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The Mushroom Lectins Show Three Types of Conserved Domain in a Bioinformatics Analysis

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ABSTRACT

The primary object of this study was to find conserved domains and sequence homology in the mushroom lectins. Mushroom lectins, a group of carbohydrate binding proteins from fungi, have attracted wider attention due to their importance in the bio-medical research. Unlike plant lectins, they are much diverse in their structures, sequences and carbohydrate recognition properties. In the present study, 22 sequences of lectins and homologous putative proteins from class *Agaricomycetes* in fungi comprising edible as well as toxic mushrooms from NCBI protein database were collected and analyzed to understand their evolutionary homology and to find presence of conserved domains. Based on the phylogeny tree, three major groups were identified. Group-1 consists of nine proteins and is characterized by the presence of Gal-Binding lectin domain, however large sequence diversity among the members was observed. Group-2 consists of six proteins and is characterized by the presence of fungal fruit body lectin domain. Members of Group-2 showed high homology with each others as compared to Group-1 and 3. Group-3 consists of five proteins and is characterized by the presence of ricin-B like domain. In the study two lectins from *Laetiporus sulphureus* and *Psathyrella velutina* were also identified that showed huge difference in the sequence from other members and characterized by unique structures. In conclusion, based on this study, mushroom lectins were divided in to three groups on the basis of conserved domains and their mutual homology.

Key words: Fungal, hemagglutinin, clustalW, genome, phylogeny

INTRODUCTION

Lectins, well known as carbohydrate binding proteins, represent a diverse group of evolutionary unrelated proteins; they are characterized for their non-immune origin and depiction of high degree of stereo-specificity in a non-catalytic manner (Khan and Khan, 2011; Bashir *et al*., 2010). The lectins have been well characterized for their properties such as-specificity (Khan *et al*., 2009), active site (Yeasmin *et al*., 2007a) and biological activity (Yeasmin *et al*., 2007b; Tanaka *et al*., 2009; Elmer-Rico and Merca, 2005; Hamid and Masood, 2009) and have wide spread applications in bio-medical research (Khan and Khan, 2011; Rahaie and Kazemi, 2010).

Lectins have been shown to play certain biological roles in cellular signaling, malignancy, host pathogen interactions, scavenging of glycoproteins from the circulatory system, cell-cell interactions in the immune system, differentiation and protein targeting to cellular compartments etc. (Springer and Lasky, 1991; Khan and Khan, 2011; Ashwell and Harford, 1982; Fokunang and Rastall, 2003). The plant and animal lectins, earlier, were studied at most for every details of their biochemical properties (Rini and Lobsanov, 1999; Rudiger and Gabius, 2001), whereas, fungal

lectin were limited only to certain aspects of their properties (Singh *et al*., 2010; Khan and Khan, 2011). Now-a-day, mushroom and other fungal lectins are gaining wider attraction due to their antitumor, antiproliferative and immunomodulatory activities (Wang *et al*., 2000; Wasser and Weis, 1999). Presence of fungal lectin is no more considered as an obscure phenomenon as it was earlier but their physiological role still remains uncertain (Tronchin *et al*., 2002; Candy *et al*., 2003; Khan *et al*., 2007).

Bioinformatics is an emerging branch of biological sciences involving statistics and computational science in the field of molecular biology. In recent years, rapid sequencing technique has generated huge amount of DNA and protein sequences from various organisms. Bioinformatics analyses of the protein and DNA sequences can be used to generate important information related to protein interaction, protein structure, drug discovery and evolutionary modeling (Aniba *et al*., 2010; Barbarini *et al*., 2010).

Amino acid sequences of several fungal and mushroom lectins have been determined and analyzed for similarity and homology with other lectins and proteins. The amino acid sequence of *Xerocomus chrysenteron* lectin showed 69 and 64% homology with *Agaricus bisporus* and *Arthrobotrys oligospora*, respectively (Birck *et al*., 2004). The amino acid sequence of *Pleurocybella porrigens* lectin showed similarity with ricin-B-chain (33%), lectin from *Polyporus squamosus* (36%) and hemagglutinin from *Clostridium botulinum*, HA-1 (40%) (Suzuki *et al*., 2009). The sequence homology and structure prediction revealed that *Clitocybe nebularis* lectin belongs to ricin B-like superfamily (Pohleven *et al*., 2009). The lectin from Grifola frondosa showed 26.1 and 22.8% homology with jacalin like plant lectins from *Helianthus tuberosus* and *Parkia platycephala*, respectively (Nagata *et al*., 2005). On the other hand, *Sclerotinia sclerotiorum* lectin showed significant similarity only to the lectin from the fungus *Ciborinia camelliae* but not with any other lectins (Candy *et al*., 2003).

In the present study, amino acids sequence of 20 *Agaricomycetes* mushrooms lectins (classification-Kingdom: Fungi; Subkingdom: Dikarya; Phylum: Basidiomycota; Subphylum: Agaricomycotina; Class: *Agaricomycetes*) were collected and analyzed by various bioinformatics tools to explore their mutual homology and presence of conserved domains.

MATERIALS AND METHODS

Amino acid sequence for mushroom lectins (class: *Agaricomycetes*) were obtained from NCBI and aligned by ClustalW2 (Larkin *et al*., 2007) (Fig. 1-4). The alignment scores, expect value (e-value) and identity/homology (%) were obtained by aligning each 'Query' sequence with 'Subject' sequence by BLASTP (Altschul *et al*., 2005) (Table 1-3).

Sequence alignment for the following *Agaricomycetes* mushroom was found in NCBI database (accession ID given in parentheses): *Agaricus bisporus* (AAA85813), *Agrocybe aegerita* (AAP93924) (Yang *et al*., 2005a), *Agrocybe cylindracea* (1WW6_A) (Ban *et al*., 2005), *Athelia rolfsii* (ACN89784), *Clitocybe nebularis* (ACD47153) (Pohleven *et al*., 2009), *Coprinopsis cinerea* (CGL3) (2R0F_B) (Walti *et al*., 2008) *Coprinopsis cinerea* okayama 7#130 (XP_001830003) (Cioci *et al*., 2006), *Grifola frondosa* (BAE43847) (Nagata *et al*., 2005), *Laccaria bicolor* (XP_001888824) (Martin *et al*., 2008), *Psathyrella velutina* (2C25_B) (Cioci *et al*., 2006), *Laetiporus sulphureus* (1W3A_A) (Mancheno *et al*., 2005), *Lyophyllum decastes* (A7UNK4) (Goldstein *et al*., 2007), *Marasmius oreades* (3EF2_A) (Kruger *et al*., 2002), *Moniliophthora perniciosa* (XP_002397199), *Paxillus involutus* (AAT91302) (Le Quere *et al*., 2006), *Pleurocybella porrigens* (BAG85345) (Suzuki *et al*., 2009), *Pleurotus cornucopiae* (BAD16585) (Sumisa *et al*., 2004a), *Pleurotus cornucopiae* (BAB63923) (Sumisa *et al*., 2004b), *Polyporus squamosus* (BAC87876) (Tateno *et al*.,

2004), *Xerocomus chrysenteron* (AAL73236) (Birck *et al.*, 2004). The study conceived and experiments were carried out in 2007-2011 in National Chemical Laboratory, India.

RESULTS AND DISCUSSION

The sequences of the lectins were obtained from NCBI non-redundant protein database and they were subjected to construction of the phylogeny tree (Fig. 1). Based on the phylogenic tree all the lectins and related proteins from mushrooms (class: *Agaricomycetes*) were divided into three groups (Fig. 1).

Group-1: Galectin-like lectins: Group-1 was represented by nine members of the 20 fungal lectins currently under study. Many members possess a galactose binding lectin domain (Gal-Bind Lectin) (pfam00337, accession ID: cl00071) according to Conserved Domain Database (CDD) (Marchler-Bauer *et al.*, 2011). The *Coprinopsis cinerea* lectin CGL1 and CGL2 (Boulianne *et al.*, 2000) showed very close homology to the CGL3 (Walti *et al.*, 2008), hence only CGL3 is included in the analysis. CGL3 showed low homology (36% identity) with lectins from *Agrocybe aegerita* (Yang *et al.*, 2005a) and *Agrocybe cylindracea* (Ban *et al.*, 2005). All three mentioned lectins are classified as galectins and possess the galactose-binding lectin (Gal-Bind Lectin) domain. The important residues (His^{60} Arg^{64}, Asn^{73}, Glu^{84}, Arg^{86}) involved in ligand binding in CGL3 (Walti *et al.*, 2008) were conserved and present in the Gal-Bind lectin domain of *Agrocybe aegerita* and *Agrocybe cylindracea* lectins. The hypothetical lectin-like protein from the *Coprinopsis cinerea* okayama 7#130 (accession no. EAU91925) did not show any homology with CGL1, CGL2 or CGL3 but did show 73% identity with the hypothetical mannose binding lectin from *Laccaria bicolor* (Martin *et al.*, 2008). In the group AAL (*Agrocybe aegerita* lectin) (Yang *et al.*, 2005a), ACL (*Agrocybe cylindracea* lectin) (Ban *et al.*, 2005) and CGL3 (*Coprinopsis cinerea* lectin) (Walti *et al.*, 2008) showed presence of consensus sequence motif of mammalian galectins (Vasta *et al.*, 2004) which consists of His^{44}, Arg^{48}, Val^{59}, Asn^{61}, Trp^{68}, Glu^{71} and Arg^{78} (number refers to position in human galectin-1) (Yang *et al.*, 2005b) (Fig. 2: position marked by '#'). AAL and ACL showed 89% identity with each other but showed only 36% identity with CGL3 (Table 1). It was also found that in dimeric *Agrocybe aegerita* lectin each protomer adopts a prototype galectin fold (Yang *et al.*, 2009).

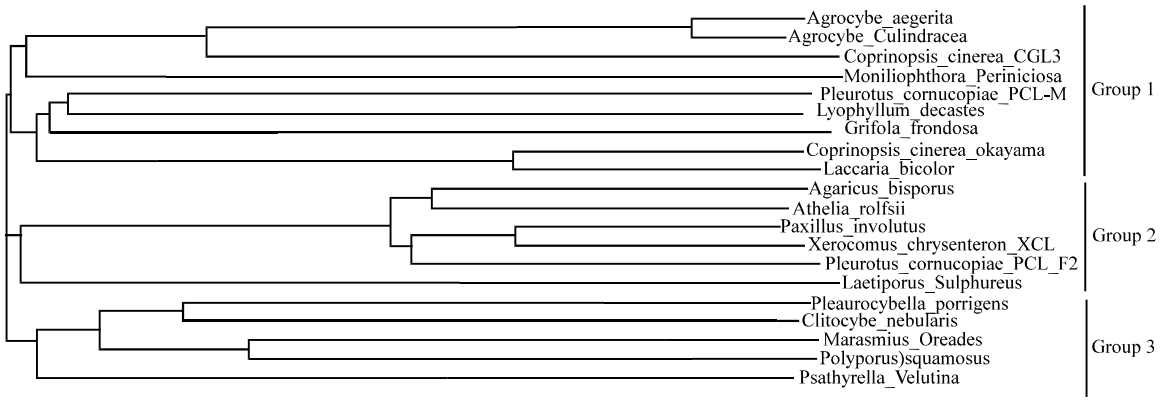

Fig. 1: Phylogeny tree of lectins. Amino acid sequences of the lectins were obtained from NCBI (http://www.ncbi.nlm.nih.gov/protein) and the phylogeny tree was prepared by the tool available at (http://www.ebi.ac.uk/Tools/clustalw2/index.html) and lectins divided into three groups following first line of phylogeny

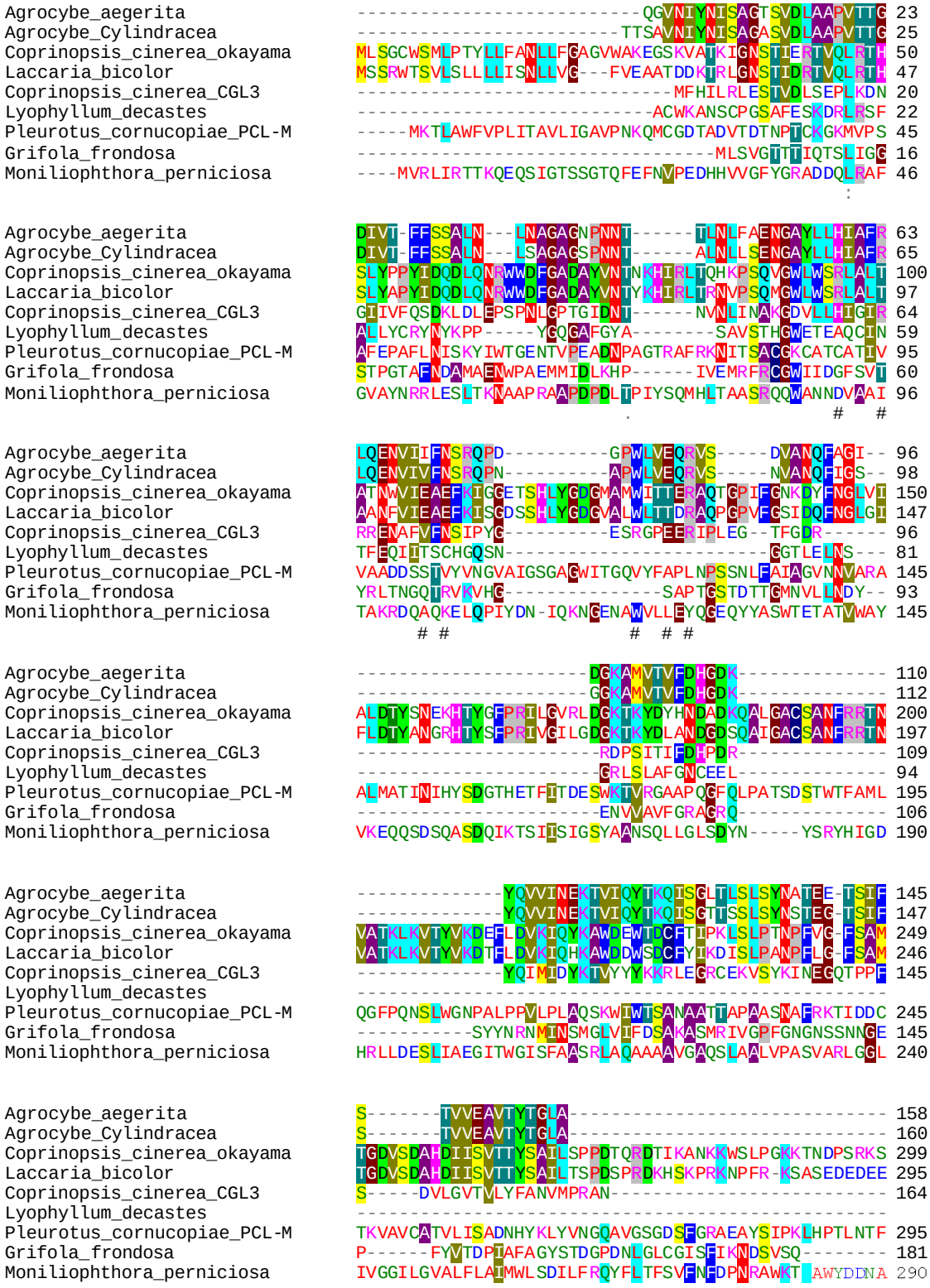

Fig. 2: Continued

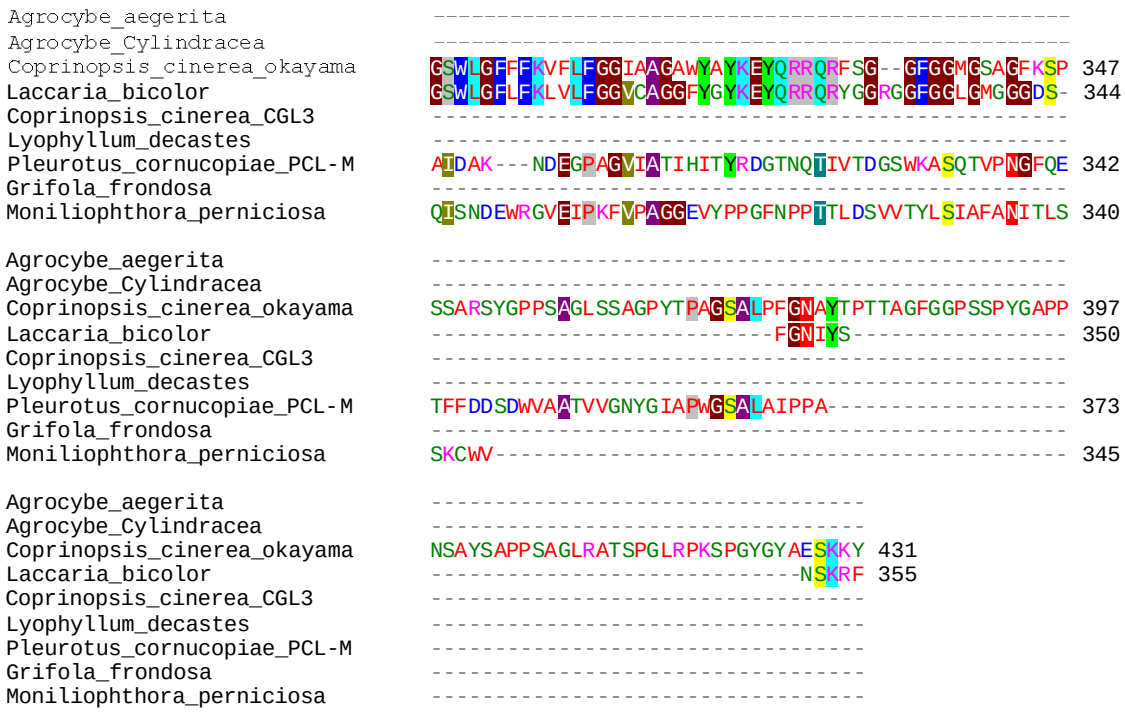

Fig. 2: Sequence alignment of Group-1 lectins. Amino acid sequences of the lectins were obtained from NCBI (http://www.ncbi.nlm.nih.gov/protein) and aligned by ClustalW2 (http://www.ebi.ac.uk/Tools/clustalw2/index.html) and manually edited and highlighted. Residues positions corresponding to consensus sequence motif of human galectin-1 are marked by '#'

The hypothetical protein from *Moniliophthora perniciosa*, however, did not show any close resemblance with any of the protein in the group but has been identified to possess a jacalin-like lectin domain. The galactosyl binding lectin from *Lyophyllum decastes* (A7UNK4) (Goldstein *et al.*, 2007) showed neither any homology with other lectins in the group nor the presence of any conservation related to galectin-like domain. The lectin from *Pleurotus cornucopiae* (Sumisa *et al.*, 2004a) was also found to possess unique amino acid sequence and it is related to stage specific development (Oguri *et al.*, 1996).

The lectin from *Grifola frondosa* (Nagata *et al.*, 2005) also showed unique sequence, without any similarity to any of the members in the Group-1. However, the lectin is reported to show similarity with jacalin-type lectins from *Helianthus tuberosus* (Van Damme *et al.*, 1999) and *Parkia platycephala* (Mann *et al.*, 2001). In the ClustalW alignment, both of the jacalin related, lectin from *Grifola frondosa* and the hypothetical protein *Moniliophthora perniciosa*, showed conservation of some residues but did not show considerable mutual homology (Fig. 2).

Group-2: Fungal fruiting body lectins: The group-2 lectins showed very high level of homology with each other. Most of the lectins in the group were found to have a conserved domain in the CDD (conserved domain database) (Marchler-Bauer *et al.*, 2011) belonging to protein superfamily FB_lectin (fungal fruit body lectin, pfam07367, accession ID: cl06418) (Wang *et al.*, 2002). The hypothetical lectin like protein from *Paxillus involutus* (Le Quere *et al.*, 2006) and lectin from *Xerocomus chrysenteron* (XCL1) (Birck *et al.*, 2004) showed maximum identity in the group

Table 1: Homology among the members of Group-1

Subject Query	Agrocybe aegerita (AAP93924)	Agrocybe cylindracea (1WW6_A)	Coprinopsis cinerea (CGL3) (2R0F_B)	Moniliophthora perniciosa (BAD16585)	Pleurotus cornucopiae (A7UNK4)	Lyophyllum decastes (BAE43847)	Grifolia frondosa okayama 7#130	Coprnosis cinerea (XP_001830003)	Laccaria bicolor (XP_001888824)
Agrocybe aegerita (AAP93924),		282, 2e-25 (89%)	80, 2e-20, (36%)	16.2, 0.7				14.2, 2	13.5, 4.1
Agrocybe cylindracea (1WW6_A)	282, 4e-81 (89%)		86.7, 4e-22, (36%)	15.8, 0.76	12.7, 6.4,		14.6, 1.6	13.5, 3.8	
Coprinopsis cinerea (CGL3) (2R0F_B)	80.5, 2e-20, (36%)	86.7, 4e-22, (36%)		15, 1.4	13.5, 3.8		16.9, 0.35		
Moniliophthora perniciosa	15, 1.6	15.8, 1.7	15.4, 2.7		17.7, 0.43	15, 2.9	28, 3.6	48.5, 0.39	65.8, 0.18
Pleurotus cornucopiae (BAD16585),			13.9, 8	92, 0.5			14.6, 4.2	15.8, 2	50.8, 0.12
Lyophyllum decastes (A7UNK4),				47.7, 0.098			15.8, 0.47	11.5, 8.7	
Grifolia frondosa (BAE43847),			16.9, 0.39	28.9, 1.6	14.6, 1.9	15.8, 0.96		13.5, 5	30, 0.47
Coprnosis cinerea okayama 7#130 (EAU91925)	14.2, 6.2	14.6, 4.5		48.5, 0.6	44.6, 2.3				452, 9e-132, (73%)
Laccaria bicolor (XP_001888824)	13.5, 9.7			48.9, 0.22	69.3, 0.093	15.4, 2.6	16.5, 1.1	471, 1e-137 (69%)	

Table 2: Homology among the members of Group-2

Subject Query	Agaricus bisporus (AAA85813)	Athelia rolfsii (ACN89784)	Paxillus involutus (AAT91302)	Xerocomus chrysenteron (AAL73236)	Pleurotus cornucopiae (BAB63923)	Laetiporus sulphureus (1W3A_A)
Agaricus bisporus (AAA85813)		177, 2e-92, (62%)	121, 9e-33, (55%)	147, 2e-40, (55%)	135, 6e-37, (52%)	28.9, 1.0
Athelia rolfsii (ACN89784),	177, 1e-49, 62%		147, 2e-40, (58%)	164, 8e-46, (56%)	149, 4e-41, (53%)	39.2, 2.2
Paxillus involutus (AAT91302)	121, 7e-33, (55%)	147, 2e-40, (58%)		172, 4e-48, (70%)	123, 2e-33, (55%)	
Xerocomus chrysenteron (AAL73236),	147, 1e-40, (55%)	164 8e-46, (56%)	172, 5e-48, (70%)		144, 9e-40, (52%)	26.6, 3.5
Pleurotus cornucopiae (BAB63923),	135, 6e-37, (52%)	149, 4e-41, (53%)	123, 2e-33, (55%)	144, 9e-46, (52%)		12.7, 4.8
Laetiporus sulphureus (1W3A_A),	28.9, 2.2	13.9, 5.0		26.6, 8.2		

(e-value: 4e-48; identity 70%). The *Agaricus Bisporus* Lectin (ABL) showed only 55% identity(e-value: 2e-40) (Table 2) with XCL but both of them share similar carbohydrate specificity for galactosamine and galactose (Trigueros *et al*., 2003). ABL, XCL1, PCL (*Pleurotus cornucopiae* lectin) and *Paxillus involutus* lectin have also been grouped with two lectins from ascomycetes (*Arthrobotrys oligospora* and *Gibberella zeae*) in a group based on sequence homology (Crenshaw *et al*., 1995; Iijima *et al*., 2002; Rosen *et al*., 1996).

The fungus *Pleurotus cornucopiae* has been reported to produce three lectins (PCL-F1, PCL-F2 and PCL-M) (Iijima *et al*., 2002; Sumisa *et al*., 2004a, b). The lectins PCL-F1 and PCL-F2 differ only by five amino acids from each other (Sumisa *et al*., 2004b) but they showed huge diversity with PCL-M and hence placed in different groups (Fig. 1). PCL-F1 and PCL-F2 showed 69% identity with lectin from *Arthrobotrys oligospora*, a nematode trapping fungi and both of the lectins are also expected to be involved in capturing nematodes (Iijima *et al*., 2002; Rosen *et al*., 1996). The hypothetical lectin from *Athelia rolfsii* showed 62% identity (*e*-value: 1e-49) with *Agaricus bisporus* lectin and showed around 50% identity with other lectins in the group (Table 2).

Among the above mentioned lectins, XCL is the only one, whose crystal structure is available. It is primarily a β-sheet sandwich structure, made up of a four stranded and six-stranded β-sheets (Birck *et al*., 2004). This kind of the structure has never been reported for any lectin superfamily and also the structure cannot be superimposed to any known lectin structure (Birck *et al*., 2004). Partial conservation was seen in the group for the residues involved in major β-sheets (Fig. 3).

The *Laetiporus sulphureus* lectin did not exhibit considerable homology to any of the lectins in the group (Table 2). This lectin is characterized by hemolytic pore-forming properties (Mancheno *et al*., 2005). This lectin exists in the form of hexamer and characterized by N-terminal lectin-like module and C-terminal pore forming module (Mancheno *et al*., 2005). In the ClustalW alignment the middle region was aligned with other lectins in the group with presence of few conserved residues but not the N- and C-terminal region (Fig. 3).

Group-3: Ricin-B like lectins: This group consists of five lectins, some of which showed presence of ricin-B like domain (pfam00652, accession ID: cl00126) (Rutenber *et al*., 1987; Rutenber and Robertus, 1991; Rutenber *et al*., 1991). The *Pleurocybella Porrigens* Lectin (PPL) showed 36% identity to *Polyporus squamosus* lectin in the group (Table 3). PPL have been reported to show some similarity with ricin (33%) (a plant lectin from *Ricinus communis*) and hemagglutinin from *Clostridium botulinum* (40%) (Suzuki *et al*., 2009). The residue (Asp and Iso, marked by # in Fig. 4) involved in galactose binding in ricin-B were conserved in lectins from *Pleurocybella porrigens* (Suzuki *et al*., 2009) and *Clitocybe nebularis* (Pohleven *et al*., 2009) (Fig. 4), whereas the conserved (Q/N)XW motif of ricin-B was also seen in the group except in *Psathyrella velutina* lectin

Table 3: Homology among the members of Group-3

Subject query	Pleurocybella porrigens (BAG85345)	Clitocybe nebularis (ACD47153)	Marasmius oreades (3EF2_A)	Polyporus squamosus (BAC87876)	Psathyrella velutina (2C25_B)
Pleurocybella porrigens (BAG85345)	32.3, 8e-06, (28%)	83.1, 2e-04 (34%)	75.5, 1e-09 (36%)	54.1, 1.3	
Clitocybe nebularis (ACD47153)	32.3 9e-06 (28%)		63.1 0.002 (27%)	78.9 3e-05 (41%)	43.1, 0.69
Marasmius oreades (3EF2_A)	70, 4e-04	63.1, 0.003		172, 2e-47 (38%)	45.8, 2.4
Polyporus squamosus (BAC87876)	75.5, 3e-09	78.9, 7e-05	172, 2e-47 (38%)		45, 1.3
Psathyrella velutina (2C25_B)	15, 4.1	30, 2.0	45.8m 3.3	45, 1.8	

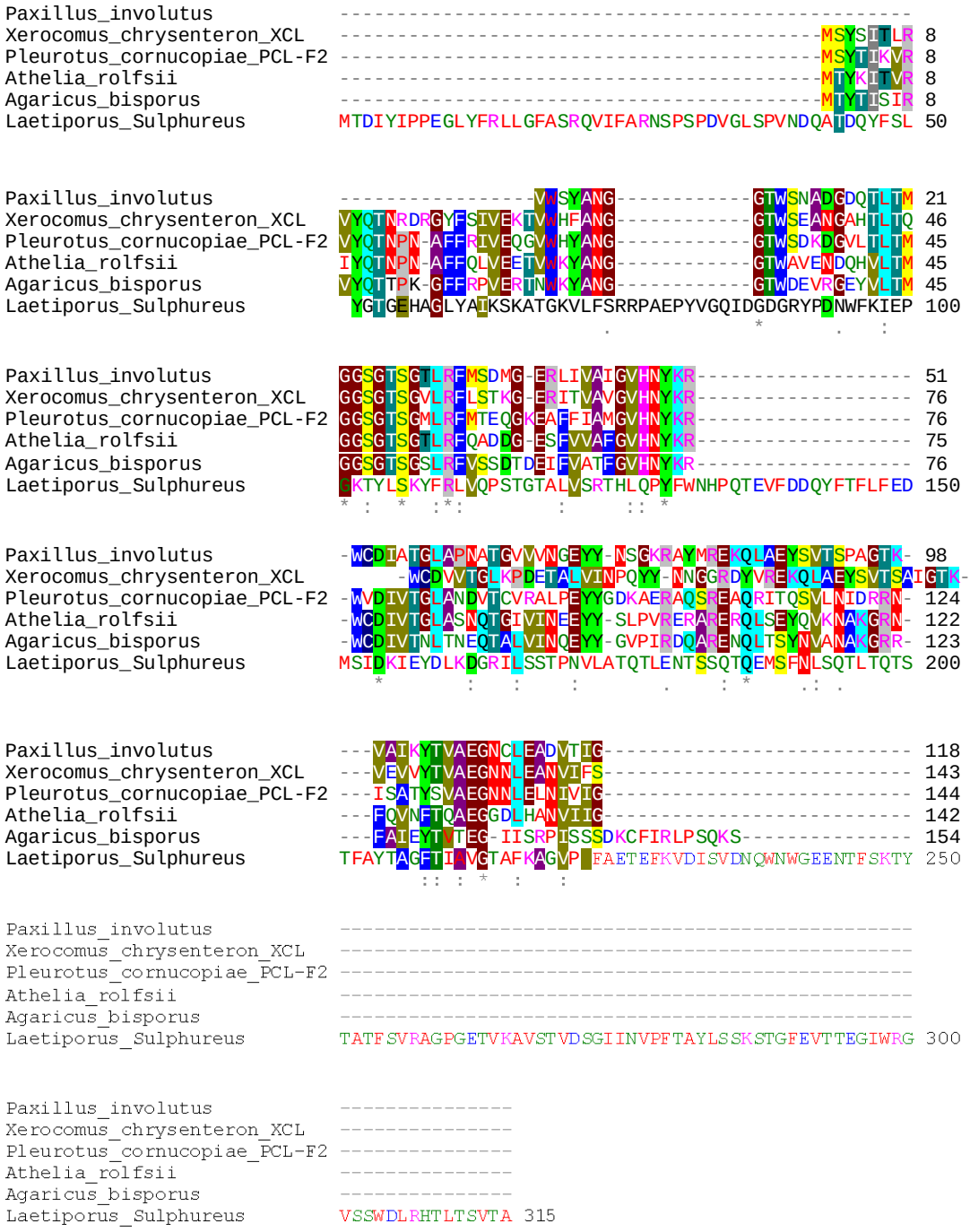

Fig. 3: Sequence alignment of Group-2 lectins. Amino acid sequences of the lectins were obtained from NCBI (http://www.ncbi.nlm.nih.gov/protein) and aligned by ClustalW2 (http://www.ebi.ac.uk/Tools/clustalw2/index.html) and manually edited and highlighted. Conserved residues are shown by '*'

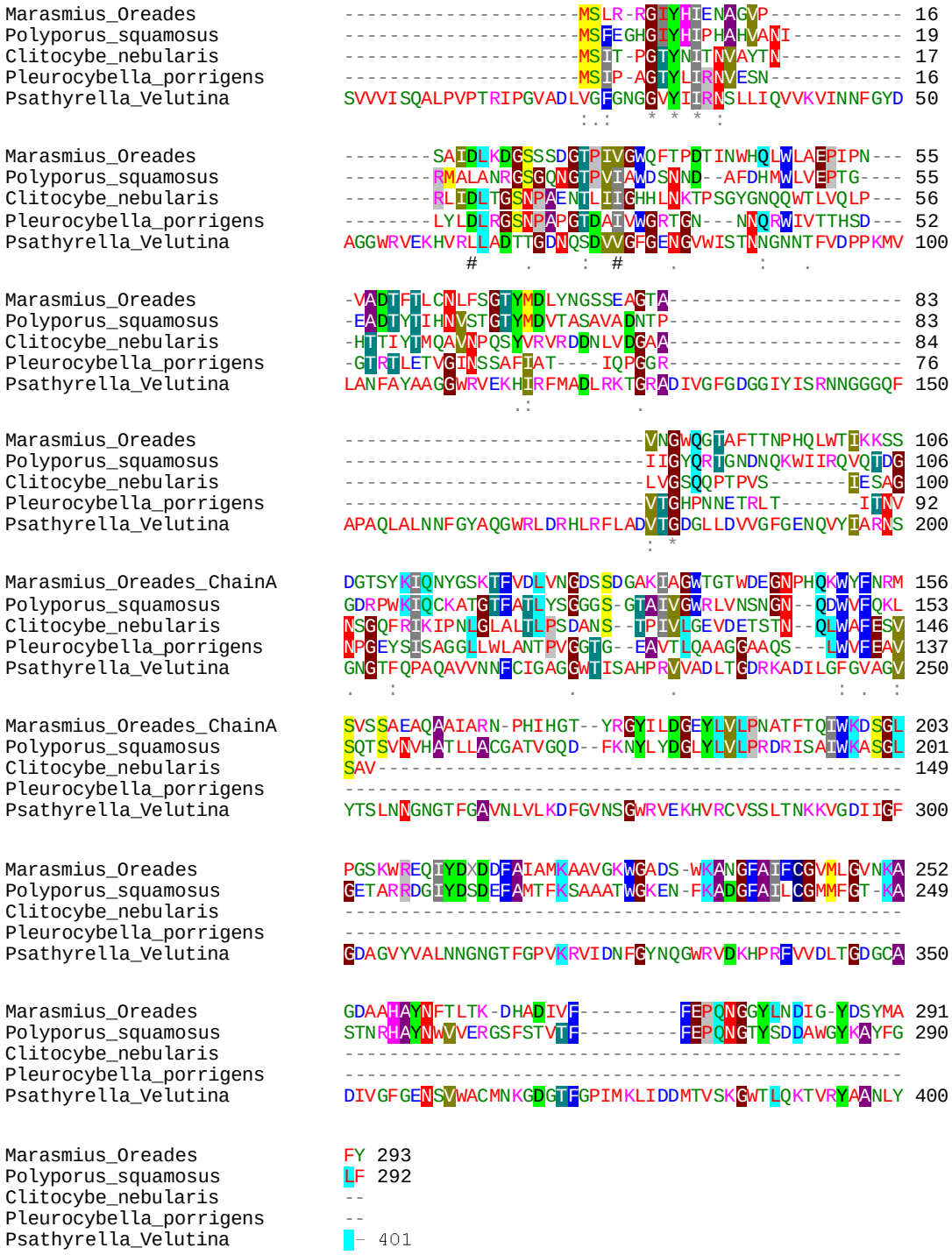

Fig. 4: Sequence alignment of Group-3 lectins. Amino acid sequences of the lectins were obtained from NCBI (http://www.ncbi.nlm.nih.gov/protein) and aligned by ClustalW2 (http://www.ebi.ac.uk/Tools/clustalw2/index.html) and manually edited and highlighted. Residues corresponding to the amino acids involved in galactose binding in ricin-B are marked by '#' and conserved residues are shown by '*'

(Fig. 4). The *Clitocybe Nebularis* Lectin (CNL) has also been reported to show 20% similarity with ricin-B which also showed presence of double repeats of (Q/N)XW motif (Pohleven *et al.*, 2009).

The *Polyporus squamosus* Lectin (PSL) (Tateno *et al.*, 2004) and *Marasmius oreades* lectin (MOA) (Kruger *et al.*, 2002) showed 38% identity with each other (Table 3) and both of the lectins also possess (Q/N)XW domain. In spite of the mentioned homology they differ in their carbohydrate binding properties. *Marasmius oreades* showed maximum affinity for Galα1, 3Galβ1, 4GlcNAc (Kruger *et al.*, 2002), whereas *Polyporus squamosus* lectin showed for Neu5Acα2,6GalB1,4GlcNAc (Tateno *et al.*, 2004). The N-terminal domain of *Marasmius oreades* lectin (residues 2-156) adopts a β-trefoil fold similar to many carbohydrate binding proteins and lectins (Grahn *et al.*, 2009).

In the group, *Psathyrella velutina* Lectin (PVL) (Cioci *et al.*, 2006) did not show homology with any of the lectins (Table 3) and appeared independent in the phylogeny tree (Fig. 1). The Genomic blast search in NCBI fungal DNA database revealed presence of a related gene with 50% identity in the genome of *Coprinopsis cinerea* okayama 7#130 strain (Cioci *et al.*, 2006). The crystal structure of this lectin indicates that the lectin adopts very regular seven-bladed β-propeller fold which could accommodate six molecules of monosaccharide N-acetylglucosamine (Cioci *et al.*, 2006). In the ClustalW alignment of Group-3 lectins, PVL shows very low homology in the N-terminal region with other lectins but almost no homology in the C-terminal region. The characteristic ricin-B domain (Q/N)XW was also absent in this lectin.

CONCLUSION

Twenty lectins and related proteins found in class *Agaricomycetes* can be classified in three major groups based on their phylogenetic distance. Most of the members in the group share moderate-to-high sequence homology and characterized by presence of characteristic domain according to the CDD (conserved domain database). However, two lectins, *Laetiporus sulphureus* lectin from Group-2 and *Psathyrella velutina* lectin from Group-3 did not show considerable homology with the other members in the group and are characterize with an independent origin in the phylogeny tree remotely related to the group. These two lectins also differ from other members in the structure and carbohydrate binding properties and shows similarity with other proteins of non-fungal origin and placed in the group as exceptions.

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