Insect Symbiosis

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BOOK REVIEWS

BOURTZIS, K. A., AND T. A. MILLER, EDITORS. 2003. Insect Symbiosis. CRC Press; Boca Raton, FL. 347 p. ISBN 0-8493-1286-8. Hardback. $119.95.

This edited volume contains a wealth of information about symbionts of insects which all entomology graduate students (and their advisors) need to be aware of. Information contained within this multi-authored volume may change the way we conduct our research or interpret data. The chapters contained within it make it clear that the biology, behavior, ecology and genetics of insects cannot be considered without considering the role of symbionts in each of these topics. This volume provides an overview of a rapidly advancing field of study, although it is not an exhaustive review of all that is known about symbionts. The entire field of symbiosis is expanding quickly and various books (including Margulis 1970, 1993; O'Neill et al. 1997; Sapp 1994; Douglas 2002; Paracer & Ahmadjian 2000; Majerus 2003) are available to discuss the symbioses found in an incredible array of organisms, giving symbiosis a prominent role in understanding ecology, behavior and evolution.

The entomological world is in the process of being revolutionized by the discovery, and increased understanding, of the various roles played by the multitude types of symbionts found in arthropods. There are several definitions of symbiosis, but in this book it involves an association where one organism (the symbiont) lives within the body of another organism (the host), regardless of the actual effect on the host; some symbioses are mutualistic, some parasitic, and some involve commensalism, in which one partner derives some benefit without either harming or benefiting the other organism.

The advent of molecular biology and the polymerase chain reaction (PCR) has made it possible to identify a wealth of hitherto-unknown microorganisms associated with their arthropod hosts that are not culturable by traditional methods. Novel fungi, bacteria, viruses, microsporidia, and protozoa are being discovered by the PCR and the complete genomic analyses of several (including two symbionts from aphids and *Wolbachia*, which are found in many arthropods and Crustacea) indicate that the field is progressing rapidly. Microscopic and molecular techniques allow scientists to resolve where these symbionts reside and how they are transmitted, while biochemical approaches allow a clearer understanding of their relationships.

Some symbionts, such as *Wolbachia*, are nearly ubiquitous in arthropods and have diverse effects on their hosts including male killing, cytoplasmic incompatibility, sterility, lethality, or 'none apparent'. For example, *Wolbachia*, an intracellular bacterium, has been identified in 76% of arbitrarily chosen insect and mite species within 16 orders and some were found to have multiple types of *Wolbachia* within them (Jeyaprakash & Hoy 2000). Chapters that include discussions of *Wolbachia* include Chapter 15 by M. Huigens and R. Stouthamer on Parthenogenesis Associated with *Wolbachia*, chapter 14 by K. Bourtzis, H. Braig and T. Karr on Cytoplasmic Incompatibility, and Chapter 13 by S. Dobson on *Wolbachia pipientis*: Impotent by Association. In addition, chapter 12 by G. Hurst, F. Jiggins and M. Majerus on Inherited Microorganisms that Selectively Kill Male Hosts: The Hidden Players of Insect Evolution?, include *Wolbachia* as well as other microorganisms that kill male embryos. In Chapter 16, F. Dedeine, C. Bandi, M. Bouletreau and L. Kramer provide Insights into *Wolbachia* Obligatory Symbiosis, describing the relationship between *Wolbachia* and filarial nematodes and contrasting it with the relationships found between *Wolbachia* and insects. In Chapter 17, S. Bordenstein describes what is known about Symbiosis and the Origin of Species, with a special emphasis on the roles of *Wolbachia* in speciation. Finally, in Chapter 18, T. Fukatsu, N. Kondo, N. Ijichi and N. Nikoh describe work that indicates that part of the *Wolbachia* chromosome has been transferred into the nuclear genome of its insect host, the Adzuki bean beetle. Integration of part of the genome of *Wolbachia* into the insect host genome is reminiscent of the transfer of genes from the mitochondrion (originally a microbial endosymbiont of the eukaryotic cell) to the nuclear genome of a eukaryotic host. Such a transfer of genes can ultimately lead to the symbiont becoming an organelle.

H. Ishikawa introduces the book (Chapter 1) with an Introduction and provides an over view of roles of gut microbes, endoparasitism, extracellular and intracellular symbiosis, including mutualistic symbionts (such as those found in aphids, cockroaches, termites, beetles and blood-sucking insects), as well as others such as sex-ratio distorters, *Spiroplasma*, microsporidia and *Wolbachia*. Ishikawa noted that "insects may provide the best material for examining the evolutionary significance of interspecific symbioses."

A. Douglas provides an overview of *Buchnera* Bacteria and Other Symbionts of Aphids in Chapter 2. The *Buchnera*-aphid relationship is ancient and intimate, involving a mutual dependence between the *Buchnera* housed in specialized cells called mycetocytes and their aphid hosts that has extended back 200 million years to the origin of the Aphidoidea. *Buchnera* provide essential amino acids to their hosts and the relationship has affected the genomes of both aphids and microbes. In chapter 3, I. Tamas and S. Andersson discuss the Comparative Genomics of Insect Symbionts, with a focus on *Buchnera*. The genomes of obligate host-associated bacteria tend to be smaller than the genomes of their closest free-living relatives. The small genome size in *Buchnera* is achieved by loss of phage, transposable elements and repeated sequences, as well as the loss of essential genes. Over the years, the *Buchnera* genome deteriorated, and *Buchnera* genomes are the most highly reduced that have been described. It also appears that the process of eliminating genes is still occurring, although *Buchnera* and their hosts are at a late stage in the co-evolutionary process. Tamas and Andersson suggest that, at this point in the aphid-*Buchnera* relationship, "it may no longer be meaningful to speak about an insect host and a bacterial guest; the two have merged to become a new, single organism."

Another fascinating story is provided in Chapter 4 by S. Aksoy about Symbiosis in Tsetse. Tsetse flies are important agricultural and medical pests in Africa that vector protozoan trypanosomes, causing sleeping sickness in humans and various diseases in animals. Tsetse flies provide a home for several bacterial symbionts, and the relationships between the fly and the bacteria range from obligate mutualists to facultative parasites. The importance of the symbionts in human affairs is demonstrated by the fact that the presence of one, *Sodalis*, has been implicated as enhancing the likelihood that tsetse flies will transmit trypanosomes, thus making tsetse a more effective disease vector. Aksoy also discusses the possibility of harnessing symbionts to control of disease transmission. Several different research approaches, including the genetic modification of one or more of the symbionts, are being evaluated with the goal of conquering human sleeping sickness, which claims over 50,000 lives per year in Africa, as well as devastating livestock production, resulting in serious social and economic problems over much of the continent.

A. Heddi reviews what is known about endosymbiosis in *Sitophilus* weevils, pests of stored cereals, in Chapter 5. These weevils contain bacteria that help their hosts to balance the nutritional deficiencies of their diet. In addition, the weevils contain *Wolbachia,* which induces cytoplasmic incompatibility, which may be a component of the reproductive isolation that can lead to speciation.

In Chapter 6, R. Durvasula, R. K. Sundaram, C. Cordon-Rosales, P. Pennington and C. B. Beard describe the relationship between the kissing bug *Rhodnius prolixus* and its symbiont, *Rhodococcus rhodnii*, an actinomycete that aids in processing B-complex vitamins and in the sexual maturation of the insect host. These authors discuss the possibility of using a genetically modified symbiont to control transmission of Chagas' disease, which kills over 50,000 people annually in Central America and northern regions of South America. The genetic modification of insect gut symbionts results in an insect that is "paratransgenic", rather than transgenic, because it is the genome of the microorganism that is modified rather than the genome of the host insect. The use of a paratransgenic approach to control Chagas' disease would be a novel pest management tactic, but the authors acknowledge that the environmental effects of releasing genetically modified gut symbionts must be understood and issues of regulation and policy pertaining to the release of genetically modified organisms must be resolved before this can be achieved.

Some symbioses involve fungi and in Chapter 7, D. Six discusses bark beetle-fungus symbioses found in the family Scolytidae. Bark beetles are associated with filamentous fungi (Ascomycotina and Basidiomycotina). In addition, bark beetles contain ascomycete yeasts, although the yeasts have been less well studied. Many bark beetles possess specialized structures called "mycangia", and these may involve an invagination of the integument that is lined with glands or secretory cells that are specialized for the acquisition and transport of fungi. Other, less elaborate, mycangia include "any structure that consistently transports fungi". The fungi are considered mutualists, although other relationships may exist, because bark beetle larvae and teneral adults feed on the mycelia and also probably feed on yeasts during development. The fungi are transported to new trees by the beetles, providing the fungi with dispersal mechanisms and protection from the environment in the beetle feeding galleries and during dispersal within the mycangia.

Not all symbioses are obligatory. In Chapter 8, C. Lauzon discusses the Symbiotic Relationships of Tephritids, which appear to be less than obligate, but still interesting for several reasons, including the possible improvement of genetic control programs. The Mediterranean fruit fly and other major agricultural pests such as apple maggot fly contain *Enterobacter agglomerans* and *Klebsiella pneumoniae*, which are present in biofilms within their guts. Lauzon speculates that artificial diets containing antibiotics, which are used in mass rearing programs for sterile insect genetic control programs, affect the health of the fruit flies. An applied aspect of this work suggests that these gut symbionts, which can be cultured, could be fed to sterilized fruit fly adults as probiotics to aid in their nutrition and fitness. Improving the fitness of sterilized males could result in huge cost savings in genetic control programs.

Digestion of cellulose is not easy for most animals but, with the aid of gut symbionts, termites have been able to exploit an abundant food resource. The relationship between termites and their symbionts is incredibly complex and diverse. The hindgut of a single termite, for example, may harbor hundreds of different types of microorganisms including bacteria, fungi, and protozoa. Although there is a clear relationship between hind gut symbionts and termite nutrition, the relationships are not limited to nutrition. K. Matsuura, in Chapter 9, describes Symbionts Affecting Termite Behavior, including novel termite-bacteria and termite-fungus interactions. Matsuura focuses on the role of symbionts in nestmate recognition, nest odor, and the evolutionary process of egg mimicry by sclerotia of a fungus. Matsuura concludes by noting that ". . . our knowledge of termite-microorganism relationships remain limited." The habits of termites are enmeshed with various microorganisms and, no doubt, additional discoveries remain to elucidate these fascinating interactions.

Symbiosis may involve a parasitic relationship and The Symbiosis of Microsporidia and Insects is described by P. Agnew, J. Becnel, D. Ebert and Y. Michalakis in Chapter 10. Microsporidia are unicellular eukaryotes that are obligate intracellular parasites that cannot live independently outside their host. Recent molecular analyses indicate that microsporidia are related to fungi. During evolution, there was a loss of cytological complexity and reduction in the size of the genomes of microsporidia compared to their free living fungal relatives. Agnew et al. indicate that microsporidia have been highly successful and are among the most common parasites of arthropods (as well as of humans and other animals).

Although *Wolbachia* have been the dominant microorganism recognized to affect sex ratios in arthropods, A. Weeks and J. Breeuwer describe A New Bacterium from the Cytophaga-Flavobacterium-Bacteroides Phylum that Causes Sex-Ratio Distortion in Chapter 11. A new undescribed bacterium from this phylum appears to cause feminization and parthenogenesis in its hosts. In the privet mite (*Brevipalpus phoenicis*), it appears to cause females to be haploid (the first apparent case of haploidy in females in the animal kingdom) and no males are normally found.

Another aspect of sex ratio distortion is described by G. Hurst, F. Jiggins and M. E. Majerus in chapter 12, Inherited Microorganisms That Selectively Kill Male Hosts: The Hidden Players of Insect Evolution?". Scientists have known for a long time that individuals from some insect populations collected from the field would yield progenies with a strongly biased sex ratio in favor of females. The diversity of organisms involved in male killing is reviewed and discussed with regard to fitness costs and effects on population size or extinction. The authors conclude that it is "premature to say we understand the population biology of these elements". However, the authors suspect that the high prevalence achieved by male killers in certain insect species may make them important in evolutionary processes, especially those involving changes in sex determination systems.

This excellent overview of some of the relationships between insects and the various microorganisms that live within them should trigger additional research on the "bugs" of interest to you. The chapters each contain numerous references and excellent illustrations, including color figures in the center of the volume. Run, don't walk, to get a copy of this book; it just may change how you think about your "bugs".

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