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

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

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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 baijnathi*, *E. stuckenbergi*), a galler (*Otitesella 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 (*Odontofroggatia corneri*, *Odontofroggatia galili* and *Walkerella microcarpae*), and a fourth native species has expanded its host range and is developing as a parasitoid of the *Odontofroggatia* species (*Sycophila punctum*). In contrast, the Asian pollinator of *F. religiosa* (*Platyscapa quadraticeps*) 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.* 2011*b*; 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.

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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: *Odontofroggatia galili* Wiebes (Pteromalidae: Epichrysomallinae) and *Walkerella microcarpae* Bouček (Pteromalidae: Otitesellinae). *Odontofroggatia 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). *Odontofroggatia* 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. *Odontofroggatia 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, *Odontofroggatia 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.* 2011*a*; 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 (Ramírez 1970; Ramírez

& 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

Odontofroggatia 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).

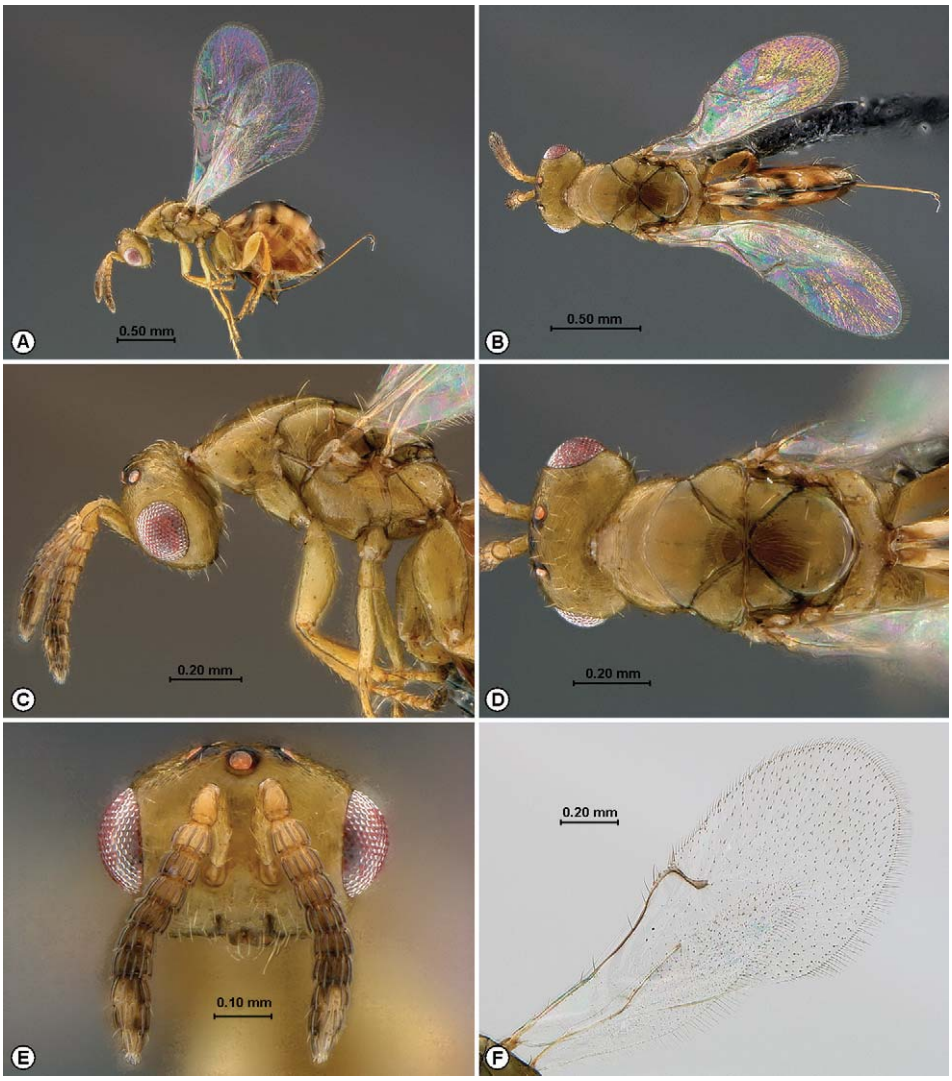

Fig. 1. *Odontofroggatia corneri* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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).

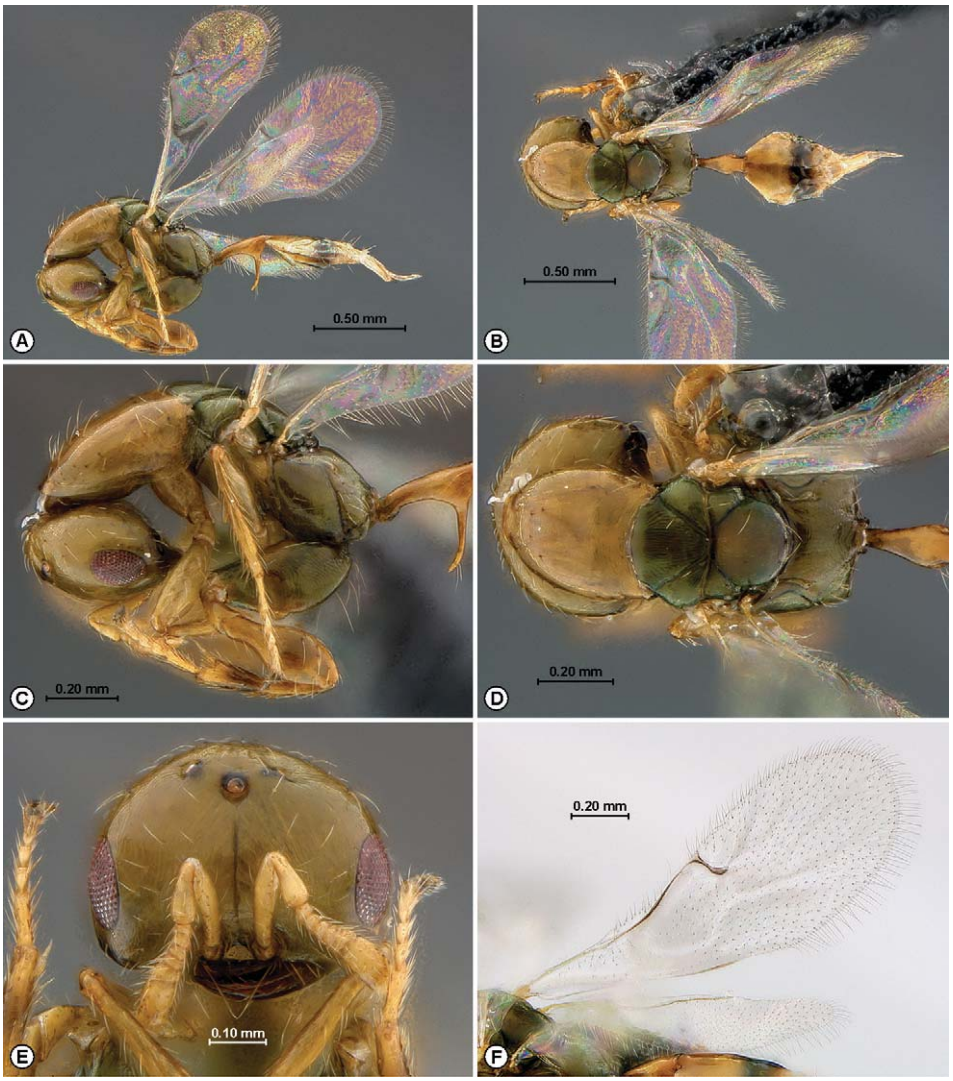

Fig. 2. *Odontofroggatia corneri* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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,

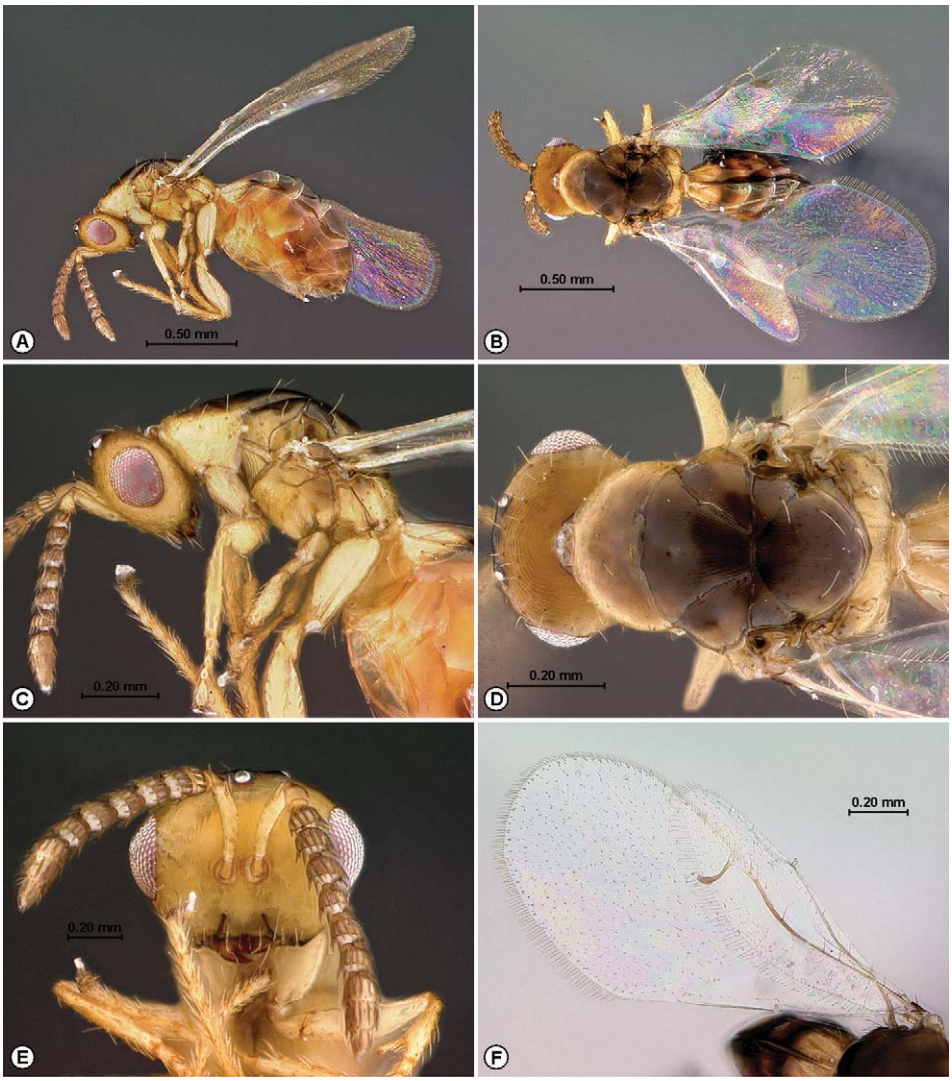

Fig. 3. *Odontofroggatia galili* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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*

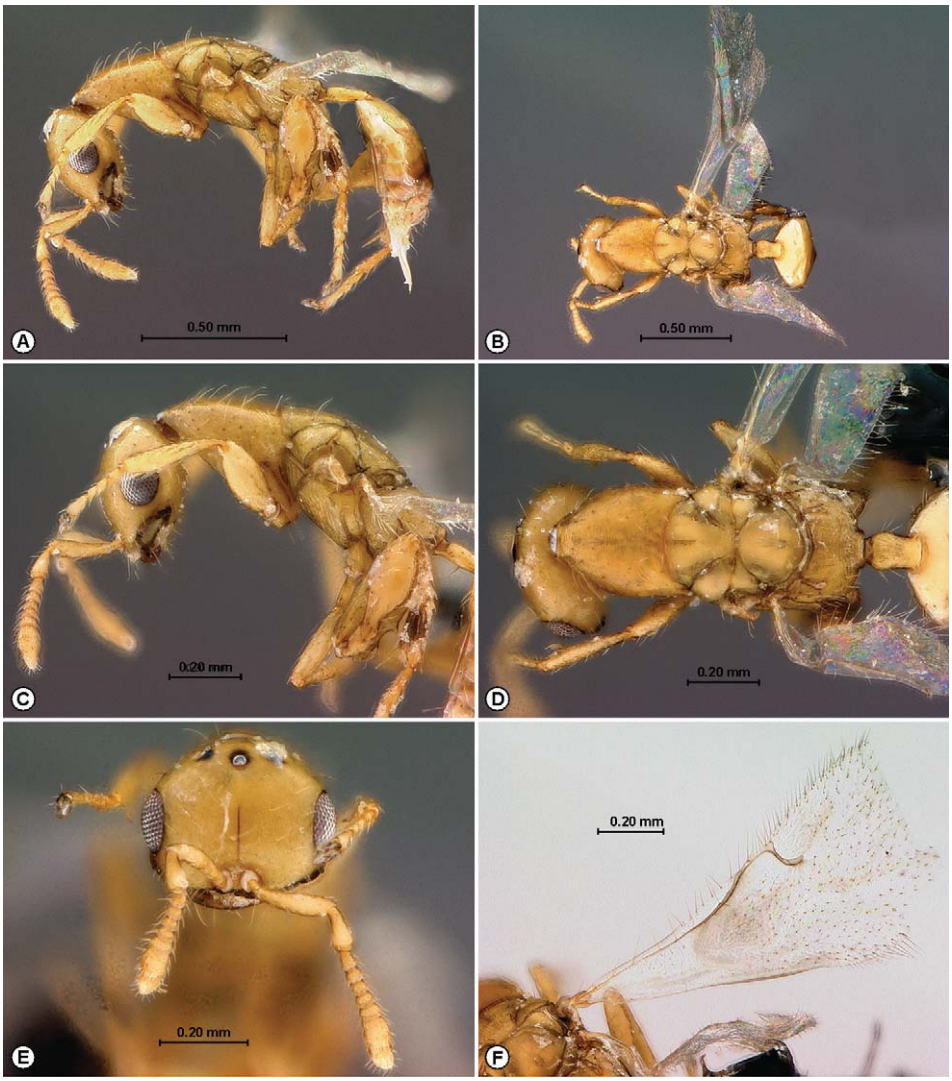

Fig. 4. *Odontofroggatia galili* male: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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,

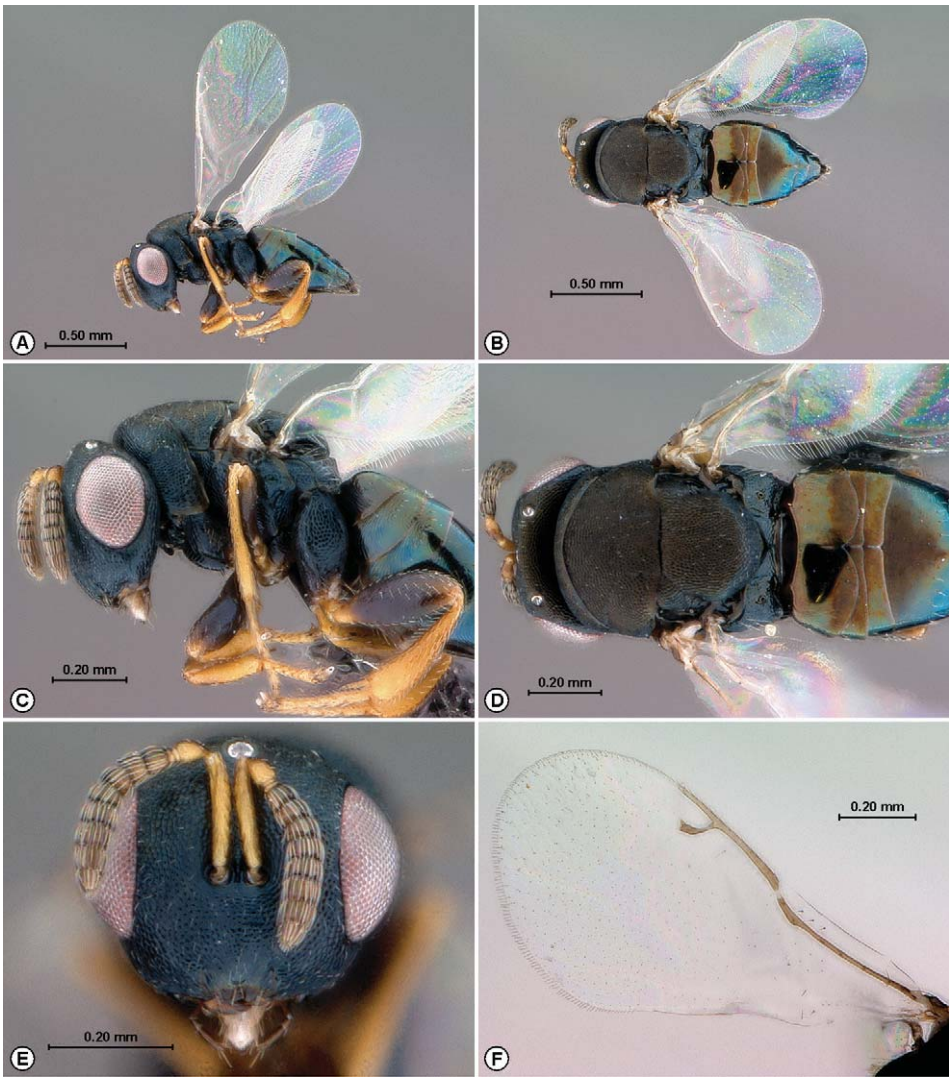

Fig. 5. *Walkerella microcarpae* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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.

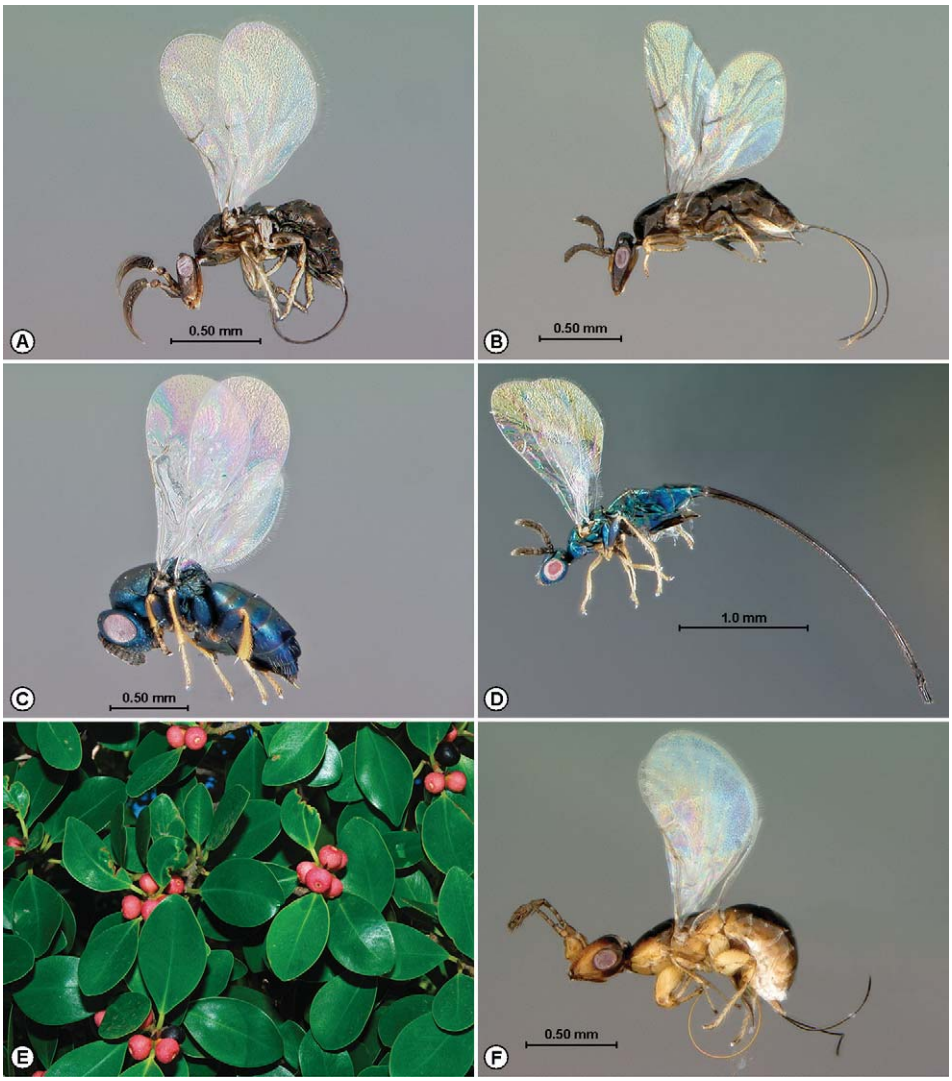

Fig. 7. (A–D) African fig wasps reared from introduced *Ficus microcarpa*: (A) *Elisabethiella baijnathi* female, lateral habitus; (B) *Elisabethiella stuckenbergi* female, lateral habitus; (C) *Otitesella uluzi* female, lateral habitus; (D) *Sycorcytes* species, lateral habitus; (E) *F. microcarpa*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

Introduced fig wasps associated with Ficus religiosa

Family Agaonidae Walker, 1871

Platyscapa 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).

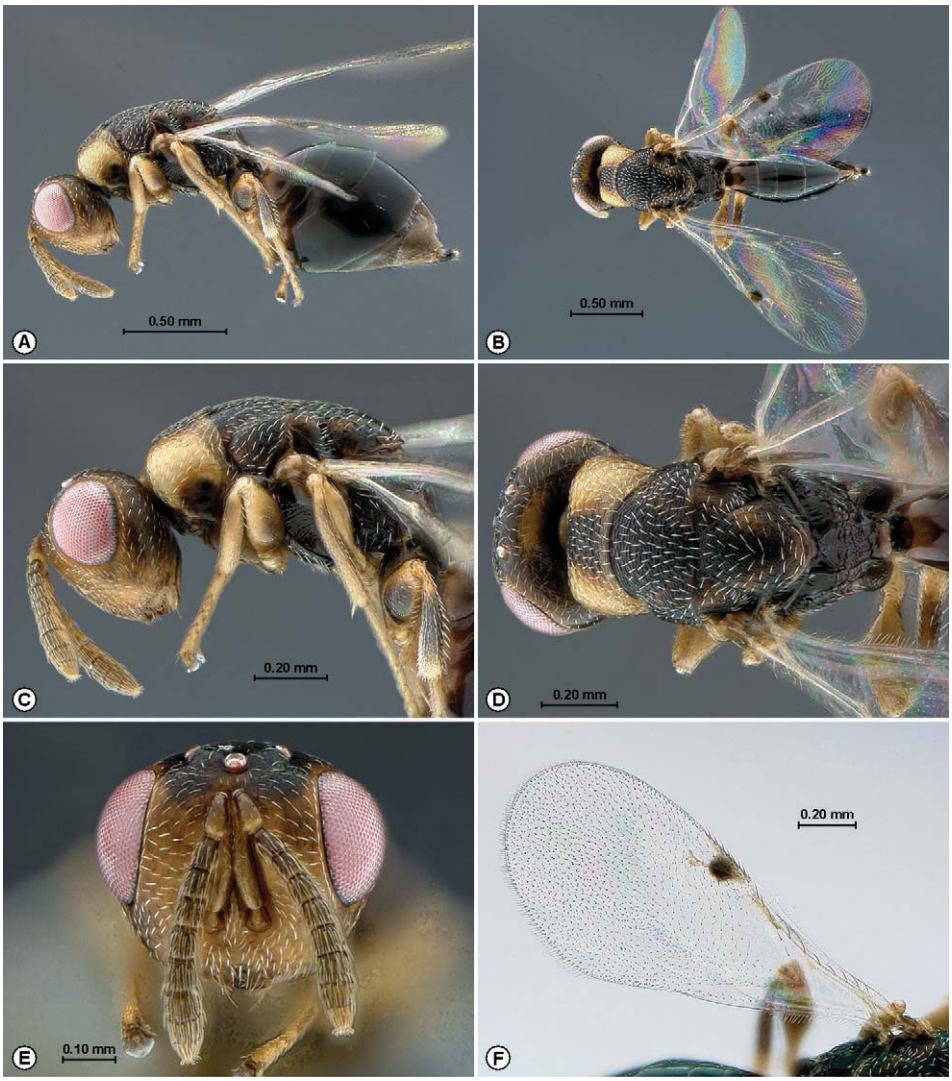

Fig. 8. *Sycophila punctum* female: (A) lateral habitus; (B) dorsal habitus; (C) head and mesosoma, lateral view; (D) head and mesosoma, dorsal view; (E) head, anterior view; (F) wings.

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 galler species associated with *Ficus microcarpa*, *Walkerella microcarpae* and *Odontofroggatia 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. *Odontofroggatia 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, *Odontofroggatia 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. *Odontofroggatia 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. baijnathi*), a putative parasitoid of the pollinator (*Sycorctes* sp. indesc. 'dark') and *Otitesella 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 epichrysomalline *Lachaisea* species (Compton & van Noort 1992), but in this crop of *F. microcarpa* would have probably been parasitizing either of the two introduced epichrysomallines, *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*).

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