# *AGANASPIS ALUJAI* (HYMENOPTERA: FIGITIDAE: EUCOILINAE), A NEW SPECIES ATTACKING *RHAGOLETIS* (DIPTERA: TEPHRITIDAE) IN THE NEOTROPICAL REGION

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## Abstract

A new neotropical species of *Aganaspis* (Hymenoptera: Figitidae, Eucoilinae) is described and compared to other *Aganaspis* species occurring in the Neotropical Region. This thelytokous species was reared from pupae of 2 species of fruit flies in the genus *Rhagoletis* (Diptera: Tephritidae), both in the *suavis* species group, and collected from 2 species of native walnuts in Mexico. Evidence of host specialization through diapause timing and notes on basic biology are provided.

Key Words: Hymenoptera, Figitidae, *Aganaspis*, *Rhagoletis*, Parasitoid

## Resumen

Una nueva especie neotropical de *Aganaspis* (Hymenoptera: Figitidae, Eucoilinae) se describe y compara con otras especies de *Aganaspis* de la región. Esta especie thelyotokica fue recuperada de pupas de dos especies de moscas de la fruta en el género *Rhagoletis* (Diptera: Tephritidae), ambas pertenecientes al grupo de especies *suavis* y obtenidas de dos especies nativas de nueces en México. Se provee evidencia de especialización a su hospedero manifestada por la regulación del tiempo de la diapausa y algunas notas sobre su biología básica.

Translation provided by the authors.

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The genus *Aganaspis* Lin (Hymenoptera: Figitidae, Eucoilinae) comprises only 6 species, which are distributed in the Neotropical and Indo-Pacific regions. The American species *A. pelleranoi* (Brèthes) and *A. nordlanderi* Wharton can be easily differentiated from the Asian species group (*A. daci* (Weld), *A. contracta* Lin, *A. ocellata* Lin, and *A. major* Lin) by several morphological features such as the shape of the scutellar disc and female antenna, absence of setae on the eyes, and lack of the median depression in the metapleuron (Wharton et al. 1998). Originally, this genus was described by Lin (1987) to accommodate Asian species. Later, following suggestions by Göran Nordlander, Ovruski (1994) placed the neotropical species *Ganaspis pelleranoi* (Brèthes) (= *G. carvalhoi* Dettmer) in *Aganaspis*. This placement has been accepted by subsequent authors (Wharton et al. 1998; Diaz & Gallardo 2000; Fontal-Cazalla et al. 2002; Guimarães et al. 2003). In a cladistic analysis of the subfamily Eucoiline (Fontal-Cazalla et al. 2002), the genus *Aganaspis* was included in the "Neotropical grade", an unresolved group of Neotropical taxa representing a morphological transition between the *Zaeucoila* group of genera and the 5 genus groups of higher eucoilines (The *Ganaspis* Foerster, *Chrestosema* Foerster, *Trybliographa* Foerster, *Rhoptromeris* Foerster, and *Kleidotoma* Westwood groups) recognized by Nordlander (1982).

*Aganaspis daci* (originally described as *Trybliographa daci* Weld), was first collected in Malaysia and Borneo, and introduced into Hawaii as a potential biocontrol agent for *Bactrocera dorsalis* (Hendel) (Clausen et al. 1965). This species is the only one of the 4 Asian species for which hosts have been recorded. *Aganaspis daci* was introduced into Florida (USA) where it established successfully on *Anastrepha suspensa* (Loew), although in low numbers (Baranowski et al. 1993). It was released in Mexico (Jiménez-Jiménez 1956), and Costa Rica (Wharton et al. 1981) for biological control of *Anastrepha* spp., but its establishment in both countries is doubtful (Wharton et al. 1998).

*Aganaspis pelleranoi* is a widespread neotropical species that occurs from México to Argentina and is most commonly found attacking *Anastrepha* larvae in several host plant species (Ovruski et al. 2000). This eucoiline species is a potential candidate for biological control of *Anas-*

*trepha* species of economic importance (Sivinski et al. 1997; Lopez et al. 1999). *Aganaspis nordlanderi* is only known from Costa Rica attacking larvae of *Ceratitis capitata* (Wiedemann) and *A. striata* Schiner (Wharton et al. 1998) and from Brazil attacking *A. bahiensis* Costa Lima, *A. striata* and one lonchaeid of the genus *Neosilba* McAlpine (Guimarães et al. 1999; 2003).

Described species of *Aganaspis* for which biological data have been gathered can be considered specialists in terms of their tephritid fruit fly host range but as generalists in terms of the number and diversity of plant species on which they are able to find their hosts. As far as their biology is concerned, no thelytokous strains have been found for any species in the genus and no described species of *Aganaspis* has previously been found to exhibit obligate diapause or infest diapausing species of temperate tephritids. Nonetheless, existence of facultative diapause was documented for populations of *A. pelleranoi* living in tropical sub-decidous and decidous forest in central Veracruz, Mexico (Aluja et al. 1998), and in subtropical rain-forest in northwestern Argentina (Ovruski et al. 2004).

In this paper, a new neotropical *Aganaspis* species, reared from *Rhagoletis ramosae* Hernandez-Ortiz on *Juglans major* var. *glabrata* (Torr.) A. Heller, and *Rhagoletis zoqui* Bush on *Juglans mollis* Engeim is described. Evidence of host specialization and diapause is furnished, and the relationships between the American *Aganaspis* species are discussed.

## MATERIALS AND METHODS

The description of *A. alujai* was based on quantitative measurements on 21 female specimens in Mexico that were reared from *Rhagoletis ramosae* and *Rhagoletis zoqui* recovered from single collections of *Juglans major* var. *glabrata* in Michoacan and *Juglans mollis* in Hidalgo, respectively. No males were reared. Quantitative measurements were made with an optical micrometer installed within Zeiss-Stemi SV6 stereo-microscopes. Scanning electron microscope (SEM) images were taken for detailed observation of characteristic morphological features. Specimens were prepared for SEM by taking them out of a 70% alcohol solution and placing them in 10% KOH for at least 10 minutes to clear structures. Specimens were then transferred to a Petri dish lined with a paper towel to allow room temperature evaporation of KOH. After 1 hour, specimens were cut with dissecting tools and placed on top of a carbon conductive tab affixed to a SEM stub. The specimens were coated with gold-palladium in a JEOL Model SINECOAT-JSC-1100. Images were taken with a JEOL Model JSM-5600LV microscope. Light microscopy images were taken with a MacroFire camera mounted on a MZ16Apo stereomicroscope and post-processed with AutoMontage™ and PhotoShop®. Terminology for the descriptions follows Wharton et al. (1998), with modifications as used by Fontal-Cazalla et al. (2002).

## RESULTS

### Species Description

### *Aganaspis alujai* Wharton & Ovruski, n. sp.
(Fig. 1a-f)

*Female*. Body length 2.5-3.0 mm; fore wing length 2.4-2.9 mm. Head and mesosoma black, metasoma mostly black, tending to castaneous brown apically and ventrally, with pattern of lighter coloration slightly variable among specimens, antennae black apically grading to dark brown over basal half, mandible brown, with apical teeth black, postgena dark brown, legs yellow brown with telotarsi, most of mid and hind coxa, and swollen portion of all femora dark brown. Head 1.9-2.2 times wider than long and 1.03-1.06 times wider than mesoscutum in dorsal view, 1.11-1.48 times higher than wide in frontal view. Toruli elevated laterally, forming short, shallow, orbital furrow between antennal base and internal eye margin. Vertex and frons bare, polished, unsculptured; occiput bare, densely and obliquely striate laterally and dorsal-laterally, smooth and polished mid-dorsally. Face shining, polished; clypeal furrows distinct, widely separated, very weakly converging dorsally, extending nearly half distance from ventral margin of clypeus to toruli; row of 3-4 long, weakly decurved setae in each clypeal furrow; 3-4 pairs of decumbent, medially directed setae above and lateral dorsal margin of clypeal furrow; longitudinal row of 6-7 setae extending along inner eye margin onto malar sulcus. Eyes weakly bulging, temples distinctly receding in dorsal view; 1.25-1.5 times higher than wide in lateral view, without visible setae at 60×. Temple 0.5-0.66 times as long as eye. Malar space 0.45-0.55 times height of eye; malar space with deep, complete malar sulcus; gena weakly striate and setose ventrally. Ocelli arranged in an isosceles triangle, posterior ocelli widely separated: distance between them 1.42-1.5 times distance between posterior ocellus and eye. Antenna (Fig. 1a) short, 2.4-2.5 times height of head, without distinct club; scape and pedicel 1.9 and 1.15 times as long as broad, respectively; first 3 flagellomeres slightly broader subapically than medially, flagellomeres 5-11 broader medially, nearly moniliform; first flagellomere slightly (1.06-1.13 times) longer than second; ratio of length to maximum width, all flagellomeres: 3.1:2.5:2.32-2.4:2.0-2.25:1.6-1.7:1.6-1.7:1.6-1.7:1.5-1.6:1.5-1.6:1.5-1.6:1.9-2.0. Mesosoma 1.25 times longer than high; 1.73-1.79 times longer than wide; 1.36-1.45 times higher than wide. Pronotal plate (Fig. 1b) protruding above anterior margin of mesoscutum, weakly notched; median bridge 1.42-1.5

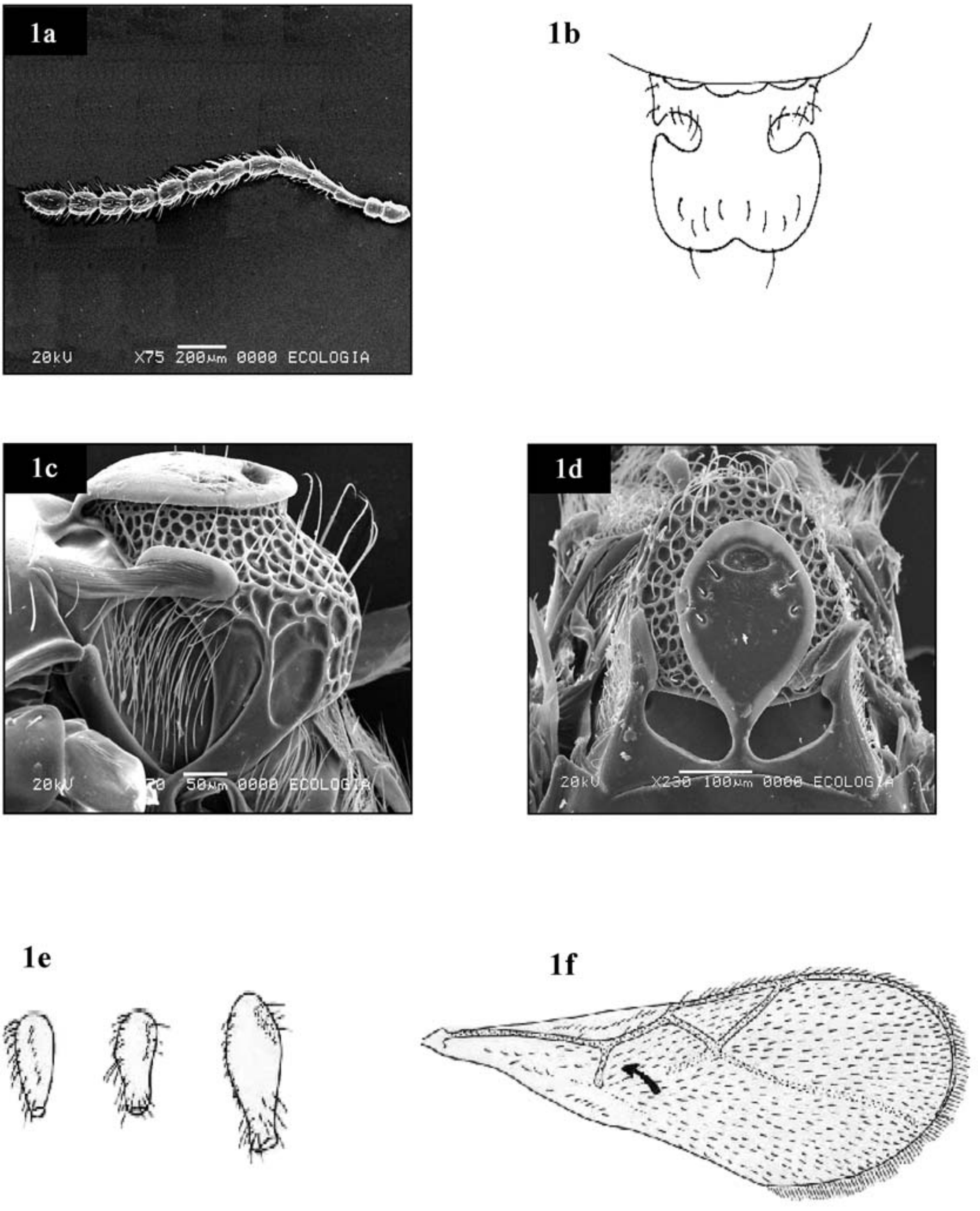


Fig. 1. *Aganaspis alujai*. a, female antenna; b, pronotal plate; c, scutellar disc and cup in profile; d, scutellar disc and cup in dorsal view; e, fore, mid, and hind coxae in lateral view; f, complete fore wing, with arrow showing the area behind Rs&M vein between Sc+R1 and basal section of Cu1.

times wider than anterior ocellus, and 0.35-0.40 times as wide as posterior part; anterior part of pronotal plate 5.65-5.70 times wider than long, with 5-6 setae on posterior margin of each lateral arm; posterior part 2.16-2.20 times wider than long, with 10-11 setae near posterior margin. Pronotum laterally polished, unsculptured, with tuft of white setae anteriorly, and 8-10 long, completely decumbent setae posteriorly. Mesoscutum 1.08-1.10 times as wide as long; notauli absent, represented by a row of 6-7 short setae on each side, each row converging anteriorly with lateral row of 8-9 short setae; parascutal impression weak, largely confined to area mesad tegula; mesonotal keel absent or barely visible as a weak median elevation anteriorly, replaced by weak median depression on posterior 0.3. Scutellar disc (Fig. 1c, d) distinctly and finely reticulate; posterior margin of disc rounded in dorsal view, sinuate in profile; height of scutellum about 0.9 times length of scutellar plate in lateral view; fovea behind lateral keel of scutellum 1.56-1.67 times higher than long. Scutellar plate (Fig. 1d) large, subrounded, 1.2-1.4 times longer than wide, posterior margin strongly rounded, never truncate, anterior margin slightly extending through scutellar fovea; width of plate 0.64-0.66 times width of disc; surface nearly flat, with either 2 or 3 pairs of lateral punctures, each bearing a short, erect seta. Pit of scutellar plate (Fig. 1d) small, elliptical, abutting posterior rim of plate, 2.0-2.15 times wider than long, and 0.3-0.4 times width of scutellar plate. Lateral bars (Fig. 1c) long, 0.92-0.96 times as long as scutellar plate, smooth to finely striate. Scutellar fovea large, deep, 2.09-2.15 times wider than long. Mesopleuron smooth, completely without setae; precoxal carina straight along ventral margin, curving dorsally along anterior 0.3 and posterior 0.2. Metanotum densely pubescent laterally. Metapleuron smooth above, rugulose ventral-posteriorly, with strongly carinate posterior margin; bare except along posterior margin. Propodeum short, 1.3-1.4 times wider than long in dorsal view, densely white-pubescent, the setae almost completely obscuring area laterad lateral propodeal carina; lateral propodeal carinae slightly diverging ventrally then abruptly broadened posteriorly delimiting a round, deep fovea posterior-medially; upper part between lateral carinae with long, dense, dorsally-directly, white setae. Anterior face of fore and mid coxae extensively covered with long setae; hind coxa anterior-medially with patch of short setae extending more than half length from base, and with patches of longer setae ventrally; mid and hind coxae with short, dense, white pubescence on postero-dorsal margin, and with some long setae directed backwards (Fig. 1e). Fore wing (Fig. 1f) 2.7-2.9 times longer than wide, with longest seta on posterior-apical margin 0.08-0.11 times maximum width of wing; marginal cell 2.5-2.7 times as long as deep, completely closed along wing margin; Rs 1.55-1.73 times longer than 2r; costal cell with a longitudinal row of setae on ventral surface extending from basal to apical section of cell, otherwise bare; cell immediately distad basal vein uniformly setose, with vertical row of 3-5 setae parallel to basal vein (Fig. 1f). Metasoma 1.39-1.45 times longer than high; syntergum 0.85-0.92 times as long as metasoma, and 1.09-1.12 times length of mesosoma; hairy ring at base of syntergum absent mid-ventrally, otherwise complete and very well-developed; syntergum emarginate dorsally, maximum length in lateral view 1.15-1.2 times length along mid-dorsal line; minute punctures present on posterior third of syntergum and on visible portions of remaining terga.

### Material Examined

The above description is based on 21 females, all reared from *Rhagoletis ramosae* from a single collection of *Juglans major* var. *glabrata*. No males were reared. Female holotype, Mexico, Michoacán, Zirimicuaro, 12-IX-02, ex. *Rhagoletis ramosae* in *Juglans major* var. *glabrata*, Diaz-Fleischer collector (Instituto de Ecología, A.C.); paratypes, same data as holotype, 6 females (Instituto de Ecología, A.C.); 12 females (Texas A&M University); 1 female (US National Museum); 1 female (University of California, Riverside). The coordinates for the site are 19°24'N, 101°58'W, at 1,306 m above sea level. The environmental conditions for the site are mean annual temperature 17°C and mean annual precipitation 1,350 mm.

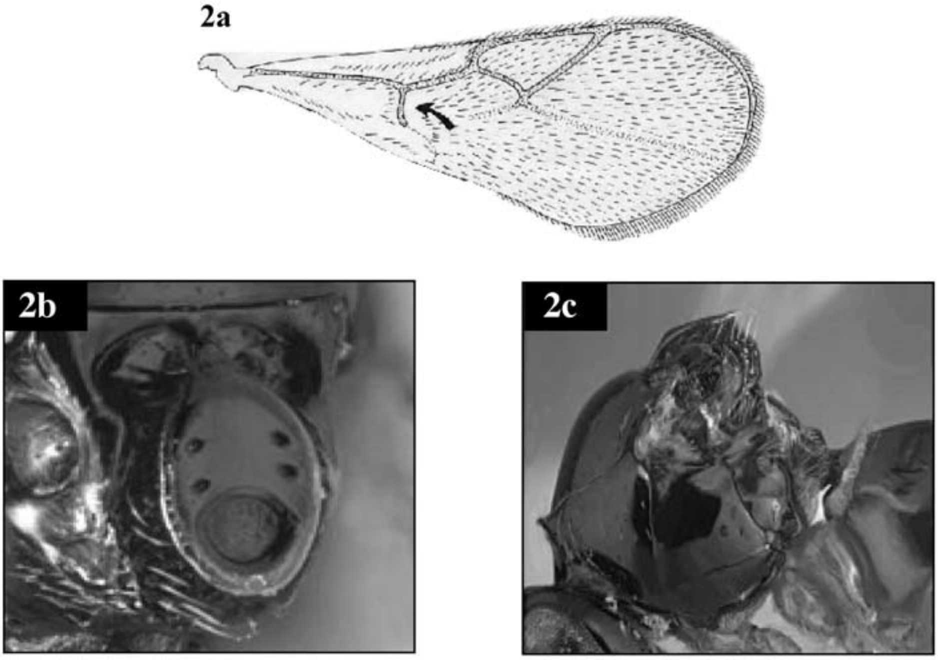
Additional examined material includes 78 females emerging from pupae of *Rhagoletis zoqui* collected in 19-IX-03, from *Juglans mollis* collected at Lagunita, Hidalgo, Mexico, 20°39'N, 99°14'W, 2621 m above sea level. Mean annual temperature and precipitation for the site are 16°C and 500 mm.

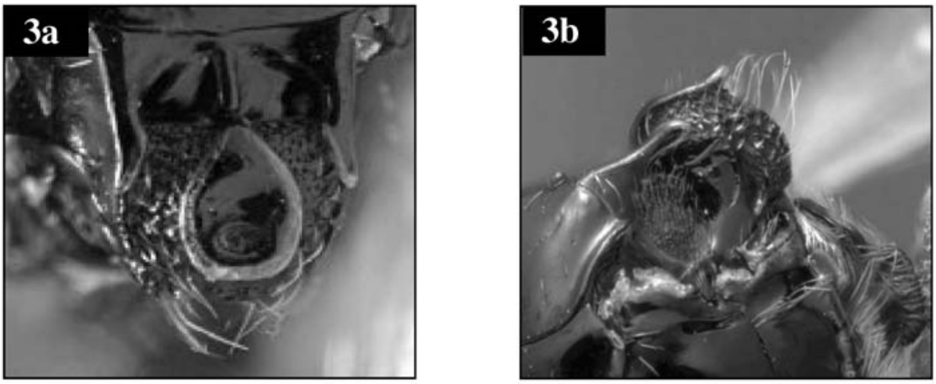
### Etymology

This species is named after Martín Aluja, in recognition of his numerous contributions to ecology and biology of neotropical fruit fly parasitoids.

### Diagnosis

This new species differs from *A. daci* and other Old World species by the absence of obvious setae on the female compound eye, possession of a scutellar disc that bulges posteriorly beyond the apex of the scutellar plate, and absence of a distinct cleft in the posterior carinate margin of the metapleuron. The new species shares these and other features with the 2 previously described New World species, *A. nordlanderi* and *A. pelleranoi*, but differs from them primarily in details of the scutellar plate, venation, and setal pattern of the fore wing. The scutellar plate extends into the scutellar fovea and is relatively flat in both *A. pelleranoi* (Fig. 2b, c) and *A. alujai* (Fig. 1c, d) whereas in *A. nordlanderi* (Fig. 3a, b) the plate does not extend into the scutellar fovea and is weakly but distinctly recurved in profile. The plate is distinctly larger (relative to the disc) and more parallel-sided in *A. pelleranoi* than in *A. alujai*. The portion of R1 between 2r and the wing margin is much longer in *A. nordlanderi* than in either of the other 2 species, resulting in a greater





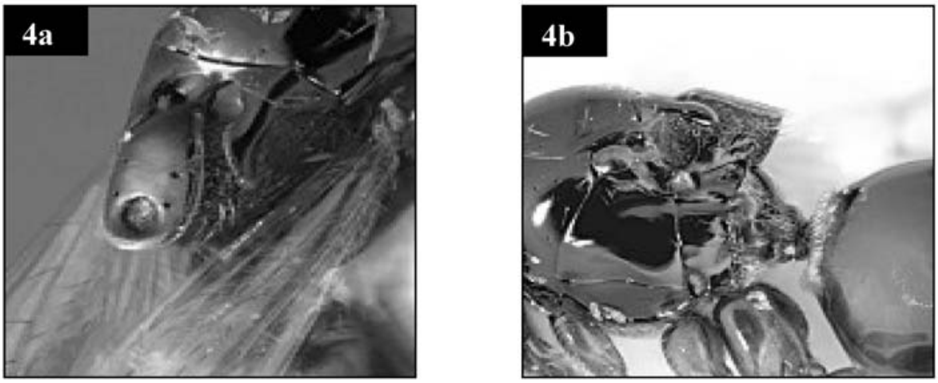


Fig. 2. *Aganaspis pelleranoi*. a, complete fore wing; b, scutellar disc in dorsal view; c, scutellar d7isc in profile.
Fig. 3. *Aganaspis nordlanderi*. a, scutellar disc in dorsal view; b, scutellar disc in profile.
Fig. 4. *Aganaspis daci*. a, scutellar disc in dorsal view; b, scutellar disc in profile.

Rs/2r ratio for *A. nordlanderi* and a marginal cell in which the greatest height is more anteriorly displaced (see Figs. 1f, 2a). The marginal cell is closed by a distinct vein in both *A. pelleranoi* and *A. alujai* (usually more distinctly pigmented in *A. alujai*), but the marginal cell is open in *A. nordlanderi*. The costal cell is densely setose in *A. nordlanderi* but largely reduced to a single median line of setae in the other 2 species (the line of setae extends the full length of the cell, but becomes a double row of setae over the apical 0.3-0.4). The cell immediately distad the basal vein is more or less uniformly setose in *A. alujai* and *A. nordlanderi* (Fig. 1f) but is bare adjacent the basal vein in *A. pelleranoi* (Fig. 2a). The new species can be separated from the previously described New World species by its darker coloration. Specimens of *A. pelleranoi* and *A. nordlanderi* that have been reared from *C. capitata* and various species of *Anastrepha* Schiner have the female metasoma generally orange and the legs entirely yellow to yellow-brown whereas the metasoma and legs are largely black in *A. alujai*.

### Comments

Based on the characters discussed above, *A. alujai* shares more features with *A. pelleranoi* than with *A. nordlanderi*. However, when compared with species such as *A. daci*, the character states found in *A. nordlanderi* appear to be derived relative to those in *A. pelleranoi* and *A. alujai*, suggesting that the resemblance between the latter 2 species may not be a result of shared, derived features. Further assessment of relationships would be premature in the absence of a clear outgroup for the New World species. Problems associated with the generic classification were discussed in Wharton et al. (1998), in which the use of the name *Trybliographa* for these species (most recently by Diaz et al. 2006) was rejected.

Prior to the description of *Aganaspis* by Lin (1987), Legner & Goeden (1987) reared an incompletely identified eucoiline figitid from the walnut husk fly, *Rhagoletis completa* Cresson, infesting *Juglans microcarpa* Berland in western Texas and southeastern New Mexico. Examination of voucher material (1 male, 1 female from Davis Mountains, TX) from the University of California, Riverside collection revealed that specimens from Texas are nearly identical to those from central Mexico and represent either another population of the same species or a very closely related species. A third specimen, collected from walnut trees in Lincoln Co., New Mexico, is identical to those from Texas. There are minor differences in venation (Cu1 is distinct in the material from Mexico, but the basal vein is shorter in specimens from the U.S., and lacks the angular extension of Cu1 ventrally) and the scutellum. Thus, we prefer to restrict the definition of *A. alujai* to material from Michoacán and Hidalgo until material from intermediate areas can be examined.

### Biology

The specimens forming the type series were reared from 1,250 puparia recovered from fruits of *J. major* var. *glabrata* in Michoacán. From these puparia, 351 *R ramosae* adults with a sex ratio roughly equivalent to 0.5 and 21 female parasitoid specimens were recovered. The remaining 878 puparia yielded no flies or parasitoids. Additional collections of *Juglans mollis* in 2003 in Lagunita, Hidalgo yielded 1000 pupae of *Rhagoletis zoqui*, from which 397 adult *R. zoqui* at a sex ratio roughly equivalent to 0.5 and 78 female parasitoid specimens were recovered. Pupae were collected from infested fruit on Sep 12, 2002, and on Sep 19, 2003, and kept at ambient temperature and humidity at the INECOL in Xalapa in a pupal rearing chamber with no temperature control. Xalapa has a mean annual relative humidity of 66% and mean annual temperature of 18.6°C (CONAGUA, http://smn.cna.gob.mx/productos/observatorios/historica/jalapa.pdf). Adult tephritid hosts from Michoacan emerged from May 8 through Aug 15, 2003 with an average time from pupal recovery to adult emergence of 298 days. Parasitoids from Michoacan also entered diapause but emerged as adults from parasitized puparia from Aug 5 through Sep 18, 2003, with an average time from pupal recovery to adult parasitoid emergence of 348 days (Fig. 5A). Adult tephritid hosts from Hidalgo emerged from Mar 24 through Aug 20, 2004 with an average time from pupal recovery to adult emergence of 294 d. Parasitoids from Hidalgo also entered diapause and emerged as adults from parasitized puparia from Aug 20 through Oct 24, 2004 with an average time from pupal recovery to adult parasitoid emergence of 387 d (Fig. 5B). In the laboratory, the average time from adult emergence from parasitized pupae until death of *A. alujai* was 12.76 d at 27°C and 75% R.H. ($n$ = 21).

## KEY

The following key includes all *Aganaspis* species occurring in the New World.

1. Eye covered with scattered setae (more readily visible in females than males); scutellar plate long, protruding behind scutellar disc (Fig. 4a, b); posterior carinate margin of the metapleuron interrupted by a median cleft or depression (Introduced to New World). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. daci* (Weld)

—Eye without setae; scutellar plate short, not extending posteriorly beyond scutellar disc (Figs. 1c, d; 2b, c; 3a, b); posterior carinate margin of the metapleuron continuous, not interrupted by a cleft . . . . . . . . . . . . 2

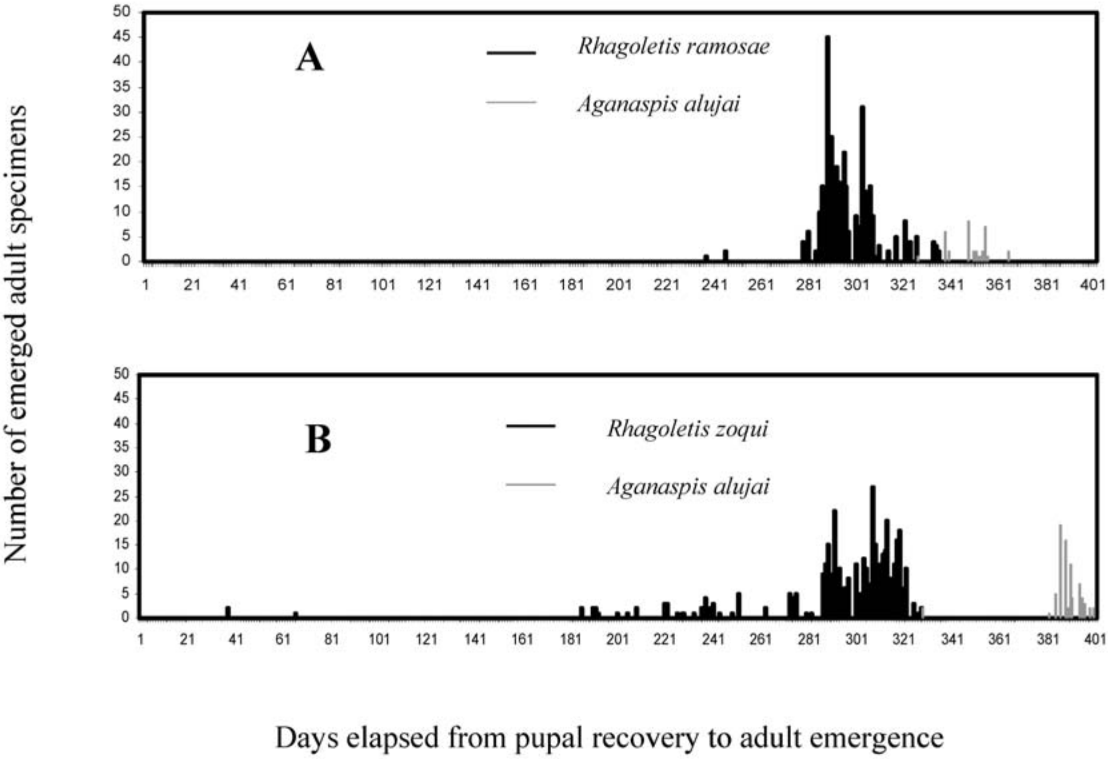


Fig. 5. Daily post-diapause emergence patterns of (A) adult *Rhagoletis ramosae* (black histogram) and adult *Aganaspsis alujai* (grey histogram), and (B) adult *Rhagoletis zoqui* (black histogram) and adult *Aganaspsis alujai* (grey histogram).

2. Costal cell densely setose; scutellar cup not extending through scutellar fovea (Fig. 3a), with a long anterior bridge; posterior margin of scutellar disc slightly concave medially and thus weakly bilobed in dorsal view; marginal cell completely open. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. nordlanderi* Wharton

—Costal cell with a single longitudinal row of setae on ventral surface, otherwise largely bare; scutellar cup extending through scutellar fovea, with a short anterior bridge (Figs. 1d, 2b); posterior margin of scutellar disc rounded in dorsal view; marginal cell completely closed . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3. Scutellar plate large (Fig. 2b), nearly parallel-sided, 0.71-0.85 times as wide as scutellar disc; fore wing with area immediately behind basal vein bare (Fig. 2a); hind leg pale, yellow to yellow-brown . . .*A. pelleranoi* (Brèthes)

—Scutellar plate small (Fig. 1d), rounded, 0.60-0.66 times as wide as scutellar disc; fore wing with area behind basal vein densely setose (Fig. 1f); hind leg (especially coxa and femur) extensively black . . . . . *A. alujai*, new species

## DISCUSSION

The observed delay in emergence of adult parasitoids with respect to that of adults of their tephritid hosts also has been documented by Feder (1995) for *Utetes canaliculatus* (Gahan) (reported as *Opius lectus* Gahan) attacking *Rhagoletis pomonella* Walsh on hawthorn. Such synchronization is undoubtedly commonplace among parasitoids of univoltine hosts, allowing the hosts to reach sexual maturity, mate, and oviposit, and allow their larvae to reach a suitable developmental stage for parasitism. (For more detailed discussion of various aspects associated with host-parasitoid synchronization, see Godfray 1994.) The synchronization between *A. alujai* and their hosts *R. ramosae* and *R. zoqui* suggests a strong degree of host specialization. Although we recognize that the temperatures at which we took longevity records for adult parasitoids might exceed those encountered in their natural habitats, we can conclude that the lifespan of adults is relatively short and therefore synchronized emergence with their host is a key adaptation if *A. alujai* is specialized to parasite walnut-infesting *Rhagoletis* flies with obligate diapause as appears to be the case.

Parasitoids of multivoltine host flies, such as *Anastrepha ludens* (Loew), *A. obliqua* (Macquart), *A. fraterculus* (Wiedemann), *A. striata*, and *A. serpentina* (Wiedemann), also may exhibit facultative diapause, allowing them to overcome periods of pronounced host scarcity (Aluja et al. 1998; Sivinski et al. 2000). For example, some *A. pelleranoi* individuals attacking *Anastrepha* larvae in *Psidium guajava* L. diapaused for up to 11 months in central Veracruz, Mexico (Aluja et al. 1998).

The sites where *Aganaspis* were found associated with walnut-infesting flies in the *Rhagoletis suavis* group are separated from each other by great distance and geographically isolated from each other by numerous barriers of orographic and climatic nature. In both sites only females were recovered from infested tephritid puparia, strongly suggesting that both strains collected are fully parthenogenic (i.e., thelytokous). Whether or not thelytoky arose independently in both cases or had a common origin could be determined through genetic analysis of individuals from both populations or by examining whether or not both strains possess and share similar strains of sex ratio distorting agents. The species of *Aganaspis* (as currently defined), thus offer exciting possibilities to explore the evolution of thelytoky in a group not known to possess this trait as well as function and evolution of diapause in temperate vs tropical taxa.

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