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TAXONOMIC NOTES ON *MESOPERIPATUS THOLLONI* (ONYCHOPHORA: PERIPATIDAE), AN ELUSIVE VELVET WORM FROM GABON

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ABSTRACT. The velvet worm *Mesoperipatus tholloni* (Bouvier, 1898) is among the least understood of the velvet worms, the only species in the genus *Mesoperipatus* Evans, 1901, and the only African Peripatidae. Despite its biogeographic and phylogenetic uniqueness, originally thought to be an intermediate between Peripatidae and Peripatopsidae, little work has been published since its original treatment in a series of papers in the late 1800s and early 1900s. Here, we provide a redescription of this species based on new material collected during a 2009 Museum of Comparative Zoology (MCZ) expedition to Gabon and examination of historical material from the original collections lodged at the MCZ and the Museu de Zoologia, Universidade de São Paulo (MZUSP). We also provide the first scanning electron micrographs of this species.

KEY WORDS: taxonomy; morphology; Africa; scanning electron microscopy

INTRODUCTION

Mesoperipatus tholloni (Bouvier, 1898) is among the least understood of the velvet worms, the only species in the genus *Mesoperipatus* Evans, 1901, and the only African

Peripatidae (Bouvier, 1898a; Evans, 1901; Oliveira *et al.*, 2012). The first specimens of this rare species (two females) were collected by French botanist and chief of exploration of the French Congo, M. Thollon, who died in Libreville on January 1897. The specimens were described by Bouvier (1898b), who erected the new species *Peripatus tholloni* as a “transitional form” between the South African peripatopsids and the American peripatids (Bouvier, 1898c; see also Bouvier, 1898d). In his original description, Bouvier (1898b) mentioned Gabon as the type locality, but subsequent papers and collection labels often refer to

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Congo or French Congo.¹ The two original specimens collected by Thollon were split between the Muséum national d'Histoire naturelle, Paris, and the Cape Museum (now the Iziko South African Museum, Cape Town) (Bouvier, 1905:349).

Later in 1903, Mr. Haug, a pastor and naturalist, sent Bouvier two additional specimens collected on 15 March (Haug, 1903). The letter was sent from Ngômô, on the Ogooué River, which was subsequently interpreted as the collection locality. Oliveira *et al.* (2012) said that the modern name of Ngômô is Ngolé,² but this is unlikely, as both are close localities in the Moyen-Ogooué Province, Ogooué et des Lacs Department: Ngômô (0.84°S, 9.98°E) and Ngolé (0.83°S, 10.07°E) (Fig. 1) (Falling Rain Software Ltd., 1996–2016). Both localities have existed for over a century, as evidenced in Schweitzer's impressions and experiences in Gabon, where he described several of the settlements of the time (Schweitzer and Campion, 1923). Schweitzer was sponsored by the Paris Evangelical Missionary society, which had taken over four stations established by American Protestants: these were at N'Gômo,³ Lambaréné, Sakita, and Talagonga; Catholics, meanwhile, were established at Lambaréné,

N'Djolé, and near Samba (Schweitzer and Campion, 1923).

Bouvier (1904) specified that E. Haug made available five specimens, including an adult male—the only one known until then for the species. All the known specimens are listed in Bouvier's monograph (1905): the two original females collected by Thollon, the first two females collected by Haug, and four additional females and one male collected by Haug in 1904. It is however possible that some of these specimens do not belong to the same species, given the variation in the number of legs reported in the redescription of the species (Bouvier, 1905). Later, in the catalogue of the onychophorans of the Muséum national d'Histoire naturelle (MNHN), Bouvier (1907a) lists the collecting date of the Thollon specimens (1883) and specifies that only one of the two original specimens from Thollon and one of the two first specimens from Haug remained in the MNHN. In that paper it is also made clear that the type locality is Gabon and cites additional specimens from Ngômô collected by Haug in 1906. In addition to these, new "beautiful" specimens from "Talagonga, near N'Djolé" were collected in 1906 by Ellenberger—another missionary working in Gabon. It is therefore not improbable that this whole suit of specimens represents more than one species.

A large female and a small male from the 1906 collections from Talagonga were donated by the MNHN to the Museum of Comparative Zoology, Harvard (MCZ) ("Talagonga près de N'Djolé, Ellenberger capt."; however, on the label, it also says "Ogooué, E. Haug"). An additional large female and small male from "près de N'Djolé, dans l'Ogooué" were also donated to the Museu de Zoologia, Universidade de São Paulo (MZUSP), "capt. Par M. Ellenberger pour M. Haug." It could be that the specimens from the MCZ and from the MZUSP are a mixed lot from the Haug 1906 and the Ellenberger 1906 collections.

¹ The French Congo, which began at Brazzaville on 10 September 1880 as a protectorate over the Bateke people along the north bank of the Congo River, was formally established as the French Congo on 30 November 1882 and was confirmed at the Berlin Conference of 1884–85. The French Congo was sometimes known as Gabon-Congo. It formally added Gabon on 30 April 1901, was officially renamed Moyen-Congo in 1903, was temporarily divorced from Gabon in 1906, and was then reunited as French Equatorial Africa in 1910.

² Ngolé is a town from the Ogooué et des Lacs Department (Lambaré.) (0°50'S, 10°04'E), Moyen Ogooué, Gabon.

³ Another spelling for Ngômô.

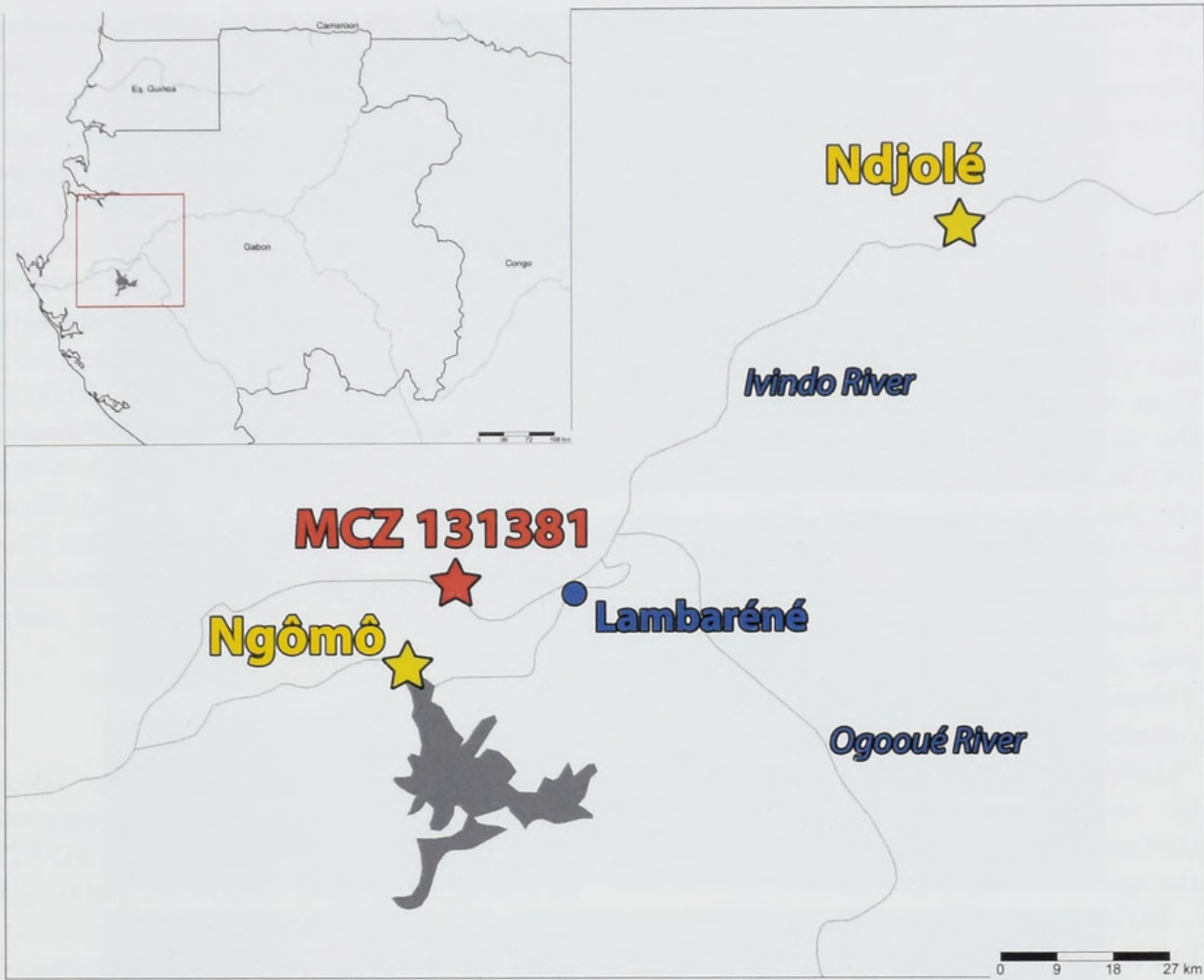


Figure 1. Map of the Middle Ogooué river section, with the traditional localities of Ngômô and Ndjolé (yellow stars), and the newer collection point west of Lambaréné (red star). Inset shows the larger region, and the red square identifies the studied region.

Although Talagonga was the “most advanced mission station” in the late 1800s and early 1900s, it is not found on modern maps but was located in the rapids of the Ogooué river, near Ndjolé (in modern spelling). These specimens are thus found quite a distance from the former ones from the Abanga-Bigne Department of the Moyen-Ogooué Province.

Few authors actually studied this species after Bouvier (but see Fedorow, 1926, 1929) because of the difficulties in obtaining fresh material from this genus endemic to the forests of the Moyen-Ogooué Province, among other

things. More recent specimens collected in January 1970 have been reported from Cameroon (Senckenberg Naturmuseum, Frankfurt).

In addition to the historical specimens in the MCZ a modern expedition to Cameroon and Gabon yielded an additional specimen of this species (or species complex). The specimen was collected by L. R. Benavides, G. Giribet, and J. Y. Muriene near Lambaréné, in the Moyen-Ogooué Province, Ogooué et des Lacs Department, on 28 June 2009. This specimen was used for molecular study by Muriene *et al.* (2014), but none of the MCZ specimens—old or new—were

studied morphologically. Here we provide the first scanning electron micrographs for this specimen and provide a redescription of some salient characters of *M. tholloni*.

MATERIALS AND METHODS

The five specimens available in the MCZ and MZUSP were examined morphologically and compared with the original description of *M. tholloni* (Bouvier, 1898a) on the basis of specimens from a single locality and the monographs written by Bouvier (1905, 1907b), in which he redescribed the species on the basis of specimens from multiple localities. Two specimens were studied using scanning electron microscopy (SEM).

Material Examined. MCZ IZ-85892: One male and one female in 70% EtOH from Talagonga, near N'Djolé, Ogooué, Gabon, collected in 1906 (no exact collection data); "Ellenberger capt." and "E. Haug" appear on the original label. Female specimen studied under SEM (images not shown, as the specimen was in bad shape).

MCZ IZ-131381: One female in 96% EtOH from near Lambaréné (0.65824°S, 10.19916°E), Moyen-Ogooué Province, Gabon; Leg. L. R. Benavides, G. Giribet, and J. Y. Murienne, 28.vi.2009. Specimen used for molecular work (Murienne *et al.*, 2014) and prepared for SEM.

MZUSP: One male and one female in 70% EtOH (no catalogue number) from near N'Djolé, Ogooué, Gabon, no collection data; "capt par Ellenberger pour E. Haug" appears on the original label.

Dental formula and descriptive terminology follow the onychophoran literature, most importantly Bouvier (1898a, 1905) and Evans (1901).

SEM imaging

From specimen MCZ IZ-131381, one antenna, one mandible, the fifth oncopod

of the left side, and a small rectangular section of the dorsal integument covering from the dorsomedian furrow to the base of the oncopods were dissected out and prepared for SEM. Additionally, from female specimen MCZ IZ-85892, a piece of the dorsal integument was dissected out and prepared for SEM. These tissues were critical point dried and mounted in SEM stubs with biadhesive carbon tape. The samples were then sputter coated with an EMS 300T D dual-headed sputter coater at the Harvard Center for Nanoscale Systems. A 5-nm platinum/palladium layer was applied. Samples were imaged with a Carl Zeiss Ultra Plus FESEM using the SE2 and backscatter detectors. Images were then edited using Adobe Photoshop CS5.

Coloration

Photographs of a life specimen were taken with a Nikon D2X digital camera equipped with an AF-S Micro Nikkor 60 mm f/2.8D ED or with an AF-S Micro Nikkor 105 mm f/2.8D ED lens and a TTL Nikon Speedlight. Coloration was described from the photographs of the living specimen (Figs. 2–4). Standard names of the 267 Color Centroids of the NBS/ISCC Color System (Mundie, 1995) were used in descriptions and given in parentheses.

TAXONOMIC RESULTS

Family Peripatidae Evans, 1901

Genus *Mesoperipatus* Evans, 1901

Mesoperipatus tholloni (Bouvier, 1898)

Figures 2–10

Peripatus tholloni Bouvier, 1898a:197; Bouvier, 1905:337.

Mesoperipatus tholloni (Bouvier, 1898): Evans (1901:478).

Emended diagnosis. Broad and narrow dorsal plicae alternating throughout the dorsal region with clear differences in the



Figures 2–4. Live female of *Mesoperipatus tholloni*. Figure 2. Whole animal in dorsal view. Figure 3. Anterior part of the animal in dorsolateral view. Figure 4. Ventral side with spinous pads in detail.

number of dorsal papillae between the two types of dorsal plicae. Dorsal papillae varying in size, the biggest ones being only present on the broader plicae. Roundish dorsal papillae close together, and primary papillae with an asymmetric apical piece with the bristle directed posteriorly. Both jaws with one accessory tooth; the inner jaw also armed with ten denticles separated from the accessory teeth by a diastema. From tip to base, the antenna has six broad rings followed by a narrow ring, then changing to alternating rings until about the 30th ring. Two crural papillae present on the two pregenital legs of the male.

Description of the studied specimens

Measurements (length/width/height in mm). Female IZ-13181: 30/4.5/1.4; Female IZ-85892: 40/4.0/3.0; Female MZUSP: 55/3.0/4.0; Male IZ-85892: 14/0.05/0.05; Male MZUSP: 15/1.0/1.0.

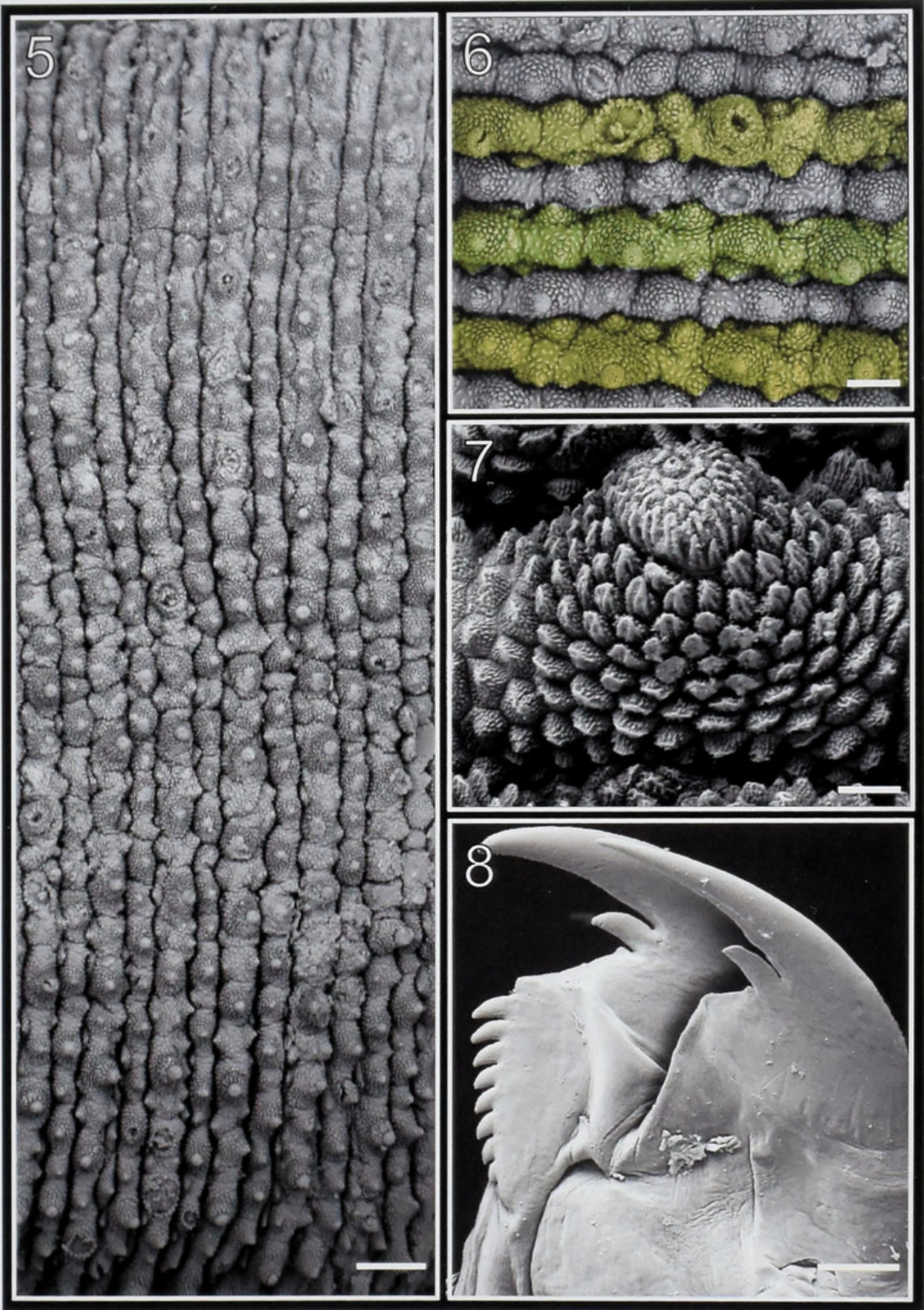
Color (for living specimens; Figs. 2–4). Dorsal body background light reddish brown (42) with dorsal light spots (primary papillae) grayish yellowish pink (10). Without dorsal patterning, with dorsomedian furrow, brownish grayish brown (61). Head color as body background and antennae grayish yellowish brown (80). Dorsal side of legs grayish pink (8), ventral body background moderate pink (5), with sparser, light papillae pale purplish blue (202) (Figs. 2, 3). Ventral organs pinkish white (9) and spinous pad light greenish gray (154) (Fig. 4).

Body description. Dorsum: dorsomedian furrow clearly visible; hyaline organs absent. With 12 broad plicae per segment, incomplete plicae absent, narrow and broad plicae alternating for all dorsal integument, seven of which cross over to the ventral side (Fig. 5). Primary and accessory papillae present on both plicae (Figs. 5, 6), but the largest

primary papillae only occur on the broad plicae (Figs. 6, 7). In all plicae, the primary papillae are always separated by accessory papillae, and the number of papillae on the large plicae is larger than on the narrow plicae (Fig. 6). On the broader plicae, the accessory papillae occur on the top or flanks of the plicae, although on the narrow plicae, the dorsal papillae only occur on the top (Fig. 6). Largest primary papillae with roundish insertion dome or conical base and asymmetrical spherical apical piece (Figs. 6, 7). Basal piece larger than apical piece, with around eight scale ranks (Fig. 7). Apical piece with three or four anterior and two or three posterior scale ranks (Fig. 7). The scales are robust on the base and thinner on the apical piece (Fig. 7). Bristles on the examined material were broken on the majority of primary papillae, probably caused by cryopreservation (Fig. 7). Smallest primary papillae with the base and apical piece not clearly distinguished. Accessory papillae similar in shape to the base of the smaller primary papillae, but smaller in size and higher in number (Fig. 6).

No evident structures or patterns on the head. Antennae with an interesting pattern of ring distribution (Figs. 2–4, 9); composed of 50 rings on both sexes. The antennal tip composed of six broad rings, excluding the disc on the top, followed by a sequence of thin and broad rings until at least ring 31 (Fig. 9). Eyes and frontal organs present ventrolateral of the antennal base. Frontal organs with length equivalent to three to five fused antennal papillae.

Venter: Mouth opening surrounded by seven lobes in a decreasing sequence from front to posterior ends of the mouth; all of them with small spines on the top, as detailed by Bouvier (1905:341). Inner and outer jaw blades both with one, long primary tooth followed by a small accessory tooth (Fig. 8). On the inner blade, a diastema separates the



Figures 5–7. SEM images of dorsal integument and jaws. Figure 5. Section of the dorsal integument corresponding to one segment on the middle of the body; note the lack of incomplete plicae. Figure 6. Detail of the dorsal broad (yellow) and narrow plicae. Figure 7. Primary papilla on dorsal view. Figure 8. Jaws of the left mandible, outer jaw in front. Inner jaw (back) with 10 denticles; the first, near the diastema, is broken, and the last is hidden on this image.

accessory tooth from a series of at least 10 denticles (Fig. 8). The inner and outer blade formulas are 1/1 and 1/1/10, respectively (Fig. 8). Females with 25 or 26 pairs of legs (Fig. 2); 24 in males; usually with three complete and sometimes with vestiges of a fourth spinous pad, without evidence of a fifth (Fig. 10).

Nephridial tubercle occurring on the fourth and fifth legs, connected on top with the third spinous pad and between two fragments of the fourth spinous pad (Fig. 10). Two prolateral and one retrolateral foot papillae in the feet of the fourth and fifth legs. Ventral and preventral organs not examined. Genital opening located close to penultimate pair of legs in both sexes, as in all species of Peripatidae, opening in a crux, and usually surrounded by tumescent lobes higher than the ventral integument. Only two pregenital legs with crural papillae (male) with one crural papilla each. Anal glands inconspicuous (male); represented only by the respective single pore on ventral part of anal aperture.

Type locality. Ngômô, Moyen-Ogooué, Gabon.

Distribution. Province Lambaréné, Talagonga, Moyen-Ogooué, Gabon; coordinates 0.65824°S, 10.19916°E (Fig. 1).

DISCUSSION

Since the first records of the species, *Mesoperipatus tholloni* has been easy to recognize because of its unique geographic distribution, being the only African Peripatidae. This unique distribution (only known from the Moyen-Ogooué Province and Cameroon) and its monotypy make this interesting genus even more important. *Mesoperipatus tholloni* has been hypothesized to be an intermediate group between the American and Asian groups of onychophorans because of their unique biogeo-

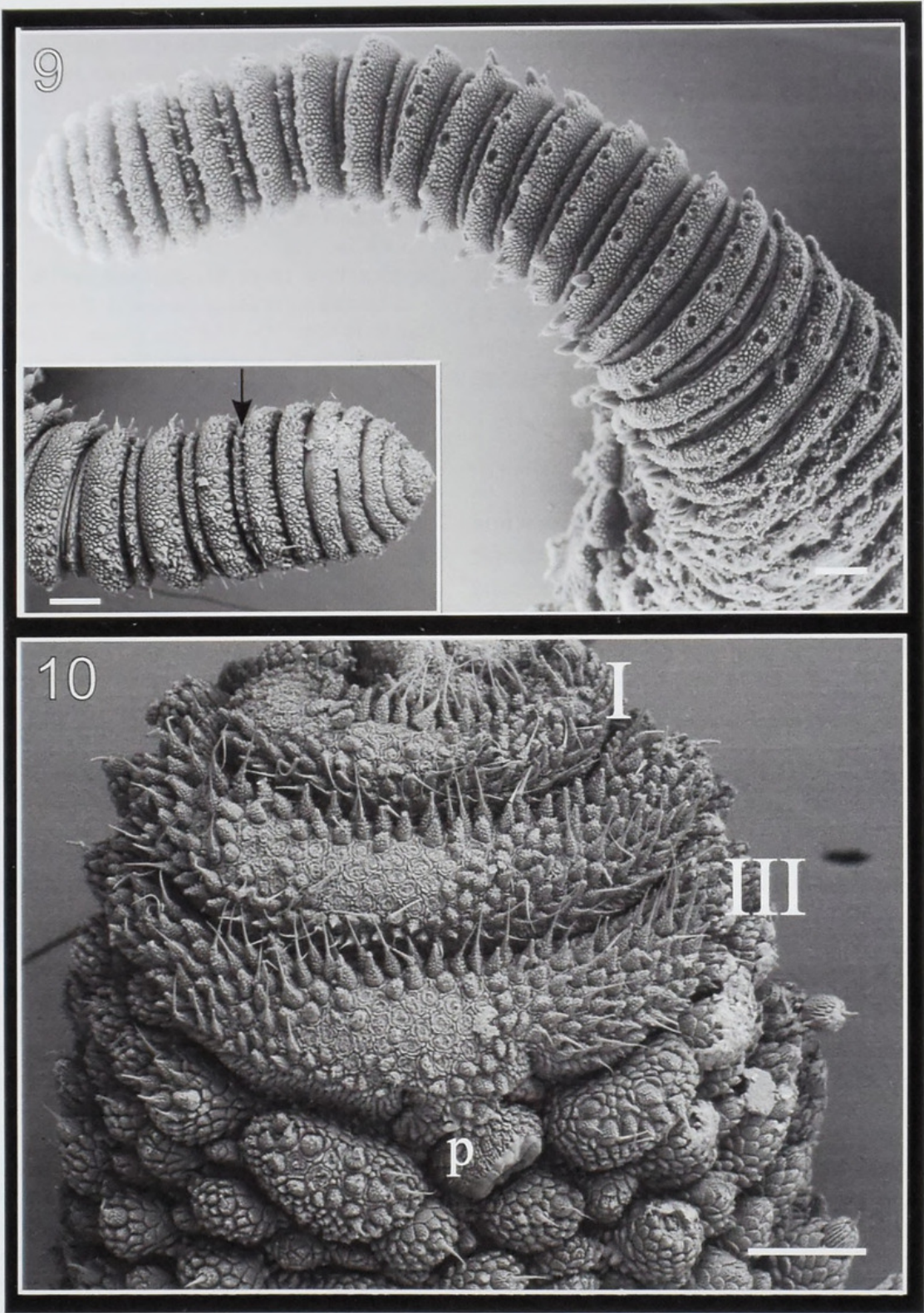
graphic distribution (Bouvier, 1898a, d; Monge-Nájera, 1995) and morphology (Evans, 1901; Bouvier, 1905) or to constitute a “link” between both groups based on phylogenetic placement using molecular data (Murienne *et al.*, 2014), which severed connections to the South American fauna after the Lower Cretaceous (Monge-Nájera, 1995) or around the Triassic (Murienne *et al.*, 2014).

Moreover, the morphology of *M. tholloni* is singular and easy to recognize because the genus has three complete and a vestige of a fourth spinous pad on the fourth and fifth legs and a random distribution (on the top or furrow) of the accessory papillae in alternating dorsal papillae. Despite the anal gland ducts opening in a single and large orifice, like *Eoperipatus* (also observed in some *Oroperipatus*), *Mesoperipatus* differs from *Eoperipatus* in the number of broad rings on the tip of the antennae and on the number of complete spinous pads and foot papillae on the fourth and fifth leg pairs.

Similar to some Neotropical Peripatidae, *M. tholloni* has alternating broad and narrow plicae on its dorsal integument, such as *Oroperipatus ecuadorensis* (Bouvier, 1902). Some dorsal plicae of *M. tholloni* could be misidentified as incomplete dorsal plicae, because they may result from some anastomosed regions of the dorsal plicae.

The number of accessory teeth on both jaws, the number of foot papillae, and the absence of incomplete plicae are shared characteristics between *Mesoperipatus* and the four most speciose genera of Onychophora in Central and South America.

Despite historical debate about the placement of *M. tholloni* in the family Peripatidae, our study of the external morphology of this species confirms that it is a unique Peripatidae species from the African continent, which seems to share external characteristics with Asian and American peripatids. The stron-



Figures 9, 10. SEM images of antenna and spinous pads. Figure 9. Left antenna; inset showing the tip of the antenna with six broad rings until interrupted by one thin ring (arrow). Figure 10. Spinous pads of the fifth leg, left side. Complete spinous pads I and III are labeled; the fourth spinous pad is formed by fragments. Urinary papilla (p) connected with third spinous pad.

gest evidence for this placement is the anal gland opening, the distribution of dorsal papillae on the plicae, and the number of spinous pads on the fourth and fifth legs. This placement is also corroborated by molecular analyses (Murienne *et al.*, 2014), which show that in spite of shared characteristics with Asian onychophorans, *M. tholloni* is more closely related to the Neotropical forms (Murienne *et al.*, 2014); it is intermediate in position between these two biogeographical regions, making this species integral in studies of Peripatidae evolution.

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