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9 Fig Wasps and Pollination

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9.1 Introduction

The following text is illustrated by the slide show '*Ficus carica* and its pollination' (Kjellberg and Lesne, 2020). Slide numbers in the text refer to slide numbers in the first version of the slide show.

The obligate mutualism between fig trees (*Ficus*, Moraceae) and their pollinating fig wasps (Agaonidae, Hymenoptera) has been in existence for some 70 million years (Cruaud et al., 2012). It entails complex patterns of reciprocal evolution between the partners that has resulted in highly constrained relationships between the pollinators and their host *Ficus* species (Ramirez, 1970; 1974; 1977; Galil, 1977; Weiblen and Bush, 2002; Cook and Rasplus, 2003; Cook and Segar, 2010; Cruaud et al., 2010; 2012). Each partner cannot reproduce without the other. *Ficus* species are entirely reliant on the specialized agaonid fig wasps (Agaonidae; Chalcidoidea; Hymenoptera; slide 26) for pollination of their florets, which are encased inside the fig, an enclosed inflorescence (slide 8). Fig wasps locate their host tree by homing in on host-specific volatiles (Barker, 1985; van Noort et al., 1989; Ware et al., 1993; Hossaert-McKey et al., 1994; Gibernau et al., 1997; Grison et al., 1999, Soler et al., 2012; Souto-Vilarós et al., 2018) emitted by glands located in the fig ostiole (Souza et al., 2015) when the florets and stigmas are receptive for oviposition and pollination (Fig. 9.1A) (slides 28, 43). On locating receptive figs, the wasps negotiate a tight bract-lined opening situated at the apex of the fig termed the ostiole (slides 8, 41), to gain access to the florets lining the inside of the central cavity (slide 8). Negotiating the ostiole is no easy task, with the female wasp having to squeeze and labor her way between the tightly closed bracts. She is, however, remarkably adapted to do so. Her body, in particular her head and thorax, is extremely flattened and elongate (Fig. 9.1A). She also has rows upon rows of backward pointing teeth on her mandibular appendage (Fig. 9.2B), situated on the underside of her head, as well as a few strong teeth on her legs (Fig. 9.2D). They then pollinate the stigmas while ovipositing (Fig. 9.1B). They oviposit by inserting their ovipositor down the style (slide 10) to deposit an egg within the flower ovule, between the inner integument and the nucellus (Jansen-González et al., 2012). The wasp larva feeds on endosperm tissue within the galled flower. This endosperm may result from the double fertilization of the ovule (Jansen-González et al., 2012) or its development is parthenogenetic (Leclerc du Sablon, 1908; Corner, 1933), initiated by the wasp larva (Borges and Kjellberg, 2014). They are not able to develop anywhere else, except within the figs of their host *Ficus* species. When the wasps become adult, they emerge from their natal fig loaded with pollen, and leave in search of a fresh receptive fig

(Fig. 9.1D). The relationship is generally highly specific although some wasps may end up in the wrong host (Compton, 1990; Ware and Compton, 1992; Moe et al., 2011; Yang et al., 2012). However, there are numerous instances where more than one pollinator species regularly develops within a host fig species, either with parapatric distributions throughout the range of the host (Rasplus, 1996; Yu et al., 2019), or pollinators may co-occur within the same location (Rasplus, 1996; Molbo et al. 2003; Herre et al., 2008; Compton et al., 2009a; Rodriguez et al., 2017). Rarely a single wasp species may be the main pollinator of two or more *Ficus* species (Rasplus, 1996; Cornille et al., 2012; Wang et al., 2016).

In some *Ficus* species, the wasps, before leaving their natal fig, walk to the stamens and load pollen into specialized pollen pockets (Frank, 1984). Once the wasps have entered a receptive fig, they extract pollen from the pollen pockets and deposit it on the stigmas (Frank, 1984). In active pollination systems in general, and in *Ficus* in particular, limited amounts of pollen are produced (Pellmyr et al., 2020).

In about one third of *Ficus* species, including *F. carica* (Galil and Neeman, 1977), pollen transport is passive (Kjellberg et al., 2001; Cruaud et al., 2012). The fig produces a large amount of pollen and the wasps become coated with pollen on emerging from their natal fig (Galil and Neeman, 1977; slides 37, 38) (Fig. 9.1D). When they enter a receptive fig, the body of the wasp will brush against the elongate stigmas ensuring their pollination (Galil and Neeman, 1977; slides 42, 43).

Two breeding systems have evolved in the mutualism. About half of the 850 fig species are monoecious (seeds and wasps develop within the same fig), and the other half are gynodioecious (functionally dioecious, where male plants produce pollen and pollen vectors and female plants produce seeds) (Cruaud et al., 2012). In receptive figs of monoecious species, pistillate flowers are stacked in several layers due to variable pedicel length. The styles vary in length so that flowers located close to the fig wall have long stigmas while flowers located closer to the fig cavity have shorter stigmas. The wasps preferentially oviposit in shorter styled flowers, located closer to the fig cavity for several reasons. One is that the larvae located closest to the fig wall are more exposed to parasitic non-pollinating wasps ovipositing through the fig wall (Al-Beidh et al., 2012). Another reason is that female wasps developing in galls located close to the fig cavity are more likely to be already mated when wasps begin to emerge from a fig, and they emerge more rapidly from the fig and are larger (Anstett, 2001). As a result, ovules located close to the fig wall mainly turn into seeds while ovules located closer to the fig cavity are mainly transformed into galls hosting wasp larvae (Nefdt and Compton, 1996). These wasps will leave the fig in search of a receptive fig to enter. They transfer pollen from their natal fig to the next fig, ensuring the male function of the tree.

In functionally dioecious species, half of the trees (Valdeyron and Lloyd, 1979) have figs presenting very long styles (Condit, 1932; Beck and Lord, 1988a), so that wasps cannot oviposit (Fig. 9.3A,B) (slides 12, 42, 43). The wasps enter these figs by mistake, effect pollination and die without producing offspring (Anstett et al., 1997). As these trees produce seeds and no wasps, they are female. The figs of the other trees have short styled female flowers (Condit, 1932; Beck and Lord, 1988a; slides 10, 12, 28–30). The wasps oviposit in many of these flowers transforming them into galls (Fig. 9.3B,C) (slides 31, 32). Non-oviposited flowers generally produce no seeds because the ovules are not fertilized. This is due, depending on species, to very precise pollination of the flowers in which the wasps oviposit (Jousselin and Kjellberg, 2001), pollen stigma incompatibilities (Jousselin and Kjellberg, 2001), stigma traits (Beck and Lord, 1988b) or lack of pollen in the fig from which the wasp emerged (Leclerc du Sablon, 1908). As the figs of these trees produce pollen, pollen vectors (wasps), and no (or almost no) seeds, these trees are functionally male (Galil and Neeman, 1977; Neeman and Galil, 1978; Bronstein et al., 1992; Kerdelhué and Rasplus, 1996a, b).

Ficus carica is a functionally dioecious species, which is hypothesized to have enabled the functional adaptation of the species to the seasonal Mediterranean climates, the area encompassing the original distribution of this species (Kjellberg et al., 1987). The pollinator *Blastophaga psenes* Linnaeus, 1758 is not able to differentiate between the two sexes and enters figs of trees of both sexes. The volatile attractants released by receptive figs of male and female *F. carica* show no difference in chemical composition (Gibernau et al. 1997; Proffit et al., 2020). Although the figs on female trees are traps for the wasps, as the females are unable to reproduce in these figs, they are fooled into entering the fig as a result of the exact mimicking of male figs (size, color), and most importantly the chemical volatiles that the pollinators home in on (Patel et al., 1995).

Although *F. carica* has been in cultivation for thousands of years, an understanding of the role that the pollinating wasp, *B. psenes* (Figs. 9.1 and 9.2) plays in the reproduction of the figs (the process of caprifigation) is only a relatively recent elucidation (Baker, 1961). The earliest detailed accounts of the caprifigation process date back to the mid-19th century (Westwood, 1840). Subsequent investigations into the biology of *F. carica* (Solms-Laubach, 1882; Eisen 1896, 1901; Du Sablon, 1908; Longo, 1909; Ravasini, 1911; Rixford, 1918; Condit, 1920, 1932; Cotte and Reyner, 1923; Grandi, 1923; Crane, 1951) have ensured the ongoing commercial success of this crop.

9.2 Pollinator Wasp and Other Organisms Associated with *Ficus carica*

Blastophaga psenes is the only known pollinator of *F. carica* (Baker, 1961; Wiebes, 1994). The species has a large distribution and ranges from the Canary Islands to Uttarakhand in northern India (where it is associated with *F. palmata*), and from northern Iran to southern Algeria. However, no genetic analysis of the species has been attempted so far. Specimens from the Mediterranean area appear morphologically similar and may represent *B. psenes*. However, slight morphological differences between specimens from eastern localities (Iran, India), mostly associated with *F. palmata* (Fig. 9.4C,D), suggest that *B. psenes* as presently diagnosed may represent a species complex. Further studies are required to better define this supposedly well-known species. Morphologically, *B. psenes* has been thoroughly described by Grandi (1920, 1923, 1929), the female is winged and the male is apterous (Fig. 9.2C,D) like all other males of agaonids.

The female is characterized by a third funicular segment subdivided into three segments (Fig. 9.2A); funiculars F5 to F8 bear one row of multiporous plate sensillae; only a residual scar is visible on the mesopleuron in place of a pollen pocket (Fig. 9.2F); a mesoscutum without a median sulcus; and metasomal spiracles with a small peritremata. In males, the metanotum is partly fused with the mesoscutum and propodeum, therefore the metapleurae are widely separated, but well defined through their internal septa (Fig. 9.2E), and the head is round bearing multiple spicules in its anterior third. Molecular phylogenies (Cruaud et al., 2012) have placed *B. psenes* within a clade of agaonids (formerly described in the genus *Dolichoris*) associated with *Ficus* subgenus *Pharmacosycea* section *Oreosycea*. This result is corroborated by morphology and suggests that the association of *B. psenes* with *F. carica* (subgenus *Ficus*) may result from an ancient host shift. The venom gland reservoir (acid gland or poison bag) of *B. psenes*, and more generally in Agaonids, is exceptionally large compared to the venom gland of other chalcid wasps (Copland et al., 1973). The secretion produced (possibly associated with larval secretion) is involved in the transformation of the flower (that has had an egg laid into the ovary) into a gall.

Females *B. psenes* have two large ovaries each containing from 130 to more than 200 ovarioles that are tightly packed (Grandi, 1929). Each ovariole contains a single egg ready for laying and no oocyte (Elias et al., 2018). Indeed, all Agaonidae are pro-ovigenic. They mature all their eggs during pre-adult

development (Grandi, 1929; Copland et al., 1973; Dunn et al., 2011; Jia et al., 2014; Elias et al., 2018) and no ovigeny occurs in adult females. Eggs of agaonids are composed of three parts, the ovum, a long peduncle and the ovariole, recognizable by the presence of a tunica propria. Because the ovariole is filled by a substance similar to the substance observed in the ovum, ovarioles were not detected by Grandi (1929) in *B. psenes*. The fate of the ovariole is still debated. In *B. psenes*, Grandi (1929) assumed the ovariole is incorporated with the peduncle into the ovum while observations in other genera suggest it may remain lodged in the flower style (Copland et al., 1973) and may be used as a cue by other ovipositing females (Dunn et al., 2011). The process of oviposition takes about two and a half minutes in *B. psenes*, and the style of the flowers in which an egg has been deposited develops a characteristic rusty coloration.

The egg of *B. psenes*, is deposited near the style insertion between the nucellus and the inner integument of the ovule. The egg hatches about 4–5 days after oviposition. The young larva is translucent, whitish and glabrous and exhibits 13 segments. The final larval instar is ventrally bent. The head bears two acute mandibles. The prothorax is longer than the two other thoracic segments, which bear ventro-laterally two rounded outgrowths. The number of larval instars is not known in *B. psenes* and is globally poorly known in Agaonidae, only having been recorded twice with four instars in *Pegoscapus* (Jansen et al., 2012) and five instars in *Ceratosolen* (Jia et al., 2014).

The post-embryonic development time of *B. psenes* depends on temperature, season and other parameters, but may take about two months (Grandi, 1929) for the spring generation. The post-embryonic development time until pupation is the same in males and females. However, males have a shorter pupation time and therefore emerge from their galls one day before females (protandry). Males copulate with multiple females while they are still enclosed in their galls (Fig. 9.1C). Females of the spring generation get abundantly dusted with pollen while in the process of emerging from their natal fig. The female lifespan of *B. psenes* is relatively short and varies from 5 to 8 days under laboratory conditions, but only two days in the natural environment (Kjellberg et al., 1988).

Most *Ficus* species have a cohort of non-pollinating fig wasps also associated with their figs, which may be gallers (Compton and van Noort, 1992; Jansen-González et al., 2014), cleptoparasites (Joseph, 1958) or true parasitoids (endo and exoparasitoids) of the galling wasp species and pollinators (Compton and van Noort, 1992; Tzeng et al. 2008; Yadav and Borges, 2018), or even hyperparasitoids (Compton et al., 2009b). The galling non-pollinating wasps (at least the two species for which data is available) feed on galled nucellus and not, as the pollinators, on endosperm (Jansen-González et al., 2014). This assemblage can vary from zero, or one or two species to well over 40 species (Compton and Hawkins, 1992; Hawkins and Compton, 1992; Chen et al., 1999; Cook and Rasplus, 2003; Segar et al., 2013; Wang et al., 2015). The wasps are generally host-specific, but in Africa and South America some non-pollinating fig wasps are true generalists exploiting a series of local *Ficus* species (McLeish et al., 2012; Farache et al., 2018). Within non-pollinating wasp communities, parapatric distributions of morphologically similar species suggest that competition is a major structuring factor (Darwell and Cook, 2017). The single known non-pollinating fig wasp associated with *F. carica* is *Philotrypesis caricae* L., 1762 (Pteromalidae, Sycoryctinae) (Figs. 9.5A–C and 9.5A–G). As do many of the non-pollinating fig wasps, *Philotrypesis* species oviposit through the fig wall into the ovules (slides 32–34) (Fig. 9.6A–C). This non-pollinating fig wasp is a cleptoparasite of the pollinator wasp larvae. The egg is laid as the pollinator egg between the inner integument and the nucellus (Joseph, 1958). It feeds initially, together with the host *Blastophaga psenes* larva, on the endosperm tissue (the development of which was initiated by the pollinator larva) inside the galled flower until the second larval instar, where after the *Philotrypesis* larvae dominates resulting in the death of the pollinator larvae (Joseph, 1958).

A diversity of other organisms develops inside figs and are transferred between figs by the pollinating wasps (Wohlfarter et al., 2011). They include mites (Jauharlina et al., 2012), nematodes (Martin et al., 1973; Van Goor et al., 2018), fungi (Caldis, 1927; Michailides et al., 1996; Michailides and Morgan, 1998), and bacteria (Grimont et al., 1979). The biology of the mites is poorly known. They have been recorded as feeding on ovule tissue, and may disperse autonomously between figs on a tree, while dispersal between trees is phoretic with the mites hitching a ride on the body of dispersing female pollinating wasps (Jauharlina et al., 2012). Fig nematodes disperse inside the body of female pollinating fig wasps, and at least in the case of *Schistonchus africanus* do not colonize the wingless pollinator males (Vovlas et al., 1998). They feed on wasp and plant tissue. The effect of nematodes on the wasps varies. *Parasitodiplogaster* nematodes appeared to have a strong effect on agaonid wasp reproductive success in Panama (Herre, 1993), while their effect is only marginal in Baja California (Van Goor et al., 2018). It has been proposed that nematodes avoid entering the lethal trap constituted by dispersing non-pollinating fig wasps that oviposit through the fig wall, never entering a fig (Herre, 1993). However, *Parasitodiplogaster* nematodes in Baja California and the *Ficus carica* nematode *Schistonchus caprifici* (Gasparrini, 1864) colonize both the pollinator and the parasitoid fig wasps (Vovlas and Larizza, 1996; Van Goor et al., 2018). Pollinating wasps also carry fungi from ripe figs to receptive figs. This is the case for *Fusarium moniliforme*, which is carried from fig to fig by *Blastophaga psenes*, the pollinator of *Ficus carica*, and is responsible for a disease called endosepsis (Davey and Smith, 1933; Michailides et al., 1996; Michailides and Morgan, 1998). The presence of *Fusarium moniliforme* strongly reduces the reproductive success of the wasp (Michailides et al., 1996; Michailides and Morgan, 1998). *Blastophaga psenes* often exits the receptive fig it has entered, so that visited figs often contain no wasp corpse (Gibernau et al., 1996). This can be seen as a wasp strategy to limit contamination by germs and parasites present in the wasp's body. Bacteria such as *Serratia ficaria* (Grimont et al., 1979) have been found to be transferred between figs by the pollinators, though no negative effect on the wasps have been observed (Grimont et al. 1979; FK, personal observation).

9.3 Pollination Biology of Wild Common Fig, *Ficus carica* in its Native Habitat

Ficus carica L. 1753, is native to the whole of the Mediterranean basin (Khadari et al., 2005b), where both cultivated plants and wild populations co-exist (Figs. 9.7A,B and 9.8A). Fossils, some of which date back 100,000 years, have been found in France (Planchon, 1864; Ambert et al., 1995; slide 3). *Ficus carica* is also present along the south-eastern coast of the Black Sea and the Caspian Sea, where it presents somewhat different phenotypes and is genetically somewhat different (Khadari et al., 2005a). These forms were described under the names *Ficus colchica* Grossh. (slides 4, 5) and *Ficus hyrcana* Grossh. They present more gracile shoots than typical *F. carica* (Fig. 9.4B). The arid- adapted species *Ficus palmata* (slides 6, 7) is the closest relative of *F. carica*, but is not conspecific (Berg and Corner, 2005; Khadari et al., 2005b). It is distributed from Ethiopia to India and Nepal (Fig. 9.4C,D).

Descriptions of the year-round phenology of *Ficus carica* are confusing, because most are based on observations of male tree cultivars. The yearly number of wasp generations varies geographically, but also depends on whether wild trees or some specific male tree cultivars are investigated. Here we first describe the year-round phenology of wild trees in the South of France, where *Ficus carica* is native, as presented by Valdeyron and Lloyd (1979) and improved by further observations in Kjellberg et al. (1987). This phenology is illustrated in slides 17–47.

Terminal buds flush in late March and the shoot grows until July. At each node, a fig bud may appear on the shoot that has developed in that year, at the axil of the leaf. Fig buds appear progressively along

the shoot, from the base to the apex of the shoot. On female trees, fig buds develop rapidly into receptive figs that become receptive from mid-June to mid-July. Often the sub-terminal fig bud remains dormant until the next spring. However, the spring development of such sub-terminal fig buds stops rapidly after onset and the fig aborts. On male trees, fig buds appear later, from late July to the end of summer. The basal ones progressively become receptive before winter. The distal fig buds, closer to the apex of the branch and representing often about half of the fig buds, do not develop into receptive figs before winter. They overwinter as fig buds and, the next spring, they develop synchronously into receptive figs. These figs, which have overwintered as fig buds, are the sole figs producing abundant, functional pollen. These delayed polliniferous male figs are visited by wasps in April and release the next generation of wasps in June–July (Fig. 9.8B). These are the sole wasps in the yearly cycle that are abundantly dusted with pollen (Fig. 9.1D). When the wasps emerge from most of these figs, there are no receptive figs on male trees, but all the figs on female trees are receptive. Hence, these wasps visit female trees, ensure pollination and die without producing offspring. The latest wasps emerging from the latest polliniferous figs reach the first figs to become receptive on the shoot of that year of male trees, in late July–early August, enter them and oviposit. In Montpellier, in these figs, the wasp larvae reach the last larval stage in September–October and do not complete their metamorphosis before next spring. The figs will ripen the following April releasing the wasps that will ensure the colonization of the polliniferous figs. Hence, there are two yearly wasp generations.

In particularly warm years or in warmer climates, the wasps developing in figs that have been visited in late July become adult before winter. As fig buds develop progressively into receptive figs along the shoot of that year, the wasps find receptive figs on the same tree and visit them. These later figs are the ones that will overwinter containing last stage fig wasp larvae inside. Hence, depending on climatic conditions, there are two or three yearly generations of wasps. Detecting the yearly number of generations of wasps in winter is easy. If the figs hosting wasps in winter are at the base of the shoot that has developed in that year, then it is a two-yearly wasp generation cycle (slide 21). If the figs hosting the wasps are higher up on the shoot of that year, then it is a three-yearly wasp generation cycle. This conclusion can be confirmed by looking for fig seeds. In most years, in Montpellier, some seeds are found in male figs visited by wasps emerging from polliniferous figs that have overwintered as fig buds. Figs that develop directly on the shoot of that year do not produce functional pollen. Hence, there are no seeds in male figs visited by wasps emerging from figs developing on the shoot of that year.

However, fig and axillary vegetative bud development are under the control of apical dominance. Lopping off the terminal bud, or any factor reducing its vigor such as strong frost in winter, will result in early development of the sub-terminal vegetative bud and of the associated fig bud, making the reading of phenology somewhat more complex, but still feasible. For instance, early figs on male trees, that have been receptive at the same time as the main female tree crop, contain not only wasp offspring, but also many seeds and they ripen sweet (Condit, 1920), while the figs that are visited following the usual natural yearly cycle are visited by late emerging wasps and contain only few seeds. This is because the last wasps to emerge from a polliniferous fig carry reduced quantities of pollen (Kjellberg et al., 2014). Another confusing factor is when fig trees grow in places allowing prolonged vegetative growth throughout summer, or when intensive pruning produces the same effect. In such cases, development of the fig bud becomes somewhat atypical (slide 81 for a cultivar in a moist climate).

Much confusion in the literature stems from the presence in cultivation of male tree genotypes presenting an atypical early onset of fig bud development (slides 65, 66). In some cultivars, fig buds begin to develop rapidly on the shoot of that year on male trees. As a result, figs become receptive in

July, when wasps are emerging from the polliniferous figs. These figs are readily visited, and they release a new generation of wasps before winter. On leaving their fig, these wasps find receptive figs on the same male tree, visit them, and their offspring overwinter in these figs. Hence, figs on the shoot of that year on male trees may release wasps before winter for two different reasons, either (i) because of a long growth season extending late in autumn, or (ii) because they develop on particular cultivated genotypes. In the 19th and 20th century literature on *Ficus carica* cultivation, the figs developing on male trees and ripening before winter are called mammoni, whatever their origin. Figs overwintering with wasps inside are called mamme, whether visited by wasps emerging from polliniferous figs or from mammoni figs, and polliniferous figs are called profichi (Condit, 1947). Because the term mammoni represents two different biological phenomena, the classical literature is almost impossible to analyze.

On wild male trees, the colonization of the first receptive figs on the shoot of that year by wasps emerging from polliniferous figs is a sensitive point during which the continuity of wasp generations is difficult to observe. In some years the continuity of generations is poor, resulting in few visited figs on few male trees. Indeed, on average, only one in several thousand female wasps produced by polliniferous figs will breed successfully. The lack of receptive figs on male trees at the time when most figs are receptive on female trees is also observed in other *Ficus* species that grow in highly seasonal climates, and that have developed grouped fig receptivity on all female trees. This is the case for *Ficus exasperata* (Patel, 1996), and *Ficus erecta* (Tzeng et al., 2006). The taxonomy and phylogeny of genus *Ficus* shows that these examples represent three independent instances of evolution of adaptation to highly seasonal climates (Cruaud et al., 2012). Hence, the succession of generations on *Ficus carica* as described above corresponds to a general pattern that may emerge when *Ficus* species adapt to seasonal climates. The reason why male trees do not produce receptive figs at the time when figs are receptive on female trees is straightforward. When such figs are present, the wasps, which are guided to receptive figs by the volatile organic compounds they release (Soler et al., 2012), move en masse to these nearby figs as described by Condit (1920) 'it is not at all uncommon to find mammoni figs with five or six females, either around the eye, or trying to force an entrance [slide 66]. If such figs are opened, the spaces between the bracts are literally packed full and black with the living and dead bodies of *Blastophaga*'. These wasps do not go to the female trees and hence, do not ensure the reproductive success of the male plant. Therefore, a male tree producing such figs is counter selected for under the premise of natural selection.

The matching of wasp emergence from overwintering figs and receptivity of the polliniferous figs lacks precision. The development of the overwintering wasps is stopped at the last larval stage by low temperatures. As a result, the overwintering wasps are all synchronized at the last larval stage. Their development resumes if sufficiently high temperatures are reached, and this sometimes happens in the middle of winter for trees growing in protected places (Joseph, 1958). If a fig-bearing branch is cut in winter and brought into a heated room in a water jar, after a few days, the wasps emerge. Conversely, the development of receptive figs depends on a sufficient period of vegetative growth, which depends on a sum of suitably warm degree-days.

Further, temperatures in April may drop below those required for wasp emergence so that emergences from figs stop for several days (Khadari et al., 2005a,b), while the receptive figs continue to grow. Hence, receptive figs need to be and are capable of waiting for several weeks for the emergence of wasps (Khadari et al., 2005a,b; slides 22, 23).

9.4 Fig Crops and Pollination

Biology of Cultivated Common Fig, *Ficus carica*, in its Native Range

Wild female *F. carica* produce sweet tasty pollinated ripe figs in autumn (Fig. 9.8A) (slide 52), but they abort unpollinated figs. In places where *F. carica* thrives as wild trees, and where fig cultivation was limited, female trees germinating in ditches along fields were often preserved and even tended (slide 53). They were pollinated by wasps emerging from nearby male trees and produced large quantities of pollinated ripe figs. In the Montpellier region (South of France), these figs were often dried by farmers for family consumption during winter and could constitute about 5–10% of the caloric diet of a family during winter (Kjellberg and Valdeyron, 1984). Pollination was generally successful because of the presence of nearby wild male trees and because only few female trees were tended. Locally appreciated wild female genotypes were sometimes multiplied through cuttings within a village, benefiting from natural pollination (Kjellberg, 1995). This was originally the case for the variety Black Bursa (Bursa Siyahi) in the Bursa region of Turkey for the production of fresh figs. These figs require pollination, but as long as cultivation remained at a small scale, the peasants relied on natural pollination. When the number of cultivated trees increased to provide figs for the Istanbul market, a large fraction of the fig crop aborted and fig-cultivation experts from Izmir were called in. They introduced the controlled pollination techniques (see below) that were locally unknown in the Bursa region (U. Aksoy, personal communication). This easy incorporation of wild plants into cultivation systems may explain the strong genetic diversity of fig cultivars at the western limit of *F. carica*'s natural range (Achtak et al., 2010) even though initial fig domestication is assumed to have occurred in the east Mediterranean. Indeed, there is no report of a genetic signature of introduction into the west Mediterranean of domesticated plants from the east Mediterranean. This is in stark contrast with the olive, another emblematic tree crop in the Mediterranean. Olive presents much more marked domestication traits and a clear signature of introductions of domesticates from the east Mediterranean to the west Mediterranean is demonstrated accompanied by some introgression in the west by local wild olive (Gros-Balthazard et al., 2019).

Some of the most important fig cultivars, including the Turkish Sari Lop or Smyrna fig, require pollination for fruit development (Condit, 1947; Gaaliche et al., 2011). The fruiting phenology of these cultivars is the same as that of wild female trees (Fig. 9.9B) (slide 57). However, they are mainly cultivated in locations that favor the natural drying of the ripe figs, i.e. where the climate at the end of summer and in autumn is warm and dry. Often the trees are planted in deep soils, in habitats where rocks are missing, i.e. where natural populations of *F. carica* are absent (Fig. 9.9A) (slides 55, 56, 58). Further, the trees are planted in large number, by far outnumbering wild local male fig trees if any are present. Therefore, the farmers need to manage pollination in a process called caprifigation. This is achieved by picking polliniferous figs (profichi in the agronomic literature) in June from male trees (caprifig trees in the agronomic literature) just before wasp emergence, and suspending them in female trees (slides 59, 61, 62). The profichi originate either locally from trees cultivated by the farmers (slides 60, 63, FK personal observation) or from wild growing local trees (Aumeeruddy-Thomas and Hmimsa, 2018) or the profichi may be provided by specialists who sell them on markets (slide 64). Often farmers use a mix of locally produced and commercial profichi figs to cover the period of fig receptivity (U. Aksoy, personal communication; FK personal observation). The farmers are conscious of the importance of the male figs that overwinter, sheltering the wasps (mamme figs) to ensure colonization of the profichi. In case of climatic accidents leading to a deficit of mamme figs on their cultivated caprifig trees, farmers may import mamme figs and suspend them in the male trees to ensure the visitation of the profichi (slide 67). Caprifigation of caprifig trees with mamme figs is reported in Turkey with mamme figs from Greece (Eisen, 1901), for the Kerkhennah islands off Tunisia (G. Valdeyron, personal communication 1982, slide 67) and for the Greek Cyclades islands (Tournefort, 1717) with mamme figs from the continent. In Turkey, along the Meander valley, some villages are specialized in the production of profichi figs. In at least one of them, the caprifig cultivar in use

produced very early receptive figs on the growth of the year facilitating local survival of the pollinating wasps despite the removal of most profichi from the trees (slides 64, 65).

A domestication trait in fig cultivars is the occurrence of parthenocarpy, i.e. fig development without pollination. Some such cultivars produce the same crop of figs that ripen in August–September as do wild female trees, and as do Smyrna figs. Such cultivars may be favored to avoid diseases transmitted by the pollinating wasps. Alternatively, male figs may be treated with fungicides (Michailides et al., 1996, slides 68–76).

In some cultivars, the sub-terminal fig bud(s) that overwinters on the tree does not abort early when growth resumes in spring. At receptivity, these figs cannot be pollinated because mamme figs on male trees contain no pollen. These figs may continue to develop as parthenocarpic fruits and ripen at the same time as the profichi, in June–July in the South of France (slides 77, 78). They bear different names in different countries such as breba figs or figues-fleurs, or first crop figs. First crop figs have overwintered as fig buds (slide 78) and their development has been affected in the same way as figs that overwintered as fig buds on male trees. They include a thicker, spongier fig wall and larger size so that flowers are less packed within the fig cavity. Their styles are also somewhat shorter than those of second crop figs (compare slides 42, 43 with slides 79, 80). First crop figs are not a natural crop on female trees and, as such, are prone to early fruit dropping. Abortion is less marked in trees that have more resources available. This may be the reason for the cultivation of some cultivars in which the first crop is parthenocarpic but not the second one, as in such cultivars, in the absence of pollination, most second crop figs abort. When such trees are cultivated in low number in the Montpellier region, because of the availability of pollinating wasps stemming from wild trees, it is worthwhile removing by hand the second crop figs. In the Montpellier region we investigated a one hectare orchard of such a cultivar. The nursery man who provided the plants included a wild germinated tree for pollination. The tree turned out to be female. Nevertheless, we recorded that second fig crops were more visited on the adjacent fig trees than in the remainder of the orchard and as a result they aborted a larger fraction of their first fig crop (Kjellberg et al., 1983). The simple explanation is that the second fig crop of the wild female tree was more attractive to the pollinators than the cultivar's figs, and hence attracted pollinating wasps that also visited neighboring trees. This trait associated with domestication has resulted in reduced attractivity of the second fig crop with an associated reduction in pollinator visits, a higher second fig crop abortion and hence more resources available for the first fig crop.

9.5 The History of Fig Cultivation and Pollination

Monkeys and apes relish eating figs produced by a diversity of *Ficus* species and early humans were probably no exception. Figs of *F. carica* were consumed by humans from early times. Indeed, charred fig seeds and even fig remains have been found in settlements along the Jordan valley dating back 11,000 BP (the occurrence of parthenocarpic figs in a site dating to 11,400 BP, in the Jordan Valley is doubtful) (Kislev et al., 2006), and figs and fig trees are regularly included in old scriptures from the region. This is no surprise as the climate of Galilea is favorable for fig tree growth and wild *F. carica* is still thriving (personal observation). More unexpectedly, charred fig seeds appear in sites of the Rakka governorate along the Euphrates in the tenth millennium BP (Willcox, 2014). The dry climate in that region is not compatible with the presence of wild *F. carica* populations. Further Willcox (2014) stated: 'finds of figs are numerous on a number of early sites in the southern Levant where they were apparently used intensively at an earlier date than in the north. However they occur well away from their natural habitats, so even in the south it appears that figs and probably the cultivation of fig trees was spreading thanks to human contact over large distances.' Fuller and Stevens (2019) provide a map of early archaeological sites presenting evidence for figs. Several sites to the East are outside what we consider the natural range of *F. carica* suggesting fig cultivation outside its natural range. There is no

early archaeological documentation of fig consumption in the Meander valley region. This contradicts the classical idea (Condit, 1947), included in the name *F. carica*, that Caria was the region of origin of the species. Indeed, the landscape in which the fig is cultivated south of Izmir is not compatible with the presence of large wild populations of fig trees.

The first known description of caprification is given by Theophrastus (391–288 BC). The term he used for caprification, *erinasmos*, is the same as used today in Greece and suffers no ambiguity as to its meaning. He states that the pollinators develop feeding on the seeds in the caprifigs. The classical Roman word for male fig tree is *caprificus*, and the verb ‘caprificare’ translates as ‘to caprify’, so this term has also survived up to today. Such indigenous terminology for caprification is in stark contrast with old Hebrew scriptures in which there is no evocation of the male fig tree and no specific word for caprification (Goor, 1965). In the Turkish language, *İncir* is the edible fig, *İncir Ağacı* is the female fig tree and the caprifig tree is called *Erkek İncir*, i.e. male fig. *İlek* is the first male crop of the season. In Turkish, *ilk* is first and *Erkek* is male. However, in some regions, the names *Tum İncir* and *Eşek İnciri* are used for caprifig trees. *Tum İncir* means the unripe fig while *Eşek İnciri* means donkey figs, i.e. a fig that can only be eaten by donkeys (Oğuzhan Çalıřkan, pers. com.). Throughout the Arab speaking countries, the caprifig tree is called *Dokkar* (or *dhakar*), which means male. This is true from Portugal, where the caprifig tree is known as *figo di toca* (Eisen, 1901), to Syria. However, in the north of Syria, in the Idlib governorate, a specific word, ‘*tub*’ is used for caprifig tree, which could originate in *Tum İncir* (Oğuzhan Çalıřkan, personal communication). These differences in terminology for caprifigs and caprification suggest independent origin of the practice of caprification in northern Syria, Turkey, Greece and Italy, while the practice of caprification may have been imported, or is of more recent origin in the south of the Mediterranean basin. A thorough comparative linguistic investigation of the terminology associated with caprification is required before firm conclusions can be drawn.

A series of historical accounts of caprification around the Mediterranean basin in the late 19th–early 20th century are provided by American authors that were involved in introducing *Blastophaga psenes* to America and in optimization of fig cultivation (Eisen, 1896, 1901; Condit, 1947). The agronomic literature describing caprification practice and the succession of fig crops in California demands some interpretation as they were conducted outside the natural range of the fig in the absence of natural populations. Eisen (1901) states that the caprifig trees should not be planted close to the female trees as they require sheltered places and shade. Indeed, female plants used for fig production are generally not planted in the natural habitat of *F. carica*. He also states that ‘The various crops of the caprifig do not always succeed each other continuously. There is a frequent lapse of time between the falling of the profichi and the appearance of the mammoni.’ Hence many of the caprifigs cultivated in California presented the typical phenology of wild caprifig trees presented above. Caprification of caprifig trees was also used early in California (Eisen, 1901). The difficult succession of crops on the male trees is still present in Condit’s 1933 account of fig culture in California. He states, ‘One weak point in the succession of crops, the break between the profichi and the mammoni crops, can in the case of some varieties be overcome by pinching back the tips of new shoots here and there over the tree, about the middle of May. This temporarily stops the terminal growth but stimulates development of lateral fruit buds which will be ready to receive blastophagas early in June.’ Lopping off the terminal bud (in May in France) is an easy way to induce the early development of the subterminal fig bud, resulting in a fig that is receptive when wasps emerge from the profichi. Progressively caprifig cultivars, in which the phenological gap between profichi and mammoni was missing, were chosen. Such a cultivar is reported in Condit’s (1955) compendium of fig cultivars ‘On trees of the Milco at Fresno, the mammoni figs appeared in numbers a week or ten days before the profichi’, and today only such cultivars are used.

Ficus carica has also been introduced for cultivation to various other parts of the world where there is a suitable climate, such as Australia (Morton, 1987), China (Morton, 1987), India (Rattanpal et al., 2017), Japan (Morton, 1987), North America (including California (USA), Mexico, Costa Rica, and the West Indies (Condit, 1920, 1933, 1955; Morton, 1987; Armstrong, 1988, 2010), South America (including Argentina, Brazil, Chile, Colombia, Venezuela) (Morton, 1987), and South Africa (Tribolet, 1912; Wohlfarter et al., 2011; Giliomee et al., 2017). In some of the introduced areas, *F. carica* has become naturalized in suitable habitats. In southern California, trees establish in riverbeds and creeks among willow and cottonwood thickets, and have become invasive (Holmes et al., 2014).

There are a huge number of varieties of *F. carica* in cultivation, in areas of origin (Achtak et al., 2010) as well as in areas of introduction with some widely known introduced cultivars. Condit (1955) provides a key for almost 700 cultivars. Adriatic, Black Ischia, Brown Turkey, Brunswick, Genoa, Celeste, and Marseilles, Poona, and Purple Genoa are favored in warmer climates and do not require pollination (Morton, 1987). These varieties are usually those that are first introduced to new regions, because they do not require the more complicated horticultural practice of caprification. The Smyrna fig and its pollinator *B. psenes* is often subsequently introduced to various parts of the world presenting Mediterranean climates to facilitate the commercial cultivation of this variety, used for the dry fig market, which if not pollinated abort their figs before they reach maturity (Tribolet, 1912). Although the Smyrna fig (known as the Calimyrna fig in California) was introduced to California around 1880, the pollinator only followed around 1899 (Morton, 1987, Tribolet, 1912), after it was discovered that it was not present in the caprifig trees that had been established 20 years earlier. Experimental deduction through the process of artificial pollination elucidated the need for the pollinator wasp to perform this duty (Tribolet, 1912). Following the successful introduction and propagation in California, the Smyrna fig was imported into South Africa in 1902/1903 and the pollinator was introduced from California in 1908, and has been cycling successfully ever since then (Tribolet, 1912; Wohlfarter et al., 2011).

In California and South Africa the caprifig trees (male trees) of *F. carica* produce three caprifig crops per year: the summer profichi crop (with galls and male flowers); an autumn mammoni crop (galls and abortive male flowers); and an overwintering mamme crop (galls and abortive male flowers) where the figs only mature the following spring (Armstrong, 1988; Giliomee et al., 2007; Tribolate, 1912). Pollen laden female fig wasps leaving the profichi crop enter the mammoni crop and oviposit into the ovules; the resulting wasp progeny leaving this crop then oviposit in the mamme crop and those wasps then complete the cycle by ovipositing in the profichi crop again. Pollen from the profichi crop is used to pollinate the Smyrna (Calimyrna) orchards in mid-summer, as the other two crops do not produce pollen in the figs (Armstrong, 2010). The wasps survive the cold winter months as larvae in the overwintering mamme crops. Female trees produce two fig crops per year: the breba crop, ripening in early summer; and the main second crop ripening in autumn. The process of caprification can aid the transmission of internal rot fungus or endosepsis (*Fusarium moniliforme* var. *fici*) (Caldis, 1927) from the male caprifigs to the female Smyrna figs (Armstrong, 2010; Caldis, 1927; Davey and Smith, 1933; Michailides and Morgan, 1998; Wohlfarter et al., 2011). Intervention is required to avoid this transmission. In California the overwintering mamme crop is harvested in spring and the figs are treated with a fungicide after being split open (Armstrong, 2010). They are then re-introduced to the orchards so that the emerging wasps can enter the profichi crop. This fungus can result in considerable crop losses, with hot and humid conditions being ideal for rapid transmission (Caldis, 1927; Michailides and Morgan, 1998; Wohlfarter et al., 2011).

Conclusion

The cultivated fig *Ficus carica* is a dioecious species that has been in cultivation for thousands of years, although an understanding of the role that the pollinating wasp *Blastophaga psenes* plays in the reproduction of the cultivated fig (the process of caprification) is only a relatively recent elucidation. The process of caprification where oviposition by the pollinator *B. psenes* is required to ensure successful ripening of the female figs still plays an important role in the cultivated fig industry. In natural wild populations of *F. carica*, figs suitable for consumption are produced on female trees only if they are pollinated by *Blastophaga psenes*, released from figs borne on male trees, which contain both wasps and pollen, and are usually not eaten. The male figs that produce the wasp pollinator were called 'caprifigs' because they were not eaten and were said to be 'only good for the goats'. Commercial cultivation of fresh figs for the consumer market usually centers on parthenocarpic cultivars, i.e. varieties that have been artificially selected for during the long association of cultivation by humans. Some of these varieties have been artificially selected to not need pollination to produce ripe figs and their propagation is via the process of cuttings (truncheons). Fig trees will normally abort their fig crop if the figs are not pollinated as the figs are then an energy cost with no benefit to the tree. This mode of vegetative propagation allowed for the anthropogenic expansion of the species' distribution to non-native regions across various parts of the world, and may have been one of the earliest forms of agricultural domestication of a plant species, predating cereal production. The best fig cultivars grown for dry fig production have mainly been cultivars that need pollination (caprification) such as the Turkish Sari Lop or Smyrna fig, which has a nutty flavor and contains seeds, in contrast to the sweeter fruit of the parthenocarpic varieties that are much softer without seeds (Armstrong, 1988; 2010; Tribolet, 1912). The pollinator has hence also been introduced to various parts of the world where *F. carica* is cultivated to enable the production and supply of figs to the dry fig market (Mars, 2003). In many regions, however, these cultivars are being progressively replaced by cultivars that do not require pollination in order to avoid sanitary problems and costs.

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Fig. 9.1. *Blastophaga psenes*. (A) A female attracted to a receptive fig by host-specific volatiles emitted by the fig ostiole, (B) female ovipositing in a receptive fig of a male tree, (C) male opening a hole into a gall containing a female, (D) female escaping the fig dusted with pollen. (Figures courtesy of F. Kjellberg and J.Y. Rasplus.)

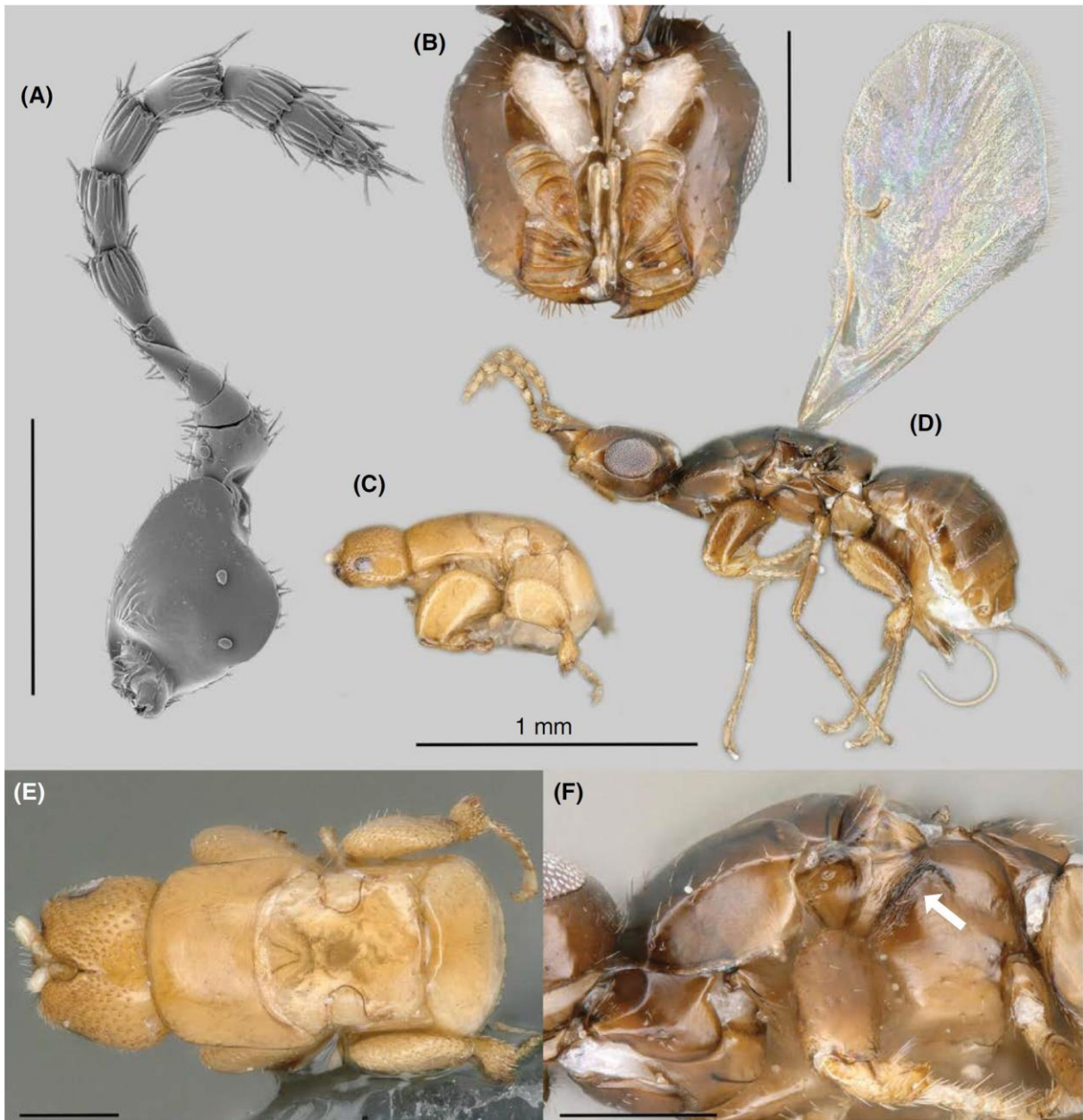


Fig. 9.2. *Blastophaga psenes*. (A) Antenna (SEM), (B) Head ventral, showing the mandibles and their appendage bearing 6 ridges, (C, D) Habitus male and female, lateral view, (E) Habitus male dorsal view, (F) Mesosoma female ventral view, white arrow shows the scar in place of pollen pocket. Scale = 200 μ m excepted for habitus = 1 mm. (Figure courtesy of J.Y. Rasplus.)

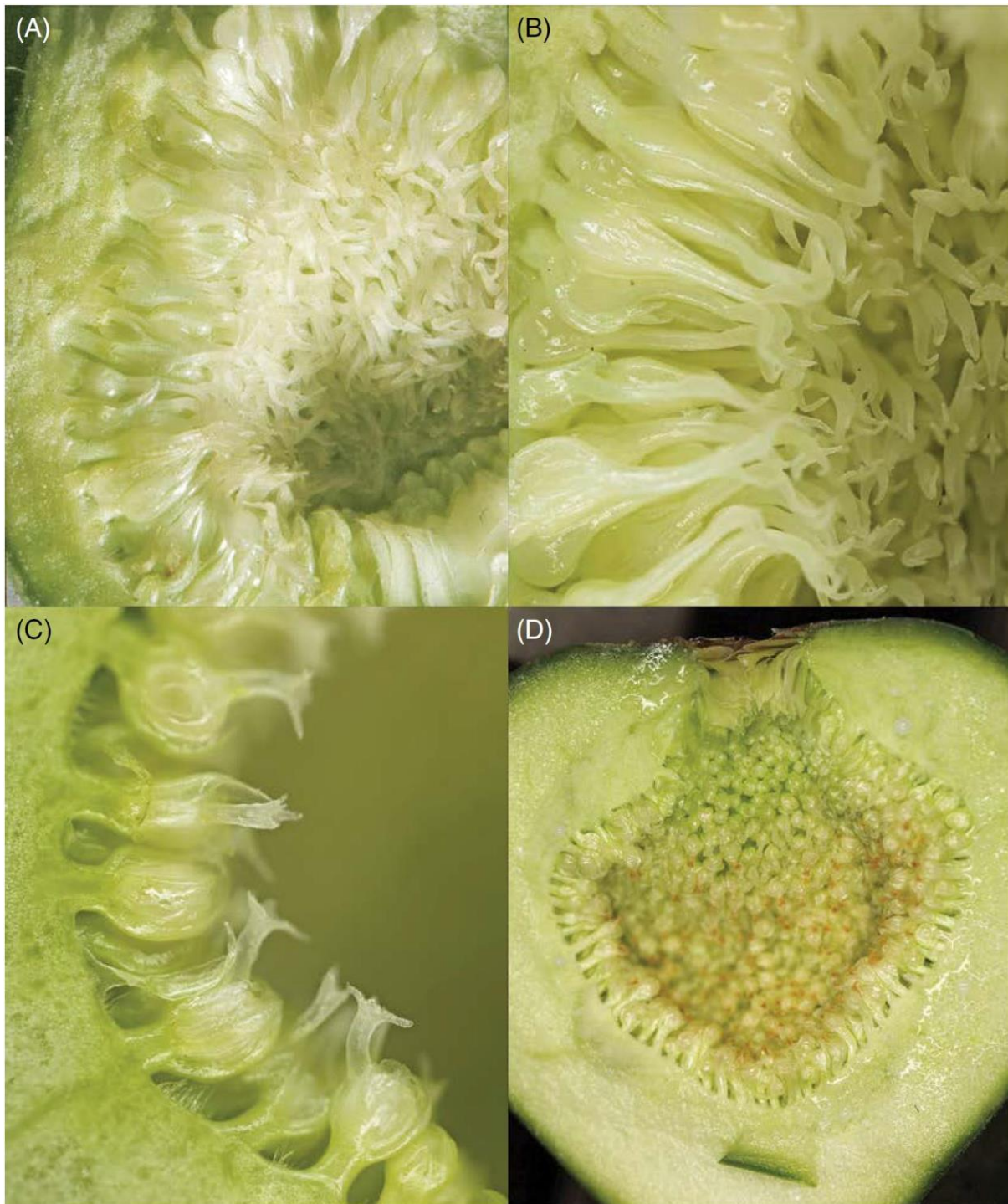


Fig. 9.3. *Ficus carica*. (A) Female tree, receptive fig; the elongate stigmas that will brush the body of the wasp, collecting pollen and ensuring seed set. (B) Detail of the elongate stigmas with papillae on which pollen will stick, the styles are long and do not allow wasp oviposition. (C) Male tree, inside a receptive fig the styles are short allowing wasp oviposition. (D) Male tree, fig a few days after oviposition; immature male flowers are visible in the upper part of the fig; in the lower part, female flowers show style with brown trace of ovipositor insertion, the pedicel elongates and the ovule begins to swell turning into a gall. (Figures courtesy of F. Kjellberg.)



Fig. 9.4. (A) *Ficus carica* (typical form), on rocks along river banks. (B) *F. carica* (form *Ficus colchica* Grossh), this is morphologically the most divergent form of *F. carica* with gracile branches and flexible leaves, Black Sea coast, Turkey. (C) *Ficus palmata*, Adiyaman Province, Turkey; *F. palmata* is distributed from Ethiopia to India and Nepal, and is the sole species closely related to *F. carica*. (D) *F. palmata* male tree with profichi. (Figures courtesy of F. Kjellberg.)

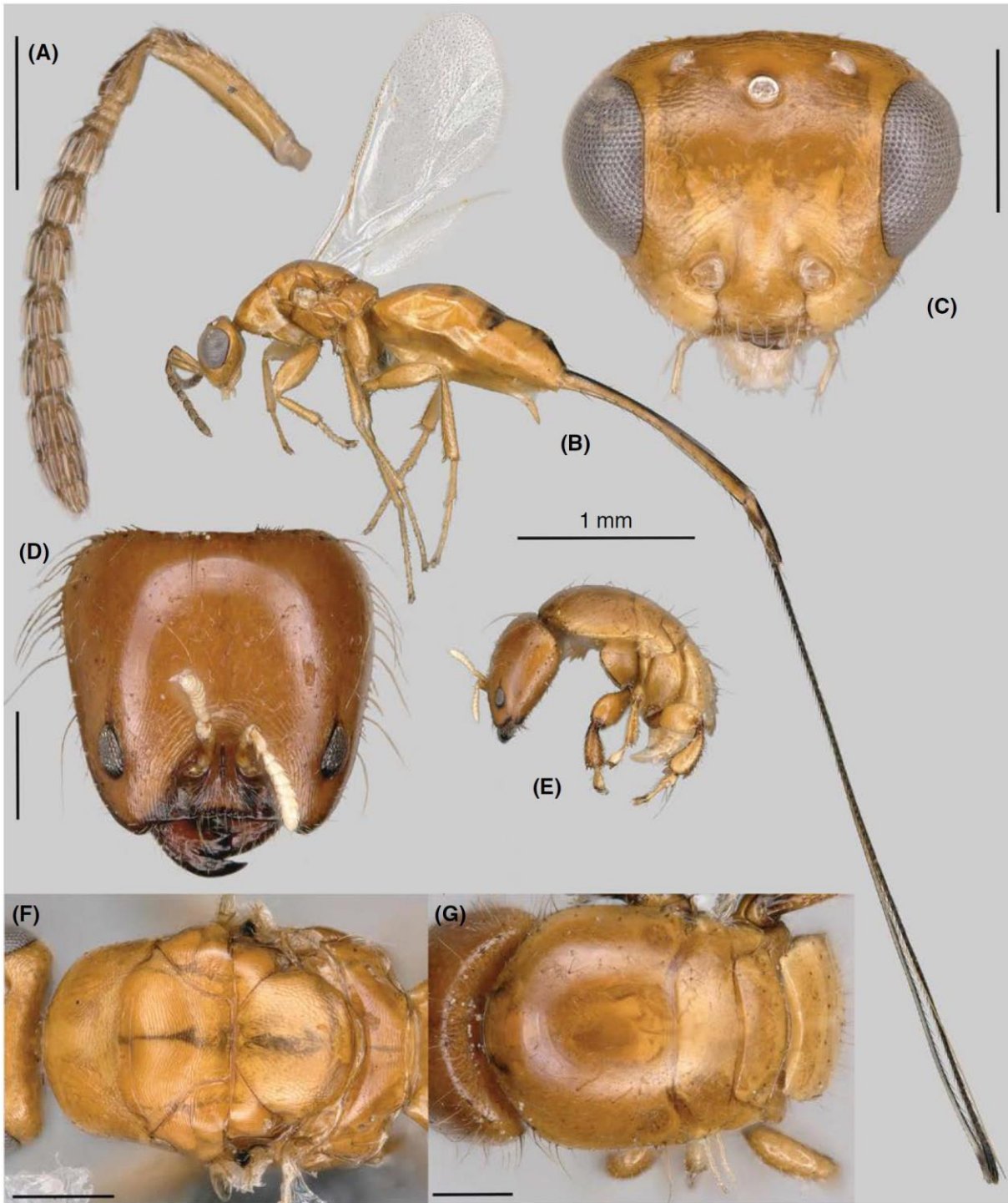


Fig. 9.5. *Philotrypesis caricae*. (A) Antenna. (B) Habitus female, lateral view. (C) Head female, frontal view. (D) Head male, frontal view. (E) Habitus male, lateral view. (F) Mesosoma female dorsal view. (G) Mesosoma male dorsal view. Scale = 200 μ m excepted for habitus = 1 mm. (Figures courtesy of J.Y. Rasplus.)

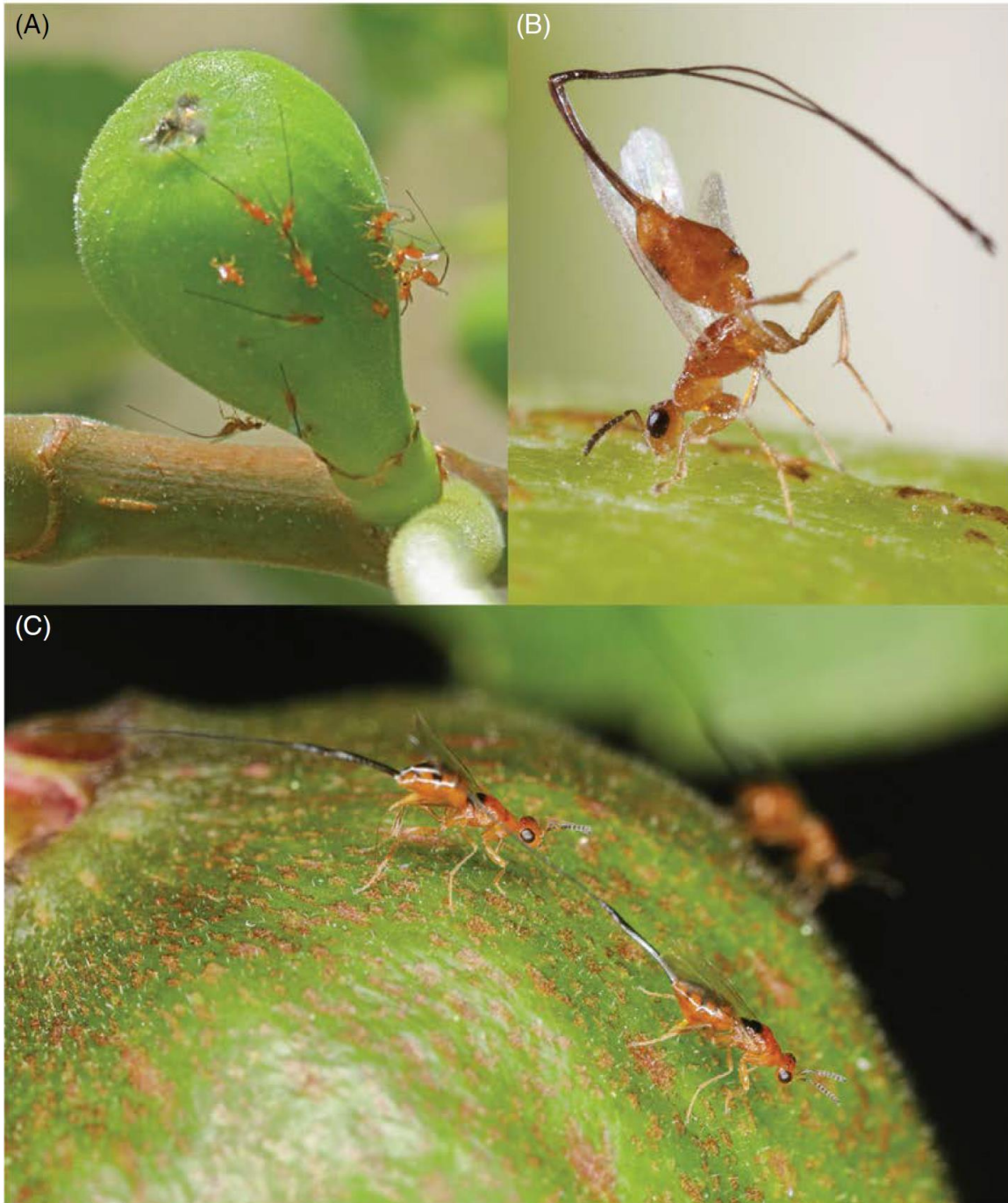


Fig. 9.6. *Philotrypesis caricae*. (A) Females ovipositing into a fig recently entered by *B. psenes*, on a male tree. (B, C) Female ovipositing and cleaning. (Figures courtesy of B. Schatz, J.Y. Rasplus and F. Kjellberg.)

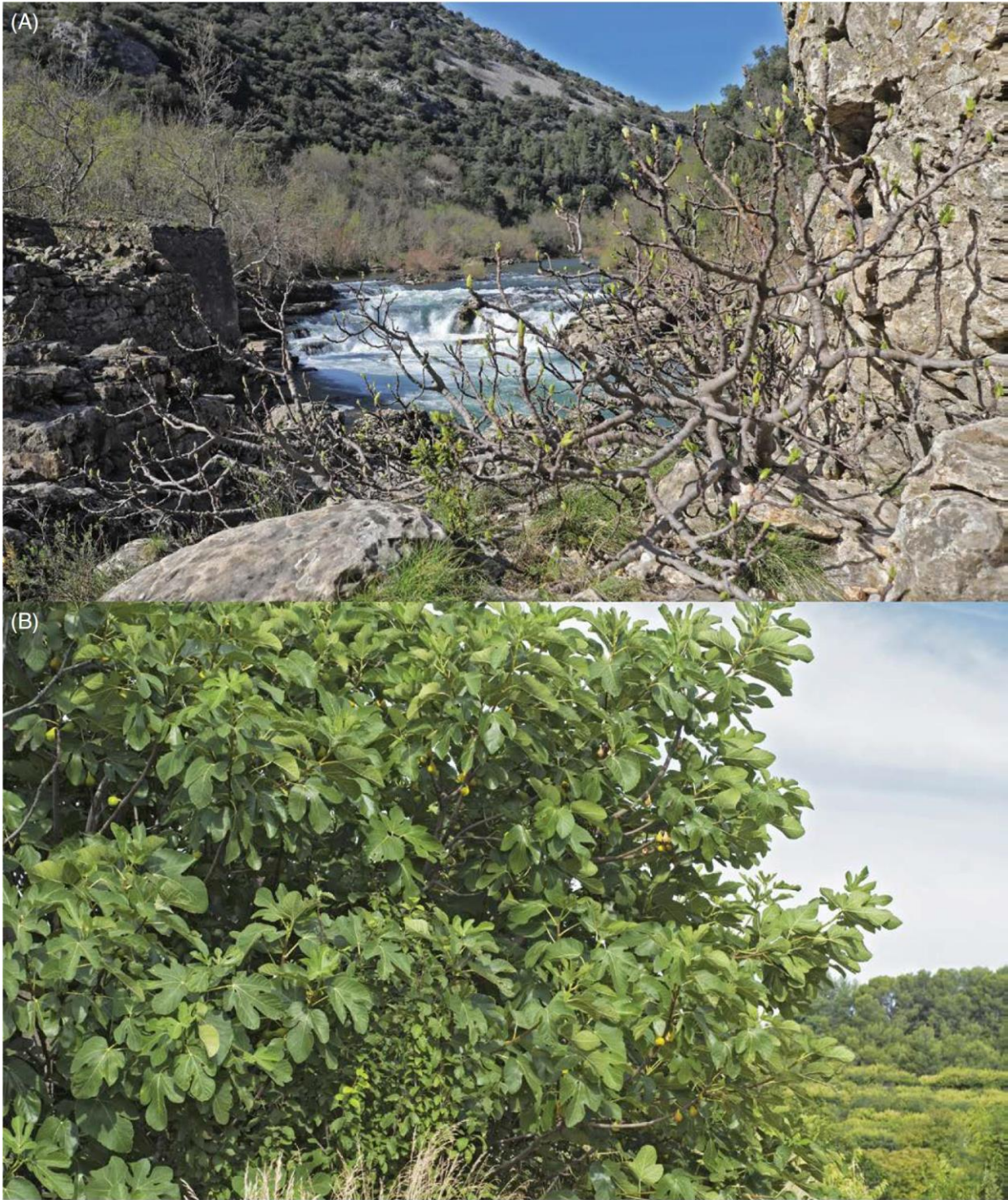


Fig. 9.7. *Ficus carica*. (A) Wild *F. carica* on the rocky bank of river Hérault, March 2020, St-Guilhem-le-désert, France. (B) Wild *F. carica* male in fields, July, Malemort, France; at that period, there are no receptive figs on male trees, the wasps can only go from male figs to figs on female trees. (Figures courtesy of F. Kjellberg and J.Y. Rasplus.)



Fig. 9.8. *Ficus carica*. (A) Wild *F. carica* female tree with ripe seed-containing figs. (B) Wild *F. carica* male, polliniferous figs at the stage of *Blastophaga psenes* emergence. (Figures courtesy of F. Kjellberg and J.Y. Rasplus.)



Fig. 9.9. (A). Fig plantation, Meander valley, Turkey. (B). Female tree, receptive figs of the second crop (= the crop present on wild female trees), requiring pollination; this phenotype is very similar to typical wild female trees, same locality. (Figure courtesy of F. Kjellberg.)