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## 3,4-Dihydroxyphenylacetaldehyde synthase and cuticle formation in insects

Chenghong Liao <sup>a, b, 1</sup>, Archana Upadhyay <sup>a, b, 1</sup>, Jing Liang <sup>c</sup>, Qian Han <sup>a, b, \*</sup>, Jianyong Li <sup>c, \*\*</sup><sup>a</sup> Key Laboratory of Tropical Biological Resources of Ministry of Education, Hainan University, Haikou, Hainan 570228, China<sup>b</sup> Laboratory of Tropical Veterinary Medicine and Vector Biology, Hainan Key Laboratory of Sustainable Utilization of Tropical Bioresources, Institute of Tropical Agriculture and Forestry, Hainan University, Haikou, Hainan 570228, China<sup>c</sup> Department of Biochemistry, Virginia Tech, Blacksburg, VA 24061, USA

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## ABSTRACT

Cuticle is the most important structure that protects mosquitoes and other insect species from adverse environmental conditions and infections of microorganism. The physiology and biochemistry of insect cuticle formation have been studied for many years and our understanding of cuticle formation and hardening has increased considerably. This is especially true for flexible cuticle. The recent discovery of a novel enzyme that catalyzes the production of 3,4-dihydroxyphenylacetaldehyde (DOPAL) in insects provides intriguing insights concerning the flexible cuticle formation in insects. For convenience, the enzyme that catalyzes the production DOPAL from L-dopa is named DOPAL synthase. In this mini-review, we summarize the biochemical pathways of cuticle formation and hardening in general and discuss DOPAL synthase-mediated protein crosslinking in insect flexible cuticle in particular.

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## 1. Introduction

In insects, the cuticle provides protection against physical injury and flexibility in inter-segmental and joint areas for mobility. The cuticle covers the body of the insect and acts as an effective barrier between the insect and its surroundings. It provides protection against desiccation, microorganisms, and predators, and simultaneously acting as an exoskeleton providing the attachment sites for muscles (Gibbs et al., 1991; Moussian, 2010; Ortiz-Urquiza and Keyhani, 2013). Our understanding of cuticular structures has largely been derived from studies of Diptera and Lepidoptera species (such as *Drosophila melanogaster*, *Manduca sexta*, etc.) (Rebers and Riddiford, 1988; Suderman et al., 2003; Moussian et al., 2006; Shibata et al., 2010; Pesch et al., 2017). Based on physical characteristics, cuticle can be further classified into rigid cuticle and flexible cuticle (or flexible cuticle structures). Flexible cuticle areas cover the segmental and joint regions, which allow insects to move or fly freely. The ability of flexible cuticle to maintain strength and

stretch to a significant degree is believed being closely related to protein crosslinking. A highly flexible cuticle is particularly crucial in female mosquitoes because their abdomen must accommodate blood meal that can be equivalent to their own body weight.

Mosquitoes are disease vectors and cause more human suffering than any other organisms or insects (Le Coupanec et al., 2013; Mores et al., 2014; Diouf and Nour, 2017). Over one million people worldwide die from mosquito-borne diseases on yearly basis (Caraballo and King, 2014). These mosquitoes not only affect humans, but also have a potential to transmit several diseases to dogs, horses and other animals. The completion of genomes for several major disease vectors (i.e. *Anopheles gambiae*, *Aedes aegypti* and *Culex quinquefasciatus*) represents a major milestone towards developing a better overall understanding of mosquito physiology (Holt et al., 2002; Nene et al., 2007; Arensburger et al., 2010). These genome sequences revealed a number of insect specific gene families and even mosquito specific gene/protein families (such as cuticle-formation/hardening, blood feeding, blood digestion and ovary/egg development related gene families, etc.) that play essential physiological roles for mosquito survival. The absence of these gene families in other species suggests they could be ideal targets for mosquito control (Jasinskiene et al., 2003; Robich et al., 2007; Honnen et al., 2016).

\* Corresponding author. Hainan University, Haikou, Hainan 570228, China.

\*\* Corresponding author.

E-mail addresses: [qianhan@hainu.edu.cn](mailto:qianhan@hainu.edu.cn) (Q. Han), [lij@vt.edu](mailto:lij@vt.edu) (J. Li).<sup>1</sup> Both authors contributed equally to this work.

## 2. Insect cuticular proteins

As most insects undergo metamorphosis, they need to shed off their old cuticle and synthesize a new one to fit the body shape and size throughout their life cycles. The newly formed cuticle (Fig. 1), mainly composed of cuticular proteins, chitin, and sclerotizing reagents, needs to be hardened through the crosslinking between cuticular proteins and sclerotizing reagents. The ability to adapt to different environments leads to the success of insects in evolution and their widespread presence on earth likely is attributable to the protection of their cuticle. Cuticular proteins and chitin are major building blocks of insect cuticle. Identification of cuticular proteins and determination of their transcriptional profile are major steps forward for gaining a better understanding of cuticle formation and hardening, but exactly how individual cuticular proteins and chitin integrate to form highly protective cuticle structures remains to be fully established.

Cuticular protein crosslinking was thought to be involved in flexible cuticle formation (Tatarenkov et al., 2001; Vavricka et al., 2011). Cuticular proteins are either synthesized by the epidermal cells or transported from the hemolymph (Csikos et al., 1999). Arthropod cuticular proteins constitute a much diverse group (Andersen et al., 1995). Thirteen families of cuticular proteins have been reported in arthropods. They were named CPR (RR1, RR2, and RR3), CPF, CPFL, TWDL, CPAP1, CPAP3, CPLCA, CPLCG, CPLCW, CPLCP, and CPTC, respectively. Certain motifs or short stretches of amino acids in cuticular proteins are used for the identification of the proteins families. Some of the families are restricted to a particular insect order. The features of each family have been described previously (Willis, 2010; Willis et al., 2012). The majority of cuticular proteins belong to the family CPR, which has the Rebers and Riddiford Consensus sequence (R&R Consensus; Pfam motif: PF00379) and was first identified by Rebers and Riddiford, (1988). Three subfamilies of CPR cuticular proteins have been reported. i.e. RR-1, RR-2, and RR-3 (Andersen, 1998, 2000; Karouzou et al., 2007). The classification was based on the presence of a Rebers and Riddiford (RR) consensus that was proposed to have affinity to chitin (Rebers et al., 1997). Cuticular proteins with RR-1 type domain are considered as flexible cuticular proteins and those with RR-2 type domain are predicted as rigid cuticular proteins (Andersen, 2000), which are used to classify flexible and rigid cuticular proteins in sequenced insect species in cuticle DB website (Magkrioti et al., 2004). However, there are exceptions. For example, RR-1 motif was also found to contribute to the differentiation of rigid cuticle during ecdysis in insects (Soares et al., 2007; Noh et al., 2015). RR-3 has only been identified in a few cuticular protein sequences and

their role in cuticle formation remains to be established (Karouzou et al., 2007; Willis, 2010; Ioannidou et al., 2014). The N-terminal of the conserved motif of RR contains abundant hydrophilic amino acids, and the conservation of the sequence is related to the type of cuticle in which the epidermis is located. The consensus region of RR-2s, located in rigid cuticle, is conserved, but the consensus motif of RR-1s in flexible cuticle is variable in many species (Rebers and Riddiford, 1988; Willis, 2010). The conserved motif of RR has a binding site for chitin (Andersen et al., 1995) and its molecular conformation is  $\beta$  sheet, which seems the necessary structural conformation for interacting with chitin. It has been proposed to cross link with reactive quinone species when binding with chitin (Guan et al., 2006; Arakane et al., 2012). Other small families also have characteristic motifs. The CPF family has no more than 44 conserved amino acid motif (CPF motif: PF 11018) (Togawa et al., 2007). CPFL (CPF-like) family lacks the conserved 44 amino acid residues but its C-terminal regions are similar to those of the CPF family (Togawa et al., 2007). The CPAP1 and CPAP3 families have a peritrophin-A motif with six distinctly spaced cysteine residues (ChtBD2 domain: PF 01607); CPAP1 has one and CPAP2 has three ChtBD2 domains (Jasrapuria et al., 2012). The CPLCA (cuticular protein of low complexity A), CPLCG, CPLCW and CPLCP families do not possess the motifs described above for other cuticular protein families (He et al., 2007; Willis et al., 2012).

Whole genome sequencing of some insects helps identify cuticular proteins of the insects. Twenty eight cuticular proteins in CPR family have been reported in *Apis mellifera* (Consortium, 2006), 101 CPR cuticular protein genes reported in *Drosophila melanogaster* (Karouzou et al., 2007), 156 CPR genes identified in *Anopheles gambiae* (Cornman et al., 2008), 148 cuticular proteins in *Bombyx mori* (Futahashi et al., 2008), and 158 CPR cuticular protein genes identified and named in *An. sinensis* (Liu et al., 2017). Total cuticular proteins of *A. mellifera*, *Dr. melanogaster*, *An. gambiae*, *B. mori* and *An. sinensis* are 46, 193, 257, 165, and 250, respectively (Liu et al., 2017). However, the exact number of cuticular protein varies from different research groups. For example, genome analysis suggested 238 putative cuticular proteins, including 136 CPR cuticular proteins in *An. sinensis* (Zhou et al., 2017), which is slightly different from what reported by another group (Liu et al., 2017).

Cuticular proteins play an important role in determining the diverse physical properties of cuticle by interactions among themselves and with chitin (Neville, 1993). The unique localization and cross-linking of specific cuticular proteins may be critical for the roles individual cuticular proteins plays. Flexibility or rigidity of cuticles is determined by the degree of cross-linking of some cuticular proteins together with dehydration. However, the functional significance and precise locations of cuticular proteins within a cuticle in insect are still not well established. Studies demonstrated that AgamCPF3 protein is localized in the adult exocuticle, while AgamCPLCG3/4 proteins are restricted to the endocuticle in *An. gambiae* (Vannini et al., 2014). CPR family RR-1s were localized in the procuticle of the soft intersegmental membrane except for one protein found in the endocuticle of rigid cuticle, while CPR family RR-2s were consistently found in rigid cuticle and not in flexible cuticle (Vannini and Willis, 2017). In *Dr. melanogaster* a single cuticular protein, Obstructor-E was reported being able to control the whole body shape of the fly (Tajiri et al., 2017). In the silk worm, *Bombyx mori*, mutation of the *BmorCPR2* gene was described for being responsible for an abnormal distribution of internodes and intersegmental folds, leading to reductions in chitin content and decrease of tensile/stretch properties in larval cuticle (Qiao et al., 2014). Functional studies in the beetle *Tribolium castaneum* suggested the roles of four major cuticular proteins (TcCPR27, TcCPR18, TcCPR4 and TcCP30) in cuticle integrity and property and adult eclosion (Noh et al., 2016).

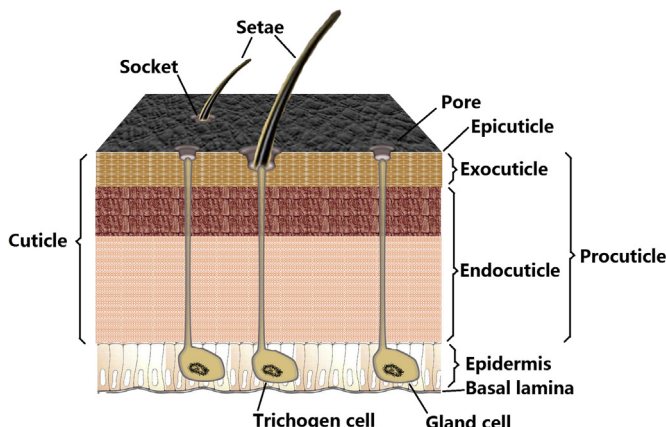


Fig. 1. Cuticle structure of insect (modified from Hackman and Goldberg, 1971).

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