Sneaky African fig wasps that oviposit through holes drilled by other species

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Watshamiella Wiebes species (Hymenoptera: Chalcidoidea: Pteromalidae: Sycoryctinae) were observed to engage, monitor and subsequently use oviposition holes made by other parasitoid fig wasp genera (*Apocrypta* Coquerel and *Sycoryctes* Mayr) to oviposit into host figs (Moraceae, *Ficus*) through the fig wall. They may be inquilines, klepto-parasitoids, or hyper-parasitoids; however, further biological investigations of larval diet are required to establish their life history strategy. *Watshamiella* species are morphologically robust, with enlarged fore femora and tibia, and aggressively interact with other fig wasps and ants. Our observations contribute towards unravelling the complex suite of behavioural adaptations and interactions involved in the community ecology of the obligate mutualism that exists between fig wasps and their host figs.

Key words: behaviour, biology, inquiline, parasitoid, ecology, *Ficus,* fig wasp, Sycoryctinae.

CONTENTS

INTRODUCTION

The mutualistic relationship between fig trees (*Ficus* spp., Moraceae) and their fig wasp pollinators (Hymenoptera, Agaonidae, Agaoninae) is well known (Janzen 1979; Weiblen 2002). Fig trees are distinguished by their unique inflorescences (figs) that have the form of a hollow ball, lined on the inside by tens, hundreds or thousands of tiny flowers. The only means of entry to the flowers is *via* a narrow, bract-lined hole, the ostiole, through which pollinator fig wasps must crawl in order to lay their eggs and pollinate the flowers. Fig wasp larvae feed on ovules galled by the female fig wasps (Wiebes 1979).

Much less is understood about the biology of non-pollinating fig wasps, twenty or more of which may be associated with each of the 112 species of fig trees in Africa (Berg & Wiebes 1992; Burrows & Burrows 2003; Compton & Hawkins 1992; van Noort & Rasplus 2004–2009). Non-pollinators were grouped within several subfamilies of Agaonidae (Bouček 1988), but this classification has been shown to be paraphyletic (Rasplus *et al*. 1998). The Sycoryctinae, Otitesellinae and Sycoecinae were reassigned to the Pteromalidae. *Watshamiella* Wiebes belongs to the Sycoryctinae, a poorly understood, non-pollinating group of inquilines or parasitoids (Berg & Wiebes 1992; Bouček 1988; Kerdelhué & Rasplus 1996; Tzeng *et al*. 2008). Some of the non-pollinating fig wasps, such as the Sycoecinae, are similar to the pollinators, in that they enter the figs to lay their eggs (Compton & van Noort 1992), but most non-pollinators, including the Sycoryctinae, possess elongate ovipositors, which they use to reach the ovules while standing on the surface of the figs (Kerdelhué & Rasplus 1996). A small number of species in the Epichrysomallinae and Eurytomidae do not utilize the ovules at all, but feed in chambers inside the fig wall, or grossly distort whole figs,

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preventing flower formation (Compton & van Noort 1992). Beyond where their larvae develop, the behaviour of most species has not been observed, but non-pollinators can be broadly divided into those species with larvae that feed on galled ovules (and to varying degrees are independent of the pollinators) and others, including the Sycoryctinae, with larvae that feed inside the galls produced by others, often the pollinator. As the galls are entirely hollowed out, many of these parasitoids may actually be inquilines or klepto-parasites that feed on galled plant material after destroying the gall causers. In general it appears that the genera of fig wasps are consistent in their feeding methods, but the association of life history trait with classification is not always congruent. Recent evidence suggests that a species of *Apocryptophagus* Ashmead, a genus belonging to the galling subfamily Sycophaginae, is in fact an inquiline/parasitoid (Wang & Zheng 2008). Some of the parasitoid species are indiscriminate, killing whichever other fig wasps are available (Compton & Robertson 1988), but at least one group (Eurytomidae) appears to specialize on non-pollinator hosts (Compton 1993). A specialist fig wasp parasitoid that did not target pollinators has also been recorded from Asia (Godfray 1988).

Here we describe the unusual ovipositional behaviour of two species of non-pollinating fig wasp belonging to the genus *Watshamiella*. The first observations were recorded during the production of a natural history film in Kenya and the second in Kibale National Park in Uganda.

MATERIALS AND METHODS

Filming of figs of *Ficus sycomorus* L. took place on Rusinga Island, located on the eastern side of Lake Victoria (00°24.760′S, 034°08.550′E) during November and December 2003. This fig tree is distributed throughout most of Africa, commonly at the sides of rivers and other water bodies. Its figs reach 30–40 mm in diameter and in Eastern Africa are borne in groups on short leafless branches or spurs arising from the trunk and major branches (Berg & Wiebes 1992).

Ficus artocarpoides Warb. is restricted to central Africa (northern Angola to eastern Uganda and west to Guinea) where it is associated with rainforest and gallery forest up to an altitude of 1600 m (Berg & Wiebes 1992; Rasplus *et al*. 2003). The species reaches its eastern limits in Uganda. Figs are borne on spurs on older wood, typically along secondary branches and on the main trunk (Berg & Wiebes 1992). Observations were carried out in August 2008 by S. van Noort and M. McLeish in the vicinity of the Makerere University Biological Field Station (MUBFS) situated in Kibale National Park located in western Uganda. An individual of *Ficus artocarpoides* (UG08-F124) located at 0°33.579′N, 30°21.796′E, at an altitude of 1552 m was observed over a period of a week. Photography of fig wasp behaviour was done *in situ* in the field by S. van Noort using a Nikon D80 and a Nikkor 105 mm macro lens.

RESULTS

Observations on *Ficus sycomorus*

Females of *Apocrypta longitarsus* Mayr were abundant on the surface of the figs. The ovipositor of *Apocrypta* Coquerel species is longer than the rest of the body combined, and it takes several minutes for it to be fully inserted and an egg to be laid. During this period their abdomens are grossly distended, generating a characteristic arched appearance (Abdurahiman & Joseph 1980) and the hind legs are used as a brace to steady the ovipositor as it descends into the fig (Figs 1A,B). *Apocrypta longitarsus* is a parasitoid that destroys the larvae of both pollinators and non-pollinators (Kerdelhué & Rasplus 1996). Because its host's galls vary greatly in size, the adults display an unusually wide variation in body size.

Also present on the figs, at the same time as *A. longitarsus,* were females of an undescribed species of the genus *Watshamiella* with a characteristic black transverse bar on the dorsal surface of the thorax and black bars across the gaster. This genus was erected by Wiebes (in Bouček *et al*. 1981) to accommodate six African and Asian species, but many more species remain to be described. The female *Watshamiella* were active on the surface of the figs, paying close attention to any *A. longitarsus* females that were in the process of ovipositing through the fig wall (Fig. 1A,B). Individual *Watshamiella* females positioned themselves facing drilling *A. longitarsus,* usually standing behind them, but sometimes to one side. While *A. longitarsus* was drilling, some of the waiting *Watshamiella* females moved forward to antennate the point where the ovipositor was penetrating the fig, or antennated its abdomen, but generally they remained relatively static, unless a second *Watshamiella* female came close. If this happened then a host guarding response was generated, with an initial rearing of the forelegs and raising of the wings (Fig. 1C). This was usually followed by an attempt to chase off the second female, which escalated into brief intense fights. No damage to the wasps was observed.

At no time did *A. longitarsus* females show any aggression towards the *Watshamiella* females. Once they had completed oviposition, and moved on, the resident *Watshamiella* immediately walked forward to antennate where *A. longitarsus* had been ovipositing, then further forward until the tip of its ovipositor was approximately over the hole. The tip of the ovipositor was then repeatedly touched onto the surface until the hole was found, whereupon it slowly moved backwards and inserted its ovipositor down the hole. The egg tube became detached from the increasingly curved sheaths (third valvulae), which nonetheless remained in position on the fig surface until about a quarter of the ovipositor had been inserted, after which they were held out behind the fig wasp (Fig. 1D). After two to three minutes, when oviposition was presumably complete, they moved forwards to extricate their ovipositors, and then walked away. If a second *Watshamiella* appeared then the ovipositing female was capable of displaying the same rearing threat behaviour. This did not escalate into a fight.

The film '*The queen of trees*' (released 2005), a Deeble and Stone Production for the BBC, includes footage of the behaviour described here. It is available on DVD through commercial outlets.

Observations on *Ficus artocarpoides*

The tree had a crop of a couple of hundred figs in C-phase development. Less than 10 of these figs at any one time of about 80 figs that were within observational limits were

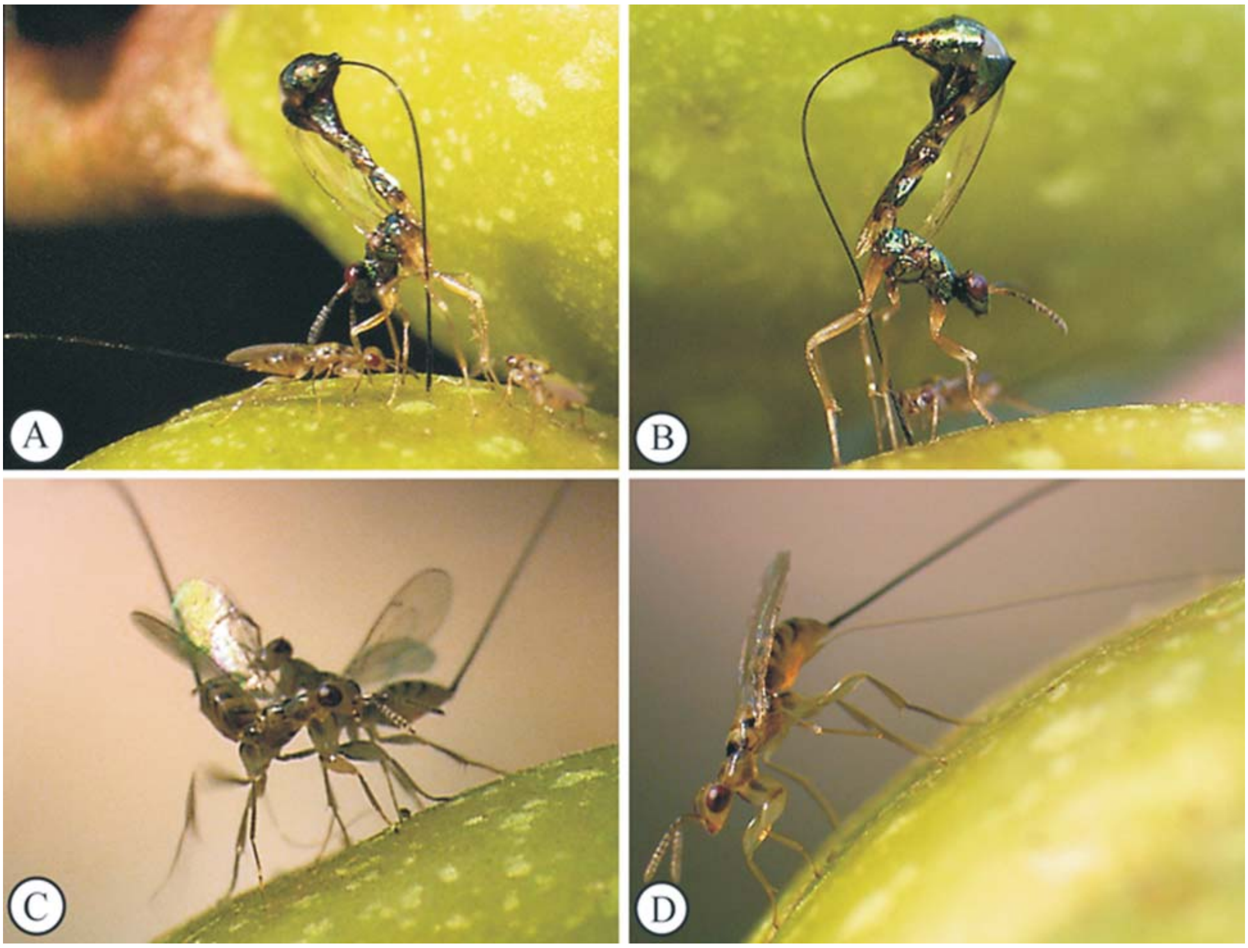

Fig. 1. **A**, Two *Watshamiella* females monitoring a probing *Apocrypta longitarsus* on the surface of a fig of *Ficus sycomorus* on Rusinga Island (Kenya). The *Watshamiella* on the left is examining the point of entry of the *Apocrypta* ovipositor with its antennae. **B**, *Apocrypta longitarsus* probing the surface of the fig, with attendant female *Watshamiella.* **C**, Two *Watshamiella* females fighting over access to an *Apocrypta longitarsus* oviposition site. Note the characteristic raised wings and that one female already has her ovipositor partly inserted. **D**, A *Watshamiella* female with her ovipositor partly inserted down the hole produced by an *Apocrypta longitarsus* female. Note that the ovipositor sheaths have become detached from the egg tube. When the egg tube is first inserted they provide a temporary, increasingly curved, brace at the fig surface.

covered with hundreds of ovipositing *Sycoryctes* Mayr (Fig. 2A). Occasionally single Sycoryc*tes* individuals explored bare figs. *Crematogaster* ants patrolling the tree were attracted to or responded to figs where ovipositing fig wasps were present. The ants moved onto these figs from the main trunk and proceeded to attack the ovipositing fig wasps (Figs 2C,D). In cases where there were 10–20 fig wasp individuals the ants often managed to chase off the wasps (Fig. 2B). In cases where the ovipositing *Sycoryctes* were present in higher densities as in Fig. 2A there was ongoing interaction between wasps and ants, with the wasps aggressively counter-attacking the ants. *Sycoryctes* individuals attacked the ants with their legs and moved around, but always retained their ovipositor inserted into the fig. These warding-off of attacks were sometimes successful, but if sufficient ants concentrated on an individual fig wasp she was overpowered and killed (Figs 2C,D). There were never more than 30 ants on a fig and they remained on the fig surface for some time after successfully chasing away ovipositing wasps (Fig. 2B).

Watshamiella individuals were observed to land on a fig with ovipositing *Sycoryctes* females and then took about 15 seconds to select an ovipositing *Sycoryctes* female. After antennating the ovipositor of the *Sycoryctes* and the oviposition site on the fig surface the *Watshamiella* female positioned herself behind the *Sycoryctes,* where she aggressively guarded her against both marauding ants and other *Watshamiella* individuals (Figs 3A,D). On occasion, when the *Watshamiella* female antennated too aggressively the *Sycoryctes* female responded antagonistically and there was a brief flurry of interaction involving antennae and legs. *Sycoryctes* females took approximately 45 minutes to oviposit from commencement of ovipositor insertion until withdrawal. After the *Sycoryctes* female had moved off, the *Watshamiella* female moved in and identified the oviposition site by antennating the surface of the fig (Fig. 3E). This process took 5–10 seconds after which she turned around and backed towards the oviposition site guiding her ovipositor onto the oviposition hole by tapping it onto the fig surface (Fig. 3F). She then commenced insertion of her ovipositor down the previously drilled hole. It took five minutes for her to completely insert her ovipositor. While in the process of oviposition she defended her site against other approaching fig wasps and ants by 'boxing'

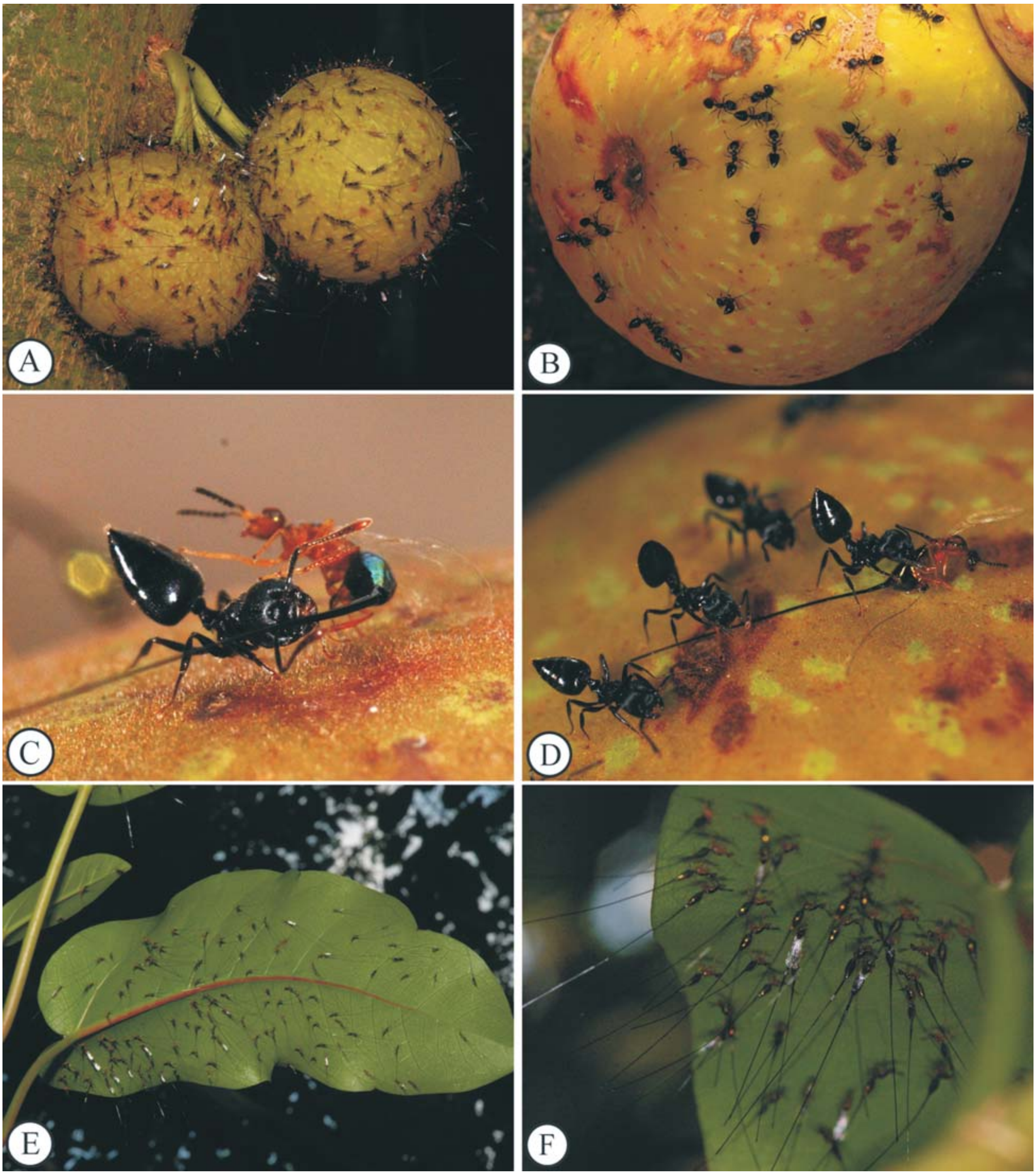

Fig. 2. A, *Sycoryctes* and *Watshamiella* females ovipositing though the exterior wall of *Ficus artocarpoides* figs in Kibale Forest (Uganda). **B**, *Crematogaster* ants patrolling the surface of a *Ficus artocarpoides* fig, excluding fig wasps from ovipositing. **C**, A *Crematogaster* ant attacking a *Sycoryctes* female in the process of oviposition. **D**, *Crematogaster* ants killing the attacked *Sycoryctes.* Note the ovipositor is still inserted in the fig. **E**, *Sycoryctes* and *Watshamiella* females resting under a leaf of *Ficus artocarpoides* within a metre of figs they have recently oviposited in. **F**, Close up of *Sycoryctes* and *Watshamiella* females resting under the leaf.

them with her large expanded fore tibia. Figs 3C,D illustrates the disparity in fore femur and tibial size between *Sycoryctes* and *Watshamiella.* The *Watshamiella* female finished oviposition within 8 minutes and then moved around on the fig searching for another suitable ovipositing *Sycoryctes* female, which she then positioned herself behind and the procedure was repeated.

Female fig wasps clustered underneath leaves of the host fig tree within a metre or so of figs with ovipositing females. These clusters were once again dominated by *Sycoryctes,* but *Watshamiella* females were also present among the *Sycoryctes.* There was some minor jostling but generally the wasps were stationary with their ovipositors hanging downwards away from the leaf surface (Fig. 3E,F).

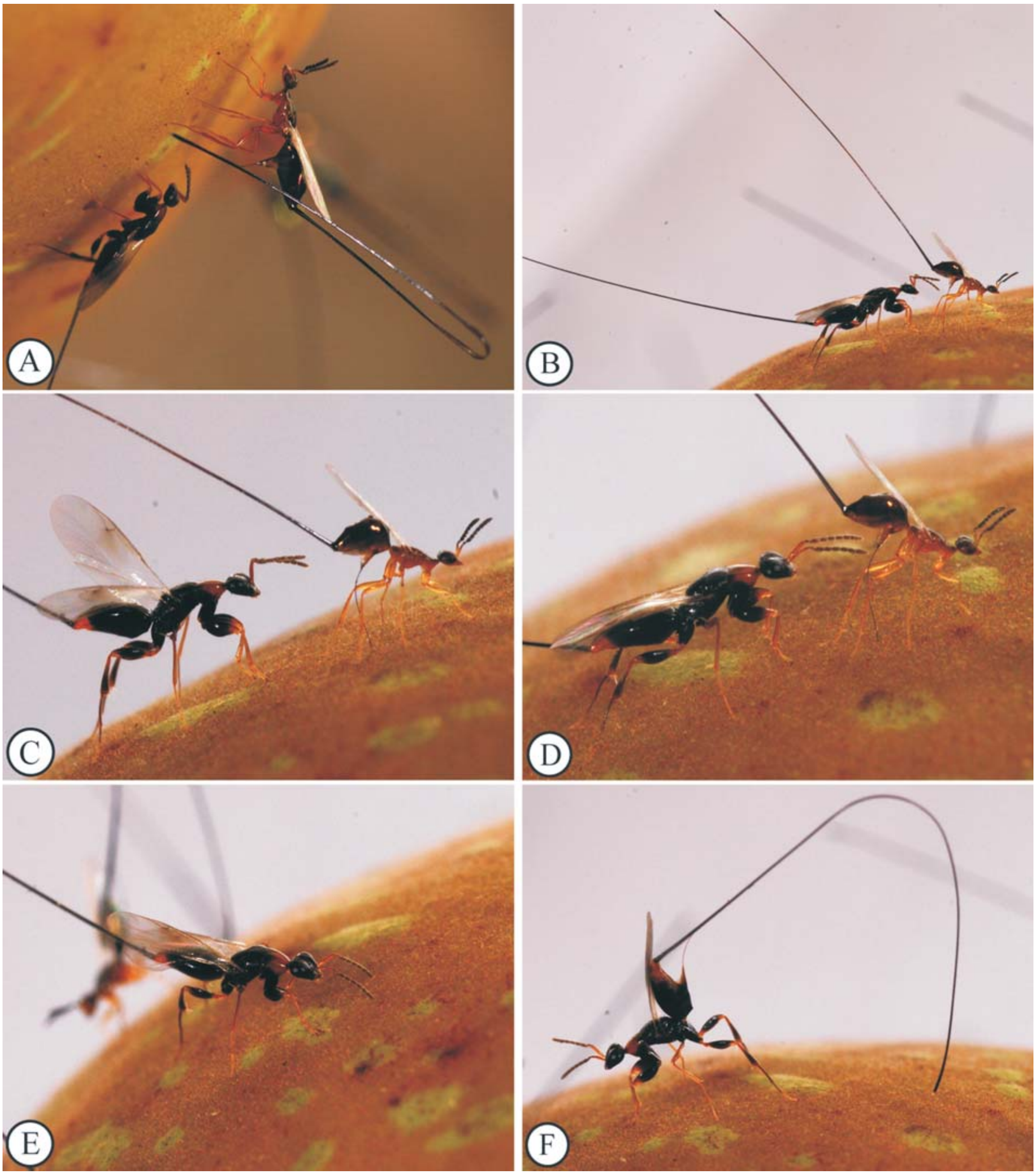

Fig. 3. **A**, A *Watshamiella* female monitoring a probing *Sycoryctes* female. **B**, A *Watshamiella* female monitoring a *Sycoryctes* female in the process of oviposition. **C**, The same *Watshamiella* female guarding the *Sycoryctes* female – she will actively chase off other *Watshamiella* females and predatory ants. **D**, *Watshamiella* female antennating the ovipositing *Sycoryctes*. **E**, *Watshamiella* female antennating the surface of the fig to locate the oviposition hole recently left by the *Sycoryctes*. **F**, *Watshamiella* female ovipositing down the oviposition hole left by the *Sycoryctes*. Careful comparison of the green blotches on the surface of the fig will illustrate that the *Watshamiella* female is ovipositing in the exact position on the fig surface that the *Sycoryctes* was ovipositing at in Fig. 3D (angle of photography is slightly different in the two images).

DISCUSSION

Taking advantage of the holes drilled by another species has several potential rewards for *Watshamiella* species. They can lay their eggs without the specialized musculature and associated structures of fig wasps such as *Apocrypta* or *Sycoryctes* and need not expend the energy that drilling requires. Perhaps more importantly, they spend much less time (8 minutes as opposed to 45 minutes) than *Apocrypta* and *Sycoryctes* with their ovipositor inserted into a fig. Predatory ants routinely patrol the surface of *F. sycomorus, F. artocarpoides* and other figs, capturing unwary fig wasps, and ovipositing individuals are clearly particularly vulnerable (Compton & Robertson 1988). Speed of oviposition, and consequently greater safety from ants, may have been an adaptive advantage of this life history strategy. The larvae devour the contents of the gall, with no plant material ever left behind. This means they are either making use of the galled plant material (most likely) or possibly letting the secondary host grow and then eating it right at the finish. They may be inquilines, klepto-parasitoids, or hyper-parasitoids, but biological mode cannot be confirmed without direct observations of the larval diet. It is possible that although the species are using oviposition holes made by other parasitoid fig wasps they are not true hyper-parasitoids. They could be parasitizing the fig wasp host of the primary parasitoid, but not the parasitoid itself. Since the primary *Sycoryctes* or *Apocrypta* parasitoid has just laid eggs a few minutes before, to be considered as a true hyper-parasitoid *Watshamiella* must oviposit within the egg of the primary parasitoid. Similar oviposition behaviour to that displayed by *Watshamiella* species has been recorded in another species of hymenopteran with hosts deep inside a plant, but not amongst fig wasps (Quicke 1997). *Pseudorhyssa* (Ichneumonidae) is a kleptoparasitoid that makes use of the hole drilled by another ichneumonid, *Rhyssa* to gain access to sawfly larvae. Its larvae hatch quickly and kill both the primary host and the eggs laid by *Rhyssa* (Couturier 1949).

No *Watshamiella* species have been described in association with *Ficus sycomorus* or *F. artocarpoides* (J. Noyes, Universal Chalcidoidea Database: http://www.nhm.ac.uk/research-curation/projects/chalcidoids/), but at least two species are associated with *F. sycomorus* and three species with *F. artocarpoides* (S. Compton, J.Y. Rasplus & S. van Noort, unpublished). The undescribed species on *F. sycomorus* from Uganda is probably the species that is more widespread in southern Africa, having been collected from Botswana, Malawi, South Africa (KwaZulu-Natal and Mpumalanga) and Zambia. The three undescribed species on *F. artocarpoides* (two black and orange species and a yellow species with black markings on the metasoma) are all known from Kibale and one of which is also known from Gabon (J.Y. Rasplus, pers. comm.). Specimens are always rare in collections.

African *Watshamiella* display several unusual features which suggest the biology of the genus as a whole may be atypical. Their ovipositors (including their surrounding sheaths) are delicate in appearance compared with species of *Apocrypta* and *Sycoryctes* and their frequency of occurrence is also unusual in that large collections of figs from a crop that produce hundreds or thousands of other fig wasps often contain just one or two individuals of this genus. Furthermore, males often appear to be rare or entirely lacking, a characteristic that may be unique amongst African fig wasps, although in some cases the sex ratio of reared individuals can be male biased. We reared five alate males and three females of one of the species from *F. artocarpoides* in Uganda; however, the other two species were only represented by females. The genus is genetically more distinct from congeneric Sycoryctinae (*Sycoryctes, Philotrypesis, Sycoscapter*) than these genera are distinct from each other. *Watshamiella,* however, has radiated more recently (last two million years) at species level, than these other sycoryctine genera, which radiated around five million years ago (M. McLeish & S. van Noort & Tolley, in prep.).

Clustering of fig wasps for oviposition on certain figs and not others may result from that particular fig having host fig wasp larvae at a suitable stage of development for parasitism, whereas the others nearby were at too early or too late a stage of development. The parasitoids would then be homing in on the fig via simultaneous response to cues released by the fig. However, the figs on *F. artocarpoides* were synchronized in development, with numerous attempts by *Sycoryctes* females to colonize novel adjacent figs for oviposition. There was a continual back and forward sparring between the fig wasps and the ants to occupy and dominate figs. It thus appears that clustering for oviposition is an adaptive trait to promote protection from predation through aggregation of many individuals. This was clearly demonstrated in our observations on *F. artocarpoides* where ants had little effect in chasing fig wasps off figs once they had reached a certain numerical threshold. It is thus possible that *Sycoryctes* females were responding to cues released by conspecific ovipositing individuals, but this adaptive trait would be counter selected for by competition for host resources. Presumably *Watshamiella* females would also be responding to the same cues. Parasitoid fig wasps had clearly arrived at the host tree in large numbers and were not all engaged in the act of oviposition. The many individuals observed roosting under leaves of the host fig tree while others were ovipositing, were clearly resting, either between oviposition events or simply waiting for a critical threshold to assimilate on a fig before they joined the oviposition party.

CONCLUSIONS

Watshamiella species have adapted a sneaky oviposition strategy to optimize their ovipositional success while reducing their predation exposure. It is likely that all species within the genus will exhibit the same life history strategy. Our observations contribute towards unravelling the complex suite of behavioural adaptations and interactions between participants involved in the community ecology of the obligate mutualism that exists between fig wasps and their host figs, but there are many facets of this fascinating interaction that still need investigation.

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