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ABSTRACT: The tropical banyan tree, Ficus microcarpa L., is pollinated by Eupristina verticillata Waterston (Agaonidae), which was purposely introduced into Hawai'i in 1938. Seeds of this tree are commonly spread by birds and germinate readily on rock faces and masonry, often creating a nuisance problem. Since 1971, eight additional species of Chalcidoidea that develop in the fruit of *F. microcarpa* have been found to be established in Hawai'i. These include two species of Otitisellinae (Agaonidae), two Epichrysomallinae (Agaonidae), two Sycoryctinae (Agaonidae), and two Eurytomidae (Eurytominae). An historical review of introductions of fig wasps associated with *F. microcarpa* into Hawai'i is presented, nomenclatural problems are discussed, and the species known to be present are identified, insofar as is possible without reference to presently unavailable types. Taxonomic information, and a key to the chalcidoid species associated with *F. microcarpa* fruit in Hawai'i, are provided.

Ficus microcarpa L., commonly called Chinese banyan or Cuban laurel, is a widely planted ornamental shade tree native to the Asiatic tropics. It occurs naturally from India and Sri Lanka eastward through south Asia to Indonesia, New Guinea, northern Australia, Bismarck Archipelago, Solomon Islands, New Caledonia, Philippines, Ryukyus and Taiwan (Hill 1967a, Wagner *et al.* 1990).

In the past, references to insects associated with Chinese banyan often cited the tree as *Ficus retusa* L. or *F. nitida* Thunb., apparently misidentifications of *F. microcarpa* (Wagner *et al.* 1990).

Eupristina verticillata and the Ficus microcarpa Weed Problem

Before 1938, when its agaonid pollinator, Eupristina verticillata Waterston, was purposely introduced into Hawai'i from the Philippines (Pemberton 1939), F. microcarpa produced neither mature fruit nor fertile seed in Hawai'i. Eupristina verticillata was introduced to facilitate propagation of the tree for reforestation. However, the ripe fruit are eaten by birds, such as the barred dove, Geopelia striata L., which distribute the seeds in their feces. Seeds that lodge in rock faces or masonry germinate readily, and the resultant seedlings are often a nuisance. Ficus microcarpa is now a well established naturalized element of the Hawaiian flora, and trees are increasing wherever conditions favor their development. More recently, E. verticillata has been spread accidentally to California, Florida, Bermuda, Mexico, Honduras, San Salvador and Brazil. As in Hawai'i, the resultant F. microcarpa seedlings have caused problems in many of these areas (Ramirez & Montero 1988).

Other Sycophilous Chalcidoidea Associated with Ficus microcarpa

In addition to their obligate agaonid pollinators, the fruit of *Ficus* species (known botanically as syconia) furnish habitat for numerous other chalcid wasps, many of which are highly specialized to live in this environment. These belong to several distinct groups (families or subfamilies) within the Chalcidoidea. A provisional world catalog of Chalcidoidea associated with syconia of *Ficus* species was published by Wiebes (1966), who

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Fig. 1. Walkerella microcarpae Bouček. A, male, dorsal aspect; B, male, dorsum of head; C, female, lateral aspect; D, female, dorsum of thorax.



Fig. 2. Micranisa yashiroi (Ishii). A, male, dorsal aspect; B, male, dorsum of head; C, female, lateral aspect; D, female, dorsum of thorax.

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listed nine species from *F. microcarpa*. This number probably represents only a small fraction of the species associated with that tree over its vast native range. For example, Timberlake (1922) reported that 22 species of chalcidoids were reared by D.T. Fullaway from *F. microcarpa* fruit collected in Hong Kong. Unfortunately, Timberlake did not enumerate the species. These specimens, now in the Bishop Museum, Honolulu, are incompletely identified, but appear to include all of the species now established in Hawai'i. Hill (1967a) listed 20 chalcidoid species, mostly incompletely identified, that were reared from *F. microcarpa* fruit in Hong Kong.

The trophic relationships of the several chalcidoid species that occur within the syconia of *Ficus microcarpa* are not well understood. A paper by Bouček *et al.* (1981) illustrates the complexities of fig wasp interrelationships. These authors found 28 species of chalcidoids, exclusive of parasites of facultative inhabitants, associated with the syconia of *Ficus thonningii* in Africa.

Accidental Establishment of F. microcarpa Sycophiles in Hawaii

Since the early 1970s there has been a gradual accidental influx of *F. microcarpa* sycophiles into Hawai'i. Before 1971 only *Eupristina verticillata* was known to inhabit *F. microcarpa* syconia there. That year a species in the subfamily Otitesellinae was discovered in Honolulu. At that time, the Otitesellinae were usually placed in the Torymidae or Pteromalidae, but more recently Bouček (1988) assigned them to the Agaonidae. The species discovered in Hawai'i was first reported as an undetermined Torymidae (Beardsley 1972), and was subsequently identified as *Otitesella* sp., near *ako* Ishii by G. Gordh, then at the U.S. National Museum (Beardsley 1977). It was placed as *Micranisa yashiroi* (Ishii) by Bouček (1993). For reasons presented in the 'Taxonomic Notes'' section of this paper, I believe that Bouček placement probably is incorrect.

In 1975 I found a wasp of the subfamily Epichrysomallinae (reported as an undetermined torymid, Beardsley 1977) in *F. microcarpa* syconia, in Honolulu. Like the Otitesellinae, the Epichrysomallinae also were transferred by Bouček (1988) from the Pteromalidae to the Agaonidae. This wasp was determined as *Epichrysomalla* sp. (Beardsley 1980b) and later as *Odontofroggatia gajimaru* Ishii by Bouček (Beardsley 1982). In fact, neither identification was correct. Apparently, two other species of *Odontofroggatia* (*O. galili* Wiebes and *O. ishii* Wiebes) had become established in Hawai'i, both of which were first collected in July 1975. Correct identification of these was not made until Wiebes's (1980) revision of *Odontofroggatia* became available.

In 1976 an eurytomid wasp, later identified as Sycophila sp. and incorrectly reported as a torymid (Beardsley 1980a), was collected in light traps on O'ahu and subsequently reared from *F. microcarpa* syconia. Rearings from fruit of this tree, from several collections made on O'ahu in 1989, yielded specimens of three species previously unreported in Hawai'i. These were a second Sycophila sp.; a second Otitesellinae that I determined as Walkerella yashiroi Ishii, but which was more recently described as a new species, *W.* microcarpae Bouček (1993), and a species of Sycoryctinae that has been identified as Philotrypesis emeryi Grandi. The Sycoryctinae, formerly in the Torymidae, also were placed in the Agaonidae by Bouček (1988).

In May 1994 a second species of *Philotrypesis* was collected in general sweeping on Moloka'i, and in July 1994 it was reared from *F. microcarpa* syconia collected in Honolulu. Since rearings from *F. microcarpa* fruit collected on O'ahu in 1989 failed to yield this species, which was abundant in 1994 rearings, it is presumed to have become established in Hawai'i relatively recently.

The continued influx of *F. microcarpa* sycophiles into Hawai'i illustrates the vagility of these tiny wasps, some of which have spread very widely in tropical and subtropical areas where their host tree is planted (Anonymous 1994, Bouček 1993, Nadel *et al.* 1992, Ramirez & Montero 1988). How the spread of these wasps has been accomplished is unknown. However, many, possibly all, are attracted to lights, and I have recovered numerous specimens of several species from light trap material collected in and around Honolulu International Airport. This suggests that the principal means for the overseas dispersal of these wasps is jet aircraft, which often load at night under lights. Such aircraft daily span the Pacific from Hong Kong, Manila, and other Asian ports in areas where F. *microcarpa* is endemic.

Taxonomic Notes on Ficus microcarpa Sycophiles in Hawaii

The chalcidoid species presently known to be associated with *Ficus microcarpa* syconia in Hawai'i are listed below, with appropriate references, following the classification proposed by Bouček (1988). Distributional data are from published records, except for previously unpublished Hong Kong records based on specimens in the B.P. Bishop Museum in Honolulu, and for Hawai'i, where unpublished species and island records are included. The Hawaiian distribution records are almost certainly incomplete as collecting on Hawaiian islands other than O'ahu has been minimal, and most of the species listed are by now probably widely distributed on all of the islands, wherever *Ficus microcarpa* occurs.

Family Agaonidae Subfamily Agaoninae

Eupristina (Parapristina) verticillata Waterston

Eupristina verticillata Waterston 1920:128; Pemberton 1939:182; Williams 1939:194; van Zwaluwenburg 1940:362; Bianchi 1964:346.

Blastophaga (Eupristina) verticillata; Grandi 1926:358; Wiebes 1966:23.

Blastophaga (Parapristina) verticillata; Hill 1967b:32.

Parapristina verticillata; Wiebes 1979:8; Nadel et al. 1992:32.

Eupristina (Parapristina) verticillata; Bouček 1993:204.

Distribution: Philippines (type locality), Hong Kong, Hawai'i (Kaua'i, O'ahu, Moloka'i, Hawai'i), California, Florida, Bermuda, Mexico, Central America, Brazil.

Remarks: This primary caprifier was purposely imported from the Philippines in 1938 and liberated on O'ahu (Pemberton 1939).

Subfamily Epichrysomalinae

Odontofroggatia galili Wiebes

Odontofroggatia galili Wiebes 1980:3; Nadel et al. 1992:33; Bouček 1993:180.

Distribution: Southeast Asia, Hong Kong, Australia, Papua-New Guinea, Hawai'i (O'abu), California, Florida, Bermuda, Israel (type locality).

Odontofroggatia ishii Wiebes

Odontofroggatia ishii Wiebes 1980:6; Bouček 1993:180.

Distribution: Southeast Asia (type locality Malaya), Hong Kong, Papua-New Guinea, Hawai'i (O'ahu), California, Florida.

Remarks: This is the first record of these *Odontofroggatia* species in Hawai'i. The earlier record (Beardsley 1982) of *O. gajimaru* Ishii apparently resulted from misidentification of one or both of the above.



Fig. 3. Sycophila spp. A, sp. A, male, lateral aspect; B, sp. A, female, lateral aspect; C, sp. A, male, dorsum of propodeum and petiole; D, sp. B, male, dorsum of propodeum and petiole.



Fig. 4. A, Eupristina verticillata Waterston, female, lateral aspect of head; B, Odontofroggatia galili Wiebes, male, frontal aspect of head (antennae removed); C, O. galili, male, hind coxa; D, O. galili, male, dorsum of propodeum and petiole.

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Females of *Odontofroggatia* species oviposit through the outside of the syconium by means of an elongate ovipositor that is coiled within the gaster when not in use. Eggs are laid into young ovaries which are transformed into small galls by larval feeding. The wasps are not parasitic on Agaoninae or other inquilines, and may occur in syconia where agaonines are not present (Bouček 1988). Males are winged and leave the syconia to mate. Sexual dimorphism is strongly developed; males have broad heads with large, falcate mandibles, petiolate gasters and other specialized structures.

Subfamily Otitesellinae

Micranisa yashiroi (Ishii)

Otitesella yashiroi Ishii 1934:93. Otitesella sp. near ako Ishii, Beardsley 1977:408. Micranisa sp., Nadel et al. 1992:33.

Micranisa yashiroi, Bouček 1993:186.

Distribution: Okinawa (type locality), Hong Kong, Hawai'i (O'ahu, Moloka'i), Florida.

Remarks: Although he did not see the type specimens, Bouček (1993) placed the *Micranisa* species that is commonly associated with *Ficus microcarpa* syconia in Hawaii and elsewhere, as that described by Ishii (1934) as *Otitesella yashiroi*, based apparently on Ishii's description of the male. Although Ishii did not specify the sex of his holotype, he described the female of *O. yashiroi* before and in greater detail than the male, which leads me to believe it likely that the holotype is a female. If so, then Bouček was probably incorrect, as Ishii's description and figure of the female antenna more closely fit the species which Bouček has described as *Walkerella microcarpae* than they do *O. yashiroi*. I suspect that when the holotype of *O. yashiroi* is examined it will prove to be a female, and Bouček's *W. microcarpae* will become a junior synonym.

Bouček was clearly correct in concluding that Ishii's description of the male of O. *yashiroi* applies to a *Micranisa* species. However, both *yashiroi* and W. *microcarpae* of Bouček may occur in the same syconium, and this may have caused Ishii to incorrectly associate a *Micranisa* male with his O. *yashiroi* female.

Although I believe that the correct name of the Walkerella species which occurs in F. microcarpa syconia should be W. yashiroi (Ishii), and that the Micranisa associated with these fruit still is without a valid name, I have used Bouček's names for both species in the present paper because to disprove Bouček's implied assumption that the type of O. yashiroi is a male requires examination of Ishii's type material, which I have been unable to accomplish.

Walkerella microcarpae Bouček

Walkerella microcarpae Bouček 1993:184.

Walkerella yashiroi (Ishii), Stange & Knight 1987:3; Nadel et al. 1992:33.

Distribution: Okinawa, Hong Kong, Hawai'i (O'ahu), California, Florida (type locality), Bermuda, Grand Cayman, Brazil.

Remarks: This species has not been reported previously from Hawai'i. It was first collected by me in general sweeping at Hickam Air Force Base, O'ahu, in May 1988, but was not reared from fig syconia and identified until June 1989.

As explained above, I have followed Bouček (1993) in using this name for the *Walkerella* species associated with syconia of *F. microcarpa*, although I believe that it may be incorrect.

In the Otitesellinae sexual dimorphism is strongly expressed. The pale, flightless males apparently do not normally leave the syconium in which they develop. The ovipositional habits of our species do not appear to have been determined. Bouček (1988) states that *Walkerella* females oviposit from the outside of small fig syconia and larvae develop in galls formed from female florets (ovaries).

Subfamily Sycoryctinae

Philotrypesis emeryi Grandi

Philotrypesis emeryi Grandi 1926:363; 1930:146-152; Stange & Knight 1987:3; Nadel et al. 1992:33; Bouček 1993:196.

Distribution: Sumatra (type locality), Hong Kong, Hawai'i (O'ahu), Florida.

Remarks: The presence of this species in Hawai'i was reported by Nadel *et al.* (1992), based on information supplied by me. Although I collected a single female specimen in general sweeping at Hickam Air Force Base, O'ahu in October 1985, it was not reared from syconia and identified until June 1989.

Philotrypesis females oviposit from outside through the syconium wall, and the larvae compete for space and food with those of agaonine pollinators in the female florets (Bouček 1988).

Two male morphotypes of *P. emeryi* have been collected in Hawai'i. The majority of males which I have seen are fully winged and, except for genitalic characters, resemble females. A single specimen of a pale, flightless male morph of this species was recovered from a *F. microcarpa* syconium in Honolulu during June 1989. See Grandi (1930) for information on male polymorphism in *Philotrypesis*.

Philotrypesis sp.

Two female specimens of a second, previously unreported *Philotrypesis* species were collected on Moloka'i in general sweeping in May 1994. Numerous additional females, and several flightless males which appear to be conspecific, were reared from *F. microcarpa* syconia collected in Honolulu in July 1994. Females of this species in the Bishop Museum, collected in Hong Kong, were reared from *Ficus retusa* (= *F. microcarpa*) by D.T. Fullaway. Except for pale scape and legs, the females are entirely black. Since no black *Philotrypesis* are recorded from *F. microcarpa*, the species may be undescribed; however, further taxonomic research is needed. I have not seen winged males of this species.

Distribution: Hong Kong, Hawai'i (O'ahu, Moloka'i).

Family Eurytomidae Subfamily Eurytominae

Following Stage & Snelling (1986) and Bouček (1988), the number of eurytomid subfamilies has been reduced to three and the Sycophilinae, in which the two species listed below were formerly placed, is no longer recognized as distinct even at the tribal level.

Sycophila sp. A.

Sycophila sp., Beardsley 1980a:173.

Distribution: Hong Kong, Hawai'i (O'ahu), California.



Fig. 5. Odontofroggatia ishii Wiebes, male. A, lateral aspect; B, frontal aspect of head; C, hind coxa; D, dorsal aspect of propodeum, petiole, and second gastral tergum.



Fig. 6. Odontofroggatia females. A, O. ishii, lateral aspect of head and antennae; B, O. galili, semilateral aspect of head and antennae; C, O. ishii, dorsum of propodeum; D, O. galili, dorsum of propodeum.

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Sycophila sp. B.

This species, not previously reported in Hawai'i, was first collected near Ewa, O'ahu in general sweeping during April 1982. It was reared from *Ficus microcarpa* syconia collected in Honolulu in July 1988.

Distribution: Hong Kong, Hawai'i (O'ahu).

Remarks: Hill (1967a) reported three Sycophila species from Ficus microcarpa in Hong Kong, two very common and one rare. Both the above listed species are represented in material from Hong Kong reared from F. microcarpa by D.T. Fullaway. Because of the present taxonomic chaos in the genus Sycophila, it has not been possible to identify either of these species beyond the genus.

The biological roles of Sycophila spp. in fig syconia are largely undetermined.

KEY TO CHALCIDOIDEA ASSOCIATED WITH SYCONIA OF FICUS MICROCARPA IN HAWAI'I

1. 	Flightless males, wings vestigial or absent (figs 1A, 2A) 2 Fully winged males and females 6
2.	Mandibles conspicuously enlarged and protruding, 2/3 as long as remainder of head or nearly so (Figs. 1B, 2B) (Otitesellinae)
	Mandibles relatively short, extending much less than 2/3 length of head
3.	Antennae inserted very close together, the toruli separated by less than width of a torulus (Fig. 1B), apical flagellomeres blackish; head capsule nearly
	rectangular in outline from above
4.	Foreleg with femur greatly enlarged; head strongly flattened dorsoventrally, lateral margins rounded in dorsal view; gaster strongly tapered, normally curved forward beneath mesosoma, the segments telescoping (Agaoninae) Eupristing verticillate Waterston
	Femur of foreleg not enlarged; head not strongly flattened, nearly rectangular from above; gaster short and flat, not curved forward beneath mesosoma or telescoping (Sycoryctinae)
5.	Setae on sides of head elongate, the length of longest equal to width of head; head, pronotum and fore tibia dark brown, remainder paler <i>Philotrypesis</i> sp.
	Setae on sides of head shorter, longest much shorter than width of head; body mostly pale except posterior part of gaster darker <i>Philotrypesis emeryi</i> Grandi
6.	Head flattened, semirectangular in outline from above; mandible with a serrate, blade-like appendage extending beneath head (fig. 4A); ovipositor exerted for distance equal to length of metasoma, strongly arched dorsally; dorsum of mesosoma shining black (Agaoninae)
	Head not flattened or rectangular in outline; mandible without such an appendage; ovipositor if strongly exerted, straight or slightly curved; body color various

^{2.} Problems in applying these names are discussed in the text.

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7. 	Pronotum large, subrectangular from above; forewing with conspicuous dark stigma-like mark on anterior margin (Eurytominae)
8. 	Marginal vein of forewing very broad over entire length, globular, with dark mark confined mostly to it (Figs. 3A,B); male gastral petiole long and slender, ca 8 times as long as wide (Figs. 3A,C); mesosoma mostly yellow (female) or yellow and black (male)
	ing extending well behind vein; male gastral petiole relatively short and thick, less than twice as long as wide (Fig. 3D); female mesosoma mostly dark brown to blackish except yellowish pronotum, male paler
9.	Female ovipositor elongate, straight or weakly curved, length behind gaster greater than that of head plus mesosoma, base covered dorsally by two elongate posterior terga; winged males with normal head shape (Sycoryc- tinae)
	Female ovipositor not as above; heads of winged males ovoid, with broad mouths and long, slender mandibles (Figs. 4B, 5B)
10. -,	Body black, scape and legs in part, paler
11.	Tarsi four-segmented; postmarginal vein of forewing not developed, stigmal vein intersecting marginal at angle of about 90°; mesosoma mostly smooth, shining, with fine linear striations; male with broad mouth and long, slender mandibles (Epichrysomalinae)
	Tarsi five-segmented; postmarginal vein well developed, stigmal vein intersecting marginal at distinctly greater than 90°; mesosoma with reticulate sculpture; males flightless (couplet 3) (Otitesellinae)
12.	Female antenna with flagellomeres dark, bearing conspicuous dark spine-like hairs extending parallel to surface, without interspersed finer hairs (Fig. 6B); propodeum without anterior arcuate ridges (Fig. 6D); male gastral petiole without lateral tooth-like projections (Fig. 4D); male hind coxa with large dorsal tooth (Fig. 4C)
	Female antenna paler, spine-like setae interspersed with finer hairs (Fig. 6A); propodeum with a pair of arcuate ridges near anterior margin (Fig. 6C); male gastral petiole with a pair of conspicuous lateral tooth-like projections (Fig. 5D); male hind coxa without a tooth (Fig. 5C)
13.	Color largely metallic blue-green; dorsum of mesosoma with weakly impressed non-uniform reticulate sculpture (i.e.: reticulations more transverse on anterior part of mesoscutum than at middle) (Fig. 2D); gaster laterally compressed, with posterior segments and ovipositor sheaths curving downward (Fig. 2C)
	Color mostly black, gaster with slight metallic cast; dorsum of mesosoma with strongly impressed, uniformly reticulate sculpture (Fig. 1D); gaster not com- pressed; posterior segments and ovipositor sheaths extending straight behind or slightly downward (Fig. 1C)

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LITERATURE CITED

Anonymous. 1994. New state records; fig wasps. Calif. Plant Pest Dis. Rep.13: 62-63.

Beardsley, J.W. 1972. Note on unidentified torymid wasp from Chinese banyan. Proc. Hawaii. Entomol. Soc. 21: 148.

. 1977. Note on torymid wasps from Chinese banyan. Proc. Hawaii. Entomol. Soc. 22: 408.

------. 1980a. Note on Sycophila sp. Proc. Hawaii. Entomol. Soc. 23: 173.

-----. 1980b. Note on Epichrysomalla sp. Proc. Hawaii. Entomol. Soc. 23: 178.

1982. Note on Odontofroggatia gajimaru Ishii. Proc. Hawaii. Entomol. Soc. 24:
6.

Blanchl, F.A. 1964. Note on Eupristina verticillata Waterston. Proc. Hawaii. Entomol. Soc. 18: 346.

Bouček, Z. 1988. Australasian Chalcidoidea (Hymenoptera). C.A.B. International, Wallingford, Oxon, U.K. 832 p.

-----., A. Watsham & J.T. Wiebes. 1981. The fig wasp fauna of the receptacles of *Ficus thonningii* (Hymenoptera, Chalcidoidea). *Tijdschr. Entomol.* 124: 149-233.

Grandl, G. 1926. Hymenoptères sycophiles recolltes à Sumatra et à Java par E. Jacobson. Treubia 8: 352-64.

———. 1930. Monografia del gen. Philotrypesis Först. Boll. Lab. Entomol. Bologna 3: 1–181.

Hill, D.S. 1967a. The figs (Ficus spp.) of Hong Kong. Hong Kong Univ. Press. viii + 154 p.

———. 1967b. Fig-wasps (Chalcidoidea) of Hong Kong. 1. Agaonidae. Zool. Verh. 89: 1-55.

Ishli, T. 1934. Fig chalcidoids of Japan. Kontyû 8: 84-102.

Nadel, H., J.H. Frank & R.J. Knight. 1992. Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. *Fla. Entomol.* 75: 29–38.

Pemberton, C.E. 1939. Note on introduction and liberation of *Eupristina verticillata* Waterston in Honolulu. *Proc. Hawaii. Entomol. Soc.* 10: 182.

Ramirez, W. & J. Montero. 1988. Ficus microcarpa L., F. benjamina L., and other species introduced in the New World, their pollinators (Agaonidae) and other fig wasps. Rev. Biol. Trop. 36: 441-46.

Stage, G.I. & R.R. Snelling. 1986. The subfamilies of Eurytomidae and systematics of the subfamily Heimbrinae (Hymenoptera: Chalcidoidea). Contrib. Sci. 375: 1–17.

Stange, L.A. & R.J. Knight. 1987. Fig pollinating wasps of Florida. Florida Dep. Agric. Consumer Serv., Div. Plant Indust., Entomol. Circ. 296, 4 p.

Timberlake, P.H. 1922. Note on insects from figs of Ficus retusa at Hong Kong. Proc. Hawaii. Entomol. Soc. 5: 5.

- Wagner, W.L., D.R. Herbst, & S.H. Sohmer. 1990. Manual of the Flowering Plants of Hawaii. Vol. 1. Univ. Hawaii Press & Bishop Museum Press, Honolulu. 988 p.
- Waterston, J. 1920. Notes on fig insects, including descriptions of three new species and a new blastophagine genus. Trans. R. Entomol. Soc. Lond. 1920: 128-36.
- Wiebes, J.T. 1966. Provisional host catalogue of fig wasps (Hymenoptera, Chalcidoidea). Zool. Verh. 83: 3-44.

—. 1967. Redescription of Sycophaginae from Ceylon and India, with descriptions of lectotypes, and a World Catalogue of the Otitesellinae (Hymenoptera Chalcidoidea, Torymidae). *Tijdschr. Entomol.* 110: 399-442.

- -----. 1980. The genus Odontofroggatia Ishii (Hymenoptera Chalcidoidea, Pteromalidae Epichrysomallinae). Zool. Meded. 56: 1-6.
- Williams, F. X. 1939. Note on Eupristina verticillata Waterston, first recovery on Oahu. Proc. Hawaii. Entomol. Soc. 10: 194.

^{. 1979.} Co-evolution of figs and their insect pollinators. Ann. Rev. Ecol. Syst. 10: 1-12.