

A Faunal Survey of Fig-wasps (Chalcidoidea: Hymenoptera) Distributed in Japan and Their Associations with Figs (*Ficus*: Moraceae)

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Abstract. Species compositions of fig-wasps were investigated in 14 figs (*Ficus*) distributed in Japan. A total of 38 species (Agaonidae: 36 spp.; Ormyridae: 1 sp.; Eurytomidae: 1 sp.) have been recognized during this survey. All fig-wasps were associated with only a single species of fig, suggesting extreme host specificity. All fig species have their own pollinators (Agaoninae), while there are considerable differences on the species richness of non-pollinating fig-wasps among fig species. Eight out of 9 species of wasps belonging to Epichrysomallinae or Otitesellinae were obtained from 3 species of monoecious figs and all but one dioecious fig did not have any wasps from these subfamilies. These facts agree with previous observations which lead to the recent hypothesis that dioecious figs evolved under the selective pressure of non-pollinating fig-wasps. However, the hypothesis should be confirmed with further studies about the ecology of non-pollinating fig-wasps. Factors which may affect differences in fig-wasp compositions between Japan and other Asian regions are also discussed.

Key words: Fig-wasp, Agaonidae, dioecious fig, monoecious fig, 'gall-former', Japan.

Introduction

All species belonging to the fig-wasp family (Agaonidae sensu Bouček, 1988) fully depend on figs (*Ficus*, Moraceae) as their food plants. They show considerable degree of host specificity and almost all the described species are recorded from only a single host species (Ramírez, 1970; Wiebes, 1979; Berg & Wiebes, 1992; Wiebes, 1994; but see Rasplus, 1996). Among the 6 subfamilies of the family, Agaoninae has the interesting ecological feature that almost all members of this subfamily are species-specific pollinators of figs. The complex interactions between pollinating fig-wasps and figs involving insect/food-plant and pollinator/plant relationships are significant cases of coevolution between insects and plants.

To study the coevolution of the interactions, basic knowledge about species relationships between fig-wasps and figs is indispensable. Although many attempts have been made to show which species of fig-wasps are associated with particular species of figs (e.g. Bouček, 1988; Berg & Wiebes, 1992; Wiebes, 1994), such kinds of study have been limited so far in Japan (Ishii, 1934; Yokoyama & Iwatsuki, 1994). Therefore it is necessary to collect the information about species relationships of the fig-wasp/fig interaction to study the coevolution between fig-wasps and figs in Japan.

In this paper, we record fig-wasps obtained from 14 out of the 15 species of figs distributed in Japan. This is the first extensive survey on the species of fig-wasps distributed in Japan covering

most fig species in this region and including non-pollinating wasps which have not received enough attention until very recently. This kind of extensive survey which focused on the single geographic region has rarely been conducted (Hong Kong: Hill, 1967b; Africa: Berg & Wiebes, 1992). Although many species of fig-wasps are still under identification or are waiting for description, we believe that it is meaningful to report the following results for understanding the outline of species relationships of the fig-wasp/fig interaction in Japan.

Materials and Methods

Collection localities of 14 fig species (3 monoecious and 11 dioecious species; identifications of figs were based on Corner (1965) and Yamazaki (1989)) and their vouchers are listed in Table 1. Voucher specimens are deposited in the Herbarium of Biological Institute, Tohoku University (TUS). The collections without voucher specimens were identified by comparing with specimens previously collected by one of the authors (JY) or those deposited in the Herbarium of University of Tokyo (TI). A total of 77 collections from 54 localities were used in this study. Syconia (urn-shaped inflorescences of figs) of the male stage before the fig-wasps began to emerge (Phase D: Galil & Eisikowitch, 1968) were collected from the field and kept in plastic bags until fig wasps emerged. For monoecious figs, 50-100 syconia from each crop were collected to obtain an enough amount of fig-wasps involving rare wasp species. For dioecious figs, however, only 5-10 syconia were usually obtained from each crop because of asynchrony of syconia production among trees. All fig-wasps were preserved in 70% ethanol until further observation. Identification was carried out with observation of morphological traits under a light microscope (Microphoto-FX, Nihon-Kogaku Co., Japan) and a scanning electron micro-

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Table 1. Samples collected in this study.

Fig species Locality (No. of individuals)	Voucher
Monoecious figs	
<i>Ficus superba</i> (Miq.) Miq. var. <i>japonica</i> Miq.	
Kanoya-shi, Kagoshima (1)	J. Yokoyama 5305
Miyawaki, Tarumizu-shi, Kagoshima (1)	none
Yamato-son, Amami-oshima Isl., Kagosima (3)	J. Yokoyama 4931
Miyagi Isl., Okinawa (1)	none
Agena, Gushigawa-shi, Okinawa Isl., Okinawa (2)	J. Yokoyama 5325
Ohama, Ishigaki Isl., Okinawa (1)	none
Kabira, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5285
<i>F. caulocarpa</i> (Miq.) Miq.	
Miyara, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5251
Ishigaki-shi, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5250
<i>F. microcarpa</i> Linn. f.	
Naze-shi, Amami-oshima Isl., Kagoshima (1)	none
Nishihara, Okinawa Isl., Okinawa (1)	Ryukyu Univ. (cult.)
Agena, Gushigawa-shi, Okinawa Isl., Okinawa (1)	J. Yokoyama 5326
Ishigaki-shi, Ishigaki Isl., Okinawa (1)	none
Tomino, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5260, 5261
Todoroki-gawa, Ishigaki Isl., Okinawa (1)	none
Miharu-Funaura, Iriomote Isl., Okinawa (1)	J. Yokoyama et al. 5224
Diocious figs	
<i>F. nipponica</i> Franch. et Savat.	
Mt. Takatori, Zushi-shi, Kanagawa (1)	J. Yokoyama 5298
<i>F. thunbergii</i> Maxim.	
Naze-shi, Amami-oshima Isl., Kagoshima (1)	J. Yokoyama 5345
Yona, Kunigami-son, Okinawa Isl., Okinawa (1)	J. Yokoyama et al. 5201
<i>F. pumila</i> L.	
Naze-shi, Amami-oshima Isl., Kagoshima (2)	J. Yokoyama 5310
Urasoe-shi, Okinawa Isl., Okinawa (1)	J. Yokoyama 5319
<i>F. erecta</i> Thunb. ex A. Murray	
Hakusan, Bunkyo-ku, Tokyo (2)	Bot. Gard., Univ. of Tokyo (cult.)
Shimoda-shi, Shizuoka (1)	none
Aoshima, Aoshima-shi, Miyazaki (1)	J. Yokoyama 4886
Hirata-Asato, Amami-oshima Isl., Kagoshima (1)	none
Benoki, Kunigami-son, Okinawa Isl., Okinawa (1)	none
Yona, Kunigami-son, Okinawa Isl., Okinawa (1)	J. Yokoyama 5366
Mt. Banna, Ishigaki Isl., Okinawa (1)	J. Yokoyama 5372

F. boninsimae Koidz.

Hatsune, Chichijima Isl., Bonin Isls., Tokyo (1)	J. Yokoyama et al. 92-018
Asahidaira, Chichijima Isl., Bonin Isls., Tokyo (1)	J. Yokoyama 93-009
Mt. Chuo, Chichijima Isl., Bonin Isls., Tokyo (1)	J. Yokoyama 93-004

Mt. Chibusa, Hahajima Isl., Bonin Isls., Tokyo (4)	J. Yokoyama & M. Ito 92-024, 92-025, 92-028, 92-039
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F. iidaiana Rehder et Wilson

Sekimon, Hahajima Isl., Bonin Isls., Tokyo (1)	J. Yokoyama & M. Ito 92-101
Uchu-zawa, Hahajima Isl., Bonin Isls., Tokyo (1)	J. Yokoyama & M. Ito 92-102

F. ampelas Burmann fil.

Naha-shi, Okinawa Isl., Okinawa (2)	J. Yokoyama 4943
Yona, Kunigami-son, Okinawa Isl., Okinawa (3)	J. Yokoyama 5367
Shirahama, Iriomote Isl., Okinawa (1)	none

F. virgata Reinw. ex Blume

Yohuke, Nago-shi, Okinawa Isl., Okinawa (1)	J. Yokoyama 5320
Maegaki, Yagachi Isl., Okinawa (1)	J. Yokoyama 5321
Mt. Banna, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5271
Yonehara, Ishigaki Isl., Okinawa (2)	none

F. variegata Blume*

Mt. Banna, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5270
Yonehara, Ishigaki Isl., Okinawa (3)	none
Mt. Omoto, Ishigaki Isl., Okinawa (1)	J. Yokoyama 5374
Iriomote Isl., Okinawa (1)	J. Yokoyama 5235

F. benguetensis Merrill

Sato, Amami-oshima Isl., Kagoshima (1)	none
Yona, Kunigami-son, Okinawa Isl., Okinawa (1)	J. Yokoyama 5280
Mt. Yonaha, Okinawa Isl., Okinawa (1)	J. Yokoyama 5212
Mt. Banna, Ishigaki Isl., Okinawa (1)	none
Urauchi, Iriomote Isl. Okinawa (1)	J. Yokoyama 4963

F. septica Burmann fil.

Maegaki, Yagachi Isl., Okinawa (1)	J. Yokoyama 5322
Mt. Banna, Ishigaki Isl., Okinawa (2)	J. Yokoyama 5373
Sukuchi, Ishigaki Isl., Okinawa (2)	none
Komi, Iriomote Isl., Okinawa (1)	J. Yokoyama 5223

*: Corner (1965) recognized 5 varieties in *F. variegata* and the Japanese population was treated as *F. v. var. garciae* (Elm.) Corner. As Yamazaki (1983) pointed out, however, leaf characters of specimens collected in this study agree with those of *F. v. var. sycomoroides* (Miq.) Corner. Based on Liu & Liao's (1976) description, the Taiwanese population seems to be intermediate states between *F. v. var. garciae* and *F. v. var. sycomoroides*. Therefore, here we did not follow the Corner's variety-level taxonomic treatment.

scope (JSM-820S, Nihon Denshi Co., Japan) and comparing with descriptions in original publications and monographic studies (e.g. Grandi, 1930; Wiebes, 1963, 1967, 1980, 1994; Ulenberg & van Pelt, 1985).

Subfamilial criteria of Agaonidae and generic categories of non-pollinating fig-wasps were based on Bouček (1988) and the generic subdivision of heterogeneous *Blastophaga* sensu lato was based on Wiebes (1994). All specimens of fig-wasps used in this study are lodged in the Biological Institute, Tohoku University.

Results

Species compositions of fig-wasp assemblages in Japan

Species of fig-wasps obtained in this study are listed in Table 2. A total of 38 species (including unnamed 'species') representing 4 subfamilies of Agaonidae, Ormyridae, and Eurytomidae were recognized from 14 species of fig. All specimens examined in this study were listed in Appendix 1. Each fig-wasp species was obtained from a single species of fig, suggesting extreme

Table 2. Fig-wasps recorded in this study and their association with figs.

Fig species Agaoninae (pollinating fig-wasps)	non-pollinating fig wasps
Monoecious figs	
<i>Ficus superba</i> (Miq.) Miq. var. <i>japonica</i> Miq.	
<i>Platyscapa ishiana</i> (Grandi) (= <i>Blastophaga ishiana</i> Grandi)	Sycoryctinae <i>Philotrypesis</i> sp. 1 <i>Sycoscapter</i> sp. 1
	Otitesellinae <i>Otitesella ako</i> Ishii
	Epichrysomallinae <i>Acophila mikii</i> Ishii <i>Camarothorax</i> sp. 1
<i>F. caulocarpa</i> (Miq.) Miq. <i>Platyscapa fischeri</i> Wiebes	Otitesellinae <i>Otitesella clarae</i> Wiebes
	Epichrysomallinae <i>Camarothorax</i> sp. 2
<i>F. microcarpa</i> Linn. f. <i>Eupristina</i> (<i>Parapristina</i>) <i>verticillata</i> Waterston	Sycoryctinae <i>Philotrypesis okinavensis</i> Ishii <i>Sycoscapter gajimaru</i> (Ishii)
	Otitesellinae <i>Walkerella yashiroi</i> (Ishii) (= <i>Otitesella yashiroi</i> Ishii)
	Epichrysomallinae <i>Odontofroggata gajimaru</i> Ishii <i>Odontofroggata galili</i> Wiebes
	Other families Ormyridae <i>Ormyrus</i> sp. 1
	Eurytomidae <i>Sycophila</i> sp. 1
Dioecious figs	
<i>F. nipponica</i> Franch. et Savat.	
	<i>Wiebesia callida</i> (Grandi) (= <i>Blastophaga callida</i> Grandi)
	<i>F. thunbergii</i> Maxim. <i>Wiebesia</i> sp. 1
	<i>F. pumila</i> L. <i>Wiebesia pumilae</i> (Hill) (= <i>Blastophaga pumilae</i> Hill)
	<i>F. erecta</i> Thunb. ex A. Murray <i>Blastophaga</i> (<i>B.</i>) <i>nipponica</i> Grandi
	Sycoryctinae <i>Sycoscapter inubiae</i> (Ishii)
	<i>F. boninsimae</i> Koidz. <i>Blastophaga</i> (<i>B.</i>) sp. 1
	<i>F. iidaiana</i> Rehder et Wilson <i>Blastophaga</i> (<i>B.</i>) sp. 2
	<i>F. ampelas</i> Burmann fil. <i>Kradibia sumatrana</i> (Grandi) (= <i>Blastophaga sumatrana</i> Grandi)
	Sycoryctinae <i>Philotrypesis jacobsoni</i> Grandi <i>Sycoscapter</i> sp. 2
	<i>F. virgata</i> Reinw. ex Blume <i>Liporrhopalum philippinensis</i> Hill
	Sycoryctinae <i>Philotrypesis</i> sp. 2 <i>Sycoscapter</i> sp. 3
	Epichrysomallinae <i>Neosycophila</i> sp. 1
	<i>F. variegata</i> Blume <i>Ceratosolen</i> (<i>C.</i>) <i>appendiculatus</i> (Mayr)
	Sycoryctinae <i>Apocrypta caudata</i> (Girault)
	<i>F. benguetensis</i> Merrill <i>Ceratosolen</i> (<i>Rothropus</i>) <i>cornutus</i> Wiebes
	Sycoryctinae <i>Philotrypesis</i> sp. 3
	<i>F. septica</i> Burmann fil. <i>Ceratosolen</i> (<i>C.</i>) <i>bisulcatus</i> <i>jucundus</i> Grandi (= <i>Ceratosolen jucundus</i> Grandi)
	Sycoryctinae <i>Apocrypta</i> sp. 1 <i>Philotrypesis spinipes</i> Mayr

species-specificity as reported in previous studies (e.g. Wiebes, 1963, 1994; Ramirez, 1970). All but one host fig records of exactly identified fig-wasp species in this study were consistent with previous reports (from Japan, see Ishii, 1934: from other region of Asia, see Appendix 2). The only exception is *Liporrhopalum philippinensis* which was obtained from *Ficus virgata* Reinw. ex Blume var. *virgata* in this study, though this species was previously recorded from *Ficus virgata* var. *philippinensis* (Bur.) Corner and *Ficus virgata* var. *virgata* had a record of its own pollinator, *L. virgatae* (Hill, 1969). However, the morphological differences between *F. virgata* var. *virgata* and *F. virgata* var. *philippinensis* pointed out by Corner (1959) are sometimes ambiguous (Yamazaki, 1983) and the subdivision of *F. virgata* into these two varieties is in need of further reinvestigation.

Fourteen species of Agaoninae representing the species-specific pollinators of all fig species examined here were identified. Among them, *Platyscapa fischeri*, *Liporrhopalum philippinensis*, and *Ceratosolen cornutus* are newly recorded from Japan. Agaoninae obtained from *F. boninsimae* and *F. iidaiana* might be undescribed species which should be closely related to

Blastophaga nipponica based on morphological characters. The wasp collected from *F. thunbergii* was also considered to be undescribed and should be closely related to *Wiebesia pumilae* (= *Blastophaga pumilae*).

Six species of Epichrysomallinae and 3 species of Otitesellinae were obtained in this study. *Odontofroggata galili* (Epichrysomallinae) and *Otitesella clarae* (Otitesellinae) were newly recorded from Japan. Records of the genera *Camarothorax* and *Neosycophila* are also new to Japan. All monoecious fig species examined here (*F. superba* var. *japonica*, *F. caulocarpa*, and *F. microcarpa*) have at least one species of Epichrysomallinae and one species of Otitesellinae. In contrast, epichrysomallid wasps were not found in all but one species of dioecious figs and no otitesellid wasps were obtained from dioecious fig species examined in this study.

Thirteen species of Sycoryctinae were recorded in this study. *Philotrypesis jacobsoni*, *Philotrypesis spinipes*, and *Apocrypta caudata* were newly recorded from Japan. Sycoryctinid wasps were found in both monoecious and dioecious figs but were not found in 6 species of fig (*F. caulocarpa*, *F. nipponica*, *F. thunbergii*, *F. pumila*, *F. boninsimae*, and *F. iidaiana*).

Outside of Agaonidae sensu Bouček (1988), *Ormyrus* sp. (Ormyridae) and *Sycophila* sp. (Eurytomidae) were obtained from *F. microcarpa*. They were also obtained from fig syconia of this species in previous studies (Bouček *et al.*, 1981; Bouček, 1988).

Species richness of non-pollinating fig-wasps on monoecious and dioecious figs

Dioecious figs examined in this study have simpler non-pollinating fig-wasp faunas than those of monoecious figs (Mann-Whitney test: $U=2$, $p<0.05$). The difference in species richness of fig-wasp fauna between monoecious and dioecious figs is due to the occurrence of epichrysomallid and otitesellid wasps as mentioned above (Mann-Whitney test for the richness of these two subfamilies: $U=0$, $p<0.01$). In contrast, there are no obvious differences in the species richness of sycoryctinid wasps between monoecious and dioecious figs ($U=11.5$, $p>0.05$). It is noteworthy that the dioecious figs which are endemic to the Bonin Islands (*F. boninsimae* and *F. iidaiana*) and those belonging to the section *Rhizocladus* (*F. nipponica*, *F. thunbergii*, and *F. pumila*; Corner, 1965) have no records of non-pollinating fig-wasps in this study. Thus these species have the simplest systems (only consist of a host fig and a pollinator) among known fig-wasp/fig interactions.

Discussion

Factors affecting differences of fig-wasp compositions among different regions

Although the results are still preliminary, this is the first extensive survey on the fig wasp fauna in Japan. Comparing with previous reports (e.g. Wiebes, 1966, 1994; Bouček, 1988), considerable differences of species composition of fig-wasps between Japan and other regions were observed in some fig species (compare Table 2 and Appendix 2). For example, in case of epichrysomallid and otitesellid wasps obtained from *F. microcarpa*, we found 2 species of *Odontofroggattia* and *Walkerella yashiroi* (Table 2) during this survey. In contrast, Bouček (1988) reported *Acophila* spp., *Epichrysomalla* sp., 2 species of *Odontofroggattia* (including 1 species which could not be found in our survey), and 2 species of *Walkerella* (both different from *W. yashiroi*) from *F. microcarpa* in the Australasian region (including Australia, New Guinea, New Zealand, and adjacent islands). At least three factors may account for the differences of species composition observed among different populations of the same fig species. First, some species of fig-wasps were not collected due to the inadequate sampling during this survey. Compton & Hawkins (1992) provided species-recruitment curves for fig-wasps on 16 South African fig species. Their results indicated that, on 5 species of fig, numbers of fig-wasp species were not saturated even when 10 or more individuals were sampled. In our survey, less than 10 individuals were collected from each fig species except *F. superba* var. *japonica*. Thus some species of fig-wasp may not have been found during this survey though we intended to collect samples extensively from the distribution area of each species in Japan. Some

epichrysomallid wasps known from *F. microcarpa* of other regions are the most probable candidates for undiscovered species in Japan. Based on the Compton & Hawkins' (1992) result, however, on figs which have less than 5 species of fig-wasps, the species-recruitment curves were saturated after 3 trees were sampled. Therefore, at least in the cases of dioecious figs, fig-wasps listed in this survey probably represent the exact faunal composition of fig-wasps on each fig species in Japan.

Second, some fig-wasps recorded from other regions could not be obtained because they have not colonized Japan for various reasons. Japan is the northern limit of distribution of *Ficus* in Asia. Thus relatively low temperatures in winter may affect the survival of fig-wasps directly (e.g. by preventing overwinterings) or indirectly (e.g. due to decreasing food supply with less syconia production in particular periods (Anstett *et al.*, 1995)). For example, Wiebes (1980) described 3 new species of *Odontofroggattia* from *F. microcarpa* in the Malay Peninsula and the Solomon Islands. All these species were also reported from Papua New Guinea by Bouček (1988: but host records were different from the original description; all species were also obtained from *F. prasinicarpa* Elmer.). Among them, however, only *O. galili* was recorded during this survey. *F. microcarpa* has been introduced to many regions and sometimes its fig-wasps, including *Odontofroggattia*, have also established themselves outside their natural distribution area. In Israel, *O. galili* inhabits the introduced *F. microcarpa* but the other 2 species do not occur there (Wiebes, 1980). One reason why these 2 species were not observed in Japan may be the occurrence of competition for resources with the other *Odontofroggattia* species, *O. gajimaru* (if *O. gajimaru* is the sister species of *O. ishii*, the difference in faunal composition may have occurred by allopatric speciation, see below). Taking the case in Israel into account, however, a more plausible reason may be that they have less ability to colonize seasonal environments than *O. galili*. Lack of some Sycophaginae or Sycoryctinae recorded from *F. variegata* in Japan may be for the same reason (Appendix 2).

Third, the allopatric speciation of fig-wasps might occur among local populations of particular fig species. In case of *Walkerella* spp. on *F. microcarpa*, for example, Bouček (1988) reported *Walkerella kurandensis* which is very close to *W. yashiroi* from Queensland, Australia. He also noted that there is another species of *Walkerella* which is also very similar to *Walkerella kurandensis* in the Papua New Guinean population of *F. microcarpa*. The most plausible explanation to the fact that each local population of *F. microcarpa* is occupied by different, but very similar, species of *Walkerella* is that they speciated from a single ancestor by geographic isolation. Difference of Sycophaginae and Sycoscapter species from *F. variegata* between Queensland and Java also may be explained by the allopatric speciation (Appendix 2). Such mode of speciation of fig-wasps may be in progress on some other fig-wasp/fig interactions, especially on Agaoninae (pollinating wasps)/fig relationships (e.g. *F. septica* is pollinated by *C. bisulcatus bisulcatus* (Mayr) or *C. b. jucundus*. The former is distributed in Indonesia and New Guinea and the latter is in

Malaysia, Philippines, Taiwan, and Japan (Wiebes, 1994; Yokoyama & Iwatsuki, 1994). For other instances, see Rasplus (1996)).

Which factors are important to account for the observed differences of faunal composition of fig-wasps may depend on the case. Further studies (e.g. extensive faunal surveys in Japan and adjacent regions, ecological investigation of fig-wasps themselves and fig-wasp/fig interactions, and phylogenetic relationships of fig-wasps) will be needed to probe the important factor in each case.

Simple fig-wasp compositions on dioecious figs

This study indicates that dioecious figs have fewer non-pollinating fig-wasps than monoecious figs. The simpler faunal compositions of fig-wasps observed on dioecious figs were also pointed out in previous studies (Corlett *et al.*, 1990; Compton & Hawkins, 1992; Kerdelhué & Rasplus, 1996b). Since dioecious figs are considered to be advanced groups which evolved from monoecious figs (Corner, 1962; Ramírez, 1980; Berg, 1990), these facts mean that the numbers of non-pollinating fig-wasps were reduced in the course of evolution of figs from monoecy to dioecy. It is still uncertain why dioecious figs usually have a simpler fig-wasp fauna than monoecious ones. Recently Kerdelhué & Rasplus (1996b) proposed the hypothesis that dioecious figs evolved under the selective pressure of non-pollinating fig-wasps. The multi-layered arrangement of female flowers in syconia of monoecious figs provides the niche for non-pollinating fig-wasps. Especially the medium layers comprising female flowers with an intermediate style length (Kerdelhué & Rasplus, 1996b) are frequently occupied by 'gall-formers' in which Epichrysomallinae, Otitesellinae, Sycoecinae, and Syco-phaginae (latter 2 subfamilies were not recorded in this study) are included (Compton & Nefdt, 1990; Compton & van Noort, 1992; Kerdelhué & Rasplus, 1996a). According to the hypothesis, the development of perfect heterostyly which is observed in extant dioecious figs can reduce the costs for being parasitized by 'gall-formers.' In Asian species, however, since there is almost no information about the ecology of non-pollinating fig-wasps and their patterns of resource use or niche separation among species, it is uncertain whether reduction of flower layers with evolution of complete heterostyly has been directly linked with a reduction of the gall-formers' niche. Furthermore, the validity of the hypothesis remains to be confirmed with more information about, for example, parasitizing rate (or relative effect) of each non-pollinating fig-wasp to particular fig species or the habits of gall-formers parasitizing dioecious figs. Since there are some dioecious fig species which have a relatively rich fauna of non-pollinating fig-wasps (e.g. *F. ampelas* or *F. variegata* outside Japan, see Appendix 2), other factors affecting species richness should be considered for a complete understanding of simple fauna of non-pollinating wasps in dioecious figs. Further studies investigating the ecology and species interactions of non-pollinating fig-wasps, their ecological relationships to pollinating wasps, and ecology of host figs are strongly required.

In this study, we found that dioecious figs in the Bonin

Islands and those of section *Rhizocladus* do not have any non-pollinating fig-wasps. In the former cases, the reason why they lack non-pollinating fig-wasps may be simple. Since the Bonin Islands are the typical oceanic islands which are located about 900 km south off the mainland Japan, they have poor insect fauna including less than 800 recorded species (Kato, 1991). Although investigations of hymenopteran fauna in the Bonin Islands are still insufficient, there are no records of Chalcidoidea except *Blastophaga*, the pollinating fig-wasps, so far from the islands. On the other hand, fig species belonging to the same sections (sect. *Ficus*) have at least one species of non-pollinating fig-wasp (*F. erecta*, the putative closest relative, has *Sycoscapter inubiae* (Ishii) (Sycoryctinae) and Kerdelhué & Rasplus (1996) reported that 2–3 species of non-pollinating fig-wasps were observed in 2 fig species of sect. *Ficus*). Thus the absence of non-pollinating fig-wasps in endemic fig species of the Bonin Islands may be solely caused by their failure to migrate to the islands.

On the other hand, why the figs from sect. *Rhizocladus* have no non-pollinating fig-wasps is unknown. There could be some mechanisms for avoiding parasitisms by non-pollinating fig-wasps (especially sycoryctinids). Particular chemical substances may be the most plausible candidates.

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Appendix 1. Specimens examined in this study

Family Agaonidae

Subfamily Epichrysomallinae

Acophila mikii Ishii*Acophila mikii* Ishii, 1934, *Kontyû*, 8: 97-98.*Specimens examined.* 6♀, Agena, Gushigawa-shi, Okinawa Isl., Okinawa, 1. VI. 1993.*Host-plant.* *Ficus superba* (Miq.) Miq. var. *japonica* Miq.*Camarothorax* sp. 1*Specimens examined.* 4♀, Miyawaki, Tarumizu-shi, Kagoshima, 29. V. 1993; 3♀, Yamato-son, Amami-oshima Isl., Kagosima, 20. V. 1991; 12♀3♂, Yamato-son, Amami-oshima Isl., Kagosima, 30. V. 1993; 1♀, Agena, Gushigawa-shi, Okinawa Isl., Okinawa, 1. VI. 1993; 7♀3♂, Miyagi Isl., Okinawa, 1. VI. 1993; 15♀, Ohama, Ishigaki Isl., Okinawa, 6. VII. 1992.*Host-plant.* *Ficus superba* (Miq.) Miq. var. *japonica* Miq.*Camarothorax* sp. 2*Specimens examined.* 9♀3♂, Miyara, Ishigaki Isl., Okinawa, 18. VII. 1993.*Host-plant.* *Ficus caulocarpa* (Miq.) Miq.*Neosycophila* sp. 1*Specimens examined.* 2♂, Yohuke, Nago-shi, Okinawa Isl., Okinawa, 2. VI. 1993; 1♀, Maegaki, Yagachi Isl., Okinawa, 2. VI. 1993.*Host-plant.* *Ficus virgata* Reinw. ex Blume*Odontofroggata gajimaru* Ishii*Odontofroggata gajimaru* Ishii, 1934, *Kontyû*, 8: 95-97.*Specimens examined.* 7♀1♂, Naze-shi, Amami-oshima Isl., Kagoshima, 22. VI. 1991; 2♀2♂, Nishihara, Okinawa Isl., Okinawa, 4. VII. 1991.*Host-plant.* *Ficus microcarpa* Linn. f.*Odontofroggata galili* Wiebes*Odontofroggata galili* Wiebes, 1980, *Zool. Meded. Leiden*, 56: 3-5.*Specimens examined.* 4♀1♂, Nishihara, Okinawa Isl., Okinawa, 4. VII. 1991; 3♀, Tomino, Ishigaki Isl., Okinawa, 20. IX. 1992; 1♀, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992; 2♂, Ishigaki-shi, Ishigaki Isl., Okinawa, 2. VII. 1992; 8♀12♂, Miharu-Funaura, Iriomote Isl., Okinawa, 1. VII. 1992.*Host-plant.* *Ficus microcarpa* Linn. f.

Subfamily Otitesellinae

Otitesella ako Ishii*Otitesella ako* Ishii, 1934, *Kontyû*, 8: 91-93.*Specimens examined.* 17♀, Kanoya-shi, Kagoshima, 29. V. 1993; 24♀, Miyawaki, Tarumizu-shi, Kagoshima, 29. V. 1993; 12♀, Yamato-son, Amami-oshima Isl., Kagosima, 20. V. 1991; 34♀1♂, Yamato-son, Amami-oshima Isl., Kagosima, 30. V. 1993; 35♀, Ohama, Ishigaki Isl., Okinawa, 6. VII. 1992; 1♀4♂, Kabira, Ishigaki Isl., Okinawa, 21. IX. 1992.*Host-plant.* *Ficus superba* (Miq.) Miq. var. *japonica* Miq.*Otitesella clarae* Wiebes*Otitesella clarae* Wiebes, 1974, *Zool. Meded. Leiden*, 48: 148-150.*Specimens examined.* 7♀, Miyara, Ishigaki Isl., Okinawa, 18. VII. 1993; 1♀, Ishigaki-shi, Ishigaki Isl., Okinawa, 21. IX. 1992.*Host-plant.* *Ficus caulocarpa* (Miq.) Miq.*Walkerella yashiroi* (Ishii)*Walkerella yashiroi* Ishii, 1934, *Kontyû*, 8: 93-94.*Walkerella yashiroi*: Wiebes, 1967, *Tijdschr. Ent.*, 110: 439.*Specimens examined.* 5♀2♂, Nishihara, Okinawa Isl., Okinawa, 4. VII. 1991; 2♀, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992.*Host-plant.* *Ficus microcarpa* Linn. f.

Subfamily Sycoryctinae

Apocrypta caudata (Girault)*Goniogastrella caudatus* Girault, 1915, *Mem. Qd. Mus.*, 4: 282.*Apocrypta caudata*: Hill, 1967, *Figs (Ficus spp.) of Hong Kong*, 93.*Apocrypta caudata*: Ulenberg & van Pelt, 1985, *Verh. Kon. Ned. Akad. Wet., afd. Natk., 2de reeks*, 83: 136-139.*Specimens examined.* 34♀20♂, Mt. Banna, Ishigaki Isl., Okinawa, 3. VII. 1991; 43♀3♂, Mt. Omoto, Ishigaki Isl., Okinawa, 21. IX. 1992.*Host-plant.* *Ficus variegata* Blume*Apocrypta* sp. 1*Specimens examined.* 3♀1♂, Mt. Banna, Ishigaki Isl., Okinawa, 6. VII. 1992; 1♀, Komi, Iriomote Isl., Okinawa, 1. VII. 1992.*Host-plant.* *Ficus septica* Burmann fil.*Philotrypesis jacobsoni* Grandi*Philotrypesis jacobsoni* Grandi, 1926, *Treubia*, 8: 359.*Specimens examined.* 26♀, Naha-shi, Okinawa Isl., Okinawa, 28. VI. 1991.*Host-plant.* *Ficus ampelas* Burmann fil.*Philotrypesis okinavensis* Ishii*Philotrypesis okinavensis* Ishii, 1934, *Kontyû*, 8: 90-91.*Specimens examined.* 1♀, Tomino, Ishigaki Isl., Okinawa, 20. IX. 1992; 4♀, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992; 1♀, Miharu - Funaura, Iriomote Isl., Okinawa, 1. VII. 1992.*Host-plant.* *Ficus microcarpa* Linn. f.*Philotrypesis spinipes* Mayr*Philotrypesis spinipes* Mayr, 1885, *Verh. Zool. Bot. Gesellsch. Wien*, 35: 223-224.*Specimens examined.* 1♀, Mt. Banna, Ishigaki Isl., Okinawa, 6. VII. 1992; 14♀, Sukuchi, Ishigaki Isl., Okinawa, 21. IX. 1992.*Host-plant.* *Ficus septica* Burmann fil.*Philotrypesis* sp. 1*Specimens examined.* 5♀, Miyagi Isl., Okinawa, 1. VI. 1993.*Host-plant.* *Ficus superba* (Miq.) Miq. var. *japonica* Miq.*Philotrypesis* sp. 2*Specimens examined.* 8♀, Maegaki, Yagachi Isl., Okinawa, 2. VI. 1993; 5♀2♂, Mt. Banna, Ishigaki Isl., Okinawa, 22. IX. 1992; 4♀, Yonehara, Ishigaki Isl., Okinawa, 21. IX. 1992.*Host-plant.* *Ficus virgata* Reinw. ex Blume*Philotrypesis* sp. 3*Specimens examined.* 13♀, Sato, Amami-oshima Isl., Kagoshima, 22. VI. 1991; 11♀3♂, Yona, Kunigami-son, Okinawa Isl., Okinawa, 27. VI. 1991; 23♀, Mt. Banna, Ishigaki Isl., Okinawa, 3. VII. 1991; 10♀2♂, Urauchi, Iriomote Isl., Okinawa, 2. VII. 1992.*Host-plant.* *Ficus benguensis* Merrill*Sycoscapter gajimaru* (Ishii)*Goniogaster gajimaru* Ishii, 1934, *Kontyû*, 8: 89.*Sycoscapter gajimaru*: Wiebes, 1964, *Nova Guinea Zool.*, 26: 83.*Specimens examined.* 7♀, Agena, Gushigawa-shi, Okinawa Isl., Okinawa, 14. VII. 1993; 13♀, Tomino, Ishigaki Isl., Okinawa, 20. IX. 1992; 2♀, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992.*Host-plant.* *Ficus microcarpa* Linn. f.*Sycoscapter inubiae* (Ishii)*Goniogaster inubiae* Ishii, 1934, *Kontyû*, 8: 87-89.*Sycoscapter inubiae*: Wiebes, 1964, *Nova Guinea Zool.*, 26: 83.*Specimens examined.* 23♀3♂, Hakusan, Bunkyo-ku, Tokyo, 8. VI. 1993; 22♀4♂, Shimoda-shi, Shizuoka, 23. V. 1993; 7♀8♂, Hirata-Asato, Amami-oshima Isl., Kagoshima, 22. VI. 1991; 3♀6♂, Benoki, Kunigami-son, Okinawa Isl., Okinawa, 2. VI. 1993; 2♀2♂, Yona,

Kunigami-son, Okinawa Isl., Okinawa, 17. X. 1993; 25♀2♂, Mt. Banna, Ishigaki Isl., Okinawa, 17. VII. 1993.

Host-plant. *Ficus erecta* Thunb. ex A. Murray

Sycoscapter sp. 1

Specimens examined. 2♀, Yamato-son, Amami-oshima Isl., Kagosima, 23. VI. 1991; 2♀, Akena, Gushigawa-shi, Okinawa Isl., Okinawa, 1. VI. 1993; 1♀5♂, Akena, Gushigawa-shi, Okinawa Isl., Okinawa, 19. VII. 1993; 3♀, Ohama, Ishigaki Isl., Okinawa, 6. VII. 1992.

Host-plant. *Ficus superba* (Miq.) Miq. var. *japonica* Miq.

Sycoscapter sp. 2

Specimens examined. 5♀, Yona, Kunigami-son, Okinawa Isl., Okinawa, 17. X. 1993.

Host-plant. *Ficus ampelas* Burmann fil.

Sycoscapter sp. 3

Specimens examined. 12♀5♂, Yohuke, Nago-shi, Okinawa Isl., Okinawa, 2. VI. 1993; 14♀, Maegaki, Yagachi Isl., Okinawa, 2. VI. 1993; 1♀, Mt. Banna, Ishigaki Isl., Okinawa, 20. IX. 1992; 21♀, Yonehara, Ishigaki Isl., Okinawa, 21. IX. 1992.

Host-plant. *Ficus virgata* Reinw. ex Blume

Subfamily Agaoninae

Blastophaga (B.) *nipponica* Grandi

Blastophaga nipponica Grandi, 1921, *Ann. Mus. Stor. nat. Genova*, 49: 304–305.

Specimens examined. 19♀, Hakusan, Bunkyo-ku, Tokyo, 8. VI. 1993; 92♀8♂, Hakusan, Bunkyo-ku, Tokyo, 24. VII. 1993; 18♀5♂, Shimodashi, Shizuoka, 23. V. 1993; 10♀5♂, Aoshima, Aoshima-shi, Miyazaki, 6. VII. 1991; 13♀7♂, Hirata-Asato, Amami-oshima Isl. Kagoshima, 22. VI. 1991; 37♀12♂, Benoki, Kunigami-son, Okinawa Isl., Okinawa, 2. VI. 1993; 6♀2♂, Yona, Kunigami-son, Okinawa Isl., Okinawa, 17. X. 1993; 19♀1♂, Mt. Banna, Ishigaki Isl., Okinawa, 17. VII. 1993.

Host-plant. *Ficus erecta* Thunb. ex A. Murray

Blastophaga (B.) sp. 1

Specimens examined. 23♀5♂, Hatsune, Chichijima Isl., Bonin Isls., Tokyo, 3. VI. 1992; 53♀37♂, Asahidaira, Chichijima Isl., Bonin Isls., Tokyo, 2. III. 1993; 34♀28♂, Mt. Chuo, Chichijima Isl., Bonin Isls., Tokyo, 26. II. 1993; 39♀7♂, Mt. Chibusa, Hahajima Isl., Bonin Isls., Tokyo, 31. V. 1992; 40♀37♂, Mt. Chibusa, Hahajima Isl., Bonin Isls., Tokyo, 28. II. 1993.

Host-plant. *Ficus boninsimae* Koidz.

Blastophaga (B.) sp. 2

Specimens examined. 49♀78♂, Sekimon, Hahajima Isl., Bonin Isls., Tokyo, 30. V. 1992; 5♀3♂, Uchu-zawa, Hahajima Is., Bonin Isls., Tokyo, 31. V. 1992.

Host-plant. *Ficus iidaiana* Rehder et Wilson

Ceratosolen (C.) *appendiculatus* (Mayr)

Blastophaga (*Ceratosolen*) *appendiculata* Mayr, 1885, *Verhandl. k. k. zool.-bot. Gesellsch. Wien*, 35: 164–166.

Ceratosolen appendiculatus: Grandi, 1928, *Boll. Lab. Ent. Bologna*, 1: 176–179.

Specimens examined. same as a previous report (Yokoyama & Iwatsuki, 1994).

Host-plant. *Ficus variegata* Blume

Ceratosolen (C.) *bisulcatus jucundus* Grandi

Ceratosolen jucundus Grandi, 1927, *Philip. J. Sci.*, 33: 320–323.

Ceratosolen bisulcatus jucundus: Wiebes, 1994, *Kon. Ned. Akad. Wet., afd. Natk., 2de reeks*, 92: 165.

Specimens examined. same as a previous report (Yokoyama & Iwatsuki, 1994).

Host-plant. *Ficus septica* Burmann fil.

Ceratosolen (*Rothropus*) *cornutus* Wiebes

Ceratosolen cornutus Wiebes, 1994, *Proc. Kon. Ned. Akad. Wet.*, 97: 129–130.

Specimens examined. 12♀5♂, Sato, Amami-oshima Isl., Kagoshima, 22. VI. 1991; 4♀5♂, Yona, Kunigami-son, Okinawa Isl., Okinawa, 27. VI. 1991; 31♀6♂, Mt. Yonaha, Okinawa Isl., Okinawa, 30. VI. 1992; 25♀4♂, Urauchi, Iriomote Isl. Okinawa, 2. VII. 1992.

Host-plant. *Ficus benguetensis* Merrill

Eupristina (*Parapristina*) *verticillata* Waterston

Eupristina verticillata Waterston, 1921, *Bull. Ent. Res.*, 12: 38–40 (♀).

Eupristina verticillata: Grandi, 1926, *Treubia*, 8: 258 (♂).

Euprista okinavensis Ishii, 1934, *Kontyû*, 8: 85–87.

Blastophaga (*Parapristina*) *verticillata*: Hill, 1967, *Zool. Verh. Leiden*, 89: 32–35.

Specimens examined. 1♀, Nishihara, Okinawa Isl., Okinawa, 4. VII. 1991; 2♀, Tomino, Ishigaki Isl., Okinawa, 20. IX. 1992; 8♀, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992; 9♀, Miharu-Funaura, Iriomote Isl., Okinawa, 1. VII. 1992.

Host-plant. *Ficus microcarpa* Linn. f.

Liporrhophalum philippinensis Hill

Liporrhophalum philippinensis Hill, 1969, *Zool. Verh. Leiden*, 100: 7–11.

Specimens examined. 11♀6♂, Yohuke, Nago-shi, Okinawa Isl., Okinawa, 2. VI. 1993; 1♀, Maegaki, Yagachi Isl., Okinawa, 2. VI. 1993; 27♀11♂, Mt. Banna, Ishigaki Isl., Okinawa, 20. IX. 1992; 62♀5♂, Mt. Banna, Ishigaki Isl., Okinawa, 22. IX. 1992; 25♀, Yonehara, Ishigaki Isl., Okinawa, 21. IX. 1992.

Host-plant. *Ficus virgata* Reinw. ex Blume var. *philippinensis* (Bur.) Corner (Hill, 1969); *Ficus virgata* Reinw. ex Blume var. *virgata* (this study).

Kradibia sumatrana (Grandi)

Blastophaga sumatrana Grandi, 1926, *Treubia*, 8: 352–353.

Kradibia sumatrana: Wiebes, 1978, *Zool. Meded. Leiden*, 53: 173.

Specimens examined. same as a previous report (Yokoyama & Iwatsuki, 1994).

Host-plant. *Ficus ampelas* Burmann fil.

Platyscapa ishiana (Grandi)

Blastophaga ishiana Grandi, 1923, *Ann. Mus. civ. Stor. nat. Genova*, 61: 101–102.

Platyscapa ishiana: Wiebes, 1977, *Neth. J. Zool.*, 27: 214–215.

Specimens examined. 48♀3♂, Kanoya-shi, Kagoshima, 29. V. 1993; 19♀15♂, Miyawaki, Tarumizu-shi, Kagoshima, 29. V. 1993; 3♀, Yamatoson, Amami-oshima Isl., Kagoshima, 20. V. 1991; 45♀1♂, Yamato-son, Amami-oshima Isl., Kagoshima, 30. V. 1993; 4♀, Akena, Gushigawa-shi, Okinawa Isl., Okinawa, 1. VI. 1993; 7♀, Ohama, Ishigaki Isl., Okinawa, 6. VII. 1992.

Host-plant. *Ficus superba* (Miq.) Miq. var. *japonica* Miq.

Platyscapa fischeri Wiebes

Platyscapa fischeri Wiebes, 1977, *Neth. J. Zool.*, 27: 220, 222.

Specimens examined. 13♀11♂, Miyara, Ishigaki Isl., Okinawa, 6. VII. 1992; 59♀5♂, Miyara, Ishigaki Isl., Okinawa, 18. VII. 1993; 2♀1♂, Ishigaki-shi, Ishigaki Isl., Okinawa, 20. IX. 1992; 2♀, Ishigaki-shi, Ishigaki Isl., Okinawa, 21. IX. 1992.

Host-plant. *Ficus caulocarpa* (Miq.) Miq.

Wiebesia callida (Grandi)

Blastophaga callida Grandi, 1927, *Boll. Soc. Ent. Ital.*, 59: 18–24.

Wiebesia callida: Wiebes, 1994, *Kon. Ned. Akad. Wet., afd. Natk., 2de reeks*, 92: 110–111.

Specimens examined. 76♀18♂, Mt. Takatori, Zushi-shi, Kanagawa, 9. V. 1992.

Host-plant. Ficus nipponica Franch. et Savat.

Wiebesia pumilae (Hill)

Blastophaga pumilae Hill, 1967, *Zool. Verh. Leiden*, 89: 27–31.

Wiebesia pumilae: Wiebes, 1994, *Kon. Ned. Akad. Wet., afd. Natk.*, 2de reeks, 92: 111–112.

Specimens examined. same as a previous report (Yokoyama and Iwatsuki, 1994).

Host-plant. Ficus pumila L.

Wiebesia sp.1

Specimens examined. 4♀5♂, Naze-shi, Amami-oshima Isl., Kagoshima, 12. VII. 1993; 2♀32♂, Yona, Kunigami-son, Okinawa Isl., Okinawa, 29. VI. 1992.

Host-plant. Ficus thunbergii Maxim.

Family Ormyridae

Ormyrus sp.1

Specimens examined. 1♀, Mihar-Funaura, Iriomote Isl., Okinawa, 1. VII. 1992.

Host-plant. Ficus microcarpa Linn. f.

Family Eurytomidae

Subfamily Eurytominae

Sycophila sp.1

Specimens examined. 1♀2♂, Todoroki-gawa, Ishigaki Isl., Okinawa, 22. IX. 1992.

Host-plant. Ficus microcarpa Linn. f.

F. microcarpa Linn. f.

Ceylon, India, south China eastwards through south-east Asia and Malaysia to New Britain, Australia (Queensland, New South Wales), Caroline Isl., Cocos and Christmas Isl. New South Wales), Caroline Isl., Cocos and Christmas Isl.

Agaoninae

Eupristina (*Parapristina*)

verticillata Waterston

(Malaysia, Sumatra, Philippines, Macao, Hong Kong: see Wiebes (1992))
Philippines, Macao, Hong Kong: see Wiebes (1992))

Sycoryctinae

Philotrypes emeryi Grandi

(Sumatra: Grandi, 1930)

Sycophaginae

According to Wiebes (1966), Timberlake's (1922) records of 'Idarninae' should be placed in this subfamily.

Otitesellinae

Walkerella kurandensis

Bouček

(Queensland: Bouček, 1988)

Walkerella sp.

(Papua New Guinea: Bouček, 1988)

Epichrysomallinae

Acophila spp.

(Australasian region: Bouček, 1988)

Epichrysomalla spp.

(Australasian region: Bouček, 1988)

Odontofroggattia corneri

Wiebes

(Malaysia, Solomon Is.: Wiebes, 1980;

China, Papua New Guinea: Bouček, 1988)

Odontofroggattia gajimaru

Ishii

(China: Bouček, 1988)

Odontofroggattia galili Wiebes

(Israel*3, Malaysia: Wiebes, 1980; Papua New Guinea, Queensland: Bouček, 1988)

Odontofroggattia ishii Wiebes

(Malaysia: Wiebes, 1980)

Other families

Ormyridae

Ormyrus spp.

(Hong Kong: Timberlake, 1922)

Eurytomidae

Appendix 2. Distribution (outside Japan) of figs in this study, their associated fig-wasp species recorded outside Japan and their known distribution.

Fig species Distribution area*1	Associated fig-wasps (their distribution: ref.)
Monoecious figs	
<i>Ficus superba</i> (Miq.) Miq. var. <i>japonica</i> Miq. Taiwan, Hong Kong, China, Hainan, Indochina, Thailand, Malaya (west coast).	Agaoninae <i>Platyscapa ishii</i> (Grandi) (Hong Kong: Hill, 1967a) Epichrysomallinae <i>Acophila mikii</i> Ishii (Hong Kong: Hill, 1967b) <i>Camarothorax</i> sp. (Queensland: Bouček, 1988)*2
<i>F. caulocarpa</i> (Miq.) Miq. Ceylon, lower Myanmar, Thailand, Malaya (Langkawi,	Agaoninae <i>Platyscapa fischeri</i> Wiebes

Appendix 2. (Continued)

Fig species Distribution area*1	Associated fig-wasps (their distribution: ref.)	
	<i>Decatomia</i> spp. (= <i>Sycophila</i> ?) (Hong Kong: Timberlake, 1922)	(Queensland: Girault, 1915; Wiebes, 1966; Bouček, 1988) <i>Eukoebelea spinatarsus</i> (Mayr) (?) ^{*6} (Java: Mayr, 1885, 1906; Wiebes, 1966)
Dioecious figs		Sycoryctinae
<i>F. nipponica</i> Franch. et Savat. Taiwan, Korea, China, Vietnam, no records Myanmar, Tibet, Assam, Sikkim, Bhutan.		<i>Apocrypta caudata</i> (Girault) (Queensland: Girault, 1915; Wiebes, 1966; Hong Kong: Hill, 1967b; Solomon Isl.: Ulenberg & van Pelt, 1985) <i>Philotrypesis bimaculata</i> Mayr (Java: Mayr, 1885) <i>Sycoscapter patellaris</i> (Mayr) (Java: Mayr, 1885; Bouček, 1988) <i>Sycoscapter subaeneus</i> (Girault) (Queensland: Girault, 1915; Wiebes, 1966; Bouček, 1988)
<i>F. thunbergii</i> Maxim. Korea, China (Szechuan). no records		
<i>F. pumila</i> L. Taiwan, China, north Indochina.	Agaoninae <i>Wiebesia pumilae</i> (Hill) (Hong Kong: Hill, 1967a; Taiwan: Ma & Wu, 1989)	
<i>F. erecta</i> Thunb. ex A. Murray Korea, Taiwan (Liu & Liao, 1976).	Agaoninae <i>Blastophaga</i> (<i>B.</i>) <i>nipponica</i> Grandi (Taiwan: Grandi, 1927b)	<i>F. benguetensis</i> Merrill Taiwan, Philippines Agaoninae <i>Ceratosolen</i> (<i>Rothropus</i>) <i>cornutus</i> Wiebes (Philippines: Wiebes, 1994)
<i>F. ampelas</i> Burmann fil. Taiwan, Philippines, Sumatra (west coast and islands), Java, Borneo (?), Bali, Lombok, Flores, Timor, Celebes, Moluccas, west New Guinea.	Agaoninae <i>Kradibia sumatrana</i> (Grandi) (Sumatra: Grandi, 1926; Java: Wiebes, 1994) Sycoryctinae <i>Philotrypesis jacobsoni</i> Grandi (Sumatra: Grandi, 1926) Epichrysomallinae <i>Neosycophila</i> sp. (Sumatra (?): Grandi, 1923) Other families Eurytomidae <i>Sycophila</i> sp. (?) (Sumatra (?): Grandi, 1923)	<i>F. septica</i> Burmann fil. Taiwan, Philippines, Sumatra, Java, Borneo, Lesser Sunda Isl., Timor, Celebes, Moluccas, New Guinea, Admiralty Isl., New Britain, New Ireland, Solomon Isl., New Hebrides, Cruz Isl., Queensland. Agaoninae <i>Ceratosolen</i> (<i>C.</i>) <i>bisulcatus bisulcatus</i> (Mayr) (Java, Krakatau, Bali, New Guinea: see Wiebes (1963, 1994)) <i>Ceratosolen</i> (<i>C.</i>) <i>bisulcatus jucundus</i> Grandi (Philippines: Grandi, 1927a; Taiwan: Grandi, 1927b; Borneo: Wiebes, 1963) Sycophaginae <i>Sycophaga sycomori</i> (L.) (?) ^{*7} (Java: Mayr, 1885) Sycoryctinae <i>Philotrypesis spinipes</i> Mayr (Java: Mayr, 1885)
<i>F. virgata</i> Reinw. ex Blume Taiwan, Philippines, Celebes, Moluccas, Flores, Alor, Wetar, Timor, Key and Aru Isl., New Guinea, New Britain, Solomon Isl., New Hebrides, New Caledonia, Queensland, Caroline Isl. (Ponape).	Agaoninae <i>Liporrhopalum virgatae</i> Hill (Solomon Isl.: Hill, 1969; Papua New Guinea: Bouček, 1988 ^{*4}) Epichrysomallinae <i>Neosycophila</i> sp. (Papua New Guinea: Bouček, 1988)	
<i>F. variegata</i> Blume Taiwan, China, north-east India to Myanmar, Indochina, South Andaman Isl., Philippines, through Malaysia to Solomon Isl. and Queensland. ^{*5}	Agaoninae <i>Ceratosolen</i> (<i>C.</i>) <i>appendiculatus</i> (Mayr) (Java, Philippines, Moluccas, Queensland, Papua New Guinea: see Wiebes (1963, 1994)) Sycophaginae <i>Apocryptophagus concisiventris</i> (Girault) (Queensland: Girault, 1915; Wiebes, 1966; Bouček, 1988) <i>Apocryptophagus fuscus</i> (Girault)	

*1: Based on Corner (1965) and Yamazaki (1983).; *2: Bouček (1988) did not indicate which collection came from Papua New Guinea or Queensland. However, *F. superba* has not been recorded from New Guinea. Thus, here we treated that his record from Queensland should be *F. superba* and that from Papua New Guinea should be *F. caulocarpa*. Although he noted the host fig as *F. superba* var. *japonica*, Corner (1965) reported that *F. s.* var. *henniana* (Miq.) Corner, instead of *F. s.* var. *japonica* was distributed in Queensland. Therefore, this record needs a reidentification of the host.; *3: Based on the record from introduced *F. microcarpa*.; *4: Bouček (1988) tentatively treated specimens from Papua New Guinea as *L. virgatae* but indicated that they do not agree with the original description.; *5: Varieties of host not mentioned in early records of fig-wasps from *F. variegata* and, as indicated in a footnote of Table 1, the Corner's variety-level taxonomy seems to need further reconsiderations. Thus areas listed here indicate the distribution range of *F. variegata* sensu lato (including all varieties) and all accessible fig-wasp records from *F. variegata* sensu lato were also listed.; *6: Mayr originally recorded as *Sycophaga sycomori* (L.) (1885) or *S. spinatarsus* Mayr (1906). Although Wiebes treated them as *Eukoebelea*, Bouček considered that most records of *Eukoebelea* in Africa and south-east Asia seems to be species of *Apocryptophagus*.; *7: Probably a species of *Apocryptophagus*.