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Ficus microcarpa L., *F. benjamina* L. and other species introduced in the New World, their pollinators (Agaonidae) and other fig wasps

William Ramírez B.
Escuela de Fitotecnia, Universidad de Costa Rica. Costa Rica, América Central.
Jorge Montero S.
Escuela de Biología, Universidad de Costa Rica. Costa Rica, América Central.

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Abstract: The invasion of the Old World fig *F. microcarpa* L. (section *Conosycea*) in U.S.A., Mexico and Central America by its Old World pollinator *Parapristina verticillata* is reported. Because of the size of the seedlings growing naturally in Florida, Honduras, and the State of Morelos, Mexico, and the fact that no seedlings were found in other parts of Mexico and El Salvador, we postulate that *P. verticillata* probably arrived to those areas within the last five years. It is probable that *P. verticillata* will move south invading all the tropical and subtropical countries where *F. microcarpa* is abundantly planted. *Walkerella*, a non-pollinating wasp was also found in Brazil and Florida inhabiting the syconia of *F. microcarpa.*
The syconia of Old World *F. benjamina* L. (section *Conosycea*) in Costa Rica, were found pollinated by the New World *Pegoscapus tristani.* the pollinator of *F. padifolia* H.B.K. (section *Americana*). The syconia of Old World *F. religiosa* L. (section *Urostigma*) in Miami, Florida, were found to be pollinated by the symbiotic agaonid of the native *F. aurea* Nutt. Hybrid seedings were found growing naturally.
Species of *Ficus* which evolved in different geographic areas, such as islands or continents could also evolve equally or similarly attracting synomones, which can confuse foreing agaonids and other sycophilous wasps when a species of fig is introduced.

Invasion of Old World species of *Ficus* in not native regions

Introduced species of *Ficus* do not set seed until their specific pollinators (the Agaonidae) are also introduced; for a review of *Ficus* transport see Ramírez (1970).

F. benjamina, F. microcarpa and *F.religiosa* are widely cultivated as ornamentals in many cities and parks in Old and New World tropical and subtropical countries. These species are ideal ornamentals because of their height, impressive crown and leaves which usually drop gradually rather than synchronously, as in many other species of *Ficus*. As the native pollinators were not introduced with the trees, the syconia, although abundant, drop to the ground while small and not juicy (for *F. microcarpa* see Galil and Copland 1981). *F. benjamina* and *F. microcarpa* are Old World *Urostigma* banyan figs which belong to section *Conosycea* (Corner 1965). *F. microcarpa* grows naturally in Ceylon, India, Southern China, Ryu Kyu and eastward throughout South-East Asia and Malaysia to New Britain, Australia, Carolina Islands, Cocos, and Christmas Island (Indian Ocean) (Corner 1965). *F. microcarpa* has often been wrongly named *F. retusa* L. or *F. nitida* Thunb (Corner 1965). The pollinator of *F. microcarpa* in Asia and Australasia is *Parapristina verticillata* (Waterston 1921). *F. benjamina* grows naturally in India and Southern China throughout Malaysia to Solomon Island, North Australia (Arhem Land Queesland) (Corner 1965). *F. benjamina* is pollinated by

Eupristina adempta (Wiebes 1966). *F. religiosa* is native in sub-Himalayan forest from Rawlpingi to Yunnan, Cochinchina to North Thailand (Corner 1965). It belongs to section *Urostigma* and is pollinated by *Platiscapa quadraticeps* (Wiebes 1986).

Stange and Knight (1987) report that two foreign fig-pollinating wasps have become established in Florida in the past few years on exotic figs. *P. verticillata* has been found in *F. microcarpa* and also in the native fig *F. aurea* Nutt. *E. masoni* Saunders (1882) occurs in the Asian fig *F. benghalensis* (section *Conosycea*) *P. verticillata* was successfully introduced into Hawaii in 1921 (Condit 1969) and was collected first in the Miami area in March, 1986 in seeded syconia of *F. microcarpa*. It is also known from Bermuda on *F. microcarpa*. Stange and Knight (1987) assumed that since many *F. microcarpa* trees are imported from Hawaii, it is probable that this was the mode of introduction of *P. verticillata* into Florida.

Stange and Knight (1987) also mention the presence in Florida of the cecidogenous fig wasp *Walkerella yashiroi* (Ishii) and *Odontofroggatia* sp. (Pteromalidae) in figs of *F. microcarpa*. H. Anderson (Ent. Dept. Univ. of California) informed Ramírez about the development of the syconia of *F. rubginosa* Desf, in California in association with the normal development of an agaonid, probably *Pleistodontes imperialis* (Saunders 1882). *F. rubiginosa* and its pollinator *P. imperialis* were introduced into Hawaii early during this century (Pemberton 1921), Galil and Eisikowitch (1968a) inform about *Platyscapa quadraticeps* in Israel normally developing in the syconia of *F. religiosa* Both, the wasp and the host are not native to Israel*.

Introduced fig wasps in Mexico, Central and South America:

During 1984, Ramírez observed ripe and almost black syconia in *F. microcarpa* in Río de Janeiro (Fig. 1), Sau Paulo and Viçosa, Brazil. A close examination of almost ripe syconia in D-phase (for developmental phases of syconia; see Galil and Eisikowitch, 1968 b), revealed the presence of non-polleniferous *Walkerella* wasps with wingless males (Wiebes, Rijmuseum van Natuurlijke Historie, Leiden; pers. com.). The invasion of *F. microcarpa* by *Walkerella* seems to be a recent phenomenon dating back about five to 10.years.

On August 24, 1985, Ramírez observed in downtown Cuernavaca, Morelos, Mexico a small *F. microcarpa* tree (planted in a pot) which had ripe, purple, juicy syconia (Fig. 2). A close examination of the fruits revealed the presence of small tunnels bored through their ostiola, which indicate that some kind of sycophilous wasp was stimulating the maturation of the syconia. Microscopic examination of other fruits in the early D. phase showed ripe syconia with developing agaonids inside. On the same day, a small seeding of *F. microcarpa* about 20 cms. high (Fig. 3) was found growing among some rocks on a wall of a hotel in Cuernavaca, Mexico.

The agaonid was later identified both by Ramírez and J. T. Wiebes as *Parapristina verticillata*, the native pollinator of *F. microcarpa* in the Old World.

During a second trip to Cuernavaca in 1985, Ramírez found *P. verticillata* normally developing in the syconia of *F. microcarpa* and many small seedings (less than 20 cms tall) growing among rocks and walls of the gardens of an Hotel (Fig. 3).

Other locations in Mexico (Tonatico, Ixtapan de la Sal and Atlixco in the states of Mexico and Puebla, Acapulco, la Y-griega in Guerrero, and in Zinapecuaro, Michoacan) had tree figs with agaonid inhabited syconia but no seedlings were found. Because of the size of the seedlings from Cuernavaca, it seems that the arrival of *P. verticillata* to this place in Mexico may have occurred less than five years ago.

All *Parapristina* wasps observed seemed to develop normally in the syconia of *F. microcarpa*. Usually only one pollinating wasp (no more than three) penetrated the female phase (B phase). Syconia observed in Mexico finished development in about 54 days. Frugivorous bats visited and collected the ripe syconia, although birds also ate the syconia during day time.

During January 1986, *P. verticillata* was also found in every adult fig tree of *F. microcarpa* in downtown San Salvador, and in the surroundings. Females were observed penetrating and developing in the most populated and polluted areas of the city. Nevertheless, no

* Ramírez and Galil found, for the first time in Nov. 1988, *P. verticillata* developing in the syconia of F. *microcarpa* in downtown Tel-Aviv. Small seedling (less than 20 mm tali) were found in a greenhouse

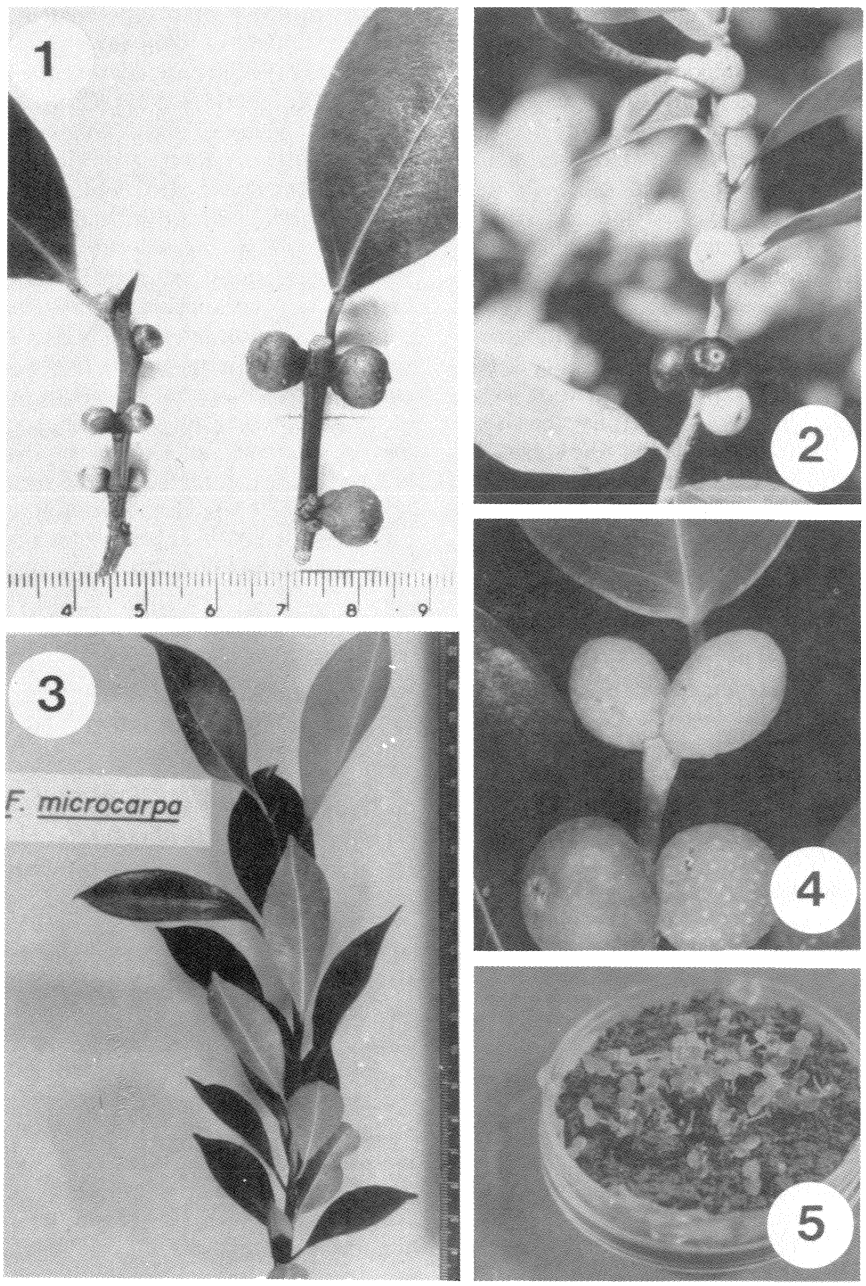

Fig. 1. Left: Branch of *Ficus microcarpa* without developing *Walkerella* sp. Right: Branch with parthenocarpic ripe syconia (large fruits) where *Walkerella* sp. is developing. Ribeirao Preto, S. Paulo, Brazil.

Fig. 2. Branch of *Ficus microcarpa* with two normal ripe syconia (dark-colored fruits) where *Parapristina verticillata* developed. Key Vaca, Florida.

Fig. 3. Naturally growing seedling of *Ficus microcarpa* in Mexico. The seedling was about two years old and measured aproximately 29 cm.

Fig. 4. Branch of *F. benjamina* with two pollinated ripe syconia (large fruits) which were penetrated by the agaonid symbiont of *F. padifolia* HBK. in San José, Costa Rica.

Fig. 5. Seedling of *F. microcarpa,* the seeds were obtained from ripe syconia pollinated by *P. verticillata* in Cuernavaca, Mexico.

seedings were found growing naturally. A visit to Honduras (Feb. 1986) revealed the presence of *P. verticillata* developing in syconia of *F. microcarpa* in downtown Tegucigalpa. Seedlings about the same age and size as those found in Cuernavaca, Mexico, were also found growing in craks of walls in dowtown Tegucigalpa. Seeds obtained from syconia in Mexico germinated in a high percentage when planted in unsterilized soil (Fig. 5).

Because of the size of the seedlings in Mexico (Fig. 3) and Honduras, it is difficult to guess in which are *P. verticillata* first arrived, but its arrival certainly was within the last five to ten years. It is possible that the Mexican *Parapristina* arrived from Florida, Marcelo D. Vázquez A. (Instituto Botánico Darwinion, Argentina) informed Ramírez about the presence of *P. verticillata* developing in *F. microcarpa* in Colombia.

Agonidae in the introduced *F. benjamina* in Costa Rica

At the same that *P. verticillata* was found pollinating *F. microcarpa* in Mexico, El Salvador and Honduras (1985-86), one of us (Montero) found a Costa Rican agaonid penetrating ths syconia of the Old World *F. benjamina* in the campus of the Universidad de Costa Rica.

The agonid pollinating *F. benjamina* in Costa Rica was tentatively identified as *Pegoscapus tristani* (Grandi 1919), a pollinator of *F. padifolia* HBK, a fig that grows on the university campus and is very abundant in the Central Valley where the university is located. *P. tristani* pollinated most of the female florest of *F. benjamina* and probably oviposited in some of them. When the rype syconia were opened (phase D), it was found that only the long-styled florets set seeds. Fifty short (galls) and long-styled (female) florets were planted separately in two Petri dishes with normal soil. Only the long-styled florets germinated, and gave origin to hybrid seedlings (probably *F. banjamina* X *F. padifolia*). In *F. benjamina* in Costa Rica, partial fertilization of the long-styled female flowers is produced by *P. tristani* and the syconia reach normal maturation (phase D) without the development of the strange agaonid. The interfloral phase of the pollinated syconia in a tree was found to be 58 days.

Wiebes (1982) considers that the pollinators of the Old World section *Conosycea* figs to which *F. benjamina* and *F. microcarpa* belong, section *Stilpnohyllum* and the New World section *Americana* (to which *F. padifolia* belongs) have coalesced male thoracic sclerites. Ramírez (1977) located the agaonids of the three fig sections mentioned on a common branch of his cladogram. Wiebes (1963) considers *Eupristina* (with which *Parapristina* was formerly included) to be the Asian analogue of American *Julianella* (a subgenus of *Pegoscapus*). This resemblance makes one suspect that the pollinators of the three fig sections *Ficus* mentioned may be related.

Since the Agaonidae usually live less than three days as adults, it is probable that the high ratio of introduction and distribution of Agaonidae wasps into new areas is associated with the era of the fast-flying airplanes.

Why do agaonids and other fig wasps penetrate and search syconia of other species of figs which are not their own host?

There are only a few reports about agaonids penetrating and pollinating species of figs which are not their normal host (Ramírez 1970, 1986, Stange and Knight 1987). According to Ramírez (1970) the evolution of mechanical and chemical barriers (specific allomones) by different isolated populations of figs and the evolution of morphological and physiological characters by their symbiotic pollinators may have contributed to the extensive speciation of *Ficus* and Agonidae and the evolution of specific pollinators in *Ficus*. Janzen (1979) suggests that each species of *Ficus* seems to have a specific odor which attracts only one specific pollinator. He also hypothesizes that the fig tree produces the species-specific synomone at the time the fig crop comes to receptive age (female phase) and that the parasitoids respond to it as do the pollinating agaonids. Nevertheless, he did not consider that each species of *Ficus* has many primary and secondary sycophilous wasps and that not all arrive when the syconia are receptive for the Agaonidae.

In the New World species of *Ficus* the noncecidogenous *Idarnes* wasps (subfamily Sycophaginae: Torymidae) usually appear at the

same time or before the pollinators arrive at the receptive syconia or slightly later. These long-ocipositor parasitic wasps are very specific to their hosts at the species and subgeneric (Gordh 1975).

We observed that in a *F. benjamina* tree in Costa Rica the pollinator *P. tristani* as well as its parasitoid *Idarnes,* were attracted at the same time to two branches with receptive syconia. Most, if not all, the syconia of two receptive branches, were penetrated by the pollinating agaonids the same day, and their attractiveness ceased completely after pollination occurred as normally happens to other species of figs. It, is probable that the cleptoparasitic torymids and the pteromalids fig wasps (subfamily Sycoryctinae) are also attracted to the syconia by the same synomones that attract the agaonid pollinators.

The attracting allomones of *Ficus* may be produced by the white receptive stigmata of the female florets which wilt and become brownish after pollination and that fertilization and, or oviposition; may cut the production of the attracting synomones (see Pemberton 1921).

F. religiosa, an Old World species, is also producing seeds which normally germinate and develop in Miami, while *F. septica* is penetrated by *P. assuetus,* the pollinator of *F. aurea* (Knight pers. com.). Ramírez also observed the same phenomenon in Miami, Florida, during 1987. The pollinator of *F. religiosa* in Florida was identified by Ramírez as the symbiont of *F. aurea* Nutt. Hybrid seedlings about 75 cm tall were found growing naturally.

Consequences of the introduction of foreign species of *Ficus* and its cecidogenous pollination and non pollinating wasps:

The production of viable seeds and pollen by introduced species of figs once they become associated with their own or a native wasp, brings about several consequences: 1) the seedings produced become epiphytes on native trees or man made structures competing with the figs and other native trees, especially when the introduced figs are more xerophytic than the native ones; 2) the production of hybrids between native and introduced figs may upset the native figs gene pools and biology of the introduced and native Agaonidae; 3) the presence of introduced wasps (agaonids and other primary sycophilous chalcidoids) stimulates the production of soft and juicy syconia which accumulate in large numbers under the trees and on sidewalks, making these areas slippery and dangerous for walking: the frugivorous bats and birds feeding on the ripe syconia, splatter their droppings onto sidewalks, cards and buildings causing damages to the paint and structures; 4) finally, the high population of fig wasps produced in towns where their host grow make them accidentally enter into the eyes of people, causing bad itching and pain.

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