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HOW TO BE A FIG WASP

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■ **Abstract** In the two decades since Janzen described how to be a fig, more than 200 papers have appeared on fig wasps (Agaonidae) and their host plants (*Ficus* spp., Moraceae). Fig pollination is now widely regarded as a model system for the study of coevolved mutualism, and earlier reviews have focused on the evolution of resource conflicts between pollinating fig wasps, their hosts, and their parasites. Fig wasps have also been a focus of research on sex ratio evolution, the evolution of virulence, coevolution, population genetics, host-parasitoid interactions, community ecology, historical biogeography, and conservation biology. This new synthesis of fig wasp research attempts to integrate recent contributions with the older literature and to promote research on diverse topics ranging from behavioral ecology to molecular evolution.

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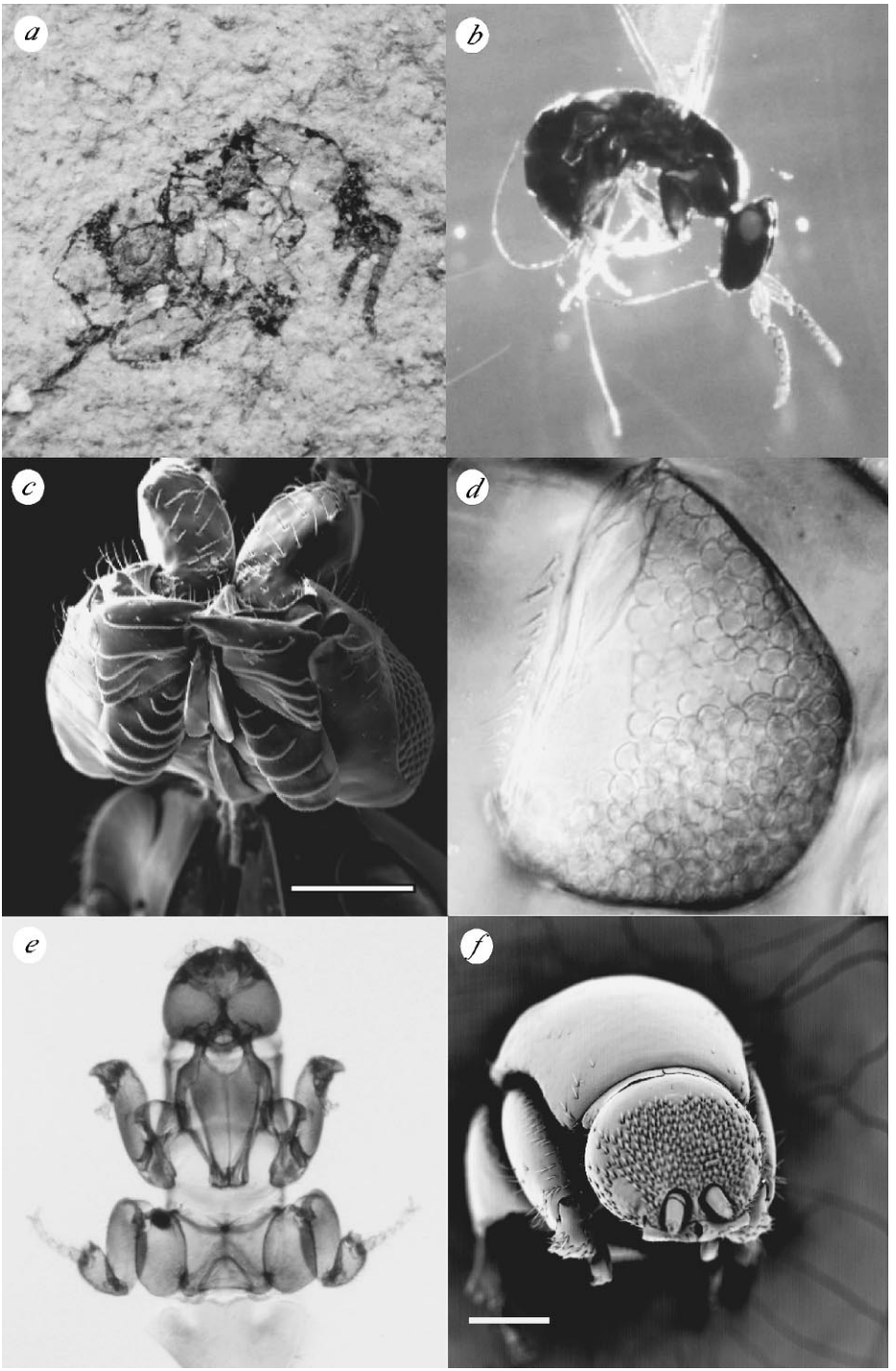
INTRODUCING FIG WASPS

The family Agaonidae (Hymenoptera: Chalcidoidea) includes several hundred parasitic wasp species that are closely associated with the fig inflorescence, an enclosed receptacle (or syconium), that characterizes the genus *Ficus* (Moraceae). All fig wasps are confined to figs as larvae, and their specialized diets are restricted to fig embryos, galled fig ovaries, or other fig wasp larvae (15). The life histories of these diminutive wasps include a fascinating variety of oviposition modes and host interactions, running the gamut from mutualism to antagonism. Molecular phylogeny suggests that the pollination mutualism evolved once and characterizes the subfamily Agaoninae (111). These pollinators of figs (Figure 1) show peculiar morphological adaptations, extreme host specificity, and life cycles that are tightly synchronized with fig phenology (177). The mutualism has been the source of much speculation on the nature and extent of the coevolutionary processes involved (133, 135, 177, 182). Comparative phylogenetic studies are possible now that phylogenies are available for fig wasps globally (111), and for Neotropical (112), Afrotropical (101) and Indo-Pacific fig pollinators (161). The first comparative studies based on molecular data have examined evolutionary hypotheses including coadaptation with host plants (159), male dimorphism (46), female virginity (165), and Hamilton's theory of kin selection (168).

Interest in fig wasps, as reflected in the number of publications, has also increased dramatically since Janzen (95) described how to be a fig more than two decades ago (Figure 2). The lifelong contribution of J.T. Wiebes also provided a taxonomic foundation for fig wasp research today. Although many hundreds of fig wasp species have yet to be described, advances in ecology and evolution have outpaced systematic studies, with international symposia held every few years (25, 34, 47). Earlier reviews have focused on evolutionary conflicts arising from the fig pollination mutualism (1, 4, 22), fig wasp biology in India (2) and Panama (85), and the similarity of fig wasp interactions to species interactions in general (86, 87, 200). The following review summarizes our current state of knowledge about fig wasps in an attempt to correct misconceptions in the older literature and to promote research on fig wasp behavior, ecology, taxonomy, phylogenetics, and evolution.

Figure 1 Pollinating fig wasps (Agaoninae: Agaonidae). (*a*) Oligocene *Tetrapus* from Florissant, Colorado (28). (*b*) Extant *Tetrapus* from Santa Catarina, Brazil. (*c*) Ventral view of the female head in *Kradibia ohuensis* showing mandibular appendage with six lamellae (scale = 0.1 mm). (*d*) Pollen pocket of *Ceratosolen kaironkensis* containing *Ficus microdictya* pollen grains. (*e*) Four-legged *Wiebesia frustrata* male with atrophied midleg. (*f*) *Kradibia ohuensis* male with vestigal eyes and dorsal spines on head (scale = 0.1 mm).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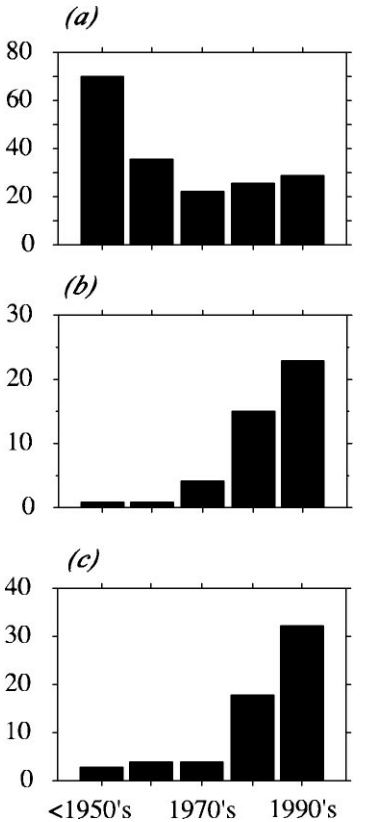

Figure 2 Numbers of publications on (*a*) fig wasp systematics, (*b*) evolution, and (*c*) ecology prior to 1960 and during each decade thereafter.

FIG WASP ECOLOGY

We begin with an overview of pollination ecology, setting aside the antagonistic interactions of nonpollinating fig wasps for later discussion. Early accounts of fig wasp ecology focused on the extreme synchrony of fig and pollinator life cycles (8, 50, 197). For example, egg-laying by pollinators is closely synchronized with the receptivity of fig flowers, and the release of adults from the fig coincides exactly with pollen presentation (12, 119, 141). Fig phenology (24, 26) and the production of fig crops (97) are also closely linked to pollinator population dynamics (5). It is perhaps not surprising, therefore, that some fig populations are pollinator limited (18). Asynchrony at the population level is a general feature of fig phenology and provides pollinators with a source of receptive figs throughout the year in many tropical climates (104). The mutualism is also constrained by the physiological requirements of fig wasps (128). High temperatures limit the survival of fig wasps

in tropical forest canopies (128), as do low temperatures in subtropical climates (27).

Pollination Ecology

Fig pollinators show morphological and behavioral specializations that are associated with the host life cycle. Among these specializations are extreme sexual dimorphisms that reflect the different activities of males and females (Figure 1). Female pollinators have functional wings and eyes and are responsible for colonizing new hosts. These females are also characterized by modifications of the head and antennae in response to the shape of the inflorescence opening (150) and by the evolution of pollen transport mechanisms (134), although the latter have been lost in some lineages (38). In particular, the female head is specially flattened and bears mandibular appendages with rows of teeth (Figure 1) that push against the inflorescence bracts lining the fig opening (or ostiole). In most pollinator species, the antennal scapes fit into a deep groove on the dorsal surface of the head, and the third segment bears a spine that serves as a hook for prying at the outer bracts and also as a point of detachment for the distal segments on contact with the inner bracts (61). The fig is at once a "tomb blossom" (13) and a "nursery," as females are trapped inside and perish after laying eggs.

Females reproduce by inserting their ovipositors into the styles of fig flowers. Only eggs deposited between the integument and nucellus of fig ovules will hatch (77), where individual larvae feed on endosperm in the galls (50, 57, 58, 77). Fertilization of fig flowers by pollinators provides the food resource for the next generation of wasps. Unique features associated with pollen transport include corbiculae on the forecoxae, pockets on the mesothorax (Figure 1), or grooves between the abdominal segments (15, 134). Two major modes of fig pollination may be distinguished by differences in wasp behavior and morphology. Actively pollinating species remove pollen from the thoracic pockets with their forelegs, depositing it on the stigmatic surface when laying eggs in a fraction of fig flowers (51, 55, 96, 99). On the other hand, passively pollinating species do not have functional pockets or active pollination behavior, and pollen is transported on the abdomen instead. Both modes of pollination are beneficial to the host plant, although pollinators also serve as vectors for the fungal pathogens that attack figs (114).

Male participation in the life cycle is restricted to the cavity of the host, and most individuals are apterous with vestigial eyes, antennae, and tarsi. Emerging males chew holes in galls containing the females, and their telescopic abdominal segments are curled beneath the body so that the genitalia may be inserted into the galls. Males associated with figs that are fluid filled during this phase also exhibit bizarre respiratory adaptations (39). The armature on the foretibia, enlarged femora, and retractable antennae (Figure 1) appear to be associated with burrowing out of the fig, providing an escape for mated and pollen-laden females.

Overall, pollinator life cycles and morphology provide a rich source of adaptive hypotheses that can be tested with behavioral, ecological, and phylogenetic data

(13, 25, 51, 54, 83, 86, 117, 133–135, 183). The extent of host specificity in fig wasp interactions is central to these issues.

Host Specificity

Pollinator associations are generally host species–specific (115, 132, 138, 177), as initiated by the arrival of females at receptive figs releasing volatile attractants (93, 152). The chemical cues attracting *Blastophaga psenes* to the edible fig (*Ficus carica*) were recently identified (65), and different species appear to have unique volatile profiles (157). Little is known about flight patterns, but trapping data (36, 154, 155) and fig paternity analysis (120–122) suggest that females disperse above the forest canopy, frequently over distances of more than 10 kilometers. In most cases, the geographic distribution of pollinator species closely matches that of the host. Rasplus (138) outlined different scenarios in which more than one species of pollinator is associated with a particular host. The cooccurrence of pollinating and cheating species of Agaoninae is known only from African *Ficus sycomorus*, which commonly supports nonpollinating *Ceratosolen galili* and pollinating *Ceratosolen arabicus* in the same fig (38). In addition, two pollinator species occasionally inhabit the same host in sympatry, as do *Ceratosolen flabellatus* and *Ceratosolen silvestrianus* in *Ficus sur* (99), and divergent habitat preference has been suggested as a means of reproductive isolation in this case (116).

The most common departure from one-to-one specificity is the situation in which two pollinator taxa are geographically isolated across the host range. Fifteen cases are known from the Indo-Pacific region (138), and these frequently involve allopatric host subspecies or varieties (e.g., *Liporrhopalum gibbosae* and *Liporrhopalum rutherfordi* from *Ficus tinctoria* ssp. *gibbosa* and ssp. *parasitica*, respectively). There are five additional cases in the region in which pollinator subspecies are allopatric across the range of a single host species (e.g., *Ceratosolen bisulcatus* ssp. *bisulcatus* and ssp. *jucundus* in the southern and northern range of *Ficus septica*) (181). Cases in which different host species are associated with the same pollinator are less common, and artifacts of botanical classification account for several of these instances (161). For example, *Ceratosolen appendiculatus* is known to pollinate widespread *Ficus variegata* and endemic *Ficus viridicarpa* in peninsular Malaysia (138). However, *F. viridicarpa* barely differs from *F. variegata* in fig coloration, and the two are considered just one species (G. Weiblen, personal observations).

The general pattern of one-to-one host specificity is also supported by experimental evidence. An example of a natural experiment involves the colonization of volcanic islands, where population expansion by colonizing fig species depended on specific pollinator species (43). Furthermore, the naturalization of exotic *Ficus* species in North America has resulted from the introduction of specific pollinators from other continents (118). A few reports of breakdown in specificity involve visits of local pollinators to exotic *Ficus* (153), but fertile F1 hybrids resulting from pollinator "mistakes" have yet to be documented. Recent pollination experiments

(162) and phylogenetic patterns (159) are also consistent with early attempts at fig breeding. Intraspecific crosses of *F. carica* were made by introducing *B. psenes*, to cultivars of the edible fig, but crosses between *F. carica* and *Ficus pumila* using the same technique failed because *B. psenes* could not be induced to enter figs of *F. pumila* (45). On the other hand, *Ficus aurea* × *religiosa* hybrid seedlings were reported in Florida, where *Pegoscapus mexicanus*, the local pollinator of *F. aurea*, was observed visiting exotic *Ficus* (137), and a similar breakdown of specificity involving a local pollinator and an exotic fig produced hybrids in Africa (32, 153). Hybrids have also been produced by artificial pollination (45), which suggests that host choice is an important pre-reproductive isolating mechanism, given that pollinators rarely make "mistakes" in natural populations (17).

Host Utilization

Host use by fig pollinators can be divided into two general strategies depending on whether the breeding system of the host fig is monoecious or functionally dioecious (hereafter dioecious). In monoecious species, pollinator offspring and viable seeds develop inside the same fig. On the other hand, pollinator production and seed set in dioecious species are divided into two types of figs occurring on different plants (Figure 3). Galil & Eisikowich (59) first reported that seed is set in long-styled flowers with ovules that are beyond the reach of pollinator ovipositors. Further studies of host use in monoecious figs showed that nearly all flowers are accessible to pollinators, but most offspring tend to develop in flowers with short styles (6, 7, 33, 125). The idea that differences in style length could regulate seed and pollinator production was criticized when monoecious style length distributions were shown to be unimodal (18), but dioecious figs are quite different in this respect.

Style length dimorphism is a defining feature of dioecious species and separates the inflorescence types into gall figs and seed figs (13). A general picture of dioecious fig pollination has emerged after more than a century of observation (8, 12, 48, 50, 55, 119, 158, 197). Female pollinators are attracted to both gall and seed figs (3, 127, 162); they pollinate both types, but their offspring only develop in gall figs (48, 55). Gall figs are functionally "male" because they foster the wasp larvae that disperse fig pollen as adults. Ovules that would otherwise produce seed instead serve to nourish wasp offspring (12, 123). On the other hand, seed figs are functionally "female" because the styles are too long for ovipositors to reach the ovules, and viable seeds result from pollination. Thus, fig ovules are allocated to each generation of seeds and wasps in a predictable fashion.

Sex Ratio

Fig wasps have also served as models for testing the predictions of sex allocation theory. Because few females lay eggs in a given fig, related male offspring are in local competition for mates, and there is a strong possibility of mating between siblings (53, 81, 82, 164, 166, 168). The effects of local mate competition and

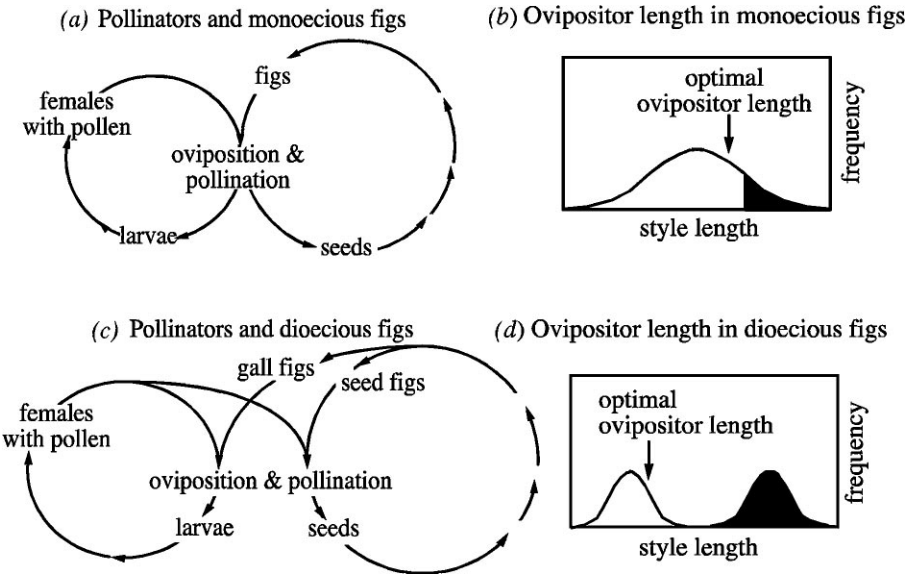

Figure 3 Life cycles of pollinating fig wasps and the interaction between ovipositor length and fig style length. (*a*) In monoecious *Ficus*, pollinator larvae and seeds mature in the same fig. (*b*) Optimal ovipositor lengths in monoecious figs are slightly longer than the average style length. Seeds in short-styled flowers are destroyed by larvae, but seeds in long-styled flowers tend to survive, as indicated by the shaded area under the curve. (*c*) In dioecious *Ficus*, there are two types of figs and both are pollinated. Wasp larvae develop in gall figs and seeds develop in seed figs. (*d*) Ovipositors associated with functionally dioecious *Ficus* are slightly longer than the style length in gall figs, but they are unable to reach the ovules in seed figs. Dimorphic style lengths divide the maturation of pollinators and seeds into seed figs (shaded) and gall figs (not shaded), respectively.

inbreeding favor the evolution of highly female-biased sex ratios (81), as predicted by Hamilton's theory of competition among male relatives for mates (78). Sex ratios in fig wasps are, in fact, negatively correlated with levels of inbreeding and local mate competition (52, 53). Herre (81) disentangled the effects of inbreeding and local mate competition in a refined model of sex ratio evolution, and empirical data across multiple species support his predictions (82, 90). The impact of virginity on fig wasp sex ratios (66) was recently formalized in a model, and according to the prediction of local mate competition theory, levels of virginity were inversely related to the size of the brood (165). Predictions of stabilizing selection theory have also been supported by sex ratios and the frequency of single-founder broods (164, 166). Tests of local mate competition theory with nonpollinating fig wasps recently showed that male fighting is correlated with female density and mating opportunity, as opposed to male relatedness (168).

Gallers, Parasitoids, and Predators

Nonpollinators are important components of fig wasp communities (21, 41), having negative impacts on the mutualism (101, 105). Three distinct guilds of nonpollinators have been identified: gall makers that attack figs from the exterior, gall makers that enter figs as do the pollinators, and parasitoids that attack other fig wasp larvae (44, 103). Parasitoids have extraordinarily long ovipositors that are capable of piercing the fig receptacle (40), and they are classified in the subfamily Sycoryctinae. They typically attack pollinator larvae, but the genus *Apocrypta* appears to specialize on gall-making *Apocryptophagus* (140, 162). Gallers in the subfamilies Epichrysomallinae, Otitesellinae, Sycoecinae, and Sycophaginae have short or long ovipositors, depending on whether they attack figs from the interior or the exterior. Overall trophic relationships are summarized in Figure 4, and these assemblages can include up to 20 taxa on a single fig species (11, 30). In African fig wasp communities, the species richness of parasitoids is correlated with that of gallers (37, 41, 80), suggesting that some parasitoids may be specialists on gall-making taxa.

Gallers feed on abnormally proliferating nucellus (56–59, 77), and therefore, do not depend directly on the fertilization of flowers by pollinators (23, 162). Parasitoids attack flowers containing other fig wasps, either by consuming the host larva or by starving it by feeding on endosperm (106). Because their development depends on other fig wasp larvae, parasitoids are rarely found in seed figs of dioecious species (162). The dynamics of host-parasite interactions are intriguing because the negative impact of nonpollinators could threaten the long-term stability of the mutualism (119). Bronstein (21) suggested that figs partition

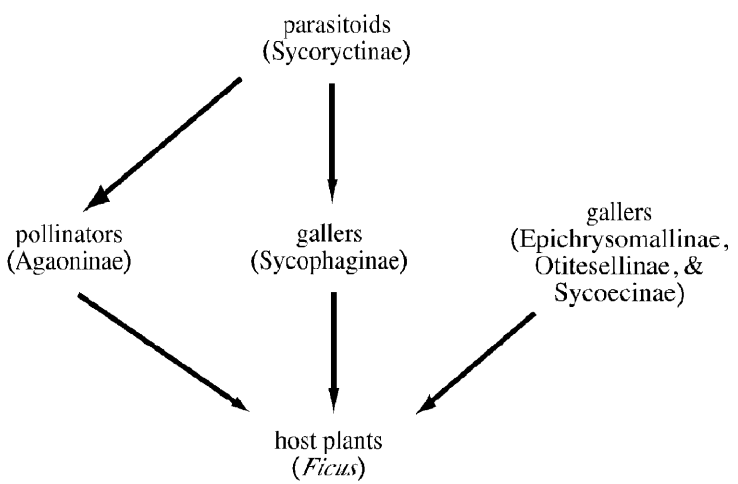

Figure 4 Trophic relationships among figs and fig wasps. Agaonid subfamilies include pollinators, gallers, and parasitoids.

resources between pollinators and nonpollinators to minimize their competition, but further studies have shown that the two compete for seed resources (163, 167) and that nonpollinators have a negative impact on pollinator population dynamics (23, 101, 105).

A key factor in stabilizing host-parasite interactions is parasitoid aggregation in space and time. If hosts are distributed in patches and the incidence of parasitism varies from patch to patch, then increasing host density reduces parasitoid search efficiency. West & Herre (167) reported that density-dependent heterogeneity is sufficient to stabilize the interaction between parasitic *Physothorax* and galling *Aepocerus* in monoecious figs. Data on the population dynamics of parasitic *Philotrypesis* and pollinating *Kradibia* also indicate that heterogeneity in the rate of parasitism is sufficient to stabilize the interaction in dioecious figs. It is interesting that there was an inverse relationship between the rate of parasitism and host density (162), which may result from a low limit on the rate of parasitism per patch and little or no aggregation of parasitoids within patches. Possible explanations include the failure by parasitoids to detect patches of high pollinator density, failure to determine where parasitoid eggs have been laid, egg limitation, or predation. Further studies are needed to explore the effects of these different factors on rates of parasitism in fig wasps.

Other topics of research on nonpollinators include the striking adaptations for intraspecific combat among males (79). Fighting occurs among males of some parasitoid species (79) but not others (66), and male dimorphism appears to be widespread in lineages exhibiting male combat (136). Polymorphisms in fighting behavior and winglessness among parasitoid males have been attributed to sexual selection (46) and may be related to population structure (90). The predators of fig wasps are also noteworthy, as they too have impacts on the mutualism. Ants are probably the most significant predators (20, 162), although phorid flies have also been recorded (35). Interactions beyond the fig wasp community become progressively more complex, as ants tending planthoppers protected figs against nonpollinating wasps (42).

FIG WASP SYSTEMATICS

The great majority of wasps associated with the fig inflorescence belong to the superfamily Chalcidoidea (Table 1), although a few braconids have been reared from figs (142). The pollinating fig wasps have received the most attention, with the taxonomic contributions of Grandi (68–76), Hill (91, 92), and Wiebes (169–176, 178–180, 184–192, 194, 196) culminating in revisions of the pollinating Agaoninae in each major tropical region (14, 193, 195). Recently, more species have been described from Taiwan (29, 30) and India (130). These various revisions have brought the total to more than 300 species of pollinators. In addition, nearly 400 species of nonpollinating Agaonidae have been described. Boucek (15) included most nonpollinators in the Agaonidae, but he assigned other genera to Orymidae, Torymidae, and Pteromalidae in his revision of neotropical fig wasps (16). Apart

TABLE 1 Hymenoptera reared from fig florescences, in alphabetical order

Family	Subfamily	Genera (number of described species)
Agaonidae	Agaoninae	*Agaon* (11), *Alfonsiella* (7), *Allotriozoon* (3), *Blastophaga* (24), *Ceratosolen* (61), *Courtiella* (13), *Deliagaon* (4), *Dolichoris* (10), *Elisabethiella* (14), *Eupristina* (13), *Liporrhopalum* (18), *Kradibia* (23), *Nigeriella* (4), *Paragaon* (2), *Pegoscapus* (45), *Platsyscapa* (19), *Pleistodontes* (18), *Tetrapus* (6), *Waterstoniella* (20), *Wiebesia* (18)
	Epichrysomallinae	*Acophila* (2), *Asycobia* (1), *Camarothorax* (6), *Eufroggattisca* (1), *Epichrysomalla* (1), *Herodotia* (2), *Meselatus* (4), *Neosycophila* (2), *Odontofroggatia* (4)
	Otitesellinae	*Aepocerus* (19), *Eujacobsonia* (2), *Grandiana* (3), *Grasseiana* (2), *Guadalia* (1), *Heterandrium* (9), *Lipothymus* (4), *Marginalia* (1), *Micranisa* (5), *Micrognathophora* (1), *Otitsella* (18), *Philosycella* (1), *Walkerella* (∼5)
	Sycoecinae	*Crossogaster* (16), *Diaziella* (12), *Philocaenus* (22), *Robertsia* (2), *Seres* (5), *Sycoecus* (10)
	Sycophaginae	*Anidarnes* (3), *Apocryptophagus* (∼30), *Eukobelea* (4), *Idarnes* (15), *Pseudidarnes* (5)
	Sycoryctinae	*Adiyodiella* (1), *Apocrypta* (24), *Arachonia* (1), *Dobunabaa* (1), *Philotrypesis* (∼50), *Philoverdance* (1), *Sycoryctes* (4), *Sycoscapter* (∼46), *Sycoscapteridea* (4), *Tenka* (1), *Watshamiella* (∼10)
Braconidae		*Ficobracon* (1), *Psenobolus* (3)
Eurytomidae		*Bruchophagus* (1), *Eurytoma* (1), *Sycophila* (3)
Orymidae		*Orymus* (2)
Pteromalidae		*Hansonia* (1), *Podivna* (1)
Torymidae		*Physothorax* (7), *Torymus* (1)

from *Apocrypta* (140), *Otitesella* (149, 151), and the Sycoecinae (64, 144–148), taxonomic revisions are needed for most nonpollinating genera.

The classification of Agaoninae has received the most attention, and a total of 16 pollinator genera are currently recognized (14, 93, 195). Wiebes (182) divided the pollinators into two tribes, Agaonini and Blastophagini, based on characters of the female head, but Boucek (15) pointed out that neither male characters nor host associations support this division. Corner (49) rejected the proposal of Ramirez (135), altering the botanical classification to better fit patterns of pollinator association, but phylogenetic analyses indicate that host use by pollinators is a strong predictor of host plant phylogeny (161). As we shall see, the discovery of new associations continues to provide opportunities to test the conservatism of host use in a phylogenetic framework (183, 186).

Phylogenetic Relationships

Phylogenetic analyses of mitochondrial DNA and morphology have also provided new insights on the classification (15, 193) and proposed relationships of fig pollinators (100, 112, 131, 139, 182). In particular, ribosomal and mitochondrial DNA (111, 113, 139) suggest that some nonpollinator subfamilies are more closely related to other chalcid families than to Agaoninae (Figure 5). Although fig wasps are not monophyletic, the pollinators (Figure 5) belong to a well-supported clade (113). Molecular phylogenies also indicate that neotropical *Tetrapus* is a sister group to the rest of the Agaoninae (111, 113), a position that is consistent with fossil evidence (28, 194), morphology, and the phylogenetic position of the host figs. The division of the fig pollinators into Agaonini and Blastophagini is not supported by results from either the separate (111) or combined evidence (161).

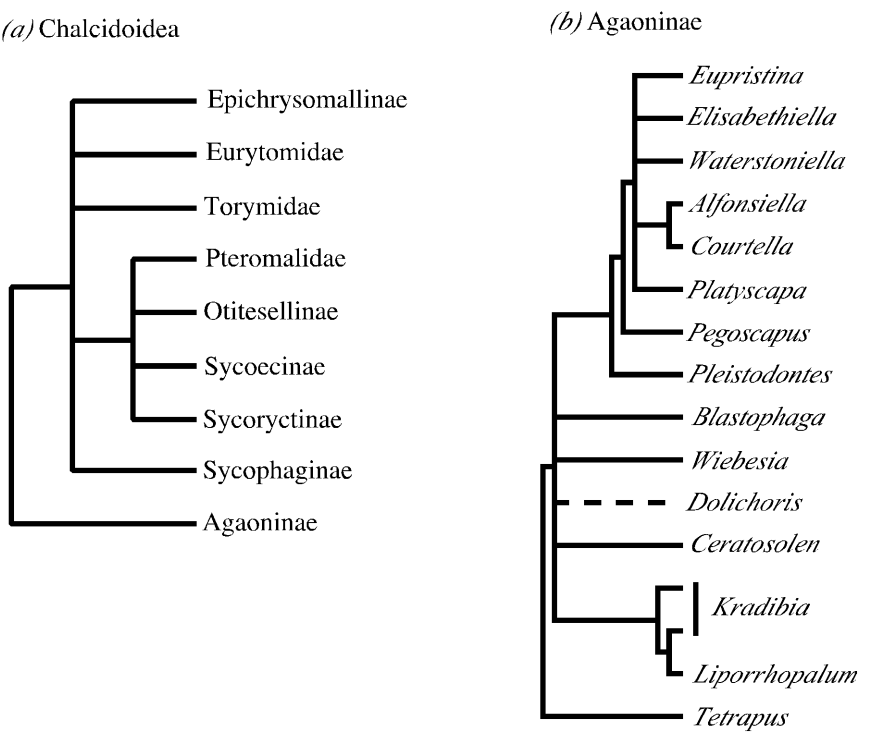

Figure 5 Phylogeny of Agaonidae. (*a*) 28S ribosomal DNA phylogeny for agaonid subfamilies and other Chalicidoidea families (139). Mitochondrial DNA also suggests that some nonpollinating fig wasps are more closely related to Pteromalidae and Torymidae than to the pollinating Agaoninae (111). (*b*) Phylogeny of fig pollinators (Agaoninae) based on mitchondrial DNA sequences (113, 161). The monophyly of *Dolichoris* is uncertain, as indicated by a dashed line.

This conclusion also agrees with Boucek (15), who regarded the two subfamilies as artificial and uncorroborated by male morphology.

Ramirez (134) suggested that the pollinators of dioecious figs constitute a monophyletic group, but Wiebes (182) argued against this on the basis of overall morphology. In particular, Wiebes (193) suggested that the dioecious fig pollinators in *Blastophaga* might be more closely related to the monoecious fig pollinators, *Platyscapa* and *Dolichoris*. The largest genus, *Ceratosolen*, includes pollinators of both monoecious and dioecious figs, and the associations of its three subgenera do not correlate with the distribution of fig breeding systems (160). Molecular analyses of these taxa support Wiebes' (193) suggestion that the pollinators of dioecious figs are not monophyletic (113, 161).

Morphological Apomorphies

Reconstructing morphological change from phylogeny also supports Wiebes' (182) view that pollinators of figs show trends toward the reduction and loss of multiple features including mouthparts, tarsi, male eyes, and female wing venation (161). In females, reductions and losses are apparent in the maxillary palpus, ventral lamellae on the mandibular appendage, front coxal combs, and ovipositor length. It has further been supposed that the elaboration of the female antennae, mandibular appendages, and mesosternal pockets are products of adaptation to host figs (131, 134). Most morphological features relevant to host use show patterns of homoplasy, providing the basis for specific tests of adaptive hypotheses in a phylogenetic framework (46, 159). There is strong evidence of similar solutions to the functional constraints imposed by hosts evolving independently in different fig wasp lineages (150).

In particular, the female head in *Pleistodontes* is apomorphic in six different characters that were previously cited as pleisiomorphic characters shared with *Tetrapus* (182). In these genera, the facial groove fitting the antennae in most pollinators is closed, the scape and pedicel are elongate, the pedicel has few axial spines, and the mandibular appendage is oriented subvertically with abundant ventral lamellae. Wiebes (181) regarded these similarities as evidence of shared ancestry, but molecular studies (111, 113, 161) indicate that *Pleistodontes* belongs to a clade of mostly Old World pollinators and is not closely related to neotropical *Tetrapus* (Figure 5). This suggests that *Tetrapus* and *Pleistodontes* have converged in modifications of the female head and the mandibular appendage (161). Convergent head shapes in African pollinating and nonpollinating fig wasps have been related to ostiole morphology (150), and the homology of head traits in *Pleistodontes* and some African pollinators as suggested by Wiebes (182) has also been questioned (111).

However, not every morphological character is homoplasious, and many serve as useful touchstones for identification. For example, *Ceratosolen* is morphologically distinct from its relatives in at least eight features. In females, the spiracular peritremata of the eighth urotergite are enlarged and ovoid. The male head is

elongate, with few dorsal spines and a prominent trilobate margin to the epistoma. The male antennae are slender, the eyes are reduced, the pronotum is elongate, and the propodeal peritremata are enlarged.

It is noteworthy that some clades with strong molecular support but without prior taxonomic designation are not marked by morphological changes. For example, the second largest clade of dioecious fig pollinators, *Kradibia* plus *Liporrhopalum*, was proposed by Wiebes (193) in an effort to reconcile pollinator and host classification. His suggestion ran contrary to early morphological cladograms (131, 182), so it is not surprising that apomorphies for this clade are lacking. In contrast, the monophyly of *Liporrhopalum* with respect to paraphyletic *Kradibia* is marked by many apomorphies including elongate funicular segments in the female antennae, a tricuspidate antaxial tooth in the female hind tibia, obsolete forewing venation, and the reduction of tarsi in mid- and hindlegs of males. The following section outlines how patterns of morphological change inferred from phylogenies are essential to the study of fig wasp evolution.

FIG WASP EVOLUTION

Fig wasps are a fantastic subject for evolutionary study, especially for investigations of coevolved mutualism between pollinators and their host plants (177). Fossil achenes indicate that fig pollination evolved at least 50 million years ago, and leaves classified as *Ficus* are present in the Cretaceous and Tertiary records (31). The earliest fossil fig wasp (28) is known from the Florissant formation in Colorado, 25–35 mya (Figure 1), and *Pegoscapus* from Dominican amber further suggests that two lineages of monoecious fig pollinators had diverged by the upper Miocene (129). Little beyond this can be concluded from the fossil record. Recent dating based on molecular divergence, however, suggests that the mutualism may be 90 million years old (113). The radiation of fig wasp genera may have occurred during the breakup of Gondwana, and the divergence of *Ceratosolen* may have coincided with the separation of Madagascar from Africa (100).

Comparative approaches to the study of fig wasp evolution were limited until recently by the ambiguity of phylogeny estimates for the lineages involved (88, 100, 111–113, 139, 159, 160, 162, 198, 199). Molecular phylogenies provide new opportunities to examine evolutionary hypotheses drawn from the specificity of fig wasp interactions (83, 133, 177). Two major components of coevolution have been addressed thus far: (*a*) phylogenetic evidence for a history of cospeciation between figs, pollinators, and parasites; and (*b*) evidence for the reciprocal adaptation of interacting traits.

Modes of Speciation

Congruence between fig and pollinator classification is suggestive of cospeciation (34, 49, 133, 183), whereas the occasional breakdown of host specificity has

suggested alternative modes of speciation (115). Cospeciation occurs when an ancestral association between species splits into descendant associations (Figure 6). On the other hand, host switching over evolutionary time can result in patterns of phylogenetic incongruence even in highly host-specific interactions (138). The cospeciation hypothesis assumes that associations are conservative, with host shifts

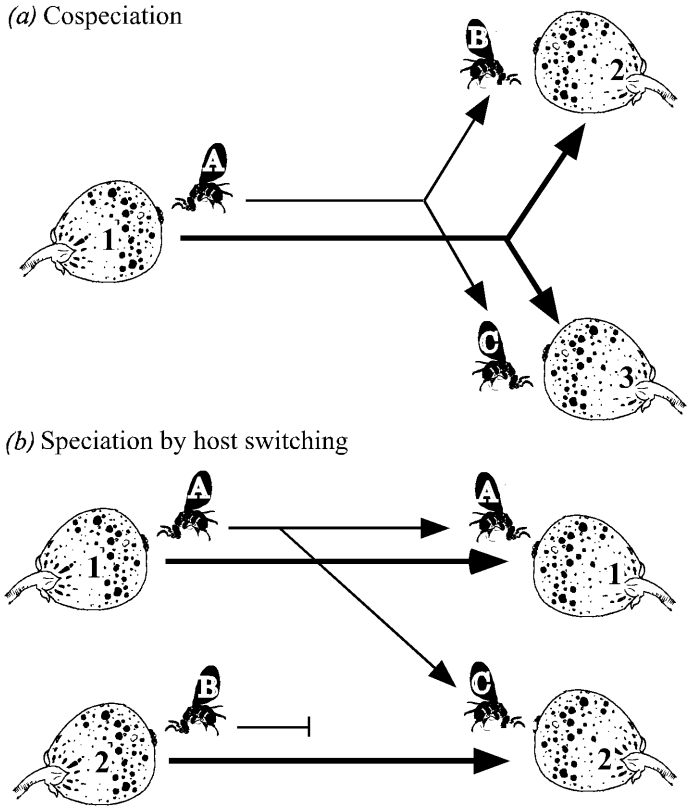

Figure 6 Modes of speciation in fig pollinators and their hosts (100, 115, 159). (*a*) Cospeciation is illustrated by the splitting of ancestral pollinator species "A" into two descendant species, "B" and "C," accompanied by the splitting of ancestral host species "1" into descendant species "2" and "3." Phylogeographic patterns suggest that speciation in rapidly evolving pollinators often preempts host speciation. (*b*) Speciation by host switching. One of several possibilities involves an individual of pollinator species "A" shifting from host species "1" to a subpopulation of host species "2" lacking the ancestral pollinator species "B." The founding pollinator population evolves into species "C." Depending on the location and timing of these events, the host population may diverge from ancestral species "2," or alternatively, two pollinator species may coinhabit host "2" as in the case of *Ficus sur* (99). Illustrations not to scale.

producing patterns of homoplasy in evolutionary reconstructions of host use. Because Wiebes (191) relied on the botanical classification in grouping his species, it is possible that congruence between pollinator classification and host associations could be a taxonomic artifact. Machado et al. (113) further suggested that morphological convergence with respect to the interaction could result in spurious agreement between the classifications. The case for cospeciation is strengthened by evidence of monophyletic groups of pollinators with conserved host associations, becoming even stronger when clades without names show conservatism.

Comparisons of fig and pollinator phylogenies at various taxonomic levels have supported cospeciation (88, 113, 159, 161, 198, 199). For example, several monophyletic genera of pollinators are uniquely associated with host sections (Figure 7), including *Blastophaga* with *Ficus*, *Platyscapa* with *Urostigma*, and *Pleistodontes* with *Malvanthera*. However, the apparent conservatism of host associations in each of these clades could be spurious if the taxonomic limits of pollinator genera were set by host classification. Pollination of section *Conosycea* by a *Eupristina-Waterstoniella* clade provides additional evidence of conservatism in this regard, as does monophyletic *Wiebesia* associated with the *Rhizocladus-Kalosyce* clade. Pollination of section *Sycidium* is also indicative of host conservatism, as *Kradibia* pollinates subsection *Sycidium* and *Liporrhopalum* pollinates subsection *Paleomorphe*.

The inference of host switching from fig classification alone can also be misleading. A case of mistaken identity having a strong effect on inferences of host switching involves *Ceratosolen nanus*, the pollinator of *Ficus pungens* in section *Sycidium*. From fig classification alone, we infer that the *C. nanus* lineage switched from section *Sycocarpus* to *Sycidium*. Wiebes (170) asserted that the pollinator undoubtedly belonged to *Ceratosolen* in spite of its association with *Kradibia*-pollinated *Sycidium*. Phylogenetic analyses based on molecular and morphological data indicate that *F. pungens* is more closely related to *Sycocarpus* than to *Sycidium* (160). Correcting for the spurious placement of *F. pungens*, we no longer infer an ancestral host shift in this case. This illustrates the importance of considering the potential for host phylogeny to affect inferences on the conservatism or lability of pollinator associations. An intriguing case of host switching may involve the pollinators of dioecious figs, *Blastophaga* and *Wiebesia*, and pollinators of the monoecious subgenus *Urostigma* (161), but more data are needed to explore this possibility. In general, we may conclude from ancestral host associations based on pollinator phylogeny that host switching has not been a major factor in the evolution of the fig/pollinator mutualism.

Nonetheless, the breakdown of host specificity in several cases suggests alternative modes of speciation (115). The most common departure from specificity involves the geographic isolation of two pollinator species across the range of a single host species. In a survey of the Indo-Pacific region, Rasplus (138) counted 20 cases of multiple allopatric pollinator species or subspecies per host species. In addition, *Platyscapa fischeri* and *Platyscapa hsui* pollinate *Ficus caulocarpa*

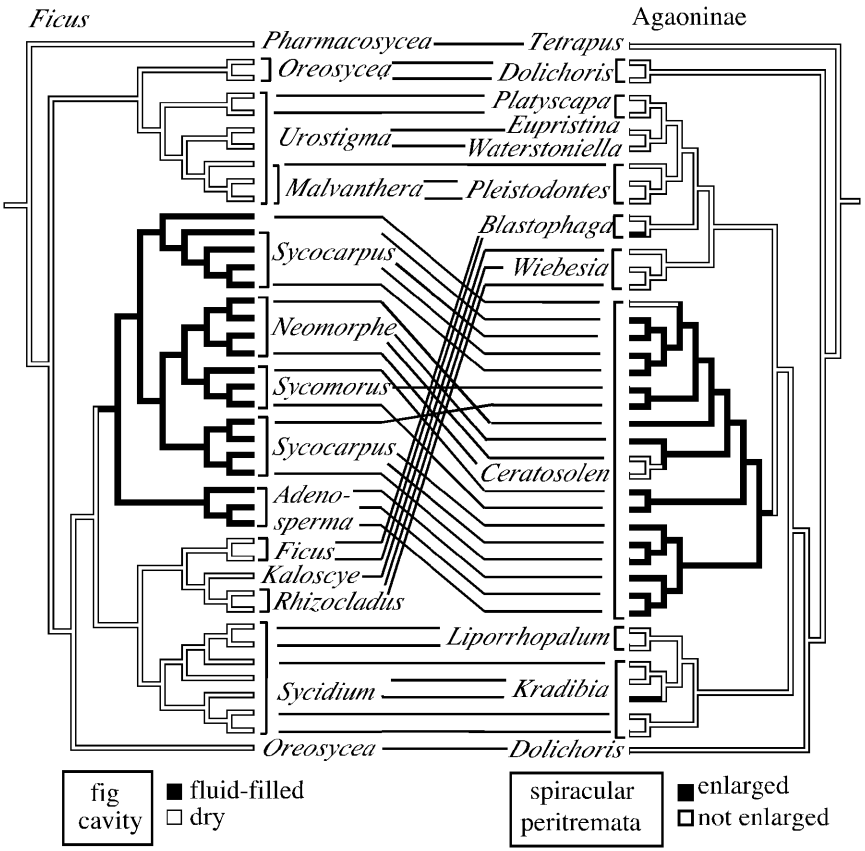

Figure 7 Coevolution of fig pollinators and their host plants. Phylogenies of Indo-Australian *Ficus* and Agaoninae based on combined analyses of morphology and DNA sequences (160, 161). The interacting clades support a history of cospeciation in the mutualism, and parsimony suggests the correlated evolution of morphological features. For example, *Ceratosolen* and their hosts share the derived features of enlarged spiracular peritremata and fluid-filled figs (159).

in different regions of the host range (29, 175). The unequal diversification rates suggested by geographical distribution patterns could result from different rates of dispersal, or alternatively, from different rates of local adaptation in pollinators and hosts. Due to linked lifecycles, the loss of a pollinator association implies the extinction of the host lineage unless accompanied by a contemporaneous host switch. The rarity of multiple pollinator species on the same host in sympatry (99, 115, 116) tends to support a model of pollinator speciation preempting host speciation under allopatric conditions. Indeed, Kerdelhué et al. (100) argued that multiple pollinator

species in *F. sur* represent the radiation of a pollinator lineage in the absence of host plant radiation.

The rarity of host switching in the mutualism is a likely consequence of extreme specialization and life cycle interdependence. Mating within the fig reduces the effective population size of pollinators (111), and the loss of genetic variation in traits pertaining to host selection and performance could constrain the evolution of host use. In addition, the linkage of fig and pollinator life cycles implies that a founder invading a new host would compete for resources with an established pollinator population. Local adaptation in the resident pollinator would favor its competitive ability against invaders. A rare but fascinating scenario is the evolution of cheating in conjunction with a pollinator host shift. Independent studies (101, 111) have shown that pollinating *C. arabicus* and nonpollinating *C. galili* in *F. sycomorus* are not sister species, suggesting that a host shift was accompanied by the transition from mutualism to cheating in this case (100). However, phylogenetic studies of other nonpollinating lineages indicate that parasitoids tend to cospeciate with the pollinators (110, 112).

Coadaptation

The correlated evolution of fig and wasp traits also provides evidence for reciprocal adaptation, or coadaptation (13, 133). Examples of adaptive scenarios include the respiratory apparatus in the inhabitants of fluid-filled figs (39), emergence behavior and the location of stamens (159), and pollination behavior in relation to the pollen/ovule ratio (134). Morphological convergence provides the opportunity to test these adaptive hypotheses in a phylogenetic framework. Convergent pollinator morphology has thus far been attributed to the similar functional constraints of host figs (88), particularly for features of the female head (161) and mouthparts (131) that interact with the fig opening (150). Some of the strongest evidence of morphological adaptation is the relationship between ovipositor length and life history. Parasitoids lay eggs through the fig wall and their ovipositor lengths are highly correlated with fig wall thickness. On the other hand, pollinator ovipositors are strongly correlated with the style length distributions of their hosts but not with fig wall thickness (159).

An intriguing case of convergence involves the breathing apparatus of pollinators and gallers inhabiting fluid-filled figs (Figure 7). These figs collect fluid during the interval between pollination and maturity (8, 14). Compton & McLaren (39) suggested that the enlarged and pillose spiracles that repel fluid are adaptations to this semi-aquatic environment. Another hypothesis concerns the emergence of pollinators from figs in relation to the positioning of staminate flowers. Stamens may be located around the fig opening or dispersed throughout the fig, depending on whether wasps escape through the fig opening or through the wall. Also correlated with the abundance of stamens are transitions between active and passive pollination behavior (60) and pollen pockets (134). The role of coadaptation in mitigating evolutionary conflicts between figs and pollinators deserves special attention.

Resource Conflicts

Fig resource tradeoffs (89) and evolutionary conflicts with pollinators (4, 67, 104, 127) have a rich literature. In particular, morphological specialization has been interpreted as an adaptation to stabilize the mutualism (13, 49, 63, 117, 134, 135, 177). Mutualisms between pollinating seed predators and their hosts are a source of evolutionary conflicts (25, 87). In the exchange of pollination services for larval food, seeds are the common currency in which the success of subsequent generations is measured (94). In theory, the consumption of too many or too few seeds by pollinators could drive a mutualism toward parasitism or extinction. However, reciprocal selection on the partners could maintain equilibrium between resource allocation by the host plant and resource consumption by the pollinator. The fitness consequences of resource trade-offs have been examined directly in particular species, but factors maintaining mutualism stability are not easily isolated (89).

Comparative phylogenetic analyses, on the other hand, have shed new light on the evolution of traits governing these conflicts (159). In particular, the role of style lengths and pollinator ovipositors in mitigating the conflict over seed resources is supported by comparative data (161). Models of coevolution predict that ovipositor and style lengths will be highly correlated owing to the increased fitness associated with access to fig ovaries. In theory, the fitness costs of seed predation will select for an optimal style length distribution (19), just as longer ovipositors will be selected so that the entire distribution is accessible (117). If, however, an efficiency cost is imposed on oviposition in longer-styled flowers, the optimum style length for oviposition will be nearer to the mean of the style length distribution (63, 124).

Monoecious figs have unimodal distributions of style length with considerably more variance than pollinator ovipositors (98). Behavioral studies indicate that ovipositors can penetrate even the longest styles in monoecious figs but that most oviposition occurs in short-styled flowers owing to time-efficiency constraints on egg-laying behavior (124). In addition, an optimal packaging model can account for variation in the length of flower pedicels, but not of styles, which vary according to the selective regime imposed by pollinators (62). The strong correlation of style and ovipositor lengths across species is consistent with the coadaptation hypothesis (124).

However, the length of the ovipositor alone does not entirely account for patterns of resource use in the fig/pollinator mutualism (98). Founder numbers are also highly correlated with fig size and may play a role in stability (2, 83). West & Herre (163) suggested that developmental barriers might protect some fig ovaries, termed "unbeatable seeds," whereas Murray (117) proposed that selective fig abortion might stabilize levels of seed and pollinator production. Herre (83) proposed that gall size could constrain pollinator egg load, thereby limiting levels of pollinator production, an idea consistent with the phylogenetic correlation of gall size and wasp body size (159). Consumption of seed resources by pollinators could also be regulated by the morphology of the fig opening affecting founder sizes and

numbers (124, 154), but this hypothesis has yet to be tested using comparative methods.

Dioecious Fig Conflicts

Molecular divergence suggests that fig pollination is ancient, and the extant diversity of pollination modes points to an ongoing dynamic equilibrium between the mutualists in patterns of resource allocation and utilization (113). Resource conflicts in dioecious fig pollination are quite different from those in monoecious figs. In particular, the style length distribution is bimodal (Figure 3), and the maturation of seeds and pollinators is segregated in two types of figs on separate plants (158). Short-styled flowers in gall figs are consumed by pollinator larvae, whereas the ovules of long-styled flowers in seed figs are unharmed (55, 104). The stability of this mutualism seems paradoxical because pollinators show no preference for gall figs in spite of the fact that seed fig pollinators leave no offspring (4, 22, 67, 94, 127).

A first glance indicates that pollinators of dioecious figs have shorter ovipositors than their monoecious-pollinating counterparts (135). The correlation between fig breeding systems and ovipositor lengths (135) has been overlooked in discussions of resource conflicts (2, 89, 98, 124), but it remains crucial to mutualism stability. Note that the ovipositor lengths of dioecious fig pollinators closely match the first mode of the style length distribution (Figure 3). The inability of dioecious fig pollinators to distinguish between gall and seed figs prior to entering the "tomb blossom" (3, 127), combined with low variability in ovipositor length, effectively prevents pollinators from reaching the second mode of the distribution. Could a mutation for increased variability in ovipositor length result in the breakdown of dioecious pollination, leading to extinction or a shift from dioecy to monoecy in the host fig population? Phylogenetic analyses of evolutionary sequences are equivocal in this respect (159).

Possible explanations for the origin and maintenance of dioecious fig pollination include seasonality, vicarious selection, and escape from parasitoids (4, 67, 102, 104, 162). Kjellberg et al. (104) argued that seasonal reproductive phenology could reduce or eliminate the opportunity for pollinators to choose between gall figs and seed figs. Alternatively, Grafen & Godfray (67) proposed "vicarious selection" to describe the situation in which seed figs act as the agent of selection on wasps in gall figs. They argued that the external similarities of the two types maintain mutualism stability, and the few data available tend to support their view (162). Choice experiments have shown no preference for gall figs in spite of the failure of founders to reproduce in seed figs (127, 162). These pollinators are capable of selecting a unique host from a range of closely related species in sympatry, presumably through olfactory cues released from figs during the period of receptivity (93), and yet they cannot distinguish between gall figs and seed figs of the same species. Thus, the simplest explanation for dioecious fig pollination is pollinator deception, with selection favoring seed figs that mimic gall figs in attractiveness

(67). Patel et al. (127) pointed out that it would be difficult to detect less stable interactions because the evolution of a gall fig preference in pollinators would rapidly drive hosts to extinction. However, dioecious fig lineages are more diverse than monoecious lineages (160), perhaps indicating that dioecious figs are no less prone to extinction than their monoecious relatives.

Kerdelhué & Rasplus (102) argued that the evolution of dioecy in figs might reduce the incidence of nonpollinators. Assuming that nonpollinators compete for fig ovaries and that competitive displacement favors the partitioning of resources according to the position of fig ovaries, they attributed lower numbers of nonpollinating species in dioecious figs compared with monoecious figs to the absence of multiple ovary layers in gall figs. The fact that nonpollinators waste time probing seed figs (162), however, suggests a more direct advantage of dioecy than that based on the partitioning of ovary layers (102). Trapping data suggest that nonpollinators do not distinguish between gall and seed figs in the search for oviposition sites, and thus, time wasted by parasites on seed figs will reduce rates of parasitism in gall figs. A model of pollinator production suggests that, with the evolution of dioecy, the male component of plant fitness could rise through increased pollinator production (162). A model of the monoecious resource conflict suggests that gains in male fitness through pollinator production would be offset by losses in female fitness through the consumption of seeds by pollinators (94). However, a reduction in parasitism through dioecy is advantageous for the pollinator and for the host plant in both fitness components. Parasitism, therefore, may have played a role in the origin and maintenance of dioecious fig pollination (102).

Molecular Evolution

Indirect comparisons suggest that rates of nucleotide substitution are several times faster in pollinators than in their hosts (159). An obvious explanation for this pattern is generation time. Fig trees reproduce over a period of decades, whereas their pollinators can undergo several generations per year, depending on the phenology of their host (95), and this implies a large difference in generation time. Inbreeding remains a weak explanation for the difference between evolutionary rates of evolution in figs and pollinators. There is a high probability of mating between sibling pollinators given that founders are few and that mating is restricted to the natal fig (81). Machado (111) showed that inbreeding, as estimated by the proportion of single foundress broods, is negatively correlated with levels of intraspecific variability in mitochondrial DNA. Although inbreeding reduces genetic variation among wasps within a fig, the abundance of figs in a population ought to minimize the effect of drift. Estimates of fig genetic diversity based on allozymes are high, which suggests that effective population sizes are rather large (121, 122). Whether differences in generation time or the breeding structure of fig and pollinator populations could contribute to differences in evolutionary rates is an intriguing area for future research. The most promising avenue for testing such hypotheses in the fig and pollinator mutualism is to examine rates of change at

comparable gene loci, such as the alcohol dehydrogenase genes of cospeciating lineages.

Molecular branch length comparisons (159) suggest that speciation in pollinators may have preceded speciation in figs, possibly owing to higher rates of local adaptation in pollinators compared with their hosts. Michaloud et al. (115) proposed modes of speciation in the fig/pollinator mutualism based on deviations from one-to-one specificity in natural populations, and the most common pattern involves the geographic isolation of two pollinator species across the range of a single host species (29, 175). In addition, reproductive isolation depends primarily on host choice, namely, the behavioral response of pollinators to volatile fig attractants (93, 152, 156, 157). Local adaptation in host choice by allopatric populations of rapidly evolving pollinators could lead to the reproductive isolation and subsequent divergence of more slowly evolving fig populations. An alternative explanation, that preemptive speciation is due to differences in dispersal rates (138), is not supported by genetic studies, indicating that pollinators are capable of traveling great distances (121, 122). In any event, the overall phylogenetic patterns are consistent with a geographical model of diversifying coevolution.

Asymmetry in the evolutionary rates of fig and pollinator lineages also has implications for reciprocal adaptation and the maintenance of evolutionary conflicts. In a simple model of gene-for-gene coevolution, change in a gene for host exploitation selects for a response in a resistance gene. In the case of figs and pollinators, unequal rates of change in the genes involved in resource conflicts could lead to extinction or a shift from mutualism to parasitism. For example, suppose that the resource tradeoff is regulated by the coadaptation of a pollinator gene for ovipositor length and a fig gene for style length. Evolution of longer ovipositors would increase pollinator fitness, but a corresponding reduction in fig fitness would select for longer styles. Countering the expectation of runaway evolution, style and ovipositor lengths are constrained by the efficiency of flower packing within figs and the time efficiency of oviposition (124). In any event, unequal rates imply that innovation in the host could be challenged rapidly by an evolving pollinator population.

BEYOND FIG WASPS

This review of fig wasp biology has attempted to synthesize recent contributions in the fields of evolution, systematics, and ecology. It is hoped that interdisciplinary approaches in the future will provide new insights on topics ranging from behavioral ecology to molecular phylogenetics. Testing of evolutionary hypotheses is facilitated by the considerable taxonomic and ecological diversity of fig wasps, and comparative phylogenetic studies of fig wasp interactions are now possible. For example, the host specificity of fig pollinators and parasitoids, combined with population genetic data, can now be used to test and refine models of speciation

for host-specific plant-insect interactions in general. Patterns of host utilization also provide the opportunity to understand the resolution of evolutionary conflicts, including resource trade-offs between mutualists and host-parasitoid interactions. A combination of ecological modeling and comparative phylogenetics can further examine the coadaptation of interacting traits, a central theme in evolutionary biology. An especially challenging and exciting question for future research is how patterns of genetic diversity and rates of molecular evolution influence these coevolving interactions.

Future studies should also extend beyond fig wasps to other webs of species interactions (84). For example, an intriguing problem relates to pollination and seed dispersal in dioecious figs. The similar external appearance of both sexes of figs prior to pollination may prevent pollinators from avoiding seed figs, but after pollination, it is advantageous for seed figs to be dispersed by frugivores and for gall figs to protect developing pollinators. Although gall and seed figs appear similar prior to pollination, they ultimately differ in size, coloration and palatability when ripe (158). Indeed, ripe gall figs are often ignored by frugivores that prefer to eat seed figs of the same species, even though gall figs may be larger when ripe (158, 162). Selection favoring gall and seed fig similarity during the pollination phase could be opposed by selection favoring dissimilarity during the dispersal phase. Examining the possibility of opposing selection on fig pollination and dispersal traits is a challenging area for future investigation (109).

Figs also support a diverse assemblage of arthropods, and fig wasp communities should be compared to other groups of phytophagous insects (10). Fig-infesting fruit flies, for example, appear to be relatively host-specific, and multiple species may even compete for resources on the same host (107, 108). However, leaf-chewing (9) and sap-sucking insects (126) show high faunal overlap among sympatric species of *Ficus*. Thus, the fig wasps represent a most extreme example of specialization in the continuum of evolving plant-insect interactions. This degree of specialization is indeed an asset to biological study, and from the many exciting developments of the past decade, we are beginning to understand how to be a fig wasp.

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