

## PREFACE

## Aphids as models for ecological and evolutionary studies

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Aphids (Hemiptera: Aphididae) are a group of phloem-feeding insects numbering more than 5 000 extant species (Favret, 2014a). Most species have complex life cycles that include both asexual (viviparous parthenogenesis) and sexual reproduction. They display a high degree of intraspecific polyphenism with multiple phenotypes from an identical genotype, and they have specialized associations with their host plants (Blackman & Eastop, 2000). Some aphid species are gall-makers and even have evolved sociality with division of labor (Aoki, 1977; Stern & Foster, 1996). Many aphid species are agricultural and forestry pests. They incur damage to plants and carry vector plant viruses (Blackman & Eastop, 2000). Due to their fascinating biological character and economic importance, aphids have long been popular animals for research in basic and applied biology, and are becoming useful research models for studying important questions in ecology and evolution, especially in the genomic era (Brisson & Stern, 2006; Huang & Qiao, 2006; Srinivasan & Brisson, 2012).

The papers in this special issue were selected from among the presentations delivered at the 9th International Symposium on Aphids (9ISA), held in June 2013 in Beijing, China. The 9ISA is the first time the International Symposium on Aphids was held in Asia. It attracted 187 participants from 66 research institutes and universities in 20 countries and regions on five “continents” (Asia, Europe, Oceania, North America, South America). The purpose of this special issue is to demonstrate the diversity and new findings of studies using aphids as research models. The issue consists of 11 original articles, one review paper (Vorburger, 2014) and one perspective paper (Favret, 2014b). These papers address a wide range of re-

search topics, including systematics, DNA barcoding, mitogenomics, new protocols for whole-mount fluorescent *in situ* hybridization (FISH), the biology of aphid pests, and interactions between aphids and their endosymbionts, parasitoids and host plants.

Aphids harbor an obligate (primary) bacterial endosymbiont, *Buchnera aphidicola*, and a wide variety of facultative (secondary) endosymbionts (Moran *et al.*, 2008; Oliver *et al.*, 2010). The obligate association of aphids and *Buchnera* is indispensable to both partners. Recent evidence suggests facultative endosymbionts also provide benefits to their aphid hosts. In this issue, Vorburger (2014) reviews empirical studies and models to explore the evolutionary ecology of facultative endosymbiont-conferred resistance to parasitoids observed in aphid populations. The paper shows that defensive symbionts (*Hamiltonella defensa*, *Serratia symbiotica*, *Regiella insecticola*) can alter the reciprocal selection between aphids and parasitoids in several ways, and therefore modify host–parasitoid coevolution. The paper also discusses the implications of symbiont-conferred resistance for biological control of aphid pests. Peccoud *et al.* (2014) investigate whether paternal transmission during sexual reproduction is a reliable mechanism of horizontal transfer of facultative endosymbionts across aphid lineages. Their experiments suggest that such paternal transmission is very rare or absent across nine host-specialized pea aphid biotypes, while confirming that maternal inheritance is routine for most secondary endosymbionts. Interestingly, they report that *Serratia symbiotica* is frequently lost during the sexual reproduction of their hosts, suggesting future studies are needed to understand various possibilities concerning inheritance or transmission patterns of secondary symbionts. By using multiple molecular markers, Wang *et al.* (2014c) report an unusual, high infection rate and diverse infection patterns of the secondary endosymbionts, *Wolbachia*, in natural aphid populations in China. The unusual widespread infection of *Wolbachia* in Chinese aphids may provide a good model for studying the

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invasion, spread and evolution of secondary endosymbionts in aphids.

As the first reported case of cospeciation between insects and bacteria, aphid–*Buchnera* symbiosis has been widely investigated and may be the best known case (Moran *et al.*, 2008). The fine-scale fidelity of aphid–*Buchnera* parallelism has been indicated by several phylogenetic studies mainly on closely related species and intraspecific lineages (see review in Liu *et al.*, 2013). However, more investigations across aphid lineages with different life cycles and at different taxonomic levels are still needed to reveal a reliable scenario for the evolutionary relationships between aphids and *Buchnera*. To understand whether relatively isolated habitats (i.e., galls) have an effect on the aphid–*Buchnera* relationship, Liu *et al.* (2014a) investigated the molecular phylogenetic relationships of gall aphids from *Pemphigus* and allied genera, and their *Buchnera* symbionts. Their results again confirm the parallel evolution at the generic and interspecific levels. Nevertheless, a new research based on much more taxa and genomic data than previous studies indicates obvious phylogenetic incongruence between aphids and *Buchnera* at the subfamily level (Liu *et al.*, 2014b). It suggests that we should rethink the cospeciation hypothesis and tread carefully when using *Buchnera* markers for inferring higher relationships among aphid lineages (e.g., Nováková *et al.*, 2013).

The taxonomic community nowadays faces particular challenges, such as the lack or loss of readily available taxonomic expertise as well as the insufficiency of funding opportunities compared to other disciplines, that is, taxonomic impediments (Ebach *et al.*, 2011). Using aphids as an example, Favret (2014b) proposes a conceptual cyber-taxonomic workflow incorporating the two most important taxonomy resources: expert knowledge and museum specimens. As global issues, taxonomic impediments can only be finally resolved through global collaboration, by using informatics tools to link taxonomic expertise and specimens in different countries. *Aphis* is the largest aphid genus and is considered the most difficult group in aphid taxonomy. Lagos *et al.* (2014) present a phylogeny of *Aphis* species groups found in the Midwestern United States, incorporating DNA sequence and morphological data. Their results are valuable for unraveling the mysterious relationships among species of this difficult genus and its allied genera.

The release of the pea aphid nuclear genome (The International Aphid Genomics Consortium, 2010) is boosting aphid genomic studies and providing opportunities for understanding fundamental questions in the complex life cycle of aphids and in applied agricultural problems. Ongoing genome sequencing projects of other aphid species

such as *Myzus persicae*, *Aphis gossypii* and *Toxoptera citricidus* will also contribute greatly. Although the mitochondrial genome has shown its importance in exploring molecular evolution, phylogenetics and population genetics, only two aphid mitochondrial genomes (*Schizaphis graminum*, *Acyrtosiphon pisum*) had been sequenced before 2013. Wang *et al.* (2013) reported the complete mitogenome of *Cavariella salicicola*, and two nearly complete mitogenomes of *Aphis glycines* and *Pterocomma pilosum*; Zhang *et al.* (2014) reported the complete mitogenome of *Diuraphis noxia*. Both studies found a unique repeat region with variable numbers of tandem repeats between tRNA<sup>Phe</sup> and tRNA<sup>Glu</sup>. In this issue, Wang *et al.* (2014b) present the mitogenome of *Cervaphis quercus*, a member of the Greenideinae, and the first mitogenome of a species outside the Aphidinae. They compare it with the previously published mitogenomes and suggest that the repeat region is unique to Aphidinae species and may have species-specific origins.

Phenotypic plasticity, the alternation of modes of reproduction, and other important biological features of aphids are at least partially regulated by differential gene expression. To study these questions and correctly detect gene expression patterns, reliable techniques are of great value. Chung *et al.* (2014) developed a new strategy for whole-mount RNA-FISH in the pea aphid, based on a comprehensive analysis of current protocols. The optimal conditions were identified, and new protocols with an improved resolution of gene detection can yield a better understanding of germ-line specification and embryonic segmentation in the pea aphid. The article provides recommendations for reliable RNA-FISH for other insects as well.

The other five papers in this issue focus on three aphid pests, the soybean aphid *Aphis glycines*, the cotton aphid *Aphis gossypii*, and the English grain aphid *Sitobion avenae*. Wang *et al.* (2014a) report the population dynamics of *A. glycines* in northeastern China based on a 3-year experiment. Their results indicate that soybean aphids are recovered in suction traps about 2 weeks earlier than in traditional field surveys, indicating the efficiency of suction traps in aphid monitoring. Using the DNA barcoding technique, Zhou *et al.* (2014) identify 15 Hymenoptera parasitoid species belonging to 10 genera of five families from the soybean aphid populations in northeastern China. Xu *et al.* (2014) report an interesting finding that the cucurbit-specialized lineages of *A. gossypii* have the potential to utilize mature or whitefly-stressed cotton plants as temporary hosts. This behavior allows the aphids to overcome food deficiency arising from senescing, but the feeding experience on cotton does not alter their specialization for cucurbits. Gao *et al.* (2014) test whether

divergent selection experienced by *S. avenae* on oat and barley promotes the evolution of host races. Their results indicate that oat- and barley-specialized aphid clones have diverged and that the fitness of barley clones tends to increase commensurate with host specialization. Hu *et al.* (2014) present the results of a laboratory experiment indicating that both brown and green color morphs of *S. avenae* perform significantly better on barley infected by *Barley yellow dwarf virus* (BYDV) than BYDV-free plants. When on BYDV-infected barley, the green aphids can develop faster than the brown. The results document synergistic damage to plants by the combination of aphids and virus, presenting important implications for the control of this aphid pest.

We hope this collection of aphid papers will facilitate the discussion and communication of recent advances in aphid research and all of its implications. We believe that aphid models will play increasingly important roles in studying fundamental questions in ecology and evolution. We wish to thank all the authors for their contributions that made this issue possible, and we thank the invited editorial committee members and reviewers for their time and effort during the peer review process. The thoughtful comments and critiques from the reviewers and editors helped improve the quality of this special issue. We are grateful to Professor Le Kang, the Editor-in-Chief, and Dr. Yun-Xian Zhao, the managing editor, for providing our aphid colleagues this opportunity to exchange ideas and new findings. Dr. Zhao's wonderful suggestions and assistance in processing the manuscripts made our job easier. Our gratitude is also due to the staff of Wiley for their support in the production of this issue.

## Acknowledgments

We thank Dr. Colin Favret for reading a draft of this article and editing the language. The work was supported by grants from the National Science Funds for Distinguished Young Scientists (31025024), National Natural Sciences Foundation of China (31272348), and the Ministry of Science and Technology of the People's Republic of China (2011FY120200).

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Accepted April 9, 2014