Sex Determination & Life Cycle Of Ficus carica

Sex Determination In Ficus carica:

The common fig (**Ficus carica**) is a gynodioecious species with bisexual trees (functional male caprifigs) and unisexual female trees. Sex determination is quite unlike other dioecious species, such as willows, marijuana, fruit flies and people.

Contrary to many authors, sex determination in **Ficus carica** is **NOT** the XX/XY method suggested for mosses, cottonwoods and willows (and the method in most people and fruit flies). According to Condit (1969), the sporophyte chromosome number for most species of **Ficus** is 2n = 26. Storey (1977) also confirms this number for **F. carica**, and states that the chromosome-bearing sex-determining alleles are indistinguishable (at least by shape and size).

Sex determination in the common fig (**Ficus carica**) may be controlled by two pairs of alleles located on one pair of homologous chromosomes. Data from breeding experiments support this hypothesis. [From Storey, W.B. 1975. **Figs** (pp. 568-589). In: **Advances in Fruit Breeding**, Purdue University Press, West Lafayette, Indiana.]

G = dominant allele for short-style female flowers
g = recessive allele for long-style female flowers
A = dominant allele for production of male flowers
a = recessive allele for suppression of male flowers

Dominant G & A genes linked on one chromosome.
g & a genes linked on homologous chromosome.

Caprifig genotypes: Homozygous GA/GA and heterozygous GA/ga.
Female fig (edible fig) genotype: Homozygous ga/ga ONLY.

The following table shows all the possible crosses between homozygous (GA/GA) & heterozygous (GA/ga) male caprifigs with homozygous (ga/ga) female figs. Possible types of gametes from parents are indicated within brackets [ ], and the sex and genotypic ratio of progeny are shown in blue:

Seed Parents	Pollen Parents	
	Homo Caprifig (GA/GA) [GA] only	Hetero Caprifig (GA/ga) [Ga] and [ga]
Homo Caprifig (GA/GA) [GA] only	All GA/GA Male	1/2 GA/GA Male 1/2 Ga/ga Male
Hetero Caprifig (GA/ga) [Ga] and [ga]	1/2 GA/GA Male 1/2 Ga/ga Male	1/4 GA/GA Male 1/2 Ga/ga Male 1/4 ga/ga Female
Female Fig (ga/ga) [ga] only	All Ga/ga Male	1/2 Ga/ga Male * 1/2 ga/ga Female *

*** = Most likely genotypic combination.**

Both long-style and short-style ovaries are fertile and occasionally "less-likely" seeds may develop inside the pollinated short-style ovaries of the caprifig (if there are no wasp larvae to consume the seed tissue inside). According to Rixford (1918) and Condit (1947), fertile seeds are commonly found in the mammoni crop, up to 75 seeds per syconium. According to Valdeyron and Lloyd (**Evolution** 33, 1979), caprifig syconia seldom contain more than 10 seeds. The seeds result from pollination by wasps from the profichi crop, and from ovaries in which the wasps failed to oviposit. A caprifig seed parent is the only way to obtain homozygous caprifig offspring (GA/GA). When crossed with female trees, homozygous caprifig pollen parents yield 100% heterozygous caprifig offspring (GA/ga).

Of all the 11 possible genotypic progeny (see above table), only two (1/4 ga/ga and 1/2 ga/ga) result in female trees. If you eliminate the "less likely" homozygous pollen parents (GA/GA) and the "less likely" caprifig seed parents (GA/GA and GA/ga), there would be a 50/50 ratio of zygotic combinations resulting in heterozygous caprifigs and homozygous female trees (1/2 GA/ga and 1/2 ga/ga). [See genotypes with asterisk in lower right box of above table.] In wild populations of the Mediterranean region, caprifig and female trees

occur in similar frequencies (Valdeyron and Lloyd, 1979).

According to Storey (**Recent Advances in Fruit Breeding**, 1975), all commercial caprifigs probably originated from common edible fig seeds (from female (ga/ga) trees) and, therefore, are heterozygous (GA/ga). According to Condit (1920), cuttings of Smyrna figs and caprifigs were introduced into California in 1882. The fruit from these trees all dropped because of the lack of caprification. In 1890 caprifig cuttings with wasp-bearing syconia were also introduced. It is impossible to be certain if any of these caprifigs were homozygous. Naturalized female trees that have been pollinated develop syconia that are conspicuously pinkish-red inside, with numerous drupelets (endocarps) containing viable seeds.

Hypotheses Regarding Sex Ratio Of Naturalized Wild Figs (Ficus carica) In San Diego County:

Why Do Male Caprifigs Outnumber Female Trees?

1. The apparent increase in male caprifigs in wild (naturalized) populations (e.g. creeks and riverbeds in the Vista area of northern San Diego County) may be due (in part) to chance caprifig seed parents giving rise to more caprifig (GA/GA and GA/ga) zygotic combinations. To test this hypothesis, caprifig syconia (mammoni crop) from naturalized populations should be studied in order to determine their percentage of viable seeds. If the original naturalized figs were caprifigs (rather than female trees), and if they were the seed **AND** pollen parents, this would most certainly favor caprifig progeny (regardless of whether they were homozygous or heterozygous caprifig parents).

2. It might also be that some of the original or present-day caprifigs in the Vista area (northern San Diego County) are homozygous (GA/GA) and would always give rise to caprifig offspring.

3. Many of the closely-spaced caprifigs in Vista populations may have originated asexually from adventitious stems.

4. There may be selective survival factors limiting the female trees. (i.e. caprifigs may survive better in wild, naturalized locations).

5. Another plausible explanation has been suggested by Boris Igic of the UCSD Department of Biology. A study by Professor J.R. Kohn of UCSD has shown that inbreeding depression affects sex ratios (**Nature** 335: 431-433, 1988). Self-pollinated populations of hermaphroditic caprifigs may not suffer negative effects from inbreeding depression. They may actually survive and multiply faster than unisexual female trees.

This hypothesis certainly deserves further research, particularly with respect to caprifig populations.

Fig Cultivation Predates Cereal Domestication

Krislev, M.E., Hartmann, A. and O. Bar-Yosef. 2006. "Early Domesticated Fig in the Jordan Valley." Science 312 (5778): 1273-1275. 2 June 2006

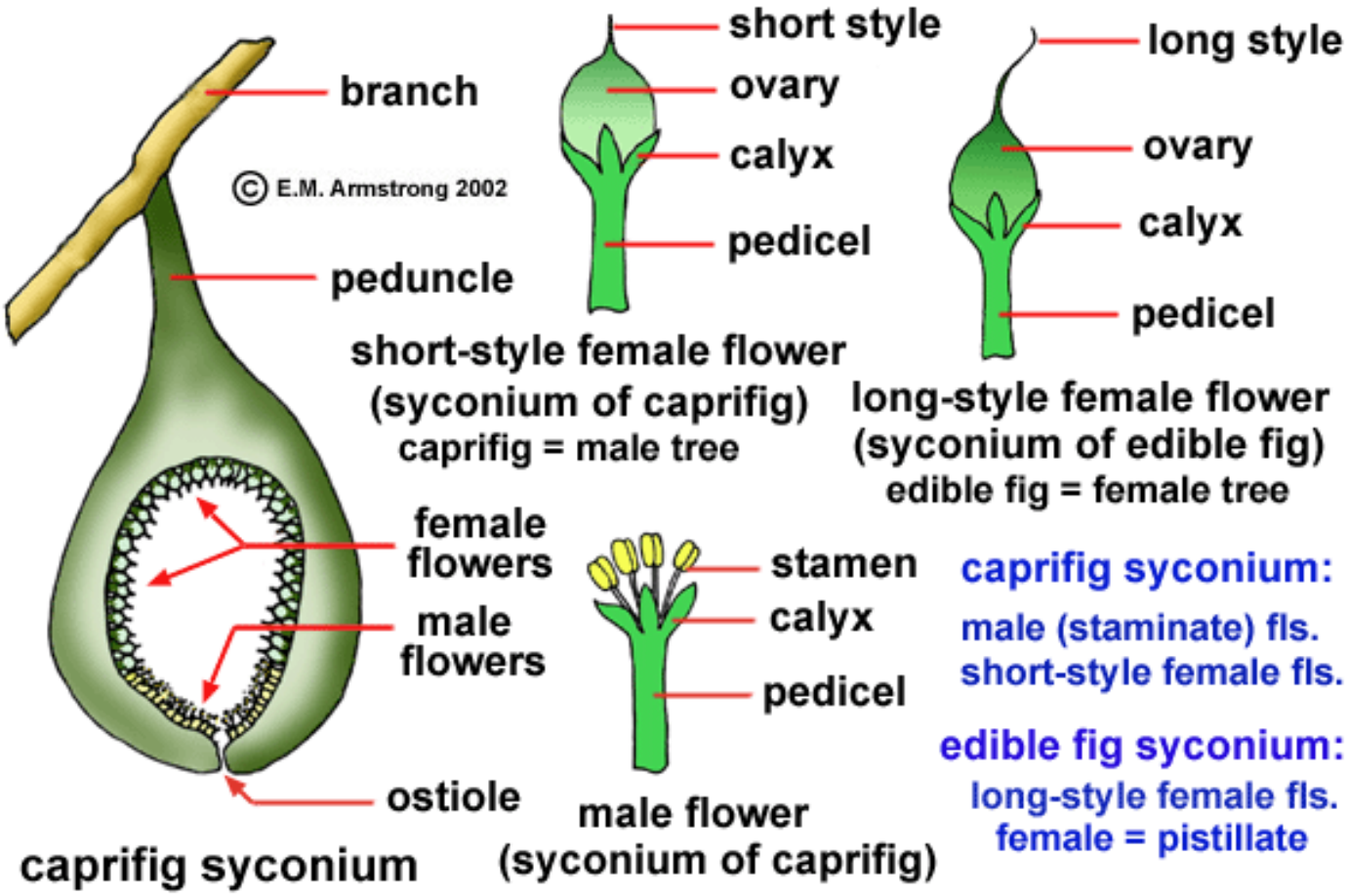
The remains of parthenocarpic fig syconia (edible figs) have been discovered in archeological sites of the Jordon Valley that date back to 11,400 years bp. The carbonized syconia are clearly parthenocarpic because the drupelets are without embryos or seeds. Wild populations of Ficus carica are gynodioecious with male trees (caprifigs) and female trees. Edible figs are produced on female trees only if they are pollinated by fig wasps (Blastophaga psenes) from the syconia of male trees. The male syconia contain wasps and pollen, and are generally not eaten. They were named "caprifigs" because they were commonly fed to goats. If pollinated, seeds develop inside the druplets within syconia on female trees. Without pollination, the immature figs are shed by the female trees. Parthenocarpy is produced by a single domant mutant gene. Female trees expressing this gene retain their developing figs to maturity, even though they are not pollinated and contain no seeds. Parthenocarpic trees must be propagated by cuttings because they do not produce seeds. They produce sweet fig fruits without the need for male trees that carry symbiotic fig wasps within their syconia. This is very advantageous to farmers in regions where the wild caprifigs and natural pollinator wasps do not occur. The presence of parthenocarpic figs in ancient settlements indicates that people recognized these rare parthenocarpic trees and propagated them by planting branches. Evidence of such activity may mark one of the earliest forms of agriculture. Fig trees could have been the first domesticated plant of the Neolithic Revolution, which preceded cereal domestication by about 1,000 years.

Summary Of The Ficus carica Life Cycle:

1. **Syconium**: Complex inflorescence (flower cluster) consisting of hollow, fleshy structure (peduncular tissue) lined on the inside with numerous tiny unisexual flowers. The ripe syconium is **NOT** a true fruit in the strict botanical sense, it is actually a fleshy, flask-shaped, modified stem lined on the inside with many tiny one-seeded fruits (drupelets). [It Is Also Called A Multiple Fruit]

See Several Syconia Of The Male Caprifig Female Syconium Packed With Long-Style Flowers

2. **Ficus carica** has 2 sexual forms, the "male" caprifig and female tree (edible fig). The caprifig is monoecious [i.e. with separate male (staminate) flowers and separate female (pistillate) flowers. It is functionally male because it produces pollen. Edible figs contain only long-style female flowers. Since functional male trees are hermaphroditic, **Ficus carica** is usually considered gynodioecious rather than dioecious.



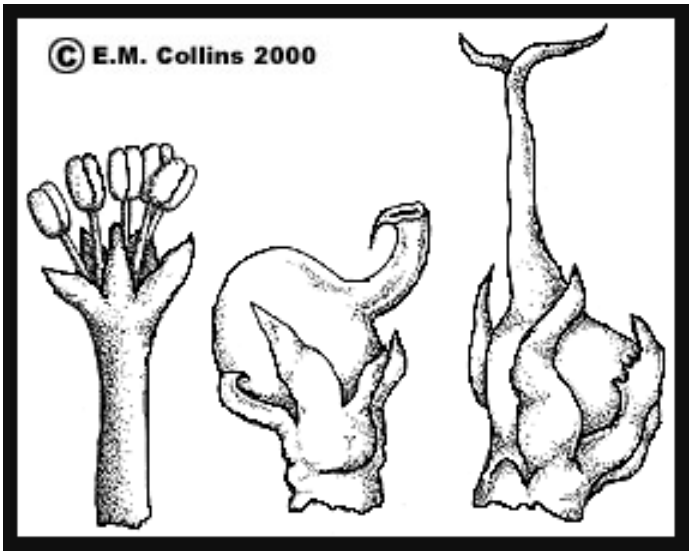
3. Short-style female flowers and male flowers are determined by a pair of dominant genes on the same chromosome [GA]; recessive alleles result in long-style female flowers and suppression of male flowers [ga]. The caprifig may be homozygous [GA/GA] or heterozygous [GA/ga], while the female tree must be homozygous recessive [ga/ga].

4. Caprifigs are native to Caria, an ancient region of Asia Minor between the Black Sea and Mediterranean Sea. This is essentially the present-day region of Turkey. The prefix **capri** refers to goat, and apparently caprifigs were fed to livestock. Old World gynodioecious figs belong to the Subgenus Ficus. Other fig species of tropical and subtropical regions belong to different subgenera, including many ornamental figs such as

the rustyleaf fig (**F. rubiginosa**), Moreton Bay fig (**F. macrophylla**), Indian laurel fig (**F. microcarpa**), benjamin fig (**F. benjamina**), sycomore fig (**F. sycomorus**), Indian rubber tree (**F. elastica**), the Bo tree (**F. religiosa**) and many other species. The latter species are monoecious, with male flowers, short-style female flowers and long-style female flowers all in the same syconium. At least 1,000 different species of **Ficus** are known, all with their own "in house" pollinator wasp. Some fig species have more than one species of wasp. Some tropical fig trees, including F**. rubiginosa**, **F. benjamina** and **F. bengalensis** become "banyans" and "stranglers" in their native habitats.

See Pollination Patterns In Dioecious Figs

5. Fig flowers have no petals and are characteristic of the Mulberry Family (Moraceae) and the closely-related Nettle Family (Urticaceae) and Marijuana Family (Cannabaceae).



Minute flowers from the dioecious syconia of the common edible fig (**Ficus carica**). Left, male flower showing 5 stamens protruding from bract-like calyx. Center and right, short and long-style female flowers consisting of a single pistil protruding from bract-like calyx. The long-style female flowers are produced in syconia on separate "female" trees, while the male flowers and short-style female flowers are produced in syconia on "male" caprifig trees.

Pollination Of The Male Caprifig:

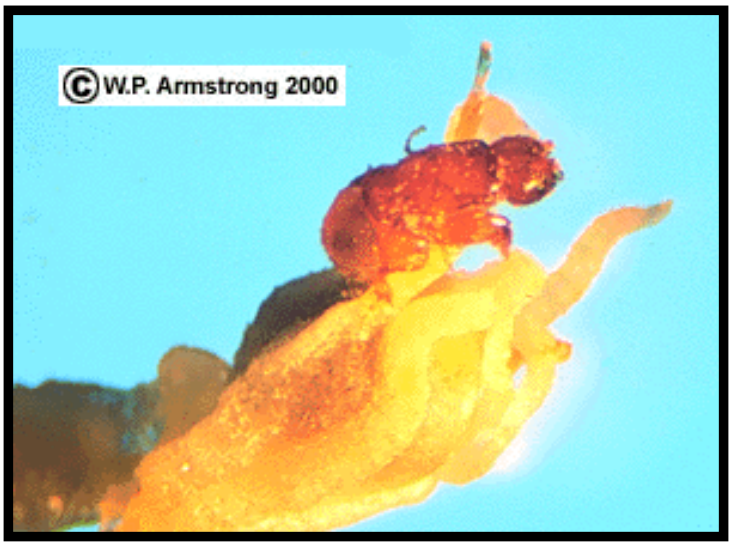
1. Winged female wasp (**Blastophaga psenes**) enters pore (ostiole) and lays an egg

(oviposits) inside each ovary of short-style female flower. She inserts her ovipositor through stylar canal into ovary of flower.

2. Wasp eggs hatch into larvae inside the ovaries, one larva per ovary. The larva feeds on the embryo sac tissue (developing endosperm) and the nucellar tissue surrounding the embryo sac, hence no seed is produced.

3. Larvae develop into adult wasps through metamorphosis in about 10-12 weeks. The males chew their way out of their ovary container and then locate female wasps still contained within ovaries of short-style female flowers.

4. **Hymenopteran Orgy Inside Syconium**: The male wasp chews a hole in the ovary containing a female wasp, inserts his long abdomen and inseminates the female inside. He goes from ovary to ovary, mating with females who he never sees and who never see him.



A male fig wasp (**Blastophaga psenes**) mounting a short-style female flower and inserting his long, slender abdomen into a fertilization hole that he cut through the ovary wall to inseminate the female fig wasp inside.

5. The female wasps emerge from their ovary containers and escape through the pore (ostiole) at the end of the syconium. The impenetrable scales that line the ostiole become passable at this crucial time of wasp exodus. Wingless males stay behind and die. Female wasps are dusted with pollen from male flowers as they leave the caprifig syconium. The anthers must mature and release pollen at precisely the right time, 3 months after the female flowers were mature and receptive. This is a classic case of protogyny in which self-pollination within the syconium does not occur.

A profichi caprifig syconium cut open showing mass of stamens protruding from region just below ostiolar scales. When the female wasp exits through to the ostiole she is dusted with pollen from the male flowers. In addition to pollen, these syconia also bear the male and female fig wasps, essentially to the survival and perpetuation of wild populations of **Ficus carica**.

6. Female wasps search for another receptive syconium containing receptive female flowers (with ovaries) to deposit eggs. The ostiole of the young syconium must be passable at this critical time. Soon after it becomes impervious to insect entry. Time is of the essence since the tiny female wasps only live a short time (several days-weeks?).

7. Caprifigs produce 3 crops of syconia per year: the **profichi** which ripen in early summer; the **mammoni** which ripen in fall; and the **mamme** which overwinter on the tree and ripen in spring. Only the ripe profichi crop shed pollen, and these are used to pollinate the smyrna-type (Calimyrna) female figs of commerce. Wasp larvae overwinter in the mamme crop. Some seeds may develop in the mammoni crop in ovaries without larvae.

Caprification: Pollination of Female Fig Via Pollen From Caprifig:

1. Female trees (incl. the Smyrna-type figs such as the Calimyrna) produce 2 crops of syconia annually: a **breba** crop (which ripens in early summer) and a **2nd** or **main** crop which ripens in fall. Smyrna-type figs are homozygous recessive for the **caducous** (early

deciduous) trait [pp] and require pollination in order for the fruit to set. Note: numerous varieties of edible figs are heterozygous for the dominant persistent gene [Pp] and do not require wasp pollination. Since [P] is lethal to the egg receiving it, homozygous dominant offspring [PP] are not possible; caprifigs may be caducous [pp] or persistent [Pp].

Ripe Calimyrna figs grown in northern San Diego County. Minute pollinator wasps (**Blastophaga psenes**) are responsible for fruit set and crunchy seeds which impart a superior nutty flavor to these delicious figs. The wasps overwinter in a nearby caprifig which appears to be **Ficus pseuodocarica**.

2. Calimyrna (California-grown Smyrna-type fig) has no male flowers; therefore it must be pollinated by fig wasp with pollen from the profichi crop of caprifig. The pollen is carried to the immature 2nd or main crop during the receptive stage (early summer).

3. Bags of wasp-filled caprifigs (profichi crop) are stapled in Calimyrna trees (June in California).

4. The emerging gravid female wasps instinctively try to lay their eggs in the most convenient syconium, which in this case are the young receptive 2nd crop of the

Calimyrna.

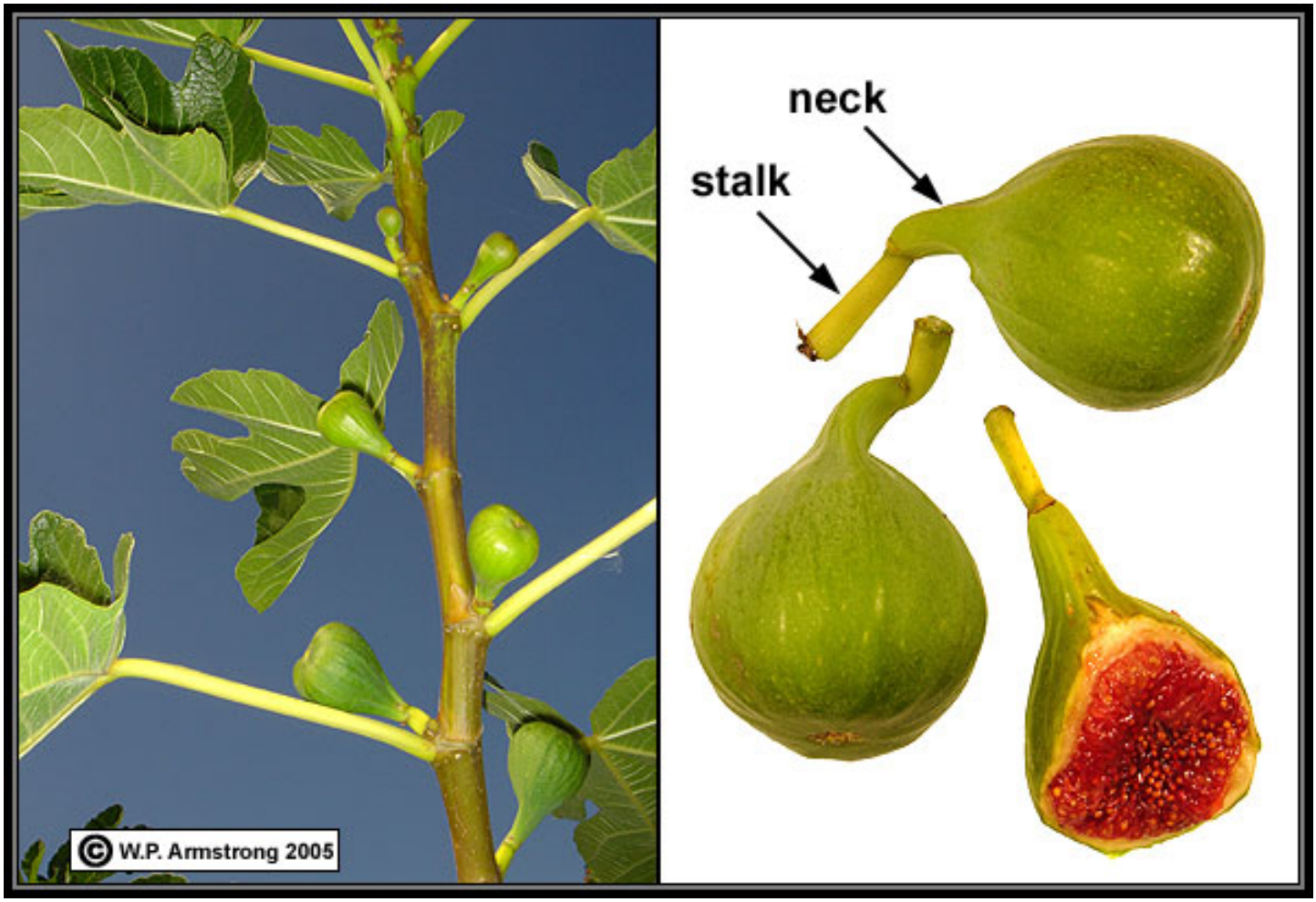
5. The styles of Calimyrna female flowers are much longer than the short-style caprifig, in fact, they are longer than the wasp's ovipositor. The female wasp is unable to lay her eggs (oviposit) in ovaries of long-style Calimyrna flowers; however, she does pollinate the flowers in her desperate attempt to oviposit. Without wasp larvae a seed develops inside each ovary, and each ovary becomes a minute one-seeded fruit (drupelet). The mature one-seeded drupelets impart a superior nutty flavor to Calimyrna figs and your fig newtons.

6. Without the fig wasp, the syconia of Calimyrna trees would not ripen and would fall off the trees. They must be pollinated in order to set fruit. The annual crop in California is worth over 2 million dollars. One disadvantage of wasp pollination is the transmission of a fruit rotting fungus ("endosepsis"). This involves the treatment of the mamme crop with a fungicide and the distribution of mamme figs among the profichi crop at the proper time in early spring. This elaborate fungus treatment plus the distribution of profichi crop to Calimyrna fig trees in June is labor intensive (and expensive).

7. There are literally hundreds of named cultivars of edible female figs with persistent syconia. Their syconia develop and set without pollination. The seedless (hollow) drupelets inside still have a hard endocarp layer and are crunchy. The term parthenocarpic is often used for these figs since they don't require pollination. Actually the term parthenocarpic only applies to the drupelets inside, which are technically the fruits developing without pollination or fertilization. Some examples of parthenocarpic fig cultivars are brown turkey, black mission, kadota, conadria, adriatic and many more.

'Brown Turkey,**'** a parthenocarpic cultivar of **Ficus carica** with brownish-purple syconia.

This parthenocarpic variety of **Ficus carica** is similar to **'**verte.**'** It produces a heavy 2nd (main crop) late in the fall (October-November). The syconia have a green outer skin and strawberry interior. They are very sweet and delicious.



A parthenocarpic variety of **Ficus carica** similar to **'**verte.**'** It produces a heavy 2nd (main crop) late in the fall (October-November). The syconia have a green outer skin and strawberry interior. This photo was taken on November 5 in San Diego County. The upper branches still contained numerous immature syconia.

'Flanders,**'** a parthenocarpic variety of **Ficus carica** created by Dr. Ira Condit and described in 1965. It is named after Dr. Stanley Flanders, professor emeritus of entomology at the University of California, Riverside and world authority on honey bees.

'Mary Lane,**'** a parthenocarpic variety of **Ficus carica**. This cultivar has very little sclerified (woody) tissue in its endocarp and is ideally suited to denture wearers.

'Pinachée,**'** a parthenocarpic variety of **Ficus carica** with alternating yellow and green striped syconia and stems. Variegated plants are often referred to as chimeras. Chimeras are organisms composed of two genetically different types of tissue. Chimeras may result from the fusion of cells or tissue. In variegated plants, a mutation in the chloroplast DNA often results in the loss of chloroplasts. Consequently, this mutant tissue has no green pigment and no photosynthesis. Colorless tissue in variegated plants may also be caused by viruses.

Chimeras

In ancient Greek mythology, the chimera was a fabulous monster having a lion's head, a goat's body and a serpent's tail. Some so-called "hybrid" animals mentioned in news articles are actually chimeras. They are produced by combining genes and cells of two species. With the modern age of biotechnology the list of possible chimeras is unlimited. Some genetically engineered chimeras are so bizarre that the combination of species used in the chimera would never be genetically compatible for in vitro or in vivo fertilizations. Hybridoma chimeras are made fusing the cells of two species. One such hybridoma cell line is referred to as a "geep" because it contains the genes of a goat and a sheep. Specific monoclonal antibodies used in cancer research are produced by plasma cells that have been fused with myeloma (cancerous) cells. Because of their tumor component, these antibody-producing cells are "immortal" and continue to divide and produce the same type of antibody. Hybridoma cells have now been created that produce monoclonal antibodies that attack and bind to the poison oak allergen. This research opens the door for an effective new treatment for a potentially serious dermatitis. A combination of the common cold and the polio virus has shown great promise in curing brain cancer. Similar combinations with HIV show promise with other diseases. There is also the potential of producing killer viruses for biological warfare by combining known pathogenic organisms. For example, could airborne strains of HIV be made by combining this deadly virus with influenza, or a deadly form of smallpox combined with Ebola? There are rumors of other super-chimeras such as veePox, a combination of smallpox and Venezuelan encephalitis.

8. In cultivated figs, parthenocarpy generally refers to the development of the ovaries of female flowers within the syconium into drupelets without fertilization. According to W.B. Storey (**Advances in Fruit Breeding**, 1975), there are 2 genetically determined forms of parthenocarpy: stimulative and vegetative. Stimulative parthenocarpy includes the insertion of the ovipositor down the stylar canal into the ovary of short style flowers. It can also be induced by blowing air into the syconium, or by spraying the syconium with a plant growth regulator. The mature drupelets may contain a wasp (if an egg was laid in the ovary) or it may be empty. Vegetative parthenocarpy involves the formation of drupelets without any external stimulation, and is responsible for the hollow drupelets inside common figs such as "black mission," "kadota," and "brown turkey." [Some author use the term parthenocarpy to describe the ripening of seedless fig syconia on the tree without any pollination or fertilization.]

9. Female trees may also produce apomictic seeds--i.e. without pollination and subsequent fertilization. In general there are two main types of apomixis:

[1] Parthenogenesis (agamogenesis): A haploid or diploid egg within the embryo sac (or diploid cell from 2 fused haploid cells of embryo sac) develops into an embryo. [Formation of haploid cells may involve crossing over during Prophase I of meiosis resulting in some genetic variability.]

[2] Agamospermy: An embryo arises from tissue surrounding the embryo sac. If this involves cells of the nucellus or inner integument it is called a nucellar embryo. Nucellar embryos are chromosomally identical to the sporophyte parent. They are essentially clones of the female tree. Apomictic seeds allow propagation of choice edible fig cultivars (female trees) without the transmission of viruses through cuttings.

Fig & Fig Wasp Hyperlinks:

The Calimyrna Fig & Its Pollinator Wasp
Creeping Fig: One Source Of Grass Jelly
Sexuality and Political Correctness In Figs
A Summary Of The Ficus carica Life Cycle
The Amazing Fig & Fig Wasp Relationship
Pollination Patterns In Dioecious Fig Species
Cauliflory In Tropical Species Of Figs (Ficus)
Strangler Figs & Banyans: Remarkable Trees
Gall Controversy--Do Fig Wasps Induce Galls?
The Evolution Of Dioecious Fig (Ficus) Species
A Petrified Fig Syconium From The Cretaceous
Nonpollinator Fig Wasps With Long Ovipositors
Figs Of The Holy Land (Their Role In Religions)
Sex Determination In Common Fig (Ficus carica)

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