

The evolution of symbiotic systems

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Symbiosis refers to close and sympatric interactions between species. The interactions involve dynamic changes of genomes, metabolisms, and signaling networks of symbiotic partners. A unified understanding of these interactions is required when studying symbiotic organisms. To emphasize the enormous variety of symbiotic consortia and the underlying commonalities that relate these systems, James Lake and I organized the 7th Okazaki Biology Conference (OBC) on “The Evolution of Symbiotic Systems,” hosted by the National Institute for Basic Biology, from January 11–14, 2010, in Kakegawa, Japan. The OBC is an international conference dedicated to providing opportunities to create new networks of scientists and to facilitate the development of future areas of fundamental research in the biological sciences. The topics ranged broadly and included early prokaryotic endosymbiosis, the evolution of plastids, diversity of endosymbionts, partner shifts, interdependent genomes, marine symbioses, insect–microbe interactions, plant–microbe interactions, and artificial symbiotic systems. Of these various symbioses ranging from intracellular to inter-specific, six topics are introduced in this multi-author review.

Apicomplexans are a group of protists that are obligate intracellular parasites in animals including humans. With some exceptions, apicomplexans have a tiny plastid-like organelle called an apicoplast that is thought to have

originated from secondary endosymbiosis of a red algae [1]. The apicoplast of parasitic apicomplexans such as the human malaria *Plasmodium falciparum* is nonphotosynthetic but has become indispensable because it functions in other metabolisms supplying essential products to the host. In contrast to the metabolisms involving the apicoplast, housekeeping functions of the organelles have remained unclear, though they are often unique or differ markedly from those of other organisms. Sato sheds light on the apicoplast and its uniqueness in the housekeeping functions.

Aphids are small, soft-bodied insects and feed exclusively on plant phloem sap. They have been associated with intracellular symbiotic bacteria that synthesize essential amino acids. In the case of the pea aphid, its symbiotic bacteria *Buchnera aphidicola* are absolutely required for host growth and reproduction. These bacteria are transmitted from mother to offspring through host generations. In 2000, Shigenobu and associates reported the complete genome sequence of *Buchnera* sp. strain APS, which is composed of one 640,681 base pair chromosome and two small plasmids [2]. Next, a draft genome sequence of the pea aphid was determined in 2010 [3]. In response to these genome sequence analyses, Shigenobu and Wilson present a refined picture of this symbiosis by linking pregenomic observations to new genomic data to understand the *A. pisum/Buchnera* APS symbiosis, including (1) lateral gene transfer, (2) host immunity, (3) symbiotic metabolism, and (4) regulation of symbiosis.

Termites are insects that are able to vigorously decompose plant wood and therefore play an important role in carbon turnover in the global environment. Furthermore, nitrogen fixation in termites is one of the most important aspects of the symbiosis because the diet of termites is usually low in nitrogen sources [4]. Termites’ abilities to

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feed on vast amounts of nitrogen-poor lignocellulose and fix atmosphere nitrogen largely depend on a symbiotic gut microbial community, which comprises >300 species of protists, bacteria, and archaea. Notably, most of them are uncultivable and constitute a multi-layered symbiotic system. Hongo overviews this multi-layered system organized by wood-feeding termites and their gut uncultivable microorganisms, focusing on the recent achievements in single-species-targeted metagenomics and metatranscriptomics studies [5].

Symbiosis between legumes and soil bacteria, collectively called rhizobia, is one of the most successful mutually beneficial plant–microbe interactions on earth. Legumes develop a special adaptive organ called a nodule in response to Nod factors from rhizobial infection. In a nodule, rhizobia provide the host plants with ammonia produced through fixing atmospheric nitrogen. In return, the host plants supply the rhizobia with their photosynthetic products. Saeki reviews the establishment and maintenance of rhizobium-legume symbiosis from the bacterial side, focusing on the ROS scavenging enzymes, the BacA protein originally found in *Sinorhizobium meliloti*, and the Type III/IV secretion systems. Recent progress in molecular genetics and genomics in model legumes, i.e., *Lotus japonicus* and *Medicago truncatula*, has enabled us to identify a number of host genes required for root nodule symbiosis [6, 7]. Yokota and Hayashi overview the evolution of root nodule symbiosis based on the plant symbiotic genes identified.

The numerous types of symbioses are complex systems such as the multilayered symbiotic system in termites. Given the diversity and complexity of symbiotic interactions in nature, one strategy is to utilize simpler systems. Artificial systems composed of a small set of living organisms can reduce the complexity and provide a platform to address many important questions about natural systems. For example, what are the potential origins of symbioses? What determines the persistence of symbioses?

How do habitat structures affect the ecology and evolution of symbioses [8]? How do symbiotic interactions generate dynamics and patterns at the community level [9]? How does symbiosis affect evolution? Shou and associates introduce artificial systems and address several important questions in order to capture essential features of natural symbioses.

One of the important aspects of symbiosis is the generation of novel adaptive traits through the cooperation. Working together, symbiotic organisms can sometimes accomplish biological feats that none can achieve alone. I hope that this multi-author review triggers a new integrated symbiosis research that none of the single aspects can achieve alone.

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