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ORIGINAL ARTICLE

How mushrooms tend to break through the genetic dead end

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Abstract – Genes, genetics, genomics, and the roles of mushrooms and toadstools in the global carbon cycle (GCC) are reviewed here. The literature survey is a tribute to the contributions made by Hungary and Hungarian scientists to fungi and mushroom research. For this reason, the names of the fungi discussed are also given in Hungarian.

Fungi – like wood eating insects – are the main decomposers (a type of consumers, *syn.:* heterotrophs) and consequently recycle the biomass produced by photosynthetic organisms (*i.e.,* the producers, *syn.*: autotrophs). Photosynthesis is driven by the solar energy day by day (by *photo-autotrophs*) (*i.e.,* primary producers of chlorophyllous plants), and primary production night by night is performed by *chemo-autotroph* prokaryotes. Only autotrophic organisms can produce organic materials in the Earth to supply food and feed the *hetero-trophs* (*e.g.,* animals, including Human), and *sapro-trophs* (*i.e.,* decomposers) including fungi and bacteria. The crucial excess oxygen from the oxygenic photosynthesis supports diverse life on Earth.

Mushrooms were found to have 100-1000 times smaller genomes than plants or animals, however, enormous genome expansions *e.g.,* of *Armillaria*s (*Eng./Hung.:* honey mushrooms / tuskógombák) have indicated recently that fungi continue to expand their genome.

Comparative genome analyses of *Polyporales* mushrooms have recently identified an ongoing transitioning from *white-rot* (WR) towards *brown-rot* (BR) life style with loss of genes encoding enzymes to decay cell wall components of plants (and woody plants, the trees) including cellulose, hemicellulases, lignin (the three together are also called lignocelluloses), and pectin. In the case of lignin, genes of *ligninase* enzymes, which are capable of digesting lignin only, developed only in wood-decay fungi which underscore their role in GCC.

Symbiosis between fungi and green algae or cyanobacteria created a new phylum the Lichens (*Mycophycophyta*) in evolution. A tripartite symbiosis among achlorophyllous (*i.e.,* parasitic) mycoheterotrophic plants ↔ mycorrhizal fungi ↔ and autotrophic green plants were re-discovered recently.

Here we review the achievements of research of *Di-caria* true fungi (*Eu-mycota*) of both *Asco-mycota* (*Eng./Hung.:* Sac fungi / Tömlős gombák) and *Basidio-mycota* (*Eng./Hung.:* Club fungi / Bazidiumos gombák) with special emphasis on genes, genetics and genomic and evolutionary relationships. In brackets, the commercial mushroom names of English (*Eng.*) and Hungarian (*Hung.*) are given.

Keywords – genes, genetics, and genomics of mushrooms

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Introduction

Photosynthesis (*i.e.,* Global Carbon Cycle, GCC) drives the fundamental basis of life on Earth (Calvin, 1961; Szalay *et al.,* 1967; Mitchell, 1978; Lehoczki *et al.,* 1992). It goes through the *'auto-troph'* organisms of both *chemo-autotroph* bacteria, and *photo-autotroph* plants by fixing CO_2 from the atmosphere and returning back O_2 into the atmosphere, and, by means of producing organic materials ('biomass') they supply organisms of *'hetero-trophs',* and *'sapro-trophs'*. These cycles have been ongoing day by day (in *photo-auto-troph chlorophyllous* *plants*), and night by night (in *chemo-auto-troph bacteria*) since the emergence of these processes (Field *et al.*, 1998; Nealson and Conrad, 1999; Gyulai *et al.*, 2019).

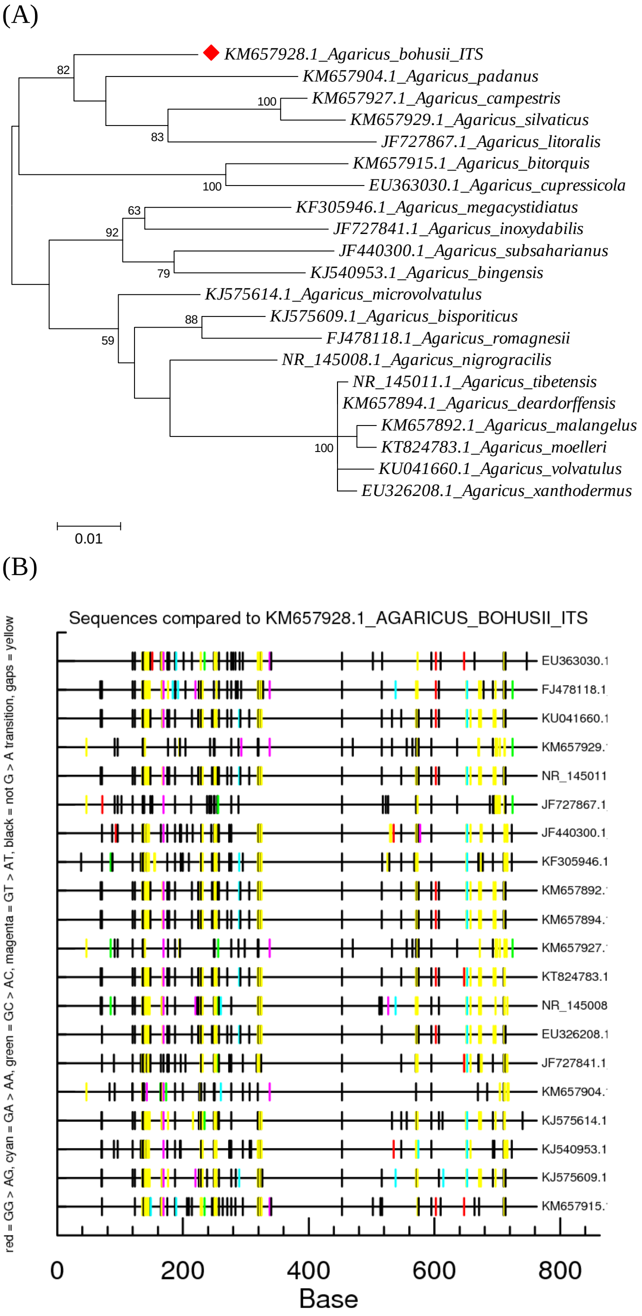

Figure 1. ML (Maximum Likelihood) (Hillis *et al.*, 1994) dendrogram (*A*) edited by MEGA7 program (Kumar *et al.*, 2016); and HyperMut (Rose and Korber, 2000) visualizations (*B*) of nucleotide changes of ITS (*Internal Transcribed Spacer* of ribosomal DNA) sequences of *Agaricus* species aligned to *A. bohusii* (named after the Hungarian mycologist Gábor Bohus, 1914-2005 (1951); by Bon, 1983) (Vasas and Dima, 2005). Sequences were downloaded from NCBI server (National Center for Biotechnology Information), and aligned to *A. bohusii* (#ID *KM657928.1*; 722 bp) (Geml *at al.*, 2004; Zhou *et al.*, 2016) by BioEdit (Hall, 1999) *(A)*. Gene Bank accession numbers are indicated.

Photoautotrophic organisms are comprised of *(i)* photosynthetic bacteria, cyanobacteria and protists; and *(ii)* chlorophyllous plants of seedless algae, moss, and ferns, and seed plants of Gymnosperm trees (all Gymnosperms are woody plants; there are no 'herbaceous Gymnosperm' species), and Angiosperm plants and trees (Calvin, 1961; Mitchell, 1978).

The GCC cycle is driven by *physical sunlight radiational energy* (*i.e.*, APAR - the *Absorbed Photosynthetically Active* solar *Radiation* within the range of 400 to 700 nm), which is converted into *chemical energy* ('biomass') by photosynthesis, which is about 1.0 – 1.15 x 10^{11} metric tons of carbon (taken from CO_2) per year with roughly equal contributions from land and oceans. The sunlight energy captured by photosynthesis is of approximately 130 terawatts globally (*i.e.*, net primary production - NPP), which is about three times bigger than the power consumption of human civilization 'currently' (Field *et al.*, 1998).

Only autotrophic organisms (*i.e.*, primary producers) can produce organic materials ('biomass') to supply food and feed to *heterotrophs* (*e.g.*, animals, including human) (Nealson and Conrad, 1999).

The 'excess' oxygen that oxygenic photosynthesis produces is the single and unique process to oxygenate and maintain diverse life on Earth. The remains and 'left-overs' of *heterotrophs* are used up further by *saprotrophs* (*i.e.*, decomposers) including bacteria and fungi of both micro and higher fungi.

Here we survey the roles of fungi and mushrooms in the global carbon cycle with special emphasis on genes, genetics, and genomics of both *(i) Ascomycota* (*Eng./Hung.:* Sac fungi / Tömlősgombák) including the main groups of (1) *Tuberales* (*Eng./Hung.*: Truffles / Szarvasgombák), (2) Pezizales (Cups / Csészegombák) and (3) *Morchella* (Morels / Kucsmagombák); and *(ii) Basidiomycota* (*Eng./Hung*.: Club fungi / Bazidiumos gombák) including the main groups of (1) *Auricula* (*Eng./Hung.*: Jelly ears / Júdásfülegombák), (2) *Agaricales* (Gill fungi / Lemezesgombák), (3) *Polyporales* (Tube fungi / Csövesgombák), and (4) Gasteromycota (Puff balls / Pöffetegek).

Literature and background

The literature survey is a tribute to the contributions made by Hungary and Hungarian scientists to fungi and mushroom research. For this reason, the names of the fungi discussed are also given in Hungarian. There were several pioneering authors of mushroom research, such as László Hollós (1911) with 534 entries at Mycobank; Gábor Bohus *et al.*, (1951) (Fig. 1) with 63 entries; József Vörös (Bánhegyi *et al.*, 1986-87) with 22 entries; József Bánhegyi (*et al.*, 1953, 1985-87) with 18 entries; László Szemere (1970) with 3 entries; and Zoltán Kalmár *et al.* (1989). The microfungi, *e.g.*, of the study of Sándor Tóth

(1966) with 23 entries at *Mycobank*, and the human pathogenic fungi (*e.g.*, *Microsporum audouinii*, MB#160505) discovered by the pioneering Dávid Gruby (1843) with 5 entries at *Mycobank* will not be discussed.

Technologies and methods

ML (Maximum Likelihood) dendrogram (*A*) edited by MEGA7 program (Kumar *et al.*, 2016); and a HyperMut (Rose and Korber, 2000) visualizations.

Sequences were downloaded from NCBI server (*National Center for Biotechnology Information*), and aligned to *A. bohusii* (#ID *KM657928.1*; 722 bp) (Geml *at al.*, 2004; Zhou *et al.*, 2016) by BioEdit (Hall, 1999) *(A)*. Gene Bank accession numbers are indicated. Genome data were downloaded from Martin *et al.*, 2010; and Nordberg *et al.*, (2014), and from *NCBI server* (Altschul *et al.*, 1997) (Fig. 2a,b).

(1) Systematics of Fungi

Fungi comprise over 98,000 species. Of them, true fungi (*Eumycota*) comprise seven phyla of *Ascomycota* (64,163 species of 6,355 genera); *Basidiomycota* (31,515 species of 1,589 genera), *Microsporidia* (1,300 unicellular species of 170 genera); *Chytridiomycota* ('chytrids') (706 species of 105 genera - some of them with flagellar zoospores; *Blastocladiomycota* (179 species of 14 genera); *Glomeromycota* (169 species of 12 genera of the arbuscular mycorrhiza); and *Neocallimastigomycota* (20 species of 6 genera) (Fig. 2a) (Moore *et al.*, 2011; Justo *et al.*, 2017).

The first systematics book of mushrooms in Europe and worldwide, was edited in Németújvár, Hungary (present-day Güssing, Austria), and printed in Antwerp, Holland, by Clusius (1601), and reprinted in Budapest, Hungary and Graz, Austria (1983)

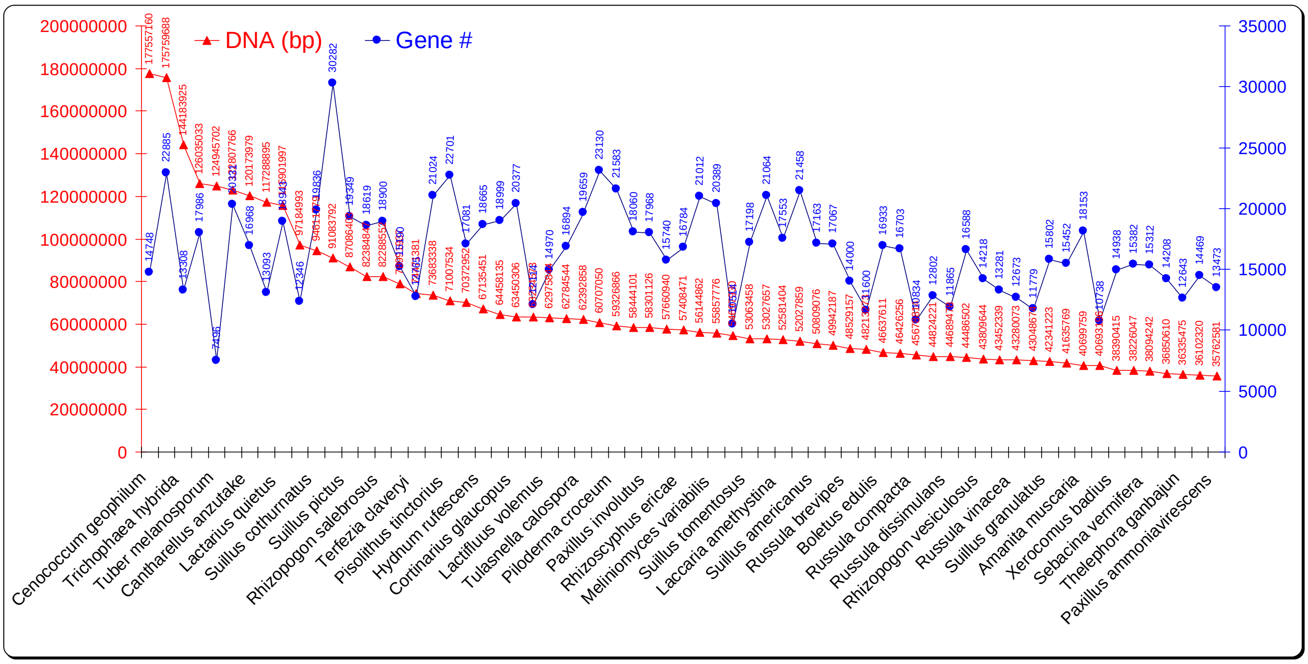

Figure 2a. Genomes sizes (DNA in bp) and gene numbers (#) of 65 mycorrhiza fungi. The EM *Cenococcum geophilum* shows the largest genome (177,557,160 bp DNA; with 14,748 encoding genes) to *Paxillus ammoniavirescens* (*Lat./Eng./Hung*: *Paxillus* / Rollrim / Cölöpgomba) with the smallest genome (35,762,581 bp DNA; with 13,473 encoding genes). The culinary important *Tuber melanosporum* (*Eng./Hung.*: black truffle / fekete szarvasgomba) has the third largest genome (124,945,702 bp DNA) due to transposon (Biemont and Vieira, 2006; Alzohairy *et al.*, 2013) activities. Genome data were downloaded from Martin *et al.*, 2010; and Nordberg *et al.*, (2014).

Hundreds of new mushroom species have been identified (Clusius, 1601, 1983; Nakasone and Eslyn, 1981; Geml *et al.*, 2004; Lukács, 2007; Zhou *et al.*, 2016; Sádlíková and Kout, 2017) including

- *Lycoperdon hungaricum* (*Eng./Hung*.: Hungarian puffball / Magyar pöffeteg) described in 1901 by Hollós (MycoBank, MB#151191);
- *Geaster hungaricum* (*Eng./Hung.*: Hungarian earthstars / Magyar csillaggomba) also described by Hollós in 1904 (MB#528059);
- *Morchella hungarica* (*Eng./Hung.*: Hungarian morel / pusztai kucsmagomba) (MB#301308) (*syn.*: *Morchella steppicola*) described in 1941 by Bánhegyi;
- *Lamprospora hungarica* (*Eng./Hung.:* Hungarian peziza / Magyar csészegomba) also described by Bánhegyi in 1941 (MB#299363); -
- *Agaricus macrosporoides* (*Eng./Hung.:* Hortobagy button / hortobágyi csiperke) described in 1947 by Bohus (MB#308354);

- *Tricholoma pannonicum* (*Eng./Hung.:* Pannonian knight / magyar pereszke) also described by Bohus in 1960 (MB#340331);
- *Agaricus bresalodanus* (*Hung.:* akác csiperke) (MB#315946) described by Bohus (1969) as well; and
- *Agaricus bohusii* (*Eng./Hung.:* Bohus button / csoportos csiperke) described by Bon (1983) (MB#108651); *etc.* (Fig. 1).

Of both Basidiomycota and Ascomycota, about 1,500 mushroom species were reported to grow naturally in Japan (Mizuno, 1995); about 3,487 species were recorded in Hungary to date (*Hungarian Mycological Society*); and approximately 5,500 known species (estimated total at 9,000) were recorded in Ireland (Cullen and Fox, 2010). Like plants and animals, many mushroom species are strictly protected (Rimóczi and Vetter, 1990; Siller *et al.*, 2006).

(2) Are fungi achlorophyllous plants?

In evolutionarily speculations, fungi were assumed to be more closely related to animals than plants based on the chemical structure of hyphal cell walls; the composition of mitochondrial and nuclear DNA, and ribosomal RNA; and the nutritional and metabolic pathways (Burnett, 1987).

An early study of amino acid composition of fungal elongation factor 3 (EF-3), and its gene (*ycf*3) was also found to be highly homologous to mammalian myosin (Beltfield, 1995). However, these speculations have not been confirmed by the current molecular methods, *e.g.*, by the sequence analyses of genes of the evolutionarily highly conserved GAPDH enzyme proteins (Gyulai *et al.*, 2019).

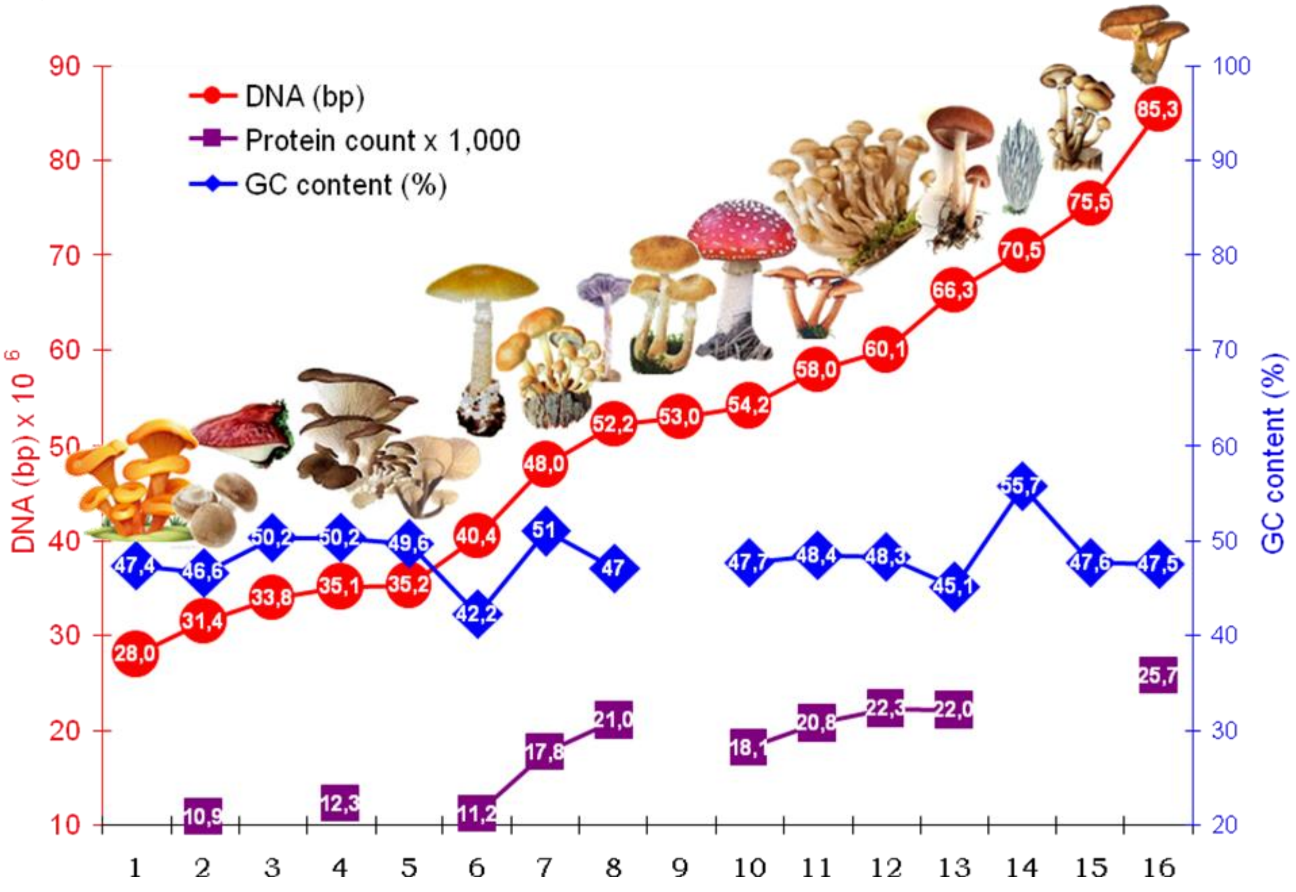

Figure 2b. Genome sizes (DNA bp x 10^6), GC content of genomic DNS (%), and protein count (x 1,000) of sixteen (1 – 16) gill fungi (*Agaricales*) species. Data were downloaded from *NCBI server* (Altschul *et al.*, 1997) and edited by MS Excel program. The NCBI ID numbers are: **(1)** *Omphalotus olearius* (*Eng./Hung.:* the Jack-O-Lantern mushroom / világító tölcsérgomba), ID 12242. **(2)** *Agaricus bisporus* (button mushroom / termesztett kétspórás csiperke), ID 14502. **(3)** *Fistulina hepatica* (beefsteak fungus / májgomba), ID 17385. **(4)** *Pleurotus ostreatus* (oyster mushroom / késői laskagomba), ID 909. **(5)** *Flammulina velutipes* (*Syn.: Collybia v.*) (velvet shank / téli fülőke), ID 16873. **(6)** *Amanita phalloides* (death cap / gyilkos galóca), ID 52888. **(7)** *Hypholoma sublateritium* (brick cap / vöröses kénvirággomba), ID 10490. **(8)** *Laccaria amethystina* (amethyst deceiver / lila pénzecskegomba), ID 17.383. **(9)** *Armillaria fuscipes*, ID 45353. **(10)** *Amanita muscaria* (fly agaric / légyölő galóca), ID 858. **(11)** *Armillaria solidipes*, (honey fungus / tuskógomba ssp.), ID 57440. **(12)** *Armillaria ostoyae*, (honey fungus / tuskógomba ssp.), ID 17578. **(13)** *Gymnopus luxurians* (*syn.*: *Collybia luxurians*) (parachute / fülőke), ID 6988. **(14)** *Clavaria fumosa* (smoky spindles / gyepkorallgomba), ID 38887. **(15)** *Armillaria cepistipes* (mullet honey fungus / hagymatönkű gyűrűs tuskógomba), ID 61177. **(16)** *Armillaria gallica* (bulbous honey fungus / gumós tuskógomba), ID 57439

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An important biochemical difference was found in the storage form of sugar (*i.e.*, carbon storage) as in *glycogen* of fungi, bacteria, protozoa and animal cells; compared to *starch* in plant cells. The first speculative hypothesis of the algal origin of fungi assumed the loss of chlorophyll (and consequently the chloroplasts) from the ancient algal cells that evolved to fungi (Martin, 1955). However, it is believed currently that fungi descended from protozoan-like ancestors (De Clerck *et al.,* 2012). Nevertheless, chlorophyll loss is not rare among parasitic plants, *e.g.*, the tropical *Cathaya argyrophylla* (NCBI# NC_014589), and the temperate zone *Cuscuta obtusiflora* (*Eng./Hung.:* dodder / aranka) (family *Orobanchaceae*) (NCBI# NC_009949). Interestingly, a new invasive mushroom species in Hungary, the *Chlorophyllum molybdites* (Eng./*Hung.:* green-spored parasol / mérgező őzlábgomba) (Massee, 1898), has chlorophyll green spores, unlikely from chlorophyll.

Phylogenetics (Frank, 1885; Heckman *et al.*, 2001; James *et al.*, 2006), and ontogenesis of fungi also shows unique characters: spores grow to haploid (n) *hyphae*, and when *hyphae* meet, they mate and fuse, and produce *dikariotic hypha* (2n) (hence the name *Dicaria*). *Hyphae* later grow a very large (up to square kilometers) net of fungal *mycelium* (Stanosz *et al.*, 1987; Smith *et al.*, 1992), which produces the fruiting bodies known as mushrooms.

Similar to the clonally propagated, largest and oldest giant flowering plants like the aquatic *Posidonia oceanica* (monocot, *Alismatales*) (Telesca *et al.,* 2015) with 100,000 year age and over 8 km long growing areas in Mediterranean Sea; and the trembling giant (*Populus tremuloides*) with 80, 000 year age (Utah, U.S.A.) (Grant, 1993), there are also giant mushrooms.

In the U.S. forests, the “giant” honey mushroom *Armillaria bulbosa* showed how the mycelium grown from a single fungal spore cell can colonize hectares (up to 15 ha) of forests and live 1,500 – 2,400 years with a final total weight of at least 10 tones to date (Smith *et al.*, 1992). This prolonged capacity to grow is attributable to the white-rot (WR) life style of *Armillaria* species, which are ‘fully armed’ with WR enzyme genes ready to degrade all woody plant cell wall components such as cellulose, hemicellulose, lignin, and pectin (Kusano, 1911; Lan *et al.,* 1994). A similar species of *Desarmillaria tabescens* (*syn.: Armillaria t.*) (*Eng./Hung.:* ringless honey fungus / csoportos tuskógomba) also can colonize hectares in the forests.

(3) Small eukaryotic fungal genome condensed in small chromosomes

Not only the transposon research, but also fungal cytogenetics started when Barbara McClintock (1945) studied and succeeded in visualizing the extremely small chromosomes of the fungus *Neurospora crassa* (the ‘today boring’ but) the former model organism of early geneticists (McClintock, 1945). Later, the invention of pulsed field gradient gel electrophoresis (PFGE) (Schwartz *et al.,* 1982; Schwartz and Cantor, 1984) opened a new era of fungal cytogenetics (Zolan, 1995; Lai *et al.,* 1989; Fekete *et al.,* 1993). Currently, genome sequencing projects revealed fundamental correlations between fungal genomes and functions (Floudas *et al.*, 2015; Sipos *et al.*, 2017). Similarly to fungi chromosome sizes, genome sizes of fungi (Fig. 2a,b) were found to be ten times smaller than the genome of the smallest known grass genome of diploid ancient grass genus *Oropetium* (245 x 10^6 bp DNA; encoding for 28,466 protein-coding genes; and with chloroplast DNA of 0.135324 x 10^6 bp) (VanBuren *et al.*, 2015).

(4) Genome evolution: Gene loss. Fungal wood decay – Evolutionarily transition from White-rot (WR) toward Brown-rot (BR) fungi with gene loss

The comparative genome sequencing of two Polyporales species of white-rot (WR) and brown-rot (BR) mushrooms of *Cylindrobasidium torrendii* (WR) compared to *Fistulina hepatica* (BR) revealed that *C. torrendii* (WR) has been at a transitioning intermediate stage from WR towards BR life style through gene loss (Floudas *et al.,* 2015).

Figure 3a. Central (heartwood / geszt) brown-rot (BR) (*syn.:* cubic rot); and mycelium of the peripheral (softwood / szijács) white-rot (WR) wood decaying fungus *Schizophyllum commune* (Split gills fungus / Hasadtlemezű gomba) on an about forty-year-old plum tree (*Prunus domestica*) (five-year cut). For scale, see the surrounding weeds (*Photo by* G. Zs. Gyulai, 2018, Gödöllő, Hungary).

Wood decaying fungi – like wood eating insects – are the main decomposers and consequently recyclers of biomass produced by photosynthesis.

One classification divides fungi into two main groups such as *saprotroph*s, which degrade non-living organic substrates, and *biotroph*s, which obtain carbon (*i.e.*, sugar) from living hosts. The ecological lifestyles of fungi include dung decay (DG), wood decay (WD), and mycorrhiza (MR) fungi (Reynolds *et al.,* 2018).

White-rot (WR) mushrooms such as *Armillaria*s (*Eng./Hung.:* honey mushroom / tuskógombák), *Ganoderma applanatum,* and *Trametes versicolor* (*Eng./Hung.:* turkey tail mushrooms / lepketapló; *Syn*.: *Coriolus versicolor*) are armed with all enzyme genes by which they can break down all major woody plant cell wall components leaving remains of white color. Wood-decaying fungi are the only eukaryotes that have evolved enzyme genes necessary to decompose lignin of wood (Loyd *et al*., 2018). These enzymes comprise the lignin-modifying enzymes (LMEs) (*e.g.*, ligninases, and laccase; EC 1.10.3.2) (Hsieh and Wu, 2001).

Figure 3b. The developed fruiting body of softwood (*Hung.* szijács) white-rot (WR) wood decaying fungus *Schizophyllum commune* (Split gills fungus / Hasadtlemezű gomba) (with 3,85 x 10^7 DNA bp, encoding for 13,210 genes; Ohm *et al.,* 2010) (*Photo by* G. Zs. Gyulai, 2018, Gödöllő, Hungary).

Brown-rot (BR) (also called: cubical rot) fungi (Fig. 3a), *e.g., Lenzites (syn.: Trametes) betulinus* of Polyporales (*Eng./Hung.*: birch mazegill / nyírfatapló) tend to lose genes from whole WR gene collection, and they primarily decay 'only' the cellulose and hemicelluloses in the wood, and leave residues of lignin which gives the brown color of decayed wood.

In addition to the two larger groups of WR and BR fungi, there are also smaller groups of soft-rot (SR) fungi which also can decay cellulose, hemicelluloses and lignin; dry-rot (DR), *e.g*., *Meruliporia incrassata* (with rhizomorphs, similar to *Armillaria*s); litter rot (LR) fungi; and moulds (*Eng./Hung*.: filamentous fungi / fonalas gombák, penészgombák). Generally, moulds (*e.g., Alternaria, Aspergillus, Cladosporium, Fusarium, Mucor, Penicillium, Rhizopus, Stachybotrys*, *Trichoderma, etc.*) are not wood-decaying fungi; they only live on the surface of the wood (and on food intended for human consumption).

(5) Genome evolution: Gene gain. Genome sequencing – Phylogenetics and Phylogenomics of Fungi

Recent studies of total genome sequencing of four *Armillaria* species (*Eng./Hung.:* honey mushrooms / tuskógombák) of *(i) A. cepistipes* (*Hung.:* hagymatönkű tg.), *(ii) A. gallica* (*syns.*: *A. bulbosa; A. lutea*) (*Hung.:* gumós tg.), *(iii) A. ostoyae* (*syns.*: *A. solidipes)*, *A. obscura*, *A. polymyces*) (*Hung*.: sötétpikkelyes tg.); and *(iv) A. solidipes (syn.: A. ostoyae)* revealed high levels of genome expansion driven by protein coding gene duplications, and not by transposons proliferations (Sipos *et al.*, 2017). Unfortunately, the genome of the most frequently harvested *A. mellea* (*Eng./Hung.:* honey mushroom / gyűrűs tg.) was highly fragmented and difficult to edit (Sipos *et al.*, 2017).

Genome sequencing of the EM *Tuber melanosporum (Eng./Hung.:* black truffle / fekete szarvasgomba) also showed an extreme genome expansion (0.125 x 10^9 bp) as a result of the proliferation of transposable elements accounting for about 58% of the genome (Fig. 2a). In contrast, this large genome only contains approximately 7,500 protein-coding genes with very rare multigene families (Martin *et al.,* 2010).

Genome sequencing of *Polyporales* (*Eng./Hung.:* tube fungi / taplógombák) species also revealed that the genome sizes of *Bjerkandera adusta* (*Eng*.: smoky polypore), *Ganoderma ssp.* (*Eng./Hung.:* reishi / pecsétviaszgomba), and *Phlebia brevispora* (described by Nakasone and Eslyn, 1981) are in the range of 39.5 x 10^6 – 49.9 x 10^6 bp and encode for 12,910–16,170 genes (Binder *et al.*, 2013), which are in a similar range to *Fistulina hepatica* (*Eng./Hung*.: Beefsteak fungus / májgomba) with total DNA length of 33.8478 x 10^6 bp, and protein count of 11.244 (Fig. 2a,b).

The structure and composition of hemicellulose and lignin components of wood cell walls are different in softwood (SW) (*Hung.:* puhafa) (Gymnosperm coniferous trees), which are rich in galactoglucomannan and guaiacyl lignin) compared to hardwood (HW) (*Hung.:* keményfa) (deciduous trees) rich in glucuronoxylan, syringyl and guaiacyl lignins). The SW trees are predominant of land plant biomass in the Northern hemisphere; however, they are more recalcitrant to wood decaying fungi than HW trees. WR basidiomycete (Polyporales) fungus *Phanerochaete carnosa* decays strictly only coniferous SW trees.

Another WR fungus *Phanerochaete chrysosporium* mainly infects hardwood trees. The genome sequencing of the two fungi revealed, that WR-SW *P. carnosa* genome is enriched (nearly doubled) with genes that encode cytochrome-P450-monooxygenases (a group of hemoproteins with plant heme cofactor) with 266 copies of P450s (CYPs) that participate in extractives degradation, and manganese peroxidases involved in lignin degradation. About 33% of the P450 genes in the *P. carnosa* genome were found tandemly duplicated. This high P450 gene number is higher than in the third species of BR *P. placenta* (236 copies of P450s) (Suzuki *et al.*, 2012).

Further genome analyses are organized by the '1,000 Fungal Genomes Projects' launched by the US Department of Energy (DOE) Joint Genome Institute (JGI) (*Nordberg et al.*, 2014) (Fig. 2a,b). One of the most current results revealed how a dry rot (DR) fungus *Serpula* (*syn.: Merulius*) *lacrymans* (Boletales) (*Eng./Hung.:* dry rot / könnyező házigomba) became a very effective brown rot (BR) fungus compared to its wild relatives and became a successful invader of timbers of pine, fir, and spruce in houses (Balasundaram *et al.*, 2018).

(6) Fungi parasitized by Plants

Myco-heterotrophy is a form of tripartite symbiosis among *(i)* achlorophyllous mycoheterotrophic parasitic plants, which parasitizes *(ii)* mycorrhizal fungi that are attached to roots of *(iii)* photosynthetic plants. In this way mycoheterotrophic plants get all or part of their mineral food from photosynthetic plants through the bridge of mycorrhizal fungi (the haustrorial parasite plants are different).

There are over 400 achlorophyllous plant species, not only orchids, in 87 genera, that are parasitic upon fungi, and exploit them for carbon source (Leake, 2005; Merckx, 2013). However, there are some green mycoheterotroph plants, *e.g.*, *Burmannia*, *Galeola*, and *Pyrola (Hung.: körtike)* capable of photosynthesis. This extraordinary mode of plant nutrition was first recognized more than a century ago (Johow, 1889; Kusano, 1911), and also studied currently, *e.g.*, between the *Gastrodia elata* (*Orchidaceae*) and *Armillariella mellea* (*Eng./Hung.:* honey mushroom / gyűrűs tuskógomba) (Lan *et al.*, 1994).

The Joint Genome Institute (JGI) framework (*Nordberg et al.*, 2014) of the Mycorrhizal Genomics Initiative (MGI) project sequences mycorrhizal fungi (both Basidiomycota and Ascomycota) (65 species to date), which include the major clades of symbiotic species associating with trees and woody shrubs, to reveal mycorrhizal symbioses, including Ericoid (ERM)-, Orchidoid (ORM)- and Ecto (EM)-mycorrhizal associations (Kohler *et al.*, 2015) (Fig. 2a).

Non-parasitic forms of symbiosis between fungi and green algae or cyanobacteria represent a new phylum, the Lichens (*Hung.:* zuzmók), with 20,000 'species' (*i.e.*, combinations of symbionts) (Gallé, 1966; Fox, 2001; Kalb and Aptroot, 2018).

(7) Transition from SAP to EM life form of Mycorrhiza fungi

EM fungi colonize the root surface of host plants and grow between the host plant cells (but do not penetrate cell walls). Mycorrhiza literally means 'fungi-roots'. Most of the 500 species of genus *Amanita*, the iconic group of mushroom-forming fungi, engage in autonomous saprotrophic (SAP) ectomycorrhizal (SAP-EM) symbioses with plants by a transition from saprotrophic (SAP) decomposition of dead organic matters to biotrophic (BT) dependence on the host plants for carbon (*i.e.*, sugar) source (Wolfe *et al.*, 2012).

Saprotrophic (SAP) (*i.e.*, free living) fungi efficiently decay celluloses of dead plant materials into sugars by producing three classes of enzymes: the endoglucanases (encoded by, *e.g.*, *eg*1 gene), cellobiohydrolases (encoded by *cbhI*), and beta-glucosidases (encoded by *bgl*), as it was detected in all investigated SAP species of *Amanita* genus of *Amanita inopinata*, *A. manicata*, *A. thiersii*, and two *Volvariella* (*Eng./Hung.:* rosegill / bocskorosgombák), *Volvariella volvacea*, and *V. bombycina*.

These enzyme genes were found to absent from most EM types of the other *Amanita* genomes, *e.g.*, *A. citrina* (*Eng./Hung.:* false deathcap / citromgalóca), and *A. muscarina* (*Eng./Hung.:* fly agaric / légyölő galóca). This gene loss suggests that EM *Amanita* species can no longer function as free-leaving saprotrophs (SAP) (Wolfe *et al.*, 2012). These results also confirmed the Martin *et al.*'s (2010) hypothesis of different 'molecular tool kits used by different mushroom species to form symbioses.

(8) Agricultural production of fungi

More than thirty cultivated mushroom species have been on the market with some species at the leading positions (%) such as *Agaricus bisporus* (*Eng./Hung.:* cultivated button mushrooms / csiperke) including *Agaricus bitorquis* (*Eng./Hung.:* pavement mushroom / ízletes csiperke) - 37,6 %; Shiitake, *Lentinula edodes* - 16,8 %; Oyster mushrooms, *Pleurotus* spp. (*Hung.:* laskagombák) - 16,3 %; *Auricularia* ssp. (*Eng./Hung.*: jelly ear / judásfülék) (mostly *Auricularia auricular-judea*) - 8,5 %; *Volvariella volvacea* (*Eng./Hung.:* paddy straw mushroom or rosegill / csíkos bocskorosgomba) - 6,1 %; and *Flammulina velutipes* (*Eng./Hung.:* velvet foot or golden needle mushroom / téli fülőke) - 4,7 %, *etc.* (Györfi, 2001; Leifa *et al.*, 2001).

Cultivation of *Flammulina velutipes* started in China from the 8th Century the *Agaricus bisporus* was cultivated in Europe from the 17th Century, and oyster mushrooms (*Pleurotus* spp.) are reported to have commenced in 1917 on tree stumps and wood logs (in Mamiro *et al.*, 2014).

The number of technologies for the cultivation of newer mushroom species have been continuously increasing. One of them is the *Pleurotus eryngii* (*Eng./Hung.*: king oyster mushrooms / ördögszekér laskagomba) (in Mamiro *et al.*, 2014; Gyenge *et al.*, 2016). Unfortunately, the highly demanding technology for growing *Calvatia gigantea* (*syn.*: *Langermannia gigantean*) (*Eng./Hung.*: giant puffball / óriás pöfeteg) has not succeeded to date (http://koronagomba.hu).

(9) Medicinal mushrooms

Many bioactive compounds have been isolated not only from fungi (as antibiotic penicillin first by Fleming, 1945) but also from higher mushrooms (Blagodatski *et al.,* 2018). There are four main groups based on chemical structure: lectins, terpenoids, proteins, and polysaccharides.

Of mushroom proteins, fungal immunomodulatory proteins (FIP), ribosome inactivating proteins (RIP), ribonucleases, laccases, have become the main sources of natural antitumor, antiviral, antimicrobial, antioxidative, and immunomodulatory agents (Xu *et al.,* 2011).

The fungal polysaccharide, lentinan is produced by shiitake mushroom (*Lentinus edodes*). A similar compound of schizophyllan (*syn.*: sizofiran) produced by *Schizophyllum commune* (*Eng./Hung.*: splitgill / hasadtlemezű taplógomba) is the most studied immunomodulating microbial β-(1,3)-D-glucan commercialized in cancer therapeutics (Giavasis, 2014). Lentinan also showed antimicrobial activity against tuberculosis and *Listeria monocytogenes* infection, as well as to *Salmonella enteritis* and *Staphylococcus aureus.*

Ganoderma lucidum (Basidiomycetes, Polyporales) (*Eng./Hung*.: reishi / pecsétviaszgomba) produces ganoderan, a β-(1,3) bioactive glucan with immunostimulating activity. *Agaricus blazei*, growing in Brazil (*Hung.:* brazil csiperke), stimulates the immune system by producing antitumor polysaccharides of β-(1,6); β-(1,3) glucan, and an acidic β-(1,6); α-(1,4) glucan. *Grifola frondosa* (*Eng./Hung*.: maitake or hen of the woods / fodros taplógomba), and *Trametes versicolor (Eng./Hung*.: turkey tail mushrooms / lepketapló) (*syn*.: *Coriolus versicolor*) also produces proteoglucan with a β-(1,3)-D-glucan chain, both used in Asia as an effective immunostimulative anticancer drug. *Pleurotus ostreatus* (*Eng./Hung.:* oyster mushroom / laskagomba) also synthesize bioactive b-glucans, such as pleuran, an insoluble β-(1,3/1,6)-D-glucan, and also a bittersweet aroma of benzaldehyde similar to bitter almonds. *Tremella* mushrooms (*Eng./Hung.:* brain mushrooms / rezgőgombák) of *T. mesenterica, T, fuciformis, T. aurantica,* and *T. cinnabarina* have an unusually high polysaccharide content of 60–70% compared to 10–30% in other mushrooms.

Microfungus *Saccharomyces cerevisiae*, the common food grade brewer's and baker's yeast also produce immunopotentiating glucans found in the cell wall. *S. cerevisiae* is also the industrial producer of zymosan, an immunomodulating cell wall proteoglucan (Giavasis, 2014).

Hallucinogenic (psychoactive) mushrooms - Psilocybin (psilocin). About 216 mushroom species in genera of *Copelandia, Gymnopilus* (*Eng./Hung.:* rustgill / lánggombák, tökegombák), *Inocybe* (*Eng./Hung.:* fibrecap / susulykák), *Mycena* (*Eng./Hung.:* bonett / kígyógombák), *Panaeolus* (*Eng./Hung.:* mottlegill / trágyagombák), *Pholiotina* (*Hung.:* tökegombácska), *Pluteus* (*Eng./Hung.:* shield / csengettyűgomba), and *Psilocybe* (*Eng./Hung.:* brownie or magic / badargomba) belong to neurotopic fungi (Guzmán *et al.*, 1998). These are divided into four groups of *(i)* psilocybin (a tryptophan derivative) producing fungi, *(ii)* species with ibotenic acid (an amino oxazol derivative) *e.g.*, *Amanita muscaria* (fly agaric / légyölő galóca), *(iii)* mycotoxin producing ergot-alkaloid fungi, *e.g.*, *Claviceps purpurea* (*Eng./Hung*.: Holy fire or St. Anthony's fire / anyarozs), and (iv) miscellaneous undetermined 'sacred' fungi.

Psilocybin (PS$^+$) fungi cause human hallucinogenic effects. In Europe, sixteen PS$^+$ species grow, *e.g.*, *Pluteus salicinus* (*Eng./Hung*.: willow shield / szürke/zöldülő csengettyűgomba). The psilocybin production is encoded by a cluster of five genes revealed very recently by genome sequencing of three PS$^+$ mushrooms of *Psilocybe cyanescens (Hung.:* kékülő badargomba) (0.53,483,841 x 10^8 bp), *Gymnopilus dilepis* (*Cortinariaceae* / Pókhálósgombák-Tőkegombák) (0.47,177,497 x 10^8 bp), and *Panaeolus (syn. Copelandia) cyanescens* (*Hung*.: Trágyagomba) (0.44,965,162 x 10^8 bp) (Reynolds *et al.*, 2018). Psilocybin gene clusters were found to spread among mushroom species by HGT (horizontal gene transfer) between divergent dung decomposers in the genera *Psilocybe* and *Panaeolus* (Szöllősi *et al.*, 2015; Reynolds *et al.*, 2018). Molecular structure of psilocybin is derived from the amino acid tryptophan, and functionally acts as a serotonin receptor antagonist similar to psychedelic drugs of psilocin, mescaline (from peyote cactus: *Lophophora williamsii*), LSD (lysergic acid diethylamide; isolated from *Claviceps*), and DMT (dimethyltryptamine isolated from *e.g., Mimosa tenuiflora*).

(10) Poisonous mushrooms

Next to *psychoactive fungi*, there are three dangerously lethal groups of mushrooms with *Amanita phalloides* (*Eng./Hung*.: death cap / gyilkos galóca) at the top, which produces alpha-amanitin, encoded by toxin gene families of α-amanitin (AMA), β-amanitin (BAM), phallacidin (PHA), *etc*.) causing fatal liver damage in 1–3 days following ingestion by inhibiting RNA polymerase II and III. The AMA is a cyclic peptide (cyclic L-asparaginyl-4-hydroxy-L-proly-(*R*)-4,5-dihydroxy-L-isoleucyl-6-hydroxy-2-mercapto-L-tryptophylglycyl-L-isoleucylglycyl-L-cysteinyl), with chemical formula $C_{39}H_{54}N_{10}O_{14}S$; and Molar mass: 918.97 g/mol.

Orellanine mycotoxin (3,3′,4,4′-tetrahydroxy-2,2′-bipyridine-*N, N′*-dioxide; $C_{10}H_8N_2O_6$) is produced by *Cortinarius* species *e.g., Cortinarius rubellus* (*Eng./Hung.:* deadly web cap / pókhálósgombák) causing kidney failure within 3 weeks after ingestion. The name orellanin was derived from *C. orellanosus* (*Eng./Hung*.: web cap / pókhálósgombák).

Monomethylhydrazine (MMH) (NH_2-NH-CH_3), which chemically is a rocket propellant, is produced by *Gyromitra* species (*Eng./Hung.:* false morels / papsapka-gombák) and cause hemolysis and brain damage. The antidote is a large dose of intravenous pyridoxine-hydrochloride.

All the other dangerously poisonous fungi, *e.g.*, *Inocybe* (*Eng./Hung.:* fibrecap / susulykák), tend to not be lethal (Kosentka *et al.*, 2013).

(11) Mycoremediation

Unlike plants, fungal cell walls are made up of mostly polysaccharides including chitin, which is the most characteristic polysaccharide found in protozoa, insects and fungi compared to plant polysaccharides which lack chitin (Ruiz-Herrera, 1992). However, unlike animal cells; plants, fungi and bacteria (except *Mycoplasma*s) have solid cell walls.

Mineral content of fungi has been compared to plants, and showed major differences with significantly low contents of Ca, due probably to fungal cell wall structure; and low Mg, due to the achlorophyllous fungal cells (Vetter, 2003). Low Ca and Fe content of the mushroom *Pleurotus* compared to leaf vegetables were also found by Mamiro *et al.* (2014).

Like phyto/dendro-remediation (Komives and Gullner, 2006; Gyulai *et al.*, 2014; Bittsánszky *et al.*, 2016) bacto-remediation and myco-remediation (Radhika *et al.*, 2016) are widely applied. In this technology, fungi clean up minerals and heavy metals from the contaminated soils, wastewaters, and air either in laboratory myco-reactors or in the environment *in situ* (Vane *et al.*, 2006). White-rot (WR) fungi (*i.e.*, *Phanerochaete chrysosporium*, *Pleurotus ostreatus*, and *Coriolus versicolor*) were found to degrade oil spills in contaminated soils (Yateem *et al.*, 1998). Mercury (Hg) bio-extraction capacity of *Coprinus comatus* (*Eng./Hung.:* shaggy ink cap / gyapjas tintagomba) was reported recently (Falandysz, 2016).

Conclusion

Genes, genetics and genomics of the systematically still mysterious mushrooms and fungi have revealed several changes in the genome expansions, which makes mushrooms (and fungi) a crucial part of the global carbon cycle.

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