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(REVIEW ARTICLE)

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Mutualistic relationship of the Agaonidae Family (Insecta: Hymenoptera) with *Ficus sp*. (Moraceae) contributing to diversity and sustainability in tropical forests

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Abstract

Species of the Family Agaonidae are associated with the genus *Ficus* , as the species of the subfamily Agaoninae behave as pollinators, while the other species are mainly parasites of pollinators or gall formers from other parts of the fig. The male's life cycle is exhausted inside the fig tree's syconium: its role is to mate with the female and, therefore, with its robust jaws, open an exit for her (it is the opposite of what happens among the Strepsiptera, in which the female never leaves the host). Once fertilized, the female will leave the host fig to lay eggs in other figs, thus completing pollination. The objective of this paper is to survey the biology, bionomy and taxonomy of the Agoanidae Family (Hymenoptera). To this end, a bibliographic survey of Agaonidae was carried out in the years 1916 to 2021. Only complete articles published in scientific journals and expanded abstracts presented at national and international scientific events. Data were also obtained from platforms such as: Academia.edu, Frontiers, Qeios, Pubmed, Biological Abstract, Publons, Dialnet, World, Wide Science, Springer, RefSeek, Microsoft Academic, Science and ERIC.

Keywords: Ecological relationship; Host fig; Pollination; Parasitoid; Life cycle

1. Introduction

1.1. Diagnosis

The Agaonidae are characterized by a marked sexual dimorphism: the female is a small insect, with wings with a marginal vein perpendicular to the anterior margin, while the male is usually wingless (or with very rudimentary wings). The middle legs are visibly thinner than the front and rear ones. The females have a clearly everted ovipositor, in some species very long (Figures 1, 2, 3, 4, 5, 6, 7, 8, 9A, 9B, 10A and 10B) [1,2,3].

Source: https://australian.museum/learn/animals/insects/fig-wasps/

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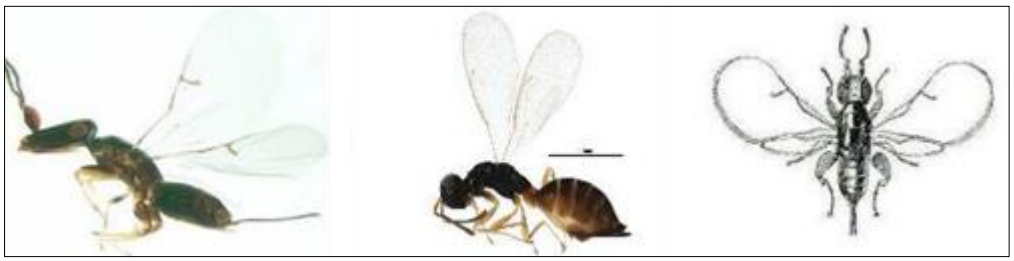
Figure 1 Specimen of Agaonidae Family

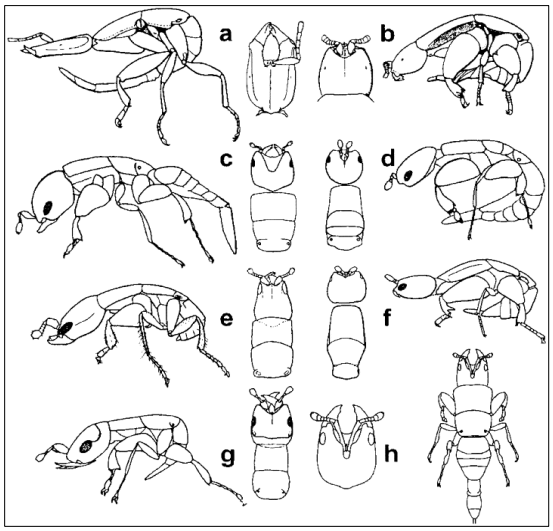


Source: https://en.wikipedia.org/wiki/Agaonidae

Figure 2 Specimens of Agaonidae Family

Source: http://www.figweb.org/fig_wasps/Diversity/index.htm

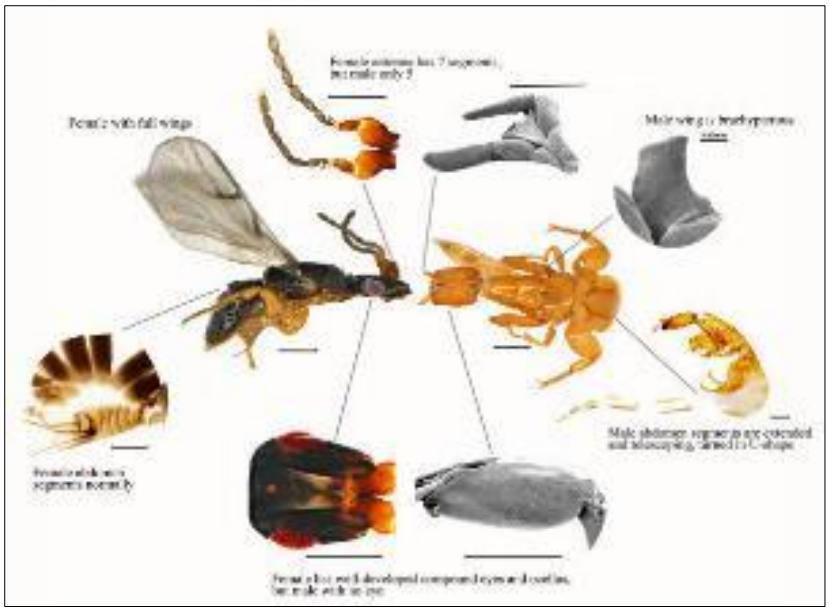
Figure 3 Fig wasp diversity (Agaonidae)



Source: https://www.sciencedirect.com/science/article/pii/S1631069103000106

Figure 4 Fighting (F) and non-fighting (NF) fig pollinating wasp males. (a) *Courtella michaloudi* (Wiebes, 1979) (F); (b) *Courtella armata* (Wiebes, 1974) (NF); (c) *Platyscapa awekei* Wiebes, 1977 (F); (d) *Platyscapa soraria* Wiebes, 1980 (NF); (e) *Alfonsiella longiscapa* Joseph, 1959 (F); (f) *Elisabethiella stuckenbergi* (Grandi, 1955) (NF); (g)

Nigeriella excavata Compton 1990(F); (h) *Pegoscapus astomus* (Grandi, 1920) (F). Note falcate mandibula, strong head, elongate scape (first antennal segment), and shortened strong thorax, in fighting males. Fighting males can retract the gaster: (a) extended position, (e, g) retracted position. Note the elongate segments of the fore tarsus in (a) compensating for their reduced number, and suggesting non-fighting ancestry, (h) redrawn after Grandi



Source: https://www.researchgate.net/figure/Extreme-morphological-dimorphism-between-female-and-male-fig-wasps-C-solmsi_fig2_259446680

Figure 5 Extreme morphological dimorphism between female and male fig wasps. Morphologically, the genders exhibit extreme differences in their compound eyes, wings, antennae, and body color. Scale bar indicates 0.2 mm for each part, except 0.02 mm for male wing

Source: https://zookeys.pensoft.net/article_preview.php?id=6529&skip_redirect=1

Figure 6 *Conidarnes sumatranae* sp. n. female. Ahabitus lateral view B antenna C head in frontal view

Source: https://zookeys.pensoft.net/article_preview.php?id=6529&skip_redirect=1

Figure 7 *Conidarnes sulcata* sp. nov. bad. Ahabitus lateral view B antenna C head in frontal view D mesoma in dorsal view E propodeum and terminal mesosoma in dorsal view F wing. Photographs by Gunther Fleck

Source: https://zookeys.pensoft.net/article_preview.php?id=6529&skip_redirect=1

Figure 8 *Conidarnes achterberg* sp. n., female. Ahabitus side view B antenna C antenna, detail

Source: https://zookeys.pensoft.net/article_preview.php?id=6529&skip_redirect=1

Figure 9A Figure *Conidarnes bergi* sp. nov. female. A mesosome in dorsal view B propodeum and terminal mesosome in dorsal view C prosternum D detail of venation. Figure 9B *Conidarnes bergi* sp. nov. bad. Ahabitus lateral view B antenna C head in frontal view D mesoma in dorsal view

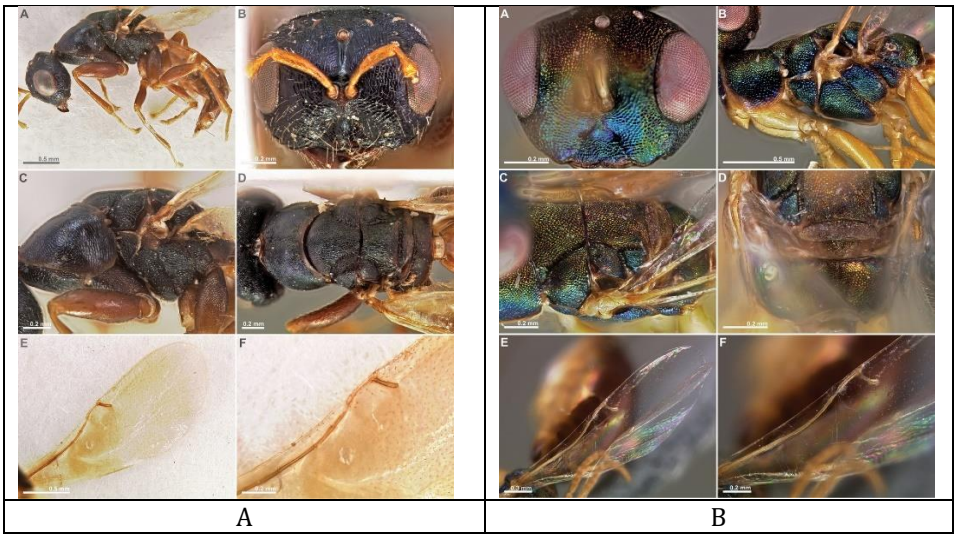
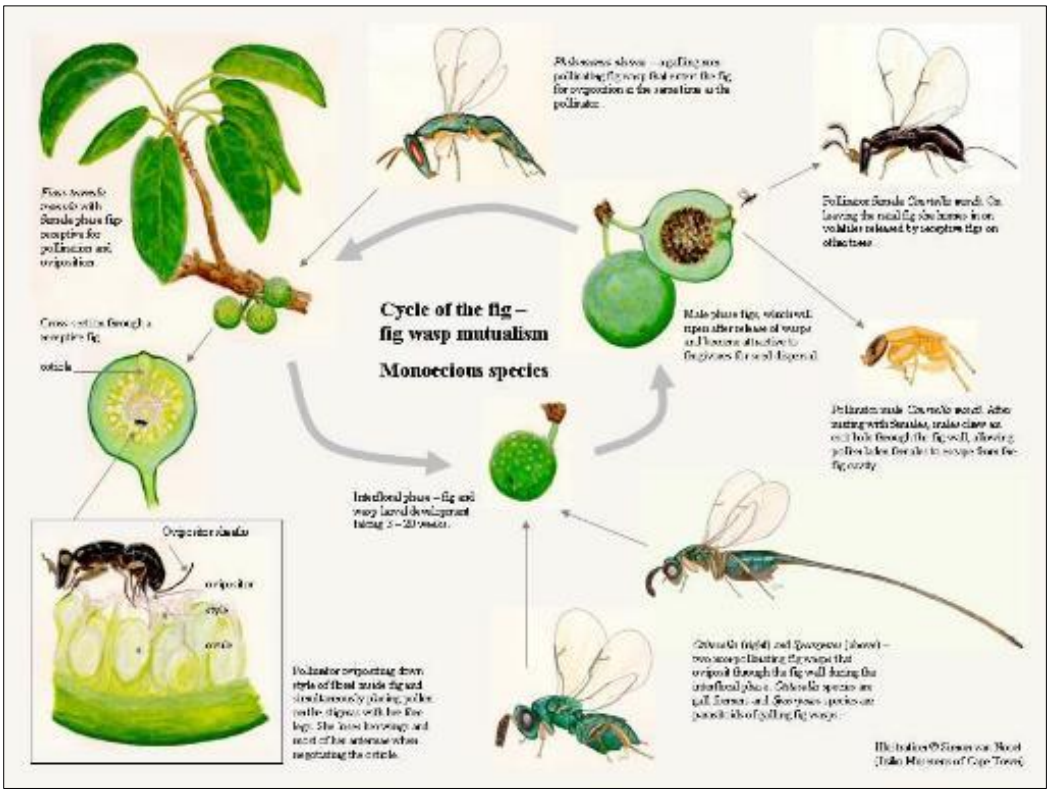


Figure 10A *Conidarnes achterbergi* sp. nov. Female. A head in frontal view B mesosoma in lateral view C mesosoma in dorsal view D propodeum and terminal mesosoma in dorsal view E wing F detail of venation. Figure 10B *Conidarnes* sp. ex *Ficus sundaica* Blume Bijdr (1825) (Moraceae) male. Ahabitus lateral view B head in frontal view C mesosoma in lateral view D mesosoma in dorsal view E wing F detail of venation

1.2. Biology, diversity and distribution

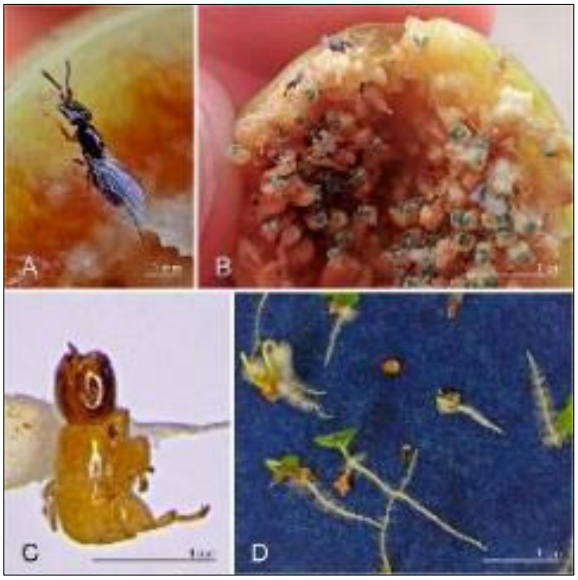
The life cycle of each species of Agaonidae is associated with a species of the genus *Ficus*; the species of the subfamily Agaoninae behave as pollinators, while the other species are mainly parasites of pollinators or gall-formers of other parts of the fig **(Figure 11)** [4,5,6].



Source: https://www.fs.fed.us/wildflowers/pollinators/pollinator-of-the-month/fig_wasp.shtml

Figure 11 Life cycle of the Agaonidae Family

The life cycle of the male is exhausted inside the syconium of the fig tree: its role is to mate with the female and therefore, with its robust jaws, to open a way out for her (it is the opposite of what happens among the Strepsiptera, in which the female never leaves the host). Once fertilized, the female will leave the host fig to go and lay the eggs on other figs, thus completing the pollination (Figures 12, 13, 14, 15, 16, 17, 18, 19 and 20) [7,8,9,10,11].



Source: Photo: Luís F. M. Coelho

Figure 12 (A) *Pleistodon imperialis* Saunders, 1882 female; (B) new *P. imperialis* generation emerging from *Ficus watkinsiana* Bailey, F.M. (1891) (Moraceae); (C) wingless *P. imperialis* male extracted from *F. watkinsiana*; (D) *F. watkinsiana* seeds germinating in the absence of its normal obligatory pollinator

Source: Photo: Luís F. M. Coelho

Figure 13 The study was published in a special issue of Acta Oecologica with four articles by scientists from Brazil. Another paper analyzes morphological differences in the ovipositors of several parasitoid wasp species

https://www2.palomar.edu/users/warmstrong/arbimg10.htm

Figure 14 Syconium (fig fruits, known as syconia, are borne singly or in pairs above the scars of fallen leaves or in axils of leaves of the present season. Flowers are staminate (male) or pistillate (female) and enclosed within the inflorescence structure. Long-styled female flowers are characteristic of the edible fruits) of Moreton Bay fig *Ficus microcarpa* L., 1758 (Moraceae) in Palomar College Arboretum. Palomar College horticulturist Tony Rangel grew viable seeds from this tree, so I suspected that the pollinator wasp (*Pleistodontes froggatti* Mayr, 1906) must be present

Source: https://www2.palomar.edu/users/warmstrong/arbimg10.htm

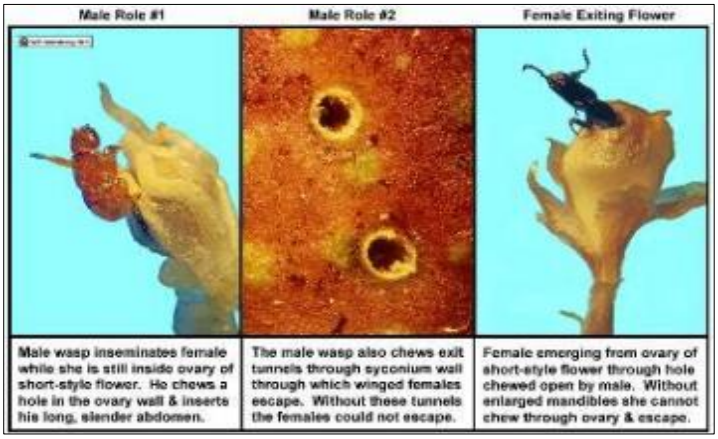
Figure 15 *Pleistodontes froggatti* Mayr, 1906 from Moreton Bay fig syconium in Palomar College Arboretum

Source: https://www2.palomar.edu/users/warmstrong/arbimg10.htm

Figure 16 *Eupristina verticillata* Waterston, 1921 from Indian laurel fig *Ficus microcarpa* L., 1758 (Moraceae) syconia on Palomar College campus. One wasp is squeezing through an exit tunnel cut by male wasps (white arrow)

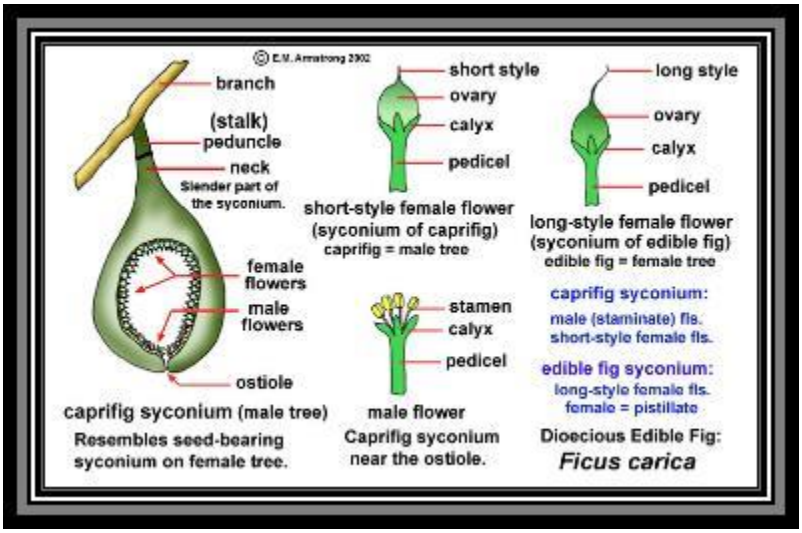
Source: https://www2.palomar.edu/users/warmstrong/arbimg10.htm

Figure 17 Naturalized figs in the Florida Keys. Strangler figs and banyans need viable seeds and a moist climate to be naturalized. Viable seeds require pollinator wasps in their syconia



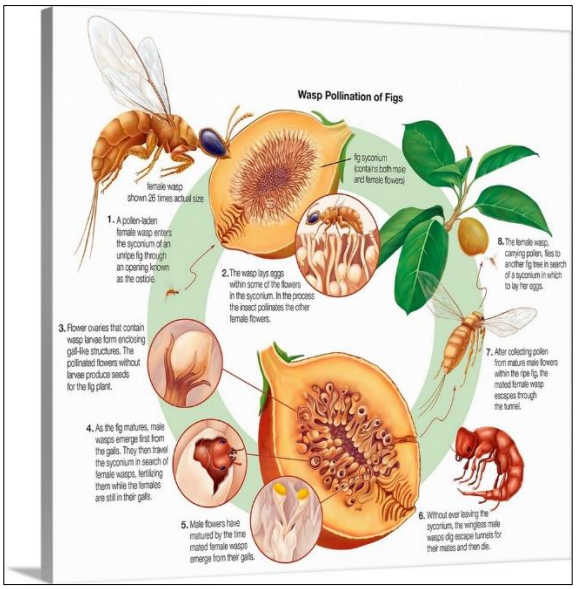
Source: https://www2.palomar.edu/users/warmstrong/arbimg10.htm

Figure 18 The male and female wasps in above image are *Blastophaga psenes* (Linnaeus, 1758) from *Ficus* carica L., 1758. The exit tunnels were made by male *Pleistodontes imperialis* Saunders, 1882 in the syconium wall of the rustyleaf fig (*Ficus rubiginosa* Desf. ex Vent). *Blastophaga* males do not cut the exit tunnels through the syconium wall. Instead, the females exit through the ostiole, becoming dusted by pollen from male flowers near the ostiolar end of the syconium



Source: https://www2.palomar.edu/users/warmstrong/arbimg10.htm

Figure 19 Life cycle of the common fig (*Ficus carica* L., 1758). Style length is genetically determined and it is vital that syconia on seed-bearing female trees have styles longer than the female wasp's ovipositor



Source: https://www.greatbigcanvas.com/view/life-cycle-of-the-fig-wasp-agaonidae,2276617/#&gid=1&pid=1

Figure 20 Life cycle of the fig wasp (Agaonidae) wall art

1.3. Taxonomy

This observation leads us to estimate the total fauna of neotropical agaonid wasps at 700 to 850 species, of which only 101 are described (12-14%) [12].

About 150 species of fig trees are known for the Neotropics, most of them endemic, and there are about 10 recently introduced by man. The endemic species belong exclusively to two subgenera and sections: *Pharmacosycea* section *Pharmacosycea* and *Urostigma* section Americana, with 20 and 120 species, respectively. Some 5 or 6 species of agaonids (Agaonidae S.d.) are specifically associated with each of the 140 species of *Ficus* (Figure 21) [13,14,15].

Source: https://guiadassuculentas.com/*Ficus* -lyrata-um-guia-completo-desta-planta/

Figure 21 Species of *Ficus* (Moraceae)

The neotropical fauna is endemic and with the exception of the introduced genera in the region with their host plants, none of the Neotropical genera are found elsewhere. Five of the six fig wasp subfamilies are found in the Neotropics (Agaoninae, Sycophaginae, Sycoryctinae, Otitesellinae, and Epichrysomallinae); most of these groups contain Neotropical and some introduced genera. The family has been recognized; it probably does not represent a monophyletic group (Figure 22, 23, 24, 25 and 26) [16,17,18].

Source: http://v3.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=157403

Figure 22 Subfamily Agaoninae

Source: http://www.figweb.org/Fig_wasps/agaonidae/Keys/Standard_dichotomous_keys/Sycophaginae_genera.htm

Figure 23 Subfamily Sycophaginae

Source: http://www.figweb.org/fig_wasps/agoanidae/Sycoryctinae/index.htm

Figure 24 Subfamily Sycoryctinae

Source: http://www.figweb.org/fig_wasps/pteromalidae/otitesellinae/index.htm

Figure 25 Subfamily Otitesellinae

Source: http://www.figweb.org/Fig_wasps/agaonidae/Epichrysomallinae/index.htm

Figure 26 Subfamily Epichrysomallinae

The plant and its pollinating hymenoptera are completely dependent on each other, since each *Ficus* species can only be pollinated by the appropriate insect species, and each insect species cannot reproduce outside the appropriate plant species. This is the case, to quote the best-known example, of the common fig (*Ficus carica* L., 1758) and of *Blastophaga psenes* (Linnaeus, 1758) (Figure 27) [17,18].

Source: https://alchetron.com/Blastophaga-psenes

Figure 27 *Blastophaga psenes* (Linnaeus, 1758 and the common fig *Ficus carica* L., 1758)

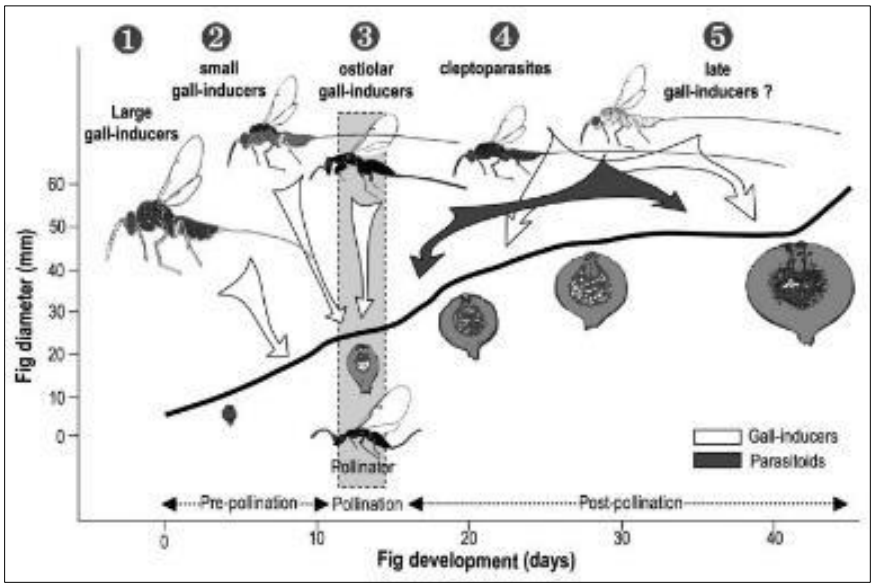
Such a close relationship suggests that both groups descend from common ancestors: an ancestral *Ficus* and its pollinating insect, from which the current species evolved by subsequent speciation. This would be a typical case of coevolution, even if the exact mechanism of this phenomenon is not yet fully understood. There are exceptions: for example, two different African species, *Ceratosolen arabicus* Mayr, 1906 and *Ceratosolen galili* Wiebes, 1964, can interact with both *Ficus sycomorus* L., 1758 (Moraceae) and *Ficus mucuso* Welw. ex Ficalho (Figures 28, 29, 30, 31 and 32) [19,20].

Source: http://www.figweb.org/Fig_wasps/agaonidae/Kradibiinae/Ceratosolen/Ceratosolen_galili.htm

Figure 28 African species, *Ceratosolen arabicus* Mayr, 1906 and *Ceratosolen galili* Wiebes, 1964

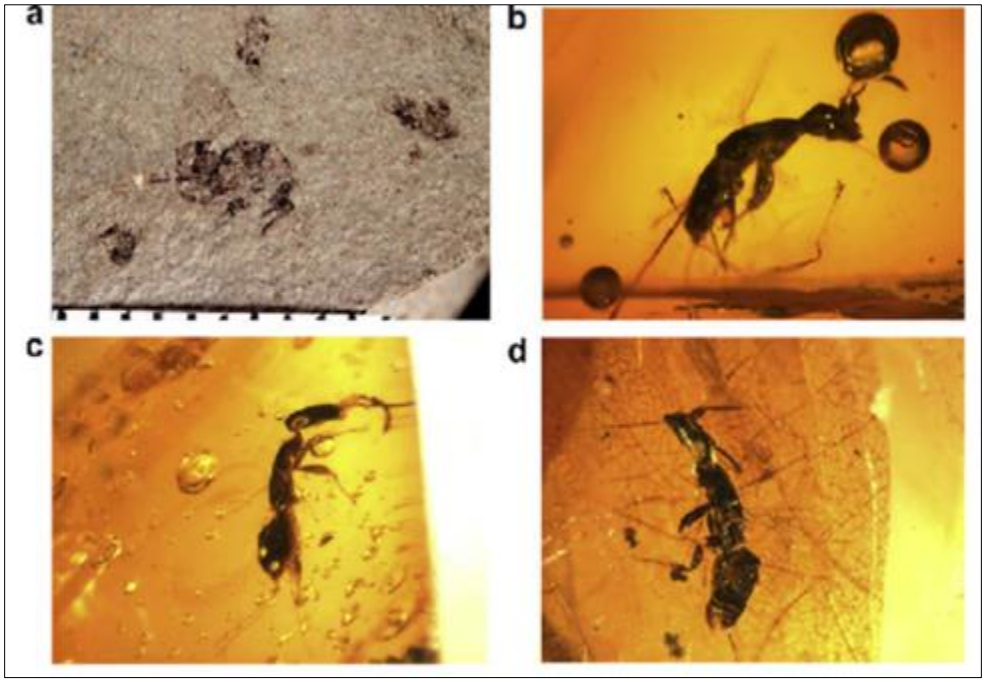
Source: https://www.prota4u.org/database/protav8.asp?g=psk&p=*Ficus* +mucuso

Figure 29 the common fig (*Ficus* carica L., 1758) and of *Blastophaga psenes* (Linnaeus, 1758)



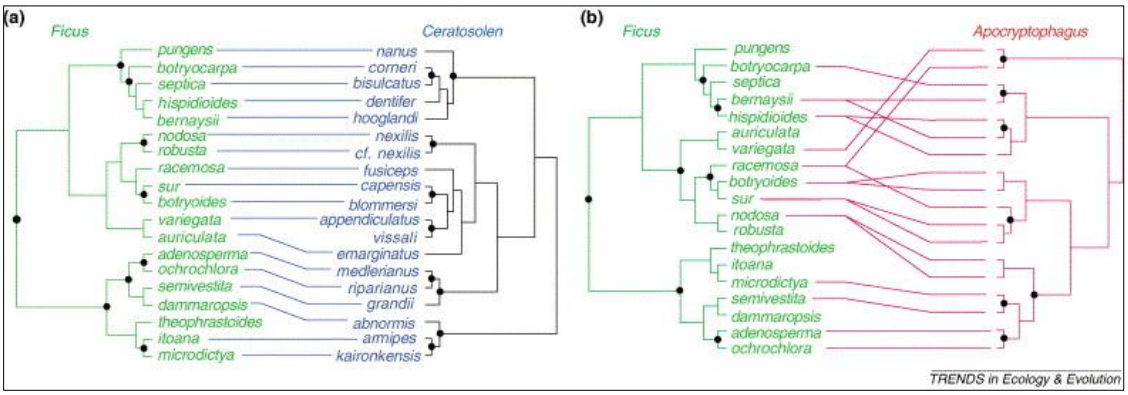
Source: https://bmcecolevol.biomedcentral.com/articles/10.1186/1471-2148-11-178

Figure 30 Ecological groups of sycophagine NPFW. The five ecological groups are depicted on the growth curve of a sycomorus fig. The arrows show the timing of oviposition of the different ecological groups of Sycophaginae



Source: https://www.researchgate.net/figure/Fossils-of-Chalcidoidea-wasps-2a-Type-of-Tetrapus-mayri-MCZ-No-2067-No-13-976-of_fig2_222675845

Figure 31 Fossils of Chalcidoidea wasps. (2a) Type of *Tetrapus mayri* (MCZ No. 2067 = No. 13,976 of the S.H. Scudder Collection) from the Florissant, Colorado, (Brues, 1910; Weiblen, 2002) (Photo by Herb Meyer). (2b) Fossils of the genus *Pegoscapus*, (Fig. 2b) and *Tetrapus* (Fig. 2c and d) from Dominican amber (photos by Laurent Soldati)



Source: https://www.sciencedirect.com/topics/agricultural-and-biological-sciences/agaonidae

Figure 32 Co-speciation of figs and their pollinators. Statistical comparisons reveal significant congruence between phylogenies of *Ceratosolen* pollinators (a) and their host figs, but not between *Apocryptophagus* gall-inducing parasites (b) and the same host figs [23]. Lines link wasps to their fig hosts whilst circles indicate nodes implied to have co-speciated in a maximum co-speciation analysis

Objective

The objective of this paper is to survey the biology, bionomy and taxonomy of the Agoanidae Family.

2. Methods

The method used to prepare this mini review was Marchiori 2021 methodology [21].

2.1. Studies conducted and selected

2.1.1 Study 1

Subfamily of Agaoninae

Agaonine wasps are attracted to receptive figs and enter through the ostiole. Once inside, the wasp probes the flowers, depositing an egg right next to the ovule on the appropriate flower and pollinates actively or not (Figure 33) [22,23,24].

Source: http://www.figweb.org/Fig_wasps/agaonidae/Agaoninae/Blastophaga/Blastophaga_psenes.htm

Figure 33 Subfamily of Agaoninae: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings

The female dies and the deposited eggs hatch; each larva develops at the expense of a single ovule transformed into a gall the size of a seed. A few weeks later, the males emerge first, looking for the female-containing galls, open the mating hole in the gall and mate with the female (Figure 34) [22,23,24].

Source: http://www.figweb.org/Fig_wasps/agaonidae/Agaoninae/Blastophaga/Blastophaga_psenes.htm

Figure 34 Subfamily of Agaoninae

The females load themselves with pollen, actively or passively. At the same time, the males dig an exit hole from the fig through which the females leave the fig. A female wasp can control the sex of her offspring. Agaonid wasps reproduce under local conditions of competition for mating, which ensures mating between individuals born inside the fig, strong bonds of relationship between them (Figure 35) [25,26,27,28].

Source: https://www.biodiversity4all.org/taxa/527669-Agaoninae

Figure 35 Subfamily of Agaoninae

Therefore, if only one female wasp enters the fig, she is producing mostly sisters and enough brothers to fertilize them. In contrast, when many females enter a fig, they must produce as many brothers as sisters, to such an extent that the situation will be very close to panmixias. Females are selected to produce increasing proportions of males with increasing numbers of foundresses (Figure 36) [25,26,27,28].

Source: https://www.semanticscholar.org/topic/Agaoninae/2416391

Figure 36 Habitus in lateral view, *Idarnes incertus* sp. group, females. (A) *Idarnes amacayacuensis* sp. nov; (B) *Idarnes amazonicus* sp. nov.; (C) *Idarnes* americanae sp. nov; (D) *Idarnes* badiovertex sp. Nov.; (E) *Idarnes* brevis sp. nov.; (F) *Idarnes brunneus* Farache & Rasplus, 2017

The design of the fig, the annual fruiting cycle, the intra-crown synchrony, the nutrient content and the diversity of presentation of the figs, are important characteristics that facilitate consumption by frugivores. Consequently, figs are considered a key resource for frugivore communities and the *Ficus* genus is the most important plant for tropical groups. In this sense, the *Ficus* -Agaoninae mutualism can be considered of great economic importance since it maintains the diversity of vertebrates and arthropods strictly associated with *Ficus* and also contributes sustain diversity in tropical forests (Figure 37) [25,26,27,28].

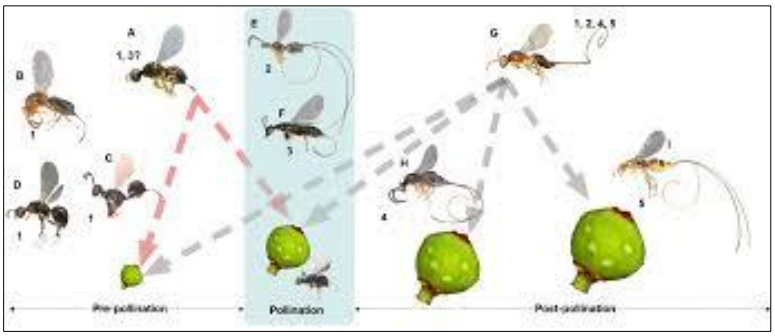
Source: https://bugguide.net/node/view/883356

Figure 37 Subfamily of Agaoninae

2.1.2 Study 2

Subfamily Sycophaginae

In the Neotropics Sycophaginae species are strictly associated with *Urostigma* figs, all other citations are doubtful. Most Sycophaginae cause galls inside flowers and can develop on unpollinated fruits. All neotropical sycophagines oviposit from the outside of figs. Species of the genus *Idarnes* show two different oviposition times in figs that correspond to two morphologically different groups (groups of species carme and uncertain). The *Idarnes* of the group incerta ovipositan long before pollination and produce small litters. The males are winged and mate with the females inside and outside the figs. Winglessness has been shown to increase with litter size (Figure 38).



Source: https://www.ffclrp.usp.br/imagens_defesas/23_06_2017__09_33_20__45.pdf

Figure 38 Schematic representation showing temporal segregation of fig wasps, represented with members of a NPFW subfamily (Sycophaginae). The taxa represented in the figure come from different hosts and biogeographic regions. Numbers represent the biology: 1 Large gall inducer 2 small gall inducer 3 ostiolar gall inducer 4 kleptoparasite 5 late "gall inducer". A New Genus B *Idarnes* (incertus species group) C *Pseudidarnes* D *Anidarnes* E *Idarnes* (*Flavicollis* sp. g.) F *Sycophaga* (ostiolar gall inducer) G *Sycophaga* (formerly *Apocryptophagus*) H *Idarnes* (*Carme* sp. g.) I *Eukoebelea*

The galls made by these wasps project into of the receptacle cavity. The carme group of species (including flavicollis) has wingless males and females with ovipositor relatively length. Species in this group use the same channels of attraction than pollinators, oviposit in the same stage of fruit development as the pollinating wasps and produce large broods (Figure 39).

Source: http://www.figweb.org/Fig_wasps/agaonidae/Keys/Standard_dichotomous_keys/Sycophaginae_genera.htm

Figure 39 Petiole conspicuous, at least as long as broad (A); four-segmented maxillary palpi; labial palpi three-segmented; postmarginal vein conspicuous (may be short) (B); associated with *Ficus* subgenus *Urostigma*, section Malvanthera, Australasia *Pseudidarnes* Girault, 1927

These wasps use the In the Neotropics Sycophaginae species are strictly associated with *Urostigma* figs, all other citations are doubtful. Most Sycophaginae cause galls inside flowers and can develop on unpollinated fruits (such as Idarnes). All neotropical sycophagines oviposit from the outside of figs. Species of the genus *Idarnes* show two different oviposition times in figs that correspond to two morphologically different groups (groups of species carme and uncertain). Idarnes of the incerta group oviposit long before pollination and produce small litters (Figure 40).

Figure 40 Antennae inserted closer to median ocellus than to clypeal margin (A); supraclypeal area higher than clypeus and laterally well delimited by line or groove (A); ovipositor sheaths with a median constriction (B) (one exception: *Anidarnes dissidens* Farache & Rasplus, 2013); scrobal cavity including the median ocellus (A); associated with *Ficus* subgenus *Urostigma* section Americana, Neotropical region Anidarnes Bouček, 1993

The males are winged and mate with the females inside and outside the figs. Winglessness has been shown to increase with litter size. The galls made by these wasps project into the cavity of the receptacle. The carme group of species (including flavicollis) has wingless males and females with relatively ovipositors (Figure 41).

Source: http://www.figweb.org/Fig_wasps/agaonidae/Keys/Standard_dichotomous_keys/Sycophaginae_genera.htm

Figure 41 Malar sulcus present and conspicuous (A, B); sculpture of the head and mesosome can be reticulated or engraved (A), or completely smooth (B); associated with *Ficus* subgenus *Sycomorus* more rarely with subgenus *Urostigma* section *Americana*; Old World *Sycophaga* Westwood, 1840

Length. Species in this group use the same channels of attraction as pollinators, lay eggs at the same stage of fruit development as pollinating wasps, and produce large broods. These wasps use the same set of flowers, and consequently there is a negative effect on the production of pollinating wasps. Additionally, it has been shown that species of *Idarnes* occur in significantly more numbers large in unpollinated figs and preferentially develop in flowers that do not contain larvae pollinators (Figure 42).

Source: Jan Celliers Park

Figure 42 *Sycophaga* sp. of *Ficus* sp.

Males emerge first from their gills and fight with other males of the same species to mate with females are unable to chew exit tunnel in the wall of the fig, and consequently depend on the behavior of pollinators.

The natural history of *Anidarnes* has been studied recently. These wasps can lay eggs long before pollination, in the same way as the *Idarnes* (incerta). *Anidarnes bicolor* (Ashmead, 1900) induces large galls on the inner wall of figs, and their progeny feed on the sterile tissue (Figure 43) [29,30,31.32,33,34,35].

Source: http://www.figweb.org/fig_wasps/agaonidae/Sycophaginae/Anidarnes/Anidarnes_bicolor.htm

Figure 43 *Anidarnes bicolor* (Ashmead, 1900)

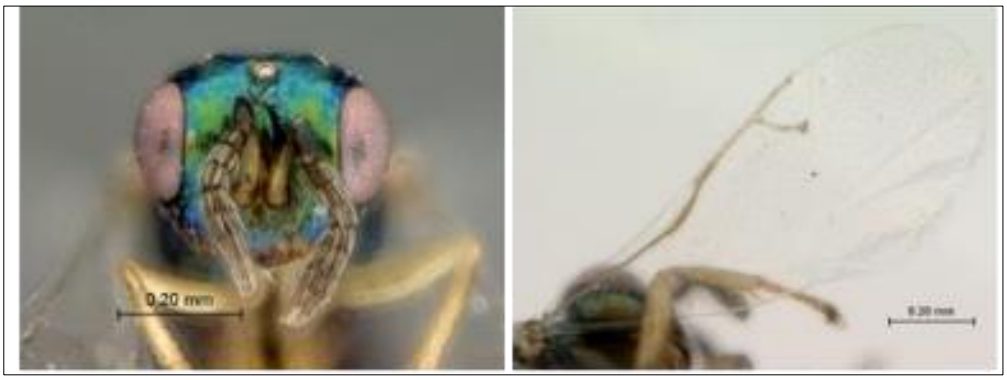
2.1.3 Study 3

Subfamily Sycoryctinae

All species of Sycoryctinae exhibit ovipositors. long to extra-long, oviposit from outside the fig and they exhibit fascinating behaviors dependent on the morphology of the ovipositor. However, the biology of the Sycoryctinae is poorly understood. *Philotrypesis* species oviposit in ovaries previously transformed into galls by the application of poison and containing the pollinator's eggs (Figure 44).

Source: https://www.researchgate.net/figure/Oviposition-behaviour-of-Sycophilomorpha-sp-A-When-Sycophilomorpha-sp-was-ovipositing_fig1_44686030

Figure 44 Oviposition behavior of *Sycophilomorpha* sp. (A) When *Sycophilomorpha* sp. was ovipositing, the fig was still covered by hood-like involucral bracts and the stipule. (B) The blue arrow indicates the position of the hidden fig. (C) The ovipositor pierced the fig wall and left a small black scar (red arrow). (D) The flowers in such young figs had not yet differentiated into ovule, style, and stigma *Philotrypesis* larvae kill the pollinator and feed on the seed that has started to develop in the ovary. Consequently, the species of *Philotrypesis* are considered tenants of the Agaoninae. The biology of *Sycoscapter* is not known (Figure 45).



Source: http://www.figweb.org/fig_wasps/pteromalidae/sycoryctinae/sycoryctini/sycoryctes/Sycoryctes_species_1_UAE.htm

Figure 45 Subfamily Sycoryctinae

Recent studies in Africa do not distinguish between the biology of a strict parasitoid or an incumbent. These oviposit from a few hours to several days after the occurrence of oviposition, depending on the species. There are few published data on the biology of *Critogaster*, but all known species are associated with *Ficus* subgenus *Pharmacosycea*.

The degrees of polyphagia are still under debate and more studies are needed; however, it seems that species are not species-specific. Rather *Critogaster* species seem to be competitors from pollinators (*Tetrapus*) and produce galls (Figure 46).

Source: http://www.figweb.org/fig_wasps/pteromalidae/sycoryctinae/sycoryctini/sycoryctes/Sycoryctes_species_1_UAE.htm

Figure 46 Subfamily Sycoryctinae

Females have been reported to taste fig and they oviposit inside the virgin flowers several days before of pollination and oviposition of pollinators, and therefore it is unsafe to state that they behave as parasitoids of *Tetrapus* (Figure 47).

Source: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13483?af=R

Figure 47 Low host specificity and broad geographical ranges in a community of parasitic non-pollinating fig wasps (Sycoryctinae; Chalcidoidea)

The males of *Apocrypta, Sycoscapter* and *Critogaster* they are wingless and die trapped in the cavity of the fig after the emergence of the females. The males have a short lifespan, maximum 48 hours while the female of *P. caricae* can live about a month. Males of *Philotrypesis* and S*ycoscapter* fight with each other and show various morphological adaptations for fighting (Figure 48) [36,37,38,39,40,41,42].

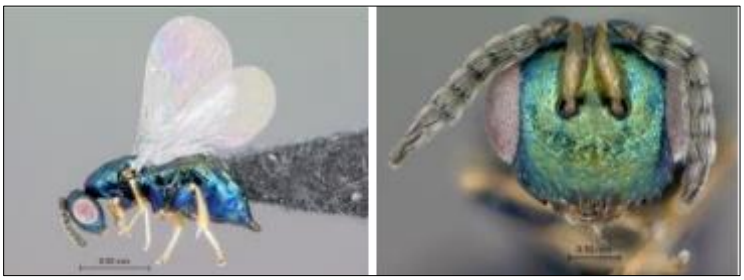
Source: https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13483?af=R

Figure 48 Females of the four wasp species landing or ovipositing from outside the figs of *Ficus auriculata* Lour. (A) Fixed sequence of behavioural events in the pollinator *Ceratosolen emarginatus* Mayr, 1906, including holding the antennae upward (A1), lowering the antennae (A2), tapping the fig surface with the tip of the final flagellomere by curving the antenna downwards (A3), and lifting the ostiolar bracts with the modified spine-like expansion of the third antennal segment (A4). The bottom pictures show aggregative oviposition by the three nonpollinators, *Sycophaga* sp. (B), *Philotrypesis Longicaudata* Mayr, 1906 (C), *Sycoscapter roxburghi* Joseph, 1957 (D).

2.1.4 Study 4

Subfamily Otitesellinae

The Otitesellinae of the Old World (such as *Micranisa* and *Walkerella*) oviposit on young figs from the outside. Generally speaking, females lay eggs on virgin flowers in the same way as pollinating wasps enter the fig cavity. Once the eggs have been deposited, the flowers turn into galls and the larva develops on tissue (Figure 49) [43,44].



Source: http://www.figweb.org/fig_wasps/pteromalidae/otitesellinae/Otitesella/Otitesella_sesquianellata.htm

Figure 49 Subfamily Otitesellinae

The New World Otitesellinae (*Aepocerus* and *Eterandrium*) are also gall-makers and grow exclusively on the *Ficus* of the American section. *Aepocerus* species can prevent abortion of unpollinated fruit and fruit in which few pollinators have developed (Figure 50).

Source: http://www.figweb.org/fig_wasps/goanidae/otitesellinae/Otitesella/Otitesella_sesquianellata.htm

Figure 50 Subfamily Otitesellinae

Aepocerus larvae are parasitized by species of *Physothorax* (Torymidae). Most *Aepocerus* and *Heterandrium* species appear to have high specificity and most *Ficus (Americana)* species exhibit one or two species of these genera [43,44].

2.1.5 Study 5

Subfamily Epichrysomallinae

The Otitesellinae of the Old World (such as *Micranisa* and *Walkerella*) oviposit on young figs from the outside. Generally speaking, females lay eggs on virgin flowers in the same way as pollinating wasps enter the fig cavity. Once the eggs have been deposited, the flowers turn into galls and the larva develops on the tissue (Figure 51).

Source: http://www.figweb.org/Fig_wasps/agoanidae/Epichrysomallinae/index.htm

Figure 51 Subfamily Epichrysomallinae

The New World Otitesellinae (*Aepocerus* and *Eterandrium*) are also gall-makers and grow exclusively on the *Ficus* of the American section. *Aepocerus* species can prevent abortion of unpollinated fruit and fruit in which few pollinators have developed. Aepocerus larvae are parasitized by species of *Physothorax* (Torymidae). Most *Aepocerus* and *Heterandrium* species appear to have high specificity and most *Ficus* (*Americana*) species exhibit one or two species of these genera. Most species oviposit on figs before hatching. pollination and lay few eggs. The ovipositor is long but coiled within gaster.

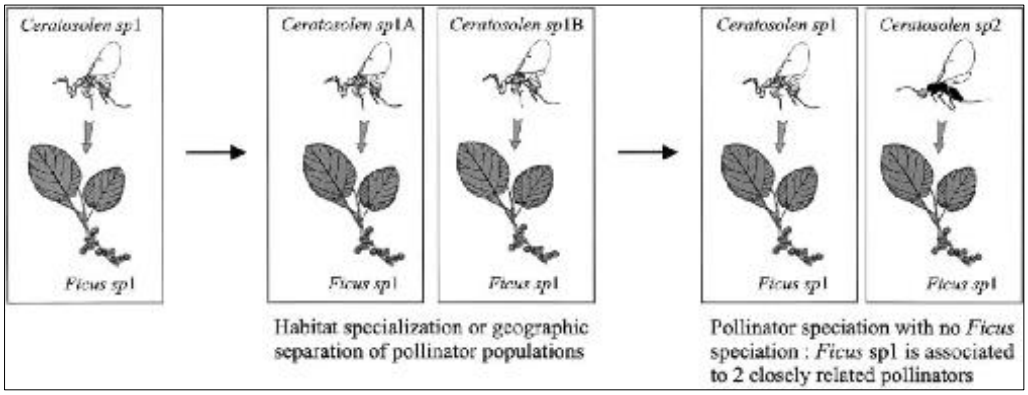
The virgin flowers develop into large, characteristic galls that project into the cavity. The adults chew their way out through the wall of the figs. Males are mostly winged and mate with females outside of figs [45,46].

2.1.6 Study 6

Ceratosolen galili Wiebes, 1964 (Figures 52 and 53).

Source: https://en.wikipedia.org/wiki/Ceratosolen

Figure 52 *Ceratosolen galili* Wiebes, 1964



Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 53 Schematization of hypothesis (ii). Two fig species evolved independently with their species-specific pollinator in different areas (e.g., *Ficus sycomorus* L. 1758 and *Costus arabicus* L.1758 in Madagascar, and *Ficus* sp. and *Costus galili* L., 1758 in Africa). If one species extends its geographical range and comes in sympatry with the other (e.g., by crossing the Mozambique Channel), subsequent host shift may occur due to biological and/or biochemical affinities of the two hosts. One of the fig hosts is then associated with two phylogenetically distant pollinators (e.g., *Ficus sycomorus* L. 1758 associated with *C. arabicus* and *C. galili)*; the other *Ficus* species might become extinct

- Distribution

Senegal, Ivory Coast, Nigeria, Democratic Republic of Congo, South Africa, Ethiopa, Kenya, Tanzania, Ghana and Uganda.

- Biology

Host figs: *Ficus sycomorus* (L.); *Ficus sycomorus gnaphalocarpa* (Miq.) C.C. Berg and *Ficus mucuso* Ficalho (Figures 54 and 55).


TANZANIA, Mkomazi
Game Reserve, nr.
Zange Gate,
4°03.47'S 37°47.56'E
28.iv.1996, S. van Noort
ex F. sycomorus L.,
dry river course, tree 1,
coll. FMK32
SAM-HYM-
P0/6428
Cratosolen
galili
det. S. van Noort 2007

Source: Photographs of living specimens © Vida van der Walt (Pretoria); mounted specimens © Simon van Noort (Iziko Museums of South Africa)

Figure 54 Foundress female fig wasps entering a receptive fig through the ostiole (the narrow, bract lined opening at the apex of the fig). Ants (a species of *Pheidole*, Formicidae) are predating the hapless female wasps

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 55 Distribution *Ceratosolen* galili Wiebes, 1964

2.1.7 Study 7

Ceratosolen grandii Wiebes 1963 (Figure 56).

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 56 *Ceratosolen grandii* Wiebes 1963

- Distribution

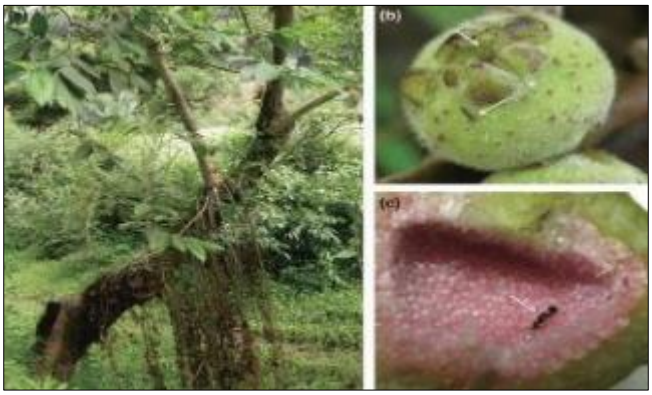
Papua New Guinea.

- Biology

Host fig: *Ficus semivestita* Corner.

Note: Iziko South African Museum and Jean-Yves Rasplus (INRA, France).

Ceratosolen gravelyi Grandi 1916 (Figure 57).



Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 57 4-methylanisole is the main signal compound in the floral scent of *Ficus semicordata* that attracts its obligate pollinator to the host figs at the precise stage required for pollination and oviposition. 4-methylanisole may thus function as a private channel (species-specificity) in this specialized obligate mutualism

- Distribution

India, Afrotropics.

- Biology

Host: *Ficus semicordata* Ham. ex Smith.

Note: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France).

Ceratosolen hooglandi Wiebes 1963 (Figure 58).

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 58 *Ceratosolen hooglandi* Wiebes 1963

- Distribution

Papa New Guinea.

- Biology

Host fig: *Ficus bernaysii* King.

Ceratosolen (Rothropus) humatus Wiebes 1963.

- Distribution

Malaysia.

- Biology

Host fig: *Ficus beccarii* King and *Ficus* subterranea Corner.

Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France).

Blastophaga psenes (Linnaeus, 1758) (Figure 59).

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 59 *Blastophaga psenes* (L., 1758) pollinator of *Ficus carica* L. and *Ficus palmata* Forssk

- Distribution

Palaearctic region; introduced to Afrotropical, Australasian, Nearctic, and Oriental regions.

- Biology

Pollinator of *Ficus carica* L. and *Ficus palmata* Forssk.

Philotrypesis finitimorum Wiebes 1971 (Figure 60).

- Biology

Host**:** *Ficus saussureana* DC.

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 60 Distribution: *Philotrypesis finitimorum* Wiebes 1971

Adiyodiella valluvanadensis Priyadarsanan, 2000 (Figure 61).

Biology: Host plant: *Ficus superba* (Moraceae).

Source: Web authors Simon van Noort (Iziko South African Museum) and Jean-Yves Rasplus (INRA, France)

Figure 61 Distribution: India *Adiyodiella valluvanadensis* Priyadarsanan, 2000

Arachonia Joseph 1957.

- Distribution

Afrotropical region, Oriental region: India and Malaysia.

- Biology

Non-pollinator parasitoid fig wasps (Figure 62) [47,48,49,50,51,52,53].

Source: Photographs © Simon van Noort (Iziko Museums of South Africa)

Figure 62 *Arachonia* Joseph 1957

3. Conclusion

Species of the Family Agaonidae are associated with the genus *Ficus* , as the species of the subfamily Agaoninae behave as pollinators, while the other species are mainly parasites of pollinators or gall formers from other parts of the fig. The male's life cycle is exhausted inside the fig tree's syconium: its role is to mate with the female and, therefore, with its robust jaws, open an exit for her (it is the opposite of what happens among the Strepsiptera, in which the female never leaves the host). Once fertilized, the female will leave the host fig to lay eggs in other figs, thus completing pollination.

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