



RESEARCH ARTICLE

Redescription of *Epiperipatus edwardsii*, and descriptions of five new species of *Epiperipatus* from Brazil (Onychophora: Peripatidae)

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ABSTRACT. *Epiperipatus edwardsii* (Blanchard, 1847) is redescribed based on fresh material collected near the type locality. Additionally, five new species of velvet worms of the genus *Epiperipatus* Clark, 1913 from Brazil are described: *Epiperipatus hyperbolicus* **sp. nov.**, *Epiperipatus lucerna* **sp. nov.**, *Epiperipatus titanicus* **sp. nov.** (Holotypes deposited in MNR]: Murici, Alagoas State), *Epiperipatus beckeri* **sp. nov.** (Holotype female deposited in MNR]: Camacan, Bahia State) and *Epiperipatus marajoara* **sp. nov.** (Holotype male deposited in MZUSP: Breves, Marajó island, Pará State). The peculiar shape of the primary papillae (artichoke-like) of *E. titanicus* **sp. nov.** and *E. beckeri* **sp. nov.** is documented for the first time. *Epiperipatus titanicus* **sp. nov.** has the largest number of pairs of oncopods (38 for males and 39 for females) among the Brazilian Onychophora. We also provide an identification key for Brazilian species of *Epiperipatus*.

KEY WORDS. French Guyana, neotropics, onychophorans, Peripatus, taxonomy.

INTRODUCTION

Epiperipatus Clark, 1913 is the most diverse genus of Neotropical Peripatidae. Currently, 26 species are known in Central and South America (Oliveira et al. 2012a). Clark (1913a) proposed Epiperipatus as a subgenus of Peripatus Guilding, 1826, and included the following species: P. (E.) edwardsii (Blanchard, 1847), P. (E.) imlhurni (Sclater, 1888), P. (E.) trinidadensis (Sedgwick, 1888), P. (E.) brasiliensis (Bouvier, 1899), P. (E.) simoni (Bouvier, 1899), P. (E.) nicaraguensis (Bouvier, 1900), P. (E.) biolleyi (Bouvier, 1902), P. (E.) isthmicola (Bouvier, 1902), P. (E.) evansi (Bouvier, 1904), and P. (E.) barbouri (Brues, 1911). The subgenus was delimited based on subjective characters, for instance shape, size and pattern of distribution of the dorsal papillae (Clark 1913a: 17). Many years later, Peck (1975) elevated Epiperipatus to genus, without performing a detailed morphological study. More recently, after evaluating scanning electron microscopy images of the integument (especially the primary papillae) of the Neotropical Peripatidae, Read (1988a) suggested that the patterns of scales ranks of the primary papillae can be used to delimit genera within peripatids.

for Zoology

Neopatida is the largest group of Peripatidae from the Neotropics. This taxonomically obscure group comprises the widespread genus *Macroperipatus* Clark, 1913, type species Peripatus torquatus von Kennel, 1883, from Trinidad, and Epiperipatus, type species Peripatus edwardsii Blanchard, 1847, from French Guiana. Those genera were included in a phylogenetic analyses of Costa (2016) and Giribet et al. (2018). Although phylogenetic studies on onychophorans have been seldom conducted including Brazilian species, the number of species described in Epiperipatus has increased considerably in the past few years. Brito et al. (2010) described Epiperipatus cratensis Brito et al., 2010 from Crato, Ceará State, Northeast Brazil. Oliveira et al. (2011) described three cryptic species of Epiperipatus, i.e., E. diadenoproctus Oliveira et al., 2011, E. adenocryptus Oliveira et al., 2011 and E. paurognostus Oliveira et al., 2011, from the Minas Gerais State, Southeast Brazil, using a molecular and morphological approach to delimit the new species. Oliveira et al. (2010) revised the taxonomic status of two species combined with Macroperipatus, M. acacioi (Marcus & Marcus, 1955) and M. machadoi Oliveira & Wieloch, 2005, and examined some characters of the integument and the crural tubercles, concluding that the two species are better combined with *Epiperipatus*. Recently, Chagas-Jr and Costa (2014) also revised a species of Macroperipatus, M. ohausi (Bouvier, 1900), and concluded that it equally belongs to Epiperipatus, not to Macroperipatus. Therefore, fourteen species of *Epiperipatus* are currently known to occur in Brazil.

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Epiperipatus edwardsii is widespread in the Neotropics, distributed on a large area from Panama, Trininad & Tobago, Venezuela, French Guiana, Suriname, Colombia and Brazil (Read 1988b, Sampaio-Costa et al. 2009, Oliveira et al. 2012a). This contrasts with the narrow distribution of other species of onychophorans restricted to less than 100 km² (Marcus and Marcus 1955, Peck 1975). Blanchard (1847) described *E. edwardsii* based only on the number of oncopods (30 pairs). Bouvier (1905) proposed an emended description, adding, for instance, the diamond-shape pattern on the dorsal body, two incomplete folds, and base of primary papillae roundish, contiguous with dorsal papillae. These characters are shared by several species of *Epiperipatus*, which makes it impossible to identify any particular species using them.

Based on findings of Costa (2016), in this paper we analyzed a specimen of *E. edwardsii* from the Nouragues Field Station, French Guyana, a few kilometers from the species type locality, in Cayenne. We redescribe *E. edwardsii* and provide images documenting the dorsal color and the scale ranks of the primary papillae. Additionally, we describe five new species in *Epiperipatus*, all from Brazil. Two new species, *Epiperipatus titanicus* sp. nov. and *E. beckeri* sp. nov., have symmetrical apical piece with one scale rank, a feature that had not been observed before in Peripatidae.

MATERIAL AND METHODS

In total, we examined 65 specimens collected between 2008 and 2014. The material examined is deposited in the following institutions: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG); Natural History Museum, London, United Kingdom (NHM); Collection of the Evolution et Diversité Biologique laboratory at Université Toulouse III Paul Sabatier, Toulouse, France (GF). Live specimens were photographed (mainly for color and body patterns) with SONY Cybershot DSC-HX1 with built-in flash, or Canon EOS Rebel XS with macrolens and flash circular cameras. The color of live specimens was described following the standard names of the 267 Color Centroids of NBS/ISCC Color System (Mundie 1995). Respective code numbers are given between parentheses following the color name.

We obtained the stacked images using a Leica MZ125 Stereomicroscope with built-in Leica DFC 290 camera, Leica Light source CLS100X series 00373 and assembled through of software Leica Application Suite version 3.3.0. We compiled descriptions, and dissection of dead specimens using a stereomicroscope. The morphological descriptive nomenclature follows the terminologies of Read (1988a), Morera-Brenes and Monge-Nájera (2010) and Oliveira et al. (2010).

Dorsal integument, jaws, legs and some antennae were photographed using Scanning Electron Microscopy (SEM). All tissues were cleaned, subjected to critical point and sputter coating. In the cleaning process, the soft parts were washed in a solution of hypochlorite 3% diluted in distilled water. The hard parts (for example jaws) were cleaned in distilled water and Ethylenediaminetetraacetic acid (or EDTA) heat solution in sonicator processor. For critical point, the tissues were dehydrated using an increasing ethanol series: 30%, 50%, 70%, 80%, 90% and 100%.

These tissues were critical point dried and mounted in SEM stubs with biadhesive carbon tape, in the critical point machines Baltec CPD 030. The sputter coating was completed using the machines Denton Desk IV gold sputter model and Balzer SCD 50 sputter coater. Generally, on average, 5 to 10 nm of gold/paladium or platinum/palladium were deposited over the tissues. We took SEM images using microscopes JEOL JSM-6390LV and DSM 940 Zeiss scanning electron. The Backscatter electron detector (BSD) function, when available on the microscope, was used to avoid the charging effects on the tissues.

The descriptions of new species are based on type series instead of just in the holotype (compound description). A full description is only provided for the first described species, *E. titanicus*, subsequent descriptions are comparative and complementary to that of *E. titanicus*.

TAXONOMY

Peripatidae Evans, 1901

Epiperipatus Clark, 1913

Peripatus (Epiperipatus) Clark, 1913: 17; Cockerell 1913: 87; Scorza 1953: 783; Froehlich 1968: 163, 165–168.

Epiperipatus Clark, 1937: 2; Arnett 1961: 218; Peck 1975: 334; Sampaio-Costa et al. 2009: 556; Morera-Brenes and Monge-Nájera 1990: 449, 2010: 1134; Morera-Brenes and León 1986: 278; Röhlig et al. 2010: 229; Chagas-Jr and Costa 2014: 979; Oliveira et al. 2010: 16, 2012a: 7, 2012b: 18, 2015: 227.

Type-species. *Peripatus edwardsii* Blanchard, 1847 by original designation.

Diagnosis. Dorsal papillae with roundish insertion. Bases of primary papillae with four to eighteen scale ranks. Apical pieces are conical, cylindrical, or rarely flat. Usually four complete and sometimes, rarely vestiges of a fifth spinous pad on the fourth and fifth legs. Nephridial tubercle on fourth and fifth pairs of legs, between third and fourth spinous pads. One to tree pregenital legs with crural papillae (male only).

Epiperipatus edwardsii (Blanchard, 1847) Figs 1–6

Peripatus edwardsii Blanchard, 1847: 140.

Peripatus (Epiperipatus) edwardsii: Clark 1913: 18.

Epiperipatus edwardsii: Peck 1975: 345; Oliveira et al. 2012a: 10.





Figures 1–6. *Epiperipatus edwardsii*, GF180312HC003-06: (1) dorsal papillae arrangement; (2) dorsal view of the distal half of the body depicting diamond shaped pattern over the dorsomedian furrow; (3) foot in ventral view; (4) primary papillae in posterior view depicting differences in the number and shape of the scales (B and P); (5) outer blade in first plan of right jaw; (6) right fourth leg in ventral view depicting spinous pad undivided (I) and divided (IV) into two unqueal parts. (AT) Accessory tooth, (B) basal piece, (DR) series of denticles, (I) first spinous pads, (IJ) inner blade, (IV) last spinous pads, (nt) nephridial tubercle, (OJ) outer blade, (P) apical piece, (PP) prolateral foot papillae, (RP) retrolateral foot papillae. Scale bars: 1, 5 = 100 μ m, 2 = 5 mm, 3 = 30 μ m, 4 = 20 μ m, 6 = 200 μ m.

Diagnosis. The background color of the body of this species is in the purple spectrum; dorsal papillae round, primary papillae bearing asymmetrical apical piece, four complete spinous pads on the fourth and fifth legs (the last broken in some specimens).

Redescription. Measurements (mm): Type: length 35.0; width 4.0; height 3.0 (based on Bouvier 1905). Additional specimen (hereafter): length 30.0, width 3.0, height 3.0. Color (living specimen). Background color of body dark purplish gray (234), dorsal surface dark grayish reddish brown (47) with purplish gray (233) diamonds overlapping light brownish gray (63) dorsomedian furrow (Fig. 2). Background color of ventral body purplish gray (233) with light gray and yellowish-brown (79) median band. Legs white (263) and ventral organs pale

pink (7). Description of body. Conspicuous dorsomedial furrow and hyaline organs on entire length of body. Twelve plicae per segment, two incomplete (not extending to insertion of legs), and seven crossing over to ventral side. Uniform width among to the dorsal plicae as mentioned by Bouvier (1905). Dorsal papillae on all plicae (Fig. 1). Primary papillae as the largest dorsal papillae, with roundish dome insertion and asymmetrical spherical apical piece (Figs 1, 4). Basal piece larger than apical piece, with a range of at least seven scale ranks. Apical piece with three posterior scale ranks (Fig. 4). Bristle directed posteriorly (Fig. 4). Accessory papillae usually the smallest, but some as large as the basal piece of a primary papilla (Fig. 1). Accessory papillae with roundish insertion. Accessory papillae more abundant than primary papillae per plica (Fig. 1). Frequently,



primary papillae separated by one to four accessory papillae. Dorsal papillae always on the plicae, although only and rarely accessory papillae present on flanks.

Head. No evident structures or color patterns on head. Antennae with 44 rings: antennal tip composed of seven broad rings, excluding the terminal disc on top. Antennal body with alternating sequence of narrow and broad rings at least up to the eighteenth. Eyes and frontal organs present on ventrolateral region of antennal base. Frontal organs as long as four fused antennal papillae. Mouth opening surrounded by small, anterior, unique lobe, and seven flanked lobes decreasing in size from anterior to posterior ends of the mouth. Dental formula of inner and outer jaws, respectively: 1/1 and 1/1/10, with second accessory tooth of inner jaw vestigial (Fig. 5).

Legs. Male with 30 pairs of legs. Ventrally, fourth and fifth pairs of legs with four complete spinous pads (the fourth are sometimes broken) without vestige of fifth spinous pad (Fig. 6). Nephridial tubercle on fourth and fifth pairs of legs, between third and fourth spinous pads, and connected at tip with third spinous pad (Fig. 6). Two pro-lateral and one retro-lateral foot papillae the feet of fourth and fifth legs (Fig. 3). Conspicuous ventral and preventral organs, gonopore close to penultimate pairs of legs in both sexes.

Sexual dimorphism. Male pregenital leg without crural papillae (these organs had not been previously described for this species). Anal glands inconspicuous (male); represented by two pores on ventral portion of anal aperture.

Material examined. 1♂, French Guiana, Cayenne, Nouragues Field Station, no further data (GF180312HC003-06). The holotype, deposited at the Muséum National d'Histoire Naturelle, Paris, France (MNHN), was not examined because the curator did not reply to our loan requests.

Distribution. French Guyana: Cayenne and adjacency of Nouragues Field Station (Bélizon, Bita, Coco).

Remarks. The type of *Epiperipatus edwardsii*, deposited at the Muséum National d'Histoire Naturelle, Paris, France (MNHN) was not examined. We tried to contact the curator to arrange a loan of this material, but the curator did not reply. *Epiperipatus edwardsii* is the most frequently misidentified species of *Epiperipatus* and for this reason some records of its distribution (e.g., Brues 1914, Clark 1914, Peck 1975, Sampaio-Costa et al. 2009) are not accepted here. The shape and distribution of the dorsal papillae, dorsal diamond pattern and number of legs are frequently misinterpreted.

According to our observations, the diamond patterns are a general feature in most species of *Epiperipatus*. Morphologically, the diagnostic features to delimit *E. edwardsii* are (1) dorsal papillae over the plicae and never on the folds, and (2) primary papillae usually separated by one or two accessory papillae (however in some cases they are close to each other). Also, *E. edwardsii* is supported by molecular data as demonstrated in Maximum Parsimony and Maximum Likelihood analyses (e.g., Costa (2016) and Giribet et al. 2018). The other records of *E. edwardsii* found in the literature, for instance from Panama, Venezuela, Colombia and Brazil (Brues 1914, Clark and Zetek 1946, Read 1988a, b, Sampaio-Costa et al. 2009, see discussion below) are probably based on undescribed species. Moreover, records of *E. edwardsii* from Aripo in Trinidad (Read 1988a) and Haut Sarare, Venezuela (Read 1988b) also correspond to an undescribed species. In conclusion, the distribution of *E. edwardsii* is likely limited to French Guyana.

Epiperipatus titanicus sp. nov.

http://zoobank.org/068FF25E-2B24-42CA-86AC-3404406284B8 Figs 7, 13–16, 37

Epiperipatus sp. 1: Sampaio-Costa et al.: 2009: 556, 557.

Diagnosis. *Epiperipatus* species with symmetrical, reduced or hidden apical piece. Body large, 29 up to 76 mm and 36 to 39 pairs of legs.

Compound description. Measurements. Males: length 29-41; width 1.0-3.0; height 1.0-2.5. Females: length 16-76; width 1.0-4.0; height 1.0-6.0. Background color of body in vivo is dark grayish red (20), with dorsal wavy band of light grayish red (18) and overlaid by diamond-shape marks, the same color as background color of body (Fig. 13). Dorsomedian furrow very dark purplish red (260) (Fig. 13). Anterior portion of head and antennae dark purple (224). Color of dorsal portion of legs the same as predominant dorsal body color. Largest primary papillae pale and distinguishable in vivo from light brown (57) color found on alternate plicae and forming longitudinal sequences on dorsal integument. The number of pale primary papillae increases near the legs. Legs and ventral surface displaying same color, pale pink (7). Description of body. Dorsal papillae aligned on top of folds, two primary papillae separated by one to three accessory papillae and rarely occurring close together. Both dorsal papillae have conical basal pieces, artichoke-like, composed of lanceolate scales that never overlap with one another at base of papillae (Figs 7, 14). The primary papillae are the largest and at their bases there are five to ten scale ranks. Apical piece can be reduced and there is just one scale rank (Fig. 7). Rank in some cases overlapped by scale rank of the base papilla, hiding the constriction between the two parts of the primary papillae (Fig. 7. See also Sampaio-Costa et al. 2009: 557, figs 6-8). The apical piece, when evident, is symmetrical and conical with narrow and elongated scales (Fig. 7). Needle-shaped sensory bristle curved or straight, placed at center of apical piece. Accessory papillae similar to primary papillae with respect to shape of scale and morphology of the base, but without an apical piece.

Head. Holotype and paratype with 44–45 antennal rings, respectively. In both specimens, antennal tip composed of seven broad rings (excluding the terminal disc on top) and followed by alternating narrow and broad rings until the eighteenth ring. Mouth opening surrounded by anterior oral lobe (unpaired lip) and seven pairs of oral lips. Jaws with two blades composed of one long curved main tooth followed by one accessory tooth (Figs 15, 16).





Figures 7–12. Shape of primary papillae (holotype, except when mentioned) of *Epiperipatus beckeri* sp. nov., *E.piperipatus lucerna* sp. nov., *Epiperipatus marajoara* sp. nov., *Epiperipatus hyperbolycus* sp. nov. and *Epiperipatus titanicus* sp. nov. (7) *Epiperipatus titanicus* sp. nov. (MNRJ 0057); (8) *Epiperipatus marajoara* sp. nov. (MZUSP 0022); (9) *Epiperipatus lucerna* sp. nov. MNRJ 0101; (10) *Epiperipatus beckeri* sp. nov. (MNRJ 0045); (11–12), *Epiperipatus hyperbolycus* sp. nov. (MNRJ 0104). Scales bars: 7, 12 (also in the small box of Fig. 9) = 10 μm, 8–11 = 20 μm.

Formulae of inner and outer jaw blades: 1/1 and 1/1/7–11 (Figs 15, 16), respectively. Legs. Males: 36–38 pairs of legs. Females: 36–39 pairs of legs. Nephridial tubercle on fourth and fifth pairs of legs, between third and fourth spinous pads (Fig. 17). On fourth and fifth pairs of legs, fifth spinous pad present and always reduced (Fig. 17).

Sexual dimorphism. Two or three pregenital legs with one crural papilla (male) each. Anal glands inconspicuous (male); represented by two pores on anterior margin of anal aperture.

Type material. Holotype. \bigcirc , BRAZIL, Alagoas State: Murici, Estação Ecológica de Murici (Mata da Bananeira area), Lo-Man-Hung, N.F. leg. (MNRJ 0057). Paratypes. \bigcirc , idem, 11–18.xiii.2009, Costa, C.S., Giupponi, A. and Chagas-Jr leg. (MNRJ 0035); 2 \bigcirc , same date but 21.vii.1995, Freitas, L.M. and Natali, M.S. leg. (DZ-UFMG-ONY 0008 and 0009); 9 \bigcirc , 4 \bigcirc and 1 unsexed, same data but, 11–18.xii.2009, Costa, C.S., Guipponi, A. and Chagas-Jr, A, leg (MNRJ 0053); 1 \bigcirc , same data but, 26–29.vii.2012, Costa, C.S., Alcântara, D.M.C., Dias, P.S. and Nihei,S.S. leg (MZUSP 0010).

Distribution (Fig. 37). Only known from the type locality (Brazil, Alagoas state, Murici, Estação Ecológica de Murici).

Etymology. The specific name *titanicus, titanica, titanicum* (L., "titanic", adjective) refers to the large size of the females, and the great number of pairs of oncopods, more numerous than in any other Brazilian species of onychophorans.

Remarks. The number of leg pairs in this species varies from 36 to 39, and these numbers overlap in males and females, 36 to 38 in males and 36 to 39 in females.

Epiperipatus lucerna sp. nov.

http://zoobank.org/0CECB928-54B3-4125-BEB4-D9D091E89F1A Figs 9, 18–20, 37

Diagnosis. Apical piece cylindrical, asymmetric, have of two scale ranks on back side and three on front side; 29 to 30 pairs of legs.





Figures 13–17. *Epiperipatus titanicus* sp. nov. habitus, dorsal plicae, spinous pad and jaws: (13) Living specimen in dorsal habitus, paratype; (14) dorsal papillae arrangement of the holotype; (15) paratype blades; (16) holotype blades with the accessory tooth broken in outer jaws; (17) spinous pad and nephridial tubercles of paratype. The Roman numbers indicate the first and last spinous pad of the leg. Black arrows point vestiges of a fifth spinous pad; (15–16) jaws with outer blade in first plane in the both figures. Scales bars: 13 = 2.7 mm, 17 = 200 µm, 14 = 15 = 100 µm, 16 = 50 µm.

Compound description. Measurements. Male: length 13-29; width 1.0-3.0; height 1.0-1.5. Female: length 23-44; width 1.0-3.0; height 2.0-4.0. Color (living specimens). In vivo background color of body on dorsal portion, arrangement of pale primary papillae, and ventral region as described for *E. titanicus*. Description of body. Dorsal papillae aligned on top of folds, with two primary papillae close together or separated by one to five accessory papillae. Dorsal papillae with conical basal piece, composed of overlapping lanceolate scales. Primary papillae regular in size, at their bases four to eight scale ranks (Fig. 19). Apical piece cylindrical, asymmetrical, composed of two scale ranks on back side and three on front side (Fig. 9). This rank overlapped by scale rank of the base papilla and hiding constriction between the two parts of primary papillae (Figs 9, 19). Needle-shaped sensory bristle curved or straight and located on back side of apical piece (Fig. 9). Head. Number of complete antennal rings in holotype 29, alternating between narrow and large rings, from the eighth to the twentieth rings. Paratype with 46 rings and ring widths alternating from the eighth to the eighteenth ring. Antennal tips composed of seven large rings and terminal

bud. Number of tooth in jaw blades as in *Epiperipatus titanicus* sp. nov. as in dental formula: (1/1; 1/1/8). Legs. Males: 27–29 pairs of legs. Females: 29–31 pairs of legs. Nephridial tubercle on fourth and fifth pairs of legs, between third and fourth spinous pads (Fig. 20). No evidence of fifth spinous pad on fourth and fifth pairs of legs.

Sexual dimorphism. One or two pregenital legs with crural papillae (male) with one crural papilla each (structure not identifiable in some adult males examined). Anal glands inconspicuous (male); represented by two pores on anterior board of anal aperture.

Type material. Holotype. MNRJ 0101, \circ , Brazil, Alagoas state, Murici, Estação Ecológica de Murici (Mata da Bananeira area), 11–18.xii.2009, Costa, C.S., Giupponi, A. and Chagas–Jr leg. Paratypes. MNRJ 0102, \circ , idem; MNRJ 0103, 13 \circ , 6 \circ and 3 unsexed, Brazil, Alagoas state, Murici, Estação Ecológica de Murici (Mata da Bananeira area), 11–18.xii.2009, Costa, C.S., Giupponi, A. and Chagas–Jr leg; MZUSP 0011, 1 \circ , idem, 26–29.vii.2012, Costa, C.S., Alcântara, D.M.C., Dias, P.S. and Nihei,S.S. leg.





Figures 18–23. *Epiperipatus lucerna* sp. nov. and *Epiperipatus hyperbolicus* sp. nov.. *Epiperipatus lucerna* sp. nov., dorsal plicae, spinous pad and jaws: (18) dorsal papillae arrangement over the plicae (holotype); (19) primary papillae, holotype. Note the scales ranks on the basal piece; (20) spinous pad and nephridial tubercles of paratype. *Epiperipatus hyperbolicus* sp. nov., dorsal plicae, spinous pad and jaw, paratype images: (21) dorsal plicae on top view. Incomplete plicae position indicate by the arrow head; (22) spinous pad and nephridial tubercles. The Roman numbers indicate the first and last spinous pad of the leg; (23) jaw. The inner and outer blades are illustrated in the large and small boxes. Scales bars: 18, 21 = 500 μ m, 19 = 20 μ m, 20 = 200 μ m, 22 = 100 μ m, 23 (also in the small box) = 50 μ m.

Distribution (Fig. 37). Only known from the type locality (Brazil, Alagoas State, Murici, Estação Ecológica de Murici).

Etymology. The specific name *lucerna* (L., "lamp", feminine noun in apposition) refers to the candle shape of the apical piece of the primary papillae of this species.

Epiperipatus hyperbolicus sp. nov.

http://zoobank.org/ED926027-E31F-4C19-80CE-321B6B6886CC Figs 11, 12, 21–23, 37

Diagnosis. Dorsal papillae with conical and small basal piece composed of truncated robust scales and primary papillae of regular size with six or seven scale ranks at base and robust and asymmetric spherical apical piece. Legs with 23 to 25 pairs. Compound description. Measurements (based on a single male): length 26, width 2.0 and height 3.0. Females: length 22–33, width 17–2.0 and height 2.0–3.0. Color (living specimens). Background color of dorsal body, arrangement of pale primary papillae, and ventral region as in *Epiperipatus titanicus* sp. nov. Description of body. Dorsal papillae aligned on top of folds, two primary papillae occurring close together or separated by one to three accessory papillae. Dorsal papillae with conical basal piece, composed of truncated scales (Fig. 21). Primary papillae regular in size with six or seven scale ranks at base and robust and asymmetric spherical apical piece (Figs 11, 12). Apical piece composed of overlapped scale ranks, six or seven on front and three on back (Figs 11, 12). Constriction between the two portions of primary papillae hidden (Figs 11, 12). Needle-shaped sensory bristle curved or straight and dislocated to back side of apical piece.



Head. In holotype antennae with 27 rings (28 rings in paratype, some females with 36, 37 and 41 antennal rings). In both holotype and paratype the antennal tips composed of seven broad rings and terminal bud. Antennal tip followed by alternating narrow and broad rings until sixteenth ring. Jaw blades as in *Epiperipatus titanicus* sp. nov. with dental formula of holotype and paratype as follows: 1/1/7 and 1/1/11 (Fig. 23). Legs. Male holotype: 23 pairs of legs. Females: 24 and 25 pairs of legs. Nephridial tubercle on fourth and fifth pairs of legs, between third and the fourth spinous pads (Fig. 22). Fourth and fifth pairs of legs without evidence of fifth spinous pad (Fig. 22).

Sexual dimorphism. One or two pairs of pregenital legs present (male) with one crural papilla on each. Anal glands inconspicuous (male); represented only by two pores on anterior margin of anal aperture.

Type material. Holotype. MNRJ 0104, \mathcal{J} , Brazil, Alagoas State, Murici, Estação Ecológica de Murici (Mata da Bananeira), 11–18.xii.2009, Costa, C.S., Giupponi, A. and Chagas-Jr leg. Paratypes. MNRJ 0105, \mathcal{Q} , idem; MNRJ 0106, $2\mathcal{Q}$, Brazil, Alagoas State, Murici, Estação Ecológica de Murici (Mata da Bananeira), 11–18.xii.2009, Costa, C.S., Giupponi, A. and Chagas-Jr leg.

Distribution (Fig. 37). Only known from the type locality (Brazil, Alagoas State, Murici, Estação Ecológica de Murici).

Etymology. The specific name *hyperbolicus, hyperbolica, hyperbolicum* (Latinized adjective "exaggerated", from Greek ύπερβολή, plus suffix *-icus*) refers to the large spherical shape of the apical piece of the primary papillae of this species.

Epiperipatus beckeri sp. nov.

http://zoobank.org/0CF05504-9F4C-4CB2-8652-F5CEE3545194 Figs 10, 24–27, 37

Diagnosis. Dorsal background color of body light orange, with dark orange dorsomedian furrow, and antennae purple brownish. Apical piece of primary papillae symmetrical, reduced, not hidden basally.

Compound description. Measurements: length 35-53, width 2.0-4.0, height 4.0. Holotype: length 53, width 4.0, height 2.0. Color (living specimens). Background color of body of the specimen is moderate yellowish pink (29) with a mid-longitudinal pale orange yellow (73) wavy stripe interrupted by well-defined background color cardioid patches (Fig. 24). Dorsomedian furrow thin, dark yellowish pink (30). Anterior portion of head strong yellowish pink (26) gradually turning to light violet (210) in antennae (Fig. 24). Arrangement of pale primary papillae as in *Epiperipatus titanicus*. Background color of body of juvenile light violet (210). Description of body. Dorsal papillae roundish and close together, rarely varying in the size. Larger, pale, primary papillae present, except in juveniles, marked only by faded aspect. Dorsal papillae aligned on top of folds. When separate there are 2 to 4 accessory papillae between two primary papillae (Fig. 25). Base of primary papillae conical and apical piece symmetrical and reduced, with some exceptions (see comments) (Fig. 10). Seven to twelve scale ranks at base and only one scale rank on apical piece (Fig. 10). Bristle on apical piece narrow and long, sometimes as long as apical piece (Fig. 10). Accessory papillae conical, generally the same size as primary papillae, but without apical piece (Fig. 26). Plicae regular, 12 per segment over legs, seven crossing to ventral side and incomplete plicae shorter than length of dorsal side (Fig. 25). Head. Holotype with 44 rings with seven broad rings on antennal tip and followed by sequence of alternating narrow and broad rings until fourteenth ring. In the other adult female there are 40 rings with the same aspect described for the holotype. Jaws (holotype) dental formula: 1/2 and 1/2/11 (Fig. 27).

Legs. Twenty-eight to thirty (juveniles included). Holotype with 30 pairs of legs. Nephridial tubercles between third and fourth spinous pads, connected by strait isthmus on top with third spinous pad. Two prolateral and one retrolateral foot papillae on feet of fourth and fifth legs.

Sexual dimorphism. Males unknown.

Type material. Holotype. \bigcirc , Brazil, Bahia State, Camacan, Reserva Particular do Patrimônio Natural Serra Bonita, 11–15. vi.2009, Chagas-Jr, A., Dill, V., Giupponi, A., Pedroso, D. & Kury, A. Leg (MNRJ 0045),. Paratypes. 1 \bigcirc and 4 juveniles, Brazil, Bahia State, Camacan, Reserva Particular do Patrimônio Natural da Serra Bonita, 14.ii to 12.iii.2009, M. Teixeira Junior leg. (MZUSP 0017).

Distribution (Fig. 37). Only known from the type locality (Brazil, Bahia State, Camacan, Reserva Particular do Patrimônio Natural Serra Bonita.).

Etymology. The specific name *beckeri* (German surname, noun with Latin ending -i of the genitive case) honoring the naturalist and entomologist Vitor O. Becker, who created and is responsible for the administration of Reserva Particular da Serra Bonita, Camacan, Bahia State.

Remarks. The main differences between juveniles and adults are the color and the kind of dorsal papillae they display. A juvenile was photographed in vivo with background color of body very dark purplish red (260), without diamond areas. The other post-fixed juvenile darker than adults, with background color of body dark brown (55), diamond areas brownish orange (54) and legs on dorsal region pale yellow (89).

The regular primary papillae and accessory papillae have similar size in the adult. In the juveniles, the largest pale primary papillae are more diverse on the dorsal plicae. These primary papillae have a spherical everted and robust apical piece, their arrangement forming longitudinal lines similar to the condition found in the holotype.

Epiperipatus marajoara sp. nov.

http://zoobank.org/0591C7B3-B49E-4897-B61C-7DC7547F741D Figs 8, 28–32, 37

Peripatus simoni: Bouvier, 1900: 753; 1905: 315; Froehlich 1968: 167 (misidentification).





Figures 24–30. *Epiperipatus beckeri* sp. nov. and *Epiperipatus marajoara* sp. nov. *Epiperipatus beckeri* sp. nov., dorsal body background and papillae and jaw, holotype, MNRJ 0045: (24) body background of dorsal side; (25) dorsal plicae and papillae arrangement. Note the incomplete plicae on the right side of the picture; (26) accessory papilla in posterior view. Note slight different shape between the accessory and primary papillae (see the Fig. 10); (27) teeth formula and shape. Note two accessory teeth for both blades. Note in the small box the denticles series of the outer blade, with eleven denticles. *Epiperipatus marajoara* sp. nov., body patterns: (28) body background of dorsal side; (29) body background of the ventral side. Note the ventral organs clearly visable. MZUSP 0022, holotype; (30) dorsal papillae arrangement around to the dorso-mediam furrow in anterior view. Note the elongate apical piece in the primary papillae and the small scale ranks (six) on the basal piece.Scale bars: 24, 28, 29 = 5.0 mm, 25 = 500 µm, 26 = 20 µm, 27 (in the small box = 50 µm), 30 = 100 µm.

Epiperipatus simoni: Clark and Zetek 1946: 211; Peck 1975: 346; Vasconcelos et al. 2004: 140; Sampaio-Costa et al. 2009: 556 (misidentification).

Diagnosis. This species has dorsal background color of body in the brown spectrum, dorsal diamond pattern inconspicuous or absent, roundish dorsal papillae, primary papillae with well-developed base, and a cylindrical apical piece.

Compound description. Measurements. Females. Length 40, 50 and 65 (specimens from NHM examined by Bouvier in his monograph). Males. Length 27–34, width 2.0–7.0, height 1.0–6.0. The single female is: length 33, width 2.8, height 1.2. Color (living specimens). Background color of body Light Grayish Brown ZOOLOGIA 35: e23366 | DOI: 10.3897/zoologia.35.e23366 | Ocotober 16, 2018

(60) overlaid with brownish pink (33) diamond-shaped makers. Dorsalmedian furrow moderate brown (58), and antennae grayish reddish brown (46) (Figs 28, 29). Largest primary papillae pale and distinguishable in vivo by the light brown (57) color. Found on alternate plicae and forming longitudinal sequences on dorsal integument. Dorsal side of legs same color as dorsal background color of body. Color uniform on ventral surface, grayish yellowish pink (32), except for white spot splashed on integument over the ventral organs (Fig. 29). The number of pale primary papillae increases towards legs. Description of body. Dorsal papillae aligned on top of folds, with two primary papillae separated by one to three accessory papillae (Fig. 30). Both have conical and artichoke-like basal pieces, and are composed of overlapping per 16. 2018 9/15





Figures 31–36. *Epiperipatus marajoara* sp. nov., *Epiperipatus cratensis, E. brasiliensis* and *E. paurognostus. Epiperipatus marajoara* sp. nov., MZUSP 0022, holotype: (31) spinous pad and the nephridial tubercle of the fifth leg; (32) inner and outer blade of right jaw. The accessory tooth is broken in the outer blade. (33, 35) *Epiperipatus cratensis*, MZUSP 0083, dorsal papillae arrangement with dorsomedian furrow on the top of image and primary papillae in lateral view, respectively. (34) *E. brasiliensis*, MZUSP 0121, primary papillae in lateral view. (36) *E. paurognostus*, UFMG 0184, dorsal papillae arrangement. Note all dorsal papillae are proeminent. Scale bars 31, 32 = 30 μ m, 33 = 500 μ m, 34 = 20 μ m, 35 = 100 μ m, 36 = 40 μ m.

lanceolate scale ranks. Primary papillae the largest dorsal papillae, bearing five to six scale ranks basally. Apical piece conical and reduced (Fig. 30), composed of three scale ranks on front side and two scale ranks on back side. Constriction between base and apical piece hidden by basal scale ranks. Bristle slightly displaced to posterior region of apical piece.

Head. Antennae composed of 43 to 47 rings. Antennal tip composed of seven broad rings, except the terminal disc on top, followed by sequence of narrow and broad rings until at least the eighteenth antennal ring. Jaws with two blades and both composed of one long curved main tooth followed by one accessory tooth. Dental formula of outer and inner for holotype and paratype are: 1/1 and 1/1/8 (Fig. 32). Legs. Males: 27 pairs of legs. Single female with 31 pairs of legs. Nephridial tubercle

on fourth and the fifth pairs of legs, between third and fourth spinous pads (Fig. 31), no evidence of fifth spinous pad.

Sexual dimorphism. One or two pregenital legs with one or two crural papillae (male), absent in females. Anal glands inconspicuous (male); represented only by two pores on anterior margin of anal aperture, absent in females.

Type material. Holotype. 3° , Brazil, Pará State, Island of Marajó, Breves, Reserva de Extrativista Mapuá, Breves; 4–8.xii.2012; Cristiano Sampaio Costa leg. (MZUSP 0022). Paratypes. Same data as holotype. 9° (MZUSP 0027). 4 3° (MZUSP 0023-0026). 3° , Breves, Marajó Island, Brazil, Amazon, 96.5.14.6-8 (NHM # 1004943, 1004944, 1004945).

Distribution (Fig. 37). Only known from the type locality (Brazil, Pará State, Breves, Reserva Extrativista Mapuá).





Figure 37. Distribution records of species of *Epiperipatus* in Brazil. Colors on the map correspond to biomes. The new species are represented by stars on the map. The absence of *E. tucupi*, is due to the inaccurate original label (the only data is "Pará state").

Etymology. The specific name *marajoara* (demonymic noun in apposition; invariable), honors the marajoara people, natives from the Island of Marajó.

Remarks. This species was discovered comparing the descriptions with *bona fide* specimens of *E. simoni* from NHM and specimens collected from the Island of Marajó, Pará State, Brazil. The type locality of *E. simoni* is Caracas in Venezuela, with records in Breves, Island of Marajó (Pará State) and Rio de Janeiro State (see Sampaio-Costa et al. 2009). We examined the specimens of *E. simoni* from Breves identified by Bouvier (1905) deposited in the NHM and we considered a misidentification of the new species here described. Also,

we examined the integument of the specimens of *E. simoni* from Rio de Janeiro (Sampaio-Costa et al. 2009: 556) and we believe both records are misidentifications and belong to undescribed species.

DISCUSSION

Since 2010, the number of species of *Epiperipatus* has increased through descriptions of new species and new combinations. After the five new species erected in this work, the genus became the most diverse of Neotropical onychophorans, now including 31 species. In Brazil, *Epiperipatus* is also the most



diverse genus of Peripatidae, with 14 species (excluding *E. edwardsii* and *E. simoni*, Fig. 37).

As stated by Bouvier (1905), the males of Epiperipatus have two pairs of pregenital oncopods with crural papillae, while males of *Peripatus* have at least two pregenital oncopods with crural papillae. Any new species described here fits in the Bouvier's definition for Epiperipatus, because three of them present one or two pairs of pregenital oncopods with crural papillae (E. hyperbolicus sp. nov., E. lucerna sp. nov. and E. marajoara sp. nov.), or two or three (E. titanicus sp. nov.). According to Read (1988a), Epiperipatus has three ranks of scales in the apical piece, and less than 12 ranks of scales in the basal piece. We also do not agreed with Read (1988a) because E. beckeri sp. nov. and E. titanicus sp. nov. have a short apical piece bearing one rank scale, E. lucerna sp. nov. and E. marajaora sp. nov. have two ranks of scales in the apical piece and E. hyperbolicus sp. nov. has three ranks of scales in the apical piece. The short apical piece bearing one rank scale is a feature never seen in other species of the genus and is described for the first time (see Figs 7, 10, Table 1).

However, the five new erected species are herein assigned to *Epiperipatus* because they share, with other species in the genus, the rounded insertion of the dorsal papillae, and distinct nephridial tubercles between the third and fourth spinous pads. They are also nested within of *Epiperipatus* based on molecular synapomorphyes of found in COI, 12S rRNA, 16S rRNA and 18S rRNA sequences (Costa 2016). Although it does not mean a phylogenetic relationship (see Costa 2016), the species of *Epiperipatus* could be divided into two groups according to the dorsal folds (complete vs. incomplete). The group with incomplete folds is formed by *E. acacioi, E. adenocryptus, E. barbadensis* (Froehlich, 1962), *E. barbouri, E. betheli* (Cockrell, 1913), *E. biolleyi, E. broadwayi* (Clark, 1913), *E. diadenoproctus, E. edwardsii, E. evansi, E. imthurni* (Sclater, 1888), *E. isthmicola, E. machadoi, E. nicaraguensis, E. ohausi, E. paurognostus, E. simoni*, *E. trinidadensis*, and *E. vespucci* Brues, 1914. While the group with complete folds is formed by *E. brasiliensis*, *E. cratensis*, *E. torrealbai* Scorza, 1953, *E. vagans* Brues, 1925 and *E. tucupi* Froehlich, 1968. Some species of *Epiperipatus* such as *E. hilkae* Morera-Brenes and Monge-Nájera, 1990 and *E. lewisi* Arnett, 1961 the dorsal folds are unknown. The five new species here present falls into the group with incomplete folds. Table 1 summarizes the morphological characteristics of *Epiperipatus* of the fourteen species present in Brazil.

Our study shows new characters to the taxonomy of Peripatidae. For instance, the few scales ranks on apical piece (see *E. titanicus* and *E. beckeri*), and the larger shape apical piece (see *E. hyperbolicus*). In resume, the new species differ from each other by the shape of the apical piece on the primary papillae. The apical piece of the primary papillae in *E. titanicus* is smaller than in *E. beckeri*. As for *E. lucerna* sp. nov. and *E. marajoara* sp. nov., they have conical apical piece, but *E. marajoara* sp. nov. has a smaller number of pairs of oncopods (27–31 pairs) and inconspicuous diamond pattern on the dorsal portion of the body. Among the five new species, *E. hyperbolicus* sp. nov. is distinguished by the particular shape of the apical piece of the primary papillae. Only in this species a robust and asymmetric spherical apical piece was observed.

Additionally, *E. lucerna* sp. nov., *E. hyperbolicus* sp. nov. and *E. titanicus* sp. nov. are the first species described in Brazil from the same locality, Estação Ecológica de Murici (Mata da Bananeira) in the Alagoas State, Brazil. This region is highland humid forest inserted in the realm of the Caatinga, and is really important to the understanding of the distribution and biogeographical history of onychophorans in the Neotropical region (Vasconcellos et al. 2004).

Due to the conservative morphology of Neotropical onychophorans, many specimens previously identified as *E. edwardsii* in the literature are not actually *E. edwardsii*. The

Species	Morphology of the apical piece	Distribution of ranks of scales ¹	Range of scale ranks ²	Incomplete plicae	Number of oncopods
E. acacioi	Spherical	Asymetrical	2 or 3	Present	24–26 (්); 26–29 (♀)
E. adenocryptus	Conical	Asymetrical	2 or 3	Present	26 and 27 (♂); 28–30 (♀)
E. brasiliensis	Conical	Symetrical	2	Absent	29 (♂); 31 and 32 (♀)
E. cratensis	Spherical	Asymetrical	2 or 3	Absent	30–33 (♂); 33–34 (♀)
E. diadenoproctus	Conical	Asymetrical	2 or 3	Present	26–28 (♂); 29 and 30 (♀)
E. machadoi	Conical	Asymetrical	2 or 3	Present	27–29 (්); 28–31 (♀)
E. ohausi	Spherical	Asymetrical	3	Present	26–28 (්); 27–29 (ූ)
E. paurognostus	Conical	Asymetrical	2 or 3	Present	26 and 27 (♂); 27–29 (♀)
E. tucupi	Conical	_	-	Absent	34 and 35 (♀)
E. beckeri sp. nov.	Conical reduced	Symetrical	1	Present	28–30 (♀)
E. hyperbolicus sp. nov	Spherical robust	Asymetrical	3	Present	23 (♂); 24 and 25 (♀)
E. lucerna sp. nov.	Conical	Asymetrical	2	Present	27–29 (්); 29–31 (♀)
E. marajoara sp. nov.	Conical	Asymetrical	2	Present	27 (්); 31 (♀)
E. titanicus sp. nov.	Conical reduced	Symetrical	1	Present	36 and 38 (ೆ); 36–39 (♀)

Table 1. The main characteristics present in the Brazilian Epiperipatus species.

¹Distribution of ranks of scales in the anterior and posterior portions of the distal end of papillae; ²Range of scale ranks on the posterior side of the apical piece.



characters that have been most often misinterpreted are the shape and distribution of the dorsal papillae, the dorsal diamond pattern, and the number of oncopods. A recent phylogenetic study revealed that E. edwardsii occurs only in Cayenne, or near this locality (Costa 2016). In addition, the specimens of E. edwardsii show diamond patterns on the dorsal side, rounded dorsal papillae, and basal and apical piece of the primary papillae covered by a small range of scale ranks. The broad distribution of E. edwardsii seems unlikely. Hence the records from Panama and Suriname (Bouvier 1905), Colombia (Brues 1914), Trinidad and Venezuela (Read 1988a, b) and Brazil (Clark and Zetek 1946, Froehlich 1968, Sampaio-Costa et al. 2009) belong to other species closely related to E. edwardsii and which share with it the similarities in the diamond shape on the dorsal pattern, and shape of the primary papillae. For the same morphological misinterpretation, we believe that all specimens from Brazil currently identified as E. simoni belong to undescribed species indeed.

Identification key for Brazilian species of Epiperipatus

1	Complete folds (Fig. 33)
1'	Incomplete folds (Fig. 21)
2	Symmetrical conical apical piece (Fig. 34), 29 pairs of legs
	(males) and 31 and 32 (females)
	<i>E. brasiliensis</i> Bouvier, 1899
2'	Asymmetrical conical apical piece (Fig. 35), 30 to 33 pairs
	of legs (males) and 33 to 34 (females)
	<i>E. cratensis</i> Brito et al., 2010
2″	Asymmetrical spherical well-developed apical piece
	(comparable with E. cratensis), 34 and 35 pairs of legs (fe-
	males) E. tucupi Froehlich, 1968
3	Conical apical piece (Figs 7–10)
3'	Spherical apical piece (Fig. 11)
4	Conical normal-sized apical piece (Fig. 9)
4'	Conical/cylindrical reduced (comparable with E. ed-
	wardsii) apical piece (Figs 7, 10)7
5	Spherical regular apical piece (Fig. 4)
5'	Spherical robust (comparable with <i>E. edwardsii</i>) apical
	piece (Fig. 11)E. hyperbolicus sp. nov.
6	Asymmetrical apical piece with cylindrical shape (Fig. 8).
	two primary papillae separated by one to three accessory
	(Fig. 30), accessory papillae occur on the flanks, 27 pairs
	of legs (males) and 31 (females)E. marajoara sp. nov.
6'	Asymmetrical apical piece with conical candle shape (Fig
0	9) dorsal papillae aligned on top of folds (Fig. 18) with
	two primary papillae separated by one to five accessory
	accessory papillae absent on flank of the folds (Fig. 18)
	27 to 29 pairs of logs (males) and 29 to 31 (females)
	E lucarna sp. pou
7	Symmetrical reduced or hidden anical piece (Fig. 7) two
/	primary papillae separated by one to three accessory (Fig.
	14) reddieb brown background color of body (<i>in vivo</i> Fig.
	14), reduisit brown background color of body (<i>in vivo</i> , Fig.
	15), dorsal papillae aligned on top of folds (Fig. 14), $36-38$
	pairs of legs (males) and 36–39 (females)
	E. titanicus sp. nov.

7'	Symmetrical reduced apical piece, dorsal papillae aligned
	on top of folds (Fig. 25), primary papillae when separat-
	ed there are two to four accessory papillae between two of
	them (Fig. 25), yellowish pink background color of body
	(Fig. 24), 28–30 pairs of legs (females) E. beckeri sp. nov.

- 9 Background brownish, 27 to 29 pairs of legs and 28 to 31 (females).....*E. machadoi* (Oliveira & Wieloch, 2005)

- 11 Male anal glands with two well-developed pores (like light spots) on the anterior board of anal aperture (Oliveira et al. 2011: fig. 5C), 26 to 28 pairs of legs (males) and 29 to 30 (females).....*E. diadenoproctus* Oliveira et al., 2011
- 11' Male unconspicuous anal gland, which was bean-shaped, hardly visible (Oliveira et al. 2011: fig. 5D), 26 and 27 pairs of legs (males) and 28 to 30 (females) without overlap between sexes*E. adenocryptus* Oliveira et al., 2011
- 12 Only primary papillae are prominent (Chagas-Jr & Sampaio 2014: fig. 6), primary papillae with robust apical piece (Chagas-Jr & Sampaio 2014: figs 8, 9), 26 to 28 pairs of legs (male) and 27 to 29 (female)*E. ohausi* Bouvier, 1900

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