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Changes in nymphal morphometric values and tarsal microstructures during postembryonic development in the Neotropical harvestman *Heteromitobates albiscriptus* (Opiliones: Gonyleptidae)

Alessandra Z. Ramin[1], **Rodrigo H. Willemart**[2,3,4] and **Pedro Gnaspini**[1,4]: [1]Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, 321, 05508-090, São Paulo, SP, Brazil; E-mail: gnaspini@ib.usp.br; [2]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; [3]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; [4]Programa de Pós Graduação em Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 321, Travessa 14, Cidade Universitária, São Paulo – SP, 05508-090 Brazil

Abstract. The postembryonic development of Opiliones (Arachnida) includes three phases: larval, nymphal (with four to eight instars), and adult (when molts cease). The present study aimed to describe the postembryonic development of *Heteromitobates albiscriptus* (Mello-Leitão, 1932) (Gonyleptidae) including both a morphometric study and SEM analysis of two structures present in the tarsus of nymphs and adults: the "tarsal aggregate pores" (TAPs) and the "tarsal perforated organ" (TPO). The nymphal phase includes five stages, which can be easily recognized by morphometric values. In contrast to the pectinate tarsal claws found in legs III–IV of adults (the main synapomorphy of the genus *Heteromitobates* in the subfamily Goniosomatinae), nymphs bear smooth claws. First nymphs lack TAPs and TPOs. TAPs seem to have a precisely defined position in both prolateral and retrolateral faces of the tarsus. The number of pores in TAPs grows from three or four among second nymphs to around 20 among adults, and measure around 2.15 μm in diameter with no clear difference between ages. An additional field of pores on legs III–IV ("ventral tarsal aggregate pores", vTAPs) was detected only among adults. The plates at the base and the apex of the TPOs differ from the ones in between. The length of the TPO and its number of plates increase with each molt. However, there is no discernible pattern of growth throughout the postembryonic development when taking into account both the average size of the plates (ranging between ~7–11 μm) and the ratio of TPO length to tarsus length.

Keywords: Morphology, glandular opening, Gonyleptidae, Goniosomatinae, ontogeny

After hatching, arthropods pass through successive molts to achieve adulthood, defining a postembryonic developmental phase. The postembryonic development of arachnids of the order Opiliones (harvestmen) includes three phases: larval, nymphal, and adult (e.g., Juberthie 1964; Gnaspini 2007). The larva hatches and molts to the first nymphal instar; after a variable number of nymphal molts, usually four to eight (mostly, six), the adult stage is reached (Gnaspini 2007). The duration of each phase varies among the suborders Cyphophthalmi, Eupnoi, Dyspnoi, and Laniatores (reviewed by Gnaspini 2007): whereas the larva of a sironid specimen of Cyphophthalmi takes four to seven days before molting into the first nymph, the larvae of the remaining suborders usually molt into the first nymph within less than an hour (e.g., Juberthie 1964; Gnaspini 2007). During postembryonic development each molt results in a larger animal. Because total body length and width may vary with the amount of food in the gut, these measurements are unsuitable for documenting growth, but the appendages seem to be more appropriate structures and have been used in most comparative studies (e.g., Table 2 in Gnaspini 2007).

According to Juberthie (1964), sexual characters usually appear in the penultimate instar (i.e., the last nymphal stage), but Muñoz-Cuevas (1971a) and Gnaspini (1995) have shown that, in the studied neotropical Laniatores, sexual characters appear in the antepenultimate instar. In many Laniatores, males can often be distinguished from females by enlarged armature of the body, but especially in legs IV (trochanter, femur and/or tibia) (e.g., from several chapters in Pinto-da-Rocha et al. 2007), and these apophyses already appear in penultimate nymphal instars (e.g., Muñoz-Cuevas 1971b; Gnaspini 1995). Especially considering Muñoz-Cuevas's (1971b) statement that sexual maturity is achieved in the penultimate stage (i.e., the last nymphal instar), this stage is frequently treated as "subadult" stage. In addition, based on the assumption that both subadults and adults were sexually mature, Gnaspini et al. (2004) suggested that the adult phase of laniatoreans included two stages, contrary to the general rule among arachnids, except for some mygalomorph spiders (in which some females may molt after sexual maturity), molts cease with adulthood. The presence of two adult stages among harvestmen was shown to be wrong and the variation observed among sexually mature males was recognized as profound differences related to sexual selection (e.g., DaSilva & Gnaspini 2009; Zatz et al. 2010; Munguía-Steyer et al. 2012).

Among Grassatores (an infraorder of Laniatores), there are typical morphological features that aid in distinguishing between nymphs and adults. All legs of Cyphophthalmi, Eupnoi, and Dyspnoi as well as legs I and II of Laniatores bear only one claw. Among "Insidiatores" (a non-monophyletic infraorder of Laniatores), legs III and IV have a complex and usually trifid claw. In Grassatores, legs III and IV have two single claws, independently inserted in the tarsus, although the claws may be fused at the base (e.g., Gnaspini 2007). In Grassatores, nymphs and adults differ in the

Table 1.—Summary of leg measurements (length, in mm) for the available material of *Heteromitobates albiscriptus* (see complete list in Appendix 1), reported as the range of values observed in each stage. The number of specimens analyzed [N] of each age is given between square brackets. The average growth of each leg (percentage) relative to the previous stage is given in parentheses.

	Nymph 1 [N=8]	Nymph 2 [N=5] (% growth)	Nymph 3 [N=11] (% growth)	Nymph 4 [N=14] (% growth)	Nymph 5 [N=3] (% growth)	Adult [N=15] (% growth)
Leg I	7.71–8.75	10.60–10.87 (29)	13.12–14.73 (31)	17.13–19.55 (33)	23.74–24.36 (27)	30.20–36.53 (35)
Leg II	19.64–23.33	26.78–28.73 (25)	34.02–39.05 (29)	43.70–48.45 (27)	57.32–58.70 (25)	73.43–84.08 (37)
Leg III	11.19–13.89	16.30–17.60 (27)	20.72–24.66 (31)	26.42–30.90 (34)	38.33–39.18 (30)	49.73–58.65 (35)
Leg IV	16.11–19.58	23.29–25.26 (26)	28.36–33.00 (30)	38.46–42.43 (29)	51.42–52.19 (28)	67.84–79.77 (39)

structures found between the two tarsal claws (e.g., Muñoz-Cuevas 1971a, b). In this group, all nymphal stages bear two typical "juvenile" structures ventrally in both third and fourth leg tarsi: one projection similar to a third tarsal claw, called a 'pseudonychium', and a "fleshy" projection, called an 'arolium'. These structures grow during nymphal development, but are not observed in adults (Muñoz-Cuevas 1971a, b; Gnaspini 1995, 2007). On the other hand, there is a third structure in most Gonyleptoidea (Cosmetidae, Cranaidae, Gonyleptidae, Manaosbiidae, Stygnidae), called a 'tarsal process', which may grow gradually with each molt, but which is fully developed only in adults (Muñoz-Cuevas 1971a, b). It is a dorsal projection on the apex of the last tarsomere, which usually bears a long and unusual seta.

Although studies concerning Eupnoi and Dyspnoi have shown that many structures develop or increase in size and/or complexity during post-embryonic development (e.g., setae of the appendages, shape of the eyemound, pseudoarticulation of femora, and the shape and size of the hood among some Dyspnoi; see review in Gnaspini 2007), studies concerning Laniatores have focused mainly on the armature of pedipalps and legs and the increase in the number of tarsomeres (Gnaspini 2007), except for the work of Townsend et al. (2009), who also added some information on body tubercles and color.

Recent studies by Willemart & Gnaspini (2003), Willemart et al. (2007, 2009, 2010), Willemart & Giribet (2010), Wijnhoven (2013) and Rodriguez et al. (2014) have reviewed the knowledge about sensory structures and glandular openings on the integument of harvestmen. Willemart et al. (2007) described six glandular openings in the articulations, trochanter, metatarsus and tarsus of the legs and one that occurs all over the body. Among them are the tarsal aggregate pores (TAPs) that were first recognized at the retrolateral and prolateral faces of the distal end of legs III and IV, close to the tarsal process (among adults), as in figs 8, 9 from Willemart et al. (2007), in both sexes. Gainett et al. (2014) showed the large morphological variation of these structures in all families of Laniatores. Another conspicuous structure on all legs is the tarsal perforated organ (TPO), which is located on the ventral surface of the most proximal tarsomere, as in figs 11, 12 from Willemart et al. (2007) and is composed of two parallel rows of allegedly perforated plates. Because of its external appearance, TPO was thought to be glandular but has recently been suggested to be a region of attachment of muscles (Proud & Felgenhauer 2013).

So far, no studies have dealt with the ontogeny and phylogenetic distribution, as well as sexual dimorphism of glandular openings, and such studies are important because they provide indirect functional evidence. Cuticular structures that only appear in adults or late instars and sexually dimorphic structures usually have a sexual function, being a product of sexual selection (Andersson 1994; Willemart et al. 2006; Buzatto et al. 2014; Fowler-Finn et al. 2014). Therefore, morphology is very important in giving clues that help to explain typical behaviors of a species.

Thus the present study aimed to describe the postembryonic development of *Heteromitobates albiscriptus* (Mello-Leitão, 1932) (Laniatores: Gonyleptidae), including a morphometric study and analysis of two common structures (tarsal aggregate pores and tarsal perforated organ) present in the tarsus in all nymphal stages as well as in adults of both sexes.

METHODS

Species studied.—Males and females for each developmental stage of the species *Heteromitobates albiscriptus* (Laniatores: Gonyleptidae: Goniosomatinae) were examined. The animals analyzed were collected previously in Gruta da Quarta Divisão, Ribeirão Pires, São Paulo, during the study by Willemart & Gnaspini (2004a, b) and preserved in 70% ethanol. See also DaSilva & Gnaspini (2009) for a redescription and taxonomic discussion.

Morphometric and meristic analysis.—Based on the methodology described by Gnaspini (1995) when studying another goniosomatine harvestman and on structures that have been used in the study of the postembryonic development of harvestmen (as listed in Gnaspini 2007), we measured the

Table 2.—Summary of the counts of tarsomeres (number of articles in tarsi) in the available material of *Heteromitobates albiscriptus* (see complete list in Appendix 1), reported as the range of values observed in each stage. The number of specimens analyzed [N] of each age is given between square brackets.

	Nymph 1 [N=8]	Nymph 2 [N=5]	Nymph 3 [N=11]	Nymph 4 [N=14]	Nymph 5 [N=3]	Adult [N=15]
Leg I	1	2	2	2	2	9–12
Leg II	1	2	2	2	2	20–27
Leg III	2	2	2	2	3	10–14
Leg IV	2	2	2	2	3	13–15

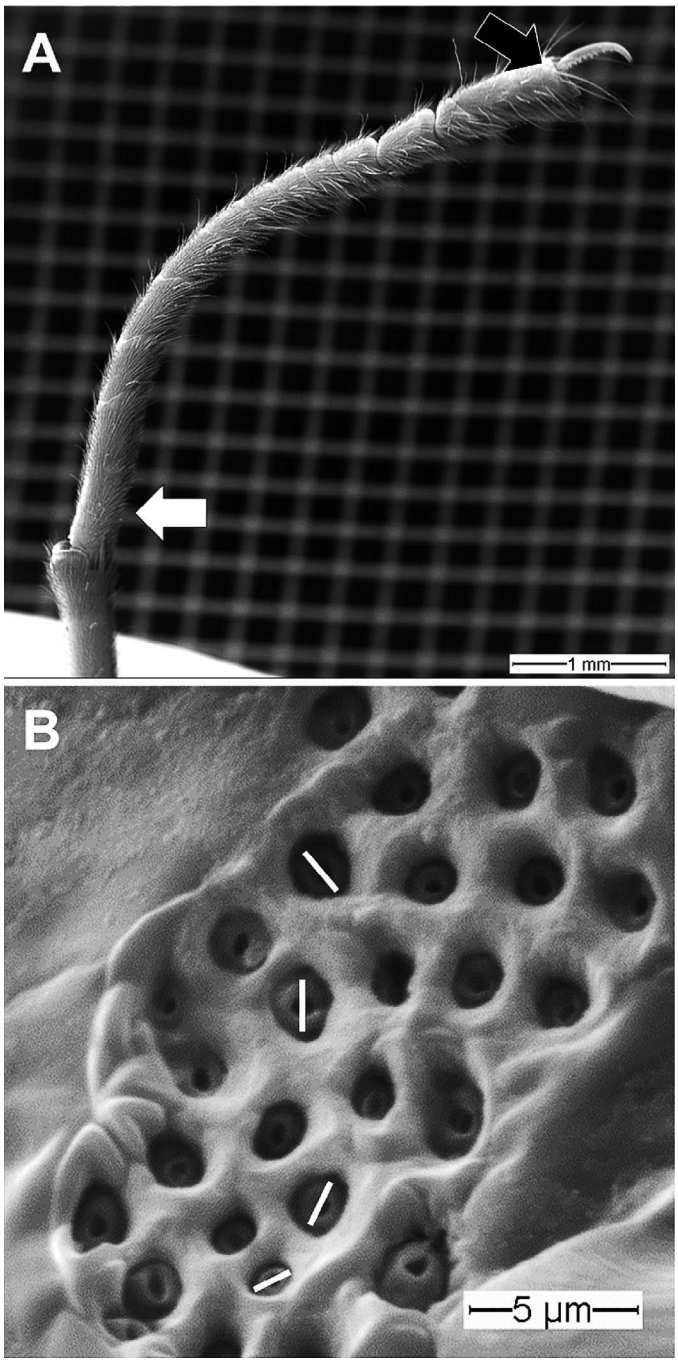

Figure 1.—**A.** Right tarsus of leg III of an adult male of *Heteromitobates albiscriptus*, showing the location of the tegumental structures studied herein under SEM. The black arrow shows the region where TAPs ("tarsal aggregate pores") are located, and the white arrow shows the position of TPO ("tarsal perforated organ"). Retrolateral view. **B.** Retrolateral view of right tarsus of leg IV of an adult male of *Heteromitobates albiscriptum*, showing measurements of the diameter taken in some pores of TAPs (white lines).

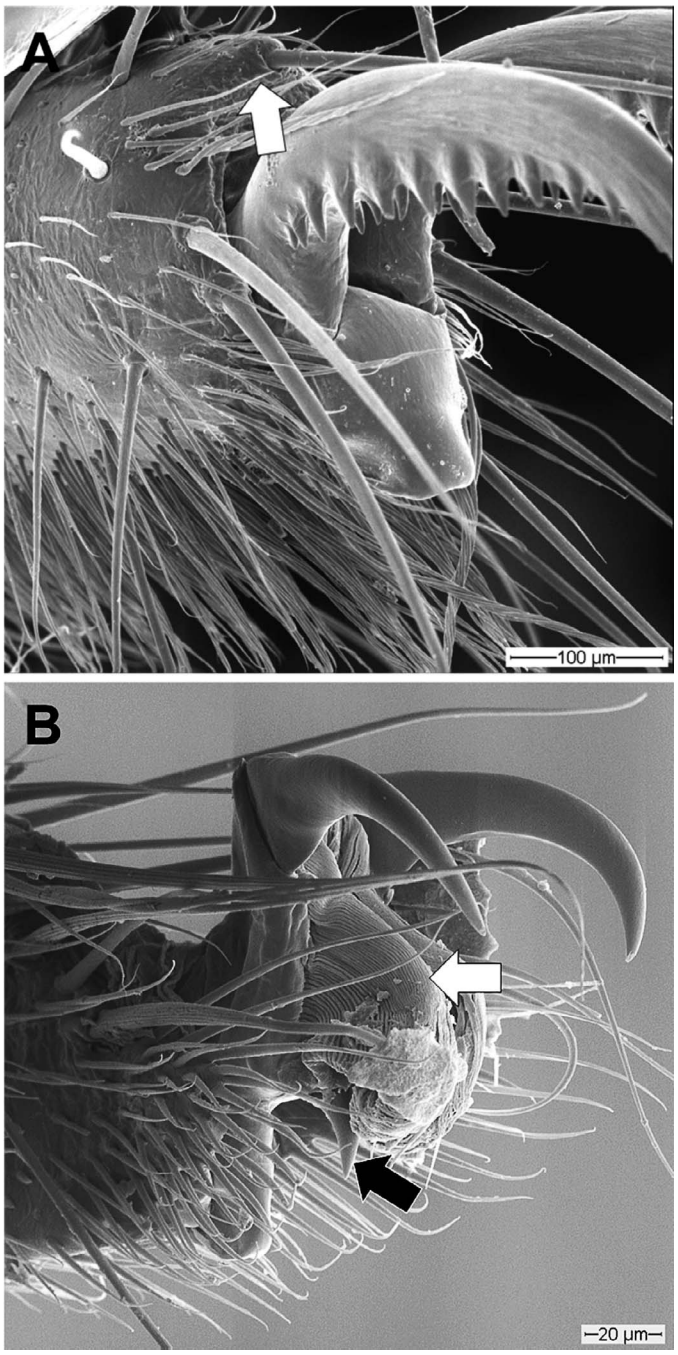

Figure 2.—**A.** Right leg IV of an adult male of *Heteromitobates albiscriptus*, showing the pectinate tarsal claws typical of the genus *Heteromitobates* and the tarsal process (arrow) typical of the adult tarsus of some gonyleptoid Laniatores. **B.** Right leg IV of a first nymph of *Heteromitobates albiscriptus*, showing the smooth tarsal claws, the arolium (white arrow) and the pseudonychium (black arrow). Retrolateral views.

following structures of all 56 individuals available: body length (from the base of chelicerae to the end of the abdomen) and width (at the widest point), total length and number of tarsal segments of each leg. Measurements were taken with a digital caliper and when necessary under a stereomicroscope. Measurements were taken on the right appendages; when a leg was missing or incomplete, the corresponding left appendage was measured. Measurements are herein expressed as the average measure ± standard deviation. Since we noticed, during the study, that sex could be recognized both in adults and last instar nymphs, we identified the sex when taking the

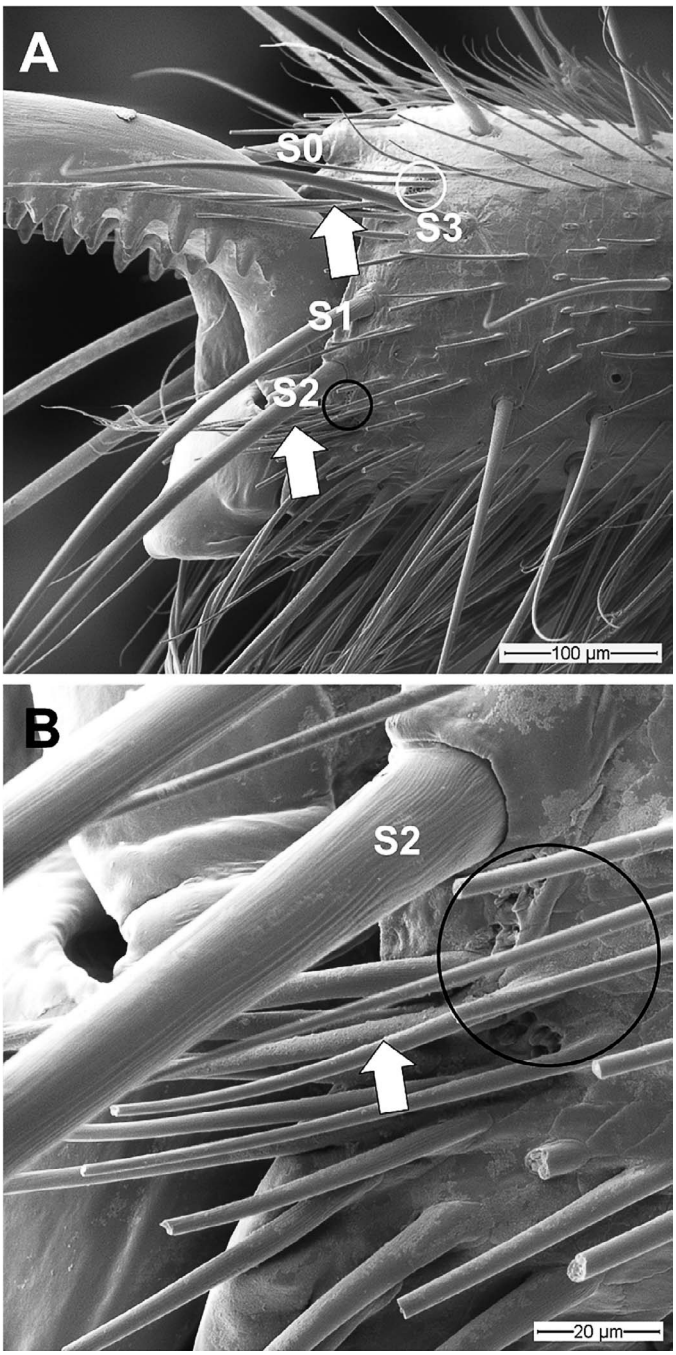

Figure 3.—**A.** Right leg III of an adult male of *Heteromitobates albiscriptus*, showing the TAPs (white circle) and vTAPs (black circle). **B.** Detail showing vTAPs. S0-S3 = setae (see text for description); arrows = associated trichomes (see text). Prolateral views.

measurements that were used in tarsal microstructural analyses, but the reduced number of females available did not allow comparisons between sexes in the morphometric analysis. Therefore, results are reported for all adults combined.

Morphological analysis of tarsal structures under SEM.—For SEM analysis, we followed the procedures described in Willemart et al. (2007, 2009, 2010). The legs were removed, cleaned ultrasonically and then mounted on a stub using silver glue. The stubs were sputter coated with gold using a Balzer SCD 50 sputter coater and then examined under the Zeiss DSM 940 SEM of the Electronic Microscope Laboratory of IBUSP. We used the right leg when available; otherwise, we used the left leg. For this study we used at least one specimen of each nymphal stage and at least one male and one female specimen for the last nymphal and the adult stages. Unfortunately, all available second nymphs had dirt adhered to their legs, hampering optimal analyses and micrographs.

In order to analyze the ontogenetic changes of the TAPs (Fig. 1A, black arrow) and TPO (Fig. 1A, white arrow) during the postembryonic development, we made a series of measurements and counts, as described below. We then compared the number and size of the studied structures in relation to the length of the tarsus along the postembryonic stages.

In the case of the TAPs, we used the micrographs to count the number of pores and to measure their diameter, in both prolateral and retrolateral groups. The numbers given here are an estimate of the real number of pores, because in some cases we could not properly see all pores due to the presence of the typical trichomes covering the group of pores. Therefore, we made several micrographs from different angles in order to allow precise counts of pores. In the case of the diameter, for comparisons among ontogenetic stages, we used the average diameter of the pores in the group; we measured as many pores as possible in each group (Fig. 1B), directly on the micrograph, using the scale bar as a reference. Although these pores were only previously detected on legs III and IV (Willemart et al. 2007), we analyzed all four legs in our study to check this information, especially considering that we included juveniles, not studied before.

In the case of the TPO, we photographed with high magnification and analyzed only one of the rows of all legs; we used the retrolateral row whenever possible, but we used the prolateral row when needed and also for comparison of structures between the two rows. We measured the total length of the organ and counted the number of plates included in the organ. Since the plates have an irregular shape, we measured the longest length of three randomly selected plates and used the mean length to make comparisons among stages.

We also observed the structures located between the two tarsal claws of legs III and IV and previously known to be exclusive of nymphs (arolium and pseudonychium) or adults (fully developed tarsal process), and looked for additional structures that could help in the recognition of ontogenetic stages and/or sexes.

RESULTS

Morphometric analysis of the postembryonic stages.—We herein recognized five stages in the nymphal phase. Tables 1 and 2 summarize the data collected in this study (Appendix 1 shows all measurements collected for all specimens studied). Clearly there is no overlap between the measured values of successive stages, which can therefore be easily recognized by morphometric values. The number of tarsomeres is initially small in nymphs and increases among adults, with a major saltational change between the two phases. Sex cannot be recognized in the first four nymphal stages. Males can be distinguished from females by the presence of an apophysis on

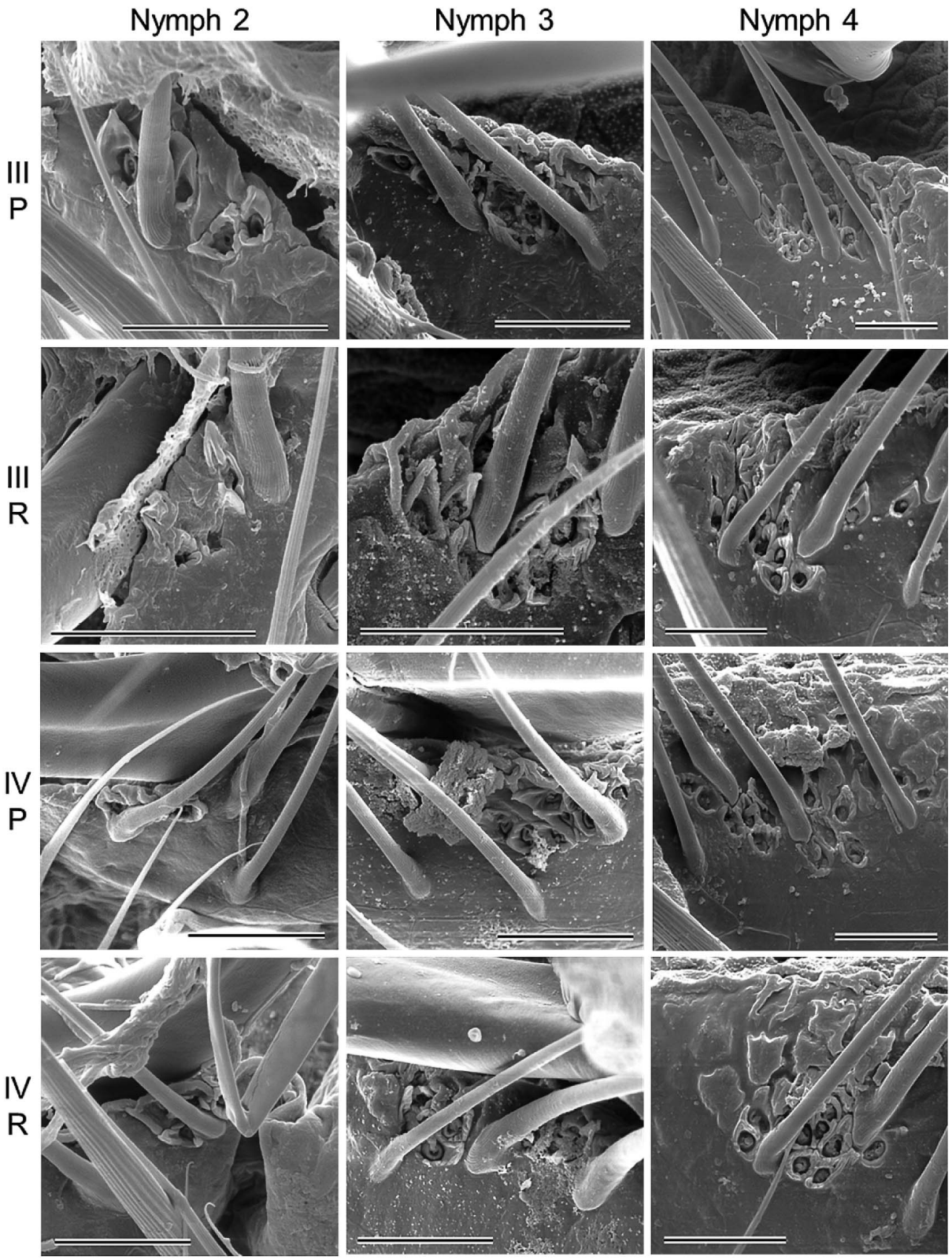

Figure 4.—Comparative plate of TAPs in both prolateral (P) and retrolateral (R) margins of legs III and IV during the postembryonic development of *Heteromitobates albiscriptus*. Nymphs 2–4 (compare to Figs. 5, 6). Scale = 20μm.

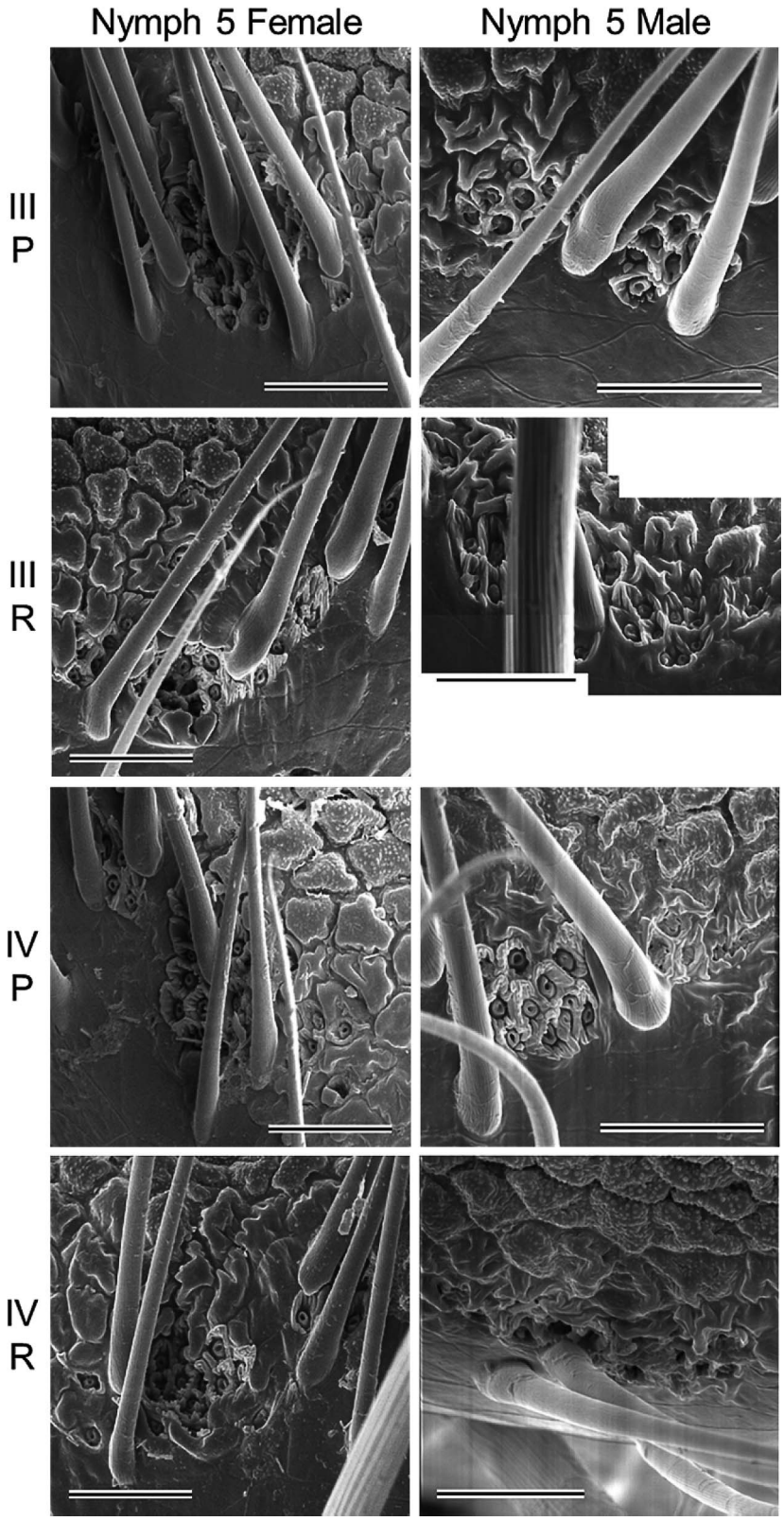

Figure 5.—Comparative plate of TAPs in both prolateral (P) and retrolateral (R) margins of legs III and IV during the postembryonic development of *Heteromitobates albiscriptus*. Nymphs 5 (compare to Figs. 4, 6). Scale = 20μm.

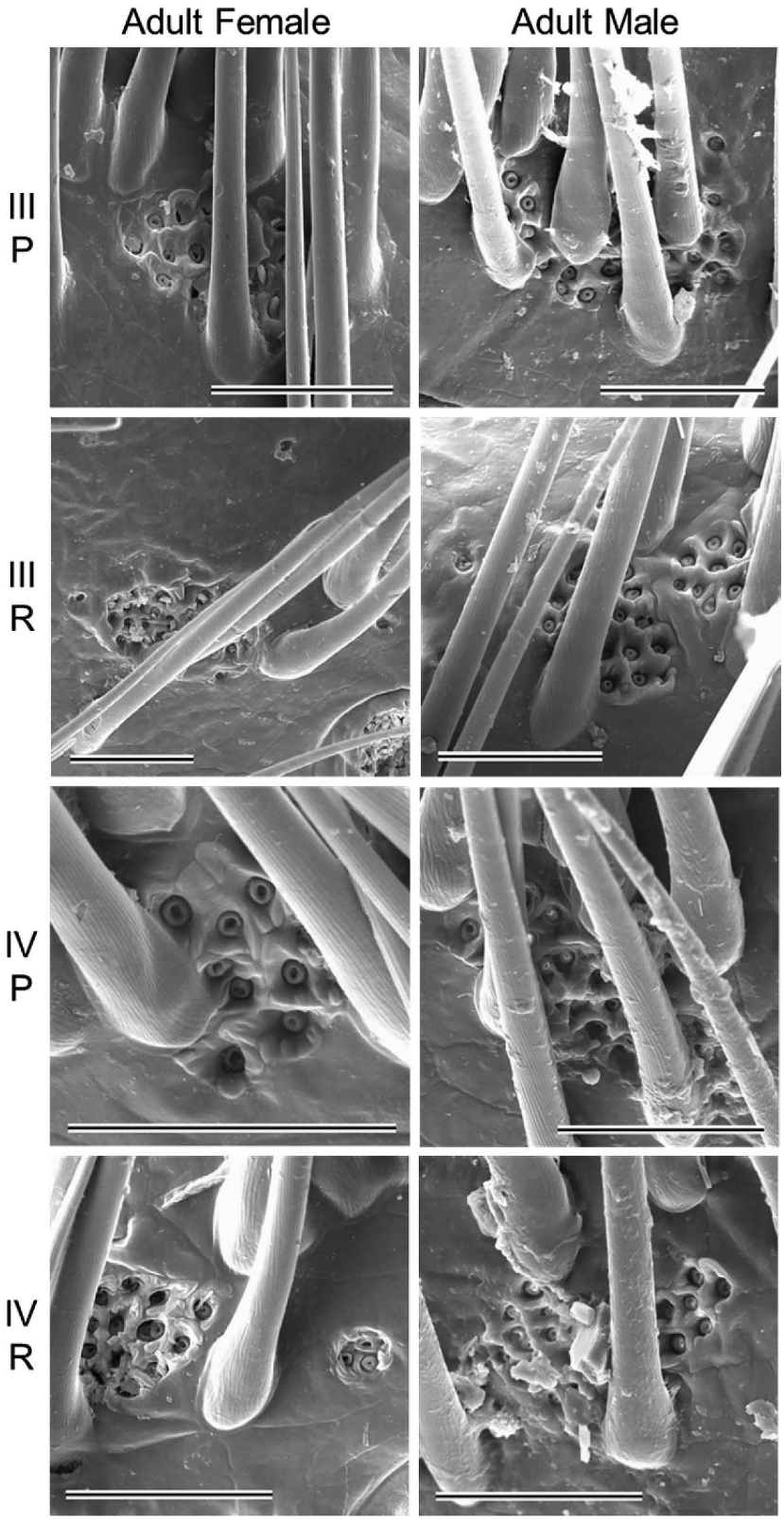

Figure 6.—Comparative plate of TAPs in both prolateral (P) and retrolateral (R) margins of legs III and IV during the postembryonic development of *Heteromitobates albiscriptus*. Adults (compare to Figs. 4, 5). Scale = 20μm.

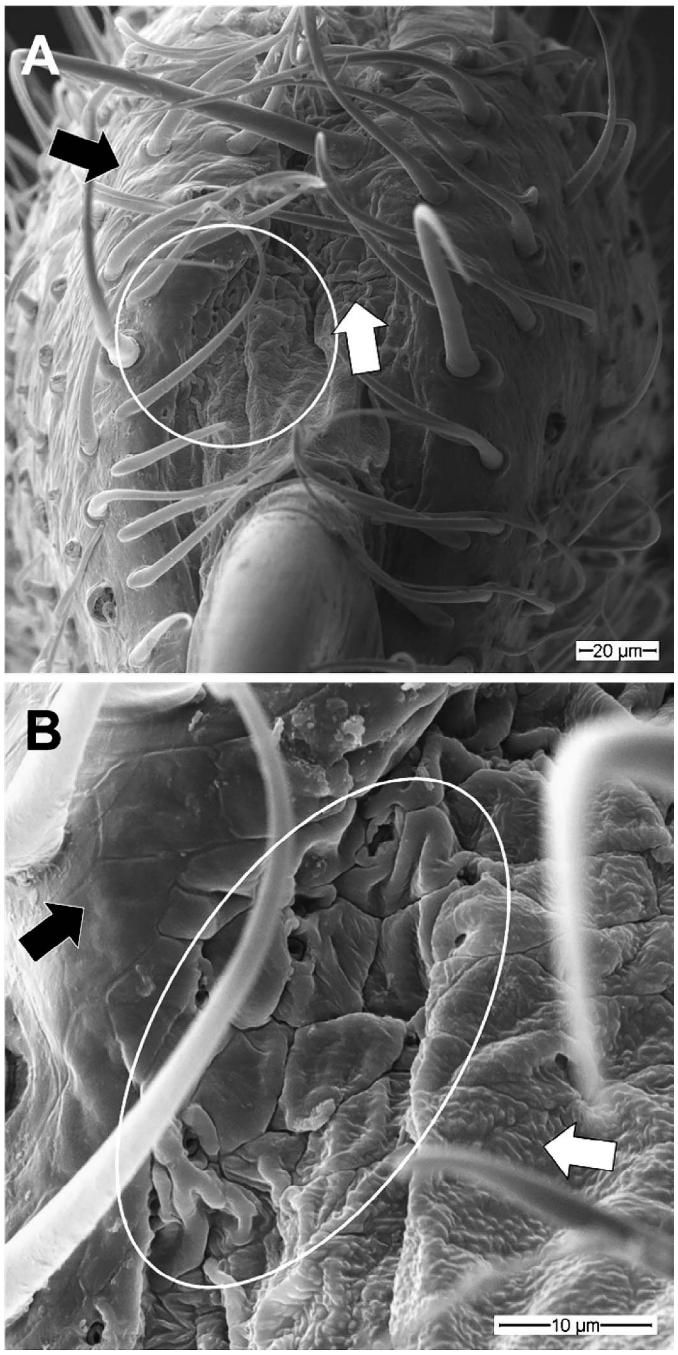

Figure 7.—**A.** Frontal view of tarsus I of an adult female of *Heteromitobates albiscriptus*, showing the different integument between the distal pleura around the articulation of the tarsal claw (white arrow) and the regular integument (black arrow). **B.** Detail of the circle in **A**, showing FAPs ("frontal tarsal aggregate pores") (ellipse); arrows show difference in integument, as in **A**.

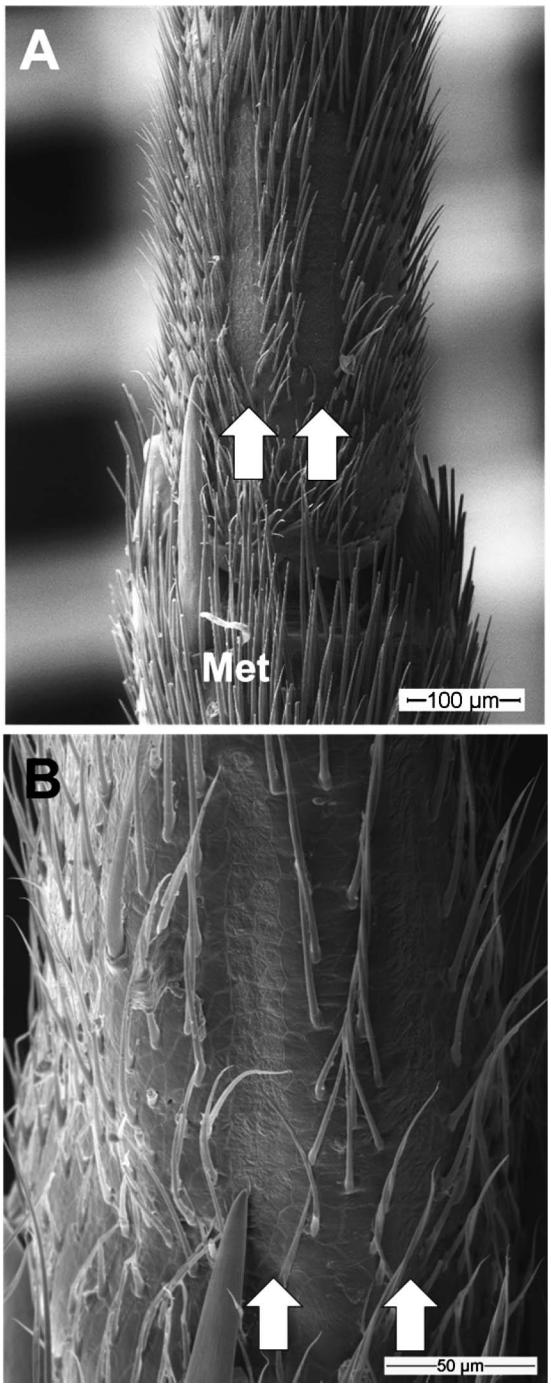

Figure 8.—Ventral view of the first tarsomere showing the pair of TPOs (arrows) running along the base of the tarsomere of *Heteromitobates albiscriptus*. **A.** Left fourth leg of an adult female. **B.** Right fourth leg of a fourth instar nymph. Met = apex of metatarsus.

trochanter IV both in the last nymphal stage and, more pronouncedly, in adults.

Additional taxonomic description of *H. albiscriptus* concerning nymphal features.—In addition to the description of *Heteromitobates albiscriptus* provided by DaSilva & Gnaspini (2009), our data allowed the recognition of important information related to nymphs. First, the color of the body and legs of nymphs is a patchy mixture of green and light grey, in both preserved and live specimens. Second, in contrast to the pectinate tarsal claws in legs III and IV of adults (Fig. 2A), nymphs bear smooth claws (Fig. 2B).

Tarsal aggregate pores: additional description and ontogenetic analysis.—Willemart et al. (2007) described the TAPs as "an aggregation of glandular openings that is always close to

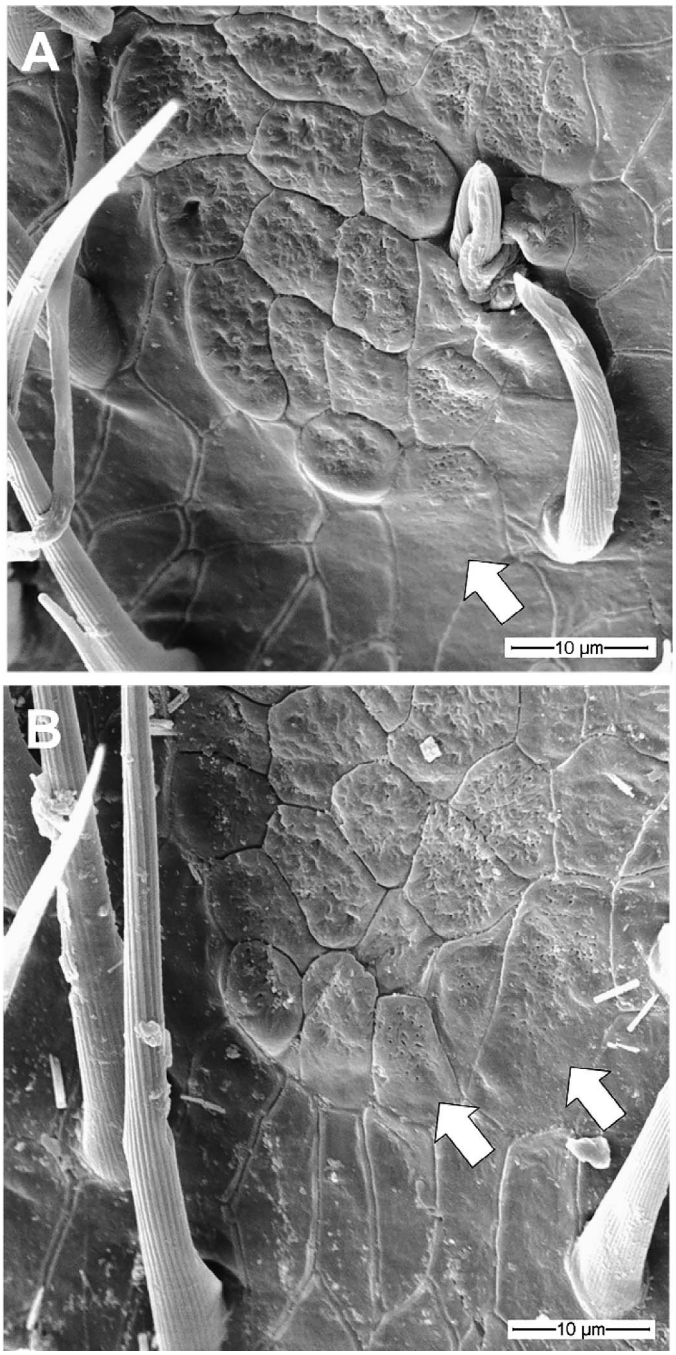

Figure 9.—Detail of the proximal portion of TPOs of *Heteromitobates albiscriptus*, showing the partially perforated nature of some of the proximally placed plates (arrows) as well as the more elongate shape of some proximal plates (both from the TPO and the surrounding integument). **A**. Leg III. **B.** Leg IV. Both are prolateral rows on the right legs from an adult female.

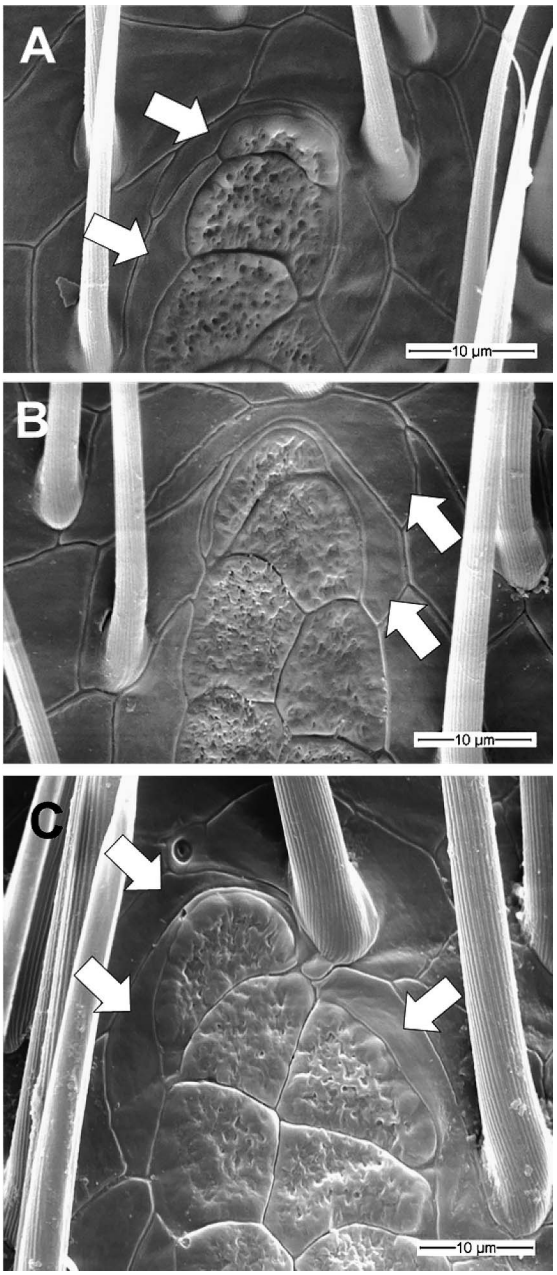

Figure 10.—Detail of the distal portion of TPOs of *Heteromitobates albiscriptus*, showing that the single cell or group of distal cells form a round margin frequently surrounded by very narrow and elongate curved tegumental plate(s) (arrows), very different from the other tegumental plates. **A, B.** Male 5th nymph, retrolateral row of left leg II and prolateral plate of right leg IV, respectively. **C.** Retrolateral row of right leg IV of an adult male.

the base of an aggregation of trichomes." They observed ~15 openings with a ca. 1 mm diameter. These associated trichomes are located at a specific position on the tarsus and are frequently twisted together (Fig. 3, arrows), so that this group of trichomes can be promptly recognized and could help to locate the TAPs. TAPs from each side of the tarsus may form a single group or they can be split into two groups located on either side of the associated trichomes. We observed up to 25 pores in total among adult males, either on a single group or split into two groups.

In addition, TAPs seem to have a precisely defined position in both prolateral and retrolateral faces of the tarsus (Fig. 3A, white circle), close to the distal margin surrounding the insertion of the tarsal claws, and close to the dorsal face of the tarsus, on both sides of a large seta (part of the tarsal process of adults but also present among nymphs; Fig. 3A, "S0"). In

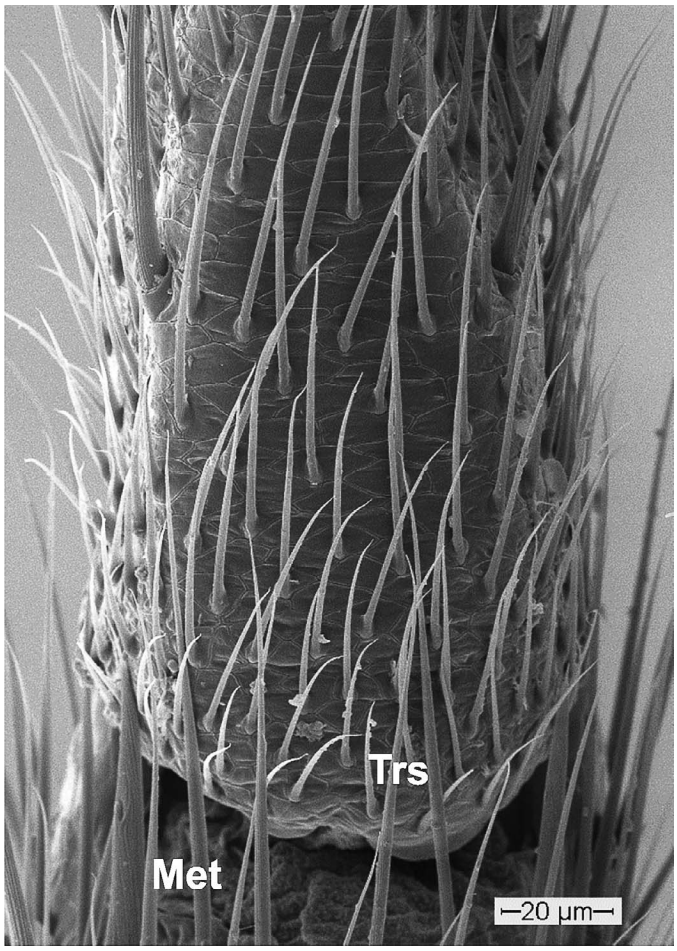

Figure 11.—Proximal region of the proximal tarsomere (Trs) of right leg IV of a first nymph of *Heteromitobates albiscriptus*, ventral view, showing the absence of TPOs. Met = apex of metatarsus.

both prolateral and retrolateral faces of legs III and IV, it is possible to recognize the following group of setae (Fig. 3A): "S0" is dorsally placed and it is attached to the tarsal process among adults or, among nymphs, it represents the position where the tarsal process will later develop, and it is placed close to the distal margin of the tarsomere; two additional large setae, "S1" and "S2", are also located close to the distal margin of the tarsomere, but are more ventral than "S0"; "S3" is located between setae "S0" and "S1" in a position somewhat displaced from the distal margin of the tarsomere. TAPs are placed inside the triangle formed by setae "S0-S1-S3", usually close to the distal margin of the tarsomere, but at a variable distance from "S0".

TAPs appear in legs III and IV of all stages except among the first nymphs, and grow in number from three or four among second nymphs to around 20 among adults (Table 3 and Figs. 4–6). The individuals analyzed usually had similar numbers of pores both on prolateral and retrolateral regions, as well as when both legs III and IV were compared. The diameter of the pores did not show a clear difference among ages, and measured 2.15 ± 0.46 µm (N = 174) (Table 3).

In our study, we identified an additional field of tarsal aggregate pores, placed more ventrally, just below "S2" (Fig. 3A, B), with similar structure to the group described above, also associated with the same kind of typical trichomes. We herein refer to this newly discovered group as the "ventral tarsal aggregate pores" (vTAPs). These groups of pores were observed only among adults (in both males and females), and usually have a smaller number of pores when compared to the "regular" TAPs. Although a similar group of the typical associated trichomes could be observed among the last instar nymphs (though less conspicuous than those of adults), the pores were absent.

Pores on the distal pleura of legs I & II.—By analyzing the distal region of the tarsi of legs I and II, which bear only one tarsal claw and lack TAPs, we recognized an additional group of pores, herein detected for the first time and informally named "frontal tarsal aggregate pores" (FAPs) in order to facilitate communication in the present text. They are placed on the distal pleura of the tarsus, around the articulation of the tarsal claw, on both sides of the tarsal claw (Fig. 7). The integument of the distal pleura (Fig. 7, white arrows) can be easily recognized from the integument of the rest of the tarsus (which is composed of smooth plates and bears trichomes and setae, as in Fig. 7, black arrows). In the material examined, we could clearly observe FAPs on legs I of males and females of both fifth nymph and adult stages; and FAPs were clearly absent on legs III of female fifth nymphs and adults and on legs IV of adult females. The rest of the material herein analyzed did not allow us to precisely identify the presence or absence of FAPs.

Tarsal perforated organ (TPO): additional description and ontogenetic analysis.—As described by Willemart et al. (2007), the "tarsal perforated organ" (TPO) is composed of a pair of rows of perforated plates located on the ventral side of the first tarsomere of all legs (Fig. 8A, B). We herein observed typical features that are frequently found in the TPOs analyzed.

Concerning the proximal portion of the rows of plates, it is common to find longitudinally elongate tegumental plates just proximally to the TPO (Fig. 9A, B), and some of the proximal plates of the TPO may also be more elongate than the others (Fig. 9A, arrow). In addition, the more proximal plates of the TPO are very frequently only perforated on their distal portion and their proximal portion is smooth, resembling the surrounding tegumental plates (Fig. 9, arrows).

Concerning the distal portion of the TPO, it is very common that the distal plate(s) has (have) a round distal margin (Fig. 10). This shape is not frequently observed among the other plates of the TPO, which are usually sub-rectangular in shape (i.e., opposed sides are frequently straight lines parallel to each other). In addition, the tegumental plates that surround the apex of the TPO are frequently narrow and very elongated when compared to the other tegumental plates, and usually contour the apex of the TPO (Fig. 10, arrows).

TPOs appear in all legs of all stages except among the first nymphs (Table 4, Figs. 11–15). Except for the second nymph, which showed lower values when compared to the other stages, there is no clear growth during the postembryonic development when both the average size of the plates (ranging between 7–11 µm) and the percentile relation between the length of TPO and the total length of the tarsus are concerned

Table 3.—Number and diameter of pores in the TAPs ("tarsal aggregate pores") during the postembryonic development of *Heteromitobates albiscriptus*. TAPs were not observed in nymphs 1. Right legs were used in the study (when they were not available, left legs were used, marked with an *). Tarsus = length of tarsus (mm); Total = total length of leg (mm); #prol = number of pores in the prolateral group; #retrol = number of pores in the retrolateral group; Φprol/Φretrol = diameter (average ± std dev., in μm) of pores in prolateral and retrolateral groups respectively (N is given in parentheses).

Instar	Leg	Tarsus	Total	# prol	# retrol	Φ prol	Φ retrol
Nymph 2	III	2.11	16.35	4	4	2.20±0.30 (3)	1.49±0.14 (3)
	IV*	2.84	24.74	3	4	2.56±0.35 (2)	1.87±0.21 (3)
Nymph 3	III	2.96	22.67	8	9	2.28±0.27 (4)	2.29±0.24 (4)
	IV	3.47	32.54	8	8	2.50±0.15 (4)	2.51±0.51 (4)
Nymph 4	III	3.57	29.28	11	12	2.31±0.23 (5)	2.41±0.22 (6)
	IV	4.65	42.48	13	11	2.74±0.44 (7)	2.65±0.45 (7)
Nymph 5 female	III	4.75	37.58	18	20	2.38±0.19 (5)	2.34±0.22 (9)
	IV	6.14	50.99	18	15	2.53±0.32 (9)	2.51±0.32 (9)
Nymph 5 male	III	4.81	38.17	16	17	2.27±0.38 (9)	2.21±0.34 (6)
	IV	5.77	51.65	15	15	2.20±0.35 (9)	2.29±0.20 (5)
Adult female	III	6.08	47.42	14	19	1.94±0.19 (5)	1.41±0.06 (5)
	IV*	7.20	65.01	15	17	1.67±0.14 (5)	1.50±0.20 (7)
Adult male	III	7.04	55.65	20	25	1.88±0.24 (9)	1.85±0.24 (16)
	IV	8.46	75.74	19	20	1.73±0.29 (5)	1.80±0.26 (9)

(Table 4). In turn, as expected based on the information above, there is a clear growth in the number of plates per TPO, as well as the length of TPO, throughout the ontogeny. Yet, the length of the TPOs is often greater among males, which usually have longer legs than females.

TPOs may be formed by one single row of cells (which is common among early stages [except first nymphs, which lack TPOs] and/or in legs I–II) or by more than one (up to four or five), which is common among the older stages and/or in legs III–IV (Figs. 12–15).

Table 4.—Morphometric analysis of TPO ("tarsal perforated organ") during the postembryonic development of *Heteromitobates albiscriptus*. Right legs were used in the study (when they were not available, left legs were used, marked with an *). Leg Total = total length of leg (mm); Tarsus = length of tarsus (mm); TPO = length of the TPO (mm); TPO/Tarsus = length of the TPO as a proportion of the length of the tarsus, expressed as a percentage; Plate = average length of single plates of the TPO (μm); #Plates = number of plates that composed the TPO.

Instar	Leg	Leg Total	Tarsus	TPO	TPO/Tarsus (%)	Plate	#Plates
Nymph 2	I	11.11	1.99	0.056	2.8	6.45	9
	II	26.02	5.10	0.056	1.1	9.06	7
	III	16.35	2.11	0.103	4.9	6.67	28
	IV*	24.74	2.84	0.063	2.2	7.11	16
Nymph 3	I	13.32	2.25	0.068	3.0	8.19	9
	II	37.31	6.58	0.063	1.0	7.62	10
	III	22.67	2.96	0.144	4.9	10.43	32
	IV	32.54	3.47	0.108	3.1	7.46	30
Nymph 4	I	18.46	2.69	0.105	3.9	8.19	16
	II	45.63	8.53	0.068	0.8	8.16	12
	III	29.28	3.57	0.201	5.6	10.11	43
	IV	42.48	4.65	0.163	3.5	10.37	36
Nymph 5 female	I	26.64	3.22	0.130	4.0	8.39	25
	II	56.88	10.39	0.093	0.9	8.71	19
	III	37.58	4.75	0.189	4.0	10.58	47
	IV	50.99	6.14	0.218	3.6	11.74	37
Nymph 5 male	I	24.43	3.15	0.139	4.4	8.33	26
	II*	59.03	10.40	0.137	1.3	8.42	26
	III	38.17	4.81	0.247	5.1	9.03	66
	IV	51.65	5.77	0.251	4.4	11.95	62
Adult female	I	30.32	4.05	0.180	4.4	9.72	36
	II	72.60	12.03	0.134	1.1	9.22	30
	III	47.42	6.08	0.249	4.1	10.00	82
	IV*	65.01	7.20	0.262	3.6	10.87	84
Adult male	I	33.96	4.30	0.226	5.3	10.71	41
	II	81.58	13.12	0.148	1.1	9.33	28
	III	56.00	7.02	0.232	3.3	10.18	81
	IV	74.57	8.12	0.301	3.7	11.67	91

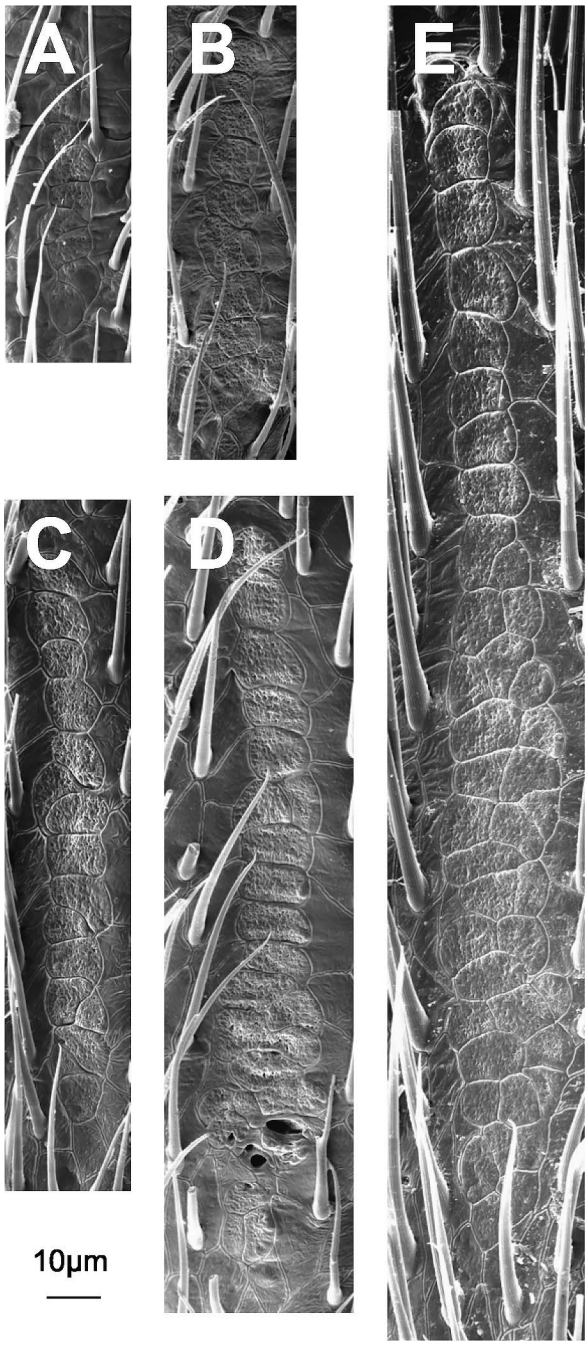

Figure 12.—Ontogenetic modification of TPOs of leg I, from 2nd nymph to the adult of *Heteromitobates albiscriptus* (**A–E**, respectively; **D** male 5th nymph and **E** adult male). All figures to the same scale (same as in Figs. 13–15).

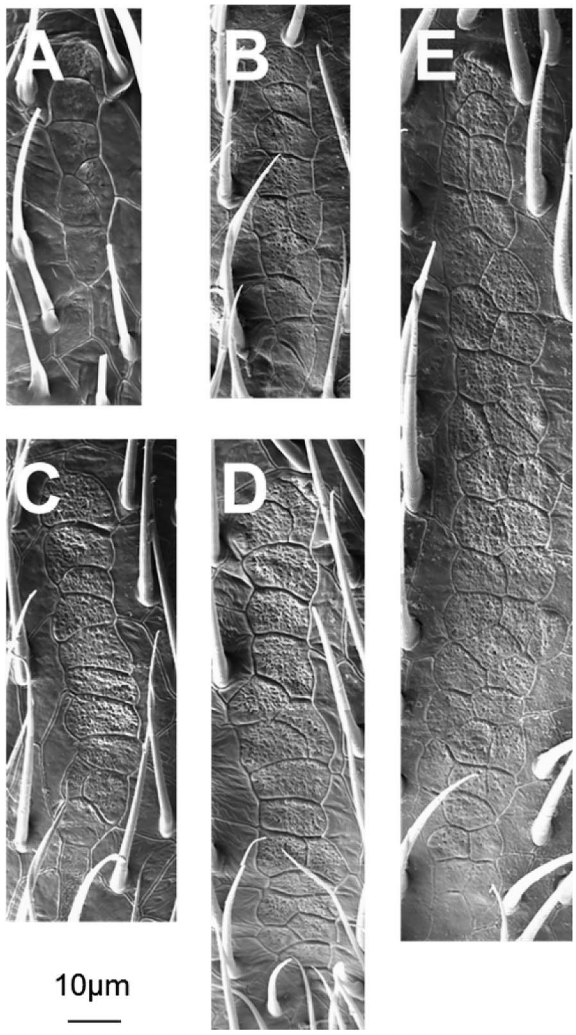

Figure 13.—Ontogenetic modification of TPOs of leg II, from 2nd nymph to the adult of *Heteromitobates albiscriptus* (**A–E**, respectively; **D** female 5th nymph and **E** adult male). All figures to the same scale (same as in Figs. 12, 14, 15).

DISCUSSION

Taxonomic remark: juvenile stages should be taken into consideration in taxonomic studies.—The fact that nymphs bear simple tarsal claws in legs III and IV (Fig. 2B) instead of the pectinate claws of adults (Fig. 2A) is important information for taxonomists, since the genus *Heteromitobates* is characterized by the presence of pectinate tarsal claws, contrasting to the other genera in the subfamily Goniosomatinae (DaSilva & Gnaspini 2009), which all bear smooth claws. In other words, if one has in hand nymphs of *Heteromitobates* with no knowledge of this information, one may describe or try to identify the species in a different (and incorrect) genus, creating a taxonomic confusion. The importance of ontogeny in taxonomy is recognized in other groups, including extant and fossil animals, as, for instance, in the controversy around pachycephalosaurid dinosaurs (e.g., Horner & Goodwin 2009).

Recognition of the postembryonic stages.—Considering that the stage recognized in previous publications as the "subadult" should be considered part of a single adult stage (as discussed by DaSilva & Gnaspini 2009; see also Zatz et al. 2010; Munguía-Steyer et al. 2012) and not the last nymphal instar (see discussion in Gnaspini et al. 2004), the number of nymphal stages herein observed (five) agrees with other goniosomatines (e.g., Gnaspini 1995, 2007), when the previous publications numbers are corrected. In contrast, the larger growth detected by Gnaspini (1995) for the molt between the first and the second nymph was not detected here; in our case,

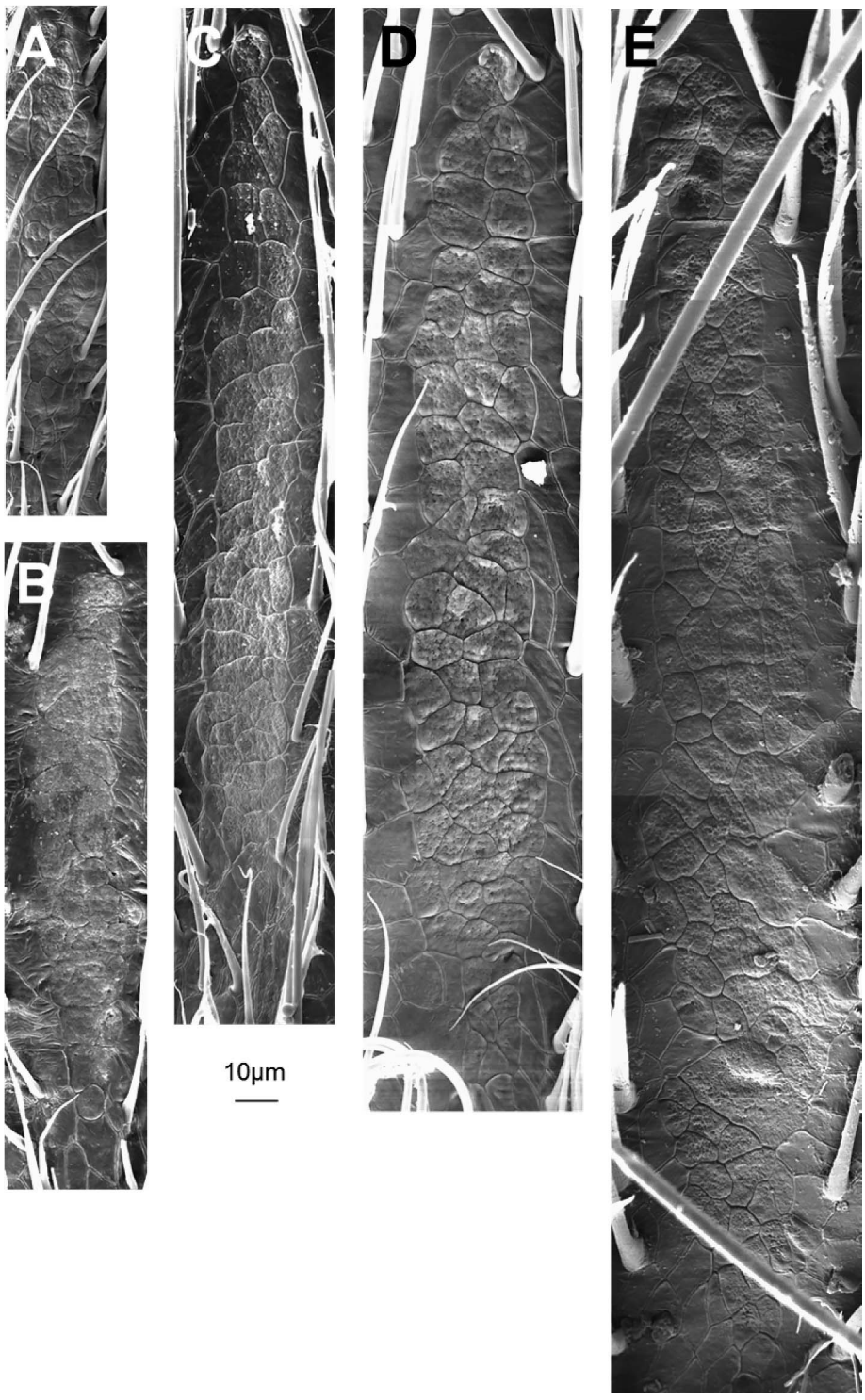

Figure 14.—Ontogenetic modification of TPOs of leg III, from 2nd nymph to the adult of *Heteromitobates albiscriptus* (**A–E**, respectively; **D** male 5th nymph and **E** adult male). All figures to the same scale (same as in Figs. 12, 13, 15).

there is no difference detected between subsequent stages (Table 1), which seems to be the case also with cranaids (Townsend et al. 2009; although the lack of information for some nymphal stages do not allow precise conclusions) and most Eupnoi and Dyspnoi studied (as summarized in Gnaspini 2007). Yet, in contrast with Gnaspini (1995), the developmental stages of *H. albiscriptum* can be easily recognized by morphometric data, with no overlap between successive stages (Table 3). Our data agreed with Gnaspini (1995) concerning the increase in the number of tarsomeres that occurs in legs III–IV in the last nymphal instar and in all legs in the molt to the adult phase. The only difference

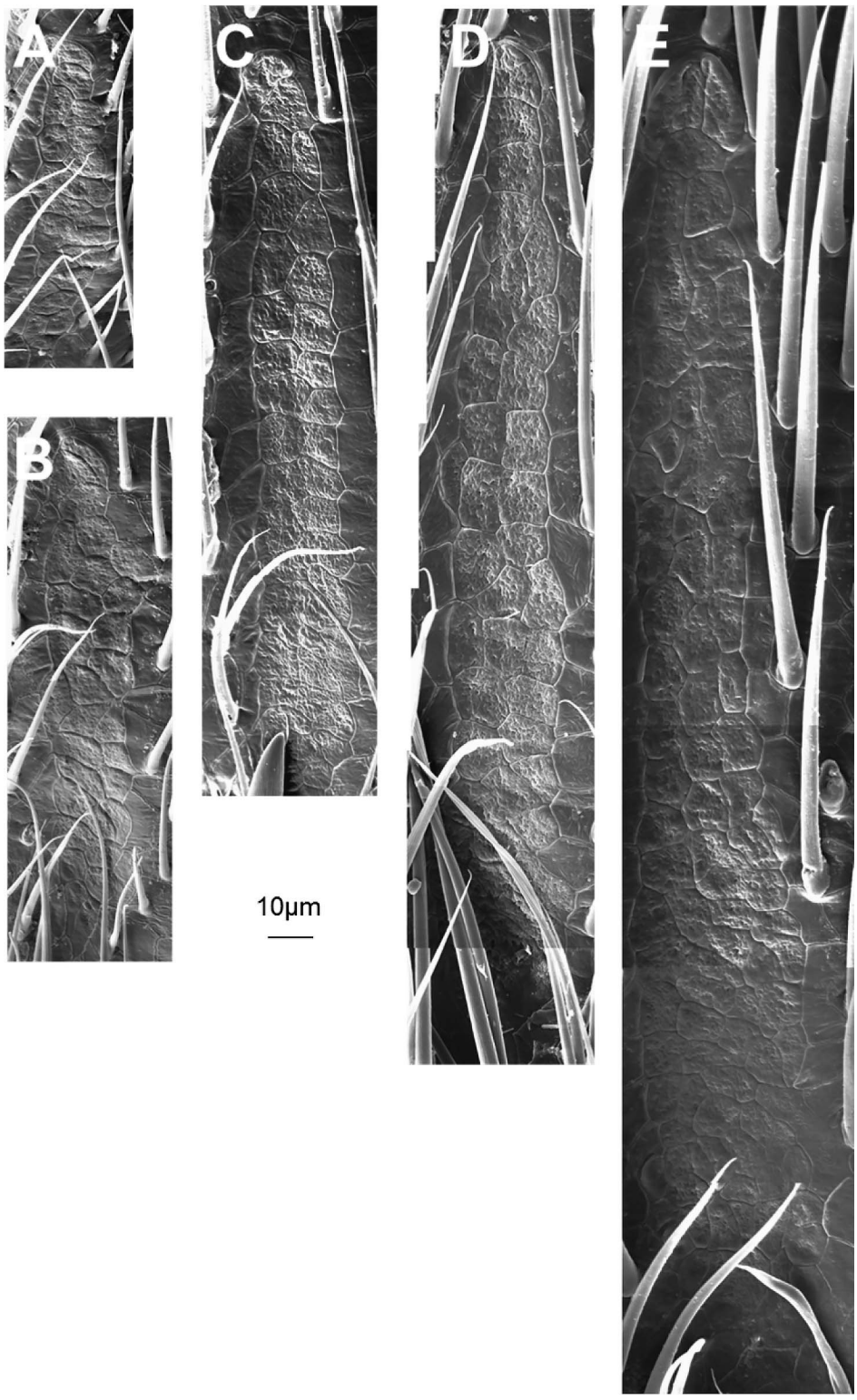

Figure 15.—Ontogenetic modification of TPOs of leg IV, from 2nd nymph to the adult of *Heteromitobates albiscriptus* (**A–E**, respectively; **D** female 5th nymph and **E** adult male). All figures to the same scale (same as in Figs. 12–14).

detected is the number of tarsomeres in legs I–II among the first nymphs, being one tarsomere in *H. albiscriptum* in contrast to the two tarsomeres detected in *Serracutisoma spelaeum* (Mello-Leitão, 1933). Therefore, the number of tarsomeres tend to be conservative among nymphs of Laniatores, based on studies focusing on Gonyleptidae (with differences possibly occurring in the first and/or last nymphs, e.g., Muñoz-Cuevas 1971b; Gnaspini 1995, 2007; Gnaspini et

al. 2004; this study) and Cranaidae (Townsend et al. 2009; although the variation is not clear due to the lack of information for some nymphal stages); in contrast with one studied species of the suborder Dyspnoi, in which the number of tarsomeres tend to increase with each molt (Avram 1973).

In addition to morphometric values, the last nymphal instar (5^{th} instar, in our case) can also be recognized by the increase in the number of tarsomeres in relation to the previous instars, although this is a much smaller increase when compared to the molt to the adult tarsus.

In addition to the well-known presence of a full grown tarsal process, our study detected one additional tarsal structure typical of the adult phase: vTAPs (on legs III–IV; Fig. 3), as well as the presence of pectinate claws, which is probably restricted to species of the genus *Heteromitobates* Roewer, 1913, as discussed above. Moreover, the number of pores in TAPs as well as the number of plates in TPOs increase with age and can also be used to recognize the ontogenetic stage of an individual.

FAPs: frontal tarsal aggregate pores on the distal pleura of legs I–II.—Glandular pores are widespread all over the integument of harvestmen (e.g., Willemart et al. 2007) and FAPs may simply be "regular" pores, and, for this reason, we preferred to use FAP as an informal term at the present time. Although we clearly detected their presence in some legs of some stages and their absence in other legs, our data are inconclusive with respect to their presence throughout postembryonic development, and, therefore, FAPs deserve a more specific approach.

TAPs: tarsal aggregate pores.—The morphology of TAPs observed herein agreed with their original description (Willemart et al. 2007) and their association with typical trichomes which frequently twist together was also commented on by Gainett et al. (2014). Here we described their specific position in the tarsus and recorded a second group of TAPs located more ventrally (vTAPs), only among adults. Although no clear difference could be detected among the different stages considering the diameter of the pores, adults seem to have smaller pores when compared to the previous instars (except for the second nymphs), which may be related to the larger number of pores in the TAPs among adults (Table 3). Having found no clear distinction between TAPs in immatures and adults or between adult males and females, we have no evidence of sexual selection influencing the development of TAPs (Andersson 1994). If histological studies confirm that they are in fact glandular as their external morphology suggests, they might therefore be used for a non-sexual purpose such as leaving chemical trails used for navigation. Chemicals left on the substrate have indeed been shown to be used in a variety of contexts in harvestmen (Willemart & Hebets 2011; Teng et al. 2012; Fernandes & Willemart 2014).

TPO: tarsal perforated organ.—Although the number of plates (and consequently the total length of TPO) and also the number of rows of plates in the TPO grow with age, the ratio of TPO length to tarsus length does not show a clear growth with age (Table 4). It is also worth noting that some unusual features may be observed in TPOs, and may represent anomalies during the integument formation. For instance, both rows of plates of the TPO usually form a single group, but in a few cases we observed gaps within them (as in the distal portion in Fig. 14E). Other types of unusual features observed in TPOs were holes (Fig. 12D; which are clearly not pores) and intrusions (Fig. 9A). These features were rarely observed and could not be related to age or to specific legs.

When the four legs are compared, the absolute number of plates in the TPO as well as the TPO absolute and percentile length in relation to the length of the tarsus of leg II are smaller when compared to the other legs, despite the fact that leg II is the longest leg. In all legs, TPOs have multi-porous plates, with no obvious difference between legs or sexes. We therefore have no evidences of any sexual role for such an organ. When Willemart et al. (2007) described the TPOs, they suggested that TPOs were the openings of contact glands. However, the recent study published by Proud & Felgenhauer (2013) provided evidence against the "contact gland" hypothesis. Those authors related the TPO to internal attachments of muscles to the inner surface of the exoskeleton. More specifically, they related TPO to the first internal pulley detected in a series of pulleys located along the tarsomeres. They could not explain why only the first pulley had external reflections in the integument, and suggested this was related to the molting process when the first pulley would be the one to maintain connection with muscles. The irregular external surface of the tegumental plates would represent scars related to the microtubules and tonofibrillae that were extended throughout the cuticular matrix. Based on our results, we would add more questions to this scenario. First, the internal connection to a pulley and the "scar nature" of TPOs may explain their irregular integument (as well as the "mistakes" observed in the integument, as described above) but do not explain the specific shape of the surrounding anterior and posterior tegumental plates, which differ from the other plates in the legs. Second, especially considering that leg II is the longest leg, the scenario does not explain why the TPO is the shortest both in absolute and in relative values (in this case 1% of the tarsus length against 4% in the other legs) on this leg. Third, we observed the absence of the TPO in first nymphs. It is known that harvestmen hatch in the form of larvae that molt into a first nymphal stage (e.g., Gnaspini 2007). Therefore, we would expect to find TPOs among first instar nymphs if they are the results of the molting process. Gnaspini & Lerche (2010) noticed that the molting process starts already inside the egg, during embryonic development. This premature molting process may explain the absence of TPO in first nymphs if TPO is actually related to molting. Although they are clear structures on the tarsus of all legs, and in spite of the great advances provided by the work of Proud & Felgenhauer (2013), there are still unanswered questions about the TPOs.

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Appendix 1.—Measurements (mm) of body length and width and total length of right appendages (L1–L4 = leg I to leg IV), and number of articles in the tarsus of each leg (T1–T4). * indicates a measurement made on a left appendage.

	Body length	Body width	L1	T1	L2	T2	L3	T3	L4	T4
1st nymph	2.28	1.59	7.71	1	19.64	1	11.19	2	16.11	2
	1.88	1.30	8.33	1	22.29	1	12.18	2	18.24	2
	2.15	1.73	8.24	1	21.79	1	13.65	2	18.91	2
	2.47	1.83	8.48	1	23.33	1	13.31	2	19.24	2
	2.35	1.62	8.47	1	23.06	1	13.40	2	19.24	2
	2.12	1.72	8.42	1	22.75	1	13.29	2	19.08	2
	2.27	1.90	8.21	1	22.88	1	13.50	2	19.44	2
	2.33	1.84	8.75	1	22.63	1	13.89	2	19.58	2
2nd nymph	2.19	1.49	10.85	2	26.78	2	16.52	2	23.29	2
	3.07	2.46	10.87	2	27.90	2	16.30	2	23.31	2
	2.77	1.90	10.82	2	28.73	2	17.00	2	24.10	2
	2.9	2.06	10.60	2	28.47	2	17.34	2	24.54	2
	3.12	2.49	10.78	2	28.34	2	17.60	2	25.26	2
3rd nymph	3.45	2.99	13.12	2	34.02	2	21.20	2	28.36	2
	2.89	2.42	13.12	2	35.24	2	20.72	2	30.14	2
	3.3	2.42	14.26	2	35.00	2	22.28*	2	30.35	2
	3.71	3.16	13.82	2	36.44	2	21.44	2	31.08	2
	3.02	2.49	14.07	2	36.01*	2	22.09	2	31.28*	2
	3.63	3.31	14.21	2	36.55	2	22.24	2	31.32	2
	3.67	2.99	14.04	2	37.06	2	23.43	2	31.40	2
	3.6	3.09	14.56	2	36.55	2	22.02	2	31.70	2
	3.47	3.09	14.49	2	39.45	2	24.66	2	32.84	2
	3.42	3.01	14.73	2	38.19	2	22.80	2	32.89	2
	3.47	2.94	14.41	2	37.64	2	23.62	2	33.00	2
4th nymph	4.08	3.79	17.13	2	43.70	2	26.42	2	38.46	2
	4.21	4.26	18.26	2	45.06	2	27.76	2	38.71	2
	3.83	3.53	18.01	2	44.66	2	29.00	2	39.28	2
	3.95	3.59	18.12	2	44.59	2	28.19	2	39.75	2
	4.27	4.00	18.34	2	45.51	2	29.29	2	39.76	2
	4.54	4.11	19.03	2	43.90	2	29.66	2	40.44	2
	4.13	3.60	19.02	2	46.43	2	30.32	2	40.47	2
	4.22	4.10	18.87	2	46.43	2	29.70	2	40.54	2
	4.16	3.84	19.21	2	48.45	2	30.15	2	40.59	2
	3.77	4.16	19.00	2	46.64	2	29.86	2	40.91	2
	4.3	4.24	19.55	2	46.91	2	30.20	2	41.24	2
	4.66	3.84	18.49	2	46.85	2	29.89	2	41.56	2
	3.81	3.73	19.35	2	47.94	2	30.90	2	42.39	2
	4.34	4.21	18.84	2	47.66	2	30.13	2	42.43	2
5th nymph female	5.69	5.31	23.98	2	57.32	2	38.33	3	51.42	3
	5.23	5.36	23.74	2	58.26	2	38.76	3	52.19	3
5th nymph male	5.21	5.04	24.36	2	58.70	2	39.18	3	51.98	3
Adult female	7.2	8.03	30.20	11	73.43	26	50.09	12	67.84	14
	7.87	7.91	36.53	9	84.08	20	58.65	11	79.77	14
Adult male	6.55	6.72	31.36	12	77.94	27	50.25	13	68.22	14
	6.86	7.04	31.89	11	75.97	20	51.26	11	68.50	13
	6.53	6.14	30.69	11	76.35	26	49.73	11	68.57	13
	6.67	6.32	31.69	12	-	-	49.84	14	69.08	15
	6.66	6.90	32.35	12	76.98	22	50.44	11	69.95	15
	6.62	6.66	31.66	11	76.30	24	51.33	12	70.29	15
	7.34	7.35	32.60	10*	79.17	25	53.89	12	72.34	15
	7.64	7.74	31.97	10	79.97	26	54.04	13	73.60	15
	7.68	7.69	33.18	11	80.58	25	54.21	13	74.02	15
	7.89	8.53	32.55	10	81.81	26	55.16	12	75.11	15
	7.93	7.98	33.17	11	82.08	21	52.28	10	75.17	15
	7.67	7.92	34.55	12	83.19	25	55.94	12	75.26	15
	7.79	8.24	34.50	11	83.13	25	56.68	12	76.40	14