

# Sexually Dimorphic Tegumental Gland Openings in Laniatores (Arachnida, Opiliones), With New Data on 23 Species

Rodrigo H. Willemart,<sup>1\*</sup> Abel Pérez-González,<sup>2</sup> Jean-Pierre Farine,<sup>3</sup> and Pedro Gnaspini<sup>4</sup>

<sup>1</sup>*Escola de Artes Ciências e Humanidades, Universidade de São Paulo, Rua Arlindo Bétio, 1000, Ermelino Matarazzo 03828-000, São Paulo, SP, Brazil*

<sup>2</sup>*Grupo de Sistemática e Biologia Evolutiva, Núcleo em Ecologia e Desenvolvimento Sócio-Ambiental de Macaé, Universidade Federal do Rio de Janeiro, C.P. 119331, 27910-970, Macaé, RJ, Brazil*

<sup>3</sup>*Faculté des Sciences, Laboratoire Développement-Communication Chimique, CNRS UMR5548, Université de Bourgogne, 6 Bd Gabriel, 21000 Dijon, France*

<sup>4</sup>*Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 321, 05508-080, São Paulo, SP, Brazil*

**ABSTRACT** Sexually dimorphic glands often release sexual pheromones both in vertebrates and invertebrates. Species of Laniatores (Arachnida, Opiliones) seem to depend on chemical communication but few studies have addressed this topic. In this study, we review the literature for the Phalangida and present new data for 23 species of Laniatores. In 16 taxa, we found previously undescribed sexually dimorphic glandular openings on the femur, patella, metatarsus, and tarsus of legs I and metatarsus of legs III and IV. For the other species, we provide scanning electron micrographs of previously undescribed sexually dimorphic setae and pegs located on swollen regions of the legs. We also list additional species in which males have swollen regions on the legs, including the tibia, metatarsus, and tarsus of legs I, trochanter and tibia of legs II, femur, metatarsus, and tarsus of legs III, and metatarsus and tarsus of legs IV. The function and biological role of the secretions released by these glands are discussed. *J. Morphol.* 271:641–653, 2010. © 2009 Wiley-Liss, Inc.

**KEY WORDS:** chemical communication; Dyspnoi; Eupnoi; Laniatores; pheromone; sexual dimorphism

## INTRODUCTION

Chemicals produced by specialized glands are widely used by arthropods for intraspecific communication. Pheromonal attraction, aggregation, alarm, individual recognition, and general orientation are some of the known functions of the secreted chemicals (Wyatt, 2003). When a sexual role exists, pheromones are usually produced by sexually dimorphic glands with distinct functions: for instance, male scorpionflies possess glands that release female attractant pheromones (Thornill, 1992); females of some cockroaches feed on secretions provided by the tergal glands of males before they copulate (Farine et al., 1989, 1996); and

males of some moths display to females with chemicals from a specialized structure (coremata) after the female has been attracted (Bezzerrides et al., 2005).

In arachnids, tegumental glands that produce secretions known to be used for sexual purposes have been described in only four orders: some ticks use sex pheromones to find females, to mount them and to find the genital pore (Sonenshine, 2006); some male scorpions rub a gland on the metasoma against the female during courtship (Peretti, 1997), and some female harvestmen and spiders feed on secretions offered by males before mating occurs (e.g. Martens, 1975; Kronstedt, 1986; Vanacker et al., 2004; Shultz, 2005). Although a wide variety of sexual pheromones is known in spiders, the glands that produce them are still mostly unknown (Gaskett, 2007; but see below).

No visual or acoustical displays are known in harvestmen (Arachnida, Opiliones) and in the absence of these two channels, chemical cues might be expected to be used for sexual purposes. Harvestmen do have contact chemoreceptors (Willemart et al., 2009) that are thought to play a

Contract grant sponsor: Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP); Contract grant numbers: 03/02557-0, 00/04686-4; Contract grant sponsor: Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); Contract grant numbers: 300326/1994-7, 155524/2006-2.

\*Correspondence to: Rodrigo H. Willemart, Escola de Artes Ciências e Humanidades, Universidade de São Paulo, Rua Arlindo Bétio, 1000, Ermelino Matarazzo 03828-000, São Paulo, SP, Brazil. E-mail: willemart@usp.br

Received 25 February 2009; Revised 15 October 2009; Accepted 19 October 2009

Published online 21 December 2009 in Wiley InterScience (www.interscience.wiley.com)  
DOI: 10.1002/jmor.10822

role in close range olfaction as well (Willemart and Chelini, 2007). Chemical communication for sexual purposes is, however, a neglected field in harvestmen biology, because only Martens (1975) and Shultz (2005) have found clear evidences that male and female harvestmen use chemicals to communicate with each other.

Four major taxa are currently recognized within Opiliones (e.g., Giribet and Kury, 2007; Pinto-da-Rocha and Giribet, 2007): Cyphophthalmi, Eupnoi, Dyspnoi, and Laniatores (the last three may be grouped into Phalangida). In Dyspnoi, cheliceral glands present only in males have been studied in details in 13 species. These are the only sexually dimorphic glands in Phalangida of which there is histological information, and they open on the basal segment of chelicera, at its most distal portion, in nine species of Nemastomatidae, three species of Sabaconidae, and two of Ischyropsalididae (Šilhavý, 1967; Martens, 1973; Dumitrescu, 1974; Martens and Schawaller, 1977; Lopez et al., 1980). In *Dicranolasma scabrum* (Dicranolasmatidae), glandular cells occur both in the basal and distal ("hand") segments (Martens and Schawaller, 1977). In *Hesperonemastoma* (Ceratolasmatidae), it opens only on the distal segment ("hand") (Gruber, 1970). In all known cases, there is a concentration of sensilla chaetica close to where the glands open. On the distal portion of the basal segment of the chelicerae, some species have an apophysis where the gland openings are visible (e.g., Martens and Schawaller, 1977). In other species for which no histological studies have been conducted, there is a concentration of setae in this same region, suggesting that glands might also occur (e.g., Martens, 1969a). Other species have no evident apophysis but do have the glands (*Carinostoma carinatum*, *Ischyropsalis hellwigi*, *I. carli*; Martens and Schawaller, 1977).

In Dyspnoi, glandular openings have also been described on the pedipalps. Gruber (1996, 1998) examined *Dicranolasma* spp. and observed that adult males have glandular openings on the distal extremity or distal half of the medial surface of the pedipalp patella. The pores are beneath a tuft of setae, similar to those of sexually dimorphic chelicerae described earlier. The patella is thinner in females and does not bear glands like in males. This sexual dimorphism occurs only in some species of this genus, such as, *D. scabrum* and *D. opilionoides*, for example. Finally, glandular tissue most probably also occurs in the pedipalps of *Dendrolasma*, *Hesperonemastoma*, and *Ortholasma*, as indicated by swellings, dense groups of setae, and thicker femora in males (Gruber, 1970; Shear and Gruber, 1983).

The only published case of a sexually dimorphic gland in laniatorean harvestmen is the metatarsal gland on leg IV in *Iporangaia pustulosa* males (Gonyleptidae, Progonyleptoidellinae: Willemart

et al., 2007). This body part is swollen compared with the female, and bears several small pores widespread on the metatarsus. Martens (1972) described a structure similar to the adenostyle (where a gland opens in Cyphophthalmi) on the legs II of males of *Ausobskya athos* (Laniatores, Phalangodidae) but further studies should be conducted to clarify whether or not it is a gland.

In this study, we investigated laniatorean species in order to find and describe sexually dimorphic tegumental glands. The aim of this study is to detect sexually dimorphic glands, which are potentially responsible for the production of sexual pheromones in several taxa and to provide a list of target species that can be studied behaviorally and chemically in the future.

## MATERIALS AND METHODS

We examined the harvestmen collections of Museu de Zoologia da Universidade de São Paulo and Museu Nacional do Rio de Janeiro (MNRJ), both in Brazil. Based on our previous knowledge and on taxonomic papers, we studied a sample of the available species of Laniatores in which males present legs with swollen areas, because this could indicate the presence of a gland (e.g., Gruber, 1970; Shear and Gruber, 1983; Mancini and Machado, 2003; Willemart et al., 2007). We used a stereomicroscope to separate species in which males possessed any swollen area from those in which no such sexual dimorphism was present. The legs of males and females of species in which such dimorphism was present were then prepared for scanning electron microscope (SEM). The portion of the leg was cleaned ultrasonically, then dried in a stove at 40°C for at least 24 h, mounted on an aluminum stub using double stick adhesive tape, sputter coated with gold (Sputter Coater Balzer SCD 50), and photographed with a SEM Zeiss DSM 940. Most species analyzed belong to Grassatores (Biantidae, Cosmetidae, Escadabiidae, Gonyleptidae, Manaosbiidae, Samoidae, Stygnommatidae, and Zalmoxidae), with one exception, a species of Triaenonychidae. One to three individuals of each species (both sexes) were studied. The complete list of species analyzed with SEM in this study can be found in Tables 1 and 2.

## RESULTS

### Male Glandular Openings in Laniatores

We describe the glandular areas of Laniatores where openings could be recognized. Leg regions where the actual openings could not be seen are described in a separate section. The sections were organized by grouping taxa that share similar structures. We emphasize that it is premature discussing these similarities as homologies (meaning synapomorphies), especially because some of these similar structures occur in different parts of the legs or in different legs among taxa.

**Groups of bordered pores.** These groups are organized in longitudinal rows, each group being easily distinguishable from the surrounding integument by a shallow depression, and each pore having a well-defined thick border. In *Litoralia junci* (Cosmetidae), males have an enlarged metatarsus I, where groups of pores are organized in rows (Fig. 1A,B) on the ventral region of the

TABLE 1. Body region and organization of male glandular openings in the laniatorean harvestmen studied

	Leg I			Leg III	Leg IV
	Tarsus	Metatarsus	Femur/patella	Metatarsus	Metatarsus
Biantidae					
<i>Caribbianes</i> sp.				Single	
Cosmetidae					
<i>Cynorta meinerti</i>	Grouped				
<i>Gryne</i> sp.					Single
<i>Litoralia junci</i>		Grouped			
Cranaidae					
Undetermined genus and species		Grouped			
Gonyleptidae					
<i>Piassagera brieni</i>	Grouped				
<i>Gonyleptoides marumbensis</i>	Grouped				Single
<i>Heliella singularis</i>	Grouped				Single
<i>Iguapeia melanocephala</i>	Grouped				Single
<i>Iporangaia pustulosa</i>	Grouped				Single
<i>Mitopernoides variabilis</i>	Grouped				Single
<i>Progonyleptoidellus striatus</i>	Grouped				Single
Manaosbiidae					
<i>Isocranaus strinatii</i>	Grouped				
Trienonychidae					
<i>Larifuga weberi</i>	Grouped				
Zalmoxidae					
<i>Guanonia multispina</i>					Single
Grassatores-family uncertain					
<i>Costabrimma</i> sp.			Single		

Grouped openings are composed of more than two glandular openings forming a clear discrete unit. All gonyleptids listed belong in the subfamily Progonyleptoidellinae, except for *Piassagera brieni* (Hernandariinae).

metatarsus, distally. In another cosmetid, *Cynorta meinerti*, males have the most proximal tarsomere of the basitarsus I enlarged, with sparse groups of pores (Fig. 1C) on the ventral and prolateral regions, distally. Finally, males of the trienonychid *Larifuga weberi* have an enlarged basitarsus I, with groups of pores also arranged in approximate rows (Fig. 1D) on the pro- and retro-lateral regions. The number of groups varies depending on the tarsomere and whether it is pro- or retro-lateral.

**Pores grouped inside a large (and generally deep) opening.** Generally, a large opening can be seen on the side of the tarsus, and a few sparse or several densely grouped pores can be observed inside. In an undetermined genus and species of a cranoid, males have an enlarged metatarsus I, where a row of ventral/lateral openings are found (Fig. 2A). No distinct texture or setae surround the glandular openings. Males of the manaosbiid *Isocranaus strinatii* have an enlarged basitarsus I (Fig. 2B), more specifically the first and second tarsomeres, with three large openings at the ventral region (one shown in Fig. 2B). In the gonyleptid *Piassagera brieni* (Hernandariinae), males have the basitarsus of legs I swollen (Fig. 2C; compare with female, Fig. 2D). The first and second most proximal tarsomeres may have one to three large openings (Fig. 2C) both in the pro- and retro-lateral regions. Smaller pores deep inside the leg might be seen (Fig. 2E,F), although the secretions often cover and hide them. In the gonyleptid

subfamily Progonyleptoidellinae, males of all the studied species (*Gonyleptoides marumbensis*, *Heliella singularis*, *Iguapeia melanocephala*, *Iporangaia pustulosa*, *Mitopernoides variabilis*, and *Progonyleptoidellus striatus*) have two glandular regions that are sexually dimorphic, the first one occurring on legs I [Fig. 3A (compare with Fig. 3B, of a female), Figs. 3C,D and 4A–F]. These males have a swollen basitarsus I (Figs. 3A,C and 4A,C,E) that bear glandular openings on the pro- and retro-lateral regions of the first, second, and sometimes third tarsomeres. Large openings with smaller openings deep inside the leg I are easily seen on the lateral region (Figs. 3C inset and 4B,D,F) and are often clogged with secretions (Fig. 3D). The second glandular region is presented below.

**Scattered pores, more densely distributed in males than among females.** The second glandular region of progonyleptoidellines is a slightly enlarged metatarsus IV, with small scattered pores (Fig. 5A) covering the dorsal, lateral, and ventral regions. The texture of the glandular region is clearly distinct from the adjacent regions of the leg or the same region in the leg of a female (Fig. 5B). Similarly to males of these gonyleptids, males of the cosmetid *Gryne* sp. have an enlarged metatarsus IV, with several small single pores (Fig. 5C) on the dorsal, lateral, and ventral regions of the leg. A distinct pattern, with the presence of specialized setae, occurs in *Caribbianes* sp. (Biantidae): males have an enlarged metatarsus III, with single



TABLE 2. Body region, family and species in which a sexual dimorphism potentially related to the occurrence of glands occur in laniatorean harvestmen

Leg	Leg region	Species	References
I	Tibia	Escadabiidae: <i>Baculigerus</i> undescr. sp. 1, <i>Baculigerus</i> undescr. sp. 2	This article (Fig. 7A)
	Metatarsus	Assamiidae: <i>Trionyxella clavipus</i> ; Cosmetidae: <i>Litoralia acerba</i> ; Cranaiidae: <i>Holocranus pectinitibialis</i> , <i>Isocranus obscurus</i> , <i>Megacranus pygoplus</i> , <i>Micropachylus metatarsalis</i> ; Stygnopsidae: <i>Potosa dybasi</i> ; Triaenonychidae: e.g., <i>Tanalaius allualdi</i>	Roewer, 1923; Goodnight and Goodnight, 1947; González-Sponga, 1992
	Tarsus	Assamiidae: <i>Dulitellus sarawakensis</i> , <i>Triaenopodium shibai</i> , <i>Triaenopodium tarsalis</i> , <i>Trionyxella clavipus</i> ; Cladonychidae: <i>Holoscotolemon fusitarsus</i> ; Cosmetidae: <i>Keonones chamberlini</i> , <i>Oligovonones brunneus</i> , <i>Zarax aenescens</i> ; Cranaiidae: <i>Isocranus obscurus</i> ; Gonyleptidae: <i>Progyndes curvibialis</i> ; Manaosbiidae: various; Stygnidae: <i>Hoplostygnus albicinctus</i> , <i>Stenostygnoides cosmetitarsus</i> ; Triaenonychidae: <i>Nuncia tumidarta</i>	Roewer, 1923, 1949; Sørensen, 1932; Forster, 1954; Suzuki, 1970, 1976; González-Sponga, 1992; Kury, 1997; A. Pérez-González, pers. obs.
II	Trochanter	Biantidae: <i>Metabiantes</i> sp.	Lawrence, 1937
	Tibia	Escadabiidae: <i>Baculigerus</i> undescr. sp. 2; Fissiphallidae: <i>Fissiphallus martensi</i> ; Pyramidopidae: <i>Conomma fortis</i> ; Zalmoxidae: <i>Stygnoleptes analis</i>	Roewer, 1923; Pinto-da-Rocha, 2004; this article (Fig. 7C,D)
III	Patella	Escadabiidae: <i>Baculigerus</i> undescr. sp. 1	This article, no figure
	Tibia	Escadabiidae: <i>Baculigerus</i> undescr. sp. 1; Zalmoxidae: <i>Minuides milleri</i>	Kury and Pérez-González, 2007; this article (Fig. 7B)
	Metatarsus	Biantidae: <i>Heterolacurbs ovalis</i> ; Cosmetidae: <i>Paecilaemula metatarsalis</i> ; Samoidae: <i>Neoscotolemon</i> sp.; <i>Pellobunus</i> sp.; Stygnommatidae: <i>Stygnomma annulipes</i> , <i>Stygnomma teapense</i>	Roewer, 1923; Pérez-González and Kury, 2007; this article (Fig. 6B–F)
	Basitarsus	Stygnidae: <i>Timesius vesicularis</i> ; Zalmoxidae: <i>Ethobunus</i> undescr. sp., various others (e.g. <i>Dapessus</i> spp.)	Roewer, 1923; Goodnight and Goodnight, 1983; Kury and Pérez-González, 2007; this article (Fig. 6A)
IV	Metatarsus	Cosmetidae: <i>Gryne orencis</i> , <i>Paecilaemula metatarsalis</i>	Roewer, 1923; Sørensen, 1932
	Tarsus	Phalangodidae: <i>Ausobskeya athos</i> ; Zalmoxidae: <i>Zalmoxis crassitarsis</i> , <i>Zalmoxis similis</i>	Martens, 1972; Suzuki, 1982

scattered glandular openings and serrated setae on the ventral region of the expanded calcaneus (Fig. 5D,E). Trichomes and sensilla chaetica (sensu Willemart et al., 2009) are not present in this glandular area, and the serrated setae found here are not seen anywhere else in the body. In *Costabrimma* sp. (family uncertain), males have a clearly sexually dimorphic femur and patella I, with the ventral region bearing several single scattered pores and no setae (Fig. 5F). Finally, males of the zalmoxid *Guanonia multispina* have an enlarged metatarsus IV with several small pores at the ventral region (Fig. 5G).

### Laniatores With Sexually Dimorphic Swollen Legs but No Conspicuous Openings

In some species studied herein, males have swollen legs but no specialized pores (= distinct from the ones found on the rest of the body) could be detected (Table 2). Instead, we found setae (Fig. 6A–F) and pegs (Fig. 7A–D) on the basitarsus, metatarsus, tibia, and patella of legs III, tibia I and II, respectively (Table 2).

**Sulcated setae.** Males of *Ethobunus* undescr. sp. (Zalmoxidae) have an enlarged basitarsus III. No evident pores or large openings could be found, but sulcated setae are very abundant (Fig. 6A). These look superficially like sensilla chaetica but are falciform and sulcated (Fig. 6A inset). Interestingly, sensilla chaetica are almost absent on this swollen part of the leg (Fig. 6A), but in other parts they occur normally.

**Enlarged metatarsus III with a distinct area covered with long setae.** Species of this group all have distinct setae on the ventral region of the calcaneus, and these are not found anywhere else in the body. Males of *Neoscotolemon* sp. (Samoidae) have a slightly enlarged metatarsus III where a high concentration of tightly distributed setae can be seen on the distal portion of the calcaneus (Fig. 6B), ventrally. In some individuals, these setae are covered with what appear to be secretions. In another species of the same family, *Pellobunus* sp., the enlarged metatarsus III of males carries a large number of tightly distributed setae on the distal portion of the calcaneus (Fig. 6C,D), ventrally. However, the setae covering

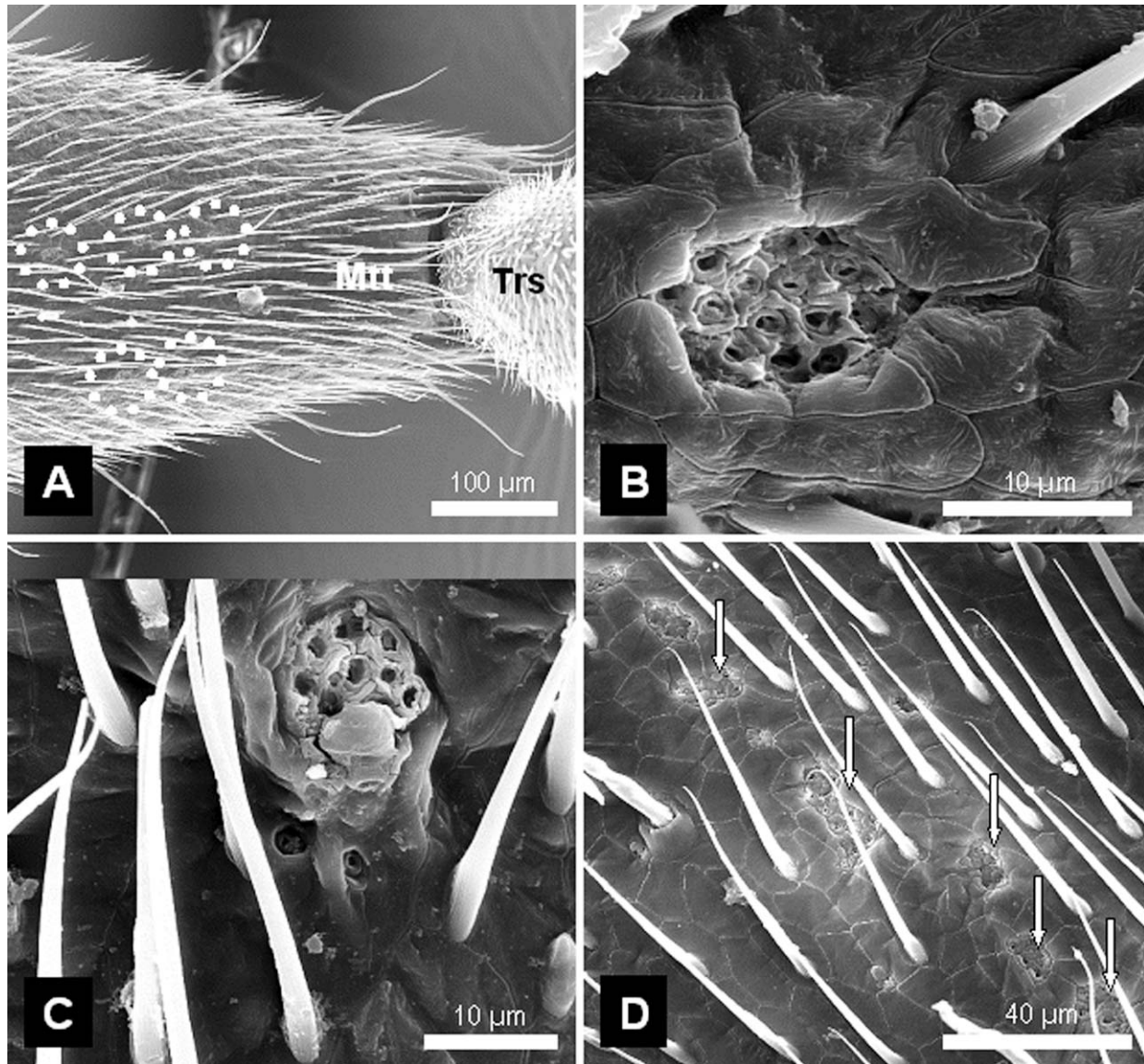


Fig. 1. Species with groups of bordered pores. **A:** *Litoralia junci* (Cosmetidae), adult male. Part of tarsus (Trs) and of swollen metatarsus (Mtt) of leg I, ventral overview. Circled regions show groups of glandular openings. **B:** Same specimen, close up micrograph of one of the regions highlighted in (A). **C:** *Cynorta meinerti* (Cosmetidae), adult male. Grouped glandular openings on the basitarsus of leg I, lateral view. **D:** *Larifuga weberi* (Triaenonychidae), adult male. Rows of grouped glandular openings (arrows) on the basitarsus of leg I, lateral view.

the calcaneus are located only at the external portion and they are morphologically similar to sensilla chaetica, which is not the case in *Caribbiantes* sp. (Fig. 5D,E) and *Neoscotolemon* sp. (Fig. 6B). Finally, males of the stygnommatid *Stygnomma teapense* have a conspicuously enlarged metatarsus III with a groove that may be covered with possible secretions (Fig. 6E,F).

**Areas with “droplet-like” pegs.** Being sensory or glandular in function, groups of pegs appear on some leg regions, exclusively in males. In *Baculigerus* undescr. sp. 1 (Escadabiidae),

males have enlarged regions in tibia of legs I (dorsally) and III (prolateral) and patella III (prolateral), with a distinctive texture at the stereomicroscope. In scanning electron micrographs, a few pores (but not more than in other leg regions) and several pegs become visible (Fig. 7A,B). Males of *Baculigerus* undescr. sp. 2, in addition to having pegs on tibia I, have a very large hump arising ventrally from tibia II (Fig. 7C), easily visible with the stereomicroscope. The entire (internal, external, and lateral portions) hump is covered with several pegs (Fig. 7C) similar to



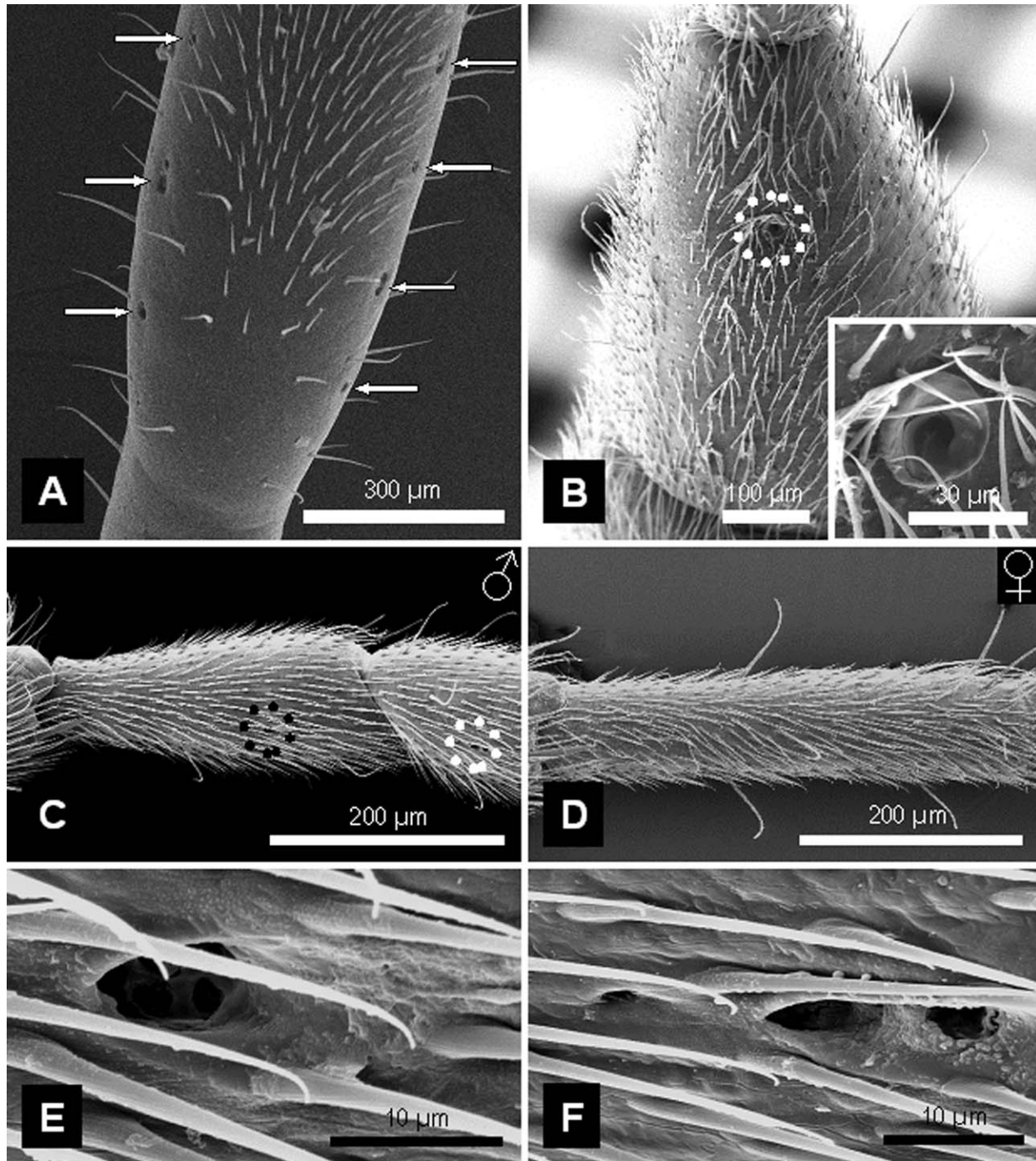


Fig. 2. Species with pores grouped inside a large opening. **A:** Undetermined Cranaiidae, adult male. Metatarsus of leg I with several openings at the sides (arrows), ventral view. **B:** *Isocranaus strinatii* (Manaosiidae), adult male. Second tarsomere of basitarsus of leg I, ventral view. Circled area shows large opening, detailed in the inset. **C:** *Piassagera brieni* (Gonyleptidae), swollen first 2 tarsomeres of leg I of an adult male, with openings (circled), retrolateral view. **D:** *Piassagera brieni*, first tarsomere of leg I of an adult female, not enlarged and with no opening, retrolateral view. **E:** *Piassagera brieni* male, detailed view of the glandular opening highlighted by a black circle in (C). **F:** *Piassagera brieni* male, detailed view of the group of glandular openings highlighted by a white circle in (C).

those of *Baculigerus* undescr. sp. 1, and a few pores (not more than in other leg regions). A similar pattern is found in the zalmoxid *Stygnoleptes*

*analis*, of which males have an enlarged tibia II with numerous droplet-like pegs (Fig. 7D) on the ventral region.

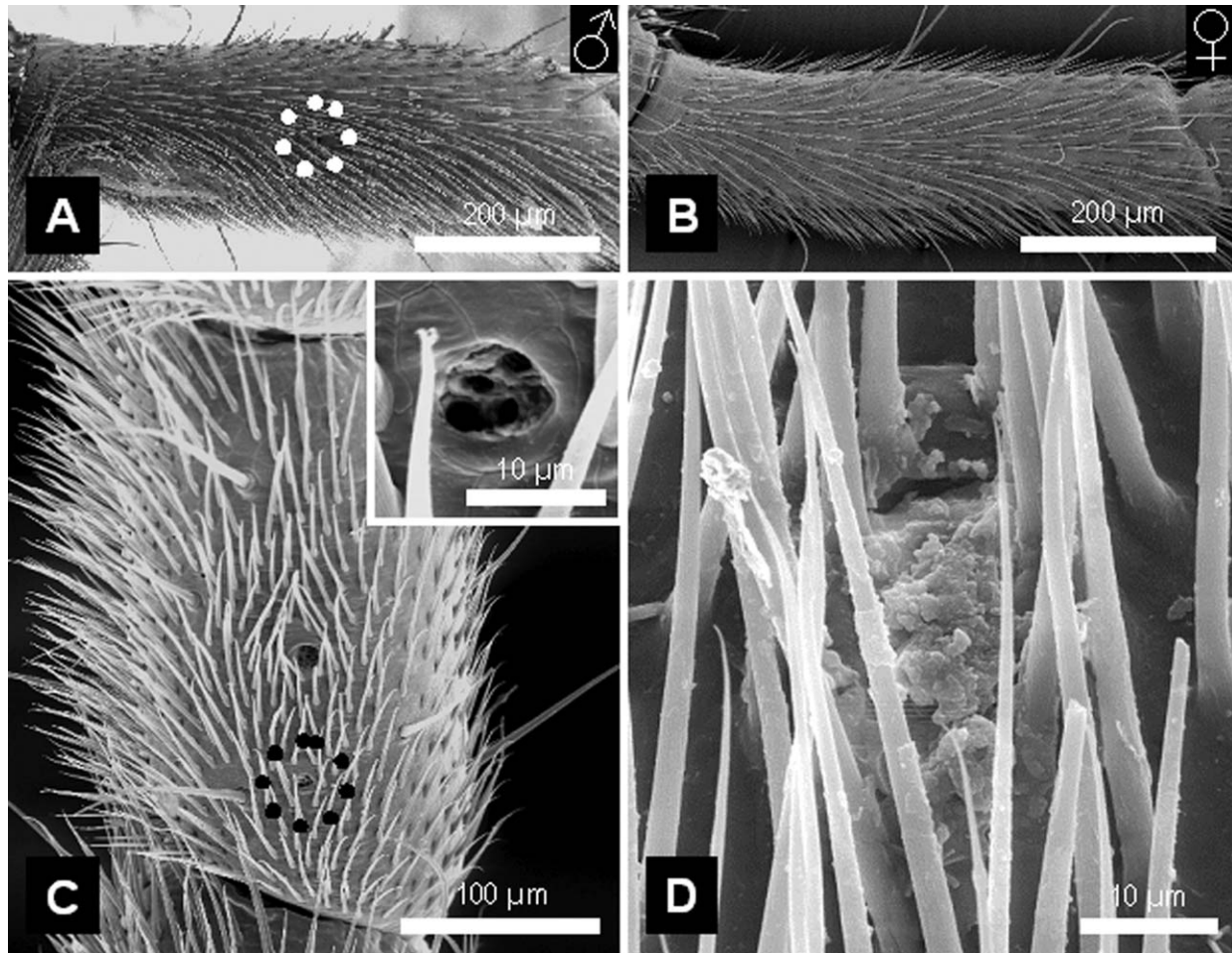


Fig. 3. Species with pores grouped inside a large opening—Progonyleptoidellinae (Gonyleptidae). **A:** *Progonyleptoidellus striatus*, slightly swollen first tarsomere of leg I of an adult male, with an opening (circled), retrolateral view. **B:** *Progonyleptoidellus striatus*, first tarsomere of leg I of an adult female, not enlarged and with no opening, retrolateral view. **C:** *Progonyleptoidellus striatus*, third tarsomere of leg I of an adult male, prolateral view. Two glandular openings are shown, several pores can be seen inside openings. The smaller, most proximal opening (circled) is detailed in the inset. **D:** *Iporangaia pustulosa*, adult male. Glandular opening of second tarsomere of leg I covered with secretions, prolateral view.

## DISCUSSION

The glandular openings described here are on distinct legs (see Fig. 8) and might be either single and widespread, or grouped, organized as discrete units (Table 1). Such pattern is found on legs of *Caribbiantes* sp. (Biantidae), *Costabrimma* sp. (Family uncertain), *Guanonia multispina* (Zalmoxidae), *Gryne* sp. (Cosmetidae), and the metatarsus of legs IV in all species of Progonyleptoidellinae (Gonyleptidae) (Fig. 5A–G). In contrast, gland openings as discrete units are found in distinct body regions in some laniatoreans (Figs. 1–4): *Larifuga weberi* (Triaenonychidae), *Litoralia junci*, *Cynorta meinerti* (Cosmetidae), *Piassagera brieri* (Gonyleptidae), an undetermined Cranaidae, *Isochranaus strinatii* (Manaosbiidae), and on legs I of the progonyleptoidellines (Gonyleptidae). In summary, all the glands we describe herein on legs I that open through discrete units (except for the

glandular openings on the femur/patella of leg I in *Costabrimma* sp., Fig. 5F) and all glands that open on legs III and IV open through single pores widespread on the metatarsus. Males of the samoids *Neoscotolemon* sp. and *Pellobunus* sp. and the stygnommatid *Stygnomma teapense* all have an enlarged metatarsus III with a distinct area covered with long setae. Such area is similar to the glandular area in the exact same leg and region of the biantid *Caribbiantes* sp. (see Fig. 5D,E). Probably, the first 3 have pores that could not be seen in the specimens we have analyzed.

Although several behavioral studies exist on sexual pheromones in arachnids, mainly in spiders (Schulz, 2004; Gaskett, 2007), morphological studies on sexually dimorphic tegumental glands in arachnids are rare. Such glands have been described in only a few spiders (e.g. Legendre and



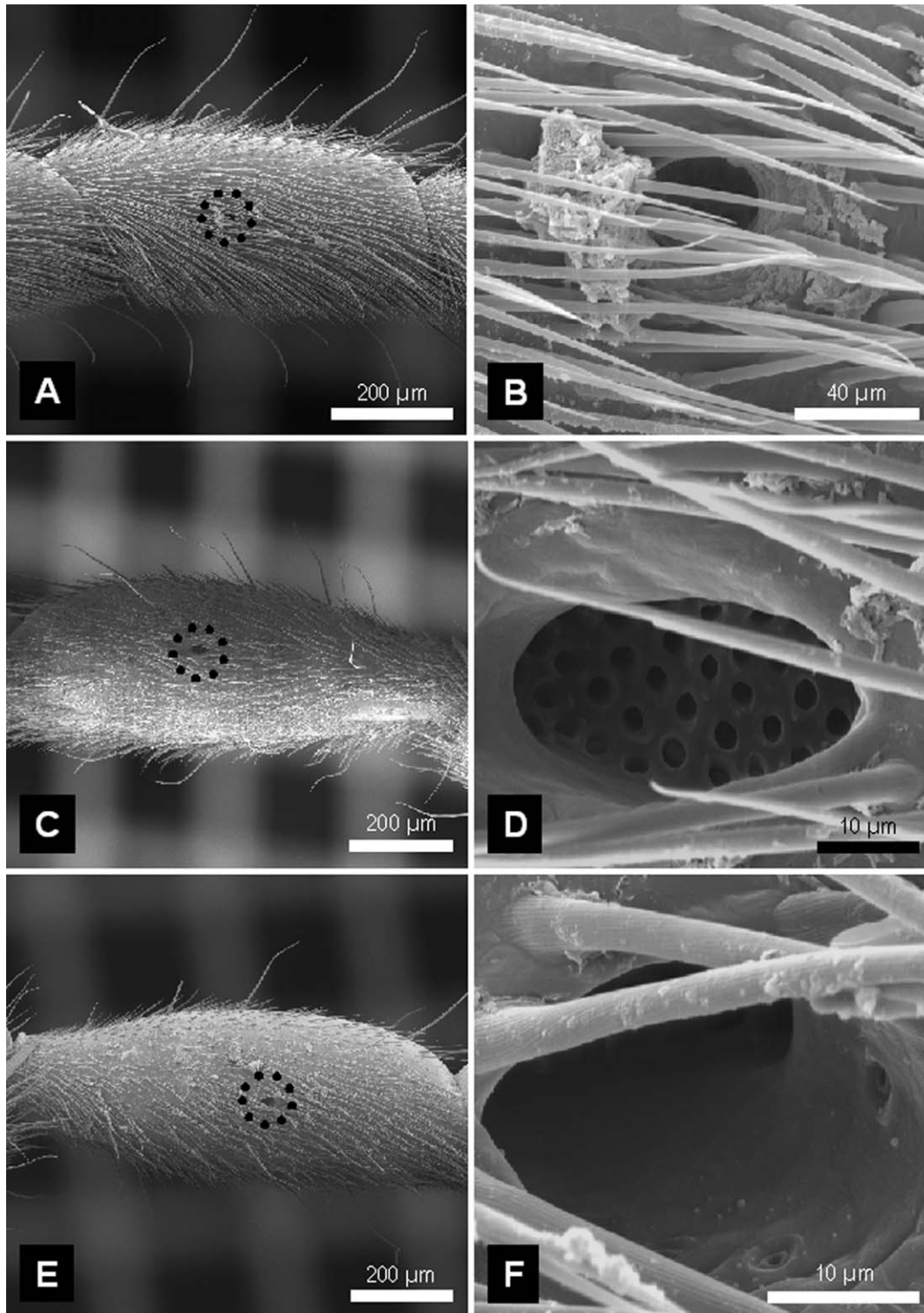


Fig. 4. Species with pores grouped inside a large opening—Progonyleptoidellinae (Gonyleptidae). **A:** *Gonyleptoides marumbensis*, adult male, second tarsomere of leg I, retrolateral view. **B:** Same specimen, close up micrograph of the region highlighted in (A). **C:** *Iguapeia melanocephala*, adult male, first tarsomere of leg I, prolateral view. **D:** Same specimen, close up micrograph of the region highlighted in (C) (large number of pores can be seen inside the main opening). **E:** *Iguapeia melanocephala*, first tarsomere of leg I, retrolateral view. **F:** Same specimen, close up micrograph of the region highlighted in (E).



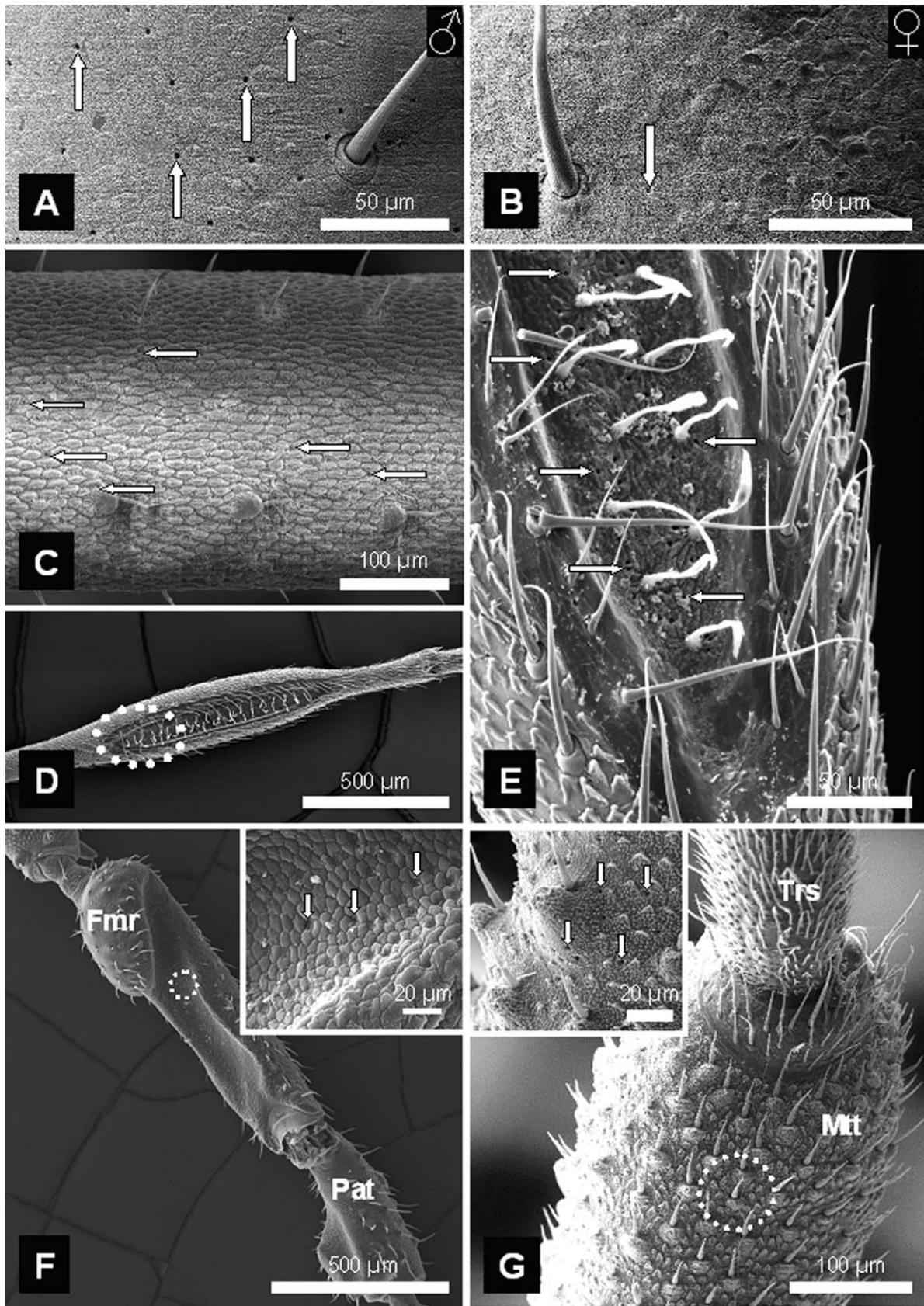


Fig. 5. Species with scattered pores more abundant in males. **A:** *Heliella singularis* (Gonyleptidae), adult male: sexually dimorphic metatarsus of leg IV, with more glandular openings (arrows) in males than in females, dorsal view. **B:** *Heliella singularis*, adult female, dorsal view: arrow shows a glandular opening. **C:** *Gryne* sp. (Cosmetidae), adult male. Glandular openings (arrows) on the metatarsus of leg IV. **D:** *Caribbiantes* sp. (Biantidae), adult male, metatarsus of leg III, ventral view. **E:** Same specimen, close up micrograph of the region highlighted in (D) (note the multiple pores, arrows). **F:** *Costabrimma* sp. (incertae sedis), adult male. Femur (Fmr) and patella (Pat) of leg I, ventral view. Circled area detailed in the inset, showing a high number of pores (arrows). **G:** *Guanonia multispina* (Zalmoxidae), adult male. Swollen metatarsus (Mtt) and part of tarsus (Trs) of leg IV, ventral view. Circled area detailed in the inset (arrows show glandular openings).



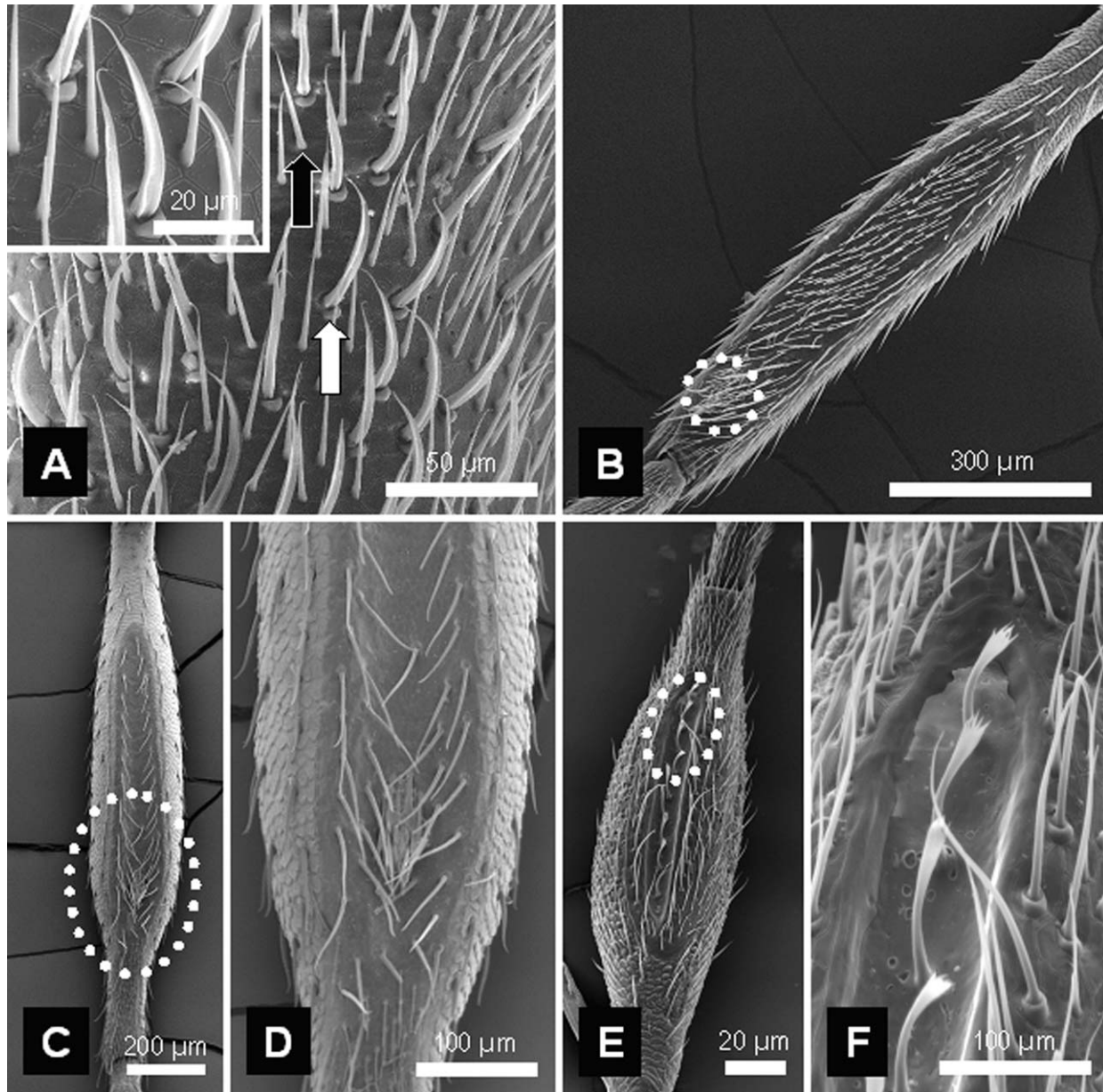


Fig. 6. Species with special setae. **A:** *Ethobunus* undescr. sp. (Zalmoxidae), adult male. Basitarsus of leg III, ventral view, showing sulcated setae (white arrow—detailed in the inset) and trichomes (black arrow). **B:** *Neoscotolemon* sp. (Samoidae), adult male. Metatarsus of leg III, ventral view. Circled region shows a high concentration of sensilla. **C:** *Pellobunus* sp. (Samoidae), adult male, metatarsus of leg III, ventral view. **D:** Same specimen, close up micrograph of the region highlighted in (C). **E:** *Stygnomma teapense* (Stygnommatidae), adult male, metatarsus of leg III, ventral view. **F:** Same specimen, close up micrograph of the region highlighted in (E), showing a concentration of previously undescribed sensilla.

Lopez, 1974; Kovoov, 1981; Kovoov et al., 1981; Wanless, 1984) and in Amblypygi: males of *Euphrynichus bacillifer* (Phrynichidae) have bacilliform apophyses on the pedipalp that are larger and have more pores in males than in females (Weygoldt, 1998; Weygoldt, 2000). Although the function is unknown in the above cited publications, in other species the male glands are used in premating behavior (spiders: Kronstedt, 1986; Vanacker et al., 2004; scorpions: Peretti, 1997). Some of these gland openings are of the “group of

pores” type (e.g. Wanless, 1984) and others are of the “single scattered pores” type (e.g. Kovoov et al., 1981; Kronstedt, 1986), though the morphology of the openings is quite different from those we have described in his paper. Also, the glands in these other arachnids are not only in the legs (Kronstedt, 1986) but also in the prosoma (Vanacker et al., 2004) and opisthosoma (Peretti, 1997).

The use of such glands in laniatorid harvestmen is still enigmatic. The deposition of pheromones on the substrate is a plausible hypothesis: this is a



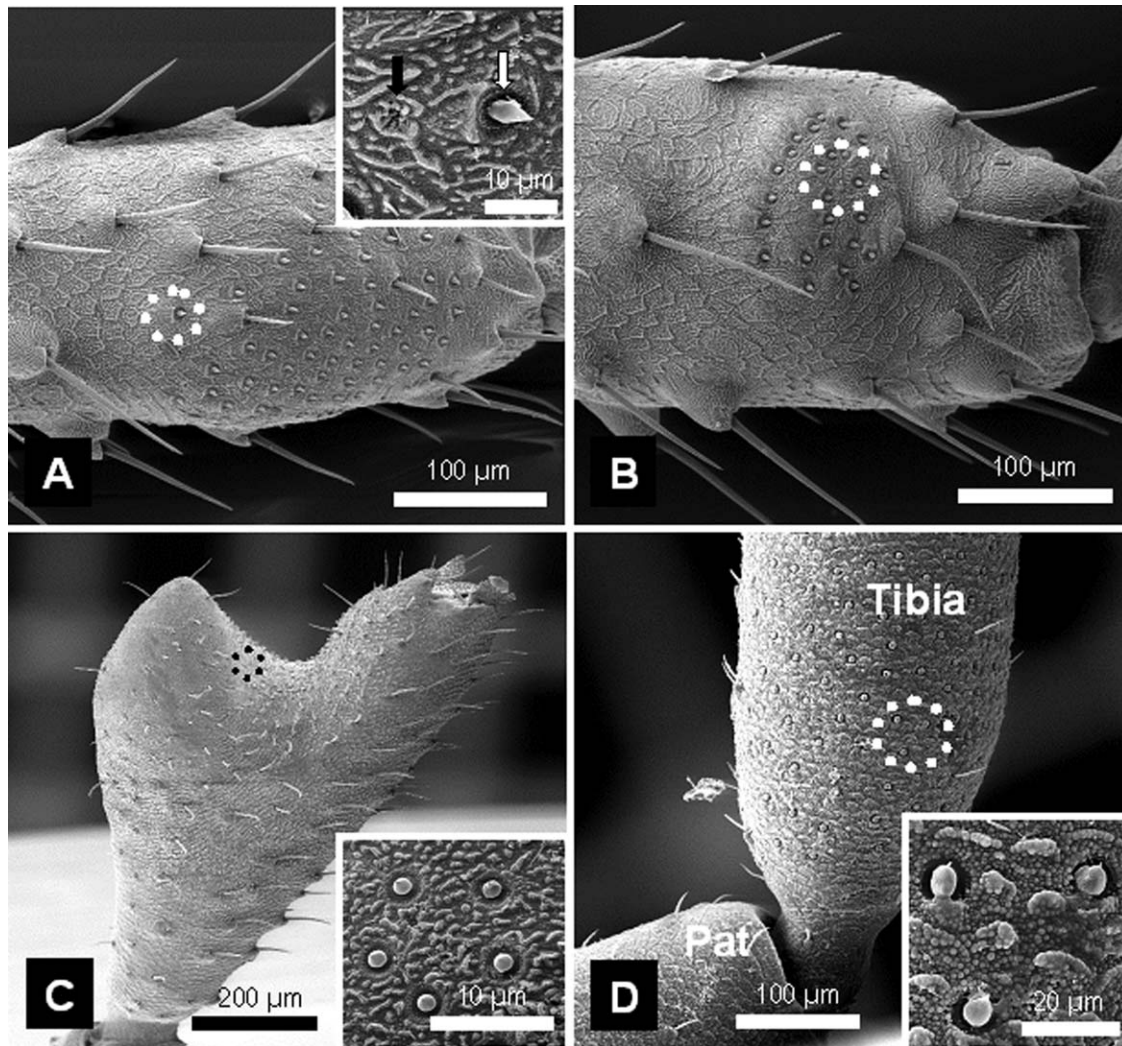


Fig. 7. **A:** *Baculigerus* undescr. sp. 1 (Escadabiidae), adult male, tibia of leg I, dorsal view. Circled area is detailed in the inset, which shows a peg (white arrow) and a pore (black arrow). Tibia I of females is not swollen and pegs are absent. **B:** *Baculigerus* undescr. sp. 1, tibia of leg III, prolateral view. Pegs (circled) are similar to those shown in the inset of (A) and are absent in females. **C:** *Baculigerus* undescr. sp. 2 (Escadabiidae), adult male. Tibia of leg I, ventral view, showing swollen area with pegs (circled area detailed in the inset). **D:** *Stygnoleptis analis* (Zalmoxidae), adult male. Swollen tibia of leg II and part of patella (Pat), ventral view. Circled area detailed in the inset.

common behavior in other arthropods, such as, insects, scorpions, and spiders (Gaffin and Brownell, 1992; Wyatt, 2003; Gaskett, 2007; Billen, 2009) and harvestmen have contact chemoreceptors on their legs (Willemart et al., 2009). Some species, namely *Neosadocus* sp. and *Iporangaia pustulosa* (both Gonyleptidae), have been seen rubbing other glands on the substrate (Willemart et al., 2007), indicating that chemicals might be used in this way. The transfer of secretions to the mouth parts of females is another possibility that is known to occur in some spiders before mating (Kronstedt, 1986; Vanacker et al., 2004). In harvestmen of the suborder Dyspnoi, cheliceral glands of males seem to release courtship gustatory pheromones (Birch, 1974), which, at least in

*Ischyropsalis luteipes* and *I. hellwigi*, females perceive by mouth contact before copulation (Martens, 1967, 1969a,b, 1975). Gruber (1978) reported probable gland secretions of the chelicerae on the pedipalps of *Ceratolasma trichanta* (Ceratolasmatidae), on the exact region that touches the gland when the animal rests. He speculated about a possible indirect role of the pedipalps in transferring secretions from the chelicerae to females, because the hood would be an obstacle (see Pinto-da-Rocha and Giribet, 2007 for general morphology of Dyspnoi). Interestingly, Meijer (1972) inferred the sexual activity of *Nemastoma lugubre* throughout the year based on the presence/absence of coagulated secretions in the cheliceral apophysis of males collected in pitfalls.

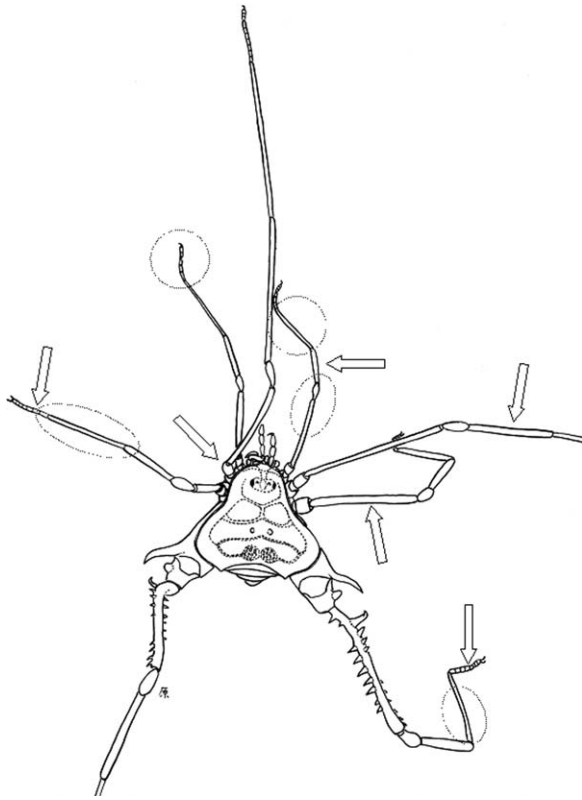


Fig. 8. Generic laniatorid harvestmen showing regions where we provide evidences of glandular openings (circles) and regions that potentially bear glands based on literature data and on our SEM micrographs (arrows). In addition to these, some species of Dyspnoi have glands that open on chelicerae and pedipalps. Drawing by M. R. Hara.

## ACKNOWLEDGMENTS

This study was conducted in the post-graduation program in Zoology of the Instituto de Biociências da USP (IBUSP). Two anonymous reviewers and the editor greatly helped with several comments on the manuscript. J. Gruber and P. Mitov and provided very helpful suggestions on parts of early drafts. M. B. da Silva and R. Pinto-da-Rocha allowed the use of specimens from Museu de Zoologia da USP (MZUSP) and helped with bibliography. A. B. Kury kindly allowed the access to the MNRJ collection and send some critical specimens to this study. L. F. de Armas, G. Giribet, and C. Viquez loaned several of the studied specimens to A. P. G. The Venezuelan material was part of the "Venezuelan Arachnological expedition project" by Fundación La Salle and MNRJ, and we thank Celsa Señaris and Osvaldo Villareal for making it available for study. M. D. Marques granted access to the SEM from MZUSP and A. A. G. F. C. Ribeiro granted access to the SEM from IBUSP. Marcio V. Cruz, Eduardo (in memoriam), and Enio Mattos greatly helped with the SEM photographs in IBUSP. C. F. Lerche helped with papers in

German. We are deeply and specially grateful to C. Fernandez for her help with bibliography. M. R. Hara kindly prepared a general scheme of a laniatorid in motion, and L. M. Lobo is thanked for all the remaining drawings.

## LITERATURE CITED

- Bezzarides AL, Iyengar VK, Eisner T. 2005. Corematal function in *Utetheisa ornatix*: Interpretation in the light of data from field-collected males. *Chemoecology* 15:187–192.
- Billen J. 2009. Occurrence and structural organization of the exocrine glands in the legs of ants. *Arthropod Struct Dev* 38: 2–15.
- Birch M. 1974. Aphrodisiac pheromones in insects. In: Birch M, editor. *Pheromones*. Frontiers of Biology, Vol. 32. Amsterdam and London: North-Holland Publishing Company. pp 115–134.
- Dumitrescu D. 1974. Les glandes chélicériennes chez les opilions. *Trav Mus Hist Nat Bucarest* 14:109–113.
- Farine JP, Brossut R, Nalepa CA. 1989. Morphology of the male and female tergal glands of the woodroach *Cryptocercus punctulatus* (Insecta, Dictyoptera). *Zoomorphology* 109:153–164.
- Farine JP, Everaerts C, Abed D, Ntari M, Brossut R. 1996. Pheromonal emission during the mating behavior of *Eurycotis floridana* (Walker) (Dictyoptera: Blattidae). *J Insect Behav* 9: 197–213.
- Forster RR. 1954. The New Zealand harvestmen (sub-order Laniatores). *Canterbury Mus Bull* 2:1–329.
- Gaffin DD, Brownell PH. 1992. Evidence of chemical signaling in the sand scorpion. *Paururoctonus mesaensis* (Scorpionida: Vaejovidae). *Ethology* 91:59–69.
- Gaskett AC. 2007. Spider sex pheromones: Emission, reception, structures, and functions. *Biol Rev* 82:27–48.
- Giribet G, Kury AB. 2007. Phylogeny and Biogeography. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge, MA: Harvard University Press. pp 62–87.
- González-Sponga MA. 1992. Arácnidos de Venezuela. Opiliones Laniatores II. Familia Cosmetidae. Caracas: Academia de Ciencias Físicas, Matemáticas y Naturales. 432 p.
- Goodnight JC, Goodnight ML. 1947. Phalangida from tropical America. *Fieldiana Zool* 32:1–58.
- Goodnight JC, Goodnight ML. 1983. Opiliones of the family Phalangodidae found in Costa Rica. *J Arachnol* 11:201–242.
- Gruber J. 1970. Die "Nemastoma"—Arten Nordamerikas (Ischyropsalididae, Opiliones, Arachnida). *Ann Nat Mus Wien* 74:129–144.
- Gruber J. 1978. Redescription of *Ceratolasma tricantha* Goodnight and Goodnight, with notes on the family Ischyropsalididae (Opiliones, Palpatores). *J Arachnol* 6:105–124.
- Gruber J. 1996. Beobachtungen zur Ökologie und Biologie von *D. scabrum* (Herbst, 1799). Teil II: Fortpflanzung, Entwicklung und Wachstum (Arachnida: Opiliones: Dicranolasmatidae). *Ann Nat Mus Wien* 98B:71–110.
- Gruber J. 1998. Beiträge zur Systematik der Gattung *Dicranolasma* (Arachnida: Opiliones. Dicranolasmatidae). I. *Dicranolasma thracium* Starega und verwandte Formen aus Südosteuropa und Südwestasien. *Ann Nat Mus Wien* 100B:489–537.
- Kovoor J. 1981. Une source probable de phéromones sexuelles: Les glandes tégumentaires de la région génitale des femelles d'araignées. *CR VIème Colloq Arachnol Ser B88 (Suppl):*1–15.
- Kovoor J, Lopez A, Emerit M. 1981. Des glandes tégumentaires particulières aux femelles chez *Leptyphantès sanctivincentii* et *Linyphia triangularis* (Araneae, Linyphiidae). *CR VIème Colloq Arachnol Ser B88 (Suppl):*53–60.
- Kronstedt T. 1886. A presumptive pheromone-emitting structure in wolf spiders (Araneae, Lycosidae). *Psyche* 93:127–132.
- Kury AB. 1997. The genera *Saramacia* and *Syncranaus* Roewer, with notes on the status of the *Manaosiidae* (Opiliones.



- Laniatores, Gonyleptoidea). Bol Mus Nac Rio de Janeiro 374: 1–22.
- Kury AB, Pérez-González AP. 2007. Taxonomy, Zalmoxidae. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. Harvestmen: The Biology of Opiliones. Cambridge, MA: Harvard University Press. pp 243–246.
- Lawrence RF. 1937. The external sexual characteristics of South African harvest-spiders. Trans R Soc S Afr 24:331–337.
- Legendre R, Lopez A. 1974. Étude histologique de quelques formations glandulaires chez les Araignées du genre *Argyrodes* (Theridiidae) et description d'un nouveau type de glande: La glande clypéale des mâles. Bull Soc Zool Fr 99:453–460.
- Lopez A, Emerit M, Rambla M. 1980. Contribution a l'étude de *Sabacon paradoxum* Simon 1879 (Opiliones: Palpatores, Ischyropsalidae). Stations nouvelles, particularités électromicroscopiques du prosoma et de ses appendices. CR VIème Colloq Arachnol 10:147–161.
- Mancini KC, Machado G. 2003. Glândula tarsal sexualmente dimórfica no opilião *Manaosbia scopulata* Roewer, 1943 (Opiliones: Manaosbiidae). IV Encontro de Aracnólogos do Cone Sul, São Pedro, São Paulo, Brazil, December 7–12, 2003.
- Martens J. 1967. Bedeutung einer Chelicerendrüse bei Weberknechten (Opiliones). Naturwissenschaften 54:346.
- Martens J. 1969a. Die Abgrenzung von Biospezies auf biologisch-ethologischer und morphologischer Grundlage am Beispiel der Gattung *Ischyropsalis* C.L. Koch 1839 (Opiliones, Ischyropsalidae). Zool Jahrb Abt Syst Ökol Geogr Tiere 96: 133–264.
- Martens J. 1969b. Die Sekretarbitung während des Paarungsverhaltens von *Ischyropsalis* C.L. Koch (Opiliones). Z Tierpsychol 26:513–523.
- Martens J. 1972. Ausobskya athos, der erste Krallenweberknecht aus Griechenland (Opiliones: Phalangodidae). Sencken Biol 53:431–440.
- Martens J. 1973. Feinstruktur der cheliceren-drüsen von *Nemastoma dentigerum* Canestrini (Opiliones: Nemastomatidae). Z Zellforschung 136:121–137.
- Martens J. 1975. *Ischyropsalis hellwigi* (Opiliones) Paarungsverhalten. Encyclopaedia. Cinematographica E 2128/1875.
- Martens J, Schawaller W. 1977. Die Cheliceren-Drüsen der Weberknechte nach rasteroptischen und lichtoptischen Befunden (Arachnida: Opiliones). Zoomorphologie 86:223–250.
- Meijer J. 1972. Some data on the phenology and the activity-patterns of *Nemastoma lugubre* (Müller) and *Mitostoma chrysomelas* (Hermann) (Nemastomatidae: Opilionida, Arachnida). Neth J Zool 22:105–118.
- Peretti AV. 1997. Relación de las glándulas caudales de machos de escorpiones Bothriuridae con el comportamiento sexual (Scorpiones). Rev Arachnol 12:31–41.
- Pérez-González AP, Kury AB. 2007. Taxonomy, Samoidae. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. Harvestmen: The Biology of Opiliones. Cambridge, MA: Harvard University Press. pp 224–226.
- Pinto-da-Rocha R. 2004. A new Fissiphallidae from Brazilian Amazon rain forest (Arachnida: Opiliones). Zootaxa 640:1–6.
- Pinto-da-Rocha R, Giribet G. 2007. Taxonomy. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. Harvestmen: The Biology of Opiliones. Cambridge, MA: Harvard University Press. pp 88–246.
- Roewer CF. 1923. Die Weberknechte der Erde. Systematische Bearbeitung der bisher bekannten Opiliones. Jena: Gustav Fischer. 1116 p.
- Roewer CF. 1949. Über Phalangodidae II. Weitere Weberknechte XIV. Senckenbergiana 30:247–289.
- Schulz S. 2004. Semiochemistry of spiders. In: Cardé RT, Millar JG, editors. Advances in Insect Chemical Ecology. Cambridge: Cambridge University Press. pp 110–150.
- Shear WA, Gruber J. 1983. The opilionid subfamily Ortholasmatinae (Opiliones: Troguloidea, Nemastomatidae). Am Mus Novit 2757:1–65.
- Shultz JW. 2005. Preliminary analysis of mating in *Leiobunum nigripes* (Opiliones) and diversification of male reproductive structures in *Leiobunum*. News Am Arachnol Soc 72:11.
- Silhavý V. 1967. Über eine Sekretmündung am ersten Cheliceren-Glied der Nemastomatiden und Ihre Anwendung in der Taxonomie (Opilionidea). Acta Entomol Bohem 64:319–321.
- Sonenshine DE. 2006. Tick pheromones and their use in tick control. Ann Rev Entomol 51:557–580.
- Sørensen W. 1932. Descriptiones Laniatorum (Arachnidorum Opilionum Subordinis). (Opus posthumum recognovit et editit Kai L. Henriksen). Mém Acad Roy Sci Let Danemark Ser 9, 3:197–422.
- Suzuki S. 1970. Report on a collection of opilionids from Nepal. J Sci Hiroshima Univ (Zool) 23:29–57.
- Suzuki S. 1976. Report on a collection of opilionids from Pasoh Forest Reserve. West Malaysia. Nat Life Southeast Asia 7:9–38.
- Suzuki S. 1982. Contributions to the taxonomy and zoogeography of the Opiliones of the Philippines. Bismark and Solomon Islands. With an appendix on some related species from the Moluccas and Sumatra. Steenstrupia 8:181–225.
- Thornill R. 1992. Female preference for the pheromone of males with low fluctuating asymmetry in the Japanese scorpionfly (*Panorpa japonica*. Mecoptera). Behav Ecol 3:277–283.
- Vanacker D, Hendrickx ML, Verraes P, Maelfait J-P. 2004. Can multiple mating compensate for slower development and shorter adult life in a male dimorphic dwarf spider? Biol J Linn Soc 82:269–273.
- Wanless FR. 1984. A review of the spider subfamily Spartaeinae nom. n. (Araneae: Salticidae) with descriptions of six new genera. Bull Br Mus Nat Hist (Zool) 46:135–205.
- Weygoldt P. 1998. Mating and spermatophore morphology in whip spiders (*Phrynichodamon scullyi* (Purcell, 1901). *Damon gracilis* nov spec., *Damon variegatus* (Perty, 1834), and *Euphrynichus bacillifer* (Gerstaecker, 1873) (Arachnida: Amblypygi: Phrynichidae). Zool Anz 236:259–276.
- Weygoldt P. 2000. Whip Spiders (Chelicerata: Amblypygi): Their Biology, Morphology and Systematics. Steenstrup: Apollo Books. 163 p.
- Willemart RH, Chelini MC. 2007. Experimental demonstration of close-range olfaction and contact chemoreception in the Brazilian harvestman *Iporangaia pustulosa*. Entomol Exp Appl 123:73–79.
- Willemart RH, Chelini MC, de Andrade R, Gnaspini P. 2007. An ethological approach to a SEM survey on sensory structures and tegumental gland openings of two neotropical harvestmen (Arachnida: Opiliones, Gonyleptidae). Ital J Zool 74:39–54.
- Willemart RH, Farine JP, Gnaspini P. 2009. Sensory biology of Phalangida harvestmen (Arachnida. Opiliones): A review, with new morphological data on 18 species. Acta Zool 90:209–227.
- Wyatt TD. 2003. Pheromones and animal behaviour, communication by smell and taste. Cambridge: Cambridge University Press. 391 p.