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Editorial overview: Parasites/parasitoids/biological control: The study of parasitoid physiology begins to mature

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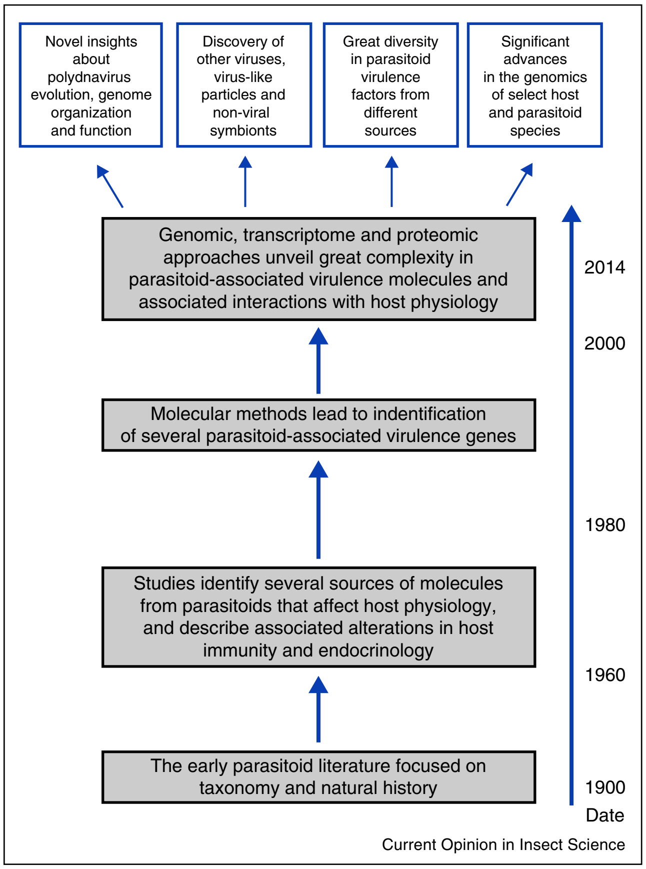
Parasitoids are free-living insects as adults, whose offspring develop by feeding in or on the body of another arthropod. This term was first used by Reuter [1] who also noted that most parasitoids complete their immature development by feeding on a single host and most hosts die as a consequence of being parasitized. Like many organisms with parasitic lifestyles, parasitoids have restricted host ranges that consist of one or a few species in the same genus, family or related families [2]. Parasitoids are also specialized in terms of: Firstly, parasitizing only one life stage of their host (egg, larval, pupal or adult parasitoids); secondly, laying eggs and offspring feeding on (ectoparasitoids) or in a host (endoparasitoids); and finally, one offspring developing per host (solitary parasitoids) or several offspring developing per host (gregarious parasitoids) [2].

Seven insect orders contain parasitoids, but ~80% of known species belong to the Hymenoptera. Parasitic Hymenoptera are among the most important insect groups, because of their high species diversity, the critical role many parasitoids play as mortality agents of other insects, and their widespread use in biological control. Yet in many respects parasitoid wasps are also greatly understudied. Their diversity creates major challenges in systematics and makes identification of field-collected specimens below the family or subfamily level very difficult outside of a handful of taxonomic experts. The biology of most parasitoids is poorly or entirely unknown due to difficulties associated with collection and rearing, while the small size of many species makes many types of experimental studies hard to conduct. These considerations have also restricted our understanding of parasitoid physiology to only a few species that are amenable to continuous culture in the laboratory.

Before the late 1960s, knowledge of parasitoid biology was largely confined to descriptions of taxonomy and natural history, a few elegantly detailed morphological studies, and a modest number of papers describing how parasitoids affect the growth and/or immune defenses of hosts (Figure 1). A few comprehensive works were also written that summarized this knowledge base [2–5]. These books and reviews provide few functional insights, but the breadth of descriptive information they present is spectacular. The perception by early workers that parasitoid larvae were responsible for altering the growth of hosts were overturned by studies conducted in the 1970s and 1980s, which showed that many parasitoids produce factors like venom and teratocytes that cause many of the alterations that occur in naturally parasitized hosts [6] (Figure 1). It was also during this period that parasitoids in certain families of the Hymenoptera were shown to carry

Figure 1



History and major developments in the study of parasitoid–host interactions.

viruses that wasps inject into hosts and which play critical roles in altering host endocrine, and immune physiology [7]. A second valuable advance during this period was terminology first used by Haeselbarth [8] who divided parasitoids into two broadly functional groups, koinobionts and idiobionts, on the basis of whether or not parasitized hosts grow beyond the life stage attacked. This terminology provided a foundation for linking data generated by physiologists to data on host range and other life history traits being generated through ecological and evolutionary studies. Many of these results were also summarized in review articles and books published in the 1980s and 1990s [6,9–12].

The first parasitoid-associated genes implicated in altering host physiology were identified in the late 1980s with additional factors identified in the 1990s through the mid 2000s [summarized in [13–16]] (Figure 1). The small size of most parasitoids together with a near absence of genetic tools, however, severely constrained the breadth of factors that could be identified and the types of functional studies that could be conducted during this period. Thus, broader insights about the virulence factors parasitoids produce and how these molecules interact with hosts were largely stymied until recent advances in deep sequencing technology and mass spectrometry made genomic, transcriptome, and proteomic studies of parasitoids and hosts possible. These methods have provided a wealth of comparative data on the network of genes, signaling pathways and effector molecules that regulate the development and immune defenses of many host species. They have also provided the means to characterize parasitoid venoms, the secretory products of teratocytes, and the complex genomes of parasitoid-associated viruses. Studies of species that parasitize model organisms like *Drosophila melanogaster*, together with RNA interference (RNAi) and other methods for manipulating gene function in non-model species further provide approaches for unraveling the complex physiological interactions that occur between different parasitoids and hosts (Figure 1).

Recent data reveal previously unimaginable variation in the virulence gene products from different parasitoids. These new findings show that a number of processes including gene duplication and horizontal gene transfer have played important roles in the divergence of virulence genes in different wasp species. They also provide insights into how parasitoid viruses function and how some virulence factors interact with host molecules to alter physiological processes (Figure 1). Advances are most apparent in the analysis of polydnaviruses and venoms. The first four entries of this issue reflect this. Jean-Michel Drezen and colleagues begin by summarizing current knowledge of symbiotic viruses associated with parasitoid wasps. The authors first present an overview of the parasitoid virus world, highlighting the Polydnaviridae and advances made in understanding the replication of polydnaviruses in the genus Bracovirus. The authors point out that bracovirus replication has evolved as a means to generate a vector for efficiently delivering virulence genes to hosts, which in turn benefit the development of parasitoid offspring. This article also discusses the many processes underlying the remarkable expansion and diversification of virulence genes that bracoviruses deliver to hosts.

The contribution by Doremus *et al.* further builds on this topic by focusing on polydnaviruses in the genus Ichnovirus. The authors first summarize the morphological and molecular features of ichnoviruses followed by a discussion of the genes on DNAs that are packaged into virions for delivery to host insects. They then discuss the known or potential roles of these virulence genes in parasitism including functions in immunosuppression and potential effects on host metabolic and cellular processes. Several of these virulence genes have diversified into multimember families, with recent results showing that some family members are strongly expressed in hosts while others are expressed very weakly. The suite of virulence genes present in ichnovirus particles is now well characterized for several species although much more study is needed to