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Biological Analogies Between Some fig–wasps (Hymenoptera: Agaonidae and Torymidae: Sycophaginae) and *Varroa jacobsoni* (Acari: Varroidae)

William Ramírez B.
Escuela de Fitotecnia, Facultad de Agronomía Universidad de Costa Rica

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Abstract: Some fig wasps (Agaonidae and Torymidae: Sycophaginae) and the mite *Varroa jacobsoni* exhibit analogous biological, morphological and behavioral characteristics that seem to have arisen through convergent evolution. Both groups develop in enclosed dark environments (small territories) with both high internal humidity and carbon dioxide concentration. The males of both groups are haploid, exhibit neoteny, and have shorter developmental phases and life spans than females. They do not fight at mating nor feed as adults. They are also less numerous and less sclerotized than the females. Male and female *Varroa* have enlarged peritremata and breathing tubes. Laminate breathing peritremal excrescenses or filaments are found in the Sycophaginae males (except *Idarnes*). The presence of large peritremata and protrudingbreathing structures, among other analogies between some fig wasps and the acarids, *Varroa,* seem to be adpatations to the humid environments in which they live during part of their life cycle.

Organisms that develop in closed microenvironments (seraglia) with very similar and constant physical, biological and feeding conditions, seem to have very constant ontogenesis and also develop specific one-to-one relationships; that is, each host has a specific associate (parasite or symbiont). This type of association leads to radiative adaptations, synchronism of development for at least one of the associates and total dependence for at least one of the partners. They also show a high degree of relatedness.

Both Agaonidae and *Varroa* fit the "Local Mate Competition Rule" of Hamilton. Other characteristics that seem to fit into Hamilton's rule are: specific relationships between host and associate, developmental synchronization, associate females usually lay a constant number of eggs; nearly constant developmental time from egg to adult of the associate, neotenic males, very constant ontogenies of one of the associates and precise sex ratios.

The mite *Varroa jacobsoni* Oud. (Varroidae) is a parasite of the honey bees *Apis cerana* Fabricius and *A. mellifera* L. (Apidae). In the latter, it develops inside both the drone and worker cells. The sycophilous wasps (Agonidae and Torymidae: Sycophaginae) develop exclusively inside of the syconia of the figs (*Ficus*).

Organisms that occupy similar habitats or microenvironments and small territories or seraglios often exhibit analogous biological characteristics that arise through convergent evolution. They also tend to develop specific relationships with host associates. Among the arthropods, some common examples of convergence are: the presence of gills in aquatic organisms, the loss of pigmentation and eyes in cave dwellers, and the loss of appendages (e.g. legs and wings) and other adult characteristics among parasites. Another characteristic of very host-specific parasistes seem to be the neoteny of one of the sexes.

Comparative studies between organisms that develop in similar environments or isolated food objects or hosts can produce clues to help understand the biology of similar but unrelated organisms. Similar constant isolated environments can induce the evolution of analogous adaptations in unrelated arthropods. This will be shown later in a comparison of certain characteristics of *V. jacobsoni,* an economically important mite parasite of the honey bee *A mellifera,* and some sycophilous fig wasp groups (Aganoidae and Torymidae). Such comparisons are not only of academic interest, they can also be of great value for a better understanding of the biology of the organisms involved. The most outstanding analogies between the fig

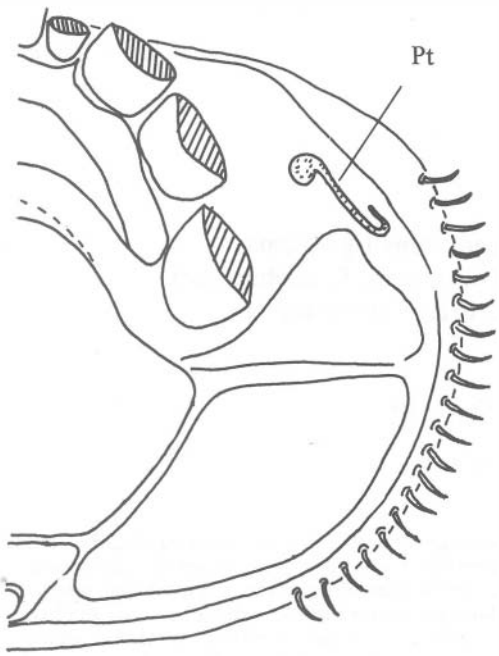

FIG. 1. Ventral view of the right side of the female mite *(Varroa jacobsoni* (Varroidae, Mesostigmata: Acarina) (legs removed) showing the peritremal tube (Pt). After Akratanakul 1975, plate 1.

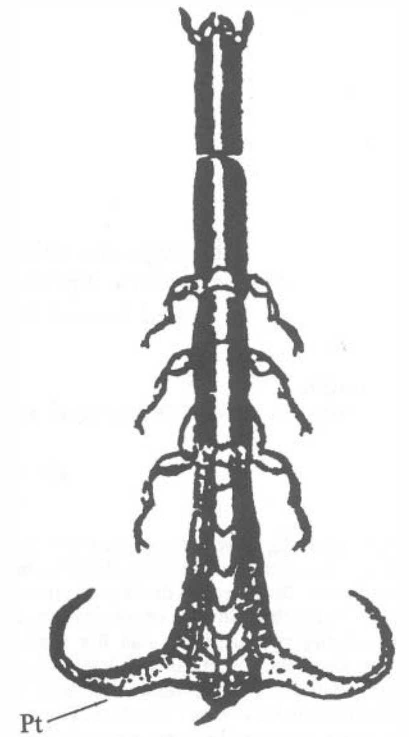

FIG. 2. Ventral view of the male fig wasp *Apocrypta perplexa* (Sycophaginae: Torymidae) . Showing the peritrenal tubes (Pt). After Coquerel, 1855, Fig. 2.

wasps (Agaonidae and some Torymidae: Sycophagini) and *Varroa jacobsoni* (Varroidae) are respiratory protruding structures (Figs. 1 and 2), reproductive and behavioral traits, and precise sex ratios.

DISCUSSION

The developmental stages of both *V. jacobsoni* (and other Varroidae) and the sycophilic fig wasps occur in enclosed, confined, dark humid habitats (seraglios) and isolated hosts: the sealed brood cell of the honey bee and the interior of the fig syconium, respectively. In all fig wasps (Agaonidae and Torymidae) and in *V. jacobsoni* the males reproduce by arrhenotoky, a mode of reproduction that readily permits the production of biased (Hamilton 1967, Joseph 1984), and precise sex ratios.

According to Halmilton (1967), it seems that male haploid organisms have found themselves preadapted to live in isolated niches or hosts of the sort characterized by his model. The evolution of male haploidy has actually accompanied, in several independent lines, an evolutionary trend to occupy such niches. Most of the arthropods listed by Hamilton (1967), which develop in isolated hosts having sibmating combined with arrhenotoky and spanandry are hymenopterous insects (including Agaonidae) and a few species of mites (e.g. Laelaptidae, Pyemotidae and Tarsonemidae). Green *et al.* (1982) suggest that an evolutionary advantage of arrhenotoky is that it makes precise sex ratios possible, wich provide a selective advantage in highly inbred parasitic wasps.

Some insects that develop in humid or aquatic environments have evolved large peritremata and breathing tubes These include: most Cyclorrhapha, especially the Tubulifera fly larvae (Fam. Syrphidae) and the hemipterans Nepidae and Belostomatidae. Breathing tubes are also found in most Sycophaginae males and in both sexes of *Varroa jacobsoni.* Hilton, (1961) points out that insect eggs that are in wet environments or become submerged have envolved chorionic plastrons which are used for gas exchange. In some species that are immersed in water there are plastrons bearing elongated respiratory horns (e.g. some Muscidae); egg shells with plastrons bearing horns have evolved independently (they are not homologous) in at least fifteen species.

Adult males of *Apocrypta, Eukoebelea, Sycophaga* and *Sycophagella* fig wasps (Torymidae: Sycophaginae, *sensu* Wiebes 1976), which spend part of their life cycle in very humid environments, have large peritremata and laminate breathing excrescenses or long filaments on the spiracles (Fig. 2) which are used as snorkels while they are submerged. The large peritremata and breathing tubes of female *Varroa* (Fig. 1) seem to be used for respiration while they are inactive and hidden in the wet brood food of the honey bee cell (De Jong 1984). When *Varroa* is submerged in the larval food of the bee, the larva seems to be in a cataleptic state (Ramírez and Otis 1986).

Some syconia of the Old World section *Sycocarpus* contain a thick liquid or "liquor" at a certain period of their development (Williams 1928, Baker 1913). This liquid can also be found in the sections *Sycomorus* and *Neomorphe (sensu* Ramírez 1977). In *Ficus nota,* this "liquor" is still present when the heteromorphous male wasps Agaonidae and the Sycophagini (family Torymidae) emerge from the galls. Males of *Eukoebelea nota* have a pair of silvery tubes which extend internally throughout the length of the body and a pair of laminate excrescences or prong-like respiratory processes which extend from the eighth urotergite of the abdomen. These structures allow the males to breath while they are submerged in the "liquor" (Williams 1928). These respiratory external structures are a common syndrome in most of the male Sycophaginae, a parasitoid group of the Agaonidae (the pollinators). Wiebes (1966, 1976) informs that the gaster of male Sycophaginae, except those of *Idarnes,* bear very long, laminate excrescences on the spiracles of the eighth urotergite. Laminate respiratory excrescences or filaments are probably related to the presence of "liquor" inside the syconium in the male phase, when the Sycophaginae males eclose from the galls. According to Wiebes (1982) *Eurokoebelea* males behave like little snakes in the humid interior of the receptable, and they have "gills" (e.g. long filaments on the spiracular peritremata). *Idarnes* (Sycophagini) develops in syconia which do not accumulate liquid at the time of eclosion of the males and does not possess respiratory excrescences. According to Galil (1984), in *Ficus sycomorus (section Sycomorus*), at the beginning of the male phase (when the male fig wasps are eclosing from the galls), the ambient is very wet and liquid accumulates within the syconium.

Unlike some Sycophaginae fig wasps, female *Varroa* have a pair of peritremal breathing tubes (poorly developed in males) which are movable, strongly looped and extrude distally from the stigma in the region of coxa IV (Delfinado and Baker 1974) (Fig. 2). The adult fertilized female mite enters the brood cells, where she buries herself in the larval food under the bee larva with its ventral side facing the larva.

Langhe and Natzkii (1977) postulated that the peritremal tubes allow *Varroa* mites to breath in the different gaseous regimes which they encounter in the hives. While developing, the mite must accommodate itself to a high carbon dioxide concentration inside the hive or during flight of the bee. It is of interest to note that *Varroa* has not been found in the nests of *Apis* dorsata and *A. florea* which build single exposed combs.

Flechtmann (1975) mentions that the elongate peritremata on the stigma are found in most predator mites of suborder Mesostigmata, to which the Varroidae belong. The tubular peritremata are reduced or abstent in the endoparasitic mites of vertebrates (Flechtmann 1975). According to the same author much evidence indicates that the tubular peritremata are involved in the mechanisms of the hydrolic balance of the mites (pers. com.).

In heteromorphic fig wasps (Fam. Agaonidae and Torymidae: Sycophaginae) as well as *Varroa* (the bee mite) the males are smaller, neotenic, and unpigmented. The similiraty of characteristics can be attributed to their development in dark and humid microenviroments; namely, the interior of the syconium and the brood cell respectively. The males of Agaonidae unlike the females, are apterous. Sycophaginae males (Sycoecini excepted) are apterous too (Wiebes 1976). There are many other similarities between the males of the two groups studied: males have shorter developmental periods and life spans (for *Varroa,* see Grobov 1977). They have precise sex ratios and are also much less abundant than females. Males of both groups usually do not abandon the site where their development and mating occur, do not feed and do not fight. Astomy is found in some male Agaonidae. Development time for *Varroa* mites is very constant for both sexes: 7.5 days for the female and 5.5 days for the male, which is completed before the adult bee emerges from the cell (Infantidis 1983).

Valerio (1976) noted that for *Baeus achaearaneus* (Hymenoptera, Scelionoidae), an endophagous parasite on the eggs of the house spider *Achaeraneae tepidariorum.* "...in general, every male seems to be able to fertilize many females". He states, quoting Dreyfus and Brever (1944) "the gregarious Sceleionoidae and some related families have developed a rather close inbreeding system, and copulation occurs right after emergence near the host, or inside it" (Valerio 1974). According to Mitchell (1973)"... all adaptations for small territories tend to result in inbreeding".

In the heteromorphic fig wasps, especially the Agaonidae, the developmental period is quite constant. In both Agaonidae and *Varroa,* few females (usually one or two) penetrate the syconium or the brood cell respectively; that is, each host is colonized by a certain small number of females and is eventually exhausted through feeding of the progenies (Ramírez 1986). Females of both groups lay a very constant number of eggs on their respective hosts. The males usually copulate (sib-mating) with related females (sisters). Both groups fit the "Local Mate Competition Rule" (LMC) of Hamilton (1987). According to Hamilton (1979) "rotting logs are a habitat which also provide intrademic inbreeding. In a species of *Pymephorus* mite, their broods with two to four males among 16 to 160 females develop and mate with the lethargic females inside the physogastric mother".

It is probable that the relative humidity and carbon dioxide concentration of the sealed honey bee brood cell are higher than in the interior of the hive, although this is yet to be measured. It is known however, that in the early stages of the male phase of the syconia of *Ficus religiosa* (when adult fig wasps *B. quadraticeps* are emerging from the galls), the internal atmosphere of the fig consists of about 10% carbon dioxide and 10% oxygen and some ethylene (Galil *et al.* 1973), as opposed to the normal 0.0033% carbon dioxide and 21% oxygen concentration of the atomosphere (Keeton 1980). The higher carbon dioxide and relative humidity in the brood cell and in the syconia could have contributed to the presence of lethargic females in Agaonidae and *Varroa* at the time of mating, as found by Hamilton (1979) in other organisms inhabiting seraglias.

Organisms like the fig wasps and *Varroa,* which develop within very constant microenvironments and food supplies seem to have very constant ontogenesis. The similar dark microenvironments, gaseous conditions and the presence of a liquid or semiliquid medium during part of the life cycle of these two unrelated arthropods have led to many biological and morphological analogies as listed in Table 1.

In insects and possibly other arthropods, neoteny exists in those species in which mating occurs in the same place where females and males develop. Other neotenic groups include the families Psychidae (most species). Lampyridae and Phengodidae (some species), and the entire order Stresiptera. In the mite *Tetranychus urticae,* which deposits its eggs and develops in circunscribed areas, the males are eight times smaller than the females and do not feed. The failure of the males to grow significantly suggests a selective regime in which males that pursue females earlier leave more daughters than the males which take time to feed and grow (Mitchell 1973). In the agaonid fig wasps, copulation occurs while the lethargic females are still inside the gall flowers in the syconium (the fig). Copulation of all the females (several hundreds) from a single fig takes only a short time (few hours). For this reason the males do not eat as adults and have to be ready for their sexual activities upon their emergence form their galls (*Varroa* males do not feed either).

The mite *Euvarroa sinhai* (which develops on *Apis florea*) is very similar to *Varroa jacobsoni* in its parasite relationships (Akratanakul 1976). The bee mites *Tropilaelaps clareae* and *T. koenigerum*, which normally develop in *A. dorsata,* also seem to have similar relationships with their host (as *V. jacobsoni*). Thus, these two species of bee mites could also fit into the "Local Mate Competion Rule" of Hamilton (1967).

LMC females seem to lay the male eggs at the beginning of the oviposition sequence. Inbreeding among LMC organisms does not seem to be deleterious since a high genetic variation does no appear to be necessary, the reason is that they spend most of their lives in very steady physical and alimentary environments.

TABLE 1

Analogies between sycophilous wasps (Fam. Agaonidae) and the parasitoids Toryminae (Sycophaginae) and Varroa jacobsoni *(Varroidae, Mesotigmata: Acari)*

		Fig. wasps	*Varroa Jacobsoni*
1)	Specific relationships	Agaonidae, Sycophaginae	+
2)	Sex ratio spanandrous*	Agaonidae	+
3)	Developmental synchronization of host and associate	Agaonidae	+
4)	Arrhenotokous reproduction*	Agaonidae, Sycophaginae	+
5)	Precise sex ratios	Agaonidae	+
6)	Females modify the developmental period of the host	Agaonidae	?
7)	Gregarious development*	Agaonidae	+
8)	Development occurs in a dark and humid environment (claustral habitat)	Agaonidae, Sycophaginae**	+
9)	Few females colonize the host (relatedness)	Agaonidae	+
10)	Females usually lay a constant number of eggs*	Agaonidae	+
11)	Male eggs usually laid at the beginning of the sequence	Agaonidae	+
12)	Development time from eggs to adult is nearly constant*	Agaonidae	+
13)	Quite constant progenies reared per host	Agaonidae	+
14)	Males born before females*	Agaonidae	+
15)	Neotenic males	Agaonidae	+
16)	Smaller males	Agaonidae	+
17)	Shorter male life span*	Agaonidae	+
18)	No feeding of males	Agaonidae, apterous Sycophaginae	
19)	No fighting of males	Agaonidae	+
20)	No oedemery of male's front legs	Agaonidae	+
21)	Mating occurs before females emergency	Agaonidae	?
22)	Polygamous males*	Agaonidae	+
23)	Sibmating more common than outcrossing*	Agaonidae	+
24)	Mating in same place of development*	Agaonidae	+
25)	Precocious local mating	Agaonidae	?
26)	Females are lethargic before and at mating	Agaonidae	?
27)	No males successfully mate outside their own group*	Agaonidae	+
28)	No abandoning of place of developement by most males (claustrophilic males)*	Agaonidae	+
29)	Females store sperm*	Agaonidae	+
30)	One insemination serves to fertilize the whole eggs production*	Agaonidae	+
31)	Finding of new host only by females*	Agaonidae, Sycophaginae	+
32)	Large peritremata in females and males	Agaonidae	+
33)	Protruding respiratory structures	male Sycophagini***	+
34)	Fighting of females at oviposition	Agaonidae	+
35)	Competition for resources biases the sex ratio	Agaonidae, Sycophaginae	+
36)	Local resources competition (LRC)	Agaonidae	+
37)	Nonrandom searching for hosts	Agaonidae	+
38)	Differential mortality of developing females occurs with superparasitism.	Agaonidae, Sycophaginae	+

* Typical characteristics of inbreeding spp., (Hamilton 1967)

** *Apocrypta, Eukoebelea, Sycophagella* and *Sycophaga Idarnes* excepted

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REFERENCES

Akratanakul, P. 1976. Biology and systematics of bee mites of the family Varroidae (Acarina: Mesostigmata). M.Sc. Thesis. Oregon Univ.: 64 p.

Barker, C.F. 1913. Astudy of caprification of *Ficus nota* Philipp. J. Sci. 8: 63-83.

De Jong. D. 1984. Current knowledge and open questions concerning reproduction in the honey bee mite *Varroa jacobsoni.* p. 547-552. *In* Advances in Invertebrate Reproduction 3, Elsevier Science Publishers, B.V.

Delfinado, M.D. 1974. Varroidae, a new family of mites on honey bees (Mesostigmata: Acarina). J. Wash. Acad. Sc. 64: 4-10.

Dreyfus, A. & M. E. Brever 1944. Chromosome and sex determination in the parasitic hymenopteran *Telenonus fariari* Lima. Genetics 29: 75-82.

Flechtmann, C.H.W. 1975. Elementos de Acarología. Livraria Nobel S.A. Sao Paulo. Brasil. 344 p.

Galil, J., M. Zeroni, & D. Bar Shalom. 1973. Carbon dioxide and ethylene effects in the coordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa.* New Phytol. 72: 1113-1127.

Galil, J. 1984. Anther dehiscense in fig syconia. p. 35-40 *In* Mini Symposium Figs and Fig Insects. Centre National de la Recherche Scientifique. France.

Green, R.F., G., Gordh & B.A. Hawkins 1982. Precise sex ratios in highly imbred parasitic wasps. Am. Nat. 120: 653-665.

Grobov, O.F. 1977. Varroasis in bees. p. 49-60 *In* Varroasis a honeybee disease: Bucharest, Apimondia Publishing House.

Hamilton, W.D. 1967. Extraodinary sex ratios. Science. 156: 47-488.

Hamilton, W.D. 1979. Wingless and fighting males in fig wasps and other insects, p. 168-220 *In* Reproduction, competition and selection of insects. M.S. Blum & N.A. Blum (eds.). New York: Academic Press.

Hilton, H.E. 1961. How some insects, especially the egg stages, avoid drowning when it rains. Proc. London Entomol. Nat. Hist. Soc.: 138-139.

Joseph, K.J. 1984. The reproductive strategies in fig wasps (Chalcidoidea: Hymenoptera). A Review. Proc. Indian Natn. Science B 50: 449-460.

Keeton, W.T. 1980. Biological Science. W.W. Norton and Co. New York and London, 3a. ed. 1080 p.

Langhe, A.B. & K. V. Natzkii. 1977. The mite *Varroaa jacobsoni* and the methods of controling it. p. 40-46. *In* Apimondia. Bucharest (op. cit.).

Mitchell, R. 1973. Growth and population dynamics of a spider mite (*Tetranychus urticae* K. Acarina: Tetranychidae). Ecology 54: 1349-1355.

Ramírez, B.W. 1977. A new classification of *Ficus.* Ann. Mo. Bot. Gdn. 64: 298-310.

Ramírez, B.W. 1986. The influence of the microenvi ronment (the interior of the syconium) in the coevolution between fig wasps (Agaonidae) and the figs (*Ficus*). p. 32 *In* Abstracts 6th Int. Symp. Insect-Plant relationships. Pau. France.

Ramírez, B.W. & G.W. Otis. 1986. Developmental phases in the life cycle of *Varroa jacobsoni,* an ectoparasite mite on honeybees. Bee World 67: 92-97.

Smirnov, A.M. 1979. Acerca de la morfología e histología del ácaro *Varroa jacobsoni.* p. 36-40 *In* Atajo y Prevención de la Varroasis. Bucharest, Apimondia Publishing House.

Valerio, C.E. 1974. Dimorfismo en avispas macho de la familia Scelionidae (Hymenoptera). Brenesia 3: 1-9.

Valerio, C.E. 1976. Significance of all-male progenies in some microhymenopteran parasites. Brenesia. 9: 25-29.

Wiebes, J.T. 1966. The structure of the ovipositing organs as a tribal character in the Indo-Australian sycophagine Torymidae (Hymenoptera). Chalcidoidea Zool. Med. 41: 151-159.

Wiebes, J.T. 1976. A short history of fig-wasps research. Gdn. Bull. Singapore 39: 207-224.

Wiebes, J.T. 1982. Fig. wasps (Hymenoptera). p. 735-755 *In* J. L. Gressit (ed.). Monographiae Biologicae.

Williams, F. X. 1928. Studies in tropical fig wasps, their bosts and associates. Bull. Hawaii Sug. Exp. Sta. Entomol. ser. 19: 1-179.