Floral Characteristics of *Ficus curtipes* and the Oviposition Behavior of Its Pollinator Fig Wasp

Author(s) :F. P. Zhang, Y. Q. Peng, S. G. Compton, and D. R. Yang

Source: Annals of the Entomological Society of America, 102(3):556-559. 2009.
Published By: Entomological Society of America
DOI: http://dx.doi.org/10.1603/008.102.0328
URL: http://www.bioone.org/doi/full/10.1603/008.102.0328

Floral Characteristics of *Ficus curtipes* and the Oviposition Behavior of Its Pollinator Fig Wasp

F. P. ZHANG,[1,2] Y. Q. PENG,[1] S. G. COMPTON,[3] AND D. R. YANG[1,4]

Ann. Entomol. Soc. Am. 102(3): 556–559 (2009)

ABSTRACT Fig wasps (Hymenoptera: Agaonidae) can only develop inside the fruit (figs) of fig trees (Moraceae; *Ficus* spp.). Figs are hollow, rounded structures lined on the inside by numerous tiny flowers. To lay their eggs, female fig wasps enter the figs and typically walk around on a platform of stigmas (synstigma) from which they insert their ovipositors through the stigmas and down the styles before reaching the ovules, where they oviposit. Previous studies have described fig wasp oviposition behavior in those *Ficus* species with a synstigma and have related ovipositor lengths to style lengths accordingly. Here, we show that this oviposition pattern is not universal within *Ficus* and that variation in fig architecture leads to the modification of oviposition behavior. Figs of the monoecious Asian fig tree *F. curtipes* and relatives (subsection *Conosycea*) lack a synstigma, which is replaced by an irregular mass of elongate stigmas. The ovipositor of the pollinator *Eupristina* sp. is sufficiently long to reach all the ovules. Despite this, and unlike other fig wasps, they do not oviposit via the top of the stigmas, but insert their ovipositors through the stigmal bases. Oviposition behavior in fig wasps is therefore responsive to variation in floral structure within their host figs.

KEY WORDS morphology, oviposition, stigma, style

The interaction between host-specific pollinating fig wasps (Hymenoptera: Agaonidae) and their host fig trees (Moraceae; *Ficus* spp.) is a striking example of mutualism and coevolution, each needing the other for reproduction (Galil and Neeman 1977, Janzen 1979). Approximately half of *Ficus* species in the world are monoecious, and others are functionally dioecious (Berg 1989, Weiblen 2000). In monoecious species, both male and female flowers develop within the same fruit, and each fig produces seeds, pollen, and fig wasps (Wiebes 1979, Ganeshaiah et al. 1995, Weiblen 2002, Jousselin et al. 2003). In dioecious species, there are two types of trees: "female" trees that have figs containing only female flowers, and "male" trees that have figs containing both male and female flowers. Male trees produce wasps and pollen, whereas female trees produce seeds only (Ramirez 1981, Berg 1990, Weiblen and Bush 2002).

Fig wasps cannot develop anywhere except in the ovules that line the inside of figs. After entering a fig via the ostiole, foundress females must reach the ovules to deposit their eggs. The stigmas typically form a more or less continuous layer (the synstigma) that lines the cavity of a fig. The females then insert the ovipositor down the length of the style via the stigma. Successful probing and oviposition are influenced by style length, the shape and length of stigma, the thickness of the style, their insertion point on the ovary, and ovular structure (Verkerke 1986, 1988).

Many studies have investigated the relationship between style length and the ovipositor length of their associated pollinators (Galil and Eisikowitch 1968, Kathuria et al. 1995, Nefdt and Compton 1996, Herre and West 1997), with measurements relating style and ovipositor lengths used routinely to address questions about accessibility of fig flowers for oviposition, and how this relates to the stability of the mutualism. In monoecious species, style length is usually not a limiting factor for oviposition. Even though pollinators may have ovipositors that are long enough to reach most or all of the ovules, the fig wasps still may not occupy them all (Nefdt and Compton 1996, Anstett 2001). The shape of the stigma (through which the ovipositor is inserted) varies between different sections of *Ficus* spp. For examples, in the figs of subgenus *Sycomorus*, the unbranched stigmas are mutually attached, with stigmatic papillae gluing the styles together to provide a well-defined synstigmatic surface, whereas the stigmas are branched in the subgenera *Urostigma* and *Pharmacoscea* (Verkerke 1989).

Pollinator oviposition behavior was first described in detail in the figs of *Ficus sycomorus* L. and involved pollinator wasps inserting their ovipositors through the tops of the stigmas (Galil and Eisikowitch 1968). This behavior is now regarded as the norm among fig wasps, but here we show that the modified stigmal

---

[1] Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, China.

[2] Graduate University of Chinese Academy of Sciences, Beijing, China.

[3] Faculty of Biological sciences, The University of Leeds, Leeds, United Kingdom.

[4] Corresponding author, e-mail: yangdr@xtbg.ac.cn.

0013-8746/09/0556–0559$04.00/0

structure present in some figs can lead to modification in pollinator oviposition behavior.

Materials and Methods

Study Site. The study was carried out in the Xishuangbanna Tropical Botanical Garden (101° 15′ E, 21° 55′ N) located in southwest China and the northern margin of tropical southeast Asia.

Study Species. *Ficus curtipes* Corner belongs to subgenus *Urostigma,* subsection *Conosycea.* This species is widely distributed in China, India, Malaysia, and Thailand. Trees grow up to 5–10 m in height and are epiphytic when young. At Xishuangbanna, this species occurs naturally in tropical forest and is also cultivated commonly in cities and villages as an ornamental tree. *F. curtipes* produces figs in synchronous crops with different trees flowering at different times throughout the year. *F. curitpes* is monoecious, with both male and female flowers developing in the same figs, which are produced in the leaf axils. There is no differentiation into separate seed and gall flowers, and all the female flowers seem capable of producing seed or galls. The developmental cycle of monoecious fig can be divided into five phases, as follows period. In prefemale phase (A-phase), the young figs first occurs as a protrusion in a leaf axil. At female phase (B-phase), the figs have a diameter of 11.76 ± 0.42 mm (mean ± SD; n = 30) and contain female flowers that are ready to be pollinated (receptive). At this stage the female pollinators, aided by their flattened heads (van Noort and Compton 1996), enter into figs through the ostiole. Once inside, the wasps oviposit and pollinate. Each of their larvae develops at the expense of a single ovule. Inter-floral phase (C-phase) is comparatively long, lasting 3–4 mo and is the period when wasp progeny and seeds are developing. At male phase (D-phase), the figs have a diameter of 15.52 ± 0.75 mm (mean ± SD; n = 47), and the seeds and wasps have completed their development. Males emerge from their galls into the fig cavity and mate with the females, which then become loaded with pollen before leaving their natal fig in search of a receptive fig. Postflower phase (E-phase) is the period after the exit of the female wasps. The figs increase in size, soften and become dark red to purplish red. The pollinator is an undescribed species of *Eupristina.*

Tree and Wasp Sampling. Forty-five receptive (female/B-phase) figs from three trees (15 figs per tree) were collected, and 30 florets per fig were sampled at random to measure their style lengths. Style and stigma morphology were also recorded based on observations from 330 figs on 10 trees. *Eupristina* sp. females were collected from figs at the developmental phase when the wasps were emerging (male [D] phase) after separation from their sheaths, and the ovipositors of 37 females were measured under a dissecting microscope. Additional female wasps were allowed to enter female phase figs, which were then cut open to observe the wasps' oviposition behavior. More than 300 female wasps were observed in this way.

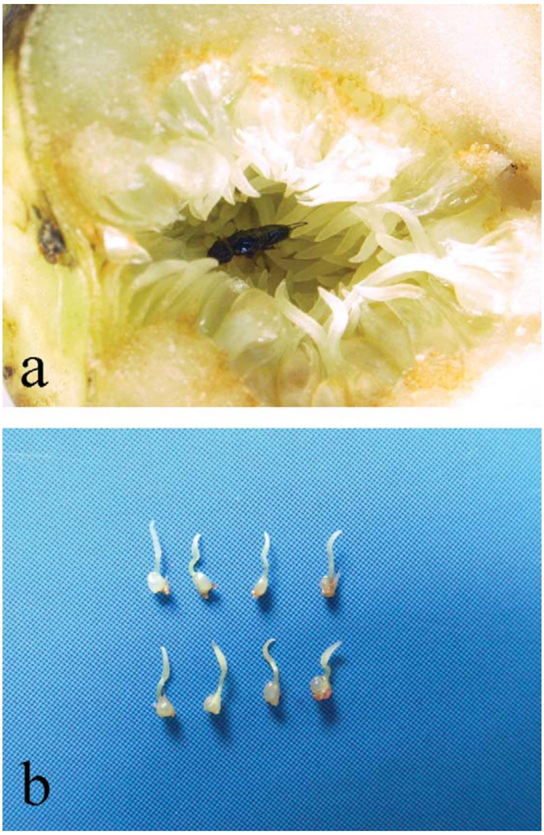

Fig. 1. Inner surface of a receptive fig of *F. curtipes*, with a pollinator female (a) and detail of female florets (b). (Online figure in color.)

Statistical Analysis. A nested analysis of variance was conducted using R 2.7.1 (R Development Core Team 2008). Means ± SD are presented.

Results

Stigmal Morphology and Floral Structure in F. curtipes. The figs of *F. curtipes* differ from previously studied *Ficus* species in both the morphology of the flowers and how they are positioned within the fig. The stigma is elongate, slightly curved, and only slightly broader than the style. They do not unite to form a synstigma (Fig. 1). Male florets are scattered among the female flowers.

Style-Length Ovipositor-Length Comparisons. The mean style length was 0.85 ± 0.25 mm (n = 1,350), with significant differences in style-length among *F. curtipes* trees (F = 921.56, df = 2, $P < 0.001$) and individual figs (F = 3.01, df = 44, $P < 0.001$). Style lengths were almost all shorter than the pollinator ovipositor lengths, which had a mean length of 1.90 ± 0.06 mm (n = 37) (Fig. 2), and they were long enough to reach 99% of the ovules.

Ovipositor Entry Points. Foundress female fig wasps lost their wings and most of their antennae while entering the figs through the ostiole. Once in-

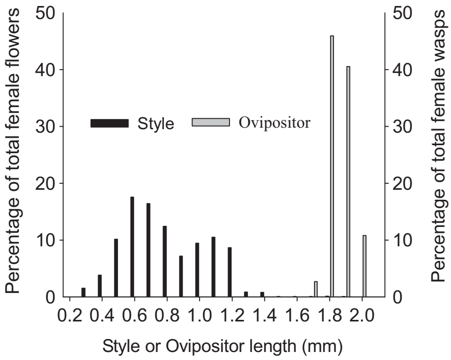

Fig. 2. Style length distribution in *F. curtipes* figs and ovipositor lengths of its pollinator *Eupristina* sp.

side, the wasp walked in the cavity of the fig (Fig. 1) and probed the flowers. The pollinators consistently inserted their ovipositors at the basal incline of the stigmas, part way down the length of the style, rather than at the top of the stigma (Fig. 3).

Discussion

Monoecious fig trees and fig wasps are potentially in conflict over the resources provided by the plant's female flowers, namely, whether the flowers produce seeds or produce wasps. The former represents the plant's female reproductive function, whereas the latter (in the form of pollen-carrying female wasps) reflects the fig's investment in male reproductive function (Herre 1989). The potential conflict arises because only wasp progeny, not seeds, are of direct benefit to ovipositing females, and so for fig wasps, it may be beneficial to use all female flowers in the fig. Several studies have attempted to determine the reasons why the wasps fail to make use of all these flowers (Galil and Eisikowitch 1968, Bronstein 1988, West and Herre 1994, Ganeshaiah et al. 1995, Nefdt and Compton 1996, Jousselin et al. 2004). Several early studies suggested that the balance between wasp and seed production in monoecious *Ficus* species is maintained by fig wasps having short ovipositors, which only allow them access to the ovaries of short-styled flowers (Galil and Eisikowitch 1968, Ramirez 1970, Galil and Neeman 1977, Murray 1985). This was later contradicted by measurements showing that many pollinator wasps have ovipositor lengths longer than the median style lengths of their hosts (Nefdt and Compton 1996). Nonetheless, pollinator wasps often largely or entirely fail to use flowers with long styles (Compton and Nefdt 1990), suggesting that other factors, including stigma structure, may be important (Verkerke 1986, 1988). Studies relating style lengths to ovipositor lengths have consistently assumed that the method of

Fig. 3. Insertion point for oviposition by females of *Eupristina* sp. in *F. curtipes*. (Online figure in color.)

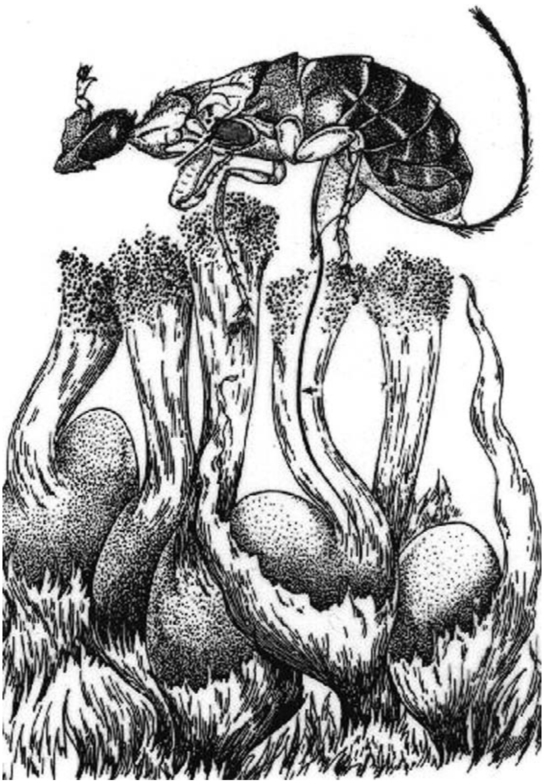

Fig. 4. Ovipositor insertion point in *Ceratosolen arabicus* Mayr, pollinator of *F. sycomorus* (from Galil and Eisikowitch 1968).

oviposition described by Galil and Eisikowitch (1968), with ovipositors inserted through the top of the stigma, is typical for the genus as a whole (Fig. 4). Our studies show that this is not always the case and that, in species such as *F. curtipes*, such comparisons potentially underestimate the numbers of flowers that are accessible for oviposition.

F. curtipes is a typical *Ficus* species, *F. curtipes* differs from other *Ficus* species in lacking well defined synstigma, the platform formed from stigmas on which ovipositing females can walk and oviposit through the tops of the stigmas (Galil and Eisikowitch 1968; Fig. 4). The stigmas of *F. curtipes* are unbranched, elongate, slightly curved, and only slightly broader than the style and because they are not mutually attached, they do not form a synstigma. The lack of a synstigma seems to hinder the pollinators, because ovipositing wasps frequently stumble and fall between different stigmas as they attempt to find oviposition sites. It does, however, allow them to insert their ovipositors at the basal incline of the stigmas, not at the top of stigma as described in other species, which reduces the length of ovipositor that has to be inserted.

In summary, fig wasp probing is not only affected by style length but also by the way that flowers are presented within a fig. Our observations of floral structure in five other *Conosycea* species (*Ficus glaberrima* Blume, *Ficus benjamina* L., *Ficus microcarpa* L., *Ficus stricta* Miquel, and *Ficus maclellandii* King) show that they also lack a synstigma, suggesting that the oviposition behavior present in *F. curtipes* is likely to be widespread among this group of fig trees.

Acknowledgments

We thank J. Y. Zhang for assistance. This study was funded by the Chinese Natural Science Foundation (30571507, 30670358) and KSCX2-YW-Z-003.

References Cited

Anstett, M. C. 2001. Unbeatable strategy, constraint and coevolution, or how to resolve evolutionary conflicts: the case of the fig/wasp mutualism. Oikos 95: 476–484.

Berg, C. C. 1989. Classification and distribution of *Ficus.* Experientia 45: 601–611.

Berg, C. C. 1990. Reproduction and evolution of *Ficus* (Moraceae): traits connected with the adequate rearing of pollinators. Mem. N Y Bot. Gard. 55: 169–185.

Bronstein, J. 1988. Mutualism, antagonism, and the fig-pollinator interaction. Ecology 69: 1298–1302.

Compton, S. G., and R.J.C. Nefdt. 1990. The figs and fig wasps of *Ficus burtt-davyi.* Mitt Inst. Allg. Bot. Hamburg 23: 441–450.

Galil, J., and D. Eisikowitch. 1968. On the pollination of *Ficus sycomorus* in East Africa. Ecology 49: 259–269.

Galil, J., and G. Neeman. 1977. Pollen transfer and pollination in the common fig (*Ficus carica* L.). New Phytol. 79: 163–171.

Ganeshaiah, K. N., P. Kathuria, and R. V. Shaanker. 1995. Evolution of style-length variability in figs and optimization of ovipositor length in their pollinator wasps: a coevolutionary model. J. Genet. 74: 25–39.

Herre, E. A. 1989. Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. Experientia 45: 637–647.

Herre, E. A., and S. A. West. 1997. Conflict of interest in a mutualism: documenting the elusive fig-wasp-seed tradeoff. Proc. R. Soc. Lond. B 264: 1501–1507.

Janzen, D. H. 1979. How many parents do the wasps from a fig have? Biotropica 11: 127–129.

Jousselin, E., F. Kjellberg, and E. A. Herre. 2004. Flower specialization in a passively pollinated monoecious fig: a question of style and stigma. Int. J. Plant Sci. 165: 587–593.

Jousselin, E., M. Hossaert-McKey, and E. A. Herre. 2003. Why do fig wasps actively pollinate monoecious figs? Oecologia (Berl.) 134: 381–387.

Kathuria, P., K. N. Ganeshaiah, R. U. Shaanker, and R. Vasudeva. 1995. Is there a dimorphism for style lengths in monoecious figs? Curr. Sci. 68: 1047–1050.

Murray, M. G. 1985. Figs (*Ficus* spp.) and fig wasps (Chalcidoidea: Agaonidae): hypotheses for and ancient symbiosis. Biol. J. Linn. Soc. 26: 69–81.

Nefdt, R.J.C., and S. G. Compton. 1996. Regulation of seed and pollinator production in the fig-fig wasp mutualism. J. Anim. Ecol. 65: 170–182.

R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http://www.R-project.org).

Ramirez, B. W. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24: 680–691.

Ramirez, B. W. 1981. Evolution and the monoecious and dioecious habit in *Ficus* (Moraceae). Brenesia 18: 207–216.

van Noort, S., and S. G. Compton. 1996. Convergent evolution of Agaoninae and Sycoecinae (Agaonidae, Chalcidoidea) head shape in response to the constraints of host fig morphology. J. Biogeogr. 23: 415–424.

Verkerke, W. 1986. Anatomy of *Ficus ottoniijolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. Proc. K. Ned. Akad. Wet. 89: 443–469.

Verkerke, W. 1988. Sycone morphology and its influence on the flower structure of *Ficus sur* (Moraceae). Proc. K. Ned. Akad. Wet. 91: 319–344.

Verkerke, W. 1989. Structure and function of the fig. Experientia 45: 612–621.

Weiblen, G. D. 2000. Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. Am. J. Bot. 87: 1342–1357.

Weiblen, G. D. 2002. How to be fig wasp. Annu. Rev. Entomol. 47: 229–230.

Weiblen, G. D., and G. L. Bush. 2002. Speciation in fig pollinators and parasites. Mol. Ecol. 11: 1573–1578.

West, S. A., and E. A. Herre. 1994. The ecology of the New World fig-parastizing wasps *Idarnes* and implications for the evolution of the fig pollinator mutualism. Proc. R. Soc. Lond. B 258: 67–72.

Wiebes, J. T. 1979. Coevolution of figs and their insect pollinators. Annu. Rev. Ecol. Syst. 10: 1–12.

Received 10 August 2008; accepted 10 November 2008.