

Review

Riptortus pedestris and *Burkholderia* symbiont: an ideal model system for insect–microbe symbiotic associations

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Received 26 November 2016; accepted 28 November 2016

Available online 10 December 2016

Abstract

A number of insects establish symbiotic associations with beneficial microorganisms in various manners. The bean bug *Riptortus pedestris* and allied stink bugs possess an environmentally acquired *Burkholderia* symbiont in their midgut crypts. Unlike other insect endosymbionts, the *Burkholderia* symbiont is easily culturable and genetically manipulatable outside the host. In conjunction with the experimental advantages of the host insect, the *Riptortus*–*Burkholderia* symbiosis is an ideal model system for elucidating the molecular bases underpinning insect–microbe symbioses, which opens a new window in the research field of insect symbiosis. This review summarizes current knowledge of this system and discusses future perspectives.

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Keywords: Insect–microbe interaction; Gut symbiosis; Stink bugs; *Riptortus pedestris*; *Burkholderia*; Evolution

1. Introduction

For the last several decades, researchers have discovered that diverse animals and plants establish intimate associations with various microorganisms that often confer beneficial effects upon their host organisms. For instance, in leguminous plants, symbiotic rhizobia are intracellularly housed in specific host organs, called “nodules”, wherein the symbionts fix atmospheric dinitrogen and provide nitrogen compounds to the host plants [1]. In the squid–*Vibrio* symbiotic system, the Hawaiian bobtail squid *Euprymna scolopes* contains bioluminescent *Vibrio fischeri* in the light organ extracellularly, and uses their light in counter-illumination to avoid encountering predators during their nocturnal activity [2]. In addition to these specific one-to-one relationships, recent advancements in sequencing

technologies have revealed that a number of animals harbor and intimately interact with specific microbiota consisting of diverse microorganisms. In the adult human intestinal tract, for example, a great number and wide variety of microbes, 10 to 100 trillion cells in total and over 1000 species in diversity, are housed [3–5]. These complex gut microorganisms independently and/or cooperatively are required for diverse aspects of the biology of the host, including food digestion, induction, training and function of the immune system, organ development, and even regulation of brain functioning. When gut microbiota is disturbed, the host health may be affected in various ways and induce disorders, including obesity, metabolic diseases, cancer, autoimmune and inflammatory disorders and neurophysiological disorders [6–8].

2. Bacterial symbioses in insects

Insects, the most diverse animal group in the terrestrial ecosystem, include more than a million species. In general, the diversity of the insect microbiota is far less complex than in

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mammals and other vertebrates [9–12]. In particular, most insect species that feed exclusively on a nutritionally poor diet or indigestible food such as plant sap, vertebrate blood or woody materials, generally possess specific symbiotic microorganisms in their bodies [13–15]. Symbiotic systems in various insects described thus far show wide variety in symbiont diversity and taxonomy, localization in the host body, transmission mechanisms and symbiont function [15]. In this review, we first summarize what is known thus far in several well investigated insect endosymbiotic systems, and then introduce a recently established useful model system, the *Riptortus*–*Burkholderia* gut symbiosis, and its recent progress.

2.1. Pea aphid microbiota

One of the most famous insect-microbe symbioses is aphid-*Buchnera* mutualistic symbiosis. The pea aphid, *Acyrtosiphon pisum*, a notorious pest of leguminous crops and known to be a model insect for studying phenotypic polymorphism and microbial symbiosis [16], possesses specialized cells called bacteriocytes, wherein an obligate intracellular bacterial symbiont, *Buchnera aphidicola*, is harbored [17]. *Buchnera* is transmitted vertically (i.e. from mother to offspring) via transovarial infection, in which *Buchnera* cells are directly passed from the maternal bacteriocytes to the embryos [18]. *Buchnera* provides the host insect with essential amino acids that are scarcely contained in plant phloem sap, improving host growth and fecundity [19,20]. The genome of *B. aphidicola* in the pea aphid is 0.64 Mb in size and lacks numerous genes required for a free-living lifestyle, being non-viable outside the host body [21]. In addition to the primary symbiont *Buchnera*, aphids also possess one or more vertically transmitted facultative symbionts such as *Hamiltonella defensa* and *Serratia symbiotica*. These facultative symbionts are found in distinct *Buchnera*-free bacteriocytes or in the hemolymph; these facultative symbionts are not essential, but are beneficial, by protecting the host against parasitoid wasps and pathogens [22,23], conferring tolerance in heat stress [24], influencing feeding preference [25] and controlling body color change [26].

2.2. Fruit fly microbiota

The most famous insect model organism *Drosophila melanogaster* and its allied species generally harbor a relatively small number of bacterial taxa in their gut (reviewed in [27]). Gut microbiota of fruit flies consists of 1–30 bacterial taxa (with 97% threshold of 16S rRNA sequence identity), which vary between laboratory-reared and wild-captured samples as well as between fly species [28]. Some of these bacteria are transmitted vertically via egg-surface contamination, most likely derived from adult feces, and new hatchlings acquiring the symbionts by feeding egg shells [29,30]. Although the gut microbes of *Drosophila* are not essential for host survival, experimental elimination of the gut microbes showed that the symbionts increase the growth rate of the insect host, for

example, via modulating insulin signaling [31]. Furthermore, it has been demonstrated that the *Drosophila* gut microbiota influences host immunity [32,33], gut homeostasis [33], gut morphogenesis [34] and mating preferences of the host fly [35]. Recently, a genome-wide association study using a number of inbred lines identified host genetic factors associated with gut microbiota-dependent nutritional phenotypes [36]. *Drosophila* species have been also studied as a useful model system for revealing the symbiotic mechanisms of the famous host sex manipulators *Wolbachia* and *Spiroplasma* [37–39].

2.3. Honey bee microbiota

The honey bee *Apis mellifera*, a model organism in social insects and an agriculturally important organism as a pollinator of diverse crops, is commonly associated with a simple gut microbiota (reviewed in [40]): in adult workers, it consists of a mere nine bacterial taxa [41]. These gut symbionts are transmitted via social interactions between bee individuals [42]. Recent studies, in conjunction with studies in bumble bees (*Bombus* spp.) belonging to the same family Apidae, whose gut microbiotas are similar to that of the honey bee, have revealed that honey bee symbionts contribute to degradation of food materials, i.e. nectar, honey, and pollen [43], and to protection against a trypanosomatid parasite *Crithidia bombi* [44]. All of the gut bacteria are culturable in axenic media, and re-infection experiments are established, making this system a useful model for insect-microbe and microbe–microbe interactions [40,45].

2.4. Microbiota of other insects

Tsetse flies, the notorious vectors of African trypanosomes, feed exclusively on vertebrate blood and house a vertically transmitted intracellular symbiont, *Wigglesworthia glossinidia*, that provides the host with B vitamins rarely contained in vertebrate blood [46]. Other well-investigated intracellular obligate symbioses are found in plant sap-feeding hemipteran insects, such as the psyllids–*Carsonella*, mealybugs–*Tremblaya*, and Auchenorrhyncha–*Sulcia* symbiotic associations [17,47]. Another famous insect-microbe symbiosis is found in termites. Lower termites are wood feeders and, exceptionally among the insects, harbor several hundred taxa of symbiotic bacteria (with 97% threshold of 16S rRNA sequence identity) as well as archaea and protists in the hindgut [48]. These symbiotic microorganisms play central roles in the digestion of the woody materials, i.e. cellulose, hemicellulose and lignin, and are vertically transmitted through a unique coprophagy mechanism [49]. In addition to termites, recent surveys using next-generation sequencers have revealed that specific gut symbioses are omnipresent among diverse insects, including beetles [50], grasshoppers and cutworms [51], etc. (a broad survey was performed in [52]). Microbial symbioses in stink bugs have been broadly and intensely investigated, as reviewed in a later section of this review (see Section 5).

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