



Fig Wasps (Hymenoptera: Chalcidoidea: Agaonidae, Pteromalidae) Associated with Asian Fig Trees (Ficus, Moraceae) in Southern Africa: Asian Followers and African Colonists

Authors: van Noort, Simon, Wang, Rong, and Compton, Stephen G.

Source: African Invertebrates, 54(2) : 381-400

Published By: KwaZulu-Natal Museum

URL: <https://doi.org/10.5733/afin.054.0208>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Fig wasps (Hymenoptera: Chalcidoidea: Agaonidae, Pteromalidae) associated with Asian fig trees (*Ficus*, Moraceae) in southern Africa: Asian followers and African colonists

Simon van Noort^{1,2}, Rong Wang³ and Stephen G. Compton^{3,4}

¹Natural History Department, Iziko South African Museum, P. O. Box 61, Cape Town, 8000 South Africa; svannoort@iziko.org.za

²Department of Zoology, University of Cape Town, Rondebosch, 7701 South Africa

³School of Biology, University of Leeds, LS2 9JT, UK; S.G.A.Compton@leeds.ac.uk

⁴Department of Zoology & Entomology, Rhodes University, Grahamstown, 6140 South Africa

ABSTRACT

The Asian and Indo-Australasian fig tree species *Ficus microcarpa* and *F. religiosa* are widely-planted street and garden ornamentals in southern Africa and elsewhere. Like other fig trees, they depend for pollination on host specific fig wasps (Agaonidae). Their pollinators have also been widely introduced, and this allows the trees to become naturalised weeds. Both trees also support numerous non-pollinating fig wasps that can reduce seed or pollinator numbers, and a sub-set of these assemblages also now have wide distributions outside their native range. Two South African pollinators (*Elisabethiella bajinathi*, *E. stuckenbergi*), a galler (*Oritesella uluzi*) and a parasitoid (*Sycoryctes* species) occasionally succeed in reproducing in the figs of *F. microcarpa*, but in very small numbers. The tree's usual pollinator is absent but three Asian gallers of *F. microcarpa* are now widely established (*Odontofroggattia corneri*, *Odontofroggattia galili* and *Walkerella microcarpae*), and a fourth native species has expanded its host range and is developing as a parasitoid of the *Odontofroggattia* species (*Sycophila punctum*). In contrast, the Asian pollinator of *F. religiosa* (*Platyscapa quadriceps*) has colonised South Africa and Zambia and is likely to be present throughout southern Africa. No non-pollinator associates have been recorded in the region. Without its usual pollinator, *F. microcarpa* cannot reproduce, but *F. religiosa* may eventually become established in areas with a suitable climate.

KEY WORDS: Afrotropical, Agaonidae, Pteromalidae, Moraceae, *Ficus*, fig wasps, introduced species, invasive species.

INTRODUCTION

Many fig trees (*Ficus* species, Moraceae) are easy to grow as roadside, hedgerow and garden trees, as well as making ideal bonsai specimens. As a result, they are common subjects in the horticultural trade and a number of species have been distributed by man around the world. There are 15 or more species of exotic fig trees present in Africa, of which at least eight are being commonly propagated (Burrows & Burrows 2003). Fig trees depend on host specific fig wasps (Agaonidae) for pollination, and consequently cannot reproduce sexually in the absence of their associated pollinator species (Janzen 1979; Wiebes 1979; McKey 1989; Weiblen 2002; Cook & Rasplus 2003; Herre *et al.* 2008; Cook & Segar 2010). Pollinator fig wasp foundresses enter the figs in order to lay their eggs in, and gall, the ovules that line the inner surface of the fig. Fig trees also support numerous species of non-pollinating fig wasps (NPFW) that also have larvae that develop inside their figs (Compton 1993; Kerdelhué & Rasplus 1996; Kerdelhué *et al.* 2000; van Noort 2003; Compton *et al.* 2009; Cook & Segar 2010; Cruaud *et al.* 2011b; McLeish *et al.* 2012). These include ovule gallers and parasitoids, and they can reduce the reproductive success of both the trees and their pollinators (Weiblen 2002; Herre *et al.* 2008; Cook & Segar 2010).

Most of the exotic fig tree species grown in southern Africa and elsewhere have none of their associated fig wasps present, and consequently cannot reproduce. Among the exceptions are the cultivated fig *Ficus carica* L., the Australian *Ficus macrophylla* Desf.

<http://africaninvertebrates.org>

urn:lsid:zoobank.org:pub:F34A12CA-6A27-4484-A230-3F68F2D5EFEA

ex Pers. and *F. rubiginosa* Desf. ex Vent., with several of their associated species now present in New Zealand (Early 2000), the Asian *F. microcarpa* L.f. (Bouček 1993), and the Indian *Ficus religiosa* L. (Galil & Eisikowitch 1968).

Blastophaga psenes (L., 1758), the pollinator of the cultivated fig *F. carica*, was introduced to South Africa from California in 1908 for the caprification of non-parthenocarpic fig varieties that otherwise would fail to produce edible fruits (Wohlfarter *et al.* 2011). Modern commercial cultivation of fresh figs for the consumer market usually focuses on artificially selected parthenocarpic cultivars that do not need pollination to produce ripe fruit, but there are still some caprifig orchards in South Africa that depend on the long-established populations of *B. psenes* for pollination (van Noort 2003; Wohlfarter *et al.* 2011).

Ficus microcarpa (sometimes known as the Malay Banyan, among numerous other common names), is also often referred to by its synonyms *F. retusa* and *F. nitida*. It is a common and widespread species, indigenous to the Asian and Indo-Australasian regions (Berg & Corner 2005; Tan *et al.* 2009). Within the native range of *F. microcarpa*, Chen *et al.* (1999) recorded 20 species of associated fig wasps in Taiwan, and there are additional species elsewhere within its natural range (Zhang & Xiao 2008; Feng & Huang 2010; Li *et al.* 2013; Wang & Compton, unpubl. data; J.-Y. Rasplus, pers. comm.). The tree is pollinated by *Eupristina verticillata* Waterston, 1921, a taxon that may represent a complex of closely-related species (Sun *et al.* 2011). Identification keys to the fig wasp species associated with *F. microcarpa* are available in publications by Chen *et al.* (1999) and Feng & Huang (2010).

Ficus microcarpa has been widely planted around the world as a garden, roadside and container tree (Condit 1969; Bouček 1988; Kobbi *et al.* 1996; Beardsley 1998; Yokoyama & Iwatsuki 1998; Chen *et al.* 1999; Burrows & Burrows 2003; Farache *et al.* 2009; van Noort & Rasplus 2010; Doğanlar 2012). In South Africa this fig tree species is cultivated in frost-free areas and is most prevalent in the coastal regions of the two Cape provinces, being particularly widespread in the Western Cape (Burrows & Burrows 2003). It is commonly planted as an ornamental roadside tree in Cape Town and Port Elizabeth and also in many of the smaller towns of the Western and Eastern Cape provinces. It is also grown as a container plant in malls and in city squares (Burrows & Burrows 2003).

Eupristina verticillata was deliberately introduced from the Philippines to pollinate *F. microcarpa* in Hawaii (Pemberton 1939), in order to promote propagation of the tree for a reforestation initiative (Beardsley 1998). However, natural seed dispersal by birds resulted in the rapid spread of *F. microcarpa* through the Hawaiian Islands (Williams 1939; van Zwaluwenburg 1940), where it has become a problematic weed (Beardsley 1998). Subsequently, *E. verticillata* spread without authorised introductions to most of the introduced range of *F. microcarpa*, including Australia (part), Bermuda, Brazil (São Paulo), Canary Islands, El Salvador, Hawaii, Honduras, Italy (Sicily), Japan (part), Madeira, Mexico, Puerto Rico, Solomon Islands, Tunisia, Turkey, United Arab Emirates, United States of America (California, Florida) (Lo Verde *et al.* 1991; Nadel *et al.*, 1992; Kobbi *et al.* 1996; Yokoyama 1996; Beardsley 1998; Yokoyama & Iwatsuki 1998; Koponen & Askew 2002; van Noort & Rasplus 2010; Doğanlar 2012). The presence of the pollinator has resulted in seedlings developing in cracks and crevices of buildings, causing structural weaknesses, as well as to the tree becoming invasive in some natural areas (Ramirez & Montero 1988; McKey 1989; Lo Verde *et al.* 1991; Beardsley 1998).

Several of the NPFW species associated with *F. microcarpa* have also become established outside their native ranges, and two species are particularly widely distributed: *Odontofroggattia galili* Wiebes (Pteromalidae: Epichrysomallinae) and *Walkerella microcarpae* Bouček (Pteromalidae: Otitesellinae). *Odontofroggattia galili* is one of five described species in the genus that have been reared from figs of *F. microcarpa* and also the closely related *F. prasinicarpa* (Bouček 1988; Feng & Huang 2010). *Odontofroggattia* species are gall-forming fig wasps that reproduce in the ovules of the host figs (Bouček 1988). Their galls are considerably larger than those formed by the pollinator. *Odontofroggattia galili* larvae can develop successfully in figs that have not been pollinated (Galil & Copland 1981). In urban environments this fig wasp is considered to be a nuisance, because gall development results in large, soft figs, which make a mess underneath the trees (Galil & Copland 1981). Over the last 40 years *O. galili* has expanded its range, probably aided by accidental transport by man inside figs. It arrived in Israel between 1970 and 1975 (presumably directly from Southeast Asia) and was subsequently reported from Florida, USA in 1986 (Galil & Copland 1981; Stange & Knight 1987). It had also reached the Greek island of Simi before September 1987, when the species was already numerous inside the figs of roadside trees (Compton 1989). Subsequently the species has also been reported from several other areas around the Mediterranean (Lo Verde & Porcelli 2010). A related species, *Odontofroggattia ishii* Wiebes, 1980 has been recently recorded from *F. microcarpa* in Turkey (Doğanlar 2012).

Walkerella microcarpae is a second ovule-gall forming species, with *F. microcarpa* as the only recorded host plant. It was originally described from the Americas, where it had colonised introduced *F. microcarpa* before the 1980s (Bouček 1993; Farache *et al.* 2009), and has been subsequently recorded from the Mediterranean area (Lo Verde *et al.* 2007; Doğanlar 2012). Within its native range its distribution extends from China to Papua New Guinea (Xu *et al.* 2005; Ma *et al.* 2013; Wang & Compton, unpubl. data; van Noort, unpubl. data).

Numerous species of fig wasps have been recorded from the figs of *Ficus religiosa* in its native range (Wiebes 1967), but only the pollinator, *Platyscapa quadraticeps* Mayr is recorded as having been introduced elsewhere. The presence of *P. quadraticeps* has been confirmed in countries around the Mediterranean (Galil & Copland 1981; van Noort & Rasplus 2010), and indirect evidence, based on the presence of *F. religiosa* seedlings, suggest that the pollinator is also present in Florida, Hawaii and Australia (Nadel *et al.* 1992; Bouček 1993; Randall 2007; Frohlich & Lau 2008). The pollinator has also been reported from Zambia and South Africa (van Noort 2003), and Hyde *et al.* (2012) reported naturalised seedlings growing from a wall in Harare (Zimbabwe) in 2007, indicating that the pollinator is also likely to be present in Zimbabwe.

Most fig tree pollinators and many NPFW are host tree specific, although there are numerous exceptions (Ramirez 1970; Michaloud *et al.* 1985, 1996; Compton *et al.* 1991; Rasplus 1996; Kerdelhué *et al.* 1997, 1999; Lopez-Vaamonde *et al.* 2002; Molbo *et al.* 2003; van Noort 2003; Machado *et al.* 2005; Haine *et al.* 2006; Erasmus *et al.* 2007; Marussich & Machado 2007; Peng *et al.* 2008; Compton *et al.* 2009; Cook & Segar 2010; Moe & Weiblen 2010; Cruaud *et al.* 2011a; Moe *et al.* 2011; Sun *et al.* 2011; Chen *et al.* 2012; Cornille *et al.* 2012; Kobmoo *et al.* 2012; McLeish & van Noort 2012; McLeish *et al.* 2012). Fig wasps are able to enter the figs of atypical hosts and can sometimes reproduce there and generate fertile seed (Ramirez 1970; Ramirez

& Montero 1988; Compton 1990). Such ‘mistakes’ appear to be more likely when fig trees are planted outside their natural range, because their pollinators are normally absent, and the figs remain attractive to fig wasps for much longer than would be the case within their natural range (Ware & Compton 1992).

Introduced fig trees have become invasive species in several parts of the world. We surveyed two Asian fig trees planted in southern Africa in order to find which of their associated fig wasps have been introduced, and in particular to determine whether their pollinators are present and are allowing them to reproduce. Based on the material obtained, we also aimed to produce high quality digital images of the introduced fig wasps, to facilitate their identification in the future by non-specialists. The surveys also allowed us to check whether any native fig wasp species were breeding in the figs of the introduced species.

MATERIAL AND METHODS

Mature (‘Phase D’) figs were removed from planted *F. microcarpa* and *F. religiosa* trees and either placed directly into 70% ethanol or in netting-covered containers so that adults of any fig wasps that emerged could be collected. The fig wasps were then preserved in 96% ethanol with representatives point-mounted on cards. Specimens used for photography were point mounted on black, acid-free card for examination using a Leica M205C stereomicroscope with LED light sources. Images were acquired using the EntoVision multiple-focus imaging system. This system comprises a Leica M16 microscope with a JVC KY-75U 3-CCD digital video camera that fed image data to a notebook computer. The program Cartograph 5.6.0 was then used to merge an image series (representing typically 10–15 focal planes) into a single in-focus image. Lighting was achieved using techniques summarised in Buffington *et al.* (2005), Kerr *et al.* (2009) and Buffington & Gates (2009). All images presented in this paper are available through the Figweb resource (<http://www.figweb.org>).

The material is deposited in the following collections: SAMC – Iziko South African Museum, Cape Town; and SGCC – Stephen G. Compton collection, Rhodes University, South Africa and University of Leeds, UK.

RESULTS

Introduced fig wasps associated with Ficus microcarpa

Family Pteromalidae Dalman, 1820

Subfamily Epichrysomallinae Hill & Riek, 1967

Odontofroggattia corneri Wiebes, 1980 (Figs 1, 2)

Material examined: SOUTH AFRICA: *Western Cape*: 3♀ 2♂ Gardens, Wesley Street, 33°55.903'S 18°25.199'E, 30 m, 3.ii.2012, S. van Noort, SA12-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046350 (SAMC); 11♀ 8♂ Somerset West, Mall parking area, 34°4.936'S 18°49.328'E, 20 m, 31.xii.2012, S. van Noort, SA12-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046340 (SAMC); 76♀ 49♂ Grand West, parking area, 33°55.038'S 18°32.789'E, 25 m, 8.i.2013, S. van Noort, SA13-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046324 (SAMC); 318♀ 50♂ Kalk Bay, Bay Primary school, 34°07.647'S 18°26.817'E, 18 m, 25.i.2013, S. van Noort, SA13-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046316 (SAMC); 66♀ 59♂ Constantia, Croft road, 34°01.929'S 18°26.119'E, 60 m, 21.ii.2013, S. van Noort, SA13-CPT-F03, ex planted *Ficus microcarpa*, SAM-HYM-P046349 (SAMC); 330♀ 157♂ Grand West, parking area, 33°55.054'S 18°32.702'E, 25 m, 10.iii.2013, S. van Noort, SA13-CPT-F04, ex planted *Ficus microcarpa*, SAM-HYM-P046356 (SAMC).

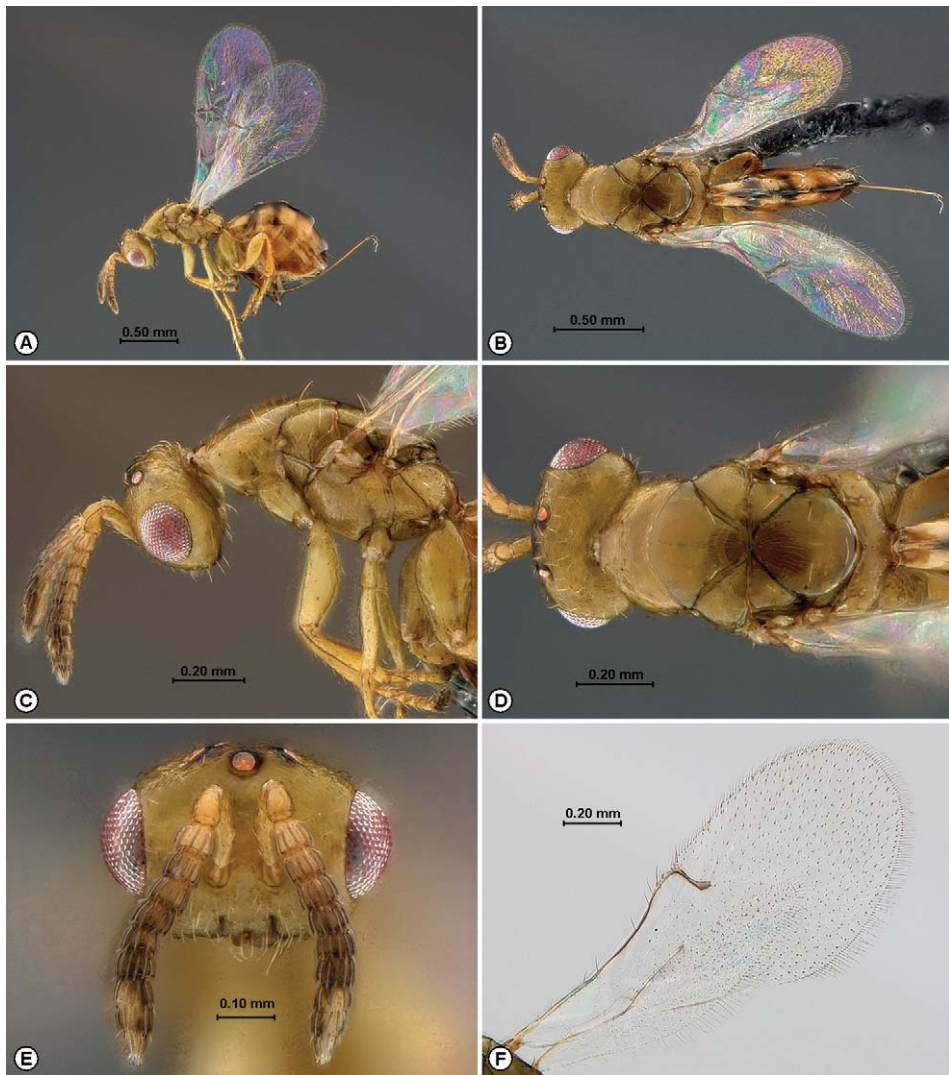


Fig. 1. *Odontofroggatia corneri* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

Global distribution: China (Guangdong, Hainan), Malaya, Papua New Guinea, Solomon Islands (Isabel Island), South Africa (new record), Taiwan (Bouček 1988; Chen *et al.* 1999; Feng & Huang 2010).

Odontofroggatia galili Wiebes, 1980 (Figs 3, 4)

Material examined: SOUTH AFRICA: *Eastern Cape*: 9♀ 11♂ Grahamstown, High Street, 33°18'43"S 26°31'23"E, 29.viii.2010, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 20♀ 8♂ same locality but 6.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 17♀ 9♂ Grahamstown, Robinson Street, 33°18'58"S 26°31'44"E, 6.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 1♀ 1♂ Port Elisabeth, 'Boardwalk' shopping complex, 33°59'06"S 25°39'32"E, 10.ix.2011, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 1♀ 1♂ same locality but 2.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC).



Fig. 2. *Odontofroggattia corneri* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

Western Cape: 1♀ 1♂ Cape Town, Vredehoek, 33°56.347S 18°25.538E, 20.vii.2007, M. Cochrane & S. van Noort, ex planted *Ficus microcarpa*, SAM-HYM-P030916 (SAMC); 5♀ 2♂ Bredasdorp, 34°32.179'S 20°02.372'E, 28.iv.2011, S. van Noort, ex planted *Ficus microcarpa*, SAM-HYM-P046323 (SAMC); 1♂ Gardens, Wesley Street, 33°55.903'S 18°25.199'E, 30 m, 3.ii.2012, S. van Noort, SA12-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046351 (SAMC); 1♀ 2♂ Kalk Bay, Bay Primary School, 34°07.647'S 18°26.817'E, 18 m, 25.i.2013, S. van Noort, ex planted *Ficus microcarpa*, SAM-HYM-P046317 (SAMC); 23♀ 7♂ Constantia, Croft road, 34°01.929'S 18°26.119'E, 60 m, 21.ii.2013, S. van Noort, SA13-CPT-F03, ex planted *Ficus microcarpa*, SAM-HYM-P046352 (SAMC).

Global distribution: Australia, Bermuda, China (Hong Kong, Guangdong, Hainan, Yunnan (Compton & Wang, unpubl. data)), Japan, Malaysia, Mediterranean region, Papua New Guinea, South Africa (new record), Taiwan, Southeast Asia, United Arab Emirates,



Fig. 3. *Odontofroggatia galili* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

USA (California, Florida, Hawaii) (Galil & Eisikowitch 1968; Bouček 1988; Compton 1989; Beardsley 1998; Yokoyama & Iwatsuki 1998; Chen *et al.* 1999; Feng & Huang 2010; van Noort & Rasplus 2010).

Subfamily Otitesellinae Joseph, 1964

Walkerella microcarpae Bouček, 1993 (Figs 5, 6)

Material examined: SOUTH AFRICA: *Eastern Cape*: 151♀ 52♂ Port Elisabeth, 'Boardwalk' shopping complex, 'Tree 1', 33°59'06"S 25°39'32"E, 10.ix.2011, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 32♀ 15♂ same locality but 2.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 220♀ 123♂ Grahamstown, High Street, 33°18'43"S 26°31'23"E, 29.viii.2010, S.G. Compton, ex planted *Ficus*

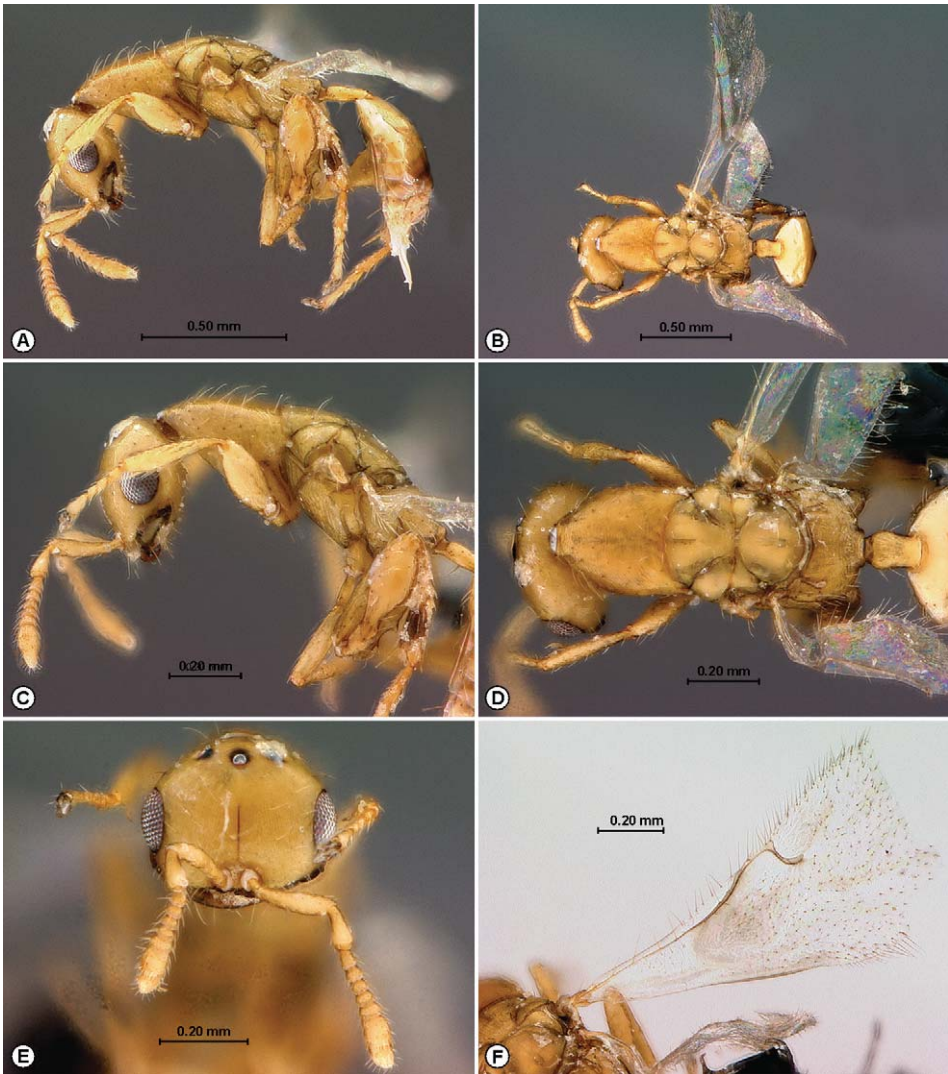


Fig. 4. *Odontofroggatia galili* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

microcarpa (SGCC); 58♀ 16♂ same locality but 6.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 14♀ 8♂ same locality but 'Tree 2', 33°18'43"S 26°31'23"E, 6.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC); 61♀ 31♂ Grahamstown, Robinson Street, 33°18'58"S 26°31'49"E, 6.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC). *Western Cape*: 4♀ 10♂ Cape Town, Bellville, Voortrekker Road, 33°54.167'S 18°38.435'E, 31.v.2007, M. Cochrane & S. van Noort, SA07-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046320 (SAMC); 128♀ 65♂ Cape Town, Vredehoek, 33°56.347'S 18°25.538'E, 20.vii.2007, M. Cochrane & S. van Noort, SA07-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P030917 (SAMC); 24♀ 5♂ same locality but 9.ix.2007, M. Cochrane, SA07-CPT-F03, ex planted *Ficus microcarpa*, SAM-HYM-P046341 (SAMC); 52♀ 12♂ Tokai, 34°03.676'S 18°27.553'E, 10 m, 16.ix.2007, S. van Noort, SA07-CPT-F04, ex planted *Ficus microcarpa*, SAM-HYM-P046342 (SAMC); 4♀ 1♂ Cape Town, Gardens, 33°55.717'S 18°24.859'E, 18.i.2009, S. van Noort, ex planted *Ficus microcarpa*, SAM-HYM-P030907 (SAMC); 168♀ 264♂ Kirstenhof, 34°04.450'S 18°26.951'E, 16.xii.2009, S. van Noort,

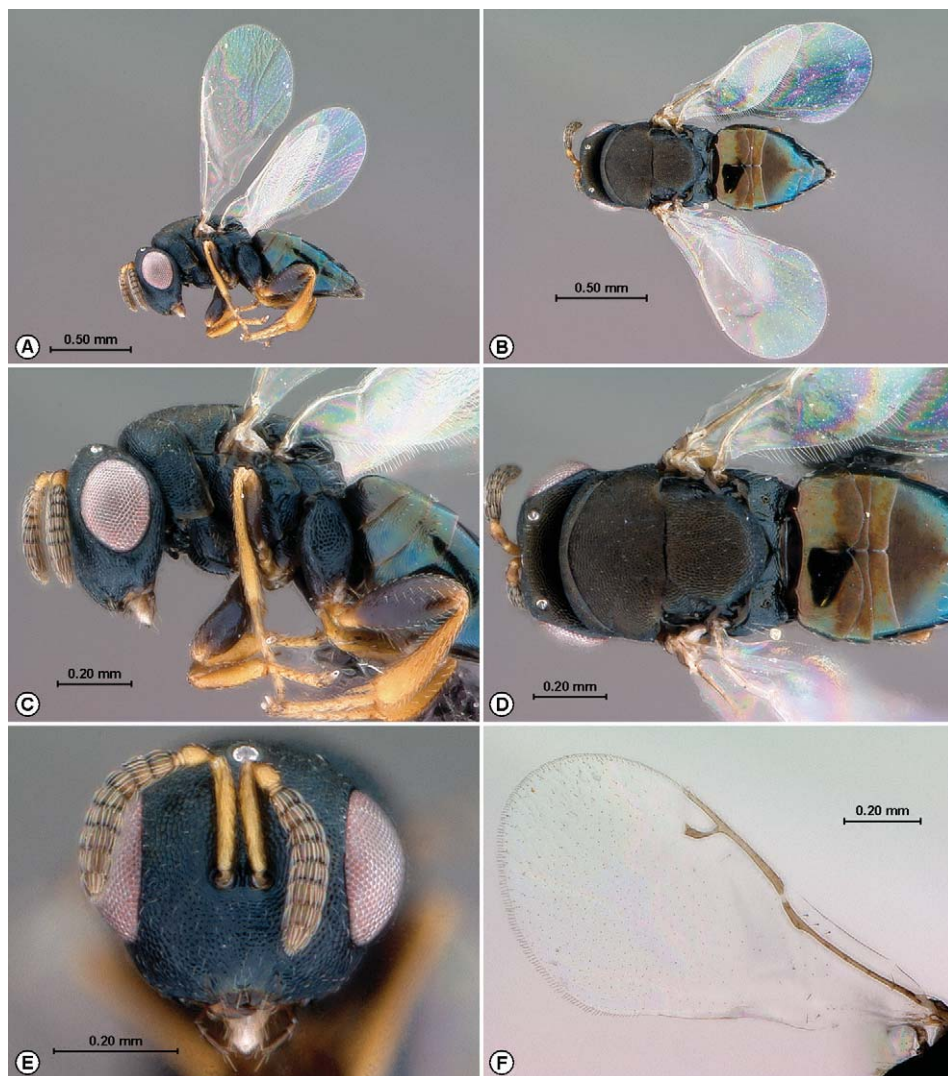


Fig. 5. *Walkerella microcarpae* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

SA09-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046343 (SAMC); 140♀ 11♂ Porterville, 33°01.068'S 18°59.593'E, 144 m, 12.ii.2010, S. van Noort, SA10-POR-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046344 (SAMC); 57♀ 34♂ Heidelberg, 34°05.577'S 20°57.784'E, 80 m, 27.ii.2010, S. van Noort, SA10-HEI-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046338 (SAMC); 90♀ 82♂ Bredasdorp, 34°32.179'S 20°02.372'E, 28.iv.2011, S. van Noort, SA11-BRE-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046322 (SAMC); 105♀ 24♂ Kirstenhof, 34°04.450'S 18°26.951'E, 21.viii.2011, S. van Noort, SA11-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046345 (SAMC); 16♀ 15♂ Muizenberg, Holland road, 34°06.251'S 18°28.211'E, 5 m, 3.ix.2011, S. van Noort, SA11-CPT-F03, ex planted *Ficus microcarpa*, SAM-HYM-P046346 (SAMC); 86♀ 40♂ Vredenberg, 32°54.137'S 17°58.953'E, 115 m, 3.x.2011, S. van Noort, SA11-VRE-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046330 (SAMC); 127♀ 63♂ Lakeside, Bunker road, 30 m, 34°05.358'S 18°27.273'E, 5.xii.2011, S. van Noort, SA11-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046319 (SAMC); 24♀ 20♂ Simonstown, Jubilee Square, 34°11.586'S 18°25.983'E, 20 m,



Fig. 6. *Walkerella microcarpae* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head of large male, anterior view; (E) head of small male, anterior view; (F) male and female recently eclosed from their natal galls (male is using his mandibles to open a gall containing another female to assist her escape and be the first to mate with her).

25.ix.2011, S. van Noort, SA11-CPT-F04, ex planted *Ficus microcarpa*, SAM-HYM-P046347 (SAMC); 30♀ 21♂ Gardens, Wesley Street, 33°55.903'S 18°25.199'E, 30 m, 3.ii.2012, S. van Noort, SA12-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046346 (SAMC); 81♀ 40♂ Somerset West, Mall parking area, 34°04.936'S 18°49.328'E, 20 m, 31.xii.2012, S. van Noort, SA12-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046339 (SAMC); 13♀ 13♂ Grand West, parking area, 33°55.038'S 18°32.789'E, 25 m, 8.i.2013, S. van Noort, SA13-CPT-F01, ex planted *Ficus microcarpa*, SAM-HYM-P046325 (SAMC); 48♀ 12♂ Grand West, parking area, 33°55.054'S 18°32.702'E, 25 m, 10.iii.2013, S. van Noort, SA13-CPT-F04, ex planted *Ficus microcarpa*, SAM-HYM-P046354 (SAMC); 152♀ 16♂ Kalk Bay, Bay Primary school, 34°07.647'S 18°26.817'E, 18 m, 25.i.2013, S. van Noort, SA13-CPT-F02, ex planted *Ficus microcarpa*,

SAM-HYM-P046318 (SAMC); 2♀ Constantia, Croft road, 34°01.929'S 18°26.119'E, 60 m, 21.ii.2013, S. van Noort, SA13-CPT-F03, ex planted *Ficus microcarpa*, SAM-HYM-P046348 (SAMC).

Global distribution: Bermuda, Brazil, Cayman Islands, China (Hong Kong), China (mainland) (Ma *et al.* 2013; Compton & Wang, unpubl. data), Japan, Malaysia (van Noort, unpubl. data), Mediterranean region (Lo Verde *et al.* 2007), Papua New Guinea (van Noort, unpubl. data), South Africa (new record), USA (California, Florida, Hawaii) (Bouček 1993; Beardsley 1998).

African fig wasps reproducing in figs of Ficus microcarpa (Fig. 7E)

Family Agaonidae Walker, 1871

Elisabethiella baijnathi Wiebes, 1989 (Fig. 7A)

Material examined: SOUTH AFRICA: *Eastern Cape*: 1♀ Grahamstown, High Street, 33°18'44"S 26°31'23"E, 7.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC).

Global distribution: South Africa.

Indigenous host: *Ficus burtt-davyi* Hutch.

Elisabethiella stuckenbergi (Grandi, 1955) (Fig. 7B)

Material examined: SOUTH AFRICA: *Western Cape*: 5♀ 1♂ Grand West, parking area, 33°55.054'S 18°32.702'E, 25 m, 10.iii.2013, S. van Noort, SA13-CPT-F04, ex planted *Ficus microcarpa*, SAM-HYM-P046353 (SAMC).

Global distribution: Mozambique, South Africa, Swaziland, Tanzania, Zimbabwe, Zambia (Bouček *et al.* 1981; Erasmus *et al.* 2007; Cornille *et al.* 2012).

Indigenous host: *Ficus burkei* (Miq.).

Family Eurytomidae Walker, 1832

Sycophila punctum Bouček, 1981 (Figs 8, 9)

Material examined: SOUTH AFRICA: *Western Cape*: 2♀ 9♂ Kalk Bay, Bay Primary school, 34°07.647'S 18°26.817'E, 18 m, 25.i.2013, S. van Noort, SA13-CPT-F02, ex planted *Ficus microcarpa*, SAM-HYM-P046315 (SAMC).

Global distribution: South Africa (new record), Zimbabwe (Bouček *et al.* 1981).

Indigenous host: *Ficus burkei* (Miq.).

Family Pteromalidae Dalman, 1820

Subfamily Otitesellinae Joseph, 1964

Otitesella uluzi Compton in van Noort & Compton, 1988 (Fig. 7C)

Material examined: SOUTH AFRICA: *Eastern Cape*: 1♀ Grahamstown, High Street, 33°18'44"S 26°31'23"E, 7.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC).

Global distribution: South Africa.

Indigenous host: *Ficus burtt-davyi* Hutch.

Subfamily Sycoryctinae Wiebes, 1966

Sycorctes sp. indesc. (Fig. 7D)

Material examined: SOUTH AFRICA: *Eastern Cape*: 1♀ 1♂ Grahamstown, High Street, 33°18'44"S 26°31'23"E, 7.iv.2012, S.G. Compton, ex planted *Ficus microcarpa* (SGCC).

Global distribution: South Africa.

Indigenous host: *Ficus burtt-davyi* Hutch.

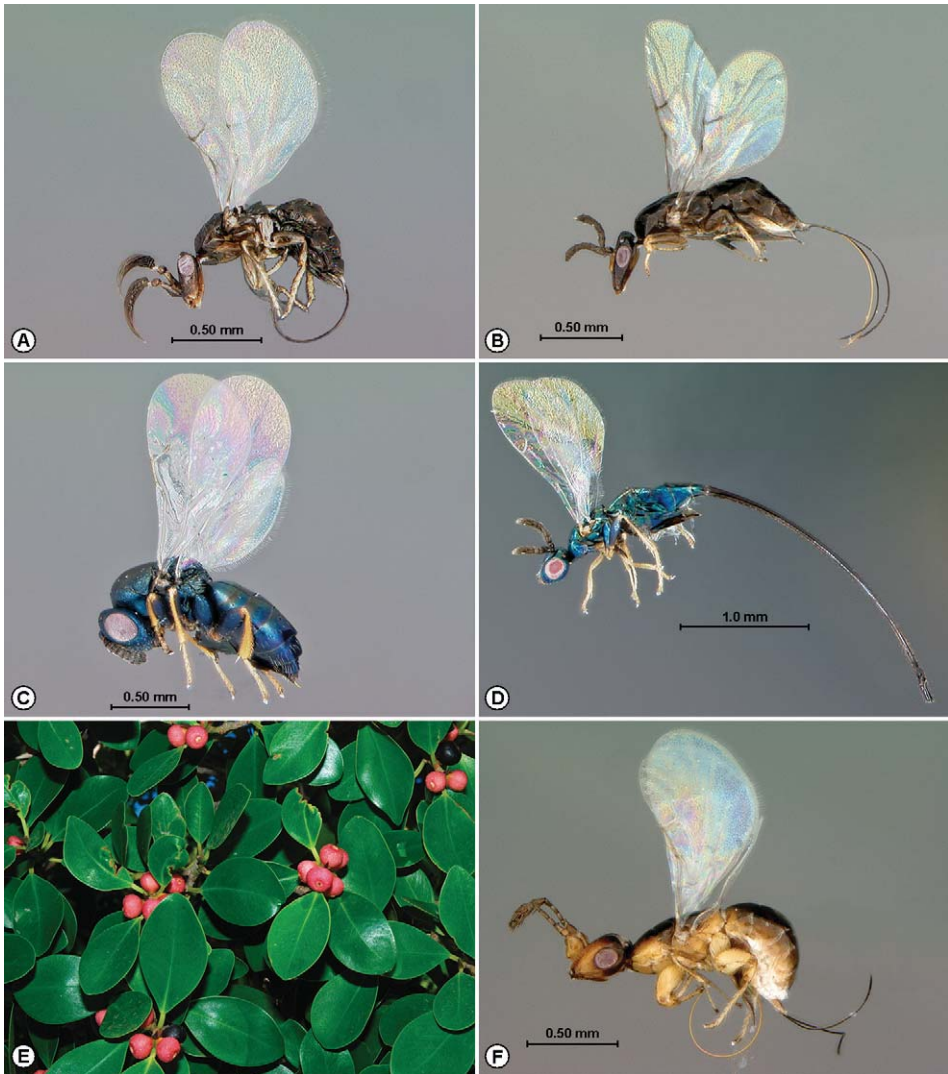


Fig. 7. (A–D) African fig wasps reared from introduced *Ficus microcarpa*: (A) *Elisabethiella bajnathi* female, lateral habitus; (B) *Elisabethiella stuckenbergi* female, lateral habitus; (C) *Otitesella uluzi* female, lateral habitus; (D) *Sycorcytes* species, lateral habitus; (E) *F. microcarpa* with D-phase figs; (F) *Platyscapha quadraticeps* female, lateral habitus, pollinator of *F. religiosa*.

Introduced fig wasps associated with Ficus religiosa

Family Agaonidae Walker, 1871

Platyscapha quadraticeps (Mayr, 1885) (Fig. 7F)

Material examined: SOUTH AFRICA: *Gauteng*: 2♀ Pretoria, University of Pretoria campus, Botany Department, 25°45.10'S 28°13.75'E, 13.xii.1999, S. van Noort, J. Greeff & F. Kjellberg, KW99-F58, planted tree, ex *Ficus religiosa*, SAM-HYM-P046355 (SAMC); 18♀ 11♂ same data but 7.xi.2000, J. Greeff, SAM-HYM-P021140 (SAMC). ZAMBIA: 24♀ 34♂ Lusaka, 6.v.1991, M. Bingham, C447, SAM-HYM-P005815 (SAMC).

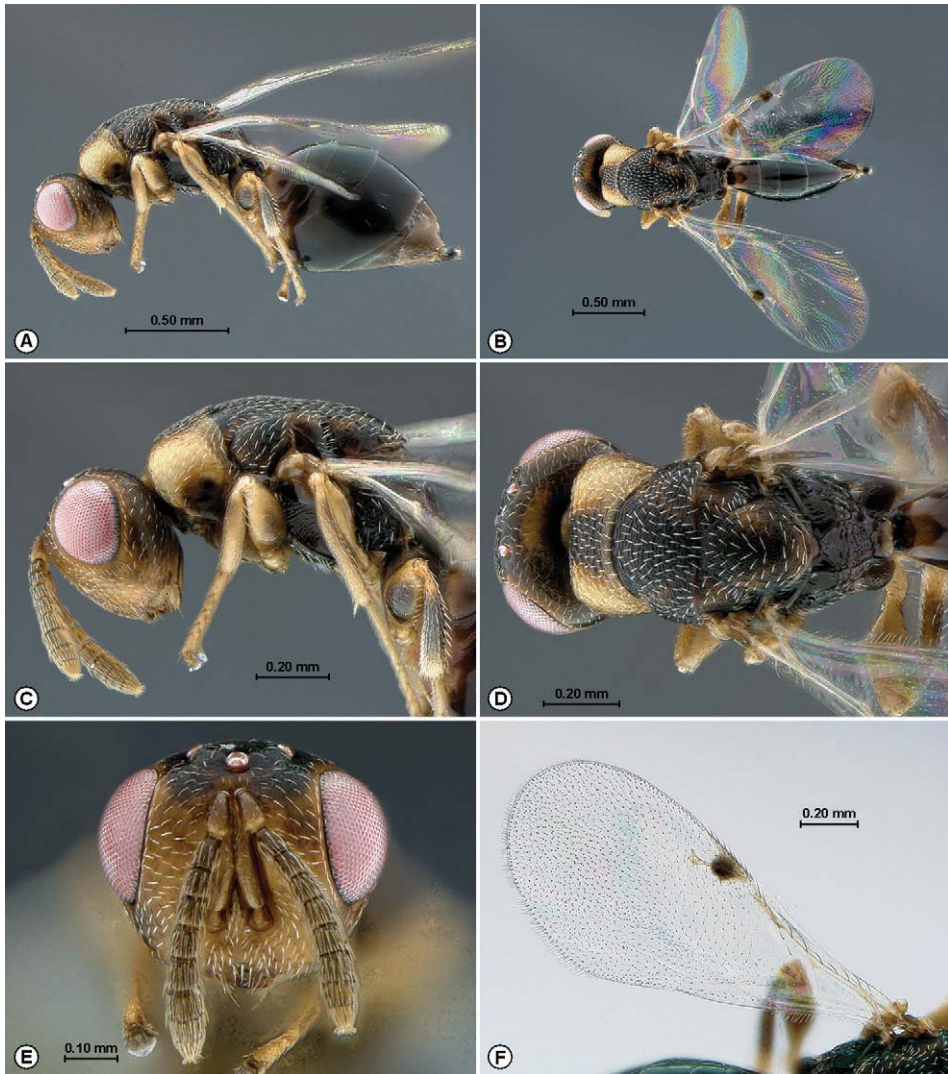


Fig. 8. *Sycophila punctum* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

Global distribution: China, India, Pakistan, Singapore, Sri Lanka, Taiwan, Thailand, Vietnam. Introduced to Iraq, Israel, Malaysia, South Africa, UAE, Zambia, Zimbabwe (Berg & Corner 2005; van Noort & Rasplus 2010; Hyde *et al.* 2012).

DISCUSSION

Globalization of invasive fig wasp species is mediated through the horticulture and bonsai trade, with the spread of fig wasp species outside their natural range likely to be facilitated by accidental transfer of their larvae inside figs as part of international trade of the host fig species. Fig wasps can rapidly expand their range in a newly colonised



Fig. 9. *Sycophila punctum* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

region. They are excellent colonisers of islands (Compton *et al.* 1988), and some species can be dispersed by wind for tens or even hundreds of kilometres (Ahmed *et al.* 2009). Consequently, once they become established in a novel area, it is highly probable that they will spread across the entire population of their host fig tree in the region, however fragmented it may be. In South Africa, *Ficus microcarpa* (Fig. 7E) is planted as a garden ornamental or as a shade tree along streets or in parking areas in suburban situations and hence subpopulations may be separated by hundreds of kilometres.

Two of the gallier species associated with *Ficus microcarpa*, *Walkerella microcarpae* and *Odontofroggattia galili* were first recorded in 2007 in Cape Town and have now

probably become established throughout the host species' planted range in the country. It is possible that they arrived in the country prior to this date and remained undetected. Of the fig wasp species associated with *F. microcarpa*, these two species (along with the tree's pollinator) have achieved the widest distribution globally. This may be related to the composition of the fig wasp species assemblage associated with the fig population from where the global horticultural stock was derived, i.e. they happened to be the species that became established in the source country that subsequently exported *F. microcarpa* figs globally, but it is also likely that features of their biology have facilitated their spread. Their ability to develop independently of the pollinator provides a clear advantage, and their adults may also be more physiologically resilient than some of the other species that have not spread beyond their native range. The situation in South Africa, where they have established in the absence of their associated pollinator fig wasp, is similar to the initial situation in Israel, where *O. galili* was the first fig wasp recorded from *F. microcarpa*, and may still be the only species present, and the Greek Isles, where this species was the first to be recorded, but now there are several additional species, including the pollinator (Compton & Wang, unpubl. data). NPFW were similarly established on *F. microcarpa* in Brazil, before the arrival of the pollinator (Neves & Isaias 1987), indicating that the current inability of *F. microcarpa* to set seed in South Africa may only be temporary. *Odontofroggata galili* is generally rarer than *W. microcarpae* in South Africa, although the two species may be equally widely distributed. In Grahamstown and Port Elizabeth each crop was found consistently to support both species, but *W. microcarpae* was much more common and could comprise over 90% of the fig wasps present in the figs. In the Cape Town region *O. galili* is much rarer and often not present in the fig crop. In February 2012 an additional species, *Odontofroggata corneri*, was recorded in Cape Town. This species now dominates the fauna in the Western Cape, with *W. microcarpae* relatively far less abundant in fig crops than prior to the arrival of *O. corneri*, although this may reflect an increased proportion of the figs being colonised, rather than competitive exclusion. *Odontofroggata galili* remains rare in the Cape Town samples. Clearly there is ongoing independent colonization occurring and it is likely that the pollinator will arrive in South Africa in the near future.

In one of the Cape Town samples two pairs of *O. galili* females were preserved *in copula* with *O. corneri* males, together with pairs of both species *in copula* with their correct males in the same sample. These two species occur together in their native range, suggesting that this inter-species copulation is not a result of an artificial introduction effect and may result in hybrids if there is not a post-fertilization barrier in place.

In contrast to *F. microcarpa*, *F. religiosa* has its pollinator present in southern Africa and is reproducing successfully, although not spreading. According to Galil and Eisikowitch (1968), *F. religiosa* is highly unlikely to establish in Israel, because of the contrast in conditions compared with the monsoonal climate of its natural distribution (Galil 1984). This is also likely to be true for much of southern Africa, but in higher rainfall areas *F. religiosa* may be able to colonise areas of natural vegetation. The pollinator has been established in Africa for at least 22 years and to date there is no indication that the host fig is problematic by colonizing new areas.

The presence of adults of three species of African fig wasps in figs from one of the *F. microcarpa* crops sampled in Grahamstown and two different species in crops from Cape Town was unexpected. The three indigenous species recorded in Grahamstown

in 2012 are all associated with the most common native fig tree in the area, *F. burtt-davyi* and comprised the tree's pollinator (*E. bajnathi*), a putative parasitoid of the pollinator (*Sycorctes* sp. indesc. 'dark') and *Otiitesella uluzi*, a species that is closely related to *W. microcarpae* and forms similar galls (Compton 1993). In 2013 two other indigenous African species both associated with *F. burkei* were recorded in Cape Town. The pollinator *Elisabethiella stuckenbergi* was represented by five females and a male in a crop from Grand West, clearly indicating that it was successfully reproducing. The other species, *Sycophila punctum* is a parasitoid, usually of indigenous epichryosomal-line *Lachaisea* species (Compton & van Noort 1992), but in this crop of *F. microcarpa* would have probably been parasitizing either of the two introduced epichrysoallines, *O. corneri* or *O. galili*, and hence is able to use hosts from different genera. All these local species were present in tiny numbers, but these records nonetheless show that fig wasps can be capable of successfully galling and completing their development in a *Ficus* species that is only distantly-related to their normal host (*F. burtt-davyi* and *F. burkei* are placed in *Ficus* subgenus *Urostigma*, section *Galoglychia*, whereas *F. microcarpa* is placed in subgenus *Urostigma*, section *Urostigma*).

ACKNOWLEDGEMENTS

SVN was funded by South African National Research Foundation grants: GUN 2068865; GUN 61497; GUN 79004; GUN 79211; GUN 81139. RW was supported by the China Scholarship Council.

REFERENCES

- AHMED, S., COMPTON, S.G., BUTLIN, R.K. & GILMARTIN, P.M. 2009. Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences of the USA* **106**: 20342–20347. (doi:10.1073/pnas.0902213106)
- BEARDSLEY, J.W. 1998. Chalcid wasps (Hymenoptera: Chalcidoidea) associated with fruit of *Ficus microcarpa* in Hawai'i. *Proceedings of the Hawaiian Entomological Society* **33**: 19–34.
- BERG, C.C. & CORNER, E.J.H. 2005. Moraceae – *Ficus*. In: *Flora Malesiana Series I (Seed Plants)*. Vol. 17, part 2. Leiden: National Herbarium of the Netherlands.
- BOUČEK, Z. 1988. *Australian Chalcidoidea (Hymenoptera): A biosystematic revision of genera and fourteen families, with a reclassification of species*. Wallingford, UK: CAB International Institute of Entomology.
- 1993. The genera of chalcidoid wasps from *Ficus* fruit in the New World. *Journal of Natural History* **27**: 173–217.
- BUFFINGTON, M.L., BURKS, R. & MCNEIL, L. 2005. Advanced techniques for imaging microhymenoptera. *American Entomologist* **51**: 50–54.
- BUFFINGTON, M.L. & GATES, M. 2009. Advanced imaging techniques II: using a compound microscope for photographing point-mount specimens. *American Entomologist* **54**: 222–224.
- BURROWS, J. & BURROWS, S. 2003. *Figs of southern & south-central Africa*. Hatfield: Umdaus Press.
- CHEN, Y.R., CHUANG, W.C. & WU, W.J. 1999. Chalcid wasps on *Ficus microcarpa* L. in Taiwan (Hymenoptera: Chalcidoidea). *Journal of Taiwan Museum* **52**: 39–79.
- CHEN, Y., COMPTON, S.G., LIU, M. & CHEN, X.-Y. 2012. Fig trees at the northern limit of their range: the distributions of cryptic pollinators indicate multiple glacial refugia. *Molecular Ecology* **21**: 1687–1701. (doi:10.1111/j.1365-294X.2012.05491.x)
- COMPTON, S.G. 1989. The Fig Wasp, *Odontofroggata galili* (Hymenoptera: Pteromalidae), in the Greek Isles. *Entomologist's Gazette* **40**: 183–184.
- 1990. A collapse of host specificity in some African fig wasps. *South African Journal of Science* **86**: 39–40.
- 1993. One way to be a fig. *African Entomology* **1**: 151–158.
- COMPTON, S.G., GREHAN, K. & VAN NOORT, S. 2009. A fig crop pollinated by three or more species of agaonid fig wasps. *African Entomology* **17**: 215–222.
- COMPTON, S.G., HOLTON, K.C., RASHBROOK, V.K., VAN NOORT, S., VINCENT, S.L. & WARE, A.B. 1991. Studies of *Ceratosolen galili*, a non-pollinating agaonid fig wasp (Hymenoptera, Agaonidae). *Biotropica* **23**: 188–194.

- COMPTON, S.G., THORNTON, I.W.B., NEW, T.R. & UNDERHILL, L. 1988. The colonisation of Krakatau by fig wasps and other chalcids. *Philosophical Transactions of the Royal Society of London, Series B* **322**: 459–470.
- COMPTON, S.G. & VAN NOORT, S. 1992. Southern African fig wasps (Hymenoptera: Chalcidoidea): resource utilization and host relationships. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C* **95**: 423–435.
- COMPTON, S.G., VAN NOORT, S., MCLEISH, M., DEEBLE, M. & STONE, V. 2009. Sneaky African fig wasps that oviposit through holes drilled by other species. *African Natural History* **5**: 9–15.
- CONDIT, I.J. 1969. *Ficus: The exotic species*. Berkeley, California: University of California.
- COOK, J.M. & RASPLUS, J.-Y. 2003. Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology and Evolution* **18**: 241–248.
- COOK, J.M. & SEGAR, S.T. 2010. Speciation in fig wasps. *Ecological Entomology* **35**: 54–66.
- CORNILLE, A., UNDERHILL, J.G., CRUAUD, A., HOSSAERT-MCKEY, M., JOHNSON, S.D., TOLLEY, K.A., KJELLBERG, F., VAN NOORT, S. & PROFFIT, M. 2012. Floral volatiles, pollinator sharing and diversification in the fig-wasp mutualism: insights from *Ficus natalensis* and its two wasp pollinators (South Africa). *Proceedings of the Royal Society B* **279**: 1731–1739. (doi:10.1098/rspb.2011.1972)
- CRUAUD, A., COOK, J., DA-RONG, Y., GENSON, G., JABBOUR-ZAHAB, R., KJELLBERG, F., PEREIRA, R.A.S., RØNSTED, N., SANTOS-MATTOS, O., SAVOLAINEN, V., UBADILLAH, R., VAN NOORT, S., YAN-QIONG, P. & RASPLUS, J.-Y. 2011a. Fig-fig wasp mutualism, the fall of the strict cospeciation paradigm? *In*: Patiny, S., ed., *Evolution of plant-pollinator relationships*. Cambridge: Cambridge University Press, pp. 68–102.
- CRUAUD, A., JABBOUR-ZAHAB, R., GENSON, G., KJELLBERG, F., KOBMOO, N., VAN NOORT, S., DA-RONG, Y., YAN-QIONG, P., UBADILLAH, R., HANSON, P.E., SANTOS-MATTOS, O., FARACHE, F.H.A., PEREIRA, R.A.S., KERDELHUÉ, C. & RASPLUS, J.-Y. 2011b. Phylogeny and evolution of life-history strategies in Sycophaginae non-pollinating fig wasps (Hymenoptera, Chalcidoidea). *BMC Evolutionary Biology* **11**: Art. 178. (doi:10.1186/1471-2148-11-178)
- DOĞANLAR, M. 2012. Occurrence of fig wasps (Hymenoptera: Chalcidoidea) in *Ficus caria* and *F. microcarpa* in Hatay, Turkey. *Turkish Journal of Zoology* **36** (5): 721–724.
- EARLY, J.W. 2000. Fig wasps (Hymenoptera: Agaonidae and Torymidae) in New Zealand. *New Zealand Entomologist* **23**: 27–32.
- ERASMUS, J.C., VAN NOORT, S., JOUSSELIN, E. & GREEFF, J.M. 2007. Molecular phylogeny of fig wasp pollinators (Agaonidae, Hymenoptera) of *Ficus* section *Galoglychia*. *Zoologica Scripta* **36**: 61–78. (doi:10.1111/j.1463-6409.2007.00259.x)
- FARACHE, F.H.A., DO Ó, V.T. & PEREIRA, R.A.S. 2009. New occurrence of non-pollinating fig wasps (Hymenoptera: Chalcidoidea) in *Ficus microcarpa* in Brazil. *Neotropical Entomology* **38** (5): 683–685.
- FENG, G. & HUANG, D.W. 2010. Description of a new species of *Odontofroggatia* (Chalcidoidea, Epichrysomallinae) associated with *Ficus microcarpa* (Moraceae) with a key to species of the genus. *Zootaxa* **2335**: 40–48.
- GALIL, J. 1984. *Ficus religiosa* L. – the tree-splitter. *Botanical Journal of the Linnean Society* **88**: 185–203. (doi:10.1111/j.1095-8339.1984.tb01570.x)
- GALIL, J. & COPLAND, J.W. 1981. *Odontofroggatia galili* Wiebes in Israel, a primary fig wasp of *F. microcarpa* L. with a unique ovipositor mechanism (Epichrysomallinae, Chalcidoidea). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C* **84**: 183–195.
- GALIL, J. & EISIKOWITZ, D. 1968. On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* **18**: 356–363.
- GARDNER, R.O. & EARLY, J.W. 1996. The naturalisation of banyan figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera: Agaonidae) in New Zealand. *New Zealand Journal of Botany* **34**: 103–110.
- HAINÉ, E.R., MARTIN, J. & COOK, J.M. 2006. Deep mtDNA divergences indicate cryptic species in a fig pollinating wasp. *BMC Evolutionary Biology* **6**: Art. 83 [1–11]. (doi:10.1186/1471-2148-6-83)
- HERRE, E.A., JANDER, K.C. & MACHADO, C.A. 2008. Evolutionary ecology of figs and their associates: recent progress and outstanding puzzles. *Annual Review of Ecology, Evolution and Systematics* **39**: 439–458.
- HYDE, M.A., WURSTEN, B.T. & BALLINGS, P. 2012. Flora of Zimbabwe: Species information: Records of: *Ficus religiosa*. www.zimbabweflora.co.zw/speciesdata/species-display.php?species_id=167380 (retrieved 31.x.2012).
- ISHII, T. 1934. Fig chalcidoids of Japan. *Kontyû* **8**: 84–100.
- JANZEN, D.H. 1979. How to be a fig. *Annual Review of Ecology and Systematics* **10**: 13–51.
- KERDELHUÉ, C., HOCHBERG, M.E. & RASPLUS, J.-Y. 1997. Active pollination of *Ficus sur* by two sympatric fig wasp species in West Africa. *Biotropica* **29**: 69–75. (doi:10.1111/j.1744-7429.1997.tb00007.x)

- KERDELHUÉ, C., LE CLAINCHE, I. & RASPLUS, J.-Y. 1999. Molecular phylogeny of the *Ceratosolen* species pollinating *Ficus* of the subgenus *Sycomorus* sensu stricto: biogeographical history and origins of the species-specificity breakdown cases. *Molecular Phylogenetics and Evolution* **11**: 401–414. (doi:10.1006/mpev.1998.0590)
- KERDELHUÉ, C. & RASPLUS, J.-Y. 1996. Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* **75**: 3–14.
- KERDELHUÉ, C., ROSSI, J.-P. & RASPLUS, J.-Y. 2000. Comparative community ecology studies on Old World figs and fig wasps. *Ecology* **81**: 2832–2849.
- KERR, P., FISHER, E. & BUFFINGTON, M.L. 2009. Dome lighting for insect imaging under a microscope. *American Entomologist* **54**: 198–200.
- KOBBI, M., CHAIEB, M., EFELIN, C. & MICHALOUD, G. 1996. Relationship between a mutualist and a parasite of the laurel fig, *Ficus microcarpa*. *Canadian Journal of Zoology* **74**: 1831–1833.
- KOBMOO, N., HOSSAERT-MCKEY, M., RASPLUS, J.-Y. & KJELLBERG, F. 2010. *Ficus racemosa* is pollinated by a single population of a single agaonid wasp species in continental South-East Asia. *Molecular Ecology* **19**: 2700–2712. (doi:10.1111/j.1365-294X.2010.04654.x)
- KOPONEN, M. & ASKEW, R.R. 2002. Chalcids from Madeira, Canary Islands and Azores (Hymenoptera, Chalcidoidea). *Vieraea* **30**: 112–117.
- LI, Z., XIAO, H. & HUANG, D.W. 2013. *Sirovena* Bouček (Pteromalidae: Pireninae), a new member of the fig wasp community associated with *Ficus microcarpa* (Moraceae). *Zootaxa* **3619** (5): 581–588. (doi:10.11646/zootaxa.3619.5.7)
- LO VERDE, G. & PORCELLI, F. 2010. First record of the non-pollinating fig wasp *Odontofroggattia galili* Wiebes, 1980 from Malta (Hymenoptera, Chalcidoidea, Agaonidae). *Bulletin of the Entomological Society of Malta* **3**: 5–8.
- LO VERDE, G., PORCELLI, F., BELLA, S. & RASPLUS, J.-Y. 2007. Imenotteri agaonidi nuovi per l'Europa e loro ruolo nella naturalizzazione di *Ficus* spp. in Italia. *Proceedings of XXI Congresso Nazionale Italiano di Entomologia, Campobasso, 11–16 giugno 2007*. P. 60.
- LO VERDE, G., PORCELLI, F. & SINACORI, A. 1991. Presenza di *Parapristina verticillata* (Waterst.) e *Odontofroggattia galili* Wiebes (Hymenoptera: Chalcidoidea Agaonidae) in Sicilia. *Atti XVI Congresso Nazionale Italiano di Entomologia, Bari-Martina Franca, Italy, 23–28 settembre 1991*. P. 139–143.
- LOPEZ-VAAMONDE, C., DIXON, D.J., COOK, J. & RASPLUS, J.-Y. 2002. Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host-plant associations. *Zoological Journal of the Linnean Society* **136**: 637–683. (doi:10.1046/j.1096-3642.2002.00040.x)
- MA, Y.-C., PENG, Y.-Q. & YANG, D.-R. 2013. Description of two new species of *Walkerella* (Pteromalidae, Otitesellinae) from China with a key to species of the genus. *Zootaxa* **3702**: 473–482.
- MACHADO, C.A., ROBBINS, N., GILBERT, M.T.P. & HERRE, E.A. 2005. Critical review of host specificity and its coevolutionary implications in the fig/fig-wasp mutualism. *Proceedings of the National Academy of Sciences of the USA* **102**: 6558–6565. (doi:10.1073/pnas.0501840102)
- MARUSSICH, W.A. & MACHADO, C.A. 2007. Host-specificity and coevolution among pollinating and non-pollinating New World fig wasps. *Molecular Ecology* **16**: 1925–1946. (doi:10.1111/j.1365-294X.2007.03278.x)
- MAYR, G. 1885. Feigeninsecten. *Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien* **35**: 147–250.
- MCKEY, D. 1989. Population biology of figs; applications for conservation. *Experientia* **45**: 661–673.
- MCLEISH, M.J., BEUKMAN, G., VAN NOORT, S. & WOSSLER, T.C. 2012. Host-plant species conservatism and ecology of a parasitoid fig wasp genus (Chalcidoidea; Sycoryctinae; *Arachonia*). *PLoS ONE* **7** (9): e44804 [1–13]. (doi:10.1371/journal.pone.0044804)
- MCLEISH, M.J. & VAN NOORT, S. 2012. Codivergence and multiple host species use by fig wasp populations of the *Ficus* pollination mutualism. *BMC Evolutionary Biology* **12**: Art. 1 [1–12]. (doi:10.1186/1471-2148-12-1)
- MICHALOUD, G., CARRIERE, S. & KOBBI, M. 1996. Exceptions to the one:one relationship between African fig trees and their fig wasp pollinators: possible evolutionary scenarios. *Journal of Biogeography* **23**: 513–520.
- MICHALOUD, G., MICHALOUD-PELLETIER, S., WIEBES, J.T. & BERG, C.C. 1985. The co-occurrence of two pollinating species of fig wasp on one species of fig. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C* **88**: 93–119.
- MOE, A.M., ROSSI, D.R. & WEIBLEN, G.D. 2011. Pollinator sharing in dioecious figs (*Ficus*: Moraceae). *Biological Journal of the Linnean Society* **103**: 546–558. (doi:10.1111/j.1095-8312.2011.01669.x)
- MOE, A.M. & WEIBLEN, G.D. 2010. Molecular divergence in allopatric *Ceratosolen* (Agaonidae) pollinators of geographically widespread *Ficus* (Moraceae) species. *Annals of the Entomological Society of America* **103**: 1025–1037.

- MOLBO, D., MACHADO, C.A., SEVENSTER, J.G., KELLER, L. & HERRE, E.A. 2003. Cryptic species of fig-pollinating wasps: implications for the evolution of the fig–wasp mutualism, sex allocation, and precision of adaptation. *Proceedings of the National Academy of Sciences of the USA* **100**: 5867–5872. (doi:10.1073/pnas.0930903100)
- NADEL, H., FRANK, J.H. & KNIGHT, R.J. 1992. Escapees and accomplices: The naturalization of exotic *Ficus* and their associated faunas in Florida. *Florida Entomologist* **75**: 29–38.
- NARENDHAN, T.C. & SHEELA, S. 1993. Descriptions of an interesting new genus and a new species of Epi-chrysomallinae (Hymenoptera: Agaonidae) from India. *Journal of the Zoological Society of Kerala* **3** (1): 7–12.
- NEVES, L.J. & ISAIAS, R.M.S. 1987. Ocorrência de agente galhador em flores de *Ficus microcarpa* L. *Bradea* **4**: 327–330.
- PEMBERTON, C.E. 1939. Note on introduction and liberation of *Eupristina verticillata* Waterston in Honolulu. *Proceedings of the Hawaiian Entomological Society* **10**: 182.
- PENG, Y.-Q., DUAN, Z.-B., YANG, D.-R. & RASPLUS, J.-Y. 2008. Co-occurrence of two *Eupristina* species on *Ficus altissima* in Xishuangbanna, SW China. *Symbiosis* **45**: 9–14.
- RAMÍREZ, W.B. 1970. Host specificity of fig wasps (Agaonidae). *Evolution* **24**: 680–691.
- 1994. Hybridization of *Ficus religiosa* with *F. septica* and *F. aurea* (Moraceae). *Revista de Biología Tropical* **42**: 339–342.
- RAMÍREZ, W.B. & MONTERO, J. 1988. *Ficus microcarpa* L., *F. benjamina* L., and other species introduced in the New World, their pollinators (Agaonidae) and other fig wasps. *Revista de Biología Tropical* **36**: 441–446.
- RASPLUS, J.-Y. 1996. The one-to-one species specificity of the *Ficus*–Agaoninae mutualism: how casual? In: van der Maesen, L.J.G., van der Burgt, X.M. & van Medenbachde Rooy, J.M., eds., *The biodiversity of African plants*. Dordrecht, The Netherlands: Kluwer Academic, pp. 639–649.
- RASPLUS, J.-Y., KERDELHUÉ, C., LE CLAINCHE, I. & MONDOR, G. 1998. Molecular phylogeny of fig wasps. Agaonidae are not monophyletic. *Compte Rendu de l'Academie des Sciences de Paris* **321**: 517–526.
- RASPLUS, J.-Y., VILLEMANT, C., PAIVA, M.R., DELVARE, G. & ROQUES, A. 2010. Hymenoptera. Chapter 12. In: Roques, A. *et al.*, eds., *Arthropod invasions in Europe*. *BioRisk* **4**: 669–776. (doi:10.3897/biorisk.4.55)
- STANGE, L.A. & KNIGHT, R.J. 1987. Fig pollinating wasps of Florida (Hymenoptera: Agaonidae). *Division of Plant Industry, Florida Department of Agriculture & Consumer Services, Gainesville, Entomology Circular* **296**: 1–4.
- SUN, X.-J., XIAO, J.-H., COOK, J.M., FENG, G. & HUANG, D.-W. 2011. Comparisons of host mitochondrial, nuclear and endosymbiont bacterial genes reveal cryptic fig wasp species and the effects of *Wolbachia* on host mtDNA evolution and diversity. *BMC Evolutionary Biology* **11**: Art. 86 [1–8]. (doi:10.1186/1471-2148-11-86)
- TAN, H.T.W., YEO, C.K. & NG, A.B.C. 2009. *Native and naturalised biodiversity for Singapore waterways and water Bodies No. 1. Ficus microcarpa, Malayan Banyan*. Singapore: Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore & Singapore-Delft Water Alliance. http://rmbr.nus.edu.sg/raffles_museum_pub/ficus_microcarpa.pdf (accessed 10.ix.2013).
- VAN NOORT, S. 2003. Fig wasps and the pollination of figs. In: Burrows, J. & Burrows, S., eds., *Figs of southern & south-central Africa*. Hatfield: Umdaus Press, pp. 12–21.
- VAN NOORT, S. & COMPTON, S.G. 1988. Two new species of *Otitesella* (Hymenoptera, Chalcidoidea, Pteromalidae) from *Ficus burtt-davyi*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C* **91**: 419–427.
- VAN NOORT, S. & RASPLUS, J.-Y. 2010. Order Hymenoptera, Chalcidoidea associated with figs (families Agaonidae & Pteromalidae). In: van Harten, A., ed., *Arthropod fauna of UAE*. Vol. 3. Sharjah, UAE: UAE Insect Project, pp. 325–355.
- VAN ZWALUWENBURG, R.H. 1940. Note on *Eupristina verticillata* Waterston on Kauai. *Proceedings of the Hawaiian Entomological Society* **10**: 362.
- WARE, A.B. & COMPTON, S.G. 1992. Breakdown of pollinator specificity in an African fig tree. *Biotropica* **24**: 544–549.
- WEIBLEN, G.D. 2002. How to be a fig wasp. *Annual Review of Entomology* **47**: 299–330. (doi:10.1146/annurev.ento.47.091201.145213)
- WIEBES, J.T. 1967. Redescription of Sycophaginae from Ceylon and India, with designation of lectotypes, and a world catalogue of the Otitesellini (Hymenoptera, Chalcidoidea, Torymidae). *Tijdschrift voor Entomologie* **110**: 399–442.
- 1979. Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics* **10**: 1–12.

- 1980. The genus *Odontofroggattia* Ishii (Hymenoptera, Chalcidoidea, Pteromalidae, Epichrysomallinae). *Zoologische Mededelingen Leiden* **56** (1): 1–6.
- 1989. Agaonidae (Hymenoptera: Chalcidoidea) and *Ficus* (Moraceae) fig wasps and their figs. III. *Elizabethiella*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen C* **92**: 127–129.
- WILLIAMS, F.X. 1939. Note on *Eupristina verticillata* Waterston, first recovery on Oahu. *Proceedings of the Hawaiian Entomological Society* **10**: 194.
- WOHLFARTER, M., GILLOMEE, J.H., VENTER, E. & STOREY, S. 2011. A survey of the arthropod pests and plant parasitic nematodes associated with commercial figs, *Ficus carica* (Moraceae), in South Africa. *African Entomology* **19**: 165–172.
- XU, L., YANG, D.-R., PENG, Y.-Q. & WEI, Z.-D. 2005. *Ficus* and the wasp community within syconia in Xishuangbanna. *Forest Research* **18**: 497–503.
- YOKOYAMA, J. 1996. The occurrence of *Eupristina* (*Parapristina*) *verticillata* Waterston (Hymenoptera, Agaonidae) in the Bonin Islands. *Japanese Journal of Entomology* **64**: 91–92.
- YOKOYAMA, J. & IWATSUKI, K. 1998. A faunal survey of fig-wasps (Chalcidoidea: Hymenoptera) distributed in Japan and their associations with figs (*Ficus*: Moraceae). *Entomological Science* **1**: 37–46.
- ZHANG, R. & XIAO H. 2008. A new species of the genus *Acophila* on *Ficus microcarpa* L. from China (Hymenoptera, Agaonidae). *Acta zootaxonomica sinica* **33**: 505–507.