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ORIGINAL ARTICLE

Description and biological traits of a new species of *Paracentrobia* (Hymenoptera: Trichogrammatidae), an egg parasitoid of the sharpshooter *Tapajosa rubromarginata* (Hemiptera: Cicadellidae) in Argentina

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During a survey of egg parasitoids of sharpshooters (Cicadellidae: Cicadellini and Proconiini), an undescribed species of *Paracentrobia* Howard was detected. It is here described and illustrated, and laboratory data on its life cycle are reported. *Paracentrobia tapajosae* sp. n. is a primary parasitoid of *Agalliana ensigera* Oman and *Tapajosa rubromarginata* (Signoret). Sixty-seven percent of the exposed host eggs were parasitized by *P. tapajosae* sp. n., and eggs with well-developed sharpshooter embryos were successfully attacked. The developmental cycle from egg to adult was 21.3 ± 2.3 days. Adult longevity was 6.8 ± 4.5 days, with females living longer than males. The sex ratio, considering only mated females, was 1:2.2 (males/females). Under laboratory conditions, *P. tapajosae* is a facultatively gregarious parasitoid. Laboratory data suggest a likely potential of this species as a biological control agent.

Durante la búsqueda de parasitoides de huevos de chicharritas (Cicadellidae: Cicadellini y Proconiini), se obtuvo una especie no descrita de *Paracentrobia* Howard, la cual se describe e ilustra en esta contribución aportando además datos sobre su ciclo de vida. *Paracentrobia tapajosae* sp. n. es un parasitoide primario de huevos de *Agalliana ensigera* Oman y *Tapajosa rubromarginata* (Signoret). La tasa de parasitoidismo obtenida en laboratorio fue del 67% de los huevos expuestos, y huevos en avanzado estado de desarrollo también fueron exitosamente atacados. El tiempo medio de desarrollo fue de $21,3 \pm 2,3$ días. La longevidad de los adultos fue de $6,8 \pm 4,5$ días, y las hembras vivieron más que los machos. La proporción de sexos, considerando solo hembras fecundadas, fue 1:2.2 (machos/hembras). En condiciones de laboratorio, *P. tapajosae* se comportó como facultativamente gregario. Los datos de laboratorio sugieren que esta especie tiene un buen potencial como agente de control biológico.

Keywords: Argentina; biocontrol agent; Cicadellinae; life cycle; *Paracentrobia*; Proconiini

Introduction

Egg parasitoids are considered among the most important natural enemies of Auchenorrhyncha (Waloff & Thompson 1980; Freytag 1985; Denno & Roderick 1990). Since the early 1990s, the glassy-winged sharpshooter, *Homalodisca vitripennis* (Germar) (Hemiptera: Cicadellidae), has proceeded to expand its numbers and its range, becoming a very serious problem pest of grapevines in California, USA. A survey of egg parasitoids of the proconiine sharpshooters (i.e., species of the leafhopper tribe Proconiini of the subfamily Cicadellinae) was initiated in 2000 in South America to identify candidate agents for the biological control of this pest in the USA (Jones 2001).

Most of Argentina north of the 40° parallel was surveyed using sentinel eggs of *Tapajosa rubromarginata* (Signoret), a native South American proconiine sharpshooter related to *H. vitripennis. Tapajosa rubromarginata* is common on many crops in the Tucumán Province of Argentina, and sometimes its populations rise notably producing damage in sugarcane crops (Costilla et al. 1972; Remes Lenicov et al. 1998). Among the 20 egg parasitoid species collected was an undescribed species of *Paracentrobia* Howard (Hymenoptera: Trichogrammatidae).

The genus *Paracentrobia* has a worldwide distribution and includes 44 described species (Noyes 2003), of which eight nominal species occur in the New World. Only two of these have known hosts:

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P. subflava (Girault) attacking *Exitianus obscurinervis* (Stål), *Amplicephalus simpliciusculus* Linnavuori, *Dalbulus maidis* (De Long & Wolcott) and *Haldorus sexpunctatus* (Berg) (Virla 1999), and *P. acuminata* (Ashmead) obtained from eggs of *Cuerna costalis* (Fabricius), *Draeculacephala minor* [=*D. producta* (Walker)], *D. mollipes* (Say), *D. portola* Ball, *Homalodisca coagulata* (Say) [=*H. vitripennis* (Germar)], *H. insolita* (Walker), *Saccharosydne saccharivora* (Westwood), *Lestes dryas* Kirby, and *Lestes unguiculatus* Hagen (according to Noyes 2003).

Here a new species of *Paracentrobia* from Argentina is described as *P. tapajosae* sp. n., and we also report on its life history parameters under laboratory conditions.

Materials and methods

Collection of specimens and taxonomic studies

Specimens of the new species were obtained from egg masses of *Tapajosa rubromarginata* collected on Johnson grass (*Sorghum halepense*) in the field at El Manantial (26°49′50.2″S, 65°16′59.4″W; elevation 495 m) and San Miguel de Tucumán (26°48′35.7″S, 65°16′25.3″W; elevation 470 m) from February to March 2004, and also from sentinel eggs of *Agalliana ensigera* Oman (Cicadellidae: Agalliini) on corn leaves exposed at El Manantial from 24 January to 2 February 2005. Each field-collected egg mass was transferred to a Petri dish with wet tissue paper and covered with clear plastic food wrap to prevent desiccation, and to keep adult wasps from escaping.

The description follows the terminology used by Pinto (2006). The measurements reported are relative, except for the total length (head to gastral tip, without the antennae), which is given in millimeters.

Maintenance of the colony and bionomic studies

Laboratory studies were carried out in PROIMI, San Miguel de Tucumán, Tucumán Province, Argentina. Duration of development, sex ratio, adult longevity, and potential factitious hosts were observed using a colony established in the laboratory for two generations. In addition, the oviposition and copulation behaviors were observed. The colony was initiated with field-collected egg masses of *T. rubromarginata* laid on *Sorghum halepense* leaves and parasitized by *P. tapajosae* sp. n. In order to obtain host eggs in the laboratory, field-collected females of *T. rubromarginata* were placed in polyethylene-terephtalate (PET) cylindrical cages (35 cm high × 18 cm diameter) on potted citrus plants (20 liter pots) which were checked daily for eggs. Although *P. tapajosae* sp. n. were obtained from host eggs on monocots, we used host eggs on citrus (*Citrus sinensis* and *C. limon*) because the leaves are resistant to rotting and desiccation after they are cut off, and thus are especially suitable for rearing egg parasitoids that need about three weeks to complete development. Desiccation or decaying of egg substrate is considered one of the major problems for breeding this kind of egg parasitoid in a laboratory (Sahad 1984; Logarzo et al. 2004).

The behavior of the new species was observed using a stereo-binocular microscope, observing different individuals throughout the two breeding generations, using the adults obtained from 33 exposed egg masses on citrus leaves (395 eggs).

Between four and seven wasps (males and females), about 12 h old, were kept in glass tubes (20 cm × 2.5 cm) with *T. rubromarginata* eggs for 24 h. One hole was covered with mesh for aeration, the other hole was fitted with cotton plugs which were moistened with water and honey as needed. After exposure, the egg masses were checked daily to ensure the freshness of the leaves until wasp emergence. The colony was kept and the experiments were conducted, at 24 ± 3°C, 70–80% relative humidity and artificial photoperiod of 14/10 h (light/dark). In the assays, we considered as "mated" all the female individuals that were kept together with males for at least 12 h following their emergence. Parthenogenetic reproduction was assessed by exposing four unmated females to newly laid egg masses (five egg masses each, a total of 172 eggs) and determining the sex of the resulting progeny.

Host eggs that changed content homogeneity and coloration after 7–9 days were considered "parasitized", while those developing eyespots of the host leafhopper were considered "unparasitized". Sharpshooter nymphs hatching from the unparasitized eggs were counted daily. After two weeks, when parasitoid emergence was nearly completed, each leaf was dissected and the host eggs remaining in the plant tissue were counted. By this time, most *P. tapajosae* individuals had attained the pupal stage, thus it was easy to distinguish parasitized from unparasitized eggs.

Development from egg to adult emergence, progeny sex ratios, and percentage of parasitism were measured using host eggs of three age ranges: ⩽24, 25–71 and 72–96 h old. The developmental time from egg to adult emergence was measured using 284 individuals, and adult longevity was monitored twice a day from this batch of wasps (143 females and 141 males), from within 12 h after emergence until death. The observations were conducted on single wasps in individual vials without host material but with a small honey drop for feeding.

We also conducted experiments with potential alternative host eggs. Host eggs less than 48 h old were exposed for 24–48 h to four to seven mated females of *P. tapajosae*. The following species and host plants were used: Fulgoroidea: Delphacidae: *Peregrinus maidis* (Ashmead) on corn (235 eggs) and *Delphacodes kuscheli* Fennah on oats (103); Membracoidea: Cicadellidae: *Chlorotettix fraterculus* (Berg) on corn (72), *Dalbulus maidis* on corn (134), *Exitianus obscurinervis* on Johnson grass (14), and *Plesiommata mollicella* (Fowler) on corn (14).

When appropriate, data were analyzed using a *t*-test for mean separation at the 0.05 level of significance, or analysis of variance (ANOVA), and means were compared with the Tukey test.

Results

Taxonomy

Paracentrobia tapajosae Viggiani, sp. n. (Figures 1, 2)

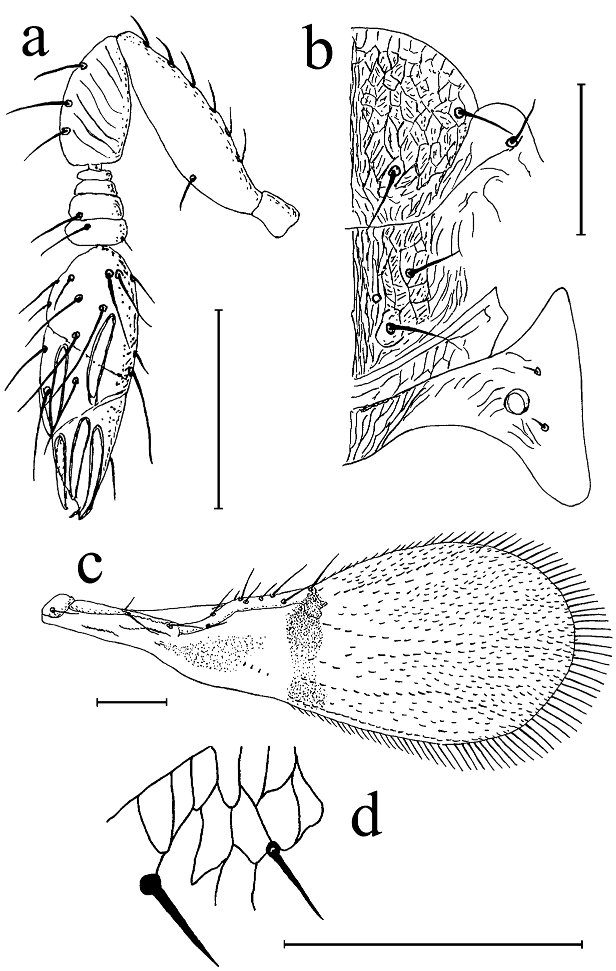

Figure 1. *Paracentrobia tapajosae* sp. n., female. (a) Antenna; (b) mesonotum (left half); (c) forewing; (d) lateral area of a gastral tergum. Scale bar: 0.1 mm.

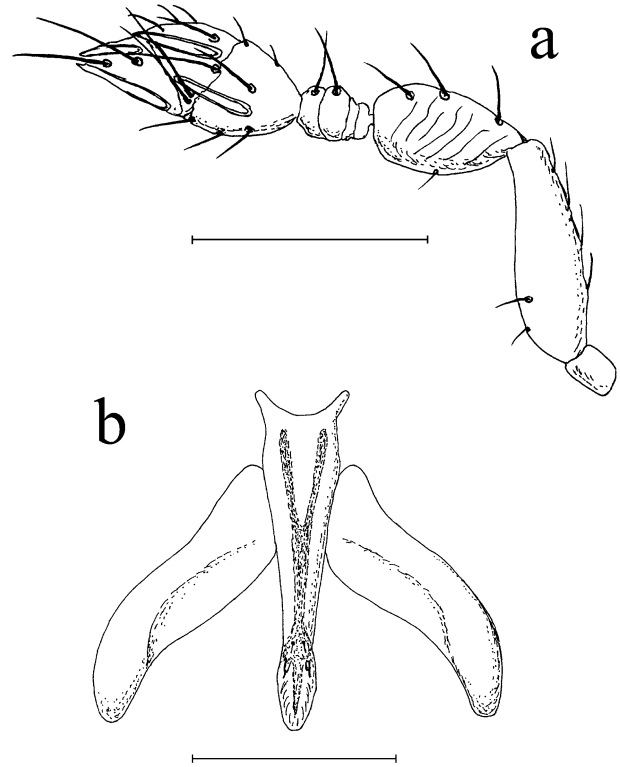

Figure 2. *Paracentrobia tapajosae* sp. n., male. (a) Antenna; (b) male genitalia with the appendages of the last sclerite, ventral view. Scale bar: 0.1 mm.

Paracentrobia sp.: Logarzo et al. 2004, p. 512.
Paracentrobia nr *acuminata* (Ashmead): Virla et al. 2005, p. 283.

Diagnosis

The new species can be distinguished by the combination of the following features: body yellow with black markings on head and mesosoma; metasoma with six pairs of black spots on each side; forewing with discal microtrichia arranged in five rows starting at level of the stigmal vein and with a moderately dense ciliation between delimited areas of disc. *Paracentrobia tapajosae* sp. n. is very close to *P. subflava*, but can be separated from the latter by the discal ciliation which is denser between the areas delimited by the rows; in *P. subflava*, these areas are mostly bare, as reported by Girault (1911), and confirmed by one of us (G. Viggiani) who examined a photograph of the type specimen of *P. subflava*.

Description

Female

Length 1.2 mm. Body yellow. Head with a black spot on each side of clypeal area, connected with a concolorous occipital stripe across malar space. Antenna yellow with some brown, mostly on first claval segment. Eye red brown. Mesosoma with pronotum having an H-shaped black marking, starting from neck area. Mesosternum with some brown. Mesopleuron with a subtriangular black spot near hind coxa and another along the ventral border. Propodeum with a thin black marking along lateral margin and part of posterior margin. Legs yellow. Metasoma with six pairs of black spots on each side. Forewing hyaline, with a black band at level of stigmal vein, more pronounced on upper half. Antenna (Figure 1a) with scape 3.5 times as long as wide; pedicel one-third shorter than scape; funicle with two anelli and two transverse funicular segments; clava 1.2 times as long as scape, three times as long as wide, with asymmetrical segments, of which first (basal) segment as long as third (apical) segment, second segment shorter, each claval segment with linear sensilla (three to four on apical segment). Mesosoma with midlobe of mesoscutum (Figure 1b), mostly longer than wide, rather irregularly reticulate, mesoscutum and scutellum each with two pairs of setae; posterior pair of the scutellar setae slightly longer. Metanotum narrow, with transverse striation. Propodeum with distal area clearly produced posteriorly and with transverse striation oriented toward tip of disc. Forewing (Figure 1c) moderately broad, 2.5 times as long as wide; vein length ratios as 15 (submarginal vein): 8 (premarginal vein): 11 (marginal vein): 4 (stigmal vein); main setae on the veins as follows: one on submarginal vein, two on premarginal vein, four on marginal vein; one seta near base of stigmal vein; discal microtrichia arranged in five rows starting at level of stigmal vein and with a moderately dense ciliation between delimited areas of disc. Longest marginal setae about one-fifth of maximum forewing width. Hind wing with one median and two submarginal rows of setae. Legs normal with middle spur shorter than corresponding basitarsus (7:13). Metasoma longer than mesosoma (10:7), metasomal terga with following setae: one pair each on first and second terga, two pairs each on third and fourth terga, with the posterior pair much stronger, one pair on fifth tergum and five pairs on sixth tergum; lateral area of terga (Figure 1d), mainly near setae, with cellulate sculpture (cells mostly longer than wide); ovipositor slightly exerted and about twice as long as metatibia.

Male

Similar to female, except antenna with a shorter clava, about twice as long as wide, apically with longer setae (Figure 2a). Metasoma about as long as mesosoma, last sternum with elongate appendages. Genitalia as typical of the genus (Figure 2b), with two very small ventral setae and vestigial digiti.

Etymology

The specific name (an adjective) refers to the generic name of the main leafhopper host of this new taxon.

Material examined

Holotype ♀ on slide [deposited in Fundación e Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (IMLA)]: Argentina, Tucumán, El Manantial (26°49′50.2″S, 65°16′59.4″W; 495 m), February to April 2004, E. Virla and E. Luft Albarracin, from eggs of *Tapajosa rubromarginata* (Signoret). Paratypes (all on slides): Argentina, Tucumán: El Manantial: February to April 2004, E. Virla and E. Luft Albarracin, from eggs of *T. rubromarginata*, 4♀ and 3♂ [1♀, 1♂ in Entomological Collection, Dipartimento di Entomologia e Zoología Agraria «Filippo Silvestri», Università degli Studi di Napoli «Federico II», Portici, Italy (IENU) and 1♀, 1♂ in Museo de la Plata, La Plata, Buenos Aires, Argentina (MLPA); remaining in IMLA]; 13–21 January 2005, E. Luft Albarracin, from eggs of *T. rubromarginata*, 3♀ (IMLA). San Miguel de Tucumán, E. Virla and E. Luft Albarracin, from eggs of *T. rubromarginata*, 3♀ and 1♂ [1♀, 1♂ in Entomology Research Museum, University of California at Riverside, California, USA (UCRC)' remaining in IMLA]. Additional (non-type) material (all specimens on slides): El Manantial, 24 January to 2 February 2005, E. Virla and E. Luft Albarracin, from eggs of *Agalliana ensigera* Oman, 4♀ and 1♂ (IMLA).

Distribution

In addition to the above-mentioned localities, *P. tapajosae* sp. n. was reared from eggs of *T. rubromarginata* on Johnson grass in Tafí Viejo (26°45′12.9″S, 65°14′40.5″W; 552 m) and Horco Molle (26°46′50.1″S, 65°19′38.3″W; 703 m), both in Tucumán Province.

Bionomics of *Paracentrobia tapajosae* sp. n

General behavior

Paracentrobia tapajosae sp. n. is a primary parasitoid of *T. rubromarginata*. All individuals obtained from the egg masses of this leafhopper, collected in the field on *S. halepense*, were solitary (only one parasitoid emerged per sharpshooter egg). Also, only one wasp per egg emerged from the field-exposed sentinel eggs of *A. ensigera*.

Under laboratory conditions, *P. tapajosae* sp. n. was facultatively gregarious, with one to four individuals emerging per host egg. We regard this phenomenon as directly related to the laboratory conditions, because we found superparasitism in 77.7% of the attacked egg masses (in 14 out of 18 egg masses). In about 30% of the attacked egg masses (n=33), the females oviposited in all the offered eggs regardless of the number of eggs available, ranging between six and 22. When females reached the last egg they continued ovipositing once again in the same eggs while walking back until they finally arrived where they had started. When more than one female was confined with a single egg mass, we commonly observed two or more females ovipositing in the same egg mass. The females spent on average 2 min for parasitizing each host egg.

Emergence took place mostly in the morning, with only a few imagines emerging in the afternoon. An adult emerged from the egg through a hole made in the apical area but never at the very tip of the egg. About 80% of the holes were made in the upper surface of the egg masses, while the remaining 20% emerged from the other side of the leaf. In a single superparasitized egg mass, individuals could emerge either via a single hole made by the first wasp or from holes made independently by each of the adults.

Parasitism rate

Twenty-six out of 33 egg masses (78.8%) exposed to *P. tapajosae* sp. n. females in the laboratory were attacked, producing 284 wasps (1.25 adults per egg were obtained) from 265 parasitized eggs (67.1%) out of 396 exposed. Not all parasitoids in the egg masses completed the development due to rotting or desiccation of the host eggs or the plant substrate, resulting in failure of the wasps to emerge from eight egg masses. A total of 46 host sharpshooter nymphs emerged from the 130 unparasitized eggs.

Eggs with well-developed sharpshooter embryos were successfully parasitized by *P. tapajosae* sp. n. Although the percentage of attacked eggs of different age was different (Table 1), the differences were not significant (F=1.87, df=30, P=0.1718). The older the attacked egg mass were, the more nymphs and fewer adult wasps emerged.

Development

The duration of development from oviposition to adult emergence of *P. tapajosae* sp. n. averaged 21.3 ± 2.3 d. Significant differences were found between adults emerging from eggs aged 25–71 h and those emerging after more than 72 h (Table 2; Figure 3). When this parameter was analyzed by sex, females and males did not show significant differences in regard to the time to reach the adult stage (t=−1.54, df=264, P=0.124) (females 21.5 ± 2.0 days; males 21.06 ± 2.6 days).

Four to five days after oviposition, the host egg content became heterogeneous, with the formation of numerous clots. One to two days later, we were able to observe clear divisions in the eggs containing the larvae in case they were superparasitized. Later on, the parasitized eggs changed coloration from creamy to dark brown or black; this was visible 6–11 days after oviposition.

Sex ratio

The wasps reproduce sexually and parthenogenetically (arrhenotoky). The overall sex ratio of *P. tapajosae* sp. n. in the laboratory was 1:2.2 (male/female), considering only the offspring generated from mated females. Sex ratio differed due to host egg age. Less than 24-h-old eggs produced 32.6% males, while older eggs produced 65.5% males (t=−2.5, df=16, P=0.02). Analysis of the data obtained from *T. rubromarginata* field-collected egg masses revealed that the sex ratio was female biased, roughly 1:4 (15 males/65 females). The sex ratio of

Table 1. Influence of host egg age on the parasitization of *Tapajosa rubromarginata* eggs by *Paracentrobia tapajosae* sp. n.

	Age of host eggs (h)		
	⩽24	25–71	⩾72
Exposed host eggs	198	112	85
Host egg masses	14	11	8
Parasitized host eggs	162	64	39
Parasitism (%)	81.8	57.14	45.8
Eggs that bred adult wasps (egg masses)	134 (9)	70 (7)	24 (2)
Emerged adult wasps	155	103	26
Ratio wasps/eggs	1.16	1.47	1.08
Hatched host nymphs n (%)	0 (0)	20 (17.9)	26 (30.6)

Table 2. Duration of development (mean ± SD) of *Paracentrobia tapajosae* n. sp. parasitizing *Tapajosa rubromarginata* eggs of different age.

	Age of host eggs (h)		
P. tapajosae developmental phases (days)	⩽24	25–71	⩾72
Egg laying to changes in host egg color	4.82 ± 0.83 a	5.51 ± 1.08 b	4.61 ± 0.49 a
n	160	43	46
Egg laying to host egg division (in superparasitism)	5.06 ± 0.53 a	8.13 ± 1.35 b	5.72 ± 1.54 c
n	140	69	14
Egg laying to black host eggs	7.83 ± 1.38 a	11.12 ± 3.61 b	8.08 ± 1.35 a
n	181	102	51
Egg laying to wasp emergence	21.50 ± 2.54 ab	20.82 ± 2.15 a	21.73 ± 1.19 b
n	155	103	26

n, number of host eggs observed. Means with the same letter are not significantly different (ANOVA, $P \geq 0.05$).

P. tapajosae sp. n. reared from the exposed sentinel eggs of *A. ensigera* was 1:3.4 (5 males/17 females).

Longevity

The average adult longevity of *P. tapajosae* sp. n. was 6.8 ± 4.5 days. We found significant differences in adult longevity between females and males, with females living longer than males ($t = 6.18 \times 10^{-9}$, df = 268, $P < 0.05$) (females 8.2 ± 4.7 days; males 5.2 ± 3.7 days).

Tests of host range

Under laboratory conditions, no eggs of Delphacidae or other species of Cicadellidae tested were attacked by *P. tapajosae* sp. n., as only host nymphs emerged. Females only examined the offered eggs of *P. mollicella* and *C. fraterculus*; however, they did not attempt to oviposit in them.

Discussion

Superparasitism

The observed facultative gregarism in *P. tapajosae* sp. n. under laboratory conditions contrasts with the habit of *Paracentrobia andoi* (Ishii), whose females showed gregarism in both laboratory and field. *Paracentrobia andoi* lays two or three eggs in a single host egg (Vungsilaburt 1978). Interestingly, in *P. tapajosae* sp. n. all the embryos reached the adult stage while in *P. andoi* only one larva per host survived (Vungsilaburt 1978). The gregarism observed in *P. tapajosae* sp. n. could be related to the lack of competitive or aggressive behavior for host eggs among the females. This aggressive behavior was observed in other species of Trichogrammatidae attacking auchenorrhynchous eggs (*Pseudoligosita krygeri* (Girault) (Bakkendorf 1934), *Paracentrobia andoi* (Miura 1992), *Ufens ceratus* Owen, and *U. principalis* Owen (Al-Wahaibi et al. 2005).

As recorded for *P. subflava* (Virla 1999), *P. tapajosae* sp. n. is able to oviposit and develop even on an advanced red-eyed host embryo. In this trait it differs from *P. andoi*, which is able to discriminate the developmental stages of the host eggs and does not oviposit in eggs with developed embryos (Vungsilaburt 1978).

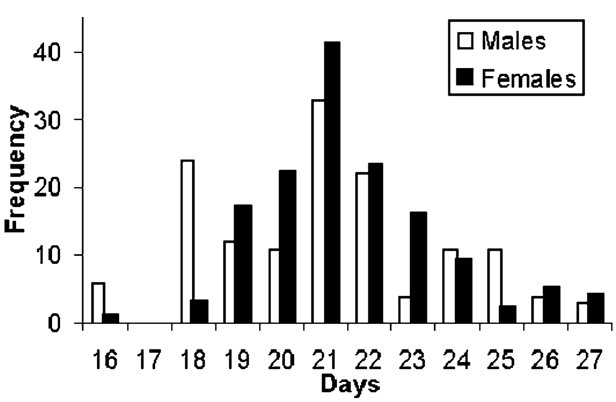

Figure 3. Frequency distribution of the egg to adult period (in days) of *Paracentrobia tapajosae* sp. n. in the laboratory.

Parasitation rates

Under laboratory conditions parasitization rates of *P. tapajosae* sp. n. (>67%) were similar to other trichogrammatid species. Logarzo et al. (2004) recorded an average 72.5% parasitism and wasp emergence of 44% for *Zagella delicata* De Santis (Trichogrammatidae), which is another *T. rubromarginata* egg parasitoid occurring in Tucumán Province, its host nymphs emerging from only 11.65% of the exposed eggs. As in *P. subflava* attacking the eggs of *Exitianus obscurinervis* (Virla 1999) and *Ceratogramma etiennei* Delvare attacking the eggs of the root weevil *Diaprepes abbreviatus* (L.) (Curculionidae) (Amalin et al. 2005), average parasitism of *P. tapajosae* sp. n. was highest in the more freshly laid eggs.

Common traits of parasitoids

Further similarities with congeneric species and other trichogrammatids comprise the egg-to-adult period (Vungsilaburt 1978; Miura 1990; Virla 1999), longevity (*P. subflava* 10 days, Virla 1999; *P. andoi* 4.1 days, Miura 1990, 15.9 d, Vungsilaburt 1978; *Z. delicata* 10 days, Logarzo et al. 2004).

Paracentrobia tapajosae sp. n. as a new biological control agent?

Several features of *P. tapajosae* sp. n. suggest that it might be a useful agent for biological control of *T. rubromarginata*, a potential pest of sugarcane, and perhaps of *Agalliana ensigera* on corn: (1) the high parasitization rate of the host eggs, (2) the successful development on advanced host embryos, (3) the female-biased sex ratio, (4) the narrow host range, and (5) the fact that the parasitoids can easily be reared in the laboratory. Furthermore, the gregarisms observed under laboratory conditions would even increase the efficiency of the rearing. A disadvantage of the species is its relatively short lifespan because it leaves only a short period for the release of laboratory-reared wasps to the field. No wasps emerged from eggs of the two Delphacidae and four Cicadellidae species tested. Although most of the *Paracentrobia* species are known to attack a broad spectrum of host species within the same group of Auchenorrhyncha (Virla 1999; Noyes 2003), up to now we do not have any evidence for further host species of *Paracentrobia tapajoase* sp. n.

Acknowledgements

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