

SHORT COMMUNICATION

Speciation in fig pollinators and parasites

GEORGE D. WEIBLEN*† and GUY L. BUSH†

*Department of Plant Biology, University of Minnesota, 1445 Gortner Avenue, Saint Paul, Minnesota 55108, USA; †Department of Zoology, 203 Natural Sciences Building, Michigan State University, East Lansing, Michigan 48824, USA

Abstract

Here we draw on phylogenies of figs and fig wasps to suggest how modes of speciation may be affected by interspecific interactions. Mutualists appear to have cospeciated with their hosts to a greater extent than parasites, which showed evidence of host shifting. However, we also repeatedly encountered a pattern not explained by either cospeciation or host switching. Sister species of fig parasites often attack the same host in sympatry, and differences in ovipositor length suggest that parasite speciation could result from divergence in the timing of oviposition with respect to fig development. These observations on fig parasites are consistent with a neglected model of sympatric speciation.

Keywords: Agaonidae, coevolution, cospeciation, mutualism, parasitism, phylogeny

Received 14 June 2001; revision received 8 January 2002; accepted 15 March 2002

Introduction

Life history adaptations affecting the process of species formation may explain why some groups of organisms are more diverse than others (Farrell 1998), but modes of speciation have rarely been compared in closely related groups that interact with other species in fundamentally different ways. Interactions between fig wasps (Hymenoptera, Agaonidae) and their host plants (*Ficus*, Moraceae) range from mutualism to parasitism, and have served to test evolutionary theories of sex allocation (Herre 1985, 1987; West *et al.* 2000), kin selection (Hamilton 1967; West *et al.* 2001) and virulence (Herre 1993). However, few data are available comparing patterns of speciation in figs, their pollinating mutualists and nonpollinating parasites (Machado *et al.* 1996; Lopez-Vaamonde *et al.* 2001). Evolutionary models of obligate mutualism predict the parallel radiation of figs and pollinators (Kiestler *et al.* 1984), but is this also the case for parasites?

All fig species are pollinated by mutualistic fig wasps (Agaonidae, Agaoninae) that feed exclusively on the developing seeds of their hosts and phylogenetic analyses indicate that fig pollination evolved once (Herre *et al.* 1996). Pollinators of figs are characterized by extreme host specificity, morphological adaptations and life cycles that depend entirely on host reproduction (Fig. 1). In theory,

resource conflicts between pollinators and hosts could threaten the persistence of mutualism (Pellmyr & Huth 1994), and yet the richness of *Ficus* (~750 species worldwide) and their pollinators suggests that the interaction is evolutionarily stable. Resembling a fruit, the fig is an enclosed inflorescence containing many unisexual flowers that are accessible to fig wasps through a narrow opening at the apex of the receptacle. Pollen-carrying females are attracted by host-specific fragrances released from receptive figs (Hossaert-McKey *et al.* 1994) and they push their way into the fig cavity, where they lay eggs in a fraction of the flowers they pollinate. Their offspring feed on fig endosperm as larvae and mate in the fig cavity as adults. Females complete the life cycle by transporting pollen from natal figs to receptive figs, where the fertilization of flowers provides the next generation of pollinators with seed resources.

A diverse assemblage of nonpollinating wasps, including gallers that compete with pollinators for fig resources, and parasitoids that attack pollinator larvae in figs may weaken the mutualism. Unlike the pollinators, some fig parasites attack the flowers by piercing the outside of the receptacle with long ovipositors (Fig. 1b). The genus *Apocryptophagus* (Agaonidae, Sycophaginae) induces abnormal development of fig ovaries into large galls (Fig. 1c), which affect the mutualism negatively by damaging flowers and by competing with pollinators. The impressive diversification of figs and pollinators is thought to be the product of cospeciation, the parallel radiation of interacting lineages

Correspondence: George D. Weiblen. Fax: 612 624 1234; E-mail: gweiblen@umn.edu

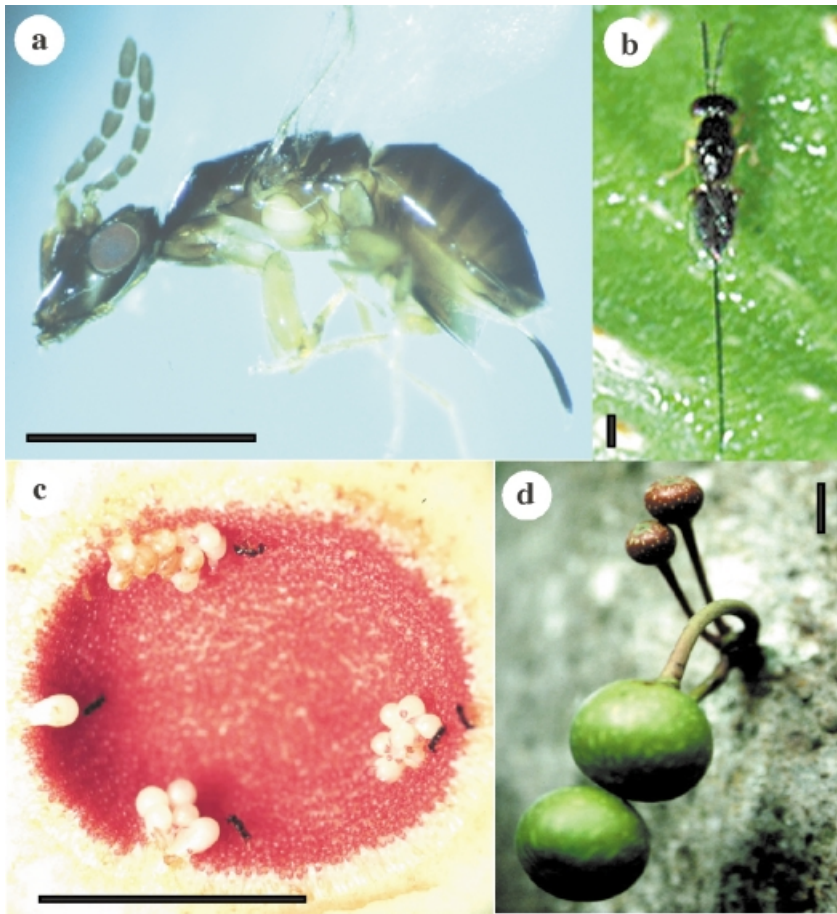


Fig. 1 (a) A pollinating fig wasp belonging to the genus *Ceratosolen*, (b) and a nonpollinating fig wasp belonging to *Apocryptophagus*, (scale bars are 1 mm). (c) The interior of a fig in cross-section showing female *Ceratosolen* pollinating flowers and laying eggs. The enlarged flowers are galls induced by *Apocryptophagus*, which lays eggs by piercing the fig wall. (d) Figs in early and late phases of development differ in wall thickness (scale bars are 1 cm).

(Kiester *et al.* 1984). On the other hand, host shifting can also lead to the formation of new species, especially in phytophagous parasites (Bush 1994). Whether fig pollinators and gallers differ in modes of speciation is unknown, and this situation provides a novel opportunity to compare the evolution of host associations in closely related mutualists and parasites (Kerdelhue *et al.* 1999).

Materials and methods

Apocryptophagus parasites specialize on figs in the subgenus *Sycomorus sensu lato*, which is monophyletic and pollinated by the genus *Ceratosolen* (Weiblen 2000, 2001). Sixteen species of *Sycomorus* s. l. from Melanesia were the focus of sampling, with the addition of three species from outside the region. Nineteen *Ceratosolen* species (Weiblen 2001) and 18 undescribed morphospecies of *Apocryptophagus* associated with the selected hosts were included in phylogenetic analyses of manually aligned partial sequences from the mitochondrial cytochrome oxidase I gene (COI). *Apocryptophagus* morphospecies (hereafter referred to as species) are distinguished on the basis of body size and ovipositor length (Table 1). Kerdelhue & Rasplus (1996)

showed that multiple species of *Apocryptophagus* on the same host differ significantly in ovipositor length and in the timing of oviposition, which are correlated with fig diameter. A single individual from each *Apocryptophagus* species was sequenced for partial COI (GenBank accession numbers AF364519-AF364535 and AF200371). GenBank accession numbers for pollinating fig wasps as described by Weiblen (2001) are 200374-AF200388 and AF200390-AF200393. Accession numbers for *Ficus* nuclear ribosomal ITS sequences from Weiblen (2000) are AF165374, AF165376, AF165378, AF165379, AF165380, AF165383, AF165388, AF165391, AF165394, AF165395, AF165396, AF165404, AF165405, AF165406, AF165408, AF165409, AF165411, AF165412 and AF165415. Heuristic searches under parsimony were conducted with PAUP* (Swofford 1998) with 1000 random addition sequence replicates, and bootstrapping with 1000 replicates provided measures of clade support.

Tests of cospeciation were performed using TREEMAP software (Page 1996) to generate a reconciled tree that maximized cospeciation and minimized duplications and losses of associations under parsimony. A randomization test estimated the probability of observing maximum cospeciation against a null distribution obtained from 10 000

Table 1 *Apocryptophagus* species included in the phylogenetic analyses. The relative timing of *Apocryptophagus* oviposition is indicated for host species with more than one parasite. Species pairs a–h in Figs 2 and 3 are also indicated. Length measurements are reported in mm. Means (and standard deviations) are based on *N* individuals from the same fig crop

Host <i>Ficus</i> species	Host voucher	Locality	Timing of oviposition	Species pair	Thorax length	Ovipositor length	<i>N</i>
<i>adenosperma</i>	GW674	New Guinea		h	0.70 (0.10)	2.91 (0.14)	5
<i>bernaysii</i>	G093	New Guinea	early	c	0.77 (0.09)	1.71 (0.09)	5
<i>bernaysii</i>	B73	New Guinea	late	b	0.61 (0.04)	2.96 (0.08)	3
<i>botryocarpa</i>	GW468	New Guinea		b	0.69 (0.10)	4.08 (0.19)	6
<i>botryoides</i>	GW841	Madagascar	early	d	0.80 (0.08)	2.32 (0.16)	3
<i>botryoides</i>	GW841	Madagascar	late	d	0.74 (0.08)	4.4 (0.42)	5
<i>hispidioides</i>	GW522	New Guinea	late		1.47 (0.16)	5.31 (0.13)	5
<i>hispidioides</i>	G013	New Guinea	early	c	1.12 (0.08)	1.6 (0.08)	3
<i>microdictya</i>	GW954	New Guinea		g	0.77 (0.04)	8.61 (0.20)	3
<i>nodosa</i>	G101	New Guinea	late	f	0.62 (0.10)	8.48 (0.21)	5
<i>nodosa</i>	B191	New Guinea	early	f	0.91 (0.12)	3.92 (0.08)	3
<i>ochrochlora</i>	GW735	New Guinea		h	0.51 (0.05)	3.49 (0.26)	5
<i>racemosa</i>	GW1075	Australia	early	a	0.70 (0.08)	4.76 (0.14)	4
<i>racemosa</i>	GW1075	Australia	late		0.56 (0.08)	7.81 (0.20)	3
<i>semivestita</i>	GW700	New Guinea		g	0.75 (0.04)	9.62 (0.12)	5
<i>sur</i>	GW840	Tanzania	early	e	1.06 (0.17)	3.02 (0.15)	5
<i>sur</i>	GW840	Tanzania	late	e	0.70 (0.07)	5.49 (1.21)	5
<i>variegata</i>	B61	New Guinea		a	0.48 (0.06)	4.78 (0.28)	4

pairs of randomly generated 19-taxon trees under the proportional-to-distinguishable model. Null (H_0) and alternative (H_1) hypotheses that the same or different histories underlie pollinator mtDNA and fig nrDNA were compared using a maximum likelihood (ML) test of heterogeneity (Huelsenbeck & Rannala 1997; Huelsenbeck *et al.* 1997). To determine the most appropriate model of nucleotide substitution under ML, nested models were compared with likelihood ratio tests (Posada & Crandall 1998). A general time reversible model (GTR) with the addition of a parameter for heterogeneity in the rate of substitution across sites (Γ) fitted the mtDNA data significantly better than simpler models (Weiblen 2001). In the case of fig nrDNA, a simpler model assuming equal rates of transitions and transversions (F81) plus Γ provided the best fit with the fewest additional parameters. Branch lengths for host, pollinator and parasite topologies were then estimated under their respective models.

The likelihood of different histories for fig nrDNA and fig wasp mtDNA (H_1) was obtained by summing the likelihoods of the data sets given different topologies, branch lengths and model parameters. Deviations from one-to-one specificity in fig parasites were accommodated by duplicating fig nrDNA sequences from hosts that had more than one parasite species, and by removing nrDNA sequences from hosts that lacked parasites. Most parsimonious trees from combined searches of fig nrDNA plus fig wasp mtDNA sequences were then used to estimate nrDNA and mtDNA branch lengths in the null case (H_0). The likelihood of identical history (H_0) was then obtained

by summing the likelihoods of the separate data sets under the same topology but given separate model parameters for nrDNA and mtDNA. Monte Carlo simulation compared the ratio of H_0 and H_1 likelihoods, given that the test statistic (δ) was not χ^2 distributed. One hundred pairs of nrDNA and mtDNA data sets were generated using the program Seq-General (Rambaut & Grassly 1997). Each data set was simulated along the combined tree assuming a Markov process with branch length estimates and model parameters based on the observed nrDNA and mtDNA. Separate and combined heuristic searches under parsimony with 10 random addition sequence replicates were then performed for each pair of data sets and the ratio of H_0 and H_1 for the simulations provided a null distribution against which to compare the observed data in a one-tailed test of significance. Fig wasp mtDNA data sets rejected the assumption of a molecular clock due to heterogeneity in substitution rates, disallowing tests of cospeciation based on Bayesian estimation (Huelsenbeck *et al.* 2000). Log-likelihood tests of the molecular clock for *Apocryptophagus* and *Ceratosolen* were $\chi^2 = 86.37$ (d.f. = 1, $P < 0.001$) and $\chi^2 = 116.18$ (d.f. = 1, $P < 0.001$), respectively.

Results and discussion

Heuristic searches yielded two most parsimonious trees for *Apocryptophagus* ($L = 819$; $CI = 0.41$, with uninformative positions excluded) based on 188 informative positions of the 402 nucleotide alignment (47% informative). For *Ceratosolen*, 167 positions were informative (42%) and heuristic searches

yielded six trees ($L = 608$; $CI = 0.43$). The pollinator topologies were highly similar to those from intensive analyses of pollinators based on 2 kb mtDNA (Weiblen 2001) and midpoint rooting of a simultaneous *Apocryptophagus*–*Ceratosolen* analysis supported the monophyly of the pollinating lineage. The phylogeny estimate for 19 host *Sycomorus* species based on the nuclear ribosomal internal transcribed spacer region (ITS) was very similar to results obtained from combined analyses of molecular and morphological data (Weiblen 2000). Fifteen trees ($L = 89$; $CI = 0.64$) were obtained from heuristic searches based on 50 informative characters out of 761 aligned positions (7%; excluding nine indels).

Phylogenies for *Apocryptophagus*, *Ceratosolen* and *Sycomorus* suggest that the pollinators have cospeciated with their host plants to a greater extent than the parasites (Fig. 2). Depending on which of the 15 host topologies was analysed, between nine and 10 cases of cospeciation for mutualists were inferred from reconciled trees (Page 1994). Fewer cospeciation events were inferred for figs and their parasites, between seven or eight according to host topology. Cospeciation between mutualists was significantly greater than expected by chance; that is, if figs and pollinators were associated at random ($P = 0.030$ – 0.009). On the other hand, chance could account for the inferred level of cospeciation between figs and parasites ($P = 0.050$ – 0.193). Although many nodes in Fig. 2 lack bootstrap support, the relationships shown are essentially in agreement with more robust phylogenies for *Sycomorus* and *Ceratosolen* based on larger samples of taxa and characters (Weiblen 2000, 2001). The number of inferred fig/pollinator cospeciations increases to 14 when the larger data sets from Weiblen (2000, 2001) were analysed, but our present discussion is limited to the smaller data set for which we have comparable information on galls.

We examined potential sources of phylogenetic incongruence between the host, pollinator and parasite data sets. Phylogenetic conflicts could be due to host switching, to unequal evolutionary rates, or to systematic error. To explore the latter possibility, we employed maximum likelihood to test whether incongruence between the interacting lineages could arise from random mutation and drift in two genes that share a common history (Huelsenbeck & Bull 1996; Huelsenbeck *et al.* 1997). The method compares the likelihood of gene sequences assuming separate and common histories for hosts and their associates. A distribution of log-likelihood differences is generated by simulating sequence data under the null hypothesis of shared history, but assuming separate DNA substitution models and parameters for each gene. Systematic error could not be ruled out as a cause of heterogeneity among the DNA sequences of the mutualists ($\delta = 28.8$; NS). On the other hand, error was rejected as an explanation for conflict between the fig and parasite phylogenies ($\delta = 79.7$; $P < 0.01$). These results suggest that other factors such as host switch-

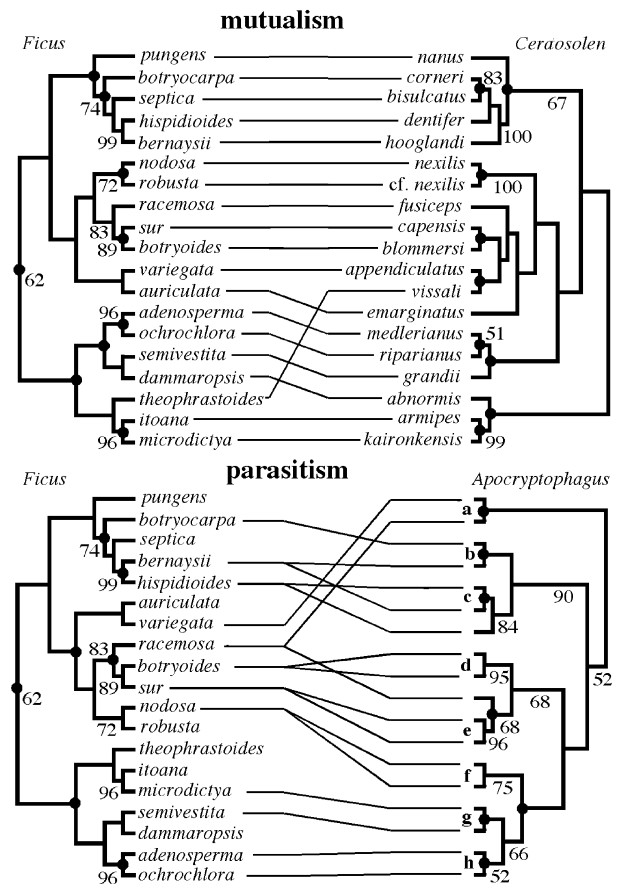


Fig. 2 Evolutionary patterns of host association in pollinating mutualists and nonpollinating parasites of *Ficus* subgenus *Sycomorus sensu lato*. Species associations between pollinating *Ceratosolen* and *Sycomorus* are pairwise, in contrast to *Apocryptophagus*, where multiple unnamed parasite species may attack a single host species and some host species are not attacked at all. Cospeciating nodes inferred from reconciled trees are marked by dots. Bootstrap percentages > 50% based on 1000 replicates are listed below the nodes. Phylogenies are based on parsimony analyses of nuclear ribosomal ITS sequences for *Ficus* and mitochondrial COI sequences for fig wasps. (a–h) refer to species pairs in Fig. 3.

ing or unequal evolutionary rates account for phylogenetic conflicts between parasites and their hosts. Mean (\pm SD) uncorrected P' distances for sister pollinator species and sister parasites were 0.16 (0.05) and 0.14 (0.05), respectively. Similar levels of mtDNA divergence in pollinators and parasites favour the mode of speciation as the most probable explanation for these patterns.

Why would fig parasites speciate differently than the mutualists? We hypothesize that nonpollinating *Apocryptophagus* are less constrained by the reproductive requirements of their hosts than are pollinating *Ceratosolen*. Floral fertilization is required to produce the endosperm on which pollinator offspring depend for survival, but parasites circumvent these steps by inducing the abnormal proliferation of the nucellus in fig ovules (Fig. 1c). Bypassing

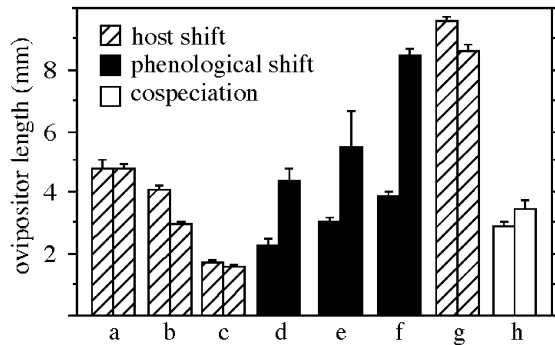


Fig. 3 Sister group comparisons of ovipositor length in the fig parasite, *Apocryptophagus*, under three alternative modes of speciation. (a–h) refer to sister groups in Fig. 2. Sister species (h) attacking sister hosts, *F. adenosperma* and *F. ochrochlora*, represent cospeciation. In contrast (a–c, g) are sister species on nonsister hosts, indicating potential instances of host switching. Closest relatives attacking the same host are represented by (d–f). We predict less divergence in ovipositor length between sister species in cases of cospeciation and host switching than in the case of a phenological shift, where divergence results from a shift in the relative timing of oviposition. Greater ovipositor length divergence between sister species (d–f) indicates a relatively large shift in the timing of oviposition, as the thickness of the fig wall increases during development (Kerdelhue & Rasplus 1996).

fertilization may enable parasites to induce galls on new host species, while pollinators shifting between host species could encounter pollen incompatibility and competition. Thus, the exchange of pollination services for larval food that defines the mutualism may also constrain the evolution of novel associations such that figs and pollinators tend to cospeciate. Speciation in parasites, on the other hand, need not be so tightly coupled with host speciation.

We expected speciation by host switching to account for the majority of cases in which two parasite species are associated with the same plant species. However, we identified three cases in which parasite species attacking the same host are nearest relatives (Fig. 2). These cases are illustrated in Fig. 3, where sister species using the same fig differ markedly in ovipositor length by at least 2 mm. On the other hand, ovipositor lengths are more similar (< 1 mm difference) between sister species that have cospeciated or switched hosts in the course of speciation (Fig. 3). It is improbable that three cases of extreme ovipositor length divergence between sister species on the same host compared to five instances of sisters on different hosts is due to chance ($P = 0.018$; Fisher's exact test with Monte Carlo simulation for small sample size; Engels 1998). Kerdelhue & Rasplus (1996) showed that ovipositor lengths in *Apocryptophagus* are related to oviposition behaviour. In *F. sur*, for example, parasites with short ovipositors specialize on thin-walled figs in the early stages of development. Parasites with long ovipositors lay eggs later in fig development when the wall is thicker. The combined ecological

and phylogenetic data suggest that divergence in the timing of oviposition with regard to fig phenology may initiate and accompany the speciation of parasites attacking the same host species.

This ecologically driven divergence is similar to the sympatric mode of speciation proposed by Gibbons (Gibbons 1979; Ramadevan & Deakin 1990) to explain the origin of three closely related sympatric *Megarhyssa* (Hymenoptera, Ichneumonidae) species that differ only in ovipositor length. *Megarhyssa* parasitize subpopulations of wood-boring *Tremex columba* (Hymenoptera, Siricidae) that feed at different depths in tree trunks. Fig parasites support the validity of Gibbons model of resource-partitioned speciation for the interactions of parasitic Hymenoptera, and are consistent with other recent models of sympatric speciation (Johnson *et al.* 1996; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999). More data on fig phenology and oviposition are needed to confirm these suppositions. A further step in phylogeny reconstruction would be to increase sampling of *Sycomorus* and associated wasps with expanded molecular data sets. The prediction of divergent selection on ovipositor lengths of sister species on the same host may also be tested in field experiments. A final integrative step would be to examine patterns of speciation in other fig-inhabiting organisms, including parasitoids and nematodes.

Acknowledgements

We would like to thank R. L. Butlin, V. Novotny, J. L. Patton, A. Yoder and two anonymous reviewers for comments. We also thank B. Isua, C. Kerdelhue, U. Koil and B. Patton for providing specimens. This work was supported by NSF grant numbers DEB 94-07297, DEB 98-01259 and Michigan State University.

References

- Bush GL (1994) Sympatric speciation in animals: new wine in old bottles. *Trends in Ecology and Evolution*, **9**, 285–288.
- Dieckmann U, Doebeli M (1999) On the origin of species by sympatric speciation. *Nature*, **400**, 354–357.
- Engels W (1998) Monte Carlo $R \times C$ contingency table test. Computer Program for the Macintosh. Department of Genetics, University of Wisconsin.
- Farrell BD (1998) 'Inordinate fondness' explained: why are there so many beetles? *Science*, **281**, 555–559.
- Gibbons JRH (1979) A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. *American Naturalist*, **114**, 719–741.
- Hamilton WD (1967) Extraordinary sex ratios. *Science*, **156**, 477–488.
- Herre EA (1985) Sex ratio adjustment in fig wasps. *Science*, **228**, 896–898.
- Herre EA (1987) Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature*, **329**, 627–629.
- Herre EA (1993) Population structure and the evolution of virulence in nematode parasites of fig wasps. *Science*, **259**, 1442–1445.
- Herre EA, Machado CA, Bermingham E *et al.* (1996) Molecular

- phylogenies of figs and their pollinator wasps. *Journal of Biogeography*, **23**, 521–530.
- Hossaert-McKey M, Gibernau M, Frey JE (1994) Chemosensory attraction of fig wasps to substances produced by receptive figs. *Entomologia Experimentalis et Applicata*, **70**, 185–191.
- Huelsenbeck JP, Bull JJ (1996) A likelihood ratio test to detect conflicting phylogenetic signal. *Systematic Biology*, **45**, 92–98.
- Huelsenbeck JP, Rannala B (1997) Phylogenetic methods come of age: testing hypotheses in an evolutionary context. *Science*, **276**, 227–232.
- Huelsenbeck JP, Rannala B, Larget B (2000) A Bayesian framework for the analysis of cospeciation. *Evolution*, **54**, 352–364.
- Huelsenbeck JP, Rannala B, Yang Z (1997) Statistical tests of host-parasite cospeciation. *Evolution*, **51**, 410–419.
- Johnson P, Hoppensteadt F, Smith J, Bush GL (1996) Conditions for sympatric speciation: a diploid model incorporating habitat fidelity and non-habitat assortative mating. *Evolutionary Ecology*, **10**, 187–205.
- Kerdelhue C, Le Clainche I, Rasplus J-Y (1999) Molecular phylogeny of the *Ceratostolen* species pollinating *Ficus* of the subgenus *Sycomorus sensu stricto*: biogeographical history and origins of the species-specificity breakdown cases. *Molecular Phylogenetics and Evolution*, **11**, 401–414.
- Kerdelhue SC, Rasplus J-Y (1996) Non-pollinating Afro-tropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos*, **75**, 3–14.
- Kiester AR, Lande R, Schemske DW (1984) Models of coevolution and speciation in plants and their pollinators. *American Naturalist*, **124**, 220–243.
- Kondrashov AS, Kondrashov F (1999) Interactions among quantitative traits in the course of sympatric speciation. *Nature*, **400**, 351–354.
- Lopez-Vaamonde C, Rasplus J-Y, Weiblen G, Cook JM (2001) DNA-based phylogenies of fig wasps: partial co-cladogenesis between pollinators and parasites. *Molecular Phylogenetics and Evolution*, **21**, 55–71.
- Machado CA, Herre EA, McCafferty S, Birmingham E (1996) Molecular phylogenies of fig pollinating and non-pollinating wasps and the implications for the origin and evolution of the fig-fig wasp mutualism. *Journal of Biogeography*, **23**, 531–542.
- Page RDM (1994) Parallel phylogenies: reconstructing the history of host-parasite assemblages. *Cladistics*, **10**, 155–173.
- Page RDM (1996) Temporal congruence revisited: comparison of mitochondrial DNA sequence divergence in cospeciating pocket gophers and their chewing lice. *Systematic Biology*, **45**, 151–167.
- Pellmyr O, Huth CJ (1994) Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, **372**, 257–260.
- Posada D, Crandall KA (1998) Model test: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.
- Ramadevan S, Deakin MAB (1990) The Gibbons speciation mechanism. *Journal of Theoretical Biology*, **145**, 447–456.
- Rambaut A, Grassly NC (1997) Seq-General: an application for the Monte Carlo simulation of DNA sequence evolution along phylogenetic trees. *Computer Applications in Bioscience*, **13**, 235–238.
- Swofford DL (1998) *Phylogenetic Analysis using Parsimony* (* and other methods). Sinauer Associates, Sunderland, MA.
- Weiblen GD (2000) Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. *American Journal of Botany*, **87**, 1342–1357.
- Weiblen GD (2001) Phylogenetic relationships of fig wasps pollinating functionally dioecious figs based on mitochondrial DNA sequences and morphology. *Systematic Biology*, **50**, 243–267.
- West SA, Herre EA, Sheldon BC (2000) The benefits of allocating sex. *Science*, **290**, 288–290.
- West SA, Murray MG, Machado CA, Griffin AS, Herre EA (2001) Testing Hamilton's rule with competition between relatives. *Nature*, **409**, 510–513.

George Weiblen is an Assistant Professor in Plant Biology at the University of Minnesota and Assistant Curator of vascular plants at the Bell Museum of Natural History. His research employs molecular phylogenetic techniques to reconstruct the history of plant–insect interactions through evolutionary time. Coevolution between figs and fig wasps has been a focus of his recent work in this area. Guy Bush is Hannah Professor Emeritus in Evolutionary Biology at Michigan State University. His research has focused on processes of speciation in phytophagous insects, particularly the apple maggot, *Rhagoletis pomonella*.
