



Mini Review

Genomics of intracellular symbionts in insects

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ABSTRACT

Endosymbiotic bacteria play a vital role in the evolution of many insect species. For instance, endosymbionts have evolved metabolically to complement their host's natural diet, thereby enabling them to explore new habitats. In this paper, we will review and give some examples of the nature of the metabolic coupling of different primary and secondary endosymbionts that have evolved in hosts with different nutritional diets (i.e., phloem, xylem, blood, omnivores, and grain). Particular emphasis is given to the evolutionary functional convergence of phylogenetically distant endosymbionts, which are evolving in hosts with similar diets.

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Introduction

In recent years, genomics and metagenomics have opened up new avenues of research into symbiotic associations. Metagenomic studies of different habitats, such as sea water, ice cores, marine sponges, or human gut (Venter et al., 2004; Bidle et al., 2007; Schmitt et al., 2007; Booijink et al., 2007) have led to the discovery of the presence of previously unknown and uncultivable bacteria, protozoa, and viruses. In particular, there are increasing numbers of genome sequences for many symbionts, revealing their complete set of genes as well as their functional contribution to their host's metabolism.

Symbiotic associations are particularly well studied in insects. Insects are the most species-rich group of organisms, and it has been estimated that at least 15–20% of all insects live in symbiotic relationships with bacteria (Buchner, 1965; Douglas, 1998). According to the location of the symbiont with respect to the cells, associations can be referred to as ectosymbiotic or endosymbiotic. Among intracellular symbioses, there are differences regarding the extent of dependence between the animal host and the symbiont and the age of the association leading to the distinction between obligate primary endosymbiont (P-endosymbiont) and facultative secondary endosymbiont (S-endosymbiont). S-symbionts are

considered facultative since they are not essential to host survival and reproduction even though, in some cases, they confer advantages to their hosts (Oliver et al., 2009). Although they are normally transmitted vertically through host generations, their distribution patterns suggest that sporadic horizontal transmission can occur (Russell et al., 2003; Russell and Moran, 2005). Insects that have established endosymbiotic associations with bacteria are characterized, in general, by feeding upon unbalanced diets, poor in essential nutrients such as amino acids, sterols, or vitamins, which are provided by the symbionts. Other symbionts provide different functions to their host, such as nitrogen recycling and storage or the provision of metabolic factors that are required for survival and fertility (Douglas, 1998; Baumann and Moran, 2000). On the other hand, the bacterium gains a permanent supply of a wide range of metabolites that are provided by the host as well as a safe environment. The first step towards obligate endosymbiosis becoming established is when a free-living bacterium infects the host. Then, both organisms coevolve to adapt to the new situation. On the bacterial side, genomic studies have revealed that the endosymbiont genome gets smaller during this adaptive process, owing to the loss of genes that are rendered unnecessary in the new environment (Gil et al., 2004; Zientz et al., 2004; Moya et al., 2008; Moran et al., 2008; Feldhaar and Gross, 2009).

To date, the following complete genomes of bacterial endosymbionts of insects have been fully sequenced: the endosymbionts of 4 aphid species (*Buchnera* spp.) (Shigenobu et al., 2000; Tamas et al., 2002; van Ham et al., 2003; Pérez-Brocal et al., 2006), 2 S-symbionts of the pea aphid (*Hamiltonella defensa* and *Regiella insecticola*) (Degnan et al., 2009a, 2009b), the endosymbionts of 2 carpenter ant

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Table 1
Functional features of intracellular symbionts.

Endosymbiont	Host	Association age	Host nutrition	Genome size (Kb)	Metabolic capacity	Insertion elements	T3SS	Accession number
<i>Buchnera aphidicola</i> Bap (γ -Proteobacteria)	<i>Acyrtosiphon pisum</i> (aphid)	150 my	Phloem (primary)	652	Amino acids, vitamins	No	Incomplete T3SS	BA000003 AP001070 AP001070
<i>Buchnera aphidicola</i> BSG (γ -Proteobacteria)	<i>Schizaphis graminum</i> (aphid)	150 my	Phloem (primary)	653	Amino acids, vitamins	No	Incomplete T3SS	AE013218 AF041836 Z21938
<i>Buchnera aphidicola</i> BBp (γ -Proteobacteria)	<i>Baizongia pistaciae</i> (aphid)	150 my	Phloem (primary)	618	Amino acids, vitamins	No	Incomplete T3SS	AE016826 AF492591
<i>Buchnera aphidicola</i> BCt (γ -Proteobacteria)	<i>Cinara tujafilina</i> (aphid)	150 my	Phloem (primary)	445	Amino acids, vitamins	No	Incomplete T3SS	–
<i>Buchnera aphidicola</i> BCC (γ -Proteobacteria)	<i>Cinara cedri</i> (aphid)	150 my	Phloem (primary)	422	Amino acids, Trp incomplete	No	Incomplete T3SS	CP000263 AY438025
^{a,b} <i>Serratia symbiotica</i> (γ -Proteobacteria)	<i>Cinara cedri</i> (aphid)	–	Phloem (primary)	In progress	Vitamins, Trp incomplete	No	No	–
<i>Halmitonella defense</i> (γ -Proteobacteria)	<i>Acyrtosiphon pisum</i> (aphid)	–	Phloem (secondary)	2100	Parasitoid wasp protection	IS elements	2 complete T3SSs	CP001277 CP001278
^a <i>Carsonella ruddi</i> (γ -Proteobacteria)	<i>Pachysylla venusta</i> (psyllid)	120 my	Phloem (primary)	160	Symbiotic role lost	No	No	AP009180
<i>Baumannia cicadellincola</i> (γ -Proteobacteria)	<i>Homalodisca vitripennis</i> (sharpshooter)	170 my	Xylem (primary)	686	Vitamins, cofactors	No	No	CP000238
^a <i>Sulcia muelleri</i> (Flavobacteria)	<i>Homalodisca vitripennis</i> (sharpshooter)	> 270 my	Xylem (primary)	246	Amino acids	No	No	CP000770
^a <i>Sulcia muelleri</i> (Flavobacteria)	<i>Diceroprocta semicincta</i> (singing cicada)	> 270 my	Xylem (primary)	277	Amino acids	No	No	CP001605
^a <i>Hodgkinia cicadicola</i> (α -Proteobacteria)	<i>Diceroprocta semicincta</i> (singing cicada)	190 my	Xylem (primary)	144	Amino acids	No	No	NC012960
<i>Wigglesworthia glossinidia</i> (γ -Proteobacteria)	<i>Glossina brevipalpis</i> (tsetse fly)	40–80 my	Blood (primary)	698	Vitamins, cofactors	No	complete T3SS	BA000021 AB063523
<i>Sodalis glossinidius</i> (γ -Proteobacteria)	<i>Glossina morsitans</i> (tsetse fly)	–	Blood (secondary)	4171	Immunity	IS elements	3 complete T3SSs	AP008232
^a <i>Blochmannia pennsylvanicus</i> (γ -Proteobacteria)	<i>Camponotus pennsylvanicus</i> (carpenter ant)	50 my	Omnivore (primary)	792	Nitrogen metabolism	No	No	CP000016
^a <i>Blochmannia floridanus</i> (γ -Proteobacteria)	<i>Camponotus floridanus</i> (carpenter ant)	50 my	Omnivore (primary)	706	Nitrogen metabolism	No	No	BX248583
<i>Blattabacterium</i> (Flavobacteria)	<i>Blattella germanica</i> (cockroach)	150 my	Omnivore (primary)	637	Nitrogen metabolism	No	No	CP001487
<i>Blattabacterium</i> (Flavobacteria)	<i>Periplaneta americana</i> (cockroach)	150 my	Omnivore (primary)	637	Nitrogen metabolism	No	No	CP001429
SOPE (γ -Proteobacteria)	<i>Sitophilus oryzae</i> (weevil)	Less than 25 my	Grain (primary)	3000 ^c	Amino acids, vitamins	IS elements	Complete T3SS	–

my, Millions of years.

^a Candidatus.

^b Secondary endosymbiont in other aphids.

^c Size estimated by pulse-field gel.

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