Fig Wasps: Mechanism of Pollen Transfer

Abstract. *The fig* (Ficus) *is absolutely dependent upon pollination by minute agaonid wasps for development of fertile seeds. In some species of the wasp genera* Agaon, Allotriozoon, Blastophaga, Ceratosolen, Elisabethiella, Liporrhopalum, *and* Pleistodontes, *the females possess concavities ("corbiculae") to carry pollen. The New World* Tetrapus *and some Old World* Blastophaga *lack pollen-carrying structures and may carry pollen dusted over the body or in the digestive tract.*

Pollination of all species of figs (*Ficus*) is effected through their unique symbiotic association with chalcid wasps of the family Agaonidae. No other means of pollination is available to the plant, and the wasps cannot develop anywhere except in the receptacles of the fig. The manner in which the minute and almost hairless wasps carry enough pollen has been in doubt. The prevailing view, based primarily on observations of *Blastophaga psenes,* the pollinator of the edible fig (*Ficus carica*), is that pollination is effected by pollen grains adhering to the wasp's body surface and perhaps to its appendages (*1*). Other reports generally support the transport of pollen on the body surface (*2–4*). Agaonid wasps inhabiting *Ficus roxburghii,* on reaching the external orifice of the fig, usually remain for a short time close to it, drying their wings and cleaning off particles of debris which adhere to their bodies (*5*). Without doubt their bodies carry pollen grains but the number is always comparatively small after the wasps have cleaned themselves. Therefore, Cunningham says that the development of embryos in *Ficus roxburghii* appears to be an asexual process (*5*).

There is a period of several weeks or months between the maturation of pistillate flowers and that of staminate flowers in the same fig (Fig. 1). It is therefore impossible for the pistillate flowers to be pollinated from the staminate flowers of the same fig. When the wasps enter the fig cavity, they presumably pollinate some of the pistillate flowers which become seeds (Fig. 1). Subsequently a female wasp lays eggs in some of the pistillate flowers, presumably only those with short stigmas. Each such gall flower (Fig. 1) nourishes a single wasp larva which reaches maturity simultaneously with the maturation of the figs. The ripening of the staminate flowers inside a fig is synchronous with the emergence of the fig wasps from their galls.

Ficus occurs in all parts of the world where desert or frost do not prevail; it extends roughly between the latitudes of 35° north and south. This genus is divided (*6*) into four distinct subgenera. (i) Subgenus Urostigma is pantropical; (ii) subgenus Pharmacosycea occurs in Melanesia, Asia, and tropical America; (iii) subgenus Sycomorus is confined mainly to Africa; (iv) subgenus Ficus is limited to the Old World.

Each of the two New World subgenera of figs (Urostigma and Pharmacosycea) has its own group of related pollinators; Urostigma species are pollinated by *Blastophaga,* and Pharmacosycea species are pollinated by *Tetrapus.* In Urostigma the ripe anthers dehisce, but spontaneous discharge of pollen does not seem to occur. In *Ficus roxburghii* pollen tends not to escape from the anthers after dehiscence until the stamens are disturbed by the wasps (*5*). In New World Pharmacosycea and in *Ficus nota* and *F. macrophylla* (*3*) the anthers dehisce and pollen is shed apparently without the help of the wasps.

The females of *Blastophaga tonduzi,* pollinators of *Ficus hemsleyana* (Urostigma), emerged from the gall flowers where they developed and moved about as though searching for anthers while still within the fig. They opened the anthers with the antennal scapes and mandibles and appeared to move the pollen with the head and antennae as if they were eating it. Wasps associated with several other species of New World Urostigma behaved similarly. Galil (*7*) observed that females of *Blastophaga quadraticeps,* the pollinator of *Ficus religiosa,* approach the staminate flowers before leaving the fig and push their heads into the pollen sacs and chew.

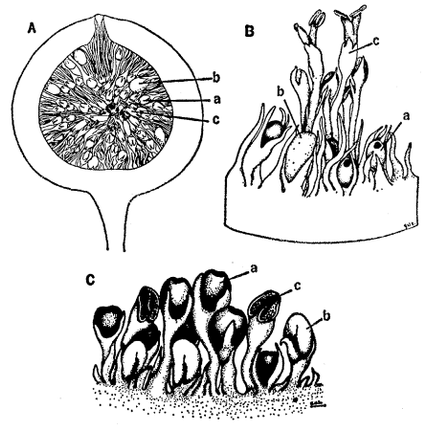

Fig. 1. (A) Cross section of a ripe Costa Rican fig [*Ficus glabrata* (Pharmacosycea)]; (*a*) gall flower; (*b*) seed; (*c*) staminate flower. (B) Section of a ripe Venezuelan fig [*Ficus radula* (Pharmacosycea)]; (*a*) gall flower; (*b*) seed; (*c*) staminate flower. (C) Section of a ripe Venezuelan fig (Urostigma); (*a*) gall flower; (*b*) seed; (*c*) staminate flower. Note the relative position of anthers in B and C.

In every New World Urostigma fig species I observed, as soon as a pollinating wasp reached the interior of the young fig to be pollinated, it pushed its head among the stigmas, in some cases for several hours; then it oviposited in the gall flowers. In *Ficus turbinata,* the wasps were still laying eggs 3 days after entering the fig.

To determine whether the wasps carry pollen externally, I put hundreds of *Blastophaga* females which emerged naturally from their Urostigma figs into small vials of alcohol, shook them violently for about 20 minutes, and centrifuged the contents of the vials. Only a few dozen pollen grains were found. When heads, thoraces, and abdomens of the female wasps were ground in alcohol, each body region separately, much pollen was found in the vials of ground thoraces. Dissections of the digestive tracts and buccal cavities of females showed no pollen, contrary to Galil's observations on *Blastophaga quadraticeps* (*7*).

New World *Blastophaga* females have pollen-holding concavities located one on each coxa of the front leg, and and two in the mesosternum (Fig. 2). Because these structures resemble the little baskets (corbiculae) used by the honey bee (*Apis mellifera*) to carry pollen, I call them corbiculae—"coxal corbiculae" for those located in the front legs and "sternal corbiculae" for the ones located in the mesosternum (Fig. 3).

The coxal corbicula is an elongate cavity in the mesal side of each front coxa, fenced by a row of bristles on one side (Fig. 3). Each sternal corbicula is a round depression, partially covered by a flap (Figs. 2 and 3) so that it opens medially. In the New World *Blastophaga* wasps, it usually has two rows or groups of hairs, one located anteriorly and the other posteriorly (Fig. 3). Corbiculae have been illustrated for fig wasps in the literature,

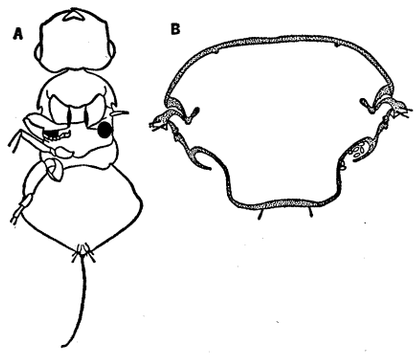

Fig. 2. (A) Ventral side of *Blastophaga jimenezi* (Central American species), with legs in part removed to show position of coxal corbiculae (elongate black spots) and sternal corbiculae (round spots). (B) Cross section of mesothorax of *Blastophaga jimenezi* showing position and shape of sternal corbiculae (pollen grains in place on right side).

without names or mention of function. Grandi (*8*) shows the sternal corbiculae of *Agaon paradoxum* and *Blastophaga estherae*, the coxal corbicula of *Blastophaga aguilari*, and both structures in *Blastophaga williamsi*. Mangabeira (*9*) and Galil and Eisikowitch (*4*) also show the sternal corbiculae of *Blastophaga lopesi* and *Ceratosolen arabicus*, respectively.

Both pairs of corbiculae are present in every species of *Blastophaga* (about 40) I have collected in Venezuela, Panama, Costa Rica, San Andres Island, and Florida, with the exception of two undescribed species, exclusive pollinators of *Ficus tuerckheimii*, which possess only the sternal corbiculae. The African *Elisabethiella stueckenbergi* and the New Caledonian *Blastophaga boschmai* also possess both sternal and coxal corbiculae. Among Old World species, sternal corbiculae only are found in *Blastophaga quadraticeps* (Africa) and *B. jacobsi* (New Guinea), in *Agaon hamiferum modestum* and *Allotriozoon prodigiosum* (Africa), in *Liporrhopalum mindanaensis* (Asia), in *Pleistodontes imperialis* (Australia) and in *Ceratosolen arabicus, C. capensis, C. galili* (Africa), and *C. pilipes* (Borneo) (*10*). Galil and Eisikowitch (*4*) report that as females of *Ceratosolen arabicus* crawl along the narrow exit made by the males among the staminate flowers their bodies become coated with pollen, but they do not mention the presence of any structure to carry pollen in this species.

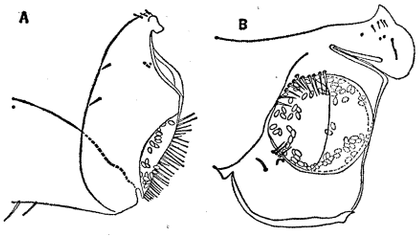

Fig. 3. (A) Coxal corbicula of Venezuelan *Blastophaga* sp. containing pollen grains. (B) Sternal corbicula of Venezuelan *Blastophaga* sp. containing pollen grains.

An unidentified species of Urostigma had an average of 344 seeds per fig in a total of 31 figs examined. A single fig of *Ficus goldmanii* pollinated by one wasp yielded 682 viable seeds. This must mean either that one wasp can pollinate at least 682 flowers (one ovule each), or that apomictic development occurred, or possibly that some pollination leads to apomictic development of other flowers in the same synconium. That the corbiculae can carry sufficient pollen for pollination is revealed by the presence of 404 grains in a single sternal corbiculae of a female *Ceratosolen arabicus*. Usually a fig is pollinated by several wasps, each with two or four corbiculae, assuring an adequate number of pollen grains. There was pollen in the corbiculae of every female wasp emerging from the ripe figs of species of New World Urostigma, but the corbiculae of wasps that had died inside the young figs after accomplishing pollination were empty or contained only few grains of pollen.

Females of *Blastophaga psenes*, the pollinator of the edible fig (*Ficus carica*), lack corbiculae but possess two longitudinal ventral cavities in the head (*11*). Several grains of pollen were present in these cavities in specimens examined, but I cannot determine whether or not these structures serve the same function as the corbiculae because the number of grains of pollen was too small. Much pollen was found, however, in the digestive tract. The ventral side of the head of New World *Blastophaga* females is smooth, not concave.

In the case of 12 species of *Tetrapus* wasps, there were no pollen-carrying structures, but much pollen was found in the digestive tract, as in *Blastophaga psenes*. The numerous anthers in pharmacosyceous figs are located more centrally than the normal and parasitized ovaries (Fig. 1) so that there is no true cavity in the figs. Thus the wasps crawling among the mass of staminate flowers become completely dusted with pollen. The stigmas of the fertile pistillate flowers in the young figs are very long, projecting into the center of the fig, so that it is possible for the egg-laying wasps to scatter pollen on the pistillate flowers while they are laying or searching for pistillate flowers in which to oviposit. Alternatively, *Tetrapus* females may carry pollen internally and regurgitate it on the stigmas of the flowers.

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X-ray and Electron Diffraction of Ocular and Bone Marrow Crystals in Paraproteinemia

Abstract. *Crystals in the cornea, conjunctiva, and bone marrow of a patient with a monoclonal gammopathy were analyzed by x-ray and selective-area electron diffraction. X-ray diffraction rings obtained from the abnormal crystalline deposits closely matched cholesteryl stearate patterns, and electron diffraction findings were suggestive of this lipid.*

Corneal and conjunctival crystals visible with the biomicroscope are rare in man. Childhood and adult cystinosis, crystalline corneal dystrophies, and paraproteinemia are the most common