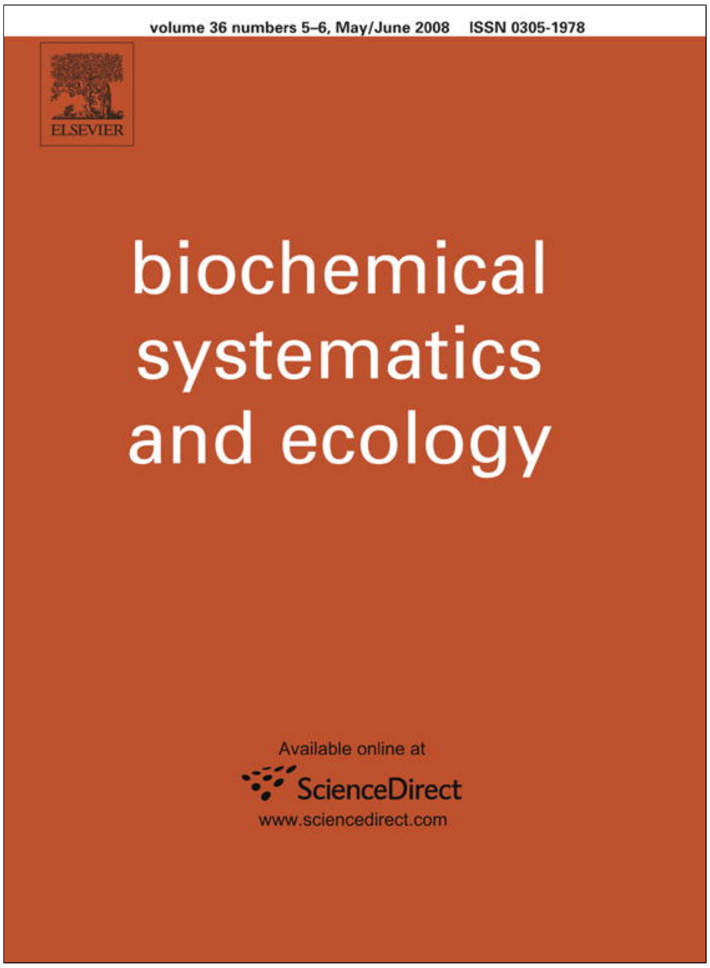

volume 36 numbers 5–6, May/June 2008 ISSN 0305-1978

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Biochemical Systematics and Ecology 36 (2008) 369–376

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Chemical and behavioral defenses of the neotropical harvestman *Camarana flavipalpi* (Arachnida: Opiliones)

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Received 9 February 2007; accepted 19 December 2007

Abstract

The defensive secretion of the harvestman *Camarana flavipalpi* (Gonyleptidae) was chemically characterized, revealing the presence of a single, highly volatile component (2-methyl-5-ethyl-phenol). Individuals do not frequently use chemical defenses and rely mainly on thanatosis as defense. Two types of emission of secretions were recorded: a globule at the gland opening without liquid displacement and liquid displacement along the lateral margins of the dorsal scute with accumulation of fluid at the lateroposterior area of the body. The anterior opening of the ozopore is covered by an integumentary dome that faces the laterodorsal area of the scute. The lateral channel is well defined near the opening of the ozopore and along the lateral margin of the dorsal scute as rows of small granules. The ozopore morphology of *C. flavipalpi* is similar to closely related species and simplified when compared with other species that promptly release chemical secretions.
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Keywords: Chemical shield; Gonyleptidae; Morphology; Ozopore; 2-Methyl-5-ethyl-phenol

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1. Introduction

One of the most conspicuous features of the order Opiliones is the presence of a pair of exocrine glands located at the anterior margins of the cephalothorax. These glands, known as scent glands or repugnatorial glands, produce a variety of volatile secretions that are released under the threat of predation (review in Gnaspini and Hara, 2007). Although all harvestman species have scent glands, some species rarely release secretions when disturbed, relying mainly on fleeing, thanatosis or crypsis as defense (Gnaspini and Hara, 2007). Two extreme cases are the manaosbiid *Zygopachylus albomarginis*, whose individuals rarely release secretions even if they are held with forceps (Cokendolpher, 1987), and the gonyleptid *Promitobates ornatus*, which presents reduced gland sacs, simplified morphology of the ozopore, and never releases chemical secretions (Hara and Gnaspini, 2003; Hara et al., 2005). Duffield et al. (1981) suggested that chemical defenses in harvestmen are only employed when evasive measures were not successful in preventing the attack of a potential predator. Moreover, even when the chemicals are emitted towards the aggressor, they are

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0305-1978/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.bse.2007.12.006

generally secreted in limited doses (Juberthie, 1961; Eisner et al., 1971), probably because production of chemical compounds in arthropods has a high energy cost (Blum, 1981, 1985).

Previous studies on species that rarely release secretion have suggested that the morphology of their gland opening (ozopore) is more simplified when compared with closely related species that promptly release chemical secretions (Hara and Gnaspini, 2003). In this study we describe the ozopore morphology and characterize the chemical composition of the defensive secretion of the neotropical harvestman *Camarana flavipalpi* (Gonyleptidae: Tricommatinae), a species that rarely releases chemical secretions, even when persistently disturbed. Our aim was to investigate if *C. flavipalpi* shows a simplification in its ozopore morphology and also in the chemical nature of the compounds produced. We compared our results with those obtained for *Pseudopachylus longipes*, another representative of the subfamily Tricommatinae, in which the emission of the defensive secretion occurs with liquid displacement through integumentary grooves (Hara and Gnaspini, 2003).

2. Material and methods

2.1. Harvestmen collection and rearing

C. flavipalpi is a secretive harvestman that is mainly found among leaf-litter and under rocks during the day, and walking on low vegetation at night. There is no information on the biology of this species, but laboratory observations show that it is mainly active at night, and individuals are predominantly solitary, but may form small diurnal aggregations of up to 10 individuals under rocks and rotting logs. Females lay isolated eggs in hidden places and do not show any additional form of parental care (G. Machado, unpublished data). Sexual dimorphism is evident, with males presenting an elongated femur IV, nearly 100% longer than that of females.

Individuals of *C. flavipalpi* used in the chemical analyses and morphological description of the ozopore were collected in Ubatuba, São Paulo State, southeastern Brazil, in December 2004. In the laboratory, 20 individuals were reared in the same terrarium (60 × 40 cm base, 35 cm high) containing soil, pieces of rocks and trunks as shelters, and a dish with water to maintain the humidity. They were fed with dead insects and an artificial diet for ants (Bhatkar and Whitcomb, 1970) twice a week. Temperature and moisture conditions were controlled and ranged from 23 to 25 °C and from 80 to 90%, respectively, and a light schedule of 13L:11D was maintained in the laboratory. For the behavioral observations, another 45 individuals (30 males and 15 females) of *C. flavipalpi* were collected in Ubatuba in November 2006. They were reared and maintained under the same conditions as described above. Voucher specimens were deposited at the Museu de Zoologia da Universidade de São Paulo (MZSP), Brazil.

2.2. Chemical analyses

Analyses were carried out using an HP 6890/5973 system equipped with HP5 fused silica capillary column (30 m × 0.25 mm × 0.25 μm). Column temperatures were programmed from 50 to 200 °C at 10 $°C\ min^{-1}$ and subsequently from 200 to 290 °C at 16 $°C\ min^{-1}$. The injector temperature was maintained at 250 °C. Helium was used as carrier gas, at flow rate of 1 $mL\ min^{-1}$. The mass spectra were taken at 70 eV and the scanning speed was 3.54 scans s^{-1} from m/z 40 to 450. NMR spectral data were acquired from Varian Inova spectrometer, operating at 499.88 MHz for ^1H NMR. $CDCl_3$ was used as solvent and TMS as an internal reference (δ 0.0). Chemical shifts δ were recorded in ppm and coupling constants J in Hertz (Hz). TLC analyses were performed on silica Merck F_{254} Aluminum Sheets and the spots were visualized by UV (254 nm). All solvents were of high analytical grade, bi-distilled before using. Cotton wool was successively extracted with bi-distilled ethyl acetate and the solvent was evaporated under vacuum.

Chemical defense exudates were collected by pressing cotton wool (50–70 mg) onto the gland openings. The exudates from seven individuals (2.1 mg total) were then either extracted with ethyl acetate (about 5 mL) and analyzed by GC–MS or with $CDCl_3$/TMS (600 μL) for the NMR experiments.

2.3. Behavioral response towards threats

To investigate under which circumstances individuals of *C. flavipalpi* release chemical secretions a modification of the protocol established by Hara and Gnaspini (2003) was used, which consisted of three steps of increasing disturbance: (1) the individual was seized in the distal region of the right femur IV for 10 s ($n = 15$); (2) the basal regions of right femurs I and II of the individual were seized at the same time for 10 s ($n = 15$); and (3) the dorsum (mesotergal areas) and venter of the individual were seized at the same time for 10 s ($n = 15$). In the three cases, the stimulus was applied using forceps whose points were covered with rubber tubes to avoid damaging the cuticle of the animals. Each individual was tested only once and randomly assigned to one of the three kinds of stimuli, since continuous disturbance of the same individual may increase the chances of releasing chemical secretions. Individuals were scored as respondent if they released chemical secretions, which are easily recognized by their strong phenolic smell and their white coloration. Releasing of only enteric fluid was recorded, but the individuals were scored as non-respondent. For the respondent individuals, the time elapsed between the release of chemical secretions and the complete evaporation of the liquid was recorded. The trials were conducted under room temperature (nearly 25 °C) from 16:00 to 19:00 h. Individuals were tested under a stereomicroscope in order to observe in detail the displacement of both the enteric fluid and chemical secretions.

2.4. Morphology of the ozopore

Specimens maintained in 70% ethanol were cleaned in a solution of a commercial detergent in water (1:3) for 15–20 s in ultrasound equipment (cf. Pinto-da-Rocha, 2002). In order to remove the detergent, the material was left in water under the ultrasound for four sessions of 15 min each, the water being replaced after each session. Finally, the material was dehydrated in 100% ethanol for 1 h and let air-drying. After dehydration, the material was mounted on a stub and gold coated in a Balzer SCD 50 Sputter Coater. The material was examined with the ZEISS DSM 940 scanning electron microscope of the Electronic Microscopy Laboratory of the Instituto de Biociências of the Universidade de São Paulo (IBUSP), Brazil. The terminology of the structures used here follows Hara and Gnaspini (2003).

3. Results

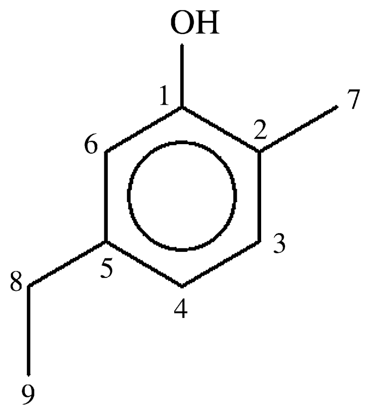
3.1. Chemical analyses

Analysis of *C. flavipalpi* defensive secretion (0.3 mg) by GC–MS and TLC revealed the presence of a highly pure substance. Comparison of the electron impact mass fragmentation (EIMS) pattern with the literature (McLafferty and Stauffer, 1992) suggested the occurrence of methyl-ethyl-phenol. However, the aromatic ring substitution pattern could not be assigned from the EIMS spectrum only. For ^{1}H NMR experiments, secretions were collected from seven specimens, totaling *ca.* 2.1 mg (0.3 mg per individual). The aromatic region displayed an evident 1,2,5 substitution pattern, with a doublet at δ 7.03 (H-3, J ortho at 7.6 Hz), a double-doublet at δ 6.70 (H-4, J ortho 7.6 Hz; J meta 1.5 Hz) and a doublet with meta coupling (H-6, J 1.5 Hz) at δ 6.40, each signal integrating for one hydrogen. NOE difference spectrum displayed 0.53% of signal increment in H-3 when the methyl group at δ 2.22 was irradiated. No increments were observed in ethyl group signals. Therefore, it was inferred that ethyl substituent was located at position 5 and the compound was then identified as 2-methyl-5-ethyl-phenol (**1**) (Fig. 1). A broad water signal was observed in ^{1}H NMR spectrum at δ 1.70, indicating that some aqueous enteric fluid was collected together with the defensive secretion.

3.2. Behavioral response towards threats

There was no respondent individual in the first two steps of disturbance ($n = 30$), although three of them emitted enteric fluid. Eight out 15 tested individuals released chemical secretions when seized by the dorsum and venter at the same time (step 3 of disturbance). Among the respondent individuals, six released chemical secretions from only one gland opening and two from both gland openings. After experimental manipulation, nearly 65% of non-respondent individuals exhibited thanatosis behavior, in which the legs were rigid (generally fully extended laterally) and the individuals became motionless for a period from 8 s to nearly 11 min (mean ± SD = 206.8 ± 190.4 s; $n = 24$; Fig. 2).

Two types of emission of secretion were recorded: (1) a globule at the gland opening without liquid displacement ($n = 1$) and (2) liquid displacement along the lateral margins of the dorsal scute with accumulation of fluid at the lateroposterior area of the body forming a droplet ($n = 7$; Fig. 3). Mixtures of chemical secretions with enteric fluid were recorded in the seven cases in which there was liquid displacement along the body of the animals. In these cases, the



(1)

Fig. 1. Chemical defense compound of the harvestman *Camarana flavipalpi*. (**1**) 2-Methyl-5-ethyl-phenol. GC−MS: *m/z* 136 (M^+, 42%), 121 (100%), 115 (3%), 107 (9%), 103 (7%), 91 (9%), 77 (16%), 65 (4%). ^{1}H NMR (499.88 MHz, $CDCl_3$, TMS) δ 7.03 (d, 1H, H-3, *J* 7.6 Hz), 6.70 (dd, 1H, H-4, *J* 7.6, 1.5 Hz), 6.40 (d, 1H, H-6, *J* 1.5 Hz), 2.57 (q, 2H, H-8, *J* 7.6 Hz), 2.22 (s, 3H, H-7), 1.70 (br s, OH), 1.22 (t, 3H, H-9, *J* 7.6 Hz).

enteric fluid was released before the chemical secretion ($n = 4$) or nearly at the same time as the chemical secretion, which was released directly into the flowing enteric fluid ($n = 3$). On two occasions it was evident that the chemical secretion was intermittently discharged into the enteric fluid.

The chemical secretion is white in color, even after the mixture with the enteric fluid. The mean time the mixture of chemical secretion and enteric fluid took to loose this white coloration was 237.3 s (SD = 138.6 s; min−max = 58−510 s; $n = 8$), and the mean time it took to completely evaporate from the body surface was 546.3 s (SD = 257.6 s; min−max = 176−1092 s; $n = 8$).

3.3. Morphology of the ozopore

The anterior opening of the ozopore of *C. flavipalpi* is covered by an integumentary dome that faces the laterodorsal area of the dorsal scute (Fig. 4A). This dome is crossed by a transversal slit, which extends from the area near the trochanter apophyses up to the apex of the integumentary dome (Fig. 4B). There is no sign of a "posterior opening" (sensu Hara and Gnaspini, 2003) of the ozopore or of a V-shaped cut in the posterior rim of the slit. The lateral channel is well defined near the opening of the ozopore and along the lateral margin of the dorsal scute as rows of small granules (Fig. 4A,B). Although some setiferous tubercles may be found nearly 0.5 mm above the lateral channel, there are no sensorial pegs along it.

4. Discussion

Quinones and phenols are widely distributed in the chemical secretions of arthropods such as insects and millipedes (Whitman et al., 1994). The phenol released by the gonyleptid *C. flavipalpi* has already been identified in chemical secretions from harvestmen species belonging to three families: the stygnommatid *Stygnomma spinifera* (Duffield et al., 1981), the cosmetids *Cynorta astora* (Eisner et al., 1977) and *Eucynortula albipunctata* (Roach et al., 1980), and the gonyleptid *Pachyloidellus goliath* (Acosta et al., 1993). Because cosmetids are the sister group of gonyleptids (Kury, 1994), similarities between the chemical secretions of their representatives may be regarded as homology. Stygnommatids, however, belong to another superfamily (Giribet and Kury, 2007) and the presence of compound (**1**) should be interpreted as an independent event of evolution of this chemical exudate. It is worth noting that in all species previously studied compound (**1**) is produced together with other substances, while *C. flavipalpi* produces it as a single chemical secretion. Few species of the suborder Laniatores have been recorded to produce only one chemical compound; among them is the gonyleptid *P. longipes*, which belongs to the same subfamily as *C. flavipalpi*, the Tricommatinae. Individuals of *P. longipes* release a secretion composed exclusively of 3-ethyl-5-methyl-phenol (Hara et al., 2005) that is isomer of the compound (**1**) produced by *C. flavipalpi*. Therefore, chemical data indicate

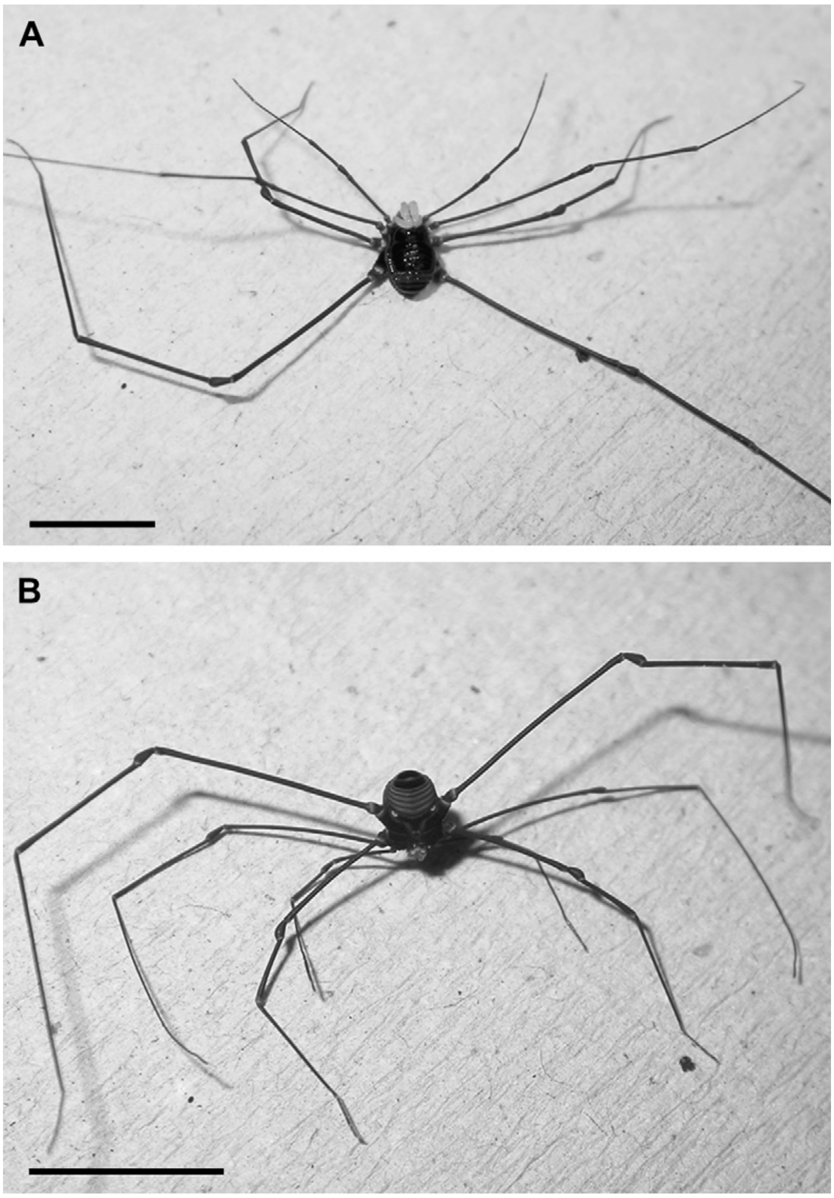


Fig. 2. Two motionless individuals of the harvestman *Camarana flavipalpi* exhibiting thanatosis behavior. Note that in (A) the legs are rigid and fully extended laterally, whereas in (B) they slightly retracted. Scale bars = 1 cm.

a close chemotaxonomic relationship between these species, suggesting possible similarities in the biosynthetic origins of defensive secretions.

The amount of secretion released by each individual of *C. flavipalpi* is only 0.3 mg, which is nearly 25 times less than the discharge of fluids released by individuals of another gonyleptid, *Acutisoma longipes* (Machado et al., 2005). Experiments with *S. spinifera* have shown that 2-methyl-5-ethyl-phenol – the major component of the secretion in this species – is extremely effective against ants and lizards (Duffield et al., 1981). It is possible that even in small amounts, the chemical secretion of *C. flavipalpi* is able to repel natural enemies. However, individuals of *C. flavipalpi* do not frequently use chemical defenses because there was no response in the first two steps of disturbance, when only the legs of the individuals were seized. Even in the third step of disturbance, when their body was gently squeezed, only 50% of the individuals released secretions. A similar disturbance evoked no emission of secretions in the manaosbiid *Z. albomarginis* (Cokendolpher, 1987), but a massive discharge in the cosmetid *Vonones sayi* (Eisner et al., 1971). Thus, different species show different degrees of responsiveness to disturbance; those that are cryptically colored and present thanatosis behavior clearly are less responsive and rarely release chemical secretions (e.g., Cokendolpher, 1987; Machado and Vasconcelos, 1998; Pereira et al., 2004). Among the few respondent individuals of

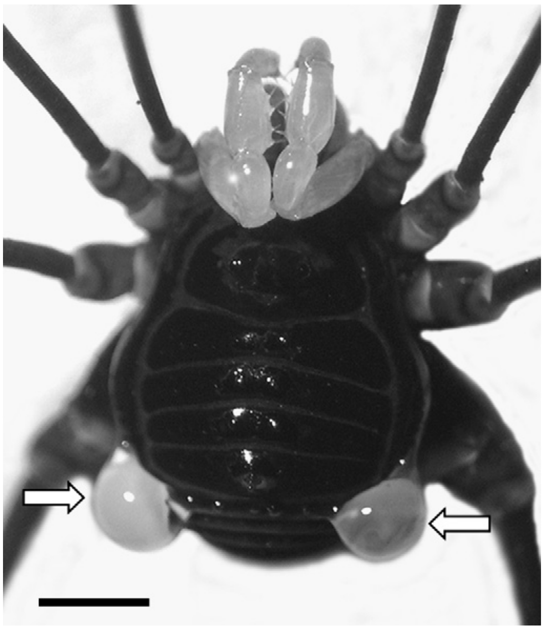


Fig. 3. Adult male of the harvestman *Camarana flavipalpi* with two droplets (arrows) formed by the mixture of enteric fluid and defensive secretion (photos: B.A. Buzatto). The fluid is released in the ozopore, runs along the lateral margins of the dorsal scute, and accumulates at the lateroposterior area of the body. Scale bar = 1 mm.

C. flavipalpi, most released chemical secretions through only one gland opening, which means they are capable of controlling the discharge of secretions in each gland sac independently. Individuals of the gonyleptid *Goniosoma spelaeum* (Gnaspini and Cavalheiro, 1998), the cosmetid *V. sayi* (Eisner et al., 1971), and the sironids *Parasiro coiffaiti* and *Siro rubens* (Juberthie, 1961) can also exercise considerable control over the quantity of fluid they emit, adjusting their output to the intensity of stimulation. Thus, independent of the species, chemical secretions are generally used conservatively so that adequate levels of defensive exudates may be maintained for future encounters with potential predators (Duffield et al., 1981).

The types of emission recorded for *C. flavipalpi* correspond to the mechanisms 1b and 2c, according to the classification of Hara and Gnaspini (2003). Mechanism 1b (emission of a secretion globule at the gland opening) has already been observed in several subfamilies of Gonyleptidae, but this study is the first to report it in the Tricommatinae. Mechanism 2c (liquid displacement along a row of tubercles at the margins of the dorsal scute), on the other hand, has already been reported for the tricommatine *P. longipes*, and it is supposed to increase the evaporating surface and to create a chemical shield around the body of the harvestman protecting the animal after the emission of secretion (Acosta et al., 1993; Hara and Gnaspini, 2003; Machado et al., 2005). Our observations showed that the chemical secretion of *C. flavipalpi* takes about 9 min to evaporate (when the droplet looses the white coloration). However, it takes up to 18 min for the remaining transparent fluid to completely evaporate from the body surface. If the transparent fluid contains traces of the compound (**1**), it is possible that the mixture may also increase the duration of the chemical shield, prolonging the time of evaporation of the chemical secretion.

The ozopore morphology of *C. flavipalpi* is similar to that of a close relative, *P. longipes* (see Fig. 5 in Hara and Gnaspini, 2003): both have a short integumentary dome facing laterally, a simple transversal slit, and both lack the ‘‘posterior opening’’ of the ozopore and the V-shaped cut in the posterior rim of the slit. However, along the lateral channel of *C. flavipalpi* the rows of tubercles are more evident than in *P. longipes* and there are no sensorial pegs. Other gonyleptids, such as *P. ornatus* and *Longiperna cancellata* (Mitobatinae), do not release chemical secretions at all (Hara and Gnaspini, 2003) and, despite the fact they are not closely related to *C. flavipalpi* (Pinto-da-Rocha, 2002), there are some convergences in their ozopore morphology: they have a short dome facing laterally and a simple opening without the V-shaped cut (Hara and Gnaspini, 2003). Contrary to *C. flavipalpi*, however, there is a marked reduction in the lateral channel and a complete absence of sensorial pegs in the Mitobatinae species. When compared to the sister family Cosmetidae or to species of other subfamilies of Gonyleptidae that promptly release large amounts of chemical secretion (e.g., Goniosomatinae, Gonyleptinae, and Progonyleptoidellinae), the ozopore morphology of

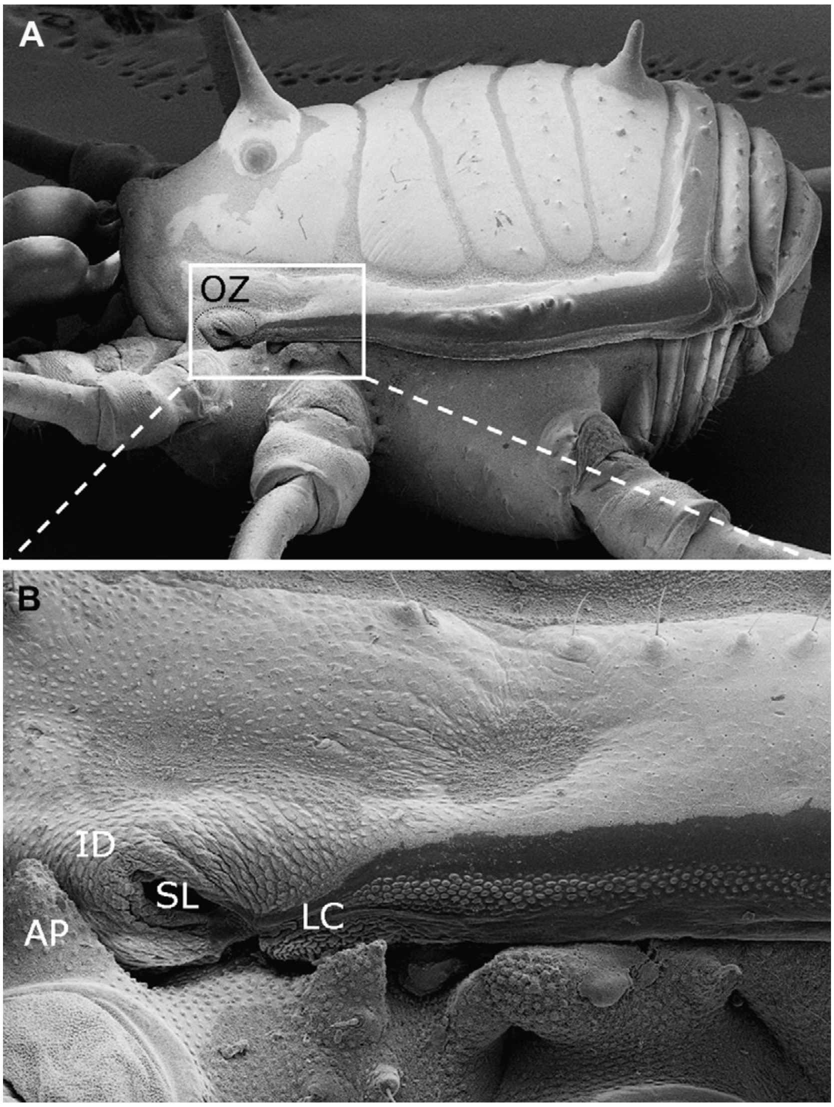


Fig. 4. External morphology of the ozopore of the harvestman *Camarana flavipalpi*. (A) Lateral view of an adult female. The rectangle indicates the area presented below. (B) Detail of the ozopore. OZ = ozopore; ID = integumentary dome; SL = slit of the integumentary dome; LC = lateral channel.

tricommatines and mitobatines is clearly simplified (Hara and Gnaspini, 2003). Therefore, the ozopore of species that never or rarely release chemical secretions are clearly more simplified than that of species that promptly release chemical secretions. Convergent simplification of ozopore morphology along with lesser frequency in the use of chemical secretions seems also to occur in certain Eupnoi that emit a gas instead of liquid, and also in certain Dyspnoi that do not emit secretion at all, even in the case of significant disturbances (Gnaspini and Hara, 2007). Future studies should explore the hypothesis of co-evolution between ozopore morphology and promptness to release chemical secretions using a large set of species within the order Opiliones.

Acknowledgements

We thank B.A. Buzatto, T.M. Del-Corso, R.T. Guido, T.M. Nazareth, and F. Osses for helping with the fieldwork; Dr. P. Gnaspini (USP) and an anonymous reviewer for critically reading the manuscript; B.A. Buzatto for the photo presented here as Fig. 3; Dr. R.H. Willemart (USP) for providing the SEM photos presented as Fig. 4, and Prof. C.H. Collins (Unicamp) for revising the final version of the paper. This study was supported by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (GM #02/00381-0; AMP, #03/09357-7 and 05/02934-4).

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