



<http://dx.doi.org/10.11646/zootaxa.3846.3.3>

<http://zoobank.org/urn:lsid:zoobank.org:pub:39732CE3-F949-4A2B-87A2-030B3EDA5013>

New species of *Pseudonannolene* Silvestri, 1895 from Brazilian limestone caves with comments on the potential distribution of the genus in South America (Spirostreptida: Pseudonannolenidae)

LUIZ FELIPE MORETTI INIESTA & RODRIGO LOPES FERREIRA¹

Centro de Estudos em Biologia Subterrânea, Setor de Zoologia Geral, Departamento de Biologia, Universidade Federal de Lavras, Minas Gerais, Brazil

¹Corresponding author. E-mail: drops@dbi.ufla.br

Abstract

Ten new species of *Pseudonannolene* Silvestri, 1895 are described from Brazilian limestone caves. The species are separated by the morphology of their gonopods and the processes of the first pair of legs of males. A pictorial identification key for the cave-dwelling species from Brazil is provided, besides comments on the distribution of the genus with a potential distribution map of *Pseudonannolene* and *Epinannolene* in South and Central America.

Key words: *Pseudonannolene*, Cave, Brazil, Conservation, Neotropics, Potential distribution

Introduction

The family Pseudonannolenidae was described by Silvestri in 1895, through samples of species *Pseudonannolene typica* Silvestri, 1895, found in Candelaria, Misiones, Argentina, and *Pseudonannolene bovei* Silvestri, 1895, from Giabibbirri, Misiones, Argentina (Silvestri 1895). The main features described were a longitudinal division of the promentum of the gnathochilarium, an elongated and cylindrical body shape, presence of 10 to 11 rows of pectinate lamellae on the mandibles, fourth corporal ring apodous and ozopores starting on the fifth ring (Silvestri 1895). The family has around 50 described species (Shear 2011), distributed in three subfamilies (Mauriès 1987; Hoffman & Florez 1995; Shelley 2003): Pseudonannoleninae Silvestri, 1895, comprising the genera *Pseudonannolene*, *Epinannolene* and *Typhlonannolene* (the validation of this genus is still under discussion); Physiostreptinae Silvestri, 1903, with the genera *Phallortus*, *Physiosreptus* and *Holopodostreptus*; and Cambalomminae Mauriès, 1974, with the single genus *Cambalomma*.

The three subfamilies are mainly separated by the morphology of the gnathochilarium. In Pseudonannoleninae the lamellae linguales are totally separated by the promentum (Brölemann 1903; Chamberlin 1923; Hoffman & Florez 1995) in Cambalomminae, they are separated only by a prolongation of the mentum (Loomis 1941); and in Physiostreptinae, the lamellae are fully connected, without a separation (Hoffman & Florez 1995).

In Brazil, the genus *Pseudonannolene* comprises the richest within the family, being frequently found in caves (Iniesta & Ferreira 2013a). Species are also found in different habitats, such as forests, monocultures, gardens and near houses (Schubart 1944).

Identification of *Pseudonannolene* is based mainly on a longitudinal bipartition of the promentum (a feature that formerly defined the family) and gonopod morphology (Mauriès 1987; Iniesta & Ferreira 2013a).

The first species described in Brazil was *P. longicornis* Porat, 1888, found in São Paulo state. The species was originally described as belonging to the genus *Alloporus* (Spirostreptidae), later being relocated to the genus *Pseudonannolene* (Brölemann 1909). In caves, the first Brazilian species described was *P. strinatii* Mauriès, 1974, found in the Gruta das Areias cave, São Paulo state (Mauriès 1974). Other species were subsequently described, mainly by Fontanetti (1996a; 1996b) and Iniesta & Ferreira (2013b, 2013c).

In this work, ten new species of *Pseudonannolene* Silvestri, 1895 are described from Brazilian limestone

caves. A pictorial identification key for the cave-dwelling species is provided, besides comments on the distribution of genus with a potential distribution map of *Pseudonannolene* and *Epinannolene* in South and Central America.

Material and methods

Collection and preservation. Type specimens were collected during 2001 and 2014 and are deposited in the Zoology Collection, Seção de Invertebrados Subterrâneos at the Universidade Federal de Lavras (UFLA), Campus Universitário de Lavras, Minas Gerais, Brazil. All specimens were captured with a brush and placed in vials containing 70% ethanol. The collections were made in limestone caves in different municipalities from Minas Gerais and Bahia states.

Specimens and laboratory procedures. Measurements and drawings were made under a stereomicroscope (Stemi 2000 (ZEISS)) and a *camera lucida* microscope (Leica MDLS). Dissections were made with fine entomological pins. The stereoscopic images were acquired using the Leica M205 A, with the program Leica Application Suite auto montage to combine the images. For the measurements of body length, length of legs, tarsal claws and antennae, the distance between two farthest points on their extremities was used. For the diameter, the maximum vertical diameter was used. The ratio between the lengths of structures with midbody diameter was made using the midbody diameter as maximum measurement (100%). For the descriptions, we use measurements on the gonopod, as shown in figure 1.

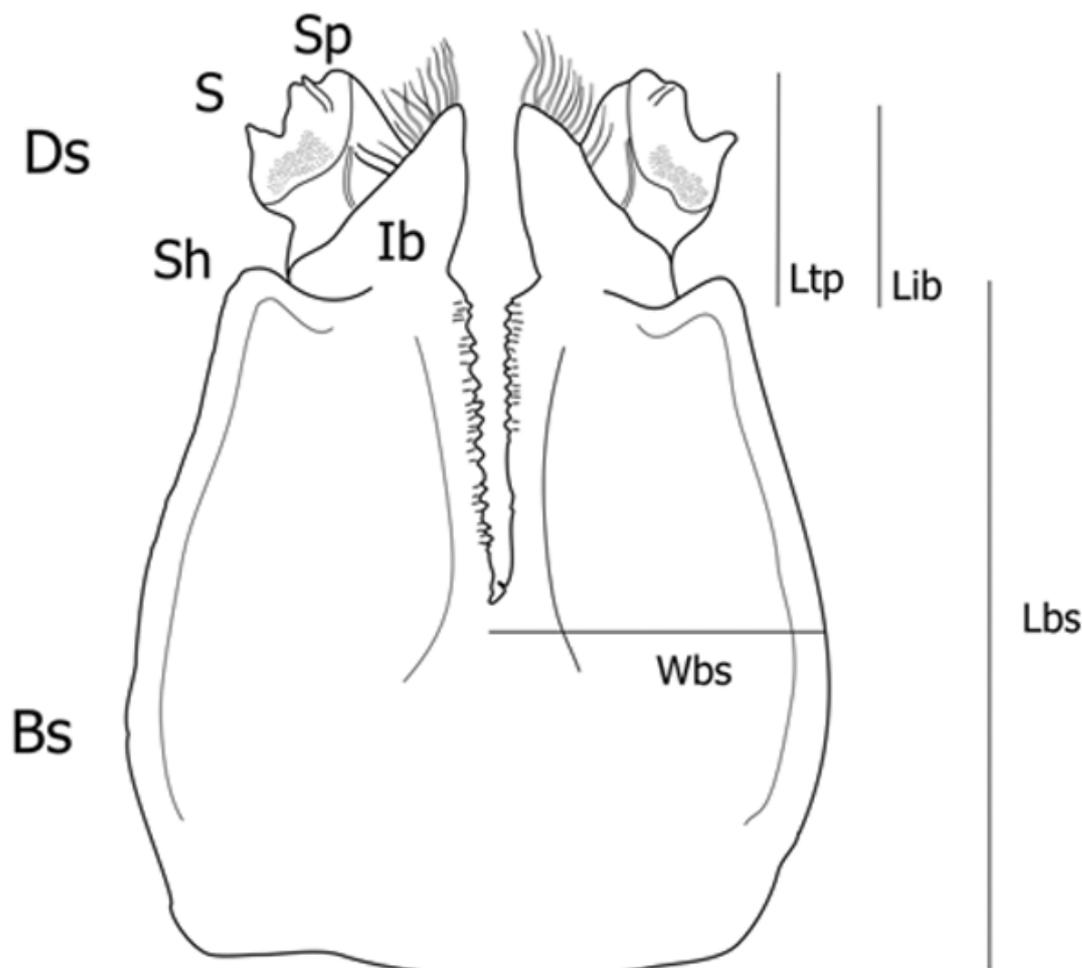


FIGURE 1. Schematic drawing of gonopod of *P. taboa* on caudal view showing the measurements and nomenclature used on this work. The bristles were made in schematic form, not corresponding to the real amount. **Abbreviations:** Bs = Basal section; Ds = Distal section; Sh = Shoulder; Ib = Internal branch; S = Solenomere; Sp = Seminal spine; Wbs = Width basal section; Ltp = Length telopodite; Lib = Length internal branch; Lbs = Length basal section.

Distribution analysis. The potential distribution maps were prepared using the method of maximum entropy from Maxent (Phillips *et al.* 2006), version 3.3.3k software. The program estimates the potential distribution of the taxon through restrictions of various environmental parameters (Phillips *et al.* 2006). We used about 90 distribution records of the genus *Pseudonannolene* and 20 records of *Epinannolene*, in South and Central Americas. The records were obtained from the literature and from data of collections in Brazilian caves conducted by the staff currently based at the Centro de Estudos em Biologia Subterrânea, Universidade Federal de Lavras. The maps were generated with a confidence level of AUC = 0.933 and 0.980, respectively. The program used eighteen environmental variables such as cloud cover, diurnal temperature variation, frequency of frost, rainfall, average temperature, maximum and minimum temperature, vapor pressure, altitude, variations of monthly precipitation in January, April, July and October, and the categorical variable of potential vegetation classes. These data were obtained from the Intergovernmental Panel on Climate Change (IPCC). The map was converted into a layer through the ArcMap software, and the scales inserted in different color schemes, with red indicating the maximum potential of occurrence of species and blues the minimum. The troglotrophic species were not used for this analysis, since their current distributions are not necessarily associated with any epigeal conditions.

Comments. The species *P. rugosetta* Silvestri, 1897 found in Cayenne, French Guyana, was not considered for the analysis of potential distribution, due to the geographic uncertainties in relation to the actual location (Mauriès 1987).

Systematic

Order Spirostreptida Brandt, 1833

Suborder Cambalidea Cook, 1895

Family Pseudonannolenidae Silvestri, 1895

Pseudonannolenidae Silvestri, 1895. Ann. Mus. civ. Stor. Nat. Genova, 34: 774. Silvestri 1895: 774.
Physiostreptidae Silvestri, 1903. Boll. Mus. Torino, 18 (433): 14. Hoffman & Florez 1995: 116; Shelley 2003: 196
Epinannolenidae Chamberlin, 1922. Notes on West Indian millipeds, 61: 2; Shelley 2003: 191
Phallorhthidae Chamberlin, 1952. Gt Basin Natur., 12:20. Hoffman & Florez 1995: 116

Subfamily Pseudonannoleninae Silvestri, 1895

Genus *Pseudonannolene* Silvestri, 1895

Pseudonannolene Silvestri, 1895. Annali del Museo Civico di Storia Naturale di Genova, 34: 775. Type species: *Pseudonannolene typica* Silvestri, 1895, by monotypy. Online publication: Sierwald, P. (ed.). 2006. *Nomenclator Generum Diplopodorum*, version 2.

Pseudonannolene taboa Iniesta & Ferreira 2014, new species

(Figs. 2, 14g)

Material examined. Holotype: 1 male (ISLA 4129) from Gruta Taboa cave (19°28'29.68"S 44°19'41.31"W), Sete Lagoas/MG, Brazil, 15/III/2005. Collected by R. L. Ferreira.

Paratypes: 2 males (ISLA 4130, 4131) from Gruta Taboa cave, Sete Lagoas/MG, Brazil, 15/III/2005. Collected by R. L. Ferreira; 3 females (ISLA 4132, 4133, 4134) from Gruta Taboa cave, Sete Lagoas/MG, Brazil, 15/III/2005. Collected by R. L. Ferreira.

Etimology. The specific epithet refers to the name of the cave in which specimens were collected: "gruta Taboa".

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 23–25 labral setae. Mandibles with 10–12 rows of pectinate lamellae (difficult to see). *P. taboa* has the internal branch of the gonopod like a shield of the solenomere, similarly to those observed in the Brazilian species *P. ambuatinga* (Iniesta &

Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbirensis*, *P. tocaiensis* (Fontanetti 1996a; Fontanetti 1996b) and *P. microzoporus* (Mauriès 1987). The branch is elongated, with the length similar to the telopodite. The solenomere is bifurcated, with seminal apophysis located on the apex of the inner branch. This morphology is similar to the species *P. chaimowiczi* and *P. imbirensis*, in which solenomere have two distinguishable tips (Fontanetti 1996a). The species *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902) have the solenomere with a bifurcated region, however, less evident. Regarding the pre-femoral process, this has rounded shape and is slightly smaller when compared to the pre-femur, as in the species *P. rolamossa*, *P. gogo*, *P. ambuatinga*, *P. tocaiensis*, *P. mesai*, *P. leucocephalus*, *P. ophiulus*, *P. halophila*, *P. chaimowiczi*, *P. strinatii* (Fontanetti 2002).

Description of adults. *Measurements:* Length from 85 up to 92 mm; maximum midbody diameter between 5.5 to 6.1 mm; body rings ranging between 72 to 78; length of antennae ranging from 5.4 to 5.7 mm (relation to diameter ranging 0.93 to 0.98); length of legs 2.8 to 3 mm (relation to diameter ranging 0.49 to 0.51); length of tarsal claw 0.14 to 0.16 mm (relation to diameter ranging 0.02 to 0.03).

Color: Visualization after fixation in 70% alcohol. Dark brown color, with the anterior region of each ring darker and the posterior region reddish.

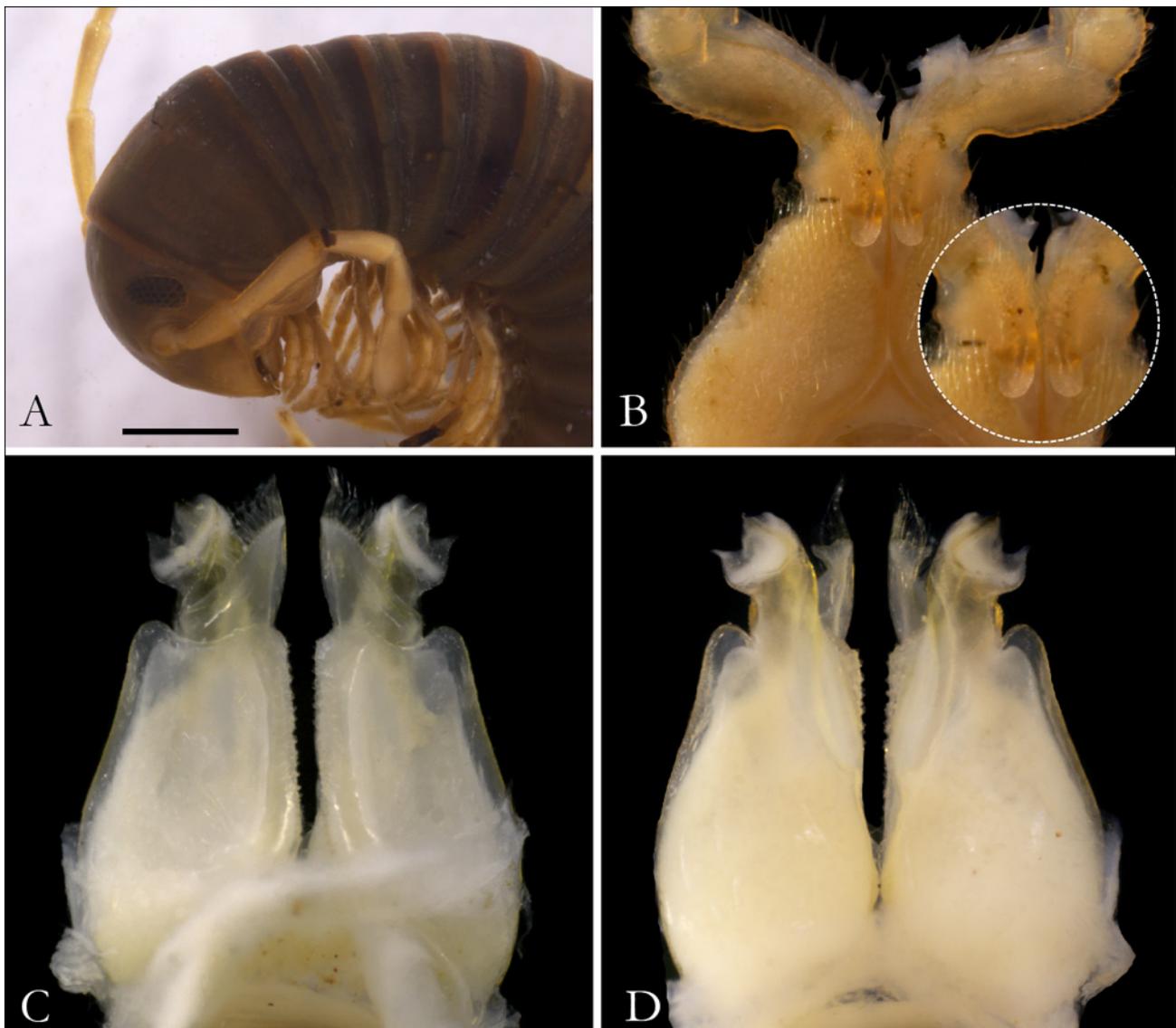


FIGURE 2. *Pseudonannolene taboa* sp.n. (holotype, ISLA 4129): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 2 mm; b) 700 µm; c) 700 µm; d) 700 µm.

Head (Fig. 2a): Head glabrous and pigmented. Labrum with a row containing 23–25 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10–12 rows of pectinate lamellae. Eyes with 34–38 ocelli arranged in 5–6 rows. Antennae pigmented and densely setose. First antennomere small, second little lower than third, fourth, fifth and sixth lower, being the last larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone brown reddish. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 2b): Coxae (**Cx**) larger than remaining legs and densely setose. Prefemur (**Prf**) with thin and elongated oral process parallel (**P**) to the coxae. Bristles arranged on base of **P**.

Gonopod (Fig. 2c, d): Gonopod elongated and slightly sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Presence of a process supporting a seta. Basal section (**Bs**) with width little larger than half of length; Basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) as long as wide and half of **Bs**. Solenomere (**S**) elongated and trunk wide; latter region rounded; squamous and with two well-marked tips (bifurcated), being the first tip containing seminal spine (**Sp**); internal branch (**Ib**) wide and elongated; like a shield of **S**; bristles exceeding the **S**.

Notes on the natural history and habitat. The Taboa cave (Fig. 15e) is located in the city of Sete Lagoas (Minas Gerais). It is a vadose cave, and its main conduit morphology of semi - meander is traversed (half extension) by a subterranean stream that enters the cavity in its deeper portion (farthest from the entrance). The distal portion of the cave is a rather damp, and food resources present include plant debris brought in by the water and especially bat guano. These organic deposits apparently constitute the staple food for the population of *P. taboa*, which tends to occur preferentially in this deepest region of the cave. The cave is in a zone with pronounced urbanization. The external vegetation has been significantly amended, currently only fragments of native vegetation being observed, primarily associated with rock outcrops, which are unfit for cultivation areas. Many outcrops have been altered or completely destroyed by mining activities. Dozens of caves have been targets of biospeleological inventories in the region where the Taboa cave is located. However, specimens of *P. taboa* were never found in other caves, indicating its apparent endemism to that cavity.

***Pseudonannolene leopoldoi* Iniesta & Ferreira 2014, new species**

(Figs. 3, 4, 14b)

Material examined. Holotype: 1 male (ISLA 4123) from Lapa do Zu cave (17°01'17.79"S 44°29'59.84"W), São João da Lagoa/MG, Brasil, 25/IX/2013. Collected by R. L. Ferreira.

Paratypes: 2 males (ISLA 4124, 4125) from Lapa do Zu cave, São João da Lagoa/MG, Brasil, 25/IX/2013. Collected by R. L. Ferreira. 3 females (ISLA 4126, 4127, 4128) from Lapa do Zu cave, São João da Lagoa/MG, Brasil, 25/IX/2013. Collected by R. L. Ferreira.

Etimology. The specific epithet is in honor of the biospeleologist Leopoldo Ferreira de Oliveira Bernardi for his contribution to our knowledge of Brazilian subterranean biology, especially cave mites.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 18–22 labral setae. Mandibles with 10–11 rows of pectinate lamellae (difficult to see). *P. leopoldoi* has an internal branch of the gonopod similar to those observed in the species *P. taboa*, besides the *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996b) and *P. microzoporos* (Mauriès 1987). The bifurcated form of the solenomere and the presence of a seminal spine on the internal apex of the branch are similar to what is observed in the species *P. taboa*, *P. chaimowiczi*, *P. imbiensis*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). About the pre-femoral process, that is rounded: its size is shorter when compared to the pre-femur, and similar to those occurring in the species *P. imbiensis*, *P. silvestri* e *P. tricolor* (Fontanetti 2002) and *P. spelaea* (Iniesta & Ferreira 2013a).

Description of adults. *Measurements:* Length from 48 up to 55 mm; maximum midbody diameter between 2.9 to 3.3 mm; body rings ranging between 62 to 64; length of antennae ranging from 3 to 3.2 mm (relation to diameter ranging 1 to 1.03); length of legs 2.3 to 2.5 mm (relation to diameter ranging 0.75 to 0.79); length of tarsal claw 0.14 to 0.16 mm (relation to diameter ranging 0.04 to 0.05).

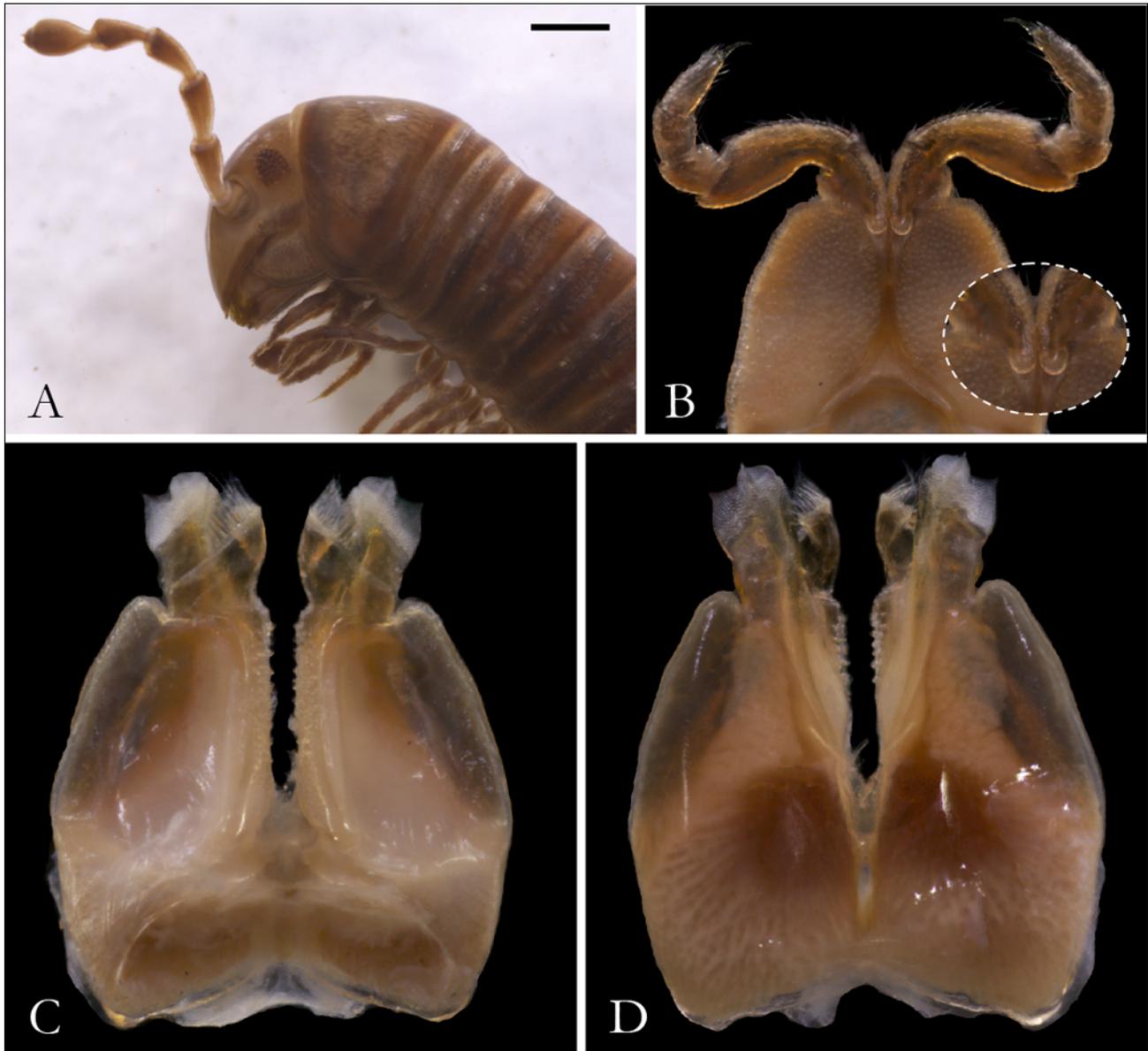


FIGURE 3. *Pseudonannolene leopoldoi* sp.n. (holotype, ISLA 4123): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 1 mm; b) 700 µm; c) 300 µm; d) 300 µm.

Color: Visualization after fixation in 70% alcohol. Reddish color, with the anterior region of each ring darker and posterior ranging from light brown to reddish.

Head (Fig. 3a): Head glabrous and pigmented. Labrum with a row containing 18–22 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10–11 rows of pectinate lamellae. Eyes with 28–36 ocelli arranged in 5 rows. Antennae pigmented and densely setose. First antennomere small, second and third similar, fourth, fifth and sixth lower and similar, being the last larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone ranging from light brown to reddish. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 3b): Coxae (**Cx**) larger; densely setose; square-shaped. Prefemur (**Prf**) with shorter oral process parallel (**P**) to the coxae. Bristles arranged on base of **P**.

Gonopod (Fig. 3c, d): Gonopod stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Presence of a process supporting a seta. Basal section (**Bs**) with width little larger than half of length; Basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) little shorter than the length of **Bs** and with width little larger than half of length. Solenomere (**S**)

elongated and with trunk wide; shorter squamous region; bifurcated, with an acute external tip and rounded internal. Internal branch (**Ib**) wide, starting right below the **Sh** line on **Bs**; like a shield of **S** and bristles not exceeding the **S**.

Notes on the natural history and habitat. The Lapa do Zu cave (Fig. 15c) comprises a limestone cave of considerable volume. It presents a single entry and receives organic material from the external environment, especially due to floods that occur during the rainy season. Thus, a large amount of plant debris is noticeable in various parts of the cave. In its distal portion, there is a large gap that leads to a drain (a small stream) that appears and disappears amid blocks of rock. This considerably increases the humidity of this portion of the cave. Individuals of *P. leopoldoi* were observed throughout the entire cave, and were associated with plant debris and deposits of bat guano. The fact that several specimens were associated with the large carcasses of a grasshopper (Caelifera), left in the cave by insectivorous bats (Fig. 3) is noteworthy. Such individuals, in many cases, clustered on one carcass, apparently feeding on fungus that developed in profusion in these carcasses.



FIGURE 4. Individuals of *Pseudonannolene leopoldoi* observed feeding on fungi that developed in carcass of grasshoppers.

***Pseudonannolene robsoni* Iniesta & Ferreira 2014, new species**

(Figs. 5, 6, 14c)

Material examined. Holotype: 1 male (ISLA 4080) from Gruta Água Limpa cave (20°27'06.99"S 45°39'10.58"W), Pains/MG, Brasil, 28/V/2009. Collected by R. Zampaulo.

Paratypes: 1 male (ISLA 4083) from Gruta do Bicho Desconhecido cave (20°24'20.04"S 45°35'24.70"W), Pains/MG, Brasil, 04/IV/2009; 1 male (ISLA 4084) from Gruta Loca dos Negros cave (20°24'05.99"S 45°39'49.49"W), Pains/MG, Brasil, 21/III/2009; 1 male (ISLA 4085) from Gruta Duas Bocas cave (20°22'07.15"S 45°41'10.10"W), Pains/MG, Brasil, 01/IV/2009. Collected by R. Zampaulo.

Other material examined. 1 male (ISLA 4079) from Gruta Zé da Fazenda cave (20°22'10.78"S 45°40'07.44"W, Pains/MG, Brasil, 09/III/2009; 1 male (ISLA 4081) from Gruta das Cerâmicas cave (20°24'15.21"S 45°35'51.15"W), Pains/MG, Brasil, 28/V/2009; 1 male (ISLA 4082) from Gruta Fumaça III cave (19°28'29.68"S 44°19'41.31"W), Pains/MG, Brasil, 12/II/2009; 1 male (ISLA 4086) from Gruta Tio Rafa II cave (20°24'47.04"S 45°39'52.73"W), Pains/MG, Brasil, 24/I/2009; 1 male (ISLA 4087) from Gruta Ninfeta de Baixo cave (20°20'18.69"S 45°36'55.67"W), Doresópolis/MG, Brasil, 25/I/2009; 1 male (ISLA 4088) from Gruta Ninfeta de Baixo cave (20°20'18.69"S 45°36'55.67"W), Doresópolis/MG, Brasil, 25/I/2009; 1 male (ISLA 4089) from Gruta Cinderela cave (20°26'45.51"S 45°35'59.83"W), Pains/MG, Brasil, 18/IX/2009; 1 male (ISLA 4090) from Gruta Dolina dos Angicos cave (20°25'05.92"S 45°40'43.74"W), Pains/MG, Brasil, 25/VI/2009; 1 male (ISLA 4091) from Gruta Capoeirão cave (20°21'55.34"S 45°40'15."W), Pains/MG, Brasil, 22/I/2009.

Etimology. The specific epithet is in honor of the biospeleologist Robson de Almeida Zampaulo for his contribution to our knowledge of Brazilian subterranean biology. It is noteworthy that the work of this biologist, developed in the region of Pains, has contributed significantly to the expansion of knowledge of the subterranean fauna of this important Brazilian karst region.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 19–23 labral setae. Mandibles with 10 rows of pectinate lamellae (difficult to see). *P. robsoni* has the internal branch of the gonopod slightly similar to a shield, being its medium-distal portion twisted over the solenomere, besides the presence of an elongated apical projection on the branch. The pre-femoral process is similar to that observed in the species *P. leopoldoi*, *P. imbiensis*, *P. silvestri*, *P. tricolor* e *P. spelaea* due to the reduced size compared to the pre-femur (Fontanetti 2002; Iniesta & Ferreira 2013a).

Description of adults. *Measurements:* Length from 70 up to 88 mm; maximum midbody diameter between 4.8 to 5.8 mm; body rings ranging between 65 to 70; length of antennae ranging from 5.2 to 5.8 mm (relation to diameter ranging 1.07 to 0.99); length of legs 3.2 to 4 mm (relation to diameter ranging 0.66 to 0.68); length of tarsal claw 0.16 to 0.32 mm (relation to diameter ranging 0.03 to 0.05).

Color: Visualization after fixation in 70% alcohol. Bicolor, with the anterior region of each ring darker and posterior reddish yellow.

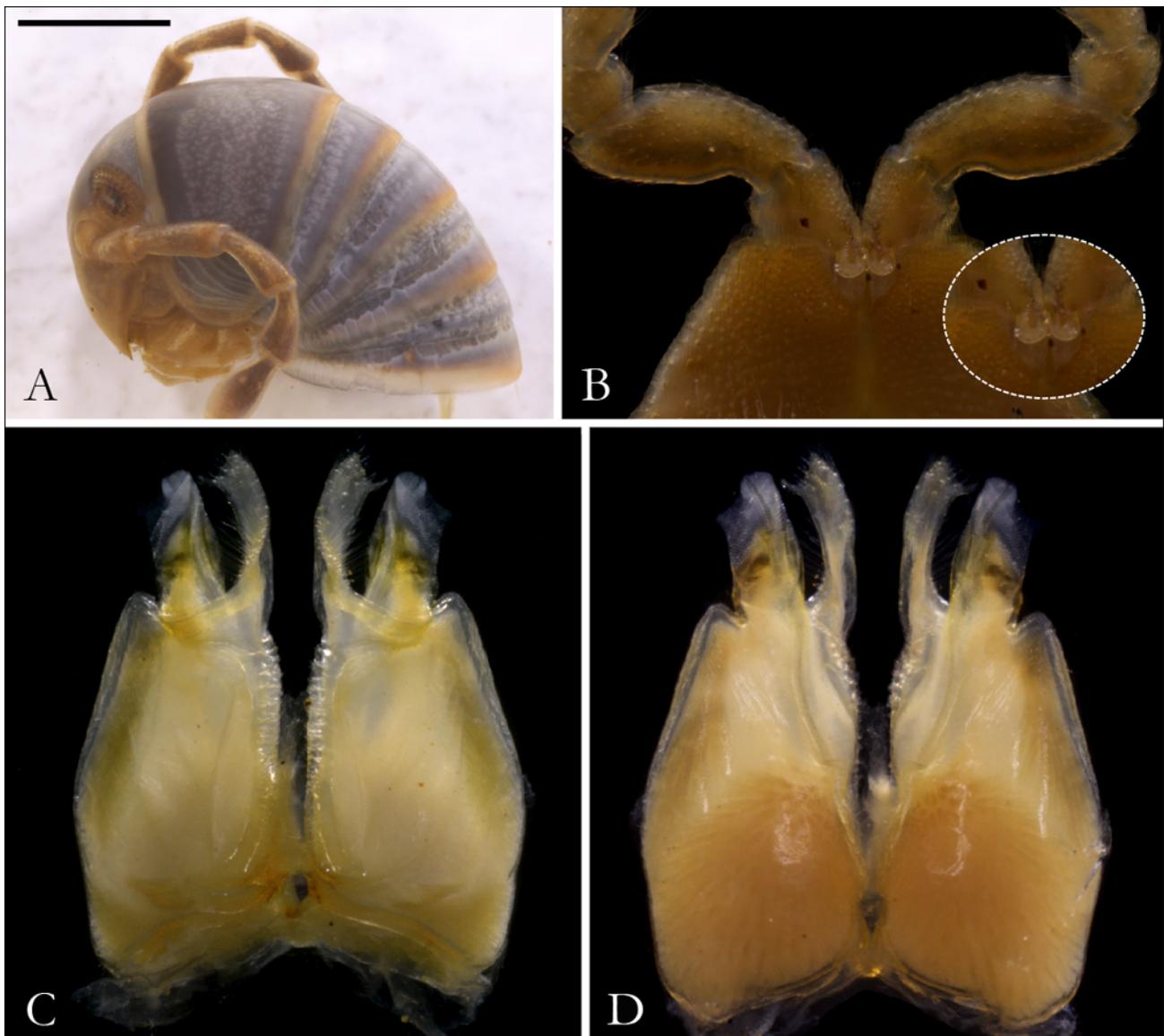


FIGURE 5. *Pseudonannolene robsoni* sp.n. (holotype, ISLA 4080): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 2 mm; b) 500 μ m; c) 700 μ m; d) 700 μ m.



FIGURE 6. Grouping of individuals of *Pseudonannolene robsoni* feeding on rodent feces.

Head (Fig. 5a): Head glabrous and pigmented. Labrum with a row containing 19–23 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10 rows of pectinate lamellae. Eyes with 36–43 ocelli arranged in 5 rows. Antennae pigmented and densely setose. First antennomere small, second and fourth similar, third longer, fifth and sixth little smaller than second and fourth, being the sixth larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone reddish yellow. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 5b): Coxae (**Cx**) larger; densely setose; square-shaped. Prefemur (**Prf**) with shorter oral process parallel (**P**) to the coxae. **P** with bristles arranged on base and base width equal to the distal region.

Gonopod (Fig. 5c, d): Gonopod short, stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (**Bs**) with width little larger than half of length; basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) slightly longer than wide and little smaller than half of length of **Bs**. Solenomere (**S**) trianguliform; elongated and little wide; trunk elongated and glabrous. Distal region squamous and slightly bifurcated, with an acute external tip and rounded internal with a seminal spine (**Sp**). Internal branch (**Ib**) with small base and a thin distal region, starting right below the **Sh** line on **Bs**. **Ib** projecting in order to interlace the **S** and exceeding his length. Longer bristles arranged on edge of **Ib**; presence of a swollen apical projection

Notes on the natural history and habitat. The karst region where populations of *P. robsoni* were found is considered an area of environmental, historical and economic importance. Furthermore, this region stands out in terms of harboring the greatest concentration of limestone caves known in Brazil at the present moment (over 1,200 recorded caves). However, since the 1960s the area has undergone intense changes due to mining activities, which

remove the limestone to produce cement and lime. Such activities are causing irreversible impacts on the landscape. In addition, it also highlights the intense changes suffered by the vegetation of the area (especially due to the expansion of agricultural activities), which has resulted in a rather fragmented landscape, where remaining vegetation is associated with only the tops of outcrops (inappropriate areas for human use). There are alterations in drainages near many caves, that in association with the loss of the original vegetation, may be leading to an intense change in import of organic resources to many caves (primarily dependent on imported organic resources from the external environment). The extraction of limestone has also often led to direct changes in the caves, ranging from partial destruction of conduits to the complete destruction of caves (Zampaulo 2010). This species is well distributed in caves in the region, although populations of every cave are often reduced. Exception is made for Brega cave (Fig. 15i), where numerous individuals were found associated with the guano of hematophagous bats (*Desmodus rotundus*) and rodent feces (Fig. 6).

***Pseudonannolene rosinei* Iniesta & Ferreira 2014, new species**

(Figs. 7, 14e)

Material examined. Holotype: 1 male (ISLA 4094) from Gruta Paranoá cave (20°21'57.13"S 45°40'11.15"W), Pains/MG, Brasil, 27/I/2009. Collected by R. Zampaulo.

Paratypes: 1 male (ISLA 4095) from Gruta Ninfeta III cave (20°20'17.78"S 45°36'55.90"W), Pains/MG, Brasil, 25/I/2009. Collected by R. Zampaulo; 1 female (ISLA 4121) from Gruta Ninfeta III cave (20°20'17.78"S 45°36'55.90"W), Pains/MG, Brasil, 25/I/2009. Collected by R. Zampaulo.

Etymology. The specific epithet is in honor to Rosinei de Oliveira, from the city of Pains. Rosinei has been actively contributing to increase knowledge of the subterranean fauna of the region Pains, which stands out on the national scene as a major hotspot of subterranean diversity.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 24 labral setae. Mandibles with 11 rows of pectinate lamellae. *P. rosinei* has the internal branch of the gonopod similar those observed in the species *P. taboa*, *P. leopoldoi*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996a) and *P. microzoporus* (Mauriès 1987). The squamous portion of the solenomere is bifurcated, as in *P. taboa*, *P. leopoldoi*, *P. chaimowiczi*, *P. imbiensis*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). The pre-femoral process is relatively larger than pre-femur, as in *P. taboa*, *P. rolamossa*, *P. gogo*, *P. ambuatinga*, *P. tocaiensis*, *P. mesai*, *P. leucocephalus*, *P. ophiulus*, *P. halophila*, *P. chaimowiczi* e *P. strinatii* (Fontanetti 2002; Iniesta & Ferreira 2013b; Iniesta & Ferreira 2013c).

Description of adults. *Measurements:* Length from 58 up to 68 mm; maximum midbody diameter between 3.96 to 4.48 mm; body rings ranging between 62 to 65; length of antennae ranging from 4.4 to 4.7 mm (relation to diameter ranging 1.04 to 1.11); length of legs 3.52 to 4 mm (relation to diameter ranging 0.88 to 0.89); length of tarsal claw 0.24 to 0.32 mm (relation to diameter ranging 0.06 to 0.07).

Color: Visualization after fixation in 70% alcohol. Bicolor, with the anterior region of each ring darker and posterior brownish yellow.

Head (Fig. 7a): Head glabrous and pigmented. Labrum with a row containing 24 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 11 rows of pectinate lamellae. Eyes with 27–30 ocelli arranged in 4 rows. Antennae pigmented and densely setose. First antennomere small, second, fourth, fifth and sixth similar, being the last larger. Third antennomere largest. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone brownish yellow. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 7b): Coxae (**Cx**) larger; densely setose; triangle-shaped. Prefemur (**Prf**) with shorter oral process parallel (**P**) to the coxae. **P** with bristles arranged on base and base width equal to the distal region.

Gonopod (Fig. 7c, d): Gonopod short, stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (**Bs**) with width little larger than half of length; basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) as long as wide

and little smaller than half of length of **Bs**. Solenomere (**S**) trianguliform; distal region squamous, bifurcated, with an acute external tip and rounded internal with a seminal spine (**Sp**). Internal branch (**Ib**) starting right below the **Sh** line on **Bs**. **Ib** like a shield and bristles exceeding the **S**.

Notes on the natural history and habitat. The species is also distributed in caves in the region of Pains (Fig. 15a), though it was never recorded in sympatry with *P. robsoni*. However, *P. rosineii* is less frequent, occurring in a few caves compared to *P. robsoni*. Their populations also tend to be small, which clearly demonstrates that populations of *P. rosineii* and *P. robsoni* also occur outside of caves, wherein the caves do not necessarily make up their main habitats. The caves where populations of *P. rosineii* were observed are small and generally dry, the main organic resource being guano of *Desmodus rotundus*.

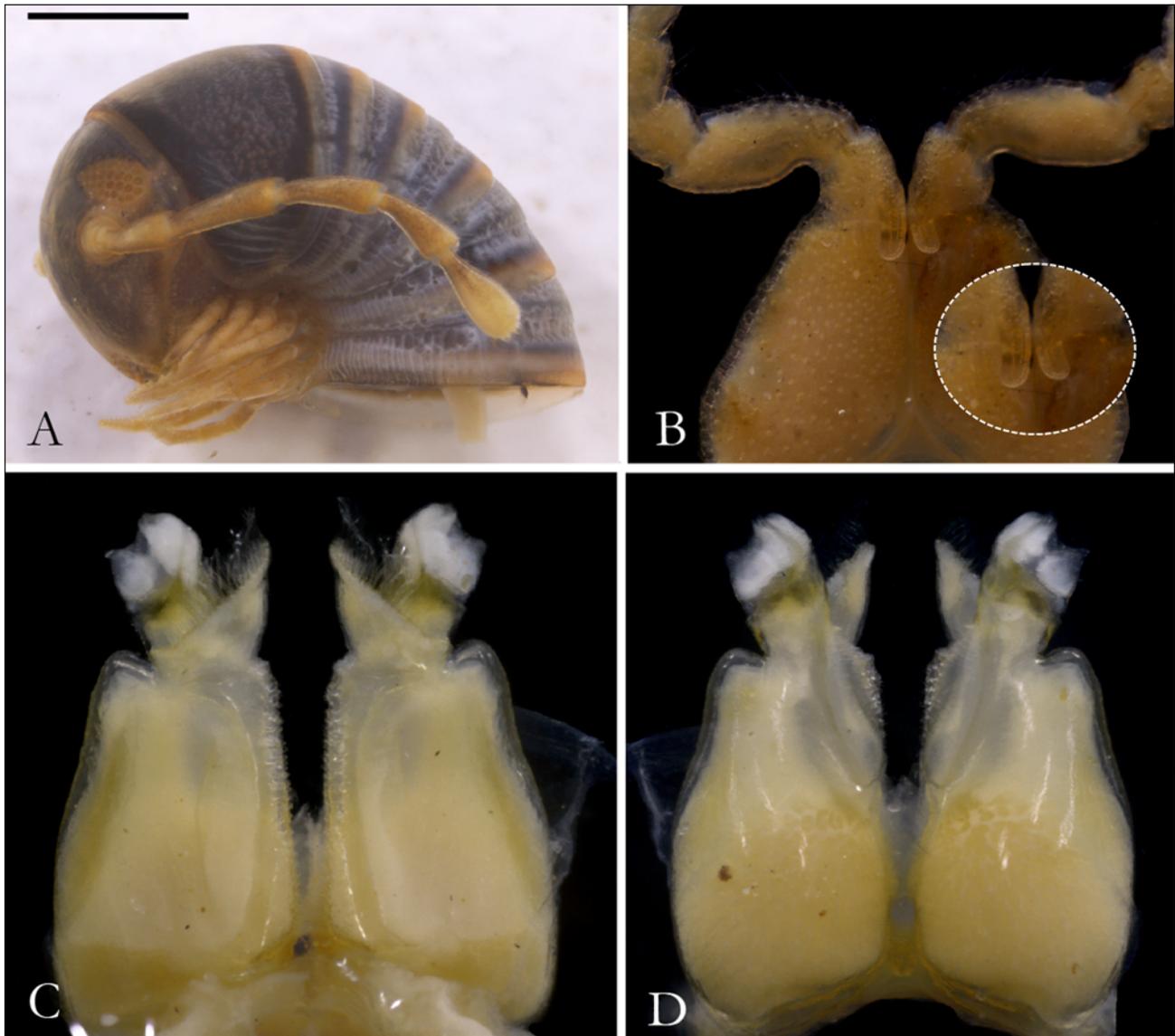


FIGURE 7. *Pseudonannolene rosineii* sp.n. (holotype, ISLA 4094): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 2 mm; b) 500 µm; c) 500 µm; d) 500 µm.

***Pseudonannolene marconii* Iniesta & Ferreira 2014, new species**

(Figs. 8, 14d)

Material examined. Holotype: 1 male (fragmented, ISLA 4106) from Gruta da Pedra Suspensa cave (15°23'31.42"S 39°44'18.41"W), Pau Brasil/BA, Brasil, 21/I/2005. Collected by R.L. Ferreira.

Etimology. The specific epithet is in honor of the biospeleologist Marconi Souza Silva for his contribution to

our knowledge of Brazilian subterranean biology. It is noteworthy that this biologist developed work in caves of the Brazilian Atlantic Forest and he has contributed significantly to the expansion of knowledge of the subterranean fauna of this biome.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 28 labral setae. Mandibles with 10 rows of pectinate lamellae (difficult to see). *P. marconii* also of the internal branch of gonopod like a shield, as those observed in the species *P. rosineii*, *P. taboa*, *P. leopoldoi*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996a; Fontanetti 1996b) and *P. microzoporus* (Mauriès 1987). However, the solenomere is slightly bifurcated, being similar to *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). A notable difference in the gonopod is the elongated shape, being the basal region with length two times longer than the width. The pre-femoral process is proportionally longer than pre-femur, as in the species *P. taboa*, *P. rosineii*, *P. imbiensis*, *P. silvestri* and *P. tricolor* (Fontanetti 2002).

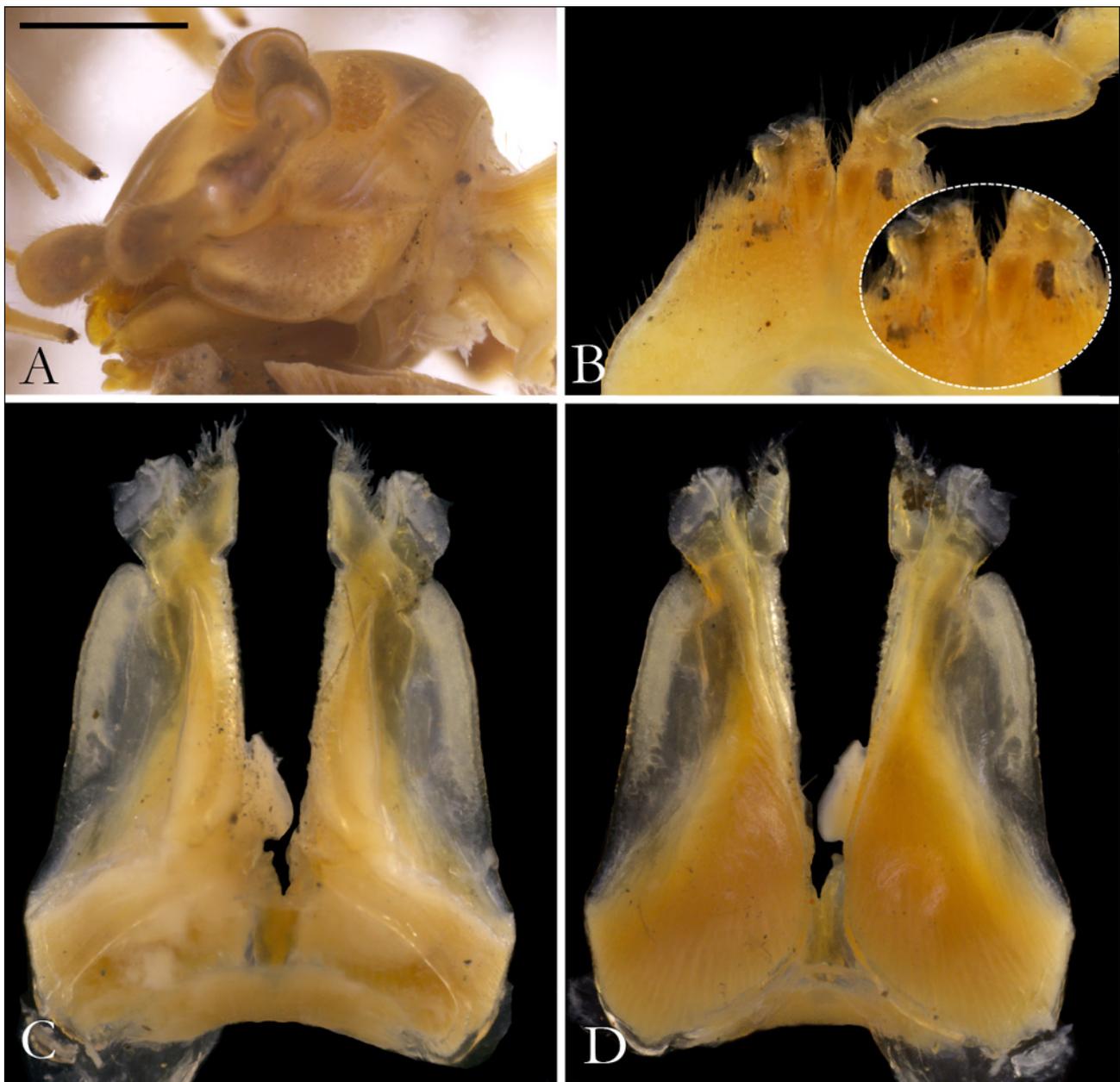


FIGURE 8. *Pseudonannolene marconii* sp.n. (holotype, ISLA 4106): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 1 mm; b) 500 µm; c) 500 µm; d) 500 µm.

Description of adults. *Measurements:* Length from 58 mm; maximum midbody diameter between 5.63 mm; 60 body rings; length of antennae ranging 3.32 mm (relation to diameter 0.59); length of legs 3.82 mm (relation to diameter 0.68); length of tarsal claw 0.24 mm (relation to diameter 0.04).

Color: Visualization after fixation in 70% alcohol. Bicolor, with the anterior region of each ring darker and posterior yellow reddish.

Head (Fig. 8a): Head glabrous and pigmented. Labrum with a row containing 28 labral setae, and above a group of 13 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10 rows of pectinate lamellae. Eyes with 34 ocelli arranged in 4 rows. Antennae pigmented and densely setose. First antennomere small, second and third similar, fourth, fifth and sixth lower and similar, being the last larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone yellow reddish. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 8b): Coxae (**Cx**) larger; densely setose; triangle-shaped. Prefemur (**Prf**) with elongated oral process parallel (**P**) to the coxae. Bristles arranged on base of **P** to the middle region; base wide and distal region short.

Gonopod (Fig. 8c, d): Gonopod elongated; thin and slightly sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (**Bs**) with length little larger than two times the width. Presence of a short process between the coxae supporting a seta. Basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) short and rounded. Distal region (**Ds**) as wide as long and little short than half of length of **Bs**. Solenomere (**S**) with a short trunk, distal portion squamous; slightly bifurcated, with an acute external tip and rounded internal. Internal branch (**Ib**) stout, wide, and like a shield of **S**. Bristles arranged in almost all edge and exceeding the **S**.

Notes on the natural history and habitat. The Pedra Suspensa cave is located in the carbonate group Rio Pardo, which occurs in the southeastern state of Bahia. This formation covers several caves; however, most of them are dry. Although the area is in Atlantic forest areas, deforestation is intense. The cave has a single entry and its conduit is almost entirely covered with guano produced by bats from different diets, among which stands out guano produced by *Desmodus rotundus*, a hematophagous species. The population of *P. marconii* is extremely large, dozens of specimens were observed throughout the cave, except for the area near the entrance. This condition differs from most species found in caves of Brazil, for which extremely large populations are not often observed. The species was found in the same karst region as *P. tricolor* (Trajano *et al.* 2000), though in different caves. The species was also found in Milagrosa (Fig. 15f) and California caves, located in the same area.

***Pseudonannolele xavieri* Iniesta & Ferreira 2014, new species** (Figs. 9, 14a)

Material examined. Holotype: 1 male (ISLA 4105) from Gruta da Fumaça cave (10°59'36.81"S 43°42'06.75"W), Iraquara/BA, Brasil, 07/I/2001. Collected by R. L. Ferreira.

Etimology. The specific epithet is in honor to the biospeleologist Xavier Prous for his contribution to our knowledge of Brazilian subterranean biology.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 24 + 2 labral setae. Mandibles with 10 rows of pectinate lamellae (difficult to see). *P. xavieri* has of the internal branch of the gonopod tumid and digitiform, similar to the observed in the species *P. saguassu* (Iniesta & Ferreira 2013b), *P. anapophysis* (Fontanetti 1996a) and *P. strinatii* (Mauriès 1974). Regarding the solenomere, it has a slightly bifurcated form, as in the species *P. marconii*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). However, differing from those species, the gonopod is short and rounded, but wider. The pre-femoral process is not elongated; however, its distal portion is wider and rounded, as in *P. leopoldoi*, *P. imbiensis*, *P. silvestri*, *P. tricolor* and *P. spelaea* (Fontanetti 2002; Iniesta & Ferreira 2013a).

Description of adults. *Measurements:* Length from 44 mm; maximum midbody diameter 3.6 mm; 60 body rings; length of antennae ranging from 3.6 mm (relation to diameter 1.07); length of legs 2.43 mm (relation to diameter ranging 0.72); length of tarsal claw 0.22 mm (relation to diameter 0.06).

Color: Visualization after fixation in 70% alcohol. Bicolor, with the anterior region of each ring darker and posterior whitish.

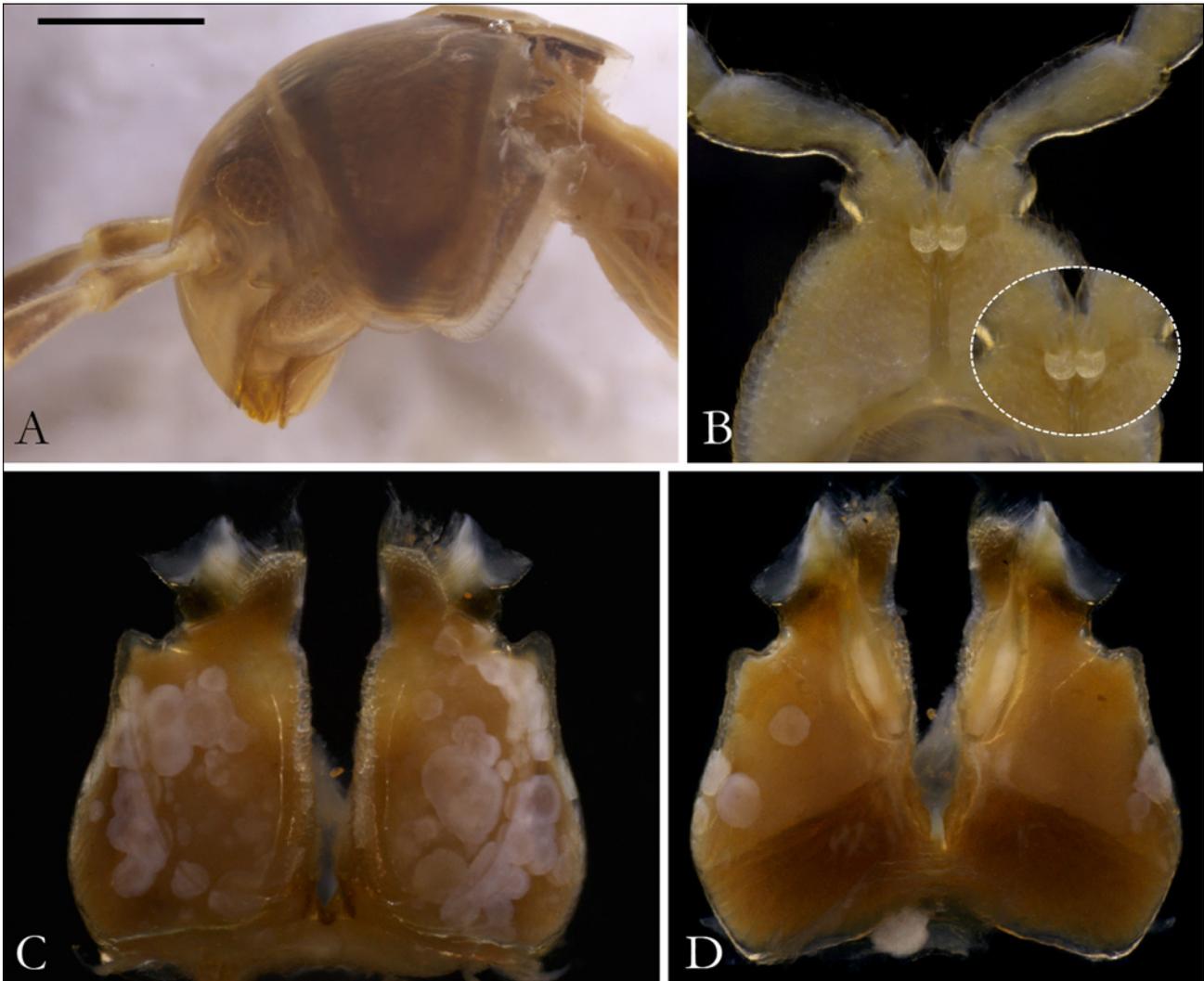


FIGURE 9. *Pseudonannolene xavieri* sp.n. (holotype, ISLA 4105): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 1 mm; b) 500 µm; c) 500 µm; d) 500 µm.

Head (Fig. 9a): Head glabrous and pigmented. Labrum with a row containing 24 + 2 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10 rows of pectinate lamellae. Eyes with 29 ocelli arranged in 4 rows. Antennae pigmented and densely setose. First antennomere small, second and third similar, fourth, fifth and sixth lower and similar, being the last larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone whitish. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 9b): Coxae (**Cx**) larger; densely setose; triangle-shaped. Prefemur (**Prf**) with elongated and rounded oral process parallel (**P**) to the coxae. Bristles arranged on base of **P**.

Gonopod (Fig. 9c, d): Gonopod short, stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Presence of a process supporting a seta. Basal section (**Bs**) with width little short than the length; basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) as long as wide and little shorter than half of the length of **Bs**. Solenomere (**S**) short but wide and with trunk wide; distal portion squamous; slightly bifurcated, with an acute external tip and rounded internal. Internal branch (**Ib**) short but swollen, starting right below the **Sh** line on **Bs**; bristles exceeding the **S** and arranged in middle-distal region.

Notes on the natural history and habitat. The Fumaça cave is located in the city of Iraquara (Bahia), as part of a diverse speleological scenario characterized by the presence of dozens of caves, some quite large. The epigeal environment is semi-arid (Caatinga) and quite urbanized, especially by the presence of several cultivated areas.

The cave is located in a region known as "Chapada Diamantina" comprising one of the most important centers of ecotourism in Brazil. Several caves in the area are open to visitors, regularly receiving hundreds of tourists throughout the year. This is the case of the Fumaça cave, which has much of its extension accessible to tourists. Among the changes that were aimed at improving the access of tourists into the cave are stairs, walkways (built by the relocation of cave soil), and railings. Such structures have changed some parts of the cave, certainly changing microhabitats. The main organic resources present consist of bat guano deposits, and the few individuals were observed always associated with this substrate. Individuals of this species also occur in other caves in the area, though always at low densities (Fig. 15h).

***Pseudonannolene caatinga* Iniesta & Ferreira 2014, new species**
(Figs. 10, 14f)

Material examined. Holotype: 1 male (ISLA 3627) from Toca dos Ossos cave (10°93'09"S 41°05'75"W), Ourulândia/BA, Brasil, 10/VI/2012. Collected by R.L. Ferreira.

Paratypes: 5 males (ISLA 3628, 3629, 3630, 3631, 3634); 3 females (3632, 3633, 3635) from Toca dos Ossos cave, Ourulândia/BA, Brasil, 10/VI/2012. Collected by R.L. Ferreira.

Etimology. Caatinga refers to a semi-arid biome that comprises the only exclusively Brazilian biome and in which the species was found. The word is formed by a combination of two words of origin of the Tupi (Brazil's indigenous language): Ka'a, meaning "forest" and Tinga meaning white. Therefore, caatinga means "White Forest".

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 20 labral setae. Mandibles with 7 rows of pectinate lamellae (difficult to see). *P. caatinga* has the internal branch of the gonopod as the observed in the species *P. rosineii*, *P. taboa*, *P. leopoldoi*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbirensis*, *P. tocaiensis* (Fontanetti 1996b) and *P. microzoporos* (Mauriès 1987). The solenomere is bifurcated, as in the species *P. rosinei*, *P. taboa*, *P. leopoldoi*, *P. chaimowiczi*, *P. imbirensis*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). The pre-femoral process is proportionally shorter than pre-femur, as observed in *P. xavieri*, *P. leopoldoi*, *P. spelaea*, *P. robsoni*, *P. imbirensis*, *P. silvestri* and *P. tricolor* (Fontanetti 2002; Iniesta & Ferreira 2013a).

Description of adults. *Measurements:* Length from 65 up to 72 mm; maximum midbody diameter between 3.2 to 4.64 mm; body rings ranging between 65 to 68; length of antennae ranging from 3.52 to 3.8 mm (relation to diameter ranging 0.81 to 1.1); length of legs 2.96 to 3.39 mm (relation to diameter ranging 0.73 to 0.93); length of tarsal claw 0.22 to 0.27 mm (relation to diameter ranging 0.06).

Color: Visualization after fixation in 70% alcohol. Bicolor, with the anterior region of each ring darker and posterior reddish brown.

Head (Fig. 10a): Head glabrous and pigmented. Labrum with a row containing 20 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 7 rows of pectinate lamellae. Eyes with 29–35 ocelli arranged in 5 rows. Antennae pigmented and densely setose. First antennomere small, second and third similar, fourth, fifth and sixth short, being the last larger. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone reddish brown. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 10b): Coxae (**Cx**) larger; densely setose; triangle-shaped. Prefemur (**Prf**) with elongated oral process parallel (**P**) to the coxae. **P** with bristles arranged on base and base width equal to the distal region.

Gonopod (Fig. 10c, d): Gonopod elongated, stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (**Bs**) with width little larger than half of length; Basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) short and rounded. Distal section (**Ds**) as long as wide and smaller than half of length of **Bs**. Solenomere (**S**) with distal region squamous, bifurcated, with an acute external tip and rounded internal with a seminal spine (**Sp**). Internal branch (**Ib**) starting right below the **Sh** line on **Bs**; short and wide, like a shield of **S**; bristles arranged in middle-distal region and exceeding the **S**.

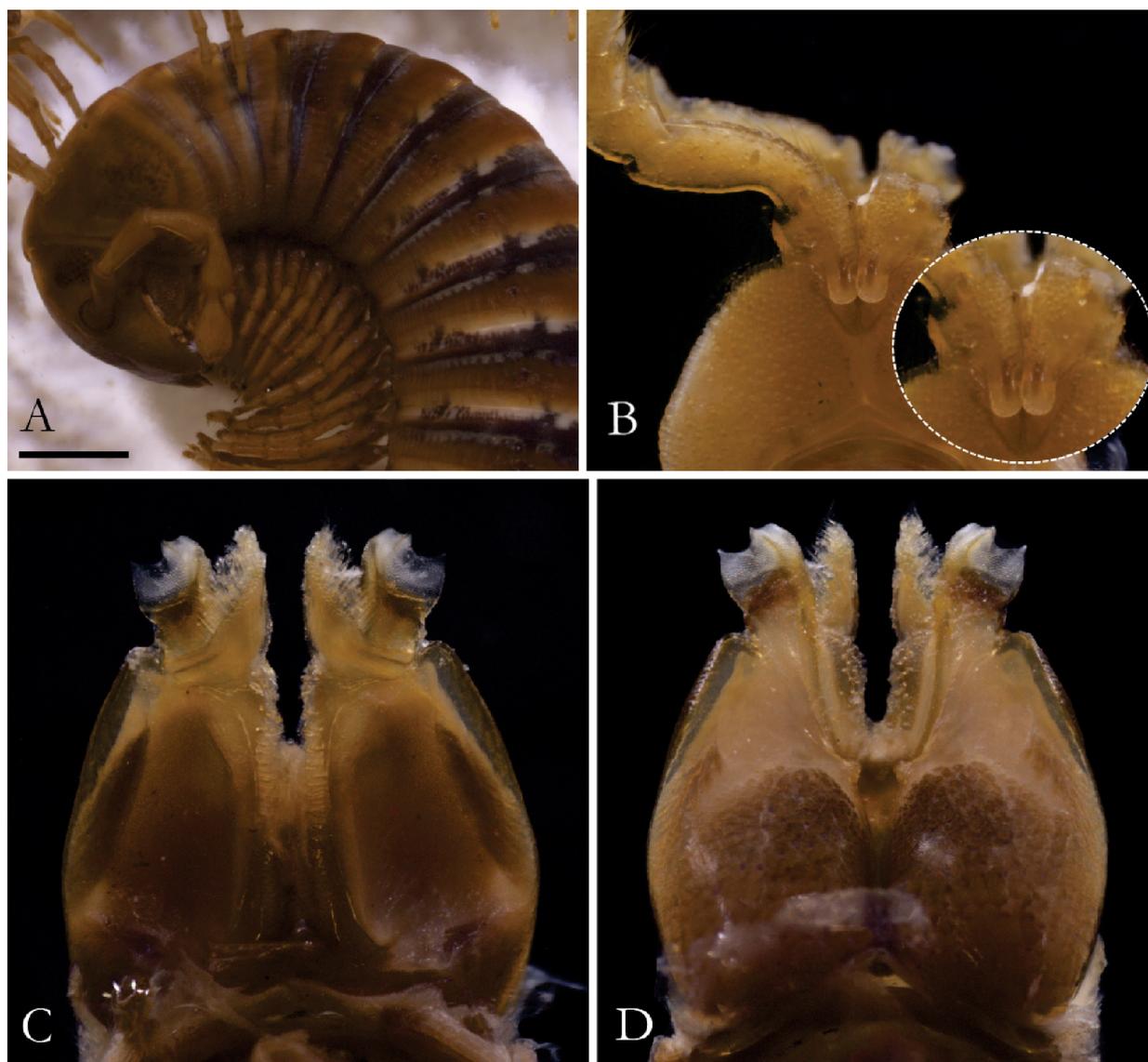


FIGURE 10. *Pseudonannolele caatinga* sp.n. (holotype, ISLA 3628): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 1 mm; b) 350 μ m; c) 700 μ m; d) 700 μ m.

Notes on the natural history and habitat. The cave (Fig. 15g) is extensive (more than 15 km long), predominantly dry, and associated with quite metamorphosed carbonates of the Una group. This cave has extremely labyrinthine architecture, presenting very heterogeneous conditions along its length. Specimens of *P. caatinga* were found only in more humid regions of the cave, which comprise few areas. Migrations of species between these areas probably occur during rainy periods, in which the cave becomes wetter. Food resources for species consist primarily of plant debris brought by the wind (that preferentially deposited near skylights) and bat guano. The outer region has undergone profound impacts of mining activities, which have intensified in the last decade. Numerous changes resulting from this activity are observed inside the cave, such as deposition of blocks, siltation and clogging of entrances, where there was mining over the cave. Fortunately, this mining is currently inactive. The population of *P. caatinga* can be considered large because in some places dozens of individuals can be seen.

***Pseudonannolene erikae* Iniesta & Ferreira 2014, new species**

(Fig. 11)

Material examined. Holotype: 1 male (ISLA 4107) from Gruta Rei do Mato cave (19°29'44.15"S 44°16'51.66"W), Sete Lagoas/MG, Brasil, 04/XI/2011. Collected by R. L. Ferreira.

Paratype: 1 male (ISLA 4108) and 1 female (ISLA 4109) from Gruta Rei do Mato cave, Sete Lagoas/MG, Brasil, 04/XI/2011. Collected by R. L. Ferreira.

Etimology. The specific epithet is in honor of the biospeleologist Érika Linzi Silva Taylor for her contribution to our knowledge of Brazilian subterranean biology, mainly cave microbiology.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 20–22 labral setae. Mandibles with 10–11 rows of pectinate lamellae (difficult to see). *P. erikae* has a notably modified gonopod in comparison to other Brazilian species. The internal branch diagonally directed markedly differs from other Brazilian species. Such structure could eventually represent a modification from a shield form to a branch, as in the species *P. rosineii*, *P. taboa*, *P. leopoldoi*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996a; Fontanetti 1996b) and *P. microzoporus* (Mauriès 1987). The triangle-shaped solenomere is similar to *P. ambuatinga* and *P. saguassu* (Iniesta & Ferreira 2013b). The pre-femoral process also is highly modified, having an irregular and concave morphology, not similar to any known Brazilian species.

Description of adults. *Measurements:* Length from 64 up to 69 mm; maximum midbody diameter between 4.2 to 4.6 mm; body rings ranging between 61 to 63; length of antennae ranging from 4.7 to 4.9 mm (relation to diameter ranging 1.06 to 1.12); length of legs 2.5 to 2.8 mm (relation to diameter ranging 0.43 to 0.6); length of tarsal claw 0.14 to 0.22 mm (relation to diameter ranging 0.03 to 0.05).

Color: Visualization after fixation in 70% alcohol. Grayish color, with the anterior region of each ring clearer.

Head (Fig. 11a): Head glabrous and pigmented. Labrum with a row containing 20–22 labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 10–11 rows of pectinate lamellae. Eyes with 28–30 ocelli arranged in 4 rows. Antennae pigmented and densely setose. First antennomere small, second, fourth, fifth and sixth similar, being the last larger. Third largest. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus, except for a male paratype that showed an irregular suture in pro-mentum.

Trunk: Body pigmented. Prozone and metazone grayish, with a posterior region clearer. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 11b): Coxae (Cx) triangle-shaped, larger than remaining legs, and densely setose. Prefemur (Prf) with an irregular and oval process (P). Bristles arranged on base of P.

Gonopod (Fig. 11c, d): Gonopod complex, stout and sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (Bs) with width little larger than half of length; Basiconic bristles arranged in rows along the entire the base of gonopod. No shoulder. Distal section (Ds) little wider than half of length and half of length of Bs. Solenomere (S) curved, elongated, trunk evident and wide; distal region short, rounded, squamous and of irregular shape. Seminal groove from the base of solenomere with the other branch. Seminal spine (Sp) on apical portion. Internal branch (Ib) starting right below the Sh line on Bs; thin and of divergent direction when compared with S.

Notes on the natural history and habitat. The Rei do Mato cave (Fig. 15b) comprises one of the most important Brazilian tourist caves. This cave is distinguished by a great wealth of formations (speleothems), which contribute great scenic beauty to this cavity. This region has hundreds of caves, considered one of the regions of greatest speleological importance in the country. Rei do Mato cave presents numerous infrastructures that have been installed to facilitate the access of tourists to its innermost portions. However, due to the rugged topography of the cavity, the building of such structures has resulted in severe changes to this cave. In almost all its length, a large metal footbridge with handrails and stairs can be seen. In addition, the cave has an electric lighting system, installed for more than two decades. Such a system creates a photoperiod in the cavity, leading to serious alterations of microclimatic and trophic conditions. Thus, the densities of many species are often low, as in the case of *P. erikae*. The few individuals observed were feeding in rare guano deposits, since the illumination of the cavity ends up scaring bats. Although the epigeal environment is severely altered (for agricultural and mining activities), the cavity is legally protected, being part of a conservation unit (Natural Monument Rei do Mato).



FIGURE 11. *Pseudonannolene erikae* sp.n. (holotype, ISLA 4107): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 2 mm; b) 700 µm; c) 700 µm; d) 700 µm.

***Pseudonannolene longissima* Iniesta & Ferreira 2014, new species**

(Fig. 12)

Material examined. Holotype: 1 male (ISLA 4110) from Gruta Rei do Mato cave (19°29'44.15"S 44°16'51.66"W), Sete Lagoas/MG, Brasil, 18/I/2001. Collected by R. L. Ferreira.

Etimology. The epithet is derived from the Latin "longus", which means something very distant. This name refers to the elongated and thin body shape of the specimen.

Comparative diagnosis. Body and eyes pigmented. Labrum with 6 supralabral setae; 19? labral setae. Mandibles with 9 rows of pectinate lamellae (difficult to see). *P. longissima* has the internal branch of the gonopod like a shield of the solenomere, being similar to *P. caatinga*, *P. rosinei*, *P. taboa*, *P. leopoldoi*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996a; Fontanetti 1996b) and *P. microzoporus* (Mauriès 1987). The solenomere also shows a bifurcated squamous region, with a seminal spineon located in the internal apex of the branch, similarly to the species *P. caatinga*, *P. rosinei*, *P. taboa*, *P. leopoldoi*, *P. chaimowiczi*, *P. imbiensis*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor*

(Brölemann 1902). The pre-femoral process is rounded and lower positioned when compared to the pre-femur, as in *P. rolamossa*, *P. gogo*, *P. ambuatinga*, *P. tocaiensis*, *P. mesai*, *P. leucocephalus*, *P. ophiulus*, *P. halophila*, *P. chaimowiczi* and *P. strinatii* (Fontanetti 2002).

Description of adults. *Measurements:* Length from 78 mm; maximum midbody diameter 2.93 mm; 65 body rings; length of antennae 3.2 mm (relation to diameter 1.09); length of legs 2.8 mm (relation to diameter 0.95); length of tarsal claw 0.12 mm (relation to diameter 0.04).

Color: Visualization after fixation in 70% alcohol. Specimen in recent post-moult. Whitish color, with some dark zone in dorsal region in each body ring.

Head (Fig. 12a): Head glabrous and slightly pigmented. Labrum with a row containing 19? labral setae, and above a row with 6 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 9 rows of pectinate lamellae. Eyes with 31 ocelli arranged in 4 rows. Antennae little pigmented and densely setose. First antennomere small, second, fourth, fifth and sixth similar, being the last larger. Third largest. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus

Trunk: Prozone and metazone whitish, with a dorsal region darker in some portions. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 12b): Coxae (Cx) triangle-shaped, larger than remaining legs, and densely setose. Prefemur (Prf) with a elongated and rounded process (P). Bristles arranged on base of P.

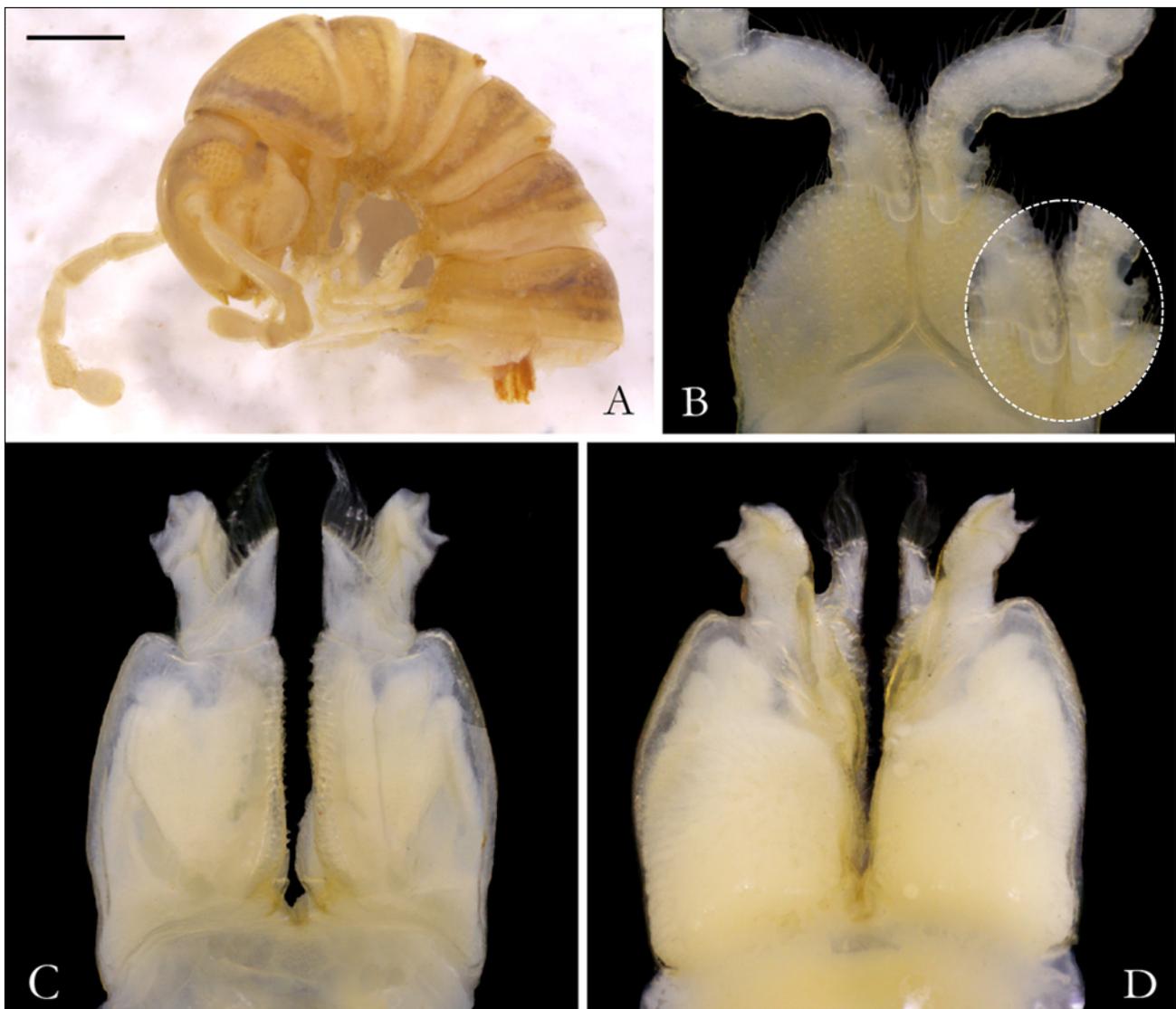


FIGURE 12. *Pseudonannolele longissima* sp.n. (holotype, ISLA 4110): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 500 μ m; b) 250 μ m; c) 250 μ m; d) 300 μ m.

Gonopod (Fig. 12c, d): Gonopod short, stout and little sclerified. Coxae reduced; glabrous and adhered to basal region of gonopod. Basal section (**Bs**) with length two times little larger than width; Basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) short and rounded. Distal section (**Ds**) with width little longer than half of length and of **Bs**. Solenomere (**S**) with trunk elongated; distal region rounded and squamous, slightly bifurcated; with an acute and short external tip and wide internal with an elongated seminal spine (**Sp**). Internal branch (**Ib**) wide and starting right below the **Sh** line on **Bs**; slightly like a shield of **S**; elongated bristles arranged in middle-distal region and exceeding the **S**.

Notes on the natural history and habitat. The single specimen of this species was found in the Rei do Mato cave (Fig. 15b) (Sete Lagoas, MG), the same cave as the type material of *P. erikae*. It is noteworthy that several collections have been conducted in this cave, so that this single observation can show that: *i*) the species has low population densities, encounters being rare or alternatively *ii*) the main habitat of this species does not include caves and the single individual collected entered accidentally in this environment. Since no systematic collections were made in the epigeal environment of the area, doubt remains about these hypotheses.

***Pseudonannolene fontanettiae* Iniesta & Ferreira 2014, new species**

(Fig. 13, 14h)

Material examined. Holotype: 1 male (ISLA 5033) from Casa da Pedra cave (21°08'23.92"S 44°11'11.43"W), Tiradentes/MG, Brasil, 25/II/2014. Collected by R. L. Ferreira.

Paratypes: 1 male (ISLA 5034) from Casa da Pedra cave (21°08'23.92"S 44°11'11.43"W), Tiradentes/MG, Brasil, 25/II/2014. Collected by R. L. Ferreira; 1 female (ISLA 5035) from Casa da Pedra cave (21°08'23.92"S 44°11'11.43"W), Tiradentes/MG, Brasil, 25/II/2014. Collected by R. L. Ferreira

Etymology. The specific epithet is in honor to the biologist Carmen Silvia Fontanetti Christofolletti for her important contribution to our knowledge of the genus *Pseudonannolene* in Brazil.

Comparative diagnosis. Body and eyes pigmented. Labrum with 5–7 supralabral setae; 22 labral setae. Mandibles with 11 rows of pectinate lamellae (difficult to see). *P. fontanettiae* has the internal branch of the gonopod like a shield, as observed in the species *P. caatinga*, *P. rosinei*, *P. taboa*, *P. leopoldoi*, *P. longissima*, *P. ambuatinga* (Iniesta & Ferreira 2013b), *P. spelaea* (Iniesta & Ferreira 2013a), *P. rolamossa*, *P. gogo* (Iniesta & Ferreira 2013c), *P. chaimowiczi*, *P. imbiensis*, *P. tocaiensis* (Fontanetti 1996a; Fontanetti 1996b) and *P. microzoporos* (Mauriès 1987). As in the species *P. robsoni*, *P. fontanettiae* shows an apical projection on the internal branch, however shorter than in the former. The solenomere has a short squamous bifurcated region, with a seminal spine on the internal part of the apex, being similar to *P. caatinga*, *P. rosinei*, *P. taboa*, *P. leopoldoi*, *P. longissima*, *P. chaimowiczi*, *P. imbiensis*, *P. rolamossa*, *P. gogo*, *P. anapophysis* (Fontanetti 1996a), *P. strinatii* (Mauriès 1974) and *P. tricolor* (Brölemann 1902). The pre-femoral process is rounded and little lower positioned than the pre-femur, as found in innumerable species of the genus (Fontanetti 2002).

Description of adults. *Measurements:* Length from 76–81 mm; maximum midbody diameter between 3.84 to 4.12 mm; 67 to 69 body rings; length of antennae ranging 4.86 to 4.96 mm (relation to diameter 1.2 to 1.26); length of legs 2.96 to 3.01 mm (relation to diameter 0.73 to 0.77); length of tarsal claw 0.17 to 0.20 mm (relation to diameter 0.04 to 0.05).

Color: Bicolor, with the anterior region of each ring darker and posterior whitish.

Head (Fig. 13a): Head glabrous and slightly pigmented. Region of labrum with three labral teeth; a row with 22 labral setae, and above a row with 5–7 supralabral setae. Mandibles slightly pigmented, with 2 external teeth, 4 internal teeth and 11 rows of pectinate lamellae. Eyes with 31 ocelli arranged in 4 rows. Antennae little pigmented and densely setose. First antennomere small, second, fourth, fifth and sixth similar, being the last larger. Third largest. Presence of basiconic sensilla in latter edge of fifth and sixth antennomere. Gnatochilarium typical of the genus.

Trunk: Body pigmented. Prozone dark and metazone whitish. Lateral region of each ring with transverse striae. Telson, anal shield and anal valve pigmented.

First male pair of legs (Fig. 13b): Coxae (**Cx**) triangle-shaped, larger than remaining legs, and densely setose. Prefemur (**Prf**) with an elongated and rounded process (**P**). Bristles arranged on base of **P**.

Gonopod (Fig. 13c, d): Gonopod short, stout and sclerified. Coxae reduced; glabrous and adhered to basal

region of gonopod. Basal section (**Bs**) about 2 times longer than wide; basiconic bristles arranged in rows along the entire the base of gonopod. Shoulder (**Sh**) evident and rounded. Distal section (**Ds**) little wider than half of length and his length is similar to half of **Bs**. Solenomere (**S**) elongated; trunk elongated and glabrous. A little distal region squamous and bifurcated, with an acute external tip and rounded internal with a seminal spine (**Sp**). Internal branch (**Ib**) elongated, starting right below the **Sh** line on **Bs**. **Ib** like a shield of **S**; with bristles arranged on edge of **Ib** and presence of a swollen but short apical projection.

Notes on the natural history and habitat. The Casa da Pedra cave (Fig. 15d) has a considerable extension in comparison to other nearby caves. It has a labyrinthine aspect with multiple entrances. A large amount of organic matter, especially leaf litter, is carried in from outside. Another important organic resource found was guano produced by frugivorous bats. The cave has no drainage, being relatively dry. It is located within the area of a mining company, and is regularly visited by tourists. Hence, there are some impacts arising from this activity, such as graffiti and small wooden bridges installed in some conduits. The surrounding vegetation has been significantly modified, being associated mainly to the limestone outcrop.

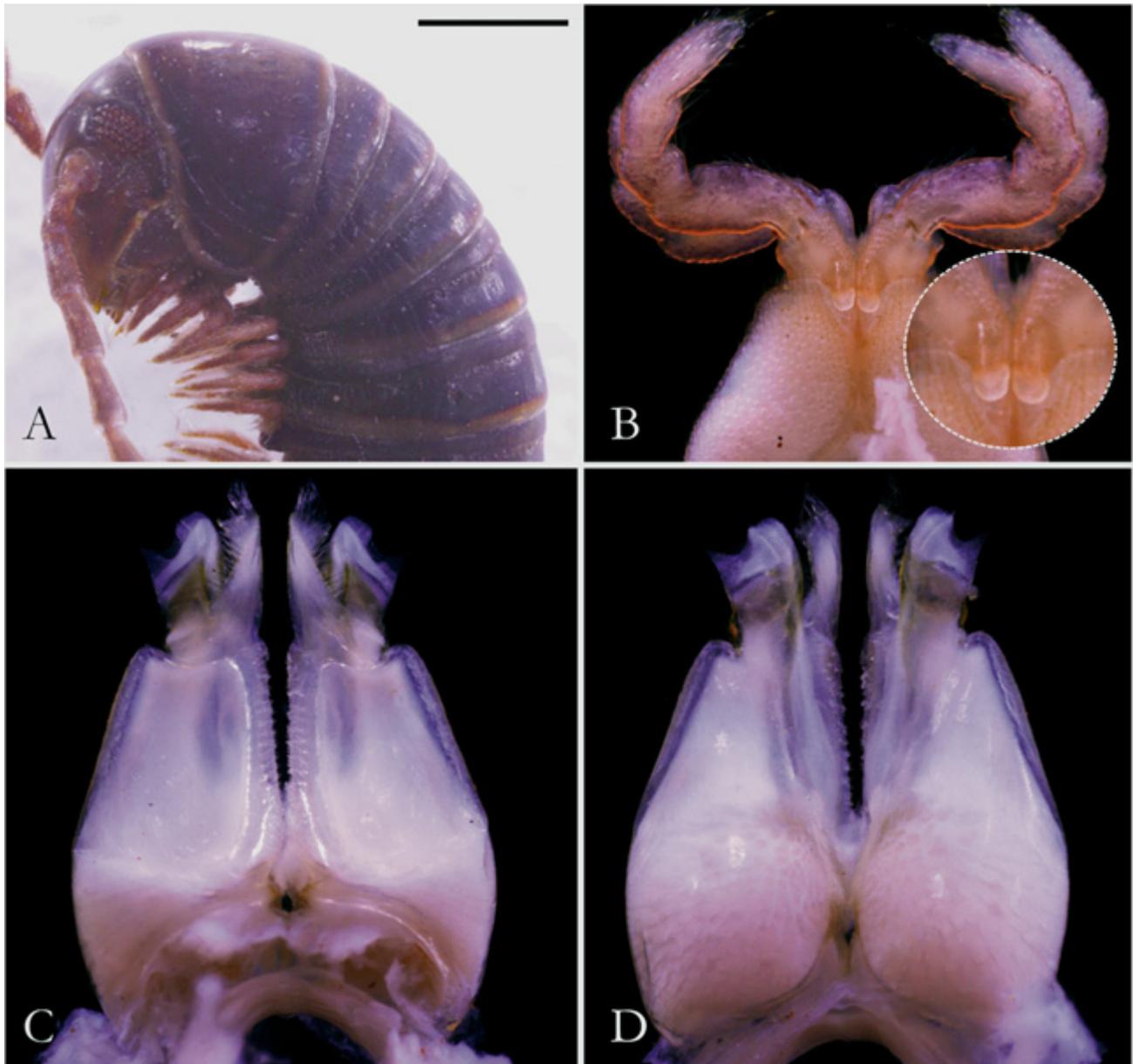


FIGURE 13. *Pseudonannolene fontanettiae* sp.n. (holotype, ISLA 5033): a) Anterior region; b) Pre-femoral process; c) Caudal view of gonopod; d) Oral view of gonopod. **Scale bar:** a) 2 mm; b) 700 µm; c) 700 µm; d) 700 µm.



FIGURE 14. Live specimens: a) *Pseudonannolene xavieri* sp.n.; b) *Pseudonannolene leopoldoi* sp.n.; c) *Pseudonannolene robsoni* sp.n.; d) *Pseudonannolene marconii* sp.n.; e) *Pseudonannolene rosineii* sp.n.; f) *Pseudonannolene caatinga* sp.n.; g) *Pseudonannolene taboa* sp.n.; h) *Pseudonannolene fontanettiae* sp.n.

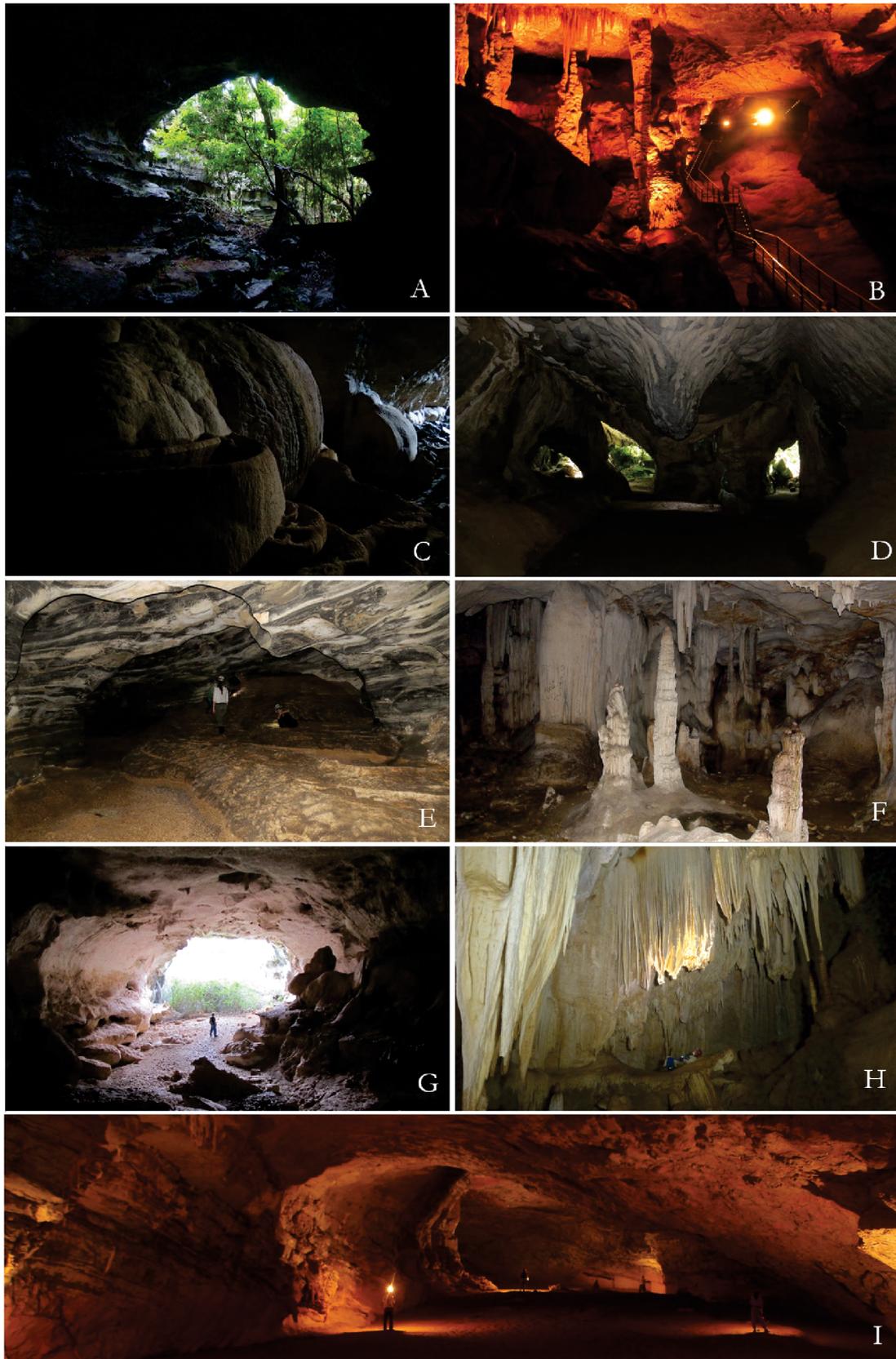


FIGURE 15. Caves where the specimens were found: a) Paranoá cave (*Prosineii* sp.n.); b) Rei do Mato cave (*P. erikae* sp.n. and *P. longisima* sp.n.); c) Lapa do Zu cave (*P. leopoldoi* sp.n.); d) Casa da Pedra cave (*P. fontanettiae* sp.n.); e) Taboa cave (*P. taboa* sp.n.); f) Milagrosa cave *P. marconii* sp.n.); g) Toca dos Ossos cave (*P. caatinga* sp.n.); h) Lapa do Baio cave (*P. xavieri* sp.n.); i) Brega cave (*P. robsoni* sp.n.).

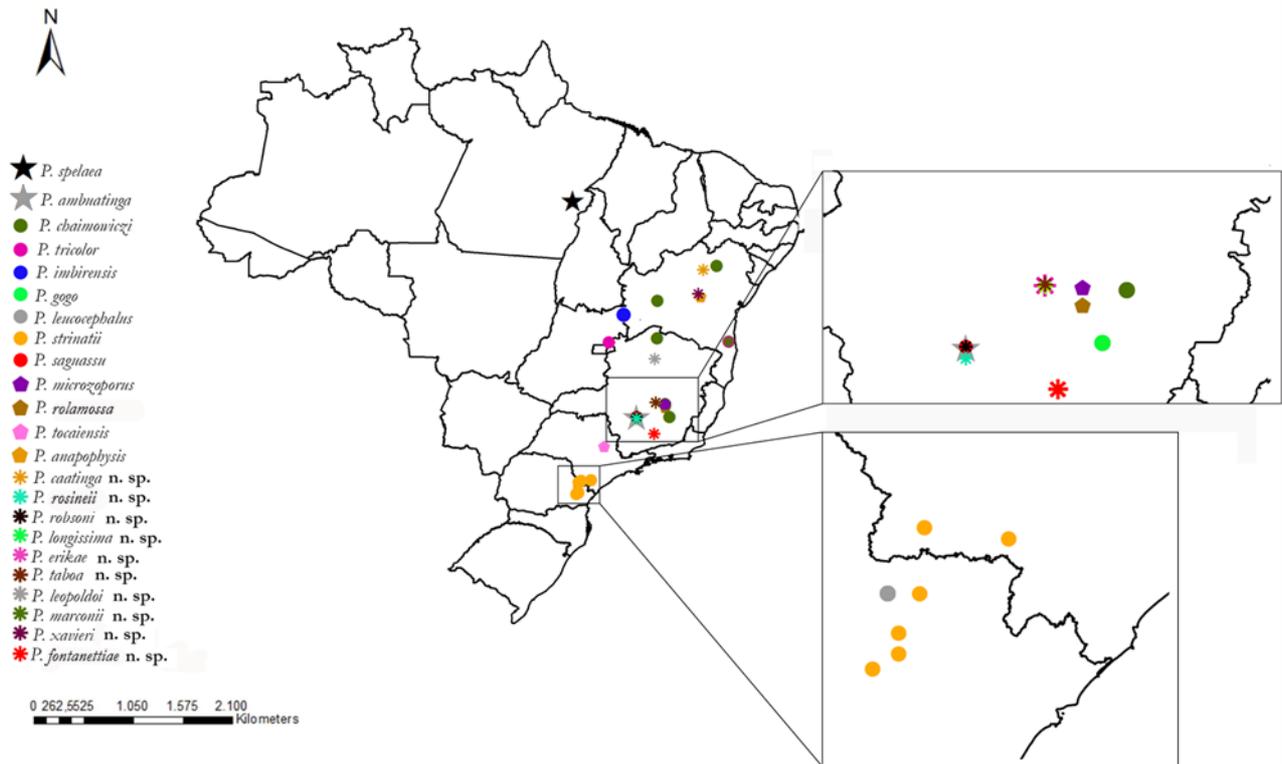


FIGURE 16. Distribution map of the cave species of the genus *Pseudonannolene* in Brazil. The species marked with stars are troglobite, while the remaining troglophiles.

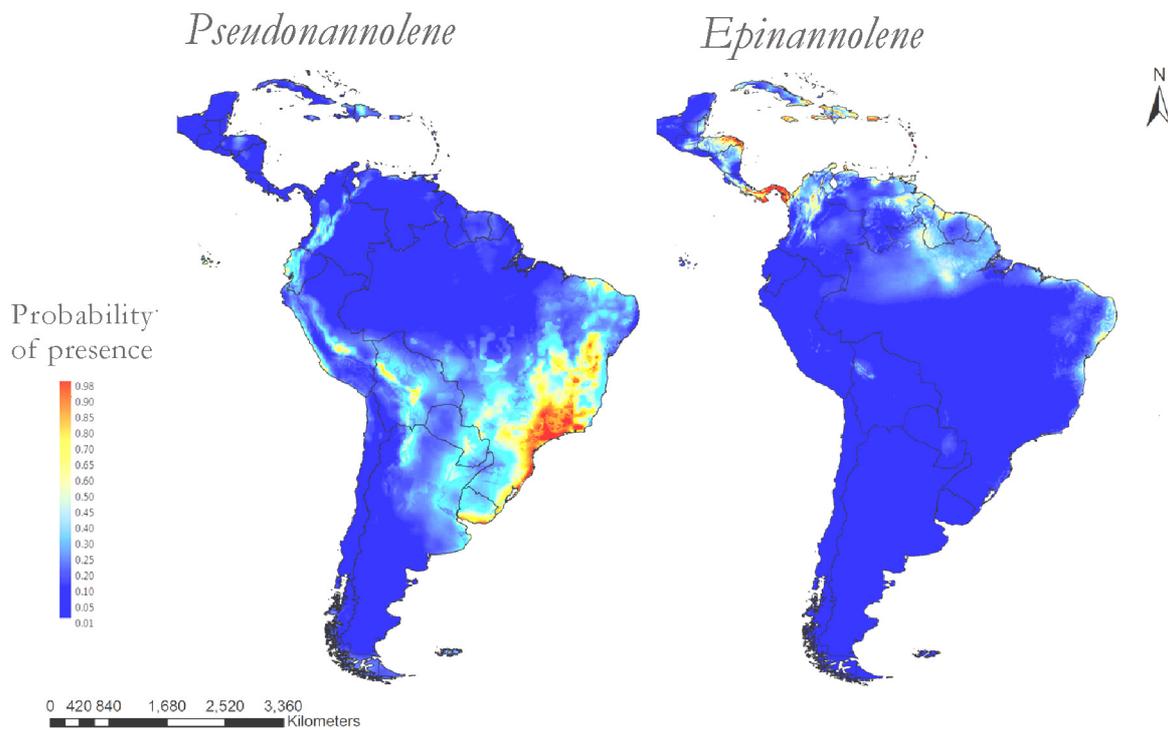


FIGURE 17. Potential distribution map of Neotropical species of *Pseudonannolene* and *Epinannolene*.

Discussion

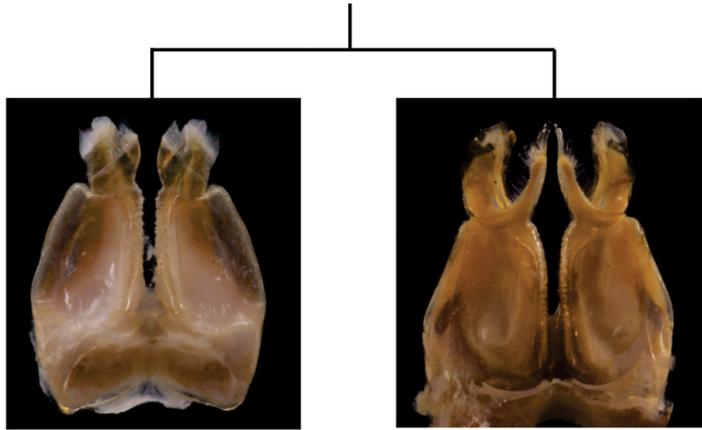
Synopsis of the cave-dwelling species of *Pseudonannolene* from Brazil

Currently there are 23 species of *Pseudonannolene* with records from Brazilian caves (Trajano *et al.* 2000; Iniesta & Ferreira 2013a; Iniesta & Ferreira 2013b; Iniesta & Ferreira 2013c). Two of these species are considered troglobites: *P. spelaea* and *P. ambuatinga* (Iniesta & Ferreira 2013a; Iniesta & Ferreira 2013b). The other species are considered troglophiles that have established populations in both the cave environment and in external areas. It stands out that some species, known only by the holotype, were considered troglophiles, although we cannot claim this status. This is the case for the species *P. saguassu* and *P. longissima*, both collected near cave entrances (Iniesta & Ferreira 2013b). The cave-dwelling species currently known for Brazil are listed below:

- Pseudonannolene spelaea* Iniesta & Ferreira, 2013: Caves from Pará state
- Pseudonannolene ambuatinga* Iniesta & Ferreira, 2013: Caves from Minas Gerais state
- Pseudonannolene saguassu* Iniesta & Ferreira, 2013: Caves from Minas Gerais state
- Pseudonannolene rolamossa* Iniesta & Ferreira, 2013: Caves from Minas Gerais state
- Pseudonannolene gogo* Iniesta & Ferreira, 2013: Caves from Minas Gerais state
- Pseudonannolene anapophysis* Fontanetti, 1996: Caves from Bahia state
- Pseudonannolene chaimowiczi* Fontanetti, 1996: Caves from Minas Gerais and Bahia states
- Pseudonannolene imbiensis* Fontanetti, 1996: Caves from Goiás state
- Pseudonannolene leucocephalus* Schubart, 1944: Caves from Paraná state
- Pseudonannolene microzoporus* Mauriès, 1987: Caves from Minas Gerais state
- Pseudonannolene strinatii* Mauriès, 1974: Caves from São Paulo and Paraná states
- Pseudonannolene tocaiensis* Fontanetti, 1996: Caves from São Paulo state
- Pseudonannolene tricolor* Brölemann, 1902: Caves from São Paulo, Bahia and Goiás states
- Pseudonannolene taboa* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene leopoldoi* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene robsoni* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene rosineii* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene marconii* **n. sp.**: Caves from Bahia state
- Pseudonannolene xavieri* **n. sp.**: Caves from Bahia state
- Pseudonannolene caatinga* **n. sp.**: Caves from Bahia state
- Pseudonannolene erikae* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene longissima* **n. sp.**: Caves from Minas Gerais state
- Pseudonannolene fontanettiae* **n. sp.**: Caves from Minas Gerais state

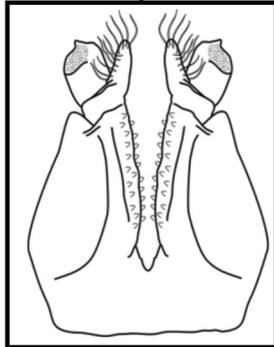
Pictorial key to Brazilian cave-dwelling species

The drawings were made based on original descriptions and other figures (Schubart 1944; Mauriès 1974, 1984; Brölemann 1902; Fontanetti 1996a, 1996b; Iniesta & Ferreira 2013a, 2013b, 2013c). For this pictorial key we used only the gonopods in caudal view. The same image was sometimes used in some steps of the key only to show some special trait.



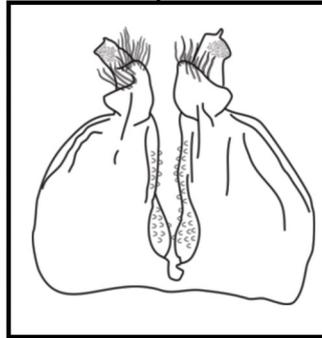
Solenomere bifurcated
(two little tips are
visible). Go to Part II.

Solenomere not bifurcated.



Shouder evident and
rounded.

P. tricolor

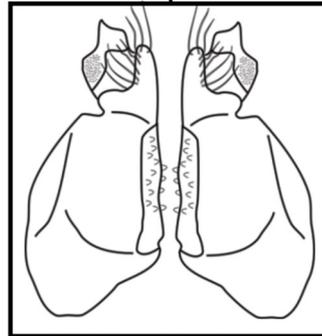


Shouder not evident.

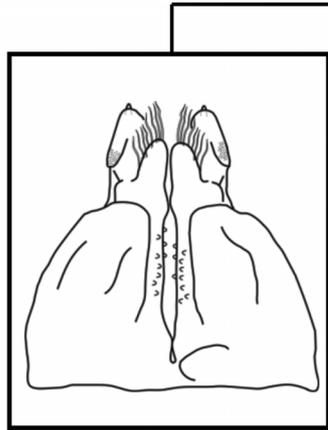


Internal branch distant from
the solenomere.

P. erikae

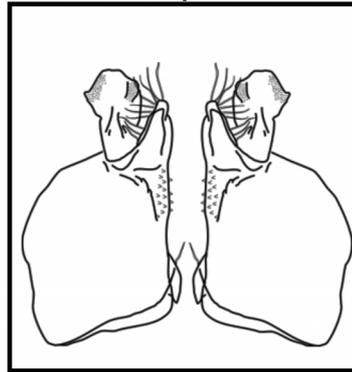


Internal branch close or
acceded to the solenomere.

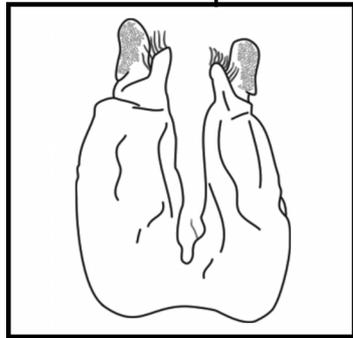


A swollen internal branch.

P. saguassu

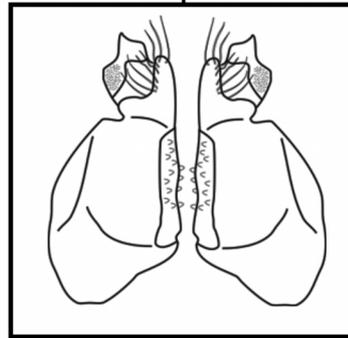


Internal branch seems like a shield of the solenomere.

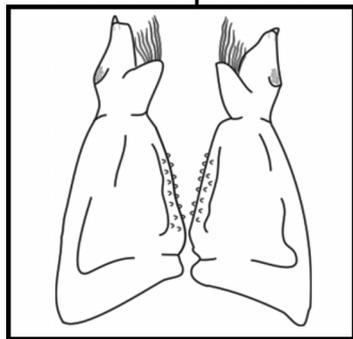


Solenomere without an apical region.

P. spelaea

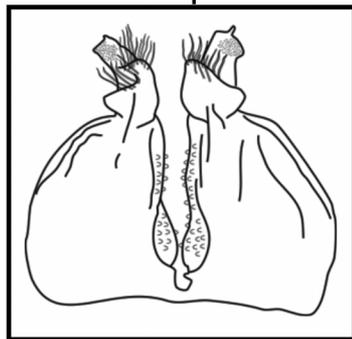


Solenomere with at least one apical region.

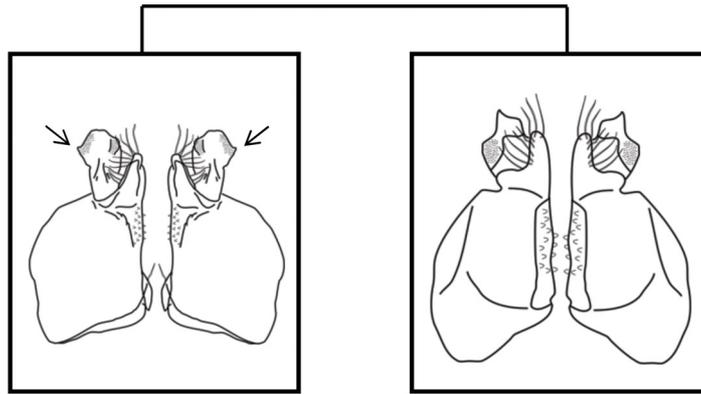


Solenomere triangle-shaped.

P. ambuatinga



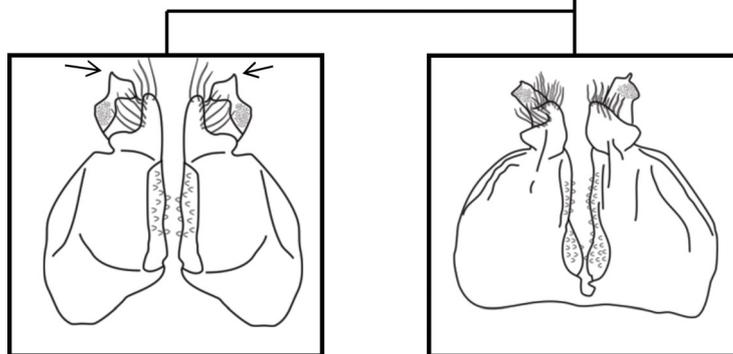
Solenomere with an irregular form.



Solenomere with a lateral projection on its medium portion.

P. microzoporus

Solenomere without a lateral projection on its medium portion.



Solenomere with a long apex.

P. tocaiensis

Solenomere without a long apex.

P. leucocephalus

Part II

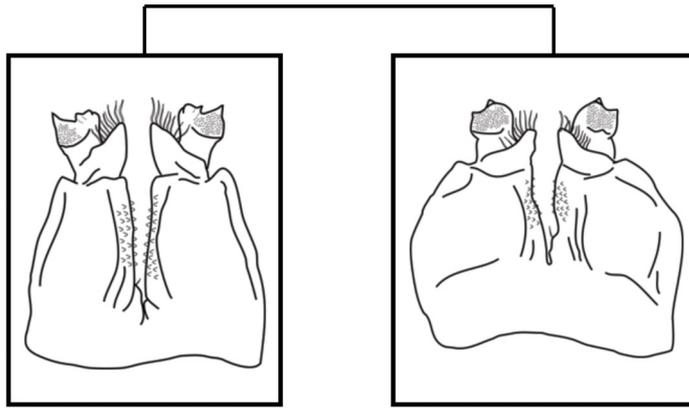


Internal branch twisted around the solenomere.

P. robsoni

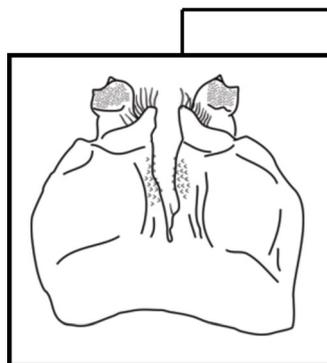


Internal branch not twisted.



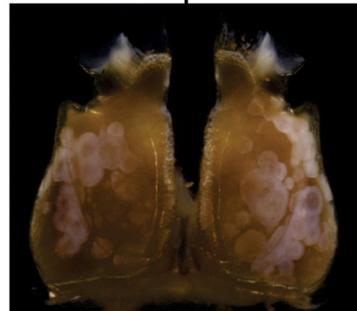
Width and length of different sizes. Go to Part III

Length and width of similar size.



Solenomere slightly bifurcated and a short internal branch.

P. gogo



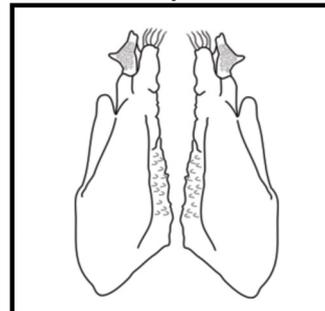
Solenomere with two pronounced tips and a wide internal branch.

P. xavieri

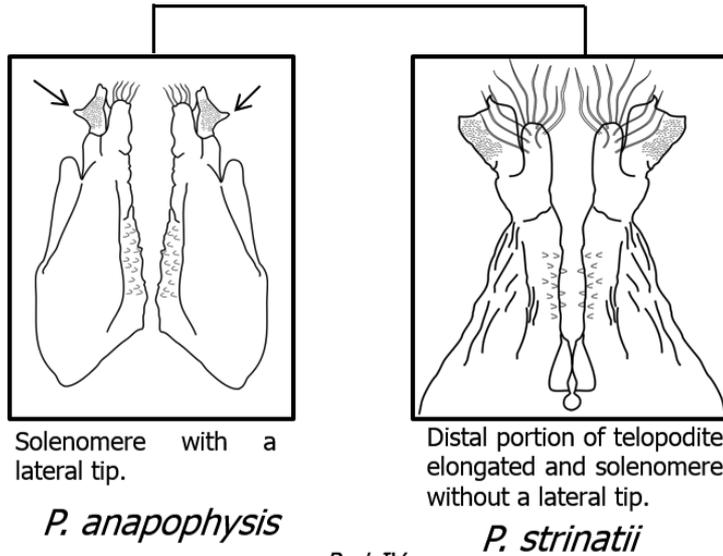
Part III



Internal branch seems like a shield of the solenomere. Go to Part IV



A tumid internal branch.

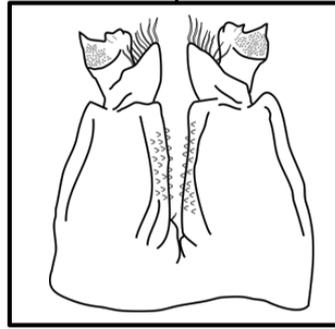


Part IV

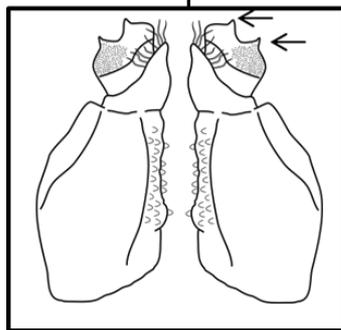


Distal region of gonopod very elongated and little wide.

P. marconii

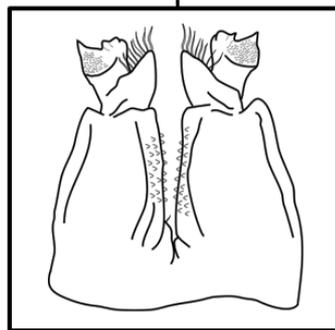


Distal region of gonopod not very elongated.



Solenomere and trunk wide and presence of two similar tips.

P. imbirensis

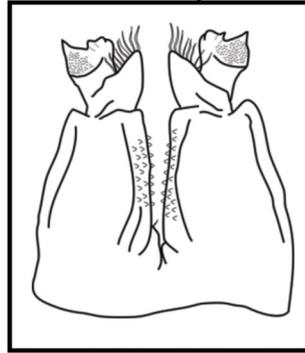


Solenomere and trunk not wide with presence of different tips.



Internal branch at the same height than the solenomere.

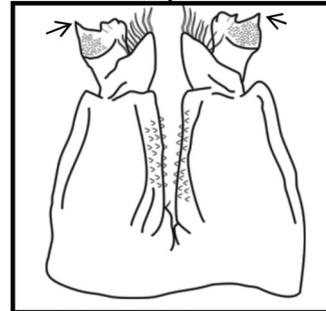
P. fontanettiae



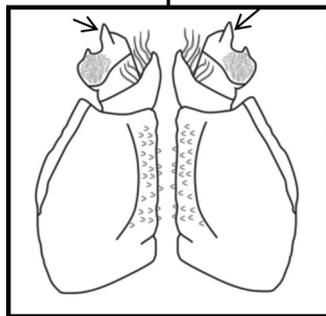
Short internal branch or reaching about 0.75 times the size of the solenomere.



The two tips of the solenomere are similar or both are pointed. Go To Part V

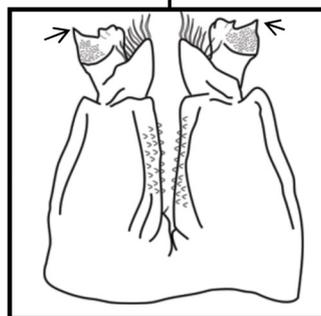


The two tips of the solenomere are unequal (one distinctly more pointed).



Internal branch with a pointed and larger internal apex.

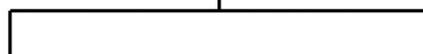
P. chaimowiczi



Internal branch with a pointed and larger external apex.

P. rolamossa

Part V



Part V

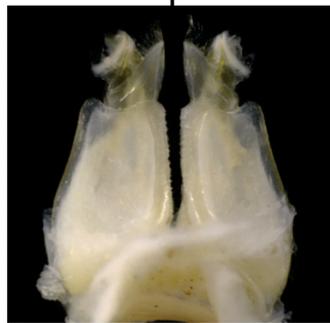


Long trunk and long setae on the internal branch.

P. longissima



Elongated internal branch with short setae.



Squamous region wider and a long and diagonal internal branch.

P. taboa

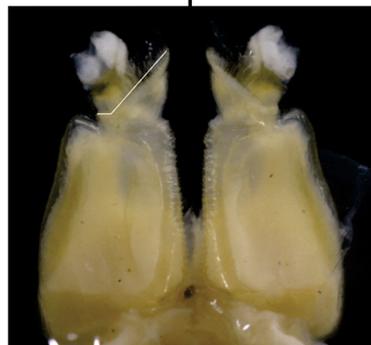


Squamous region not so wider than trunk of solenomere.



Internal branch starting just above the shoulder line emerging diagonally from the solenomere.

P. leopoldoi

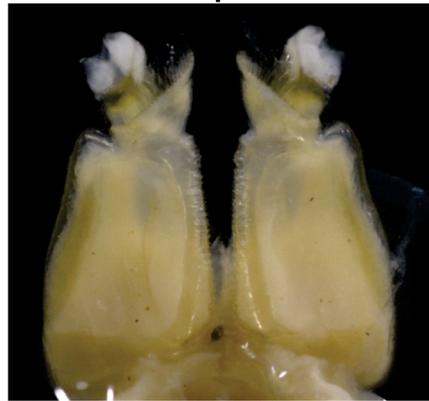


Internal branch emerging straight and turning up diagonally from the solenomere.



Internal branch starting just below the shoulder line and ending close to the internal apex.

P. caatinga



Internal branch starting just above the shoulder line and ending before of end of the internal apex.

P. rosineii

Distribution of cave-dwelling species from Brazil

In Brazil, most of the species that were found in caves tend to have disjunct distributions, although there are areas with high species overlap (Fig. 16). Among these areas, the central region of Minas Gerais state certainly deserves attention, home to at least 13 species. This region coincides with one of the areas of highest potential of species occurrence in the genus (Fig. 17). In addition, there are many distinct lithologies in the area, which may have contributed for the isolation of populations in small areas, increasing the number of species. It is important to note that all species known to Brazilian caves are distributed preferentially in the axis of the Northeast-Southeast-South regions, with the exception of *P. spelaea*, a troglobite species, found in the Amazon region. This may be due to two factors : *i*) most Brazilian known caves are located in this axis, since these regions concentrate large occurrences of carbonate rocks, and/or *ii*) the dearth of studies in North and Midwest regions lead to an absence of records of species of the genus for these regions.

According to Trajano *et al.* (2000), the species *P. chaimowiczi* has a wide distribution along the axis, being found from the central region of Minas Gerais (type locality) to the north of Bahia (Fontanetti 1996a; Trajano *et al.* 2000). Regarding *P. strinatii*, this also presents a wide distribution, however, smaller than *P. chaimowiczi*, which was found in several areas between the border of the states of São Paulo (type locality) and Paraná (Trajano *et al.* 2000). Thus, the distribution of both species also allows inferring that the genus has a large dispersal capacity in the Northeast-Southeast-South region.

Potential distribution of species of genera *Pseudonannolene* and *Epinannolene* from South and Central Americas

The genus *Pseudonannolene* is typically Neotropical (Schubart 1944; Mauriès 1987), having a distribution throughout almost all Brazil, besides Argentina, Uruguay, Paraguay and Bolivia (Mauriès 1987). One factor that explains its wide distribution, according to Schubart (1944), would be its low ecological specialization, so that any conditions and habitats that provide more or less favorable resources would allow a population to be established. The potential distribution map of the genus for South America (Fig. 17) indicates that the *Pseudonannolene* species have a higher probability of occurrence in the southeastern region of Brazil and south-central Bahia (Northeast-Southeast-South axis), and the seaside coast of Paraná, Santa Catarina, Rio Grande do Sul and southern Uruguay. Note that parts of the states of Minas Gerais and Bahia, which have great potential for species occurrence, coincides with the karstic regions of the Groups Bambuí, Una, Caatinga and Canudos. Thus, such regions would

certainly represent important areas that should be intensively inventoried, which will surely add a lot of knowledge about the genus.

Other places like northern Ceará, central and northwestern Bolivia, central Peru, western Ecuador and west-central Colombia also have small areas with probability of occurrence.

Among the environmental parameters used in the program, the pressure of water vapor was the most influential for the potential distribution of *Pseudonannolene*. This fact allows deducing that the relative humidity is an important condition for the establishment of the genus, since its species prefers more humid environments.

Differently from the potential distribution of *Pseudonannolene*, the genus *Epinannolene* is found primarily in the Central American region and in northern and northwestern South America, mainly over the Amazon basin (Mauriès 1974; Hoffman 1984; Mauriès 1987; Golovatch *et al.* 1997.; Adis *et al.* 2002). In the potential distribution map of the genus, all of Panama, part of Costa Rica, Nicaragua and the western part of Honduras were the areas of highest probability of occurrence. Some regions such as Jamaica, western Cuba, Haiti and Puerto Rico, plus the Lesser Antilles also have great potential for occurrence (Fig. 17).

Regarding Brazil, a few species are known from the Amazon region, and this area along with the northern state of Rio Grande do Norte, coast of Paraíba, Pernambuco and Alagoas makes up distant regions in which the genus may possibly be found.

For *Epinannolene*, the main environmental variables influencing their distribution were precipitation in July and diurnal temperature variation. The influence of these variables confirms that the high humidity in the region is a condition of extreme importance to the genus, just as it is to *Pseudonannolene*.

According Mauriès (1974, 1987) the geographical division between the genera *Pseudonannolene* and *Epinannolene* is very characteristic, however, with overlapping areas. The species *Epinannolene semicincta* Mauriès, 1987 found in Chillacocha, Ecuador, has a distribution that partly overlaps the area of potential occurrence of *Pseudonannolene* (Mauriès 1987). Regions such as northern Brazil, throughout the Amazon River, and part of Colombia, Peru and Venezuela, may possibly be other syntopic sites of both genera. However, it is indeed possible to distinguish large areas where different genera are found. While *Pseudonannolene* is mainly found in the east-central southeastern portion of South America, the genus *Epinannolene* replaces it in Central America and parts of South America.

The distribution map of both genera allows deducing that the north of South America and part of Central America were the great center of endemism of the Pseudonannolenidae, and later, part of its species tended to follow a southernmost colonization direction toward the southeastern portion of South America, as in *Pseudonannolene* species. In other species (and especially *Cambalomma* and *Epinannolene*) the dispersion has followed a more northerly direction, towards the Central American region.

From northern South America *Phallortus* Chamberlin, 1952, from Colombia, *Physiostreptus* Silvestri, 1903 and *Holopodostreptus* Carl, 1913, both genera from Ecuador (Carl 1913; Hoffman & Florez 1995; Sierwald 2006), are known. Such genera correspond to the subfamily Physiostreptinae Silvestri, 1903, characterized by the absence of a promentum separating the lamellae linguales (Hoffman & Florez 1995; Shelley 2002; Sierwald 2006). In the West Indies, the genus *Cambalomma* Loomis, 1941 occurs in Haiti, the only representative of the subfamily Cambalomminae Loomis, 1941, which is identified by the presence of a distal projection of the mentum (secondary mentum) partially separating the lamellae linguales (Loomis 1941; Mauriès 1987; Florez & Hoffman 1995, Shelley 2002; Sierwald 2006). Finally, the records further north in the West Indies, besides *Cambalomma*, are of the genus *Epinannolene* Brölemann 1903, found in Antilhas, Bermudas and Guadeloupe (Loomis 1968; Mauriès 1987), and those of southernmost South America are of *Pseudonannolene*. Both genera belong to the subfamily Pseudonannoleninae Silvestri, 1895 due to the presence of a promentum separating the lamellae linguales.

Finally, it is important to mention that possibly Physiostreptinae corresponds to the most plesiomorphic subfamily, due to no separation of lamellae linguales, followed by Cambalomminae, due to the presence of a secondary mentum, and the more apomorphic Pseudonannoleninae, which presents a promentum. The genus *Pseudonannolene* possibly corresponds to the most derivative, because of the promentum being separated into two parts by a longitudinal suture, unlike the related genera *Epinannolene* and *Typhlonannolene*.

Morphology of the Gonopod

The structure of gonopod in Diplopoda is the main morphological character for species differentiation (Miley 1927; Berns 1968; Mwabvu 2013). Thus, for the genus *Pseudonannolene* descriptions are based especially on the

gonopod morphology and its shared traits (Fontanetti 1996a; Fontanetti 1996b; Fontanetti 2002; Iniesta & Ferreira 2013a; Iniesta & Ferreira 2013b; Iniesta & Ferreira 2013c). In this genus, although no clear correlation is known between the parts of the legs and the gonopod, in recent species descriptions it is possible to recognize some gonopod divisions (Schubart 1994; Mauriès 1987; Fontanetti 1996a; Iniesta & Ferreira 2013a). Thus, the gonopod is currently being divided in two distinct parts: a basal region, composed primarily of the coxae, and a distal telopodite, containing two well-developed branches, an inner (surrounded by bristles) and an outer branch (solenomere) having a smooth trunk, a squamous region and a seminal spine (Fig. 1). In relation to differences between species, both portions are extremely important. The basal region may or may not have an apparent upper lateral shoulder (near the distal portion) and width/length can vary. Species like *P. gogo* Iniesta & Ferreira, 2013 and *P. xavieri* have a ratio between these measures almost equivalent (although differentiated by the morphology of the internal branch and solenomere). On the other hand, *P. marconii* has a basal region clearly more elongated than the other species, with smaller width. On the internal branch of the telopodite two different and more recurrent forms are found: one generally thinner, long and forming a shield over the base of the solenomere and the other more swollen, elongated or not. The first branch morphology is the most abundant in the genus, the telopodite may be as elongated as the solenomere, and clearly forming a groove (seminal groove?) between the two branches. The second form, thicker, found in *P. strinatii* Mauriès, 1974, *P. ambuatinga* Iniesta & Ferreira, 2013 and *P. anapophysis* Fontanetti, 1996 (Mauriès 1974; Fontanetti 1996a; Iniesta & Ferreira 2013b) is more rare. For *P. erikae*, the branch was highly modified with a sturdy format, positioning divergent to the other branch, thus forming a large space for the supposed seminal groove.

Regarding the solenomere, there are also some significant differences between species in which three main morphological patterns were identified: *i*) bifurcated distal region with an external and an internal tip, carrying the seminal spine; *ii*) triangle-shaped region, with a central apex and carrying a spine; and *iii*) a more rounded shape without a distinguishable tip. Among these morphologies, the bifurcated appearance, which may be clear or slightly modified, is shared with the greatest number of species. As to the more rounded shape, is quite evident for *P. spelaea* Iniesta & Ferreira, 2013, in which no apex and seminal spine are viewed (Iniesta & Ferreira 2013a). Again, in the species *P. erikae*, the solenomere proved to be quite modified with a tortuous and divergent position regarding the internal branch, plus a slight triangle-shape.

Another important feature is the ratio between the internal branch and the telopodite. Species like *P. ambuatinga* Iniesta & Ferreira, 2013, *P. saguassu* Iniesta & Ferreira, 2013, *P. rolamossa* Iniesta & Ferreira, 2013, *P. chaimowiczi* Fontanetti, 1996a, *P. leucocephalus* Schubart, 1944, *P. robsoni*, *P. erikae*, *P. longissima* and *P. fontanettiae* has the branch equal to or near half the total length of telopodite. However, in the species *P. tricolor* Brolemann, 1902, *P. caatinga* and *P. marconii*, the length of both are similar.

Despite the huge importance of the gonopod structures for the taxonomy of the genus, in some species their gonopods are not known, as in the case of *Pseudonannolene segmentata* Silvestri, 1895 and *Pseudonannolene rugosetta* Silvestri, 1897, in which the descriptions were based solely on morphological characters of females (Silvestri 1902; Mauriès 1987). The species *Pseudonannolene meridionalis* Silvestri, 1902, was also described based only on females, although Mauriès (1987) has described a gonopod that could possibly be from the species.

Finally, the shape of the pre-femoral process of the first pair of legs of males has also been shown as an important taxonomic trait for the genus (Fontanetti 2002). This structure can be found in two main forms: elongate over a short pre-femur and a smaller one over a larger pre-femur (Fontanetti 2002). It is noteworthy that the species *P. anapophysis* Fontanetti, 1996 has no pre-femoral process and in *P. erikae* the process is quite modified, having a more oval form, and a not so elongated projection.

Conservation

Currently in Brazil caves are protected under the Decree Law No. 6,640, which mandates that they can only be exploited after a categorization indicating their relevance, and those defined as being of utmost importance being under maximum protection. To categorize a cave, several parameters, both geological and biological, are taken into account. Thus, in the case of the genus *Pseudonannolene*, with several species often found in caves, the preservation of these environments is crucial to their survival, thus allowing that further studies on the group be conducted.

Regarding species restricted to the caves, this makes up one of the main attributes for defining the degree of relevance of caves. In the country, only 2 troglobitic species are known, *P. spelaea* Iniesta & Ferreira, 2013, found

in iron ore caves from the Amazon region (Pará) and *P. ambuatinga* Iniesta & Ferreira, 2013, from limestone caves of the municipality of Pains (Minas Gerais) (Iniesta & Ferreira 2013a; Iniesta & Ferreira 2013b). The habitats of these species are preserved only due to their presence. Accordingly, a single troglobitic species can protect a whole system, and this is why new inventories have to be urgently conducted. Thus, species of *Pseudonannolene* are revealing themselves as good tools for cave conservation, at least in Brazil.

Acknowledgements

Acknowledgments to all the team from the Centro de Estudos em Biologia Subterrânea (UFLA) for their help in collecting material, to Dr. Julio N.C. Louzada (Department of Ecology—UFLA) for the use of stereoscopic image capture and to CAPES – edital Pró-equipamento 2010 for the automatic mounting equipment. We are also grateful to Dr. William Shear for his attention and advices, to Dr^a. C. Fontanetti for the attention and for sending important literatures and the anonymous reviewers. R. Ferreira is grateful to the National Council of Technological and Scientific Development (CNPq) for the research grant (process No. 301061/2011-4) and to the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for funding support (processes CRA—APQ 01826-08 and CRA—PPM-00433-11). L. F. M. Iniesta is grateful to the National Council of Technological and Scientific Development (CNPq, process 129126/2012-8, 137717/2013-0) and to the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for funding support (FAPEMIG, CRA – APQ 01046-12).

Bibliographic references

- Adis, J., Foddai, D., Golovatch, S.I., Hoffman, R.L., Minelli, A., de Moraes, J.W., Pereira, L.A., Scheller, U., Schileyko, A.A. & Wurmli, M. (2002) Myriapoda at “Reserva Ducke”, Central Amazonia/Brazil. *Amazoniana*, 17, 15–25.
- Berns, M.W. (1968) The development of the copulatory organs (gonopods) of a spirobolid millipede. *Journal of Morphology*, 126, 447–462.
- Brölemann, H.W. (1902) Myriapodes du Musee de Sao Paulo. *Revista do Museu Paulista*, 5, 35–237.
- Brölemann, H.W. (1903) Myriapodes recueillis à l'isla de Cocos par M. le Professeur P. Biolley. *Annales de la Société Entomologique de France*, 72, 128–143.
- Brölemann, H.W. (1909) *Catálogos da Fauna Brasileira*. Museu Paulista, São Paulo, Brasil, 236 pp.
- Carl, J. (1913) Diplopodenstudien II. Eine neue Physiostreptiden-Gattung. *Zoologischer Anzeiger*, 62, 212–216.
- Chamberlin, R.V. (1922) Notes on West Indian millipeds. *Proceedings U. S. National Museum*, 61(10), 1–19.
<http://dx.doi.org/10.5479/si.00963801.61-2431.1>
- Chamberlin, R.V. (1923) Results of the Bryannt Walker Expeditions of the University of Michigan to Colombia, 1913, and British Guiana, 1914. *Occ. Pap. Mus. Univ. Mich.*, 133, 1–143.
- Chamberlin, R.V. (1952) Further records and descriptions of American millipeds. *Great Basin Naturalist*, 12, 13–34.
- Fontanetti, C.S. (1996a) Description of three cave diplopods of *Pseudonannolene* Silvestri (Diplopoda, Pseudonannolenida, Pseudonannolenidae). *Revista Brasileira de Zoologia*, 13 (2), 427–433.
- Fontanetti, C.S. (1996b) Description of a new species and the karyotype of the cavernicolous millipede *Pseudonannolene* Silvestri and the karyotype of *Pseudonannolene Strinatti* Mauriès (Diplopoda, Pseudonannolenida, Pseudonannolenidae). *Revista Brasileira de Zoologia*, 13 (2), 419–426.
<http://dx.doi.org/10.1590/S0101-81751996000200012>
- Fontanetti, C.S. (2002) Taxonomic Importance of the Prefemoral Process of the first Pair of Legs in Males of the Genus *Pseudonannolene* (Diplopoda, Spirostreptida). *Folia biologica (Kraków)*, 50, 199–202.
- Golovatch, S.I., Hoffman, R.L., Adis, J., Vohland, K. & Mármol, A. (1997) On the identity of further two millipede species (Diplopoda) from environs of Manaus, Central Amazonia, Brazil. *Amazoniana*, 16, 301–309.
- Hoffman, R.L. & Florez, E. (1995) The millipede genus *Phallorthis* revalidated: another facet of a taxonomic enigma (Spirostreptida: Pseudonannolenidae). *Myriapodologica*, 3, 115–126.
- Hoffman, R.L. (1984) A new species of *Epinannolene* from the Amazon Basin, Brazil (Spirostreptida: Pseudonannolenidae). *Myriapodologica*, 1 (13), 91–94.
- Iniesta, L.F.M. & Ferreira, R.L. (2013a) The first troglobitic *Pseudonannolene* from Brazilian iron ore caves (Spirostreptida: Pseudonannolenidae). *Zootaxa*, 3669 (1), 85–95.
<http://dx.doi.org/10.11646/zootaxa.3669.1.9>
- Iniesta, L.F.M. & Ferreira, R.L. (2013b) Two new species of *Pseudonannolene* Silvestri, 1895 from Brazilian limestone caves (Spirostreptida: Pseudonannolenidae): syntopy of a troglophilic and a troglobiotic species. *Zootaxa*, 3702 (4), 357–369.
<http://dx.doi.org/10.11646/zootaxa.3702.4.3>
- Iniesta, L.F.M. & Ferreira, R.L. (2013c) Two new species of *Pseudonannolene* Silvestri, 1895 from Brazilian iron ore caves

- (Spirostreptida: Pseudonannolenidae). *Zootaxa*, 3716 (1), 75–80.
<http://dx.doi.org/10.11646/zootaxa.3716.1.6>
- Loomis, H. F. (1941) New genera and species of millipeds from the southern peninsula of Haiti. *Journal of the Washington Academy of Sciences*, 31 (5), 187–195.
- Loomis, H.F. (1968) *A checklist of the millipeds of Mexico and Central America*. Bulletin of the U.S. National Museum 266, 137 pp.
- Mauriès, J.P. (1974) Un cambalide cavernicole du Brésil, *Pseudonannolene strinatii* n. sp. (Myriapoda, Diplopoda). *Revue Suisse de Zoologie*, 81 (2), 545–550.
- Mauriès, J.P. (1987) Cambalides nouveaux et peu connus d'Asie, d'Amérique et d'Océanie. II. Pseudonannolenidae, Choctellidae (Myriapoda, Diplopoda). *Bull. Mus. natn. Hist. nat. Paris*, 9, 169–199.
- Miley, H.H. (1927) Development of the male gonopods and life history studies of a polydesmid millipede. *The Ohio Journal of Science*, 27 (1), 25–43.
- Mwabvu, T., Lamb, J., Slotow, R., Hamer, M. & Barraclough, D. (2013) Is millipede taxonomy based on gonopod morphology too inclusive? Observations on genetic variation and cryptic speciation in *Bicoxidens flavicollis* (Diplopoda: Spirostreptida: Spirostreptidae). *African Invertebrates*, 54 (2), 349–356.
<http://dx.doi.org/10.5733/afin.054.0203>
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.
<http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026>
- Schubart, O. (1944) Os Diplopodos de Pirassununga. *Acta zool. Lilloana*, 2 (2), 321–440.
- Shear, W. (2011) Class Diplopoda de Blainville in Gervais, 1844. In: Zhang, Z.-Q. (Ed.) *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa*, 3148, 159–164.
- Shelley, R.M. (2003) A revised, annotated, family-level classification of the Diplopoda. *Arthropoda Selecta*, 11 (3), 187–207.
- Sierwald, P., Jeekel, C.A.W., Hoffman, R.L., Shelley, R.M., Kiser, S.B. & Golovatch, S.I. (2006) Nomenclator Generum Diplopodorum, Version 2. A complete listing of all genus-group names in the class Diplopoda from 1758 through 1999. On-line publication: This Excel file is available to download. Available from: http://www.fieldmuseum.org/research_collections/zoology/zoo_sites/millipeet/pdfsFullarticles/MILLGEN.xls (accessed 31 March 2014)
- Silvestri, F. (1895) *Chilopodi e diplopodi raccolti dal Capitano G. Bove e dal Prof. L. Balzan nell'America Meridionale*. Annali del Museo Civico di Storia Naturale di Genova, 34, 839 pp.
- Silvestri, F. (1902) Viaggio del Dr. A. Borelli nel Matto Grosso. *Boll. Musei. Zool. Anat. Comp. R. Univ. Torino*, 17 (432), 1–25.
- Trajano, E., Golovatch, S.I., Geoffroy, J.J., Pinto-da-rocha, R. & Fontanetti, C.S. (2000) Synopsis of brazilian cave-dwelling millipedes (Diplopoda). *Papéis Avulsos de Zoologia*, 18, 259–287.
- White, W.B. & Culver, D.C. (2012) *Encyclopedia of caves*. Elsevier Academic Press, Oxford, San diego, 966 pp.
- Zampaulo, R.A. (2010) *Diversidade de invertebrados cavernícolas na Província Espeleológica de Arcos, Pains e Doresópolis (MG): subsídios para a determinação de áreas prioritárias para conservação*. Dissertação (Mestrado em Ecologia Aplicada) - Universidade Federal de Lavras, Lavras, 190 pp.