Putative adhesive setae on the walking legs of the Paleotropical harvestman *Metibalonius* sp. (Arachnida: Opiliones: Podoctidae)

Guilherme Gainett[1,2], **Prashant P. Sharma**[2], **Gonzalo Giribet**[3] and **Rodrigo H. Willemart**[1,4,5]: [1] Laboratório de Ecologia Sensorial e Comportamento de Artrópodes, Escola de Artes, Ciências e Humanidades, Universidade de São Paulo, Rua Arlindo Béttio, 1000, Ermelino Matarazzo, São Paulo, SP 03828-000, Brazil; E-mail: guilherme.gainett@wisc.edu; [2] Department of Integrative Biology, University of Wisconsin-Madison, 352 Birge Hall, 430 Lincoln Drive, Madison, WI 53706 USA; [3] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA; [4] Programa de Pós-Graduação em Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 321, Travessa 14, São Paulo, SP 05508-090, Brazil; [5] Programa de Pós-Graduação em Ecologia e Evolução, Universidade Federal de São Paulo, Campus Diadema, Rua Professor Artur Riedel, 275, Jardim Eldorado, Diadema, SP 09972-270, Brazil.

Abstract. We provide a first scanning electron microscopy examination of the Paleotropical harvestman family Podoctidae (Opiliones: Laniatores), focusing on the distitarsus of the legs of *Metibalonius* sp. Distitarsi I and II are mostly equipped with olfactory sensilla chaetica with wall pores, while those of legs III and IV have gustatory sensilla chaetica with a tip pore, ventral trichomes with ovate tips (non-sensory) and a type of spatulate seta. Spatulate setae are present in adults of both sexes, with no apparent sexual dimorphism, but they are absent in the nymph. Seven of these setae are inserted on the frontal surface of the last tarsomere of legs III and IV, with the tips oriented ventrally. Each seta has an s-shaped socketed shaft, which terminates distally in a spatula-shaped structure. The distribution of spatulate setae, restricted to legs III and IV (walking legs), the position on the distitarsi, and the typical spatulate shape suggest an adhesive function for these structures. Morphology and position suggest that the socketed spatulate setae of *Metibalonius* sp. and the previously reported scopular spatulate setae of other harvestmen constitute two distinct types of adhesive structures, highlighting the diversity of adhesive structures in Laniatores. Future investigations about the natural history of this species and internal morphology of spatulate setae are necessary to test further functional hypotheses and to determine their behavioral role.

Keywords: Sensilla, Laniatores, spatulate setae, SEM, adhesion

Scanning electron microscopy surveys of integumental structures are inherently important for their potential to reveal informative characters for systematics, inspire engineering devices (e.g., bio-inspired adhesives) and give insights on the behavior of animals (Stork 1980; Gorb 2008; Wolff & Gorb 2016). Extensive SEM surveys have been conducted in insects, building a solid body of work on the diversity of forms and functions of the arthropod cuticle (e.g., Stork 1980; Beutel & Gorb 2001; Chapman 2013). In arachnids, most surveys have focused on spiders, mites and ticks (e.g., Alberti & Coons 1999; Coons & Alberti 1999; Ramírez 2014), but knowledge of the integument of other arachnid taxa, such as Opiliones (harvestmen or daddy-long-legs), remains relatively scarce (see below).

Studies in harvestmen have rapidly increased in the last decade, focusing mostly on the largest suborder, Laniatores, a group with approximately 30 families distributed worldwide (Kury 2013; Giribet & Sharma 2015). Researchers have mostly investigated the ultrastructure of the integument (Townsend et al. 2009; Rodriguez & Townsend 2015; Rodriguez et al. 2014a, b; Ramin et al. 2016), sensory organs (Willemart et al. 2007, 2009; Willemart & Giribet 2010; Gainett et al. 2014, 2017) and glands (Willemart et al. 2010; Gnaspini & Rodrigues 2011; Proud & Felgenhauer 2011, 2013; Gainett et al. 2014; Ramin et al. 2016). However, even in the better studied Laniatores, the members of a few families have never been closely investigated by SEM, Podoctidae being one of these. Podoctidae is a small family of Paleotropical harvestmen, whose precise sister-group relationship to other laniatorid families is still contentious (Fernández et al. 2017), and whose traditional systematics has recently been largely rearranged based on molecular evidence (Sharma et al. 2017). Therefore, knowledge about the integument of a podoctid could provide important information for the taxonomy and biology of this poorly known family. We thus used SEM to investigate the distitarsus of legs I–IV of the podoctid *Metibalonius* sp. (Fig. 1a–c), reporting a previously undescribed setal type.

METHODS

Metibalonius sp. is a small species, with a body length of 1.5 mm (Fig. 1). Specimens were obtained from the Invertebrate Zoology Collection in the Museum of Comparative Zoology, Harvard University. *Metibalonius* sp. individuals (MCZ-131275, available online at http://mczbase.mcz.harvard.edu/guid/MCZ:IZ:131275) were collected in Australia (Ella Bay N. P., Queensland; above waterfall, next to dirt road; 17° 28′ 39.3″ S, 145° 04′ 22.2″ E; collected by P.P. Sharma & R.M. Clouse, 1.V.2011). We sampled 3 males, 6 females, 1 nymph, and selected one male and one female for scanning electron microscopy (SEM). For SEM, legs of specimens were cleaned using a Branson 200 sonicator, in a 1:10 dilution of detergent, and subsequently in deionized water only. Some of the appendages were intentionally left uncleaned for the investigation of possible secretions. Cleaned appendages were dried in 100% acetone and mounted on 12 mm SEM stub mounts

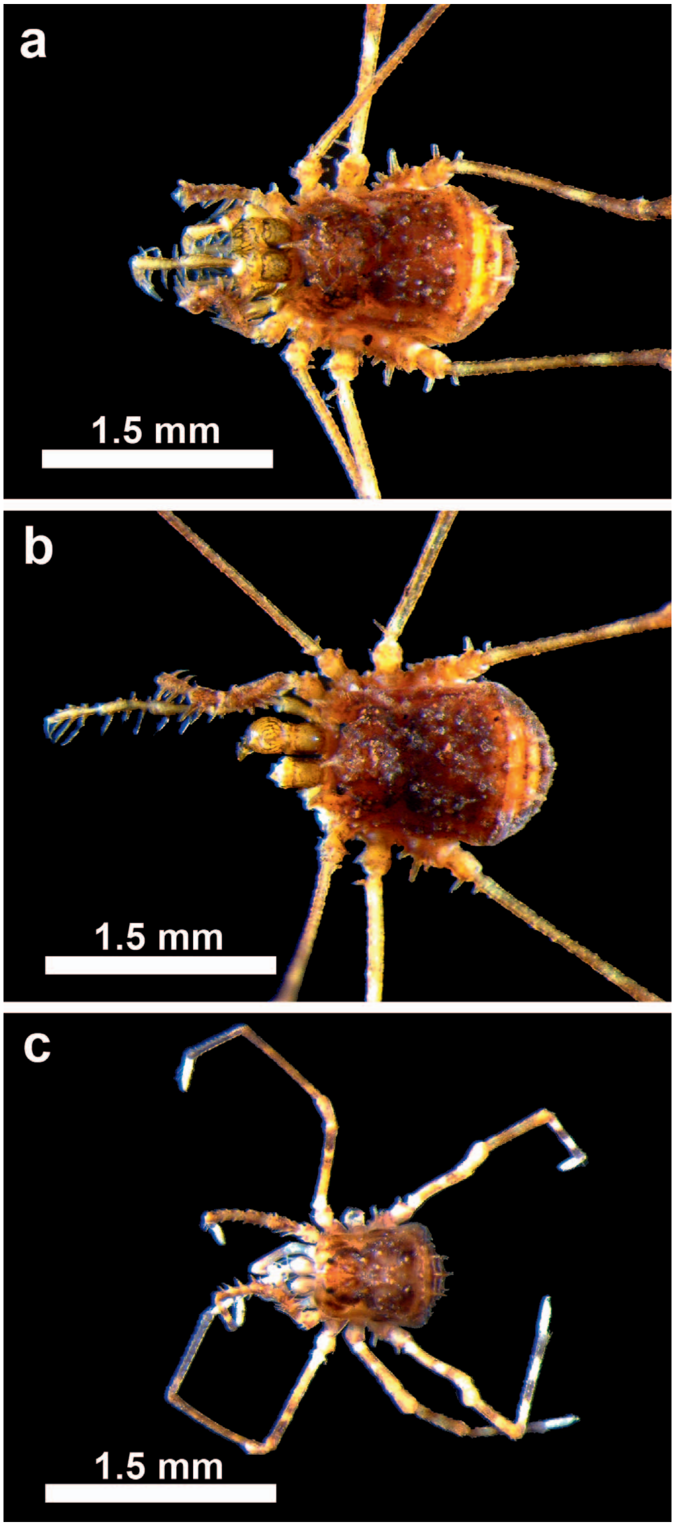

Figure 1.—Automontage pictures of individuals *Metibalonius* sp. (Podoctidae) in dorsal view. a: Adult female. b: Adult male. c: Nymph.

(Electron Microscopy Sciences) using Ultra-Smooth carbon adhesive tabs (Electron Microscopy Sciences). Samples were coated with Pt-Pd, using a Cressington 208HR sputter coater and imaged in a Zeiss Ultra-Plus (field emission scanning electron microscope; accelerating voltage: 5–6 kV) at the Center for Nanoscale Systems, Harvard University. Measurements were taken using the open source software ImageJ 1.48v (available online at https://imagej.nih.gov/ij).

RESULTS

Legs I and II differ from legs III and IV with respect to shape and setal composition (Figs. 2, 3). The distal tarsomeres of the anterior legs (I and II) are relatively more elongated than those in posterior legs (III and IV) (Figs. 2, 3). The most distal tarsomeres of the anterior legs have almost no trichomes and are mostly covered in sensilla chaetica with wall pores and some sensilla chaetica with a tip pore (Fig. 2a–c). On both legs, setae are evenly distributed on most tarsomeres, having a higher density only around the small single claw (Fig. 2). Legs I and II show a similar density and distribution of setae, with no evident sexual dimorphism (Fig. 2a–c). Distitarsi of posterior legs III and IV have trichomes along all surfaces of the tarsomeres, with higher density on the ventral side (Fig. 3b, c). Some of the distal ventral trichomes of the most distal tarsomeres III and IV of *Metibalonius* sp. have a curved shape ending in an expanded apex instead of tapering gradually toward the distal portion (Figs. 3b, c; 4f). The apex has an ovate shape of approximately 1.5 μm wide and 3.5 μm long. When broken, the shaft appears solid. These trichomes occur in specimens of both sexes, with no apparent sexual dimorphism. Posterior distitarsi also have sensilla chaetica with a tip pore (*sensu* Gainett et al. 2017) and a peculiar undescribed type of spatulate setae on the most distal tarsomeres.

These spatulate setae occur on the most distal part of the last tarsomere of legs III and IV of adults of both sexes, with no apparent sexual dimorphism (Fig. 3a–c). These structures are inserted in sockets on the frontal part of the tarsomere, three of them inserted retrolaterally and four prolaterally (Fig. 3a–c). The setae are sigmoidally curved towards the tip of the leg, with the tip of the setae facing down (Fig. 4a). The shaft is approximately 80 μm long. The proximal part of the shaft is cylindrical, with a diameter at the base of 5.8 μm (Fig. 4a). The wall of the shaft is externally smooth at this region. This cylindrical profile of the shaft becomes progressively flattened at 2/3 of its length towards the tip (Fig. 4a–d). Wall pores were not detected, and broken shafts reveal a lumen. The apex is expanded, flattened, and spatula-like, and the dorsal and ventral surfaces have different textures. The spatula is approximately 12 μm wide. The dorsal surface is similar in texture to the rest of the seta, but showing some ridges (Fig. 4b), while the ventral side of clean samples appears rough and wrinkled, bearing several microfolds (Fig. 4d, e). In uncleaned samples, this ventral surface is covered with particles, and a marked oval disc with clear margins was discernible (Fig. 4c, brackets). The particles were more concentrated in the ventral side of the spatula than in the rest of the shaft (Fig. 4c, brackets). The approximate area of the wrinkled ventral surface of the spatula is 90 μm^2, which implies a total contact surface of approximately 630 μm^2 per leg, and 2520 μm^2 for all walking legs (III and IV). Only the nymph (Fig. 1c) has an arolium on the frontal region of legs III and IV (absent on legs I and II), and lacks spatulate setae (See Supplementary Fig. 1, available online at http://dx.doi.org/101636/JoA-S-17-047.S1).

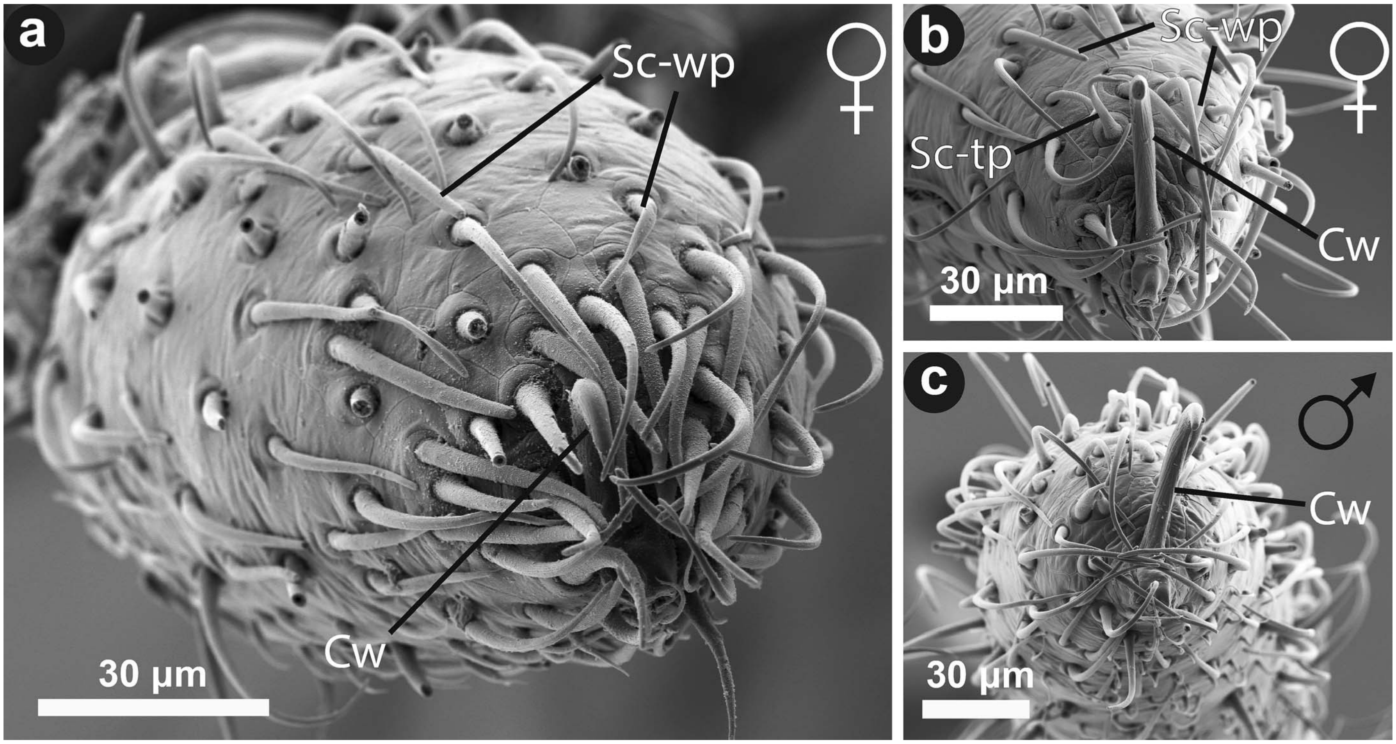

Figure 2.—Scanning electron micrographs of the frontal view of distitarsi I and II of *Metibalonius* sp. a: Leg I, female. b: Leg II, female. c: Leg II, male. Cw: claw; Sc-tp: sensilla chaetica with a tip pore; Sc-wp: sensilla chaetica with wall pores.

DISCUSSION

We have reported a distinctive socketed spatulate seta on the most distal tarsomeres III and IV of *Metibalonius* sp. The expanded spatulate tip clearly suggests an adhesive function. A spatulate shape is typical of adhesive setae and this shape has independently evolved in distantly related animal groups, including geckos, insects and arachnids (Foelix et al. 1984; Autumn et al. 2000; Beutel & Gorb 2001; Gorb 2001; Wolff & Gorb 2016). In comparison with blunt tips, spatulate structures increase the contact surface, which has been demonstrated both experimentally and theoretically to generate high adhesive forces (Autumn et al. 2000; Persson & Gorb 2003; Varenberg et al. 2010). Moreover, the spatulate setae in *Metibalonius* sp. have dorsal ridges and a lumen probably filled with liquid, features that have been observed in adhesive setae in insects (Gorb 1998). These features are thought to assist in stabilizing and spreading the contact zone over the substrate (Eimüller et al. 2008), conferring visco-elastic properties important for adhesion (Persson & Gorb 2003). In addition, the ventral surface of the spatula displays a wrinkled soft cuticle when dried. Similar ultrastructure has been reported in insects and could be explained by the presence of hydrated proteins (Peisker et al. 2013). In the ladybug beetle *Coccinella septempunctata*, it has been shown that the spatulate tips of adhesive setae have a high concentration of the protein resilin, which may be important to resist abrasion, and for optimizing contact zone and stability (Peisker et al. 2013).

The setae of *Metibalonius* sp. are also particularly similar in shape to the adhesive tenent setae observed in many beetle species (Stork 1980; Gnaspini et al. 2017). Even though the number of units of adhesive setae is usually higher than in the harvestman, some beetles may show comparable numbers. For instance, the beetle *Colenisia zelandica* (Leodidae) (body length: ~1.5 mm; Leschen 1999) has only 8 large putative adhesive setae on each tarsus (Gnaspini et al. 2017). Therefore, an adhesive mechanism as seen in these insects, presumably relying on a liquid secretion and capillarity, seems plausible for the setae in this harvestman. Our scanning electron micrographs of spatulate setae of *Metibalonius* sp. show no slits or pores in the shaft and socket, but we cannot rule out that a liquid is secreted, as openings sometimes are only detectable with transmission electron microscopy. Nonetheless, some secretion-like material is clearly more concentrated on the putative adhesive surface of the spatula (Fig. 4c), which further supports this idea.

Setae presenting a single large terminal spatula and that rely on a liquid to adhere are very common in beetles and flies (Gorb 2001), but are relatively rare in Arachnida (reviewed in Wolff & Gorb 2016). In ricinuleids, a putative adhesive seta with spatulate tip has been shown to possess a secretory system that oozes at the base of the shaft (Talarico et al. 2006; Wolff & Gorb 2016). Other cases of setae with single terminal spatula in arachnids have only been reported for Opiliones of the suborder Laniatores (Rambla 1990; Wolff & Gorb 2016). They occur in the families Biantidae (Stenostygninae), Samoidae, Epedanidae, Stygnidae and Podoctidae ("Ibaloniinae" only), as a dense aggregation termed scopula (Rambla 1990; Pinto-da-Rocha et al. 2007; Wolff & Gorb 2016). Scopular setae also have some secretion-like material associated with the broadened tips (Wolff & Gorb 2016), similar to

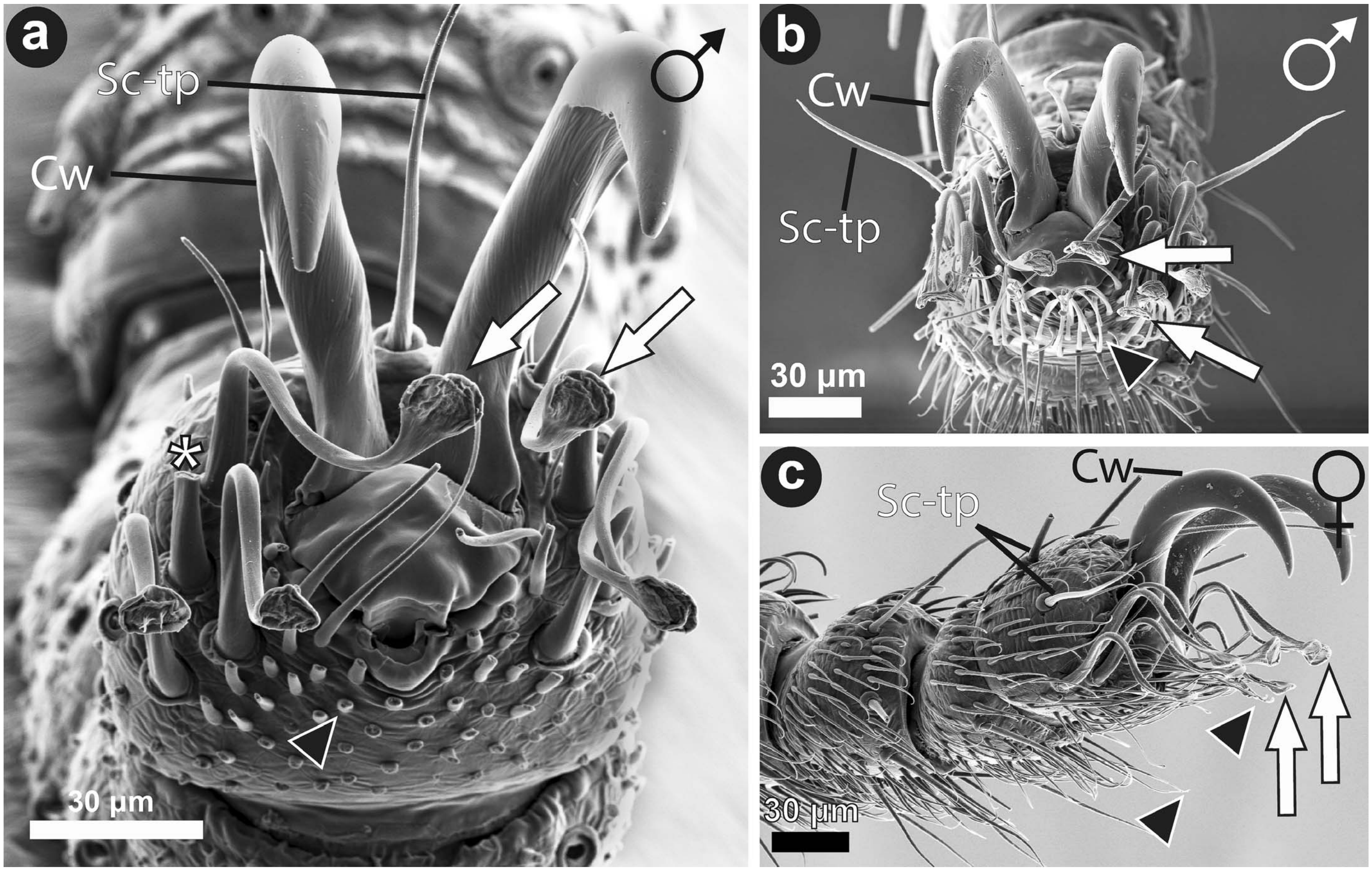

Figure 3.—Scanning electron micrographs of frontal (a, b) and lateral (c) views of distitarsi III and IV of *Metibalonius* sp. a: Male, leg III. Note that ventral trichomes (black arrowhead) are broken. b: Male, leg IV. c: Female, leg IV. Arrow: spatulate setae; Asterisk: broken spatulate seta; Black arrowhead: trichome with expanded tip; Cw: claw; Sc-tp: sensilla chaetica with a tip pore.

what we observe in *Metibalonius* sp. However, scopular setae differ from the setae here described in some respects. The scopular setae occur in a much higher density, when compared to only 7 units of socketed spatulate setae per leg in *Metibalonius* sp. Also, described scopular spatulate setae have slender shafts, sometimes band-like flattened (e.g., *Metacrobunus* sp.; Epedanidae; Wolff & Gorb 2016), while the setae we report have tubular shafts proximally, with a lumen. Moreover, the tip of a scopular seta is either lanceolate or slightly broadened, and ranges from approximately 2 to 6 µm in width (Wolff & Gorb 2016), while the type of spatulate setae in *Metibalonius* sp. has a spatula-shaped tip with more than twice this size. The scopular setae morphology more closely resembles the ovate-tip trichomes herein reported, which co-occur with the socketed spatulate setae in *Metibalonius* sp. It is currently unknown if the described scopular setae have true sockets and shafts with a lumen, characteristics which would indicate similarity with the spatulate setae in *Metibalonius* sp. (see Rambla 1990; Wolff & Gorb 2016). Nonetheless, scopular setae have shaft dimensions and tip morphology resembling the ovate-tip trichomes, which have solid shafts and no apparent socket. Moreover, the density and distribution of scopular setae (ventral) in all reported cases in Laniatores (Wolff & Gorb 2016) is very similar to non-spatulate trichomes on the ventral surface of the most distal tarsomeres of other laniatorean harvestmen (Willemart & Gnaspini 2003), which suggests that they may be the same type of structure. Therefore, the socketed spatulate setae likely constitute a different type of adhesive setae in harvestmen. This observation and the fact that scopular spatulate setae have evolved multiple times in harvestmen (Wolff & Gorb 2016) further highlights the diversity of adhesive structures in these arachnids.

In other families of Laniatores, the corresponding region where socketed spatulate setae occur is equipped mainly with sensilla chaetica with a tip pore (Willemart et al. 2009; Gainett et al. 2017). In *Heteromitobates albiscriptus* (Mello-Leitão, 1932) (Gonyleptidae), six sensilla chaetica occur in this region, termed S1, S2 and S3 (pro- and retrolateral) (Ramin et al. 2016), and are precisely located in the correspondent position where spatulate setae occur in *Metibalonius* sp. Moreover, the morphology of the socket of spatulate setae in *Metibalonius* sp. is also similar to that of sensilla chaetica with a tip pore (compare in Fig. 4a). Therefore, socketed spatulate setae may be modified tip-pored sensilla chaetica, which are typical gustatory and touch-sensitive sensilla in harvestmen (Guffey et al. 2000; Willemart et al. 2009; Gainett et al. 2017). Modification of sensilla chaetica into setae with a new function has also been suggested for the glandular sensilla of some harvestmen (Wolff et al. 2016b).

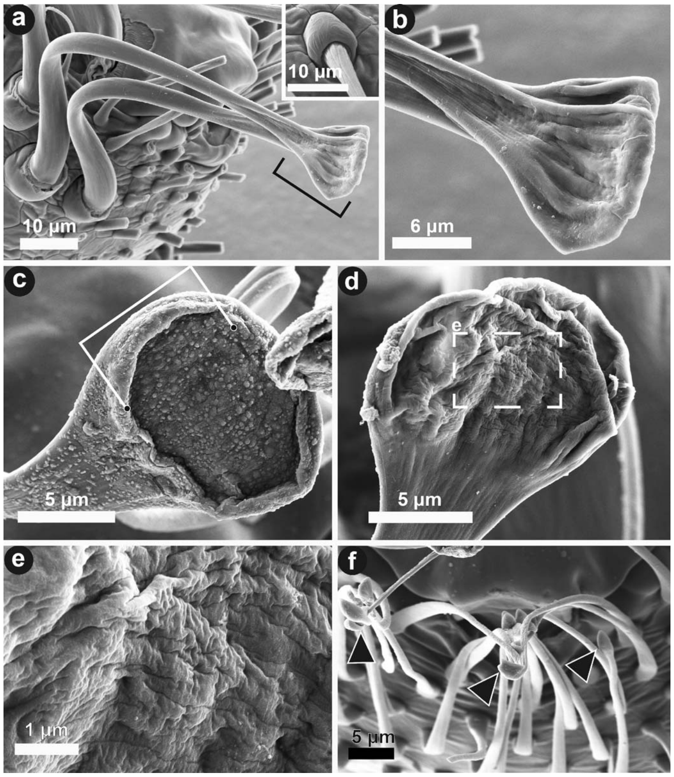

Figure 4.—Scanning electron micrographs of spatulate setae and trichomes on the most distal tarsomeres III and IV of *Metibalonius* sp. a: Lateral view of spatulate setae on the most distal tarsomere III, adult male. Bracket indicates the spatulate tips of two adjacent setae. Inset: socket of a sensillum chaeticum, leg III, male. b: Close-up of spatula tips shown in "a". c: Ventral surface of an uncleaned spatula, leg IV, female. Brackets indicate the limits of the oval disc with higher concentration of particles. d: Ventral surface of a cleaned spatula, leg III, male. e: Detail of the wrinkled surface of the spatula shown in "d" (dashed square). f: Frontal view of the ventral trichomes on the most distal tarsomere IV, male. Note the ovate shape of the tips (black arrowhead).

Apparent absence of terminal pores in spatulate setae disfavors chemoreception (Altner & Prillinger 1980; Keil & Steinbrecht 1984), but the presence of a hollow cuticular shaft inserted in a socket with articulating membrane is typical of mechanoreceptive sensilla of arachnids (Foelix 1985), and also of some adhesive setae in spiders (Foelix et al. 1984). On the other hand, legs I and II of *Metibalonius* sp. lack spatulate setae altogether, and are equipped with sensilla chaetica with wall pores (olfactory) (see also Gainett et al. 2017). This distribution is in accordance with what has been described for other laniatorean species: legs I and II (sensory appendages) concentrate the highest diversity of sensillar structures, including olfactory sensilla; and legs III and IV (walking legs) are equipped with trichomes (non-sensory) and a smaller diversity of sensilla, mostly touch detectors and contact-chemoreceptors (Willemart et al. 2009; Gainett et al. 2017).

Adhesion in arthropods may serve various functions, including prey capture, defense against predators and locomotion (Rovner 1980; Eisner & Aneshansley 2000; Betz & Kölsch 2004; Willemart et al. 2011; Wolff et al. 2015). For the spatulate setae here described, a role in prey capture, similar to glandular sensilla in other harvestmen (Wolff et al. 2014), seems unlikely, since spatulate setae occur on legs III and IV, the walking legs. The adhesive arolium of *Metibalonius* sp. nymph, as in other laniatorean harvestmen, occurs only on leg pairs III and IV and is absent in adults. Interestingly, spatulate setae are absent in the nymph, but occur on leg pairs III and IV of adults. The same pattern has also been reported for the arolium and scopular setae of *Hinzuanius flaviventris* Pocock, 1903 (Laniatores, Biantidae) (Wolff & Gorb 2016). These observations raise the question of why adults still need adhesion similar to immature individuals. It has been proposed that immature laniatorean harvestmen have arolia because they have to molt, which often requires being upside down (Gnaspini 1995, 2007). However, molting is generally assumed not to occur in adult harvestmen (Gnaspini 2007), so a general role of spatulate setae in substrate adhesion should be considered as more likely. Alternatively, emergence of spatulate setae only in the sexually mature stage of development may also indicate a sexual role (see Andersson 1994). Unfortunately, relatively little is known about the natural history of Podoctidae, and even less so for *Metibalonius*. Described features for other podoctids include the attachment of debris to the body (Martens 1993; Wolff et al. 2016a) and the iconic presence of eggs attached to legs IV of two male specimens of *Leytpodoctis oviger* Martens, 1993, indirectly suggesting paternal care (Martens 1993; but see Sharma et al. 2017). Therefore, basic natural history data on habitat use and biology of *Metibalonius* and other podoctids are needed to understand the behavioral role of these setae. Spatulate setae of similar morphology and in comparable numbers have also been observed in other species of the same genus, i.e., *Metibalonius esakii* Suzuki, 1941 (G. Machado, pers. comm.). Therefore, it would be interesting to inspect more species for the presence of these conspicuous setae, which can potentially reveal a new diagnostic character for the recently revised systematics of the family (Sharma et al. 2017).

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