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## Comparative genome analysis of Basidiomycete fungi

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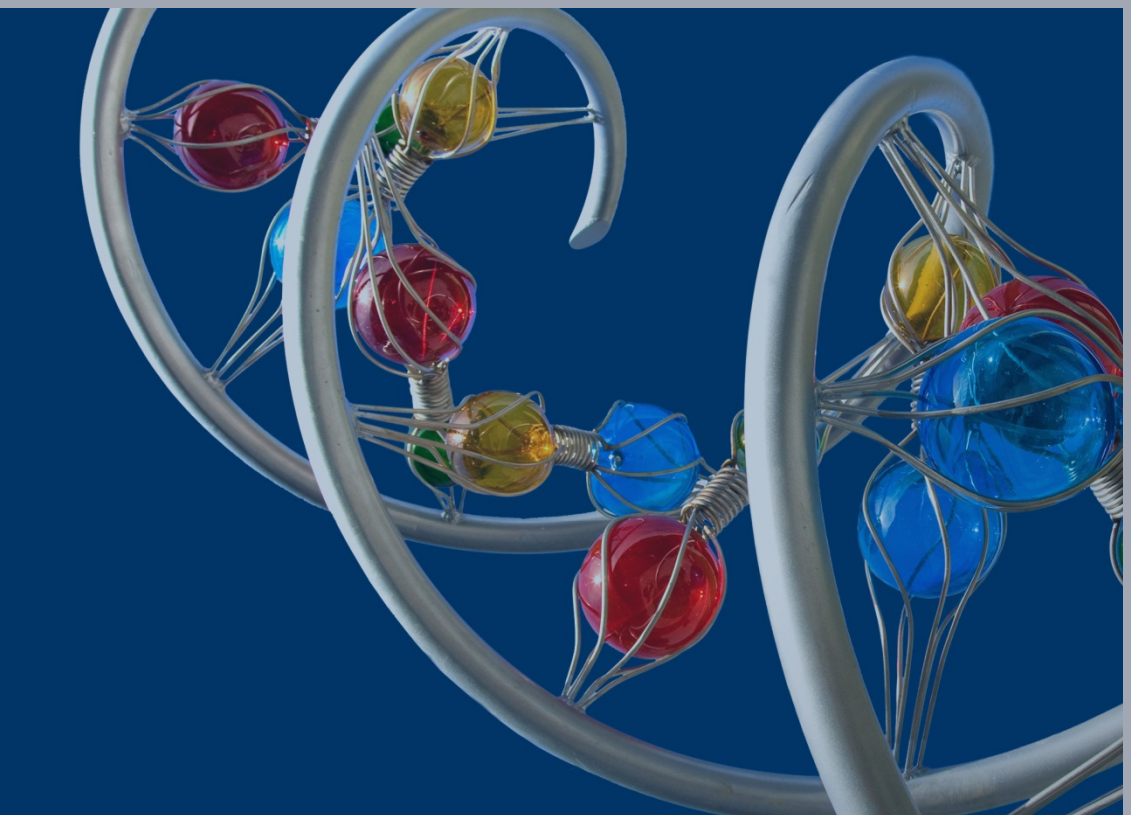
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**Abstract**  
Fungi of the phylum Basidiomycota (basidiomycetes), make up some 37% of the described fungi, and are important in forestry, agriculture, medicine, and bioenergy. This diverse phylum includes symbionts, pathogens, and saprotrophs including the majority of wood decaying and ectomycorrhizal species. To better understand the genetic diversity of this phylum we compared the genomes of 35 basidiomycetes including 6 newly sequenced genomes. These genomes span extremes of genome size, gene number, and repeat content. Analysis of core genes reveals that some 48% of basidiomycete proteins are unique to the phylum with nearly half of those (22%) found in only one organism. Correlations between lifestyle and certain gene families are evident. Phylogenetic patterns of plant biomass-degrading genes in Agaricomycotina suggest a continuum rather than a dichotomy between the white rot and brown rot modes of wood decay. Based on phylogenetically-informed PCA analysis of wood decay genes, we predict that that *Botryobasidium botryosum* and *Jaapia argillacea* have properties similar to white rot species, although neither has typical ligninolytic class II fungal peroxidases (PODs). This prediction is supported by growth assays in which both fungi exhibit wood decay with white rot-like characteristics. Based on this, we suggest that the white/brown rot dichotomy may be inadequate to describe the full range of wood decaying fungi. Analysis of the rate of discovery of proteins with no or few homologs suggests the value of continued sequencing of basidiomycete fungi.



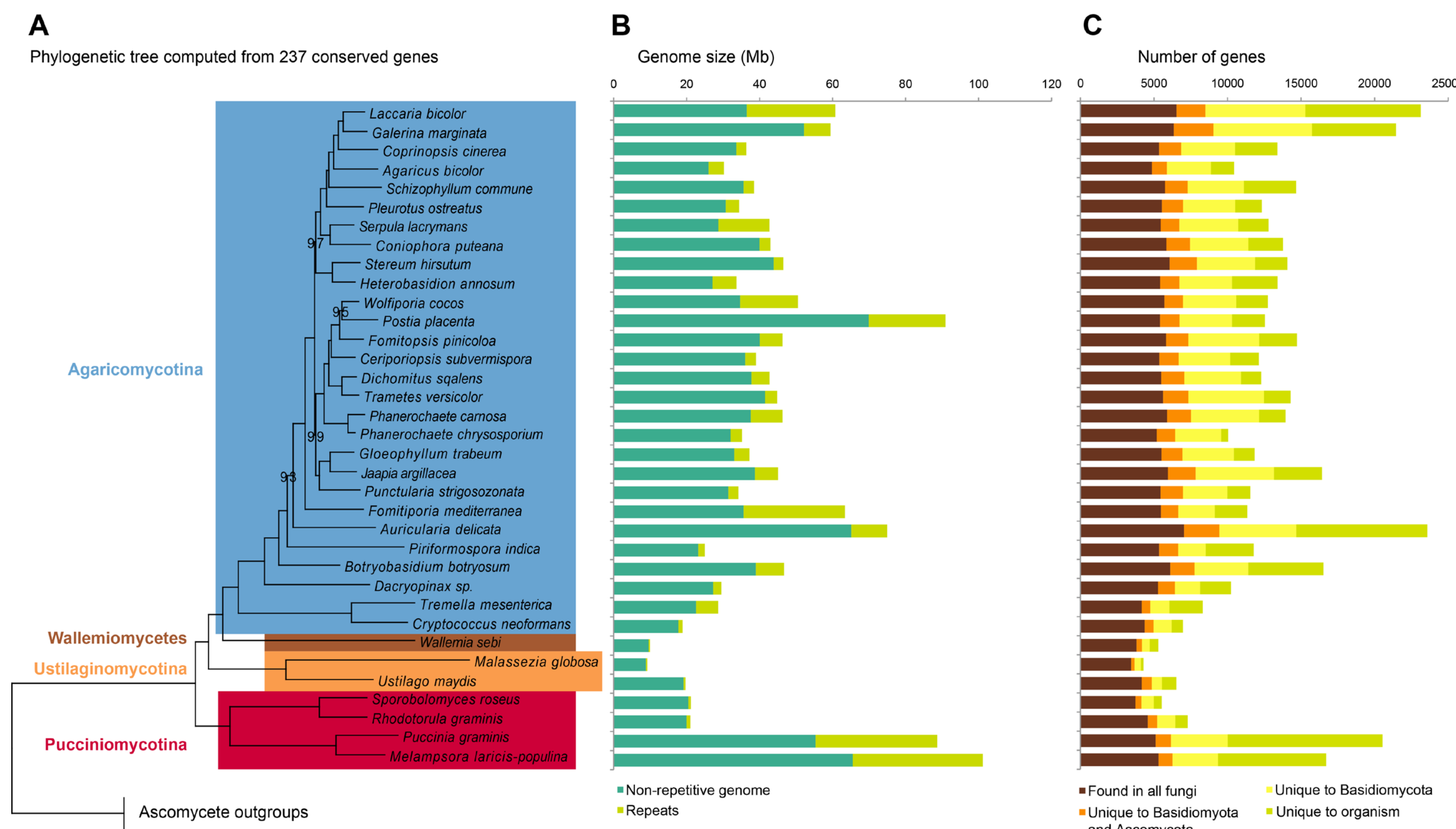
http://jgi.doe.gov/fungi

**Fungal Genomics Program**  
Exploration of fungal diversity

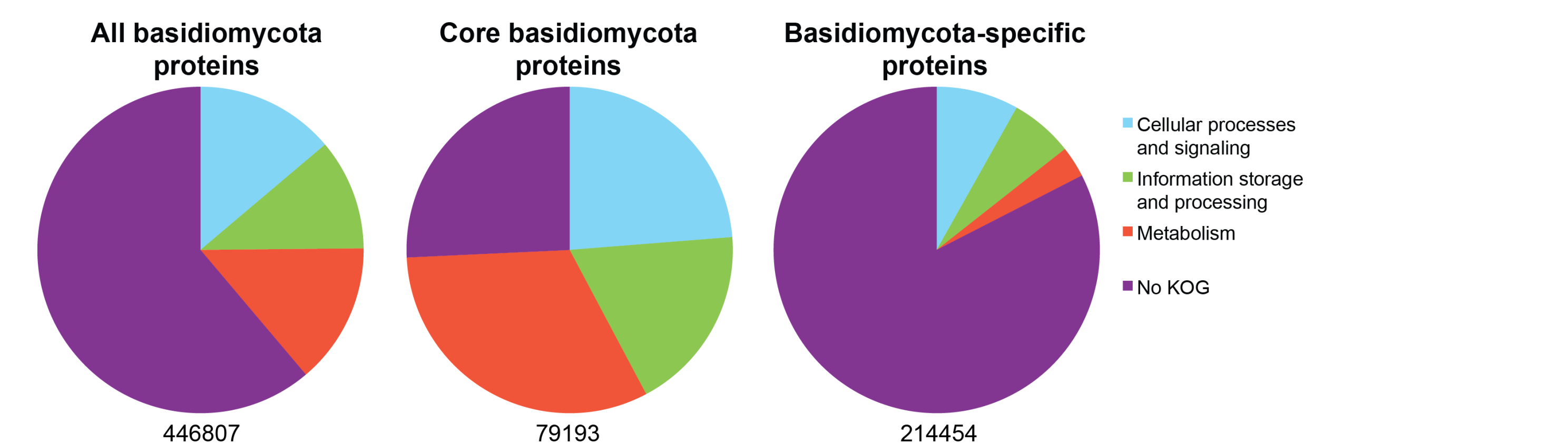
**Genomic Encyclopedia of Fungi**

**MycosCosm**  
the fungal genomics resource

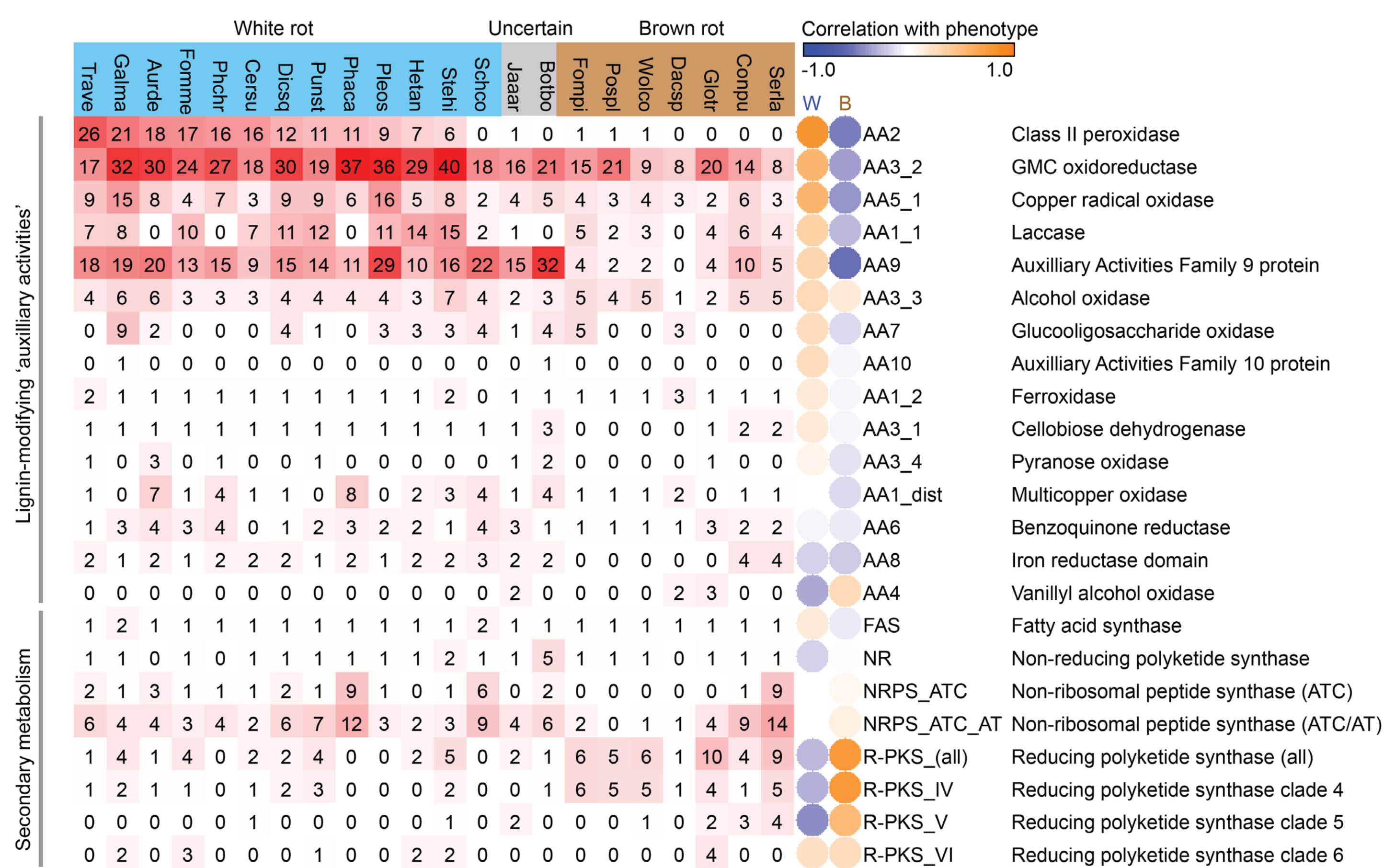
Subphylum	Order	Organism	Genome size (Mb)	Gene number		
Agaricomycotina	Agaricales	<i>Agaricus bisporus</i>	30.2	10438		
		<i>Coprinopsis cinerea</i>	36.3	13393		
		<i>Galerina marginata</i>	59.4	21461		
		<i>Laccaria bicolor</i>	64.9	19036		
		<i>Pleurotus ostreatus</i>	34.3	12330		
		<i>Schizophyllum commune</i>	38.5	13210		
		Auriculariales	<i>Auricularia delicata</i>	74.9	23577	
		Boletales	<i>Serpula lacrymans</i>	42.8	12917	
			<i>Coniophora puteana</i>	43.0	13761	
		Cantharellales	<i>Botryobasidium botryosum</i>	46.7	16526	
		Corticiales	<i>Punctularia strigosozonata</i>	34.2	11538	
			<i>Dacryopinax sp.</i>	29.5	10242	
		Gloeophyllales	<i>Gloeophyllum trabeum</i>	37.2	11846	
			<i>Hymenochaetales</i>	<i>Fomitiporia mediterranea</i>	63.4	11333
		Jaapiales	<i>Jaapia argillacea</i>	45.1	16419	
		Polyporales	<i>Dichomitus squalens</i>	42.7	12290	
			<i>Ceriporiopsis subvermispora</i>	39.0	12125	
			<i>Fomitopsis pinicola</i>	46.3	14724	
			<i>Phanerochaete camosa</i>	46.3	13937	
			<i>Phanerochaete chrysosporium</i>	35.1	10048	
			<i>Postia placenta</i>	90.9	9113	
			<i>Trametes versicolor</i>	44.8	14296	
			<i>Wolfiporia cocos</i>	50.5	12746	
			Russulales	<i>Heterobasidium annosum</i>	33.6	13405
				<i>Stereum hirsutum</i>	46.5	14072
			Sebacinales	<i>Piriformospora indica</i>	25.0	11767
			Tremellales	<i>Cryptococcus neoformans</i>	18.9	6967
		Pucciniomycotina	Pucciniales	<i>Tremella mesenterica</i>	28.6	8313
				<i>Puccinia graminis</i>	88.6	20534
				<i>Melampsora laricis-populina</i>	101.1	16831
		Sporidiobolales	<i>Rhodotorula graminis</i>	21.0	7283	
			<i>Sporobolomyces roseus</i>	21.2	5536	
		Ustilaginomycotina	Ustilaginales	<i>Ustilago maydis</i>	19.7	6522
			Malasseziales	<i>Malassezia globosa</i>	9.0	4286
		Unclassified	Wallemiales	<i>Wallemia sebi</i>	9.8	5284



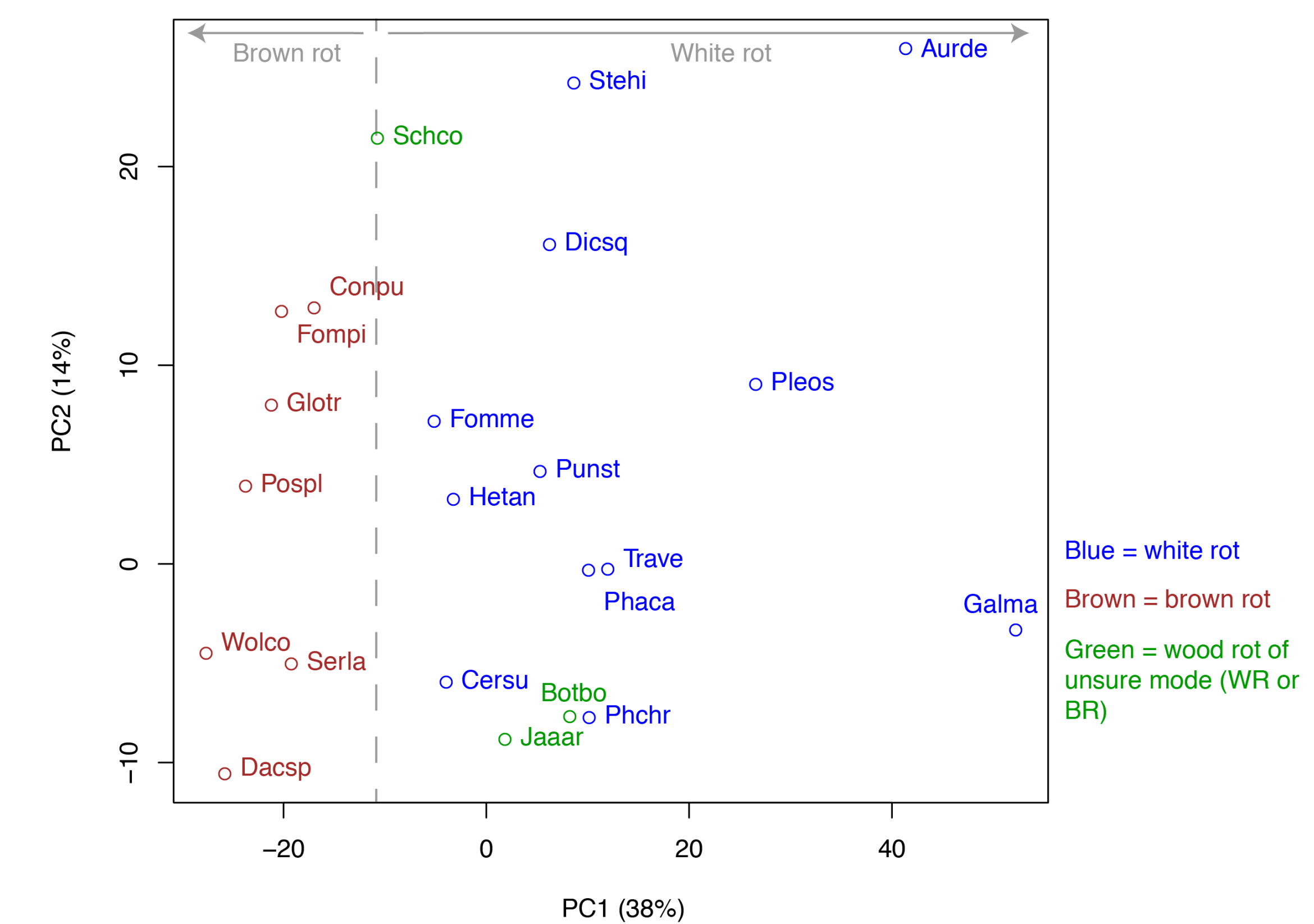
Phylogeny, genome size and repeats, gene conservation. **A.** Maximum likelihood tree of 35 basidiomycetes based on concatenated alignments of 237 widely conserved genes. Ascomycete outgroups are omitted from figure. Bootstrap values of branches are 100% except where indicated. **B.** Repeat content in basidiomycetes is highly variant, ranging from 1% to 44%. **C.** About 42% of basidiomycete genes are conserved in all published fungi. Some 10% are unique to Basidiomycota and Ascomycota; 26% are unique to basidiomycetes, and another 22% are organism-specific within basidiomycetes, which, while biased by taxon sampling, highlights the novel functions yet to be uncovered in the phylum.



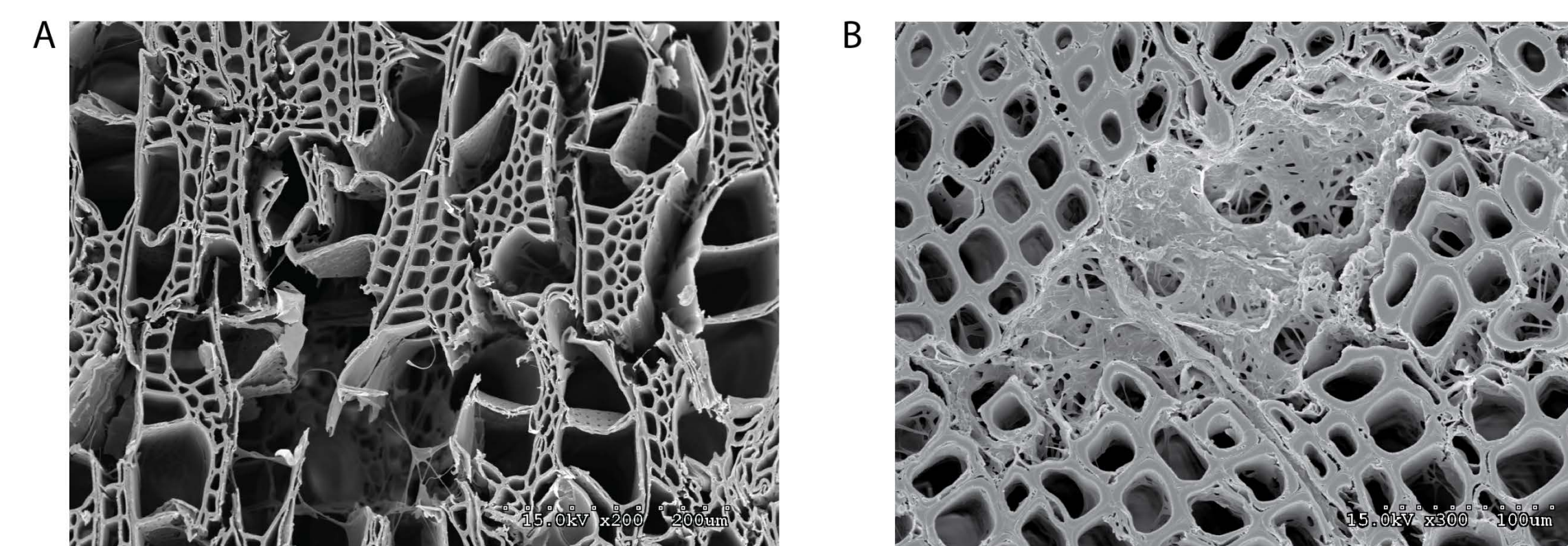
Core genes of Basidiomycota. Notice that half of basidiomycete proteins have no KOG annotation (function unknown); 92% of core basidiomycete proteins have a KOG annotation (putative function predicted) and that 78% of non-core basidiomycete proteins have no KOG annotation (function unknown)



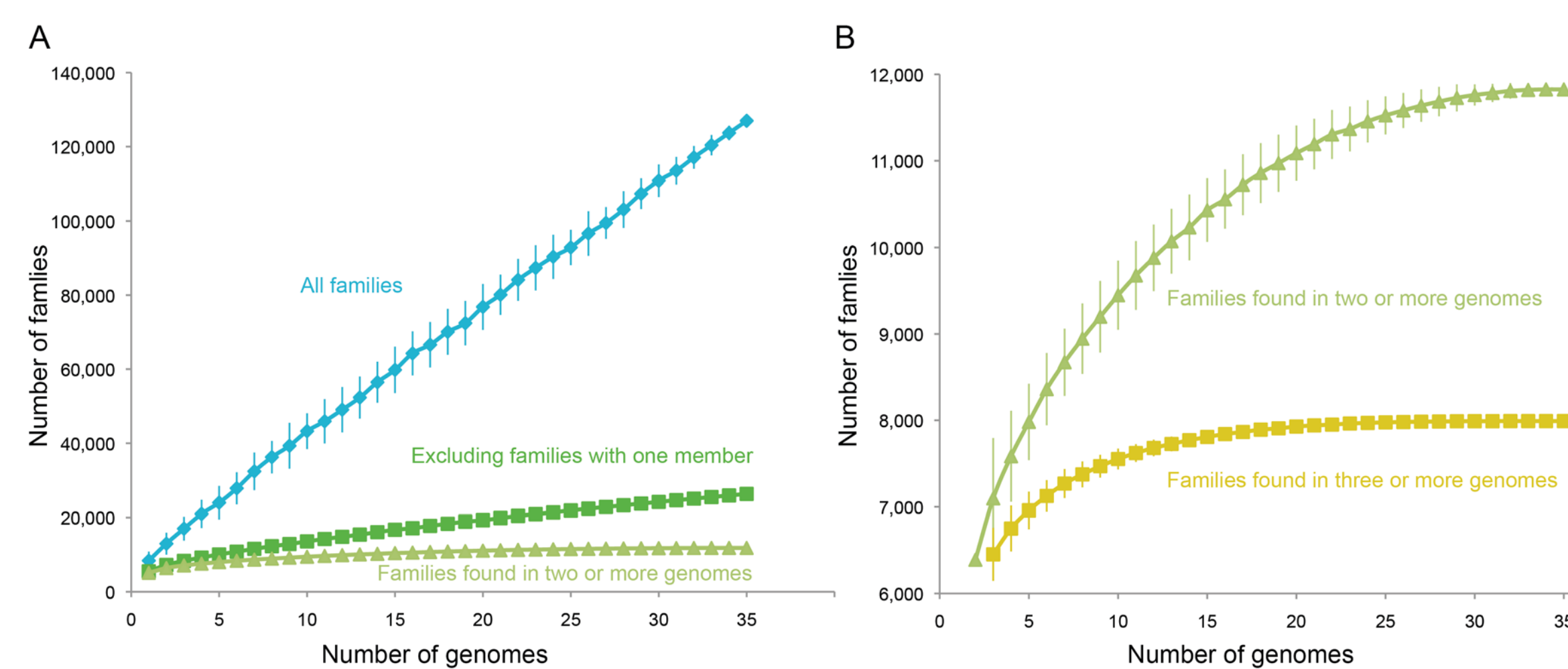
Lignin-degrading and secondary metabolism in wood-decaying fungi. Gene copy number is shaded red/white and independent contrasts correlation(36) of enzyme with rot type shaded orange/blue. Notice the white/brown rot dichotomy with respect to the lignin peroxidase-containing category AA2 (containing the PODs), and blurred line between white/brown rots with the other enzymes. *B. botryosum* and *J. argillacea* lack PODs but possess other enzymes potentially involved in lignin breakdown. The distribution of secondary metabolism enzymes suggests that the reducing polyketide synthase (R-PKS) enzymes are expanded in the brown rot fungi.



Wood-decaying basidiomycetes plotted on the first two principal components from phylogenetic PCA of CAZymes (including lignin-related auxiliary activities) of the organisms. Note the separation of brown rot fungi (brown), white rot fungi (blue) on PC1, which explains 38% of the variability. *B. botryosum* and *J. argillacea* group with *C. subvermispora* and *P. chrysosporium*, suggesting possible similarities to these fungi known to produce white rot. *S. commune*, previously characterized as able to produce white rot, is midway between white and brown rot. Though the brown rot fungi are all together on PC1, the polypores *F. pinicola*, *P. placenta*, and *W. cocos*, are spread out on PC2 (14% of variability), suggesting the power of phylogenetic PCA to deconvolute phylogenetic similarities of organisms.



Wood decay experiments indicating white rot-like mode of decay in *Botryobasidium botryosum* and *Jaapia argillacea*. **A.** Micrograph of *B. botryosum* on aspen wood with vessel, fiber and parenchyma cell walls degraded. All cell wall layers are degraded resulting in small voids in the wood. Mycelia are visible growing through voids. **B.** Micrograph of *J. argillacea* on pine showing an area within the wood where the fungus has caused a localized simultaneous decay of the cells. Residual cell wall material and hyphae fill the degraded zone.



Rate of protein family discovery from newly sequenced basidiomycete genomes. MCL clustering of protein sequences was used to identify protein families. For each number of genomes, samples of genomes of a given number were randomly generated, and the protein families were counted. Panel A illustrates that many new protein families are still being discovered from each new basidiomycete genome sequenced, and that the gains are more modest, but still increasing, for families with more than one member. Panel B indicates that most of the families conserved in multiple genomes have been discovered by sequencing efforts.