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Distribution of methionine sulfoxide reductases in fungi and conservation of the free-methionine-*R*-sulfoxide reductase in multicellular eukaryotes

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Running title: Methionine sulfoxide reductases in fungi

Keywords: fungi, genome, horizontal gene transfer, methionine sulfoxide, methionine sulfoxide reductase, protein oxidation, thiol oxidoreductase.

Highlights:

- Free and protein-bound methionine can be oxidized into methionine sulfoxide (MetO).
- Methionine sulfoxide reductases (Msr) reduce MetO in most organisms.
- Sequence characterization and phylogenomics revealed strong conservation of Msr in fungi.
- fRMsr is widely conserved in unicellular and multicellular fungi.
- Some *msr* genes were acquired from bacteria via horizontal gene transfers.

Abstract

Methionine, either as a free amino acid or included in proteins, can be oxidized into methionine sulfoxide (MetO), which exists as *R* and *S* diastereomers. Almost all characterized organisms possess thiol-oxidoreductases named methionine sulfoxide reductase (Msr) enzymes to reduce MetO back to Met. MsrA and MsrB reduce the *S* and *R* diastereomers of MetO, respectively, with strict stereospecificity and are found in almost all organisms. Another type of thiol-oxidoreductase, the free-methionine-*R*-sulfoxide reductase (fRMsr), identified so far in prokaryotes and a few unicellular eukaryotes, reduces the *R* MetO diastereomer of the free amino acid. Moreover, some bacteria possess molybdenum-containing enzymes that reduce MetO, either in the free or protein-bound forms. All these Msrs play important roles in the protection of organisms against oxidative stress. Fungi are heterotrophic eukaryotes that colonize all niches on Earth and play fundamental functions, in organic matter recycling, as symbionts, or as pathogens of numerous organisms. However, our knowledge on fungal Msrs is still limited. Here, we performed a survey of *msr* genes in almost 700 genomes across the fungal kingdom. We show that most fungi possess one gene coding for each type of methionine sulfoxide reductase: MsrA, MsrB, and fRMsr. However, several fungi living in anaerobic environments or as obligate intracellular parasites were devoid of *msr* genes. Sequence inspection and phylogenetic analyses allowed us to identify non-canonical sequences with potentially novel enzymatic properties. Finaly, we identified several ocurences of *msr* horizontal gene transfer from bacteria to fungi.

1. Introduction

Life in the presence of dioxygen necessarily exposes the biological systems to oxidant molecules. Due to its high reactivity, dioxygen can be converted to reactive oxygen species (ROS), which play key roles in physiological and pathological contexts through redox modifications of macromolecules [1]. Met, either as a free amino acid or as a residue included in a protein, can be oxidized into Met sulfoxide (MetO) by the addition of an oxygen atom to the sulfur of the lateral chain. MetO exists as diastereomer *R* or *S* (Met-*R*-O and Met-*S*-O, respectively) [2], and can be reduced back to Met by the action of oxidoreductases called methionine sulfoxide reductases (Msr). The two main types are the (seleno)thiol-containing MsrA and MsrB, which display strict stereoselectivities toward the *S*- and the *R*-diastereomer of MetO, respectively [3–5]. Whereas MsrA reduces free MetO and protein-bound MetO with similar catalytic efficiencies, MsrB generally only reduces efficiently the protein-bound MetO [6]. Another enzyme, fRMsr (free methionine-(R)-sulfoxide reductase) specifically reduces the free form of Met-*R*-O [7–9]. Some bacteria also possess several molybdoenzymes that reduce exclusively the free MetO [10,11] or both the free and protein-bound MetO [12–15]. Despite the lack of sequence and structure similarities, MsrA, MsrB and fRMsr generally catalyze the reduction of MetO using a similar 3-steps-mechanism [9,16] : i) a *'catalytic'* Cys (or, less frequently, a selenocysteine, Sec) reduces the target MetO and is converted into a sulfenic (or selenic) acid [17], ii) an internal *'resolving'* Cys reduces it through the formation of an intramolecular disulfide bond, and finally iii) the oxidized Msr is regenerated through disulfide exchange with a thioredoxin [18]. Variations of this mechanism exist, with some Msrs devoid of any resolving Cys, in which the sulfenic acid is directly reduced by an external reducer [19–21]. Alternatively, in other Msrs, a disulfide exchange occurs with a second internal resolving Cys before regeneration by the thioredoxin [7,22,23]. Genome mining analyses indicated that *msrA* and *msrB* genes originated from early prokaryotes and are now present in all organisms across the tree of life, with few exceptions [24–26]. Most organisms have few *msr* genes, generally one of each type [24–26], but this number is generally higher in plants (e.g. up to 5 *msrA* and 9 *msrB* genes in *Arabidopsis thaliana* [25]). Moreover, some bacteria encode a bifunctional MsrA/MsrB fusion and some others lack a MsrB, but no organism of any kind was so far described with only a MsrB [24,26]. Finally, only very few organisms do not possess any *msr* gene at all, such as a few endosymbiotic or obligatory parasitic bacteria and some archaea [24,26]. fRMsr were so far only reported in bacteria and a few unicellular eukaryotes [7–9]. Most interestingly, the only eukaryote for which the absence of *msr* gene was observed is the fungus *Encephalitozoon cuniculi*, a microsporidium having a remarkably reduced genome (~2.9 Mb) and living as intracellular parasite of mammals [24,27]. The conservation of typical MsrAs and MsrBs in almost all known organisms argues for the critical role of MetO reduction in cellular metabolism, and numerous studies showed that Msrs are involved in the protection against oxidative stress and the regulation of protein functions. Schematically, Msr protective roles against oxidative injuries occur through two main functions: i) the repair of oxidized proteins, and

ii) an antioxidant function through ROS scavenging by cyclic Met oxidation and reduction. Moreover, the reversible Met oxidation was shown to act as a post-translational modification responsible for the activation of enzymes and transcription factors or the regulation of protein-protein interactions [28–30]. The role of fRMsr has been far less studied, but it is suspected to have an antioxidant function by reducing free MetO and maintaining the pool of Met available for protein synthesis and for the production of sulfur-containing metabolites [8,31]. Overall, these functions were well established in animals, bacteria and plants, and have recently been reviewed [32–36].

Fungi are heterotrophic eukaryotes that colonize virtually all niches on Earth and exist as unicellular or multicellular organisms. They can have numerous lifestyles, either as free living organisms playing key roles in organic and inorganic matter cycling, or as symbionts or pathogens with crucial impacts on plant and animal health [37]. As any other organism living in aerobic conditions and exposed to environmental constraints, fungi are exposed to oxidative constraints and protein oxidation [38]. However, the effects of Met oxidation and the roles of Msrs were largely overlooked in these eukaryotes. The Msr system was mainly characterized in the yeast *Saccharomyces cerevisiae,* which possesses one Msr of each type [6,8]. In *S. cerevisiae,* MsrA is located in the cytosol, MsrB is found in mitochondria and in the cytosol and fRMsr is located both in the cytosol and the nucleus [39,40]. Genetic manipulations have shown that these Msrs are involved in the protection against oxidative stress and in maintaining the yeast lifespan [6,8,41,42]. Consistently, the overexpression of *msrA* in the basidiomycete *Pleurotus ostreatus* and of *msrB* in the yeast *Schizosaccharomyces pombe* increased the resistance to oxidative constraints [43,44]. Moreover, the filamentous fungus *Aspergillus nidulans* possesses one *msrA* and one *msrB* genes, and the deletion of one or both genes increased the sensitivity of the fungus to oxidative treatments [45]. Few proteins with oxidized Met residues have been characterized in fungi, but remarkably interesting findings were obtained. For instance, in *S. cerevisiae*, the reversible oxidation of Met regulates the oligomerization state of the ataxin-2 protein and the activity of the co-chaperone Fes1 [40,46]. Moreover, Met oxidation enhanced the activity of an α-galactosidase in *Trichoderma reesei* [47]. Finally, in *A. nidulans,* it was demonstrated that the nuclear localization of the nitrate-responsive transcription factor NirA was actively regulated through cyclic Met oxidation [48]. These data indicate that, as for other organisms, fungal Msrs certainly play key roles under many conditions of oxidative stress, such as biotic interactions or abiotic constraints.

In this study, we searched for *msr* genes in about 700 fungal genomes. We show that the great majority of fungi have one *msrA* and one *msrB* genes. Moreover, we identified *fRmsr* genes in almost all the fungi we analyzed and thereby demonstrate that the enzyme is conserved in these multicellular eukaryotes. Finally, using a phylogenetic analysis and a close inspection of the sequence features, we identified fungal Msrs with unusual sequence characteristics and uncovered horizontal gene transfers from bacteria to fungi.

2. Material and methods

2.1. Search for Msr homologs in fungi.

The protein sequence of MsrA (Uniprot accession # C8Z745), MsrB (Uniprot accession # P25566) and fRMsr (Uniprot accession # P36088) from *S. cerevisiae*, MsrP (Uniprot accession # P76342) and BisC (Uniprot accession # P20099) from *Escherichia coli*, TorZ (Uniprot accession # P44798) from *Haemophilus influenzae*, and DorA (Uniprot accession # Q57366) from *Rhodobacter sphaeroides* were used as BLASTP and TBLASTN [49] queries to identify *msr* genes in 683 genomes available in the MycoCosm database [50] (https://mycocosm.jgi.doe.gov/mycocosm/home).

2.2. List of all explored fungal genomes.

Aaosphaeria arxii CBS 175.79 v1.0; Amniculicola lignicola CBS 123094 v1.0; Ampelomyces quisqualis HMLAC05119 v1.0; Aplosporella prunicola CBS 121.167 v1.0; Aulographum hederae v2.0; Bimuria novae-zelandiae CBS 107.79 v1.0; Byssothecium circinans CBS 675.92 v1.0; Cercospora zeae-maydis v1.0; Clathrospora elynae CBS 161.51 v1.0; Cucurbitaria berberidis CBS 394.84 v1.0; Decorospora gaudefroyi v1.0; Delitschia confertaspora ATCC 74209 v1.0; Delphinella strobiligena CBS 735.71 v1.0; Didymella exigua CBS 183.55 v1.0; Dissoconium aciculare v1.0; Dothidotthia symphoricarpi v1.0; Elsinoe ampelina CECT 20119 v1.0; Eremomyces bilateralis CBS 781.70 v1.0; Hortaea acidophila CBS 113389 v1.0; Karstenula rhodostoma CBS 690.94 v1.0; Lentithecium fluviatile v1.0; Lindgomyces ingoldianus ATCC 200398 v1.0; Lineolata rhizophorae ATCC 16933 v1.0; Lizonia empirigonia CBS 542.76 v1.0; Lophiostoma macrostomum v1.0; Lophiotrema nucula CBS 627.86 v1.0; Lophium mytilinum CBS 269.34 v1.0; Macroventuria anomochaeta CBS 525.71 v1.0; Massarina eburnea CBS 473.64 v1.0; Massariosphaeria phaeospora CBS 611.86 v1.0; Melanomma pulvis-pyrius v1.0; Microthyrium microscopicum CBS 115976 v1.0; Myriangium duriaei CBS 260.36 v1.0; Mytilinidion resinicola CBS 304.34 v1.0; Ophiobolus disseminans CBS 113818 v1.0; Patellaria atrata v1.0; Phoma tracheiphila IPT5 v1.0; Piedraia hortae CBS 480.64 v1.1; Pleomassaria siparia v1.0; Polychaeton citri v1.0; Polyplosphaeria fusca CBS 125425 v1.0; Pseudovirgaria hyperparasitica CBS 121739 v1.0; Rhizodiscina lignyota CBS 133067 v1.0; Saccharata proteae CBS 121410 v1.0; Setomelanomma holmii CBS 110217 v1.0; Sporormia fimetaria v1.0; Teratosphaeria nubilosa CBS 116005 v1.0; Tothia fuscella CBS 130266 v1.0; Trematosphaeria pertusa CBS 122368 v1.0; Trichodelitschia bisporula CBS 262.69 v1.0; Verruculina enalia CBS 304.66 v1.0; Viridothelium virens v1.0; Westerdykella ornata CBS 379.55 v1.0; Zasmidium cellare ATCC 36951 v1.0; Zopfia rhizophila v1.0 [51]*; Acaromyces ingoldii MCA 4198 v1.0; Ceraceosorus guamensis MCA 4658 v1.0; Jaminaea sp. MCA 5214 v1.0; Meira miltonrushii MCA 3882 v1.0; Pseudomicrostroma glucosiphilum gen et sp. nov. MCA 4718 v1.0; Testicularia cyperi MCA 3645 v1.0; Tilletiopsis washingtonensis MCA 4186 v1.0;*

Violaceomyces palustris SA 807 v1.0 [52]; *Acidomyces richmondensis BFW; Acidomyces richmondensis BFW* [53]; *Acremonium chrysogenum ATCC 11550* [54]; *Agaricus bisporus var bisporus (H97) v2.0; Agaricus bisporus var. burnettii JB137-S8; Gigaspora rosea v1.0; Rhizophagus cerebriforme DAOM 227022 v1.0; Rhizophagus diaphanus v1.0* [55]; *Amanita muscaria Koide v1.0; Gymnopus luxurians v1.0; Hebeloma cylindrosporum h7 v2.0; Hydnomerulius pinastri v2.0; Hypholoma sublateritium v1.0; Laccaria amethystina LaAM-08-1 v2.0; Paxillus adelphus Ve08.2h10 v2.0; Paxillus involutus ATCC 200175 v1.0; Piloderma croceum F 1598 v1.0; Pisolithus microcarpus 441 v1.0; Pisolithus tinctorius Marx 270 v1.0; Plicaturopsis crispa v1.0; Scleroderma citrinum Foug A v1.0; Sebacina vermifera MAFF 305830 v1.0; Sphaerobolus stellatus v1.0; Suillus luteus UH-Slu-Lm8-n1 v3.0; Tulasnella calospora AL13/4D v1.0; Oidiodendron maius Zn v1.0* [56]; *Amanita thiersii Skay4041 v1.0* [57]; *Ambrosiozyma philentoma NRRL Y-7523; Candida boidinii NRRL Y-2332; Citeromyces matritensis NRRL Y-2407; Nakazawaea wickerhamii NRRL Y-2563; Peterozyma xylosa NRRL Y-12939; Saccharomycopsis capsularis NRRL Y-17639; Saturnispora dispora NRRL Y-1447* [58]; *Amorphotheca resinae v1.0; Meliniomyces bicolor E v2.0; Meliniomyces variabilis F v1.0; Rhizoscyphus ericae UAMH 7357 v1.0* [59]; *Anaeromyces robustus v1.0; Neocallimastix californiae G1 v1.0; Piromyces finnis v3.0; Piromyces sp. E2 v1.0* [60]; *Antonospora locustae HM-2013* [61]; *Armillaria cepistipes B5; Armillaria gallica 21-2 v1.0; Armillaria ostoyae C18/9; Armillaria solidipes 28-4 v1.0* [62]; *Armillaria mellea DSM 3731* [63]; *Arthrobotrys oligospora ATCC 24927* [64]; *Ascobolus immersus RN42 v1.0; Choiromyces venosus 120613-1 v1.0; Morchella importuna CCBAS932 v1.0; Terfezia boudieri ATCC MYA-4762 v1.1; Tuber aestivum var. urcinatum v1.0; Tuber borchii Tbo3840 v1.0; Tuber magnatum v1.0* [65]; *Ascochyta rabiei ArDII* [66]; *Ascocoryne sarcoides NRRL50072* [67]; *Ascodesmis nigricans CBS 389.68 v1.0* [68]; *Aspergillus aculeatinus CBS 121060 v1.0; Aspergillus brunneoviolaceus CBS 621.78 v1.0; Aspergillus costaricaensis CBS 115574 v1.0; Aspergillus ellipticus CBS 707.79 v1.0; Aspergillus eucalypticola CBS 122712 v1.0; Aspergillus fijiensis CBS 313.89 v1.0; Aspergillus heteromorphus CBS 117.55 v1.0; Aspergillus homomorphus CBS 101889 v1.0; Aspergillus ibericus CBS 121593 v1.0; Aspergillus indologenus CBS 114.80 v1.0; Aspergillus japonicus CBS 114.51 v1.0; Aspergillus neoniger CBS 115656 v1.0; Aspergillus niger (lacticoffeatus) CBS 101883 v1.0; Aspergillus niger (phoenicis Corda) Thom ATCC 13157 v1.0; Aspergillus niger NRRL3; Aspergillus niger van Tieghem ATCC 13496 v1.0; Aspergillus piperis CBS 112811 v1.0; Aspergillus saccharolyticus JOP 1030-1 v1.0; Aspergillus sclerotiicarbonarius CBS 121057 v1.0; Aspergillus sclerotioniger CBS115572 v1.0; Aspergillus uvarum CBS 121591 v1.0; Aspergillus vadensis CBS 113365 v1.0; Aspergillus violaceofuscus CBS 115571 v1.0; Aspergillus welwitschiae CBS139.54b v1.0* [69]; *Aspergillus aculeatus ATCC16872 v1.1; Aspergillus brasiliensis v1.0; Aspergillus carbonarius ITEM 5010 v3; Aspergillus glaucus v1.0; Aspergillus luchuensis CBS 106.47 v1.0; Aspergillus sydowii CBS 593.65 v1.0; Aspergillus tubingensis v1.0; Aspergillus versicolor v1.0; Aspergillus wentii v1.0; Aspergillus zonatus v1.0; Penicillium chrysogenum v1.0* [70]; *Aspergillus bombycis NRRL 26010* [71]; *Aspergillus calidoustus* [72]; *Aspergillus campestris IBT 28561 v1.0;*

Aspergillus candidus CBS 102.13 v1.0; Aspergillus novofumigatus IBT 16806 v1.0; Aspergillus ochraceoroseus IBT 24754 v1.0; Aspergillus steynii IBT 23096 v1.0; Aspergillus taichungensis IBT 19404 v1.0; Aspergillus albertensis v1.0; Aspergillus alliaceus CBS 536.65 v1.0; Aspergillus arachidicola v1.0; Aspergillus avenaceus IBT 18842 v1.0; Aspergillus bertholletius IBT 29228 v1.0; Aspergillus caelatus CBS 763.97 v1.0; Aspergillus coremiiformis CBS 553.77 v1.0; Aspergillus leporis CBS 151.66 v1.0; Aspergillus minisclerotigenes CBS 117635 v1.0; Aspergillus nomius IBT 12657 v1.0; Aspergillus novoparasiticus CBS 126849 v1.0; Aspergillus parasiticus CBS 117618 v1.0; Aspergillus parvisclerotigenus CBS 121.62 v1.0; Aspergillus pseudocaelatus CBS 117616 v1.0; Aspergillus pseudonomius CBS 119388 v1.0; Aspergillus pseudotamarii CBS 117625 v1.0; Aspergillus sergii CBS 130017 v1.0; Aspergillus tamarii CBS 117626 v1.0; Aspergillus transmontanensis CBS 130015 v1.0 [73]*; Aspergillus clavatus NRRL 1 from AspGD; Aspergillus flavus NRRL3357; Aspergillus nidulans; Aspergillus oryzae RIB40; Aspergillus terreus NIH 2624; Neosartorya fischeri NRRL 181* [74]*; Aspergillus cristatus GZAAS20.1005* [75]*; Aspergillus fumigatus A1163* [76]*; Aspergillus fumigatus Af293 from AspGD* [77]*; Aspergillus kawachii IFO 4308* [78]*; Aspergillus niger ATCC 1015 v4.0* [79]*; Aspergillus niger CBS 513.88* [80]*; Aspergillus nomius NRRL 13137; Aspergillus ochraceoroseus SRRC1432; Aspergillus rambellii SRRC1468* [81]*; Aspergillus udagawae IFM 46973* [82]*; Aureobasidium pullulans var. melanogenum CBS 110374; Aureobasidium pullulans var. namibiae CBS 147.97; Aureobasidium pullulans var. pullulans EXF-150; Aureobasidium pullulans var. subglaciale EXF-2481* [83]*; Auricularia subglabra v2.0; Coniophora puteana v1.0; Dichomitus squalens LYAD-421 SS1 v1.0; Fomitiporia mediterranea v1.0; Fomitopsis pinicola FP-58527 SS1 v3.0; Gloeophyllum trabeum v1.0; Punctularia strigosozonata v1.0; Stereum hirsutum FP-91666 SS1 v1.0; Trametes versicolor v1.0; Wolfiporia cocos MD-104 SS10 v1.0; Dacryopinax primogenitus DJM 731 SSP1 v1.0; Tremella mesenterica Fries v1.0* [84]*; Auriculariopsis ampla NL-1724 v1.0* [85]*; Baudoinia compniacensis UAMH 10762 (4089826) v1.0; Cochliobolus heterostrophus C4 v1.0; Cochliobolus heterostrophus C5 v2.0; Cochliobolus lunatus m118 v2.0; Cochliobolus sativus ND90Pr v1.0; Hysterium pulicare; Rhytidhysteron rufulum; Septoria musiva SO2202 v1.0; Septoria populicola v1.0; Setosphaeria turcica Et28A v2.0* [86]*; Beauveria bassiana ARSEF 2860* [87]*; Bjerkandera adusta v1.0; Ganoderma sp. 10597 SS1 v1.0; Phlebia brevispora HHB-7030 SS6 v1.0; Neofusicoccum parvum UCRNP2; Eutypa lata UCREL1; Phaeoacremonium aleophilum UCRPA7* [88]*; Blastobotrys (Arxula) adeninivorans* [89]*; Blastomyces dermatitidis SLH14081* [90]*; Blumeria graminis f. sp. hordei DH14; Blumeria graminis f. sp. hordei Race1* [91]*; Blumeria graminis f. sp. tritici 96224* [92]*; Botryobasidium botryosum v1.0; Galerina marginata v1.0; Jaapia argillacea v1.0; Pleurotus ostreatus PC15 v2.0; Ascoidea rubescens NRRL Y17699 v1.0; Babjeviella inositovora NRRL Y-12698 v1.0; Candida arabinofermentans NRRL YB-2248 v1.0; Candida tanzawaensis NRRL Y-17324 v1.0; Cyberlindnera jadinii NRRL Y-1542 v1.0; Hanseniaspora valbyensis NRRL Y-1626 v1.1; Hyphopichia burtonii NRRL Y-1933 v1.0; Lipomyces starkeyi NRRL Y-11557 v1.0; Metschnikowia bicuspidata NRRL YB-4993 v1.0; Nadsonia fulvescens var. elongata DSM 6958 v1.0; Ogataea polymorpha NCYC 495 leu1.1 v2.0;*

Pachysolen tannophilus NRRL Y-2460 v1.2; Pichia membranifaciens v2.0; Tortispora caseinolytica Y-17796 v1.0; Wickerhamomyces anomalus NRRL Y-366-8 v1.0; Saitoella complicata NRRL Y-17804 v1.0 [93]*; Botryosphaeria dothidea* [94]*; Botrytis cinerea v1.0* [95]*; Byssochlamys spectabilis No. 5* [96]*; Candida albicans SC5314* [97]*; Candida tenuis NRRL Y-1498 v1.0; Spathaspora passalidarum NRRL Y-27907 v2.0* [98]*; Capronia coronata CBS 617.96; Capronia epimyces CBS 606.96; Capronia semiimmersa CBS27337; Cladophialophora bantiana CBS 173.52; Cladophialophora carrionii CBS 160.54; Cladophialophora immunda CBS83496; Cladophialophora psammophila CBS 110553; Cladophialophora yegresii CBS 114405; Cyphellophora europaea CBS 101466; Exophiala aquamarina CBS 119918; Exophiala mesophila CBS40295; Exophiala oligosperma CBS72588; Exophiala sideris CBS121828; Exophiala spinifera CBS89968; Exophiala xenobiotica CBS118157; Fonsecaea multimorphosa CBS 102226; Fonsecaea pedrosoi CBS 271.37; Coniosporium apollinis CBS 100218; Verruconis gallopava* [99]*; Cenococcum geophilum 1.58 v2.0; Glonium stellatum CBS 207.34 v1.0; Lepidopterella palustris v1.0* [100]*; Ceriporiopsis (Gelatoporia) subvermispora B* [101]*; Chaetomium globosum v1.0* [102]*; Chaetomium thermophilum var thermophilum DSM 1495* [103]*; Cladonia grayi Cgr/DA2myc/ss v2.0* [104]*; Cladosporium fulvum v1.0; Dothistroma septosporum NZE10 v1.0* [105]*; Cladosporium sphaerospermum UM 843* [106]*; Clavispora lusitaniae ATCC 42720; Lodderomyces elongisporus NRRL YB-4239; Meyerozyma guilliermondii ATCC 6260* [107]*; Coccidioides immitis RS ; Coccidioides posadasii C735 delta SOWgp; Histoplasma capsulatum NAm1; Uncinocarpus reesii UAMH 1704* [108]*; Cochliobolus carbonum 26-R-13 v1.0; Cochliobolus miyabeanus ATCC 44560 v1.0; Cochliobolus victoriae FI3 v1.0* [109]*; Colletotrichum chlorophyti NTL11* [110]*; Colletotrichum fioriniae PJ7* [111]*; Colletotrichum graminicola M1.001* [112]*; Colletotrichum higginsianum IMI 349063* [113]*; Colletotrichum incanum MAFF 238712* [114]*; Colletotrichum nymphaeae SA-01; Colletotrichum salicis CBS607.94; Colletotrichum simmondsii CBS122122; Trichoderma gamsii T6085* [115]*; Colletotrichum orbiculare 104-T* [116]*; Colletotrichum orchidophilum IMI 309357* [117]*; Colletotrichum tofieldiae 0861* [118]*; Conidiobolus coronatus NRRL28638 v1.0; Coemansia reversa NRRL 1564 v1.0; Gonapodya prolifera v1.0* [119]*; Coniochaeta ligniaria NRRL 30616 v1.0* [120]*; Coniochaeta sp. 2T2.1 v1.0* [121]*; Coniophora olivacea MUCL 20566 v1.0* [122]*; Coprinellus micaceus FP101781 v2.0; Coprinopsis marcescibilis CBS121175 v1.0; Crucibulum laeve CBS 166.37 v1.0; Dendrothele bispora CBS 962.96 v1.0; Heliocybe sulcata OMC1185 v1.0; Peniophora sp. CONTA v1.0; Pluteus cervinus NL-1719 v1.0; Polyporus arcularius v1.0; Pterula gracilis CBS309.79 v1.0* [123]*; Coprinopsis cinerea* [124]*; Coprinopsis cinerea AmutBmut pab1-1 v1.0* [125]*; Cordyceps militaris CM01* [126]*; Corynespora cassiicola CCP v1.0* [127]*; Cronartium quercuum f. sp. fusiforme G11 v1.0* [128]*; Cryphonectria parasitica EP155 v2.0* [129]*; Cryptococcus curvatus ATCC 20509 v1.0; Cryptococcus terricola JCM 24523 v1.0* [130]*; Cryptococcus neoformans var neoformans JEC21* [131]*; Cryptococcus neoformans var. grubii H99* [132]*; Cylindrobasidium torrendii FP15055 v1.0; Fistulina hepatica v1.0* [133]*; Cystobasidium minutum MCA 4210 v1.0* [134]*; Daedalea quercina v1.0; Exidia glandulosa v1.0; Fibulorhizoctonia sp.*

CBS 109695 v1.0; Laetiporus sulphureus var. sulphureus v1.0; Neolentinus lepideus v1.0; Peniophora sp. v1.0; Sistotremastrum niveocremeum HHB9708 ss-1 1.0; Sistotremastrum suecicum v1.0; Calocera cornea v1.0; Calocera viscosa v1.0 [135]*; Daldinia eschscholtzii EC12 v1.0; Hypoxylon sp. CI-4A v1.0; Hypoxylon sp. CO27-5 v1.0; Hypoxylon sp. EC38 v3.0* [136]*; Debaryomyces hansenii* [137]*; Dekkera bruxellensis CBS 2499 v2.0* [138]*; Dentipellis sp. KUC8613 v1.0* [139]*; Dichomitus squalens CBS463.89 v1.0; Dichomitus squalens CBS464.89 v1.0; Dichomitus squalens OM18370.1 v1.0* [140]*; Encephalitozoon cuniculi GB-M1* [141]*; Encephalitozoon hellem ATCC 50504; Encephalitozoon romaleae SJ-2008* [142]*; Encephalitozoon intestinalis ATCC 50506* [143]*; Endocarpon pusillum Z07020* [144]*; Endogone sp FLAS 59071; Jimgerdemannia flammicorona AD002; Jimgerdemannia flammicorona GMNB39; Jimgerdemannia lactiflua OSC166217* [145]*; Enterocytozoon bieneusi H348* [146]*; Eremothecium gossypii ATCC 10895* [147]*; Erysiphe necator c* [148]*; Eurotium rubrum v1.0* [149]*; Exophiala dermatitidis UT8656* [150]*; Fibroporia radiculosa TFFH 294* [151]*; Fonsecaea monophora CBS 269.37* [152]*; Fonsecaea nubica CBS 269.64* [153]*; Fusarium fujikuroi IMI 58289* [154]*; Fusarium graminearum v1.0* [155]*; Fusarium oxysporum f. sp. conglutinans race 2 54008 (PHW808); Fusarium oxysporum f. sp. cubense tropical race 4 54006 (II5); Fusarium oxysporum f. sp. lycopersici MN25 (FoMN25) NRRL 54003; Fusarium oxysporum f. sp. radicis-lycopersici 26381 (CL57); Fusarium oxysporum f. sp. raphani 54005; Fusarium oxysporum f. sp. vasinfectum 25433 (Cotton); Fusarium oxysporum Fo47; Fusarium oxysporum NRRL 32931* [156]*; Fusarium oxysporum f. sp. lycopersici 4287 v2; Fusarium verticillioides 7600 v2* [157]*; Fusarium oxysporum f. sp. melonis (FoMelon) NRRL 26406* [158]*; Fusarium oxysporum f. sp. pisi HDV247* [159]*; Fusarium pseudograminearum CS3096* [160]*; Gaeumannomyces graminis var. tritici R3-111a-1; Magnaporthiopsis poae ATCC 64411* [161]*; Glarea lozoyensis ATCC 20868* [162]*; Grosmannia clavigera kw1407* [163]*; Gymnopus androsaceus JB14 v1.0; Chalara longipes BDJ v1.0* [164]*; Heterobasidion annosum v2.0* [165]*; Homolaphlyctis polyrhiza JEL142 v1.0* [166]*; Hortaea werneckii EXF-2000 M0 v1.0* [167]*; Ilyonectria sp. v1.0* [168]*; Kazachstania africana CBS 2517; Torulaspora delbrueckii CBS 1146* [169]*; Kluyveromyces lactis; Yarrowia lipolytica (strain CLIB122)* [170]*; Kuraishia capsulata CBS 1993* [171]*; Laccaria bicolor v2.0* [172]*; Lentinula edodes B17 v1.1* [173]*; Lentinula edodes W1-26 v1.0* [174]*; Lentinus tigrinus ALCF2SS1-6 v1.0; Lentinus tigrinus ALCF2SS1-7 v1.0* [175]*; Leptosphaeria maculans* [176]*; Leucoagaricus gongylophorus Ac12* [177]*; Leucosporidiella creatinivora 62-1032 v1.0; Kockovaella imperatae NRRL Y-17943 v1.0; Naematella encephela UCDFST 68-887.2 v1.0; Clohesyomyces aquaticus v1.0; Pseudomassariella vexata CBS 129021 v1.0; Protomyces lactucaedebilis 12-1054 v1.0; Lobosporangium transversale NRRL 3116 v1.0; Absidia repens NRRL 1336 v1.0; Hesseltinella vesiculosa NRRL3301 v2.0; Rhizopus microsporus var. microsporus ATCC52813 v1.0; Syncephalastrum racemosum NRRL 2496 v1.0; Basidiobolus meristosporus CBS 931.73 v1.0; Linderina pennispora ATCC 12442 v1.0; Catenaria anguillulae PL171 v2.0; Rhizoclosmatium globosum JEL800 v1.0* [178]*; Lichtheimia corymbifera JMRC:FSU:9682* [179]*; Macrophomina phaseolina MS6* [180]*; Magnaporthe oryzae 70-15 v3.0* [181]*; Malassezia globosa*

[182]*; Malassezia sympodialis ATCC 42132* [183]*; Marssonina brunnea f. sp. multigermtubi MB_m1* [184]*; Melampsora larici-populina v2.0; Puccinia graminis f. sp. tritici v2.0* [185]*; Melampsora lini CH5* [186]*; Metarhizium acridum CQMa 102;* [187]*; Metarhizium robertsii ARSEF 23;* [188]*; Metschnikowia bicuspidata single-cell v1.0; Dimargaris cristalligena RSA 468 single-cell v1.0; Piptocephalis cylindrospora RSA 2659 single-cell v3.0; Syncephalis pseudoplumigaleata Benny S71-1 single-cell v1.0; Thamnocephalis sphaerospora RSA 1356 single-cell v1.0; Blyttiomyces helicus single-cell v1.0; Caulochytrium protostelioides ATCC 52028 v1.0; Rozella allomycis CSF55 single-cell v1.0* [189]*; Metschnikowia fructicola 277* [190]*; Microbotryum lychnidis-dioicae p1A1 Lamole* [191]*; Microdochium bolleyi J235TASD1 v1.0* [192]*; Microsporum canis CBS 113480; Trichophyton rubrum CBS 118892* [193]*; Mitosporidium daphniae UGP3* [194]*; Mixia osmundae IAM 14324 v1.0; Tilletiaria anomala UBC 951 v1.0* [195]*; Moesziomyces aphidis DSM 70725* [196]*; Monacrosporium haptotylum CBS 200.50* [197]*; Moniliophthora perniciosa FA553* [198]*; Morchella importuna SCYDJ1-A1 v1.0* [199]*; Mortierella elongata AG-77 v2.0* [200]*; Mucor endophyticus; Mucor fuscus; Mucor lanceolatus; Mucor racemosus* [201]*; Mucor lusitanicus (circinelloides) MU402 v1.0* [202]*; Mucor lusitanicus CBS277.49 v2.0; Phycomyces blakesleeanus NRRL1555 v2.0* [203]*; Myceliophthora thermophila (Sporotrichum thermophile) v2.0; Thielavia terrestris v2.0* [204]*; Mycosphaerella graminicola v2.0* [205]*; Nakaseomyces bacillisporus CBS 7720; Nakaseomyces delphensis CBS 2170* [206]*; Nectria haematococca v2.0* [207]*; Nematocida parisii ERTm1* [208]*; Neolecta irregularis DAH-1 v1.0* [209]*; Neonectria ditissima R09/05* [210]*; Neurospora crassa FGSC 73 trp-3 v1.0* [211]*; Neurospora crassa OR74A v2.0* [212]*; Neurospora tetrasperma FGSC 2508 mat A v2.0; Neurospora tetrasperma FGSC 2509 mat a v1.0* [213]*; Nosema ceranae BRL01* [214]*; Obba rivulosa 3A-2 v1.0* [215]*; Omphalotus olearius* [216]*; Ophiostoma novo-ulmi subsp. novo-ulmi H327* [217]*; Ophiostoma piceae UAMH 11346* [218]*; Orpinomyces sp.* [219]*; Paecilomyces niveus CO7 v1.0* [220]*; Paecilomyces variotii CBS 101075 v1.0; Paecilomyces variotii CBS144490 HYG1 v1.0* [221]*; Paracoccidioides brasiliensis Pb03; Paracoccidioides brasiliensis Pb18* [222]*; Paraconiothyrium sporulosum AP3s5-JAC2a v1.0; Pyrenochaeta sp. DS3sAY3a v1.0; Stagonospora sp. SRC1lsM3a v1.0; Alternaria alternata SRC1lrK2f v1.0* [223]*; Penicillium antarcticum IBT 31811; Penicillium coprophilum IBT 31321; Penicillium decumbens IBT 11843; Penicillium flavigenum IBT 14082; Penicillium nalgiovense FM193; Penicillium polonicum IBT 4502; Penicillium solitum IBT 29525; Penicillium steckii IBT 24891; Penicillium vulpinum IBT 29486* [224]*; Penicillium chrysogenum Wisconsin 54-1255* [225]*; Penicillium digitatum Pd1; Penicillium digitatum PHI26* [226]*; Penicillium expansum d1; Penicillium italicum PHI-1* [227]*; Penicillium griseofulvum PG3* [228]*; Penicillium nordicum DAOMC 185683* [229]*; Penicillium oxalicum 114-2* [230]*; Penicillium subrubescens FBCC1632 / CBS132785* [231]*; Penicillium thymicola DAOMC 180753 v1.0* [232]*; Periconia macrospinosa DSE2036 v1.0; Cadophora sp. DSE1049 v1.0* [233]*; Phaeomoniella chlamydospora UCRPC4; Diplodia seriata DS831; Diaporthe ampelina UCDDA912* [234]*; Phanerochaete carnosa HHB-10118-Sp v1.0* [235]*; Phanerochaete chrysosporium RP-78 v2.2* [236]*; Phialocephala scopiformis 5WS22E1 v1.0* [237]*; Phialophora attae*

CBS 131958 [238]*; Phlebia centrifuga FBCC195* [239]*; Phlebia radiata Fr. (isolate 79, FBCC0043)* [240]*; Phlebiopsis gigantea v1.0* [241]*; Phyllosticta capitalensis CBS 128856 v1.0; Phyllosticta citriasiana CBS 120486 v1.0; Phyllosticta citribraziliensis CBS 100098 v1.0; Phyllosticta citricarpa CBS 127454 v1.0; Phyllosticta citrichinaensis CBS 130529 v1.0; Phyllosticta paracitricarpa CBS 141357 v1.0; Phyllosticta sp. CPC 27913 v1.0* [242]*; Pichia kudriavzevii CBS573* [243]*; Pichia pastoris* [244]*; Piriformospora indica DSM 11827 from MPI* [245]*; Pleurotus ostreatus PC9 v1.0* [246]*; Pneumocystis jirovecii;* [247]*; Pochonia chlamydosporia 170* [248]*; Podospora anserina S mat+* [249]*; Polyporus brumalis BRFM 1820 v1.0* [250]*; Postia placenta MAD 698-R v1.0* [251]*; Postia placenta MAD-698-R-SB12 v1.0* [252]*; Pseudocercospora (Mycosphaerella) fijiensis v2.0* [253]*; Pseudogymnoascus destructans 20631-21* [254]*; Pseudozyma antarctica T-34* [255]*; Pseudozyma hubeiensis SY62* [256]*; Psilocybe cubensis v1.0; Psilocybe serbica v1.0* [257]*; Puccinia coronata avenae 12NC29; Puccinia coronata avenae 12SD80* [258]*; Puccinia graminis f. sp. tritici 21-0 haplotype A; Puccinia graminis f. sp. tritici 21-0 haplotype B; Puccinia graminis f. sp. tritici Ug99 haplotype A; Puccinia graminis f. sp. tritici Ug99 haplotype C* [259]*; Puccinia striiformis f. sp. tritici 104 E137 A*- [260]*; Puccinia striiformis f. sp. tritici PST-130* [261]*; Puccinia striiformis f. sp. tritici PST-78 v1.0; Puccinia triticina 1-1 BBBD Race 1* [262]*; Pycnoporus cinnabarinus BRFM 137* [263]*; Pycnoporus coccineus BRFM 310 v1.0; Pycnoporus puniceus CIRM-BRFM 1868 v1.0; Pycnoporus sanguineus BRFM 1264 v1.0; Ramaria rubella (R. acris) UT-36052-T v1.0* [264]*; Pyrenophora teres f. teres* [265]*; Pyrenophora tritici-repentis* [266]*; Pyronema confluens CBS100304* [267]*; Rhizoctonia solani AG-1 IB* [268]*; Rhizophagus irregularis A1 v1.0; Rhizophagus irregularis A4 v1.0; Rhizophagus irregularis A5 v1.0; Rhizophagus irregularis B3 v1.0; Rhizophagus irregularis C2 v1.0; Rhizophagus irregularis DAOM 197198 v2.0* [269]*; Rhizophagus irregularis DAOM 181602 v1.0* [270]*; Rhizopogon vesiculosus Smith; Rhizopogon vinicolor AM-OR11-026 v1.0* [271]*; Rhizopus delemar 99-880 from Broad* [272]*; Rhizopus microsporus ATCC11559 v1.0; Rhizopus microsporus var. microsporus ATCC52814 v1.0* [273]*; Rhizopus microsporus var. chinensis CCTCC M201021* [274]*; Rhodosporidium toruloides IFO0559_1; Rhodosporidium toruloides IFO0880 v2.0; Rhodosporidium toruloides IFO1236_1* [275]*; Rhodosporidium toruloides IFO0880 v4.0* [276]*; Rhodosporidium toruloides NP11* [277]*; Rhodotorula graminis strain WP1 v1.1* [278]*; Rhodotorula sp. JG-1b* [279]*; Rickenella fibula HBK330-10 v1.0* [280]*; Rickenella mellea v1.0 (SZMC22713;* [281]*; Rigidoporus microporus ED310 v1.0* [282]*; Rozella allomycis CSF55* [283]*; Saccharomyces arboricola H-6* [284]*; Saccharomyces cerevisiae M3707 Dikaryon; Saccharomyces cerevisiae M3836 v1.0; Saccharomyces cerevisiae M3837 v1.0; Saccharomyces cerevisiae M3838 v1.0; Saccharomyces cerevisiae M3839 v1.0; Arthroderma benhamiae CBS 112371; Trichophyton verrucosum HKI 0517* [285]*; Saccharomyces cerevisiae S288C* [286]*; Saksenaea vasiformis B4078* [287]*; Scheffersomyces stipitis NRRL Y-11545 v2.0* [288]*; Schizophyllum commune H4-8 v3.0* [289]*; Schizopora paradoxa KUC8140 v1.0* [290]*; Schizosaccharomyces cryophilus OY26; Schizosaccharomyces japonicus yFS275; Schizosaccharomyces octosporus yFS286* [291]*; Schizosaccharomyces pombe* [292]*; Sclerotinia* *sclerotiorum v1.0* [293]; *Serpula himantioides (S.lacrymans var shastensis) MUCL38935 v1.0* [294]; *Serpula lacrymans S7.3 v2.0; Serpula lacrymans S7.9 v2.0* [295]; *Smittium culicis GSMNP; Smittium culicis ID-206-W2; Smittium mucronatum ALG-7-W6; Zancudomyces culisetae COL-18-3* [296]; *Sodiomyces alkalinus v1.0* [297]; *Sphaerosporella brunnea Sb_GMNB300 v2.0* [298]; *Spizellomyces punctatus DAOM BR117* [299]; *Sporisorium reilianum SRZ2* [300]; *Stagonospora nodorum SN15 v2.0* [301]; *Stemphylium lycopersici CIDEFI-216* [302]; *Suillus brevipes Sb2 v2.0* [303]; *Talaromyces borbonicus CBS 141340* [304]; *Talaromyces marneffei ATCC 18224* [305]; *Taphrina deformans* [306]; *Thermomyces lanuginosus SSBP* [307]; *Tolypocladium inflatum NRRL 8044* [308]; *Trametes pubescens FBCC735* [309]; *Trichoderma arundinaceum IBT 40837; Trichoderma brevicompactum IBT40841* [310] *; Trichoderma asperellum CBS 433.97 v1.0; Trichoderma citrinoviride TUCIM 6016 v4.0; Trichoderma guizhouense NJAU 4742; Trichoderma harzianum CBS 226.95 v1.0; Trichoderma longibrachiatum ATCC 18648 v3.0* [311]; *Trichoderma asperellum TR356 v1.0; Trichoderma harzianum TR274 v1.0* [312]; *Trichoderma atrobrunneum ITEM 908* [313]; *Trichoderma atroviride v2.0; Trichoderma virens Gv29-8 v2.0* [314]; *Trichoderma hamatum GD12* [315]; *Trichoderma parareesei CBS 125925* [316]; *Trichoderma pleuroti TPhu1* [317]; *Trichoderma reesei QM6a* [318]; *Trichoderma reesei RUT C-30 v1.0* [319]; *Trichoderma reesei v2.0* [320]; *Trichosporon asahii var. asahii CBS 2479* [321]; *Trichosporon asahii var. asahii CBS 8904* [322]; *Trichosporon oleaginosus IBC0246 v1.0* [323]; *Tuber melanosporum Mel28 v1.2* [324]; *Ustilaginoidea virens* [325]; *Ustilago hordei Uh4857_4* [326]; *Ustilago maydis 521 v2.0* [327]; *Venturia inaequalis; Venturia pirina* [328]; *Verticillium alfalfae VaMs.102; Verticillium dahliae VdLs.17* [329]; *Volvariella volvacea V23* [330]; *Wallemia ichthyophaga EXF-994* [331]; *Wallemia mellicola v1.0* [332]; *Xylona heveae TC161 v1.0* [333]; *Yarrowia lipolytica CLIB89(W29)* [334]; *Yarrowia lipolytica FKP355 v1.0* [335]; *Yarrowia lipolytica PO1f v1.0; Yarrowia lipolytica YlCW001 v1.0* [336]; *Yarrowia lipolytica YB392 v1.0; Yarrowia lipolytica YB419 v1.0; Yarrowia lipolytica YB420 v1.0; Yarrowia lipolytica YB566 v1.0; Yarrowia lipolytica YB567 v1.0* [337]; *Zygosaccharomyces rouxii CBS732* [338]; *Zymoseptoria ardabiliae STIR04_1.1.1; Zymoseptoria pseudotritici STIR04_2.2.1* [339]; *Zymoseptoria brevis Zb18110* [340]; *Melampsora allii-populina 12AY07 v1.0; Melampsora americana R15-033-03 v1.0* (unpublished).

2.3. Protein sequence analysis and search for potential subcellular targeting.

The protein sequences were aligned using Clustal Omega [341] (https://www.ebi.ac.uk/Tools/msa/clustalo/) and manually checked. The predictions for subcellular localizations were done based on the assessment obtained from the TargetP [342] (http://www.cbs.dtu.dk/services/TargetP/), SignalP [343] (http://www.cbs.dtu.dk/services/SignalP/abstract.php), WolfPsort [344] (https://wolfpsort.hgc.jp/) and ESLpred [345] (http://crdd.osdd.net/raghava/eslpred/) software suites.

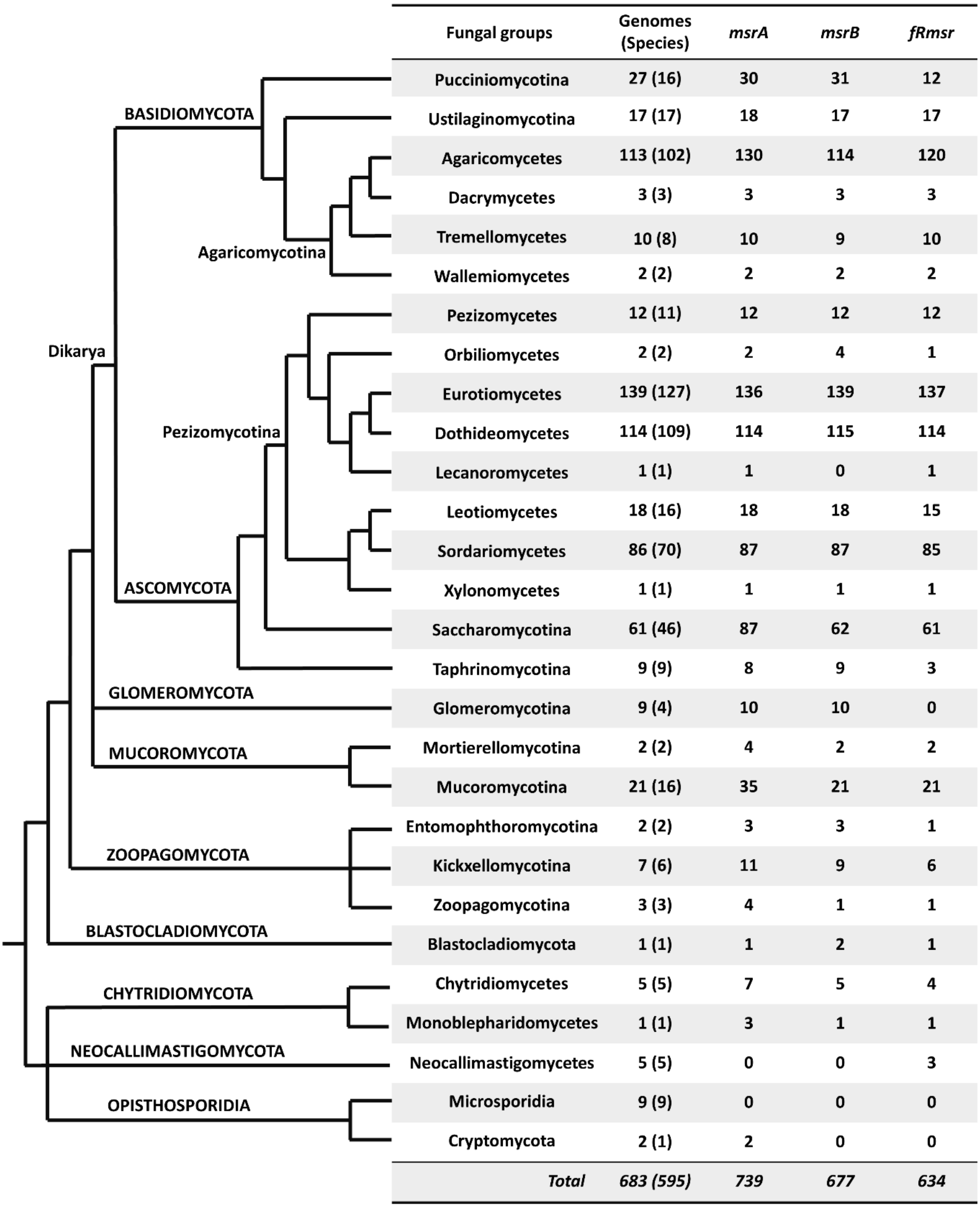
2.4. Phylogenomic analyses and search for horizontal gene transfers.

For each type of Msr, we built a multiple sequence alignment with all the identified sequences using MAFFT version v7.429 [346]. Each alignment was trimmed to remove poorly aligned regions using trimAl 1.2 [347] and manually inspected for the conservation of the catalytic residues. A phylogenetic tree was constructed for each type of Msr using RAxML Master Pthread [348] version 8.2.12 (PROTGAMMAWAG model and 500 bootstraps). The phylogenetic tree was represented using iTOL (https://itol.embl.de/) [349]. To investigate potential horizontal gene transfers, the non-canonical Msr sequences along with the sequences whose phylogeny did not fit the species phylogeny were retrieved. Those sequences were used as BLAST queries against the non-redundant protein sequence (nr) database of NCBI (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastp&PAGE_TYPE=BlastSearch&LINK_LOC=blasthome) and the best 100 hits were retrieved. The fungal sequences for which protein accessions outside the fungal kingdom were identified among the highest identity scores were in further used as BLAST queries against nr excluding the taxon Fungi (taxid: 4751) and the 25 hits with the highest identity scores were retrieved. In parallel, the same fungal genes were used as queries against the fungal nr database and the 50 hits with the highest identity scores were retrieved, excluding those with 100% identity with the query. The retrieved fungal hits were manually inspected to exclude incomplete sequences. Non-canonical sequences (lacking canonical active site or of abnormal length) were also removed to avoid potential inconsistencies and long branches in the phylogenetic trees. Finally, for each type of Msr, a phylogenetic tree was constructed that included the candidate fungal gene for horizontal gene transfer, plus 25 non-fungal and 25 fungal sequences with the highest identity scores. For each candidate to HGT, the numbers of exons, the GC content of the coding sequence and the GC content at the third positions of the codons were calculated using the gene structures and coding sequences downloaded from the MycoCosm database. The GC content on the third positions of the codons were calculated only for the coding sequences starting with ATG. All calculations were made using Microsoft® Excel® version 2101.

3. Results

3.1. MsrA, MsrB and fRMsr are largely conserved across the fungal kingdom.

Currently, around 136,000 species of fungi are known and classified into 9 phyla (**Figure 1**) [37,350]. Together, the Ascomycota and the Basidiomycota form the subkingdom Dikarya, which regroups more than 97 % of all described fungal species (~84,000 species and ~48,000 species, respectively) [350]. Each phylum contains three monophyletic subphyla (Pucciniomycotina, Ustilaginomycotina and Agaricomycotina for the Basidiomycota, and Taphrinomycotina, Saccharomycotina and Pezizomycotina for the Ascomycota). The other seven phyla are described as *'early-diverging fungi'* [350] (**Fig. 1, Data S1**). Using the *S. cerevisiae* MsrA, MsrB and fRMsr protein sequences as queries, we used the BLASTP and TBLASTN software suites to search for *msr* genes in 683 available genomes in the MycoCosm database [50]. The selected genomes were from 595 species that spanned the kingdom Fungi (**Fig. 1, Data S1**), including 65% Ascomycota species, 25% Basidiomycota species and 10% early-diverging fungi. We found that the very great majority of these genomes contained one gene coding for a MsrA and one coding for a MsrB (**Fig. 1, Data S1**), indicating that most fungi have a simple Msr system dedicated to protein oxidation repair, similarly to most other known organisms [24,26]. Most interestingly, we found that a *fRmsr* gene was present in almost all the analyzed genomes (**Fig. 1, Data S1**). The distribution of *fRmsr* across the fungal kingdom clearly showed that the presence of fRMsr is not limited to bacteria and unicellular eukaryotes as previously described [7–9]. Of note, the search for homologs of the bacterial molybdoenzymes able to reduce MetO gave no significant hits (**data not shown**).



Fungal groups	Genomes (Species)	*msrA*	*msrB*	*fRmsr*
Pucciniomycotina	27 (16)	30	31	12
Ustilaginomycotina	17 (17)	18	17	17
Agaricomycetes	113 (102)	130	114	120
Dacrymycetes	3 (3)	3	3	3
Tremellomycetes	10 (8)	10	9	10
Wallemiomycetes	2 (2)	2	2	2
Pezizomycetes	12 (11)	12	12	12
Orbiliomycetes	2 (2)	2	4	1
Eurotiomycetes	139 (127)	136	139	137
Dothideomycetes	114 (109)	114	115	114
Lecanoromycetes	1 (1)	1	0	1
Leotiomycetes	18 (16)	18	18	15
Sordariomycetes	86 (70)	87	87	85
Xylonomycetes	1 (1)	1	1	1
Saccharomycotina	61 (46)	87	62	61
Taphrinomycotina	9 (9)	8	9	3
Glomeromycotina	9 (4)	10	10	0
Mortierellomycotina	2 (2)	4	2	2
Mucoromycotina	21 (16)	35	21	21
Entomophthoromycotina	2 (2)	3	3	1
Kickxellomycotina	7 (6)	11	9	6
Zoopagomycotina	3 (3)	4	1	1
Blastocladiomycota	1 (1)	1	2	1
Chytridiomycetes	5 (5)	7	5	4
Monoblepharidomycetes	1 (1)	3	1	1
Neocallimastigomycetes	5 (5)	0	0	3
Microsporidia	9 (9)	0	0	0
Cryptomycota	2 (1)	2	0	0
Total	*683 (595)*	*739*	*677*	*634*

Figure 1. Numbers of *msrA, msrB* and *fRmsr* genes identified in fungal genomes. The simplified phylogenetic tree was built according to [37,350]. The precise number of *msr* genes per genome is available in **Data S1**.

We observed some variations in the numbers of *msr* genes in several genomes. We found 72 genomes, corresponding to 57 species, that had more than one copy of at least one *msr* gene (**Table 1, Data S1-4**). We found 42 genomes having two copies of *msrA* and 17 having three or four copies (**Table 1, Data S1-2**). The highest number of *msrA* copies was 4 in the genome of the Agaricomycetes *Crucibulum laeve* CBS 166.37 and *Dendrothele bispora* CBS 962.96 (**Table 1**). In the case of *msrB*, only 14 genomes had two gene copies (**Data S1, S3**), and the Kickxellomycotina *Smittium culicis* GSMNP was the only genome with three copies (**Table 1**). For *fRmsr*, only six genomes had two copies (**Data S1, S4**), and the Agaricomycetes *Ramaria rubella* (*R. acris*) UT-36052-T and *Coprinellus micaceus* FP101781 had 4 and 3 gene copies, respectively (**Table 1**). Overall, for the three types of Msr, the fungal species having more than one copy were sporadically spread across the fungal kingdom (**Table 1, Data S1-4**), indicating that gene enrichment was not a characteristic of a specific fungal group.

Table 1. Fungi with five or six Msr genes.

Genome	MsrA	MsrB	fRMsr	Lifestyle	Nb. Genes (Genome size in Mbp)	Ref.
Agaricomycetes						
Crucibulum laeve CBS 166.37 v1.0	4	1	1	Aerobic (saprotroph)	14,218 (44)	[351]
Dendrothele bispora CBS 962.96 v1.0	4	1	1		33,645 (131)	[351]
Tulasnella calospora AL13/4D v1.0	3	1	1		19,659 (62)	[352]
Ramaria rubella (R. acris) UT-36052-T v1.0	1	1	4		14,207 (62)	[353]
Coprinellus micaceus FP101781 v2.0	1	1	3		23,559 (77)	[351]
Dothideomycetes						
Hortaea werneckii EXF-2000 M0 v1.0	2	2	2	Aerobic	15,748 (50)	[167]
Sordariomycetes						
Coniochaeta sp. 2T2.1 v1.0	2	2	2	Aerobic (phytopathogen)	24,735 (74)	[121]
Saccharomycotina						
Pichia kudriavzevii CBS573	3	1	1	Aerobic	5,140 (11)	[354]
Yarrowia lipolytica (strain CLIB122)	3	1	1		6,447 (21)	[355]
Yarrowia lipolytica CLIB89*(W29)*	3	1	1		7,919 (21)	[356]
Yarrowia lipolytica FKP355 v1.0	3	1	1		6,858 (20)	[357]
Yarrowia lipolytica PO1f v1.0	3	1	1		6,798 (20)	[358]
Yarrowia lipolytica YB392 v1.0	3	1	1		6,750 (20)	[359]
Yarrowia lipolytica YB419 v1.0	3	1	1		6,751 (20)	[359]
Yarrowia lipolytica YB420 v1.0	3	1	1		6,772 (20)	[359]
Yarrowia lipolytica YB566 v1.0	3	1	1		6,764 (20)	[359]
Yarrowia lipolytica YB567 v1.0	3	1	1		6,776 (20)	[359]
Yarrowia lipolytica YlCW001 v1.0	3	1	1		6,800 (20)	[358]
Mucoromycotina						
Absidia repens NRRL 1336 v1.0	3	1	1	Aerobic (saprotroph)	14 919 (47)	[360]
Rhizopus microsporus ATCC11559 v1.0	2	1	2	Aerobic (phytopathogen)	11,135 (24)	[273]
Rhizopus microsporus var. *chinensis* CCTCC M201021	2	1	2		17,676 (46)	[274]
Kickxellomycotina						
Smittium mucronatum ALG-7-W6	3	1	1	Anaerobic (insect gut)	8 247 (102)	[361]
Smittium culicis GSMNP	2	3	1		12 166 (77)	[361]
Monoblepharidomycetes						
Gonapodya prolifera v1.0	3	1	1	Aerobic (aquatic)	13 902 (49)	[362]

Also, we found only 74 genomes (58 species), in which one or more Msr types were absent (**Table 2**). Among them, the nine Microsporidia species, two Neocallimastigomycetes species (out of five species analyzed) and one Taphrinomycotina species, *Pneumocystis jirovecii* (out of eight species analyzed) lacked all three Msr types. These species are either obligate intracellular parasites (Microsporidia and *Pneumocystis jirovecii*) or live in the anaerobic conditions of the animal gut (*Piromyces finnis* and *Piromyces* sp. E2) [37,363]. Interestingly, the three other Neocallimastigomycetes species (*Anaeromyces robustus, Neocallimastix californiae* G1 and *Orpinomyces* sp.), also living in anaerobic conditions [350], do not possess MsrA nor MsrB but have a gene coding for a fRMsr (**Table 2**). Our results show that, additionally to *Encephalitozoon cuniculi*, previously identified as the unique eukaryote lacking both MsrA and MsrB [24], 14 other fungal species are devoid of any protein-bound MetO reduction enzyme (**Table 2**). Furthermore, we found six species lacking *msrA* but having a *msrB* and a *fRmsr* gene (**Table 2**). These are the agaricomycete *Moniliophthora perniciosa*, the eurotiomycetes *Cladophialophora immunda*, *Penicillium coprophilum* and *Penicillium flavigenum*, the sordiariomycete *Magnaporthiopsis poae* and the saccharomycotina *Saturnispora dispora*. To our knowledge, they constitute the first species, over all kingdoms, described to have only a MsrB to reduce and repair oxidized proteins, as none was found so far in genome surveys [24,26]. Of note, we did not find fungal species having only a MsrB, as these six species also possessed a fRMsr (**Table 2**). We found that the five species *Trichosporon asahii* (Tremellomycetes), *Clohesyomyces aquaticus* (Dothideomycetes), *Cladonia grayi* (Lecaronomycetes) and *Piptocephalis cylindrospora* (Zoopagomycotina) possessed a MsrA and a fRMsr but lacked a MsrB and that the Zoopagomycotina *Syncephalis pseudoplumigaleata* had a MsrA only (**Table 2**). Finally, we found only 27 species having both a MsrA and a MsrB but lacking a fRMsr (**Table 2**). These species were sporadically dispersed among the fungal kingdom, but three groups stood out as remarkable: the Glomeromycotina, for which none of the four species analyzed had a fRMsr, the Taphrinomycotina for which six species out of eight analyzed (including the four *Schizosaccharomyces* species analyzed) were devoid of fRMsr, and the Pucciniomycotina for which all the *Melampsora* and *Puccinia* species analyzed here lacked a fRMsr (**Table 2**).

Altogether, these results showed that the great majority of fungi possess one gene coding for each protein-repairing Msr type (i.e. MsrA and MsrB), as well as one gene coding for the free MetO reductase fRMsr.

Table 2. Fungal genomes lacking one or more Msr types.

Genome	MsrA	MsrB	fRMsr	Lifestyle	Nb. Genes (Genome size in Mbp)	Ref.
Microsporidia						
Antonospora locustae HM-2013	N	N	N	Intracellular parasite of metazoans	2,606 (6)	[364]
Encephalitozoon cuniculi GB-M1	N	N	N		1,996 (2)	[365]
Encephalitozoon hellem ATCC 50504	N	N	N		1,847 (2)	[366]
Encephalitozoon intestinalis ATCC 50506	N	N	N		1,833 (2)	[367]
Encephalitozoon romaleae SJ-2008	N	N	N		1,831 (2)	[366]
Enterocytozoon bieneusi H348	N	N	N		3,632 (4)	[368]
Mitosporidium daphniae UGP3	N	N	N		3,330 (6)	[369]
Nematocida parisii ERTm1	N	N	N		2,661 (4)	[370]
Nosema ceranae BRL01	N	N	N		2,060 (8)	[371]
Neocallimastigomycetes						
Piromyces finnis v3.0	N	N	N	Anaerobic (ruminant gut)	10,992 (56)	[372]
Piromyces sp. E2 v1.0	N	N	N		14,648 (71)	[372]
Anaeromyces robustus v1.0	N	N	Y		12,832 (72)	[372]
Neocallimastix californiae G1 v1.0	N	N	Y		20,219 (193)	[372]
Orpinomyces sp.	N	N	Y		18,936 (101)	[373]
Taphrinomycotina						
Pneumocystis jirovecii	N	N	N	Intracellular parasite of metazoans	3,520 (8)	[374]
Neolecta irregularis DAH-1 v1.0	Y	Y	N	Aerobic	6,674 (15)	[375]
Schizosaccharomyces cryophilus OY26	Y	Y	N		5,180 (12)	[376]
Schizosaccharomyces japonicus yFS275	Y	Y	N		4,878 (12)	[376]
Schizosaccharomyces octosporus yFS286	Y	Y	N		4,986 (12)	[376]
Schizosaccharomyces pombe	Y	Y	N		5,134 (13)	[377]
Agaricomycetes						
Moniliophthora perniciosa FA553	N	Y	Y	Aerobic (phytopathogen)	13,560 (18)	[378]
Eurotiomycetes						
Penicillium coprophilum IBT 31321	N	Y	Y	Aerobic	8,999 (28)	[379]
Penicillium flavigenum IBT 14082	N	Y	Y		10,994 (33)	[379]
Penicillium polonicum IBT 4502	N	Y	Y		10,694 (32)	[379]
Aspergillus bombycis NRRL 26010	Y	Y	N		12,265 (37)	[380]
Aspergillus zonatus v1.0	Y	Y	N		9,886 (29)	[70]
Sordiariomycetes						
Magnaporthiopsis poae ATCC 64411	N	Y	Y	Aerobic (phytopathogen)	12,335 (40)	[381]
Pochonia chlamydosporia 170	Y	Y	N	Aerobic (animal pathogen)	14,204 (44)	[382]
Saccharomycotina						
Saturnispora dispora NRRL Y-1447	N	Y	Y	Aerobic	4,881 (10)	[383]
Tremellomycetes						
Trichosporon asahii var. *asahii* CBS 2479	Y	N	Y	Aerobic (human pathogen)	8,300 (24)	[384]
Trichosporon asahii var. *asahii* CBS 8904	Y	N	Y		8,507 (25)	[385]
Dothideomycetes						
Clohesyomyces aquaticus v1.0	Y	N	Y	Aerobic (saprotrophic)	15,810 (50)	[360]
Lecaronomycetes						
Cladonia grayi Cgr/DA2myc/ss v2.0	Y	N	Y	Aerobic (lichen)	11,389 (35)	[386]
Zoopagomycotina						
Piptocephalis cylindrospora RSA 2659 single-cell v3.0	Y	N	Y	Aerobic (mycoparasite)	4,301 (11)	[387]

Syncephalis pseudoplumigaleata Benny S71-1 single-cell v1.0	Y	N	N		6,123 (16)	[387]
Thamnocephalis sphaerospora RSA 1356 single-cell v1.0	Y	Y	N		6,857 (18)	[387]
Pucciniomycotina						
Melampsora allii-populina 12AY07 v1.0	Y	Y	N	Aerobic (phytopathogen)	23,089 (336)	-
Melampsora americana R15-033-03 v1.0	Y	Y	N		15,984 (112)	-
Melampsora larici-populina v2.0	Y	Y	N		19,550 (110)	[388]
Melampsora lini CH5	Y	Y	N		16,335 (190)	[389]
Puccinia coronata avenae 12NC29	Y	Y	N		28,270 (166)	[390]
Puccinia coronata avenae 12SD80	Y	Y	N		26,323 (150)	[390]
Puccinia graminis f. sp. *tritici* v2.0	Y	Y	N		15,979 (89)	[388]
Puccinia striiformis f. sp. *tritici* 104 E137 A-	Y	Y	N		30,249 (157)	[391]
Puccinia striiformis f. sp. *tritici* PST-130	Y	Y	N		18,021 (65)	[392]
Puccinia striiformis f. sp. *tritici* PST-78 v1.0	Y	Y	N		20,482 (117)	[393]
Puccinia triticina 1-1 BBBD Race 1	Y	Y	N		15,685 (135)	[393]
Leotiomycetes						
Blumeria graminis f. sp. *hordei* DH14	Y	Y	N	Aerobic (phytopathogen)	7,118 (125)	[394]
Blumeria graminis f. sp. *hordei* Race1	Y	Y	N		7,239 (116)	[394]
Blumeria graminis f. sp. *tritici* 96224	Y	Y	N		6,525 (159)	[395]
Glomeromycotina						
Gigaspora rosea v1.0	Y	Y	N	Aerobic (arbuscular mycorrhizal)	31,291 (568)	[396]
Rhizophagus cerebriforme DAOM 227022 v1.0	Y	Y	N		21,549 (137)	[396]
Rhizophagus diaphanus v1.0	Y	Y	N		23,252(129)	[396]
Rhizophagus irregularis A1 v1.0	Y	Y	N		26,659 (126)	[397]
Rhizophagus irregularis A4 v1.0	Y	Y	N		25,760 (138)	[397]
Rhizophagus irregularis A5 v1.0	Y	Y	N		26,585 (131)	[397]
Rhizophagus irregularis B3 v1.0	Y	Y	N		25,164 (125)	[397]
Rhizophagus irregularis C2 v1.0	Y	Y	N		26,756 (123)	[397]
Rhizophagus irregularis DAOM 197198 v2.0	Y	Y	N		26,183 (137)	[397]
Mucoromycotina						
Jimgerdemannia lactiflua OSC166217	Y	Y	N	Aerobic (ectomycorrhizal)	12,651 (180)	[362]
Lichtheimia corymbifera JMRC:FSU:9682	Y	Y	N	Aerobic (saprotrophic/ human pathogen)	13,404 (34)	[398]
Entomophthoromycotina						
Basidiobolus meristosporus CBS 931.73 v1.0	Y	Y	N	Aerobic (sapotrophic/animal pathogen)	16,111 (89)	[360]
Kickxellomycotina						
Dimargaris cristalligena RSA 468 single-cell v1.0	Y	Y	N	Aerobic (mycoparasite)	7,456 (31)	[387]
Chytridiomycetes						
Caulochytrium protostelioides ATCC 52028 v1.0	Y	Y	N	Aerobic (mycoparasite)	6,168 (22)	[387]

Y, presence of one or more genes coding for the Msr; N, absence of gene coding for the Msr.

3.2. Fungal Msrs globally retained canonical sequence features for activity.

Sequence analysis and enzymatic characterizations of MsrAs from several organisms showed that the catalytic residue is located within a G[C/U]FW motif, located in the N-terminal part of the protein [6,16,17,399,400]. The great majority of known MsrAs possess a catalytic Cys, whereas a few Sec-containing proteins are found in some insects, marine organisms and unicellular algae [25,400]. In canonical MsrAs, the resolving Cys, involved in the regeneration of the catalytic Cys, is located in the C-terminal part of the protein, althought the number and positions of resolving Cys vary [6,17,22,23]. To determine whether the fungal MsrAs share these properties, we analyzed the 709 full length MsrAs identified. These MsrAs ranged from 142 to 322 amino acids, and all of them were made of a single MsrA domain (**Data S2A**). The length differences were mostly due to the presence of N-terminal extensions of variable sizes, indicating the possible presence of signal peptides for protein distribution in subcellular compartments. We used several targeting prediction programs (see section 2.3) to evaluate the potential subcellular localization of the fungal MsrAs (**Data S2A**). Most MsrAs were predicted to be localized into the cytoplasm (45 %) or in the mitochondria (44 %) (**Fig. 2A, Data S2A**). The other sequences were predicted to be secreted (6%), to be localized in other compartments, or had no clearly assigned localization (6%) (**Fig. 2A, Data S2A**). The alignment of the primary sequences revealed that the great majority (~ 90 %) shared common features with the previously characterized *S. cerevisiae* MsrA [6,401] (**Fig. 3A, Data S2B**). The catalytic Cys (position 25 in the *S. cerevisiae* MsrA) was located in the conserved motif ^{24}GCFW^{27}. The Tyr^{64}, Glu^{76}, Asp^{111} and Tyr^{116} residues involved in substrate stabilization and catalysis [399], and the residues Gly^{47}, His^{100}, Gln^{108}, Gly^{113}, His^{163} and Tyr^{166} were also conserved. Finally, the Cys^{176}, previously identified as resolving Cys [6,401], was included in the ^{173}GYXC^{176} motif (**Fig. 3A, Data S2B**). Because of their predominance in all the fungal kingdom, we defined the fungal MsrAs having these properties as *'canonical'* sequences. The fungal MsrAs that did not match these sequence features were defined as *'non-canonical'* MsrAs (**Data S2A, C, D**). Particularly, we observed that in ~ 5 % of the identified sequences, the Phe^{26} residue in the ^{24}GCFW^{27} motif containing the catalytic Cys, was substituted by a Tyr. We also observed the replacement of Asp^{111} by an Asn residue in few sequences (~ 2 %) (**Data S2C**). Moreover, some variations were also observed for the resolving Cys (**Data S2C**). Fourteen sequences (~ 2 %) lacked the conserved ^{173}GYXC^{176} motif but possessed two to four Cys in a Q[C/S/K]X$_2$KX[C/N][C/X]XI[R/L]CYG motif, similar to poplar MsrAs [23]. Some other sequences possessed a Cys residue in the C-terminal region, but not in a GYXC motif, and others lacked any potential resolving Cys (**Data S2C**). Finally, a special case could be made for MsrAs from the early-diverging fungus *Gonapodya prolifera* (Monoblepharidomycetes). This fungus has three non-canonical MsrAs, two of which had the catalytic Cys replaced by a Sec [402]. Each had another Cys outside the conserved position of the resolving Cys in canonical fungal MsrAs. These two MsrA sequences had high similarity with the Sec-MsrAs from the bacterium *Alkaliphilus* *oremlandii* and the single-cell green alga *Chlamydomonas reinhardtii*, previously shown to use the Sec residue for the regeneration of their activity [400,403] (**Data S2D**).

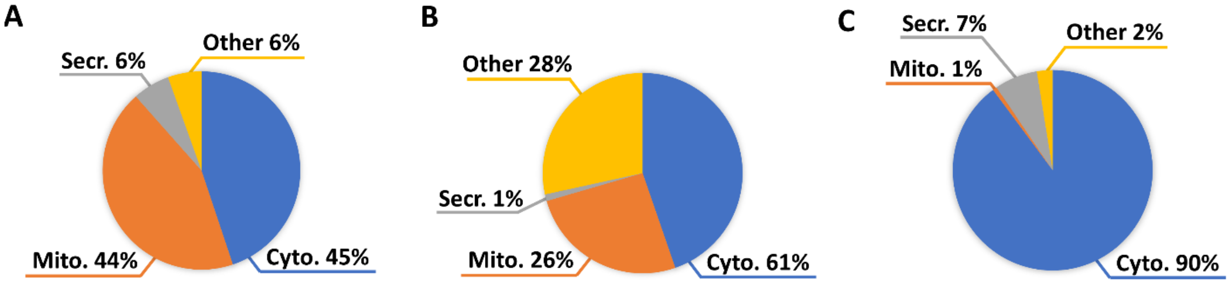


Figure 2. Potential subcellular targeting of fungal Msrs. The circle charts show the subcellular predictions for fungal MsrA (**A**), MsrB (**B**) and fRMsr (**C**), the proportion of proteins predicted to be localized in the cytosol ('*Cyto.*'), to be addressed to the mitochondria ('*Mito.*') or secreted ('*Secr.*'). The label *'Other'* indicates the proportion of proteins predicted to be addressed to other compartments or for which no consensus prediction was obtained.

In the case of MsrBs, previous biochemical characterizations demonstrated that the catalytic Cys is located in a RXCXN motif in the C-terminal part of the protein [16,21,404–407]. Mammals express a Sec-containing form in which the Asp is replaced by a Phe [404]. The resolving Cys is generally located in a CGWP motif present in the N-terminal part of the protein [21,406]. In the case of mammalian MsrBs, one or two resolving Cys, located in the N-terminal extremity of the protein, can be involved in the regeneration process [404,408]. Of note, most MsrBs possess two CX_2C clusters coordinating a structural Zn atom [409]. Here, we analyzed the 651 complete fungal MsrB protein sequences. The fungal MsrBs consisted of a single domain and ranged in length from 95 to 289 amino acids (**Data S3A**). Most of the variations in size were due to the presence of an N-terminal extension potentially involved in subcellular targeting. The majority of fungal MsrBs were predicted to be addressed to the cytosol (61 %) (**Fig. 2B, Data S3A**). The other proteins were either predicted to be localized in the mitochondria (26 %), secreted (1 %), targeted to another compartment, or were not clearly predicted to be addressed to a subcellular compartment (28 %) (**Fig. 2B, Data S3A**). Almost all fungal MsrBs (> 99 %) possessed the features of the *S. cerevisiae* enzyme (**Fig. 3B, Data S3B**): i) the two CX_2C motifs involved in the coordination of a Zn atom, ii) the resolving Cys^{97} (according to *S. cerevisiae* MsrB residue numbering) included in a ^{97}CGW^{99} motif, iii) the conserved His^{134} and His^{136} implicated in substrate binding, together with Arg^{155} and Asn^{159} [16,405], and iv) the catalytic Cys^{157} located in the ^{155}RXCXN^{159} motif. The Gly^{98}, Gly^{135}, Val^{137}, Phe^{138} and Glu^{141} residues were also conserved in all these canonical fungal MsrBs (**Fig. 3B, Data S3B**). Only four sequences (< 1 %), from the orbiliomycetes *Arthrobotrys oligospora* and *Monacrosporium haptotylum*, the taphrinomycotina *Protomyces lactucaedebilis* and the chytridiomycete *Blyttiomyces helices*, presented remarkable differences in primary sequence features (**Data S3C**). These MsrBs lacked the resolving Cys at position 97, which was substituted by a Ser or a Thr, like plant and human orthologs that use an unusual regeneration process [20,21,408]. Finally, another unusual feature was found in the MsrB from the taphrinomycotina *Protomyces lactucaedebilis*, with the location of the catalytic Cys in an HYCIN motif, instead of the typical RXCXN motif (**Data S3C**). Interestingly, searching in the NCBI nr database, we found 50 sequences, mainly from poorly characterized bacteria and archaea, that possessed this unusual motif (**Data S3D**). Considering His and Arg have similar physicochemical properties, we anticipate such non-canonical MsrBs might have conserved a catalytic activity.

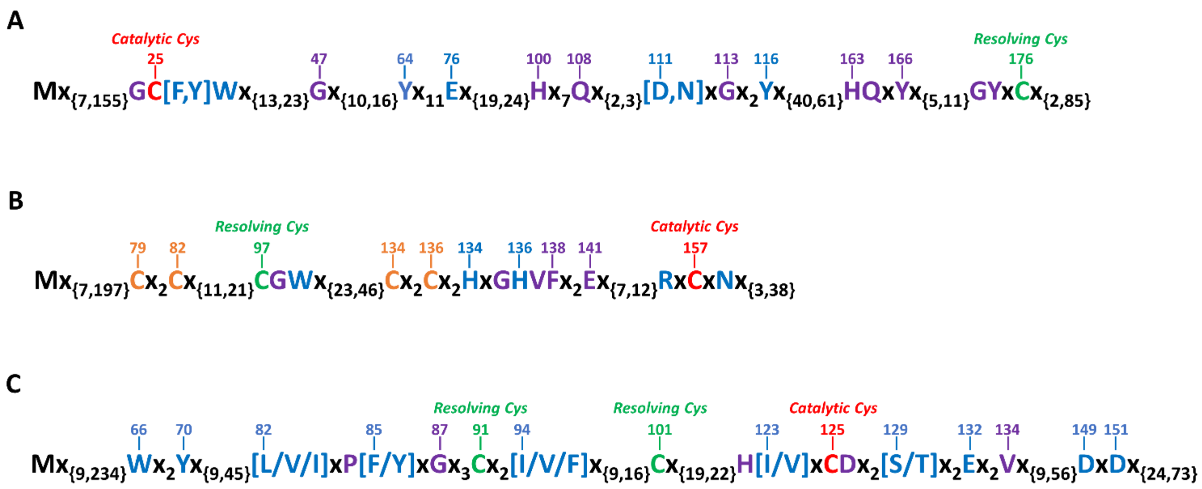


Figure 3. Protein sequence characteristics of canonical fungal Msrs. In this representation of canonical MsrAs (**A**), MsrBs, (**B**) and fRMsrs (**C**), the catalytic Cys (in *red*), the resolving Cys (in *green*) and the residues previously shown to be involved in catalysis and/or substrate binding (in *blue*) are shown. The residues in *purple* are conserved in all canonical fungal Msrs. In **B**, the Cys residues labeled in *orange* correspond to Zn binding residues. The numberings are based on *S. cerevisiae* MsrA (**A**), MsrB (**B**) and fRMsr (**C**).

Very few fRMsrs have been characterized so far. However, sequence comparison studies and biochemical characterizations indicated that the catalytic Cys is located in the HIAC motif situated in the middle of the protein sequence and that the two resolving Cys are located ~30 and ~40 amino acids upstream in the N-terminal direction [7–9]. The 589 full length fRMsr sequences analyzed here had a single fRMsr domain. Their length varied from 77 to 394 amino acids, with variations in the size of the N-terminal extension (**Data S4A**). Most of the proteins (90 %) were predicted to be localized in the cytoplasm (**Fig. 2C, Data S4A**). A few proteins were predicted to be secreted (7 %), targeted to the mitochondria (1 %), to other compartments or had no reliable prediction for subcellular targeting (2 %) (**Fig. 2C, Data S4A**). Similar to MsrAs and MsrBs, fRMsrs showed a strong conservation of the sequence features. Almost all (> 99 %) sequences possessed the catalytic Cys^{125} included in a ^{122}H[I/V]XCD^{126} motif and the resolving Cys in positions 91 and 101 (according to the *S. cerevisiae* fRMsr residue numbering) (**Fig. 3C, Data S4B**). We also observed the strict conservation of Trp^{66}, Tyr^{70}, Glu^{132}, Asp^{149} and Asp^{151}, previously shown to be involved in substrate binding and catalysis. Other important residues involved in substrate binding and catalysis [7] were also conserved or substituted by residues with similar properties in positions 82, 85, 94, 123, 129 and 132. The Pro^{84}, Gly^{87}, His^{122} and Val^{134} were also strictly conserved in these canonical fungal fRMsrs (**Fig. 3C, Data S4B**). Only three fRMsr sequences from the Agaricomycetes *Scleroderma citrinum*, *Dendrothele bispora* and *Pisolithus tinctorius* presented non-canonical characteristics. The first two lacked the potential resolving Cys^{101} and may be still able to reduce the free MetO, but in the latest, the catalytic Cys^{125} was substituted by an Arg, likely precluding catalytic activity (**Data S4C**).

Altogether, these results uncover few proteins with non-canonical sequence features, but principally showed that for each Msr type, the residues involved in catalysis are globally conserved throughout the fungal kingdom.

3.3. The phylogenetic analysis of fungal Msrs revealed horizontal gene transfers from bacteria.

The phylogenetic relationship of fungal MsrAs globally matched the expected clustering for early-diverging fungi, Ascomycota and Basidiomycota sequences (**Fig. S1-3**). However, a few Ascomycota MsrA sequences clustered with Basidiomycota sequences (indicated by an asterisk on **Fig. S1**). We also noticed the clustering of all the MsrB sequences from Pucciniomycotina (Basidiomycetes) species with Ascomycota sequences (**Fig. S2**). Strikingly, the MsrB sequences from early-diverging fungi did not group in a single cluster but were interspersed in clusters containing Basidiomycota or Ascomycota sequences (**Fig. S2**). For fRMsrs, we observed three distinct clusters containing the protein sequences from Basidiomycota, Ascomycota and early-diverging fungi, respectively (**Fig. S3**). However, two sequences from early-diverging fungi were included in the cluster containing the Ascomycota sequences (**Fig. S3**). Altogether, these results showed that the phylogeny of Msrs was globally congruent with the phylogeny of the species, except for a few protein sequences.

Several discrepancies suggested that some Msrs could have arisen from horizontal gene transfer. These discrepancies were: i) the positioning in phylogenetic clusters not reflecting the phylogeny of the species from which they were isolated (**Fig. S1-3**), ii) the presence of non-canonical sequence features (**Data S2-4**), and iii) the presence of *fRmsr* genes in the genome of three strictly anaerobic neocallimastigomycetes, whereas other organisms from the same phylum had no *msr* genes (**Table 2**).

To evaluate the possibility of horizontal gene transfers, we selected all Msr sequences (67 MsrAs, 48 MsrBs and 8 fRMsrs) with one or more of these discrepancies and searched for their closest putative homologs by BLASTP search in all organisms recorded in the NCBI nr database. We discarded all the sequences for which the closest homologs were found in other fungal taxa. Indeed, because of the strong conservation of the protein sequences, it would be difficult to ascertain the occurrence of fungus-to-fungus horizontal gene transfers. We retrieved 17 MsrA, three MsrB and three fRMsr protein sequences for further analysis (**Fig. 4-6**). For each type of Msr, we used the selected protein sequences, together with the respective 25 sequences with the highest identity score from fungi on the one hand and from non-fungal organisms on the other hand for phylogenetic analyses (**Fig. 4-6**). The phylogenetic trees highlighted two MsrA, three MsrB and three fRMsr sequences, among the selected candidates, clustering with bacterial and amoeba homologs (**Fig. 4-6, Table 3**). Moreover, we identified two additional fungal fRMsrs, not included in our primary data set, which clustered with bacterial proteins (**Fig. 6, Table 3**). Except for two MsrBs from Orbiliomycetes (Ascomycota), all these Msr sequences were from early-diverging fungi (**Table 3**). Interestingly, in the cases of MsrA and MsrB, they were all from organisms having another gene coding for a canonical enzyme in their genomes (**Data S1-3**).

For MsrAs, a potential horizontal gene transfer was observed for the two selenocysteine-containing enzymes from *Gonapodya prolifera* (**Table 3**). Very interestingly, their closest homolog was also a selenocysteine-containing MsrA, from the bacteria *Alkaliphilus oremlandii*. Bacteria from the genus *Alkaliphilus* are found in sediments and ponds [410], and *Gonapodya prolifera* occurs on fruits submerged into ponds [411]. The presence of both organisms in a same ecological niche could have favored the horizontal gene transfer. The similarity between the two *Gonapodya prolifera* Sec-MsrA suggested they arose from one horizontal gene transfer event followed by a gene duplication (**Fig. 4, Fig. S4**).

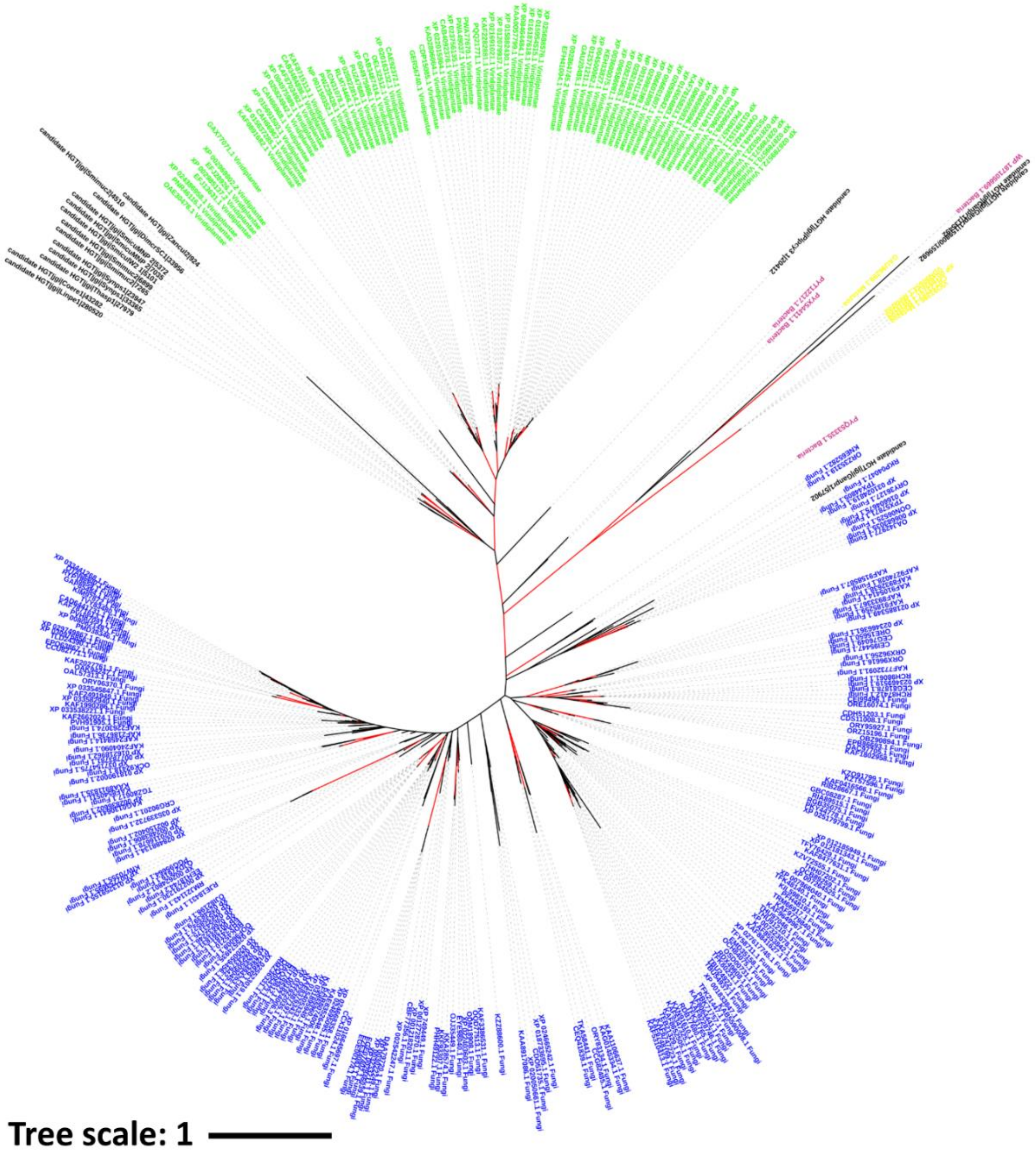


Figure 4. Phylogenetic analysis of MsrA candidates to horizontal gene transfer. The fungal MsrAs tested for horizontal gene transfer (in *black*) are from the following fungal genomes (protein accessions in brackets): *Piptocephalis cylindrospora* RSA 2659 single-cell v3.0 (20412); *Syncephalis pseudoplumigaleata* Benny S71-1 single-cell v1.0 (33365; 23947); *Thamnocephalis sphaerospora* RSA 1356 single-cell v1.0 (27979); *Coemansia reversa* NRRL 1564 v1.0 (43282); *Dimargaris cristalligena* RSA 468 single-cell v1.0 (33956); *Linderina pennispora* ATCC 12442 v1.0 (280520); *Smittium culicis* GSMNP (5372; 7035); *Smittium culicis* ID-206-W2 (5101; 8129); *Smittium mucronatum* ALG-7-W6 (4510; 6899; 7265); *Zancudomyces culisetae* COL-18-3 (924) and *Gonapodya prolifera* v1.0 (135492; 159800/159692; 57902). The MsrA sequences from fungi, plants, amoeba and bacteria are in *blue*, *green*, *yellow* and *purple*, respectively. The phylogenetic tree was built with RAxML v. 8.2 [348] and represented using iTOL (https://itol.embl.de/) [412]. The branches with bootstrap values over 70 are in *red*.

Table 3. Potential horizontal *msr* gene transfers from bacteria to fungi

Genome	Candidate gene				Mean of all genes from the scaffold			Organisms with the closest Msr homolog
	Protein accession (Scaffold number)	**Nb. of exons**	**GC content (%)**	**GC third base (%)**	**Nb. of exons**	**GC content (%)**	**GC third base (%)**	
MsrA								
Monoblepharidomycetes								
Gonapodya prolifera v1.0	135492[a] (36)	3	56.4	61.3	5.7 ± 4.8	56.5 ± 3.4	65.2 ± 8.5	*Alkaliphilus oremlandii* OhILAs
Gonapodya prolifera v1.0	159800/ 159692[a] (105)	4	58.9	69.6	5.8 ± 3.8	57.3 ± 4.2	67.4 ± 8.2	
MsrB								
Orbiliomycetes								
Arthrobotrys oligospora ATCC 24927	9001 (00170)	1	55.6	56.5	3.0 ± 2.3	48.0 ± 2.4	48.0 ± 4.6	*Sphingomonas* bacterium
Monacrosporium haptotylum CBS 200.50	10089 (00497)	1	55.8	58.0	4.3 ± 4.3	49.0 ± 2.7	52.9 ± 5.3	*Sphingomonas* bacterium
Taphrinomycotina								
Protomyces lactucaedebilis 12-1054 v1.0	391028 (3)	1	54.9	52.1	1.6 ± 1.0	52.6 ± 1.9	54.4 ± 5.9	*Calothrix parasitica*
fRMsr								
Neocallimastigomycetes								
Anaeromyces robustus v1.0	328892[b] (243)	1	30.1	14.8	4.2 ± 4.5	26.3 ± 5.0	11.8 ± 3.3	*Pseudobutyrivibrio* sp. LB2011
Neocallimastix californiae G1 v1.0	697339 (7)	1	27.5	9.8	4.6 ± 4.4	28.8 ± 4.4	16.7 ± 5.4	*Erysipelotrichaceae* bacterium
Orpinomyces sp.	1191427 (d_7180000085738)	1	34.8	22.5	3.0 ± 2.9[d]	27.2 ± 5.4[d]	16.0 ± 7.8[d]	*Pseudobutyrivibrio ruminis*
Piromyces sp.	AWI66787.1[b,c]	1	31.3	9.9	n.d.	33.2 ± 5.7	23.3 ± 11.1	*Pseudobutyrivibrio ruminis*
Mucoromycotina								
Mortierella sp. GBA39	KAF9144191.1[c] (77)	1	55.2	62.4	1.4 ± 0.7	57.1 ± 3.5	71.3 ± 6.0	*Paenibacillus rhizosphaerae*

[a] For both *Gonapodya prolifera* selenocysteine-containing MsrAs, the MycoCosm accession numbers presented here refer to only a part of the proteins. Their reconstructed complete gene structures are presented in **Fig. S4**.

[b] The horizontal gene transfers of *Anaeromyces robustus* and *Piromyces* sp. *fRmsr* genes have been shown recently [413].

[c] The protein accessions are from NCBI (https://www.ncbi.nlm.nih.gov/protein).

[d] The positions of *Orpinomyces* sp. genes on the scaffolds are not publically available. The calculations were made on the complete genome.

n.d, not determined.

In the case of MsrBs, the three selected sequences clustered with bacterial MsrBs (**Fig. 5**). The two MsrBs from the Orbiliomycetes species *Arthrobotrys oligospora* and *Monacrosporium haptotylum* had MsrBs from *Sphingomonas* bacteria as closest homologs. Both fungi trap nematodes in soil [197], and sphingomonads have been isolated from many different land and water habitats [414], indicating that the co-occurrence in the same habitat of a sphingomonad donor and a common ancestor of *A. oligospora* and *M. haptotylum* is plausible, which could have allowed horizontal gene transfers. Another potential horizontal gene transfer for MsrB was identified, from a donor cyanobacterium related to the marine *Calothrix parasitica* to the plant pathogen fission yeast *Protomyces lactucaedebilis* (Taphrinomycotina) (**Table 3**). In this case, the ecology of the extant candidate donor and acceptor do not support the co-occurrence of both organisms in a same ecological niche.

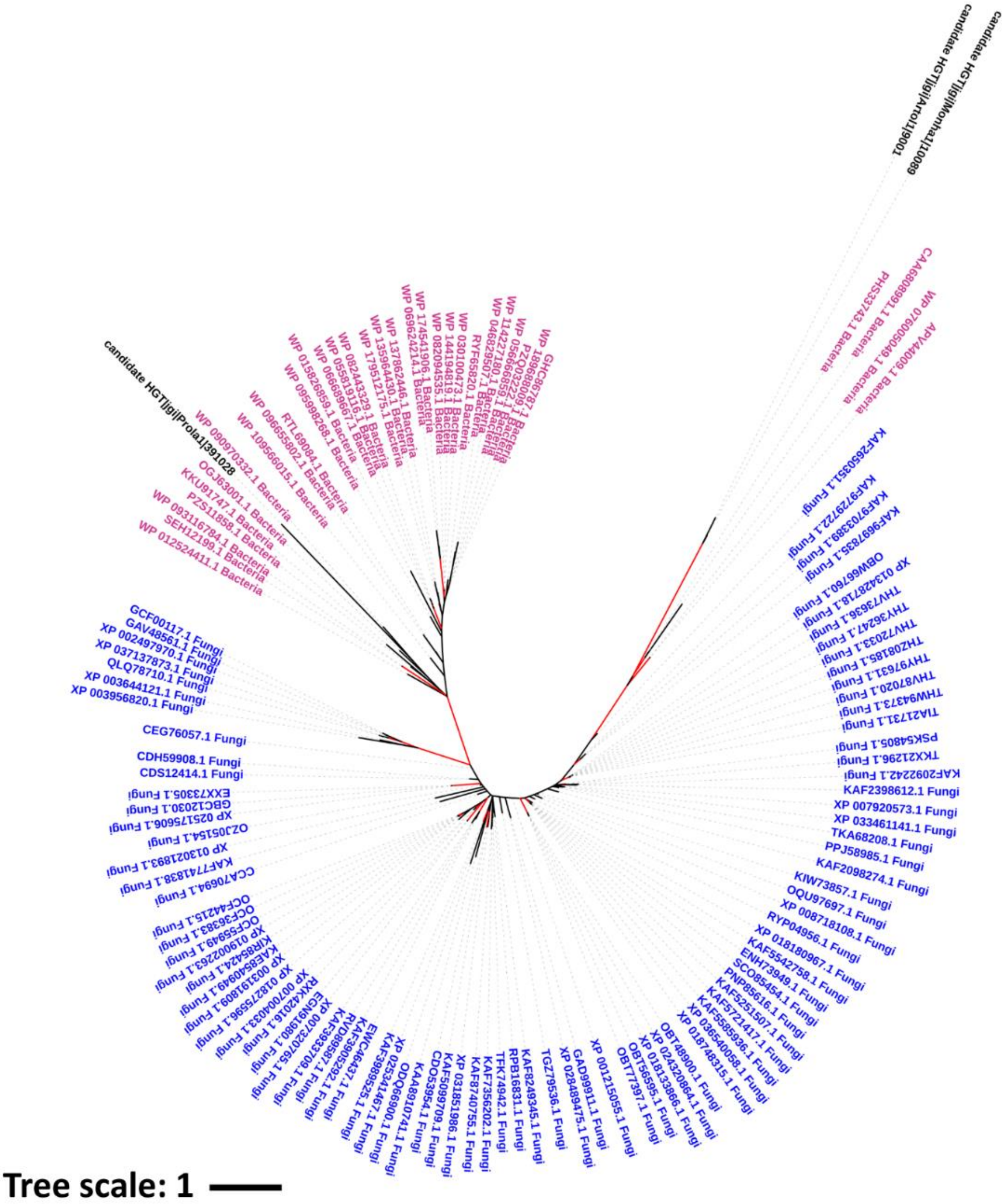


Figure 5. Phylogenetic analysis of MsrB candidates to horizontal gene transfer. The fungal MsrBs tested for horizontal gene transfer (in *black*) are from the following genomes (protein accessions in brackets): *Arthrobotrys oligospora* ATCC 24927 (9001); *Monacrosporium haptotylum* CBS 200.50 (10089) and *Protomyces lactucaedebilis* 12-1054 v1.0 (391028). The MsrBs sequences from fungi and bacteria are in *blue* and *purple*, respectively. The phylogenetic tree was built with RAxML v. 8.2 [348] and represented using iTOL (https://itol.embl.de/) [412]. The branches with bootstrap values over 70 are in *red*.

The three fRMsrs we selected as candidates to horizontal gene transfer were from the neocallimastigomycetes species *Anaeromyces robustus*, *Neocallimastix californiae* and *Orpinomyces sp.* (**Table 3**). In our phylogenetic analysis, they clustered with sequences of bacteria from the phylum Firmicutes which, similarly to neocallimastigomycetes, live in the gut of ruminants (**Fig. 6**). Interestingly, two other fungal fRMsr sequences, one from *Piromyces* sp. and one from *Mortierella* sp. GBA39, were also present in the same cluster. These two sequences were omitted from our genomic search because of the absence of the corresponding genomes in the MycoCosm database. Of note, the horizontal transfer of *fRmsr* genes from Firmicutes to neocallimastigomycetes has been shown recently for *Anaeromyces robustus* and *Piromyces* sp. [413]. Altogether, these results strongly argue for the fact that the presence of *fRmsr* in the genomes of these anaerobic fungi arose from horizontal gene transfers from Firmicutes (**Table 3**).

In addition to the phylogenetic method, we performed a parametric analysis of the numbers of exons, the overall GC contents of their coding sequence (CDS), and the GC contents of the third position of each codon to identify potential bias as supporting arguments of horizontal gene transfer (**Table 3**). The comparison of these parameters with those of the other genes included in the same genomic scaffold were shown as potential indicators of horizontal gene transfers [415]. Excepted for the two *Gonapodya prolifera msrA* genes, which had no distinguishable values from the other genes included in their scaffolds, all other genes coding MsrBs or fRMsrs, had extreme values for at least two of the three parameters considered (**Table 3**). First of all, all these eight genes were made of a single exon, like bacterial genes. The global GC content of *Arthrobotrys oligospora* and *Monacrosporium haptotylum msrB* genes coding sequences were the highest of all those included in their scaffold. Similarly, the global GC content of *Protomyces lactucaedebilis msrB*, *Anaeromyces robustus fRmsr* and *Orpinomyces* sp. *fRmsr* were among the highest (**Table 3**). In the cases of *fRmsrs* from *Neocallimastix californiae, Piromyces* sp. and *Mortierella* sp., the GC contents of the third base of the codons were among the lowest by comparison with the other genes present in the scaffold. Noticeably, we also observed a lower GC content at the third position of the codons in the *fRmsr* gene from *Piromyces* sp., for which the acquisition via HGT was previously shown [412].

Altogether, these analyses showed that the phylogeny of fungal Msrs globally matched the phylogeny of the fungi, in accordance with vertical inheritance of the genes from bacterial ancestors [8,9,24,26]. However, a few horizontal gene transfer events occurred in each Msr family, that contributed to the distribution of Msr genes in extant species.

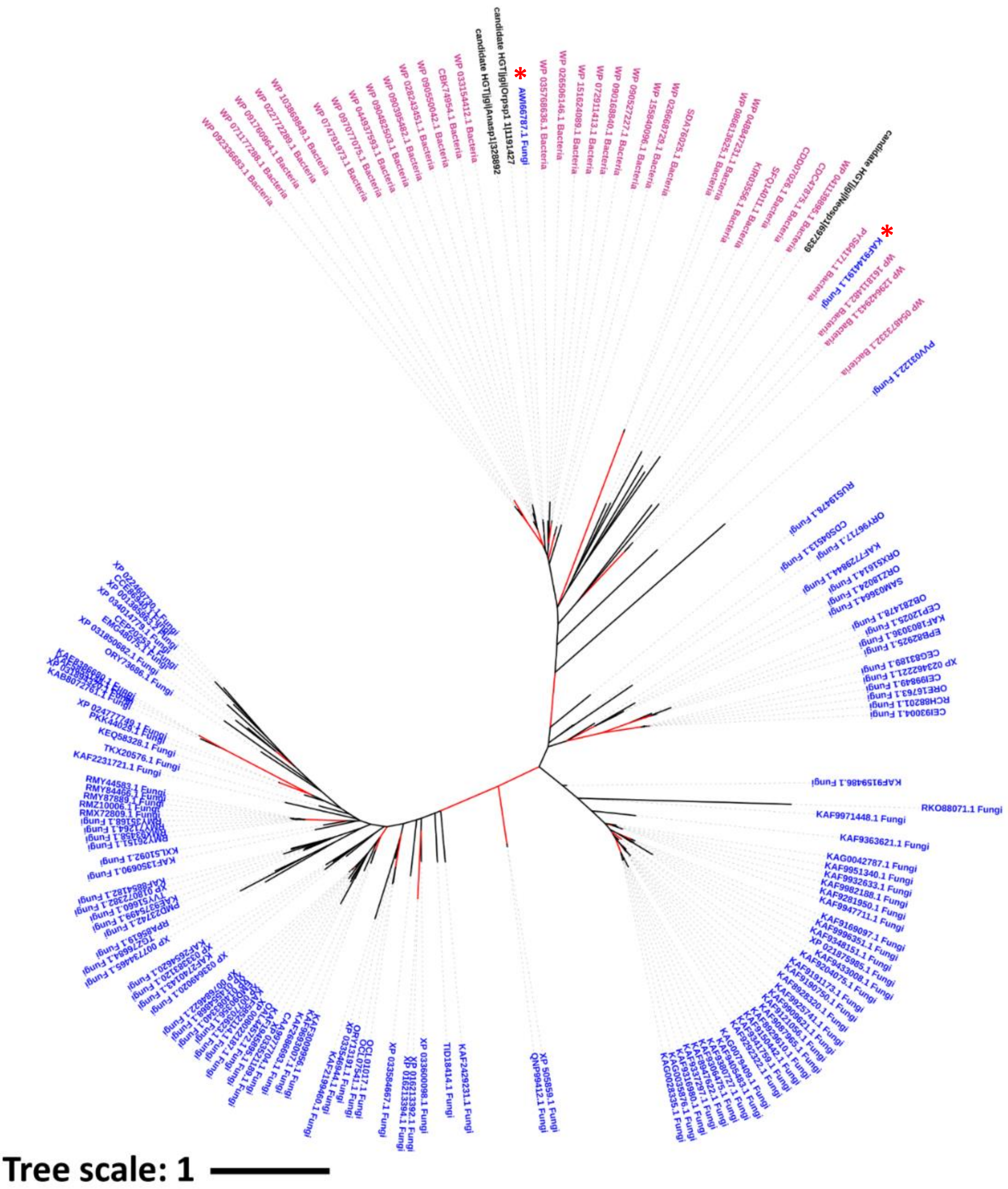


Figure 6. Phylogenetic analysis of fRMsr candidates to horizontal gene transfer. The fungal fRMsrs tested for horizontal gene transfer (in *black*) are from the following genomes (protein accessions are in brackets): *Anaeromyces robustus* v1.0 (328892); *Neocallimastix californiae* G1 v1.0 (697339) and *Orpinomyces sp* (1191427). The fRMsrs sequences from fungi and bacteria are in *blue* and *purple*, respectively. *Red* stars indicate *fRmsr* genes possibly acquired by horizontal gene transfer, which were not identified in our genomics search but found as homologs of the selected fungal fRMsr candidates. The phylogenetic tree was built with RAxML v 8.2 [348] and represented using iTOL (https://itol.embl.de/) [412]. The branches with bootstrap values over 70 are in *red*.

4. Discussion

This global genomic search for *msr* genes in nearly 700 fungal genomes covering the fungal kingdom showed that most fungi contain one gene coding for each thiol-oxidoreductase type, i.e., MsrA, MsrB and fRMsr. The phylogenetic analyses and inspection of protein sequence features revealed that Msrs from each type are globally strongly conserved across the fungal kingdom. This is consistent with the prokaryotic origin of these genes. Yet, the identification of *fRmsr* genes in almost all genomes across the fungal kingdom was surprising. Indeed, no *fRmsr* genes were identified so far from multicellular eukaryotes [8]. Very likely, the most obvious reason was the smaller number of eukaryotic genomes considered (i.e. 160), and the smaller number of fungal genomes available at the time of the previous study [8,50]. Because the number of sequenced genomes has increased dramatically in the last years, we took the opportunity of this study to reevaluate the presence of *fRmsr* genes in other multicellular eukaryotes. We searched for *fRmsr* genes in the plant and animal genomes available in the nr database of NCBI by BLAST search and found only a handful of multicellular eukaryotes apparently possessing a gene coding for a fRMsr (**Table S1**). These organisms, a plant and a few insects, are not phylogenetically related, indicating that the gene is not conserved in their lineage. This highlights the prevalence of *fRmsr* genes in the fungal kingdom, as opposite to their extremely low occurrence in other multicellular eukaryotes. What would be the advantage for the fungi to produce fRMsr whereas other multicellular organisms do not? An obvious possibility would be to protect the intracellular free Met during exposure to oxidative constraints as it was shown for *S. cerevisiae* [8]. Another possibility would be to allow the reduction of the free MetO coming from the external environment or after the degradation of proteins assimilated by the fungi and its use in protein synthesis and in sulfur metabolism. Combined with MsrA, the presence of fRMsr could virtually allow to reduce the complete pool of MetO coming from the external environment. This hypothesis arose from the observation of the presence of *fRmsr* genes in four Neocallimastigomycetes species that lacked MsrA and MsrB. Living in the anaerobic environment of ruminant gut, the fungi very likely do not suffer oxidative stress and the fRMsr could reduce the MetO coming from the animal’s food. Interestingly, the *fRmsr* genes in these Neocallimastigomycetes have been probably acquired through horizontal gene transfer, reinforcing the idea that a fRMsr would provide a selective advantage in an environment unlikely to generate oxidative constraints.

We found few variations in the numbers of gene copies of each type of Msr, with only 74 genomes lacking one gene, and 72 genomes with an extra copy of at least one *msr* gene. In both cases, it roughly corresponded to 10 percent of the analyzed genomes. Our study revealed the absence of both MsrA and MsrB in 15 species of fungi, twelve of these being also devoid of fRMsr. The lack of all Msr appears to be related to the fungal lifestyles, since it concerned the nine Microsporidia, and the *Pneumocystis jirovecii* species, which live as intracellular parasites of metazoans. These 10 species have small genomes with reduced numbers of genes, from 1,831 for *Encephalitozoon romaleae* SJ-2008 to

3,632 for *Enterocytozoon bieneusi* H348, as compared to the average ~12,200 genes for the fungal genomes considered in this study. It has been proposed that the intracellular lifestyle allowed for genome compaction and gene loss, making the fungi highly dependent on the infected cell for numerous biochemical pathways [27]. Our results suggest the fungi could also rely on the host detoxication system for the protection against oxidative constraints and limitation of protein oxidation. The absence of Msr was also observed in Neocallimastigomycetes, which live in the anaerobic environment of ruminant gut, where the protection of proteins from oxidative damage is likely not crucial. This hypothesis is reinforced by the fact that the numbers of genes in Neocallimastigomycetes genomes is above the average of the analyzed fungi (~15,500) and thus, the loss of *msr* genes was not due to a global genome compaction, but potentially due to the lack of selection pressure. Besides these species, for which the lack of Msr is consistent with the lifestyle, we also identified 12 other species for which *msrA* or *msrB* genes were absent from the genomes. As they are very likely living in aerobic conditions and are probably exposed to protein oxidation, the lack of MsrA or MsrB is surprising and we cannot exclude that the missing genes are due to incomplete genome sequencing. On the other hand, most of the 37 analyzed genomes from Glomeromycotina, Pucciniomycotina (*Melampsora* and *Puccinia*) and Taphrinomycotina (*Schizosaccharomyces*) species lacked the fRMsr. These fungi may have lost the capacity to reduce the free Met-*R*-O, as it has been shown for mammals [416], or the MsrB might have significant activity on the free Met-*R*-O, as suggested for plants [417].

Regarding the presence of supernumerary copies of *msr* genes in few genomes, it seems not to be related to the phylogeny, nor to the numbers of genes per genome, as the genomes of fungi having two copies or more of one *msr* gene contain an average number of ~12,700 genes, similar to the average number of genes in the considered genomes (~12,200). In most cases, the presence of several copies was due to gene duplications, as indicated by the close phylogenetic relationships of paralogous proteins and the conservation of canonical features. However, in few fungi, the presence of extra copies was due to horizontal gene transfers, like for *msrsA* genes in *Gonapodya prolifera*, and *msrB* genes in *Arthrobotrys oligospora*, *Monacrosporium haptotylum* and *Protomyces lactucaedebilis*. Together with the horizontal transfers of *fRmsr* genes in *Neocallimastigomycetes*, most of these events were strongly supported by the phylogeny and parametric values as well as by shared ecological niches for donor bacteria and recipient fungi. The case of *Gonapodya prolifera msrA* was remarkably interesting as it illustrated a prokaryote-to-eukaryote transfer of a selenoprotein gene. If such a transfer was observed from bacteria to archaea [418], to our knowledge, the bacteria-to-eukaryote transfer of a selenoprotein gene has never been described. As this fungus possesses an eukaryotic selenocysteine insertion machinery [402], we hypothesize that the transferred prokaryotic *msrA* gene was compatible with the eukaryotic machinery, or that it was modified after the transfer to allow proper Sec insertion. In all cases, the presence of several Msr gene copies could allow a beneficial increase in gene dosage or, alternatively, different spatial and temporal expression profiles during the life cycle of the fungi through distinct transcriptional activities. It could also allow different subcellular targeting as shown for plant Msrs [419]. Indeed, in 23 fungal genomes, out of the 59 having more than one *msrA* gene, the MsrAs were predicted to be addressed to different subcellular compartments. Similarly, MsrBs from 7 genomes out of the 15 with more than one gene were predicted to be addressed to different cellular compartments. Conversely, all the multicopy fRMsrs were predicted to be cytoplasmic. Our results indicate that, as experimentally demonstrated for yeast [39], most fungi might not have the ability to reduce the two diastereomers of protein-bound MetO in each subcellular compartment, suggesting variations in protein oxidation in the different cellular compartments. Another interesting aspect is the presence of potentially secreted Msrs in few fungal species, mostly from the Ascomycota genera *Aspergillus* and *Penicillium*. Although it remains to be demonstrated experimentally, the presence of Msrs in the extracellular environment of the fungal cells could help to protect from oxidation the numerous secreted carbohydrate-active enzymes ('*CAZymes*') and other enzymes used by saprotrophic and pathogen fungi to degrade plant cell walls or insect chitins [231].

Finally, we observed that most MsrAs, MsrBs and fRMsrs had conserved canonical features, but we also highlighted potentially interesting discrepancies. For the three types of Msrs, a few sequences lacked the resolving Cys at conserved positions and might use alternative Cys residues for the regeneration of their activity, whereas others possessed only the catalytic Cys and might be regenerated by the direct reduction of the sulfenic acid formed after MetO reduction, as shown for Msrs from other organisms [20,408]. The presence of Sec in two *Gonapodya prolifera* MsrAs might confer them a catalytic advantage, similarly to other Sec-MsrAs [400]. We also observed that ~5% of fungal MsrAs harbor a GCYW motif containing the catalytic Cys, where the Tyr residue replaces the Phe residue of the canonical GCFW motif. To our knowledge, no MsrA with such motif has been described to date. Because of the similarity between Phe and Tyr physicochemical properties, this substitution should not prevent the catalysis, but it could induce a change in substrate specificity, as demonstrated for the *E. coli* MsrA. Indeed, direct evolution assays showed that the substitution of the Phe by a Leu conferred to the enzyme the capacity to efficiently reduce alkyl-aryl sulfoxides [420]. Similarly, the atypical HYCIN motif of the *Protomyces lactucaedebilis* MsrB could modify the enzyme substrate specificity. The substitution of residues around the catalytic Cys of Msrs could affect the specificity for oxidized protein substrates or free MetO, but also potentially confer to the enzymes the ability to reduce other molecules such as the oxidized thioether-containing metabolites involved in sulfur metabolism (e.g S-adenosyl homocysteine, methylthio-ribose…) [421]. It would be interesting to evaluate the catalytic properties of these atypical Msrs on various sulfoxide-containing substrates.

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Declaration of competing interest.

None.

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