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Nutrition-dependent control of insect development by insulin-like peptides

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In metazoans, members of the insulin-like peptide (ILP) family play a role in multiple physiological functions in response to the nutritional status. ILPs have been identified and characterized in a wide variety of insect species. Insect ILPs that are mainly produced by several pairs of medial neurosecretory cells in the brain circulate in the hemolymph and act systemically on target tissues. Physiological and biochemical studies in Lepidoptera and genetic studies in the fruit fly have greatly expanded our knowledge of the physiological functions of ILPs. Here, we outline the recent progress of the structural classification of insect ILPs and overview recent studies that have elucidated the physiological functions of insect ILPs involved in nutrient-dependent growth during development.

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Introduction

Nutrients are critical environmental signals influencing growth and development in animals. Although each cell in a multicellular organism responds directly to nutrition, the growth and development of the entire organism needs to be coordinated by adjusting growth between tissues and controlling the consumption of stored nutrients. The coordination of systemic organismal growth in response to the nutritional status is primarily mediated by the insulin-like peptide (ILP) family, which includes insulin and insulin-like growth factors (IGFs) in vertebrates, as well as multiple ILPs in invertebrates.

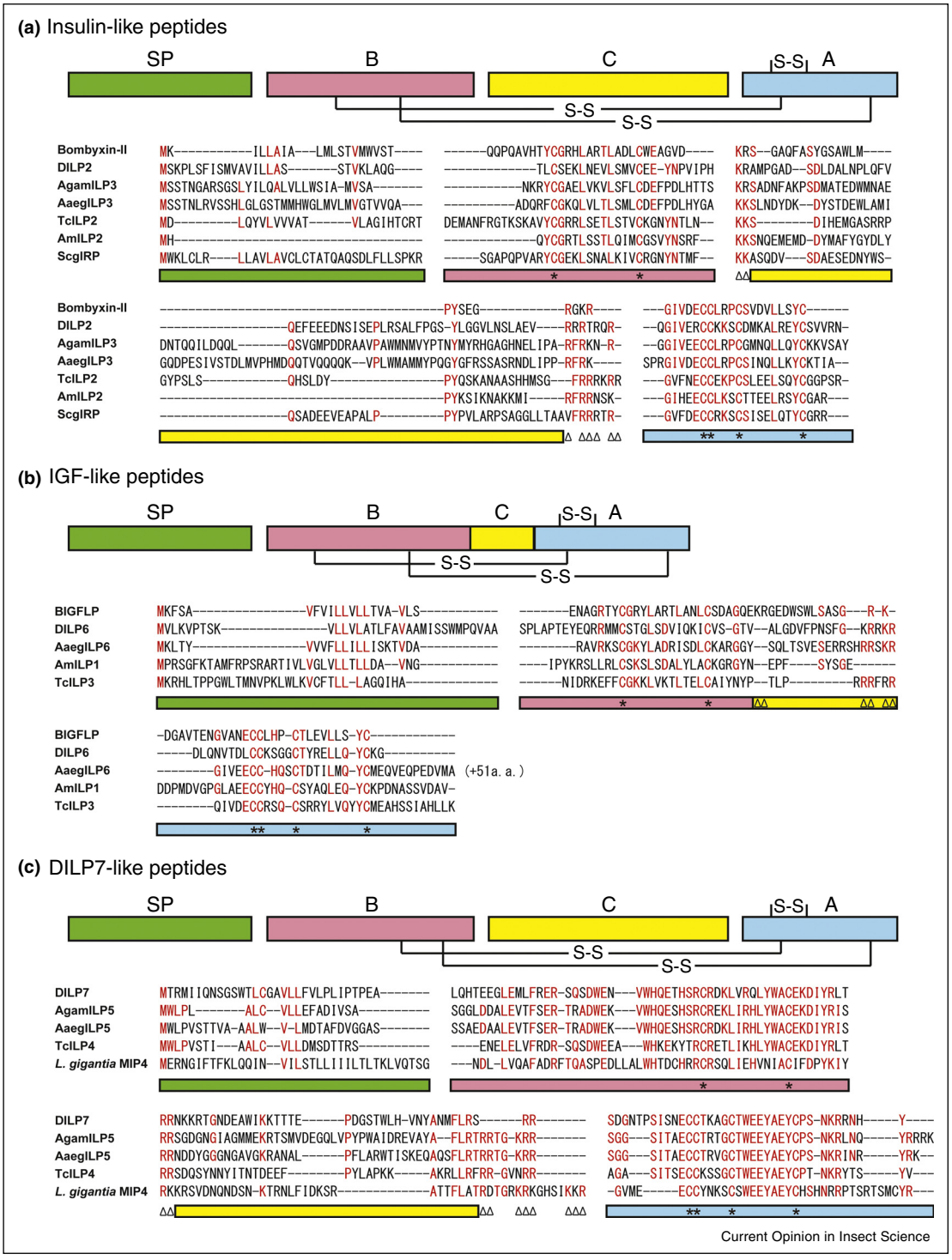
In vertebrates, insulin and IGFs regulate metabolism, growth and development in response to nutritional availability. Although insulin and IGFs have similar amino acid sequences, they have different physiological functions that are meditated by distinct receptor tyrosine kinases (RTKs), the insulin receptor and IGF-I receptor, respectively [1]. The major function of insulin is to control carbohydrate and lipid metabolism [2], whereas that of IGFs is to promote tissue and body growth during development [3]. Numerous studies have shown that the key regulator of the activities of insulin and IGFs is the nutritional status [4]. The production and secretion of insulin by pancreatic β-cells are tightly regulated by the nutrient status [5]. Nutritional availability also influences the production, serum concentration, and action of IGF-I in regulating appropriate tissue and body size [6]. Another class of ILP family peptides in vertebrates, relaxins and relaxin-like peptides, function through leucine-rich repeat-containing G protein-coupled receptors (GPCRs) and have multiple functions, especially associated with reproduction [7].

ILPs have been identified and characterized in a wide variety of invertebrate phyla and in arthropods, including insects [8]. In insects, ILPs are involved in multiple biological processes, including growth, metabolism, reproduction, immunity, behavior, stress resistance, diapause, and lifespan [8–15]. Recently, powerful genetic studies using the fruit fly *Drosophila melanogaster* have greatly enhanced our understanding of the conserved functions of ILPs, as well as their downstream signaling pathways called the insulin/IGF signaling (IIS) pathways [9–15]. In this review, we will first focus on the structural classification of ILPs in insects. We will then overview the recent progress in our understanding of the physiological functions of insect ILPs, especially as it relates to nutrient-dependent growth during development. Through this review, we aim to provide insights into the diverse yet conserved roles of insect ILPs in the coordination of systemic organismal growth, as well as tissue-specific growth, in response to the nutritional status during development.

Structural classification of insulin-like peptides in insects

ILP family members have been identified in multiple insect species, with their numbers varying significantly between only one in some orthopteran species and more than 40 in the silkworm *Bombyx mori* [8,16]. The amino acid sequences of insect ILPs are highly divergent between

Figure 1



Predicted insulin-like, IGF-like and DILP7-like peptides in insects. **(a)** Amino acid sequences of the representatives of predicted insulin-like peptides from *Bombyx* (bombyxin-II), *Drosophila* (DILP2), *Anopheles* (AgamILP3), *Aedes* (AaegILP3), *Apis* (AmILP2), *Tribolium* (TcILP2), and *Schistocerca* (ScgIRP) are aligned. **(b)** Amino acid sequences of the representatives of predicted IGF-like peptides from *B. mori* (BIGFLP), *Drosophila* (DILP6), *Aedes* (AaegILP6), *Apis* (AmILP1), and *Tribolium* (TcILP3) are aligned. **(c)** Amino acid sequences of the representatives of predicted highly conserved ILP group (DILP7-like peptides) from *Drosophila* (DILP7), *Anopheles* (AgamILP5), *Aedes* (AaegILP5), *Tribolium* (TcILP4), and *Lottia* (molluscan insulin-related peptide 4, MIP4) are aligned. Highly conserved amino acid residues are shown in red. Color bars indicate the predicted domains in the precursor peptides: green, signal peptide; red, B-chain; yellow, C-peptide; blue, A-chain. Asterisks on the color bars below the alignment denote Cys residues, and paired triangles denote potential cleavage sites (dibasic amino acids).

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