

GENETICS: RELATION OF LOCAL POPULATIONS TO THE WHOLE "SPECIES" – IMPLICATIONS FOR HOST RANGE TESTS

Keith R. HOPPER¹, Angela M. I. DE FARIAS², James B. WOOLLEY³,
John M. HERATY⁴, and Seth C. BRITCH¹

¹Beneficial Insect Introductions Research Unit, Agricultural Research Service
United States Department of Agriculture
Newark, DE 19736, U.S.A.
khopper@udel.edu

²Universidade Federal de Pernambuco,
Departamento de Zoologia, Cidade Universitaria
50.670-420 Recife, Pernambuco, Brazil
amif33@hotmail.com

³Department of Entomology, Texas A&M University
College Station, TX 77843, U.S.A.
JimWoolley@tamu.edu

⁴Department of Entomology, University of California
Riverside, CA 92521, U.S.A.
john.heraty@ucr.edu

665

ABSTRACT

Populations of parasitoids collected from different host species or geographical regions can differ in host specificity. Where the necessary research has been done, such populations have usually been found to represent various stages of speciation. Here, we review the literature on variation in host specificity among populations and sibling species of parasitoids. We then summarize our results on the evolution and genetics of host specificity in *Aphelinus varipes* Foerster and *Aphelinus albipodus* Hayat and Fatima (Hymenoptera: Aphelinidae). Populations of *A. varipes/albipodus* from *Diuraphis noxia* (Mordvilko), *Ropalosiphum padi* (L.), and *Aphis glycines* Matsumura (Homoptera: Aphididae) collected in France, Georgia, Israel, China, Korea, and Japan differed in parasitism of seven aphid species in five genera and two tribes on four host plant species in no-choice laboratory experiments. Some populations showed narrow to monospecific host use, others attacked most or all host species tested. Most populations were reproductively isolated by pre-zygotic, behavioral barriers involving female choice. However, some allopatric populations were partially or completely reproductively compatible in laboratory crosses, although they differed in host specificity. A molecular phylogeny based on three nuclear and two mitochondrial genes indicated that these compatible, allopatric populations are distinct lineages, and morphometric analyses showed subtle differences

between them. Our conclusion is that *Aphelinus varipes/albipodus* is a rich complex, with populations in various stages of speciation. Although there was some concordance between phylogenetic affinities of host species and parasitoid species, other cases showed flips in host use between closely related taxa in the complex. We have been able to introgress genes for use of a novel aphid species from one parasitoid species to another in laboratory crosses, and we are using these crosses to map genes involved in host specificity. The take-home lessons for biological control are: (1) parasitoids in what appears to be a single species, but collected from widely different geographical regions or from different host species, may differ greatly in host specificity and thus should be tested separately, and (2) allopatric sibling species with different patterns of host use may introgress if placed in sympatry, which could lead to evolutionary changes in host use.

INTRODUCTION

Populations of parasitoids collected from different host species or geographical regions can differ in host specificity. Parasitoid species may consist of distinct host races that switch little between host species in the field (Cameron *et al.* 1984; Henter *et al.* 1996; Hufbauer 2002; Nemeč and Stary 1983; Powell and Wright 1988; Stary 1983). Differences in host use among populations may often be explained by unrecognized sibling species. Evidence accumulated during the last decade suggests that sibling species of parasitoids may be far more common than previously realized (Campbell *et al.* 1993; Clarke and Walter 1995; Gauld and Janzen 2004; Kazmer *et al.* 1996; Pinto *et al.* 2003). Here, we review some of the literature on variation in host specificity among populations and sibling species of parasitoids, summarize our results on this issue, and draw conclusions concerning biological control introductions.

LITERATURE REVIEW

Microctonus aethiopoides (Hymenoptera: Braconidae) from different regions and host species differ in parasitism of *Hypera postica* versus *Sitona* spp. (Coleoptera: Curculionidae) (Sundaralingam *et al.* 2001) and also in parasitism of different *Sitona* spp. (Loan and Holdaway 1961; Phillips *et al.* 2002; Sundaralingam *et al.* 2001). Some of the differences in parasitism result from differences in encapsulation by the host (Phillips *et al.* 2002). *Microctonus aethiopoides* from different sources differ in nuclear and mitochondrial DNA sequences (Vink *et al.* 2003). Although Vink *et al.* (2003) found no morphological differences among sources, Sundaralingam (1986) was able to discriminate between parasitoids from *H. postica* in France and those from *Sitona discoideus* in Morocco using eight quantitative traits. Furthermore, parasitoids from *H. postica* in France and *S. discoideus* in Morocco were partially reproductively isolated, with much lower frequencies of males courting and females accepting insects from the other source (Sundaralingam *et al.* 2001). These results suggest that some of the differences in host use among populations of *Microctonus aethiopoides* can be explained by confounding of cryptic, sibling species.

Aphidius ervi (Hymenoptera: Braconidae) comprises a complex of populations, some of which have been recognized as host races or sibling species based on patterns in parasitism of

their aphid hosts, reproductive compatibility, morphology, and molecular markers (Atanassova *et al.* 1998; Pennacchio *et al.* 1994). Stary (1975) synonymized many species in a morphology-based revision of *Aphidius colemani* (Hymenoptera: Braconidae), another major parasitoid of aphids. But subsequent research has shown that *A. colemani* is a complex of reproductively isolated sibling species with different patterns in host use (Messing and Rabasse 1995; Ode and Hopper, unpublished data).

Populations of *Apocephalus paraponerae* (Diptera: Phoridae), a parasitoid ants in Central and South America, show differences in morphology, molecular markers, and host specificity sufficient to consider them cryptic species (Morehead *et al.* 2001). Populations of *Pseudacteon tricuspis* (Diptera : Phoridae) appear to be cryptic species with different host ranges (Porter and Gilbert 2005). Populations of *Pseudacteon curvatus* (Diptera : Phoridae), which are being introduced to control imported fire ants in North America, also show differences in host specificity which may affect their potential for impact on non-target native ants (Porter and Gilbert 2005; Vazquez *et al.* 2004;).

Leptopilina bouvardi (Hymenoptera: Figitidae), a parasitoid of *Drosophila* spp., shows geographical variation with a genetic basis in responses to different host-associated odors (Campan *et al.* 2002) and ability to avoid encapsulation by its hosts (Dupas *et al.* 2003). *Asobara tabida* and its sibling species *Asobara rufescens* (Hymenoptera: Braconidae) also show geographical variation in ability to overcome encapsulation by their hosts (Kraaijeveld and Godfray 1999; Kraaijeveld *et al.* 1994).

HOST USE IN *APHELINUS VARIPES* COMPLEX

Although *Aphelinus varipes* has been reported from 40 host species across several genera of aphids (Kalina and Stary 1976), we found distinct patterns of host use among *A. varipes* from different hosts and regions (Fig. 1) as well as different populations within a region (Fig. 2). We measured host use in single-host-species laboratory experiments, where female parasitoids had the choice of whether to oviposit or not in a particular host species. This is frequently the choice parasitoids make in the field. “Choice” tests in the laboratory provide different species in close spatial and temporal proximity, but the behavior on encountering a particular host is still whether to parasitize in or not. Our goal was to determine host acceptance/suitability in an environment that appears to harbor only one aphid species on only one plant species and where parasitoid females re-encounter this combination repeatedly with a full egg complement after a relatively long period without encountering other host species. In these experiments, we exposed 100 aphids (mixed stages) on host plant to individual, naïve, mated female wasps for 1 day, with 10-20 replicates per host-species/parasitoid-source combination. We measured parasitism as the number of mummified aphids produced during this exposure.

Most of these populations in the *A. varipes* complex had fixed differences in DNA sequences, subtle but highly significant differences in morphology, and were reproductively incompatible. It appears that *Aphelinus varipes/albipodus* is a rich complex, with populations in various stages of speciation. Thus, the host range reported in the literature for *A. varipes* is incorrect because sibling species have been confounded.

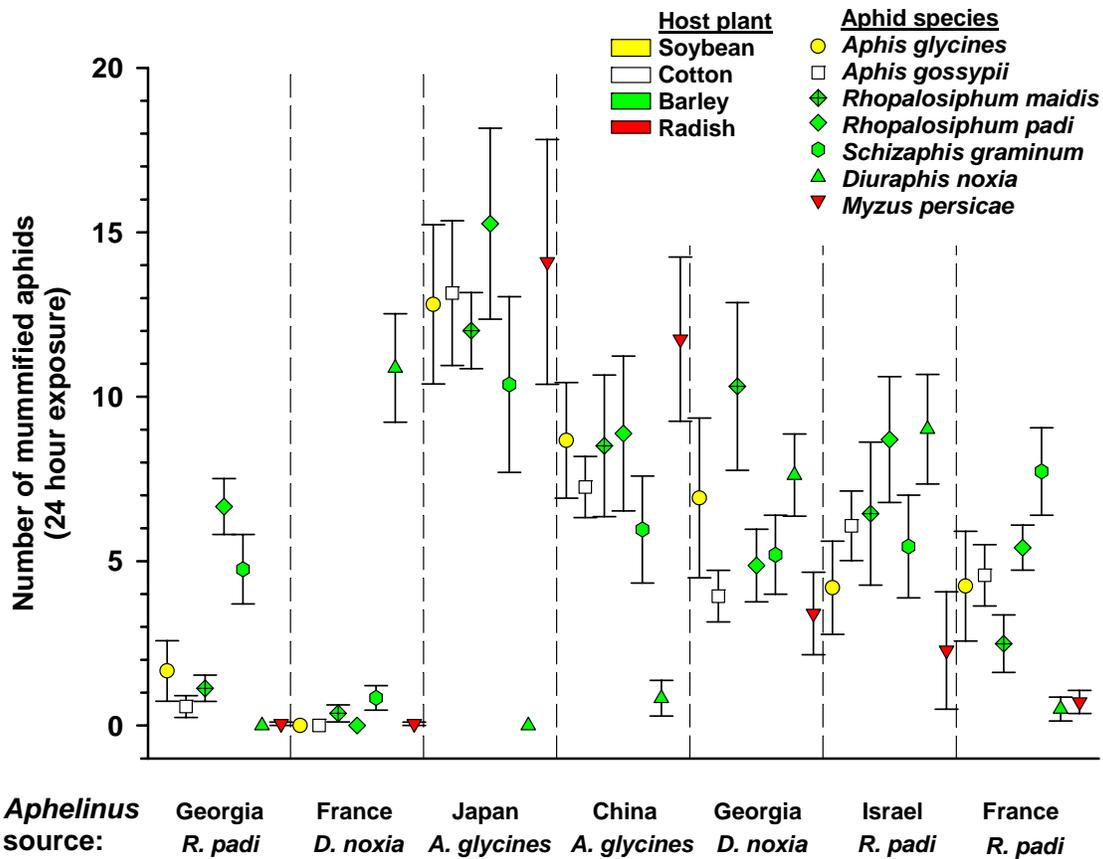


Figure 1. Host specificity in *Aphelinus varipes* complex: differences among host and regional sources.

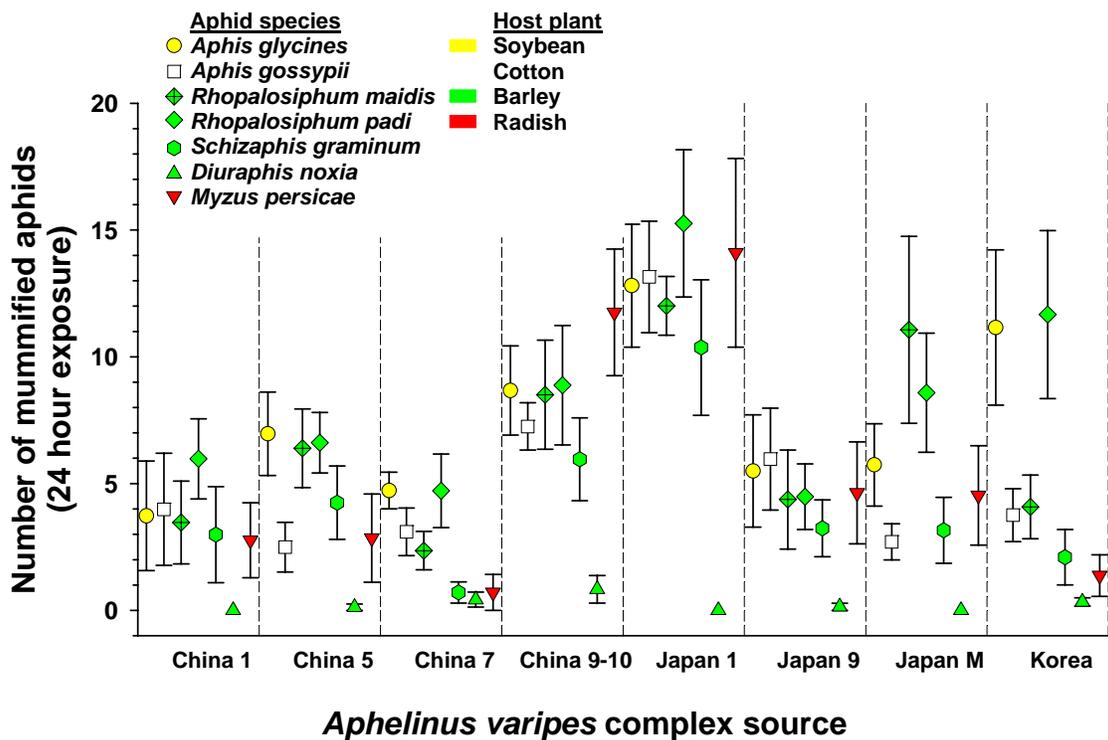


Figure 2. Host specificity in *Aphelinus varipes* complex: differences among populations from *Aphis glycines* in the Far East.

Although closely related species sometimes show similar patterns of host specificity, phylogenetic affinity was not a reliable indicator of host specificity. Even among the rather closely related species and populations in the *A. varipes* complex, use of some host species roughly maps onto the parasitoid phylogeny, but use of other species does not.

Therefore, we need to examine the genetic basis of host switches if we are to predict when they will occur. Two populations in the *A. varipes* complex, one from *D. noxia* in Georgia ('Georgia-*D. noxia*') and the other from *A. glycines* in Japan ('Japan-*A. glycines*') were reproductively compatible, despite differences in DNA sequences, morphology, and host use. 'Japan-*A. glycines*' parasitoids do not parasitize *D. noxia*, whereas 'Georgia-*D. noxia*' parasitoids readily parasitize this host (Fig. 1). By crossing and backcrossing, we have introgressed genes from 'Georgia-*D. noxia*' into the 'Japan-*A. glycines*' background and produced hybrids segregating for parasitism of *D. noxia*.

CONCLUSIONS

The take-home lessons for biological control are: (1) parasitoids in what appears to be a single species, but collected from widely different geographical regions or from different host species, may differ greatly in host specificity and thus should be tested separately, and (2) allopatric sibling species with different patterns of host use may introgress if placed in sympatry, which could lead to evolutionary changes in host use.

REFERENCES

- Atanassova, P., Brookes, C. P., Loxdale, H. D., and Powell, W. 1998. Electrophoretic study of five aphid parasitoid species of the genus *Aphidius* (Hymenoptera: Braconidae), including evidence for reproductively isolated sympatric populations and a cryptic species. *Bulletin of Entomological Research* **88**, 3-13.
- Cameron, P. J., Powell, W., and Loxdale, H. D. 1984. Reservoirs for *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae), a polyphagous parasitoid of cereal aphids (Hemiptera: Aphididae). *Bulletin of Entomological Research* **74**, 647-656.
- Campan, E., Couty, A., Carton, Y., Pham-Delegue, M. H., and Kaiser, L. 2002. Variability and genetic components of innate fruit odour recognition in a parasitoid of *Drosophila*. *Physiological Entomology* **27**, 243-250.
- Campbell, B. C., Steffen-Campbell, J. D., and Werren, J. H. 1993. Phylogeny of the *Nasonia* species complex (Hymenoptera: Pteromalidae) inferred from an internal transcribed spacer (ITS2) and 28S rDNA sequences. *Insect Molecular Biology* **2**, 225-237.
- Clarke, A. R., and Walter, G. H. 1995. "Strains" and the classical biological control of insect pests. *Canadian Journal of Zoology* **73**, 1777-1790.
- Dupas, S., Carton, Y., and Poirie, M. 2003. Genetic dimension of the coevolution of virulence-resistance in *Drosophila* - parasitoid wasp relationships. *Heredity* **90**, 84-89.

- Gauld, I. D., and Janzen, D. H. 2004. The systematics and biology of the Costa Rican species of parasitic wasps in the *Thyreodon* genus-group (Hymenoptera : Ichneumonidae). *Zoological Journal of the Linnean Society* **141**, 297-351.
- Henter, H. J., Brasch, K., and van Lenteren, J. C. 1996. Variation between laboratory populations of *Encarsia formosa* in their parasitization behavior on the host *Bemisia tabaci*. *Entomologia Experimentalis Et Applicata* **80**, 435-441.
- Hufbauer, R. A. 2002. Evidence for nonadaptive evolution in parasitoid virulence following a biological control introduction. *Ecological Applications* **12**, 66-78.
- Kalina, V., and Sary, P. 1976. A review of the aphidophagous Aphelinidae (Hymenoptera, Chalcidoidea), their distribution and host range in Europe. *Studia Entomologica Forestalia (Praha, Czechoslovakia)* **2**, 143-170.
- Kazmer, D. J., Maiden, K., Ramualde, N., Coutinot, D., and Hopper, K. R. 1996. Reproductive compatibility, mating behavior, and random amplified polymorphic DNA variability in some *Aphelinus asychis* (Hymenoptera: Aphelinidae) derived from the Old World. *Annals of the Entomological Society of America* **89**, 212-220.
- Kraaijeveld, A. R., and Godfray, H. C. J. 1999. Geographic patterns in the evolution of resistance and virulence in *Drosophila* and its parasitoids. *American Naturalist* **153**, S61-S74.
- Kraaijeveld, A. R., Voet, S., and Van Alphen, J. J. M. 1994. Geographical variation in habitat choice and host suitability in the parasitoid *Asobara rufescens*. *Entomologia Experimentalis et Applicata* **72**, 109-114.
- Loan, C. C., and Holdaway, F. C. 1961. *Microctonus aethiops* (Nees) auct. and *Perilitus rutilus* (Nees) (Hymenoptera: Braconidae) European parasites of *Sitona* weevils (Coleoptera: Curculionidae). *Canadian Entomologist* **93**, 1057-1079.
- Messing, R. H., and Rabasse, J. M. 1995. Oviposition behavior of the polyphagous aphid parasitoid *Aphidius colemani* Viereck (Hymenoptera, Aphidiidae). *Agriculture Ecosystems and Environment* **52**, 13-17.
- Morehead, S. A., Seger, J., Feener, D. H., and Brown, B. V. 2001. Evidence for a cryptic species complex in the ant parasitoid *Apocephalus paraponerae* (Diptera: Phoridae). *Evolutionary Ecology Research* **3**, 273-284.
- Nemec, V., and Sary, P. 1983. Genetic polymorphism in *Aphidius ervi* Hal (Hym, Aphidiidae), an aphid parasitoid on *Microlophium carnosum* (Bckt). *Z. Angew. Entomol.* **95**,345-350,
- Pennacchio, F., Digilio, M. C., Tremblay E., and Tranfaglia, A. 1994. Host recognition and acceptance behaviour in two aphid parasitoid species: *Aphidius ervi* and *Aphidius microlophii* (Hymenoptera: Braconidae). *Bulletin of Entomological Research* **84**, 57-64.

- Phillips, C. B., Cane, R. P., Mee, J., Chapman, H. M., Hoelmer, K. A., and Coutinot, D. 2002. Intraspecific variation in the ability of *Microctonus aethioides* (Hymenoptera: Braconidae) to parasitise *Sitona lepidus* (Coleoptera : Curculionidae). *New Zealand Journal of Agricultural Research* **45**, 295-303.
- Pinto, J. D., Platner, G. R., and Stouthamer, R. 2003. The systematics of the *Trichogramma minutum* species complex (Hymenoptera: Trichogrammatidae), a group of important North American biological control agents: the evidence from reproductive compatibility and allozymes. *Biological Control* **27**, 167-180.
- Porter, S. D., and Gilbert, L. E. 2005. Parasitoid case history: an evaluation of methods used to assess host ranges of fire ant decapitating flies. In M. S. Hoddle [ed.], *Second International Symposium of Biological Control of Arthropods*, Davos, Switzerland.
- Powell, W., and Wright, A. F. 1988. The abilities of the aphid parasitoids *Aphidius ervi* Haliday and *A. rhopalosiphum* De Stefani Perez (Hymenoptera: Braconidae) to transfer between different known host species and the implications for the use of alternative hosts in pest control strategies. *Bulletin of Entomological Research* **78**, 683-93.
- Sary, P. 1975. *Aphidius colemani* Viereck - Its taxonomy, distribution and host range (Hymenoptera, Aphidiidae). *Acta Entomologica Bohemoslovaca* **72**, 156-163.
- Sary, P. 1983. Colour patterns of adults as evidence on *Aphidius ervi* biotypes in fields environments (Hymenoptera, Aphidiidae). *Acta Entomologica Bohemoslovaca* **80**, 377-84.
- Sundaralingam, S. 1986. Biological, morphological, and morphometric analyses of populations of *Microctonus aethioides* Loan (Hymenoptera: Braconidae), MS Thesis, Pennsylvania State University, University Park, PA, U.S.A.
- Sundaralingam, S., Hower, A. A., and Kim, K. C. 2001. Host selection and reproductive success of French and Moroccan populations of the parasitoid, *Microctonus aethioides* (Hymenoptera: Braconidae). *Biocontrol* **46**, 25-41.
- Vazquez, R. J., Porter, S. D., and Briano, J. A.. 2004. Host specificity of a biotype of the fire ant decapitating fly *Pseudacteon curvatus* (Diptera: Phoridae) from northern Argentina. *Environmental Entomology* **33**, 1436-1441.
- Vink, C. J., Phillips, C. B., Mitchell, A. D., Winder, L. M., and Cane, R. P. 2003. Genetic variation in *Microctonus aethioides* (Hymenoptera : Braconidae). *Biological Control* **28**, 251-264.