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Description and behavioural biology of two *Ufens* species (Hymenoptera: Trichogrammatidae), egg parasitoids of *Homalodisca* species (Hemiptera: Cicadellidae) in southern California

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Abstract

The morphology, distribution, and hosts of two egg parasitoids, *Ufens principalis* Owen **sp. n.** and *U. ceratus* Owen **sp. n.** (Hymenoptera: Trichogrammatidae), are described for the first time. These species are compared to *U. niger* (Ashmead), the only species of *Ufens* s. str. currently described from the Nearctic, and diagnostic differences are presented. The behavioural biology of *U. principalis*, and *U. ceratus* to a smaller extent, is also described for the first time. *Ufens principalis* exhibited a rapid and long-distance response in the form of directional flight toward freshly laid eggs of *Homalodisca* species, its primary hosts in southern California. Parasitism involved aggregations of female *U. principalis* on fresh *Homalodisca* egg masses, which remained attractive to *U. principalis* for a relatively short time. The level of oviposition by *U. principalis* females was low during most of the day and peaked before sunset in tandem with a peak in *Homalodisca* oviposition. Oviposition behaviour of *U. principalis* is described and the distribution of ovipositor probe durations showed that most probes were generally of very short duration. Mating of both *Ufens* species occurred on the egg mass, with males showing aggressive behaviour towards each other as they competed for emerging females. *Ufens ceratus* males displayed greater aggression towards other males than *U. principalis* males. By contrast, fights among *U. principalis* males involved more individuals and lasted longer than corresponding fights between *U. ceratus* males.

Keywords: Biological control, male aggression, searching behaviour, mating behaviour, eclosion, host location, swarming, *Ufens*, *Homalodisca*, Chalcidoidea, taxonomy, new species, leafhoppers

Introduction

The glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae), was introduced into California from the southeastern United States (Sorensen & Gill, 1996), and is an important vector of the gram-negative xylem-limited bacterium, *Xylella fastidiosa* Wells *et al*. (Wells *et al*., 1987), which causes diseases on several crops and ornamentals including Pierce's disease of grapes, phony peach disease, almond leaf scorch, alfalfa dwarf and oleander leaf scorch (Blua *et al*., 1999; UCOP, 2000; Varela *et al*., 2001). The smoketree sharpshooter, *Homalodisca liturata* Ball (= *H. lacerta* (Fowler)) (Hemiptera: Cicadellidae) (Burks & Redak, 2003), a closely related California endemic, is also a known vector of Pierce's disease

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and oleander leaf scorch (Freitag *et al*., 1952; Purcell *et al*., 1999).

Eggs of *Homalodisca* species are laid just below the epidermis of leaves as a cluster with individual eggs orientated nearly parallel to one another. Confirmed egg parasitoids attacking *Homalodisca* species in California include *Gonatocerus* spp. (Hymenoptera: Mymaridae), *Ufens* spp., and *Zagella* spp. (both Hymenoptera: Trichogrammatidae) (Turner & Pollard, 1959; Huber, 1988; Triapitsyn *et al*., 1998). Powers (1973) reported an *Ufens* sp. attacking *H. liturata* on *Hibiscus syriacus* L. (Malvaceae) in San Diego in 1972–1973. Pinto *et al*. (1987) reported the presence of an *Ufens* sp. on jojoba, *Simmondsia chinensis* (Link) Schneider (Simmondsiaceae), in four locations in Riverside County but did not associate this *Ufens* species with *H. liturata* egg masses on the same host plant. One or more *Ufens* spp. were found parasitizing a low proportion of *Homalodisca* egg masses (1.9%) on citrus (Rutaceae) as discerned from characteristic exit holes in old egg masses assessed in November 1999 (Al-Wahaibi & Morse, 2000). Morgan *et al*. (2000) also reported the presence of an undescribed *Ufens* sp. from citrus. More recent observations suggested that egg masses of *Homalodisca* on plants native to southern California (e.g. jojoba) were predominantly parasitized by two *Ufens* species (Al-Wahaibi, 2004). These *Ufens* parasitoids were also shown to be responsible for a large proportion of *Homalodisca* egg parasitism on cultivated plants such as citrus in Riverside, California during late summer and autumn (Al-Wahaibi, 2004). There has been interest in introducing *Ufens* species into California as part of a classical biological control effort against *H. coagulata* (Triapitsyn & Hoddle, 2001, 2002; Triapitsyn *et al*., 2002). However, this effort was hampered by difficulties in rearing exotic *Ufens* species in quarantine. These difficulties led to the hypothesis that *Ufens* species might be hyperparasitoids, attacking *Gonatocerus* species (primary parasitoids) inside *Homalodisca* eggs (Triapitsyn, 2003). This hypothesis is clearly contradicted by the findings presented in this paper.

A description of *Ufens* Girault (1911) can be found in Doutt & Viggiani (1968) and Pinto (1997), and a catalogue of species in Lin (1994). *Ufens* is recognized by having antennae with 2 anelli, 2 broadly joined funicular segments, 3 club segments in females, and 4 in males, including a comparatively small terminal segment. Antennal setae are arranged in whorls, and are especially conspicuous in males. Fore wings are broad, often nearly truncate apically, with the marginal vein and stigmal vein generally subequal in length. Setal tracks, including RS1, are discernible. Maxillary palpi are 1-segmented. The antennal formula of males (2 funicular and 4 club segments) combined with the 1-segmented palpi separate *Ufens* from all other trichogrammatid genera.

Like many genera of the Trichogrammatidae, *Ufens* is still poorly understood, with the majority of its species undescribed. The only species of *Ufens* s. str. currently described from the Nearctic is *U. niger* (Ashmead), the type species. In this paper, two new species, *Ufens principalis* Owen and *Ufens ceratus* Owen, are described. Both have been collected predominantly in the southwestern United States, but are also known from other areas in the United States and Mexico.

Because of the evident contribution of these undescribed *Ufens* species to the biological control of *H. coagulata*, there was a need to examine their taxonomy and biology. In this article, the *Ufens* species known to parasitize *Homalodisca* species in southern California are described, and the behavioural biology of these egg parasitoids, especially *U. principalis*, is reported.

Species descriptions

Descriptive and anatomical terms primarily follow Doutt & Viggiani (1968). Terms for antennal sensilla and setation follow Pinto (1999). Note that only the types of sensilla that aid in species differentiation are presented here, i.e. placoid sensilla and unsocketed setae.

Characterization of colour was determined from card-mounted specimens. All measurements for length and width represent maximum dimensions and were determined using hexamethyldisilazane-dried (Heraty & Hawks, 1999), slide-mounted specimens. In all cases, $n = 10$ total (5♂ and 5♀). An attempt was made to measure individuals representing both the size and geographical variability of the species. Specimens examined were slide-mounted unless otherwise indicated; in which case, the total number of specimens is given followed by the number card-mounted.

Body length was the maximum length from the anterior margin of the pronotum to the posterior margin of the last tergum. Individual segments of the flagellum are presented as funicle 1, funicle 2, club 1, club 2, etc. The width of the marginal vein was measured transversely at its midpoint. A field of structures posterior to the radial process, appearing as minute cuticular nub-like projections, are referred to as alar acanthae. The minimum and maximum distances between setal tracks r-m and M were measured according to figs 2e and 3c. Wing fringe setae were measured along the posteroapical margin of the fore wing.

Ufens ceratus Owen sp. n.
(figs 1a,b, 2a–h)

Diagnosis. Marked colour sexual dimorphism; females dark brown, males light yellow. Females have a comparatively long second funicular segment densely covered with placoid sensilla. Males have a set of forward-projecting stout setae on the lateral margins of the clypeus and two adjacent pairs on the genae. Male genitalia with anteroventral margin deeply invaginated. Fore wing setal tracks r-m and M slightly divergent with one complete row of setae between.

Description. Colour sexually dimorphic (see below). Head width 1.4× the hind tibial length. Mesoscutal sculpturing longitudinally striate, narrowing slightly medially, with interstitia transversely ridged. Fore wing length 1.5× its width and 2.8× hind tibial length; premarginal vein, marginal vein, and stigmal vein subequal in length; alar acanthae absent; 17–22 setal tracks distinct, most setae associated with tracks; costal cell with two setal tracks, anterior track with 5–8 setae, posterior track incomplete, consisting of 1–4 more widely spaced setae; premarginal vein campaniform sensilla varying from nearly touching to separated by more than twice their diameter; marginal vein *c*. 2.5× as long as wide; fringe setae short, 0.05 wing length; r-m and M setal tracks slightly divergent, maximum/minimum distance 1.7, with a single row of setae between. Hind wing length 7.5× its width, with three complete setal tracks.

Male. Colour primarily yellow with midlobe of mesoscutum brown medially; scutellum brown; metanotum brown laterally;

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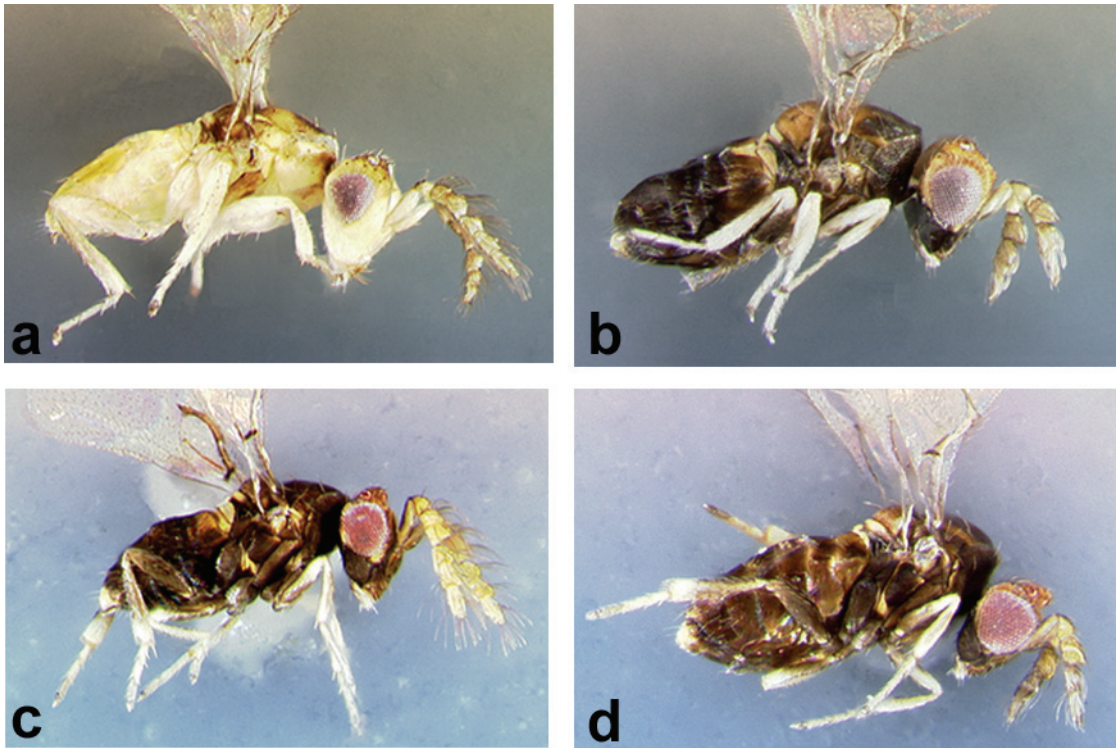

Fig. 1. *Ufens* spp. habitus. (a) *U. ceratus* ♂; (b) *U. ceratus* ♀; (c) *U. principalis* ♂; (d) *U. principalis* ♀.

genae generally yellowish, but sometimes darker than the rest of the head. Head with 6 forward-projecting robust setae: 1 pair on clypeus near lateral margins; 2 pairs adjacent to clypeus on genae (not equally stout in all specimens but always distinct from surrounding setae). Genital capsule approximately twice as long as wide, and 0.7× hind tibial length; anteroventrally invaginated for 0.26 genital capsule length; anterodorsal aperture 0.49× capsule length; parameres 0.46× capsule length.

Female. Colour dark brown with dorsal portion of the head brownish-orange; genae dark brown and distinctly darker than the rest of the head; antennae tan; femora yellow or banded dark brown and yellow; tibiae and tarsi yellow; midlobe of mesoscutum light brown medially; scutellum light brown; metanotum yellow medially. Club segments broadly joined; club 1.7× as long as funicle; funicle 2 is 1.7× as long as funicle 1; funicle 1 with 7–11 unsocketed setae; funicle 2 with 5–10 placoid, 6–10 unsocketed setae; club 1 with 3–7 unsocketed setae; club 2 lacking unsocketed setae; club 3 with 0–2 unsocketed setae. Ovipositor length subequal to hind tibial length.

Distribution. Known from the southwestern and southeastern United States, Baja California, and northern Mexico.

Host associations. Ufens ceratus has been reared from *Oncometopia clarior* (Walker) (Hemiptera: Cicadellidae) ['?' on original label], from *H. coagulata* on citrus, *S. chinensis* (jojoba), and *Cercis* sp. (redbud) (Fabaceae), and from *H. liturata* on *S. chinensis* and *Cassia* sp. (Fabaceae). It is also know from undetermined leafhopper hosts on *Vitis* sp. (grape) (Vitaceae) and Ulmus sp. (elm) (Ulmaceae), and from undetermined hosts on *Hyptis* sp. (Lamiaceae) and *S. chinensis*.

Material examined. Holotype ♂, Allotype ♀. UNITED STATES: California, San Bernardino County, 'Crafton Hills, 13.iii.2003, L. Higgins, ex. Glassy-winged sharpshooter eggs on citrus leaves, Key: 003-03-13-01' (deposited in the National Museum of Natural History, Washington, D.C.). Paratypes 8♂, 5♀; 2♂, 2♀ card mounted. Same data (1♂ and 1♀, deposited in The Natural History Museum, London, remainder deposited in the University of California, Riverside, Entomology Research Museum). Other material: UNITED STATES: Arizona, Pinal County, 7 mi. W. Superior, 3♂, 4♀, 716.3 m, 26.iv.1980, S. Manweiler, ex. eggs inserted in leaf of *S. chinensis*, Jojoba project 291042; 1♀, 716.3 m, 9.v.1980, S. Manweiler, on *S. chinensis*, Jojoba project 290366; 1♂, 1762.0 m, 25.v.1980, em. 10.vi.1980 from *S. chinensis*, Univ Calif Insect Survey specimen #290386; 1♂762.0 m, 25.v.1980, em. 10.vi.1980 from *S. chinensis*, University of California Insect Survey specimen #290386; 1♀, 762.0 m, 21.vi.1980, S.A. Manweiler, beaten from *S. chinensis*, Jojoba project 291158; 1♂, 1♀, 716.3 m, 4.x.1980, S. Manweiler, on *S. chinensis*, em. i.1981, Jojoba project 291328. California, Imperial County, Salton City (1517 Niles), 1♂, 4♀; 3♀ card mounted, ex. smoketree sharpshooter egg mass on *Cassia* seed pod, via R.S. Mendés Riverside County, Coachella, "Old Shop", 1♂, 12.vii.1989, D. Gonzalez, ex. Grape leaves with leafhopper eggs; 1♂, 6♀, Deep Canyon, unknown host on *Hyptis*, 23.iii.1963; Indio, 2♂, 4♀, 30.x.1986, D. Goodward coll., ex. leafhopper eggs on Siberian elm leaf; Palm desert, 4♂, 6♀; 2♂, 2♀ card mounted, 21.viii/17.ix.1986, D. Goodward, ex leafhopper eggs on elm; Riverside, UCR Agricultural Experiment Station, Field 7E, 2♂, 2♀, 3.vii.2000, A.K. Al-Wahaibi, ex. *Homalodisca* sp. on *S. chinensis*; 5.6 mi. S. Sage on R3, Sec. 32 T.75, R.IE. site 2, 116° 54′ W, 33° 31′ N, 2♂, 1♀, 24–29.ii.1980, Jojoba project #303378, 303388; 5.6 mi. S. Sage on R3, 29-II-1980, Sec. 32

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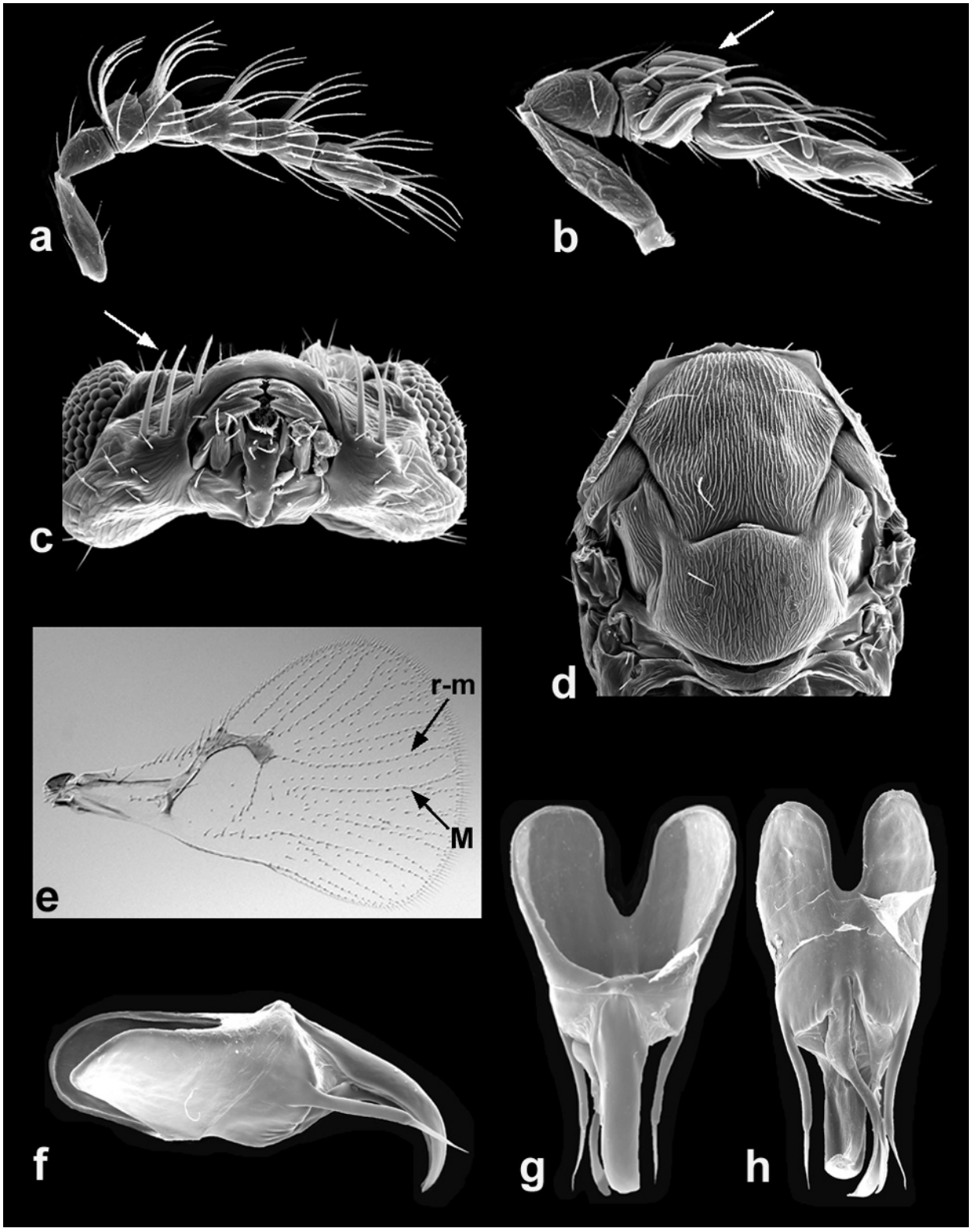

Fig. 2. *Ufens ceratus*. (a) ♂ antenna, medial; (b) ♀ antenna, medial (arrow showing enlarged funicle 2 with many placoid sensilla); (c) head, ventral (arrow showing stout setae on the lateral margins of the clypeus and on the genae); (d) mesosoma, dorsal; (e) fore wing, dorsal (arrow showing radial-medial (r–m) cross vein and median (M) setal track); (f) ♂ genitalia, lateral; (g) ♂ genitalia, dorsal; (h) ♂ genitalia, ventral.

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T.75, R.IE. site 2, 116° 54′ W, 33° 31′ N, 1♀, em. 4.iv.1980, S. Frommer, ex. eggs on *S. chinensis*, Jojoba project #302019. Florida, Jefferson County, Monticello, ARC, 1♂, 11♀, ex. *H. coagulata* eggs on redbud, vi–viii.1979, J.C. Ball. Texas, Hidalgo County, Bentsen Rio Grande State Park, 1♂ VI-19-1986, J.B. Woolley, screen sweep, River Hiking Trail; Presidio County, Big Bend Ranch SNA, Yedra Canyon, 1♂, VI-20-1991, J.B. Woolley, 91/029; Big Bend Ranch SNA, Agua Adentro, 1♂, 18/23.vi.1991, R. Wharton. MEXICO: Baja California Sur, La Paz, 10 km. W, 1♂, 1♀, 28.x.1983, J.D. Pinto, screen sweep. Nuevo Leon, Allende, 6 km. S., roadside of Hwy. 85, Sanatorio Naturista de Canoas, 1♂, 1♀, ex. *Oncometopia clarior* (Walker) ['?' on original label] eggs on orange, 10.iv.2000, L. Bezark & S. Triapitsyn, S&R # 00-07-01. Tamaulipas, Llera de Canales, 3♂, 3♀, 8.iii.2000, ex. sharpshooter egg mass on orange leaf in private garden, S. Triapitsyn, coll.

Etymology. Keros, Greek for horn, in reference to the horn-like setae on the margin of the clypeus and genae of males of this species.

Comments. Ufens ceratus was treated as *Ufens* sp. by Triapitsyn *et al*. (2002) and Triapitsyn (2003). See Comments under *U. principalis* for a discussion of diagnostic features of both species.

Ufens principalis Owen sp. n.
(figs 1c,d, 3a–f)

Diagnosis. Males and females similarly coloured. Female antenna with funicular segments subequal; funicle 2 with few placoid sensilla. Numerous unsocketed setae on all segments of flagellum, except club 2. Males lack stout setae on the clypeus and genae. Genitalia elongate, anterior margin not invaginated. Fore wing densely setose, with many setae not assignable to tracks; setal tracks r-m to M diverge widely, separated by many setae.

Description. Morphology the same as *U. ceratus*, with the following differences. Colour not sexually dimorphic: dark brown with dorsal portion of head brownish-orange; genae dark brown and distinctly darker than rest of head; antennae tan to yellow; femora dark to light brown; tibiae and tarsi yellow and brown; mesoscutum and scutellum dark and light brown (sometimes lighter medially); metanotum yellow medially. Fore wing length 1.4 × its width and 3.0 × hind tibial length; 4–11 alar acanthae present; 12–17 setal tracks distinct, many setae not falling into tracks; posterior row of setae in costal cell incomplete, consisting of 3–5 setae, often widely spaced and therefore of similar total length to anterior row; marginal vein *c*. 2.8 × as long as wide; fringe setae short, 0.04 × wing length; r-m to M vein tracks widely divergent, maximum/minimum distance 3.7 and separated apically by many setae not conforming to a single track. Hind wing length 8.6 × its width, with three complete setal tracks.

Male. Lacking robust setae on the clypeus and genae. Club twice the length of funicle. Genital capsule *c*. 3.6 × as long as wide, and subequal to hind tibial length; anteroventral invagination slight to non-existent (*c*. 0.003 genitalia length); anterodorsal aperture 0.45 × capsule length; parameres 0.34 × capsule length.

Female. Club 2 × the funicle length. Funicle 2 length subequal to funicle 1; funicle 1 with 10–13 unsocketed setae; funicle 2 with 10–14 unsocketed setae; club 1 with 9–17 unsocketed setae; club 3 with 4–5 unsocketed setae. Ovipositor length 0.8 × hind tibial length.

Distribution. This species is known only from the southwestern United States.

Host associations. Ufens principalis has been reared from *Homalodisca* species on host plants including *S. chinensis*, *Cercis* sp., *Parthenium argentatum* Gray (guayule) (Asteraceae), *Baccharis salicifolia* (Ruiz, Lopez & Paron) (mule fat) (Asteraceae), *Schinus terebinthifolius* Raddi (Brazilian pepper tree) (Anacardiaceae), *Salix* nr. *lucida* (willow) (Salicaceae), *Vitis* sp., *Erythrina* sp. (coral tree) (Fabaceae), and several types of citrus.

Material examined. Holotype ♂, Allotype ♀. UNITED STATES: California, Riverside County, 'Riverside, UCR Ag. Exp. Station, Field 7E, ex. *Homalodisca* sp. on jojoba, coll. 2.viii.2001, em. 8.viii.2001, Ali K. Al-Wahaibi, Ref 2001J54, Key: 001-08-02-01' (deposited in the National Museum of Natural History, Washington, D.C.). Paratypes 7♂, 16♀; 2♂, 13♀ card mounted. Same data (1♂ and 1♀, deposited in The Natural History Museum, London, remainder deposited in the University of California, Riverside, Entomology Research Museum). Other material: UNITED STATES: Arizona, Cochise County, Coronado National Forest, Barfoot Mtn., 1♂, 11.ix.1978, G. Gordh; Dragoon Mtns., Jordan Canyon, 31° 59.33′ N, 110° 01.07″ W, 1♂, 11.viii.2001, A.K. Owen, screen sweep. Santa Cruz County, Patagonia, 31° 53′ N, 110° 77′ W, 1♂, 16.vi.1994, MT, E. Wilk & B. Brown. California, Los Angeles County, Altadena, 1♂, 1.x/11.xii.1990, R.H. Crandell. Riverside County, Riverside, UCR Agricultural Operations, 1♂, 1♀, ex. *Homalodisca coagulata* in tangerine leaf, 13.v.1999, J. Bethke; UCR Agricultural Operations, Field 7E, 1♂, 2♀, ex. *Homalodisca* sp. in jojoba, 3.vii.2000, A.K. Al-Wahaibi; UCR campus, 4♂, 4♀; 2♂, 2♀ card mounted ex. *Homalodisca* sp. eggs in unknown leaf, 25.ix.2000, A.K. Owen; UCR campus, 1♂, 3♀; 2♀ card mounted ex. cicadellid eggs in *Erythrina*, 18.ix.2000, A.K. Owen; UCR Agricultural Operations, 1♂, ex. *Homalodisca* sp. eggs in grapefruit leaf, 5.viii.2000, A.K. Al-Wahaibi; UCR Botanical Gardens, 2♂, 1♀, ex. *Homalodisca* eggs in Jojoba leaf, 30.viii.2001, A.K. Owen; 1♂, 1♀, UCR campus, ex. *Homalodisca* sp. eggs in redbud leaves, 03.x.2001, A.K. Owen & S. Triapitsyn; UCR campus, 3♂, 3♀; 1♂, 1♀ card mounted ex. *Homalodisca* sp. eggs in redbud leaves, em. 2–3.x.2001, S. Triapitsyn; UCR Agricultural Operations, 1♂, ex. *Homalodisca* sp. eggs on grape leaves, 19.viii.2002, R. Burks; Santa Rosa Plateau Ecological Reserve, 33° 32.538′ N, 117° 14.758′ W, 1♂, Malaise trap, 14.viii–7.ix.2001. New Mexico, Hidalgo County, Gray Ranch, E. slope Animas Mtns., Indian Creek Wash, N. of Culberson Camp, 31° 25.31′ N, 108° 40.52′ W, 1♂ screen sweep, 5.viii.2002, J. George & M. Gates.

Etymology. From Principali, Latin for first in time or rank, in reference to the quickness with which this species arrives at host egg masses.

Comments. Ufens principalis has generally been collected and reared more frequently than *U. ceratus* where the species are sympatric, such as in Riverside, California. However, there is an indication that in some areas of sympatry, such as in some of the desert regions of California and Arizona, *U. ceratus* is more abundant than *U. principalis* (e.g. Desert Center; Al-Wahaibi, 2004).

Triapitsyn (2003) separates *Ufens ceratus* (as *Ufens* sp.) from the type species *U. niger*, primarily by the width of the marginal vein and hind wing, and by the number of complete setal tracks in the hind wing. In fact, both *U. ceratus* and *U. principalis* are separated from *U. niger* by the thickness of the marginal

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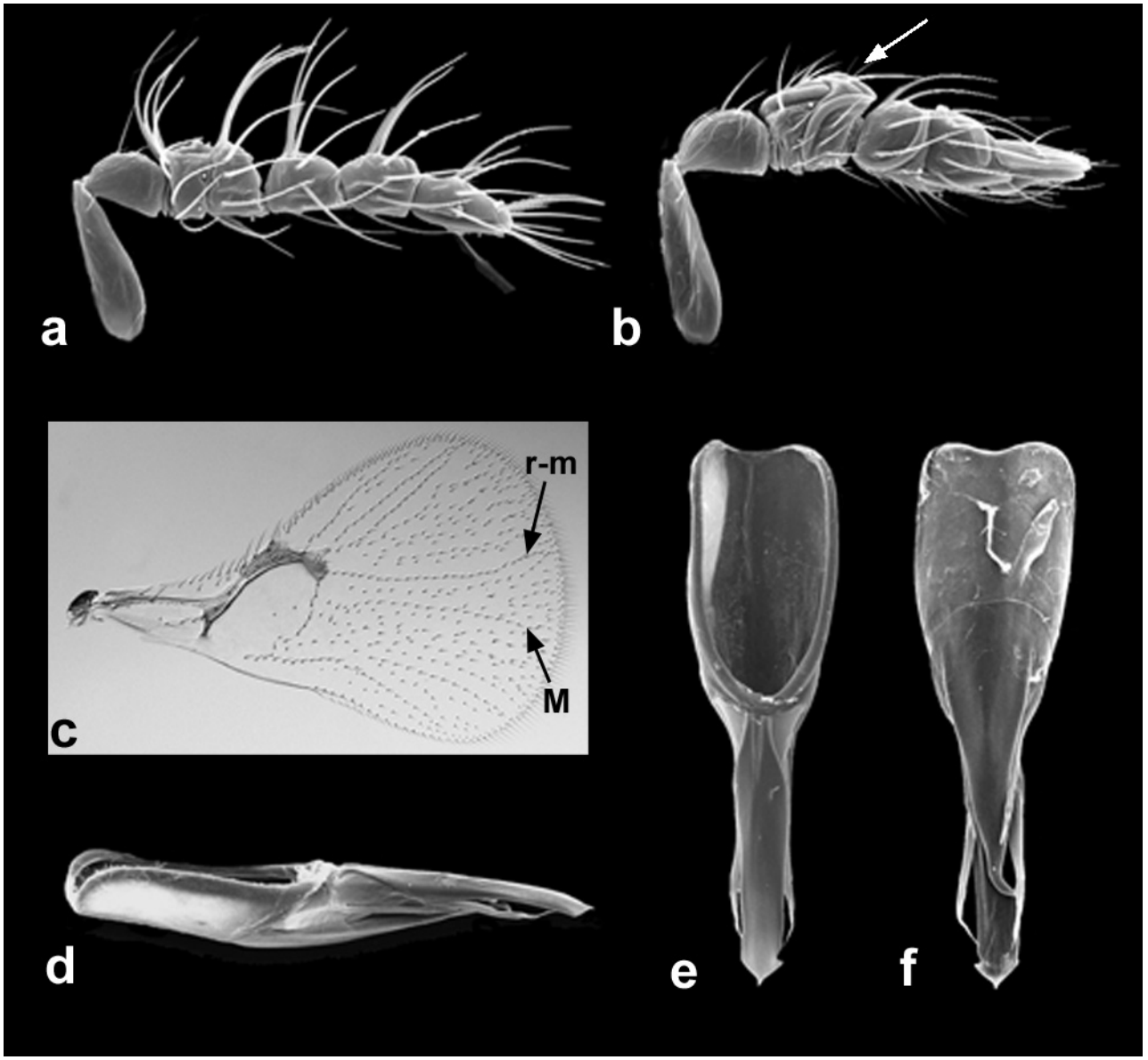

Fig. 3. *Ufens principalis*. (a) ♂ antenna, medial; (b) ♀ antenna medial (arrow showing comparatively smaller funicle 2 with disparate placoid sensilla); (c) fore wing, dorsal (arrow showing radial-medial (r-m) cross vein and median (M) setal track); (d) ♂ genitalia, lateral; (e) ♂ genitalia, dorsal; (f) ♂ genitalia ventral.

vein, and the wider hind and fore wings. Triapitsyn (2003) reported a hind wing length to width of 14.5 for *U. niger*, whereas the newly described species have mean values of 7.5 and 8.6. However, the number of complete setal tracks in the hind wing is not consistent within *U. niger*, as most individuals possess three complete tracks rather than two as reported. Both new species can also be separated from *U. niger* by their longitudinally striate mesoscutal sculpturing. In *U. niger* the sculpturing is longitudinally cellulate, with wider, lightly rugulose interstitia. Females of both new species have ovipositor lengths subequal to the hind tibial length, whereas the ovipositor of *U. niger* is longer, 1.5–2× the hind tibial length (Triapitsyn 2003). *Ufens ceratus* can also be distinguished from *U. niger* by the more disparate setae in the fore wing forming more distinct tracks, and the narrowly diverging r-m and M setal tracks separated by a single row of setae. In addition, males can be differentiated by their unique genitalia, coloration, and stout setae on the clypeus and genae. Females are further distinguished by the numerous placoid sensilla on the enlarged funicle 2.

Based upon the similarities shared between *U. niger* and *U. principalis*, such as similar wing venation and male genitalia, it is likely that these two species are more closely related to each other than either one is to *U. ceratus*.

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Materials and methods

Laboratory observations on emergence, mating and male competition behaviours

Ufens-parasitized egg masses of *Homalodisca* (unparasitized egg masses are white to light yellow whereas parasitized ones have an intense yellow to orange colour) were collected on jojoba, *S. chinensis*, from Field 7E at Agricultural Operations, University of California, Riverside during mid August to late September 2002. These egg masses were incubated at 24° C, 50–60% RH, and exposed to ambient light near a window facing east in addition to laboratory lighting from *c*. 0600 h to 2200 h inside 50 × 9 mm diameter Petri dishes. Egg masses were checked in the early morning (0600–0700 h) in late August to early October 2002 for signs of the initiation of emergence (tiny cracks or holes), or for newly emerged adults. Egg masses with one to two emerged adults or with signs of adults in the process of emerging were observed continuously for up to 2 h using a dissecting microscope fitted with a Sony CCD-IRIS camera (model DXC-107A, Sony Electronics, Tokyo, Japan) connected to a Sony monitor (model PVM-1351Q) and a Panasonic VCR (model AG 5700, Panasonic Matsushita, Secaucus, New Jersey). Emergence, courtship, and other behaviours were recorded on VHS tape for ten egg masses with *U. principalis* and ten egg masses with *U. ceratus*. Videotapes were reviewed and the following times were measured: emergence time (time between first observation of a tiny crack in the leaf epidermis and emergence of an adult parasitoid), mating time, and time spent by males in bouts of aggressive behaviour toward other males. The number of males involved in a fight or standoff was also determined. Details of emergence, courtship, mating, and aggressive male behaviour were noted and when possible, documented with photographs taken with a Nikon Cool Pix 990 digital camera (Nikon USA, Melville, New York).

Diurnal rhythm of oviposition in the field

On each day of five days in the week of 2 September 2002 and for five days between 18 April and 16 May 2003 (the two sets of five days had similar day lengths and followed daylight savings time; the spring 2003 choice of non-continuous observation days was mandated by weather and logistics), two jojoba shrubs in Field 7E were examined for 10 min per shrub, searching for *Homalodisca* egg masses attended by *Ufens* females that had assumed an oviposition stance. These daily observations were repeated five times each observation day at 0700 h, 1000 h, 1300 h, 1600 h and 1900 h. The number of *Homalodisca* egg masses with *Ufens* females and the number of egg masses with female *Homalodisca* near the egg mass (either in the process of oviposition or just after completion of oviposition and before they had flown away) were recorded. These two variables were compared among the five times of the day using a one-way ANOVA with the time of day as the effect tested (JMP IN, SAS Institute, 1996). To test the hypothesis that ovipositing *Ufens* females were associated with freshly deposited *Homalodisca* egg masses, the relationship between the variation in the number of egg masses with *Ufens* females (indicating ovipositing *Ufens*) and the variation in the number of egg masses with female *Homalodisca* (indicating freshly-laid egg masses) was tested using correlation analysis. The identification of *Ufens* females to species for all observations was not attempted due to the difficulty of close examination in the field. However, females examined in laboratory checks ($n = 5$) from some of the field observations were determined to be *U. principalis*.

Field searching behaviour and attraction to Homalodisca *egg masses*

During September 2003, in the late afternoon (*c*. 1730–1915 h), jojoba shrubs in Field 7E were checked for *Homalodisca* females in the process of oviposition or in the process of selecting a suitable leaf site on which to begin the oviposition process. Before ovipositing, *Homalodisca* females usually landed on or close to the terminal leaf of a branch and began pacing several times back and forth on the leaf, apparently testing its suitability for oviposition. They then either accepted the leaf and assumed a typical oviposition stance (in which the tip of the metasoma is curved downwards as the ovipositor is inserted into the leaf tissues) or left the leaf to search for an alternative oviposition site. The time of the initiation of the observation (female sharpshooter already ovipositing or starting oviposition) was noted. For cases where oviposition by female *Homalodisca* was noted from the beginning, the time to the nearest minute from initiation of oviposition to the arrival of the first *Ufens* female at or by the egg mass-to-be was noted. The flight of female *Ufens* toward the egg mass and aspects of their behaviour as they landed on the leaf and approached the egg mass were noted. For all observed egg masses, the estimated number of *Ufens* females on the egg mass was recorded at intervals of 1–15 min. Each egg mass was observed closely until the last female *Ufens* had left the egg masses. Each egg mass was then re-visited after 20–30 min to ascertain whether there were any *Ufens* females on the egg mass. If there were no *Ufens* females on the egg mass, Tanglefoot® (sticky material) (The Tanglefoot Company, Grand Rapids, Michigan) was applied carefully and lightly to the egg mass. The stem immediately connected to the leaf with the egg mass was then flagged. The egg mass was checked after a week for any trapped *Ufens* females. In addition, Tanglefoot® was also applied to one freshly-laid egg mass after shaking off *Ufens* females that were on it and then the egg mass was checked after 30 min to determine if it remained attractive despite the application of the sticky material. Video recordings of *Ufens* flight toward egg masses were produced using a Panasonic camera (model Digital 5100) equipped with a zooming macro lens (18-108/2.5) connected to a VHS Panasonic VCR (model AG-6730) and a Sony monitor (model PVM-1351Q). Forty-second video clips were also taken using a Nikon Cool Pix 990 digital camera. Females examined in laboratory checks ($n = 5$) from some of the field observations were determined to be *U. principalis*.

Details of field oviposition behaviour

Jojoba shrubs in Field 7E, Riverside, California were checked in late afternoon (*c*. 1730–1915 h) during September 2003 for egg masses with ovipositing female *Ufens*. When a cohort of *Ufens* was found ovipositing on a *Homalodisca* egg mass, the stem of jojoba with the leaf containing the egg mass was cut gently with pruning scissors to avoid disturbing the parasitoids. The leaf was then excised gently by hand and placed in moulding clay in a small Petri dish (50 × 9 mm) with the egg mass facing upwards and with the dish cover removed. Immediately after collecting the egg

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mass, ovipositing female *Ufens* were observed using a field set-up consisting of a dissecting microscope fitted with a Sony CCD-IRIS camera (model DXC-107A) connected to a Sony monitor (model PVM-1351Q) and a Panasonic VCR (model AG 5700). The behaviour of each cohort of ovipositing *Ufens* females was observed and recorded until all *Ufens* females walked or flew away from the egg mass. Behaviour of ovipositing females was recorded for 21 cohorts of ovipositing females (each cohort with 1–15 females) on 21 different egg masses. Details of the oviposition behaviour were noted. The duration of the oviposition process from the time of insertion until withdrawal of the ovipositor was measured using the timer on the VCR. This variable was measured for each probe made by each of 1–7 females in each of the 21 cohorts. The direction of movement of single females or multiple females over egg masses (relative to the longitudinal axis of eggs) was noted. *Ufens* oviposition behaviour was also documented with photographs and short video clips taken with a Nikon Cool Pix 990 digital camera. All *Ufens* females observed were *U. principalis*.

Statistical tools

T-tests, one-way ANOVA, multi-way model fitting, mean comparison descriptive statistics, histograms, and chi-square tests were conducted using JMP IN Version 3 (SAS Institute, 1996).

Results

Laboratory observations on emergence, mating and male competition behaviours

The emergence of both *Ufens* species commenced when the young adult inside the host egg started chewing a tiny hole through the chorion of the egg and the leaf epidermis with its mouthparts. The adult continued chewing an almost circular hole about the width of the front of its head. The chewing process was usually performed by the adult with the lateral aspect of the body parallel to the surface of the leaf or with the sternum partially, if not fully, facing the leaf surface. The emergence process lasted on average 71.0 ± 3.3 min ($n = 50$) for *U. principalis* and 57.0 ± 7.7 min ($n = 4$) for *U. ceratus*. Unlike the emergence of *Gonatocerus* species from *Homalodisca* eggs (Al-Wahaibi, personal observation), emergence by *Ufens* species left a notable pile of chewed debris, possibly due to the brittle nature of the chorion of host eggs parasitized by *Ufens* species. When the emergence hole was complete, the adult crawled out of the host egg onto the leaf epidermis. Rarely, the emerging adult cut a hole too small to allow its safe exit, resulting in the adult becoming trapped and dying while attempting to emerge. If the adult (either male or female) was the first individual emerging from the egg mass or was not noticed by males that emerged earlier, its first behaviours tended to involve grooming the antennae with the forelegs and opening the folded, crumpled wings with the hind legs. The wings started expanding soon after initiation of the unfolding process, ultimately taking their normal shape and size in a few minutes. Two dark longitudinal lines on either side of the yellowish mesosoma were distinct on both newly emerged males and females, but became non-apparent in 2–3 h as the surrounding mesosoma melanized to dark brown.

After emergence, males of both *Ufens* species tended to gather on the egg mass waiting for females to emerge. After a male had sensed the presence of an adult chewing its exit hole, he would wait next to the enlarging hole. Some males could be seen standing next to an empty hole, seemingly unaware that the occupant of the hole had emerged. When emerged males were present, the courtship process commenced immediately upon the protrusion of the female's head from the emergence hole. The male then turned to face the female's posterior end, buzzed his wings rapidly above his head (at a right angle to his body axis), and extended his forelegs to grip the emerging female's mesosoma. While the female gaster was clearing the exit hole, the male kept a tight grip on the female with his legs and immediately started copulating. The mating posture occurred with the male's body axis at a 45–90° angle to the axis of the female's. The whole process, from mounting to copulation, to disengagement, was rapid, lasting 24.8 ± 3.0 s ($n = 34$) in *U. principalis* and 13.4 ± 1.2 s ($n = 29$) in *U. ceratus*. An individual male often mated with several virgin females as they emerged from host eggs.

Once mated, females appeared unresponsive to male mating attempts, showing their lack of interest by rapid kicks with the hind legs at the males behind them as they tried in vain to engage the females. Females usually rushed to the edge of the leaf or to the underside of the leaf to perform grooming and wing expansion behaviours and rarely revisited the egg mass they had developed in.

In both *U. principalis* and *U. ceratus*, there was evidence of aggressive behaviour of males toward fellow males as they competed to mate with as many females as possible. In *U. principalis*, this behaviour consisted of fights with males using their heads (fig. 4a). Typically, if a male found another male waiting for an emerging female, he contacted him face to face, or with the front of the head pushing at the lateral aspect of the head, mesosoma, or gaster of his counterpart. Usually, more than two males were involved in the standoff resulting in a pile-up. This pile-up sometimes slowed or hindered the emergence of the disputed female. At times, males were so busy fighting with each other, that emerging females escaped unnoticed and unmated by these competing males. In egg masses with a relatively large population of emerged *U. principalis* males, 2–4 groups of fighting males were seen concurrently. *Ufens principalis* males were observed in apparent attempts to mate with other males in several scenarios. First, males sometimes apparently mistook newly-emerging males for females and would attempt copulation with the just-emerged male, who would show his refusal by kicking at the male behind him. Males also sometimes mounted other males near egg masses, apparently as part of the aggressive behaviour of one male toward another, and sometimes mounted other males on the walls of the observation container.

The aggressive behaviour of *U. ceratus* seemed even more extreme. In this species, a larger, dominant male tended to chase away other males attempting to enter the egg mass zone he was patrolling. If the intruding male was not responsive to threats by the incumbent male, a fight usually resulted in which the dominant male used his antennae to push and lift the weaker rival off the leaf surface until the rival retreated.

The average number of males involved in fights was 2.3 ± 0.1 ($n = 77$) for *U. principalis* and 2.0 ± 0.0 ($n = 74$) for *U. ceratus*, while the average duration of the fights was

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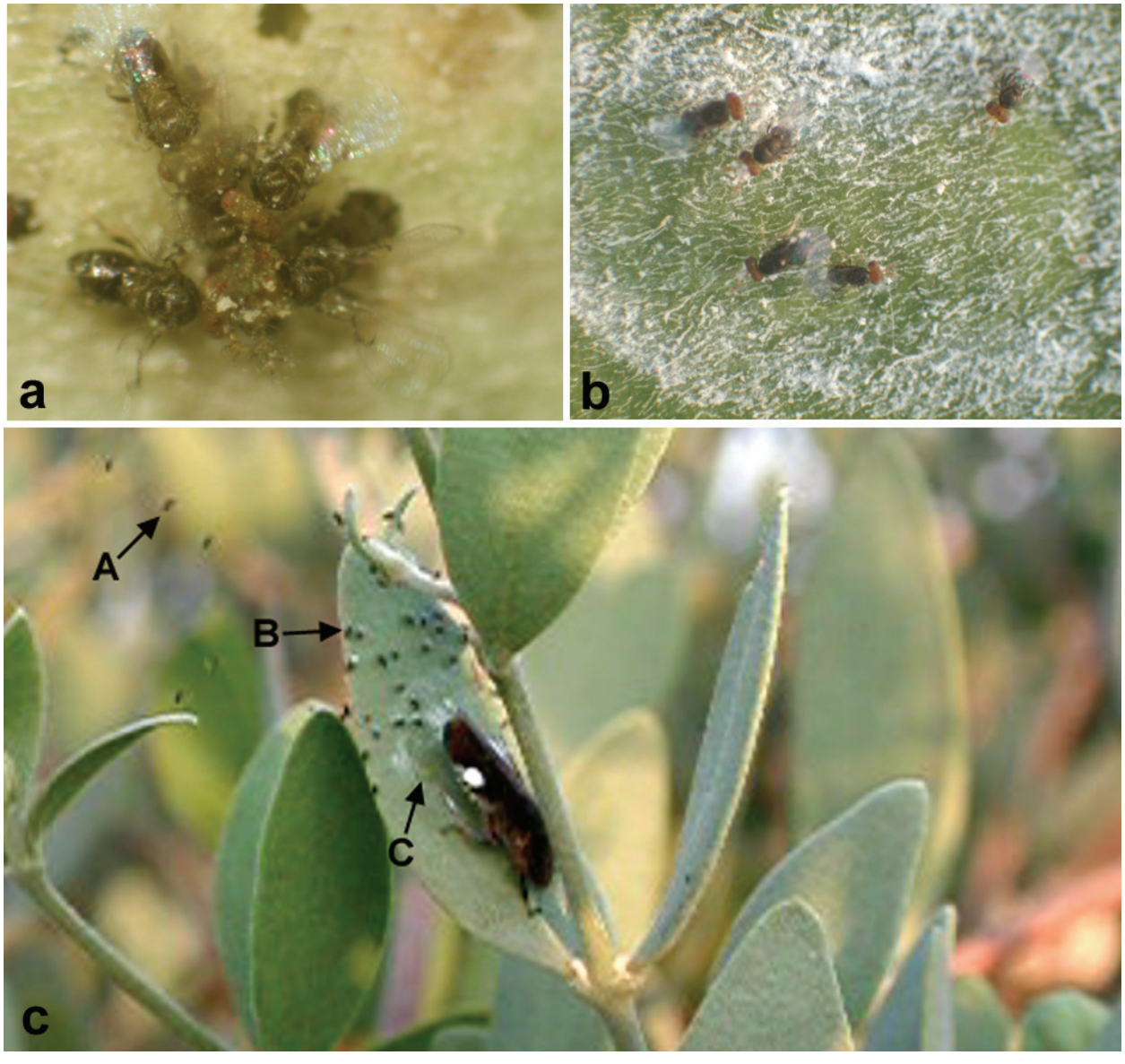

Fig. 4. Male aggression and female oviposition behaviours in *Ufens principalis*: (a) five males engaged in aggressive behaviour, forcing their heads against each other; (b): a group of five *U. principalis* females in oviposition postures on an *H. coagulata* egg mass covered with snow-like brochosomes; (c) attraction of *Ufens principalis* females to an egg mass being laid by a female *Homalodisca coagulata* on jojoba. Arrows A–C point to [A] *U. principalis* in flight towards the egg mass; [B] abundance of *U. principalis* gathered on a leaf by the egg mass; and [C] *H. coagulata* egg mass. Note the white discs on the forewings of the sharpshooter, which contain a store of secreted brochosomes which the sharpshooter removes with her hind legs to cover the egg mass. This image is frame extracted from a 40 s video clip (shot using a Nikon Coolpix 990 digital camera) taken in Field 7E, Agricultural Operations, University of California, Riverside on 27 August 2003.

88.9 ± 19.2 s ($n = 77$) for *U. principalis* and 3.9 ± 0.7 s ($n = 73$) for *U. ceratus*.

Diurnal rhythm of oviposition in the field

Results from observations during September 2002 indicated that at this time of year, oviposition frequency by *U. principalis* (no *U. ceratus* females were observed in laboratory checks) was generally low during most of the day with a noticeable surge in oviposition (number of egg masses with ovipositing female *U. principalis*) towards the end of the day, between 1600 h and 1900 h. An ANOVA test comparing the five observation times resulted in the 1900 h observation time showing a significantly higher incidence of egg masses with ovipositing *U. principalis* ($P < 0.0001$, $n = 10$). The number of egg masses with ovipositing *Homalodisca* females followed the same pattern with the 1900 h observation time having a higher incidence of ovipositing *Homalodisca* ($P < 0.0001$, $n = 10$). Correlation analysis between the number of egg masses with ovipositing *U. principalis* females and the

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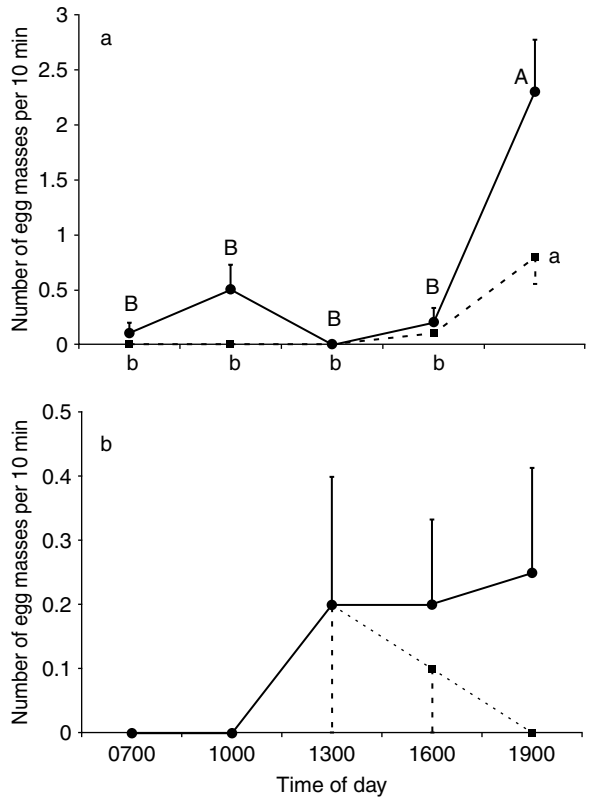

Fig. 5. Diurnal rhythm of *Ufens principalis* and *Homalodisca* oviposition on jojoba (Field 7E, Agricultural Operations, University of California, Riverside) on five contiguous days in summer 2002 (fig. 5a) and five non-contiguous days in spring 2003 (fig. 5b) (see text for details). Separate ANOVAs were conducted to compare the number of egg masses with *U. principalis* (–●–) and number of egg masses with *Homalodisca* (- -■- -) egg masses observed at different times of the day. (a) Upper-case letters indicate Tukey-Kramer HSD mean separations for egg masses with *U. principalis* (ANOVA, $P < 0.0001$), while lower-case letters indicate Tukey-Kramer HSD mean separations for egg masses with *Homalodisca* (ANOVA, $P < 0.0001$). Means with the same letter are not significantly different. (b) No significant differences were found among the number of egg masses with *U. principalis* ($P = 0.483$) or among the number of egg masses with *Homalodisca* ($P = 0.566$). Standard errors of the mean are presented as error bars. Ten jojoba shrubs in summer 2002 and ten different jojoba shrubs in spring 2003 were checked for egg masses with *U. principalis* and *Homalodisca* at each of the five times of the day.

number of egg masses with ovipositing *Homalodisca* females revealed a high correlation (r = 0.572, $n = 50$, $P < 0.0001$) (fig. 5a).

Data from April–May 2003 indicated that egg masses with ovipositing *U. principalis* were observed only during the afternoon, with relatively high numbers observed between 1000 h and 1300 h and then rising further to a maximum at 1900 h. However, there was no significant difference among the five observation times ($P = 0.483$, $n = 8$–10), probably due to low sample sizes for all observations. No egg masses with ovipositing *Homalodisca* were observed in the morning and evening (1900 h). A peak in the number of egg masses with ovipositing *Homalodisca* was apparent around 1300 h and this variable was relatively high at 1600 h. Nonetheless, there was no evidence of a significant difference among observation times for this variable ($P = 0.566$, $n = 8$–10), again likely due to low values for all observations. Correlation analysis revealed a strong association between the number of egg masses with ovipositing *U. principalis* females and the number of egg masses with ovipositing *Homalodisca* (r = 0.783, $n = 48$, $P < 0.0001$) (fig. 5b).

Field searching behaviour and attraction to Homalodisca *egg masses*

Typically, soon after a female *H. coagulata* started ovipositing into a jojoba leaf, a swarm of flying *U. principalis* females (no *U. ceratus* females were observed in laboratory checks) could be seen close to the leaf containing the sharpshooter (fig. 4c). Individual flying *U. principalis* females were observed up to a distance of approximately 30 cm from where the egg mass was being laid.

From the cloud of flying insects, female *U. principalis* started alighting, usually on the leaf side opposite to where the female *Homalodisca* was laying its eggs (but sometimes immediately adjacent to the still-forming egg mass). The time from initiation of oviposition by the *H. coagulata* female to alighting of the first *U. principalis* female on the leaf containing the egg mass averaged 2.9 ± 0.5 min ($n = 10$). If the egg mass laid was large enough and the female sharpshooter had moved far enough away from one end of the egg mass (egg masses are typically laid sequentially from one end to the other), some of the *U. principalis* females would slowly start walking towards the forming egg mass. Once they contacted the first host egg, they immediately assumed the stereotypical ovipositional posture (see below). This 'sneaking-in' behaviour behind the ovipositing female sharpshooter was risky at times because the hind legs of the sharpshooter typically thrashed on the leaf surface in rapid vigorous movements transferring its brochosome load from chalk-like discs on the forewings. Sometimes, *U. principalis* females were dislodged or crushed by the vigorous movement of the hind legs of the leafhopper. If the egg mass was small and was laid in a relatively short time, then *U. principalis* females would usually start approaching it immediately after the female sharpshooter had finished ovipositing. This approach towards the egg mass appeared synchronized among the attendant *U. principalis* females, which moved onto the egg mass at the same time and from different directions. Group oviposition by *U. principalis* females would then begin.

After the sharpshooter had left its egg mass, other *U. principalis* females would continue swarming towards the fresh egg mass. *Ufens principalis* females were observed flying towards freshly laid egg masses even after darkness fell. Typically, the highest density of *U. principalis* females on an egg mass occurred immediately after the female sharpshooter had finished ovipositing and had left, and the number of *U. principalis* females observed on the egg mass fluctuated to some degree with the advance of time. However, as time passed, the general trend was toward a drop in numbers until no *U. principalis* females were seen on the egg mass (fig. 6). In general, the number of *U. principalis* females parasitizing an egg mass at the same time averaged 3.7 ± 0.5 (range 1–25, $n = 66$). On average, the time elapsing between the arrival of the first *U. principalis* female on a leaf containing freshly laid eggs and the last time an *U. principalis*

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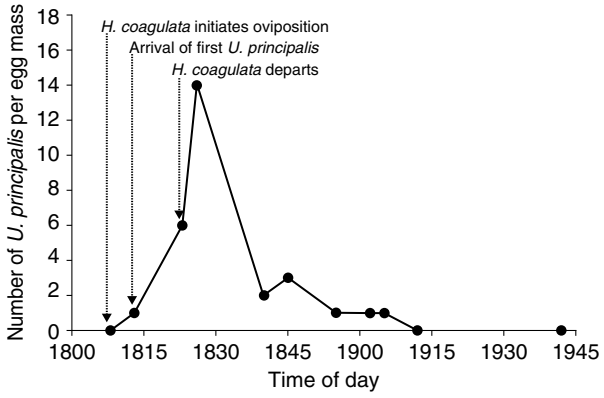

Fig. 6. A typical profile showing the variation in the number of *Ufens principalis* females per egg mass with time. This profile is based on observations performed 27 September 2003 on jojoba (Field 7E, Agricultural Operations, University of California, Riverside). Arrows point to the three key events characteristic of the profile: initiation of oviposition by *Homalodisca coagulata*, arrival of the first *U. principalis* female near the egg mass, and completion of oviposition by *H. coagulata* and its departure from the egg mass.

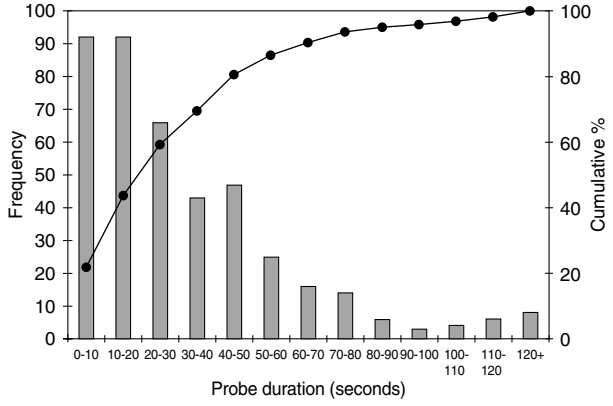

Fig. 7. The frequency distribution of ovipositor probe durations observed for *Ufens principalis* females. Both the frequency counts of probes (▭) and their cumulative relative frequency (–•–) are indicated for the given probe duration ranges. The distribution is based on 422 probes made by 1–7 *U. principalis* females on each of 21 cohorts of ovipositing females on 21 *H. coagulata* egg masses on jojoba (Field 7E, Agricultural Operations, University of California, Riverside) in September 2003.

female was seen on the egg mass (verified by checking again after 20–30 min) was 46.5 ± 7.2 min (range 21–87, $n = 11$). A week after Tanglefoot® was applied to egg masses immediately after the lapse of this initial *U. principalis* oviposition period, only 2 out of 26 egg masses had *U. principalis* females trapped in the Tanglefoot® and in both cases, there was a single female immediately next to the egg mass but not on it. Half an hour after the application of Tanglefoot® on an egg mass from which parasitizing *U. principalis* females were previously removed (by carefully shaking the females off), 4–6 females were observed trapped in the sticky material.

Details of field oviposition behaviour

During September 2003, parasitism by *U. principalis* on *Homalodisca* egg masses was usually gregarious (fig. 4b). During oviposition, *U. principalis* females normally orientated either parallel or perpendicular to the longitudinal axis of the host eggs, rarely at an acute angle to that axis. Individual *U. principalis* females entering either parallel or perpendicular to the longitudinal axes of host eggs in an egg mass tended to take linear paths that ultimately became locked into a circular movement at the periphery of the egg mass. Occasional deviations from this trajectory resulted from a female accidentally bumping into another female (this was rare), or when one female blocked the path of another, although females were observed readjusting to a more or less linear path when their path was blocked.

After arriving on an egg mass, a female *U. principalis* immediately started probing the host egg directly beneath her with her ovipositor. She inclined her body axis at an approximately 45° angle, unsheathed her ovipositor, and pierced through the leaf epidermis covering the host egg, bracing herself with all six legs. The female rocked sideways as she drilled with her ovipositor into the tissue below. When probes were long, lasting greater than *c*. 40 s, pumping movements in the metasoma were observed. The final stages of these long probes consistently ended with the whole body vibrating, including the antennae. This vibration occurred a few seconds before the female withdrew her ovipositor from the leaf. Probes lasted on average 33.1 ± 1.5 s ($n = 422$, range 2–202 s). A majority of the probes (70%) were shorter than 40 s (fig. 7).

After the female had completed a probe, she moved a short distance across the egg mass, usually not more than the length of her body, and re-probed another spot (either a different spot on the same egg or on an adjacent egg) on the egg mass with her ovipositor. *Ufens principalis* females touched the leaf surface lightly with the tip of their antennal clubs as they moved from one probe to another. The diverging antennae were moved slowly as they touched the leaf surface. Females tended to preen themselves as they moved to a new probing position but this behaviour took up little of their time. They were never observed feeding on the host egg, on the leaf, or on other materials on the leaf. Immediately after a female's last probe on a particular egg mass (which tended in most cases to be brief, lasting less than *c*. 40 s), she quickly left the egg mass by either walking or jump-flying away. The average number of probes observed for each *U. principalis* female per egg mass was 6.2 ± 0.5 ($n = 68$, range 1–25). This could be an under-estimate because observations of *U. principalis* females were mostly started minutes after their arrival on the egg mass.

Discussion

Emergence

There was evidence for a pre-dawn emergence of males of both *Ufens* species. During observations of emergence and mating behaviours of *U. principalis* and *U. ceratus* using egg masses exposed, for the most part, to ambient light conditions, during late August to early October, it was difficult to begin observations past 0600–0700 h without the prior emergence of at least one male. These early-emerging males required an average of an hour to complete emergence, so they probably initiated emergence sometime between 0500 h

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and 0600 h. From these same recordings of emergence and mating behaviours, it was observed that the initiation of *U. ceratus* emergence generally tended to start earlier than for *U. principalis*. For this reason, it was not possible to assess emergence time for most *U. ceratus* males (this variable was assessed successfully for only four *U. ceratus* adults vs. 50 *U. principalis* adults). Very early morning emergence is possibly related to the phenomenon of aggressive male competition, as it seems likely that early-emerging males would outcompete late-emerging rivals for mates.

No records were found in the literature for the time it takes other trichogrammatids to cut their exit holes and emerge, making within-family comparisons impossible. In both *U. principalis* and *U. ceratus*, individuals from the same egg tended to display independent cutting of their emergence holes which is in contrast with *Gonatocerus fasciatus* Girault (Hymenoptera: Mymaridae), where 6–7 adults of this species emerged through 2–3 exit holes in the same host egg (Triapitsyn *et al*., 2003).

Mating and male competition behaviours

The courtship and mating behaviour of *Ufens* species reported in this study were similar to that of other trichogrammatids and mymarids. A male generally approaches the female from behind and holds her during copulation (Bakkendorf, 1934), with a bending (as if stinging) of the metasoma below the male's head and mesosoma to form the shape of the letter 'C'. Mating in many parasitic Hymenoptera is brief, lasting less than 1 min (Quicke, 1997). Henriquez & Spence (1993) reported a mating time averaging 67 s for *Lathromeroidea* sp. (Hymenoptera: Trichogrammatidae), which is considerably longer than for the *Ufens* species in the present study (13.4 and 24.8 s for *U. ceratus* and *U. principalis*, respectively).

Bakkendorf (1934) stated that males of *Oligosita krygeri* Girault (cited as *Chaetostricha pulchra* Kryger) (Hymenoptera: Trichogrammatidae) engaged in 'cock fights' when encountering one another and tried to come behind one another attempting to take up a mating position. Although Miura (1992) did not mention aggressive behaviour in males of *Paracentrobia andoi* (Ishi) (Hymenoptera: Trichogrammatidae), he reported aggressive behaviour in females of this species and compared such behaviour to that of scelionid females. According to Miura (1992), the fights among *P. andoi* and among scelionid females illustrate two scenarios for fights among adult egg parasitoids. In one scenario, exemplified by *P. andoi*, both the resident and intruder females fight and usually the fight results in both females losing and leaving the host egg mass. In the other scenario, exemplified by scelionid wasps, a resident female defends her host patch aggressively and is usually successful in driving away approaching intruders. The males of *U. principalis* and *U. ceratus* followed scenarios similar to the two cases described by Miura (1992), respectively. *Ufens principalis* male aggressive behaviour was characterized by a more or less equal match between contestants and the fights were generally mild in nature, sometimes reaching the extreme of a pile-up. The males in this contest often lost their prize females because they were too busy fighting, leading to a rival male sneaking in to mate or a female leaving. *Ufens ceratus* male aggressive strategy exhibited extreme territoriality with little tolerance and consisted of chasing away rival males before setting foot on the egg mass. If the rival was not easily chased away, a fight erupted.

Host location and oviposition

The observed directed, active, and gregarious flight of *U. principalis* females within a few minutes after host eggs were laid is unique for the Trichogrammatidae, and even for egg parasitoids in general, as can be judged from the available literature. It is hypothesized that *Ufens principalis* is attracted by: (i) a kairomone possibly emanating from accessory gland products secreted by female *Homalodisca* on her eggs as they are laid inside leaf tissue; or (ii) by the combined effects of injury to leaf tissue due to insertion of the ovipositor and such an accessory gland kairomone. Support for the latter hypothesis comes from the example of *Trichogramma maidis* Pintureau & Voegelé (Hymenoptera: Trichogrammatidae) females which responded to a combination of odours from host eggs, host sex pheromone, and an extract from maize (the host plant), but not to any one of these olfactory stimuli by themselves (Kaiser *et al*., 1989). Moreover, it is known that the saliva of caterpillars of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), in combination with injured plant parts, can release highly volatile terpenoids that attract the parasitoid *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) (Turlings *et al*., 1990, 1991).

The oviposition activity of *U. principalis* was correlated with the oviposition activity of its host sharpshooter. Both insects had their peak oviposition activity in the afternoon in spring and summer. Especially on hot summer days (as in early September 2002), the period of ovipositional activity of *U. principalis* and *Homalodisca* occurred close to 1–2 h before sunset. In our study, this pre-dusk increase in *Homalodisca* ovipositonal activity on jojoba (mostly *H. coagulata*) was probably associated with migration of female sharpshooters to jojoba from neighbouring plants, such as the ubiquitous citrus in the vicinity of the University of California, Riverside jojoba field under study. Casual observations suggested that during most of the day, the majority of *Homalodisca* individuals observed on jojoba were *H. liturata* and rarely was *H. coagulata* observed. From 1730 h until sunset (in September 2002 and 2003) and as temperatures cooled down and the light intensity decreased, one could hear the buzzing sound of *Homalodisca* females as they began flying toward stem apices of jojoba. Kersting & Baspinar (1995) reported a similar pre-dusk surge in flight activity of the leafhopper, *Circulifer haematoceps* Mulsant & Rey (Hemiptera: Cicadellidae), in Turkey at the end of August. However, these authors stated that the majority of flying *C. haematoceps* were males and they did not associate the increase in flight activity with a surge in oviposition.

Field observations made in this study indicated that *U. principalis* (and also likely *U. ceratus*) is a primary parasitoid of *Homalodisca* eggs as this parasitoid directly attacked freshly laid eggs of *Homalodisca* before other parasitoids could have access to them. Moreover, the absence of *U. principalis* females on sticky material placed on egg masses one week after initial attack indicates that this species has a restricted window of time in which it parasitizes its host. This window of susceptibility of *Homalodisca* eggs to attack by *U. principalis* appears to be 1–87 min from the initiation of oviposition by female *Homalodisca*. No egg parasitoids other than *U. principalis* were observed on these very young egg masses.

Such observations strongly support the notion that other *Ufens* spp. imported into California for control of *H. coagulata* that were suspected of not being primary parasitoids (Triapitsyn, 2003) because of the failure to rear them in quarantine (Triapitsyn *et al*., 2002; Triapitsyn & Hoddle, 2002), could, after all, be primary parasitoids of *H. coagulata*. The lack of success in rearing these species could have arisen from the requirement of very young host eggs, a condition usually not met using standard parasitoid-rearing protocols.

The oviposition behaviour described for *U. principalis* is similar in general terms to that for other Trichogrammatidae such as *Trichogramma evanescens* Westwood (Van Dijken & Waage, 1987), *T. chilonis* Ishii (Suzuki *et al*., 1984), *O. krygeri* (Bakkendorf, 1934), and *P. andoi* (Vungsilabutr, 1978; Miura, 1992). In these species, oviposition involves a series of behaviours which include tapping of the antennae on the host egg, stopping, unsheathing the ovipositor, insertion of the ovipositor into the host egg (directly or through the plant), drilling, egg deposition, and withdrawal of the ovipositor. Abdominal vibration or trembling toward the end of ovipositional probes, as observed in *U. principalis*, was similarly reported by Van Dijekn & Waage (1987) for *T. evanescens* and by Suzuki *et al*. (1984) for *T. chilonis*. The ovipositional probe duration (mean 33.1 s) observed in *U. principalis* was shorter than that observed for other Trichogrammatidae such as *P. andoi* (147.9 s; Miura, 1992), *C. pulchra* (2–3 min; Bakkendorf, 1934), *Megaphragma mymaripenne* Timberlake (0.5–7.5 min; Hessein & McMurtry, 1988) and *T. chilonis* (400 s; Suzuki *et al*., 1984). This short probe time in *U. principalis* could be a result of several factors. First, its host eggs have relatively thin chorions (in comparison to hosts such as lepidopteran eggs) and are laid at a shallow depth below the surface of the leaf. Second, over evolutionary time, gregarious parasitism and competition for limited host egg resources may have caused individual *U. principalis* females to reduce the time spent in ovipositional probes in order to parasitize the highest number of eggs per unit time. Third, the small window of time in which host eggs can be parasitized could result in more efficient use of time so that the largest number of very young egg masses could be parasitized by an individual parasitoid.

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