Austin Biology

Open Access

Austin Publishing Group

Review Article

Lectin in Innate Immunity of Crustacea

Maghil Denis*, Karthigayani Thayappan, Sivakumar Mullaivanam Ramasamy, Arumugam Munusamy

Department of Zoology, University of Madras, India

***Corresponding author:** Maghil Denis, University of Madras, Kotturpuram Road, Guindy Campus, Chennai, Tamilnadu, India

Received: February 17, 2016; **Accepted:** March 25, 2016; **Published:** March 29, 2016

Abstract

Lectins are protein or glycoprotein with binding specificity to sugars and as pattern recognition molecule recognize glycosylated surface of pathogens. In crustacea, lectins are diverse and species specific and the mechanism of recognition by the lectin have an impact on immune response and immune regulation. The present review explains the evolutionary success of innate immunity based on the diversity of these recognition molecules.

Keywords: Crustacea; Lectins; Opsonin; Innate Immunity; Receptor

Introduction

The innate immunity of invertebrate appears to have evolved to a complex adaptive immune mechanism in vertebrates. The simple process of antigen or nonself recognition of innate immune response are transformed from a single step process to pathways or cascades involving receptor selection and regulatory process that target and attenuate adaptive immune responses [1]. The recognition and distinguishing of the nonself are based on recognition of cell surface glycoconjugate [2]. The modulations in carbohydrate molecules appear to be specific for species and are the basis of pathogen recognition. The glycosylated Pathogen Associated Molecular Pattern (PAMP) include, Lipopolysaccharide (LPS), Peptidoglycan (PGN), and diverse sugars including β1-3 glucan and sialic acid, recognized by Pattern Recognition Receptors (PRR) that activate an immune response to eliminate the pathogen [3]. Lectins are molecules of ubiquitous occurrence and distinguish the nonself by binding specifically to the glycan of cell surface [4]. The report on the roles of lectins in enhancement of cellular immune responses also elaborates the function of lectin not only as recognition molecules but also as an opsonin [5]. The ability of lectin to bind to microbial glycosylated surface and induce a cascade of response leading to its elimination of invading pathogen was found to vary among the organisms [6]. The diverse ligand specificity and cell-cell interactions are the basis of multiple functions and pathways of immune response. In crustacea the structural and functional diversity of the lectins based on its sugar specificity appear to display diverse innate immune responses. The present review attempts to summarize the reported role of lectins in immunological functions in crustacea.

Carbohydrate Recognition Domain (CRD) in lectins

The Ca^{2+}-dependent carbohydrate-binding lectin are termed the C-type lectins are mediated by a compact module known as the 'Carbohydrate Recognition Domain' (CRD) present in all Ca^{2+}-dependent lectins but not in other types of animal lectins [7]. This domain, shows specific, but weak calcium-dependent binding to a variety of monosaccharides [8]. C-type lectin CRDs are found as building blocks in a variety of multi-domain proteins involved in organizing the extracellular matrix, endocytosis, the primary immune system and interactions of blood cells [9]. The CRD from various species of crustacea are summarized in (Table 1). The CRD with sequence QPD (Gln-Pro-Asp) motif was predicted with binding specificity for galactose and the CRD comprised of EPN (Glu-Pro-Asn) motif for mannose [10]. The C-type lectins of the shrimps PmLT, *Penaeus monodon* [11], *Fc-Lec2 Fenneropenaeus chinensis* [12] and LvLT *Litopenaeus vannamei*, [13], had the two CRD with binding specificity for galactose and mannose. The lectins from shrimps possessed CRD with binding specificity for either one of the two sugars, the CRD for galactose QPD in *Fc-Lec5* lectin from *F. chinensis* [14] and LvLectin 2 from *L. vannamei*, [15] and EPN CRD for mannose in, LvCTL of *L. vannamei* [16] and Fc-hsL of *F. chinensis* [16]. The phylogeny of the CRD for mannose and galactose from different species of shrimps appear conserved and despite the similarity in sugar binding specificity the amino acid sequence of the lectins appear divergent [13,18,19]. The evolutionary relationship of these CRDs in shrimp imply that the motif of amino acid sequence of the lectin protein though appear conserved differ with the binding glycan cluster [20]. The C-type lectin PtLP from the swimming crab *Portunus trituberculatus* contains a single CRD domain with six conserved cysteine residues does not contain a typical EPN or QPD motif in phylogenetic analysis was found in the a large cluster together with black tiger shrimp lectin PmAV [18]. The report of C-type lectins EsLecA and EsLecG from Chinese mitten crab, *Eriocheir sinensis* showed conserved CRD of QPD (Gln-Pro-Asp) motif for galactose in EsLecA, whereas the EsLecG had a key "EPE" (Glu-Pro-Glu) motif a mutated expression of mannose [21]. This clearly demonstrated the diversification of CRD by mutations and also explains convergence by retaining the conserved CRD. The CRD in lectin from different species of crustacea fail to explain the ligand specificity which appears to be determined either by multivalency of CRD developed within the primary structure of the protein or by clustering in cell surface glycans [22]. This amply describes the diversity in PAMP that enables the evolution under selection pressure of CRD in lectins.

Lectin as Pathogen Recognition Receptor (PRR)

Of the different types of PRR identified in crustacea the C-type lectins are found to vary in binding specificities and immune functions [23]. The purified recombinant lectin Fc-hsL [17], Fc-Lec2 [12], Fc-Lec5 [14] and rFcCTL [24] from the hepatopancreas of Chinese shrimp *F. chinensis* functions as PRR against Gram-positive and Gram-negative bacteria. However rFcCTL showed higher antimicrobial activity against Gram-positive bacteria than against Gram-negative bacteria and fungi. FcCTL expression was up-regulated in hepatopancreas and gills after White Spot Syndrome Virus (WSSV) challenge. The lectin Fc-Lec2and Fc-hsL agglutinated some Gram-positive and

Citation: Denis M, Thayappan K, Ramasamy SM and Munusamy A. Lectin in Innate Immunity of Crustacea. Austin Biol. 2016; 1(1): 1001.

Table 1: Carbohydrate Recognition Domain in cDNA of lectins from crustacea.

S. No	Species in Crustacea	lectins	Amino acids	ORF*(bp)	CRD**	References
1	*Eriocheir sinensis*	EsLecAEsLecG EsERGIC-53 EsVIP36, EsLecF	159 154 501 327	480 465 1506 984 477-	 QPN'' (Gln-Pro-Asn)	[21] [33] [70]
2	*Fenneropenaeus chinensis* •	FC-L FcCTL *Fc-Lec2* FcLec5 Fc-hsL	220 333 159	859 1002 1,137 480	 EPGD EPN(Glu-Pro-Asn) mannose binding QPD(Gln-Pro-Asp) galactose binding Gln-Pro-Asp (QPD Glu-Pro-Gln (EPQ EPN(Glu-Pro-Asn) mannose binding	[17] [24] [16] [24] [17]
3	*Fenneropenaeus merguiensis*	FmL				[71]
4	*Litopenaeus vannamei*	*LvLec1* *LvCTL4* LvCTL1 LvLectin-1 LvLectin-2 (LvLT)	169 156 156 345	510 563 638 567 625	EPA' (Glu-Pro-Ala) EPN (Glu(99)-Pro(100)- Asn(101 EPN QPN (Gln122ePro123eAsn124) QPD (Gln128ePro129eAsp13 EPN (mannose) QPD (galactose)0	[26] [25] [16] **[72]** [13]
5.	*Marsupenaeus japonicus*	MjLecA, MjLecB, and MjLecC)				[19]
6	*Marsupenaeus japonicus*	MjLectin	336	1011	rare mutant LPN (Leu_{134}-Pro_{135}-Asn_{136}) in CRD1 EPN (Glu_{299}-Pro_{300}-Asn_{301}) in CRD2,	[73]
7	*Penaeus monodon*	PmLT			QPD EPN	[11]
8	*Penaeus monodon*	PmLec	182	546		[74]
9	*Portunustrituberculatus*	PtLP	164	923	CTLD	[18]

CTLD- C-type lectin like-domain (CTLD
*ORF-open reading frame

Gram-negative bacteria in a calcium-dependent manner and Fc-hsL exhibited antimicrobial activity against Gram-positive and Gram-negative bacteria [8,13]. C-type lectin from the shrimp *L. vannamei* (LvCTL1), showed activity against the WSSV [12] and LvCTL4 demonstrated antibacterial activity against *Vibrio parahaemolyticus* [25]. The cloned C-type lectin from hepatopancreasLvLec1 showed antibacterial activity against *Micrococcus lysodeikticus* and WSSV with sugar affinity to D-mannose, D-glucose, D-galactose and N-Acetyl-D-mannose [26]. The Pacific white shrimp, *Litopenaeus vannamei* and the Atlantic white shrimp, *Litopenaeus Setiferus*. RNA from the hemocytes and hepatopancreas expressed different immune functions [27]. A lectin from the hemolymph of the banana shrimp *Penaeus (Fenneropenaeus) merguiensis* agglutinated *Vibrio harveyi* and *V. parahemolyticus*, which are pathogenic to *P. merguiensis*, and to a lesser extent, *V. vulnificus*, but had no effect on the non-pathogenic *V. cholerae, Salmonella typhi* and *Escherichia coli* [28].

The mRNA transcript of C-type lectin PmLT from the shrimp *Penaeusmonodon* in hepatopancreas tissue appeared to decrease on WSSV infection initially and then gradually increased. The antibody of the recombinant lectin anti-rPmLT antibody, detected PmLT only in the Hepatopancreas Specific F cells (HPF). The lectin showed anti-viral response against WSSV to clearly indicate its role as PRR and activated anti-bacterial immune responses. Moreover, rPmLT coated agarose beads appeared to enhance encapsulation by the hemocytes [11]. Reports of C-type lectin, PmLec from the serum of the shrimp *Penaeus monodon* with PRR and opsonc function. The lectin was specific for bacterial LPS and the binding was mediated through the O-antigen. It had strong hemagglutinating and bacterial-agglutinating activity and by its binding affinity served as opsonin by enhancing hemocyte phagocytosis [29].

The C-type lectin, PcLT, from the red swamp crayfish *Procambarusclarkii* contained a Carbohydrate Recognition Domain

(CRD) with the ability to bind to *Vibrio alginolyticus* and WSSV [30]. Expressions of Pc-Lec1 from *P. clarkii* were up-regulated in the hepatopancreas and gills of crayfish challenged with *Vibrio anguillarum*, *Staphylococcus aureus*, or WSSV [31]; however expression of PcLec4appeared upregulated after challenge with the bacteria *V. anguillarum* [32]. The lectin PcLec 5 from *P. clarkia* showed binding affinity to PGN, lipoteichoic acid and highest affinity to LPS of bacteria and selectively facilitated the clearance of injected bacteria [33].

The C-type lectins from mud crab *Scylla paramamosain* SpLec1 and SpLec2 mRNA in the megalopa a stage was first increased and were expressed mainly in haemocytes, muscle and hepatopancreas, with the highest expression level found in hepatopancreas [34]. In *Marsupenaeus japonicus*, three lectins, MjLecA, MjLecB, and MjLecC interact with WSSV and reduce the viral infection rate *in vitro* Sequence analysis indicated MjLecA and MjLecB are likely to belong to the same lectin sub-family, while MjLecC belongs to another sub-family [19]. A C-Type Lectin Like-Domain (CTLD)-containing protein (PtLP) from the swimming crab *Portunus trituberculatus* contains a single CRD domain with six conserved cysteine residues with amino acid sequence identity to fleshy prawn *F. chinensis* C-type lectin [18].

Opsonin function of lectin

The cellular immune mechanism of phagocytosis appears conserved in invertebrates and vertebrates. The process of antigen recognition, internalization and elimination in innate immune response of invertebrates show increase in complexity in adaptive immunity of vertebrates. Opsonins are molecules that recognize pathogens and bind to the receptors on the surface of phagocytes to enhance phagocytosis. The lectins as carbohydrate binding molecules serve as opsonins for hemocytes in several species of crustacea.The lectin from the shrimp *P. monodon* PmLec [29], the red swamp crayfish and *Procambarus clarkia*, Pc-Lec1 [31], serve as opsonin to interact with hemocytes in clearance of bacteria. The C-type lectin FcLec4 from Chinese white shrimp *F. chinensis* functions as an opsonin to facilitate bacterial clearance. The purified FcLec4 protein confirmed its opsonic activity by interaction with β-integrin on phagocyte of kuruma shrimp *M. japonicas* for phagocytosis of *V. anguillarum*. The interaction between FcLec4 and β-integrin did not rely on the carbohydrate recognition domain but on the N-terminus of FcLec4 [35]. In *Penaeus japonicus*, N-acetylglucosamine (GlcNAc) specific lectin was shown to have opsonic activity [36].

The lectin with *O*-actyl neuraminic acid specificity was isolated from the hemolymph of the freshwater crab *Paratelphusa jacquemontii* and served as an opsonin in the phagocytosis of rabbit erythrocyte the desialylated rabbit erythrocyte failed to bind to opsonin or the hemocyte for phagocytosis and revealed that sugar specificity of the lectin was essential for immune function [37]. In *Macrobrachium rosenbergii* the phagocytic mechanism of hemocyte are mediated by recognition of nonself cells in the hemocyte membrane by two independent mechanisms: specific, via *O*-acetylsialic acid, as well as N-acetylated sugars on recognized cells and a nonspecific one [32]. The carcinolectins 5, CL5a and CL5b (counterparts of TL5a and TL5b, respectively) in the horseshoe crab *C. rotundicauda*, are the major lectin proteins that bind all representative microbes and initiate the activation of a novel complement-like system, leading to the phagocytosis of pathogens [39].

Diversity in lectin function

Lectins often bind to natural polysaccharides with much higher affinity than to simple monosaccharides and it has been attributed to extended binding sites, where the terminal sugar bind to the lectin and other sugars of the oligosaccharide bind specifically or non-specifically to the protein. The binding affinity also appears to be enhanced to an extended oligosaccharide by multiple binding in a cluster of several identical binding sites, often achieved through protein oligomerization [40]. The review demonstrate the increase in binding sites or diversified structure, for multiple binding sites of the lectin are essential for its role as Pattern Recognition Receptors (PRR) in innate immunity of crustacean. As a living fossil with more than 500 million years of survival, the horseshoe crab *Tachypleus tridentatus* shows a repertoire of lectins with diverse ligand specificities having undefined function [41,42]. Tachylectins (TL) 1-4, which exhibit diverse *in vitro* ligand specificities, are confined to the hemocytes and their functions remains unknown. The activity was also inhibited more strongly by bacterial S-type LPS but not by R-type LPS lacking O-antigen There is no significant sequence similarity to any other known LPS-binding lectins, whereas tachylectin-4 is homologous to the NH_2-terminal domain with unknown functions of *Xenopus laevis pentraxin* 1 [43]. The recombinant protein of TPL-1 and -2 showed specific PGN and LPS-binding activity suggesting a role in trapping Gram-positive and Gram-negative bacteria respectively in innate immunity [44].

Tachylectin-1 and 3 from amoebocytes are nonglycosylated proteins and exist as dimer of a glycoprotein of molecular mass 36 kDa and 29 kDa respectively. The deduced amino acid sequence of TPL-2 with an N-glycosylation site, Asn-Cys-Thr, at positions 3-5 shared sequence identity with tachylectin-3. However the reported TPL-2 also a dimer of a glycoprotein with an apparent molecular mass of 36 kDa showed functional similarity with TPL-1 to bind and entrap Gram-positive and Gram-negative bacteria or any other invading organisms [45]. TLs and TPLs have different properties. TPL-1 and -2 found in plasma with completely different ligand specificities also found in Carbohydrate Reactive Proteins (CRP) consist of closely related family-of proteins with polymorphic ligand-specificity have sequence identities encoded by multiple genes [41]. The multiple form of proteins enable PAMP recognition by diverse ligand specificity encoded in the different forms of the proteins that serve as PRR of the host [46]. Two lectins, tachylectins 5A and 5B (TL-5A and TL-5B) were identified in the hemolymph plasma of *T. tridentatus* TLs-5 agglutinated Gram-negative and Gram-positive bacteria, and the activity was more efficient for Gram-negative than for Gram-positive bacteria however had no antimicrobial activity against these bacteria. The fibrinogen-like domain of mammalian ficolins sequence identity of up to 51%, in TL-5A and TL-5B. Interestingly, a collagenous domain found in ficolins was found missing in the corresponding regions of TLs-5, which are conserved in TL-5A (Asp-198 and Asp-200) and TL-5B (Asp-215 and Asp-217). The horseshoe crab with a unique functional homologue of vertebrate fibrinogen, coagulogen, as the target protein of the clotting cascade, implicated s fibrinogen-related molecules in hemolymph plasma. As a nonself-recognizing protein [47]. The lectin from demosponge *Suberites domuncula*,

termed Suberites lectin a transmembrane protein shared the highest sequence similarity with lectin from the horseshoe crab *Tachypleus trunculus* of 27 kDa size [48].

The lectin Dorin M from soft tick, *Ornithodoros moubata* revealed significant sequence similarity with lectins from *T. tridentatus* Tl-5A, Tl-5B and vertebrate ficolins [49]. However, the collagen-like domain found in ficolins was missing in Dorin M and likewise in the corresponding region of TL-5. The cysteines form two disulfide bridges in native TL-5A and TL-5B [50] and have analogues in the sequence of native Dorin M. This implied similar folds of the secondary structure and the related binding to glycan surface of pathogens. The protein sequence similarity of Dorin M with TL-5A lectin of *T. tridentatus* and mammalian ficolins suggested the evolutionary conservation among the effector proteins in both vertebrates and invertebrates with regards to their innate immunity. The carcinolectins 5, CL5a and CL5b, the CL5 isoforms of horseshoe crab, *Carcinoscorpius rotundicauda*, of molecular size 36 and 40 kDa, respectively are prominent plasma lectins that bind all representative microbes and pathogen-associated molecular pattern molecules [39].

The occurrence of multiple lectins in primitive horse shoe crabs explains the function of innate immune system dependent on the multiplicity or diversity of the pathogen recognition molecules to defend against the continuous diversification of invading pathogens in evolution. In vertebrates the adaptive immunity diversified the recognition mechanism by variable binding ability of immunoglobulin molecule. The multiple lectins BRA-1, BRA-2 and BRA-3 were identified and isolated from the coelomic fluid of the acorn barnacle, *Megabalanus rosa*. The BRA-3 lectin was composed of 4 identical subunits of 138 amino acids forming dimers cross-linked by 5 disulfide bridges with homology to *Sarcophaga* (flesh fly) lectin [51]. The BRA-2 lectin of six identical subunits consisting of 173 amino acids cross-linked by disulfide bonds formed a dimer with one intrachain and two interchain disulfide bonds identified as Cys-53, Cys-61, Cys-14, and Cys-50, Cys-14 respectively. The two intrachain disulfide bonds are conserved through all invertebrate lectins and calcium-dependent animal lectins. From the evolutionary stand point, the marked homology of the invertebrate lectins suggests that the gene for the lectin evolved by gene duplication from a common ancestral gene. The differential expressions arise by physiological modulation as explained from isolated cDNA clones of BRA-3. A polymorphism in the *BRA-3* mRNA was revealed, with single-nucleotide differences at three positions within the coding region and cause conserved changes in the amino acid. The *BRA-3* mRNA and BRA-3 protein levels increased during early summer in a similar fashion, indicating that BRA-3 production is regulated mainly at the level of transcription [52].

The serum lectins in the freshwater prawn, *Macrobrachium rosenbergii* specific to N-acetylated sugars and α2,3, α 2,6 linked or 9-O-acetyl sialic acid residues agglutinated *Pseudomonas hemolytica* and *Pseudomonas multicoda* defining its role as recognition molecule [53]. A similar lectin on the surface of granular hemocytes with phagocytic function suggested variance in localization of the lectin. The predicted amino acid sequence of the sialic acid specific serum lectin Mrl (9.5 kDa) showed homology to hyperglycemic hormone from *M. rosenbergii* and to the variable region of the human immunoglobulin kappa and lambda light chains [54].

In another report lectin aggregates MrL circulating in the hemolymph of the prawn as high-molecular weight MrL aggregates (MrL-I) that lack hemagglutinating activity of 62.1, 67.1 and 81.4 kDa proteins and MrL-III, showed hemagglutinating activity of 9.6 kDa protein. Edman degradation indicated NH_2-terminal sequence of five amino acids for the 9.6 kDa MrL-III (DVPLL/A) and eleven for the main 81.4 kDa band identified in MrL-I (DVPLL/AXKQQQD); analysis by MALDI-TOF indicated a different tryptic pattern for MrL-I and MrL-III. MrL-I was recognized by monoclonal antibodies against MrL-III. Circular dichroism indicated similarity in secondary structure and clearly indicated differential post translational processes to favor aggregations involved in regulation and activity of the lectins [55].

The multiplicity of the lectins as molecules of immune response apparently under continuous selective pressure, modulates its functions to enhance its efficiency at levels of post transcription or post translation though retaining nucleotide sequence of the gene or amino acid sequence of the protein at primary or secondary structure with changes in tertiary structure to bind to the glycosylated cell surface of the pathogen. Further studies on *M. rosenbergii* contend with the view on immune functions of lectins. About 20 lectins including C-type lectins [dual-Carbohydrate Recognition Domain (CRD) type and single-CRD type], L-type lectin, and lectin with Low-Density Lipoprotein Class A (LDLa) domain were identified under spiroplasma strain MR-1008 challenge and were found mainly distributed in the hepatopancreas, hemocytes, nerve, intestine, and heart. The lectin expression were upregulated at different times after the challenge (except Lectin 15) to indicate that lectins are variable and function in early or late immune responses against the recognized pathogen [56]. The gene expression for the lectin protein appears modulated at different levels of expression and controlled by factors that enhance immunity.

The existence of multiple lectins has been demonstrated in prawns and shrimps [19,11,17], also the lobsters *Homarus americanus* and species of *Jasus* have equipped the effector immune response by diverse forms of lectin [57, 58].

Sialic acid specific lectins

Sialic acids a family of 9-carbon carboxylated sugars with diverse forms arising by substitution or modification of its side chain and occupy the terminal position of glyconjugates on the cell surface of deuterostomes, developmental larval stages of protostomes [59] and some microbes [60]. The structural diversity of sialic acids and variation in binding affinity of lectins affected by structural modulations explains the diversity with an apparent evolutionary basis for host or pathogen recognition. The species in crustacea possess lectins with an ability to recognize diverse forms of sialic acid, N-acetyl neuraminic acid, Neu5Ac [61], N-glycolyl neuraminic acid, Neu5Gc [62], *O*-acetyl NeuAc [63, 64, 65]. The species in crustacea belong to protostomes and lack the enzymes for synthesis of sialic acid and the gene for sialic acid specific lectin was probably an event of lateral transfer among bacteria or vertebrate host or bacterial infection by vector and lead to convergent evolution [66]. Dorin M lectin from the tick *O. moubata* with binding specificity for sialic acids, recognize and bind to sialic acid on the cell wall of spirochete *Borreliaburgdorferi*) and *B. duttoni*, the causative agent of relapsing

fever and transmitted by the vector tick [67]. The microbial transfer of the sialic acid specific lectin to microbes and even the host explains lateral transfer of genes [68]. The repertoire of sialic acid specific lectins in crustacea represents the evolutionary changes that occur in glycosylated surface of pathogens and their recognition. Further elucidation of lectin based innate responses probably explains pathogenesis with related glycosylated cell surface of the pathogen.

Conclusion

The innate immune response in invertebrates functions with an array of PRR to identify and recognize the diversification in the glycosylated surface of PAMP in pathogens. The lectins as effector molecules of innate response is involved in recognition and antibacterial activity, also as opsonin in cellular defense reactions of encapsulation and phagocytosis. The lectin molecule from crustacea in its structure has shown homology to the lectin from the simplest demosponge *Suberites domuncula* [48] to a complex variable region of the human immunoglobulin. However lectins from crustacea are variant forms with the amino acid sequence showing low identity or homology [54]. This diversity in C-type lectin is evident in crustacea though the CTLD in vertebrates occur with few modifications within the vertebrate lineage during evolution from fish to mammals [69]. The diversity in structural forms of lectin was probably directed to increase the binding sites and the specific binding affinity with more than one sugar. The evolution of the gene for lectin probably from multigene ancestors as of multi-segmental, multi-gene origin of immunoglobulin, probably explains the origin of diverse forms of lectin in a species. However, homology among the multiple forms of lectin in a species indicate the origin of the gene for lectin by duplication of a common ancestral gene, also oligomerization of protein increases the diversity in glycan binding affinity. Moreover the regulation of gene transcription and post- translation modulations are also factors that play an important role in the production of variant secondary or tertiary structures of lectin in response to the diversifying PAMP of pathogen. The crustacean lectins appear to have diversified against the challenge of mutating pathogens in the defensive process to survive and in the course of evolution the crustacean lectins are diverse with common function of PRR.

References

1. Litman GW, Rast JP, Fugmann SD. The origins of vertebrate adaptive immunity. Nat Rev Immunol. 2010; 10: 543-553.
2. Gordon S. Pattern recognition receptors: doubling up for the innate immune response. Cell. 2002; 111: 927-930.
3. Janeway CA Jr, Medzhitov R. Innate immune recognition. Annu Rev Immunol. 2002; 20: 197-216.
4. Sharon N, Lis H. History of lectins: from hemagglutinins to biological recognition molecules. Glycobiology. 2004; 14: 53R-62R.
5. Fujita T, Matsushita M, Endo Y. The lectin-complement pathway-its role in innate immunity and evolution. Immunol Rev. 2004; 198: 185-202.
6. Petersen SV, Thiel S, Jensenius JC. The mannan-binding lectin pathway of complement activation: biology and disease association. Mol Immunol. 2001; 38: 133-149.
7. Weis WI, Taylor ME, Drickamer K. The C-type lectin super family in the immune system. Immunol Rev. 1998; 163: 19-34.
8. Drickamer K. Evolution of Ca (2+)-dependent animal lectins. Prog Nucleic Acid Res Mol Biol. 1993; 45: 207-232.
9. Gabius HJ. Animal lectins. Eur J Biochem. 1997; 243: 543-576.
10. Drickamer K. Engineering galactose-binding activity into a C-type mannose-binding protein. Nature. 1992; 360: 183-186.
11. Ma TH, Benzie JA, He JG, Chan SM. PmLT, a C-type lectin specific to hepatopancreas is involved in the innate defense of the shrimp Penaeus monodon. J Invertebr Pathol. 2008; 99: 332-341.
12. Zhang XW, Xu WT, Wang XW, Mu Y, Zhao XF, Yu XQ, et al. A novel C-type lectin with two CRD domains from Chinese shrimp *Fenneropenaeus chinensis* functions as a pattern recognition protein. Mol Immunol. 2009; 46: 1626-1637.
13. Ma TH, Tiu SH, He JG, Chan SM. Molecular cloning of a C-type lectin (LvLT) from the shrimp *Litopenaeus vannamei*: early gene down-regulation after WSSV infection. Fish Shellfish Immunol. 2007; 23: 430-437.
14. Xu WT, Wang XW, Zhang XW, Zhao XF, Yu XQ, Wang JX. A new C-type lectin (FcLec5) from the Chinese white shrimp *Fenneropenaeus chinensis*. Amino Acids. 2010; 39: 1227-1239.
15. Wei X, Liu X, Yang J, Fang J, Qiao H, Zhang Y, et al. Two C-type lectins from shrimp *Litopenaeus vannamei* that might be involved in immune response against bacteria and virus. Fish Shellfish Immunol. 2012; 32: 132-140.
16. Zhao ZY, Yin ZX, Xu XP, Weng SP, Rao XY, Dai ZX, et al. A novel C-type lectin from the shrimp *Litopenaeus vannamei* possesses anti-white spot syndrome virus activity. J Virol. 2009; 83: 347-356.
17. Sun YD, Fu LD, Jia YP, Du XJ, Wang Q, Wang YH, et al. A hepatopancreas-specific C-type lectin from the Chinese shrimp *Fenneropenaeus chinensis* exhibits antimicrobial activity. Mol Immunol. 2008; 45: 348-361.
18. Kong HJ, Park EM, Nam BH, Kim YO, Kim WJ, Park HJ, et al. A C-type lectin like-domain (CTLD)-containing protein (PtLP) from the swimming crab *Portunus trituberculatus*. Fish Shellfish Immunol. 2008; 25: 311-314.
19. Song KK, Li DF, Zhang MC, Yang HJ, Ruan LW, Xu X. Cloning and characterization of three novel WSSV recognizing lectins from shrimp *Marsupenaeus japonicus*. Fish Shellfish Immunol. 2010; 28: 596-603.
20. Drickamer K, Taylor ME. Recent insights into structures and functions of C-type lectins in the immune system. Curr Opin Struct Biol. 2015; 34: 26-34.
21. Jin XK, Li WW, Cheng L, Li S, Guo XN, Yu AQ, et al. Two novel short C-type lectin from Chinese mitten crab, Eriocheir sinensis, are induced in response to LPS challenged. Fish Shellfish Immunol. 2012; 33: 1149-1158.
22. Drickamer K, Taylor ME. Identification of lectins from genomic sequence data. Methods Enzymol. 2003; 362: 560-567.
23. Wang XW, Wang XJ. Pattern recognition receptors acting in innate immune system of shrimp against pathogen infections. Fish Shellfish Immunol. 2011; 34: 981-989.
24. Lai X, Kong J, Wang Q, Wang W, Meng X. Identification and molecular characterization of a C-type lectin-like protein from Chinese shrimp (*Fenneropenaeus chinensis*). Mol Biol Rep. 2013; 40: 2223-2230.
25. Li H, Chen Y, Li M, Wang S, Zuo H, Xu X, et al. A C-type lectin (LvCTL4) from *Litopenaeus vannamei* is a downstream molecule of the NF-κB signaling pathway and participates in antibacterial immune response. Fish Shellfish Immunol. 2015; 43: 257-263.
26. Luo Z, Zhang J, Li F, Zhang X, Liu C, Xiang J. Identification of a novel C-type lectin from the shrimp Litopenaeus vannamei and its role in defense against pathogens infection. Chinese Journal of Oceanology and Limnology, 2011; 29: 942.
27. Gross PS, Bartlett TC, Browdy CL, Chapman RW, Warr GW. Immune gene discovery by expressed sequence tag analysis of hemocytes and hepatopancreas in the Pacific White Shrimp, *Litopenaeus vannamei*, and the Atlantic White Shrimp, *L. setiferus*. Dev Comp Immunol. 2001; 25: 565-577.
28. Utarabhand P, Rittidach W, Paijit N. Bacterial Agglutination by Sialic Acid-Specific Lectin in the Hemolymph of the Banana Shrimp, *Penaeus* (*Fenneropenaeus*) *merguiensis* Science Asia. 2007; 33: 41-46.
29. Luo T, Yang H, Li F, Zhang X, Xu X. Purification, characterization and cDNA

cloning of a novel lipopolysaccharide-binding lectin from the shrimp *Penaeus monodon*. Dev Comp Immunol. 2006; 30: 607-617.

30. Chen DD, Meng XL, Xu JP, Yu JY, Meng MX, Wang J. PcLT, a novel C-type lectin from *Procambarus clarkii*, is involved in the innate defense against *Vibrio alginolyticus* and WSSV. Dev Comp Immunol. 2013; 39: 255-264.

31. Zhang H, Chen L, Qin J, Zhao D, Wu P, Qin C, et al. Molecular cloning, characterization and expression of a C-type lectin cDNA in Chinese mitten crab, *Eriocheir sinensis*. Fish Shellfish Immunol. 2011; 31: 358-363.

32. Zhang XW, Liu YY, Mu Y, Ren Q, Zhao XF, Wang JX. Overexpression of a C-type lectin enhances bacterial resistance in red swamp crayfish *Procambarus clarkii*. Fish Shellfish Immunol. 2013; 34: 1112-1118.

33. Zhang XW, Ren Q, Zhang HW, Wang KK, Wang JX. A C-type lectin could selectively facilitate bacteria clearance in red swamp crayfish, *Procambarus clarkia*. Fish Shellfish Immunol. 2013; 35: 1387-1394.

34. Jiang K, Zhang D, Zhang F, Sun M, Qi L, Zhang S, et al. Isolation of the C-type lectin like-domain cDNAs from the mud crab *Scylla paramamosain* Estampador, 1949, and its expression profiles in various tissues, during larval development, and under *Vibrio* challenge. Crustaceana. 2012; 85: 817-834.

35. Wang XW, Zhao XF, Wang JX. C-type lectin binds to *β*-integrin to promote hemocytic phagocytosis in an invertebrate. J Biol Chem. 2014; 289: 2405-2414.

36. Kondo M, Matsuyama H, Yano T. The opsonic effect of lectin on phagocytosis by hemocytes of Kuruma Prawn, *Penaeus japonicus*. Fish Pathol. 1992; 27: 217-222.

37. Denis M, Thayappan K, Ramasamy SM, Munusamy A. Opsonic function of sialic acid specific lectin in freshwater crab Paratelphusa jacquemontii. Springerplus. 2015; 4: 601.

38. Vázquez L, Maldonado G, Agundis C, Pérez A, Cooper EL, Zenteno E. Participation of a sialic acid-specific lectin from freshwater prawn *Macrobrachium rosenbergii* hemocytes in the recognition of non-self cells. J Exp Zool. 1997; 279: 265-272.

39. Zhu Y, Thangamani S, Ho B, Ding JL. The ancient origin of the complement system. EMBO J. 2005; 24: 382-394.

40. Weis WI, Drickamer K. Structural basis of lectin-carbohydrate recognition. Annu Rev Biochem. 1996; 65: 441-473.

41. Iwaki D, Osaki T, Mizunoe Y, Wai SN, Iwanaga S, Kawabata S. Functional and structural diversities of C-reactive proteins present in horseshoe crab hemolymph plasma. Eur J Biochem. 1999; 264: 314-326.

42. Ng PM, Jin Z, Tan SS, Ho B, Ding JL. C-reactive protein: a predominant LPS-binding acute phase protein responsive to *Pseudomonas* infection. J Endotoxin Res. 2004; 10: 163-174.

43. Saito T, Hatada M, Iwanaga S, Kawabata S. A newly identified horseshoe crab lectin with binding specificity to O-antigen of bacterial lipopolysaccharides. J Biol Chem. 1997; 272: 30703-30708.

44. Kuo TH, Chuang SC, Chang SY, Liang PH. Ligand specificities and structural requirements of two Tachypleus plasma lectins for bacterial trapping. Biochem J. 2006; 393: 757-766.

45. Chen SC, Yen CH, Yeh MS, Huang CJ, Liu TY. Biochemical properties and cDNa cloning of two new lectins from the plasma of Tachypleus tridentatus: Tachypleus plasma lectin 1 and 2. J Biol Chem. 2001; 276: 9631-9639.

46. Kawabata S, Tsuda R. Molecular basis of non-self recognition by the horseshoe crab tachylectins. Biochim Biophys Acta. 2002; 1572: 414-421.

47. Gokudan S, Muta T, Tsuda R, Koori K, Kawahara T, Seki N, et al. Horseshoe crab acetyl group-recognizing lectins involved in innate immunity are structurally related to fibrinogen. Proc Natl Acad Sci U S A. 1999; 96: 10086-10091.

48. Schröder HC, Ushijima H, Krasko A, Gamulin V, Thakur NL, Diehl-Seifert B, et al. Emergence and disappearance of an immune molecule, an antimicrobial lectin, in basal metazoa. A tachylectin-related protein in the sponge *Suberites domuncula*. J Biol Chem. 2003; 29; 278: 32810-32817.

49. Rego RO, Kovár V, Kopácek P, Weise C, Man P, Sauman I, et al. The tick plasma lectin, Dorin M, is a fibrinogen-related molecule. Insect Biochem Mol Biol. 2006; 36: 291-299.

50. Kairies N, Beisel H.-G, Fruentes-Prior P, tsuda r, Muta T, Iwanaga S, et al. The 2-Å crystal structure of tachylectin 5A provides evidence for the common origin of the innate immunity and the blood coagulation systems. Proc Natl Acad Sci U.S.A. 2001; 98: 13519-13524.

51. Muramoto K, Kamiya H. The amino-acid sequence of multiple lectins of the acorn barnacle *Megabalanus rosa* and its homology with animal lectins. Biochim Biophys Acta. 1990; 1039: 42-51.

52. Takamatsu N, Takeda T, Kojima M, Heishi M, Muramoto K, Kamiya H, et al. Acorn barnacle *Megabalanus rosa* lectin (BRA-3): cDNA cloning, gene structure and seasonal changes of mRNA and protein levels. Gene. 1993; 128: 251-255.

53. Vazquez L, Maldonado G, Agundis C, Perez A, Cooper E, Zenteno E. Participation of a sialic acid specific lectin from freshwater prawn *Macrobrachium rosenbergii* hemocytes in the recognition of non-self cells. J Exp Zool. 1997; 279: 265-272.

54. Zenteno R, Vazquez L, Sierra C, Pereyra A, Slomianny MC, Bouquelet S, et al. Chemical characterization of the lectin from the freshwater prawn *Macrobrachium rosenbergii* (De Man) by MALDI-TOF. Comp Biochem Physiol B Biochem Mol Biol. 2000; 127: 243-250.

55. Pereyra A, Zenteno R, Vázquez L, Martínez-Cairo S, Rodríguez A, Mendoza-Hernández G, et al. Characterization of lectin aggregates in the hemolymph of freshwater prawn *Macrobrachium rosenbergii*. Biochim Biophys Acta. 2004; 4:1673: 122-130.

56. Zhu H, Du J, Hui KM, Liu P, Chen J, Xiu Y, et al. Diversity of lectins in Macrobrachium rosenbergii and their expression patterns under spiroplasma MR-1008 stimulation. Fish Shellfish Immunol. 2013; 35: 300-309.

57. Battison AL, Summerfield RL. Isolation and partial characterisation of four novel plasma lectins from the American lobster *Homarus americanus*. Dev Comp Immunol. 2009; 33: 198-204.

58. Kamiya H, Imai T, Goto R, Kittaka J. Lectins in the rock lobster *Jasus novaehollandiae* Hemolymph. Crustaceana. 1994; 67: 1.

59. Saito M, Kitamura H, Sugiyama K. Occurrence of gangliosides in the common squid and pacific octopus among protostomia. Biochim Biophys Acta. 2001; 1511: 271-280.

60. Vimr ER, Kalivoda KA, Deszo EL, Steenbergen SM. Diversity of microbial sialic acid metabolism. Microbiol Mol Biol Rev. 2004; 68: 132-153.

61. Hall JL, Rowlands DT Jr. Heterogeneity of lobster agglutinins II. Specificity of agglutinin-erythrocyte binding. Biochemistry. 1974; 13: 828-832.

62. Mercy PD Sr, Ravindranath MH. An agglutinin with unique specificity for N-glycolyl sialic acid residues of thyroglobulin in the hemolymph of a marine crab *Scylla serrata* (Forskal). Experientia. 1992; 48: 498-500.

63. Ravindranath MH, Paulson JC. O-acetylsialic acid-specific lectin from the crab *Cancer anntenarius*. Methods Enzymol. 1987; 138: 520-527.

64. Fragkiadakis GA, Stratakis EK. The lectin from the crustacean *Liocarcinus depurator* recognizes O-acetylsialic acids. Comp Biochem Physiol B Biochem Mol Biol. 1997; 117: 545-552.

65. Denis M, Palatty PD, Bai NR, Suriya SJ. Purification and characterization of a sialic acid specific lectin from the hemolymph of the freshwater crab *Paratelphusa jacquemontii*. Eur J Biochem. 2003; 270: 4348-4355.

66. Gagneux P, Varki A. Evolutionary considerations in relating oligosaccharide diversity to biological function. Glycobiology. 1999; 9: 747-755.

67. Felsenfeld O. *Borrelia*: strains, vectors, human and animal borreliosis. St Louis (MO): Warren H Green, Inc. 1971.

68. Hulinska D, Volf P, Grubhoffer L. Surface carbohydrates of Borreliaburgdorferi. In: F. Dusbabek and V. Bukva (Eds.), Modern Acarology. Academia Prague and SPB Academic, The Hague. 1991; 2: 73-78.

69. Zelensky AN, Gready JE. C-type lectin-like domains in Fugu rubripes. BMC Genomics. 2004; 5: 51.

70. Jin XK, Guo XN, Li S, Wu MH, Zhu YT, Yu AQ, et al. Association of a hepatopancreas-specific C-type lectin with the antibacterial response of *Eriocheir sinensis*. PLoS One. 2013; 8: e76132.

71. Rittidach W, Paijit N, Utarabhand P. Purification and characterization of a lectin from the banana shrimp *Fenneropenaeus merguiensis* hemolymph. Biochim Biophys Acta. 2007; 1770: 106-114.

72. Wei X, Liu X, Yang J, Fang J, Qiao H, Zhang Y, et al. Two C-type lectins from shrimp *Litopenaeus vannamei* that might be involved in immune response against bacteria and virus. Fish Shellfish Immunol. 2012; 32: 132-140.

73. Zhang M, Mao Y, Wang J, Feng W, Song X, Su Y. Molecular characterization and expression analysis of a novel dual-CRD C-type lectin in kuruma shrimp (*Marsupenaeus japonicus*) Acta Oceanol Sin. 2015; 34: 74-83.

74. Luo T, Yang H, Li F, Zhang X, Xu X. Purification, characterization and cDNA cloning of a novel lipopolysaccharide-binding lectin from the shrimp *Penaeus monodon* Dev Comp Immunol. 2006; 30: 607-617.

Citation: Denis M, Thayappan K, Ramasamy SM and Munusamy A. Lectin in Innate Immunity of Crustacea. Austin Biol. 2016; 1(1): 1001.