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Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilization and host relationships

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ABSTRACT

We investigated the host relationships of the fig wasps (Hymenoptera: Chalcidoidea) associated with 26 of the 32 *Ficus* species recorded from southern Africa. The fig wasp assemblages were composed mainly of species which gall the ovules, and their parasitoids. Host specificity was found to be extreme in pollinating fig wasps (Agaoninae), but less so in some non-pollinating species (Sycoecinae). Most subsections of *Ficus* supported characteristic genera of fig wasps, not recorded elsewhere, suggesting that both the pollinating and some nonpollinating fig wasps may have radiated in parallel with their hosts.

INTRODUCTION

Fig trees (*Ficus* spp., Moraceae) and pollinating fig wasps, (Agaoninae, Agaonidae, Hymenoptera, *sensu* Bouček, 1988) are obligate mutualists. Female agaonines pollinate the trees while ovipositing in the ovules, where their larvae subsequently develop (Galil, 1977). The relationship is believed to be highly specific, with one wasp species typically associated with each species of tree (Michaloud *et al.*, 1985; Wiebes & Compton, 1990; Compton *et al.*, 1991). Agaonine host specificity is linked to the wasps' responses to tree-specific volatile attractants, released when the figs are ready to be pollinated (van Noort *et al.*, 1989). The structure of the fig itself may form a secondary, physical barrier to oviposition by non-adapted species (Janzen, 1979; Ware & Compton, in press).

A fig has the appearance of a hollow ball, lined on its inner surface by hundreds or thousands of highly reduced unisexual flowers (Verkerke, 1989). In order to oviposit, female agaonines must force their way through the ostiole, a bract-lined tunnel, into the fig cavity. Once inside, the wasps pollinate the

flowers and lay eggs in some of the ovules. Oviposition is achieved by inserting their ovipositors down the full length of the styles (Galil, 1977). In both monoecious and dioecious *Ficus* species from southern Africa style lengths show a unimodal frequency distribution, with most styles of intermediate length and no division into discrete 'long' and 'short' styled flowers (Nefdt & Compton, in preparation). In monoecious figs the wasps generally have ovipositors that can reach most of the ovules, although the majority of eggs are laid into the flowers with shorter styles, leaving the longer styled flowers to mainly produce seeds (Compton & Nefdt, 1990).

Related trees generally support congeneric agaonines (Wiebes & Compton, 1990) and there is a generally close correspondence between the phylogenies of the wasps and their host trees (Wiebes, 1982, 1990). This has led to the suggestion that they have cospeciated (Jermy, 1984). Thompson (1989) concluded that cospeciation was most likely to occur in systems such as figs and agaonines, where the behaviour of a pollinator limits gene flow of a host plant, but that cospeciation was not the only possible explanation for their parallel phylogenies.

Agaonines form only a small proportion of the wasps associated with fig trees, although they are the only pollinators. The fig wasp assemblages associated with 14 well-studied *Ficus* species were summarized by Bouček *et al.*, 1981. Non-pollinating fig wasps belong to the remaining subfamilies of Agaonidae and other families of the Chalcidoidea (Bouček, 1988). They include both gall-forming phytophages and parasitoids, but their systematics and ecology is generally poorly understood. Host tree specificity of non-pollinating fig wasps appears to be well developed, with most species recorded from only a single host (exceptions in Bouček *et al.*, 1981 and Wiebes, 1981). This could be a consequence of the small proportion of fig wasp species that have been described, although Ulenberg found extreme host specificity in her revision of the parasitoid genus *Apocrypta* (Ulenberg, 1985).

In this paper we examine base-line questions about the biology of the fig wasps found in southern Africa. These are: which genera of fig wasps are associated with the various sub-groups of *Ficus*? what do the fig wasps eat? and, for selected wasp assemblages/ taxa, how host-tree specific are they? and do the parasitoids display host-insect specificity?

Southern African fig trees

Africa south of the Zambezi river has 32 of the 105 African *Ficus* species recognised by Berg (1990a). Three of these species are dioecious (subgenus *Ficus*), the remainder monoecious (three species of subgenus *Sycomorus* and 26 species of subgenus *Urostigma*).

The greatest diversity of *Ficus* species occurs in the warm and humid north and east of the sub-continent, whereas the large, arid zone of the Kalahari-Namib-Karoo supports few species. Of the 32 species south of the Zambezi, 17 are widespread throughout Africa, 9 are shared with East Africa, and 6 are more or less restricted to the area. The sub-continent is therefore characterised by a

large proportion of widely distributed species, with relatively few endemics and sub-endemics (Berg, 1990b).

METHODS

For the classification of *Ficus* we follow Berg (1990a) and for fig wasps Bouček (1988), except that *Sycoryctes*, *Sycoscapteridea*, and *Sycoscapter* are kept distinct as they are readily distinguished in southern African collections.

Figs were collected as the wasps were beginning to emerge and placed in netting-covered containers. Observations on the origins of the wasps were carried out as they were being removed, prior to card-mounting for subsequent identification. Most of the non-pollinating wasps are undescribed and were placed as morpho-species. Except for members of the Agaoninae and Sycoecinae, no attempt was made to routinely distinguish between congeneric species reared from different host trees. A small proportion of the figs also contained fly, beetle or moth larvae/pupae. These were retained and any emerging parasitoids were recorded.

Wasps from 312 trees were obtained in the following southern African countries: South Africa, Zimbabwe, Botswana, Namibia, Zambia and Malawi. Eight additional collections of wasps from tree species that occur in southern Africa were obtained in Kenya, Uganda and Cameroun. Overall, the collections covered 28 nominal tree taxa, representing 26 of the *Ficus* species recognised by Berg (1990a), plus two distinct subspecies/forms. Voucher specimens of the wasps are retained in the author's collection.

Determination of host-tree specificity is dependent on satisfactory taxonomic studies of both the wasps and the trees. African *Ficus* species have been revised by Berg (1990a), but knowledge of African fig wasps is more limited. In addition to Ulenberg's (1985) study of *Apocrypta*, information is available on the systematics of two groups of African fig wasps, the Agaoninae (Wiebes & Compton, 1990 and Compton, unpublished) and the Sycoecinae (van Noort, in preparation). Here we describe the degree of tree specificity in the latter two groups.

Information on the host insects utilised by the parasitoid fig wasps was generally not obtained, due to the collecting methods employed. However, detailed observations were carried out on the wasps associated with three *Ficus* species growing near Grahamstown in the eastern Cape Province of South Africa. Food webs of the three assemblages were produced.

RESULTS

Trophic relationships

Table 1 summarises the oviposition methods and trophic relationships of the fig wasps. The latter are extrapolated from observations on a limited number of species in each genus. More detailed surveys may show that their biologies are more diverse than indicated, as only a small proportion of the species were observed in detail. 'Internal' ovipositing species, such as agaonines and sycoecines, enter the figs via the ostiole prior to oviposition. With the exception of

some species of *Phagoblastus* (Sycoecinae), (G. Michaloud and R. Nefdt, personal communications), internal ovipositing species are unable to escape and have to lay all their eggs inside a single fig. Species which lay their eggs from the outside of the figs ('external' ovipositors) are characterized by their long ovipositors.

Galled ovules provided the larval food of the great majority of the phytophagous fig wasps. Galling of two other tissues inside the figs was also observed. Epichrysomallines galled the figs of *F. fischeri* and *F. glumosa* at a very early stage in their development, before features such as the flowers had differentiated. The epichrysomalline larvae developed in chambers encircling a slit-like hollow centre, all that remained of what would have been the ostiole and fig cavity. Such galled figs were unsuitable for the other phytophagous fig wasps, and the gallers were parasitised by eurytomids not recorded from normal figs. A further gall type was present in the walls of *F. sansibarica* figs. The galls, apparently produced by a eurytomid, consisted of small chambers scattered just beneath the fig surface and caused no apparent damage to the other fig inhabitants. An ormyrid and several eurytomid species were reared from these galls.

Parasitoid fig wasps were typically solitary, like their hosts. The only observed exception was *Apocrypta quineensis* Grandi, where pairs of wasps occasionally emerged from the large galls of *Apocryptophagus* in the figs of *F. sur*.

In addition to the fig wasps, potential hosts for parasitoids inside the figs were insects belonging to the Curculionidae, Drosophilidae, Phoridae, Cecidomyiidae and Pyralidae. Parasitoids of these other fig-feeding insects (species from the Braconidae, Ichneumonidae, Eulophidae and Eupelmidae) were uncommon and no fig wasps were reared.

Tree specificity

Each *Ficus* species generally had its own unique pollinator (Table 2), although

Table 1. The oviposition methods and trophic relationships of the fig wasps associated with southern African *Ficus*.

Fig wasps		Mode of oviposition	Resources utilised			
Family	Subfamily/tribe		Galled ovules	Galled primordia	Galled cortex	Wasp larvae
Agaonidae	Agaoninae	internal	+			
Agaonidae	Sycoecinae	internal	+			
Agaonidae	Epichrysomallinae	external	+	+		
Agaonidae	Otitesellinae	external	+			
Agaonidae	Sycophaginae	both	+			
Agaonidae	Apocryptini	external				+
Agaonidae	Sycoryctini	external	?			+
Ormyridae	Ormyrinae	external				+
Eurytomidae	Eurytominae	external	?			+

Table 2. The agaonines and sycoecines associated with some southern African *Ficus*.

Subgenus	Section/ Subsection	<i>Ficus</i> species	Species No.	No. of samples	Pollinator	Sycoecines
<i>Ficus</i>	Sycidium	<i>F. capreifolia</i>	1	3	<i>Kradibia gestroi</i> (Grandi)	-
<i>Sycomorus</i>		<i>F. sycomorus</i>	2	30	<i>Ceratosolen arabicus</i> Mayr*	-
		<i>F. sur</i>	3	39	<i>Ceratosolen capensis</i> Grandi	-
		<i>F. vallis-choudae</i>	4	3	<i>Ceratosolen megagephalus</i> Grandi	-
		<i>F. ingens</i>	5	16	<i>Platyscapa soraria</i> Wiebes	-
<i>Urostigma</i>		<i>F. c. cordata</i>	6	18	<i>Platyscapa desertorum</i> Compton	-
		<i>F. c. salicifolia</i>	7	11	<i>Platyscapa awekei</i> Wiebes	-
		<i>F. verruculosa</i>	8	8	<i>Platyscapa binghami</i> Wiebes	-
		<i>F. lutea</i>	9	12	<i>Allotriozoon heterandromorphum</i> Grandi	'Crossogaster' silvestrii Grandi.
<i>Galaglychia/Platyphylac</i>	<i>Galaglychia/</i>	<i>F. bussei</i>	10	3	<i>Elisabethiella</i> sp. indesc.	<i>Phagoblastus</i> A.
	<i>Platyphylac</i>	<i>F. glumosa</i>	11	24	<i>Elisabethiella glumosae</i> Wiebes	<i>Phagoblastus</i> B, <i>Crossogaster</i> A, <i>Crossogaster</i> B, <i>Phagoblastus</i> C, <i>Phagoblastus</i> <i>barbarus</i> Grandi, <i>Crossogaster</i> <i>odorans</i> Wiebes.
		<i>F. stuhlmannii</i>	12	12	<i>Alfonsiella binghami</i> Wiebes	

Table 2. (continued)

Subgenus	Section/ Ficus species	Species No.	No. of samples	Pollinator	Sycococines
	<i>F. nigro-punctata</i>	13	1	<i>Alfonsiella bergi</i> Wiebes	-
	<i>F. tettensis</i>	14	6	<i>Nigeriella excavata</i> Compton	-
	<i>F. abutilifolia</i>	15	18	<i>Elisabethiella comptoni</i> Wiebes	Phagoblastus D.
	<i>F. trichopoda</i>	16	13	<i>Elisabethiella bergi</i> Wiebes	Crossogaster C. Philoacaenus A.
Galglychia/ Chlamydodora	<i>F. fischeri</i>	17	3	<i>Elisabethiella platyscapa</i> Wiebes	-
	<i>F. craterostoma</i>	18	2	<i>Alfonsiella</i> sp. indesc.	Phagoblastus E.
	<i>F. natalensis A</i>	19	6	<i>Elisabethiella socotrensis</i> (Mayr)	Crossogaster odorans. Phagoblastus barbarus.
	<i>F. natalensis B</i>	20	2	<i>Alfonsiella longiscapa</i> Joseph	Crossogaster D. Philoacaenus B.
	<i>F. burtt-davyi</i>	21	18	<i>Elisabethiella bajinathi</i> Wiebes	Phagoblastus F.
	<i>F. ilicina</i>	22	11	<i>Elisabethiella enriquezi</i> (Grandi)	-
	<i>F. thonningii</i>	23	40	<i>Elisabethiella stuckenbergi</i> (Grandi)	Phagoblastus barbarus, Crossogaster odorans. Philoacaenus B.
Galglychia/ Caulocarpace	<i>F. l. tremula</i>	24	6	<i>Courtella wardi</i> Compton	Seres A
	<i>F. p. polita</i>	25	4	<i>Courtella bekilensis</i> (Risbec)	-
	<i>F. bizanae</i>	26	4	<i>Courtella</i> sp. indesc.	-
	<i>F. sansibarica</i>	27	6	<i>Courtella armata</i> (Wiebes)	Seres B, Seres C.
	<i>F. bubu</i>	28	1	<i>Courtella michaloudi</i> (Wiebes)	Seres D.

* Also the non-pollinating agaonine *Ceratosolen galilii* Wiebes

the agaonines reared in southern Africa from *F. craterostoma* and *F. natalensis* were different to those described from the same trees elsewhere in Africa (Wiebes & Compton, 1990). The two sub-species of *F. cordata* also had separate agaonines, while trees identified as *F. natalensis* were pollinated by either *Elisabethiella socotrensis* (*F. natalensis* 'A') or *Alfonsiella longiscapa* (*F. natalensis* 'B'). The two forms of *F. natalensis* also supported several different non-pollinating fig wasps, as did *F. c. cordata* and *F. c. salicifolia*. Evidently the wasps consistently regard all four taxa as distinct.

The fig wasp assemblage associated with *F. natalensis* A was also atypical in that it contained no species other than the pollinator, which could be distinguished from species recorded from *F. thonningii*. Furthermore, some trees identified as *F. natalensis* A produced agaonines that were intermediate in appearance between *E. socotrensis* and *E. stuckenbergi*, the pollinator of *F. thonningii* (Wiebes, pers. comm.). The status of both *F. natalensis* A and *E. socotrensis* is therefore problematic.

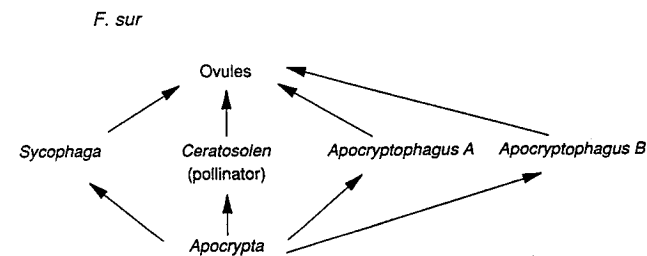
The tree specificity of the sycococine fig wasps was generally as absolute as in agaonines. However, three species recorded from *F. thonningii* were also reared from other trees, pollinated by *Alfonsiella* species rather than *Elisabethiella*.

Host-insect specificity

Figures 1-3 illustrate food webs inside the figs of three *Ficus* species growing near Grahamstown. Parasitoid host preferences were not absolute inside the figs of *F. burtt-davyi*, with *Philotrypesis* and *Sycoryctes* mainly, but not exclusively, utilising the larvae of the pollinator. Conversely, the eurytomid species in the figs of *F. ingens* were only seen to emerge from the large galls of epichrysomallines, while those produced by the pollinators were ignored. No such specificity was shown by *A. quineensis* in the figs of *F. sur*, where all the potential hosts were attacked.

Host-tree relationships

Ficus subsections *Platyphyllae* and *Chlamydodora* and their pollinators provide an exception to the generally close agreement between *Ficus* subgroups and

Fig. 1. Food web of the fig wasps associated with *Ficus sur* in the Grahamstown area of South Africa.

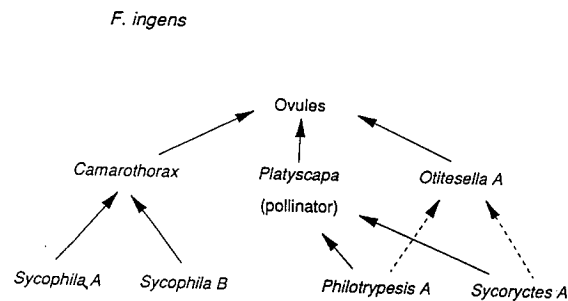


Fig. 2. Food web of the fig wasps associated with *Ficus ingens* in the Grahamstown area of South Africa. Dashed lines indicate rare utilization of hosts.

their pollinator genera (Wiebes & Compton 1990). In these subsections the trees are pollinated by wasps in any of the genera *Elisabethiella*, *Alfonstiella* or *Nigeriella* (Table 2). The sycoecine genera displayed host relationships which parallel those of the pollinators, with combinations of *Crossogaster* group B, *Phagoblastus* and *Philocaenus* species found in these two subsections. In contrast, *Crossogaster* group A (a distinct species group, van Noort, in preparation) was unique to *F. lutea* (and other trees of subsection *Galoglychia* elsewhere in Africa), while *Seres* was restricted to subsection *Caulocarpae*, where no other sycoecine genera have been recorded.

The total composition of the fig wasp assemblages is summarised in Table 3. All the wasps, except for *Ormyrus* and some of the eurytomids, belong to higher taxa that are exclusively associated with figs. Some fig wasp genera have wide host ranges within *Ficus*, occurring in most of its sub-groups (for example *Sycoryctes* and *Philotrypesis*), but the majority have more taxonomically restricted distributions. This results in most *Ficus* subsections having one or more characteristic wasp genera associated with them (Table 4). Subsections *Chlamydodora* and *Platyphyllae* are again exceptional, having no uniquely associated genera, but several characteristic genera that are shared between them. The patterns of host utilization displayed by the non-pollinating fig wasp genera are therefore

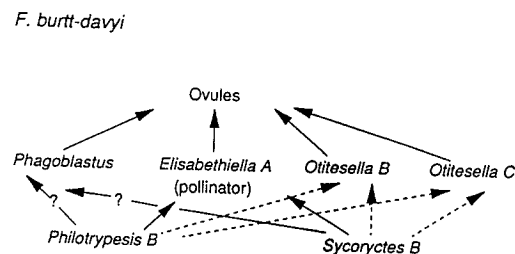


Fig. 3. Food web of the fig wasps associated with *Ficus burtt-davyi* in the Grahamstown area of South Africa. Dashed lines indicate rare utilization of hosts.

broadly consistent with those of the pollinators. Evidence for host-switching across *Ficus* subsections is also present, however, with one isolated species of *Sycosapteridea*, (typically found in *Sycomorus* and *Caulocarpae* figs) recorded from subsection *Platyphyllae* (Table 3).

DISCUSSION

Galled ovules are the food utilized by most of the phytophagous fig wasps, including the pollinators (Verkerke, 1989) and thus form the specific resource around which southern African fig wasp communities are centred. There is no evidence that any fig wasps are typical seed predators, requiring pollinated ovules (Compton *et al.*, 1991; Bronstein, personal communication), although agaonine larval mortalities are increased if they develop in unpollinated ovules (Galil & Eisikowitch, 1971). The fig wasp assemblages are self-contained in that almost all the wasp species are only associated with figs, and most belong to higher taxa that are also associated only with *Ficus* (Bouček, 1988). Exceptions are the Eurytomidae and Ormyridae, most species of which are not associated with figs. Ormyridae are associated with a wide range of plant galls, while eurytomids are also recorded from non-galling endophagous plants (Bouček, 1988). These two families are also exceptional in that they apparently include some species associated with both figs and galled leaf buds on fig trees (Bouček *et al.*, 1981; Watsham, 1984; Compton, unpublished). Parasitoid fig wasps only utilise other fig wasps as hosts, and there is no overlap with the parasitoids that attack the caterpillars and other insects feeding inside the figs.

Fig wasp communities appear to be composed mainly of host-plant specialists, with species in the best-studied groups of both gallers (Agaoninae, Sycoecinae) and parasitoids (*Apocrypta*, Ulenberg, 1985) generally displaying absolute tree specificity. Where tree specificity completely breaks down, as for example with the wasps associated with *F. thonningii* and *F. natalensis* A, we may be dealing with trees that are sister species, or the status of the host trees may need to be re-evaluated. Among the parasitoids, specificity sometimes extends to the species of wasp hosts, but other species appear to be oligophagous (Figs. 1–3; Godfray, 1988). One species of *Philotrypesis* (Sycoryctinae) has been recorded as first attacking agaonid larvae and then feeding on the surrounding ovular tissue (Joseph, 1984). Such 'inquiline' or 'entomophytophagous' feeding behaviour has also been recorded in eurytomids (Zerova and Fulsov, 1991) and could be widespread among fig wasps, but our sampling methods prevented confirmation of this.

The relative numbers of putative parasitoids in the communities are low compared with other well studied systems such as leaf miners and cynipid gall wasps, where parasitoid species consistently outnumber their hosts (Askew, 1975; Askew & Shaw, 1986). This paucity of parasitoids may be linked to one of the features of *Ficus* phenology, in that the development of all the wasps must be completed at the same time. Once the pollinators have left, the figs quickly become attractive to dispersers such as birds and bats, which will destroy any remaining insects. This places constraints on the life-styles of the parasitoids.

Table 3. The numbers of fig wasp species associated with some southern African *Ficus* subsections and species codes (see table 2)

Wasps	Syc. Sycomorbus			Urostigma Gato.					Platyphylae								Chlamydodorae								Caulocarpace			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Agoninae</i>																												
Kradibia	1																											
Ceratosten		2	2	1																								
Platyscapa					1	1	1	1																				
Allotriozoon									1																			
Elisabethella										1																		
Alfonsetia											1																	
Nigrella												1																
Courtella													1															
<i>Sycerinae</i>																												
Phagoblastus																												
Crossogaster A									1																			
Crossogaster B																												
Philocaenus																												
Seres																												
<i>Epichrysomallinae</i>																												
*Camarthorax**																												
Camarthorax					1	1				3	4	5	3				1	1	3	1	4	3						
Acophila																												

Table 3. (continued)

Wasps	Syc. Sycomorbus				Urostigma Gato.					Platyphylae								Chlamydodorae								Caulocarpace			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
<i>Otitellinae</i>																													
Otitessella A**																													
Otitessella B																													
Phillosycus																													
Genus indesc																													
<i>Sycophaginae</i>																													
Sycophaga																													
Apocryptophagus																													
<i>Apocryptini</i>																													
Apocrypta																													
<i>Sycoryctini</i>																													
Sycoryctes																													
Wasshaniella																													
Sycoscapier																													
Sycoscaperida																													
Philotrypesis																													
<i>Omyrini</i>																													
Omyrus																													
<i>Eurytomidae</i>																													
Genera indet																													
	4	1		5					5	3	4	3		4	4	2		6	2		7		2		2		4		

Camarthorax 'in the broad sense of Bouček *et al.*, 1981 probably with several constituent genera.The *Otitessella digitata* species group (Wiebes, 1969).

For example, oviposition into galls containing mature larvae or pupae is likely to be an unsuccessful strategy, because the parasitoids would not have sufficient time to complete their development. Further constraints on the parasitoids result from the common within-tree synchrony of fig production, with gaps of months or even years between crops. Consequently there can usually be no cycling on individual trees and the females of each generation can usually be in search of new trees with figs at the correct stage of development. Such constraints also apply to gallers, but in addition parasitoids must also find host insects at a suitable stage for oviposition.

The phylogeny of pollinating fig wasps parallels that of their hosts, suggesting that the two groups have evolved together (Wiebes, 1982). Related species of the parasitoid genus *Apocrypta* also utilize related trees (Ulenberg, 1985), which raises the possibility that fig wasps in general may have evolved in parallel with *Ficus*. Although the results presented here on the distribution of fig wasp genera are too coarse-grained to provide an answer to this question, several genera are restricted to particular subgroups of *Ficus*, and their distributions are therefore consistent with parallel evolution. This is not the case for all the genera, however, and in the case of *Sycosapteridea* it is the large size of their host figs, rather than taxonomic factors, which appears to characterise their distribution. Fig wasp lineages therefore appear to have responded differently to the radiation of their hosts. Detailed phylogenies of wasps from different subfamilies will be required before any overall pattern can be established.

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Table 4. Taxa of non-pollinating fig wasps with restricted distributions in southern African *Ficus* species.

Ficus Subsection(s)	Pollinators	Characteristic Non-pollinators
Sycidium	Kradibia	(Eukoebelea)*
Sycomorus	Ceratosolen	Sycophaga, Apocryptophagus, Apocrypta
Urostigma	Platyscapa	Otitesella A, Camarothorax, Acophila
Galoglychia	Allotriozoon	Crossogaster A
Platyphyllae & Chlamydodora	Elisabethiella, Alfonsiella & Nigeriella	Crossogaster B, Phagoblastus, Philocaenus
Caulocarpace	Courtella	Seres, Philosycus,

* Recorded by Bouček, 1988, but not seen in the present study.

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