GENETIKA HUB

1. Genetické aspekty sexuální reprodukce u hub.
2. Genetické aspekty asexuální reprodukce u hub. Parasexuální hybridizace.

mvkolarik@biomed.cas.cz

21st Century Guidebook to Fungi, SECOND EDITION
by David Moore, Geoffrey D. Robson and Anthony P. J. Trinci

revised 2020 edition

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http://www.davidmoore.org.uk/21st_Century_Guidebook_to_Fungi_PLATINUM/

Houby jako ideální modelové organismy

• Jednoduchá stavba – mycelium, rozmnožovací a dormantní struktury…

• Rychlý růst a krátká generační doba, neomezený růst

(dostatek biomasy), snadné uchovávání

• Velká produkce potomstva

• Jednoduchý genom

• Převážně haploidní (snadná generace knockoutů)

•Ophistoconta, tj. jsou příbuzní živočichům

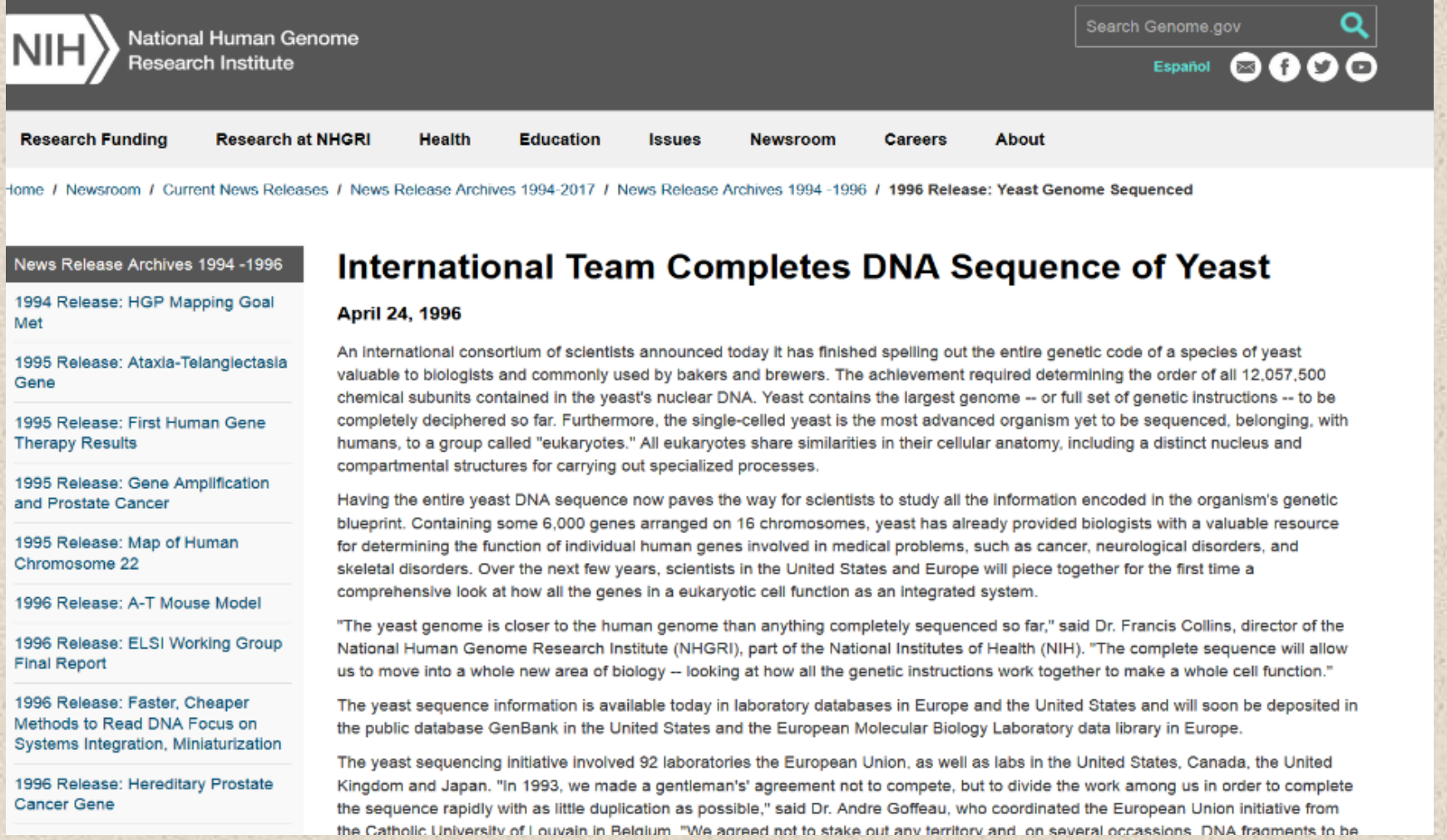
Saccharomyces cerevisiae

- prototrof, pohlavní i nepohlavní rozmnožování
- generační doba 1,25 – 2 h
- první genom eukaryota, 1996
- 12 Mbp, 16 chromozomů, cca 6300 genů (5800 je funkčních)
- *Schizosaccharomyces pombe* (WGS 2002, 4970 genů)

Sp - Fission yeast

Sc - budding yeast

Schizosaccharomyces pombe - pombe = millet beer



The yeast sequencing initiative involved **92 laboratories** the European Union, as well as labs in the United States, Canada, the United Kingdom and Japan. "In 1993, we made a gentleman's' agreement not to compete, but to divide the work among us in order to complete the sequence rapidly with as little duplication as possible," said Dr. Andre Goffeau, who coordinated the European Union initiative from the Catholic University of Louvain in Belgium. "We agreed not to stake out any territory and, on several occassions, DNA fragments to be sequenced were redistributed according to the respective abilities of the sequencing teams."

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£50 per genome	£70 per genome	£100 per genome
Get a quote	Get a quote	Get a quote

Saccharomyces cerevisiae

•*Saccharomyces* genome deletion project (2004), *Schizosaccharomyces pombe* genome deletion project (2010)

•Gene–Protein–Function Association via Mutants – the fundamental data about the gene function

•Only 18% of genes is essential for the prototrophic growth (26% in *S. pombe*)

• 31% shared with humans (incl. cancer related genes)

• The first synthetic chromosome (2.7 Mbp, rok 2014)

• fundamental knowledge about cell cycle, cell signalisation, senencence, cell division, DNA reparation….

Scherens B, Goffeau A (2004) The uses of genome-wide yeast mutant collections. Genome biology 5:229

SGD Saccharomyces GENOME DATABASE

Analyze | Sequence | Function | Literature | Community | search: actin, kinase, glucose

Categories
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- Conferences
- Data updates
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- New Data
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New & Noteworthy

A Nobel Prize for Work in Yeast. Again!

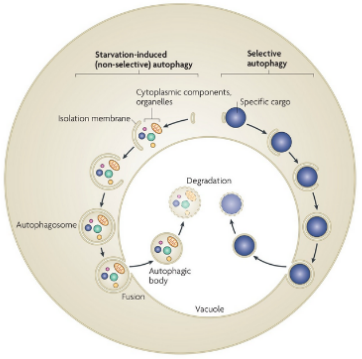
To se mi líbí 0 | Tweet

October 03, 2016

Dr. Yoshinori Ohsumi has won the 2016 Nobel Prize in Physiology or Medicine for his groundbreaking work on autophagy in yeast. This is the process whereby cells recycle their worn out parts or where a cell, like Mobius, the snake eating its own tail, eats less essential bits of itself to stay alive during times of starvation. Think Scarlett O'Hara using her drapes as a dress in Gone With the Wind (or Carol Burnett's hilarious parody).

Like many, many Nobel Prizes in the past, Ohsumi's work uncovered basic biological properties using a model organism. In this case he used our favorite lab workhorse, the yeast *Saccharomyces cerevisiae*, to piece together the steps involved in the recycling of a cell's own internal structures.

And like many other basic biological studies, this one has important medical applications. In this case the two most obvious are chemotherapy resistance and amyloid-β aggregation in Alzheimer's disease, but it isn't restricted to just these two. For example, a specialized form of autophagy that targets damaged mitochondria, mitophagy, may not be working well in people with Parkinson's disease.



Dr. Yoshinori Ohsumi has won the 2016 Nobel Prize in Physiology or Medicine for his groundbreaking work on autophagy in yeast. *Image from freethoughtblogs.com.*

The key to Ohsumi's work was finding a way to disrupt this process in yeast so that he could find the important genes underlying autophagy using the awesome power of yeast genetics (#APOYG!). It turns out that this is trickier than it might seem because yeast and their autophagosomes, the little vesicles that surround and encase the bits to be degraded, are very small and so hard to see. In fact, they

https://www.yeastgenome.org/blog/category/yeast-and-human-disease

- Leland H. Hartwell, R. Timothy (Tim) Hunt, and Paul M. Nurse won the 2001 Nobel Prize in Physiology or Medicine for their discoveries of "key regulators of the cell cycle".

- Roger D. Kornberg won the 2006 Nobel Prize in Chemistry "for his studies of the molecular basis of eukaryotic transcription".

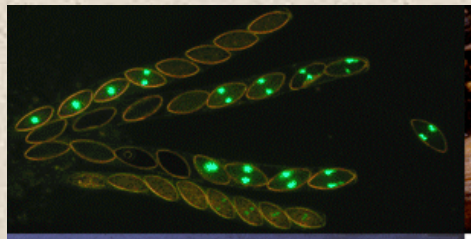
- Elizabeth H. Blackburn, Carol W. Greider, and Jack W. Szostak won the 2009 Nobel Prize in Physiology or Medicine "for the discovery of how chromosomes are protected by telomeres and the enzyme telomerase".

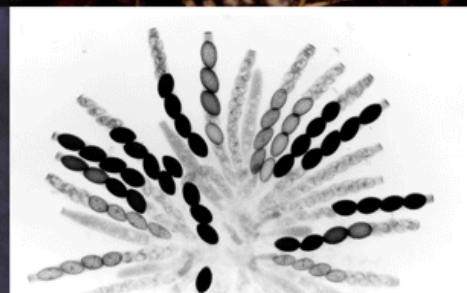
- James E. Rothman, Randy W. Schekman, and Thomas C. Südhof won the 2013 Nobel Prize in Physiology or Medicine "for their discoveries of machinery regulating vesicle traffic, a major transport system in our cells".

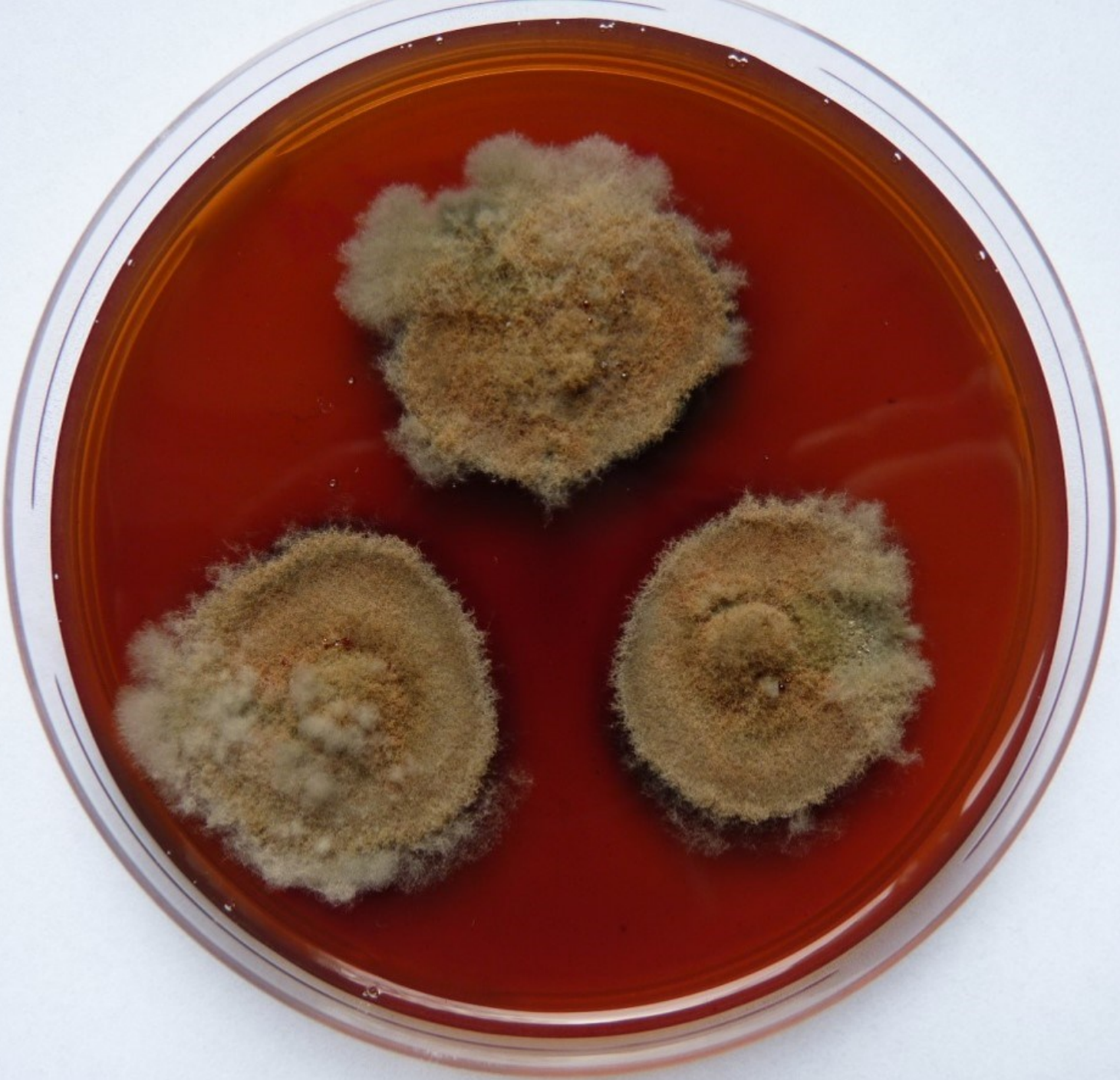
Neurospora crassa (Sordaryomycetes)

- Red-bread mold
- Prototrof
- Velmi rychlý růst ~3 mm/h
- První genom mnohobuněčného Eukaryota, 2003
- 43 MB, 10 000 genů, 7 chromozomů (o 25% méně než *Drosophila*)
- Studium knock-outů zásadně přispělo k osvětlení funkce jednotlivých genů
- Základní práce o buněčné fůzi, polaritě, gene silencingu a cirkadiálních rytmech…

- Studium příbuzných druhů a rodů
- *Neurospora* spp., *Podospora anserina*

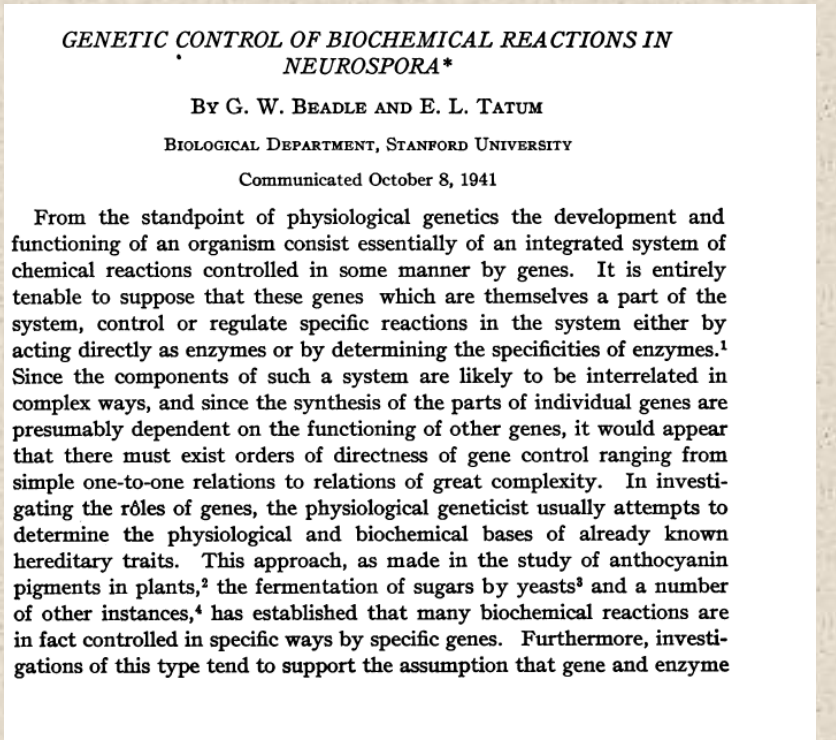






Neurospora crassa (Sordaryomycetes)

- 1941 G. Beadle a E. Tatum - ozařováním získaly mutantní kmeny u kterých porovnávali enzymatické aktivity.
- první definice genu - "one gene, one enzyme„
- Nobelova cena 1958



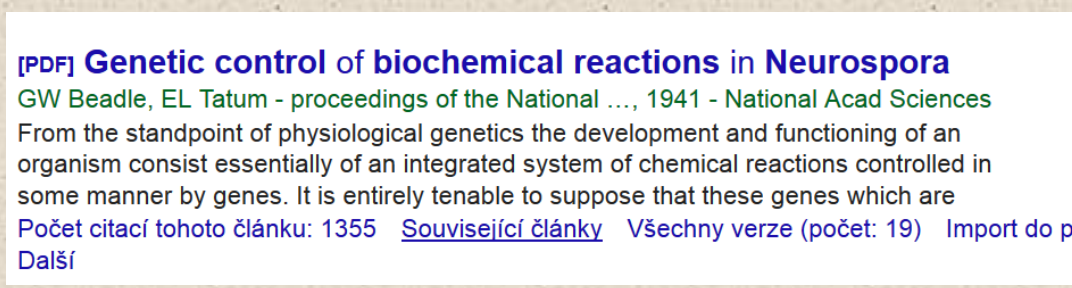
*GENETIC CONTROL OF BIOCHEMICAL REACTIONS IN NEUROSPORA**

By G. W. Beadle and E. L. Tatum

Biological Department, Stanford University

Communicated October 8, 1941

From the standpoint of physiological genetics the development and functioning of an organism consist essentially of an integrated system of chemical reactions controlled in some manner by genes. It is entirely tenable to suppose that these genes which are themselves a part of the system, control or regulate specific reactions in the system either by acting directly as enzymes or by determining the specificities of enzymes.[1] Since the components of such a system are likely to be interrelated in complex ways, and since the synthesis of the parts of individual genes are presumably dependent on the functioning of other genes, it would appear that there must exist orders of directness of gene control ranging from simple one-to-one relations to relations of great complexity. In investigating the rôles of genes, the physiological geneticist usually attempts to determine the physiological and biochemical bases of already known hereditary traits. This approach, as made in the study of anthocyanin pigments in plants,[2] the fermentation of sugars by yeasts[3] and a number of other instances,[4] has established that many biochemical reactions are in fact controlled in specific ways by specific genes. Furthermore, investigations of this type tend to support the assumption that gene and enzyme



[PDF] **Genetic control** of **biochemical reactions** in **Neurospora**

GW Beadle, EL Tatum - proceedings of the National ..., 1941 - National Acad Sciences

From the standpoint of physiological genetics the development and functioning of an organism consist essentially of an integrated system of chemical reactions controlled in some manner by genes. It is entirely tenable to suppose that these genes which are

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Další

https://www.nobelprize.org/prizes/medicine/1958/beadle/lecture/

Genetické pozadí rozmnožování

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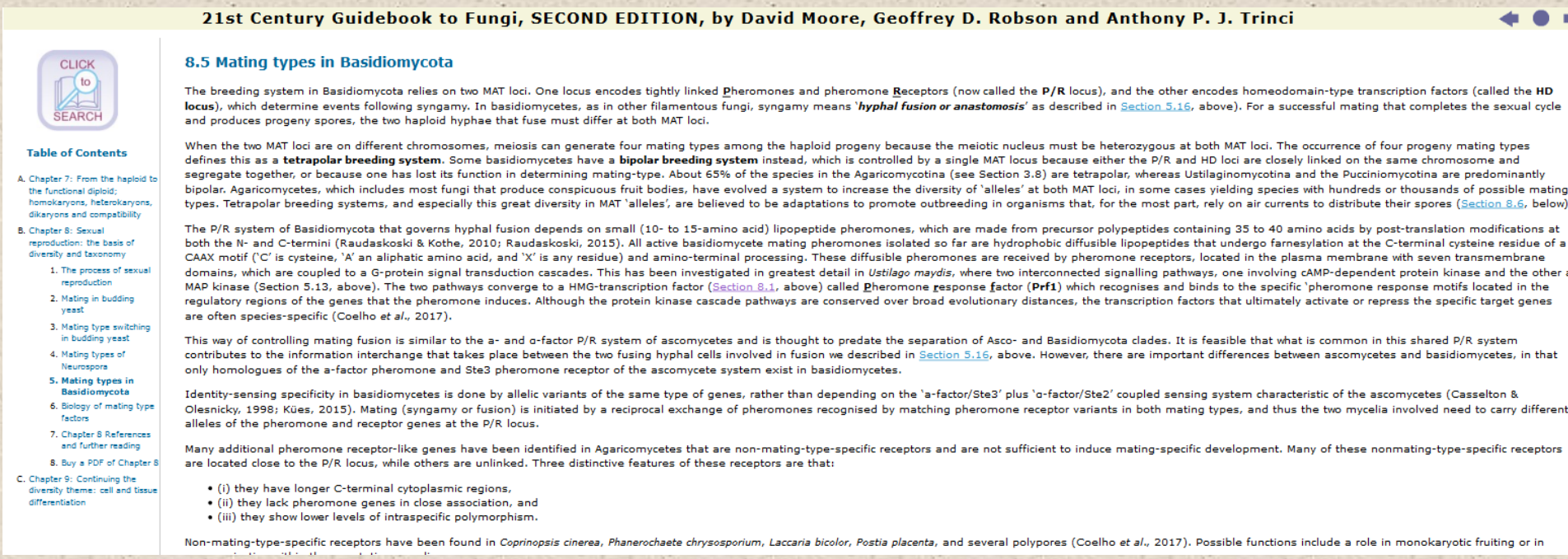

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5. **Mating types in Basidiomycota**
6. Biology of mating type factors
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8.5 Mating types in Basidiomycota

The breeding system in Basidiomycota relies on two MAT loci. One locus encodes tightly linked **P**heromones and pheromone **R**eceptors (now called the **P/R** locus), and the other encodes homeodomain-type transcription factors (called the **HD locus**), which determine events following syngamy. In basidiomycetes, as in other filamentous fungi, syngamy means '***hyphal fusion or anastomosis***' as described in Section 5.16, above). For a successful mating that completes the sexual cycle and produces progeny spores, the two haploid hyphae that fuse must differ at both MAT loci.

When the two MAT loci are on different chromosomes, meiosis can generate four mating types among the haploid progeny because the meiotic nucleus must be heterozygous at both MAT loci. The occurrence of four progeny mating types defines this as a **tetrapolar breeding system**. Some basidiomycetes have a **bipolar breeding system** instead, which is controlled by a single MAT locus because either the P/R and HD loci are closely linked on the same chromosome and segregate together, or because one has lost its function in determining mating-type. About 65% of the species in the Agaricomycotina (see Section 3.8) are tetrapolar, whereas Ustilaginomycotina and the Pucciniomycotina are predominantly bipolar. Agaricomycetes, which includes most fungi that produce conspicuous fruit bodies, have evolved a system to increase the diversity of 'alleles' at both MAT loci, in some cases yielding species with hundreds or thousands of possible mating types. Tetrapolar breeding systems, and especially this great diversity in MAT 'alleles', are believed to be adaptations to promote outbreeding in organisms that, for the most part, rely on air currents to distribute their spores (Section 8.6, below).

The P/R system of Basidiomycota that governs hyphal fusion depends on small (10- to 15-amino acid) lipopeptide pheromones, which are made from precursor polypeptides containing 35 to 40 amino acids by post-translation modifications at both the N- and C-termini (Raudaskoski & Kothe, 2010; Raudaskoski, 2015). All active basidiomycete mating pheromones isolated so far are hydrophobic diffusible lipopeptides that undergo farnesylation at the C-terminal cysteine residue of a CAAX motif ('C' is cysteine, 'A' an aliphatic amino acid, and 'X' is any residue) and amino-terminal processing. These diffusible pheromones are received by pheromone receptors, located in the plasma membrane with seven transmembrane domains, which are coupled to a G-protein signal transduction cascades. This has been investigated in greatest detail in *Ustilago maydis*, where two interconnected signalling pathways, one involving cAMP-dependent protein kinase and the other a MAP kinase (Section 5.13, above). The two pathways converge to a HMG-transcription factor (Section 8.1, above) called **P**heromone **r**esponse **f**actor (**Prf1**) which recognises and binds to the specific 'pheromone response motifs located in the regulatory regions of the genes that the pheromone induces. Although the protein kinase cascade pathways are conserved over broad evolutionary distances, the transcription factors that ultimately activate or repress the specific target genes are often species-specific (Coelho *et al*., 2017).

This way of controlling mating fusion is similar to the a- and α-factor P/R system of ascomycetes and is thought to predate the separation of Asco- and Basidiomycota clades. It is feasible that what is common in this shared P/R system contributes to the information interchange that takes place between the two fusing hyphal cells involved in fusion we described in Section 5.16, above. However, there are important differences between ascomycetes and basidiomycetes, in that only homologues of the a-factor pheromone and Ste3 pheromone receptor of the ascomycete system exist in basidiomycetes.

Identity-sensing specificity in basidiomycetes is done by allelic variants of the same type of genes, rather than depending on the 'a-factor/Ste3' plus 'α-factor/Ste2' coupled sensing system characteristic of the ascomycetes (Casselton & Olesnicky, 1998; Kües, 2015). Mating (syngamy or fusion) is initiated by a reciprocal exchange of pheromones recognised by matching pheromone receptor variants in both mating types, and thus the two mycelia involved need to carry different alleles of the pheromone and receptor genes at the P/R locus.

Many additional pheromone receptor-like genes have been identified in Agaricomycetes that are non-mating-type-specific receptors and are not sufficient to induce mating-specific development. Many of these nonmating-type-specific receptors are located close to the P/R locus, while others are unlinked. Three distinctive features of these receptors are that:

- (i) they have longer C-terminal cytoplasmic regions,
- (ii) they lack pheromone genes in close association, and
- (iii) they show lower levels of intraspecific polymorphism.

Non-mating-type-specific receptors have been found in *Coprinopsis cinerea*, *Phanerochaete chrysosporium*, *Laccaria bicolor*, *Postia placenta*, and several polypores (Coelho *et al*., 2017). Possible functions include a role in monokaryotic fruiting or in

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Jaderné poměry u hub

- **Monokaryotické** mycelium – askomycety, primární mycelium basidiomycetů. Jedno jaderné.
- **Dikaryotické** – sek. mycelium bazidiomycetů, askogenní hyfa. Dvou jaderné.

- **Polykaryotické** – Glomeromycota, a další bazální linie, Dikarya daleko méně. Mnoho jaderné.

- **Homokaryotické** – všechna jádra geneticky identická

- **Heterokaryotické –** jádra geneticky odlišná (terminologie platí pro mono-, di-, i polykaryotické houby)

Pohlavní proces - výhody

•rekombinace zvětšuje genetickou diverzitu, která je k dispozici přírodnímu výběru. Prospěšné znaky se tak mohou dostat z vazby znaků horších

•neprospěšné mutace mohou být vyloučeny z populace

•zásadní u hub žijících v proměnlivém prostředí (Red Queen Hypothesis) (experimenty s kvasinkami ukazují důležitost rekombinace pro život ve stresu)

• možnost uplatnění pohlavního výběru u hub odpadá, mají zanedbatelný pohlavní dimorfismus

Pohlavní proces - nevýhody

• Hlavní nevýhoda pohlavnosti u jiných organismů, tj. že samci nemůžou rodit potomky, u hub neplatí (mají velmi omezený pohl. dimorfismus)

• Ve stabilním prostředí může být rozbíjení ustálených kombinací genů nevýhodou (hostitelsky specifičtí a adaptovaní symbionti)

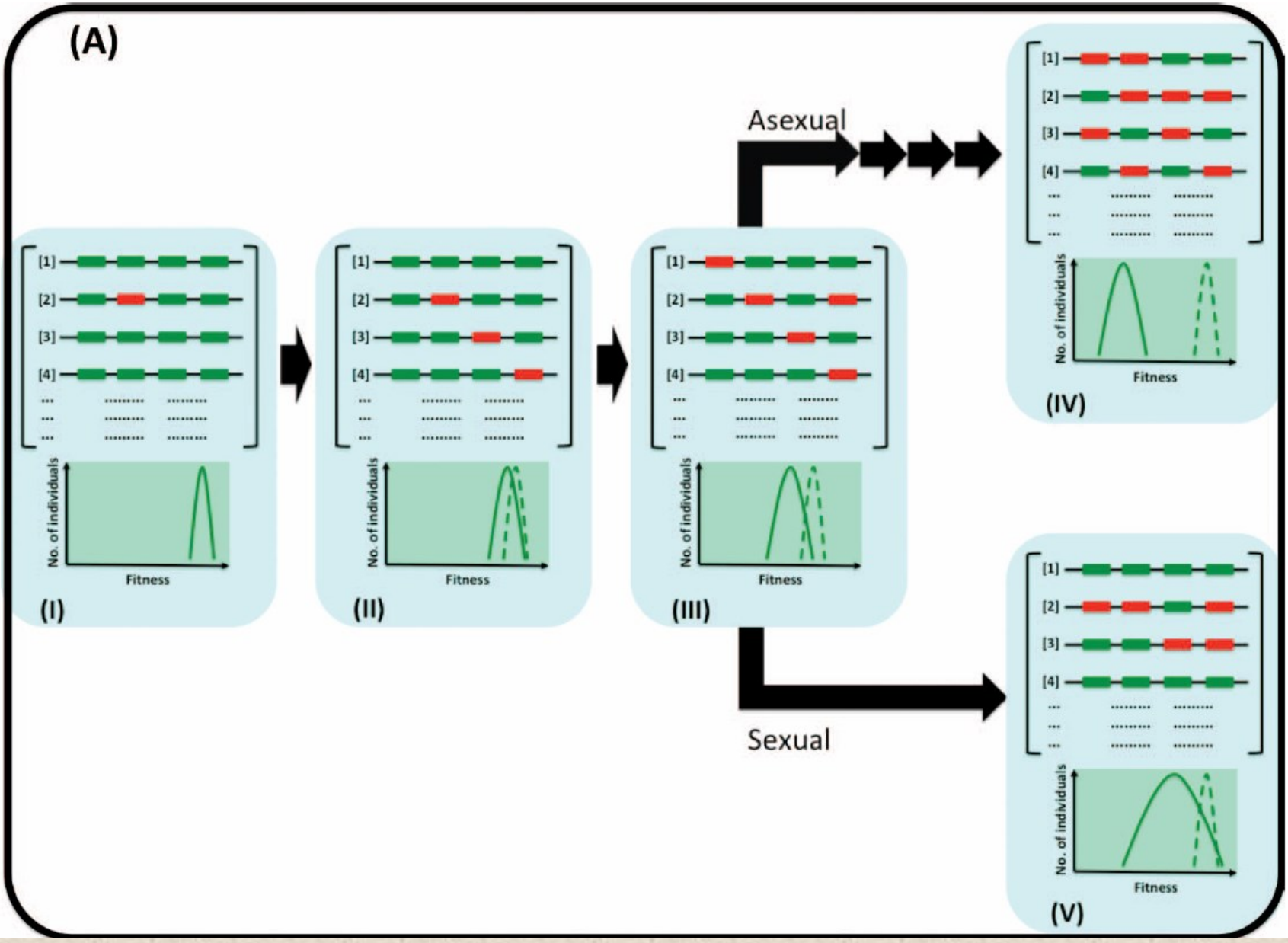
• Pohlavní proces nese riziko přenosu virů, defektních organel a plazmidů

• Asexuálních spor se může tvořit řádově více, a rychleji než sexuálních

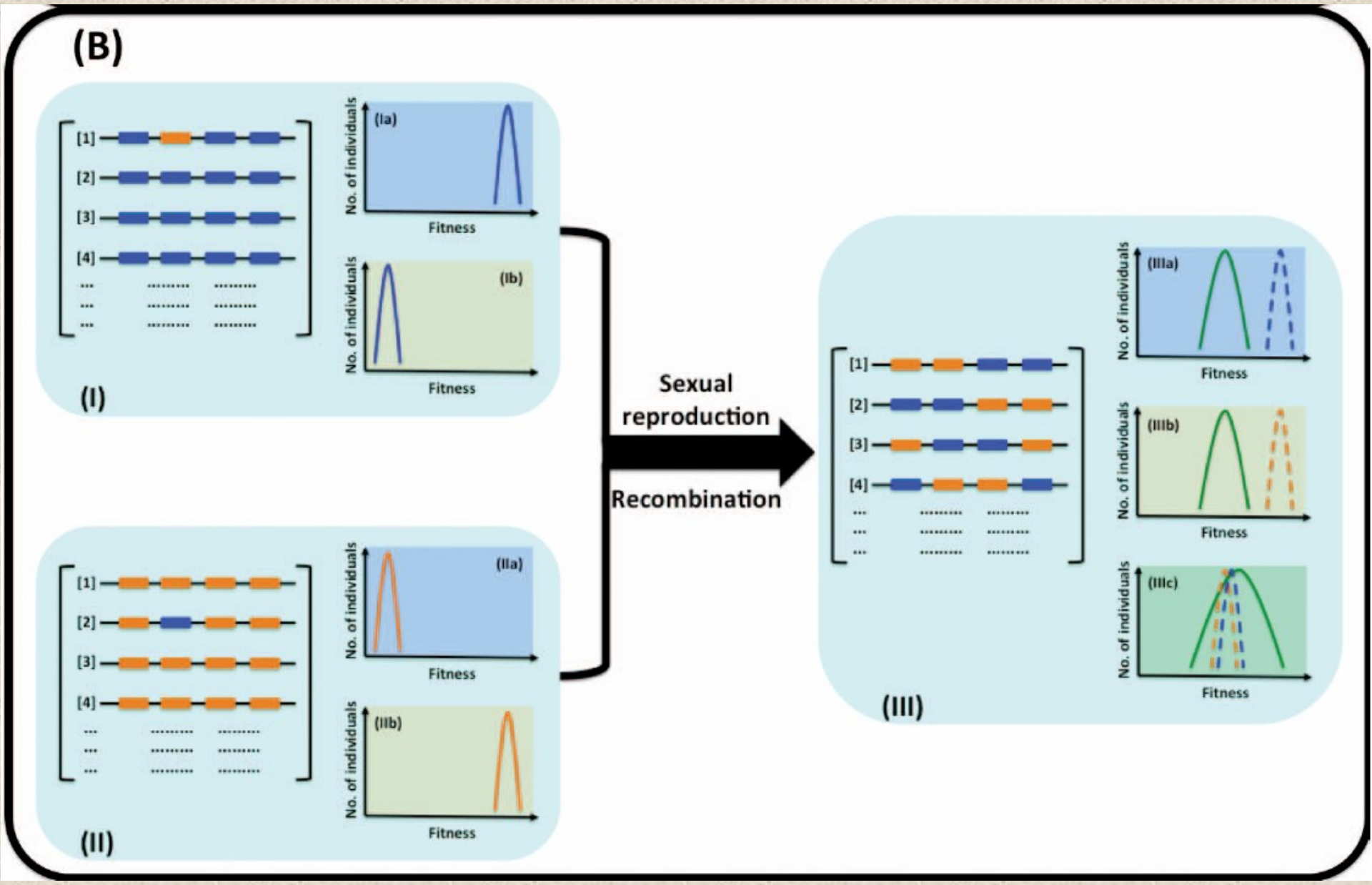
- mitóza je rychlejší a méně náročnější než meióza

- meiospora (asko-, bazidiospora) bývá stavebně náročnější

https://doi.org/10.3852/12-253



Zelené alely jsou nepoškozené. V nepohlavní populaci se hromadí škodlivé mutace (červeně) a časem v ní nenajdeme „perfektního“ jedince. Díky pohlavnímu procesu (či parasexualnímu) může opět vzniknout perfektní jedinec..



Nevýhodnou nepohlavnosti je rozbití výhodných, ustálených kombinací alel. To je problém u vysoce adaptovaných populací. Z tohoto důvodu jsou například symbiotické houby velmi často nepohlavní

Current Biology 20, 1350–1355, August 10, 2010 ©2010 Elsevier Ltd All rights reserved DOI 10.1016/j.cub.2010.05.060

Report

Fitness-Associated Sexual Reproduction in a Filamentous Fungus

Sijmen Schoustra,[1,2,*] Howard D. Rundle,[1,2] Rola Dali,[1] and Rees Kassen[1]
[1]Department of Biology, Center for Applied Research in Environmental Genomics, University of Ottawa, 30 Marie Curie, Ottawa, Ontario K1N 6N5, Canada

Facultative sexual species often engage in sexual reproduction in response to environmental stress or degradation, suggesting that individuals in poor condition are more likely to undergo sex [11]. It is also well known, for instance, that the protocol for inducing a sexual cycle in eukaryotic model micro-

- allocate disproportionately more resources to sex when their fitness is low (fitness-associated-sex)
- unfavourable conditions stimulates sexual reproduction which offers new haplotypes to the natural selection
- E.g. Nitrogen starvation is used as a startert of yeast sexual cycle

JOURNAL OF BACTERIOLOGY, Apr. 1980, p. 276–284 Vol. 142, No. 1
0021-9193/80/04-0276/09$02.00/0

Sporulation in *Hansenula wingei* Is Induced by Nitrogen Starvation in Maltose-Containing Media

MARJORIE CRANDALL* AND L. J. LAWRENCE

Pohlavní proces - nevýhody

•Pohlavní proces vyžaduje najít geneticky kompatibilního partnera (2, 4, či více pohlaví)

•Homothalické druhy rodu *Neurospora* (můžou se pářit sami se sebou) nemají konidiální stádium, kdežto heterothalické ano

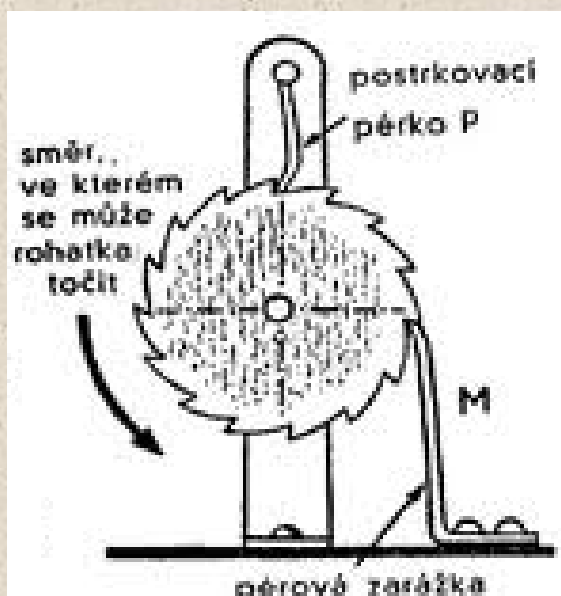
Neurospora sitophila, heterothalický druh se silnou produkcí konidií

Nevýhody nepohlavnosti – Mullerova rohatka

• klonálost by měla vést k postupné akumulaci škodlivých mutací.
• částečně lze obejít velkou produkcí diaspor - část z nich bude mít nezměněné *fitness*

• lze obejít díky **Parasexuálnímu procesu** – možnost rekombinace bez pohlavního procesu

• Popsán u *Aspergillus nidulans* (1956)
• *Fusarium monoliforme, Penicillium roqueforti, Verticillium dahliae, Verticillium alboatrum, Pseudocercosporella herpotrichoides, Ustilago scabiosae, Magnaporthe grisea, Cladosporium fulvum….*



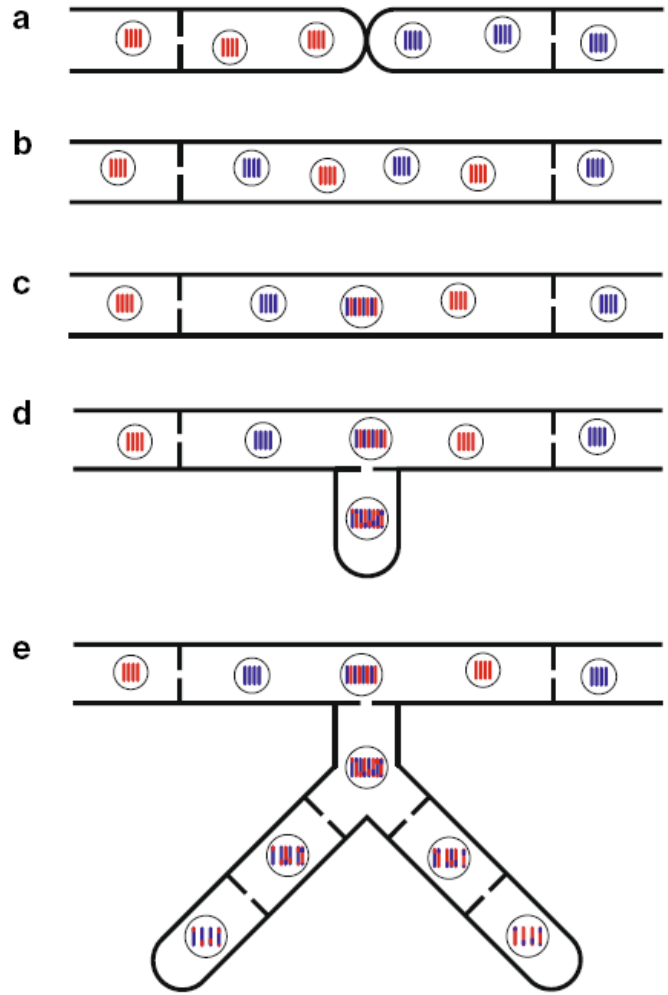


Fig. 1 The parasexual cycle. The parasexual cycle parallels events in the sexual cycle, resulting in genetically unique haploid offspring but without a meiotic reduction. **a** Hyphae of genetically unique homokaryotic parents grow towards each other by chemotaxis and fuse. **b** Nuclei from each unique strain migrate within the fused hypha, which is now considered a heterokaryon. **c** Haploid nuclei in the heterokaryon undergo karyogamy to create a heterozygous diploid nucleus. **d** The diploid nucleus undergoes mitotic recombination to produce a recombined genotype. **e** In growing hyphae, gradual loss of chromosomes due to repeated rounds of mitotic non-disjunction results in haploidization and unique genotypes in various sectors of mycelium

• Děje se v rámci kmene i mezi kmeny („křížení“) stejné *Vegetative compatibiilty group* (VCG)

•Kmeny ze stejné VCG tvoří anastomózy (snadno sledovatelný biologický znak)

•Následuje fúze jader (2n, i vícenásobná, endopolyploidie)

•vznikne heterokaryon – stejně jako u pohl. rozmnož., ale s daleko menší pravděpodobností - 10^{-6}-10^{-5} jader u *A. nidulans*)

•Karyogamie – vzniklé 2n jádro je nestabilní

Strom and Bushley *Fungal Biol Biotechnol* (2016) 3:4
DOI 10.1186/s40694-016-0022-x

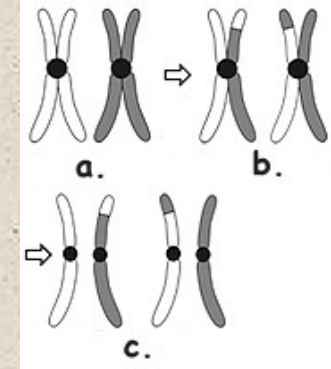
Parasexuální proces jako zdroj variability

- Během následných mitotických dělení dochází k poruchám v rozchodu chromatid, což vede k **aneuploidii**, a genetické rekombinaci

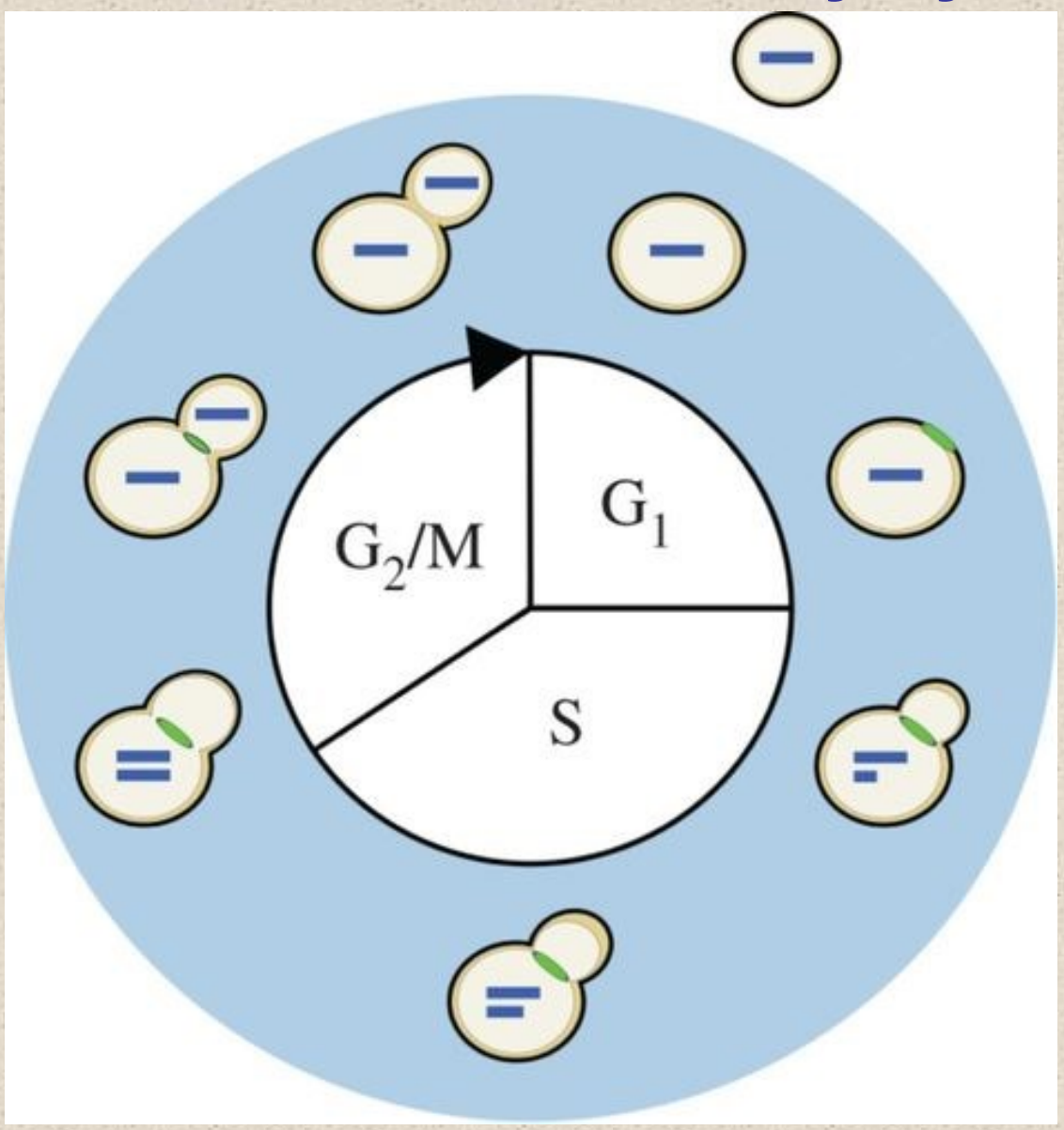
- **Aneuploidi** mají o jednu chromatidu méně či více oproti diploidnímu stavu (2n+1, 2n-1), následným dělením dochází k haploidizaci.
  - Obrovský zdroj variability genomu

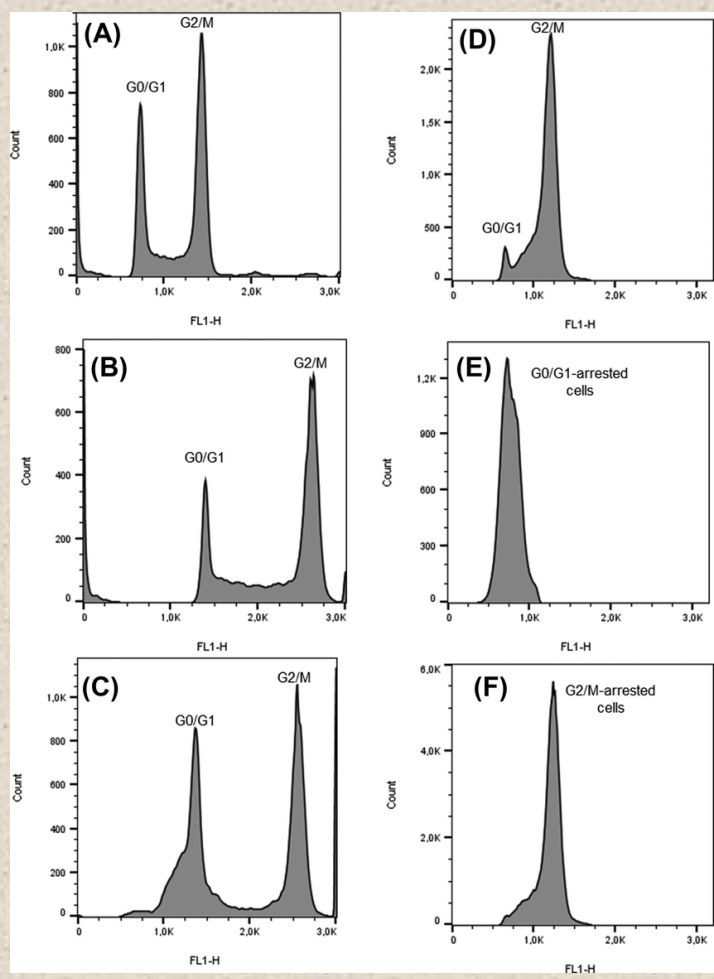
- Mitotický *crossing over* (1/500 dělení) umožňuje další rekombinaci

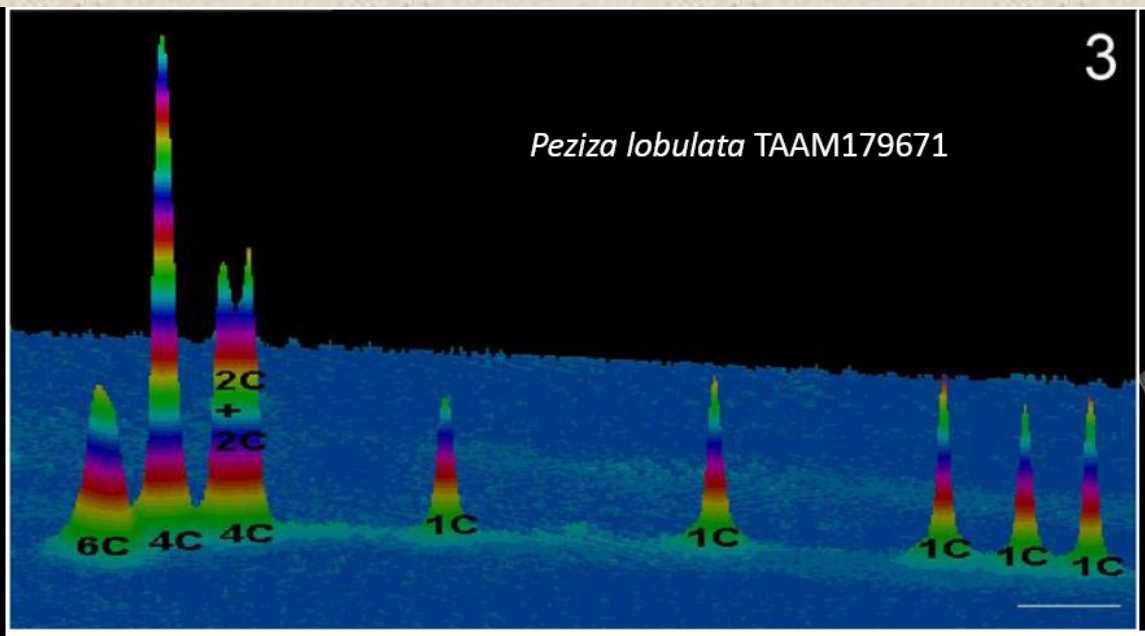
crossing-over může být i nerovnoměrný, což vede k duplikacím/delecím určitých částí genomu



Buněčný cyklus







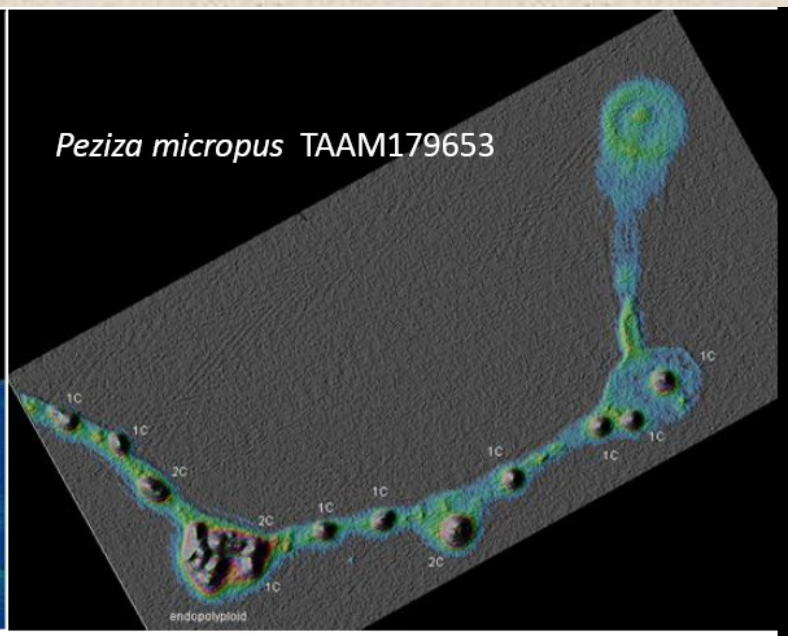
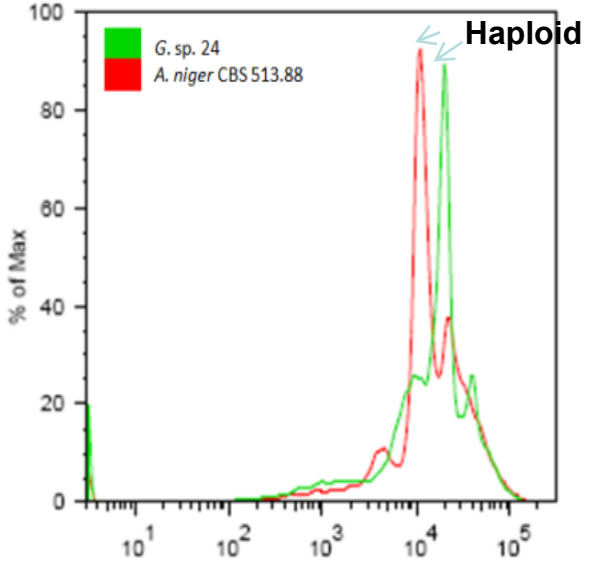


Fig. 3. Relative nuclear DNA content in the hyphae of a pure culture of *Peziza lobulata* TAA179671. The ultimate nucleus has higher growth potential compared with its sister nucleus. Replication in the nucleus of the top cell is faster than division, while the posterior nuclei can be divided without replication and stop at the 1C value.
As a result, there arise **endopolyploidization** (in the apical cells) and **haploidization** (in the posterior cells).
C – the C-value which corresponds to genome size. Bar = 5 ųm (Kullman and Teterin 2006).

Parasexuální proces jako zdroj variability

- Velké rozpětí v počtu chromosomů (6-11) i ve velikosti genomu (14,0-28,7 Mb) bylo nalezeno u *Pleurotus ostreatus* a *P. pulmonarius* (17,9-44,1 Mb)
- Plodnice *P. ostreatus* vytvářela dvě subpopulace spor lišícími se velikostí i množstvím DNA.

Variabilita velikosti spor

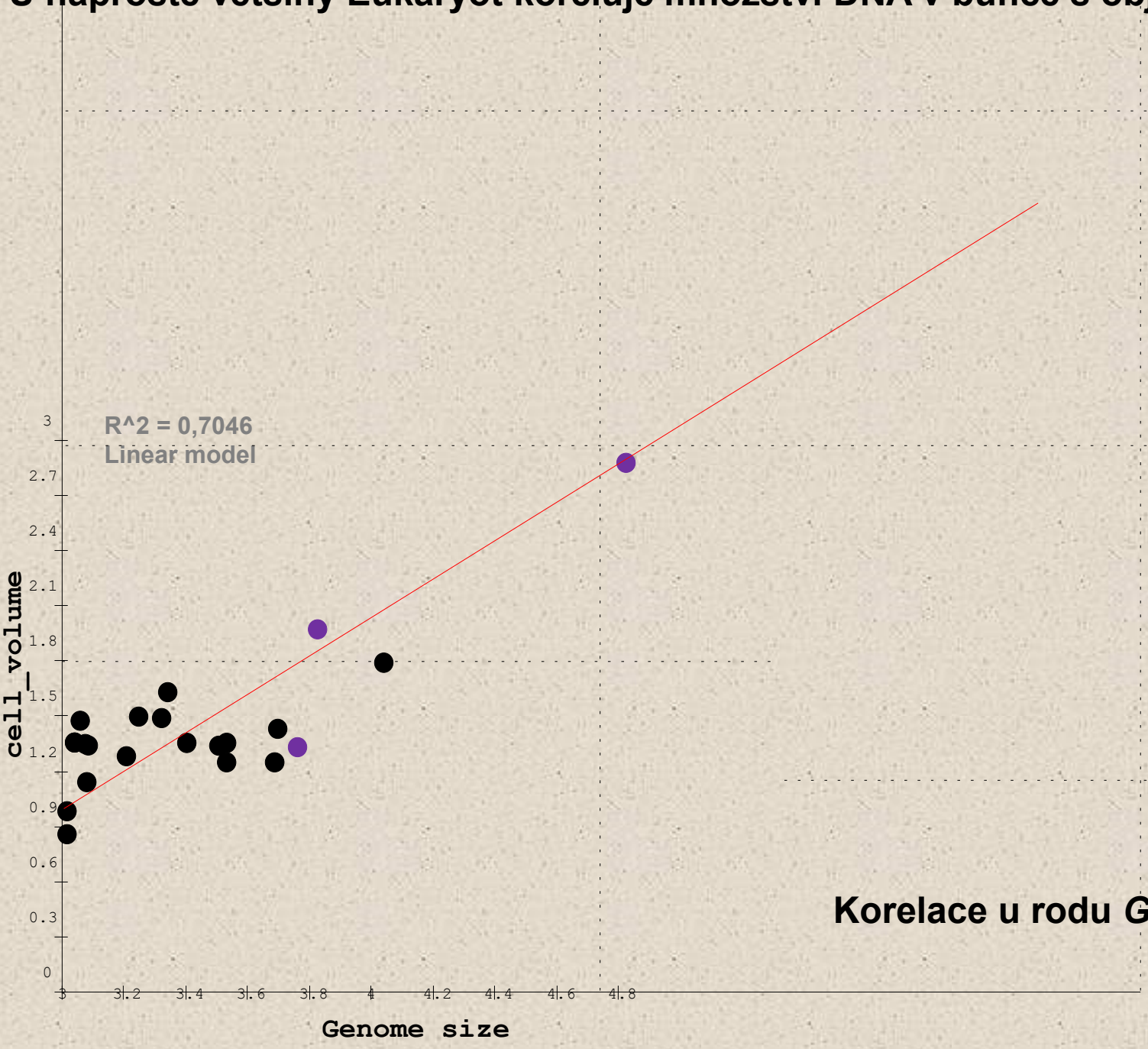


Haploid peak

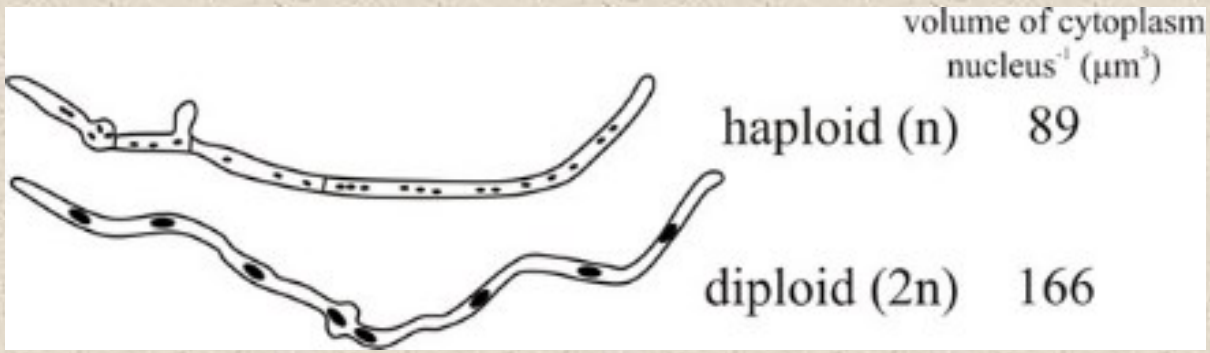
Konidie druhu *Geosmithia* sp. 24

10 µm

U naprosté většiny Eukaryot koreluje množství DNA v buňce s objemem buňky



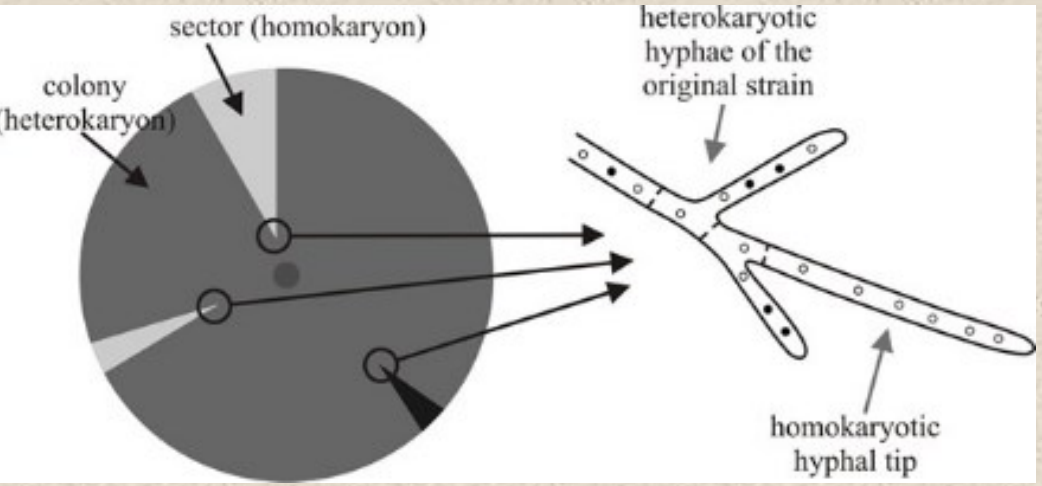
Korelace u rodu *Geosmithia*

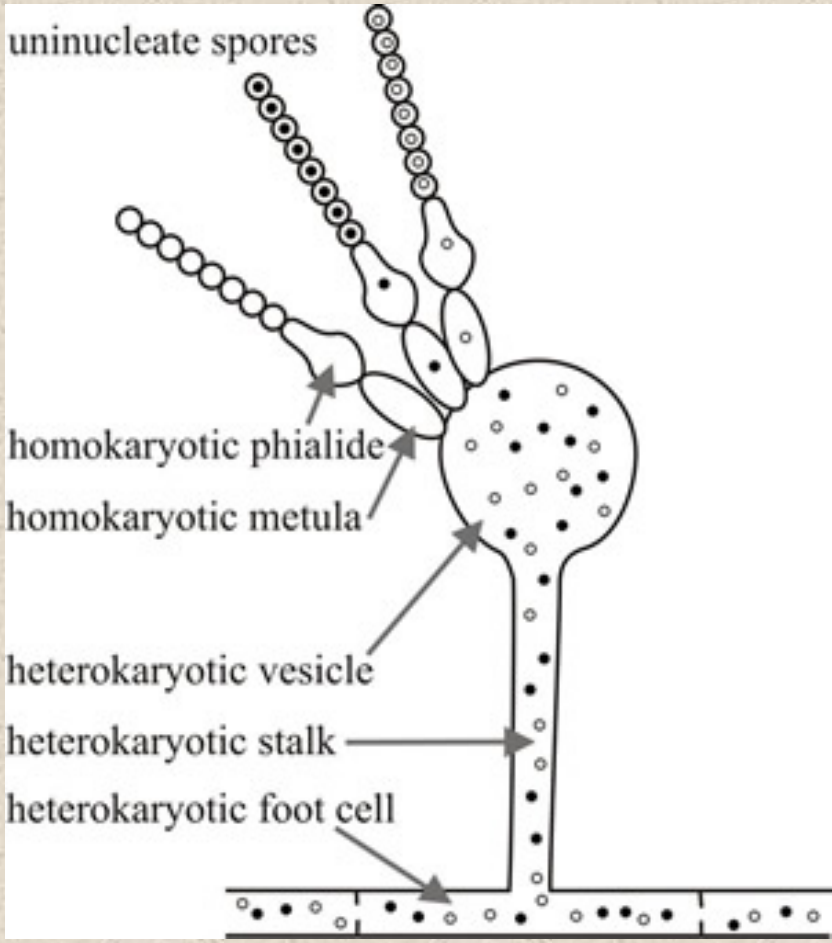


Diagrammatic comparison of germinating haploid and diploid spores of *Aspergillus nidulans*. Redrawn from camera lucida drawings in Fiddy & Trinci, 1976.

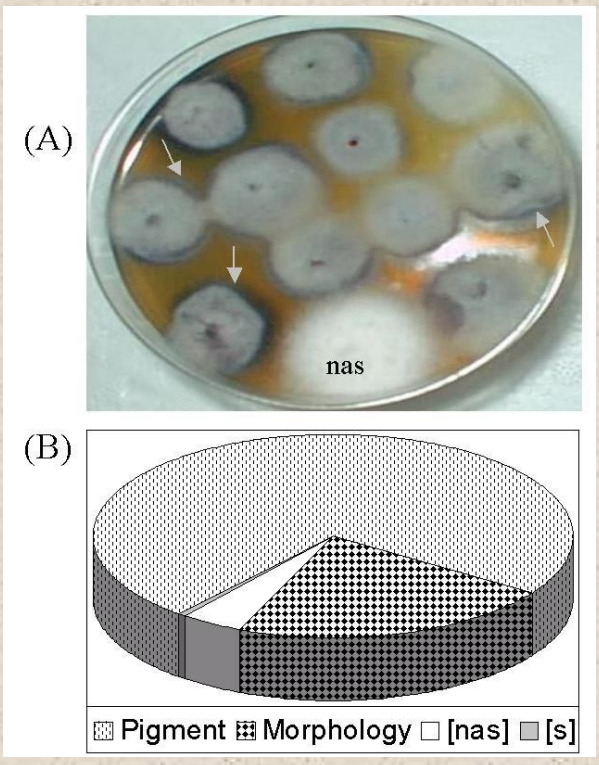
větší jádra = vice cytoplazmy

Parasexuální proces jako zdroj variability

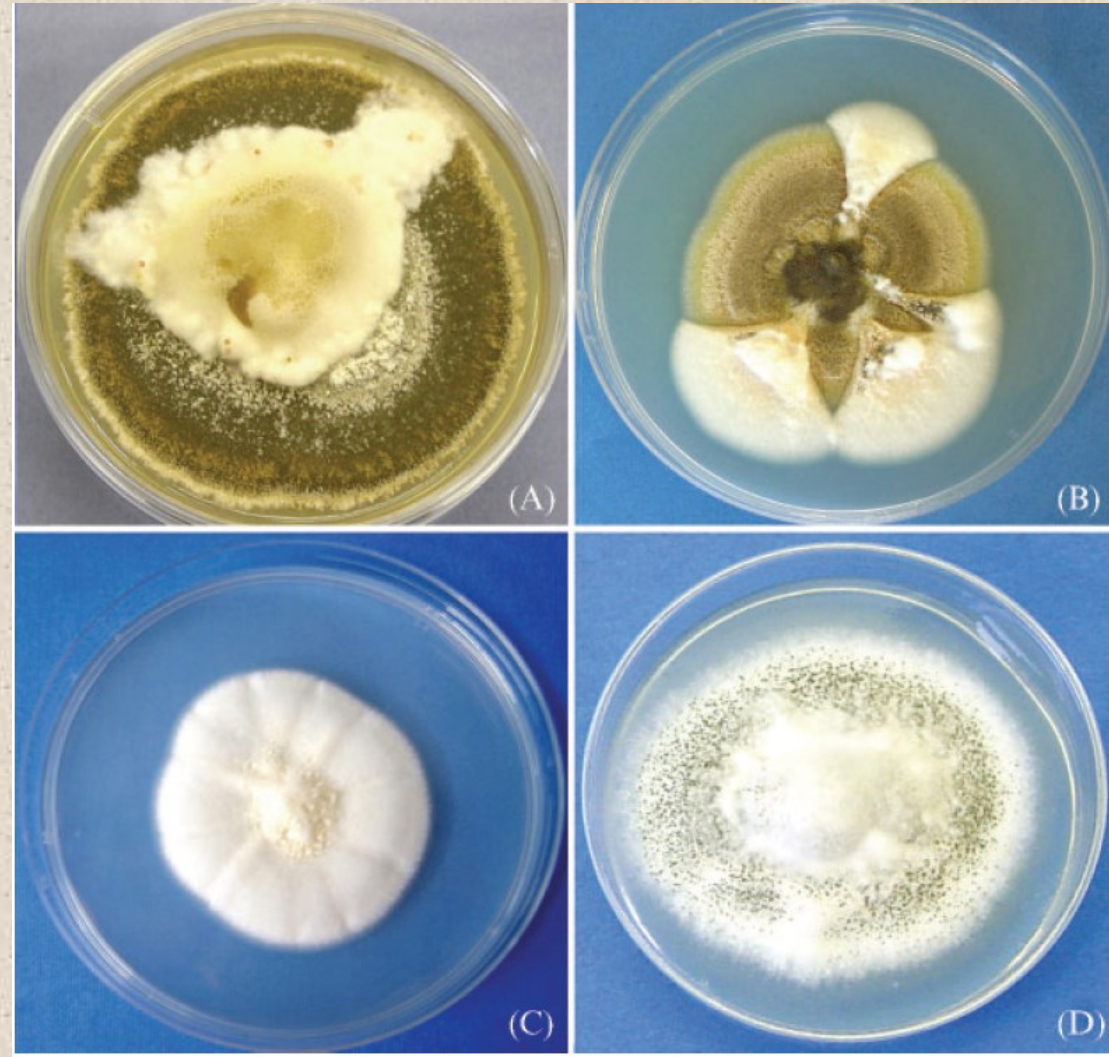




Moore, D., Robson, G.D. & Trinci, A.P.J. (2011). 21st Century Guidebook to Fungi. Cambridge, UK: Cambridge University Press. ISBN: 9780521186957.



BMC Biology2004**2**:18
https://doi.org/10.1186/1741-7007-2-18



Kombinace pohl. a nepohlavnosti

- Malé konidie jsou vhodné na rychlé rozšíření na krátkou vzdálenost
- Meiospory (asko či bazidiospory) jsou obecně odolnější vůči stresu (teplo. sucho)
- *Claviceps* – askospory přežívají zimu a malé konidie slouží k sekundární infekci během sezóny

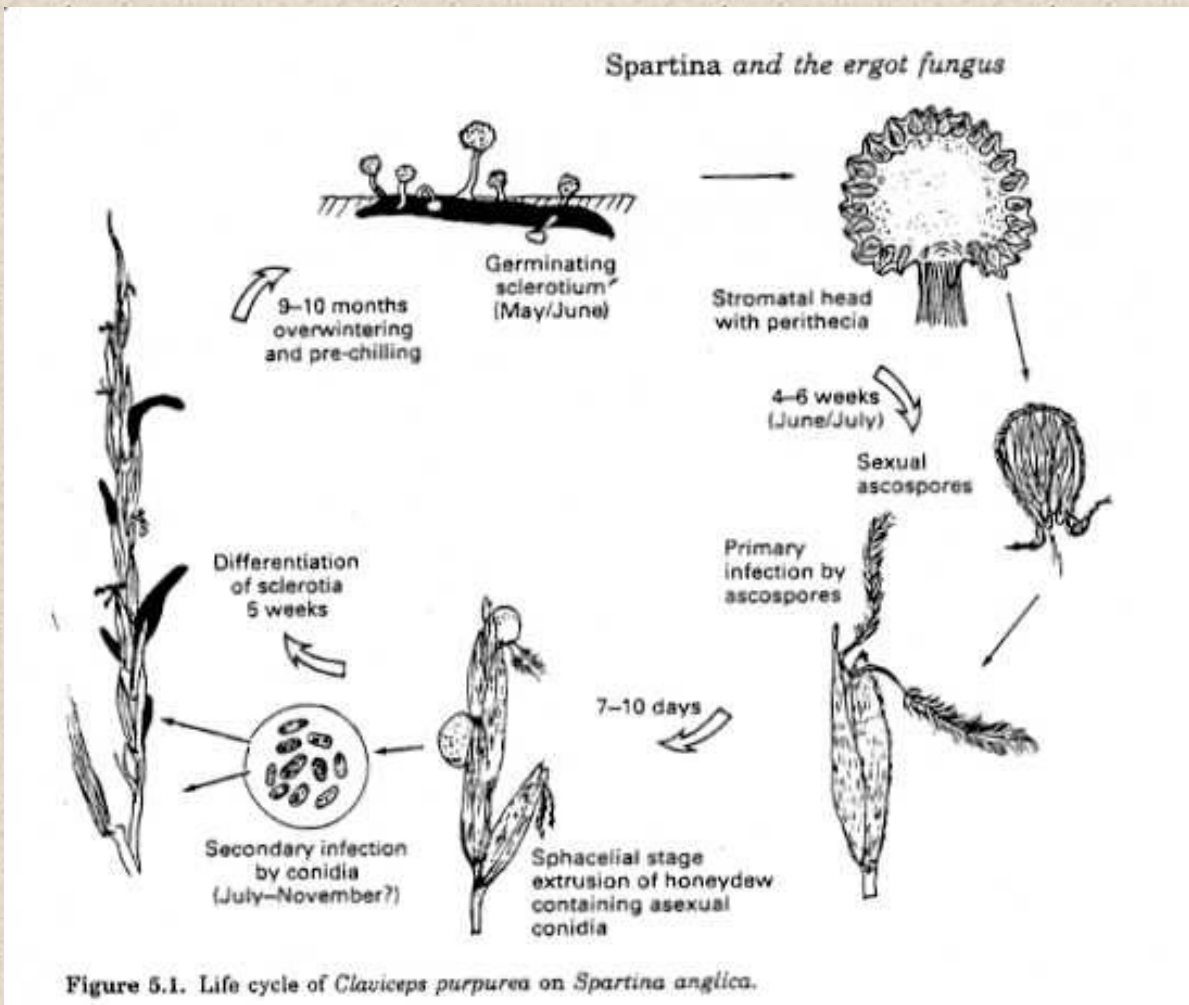
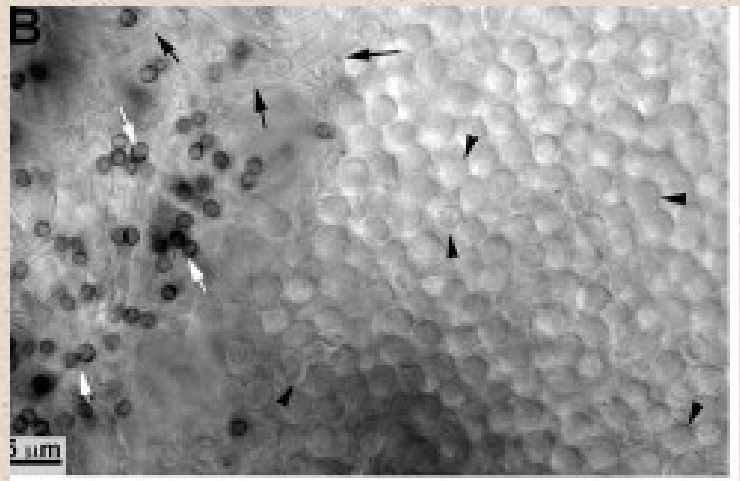


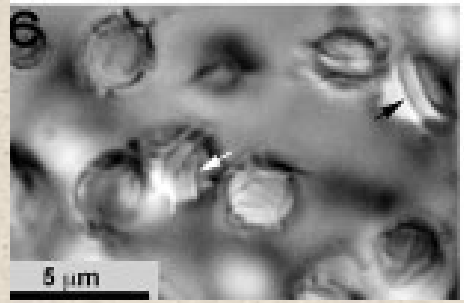
Figure 5.1. Life cycle of *Claviceps purpurea* on *Spartina anglica*.

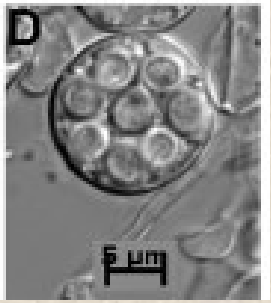
Odolné meiospory

- *Aspergillus fumigatus* – 70°C a 30 minut zničí konidie
- askospory jsou tolerantní k extrémním teplotám

  - možnost izolace meiospor od mitopor







Identification and Characterization of an *Aspergillus fumigatus* "Supermater" Pair

Janyce A. Sugui,[a] Liliana Losada,[b] Wei Wang,[b] John Varga,[b] Popchai Ngamskulrungroj,[a] Mones Abu-Asab,[c] Yun C. Chang,[a] Céline M. O'Gorman,[d] Brian L. Wickes,[e] William C. Nierman,[b] Paul S. Dyer,[d] and Kyung J. Kwon-Chung[a]

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Shrnutí

TABLE I. Comparison between sexual and asexual reproduction

	Sexual reproduction[a]	Asexual reproduction[a]
Energy cost	High a	Low b
Chance of genetic/organelle conflicts	High	Low
Recombination load[b] (i.e. breaking down of co-adapted gene combinations)	High	Low
Genetic diversity	Stable or increase c	Stable or decrease d
Adaptation to changing/fluctuating environment	Fast e	Slow f
Purging deleterious mutations[b]	More efficient	Less efficient
Selection of beneficial mutations	More efficient	Less efficient

[a] a: Require energy for finding and interacting with mating partner; meiosis is more energy consuming than mitosis. b: No energy needed to find and interact with mating partner; mitosis is more energy efficient. c: Stable if the population is in linkage equilibrium; increase if linkage disequilibrium is present in the population. In addition, meiosis may be mutagenic, which can introduce substitutions and ploidy changes at a higher rate than mitosis. d: Stable if there is no selection; decrease if there is clonal expansion. e: In some microorganisms such as fungi, sexual reproduction can also produce spores that can better resist harsh environments, as well as be better dispersed. f: The adaption of asexual population also can be fast, if a favorable genotype emerges and takes over the population by selective sweep.

[b] See FIG. 3.

Mycologia, 105(1), 2013, pp. 1–27. DOI: 10.3852/12-253

Issued 8 January 2013

Nepohlavnost je patrně je krátkodobou evoluční strategií

•U 20% hub není známo pohlavní stádium (Pringle et al. 2005). Typicky jde o odvození skupiny v rámci dané linie. Velmi často klonální populace, pouze jeden párovací typ. Nepohlavnost není dlouhodobou evoluční strategií.

•Glomeromycota - jediná skupina, u které se věří, že je čistě nepohlavní.

- Nebyla pozorována pohlavní struktura
- tvoří klonální populace (alely jsou v silné vazbě)

X

- *Glomus intraradices* - identifikovány geny výhradně spojené s meiozou (Tisserant et al. 2012)
- Geny *sexP* and *sexM* v genomu *Glomus intraradices* jsou předchůdci MAT genů

Using a meiosis detection toolkit to investigate ancient asexual "scandals" and the evolution of sex

Andrew M. Schurko and John M. Logsdon Jr*

BioEssays 30:579–589, © 2008 Wiley Periodicals, Inc.

BioEssays 30.6 579

- Geny spojené s meiozou ukazující na aktuální či nedávno ztracenou schopnost pohlavního rozmnožování
- Známy univerzální primery na celá Eukaryota

Table 1. Distribution of genes in the meiosis detection toolkit among representative eukaryotes

		SPO11	HOP1	HOP2	MND1	REC8	RAD21	DMC1	RAD51	MSH4,5	MSH2,6
ANIMALS	*Homo*	+	+	+	+	+	+	+	+	+,+	+,+
	Drosophila	+	–	–	–	+	+	–	+	–,–	+,+
	Caenorhabditis	+	+	–	–	+	+	–	+	+,+	+,+
FUNGI	*Saccharomyces*	+	+	+	+	+	+	+	+	+,+	+,+
	Schizosaccharo.	+	+	+	+	+	+	+	+	–,–	+,+
	Aspergillus	+	+	+	+	+	+	+	+	+,+	+,+
	Cryptococcus	+	+	+	+	+	+	+	+	+,+	+,+
PLANTS	*Arabidopsis*	+	+	+	+	+	+	+	+	+,+	+,+
	Oryza/Zea	+	+	+	+	+	+	+	+	+,+	+,+
	Cyanidioschyzon	+		+	+	+	+	+	+	+,+	+,+
PROTISTS	*Entamoeba*	+	–	+	+		+	+	+	+,+	+,+
	Plasmodium	+	+	+	+		+	+	+	–,–	+,+
	Trypanosoma	+	+	+	+		+	+	+	+,+	+,+
	Giardia	+	+	+	+			+	–	–,–	+,+

Gene names in black background/shaded columns are meiosis-specific. "+" = gene present and "–" = gene absent. Open spaces indicate genes that have not yet been found, but for which genome data are insufficient and/or levels of sequence conservation may be too low for detection.

Self-, non-self-recognition

- basic for species boundary maintenance

- **Vegetative incompatibility – ability of cell fusion**

- **Sexual incompatibility – ability of mating, recombinatin**

prezygotic barriers

---

postzygotic barriers

- **Meiotic mutants**
- **Spore Killers**
- **Intersterility**
- **Lower fitness**

Homo- vs. Heterogenická inkompatibilita

- **Heterogenická inkompatilita** – kompatibilní jedinci jsou geneticky shodní

  - typicky při rozpoznávání somatické inkompatibility (což je první krok při parasexuálním procesu), nutnost shody ve velkém počtu genů

  - podporuje inbreeding a tvorbu geneticky izolovaných linií

- **Homogenická inkompatibilita** – kompatibilní jedinci jsou geneticky odlišní

  - typicky při regulaci pohlavního cyklu (postplazmogamické procesy)

  - nutnost shody v menším počtu genů (1-2)

  - podporuje outbreeding, rekombinaci a speciaci

- **Tyto antagonistické pochody jsou hnací silou evoluce**

- analogie s histokompatibilitou tkání (nutnost genetické shody) vs pohlavní rozmnožování (nutnost opačné genetické výbavy) rostlin a živočichů

Somatická (vegetativní) inkompatibilita

- **Zamezení fúze hyf mezi mycelii, jako následek jejich genetické výbavy, jiné než je určeno faktory párovacích typů (mating- types factors, MTFs)**

- somatická inkompatibilita (somatic incopatibility, SI) = myceliární inkompatibilita = heterokaryonová inkompatibilita nebo nejčastěji vegetativní inkompatibilia

- Pouze u askomycetů a bazidiomycetů.

- Zajišťuje, že dojde k fúzí pouze velmi podobných jedinců

- adaptivní funkcí vegetativní inkompatibility je obrana kmene houby proti transferu cizorodé cytoplazmatické DNA. Může se jednat o mutované mitochondrie, viry a plazmidy.

Somatická (vegetativní) inkompatibilita

- řízeno geny ***het*** (alely pro heterokaryonovou inkompatibilitu)= ***vic*** (alely pro vegetativní inkompatibilitu, multilokusové. Dále ne-alelickým systémem genů.

- Kompatibilita = fúze jader, shoda ve všech *het* lokusech, příslušnost ke stejné *vegetative inkompatibility group* (VCG) = *intersterility group (i-s)*

- VCG jsou v různém pojetí používány jako biologická rasa, ale převážně nekoreluje s biologickým druhem

- Nekompatibilita = alespoň některé lokusy rozdílné
  - fúze buněk, transfer protoplastu a následná denaturace cytoplazmy. Ostatní sektory hyfy se brání tím, že uzavřou pór v buněčné stěně nebo vytvoří novou cytoplazmatickou membránu. Možný transfer cytoplazmatických elementů. V kontaktní zóně vzniká makroskopicky pozorovatelná *barrage*

  - k fúzi nedochází, vytvoří se *barrage*

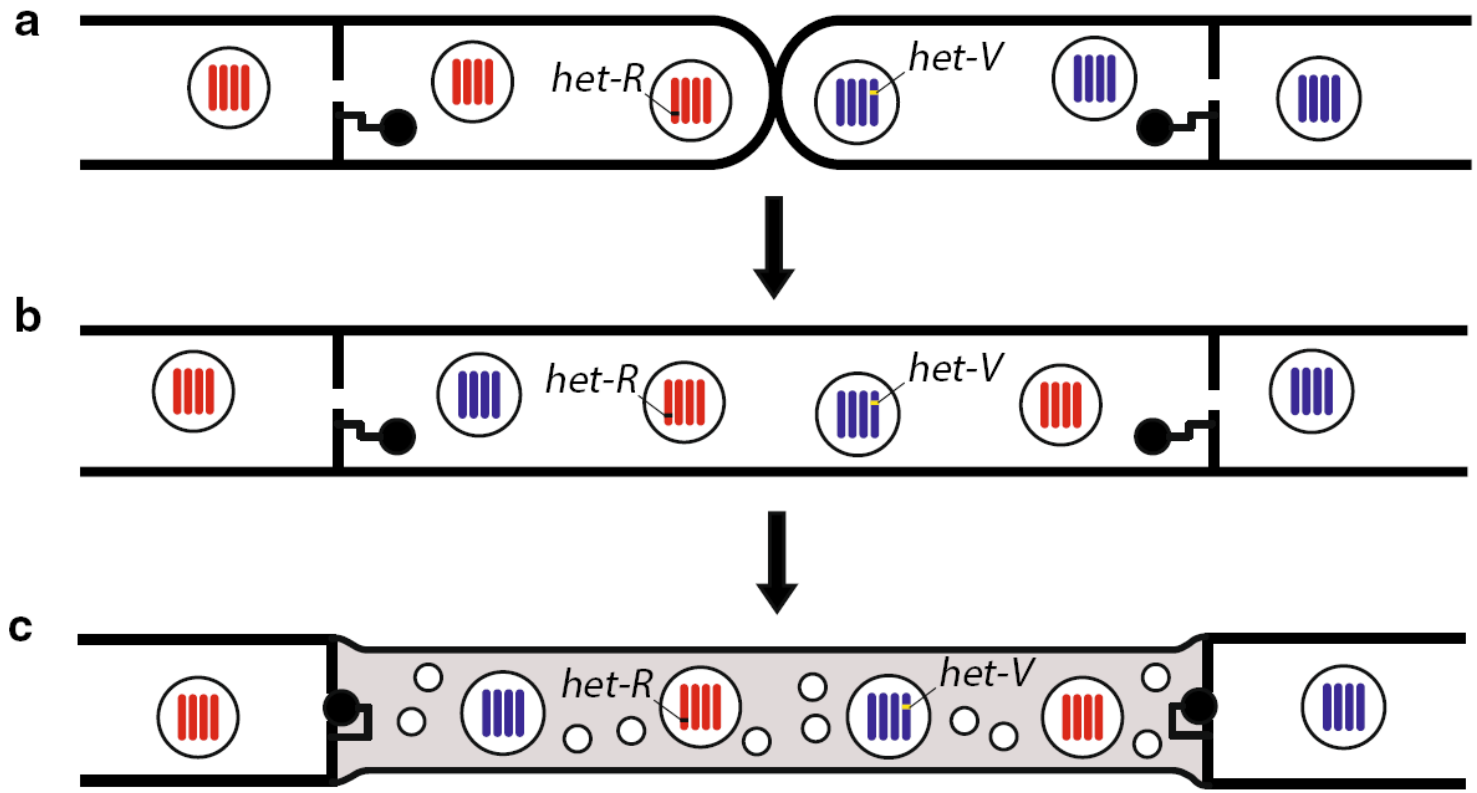

Fig. 3 Vegetative incompatibility. **a** Hyphae of vegetatively incompatible filamentous fungi grow towards each other by chemotaxis. **b** Hyphal fusion occurs, resulting in a heterokaryon. **c** Expression of incompatible *het* genes in the heterokaryon leads to sealing of septal pores, autophagy, and programmed cell death. Vacuolization and the formation of additional septa (not pictured) also occur. Autophagy (represented by small circles in the cytoplasm of the heterokaryon) may prevent the spread of pro-death signals and is not thought to contribute to the cell death process. Thinning of the heterokaryotic filament accompanies cell death

Strom and Bushley *Fungal Biol Biotechnol* (2016) 3:4
DOI 10.1186/s40694-016-0022-x

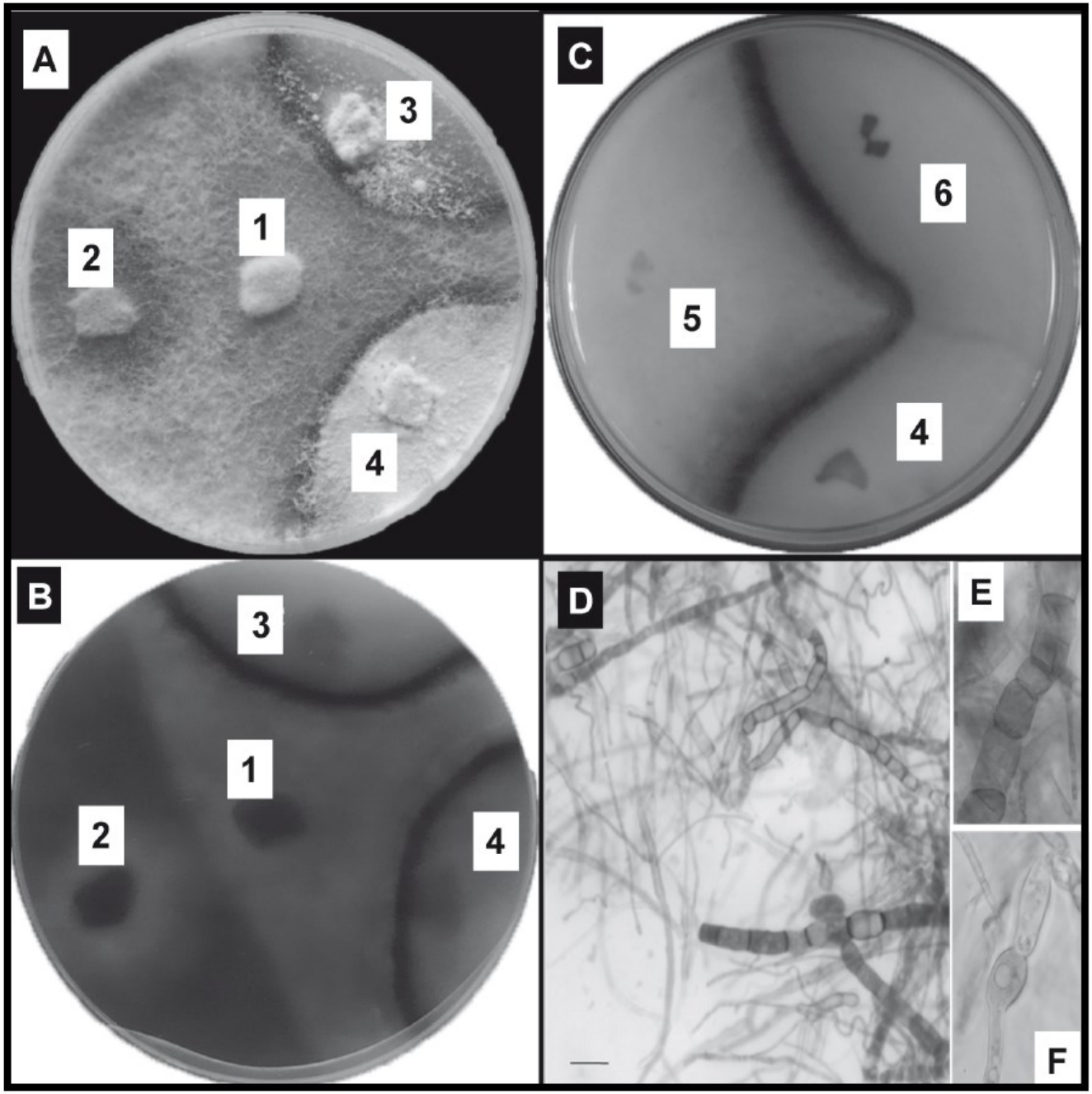

FIGURE 3 - Somatic incompatibility assays between *Diaporthe phaseolorum* var. *meridionalis* obtained from soybean fields) and *D. caulivora* isolates. **A. B**. Front and reverse of the mycelia growing in PDA: 1, *D. phaseolorum* var. *meridionalis* (HQ130439, Argentina); 2, *D. phaseolorum* var. *meridionalis* (HQ130438, Paraguay); 3, *D. caulivora* (HM625760, Argentina); 4, *D. caulivora* (HM625758, Argentina); **C**. Reverse of the mycielia growing in PDA: 5, *D. phaseolorum* var. *meridionalis* (HQ130440, Argentina); 6, *D. caulivora* (HM625770, Argentina). The darkened contact zone represents barrage formation. **D-F**. Hyphae from the barrage zone from confrontation HM625770 vs HQ130440; **D.** Thin and thickened brown hyphae; **E.** String of empty brown cells; **F.** Vacuolized cells. Bar= 10 µm.


O


P

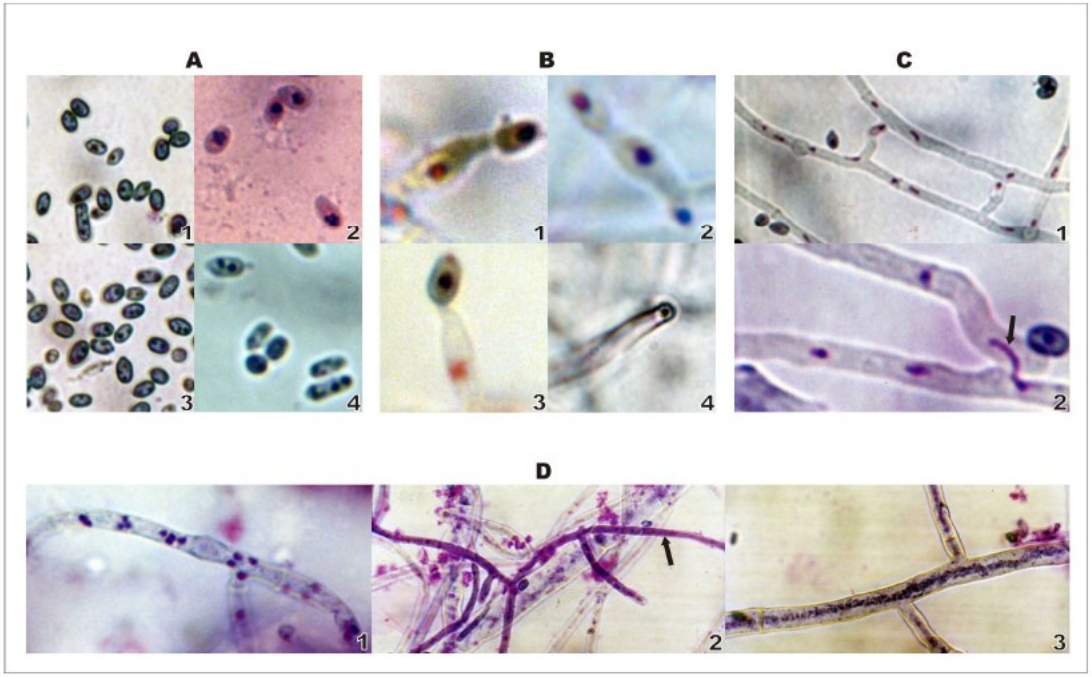

Figure 3. Nuclear staining of conidia, conidiogenesis, and of the heterokaryotic colony, with the HCl- Giemsa method. (A) Nuclear staining of conidia. 1 – parental strain 12L; 2 – parental strain 9L; 3 – heterokaryotic colony; 4 – recombinant strain 18 R. (B) Nuclear distribution of nuclei during the conidiogenesis. 1 – parental strain 12L; 2 and 3 – heterokaryotic colony; 4 – recombinant strain 23R. (C) Nuclear staining at hyphal anastomosis regions in the heterokaryon. 1 – a region of contact and initial anastomosis process; 2 – anastomosis region showing a nucleus with an active movement (arrow); (D) Nuclear staining of heterokaryotic colony. 1 – multinucleated hyphae compartments containing integral nuclei; 2 – intensely stained hyphae (arrow), that may be an indication of a cellular death process; 3 – hyphal compartment showing a cytoplasmatic grainy material; (Magnification, 1,000 X).

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LIMITED VEGETATIVE COMPATIBILITY AS A CAUSE OF SOMATIC RECOMBINATION IN *Trichoderma pseudokoningii*

Fernando Gomes Barcellos[1*], Mariangela Hungria[2], Aline Aparecida Pizzirani-Kleiner[3]

Somatická (vegetativní) kompatibilita

- *Neurospora crassa* - 11 *het* lokusů (8 lokusů bialelických)
- *A. nidulans - 8 het* lokusů, jeden z nich *het-C*, má tři alely a *het-B* má čtyři alely
- Počet VCG se různí dle biologie i ekologie houby. Lokusy (dle síly vazby) mohou rekombinovat během pohlavního rozmnožování. Tak například 10 lokusů se dvěma alelami může generovat 1000 VCG (v praxi nalézáme počty daleko menší).
- *Cryptonectria parasitica* izolované z jednoho místa v průběhu čtyř následných let patřily k 6, 11, 38 a 48 VCG. Možné vysvětlení tohoto narůstajícího počtu VCG je postupný meziroční vznik nových VCG rekombinací.

- žádné VCG u *Verticllium longisporum ,* 3 VCG u *V. dahliae*

- 125 VCG u *Fusarium oxysporum*

- **Heterokaryon self-incompatibility** – omezená schopnost tvorby anastomóz u některých kmenů, 1-2% kmenů z přírody. Určeno ne-alelickým systémem

Somatická (vegetativní) inkompatibilita

- nekompatibilní SI reakce většinou nezabrání následnému úspěšnému pohlavnímu procesu mezi izoláty z různých VCG (*Aspergillus nidulans,* je předpoklad že exprese *het* genů je potlačena), kdežto u příbuzného druhu *A. amstelodami* k pohlavnímu procesu mezi různými VCG nedochází
- Vyjímečně (*N. crassa*) faktory MAT vystupují zároveň jako faktory SI

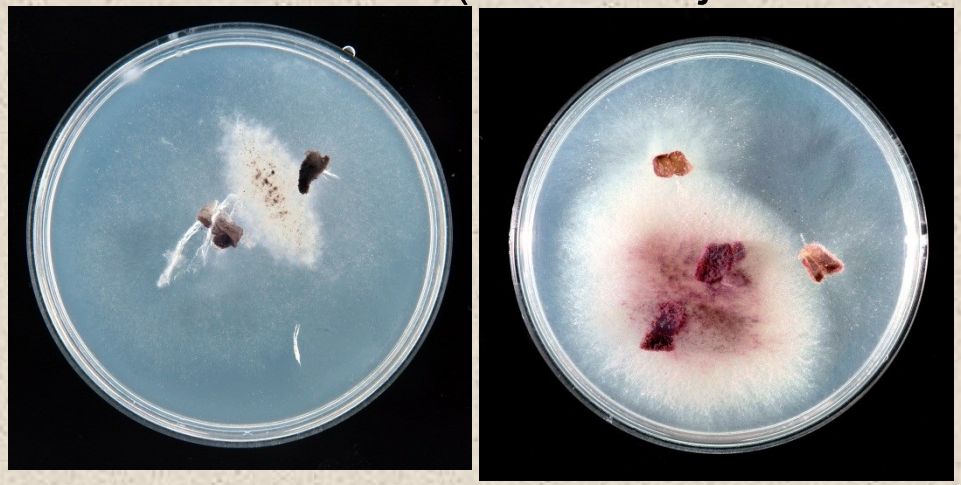
TABLE 1 Molecularly characterized genes involved in vegetative incompatibility (inc.)

Species and gene	Class of gene	Nature of the protein and its functional motifs	References
Neurospora crassa			
mat A-1	Allelic *het* gene	Mating-type transcriptional regulator; α-domain (Matα1p)	44
mat a-1	Allelic *het* gene	Mating-type transcriptional regulator; HMG box	108
tol	Mediator, *mat* inc.	Coiled-coil, leucine-rich repeat, region with similarity to HET-6 and HET-E	104
het-c	Allelic *het* gene	Signal peptide, variable domain (specificity), glycine-rich region	102, 103
un-24	Nonallelic *het* gene	Ribonucleotide reductase; allosteric activity site, variable domain (specificity)	105, 106
het-6	Nonallelic *het* gene	Region with similarity to TOL and HET-E	106
Podospora anserina			
het-s	Allelic *het* gene	Prion analog; single amino acid differences alters allelic specificity	28, 109
het-e	Nonallelic *het* gene	GTP-binding domain, WD repeat, region with similarity to TOL and HET-6	38, 98
het-c	Nonallelic *het* gene	glycolipid transfer protein; amphipathic α-helix, single amino acid differences alters allelic specificity	97
mod-D	Modifier, *het-C/E* inc.	α-subunit of G protein; GTP-binding site	73
mod-E	Modifier, *het-R/V* inc.	Heat-shock protein (Hsp90 family)	72
idi-2	Induced by *het-R/V* inc.	Signal peptide	21
mod-A	Modifier, nonallelic inc.	SH3-binding domain	7
idi-1, idi-3	Induced by nonallelic inc.	Signal peptide	21
pspA	Induced by nonallelic inc.	Serine (vacuolar) protease	100

GLASS ■ JACOBSON ■ SHIU

Somatická (vegetativní) kompatibilita

- Pozorováním morfologie mycelia na hraniční zóně (barrage)
- Studium VCG pomocí nitrát-reduktázových mutantů (nejpřesnější metoda)
- $KClO_4$ je mutagen - většina chloristan-rezistentních kmenů (cca 90 % u *G. lavendula*) je zároveň mutována v nitrát reduktáze (*nit* mutanty)
- rozdělení na nit1,2,3, nitM pomocí schopnosti růstu na hypoxanthinu, nitritu a nitrátu (mutace v jiném úseku genu)



*Geosmithia lavendula, a*uxotrofní mutanti fúzují za vzniku prototrofního jedince

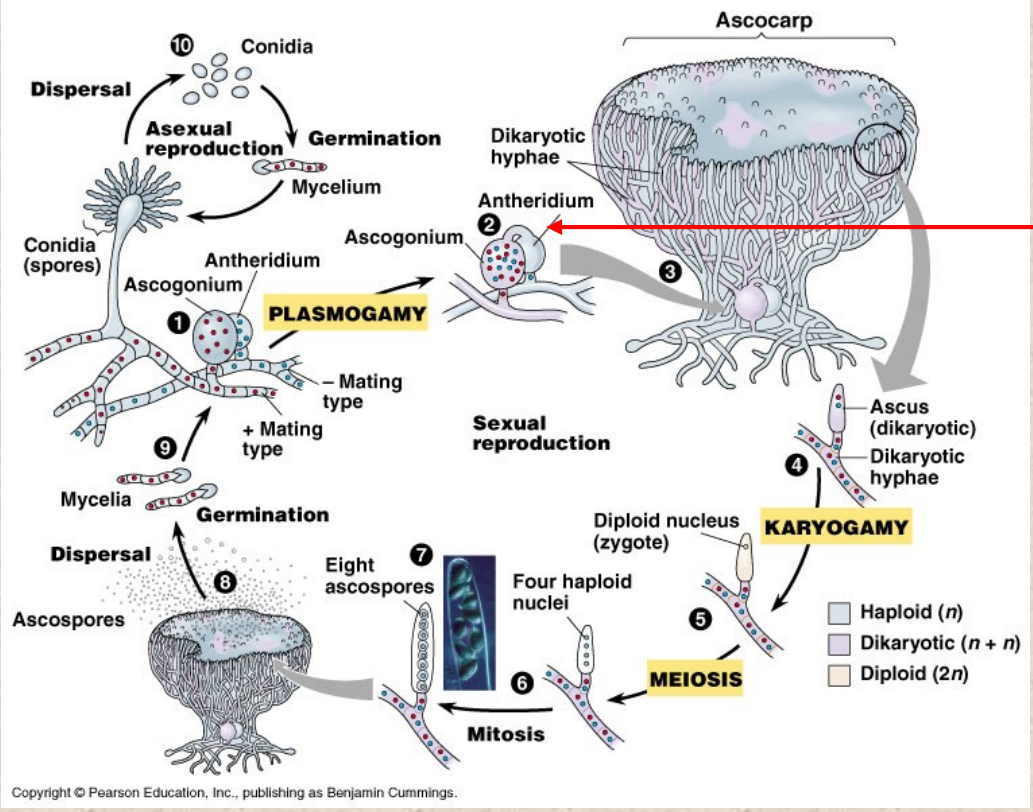
Parameiotický cyklus

- Obdobou parasexuálního cyklu, ale 2n jádro je velmi nestabilní a k haploidizaci dochází už v samotné hyfě, kde došlo ke karyogamii.
- Tj. velmi podobné pohlavnímu rozmnožování
- Známo u *Beauveria bassiana, Metarhizium anisopliae* a *A. nidulans*

Pohlavní rozmnožování askomycet

- Pohlavní rozmnožování u askomycet je velmi podrobně prostudované a bylo již identifikováno mnoho genů (200-500) zapojených v sexuálním procesu. Klíčové jsou párovací geny (mating-type genes, MAT genes).

- Jednolokusový, dvoualelový systém (= dimiktický, bipolární – „dvě pohlaví“)
- Regulační bod je **před tvorbou gametangia a při jejich kontaktu**



Nebo prostá hyfa, makro i mikrokonidie

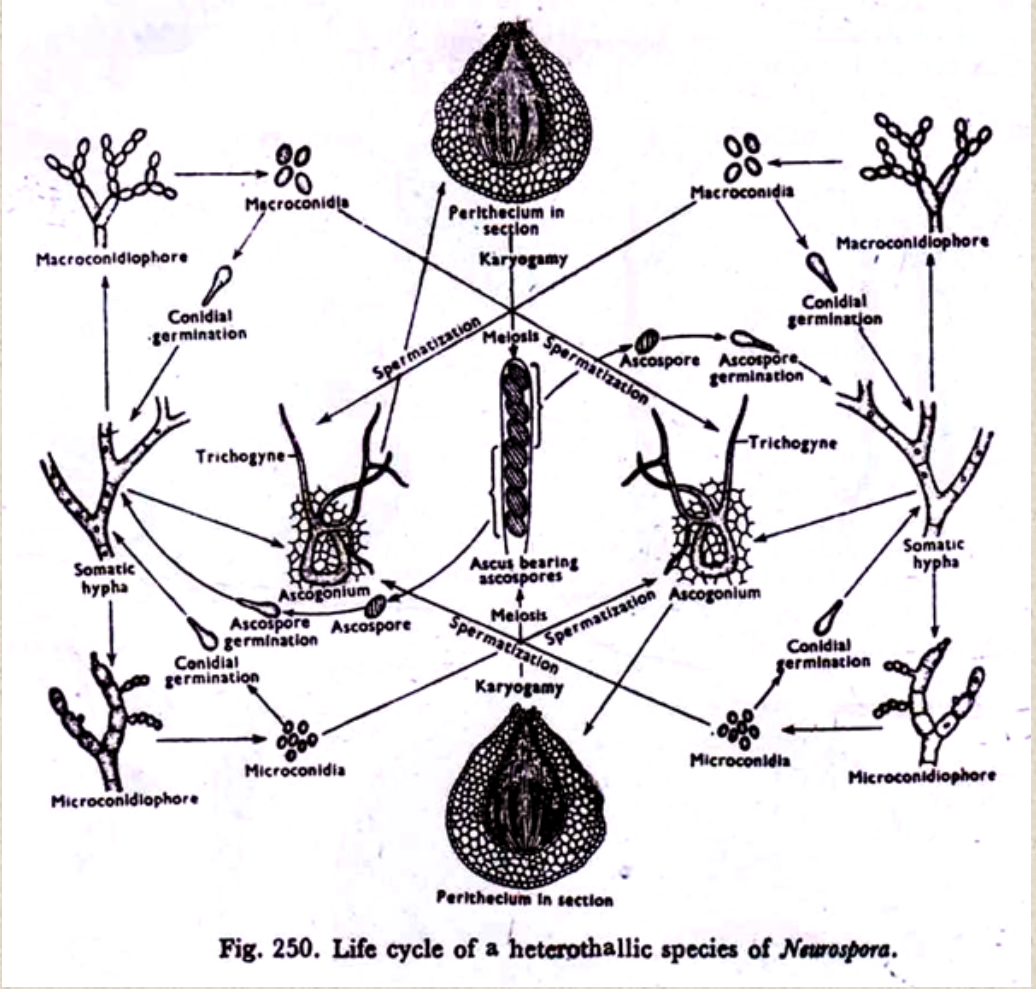
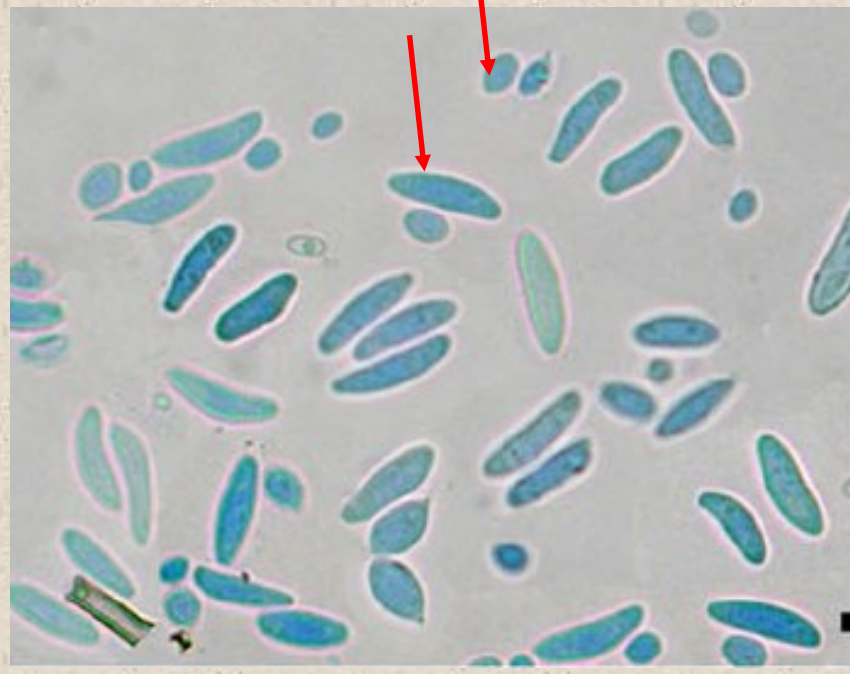


Fig. 250. Life cycle of a heterothallic species of *Neurospora*.

Claviceps



- produkce jednoho typu konidií, které slouží jako propagule i spermacie
- makrokonidie a mikrokonidie jako propagule i jako spermacie (*Neurospora*)
- mikrokonidie neklíčí v kultuře a patrně slouží pouze jako spermacie (*Claviceps*)

Pohlavní rozmnožování askomycet

- V MAT lokusu (přesněji MAT1 lokusu) mohou být **dva různé typy MAT genů** označovány jako MAT1-1 / MAT1-2 (či zkráceně MAT1 a MAT2), či MATa / MATA nebo MAT+ a MAT- případně jako MAT α /MATa u kvasinek.

- MAT1-1 a MAT1-2 jsou sice příbuzné, ale sekvenčně i funkčně značně odlišné (5301 bp vs 3235 bp u *N. crassa*) a u heterothalických druhů se nazývají **idiomorfy.** U homothalických hovoříme pouze o MAT lokusech. Použití termínů je značně chaotické. Chyba je nazývat je MAT alelami.
- MAT1-1 kóduje **alpha box (domain) mating type protein** s funkcí aktivátoru transkripce. Reguluje signalizaci založenou na feromonech a receptorech. MAT1-1 protein může přímo interagovat s MAT1-2 proteinem
- MAT1-2 kóduje protein s **HMG (high mobility group) DNA binding** doménou (protein, který se váže na DNA), regulátor transkripce.

FUNGAL BIOLOGY REVIEWS XXX (2017) 1–13

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Review

Which *MAT* gene? Pezizomycotina (Ascomycota) mating-type gene nomenclature reconsidered

P. Markus WILKEN[a,*], *Emma T. STEENKAMP*[b], *Michael J. WINGFIELD*[a], *Z. Wilhelm DE BEER*[b], *Brenda D. WINGFIELD*[a]

[a]*Department of Genetics, DST/NRF Centre of Excellence in Tree Health Biotechnology (CTHB), Forestry and Agricultural Biotechnology Institute (FABI), Faculty of Natural and Agricultural Sciences, University of Pretoria, Private Bag X20, Pretoria, 0028, South Africa*

[b]*Department of Microbiology and Plant Pathology, DST/NRF Centre of Excellence in Tree Health Biotechnology (CTHB), Forestry and Agricultural Biotechnology Institute (FABI), Faculty of Natural and Agricultural Sciences, University of Pretoria, Private Bag X20, Pretoria, 0028, South Africa*

Pohlavní rozmnožování askomycet

- Homothalické (=homomiktické) druhy jsou schopny samo-oplození (= autogamie, self-fertile) bez nutnosti křížení s partnerem

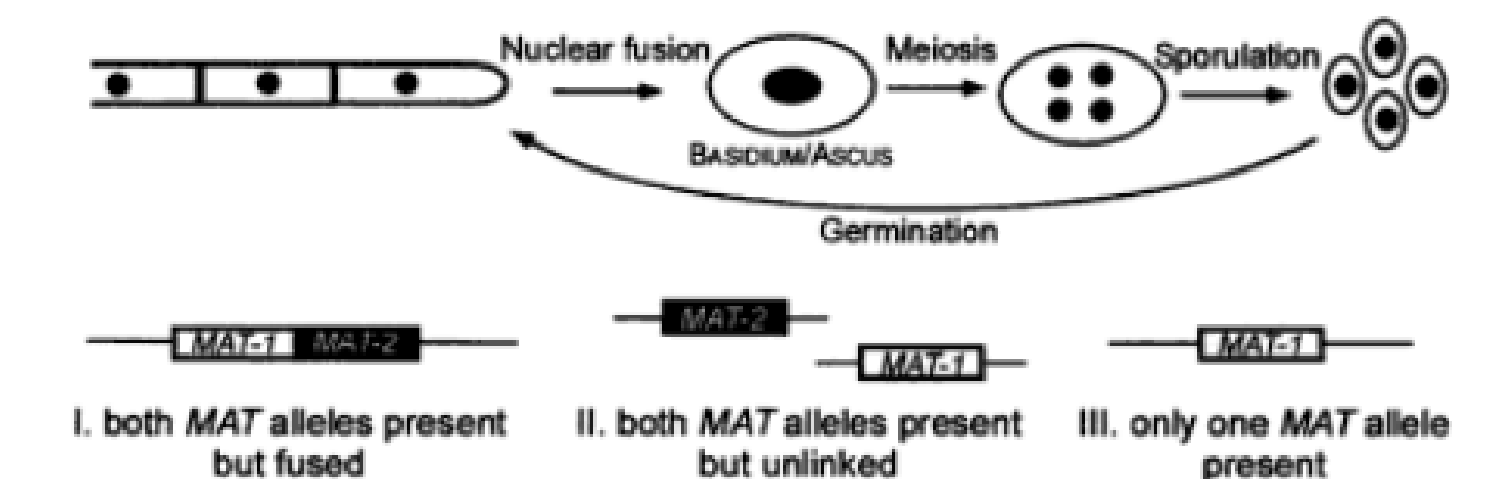
- Homothalické druhy jsou zároveň schopné tvorby askospor s kompatibilním partnerem při vhodných podmínkách prostředí, což znamená, že mohou profitovat z výhod rekombinace.

- Homothalická sexuální reprodukce samooplozením je z genetického hlediska v podstatě klonální a stejná, jako asexuální reprodukce (Nauta & Hoekstra 1992).

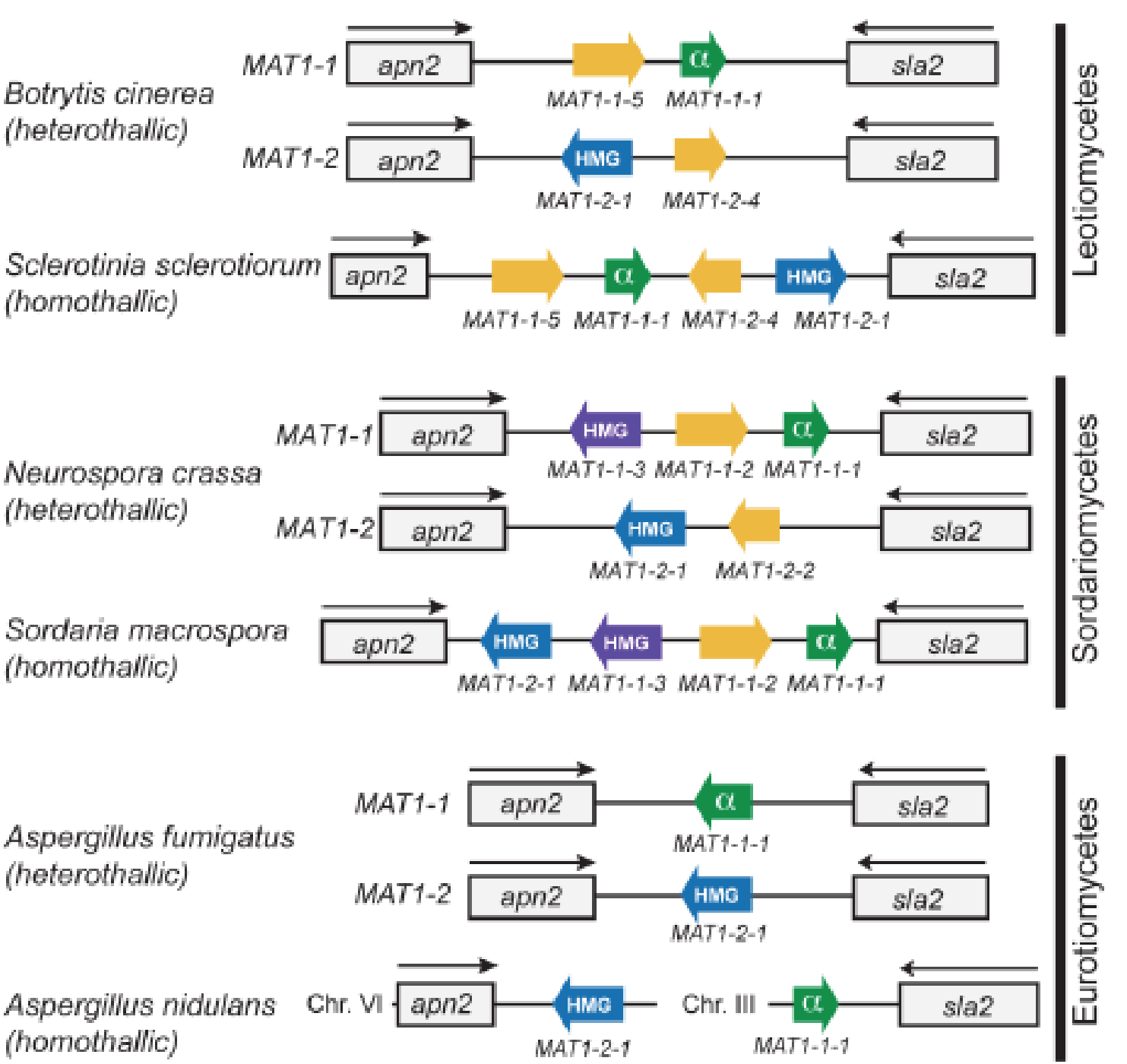
- heterothalické druhy (=heteromictic) nejsou schopny pohlavního rozmnožování pomocí samooplození, ale musí se zkřížit s partnerem opačného párovacího typu (=alogamie).

Pohlavní rozmnožování askomycet

- MAT1-1 i MAT1-2 idiomorfy mohou mít více alel (MAT1-1-1, MAT 1-1-2 a MAT1-1-3)
- U heterothalických hub nese každý jedinec jeden párovací typ (kompatibilní kombinace je MAT1-1 a MAT1-2)
- U homothalických jsou MAT1-1 a MAT1-2 spojeny v jednom lokusu, či se nacházejí v samostatných lokusech v rámci jednoho genomu, nebo je vzácně (Cryptococcus, Candida) přítomna pouze jedna idiomorfa (same-sex mating)

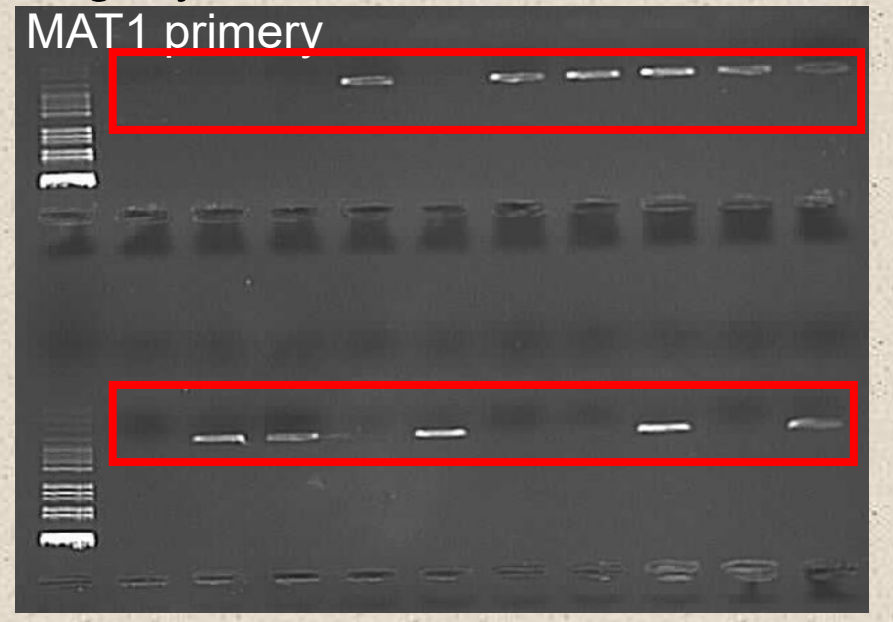


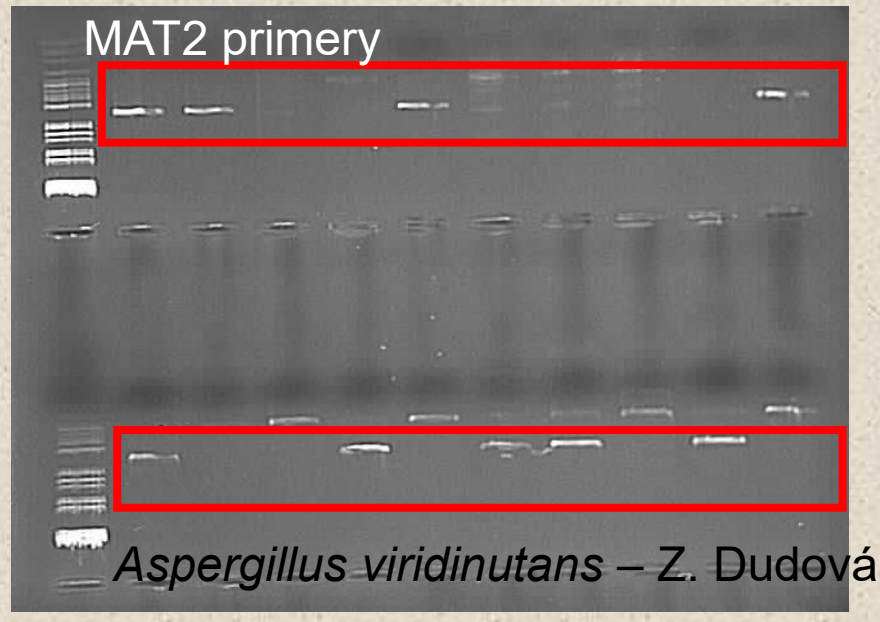
Nezbytné jsou pouze
MAT1-1-1
MAT1-2-1



Pohlavní rozmnožování askomycet

- Určování pohlavnosti pomocí primerů, chybí univerzální primery
- MAT lokusy jsou ohraničeny konzervativními geny - proteiny s GTPázovou aktivitou, geny pro β-glukosidázu, geny pro cytoskeletární proteiny, SLA2 gen …
- Tyto konzervativní oblasti lze využít při hledání PCR primerů pro MAT geny.





Aspergillus viridinutans – Z. Dudová

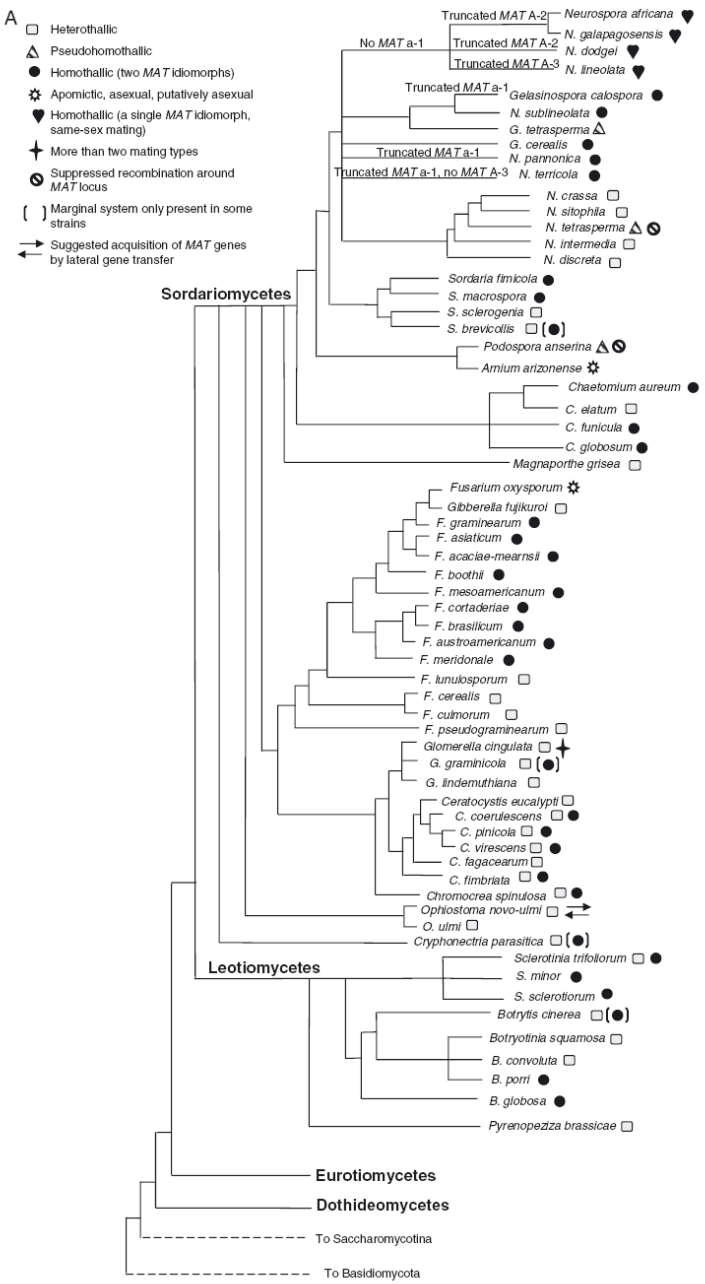
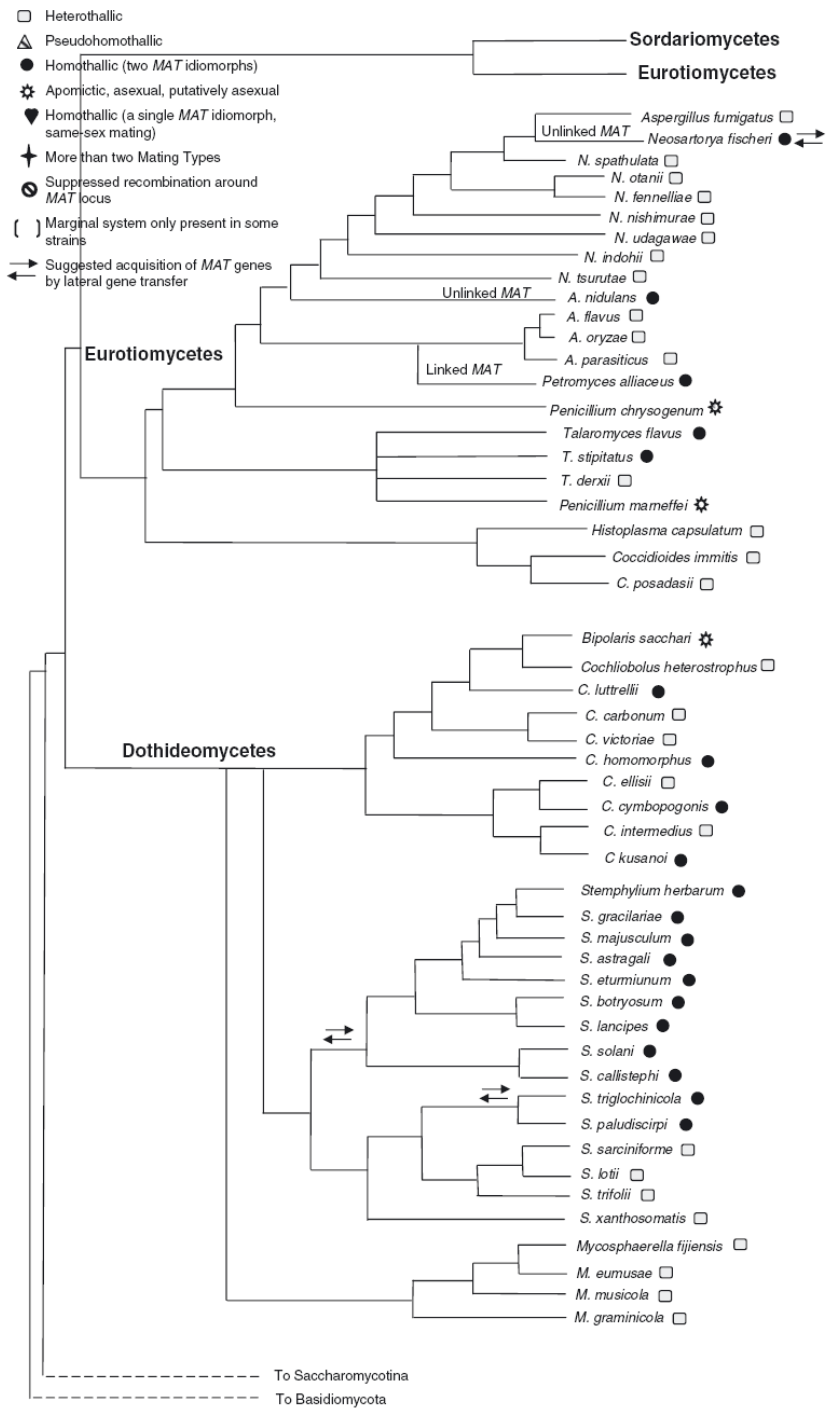
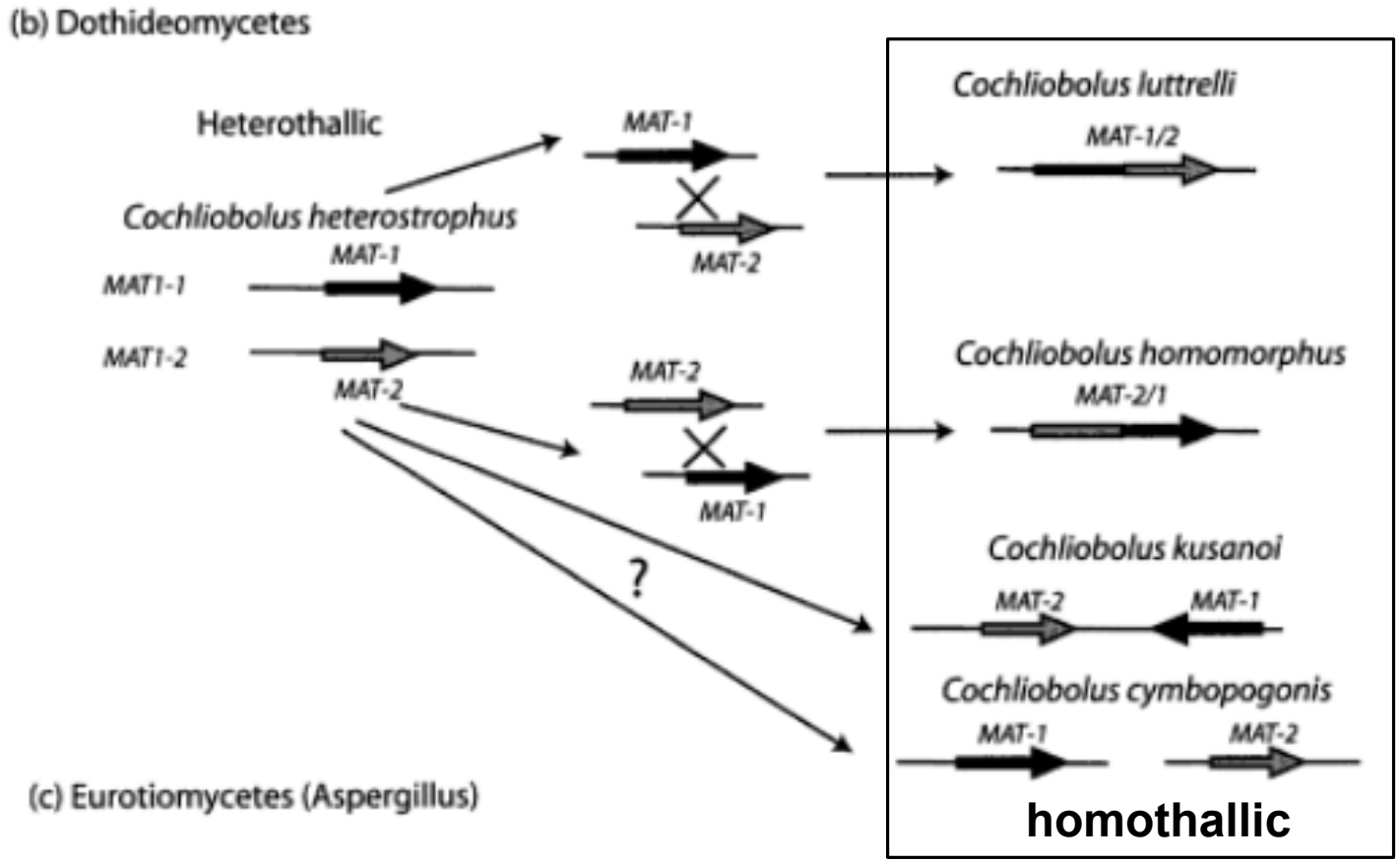
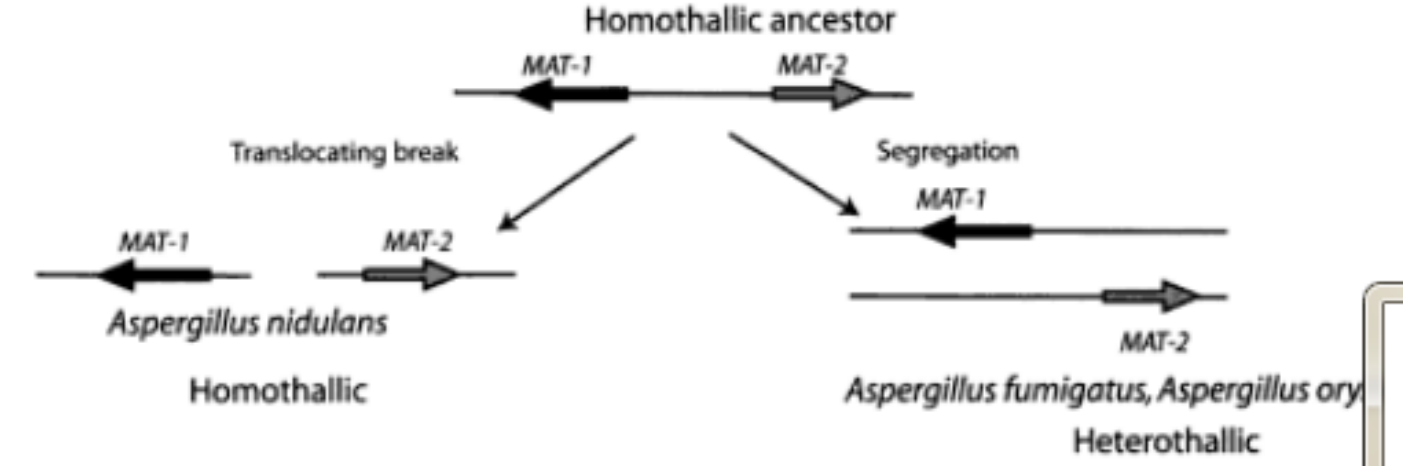


Fig. 5. Legend on previous page.


Heterothallic
Pseudohomothallic
Homothallic (two MAT idiomorphs)
Apomictic, asexual, putatively asexual
Homothallic (a single MAT idiomorph, same-sex mating)
More than two Mating Types
Suppressed recombination around MAT locus
Marginal system only present in some strains
Suggested acquisition of MAT genes by lateral gene transfer
Sordariomycetes
Eurotiomycetes
Aspergillus fumigatus
Unlinked MAT
Neosartorya fischeri
N. spathulata
N. otanii
N. fennelliae
N. nishimurae
N. udagawae
N. indohii
N. tsurutae
Unlinked MAT
A. nidulans
A. flavus
A. oryzae
A. parasiticus
Linked MAT
Petromyces alliaceus
Eurotiomycetes
Penicillium chrysogenum
Talaromyces flavus
T. stipitatus
T. derxii
Penicillium marneffei
Histoplasma capsulatum
Coccidioides immitis
C. posadasii
Bipolaris sacchari
Cochliobolus heterostrophus
C. luttrellii
C. carbonum
C. victoriae
C. homomorphus
Dothideomycetes
C. ellisii
C. cymbopogonis
C. intermedius
C kusanoi
Stemphylium herbarum
S. gracilariae
S. majusculum
S. astragali
S. eturmiunum
S. botryosum
S. lancipes
S. solani
S. callistephi
S. triglochinicola
S. paludiscirpi
S. sarciniforme
S. lotii
S. trifolii
S. xanthosomatis
Mycosphaerella fijiensis
M. eumusae
M. musicola
M. graminicola
To Saccharomycotina
To Basidiomycota


B
Heterothallic
Homothallic by MAT switching (silent cassettes are present)
Homothallic without switching by same-sex mating
Putatively asexual
3 Three MAT loci are present despite lack of MAT switching
Saccharomyces cerevisiae
Saccharomyces paradoxus
Candida glabrata
Kluyveromyces delphensis
Candida castellii
Zygosaccharomyces rouxii
Kluyveromyces thermotolerans 3
Saccharomyces kluyveri
Kluyveromyces lactis var. lactis 3
Eremothecium (Ashbya) gossypii 3
Candida albicans
Candida tropicalis
Candida parapsilosis
Lodderomyces elongisporus
Candida (Pichia) guilliermondii
Debaryomyces hansenii
Candida (Clavispora) lusitaniae
Yarrowia lipolytica
Schizosaccharomyces pombe
C
Heterothallic
Pseudohomothallic (spores including nuclei with different mating types)
Homothallic by mating type switching
Homothallic by same sex mating
Tetrapolar
Bipolar
Multiple mating types
2 Two mating types
Region of supressed recombination
Uniparental mitochondrial inheritance at plasmogamy
Uniparental mitochondrial inheritance at plasmogamy controlled by mating type
Biparental mitochondrial inheritance at plasmogamy
{ } Marginal system only present in some strains
Agrocybe aegerita
Agaricus bisporus
Agaricus bitorquis
Coprinus cinereus
Coprinellus disseminatus
Armillaria bulbosa
Pleurotus djamor
Schizophyllum commune
Lentinula edodes
Stropharia rugosoannulata
Pholiotoa nameko 2
Laccaria bicolor
Amylostereum areolatum
Heterobasidion insulare
Heterobasidion annosum
Ganoderma boninense
Thyphula ishikariensis
Thanatephorus cucumeris 2
Cryptococcus neoformans 2
Sporisorium reilianum
Ustilago maydis
Ustilago hordei 2
Microbotryum violaceum 2
Rhodosporium turoloides 2

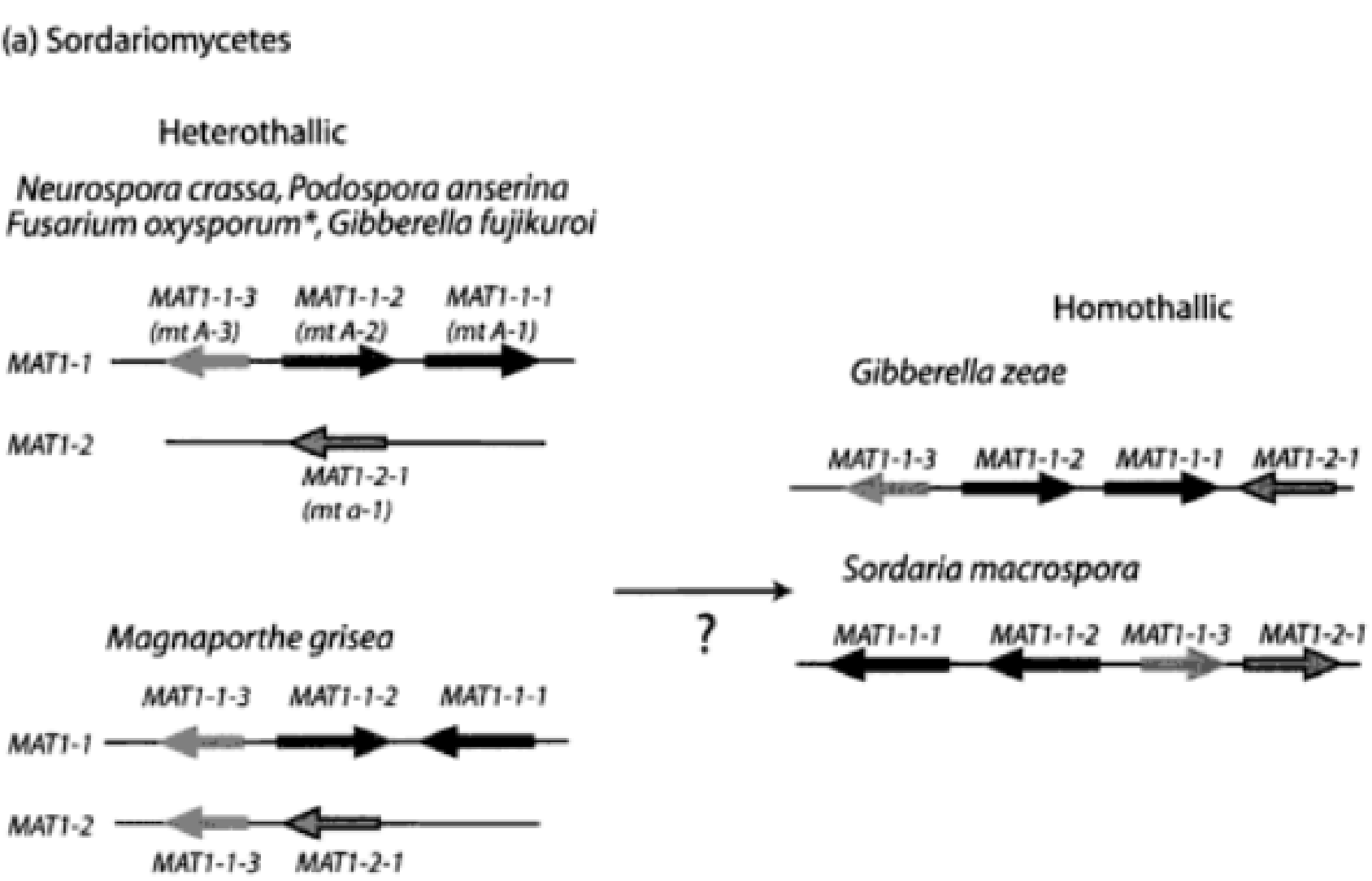




Alpha box

HMG domain

Heitmann et al. Eds (2007)



Heitmann et al. Eds (2007)

Pohlavní rozmnožování askomycet

- V areálu musí být k dispozici oba párovací faktory
  - *Phytophthora infestans*, v Evropě dlouho byli jen jedinci stejného pohlaví
  - *Pseudogymnoascus destructans.* V USA jen jeden párovací typ, v Eurasii oba
- Řada čistě nepohlavních druhů má jen jedince stejného pohlaví

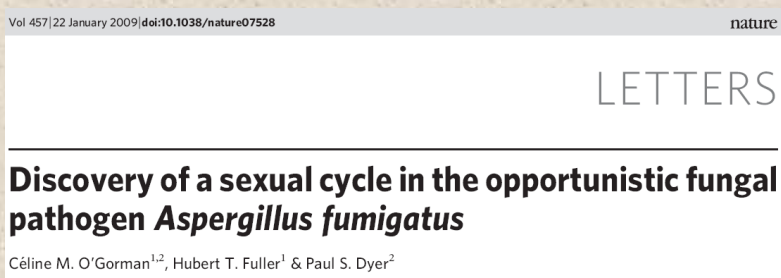
- Ztráta kompatibilního partnera je silný nástroj speciace (často u dermtofyt)

Organismus	Procentuální zastoupení MAT1 : MAT2	Počet hodnocených izolátů	Reference
Aspergillus fumigatus	49,4 : 50,6	91	O'Gorman et al. (2009)
Aspergillus terreus	60 : 40	25	Eagle (2009)
Neosartorya udagawae	41,6 : 58,3	12	Sugui et al. (2010)
Trichophyton mentagrophytes (druhový komplex)	86 : 13,24	68	Symoyens et al. (2011)
Cryphonectria parasitica	97 : 1	539	

Tabulka 5. Procentuální zastoupení MAT1 a MAT2 v populaci různých druhů

(převzato z Dudová 2011)

- Cíleným křížením lze hledat neznámé teleomorfy. Křížit se musí jen kompatibilní jedinci s velkou genetickou podobností


Vol 457|22 January 2009|doi:10.1038/nature07528 nature

LETTERS

Discovery of a sexual cycle in the opportunistic fungal pathogen *Aspergillus fumigatus*

Céline M. O'Gorman[1,2], Hubert T. Fuller[1] & Paul S. Dyer[2]

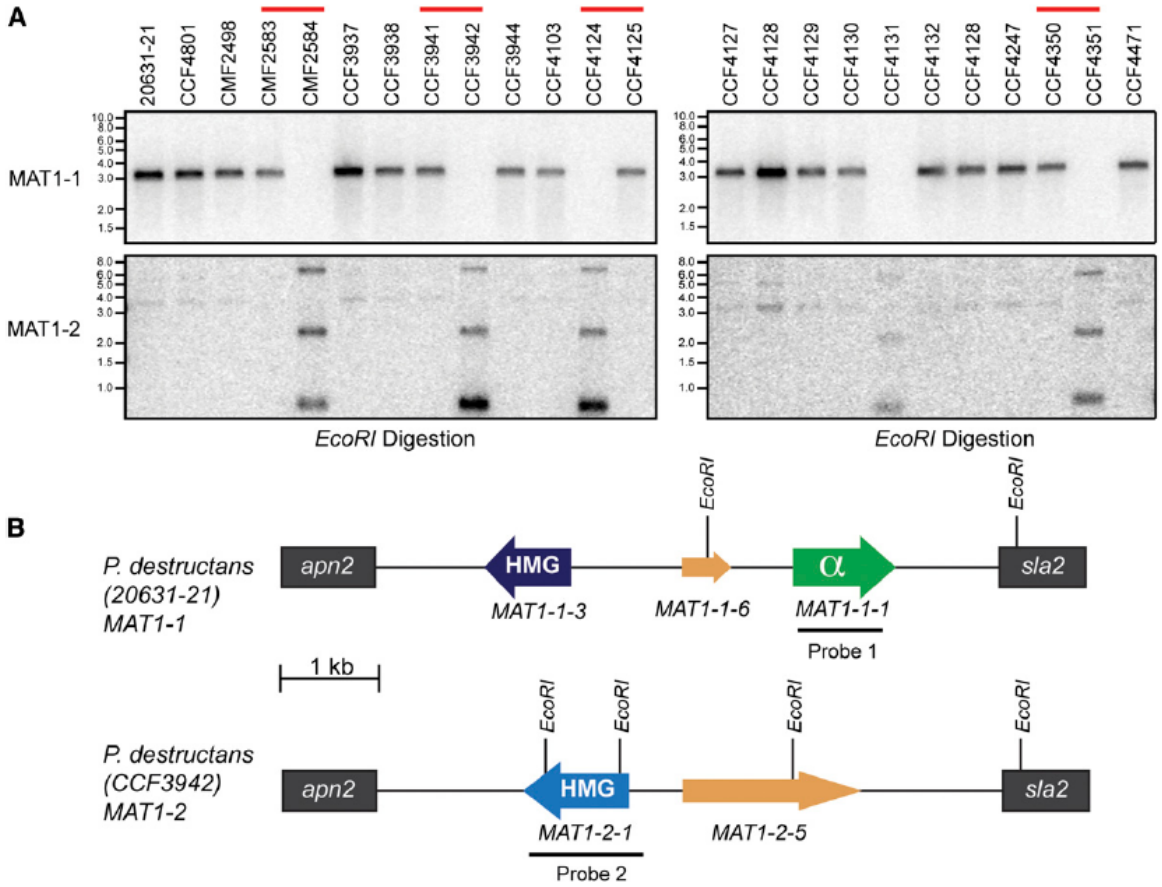


Figure 3 Central European isolates of *P. destructans* have two mating types (*MAT1-1* or *MAT1-2*). (A) Southern blot of the *MAT* locus of the North American isolate (20631-21) and 23 isolates from central Europe. Expected banding patterns for an *EcoRI* digestion of *MAT1-1* strains is a single band of 3.183 kb. Expected banding pattern for *EcoRI* digestion using *MAT1-2* as a probe is three bands of 2.6 kb, 2.063 kb, and 0.699 kb. European isolates of *P. destructans* collected from the same hibernaculum and date, different individual bats, but opposite mating types are demarcated with a red line above the isolate name. (B) Schematic of the two *MAT* idiomorphs in *P. destructans* illustrating the gene prediction structure and restriction enzyme cut sites. Radio-labeled probes used in the Southern blot are indicated by a black line.

Molecular Characterization of a Heterothallic Mating System in *Pseudogymnoascus destructans*, the Fungus Causing White-Nose Syndrome of Bats

Jonathan M. Palmer,* Alena Kubatova,† Alena Novakova,‡,§ Andrew M. Minnis,* Miroslav Kolarik,†,§ and Daniel L. Lindner*,1

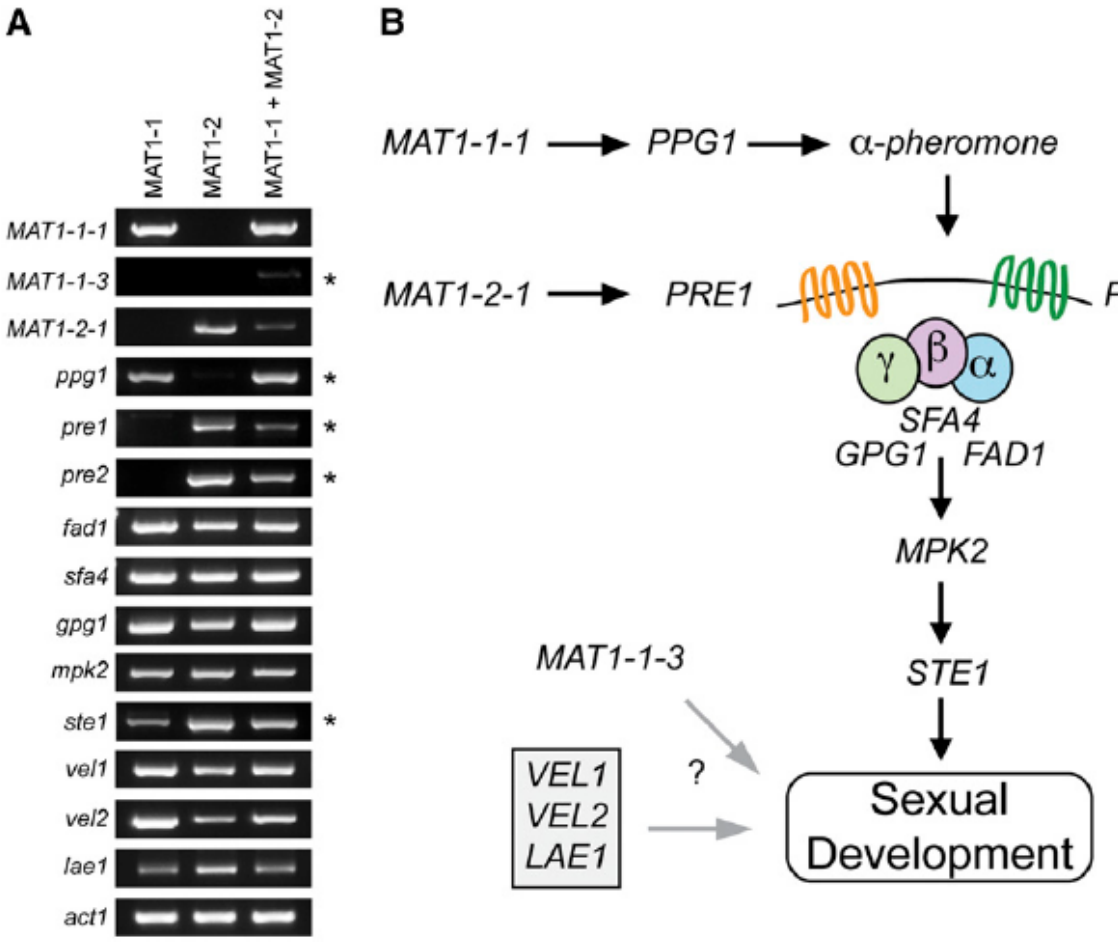


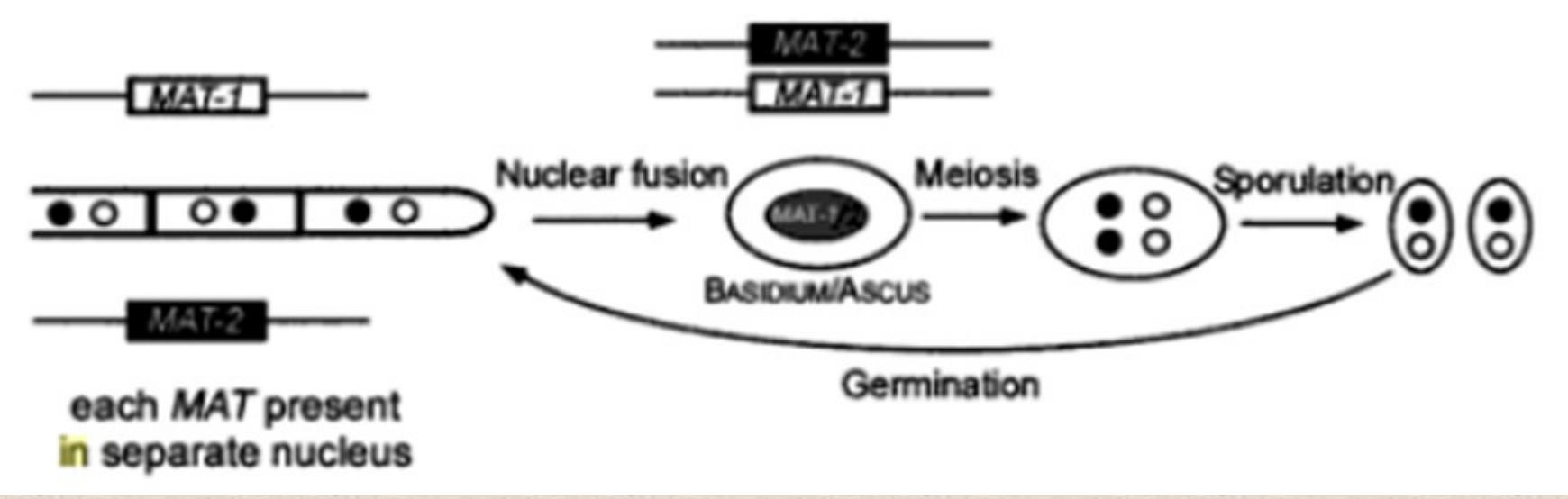
Figure 4 Putative genes involved in sexual reproduction are expressed in laboratory culture. (A) Semi-quantitative reverse-transcriptase PCR was used to measure gene expression of genes predicted to be involved in sexual reproduction. All PCR reactions were conducted with 32 amplification cycles except for those marked with an asterisk (*), where 42 amplification cycles were used. Mating type *MAT1-1* is required for expression of the precursor to alpha-pheromone (*ppg1*), whereas *MAT1-2* is required for expression of the G-protein-coupled receptors *pre1* and *pre2*. Expression of *MAT1-1-3* is only found when both mating types were co-cultured. (B) Proposed diagram of genes involved in sexual reproduction in *P. destructans* based on homology and expression in laboratory culture.

Pohlavní rozmnožování askomycet

- Pseudohomothalismus (sekundární homothalismus)

- tvoří se dva typy askospor. První, dvoujaderný typ askospor je častější a obsahuje dvě geneticky odlišná jádra, uzavřená v jediné pohlavně vzniklé askospoře. Askospory bývají ve čtyřsporých vřeccích a funkčně jsou homothalické

- Druhý typ akospor je menší a méně častý. Tento typ je haploidní a vzniklí jedinci se chovají jako heterothaličtí.
- *Podospora anserina*, *Neurospora tetrasperma* a *Gelasinospora tetrasperma*



Phylogenetic species →				int	int	int	int	int	int
↓ Biological species →				int	int	int	int	int	int
↓ Original sp. →				int	int	int	int	int	int
↓ Region →				India	India	India	India	India	India
↓				a↓A→	D44	D48	D101	D108	D128	D129
int	int	int	India	D43	6/6	6/6	6/6	6/6	6/6	6/6
int	int	int	India	D47	5/5	6/6	6/6	5/6	6/6	6/6
int	int	int	India	D109	6/6	6/6	6/6	6/6	6/6	6/6
int	int	int	India	D127	6/6	5/6	5/6	6/6	6/6	6/6
int	int	int	India	D130	5/6	4/6	6/6	6/6	6/6	6/6
int	int	int	Carib	D22	0/0	6/6	0/5	6/6	1/0	6/6
int	int	int	Carib	D16	6/6	6/6	6/6	6/6	6/6	6/6
int	int	int	Carib	D25	6/6	6/6	6/6	6/6	0/6	6/6
int	int	int	Africa	D66						
int	int	int	Africa	D81						
int	int	int	Africa	D73						
int	int	int	Africa	D79						
int	int	int	Asia	D2						
int	int	int	Asia	D3						
int	int	int	Asia	D35						
int	int	int	Asia	D8	2/1	2/5	2/2	2/1	1/1	2/4
cra	cra	cra	India	D103						
cra	cra	cra	India	D104						
cra	cra	cra	India	D106						
cra*	cra*	hyb*	India	D42	2/2	2/2	2/2	2/1	3/3	2/1
cra*	cra*	hyb*	India	D100	2/2	0/1	0/1	1/1	1/0	1/1
cra	cra	cra	Carib	D116	5/0	3/3	3/3	3/2	3/0	3/3
cra	cra	cra	Carib	D85	1/1	3/3	3/3	3/3	3/0	1/3
cra	cra	cra	Carib	D59	2/0	3/3	3/1	2/1	3/3	3/3
cra	cra	cra	Carib	D60	2/1	3/3	3/3	3/1	3/0	3/3
cra	cra	cra	Carib	D88	3/0	3/3	2/2	3/1	3/0	3/3

- **Další geny odpovídají za správnou tvorbu plodnic a spor**
- **Neshoda v *fmf-1* genu (female/male fertility) vede ke tvorbě plodniček bez askopor u *N. crassa***

Category of Reproductive Success	
6	>50% black ascospores
5	15-50% black ascospores
3 & 4	<1% black ascospores; & 1-15% black ascospores
2	perithecia developed ostioles, no ascospores ejected
0 &1	sterile, no perithecia produced; & barren perithecia, no ostiole developed

Evolution, 57(12), 2003, pp. 2721–2741

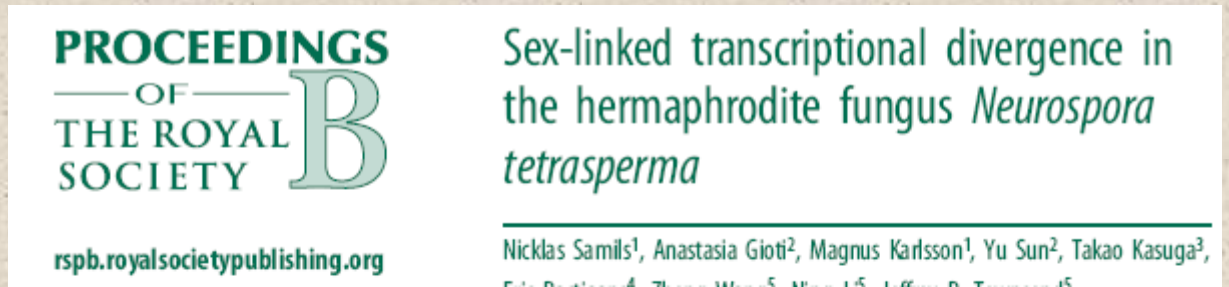
REPRODUCTIVE ISOLATION AND PHYLOGENETIC DIVERGENCE IN *NEUROSPORA*: COMPARING METHODS OF SPECIES RECOGNITION IN A MODEL EUKARYOTE

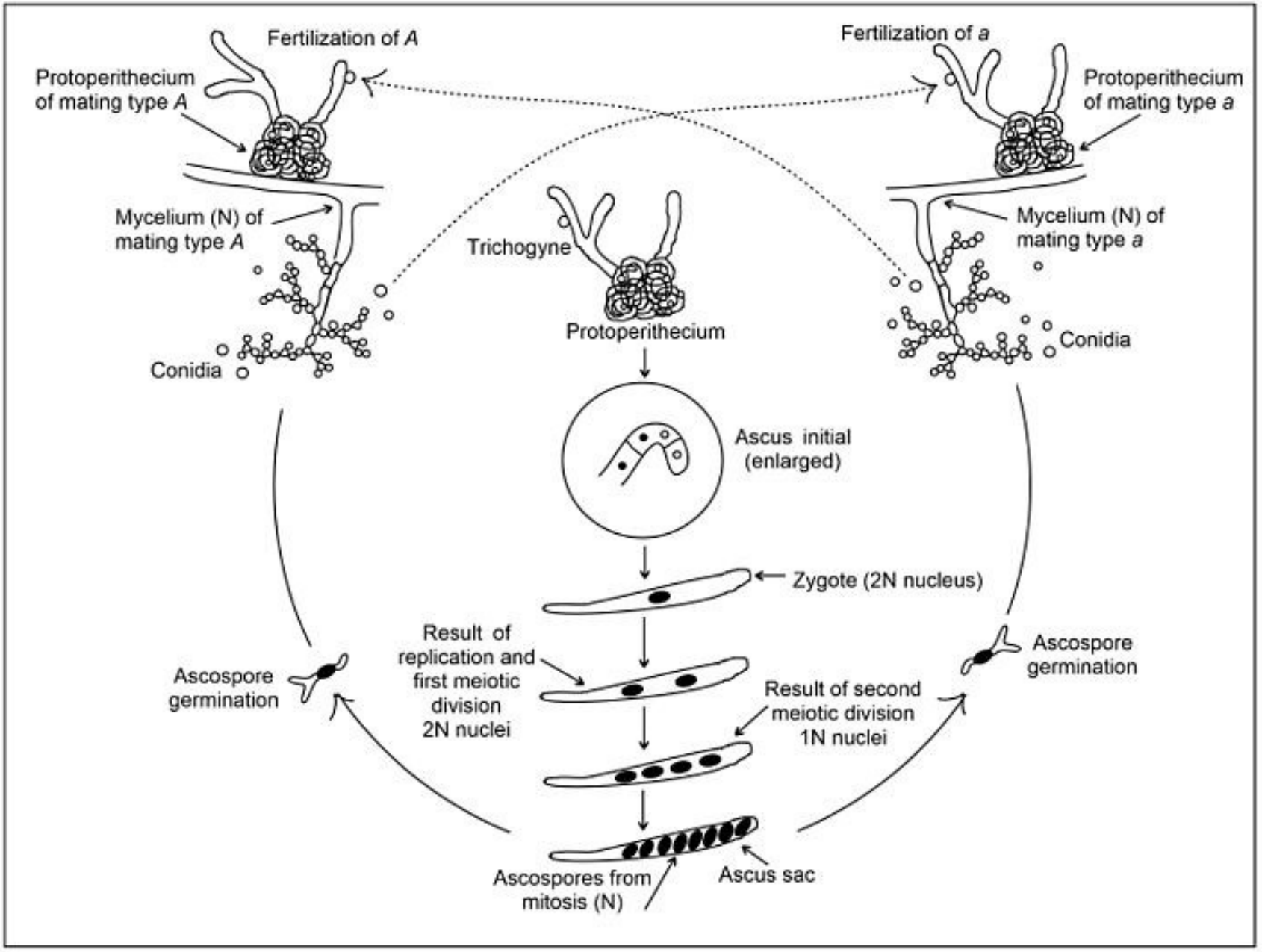
JEREMY R. DETTMAN,[1,2] DAVID J. JACOBSON,[2,3] ELIZABETH TURNER, ANNE PRINGLE, AND JOHN W. TAYLOR[4]

Pohlavní dimorfismus

- **Obě pohlaví tvoří samčí i samičí pohlavní orgány**

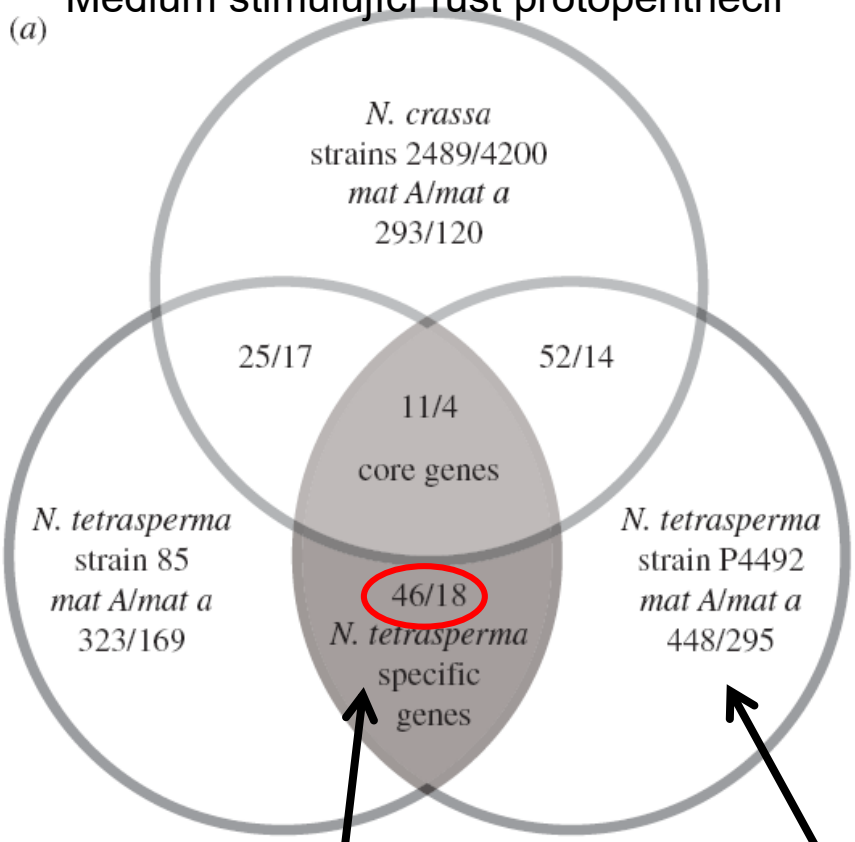
- Jednotlivé pohlaví se liší hlavně v MAT genech. Více známo jen u *Neurospora*.
- oblast chromozómu (7 Mbp) s MAT lokusem u *Neurospora tetrasperma* má omezenou rekombinaci. MAT1-1 či MAT1-2 jedinci se liší expresí těchto genů (Samils et al. 2013). Podobně tomu je i u *Microbotryum violaceum*, kde navíc známe pohlavní dimorfismus v karyotypu. Dimorfismums se zdá být na úrovni míry exprese genů
- MAT1-1 a MAT1-2 jedinci mají jiné optima i morfologii (barva mycelia, konidií, protoperitecia). MAT1 je optimalizovaný na pohlavní rozmnožování a MAT2 na růst a rozmnožování (*N. tetrasperma*)
- Nicméně *N. crassa* žádný dimorfismus nevykazuje.





http://en.wikipedia.org/wiki/File:Neurospora_crassa_life_cycle.jpg

Médium stimulující růst protoperithécií



Medium podporující vegetativní růst

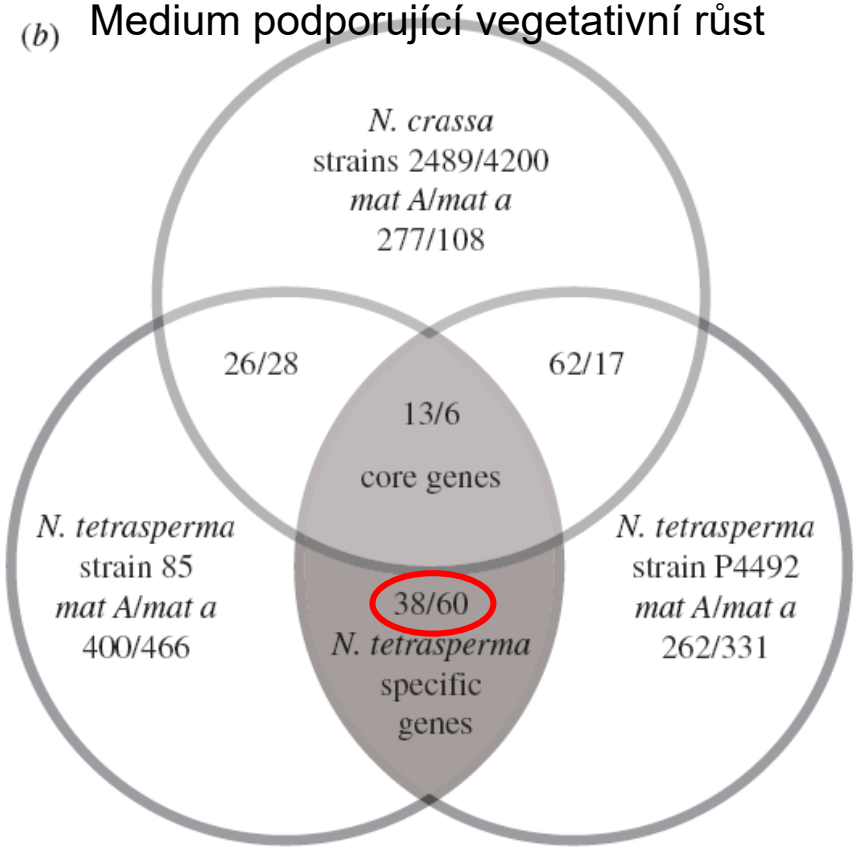


Figure 2. Venn diagrams showing the number of differentially expressed genes ($p < 0.05$), between *Neurospora* strains of different mating type (upregulated in the *mat A* strain/upregulated in the *mat a* strain) in *N. crassa* and in *N. tetrasperma*. Each diagram shows the number of genes that are specifically differentially expressed in each medium, (*a*) crossing medium and (*b*) medium inducing vegetative growth. Numbers in overlapping regions represent genes differentially expressed in more than one pair of strains of different mating type: grey areas represent the *N. tetrasperma* mating-type biased genes, and this is subdivided into the core *Neurospora* mating-type biased genes (upper grey areas) and the *N. tetrasperma* specific mating-type biased genes (lower grey areas).

geny s vyšší expresí u MAT1/ a MAT2.Kmenově specifické

geny s vyšší expresí u MAT1/ a MAT2 sdíleny dvěma kmeny

- MAT1-1 kmeny mají větší expresi genů spojených s tvorbou protoperithecia.
- MAT1-2 kmeny mají větší expresi genů spojených s vegetativním růstem

Pohlavní rozmnožování homobazidiomycetů

- **Dvojlokusový, multialelický systém (tetrapolární)**

- **Lokusy A a B** (= **mating type factor,** nesprávně jako geny), v každém jsou dva další lokusy (či sublokusy), nazývané **α a β lokusy** či **α a β komplexy**

- Alternativní označení pro **lokus A = HD factor** (homeodomain transcription factor, geny HD1 a HD2). **B lokus** = PR faktor (pheromone receptors)
- Kódování A**α1 β1,** A**α2 β2**
- **pokud jsou oba faktory odlišné, tak jde křížit**

- **Pro srozumitelnost se požívá dělení na čtyři pohlaví - A1B1, A1B2, A2B1, A2B2 (mating types generované na jedné bazidiospoře jednoho kmene tetrapolární houby)**

https://slideplayer.com/slide/12681990/

http://www.davidmoore.org.uk/21st_Century_Guidebook_to_Fungi_PLATINUM/Ch08_05.htm

Pohlavní rozmnožování homobazidiomycetů

- - 49-55% druhů je tetrapolárních (*Schizophyllum commune, Coprinus cinereus*)
  - 35-37% druhů je bipolárních (*C. comatus*)
  - 10-15% je homothalických (*Coprinus sterquilinus*) = z jedné spory lze vypěstovat plodnici

- **U tetrapolárních hub jsou A a B lokusy na odlišných chromozomech**

- **U bipolárních hub jsou vedle sebe (popřípadě jeden z nich přestal být nutný)**

TABLE I. Summary of locus and gene nomenclature used in this paper

Acronym[a]	Gene/locus	Distribution	Other names[c]
HD	homeodomain encoding MAT locus	Basidiomycota	*MAT-A* (*Coprinellus disseminatus, Phanerochaete chrysosporium*)[d] *A* locus (*Coprinopsis cinerea, Schizophyllum commune*) *b* locus (*Ustilago maydis*)
P/R	pheromone and receptor encoding MAT locus	Basidiomycota	*MAT-B* (*Cyathus stercoreus, Serpula lacrymans*) *B* locus (*Coprinopsis cinerea, Schizophyllum commune*) *a* locus (*Ustilago maydis*)
HD1	homeodomain encoding protein type 1 (atypical)	Basidiomycota	*a1/b1* (*Coprinopsis cinerea*) *bE* (*Ustilago maydis*) *Sxi1α* (*Cryptococcus neoformans*) *Z* (*Schizophyllum commune*)
HD2	homeodomain encoding protein type 2 (typical)	Basidiomycota	*a2/b2* (*Coprinopsis cinerea*) *bW* (*Ustilago maydis*) *Sxi2α* (*Cryptococcus neoformans*) *Y* (*Schizophyllum commune*)
Ste3[b]	G-protein coupled pheromone receptor (a-factor type)	Dikarya	*Bar/Bbr* (Schizophyllum commune) *CPRα/CPR2* (*Cryptococcus neoformans*) *RCB1,2,3* (*Coprinopsis cinerea*) *SlRCB1,2,3* (*Serpula lacrymans*)
Prf	pheromone response factor, High Mobility Group (HMG) DNA binding protein	Basidiomycota?	Prf-1 (*Ustilago maydis*)
Ste20	p21-activated kinase	Dikarya	CLA4 (*Coprinellus disseminatus, Pleurotus djamor*)
MAPK	mitogen-activated protein kinase	Dikarya	Kss1, Fus3 (*Saccharomyces cerevisiae*)
MAPKK	mitogen-activated protein kinase-kinase	Dikarya	Ste7 (*Saccharomyces cerevisiae*) MEK (*Saccharomyces cerevisiae*)
MAPKKK	mitogen-activated protein kinase-kinase-kinase	Dikarya	Ste11 (*Saccharomyces cerevisiae*) MEKK (*Saccharomyces cerevisiae*)
Gα, Gβ, Gγ	subunits of the trimeric GTPase protein	Dikarya	Gpa1, Ste4, Ste18 (*Saccharomyces cerevisiae*)
MIP	mitochondrial intermediate peptidase	Eukaryotes	MEP (*Schizophyllum commune*)

[a] A vast array of names has been used in the literature to represent the mating type loci, the genes they encode and the other genes involved in mating or signal transduction in Dikarya. We suggest simplifying by naming of MAT loci with *HD* for the *MAT* locus-encoding homeodomain genes and *P/R* for the *MAT* locus encoding a pheromone receptor(s) and pheromone(s).

[b] *STE* genes have been identified as non-complementing mutations leading to sterility in *Saccharomyces cerevisiae* (Bardwell 2004).

[c] Here we provide examples where alternative nomenclature has been used before, but the list is not exhaustive.

[d] In bipolar Agaricomycetes, such as *Coprinellus disseminatus* and *Phanerochaete chrysosporium*, the single *MAT* locus has been referred to as *MAT-A* because it contains HD genes but not P/R genes. Suggested nomenclature for the *MAT* locus of such species is *MAT-HD* or simply *HD*.

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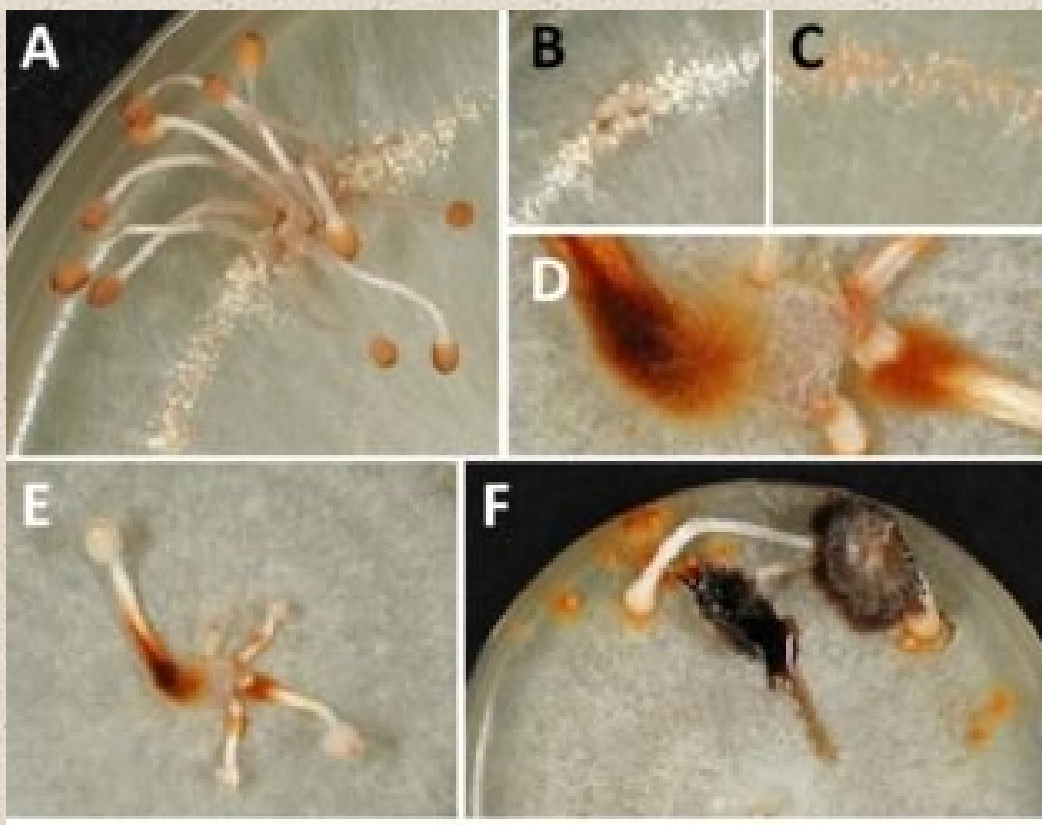
Modelové druhy

- *Coprinus* spp. - hnojník
- *Schizophyllum commune* – klanolístka
- *Agaricus* – pečárka
- *Ustilago maydis* – snět kukuřičná



https://doi.org/10.1111/myc.12527

21st Century Guidebook to Fungi, SECOND EDITION, by David Moore, Geoffrey D. Robson and Anthony P. J. Trinci

8.5 Mating types in Basidiomycota

The breeding system in Basidiomycota relies on two MAT loci. One locus encodes tightly linked **P**heromones and pheromone **R**eceptors (now called the **P/R** locus), and the other encodes homeodomain-type transcription factors (called the **HD locus**), which determine events following syngamy. In basidiomycetes, as in other filamentous fungi, syngamy means '***hyphal fusion or anastomosis***' as described in Section 5.16, above). For a successful mating that completes the sexual cycle and produces progeny spores, the two haploid hyphae that fuse must differ at both MAT loci.

When the two MAT loci are on different chromosomes, meiosis can generate four mating types among the haploid progeny because the meiotic nucleus must be heterozygous at both MAT loci. The occurrence of four progeny mating types defines this as a **tetrapolar breeding system**. Some basidiomycetes have a **bipolar breeding system** instead, which is controlled by a single MAT locus because either the P/R and HD loci are closely linked on the same chromosome and segregate together, or because one has lost its function in determining mating-type. About 65% of the species in the Agaricomycotina (see Section 3.8) are tetrapolar, whereas Ustilaginomycotina and the Pucciniomycotina are predominantly bipolar. Agaricomycetes, which includes most fungi that produce conspicuous fruit bodies, have evolved a system to increase the diversity of 'alleles' at both MAT loci, in some cases yielding species with hundreds or thousands of possible mating types. Tetrapolar breeding systems, and especially this great diversity in MAT 'alleles', are believed to be adaptations to promote outbreeding in organisms that, for the most part, rely on air currents to distribute their spores (Section 8.6, below).

The P/R system of Basidiomycota that governs hyphal fusion depends on small (10- to 15-amino acid) lipopeptide pheromones, which are made from precursor polypeptides containing 35 to 40 amino acids by post-translation modifications at both the N- and C-termini (Raudaskoski & Kothe, 2010; Raudaskoski, 2015). All active basidiomycete mating pheromones isolated so far are hydrophobic diffusible lipopeptides that undergo farnesylation at the C-terminal cysteine residue of a CAAX motif ('C' is cysteine, 'A' an aliphatic amino acid, and 'X' is any residue) and amino-terminal processing. These diffusible pheromones are received by pheromone receptors, located in the plasma membrane with seven transmembrane domains, which are coupled to a G-protein signal transduction cascades. This has been investigated in greatest detail in *Ustilago maydis*, where two interconnected signalling pathways, one involving cAMP-dependent protein kinase and the other MAP kinase (Section 5.13, above). The two pathways converge to a HMG-transcription factor (Section 8.1, above) called **P**heromone **r**esponse **f**actor (**Prf1**) which recognises and binds to the specific 'pheromone response motifs located in the regulatory regions of the genes that the pheromone induces. Although the protein kinase cascade pathways are conserved over broad evolutionary distances, the transcription factors that ultimately activate or repress the specific target genes are often species-specific (Coelho *et al.*, 2017).

This way of controlling mating fusion is similar to the a- and α-factor P/R system of ascomycetes and is thought to predate the separation of Asco- and Basidiomycota clades. It is feasible that what is common in this shared P/R system contributes to the information interchange that takes place between the two fusing hyphal cells involved in fusion we described in Section 5.16, above. However, there are important differences between ascomycetes and basidiomycetes, in that only homologues of the a-factor pheromone and Ste3 pheromone receptor of the ascomycete system exist in basidiomycetes.

Identity-sensing specificity in basidiomycetes is done by allelic variants of the same type of genes, rather than depending on the 'a-factor/Ste3' plus 'α-factor/Ste2' coupled sensing system characteristic of the ascomycetes (Casselton & Olesnicky, 1998; Kües, 2015). Mating (syngamy or fusion) is initiated by a reciprocal exchange of pheromones recognised by matching pheromone receptor variants in both mating types, and thus the two mycelia involved need to carry differen alleles of the pheromone and receptor genes at the P/R locus.

Many additional pheromone receptor-like genes have been identified in Agaricomycetes that are non-mating-type-specific receptors and are not sufficient to induce mating-specific development. Many of these nonmating-type-specific receptors are located close to the P/R locus, while others are unlinked. Three distinctive features of these receptors are that:

- (i) they have longer C-terminal cytoplasmic regions,
- (ii) they lack pheromone genes in close association, and
- (iii) they show lower levels of intraspecific polymorphism.

Non-mating-type-specific receptors have been found in *Coprinopsis cinerea*, *Phanerochaete chrysosporium*, *Laccaria bicolor*, *Postia placenta*, and several polypores (Coelho *et al.*, 2017). Possible functions include a role in monokaryotic fruiting or in

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1535-9778/10/$12.00 doi:10.1128/EC.00319-09

Basidiomycete Mating Type Genes and Pheromone Signaling[▽]

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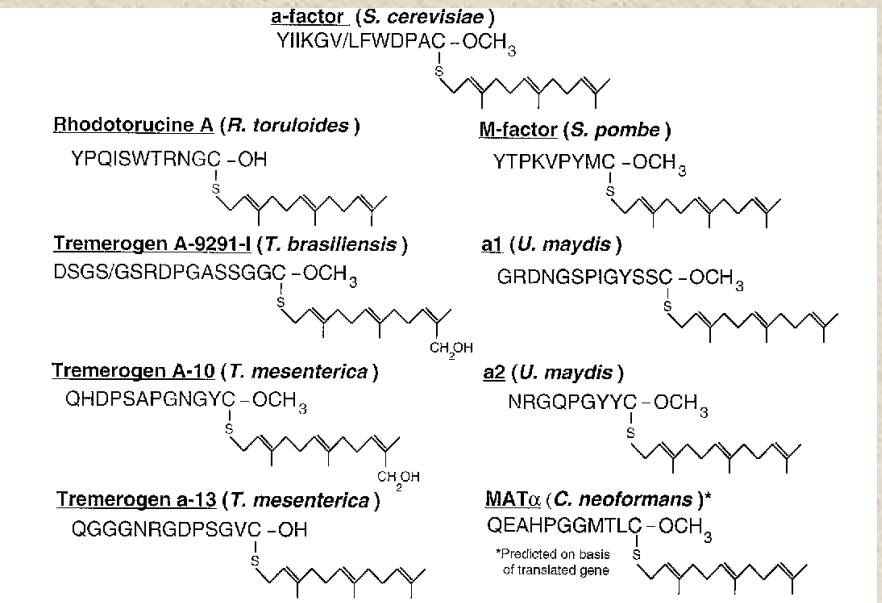
The genome sequences of the basidiomycete *Agaricomycetes* species *Coprinopsis cinerea*, *Laccaria bicolor*, *Schizophyllum commune*, *Phanerochaete chrysosporium*, and *Postia placenta*, as well as of *Cryptococcus neoformans* and *Ustilago maydis*, are now publicly available. Out of these fungi, *C. cinerea*, *S. commune*, and *U. maydis*, together with the budding yeast *Saccharomyces cerevisiae*, have been investigated for years genetically and molecularly for signaling in sexual reproduction. The comparison of the structure and organization of mating type genes in fungal genomes reveals an amazing conservation of genes regulating the sexual reproduction throughout the fungal kingdom. In agaricomycetes, two mating type loci, *A*, coding for homeodomain type transcription factors, and *B*, encoding a pheromone/receptor system, regulate the four typical mating interactions of tetrapolar species. Evidence for both *A* and *B* mating type genes can also be identified in basidiomycetes with bipolar systems, where only two mating interactions are seen. In some of these fungi, the *B* locus has lost its self/nonself discrimination ability and thus its specificity while retaining the other regulatory functions in development. *In silico* analyses now also permit the identification of putative components of the pheromone-dependent signaling pathways. Induction of these signaling cascades leads to development of dikaryotic mycelia, fruiting body formation, and meiotic spore production. In pheromone-dependent signaling, the role of heterotrimeric G proteins, components of a mitogen-activated protein kinase (MAPK) cascade, and cyclic AMP-dependent pathways can now be defined. Additionally, the pheromone-dependent signaling through monomeric, small GTPases potentially involved in creating the polarized cytoskeleton for reciprocal nuclear exchange and migration during mating is predicted.

- **B lokus** - geny kódující feromony (lipopeptid, 10-15 AMK) a receptory
- β a α lokusy obsahují více genů s nejasnou funkcí či bez vazby na rozmnožování
- Opět ohraničeno konzervativními geny (*mip*)



tures of lipopeptide mating pheromones of various fungi. The *C. neoformans* pheromone has not yet been isolated; its structure is b ence from the gene and putative processing events analogous to those that occurs with other lipopeptide pheromones. Amino aci

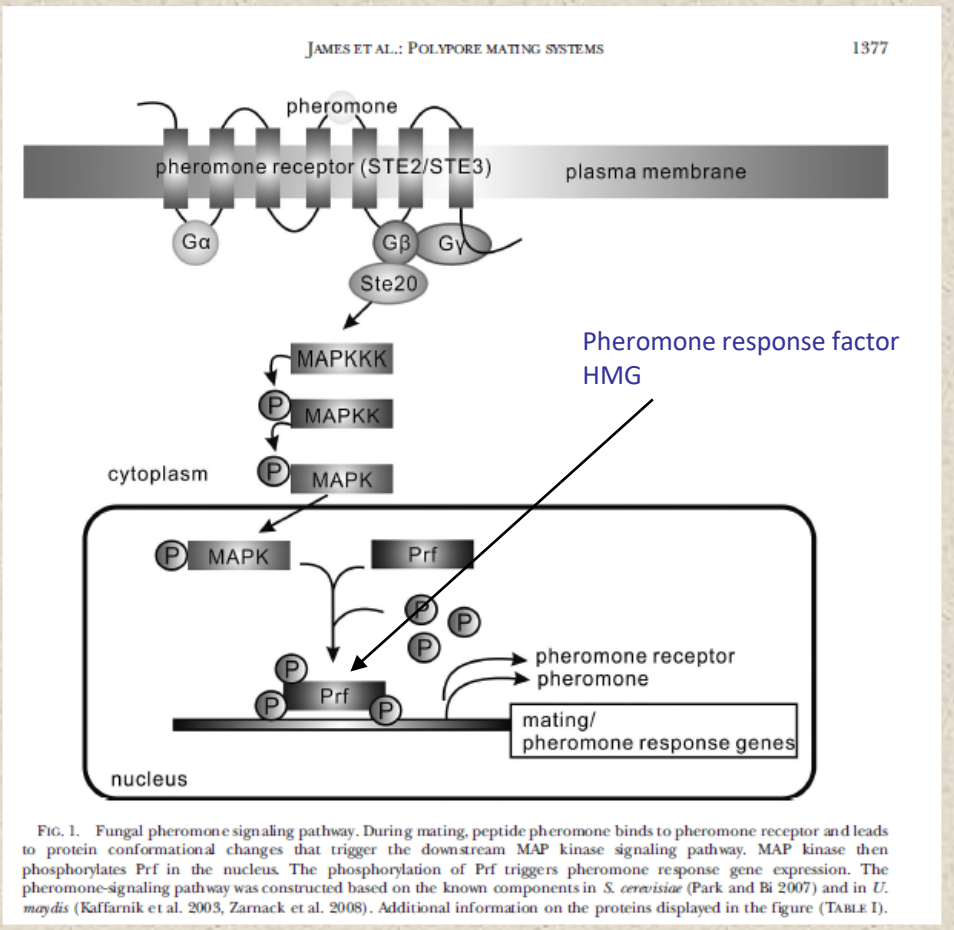


FIG. 1. Fungal pheromone signaling pathway. During mating, peptide pheromone binds to pheromone receptor and leads to protein conformational changes that trigger the downstream MAP kinase signaling pathway. MAP kinase then phosphorylates Prf in the nucleus. The phosphorylation of Prf triggers pheromone response gene expression. The pheromone-signaling pathway was constructed based on the known components in *S. cerevisiae* (Park and Bi 2007) and in *U. maydis* (Kaffarnik et al. 2003, Zarnack et al. 2008). Additional information on the proteins displayed in the figure (TABLE I).

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- **A lokus** - zásadní jsou homeodoménové geny (HD1, HD2) důležité transkripční faktory, které se vážou na DNA

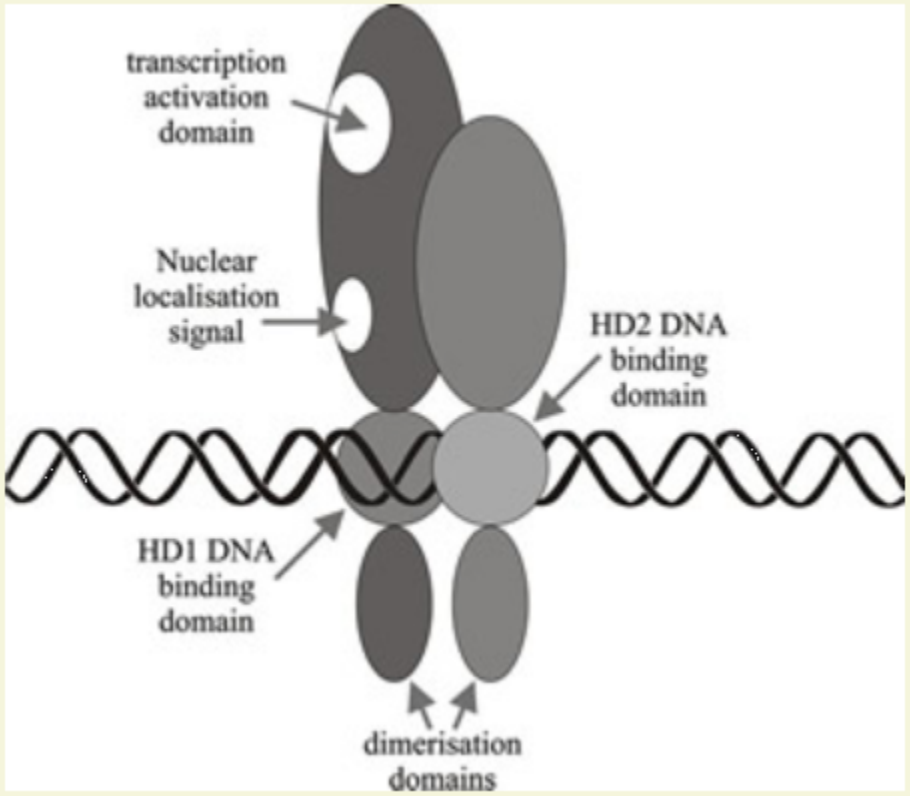

Fig. 10. Schematic diagram illustrating a simplified model of homeodomain protein interactions involved in *A* (***HD locus***) mating type factor activity in *Coprinopsis*. Modified from Chapter 2 in Moore & Novak Frazer, 2002.

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Coprinus cinereus (Coprinopsis cinerea)

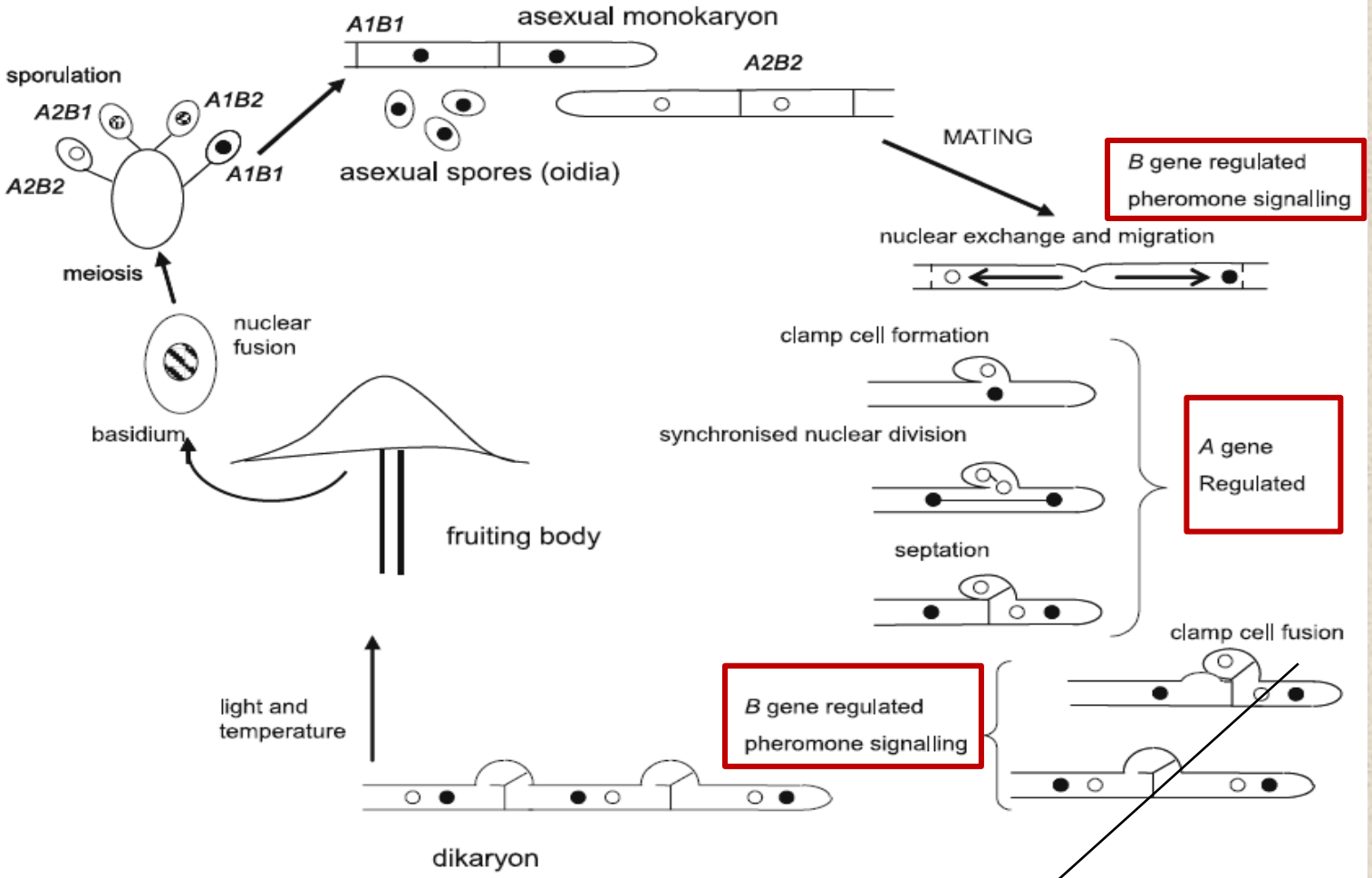

Fig. 17.2. Life cycle of the saprophytic mushroom *Coprinus cinereus* (*Coprinopsis cinerea*)

- **B faktor,** first compatibility checkpoint, odpovídá za produkci feromonu, plazmogamii a částečně migraci jader, na tomto kroku se podílí i *het* geny somatické inkompampability
- **A faktor** second compatibility checkpoin, odpovídá za migraci jader a pravidelnou dikaryotizaci (+ tvorba přezek) a septaci. Při nekompatibilitě vzniká kolonie s velmi řídkým "vodnatým" myceliem (transparentní, tzv. flat-mycelium)

Table 2.4 The consequences of encounters between primary mycelia of *Coprinus cinereus* of different mating type

Type of encounter	Example of mating type	Consequence
A = B =	$A_1B_1 \times A_1B_1$	Dikaryon formation not initiated
A = B ≠	$A_1B_1 \times A_1B_2$	Dolipore septa are converted into simple perforate septa and nuclear migration occurs, but no synchronization of nuclear division or formation of clamp connections
A ≠ B =	$A_1B_1 \times A_2B_1$	Only a few dikaryotic cells and clamp connections are formed, since nuclear migration cannot occur and most cells remain monokaryons
A ≠ B ≠	$A_1B_1 \times A_2B_2$	Nuclear migration and dikaryon formation occur, the secondary mycelium develops clamp connections, and fruiting bodies are formed

Z Carlile et al. 2001

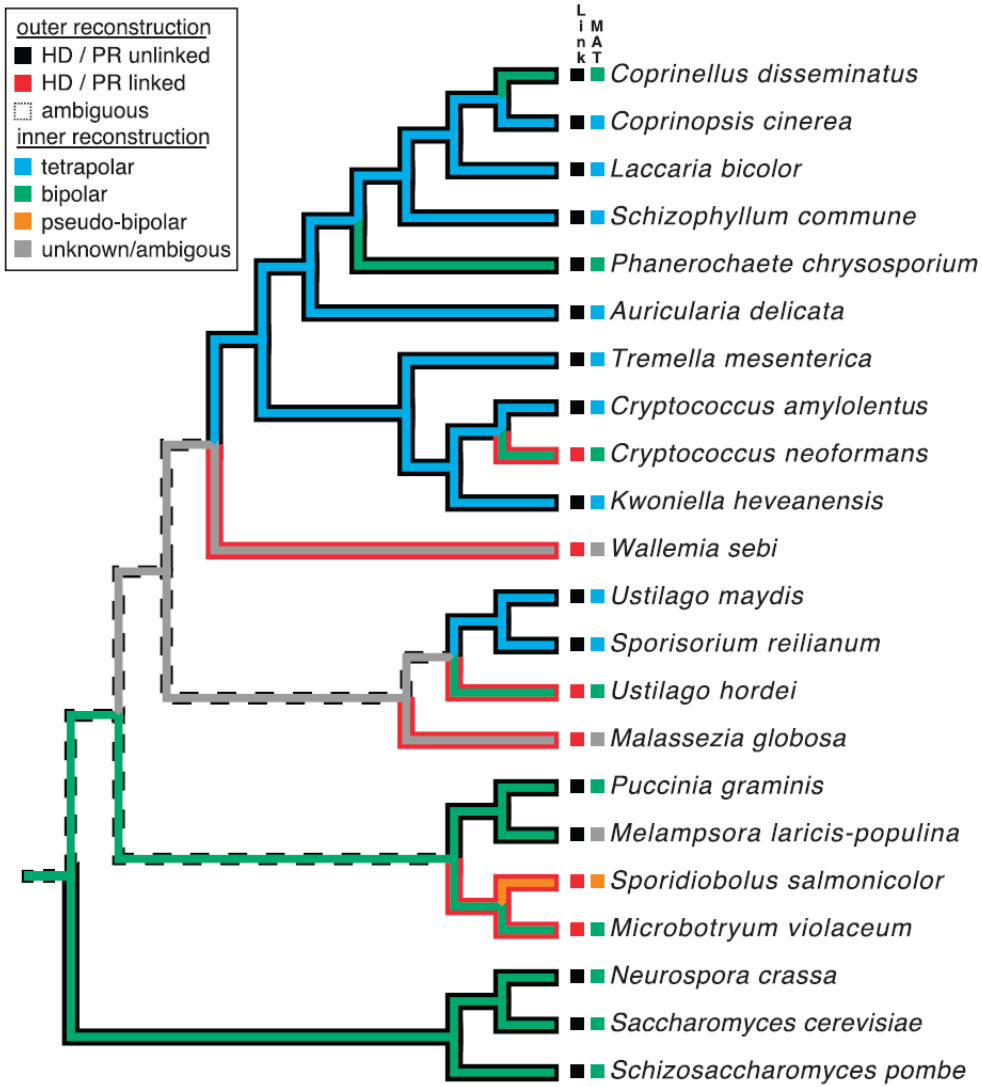

FIG. 7. Phylogenetic reconstruction of the evolution of mating systems and linkage between *HD* and *P/R* loci in the Basidiomycota. On the outer layer of the branches is the ancestral state reconstruction under parsimony of the physical linkage between *HD* and *P/R* loci. In some cases (e.g. *Melampsora larici-populina*), absence of linkage is inferred by association of *HD* and *P/R* loci to different scaffolds of draft genome sequences, and this may not be equivalent to chromosomal linkage. The inner portion of the branches reconstructs ancestral mating systems, where known. The character states of species included in the tree are given to the left of the names, where "Link" refers to linkage of *HD* and *P/R* and "*MAT*" refers to mating system. The phylogeny is based on (Aime et al. 2006, Hibbett 2006, Matheny et al. 2006, Kellner et al. 2011).

- Velká diverzita alel v populaci v α a β lokusech (u 114 kmenů *S. commune* bylo 9 Aα alel, 32 Aβ alel, 9 Bα alel a 9 Bβ alel = 288 různých A faktorů a 81 B faktorů
- - 288 x 81 = 23 328 rozdílných vzájemně kompatibilních plodných spojení
- - α a β jsou v silné vazbě, ale mají možnost rekombinovat
- -ochrana proti inbreedingu (křížení jedinců z jedné plodnice, či příbuzných jedinců)

- U tetrapolárních hub je pouze 25% potomstva z jedné plodnice schopno křížení (inbrední potencíál 25% oproti 50% u bipolárních hub)

- kdežto potomci různých plodnic budou velmi pravděpodobně kompatibilní (důsledek multialelismu viz. *S. commune*)

Table 5.2 Mating among the haploid progeny from the fruiting body of a Basidiomycete with tetrapolar incompatibility. The basidium nuclei have the mating genotype A_1A_2, B_1B_2. Meiosis gives rise to haploid progeny with four possible mating type genotypes – A_1B_1, A_1B_2, A_2B_1, A_2B_2. Mating is only completed successfully if encounters are between mycelia that differ with respect to both mating type factors. The chequerboard shows that only 25% of the possible encounters satisfy this condition. The inbreeding potential is thus 25%.

	A_1B_1	A_1B_2	A_2B_1	A_2B_2
A_1B_1	–	–	–	+
A_1B_2	–	–	+	–
A_2B_1	–	+	–	–
A_2B_2	+	–	–	–

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TABLE 4.3 Characteristics and Examples of Fungi Having Different Mating Systems that Promote Outcrossing

System	Examples	Number of mating type loci	Number of different alleles at each locus in the whole population	Designation of mating types	Inbreeding potential (%)[a]	Outbreeding potential (%)[b]
Two mating types	Most zygomycetes; *Neurospora crassa* (Ascomycota); *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* (Ascomycota, yeast)	1	1	±, *Aa*, *aα*	50	50
Unifactorial (bipolar) incompatibility	*Coprinus disseminatus* and *Stereum gausapatum* (Basidiomycota)	1	Many	$A_1 \ldots A_n$	50	Nearly 100
Bifactorial (tetrapolar) incompatibility	*Coprinopsis cinerea* and *Schizophyllum commune* (Basidiomycota)	2	Many	$A_1 B_1 \ldots A_n B_n$	25	Nearly 100
Modified tetrapolar incompatibility	*Ustilago maydis* (Basidiomycota, smut)	2	2 at locus *a*, many at locus *b*	$A_1 B_1 \ldots A_2 B_n$	25	50

[a]*The probability that a randomly encountered sibling (product of the same diploid parent) will be compatible.*

Pseudo-homothalismus

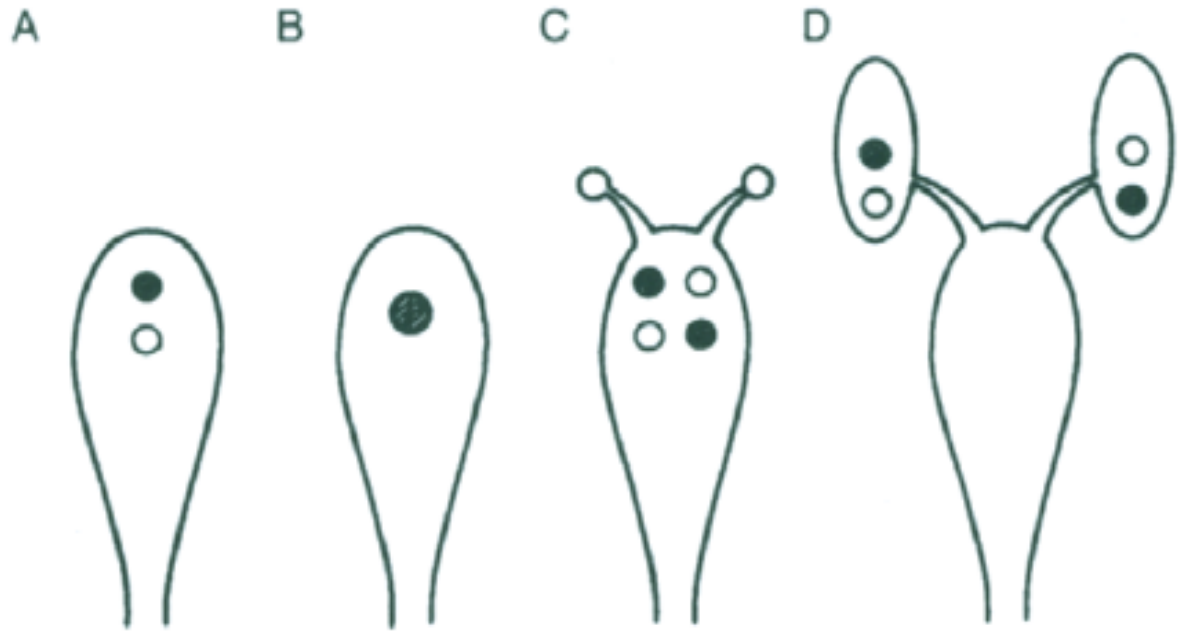

Figure 2.23 Diagram of basidiospore development in *Agaricus bisporus*. A, A basidium with two haploid nuclei of compatible mating types. B, A diploid nucleus has resulted from nuclear fusion. C, Meiosis has occurred, and since *A. bisporus* is bipolar, two nuclei are of one parental mating type and two of the other. Sterigmata have been formed and the basidiospore initials have begun to swell. D, Two nuclei have moved into one spore and two into the other. The basidia of other Agarics (e.g. *Coprinus cinereus*) are very similar, but bear four spores each of which receives a single nucleus.

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- Pro křížení potřebujeme monokaryony každého ze 4 párovacích typů z každé plodnice (vstupní materiál je čerstvá plodnice, nutno počítat s dvoujadernými sporami)
- Vícejaderné buňky je možné dedikaryotizovat (izolace protoplastů či jinak)
- **Využití v hledání hranice biologických druhů – taxonomie** (zdlouhavé)

Mycol Progress (2009) 8:337–349
DOI 10.1007/s11557-009-0607-3

ORIGINAL ARTICLE

Mating tests in *Agrocybe cylindracea* sensu lato. Recognition of *Agrocybe wrightii* as a novel species

Marina Uhart · Edgardo Albertó

FUNGAL BIOLOGY REVIEWS 30 (2016) 152–162

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Review

Vegetative incompatibility in fungi: From recognition to cell death, whatever does the trick

Mathieu PAOLETTI

Non self recognition in fungi, Institut de Biochimie et Génétique Cellulaire, UMR5095 CNRS-Université de Bordeaux, 1 rue Camille Saint-Saëns, 33077 Bordeaux Cedex, France

Table 2 Intra-strain crossings between monokaryotic isolates (MIs) of the *A. cylindracea* strain WT-49. Mating types were assigned to MIs as follows: MIs Tai 9 and 13, mating type A_1B_1; Tai 7, 12 and 15, A_1B_2; Tai 1, 10, and 14, A_2B_2; Tai 2 and 8, A_2B_1

	Tai 1 A_2B_2	Tai 7 A_1B_2	Tai 9 A_1B_1	Tai 10 A_2B_2	Tai 12 A_1B_2	Tai 13 A_1B_1	Tai 14 A_2B_2	Tai 15 A_1B_2
Tai 1 A_2B_2		- - -	+ + +	- - -	- - -	+ + +	- - -	- - -
Tai 7 A_1B_2			- - -	- - -	- - -	- - -	- - -	- - -
Tai 9 A_1B_1				+ + +	- - -	- - -	+ + +	- - -
Tai 10 A_2B_2					- - -	+ + +	- - -	- - -
Tai 12 A_1B_2						- - -	- - -	- - -
Tai 13 A_1B_1							+ + +	- - -
Tai 14 A_2B_2								- - -
Tai 2 A_2B_1								+ + +
Tai 5								- - -
Tai 6								- - -
Tai 11								- - -
Tai 18								- - -
Tai 8 A_2B_1	- - -					- - -		+ + +

+ Presence of clamp connections, - absence of clamp connections

- Roztřídění monokaryonů

na párovací typy

Table 5 Inter-strain crossings between monokaryotic isolates of *A. cylindracea* sensu lato

		WT-49 (China)				WT-22 (Belgium)			WT-54 (Ar.)	WT-43 (Gu.)
		Tai 13	Tai 1	Tai 15	Tai 8	Bel 15	Bel 22	Bel 24	Mis 2	Gua 2
Ac-1 (Japan)	Chax 8	- - -			- -	- + - NF			- + - NF	- + - F
	Chax 11		- + + F			- + + NF			- + - NF	- + - FG
	Chax 14	- - -	- - -							
	Chax 18			- + + F	+ + - NF					
WT-49	Tai 13					- + - F	- + - FG		- + - NF	- + - F
	Tai 1						- - -		- + - NF	- - -
	Tai 15					- + - ND		- -	- -	- + - FG
	Tai 8							- -	- + - NF	- - -
WT-22	Bel 15								- + - F	- - -
	Bel 22								- - -	- - -
	Bel 24								- + - F	
WT-54	Mis 2									- - -

Ar Argentina, *Gu* Guatemala
\+ Presence of clamp connections, - absence of clamp connections
F The dikaryotic mycelia product of the crossing fructified, *NF* the dikaryotic mycelia product of the crossing did not fructified, *FG* the dikaryotic mycelia product of the crossing fructified and the spores isolated germinated under appropriate conditions, *ND* not determined

- vyhodnocení tvorby dikaryonu
- Vyhodnocení fruktifikace
- Vyhodnocení klíčivosti spor z vypěstovaných plodnic
- Korelace s jinými markery
- Popis nového druhu

Somatická inkompatibilita

- heterogenická
- **Reguluje fúzi dikaryotického mycelia**
- fúze monokaryonů či di- s monokaryonem je pod kontrolou sexuální kompatibility

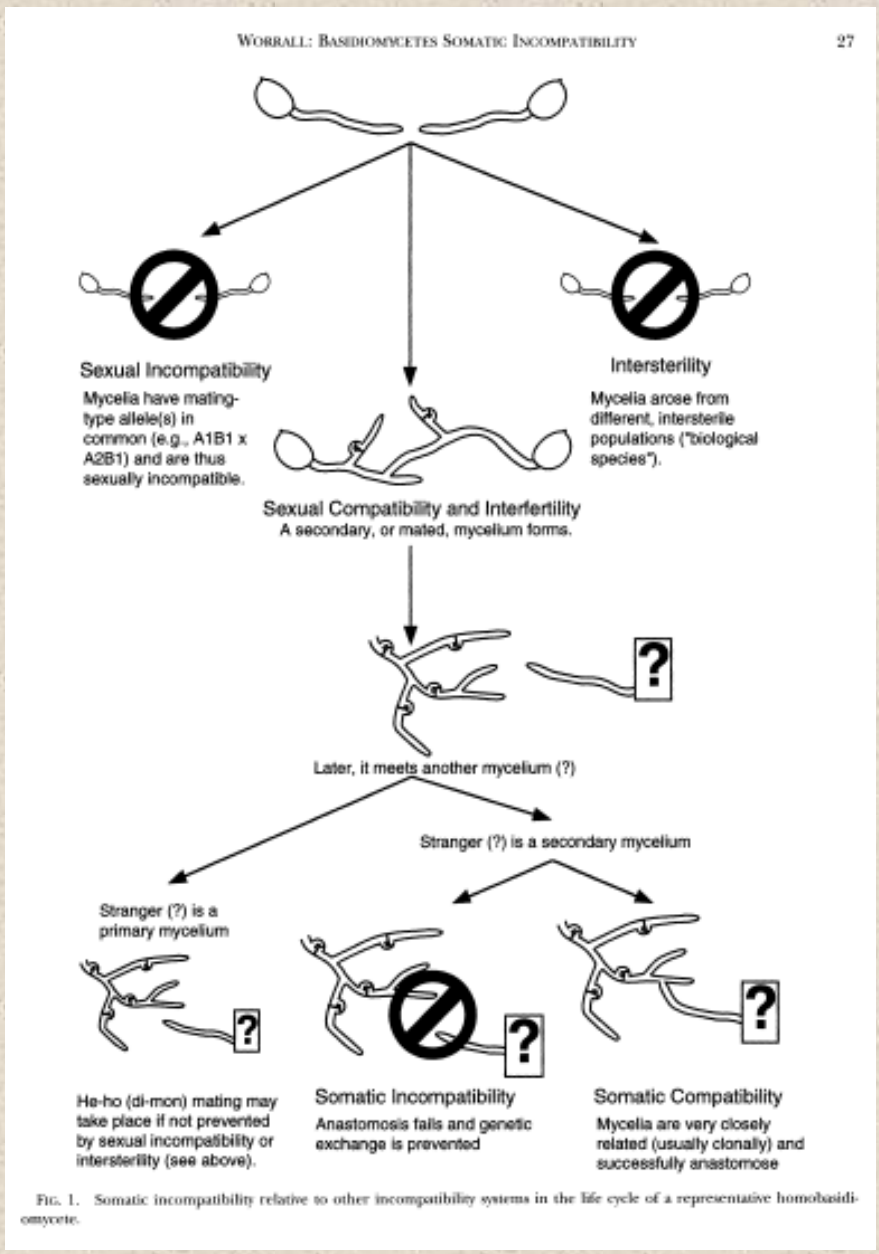

FIG. 1. Somatic incompatibility relative to other incompatibility systems in the life cycle of a representative homobasidiomycete.

TABLE II. Frequency of somatic incompatibility among pedigreed secondary mycelia

Type of pairing	Example	Species	Frequency of incompatibility (%)	Reference
Nonsibcomposed, unrelated mycelia	1a2a × 3a4a[a]	*Coprinus cinereus*	100	(May, 1988)
		Armillaria luteobubalina	100	(Kile, 1983)
		Phaeolus schweinitzii	90[b]	(Barrett and Uscuplic, 1971)
Nonsibcomposed mycelia having 1 or 2 of 4 mating alleles in common	1a2a × 3a–[c]	*A. luteobubalina*	90	(Kile, 1983)
Sibcomposed mycelium with unrelated field isolate	1a1b × 2	*Fomitopsis cajanderi*	100	(Adams and Roth, 1967)
		P. schweinitzii	85	(Barrett and Uscuplic, 1971)
Sibcomposed mycelia from different parents	1a1b × 2a2b	*Echinodontium tinctorium*	95	(Wilson, 1991)
		P. schweinitzii	62	(Barrett and Uscuplic, 1971)
Sibcomposed mycelia from same parent but no nucleus in common	1a1b × 1c1d	*Marasmius androsaceus*	100	(Holmer and Stenlid, 1991)
		Pleurotus ostreatus	96	(Kay and Vilgalys, 1992)
		F. cajanderi	83	(Adams and Roth, 1967)
		Armillaria spp.	44–55[d]	(Kile, 1983; Korhonen, 1978)
Sibcomposed mycelia from same parent, one nucleus in common	1a1b × 1a1c	*F. cajanderi*	65	(Adams and Roth, 1967)
Nonsibcomposed mycelia with one nucleus in common	1a2a × 1a3a	*Coprinus cinereus*	92	(May, 1988)
		Phaeolus schweinitzii	63	(Barrett and Uscuplic, 1971)
Sibcomposed mycelium with parental field isolate	1a1b × 1	*Collybia subnuda*	98	(Murphy and Miller, 1993)
		Phellinus sulphurascens	93	(Hansen, 1979)
		Pleurotus ostreatus	90	(Kay and Vilgalys, 1992)
		F. cajanderi	59	(Adams and Roth, 1967)
		Phaeolus schweinitzii	18	(Barrett and Uscuplic, 1971)
		Marasmiellus praeacutus	15	(Murphy and Miller, 1993)
Nonsibcomposed mycelia with one nucleus in common, the other nuclei being sib-related	1a2a × 1b2a	*Phellinus gilvus*	50	(Rizzo et al., 1995)

[a] Numbers refer to secondary mycelia from the field; letters refer to their single-spore progeny. For example, 1a is a single-basidiospore isolate from the parental mycelium 1. Synthetic secondary mycelia are indicated by the component single-spore isolates.

[b] Incompatibility in these pairings would have been absolute but for one aberrant isolate.

[c] Some pairings, including all compatible ones, involved a common parent.

[d] It was not explicitly stated that no monosporous isolates were in common.

Mycologia, 89(1), 1997, pp. 24–36.

Somatic incompatibility in basidiomycetes

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A WIDESPREAD PHENOMENON

Somatic incompatibility, under various names and with varying details, appears to be widespread in bi-

A co když monokaryon potká dikaryon?

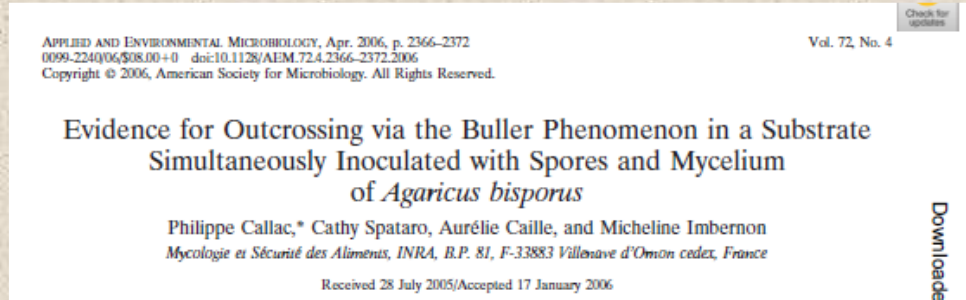
- **Bullerův fenomén (1932)**

- Opět nutná kompatibilita
- di-mon mating
- Monokaryon může párovat s dikaryonem
- Následně je monokaryon dikaryotizovan (popřípadě vznikají atypické počty jader v jedné buňce)
- Lze řadit mezi pohlavní rozmnožování

Na příkladu tetrapolární houby

- 1. Legitimní kombinace –(A1B1+A2B2)x A3B3
- 2. Hemikompatibilní kombinace (**A1B1**+A2B2) x **A1B1** (pouze jedno jádro komp.)
- 3. Nelegitimní kombinace – (A1B1+A2B2)x A1B2 nebo A2B1

Mimo přednášku a zkoušku – téma pro samostudium



APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Apr. 2006, p. 2366–2372 Vol. 72, No. 4
0099-2240/06/$08.00+0 doi:10.1128/AEM.72.4.2366–2372.2006

Evidence for Outcrossing via the Buller Phenomenon in a Substrate Simultaneously Inoculated with Spores and Mycelium of *Agaricus bisporus*

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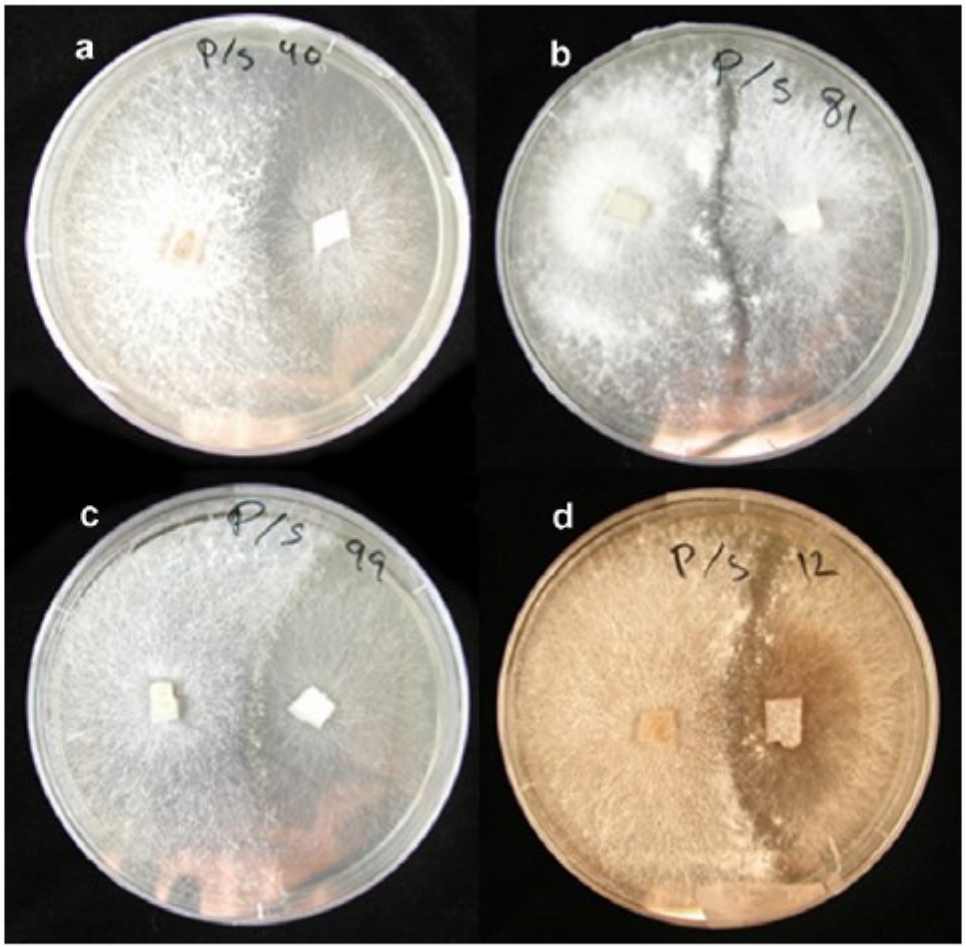

Fig. 1. Pairings between *H. annosum s.l.* heterokaryons. The mycelia in each pairing contain one common sib-nucleus (40, 81, 99 or 12) and either a TC-122-12 (parental) or a TC-39-7 (unrelated) nucleus. The pairings exemplify: (a) compatible (score 1), (b) incompatible (4), (c) weakly incompatible (2), (d) incompatible (4) interactions.

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Genetics and QTL mapping of somatic incompatibility and intraspecific interactions in the basidiomycete *Heterobasidion annosum s.l.*

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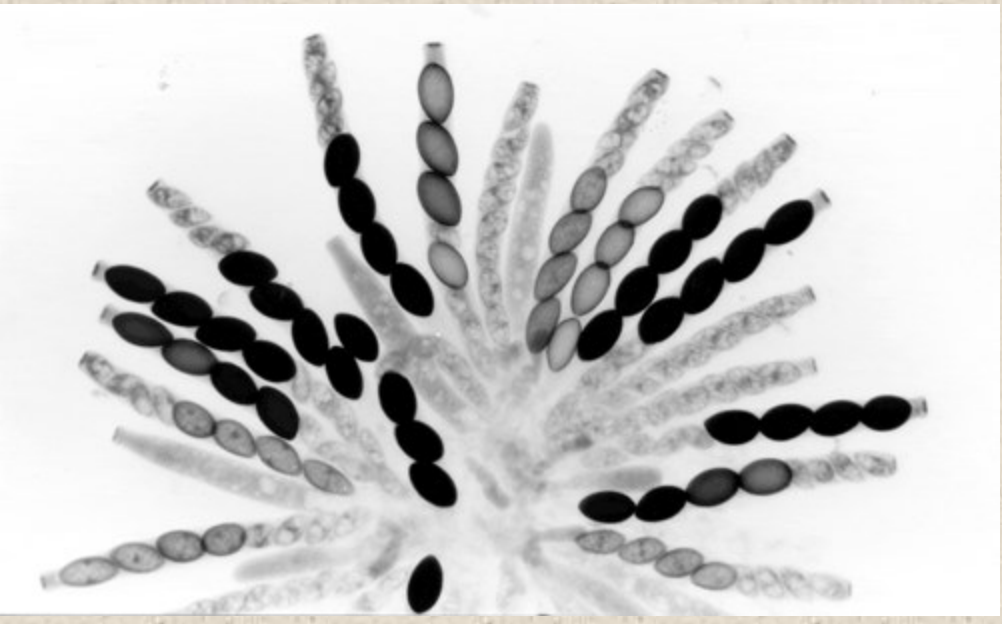
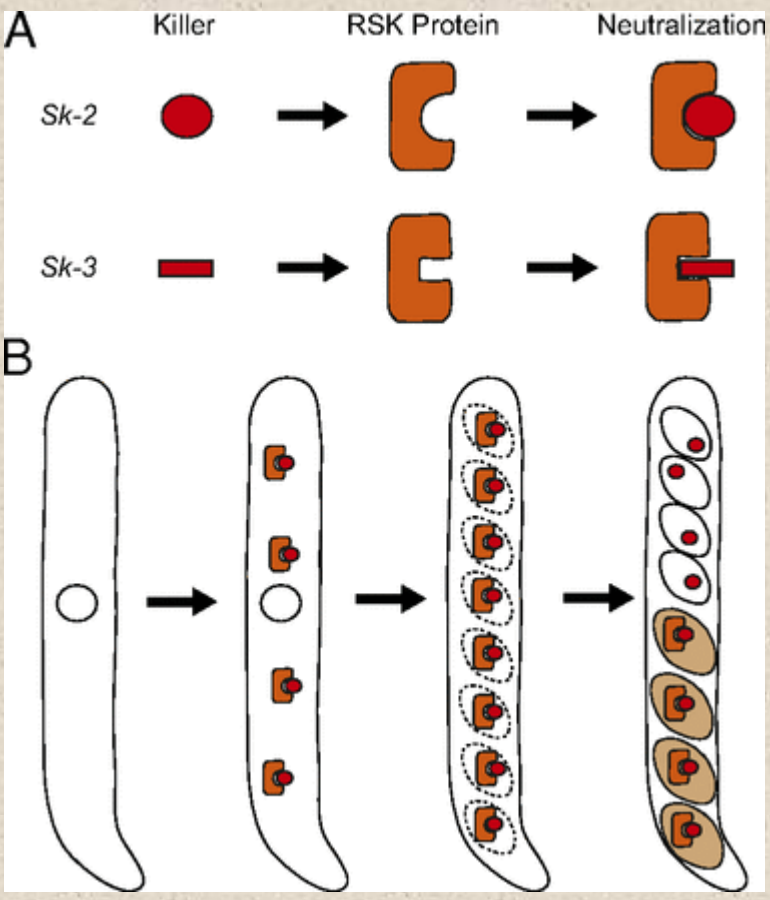
Spore killers

- Objeveno u *Neurospora* v roce 1979
- faktory aborce askospor – Spore killers (sk)
- exprimují se ve vřecku před tvorbou askospory





Hammond T M et al. PNAS 2012;109:12093-12098
Raju 1979, Genetics 93: 607-623.

Mimo přednášku a zkoušku – téma pro samostudium

Mimojadarná dědičnost

- **Mitochondriální dědičnost**

  - anisogamní houby (vláknité askomycety, některé rzi). Typicky fůze malé spermatie a velkého ascogonia. mtDNA je nejčastěji **maternálně dědičná (uni-parentální)**.

  - isogamní houby (kvasinky a většina bazidiomycetů). Při fůzi somatických buněk přechází jádro, ale nemusí přecházet mitochondrie. Případně dochází k následné segregaci mitochodnrií z jedné gamety a v obou případech je dědičnost **uni-parentální**. U některých druhů známe **bi-parantální** dědičnost.

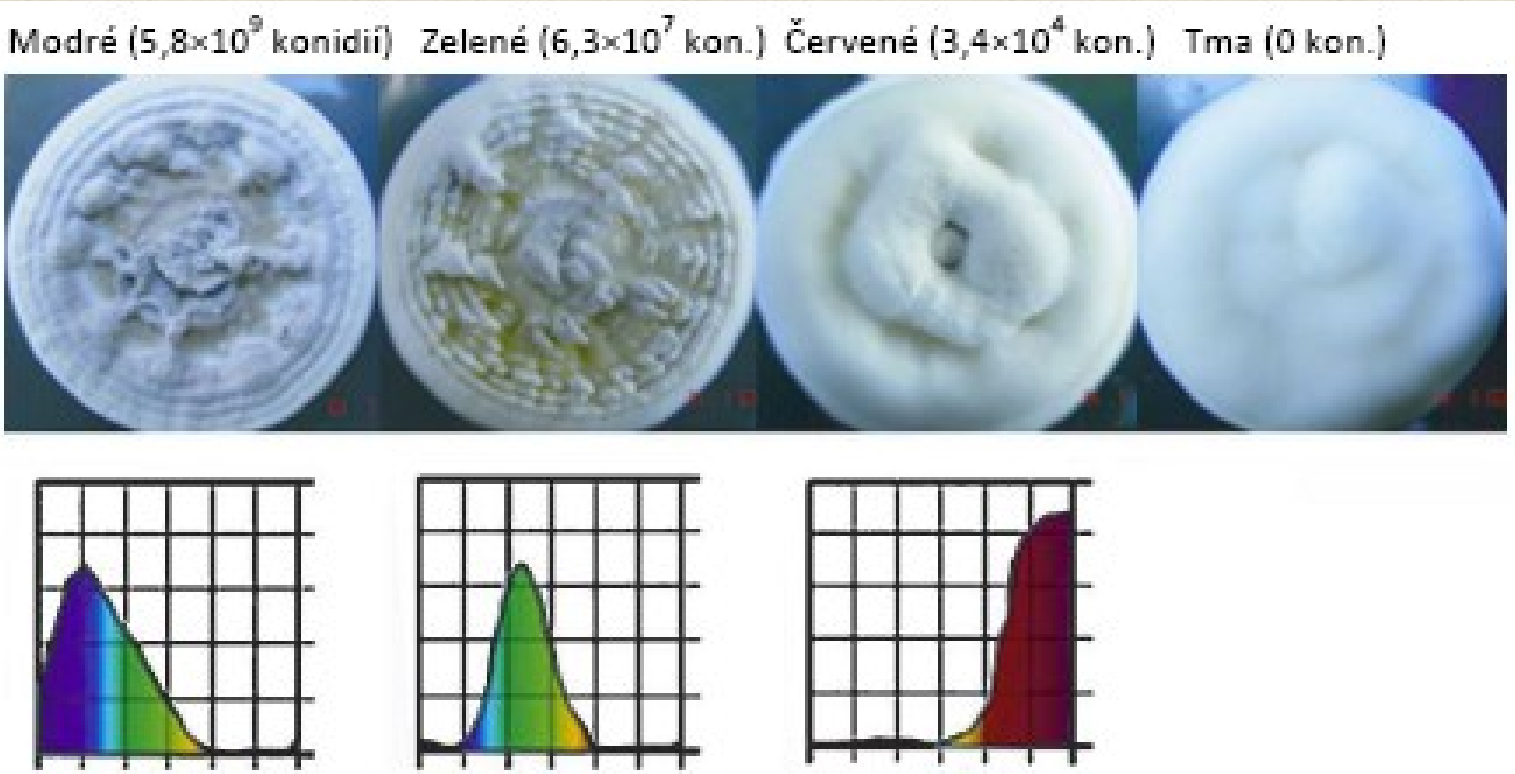
- **plazmidy**

Navození sporulace

Obecně lze ale říci, že je to stres (limitní faktory), který stimuluje sporulaci (Klebsova pravidla). V praxi je větší sporulace dosahováno použitím polopřirozených médií (např. rostlinný materiál), regulací světelného a teplotního režimu v kultivačních termostatech a dlouhodobou kultivací. Vědecky jsou studovány faktory jako je světlo, teplota, dostupnost vody, vystavení vzduchu a vysychání, dostupnost živin a esenciálních látek, osmolarita média a další faktory.

Faktor prostředí	Organismus	Mechanismus iniciace
Vysychání	*Penicillium griseofulvum*	ztráta vody z mycelia
Hyperoxie	*Neurospora crassa*	hyperoxidovaný stav
Světlo	*Penicillium cyclopium*	Nedefinováno
	Neurospora crassa	aktivace WC-1 transkripčního faktoru
	Trichoderma viride	Nedefinováno
	Aspergillus nidulans	inaktivace represoru konidiace VeA
	Septoria viciae	nedefinováno (Tan 1978)
	Phoma pinodella	nedefinováno (Tan 1978)
Osmotický stres (soli)	*Aspergillus nidulans*	Nedefinováno
	Aspergillus oryzae	Nedefinováno
	Neurospora crassa	nedefinováno (osmosenzor?)
Nedostatek dusíku	*Penicillium griseofulvum*	Nedefinováno
Nedostatek uhlíku	*Penicillium chrysogenum*	Nedefinováno
	Neurospora crassa	glukózový senzor
Nedostatek uhlíku a/nebo dusíku	*Aspergillus nidulans*	Nedefinováno
Vápník	*Penicillium* spp.	skrz konidiogenone
	Trichoderma viride	nedefinováno (Simkovic et al. 2008)
Nízké teploty	*Eurotium herbariorum*	Nedefinováno (Turian 1978)

Přehled faktorů navozujících sporulaci (převzato z Dudová 2011)



Obrázek 1. Morfologie kultur *Paecilomyces fumosoroseus* kultivovaných při různých vlnových délkách světla s počtem získaných konidií (Sánchez-Murillo et al. 2004).

(převzato z Dudová 2011)