# Symbiont-induced Speciation and Endoparasitoid Insects

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ABSTRACT: The conditions discussed by Thompson (1987) favoring symbiont-induced speciation appear to be satisfied in the case of some endoparasitoid wasps and their symbiotic polydnaviruses. It is suggested that the phylogenetic study of these wasps and their viruses would prove fruitful in the investigation of symbiont effects on organismal evolution; a preliminary research program for such study is discussed.

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In a recent paper, Thompson (1987) reviewed the proposed cases of speciation induced by symbiotic organisms and suggested a new set of conditions under which symbiont-induced speciation might be favored. The advantage of his speciation model is that it does not depend upon hybrid inferiority and selection for genes promoting pre-mating isolating mechanisms. Instead, it relies upon theoretical demonstrations that populations can diverge even in the presence of some gene flow between them when strong environmental or habitat gradients in selection occur (Barton and Charlesworth, 1984; Endler, 1977; Slatkin, 1985). If genotypic variation is present, and each genotype varies in its interactive selective value across different environments (as considered in Thompson, 1988), then different host/symbiont allele combinations could be favored in the various environment (habitat) types.

The examples considered by Thompson (1987) include a number of microbial symbionts ranging from rickettsiae to protozoans and from parasitic to mutualistic. I suggest that his model of symbiont-induced speciation, if genetically realistic, should apply as well to several large groups of animal species, namely some endoparasitoid lineages of braconid and ichneumonid wasps, amounting to some tens of thousands of species.

Adult female endoparasitoid wasps insert their eggs into other species of arthropods, primarily insects. The larvae, after hatching, feed internally on the host tissues, before emerging from and ultimately killing the host. In the last ten to twelve years it has been demonstrated that many species of these wasps maintain replicating cultures of viruses in their ovarian calyx epithelial cells. These unique, somewhat baculovirus-like viruses (Stoltz et al., 1984) are injected with the parasitoid wasp eggs into the host insects, and appear to induce a number of physiological changes in the hosts (Cook et al. 1984; Edson et al. 1981; Stoltz 1986; Stoltz and Cook 1983). Such changes include suppression of the host cellular immune response (Edson et al., 1981; Fedderson et al., 1986; Stoltz and Guzo 1986), apparently by antigenic mimicry of a host protein (Berg et al., 1988) and interaction with the wasp venom (Stoltz et al., 1988). In at least most studied cases, it is apparent that parasitism by the wasp is not successful without the active virus. In some cases at least, portions of the viral genome are even integrated into wasp somatic DNA (Fleming and Summers, 1986), although detrimental effects on the immune system are apparent only in the host caterpillars. Despite this, transmission of the viruses appears to be entirely maternal and vertical. Thus, the relationships between viruses and parasitoid wasps appear at present to be obligately mutualistic.

These endoparasitoid wasps attack a more or less limited array of host insects, often with varying success (Salt, 1968, 1976). As success of a parasitoid/virus combination varies in different host insects (environments), and if there is differential success of parasitoids bearing different virus genotypes in the same host species, Thompson's (1987) conditions favoring symbiont-induced speciation would appear to be satisfied. In addition, many parasitoid species (although not all) are known to possess mating systems favoring local reproductive isolation (Askew, 1968), especially in the immediate vicinity of the host.

The opportunities for investigation of possible symbiont-induced speciation in endoparasitoid insects are almost endless. Among the taxonomic groups of wasps possessing viral symbionts are hundreds of closely-related, morphologically similar species that differ in their natural host spectra. Biologically well-known species exhibiting

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geographic variation in host specificity or apparent "host races" would be most promising for analysis.

One approach currently being pursued to study viral effects on wasp evolution includes a species- and population-level analysis of a closely-related complex of parasitoid wasps, combined with an assessment of genetic variation among their corresponding symbiotic viruses. Mitochondrial DNA (mtDN A) variation has proven to be the most useful tool for investigating population- and species-level phylogenies because of its rapid rate of evolution (Brown et al., 1979) and its maternal, effectively haploid transmission between generations (Avise, 1989; Avise et al., 1987; Wilson et al., 1985). The recent development of the polymerase chain reaction (PCR) for amplification of DNA segments (for review see White et al., 1989) has now made it possible to study mtDNA variation among individual parasitoid wasps. I have recently amplified (S.A. Cameron & J.B. Whitfield, unpublished data) a 1700 base-pair region of the 12s and 16s ribosomal RNA genes of the mtDNA of a species of *Pholetesor*, a braconid genus for which many host/parasitoid and distributional data are available (Whitfield & Wagner, 1988). To amplify the mtDNA we used primers that were previously successful with other Hymenoptera such as bumble bees and honey bees (S. A. Cameron, unpublished data). Nucleotide sequences from this portion of the mtDNA reveal enough base-pair homology to allow comparisons between hymenopteran groups and suffcient sequence variation for intraspecific studies. Similar work is in progress to obtain sequences from other related parasitoid species.

Successful techniques are also available for extraction of viral DNA and investigation of genetic variation among the polydnaviruses, both in braconid (Jones et al., 1986) and ichneumonid (Fleming & Summers, 1986) wasps. Until suitable primers are available for PCR, assessment of polydnavirus relationships will likely depend on phylogenetic analysis of restriction fragment length polymorphisms (DeBry & Slade, 1985; Templeton, 1983). When inferred phylogenies of both the wasps and associated polydnaviruses are available, investigation of co-phylogeny can proceed using techniques developed for comparisons of host and parasite phylogenies (Brooks, 1988). Explicit co-phylogenetic hypotheses can then be used to frame specific questions about symbiont-induced speciation in the wasps.

One of the major difficulties in coevolutionary analysis may be in the viral taxonomy, an area of much current controversy (Calisher, 1988; Harrison, 1985; Kingsbury, 1988; Milne, 1988) due in part to the difficulties of applying species and lower category concepts to entities that can incorporate host DNA into their own genomes. Despite the complex problems to be solved, the possibility that viral symbionts have influenced the speciation of, and evolution of endoparasitism in, parasitoid wasps is a major biological question we are now equipped to address.

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