A Key To Subgroups Of Dioecious* (Gynodioecious) Figs Based On Fig Wasp/Male Syconium Pollination Patterns

by Wayne P. Armstrong & Steven Disparti (4 April 1998)

E-Mail Professor Armstrong: mrwolffia@waynesword.net

Also See Evolution Of Dioecious Figs

1A. Wasp pollination purposive (i.e. deliberately collecting & transferring pollen).....**2A**

1B. Wasp pollination passive (i.e. not deliberately collecting & transferring
pollen).....**5A**

2A. Exit through ostiole of male syconium. [from 1A]
.....**3A**

2B. Exit through tunnels in syconium wall cut by male wasps. [from 2A]
.....**4A**

3A. Female wasps with pollen baskets.** [from 2A]
-------**Subgenus Sycomorus (some spp.); Subgenus Ficus, Section Sycidium**.

3B. Female wasps without pollen baskets (i.e. pack pollen into intersegmental folds on body)-----**We Have Found No Examples Of This Method**.***

4A. Female wasps with pollen baskets. [from 2B]
-------**Subgenus Urostigma (most species)**. [Only Group That "Fits" Vicarious Selection Example In Chapter 10 of Dawkin's **Climbing Mount Improbable**.]

4B. Female wasps without pollen baskets. [from 4A] [See Also 6B]
-------**Subgenus Urostigma (some spp.); Subgenus Pharmacosycea, Sect. Pharmacosycea** [**The Authors Are Not Certain Whether Pollination In These Groups Is Purposive Or Whether It Is Passive**.]********

5A. Female wasps with pollen baskets. [from 1B]
-------**We Have Found No Examples Of This Method**.

5B. Female wasps without pollen baskets [from 5A] **6A**

6A. Exit through ostiole of male syconium. [from 5B]
-------**Subgenus Ficus, Section Ficus, Subsection Ficus, Series Cariceae, Erythrogyneae & Podosyceae**. [**This Is Pattern Of Common Edible Fig**.]

6B. Exit through tunnels cut by male wasps. [from 6A]
-------**Subgenus Urostigma (some spp.); Subgenus Pharmacosycea, Sect. Pharmacosycea**. [**The Authors Are Not Certain Whether Pollination In These Groups Is Passive Or Whether It Is Purposive**]********

*****Gynodioecious: Fig species with male and female trees in the population. Male trees (caprifigs) bear "male" syconia containing pollen-bearing male flowers and

short-style female flowers. The ovaries of short-style female flowers often contain a male or female wasp larva if eggs were oviposited inside them. Female trees only bear female syconia containing seed-bearing long-style female flowers and no male flowers. About half the world's 1000+ fig species are gynodioecious, the other half being monoecious with male flowers, short-style and long-style female flowers in the same syconium (i.e. without separate male and female trees).

** Pollen Basket = Pollen-Collecting Device: A specially-adapted collective cavity or bristles on female wasp where pollen is purposively deposited before leaving the male (caprifig) syconium. [We are using a broad definition here--including coxal and sternal corbiculae, and other pollen-holding devices on the body of female wasps.]

*** Based on all the references we have consulted thus far in our research.

**** It seems more likely that pollination in wasps without any pollen baskets or special pollen-collecting devices is passive rather than purposive. [Whether female wasps would deliberately dust their bodies with pollen or pack pollen into their intersegmental folds remains an enigma.]

Other WAYNE'S WORD Articles About Figs And Their Wasps:

- **Gall Flowers In Figs**
- **The Fig/Fig Wasp Relationship**
- **Sexuality In Figs And Other Flowering Plants**
- **Figs Of The Holy Land (Their Role In World Religions)**

Evolution Of Dioecious Figs

According to Carole Kerdelhue and Jean-Yves Rasplus (**Oikos** Vol. 77: 163-166, 1996), dioecious figs may have evolved from monoecious ancestral fig species due to selection pressure by non-pollinator fig wasps. Although these non-pollinator wasps belong to the same Order Chalcidoidea as pollinators, many of them belong to different families. They do not benefit the fig and may even be harmful--especially when they compete with and/or parasitize the beneficial pollinator wasps.

Monoecious syconia of **Ficus sur** contain long-style and short-style female flowers densely packed together in a layer that lines the inner cavity of the syconium. Although the styles all form a relatively continuous stigmatic layer called a synstigma (i.e. all stigmas in the same plane) within the syconium, the ovaries may be deep or shallow relative to the synstigma depending on the length of their flower stalks (pedicels). Generally, the deep-seated ovaries (on short pedicels) with long styles each contain a seed, while the shallow ovaries (on long pedicels) with short styles each contain a wasp larva. A pollinator wasp walking on this "bed" of styles (synstigma) can insert her ovipositor down the short style and easily penetrate the ovary where she lays an egg. The deep-seated, long-style ovaries are out of reach for her ovipositor (style longer than her ovipositor), and consequently these ovaries develop seeds rather than wasp larvae.

Because of intermediate style lengths (between long and short) and different ovary heights due to the length of flower stalks (pedicels), the ovary position of female flowers in monoecious fig syconia often forms a stratification. According to Kerdelhue and Rasplus (1996), there are at least 4 different ovary layers occupied by beneficial (pollinator) and non-beneficial and/or harmful non-pollinator wasps. These layers are listed according to their position (depth) from the stigmatic surface (synstigma) within the syconial cavity. See the following Figure 1:

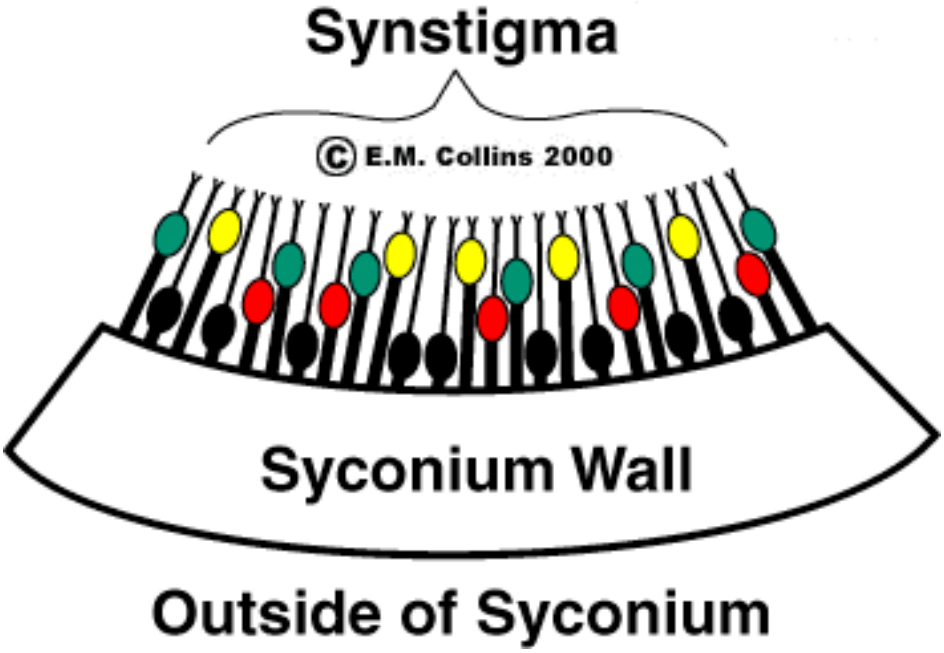

Figure 1. Heterostyly and four ovary layers (stratification) within the syconium of a monoecious fig (**Ficus sur**). (1) Yellow: The most shallow ovaries (near surface) with shortest styles which typically contain a pollinator wasp larva; (2) Green and (3) Red: Slightly deeper ovaries that typically contain non-pollinator wasp larvae; (4) Black: The deepest ovaries with longest styles that typically bear mature seeds.

1. The shallow ovary layer of short-style flowers (yellow ovaries in Figure 1) are mostly occupied by larvae of wasps that oviposit from the synstigma within the syconium cavity, including **Ceratosolen** (pollinator) and **Sycophaga** (non-pollinator gall-maker), and by their parasitic wasp larvae (parasitoids or inquilines).

2. A second slighter deeper ovary layer (green ovaries in Figure 1) includes the wasps of layer 1 (above) plus some additional gall-makers which lay eggs from the outside (**Apocryptophagus**).

3. A third deeper ovary layer (red ovaries in Figure 1) produces a few seeds and provides shelter and food (galled endosperm tissue) for mainly **Apocryptophagus** and a few **Sycophaga** individuals.

4. A fourth, deepest ovary layer (black ovaries in Figure 1) produces mostly seeds and some wasps, including some **Sycophaga** and a few **Apocryptophagus**.

If the non-pollinating wasps are very numerous, the medium layers 1 and 2 (yellow and green ovaries) will be occupied entirely by exploiters and these occupied flowers will not produce seeds or pollinator wasps. According to Kerdelhue and Rasplus (1996), this probably represents a high cost to the fig with regard to seed production.

Conclusions:

Although fig syconia are often occupied by a single species of symbiotic, mutualistic pollinator wasp (Family Agaonidae), there may be several-many other species of non-pollinator wasps competing in the same crowded syconium. Some of these non-pollinators oviposit within the syconium cavity (from the synstigma), while others (with extra-long ovipositors) can oviposit through the syconium wall from the outside. Some of these non-pollinators induce gall formation within the short-style flowers, and some lay eggs that hatch into larvae which parasitize the larvae of beneficial pollinator wasps.

If the non-pollinators are very successful and literally outnumber the pollinators, this could be very disadvantageous to the fig tree. Fewer pollinator adults would be released to pollinate receptive fig syconia, resulting in fewer seeds in these syconia when they are ripe. Because of the reduced (or lack of) flower stratification in the male and female syconia of dioecious figs, fewer species of non-pollinator wasps can survive in these syconia (i.e. fewer niches for these species). Herein lies the adaptive advantage of dioecy in figs (dioecious fig species).

Dioecious fig syconia have essentially 2 ovary positions, deep-seated ovaries with long styles in female syconia (on female trees) and shallow ovaries with short styles in male syconia (on male trees). The dioecious syconia contain fewer competing species of non-pollinator wasps, resulting in a higher percentage of adult pollinator wasps emerging from the short-style flowers of male syconia and more mature seeds in the long-style flowers of female syconia. See Figure 2 below:

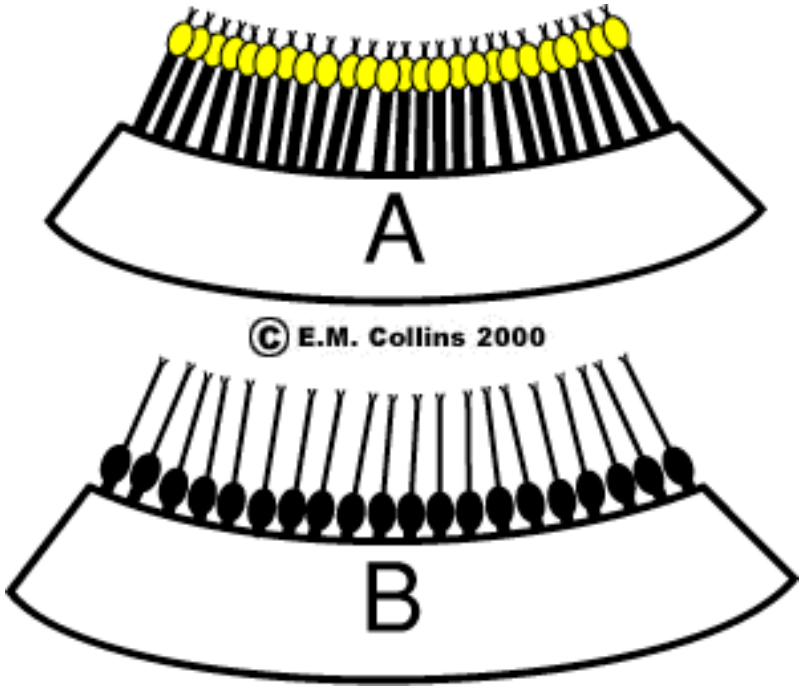

Figure 2. A. Short-style female flowers inside male syconium of dioecious fig. [male flowers also occur in this syconium.] B. Long-style female flowers inside the female syconium of dioecious fig. These syconia do not have the intermediate ovary positions of monoecious figs, and they do not harbor all the non-pollinator wasp species of monoecious figs.

According to Kerdelhue and Rasplus (1996), non-pollinator, parasitic wasps never occur in the long-style flowers of female syconia of female trees, and non-pollinator gall-makers are uncommon in the male syconia of male trees. Therefore, seed production in female syconia and pollinator wasp production in male syconia are not diminished as in the syconia of monoecious figs with stratified ovaries containing all of the non-pollinator wasp species. In addition, no gall-makers that lay eggs through the syconium wall (after pollination by pollinator wasps) have ever been found so far in dioecious figs. For the fig, having separate male and female trees (bearing male or female syconia) in the population may have a distinct adaptive advantage with regard to pollination and seed production.

References:

1. Bronstein, J.L. 1991. "The Non-Pollinating Wasp Fauna of **Ficus pertusa**: Exploitation or Mutualism?" **Oikos** 61: 175-186.

2. Bronstein, J.L. 1988. "Mutualism, Antagonism, and the Fig-Pollinator Interaction. **Ecology** 69: 1298-1302.

3. Dawkins, R. 1996. **Climbing Mount Improbable**. W.W. Norton & Company, New York.

4. Galil, J. 1977. "Fig Biology." **Endeavor** 1: 52-56.

5. Grafen, A. and H.C.J. Godfray. 1991. "Vicarious Selection Explains Some Paradoxes in Dioecious Fig-Pollinator Systems." **Proc. R. Soc. Lond.** 245: 73-76.

6. Kerdelhue, C. and J.-Y. Rasplus. 1996. "The Evolution of Dioecy Among **Ficus** (Moraceae): An Alternative Hypothesis Involving Non-Pollinating Fig Wasp Pressure on the Fig-Pollinator Mutualism." **Oikos** 77: 163-166.

7. Nefdt, R.J.C. and S.G. Compton. 1996. "Regulation of Seed and Pollinator Production in the Fig-Fig Wasp Mutualism. **Journal of Animal Ecology** 65: 170-182.

8. Ramirez, B.W. 1977. "A New Classification of **Ficus**." Ann. Missouri Bot. Garden 64: 296-310.

9. Ramirez, B.W. 1980. "Evolution of the Monoecious and Dioecious Habit in **Ficus** (Moraceae). **Brenesia** 18: 207-216.

10. Verkerke, W. 1989. "Structure and Function of the Fig." **Experientia** 45: 612-622.


Return To The WAYNE'S WORD Home Page


Return To The NOTEWORTHY PLANTS Menu


See Another WWW Site By Mr. WOLFFIA