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

3

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5

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9

10 **Running title:** Methionine sulfoxide reductases in fungi

11

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

14

15 **Highlights:**

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

21

22 **Abstract**

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

41

## 42 1. Introduction

43 Life in the presence of dioxygen necessarily exposes the biological systems to oxidant  
44 molecules. Due to its high reactivity, dioxygen can be converted to reactive oxygen species (ROS),  
45 which play key roles in physiological and pathological contexts through redox modifications of  
46 macromolecules [1]. Met, either as a free amino acid or as a residue included in a protein, can be  
47 oxidized into Met sulfoxide (MetO) by the addition of an oxygen atom to the sulfur of the lateral  
48 chain. MetO exists as diastereomer *R* or *S* (Met-*R*-O and Met-*S*-O, respectively) [2], and can be  
49 reduced back to Met by the action of oxidoreductases called methionine sulfoxide reductases (Msr).  
50 The two main types are the (seleno)thiol-containing MsrA and MsrB, which display strict  
51 stereoselectivities toward the *S*- and the *R*-diastereomer of MetO, respectively [3–5]. Whereas MsrA  
52 reduces free MetO and protein-bound MetO with similar catalytic efficiencies, MsrB generally only  
53 reduces efficiently the protein-bound MetO [6]. Another enzyme, fRMsr (free methionine-(*R*-  
54 sulfoxide reductase) specifically reduces the free form of Met-*R*-O [7–9]. Some bacteria also possess  
55 several molybdoenzymes that reduce exclusively the free MetO [10,11] or both the free and protein-  
56 bound MetO [12–15]. Despite the lack of sequence and structure similarities, MsrA, MsrB and fRMsr  
57 generally catalyze the reduction of MetO using a similar 3-steps-mechanism [9,16] : i) a ‘*catalytic*’  
58 Cys (or, less frequently, a selenocysteine, Sec) reduces the target MetO and is converted into a sulfenic  
59 (or selenic) acid [17], ii) an internal ‘*resolving*’ Cys reduces it through the formation of an  
60 intramolecular disulfide bond, and finally iii) the oxidized Msr is regenerated through disulfide  
61 exchange with a thioredoxin [18]. Variations of this mechanism exist, with some Msrs devoid of any  
62 resolving Cys, in which the sulfenic acid is directly reduced by an external reducer [19–21].  
63 Alternatively, in other Msrs, a disulfide exchange occurs with a second internal resolving Cys before  
64 regeneration by the thioredoxin [7,22,23]. Genome mining analyses indicated that *msrA* and *msrB*  
65 genes originated from early prokaryotes and are now present in all organisms across the tree of life,  
66 with few exceptions [24–26]. Most organisms have few *msr* genes, generally one of each type [24–  
67 26], but this number is generally higher in plants (e.g. up to 5 *msrA* and 9 *msrB* genes in *Arabidopsis*  
68 *thaliana* [25]). Moreover, some bacteria encode a bifunctional MsrA/MsrB fusion and some others  
69 lack a MsrB, but no organism of any kind was so far described with only a MsrB [24,26]. Finally, only  
70 very few organisms do not possess any *msr* gene at all, such as a few endosymbiotic or obligatory  
71 parasitic bacteria and some archaea [24,26]. fRMsr were so far only reported in bacteria and a few  
72 unicellular eukaryotes [7–9]. Most interestingly, the only eukaryote for which the absence of *msr* gene  
73 was observed is the fungus *Encephalitozoon cuniculi*, a microsporidium having a remarkably reduced  
74 genome (~2.5 Mb) and living as intracellular parasite of mammals [24,27]. The conservation of  
75 typical MsrAs and MsrBs in almost all known organisms argues for the critical role of MetO reduction  
76 in cellular metabolism, and numerous studies showed that Msrs are involved in the protection against  
77 oxidative stress and the regulation of protein functions. Schematically, Msr protective roles against

78 oxidative injuries occur through two main functions: i) the repair of oxidized proteins, and ii) an  
79 antioxidant function through ROS scavenging by cyclic Met oxidation and reduction. Moreover, the  
80 reversible Met oxidation was shown to act as a post-translational modification responsible for the  
81 activation of enzymes and transcription factors or the regulation of protein-protein interactions [28–  
82 30]. The role of fRMsr has been far less studied, but it is suspected to have an antioxidant function by  
83 reducing free MetO and maintaining the pool of Met available for protein synthesis and for the  
84 production of sulfur-containing metabolites [8,31]. Overall, these functions were well established in  
85 animals, bacteria and plants, and have recently been reviewed [32–36].

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

109 In this study, we searched for *msr* genes in about 700 fungal genomes. We show that the great  
110 majority of fungi have one *msrA* and one *msrB* genes. Moreover, we identified *fRmsr* genes in almost  
111 all the fungi we analyzed and thereby demonstrate that the enzyme is conserved in these multicellular  
112 eukaryotes. Finally, using a phylogenetic analysis and a close inspection of the sequence features, we

113 identified fungal Msrs with unusual sequence characteristics and uncovered horizontal gene transfers  
114 from bacteria to fungi.

## 115 **2. Material and methods**

### 116 **2.1. Search for Msr homologs in fungi.**

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

123

### 124 **2.2. List of all explored fungal genomes.**

125 *Aaosphaeria arxii* CBS 175.79 v1.0; *Amniculicola lignicola* CBS 123094 v1.0; *Ampelomyces*  
126 *quisqualis* HMLAC05119 v1.0; *Aplosporella prunicola* CBS 121.167 v1.0; *Aulographum hederiae*  
127 v2.0; *Bimuria novae-zelandiae* CBS 107.79 v1.0; *Byssothecium circinans* CBS 675.92 v1.0;  
128 *Cercospora zae-maydis* v1.0; *Clathrospora elyanae* CBS 161.51 v1.0; *Cucurbitaria berberidis* CBS  
129 394.84 v1.0; *Decorospora gaudefroyi* v1.0; *Delitschia confertaspera* ATCC 74209 v1.0; *Delphinella*  
130 *strobiligena* CBS 735.71 v1.0; *Didymella exigua* CBS 183.55 v1.0; *Dissoconium aciculare* v1.0;  
131 *Dothidotthia symphoricarpi* v1.0; *Elsinoe ampelina* CECT 20119 v1.0; *Eremomyces bilateralis* CBS  
132 781.70 v1.0; *Hortaea acidophila* CBS 113389 v1.0; *Karstenula rhodostoma* CBS 690.94 v1.0;  
133 *Lentithecium fluviatile* v1.0; *Lindgomyces ingoldianus* ATCC 200398 v1.0; *Lineolata rhizophorae*  
134 ATCC 16933 v1.0; *Lizonia empirigonia* CBS 542.76 v1.0; *Lophiostoma macrostomum* v1.0;  
135 *Lophiotrema nucula* CBS 627.86 v1.0; *Lophium mytilinum* CBS 269.34 v1.0; *Macroventuria*  
136 *anomochaeta* CBS 525.71 v1.0; *Massarina eburnea* CBS 473.64 v1.0; *Massariosphaeria phaeospora*  
137 CBS 611.86 v1.0; *Melanomma pulvis-pyrius* v1.0; *Microthyrium microscopicum* CBS 115976 v1.0;  
138 *Myriangium duriaei* CBS 260.36 v1.0; *Mytilinidion resinicola* CBS 304.34 v1.0; *Ophiobolus*  
139 *disseminans* CBS 113818 v1.0; *Patellaria atrata* v1.0; *Phoma tracheiphila* IPT5 v1.0; *Piedraia hortae*  
140 CBS 480.64 v1.1; *Pleomassaria siparia* v1.0; *Polychaeton citri* v1.0; *Polyplosphaeria fusca* CBS  
141 125425 v1.0; *Pseudovirgaria hyperparasitica* CBS 121739 v1.0; *Rhizodiscina lignyota* CBS 133067  
142 v1.0; *Saccharata proteae* CBS 121410 v1.0; *Setomelanomma holmii* CBS 110217 v1.0; *Sporormia*  
143 *fimetaria* v1.0; *Teratosphaeria nubilosa* CBS 116005 v1.0; *Tothia fuscilla* CBS 130266 v1.0;  
144 *Trematosphaeria pertusa* CBS 122368 v1.0; *Trichodelitschia bisporula* CBS 262.69 v1.0; *Verruculina*  
145 *enalia* CBS 304.66 v1.0; *Viridothelium virens* v1.0; *Westerdykella ornata* CBS 379.55 v1.0;  
146 *Zasmidium cellare* ATCC 36951 v1.0; *Zopfia rhizophila* v1.0 [51]; *Acaromyces ingoldii* MCA 4198

147 v1.0; *Ceraceosorus guamensis* MCA 4658 v1.0; *Jaminaea* sp. MCA 5214 v1.0; *Meira miltonrushii*  
148 MCA 3882 v1.0; *Pseudomicrostroma glucosiphilum* gen et sp. nov. MCA 4718 v1.0; *Testicularia*  
149 *cyperi* MCA 3645 v1.0; *Tilletiopsis washingtonensis* MCA 4186 v1.0; *Violaceomyces palustris* SA  
150 807 v1.0 [52]; *Acidomyces richmondensis* BFW; *Acidomyces richmondensis* BFW [53]; *Acremonium*  
151 *chrysogenum* ATCC 11550 [54]; *Agaricus bisporus* var *bisporus* (H97) v2.0; *Agaricus bisporus* var.  
152 *burnettii* JB137-S8; *Gigaspora rosea* v1.0; *Rhizophagus cerebriforme* DAOM 227022 v1.0;  
153 *Rhizophagus diaphanus* v1.0 [55]; *Amanita muscaria* Koide v1.0; *Gymnopus luxurians* v1.0;  
154 *Hebeloma cylindrosporum* h7 v2.0; *Hydnomerulius pinastri* v2.0; *Hypholoma sublateralitium* v1.0;  
155 *Laccaria amethystina* LaAM-08-1 v2.0; *Paxillus adelphus* Ve08.2h10 v2.0; *Paxillus involutus* ATCC  
156 200175 v1.0; *Piloderma croceum* F 1598 v1.0; *Pisolithus microcarpus* 441 v1.0; *Pisolithus tinctorius*  
157 Marx 270 v1.0; *Plicaturopsis crispa* v1.0; *Scleroderma citrinum* Foug A v1.0; *Sebacina vermifera*  
158 MAFF 305830 v1.0; *Sphaerobolus stellatus* v1.0; *Suillus luteus* UH-Slu-Lm8-n1 v3.0; *Tulasnella*  
159 *calospora* AL13/4D v1.0; *Oidiodendron maius* Zn v1.0 [56]; *Amanita thiersii* Skay4041 v1.0 [57];  
160 *Ambrosiozyma philentoma* NRRL Y-7523; *Candida boidinii* NRRL Y-2332; *Citeromyces matritensis*  
161 NRRL Y-2407; *Nakazawaea wickerhamii* NRRL Y-2563; *Peterozyma xylosa* NRRL Y-12939;  
162 *Saccharomyces capsularis* NRRL Y-17639; *Saturnispora dispota* NRRL Y-1447 [58];  
163 *Amorphotheca resinae* v1.0; *Meliniomyces bicolor* E v2.0; *Meliniomyces variabilis* F v1.0;  
164 *Rhizoscyphus ericae* UAMH 7357 v1.0 [59]; *Anaeromyces robustus* v1.0; *Neocallimastix californiae*  
165 G1 v1.0; *Piromyces finnis* v3.0; *Piromyces* sp. E2 v1.0 [60]; *Antonospora locustae* HM-2013 [61];  
166 *Armillaria cepistipes* B5; *Armillaria gallica* 21-2 v1.0; *Armillaria ostoyae* C18/9; *Armillaria solidipes*  
167 28-4 v1.0 [62]; *Armillaria mellea* DSM 3731 [63]; *Arthrotrichum oligospora* ATCC 24927 [64];  
168 *Ascobolus immersus* RN42 v1.0; *Choiromyces venosus* 120613-1 v1.0; *Morchella importuna*  
169 CCBAS932 v1.0; *Terfezia boudieri* ATCC MYA-4762 v1.1; *Tuber aestivum* var. *urcinatum* v1.0;  
170 *Tuber borchii* Tbo3840 v1.0; *Tuber magnatum* v1.0 [65]; *Ascochyta rabiei* ArDII [66]; *Ascocoryne*  
171 *sarcoides* NRRL50072 [67]; *Ascodesmis nigricans* CBS 389.68 v1.0 [68]; *Aspergillus aculeatinus*  
172 CBS 121060 v1.0; *Aspergillus brunneoviolaceus* CBS 621.78 v1.0; *Aspergillus costaricensis* CBS  
173 115574 v1.0; *Aspergillus ellipticus* CBS 707.79 v1.0; *Aspergillus eucalypticola* CBS 122712 v1.0;  
174 *Aspergillus fijiensis* CBS 313.89 v1.0; *Aspergillus heteromorphus* CBS 117.55 v1.0; *Aspergillus*  
175 *homomorphus* CBS 101889 v1.0; *Aspergillus ibericus* CBS 121593 v1.0; *Aspergillus indologenus*  
176 CBS 114.80 v1.0; *Aspergillus japonicus* CBS 114.51 v1.0; *Aspergillus neoniger* CBS 115656 v1.0;  
177 *Aspergillus niger* (*lacticoffeatus*) CBS 101883 v1.0; *Aspergillus niger* (*phoenicis* Corda) Thom ATCC  
178 13157 v1.0; *Aspergillus niger* NRRL3; *Aspergillus niger* van Tieghem ATCC 13496 v1.0; *Aspergillus*  
179 *piperis* CBS 112811 v1.0; *Aspergillus saccharolyticus* JOP 1030-1 v1.0; *Aspergillus*  
180 *sclerotii-carbonarius* CBS 121057 v1.0; *Aspergillus sclerotioniger* CBS115572 v1.0; *Aspergillus*  
181 *uvarum* CBS 121591 v1.0; *Aspergillus vadensis* CBS 113365 v1.0; *Aspergillus violaceofuscus* CBS  
182 115571 v1.0; *Aspergillus welwitschiae* CBS139.54b v1.0 [69]; *Aspergillus aculeatus* ATCC16872  
183 v1.1; *Aspergillus brasiliensis* v1.0; *Aspergillus carbonarius* ITEM 5010 v3; *Aspergillus glaucus* v1.0;

184 *Aspergillus luchuensis* CBS 106.47 v1.0; *Aspergillus sydowii* CBS 593.65 v1.0; *Aspergillus*  
185 *tubingensis* v1.0; *Aspergillus versicolor* v1.0; *Aspergillus wentii* v1.0; *Aspergillus zonatus* v1.0;  
186 *Penicillium chrysogenum* v1.0 [70]; *Aspergillus bombycis* NRRL 26010 [71]; *Aspergillus calidoustus*  
187 [72]; *Aspergillus campestris* IBT 28561 v1.0; *Aspergillus candidus* CBS 102.13 v1.0; *Aspergillus*  
188 *novofumigatus* IBT 16806 v1.0; *Aspergillus ochraceoroseus* IBT 24754 v1.0; *Aspergillus steynii* IBT  
189 23096 v1.0; *Aspergillus taichungensis* IBT 19404 v1.0; *Aspergillus albertensis* v1.0; *Aspergillus*  
190 *alliaceus* CBS 536.65 v1.0; *Aspergillus arachidicola* v1.0; *Aspergillus avenaceus* IBT 18842 v1.0;  
191 *Aspergillus bertholletius* IBT 29228 v1.0; *Aspergillus caelatus* CBS 763.97 v1.0; *Aspergillus*  
192 *coremiiiformis* CBS 553.77 v1.0; *Aspergillus leporis* CBS 151.66 v1.0; *Aspergillus minisclerotigenes*  
193 CBS 117635 v1.0; *Aspergillus nomius* IBT 12657 v1.0; *Aspergillus novoparasiticus* CBS 126849  
194 v1.0; *Aspergillus parasiticus* CBS 117618 v1.0; *Aspergillus parvisclerotigenus* CBS 121.62 v1.0;  
195 *Aspergillus pseudocaelatus* CBS 117616 v1.0; *Aspergillus pseudonomius* CBS 119388 v1.0;  
196 *Aspergillus pseudotamarii* CBS 117625 v1.0; *Aspergillus sergii* CBS 130017 v1.0; *Aspergillus*  
197 *tamarii* CBS 117626 v1.0; *Aspergillus transmontanensis* CBS 130015 v1.0 [73]; *Aspergillus clavatus*  
198 NRRL 1 from AspGD; *Aspergillus flavus* NRRL3357; *Aspergillus nidulans*; *Aspergillus oryzae*  
199 RIB40; *Aspergillus terreus* NIH 2624; *Neosartorya fischeri* NRRL 181 [74]; *Aspergillus cristatus*  
200 GZAAS20.1005 [75]; *Aspergillus fumigatus* A1163 [76]; *Aspergillus fumigatus* Af293 from AspGD  
201 [77]; *Aspergillus kawachii* IFO 4308 [78]; *Aspergillus niger* ATCC 1015 v4.0 [79]; *Aspergillus niger*  
202 CBS 513.88 [80]; *Aspergillus nomius* NRRL 13137; *Aspergillus ochraceoroseus* SRRC1432;  
203 *Aspergillus rambellii* SRRC1468 [81]; *Aspergillus udagawae* IFM 46973 [82]; *Aureobasidium*  
204 *pullulans* var. *melanogenum* CBS 110374; *Aureobasidium pullulans* var. *namibiae* CBS 147.97;  
205 *Aureobasidium pullulans* var. *pullulans* EXF-150; *Aureobasidium pullulans* var. *subglaciale* EXF-  
206 2481 [83]; *Auricularia subglabra* v2.0; *Coniophora puteana* v1.0; *Dichomitus squalens* LYAD-421  
207 SS1 v1.0; *Fomitiporia mediterranea* v1.0; *Fomitopsis pinicola* FP-58527 SS1 v3.0; *Gloeophyllum*  
208 *trabeum* v1.0; *Punctularia strigosozonata* v1.0; *Stereum hirsutum* FP-91666 SS1 v1.0; *Trametes*  
209 *versicolor* v1.0; *Wolfiporia cocos* MD-104 SS10 v1.0; *Dacryopinax primogenitus* DJM 731 SSP1  
210 v1.0; *Tremella mesenterica* Fries v1.0 [84]; *Auriculariopsis ampla* NL-1724 v1.0 [85]; *Baudoinia*  
211 *compniacensis* UAMH 10762 (4089826) v1.0; *Cochliobolus heterostrophus* C4 v1.0; *Cochliobolus*  
212 *heterostrophus* C5 v2.0; *Cochliobolus lunatus* m118 v2.0; *Cochliobolus sativus* ND90Pr v1.0;  
213 *Hysterium pulicare*; *Rhytidhysterium rufulum*; *Septoria musiva* SO2202 v1.0; *Septoria populicola* v1.0;  
214 *Setosphaeria turcica* Et28A v2.0 [86]; *Beauveria bassiana* ARSEF 2860 [87]; *Bjerkandera adusta*  
215 v1.0; *Ganoderma* sp. 10597 SS1 v1.0; *Phlebia brevispora* HHB-7030 SS6 v1.0; *Neofusicoccum*  
216 *parvum* UCRNP2; *Eutypa lata* UCREL1; *Phaeoacremonium aleophilum* UCRPA7 [88]; *Blastobotrys*  
217 (*Arxula*) *adeninivorans* [89]; *Blastomyces dermatitidis* SLH14081 [90]; *Blumeria graminis* f. sp.  
218 *hordei* DH14; *Blumeria graminis* f. sp. *hordei* Race1 [91]; *Blumeria graminis* f. sp. *tritici* 96224 [92];  
219 *Botryobasidium botryosum* v1.0; *Galerina marginata* v1.0; *Jaapia argillacea* v1.0; *Pleurotus*  
220 *ostreatus* PC15 v2.0; *Ascoidea rubescens* NRRL Y17699 v1.0; *Babjeviella inositovora* NRRL Y-



221 12698 v1.0; *Candida arabinof fermentans* NRRL YB-2248 v1.0; *Candida tanzawaensis* NRRL Y-  
222 17324 v1.0; *Cyberlindnera jadinii* NRRL Y-1542 v1.0; *Hanseniaspora valbyensis* NRRL Y-1626  
223 v1.1; *Hyphopichia burtonii* NRRL Y-1933 v1.0; *Lipomyces starkeyi* NRRL Y-11557 v1.0;  
224 *Metschnikowia bicuspidata* NRRL YB-4993 v1.0; *Nadsonia fulvescens* var. *elongata* DSM 6958 v1.0;  
225 *Ogataea polymorpha* NCYC 495 leu1.1 v2.0; *Pachysolen tannophilus* NRRL Y-2460 v1.2; *Pichia*  
226 *membranifaciens* v2.0; *Tortispora caseinolytica* Y-17796 v1.0; *Wickerhamomyces anomalus* NRRL  
227 Y-366-8 v1.0; *Saitoella complicata* NRRL Y-17804 v1.0 [93]; *Botryosphaeria dothidea* [94]; *Botrytis*  
228 *cinerea* v1.0 [95]; *Byssochlamys spectabilis* No. 5 [96]; *Candida albicans* SC5314 [97]; *Candida*  
229 *tenuis* NRRL Y-1498 v1.0; *Spathaspora passalidarum* NRRL Y-27907 v2.0 [98]; *Capronia coronata*  
230 CBS 617.96; *Capronia epimyces* CBS 606.96; *Capronia semiimmersa* CBS27337; *Cladophialophora*  
231 *bantiana* CBS 173.52; *Cladophialophora carrionii* CBS 160.54; *Cladophialophora immunda*  
232 CBS83496; *Cladophialophora psammophila* CBS 110553; *Cladophialophora yegresii* CBS 114405;  
233 *Cyphellophora europaea* CBS 101466; *Exophiala aquamarina* CBS 119918; *Exophiala mesophila*  
234 CBS40295; *Exophiala oligosperma* CBS72588; *Exophiala sideris* CBS121828; *Exophiala spinifera*  
235 CBS89968; *Exophiala xenobiotica* CBS118157; *Fonsecaea multimorphosa* CBS 102226; *Fonsecaea*  
236 *pedrosoi* CBS 271.37; *Coniosporium apollinis* CBS 100218; *Verruconis gallopava* [99]; *Cenococcum*  
237 *geophilum* 1.58 v2.0; *Glonium stellatum* CBS 207.34 v1.0; *Lepidopterella palustris* v1.0 [100];  
238 *Ceriporiopsis (Gelatorporia) subvermispota* B [101]; *Chaetomium globosum* v1.0 [102]; *Chaetomium*  
239 *thermophilum* var *thermophilum* DSM 1495 [103]; *Cladonia grayi* Cgr/DA2myc/ss v2.0 [104];  
240 *Cladosporium fulvum* v1.0; *Dothistroma septosporum* NZE10 v1.0 [105]; *Cladosporium*  
241 *sphaerospermum* UM 843 [106]; *Clavispota lusitaniae* ATCC 42720; *Lodderomyces elongisporus*  
242 NRRL YB-4239; *Meyerozyma guilliermondii* ATCC 6260 [107]; *Coccidioides immitis* RS;  
243 *Coccidioides posadasii* C735 delta SOWgp; *Histoplasma capsulatum* NAm1; *Uncinocarpus reesii*  
244 UAMH 1704 [108]; *Cochliobolus carbonum* 26-R-13 v1.0; *Cochliobolus miyabeanus* ATCC 44560  
245 v1.0; *Cochliobolus victoriae* FI3 v1.0 [109]; *Colletotrichum chlorophyti* NTL11 [110]; *Colletotrichum*  
246 *fiorinae* PJ7 [111]; *Colletotrichum graminicola* M1.001 [112]; *Colletotrichum higginsianum* IMI  
247 349063 [113]; *Colletotrichum incanum* MAFF 238712 [114]; *Colletotrichum nymphaeae* SA-01;  
248 *Colletotrichum salicis* CBS607.94; *Colletotrichum simmondsii* CBS122122; *Trichoderma gamsii*  
249 T6085 [115]; *Colletotrichum orbiculare* 104-T [116]; *Colletotrichum orchidophilum* IMI 309357  
250 [117]; *Colletotrichum tofieldiae* 0861 [118]; *Conidiobolus coronatus* NRRL28638 v1.0; *Coemansia*  
251 *reversa* NRRL 1564 v1.0; *Gonapodya prolifera* v1.0 [119]; *Coniochaeta ligniaria* NRRL 30616 v1.0  
252 [120]; *Coniochaeta* sp. 2T2.1 v1.0 [121]; *Coniophora olivacea* MUCL 20566 v1.0 [122]; *Coprinellus*  
253 *micaceus* FP101781 v2.0; *Coprinopsis marcescibilis* CBS121175 v1.0; *Crucibulum laeve* CBS 166.37  
254 v1.0; *Dendrothele bispota* CBS 962.96 v1.0; *Heliocybe sulcata* OMC1185 v1.0; *Peniophora* sp.  
255 CONTA v1.0; *Pluteus cervinus* NL-1719 v1.0; *Polyporus arcularius* v1.0; *Pterula gracilis*  
256 CBS309.79 v1.0 [123]; *Coprinopsis cinerea* [124]; *Coprinopsis cinerea* AmutBmut pab1-1 v1.0  
257 [125]; *Cordyceps militaris* CM01 [126]; *Corynespora cassiicola* CCP v1.0 [127]; *Cronartium*

258 *quercuum* f. sp. *fusiforme* G11 v1.0 [128]; *Cryphonectria parasitica* EP155 v2.0 [129]; *Cryptococcus*  
259 *curvatus* ATCC 20509 v1.0; *Cryptococcus terricola* JCM 24523 v1.0 [130]; *Cryptococcus*  
260 *neoformans* var. *neoformans* JEC21 [131]; *Cryptococcus neoformans* var. *grubii* H99 [132];  
261 *Cylindrobasidium torrendii* FP15055 v1.0; *Fistulina hepatica* v1.0 [133]; *Cystobasidium minutum*  
262 MCA 4210 v1.0 [134]; *Daedalea quercina* v1.0; *Exidia glandulosa* v1.0; *Fibulorhizoctonia* sp. CBS  
263 109695 v1.0; *Laetiporus sulphureus* var. *sulphureus* v1.0; *Neolentinus lepideus* v1.0; *Peniophora* sp.  
264 v1.0; *Sistotremastrum niveocreameum* HHB9708 ss-1 1.0; *Sistotremastrum suecicum* v1.0; *Calocera*  
265 *cornea* v1.0; *Calocera viscosa* v1.0 [135]; *Daldinia eschscholtzii* EC12 v1.0; *Hypoxylon* sp. CI-4A  
266 v1.0; *Hypoxylon* sp. CO27-5 v1.0; *Hypoxylon* sp. EC38 v3.0 [136]; *Debaryomyces hansenii* [137];  
267 *Dekkera bruxellensis* CBS 2499 v2.0 [138]; *Dentipellis* sp. KUC8613 v1.0 [139]; *Dichomitus squalens*  
268 CBS463.89 v1.0; *Dichomitus squalens* CBS464.89 v1.0; *Dichomitus squalens* OM18370.1 v1.0 [140];  
269 *Encephalitozoon cuniculi* GB-M1 [141]; *Encephalitozoon hellem* ATCC 50504; *Encephalitozoon*  
270 *romaleae* SJ-2008 [142]; *Encephalitozoon intestinalis* ATCC 50506 [143]; *Endocarpon pusillum*  
271 Z07020 [144]; *Endogone* sp. FLAS 59071; *Jimgerdemannia flammicorona* AD002; *Jimgerdemannia*  
272 *flammicorona* GMNB39; *Jimgerdemannia lactiflua* OSC166217 [145]; *Enterocytozoon bieneusi* H348  
273 [146]; *Eremothecium gossypii* ATCC 10895 [147]; *Erysiphe necator* c [148]; *Eurotium rubrum* v1.0  
274 [149]; *Exophiala dermatitidis* UT8656 [150]; *Fibroporia radiculosa* TFFH 294 [151]; *Fonsecaea*  
275 *monophora* CBS 269.37 [152]; *Fonsecaea nubica* CBS 269.64 [153]; *Fusarium fujikuroi* IMI 58289  
276 [154]; *Fusarium graminearum* v1.0 [155]; *Fusarium oxysporum* f. sp. *conglutinans* race 2 54008  
277 (PHW808); *Fusarium oxysporum* f. sp. *cubense tropical* race 4 54006 (II5); *Fusarium oxysporum* f.  
278 sp. *lycopersici* MN25 (FoMN25) NRRL 54003; *Fusarium oxysporum* f. sp. *radicis-lycopersici* 26381  
279 (CL57); *Fusarium oxysporum* f. sp. *raphani* 54005; *Fusarium oxysporum* f. sp. *vasinfectum* 25433  
280 (Cotton); *Fusarium oxysporum* Fo47; *Fusarium oxysporum* NRRL 32931 [156]; *Fusarium oxysporum*  
281 f. sp. *lycopersici* 4287 v2; *Fusarium verticillioides* 7600 v2 [157]; *Fusarium oxysporum* f. sp. *melonis*  
282 (FoMelon) NRRL 26406 [158]; *Fusarium oxysporum* f. sp. *pisi* HDV247 [159]; *Fusarium*  
283 *pseudograminearum* CS3096 [160]; *Gaeumannomyces graminis* var. *tritici* R3-111a-1;  
284 *Magnaportheopsis poae* ATCC 64411 [161]; *Glarea lozoyensis* ATCC 20868 [162]; *Grosmannia*  
285 *clavigera* kw1407 [163]; *Gymnopus androsaceus* JB14 v1.0; *Chalara longipes* BDJ v1.0 [164];  
286 *Heterobasidium annosum* v2.0 [165]; *Homolaphlyctis polyrhiza* JEL142 v1.0 [166]; *Hortaea werneckii*  
287 EXF-2000 M0 v1.0 [167]; *Ilyonectria* sp. v1.0 [168]; *Kazachstania africana* CBS 2517; *Torulaspora*  
288 *delbrueckii* CBS 1146 [169]; *Kluyveromyces lactis*; *Yarrowia lipolytica* (strain CLIB122) [170];  
289 *Kuraishia capsulata* CBS 1993 [171]; *Laccaria bicolor* v2.0 [172]; *Lentinula edodes* B17 v1.1 [173];  
290 *Lentinula edodes* W1-26 v1.0 [174]; *Lentinus tigrinus* ALCF2SS1-6 v1.0; *Lentinus tigrinus*  
291 ALCF2SS1-7 v1.0 [175]; *Leptosphaeria maculans* [176]; *Leucoagaricus gongylophorus* Ac12 [177];  
292 *Leucosporidiella creatinivora* 62-1032 v1.0; *Kockovaella imperatae* NRRL Y-17943 v1.0;  
293 *Naematella encephala* UCDFST 68-887.2 v1.0; *Clohesyomyces aquaticus* v1.0; *Pseudomassariella*  
294 *vexata* CBS 129021 v1.0; *Protomyces lactucaedebilis* 12-1054 v1.0; *Lobosporangium transversale*

295 NRRL 3116 v1.0; *Absidia repens* NRRL 1336 v1.0; *Hesseltinella vesiculosa* NRRL3301 v2.0;  
296 *Rhizopus microsporus* var. *microsporus* ATCC52813 v1.0; *Syncephalastrum racemosum* NRRL 2496  
297 v1.0; *Basidiobolus meristosporus* CBS 931.73 v1.0; *Linderina pennispora* ATCC 12442 v1.0;  
298 *Catenaria anguillulae* PL171 v2.0; *Rhizoclostridium globosum* JEL800 v1.0 [178]; *Lichtheimia*  
299 *corymbifera* JMRC:FSU:9682 [179]; *Macrophomina phaseolina* MS6 [180]; *Magnaporthe oryzae* 70-  
300 15 v3.0 [181]; *Malassezia globosa* [182]; *Malassezia sympodialis* ATCC 42132 [183]; *Marssonina*  
301 *brunnea* f. sp. *multigermtubi* MB\_m1 [184]; *Melampsora larici-populina* v2.0; *Puccinia graminis* f.  
302 sp. *tritici* v2.0 [185]; *Melampsora lini* CH5 [186]; *Metarhizium acridum* CQMa 102; [187];  
303 *Metarhizium robertsii* ARSEF 23; [188]; *Metschnikowia bicuspidata* single-cell v1.0; *Dimargaris*  
304 *cristalligena* RSA 468 single-cell v1.0; *Piptocephalis cylindrospora* RSA 2659 single-cell v3.0;  
305 *Syncephalis pseudoplumigaleata* Benny S71-1 single-cell v1.0; *Thamnocephalis sphaerospora* RSA  
306 1356 single-cell v1.0; *Blyttomyces helicus* single-cell v1.0; *Caulochytrium protostelioides* ATCC  
307 52028 v1.0; *Rozella allomycis* CSF55 single-cell v1.0 [189]; *Metschnikowia fructicola* 277 [190];  
308 *Microbotryum lychnidis-dioicae* p1A1 Lamole [191]; *Microdochium bolleyi* J235TASD1 v1.0 [192];  
309 *Microsporum canis* CBS 113480; *Trichophyton rubrum* CBS 118892 [193]; *Mitosporidium daphniae*  
310 UGP3 [194]; *Mixia osmundae* IAM 14324 v1.0; *Tilletiaria anomala* UBC 951 v1.0 [195];  
311 *Moesziomyces aphidis* DSM 70725 [196]; *Monacrosporium haptotylum* CBS 200.50 [197];  
312 *Moniliophthora perniciosa* FA553 [198]; *Morchella importuna* SCYDJ1-A1 v1.0 [199]; *Mortierella*  
313 *elongata* AG-77 v2.0 [200]; *Mucor endophyticus*; *Mucor fuscus*; *Mucor lanceolatus*; *Mucor*  
314 *racemosus* [201]; *Mucor lusitanicus (circinelloides)* MU402 v1.0 [202]; *Mucor lusitanicus*  
315 CBS277.49 v2.0; *Phycomyces blakesleeanus* NRRL1555 v2.0 [203]; *Myceliophthora thermophila*  
316 (*Sporotrichum thermophile*) v2.0; *Thielavia terrestris* v2.0 [204]; *Mycosphaerella graminicola* v2.0  
317 [205]; *Nakaseomyces bacillisporus* CBS 7720; *Nakaseomyces delphensis* CBS 2170 [206]; *Nectria*  
318 *haematococca* v2.0 [207]; *Nematocida parisii* ERTm1 [208]; *Neolecta irregularis* DAH-1 v1.0 [209];  
319 *Neonectria ditissima* R09/05 [210]; *Neurospora crassa* FGSC 73 trp-3 v1.0 [211]; *Neurospora crassa*  
320 OR74A v2.0 [212]; *Neurospora tetrasperma* FGSC 2508 mat A v2.0; *Neurospora tetrasperma* FGSC  
321 2509 mat a v1.0 [213]; *Nosema ceranae* BRL01 [214]; *Obba rivulosa* 3A-2 v1.0 [215]; *Omphalotus*  
322 *olearius* [216]; *Ophiostoma novo-ulmi subsp. novo-ulmi* H327 [217]; *Ophiostoma piceae* UAMH  
323 11346 [218]; *Orpinomyces* sp. [219]; *Paecilomyces niveus* CO7 v1.0 [220]; *Paecilomyces variotii*  
324 CBS 101075 v1.0; *Paecilomyces variotii* CBS144490 HYG1 v1.0 [221]; *Paracoccidioides brasiliensis*  
325 Pb03; *Paracoccidioides brasiliensis* Pb18 [222]; *Paraconiothyrium sporulosum* AP3s5-JAC2a v1.0;  
326 *Pyrenochaeta* sp. DS3sAY3a v1.0; *Stagonospora* sp. SRC1lsM3a v1.0; *Alternaria alternata*  
327 SRC1lrK2f v1.0 [223]; *Penicillium antarcticum* IBT 31811; *Penicillium coprophilum* IBT 31321;  
328 *Penicillium decumbens* IBT 11843; *Penicillium flavigenum* IBT 14082; *Penicillium nalgiovense*  
329 FM193; *Penicillium polonicum* IBT 4502; *Penicillium solitum* IBT 29525; *Penicillium steckii* IBT  
330 24891; *Penicillium vulpinum* IBT 29486 [224]; *Penicillium chrysogenum* Wisconsin 54-1255 [225];  
331 *Penicillium digitatum* Pd1; *Penicillium digitatum* PHI26 [226]; *Penicillium expansum* d1; *Penicillium*

332 *italicum* PHI-1 [227]; *Penicillium griseofulvum* PG3 [228]; *Penicillium nordicum* DAOMC 185683  
333 [229]; *Penicillium oxalicum* 114-2 [230]; *Penicillium subrubescens* FBCC1632 / CBS132785 [231];  
334 *Penicillium thymicola* DAOMC 180753 v1.0 [232]; *Periconia macrospinosa* DSE2036 v1.0;  
335 *Cadophora* sp. DSE1049 v1.0 [233]; *Phaeomoniella chlamydospora* UCRPC4; *Diplodia seriata*  
336 DS831; *Diaporthe ampelina* UCDDA912 [234]; *Phanerochaete carnosae* HHB-10118-Sp v1.0 [235];  
337 *Phanerochaete chrysosporium* RP-78 v2.2 [236]; *Phialocephala scopiformis* 5WS22E1 v1.0 [237];  
338 *Phialophora attae* CBS 131958 [238]; *Phlebia centrifuga* FBCC195 [239]; *Phlebia radiata* Fr.  
339 (isolate 79, FBCC0043) [240]; *Phlebiopsis gigantea* v1.0 [241]; *Phyllosticta capitalensis* CBS 128856  
340 v1.0; *Phyllosticta citriasiana* CBS 120486 v1.0; *Phyllosticta citribraziliensis* CBS 100098 v1.0;  
341 *Phyllosticta citricarpa* CBS 127454 v1.0; *Phyllosticta citrichinaensis* CBS 130529 v1.0; *Phyllosticta*  
342 *paracitricarpa* CBS 141357 v1.0; *Phyllosticta* sp. CPC 27913 v1.0 [242]; *Pichia kudriavzevii* CBS573  
343 [243]; *Pichia pastoris* [244]; *Piriformospora indica* DSM 11827 from MPI [245]; *Pleurotus ostreatus*  
344 PC9 v1.0 [246]; *Pneumocystis jirovecii* [247]; *Pochonia chlamydosporia* 170 [248]; *Podospora*  
345 *anserina* S mat+ [249]; *Polyporus brumalis* BRFM 1820 v1.0 [250]; *Postia placenta* MAD 698-R  
346 v1.0 [251]; *Postia placenta* MAD-698-R-SB12 v1.0 [252]; *Pseudocercospora (Mycosphaerella)*  
347 *fijiensis* v2.0 [253]; *Pseudogymnoascus destructans* 20631-21 [254]; *Pseudozyma antarctica* T-34  
348 [255]; *Pseudozyma hubeiensis* SY62 [256]; *Psilocybe cubensis* v1.0; *Psilocybe serbica* v1.0 [257];  
349 *Puccinia coronata avenae* 12NC29; *Puccinia coronata avenae* 12SD80 [258]; *Puccinia graminis* f. sp.  
350 *tritici* 21-0 haplotype A; *Puccinia graminis* f. sp. *tritici* 21-0 haplotype B; *Puccinia graminis* f. sp.  
351 *tritici* Ug99 haplotype A; *Puccinia graminis* f. sp. *tritici* Ug99 haplotype C [259]; *Puccinia striiformis*  
352 f. sp. *tritici* 104 E137 A- [260]; *Puccinia striiformis* f. sp. *tritici* PST-130 [261]; *Puccinia striiformis* f.  
353 sp. *tritici* PST-78 v1.0; *Puccinia triticina* 1-1 BBBB Race 1 [262]; *Pycnoporus cinnabarinus* BRFM  
354 137 [263]; *Pycnoporus coccineus* BRFM 310 v1.0; *Pycnoporus puniceus* CIRM-BRFM 1868 v1.0;  
355 *Pycnoporus sanguineus* BRFM 1264 v1.0; *Ramaria rubella (R. acris)* UT-36052-T v1.0 [264];  
356 *Pyrenophora teres* f. *teres* [265]; *Pyrenophora tritici-repentis* [266]; *Pyronema confluens* CBS100304  
357 [267]; *Rhizoctonia solani* AG-1 IB [268]; *Rhizophagus irregularis* A1 v1.0; *Rhizophagus irregularis*  
358 A4 v1.0; *Rhizophagus irregularis* A5 v1.0; *Rhizophagus irregularis* B3 v1.0; *Rhizophagus irregularis*  
359 C2 v1.0; *Rhizophagus irregularis* DAOM 197198 v2.0 [269]; *Rhizophagus irregularis* DAOM  
360 181602 v1.0 [270]; *Rhizopogon vesiculosus* Smith; *Rhizopogon vinicolor* AM-OR11-026 v1.0 [271];  
361 *Rhizopus delemar* 99-880 from Broad [272]; *Rhizopus microsporus* ATCC11559 v1.0; *Rhizopus*  
362 *microsporus* var. *microsporus* ATCC52814 v1.0 [273]; *Rhizopus microsporus* var. *chinensis* CCTCC  
363 M201021 [274]; *Rhodosporidium toruloides* IFO0559\_1; *Rhodosporidium toruloides* IFO0880 v2.0;  
364 *Rhodosporidium toruloides* IFO1236\_1 [275]; *Rhodosporidium toruloides* IFO0880 v4.0 [276];  
365 *Rhodosporidium toruloides* NP11 [277]; *Rhodotorula graminis* strain WP1 v1.1 [278]; *Rhodotorula*  
366 sp. JG-1b [279]; *Rickenella fibula* HBK330-10 v1.0 [280]; *Rickenella mellea* v1.0 (SZMC22713)  
367 [281]; *Rigidoporus microporus* ED310 v1.0 [282]; *Rozella allomyces* CSF55 [283]; *Saccharomyces*  
368 *arboricola* H-6 [284]; *Saccharomyces cerevisiae* M3707 Dikaryon; *Saccharomyces cerevisiae* M3836

369 v1.0; *Saccharomyces cerevisiae* M3837 v1.0; *Saccharomyces cerevisiae* M3838 v1.0; *Saccharomyces*  
370 *cerevisiae* M3839 v1.0; *Arthroderma benhamiae* CBS 112371; *Trichophyton verrucosum* HKI 0517  
371 [285]; *Saccharomyces cerevisiae* S288C [286]; *Saksenaea vasiformis* B4078 [287]; *Scheffersomyces*  
372 *stipitis* NRRL Y-11545 v2.0 [288]; *Schizophyllum commune* H4-8 v3.0 [289]; *Schizopora paradoxa*  
373 KUC8140 v1.0 [290]; *Schizosaccharomyces cryophilus* OY26; *Schizosaccharomyces japonicus*  
374 yFS275; *Schizosaccharomyces octosporus* yFS286 [291]; *Schizosaccharomyces pombe* [292];  
375 *Sclerotinia sclerotiorum* v1.0 [293]; *Serpula himantioides* (*S.lacrymans* var *shastensis*) MUCL38935  
376 v1.0 [294]; *Serpula lacrymans* S7.3 v2.0; *Serpula lacrymans* S7.9 v2.0 [295]; *Smittium culicis*  
377 GSMNP; *Smittium culicis* ID-206-W2; *Smittium mucronatum* ALG-7-W6; *Zancudomyces culisetae*  
378 COL-18-3 [296]; *Sodiomyces alkalinus* v1.0 [297]; *Sphaerosporella brunnea* Sb\_GMNB300 v2.0  
379 [298]; *Spizellomyces punctatus* DAOM BR117 [299]; *Sporisorium reilianum* SRZ2 [300];  
380 *Stagonospora nodorum* SN15 v2.0 [301]; *Stemphylium lycopersici* CIDEFI-216 [302]; *Suillus*  
381 *brevipes* Sb2 v2.0 [303]; *Talaromyces borbonicus* CBS 141340 [304]; *Talaromyces marneffeii* ATCC  
382 18224 [305]; *Taphrina deformans* [306]; *Thermomyces lanuginosus* SSBP [307]; *Tolypocladium*  
383 *inflatum* NRRL 8044 [308]; *Trametes pubescens* FBCC735 [309]; *Trichoderma arundinaceum* IBT  
384 40837; *Trichoderma brevicompactum* IBT40841 [310]; *Trichoderma asperellum* CBS 433.97 v1.0;  
385 *Trichoderma citrinoviride* TUCIM 6016 v4.0; *Trichoderma guizhouense* NJAU 4742; *Trichoderma*  
386 *harzianum* CBS 226.95 v1.0; *Trichoderma longibrachiatum* ATCC 18648 v3.0 [311]; *Trichoderma*  
387 *asperellum* TR356 v1.0; *Trichoderma harzianum* TR274 v1.0 [312]; *Trichoderma atrobrunneum*  
388 ITEM 908 [313]; *Trichoderma atroviride* v2.0; *Trichoderma virens* Gv29-8 v2.0 [314]; *Trichoderma*  
389 *hamatum* GD12 [315]; *Trichoderma parareesei* CBS 125925 [316]; *Trichoderma pleuroti* TPhu1  
390 [317]; *Trichoderma reesei* QM6a [318]; *Trichoderma reesei* RUT C-30 v1.0 [319]; *Trichoderma*  
391 *reesei* v2.0 [320]; *Trichosporon asahii* var. *asahii* CBS 2479 [321]; *Trichosporon asahii* var. *asahii*  
392 CBS 8904 [322]; *Trichosporon oleaginosus* IBC0246 v1.0 [323]; *Tuber melanosporum* Mel28 v1.2  
393 [324]; *Ustilaginoidea virens* [325]; *Ustilago hordei* Uh4857\_4 [326]; *Ustilago maydis* 521 v2.0 [327];  
394 *Venturia inaequalis*; *Venturia pirina* [328]; *Verticillium alfalfae* VaMs.102; *Verticillium dahliae*  
395 VdLs.17 [329]; *Volvariella volvacea* V23 [330]; *Wallemia ichthyophaga* EXF-994 [331]; *Wallemia*  
396 *mellicola* v1.0 [332]; *Xylona heveae* TC161 v1.0 [333]; *Yarrowia lipolytica* CLIB89(W29) [334];  
397 *Yarrowia lipolytica* FKP355 v1.0 [335]; *Yarrowia lipolytica* PO1f v1.0; *Yarrowia lipolytica* Y1CW001  
398 v1.0 [336]; *Yarrowia lipolytica* YB392 v1.0; *Yarrowia lipolytica* YB419 v1.0; *Yarrowia lipolytica*  
399 YB420 v1.0; *Yarrowia lipolytica* YB566 v1.0; *Yarrowia lipolytica* YB567 v1.0 [337];  
400 *Zygosaccharomyces rouxii* CBS732 [338]; *Zymoseptoria ardabiliae* STIR04\_1.1.1; *Zymoseptoria*  
401 *pseudotritici* STIR04\_2.2.1 [339]; *Zymoseptoria brevis* Zb18110 [340]; *Melampsora allii-populina*  
402 12AY07 v1.0; *Melampsora americana* R15-033-03 v1.0 (unpublished).

403

### 404 **2.3. Protein sequence analysis and search for potential subcellular targeting.**

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

411

### 412 **2.4. Phylogenomic analyses and search for horizontal gene transfers.**

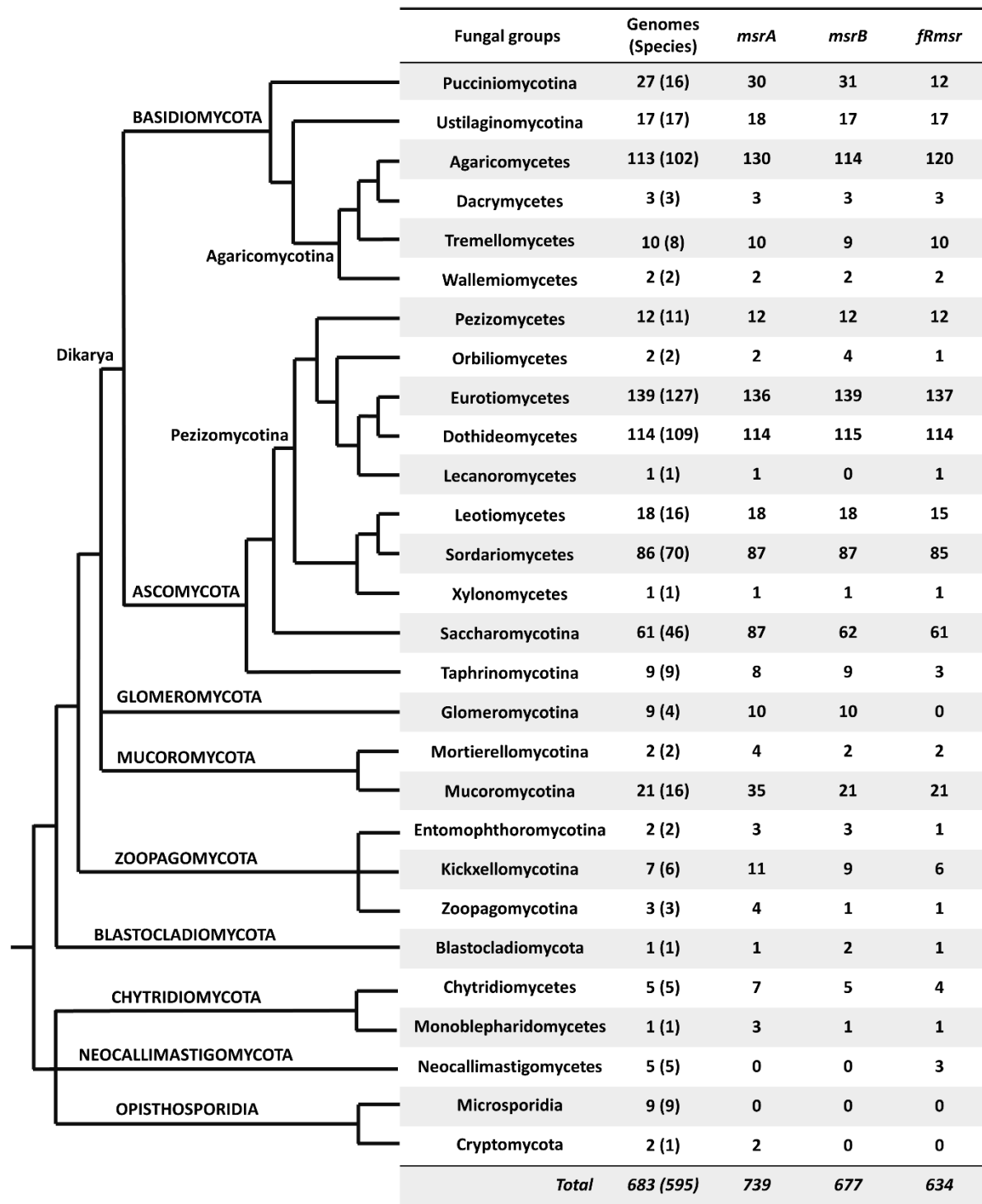
413 For each type of Msr, we built a multiple sequence alignment with all the identified sequences  
414 using MAFFT version v7.429 [346]. Each alignment was trimmed to remove poorly aligned regions  
415 using trimAl 1.2 [347] and manually inspected for the conservation of the catalytic residues. A  
416 phylogenetic tree was constructed for each type of Msr using RAxML Master Pthread [348] version  
417 8.2.12 (PROTGAMMAWAG model and 500 bootstraps). The phylogenetic tree was represented using  
418 iTOL (<https://itol.embl.de/>) [349]. To investigate potential horizontal gene transfers, the non-canonical  
419 Msr sequences along with the sequences whose phylogeny did not fit the species phylogeny were  
420 retrieved. Those sequences were used as BLAST queries against the non-redundant protein sequence  
421 (nr) database of NCBI  
422 ([https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastp&PAGE\\_TYPE=BlastSearch&LINK\\_LO](https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastp&PAGE_TYPE=BlastSearch&LINK_LO)  
423 [C=blasthome](https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM=blastp&PAGE_TYPE=BlastSearch&LINK_LO)) and the best 100 hits were retrieved. The fungal sequences for which protein accessions  
424 outside the fungal kingdom were identified among the highest identity scores were in further used as  
425 BLAST queries against nr excluding the taxon Fungi (taxid: 4751) and the 25 hits with the highest  
426 identity scores were retrieved. In parallel, the same fungal genes were used as queries against the  
427 fungal nr database and the 50 hits with the highest identity scores were retrieved, excluding those with  
428 100% identity with the query. The retrieved fungal hits were manually inspected to exclude  
429 incomplete sequences. Non-canonical sequences (lacking canonical active site or of abnormal length)  
430 were also removed to avoid potential inconsistencies and long branches in the phylogenetic trees.  
431 Finally, for each type of Msr, a phylogenetic tree was constructed that included the candidate fungal  
432 gene for horizontal gene transfer, plus 25 non-fungal and 25 fungal sequences with the highest identity  
433 scores. For each candidate to HGT, the numbers of exons, the GC content of the coding sequence and  
434 the GC content at the third positions of the codons were calculated using the gene structures and  
435 coding sequences downloaded from the MycoCosm database. The GC content on the third positions of  
436 the codons were calculated only for the coding sequences starting with ATG. All calculations were  
437 made using Microsoft® Excel® version 2101.

### 438 3. Results

#### 439 3.1. MsrA, MsrB and fRMsR are largely conserved across the fungal kingdom.

440 Currently, around 136,000 species of fungi are known and classified into 9 phyla (**Figure 1**)  
441 [37,350]. Together, the Ascomycota and the Basidiomycota form the subkingdom Dikarya, which  
442 regroups more than 97 % of all described fungal species (~84,000 species and ~48,000 species,  
443 respectively) [350]. Each phylum contains three monophyletic subphyla (Pucciniomycotina,  
444 Ustilaginomycotina and Agaricomycotina for the Basidiomycota, and Taphrinomycotina,  
445 Saccharomycotina and Pezizomycotina for the Ascomycota). The other seven phyla are described as  
446 ‘early-diverging fungi’ [350] (**Fig. 1, Data S1**). Using the *S. cerevisiae* MsrA, MsrB and fRMsR  
447 protein sequences as queries, we used the BLASTP and TBLASTN software suites to search for *msr*  
448 genes in 683 available genomes in the MycoCosm database [50]. The selected genomes were from 595  
449 species that spanned the kingdom Fungi (**Fig. 1, Data S1**), including 65% Ascomycota species, 25%  
450 Basidiomycota species and 10% early-diverging fungi. We found that the very great majority of these  
451 genomes contained one gene coding for a MsrA and one coding for a MsrB (**Fig. 1, Data S1**),  
452 indicating that most fungi have a simple Msr system dedicated to protein oxidation repair, similarly to  
453 most other known organisms [24,26]. Most interestingly, we found that a *fRmsr* gene was present in  
454 almost all the analyzed genomes (**Fig. 1, Data S1**). The distribution of *fRmsr* across the fungal  
455 kingdom clearly showed that the presence of fRMsR is not limited to bacteria and unicellular  
456 eukaryotes as previously described [7–9]. Of note, the search for homologs of the bacterial  
457 molybdoenzymes able to reduce MetO gave no significant hits (**data not shown**).

458



459

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

463



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

476 **Table 1.** Fungi with five or six Msr genes.

Genome	MsrA	MsrB	fRMsr	Lifestyle	Nb. Genes (Genome size in Mbp)	Ref.
<b>Agaricomycetes</b>						
<i>Crucibulum laeve</i> CBS 166.37 v1.0	4	1	1		14,218 (44)	[351]
<i>Dendrothele bispora</i> CBS 962.96 v1.0	4	1	1		33,645 (131)	[351]
<i>Tulasnella calospora</i> AL13/4D v1.0	3	1	1	Aerobic (saprotroph)	19,659 (62)	[352]
<i>Ramaria rubella</i> ( <i>R. acris</i> ) UT-36052-T v1.0	1	1	4		14,207 (62)	[353]
<i>Coprinellus micaceus</i> FP101781 v2.0	1	1	3		23,559 (77)	[351]
<b>Dothideomycetes</b>						
<i>Hortaea werneckii</i> EXF-2000 M0 v1.0	2	2	2	Aerobic	15,748 (50)	[167]
<b>Sordariomycetes</b>						
<i>Coniochaeta</i> sp. 2T2.1 v1.0	2	2	2	Aerobic (phytopathogen)	24,735 (74)	[121]
<b>Saccharomycotina</b>						
<i>Pichia kudriavzevii</i> CBS573	3	1	1		5,140 (11)	[354]
<i>Yarrowia lipolytica</i> (strain CLIB122)	3	1	1		6,447 (21)	[355]
<i>Yarrowia lipolytica</i> CLIB89(W29)	3	1	1		7,919 (21)	[356]
<i>Yarrowia lipolytica</i> FKP355 v1.0	3	1	1		6,858 (20)	[357]
<i>Yarrowia lipolytica</i> PO1f v1.0	3	1	1		6,798 (20)	[358]
<i>Yarrowia lipolytica</i> YB392 v1.0	3	1	1	Aerobic	6,750 (20)	[359]
<i>Yarrowia lipolytica</i> YB419 v1.0	3	1	1		6,751 (20)	[359]
<i>Yarrowia lipolytica</i> YB420 v1.0	3	1	1		6,772 (20)	[359]
<i>Yarrowia lipolytica</i> YB566 v1.0	3	1	1		6,764 (20)	[359]
<i>Yarrowia lipolytica</i> YB567 v1.0	3	1	1		6,776 (20)	[359]
<i>Yarrowia lipolytica</i> YICW001 v1.0	3	1	1		6,800 (20)	[358]
<b>Mucoromycotina</b>						
<i>Absidia repens</i> NRRL 1336 v1.0	3	1	1	Aerobic (saprotroph)	14 919 (47)	[360]
<i>Rhizopus microsporus</i> ATCC11559 v1.0	2	1	2		11,135 (24)	[273]
<i>Rhizopus microsporus</i> var. <i>chinensis</i> CCTCC M201021	2	1	2	Aerobic (phytopathogen)	17,676 (46)	[274]
<b>Kickxellomycotina</b>						
<i>Smittium mucronatum</i> ALG-7-W6	3	1	1		8 247 (102)	[361]
<i>Smittium culicis</i> GSMNP	2	3	1	Anaerobic (insect gut)	12 166 (77)	[361]
<b>Monoblepharidomycetes</b>						

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

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

508

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

Genome	MsrA	MsrB	fRMsr	Lifestyle	Nb. Genes (Genome size in Mbp)	Ref.
<b>Microsporidia</b>						
<i>Antonospora locustae</i> HM-2013	N	N	N		2,606 (6)	[364]
<i>Encephalitozoon cuniculi</i> GB-M1	N	N	N		1,996 (2)	[365]
<i>Encephalitozoon hellem</i> ATCC 50504	N	N	N		1,847 (2)	[366]
<i>Encephalitozoon intestinalis</i> ATCC 50506	N	N	N	Intracellular parasite of metazoans	1,833 (2)	[367]
<i>Encephalitozoon romaleae</i> SJ-2008	N	N	N		1,831 (2)	[366]
<i>Enterocytozoon bieneusi</i> H348	N	N	N		3,632 (4)	[368]
<i>Mitosporidium daphniae</i> UGP3	N	N	N		3,330 (6)	[369]
<i>Nematocida parisii</i> ERTm1	N	N	N		2,661 (4)	[370]
<i>Nosema ceranae</i> BRL01	N	N	N		2,060 (8)	[371]
<b>Neocallimastigomycetes</b>						
<i>Piromyces finnis</i> v3.0	N	N	N	Anaerobic (ruminant gut)	10,992 (56)	[372]
<i>Piromyces</i> sp. E2 v1.0	N	N	N		14,648 (71)	[372]
<i>Anaeromyces robustus</i> v1.0	N	N	Y		12,832 (72)	[372]
<i>Neocallimastix californiae</i> G1 v1.0	N	N	Y		20,219 (193)	[372]
<i>Orpinomyces</i> sp.	N	N	Y		18,936 (101)	[373]
<b>Taphrinomycotina</b>						
<i>Pneumocystis jirovecii</i>	N	N	N	Intracellular parasite of metazoans	3,520 (8)	[374]
<i>Neoelecta irregularis</i> DAH-1 v1.0	Y	Y	N		6,674 (15)	[375]
<i>Schizosaccharomyces cryophilus</i> OY26	Y	Y	N		5,180 (12)	[376]
<i>Schizosaccharomyces japonicus</i> yFS275	Y	Y	N	Aerobic	4,878 (12)	[376]
<i>Schizosaccharomyces octosporus</i> yFS286	Y	Y	N		4,986 (12)	[376]
<i>Schizosaccharomyces pombe</i>	Y	Y	N		5,134 (13)	[377]
<b>Agaricomycetes</b>						
<i>Moniliophthora perniciosa</i> FA553	N	Y	Y	Aerobic (phytopathogen)	13,560 (18)	[378]
<b>Eurotiomycetes</b>						
<i>Penicillium coprophilum</i> IBT 31321	N	Y	Y	Aerobic	8,999 (28)	[379]
<i>Penicillium flavigenum</i> IBT 14082	N	Y	Y		10,994 (33)	[379]
<i>Penicillium polonicum</i> IBT 4502	N	Y	Y		10,694 (32)	[379]
<i>Aspergillus bombycis</i> NRRL 26010	Y	Y	N		12,265 (37)	[380]
<i>Aspergillus zonatus</i> v1.0	Y	Y	N		9,886 (29)	[70]
<b>Sordariomycetes</b>						
<i>Magnaportheopsis poae</i> ATCC 64411	N	Y	Y	Aerobic (phytopathogen)	12,335 (40)	[381]
<i>Pochonia chlamydosporia</i> 170	Y	Y	N	Aerobic (animal pathogen)	14,204 (44)	[382]
<b>Saccharomycotina</b>						
<i>Saturnispora dispersa</i> NRRL Y-1447	N	Y	Y	Aerobic	4,881 (10)	[383]
<b>Tremellomycetes</b>						
<i>Trichosporon asahii</i> var. <i>asahii</i> CBS 2479	Y	N	Y	Aerobic (human pathogen)	8,300 (24)	[384]
<i>Trichosporon asahii</i> var. <i>asahii</i> CBS 8904	Y	N	Y		8,507 (25)	[385]
<b>Dothideomycetes</b>						
<i>Clohesyomyces aquaticus</i> v1.0	Y	N	Y	Aerobic (saprotrophic)	15,810 (50)	[360]
<b>Lecaronomycetes</b>						
<i>Cladonia grayi</i> Cgr/DA2myc/ss v2.0	Y	N	Y	Aerobic (lichen)	11,389 (35)	[386]
<b>Zoopagomycotina</b>						
<i>Piptocephalis cylindrospora</i> RSA 2659 single-cell v3.0	Y	N	Y	Aerobic (mycoparasite)	4,301 (11)	[387]
<i>Syncephalis pseudoplumigaleata</i> Benny	Y	N	N		6,123 (16)	[387]

S71-1 single-cell v1.0						
<i>Thamnocephalis sphaerospora</i> RSA 1356 single-cell v1.0	Y	Y	N		6,857 (18)	[387]
<b>Cryptomycota</b>						
<i>Rozella allomycis</i> CSF55	Y	N	N	Aerobic	6,350 (12)	[283]
<i>Rozella allomycis</i> CSF55 single-cell v1.0	Y	N	N	(mycoparasite)	6,694 (13)	[387]
<b>Pucciniomycotina</b>						
<i>Melampsora allii-populina</i> 12AY07 v1.0	Y	Y	N		23,089 (336)	-
<i>Melampsora americana</i> R15-033-03 v1.0	Y	Y	N		15,984 (112)	-
<i>Melampsora larici-populina</i> v2.0	Y	Y	N		19,550 (110)	[388]
<i>Melampsora lini</i> CH5	Y	Y	N		16,335 (190)	[389]
<i>Puccinia coronata avenae</i> 12NC29	Y	Y	N		28,270 (166)	[390]
<i>Puccinia coronata avenae</i> 12SD80	Y	Y	N	Aerobic	26,323 (150)	[390]
<i>Puccinia graminis</i> f. sp. <i>tritici</i> v2.0	Y	Y	N	(phytopathogen)	15,979 (89)	[388]
<i>Puccinia striiformis</i> f. sp. <i>tritici</i> 104 E137 A-	Y	Y	N		30,249 (157)	[391]
<i>Puccinia striiformis</i> f. sp. <i>tritici</i> PST-130	Y	Y	N		18,021 (65)	[392]
<i>Puccinia striiformis</i> f. sp. <i>tritici</i> PST-78 v1.0	Y	Y	N		20,482 (117)	[393]
<i>Puccinia triticina</i> 1-1 BBBB Race 1	Y	Y	N		15,685 (135)	[393]
<b>Leotiomyces</b>						
<i>Blumeria graminis</i> f. sp. <i>hordei</i> DH14	Y	Y	N		7,118 (125)	[394]
<i>Blumeria graminis</i> f. sp. <i>hordei</i> Race1	Y	Y	N	Aerobic	7,239 (116)	[394]
<i>Blumeria graminis</i> f. sp. <i>tritici</i> 96224	Y	Y	N	(phytopathogen)	6,525 (159)	[395]
<b>Glomeromycotina</b>						
<i>Gigaspora rosea</i> v1.0	Y	Y	N		31,291 (568)	[396]
<i>Rhizophagus cerebriforme</i> DAOM 227022 v1.0	Y	Y	N		21,549 (137)	[396]
<i>Rhizophagus diaphanus</i> v1.0	Y	Y	N		23,252(129)	[396]
<i>Rhizophagus irregularis</i> A1 v1.0	Y	Y	N	Aerobic (arbuscular mycorrhizal)	26,659 (126)	[397]
<i>Rhizophagus irregularis</i> A4 v1.0	Y	Y	N		25,760 (138)	[397]
<i>Rhizophagus irregularis</i> A5 v1.0	Y	Y	N		26,585 (131)	[397]
<i>Rhizophagus irregularis</i> B3 v1.0	Y	Y	N		25,164 (125)	[397]
<i>Rhizophagus irregularis</i> C2 v1.0	Y	Y	N		26,756 (123)	[397]
<i>Rhizophagus irregularis</i> DAOM 197198 v2.0	Y	Y	N		26,183 (137)	[397]
<b>Mucoromycotina</b>						
<i>Jimgerdemannia lactiflua</i> OSC166217	Y	Y	N	Aerobic (ectomycorrhizal)	12,651 (180)	[362]
<i>Lichtheimia corymbifera</i> JMRC:FSU:9682	Y	Y	N	Aerobic (saprotrophic/human pathogen)	13,404 (34)	[398]
<b>Entomophthoromycotina</b>						
<i>Basidiobolus meristosporus</i> CBS 931.73 v1.0	Y	Y	N	Aerobic (saprotrophic/animal pathogen)	16,111 (89)	[360]
<b>Kickxellomycotina</b>						
<i>Dimargaris cristalligena</i> RSA 468 single-cell v1.0	Y	Y	N	Aerobic (mycoparasite)	7,456 (31)	[387]
<b>Chytridiomycetes</b>						
<i>Caulochytrium protostelioides</i> ATCC 52028 v1.0	Y	Y	N	Aerobic (mycoparasite)	6,168 (22)	[387]

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

511

### 512 3.2. Fungal Msrs globally retained canonical sequence features for activity.

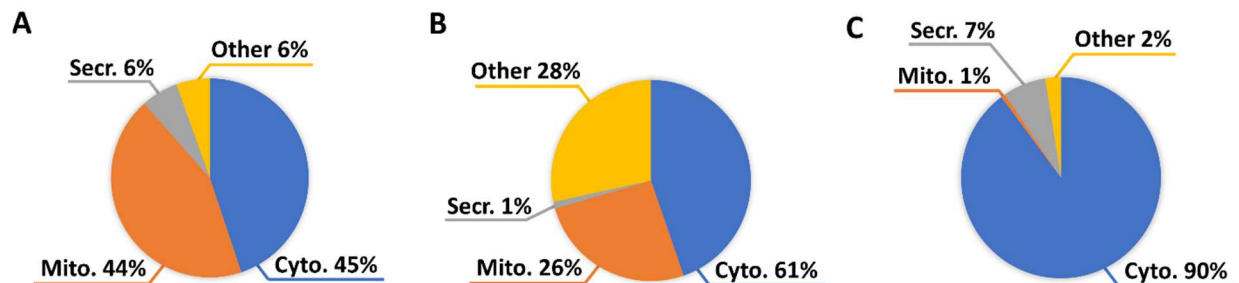
513 Sequence analysis and enzymatic characterizations of MsrAs from several organisms showed  
514 that the catalytic residue is located within a G[C/U]FW motif, located in the N-terminal part of the  
515 protein [6,16,17,399,400]. The great majority of known MsrAs possess a catalytic Cys, whereas a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

548 single-cell green alga *Chlamydomonas reinhardtii*, previously shown to use the Sec residue for the  
549 regeneration of their activity [400,403] (**Data S2D**).

550

551

552



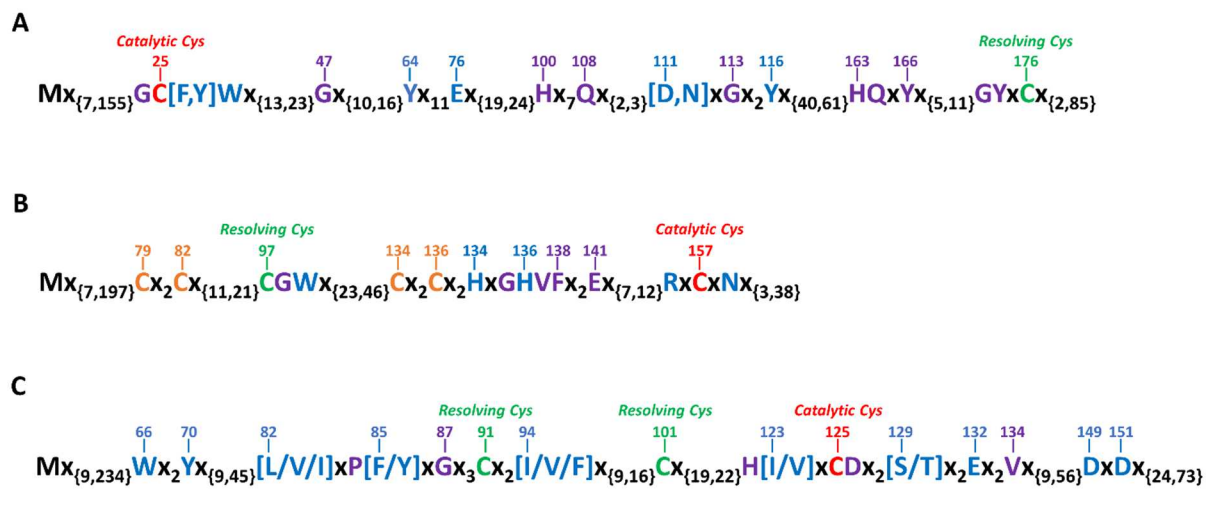
553 **Figure 2. Potential subcellular targeting of fungal Msrs.** The circle charts show the subcellular  
554 predictions for fungal MsrA (A), MsrB (B) and fRMsr (C), the proportion of proteins predicted to be  
555 localized in the cytosol ('Cyto. '), to be addressed to the mitochondria ('Mito. ')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

558

559 In the case of MsrBs, previous biochemical characterizations demonstrated that the catalytic  
560 Cys is located in a RXCXN motif in the C-terminal part of the protein [16,21,404–407]. Mammals  
561 express a Sec-containing form in which the Asp is replaced by a Phe [404]. The resolving Cys is  
562 generally located in a CGWP motif present in the N-terminal part of the protein [21,406]. In the case  
563 of mammalian MsrBs, one or two resolving Cys, located in the N-terminal extremity of the protein,  
564 can be involved in the regeneration process [404,408]. Of note, most MsrBs possess two CX<sub>2</sub>C  
565 clusters coordinating a structural Zn atom [409]. Here, we analyzed the 651 complete fungal MsrB  
566 protein sequences. The fungal MsrBs consisted of a single domain and ranged in length from 95 to 289  
567 amino acids (**Data S3A**). Most of the variations in size were due to the presence of an N-terminal  
568 extension potentially involved in subcellular targeting. The majority of fungal MsrBs were predicted  
569 to be addressed to the cytosol (61 %) (**Fig. 2B, Data S3A**). The other proteins were either predicted to  
570 be localized in the mitochondria (26 %), secreted (1 %), targeted to another compartment, or were not  
571 clearly predicted to be addressed to a subcellular compartment (28 %) (**Fig. 2B, Data S3A**). Almost  
572 all fungal MsrBs (> 99 %) possessed the features of the *S. cerevisiae* enzyme (**Fig. 3B, Data S3B**): i)  
573 the two CX<sub>2</sub>C motifs involved in the coordination of a Zn atom, ii) the resolving Cys<sup>97</sup> (according to *S.*  
574 *cerevisiae* MsrB residue numbering) included in a <sup>97</sup>CGW<sup>99</sup> motif, iii) the conserved His<sup>134</sup> and His<sup>136</sup>  
575 implicated in substrate binding, together with Arg<sup>155</sup> and Asn<sup>159</sup> [16,405], and iv) the catalytic Cys<sup>157</sup>  
576 located in the <sup>155</sup>RXCXN<sup>159</sup> motif. The Gly<sup>98</sup>, Gly<sup>135</sup>, Val<sup>137</sup>, Phe<sup>138</sup> and Glu<sup>141</sup> residues were also  
577 conserved in all these canonical fungal MsrBs (**Fig. 3B, Data S3B**). Only four sequences (< 1 %),

578 from the orbiliomycetes *Arthrotrrys oligospora* and *Monacrosporium haptotylum*, the  
 579 taphrinomycotina *Protomyces lactucaedebilis* and the chytridiomycete *Blyttomyces helices*, presented  
 580 remarkable differences in primary sequence features (**Data S3C**). These MsrBs lacked the resolving  
 581 Cys at position 97, which was substituted by a Ser or a Thr, like plant and human orthologs that use an  
 582 unusual regeneration process [20,21,408]. Finally, another unusual feature was found in the MsrB  
 583 from the taphrinomycotina *Protomyces lactucaedebilis*, with the location of the catalytic Cys in an  
 584 HYCIN motif, instead of the typical RXCXN motif (**Data S3C**). Interestingly, searching in the NCBI  
 585 nr database, we found 50 sequences, mainly from poorly characterized bacteria and archaea, that  
 586 possessed this unusual motif (**Data S3D**). Considering His and Arg have similar physicochemical  
 587 properties, we anticipate such non-canonical MsrBs might have conserved a catalytic activity.

588



589

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

596

597 Very few fRMsrs have been characterized so far. However, sequence comparison studies and  
 598 biochemical characterizations indicated that the catalytic Cys is located in the HIAC motif situated in  
 599 the middle of the protein sequence and that the two resolving Cys are located ~30 and ~40 amino  
 600 acids upstream in the N-terminal direction [7–9]. The 589 full length fRMsr sequences analyzed here  
 601 had a single fRMsr domain. Their length varied from 77 to 394 amino acids, with variations in the size  
 602 of the N-terminal extension (**Data S4A**). Most of the proteins (90 %) were predicted to be localized in  
 603 the cytoplasm (**Fig. 2C, Data S4A**). A few proteins were predicted to be secreted (7 %), targeted to

604 the mitochondria (1 %), to other compartments or had no reliable prediction for subcellular targeting  
605 (2 %) (**Fig. 2C, Data S4A**). Similar to MsrAs and MsrBs, fRMsrs showed a strong conservation of the  
606 sequence features. Almost all (> 99 %) sequences possessed the catalytic Cys<sup>125</sup> included in a  
607 <sup>122</sup>H[I/V]XCD<sup>126</sup> motif and the resolving Cys in positions 91 and 101 (according to the *S. cerevisiae*  
608 fRMsr residue numbering) (**Fig. 3C, Data S4B**). We also observed the strict conservation of Trp<sup>66</sup>,  
609 Tyr<sup>70</sup>, Glu<sup>132</sup>, Asp<sup>149</sup> and Asp<sup>151</sup>, previously shown to be involved in substrate binding and catalysis.  
610 Other important residues involved in substrate binding and catalysis [7] were also conserved or  
611 substituted by residues with similar properties in positions 82, 85, 94, 123, 129 and 132. The Pro<sup>84</sup>,  
612 Gly<sup>87</sup>, His<sup>122</sup> and Val<sup>134</sup> were also strictly conserved in these canonical fungal fRMsrs (**Fig. 3C, Data**  
613 **S4B**). Only three fRMsr sequences from the Agaricomycetes *Scleroderma citrinum*, *Dendrothele*  
614 *bispora* and *Pisolithus tinctorius* presented non-canonical characteristics. The first two lacked the  
615 potential resolving Cys<sup>101</sup> and may be still able to reduce the free MetO, but in the latest, the catalytic  
616 Cys<sup>125</sup> was substituted by an Arg, likely precluding catalytic activity (**Data S4C**).

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

620

### 621 **3.3. The phylogenetic analysis of fungal Msrs revealed horizontal gene transfers from bacteria.**

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

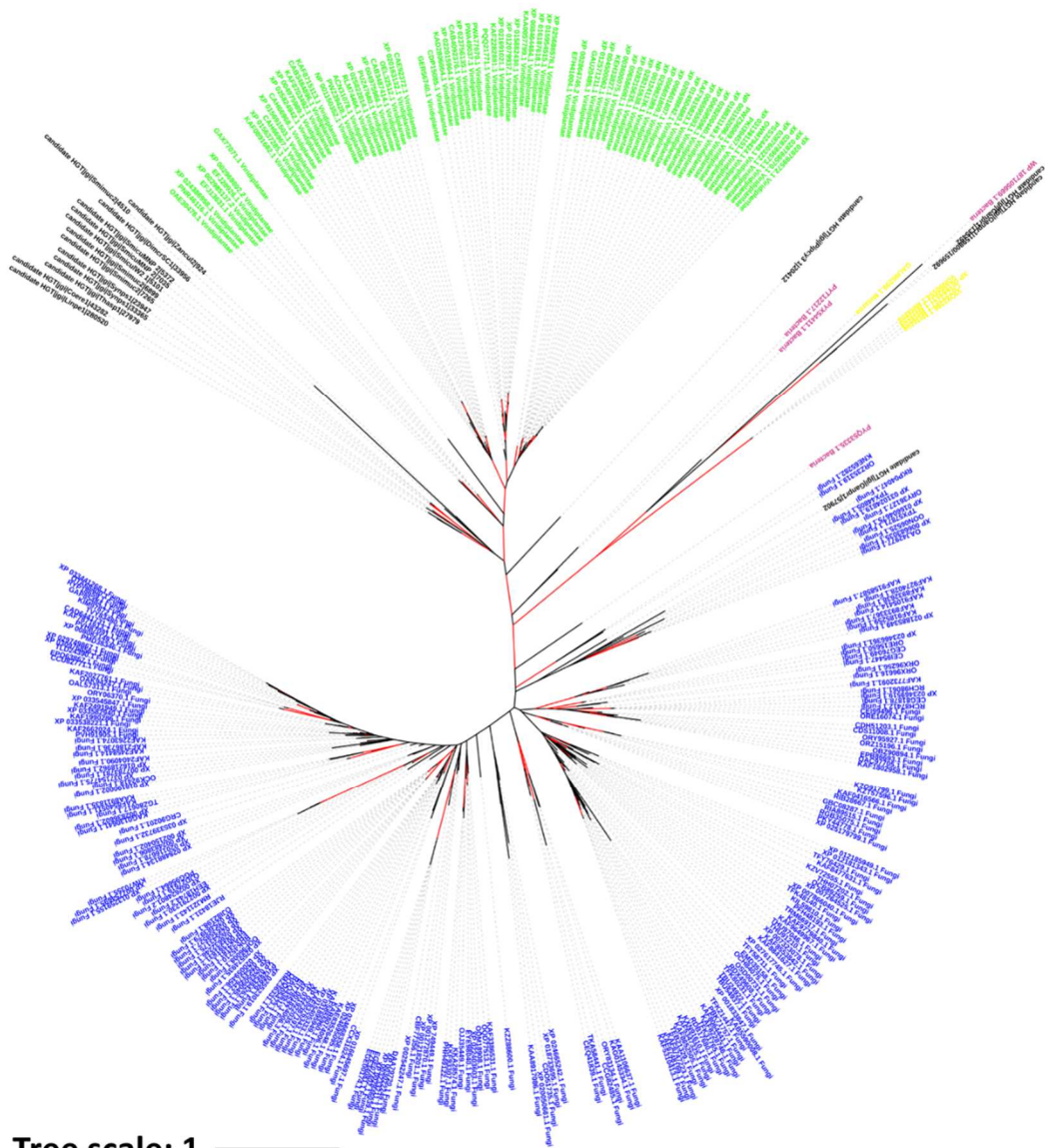
634         Several discrepancies suggested that some Msrs could have arisen from horizontal gene  
635 transfer. These discrepancies were: i) the positioning in phylogenetic clusters not reflecting the  
636 phylogeny of the species from which they were isolated (**Fig. S1-3**), ii) the presence of non-canonical  
637 sequence features (**Data S2-4**), and iii) the presence of *fRmsr* genes in the genome of three strictly



638 anaerobic neocallimastigomycetes, whereas other organisms from the same phylum had no *msr* genes  
639 (**Table 2**). To evaluate the possibility of horizontal gene transfers, we selected all Msr sequences (67  
640 MsrAs, 48 MsrBs and 8 fRMsrs) with one or more of these discrepancies and searched for their closest  
641 putative homologs by BLASTP search in all organisms recorded in the NCBI nr database. We  
642 discarded all the sequences for which the closest homologs were found in other fungal taxa. Indeed,  
643 because of the strong conservation of the protein sequences, it would be difficult to ascertain the  
644 occurrence of fungus-to-fungus horizontal gene transfers. We retrieved 17 MsrA, three MsrB and three  
645 fRMsr protein sequences for further analysis (**Fig. 4-6**). For each type of Msr, we used the selected  
646 protein sequences, together with the respective 25 sequences with the highest identity score from fungi  
647 on the one hand and from non-fungal organisms on the other hand for phylogenetic analyses (**Fig. 4-**  
648 **6**). The phylogenetic trees highlighted two MsrA, three MsrB and three fRMsr sequences, among the  
649 selected candidates, clustering with bacterial and amoeba homologs (**Fig. 4-6, Table 3**). Moreover, we  
650 identified two additional fungal fRMsrs, not included in our primary data set, which clustered with  
651 bacterial proteins (**Fig. 6, Table 3**). Except for two MsrBs from Orbiliomycetes (Ascomycota), all  
652 these Msr sequences were from early-diverging fungi (**Table 3**). Interestingly, in the cases of MsrA  
653 and MsrB, they were all from organisms having another gene coding for a canonical enzyme in their  
654 genomes (**Data S1-3**).

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

663



Tree scale: 1 —

664

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

677

678 **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 (%)	
<b>MsrA</b>								
<b>Monoblepharidomycetes</b>								
<i>Gonapodya prolifera</i> v1.0	135492 <sup>a</sup> (36)	3	56.4	61.3	5.7 ± 4.8	56.5 ± 3.4	65.2 ± 8.5	<i>Alkaliphilus oremlandii</i> OhILAs
<i>Gonapodya prolifera</i> v1.0	159800/ 159692 <sup>a</sup> (105)	4	58.9	69.6	5.8 ± 3.8	57.3 ± 4.2	67.4 ± 8.2	
<b>MsrB</b>								
<b>Orbiliomycetes</b>								
<i>Arthrotrrys oligospora</i> ATCC 24927	9001 (00170)	1	55.6	56.5	3.0 ± 2.3	48.0 ± 2.4	48.0 ± 4.6	<i>Sphingomonas</i> bacterium
<i>Monacrosporium haptotylum</i> CBS 200.50	10089 (00497)	1	55.8	58.0	4.3 ± 4.3	49.0 ± 2.7	52.9 ± 5.3	<i>Sphingomonas</i> bacterium
<b>Taphrinomycotina</b>								
<i>Protomyces lactucaedebilis</i> 12-1054 v1.0	391028 (3)	1	54.9	52.1	1.6 ± 1.0	52.6 ± 1.9	54.4 ± 5.9	<i>Calothrix parasitica</i>
<b>fRMsr</b>								
<b>Neocallimastigomycetes</b>								
<i>Anaeromyces robustus</i> v1.0	328892 <sup>b</sup> (243)	1	30.1	14.8	4.2 ± 4.5	26.3 ± 5.0	11.8 ± 3.3	<i>Pseudobutyrvibrio</i> sp. LB2011
<i>Neocallimastix californiae</i> G1 v1.0	697339 (7)	1	27.5	9.8	4.6 ± 4.4	28.8 ± 4.4	16.7 ± 5.4	<i>Erysipelotrichaceae</i> bacterium
<i>Orpinomyces</i> sp.	1191427 (d_7180000085738)	1	34.8	22.5	3.0 ± 2.9 <sup>d</sup>	27.2 ± 5.4 <sup>d</sup>	16.0 ± 7.8 <sup>d</sup>	<i>Pseudobutyrvibrio ruminis</i>
<i>Piromyces</i> sp.	AWI66787.1 <sup>bc</sup>	1	31.3	9.9	n.d.	33.2 ± 5.7	23.3 ± 11.1	<i>Pseudobutyrvibrio ruminis</i>
<b>Mucoromycotina</b>								
<i>Mortierella</i> sp. GBA39	KAF9144191.1 <sup>c</sup> (77)	1	55.2	62.4	1.4 ± 0.7	57.1 ± 3.5	71.3 ± 6.0	<i>Paenibacillus rhizosphaerae</i>

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

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

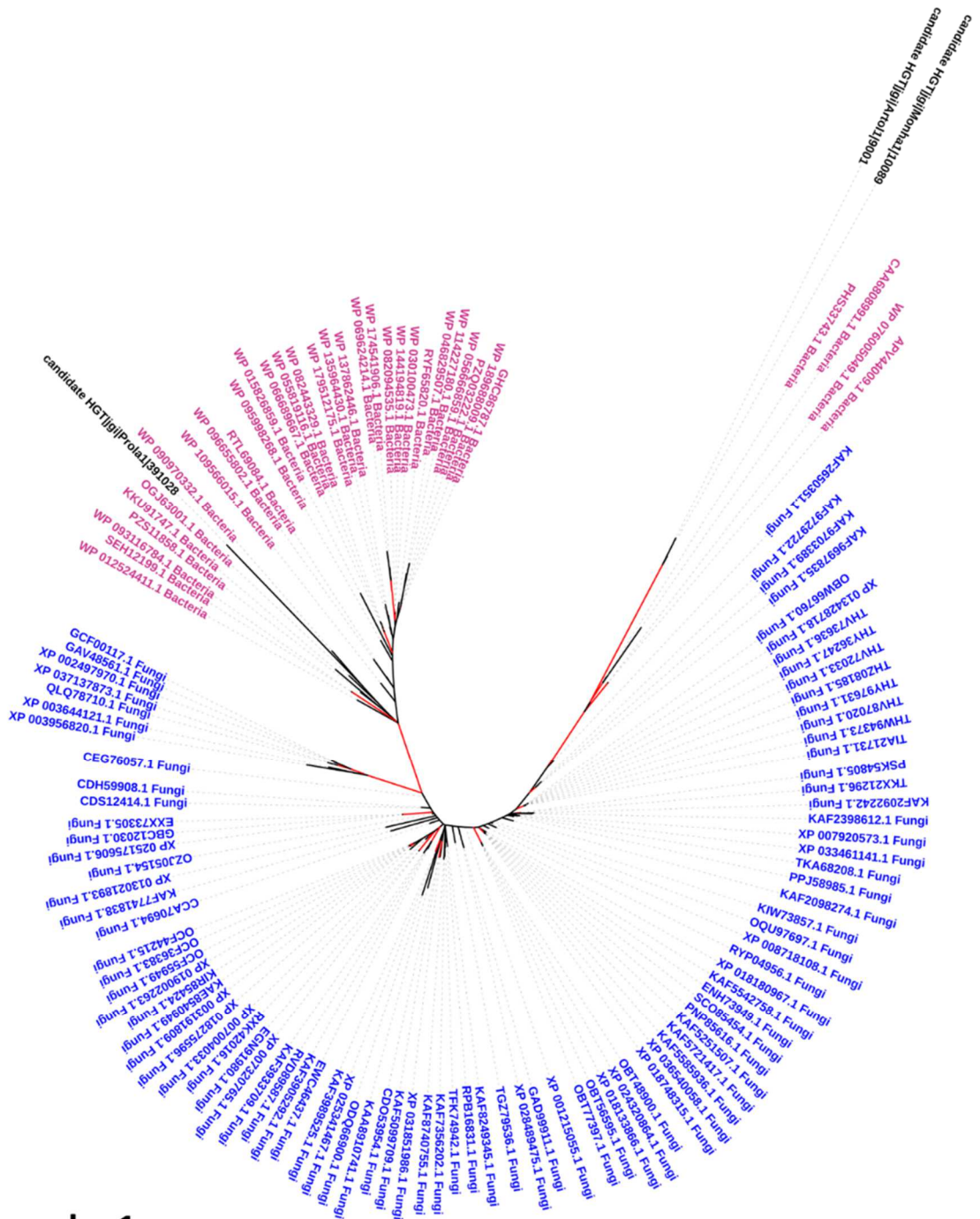
682 <sup>c</sup> The protein accessions are from NCBI (<https://www.ncbi.nlm.nih.gov/protein>).

683 <sup>d</sup> The positions of *Orpinomyces* sp. genes on the scaffolds are not publically available. The calculations were made on the  
684 complete genome.

685 n.d, not determined.

686

687           In the case of MsrBs, the three selected sequences clustered with bacterial MsrBs (**Fig. 5**). The  
688 two MsrBs from the Orbiliomycetes species *Arthrobotrys oligospora* and *Monacrosporium*  
689 *haptotylum* had MsrBs from *Sphingomonas* bacteria as closest homologs. Both fungi trap nematodes  
690 in soil [197], and sphingomonads have been isolated from many different land and water habitats  
691 [414], indicating that the co-occurrence in the same habitat of a sphingomonad donor and a common  
692 ancestor of *A. oligospora* and *M. haptotylum* is plausible, which could have allowed horizontal gene  
693 transfers. Another potential horizontal gene transfer for MsrB was identified, from a donor  
694 cyanobacterium related to the marine *Calothrix parasitica* to the plant pathogen fission yeast  
695 *Protomyces lactucaedebilis* (Taphrinomycotina) (**Table 3**). In this case, the ecology of the extant  
696 candidate donor and acceptor do not support the co-occurrence of both organisms in a same ecological  
697 niche.  
698



Tree scale: 1 —

699

700 **Figure 5. Phylogenetic analysis of MsrB candidates to horizontal gene transfer.** The fungal MsrBs  
 701 tested for horizontal gene transfer (in *black*) are from the following genomes (protein accessions in  
 702 brackets): *Arthrotritys oligospora* ATCC 24927 (9001); *Monacrosporium haptotylum* CBS 200.50  
 703 (10089) and *Protomyces lactucaedebilis* 12-1054 v1.0 (391028). The MsrBs sequences from fungi and  
 704 bacteria are in *blue* and *purple*, respectively. The phylogenetic tree was built with RAxML v. 8.2 [348]  
 705 and represented using iTOL (<https://itol.embl.de/>) [412]. The branches with bootstrap values over 70  
 706 are in *red*.

707

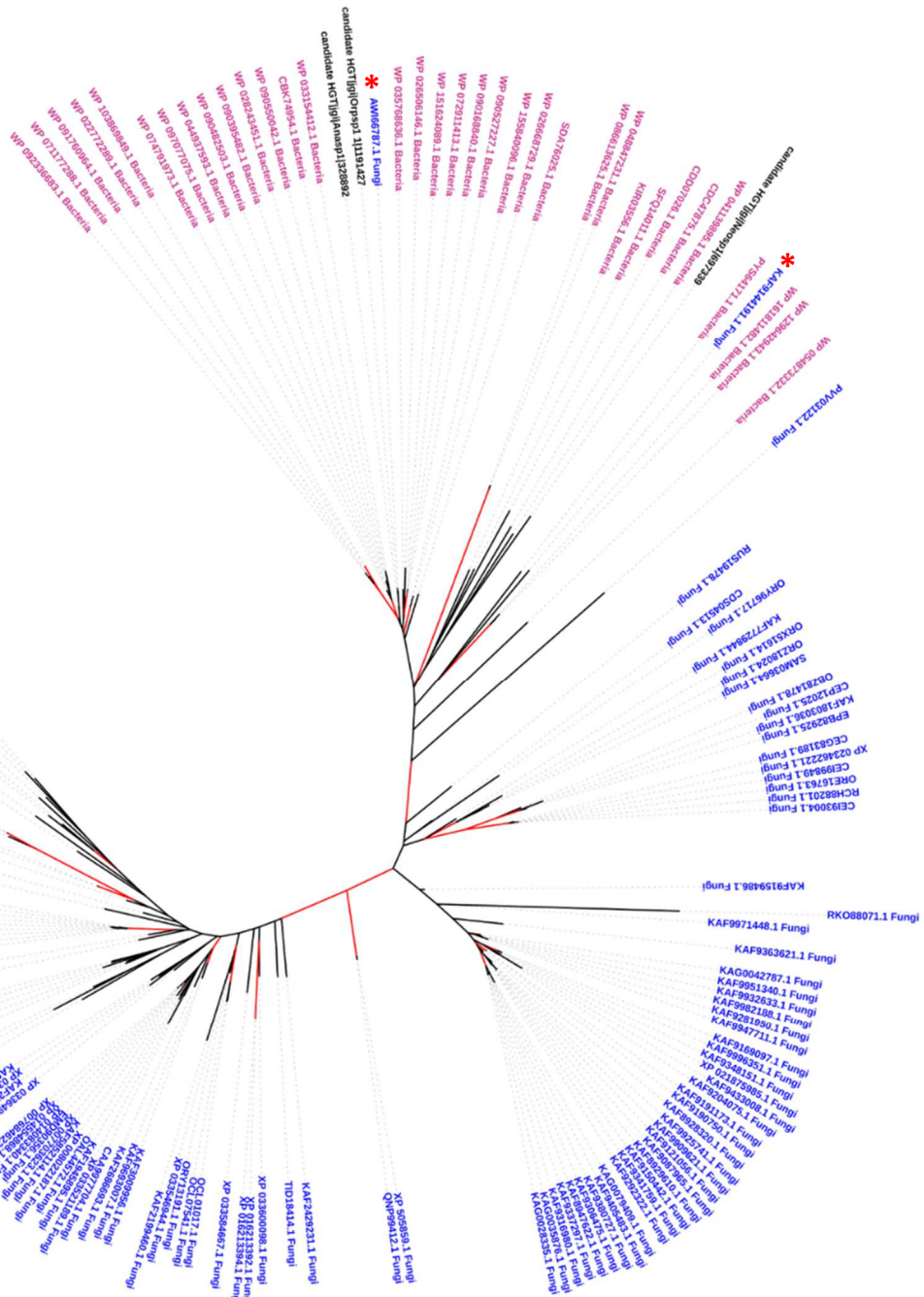
708

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

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

736 Altogether, these analyses showed that the phylogeny of fungal Msrs globally matched the  
737 phylogeny of the fungi, in accordance with vertical inheritance of the genes from bacterial ancestors  
738 [8,9,24,26]. However, a few horizontal gene transfer events occurred in each Msr family, that  
739 contributed to the distribution of Msr genes in extant species.

Tree scale: 1 



740

741 **Figure 6. Phylogenetic analysis of fRMsr candidates to horizontal gene transfer.** The fungal  
 742 fRMsrs tested for horizontal gene transfer (in *black*) are from the following genomes (protein  
 743 accessions are in brackets): *Anaeromyces robustus* v1.0 (328892); *Neocallimastix californiae* G1 v1.0  
 744 (697339) and *Orpinomyces sp* (1191427). The fRMsrs sequences from fungi and bacteria are in *blue*  
 745 and *purple*, respectively. *Red* stars indicate *fRmsr* genes possibly acquired by horizontal gene transfer,  
 746 which were not identified in our genomics search but found as homologs of the selected fungal fRMsr  
 747 candidates. The phylogenetic tree was built with RAxML v 8.2 [348] and represented using iTOL  
 748 (<https://itol.embl.de/>) [412]. The branches with bootstrap values over 70 are in *red*.

749

750

#### 751 4. Discussion

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

780 We found few variations in the numbers of gene copies of each type of Msr, with only 74  
781 genomes lacking one gene, and 72 genomes with an extra copy of at least one *msr* gene. In both cases,  
782 it roughly corresponded to 10 percent of the analyzed genomes. Our study revealed the absence of  
783 both MsrA and MsrB in 15 species of fungi, twelve of these being also devoid of fRMsr. The lack of  
784 all Msr appears to be related to the fungal lifestyles, since it concerned the nine Microsporidia, and the  
785 *Pneumocystis jirovecii* species, which live as intracellular parasites of metazoans. These 10 species  
786 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 fRMs. 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 *msrA* genes in *Gonapodya prolifera*, and *msrB* genes in *Arthrobotrys oligospora*, *Monacrosporium haptotylum* and *Protomyces lactucaedebilis*. Together with the horizontal transfers of fRMs 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

823 through distinct transcriptional activities. It could also allow different subcellular targeting as shown  
824 for plant Msrs [419]. Indeed, in 23 fungal genomes, out of the 59 having more than one *msrA* gene, the  
825 MsrAs were predicted to be addressed to different subcellular compartments. Similarly, MsrBs from 7  
826 genomes out of the 15 with more than one gene were predicted to be addressed to different cellular  
827 compartments. Conversely, all the multicopy fRMsrs were predicted to be cytoplasmic. Our results  
828 indicate that, as experimentally demonstrated for yeast [39], most fungi might not have the ability to  
829 reduce the two diastereomers of protein-bound MetO in each subcellular compartment, suggesting  
830 variations in protein oxidation in the different cellular compartments. Another interesting aspect is the  
831 presence of potentially secreted Msrs in few fungal species, mostly from the Ascomycota genera  
832 *Aspergillus* and *Penicillium*. Although it remains to be demonstrated experimentally, the presence of  
833 Msrs in the extracellular environment of the fungal cells could help to protect from oxidation the  
834 numerous secreted carbohydrate-active enzymes ('CAZymes') and other enzymes used by saprotrophic  
835 and pathogen fungi to degrade plant cell walls or insect chitins [231].

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

855

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864

865 **Declaration of competing interest.**

866 None.

867

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