



Assessing troglomorphic and phylogenetically informative traits in troglobionts: a new cave-dwelling centipede illuminates the evolution of a soil-dwelling lineage (Chilopoda: Geophilidae)

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Abstract

Cave-dwelling species are of special interest in evolutionary biology, because (i) many share particular traits associated with the cave habitat (troglomorphic traits), and (ii) some represent relict lineages that may conserve ancestral traits or possibly transitional traits, which may provide insights into the evolution of other highly derived species. However, these different kinds of characters are hard to assess thoroughly in troglobionts belonging to little known terrestrial arthropod groups. We describe a new species of centipedes from the Areias System caves, Brazil, namely, *Plutogeophilus jurupariquibaba* gen.n. sp.n., which adds to the few putative troglobionts known among Chilopoda Geophilomorpha. We analyzed a suite of characters in the light of a phylogenetic analysis and by direct comparison with epigeal relatives, controlling for interindividual variation and its confounding sources. We found that: (i) troglomorphic traits of *P. jurupariquibaba* may include large body, elongate antennae, elongate legs and claws, and possibly also elongate setae and large coxal pores; (ii) the cave-dwelling *Plutogeophilus* is the sister lineage of the soil-dwelling *Macronicophilus*, whose morphology is highly derived and whose phylogenetic position remained unclear; (iii) compared with other extant geophilids, symplesiomorphic traits and apparently intermediate traits found in *Plutogeophilus* provide insights on the origin of the morphology of *Macronicophilus*, suggesting a stepwise modification of labrum, forcipular apparatus and ultimate legs, and the derivation of the unique rounded and spiny tip of the second maxillae from a pointed claw.

Keywords Neotropics · Chilopoda · *Macronicophilus* · *Plutogeophilus jurupariquibaba* · Transitional morphology · Troglomorphy

Introduction

Animal species living only in caves (“troglobionts” in the ecological classification revised by Sket, 2008) have fascinated naturalists since long and are still the focus of many research programs of evolutionary biology (see, e.g., Barr & Holsinger, 1985; Jeffery, 2008; Juan et al., 2010; Sánchez-Fernández et al., 2018). Even though the uniqueness of troglobionts has been sometimes overemphasized (see Pipan & Culver, 2012), the peculiar morphological features

often found in these animals provide insightful material to address major questions on evolutionary processes.

Many troglobionts show similar traits that evolved most probably in association with the colonization of the cave habitat (so-called troglomorphic traits; Howarth, 1993; Fišer, 2019; Christiansen, 2012). Therefore, they allow to investigate general mechanisms of developmental plasticity, evolutionary adaptation, and convergent evolution (e.g., Bendik et al., 2013; Bilandžija et al., 2020; Derkarabetian et al., 2010).

Moreover, some troglobionts represent evolutionary lineages that have no extant close representatives in the epigeal biota (so-called relict; see Grandcolas et al., 2014). Nevertheless, when the phylogenetic relationships between a relict lineage and its closest relatives are estimated (as exemplified in Fig. 1), different characters may be compared among the extant species upon their phylogeny, and the probable states of these characters may be inferred also for the nodes (Cunningham et al., 1998; Griffith et al., 2015).

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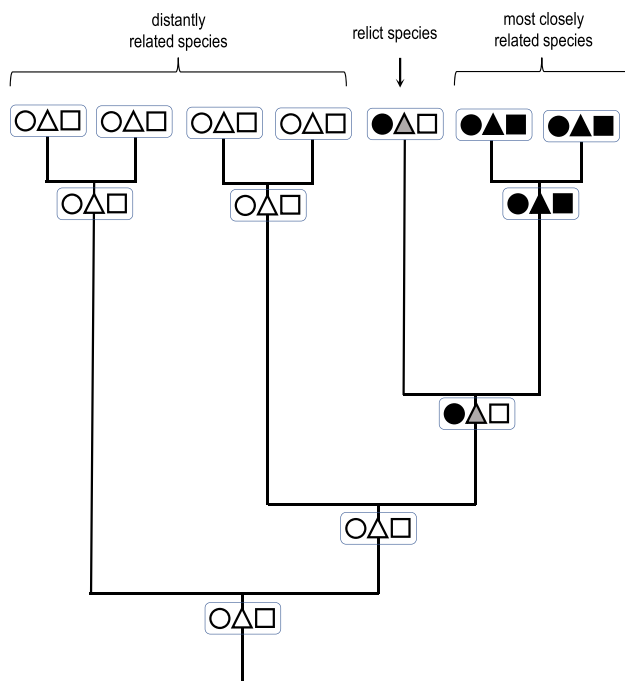


Fig. 1 Hypothetical phylogeny with an evolutionarily relict species and different cases of character state reconstruction. Different shapes indicated different characters. Empty shapes indicate an ancestral state, black shapes indicate a derived state, and gray shapes indicate an intermediate (possibly transitional) state. For the circle-character, the relict species shares a derived state with the most closely related species (synapomorphy). For the square-character, it shares an ancestral state with the other more distantly related species (symplesiomorphy). For the triangle-character, it has an apparently intermediate state between an ancestral state and a derived state (possibly transitional)

For some characters, it is expected that the states exhibited by the relict species are also shared by the species most closely related to them, rather than other species. Furthermore, these states can be reasonably interpreted as “derived” (= apomorphic) when compared to alternative states. These shared derived states are referred to as “synapomorphic” (Hennig, 1966; Patterson, 1982; Richter, 2017).

On the other hand, for other characters, because of the relatively isolated phylogenetic position of the relict species, it is expected that the states shown by the relict species differ from those shown by the most strictly related species. In some cases, these states are shared with some more distantly related species and may be interpreted as “ancestral” (= plesiomorphic) in comparison with the derived states exhibited by the closest relatives. These shared ancestral states are referred to as “symplesiomorphic” (Hennig, 1966; Patterson, 1982; Richter, 2017).

However, some characters may display a unique state in the relict species and differ from both the closest relatives and all other more distantly related species. When this unique state appears “intermediate,” on a purely phenotypic sense, between a derived state displayed by the closest

relatives and an ancestral state displayed by other distantly related species, it is plausible that (i) such intermediate condition has been inherited by a common ancestor between the relict species and the most strictly related species, and that (ii) this state underwent a further transformation only in the lineage leading to the most strictly related species (Fig. 1). In other words, such morphologically intermediate character state observed in the relict species may correspond to a “transitional” state in the evolution from an ancestral to a derived condition, within a related lineage (e.g., Corush, 2019; Di Giulio, 2013; Rosenberg, 1996; Whittington et al., 2022). We note here explicitly that we are referring to a reasonable hypothesis grounded on a rigorous cladistic interpretation and character optimization. Instead, we reject any fallacious argument that confuses the array of character states observed in extant species and the temporal series of character states evolving along a single lineage (Saether, 1979; Jenner, 2018).

In summary, some relict troglobionts offer crucial evidence to infer the evolutionary pathways that led to unique characters shown by epigeal organisms.

However, detecting genuine troglomorphic traits, separating synapomorphic and symplesiomorphic traits, and highlighting putative transitional traits are not straightforward in many troglobionts. A rigorous approach will require a comprehensive comparison of all candidate morphological characters among representative samples of specimens of the troglobiont species and of epigeal relatives, within an explicit phylogenetic hypothesis (see, e.g., Desutter-Grandcolas, 1997), controlling for other expected confounding factors like developmental allometry and sex dimorphism. For many putative troglobionts of little known arthropod groups, in particular among many terrestrial arthropods other than insects (e.g., springtails, isopods, myriapods, arachnids), only some of the many examples of alleged troglomorphic traits have been inferred or tested with a robust approach, and transitional traits are rarely reported and discussed based on a character state reconstruction upon an explicitly phylogeny (e.g., Acosta, 2019; Arnedo et al., 2007; Miller, 2005).

Among centipedes (Chilopoda), many species have been recorded only in caves and have been regarded as living only in caves (troglobionts). However, the little number of specimens available to study and the scarcity of published information on most centipede species have often hindered a phylogenetically informed analysis of the evolutionary significance of the morphological traits of the troglobionts.

In the present paper, we describe a still unnamed cave-dwelling species of centipedes from the cave biota of the Areias Cave System (São Paulo state, Brazil). The existence of a geophilomorph species in this cave system had been mentioned since long (e.g., Trajano, 1987; Trajano & Bichuette, 2010; Souza Silva & Ferreira, 2016) and this species has been recently cited under the genus

Ribautia Brölemann, 1909 (Chagas-Jr & Bichuette, 2018; Fonseca et al., 2019a), but its morphology has remained fully unknown. After describing the species in detail, we assessed its distinctive characters to sort out the traits that are probably troglomorphic and other traits that could provide insights on the evolutionary differentiation of other related centipedes, including ancestral traits and putative transitional traits.

The new troglobiont species contributes substantially to clarify the evolutionary origin of morphological peculiarities of the enigmatic *Macronicophilus* Silvestri, 1909. This is a small lineage of Neotropical soil-dwelling centipedes, with a highly derived morphology that puzzled taxonomists for long time. Especially unique in *Macronicophilus* are the tips of the second maxillae, which end with a swollen, rounded, spiny additional article, instead of a claw like in most other centipedes.

Material and methods

Morphological analysis

Five specimens of the new species were collected in the caves of the Areias Cave System (Alto Ribeira karstic area, near Iporanga, São Paulo state, Brazil) by one of the author (R.L. Ferreira), by mean of forceps, during multiple speleological visits in the years 2012–2014: 1 ♀ (ISLA 47687) from Ressurgência das Areias cave, 6.IV.2012; 2 ♂♂ (ISLA 11879, ISLA 12865b) and 1 ♀ (ISLA 12865a) from Areias de Cima cave, 7.IV.2012; 1 ♀ (ISLA 12866) from Areias de Baixo cave, 19.II.2014. All specimens were examined by light microscopy, measures were taken with a micrometer applied to the ocular lens, and stacks of photographs were taken with a camera applied to the microscope and mounted with CombineZ (Hadley, 2008).

We also examined seven specimens of *Macronicophilus*, representative of two species: *Macronicophilus abbreviatus*, 1 ♀ (PD-G 1385), from N of Manaus (Brazil), collected by M. Olivia de A. Ribeiro, VII.1990-II.1991; *Macronicophilus venezolanus*, 1 ♀ (PD-G 1359, holotype) and 1 juvenile (PD-G 1386), both from Guaramacal (Venezuela), collected by M.G. Paoletti, II.1987; *Macronicophilus venezolanus*, 1 ♀ (ICN-MCh-0515: b), 1 ♂ (ICN-MCh-0515: a), and 2 juveniles (ICN-MCh-0421: c, d), all from near Icononzo (Colombia), collected by D. Triana, C. Prado, D. Molina, and S. Galvis, 15.III.2015.

Phylogenetic analysis

We performed a phylogenetic analysis of Geophilidae s.l. (sensu Bonato et al., 2014, i.e., including clades often distinguished as Aphilodontidae, Dignathodontidae, Linotaenidae, and Macronicophilidae). We included the new species,

all known species of *Macronicophilus* and selected representatives of all other major lineages of Geophilidae s.l. and the related Eriphantidae, Gonibregmatidae, and Neogeophilidae, for a total of 48 species (Table 1). We also included a species of Zelanophilidae as outgroup (Table 1).

Of all the characters employed in the most recent phylogenetic analysis of Geophilomorpha (Bonato et al., 2014), we considered only those that were variable and parsimony-informative among the included species. We also added 13 newly defined characters, to describe variation among the *Macronicophilus* species and the new species. A total of 81 characters were employed (Table 1). The characters previously employed are defined in Table S2 in Bonato et al. (2014), whereas the new characters are defined as follows:

- Ch. 7) labrum: lateral part: width/length: (0) > 2; (1) < 2
- Ch. 29) second maxillae: pretarsus: (0) claw-like, variously reduced; (1) swollen, rounded, and spiny
- Ch. 33) forcipular coxosternite: ventrally exposed surface: width/length: (0) < 2.0; (1) > 2.0
- Ch. 43) forcipular trochanteroprefemur: length/width: (0) > 0.9; (1) < 0.9
- Ch. 48) forcipular tarsungulum/trochanteroprefemur length: (0) < 1.4; (1) > 1.4
- Ch. 49) forcipular tarsungulum/trochanteroprefemur length: (0) < 2.0; (1) > 2.0
- Ch. 50) forcipular tarsungulum: basal denticle: (0) no; (1) yes
- Ch. 53) forcipular tarsungulum: ungulum: shape: (0) not dorso-ventrally flat, at most slightly depressed; (1) distinctly dorso-ventrally flat
- Ch. 58) anterior third of trunk: leg pretarsus: anterior accessory spine: (0) yes; (1) no
- Ch. 67) intermediate part of trunk: pore-field: (0) more or less separated into two paired groups of pores; (1) without mid-longitudinal constriction
- Ch. 71) ultimate leg-bearing segment: metasternite: sexual dimorphism of length/width: (0) no; (1) yes, proportionally narrower in female than in male
- Ch. 73) ultimate leg: coxal organs: pores on dorsal side: (0) no; (1) yes
- Ch. 77) ultimate leg: tarsus 2/tarsus 1 length in male: (0) > 0.6; (1) < 0.6

All characters were defined as binary. Non-applicable states were scored as “–” and unknown or variable states with “?”.

The most parsimonious trees were searched with the heuristic procedure implemented by T.N.T. 1.5 (Goloboff & Catalano, 2016), both under equal weight and under implicit weight with variable values of the constant of concavity ($K = 1, 3, 10, \text{ and } 50$), with “traditional search” through 1000 random addition sequences, tree bisection and

Table 1 (continued)

Character code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40												
Code in Bonato et al. (2014)	4	13	19	20	28	29	-	33	37	38	45	50	51	68	69	70	71	77	78	79	80	81	87	89	92	95	96	99	-	101	104	110	-	114	115	116	117	119	120	121												
<i>Henia bicarinata</i>	0	0	0	0	0	0	-	1	0	0	?	?	?	1	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1									
<i>Henia illyrica</i>	0	0	0	0	0	0	-	1	0	0	?	?	?	1	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	1	0	0	0	0	0	0	1	0	1	0	1								
<i>Henia vesuviana</i>	0	0	0	0	0	0	-	1	0	0	0	?	?	1	0	1	1	1	0	0	0	1	0	1	0	0	1	0	0	-	0	0	1	0	0	0	0	0	0	1	0	1	0	1								
<i>Hyphidrophilus adisi</i>	1	0	1	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	1	0	1	0	1	0	1	0	0	0	1	0	1								
<i>Macronicophilus abbreviatus</i>	0	1	1	0	0	1	1	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	-	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0							
<i>Macronicophilus ortoneidae</i>	0	?	1	0	0	0	1	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	-	0	0	1	0	0	0	0	0	1	0	0	1	0	0								
<i>Macronicophilus unguiseta</i>	0	0	1	0	0	0	1	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	-	?	0	1	0	0	0	0	0	0	1	0	0	1	0	0							
<i>Macronicophilus venezolanus</i>	0	1	1	0	0	0	1	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	-	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0						
<i>Nothogeophilus turki</i>	0	0	0	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1					
<i>Pachymerium ferrugineum</i>	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0						
<i>Plateurytion tenebrosus</i>	1	0	1	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0					
<i>Pleurogeophilus mediterraneus</i>	0	0	0	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1					
<i>Platogeophilus jurapariquibaba</i> gen.n. sp.n.	0	0	1	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1				
<i>Polyericus</i> sp.	1	0	1	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0			
<i>Polygonarea</i> sp.	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1		
<i>Ribautia centralis</i>	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0			
<i>Schendyloides alacer</i>	1	1	1	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0				
<i>Sogona michoacana</i>	0	0	0	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1		
<i>Stenurytion antipodum</i>	1	0	1	0	0	0	0	1	1	0	1	0	1	1	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0		
<i>Stenotania sorrenina</i>	0	0	0	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	0	0	1	0	1	0	1			
<i>Strigamia crassipes</i>	0	0	0	0	0	0	-	1	0	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Strigamia maritima</i>	0	0	0	0	0	0	-	1	0	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Strigamia svenhedini</i>	0	0	0	0	0	0	-	1	0	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Tuoba possidonis</i>	0	1	0	0	0	0	0	1	1	0	?	?	?	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 1 (continued)

Character code	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81			
Code in Bonato et al. (2014)	122	125 -	126	128	129	130 -	-	-	131	132 -	133	141	143	144 -	150	151	152	156	160	161	162	163 -	167	168	169 -	170 -	179	180	182 -	183	185	186	190											
<i>Geophilus carpophagus</i>	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	?	?	0	0	0	1	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1			
<i>Geophilus electricus</i>	0	0	0	1	0	0	0	1	0	0	0	0	?	0	?	?	?	0	0	0	1	0	1	?	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1			
<i>Geophilus flavus</i>	1	0	0	1	0	0	0	1	0	0	0	0	?	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Geophilus truncorum</i>	1	0	0	1	0	0	0	1	0	0	0	?	0	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1		
<i>Gnathoribautia bonensis</i>	0	0	0	1	0	0	0	1	0	1	0	?	0	?	?	?	?	0	0	0	0	0	0	-	-	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	-	1		
<i>Henia bicarinata</i>	0	?	1	1	0	0	1	1	0	0	0	0	?	1	0	1	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1		
<i>Henia illyrica</i>	0	?	1	1	0	0	1	1	0	0	0	?	1	?	?	?	?	0	0	0	0	1	?	1	0	-	0	0	0	0	0	0	0	0	0	1	0	1	0	1	-	1		
<i>Henia vesuviana</i>	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1	1	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Hydrophilus adisi</i>	1	0	0	0	1	0	0	0	1	0	1	0	?	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Macronicophilus abbreviatus</i>	0	0	1	1	0	0	1	1	0	0	0	0	?	0	?	?	?	1	0	0	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	1		
<i>Macronicophilus ortonedae</i>	0	0	1	1	0	0	1	1	0	0	0	1	?	0	?	?	?	0	0	0	0	1	?	0	0	1	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1		
<i>Macronicophilus unguiseta</i>	0	0	1	1	0	0	1	1	0	0	0	1	?	0	?	?	?	1	0	0	0	0	1	?	0	0	1	0	0	1	?	0	1	0	0	1	1	0	0	0	?	?		
<i>Macronicophilus venezolanus</i>	0	0	1	1	0	0	1	1	0	0	0	1	?	0	?	?	?	1	0	0	0	0	1	?	0	0	1	0	0	1	?	0	0	1	0	0	1	1	0	0	0	1		
<i>Nothogeophilus turki</i>	1	0	0	0	0	0	1	0	0	0	1	0	?	0	?	?	?	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pachymertum ferrugineum</i>	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Plateurytion tenebrosus</i>	0	0	0	1	0	0	0	1	0	1	0	?	0	?	?	?	?	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Pleurogeophilus mediterraneus</i>	0	0	0	1	0	0	1	0	1	0	0	0	?	0	0	1	0	0	0	0	1	0	1	0	1	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Pleurogeophilus jurupariq-utababa</i> gen.n. sp.n.	1	0	0	1	0	0	1	0	1	0	0	0	?	0	?	?	?	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Polyericus sp.</i>	0	0	0	1	0	0	0	1	0	1	0	?	0	?	?	?	?	0	0	0	0	0	1	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
<i>Polygonarea sp.</i>	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Ribautia centralis</i>	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	?	?	0	0	0	0	0	1	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Schendylodes alacer</i>	0	0	0	0	0	0	0	1	0	1	0	1	0	?	?	?	?	0	0	0	0	0	1	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table 1 (continued)

Character code	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	
Character code	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	
Code in Bonato et al. (2014)	122	125	-	126	128	129	130	-	-	131	132	-	133	141	143	144	-	150	151	152	156	160	161	162	163	-	167	168	169	-	170	-	179	180	182	-	183	185	186	190		
<i>Sogona michoacana</i>	0	0	0	1	0	0	0	1	0	0	0	0	0	?	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	
<i>Stenurytion antipodum</i>	0	0	0	0	1	0	0	0	0	0	0	0	1	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Stenotaenia sorrentina</i>	0	0	1	1	0	0	0	1	1	0	0	0	0	?	0	?	?	0	0	0	0	1	?	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
<i>Srigania crassipes</i>	0	0	1	1	0	0	0	0	0	1	0	0	?	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Srigania maritima</i>	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Srigania svenhedini</i>	0	0	1	1	0	0	0	0	1	0	0	0	?	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Tuoba poseidonis</i>	0	0	1	1	0	0	0	0	1	0	0	0	?	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1

reconnection and holding 10 trees per replication. Branch statistical supports were estimated by bootstrap and jack-knife by means of 1000 replicates, each with 1000 random addition sequences, tree bisection and reconnection, holding 10 trees per replication.

Comparative analysis for troglomorphy

We considered all morphological characters that are often reported as affected by troglomorphy in terrestrial arthropods (Fišer, 2019; Howarth & Moldovan, 2018). We compared these characters between all specimens of the new species and all available specimens of the most strictly related species (according to the phylogenetic analysis, see above). In comparing specimens of different species, we took into account the body size of the specimens and the expected allometric variation of the characters as known in other geophilids (see, e.g., Horneland & Meidell, 2009; Bonato et al., 2016). The comparison was extended to all other known geophilid species, by considering all published original morphological accounts. Character states in the new species were deemed as probably troglomorphic whenever unique to the species in comparison with all other known soil-dwelling geophilids, and demonstrated or reliably interpreted as troglomorphic in other terrestrial arthropods (Fišer, 2019; Howarth & Moldovan, 2018).

Comparative analysis for transitional traits

We considered all character states of the new species that appear phenotypically intermediate between the states observed in other species. To identify those intermediate states that may have been inherited as “transitional” states (in the evolution from a common ancestor to the closest relatives of the new species; see “Introduction” and Fig. 1), we considered the character transformations as optimized in the maximum parsimony phylogenetic tree (see above). Additionally, we carefully considered the intraspecific variation of each character, within the new species as well as within the closest relatives, through direct examination of all available specimens and the published descriptions and illustrations.

Results

Morphology of the new species

Plutogeophilus gen.n. (Figs. 2, 3, and 4)

Diagnosis. Geophilidae with cephalic capsule about as long as wide or slightly elongate. Antennae slender.

Clypeus with a medial clypeal area. Intermediate part of labrum relatively wide and bearing tubercles. Lateral parts of labrum distinctly outlined, far apart from each other and fringed with bristles. First maxillae with entire coxosternite and biarticulated telopodite. Second maxillary coxosternite remarkably shortening mid-longitudinally, the anterior margin deeply angulated and the intermediate part weakly sclerotized, without anterior projections and without statumina or other distinctly sclerotized elements. Second maxillary telopodite composed of three articles, with pretarsus in shape of an elongate, subconic, slightly bent claw. Forcipular tergite subtrapezoidal, with lateral margins distinctly converging forward, about as wide as the cephalic plate and only slightly narrower than the subsequent tergite. Forcipular coxosternite distinctly wider than long, with chitin-lines, without denticles. Coxopleural sutures complete, entirely ventral, sinuous, and diverging forward. Forcipule composed of relatively stout trochanteroprefemur, distinct intermediate articles, elongate and uniformly curved tarsungulum, with a basal denticle. Leg-bearing trunk depressed, uniformly wide for most part and slightly narrowing backward. Trunk metasternites without “carpophagus” pits, with a posterior sub-elliptical transverse pore field, which may be separated into two paired fields. Leg claws simple, with a pair of accessory spines. Ultimate leg-bearing segment with entire pleuropretergite, without sulci. Coxopleura swollen in both sexes. Coxal pores sparse from the ventral to the dorsal sides. Metasternite of the ultimate leg-bearing segment distinctly narrower and shorter than the penultimate, subtrapezoid, distinctly more elongate in the female than in the male. Ultimate telopodite comprising 6 articles and a claw-like pretarsus in both sexes. Additional short dense setae on the ventral side of the ultimate legs and on the posterior part of the coxopleura and relevant metasternite, in both sexes. No anal pores.

Etymology: from the ancient Greek “Ploutōn,” who was the ruler of the underworld in classical mythology.

Type species: *Plutogeophilus jurupariquibaba* sp.n.

***Plutogeophilus jurupariquibaba* sp.n.** (Figs. 2, 3, and 4)

Diagnosis. A *Plutogeophilus* species reaching a body length of ca. 5 cm, with around 53–57 pairs of legs. Cephalic plate without transverse suture. Antenna ca. 4 times as long as the head. Antennal articles elongate, both the distal and the intermediate ones ca. 2 times as long as wide. Three to four pairs of clypeal setae, including one inside the clypeal area. Labrum with ca. 8–10 sclerotized tubercles in the adult. Each lateral part of labrum ca. 3 times as wide as long. Cephalic pleurites without setae, with an additional suture across the anterior part. Mandibular lamella with > 25 elongate teeth in the adult. Second maxillary claw > 4 times

as long as wide at the basis, and slightly shorter than the third article. Exposed part of the forcipular coxosternite ca. 1.8 times as wide as long. Chitin-lines incomplete, pointing lateral to the condyles. Forcipular trochanteroprefemur about as long as wide, tarsungulum ca. 1.5 times as long as the latter, with a stout basal denticle and not distinctly flattened distally. Poison calyx poorly elongate, inside intermediate articles. Trunk metasternites about as long as wide in the anterior part of trunk, longer than wide in the posterior part. Pore fields entire only on the most anterior segments, where they are ca. 3 times as wide as long, with the anterior margin slightly concave, and on the most posterior segments, where they are ca. 1.5 times as wide as long. Legs slightly longer than the width of the body, except for the first pair. Leg claws ca. 4–5 times as long as wide, with the anterior accessory spine distinctly longer than the posterior one. Metatergite of the ultimate leg-bearing segment ca. 1.3 times as wide as long, posterior margin medially truncate. Coxal pores > 30 in the adult. Metasternite of the ultimate leg-bearing segment 1.4–1.5 times as long as wide in the female, ca. as long as wide in the male. Female ultimate telopodite slender, with tarsus 2 much elongate and only slightly shorter than tarsus 1. Male ultimate telopodite moderately swollen, with tarsus 2 poorly elongate and only half the length of the tarsus 1. Ultimate claw without accessory spines. Male gonopods apparently uni-articulated.



Fig. 2 Living specimen of *Plutogeophilus jurupariquibaba* gen.n. sp.n. in the Areias de Cima cave, 7.IV.2012 (photo by Robson Zampaulo)

Etymology: from the Tupi-Guarani “jurupariquibaba,” which literally means “devil’s comb” and is used by Brazilian Indians to refer to centipedes.

Holotype: ISLA 11879, ♂ with developed gonopods, 42 mm long, collected by R.L. Ferreira, 7.IV.2012, in ethanol; originally entire, subsequently divided into three pieces (cephalic capsule, including antennae; maxillary complex and mandibles; trunk). A detailed description is in [Appendix](#).

Type locality: Brazil, São Paulo, near Iporanga, Areias System, Areias de Cima cave.

Phylogenetic position of the new species

The phylogenetic analysis of 81 equally weighted characters produced 1444 equally most-parsimonious trees. The relationships between most geophilids remained unresolved in

the consensus tree (Fig. 5). However, *P. jurupariquibaba* was invariably recovered sister to *Macronicophilus*, without statistical support but with 3 unambiguous synapomorphies, all referring to the ultimate leg-bearing segment: the metasternite is longer than wide, instead of wider than long as in most other geophilids (Ch. 70: 1; Fig. 6g–i), and is also sexually dimorphic, i.e., narrower and more elongate in the female than in the male, which is unique among the geophilids (Ch. 71: 1; Fig. 4g–h); moreover, in the male, the tarsus 2 is distinctly shorter than the tarsus 1, which is unusual among geophilids (Ch. 77: 1; Fig. 6j–o). Alternative analyses with implicit weighting confirmed this relationship but did not provide higher statistical support.

All the four species of *Macronicophilus* clustered in a monophyletic group with high statistical support and 5 unambiguous synapomorphies: the lateral parts of labrum are relatively more longitudinally elongate than in all other geophilids (Ch. 7: 1; Fig. 7a–c); the pretarsus of second maxillae

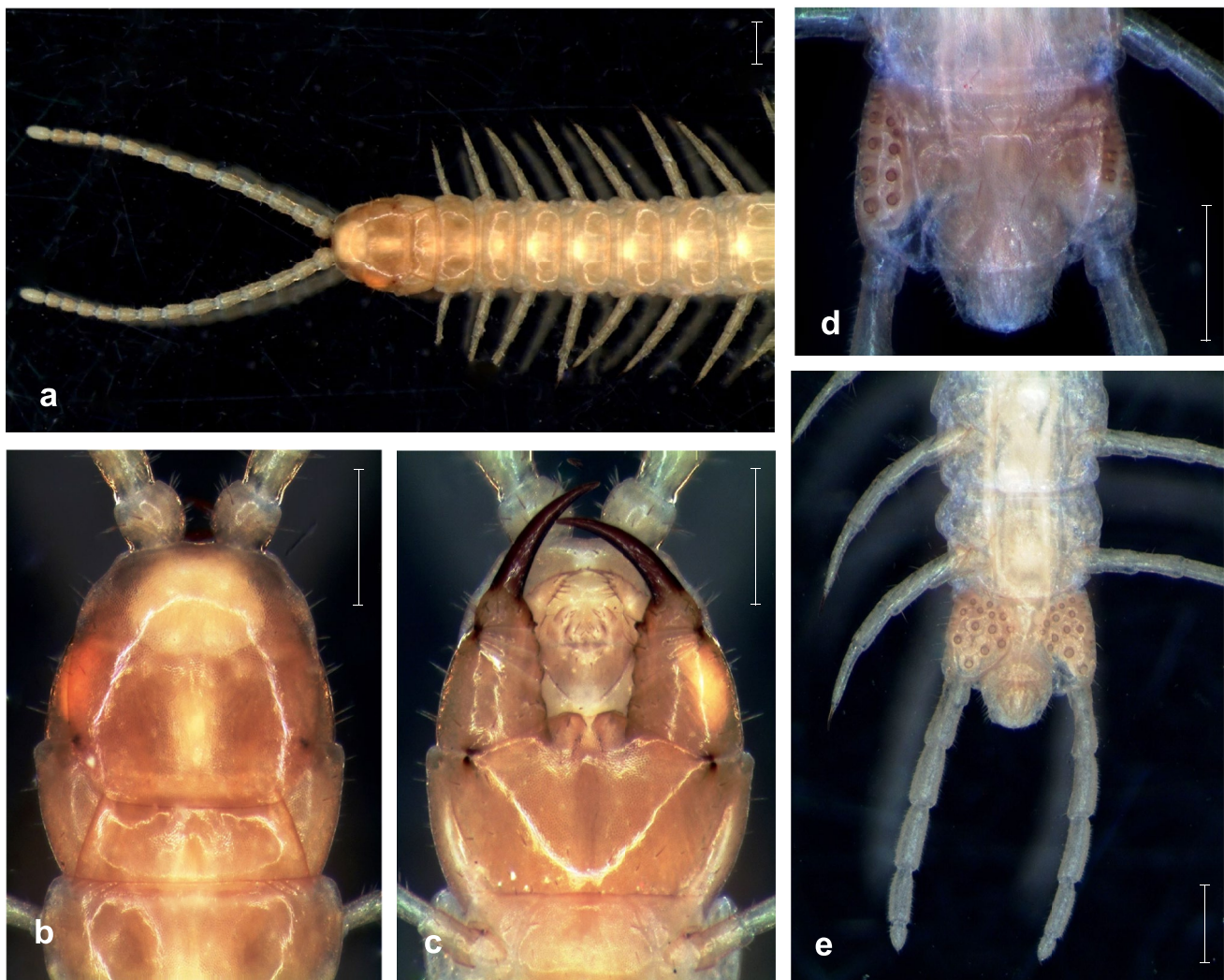


Fig. 3 *Plutogeophilus jurupariquibaba* gen.n. sp.n.: **a** anterior part of body, dorsal view; **b–c** head and forcipular segment, dorsal and ventral views, respectively; **d–e** posterior part of body, dorsal and ventral views, respectively. Photos: ♂, ISLA 11879, holotype. Scale bars: 0.4 μm

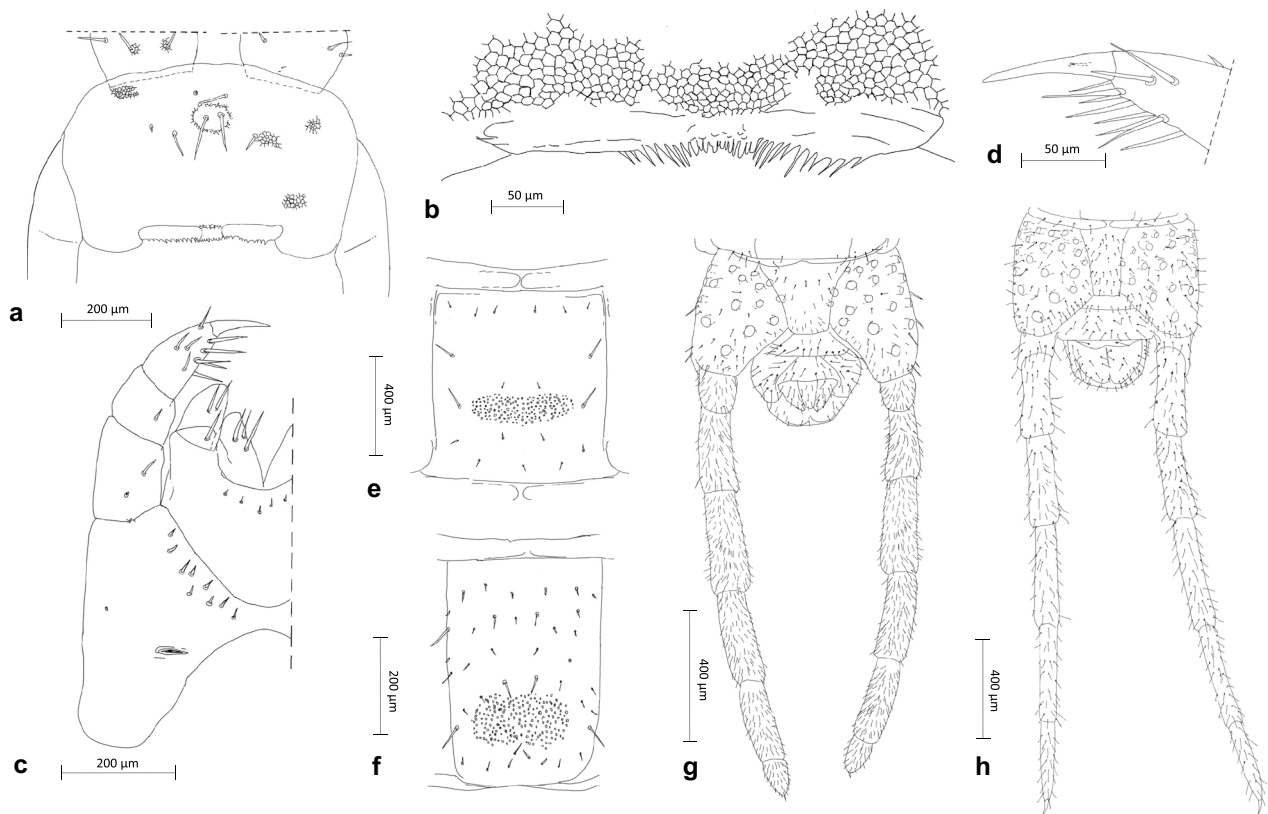


Fig. 4 *Plutogeophilus jurupariquibaba* gen.n. sp.n.: **a** clypeus, ventral view; **b** labrum, ventral view; **c** right half of maxillae, ventral view; **d** right pretarsus of second maxillae, dorsal view; **e** metasternite of leg-bearing segment 12, ventral view; **f** metasternite of penultimate leg-bearing segment, ventral view; **g** ultimate leg-bearing segment and postpedal segments of adult ♂, ventral view; **h** ultimate leg-bearing segment and postpedal segments of adult ♀, ventral view. Line-drawings from photos: **a–g** ♂, ISLA 11879, holotype; **h** ♀, ISLA 12865a, paratype. Areola partially omitted

features as a swollen, rounded, and spiny article instead of a claw (Ch. 29: 1; Fig. 7d–f); the forcipular coxosternite has no chitin-lines (Ch. 40: 0; Fig. 6a–c); all sternal pore-fields are entire, without any obvious mid-longitudinal constriction (Ch. 67: 1; Fig. 7g–i); the legs of the ultimate pair have a single tarsal article, at least in the male (Ch. 76: 1; Fig. 6j–o). The first two synapomorphies are unique at least among the geophilids, whereas the remaining synapomorphies have been recovered convergently also in other geophilids.

Troglomorphic traits of the new species

The comparison of the new species with *Macronicophilus* and other soil-dwelling geophilids (Table 2) suggests that the following distinguishing characters of *P. jurupariquibaba* may be genuinely troglomorphic, i.e., they evolved probably in association with the colonization of the cave habitat:

- Larger body: the maximum body length among the few specimens of *P. jurupariquibaba* (48 mm, $n=5$) is higher than the maximum found in most geophilids (rarely surpassing 4 cm).
- More elongate antennae: the antennal articles of *P. jurupariquibaba* are relatively slenderer and longer than those of most other geophilids.
- More elongate legs: the legs of *P. jurupariquibaba* differ from those of most other geophilids for their overall elongation in comparison with the body as well as for the relative elongation of their articles and their claws.

Other characters could represent troglomorphic traits, according to their functional interpretations. They include elongate setae and larger coxal pores. However, setae and coxal pores of similar size are known also in other geophilids (Table 2).

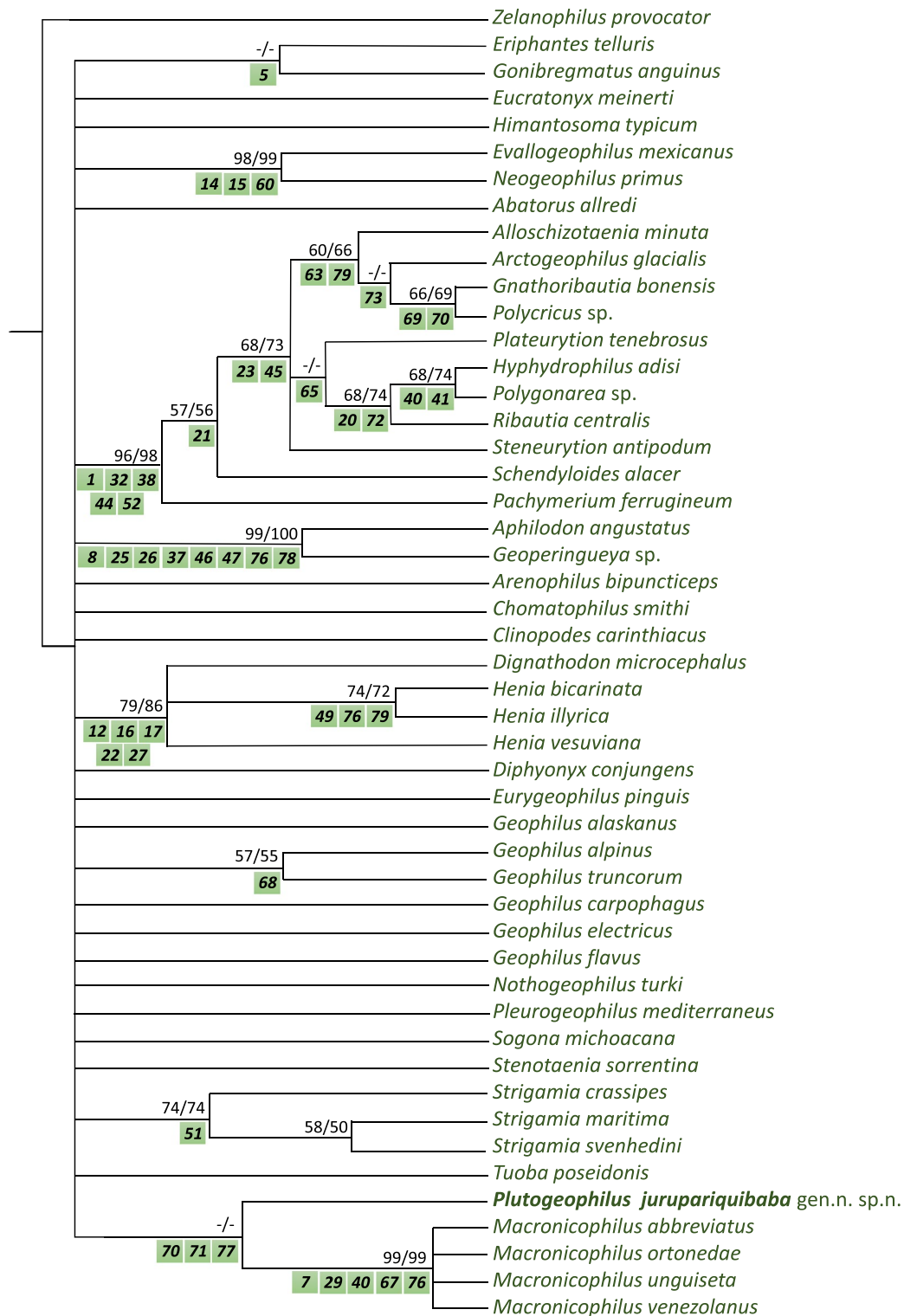


Fig. 5 Consensus tree obtained from the maximum parsimony phylogenetic analysis of Geophilidae s.l. under equal weighting of characters. Bootstrap and jackknife frequencies are indicated above nodes, in this order, when > 50%. Synapomorphies are indicated below nodes (see “Material and methods” for the character codes)

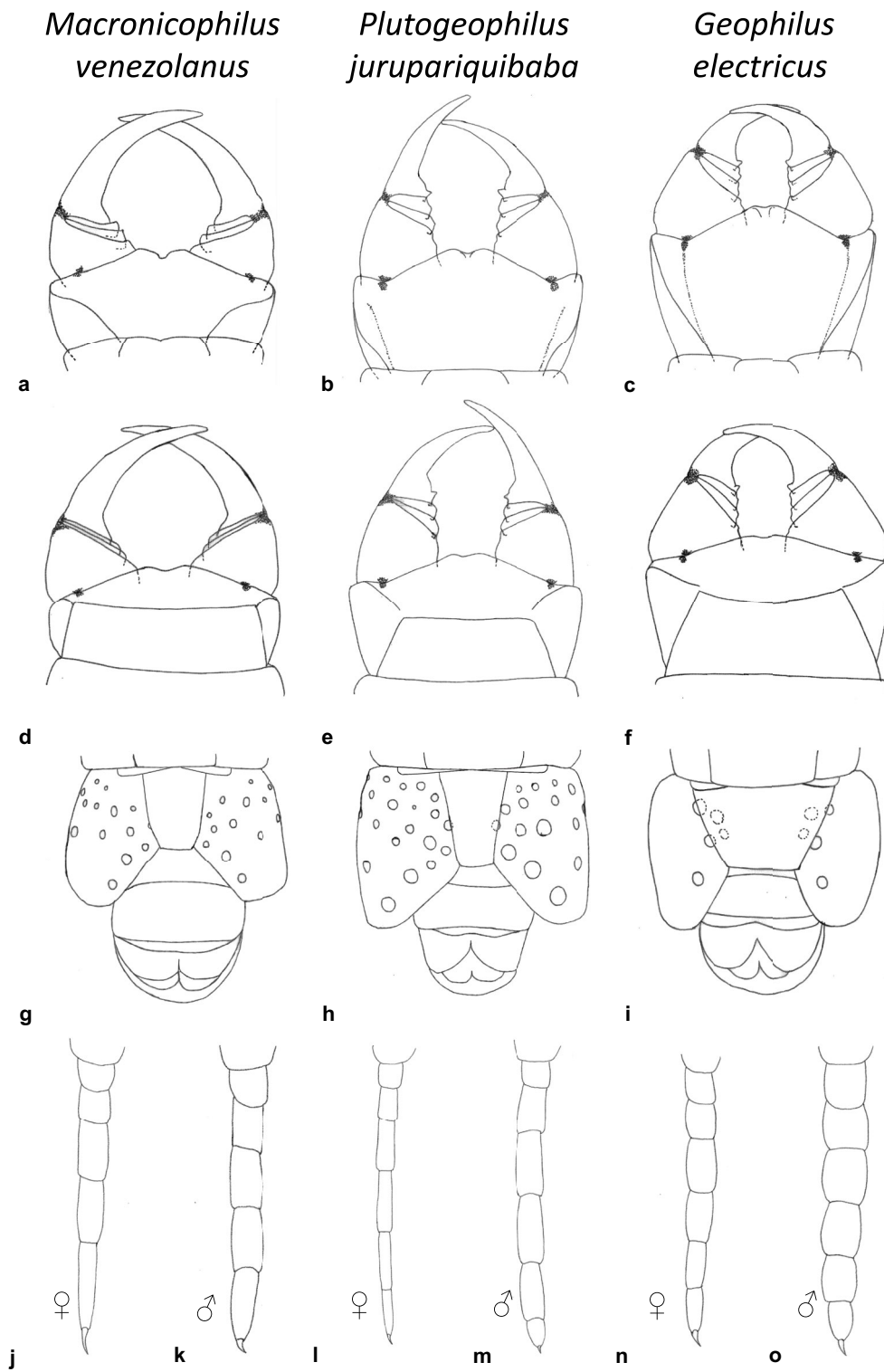


Fig. 6 Comparison between *Plutogeophilus* gen.n., *Macronicophilus*, and another Geophilidae: **a–c** forcipular segment, ventral view; **d–f** forcipular segment, dorsal view; **g–i** ultimate leg-bearing segment of adult ♀, without telopodites, ventral view; **j–o**, right leg of the ultimate pair, ventral view. Line drawings from photos, setae omitted: **a, d, g, j** PD-G 1359; **b, e, m** ISLA 11879; **c, f, i, n** PD-G 230; **h, l** ISLA 12866; **o** PD-G 1510. Redrawn from: **k** Pereira et al., 2000

Discussion

Troglobiosis and troglomorphy of *Plutogeophilus*

Among the > 1000 named species of geophilomorph centipedes (Chilopoda Geophilomorpha), almost all are thought to spend most part of their life in the upper soil layers. Some are known to move regularly on the surface (epigean species), whereas others are thought to live only inside the soil (edaphic or endogean species) (Voigtländer, 2011; Tuf, 2015; Peretti & Bonato, 2018), and a few are thought to be particularly adapted to deep soil layers (Bonato et al., 2016). Specimens of different species of geophilomorphs have been frequently found in caves throughout the world, even in the Neotropical region (e.g., Chagas-Jr & Bichuette, 2018). Also some specimens of *Macronicophilus* have been found in caves (Fonseca et al., 2019b) but most other specimens of the genus have been collected in forest soils (Silvestri, 1909; Pereira et al., 2000). Indeed, only very few

species of geophilids have been recorded exclusively in caves and may be regarded as living only in caves (hypogean or troglobiont species). They include two species of *Geophilus* Leach, 1814 that have been found in a few European caves, in the Pyrenees and the Dinarides, respectively, and show obviously troglomorphic traits (Table 3). Another species has been recently claimed as troglobiont: a new species of *Schendylops* found in a Brazilian cave (Nunes et al., 2019; Table 3). However, the putative troglomorphic traits of the latter species remain to be tested explicitly by a quantitative comparison with related epigean species.

With regard to *P. jurupariquibaba*, different observations suggest that it could be a truly troglobiont species and therefore one of the few troglobiont species of Geophilomorpha in the world. In total, more than 10 specimens have been reported so far and all from inside the caves of the Areias System (Trajano, 1987; Trajano & Bichuette, 2010; Souza Silva & Ferreira, 2016; Chagas-Jr & Bichuette, 2018). Moreover, all five specimens here reported by us have been found

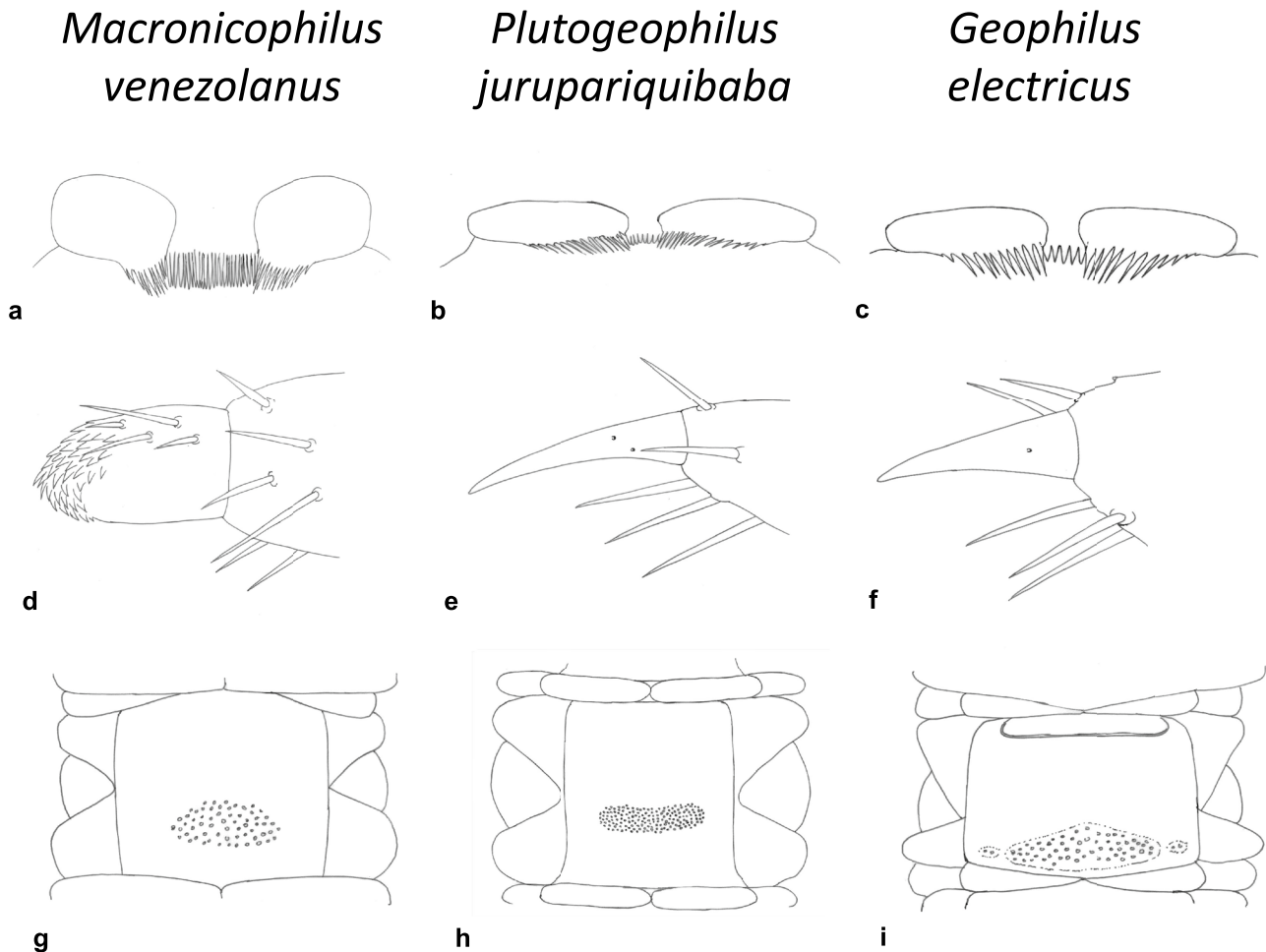


Fig. 7 Comparison between *Plutogeophilus* gen.n., *Macronicophilus*, and another Geophilidae: **a–c** labrum, ventral view; **d–f**, left pretarsus of second maxillae, ventral view; **g–i**, metasternite at ca. 20% of the antero-posterior series of leg-bearing segments, ventral view. Line drawings from photos, setae omitted: **a, d, g** PD-G 1359; **b, e, h** ISLA 11879; **c, f, i** PD-G 230

Table 2 Differences between *Plutogeophilus jurupariquibaba* gen.n. et sp.n., all known species of *Macronicophilus*, and most of other Geophilidae s.l. Character states of *Plutogeophilus* are tentatively interpreted as follows: troglomorphic, i.e., evolved in association with life in caves (Trogl.); synapomorphic with *Macronicophilus* (Synap.); ancestral with respect to *Macronicophilus* (Anc.); transitional between the ancestral state in other geophilids and the derived state of *Macronicophilus* (Trans.)

Species	<i>Plutogeophilus jurupariquibaba</i> gen.n. et sp.n.			<i>Macronicophilus</i>			Most other Geophilidae s.l.	Condition of <i>Plutogeophilus</i>
	orig. obs.	orig. obs.	orig. obs.	<i>M. venezolanus</i> Pereira et al., 2000	<i>M. ortonedae</i> Silvestri, 1909 ^a	<i>M. unguiseta</i> Pereira, 2000 ^a		
Sources	orig. obs.	Pereira et al., 2000; also orig. obs.	Silvestri, 1909; Ribaut, 1912	Pereira et al., 2000	Pereira et al., 2000	Pereira et al., 2000	Various	
<i>N</i> specimens ^b	5 (♂,♀)	12 (♂,♀)	≥ 5 (♂,♀)	1 (♂)	5 (♂,♀)	5 (♂,♀)	–	
Range (<i>N</i> localities ^b)	Alto Ribeira (3 localities)	Venezuelan Coastal Range and Northern Andes (3 localities ^c)	Ecuadorian Andes (1 locality)	Central Amazonas (1 locality)	Central Amazonas (3 localities)	Central Amazonas (3 localities)	–	
Maximum body length (mm)	48	32	27	18	16	16	10–40	Trogl.
Antenna	Antenna/head length 3.2–4.1	3.0–3.7	> 2	3.0	3.1	3.1	1.9–3.7	? Trogl.
	Intermediate articles: max length/width	1.3–1.4	Slightly > 1	1.1	1.0	1.0	1.0–1.7	Trogl.
Setae: max length (µm)	90–100	80–100	?	50–60	50–60	50–60	50–100	? Trogl.
Articles IX and XIII: dark spear-like sensilla	–	+	?	–	+	+	–	? Anc.
Clypeus	Clypeal area: ventral projection ^d	–	+	–	–	–	–	–
Labrum	Posterior plagula	–	+	–	–	–	–	–
	Lateral part: width/length	3.0	1.4–1.6	1.6–1.7	1.6–1.7	1.4–1.5	2–4	Anc.
Cephalic pleurite	Setae	–	+	+	+	+	–	? Anc.
	Transverse suture	+	–?	?	–?	–?	–	–
Mandible	<i>N</i> teeth	> 20	< 20	< 20	< 20	< 20	10–30	–
	Teeth: length/width	> 4	< 4	< 4	< 4	< 4	> 4	? Anc.
Second maxillae	Coxosternite: medial/max length	< 0.1	0.3	0.3	0.3	0.3	0.1–0.5	–
Pretarsus: shape	Claw	Claw	Spiny, rounded	Spiny, rounded	Spiny, rounded	Spiny, rounded	Claw	Anc.

Table 2 (continued)

Species	<i>Platogeophilus juru-pariquibaba</i> gen.n. et sp.n.				<i>Macronicophilus</i>		Most other Geophilidae s.l.	Condition of <i>Platogeophilus</i>
	<i>M. venezolanus</i> Pereira et al., 2000	<i>M. ortonedae</i> Silvestri, 1909 ^a	<i>M. unguiseta</i> Pereira, 2000 ^a	<i>M. abbreviatus</i> Pereira, 2000 ^a				
Forcipular segment	Sub-trapezoid	Sub-rectangular	Sub-rectangular	?	Sub-rectangular	Sub-rectangular	Sub-trapezoid	? Anc.
Exposed part of coxosternite: max width/length	1.8	2.5–2.9	2.6	2.1	2.1	2.1	1.0–1.7	Trans.
Coxosternite: chitin-lines	+	–	–	–	–	–	+	Anc.
Trochanteroprefemur: length/width	1.0	0.7–0.8	0.8	0.8	0.8	0.8	0.8–1.6	–
Tarsungulum/trochanteroprefemur length	1.5	2.5–3.0	2.3	2.5	2.2	2.2	0.9–1.5	Trans.
Tarsungulum: basal denticle	+	–	–	–	–	–	+	Anc.
Ungulum: shape	Not flattened	Distinctly flat	Distinctly flat	Distinctly flat	Not flattened	Not flattened	Not flattened	? Anc.
Poison calyx: elongation and position	Poorly elongate, inside intermediate articles	Very elongate, inside trochanteroprefemur	Very elongate, inside trochanteroprefemur	Very elongate, inside trochanteroprefemur	Moderately elongate, inside trochanteroprefemur	Moderately elongate, inside trochanteroprefemur	Poorly elongate, inside intermediate articles	? Anc.
Legs	<i>N</i> leg pairs	53, 55 (♂) 57 (♀)	53–59 (♂) 55–61 (♀)	53 (♂)	57, 61 (♂) 59 (♀)	39 (♂) 41 (♀)	Various	–
Anterior third of trunk	Leg length/width	7–8	6–7	4–5	5	7	4–7	? Trogl.
	Leg length/head width	1.3–1.5	1.0	0.8	?	0.8	0.5–1.0	Trogl.
	Tarsus: length/width	4–5	2–3	3	2–3	2–3	2.5–3.5	Trogl.
	Leg: setae: max length (µm)	100–120	80–90	?	?	30–40	50–100	? Trogl.
	Pretarsus: length/width	3.8–4.7	3–4	3–4	3–4	3–4	3–4	? Trogl.
	Pretarsus: anterior accessory spine	+	–	?	?	–	+	? Anc.
	Pore-field: anterior margin	Straight to concave	Straight to convex	Straight to convex	Straight to convex	Straight to convex	Various	–
Intermediate third of trunk	Pore-field: medial division	+	–	–	–	–	Various	? Anc.

Table 2 (continued)

Species	<i>Platigeophilus juru-pariquibaba</i> gen.n. et sp.n.			<i>Macronicophilus</i>			Most other Geophilidae s.l.	Condition of <i>Platigeophilus</i>
	<i>M. venezolanus</i> Pereira et al., 2000	<i>M. ortonedae</i> Silvestri, 1909 ^a	<i>M. unguiseta</i> Pereira, 2000 ^a	<i>M. abbreviatus</i> Pereira, 2000 ^a				
Sub-ultimate leg-bearing segments	-	+	?	-	-	-	-	-
Ultimate leg-bearing segment	1.4-1.5/1.0-1.1	1.6-2.0/1.2-1.5	> 1.5/1.1	?/1.0	1.6/1.0	1.6/1.0	0.7-1.0	Synap.
Metasternite: length/width (♀/♂)	> 1	> 1	> 1	?	> 1	> 1	1	Synap.
Metasternite: (length/width ♀)/(length/width ♂)								
Coxopleuron: N pores	23-42	22-40	24-29	11-13	9	9	Various	-
Coxal pore: max diameter (µm)	45-50	25-30	?	10	15-20	15-20	10-30	? Trogl.
Telopodite: N articles, excl. pretarsus (♀/♂)	6/6	5/5	5/5	?/5	5/5	5/5	6/6	Anc.
Telopodite: swelling (♀/♂)	-/moderate	-/-	-/-	?/-	-/much	-/much	-/+	-
♂ tarsus 2/tarsus 1 length	0.5	0	0	0	0	0	0.8-1.0	Synap., Trans.
Leg: ventral dense setae (♀/♂)	+/+	-/-	-/-	?/-	-?/+	-?/+	-/+	-
Postpedal segments	-	+	+	+	+	+	+	-
Anal pores	-	+	+	+	+	+	+	-

^athe intraspecific variation of most characters is unknown for these species, because characters have been evaluated on a single specimen only; ^bother ≥ 3 specimens of *Macronicophilus* sp. have been reported from three caves (Fonseca et al., 2019a; also orig. data), whereas specimens from another site in southern Brazil originally reported as *Macronicophilus* sp. (Calvanese & Pereira, 2013) are actually belonging to *Schendyllops demelloi* (Verhoeff, 1938) (V. Calvanese, com. pers.); ^cspecimens from a locality in the Colombian Andes had been originally recorded as *Macronicophilus* sp. (Prado-Sepúlveda et al., 2016) and are here identified by us as *M. venezolanus*; ^dpossibly an artifact, because variable conditions were found in specimens of *P. jurupariquibaba*

Table 3 Putative troglomorphic traits in the putative troglobiont species of Chilopoda Geophilomorpha

Species	<i>Geophilus persephones</i> Foddai & Minelli, 1999	<i>Geophilus hadesi</i> Stoev et al., 2015	<i>Schendylops janelao</i> Nunes et al., 2019	<i>Plutogeophilus jurupariquibaba</i> gen.n. sp.n.
Cave system	Pyrenees: La Pierre Saint-Martin (=Lépineux = La Verna)	Dinarides: Velebit: Muda labudova; Munižaba; ? Lukina jama–Trojama	Brazilian Highlands: Peruaçu: Gruta do Janelão	Brazilian Highlands: Alto Ribeira: Areias: Ressurgência das Areias; Areias de Cima; Areias de Baixo
<i>N</i> collected specimens	1	2 (+ 1?)	3	> 10
Sources for morphology	Foddai & Minelli, 1999	Stoev et al., 2015	Nunes et al., 2019	Orig.
Larger body	–	?	–	+
Longer setae	–	?	?	?
Elongate appendages	+	+	+	+
Slender claws	+	+	?	+
Larger coxal pores	–	+	–	?

in deep portions of the caves, none in the shallower parts of the caves or outside, despite that the surroundings are covered with forests (Brazilian Atlantic Forest) and host other soil-dwelling geophilomorphs (pers. obs.). Additionally, both adults and juveniles have been found in the caves, and specimens have been spotted repeatedly while walking on speleothems or above muddy compacted sediments (Fig. 2). The fact that specimens of *P. jurupariquibaba* have been found in all the three caves of the Areias System (Areias de Cima, Areias de Baixo, Ressurgência das Areias) may be explained by the fact that the three caves constitute an interconnected system, both structurally and functionally, with the Areias subterranean stream connecting the caves. Indeed, most of the troglobiont species living in the system are found in all three caves (Souza Silva & Ferreira, 2016), suggesting the possibility of hypogean dispersal among the caves. Worth noting, the Areias System is one of the two primary hotspots of subterranean biodiversity in the Neotropic region: to date, 28 endemic animal species have been recorded, only part of which have been already described and named (Souza Silva & Ferreira, 2016).

The troglobiosis of *P. jurupariquibaba* is also suggested by some derived morphological traits that can be interpreted as troglomorphic confidently, i.e., the relatively large body and the relatively elongate antennae and legs (Table 2). Even though these and other traits are repeatedly found in cave-dwelling animals and are often interpreted as convergently evolved as adaptation to the hypogean habitat (Fišer, 2019; Friedrich, 2019), the recognition of genuinely troglomorphic traits in geophilomorphs is not straightforward. In general, common troglomorphic characters are often shown by soil-dwelling animals as well, especially by endogean species (Christiansen, 2012; Deharveng & Bedos, 2018), and this is especially the case with all geophilomorph centipedes.

As corroborated by our phylogenetic analysis, the cave-dwelling *P. jurupariquibaba* evolved from soil-dwelling animals that already shared some apparently troglomorphic

characters that evolved most probably for adaptation to the soil habitat and not to caves. In detail, the full regression of eyes, a significant reduction of the integument thickness, and the suppression of pigments in the integument evolved most probably at the origin of the entire Geophilomorpha, without any subsequent reversal (Edgecombe, 2011). It has been hypothesized that such traits may facilitate the colonization of cave habitats and the further evolution of endogean species into troglobiont species (Christiansen, 2012). However, troglobiont species are actually rare in some endogean arthropod lineages, e.g., the Anillini carabid beetles and the Isotomidae springtails (Christiansen, 2012). Similarly, within Chilopoda, cave colonization and specialization seem to have occurred more frequently among lineages of primarily epigeal centipedes (especially Lithobiomorpha) than among blind, poorly sclerotized, and depigmented lineages of endogean centipedes (Geophilomorpha and a subgroup of Scolopendromorpha) (Shear & Krejca, 2019; Stoev et al., 2015). Although hypothetical, it seems that strictly endogean arthropods are less prone to differentiate in caves, given their capability of moving between caves and other subterranean habitats (including shallow subterranean habitats). However, this may be not a general rule: for instance, within palpigrades, which are primarily blind and depigmented soil-dwellers, several troglobiont species exist around the world (Mammola et al., 2021).

We reasonably highlighted some probably genuine troglomorphic traits in *P. jurupariquibaba* (Table 2) by comparison with specimens of other geophilids and by taking into account the body size and the expected allometric variation as known in other geophilids (see “Material and methods”). In the case of *P. jurupariquibaba*, the transition to the cave habitat has been apparently associated with an increase of the body size, a proportional elongation of the sensorial and walking appendages, as well as of the leg claws and their associated spines. Additionally, it could have been accompanied also by a moderate elongation of the setae (sensilla

trichodea) and a moderate widening of the coxal pores (possibly involved in osmoregulation; see, e.g., Littlewood, 1991; Rosenberg et al., 2011).

Phylogenetic position of *Plutogeophilus*

Even though we tried to extract DNA from the few collected specimens of *Plutogeophilus*, they resulted unsuitable for molecular phylogenetics. Nevertheless, morphological evidence alone provided compelling evidence that *Plutogeophilus* belongs to the Geophilidae s.l. and, among extant geophilids, it probably represents the sister lineage of the enigmatic *Macronicophilus*.

In detail, the following characters of *Plutogeophilus* are known as synapomorphies of the Geophilidae s.l. (Bonato et al., 2014): in the labrum, the side-pieces are represented by single sclerites, instead of two sclerites (so-called alae; Bonato et al., 2010; Figs. 4b, 7a–c) and the posterior margin of the side-pieces is fringed with so-called bristles (i.e., delicate branching projections; Bonato et al., 2010; Fig. 4a–b); additionally, in the females, the gonopods are coalescent into a short, entire lamina (Bonato et al., 2014; Fig. 4h).

Moreover, some similarities between *Plutogeophilus* and *Macronicophilus* in the ultimate leg-bearing segment were retrieved as unambiguous synapomorphies of *Plutogeophilus* + *Macronicophilus* in our phylogenetic analysis. In detail, the metasternite is similar in the general shape (subtrapezoid as in many other geophilids, but unusually longer than wide; Fig. 6g–i) and in the relative size (distinctly smaller than the penultimate metasternite and distinctly narrower than the overall breadth of the coxopleura; Fig. 6g–i). Actually, shape and size of the metasternite of *Plutogeophilus* and *Macronicophilus* resemble those found in some Aphilodontinae (Calvanese et al., 2019) and some species of *Geoperingueyia* Attems, 1926 (Lawrence, 1955; Pereira, 1981). However, Aphilodontinae and *Geoperingueyia* are very different from *Plutogeophilus* and *Macronicophilus* in other morphological characters (Calvanese et al., 2019) and there is no evidence for a close relationship (Fig. 5). Additionally, the sexual dimorphism of the metasternite in both *Plutogeophilus* and *Macronicophilus* (forward broader in the male than in the female; Fig. 4g–h) is unique among the geophilids, and—to the best of our knowledge—among Geophilomorpha at large. Indeed, such sexual dimorphism had not been reported explicitly for *Macronicophilus* before, but we observed it in both of the examined species (*M. abbreviatus* and *M. venezolanus*) and published drawings confirm it also in the other two species (*M. ortonedae* and *M. unguiseta*).

Plutogeophilus and *Macronicophilus* are very similar also in the modification of the distal part of the ultimate legs of males: the ultimate article is remarkably reduced (in *Plutogeophilus* males) or fully missing (in *Macronicophilus* males), in comparison with the females and with most

other geophilids of both sexes. Actually, apparently similar modifications (ultimate legs composed of a lower number of articles, either in the males only or in both sexes) are known in other geophilids (Aphilodontinae, *Apogeophilus* Silvestri, 1905, *Geomerinus* Brölemann, 1912, *Geoperingueyia*, some species of *Henia* C.L. Koch, 1847, *Navajona* Chamberlin, 1930, *Timpina* Chamberlin, 1912; Edgecombe et al., 2011). However, other major morphological differences suggest that all these geophilids are not strictly related to *Plutogeophilus* + *Macronicophilus*.

Besides the above-mentioned synapomorphies, which are corroborated by the phylogenetic analysis, other similarities between *Plutogeophilus* and *Macronicophilus* may be interpreted as additional evidence of their close relationship.

For instance, considering the forcipular apparatus, in *P. jurupariquibaba* and all four species of *Macronicophilus* the coxosternite is relatively short and the tarsungula are distinctly elongate when compared to most other geophilids (Fig. 6a–c). Similarly shortened forcipular apparatuses are found sparsely in other distantly related geophilids (*Chomatophilus* Pocock, 1896, *Tampiya* Chamberlin, 1912, *Eurygeophilus* Verhoeff, 1899, some species of *Stenotaenia* C.L. Koch, 1847, most Dignathodontinae), but other major anatomical differences—also in the forcipular apparatus—suggest that they are not strictly related to *Plutogeophilus* + *Macronicophilus* and none of them lives in South America.

Considering the body trunk, in *P. jurupariquibaba* and all species of *Macronicophilus* the clusters of ventral glandular pores (the so-called pore-fields) have a similar shape (each pore-field is transversally sub-elliptical and broadly rounded—instead of distinctly narrowing—on the lateral sides; Fig. 7g–i) and a similar pattern of longitudinal variation along the trunk (pore-fields are present from the first to the penultimate leg-bearing segment and the most posterior ones extend forward broadly; Fig. 4f). Very different shapes and patterns of pore-fields are present in different clades of geophilids (Turcato et al., 1995), and somehow similar conditions are found only in the Western Palearctic *Clinopodes* C.L. Koch, 1847, which however differs from both *Plutogeophilus* and *Macronicophilus* in other traits (Edgecombe et al., 2011).

Plutogeophilus and *Macronicophilus* share also an unusually high number of coxal pores when compared to most other geophilids (up to a few tens of pores on each coxopleuron, in individuals that are some centimeters long; Fig. 4g–h), as well as an unusual arrangement of the pores (sparse quite uniformly on the entire exposed surface of the coxopleura, from the medio-ventral, through the lateral to the medio-dorsal sides; Figs. 3d–e, 6g–i). The variability documented between specimens of different species of *Macronicophilus* is consistent with the expected intraspecific positive correlation between number of pores and body size (e.g., Horneland & Meidell, 2009). Among other

geophilids, high numbers of sparse coxal pores are known only in some species referred to *Polycricus* Saussure & Humbert, 1872, *Telocricus* Chamberlin, 1915, *Geomerinus* Brölemann, 1912, and *Stenurytion* Attems, 1909. All these nominal genera are known inadequately; however, some major characters suggest that they are only distantly related to *Plutogeophilus* and *Macronicophilus*.

Insights into the evolution of *Macronicophilus*

For some characters, *Plutogeophilus* shows a condition that is different from that found in *Macronicophilus* and instead shared with most of the other geophilids (Table 2, Figs. 6 and 7). These traits, which are recognized as symplesiomorphic according to the phylogeny (Fig. 5), may provide hints on the evolution of many unusual, derived characters of *Macronicophilus*, and even on the ancestral condition of peculiar traits that have remained hard to homologize.

The unusual labrum of *Macronicophilus* may be confidently traced back to the ancestral structure of the labrum of geophilids through the longitudinal expansion of the lateral parts (Fig. 7a–c).

The unique shape of the second maxillae of *Macronicophilus* probably originated through the overall transformation of the claw-like pretarsus into a swollen, spinous element (Fig. 7d–f). The bizarre spinous terminal structure was noticed as the most remarkable and puzzling feature of *Macronicophilus* and was often interpreted as a supernumerary article (in addition to the three articles found in most other geophilids) instead of a modified pretarsus (Silvestri, 1909; Pereira et al., 2000). Indeed, the presence of setae on this peculiar structure (Fig. 7d) may support this alternative hypothesis, because setae are commonly found on the articles of the centipede appendages but not on their pretarsi. However, we did not find transitional conditions suggesting the evolutionary addition of a novel article coupled with the suppression of the pretarsus. Moreover, other lineages of geophilids experienced modifications of the second maxillary pretarsus, even though most often through size reduction and shape simplification into a spinous tubercle or a single spine (e.g., some *Geophilus*, the Aphilodontinae and most Dignathodontinae and Linotaeniinae).

Instead, the walking legs underwent the suppression of the anterior accessory spines of the claws and the ultimate legs underwent the suppression of the claw and of the entire terminal article (Fig. 6j–o).

For some characters, *Plutogeophilus* shows an apparently intermediate condition between the probable ancestral condition shared by most geophilids and the derived condition shown by *Macronicophilus*. If such extant intermediate traits actually resemble transitional traits evolved in the common ancestor between *Plutogeophilus* and *Macronicophilus*, they may contribute additional insights into the evolution of the

very distinctive morphology of *Macronicophilus*. In particular, considering the forcipular apparatus, *Plutogeophilus* shows a relatively stouter coxosternite and relatively elongate tarsungula in comparison with most other geophilids, and this condition appears transitional towards an even more strongly stout coxosternite and a much more elongate tarsungula of *Macronicophilus* (Table 2; Fig. 6a–c). This suggests a stepwise evolutionary modification through the lateral expansion of the tergite, the shortening of the coxosternite and the suppression of the chitin-lines, the shortening of the trochanteroprefemora, the elongation of the tarsungula, and the suppression of all denticles.

In the same way, considering the ultimate legs, the ultimate article of *Plutogeophilus* is conspicuously reduced in the males, in comparison with most other geophilids, and this condition appears transitional towards the full suppression of that article in the males of all species of *Macronicophilus* and even in the females of at least 3 of the 4 species (Table 2; Fig. 6j–o).

Conservation issues

During several years, Brazilian caves were integrally protected. In 2008, a presidential decree (decree 6640) brought rules based on geological, biological, and cultural parameters to classify caves in degrees of relevance, giving full protection only to those classified as presenting maximum relevance. However, a recent presidential decree (decree 10,935) started to allow the destruction of even those caves of maximum relevance, thus representing an enormous risk to all Brazilian subterranean biodiversity (Ferreira et al., 2022). Troglobiont species like *P. jurupariquibaba* are particularly threatened, as they are endemic to one or a few caves, since their dispersal capability is dependent on the occurrence of subterranean voids that are often limited by several types of geological barriers. Hence, currently, even caves hosting exclusive troglobiont species may be destroyed in Brazil, and dozens of such species may go extinct in the next years.

Even though the Areias Cave System is inside a protected area, the headwaters of the drainages that supply the caves inhabited by *Plutogeophilus* are located outside the limits of this area. Hence, impacts occurring in the surrounding region can severely affect this cave system in different ways, from changing the organic supply to the caves to altering microhabitats, for example, through the silting of the subterranean drainages.

Considering the importance of the new species herein described, associated with the several other troglobiont species inhabiting the Areias Cave System (and other important caves in the country), it is of paramount importance that the Brazilian policy regarding cave protection be reviewed.

Scientists should conduct such revision, considering not only the obvious need of preserving karst systems due to their biodiversity and endemic species, but also due to the essential ecosystem services they provide.

Appendix

Description of holotype of *Plutogeophilus jurupariquibaba* sp.n.

ISLA 11879 (Figs. 3, 4a–g).

General features. Body depressed and almost uniformly wide along the trunk, only slightly narrowing backward. Color (in ethanol) uniformly brownish yellow, head and forcipular segment slightly darker.

Cephalic capsule. Cephalic plate sub-quadrangle, about as long as wide, lateral margins slightly narrowing more forward than backward; scutes approximately isometric and up to 10 µm wide in the anterior half of the cephalic plate, only slightly elongated longitudinally in the posterior half; transverse suture absent; setae up to ca. 80 µm long. Clypeus ca. 2.3 times as wide as long, with lateral margins complete; uniformly areolate, the scutes being up to 10 µm wide, with a single medial clypeal area, distinctly projecting ventrally; 3 pairs of setae, including one inside the clypeal area, one anterior and one latero-posterior. Pleurites uniformly areolate, without setae; an additional suture across the anterior part of the pleurite, almost reaching the lateral margin of the cephalic plate. Intermediate part of labrum ca. 1.5 times as wide as long, bearing ca. 8 stout tubercles, which are relatively sclerotized, stout but with a very short apical spine. Lateral parts of labrum far apart from each other, each bearing a row of a dozen marginal bristles, which are poorly sclerotized.

Antennae. Slender, ca. 3.8 times as long as the head width. Intermediate articles up to ca. 2.0 times as long as wide. Article XIV ca. 2.4 times as long as wide, ca. 1.6 times as long as article XIII. Setae gradually denser and shorter from the basal articles to the distal ones, both ventrally and dorsally, up to 80 µm long on article I but less than 50 µm long on article XIV. Apical sensilla ca. 15 µm long, spear-like, without projections, distinctly narrowing at about the mid-length. Club-like sensilla ca. 10 µm long, only on article XIV, grouped on the distal parts of both the internal and external sides. Three longitudinal rows of 1–5 proprioceptive spine-like sensilla at the bases of the antennal articles, approximately dorsal, ventro-internal, and ventro-external; ventral rows poorly detectable on articles I–II; rows reduced to 0–1 sensilla on antennal articles VI, X, and XIV. A few sensilla, similar to the apical ones, up to 5 µm long, on both dorso-external and ventro-internal position, close

to the distal margin of articles V, IX, and XIII; no distinctly darker spear-like sensilla (type “c” in Pereira et al., 2000).

Mandibles. A single pectinate lamella, with ca. 25 teeth, on each mandible; most teeth elongate, more than 4 times as long as wide at the basis.

First maxillae. Coxosternite entire, without mid-longitudinal sulcus, with 5 setae. Coxal projection sub-triangular, wider than long, bearing 8 setae. Telopodite composed of two articles, the distal one with 4–5 setae. A pair of short, round lappets on the basal articles only, fully concealed from below.

Second maxillae. Coxosternite remarkably shortening mid-longitudinally (< 0.1 of the maximum length), the anterior margin deeply angulated and with approximately straight converging sides, the intermediate part weakly sclerotized and with mid-longitudinally sulcus; 23–24 setae, all in the medial part or close to the anterior margin; no anterior projections; metameric pores featuring as transverse slits, without statumina or other distinctly sclerotized elements. Telopodite composed of three articles, only slightly narrowing towards the tip; 2–3 short ventral setae on the basal article, 1–2 mesal setae on the intermediate article, ca. 14 long setae on the distal article, most of which on the ventral side; pretarsus in shape of an elongate claw, ca. 0.8 times as long as the distal article, and ca. 4.5 times as long as wide at the basis, subconic and slightly bent; 3 pore-like sensilla on each pretarsus, one on the antero-dorsal side and the other two on the ventral side.

Forcipular segment. Tergite subtrapezoidal, ca. 2.3 times as wide as long, with lateral margins strongly converging forward, ca. 0.8 times as wide as the subsequent tergite, partially covered by both the cephalic plate and the subsequent tergite. Pleurites without scapular ridge. Exposed part of the coxosternite ca. 1.8 times as wide as long; anterior margin slightly projecting forward, without denticles but with a medial shallow concavity; coxopleural sutures complete, entirely ventral, sinuous, and diverging forward; chitin-lines incomplete, pointing lateral to the condyles. Basal distance between the forcipules ca. 0.2 of the maximum width of the coxosternite. Forcipular trochanteroprefemur approximately as long as wide and intermediate articles distinct, without denticles. Tarsungulum ca. 3.0 times as long as wide, and 1.5 times as long as the trochanteroprefemur; both the external and the internal margins uniformly curved, but for a mesal moderate basal bulge bearing a subconic, stout denticle; ungulum not flattened. Poison calyx elongate, ca. 2 times as long as wide, in the forcipular intermediate articles.

Leg-bearing segments. A total of 53 pairs of legs. Metatergite 1 slightly wider than the subsequent one, without pretergite. No paratergites. Metasternites about as long as wide in the anterior part of trunk, whereas up to 1.5 times

as long as wide in the posterior part. No obvious “carphagus” pits. Glandular pores arranged into a sub-elliptical transverse field on the posterior part of each metasternite, from the first to the penultimate leg-bearing segments, but separated into two paired fields between leg-bearing segment 19 and 50. The entire pore fields on the anterior part of the trunk are ca. 3 times as wide as long, with the anterior margin slightly concave, those on the most posterior segments are ca. 1.5 times as wide as long. Legs of the first pair slightly smaller than the subsequent ones, which are slightly longer than the width of the trunk. Leg claws simple, uniformly bent; a pair of accessory spines, the anterior one reaching ca. 30–40% of the length of the claw, the posterior one much shorter.

Ultimate leg-bearing segment. Pleuropretergite without sulci separating pleurites. Metatergite subtrapezoid, ca. 1.3 times as wide as long, lateral margins convex and converging backward, posterior margin medially truncate. Metasternite subtrapezoid, about as long as wide, forward ca. 1.9 times as wide as backward, lateral margins slightly concave and converging backwards; setae denser close to the posterior margin. Coxopleuron ca. 1.8 times as long of the metasternite; setae denser close to the postero-mesal and posterior margin. Coxal organs of each coxopleuron opening through ca. 25 independent pores, scattered on the ventral (13 on the right, 16 on the left), lateral (6 on the right, 5 on the left) and dorsal (4 on the right, 5 on the left) sides; the largest pores ca. 45–50 μm wide. Telopodite ca. 9–10 times as long as wide, ca. 1.3 times as long and ca. 1.3 times as wide as the penultimate telopodite; 6 articles, all similar in width, the tarsus 2 ca. 1.4 as long as wide and ca. 0.5 as long as the tarsus 1; lateral and ventral side with dense setae mostly less than 50 μm long. Pretarsus claw-like, distinctly shorter than the claws of the preceding legs, apparently without accessory spines.

Postpedal segments. Genital sternite separated by oblique sulci from pleurites. Gonopods elongate, apparently unarticulate, separated at the basis, with penis in between. Anal organs apparently lacking.

Differences in a paratype of *Plutogeophilus jurupariquibaba* sp.n.

ISLA 11866 (Fig. 4h).

General features. Color (in ethanol) of head and some most anterior trunk segments slightly darker than remaining body.

Cephalic capsule. Cephalic plate ca. 1.1 as long as wide. Clypeal area not projecting ventrally. Labrum and mandibles: not examined.

Antennae. Ca. 4.1 times as long as the head width. Setae up to 100 μm long on article I.

Leg-bearing segments. A total of 57 pairs of legs. Two paired fields, instead of a single entire pore-field, between leg-bearing segments 20 and 54.

Ultimate leg-bearing segment. Coxal organs on each coxopleuron (right/left): 17/15 ventral, 6/6 lateral, 10/12 dorsal. Metasternite ca. 1.4 times as long as wide, forward ca. 1.9 times as wide as backward, lateral margins approximately straight and converging backwards. Telopodite ca. 1.1 times as long and ca. 1.1 times as wide as the penultimate telopodite; articles gradually decreasing in width, the tarsus 2 ca. 4.5 as long as wide and ca. 0.8 as long as the tarsus 1; dense short setae on the lateral and ventral sides of trochanter, prefemur, femur and tibia, fewer on tarsus 1, none on tarsus 2.

Postpedal segments. No oblique sulci separating pleurites and genital sternite. Gonopods represented by a short bilobate lamina, without penis. Anal organs apparently lacking.

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Author contribution Both authors contributed to the study conception and design. The material was collected by RLF. Data were collected and analyzed by LB. The first draft of the manuscript was written by LB. Both authors approved the final manuscript.

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Data availability Data are available from the corresponding author on request.

Declarations

Competing interests The authors declare no competing interests.

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