Sex Life Of Figs: Part 1 Part 2 Cystoliths Palomar Pollinators

Fig Pollinators At Palomar College

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Pollination & Dispersal Of Australian Figs At Palomar College

Pollination By Fig Wasps & Dispersal By Birds

Fig Wasps & Viable Seed Production

On the Palomar College campus & Arboretum I discovered the symbiotic pollinator wasps for 3 species of Australian figs: Indian laurel fig (Ficus microcarpa), rustyleaf fig (F. rubiginosa), and Moreton Bay fig (F. macrophylla). A 4th species called banana fig (F. pleurocarpa) produced seeds but its pollinator (if any) is unknown. A 5th species (F. carica caprifig) also has its pollinator wasp on campus. [It is discussed on a comprehensive coevolution fig page at the following link.] Without their pollinator wasps, these fig species cannot produce viable (fertile) seeds. I recently noticed offspring from two Australian trees at the north end of campus, indicating wasp pollination and seed dispersal presumably by birds. Some fig seedlings were even in the crowns of large, Canary Island date palms. In tropical regions with abundant rainfall, fruit-eating bats & primates are also major agents of fig dispersal. This remarkable relationship between minute wasps and vertebrates is well-known in southern Florida, Hawaii and tropical countries. With 876 fig species worldwide, many with multiple symbiotic wasps (pollinator & nonpollinator), this is truly a remarkable and extraordinarily complex relationship between minute insects and their host trees. In fact, the DNA cladograms for figs and their wasps are absolutely mind-boggling!

Pollination of Ficus carica on Special Coevolution Fig Page

Table Of Contents

Subgenus Urostigma Section Conosycea

1. Indian Laurel Fig (Ficus microcarpa)

Subgenus Urostigma Section Malvanthera

- 2. Rustyleaf Fig (Ficus rubiginosa)
- 3. Moreton Bay Fig (Ficus macrophylla)
- 4. Banana Fig (Ficus pleurocarpa)

Indian Laurel Fig (Ficus microcarpa)

An Indian laurel fig (**Ficus microcarpa**) with massive trunk near the music building complex at Palomar College. It is also a popular indoor container plant used for bonsai. Some of these remarkable growth variations may be attributed to cultivars, such as 'Golden Gate' grown primarily for bonsai.





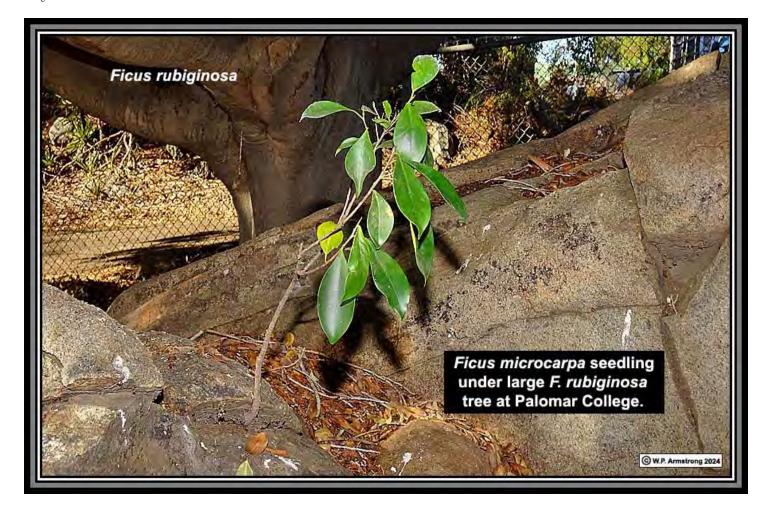
Indian laurel fig (**Ficus microcarpa**) and its symbiotic wasp (**Eupristina verticillata**) from syconia on Palomar College campus. One wasp is squeezing through an exit tunnel cut by male wasps (white arrow).

The Pollinator Wasps For Ficus microcarpa) Are Really Minute!



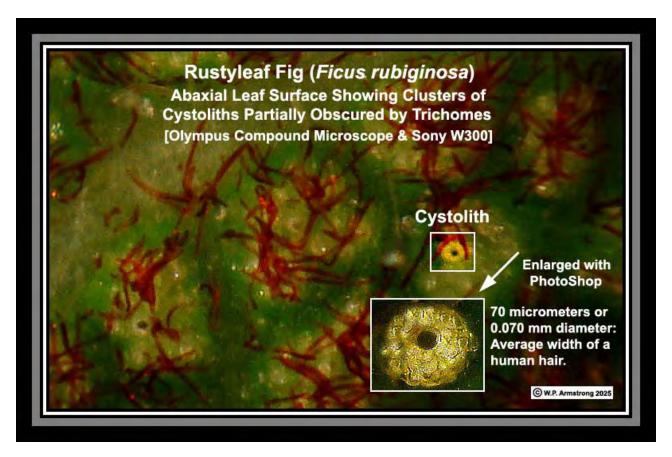
The following online article shows many images of how wasp-pollinated, invasive **Ficus microcarpa** has spread in southern California, & why I decided not to plant this tree in my front yard!

Richard E. Riefner Jr. 2016. *Ficus microcarpa* (Moraceae) naturalized in southern California, U.S.A.: Linking plant, pollinator, and suitable microhabitats to document the invasion process. <u>Invasion Of Ficus microcarpa in Southern California</u>



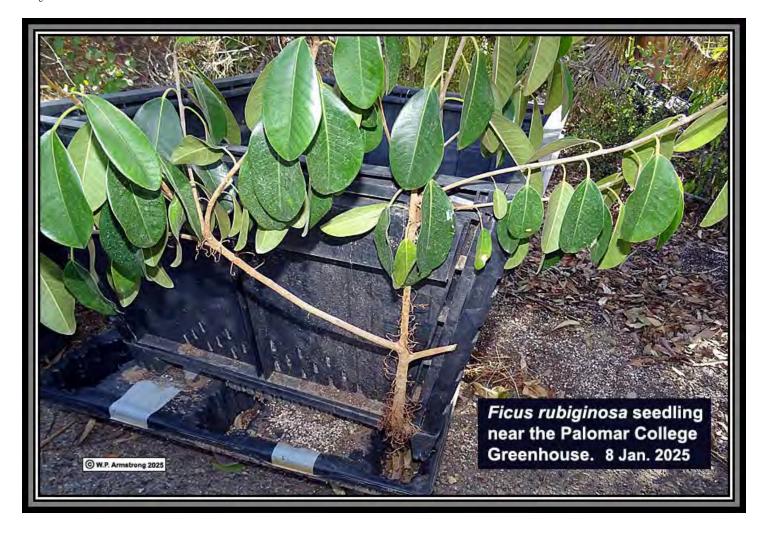
Indian laurel fig (**Ficus microcarpa**) seedling growing from crack in granitic outcrop at north end of campus. It is under a large rustyleaf fig (**F. rubiginosa**). **Ficus** species are well-adapted to grow in shade with microscopic, calcareous structures called cystoliths in their leaves. The glistening cystoliths transfer light to photosynthetic, chloroplast-bearing cells.

Rustyleaf Fig (Ficus rubiginosa)

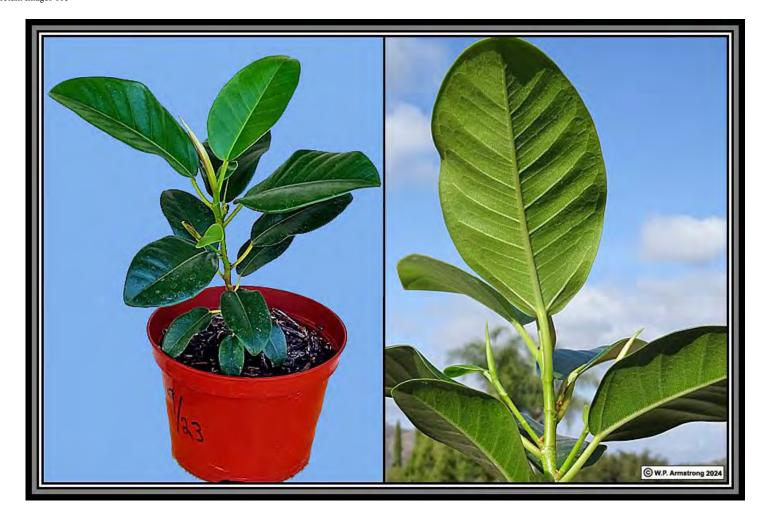


The brown hairs (trichomes) on underside of rustyleaf fig leaves produce unique rust color of abaxial leaf surface; however, the color is variable depending on density of hairs. This species is easily distinguished from leaves of **F. microcarpa**. Unlike the scattered cystoliths of **F. microcarpa**, the cystoliths of **F. rubiginosa** occur in clusters and are partially concealed by the hairs.

We have typical rustyleaf fig (**Ficus rubiginosa**) on Palomar College campus, and so-called "glabrous" rustyleaf fig, in the Palomar College Arboretum. In my opinion, the specimen I have observed in Arboretum is technically not glabrous: Minute hairs may be visible on underside of leaves (abaxial surface), especially on veins, with 10x magnification (hand lens or dissecting microscope). Some authors list it as var. **glabrescens**; however, World Flora Online lists var. **glabrescens** as a synonym for this variable species. It is also listed as **Ficus rubiginosa f. glabrescens** (F.M. Bailey) D.J. Dixon. The small f is a secondary taxon rank below variety. It denotes a special form of that species or variety.



Rustyleaf fig seedling from nearby tree near campus greenhouse.

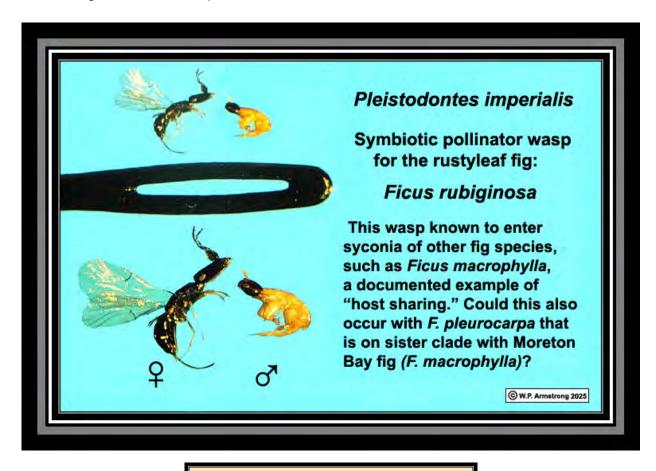




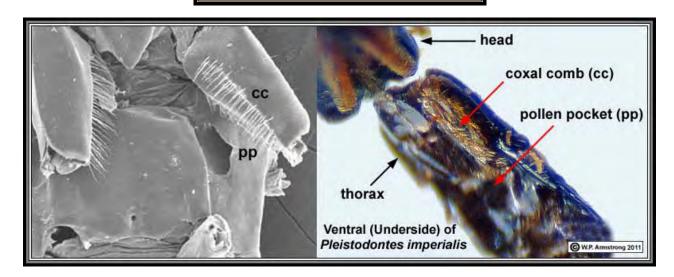
Abaxial (lower) leaf surface & veins of this tentatively identified rustyleaf fig seedling in south Escondido have relatively few hairs (trichomes), but in my opinion, they are not truly glabrous. The trichomes are interspersed with cystoliths (white dots in photo). Glabrous means smooth, glossy, and without hairs or bristles (i.e. lacking surface projections).

Seedling discovered by Steve Disparti in south Escondido tentatively identified as *Ficus rubiginosa*. It may have been introduced by birds.

Several exotic fig species, such as the commonly cultivated Benjamin fig (Ficus benjamina), Indian laurel fig (F. microcarpa), rustyleaf fig (F. rubiginosa), and Moreton Bay fig (F. macrophylla), often develop as hemiepiphytes (spending part of their life as epiphytes) with numerous aerial roots in their native habitats of Malaysia and tropical Australia. They sometimes germinate in the crowns of palms and crevices of buildings in moist climates, such as southern Florida. Due to the introduction of symbiotic wasp pollinators, some of these tropical figs in southern California, including Palomar College campus in San Diego County, produce viable seeds. They sometimes germinate in the crowns of palms; however, it is generally too arid for them to send aerial roots to the ground and develop into mature trees.



Pollination Behavior In Different Wasp Genera



A deceased female fig wasp (Pleistodontes imperialis) extracted from the ostiole of Ficus

rubiginosa. Note the coxal comb at the base of front leg that it used to actively gather pollen from syconium and store it in ventral thoracic pocket (pollen pocket). Inset (left): SEM from Kjellberg, F., Jousselin, E., Bronstein, J.L., Patel, A., Yokoyama, J., and J.-Y. Rasplus. 2001. "Pollination Mode in Fig Wasps: The Predictive Power of Correlated Traits." *Proceedings of the Royal Society of London* 268: 1113-1121.

Epiphytic Strangler Fig On Canary Island Date Palm At Palomar College



An unusual sight on the campus of Palomar College in San Diego County, California: A rustyleaf fig (**Ficus rubiginosa**) that has developed from a seed in the leaf bases of a Canary Island date palm (**Phoenix canariensis**). If the climate was more humid, with frequent rain showers, this fig could probably send aerial roots to the ground and become a full-fledged strangler. In fact, aerial root resembling "botanical boa constrictor" appears in upper left of above image (red arrow).



The rustyleaf fig (**Ficus rubiginosa**) in distance produces numerous crops of seed-bearing syconia bearing symbiotic fig wasps (**Pleistodontes imperialis**). For birds feeding on the sweet syconia, it is a relatively short distance to the Canary Island date palms where fig seeds could be deposited with their feces.

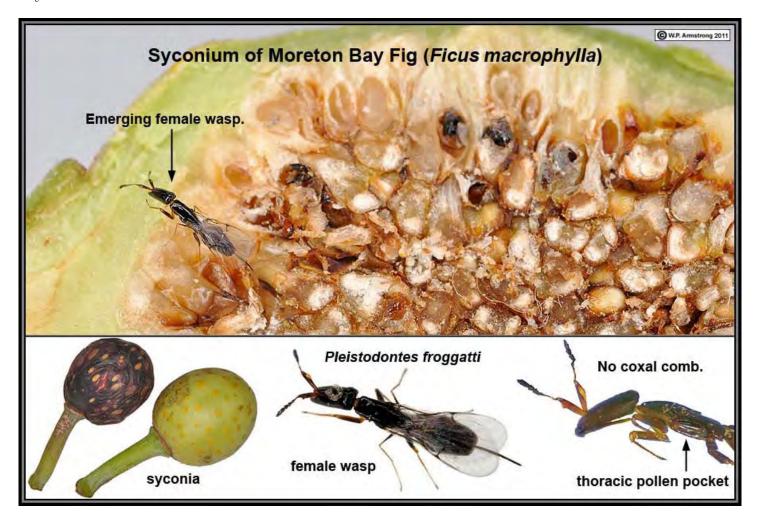
How Date Palms Support Fig Seedlings In Dry Southern Calif. Climate

Ficus seeds can germinate in date palms because the environment within a date palm's fruit cluster provides the necessary conditions for germination, including moisture, warmth, and a suitable substrate for the seeds to root in; essentially, the date palm acts as a "nurse tree" offering a protected microclimate for the fig seeds to sprout, especially if the seeds happen to be deposited there by birds. In addition to a moist & sheltered environment, decaying organic matter in date palm fruit cluster also provides nutrient source for developing fig seeds.

Moreton Bay Fig (Ficus macrophylla)



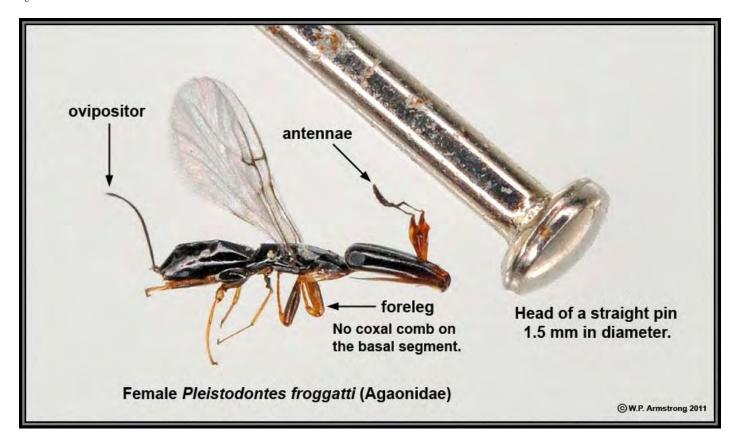
Massive trunk and surface roots of a Moreton Bay fig (**Ficus macrophylla**) in the Palomar College Arboretum. In its native Australia it is a strangler fig.



Syconium of Moreton Bay fig (**Ficus macrophylla**) in Palomar College Arboretum. Palomar College horticulturist Tony Rangel grew viable seeds from this tree, so I suspected that the pollinator wasp (**Pleistodontes froggatti**) must be present.



Unlike the similar **P. imperialis** of rustyleaf figs (**F. rubiginosa**), **P. froggatti** does not have a coxal comb at the base of its front legs. According to Cook, J.M. et al. (2004), the lack coxal combs indicates passive rather than active (purposive) pollination; however, they also state that "pollen pockets provide a good but imperfect index." In Table 1 of their article they state that pollination by **P. froggatti** is passive. Prior to my discovery of **P. froggatti** in the Moreton Bay fig at Palomar College (December 2011), the only fig wasps I have documented on campus are **P. imperialis** on rustyleaf figs and **Eupristina verticillata** on the Indian laurel fig (**Ficus microcarpa**).



Pleistodontes froggatti from Moreton Bay fig syconium in Palomar College Arboretum.

Disclaimer: If I am incorrect on my identification of *Pleistodontes froggatti*, then the above wasp is most likely the similar rustyleaf fig wasp (*P. imperialis*) that is known to enter syconia of Moreton Bay fig (*Ficus macrocarpa*) outside of its natural range. Host-sharing & host-switching are fascinating phenomena in fig biology that may lead to hybridization and diversity in *Ficus* species. More about this topic in the following section under *F. pleurocarpa*.

Banana Fig (Ficus pleurocarpa)

Seed germination of the banana fig (**Ficus pleurocarpa**) in the campus greenhouse area is perplexing because no wasp pollinators have been observed. There is no conclusive evidence that the banana fig on campus is pollinated by fig wasps. It was originally introduced without syconia, so it is doubtful that its native pollinator wasp species (**Pleistodontes regalis** and **P. deuterus**) were introduced. Its syconia appear to be packed with very hard-shelled "seeds" that sink in water. This is truly an enigma. If these "seeds" (technically drupelets) germinate, then how did they get pollinated? Were they pollinated by **Pleistodontes imperialis** from nearby rustyleaf fig (**Ficus rubiginosa**)?

Host Sharing & Pollinator Sharing

Host Sharing: 2 or more pollinator wasp species per host. Pollinator Sharing: 2 or more fig host species per pollinator.

Fig & Fig Wasp Pollination May Be Even More Complicated

When I began studying figs (Ficus) with horticulturist Steven Disparti over 30 years ago, I thought each species of fig had it own unique, symbiotic pollinator. This may still be true for some of the 876 species of Ficus; however, multiple pollinators and evidence from host & pollinator sharing data have complicated the fig & fig wasp story. The relationships undoubtedly follow kinships within subgenera & sections depicted in enormous Ficus DNA cladograms (evolutionary trees). There are 4 pollinated Australian fig species on campus in subgenus Urostigma and at least 3 verified species of Australian fig wasps: (12 possible interactions). If you exclude Section Conosycea & wasp Eupristina, and only consider the more closely related Section Malvanthera & 2 Pleistodontes wasp species on campus, there would be 7 possible interactions. Another complicating factor introduced into seedling diversity is possible hybridization between fig species pollinated by multiple wasp species each coming from at least 2 different host fig species. In fact, some authorities have speculated that host-sharing and hostswitching by fig wasps may have lead to the enormous number of fig species. In host-sharing multiple fig species share the same pollinator wasp, while in host-switching a pollinator wasp evolves to use a different fig species as its primary host.

Carlos A Machado, Nancy Robbins, M Thomas P Gilbert, & Edward Allen Herre. 2005. "Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism." Proc Natl Acad Sci U S A. 2005 Apr 25; 102 (Suppl 1):6558-6565. doi: 10.1073/pnas.0501840102

Gang Wang, et al. 2023. "Genomic evidence of prevalent hybridization throughout the evolutionary history of the fig-wasp pollination mutualism." https://doi.org/10.1038/s41467-021-20957-3

he banana fig (**Ficus pleurocarpa**) is endemic to wet tropical rainforests of northeastern Australia. It has distinctive, elongate, orange-red syconia different from other fig species. It starts out as an epiphytic strangler (hemiepiphyte) and later develops into a tree up to 25 meters tall in Australia.

Receptive Australian Ficus Species At Palomar College

F. microcarpa Fig Wasps & F. rubiginosa F. macrophylla F. pleurocarpa Fig Species Conosycea Malvanthera Malvanthera Malvanthera Eupristina **Natural Host Improbable** verticillata **Improbable Improbable** (Conosycea) **Pleistodontes Improbable Natural Host** ? imperialis (Malvanthera)

Pleistodontes
froggatti
(Malvanthera)

Improbable

? Natural Host
?

Table Showing Possible Fig Pollinations At Palomar College

Red: Improbable (Between Different *Ficus* Sections Conosycea & Malvanthera) Green Squares Containing Question Mark? (Unverified at Palomar College)

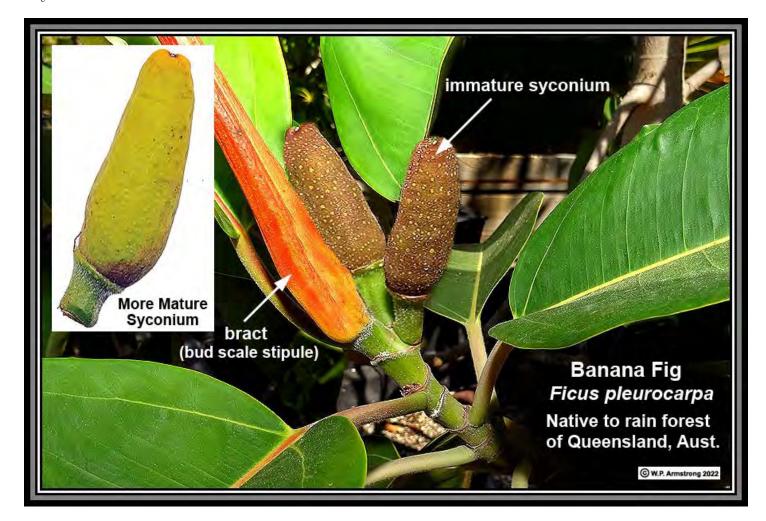
As I stated above, the symbiotic pollinator wasp for *F. carica*, *Blastophaga psenes*, is also on campus. It was introduced with my 'Vista Caprifig' donation. Although it is an improbable pollinator of *F. pleurocarpa*, nothing would surprise me the more I learn about the complex biology of fig pollination.

The pollination story for **Ficus rubiginosa** is even more complicated. According to C.T. Darwell, et al. (2014), the **Pleistodontes imperialis** wasps pollinating rustyleaf figs have diversified (evolved) into 5 distinct species across their entire host plant range along the east coast of Australia.

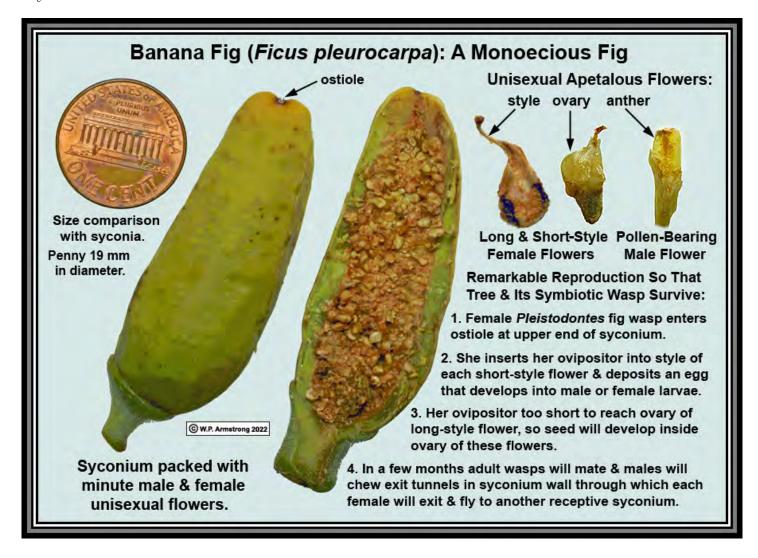
Clive T Darwell, Sarah al-Beidh, and James M Cook. 2014. "Molecular species delimitation of a symbiotic fig-pollinating wasp species complex reveals extreme deviation from reciprocal partner specificity. Darwell et al. BMC Evolutionary Biology 2014, 14:189

http://www.biomedcentral.com/1471-2148/14/189

The native pollinator of Ficus macrophylla is Pleistodontes froggatti; however, outside its native range, the syconia of F. macrophylla are also visited by P. imperialis, the pollinator for F. rubiginosa (J.M. Cook & D.W. Dunn, unpublished). In addition, DNA cladograms indicate that F. macrophylla and F. pleurocarpa are sister clades and are thus closely related species. Some interesting pollination hypotheses can be drawn from these documented observations. If the rustyleaf fig's pollinator (P. imperialis) is known to pollinate F. macrophylla, and if F. macrophylla is very closely related to F. pleurocarpa, could it also pollinate F. pleurocarpa?



As I stated in a Facebook note, the coevolution of nearly 900 species of figs, each with their symbiotic wasps, is the most amazing story of my biology career. It is difficult to summarize in a lecture because of its complexity. In fact, oversimplifications and generalizations by authors has contributed to errors in some publications.



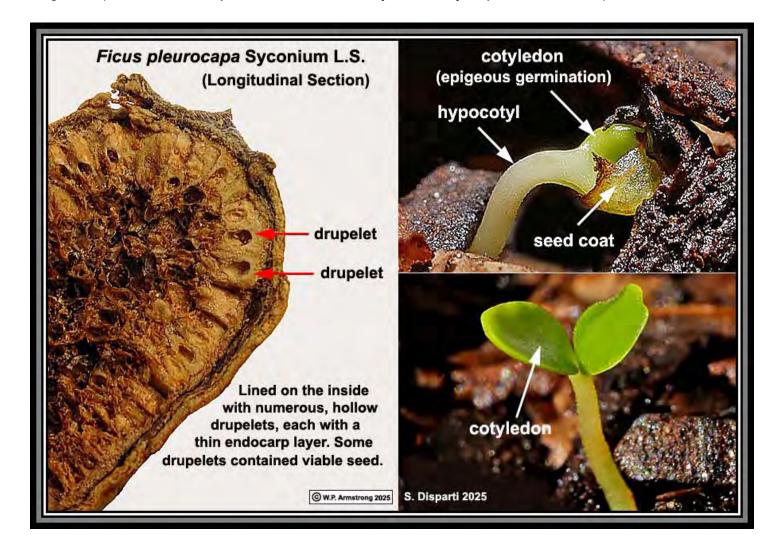
As of 4 January 2025, how this fig was pollinated at Palomar College is an enigma. No **Pleistodontes** wasps were found in **F. pleurocarpa** syconia with mature anthers to disperse the pollen.

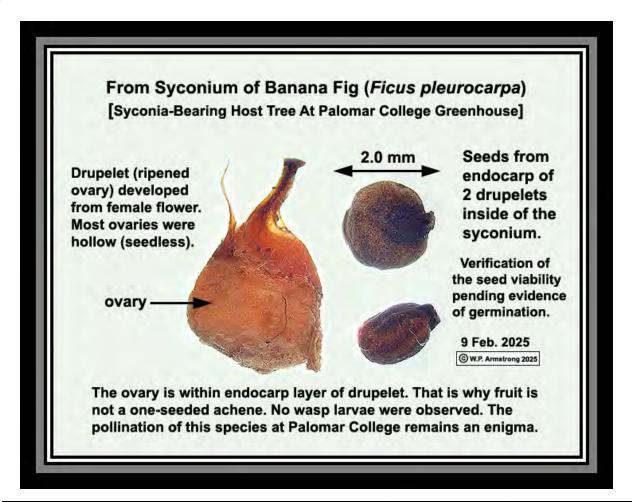
n its native rainforests of northeastern Australia, **Ficus pleurocarpa** is pollinated by two species of fig wasps, **Pleistodontes regalis** and **P. deuterus** in the same syconium. This is a good example of host sharing where 2 species of fig wasps enter syconia of the same fig species. In fact, the assumption that fig species are usually pollinated by just one species of fig wasp was challenged by the discovery of species like the banana fig. We also have tentatively identified **Pleistodontes froggatti** in the Edwin & Frances Hunter Arboretum that pollinates the Moreton Bay fig (**F. macrophylla**) and **P. imperialis** that pollinates the rustyleaf fig (**F. rubiginosa**) on campus. As I stated above, outside its native range the syconia of **F. macrophylla** may also be visited by **P. imperialis**, the pollinator for **F. rubiginosa**. Without pollination there are typically no viable seeds in the syconium and no seedling trees.

Another Australian strangler fig (**Ficus watkinsiana**) is closely related to **F. rubiginosa**. In fact, some DNA cladograms show the 2 species as sister clades. Its native Australian pollinator wasp is **Pleistodontes nigriventris**. This fig has been introduced to Kauai, Hawaii, where it is pollinated by **P. imperialis**. An impressive specimen of **Ficus watkinsiana** is the centerpiece of the "Monkey Trails" habitat at the San Diego Zoo. According to the Zoo's online Fig Web Page, it produces seedlings; therefore, pollinator wasps must be present. Could the pollinator be the rustyleaf fig wasp (**P. imperialis**)?

The drupelet contents of several **F. pleurocarpa** syconia from Palomar College were placed in soil by Mr. Disparti in December 2024. As of January 2025 several **F. pleurocarpa** seedlings appeared in the flower pots. [Their ID was confirmed with root-bearing **F. pleurocarpa** drupelets.]

The term "drupelet" refers to the minute fruits of banana fig that line the inner walls of syconium. Some references refer to them as "fruitlets." They are ripened ovaries from female flowers. The mature drupelet has an inner layer called endocarp that makes them technically different from achenes. References calling them achenes are incorrect according to fig authorites Ira J. Condit & William B. Storey at UC Riverside. If the female flower was pollinated the endocarp layer would typically enclose a minute, viable seed. Most of the **F**. **pleurocarpa** syconia I examined were empty (hollow) and seedless, indicating lack of pollination. The center of mature syconia was occupied by pollen-laden male flowers (anthers). At this time the female flowers were no longer receptive. Unfortunately, I never observed a **F**. **pleurocarpa** syconium with receptive female flowers.







Ficus pleurocarpa seedlings from drupelet-bearing syconia at Palomar College. Image shows drupelet still attached to narrow cotyledons. Upper right shows pair of cotyledons & first true leaves.

Conclusions Regarding Pollination of Banana Fig

There is no evidence of the 2 native pollinator wasps for **F. pleurocarpa** on the Palomar campus, and no evidence of **Pleistodontes** wasps from other figs on campus in the mature **F. pleurocarpa** syconia; however, I have not checked the syconia at early stage when they are small and receptive to pollen-bearing wasps. Could a **Pleistodontes** from nearby rustyleaf fig or Moreton Bay fig possibly visit the **F. pleurocarpa** syconia?

Could **F. pleurocarpa** at Palomar be self-pollinated? All the references I have consulted state that this species exhibits obligate mutualism: It must be pollinated by one or more fig wasps of the genus **Pleistodontes**. I have never observed any fig wasps in it's syconia when anthers were shedding pollen (when female flowers appeared to be past their receptive stage). Figs are typically protogynous: I.e. female flowers receptive before male flowers (anthers) shed pollen. I must conclude that pollen would typically be carried into syconium from another fig tree (possibly host-sharing). I am not aware of any other insects that could accomplish pollination or induce seed production without pollination.

There may be other factors involved in seed formation in **Ficus pleurocarpa**; however, as I have stated above, the explanation remains an enigma in my opinion.

Addendum:

My colleagues have offered some hypotheses to explain seeds in *Ficus pleurocarpa* syconia at Palomar College.

- 1. In some figs (**Ficus carica**) the syconia and ovaries of female flowers develop by parthenocarpy, which means they form enlarged (ripened) syconia containing seedless drupelets without fertilization by fig wasps. Parthenocarpic varieties of common edible are commonly sold at nurseries. This process is different from parthenogenesis, when an unfertilized egg develops into an embryo within a seed. The latter mechanism comes under the heading of apomixis that is very unlikely in figs according to the literature.
- 2. Self pollination: This can be ruled out because **F. pleurocarpa** is clearly protogynous; i.e. the female flowers mature before male flowers. By the time anthers are shedding pollen the female flowers are no longer receptive. This strategy favors cross pollination.
- 3. Activity of other minute arthropods (Collembola, Amphipods, etc.) inside syconia, possibly spread by birds, resulting in pollination of some receptive female flowers. This would explain the paucity of seeds in **F. pleurocarpa** syconia.
- 4. Pollination of some receptive flowers in **Ficus pleurocarpa** syconia by fig wasp (e.g. **Pleistodontes**) from another campus fig species who happens to enter receptive ostiole. Host-sharing has been documented for **Pleistodontes** and a large **F. rubiginosa** grows near greenhouse location for banana fig. The female wasp may be unwilling or unable to lay her eggs and she is absorbed by syconium enzymes (ficin) by the time it matures, leaving no evidence of fig wasp. This also explains the paucity of seeds. In my opinion this hypothesis fits the principle of parsimony basic to all science and tells us to choose the simplest scientific explanation that fits the evidence and peer-reviewed literature.

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