

Biosystematics of fig wasps (Chalcidoidea : Hymenoptera)

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Abstract. The fig wasps form a heterogenous group of microhymenopterans showing convergent evolution in response to adaptations for life in their unique habitat—the interior of the syconia of the different *Ficus* species. Sexual dimorphism is very common among the various tribes of the chalcidoid families constituting the fig wasps. This is in response to the different types of functions that the female and the male sexes are called upon to perform in their specialized habitat. The unisexual variations commonly met with in the male sex and rarely in the female sex, in the cleptoparasitic tribes belonging to the *Torymidae* and the *Pteromalidae* may be attributed to competitive feeding on a limited provision of food—a trophic factor. In the homeomorphic sexes of the subfamily *Epichrysomallinae* (*Pteromalidae*) copulation takes place outside on the top of the syconia. The importance of making observations on the biology including mating behaviour of the dimorphic (apterous and alate) males in the subfamily *Sycophaginae* (*Torymidae*) for the proper study of the systematics of this group is stressed.

The true fig wasps which are the fig pollinators (*Agaonidae*) are generally highly host specific, i.e. only one species of these pollinators is associated with a given species of *Ficus*. The *Ficus* species and its wasp pollinator are in intimate symbiotic relationship. There has been co-evolution of the *Ficus* species with its specific wasp pollinator. The females of these pollinator wasps often possess pollen storing structures as well as the behavioural attributes for the active collection of pollen from the stamens of the ripe fig and for the active dispersal of pollen on to the stigmas of the ovaries of flowers of tender figs into which these females penetrate for oviposition.

The ecological niche of the *Ficus* syconia is virtually identical to that of many plant galls and as such attract many species of gall-inhabiting *Eurytominae* (Family *Eurytomidae*). Such *Eurytominae* include a variety of genera, with numerous species both of phytophagous and entomophagous habits.

The modern systematics of the fig wasps is based on the above aspects of their functional morphology, biology, convergent evolution, sex-limited variations, sex-limited dimorphism, host specificity, behavioural attributes, etc. A conspectus of the modern classification of the fig *Chalcidoidea* is presented.

Keywords. Fig wasps; chalcidoidea; biosystematics.

1. Introduction

Classical systematics based on the study of only morphological features of organisms and built on the highly static type concept, over the years developed a reputation of being a matter of sterile pigeon holing (Hanson 1958). Effective research and action programme in basic and applied biology demand a sound taxonomic base (Lattin and Riley 1984). This is provided for in the newer trend in systematics or what is called biosystematics. Biosystematics is based on data derived not only from the study of morphology but necessarily also on studies of physiological, biochemical, eco-behavioural and genetic features of organisms as well as from their biometric analysis. Thus biosystematics is a dynamic area of study and research. The study of insect biosystematics has become increasingly significant in explaining problems which go beyond the classical systematic approach (Howse and Clement 1981) and

which are often of great importance in various aspects of agriculture, medicine and forestry.

Several genera and species of microhymenopterans belonging to families *Agaonidae*, *Torymidae*, *Pteromalidae* and *Eurytomidae*, because they develop in the receptacles of figs (*Ficus* spp.), form a heterogenous group—commonly called as fig wasps. Of the different families, the agaonids alone are true fig wasps in the sense that they lead a true symbiotic life and are responsible for pollination in *Ficus*. Others live either as parasites (torymid and pteromalid fig wasps) or as inquilines (eurytomid fig wasps). Owing to the unique habitat these wasps share, they show remarkable convergent evolution. Almost all species of fig wasps are characterised by pronounced sexual dimorphism: this is in response to the different functions that the male and female sexes are called upon to perform in their specialised habitat. The prevailing ecological niche—the ovary of the female flowers in the fig syconia—is more or less similar to that of many plant galls and as such attract many species of gall-inhabiting *Eurytomidae*. Fig wasp systematics to be sound and authoritative, should not be merely a descriptive compendium of morphological features, but should also effectively take into consideration the various aspects of their life such as functional morphology, biology, host-specificity, eco-behavioural attributes, sexual dimorphism, unisexual variations, unisexual dimorphism, convergent evolution, etc.

2. Review of literature

Though taxonomic descriptions of several species of fig wasps are available, only a few workers have attempted to study the biology and phylogeny of the group. Among these, the works of Grandi (1920, 1921, 1925, 1929, 1930, 1959 and 1961), Joseph (1953–1956, 1958, 1959a,b, 1966, 1984), Abdurahiman and Joseph (1976, 1978a,b, 1979), Wiebes (1963, 1973, 1976 and 1982–1986), Galil and Eisikowitch (1968, 1969, 1971), Galil *et al* (1973), Hill (1967) and Boucek *et al* (1981) are important. Their contributions have thrown light on the intricate relationships that exist between figs and fig wasps, the wasp adaptations—morphological, physiological and behavioural—involved, their reproductive strategies, life-cycles, co-evolution, phylogeny, etc. In this paper an attempt has been made to correlate the morphological, biological and behavioural attributes of this peculiar group of insects to their systematic affinities and diversities.

3. Observations

3.1 *Biological features*

A coordination of the developmental periods of the wasps and figs is a vital factor in the fig–fig wasp symbiosis. This has, in the course of evolution, caused extreme plasticity of adaptive mechanisms that are essential for the survival of both participants in the symbiosis. The success of this symbiosis is assured by the imposition of the developmental rhythm of the wasp with that of the plant partner. The viability and maturity of the unpollinated syconia, due to occupation by the wasp, is of utmost importance for the completion of the developmental cycle of the wasps.

At the early stage of development of the fig, the oviposition by the agaonid prevents the dropping of the tender figs and ensures the development of the figs to

final ripening. Longo (1909) and Leclerc du Sablon (1906) showed that as a result of oviposition by the agaonid, *Blastophaga psenes*, into the ovary of its host *Ficus carica*, the secondary nucellus is induced to divide, leading to the parthenogenetic development of the endosperm which serves as provision of food for the developing stages of the insect. It is quite likely that the determinant of this excitation for division is contained in the acid gland of the agaonids (Grandi 1920, 1961; Joseph 1958; Abdurahiman and Joseph 1978a,b). Joseph (1958) and later Abdurahiman and Joseph (1978a,b) found that the Pteromalid, *Philotrypesis* spp. and the torymid, *Apocrypta bakeri*, breeding in the receptacles of *F. carica* and *F. hispida*, are subjected to partial larval starvation as a result of their cleptoparasitic mode of life on their agaonid hosts. Both the larvae of the agaonid and the pteromalid/torymid develop simultaneously up to their second instars inside a given *Ficus* ovary, feeding on the provisions made available by the agaonid female for its own larva. But as the quantity of the food left over at the disposal of the trophically competing larvae get depleted, the more robust cleptoparasitic larva manages to win over the agaonid, resulting in its death. This competition for food, however, leads to the partial larval starvation of the torymid/pteromalid. The quantity of the food left over at the disposal of the developing pteromalid/torymid larvae in the different ovaries of a given syconium can vary depending on the duration for which the agaonid larva in each case has managed to survive. This leads to the production of variously sized torymid/pteromalid larvae. The size of the adults depends directly upon the size of the larvae, which itself is determined by the size of the cells of the larvae (Grosch 1948). This trophic factor, therefore, has a direct bearing upon the unisexual variations and unisexual polymorphism met with in the populations of certain species of torymid and pteromalid fig wasps.

This unisexual polymorphism is more commonly met with among the males and rarely among the females. In parasitic Hymenoptera, as shown by various authors, there occurs a differential mortality of the sexes as a result of partial larval starvation. Genieys (1925) showed in the case of *Habrobracon brevicornis* that partial larval starvation is less unfavourable to the male sex than to the female sex. According to Grosch (1948), it is haploidy rather than masculinity that enables animals to survive better under conditions of partial larval starvation. The female larvae which suffered from starvation would be eliminated while the males survive as dwarf individuals. This is probably why in cleptoparasitic fig wasps, dwarfism is rare among the females, while it is commonly met with in males.

Joseph (1959b) described the torymid species *Sycobiomorpha bimasculinum*, having two types of males: the alate and the apterous. The presence of these two types of males is advantageous to the species. It is suggested (Joseph 1984) that the existence of both apterous and alate males assures the fertilization of the maximum number of females by the apterous males inside the cavity of the syconium; those females that escape outside unfertilized, are fertilized by the alate males which await them on the surface of the fig wall. The importance of making observations on several aspects of biology including the mating behaviour of the fig wasps is therefore obvious and has great relevance to our understanding of the systematics of the group.

3.2 *Host specificity*

In general, the wasp pollinators (Agaonidae) do appear to be specific to their host fig, but exceptions do occur (Wiebes 1986). The best known of such exceptions is that of

Ceratosolen galili which is cleptoparasitic on *Ceratosolen arabicus* which lives in symbiosis with *Ficus sycomorus* (Galil and Eisikowitch 1968, 1969). However, *C. galili* does not pollinate its host plant. Michaloud *et al* (1985) found that two species of agaonids pollinate *Ficus ottoniifolia* in Gabon. The normal pollinator of *F. ottoniifolia* in localities from Zambia and Kenya in the south-west, to Gabon and the Cameroons more to the north-west, is *Courtella camerunensis*. However, only in Gabon, a second species, *Courtella gabonensis*, also pollinates the flowers of *F. ottoniifolia*. Berg (unpublished results) distinguished 5 subspecies of *F. ottoniifolia*, 3 of which are pollinated by *C. camerunensis*, a fourth by *C. gabonensis* and the fifth by *C. scobinifera*.

In the other families containing fig wasps (Torymidae, Pteromalidae and Eurytomidae) though the present state of our knowledge of the systematics does not permit a generalization, it may be stated that host specificity is generally found. It may be noted that related species of *Ficus* harbour related species of fig chalcidoids. The total fig wasp fauna of a Rhodesian fig, *F. thonningii* including 3 species of *Agaonidae*, appeared to consist 28 different species (Boucek *et al* 1981). Evidently more research on the insufficiently known fig wasps, is needed to throw more light on these and other exceptions to host specificity.

3.3 Pollination

It was Ramirez (1969) in Costa Rica and Galil and Eisikowitch (1969) in Israel, who almost simultaneously showed the presence of specialised structures and behaviours involved in pollination by fig wasps. Two kinds of containers for pollen transfer were subsequently recognised: mesosternal 'pollen pockets' and coxal 'corbiculae' on the fore legs. Ramirez (1978) envisaged the evolution of pre-agaonid wasps visiting the pre-*Ficus* inflorescence (to feed on pollen), by natural selection favouring the development of those forms with more setae on the mesosternum and coxae, in addition to those carrying pollen in the digestive tract. He distinguished 4 main systems of pollen transport viz (i) enhanced capacity to carry pollen in the buccal cavity or other hidden areas of the body (e.g. *Blastophaga psenes*); (ii) hairiness of the mesosternum (*Phagoblastus* sp.); (iii) corbiculae on front coxae (*Dolichoris* sp.); and (iv) mesosternal pollen pockets, with a transformation series, having the mesosternum with setae only, or with incipient pollen pockets, or with enlarged ones, or with almost closed pockets of the type Galil and Switzer-Pasternak (1970) described for *Platyscapa quadraticeps*.

Ramirez (1981) produced a cladogram for *Ficus* as well as for the agaonids. In general, it is possible to conclude that there is 'good fit' between the cladograms for the agaonid wasps and their *Ficus* hosts, in that most sections of *Ficus* have their own genus of pollinating wasps. On a higher level this need not work, as there are many other factors that influence the course of the phylogeny in agaonids.

3.4 Morphological features

Fig wasps exhibit wonderful adaptations for life inside the fig syconia. Pronounced sexual dimorphism is common as perhaps the most important of their adaptations. With few exceptions, the males are vermiform, apterous and live only for a short

duration of a few hours during which time they accomplish their sole functions of locating and fertilizing their females. Their strongly chitinized integument, greatly developed prothorax, well developed anterior and posterior legs and small middle legs, their apterism, vermiform shape and peculiar telescopic arrangement of the 7th, 8th and 9th abdominal segments (in agaonids), are all adaptations for facilitating these functions. A detailed analysis of their morphological features and transformations in different groups of agaonids are discussed by Wiebes (1982a,b). The important morphological features pertaining to the females of agaonids are given below.

3.4a *Shape of the head*: The dorso-ventrally depressed and distinctly longer head, facilitates entry through a tubular ostiolar opening of the syconium, as found in the figs of sections *Galoglychia*, *Malvanthera* and *Pharmacosycea*.

3.4b *Structure of antenna*: Normally, the scape is short and robust, but in some genera it is more or less lengthened (e.g. *Agaon*, *Alfonsiella*, *Allotriozone*, *Elizabethiella*, *Paragaon*, *Pleistodontes*, *Nigeriella*, *Tetrapus*). The long scape may be used as levers pushing apart the bracts while entering the syconia through the ostiole. Presumably the short scapes are also used in the same way.

In most genera, the pedicel is distinctly longer than wide and bears a number of backwardly directed conspicuous spines. As far as the shape and conformation of the third segment is concerned, there appears to exist a transformation series, from its simple nature without a pronounced apical elongation (e.g. *Alfonsiella*) to a segment that is produced more apically (e.g. *Agaon*), in which the elongation forms a distinct appendage. The appendage may be secondarily segmented as in *Ceratosolen*.

3.4c *Reduction of mouth parts*: The most primitive state of reduction is the one in which the maxilla consists of a distinct galea and stipes and bears a palpus, and also the labium has a palpus (e.g. *Tetrapus*). At the end of the process of reduction, the labium and maxilla are reduced to one composite structure in which the labium may be unrecognisable (e.g. *Liporrhopalum*).

The appendage of the mandible may be completely fused with the body of the latter and bear ventral lamellae (as in the *Blastophaginae*), or it may be truly appended to the mandible and bear ventral rows of teeth (as in the *Agaoninae*).

3.4d *Length of the ovipositor*: Ramirez (1974) believed that a long ovipositor is a primitive character. He also related the change from monoecious figs as hosts, to dioecious figs, with a change from long to short ovipositors, and finally back to long ovipositors when the figs revert to monoecious state.

In the case of males, the following characters are relevant.

3.4e *Reduction of the antenna*: The most complete antenna has 7 or 8 segments, viz the scape, pedicel, 3 funicular segments and a club formed of 2 or 3 parts (e.g. *Platyscapa awekei*) but usually the number is smaller, i.e. only 4 in some *Blastophaga* spp.

3.4f *Antennal torulae*: A shifting of the toruli seems to have occurred in two steps: viz their approximation towards each other in the mid line, and their restriction in

separate pockets in the head capsule. Widely separated toruli are found in *Alfonsiella*, *Nigeriella*, *Platyscapa* etc while in *Blastophaga*, *Kradibia*, *Liporrhopalum* etc they are approximated and can be pulled back into pockets. This condition is even better developed in *Ceratosolen*, where the scrobes may be open, half closed or closed over almost the whole length.

3.4g *Reduction of some mouth parts*: As in female, the labium and maxillae are greatly reduced or lost. However, distinct labium and maxillae are present in most of the species of *Ceratosolen*, *Dolichoris*, *Pegoscopus*, *Pleistodontes* and *Tetrapus*. In some there are remnants of maxillo-labial complex (e.g. *Alfonsiella*, *Allotriozone* and *Kradibia*), while in certain others they are much reduced or totally absent (e.g. *Agaon*, *Dielagaon*, *Liporrhopalum*, *Eupristina* etc).

3.4h *Tarsal segments*: The primitive condition is that all tarsi have 5 segments. In several genera there is a reduction in the number of tarsal segments of the fore, mid and hind legs.

3.4i *Genital armature*: In some genera, the male genitalia carry digiti, with or without claws, as in a few *Blastophaga*, most *Ceratosolen*, *Dolichoris*, *Kradibia*, some *Liporrhopalum*, 2 species of *Platyscapa*, most *Pleistodontes* and *Tetrapus*. The digiti are usually absent in other groups.

3.5 *Behavioural aspects*

The males of all fig chalcidoids are protandrous. On emergence they gnaw a hole in the wall of the fig ovary in which they developed and emerge into the cavity of the syconium. Now they start their search for, and unerringly locate the particular fig ovaries enclosing their respective females. This ability of the males to locate the ovaries containing their own females without any trial and error is reasonably supposed to be based on the chemoreception and the detection of specific chemicals (pheromones) produced by the females, by the sensillae located on the tip of the antennae of the male concerned (Joseph 1958). The protandrous males also make exit holes in the wall of the fig ovaries enclosing their teneral females. This act is carried out, irrespective of whether copulation takes place with the female while it is still enclosed in the fig ovary as in Agaonidae or after it has emerged into the syconial cavity as in the torymid (*Apocryptini*) and pteromalid (*Philotrypesini*) fig wasps, or outside the ostiolar opening on the external surface of the fig syconium as in the pteromalid (*Epichrysomallini*) fig wasp, *Odontofroggattia galili* and most likely in the eurytomid fig wasps. It has also been found that at least in the case of *Philotrypesis*, the male helps the females to go out of their gall flowers by slightly pulling them out by means of the mandibles and then allowing them to come out on their own.

In the case of the *Agaonidae*, the male cuts out a hole on the wall of the fig ovary enclosing the female and introduces its tubular abdomen to copulate with the teneral female inside. In the torymid *A. bakeri* (Abdurahiman and Joseph 1978a,b) and the pteromalid *Philotrypesis caricae* (Lichtenstein 1919; Grandi 1921; Joseph 1958), copulation occurs soon after the females emerge from their gall ovaries. However, in the pteromalid *O. galili*, the males tunnel through their syconial wall, close to the ostiolar area, by means of their large, sickle-shaped mandibles, generally making a

circular hole (0.4 mm dia), through which they crawl out. Several such males assemble on the top of their syconia, running excitedly here and there around the ostiole; they even push each other. As the first female emerges through the ostiole, one of the males grasps her firmly with his legs and mounts her from above. The female now runs about carrying the amatory male rider; the male curls his abdomen underneath the female's gaster and copulation follows.

4. Discussion

4.1 Classification

So far the main criterion adopted for classification of fig wasps has been an analysis of the morphological characters, supplemented by some biological evidence wherever available. Such analysis seems to suggest that at least some of the relevant groups have nothing to do with the family *Torymidae* under which most of the fig wasps (other than the agaonids) had been classified (Bouček *et al* 1981). The Agaonidae form a distinctly separate family. It seems that the subfamily *Sycoecinae* which is yet unplaced, is related to the *Agaonidae*, probably as a less specialised (plesiomorphic) group, pointing to their common origin.

The *Agaonidae* is divided into two subfamilies—the *Agaoninae* and the *Blastophaginae*. On the basis of the characters discussed above, some groupings become apparent, though the characters applied in such groupings must be used with caution (Wiebes 1982b). The tripartition of the *Agaoninae* has been made mainly based on zoogeographical arguments. The subfamily *Blastophaginae* show an accumulation of presumably primitive character-states in some genera, each of which may be quite recognisable, but only with difficulty, united with the others. The classification of the families *Agaonidae* and *Ficus*, in certain aspects, run almost parallel, i.e. at the level of fig sections. On a higher level this poses problems. It seems inevitable that the classification of the *Agaonidae* needs to be refined, in order to clear up the many unresolved relationships. It is, therefore, essential that more and more aspects of the biology of these insects are involved and treated in detail so that the analysis is based more on secure foundations.

In the family *Torymidae*, the subfamilies *Toryminae* and *Sycophaginae* undoubtedly have had closer links. The *Sycoryctinae* constitutes another torymid subfamily—but this view is rather questionable, as there are some reasons to classify them under the *Pteromalidae* as well (Bouček *et al* 1981). The subfamilies *Otitesellinae* and *Epichrysomallinae*, closely related to each other, could well be placed under the *Pteromalidae*. However, the *Epichrysomallinae* seem to be closely related to the eurytomids. The remaining groups of fig wasps, viz *Eurytomidae* and *Ormyrinae* do not pose many problems. Among these, the ormyrids show very close affinity with the *Torymidae* and may, therefore, be regarded even as a subfamily of *Torymidae*.

In the light of the above discussion, a brief classification of the fig chalcidoidea (modified from that given by Bouček *et al* 1981) emerges. Based on the present state of our knowledge of the biosystematics of the fig wasps, an attempt has been made to place most of the various genera under the categories of tribes, subfamilies and families as given in table 1.

Table 1. Placement of the genera of fig wasps (superfamily *Chalcidoidea*) under the categories of tribes, subfamilies and families.

Genera	Tribe	Subfamily	Family
<i>Tetrapus, Agaon, Nigeriella, Pleistodontes, Allotriozoon, Elizabethiella, Alfonsiella</i>	—	Agaoninae	
<i>Blastophaga, Eupristina, Watersioniella, Platyscapa, Dolichoris, Kradibia, Ceratosolen, Mamiella, Deilagaon, Liporrhopalum, Pegoscapus</i>	—	Blastophaginae	Agaonidae
<i>Crossogaster, Phagoblastus</i>	—	Sycoecinae	(unplaced, Boucek <i>et al</i> 1981)
<i>Physothorax</i>	—	Toryminae	
<i>Sycophaga, Eukoebelea, Parakoebelea, Idarnes</i>	Sycophagini	Sycophaginae	Torymidae
<i>Apocrypta</i>	Apocryptini		
<i>Ormyrus</i>	—	Ormyrinae	Torymidae or Pteromalidae
<i>Philotrypesis</i>	Philotrypesini		
<i>Sycoscapter, Arachonia, Sycoryctes, Sycoscapteridea, Sycorycteridea, Watshamiella</i>	Sycoryctini	Sycoryctinae	Pteromalidae
<i>Otitesella, Micranisa, Walkerella, Grandiana, Grasseiana</i>	—	Otitesellinae	Pteromalidae
<i>Sycobia, Pembertonia, Sycophilodes, Sycophilomorpha, Sycotetra, Camarothorax</i>	—	Epichrysomallinae	Pteromalidae
<i>Eurytoma, Syceurytoma, Ficomila, Sycophila</i>	—	Eurytominae	Eurytomidae

5. Conclusion

In the systematics of fig wasps, we are confronted with two basic problems. Firstly, there exists a number of genera and subgenera the definitions of which are extremely vague and limits of variation little known. Secondly, in many cases the host *Ficus* spp. occur as well defined and genetically distinct varieties, each species of *Ficus* having its own specific agaonid pollinator. Yet another problem is that of the occurrence of considerable convergence in various characters of the fig wasps, presumably brought about from the similarities of the microhabitats of the wasps involved. These characters may be very successful as specific determinators but are often of limited value as generic or tribal characters. In the males, they include the reduction of the mid leg, oligomery of tarsal segments, fusion of thoracic terga, loss

or reduction of eyes and reduction of mouth parts. In the females, elongation of the head, lengthening of the mandibular appendage, obsolescence of venation, loss of tibial spurs and reduction of mouth parts are some of them (Hill 1967). Such similarities in the morphological modifications of the fig wasps are obviously correlated with similarities observed in their biology, ecology and behaviour.

The taxonomy of only about 100 species of fig wasps have been worked out, though about 900 species of *Ficus* (which are mostly tropical in distribution) are known; the biology and pollination ethology of only about 10 species of wasps have been studied so far. Also very little work has been undertaken to elucidate the morphological aspects of fig wasps using the scanning electron microscope (Joseph and Abdurahiman 1984). The combined efforts of entomologists and botanists of different parts of the world aimed at in-depth studies on the agaonid—*Ficus* symbiosis, will enable us to understand the phylogeny and co-evolution of the different sections of the genus *Ficus* and of the different associated genera and species of fig wasps.

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