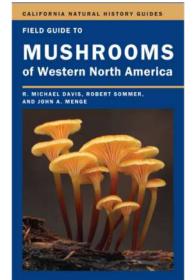
State of LA Fungi

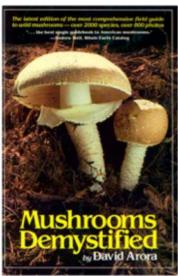
March 28, 2023

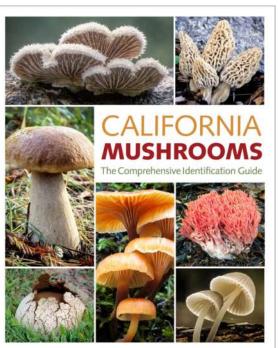


Los Angeles Mycological Society

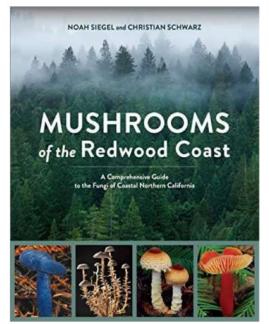
- I. Look back on March
- II. Reproduction and mating types in Basidiomycota
- III. Mushrooms in the chaparral
- IV. Evolution and ecology of psilocybin in nature







Dennis E. Desjardin · Michael G. Wood · Frederick A. Stevens







Southern California O

7,819

300

1,588



Common Fieldcap



Hairy Curtain Crust



Splitgill Mushroom



Oak-loving Elfin Saddle



Yellow Fieldcap





Mulch Maids





Pale Brittlestem



Golden Ear



Springtime Amanita



Turkey-Tail



Western Destroying A...



Crystal Brain Fungus



Deer Mushroom



Black Witches' Butter



Flocculose Inkcap







https://www.inaturalist.org/observations?d1=2023-03-01&d2=2023-03-28&place id=51727&taxon id=47170&view=species

iNaturalist: Most Common Fungal Species in SoCal, March 2023





Southern California •

4,181

283

1,011





Splitgill Mushroom



Hairy Curtain Crust



Oak-loving Elfin Saddle



Western Jack-O'-Lant...



Turkey-Tail



Rosy Navel



Golden Ear



Blewit



Springtime Amanita



Desert Shaggymane



Western Destroying A...



Yellow Cobblestone Li...



Rufous Candy Cap



Giraffe Spots



Blushing Bride Amanita



Field Bird's Nest Fungus



Stork's-bill Chytrid



Yellow Fieldcap



https://www.inaturalist.org/observations?d1=2023-03-01&d2=2023-03-28&place id=51727&taxon id=47170&view=species

iNaturalist: Most Common Fungal Species in SoCal, February 2023

III

Fungal reproduction.

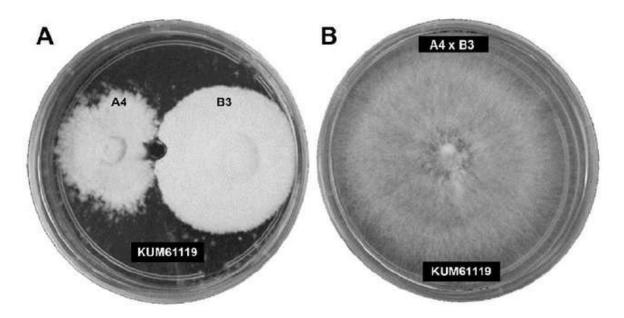


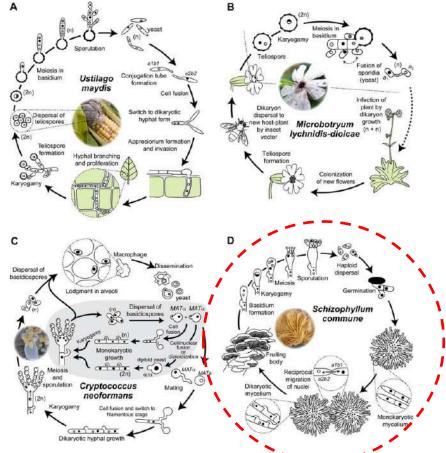
Fig. 1: Cross compatibility test. (A) A compatible mating between two selected monokaryotic isolates of A4 and B3 (obtained from KUM61119 strain). (B) Successfully crossed strain (dikaryotic). Avin et al., 2014.



Diversity in mating system complexity *just* in Basidiomycota

https://en.wikipedia.org/wiki/Basidiomycota

Mating in other fungal lineages: https://en.wikipedia.org/wiki/Mating in fungi



Most common system in mushroom-forming fungi.

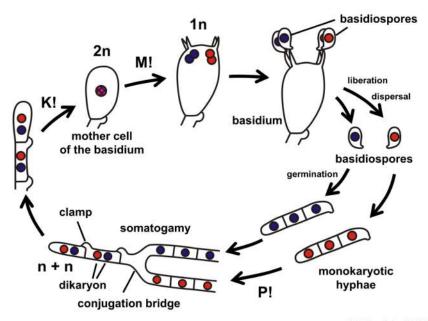
Figure: Coelho MA, Bakkeren G, Sun S, Hood ME, Giraud T. Fungal Sex:

The Basidiomycota. Microbiol Spectr. 2017 Jun;5(3):10.

https://journals.asm.org/doi/10.1128/microbiolspec.FUNK-0046-2016

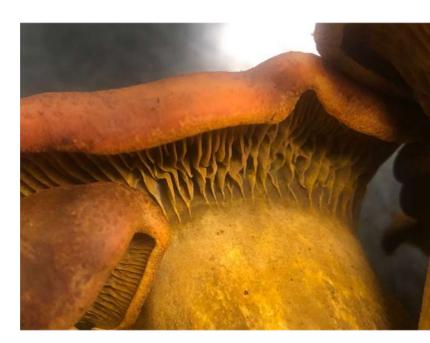
Basidiomycete Mating Types

David Bermudes



® M. Piepenbring, CC BY-SA

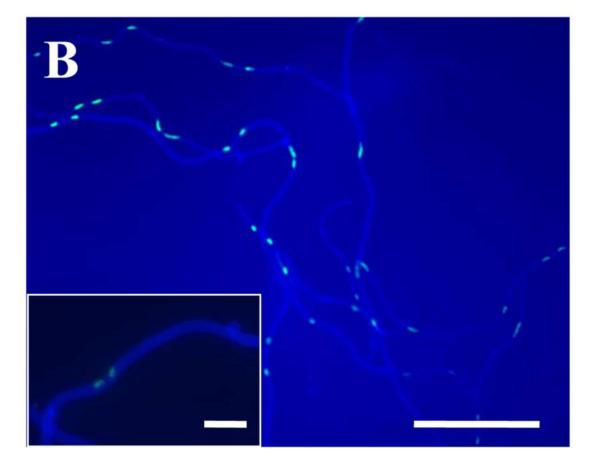
https://bio.libretexts.org/Bookshelves/Botany/A Photographic Atlas for B otany %28Morrow%29/03%3A Fungi and Lichens/3.06%3A Basidiomy cota %28Club Fungi%29/3.6.03%3A Life Cycles of Basidiomycetes



Omphalotus olivascens

Haploid nuclei – alone but together.

The mycelium of a mushroom that has mated spends its life with two haploid nuclei that are paired within the same septal division (genetically referred to as haploid dikaryotic or n + n)



Guerreiro et al., 2013 Eukaryotic Cell 12: 5 746-760 How does a basidiomycete go from haploid to haploid dikaryotic?

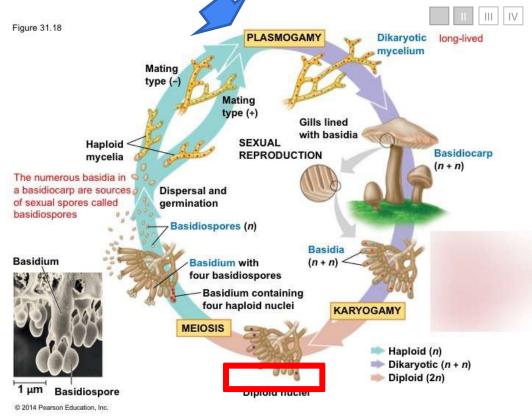
Several functions need to be performed to become a dikaryon:

Haploids need to sense each other and grow toward each other (pheromone production and pheromone receptors)

Cell wall dissolution at the tips needs to occur followed by cell fusion (plasmogamy)

Nuclei of each haploid need to migrate to the opposing cell

Clamp connections (many but not all basidiomycetes) need to form that are also involved with septal dissolution and nuclear migration

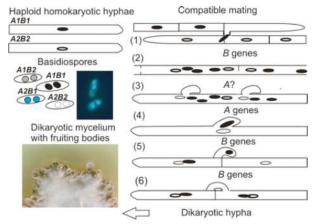


https://quizlet.com/287338501/basidiomycete-mushroom-forming-life-cycle-diagram/

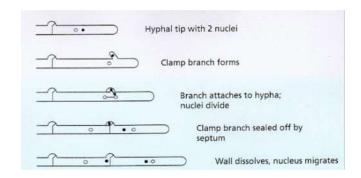
Ascomycetes and Basidiomycetes (The Dikarya)



- 90% are heterothallic
- Many are tetrapolar, having two unlinked mating loci
 E.g., A1 A2, B1 B2
- Mating compatibility requires different specificities in the functions relating to the process of dikaryonization
- Dikaryonization requires the entire set (A1 B1 A2 B2) which the individual haploids don't have.
- This is a process of complementation that results in a complete set of genes required for the process. The loci are often referred to as "opposite", but <u>complementary</u> is more accurate
 - E.g., two haploids that are complementarity are A1 B1 and A2 B2
 Thought to promote outcrossing
 - "A" genes are involved in clamp initiation and "B" genes are involved in the completion of clamp connections. Some of the "A" genes are signal transduction factors.
 - "B" genes are involved in the initial recognition through pheromones and pheromone receptors. "B" genes regulate the reciprocal nuclear migration, illustrated by movement of a nucleus via a hyphal fusion through broken septa from one haploid hypha into the other.



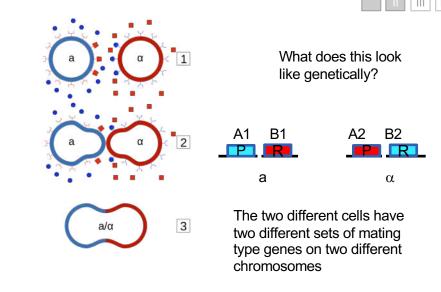
Eukaryot Cell. 2010 Jun; 9(6): 847-859.



http://archive.bio.ed.ac.uk/jdeacon/microbes/basidio.htm

Hormonal (Pheromone) Control of Mating

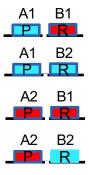
- Mating (cell fusion) is dictated by mating types that are controlled by:
- 1) Cell surface receptors
- 2) Pheromones
- 3) Transcription factors
- Cells must be of compatible (sometimes referred to as opposite) mating types
 - $\circ \quad \text{ E.g., a and } \alpha$
 - (arbitrary designations)



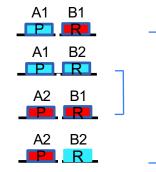
In yeast, type a produces a pheromone ullet that is specific for the receptor on α type. Type α produces a pheromone \square that is specific for the receptor on a type. There are also two different receptor types \ullet and \ullet that are specific for the pheromones.

https://www.youtube.com/watch?v=Qy2HPA3W9JM

What are all the possibilities from spore production in basidia?



Which ones are compatible?



Each one is only compatible with 1 out of 4?

Why Are "Opposite" (Complementary) Loci Required?

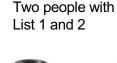


Analogy: Working Together to Build a Car

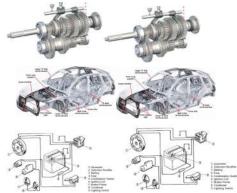
- Requirements include:
 - List 1 List 2
 - Wheels Transmission
 - Engine Chassis
 - FuelElectrical

Two people with the same list 1

Two people with the same list 2







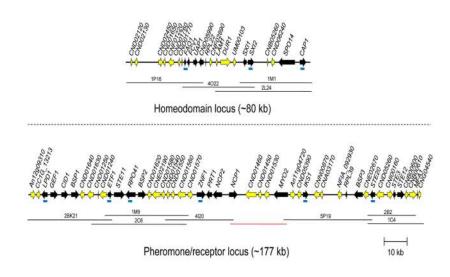


This one is the only functional one



Control of Mating in Fungi is Governed by the MAT Loci Homeodomain (A) and The Pheromone/Receptor Locus (B)

- Mating is controlled by MAT loci
 - Complex multi-gene regions of the chromosome
- The MAT loci contain numerous genes related to mating and maintenance of dikaryotic cells
 - Pheromone
 - Pheromone receptor
 - Signal transduction
 - Clamp connections and septation
 - Nuclear migration
 - Others
- Cells must be of compatible/complementary (opposite) mating types
 - \circ E.g., a and α
 - (arbitrary designations)

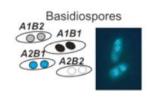


Because these loci have entirely different compositions, they are referred to as idiomorphs rather than alleles

MAT Loci Control of Mating in Fungi: Effects Observable at the Macroscopic and Microscopic Levels

II III IV

- The roles of combined (complementary) A and B genes
- Hyphae may fuse, but the process of creating a dikaryon is incomplete
- This can be observed on a petri plate and with a microscope



Pairing of strains with:	Events observed
Different A, different B idiomorphs (dikaryon)	Septal dissolution
Fertile	2. Nuclear migration
	Clamp branches arise and fuse with hypha
Cemmon A, different B idiomorphs Flat	Septa dissolve Nuclei migrate
Common B, different A idiomorphs Barrage	Septa remain intact No nuclear migration
0	3. Clamp branches arise but do not fuse
CAMERICA Demmon B idiomorphs	No septal dissolution
	No nuclear migration
	No clamp connections

Deacon 2006, Fungal Biology, Table 5.2.



Arbitrarily: A1 B1 x A2 B2

This picture shows a progression of a mating between <u>Omphalotus olivascens</u> that produced clamp connections and septa. Mycelial contact zone was robust. Initially only the colony on the left was pigmented, but after enough growth both sides turned out to be highly pigmented. Pictures taken about two weeks apart

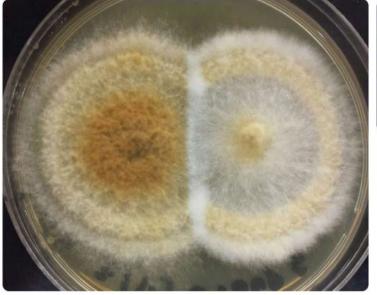




A1 B1 x A1 B2 (same A different B)



Two weeks progression of mating type growth that produced a flat reaction.





Microscopy shows false clamps

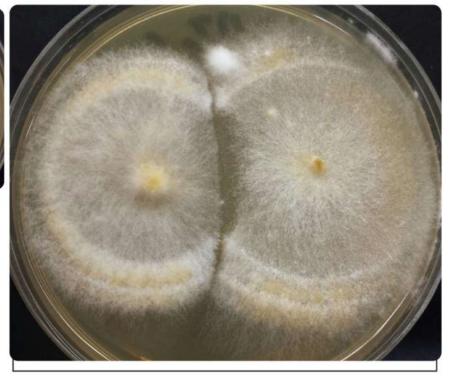
A1 B1 x A2 B1 (same B)

This photo shows a two week progression between mating types which produced false clamps. Mycelial contact zone is barrage.





A1 B1 x A1 B1 (same A same B)
"Overlap"
No clamp connections
No septal dilution
No nuclear migration



















FEMS Microbiology Reviews 18 (1996) 65-87

Tetrapolar fungal mating types: Sexes by the thousands

Erika Kothe * Philipps-Universität, Biologie-Molekuargenetik, Karl-von-Frisch-Str., D-35032 Marburg, Germany

Received 28 August 1995; accepted 16 January 1996

PLANET EARTH

THE MAGAZINE

Why This Fungus Has Over 20,000 Sexes

THE SCIENCES | MIND | TECHNOLOGY | HEALTH | ENVIRONMENT | PLANET EARTH

D-brief | By Nathaniel Scharping | Nov 6, 2017 1:23 PM







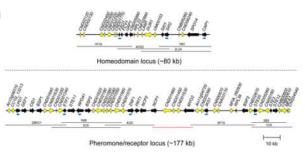


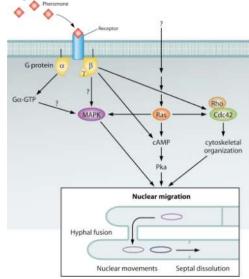


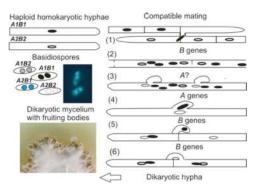


Mating loci contain multiple linked genes

- Different A genes (combination)
 - Pheromones
 - Short peptides
 - Pheromone receptors
 - Cell membrane G protein
 - Different B genes (combination)
 - Transcription factors respond to G protein coupled signals
 - Clamp connections
 - Nuclear migration
 - Septation

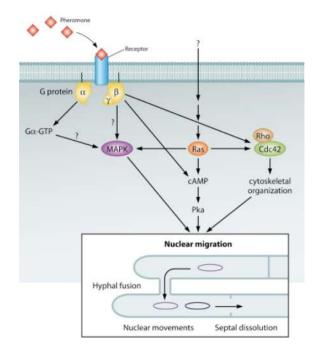








Higher numbers of mating types is due to variations in some of the individual genes. Example, Y and Z signal transduction proteins



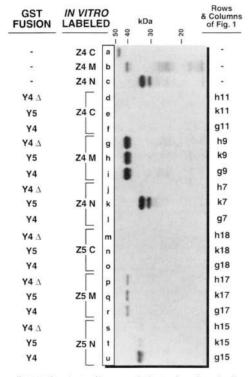


FIGURE 3.-Autoradiogram of electrophoretic gels displaying the results of protein affinity assays between fulllength GST-fusion proteins Y4, Y5 and Y4AFL 19, 81,928 and in vitro translated proteins: Z5N, N-terminal amino acids 1-289; Z5M, mid-region amino acids 288-494; Z5C, C-terminal amino acids 493-755; Z4N, N-terminal amino acids 1-271; Z4M, mid-region amino acids 270-544; Z4C, C-terminal amino acids 543-930. Procedures as described for Figure 2.

BIPOLAR MATING TYPES

alternative pathways for biosynthesis of trisporic acid leads to physiological complementation

ascomycetes Saccharomyces cerevisiae mating type a encodes diploids form al and a1/a2 heterodimer which is an active homeodomain transmating type a encodes al and transcription factor mating type switching is seen Neurospora crassa mating type A mtA-1 induces A pheromone and a-factor receptor mating type a mta-1 induces a phero-

the mating type loci are ideomorphic and show no homology

basidiomycetes

mone and A-recep-

Ustilago hordei

linkage of independent a and b loci lead to a phenotypically bipolar mating behaviour

TETRAPOLAR MATING TYPES

basidiomycetes Ustilago mavdis bi-allelic a locus each locus encodes a pheromone and a pheromone receptor for the other pheromone receptor activation leads to cell fusion multiallelic b locus homeodomain transcription factors b1 b_{East} and b_{West} form active heterodimers if b loci of mates differ: heterodimers induce filamentous growth Coprinus cinereus multiallelic A archaetype with 4 pairs 2of homeodomain trans-Aa1-1 ... cription factors: Ab1-1 ... active heterodimers Ac1-1 ... induce pseudoclamp Ad1-1 ... formation multiallelic B multiple sets of pheromones and receptors: activation essential for fully compatible mating and spore for-Schizophyllum commune multiallelic A each locus encodes a pair of homeodomain Aq1 ... 9 transcription factors: active heterodimers in-AB1 ... 32 duce clamp cell formation multiallelic B pheromone receptors and multiple pheromones; Ba1 ... 9 receptor activation leads to nuclear mig-B61 ... 9 ration and fully compatible mating

Based on the subvariants, there are a large number of theoretical sexes. Some of the variations such as having multiple pheromones and multiple pheromone receptors expand compatibility, while others such as incompatible within signal transduction factors such as Y and 7 diminish compatibility.

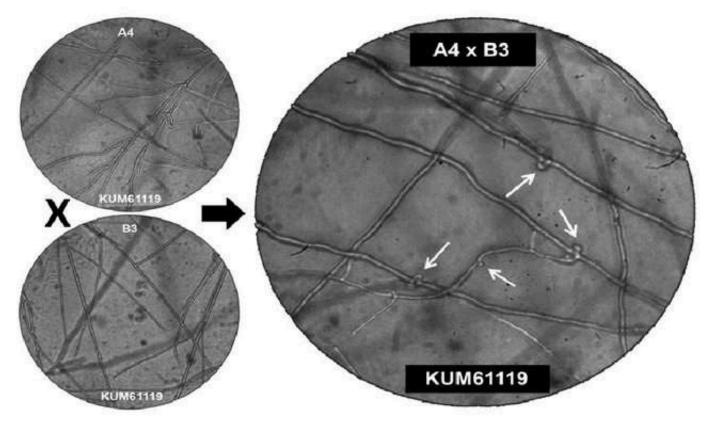


Fig. 2: Detection of compatibility by mating test. The crosses were scored as compatible if clamp connections observed. Avin et al., 2014.

Evolutionary forces in mating type multiplicity:

Gene duplication – Sequence divergence – Chromosome rearrangements

Functional integration

How could it be the case?

- Fungi have an extreme capacity for tolerating internal and external (genetic and environmental) disturbance
- After it has appeared, redundant genetic features could become linked with novel genetic variation that fulfills important life history and ecological functions.





Common moss mushroom look-alikes.







San Gabriel Mts. March 2023. SP https://www.inaturalist.org/observations/150748901

Murrieta, CA. March 2023. RD https://www.inaturalist.org/observations/149713015



Temecula, CA. 17 March 2023 SP











Entoloma subg. Cyanula Entolomataceae, Agaricales



Temecula, CA. 17 March 2023. RD https://www.inaturalist.org/observations/151466408



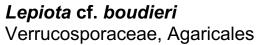


Cystolepiota sp. Verrucosporaceae, Agaricales

Under Eriogonum fasciculatum.









Chiquito Basin. 18 March 2023. RD https://www.inaturalist.org/observations/151656946





Cortinarius (Telamonia) Cortinariaceae, Agaricales

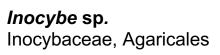
Under Adenostoma fasciculatum (chamise).



Temecula, CA. 17 March 2023. RD https://www.inaturalist.org/observations/151465563







Under scrub oak.





Temecula, CA. 17 March 2023. RD https://www.inaturalist.org/observations/151465686





Balsamia sp. Helvellaceae, Pezizales

Under scrub oak.



Santa Monica Mts. Feb. 2023. SP https://www.inaturalist.org/observations/148562000



Melanogaster sp.
Melanogastraceae, Boletales









Inocybe corydalina





Psilocybin-producing fungi



Alan Rockefeller https://www.inaturalist.org/observations/4675516



Massospora spp. https://www.sciencedirect.com/science/article/pii/S1754504819300352



Panaeolus cinctulus, RD





Pluteus americanus https://en.wikipedia.org/wiki/Pluteus_americanus

Psilocybe spp.

Psilocybe species diversity. Basidiomata of (A) Psilocybe serbica (jonagruska, CC-BY-SA 3.0), (B) P. mescalenroensis (Alan Rockefeller, CC BY-SA 4.0), (C) P. cubensis (Ricardo Arredondo, CC BY-NC), (D) P. ovoideocystidiata (Shroomydan, CC-BY-SA 3.0), (E) P. allenii (Alan Rockefeller, CC-BY-SA 3.0), (F) P. azurescens (Shroom360, CC BY-SA 3.0), (G) P. cyanescens (Alan Rockefeller, CC BY-SA 3.0), (H) P. subaeruginosa (ericos_bob, CC BY-SA 3.0), (I) P. angulospora (Inski, CC BY-NC-SA), (J) P. baeocystis (Caleb Brown, CC-BY-SA 3.0), (K) P. pelliculosa (Scottdarbey, CC-BY-SA 3.0), (L) P. semilanceata (Alan Rockefeller, CC-BY-SA 3.0), (M) P. hoogshagenii (Brayan Coral Jaramillo, CC BY-SA 3.0), (N) P. mexicana (Alan Rockefeller, CC-BY-SA 3.0), (N) P. mexicana (Alan Rockefelle CC BY-SA 4.0), (O) P. neoxalapensis (David Morales, CC-BY-NC 4.0), (P) P. zapotecorum (Alan Rockefeller, CC-BY-SA 3.0).

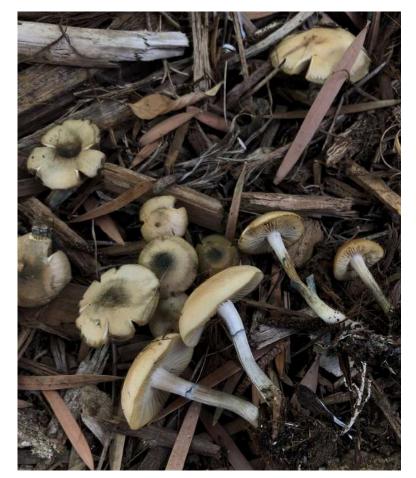
Genera with psilocybin-producing species

Genus	Family	Lifestyle	Morphology	Sclerotia
Panaeolus	Bolbitiaceae	Saprobic	Agaricoid, Secotioid	Variable
Pholiotina	Bolbitiaceae	Saprobic	Agaricoid	No
Gymnopilus	Hymenogastraceae	Saprobic	Agaricoid	No
Psilocybe	Hymenogastraceae	Saprobic	Agaricoid, Secotioid	Variable
Pluteus	Pluteaceae	Saprobic	Agaricoid	Variable
Inocybe	Inocybaceae	Ectomycorrhizal	Agaricoid	Variable
Massospora	Entomophthoraceae	Insect Pathogenic	Abdominal Spore Mass	No

Table 1, Meyer & Slot 2023: https://papers.ssrn.com/sol3/papers.cfm?abstract_id=4384673

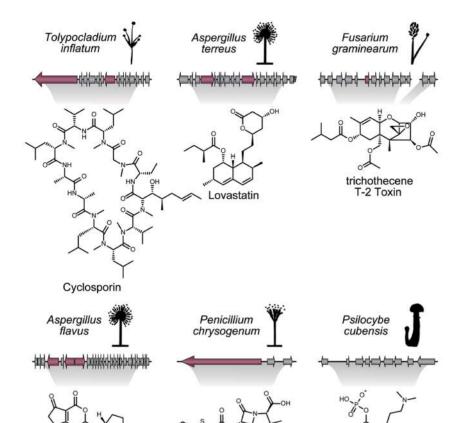
"Secondary metabolites (SMs) are generally defined as small organic molecules produced by an organism that are not essential* for their growth, development and reproduction."

From: Biotechnology and Biology of Trichoderma, 2014



Psilocybe ovoideocystidiata - West LA, Sept. 2022. RD

^{*} i.e., a molecule *in addition* to the standard toolkit shared by most branches of the tree of life.



Penicillin O

Aflatoxin

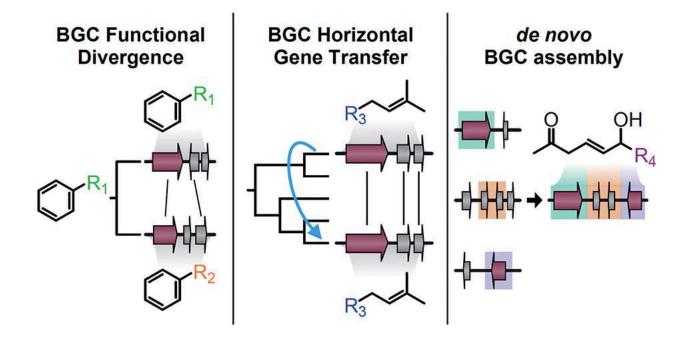
Secondary metabolites are end products in a careful process of construction and modification, encoded genetically in groups of genes called biosynthetic gene clusters (BGCs).

These genes encode different proteins with different functions in the constructive process.

They include enzymes, transporters, and transcription factors, as well as enzymes that confer resistance to the final metabolite.

Psilocybin

Mechanisms for the evolution of BGCs and fungal chemodiversity:



Horizontal gene cluster transfer increased hallucinogenic mushroom diversity

Hannah T. Reynolds,^{1,2,*} Vinod Vijayakumar,^{1,*} Emile Gluck-Thaler,^{1,*} Hailee Brynn Korotkin,³ Patrick Brandon Matheny,³ and Jason C. Slot^{1,4} 2018

Abstract

Secondary metabolites are a heterogeneous class of chemicals that often mediate interactions between species. The tryptophan-derived secondary metabolite, psilocin, is a serotonin receptor agonist that induces altered states of consciousness. A phylogenetically disjunct group of mushroom-forming fungi in the Agaricales produce the psilocin prodrug, psilocybin. Spotty phylogenetic distributions of fungal compounds are sometimes explained by horizontal transfer of metabolic gene clusters among unrelated fungi with overlapping niches. We report the discovery of a psilocybin gene cluster in three hallucinogenic mushroom genomes, and evidence for its horizontal transfer between fungal lineages. Patterns of gene distribution and transmission suggest that synthesis of psilocybin may have provided a fitness advantage in the dung and late wood-decay fungal niches, which may serve as reservoirs of fungal indole-based metabolites that alter behavior of mycophagous and wood-eating invertebrates. These hallucinogenic mushroom genomes will serve as models in neurochemical ecology, advancing the (bio)prospecting and synthetic biology of novel neuropharmaceuticals.

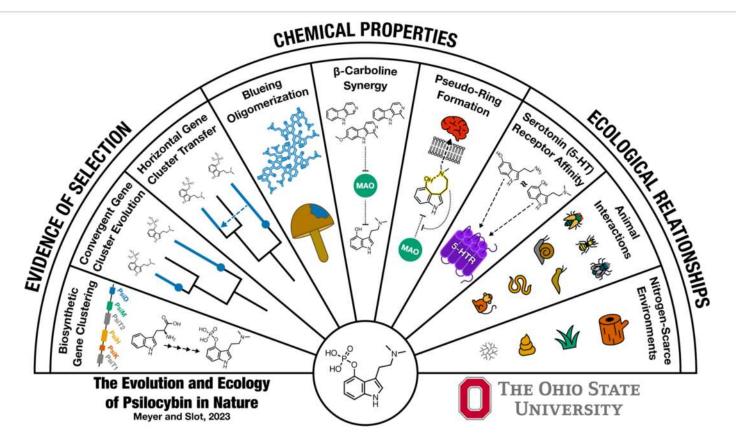
Hannah T. Reynolds, Vinod Vijayakumar, Emile Gluck-Thaler, Hailee Brynn Korotkin, Patrick Brandon Matheny, Jason C. Slot, Horizontal gene cluster transfer increased hallucinogenic mushroom diversity, *Evolution Letters*, Volume 2, Issue 2, 1 April 2018, Pages 88–101, https://doi.org/10.1002/evl3.42

Convergent evolution of psilocybin biosynthesis by psychedelic mushrooms

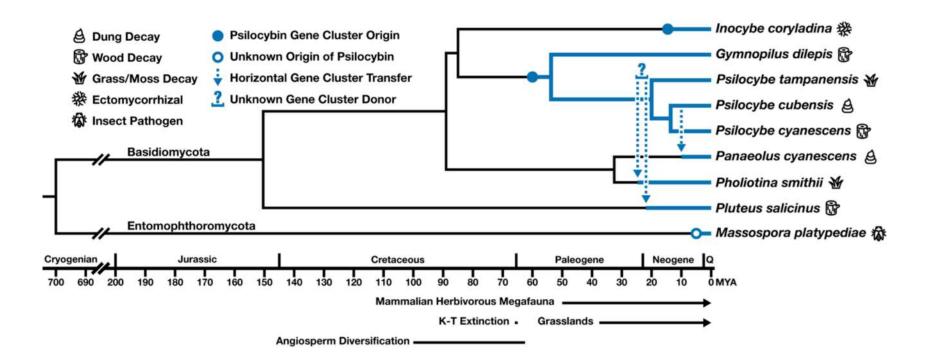
Ali R.Awan, Jaclyn M. Winter, Daniel Turner, William M. Shaw, Laura M. Suz, Alexander J. Bradshaw, Tom Ellis, Bryn T.M. Dentinger 2018 https://www.biorxiv.org/content/10.1101/374199v2.full

Abstract

Psilocybin is a psychoactive compound with clinical applications produced by dozens of mushroom species¹. There has been a longstanding interest in psilocybin research with regard to treatment for addiction², depression³, and end-of-life suffering⁴. However, until recently very little was known about psilocybin biosynthesis and its ecological role. Here we confirm and refine recent findings⁵ about the genes underpinning psilocybin biosynthesis, discover that there is more than one psilocybin biosynthesis cluster in mushrooms, and we provide the first data directly addressing psilocybin's ecological role. By analysing independent genome assemblies for the hallucinogenic mushrooms *Psilocybe cyanescens* and *Pluteus salicinus* we recapture the recently discovered psilocybin biosynthesis cluster^{5,5} and show that a transcription factor previously implicated in its regulation is actually not part of the cluster. Further, we show that the mushroom *Inocybe corydalina* produces psilocybin but does not contain the established biosynthetic cluster, and we present an alternative cluster. Finally, a meta-transcriptome analysis of wild-collected mushrooms provides evidence for intra-mushroom insect gene expression of flies whose larvae grow inside *Psilocybe cyanescens*. These larvae were successfully reared into adults. Our results show that psilocybin does not confer complete protection against insect mycophagy, and the hypothesis that it is produced as an adaptive defense compound may need to be reconsidered.



Meyer & Slot 2023: https://papers.ssrn.com/sol3/papers.cfm?abstract_id=4384673



Meyer & Slot 2023: https://papers.ssrn.com/sol3/papers.cfm?abstract_id=4384673

The most common factor among the

various ecological niches of psilocybin-producing fungi appears to be their low-nitrogen substrates. For example, the late stages of wood and dung decay are nitrogen-poor environments (Chen et al., 2013; Cowling and Merrill, 1966; Hao et al., 2004; Hess et al., 2021; Petersen et al., 1998), and ectomycorrhizal species are effective nitrogen scavengers for their host plants (Hernández et al., 2002; Mbarki et al., 2008; Stamets, 1996). Yet, despite environmental limitations, a large portion of nitrogen is allocated to psiloids. For example, psilocybin can make up to 1.6% of a mushroom's total nitrogen content (Borner and Brenneisen, 1987; Braaksma and Schaap, 1996; Gartz, 1994; Kamata et al., 2005). The high nitrogen allocation to psilocybin production suggests that its benefits outweigh any cost to nitrogen-limited growth and reproduction processes.

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Psilocybin construction starts with the essential amino acid tryptophan,

which then undergoes a series of modifications through its interactions with specific proteins.

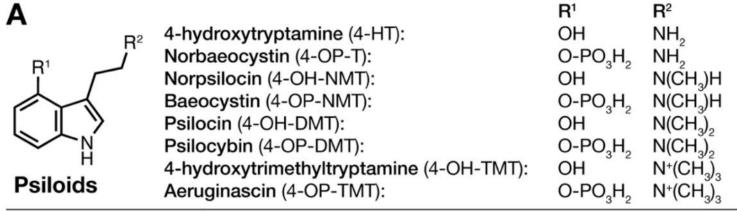




Fig. 1. Tryptophan-derived compounds in psychedelic/magic mushrooms (Gurevich, 1993; Lenz et al., 2021b). (A) Psiloids: the eight known natural 4-substituted tryptamine metabolites of the psilocybin biosynthesis pathway (Fricke et al., 2017; Stijve, 1984) found primarily in mushroom fruiting bodies (Blei et al., 2020). (B) Serotonin: a key signaling molecule found in all domains of life (Erland et al., 2019) and a key neurotransmitter in animals (Andrés et al., 2007).

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Another tryptophan-derived molecule is serotonin, which fulfills diverse cell signaling functions across all lifeforms.

The structural similarity of Psilocin to Serotonin allows Psilocin to interact with animal Serotonin-receptor proteins.

Evolutionary genomics is a powerful tool that can provide insights into the ecological role of psilocybin production. By studying rare molecular evolutionary events surrounding psilocybin's biosynthetic pathway (i.e., gene clustering, convergent evolution, HGT), we are given clues as to how these species have adapted to their environments. Two convergent origins of the psilocybin gene cluster in Agaricales have been established in wood-decay (the inferred ancestral state of Gymnopilus and Psilocybe) and in the ectomycorrhizal Inocybe, with another possible convergence in Entomophthoromycota (Awan et al., 2018; Boyce et al., 2019; Reynolds et al., 2018). Most other known psilocybin producers are saprobes and likely acquired the wood-decayassociated cluster through HGT (Fig. 2A) (Reynolds et al., 2018). This suggests that psilocybin may have different functions in different ecological niches but is most useful in decay niches. The ancestral ecologies of the cluster donor species were likely similar saprobic niches to their recipients, leading to physical contact between them and increasing the chances of HGT (Gluck-Thaler and Slot, 2015; Reynolds et al., 2018). Horizontal acquisition of psilocybin production may also facilitate expansion into new ecological niches (Slot, 2017). For instance, the HGT between the Ps. cubensis and Pa. cyanescens lineages likely occurred in their shared dung decay niche (Reynolds et al., 2018), suggesting both species faced similar pressures that psilocybin may have at least partially alleviated. Psilocybin production may defend against cohabiting animals, especially insects, that compete for resources or consume the fungus. An ecological association with insects is further supported by the likely convergent origin of psilocybin in M. levispora/platypedia, a fungus that is directly antagonistic to an insect.

https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7004109/pdf/ANIE-59-1450.pdf

Ecological function in the blue bruising reaction?

Caused by "rapid conversion of phosphorylated psiloids into their hydroxylated counterparts, followed by oxidative coupling that forms blue oligomers."

"Chromophoric oligomers may serve a defensive ecological function due to their polyphenolic and aryl-coupling properties. When ingested, these compounds generate reactive oxygen species, causing intestinal lesions in insects (Barbehenn and Peter Constabel, 2011; Salminen and Karonen, 2011)."

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IV

Do we why know why mushrooms produce psilocybin?

No. But it must be important different ways in different fungal lineages, whatever they're doing...