative structures of unknown function differentiated by *P. anserina* thalli. Left, lasso-like hyphae; right, miscrosclerotic stuctures.

nutrients, such as M4 and wood shavings, hay or miscanthus media, small sclerotic-like structures having a diameter of about 50 µm (figure 38). The exact nature as well as the role of these structures is also unknown. *P. anserina* may also be able to form sclerotes with larger sizes, however, these are seldom observed and conditions enabling their production have yet to be defined.

The gametes

P. anserina differentiates both male and female gametes on the mycelium and hence display an "ascohymenial" development. On M2, differentiation starts after two days of growth and fertilization can proceed on 3-day-old thalli, showing that both types of gamete are functional at that time. Both the *mat+* and *mat-* thalli differentiate the two kinds of gametes. In fact, we know that the mating type locus is

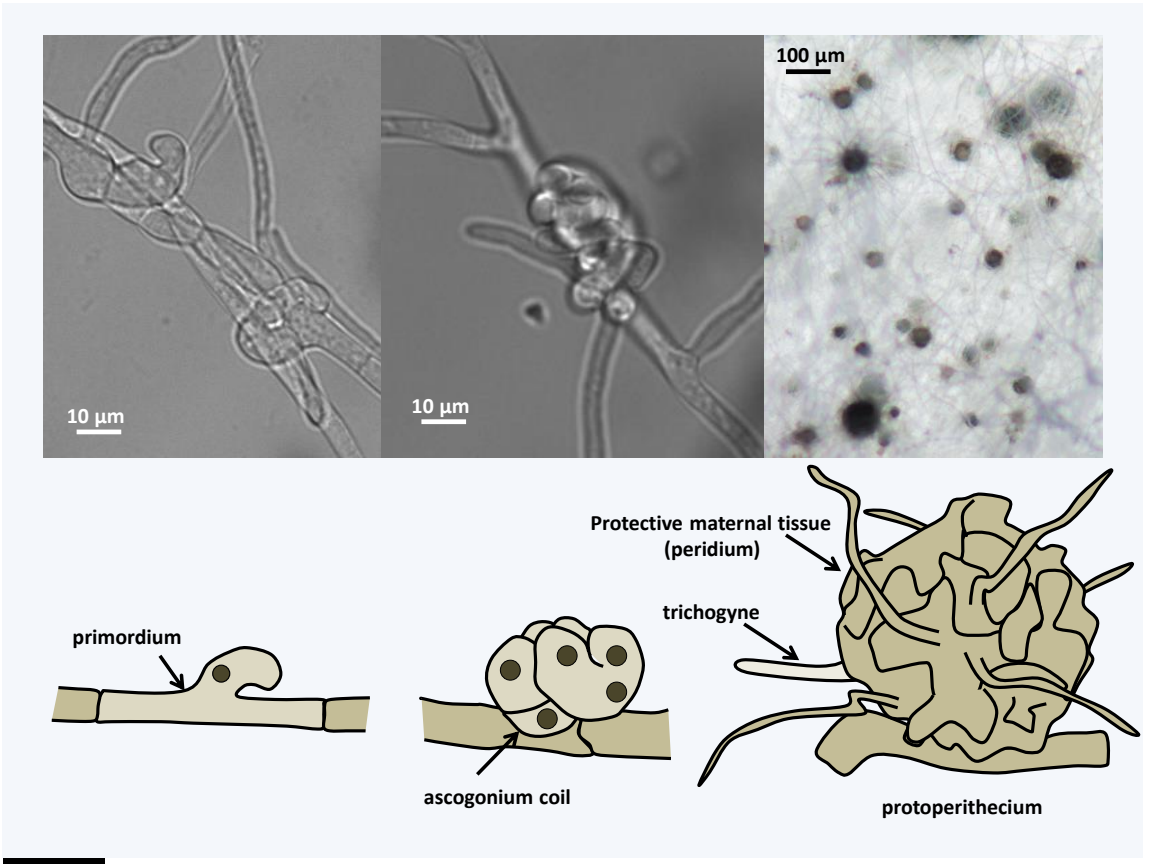


Figure 39 Differentiation of the *P. anserina* female gametangium. The fertile tissue is colored in a lighter color compared to the maternal one. See text for description.

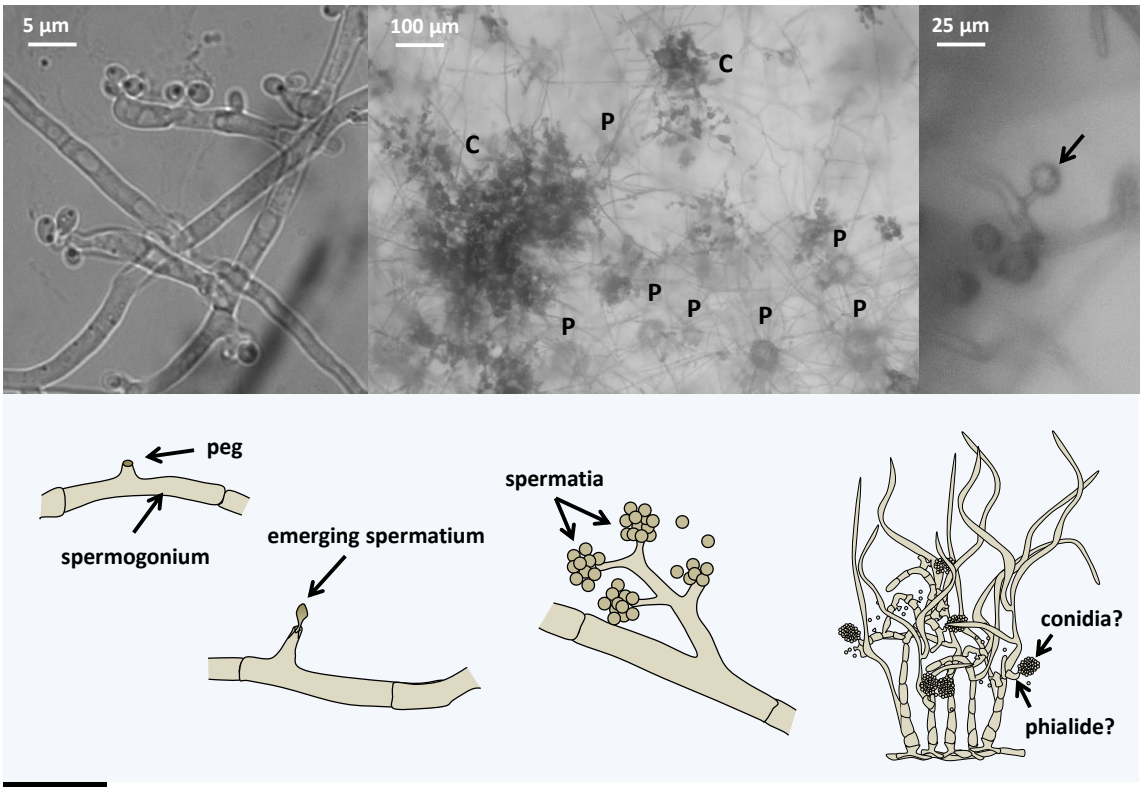


Figure 40 Differentiation of the *P. anserina* male gametes. Usually, spermatia are born at the apex of a peg developing from a spermogonium. Repetitive budding produces small cluster of spermatia. Under some conditions (here top middle and top right in the dark at 18°C on M2 + cellophane), a proliferation of spermogonia and spermatia occurs. Erected sterile hyphae also differentiate in these structures that strikingly resemble *Cladorrhinum*/*Bahupaathra* anamorphs. P: protoperithecia, arrow shows a cluster of spermatia/conidia in the anamorphic-like structures. See text for details.

dispensable for gamete differentiation.

Female gametes - or more properly gametangia since they are pluricellular when mature - are typical ascogonia/protoperithecia (figure 39). Differentiation starts with characteristic hooked hyphae that will continue their differentiation by generating a pluricellular and multinucleated ascosgonium coils. These coils will then be embedded by neighboring hyphae to generate protoperithecia that may reach large sizes (some exceed 100 µm). At that stage, the gametangia are already composed of two different tissues: the female sexual tissue awaiting fertilization in the center originating from the ascogonium coil and that reaches the outside thanks to special hyphae called trichogynes, and several layers of sterile maternal tissue that protects the sexual tissue and that will shape the fruiting body. This sterile tissue has

thus a maternal origin and results from the proliferation of the hyphae that surround the ascogonium coil. In *P. anserina*, the protoperithecia (and later perithecia) have protruding hyphae that may be mistaken for trichogynes. It is therefore not known whether a single or multiple trichogynes is/are produced per fruiting body.

Male gametes are differentiated on pegs emerging from special hyphae called spermogonia (sing. spermogonium, figure 40). They are small spherical cells having a diameter of 2 µm. They contain a single nucleus and a single mitochondrion. They are produced in small clusters and are very easily released from the spermogonium so that it is very difficult to see them attached to the peg (see figure 40 top left). Attempts to germinate spermatia have so far failed. Indeed, although a paper reported their germination at a rate of 1% on media containing yeast extract and sorbose, this rate was not reproduced recently on this medium and germination proceeds at a frequency of 1 out of one million spermatia in all tested conditions. Intriguingly, in some situations, *P. anserina* differentiates *Cladorrhinum*/*Bahupaathra* anamorph structures (figure 40, see figure 11 for comparison). Here, there are dozens of “spermatia” carried on “spermogonia”, questioning whether these are in fact “conidia” on “phialides” (conidiophores with peg-like structures to carry the spores). Indeed, their sheer number suggests that they may be used for dispersal rather than fertilization. However, these also germinate at a very low rate. Until conditions that reproducibly trigger their germination are found, these are thus better seen as spermatia.

Once the gametes are differentiated, fertilization occurs rapidly between mating compatible gametes (see chapter on the sexual cycle and genetical analysis). Based on experiments with successive waves of fertilization with genetically-different nuclei, fertilization is rapid and efficient since most female gametes are fertilized in 10 minutes. During this event, the nucleus from the spermatium enters the trichogyne and migrates to the ascogonium body. This is followed by the rapid development of the perithecium.

The perithecium

Maturation of the perithecium from fertilization to the first expulsion of ascospores lasts about four days on M2 medium at 27°C. While unfertilized protoperithecia may reach large sizes, typically about 50 µm, sometime more, they never present the neck and ostiole characteristic of fertilized perithecia and through which ascospores are expelled (see figure 41). As stated above, protoperithecia are composed of

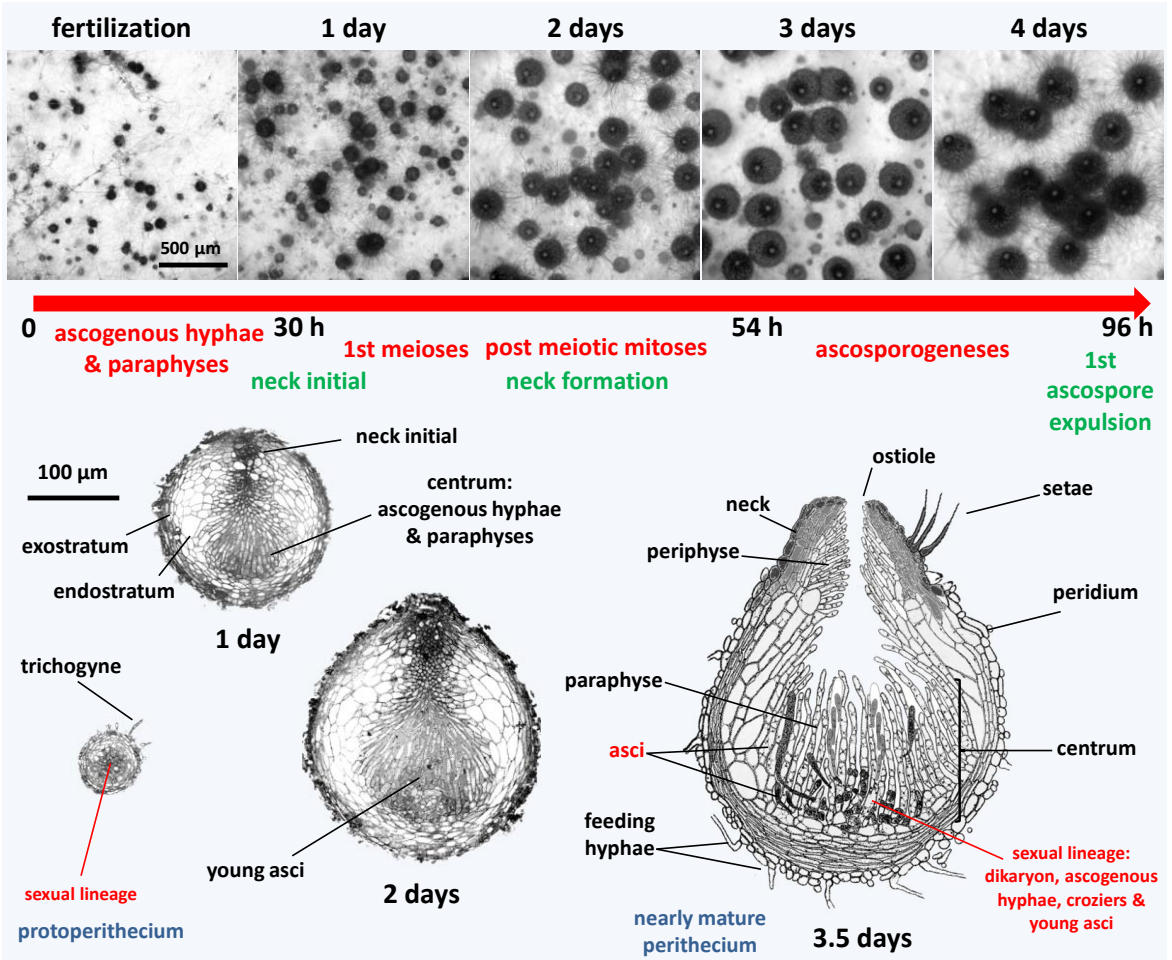


Figure 41 Differentiation of the *P. anserina* perithecium. Top, overall morphological evolution during perithecium development with timeline of main events. Bottom, schematic representation of sectioned perithecia with main tissues.

three to five layers of flattened and pigmented cells protecting the ascogonium that is embedded with sterile maternal tissues. Hairs and trichogynes emerge from the protective layer: at that time the protoperithecium looks thus like a small urchin (figure 41). Upon fertilization, development proceeds and the perithecium enlarges (figure 41). The protective cells differentiate a peridium having two layers: in the inside, the endostratum formed by hyaline polygonal cells of about 12-25 µm, and, on the outside, the exostratum formed by melanized thick-walled polygonal cells of about 10-20 µm. Twenty four hours after fertilization the neck initial is visible on the top of the developing fruiting body as a small area with

increased pigmentation. Meanwhile, the first paraphyses differentiate as early as 24h after fertilization. They are elongated unbranched hyphae composed of several articles. They occupy the centrum along with the first binucleated ascogenous hyphae emerging from the fertilized ascogonium. These produce croziers about 30 hours after fertilization and the first meioses occur just after (figure 37). Two days (48 h) after fertilization the centrum is a mix of croziers, young asci at different stages of development and upward paraphyses (figure 41 and 42). The largest increase in size occurs at day 3 and day 4, at which time the perithecium reach a diameter of about 300-350 µm. The neck is growing upward and the ostiole is forming. On the outside, the cells of the neck undergo intense pigmentation and a small tuff of darkly pigmented hairs (the setae) appears at the end of the third day on many but not all fruiting bodies. On the inside, the neck is lined with special cells, the periphyses. The centrum proliferates, producing more and more asci. These mature and the first delimitated ascospores are seen 54 hours after fertilization. Rapidly, they enlarge, mature and get pigmented. The centrum occupies then the largest part of the fruiting body and is easily separated from the peridium.

The development of the sexual tissues is typical for the *Pezizomycotina* (figure 42). The fertilized ascogonium produces several multinucleated cells from which binucleated cells emerge: the ascogenous hyphae. These binucleated cells have two genetically different nuclei and are thus dikaryotic (see chapter on the sexual cycle and genetical analysis). The dikaryotic binucleated state is propagated during cell divisions thanks to the special divisions of the croziers. The apex of this cell forms a hook. After the

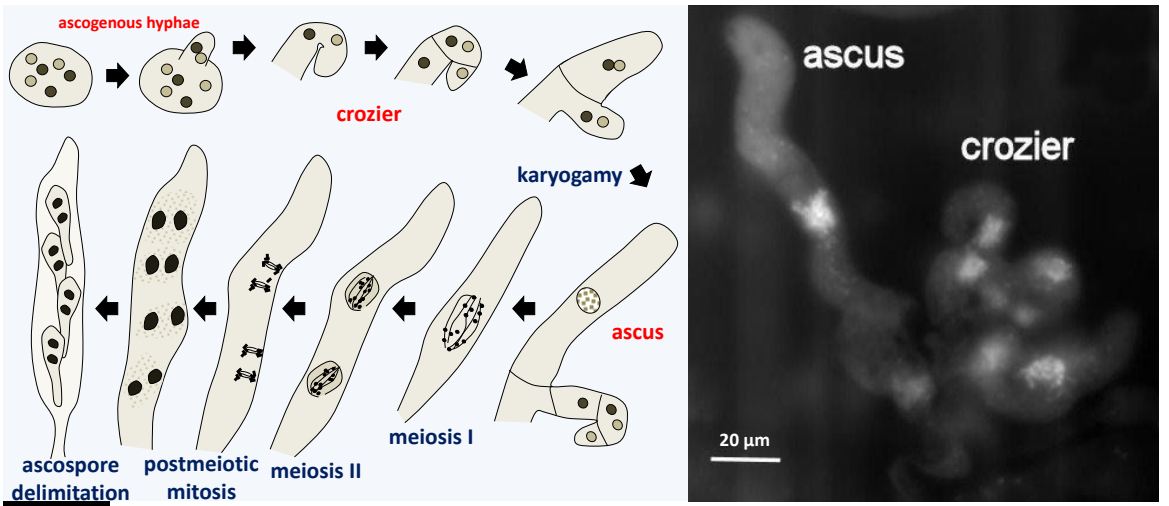


Figure 42 Development of the *P. anserina* sexual tissues. See text for explanation. Right, picture V. Berteaux-Lecellier.

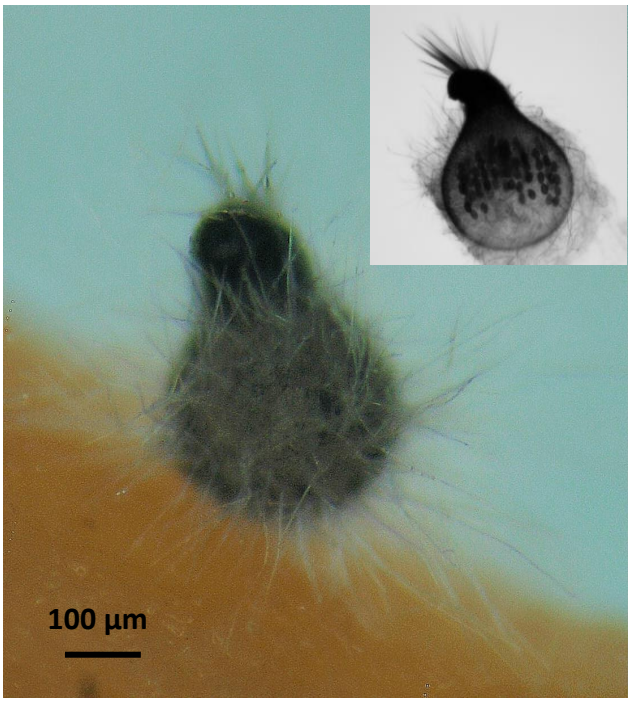


Figure 43 **Mature *P. anserina* fruiting bodies.**

coordinated division of the two nuclei, two septa form and individualize a binucleated dikaryotic cell that becomes the ascus and two uninucleated cells that undergo cell fusion to restore a binucleated dikaryotic cell. This cell will divide further to produce new croziers. Meanwhile, the ascus enlarges, undergoes karyogamy, then immediately meiosis and a postmeiotic mitosis. The orientation of the division spindles is parallel to the axis of the ascus during the meiotic division and transverse in the postmeiotic mitosis. Then nuclei glide as to associate two by two non-sister nuclei. The process ends by the differentiation of the ascospores that will be the subject of the next section. Once mature (figure 43), perithecia may produce a few hundreds to a thousands of ascospores for three to ten days depending upon the growth medium and humidity of the atmosphere.

The asci and the ascospores

Ascus and ascospore maturation lasts for about two to three days on M2 at 27°C. After bursting open mature perithecia and collecting the centrum, the whole sequence of asci and ascospore maturation may be seen in the rosettes (figure 44). Just after their delimitation around two nuclei by two membranes, ascospores have a club shape

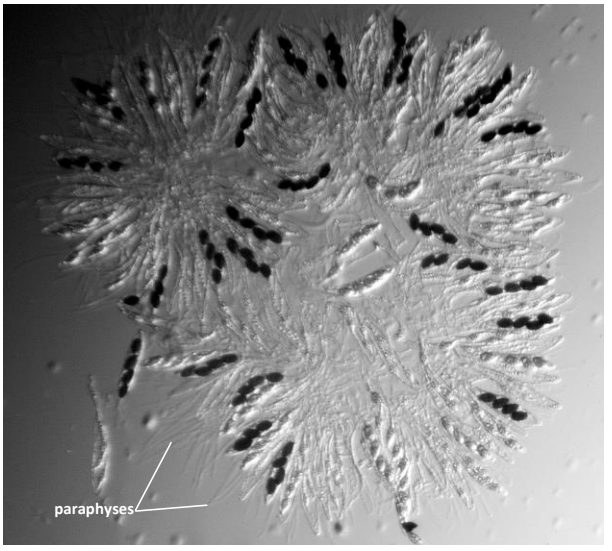


Figure 44 ***P. anserina*** **rosettes of asci with paraphyses.**

(figure 42 & 45). Rapidly, the two nuclei undergo mitoses to yield four nuclei, three of which remain in the head of the ascospore and the fourth one migrates into the tail (figure 45). A septum is then laid down between the head and tail parts of the ascospore when melanin is deposited in the head cell. The nuclei of the tail cell degenerates and the tail cell dies. This dead cell becomes the primary appendage of the ascospore that gives the name to the genus *Podospora* (spore with foot). Meanwhile, the three nuclei of the head part undergo further mitoses and the cell enlarges. When mature, ascospores have around thirty nuclei. The cell wall of the head cell gets heavily melanized by the deposit of three successive layers of melanin, giving it a black color.At least, two gelatinous appendages, the secondary appendages, are laid at the opposite poles of the spores: one at the distal tip of the tail cell and one near the apex of the spore head. They consist of gelatinous materials that are deposited between the two membranes of the

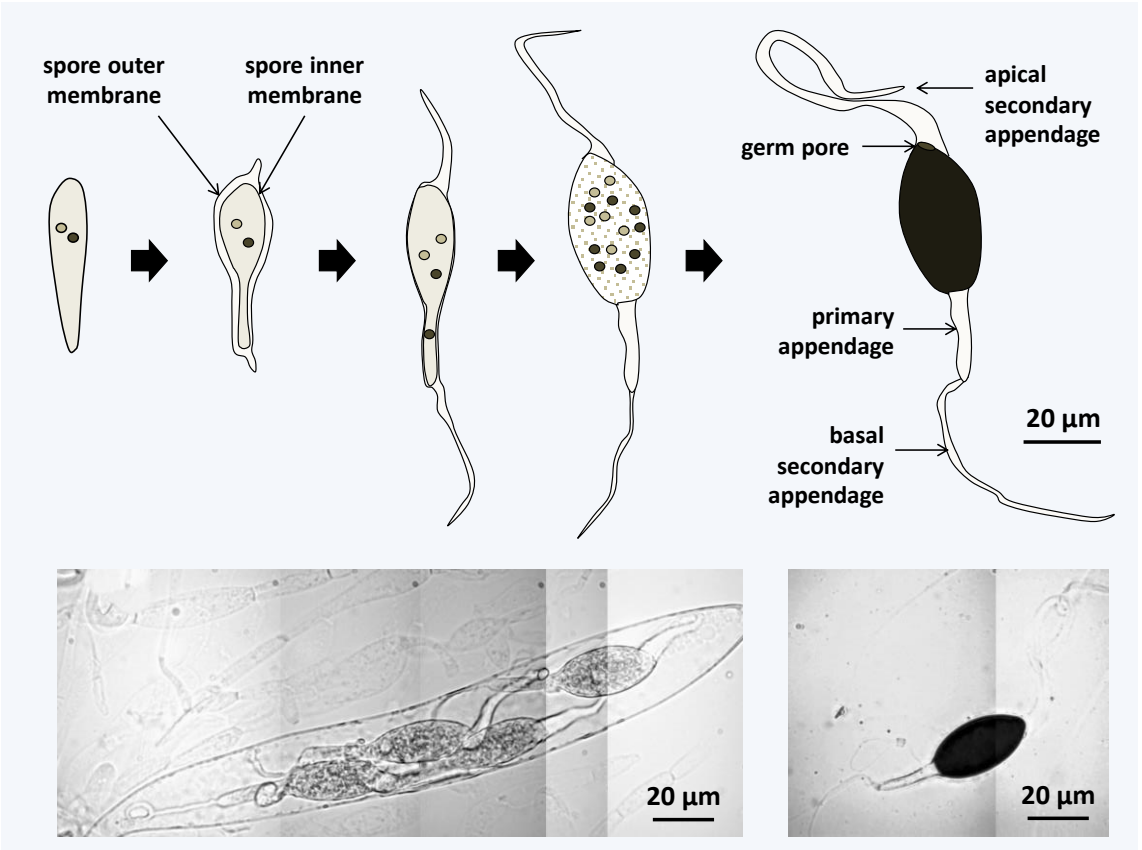


Figure 45 Development of the *P. anserina* ascospores. See text for explanation.

spores. Two smaller ones may also be present on the primary appendage. Their role is unknown. In addition, the four ascospores in the ascus are linked together by a rope of actin that is the remnants of the actin fibers that allow migration of nuclei during the maturation of the ascus and scaffold the delimitation of the ascospores. The last feature of the ascospores is the presence of a germ pore at the apex through which germination will proceed. When mature, the spore head is ~19 x 35 µm and the primary appendage (also called the pedicel) is ~5 x 20 µm.

Asci measure about 25 x 200 µm. Their apices have a simple structure (figure 46). They typically contain four dikaryotic or "big" ascospores (figure 44 & 46). However, asci with abnormally-delimitated ascospores are frequent. Their frequency can be increased by incubating developing perithecia with anesthetics such as chloroform (to do so, a cotton wool dipped in the anesthetics is placed along with the Petri plate carrying the developing perithecia in a sealed container). They are due to defects in the positioning of the spindles during the meiotic and postmeiotic divisions, resulting in abnormally-placed nuclei. Indeed, ascospore delimitation is driven by the spindle pole body. If far apart, nuclei will be incorporated in different ascospores, while close nuclei are packed inside the same ascospore. The most common is the five-spored ascus, with three big dikaryotic ascospores and two "small" homokaryotic ones (figure 46). Often, the two small ascospores stem from the alteration of a big ascospore. They result from defects in a single postmeiotic spindle resulting in two sister nuclei being too far apart. However, more complex situations may be found, such as the one depicted in figure 46, where the two small

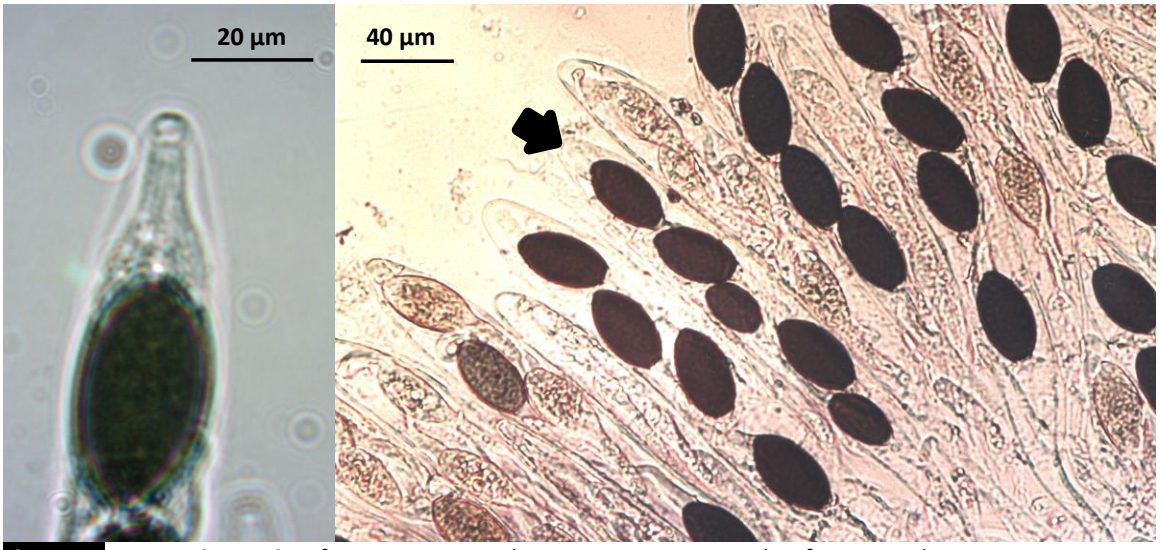


Figure 46 ***P. anserina*** **asci.** Left, ascus apex. Right, arrow points towards a five-spored ascus.

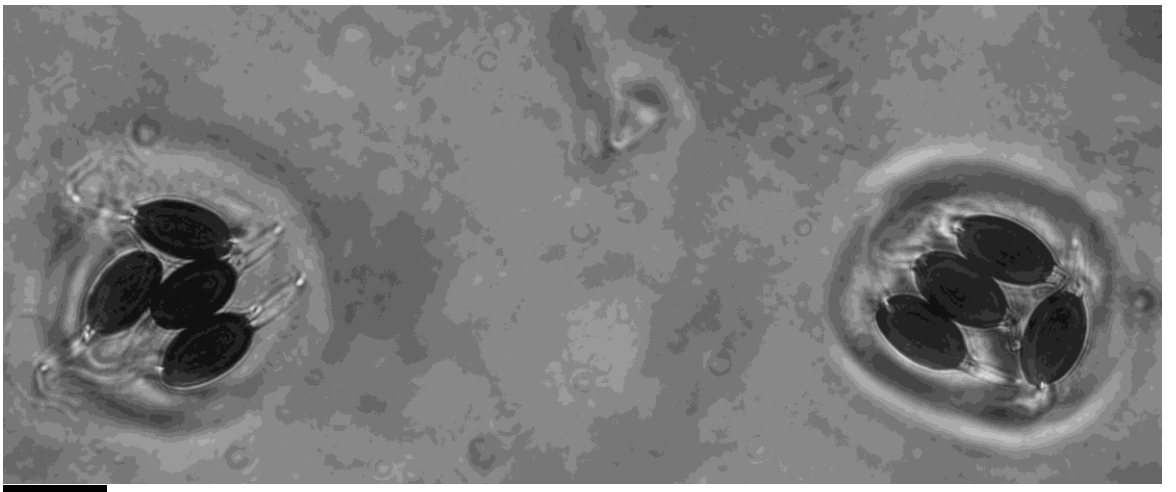


Figure 47 ***P. anserina*** **asci after expulsion from the perithecium.** These two asci were collected onto an agar plate laid over a cross plate as depicted on figure 23.

ascospores and the big ascospore between them arise from the bad delimitation of two postmeiotic spindles. Two centrally-placed nuclei formed the big ascospore and the left over nuclei the small ones. Asci with two big and four small ascospores, as well as one big and six small or even eight small ascospores are also encountered, the first one being fairly common, while the last type with eight ascospores being extremely rare. Other atypical asci carry “giant” ascospores resulting from the formation of the ascospores around three, four, five, six, seven or even eight nuclei, the more nuclei the larger the ascospore. All combinations of giant, normal and small ascospores may be encountered. However, they are rather rare. For example, delimitation encompassing eight nuclei yields ascospore with the shape of a banana. They are seen only if anesthetics are applied. The most frequently atypical asci with giant ascospores encountered in usual conditions is two big, one small and one giant ascospore. Frequency of abnormal asci depends upon many factors including the medium, the temperature and the strain. For example our reference strain “S”, like most *P. anserina* strain, has a frequency of 5-spored asci of about 1% and giant ascospore-containing asci of about 1‰. Usually, abnormal asci are more abundant early in the production of the ascospores by the perithecium.

Once mature, the four ascospores of an ascus are expelled together, because they are linked with an actin rope as stated earlier (figure 47). A film depicting this event can be seen at the following URL: https://doi.org/10.1371/journal.pone.0003237.s002. Average expulsion speed is 21 m/s, enabling to eject the ascospores about 20 cm away. To do so, ascospores are accelerated with the staggering rate of

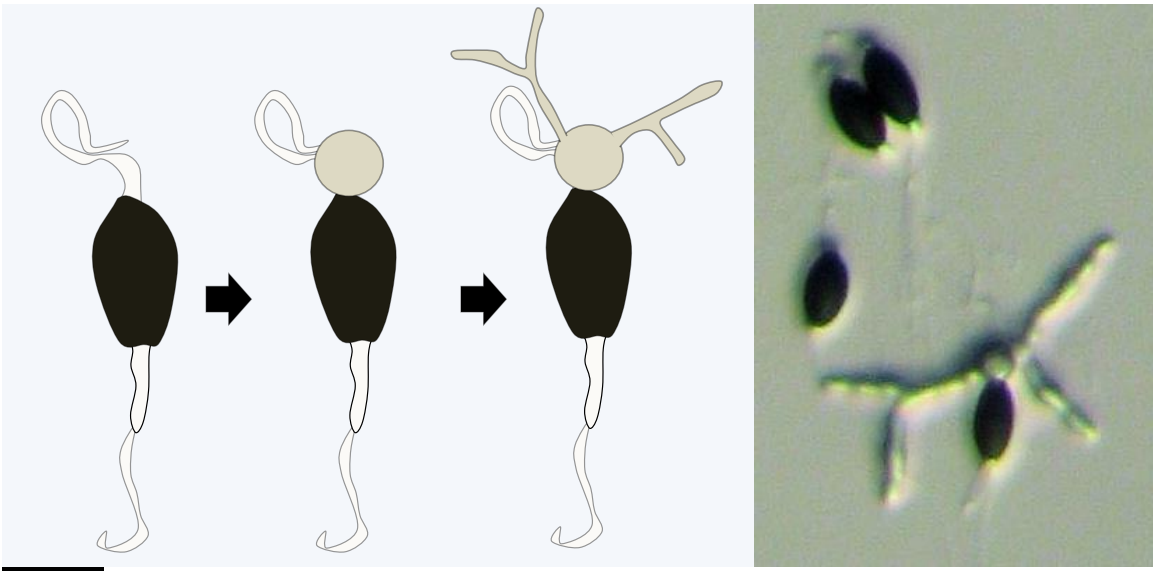


Figure 48 ***P. anserina*** **ascospore germination.** See text for details.

1 500 000 m/s^2! Surprisingly, this does not require extravagant turgor pressure. Indeed, presence of erythritol and pinitol at a combined concentration of 70 mM appears sufficient to do the trick and create the required pressure of 0.4 MPa.

After their landing, ascospores await a trigger for their germination (see chapter Physiological and molecular analysis: deciphering developmental pathways - Ascospore germination). They usually do so by extruding a germination vesicle (also called peg) from the germ pore a few hours after being triggered to germinate (figure 48). From this vesicle, hyphae rapidly emerge to create a new mycelium. Movie n°3 shows these events in an accelerated manner. Note that damaged ascospores may germinate from the breakage points. In addition, few immature ascospores are sometime ejected from the perithecia; these may also germinate from any part of the ascospore.

The sexual cycle and genetical analysis

The lifecycle of *P. anserina*

In the previous chapter, we have studied the various structures differentiated by *P. anserina*, especially those involved in the sexual reproduction. We shall now see how these differentiations are orchestrated during the life cycle of the fungus. *P. anserina* is a heterothallic "pseudo-homothallic" filamentous ascomycete, whose haplobiontic sexual cycle displays interesting features (figure 49). The fungus has thus mating types, *i.e.*, a system of genetic incompatibility/compatibility for fertilization, yet

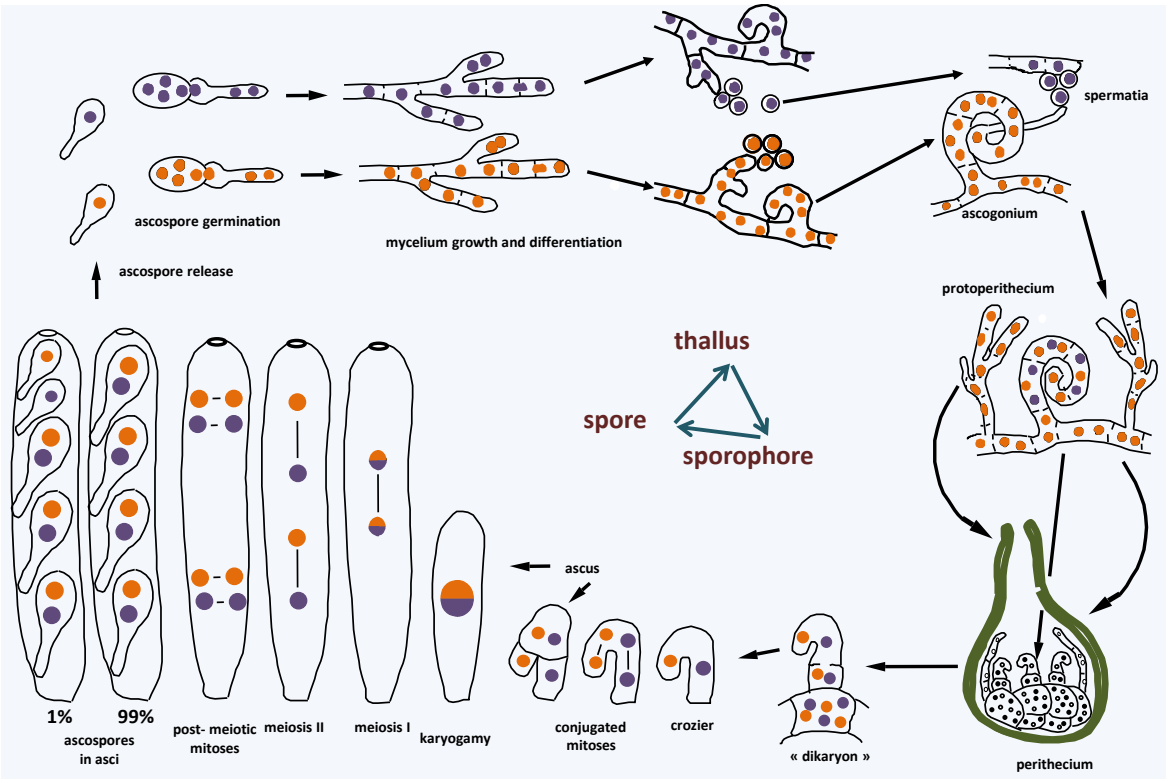


Figure 49 ***P. anserina* life cycle.** See text for details. I thank D. Zickler for the original drawing of this cycle.

produces ascospores generating mycelia able to mate with themselves.

Under appropriate conditions (see the section on Physiological and molecular analysis: deciphering developmental pathways – Sexual reproduction), mycelia of each mating-type (*mat+* and *mat-*) are able to differentiate both the male (spermatia) and the female (ascogonia) "organs". However, fertilization can only occur between a spermatium and an ascogonium of opposite mating-types. It works in both directions: ♂ *mat-* x ♀ *mat+* and ♂ *mat+* x ♀ *mat-*. To do so, the ascogonium produces a trichogyne, a dedicated hyphae that is attracted to the spermatia thanks to a pheromone/receptor system and “catches" them. The pheromone produced by the spermatium is specific for each mating type as is the compatible receptor expressed in the trichogyne. Once a spermatium caught, its fertilizing male nucleus enters the ascogonium. A trichogyne is fertilized by a single male nucleus, because to date ascogonia fertilized by genetically different nuclei have never been seen. Note that nuclei from the vegetative mycelium can also be used as male gametes, because fragmented mycelia lacking spermatia are able to fertilize compatible ascogonia. As stated in the previous chapter, an interesting point is that this fertilization event is not immediately followed by nuclear fusion or karyogamy. The two nuclei first divide in a common cytoplasm to form a syncitium. The resulting nuclei migrate by pairs of opposite mating type in specialized cells: the ascogenous hyphae. These hyphae give rise, after divisions, to the crozier cells, where the two nuclei divide synchronously. A special septum is formed to yield three cells. Karyogamy takes place in the upper binucleated cell. It is immediately followed by meiosis, a postmeiotic mitosis and formation of asci. Therefore, many asci are produced after a single fertilization event. Note that all events following a single fertilization take place in a single perithecium, because a single fertilization has never been reported to produce more than one fruiting body.

As stated in the previous chapter, asci usually contain four big ascospores or, in 1% of the cases, five, *i.e.*, three big and two small ascospores. The big ascospores usually carry *mat+* and *mat-* nuclei and thus generate mycelia able to self-fertilize, hence the term pseudo-homothalism used to characterize the breeding system of *P. anserina*. Small ascospores, but also few large ascospores, carry nuclei of a single mating type. They produce homokaryotic self-sterile mycelia that will need a compatible partner of opposite mating type to carry out sexual reproduction. Such large ascospore may be present in five-spored asci resulting from defect in more than one spindle (as the one in figure 46), but also in four-spored asci in which the mating type locus has undergone a first division segregation (see below). Availability of both heterokaryotic and homokaryotic mycelia entails that there are several ways to set up

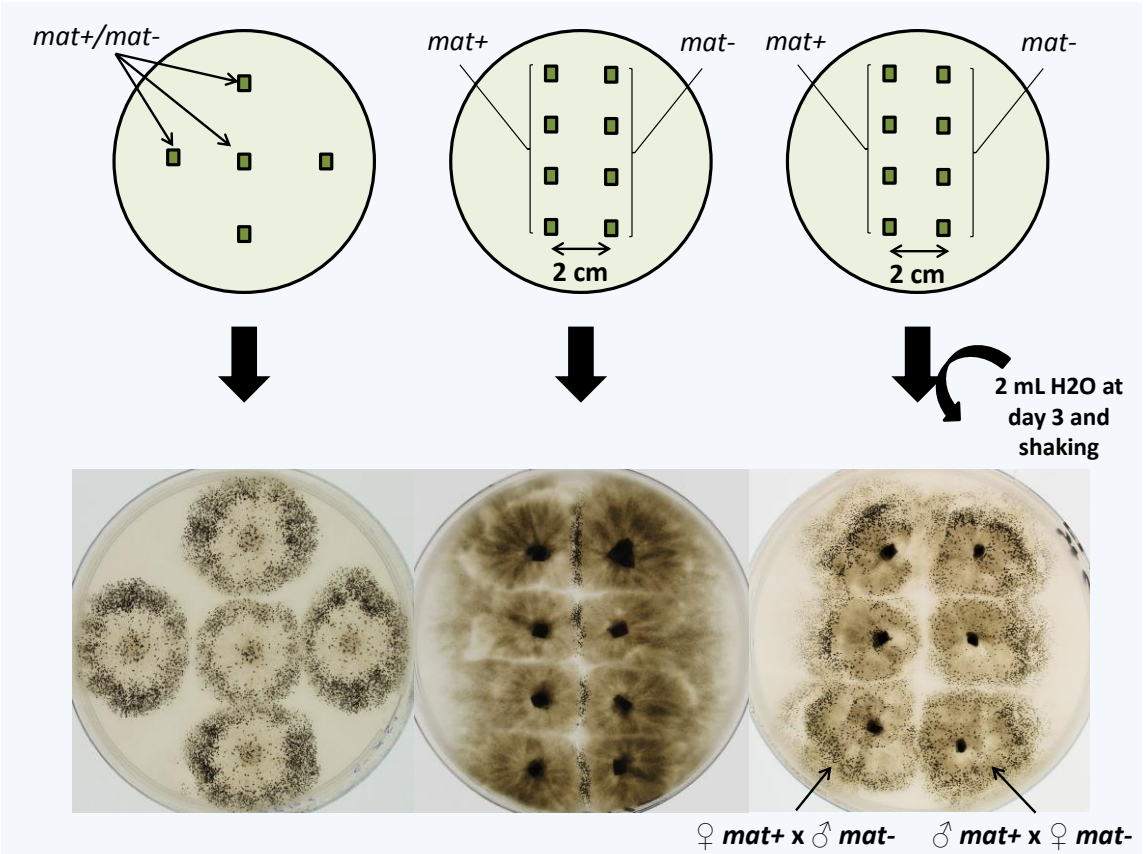


Figure 50 Three frequent setups for *P. anserina* crosses. See text for details.

sexual crosses with *P. anserina* (figure 50). Self-fertile mycelium (obtained from a *mat+/mat-* big spore or by mixing *ma+* and *mat-* fragmented mycelia) may be inoculated at one or more locations in a Petri plate. This will give rise to the typical ring of perithecia mentioned at the end of the chapter "*Podospora anserina* in the tree of life: classification of the species" (see figures 19 and 50). Alternatively, homokaryotic mycelia can be crossed with various setups. The two major ones are "confrontation" and "confrontation arrosée". In the first one, plugs for compatible mycelia are deposited 2 cm apart and incubated without further manipulation. This will result in the production of a line of perithecia at the confrontation between the perithecia (figure 50). Confrontations are for example used to test for the mating type (figure 51). In "confrontation arrosée", three days after setting the plugs, some sterile water (2 mL for an 8-cm Petri plate) is added and the plate is gently shaken. This will dislodge spermatia but not ascogonia. Fertilization will thus specifically proceed with ♀ *mat+* x ♂ *mat-* on one side of the plate and ♂

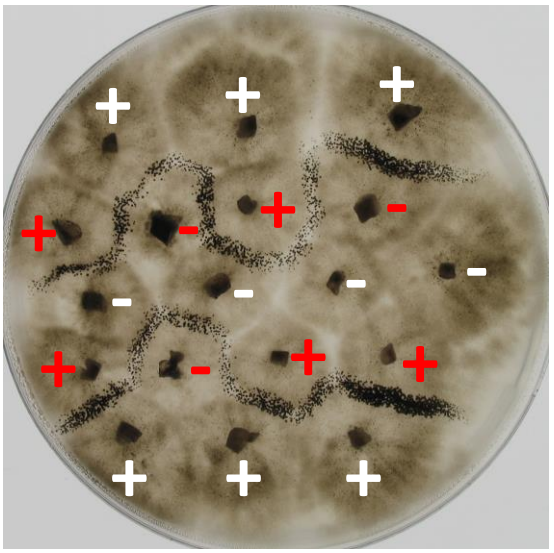


Figure 51 Typical mating type tests. On this plate, *mat+* and *mat-* tester strains (in white) were confronted to eight thalli to ascertain their mating type. Deduced mating types are indicated in red.

mat+ x ♀ *mat-* on the other side (figure 50). *In P. anserina*, it thus very easy to orient the crosses as desired, in order for example to study cytoplasmic versus nuclear segregations. To do so, one needs only to do "confrontation arrosée" and remove with a scalpel the mycelium used as male. Ascospores can then be recovered as usual from the remaining female thallus.

An important feature of *P. anserina* sexual cycle is its rapidity. Overall, it takes about eight days to complete the cycle from ascospore germination to the next generation of ascospores. Ascospore germination occurs overnight (on G medium or after a heat shock). If inoculated on M2, three days after gametes are differentiated. Finally, the process from fertilization to ascospore maturation takes in optimal condition about 4 days at the end of which the ascospores are ejected out of the perithecium. This is much faster than *Neurospora crassa* and *Aspergillus nidulans*. In these two species, the complete cycle lasts two to three weeks. Ascospore production by *P. anserina* crosses lasts for about three to ten days depending upon the medium used and humidity of the incubation chamber. Plates producing ascospores may be stored at 4°C, but no more than a few days (usually at most three days), because ascospore ejection won't resume if longer incubation time is used. Ascospores stored on "Agar plates" will germinate with 100 % efficiency when collected rapidly. However, germination efficiency will drop after three to four weeks at 4°C. Similarly, mycelia issued from germinated ascospores won't keep more than a few weeks on G medium at 4°C, while they may last two to three years on M2 medium at 4°C.

Sexual reproduction appears to be the principal mean of dispersion of *P. anserina* as it seemingly lacks any special mean of asexual reproduction, especially the fertilizing spermatia do not seem to germinate (see previous chapter). However, fragmentation of the mycelium will regenerate new thalli able to complete the whole lifecycle. This is a routine procedure used in the labs. Note that although it is frequently assumed that any cell from fungi is totipotent and could regenerate thalli fully able to

complete the whole lifecycle, spermatia, but also ascogonia and also many cells from the centrum of the perithecia appear unable to do so in *P. anserina*. This has been reported by some of the older authors working on *P. anserina* development but also observed by Robert Debuchy and myself.

Mutant generation

UV mutagenesis at 254 nm is the most convenient method to recover mutants. Doses for wild type range from 100 J/m^2 to 300 J/m^2, the best dose being usually 200-250 J/m^2. It corresponds to 1% survival when measured with protoplasts regenerative potential. Screens obviously depend upon the desired mutants. Positive screens may be started from fragmented mycelium. UVs are usually applied one day after inoculation when the mycelium fragments have started to regenerate and form a "veil" of very young mycelium on the plate. However, if no mutants are obtained with a direct screen or a negative screen is to be used, there is still the possibility to do mutagenesis on protoplasts. Most are uninucleated (and haploid), hence any mutation will immediately express its phenotype. To do this, one needs to do protoplasts as indicated in the section "Methods for macromolecules extraction and genetic transformation - Protoplasts preparation"; then one spreads them onto RG medium at a concentration of 10^4 per plate. Irradiate with UV at 200 J/m^2. Incubate in the dark at 27°C. Regenerants can be picked up after 48h under the binocular to test them individually. At least 5000 of them should be scrutinized before giving up!

Another way to recover mutants is to tape into the genetic diversity of the *P. anserina* species complex. Indeed, some species may present interesting features not present in *P. anserina*, such as the development of "sectors", spore killer genes, the ability to use some carbon sources more efficiently, *etc.* It is possible to analyze the genetic bases of these differences by crossing the interesting species with the sequenced reference strain S (or s) of *P. anserina.* Fertility of these interspecific crosses is poor, but it is possible to obtain few ascospores that in turn will have a better fertility when crosses with both parental strains. It is thus possible to start an "isogenization" process during which the interesting genetic difference (hopefully due to a single polymorphism) can be progressively associated with more and more of the genome of the *P. anserina* reference strain S. We usually do 10 backcrosses with strain S, at which time, the final isogenized strain contains the polymorphic locus and few neighboring genes from the other species, while the rest of its genome comes from S.

Genetical analyses: segregation, dominance/recessivity and complementation

As stated in the previous chapter, spindle positioning and ascospore delimitation is completely defined in *P. anserina* asci and can be summarized as depicted in figure 52. This entails some interesting features for genetic analyses. Firstly, if no crossovers occurred between a gene (with a+ and a- alleles involved in the cross) and its centromere, the ascus contains two ascospores with two a- nuclei and two with two a+ nuclei (see how centromeres behave in figure 52). Secondly, if a crossover has occurred between the gene and its centromere, the ascus contains four ascospores with one a- nucleus and one a+ nucleus (see how the mating type idiomorphs behave in figure 52). Therefore, first (FDS) and second (SDS) division segregation frequencies can be easily calculated (figure 53). Note that this allows doing ordered tetrad analysis with disordered tetrad!

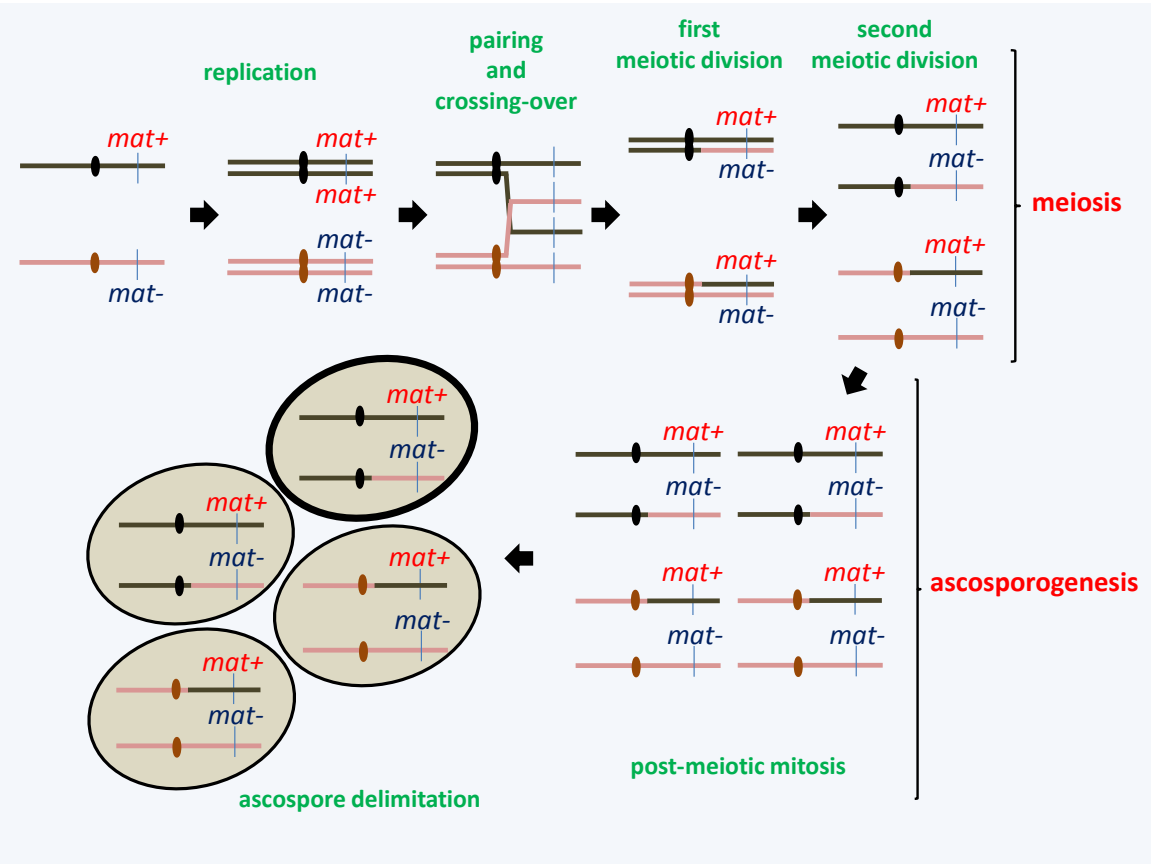


Figure 52 Meiosis and gene segregation in *P. anserina*. Centromeres are the black and brown dots. Only chromosome 1 carrying the mating type locus is represented.

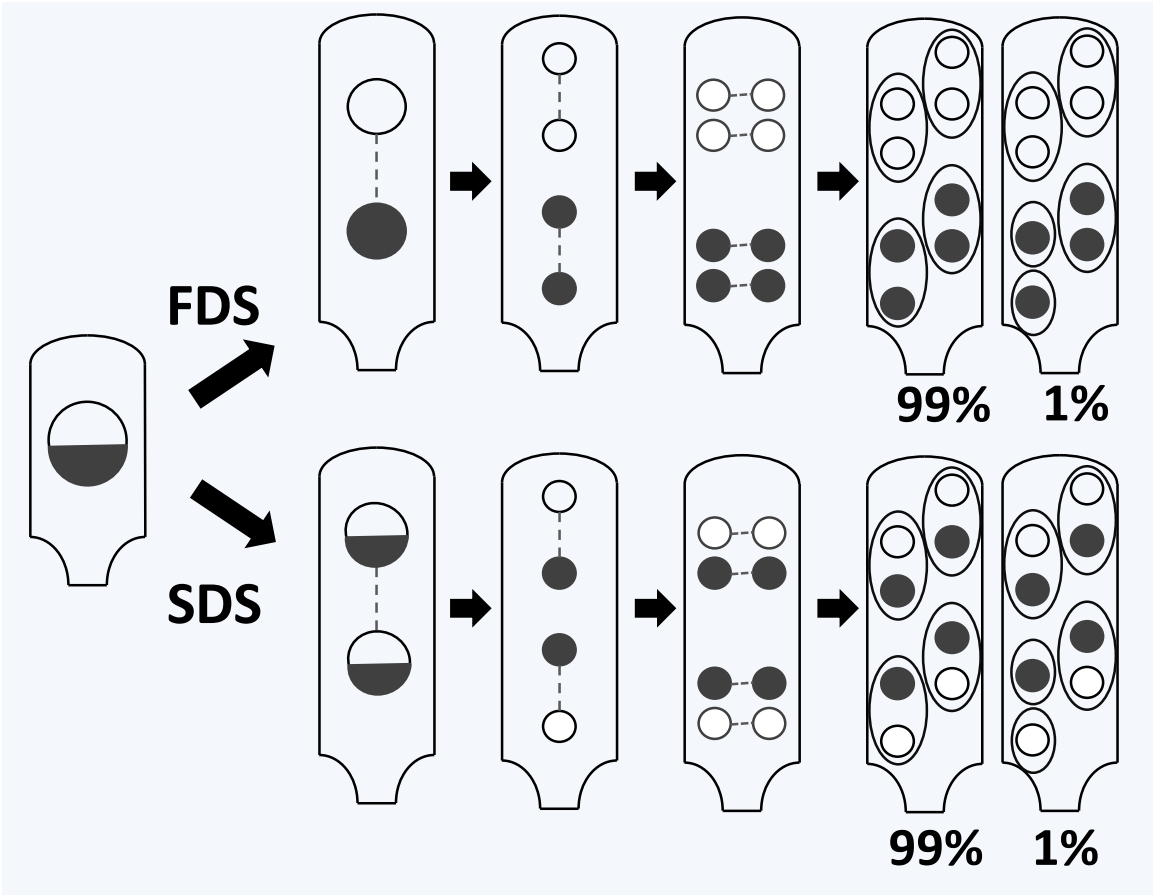


Figure 53 First division (FDS) and second division (SDS) segregation in *P. anserina*.

A second important feature of *P. anserina* meiosis is the positive interference exhibited by crossing-overs, *i.e.*, the presence of one crossing-over inhibits the occurrence of a second one nearby. The interference is so powerful in *P. anserina* that only one crossing-over usually happens over large regions. Especially, in 98-99 % of the meiosis, a single crossing-over occurs between the mating type and its centromere on chromosome 1, allowing for the recovery of *mat+/mat-* ascospores yielding self-fertile mycelia in nearly all asci. Note that on this chromosome arm a second crossing-over usually takes place between the mating type locus and the telomere. This situation is encountered for many chromosomes, with a first crossing-over between the centromere and a region located at about two thirds of the chromosome arms and a second one more distal. Therefore, SDS frequencies usually increase as the genes are positioned farther away from the centromere then decrease to reach the 66 % usually seen

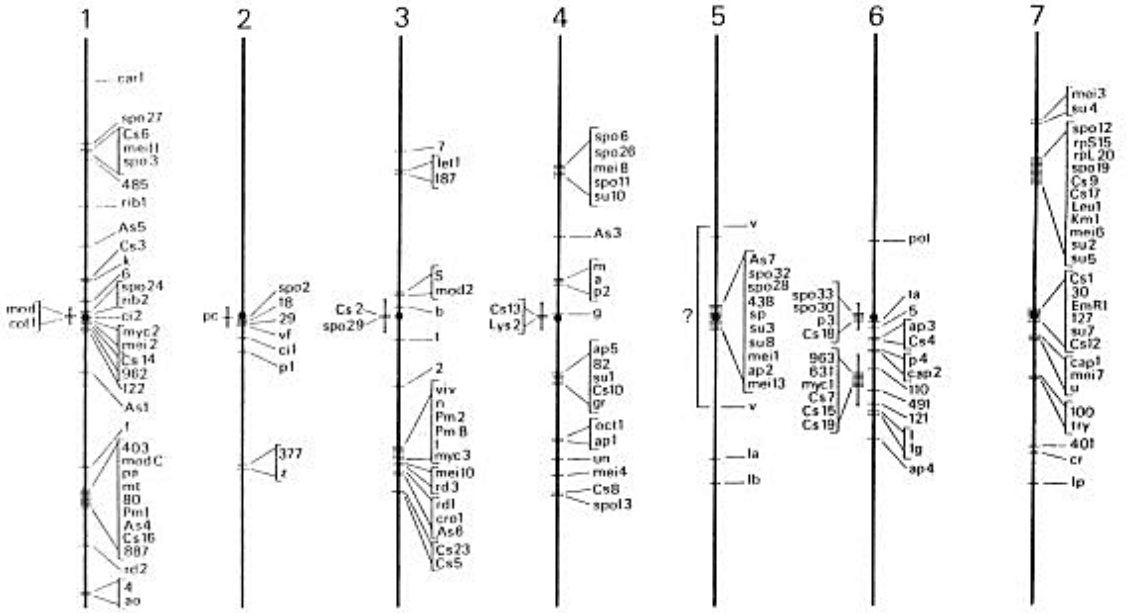


Figure 54 **Linkage map of *P. anserina*.** Positive interference of crossing-overs results in most genes grouped together around the centromere and in the middle of the chromosome arms. The black dots are centromeres. Further analyses carried out since this last official version of the map was published in 1982 have filled some of the gaps between the clustered genes (see figure 63 for an updated version of the genome map). The “left” arms are at the top and the “right” ones at the bottom.

when multiple crossing-overs are present other the same chromosome arm. This entails a linkage map quite different from the ones of other model organisms (figure 54) and the possibility to easily order genes along the chromosome arms. Indeed, parental ditypes, tetraypes and non-parental ditypes are easily determined (figure 55). When two genes are on the same chromosome, non-parental ditype are rare. Moreover, if they are on the same arm, one of the tetratype asci will be more frequent: the one with the gene closest to the centromere segregating with FDS and the most distal with SDS (figure 55).

P. anserina having a haplobiontic life cycle, vegetative diploids are difficult to select and are highly unstable (see the next section on the parasexual cycle). So, apart from the mutations that act between fertilization and meiosis, dominance/recessivity tests must be performed with heterokaryons. There are several simple ways to obtain heterokaryons. They can be directly obtained after sexual reproduction from the big spores. Mycelia of both mating type may be mixed together by simply grinding them in an Eppendorf tube with a spatula or by using a shaking apparatus such as a Fastprep and then

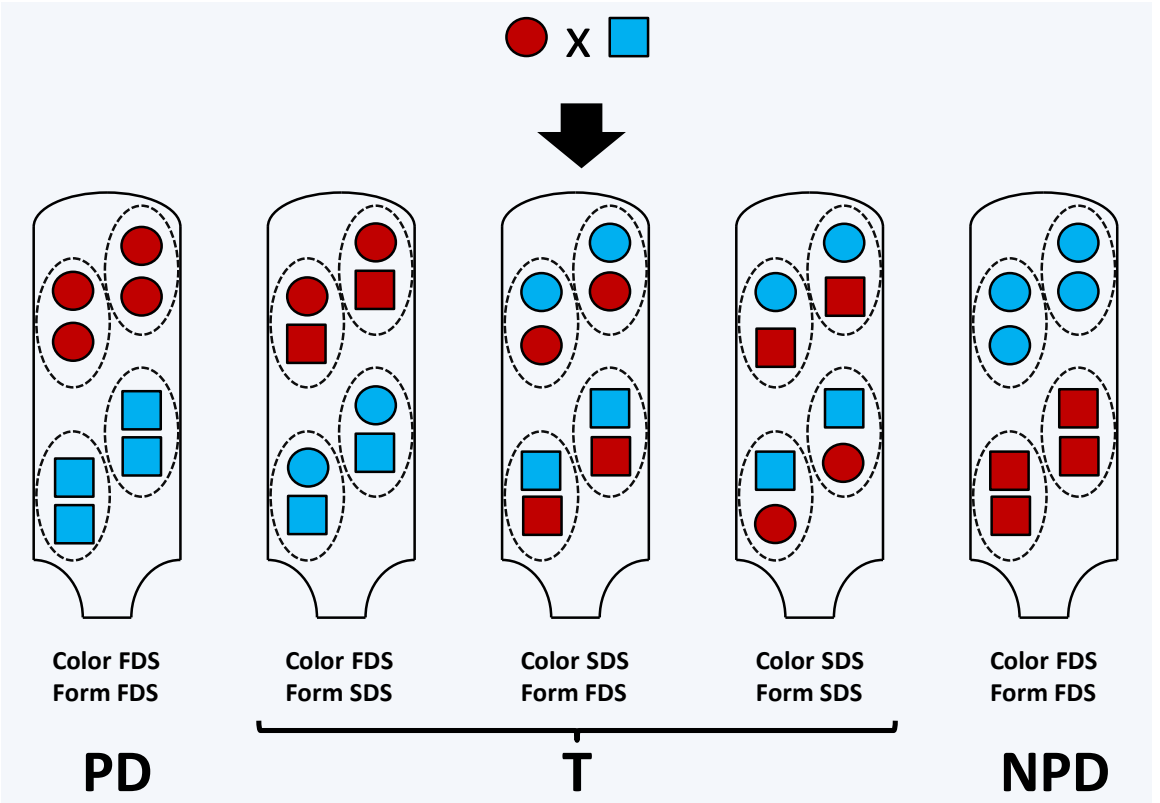


Figure 55 Segregation of two couples of alleles in *P. anserina*. PD: parental ditype, NPD: non-parental ditype and T: tetratype.

inoculating the mix on a fresh Petri plate. Note that these tests in heterokaryons can produce some interpretation problems since very often mutant nuclei (sometime wild-type ones) can be easily lost. To circumvent this, there are simple genetics tricks. One can use strains with complementary mating types, allowing checking through the presence of perithecia if both nuclear types are present. Association of the mutation to be tested with the *leu1-1* (or *lys2-1*) mutations will permit to make forced balanced heterokaryons with *lys2-1* (or *leu1-1*). Testing on minimal medium will ensure that both types of nuclei are present. Note that a problem frequently encountered in heterokaryon construction is the "vegetative incompatibility". Indeed, when anastomoses occur between thalli of the same strain, heterokaryons will readily form and proliferate. However, when anastomoses occur between different wild-type strains, frequently heterokaryotic hyphae will die in a violent death reaction called incompatibility reaction (see section on “Hyphal Interference and Vegetative/heterokaryon Incompatibility”). This occurs for example

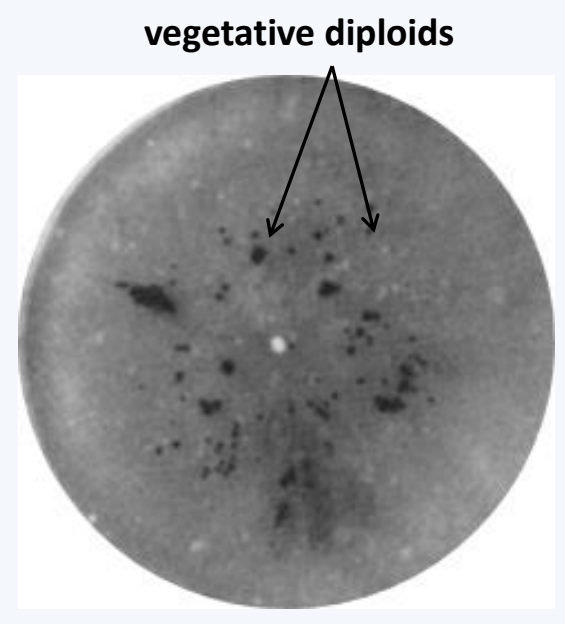


Figure 56 Vegetative diploids using the *SP40* mutant. Taken from the thesis of V. Berteaux-Lecellier

when the S (BIG S) strain is confronted with the s (small s) strain. These two strains are the most commonly used for genetical analysis! In summary, it is advised to construct heterokaryons with compatible strains! Note that complementation tests are often carried out with heterokaryons as described above for dominance/recessivity.

Parasexual cycle

P. anserina, like many ascomycete fungi, is able to form vegetative diploids and hence undergoes a parasexual cycle. However, as stated above, vegetative diploids are quite difficult to obtain. Indeed, they are rare and unstable. There is a way to visualize them by using the *SP40* mutant that carries a reciprocal translocation. When it is crossed with the wild type, some big ascospore progeny gives rise to spindly unpigmented thalli. In such thalli, the two nuclear components carry unbalanced sets of chromosomes. Hence, homokaryons would be non-viable and both types of nuclei must stay in the thalli for their survival. However, in the spindly thalli, complementation between the nuclei is weak, resulting in poor growth. On these spindly thalli, dense patches of pigmented mycelium frequently appear (figure 56). These result from vegetative karyogamy followed by “haploïdization” of the nuclei. This occurs *via* chromosome loss restoring a balanced set of seven nuclear chromosomes. Mitotic crossing-overs as described in the parasexual cycles of other fungi may also occur. Note that the sexual cycle of *P. anserina* is so efficient that the parasexual cycle is used only in special conditions, such as to test whether karyogamy can proceed in some mutants. Moreover, the *SP40* strain seems to have been lost from collection…

Developmental genetics: grafting and genetic mosaics

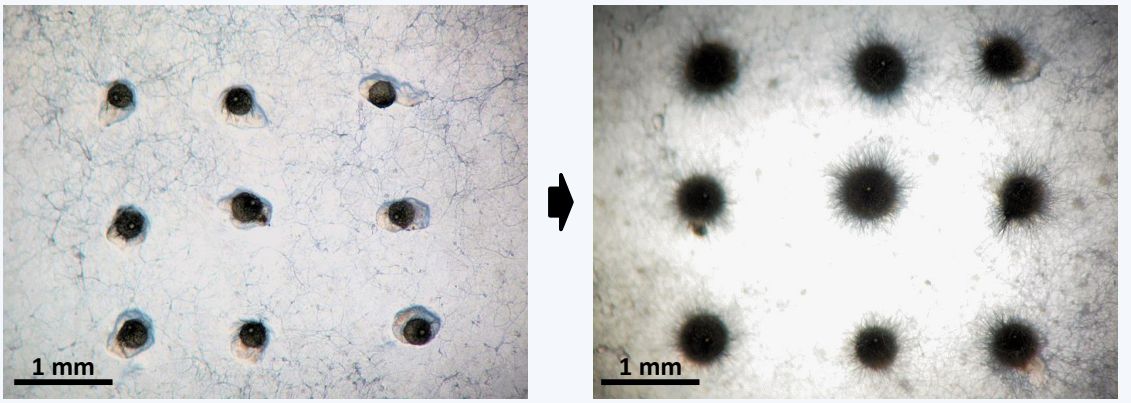


Figure 57 Grafting of perithecia to study their development in *P. anserina*. Nine 2-day-old wild-type perithecia were placed onto a homokaryotic wild-type thallus (left). Two days later (right), transplanted perithecia have completed their development.

Because fruiting body development is the most complex differentiation process exhibited by *P. anserina*, several tools enabling to analyze it genetically have been designed. Firstly, developing perithecia may be transplanted onto other genetically-identical or genetically-different mycelia (figure 57). To do so, simply lift a perithecium along with the smallest amount of underneath agar and gently put it onto the desired mycelium. This should be optimized as taking too little underlying agar will result in perithecium drying and bursting, while taking too much may obscure the results (see movie n°1). When wild-type perithecia are transplanted onto wild-type mycelia, development resume as if nothing happened and nearly 100 % of the grafted fruiting bodies will mature in four days as control non-grafted ones. Note that success rate with one-day-old perithecia may be lower since at that stage it is still difficult to differentiate fertilized from unfertilized protoperithecia. As seen in figure 58, if transplanted onto mutant mycelia, the fruiting body may or may not complete development depending whether the gene affected in the mutant is required or not in the mycelium. The same reasoning applies for mutant perithecia transplanted onto the wild type: maturation will proceed only if the gene affected in the mutant is dispensable in the fruiting body. Note that this kind of experiments with perithecia from mutants is not frequently done because some fruiting body development is needed for grafting to proceed!

Mosaic analyses with the *Δmat* and *pks1-193* mutants enables to gain further insight into the role of genes during development. The *Δmat* strain is a mutant for which the mating type locus has been

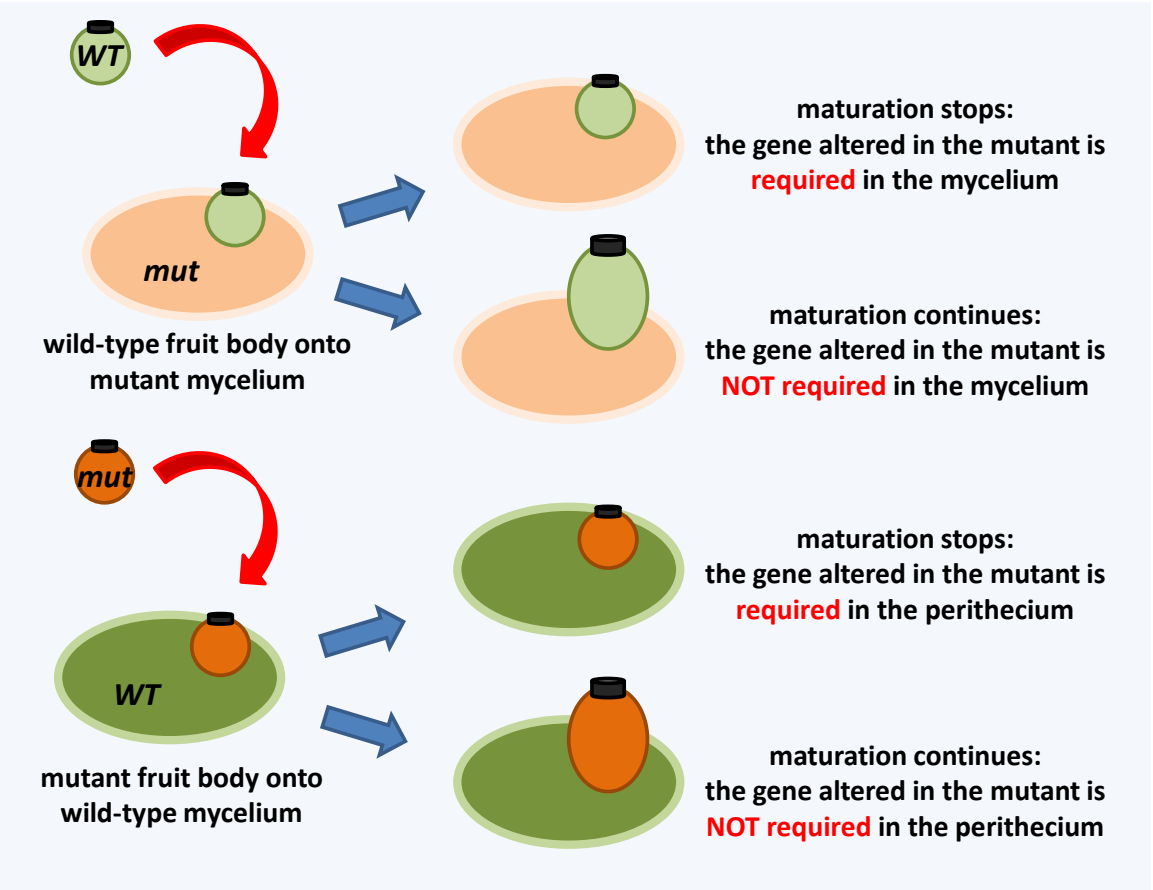


Figure 58 Grafting of perithecia to study their development in *P. anserina*. See text for details.

deleted. This strain is unable to engage fertilization, yet its mycelium is like that of the wild-type. It can thus be used to complement mycelium defect(s) impairing perithecium development. Noteworthy, it is able also to complement maternal defects, but of course not zygotic ones. Hence, when *mat+/mat-* heterokaryotic mutant mycelia are mixed together with *Δmat* in a trikaryon, development of perithecia on the trikaryon means that the gene affected in the mutant is dispensable in the zygotic lineage, while lack of fruiting body entails that this gene is required in the zygotic lineage (figure 59). Note that analyses of the defects in the trikaryons may also enable to dissociate maternal and zygotic defects for genes acting at multiple steps during development. Mosaic analyses with *pks1-193* permit to address whether the development defects are due to mycelium or maternal tissues defects. The *pks1-193* mutants carry a mutation in the gene encoding the polyketide synthase that acts at the first step of the biosynthesis of

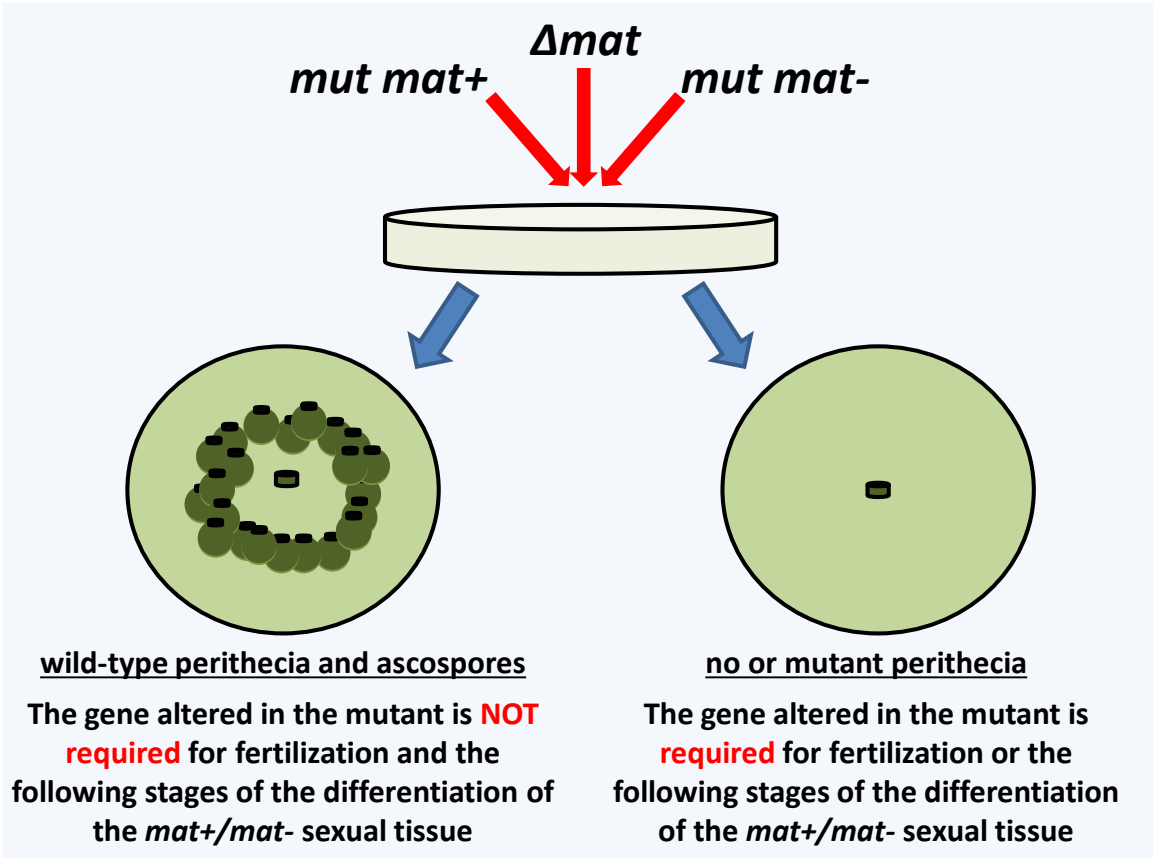


Figure 59 Trikaryon analyses with *Δmat* to study development in *P. anserina*. see text for detail.

melanin. In *P. anserina* this mutation is cell autonomous, because melanin pigments do not diffuse in hyphae. Also the gene acts at all stages of *P. anserina* development: ascospores, mycelia and fruiting bodies, all lack pigments in the mutant (fruiting bodies are also slightly smaller in the mutant). When heterokaryons of compatible mating types are made between the wild type and *pks1-193,* two kinds of perithecia may be observed: pigmented (or dark) ones and non-pigmented (or light) ones (figure 60). The maternal tissues of the pigmented perithecia stems from the wild type and from *pks1-193* in the non-pigmented ones. Note that very few mosaic perithecia with part of their peridium pigmented and part non-pigmented are observed. This suggests that few nuclei are involved in setting up the differentiation of the maternal tissues of the perithecium. When the mosaics are made with a developmental mutant lacking the ability to differentiate fruiting bodies (*i.e.*, a mutant x *pks1-193* heterokaryon of compatible

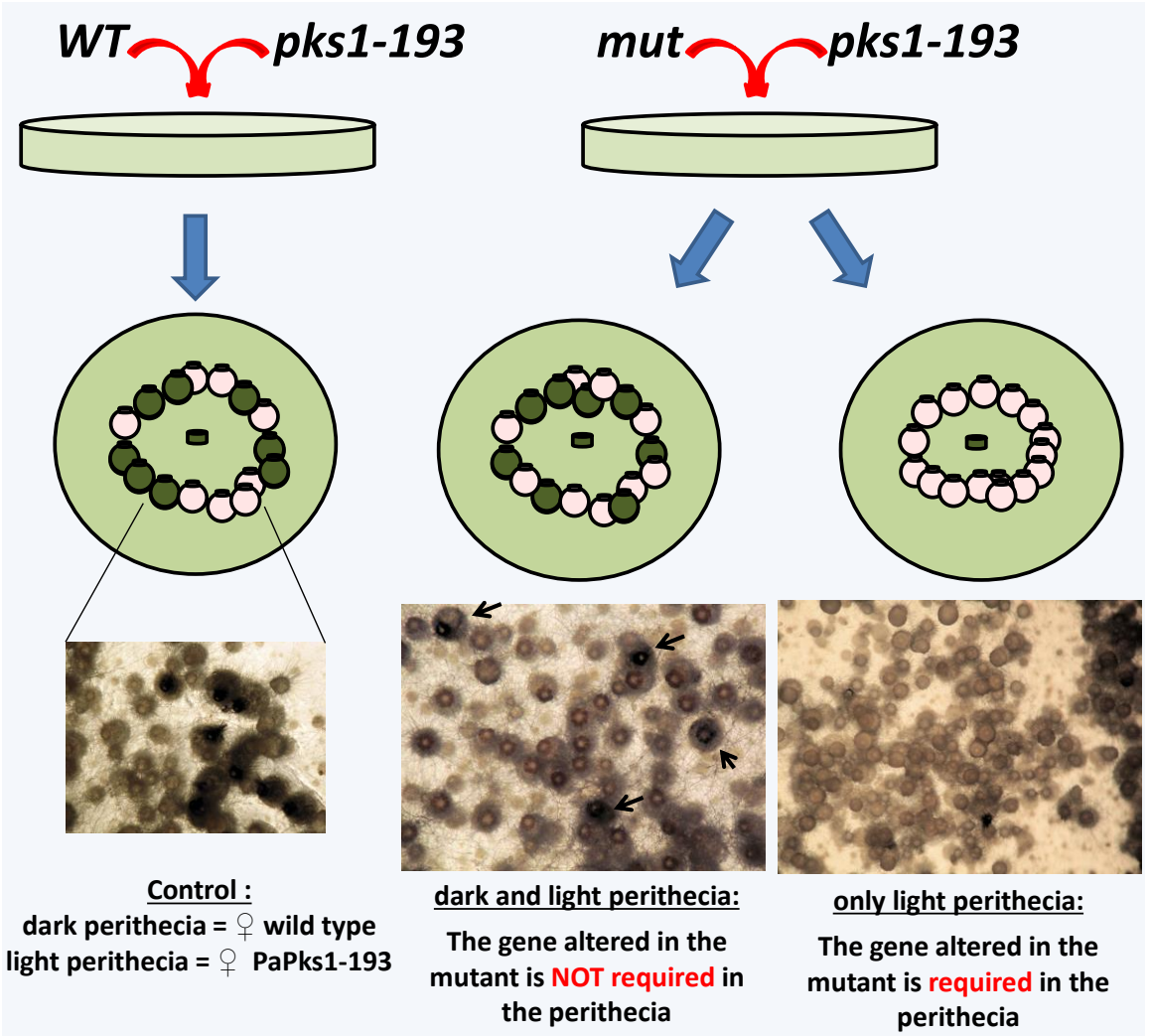


Figure 60 **Mosaic analyses with *pks1-193* to study development in *P. anserina*.** Arrows: dark (=pigmented) perithecia. See text for detail.

mating types), two different outcomes may usually be observed (figure 60). Firstly, no pigmented perithecia may be recovered. This suggests that only perithecia with *pks1-193* maternal tissue may develop and hence that the gene affected in the developmental mutant is required in the developing perithecium. On the contrary, if both pigmented and non-pigmented perithecia are observed, this indicates that the altered gene is not required in the developing fruiting body. Note that a third situation may be observed: the presence in high number of mosaic perithecia with part of their peridium

pigmented and part non-pigmented. This is accounted for if the product encoded by the mutant gene can diffuse from cell to cell and hence in this case the wild type allele of the gene is not required in all the cells of the fruiting body.

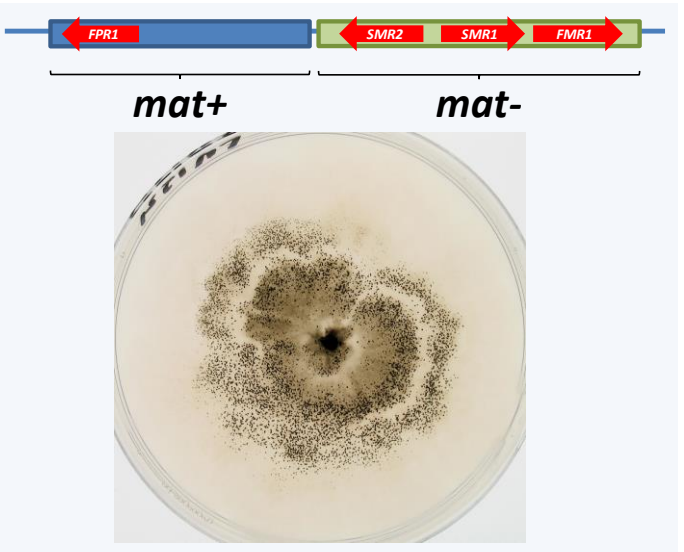


Figure 61 PM154: structure of the mating type locus and phenotype.

The last tool generated to study development is the *PM154* strain. This strain carries both mating type idiomorphs (*mat+_mat-*) in tandem at the mating-type locus on chromosome 1, without any additional genetic modification (figure 61). It is self-fertile and able to fertilize both *mat+* and *mat-* strains. Although it generates abnormal progeny with many incomplete asci, it can be used to easily select sterile mutants, including those affected with recessive mutations in genes acting in the zygotic tissues. Note that in crosses with *mat+* and *mat-* strains, there is a large distortion of segregation with the preferential recovery of *mat+_mat-* progeny.

Genes and genome

With the advent of sequencing and genetic transformation, genetic analyses in many organisms including *P. anserina* have for a time shifted towards more gene-based approaches. In these so called reverse genetic analyses, interesting genes are identified thanks to various methods such as evolutionary conservation or expression in response to stimuli. The function(s) is(are) then determined owing to gene inactivation, as depicted in the chapter “Methods for macromolecules extraction and genetic transformation”. However, with the development of the next generation sequencing (NGS) technologies, gene and mutation identification through complete sequencing of mutant genome have recently been back to the fore, reinvigorating the classic genetic analyses, *i.e.*, the search for mutants affected in

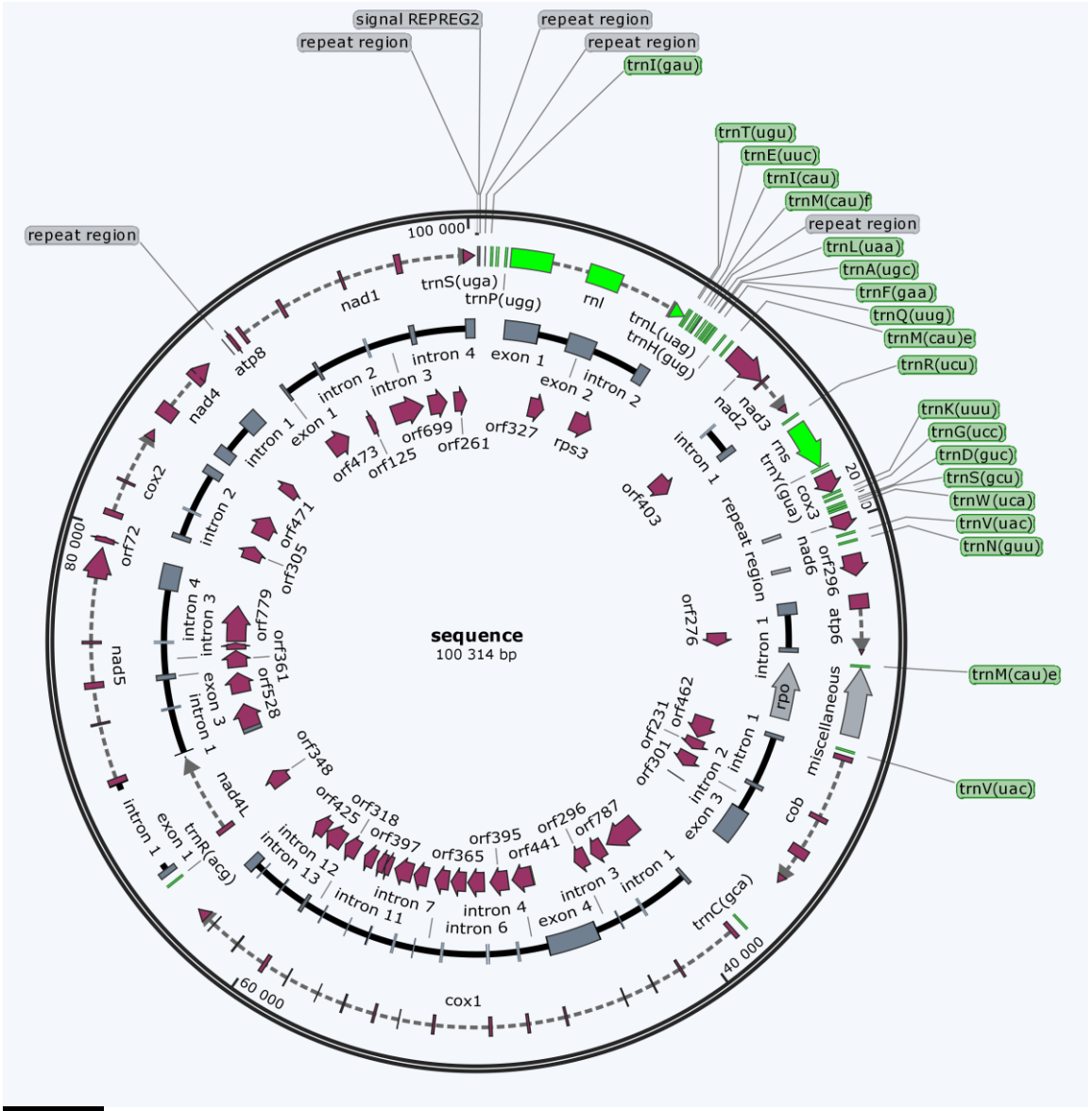


Figure 62 Schematic representation of the *P. anserina* circular mitochondrial genome as defined in 1990. This genome is a composite of the genome of strain s (small s) with three additional sequences (optional introns) from strain A.

defined phenomena and the subsequent identification of the involved genes. Nowadays, genetic analyses rely on both methods, depending on the needs. Importantly, all these genetic methods require the availability of a high-quality sequence of the *P. anserina* genome and more recently on microarray data or

RNAseq transcriptomes for expression-based selection of candidate genes.

In fact, *P. anserina* was one of the first organisms to enter the genomic era, even before it was fashionable. Indeed, as early as 1990, the complete sequence of its circular mitochondrial genome was available. At that time it was the longest contig present in the GeneBank/EMBL/DDBJ databases! The sequence has been determined by the Maxam and Gilbert method for the complete 91 192-bp genome of strain s (small s), as well as for three additional sequences present in strain A with a genome of 100 314 bp (figure 62). Those who do/did sequencing with the Maxam and Gilbert method can truly appreciate the efforts engaged in determining this sequence! The more recent releases of the genome sequence of strain S (BIG S) and s (small s) established with NGS data largely confirmed the sequence obtained then. However, the new sequences contain about 70 differences with the old one. Note that the new mitochondrial sequence of strain S (BIG S) has only one polymorphism with that of strain s (small s), indicating that the differences with the 1990 version are not due to *de novo* mutations during domestication but rather are errors in the old sequence. Presently, annotation of the genomes of both strains (Table 6) defines the following genes: the large (*rnl*) and small (*rns*) precursor of the ribosomal RNA (rRNA), 27 functional and one non-functional tRNA enabling to decode mRNAs using a non-standard genetic code in which UGA is not a stop codon but a tryptophane (W) sense codon, and 53 protein coding genes. In addition, there is a remnant in the genome of an integrated copy of the pAL2-1 plasmid. The free linear pAL2-1 plasmid is present in some strains of *P. anserina*, but not in S and s. Among the 53 protein coding genes some may not be actual genes and most proteins are intron-encoded proteins involved in intron splicing, as is customary in many fungal mitochondrial genomes. The proteins involved in the respiratory pathway are cox1, cox2, cox3, cob, NAD1, NAD2, NAD3, NAD4, NAD4L, NAD5, NAD6, ATP6 and ATP8. This set is typical to what is found in related species. There is also a ribosomal protein (rps3) encoded within an intron of *rnl*.

Additionally, the nuclear genome sequence of *P. anserina* was one of the first available. Decision to establish the sequence was made in 1999 and the first proposal deposited as an answer to a call by Genoscope, at that time the main agency for genomic analysis in France, at the beginning of the year 2000. Because establishing the complete genome sequence appeared an unsurmountable task for the small community working with the friendly mold without additional information, the proposal aimed first at establishing the genome sequence around the centromere of chromosome 5 of strain S. The project was accepted, provided that the DNA came from bacterial artificial chromosomes (BAC) and not cosmids

Table 6: main features of strain S genome		
number of chromosomes	7 nuclear + 1 mitochondrial	the number of chromosome is as expected similar to the one determined by classical genetics (see map figure 54)
genome size (nuclear + mitochondrial)= 36.06 Mb + 94.2 Kb		
chromosome 1	~8 838 400	7 gaps remain on this chromosome; the left telomere sequence is not available
chromosome 2	~5 260 700	4 gaps remain on this chromosome; the right telomere sequence is not available
chromosome 3	~4 736 000	the rDNA locus is present in a sub-telomeric position of the left arm; estimation of the number of rDNA repeats is 70; 3 gaps remain on this chromosome
chromosome 4	~3 887 200	7 gaps remain on this chromosome
chromosome 5	~4 864 800	2 gaps remain on this chromosome; the left and right telomere sequences are not available
chromosome 6	~4 300 800	no internal gap remain on this chromosome, but the right telomere sequence is not available
chromosome 7	~4 174 400	11 gaps remain on this chromosome; the right telomere sequence is not available
mitochondrial chromosome	94 198	the genome is circular
nuclear gene number: protein coding + tRNA + 5S rRNA (pseudogenes)= 10757 (434) + 361 (5) + 87 (8)		
chromosome 1	2711 (84) + 66 (1) + 23 (2)	
chromosome 2	1618 (53) + 42 (2) + 17 (2)	
chromosome 3	1232 (52) + 49 (1) + 13 (2)	
chromosome 4	1158 (45) + 50 (0) + 9 (1)	
chromosome 5	1470 (116) + 63 (0) + 8 (0)	
chromosome 6	1321 (52) + 44 (0) + 12 (1)	
chromosome 7	1247 (32) + 47 (1) + 12 (1)	
mitochondrial genes: 53 protein coding genes + 27 tRNA + 1 tRNA pseudogene + small rRNA + large rRNA		

(which required the construction of the BAC library and its screening for centromere of chromosome 5 DNA). About 480 kb of sequence was established and annotated. The paper reporting the data was published in 2003. This success, as well as decreases in sequencing costs and introduction of better informatics programs for genome sequence assembly, led to the proposal at Genoscope to establish the complete sequence of strain S *mat+* by sequencing the extremities of plasmids having 3 kb or 12 kb inserts, as well as those of BACs and cosmids, with the Sanger methods using fluorescent dyes. To facilitate annotation, the sequences of about 50 000 cDNAs was also established. All the data were made available through internet as early as the end of 2006 and the official paper was published in 2008. Since then, the genome assembly and accuracy of strain S *mat+* has been refined by 454 and Illumina NGS data. The annotation has also been improved thanks to RNAseq information from many developmental stages of the fungus (one-day-old and four-day-old mycelia, two-day-old and four-day-old perithecia, non-germinated ascospores and eight-hour-old germinated ascospores, see “Methods for macromolecules

extraction and genetic transformation - Tools for expression analysis"). Note that the assembly has been confirmed by genetic data, especially by a high-density recombination map generated with markers (mainly microsatellites) polymorphic between the S and T strains (figure 63). A progeny of about 50 descendants of a S x T cross has been analyzed for about 250 markers scattered all over the genome, enabling to build the map. The genome sequence of strain S *mat-* has also been determined and compared to that of S *mat+*. Differences were only found at and around the mating type locus in the 800-kb region devoid of recombination (figure 63). These updated versions of the genome of strain S are available at GenBank and that of S *mat+* also at the "*Podospora anserina* Genome Project webpage" (http://podospora.i2bc.paris-saclay.fr/) and at the Mycocosm portal of the JGI (https://genome.jgi.doe.gov/programs/fungi/index.jsf).

The genomes of additional *P. anserina* strains have been recently released. Firstly, the genome of an undefined strain was made available at Mycocosm. Although this strain has no name, it is related to the s (small s) *mat+* strain, because it has the s sequence at the HET-s/S locus. Sequence was generated by PacBio and has few gaps, especially sequences for the 7 centromeres have been determined. However, sequences for some telomeric ends are still not available for all chromosomes. Extensive RNAseq data of the fungus grown on various food sources are also available for this JGI Strain. Secondly, Vogan et al. (2019) released the genome sequences of 10 *P. anserina* strains (Wa21-, Wa28-, Wa46+, Wa53-, Wa58-, Wa63+, Wa87+, Wa100+, Y+ and TG+). The genomes *P. comata* T *mat+* and *P. pauciseta* CBS237.71 *mat-* are also available as drafts; the former definitively establishing that strain T belongs to a separate species. RNAseq data are also available for strain T *mat+*. They were established on a mix of mRNA extracted from several developmental stages. It is likely that rapidly, additional RNAseq data for strain S, as well as genome sequences and RNA seq data for other strains of *P. anserina* as well as other species of the *P. anserina* species complex will be available shortly. It is beyond the scope of this book to enter into the details of all these genomes and expression data. However, main characteristics of the strain S *mat+* genome are summarized in Table 6. The nuclear genome of this strain measures about 36 Mb. It is predicted to encode 10 757 protein coding genes, 361 tRNAs and 87 copies of the 5S rRNA gene. In addition, it contains 434 pseudogenes of protein coding genes, 5 pseudogenes of tRNA and 8 pseudogenes of 5S rRNA gene. Note that the pseudogene number is even higher in strain T in which more than 800 have been identified!

The nuclear chromosomes are organized like most eukaryotic chromosomes. Centromeres are

composed of AT-rich sequences originating from transposons, likely through the accumulation of RIP

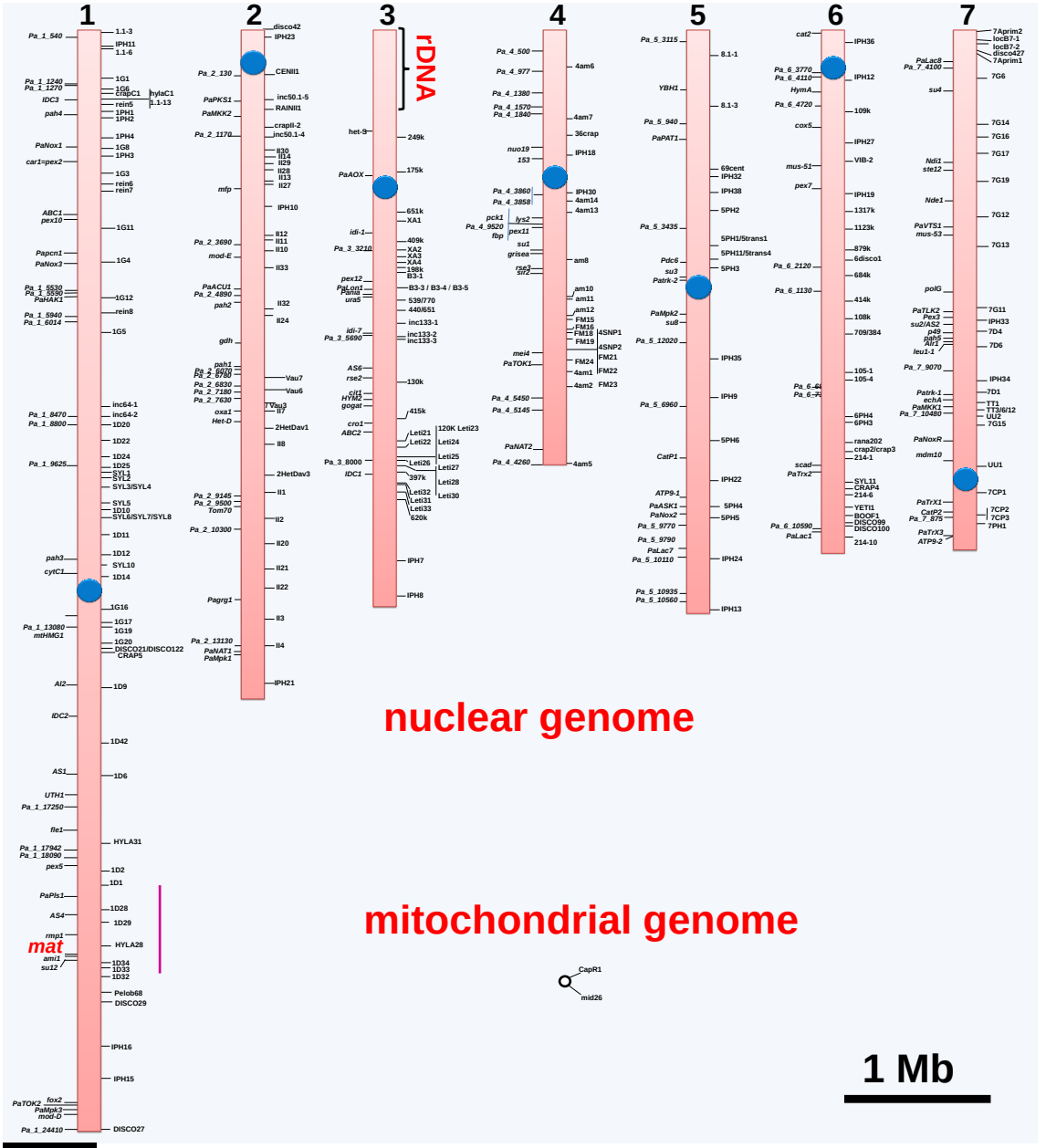


Figure 63 Schematic representation of the *P. anserina* genome as defined by complete sequencing. The chromosome are to scale (note the very small size of the mitochondrial chromosome). The blue dots are the centromeres. Main genetic markers are indicated on the left side, including classical genetic markers (*i.e.*, mostly the mutations generated in strains S or s) and newly-constructed gene deletions. On the right side are the polymorphisms with strain T used to help with genome assembly. The rDNA is on the left arm

of chromosome 3 in a sub-telomeric position. The purple line identifies the region devoid of recombination around the mating type.

mutations. RIP is a phenomenon first described in *N. crassa* and later on in *P. anserina*. This phenomenon results in the accumulation of C to T mutations in duplicated sequences. Only sequences duplicated in the same nucleus are inactivated, while those present in single copy in the other nucleus are not affected. The mutations may thus be prompted during the dikaryotic stage of the sexual tissues. While very efficient in *N. crassa*, the phenomenon is less pronounced in *P. anserina*, since only ascospores produced late harbor mutations and the mutation frequency is low (0.3 -with unlinked repeats- to 15 –with tandem repeats- mutations per kb were detected by sequencing). Nevertheless, duplicated sequences such as transposons accumulate C to T mutations through multiple rounds of sexual reproduction, resulting in high AT content. In the centromere, this percentage is about 75%. Centromeres measures from 56.5 kb for chromosome 3 to 87.5 kb for chromosome 2. Chromosome 1 centromere may be bipartite. This chromosome is twice as big as the others (Table 6, figure 63) and may have resulted from the fusion of two acrocentric chromosomes by their centromere-carrying ends. Indeed, there are two large AT-rich regions of 81 kb and 38 kb separated by a 500-kb region devoid of recombination. The 81-kb region has been assigned the role of centromere, but lack of recombination between the two regions may be indicative that the 38-kb one may also play a role as centromere.

Telomeres are also typical for eukaryotes. They end by GGGTTA repeats. Although not all ends are properly assembled, there are sequence reads containing these repeats necessary for all chromosome ends being capped this way. In sub-telomeric regions, there are also transposons inactivated by RIP. These regions have variable sizes, ranging from 2-3 kb to several dozens of kb. They often contain a degenerate helitron, as described in other fungi. Transposons, often associated with small segmental duplications, are present within the chromosome arms. They are mostly nested together in regions that may reach sizes up to 50 kb. RIP has also acted on these regions, which are thus rich in AT. There are at least 51 different transposons (Table 7), few being functional due to inactivation by RIP. The largest is the retrotransposon “Grenouille”, measuring nearly 12 kb, and the smallest is the retrotransposon "Eleutherodactylus”, which is only present as LTR (Long Terminal Repeat) of 58 bp. Note that many repeated sequences are of unknown affinity (Table 7). Annotation of these sequences is ongoing, since assembly of the repeated regions still contains gaps. Overall, these repeated regions cover about 5-10% of the genome.

Other repeated regions are the ones coding for the rRNA. There are 87 copies of the 5S rDNA

gene scattered all over the genome (Table 6) and the rDNA locus, which is in a sub-telomeric position on

Table 7: *P. anserina* strain S transposons and repeated sequences of unknown affinity

Family	Name	Element size (bp)		Estimated copy number	
DNA transposons			ITR size		
mutator-like	dendrobates	3 449	65	3	
Tc1/mariner-like	discoglosse	1 867	49	153	
	pelobate	1 948	45	20	
	rainette	1 298	41	9	
	scaphiopus	1 428	23	1	
MITE	altiphrynoides	403	50	5	
	discodeles	257	40	49	
	mantella	383	46	18	
LTR retrotransposons		full element	LTR	full element	solo LTR
copia/Ty1	centrolene	5 918	182	18	14
	hyla	6 466	630	10	63
	nephelobates	5 594	445	7	0
gypsy/Ty3	crapaud	7 372	400	80	>300
	grenouille	11 866	360	20	53
	pipa	>4 242	?	1	0
	yeti	6 943	355	2	37
solo LTR	boophis	?	367	0	3
	alytes	?	230	0	3
	arthroleptis	?	238	0	10
	ascaphus	?	170	0	6
	astylosternus	?	172	0	12
	atelopus	?	601	0	9
	bufoides	?	153	0	6
	capensibufo	?	256	0	11
	cochranella	?	155	0	18
	crepidophryne	?	137	0	6
	cyclorana	?	194	0	8
	dendrophryniscus	?	73	0	5
	eleutherodactylus	?	58	0	14
	nyctibates	?	169	0	5
	pelodytes	?	128	0	8
	rana	?	508	0	17
	xenopus	?	235	0	16
helitron					
	epipadobates	8388		22	
unknown affinity					
	adenomus	382		14	
	allophryne	268		9	
	amolops	585		31	
	andinophryne	122		12	
	ansonia	90		5	
	batrachyla	192		20	
	bombina	680		10	
	bombinator	472		5	
	brachycephalus	259		5	
	bufo	699		9	
	callulops	302		5	
	cardioglossa	182		5	
	churamiti	143		6	
	lechriodus	246		13	
	leptodactylodon	570		22	
	leptopelis	112		6	
	microhyla	1179		8	
	platymantis	593		8	
	schoutedenella	241		7	

the left arm of chromosome 3. Based on the frequency of sequence reads for the rDNA versus that of single copy regions, the number of copy of the rDNA has been estimated to 70, which is in line with the 87 copies for the 5S genes. The rDNA unit measures 8 083 pb and is organized classically: 18S precursor – ITS1 – 5.8S precursor- ITS2 – 28S precursor- large intergenic region. Note that the large intergenic region contains 3 different small repeated sequences of about 40, 100 and 150 bp.

On figure 63, in addition to the polymorphic markers used to construct the linkage map used for assembly are indicated some of the available genetic markers that can be used for genetic mapping. These results from both forward genetic mutants for which the affected gene has been identified and reverse genetic mutants. As seen, the genome, including the mitochondrial chromosome, is well covered. Important markers are firstly the mating type, with its two idiomorphs *mat+* and *mat-*, located on chromosome 1. As exposed above, this locus has been deleted and the resulting strain is used in developmental genetic analyses (see "Developmental genetics: grafting and genetic mosaics"). A chimaeric *mat+_mat-* locus is also available in strain *PM154, a* strain also used to study fruiting body development (see also "Developmental genetics: grafting and genetic mosaics"). The second important marker is the mid26 one. It is located in the mitochondria and is the clean elimination of the first intron of the *cox1* gene. This intron is involved in the shortening of the life span of the fungus. Without the intron, strains live three times longer! Introducing this marker into short-live strains make them more amenable to analysis. First obtained in the s (small s) strain, this marker has since been introgressed into the S (BIG S) genetic background by 10 backcrossed with the S strain. Introduction is simply done by crossing the desired strain as male to the mid26 strain as female. All progeny will carry the mid26 marker.

Part 2: *Podospora anserina* as a model for physiological and molecular analysis

In this second part of the book, several features of *P. anserina* lifecycle and lifestyle will be introduced, especially those that involves analysis of molecular pathways. Note that studies of these have often led to a better understanding of biology. Indeed, *P. anserina*, owing to its ease of use and speed of the sexual cycle, is an excellent model to tackle problems that would be hard to study with other organisms such as ageing or recognition of self-*versus*-non-self. However, the smallness of the community working with this fungus makes it such that our knowledge on many subjects is often patchy. We shall see in turn all aspects of the *P. anserina* stages: spore, vegetative thallus, namely the mycelium and finally the reproductive phase.

Ascospore ejection and germination

As the first stage of the lifecycle of the fungus, ascospores have two roles: dispersal and persistence. Surprisingly, modalities of both phenomena are poorly known for *P. anserina*. As previously stated, ascospore are forcibly discharged out of the fruiting body thanks to a turgor pressure-operated mechanisms. The deletion of the *Trk-1* gene involved in potassium import inside the cell impairs this process, while deletion of the genes involved in export results also in lack of spore ejection on medium with high potassium concentration. This suggests that proper turgor driven by intracellular potassium concentration is essential for correct ascospore ejection. Asci are ejected one at the time out of the fruiting body and the four (or five) ascospores often stick together thanks to the actin rope that links spores. Ejection distance is a few dozen centimeters and it is probable that wind also participate in later stages of dispersal before asci land on neighboring plants. How long in the wild ascospores may persist is not known, but it is likely that their lifespan outside the fruiting bodies is short. Indeed, in the lab we know that ascospores kept a few weeks at 4°C on agar covers fail to germinate and that their drying results in complete failure of further germination. However, we also know that *P. anserina* is able to resist in the wild on dried dung for a long time (several weeks) and renew rapidly ejection of viable ascospore when rehydrated. Yet, on Petri plates, ascospore production and ejection is irreversibly stopped if the conditions are too dry or two cold. Finally, we know that drying fertile mycelium with fruiting body-carrying ascospores overnight at 65°C does not result in death of the fungus. From all of these scattered data, the best guess is that ascospore ejection is sensitive to drying but that somehow natural drying; which may be slower that what is done in the lab, may result in preservation of the ejection function. Also, ascospores drying inside the fruiting body may survive, while they are much more fragile after ejection.

In the wild, the next step for ascospores is to be ingested by an herbivore to trigger germination. This stimulus is complex as it involves heat shock (37°C is a lethal temperature for the fungus, while 36°C is not…), drastic pH change that may differ from one type of animal to the other, attack by proteases, carbohydrate hydrolases and biliary salts… While some fungi require an exact combination of these for

germination, *P. anserina* is not demanding in its germination conditions, accounting for its presence not only in dung but in other biotopes. Indeed, while the G medium is routinely used to obtain 100% germination, high percentage of germination (often >80%) can be obtained by treating ascospores with heat shock (55-65°C for ~30 minutes), H_2O_2 (3% for 20 minutes), phenolic compounds (10^{-3}-10^{-4} M) and action of pancreatin (1-2 h at 37°C). It is likely that many other as yet untested stresses can trigger germination of *P. anserina* ascospores.

The molecular pathway involved in the triggering of germination has been addressed by

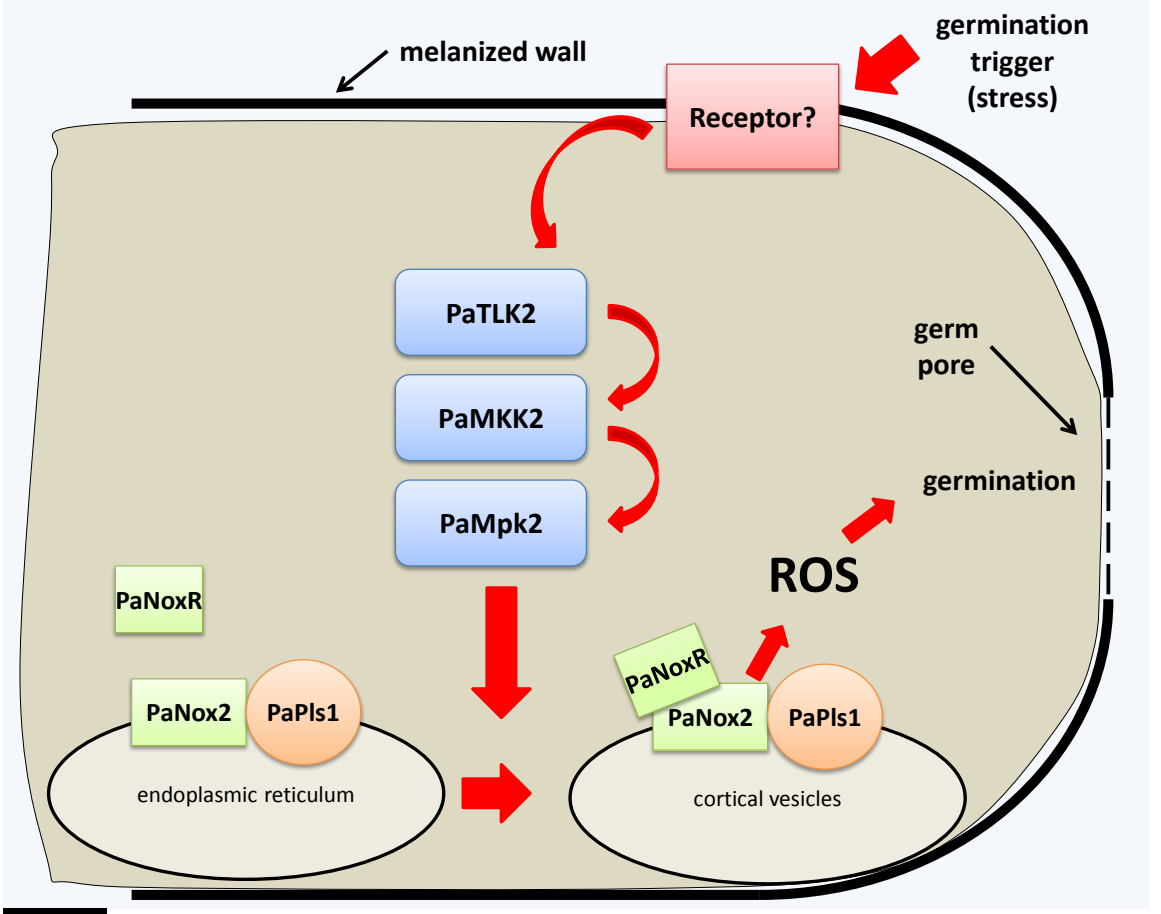


Figure 64 Schematic representation of the *P. anserina* ascospore germination pathway. Germination is triggered by several stresses that may act through different and as-yet unknown receptors. These activate through unknown mechanisms the PaMpk2 MAPK kinase pathway, which in turn activates the PaNox2/PaPls1 NADPH oxidase. Activation of this complex results in reactive oxygen species (ROS) production, likely superoxide anions. This promotes the breaching of the germination pore by the germination hyphae and germination of the ascospore.

identifying mutants impaired in germination. These are affected in the PaNox2 NADPH oxidases, the PaPls1 tetraspanin and the PaMpk2/PaMKK2/PaTLK2 MAP kinase module. In these mutants, ascospore germination is completely abolished. Conversely, a mutant having a constitutively active PaMpk2 MAP kinase germinates spontaneously at high frequency. Introducing the constitutive mutation into the PaNox2 and PaPls1 mutant background fails to restore germination suggesting that the MAPK module acts upstream of PaPls1 and PaNox2. A model presenting the germination pathway in *P. anserina* is proposed in figure 64. Pigmentation is also an important factor in the process since lack of pigment, effected either by genetic or chemical inactivation of the melanin pathway (see next chapter) results in spontaneous germination, even in the presence of the PaNox2, PaPls1 and PaMpk2 mutations. Other mutants presenting ascospore germination defects are known, especially those affected in peroxisomal proteins. However, peroxisomal mutants also present ascospore pigmentation defects, making it difficult to know whether germination impairment is a direct consequence of the mutation or an indirect one linked to pigmentation problems. Interestingly, a connection between ascospore germination and development of appressorium-like structures involved in biomass penetration has been found. Indeed both processes are under the same genetic control (see next chapter).

As explained in the chapter on morphology, *P. anserina* is able to produce sometime in very large amount spermatia, questioning their possible role as dispersal units. Cytological analysis revealed that spermatia contain one nucleus and a mitochondrion embedded inside a fair volume of cytoplasm. They carry thus everything needed to germinate. Yet all attempts, but one that could not be reproduced recently, made to trigger germination failed. Even in the successful case, only 1% germination was achieved. Pending the discovery of efficient conditions for germination, spermatia are thus best considered as serving only as male gametes.

Mycelium growth and development

Owing to the small sizes of the hyphae, *P. anserina* is not routinely used to study the basic mechanisms involved in mycelium growth, unlike *N. crassa* in which many studies are made. I will thus rather emphasize phenomena occurring during the vegetative phase, namely, Senescence, Crippled Growth and other phenotypic instabilities, vegetative/heterokaryon incompatibility including its control by the Het-s prion, hyphal interference and differentiation of appressorium-like structures. I will start with some basic description of the physiology and metabolism of the mycelium.

Growth of the fungus is best achieved on medium with a pH=7.2-7.6, which is the pH value of the M2 medium. After growth the pH is still equal to about 7, indicating that *P. anserina* does not drastically alter the pH of its growth medium. The usually-used temperature for cultivation is 27°C. Lethal temperatures are over 36°C. In many strains, as previously stated in Part 1, there is a polymorphic gene closely linked to the mating type that influences growth at high temperature. In many strains, including strain S, the *mat-* isolates grow better than *mat+* ones at high temperature. For example at 36-37°C, the S *mat-* isolates differentiate aerial hyphae, while the S *mat+* ones do not. This gene also controls longevity (see below). As expected, the fungus grows slowly at low temperatures and it still grows at 10°C. Light is not necessary for growth but is required for proper pigmentation. Major pigments are melanin synthesized by the dihydroxynaphtalene (DHN) pathway. The PKS acting at the first stage of the pathway has been identified and is required for pigmentation at all stages of the lifecycle (mycelium, fruiting bodies and ascospores). On the contrary, only the laccases acting in the ascospores have been identified. These enzymes are involved at the last stage of pigment production, *i.e.*, during the polymerization of the 1-8-dihydroxynaphtalene precursors into melanin inside the cell wall. Hyphae need to be about two-day-old to start to accumulate pigment. In the absence of melanin, the mycelium often accumulates after a few days a pinkish color, likely resulting from the oxidation of cytochromes.

The fungus is able to consume various carbon sources to promote mycelium growth, but not all of them may sustain further sexual development. Indeed, glucose is efficiently utilized for vegetative

growth but results in severely diminished fertility, when compared to dextrin, starch or amorphous cellulose (paper). Hence, the fungus is almost sterile on potato dextrose agar (PDA). Noteworthy, *P. anserina* lacks invertase and is thus unable to consume sucrose. Intriguingly, glycerol is also not metabolized well, although *P. anserina* possesses the transporters and enzymatic pathway to metabolize this compound. The fungus thrives on complex biomass, including dried hay, straw, miscanthus, oat meal, cotton seed hulls, soybean hulls and many woody substrates. Dung is of course well used; however, we see some fluctuation in the ability of the fungus to produce mycelium and fruiting bodies on different dung pellets, even from originating from the same animals. Growth requires oxygen since the fungus does not propagate, but does not die, in anaerobiosis. Nitrogen also has a large impact on growth and fertility. The fungus is for example sterile on media containing more than 1 g/L of yeast extract. It is also sterile in the presence of too much ammonium ions. The fungus is thus routinely grown on autoclaved urea, but it can also use nitrate and various amino acids. It requires thiamin for growth and both thiamin and biotin for fertility (see below the section on sexual reproduction). In summary, *P. anserina* can grow on many media, but is rather fussy when it comes to sexual reproduction, then the growth medium must not be too rich in both carbon and nitrogen sources, and must contain biotin. Please, see below the section on “Fruiting body production and repartition” in the chapter on “Sexual Reproduction” for detailed analysis of the parameters enabling sexual reproduction.

All the above parameters influence the morphology of the mycelium that may or may not follow rhythms. Rhythmic growth is also under a genetic control since many mutants having such pattern of growth on all media have been described.

Senescence and the Premature Death Syndrome

Unlike what is observed in many fungi, the vegetative growth of *P. anserina* is not unlimited. It stops definitively at one point and is accompanied by the death of the apical cells (figure 65). This phenomenon is called Senescence and is used as a simple model to study ageing. In fact, despite the claim by many that senescence was first observed on human fibroblasts, limited cell division was first described in *P. anserina* as the publication dates of the papers attest (1953 for *P. anserina* and 1961 for fibroblasts). To date, all strains taken from nature that belong to one of the seven species of the *P.*

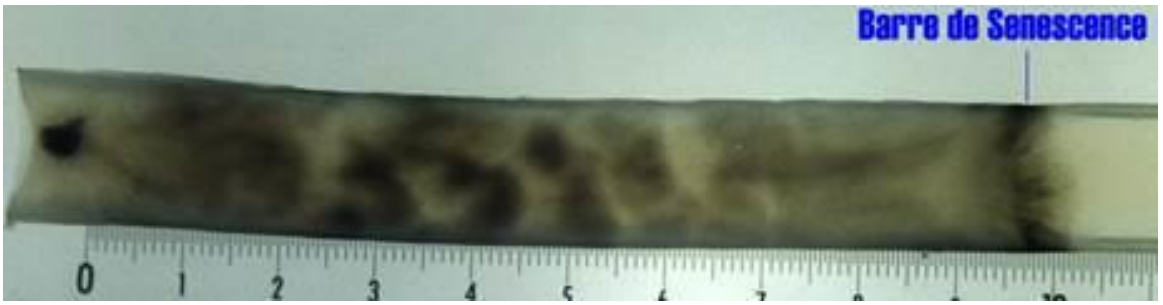


Figure 65 **Senescence in *P. anserina.*** On this culture grown in race tubes, ascospore germination occurred on the left. The mycelium then developed toward the right until growth ceased. Intense pigmentation or "Barre de Sénescence" accompanies the growth stoppage. In Barre de Sénescence, cells are dead. Cells located closer from the germination point are still alive. This culture grew for about three weeks, *i.e.*, for 10 cm, before dying.

anserina species complex have been observed to undergo Senescence, albeit with different life span that may range from 2-3 centimeters to more than 20 cm on M2 medium, indicating that Senescence is a constant features of these fungi.

At the cellular level, Senescence is accompanied by a drastic reorganization of the internal membrane networks (mitochondria and the nuclear membrane/endoplasmic reticulum network). Often the fungus is female-sterile close to the "Barre de Senescence", although few and abnormally-maturing perithecia may sometime be differentiated. Male fertility appears not drastically affected. At the molecular level, Senescence is correlated with mitochondrial DNA modifications (figure 66). The one that is the most often observed is the accumulation as a circular plasmid deriving from the first intron of the *COX1* genes. This DNA molecule is called senDNAα or plDNA. Nevertheless, other parts of the mitochondrial DNA may amplify as circular molecules during Senescence, the senDNAβ and senDNAγ. Intriguingly, the PAL2-1 linear plasmid hosted by the mitochondria of some strains promotes long life (similar plasmids are known to trigger senescence-like processes in *Neurospora spp.*). Early formal analyses have shown that Senescence is caused by the accumulation of a cytoplasmic and infectious element, called the "determinant of Senescence" and whose molecular nature is still unknown. This was demonstrated by several experiments, including formal analysis of the longevity of subcultures (figure 67), analysis of the segregation patterns of senescence (figure 68) and micromanipulation of hyphae under the microscope (figure 69). The relationship between the mitochondrial DNA modifications and the cytoplasmic and infectious determinant is not clear, since they were shown not to co-segregate both

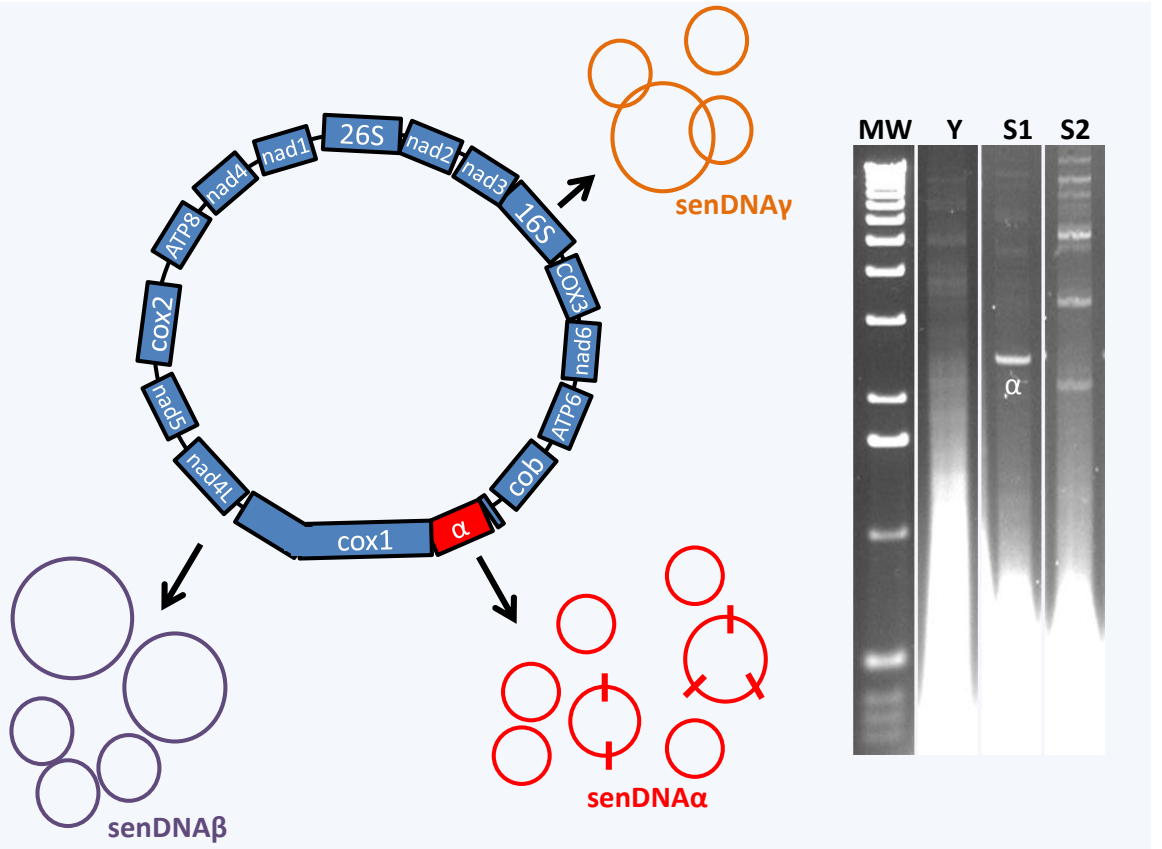


Figure 66 **Mitochondrial DNA modifications observed during Senescence in *P. anserina*.** Left, scheme of the mitochondrial DNA in young cultures and origins of the senDNA molecules amplified during Senescence. Right, agarose gel stained with ethidium bromide showing the structure of the mitochondrial DNA molecules in young (Y) cultures and in senescent ones (S1 & S2). In S1, the amplified molecule is senDNAα while senDNAα is not amplified in S2. MW: molecular weight.

during contamination experiments and meiosis. Especially, senDNAα, which was thought at one point to be the determinant of Senescence, does not accumulate in some senescing strains. Moreover, a strain deleted for the first intron of COX1, and thus unable to amplify senDNAα, was found to undergo Senescence, albeit with a longer lifespan.

Longevity can be easily monitored with *P. anserina* since it can be measured in centimeters of growth! There is thus no need for constant surveillance of the culture to accurately measure longevity, a feature that is not possible in many models, especially in animals that need constant surveillance to determine the actual time of death. Longevity is under the control of numerous nuclear genes,

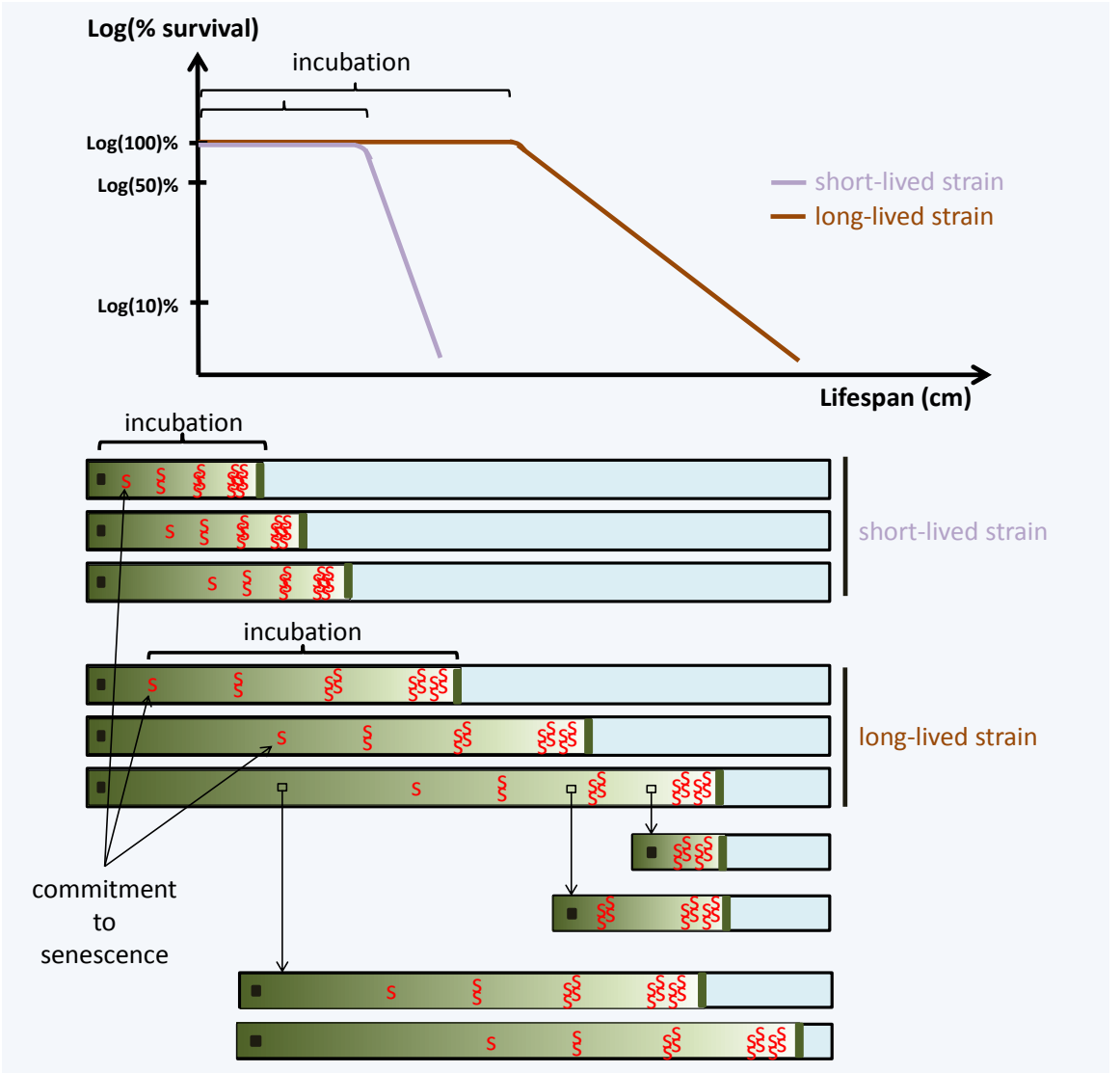


Figure 67 Lifespan analysis in *P. anserina*. Top, lifespan curves of two strains, one short-lived and the other long-lived. The logarithm of the percentage of surviving cultures is given as function of the distance between the inoculation point and the Barre de Senescence. These curves have two different parts. The first one in which the percentage is equal to 100 % shows that all cultures are able to grow for certain duration, called the incubation period. The second one is typical of the occurrence of a random event with a constant probability (given by the slop of the line). Interpretation of these curves is given below. In cultures, a random event occurs, the commitment to Senescence (*i.e.*, the appearance of the Determinant of Senescence; red S). Once this determinant has appeared, it amplifies exponentially following a constant kinetics before it kills the cells. This model can be verified by re-inoculating explant to new medium: those taken after commitment yields short-lived cultures, while those taken before commitment will generate various lifespans following the same curve as the first cultures.

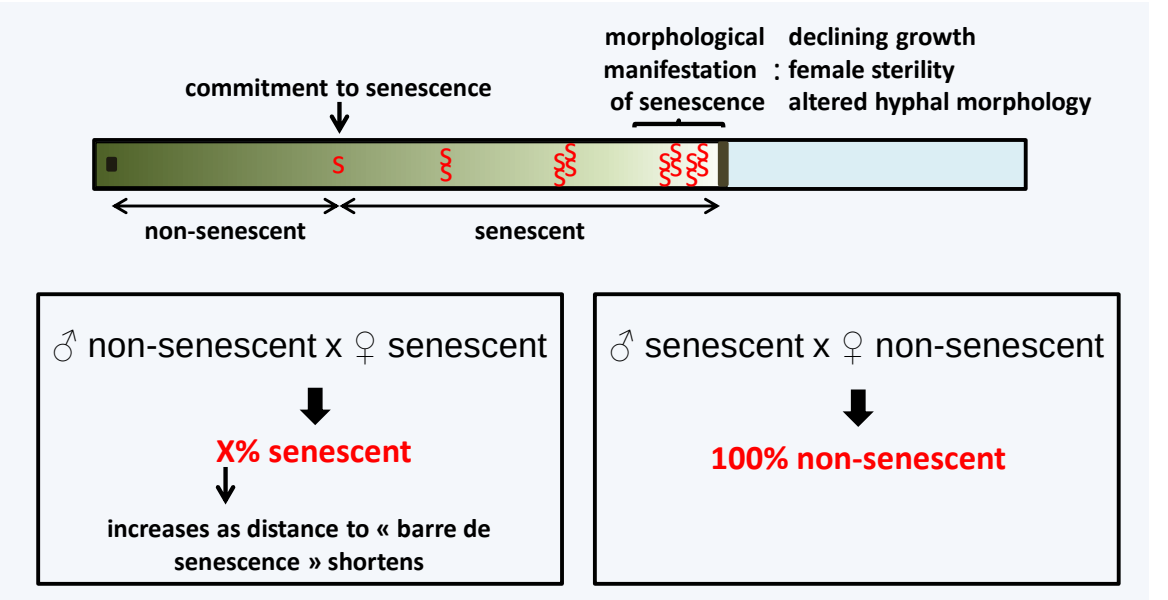


Figure 68 Segregation analysis of Senescence in *P. anserina*. Senescence is transmitted to the progeny only when the maternal parent is senescent showing that the Determinant of Senescence is located within the cytoplasm. When transmitted during ascospore formation, senescent thalli resulting from the germination of ascospore carrying the determinant are very short-live (< 1-2 cm). Their percentage increases exponentially as the maternal parent is nearer to the Barre de Senescence, confirming that Senescence results from the exponential accumulation of a cytoplasmic factor.

mitochondrial ones and some less defined cytoplasmic genetic elements. It is also highly sensitive to environmental conditions and various chemical compounds. We shall now see in turn each of these parameters, starting with the role of nutrients and chemicals.

Composition of the growth medium greatly affects longevity. For example, longevity is three to four times shorter on M2 than on Corn Meal (MR) medium. Paramount is the quantity of carbon source since caloric restriction delays all symptoms of Senescence, but the nitrogen source is also important (for example presence of yeast extract alters the life span, but in a complex manner depending upon the concentration). Longevity is also dependent upon temperature with the hotter the incubation, the shorter the lifespan. Low temperature can even trigger rejuvenation, as do surprisingly prolonged incubation at high temperature and many treatments that inhibit growth such as incubation in distilled water, storage under oil or incubation under nitrogen air. Unexpectedly, light shortens lifespan by an unknown mechanism.

Presence of many chemical compounds in the growth medium also affects the life span. I shall

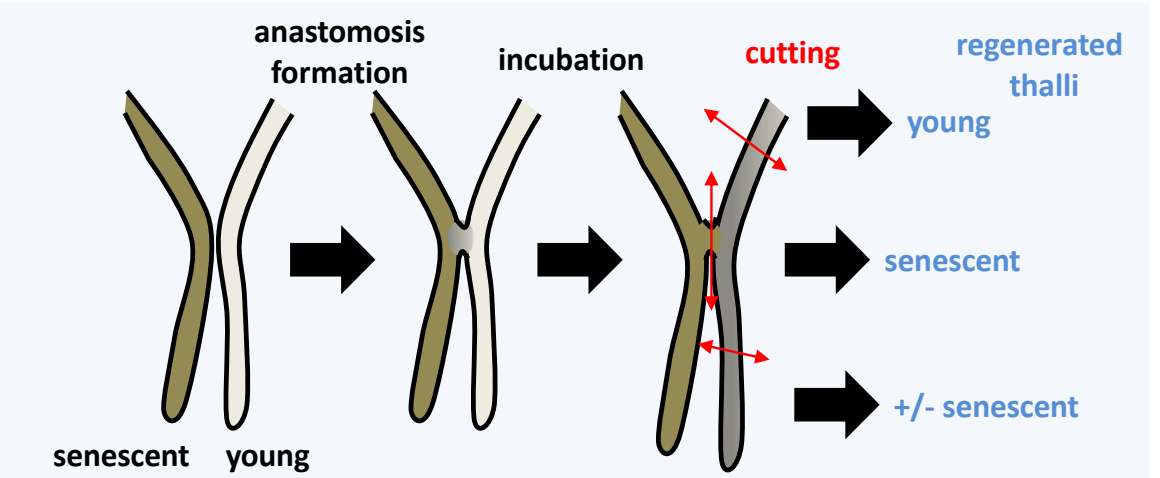


Figure 69 **Micromanipulation analysis of Senescence in *P. anserina*.** Young and senescent hyphae are brought together under a microscope as to observe anastomosis formation, which proceeds after a few hours. Once anastomoses are formed, the hyphae are incubated for 10 hours. Hyphae continue their growth, especially the young ones. At the end of the incubation, the formerly young hyphae are fragmented with a micromanipulator and new cultures are generated from the isolated fragments. Longevity analysis shows that fragments taken close to the anastomosis are invariably senescent, while those farther away are more or less senescent or even still young, demonstrating the infectious nature of the Determinant of Senescence.

only emphasize those that inhibit the respiratory chain that increase life span up to near-immortalization especially chloramphenicol and ethidium bromide that can cure senescence and rejuvenate the culture. Ethidium bromide was the most studied compound and it was shown that its action result in the elimination of the Determinant of Senescence as well as the restoration of an intact mitochondrial DNA. Contrary to inhibitors of mitochondrial functions, inhibitors of cytosolic translation, especially cycloheximide, shorten lifespan.

Genetic determinants of lifespan have also been thoroughly investigated. The first genetic determinant discovered by G. Rizet was a nuclear one called *incolore* (also known as *incoloris*). *Incolore* mutants have pleiotropic defects, including low pigmentation, profuse aerial hyphae and spermatia, female sterility and longer lifespan. To date, the affected gene in the first identified *Incolore* mutant, *IncA*, has not been identified. I will further discuss the incolore mutants later on this chapter. *Incolore* is only one of the many mutants modifying lifespan. Indeed, a survey of known mutants and of strains generated by insertional mutagenesis, the first one to be performed on any organism, indicated that between 10 and 50% of the genes likely control lifespan, *i.e.*, between 1000 and 5000 genes. Among those, genes

involved in mitochondrial biology and in cytosolic translation appear the most important.

Firstly, mutants affected in the respiratory chain have increased lifespan. Overexpression of the alternative oxidase, an enzyme able to replace the cytochrome C oxidase, in these mutants restore a normal lifespan along with a more efficient respiration and lower reactive oxygen species production. When the mutations are present in mitochondrial genes, effect on longevity can be tremendous and many mitochondrial mutants affected in genes encoding subunits of the respiratory chain are immortal. At the present time, it is not clear how the activity of the respiratory complexes controls Senescence, through metabolism, through reactive oxygen species or other processes. Indeed, mutants often have pleiotropic defects, including retrograde effects on nuclear gene expression, making it difficult to disentangle their actions on lifespan. Mitochondrial fusion and fission, mitophagy and other autophagy pathways, mitochondrial import, protein quality control and many other processes related to mitochondrial physiology (e.g., reactive oxygen species production and removal, programmed cell death…) have been shown to control lifespan. It is thus likely that each mutation involved in mitochondrial biology alters several lifespan-prolonging and lifespan-reducing pathways. It is beyond the scope of this book to present in detail all the researches carried out on the mitochondria roles in Senescence and longevity control in *P. anserina*, which is still a very active field of research. There are several reviews on the subject referenced in the appropriate section of this book.

Secondly, cytosolic translation, the main energy consumer of the cell, is also a major actor of lifespan control, linking again energy metabolism with ageing as in other organisms (*e.g.*, *Caenorhabditis elegans*). Some translation mutants may even be immortal without any obvious additional physiological defect. Indeed, mitochondria-related mutants, especially the immortal ones affected in mitochondrial genes, are slow and spindly growing, lack pigmentation and aerial hyphae, and are female sterile. On the contrary, I have obtained an immortal strain having no obvious defect during growth of the mycelium (same speed, color morphology, etc.) and sexual reproduction (fruiting bodies are differentiated in similar amount and with the same kinetics as in the wild type). This strain carries two different alleles of the genes encoding the cytosolic translation elongation factor eEF1A. Once again, how cytosolic translation affects Senescence and lifespan is not understood and its action may be through modification of several lifespan-prolonging and lifespan-reducing pathways. An additional very interesting feature of the translation mutants, especially those modifying its accuracy, is that they change the spectrum of the mitochondrial DNA modification observed in dying hyphae. Indeed, some have impaired amplification of

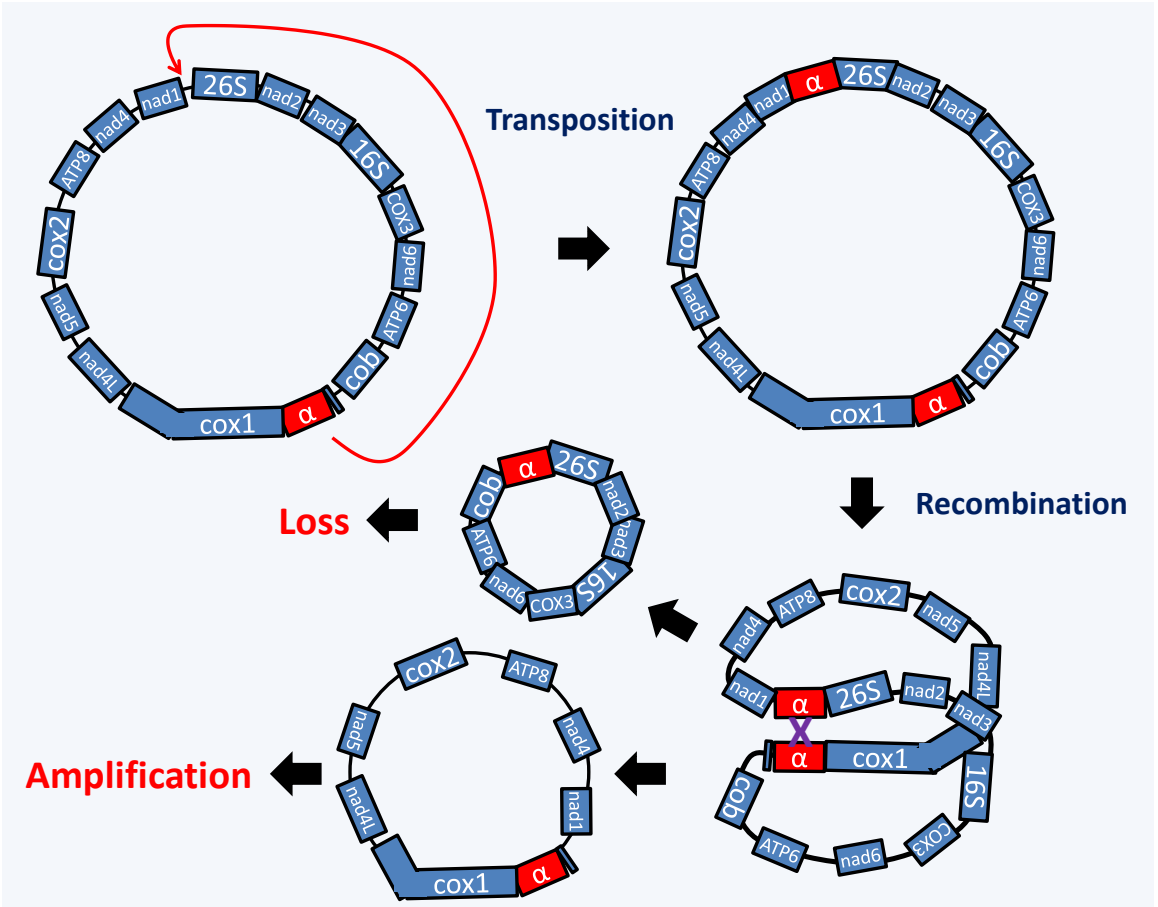


Figure 70 **Genesis of the deletion amplified during the Premature Death Syndrome in *P. anserina*.** Following transposition of the class II intron α (the first intron of the *COX1* gene), two copies are present in the same orientation in the mitochondrial genome. Such molecule can be detected by PCR amplification in all tested strains. A recombination between the two copies yields two molecules. Only the large one amplifies during the Premature Death Syndrome.

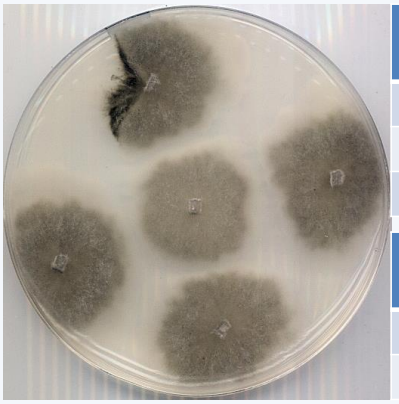
the senDNAα and thus carry exclusively other amplified molecules belonging to the senDNAβ and senDNAγ families (see S2 in figure 66). The most interesting one is the *AS1-4* mutation affecting the *AS1* gene encoding the S12 protein of the small ribosomal subunit. Indeed, this mutation triggers a near immortality in S *mat+* cultures and a very short lifespan in S *mat-* ones (1-2 cm). This latter short lifespan has been coined as "Premature Death" owing to the fact that the DNA modification observed in dying hyphae is unique and not seen during normal Senescence. It consists in the deletion of one third of the mitochondrial DNA (figure 70). Interestingly, one of the borders of the deletion is the intron α amplified

as senDNAα during senescence. It has been shown that this intron is also a transposon that integrates near the tRNA inserting serine during mitochondrial translation. The deletion amplified during Premature Death is the result of an intramolecular recombination between the two copies of the intron/transposon (figure 70). Why only one of the two molecules generated by the recombination (figure 70) is amplified is unknown. Interestingly, senDNAα is likely generated in a similar manner. Transposition of intron α just upstream itself could yield a tandem duplication of the intron. A recombination between the two copies can then generate the first extrachromosomal circular copy of senDNAα, which can subsequently be amplified either by the same mechanism or by replicating. Finally, the genetic determinant linked to the mating type that modulates the lifespan difference between the *mat-* and *mat+* isolate has been identified. It is the *rmp1* gene that contains a polymorphism between the *mat+* and *mat-* in some, but not all, natural isolates. This polymorphism also controls thermosensitivity (see above) and the long-known difference in longevity between the *mat+* and *mat-* isolates in some strains.

Overall, a lot has been learned by studying Senescence in *P. anserina*, especially on the physiology of respiration in connection with mitochondrial normal and abnormal functioning in an obligate aerobic organism. Yet, owing to the complexity of the phenomenon, much remain to be understood. With the advent of omics data, study of Senescence has now been upgraded to the study of whole pathways instead of single genes, which should further deepen our understanding of ageing.

Crippled Growth and other phenotypic instabilities

Another cell degeneration process affecting the growth of *P. anserina* was discovered more recently. Hyphae affected by this so-called “Crippled Growth” phenomenon grow more slowly, have abnormal morphology and often accumulate high level of pigments. On the whole thallus, Crippled Growth manifests as random-appearing sectors of extending altered growth with fewer and pigmented hyphae (figure 71). In the sector, there is no aerial hyphae and the mycelium is female sterile. The degeneration occurs only in *P. anserina* (but is present in all investigated strains) and not in its sibling species, unlike Senescence. It also develops specifically on some media such as M2 supplemented with yeast extract (figure 71), while wild-type strains of *P. anserina* never present Crippled Growh on the M2 medium. Like Senescence it is linked to the presence of a cytoplasmic and infectious factor (figure 72). However, unlike Senescence this factor, called *C*, accumulate in stationary phase hyphae (figure 73).



Growth regimen	M2	M2+YE	M2+ Ac. NH_4
WT	NG	NG/CG	NG
IDC	NG	NG	NG
PDC	NG/CG	NG/CG	NG/CG++

Presence of *C* in stat. ph.	M2	M2+YE	M2+ Ac. NH_4
WT	+	+	+
« pink » *IDC*	-	-	-

Figure 71 **Crippled Growth in *P. anserina*.** Left, a "Crippled Growth" sector develops on the uppermost thallus. Top right table, Growth regimen observed on different media for wild type (WT), mutants impaired for Crippled Growth (*IDC*) and those promoting Crippled Growth (*PDC*); NG: only Normal Growth occurs. NG/CG: Normal Growth with sectors of Crippled Growth. NG/CG++: sectors have a much altered growth as compared with M2+YE. Bottom right table, *C* is always present in wild-type (WT) mycelia during stationary phase and is absent from "pink" IDC mutants.

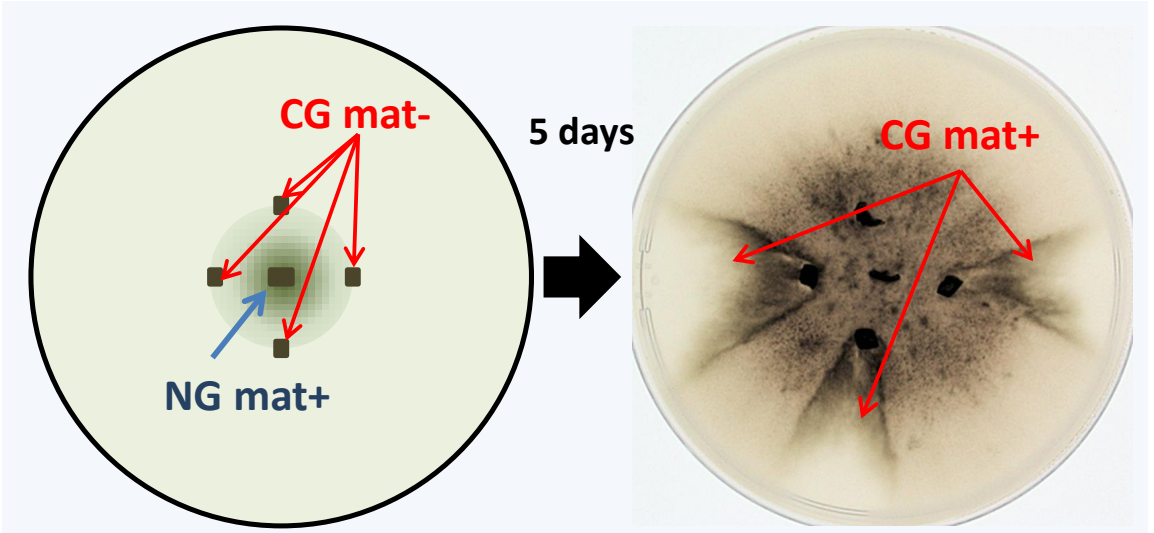


Figure 72 **Contamination experiments showing that Crippled Growth is linked to the presence of a cytoplasmic and infectious factor.** Left, a two-day-old Normal Growing thallus is inoculated with explants of Crippled Growing mycelium. After 5 days of incubation, Crippled Growing sectors develop downstream three out of the four tested CG explants. Marking the nuclei with the mating types indicates that CG sectors are of the recipient mating type, showing that Crippled Growth is due to the spreading of a cytoplasmic and infectious element.

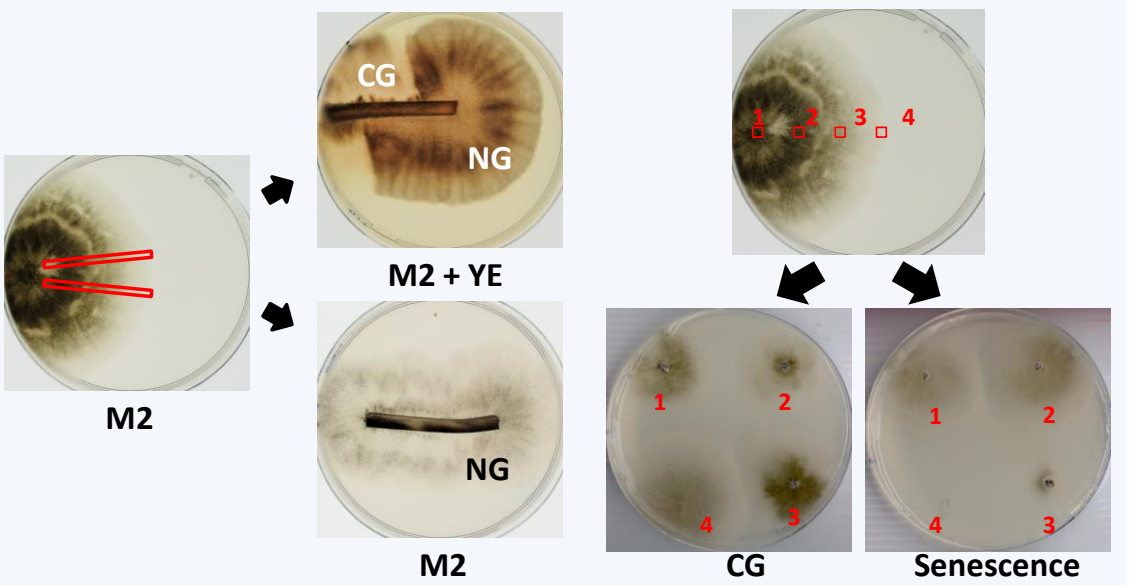


Figure 73 ***C* is induced in stationary phase.** Left, a 5-day-old Normal Growing wild-type culture on M2 is sliced as depicted by the two red rectangles. When inoculated on M2+YE, the slice gives a two-part cultures with on the right hyphae from the apical side of the slice regenerating Normal Growing hyphae and those on the left from the stationary phase side Crippled Growing ones. Note that on this plate the upper aerial part of the slice is on the top and the part that was at the bottom of the initial plate is at the bottom. The unequal shape of the Crippled Growth area of the new culture shows that *C* is induced earlier in the aerial part of cultures when compared with the bottom one. Contrary to what happens when the slice is inoculated on media permitting CG, inoculation on media not permitting CG, such as M2, yields only Normal Growing hyphae. Overall, this shows that *C* is induced in stationary phase hyphae even in conditions not permitting Crippled Growth, but will amplify in growing hyphae only in defined conditions, *i.e.*, those in which Crippled Growth sectors occur. Right, the fact that the cytoplasmic and infectious factors responsible for Crippled Growth and Senescence amplify in different kinds of hyphae (only stationary ones for Crippled Growth when growing on M2 and apical ones for Senescence) is easily visualized by testing explants taken at various distances from the inoculation point. In the case of Crippled Growth, explants from the center of the culture regenerate sick cultures if inoculated on permissive medium, while explants from the outer part of the culture generate sick cultures in the case of Senescence

Surprisingly, *C* accumulates during stationary phase even in conditions that did not permit the development of Crippled Growth sector such as growth on M2 (figure 73). An interesting property of Crippled Growth is its sensitivity to stresses. Indeed cultures growing Crippled can easily be forced to reverse to a Normal Growing regimen by stressing them. Intriguingly, all tested stresses are able to do so: heat shock, cold shock, presence of noxious substances or of osmolytes in large amounts, ultraviolet irradiation… One of the most efficient ones is physical stress. Indeed, shaking a Crippled Growing

mycelium with a Fastprep in order to break apart the hyphae results in fragments regenerating Normal Growing-mycelia. Another way to revert Crippled Growth is to undergo a sexual cycle. As stated above the Crippled Growing mycelium is female sterile. It is however male fertile. Male gametes never transmit C. Also, when sexual reproduction occurs, *i.e.*, during stationary phase *C* is present in maternal hyphae; yet freshly germinated ascospores never present Crippled Growth directly after germination. Overall, the cytoplasmic and infectious factor *C* has a complex determinism, which is summarized in figure 74: induction by stationary phase, reversal by stresses and role of growth condition, (*i.e.*, development of sectors only in medium containing yeast extract)

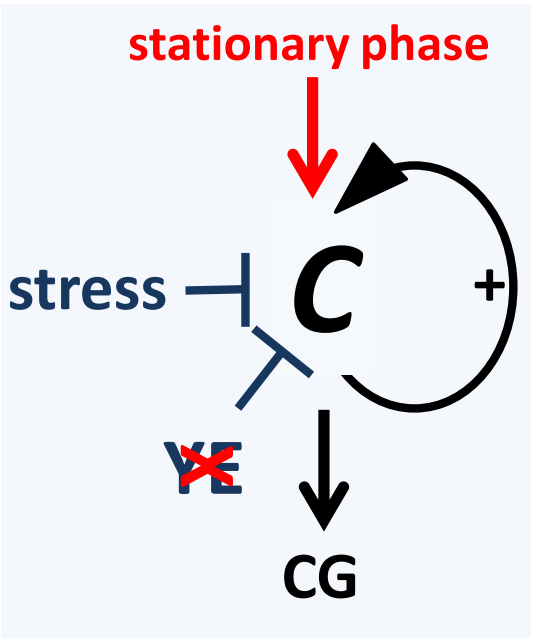


Figure 74 **Summary of the properties of *C*.**

To understand the molecular mechanism involved in the generation of *C* and the development of Crippled Growth sectors, a classical genetic approach has been undertaken. Note that purification of *C* was not feasible because, in order to follow its presence during *in vitro* purification, it would have been necessary to reintroduce it in hyphae, which could only be done by stressing them and thus reverting Crippled Growth. Mutants impairing Crippled Growth (*IDC* mutants) and mutants promoting Crippled Growth (*PDC* mutants) were selected (figure 71).

Two major classes of *IDC* mutants were retrieved. The first one still accumulated *C* during stationary phase and thus mutants from this class were likely constitutively-stressed during growth, which resulted in *C* elimination. Accordingly, all these mutants have additional phenotypes. The gene affected in only one of these mutants has been identified and encodes a potassium transporter. Defect in potassium transport can indeed be stressful during growth. The second class did not produce *C*, even in stationary phase and were thus likely affected in the pathway directly involved in the making of *C*. In addition to their effect on Crippled Growth, all these mutants have the same set of defects, including lack of pigments, aerial hyphae, anastomosis and development of fruiting bodies after fertilization. Interestingly, these are features occurring as the fungus enters into stationary phase, in accordance with

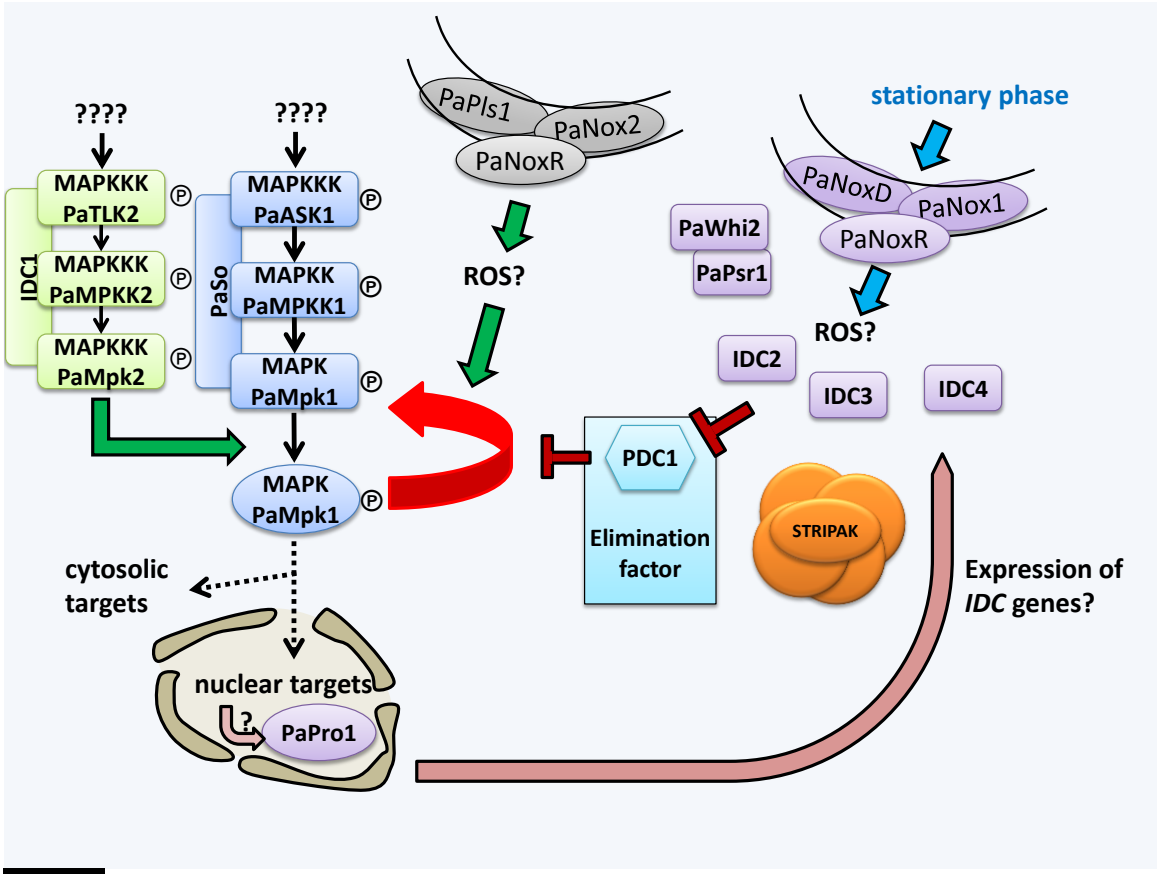


Figure 75 **A model to account for Crippled Growth.** See text for details.

the induction of *C* during this phase. Identification of the genes mutated in the *IDC* and the *PDC1* mutants followed by reverse genetic analyses of candidate genes and phenotypic analyses of single and double mutants, led to the proposal of a model whereby the *C* element is a self-activated MAP kinase pathway (figure 75). On M2 medium, this pathway is normally off in growing hyphae thanks to an "Elimination Factor" and activates upon entrance into stationary phase. This is seen by the re-localization of the PaMpk1 MAP kinase inside nuclei specifically during stationary phase. Activation is prompted by the action of the PaNox1 NADPH oxidase complex, which produces ROS. The ROS signal likely travels through the IDC2 and IDC3 proteins that contain conserved cysteines crucial for their activity. It ends up in the PDC1 protein, which also contains conserved cysteines crucial for its activity. This protein represses the PaMpk1 pathway and is thus part of the "Elimination Factor". Once lifted, activation of PaMpk1 can proceed and signal production of pigments, anastomosis, erection of hyphae and likely mobilization of

reserve to properly built the fruiting bodies. How activation is achieved is still mysterious since phosphorylation of the TxY motif conserved in MAP kinases that usually activates these proteins is constitutive. Activation is thus achieved through another mechanism as observed for some MAP kinases in protists. Activation also requires an intact PaMpk2 MAP kinase pathway. Requirement of the PaMpk2 pathway for activity of PaMpk1 has been observed in related fungi. Upon growth renewal after transfer on fresh medium, the "Elimination Factor" is reactivated, PaMpk1 is inactivated and growth can again proceed normally.

On M2 + YE medium, the pathway is also usually off and hence growth proceeds normally. Like on M2, the pathway activates using the same actors during stationary phase. Nevertheless, on M2 + YE, the mechanism repressing *C* that contains PDC1 is inactive during growth. Thus upon transfer to fresh medium, PaMpk1 is not inactivated and Crippled Growth occurs because signaling for features specific of resting hyphae (pigment, anastomoses, erection of hyphae and preparation of sexual reproduction) are expressed in dividing ones . Similarly, during growth PaMpk1 can activate spontaneously and sectors of Crippled Growth ensue. This spontaneous activation of PaMpk1 may be effected by both the PaNox1 and PaNox2 NADPH oxidase complexes.

This model has been confirmed by many experiments, but much remains to be done to clearly understand how *C* is created and how it affects growth. Many factors affecting Crippled Growth are poorly characterized and their position in the pathway is unclear: IDC4, PaPsr1/PaWhi2, the STRIPAK complex… Especially, the role of the transcription factor PaPro1 within the cascade is unclear. It has been shown to activate the expression of some of the genes involved in Crippled Growth, but in a marginal way. Whether this factor is also part of the self-activation of the pathway should to be determined. Similarly, the genes in many *IDC* and especially in many *PDC* mutants remain to be identified. It is very likely that the actual functioning of the PaMpk1 pathway during Normal and Crippled Growth is much more complex than what the model of figure 75 depicts. Finally, we will further discuss this PaMpk1/PaMpk2 pathway during the analysis of sexual reproduction and self-versus non-self-recognition, since it is a major regulator of both phenomena.

In addition to Senescence and Crippled Growth, *P. anserina* and/or its sibling species is the subject of additional phenotypic instabilities, *i.e.*, repetitive variable appearance of the mycelium in well-defined conditions. Foremost, all accumulate with great frequency *Incolore* mutations (figure 76). Indeed, *Incolore* mutations are dominant and confer a selective advantage to nuclei that carry them: these divide

Figure 76 ***Incolore* mutants in the *P. anserina* species complex.** *Incolore* is due to dominant nuclear mutations conferring selective advantage to nuclei both during growth and stationary phase.

in syncitia to the detriment of the wild-type nuclei and mycelia carrying them grow faster and produce abundant aerial hyphae. Hence, in laboratory conditions enabling nuclear division (*i.e.*, when incubated at temperatures enabling cell division), *Incolore* nuclei accumulate in mycelia that are resting, even though the mutation rate of their appearance is low. Upon re-inoculation onto fresh media, nuclei carrying an *Incolore* mutation frequently and annoyingly take over the mycelium thanks to the faster growth of the *Incolore* mycelium. It is thus not recommended to store *P. anserina* and its sibling species at temperature above 4°C, if one does not want accumulation of *Incolore* mutations. *Incolore* nuclei, often mixed with wild-type ones, are found for example in most strains conserved in public collections (CBS, ATCC, DSMZ…). *Incolore* mutants are strongly counter-selected in nature since they are female sterile. Genetic analyses showed that *Incolore* mutations arise in several genes, none of which has been identified.

Vauban is another instability that manifests as highly frequent sectors (arrowheads) of abnormal growth. *Vauban* thalli end up looking like fortresses built by Vauban (1633-1707) as seen in figure 77.

Figure 77 ***Vauban*.** Left, a typical thallus of *P. comata* strain T with numerous *Vauban* sectors at its edge. Middle, part of Neuf-Brisach fortress built by Vauban. Right, contamination experiments demonstrating that *Vauban* is due to the presence of a cytoplasmic and infectious factor.

Although *Vauban* and Crippled Growth sectors look alike with more pigments, no aerial hyphae and female sterility and although they are likewise due to the presence of a cytoplasmic and infectious factors (figure 77), they are due to different molecular mechanisms. Indeed, *Vauban* sectors are not induced by stationary phase, they cannot be cured by applying stresses and they develop on M2 medium. *Vauban* has been detected in strains of *P. comata*, *P. pseudoanserina* and *P. pseudopauciseta*, but has not yet been observed in any strain of *P. anserina*. The mechanism generating *Vauban* is to date unknown, but similar sector phenomena are present in many filamentous ascomycetes and are suspected to be due to prions. Interestingly, *P. anserina* possesses a true prion that will be discussed in the next section. This prion does not cause any obvious morphological modification.

A last phenotypic instability called Wavy (figure 78) has been observed in mutants affected in potassium transporters of the TRK family. Unlike the above-described phenomena, the instability leads to several distinct phenotypes (at least three in addition to the "normal" one that looks like the phenotype of the wild type: "green and flat", "green and zoned" and "white and zoned"). At the present time, it is unclear whether the various phenotypes result from a graded change in a single phenomenon, the mixing in various proportions of hyphae affected by a single bistable process or to several distinct phenomena. However, upon replica onto fresh medium, one usually observe a sequence of changes from "Normal", to "green and flat", then "green and zoned" and finally "white and zoned". The switch is greatly influenced by the temperature (low temperatures promote the change towards the "white and zoned" phenotype, while high temperatures tend to promote the direction toward the "normal" phenotype). This suggests therefore that Wavy multistability is likely linked to changes in a single process. This is confirmed by the

Figure 78 ***Wavy*, a multi-stable phenotypic instability.** Left and middle, the various phenotypes exhibited by the *PaTrk1*^{452} mutant. Right, Right, contamination experiments demonstrating that *Wavy* is due to the presence of a cytoplasmic and infectious factor.

fact that it is also created by a cytoplasmic and infectious factor (figure 78). There are two genes encoding such transporters in *P. anserina*, *Patrk1* and *PaTrk2*. The most important appears to be *PaTrk1,* because the phenotypic instability is more frequent in the mutants of this gene than in the one of *PaTrk2*. Paradoxically, mutants of *PaTrk1* impair Crippled Growth, as stated above. In these mutants, the Crippled Growth degeneration is thus replaced by the Wavy one!

Finally, as for other fungi, *P. anserina* mycelia exhibit phenotypic plasticity, *i.e.*, their morphology is highly dependent upon growth conditions. For example, the origin of the water used to make the growth media has some influence on mycelium morphology and pigmentation, owing to the variable presence in trace amounts of various compounds such as calcium, manganese or even proteins produced by biofilms growing inside pipe tubes. This coupled with the above-discussed phenotypic instability makes it that mycelia on Petri plates from the same strain often look different with various shades of pigmentation, amounts of aerial hyphae, presence of more or less "waves" in the mycelium… Especially, mycelium features are affected by history. For example, longevity is dependent on the sizes of the explants used to inoculate mycelia onto fresh medium: the smaller the explants the shorter the longevity. Similarly, it is worth reminding that passage into stationary phase triggers Crippled Growth while stresses cure it… Nevertheless, *P. anserina* mycelia are easily recognizable and can be easily tamed, provided that few guidelines are followed for their handling. The most important ones are

- always replicate from the center of the thallus to avoid Senescence
- never store for a long time above 4°C to avoid *Incolore* mutation
- remember that if you replicate onto media enabling Crippled Growth, the degeneration will occur with nearly 100% frequency if the explants are taken in the center of the culture, which one does to avoid Senescence…

Hyphal Interference and Vegetative/heterokaryon Incompatibility

Another field of intense research in *P. anserina* is the deciphering of molecular mechanisms of self *versus* non-self recognition. Indeed, G. Rizet discovered that *P. anserina* undergo a phenomenon now called vegetative, protoplasmic or heterokaryon incompatibility which involves recognition between *P. anserina* strains, as previously described for some other fungi (the phenomenon was first described in *Diaporthe perniciosa* in 1923 by D.M. Cayley). More recently, I pointed out that the friendly mold is also

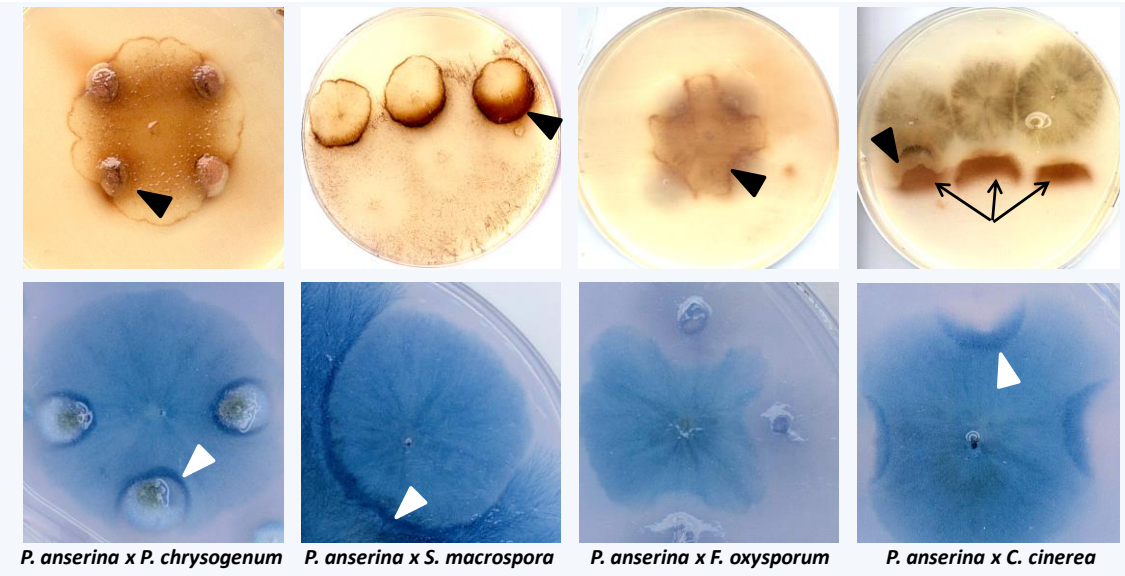


Figure 79 **Hyphal Interference in *P. anserina*.** Top, when *P. anserina* is confronted to other filamentous fungi, it produces at the meeting point high amounts of peroxide (black arrowheads), as visualized by the accumulation of the brown precipitate of diaminobenzidine. Similar processes called oxidative bursts are encountered in other instances of innate immunity in animals and plants, but also in other fungi such as *Coprinopsis cinerea* (arrows). Bottom, blue Evans/Trypan staining demonstrates that the contact may be associated with hyphal death (white arrowheads) or not as in the case of the confrontation of *P. anserina* with *Fusarium oxysporum*. *P. anserina* kills *Penicillium chrysogenum* and *Sordaria macrospora*. It is however killed by *C. cinerea*.

able to defend itself against competitors by Hyphal Interference, a process previously discovered only in basidiomycetes by F.E. Ikediugwu & J. Webster in 1970, that involves the recognition of hyphae from other species of filamentous fungi. Hence, *P. anserina* is also able to recognize its hyphae from those of another species, but also differentiates between hyphae from vegetatively-compatible versus incompatible strains.

We shall briefly discuss first Hyphal Interference because much less is known on this process than on Vegetative Incompatibility. When *P. anserina* is confronted with other fungal species, it produces an oxidative burst (figure 79), a reaction commonly encountered during innate immunity reactions in animals and plants. The oxidative burst occurs specifically when *P. anserina* is confronted with hyphae of ascomycetes or basidiomycetes and not when confronted with inert materials such as glass or plastic, yeasts, bacteria or hyphae from *Mucoromycotina*. Hence, *P. anserina* is able to recognize that it encounters another *Dikarya* filamentous fungus. Importantly, when confronted with another *P. anserina*

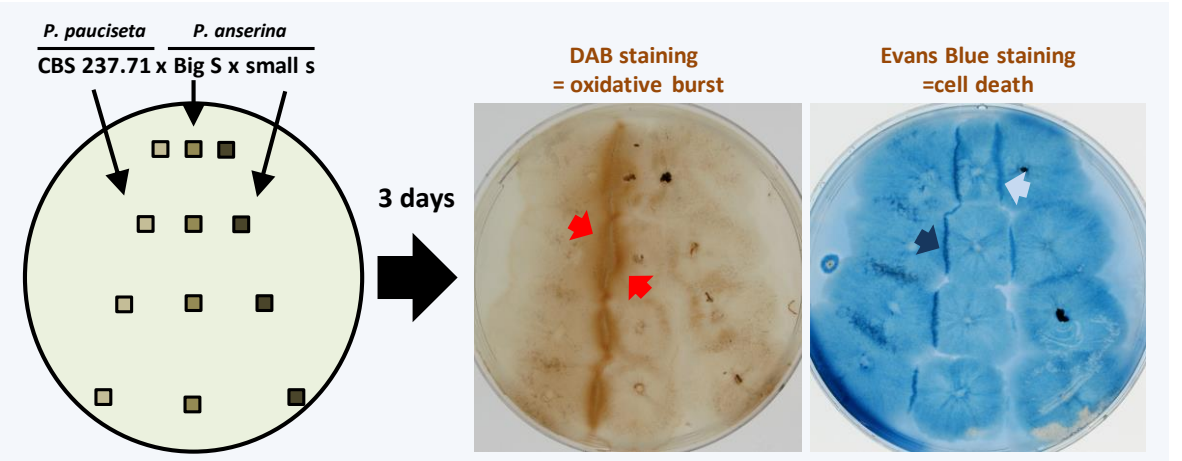


Figure 80 **Lack of Hyphal Interference between strains of *P. anserina* and presence of hyphal interference between *P. anserina* and *P. pauciseta*.** *Podospora pauciseta* CBS 237.71 and the BIG S and small s strains of *P. anserina* were inoculated along diverging lines as indicated on the left scheme. After three days, the DAB staining shows a lack of oxidative burst when the BIG S and small s strains of *P. anserina* are confronted; yet cell death due to vegetative incompatibility (light blue arrow) occurs at the confrontation between the two vegetatively-incompatible strains of *P. anserina* as shown by the Evans Blue staining. On the contrary, an intense oxidative burst on both *P. anserina and P. pauciseta* mycelia (red arrows) occurs at the junction between *P. anserina* and *P. pauciseta*, along with many hyphal death (dark blue arrow).

strain, such as in the confrontation between the vegetatively-incompatible BIG S and small s strains, no oxidative burst happen (figure 80), showing that the fungus can differentiate between self and non-self at the species level. This recognition does not necessitate the fusion of hyphae, but requires nonetheless a contact between the hyphae of the two contestants. Although the burst is a constant feature during the interactions between *P. anserina* and another species, the outcome is variable. Indeed, confrontation may or may not be accompanied by the death of the contestant or that of *P. anserina* (figure 79). Interestingly, an oxidative burst often associated with cell death occurs at confrontations between strains of the different species of the *P. anserina* species complex (figure 80 and 81), further confirming that these are *bona fide* species.

Analyses of mutants have shown that the burst and death during confrontation with *Penicillium chrysogenum*, the main fungus used in Hyphal Interference test, is under the control of the PaMpk1 MAP kinase pathway and in part the PaNox1 NADPH oxidase complex, but does not require the PaMpk2 and PaMpk3 MAP kinase pathways or the PaNox2 and PaNox3 NADPH oxidase complexes. Intriguingly, some of these complexes and pathways control Crippled Growth (see previous section); yet, the connections

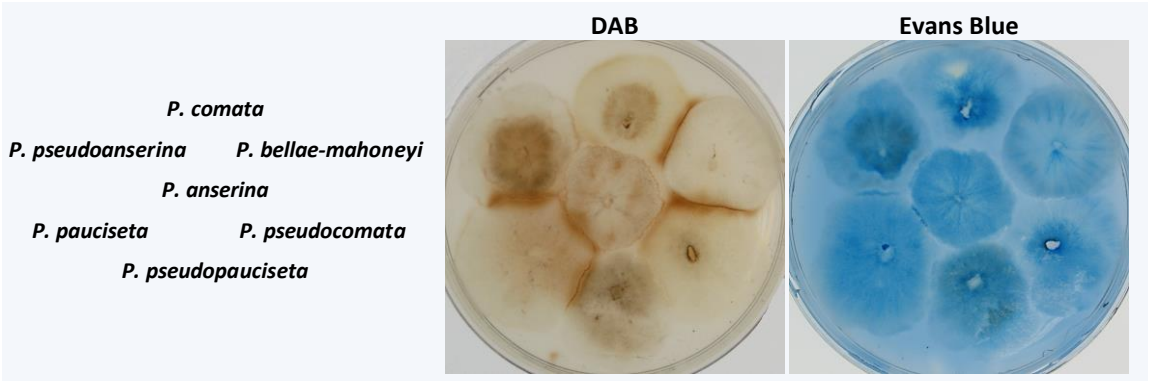


Figure 81 **Hyphal Interference between strains of *P. anserina* species complex.** Species of the complex show variable amount of oxidative burst and cell death when confronted with each other.

between the two phenomena are unclear. However, Hyphal Interference against *Penicillium chrysogenum* is efficient in *P. anserina*, which present Crippled Growth, and inefficient or even absent in other species of the *P. anserina* species complex that do not present Crippled Growth. Mutant analyses have also shown that the oxidative burst and hyphal death are not correlated, for example a mutant affected in the TIM54 protein controlling the import in the mitochondria has a large increase of the oxidative burst and a much decreased hyphal death. At the present time, little more is known about this fascinating process.

Unlike Hyphal Interference, Vegetative Incompatibility requires the fusion by anastomosis of hyphae to take place. This phenomenon occurs thus when two genetically-different strains of *P. anserina* meet (figure 82). The phenotypic features of the incompatibility reaction include morphological modifications of the vacuoles from tubular to round, increased septation, accumulation of lipid droplets, abnormal deposition of cell wall, reduction in cytosolic protein translation and activation of phenoloxidases, dehydrogenases and proteases. This culminates with the cell death of the hyphae containing the genetically-incompatible nuclei (hence the alternative name of Heterokaryons Incompatibility), likely due to the ruptures of the membranes of the vacuoles and the whole cell. Interestingly, a role of autophagy in delaying cell death has been evidenced.

The genetic differences that trigger the incompatibility reaction are located in specific genes, called *het* genes (for heterokaryons incompatibility genes). Nine het genes have been identified so far in *P. anserina* (figure 83). Two kinds of incompatibilities are known: allelic incompatibilities in which presence of different alleles of the same gene inside the same cytoplasm triggers the death reaction and

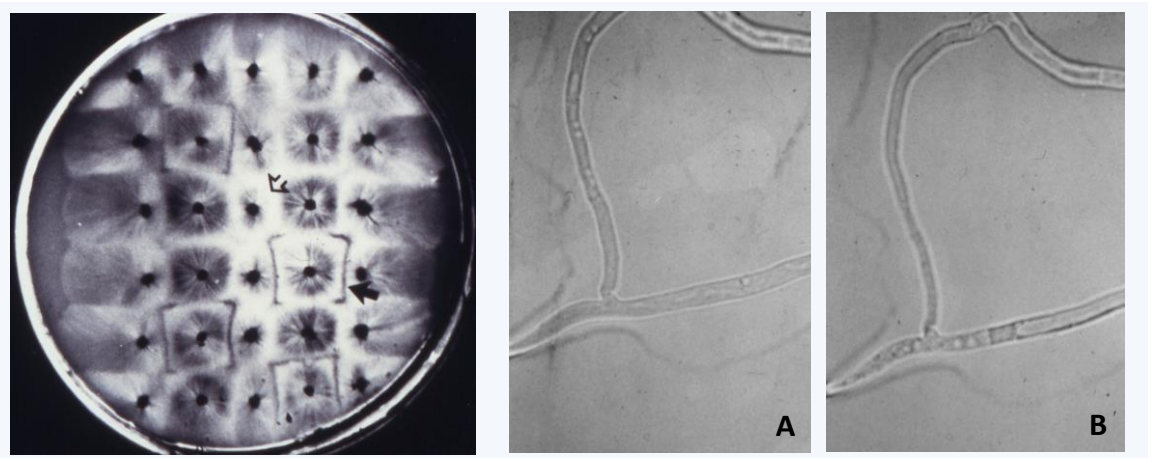
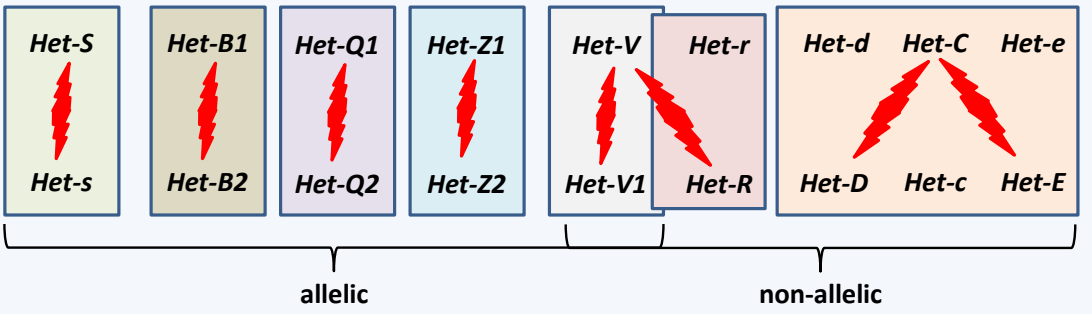


Figure 82 **Vegetative incompatibility between the S and s strains.** Left, compatible (white arrow) and incompatible (black arrow) confrontations between the progeny of a S x s cross and a S tester. Right, microscopic visualization of the incompatibility reaction: (**A**) hyphae after anastomosis formation and (**B**) a few minutes later when the incompatibility reaction has occurred. Photos courtesy B. Turcq.

non-allelic incompatibilities in which specific combinations of alleles of different genes inside the same cytoplasm cause the incompatibility reaction (figure 83). The multiplicity of *het* genes, along with the multiplicity of alleles in non-allelic incompatibility (figure 83), results in a large number of different compatibility group and warrants that in the wild, most encounter between *P. anserina* strains are incompatible.

The identification of *het* genes has led to very interesting insights into the mechanisms of allorecognition in fungi, as well as to the identification of a prion protein; indeed, Rizet showed in the early fifties that the *het-s* allele involved in the allelic *het-S*/*het-s* vegetative incompatibility exhibits a peculiar behavior that is now explained by the ability of the het-s protein to self-catalyze a fold change into amyloid aggregates, a hallmark of prion. It is beyond the content of this book to retrace the whole history of the discovery of the het-s prion and I refer to the numerous reviews on the subject, suffice to say that the prion was first discovered genetically by G. Rizet thanks to the weird changing properties of the het-s allele in incompatibility reaction (figure 84). Identification of the *het-s* and het-S genes and subsequent analyses demonstrated clearly that het-s was a prion, while het-S was not (figure 84). It was the first cellular prion for which infectivity was clearly linked to aggregation by transforming recipient prion-free strains with amyloids and for which a structure of the aggregated form was obtained (figure85). Importantly, the het-s amyloids are not toxic to the fungus *per se*, but must interact with an



	het-d1	het-d2	het-d3	het-e1	het-e2	het-e3	het-e4
het-c1, c5					☹	☹	
het-c2	☹			☹			
het-c3, c6					☹		
het-c4, c10, c11	☹	☹			☹	☹	
het-c7	☹	☹		☹			
het-c8	☹			☹	☹	☹	
het-c9	☹	☹			☹		

Figure 83 **Genetic control of Vegetative Incompatibility in *P. anserina*.** Top, nine identified loci involved in the control of Vegetative Incompatibility. Bottom, ☹ identifies lethal combinations of het-c/het-d and het-c/het-e alleles.

additional partner to trigger death. This partner can be the het-S protein. Upon binding of the het-S protein to the het-s amyloid, a Helo domain of het-S is unmasked. This Helo domain interacts with the cell membranes that it disrupts. It is most likely that cell death results for leakage of the cellular content. In this system, recognition between self and non-self is thus effected by the prion-like aggregation of het-S templated by the het-s prion.

Interestingly, it has been observed that a gene encoding a NOD-like receptor called *nwd2* lies beside *het-S*, while it is present as a pseudogene beside *het-s* (figure 84). NOD-like receptors bind ligands, especially, pathogen-associated-molecular-pattern or pamp that are accompanying pathogens, resulting in a conformational change of the receptor and transmission of a signal to counteract the pathogens. Pamp recognition is accomplished by a WD domain, carrying WD40 repeats. The genome of *P. anserina* S strain contains 77 of such genes. Interestingly, the *het-d*, *het-e*, *het-r* and *het-z* genes also encode NOD-

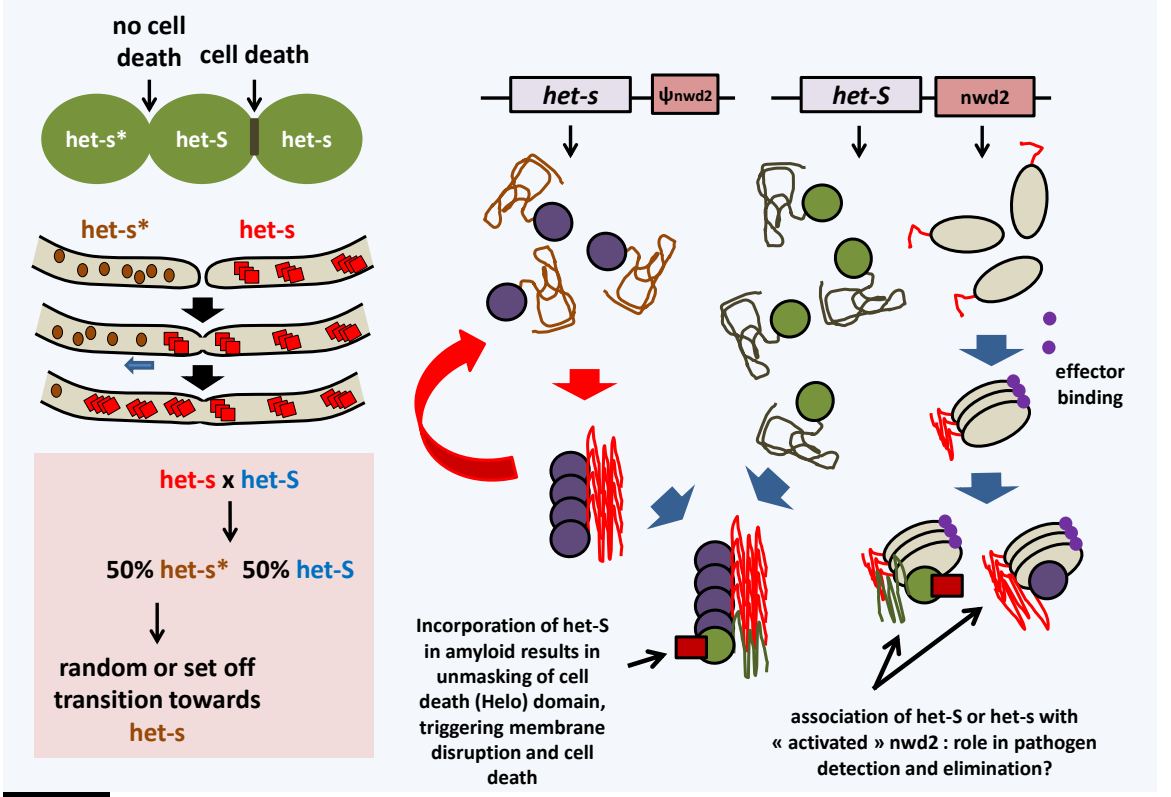


Figure 84 **The het-s prion.** Left, Rizet observed that strains carrying the het-s allele can adopt two mutually exclusive phenotypes: the het-s one in which the cultures are incompatible with strains carrying het-S and the het-s* one, in which the cultures are compatible (top left). Rizet observed that het-s* cultures convert spontaneously at low frequency towards het-s and that this can be triggered with 100% efficiency when het-s* is in contact with het-s and anastomoses occur (middle left): het-s is thus infectious to the detriment of het-s*, so that eventually all cultures carrying het-s end up being het-s. Het-s* cultures can nonetheless be recovered after sexual reproduction since progeny carrying the het-s allele are het-s* (bottom left); note that if the female parent is het-s, some progeny is directly het-s. All the properties of the het-s allele and its interactions with the het-S one are now explained by the prion properties of het-s (right). Upon translation of its messenger, the C-terminus of the het-s protein, which is the prion-forming domain, is unfolded and the het-s protein does not interact with het-S: the strain is thus het-s*. Folding of the het-s prion-forming domain into an amyloid structure is spontaneous at low frequency and results in more het-s monomers joining the amyloid fibers, explaining the spontaneous conversion of the het-s* phenotype into het-s and the infectiosity of het-s. Importantly, the het-S protein is also able to join the het-s amyloids, although it cannot form alone amyloid. Upon joining the amyloid a Helo domain carried by het-S is unmasked (this Helo domain is not present in het-s). The unmasked Helo domain disrupts membranes triggering cell death, which occurs thus only in the presence of both the het-s amyloids and het-S. It has been demonstrated that the ndw2 protein, whose gene is located beside het-S (this gene is present as a pseudogene beside het-s) can also template amyloid formation. It is speculated that it is triggered to do so by an as-yet unknown effector and that the formed complexes with het-s and/or het-S may be involved in pathogen recognition and elimination.

Figure 85 Structure of the het-s prion-forming domain. The prion-forming domain of het-s is located at the C-terminus f the protein. Here, several monomers are folded into an amyloid fiber.

like receptors and a model has been proposed and demonstrated to account for their role in vegetative incompatibility. In the case of nwd2, it has been demonstrated that chimaeric NWD2 proteins carrying WD-domain with known activating effectors is able to seed the formation of the het-s prion when they are activated by the cognate ligand, showing that the amyloid fold can be transmitted to het-s by an activated NOD-like receptor. The actual activating effector of the NWD2 protein is unknown, but is speculated that it is a pamp and that upon activation by the effector the fold is transmitted to the het-S or het-s proteins and that this participate in the pathogen detection and/or elimination (figure 84).

In the case of het-d and het-e, the fold change is transmitted to the het-c protein. Cloning identified *het-c* as a gene encoding a glycolipid transfer protein able to transfer glycolipids between vesicles *in vitro*, but whose cellular role in still unknown. Inactivation of *het-c* led to a defect in the production of normal ascospores, indicating an important role during their maturation. Presently, 11 different alleles of this gene have been identified in natural populations. They define seven specificity groups of incompatibility with *het-d*/*het-e* alleles (figure 83). Like for the het-s/het-S complexes, the incompatible het-c/het-d or het-c/het-e complexes interact with the plasma membrane, resulting in its disruption. In the case of het-z, the protein interacting with the het-z1/het-z2 complex and effecting death is PaSec9, an essential SNARE protein involved in vesicle fusion, suggesting that membrane disruption is also involved in hyphal death in this incompatibility system. At the time of writing this book, the het-r protein has not been investigated thoroughly and the *het-v*, *het-B* and *het-Q* genes have not been identified.

The involvement of NOD-like receptor suggests that in nature the components involved in Vegetative Incompatibility not only act to monitor self *versus* non-self recognition in *P. anserina*, but also as a defense system against pathogens, especially bacteria. This hypothesis is further supported by the fact that the transcriptional responses to the presence of bacteria and the one during an incompatible

reaction overlap. During Vegetative Incompatibility, the system would act to limit the spreading of potential deleterious elements present in the cytoplasm, especially virus-like particle as shown in *Cryphonectria parasitica* (there is presently no true viruses having an extracellular phase described in fungi, but genetic elements having all hallmarks of viruses are widespread in these organisms), or mitochondrial plasmids that may alter lifespan. It has also been postulated that the death system active during Vegetative Incompatibility could be activated to provide nutrients during stationary phase and especially during sexual reproduction in the hyphae underlying maturing fruiting bodies. Indeed, many mutants having suppressed Vegetative Incompatibility are female sterile, have increased amounts of aerial hyphae and impairment in growth renewal after exit of stationary phase. Moreover, Vegetative incompatibility between strains is often associated with sexual incompatibility, *i.e.*, in many instances, crosses between vegetatively-incompatible strains are partially or totally sterile and these sterilities are controlled by the *het* genes. Whatever the actual roles of this executed hyphal death, the polymorphism of the genes involved in Vegetative Incompatibility is under balanced selection, suggesting an active evolutionary force to maintain the polymorphisms of the *het* genes, a feature compatible with a role in pathogen defense and self *versus* non-self recognition. This is clearly exemplified by the het-z/sec9 incompatibility system, since it is conserved in *Neurospora crassa*, but also in the distantly related *C. parasitica*.

Appressorium-like structure differentiation

The full extent of cellular differentiation during vegetative growth that *P. anserina* is able to achieve is unknown. We know that it is able to produce small apical hyphae and that in stationary phase larger hyphae are produced, especially those that underlie the maturing fruiting bodies. *P. anserina* is also able to produce aerial hyphae in about 24 hours, most likely coated with hydrophobins and it is very efficient to produce anastomoses as early as 4 hours after growth (see chapter on morphology and cytology of the mycelium; figure 86). Nevertheless, the most striking hyphal differentiations that *P. anserina* is able to produce are the appressorium-like structures, penetration pegs and haustorium-like structures involved in plant biomass penetration (see chapter on morphology and cytology of the mycelium; figure 86). These are easy to visualize when the fungus is grown on cellophane overlaying a medium devoid of glucose (such as M2 and M0, see figure 37) and differentiate in 12-24 hours. Note that

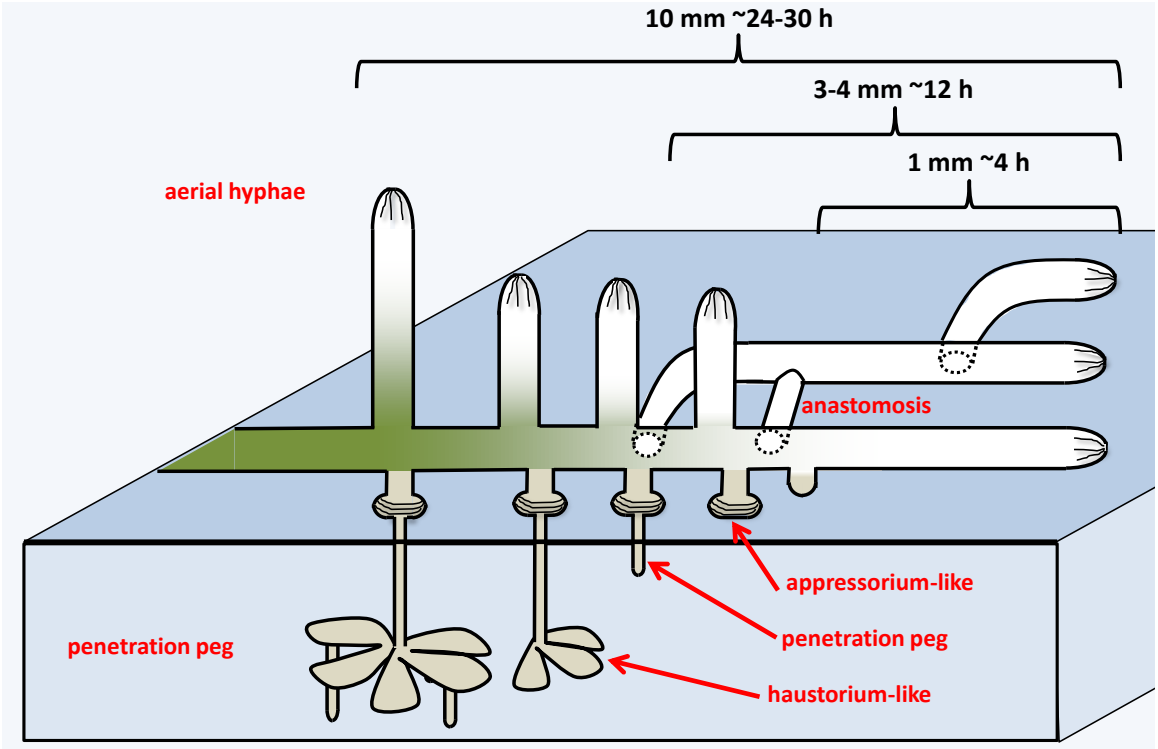


Figure 86 **Differentiation during the vegetative phase of *P. anserina*.** See figures 33, 35 and 37 for actual pictures.

if we don't known the molecular pathways implicated in the erection of hyphae, anastomosis is under the control of the *IDC* genes involved in the making of the *C* element associated with Crippled Growth (see section on Crippled Growth). For penetration of cellophane, it was shown that reorientation of hyphae towards cellophane and formation of the appressorium-like structures are under the control of the same molecular pathway as the one controlling ascospore germination, *i.e.*, the PaNox2/PaPls1 NADPH oxidase complex and the PaMpk2 MAP kinase (see section on ascospore ejection and germination). Later stages of the differentiation are less well known; however, the formation of the penetration peg is under the control of the PaNox1/PaNoxD NADPH oxidase.

Sexual reproduction

Sexual reproduction of *P. anserina* has been under scrutiny for a long time. Indeed, the first studies using *P. anserina* as an experimental system, *i.e.*, those of Wolf in 1912 and Satina in 1916, were on sexual development. Since then, numerous studies have been published; including some dealing with the recognition between the sexual partners, *i.e.*, the mating system of *P. anserina*, the differentiation of its fruiting bodies and their production and repartition on the mycelium. Additional mechanisms acting during sexual reproduction have also been studied, including Spore Killers and RIP.

Mating and mating types

As explained in the section dealing with the life cycle of *P. anserina*, the fungus is pseudo-homothallic, implying that fertilization can only proceed between sexually-compatible partners: one *mat+* and one *mat-*. Genetic analyses have indicated, that half the nuclei obtained after meiosis are *mat+* while the other half is *mat-*; the mating system of *P. anserina* is thus akin to the bipolar heterothallism found in many ascomycetes. Hence, there is a single sexual locus with two alternative versions, one conferring the *mat+* identity and the other the *mat-* one. As the mating type was the first genetic marker available for *P. anserina*, this *mat* locus, which branded genetically a first chromosome, was positioned on chromosome 1.

Identification of the two *mat* loci was achieved with the help of the cloned *matA* locus of *Neurospora crassa*, by heterologous hybridization of a genomic bank. We now know that the *mat+* idiomorph contains one gene, *FPR1*, while the *mat-* idiomorph contains three genes, *FMR1*, *SMR1* and *SMR2* (idiomorphs are alternative versions of a locus that contain different genes rather than different alleles of the same gene(s); figure 87). *FPR1* and *FMR1* are the two genes important for the recognition between the partners, e.g., for fertilization, while *SMR1* and *SMR2* are important for ensuing ascospore formation. As stated in the section on “Developmental genetics: grafting and genetic mosaics”, the

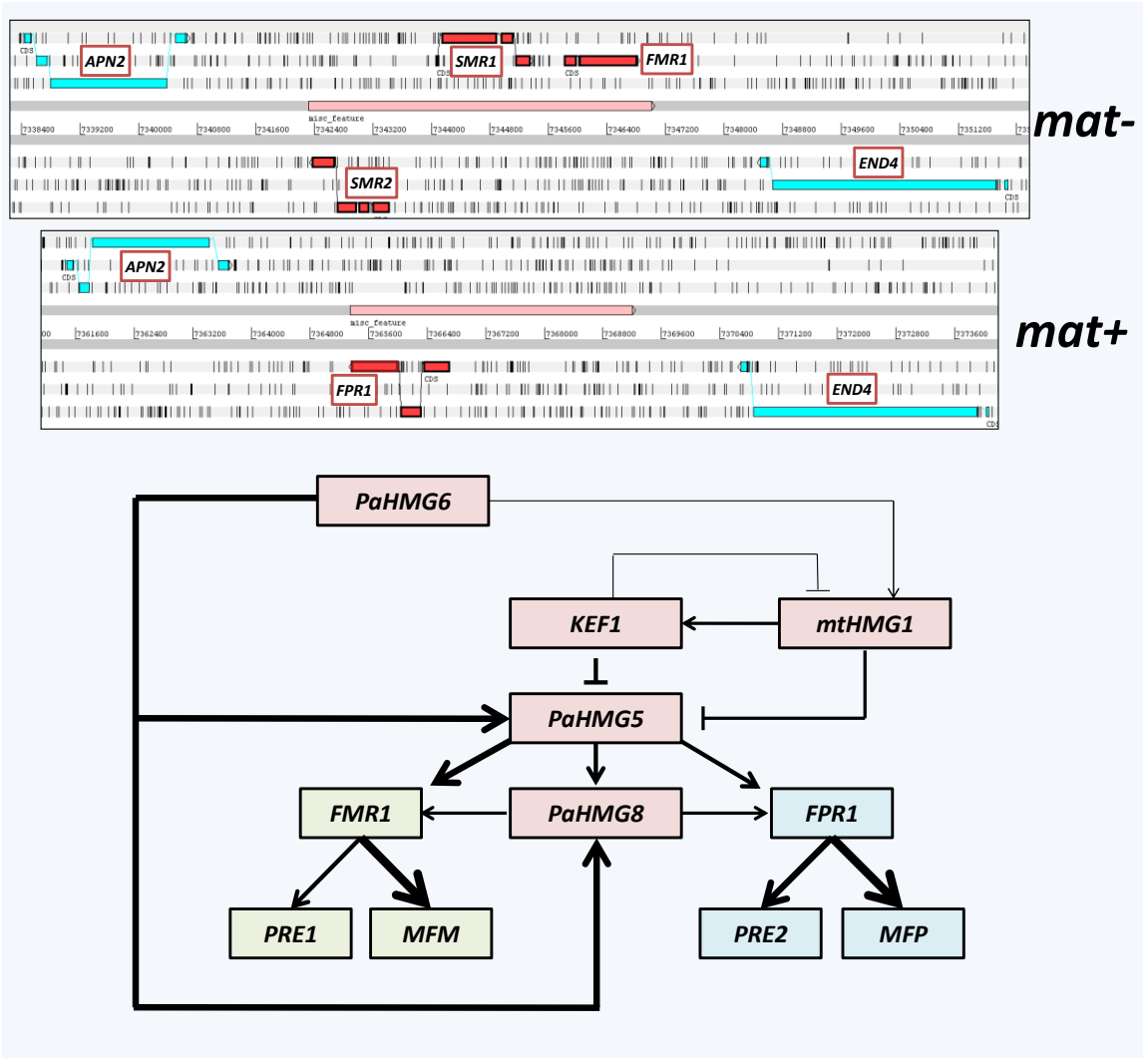


Figure 87 **Structure and regulation of the mating type loci of *P. anserina*.** Top, like in most ascomycetes the mating type loci of *P. anserina* are bordered by the *APN2* and *END4* genes. The region different between the *mat+* and *mat-* strains are boxed in pink and the mating type genes are in red. Bottom, the network of HMG-box transcription factors involved in regulating the expression of the *FMR1* and *FPR1* mating type genes, which in turn activates the PRE1/MFM and PRE2/MFP receptor pheromones genes, respectively. The thickness of the arrows is proportional to the strength of the activation (arrow) and repression (blunted line)

deletion of the mating type result in a strain (*Δmat*) completely unable to engage fertilization with either a *mat+* or a *mat-* partner. However, *Δmat* differentiate normally spermatia and ascogonia. It also produces protoperithecia. This underscores that the mating type solely controls the formation of the

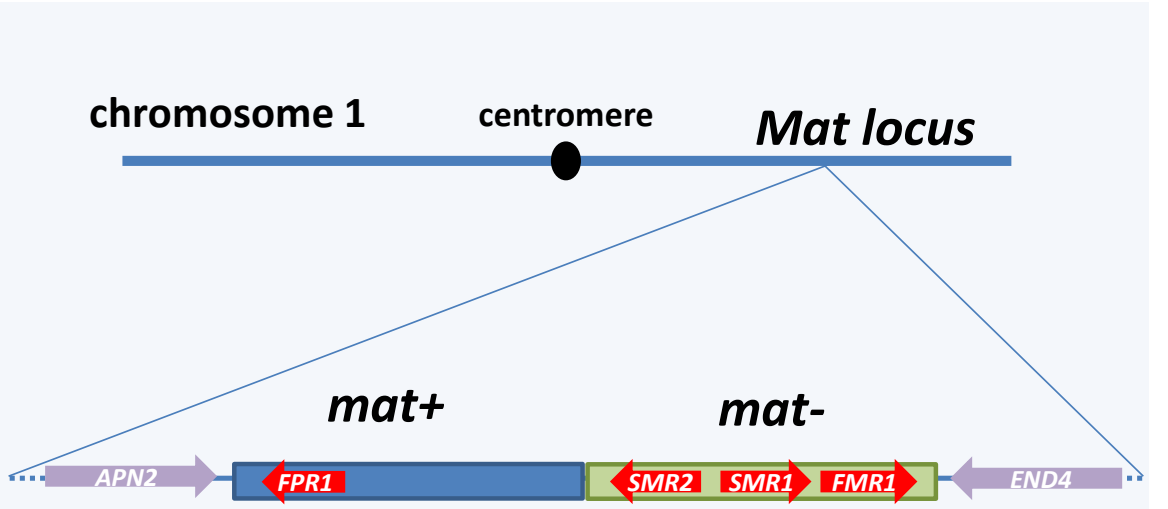


Figure 88 **Structure of the mating type locus of *the mat+_mat-* dual mater strain PM154**

zygotic tissue of the fruiting body, but not that of the gametes and the first stages of the maturation of the ascogonia into protoperithecia. Through *SMR1* and *SMR2*, but also *FPR1* and *FMR1*, the mating type locus also controls later stages of ascospore production, especially the nuclear recognition that must take place for the production of the dikaryotic *mat+/mat-* ascogenous hyphae that will lead to ascus genesis. *Δmat* can also be used to help the development of mutant affected in the maternal tissue of the fruiting body (see section on "Developmental genetics: grafting and genetic mosaics"), indicating that the mating-type locus is not involved in the differentiation of the maternal tissues of the fruiting bodies, but solely the zygotic one. Alternatively, there is a mutant of *P. anserina*, called *vacua*, in which normal looking perithecia are developing in the absence of fertilization. These contain only paraphyses and are devoid of asci, confirming that it is possible to uncouple the development of the zygotic tissues resulting from fertilization from that of the maternal tissue, *i.e.*, the peridium and other non-zygotic tissue of the centrum.

Introduction of a *mat+* idiomorph into a *mat-* strain results in a mutant able to mate with both *mat+* and *mat-* strains, but also able to self-fertilize. A *mat+_mat-* dual mating strain was even created by introducing cleanly (*i.e.*, without additional sequences) the *mat+* idiomorph beside the *mat-* one at the mat locus of chromosome 1: the *PM154* strain (figure 88; see section on "Developmental genetics: grafting and genetic mosaics" for the use of this strain in mutant search).

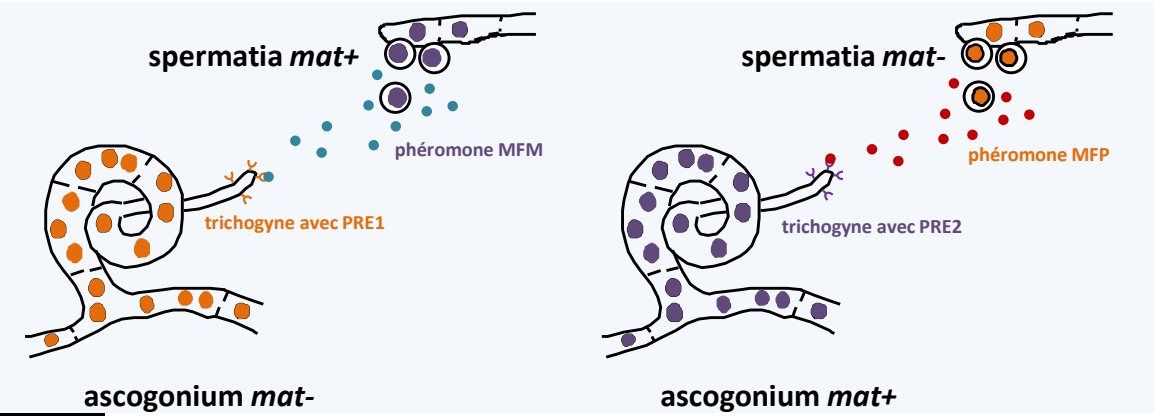


Figure 89 **Roles of *P. anserina* pheromones and receptors in mating.** Targeted deletions have shown that mutants lacking *MFM* or *MFP* are male sterile in a mating-type specific manner: *mat+* spermatia lacking *MFM* are unable to engage fertilization while *mat+* spermatia lacking *MFP* are fully functional; the converse is true for *mat-* spermatia. Similarly, mutants lacking *PRE1* or *PRE2* are female sterile in a mating-type specific manner: *mat-* ascogonia lacking *PRE1* are unable to engage fertilization while *mat-* ascogonia lacking *PRE2* are fully functional; the converse is true for *mat+* ascogonia. Therefore, *mat+* spermatia attract the *mat-* trichogynes expressing PRE1 through the production of the MFM pheromone and the *mat-* spermatia attract the *mat+* trichogynes expressing PRE2 through the production of the MFP pheromone.

In *P. anserina*, gametes are present on mycelia older than three days. Accordingly, expression of *FMR1* and *FPR1* is significant only after three days. It was shown that expression of both genes is under the complex control of a set of transcription factors containing HMG-box as DNA-binding domain (figure 87). Note that three out of the four genes present at the mating type locus (*FPR1*, *FMR1* and *SMR2*) also encode transcription factors containing HMG-box, while the last one (*SMR1*) has no obvious associated function or known domain and is not actually involved in defining sexual identity (this gene is necessary for ascospore production but can act in the *mat+* and *mat-* nuclei or in both, it appears involved at later stages of the fruiting body development than *FPR1*, *FMR1* and *SMR2*). Overall, 11 out of 12 HMG-box-containing proteins encoded in the *P. anserina* genome are involved in the sexual cycle, many of which participate in conferring sexual identity. Intriguingly, a similar function has been attributed to HMG-transcription factors in mammals!

The whole sets of targets of *FMR1* and *FPR1* were identified through microarray analyses. Functional analyses of these targets identified few genes actually involved in sexual development apart from the receptors PRE1/PRE2 and the previously characterized mating pheromones MFP/MFM (figure 87). Functional analyses have shown that, as expected, spermatia produce sex-specific pheromones that

attract the trichogyne of opposite mating type and expressing the cognate receptor (figure 89). The fact that many genes regulated by *FPR1* and *FMR1* are not involved in sexual reproduction suggests that both mating-type transcription factors are involved in the control of other processes in *P. anserina*.

Finally, it worth mentioning that the mating type locus is embedded in a 800 kb-region devoid of recombination, so that numerous polymorphisms exist between the S *mat+* and S *mat-* strains in this region, while their sequences is strictly identical in the rest of the genome. Additionally, many genes are differentially regulated between the *mat+* and *mat-* strains independently of the mating-type locus, *i.e.*, thanks to differences present in the non-recombining region. In some *Neurospora tetrasperma* strains, another pseudo-homothallic fungus, lack of recombination is linked to the presence of inversions in the genome. In *P. anserina*, the mechanisms preventing recombination is still mysterious as no inversion have been detected around the mating type locus. As explained in the chapter on "the sexual cycle and genetical analysis", *mat+/mat-* dikaryotic ascospores are obtained through a defined arrangement of nuclei in the postmeotic mitosis coupled with the fact that in most meiosis (in ~99% of them) a single crossing-over occurs between the centromere of chromosome 1 and the mating-type locus. Possibly, the same mechanism that regulates the positive interference inhibiting the occurrence of a second crossing-over between the centromere and the *mat* locus also intervene to inhibit the recombination around the mating type. Whatever the mechanism, the differences observed in the non-recombining region are not involved in the maintenance of the heterokaryosis necessary for self-fertilization through fitness-enhancing complementation. Indeed, heterokaryons are very stable in *P. anserina*, whatever their genetic constitution at the mating-type locus.

Fruiting body differentiation

Fruiting body differentiation is also intensively studied in *P. anserina*. As explained in the perithecium section on "Morphology and cytology" chapter and the section on "Developmental genetics: grafting and genetic mosaics" of the chapter on "The sexual cycle and genetical analysis", the fruiting body is made up of zygotic tissues (the lineage leading to asci) resulting from fertilization and maternal ones that originate from hyphae neighboring the fertilized ascogonium (figure 90). The mycelium is also an important partner acting in the feeding of the perithecia and dedicated large hyphae connect maturing fruiting bodies to the underlying mycelial network (figure 90). Respective roles of genes in these

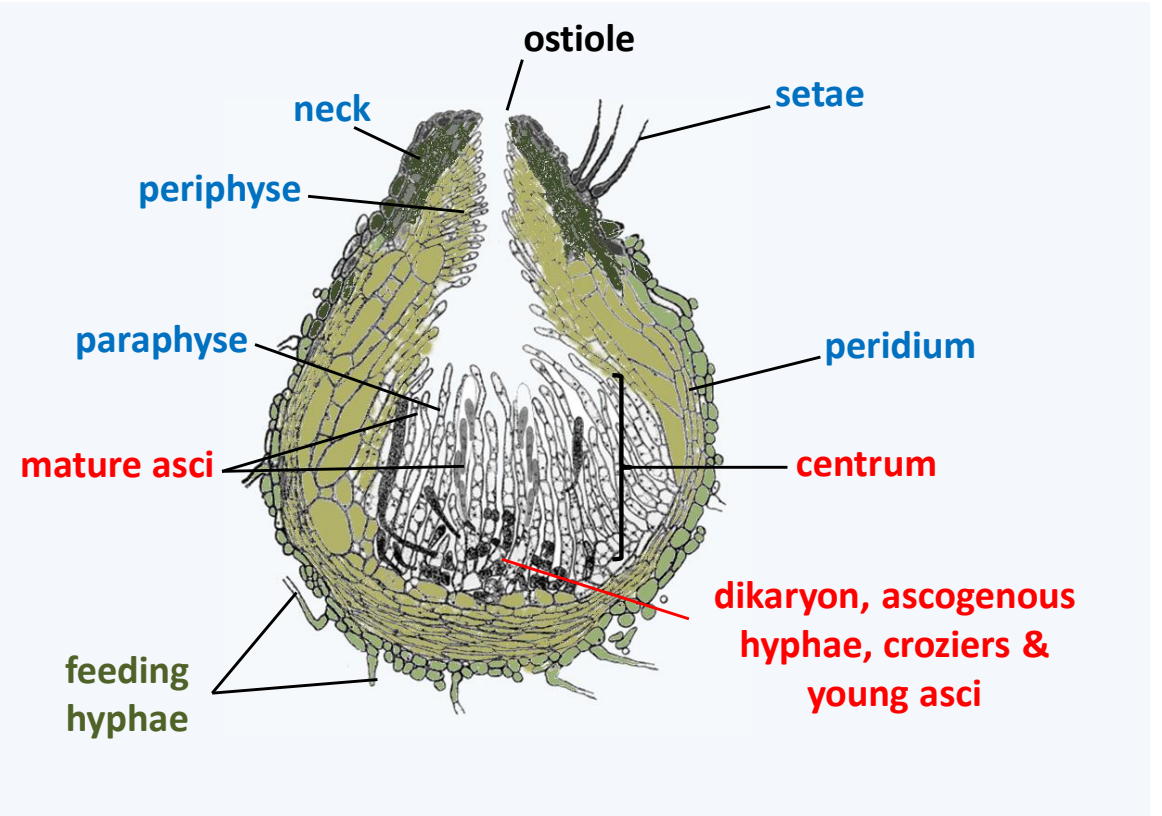


Figure 90 **The three components interacting to produce mature fruiting bodies.** In red, the zygotic tissues, in blue the maternal tissues and in green the mycelium.

three interacting components involved in the elaboration of the fruiting body can be analyzed thanks to genetic analyses adapted from embryology technics developed in animals, *e.g.*, genetic mosaics and grafting (see "Developmental genetics: grafting and genetic mosaics" section of the chapter on "The sexual cycle and genetical analysis").

The zygotic lineage develops only after fertilization. Fertilization leads first to the production of a plurinucleated cell containing both *mat+* and *mat-* nuclei. From this plurinucleated cell, ascogenous hyphae emerge. These carry a single *mat+* nucleus and a single *mat-* one. How, nuclei of opposite mating types recognize each other is unknown. Based on the phenotypes of *FPR1*, *FMR1* and *SMR2* mutants it has been proposed that the three mating type genes also participate in the recognition between the sexual partners at this stage (mutants of these genes produce selfish nuclei that engage ascus development in the absence of a mating partner and hence undergo haploid meiosis). Note that at this

stage, recognition occurs between nuclei. Accordingly, recognition does not require the mating pheromones and their receptors. Once two nuclei have properly recognized each other, *SMR1* would be required to lift a process that blocks further development of the zygotic lineage. Indeed, the *SMR1* gene of the *mat-* mating type is required for the production of the ascogenous hyphae. The PaRID DNA methyl transferase is also required at this stage. DNA methyltransferases are involved in defining DNA methylation patterns. In *P. anserina* as in other *Pezizomycotina*, RID DNA methyltransferases are also involved in the Repeat-Induced Point mutation process or RIP, a feature that will be discussed in a previous section (see the "RIP" paragraph in the section on "Genes and genome" in the chapter on "The sexual cycle and genetical analysis"). How PaRID control development is unknown, especially since no DNA methylation has been observed yet in *P. anserina*, and since, unexpectedly, the methyltransferase catalytic domain is important for the function of PaRID during development. However, transcriptome analyses have shown that genes regulated by PaRID overlap those regulated by the mating type. Note that, alternatively to *mat+* and *mat-*, the two nuclei engaging recognition can be viewed as paternal and maternal ones. Owing to the different ontogeny of spermatia and ascogonia, it is possible that their nuclei are branded with different epigenetic marks (imposed by PaRID?), which could facilitate the recognition between the two nuclei (and a feature that would also explain the lack of germination of spermatia).

Nothing is known about the coordinate divisions of the ascogenous hyphae preceding the production of croziers. More is known about the genesis of croziers. They require the *cro1* and *ami1* genes since mutants of these genes have abnormal croziers, plurinucleated ones for *cro1* mutants and uninucleated ones for ami1 mutants. The cro1 protein shares some similarity with UCS proteins that are involved in folding, assembly and function of myosin, while ami1 is similar to *Aspergillus nidulans* apsA, a cortical protein that controls spindle positioning during mitosis. Both mutants have additional defects, indicating supplementary roles. The *ami1* mutants have abnormal nuclear positioning in mycelia and asci and produce anucleated spermatia and periphyses. The *cro1* mutants display normal septation and nuclear positioning, but have abnormal mycelium morphology and a germination defect. The next step of sexual development, *i.e.*, the commitment of croziers into meiocytes (ascus) in which caryogamy proceeds necessitates some as yet undefined peroxisomal protein(s) as many of the proteins involved in peroxisomal import accumulate croziers that do not engage into further development (figure 91).

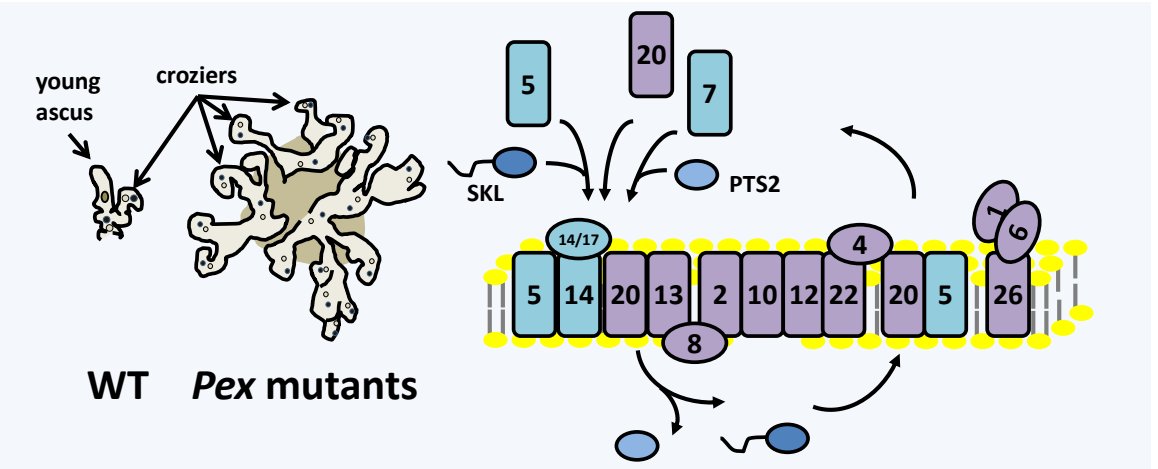


Figure 91 **Peroxisomes and ascus development.** Left, phenotype of the wild type and of peroxisome mutants, in which croziers accumulate without engaging into ascus development. Right, the subunits of the peroxisome import machinery labelled in purple are required for commitment into meiocytes, those in blue are not. The actual peroxisomal protein(s)/product(s) required for the transition are(is) unknown).

The next stage of sexual development is meiosis. *P. anserina* is not as used as *Sordaria macrospora* for meiosis analyses owing to the small size of its nuclei during this stage. Nevertheless several mutants affected in meiosis are available. Two have been studied. Firstly, mutants of the mitochondrial citrate synthase, the initial enzyme of the Krebs respiratory cycle are blocked at the diffuse stage of the first meiotic prophase, identifying a metabolic checkpoint for meiosis progression beyond this point. Secondly, the PaMe4 encoded by the *mei4* gene is a component of the synaptonemal complex and spindle pole body having crucial roles in their morphogenesis and later in recombination complex formation. Intriguingly, the Meiotic Silencing by Unpaired DNA (MSUD) process present in some *Neurospora spp.* appears absent in *P. anserina* since unpaired essential genes, such as the *AS4* gene encoding the cytosolic elongation factor, can pass through meiosis without problem. MSUD silences DNA regions that are not paired during prophase of the first meiosis through an RNA interference mechanism. Nevertheless, the expected fluorescence of proteins tagged with the GFP or mCherry proteins is often absent in the young sexual tissues for an unknown reason. Note that we also have no convincing evidence for the occurrence in *P. anserina* of Quelling, a second RNA interference mechanism acting during the vegetative phase in *Neurospora crassa*, although we sometime observe extinction of transgenes expressing proteins tagged with GFP or mCherry in the mycelium.

Several mutants having defects in later stages of development, *i.e.*, ascospore formation and

expulsion are available. It is however not known whether these have specific alterations in the ascospore formation developmental program have general disturbance in metabolism, which being higher during ascospore formation could result in various impairments. For example, many peroxisomal mutants have abnormally-pigmented ascospores that germinate at lower frequency. Fidelity of the cytosolic translation has also been shown to have a major impact on fertility. Mutants with lower fidelity are female-sterile, while some with higher translation accuracy have ascospore formation defects and others are female sterile. It has been shown that the ascospore formation defect is linked to increased accuracy, suggesting that mistranslation of some key regulator(s) is required for proper development of ascospores. Also, some mutants of potassium transporters do not properly expel their ascospores unless the medium is supplemented with large amounts of potassium, while others have the opposite phenotype, depending on whether they are involved in taking in potassium or expelling excess of it. One more mutant is worth of mention: the one affected in the *PaAlr1* gene, encoding a magnesium transporter. Null mutant of this gene has the development of all its ascospores arrested at the stage when they contain two nuclei. Reason for such a distinct defect is unknown.

As seen from the above text, our knowledge of zygotic tissues development in *P. anserina* is still very patchy. One of the reasons for this fact is that few mutants affected in the zygotic lineage are available. Indeed, for a long time, it was difficult to isolate recessive mutations with zygotic defect since *P. anserina* being formally heterothallic; mutations need hence to be present in both parents to exert their effect (note that mutants affecting maternal tissues were easily obtained since they were female-sterile!). Screening for recessive mutants required thus time-intensive genetic manipulation on many candidates to obtain few interesting mutants. Thanks to the availability of the *mat+_mat-* self-fertile strain PM154 screening of recessive mutants is now very easy (see “Developmental genetics: grafting and genetic mosaics” section of the chapter on “The sexual cycle and genetical analysis”). So far a single mutant obtained thanks to this strain has been thoroughly analyzed; it has both zygotic and maternal defects: *spod1*. The zygotic defect in *spod1* occurs after the first prophase of meiosis. Older asci are enlarged; they contain many nuclei and later on undergo lysis. The *spod1* mutant has also a strong maternal defect and produce tiny abortive fruiting body. The gene affected in *spod1* encodes an inositol-phosphate polykinase, a protein involved in signaling through phosphorylation of inositol-phosphate molecules in eukaryotes. We shall again return to this mutant in the next section because it has interesting phenotypes pertaining to the localization of fruiting bodies on the mycelium. But before we

do so, we must discuss the signaling pathways involved in the development of the maternal tissues. Indeed, in addition of *spod1*, many mutants affected in maternal tissues development have been analyzed in *P. anserina*.

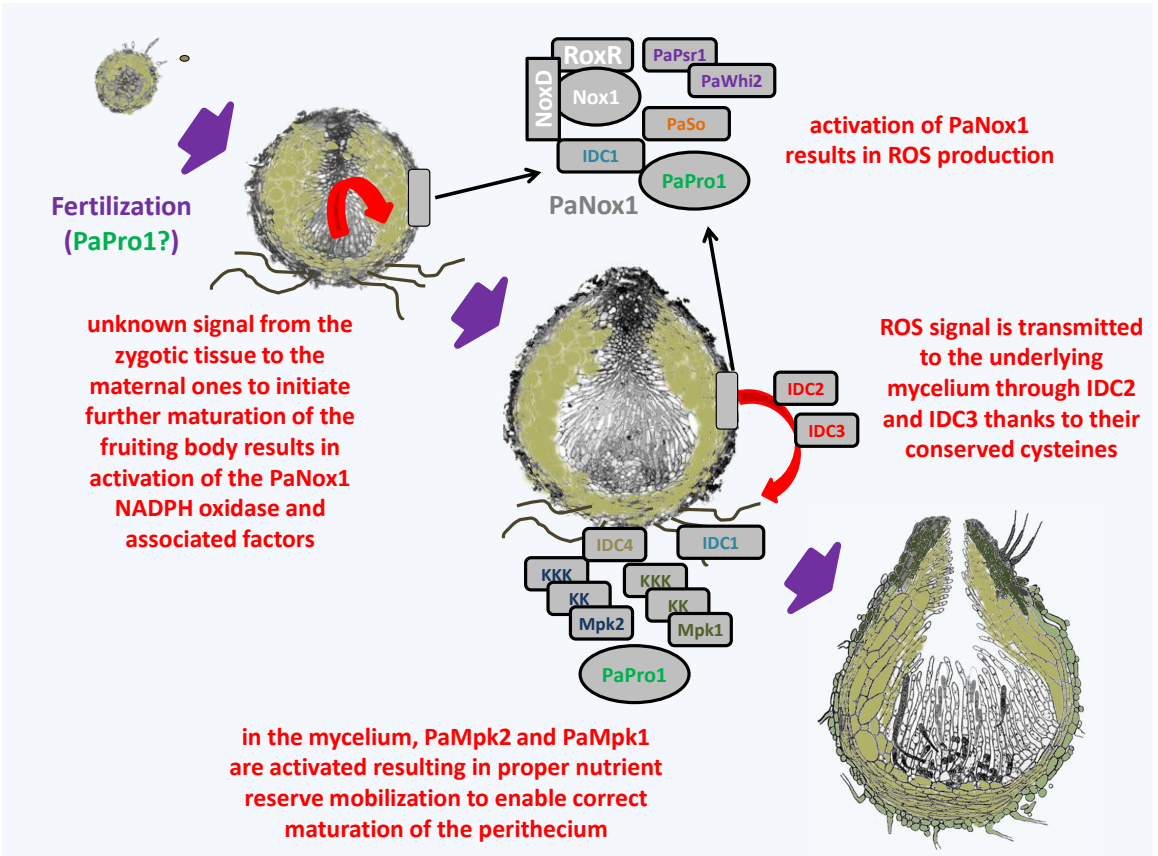


Figure 92 **Model of action of the roles of *IDC* genes during perithecium maturation.** From top left to bottom right. Development starts with fertilization. This triggers the release of an unknown signal from the zygotic tissues towards the maternal ones. In the maternal tissues, the PaNox1 NADPH oxidase complex is activated and starts to produce reactive oxygen species (ROS). The PaPsr1, PaWhi2, PaSo, IDC1 and PaPro1 proteins are also required in the maternal tissues for proper development. The ROS signal is likely transmitted through the voyage of vesicles containing oxidized IDC2 and IDC3 proteins; these proteins contains evolutionary-conserved cysteines required for their activity and genetic mosaics indicated that they act in a cell-non-autonomous manner (hence diffuse from cells to cells). Once in the underlying mycelium, they transmit their signal to the PaMpk1 and PaMpk2 MAP kinases pathways (in a manner that do not require thioredoxins). Once activated MAP kinases likely orchestrate the mobilization of the nutrients required for proper maturation of perithecia. The IDC1, IDC4 and PaPro1 proteins are also required in the mycelium. Not depicted here is the STRIPAK complex that is also important for perithecium production, it is required in the zygotic tissues but at a late stage of ascospore production, in the maternal tissues and in the underlying mycelium.

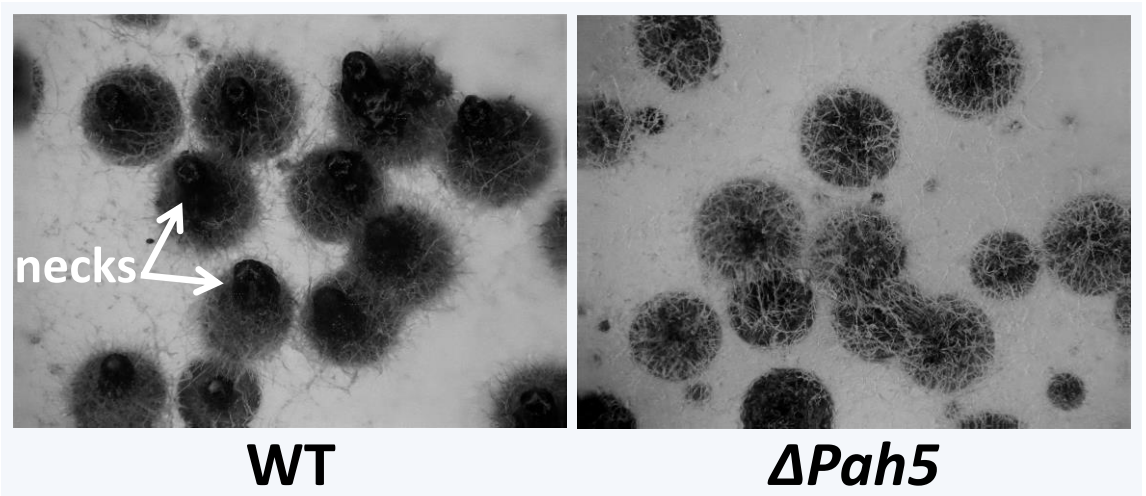


Figure 93 **Lack of neck in mutants affected in homeodomain transcription factors.** *Pah5* has the strongest effect since all perithecia produced by null mutants of *Pah5* lack neck, while null mutants affected in *Pah2* produce 30% of neckless perithecia. Other *Pah* genes have modulatory effect on the percentage of neckless perithecia produced by *Pah2* mutants. For example, a double mutant affected in both *Pah1* and *Pah2* produce 95% of neckless perithecia.

First and foremost are the *IDC* mutants involved in Crippled Growth. Indeed, as stated in the section on "Crippled Growth and other phenotypic instabilities", mutants involved in making up *C*, the infectious element associated with Crippled Growth, lack development of fruiting bodies after fertilization, while they produce male and female gametes. Only one of these mutants, the one affected in the PaPro1 transcription factor is affected in the formation of the zygotic tissues, all the other are dispensable for proper development of the zygotic tissues and hence their fertility defect is due to impairment in the production of the maternal tissues. How PaPro1 is involved in the formation of the zygotic tissues is unknown, but its action takes place very early during the process and may even occur at the fertilization stage. For the other *IDC* mutants, analyses using genetic mosaics and grafting has enabled to determine which component(s), *i.e.*, the mycelium or the maternal tissues, is(are) important for the maturation of the fruiting bodies, leading to the model depicted in figure 92. The major feature of this model is that fruiting body development results from the Reactive Oxygen Species (ROS) emitted by the maturing fruiting bodies thanks to the activation of the PaNox1 NADPH oxidase complex to the underlying mycelium through vesicular transport of the oxidized IDC2 and IDC3 proteins. There, they activate the PaMpk1 and PaMpk2 MAP kinases, which participate in nutrient mobilization to feed the maturing perithecia. Accordingly, microarray analyses of transcriptomes have shown that PaMpk1 and

PaMpk2 regulate genes involved in carbohydrate metabolism.

Transcription factors have also been analyzed for their involvement in the development of the maternal tissues of the fruiting bodies. The HMG transcription factors Pahmg6, Pahmg8 and kef1 are required in them for maturation of perithecia, while Pahmg1 is required in both the maternal and zygotic tissues. Transcription factors containing homeodomain have also been investigated and some were shown to be specifically involved in neck differentiation. The Pah2 and especially Pah5 transcription factors are important for this task since mutants have neck defects (figure 93). Note that the neck is a major morphological attribute and an important feature of the fruiting body enabling correct expulsion of ascospores. Most species related to *P. anserina* produced perithecia with neck, but a few ones produced neckless perithecia, that are then coined cleithothecia or more properly cleistothecoid perithecia.

In conclusion, *P. anserina* is invaluable in deciphering the development of the fruiting body. The pathways identified in the friendly mold have been shown to participate in development in other fungi, especially in its cousins *Neurospora crassa* and *Sordaria macrospora*, indicating as expected a conservation of these pathways in related fungi. However, there is still a lot of work to be done since, like in the other studied fungi, our understanding of its development is incomplete. The friendly mold is invaluable since the genetic tools used to differentiate the place(s) of action of the various actors (*e.g.*, the genetic mosaics and grafts) are to date implemented only in this species.

Fruiting body production and repartition

As stated in the chapter on “Mycelium growth and development”, *P. anserina* is rather fussy when it comes to produce perithecia, at least more than during its vegetative phase. In addition, there are likely complex interactions between the factors regulating sexual development, because factors found to be absolutely required for perithecium production by some researchers, are found dispensable by others. For example, James E. Pehram in his thesis states that biotin can be omitted from the medium for optimal fertility, while we find it mandatory to obtain perithecia. Caution must thus be taken when interpreting the factors described below. Firstly, as stated in the chapter on “Mycelium growth and development, ”*P. anserina* requires a medium not too rich in easily digestible carbon and nitrogen sources (such as glucose and ammonium). On rich medium, *P. anserina* produces large amount of mycelium, especially aerial hyphae, but remain sterile or produces usually with a delay abnormal

Figure 94 **Effect of light on perithecium development in *P. anserina*.** Left, M2 Petri plates were inoculated with *mat+/mat-* heterokaryotic inocula and incubated for eight days with or without light. The illuminated plate has more perithecia that have already started to expel ascospores, while the non-illuminated one has much fewer perithecia that are not yet mature. Right, M2 Petri plates were inoculated with *mat+/mat-* heterokaryotic inocula and incubated for eight days in constant illumination coming from above either with the lid on top or with the lid on the bottom, hence with plates upside down. On the plate with lid on the top, necks have an upright position pointing towards light, while on the plate with the lid on the bottom, necks tends to curve towards the medium, hence trying to also point towards the direction the light is coming from. Note that in both instances, necks are differentiated from the middle of the part of the perithecia that is sticking into air, and not within the medium for upside down plates.

perithecia producing few asci. Secondly, as stated above, in addition to thiamin, it requires biotin for optimal perithecium production, hence the presence of both vitamins in the minimal M2 medium. Thirdly, it requires light. Indeed,continuous light speeds up maturation and increases greatly maturation (figure 94). Light also directs the orientation of necks and hence the path of ascospore ejection (figure 94). Fourthly, efficient perithecium production requires air. On M2, perithecia are produce at the interface between the medium and the air. In M2 liquid cultures, *P. anserina* produces abortive perithecia, except for those few that are fortunate to develop at the interface between liquid and air. The likeliest explanation is that high levels of oxygen are required for the “Reactive Oxygen Species” production that controls perithecium production (see previous section). In other medium, such as M4, perithecia may be produced within the agar, always more slowly than at the air/medium interface. Their necks tend then to be produced arbitrarily on the top part of the fruiting body (“horizontal” perithecia are frequent when they develop inside the medium). This suggests a negative geotropism of the determinants that determine the position where they are differentiated. Finally, temperature is also important, since perithecia are efficiently produced between 18°C and 27°C. At lower temperature, the slow growth speed and very slow timing of perithecium production makes it difficult to obtain them. At 18°C on M2, perithecia take about three weeks after mycelium inoculation to mature, at 23°C they take

Figure 95 **Non-random repartition of fruiting bodies on *P. anserina* thallus.** Left: typical repartition of fruiting body along a ring when *P. anserina* is cultivated on M2 at 27°C with constant illumination. Right, a fairy ring differentiated by basidiomycetes.

about 9-10 days, and at 27°C the optimal temperature, they take 7 days. Importantly, at temperature above 29°C/30°C, no fruiting body is ever observed, while mycelium growth still proceeds up to 37°C.

As stated in the section on “The mycelium” in the chapter on “Morphology and Cytology”, an interesting feature of *P. anserina* fructification is the non-random repartition of the fruiting body on the mycelium, especially when grown on M2 medium. Indeed, on M2, the friendly mold differentiates perithecia mostly along a ring with an inner diameter of 2 cm and a width of 1 cm (figure 95). Such ring is reminiscent of the “fairy rings” produced by many basidiomycetes. This ring feature is typical of *P. anserina* and the other species of the *P. anserina* species complex may differentiate other types of repartition with or without an obvious ring pattern (see figure 19).

Ring differentiation is robust and occurs without fail on M2 provided that the cultures are not senescent (see the many figures showing *P. anserina* M2 *mat+ mat-* heterokaryotic cultures in this book, *i.e.*, figures 3, 19, 36, 94, 95, 96 and 97). It is nonetheless affected by many factors including temperature, light, nutrients and genetic factors, the general trends being that the lower the fertility, the larger and more diffuse the ring (figure 96). However, this may not be so simple, as seen with the homedomain transcription factor mutants (figure 96). The most intriguing feature of the ring formation is the central zone devoid of perithecia (that is lacking in the *ΔPah7* mutants). Indeed, male and female gametes

appear to differentiate uniformly on the thallus. The outer zone can be explained if maturation of the first-produced perithecia inhibits further differentiation of additional fruiting bodies. Yet, there is nothing obvious that should impede differentiation of fruiting bodies within the central zone. Intriguingly, when the fungus is inoculated in two close points, the central zone takes the shape of googles (figure 96), suggesting an active mechanism to inhibit production in the central zone (if nothing would inhibit production, the shape should be two interlocked rings).

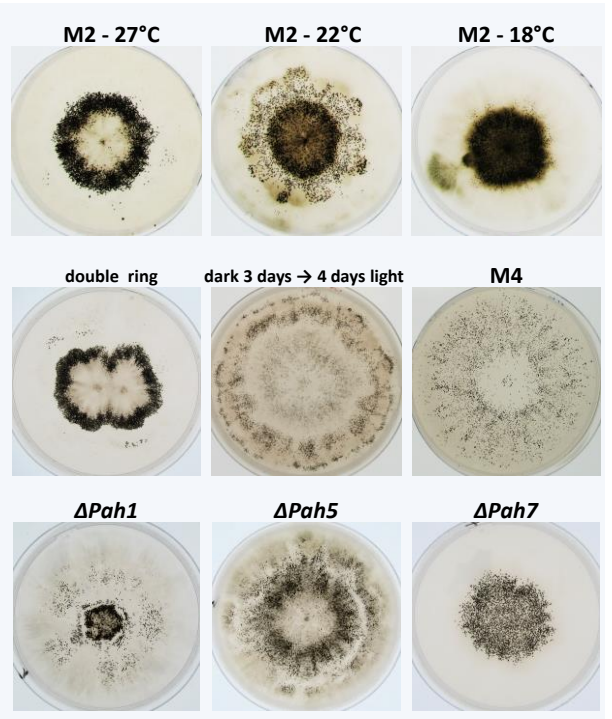


Figure 96 Environmental and genetic influence of the non-random repartition of fruiting bodies in *P. anserina* thallus. Top, influence of the temperature; Middle, effect of inoculation point, light and carbon source (M4 contains crystalline cellulose); bottom, genetic control with the examples of three mutants inactivated for the genes *Pah1*, *Pah5* and *Pah7* encoding homedomain transcription factors.

Little is known about the molecular pathways controlling both the amounts of perithecia and their repartition. However, the inositol phosphate pathway appears to be a major player as shown in other fungi. Indeed, in the previous section, I mentioned the *spod1* mutant affected in an inositol phosphate polykinase and showing impairment in differentiation of both the maternal and zygotic tissues of the perithecia. This mutant has an additional interesting phenotype: when crossed with the wild type by "confrontation arrosée", perithecia differentiate along a triangle pointing within the *spod1* thallus (figure 97). Additional experiments have shown that this pattern is due to diffusion of a factor promoting perithecium development, which is not the inositol phosphate polykinase enzyme, but possibly its reaction products (*i.e.*, the inositol-(1,3,4,5,6)-pentaphosphates made from inositol-(1,4,5)-triphosphates). Interestingly, addition of inositol in M2 increases drastically the amounts of developing perithecia (figure 97) up to such levels that they fail to mature (possibly due to lack of enough nutrients). Inositol cannot be

used as food source by the friendly mold, indicating a signaling role of inositol and its phosphates derivatives, in accordance with the phenotypes of the *spod1* mutants.

Meiotic Drive Elements: Spore Killers

Meiotic Drive Elements are genetic loci that subvert the law of Mendel that posits equipartition of alleles/idiomorphs during meiosis by eliminating nuclei that do not contain them. Meiotic Drive Elements

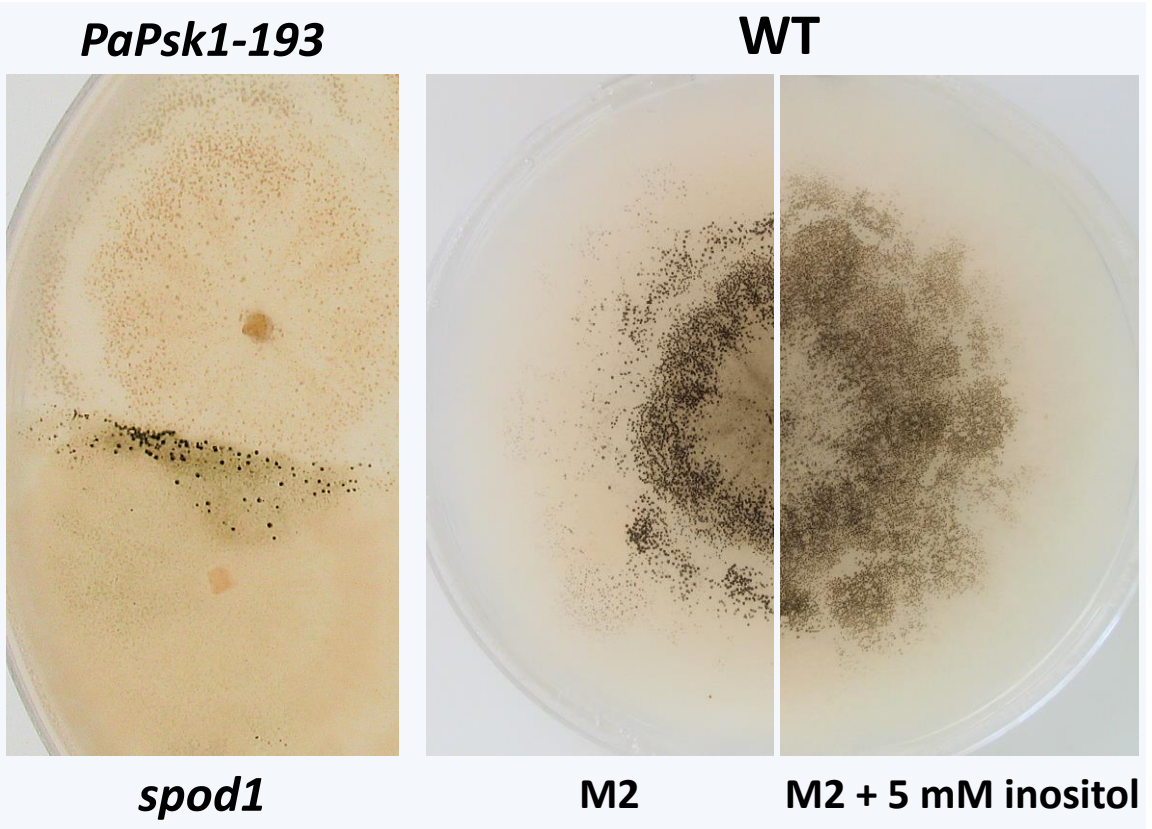


Figure 97 Involvement of inositol and inositol polyphosphates in perithecium production and repartition. Left: a cross between the *PaPks1-193* mutant lacking melanin and *spod1* produces a triangle of pigments and perithecia on the *spod1* thallus. The dark color of these perithecia shows that their maternal tissues are from *spod1* (for comparison, those on the *PaPks1-193* mutants lacking pigments have maternal tissues from *PaPks1-193* as expected). Right, addition of inositol in the M2 medium greatly increases perithecium production; these are smaller than on M2 because they fail to fully mature.

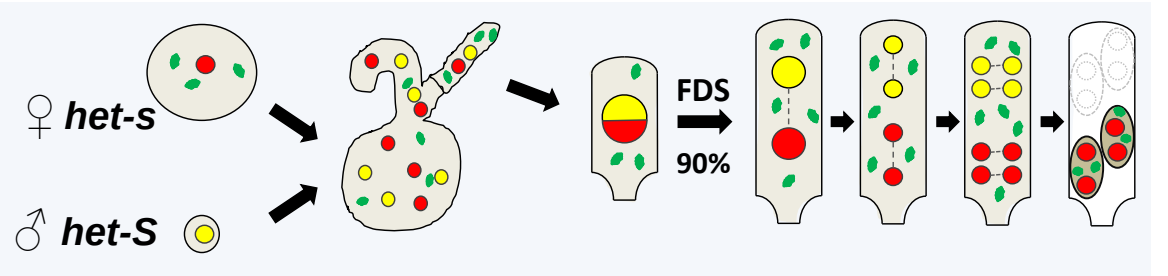


Figure 98 The *het-s/het-S P. anserina* spore killer. The spore killing phenomenon occurs at 18°C in early-produced asci when ascogonia from the *het-s* strain carrying the het-s prion are fertilized by male gametes carrying the *het-S* allele. Prion amyloids may then be present in early asci. If *het-s* and *het-S* are segregated during the first meiotic division, ascospores carrying two het-S nuclei will produce the het-S protein which in the presence of the het-s prion will promote a reaction killing the two het-S ascospores, while the two het-s ones survive and carry the prion. It is not clear what happens to second division segregation asci (SDS) of such crosses (do all the ascospores die?), but the phenomenon occurs in a minority of asci, indicating an inefficient transmission of the het-s prion, especially at temperature above 20°C where the phenomenon is not observed. Lack of spore killing in late-produced asci confirms this assumption: as the dikaryotic lineage produces croziers and asci, the het-s amyloids may be irreversibly lost, freeing asci from the presence of the prion.

carry thus at least two activities: one that kills and the other one that enables resistance. In most investigated instances, these two activities are carried out by two different factors, encoded by two different loci that remained linked through meiosis (often thanks to the presence of genomic inversions that results in recombination inhibition). In fungi, meiotic products end up in meiospores (e.g., ascospores in the *Ascomycota*), meiotic drive element are thus called “Spore Killer”.

Jean Bernet described the first Spore Killer ever in crosses between the *het-s* and *het-S* strains that we now know is related to the presence of the het-s prion and its interaction with the het-S protein (figure 98). Indeed, he observed that at low temperature (18°C) the asci produced early frequently contained two mature spores instead of the expected ones, in crosses involving the *het-s* strain (that we now know contains the het-s prion) as maternal parent and the *het-S* one as paternal parent. On the contrary, he did not observed the phenomenon when *het-s* was used as paternal parent and *het-S* as the maternal one, nor with the *het-s** strain (that we now know are devoid of prion). He also observed that the ascospores from the two-spored asci are het-s (and thus contain the prion) and not het-s*. We now interpret easily Bernet’s observations, through the maternal inheritance of the het-s prion that can only be transmitted by *het-s* ascogonia and its incompatible interaction in ascospores with the het-S protein in asci where the *het-s/het-S* alleles are segregated in first division (figure 98).

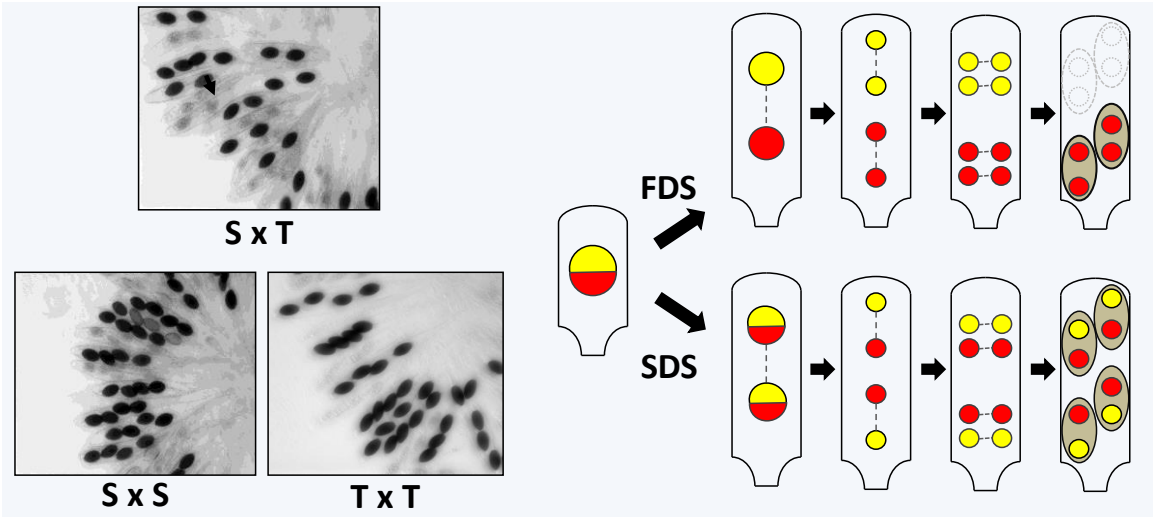


Figure 99 **The T x S *P. anserina* spore killer.** The spore killer action is observed in S x T crosses, which mostly produce two-spored asci, while S x S and T x T crosses yield the usual four-spores asci. Right, interpretation of the spore killer (in red) action by killing ascospores carrying only the sensitive allele/idiomorph (in yellow). Proportion of two-spored asci depends on the first segregation frequency of the Spore Killer locus and hence its chromosomal location: as seen on the left the T meiotic drive element is located close to its centromere resulting in more than 95% two-spored asci (one four-spored is shown for comparison in the S xT picture). Note that lethal mutations acting during ascospore formation will also yield two-spored asci. However, in such instance, surviving ascospores will carry a wild-type allele and upon further crosses these survivors will yield four-spored asci, contrary to spore killers that will always yield two-spored ones.

Jean Bernet described another Spore Killing phenomenon between the T and T' strains of "*P. anserina*". We now know that strain T, which contained the meiotic drive element, is a *P. comata* strain, while we don't know what was strain T'. Nevertheless, the spore killing effect can be seen in crosses between the T and S strains (figure 99). Identification of the locus responsible for the T x S led to the surprising discovery that both the survival and killing activities are carried out by a single gene called *Spok1*. This gene encodes for a protein with a nuclease and kinase domains responsible for killing and resistance, respectively. It conserved its activity when transferred into *Sordaria macrospora*. Surprisingly, the S strain also contains a *Spok* gene encoding a protein very similar to the Spok1 protein (87% identity between Spok1 and Spok2), called *Spok2*. *Spok2* is inactive in the presence of *Spok1*, but proved fully active in its absence. Two additional *Spok* genes, *Spok3* and *Spok4*, were discovered in some strains of *P. anserina* and in another strain of the *P. anserina* species complex, *P. pauciseta*. These also act as Spore Killers and interact in complex fashion with *Spok1*. Indeed, *Spok1* provides resistance also to *Spok3* and

Spok4, while *Spok4* provides resistance to *Spok1* and *Spok3* does not. Note that *Spok2*, *Spok3* and *Spok4* do not interact, *i.e.*, do not inhibit their respective killing and do not provide resistance. All four genes account for the known complex Spore Killer patterns detected in *P. anserina* populations, but for the *het-s/het-S* one.

Owing to their distortion effect on meiosis, Spore Killers are preferentially transmitted to the progeny. Not surprisingly, *het-s* strains are twice as frequent as *het-S* ones and more than 90% of them naturally contain the het-s prion. In the case of the *Spok* genes, the full pattern of their presence in the various members of the *P. anserina* species complex is not known. The *Spok2* gene appears present in most strains of *P. anserina* and in the *P. pauciseta* strain that has been sequenced. On the contrary, *Spok1* is present only in the *P. comata* T strain, while *Spok3* and *Spok4* have an intermediate distribution.

Natural products biosynthesis

Since the release of the genome sequence of *P. anserina*, it has been realized that the friendly mold is able to produce compounds with industrial value. These may have use principally in pharmaceutical, remediation and biofuels technologies. Two major kinds of products are presently studied: secondary metabolites and enzymes.

Secondary metabolites

Genome analysis indicates that *P. anserina* may be able to produce nearly 40 secondary metabolites, since its genome encodes that many secondary metabolites pathways (Figure 100). Biochemical analyses have so far shown that the friendly mold synthesizes anserinones A and B, two quinones with antifungal, antibacterial and anticancer activities. Additionally, one species of the *P. anserina* species complex (unfortunately, we don't know which one, since the paper did not provide the actual ITS sequence, but only states that it is 99% identical to that of the reference strain S) is able to produce sterigmatocystin, secosterigmatocystin, and 13-hydroxyversicolorin B, a derivative of anthraquinone. The sterigmatocystin produced by the friendly mold was shown to be able to efficiently kill *Anopheles gambiae* mosquito larvae.

Most genes involved in secondary metabolite production are clustered as observed in other fungi. Yet, the first analyzed pathway, the one enabling to produce dihydroxynaphtalene (DHN)-melanin, has its genes scattered all over the genome. The production of DHN-melanin starts with a polyketide synthase whose gene is located at the centromere of chromosome 2 (figure 100). The *PaPks1* gene has many mutants, which are used in many genetical and cytological analyses (see Developmental genetics: grafting and genetic mosaics). The rest of the genes involved in DHN-melanin synthesis have not been thoroughly analyzed. However, some the laccases involved at the last step of polymerization of melanin in ascospores have been identified. Surprisingly, they are not canonical laccases, and are related to ascorbate oxidases and ferroxidases.

Region	Type	From	To	Most similar known cluster		Similarity
Region 1.1	NRPS-like,NRPS,T1PKS	1,796,876	1,878,895			
Region 1.2	T1PKS	4,090,203	4,138,115			
Region 1.3	terpene	5,383,359	5,405,264			
Region 2.1	T1PKS	501,510	537,011	naphthalene	Polyketide	22%
Region 2.2	T1PKS	2,769,119	2,813,891			
Region 2.3	T1PKS	2,933,411	2,979,798	sterigmatocystin	Polyketide	46%
Region 2.4	NRPS	3,069,555	3,120,058			
Region 3.1	T1PKS	1,299,909	1,348,569			
Region 3.2	NRPS	4,460,651	4,506,700	biotin	Other	66%
Region 4.1	T1PKS,NRPS-like	31,355	66,381			
Region 4.2	indole	408,609	431,472			
Region 4.3	NRPS-like	606,778	641,809			
Region 4.4	T1PKS	1,547,198	1,596,340	solanapyrone D	Polyketide	33%
Region 4.5	T3PKS	1,991,727	2,032,583			
Region 4.6	NRPS-like	3,569,794	3,607,322			
Region 4.7	NRPS	3,674,808	3,737,150			
Region 4.8	NRPS	3,756,520	3,811,587			
Region 5.1	indole	272,223	286,753			
Region 5.2	T1PKS	327,606	374,381	9-methylstreptimidone	Polyketide:Modular type I	6%
Region 5.3	indole	431,684	453,478			
Region 5.4	T1PKS	473,503	519,108			
Region 5.5	NRPS	700,654	743,925			
Region 5.6	T1PKS	941,446	986,835			
Region 5.7	NRPS,T1PKS	1,568,699	1,619,177	UNII-YC2Q1O94PT	Polyketide	100%
Region 5.8	terpene	1,996,169	2,017,799	squalestatin S1	Terpene	40%
Region 5.9	NRPS-like	2,812,617	2,854,255			
Region 5.10	T1PKS	2,890,310	2,930,372			
Region 5.11	NRPS,T1PKS	3,093,531	3,146,847	phyllostictine A / phyllostictine B	NRP + Polyketide	40%
Region 5.12	T1PKS	3,338,185	3,378,460			
Region 5.13	T1PKS	4,554,977	4,601,222			
Region 6.1	T1PKS	14,818	48,227			
Region 6.2	T3PKS,T1PKS	2,921,451	2,973,589			
Region 6.3	T1PKS,NRPS	3,219,215	3,270,835			
Region 6.4	NRPS-like	3,850,773	3,890,945			
Region 6.5	NRPS	3,935,957	4,001,083			
Region 6.6	T1PKS	4,020,000	4,068,750	solanapyrone D	Polyketide	33%

Figure 100 Prediction of secondary metabolite clusters of *P. anserina* with antiSMASH. The fungal version of the antiSMASH prediction tool 5.0 identified 37 secondary metabolite gene clusters using the relaxed parameters. DHN-melanin biosynthesis is initiated by the polyketide synthase of the region 2.1 that produces naphtalene. The other genes involved in the melanin biosynthesis are not linked to region 2.1.

The second secondary metabolite pathway that has been characterized by molecular genetics analyses is the one predicted to produce sterigmatocystin, a toxic polyketid. It is thus most likely that sterigmatocystin and secosterigmatocystin detected by biochemical analyses are produced thanks to this cluster. It has been horizontally transferred from *Eurotiales* into the chromosome 2 of the genome of the ancestors of the *P. anserina*. Deletion of the cluster results in sensitivity to oxidative stress. Based on the genome analysis (figure 100), *P. anserina* has thee ability to produce additional polyketides, but also non-

ribosomal peptides and terpene(s). It also likely synthesizes more complex compounds since its genome encodes for proteins having fused polyketide and non-ribosomal peptide synthase domains.

In addition to the above-discussed secondary metabolites, *P. anserina* synthesizes various oxylipins of the icosanoid and isoprostanoid families thanks to lipoxygenases and cyclooxygenases. These are in turn transformed into organic volatile compounds, often with 8 carbons, that are used by the fungus to repel nematodes.

Enzymes

The other natural products of industrial value made by *P. anserina* are enzymes. These may be used directly or the genes that encode them are used to optimize production of natural compounds in biotechnological application. An example of the latter is the use of a 3-dehydroshikimate dehydratase gene to optimize the production of vanillin from glucose by *Schizosaccharomyces pombe*. Vanillin is an aromatic aldehyde that is extensively used as a flavoring and aromatic agent in food, cosmetics, cleaning products, etc. We don't know whether the optimized strains carrying the *P. anserina* enzyme are presently used in industrial scale production of vanillin. Another example is the potential use of arylamine N-acetyltransferases in detoxification of anilines. Indeed, *P. anserina* produce two such enzymes, one of which is very efficient to acetylate anilines, including 3,4-dichloroanilin or DCA. DCA is a degradation product of diuron, a widely used herbicide. DCA is highly toxic and contaminate many sites all over the world. It was shown that adding the fungus to soil, contaminated in a way that prevent seed germination, restores some health to the soil as to permit germination.

By far the most investigated enzymes in view of industrial applications are those involved in biomass degradation or CAZYmes (figure 101). Indeed, analysis of the genome sequence has permitted to discover a large array of genes involved in plant biomass degradation, including orthologues of genes acting during lignin degradation in basidiomycetes. Biochemical analyses have confirmed that *P. anserina* secretes indeed in the medium many enzymes having activities including cellulase, xylanase, pectinase, arabinofuranosidase, arabinanase, galactanase, laccase and tyrosinase. Many enzymes encoded by these genes are under scrutiny for their ability to enhance the enzymatic cocktails dedicated to breakdown the complex lignocellulosic biomass into simple sugars for second-generation biofuel production. *Trichoderma reesei*, the fungus used in industry to produce the cocktails, is an efficient cellulase

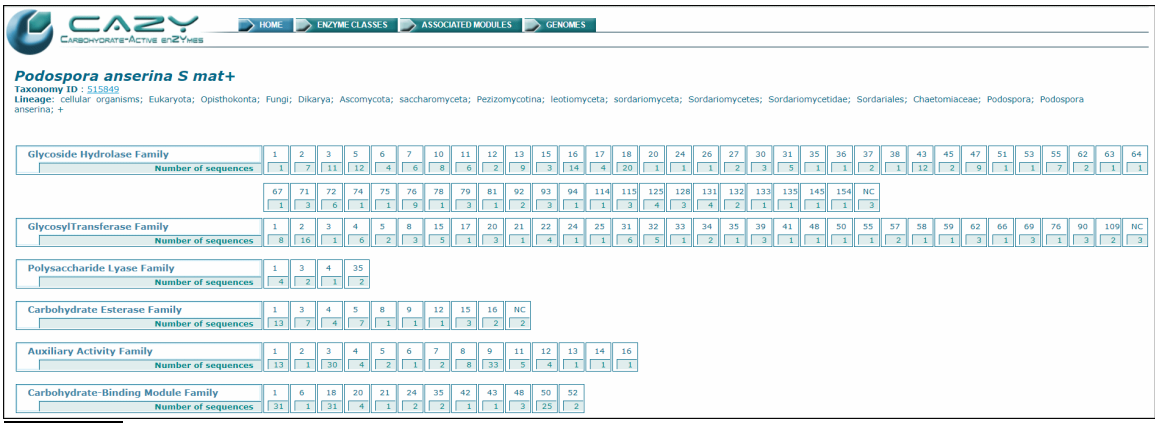


Figure 101 ***P. anserina*** **CAZYmes present in the CAZY database as of december 2019.** Of note is the presence of numerous Auxilliary Activity enzymes potentially involved in lignin break down.

producer, but is naturally endowed with surprisingly little diversity of enzymes. Cocktail supplementations with *P. anserina* enzymes produce in *Pichia* yeasts often confer greatly improved activity. Paramount for such a task are the Lytic Polysaccharide MonoOxygenases or LPMOs. LPMOs can cleave by oxidation various polysaccharides, including cellulose, and have thus been reassigned from class GH61 to classes AA9, AA10, AA11 & AA13. The *P. anserina* genome encodes 33 LPMOs. Laccases and especially the thermostable billirubin-like ones are also promising enzymes to improve not only biomass degradation, but also to partake in the removal of toxic xenobiotics and some plastics. Note that in addition to the CAZYmes listed in figure 101, *P. anserina* also possesses over 110 cytochrome P450 genes, 9 peroxidases (not counting the catalases), many Glutathione S-transferases… All these enzymes may participate in lignocellulose and plastic breakdown and/or detoxification of noxious compounds.

It is worth mentioning, that while *Neurospora crassa* is now used as a model to understand the degradation of cellulose and its regulation, *P. anserina* is presently considered as a promising model to understand the complex process of lignocellulose breakdown by fungi, through the analyzes of both the penetration of biomass (see Appressorium-like structure differentiation) and the action of enzymes encoded by the CAZYmes genes, but also the other enzymes potentially participating in the process. *P. anserina* is able to complete its lifecycle on wood and it is thus easy to finely assess whether mutant have defects in scavenging nutrients from wood. Gene inactivation of all the laccase genes has already shown that many of those are necessary for growth on lignocellulose. Similarly, the genes encoding catalases are required for growth in the presence of lignin. On the contrary, many enzymes shown to be potent to degrade lignocellulose in basidiomycetes appear dispensable for the growth and fertility of *P. anserina* on

wood (at least in a laboratory setting).

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Appendix 1: Original descriptions of *Podospora anserina*

Documents of specimens provided by Prof. Uwe Braun
Institut für Biologie, Geobotany and Botanical Garden, Herbarium
Martin-Luther-Universität Halle-Wittenberg

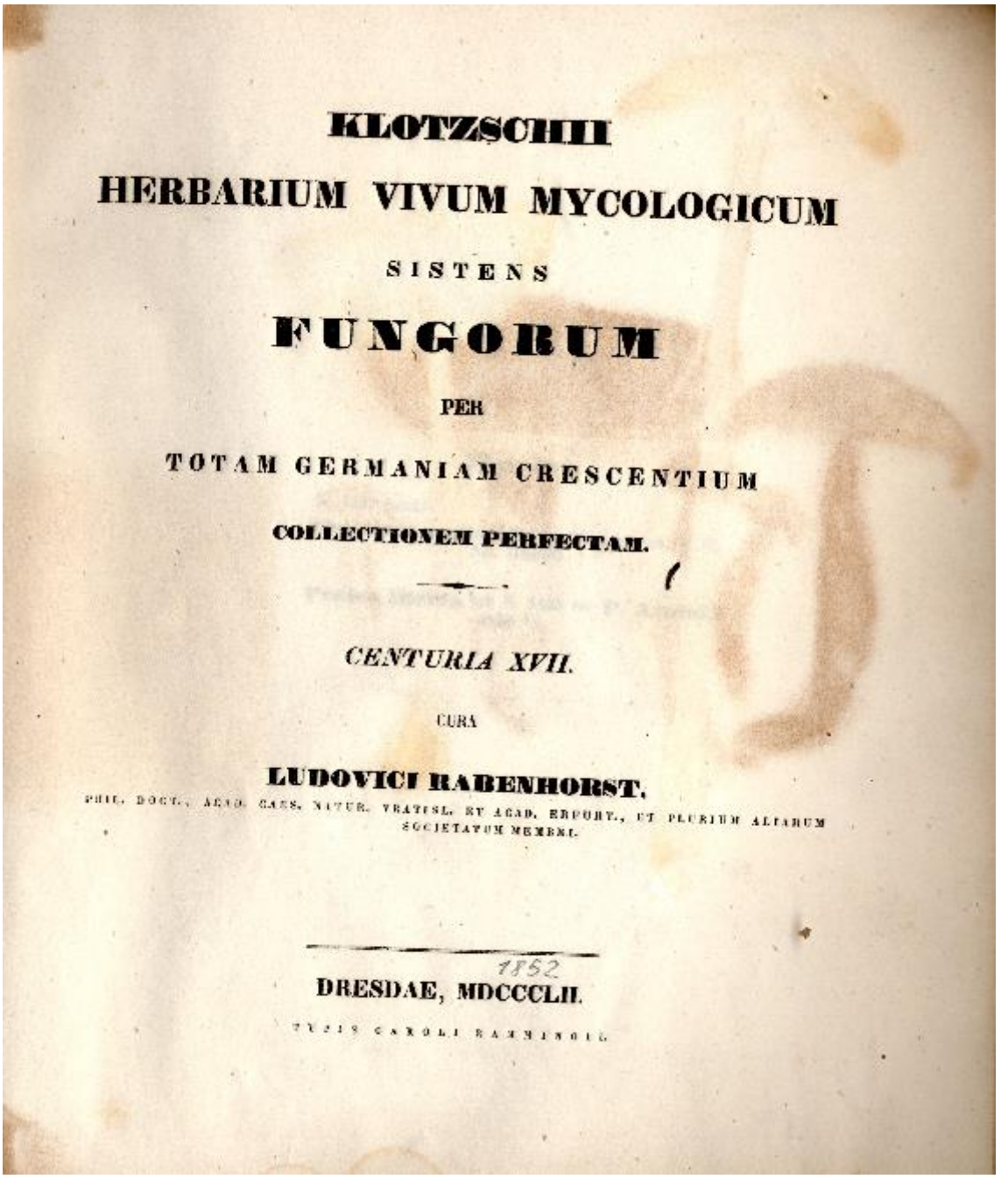
Cesati, V.

(1852).

1642. *Sphaeria pauciseta.*

Klotzschii herbarium vivum mycologicum sistens fungorum per totam germaniam crescentium collectionem perfectam

***Centuria XVII*. L. Rabenhorst.**



KLOTZSCHII

HERBARIUM VIVUM MYCOLOGICUM

SISTENS

FUNGORUM

PER

TOTAM GERMANIAM CRESCENTIUM

COLLECTIONEM PERFECTAM.

CENTURIA XVII.

CURA

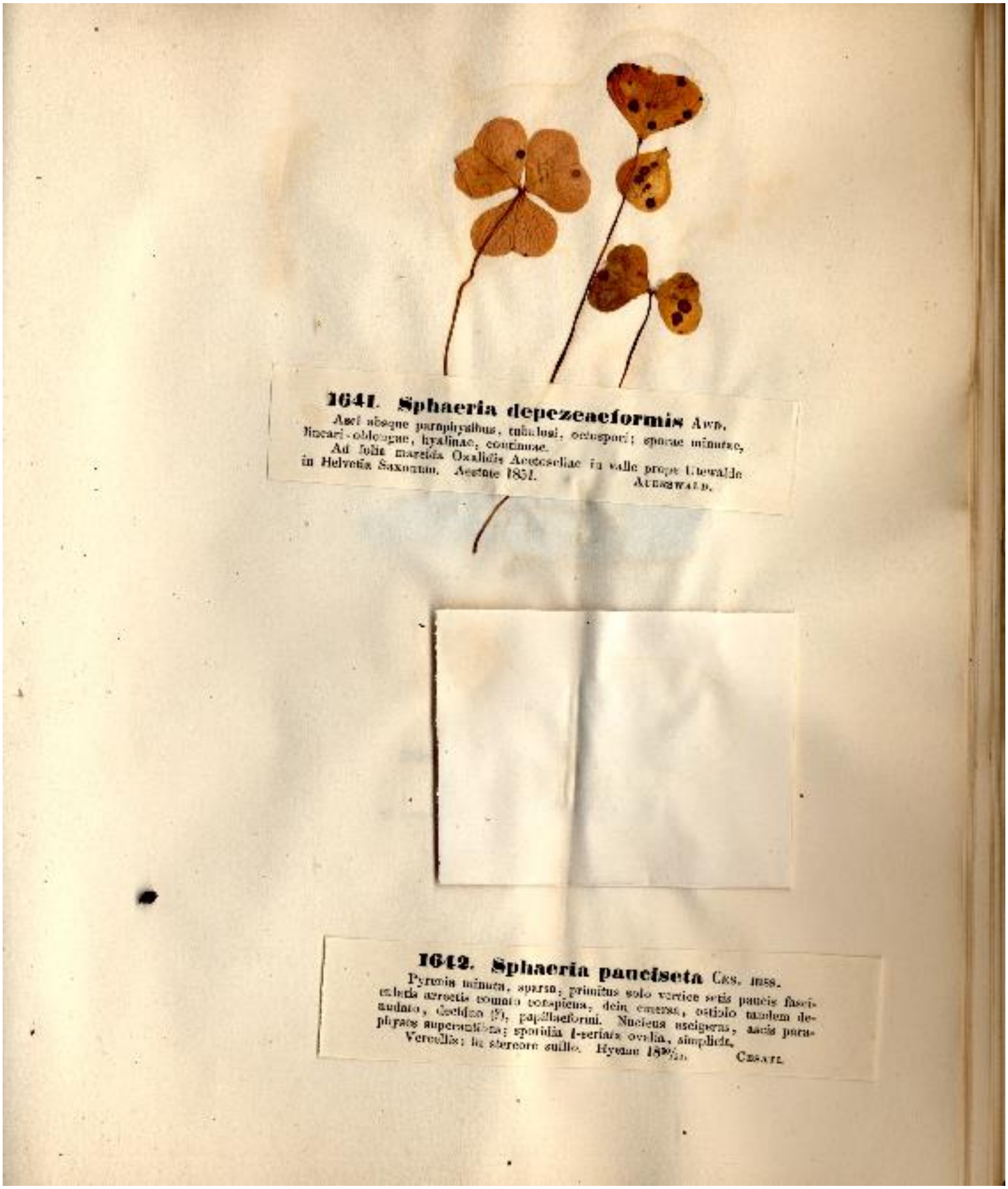
LUDOVICI RABENHORST,

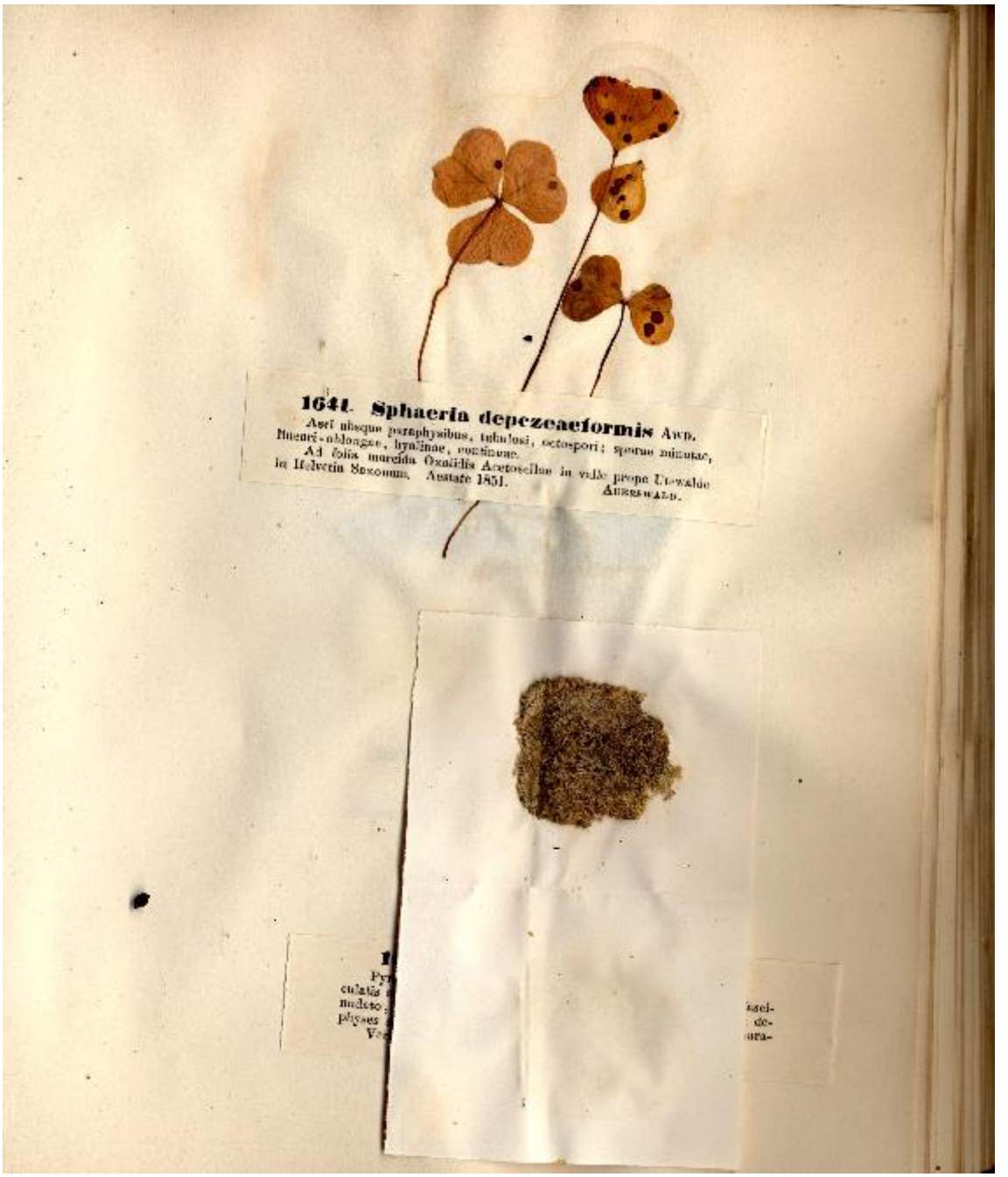
PHIL. DOCT., ACAD. CAES. NATUR. CURIOSL. ET ACAD. ERFURT., ET PLURIUM ALIARUM SOCIETATUM MEMBRI.

1852

DRESDAE, MDCCCLII.

TYPIS CAROLI BAMMINGII.


1641. Sphaeria depezeaeformis Awd.
Asci absque paraphysibus, tubulosi, octospori; sporae minutae,
lineari-oblongae, hyalinae, continuae.
Ad folia marcida Oxalidis Acetosellae in valle prope
in Helvetia Saxonum. Aestate 1851.
1642. Sphaeria pauciseta Ces. mss.
Pyrenia minuta, sparsa; primitus solo vertice setis paucis
conspicua, dein emersa, ostiolo tandem
papillaeformi. Nucleus ascigerus, ascis
sporidia 1-seriata ovalia, simplicia.
Vercellis; in stercore suillo.
Cesati.


1641. Sphaeria depezeaeformis Awd.
Asci ubique paraphysibus, tubulosi, octospori; sporae minutae,
fuscae-oblongae, hyalinae, continuae.
Ad folia marcida Oxalidis Acetosellae in valle prope Ilsenburg
in Helvetia Saxonum. Aestate 1851.
Auerswald.

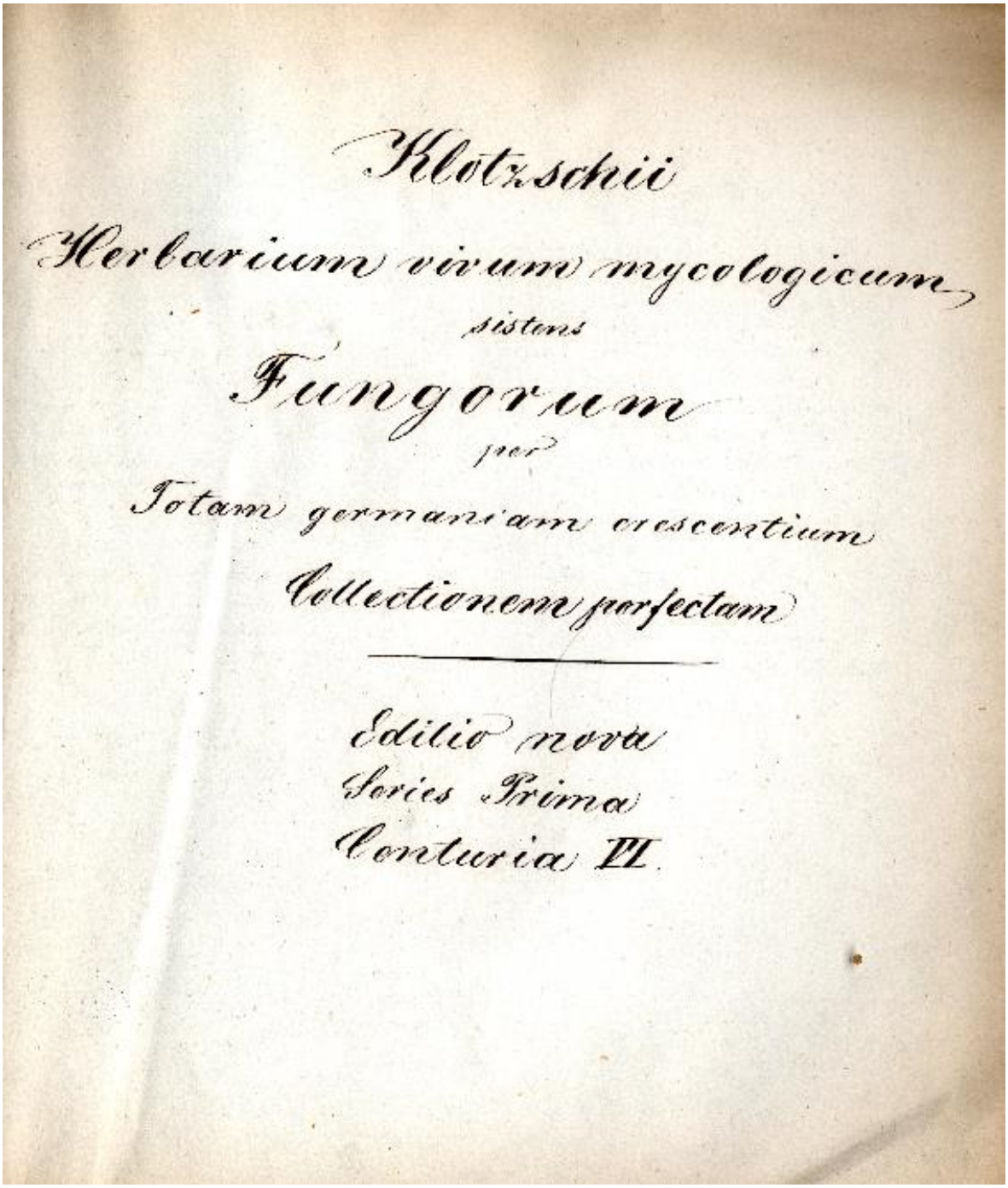
Cesati, V.

(1857)

526. *Malinvernia Rabenh.*

Klotzschii herbarium vivum mycologicum sistens fungorum per totam germaniam crescentium collectionem perfectam

***Editio nova Series Prima Centuria VI*.**



Klotzschii

Herbarium vivum mycologicum

sistens

Fungorum

per

Totam germaniam crescentium

Collectionem perfectam

Editio nova

Series Prima

Centuria VI.

Rabenhorst, Herb. mycologicum. Ed. II.

526. Malinvernia Rabenh. Hedwigia N. 18.

M. anserina Rabenh.

Sphaeria (Hypocopra) anserina Ces. in litt.

Vercellis; in fimo anserino, exeunte Octobri—Novbr.

In facie terram spectante excrementorum Anseris putrefactionem jam ineuntium puncta nigra perspiciuntur, quae sub lente vitrea pro sphaerulis ad verticem fasciculo setarum praeditis, et nisi senio omnino calvis facile intelliguntur. — Pyrenia plerumque gregaria occurrunt, nonnunquam, dio humido favente, denso agmine fere stipata, primitus obtecta et nisi setis porrigentibus (saepe coalitis ostiolum Sphaeriae dryinae mentientibus) revelata, pseudostromati tenuissimo atro insidentia, demum emersa, imo omnino liberata et tunc facile decalvata, anista, atra, opaca, laevia, ovata, ostiolo mamillari. Setae 5—6 vel plures (tunc fasciculatae) concolores, breves, rigidae, demum deciduae, non septatae. Asci cylindracei, apice constricto, basi in pedicellum fere dimidium asci attingentem producta, sporis quatuor! ellipsoideis primitus intense viridibus demum atrovirentibus, guttula s. nucleo obscuriori fartis, caudatis, cauda persistenti duplum Sporae longa. Paraphyses aequitantes, ramosae, filiformes, gelatinosae. Asci — $^{43}/_{100}$ mill. long. Sporae — $^{29}/_{100}$ mill. long. $^{3-6}/_{100}$ mill. lat.

Obs. Alterum pyrenomycetem deprehendi, sed perrarum, in eadem matrice et jam effectum, cujus sporae forma et colore illis Sphaeriae nostrae similllimae, sed $^1/_3$ minores et caudatae in illo disseminationis stadio. Sed basis quadantenus trumatula vel appendicis, vel basidii (ut in Diplodiis — et tunc Diplodia caret spora non septata) indicium praestabut. Pyrenia atra nitentia, chartacea, cellularia. Ulteriori servandus examini. Cesati.

Appendix 2: Early papers on *Podospora anserina*

Description of *Sphaeria pauciseta*

in

Botanische Zeitung (1852) 10: 285-288

den Blüthenkolben aufnimmt; beim *ungeschlossenen* entstehen die untersten Scheiden zuerst, in ihren Achseln die untersten Aeste, an ihnen die Scheiden, dann die Aeste zweiter Ordnung u. s. f. Es erscheinen daher alle Verzweigungen des Blüthenkolbens anfangs dicht von Scheidenblättern eingehüllt.

Die Entwickelung des Blüthenkolbens vom ersten Anfange, welcher oft lange vor das völlige Auswachsen des Mutterblattes fällt, bis zum Blühen nimmt meist mehrere, bei manchen bis 10 Jahre in Anspruch.

(§. 100.) Bei einigen *Lepidocaryinen*, namentlich *Calamus* und *Daemonorops* ist oft die Hauptachse, selten der ganze Blüthenkolben in ein langes, dünnes, stachliges Seil umgewandelt.

(*Fortsetzung folgt.*)

In Gersdorf's Repert. No. XX. v. 1851 ist S. 77 ff. eine Anzeige von: „C. H. Schultz Die Verjüngung im Pflanzenreiche", in welcher den Ansichten dieses Verf.'s gegen die von Al. Braun das Wort gesprochen wird.

Sammlungen.

Klotzschii Herbarium vivum Mycologicum etc. Centuria XVII. cura Lud. Rabenhorst Phil. Dr. etc.. Dresdae MDCCCL. II. 4.

Wir haben im 36. und 37. Stück dieser Zeitung, also vor einem halben Jahre die 16. Centurie dieser Pilzsammlung angezeigt und können von einer neuen Centurie, die vielerlei Interessantes, namentlich auch den vielbesprochenen den Weinstock heimsuchenden Schimmel enthält, Nachricht geben und deren Inhalt unsern Lesern vorlegen:

1601. *Agaricus* (*Volvaria*) *speciosus* Fr. 2. *A.* (*Tricholoma*) *flavo-brunneus* Fr. 3. *A.* (*Russula*) *fallax* Krombh. 4. *A.* (*Omphalia*) *scyphoides* Fr. 5. *Cantharellus glaucus* Fr. NB. Transitio ad Ag. tremulum hinc inde patens; sed plura specimina C. muscigenum praedicant. 6. *Polyporus salebrosus* Lasch Mspt. P. suberoso-lignosus tenuis; pileis dense tuberculoso-erumpentibus, reflexis, tomentosis, ferrugineis, dein longe lateque confluentibus; poris majusculis, brevibus, angulatis, pallidioribus, margine dein subdentatis, albidis. (Polyp. noduloso Fr. epicr. p. 474. N. 200. proximus!) 7. *Radulum laetum* Fr. NB. Color mox expallescens! 8. *Grandinia crustosa* Fr. 9. *Clavaria luticola* Lasch. Gregaria v. sparsa, simplex, subfragilis, farcta, ex pallido fuscescens, superne incrassato-obtusa, inferne in stipitem longum attenuata. 10. *Cl. fragilis* Holmsk. b. — Als Supplemente sind hier eingeschoben: (240.) *Cl. Klotzschii* Lasch. nov. spec. teste Lasch. Quercicola, typhuloides, gracillima! (1122.) *Cl. rugosa* Bull. vera! — 11. *Exidia saccharina* Fr. 12. *Cyphella* (olim Peziza) *Capula* Fr. Epicr. 568. var. b. *cernua* (Pez. cernua Schum.). Pulchella, candida; in vivo valde tenera et decidua, sicca indurescit et facile senior quoque nigrefacta. — Ad gramina adhuc vegeta, sed potissimum ad basin caulium Galegae inter herbas sepultam, gregatim autumno. 13. *Geoglossum viride* Pers. 14. *Peziza* (Dasyscyphus) *Galegae* Ces. mss. Valde insignis et pro aetate varians. — Gregaria, sessilis, Primitus clausa, depresso-globularis, amoene caesia, dense flocculosa; serius urceolata nigrescens disco pallido; fructificans explanata, irregularis, disco virente-luteo vel rufescente. 15. *P. Pteridis* Alb. et Schw. 16. *P. Lychnidis* Ces. pro inter. P. cyathoideae forma! 17. a) *P. cyathoidea* v. *Umbellatarum*. Diff. a forma typica colore pallido, cupula versus marginem albo-floccoso-pubescente, stipite aequali (non incrassato!). 17. b) *P. platealis* Ces. pro inter. P. cyathoideae forma!? (335.) *P. Artemisiae* Lasch. 18. *P. Urticae* Awd. Mspt. 19. *P. litorea* Fr. vera! 20. *P. pellucens* Ces. Mspt. Microscopica, hyalina, extus puberula, cito explanata. 21. *P. scutellata* Linn. 22. *P. ciliaris* Schrad. 23. *P. lacustris* Fr. syst. II. 143. Nunc brunnea, nunc pallida occurrit; mihi ex affinitate P. epiblastematicae (N. 1016) et P. Cerastiorum (N. 1420) visa. 24. *P. miliaris* Wallr.? Carnea, demum expallens, marginata! 25. *Pistillaria coccinea* Fr. 26. *P. muscicola* Fr. 27. *Vibrissea flavipes* Rabenh. Mspt. Gregaria et subcaespitosa s. sparsa, simplex, in matrice radicans; stipite 1 — 3‴ longo, erecto vel curvato, tereti, flavo, saepius pulveraceo; capitulo e viridulo glauco-cinerascente, ascis erumpentibus flocculoso. Ad Vitis viniferae truncos vetustos, putredine solutos, locis suffocatis, hinc inde, e. g. pr. Pemplin jam 1849 specimina pauca invenit W. Kannenberg et benevole nobis tribuit; 1851 ad Dresdam (ipse), pr. Lipsiam (Auerswald). 28. *Leotia lubrica* Pers. v. *lacunosa* Er. 29. *Verpa digitaliformis* Pers. 31. *Physarum columbinum* Pers. 30. *Pilobolus crystallinus* Tode. Certo certius adserere ausim Pilobolum e basi sclerotiodea (forma non substantia) s. e tuberculo luteo sistere. Doleo recentissimam monographiam cl. Cohn nondum vidisse; caeterum plura quae in Pilob. anomali nostri (N. 1542) evolutione videram et in hac specie observare contigit. 32. *Trichia pyriformis* forte var. T. fasciculato-stipitata; perid. obovato-pyriformi, laevi, nigro, nitido; stipite inaequali, ruga atropurpurea insigni; capillitio spo-

ridiisque cinnamomeis. 33. *Stictis* (*Propolis*) *versicolor* v. *fusca* Fr. 34. *Geaster Cesatii* Rabenh. in Mohl et Schlecht. bot. Zeit. 1851. 35. *Lycoperdon pusillum* Batsch. 36. *Erysiphe Leguminosarum* Lk. *E. Pisi* DeC. 37. *E. clandestina* (Wallr.). 38. *Sphaeria serpens* β. *lumbricoides*. 39. *Sph. Eryngii* Fr. 40. (1527.) *Sph. rubella* Pers. 41. *Sph. depazeaeformis* Awd. Asci absque paraphysibus, tubulosi, octospori; sporae minutae, lineari-oblongae, hyalinae, continuae. 42. *Sph. paucisela* Ces. mss. Pyrenia minuta, sparsa, primitus solo verice setis paucis fasciculatis arrectis comato conspicua, dein emersa, ostiolo tandem denudato, deciduo (?), papillaeformi. Nucleus ascigerns, ascis paraphyses superantibus; sporidia 1-seriata ovalia, simplicia. 43. *Sph. flavovirens* Fr. v. brevis interrupta, erumpens! Conf. N. 1243. 44. *Massaria mamillana* (Fr.) Rabenh. M. sporis majusculis, oblongo-ellipticis, fuscis, uniseptatis; nucleo gelatinoso nigro cirrhi forma profluente! 45. *Vermicularia trichella* Fr. 46. *Depazea Phillyreaecola* Rabenh. Mspt. D. sporis simplicibus hyalinis! 47. *D. Clematidis* Rabenh. in litt. 48. *D. Adoxaecola* Lasch Mspt. 49. *D. juglandina* Fr. NB. Haud raro una cum Perisporio atque Phyllerio obvia. 50. *D. Calthaecola* DeC. NB. Maculae pallidae, exaridae, illimitatae, mox fusco-nigrescentes. 51. *D. Aquilegiae* Rabenh. 52. *D. Ribicola* Fr. 53. *D. Saponariae* (DeC.). 54. *D. Hepaticaecola* Duby Bot. gall. II. p. 712. 55. *Ascochyta Geranii* Rabenh. Mspt. 56. *A. Epilobii* Rabenh. Mspt. 57. a) *Sporocadus Ruscicola* Rabenh. Mspt. V. sporis rectis, cylindraceis s. fusiformibus, triseptatis, brevipedicellatis, fuscis; pedicello hyalino. b) *Sphaeria Rusci* Wallr. 58. *Hysterium juniperinum* Grev. 59. *Sphaeronaema Uredineorum* Fiedl. Mspt. Erumpens. Perithecia gregaria, obovato-globosa, atra, nitida, nucleo albo farcta; sporidiis oblongo-cylindricis, guttatis, ex ostiolo guttulae s. cirrhorum alborum instar erumpentia. 60. *Trullula* (*Blennoria reformata*?) *Oreoselini* Ces. mss. Totus caulis primitus pustulis farinaceis obtectus, quarum centrum ab ostiolo serius perforatus; quod et in Blennoria Rubi (Mtgne.) videre licet. Quare eo magis suspicio subrepit, meum genus Trullulae cum Blennoria, hujus charactere reformato ob legitimi Pyrenii membranacei praesentiam forsan jungendum esse. — Perrare Cenangium Oreoselini (Nob.), nova species, immixtum reperi. 61. *Tr. leguminum*, a) *Spartii*, b) *Robiniae* Ces. Mspt. Sporidia

obscura biseptata! 62. *Phoma Agaves* Rabenh. Mspt. A Ph. concentrica Desmaz. Crypt. de France N. 1085 sat diversa! 63. *Pestalozzia macrospora* Ces. Mspt. 64. a) *Nemaspora* (*Myxosporium*) *Plantaginis* Ces. Mspt. b) *Phoma occultum* Ces. Mspt. 65. *Isaria filiformis* Wallr. 66. *I. farinosa* Fr. syst. 67. *Graphium penicilloides* Corda. 68. *Polyactis Sclerotiophila* Rabenh. Mspt. Fasciculatim e Sclerotio duro, praesertim in Polygonis, erumpit.

(*Beschluss folgt.*)

Personal-Notiz.

Thomas Moore.

Der Verfasser von Lalla-Rookh und anderer Dichtungen, der auch durch mehrere historische Schriften berühmte Irländer Thomas Moore war zu Dublin am 28. December 1780 geboren und starb in Sloperton-Cottage nicht weit von Devizes (Wiltshire) am 26. Februar 1852. Die berlinischen Nachrichten von Staats- und gelehrten Sachen widmen ihm in der ersten Beilage zur diesjährigen Nummer 60 eine ausführliche biographische Notiz, die mit den Worten schliesst: „Weniger bekannt ist es vielleicht, dass er sich mit Arbeiten beschäftigte, welche von seinem Geschmack für die Natur, für Gärtnerei und Botanik zeugen und die wahrscheinlich von seinen ländlichen Umgebungen erweckt und genährt wurden. Dahin gehören seine Werke über den *Anbau der Gurken und Melonen* und sein *Handbuch der britischen Farrenkräuter.*" Findet hier eine Namensverwechselung nicht statt *), dann bleibt es bemerkenswerth, dass schon hundert Jahre früher ein Thomas More ebenfalls über Gartenbau und namentlich Gurken (*Cucumbers*) geschrieben hat. Cf. No. 7139 des Pritzel'schen Thesaurus.

*) Von Thomas Moore ist ein „Handbook of British Ferns" erschienen, wie ich aus desselben Verf.'s Aufsatz im 1. Bde. d. Bot. Gaz. v. 1849 ersehe. Dieser Aufsatz ist ein am 2. Nov. 1849 vor der Bot. Gesellsch. zu Londoo gehaltener Vortrag über „Dr. Dickie's Cystopteris" eine Form von *Cyst. fragilis*. Jenes Handbuch, welches auch Abbildungen enthält, wie sich aus demselben Citat ergiebt, ist aber nicht von Hooker und Arnott bei ihrer British Flora benutzt. — Es giebt ausserdem noch einen schottischen Botaniker David Moore, welcher ein Paar kleine Aufsätze im Phytologist publicirte. Das Werk über Cucumbers ist mir gänzlich unbekannt. *S—l.*

Redaction: Hugo von Mohl. — D. F. L. von Schlechtendal.
Verlag von A. Förstner in Berlin. — Druck: Gebauer-Schwetschke'sche Buchdruckerei in Halle.

Renaming of *Sphaeria pauciseta* as *Sordaria pauciseta*

in

Cesati, V. and G. De Notaris (1853). *Sordaria*. Schema di classificazione degli sferiacei italici aschigeri: 51-53

B. Bombarda Erbar. Crittog. ital. n. 876. — *Sphaeria Bombarda* Bâtsch — Fries Syst. II. 456. Sclerom. suec. n. 266. Berkel. Outl. 395. tab. 24 fig. 5. — *Bombardia fasciculata* Rabenh. Herb. mycol. ed. I. n. 1559 et 1939.

Sphaeria verrucosa *Grev. Scott. Fl. tab.* 39, ex habitu.

VENTURIA

DNtrs Cenn. in att. VI. riun. scienz. 484.

V. Rosae DNtrs l. c. tab. I. fig. 1.

V. Dianthi DNtrs l. c. tab. I. fig. 2.

V. Dickiei — Sphaeria Dickiei *Berk. et Br. Brit. fung. n.* 517. *tab.* X. *fig.* 8.

V. macrotrichia — Sphaeria macrotrichia *Berk. et Br. l. c. n.* 619. *tab. IX. fig.* 2.

V. eres — Sphaeria eres *Berk. et Br. l. c. n.* 621. *tab. IX. fig.* 3.

V. Chaetomium — Sphaeria Chaetomium *Corda Icon. II. fig.* 102. *Berk. et Br.* l. c. n. 620. *tab. IX. fig.* 4.

Sphaeria polytrichia *Wallr. Fl. cryptog. II.* 784. *Rabenh. Herb. mycol. n.* 328. ex habitu huc spectat.

SORDARIA

Sphaeriae specc. Auctor. — Hypocoprae specc. Fries — Enterobotryum Preuss — Podospora Cesat. — Hypoxyli specc. Fries — Malinvernia Rabenh.

Pyrenia sparsa, sphaeroidea, vel ovoideo-conica, crassiuscula, rugulosa, vel setulosa, vertice osculo minuto hiantia, senio vulgo fracta. Asci 4-8 spori, cylindracei, obtusi, paraphysibus obvallati. Sporidia ovoidea, simplicia, badio-fusca, interdum omnino opaca, in nonnullis polo inferiore (saltem juvenilia) caudato.

S. sordaria — *Sphaeria sordaria* Fries Syst. II. 458. Sclerom. suec. n. 270. DNtrs Microm. ital. IX. n. 3.

52

S. LIGNIARIA — *Sphaeria ligniaria* Grev. Scott. tab. 82. Desmaz. X. not. n. 26. — *Sphaeria asperula* Ces. et Mont. in Ann. sc. natur. sér. IV. VII. 140.

S. PULVERACEA — *Sphaeria pulveracea* Ehrh — Fries Syst. II. 459. Sclerom. suec. n. 121. Rabenh. Fung. europ. n. 338.

S. conica — Enterobotryum conicum *Preuss Fung. Hoyersw. in Linn. XXV.* 733, ex Diagnosi.

S. FIMETI — *Sphaeria fimeti* Pers. — Fries Syst. II. 373. Sclerom. suec. n. 269. — *Hypocopra fimeti* Fries Summ. 397. Cesat. in Hedw. I. 1856. n. 15. tab. XIV. B. fig. I. 1.

S. COPROPHILA — *Hypoxylon coprophilum* Fries Summ. 384. — *Sphaeria coprophila* Fries Syst. II. 342. Cesat. Hedw. 15. tab. XIV. B. fig. 2-5. et in Rabenh. Herb. mycol. ed. nov. 257.

S. FIMISEDA — *Podospora fimicola* Cesat. in Rabenh. Herb. mycol. ed. nov. n. 259 et Hedwig. n. 15. tab. XIV. A. — *Schizothecium fimicola* Corda ? ad specimen exoletum.

S. fimicola — Sphaeria fimicola *Roberg. in Desmaz. XVII. Not.* (1849) *n.* 40 ex Diagnosi.

S. inspersa — Sphaeria inspersa *Berkel. Decad. of fung. VIII. n.* 73. ex specimine.

S. PAUCISETA — *Sphaeria pauciseta* Cesat. in Rabenh. Hedw. n. 18. cum icone. — Asci 4-spori.

S. CLAVARIAE — *Sphaeria Clavariae* Desmaz — Rabenh. Fung. europ. n. 252. Sporidia ovalia, simplicia, fusca.

S. OXYACANTHAE — *Sphaeria oxyacanthae* Mont. Syll. 233.

E qui si potranno soggiungere, avuto riguardo al carattere degli sporidii.

Sphaeria lugubris *Roberg. in Desmaz. XIX. not.* p. 14 e spec. a Cl. Lenormand.

Sphaeria punctulata *Roberg. l. c. p.* 19. ex spec. a Cl. Lenormand.

Sphaeria clivulosa *Mont. Syll.* 239. ex specimine.

Sphaeria obliquata *Sommerf.* ex specimine.

Le Sordarie accennano al gruppo delle Rosellinie. Mal-

grado le insigni differenze tra le specie fimicole, lignatili ed erbicole, non crediamo per ora di distinguerne le specie in sezioni separate. Meritevole di attenzione è l' *habitat* di *Sph. lugubris*, *tumulosa*, *punctulata*, su foglie di glumacee od affini, perchè i pirenii delle specie fimicole si trovano talvolta impiantati su frammenti di foglie e di steli di piante graminacee. Notevole eziandio la somiglianza degli sporidii delle specie fimicole, diciamo somiglianza di forma, colorito e dimensioni, cogli sporidii di alcuni *Ascobolus*, che del pari crescono sul fimo degli erbivori. Notevole la frequenza di produzioni picnidiformi, con sporidii ellissoidi fuligginei sulle mete vaccine. Noi non procederemo ad illazioni, che comunque non prive di verosimiglianza, potrebbero essere assolutamente destituite di fondamento.

ROSELLINIA

DNtrs Cenn. in att. VI. riun. scienz. 485. emend.

Pyrenia, in ordine, majuscula, superficialia, subcrustacea et interdum byssiseda, vel lignescentia, vertice rotundato ut plurimum papillata. Asci 8-spori, subinde apice capitellati. Sporidia perfecta simplicia, badio-fusca, elliptica, oblongata aut fusoidea.

1. Pyrenia subcrustacea fragilia, in nonnullis stromate dematiaceo insidentia.

R. AQUILA DNtrs l. c. fig. 1. — *Sphaeria Aquila* Fries Syst. II. 442. Schmidt et Kunze exs. n. 58. Guep. exs !

R. MAMMAEFORMIS — *Sphaeria mammaeformis* Fries Scler. suec. n. 347.

2. Pyrenia lignescentia, pachypleura.

R. TASSIANA Cesat. et DNtrs in Tass. Fl. senes. 3 cum icone.

R. MEDULLARIS — *Sphaeria medullaris* Wallr. Fl. cryptog. II. 772. Montagn. Cent. VIII.

Si citano sotto questo titolo le seguenti, per noi tut-

First description of *Malinvernia anserina*

in

Rabenhorst, L. (1857). "Erklärung der Taf. XV." Hedwigia 1: 116 - pl. 115 fig.114

digiosa besteht stets aus kugelrunden Zellen, deren Durchmesser zwischen $^1/_{2090}$ bis $^1/_{3000}$‴ schwankt. Etwas sehr Characteristisches ist auch das, daß sie sich auf amylonhaltigen Substanzen, wie Semmel, Brod, Reis und dergl. nicht entwickelten, auf denen bekanntlich die P. prodigiosa sich vorzugsweise erzeugt.

L. Rabenhorst.

Erklärung der Taf. XV.

F. 1. **Leptospora Rabenh.**
Sphaeriacearum nov. genus.

Perithecia e basi depresso-hemisphaerica in collum brevem producta, quasi phialaeformia, atra, vertice pertusa. Asci numerosissimi, colorati, cylindraceo — clavati octospori, paraphysibus filiformibus subaequilongis hyalinis immixtis. Sporae aciculares (rhaphidioides), unicellulares, rectae v. curvatae.

Diese neue Gattung steht der Rhaphidospora Montagne sehr nahe, unterscheidet sich aber sehr wesentlich durch die einfachen Sporen.

Als Repräsentant führen wir hier nur eine Art auf:

L. porphyrogona Fig. a. b. c. d. Sphaeria rubella Duby pr. p. Sph. porphyrogona Tode Fung. Meckl. Sph. rubella var. porphyrogona Pers. Syn. Desmaz. Crypt. de Fr. Ed. I. N. 977.

F. 2. **Auerswaldia Rabenh.** Mspt.
Sphaeriacearum nov. genus.

Perithecia hemisphaerica in collum longissimum tubulosum protucta, ore laciniato-fimbriato. Asci ventricosi stipitati 4(—8)-spori, paraphysibus crassiusculis plus minus numerosis immixtis. Sporae ovales, unicellulares.

A. lagenaria Rabenh.

Ceratostoma lagenarium Fr. Summ. 396. Sphaeria lagenaria Pers. et Auct.

F. 3. **Clathrospora Rabenh.** Mspt.
Sphaeriacearum nov. genus.

a) Asci octospori, b) Sporae clathratae.

C. Elynae Rabenh.

Sphaeria Elynae Awd. in litt.

F. 4. **Malinvernia Rabenh.** Mspt.
Sphaeriacearum nov. genus.

M. anserina Rabenh.

Sphaeria anserina Ces. in litt.

a. Perithecium, vario stadio evolutionis, magnopere auctum.
b. Perith. liberatum, adhuc magis auctum.
c. Pars nuclei immaturi.
d., e. Asci, vario maturitatis gradu. Long. = $^{45}/_{500}$ mill.
f. Sporae maturae. Long. = $^{10}/_{500}$ mill.; lat. = $^{5-6}/_{500}$ mill.

F. 5. **Valsa leucostoma** (Pers.) Fr.
a) magn. nat., b) valde aucta, c) Asci 8-sp., d) spor. $^{300}/_1$ auctae.

F. 6. **Cucurbitaria Pteridis.**
a) Perith. auctum, b) Asci 4-spori, c) Spor. multicellulares.

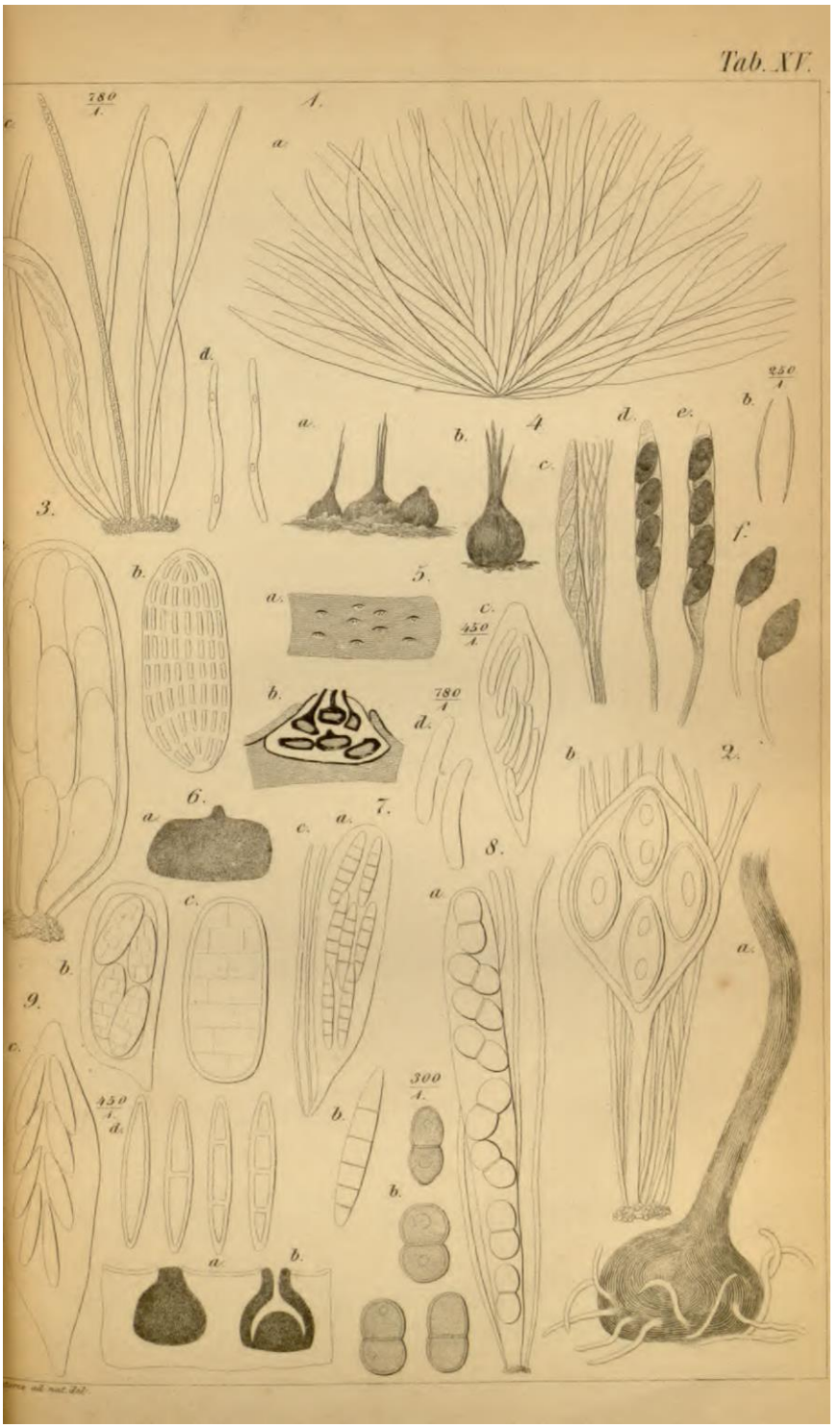
F. 7. **Sphaeria Nardi Fr.**
a) Asci 8-sp., paraphysibus immixtis (Fig. c.), b) Sporae.

F. 8. **Sphaeria insitiva Fr.**
a) Asci 8-sp. c. paraphysibus, b) Sporae diversiformes.

F. 9. **Sphaeria ditopa Fr.**
a) b) Perithecia, c) Asci 8-sp., d) Spor. 1—4-cellulares.

Redaction:
L. Rabenhorst in Dresden.

Druck von
C. Heinrich in Dresden.


Tab. XV.
780/1
A.
a.
d.
250/1
b.
4
d.
e.
c.
3.
f.
b.
5.
a.
c.
450/1
780/1
b.
d.
6.
2.
b
a.
7.
c.
a.
8.
c.
a.
b.
9.
c.
450/1
d.
300/1
b.
a.
b.

Description of *Malinvernia anserina*

in

Fuckel, K. W. G. L. (1869). 205. *Malinvernia. Symbolae mycologicae*. Beiträge zur Kenntniss der Rheinischen Pilze: 243-244

Von allen verwandten Arten durch die grossen Perithecien und durch di langen Mündungen derselben unterschieden.

d. Sporidia polyplasta, non secedentia.

204. Pleophragmia nov. gen.

Perithecia sparsa, simplicia, carbonacea, globosa, perforata. Asci oblique stipitati, oblongo-cylindracei, 8spori. Sporidia subdisticha, oblonga, perparum curvata, umbrino-fusca, e catenulis tribus, singulis 10loculatis, parallele connatis, ut sporidium triangulare appareat, composita, non secedentia, ad septa constricta, annulo hyalino cincta. Paraphyses nullae.

Von Sporormia bestimmt unterschieden durch die in ihre einzelnen Glieder niemals zerfallenden Sporen.

1. **P. leporum** nov. sp. — F. rh. 2272. — Peritheciis tectis, majusculis, globosis, atris, ostiolo prominulo, papillato, demum perforato; ascis 152 Mik. long. (pars sporifer.), 20 Mik. crass.; sporidiis 48 Mik. long., 12 Mik. crass. Cetera generis. Tab. VI. Fig. 26. sporidium.

Auf faulem Hasenkoth, der in einem Tannenwald lag, nur einmal gefunden, im Herbst. Im Tannenwald links zwischen Königstein und Glashütten.

Auf demselben Koth in Gesellschaft von Delitschia minuta †. s. d.

2. Sporidia unicaudata.

205. Malinvernia Rabenhorst in Hedwig. I. p. 116.

Nur Schlauchfrüchte bekannt.

1. **M. anserina** Rbh. in Hedw. I. No. 18. — Rbh. Hb. myc. II. 526. (Cesati). — F. rh. 1585. — Ascis cylindraceis, stipitatis, 4sporis, 102 Mik. long. (pars sporifer.), 19 Mik. crass.; sporidiis oblique monostichis, ellipsoideis, opacis, antice obtusiusculis, basi caudatis, cauda sporidio subduplo longiori, 30 Mik. long. (sine cauda), 16 Mik. crass.

An faulem Koth von Gänsen, sehr selten, im Herbst. In einem breiten Waldweg, der zur Gänschut benutzt wird, bei Grossgerau.

Die wenigen, am Scheitel stehenden Haare sind gewöhnlich so lang als das Perithecium und oft, gleichsam zu einer Spitze, vereinigt.

2. **M. breviseta** †. — Sphaeria pauciseta Rbh. in litt. — F. rh. 1002. — Ascis oblongis, longe stipitatis, 8sporis, 140 Mik. long. (pars sporifer.), 32 Mik. crass.; sporidiis subdistichis, ellipsoideis, opacis, antice subtiliter, hyaline apiculatis, basi caudatis, cauda plerumque curvata, sporidium aequante, 28 Mik. long., 14 Mik. crass.

Auf faulem Kuhmist, selten, im Herbst. Auf Waldwiesen bei Eberbach und im Oestricher Wald.

Von M. anserina unterscheidet sie sich, ausser durch die constant 8sporigen Schläuche und den abweichenden Sporenbau, durch die am Scheitel des Perithe-ciums stehenden, viel kürzeren, kronförmig abstehenden, niemals vereinigten Haare.

Dass aber beide zu einem und demselben Genus gehören, ist ausser allem

16*

Zweifel, nur wären dann im Genuscharakter, wie ihn Rbh. l. c. aufstellte, „die 4-sporigen Schläuche in „4—8sporige“ umzuändern.

Schliesslich bemerke ich noch, dass ich den früheren Namen „pauciseta“ in den passenderen „breviseta“ umgeändert.

206. Sordaria (Ces. & de Ntrs. Schem. Sfer. 51. pr. p.) Fckl.

Perithecia plerumque conferta subconfluentiave, in stromate spurio, crustaceo semiimmersa, globosa, extus sordida, brevissime tomentosa, ostiolo obtuso-conico, atro. Asci stipitati, 8spori. Sporidia subdisticha, ellipsoidea, monoplasta, opaca, basi longe appendiculata, appendiculo hyalino. Spermatia in peritheciis juvenilibus minutissima, cylindracea, curvata, hyalina.

1. **S. coprophila** Ces. & d. Ntrs. Schem. sfer. 52. — d. Ntrs. Sfer. ital. No. 20. c. ic. — Sphaeria c. Fr. Syst. myc. II. p. 342. — Hypoxylon c. Fr. S. v. Sc. p. 384. — F. rh. 1057 (unter Hypoxylon c. Fr.) — Sporidiis ellipsoideis, monoplastis opacis, appendiculo sporidio duplo longiori, hyalino, sporidiis sine appendiculo 22 Mik. long., 11 Mik. crass. Spermatiis minutissimis, cylindraceis, curvatis, hyalinis.

Auf faulem Kuhmist, nicht selten, im Herbst. Im Oestricher Wald.

3. Sporidia bicaudata.

207. Cercophora Fckl.

Perithecia sparsa, superficialia, oblongo-ovata, in rostrum obtusissimum, conicum, perforatum, quandoque curvatum attenuata, villosa. Asci stipitati, 8spori. Sporidia disticha, ovata, monoplasta, opaca, utrinque appendiculata, appendiculo inferiori longissimo, subrecto, cylindraceo, superiori breviori, ventricoso cylindraceove, hamato rectove, hyalino. Stylosporae endosporis similes, in peritheciis separatis.

1. **C. fimiseda** †. — I. Fungus pycnidium. Haplosporium tetragonum Fckl. in schedis. — Peritheciis gregariis, subconfluentibus, semiimmersis liberisve, majusculis, lineam altis, ovatis, villo sordido, rigido, dense tecto, rarius globosis, atris, in collum crassum glabrum, quadrangulare, obtusum, perithecium dimidium aequans, quandoque curvatum, demum pertusum attenuatis; stylosporis in gelatina filamentosa, stipite hyalino, immaturis oblongis, hyalinis fuscisque, quandoque apice appendiculo hyalino, maturis oblique ovatis, opacis, simplicibus, 50 Mik. long., 32 Mik. crass. Tab. IV. Fig. 1. stylospora immatura maturaque.

An faulenden Stengeln des Kopfkohls, welche an einem sehr feuchten schattigen Orte lagen. Ich fand diesen merkwürdigen Pilz nur einmal, im Winter, bei Oestrich.

Ohne Zweifel gehört er zu der Gattung Haplosporium Montagne's. Was derselbe aber von verschwindenden Schläuchen (s. dessen Sylloge p. 266) sagt, kann ich hier nicht finden. Im Gegentheil werden die Sporen auf Stielen gebildet, was ich bei den allerjüngsten (hyalinen) bestätigt fand, ganz so, wie bei Diplodia. Ausser allem Zweifel ist die genetische Verwandtschaft mit Cercocopra! Merkwürdiger Weise sind es auch hier die faulenden Kohlstengel, die auch bei Ascobolus (also auch Mistbewohnern), so bei A. glaber (siehe diesen), eine Ausnahme

A preliminary survey of the genus *Sordaria*

in

Winter, G. (1873). "Einige vorlaüfige Mittheilungen über di Gattung Sordaria." Botanische Zeitung 31(1. august 1873): 481-485

31. Jahrgang. № 31. 1. August 1873.

BOTANISCHE ZEITUNG.

Redaction: *A. de Bary.* — *G. Kraus.*

Einige vorläufige Mittheilungen über die Gattung Sordaria.

Von

Georg Winter.

(*Beschluss.*)

Gänzlich isolirt in dieser Gruppe und sehr an manche *Rosellinia*-Arten erinnernd, ist *Sordaria discospora* Awld., die jedoch, vermöge der durchaus häutigen, durchscheinenden Beschaffenheit der Perithecienwände zu *Sordaria* zu ziehen ist. Wie schon der Name sagt, ist sie charakterisirt durch die scheibenförmigen Sporen, die in Folge dieser Gestalt, von verschiedenen Seiten gesehen, mannichfaltige Ansichten darbieten und verschieden geformt zu sein scheinen. Dieser Umstand war die Veranlassung, dass Auerswald daraufhin irrthümlicher Weise seine *S. heterospora*, die nicht im Geringsten von *S. discospora* abweicht, aufstellte. Jedoch besitze ich von Auerswald Exemplare seiner *S. heterospora*, die bedeutend grössere Perithecien mit längerem Collum zeigen, und die ich daher als *Forma major* W. von der Normart abzweigen möchte, indem ich *S. heterospora* Awld. (pr. p.!) als Synonym dazuziehe, zum Theil nur deshalb, weil, wie schon oben gesagt, andere von Auerswald als *S. heterospora* vertheilte Exemplare obige Unterschiede nicht zeigen. *Sordaria maxima* Niessl. und *S. bombardioides* Awld. schliessen die Reihe der *Hypocopra*-Arten, indem sie zugleich durch die Wachsthumsweise und Gestalt ihrer Perithecien den Uebergang zur folgenden Gruppe, die mit *S. fimiseda* Cés. u. de Not. beginnt, bilden. Beide sind ausgezeichnet durch die Grösse ihrer Perithecien, den Mangel eines Collum u. a. m. Die Perithecien von *S. bombardioides* sind am Gipfel seitlich unter der Spitze etwas eingedrückt, die Spitze selbst ein wenig nach dieser Stelle übergebogen, so dass das Ganze ein helmförmiges Aussehen erhält; die Asci sind äusserst lang gestielt und enthalten 8 Sporen. *S. maxima* Niessl dagegen hat Perithecien, deren Gipfel vollständig gleichmässig abgerundet und ohne Papille oder Collum ist; bei ihr scheint die Anzahl der Sporen eines Schlauches constant 4 zu sein. Jedenfalls stehen sich beide Arten sehr nahe.

Gehen wir nun zu der dritten Gruppe über, die ich als *Eusordaria* bezeichne, so ist es am räthlichsten, an ihre Spitze *S. fimiseda* Cés. u. de Not. zu stellen, theils wegen der Aehnlichkeit ihrer Perithecien mit denen der beiden vorigen Arten, theils, weil sie die typischste Art des Subgenus *Eusordaria* ist. Sie und *Sordaria coprophila* Cés. u. de Not., die ihr unter den bis jetzt bekannten Arten am nächsten steht, sind durch Woronin's vortreffliche Arbeit (s. o.) hinlänglich bekannt, so dass ich hier darüber nichts weiter zu bemerken brauche. Dass die von Fuckel (l. c.) aufgestellte *Cercophora mirabilis* mit *S. coprophila* Cés. u. de Not. identisch ist, wurde schon oben gesagt. Der letzteren Art steht Fuckel's *S. lignicola* sehr nahe, ist jedoch hinreichend unterschieden, um sie als gute Art betrachten zu können. Form, Wachs-

thumsverhältnisse und Grösse der Perithecien sind ganz andere, ebenso die Grössenverhältnisse der Asci und Sporen. Am charakteristischsten für *S. lignicola* Fckl. sind jedoch die Anhängsel zweiter Ordnung an den Sporen, die hier sehr kurze, scharfe, gekrümmte Spitzchen, bei *S. coprophila* hingegen, lange, pfriemenförmige, ebenfalls gekrümmte stachelartige Fortsätze darstellen. Hieran reihen sich nun 2 Arten, die durch mannichfaltige Charaktere wohl leicht und sicher von den vorhergehenden und nachfolgenden Species zu trennen, deren Unterschiede unter einander jedoch nur gering sind. Es sind dies *Sordaria decipiens* Wint. und *S. pleiospora* Wint. Erstere besitzt weit kleinere Schläuche, jedoch bedeutend grössere Sporen als *S. pleiospora;* ihre Schläuche sind constant 8sporig, während die Zahl der Sporen bei *S. pleiospora* Wint. nie unter 16 heruntergeht, meist dagegen zwischen 32 und 64 schwankt. Trotzdem nun, wie man sieht, diese Unterschiede nicht bedeutend sind, auch die Entwickelungsgeschichte der Sporen bei beiden vollständig übereinstimmt, glaube ich mich doch berechtigt, sie als Arten zu trennen, da lange fortgesetzte und zahlreiche Culturen beider Arten stets constante Resultate ergeben haben.

Eine ausgezeichnete, zierliche, aber wie es scheint, äusserst seltene Art ist die von mir aufgefundene *S. setosa* Winter. Obgleich sowohl die Entwickelungsgeschichte der Sporen derjenigen von *S. coprophila* Cés. u. de Not. ähnlich ist (Ausführliches darüber findet man in meiner Monographie), ebenso das Verhalten der Anhängsel dem bei *S. coprophila* bekannten sich analog verhält, so habe ich doch, wegen der Bekleidung der Perithecien, die der von *S. curvicolla* Wint. und *S. anserina* (Rabh.) Wint. fast gleich ist, es für besser gehalten, sie in die Nähe dieser zu bringen. Die Perithecien dieser Art, ebenso wie die von *S. curvicolla* Wint. und *S. anserina* (Rabh.) sind nämlich nach dem Gipfel zu, besonders am Collum mit Büscheln langer, dunkelbrauner Borsten bekleidet. *S. setosa*, im Allgemeinen der *S. curvicolla* m. sehr ähnlich, unterscheidet sich von dieser leicht durch die Grösse der Schläuche, die Farbe der Sporen und Perithecienwandungen, insbesondere aber durch die Form der Schläuche; dieselben sind bei *S. setosa* nach der Spitze zu stark verschmälert, nur wenig bauchig, breit cylindrisch; bei *curvicolla* dagegen ist der Schlauch dicht unterhalb der Spitze am breitesten, an dieser selbst breit und stumpf abgerundet, äusserst weit bauchig, fast verkehrt eiförmig. Uebrigens

haben beide Arten als gemeinschaftliche Merkmale die Form und Bekleidung der Perithecien und die 128sporigen Schläuche. Ihnen ist *Sordaria anserina* (Rbh.) Wint. zunächst verwandt, ausgezeichnet durch die meist 4, mitunter auch nur 2 Sporen enthaltenden Schläuche. Während bei den beiden andern Arten die Borsten an oder dicht unterhalb der Spitze des Collums stehen, finden sie sich hier immer an der Stelle, wo das Perithecium in den Hals übergeht, und zwar, da dieser gekrümmt ist, stets auf der convexen Seite desselben. Die Dimensionen der Sporen sind sehr variabel, je nachdem die Schläuche 4 oder nur 2 Sporen enthalten; im ersteren Falle sind sie kleiner, im zweiten bedeutend grösser, mitunter doppelt so gross.

Wie sich die drei vorhergehenden Arten durch die borstige Bekleidung ihrer Perithecien auszeichneten, so sind es bei den beiden nun folgenden Arten, *Sordaria minuta* Fckl. und *S. curvula* de By. ebenfalls die Haare oder Haarbüschel, mit denen die Perithecien besetzt sind, die das charakteristischste Kennzeichen beider Arten liefern. *S. minuta* Fckl., die kleinste aller Sordarien, (soweit sie mir bekannt sind), besitzt Perithecien, die auf ihrer Oberfläche, besonders nach dem Collum hin mit eigenthümlichen, einzeln stehenden Haaren, an der Mündung aber mit einem dichten Kranz ebensolcher besetzt sind. Sie ist ferner ausgezeichnet durch die Kleinheit aller Theile im Gegensatz zu *S. curvula* de By. Die eigentliche Fuckel'sche *S. minuta* hat nun 8sporige Schläuche, die mitunter mit 4sporigen untermischt sind. Es finden sich jedoch auch häufig Perithecien, die stets nur 4sporige Schläuche produciren. Derartige Exemplare habe ich zuerst aufgefunden, und sie als *Sordaria tetraspora* Winter (in Hedwigia 1871 No. 11) veröffentlicht. Als ich nun Fuckel'sche Originale seiner *S. minuta* erhielt, die, ausgenommen die Zahl der Sporen, in allem Uebrigen mit meiner *S. tetraspora* vollständig übereinstimmt, so musste ich meinen Namen fallen lassen, und nahm den Fuckel'schen Namen an, indem ich *S. tetraspora* Wint. als Synonym dazuziehe. Den Schluss bildet die vielnämige *Sordaria curvula* de By. Sie scheint zuerst von Corda aufgefunden worden zu sein, wenigstens schliesse ich aus dessen Beschreibung und Abbildung[16]) von *Schizothecium fimicolum*, dass dieser Pilz mit obiger *S. curvula* de By., nicht

16) Corda, *Icones fungorum* Tom. II. pag. 29. t. XIII. fig. 105.

wie Césati u. de Notar. (l. c.) annehmen, mit *S. fimiseda* synonym ist. Herr Prof. de Bary belegte unsre Art, wie er mir mitzutheilen die Güte hatte zunächst in Briefen mit obigem Namen, später findet sie sich in des Autors bekanntem Werke: Morphologie und Physiol. der Pilze etc. pag. 209 erwähnt, doch ist sie nirgends beschrieben worden. Auerswald, der keine Exemplare der de Bary'schen Art besass, fand sie mehrfach auf, betrachtete sie als neu und gab ihr den Namen *S. appendiculata*. Eine später zu besprechende Form derselben Art wurde dann von Rabenhorst *Malinvernia pauciseta* benannt, was Fuckel in den Symbolae in *breviseta* umänderte. Ebenda beschreibt letzterer eine *Cercophora conica*, die ebenfalls zu unsrer *Sordaria curvula* gehört, während auch Karsten in den *Fungi fenninci* No. 955 eine *Ixodiopsis fimicola* ausgab, die sich in Nichts von *Sord. curvula* unterscheidet. Eine zweite, sehr ausgezeichnete Form dieser Species, die gleichwohl eben nur als Form, nicht aber als Art betrachtet werden kann, ist Fuckel's *Sord. aloides*[17]), die ebenfalls unten kurz betrachtet werden wird. *Sord. curvula* de By. ist eine der best charakterisirten Arten, besonders auffallend durch die Haarbekleidung der Perithecien. Die einzelnen Haare ähneln sehr denen von *S. minuta* Fckl., sie stehen jedoch nur selten und nur bei der Normart einzeln, sind vielmehr häufiger zu mehr oder weniger dicken Büscheln gleichsam verklebt. Die *Forma coronata* m. (= *Malinvernia pauciseta* Rbh., *M. breviseta* Fckl.), ebenso wie die *forma aloides* m. (= *Sordaria aloides* Fckl.) unterscheidet sich nur durch die Länge dieser Haare, die Dicke und Länge, sowie Stellung und Form der von ihnen gebildeten Büschel. Alle übrigen Merkmale, insbesondere die Schläuche und Sporen sind bei beiden Formen mit denen der Normart übereinstimmend. Die weiteren Eigenthümlichkeiten dieser interessanten Species findet man in meiner Monographie ausführlich besprochen.

Halle a/S., Juli 1873.

Gesellschaften.

Thesen über den mechanischen Aufbau der Gefässpflanzen, speciell der Monocotylen.

Von S. Schwendener.

(Auszug aus zwei Vorträgen, gehalten im Januar und Februar 1873.)

1) Die Pflanzen sind den mechanischen Bedingungen, unter welchen sie vegetiren, mehr oder weniger angepasst. Organe, welche in der Luft leben, wie z. B. Stämme, Blüthenschäfte etc., bedürfen in erster Linie einer gewissen Biegungsfestigkeit, um den seitlich wirkenden Kräften (Wind, excentrische Belastung u. dgl.) Widerstand zu leisten. Andere Organe, welche im Boden oder in rasch fliessendem Wasser vegetiren, desgleichen die Ranken und schlingenden Stengel etc. werden vorzugsweise durch Zugkräfte in Anspruch genommen und bedürfen daher der Zugfestigkeit. Wieder andere sind von wasserdurchtränkter Erde umgeben (Rhizome, Wurzeln) und dem entsprechend von grossen Luftcanälen durchzogen, welche eine feste äussere Umhüllung erheischen, um gegen radiale Druckkräfte geschützt zu sein, u. s. w. Diesen verschiedenen Anforderungen sucht die Pflanze durch besondere Einrichtungen, welche nach mechanischen Principien construirt sind, Genüge zu leisten.

2) Wie bei allen höher differenzirten Gewächsen die Function der Durchlüftung grossentheils den Zellformen des trachealen Systems, die Leitung eiweissartiger Stoffe den Cambiformzellen, der Schutz nach aussen der Cuticula und dem anatomisch wohl characterisirten Periderm u. s. w. übertragen ist; wie also fast jeder wichtigeren Verrichtung ein besonderes System von Elementarorganen vorsteht: so sind es auch bestimmte, anatomisch ausgezeichnete Zellen, welche die Herstellung der nöthigen Festigkeit übernehmen. Diese Zellen bilden das mechanische System der Gewächse, von dem sich nachweisen lässt, dass es ganz nach den Grundsätzen der Mechanik gebaut ist.

3) Als specifisch mechanische Elemente der Vegetationsorgane sind nur die Bastzellen und die bastähnlichen Collenchymzellen zu betrachten, welche mit jenen eine zusammenhängende Formenreihe bilden, deren extremste Glieder durch alle möglichen Uebergänge verbunden sind. Es sind langgestreckte prosenchymatische Zellen, mit oder ohne Querwände, aber stets mit mehr oder weniger verdickten Membranen, deren Molecularreihen longitudinal oder in linksschiefer Schraubenlinie verlaufen. Diese Richtung der Molecularreihen verräth sich schon durch die spaltenförmigen Poren, wo solche vorhanden sind.

4) Die mechanischen Zellen besitzen einen hohen Grad von Widerstandsfähigkeit. Stark verdickte Bastzellen, wie sie bei Liliaceen, Palmen, Gramineen etc. vorkommen, erreichen nahezu die Zugfestigkeit des Schmiedeeisens, sofern blos die Spannungen innerhalb der Elasticitätsgrenze in Betracht gezogen werden. Ich habe Fälle beobachtet, wo eine Belastung von 15—20 Kilo pro Quadratmilli-

17) Fuckel, Symb. mycol. Nachtr. II. pag. 43.

Description of *Sordaria anserina*

in

Winter, G. (1873). 20. *Sordaria anserina* (Rabh.) Winter - Die Deutschen Sordarien - Abhandlungen der Naturf. Gesellschaft zu Halle 13: 1-43 + Taf. VII-XI

In fimo murino in sylvis prope Oederan (Saxoniae) ipse legi.

Diese und die vorhergehende Art sind durch die 128-sporigen Schläuche so scharf charakterisirt und stehen durch dies Merkmal so isolirt von den übrigen Arten, dass sie, hätte man sie früher gekannt, wahrscheinlich zu Repräsentanten einer besonderen Gattung gemacht worden wären. Es ist natürlich, dass ich die Anzahl der Sporen nicht öfter gezählt habe; ich habe einen Schlauch apart herauspräparirt, aus diesem, nachdem ich mich überzeugt hatte, dass er noch unversehrt war, die Sporen vorsichtig entleert und gezählt; aus dem Resultate dieser einen Zählung habe ich dann einen Schluss gezogen auf den Inhalt auch der andern Schläuche. Es ist wahrscheinlich, dass auch hier nicht immer sämmtliche Sporen ausgebildet werden; jedoch erlangen bei diesen beiden Arten die Sporen eines Schlauches ihre Reife sämmtlich zu gleicher Zeit. An *S. anserina* (und deshalb von mir in ihre nächste Nähe gestellt) erinnern beide Arten durch die langen steifen Borsten, die jedoch hier nicht wie bei *S. discospora* über die ganze Oberfläche des Peritheciums oder des Collums desselben vertheilt sind, sondern in einem dicken Büschel die Spitze des Collums oder den Hals etwas seitlich unterhalb der Spitze krönen. Die einzelnen Haare sind braun, durchscheinend, septirt.

20. *Sordaria anserina* (Rabh.) Winter.

Peritheciis dense gregariis, semiimmersis, opaco fusco-atris, rugulosis, basi villo arachnoideo, repente, concolore cinctis et sursum sparsim ab eo vestitis, e basi globosa vel subovata conicis, in collum crassum, rugosum, nigrum, longe conicum, curvatum attenuatis; collo longe infra apicem in latere convexo setis longissimis, rigidis, fuscis, dense fastiatimque obsitis; peritheciis 280 — 330 Mikr. latis; ascis cylindraceis, utrinque attenuatis, apice rotundatis, basi longissime pedicellatis, 2-, 4- sporis, 110 — 125 Mikr. long., 20 — 22 Mikr. crass.; paraphysibus filiformibus, ramosis, gelatinosis, ascis duplo longioribus; sporidiis monostichis, ovatis, fuscis, guttulo oleoso, basi appendiculo hyalino, recto, sporidium aequante, 33 — 42 Mikr. long., 19 — 21 Mikr. crass.

Syn.: *Malinvernia anserina* Rab., *Hypocopra anserina* Cés. in litt.

Auf Gänsekoth bei Vercellis (Italiae) lg. Césati, ca. Grossgerau pr. Darmstadt lg. Fuckel.

Diese Art steht der *S. setosa* mihi sehr nahe; diese aber ist vermöge ihrer Entwicklungsgeschichte von *Sordaria* nicht zu trennen, so dass auch *S. anserina* zu

5*

dieser Gattung gebracht werden muss, obgleich ich, aus Mangel an lebenden Exemplaren, sie noch nicht entwicklungsgeschichtlich prüfen konnte. Es kommen bei dieser Species mitunter zwischen den 4sporigen auch zweisporige Schläuche vor, deren einen ich gezeichnet habe. Die Sporen sind in diesem Falle weit grösser als die Sporen der normalen Schläuche. Dies, sowie *S. fimiseda*, die ja auch mit 4- und 8-sporigen Schläuchen vorkommt, und *S. pleiospora*, bei der die Anzahl der Sporen noch schwankender ist, sind die besten Beweise für die Unzuverlässigkeit der Sporenzahl als Art-Merkmal. Diese Art bedeckt, nur mit dem Haarschopf und dem Collum hervorbrechend, in dichten Rasen die Miststücke, scheint übrigens zu den seltensten zu gehören.

21. *Sordaria minuta* Fckl., Symbolae mycol, Nachtrag II. pag. 44.

Peritheciis sparsis, superficialibus, elongato-ovatis, sive exacte conicis, apice attenuatis, rotundatis vel obtusis, pallide luteo-fuscis, ostiolo nigro-fusco, rugulosis, pilis brevibus, articulatis, concoloribus, mox decidentibus sparsim, apice densius obsitis, basi pilis tenuibus, filiformibus, repentibus cinctis, ca. 400 Mikr. alt., 220 Mikr. lat.; ascis cylindraceis, longe pedicellatis, apice attenuatis, membrana duplici apice incrassata, 4—8 sporis, 80—110 Mikr. long. (pars sporifer), 14 Mikr. crass.; paraphysibus filiformibus, ascis longioribus; sporidiis oblique monostichis, ovatis, utrinque attenuatis, monoplastis, antice massa gelatinosa, variae formae, hyalino, mox deciduo, basi appendiculo hyalino, recto, sporidium dimidium aequante, fuscis, 16—22 Mikr. long., 10 Mikr. crass.

Synon.: *Sord. tetraspora* Winter, Hedwigia 1871, p. 161.

In fimo murino prope Oederan, (Saxoniae), in fimo murino, leporino et vulpino in sylva Harth prope Lipsiam ipse legi, ad fimum equinum prope Ems (Nassoviae) leg. Dr. Lange, ad fimum ovinum et ad fimum cuniculorum pr. Halam (Saxon.) leg. ipse.

Zu dieser Species muss ich zunächst bemerken, dass meine Beschreibung von *S. tetraspora* in der Hedwigia, die nur nach einem einzigen Perithecium entworfen war, in Folge dessen sehr mangelhaft ausgefallen ist. Ich selbst habe die Art wild und cultivirt in Hunderten von Exemplaren untersucht und stets 4-sporig gefunden; da überbrachte mir kurz vor dem Druck dieser Arbeit Herr Dr. Lange von Ems Exemplare einer Sordaria, die in Allem mit meiner *S. tetraspora* übereinstimmten, nur dass sie neben 4-sporigen auch 8-sporige Schläuche besassen. Herr Fuckel

Taf. XI.

Fig. 20. *Sordaria anserina* (Rabh.) Winter.
aa. Zwei Perithecien. b. ein normal viersporiger Schlauch. c. ein zweisporiger Schlauch. d. eine reife Spore.

Fig. 21. *Sordaria minuta* Fckl.
a. ein Perithecium von *S. tetraspora* Wint. b. ein solches von einem Fuckel'schen Original von *S. minuta*. c. Haarbesatz am Collum des Peritheciums. d. ein viersporiger Schlauch von *S. tetraspora*. e. ein 8-sporiger Schlauch von Fuckel's Original von *S. minuta*. f. eine reife Spore.

Fig. 22. *Sordaria curvula* de By.
a. ein Perithecium von Hermsdorfer frischen Expl. b. ein reifer Schlauch von demselben Expl. c. Haare von der Wand des Peritheciums. d. dieselben, jedoch ein andrer Büschel, stark vergrössert. e. Conidien von einem cultivirten Expl. von Schleussig. f. Spore von einem Auerswald'schen Expl. seiner *S. appendiculata*. g. Spore von obigem Hermsdorfer Expl. h. ein frischer Schlauch, kurz vor dem Zusammenfallen der Membran gezeichnet. i. oberer Theil eines Peritheciums der *Forma coronata* m. von einem Fuckel'schen Exemplar der *Malinvernia breviseta*. k. ein Perithecium der *Forma aloides* (Fuckel) mihi von einem Expl. von Morthier. l. zwei Schläuche desselben Exemplars in verschiedener Vergrösserung. m. ein Stück eines der grossen Haarbüschel, die an der Spitze des Peritheciums der *Forma aloides* stehen. n. zwei Sporen von demselben Morthier'schen Exemplar.

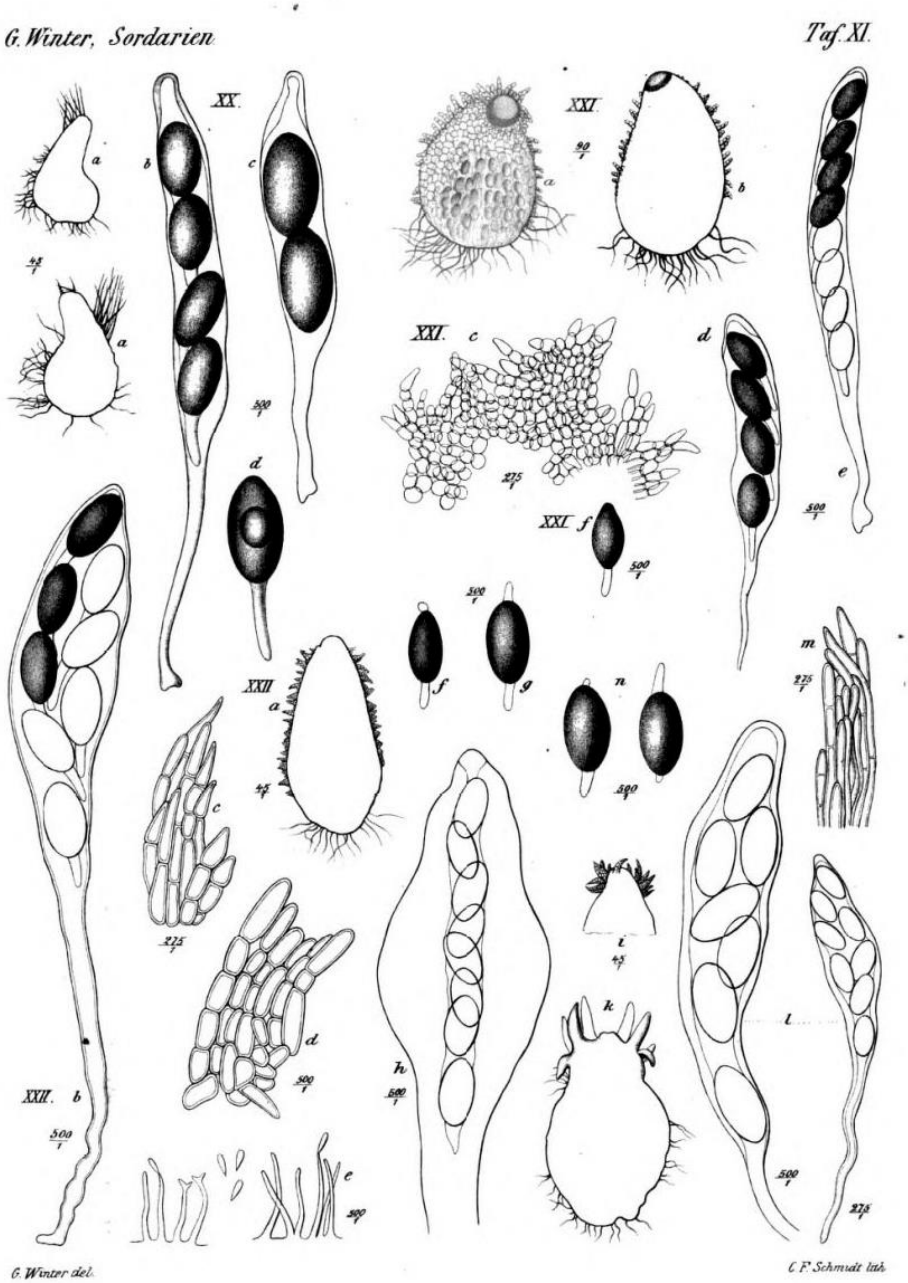

G. Winter, Sordarien
Taf. XI.
G. Winter: del.
C. F. Schmidt lith.

Illustration of *Sordaria anserina*

in

Hansen, E. C. (1876). Tavle VIII. Les champignons stercoraires du Danemark: 352-353 - Pl. VIII

Sordaria curvula De By. (Fig. 9—14).

9—14. Sporer, hvoraf to umodne, Fig. 9 og 14; i dennes Hovedvedhæng sees en Tverskillevæg, hin er udstyret med abnorme, gelatinose Vedhæng. Fig. 10 og 13 fremstille normale Sporer og vise, at de ere forsynede med alle de for Subgenus *Eusordaria* characteristiske Vedhæng; i Fig. 11 er den egentlige Spore vorteformigt tilspidset foroven, og dens nederste, gelatinose Vedhæng mangler. Fig. 12 forestiller en Spore med abnorme Vedhængsdannelser, udspringende fra Hovedvedhænget. $^{350}/_{1}$.

Sordaria anserina (Rabh.) Wint. (Fig. 15—21).

15. En normal Spore, afbildet for at vise, at ogsaa her optræde alle de for Subgenus *Eusordaria* characteristiske Vedhæng. $^{350}/_{1}$.
16—17. To Sporecarpier, hvoraf det enes Hals er nøgent, det andets kortborstet. $^{19}/_{1}$.
18. En Ascus, hvis tre nederste Sporer ere vorteformigt tilspidsede. $^{155}/_{1}$.
19. Den øverste Ende af en Ascus, med en normal og en misdannet Spore. $^{350}/_{1}$.
20. En misdannet Spore. $^{350}/_{1}$.
21. En normal Spore, hvis nederste, gelatinose Vedhæng er svagt udviklet. $^{350}/_{1}$.

Sordaria sp.? (Fig. 22—28).

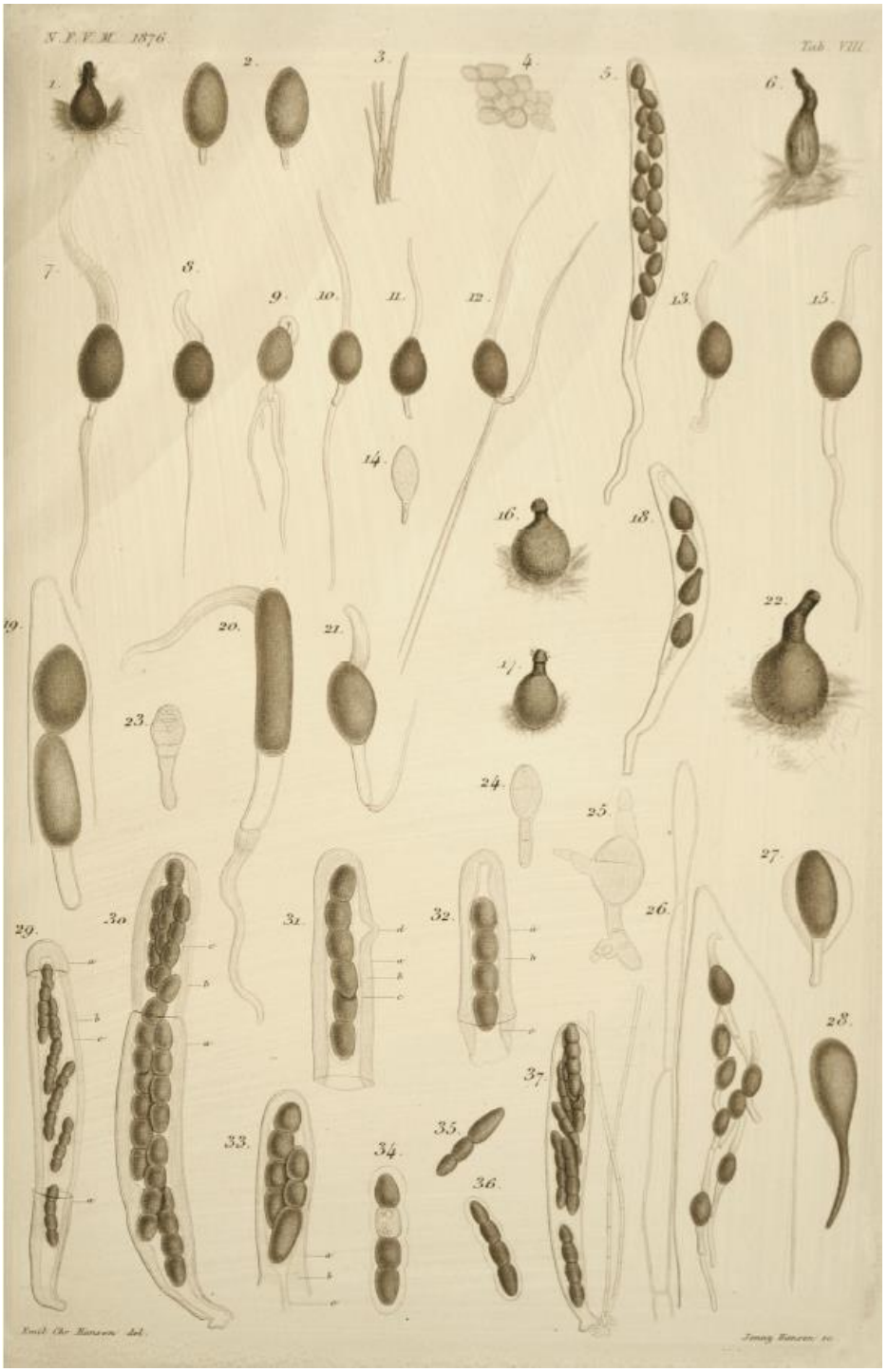
22. Et Sporecarpium. $^{15}/_{1}$.
23—25. Tre umodne, med flere Tverskillevægge udstyrede Sporer, hvoraf den ene, Fig. 25, har udsendt fire Spiretraade. $^{350}/_{1}$.
26. Den øverste Del af en Ascus og af en Paraphyse. $^{120}/_{1}$.
27—28. To misdannede Sporer. $^{350}/_{1}$.

Sporormia intermedia Awd. (Fig. 29—34).

29. En opsprungen Ascus, hvis Vægs Yderhinde er bristet paatvers og nu som en Hætte foroven bedækker den fremskudte, opsvulmede Inderhinde. I denne og de følgende Figurer betyder *a* Ascusvæggens Yderhinde, *b* dens Inderhinde, *c* „Primordialschlauch". $^{155}/_{1}$.
30. En opsprungen Ascus, hvor Væggens Yderhinde er bristet i Spidsen; foroven sees den fremskudte Inderhinde. $^{350}/_{1}$.
31—33. De hætteformede, øverste Partier af Asci, hos hvilke hele Væggen under Dækglassets Tryk er bristet paatvers. I Fig. 31 træder Inderhinden frem gjennem den ved *d* itubrudte Yderhinde; i Fig. 32 og 33 sees Sporer med indbyrdes forskjellige Endeled. $^{350}/_{1}$
34. En abnorm Spore, hvis ene Mellemled er forblevet lysegult og indeholder Vacuoler; det gelatinøse Hylster er bevaret. $^{350}/_{1}$.

Sporormia minima Awd. (Fig. 35).

35. En abnorm, treleddet Spore. $^{350}/_{1}$.


N. F. V. M. 1876.
Tab. VIII.

Description of *Hypocopra erecta*

in

Spegazzini, C. (1880). "*Fungi Argentini*." Anales de la Sociedad Científica Argentina 10: 5-33

toruloso mucosis obvallati, octospori; sporidia disticha, ellipsoidea, primo 1-3 pseudoseptata, hyalina, dein continua, fuliginea (28-32×18-20), iodi ope nucleo obscuriore hyalino-ocellato donata, apice cauda (quandoque deficiente) contorta, mox fluxili ornata, basi appendicem (20-30×4-8) cylindraceam persistentem, rectam (in prima aetate 1-3 pseudoseptatam, dein continuam) hyalinam gerentem.

Hab. In fimo vaccino putrescente secus Rio de la Plata, cerca de la Recoleta, Apr. 1880.

Obs Species *S. decipienti* sat similis, sed characteribus citatis recedens.

61. HYPOCOPRA ERECTA Sp. (n. sp.).

Diag. Perithecia elliptica vel ovoidea ($\frac{1}{2}$-$\frac{2}{3}$ alt., $\frac{1}{4}$-$\frac{1}{5}$ crass.), erecta, superficialia, glabra, vel pruinulosa, griseo-fuliginea, basi hyphis radiantibus ornata; asci cylindraceo-clavati, sursum truncato-rotundati, deorsum in pedicello longo ac gracili attenuati (200-220×25-30), tetraspori rarissime 5-6 spori, aparaphysati; sporidia monosticha, elliptico-navicularia, utrinque attenuato-rodundata (38-42 × 20), atque caudibus cylindraceis rectis vel runcinato-curvatis sporidium aequantibus, mox fluxilibus ornata.

Hab. In fimo vaccino prope San José de Flores, Apr. 1880.

62. HYPOCOPRA MICRURA Speg. (n. sp.).

Diag. Perithecia minuta (150-180), levia, globoso-lenticularia, matrici immersa, ostiolo papillato subcarbonaceo exerto, hyphis repentibus anastomasantíbus ornata, contextu membranaceo, parenchymatico, olivaceo-fuligineo; asci clavato-elongati sursum rotundati, deorsum in pedicello breviusculo attenuati (160-180 × 20-25), octospori, paraphysibus mucosis, filiformibus obvallati; sporidia subdisticha elliptico-limoniformia (20-25×15), fuliginea, basi cauda hyalina parvula (8-10×2) donata.

Hab. In fimo *Caviae leucopygae* in pratibus prope San José de Flores, Maj. 1880.

Obs. Species *H. curvulae* affinis obsporidia simillima, sed perithecii papillarum absentia, asci aparaphysatione atque pediculi brevitate recedens.

Description of *Sordaria anserina*

in

Sacchardo, P. A. (1882). II. *Malinvernia*: ascis tetrasporis. *A Sylloge fungorum omnium hucusque cognitorum*. 1: 238

cato donatis, e sporidiis exsilientibus sæpius atro-areolatis; ascis cylindraceo-clavatis, sursum obtuse rotundatis, deorsum in pedicellum longiusculum attenuatis, 100–110 ≃ 16–17 p. sporif., 60–80 ≃ 4–6 ped., octosporis, paraphysibus filiformibus, longioribus, crassiusculis obvallatis; sporidiis recte v. oblique distichis, ellipticis, utrinque acutiuscule rotundatis, opace fuligineis, 28–30 ≃ 10–12, deorsum caudâ cylindraceo-clavatâ, 14 ≃ 5, hyalinâ, facillime deciduâ auctis.

Hab. in parte interiore humo obducta trunci vetusti ac cæsi Pireuniæ dioicæ prope S. José de Flores, Argent. Amer. austr. — Var. *Agavis americanæ* Speg. Fungi Arg. Pug. IV, n. 129. A typo recedit perithecii nonnihil minoribus, 200–250, magis coriaceis, ascis brevius stipitatis crassioribusque, 140–150 ≃ 20, paraphysibus ægre visibilibus; sporidiorum magnitudine 24–30 ≃ 12–14, colore atque cauda, 15–20 ≃ 2–4, ut in typo. Hæc forma in ligno denudato vigens nonnihil ad *Rosellíniam* vergit. — In ejusdem ligno dejecto putrescente prope el Bañado de S. José de Flores, Argent. Amer. austr.

26. **Sordaria Cirsii** Crouan Finist. p. 22. — Perithecíis pyriformibus, 2–3 mill. alt., nigricantibus, glabris, hinc vero hyphis mycelicis inspersis; ascis magnis, clavatis, apice mamillatis, deorsum attenuatis, e placenta filamentoso-cellulari oriundis, octosporis; sporidiis ovoideis, monostichis, flavis, dein nigricantibus, polis appendicula hyalina incurva, attenuata auctis. 863

Hab. in basi putrida Cirsii palustris in paludibus Finistère (Gallia).

II. *Malinvernia:* ascis tetrasporis.

27. **Sordaria anserina** (Rabh.) Wint. Sord. 35, t. XI, fig. 20, Sacc. Fungi Ven. V, p. 178, *Malinvernia anserina* Rabh., *Hypocopra anserina* Ces. in litt. — Perithecíis semiimmersis, majusculis, 1/3–1/2 mill. crass., globoso-conoideis, hyphis repentibus conidiophoris basi cinctis, verticeque setis rigidulis ex hyphis coalitis fuligíneis instructis; contextu parenchymatico fuligineo (in forma *anserina* subcarbonaceo, in forma *ovina* et *equina* submembranaceo); ascis fusoideo-clavatis, p. sporif. 160–180 ≃ 30–32, stip. 110–115 ≃ 7–9, tetrasporis; sporidiis monostichis ovato-ellipsoideis, obtusiusculis, 40–42 ≃ 22, opace fuligíneis, caudâ hyalinâ, 35 ≃ 5, basi donatis. 864

Hab. in stercore anserino, ovino, vaccino, equino, cuniculorumque in Germania et Italia boreali.

Creation of the genus *Podospora*

in

Niessl (1883). "Ueber die Theilung der Gattung Sordaria." Hedwigia 22: 153-156

Mnium hornum Hedw. Breitethal am Ufer der Holtemme. K. !!

Mn. serratum Brid. An feuchten Felsen b. d. Marmormühle unweit Rübeland. !!

Bryum capillare L. Salzthal auf Waldboden zahlreich. !! Graben hinter Niewerth. K.

Br. turbinatum Schwgr. Bollhasenthal. W.

Br. inclinatum Schpr. Antonsgrotte an Porphyr. (?) !!

Br. pseudotriquetrum Schwgr. Bollhasenthal. W.

Webera nutans Hedw. Var. longiseta Schpr. Hurley-Klippe. K. !

W. cruda Schpr. Mühlenthal am Eichberghang auf Thonschiefer. W. !!

Fam. Funariaceae.

Physcomitrium pyriforme Brid. Bollhasenthal. W.

(Schluss folgt.)

Ueber die Theilung der Gattung Sordaria.

Während Dr. Winter in seiner schönen Monographie sich begnügte, drei Unterabtheilungen der Gattung Sordaria zu bilden, wurde dieselbe sowohl schon früher von Fuckel (Note: im 3. und letzten Nachtrage hat Fuckel jedoch den Namen Sordaria wieder bei gigaspora verwendet, welche nach seinen früheren Aufstellungen eigentlich zu Hypocopra gehören würde), als auch in neuerer Zeit von Saccardo in der Sylloge I, in mehrere Gattungen getheilt. Von den Gattungen Saccardo's entsprechen drei, nämlich: Coprolepa (mit Stroma), Hypocopra (Sporen ohne Anhängsel) und Sordaria (Sporen mit Anhängsel) den Unterabtheilungen Winter's und theilweise den Gattungen Fuckel's, während Philocopra jene Arten umfasst, deren Schläuche mehr als 8 Sporen enthalten (Saccardo nennt die Schläuche „polyspori"), welche übrigens, mit wenigen Ausnahmen, geschwänzt sind.

Was nun zunächst diese letztere Gattung betrifft, so ist es allerdings Ansichtssache, ob das hervorgehobene Criterium die Abtrennung hinlänglich begründe, es wird aber vielleicht gestattet sein, darauf aufmerksam zu machen, dass dieses Merkmal bei den Sordarien nicht in analoger Weise auftritt, wie bei anderen Pyrenomyceten (z. B. bei Valsa — Valsella u. dgl.). Es scheint mir nämlich, dass man hier nicht in gleicher Art die Schläuche typisch als „polyspori" bezeichnen könne. Betrachtet man nämlich die Arten, bei welchen die Zahl der Sporen in einem Schlauche über 8 hinausgeht, so hat man (wenn richtig beobachtet) zunächst

die 12sporige S. zygospora Speg., dann die 16sporigen S. similis Hans., dubia Hans. und pleiospora Wint., welch letztere, und zwar nicht selten, auch 24-, 32- und 64sporige Schläuche zeigt. Endlich bieten S. curvicolla Wint. und setosa Wint. Schläuche mit normal 128 Sporen. Dies sind lauter Multipla der typischen acht — oder in einem Falle von vier — und es sagt hier der Ausdruck: asci polyspori zu viel und auch zu wenig. Dass in der Beschreibung einiger Arten (auch solcher, die Winter schon sehr hübsch charakterisirte) bei Saccardo andere Angaben für die Sporenzahl vorkommen, wie 40—60, 60—84, 80—100, halte ich nicht für maassgebend, weil sehr oft nicht alle Sporen zur Ausbildung gelangen. Auch bei den anderen Sphaeriaceen bezeichnet man die Schläuche nicht als 1—8sporig, obwohl sich in jedem Perithecium solche finden, deren Sporenzahl geringer als 8 ist, sondern man sucht die typische Zahl zu bestimmen und giebt diese an. In unserem Falle ist diese, wie schon gesagt, ein ziemlich wechselndes Vielfaches von 8 (oder 4) und ich bin daher gleich Winter der Ansicht, dass dieses Merkmal nicht einmal zur Charakterisirung von Unterabtheilungen taugt, viel weniger eine Gattung begründe. Selbst die Anordnung der Arten in der Gattung würde ich nach der allgemeinen Verwandtschaft, ohne Rücksicht auf die Sporenzahl vornehmen, was freilich schwieriger ist und eine genaue Kenntniss der betreffenden Formen voraussetzt.

Das Merkmal der sporae appendiculatae vel caudatae scheint mir jedoch bei den Sordarien gewichtiger, als bei manchen anderen Sphaeriaceen, weil mit demselben fast immer eine Summe anderer Eigenthümlichkeiten verbunden ist. Auch das Vorhandensein des Stromas kann als charakteristisch gelten. In Bezug auf die Bezeichnung der Gattungen möchte ich jedoch an Fries anknüpfen. Von den drei als Coprolepa ausgeschiedenen Arten hat nämlich schon Fries (in der Summa veg. p. 397) S. merdaria und fimeti im Subgenus Hypocopra genannt, die dritte war ihm nicht bekannt. Frägt man sich, warum diese Gattung nun Coprolepa heissen und warum Hypocopra auf eine andere Gruppe übertragen werden soll, so findet man keinen anderen Grund, als den Irrthum Fuckel's, welcher die stromalose S. fimicola Rob. für S. fimeti Pers. hielt und darnach den Namen Hypocopra auf die stromalosen Arten übertrug. Da wir aber namentlich durch Winter in dieser Hinsicht volle Klarheit haben, so ist nicht einzusehen, warum die Bezeichnung Hypocopra nicht im Sinne von Fries für die stromatici restituirt werden sollte. Der disponibel werdende Name Copro-

lepa könnte jedoch immerhin auf jene stromaführenden Arten angewendet werden, deren Sporen mit Anhängsel versehen sind. Eine solche ist nämlich die von Oudemans (Hedwigia 1882, 11) beschriebene Coprolepa Saccardoi.

Die übrigen Sordarien mit ungeschwänzten Sporen, für welche hiernach die Bezeichnung Hypocopra selbstverständlich entfällt, vermehrt um die wenigen mehrsporigen Arten aus der Gattung Philocopra, hätten dann den Namen Sordaria zu behalten, während ich für die Arten ohne Stroma, deren Sporen mit Anhängsel versehen sind (Sordaria Sacc. und Philocopra Sacc. zum grösseren Theil), den alten Namen Podospora wieder aufnehmen möchte, welchen Cesati (Hedwigia 1856, 15) für den später als Sordaria fimiseda bezeichneten Pilz gebraucht hat.

Da in der grundlegenden fast allgemein anerkannten Arbeit von Winter die Fuckel'schen Benennungen nur für die Subgenera gebraucht sind, so haben dieselben, ausser bei Saccardo, bisher nicht viele Anwendung gefunden und man darf wohl nicht besorgen, durch die vorgeschlagenen begründeten Aenderungen gegen Gewohntes allzusehr zu verstossen.

Die wichtigeren mir bekannten, oder doch gut beschriebenen Arten würden sich folgendermaassen einreihen:

I. Stromatici.

Hypocopra Fries. Sporae muticae, seu sine appendiculo: merdaria Fries, equorum (Fckl.), fimeti (Pers.) Fries.

Coprolepa Fuckel emend. Sporae appendiculatae: Saccardoi Oudem.

II. Astromatici seu simplices.

Sordaria Ces. et de Not. emend. Sporae sine appendiculo:

a) Glabrae: gigaspora Fuckel, captura Speg., macrospora Aw., Winteri Oudem., Rabenhorstii Nssl., superba de Not., bombardioides Aw., maxima Nssl.; (?) stercoraria (Sow.), fimicola (Rob.) Ces. et de Not., humana (Fuckel) Aw., fermenti (Fckl.) Aw., aviaria Karst. (die letzteren 3 vielleicht zu fimicola gehörig), argentina Speg., papyricola Wint., phyllogena (Sacc.), minima Sacc. et Speg.

b) Villosae vel Pilosae: vesticola (Berkl. et Br.), Rotula (Cooke), vagans de Not. (Alle 3 nur ungenau bekannt.)

c) Setosae: scatigena (Berkl. et Br.) (hierher gehört der Beschreibung nach wahrscheinlich auch S. platyspora Plowr., sowie die Variet. major Wint. von S. discospora Awld.), discospora Awld., microspora Plowr., Hanseni Oudem. Omnes sporis discoideis, barbata Hans. sporis ovoideis.

Podospora Ces. em. Sporae appendiculatae.

a) Glabrae: neglecta (Hans.), communis (Speg.), dubia (Hans.), micrura (Speg.), erecta (Speg.), carbonaria (Plowr.), (?) multifera (B. et Rav.), (?) myriospora (Cr.). Bei genauerer Kenntniss werden wohl einige dieser Arten in die folgenden Gruppen kommen. Unter Sordaria sind die kahlen Perithecien häufiger, bei Podospora die bekleideten.

b) Villosae vel Pilosae: fimiseda (Ces. et de Not.), Winteri (Karst.), californica (Plowr.), hirta (Hans.), appendiculata Nssl., insignis (Hans.), decipiens (Wint.), pleiospora (Wint.), zygospora (Speg.), similis (Hans.), coprophila (Fries.), lignicola (Fuckel), natalitia (Speg.), australis (Speg.), dann die Gruppe: Arnium: lanuginosa (Preuss.), tomentosa (Speg.), caudata (Curr.), culmigena (Sacc. et Spegaz.), leucotricha (Speg.).

c) Setosae: curvula (de By.), minuta (Fckl.), platensis (Speg.), valsoides (Peck.), squamulosa (Cr.), anserina (Rabh.), curvicolla (Wint.), setosa (Wint.). — S. squamulosa Crouan ist sehr ungenau bekannt und könnte auch zu curvula gehören. Dies gilt habituell auch von valsoides, nur die Sporen werden etwas grösser angegeben (curvula 29×15, valsoides 27—33, ohne Breitenangabe).

Schliesslich möchte ich noch bemerken, dass ich die Sordarieae als eine natürliche Sippe betrachte, zu welcher nothwendig auch Delitschia und Sporormia gehören, und dass ich nicht beabsichtige, die Gattungen mit Stroma davon zu trennen, da die Affinität der übrigen Merkmale mir wesentlicher erscheint, als das Vorhandensein des Stromas.

Brünn, September 1883. Niessl.

Repertorium.

Saccardo, P. A. Sylloge Fungorum omnium hucusque cognitorum. Vol. II. (Patavii 1883.)

Es gereicht uns zu grossem Vergnügen, den zweiten Band dieses hochwichtigen Werkes anzeigen zu können. Die Bearbeitung eines derartigen zusammenfassenden Handbuches der systematischen Mycologie war unbedingt nothwendig, wenn anders diese Wissenschaft nicht ein Chaos werden sollte — wozu sie bereits auf dem besten Wege ist. Dass bei einem Werke von dem Umfange des vorliegenden eine kritische Sichtung des ungeheuren Materials von vornherein nicht oder nur in sehr beschränktem Maasse Platz greifen konnte, ist eigentlich selbstverständlich und

Description *Podospora anserina*

in

Winter, G. (1887). CLXI. Podospora. Dr. L. Rabenhorst's Kyrogamen-Flora von Deutschland, Oesterreich und der Schweiz Zweite auflage. 1: 169-177

schwarz, 600—650 μ hoch, ca. 500 μ dick. Schläuche ziemlich weit cylindrisch, sehr lang gestielt, nach oben verjüngt, unter der Spitze mit rundlichem, glänzenden Körper, 8sporig, 152 μ lang (pars sporif.), 14 μ dick. Sporen eiförmig, am Grunde gestutzt und mit cylindrischem, farblosen, gekrümmten Anhängsel versehen, an dessen Ende, ebenso wie am oberen Pole der Spore ein weiteres, gelatinöses, stachelförmiges, hyalines Anhängsel inserirt ist; Sporen reif braun, 15 μ lang, 8—10 μ dick. Paraphysen sehr zart, fadenförmig.

Auf faulendem Buchenholz. (Rheingau).

2988. **P. decipiens** (Winter).

Synon.: Sordaria decipiens Winter (deutsche Sord. pag. 28).
Sordaria lancisperma Fckl. (in litt.).

Perithecien halb eingesenkt, später oberflächlich, einem sehr zarten, spinnwebartigen, grauschwarzen Filz innesitzend und von ihm bekleidet, kugelig-kegelförmig, in einen cylindrischen, gekrümmten, kahlen, tiefschwarzen (150—160 μ langen) Hals verjüngt, durchscheinend grauschwarz, 400—450 μ im Durchmesser. Schläuche weit, beidendig verjüngt, kurz gestielt, mit verdickter Scheitel-Membran, 8sporig, ca. 210 μ lang, 40—50 μ dick. Paraphysen röhrig, gegliedert. Sporen ordnungslos zusammengehäuft, elliptisch, schwarz, am Grunde mit der Spore ungefähr gleichlangem, cylindrischen, hyalinen Anhängsel mit Cellulosemembran, am Scheitel von einer verschieden geformten, gelatinösen Masse gekrönt, 36—48 μ lang, 19—22 μ dick.

Auf Pferde-, Kuh- und Gänsemist, verbreitet.

2989. **P. anserina** (Rabh.).

Synon.: Malinvernia anserina Rabh. (in Herb. myc. No. 526).
Hypocopra anserina Cés. (in litt.).
Sordaria anserina Winter (Deutsche Sordarien pag. 35).
Exsicc.: Fuckel, Fungi rhenan. 1585, Rabh., Herb. myc. 526.

Perithecien dicht heerdenweise, halb eingesenkt, aus fast eiförmiger oder kugliger Basis kegelförmig, in einen langen, dicken, oft gekrümmten Hals verjüngt, der unter der Spitze, auf seiner convexen Seite mit dicht büscheligen, sehr langen, steifen, braunen Borsten besetzt ist, während die Perithecien mit spärlichem, zarten Hyphengeflecht bekleidet, runzelig, schwarzbraun gefärbt sind. Asci cylindrisch, nach oben verschmälert, am Ende abgerundet, sehr lang gestielt, 2—4sporig, 110—125 μ lang, 20—22 μ dick. Paraphysen

fädig, verästelt, gelatinös. Sporen einreihig, elliptisch, braun, am Grunde mit cylindrischem, geraden, hyalinen Anhängsel, 33—42 μ lang, 19—21 μ dick.

Auf Gänsekoth, seltener auf Mist anderer Thiere.

2990. **P. minuta** (Fuckel).

Synon.: Sordaria minuta Fuckel (Symbol. Nachtr. II. pag. 44).
Sordaria tetraspora Winter (in Hedwigia 1871. pag. 161).
Exsicc.: Rabh., Fungi europ. 1529, Rehm, Ascom. 199.

Perithecien zerstreut, oberflächlich, länglich-ei- oder kegelförmig, mit verjüngtem, abgerundeten oder stumpfen Scheitel, durchscheinend licht-braun, mit dunklerer Mündung, runzelig und mit zerstreuten, oberwärts dichter stehenden, kurzen, gegliederten Härchen besetzt, ca. 400 μ hoch, 220 μ dick. Asci cylindrisch, lang gestielt, nach oben verjüngt, am Scheitel verdickt, 4- oder 8sporig, 80—110 μ lang (pars sporif.), 14 μ dick. Paraphysen fadenförmig. Sporen schräg einreihig, elliptisch, braun, am oberen Pole mit einem gallertartigen, verschieden geformten, hyalinen, bald verschwindenden Anhängsel, am Grunde mit persistirendem, cylindrischen, farblosen Anhängsel, 16—22 μ lang, 10 μ dick.

Auf faulendem Koth, besonders kleinerer Thiere (Mäuse, Kaninchen etc.), doch auch auf Pferdemist.

2991. **P. curvula** (de By.).

Synon.: Sordaria curvula de By. (Morphol. und Physiol. der Pilze I. Aufl. pag. 209).
? Schizothecium fimicolum Cda. (Icones II. pag. 29).
Sphaeria fimiseda Fuckel (Fungi rhenani 2037).
Cercophora conica Fuckel (Symbolae pag. 245).
Ixodiopsis fimicola Karst. (Fungi fennici 955).
Exsicc.: Fuckel, Fungi rhenan. 2037, Kunze, Fungi selecti 102, Rehm, Ascom. 138, 200, Thümen, Fungi austr. 1152.

Perithecien zerstreut, oberflächlich oder halb eingesenkt, länglich-kegelförmig, oft gekrümmt, schwach runzelig, mit dicken, gegliederten, meist büschelweis verbundenen, gleichsam verklebten Haaren dicht bekleidet, schwarzbraun, rings um die Mündung dunkler, 750—800 μ hoch, 350—400 μ dick. Asci weit cylindrisch, lang gestielt, 8sporig, mit am Scheitel verdickter Membran, 130 μ lang, (pars sporif.), 38 μ dick. Paraphysen röhrig, gegliedert. Sporen elliptisch, schwarzbraun, an der Spitze mit verschieden gestaltetem (bald grossem, dick hakenförmigen, bald dünner cylindrischem, bald endlich kleinem, spitzenförmigen) Anhängsel von gallertartiger Consistenz, am

Description of *Sordaria penicillata*

in

Ellis, J. B. and B. M. Everhart (1892). Sordaria penicillàta (E &E). North american pyrenomycetes: 131

70 μ, mostly 8-spored. Sporidia mostly biseriate, elliptical, 50–60 x 28–30 μ, dark brown, with a long, cylindrical, often curved appendage of cellulose membranaceous structure below, and at the end of this appendage, and also at the apex of the sporidium, with a gelatinous appendage of various form. Paraphyses filiform, septate, longer than the asci.

On cow dung, New York State (Peck).

Pod. striàta, (E. & E.)

Sordaria striata, E. & E. Journ. Mycol. IV, p. 79.

Gregarious. Perithecia ovate-conical, $\frac{2}{3}$ mm. high and $\frac{1}{2}$ mm. broad, black, tubercular-roughened, the tubercles seriate above so as to cause the conical ostiola to appear striate. The tubercles are at first capped with a few light colored granules, like grains of white sugar, but these at length disappear. Asci linear-lanceolate, contracted towards each end and perforated above, 200 μ long and over, (including the filiform base) and 12–15 μ wide, with abundant paraphyses. Sporidia biseriate, elliptical, brown, 14–16 x 8–10 μ, the upper end acute or with a short hyaline appendage 8–12 μ long, the lower end prolonged into a yellowish-hyaline, cylindrical, curved appendage 35–40 x 5 μ.

On decaying stems of some large weed, St. Martinsville, La. (Langlois).

Pod. penicillàta, (E. & E.)

Sordaria penicillata, E. & E. Journ. Mycol. IV, p. 78.

Perithecia gregarious, ovate, $\frac{1}{3}$–$\frac{1}{2}$ mm. diam., at first entirely buried except the protruding ostiolum, at length with the upper half emergent; ostiolum short-cylindrical or obtusely conical and surrounded by a tuft of straight, erect, closely crowded, pale brown, continuous hairs $\frac{1}{3}$–$\frac{1}{2}$ mm. long. Asci oblong-cylindrical, about 150 x 20–25 μ, 4-spored, with indistinct paraphyses. Sporidia subhyaline and clavate-cylindrical at first, then olivaceous with a single large nucleus, finally elliptical and opake, 25–30 x 18–20 μ, with a cylindrical, nearly straight, hyaline appendage 12–15 x 4–5 μ at the lower end, and the upper end obtusely pointed or subtruncate.

On an old decaying Chinese mat., St. Martinsville, La. (Langlois).

The measurements of the perithecia given in Journ. Mycol. for this and *Philocopra lutea* were too small.

Description of *Sordaria penicillata*

in

Ellis, J. B. and B. M. Everhart (1888). "New Species of Fungi from Various Localities (Continued)." The Journal of Mycology 4(8): 73-82

about 60 x 10 micr., with imperfectly developed paraphyses. Sporidia crowded biseriate, clavate-oblong or fusoid-oblong, slightly curved, yellowish-hyaline, 2—3—nucleate, 14—16 x 3½—4. Differs from Botryosphæria minor on the same stems in its solitary perithecia and narrow sporidia.

THYRIDARIA EUTYPOIDES, E. & E.—On bark of decaying Melia. Louisiana, July, 1888. Langlois, No. 1377. Perithecia minute (110—120 micr. diam.), immersed, scattered quite uniformly through the blackened and subcarbonized substance of the bark but lying mostly near the surface and here and there collected in valsiform groups. Ostiola short cylindrical with a round opening at the subtruncate and slightly swollen apex and so numerous as to appear under the lens like a fine black pubescence. Asci (p. sp.) about 35 x 7 micr. or with the short stipe like base 40—45 micr. long, surrounded with abundant filiform paraphyses. Sporidia biseriate, oblong or clavate-oblong, 3-septate and slightly constricted at the septa, olive-brown, slightly curved, ends subobtuse, 10—12 x 2½—3. On the same specimens was a Valsa of the section Eutypella, agreeing well with the description of *Eutypella paradisaica*, Speg.

CERATOSPHÆRIA MICRODOMA, E. & E.—On bark of decaying (Sambucus) ? St. Martinsville, La., June 1888. Langlois No. 1310. Perithecia barely covered by the bark, densely gregarious, minute, not over one-sixth mm. in diam., ostiola projecting, cylindrical, 1-3 mm. long, rough and more or less overrun with a brown tomentum (which however may be only accidental). Asci oblong-cylindrical or clav-cylind. 50—55 x 7—8 subsessile with rather stout filiform paraphyses. Sporidia biseriate or crowded, oblong or clavate-oblong 3-septate and slightly constricted at the septa, olive-brown 11—12 x 2½—3.

SORDARIA PENCILLATA, E. & E.—On an old decaying Chinese mat. St. Martinsville, La., July 1888. Langlois No. 1449. Perithecia gregarious, ovate, ¼—1-3 mm. diam., at first entirely buried except the protruding ostiolum, at length with upper half emergent, ostiolum short-cylindrical or obtusely-conical and surrounded by a tuft of straight, erect, closely crowded pale brown continuous hairs 1-3—½ mm. long. Asci oblong cylindrical about 150 x 20—25, 4-spored, with indistinct paraphyses. Sporidia subhyaline and clavate-cylindrical at first, then olivaceous with a single large nucleus, finally elliptical and opake, 25—30 x 18—20, with a cylindrical, nearly straight, hyaline appendage 12—15 x 4—5 at the lower end and the upper end obtusely pointed or subtruncate.

Description of the genus *Pleurage*

in

Kuntze, o. (1898). *Pleurage*. *Revisio generum plantarum*. 3(2): 504-505

= ( ), bezw. älteren Synonymen in [ ] nach Saccardo Sylloge, bez. Hennings in Engler's Pfl.-Fam. l. c. übertragen und betreffen die Section (resp. Genus?) *Gymnochilus* mit Lamellen, die vom Stiele nicht getrennt sind: Pilosace (Gymnochilus) aequatorius [Mont.](*Ps.* Sacc.; *Pr.* Henn.), ascevus [Berk. & Br.](Sacc.), Barlae (Bres.), bifrons [Berk.](Sacc.), bipellis (Quél.; Henn.), bulbillosus [Fries](Henn.), calvescens [Berk.](Sacc.), commiscibilis [Berk.] (Sacc.; Henn.), conopilus [Fries](Sacc.), corrugis [Pers.](Sacc.), cubisporus [Mont.](Henn.), efflorescens [Berk. & Br.](Sacc.), epibates [Fries](Sacc., Henn.), exsignatus (Britz.), fagicola [Lasch](Sacc.; Henn.), Falkii [Weinm.](Sacc.; Henn.), fatuus [Fries](Sacc.), fibrillosus [Pers.](Sacc.), frustulentus [Fries] (Sacc.), fusconiveus [Berk. & C.](Sacc.), gastrodes [Mont.](Sacc.; Henn.), glareosus [Berk. & Br.](Sacc. „*gloreosa*" Henn.), Gordonii [Berk. & Br.](Sacc.), gossypinus [Bull.](Sacc.), griseobadius (Pat.), helobius (Kalchbr.), laurinus (Quél.), Loscosii [Rabh.](Sacc.), lucipetus [Berk. & Br.](Sacc.; Henn.), mastiger [Berk. & Br.](Sacc.), microrhizus [Lasch](Sacc.), Nassa [Berk.], neglectus (Massee), Noli-tangere [Fries](Sacc.), ocreatus [Berk. & Br.](Sacc.; Henn.), oenochrous [Mont.](Sacc.), ombrophilus (P.A.Karst.), pallens (P.A.Karst.), pennatus [Fries](Sacc.), persimplex (Britz.), pholidotus [Mont.](Sacc.; Henn.), plumiger [Berk. & C.](Sacc.), polytrichophilus [Peck](Sacc.; Henn.), porphyrellus [Berk. & Br.](Sacc.), pseudo-tenerus [Fries](Sacc.; Henn.), Schulzeri [Quél.](Henn.), semivestitus [Berk. & Br.](Sacc.), silvaticus [Peck](Sacc.), solitarius (P.A.Karst.), sonderianus [Berk.](Sacc.; Henn.), spadiceogriseus [Schaeff.](Sacc.; Henn.), spadiceus [Schaeff.](Schroet.), squamosus (P.A.Karst.), stenophyllus [Mont.](Sacc.; Henn.), strictus [Trog.](Sacc; Henn.); subliquescens [Schum.](Sacc.; Henn.), subnudus [P.A.Karst.](Sacc.; „*subunda*" Henn.), subobtusus (Britz.), subvinosus [Berk.](Sacc.), supernulus (Britz.), tenuiculus [P.A.Karst.] („*tamicula*" Henn.), torpens [Fries](Sacc.; Henn.), Typhae [Kalchb.](Sacc.; Henn.), tythus [Berk. & Br.](Sacc.), urticicola [Berk. & Br.] (Sacc.)OK.

Pinuzza = Solenia Hill.

Piptostoma Sacc. „Berk. & Br." = **Neopiptostoma.**

Pisomyxa = Bryocladium.

Plectania = Scutellinia.

Pleochaete = Uncinula.

Pleurage Fries 1849 Summ. veg. Scand. II 418 in adnot. pro *Schizothecio* Corda 1838 (non Schizotheca Ehrb. 1832!) propositum = *Podospora* Rabh. 1852, Ces. (non *Podosporium* Schweinitz 1832) = *Malinvernia* Rabh. 1856 = *Sordaria* Ces. & De Not. 1861 = *Cercophora, Hypocopra* Fuck. ± 1870 (non § Fries 1849) = *Arnium* Nitschke = *Philocopra* Speg. 1880. Für *Sordaria* in der weiteren Fassung von Schroeter & Lindau in Engler's Pfl.-Fam. existiren 3 ältere Namen, von denen Dr. Lindau aber den ältestgiltigen Pleurage übersehen hat. *Schizothecium* wäre zwar noch älter, kann aber, ebenso wie *Podosporia* wegen älterer Homonyme, die sich nur durch *-a: -ium* unterscheiden, nicht erneuert werden. Es ist *Schizothecium fimicolum* Corda 1838 ic. II 29 t. 13 fig. 105 = *Podospora fimicola* Ces. = *Sordaria fimiseda* Ces. & De Not. = Pleurage fimicola OK.; während *Hypocopra fimicola* Sacc. = *Sordaria fimicola* Ces. & De Not. = *Sphaeria fimicola* Rob. 1849 = Pleurage Robinii OK. genannt sei. *Malinvernia* mit dem Typus *M. anserina* Rabh. (Pers.) = *Sordaria ans.* Wint. = *Hypocopra ans.* Sacc. „Ces." wird Pleurage anserina OK.

Die anderen Arten sind nach Saccardo Sylloge übertragen, wobei Autorcitate in ( ) ohne sonstige Angabe für *Sordaria* gelten, [ ] ältere Synonyme andeutet, ferner *H.* = *Hypocopra* und *Ph.* = *Philocopra* bedeutet. Vorher sind noch Artennamen zu ändern: *Sordaria lanuginosa* Sacc.(Preuss 1853) = *Sphaeria Brassicae* Kl. 1836 = Pleurage Brassicae OK. *Hypocopra* & *Sordaria Winteri* Oud. 1882 non *Sordaria Winteri* P.A.Kasten ± 1875 = Pleurage Cameli OK. Pleurage amphicornis (Ellis), appendiculata (Niessl), argentina (Speg.; *H.* Sacc.), australis [*H.* Speg.](Sacc.), austro-americana [*H.* Speg.](Sacc.), aviaria (*H.* Karst.), barbata (Hansen; *H.* Sacc.), Bolbitonii [Quélet; *H.* Sacc.], bombardiodes (Awd.; Sacc. I No. 847 = 881), californica (Plowr.), canina [Peck](*Ph.* Sacc.), capturae (Speg.; *H.* Sacc.), carbonaria [Plowr.](Sacc.), caudata [Currey](Sacc.), Cirsii (Crouan), clavata (Pat.), communis [*H.* Speg.](Sacc.), coprophila [Fries](Ces. & De Not.), culmigena (Sacc. & Speg.), curvicolla (Wint.; *Ph.* Sacc.), curvula (De Bary), Darwinii (*H.* Speg.), decipiens (Wint.), discospora (Awd.; *H.* Fckl.), dubia (Hansen; *Ph.* Sacc.), dunarum (*H.* Mont.), elephantina (P.Henn.), equina [Fries] (*H.* Sacc.), erecta [*H.* Speg.](Sacc.), fermenti (*H.* Fckl.), gigaspora [Fckl.; *H.* Sacc.], gregaria (Otth), grisea (Cesati), Hansenii (*Ph.* Otth), hippica (*H.* Sacc.), hirta (Hansen), hypocoprodes (Speg.), humana (*H.* Fckl.), insignis (Hansen; *H.* Sacc.), jowana (*H.* Ellis & Holw.), leucoplaca [Berk. & Rav.] (*H.* Sacc.), leucotricha (Speg.), lignicola (Fckl.), lojkaeana (Rehm), lutea (Ellis & Ev.), macrospora (Awd.; *H.* Sacc.), macrotheca [Crouan] (*H.* Sacc.), maxima (Niessl; *H.* Sacc.], microspora (Plowr.; *H.* Sacc.), micrura [*H.* Speg.](Sacc.), minima (Sacc. & Speg.; *H.* Sacc.), minuta (Fckl.), multifera [Berk. & Rav.](*Ph.* Sacc.), myriospora (Crouan; *Ph.* Sacc.), natalitia [*H.* Speg.](Sacc.), neglecta (Hansen), ornithophila (*H.* Speg.), papyricola (Wint.; *H.* Sacc.), parvicaudata (*H.* Speg.), patagonica (*H.* Speg.), penicillata (Ellis & Ev.), pilosa (Mouton), pilosella (*H.* Speg.), platyspora (Plowr.; *H.* Sacc.), platensis (*Ph.* Speg.), pleiospora (Wint.; *Ph.* Sacc.), polyspora (Phill. & Plowr.; *Ph.* Sacc.), pruinicola (Otth), Pseudominuta (Speg.), punctiformis (Ces.; *H.* Sacc.), pusilla (*Ph.* Mouton), Rabenhorstii (Niessl; *H.* Sacc.), Saccardoi (*H.* March.), sarawacensis (Cesati), scatigena [Berk. & Broome](*H.* Sacc.), serignanensis (*H.* H. Fabre), setosa (Wint.; *Ph.* Sacc.), similis (Hansen; *Ph.* Sacc.), sparganicola (Phill. & Plowr.), sphaerospora (Ellis & Ev.; *H.* Sacc.), squamulosa (Crouan), stercoraria [Sow.] (*H.* Sacc.), striata (Ellis & Ev.), superba (De Not.; *H.* Sacc.), tomentosa [*H.* Speg.](Sacc.), vagans (De Not.; *H.* Sacc.), valsodes [Peck](Sacc.), vesticola [Berk. & Broome] (*H.* Sacc.) Wiesneri (Zukal), Winteri (P.A.Karst.), zygospora (Speg.; *Ph.* Sacc.)OK.

Pleuroceras Riess 1854 Hedwigia I 25 tab. VI Fig. 5 & in Rabh. herb. viv. myc. No. 1822 = *Cryptoderis* Awd. post 1860. Es ist *Pleuroceras ciliatum* Riess = *Sphaeria cryptoderis* Lév. 1848 = *Sph. lamprotheca* Desm. 1851 = *Cryptoderis lamprotheca* Awd. = Pleuroceras cryptoderis OK. Die anderen Arten sind nach Saccardo Syll. von *Cryptoderis* = ( ) übertragen: Pleuroceras Chaemaemori [Fries](Sacc.), melanostyla [DC.](Wint.; *Gnomoniella* Sacc.), misella [Niessl](Sacc.), oligotheca (Starb. & Grev.), pleurostyla [*Gnomonia* Awd.](Wint.), riparia [Niessl](Sacc.)OK.

Pleurotus = Dendrosarcus.

Pocillaria P.Br. 1756 (cfr. Rev. gen. II: 865 = *Lentinus* Fries 1825) incl. *Panus* Fries 1838. P. Hennings in Engler's Pfl.-Fam. I**: 222—226 vereinigt Panus mit Lentinus, verschweigt aber unwissenschaftlich

Description of *Sordaria communis*

in

Spegazzini, C. (1899). "Fungí argentini novi v. critici." Anales del Museo Nacional de Historia Natural de Buenos Aires Ser. 2 6: 289-365

et praecitatis simillima vix peritheciorum forma atque natura recedens; an ejusdem varietas tantum?.

547. **Sordaria cirrifera** Speg. (n. sp.).

Diag. Bicaudata subglabra; perithecia immersa globulosa mediocria; asci tetra-v. octo-spori aparaphysati: sporae ellipsoideae majusculae utrimque caudis cirrosis auctae.

Hab. In fimo vaccino putrescente prope La Plata. Maj. 1888.

Obs. Perithecia sparsa v. hinc inde laxe gregaria matrice immersa globosa glabra vix basi hyphis nonnullis repentibus ornata, sursum breviter papillato-umbonata ostiolo subcarbonaceo atro coronata, membranacea contextu parenchymatico olivaceo; asci subfusoideo-clavulati (prt. sprf. 200 μ long. = 40–50 μ crass.) antice attenuati postice modice cuneato-pedicellati aparaphysati, quandoque octospori quandoque (in eodem perithecio) tetraspori; sporae monostichae v. distichae ellipsoideae utrimque subacutiuscule rotundatae (42–55 μ long. = 20–28 μ diam.) rarius subbiconicae v. sublimoniformes (60 μ long. = 10 μ diam.) opace fuligineae utrimque caudatae, caudis hyalinis crassis in juventute spora conspicue brevioribus, supera brevi bis spiraliter torta, infera subconoidea v. inflexa, per aetatem exappendiculatae.

548. **Sordaria communis** (Speg.) Sacc.—Sacc., l. c., 1. f. 231.

Hab. In fimo vaccino et equino prope La Plata, per ann. 1893–96.

Obs. Species vulgata peritheciis plus minusve fimo immersis glabris v. vix basi hyphis nonnullis perpaucis cinctis membranaceis, ostiolo mammillato plus minusve exerto subcarbonaceo donatis; formae magis conspicuae sequentes:

a/ tetraspora; perithecia immersa majora (250–250 μ diam.) glabra; asci tetraspori fusoideo-cylindracei (900 μ long. = 20–24 μ crass.) paraphysibus articulatis simplicibus v. ramosis paucis obvallati; sporae ellipsoideae (34–38 μ long. = 18–20 μ diam.) monostichae opace fuligineae utrimque subacutiuscule rotundatae, cauda supera inflexa v. erecto-subuncinata subtorulosa (20–35 μ long. = 4 μ cras.) mox diffluente, infera cylindracea recta (20–30 μ long. = 4–5 μ crass.) apicem versus attenuata subacutiuscula persistente.

b/ brachyura; perithecia immersa majora (250–300 μ diam.) basi saepius hyphis paucis divaricatis ornata; asci subclavulati (prt. sprf. 120–140 μ long. = 40 μ crass. = ped. 50–60 μ long.) aparaphysati octospori; sporae ellipsoideae (28–34 μ long. =

Description of *Pleurage anserina*

in

Griffiths, D. (1901). North american *Sordariaceae*. Memoirs of the Torrey Botanical Club. 11: 59-61, 127 - Pl. 125, Fig. 124-126.5

Emma, Mo., Aug. 1899 (Demeterio); cow, rabbit, and burro dung, Tucson, Ariz., Jan. 1900 (Tyler); horse, cow, dog, and rabbit dung, Austin, Texas, Jan. 1900 (Long); cow, sheep, and horse dung, Brookings, S. D., Nov. 1899 (Carter); rabbit and horse dung, Biloxi, Miss., Sept. 1899 (Tracy); horse, cow, and rabbit dung, Auburn, Ala., Aug. 1899 (Earle); cow dung, Kingston, R. I., Nov. 1899 (Underwood); horse and cow dung, Tucson, Ariz., Sept. 1900.

This is a common and distinctive species which in some respects closely resembles *P. hirta* Hansen and *P. australis* Speg. It may be distinguished from the former by somewhat larger spores, hyaline apicula and longer convoluted gelatinous appendages, and from the latter by having the spores in one series and by the apicula.

The principal variation observed in the comparison of specimens from different localities, pertains to the hairiness of the perithecia and the characteristics of the gelatinous appendages. The Texas specimens had almost smooth perithecia, and those on horse dung were completely sunken with only the beak projecting. In all other respects the specimens did not differ from the others. The convolutions of the gelatinous appendages are not always visible, owing to the immaturity of the spores. The best way to distinguish them is to examine the specimens at the time that the spores are being erupted from the asci. As the asci enlarge the appendages enlarge also, and the cross striations become more readily seen. They can, however, be distinguished in a nearly mature ascus before enlargement begins.

4. PLEURAGE ANSERINA (Rabh.) Kuntze, Rev. Gen. Plant. **3**[3]: 504. 1898

Malinvernia anserina Rabenh. Herb. Mycol. no. 526.* Hedwigia, **1**: 116. *pl. 15. fig. 4.* 1857.

Sordaria anserina (Rabenh.) Wint. Abhand. naturforsch. Gesell. zu Halle, **13**: 100. *pl. 11. f. 20.* 1873. Zeitschrift gesammt. Naturwissen. (Halle), **56**: 541. 1883. Saccardo, Syll. Fung. **1**: 238. 1882. Natur. For. i Kjoben. Vidensk. Middel. for Aarene, 321, 353. *pl. 8. f. 21.* 1876.

Sordaria penicillata E. & E. Jour. Mycol., **4**: 78 (by error 66). 1888.

* Specimen not seen.

Podospora penicillata (E. & E.) E. & E. N. Am. Pyren. 131. 1892.

Podospora anserina (Rabenh.) Rehm; Rabenhorst Kryptogamen-Flora, I^2: 173. 1887.

Perithecia usually half sunken but often entirely superficial, scattered uniformly or aggregated in clusters of 2 to 6, 300–350 μ × 400–500 μ, pyriform, black above and greenish below, thin and membranaceous but not transparent; beak papillifom or slightly cylindrical, usually curved and bearing several tufts of long dark brown very sparingly septate hairs on the convex surface.

Asci 4-spored, cylindrical, slightly contracted and rounded above, and contracted below into a long slender crooked stipe, quite persistent, 17–22 μ × 200–400 μ: paraphyses filiform or slightly ventricose below, decreasing in diameter upward, 1½–2 times the length of the ascus.

Spores uniseriate, elliptical, ranging from hyaline when young through olivaceous to dark brown and opaque, 18–20 μ × 34–42 μ, terminated below by a short hyaline primary appendage 1–1½ times the length of spore, this as well as the apex of the spore is terminated by a long lash-like gelatinous appendage of variable length, which by proper illumination can be resolved into two closely united strands which gradually merge into one another distally. (*Pl. 5, f. 4–6.*)

Distinctive characters: Dorsal tufts of long hairs and 4-spored ascus.

Dried specimens: On old pasteboard, Newfield, N. J., Aug. 1894 (Ellis); Chinese mats, St. Martinville, La., July, 1888 (Langlois); sheep dung, Lafayette, Ind., Feb. 1896 (Arthur).

Cultivated specimens: On cow and horse dung, Englewood, N. J., Sept. 1899; cow dung, Ft. Lee, N. J., July, 1899; horse dung, New York City, Aug. 1899; cow and horse dung, Aberdeen, S. D., Sept. 1899 (Towne); horse dung, Highmore, S. D., July, 1899 (Carter); cow dung, Doland, S. D., July, 1899 (Carter); horse, cow and sheep dung, Brookings, S. D., Nov. 1899 (Carter); rabbit dung, Mesilla Park, N. M., Jan. 1900 (Wooton); rabbit, dog, sheep and cow dung, Tucson, Ariz., Jan. 1900 (Tyler); horse dung, Emma, Mo., Sept. 1899 (Demetrio); cow dung, De Soto, La., Aug. 1899 (Frierson); cow dung, London, Canada, Aug. 1899 (Dearness); cow dung, Newfield, N. J., Aug. 1899 (Ellis); dog, horse, and cow dung, Austin, Tex., Jan. 1900 (Long); horse dung, Gunnison, Colo., Aug. 1899 (Bartholomew); horse

and cow dung, Proctor, Vt., Aug. 1899 (Banker); cow dung, Rooks Co., Kan., July, 1899 (Bartholomew).

Although this species is described in our literature with simple gelatinous appendages, there is no question but the European as well as the American forms have these appendages double. This feature is not always easy to determine in dried specimens but it can always be readily determined in fresh material when the spores are first released from the asci. All of the Italian * exsiccati at hand show unmistakable evidences of this characteristic even in the dry state. The hairiness of the beak of the perithecium is a characteristic of considerable variation. Some of the Missouri and Highmore, S. D., specimens show only a very few, short, scattered hairs, while others from other localities show all gradations between these forms and the typical ones. Careful examination of New York material has revealed the fact that these hairs are rather later in their development than similar structures in other species. Often one may find perithecia containing spores which are apparently mature with only very young imperfectly formed hairs on them. Later these develop into the normal condition. It would appear that the maturity of the spores can not be determined by the arbitrary characteristic of coloration, for they are not ejected from the ascus in this species until the external ornamentation of the perithecium has become mature. In other species, on the contrary, the spores are discharged as soon as they assume the brown coloration, and the asci will stretch in water even while the spores are greenish in color.

The mycelium of this species develops very rapidly in all directions from the germinating spores. In several cultures the perithecia developed on paper at a distance of 2–6.5 cm. from the substratum containing the spores. Indeed, in nearly every culture made, the perithecia developed on the paper which was placed under the dung, to a greater or less extent. The species appears to be suited to a paper medium as well as the *Chaetomiaceae* or *Sordaria fimicola*. As shown above, the species has often been collected on paper and similar substrata in nature.

* Saccardo, Mycotheca Veneta nos. 1178 and 1179; Cavara, Fungi Longobardiae exsic. no. 226.

PLATE 3

1–3. *Sordaria Montanensis*. 1. Perithecium. 2. Ascus. 3. Spore.

4–8. *Sordaria discospora*. 4. Perithecium. 5. Ascus with uniseriate spores. 6 Ascus with biseriate spores; 5 and 6 are from the same perithecium. 7–8. Different views of spores.

9–15. *Sordaria leucoplaca*. 9. Perithecium on cow dung from Highmore, S. D. 10–12. Perithecia on horse dung from New York City. 13. Asci, one of which shows the aborting spores. 14. Ascus with slightly larger spores from New York City. 15. Three spores.

16–18. *Sordaria humana* on dog dung, New York City. 16. Perithecium. 17. Ascus. 18. Spore.

19–21. *Sordaria fimicola* on dead culms of *Eleocharis* from Aberdeen, S. D. 19 Perithecium. 20. Ascus. 21. Spore.

22–24. *Sordaria humana* on goat dung from New York City. 22. Perithecium. 23. Ascus slightly stretched. 24. Spores.

25–27. *Sordaria minima*. 25. Two perithecia. 26. Ascus. 27. Spore. Ascus and spore not fully mature.

28–30. *Sordaria hyalina* 28. Perithecium. 29. Ascus. 30. Spores.

PLATE 4

1–3. *Pleurage tetraspora*. 1. Perithecium. 2. Ascus. 3. Spore.

4–7. *Sordaria bombardioides*. 4. Perithecium with perfectly diagrammatic substratum to show extent to which it is sunken. 5. Outline of perithecium after removal of outer layer. 6. Ascus. 7. Spore.

8–10. *Sordaria fimicola* drawn from specimens on cow dung in Columbia greenhouse. 8. Perithecium. 9. Ascus. 10. Spore.

11–13. *Pleurage crotrata*. 11. Perithecium. 12. Ascus. 13. Spore.

14–16. *Sordaria humana* on human ordure, Newfield, N. J. (Ellis). 14. Perithecium. 15. Ascus. 16. Spore.

17–19. *Sordaria philocoproides*. 17. Perithecium. 18. Ascus. 19. Spore.

20–21. Germinating spores of *Pleurage curvula*.

PLATE 5

1–3. *Pleurage Ellisiana*. 1. Perithecium. 2. Ascus. 3. Spore.

4–6. *Pleurage anserina*. 4. Perithecium. 5. Ascus. 6. Spore. The gelatinous appendages at base of spore are not often present.

7–9. *Pleurage anomala*. 7. Perithecium. 8. Ascus. 9. Spore.

10–13. *Pleurage albicans*. 10. Perithecium. 11. Ascus. 12. Mature spore. 13. Young spore.

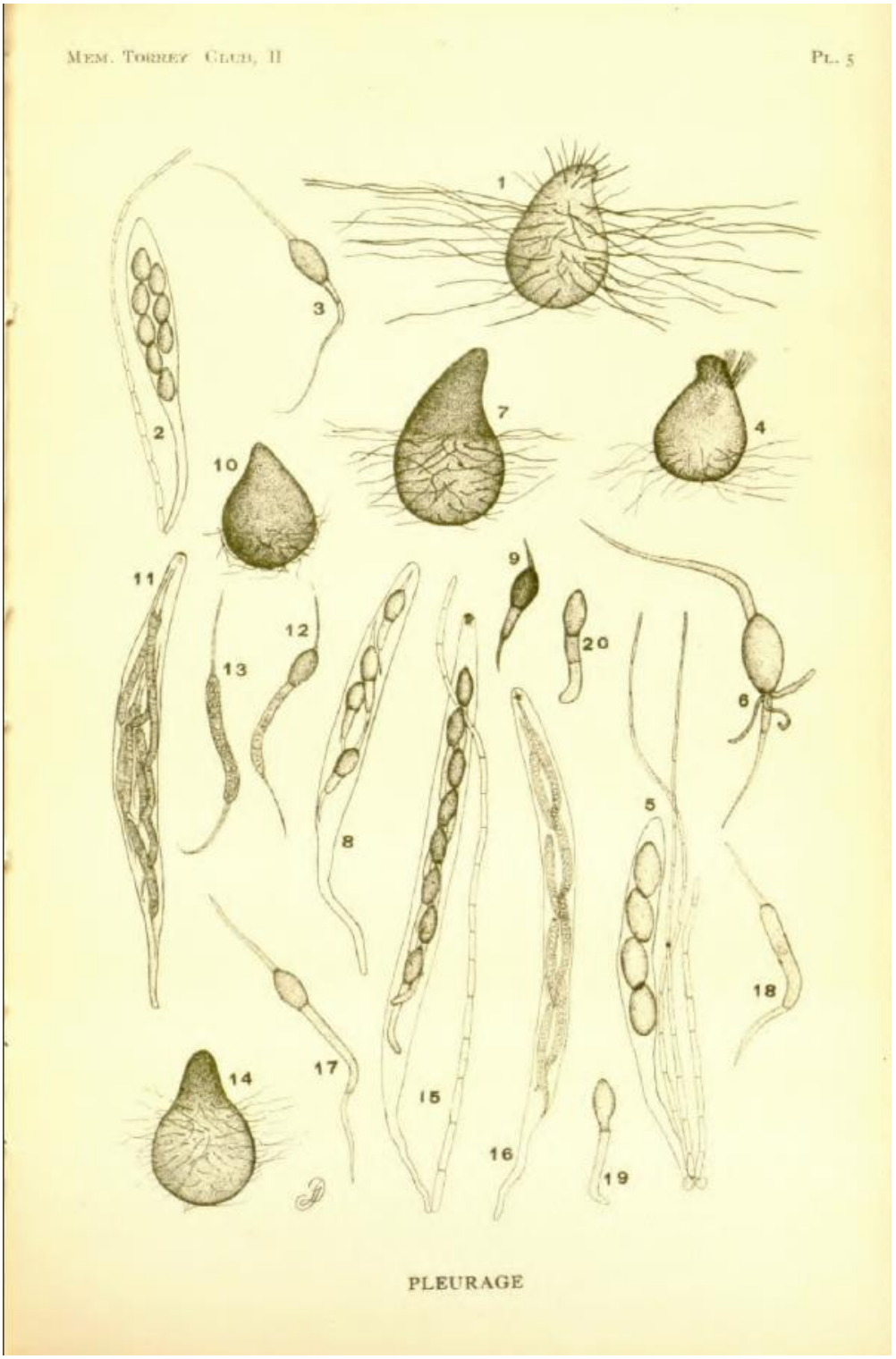
14–20. *Pleurage arachnoidea*. 14. Perithecium. 15. Mature ascus. 16. Young ascus. 17. Spore. 18. Young spore. 19. Spore showing removal of septum downward. 20. Spore showing a septum in the primary appendage.

PLATE 6

1–3. *Pleurage taenioides*. 1. Perithecium. 2. Ascus. 3. Spore.

4–6. *Pleurage Arizonensis*. 4. Perithecium. 5. Ascus. 6. Spore.

7–9. *Pleurage multicaudata*. 7. Perithecium. 8. Ascus. 9. Spore.


MEM. TORREY CLUB, II
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PLEURAGE

Description of *Podospora pauciseta*

in

Traverso, J. B. (1907). Vol. II Fasc. 2: *Pyrenomycetae. Sphaeriaceae: Allantosporae, Hyalosporae, Phaeosporae Flora Italica Cryptogama ParsI: Fungi*. 2(2): Fig. S7.1-3 p425 & pp431-432

moso-attenuatis, atris, tenuiter villosis, cellulis stratosis contextis, in sicco fragilibus; ascis e basi tenuata teretibus, octosporis, juventute apice subcapitellatis, aparaphysatis (?); sporidiis sphaeroideis vel sphaeroideo-ellipsoideis, badio-fuscis, parce translucidis. — Affinis sed satis diversa a *S. macrospora* Auersw.

Hab. in fimo *Leporis variabilis*. — Piemonte, a Riva Valsesia (CARESTIA).

Ar. distr. Italia bor. (Piem.).

Oss. Negli esemplari dell'Erbario De Notaris conservato nel R.° Istituto Botanico di Roma, io ho potuto misurare soltanto delle spore, imperocchè gli aschi erano stati riassorbiti. Tali spore, quasi globose, misuravano 10-12 * 8-10 µ. Siccome però il De Notaris nella diagnosi originale dice che questa specie è affine a *S. macrospora*, a spore molto più grandi, io non posso assicurare che le spore da me misurate sieno realmente quelle viste dal De Notaris, quantunque la forma corrisponda a quella che egli descrisse per le sue. — In altri esemplari della stessa località conservati nell'Erbario Saccardo non ho trovato che una *Sporormia* immatura.

Genus LXXX. *Podóspora* Cesati (1856)

in Rabh. *Herb. myc.*, n.° 259, et in *Hedw.* I, pag. 103; Winter, *Pilze*

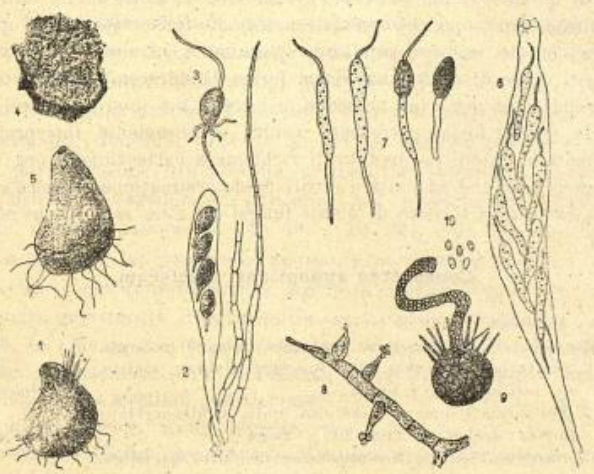


Fig. 87. 1-3. *Podospora pauciseta*: 1 perithecium, 2 ascus, 3 sporidium.
4-10. *Pod. coprophila*: 4 habitus fungi, 5 perithecium, 6 ascus immaturus, 7 sporidia varie evoluta, 8 status conidicus, 9 status pycnidicus: pycnidium, 10 sporulae.

Hab. in fimo vaccino, rarius asinino, caprino, leporino, etc. Piemonte, Veneto, Trentino, Toscana, Lazio, Sicilia.

Ar. distr. Europa, Amer. boreale.

Oss. Specie distinta sopratutto per i periteci rivestiti, almeno quando sono giovani, di tomento miceliare biancastro. Le spore si trovano molto spesso e per lungo tempo nello stadio giovanile, cioè jaline, cilindraceo-vermiformi, misuranti circa 50 - 65 × 5 ed appendicolate alle due estremità.

Secondo le ricerche di Woronin (*Beitr.* III, pag. 23) questa specie presenta uno stato picnidico ed uno stato conidico. I picnidii sono globulosi, brunastri, piccoli (50 - 70 μ diam.), con ostiolo minuto, circolare, circondato da 10 - 12 setole, e contengono delle sporule minutissime, jaline, sferoidali od ovoidee, che a maturità vengono eruttate in lunghi cirri. Lo stato conidico è rappresentato da conidiofori numerosi, brevi, in forma di fiasco, dalla cui estremità escono dei corpuscoli sferoidali, piccoli, circondati da una membrana e con un nucleo centrale molto rifrangente. Quale sia l'ulteriore sviluppo di questi cosidetti conidii non si può ancora dire con certezza.

Formazioni conidiche simili a quelle ora descritte per questa specie furono riscontrate anche in altre specie di *Podospora* e di *Sordaria*.

6. **Podospora pauciséta** (Ces.) Trav. (1906). — *Sphaeria pauciseta* Ces. in Klotzsch, Herb. myc. n.° 1642 et in Botan. Zeit. X, pag. 287 (1852); Ces. et De Not. Schema Sfer., pag. 226. — *Malinvernia anserina* Rabh. in Herb. myc., ed. II, n.° 526, et in Hedw. I, pag. 116 (1857). — *Hypocopra anserina* Ces. in litt. — *Sordaria anserina* Winter, Deutsche Sordar., pag. 35; Sacc. Syll. I, pag. 238. — *Podospora penicillata* Ell. et Ev., North-Amer. Pyren., pag. 131. — *Pleurage anserina* Kuntze, Rev. gen. pl., III, 3, pag. 504; Griffiths, North-Amer. Sordar., pag. 59.

Exs. Klotzsch, *Herb. myc.* 1642; Rabh. *Herb. myc.*, ed. II, 526; Sacc. *Myc. ven.* 1178, 1179; Cavr. *Fung. Langob.* 226.

Icon. Rabh. in *Hedw.* I, tab. XV, fig. 4; Winter, *Deutsche Sordar.*, tab. XI, fig. 20; Griffiths, *loc. cit.*, tab. V, fig. 4 - 6; Hansen, *Champ. stercor. Danem.*, pl. VIII, fig. 15 - 21; Icon. nostr. fig. 87, 1 - 3.

Bibl. 209, 397, 398, 409, 1036, 1112, 1222.

Peritheciis sparsis vel hinc inde 2 - 6 gregariis, semiimmersis, haud raro vero subsuperficialibus, ⅓ - ½ mm. diam., e globoso conoideis, in ostiolum breve, saepe incurvum, parte dorsali setuloso-penicillato (setulis fuligineis) productis, basi hyphis repentibus conidiophoris cinctis, membranaceis vel subcarbonaceis, nigricantibus; ascis clavato-fusoideis, longe pedicellatis, 250 - 350 × 20 - 25 (p. sp.

150-200 μ longa), tetrasporis vel, rarissime, bisporis; paraphysibus filiformibus, septulatis, copiosis, asco longioribus; sporidiis monostichis, ellipsoideis, e luteo opace fuligineis, 35-42 × 18-22, basi appendiculâ hyalinâ sporidii longitudinem subaequanti auctis.

Hab. in fimo anserino, cuniculino, equino, ovino, suino, vaccino. — Piemonte, Lombardia, Veneto.

Ar. distr. Ital. bor., German., Olanda, Amer, bor.

Oss. A proposito dell'identificazione di *Sphaeria pauciseta* Ces. con *Malinvernia anserina* Rabh. io debbo osservare che negli esemplari dell'exsiccata di Klotzsch non ho trovato altro che la *Sporormia intermedia* e nessuna *Podospora*; ma il fatto che Cesati e De Notaris nello *Schema* (pag. 226) citano sotto il nome di *Sordaria pauciseta* Ces. la figura di *Malinvernia anserina* in *Hedwigia* I, tab. XV, fig. 4, induce a credere che i due nomi indichino sempre la stessa specie.

7. **Podospora Brássicae** (Klotzsch) Winter, Pilze II, pag. 171 (1887). — *Sphaeria Brassicae* Klotzsch in Smith, Engl. Fl., V, pag. 261 (1826). — *Sph. lanuginosa* Preuss, in Linnaea XXVI, pag. 714 (1853). — *Arnium lanuginosum* Nitschke in Fuck. Symb. myc., Nachtr. I, pag. 38. — *Sordaria Curreyi* Auersw. in Niessl, Beitr., pag. 42. — *Sordaria lanuginosa* Sacc. Fung. ven., ser. VI, pag. 26; Syll. I, pag. 237. — *Pleurage Brassicae* Griffiths, North-Amer. Sordar., pag. 84.

Icon. Brefeld, *Untersuch.*, X Heft, tab. VI, fig. 1-2; Griffiths, *loc. cit.*, fig. 6 (pag. 84).

Bibl. 209, 907, 1036, 1112, 1222.

Peritheciis superficialibus, subgregariis, sphaeroideo-ovoideis, 800 × 600 μ circ., in ostiolum papillato-conoideum productis, filamentis mycelicis intricatis griseis undique lanoso-vestitis; ascis cylindraceis, breviter pedicellatis, 200-300 × 30-40 (p. sp. 150-250 μ longa), paraphysibus tenuibus filiformibus obvallatis; sporidiis oblique monostichis vel subdistichis, ellipsoideo-oblongis, opace fuligineis, 42-55 × 20-26, utrinque appendiculâ hyalinâ, cylindraceâ, curvulâ, variae longitudinis auctis.

Hab. in caulibus et ramis putrescentibus *Brassicae, Cirsii, Helianthi, Sambuci, Saponariae, Ulmi*, etc., nec non in mallo *Juglandis*. — Veneto, a Selva ed a Conegliano (Sacc., Speg.); Napoletano, ad Avellino (Peglion).

Ar. distr. Italia, Germania, Inghilterra, Olanda, Amer. bor.

Oss. Il Brefeld descrive per questa specie una forma conidica simile a quella della *P. coprophila* ed il Niessl dice che vi è anche una forma picnidica con picnidii molto simili ai periteci e sporule ellissoidali, brune, spesso jalino-appendicolate.

First utilization of *Podospora anserina* as an experimental model

in

Wolf, F. A. (1912). "Spore formation in *Podospora anserina* (Rahb.) Winter." Annals of Mycology 10: 60-64.

including a footnote by G.F. Atkinson

Spore formation in Podospora anserina (Rabh.) Winter[1]).

By Fred. A. Wolf.

A peculiar interest attaches to the genus *Podospora*[2]) because of the variation among different species in the number of the functional spores formed, the number ranging from four to sixteen or more in a few species. *Podospora anserina* is one of the tetrasporous species and was made the subject of an investigation for the purpose of observing nuclear phenomena in the formation of the four spores. There has grown up in the last fifteen years a vast literature on nuclear phenomena in the Ascomycetes but the tetrasporous forms have not been particularly investigated.

Podospora anserina is a saprophyte, occurring commonly on the excreta of animals. The fungus which I have studied appeared as a contamination in a poured plate culture of some leaf spot fungi. It is peculiarly adapted

1) Contribution from the Department of Botany, Cornell University, No. 147.

2) The generic name *Podospora* Cesati (in Rabenh. Herb. Mycol. No. 259, and in Hedw. 1, 103, 1852). is employed here for the following reasons. Ist. It has been in use for more than half a century and is employed by Winter in Rabenh. Krypt. Flora, etc., 1, 2d Abth. 169, 1887. 2d. The genus *Pleurage* Fr. (Summa Veg. Scand., 418, 1849), resurrected by O. Kunze (Rev. Gen. Plant. 33. 504, 1898) and used by some recent writers, occupies a very questionable position. Fries merely proposed *Pleurage* in a foot-note, although in the body of the text preceding, on the same page, he uses *Schizothecium* Corda (Icones Fung. 2, 29, pl. 13, 105, 1838). Fries states that he does not know this genus, but that if it is a good one the name ought to be changed on account of *Schizotheca* Ehrb. 1832. According to Art. 57 of the International Rules of Botanical Nomenclature adopted at Vienna in 1905, *Schizothecium* would not be changed on account of an earlier *Schizotheca*. (It may be said in addition that the latter name is regarded as a synonym of another valid genus name in the Alsineae.) Fries' mention of *Schizothecium* Fenzl is a mistake (Professor Farlow informs me that there is no *Schizothecium* Fenzl, and probably Fries meant *Schizothecium* E. Fenzl 1833 in „Versuch einer Darstellung der geographischen Verbreitungs- und Verteilungsverhältnisse der natürlichen Familie der Alsineen," etc.). *Schizothecium* Corda therefore has precedence over *Pleurage* Fr. It is extremely doubtful if we can now determine what species Corda placed in *Schizothecium*. It therefore seems better, pending the adoption of lists of genera conservanda und excludenda, to employ a genus name which has been in use for many years by specialists in this group. Geo. F. Atkinson.

to growing on paper but cannot be sectioned successfully on this substratum since the fibers of the paper do not permit the sections to cling in ribbons. If, however, the paper is carefully cut away this difficulty is avoided. When cultured on nutrient agar perithecial formation is readily secured. Small blocks of agar on which the fungus is growing may be cut out, fixed, microtomed and stained. Flemming's medium fixing solution seemed to give the most satisfactory results when used with Haidenhain's iron-alum-haematoxylin or with triple stain. Merkel's fluid and Flemming's strong and weak solutions were also used.

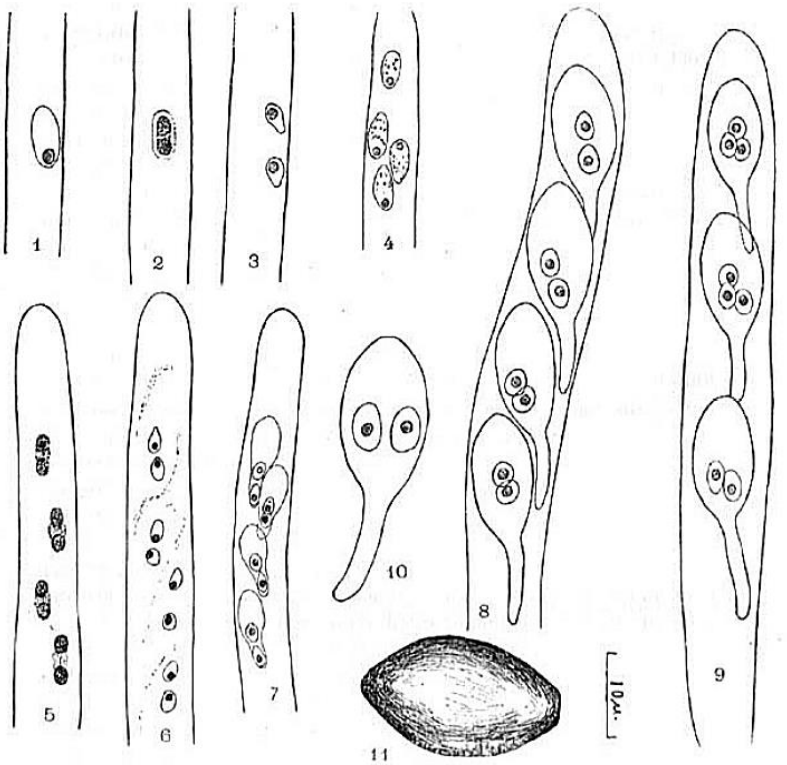
The perithecia arise from hyphal coils. The coiling of the two threads was observed both in living and fixed material. The nuclei are so small, the filaments themselves being only 3 μ in diameter, that none of the stages in fusion were observed. That this association of the two filaments represents the sexual process is however very probable. A sphere of parenchymatous tissue develops from this coil. When this structure, the perithecium, has attained about half its mature size the neck begins to be formed, the perithecium being pear shaped at maturity. At this stage of development the asci are formed in the base of the perithecium. The asci arise in a tuft, in young perithecia several being seen to branch from a single hypha. The cells of the perithecial wall, the filiform paraphyses and the vegetative mycelium are multinucleate.

When the ascus has attained about one-third its mature length it contains one large nucleus, the primary nucleus, much larger than those of the vegetative mycelium. Its position is normally near the center of the ascus and its diameter equal to one-half that of the ascus (Fig. 1). That some process of karyokinetic division occurs is quite apparent. But few of the stages could be seen in the preparations used. The first two divisions, probably heterotypic and homeotypic respectively, follow each other in rapid succession. The chromatic material in the binucleated stage is half that of the uninucleated stage and there is but little stainable plasma in the clear court surrounding the nucleolus. Fig. 2 shows one of the final stages in the division of the primary nucleus, the daughter nuclei being nearly formed. Fig. 3 is a later stage in which the nuclei have separated preparatory to the second division. After the second division there is a short period of rest. The nuclei enlarge and knots of chromatin appear but whether these can properly be termed chromosomes is impossible to state (Fig. 4). Brooks[1]) finds in *Gnomonia erythrostoma* that the four nuclei rest for some time before undergoing the third division, the chromatin net-work becoming clearly marked. While this rest period of a longer or shorter duration is not specially emphasized by other students of the Ascomycetes yet an examination of their figures

[1]) Brooks, F. T., Development of Gnomonia erythrostoma Pers. Ann. Bot. 24: 585—605. Pl. XLVIII—XLIX. 1910.

would indicate that it must occur. In *Pyronema confluens*[1]) the four nuclei have become much enlarged before the third division, indicating that some time elapses before this last division occurs.

In Fig. 5 is represented one of the late stages in the third division. The chromatin is arranged in two groups some of the nuclei showing



faintly the spindle fibers. The daughter nuclei remain in pairs close together so that at this time there are eight free nuclei within the ascus. Presently hyaline cleavage zones can be seen between the pairs of nuclei (Fig. 6). No clearly defined membrane is laid down but the granular protoplasm is less dense in these zones. The details in the process of

[1]) Harper, R. A., Sexual Reproduction in Pyronema confluens and the Formation of the Ascocarp. Ann. Bot. 14: 321—400. Pl. XIX—XXI. 1900.

spore delimitation and the subsequent laying down of the spore membrane could not be determined. The fact remains, however, that two nuclei are included within each of the four spores formed, none of the eight free nuclei disintegrating in the epiplasm (Fig. 7—8). In *Phyllactinia*[1]) there is a stage in development in which the ascus contains eight free nuclei. As a rule, however, only two spores are formed leaving the six supernumerary nuclei to disintegrate in the epiplasm. One exception to this binucleated condition in *Podospora* was noted. In this case three spores were formed within the ascus (Fig. 9), the two upper ones containing three nuclei each and the lower one two nuclei.

It has been shown also that one-celled ascospores are not regularly uninucleate although Harper[2]) in his early work believed that they were. The spores of *Tuber aestivum* are multinucleate[3]). Around four or five of the nuclei and in close proximity to their membranes the cell walls of the ascospores are developed. The nuclei increase in size and number until there are about eight in a spore. Details in the process of spore delimitation for such multinucleate spores are not described. Nuclear division, however, in ascospores without cell division has been pointed out by other investigators[4]).

In *Podospora anserina* whether only one nucleus of each pair takes part in this process of spore delimitation or wheter both nuclei are concerned and the astral rays flow together from opposite directions could not be determined. Judging from the fact that the nuclei always lie in the axis of the newly formed spore and near the lower end, it seems quite probable that only the lower one of each pair is concerned in the formation of the wall. The young spores soon become broader at the upper end (Fig. 7). The lower part becomes the hyaline appendage[5]) of the mature spore and the upper part of the dark spore has become prominently enlarged, one nucleus lies within the end which is to become the appendage. As the spores increase in size there is a corresponding growth of the nuclei which come to lie near the center of spore (Fig. 8). When the spores reach the size shown in Fig. 10, they begin to change from hyaline to greenish. This color gradually darkens becoming at length

[1]) Harper, R. A., Sexual Reproduction and Organization of the Nucleus in Certain Mildews. Carnegie Inst. of Washington Pub. **31**: 1—104. Pl. I—VII. 1905.

[2]) Harper, R. A., Cell Division in Sporangia and Asci. Ann. Bot. **13**: 467—525. Pl. XXIV—XXVI. 1899.

[3]) Dixon, H. H., The Possible Function of the Nucleolus in Heredity. Ann. Bot. **13**: 269—278. 1899.

[4]) Dittrich, C. G., Zur Entwicklungsgeschichte der Helvellineen. Beiträge zur Biol. der Pflanzen. Bd. VIII Heft. 1, 17—52, t. IV—V. 1899.

[5]) Some spores have an appendage at the apex of the spore in addition to the basal appendage.

dark brown. The appendage which is nearly equal in length to the body of the spore remains hyaline and may entirely disappear in very old spores (Fig. 11).

In a recent paper Lewis[1]) has found that eight free nuclei are formed in *Podospora zygospora*. From these the eight uninucleated sporogenous cells are formed. By the development of these cells and the division of the primary spore nucleus, a multinucleated filamentous spore is formed. Septa may or may not be formed. In case they do occur each cell is uninucleate. Each end of the filament may develop into a fertile cell or functional spore. No multinucleated fertile cells were observed. In the case, however, of *Podospora anserina*, the spores are binucleated from the first and no subsequent nuclear division occurs up to the time the mature spore has been formed.

[1]) Lewis, I. M., The Development of Spores in Pleurage zygospora. Bot. Gaz. **51**: 369—373. Pl. XIX. 1911.

Description of *Bombardia anserina*

in

Migula, W. (1913). Gattung Bombardia Fr. Thome's Kryptogamic Flora. 10: 123-129.

flächlich, mit kurzem, papillenförmigem Halse, sehr zartwandig, von einem kurzen, schwefelgelbem Filze überzogen, der aus sehr dünnen und zarten, oft zu Strängen vereinigten Hyphen besteht. Hals nackt oder kurz behaart, derb, schwarz. Reife Schläuche cylindrisch, kurzgestielt, vor der Ausstreuung der Sporen etwa 32 μ dick, an der Spitze ohne Verdickung, achtsporig. Sporen ellipsoidisch, mit kleinem papillenförmigem, 6—9 μ langem, farblosem oder blassbräunlichem Anhängsel, ausserdem mit dicker Gallerthülle, schwarz, 40—52 μ lang, 20—28 μ dick. — Auf Schafmist.

312. **S. insignis** Hansen. — Fruchtkörper zerstreut, halb eingesenkt, kugelig, kurz birnförmig oder länglich, um die warzenförmige Mündung mit schwarzen, gegliederten Haaren besetzt, ungefähr 1 mm im Durchmesser. Schläuche keulenförmig oder cylindrisch, oben etwas verschmälert und abgeflacht, nach unten in den ziemlich langen Stiel verschmälert, achtsporig, 240 μ lang, 68 μ breit. Sporen ein- oder zweireihig, im ersteren Falle die Schläuche nur von halber Breite, eiförmig, schwarzbraun, am unteren Ende abgestutzt und mit einem kurzen, farblosen Anhängsel versehen, mit Gallerthülle, 48—52 μ lang, 24—25 μ breit. Paraphysen fädig, septiert, die Schläuche überragend (Kirschstein). — Auf Pferdemist. Hasenheide bei Berlin.

Gattung Bombardia Fr.

Fruchtkörper zuletzt fast immer oberflächlich, häutig oder lederartig, braun oder schwarz. Schläuche meist achtsporig, cylindrisch, keulig oder ellipsoidisch. Sporen bei der Reife braun oder schwarz, ohne Gallerthülle, aber mit farblosen Anhängseln. Stroma fehlt.

Übersicht der Arten.

1. Schläuche bis achtsporig. 2.
   Schläuche mehr als achtsporig. 16.
2. Schläuche zwei- bis viersporig. **B. anserina.**
   Schläuche vier- bis achtsporig. 3.
3. Sporen unten mit einfachem Anhängsel. 4.
   Sporen unten mit doppeltem Anhängsel. 11.
4. Unteres Anhängsel kürzer oder so lang als die Spore. 5.
   Unteres Anhängsel länger als die Spore. 10.
5. Oberes Anhängsel, wenn vorhanden niemals fädig. 6.
   Oberes Anhängsel fädig. 8.
6. Reife Sporen bis 18 μ lang. **B. comata.**
   Reife Sporen über 25 μ lang. 7.
7. Oberes Anhängsel breit, längsstreifig. **B. decipiens.**
   Oberes Anhängsel nicht längsstreifig. **B. Cirsii.**

8. Perithecien gegen 0,8 mm hoch. **B. Brassicae.**
   Perithecien gegen 0,4 mm hoch. 9.
9. Schläuche 38 μ breit. **B. curvula.**
   Schläuche 14 μ breit. **B. minuta.**
10. Oberes Anhängsel kurz, warzenförmig. **B. hydrophila.**
    Oberes Anhängsel lang fadenförmig. **B. nigropapillata.**
11. Zweites unteres Anhängsel in Einzahl. 12.
    Zweite untere Anhängsel zu drei bis vier. **B. vestita.**
12. Fruchtkörper viel länger als breit. 13.
    Fruchtkörper meist kugelig. 15.
13. Fruchtkörper nach oben verjüngt, kegelig. 14.
    Fruchtkörper nach oben verbreitert, keulen- oder eiförmig. **B. bombarda.**
14. Sporen unter 30 μ lang. **B. coprophila.**
    Sporen über 30 μ lang. **B. fimiseda.**
15. Anhängsel II. Ordnung, borstig. **B. lignicola.**
    Anhängsel II. Ordnung lang, peitschenförmig. **B. ambigua.**
16. Sporen 16—64 im Schlauch. **B. pleiospora.**
    Sporen 128 im Schlauch. 17.
17. Sporen nur am unteren Ende mit Anhängsel. **B. curvicolla.**
    Sporen an beiden Enden, am unteren mit doppeltem Anhängsel. **B. setosa.**

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313. **B. anserina** (Rabenh.). — Malinvernia anserina Rabenh. — Hypocopra anserina. — Sordaria anserina Winter. — Podospora anserina Winter. — Perithecien dicht herdenweise, halb eingesenkt, aus fast eiförmiger oder kugeliger Basis kegelförmig, in einen langen, dicken, oft gekrümmten Hals verjüngt, der unter der Spitze auf seiner konvexen Seite mit dicht büscheligen, sehr langen, steifen, braunen Borsten besetzt ist, während die Perithecien mit spärlichem, zartem Hyphengeflecht bekleidet, runzelig, schwarzbraun gefärbt sind. Schläuche cylindrisch, nach oben verschmälert, am Ende abgerundet, sehr lang gestielt, zwei- bis viersporig, 110—125 μ lang, 20 bis 22 μ dick. Paraphysen fädig, verästelt, gelatinös. Sporen einreihig, ellipsoidisch, braun, am Grunde mit cylindrischem, geradem, farblosem Anhängsel, 33—42 μ lang, 19—21 μ dick. — Auf Gänsekot, seltener auf Mist anderer Tiere.

314. **B. comata** Kirschstein. — Fruchtkörper zerstreut, kugelig, zur Hälfte hervorragend, mit kurzer, abgerundeter, etwas glänzender Mündung, 300—400 μ im Durchmesser. Gehäuse schwarz, häutig, mit braunen, verzweigten, 2 μ dicken, wellig gebogenen Haaren bekleidet. Schläuche cylindrisch-keulig, oben flach gerundet, mit einem kugeligen, glänzenden Körper, ziemlich lang gestielt, achtsporig, 120—150 μ lang, 16—18 μ breit. Sporen

Second utilization of *Podospora anserina* as an experimental model

in

Satina, S. (1916). "Studies in the development of certain species of the *sordariaceae*." Bulletin de la Société impériale des naturalistes de Moscou, nouvelle serie. 30: 106-142 Pl. 101-102

of the nuclei is here only as a result of the dividing of them, one can then perhaps explain the formation of large and small nuclei in such sense, that the large nuclei are grown and ready to divide nuclei, and the small ones in this case must be considered as the result of the dividing of same.

To conclude the description of the development of P. curvula, one has only to add that the processes, which take place during the formation and development of the asci, ran their ordinary course. The pairing of nuclei in ascogenous hyphae is distinctly marked already, at a small distance from the ascogonium. At the base of the ascogenous hyphae the picture is not so distinct, for the latter send out branches very thickly and profusely, which cling heavily to each other.

Podospora anserina.

All above stated about the development of P. curvula can be fully attributed to P. anserina. The difference consists only in the smaller dimensions of the nuclei of the ascogonium (fig. 28). Here also it was possible to ascertain the origin of the ascogenous hyphae from several cells of the ascogonium. This species is especially convenient for watching the pairing of the nuclei in ascogenous hyphae (fig. 29). The fusion of two coiled threads, which Wolf takes for a sexual process, could not be observed here, and the antheridia, as shown on fig. 27, do not develop here at all.

As to the development of the ascus, peculiar on account of its containing only four spores, the informations obtained fully affirm the description of this process by Wolf. In fact, after the formation of eight nuclei in the ascus, the pairing nuclei do not separate, but only slightly withdraw from each other. Next to each such pair, appears a clear zone, which separates the nuclei from the surrounding dense protoplasm (fig. 30). This zone at first, is not very distinct and, only after a certain time, it becomes prominent. After this around the clear spaces a sheath is formed, and the spore so produced, from the beginning, contains two sister nuclei. Such two nuclei in the spores can be noticed till its full maturing, that is till its sheath darkens. As reported by Wolf, one could meet asci with three spores, two of which had three nuclei and one had two.

Description of *Podospora anserina*

in

Chenantais, J. E. (1919). "Recherches sur les Pyrenomycètes (Suite et Fin)." Bull. Soc. Mycol. Fr. 35: 113-139 & Pl. II-III

logie de la graine ne change pas davantage, sauf atrophie de certains appendices suivant les conditions locales dans l'asque.

Podospora decipiens pleiospora (Wint.) Chen.

Traverso. Fl. it. crypt., p. 236, s'exprime ainsi sur *P. pleiospora* : « Questa specie è caratterizzata *abbastanza*, oltre che dal numero delle spore, dalla forma degli aschi e dalla disposizione delle appendici delle spore ».

Ce « suffisamment » est une affirmation bien superficielle puisqu'elle se base sur le nombre des spores, ce qui entraîne forcément un développement proportionnel de l'asque et quelques modifications de dimensions dans les appendices qui s'adaptent à des conditions locales un peu différentes. Morphologie et disposition générale, structure, tout est la reproduction fidèle de *decipiens*. Pour qui connaît bien les deux formes, l'identité ne fait pas pas de doute, *pleiospora* est la « variété » polyspore de *decipiens*. Une « espèce » fondée sur des caractères quantitatifs est sans valeur.

Quant au caractère pileux du périthèce, il est sujet à caution. Sur des centaines de périthèces, in fimo vaccino et cuniculino, je n'ai trouvé qu'une fois un lacis de poils minces hyphiformes et très fuscescents au-dessous de l'ostiole. La courbure du col est un phénomène héliotropique qui se produit chez la plupart des Sordariées. Il n'a aucune valeur de diagnose dans les formes membraneuses émergeant plus ou moins du support (Pl. I, fig. 11 et 12).

Podospora pauciseta (Ces.) Trav.

Syn. — *Podospora pauciseta* (Ces.) Trav. (1906). — *Sphæria pauciseta* Ces. (1852). — *Malinvernia anserina* Rabh. — *Hypocopra anserina* Ces. in litt. — *Sordaria anserina* Wint. — *Podospora penicillata* Ell. et Er. — *Pleurage anserina* Kuntze. C. f. r. Trav. Fl. it. crypt., p. 431, icon.

Nous rattachons à cette forme les variantes suivantes dont l'ensemble constitue un groupe-espèce :

Sordaria pilosa Mout. *Bull. Soc. bot. Belg.*, p. 144, Pl. IV. Pourrait être la forme octospore de *pauciseta*. La disposition des poils entourant le col a été retrouvée par nous plusieurs fois sur les formes polyspores suivantes :

Philocopra setosa Wint. Sacc. — *Ph. curvicolla* Wint. Sacc. Il est évident que ces deux formes sont synonymes, la courbure

du col est contingente comme dans *curvula* et bien d'autres Sordariées. L'écart des spores, 17-19 = 10-12 μ dans *setosa*, 14-16 = 9-11 dans *curvicolla*, ne peut être pris en considération. Mêmes réflexions pour les formes suivantes. (Syll. 1, p. 239 et 250).

Philocopra platensis Speg. — *Ph. dakotensis* (Griff.) Saec. Spores respectivement de 20-22 = 15-17 et de 18-23 = 12-15 (Syll. XVII, p. 607 et I, p. 250).

Philocopra similis (Hans.) Sacc. Spores un peu plus fortes, 27-33 = 17-18 (Syll. I, p. 251).

Philocopra adelura (Griff.) Sacc. et D. Sacc. Les spores, de tout point comparables à celles des formes précédentes, mesurent 26-32 = 13-19 pour 64 spores dans l'asque. Cette forme, que j'ai trouvée abondante sur crottes de lapin, avait des spores de 20-23 = 12-15 pour 128, 324 ou 512 spores dans l'asque. Nous considérons cette forme comme une variété glabre de *Podospora pauciseta setosa* (Syll. XVII, p. 607).

Choix du type. — Sans être aussi fréquente que chez les Discomycètes, la polysporité n'est pas rare chez les Pyrénomycètes; l'avortement de 4 spores sur 8 n'est pas exceptionnel. La création de genres spéciaux pour ces phénomènes : *Fracchiæa*, *Pleurostoma*, *Valsella*, *Philocopra* et *Aglaospora*, *Malinvernia*, etc., ne se justifie que si des caractères morphologiques différents de ceux des genres d'où ils ont été retirés sont constatés, soit du côté des périthèces, soit du côté des spores. Or, dans toutes les formes précédentes, le périthèce a la même disposition typique des poils sur le col et l'ontogénèse de la spore est identique. Une seule forme est glabre, mais ses spores ne diffèrent pas de celles des autres.

On peut s'étonner que nous ayons choisi une forme notoirement tétraspore pour type d'une espèce dont les bipartitions nucléaires varient de 32 à 512. On ne sépare plus maintenant *S. minuta* tétraspore de sa variété octospore. A mon avis, il est possible que la forme octospore de *P. pauciseta* soit réalisée par *S. pilosa* Mout. Elle se présente, il est vrai, avec des poils en couronne autour du col, mais cette dissociation des fascies assez rare se voit également chez *setosa-curvicolla* (1). L'objection la plus sérieuse serait tirée du volume des spores de *P. pauciseta*. Mais on a constaté que ces spores sont « binucléées » et, si l'on supposait la forme octospore réalisée, les spores originairement de 35-42 = 18-22 se rapprocheraient par dédoublement des noyaux de 17-21 = 9-11,

(1) De toutes façons, *S. pilosa* Mout. tient étroitement à *Ph. setosa-curvicolla*.

soit de celles de *S. pilosa* Mout. qui mesurent 17-22 = 11-14. Quoi qu'il en soit, il nous paraît difficile de ne pas rattacher nos *Philocopra* à une forme qui présente tous leurs caractères essentiels.

Si l'on s'en tenait à la morphologie de la spore seule, il n'y aurait pas lieu de séparer *pauciseta* de *fimiseda* ; sans leur volume inégal, elles seraient « superposables » ; le périthèce est facile à différencier chez ces deux formes et n'autorise pas à regarder l'une comme une variante de l'autre. Il est donc logique, étant donnée la similitude absolue du périthèce et des spores de *P. pauciseta* avec celle de certains *Philocopra* de choisir cette forme comme type de l'espèce.

Obs. — Pendant quatre ans, j'ai recueilli et élevé de nombreux échantillons de *Philocopra* in fimo cuniculino et j'ai étudié *P. pauciseta* sur échantillon provenant de Bizerte in fimo Cameli.

Périthèces. — Le périthèce de *P. pauciseta* n'est pas exclusivement membraneux et transparent comme celui des formes polyspores. Il est opaque et cette opacité est due à un léger revêtement carbonacé discontinu qui recouvre l'enveloppe membraneuse. Je me suis demandé à ce sujet quelle différence il y a entre l'expression « sub-carbonacé » (*anserina*) et « sub-membraneux » (*ovina* et *equina*) employée au Syll. I, p. 238. Les périthèces que j'ai étudiés justifiaient l'une et l'autre expression. Cette consistance spéciale distingue à première vue *P. pauciseta* des variantes polyspores.

La distribution des poils, sur ou autour du col, présente des dispositions assez variées quoique toujours localisées à cette région. La figure de Traverso (Fl. it. crypt., p. 87) représente une fascie unique sur le col. On la retrouve dans notre Planche III. Cette disposition n'est pas absolument typique. Sur *P. pauciseta* et les formes qui en dépendent, notamment *setosa-curvicolla*, il y a le plus souvent apparence de fascie unique alors qu'il y a deux groupes pileux plus ou moins accolés. Les fascies peuvent être opposées, simulant deux cornes de chaque côté du col ; le plus souvent trois fascies sont associées par la base d'un seul côté. On peut trouver encore 4 groupes symétriques ou une dissociation à peu près complète des poils autour du col. Ceux-ci sont souvent simples ou faiblement septés, vert-brunâtre et pâlissent en séchant. C. f. r. fig. 1, Pl. III. La forme *adelura* en est dépourvue ; on en trouve cependant parfois quelques-uns qui simulent des hyphes dans les environs du col. Il y a donc tous les intermédiaires entre

la forme pileuse et la forme glabre, la spore témoin est identique.

L'ostiole se présente au début comme un bouton aplati sur le col étranglé, puis il s'allonge, se redresse en se courbant plus ou moins. La dimension des périthèces oscille entre 4 à 600 μ. Ils sont transparents et permettent de voir le contour des asques bourrés de spores (Pl. III, fig. 2).

Spores.— Pour étudier la filiation des *Philocopra*, il faut examiner un grand nombre de spores, particulièrement celles qui se trouvent dans les mêmes conditions que chez les *Podospora* octospores. Ce sont celles qui occupent les environs du sommet de l'asque et la périphérie de la masse, où elles sont en connexion avec les parois. Là seulement on pourra trouver des appendices fondamentaux ou adventifs suffisamment caractérisés. Faute de cet examen méthodique on signalera une spore sans appendices avec une cauda (vestigium) et on pourrait en conclure en se fiant à la loi de fréquence que les appendices font défaut. Il n'en est rien, mais les spores centrales tassées sur elles-mêmes ne sont plus reliées que par quelques filaments à peine perceptibles (Pl. III, fig. 4). Dans les environs du sommet, toujours libre, comme chez *P. fimiseda* et *pauciseta*, s'insère l'appendice supérieur plus ou moins droit ou enroulé à son extrémité. A la base du vestigium on trouve l'appendice inférieur très fragile, difficile à voir et qui manque souvent comme les appendices adventifs pour les raisons signalées plus haut. Ces appendices adventifs figurés par Traverso (*l. c.*) dans *P. pauciseta* ne sont pas notés dans sa description. Je ne les ai jamais vus dans cette forme pas plus que dans *P. fimiseda*. En revanche, dans la diagnose de Fl. it. crypt. on confond le vestigium avec l'appendice inférieur et il n'est pas question de l'appendice supérieur. Winter, in Rabh. Krypt. Flor., fig. 3, p. 162, est aussi muet sur l'appendice supérieur si caractéristique de *P. decipiens*. Ces détails anatomiques négligés autrefois devraient être pris en considération dans des ouvrages aussi modernes que l'ouvrage italien. L'appendice supérieur de *pauciseta* peut être aussi volumineux que celui de *fimiseda* et il ne manque jamais. Les spores des *Philocopra* ont, comme celles de *P. pauciseta*, le sommet légèrement tronqué, mais chez eux l'épispore ne recouvre pas totalement le pore germinatif. Cette zone est nettement figurée par un petit cratère ouvert au fond duquel on aperçoit l'endospore brillante et hyaline (Pl. III, fig. 6).

Un coup d'œil jeté sur nos figures suffit à justifier nos vues synthétiques. La variété glabre *adelura* a été rapprochée de *P. deci-*

piens par GRIFFITHS. Le périthèce est lisse comme dans cette forme, mais cette affinité superficielle est démentie par l'identité des spores de *Ph. adelura* avec celle des variantes polyspores de *P. pauciseta*.

Les variations des dimensions sporales sont peu considérables dans les formes étudiées par moi et répondant à *pilosa*, *setosa*, *curvicolla* ou *adelura*; elles oscillent de 18-22 = 12-15 μ. La variante *similis* Hans. sp. 27-34 = 17-18 et la variante *adelura* Griff. sp. 26-32 = 18-19 pour 64 spores ne diffèrent pas sensiblement. Chez les nombreux types glabres que j'ai rencontrés, j'ai trouvé les dimensions 20-23 = 12-15, mais il faut noter que le nombre de spores était au minimum de 128 et 324. Sans pouvoir établir une loi de proportionnalité entre le volume et le nombre des spores, il y a là au moins une coïncidence qui peut n'être pas fortuite.

Podospora hirsuta Dangeard.

M. DANGEARD, dans ses études sur le développement des périthèces, cultive sur agar-agar des excréments variés et ne s'enquiert pas des espèces qu'ils contiennent avant l'ensemencement. Cette méthode est originale. Ainsi il nous cache absolument, non seulement l'origine, mais le crottin ou bouse qui a donné naissance à une Sordariée polyspore qu'il a baptisée *Podospora hirsuta* Dang. (*Le Botaniste*, 1907, p. 345).

Il n'y aurait pas lieu de prendre en considération une expérience réalisée dans des conditions aussi peu scientifiques, si les auteurs du Sylloge, en cela du reste couverts par l'autorité de l'auteur, n'avaient cru devoir l'enregistrer comme valable aux yeux de la postérité. Ils disent bien : Hab. *in excrementis*? Crottin? Bouse? C'est discret au possible. Nous demanderons plus. Quelle est la Sordariée que vous avez ensemencée?

Voyons votre phénomène :

Périthèces.— A retenir le tomentum blanc formé d'hyphes abondants. Résultat du milieu spécial. Ce qu'il y a de plus typique, ce sont les poils rigides entourant l'ostiole. *P. setosa* et *curvicolla* se présentent de la même façon in fimo cuniculorum.

Asque. — M. DANGEARD découvre l'orientation définie des spores dans l'asque, la tête étant toujours dirigée vers le sommet. M. BAINIER, comme nous l'avons vu, a fait la découverte inverse

Les périthèces, les asques et les spores ont bien tous les caractères des Massariées, c'est ce qui nous a conduit à placer dans le genre *Massarinula* cette forme qui paraît s'y apparenter par ses spores à épispore épaisse revêtue d'une mince couche hyaline, peu apparente, je dois le dire, et qu'il faut rechercher avec soin, au moins dans les exemplaires que je possède et qui ont peut-être été recueillis déjà fort âgés.

EXPLICATION DES PLANCHES.

Planche I.

Fig. 1. — Deux spores, la première de *Lasiosphæria spermoides*, la seconde de *L. strigosa*.

Fig. 2. — Deux spores de *Lasiosphæria immersa* avec spicules très caducs.

Fig. 3. — Trois spores de *Lasiosphæria orina* dont une complètement septée.

Fig. 4. — Quatre spores de *Lasiosphæria crinita* = *subcaudata* = *erinacea*.

Fig. 5. — Une spore de *Lasiosphæria ferruginea*.

Fig. 6. — *Lasiosordaria ambigua* : *a*, spore fucescente avec commencement de différenciation de la tête ; *c*, tête seule fucescente et cloisonnée ; *d*, phase intermédiaire, fucescence de la tête sans cloison ; *e*, phase terminale, opacité de la tête ; *b*, spore involuée témoignant de la filiation lasiosphæriée.

Fig. 7. — Trois spores de *Lasiosordaria vagans*.

Fig. 8. — Deux spores de *Lasiosordaria coprophila*.

Fig. 9. — *Podospora fimiseda* : *a*, spore jeune en massue ; *b*, spore adulte.

Fig. 10. — *Podospora curvula* : *b*, spore jeune ; *a*, spore adulte.

Fig. 11. — *Podospora decipiens*.

Fig. 12. — *Podospora decipiens pleiospora* et une spore hyaline involuée témoin.

Fig. 13. — *Podospora pauciseta setosa* = *curricolla*.

Fig. 14. — *Podospora vestita* d'après Zopf.

Fig. 15. — *Sordaria carbonaria* : trois spores.

Fig. 16. — *Podospora lanuginosa* : *a*, spore mure, *b*, spore jeune avec indication de l'isolement de la loge inférieure.

Fig. 17. — *Sordaria fimicola*, interruption de la zone au pore germinatif.

Planche II.

Fig. 1. — *Podospora decipiens* : *a*, disposition des appendices adventifs dont deux sont soudés au vestigium ; *b*, rétraction de tous les cordons protoplasmiques à la base de la spore ; *c*, séparation en deux languettes et allongement de l'appendice supérieur ; *d*, élongation du même appendice.

FIG. 2. — *Podospora decipiens pleiospora* : *a* et *b*, dispositions variées des appendices « adventifs » dans la masse justifiant cette dénomination.

FIG. 3.— *Podospora curvula* : *a*, une chaîne de spores expulsées normalement, celles du sommet entraînent des lambeaux du canal intérieur de l'asque ; *b*, élongation de l'appendice supérieur et appendices adventifs de la base ; *c*, un appendice adventif sur le vestigium ; *d*, dissociation fasciculaire de l'appendice supérieur ; *e*, languettes adventives.

FIG. 4.— *Podospora fimiseda* : *a*, dissociation des cordons à la base de l'appendice supérieur ; *b*, à la base de l'appendice inférieur prolongeant le vestigium flétri ; dissociation et étirement considérable des deux appendices.

FIG. 5.— *Podospora curvula minuta* : spore ayant entraîné un lambeau de la paroi du canal des spores.

FIG. 6.— *Podospora pauciseta setosa* : une spore avec vestigium très court et un long appendice supérieur.

PLANCHE III.

FIG. 1. — *Podospora pauciseta setosa* (*Philocopra*) : *a*, *b*, *c*, *d*, dispositions variées des poils autour du col ; *e*, forme chauve (*Ph. adelura*), exemplaires jeunes.

FIG. 2. — *Podospora pauciseta adelura* : périthèce jeune laissant voir par transparence deux asques à 512 spores.

FIG. 3. — *Podospora pauciseta setosa* : un groupe de poils fasciés autour du col.

FIG. 4. — *Podospora setosa adelura* : *a*, appendice en cupule ou ventouse d'une spore du sommet de la masse vu de face avec ses cordons constituants ; *b*, une autre spore dont les cordons apicaux sont dissociés ; *c*, appendice fondamental inférieur régulier ; *d*, filaments adventifs reliant les spores entre elles ; *e*, spore jeune ; *f*, *h*, languettes provenant de la paroi du canal de l'asque ; *g*, type régulier à plus faible grossissement ; *i*, insertion excentrique normale de l'appendice supérieur.

FIG. 5. — *P. setosa adelura* : *a*, *b*, *c*, *d*, 4 spores à 2 grossissements différents provenant d'un asque à 128 spores dont les appendices supérieurs sont plus développés.

FIG. 6. — *P. setosa-curvicolla* : dispositif du sommet de la spore tronqué et vu en coupe montrant le pore germinatif.

FIG. 7. — Aspect d'un asque à 512 spores montrant l'aspect réticulé du manchon infiltrable.

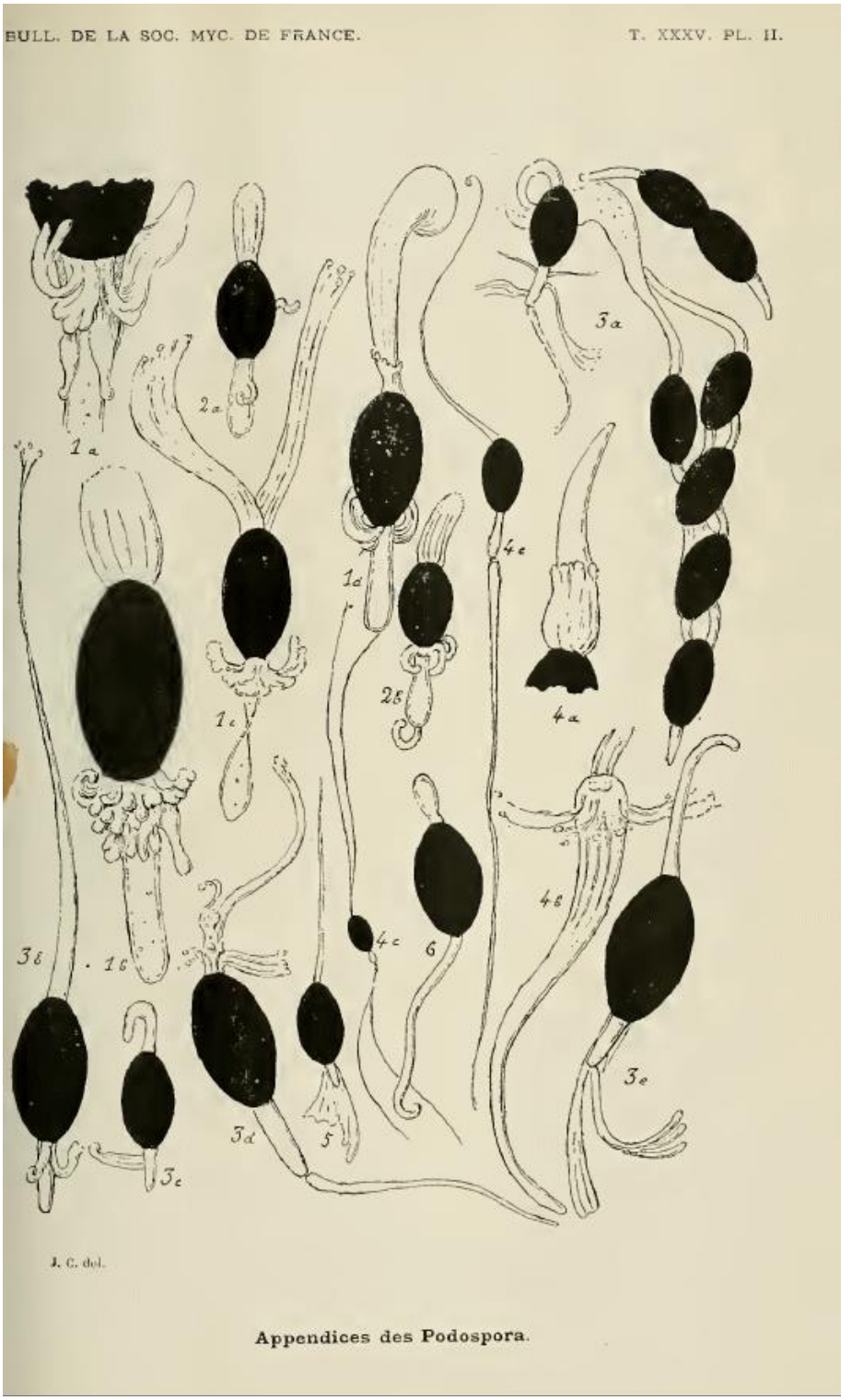
PLANCHE IV.

FIG. 1. — *Lasiosphæria immersa* : *a*, tractus protoplasmiques s'insérant sur le globule du sommet, partant de la spore et de l'anneau de la voûte de l'asque ; *b*, coloration par le bleu lactique du contenu de l'asque et de quelques tractus reliant la première spore à l'anneau de la voûte resté blanc.

FIG. 2. — *Lasiosphæria ovina* : sommet d'un asque ; les tractus se sont condensés en un cordon visible mais faiblement adhérent à l'épispore.

FIG. 3. — Insertions des spicules plus résistants chez les *Lasiosordaria*.

FIG. 4. — *Sordaria fimicola* : l'anneau de renforcement de la voûte vu en coupe.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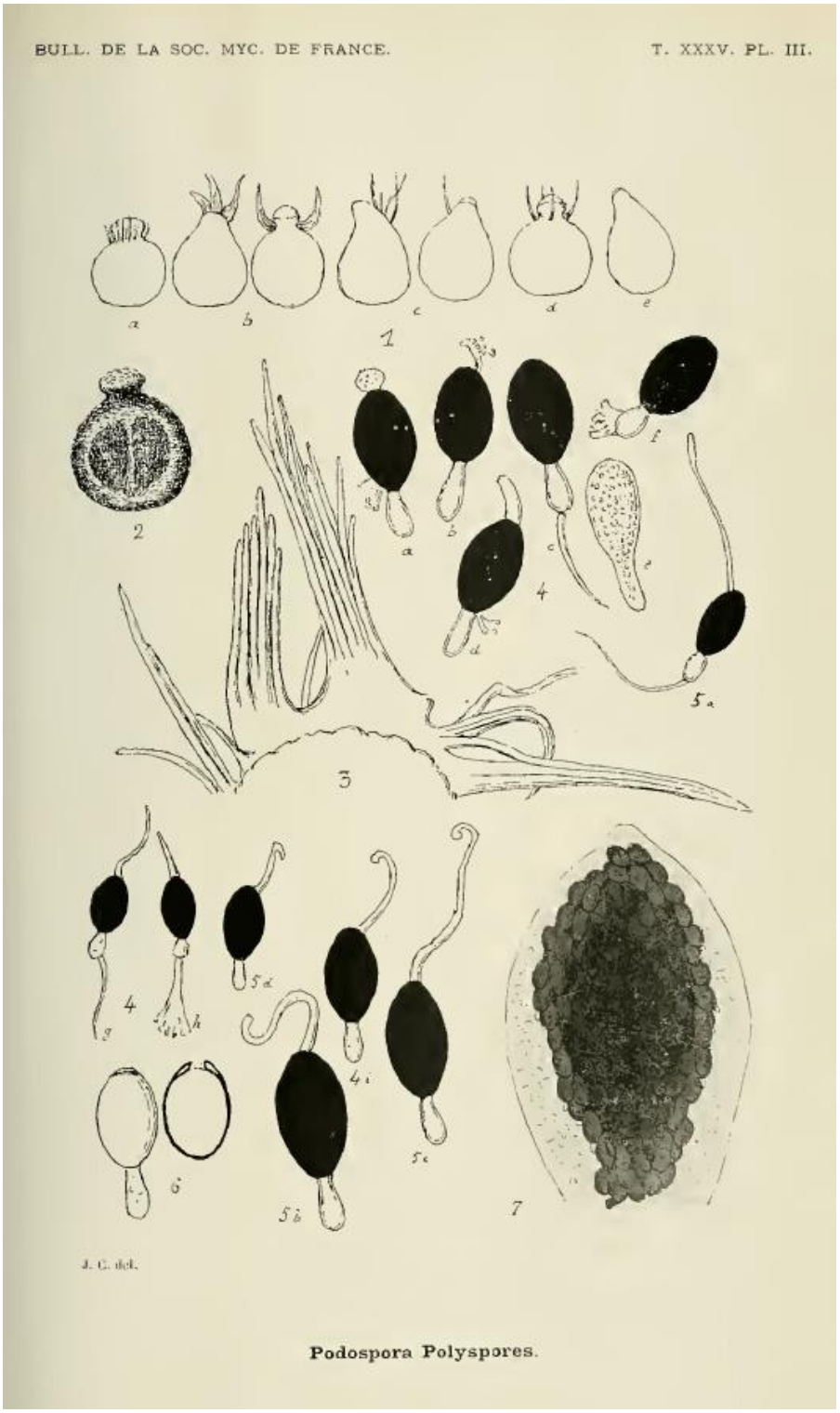
Appendices des Podospora.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Podospora Polyspores.

Podospora anserina

Podospora anserina is a model used in several laboratories to study various facets of biology, including ageing, prions, sexual compatiblity and development, genome evolution, phenotypic instability, biomass degradation, natural, product production, *etc.* Its ease of culture, preservation and sophistication of its genetic analyses make of this fungus an asset in experimental research, hence its common name: the "friendly mold".

This book aimed at providing an up to date presentation of *Podospora anserina*. In a first part, the general biology of the model fungus is presented. It is followed in a second part by a review of the main results obtained while using the friendly mold in molecular genetic analyses. The author hopes that this book will help both researchers already using the fungus and those that may wish to use it.

Philippe Silar is professor at Université de Paris since 1999, where he teaches Eukaryotic Microbiology and Genetics. His research work focuses on the genetics and physiology of fungi, using mostly the model fungus *Podospora anserina* since 1991.

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