Research Article

A new and critically endangered species and genus of Onychophora (Peripatidae) from the Brazilian savannah — a vulnerable biodiversity hotspot

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In recent years, a high number of endemic species might have gone extinct silently in the Brazilian savannah (=Cerrado), a biodiversity hotspot, as researchers are not able to describe them as fast as their natural habitats are being destroyed. This especially holds true for onychophorans, or velvet worms, which include many point endemic species and, in this biome, only occur in small gallery forests susceptible to disturbances. In the present work, we use a combined morphological and molecular approach to describe a relict and critically endangered onychophoran species from the Cerrado. Our morphological analyses using light and scanning electron microscopy revealed novel characters and character states for Peripatidae, such as six interpedal structures per segment, modified scales on the genital and posterior body region of females and a third class of dermal papillae, herein named peripheral accessory papillae. Since Cerradopatus sucuriuensis gen. et sp. nov. showed a unique set of morphological characters and could not be assigned to any described genus of Peripatidae, a new genus is raised for this species herein. In addition to morphological data, the new taxon is supported by karyotypic, slime protein profiling and molecular data, including sequences of the mitochondrial genes COI and 12S rRNA. Unfortunately, Cerradopatus sucuriuensis gen. et sp. nov. is prone to an extremely high risk of extinction in the wild, as it only occurs in specific humid patches within three small, unprotected fragments of forest that are being progressively affected by human activities. According to the IUCN Red List categories and criteria, this species is classified as Critically Endangered and requires urgent conservation efforts.

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Key words: Brazil, Cerrado, conservation biology, molecular phylogeny, morphological diversity, taxonomy, threatened species, velvet worms

Introduction

In recent years, the progressive loss of natural habitats has intensified the discussion of strategies for conservation of biodiversity. However, little attention has been given to the actual recording of this biodiversity and many species become extinct even before they can be described (Lewinsohn, Freitas, & Prado, 2005; Mesibov, 2004). This situation is sometimes exacerbated by the fact that conservation efforts are mainly focused on vertebrates (e.g. mammals and birds) and rarely on small and cryptic invertebrates (Böhmer, Kemp, Baillie, & Collen, 2012; New, 1995), even though these are by far more diverse than the former (Scheffers, Joppa, Pimm, & Laurance, 2012; Wilson, 1987). Among the few invertebrate groups considered for conservation, onychophorans, or velvet worms, are important flagship species for habitat protection, due to the point endemism of species and their...
restriction to humid environments susceptible to disturbance (New, 1995).

One example of the high impact of onychophorans for conservation is the establishment of a natural reserve in Brazil based on the limited distribution of the species *Epiperipatus acacioi* (Conselho Estadual de Política Ambiental [COPAM], 1988) — one of the rare cases worldwide and the only one in Brazil (see Lewinsohn et al., 2005), in which a nature reserve has been established based on a single invertebrate species. The peculiar biology of onychophorans led the International Union for Conservation of Nature (=IUCN) to suggest that all representatives of this group should be treated as at least ‘Vulnerable’ (IUCN, 2013; Wells, Pyle, & Collins, 1983), although individual species might be allocated to different ‘threatened’ categories (IUCN, 2013; New, 1995). However, the limited information on most species still hampers the evaluation of their vulnerability (New, 1995), and currently only 11 onychophoran species are effectively included in the IUCN Red List (IUCN, 2013).

In the last few years, several species of both Peripatidae and Peripatopsidae — the two major onychophoran subgroups — have been described (e.g. Daniels, McDonald, & Picker, 2013; McDonald, Rubberg, & Daniels, 2012; Oliveira, Franke, et al., 2012; Oliveira, Lacorte, Fonseca, Wieloch, & Mayer, 2011; Oliveira, Schaffer, et al., 2013; Rubberg & Daniels, 2013). Yet, the 205 nominal taxa of Onychophora might represent only a minor part of the expected diversity of the group (see Daniels et al., 2013; Oliveira, Franke, et al., 2012; Oliveira, Read, & Mayer, 2012; Oliveira, Schaffer, et al., 2013; Rubberg & Daniels, 2013). For example, only 16 species have been reported from Brazil (Table 1), although recent findings suggest that a new onychophoran species might occur every 20–30 km in this country (Oliveira et al., 2011). Considering that Brazil covers an area of 8,515,767 km² and shows a great variety of landscapes and biomes (Fig. 1), it would be expected that this country alone houses several hundred new species. On the other hand, the accelerated rate of habitat destruction in Brazil (Laurance, 2010) also suggests that many of these species might go extinct even before they can be described.

In the present study, we investigate a new species of Peripatidae from the Brazilian savannah (=Cerrado), one of the richest and most threatened environments worldwide (CI, 2004). Included among the 25 world biodiversity hotspots (Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000), the Cerrado originally occupied 22% of the Brazilian territory (Oliveira & Marquis, 2002), but recent estimates suggest that only one-fifth of its vegetation still exists (Myers et al., 2000) and no more than 1.4% of its original extent corresponds to effectively protected areas (CI, 2014). The occurrence of Onychophora in the Cerrado remains largely unexplored and only two onychophoran species have been described from this environment to date (Fig. 1; Table 1; Carvalho, 1941, 1942; Marcus, 1937). Herein, we use various morphological and molecular methods, as well as previously

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Table 1. List of described onychophoran species reported from Brazil and the biomes where they occur.

| Species                        | Type locality                                                                 | Biome                          |
|-------------------------------|-------------------------------------------------------------------------------|--------------------------------|
| *Cerradopatus sucuriuensis*   | Brazil, MS, Chapadão do Sul, environs of the PCH (=small power plant) Porto  | Cerrado (savannah)             |
|                               | das Pedras                                                                    |                                |
| *Epiperipatus acacioi*        | Brazil, MG, Ouro Preto, Ecological Station of Tripui                          | Atlantic rainforest            |
| (Marcus & Marcus, 1955)       |                                                                                |                                |
| *Epiperipatus adcnocryptus*   | Brazil, MG, Santa Bárbara do Leste, córrego dos Ferreiras                     | Atlantic rainforest            |
| Oliveira et al., 2011         |                                                                                |                                |
| *Epiperipatus brasilensis*    | Brazil, PA, Santarém                                                          | Amazon rainforest              |
| Bouvier, 1899a                |                                                                                |                                |
| *Epiperipatus cratensis*      | Brazil, CE, Crato, Rio Batateiras                                             | Atlantic rainforest            |
| Brito et al., 2010            |                                                                                |                                |
| *Epiperipatus diadenoproctus* | Brazil, MG, Simonésia, RPPN Mata dos Sossego                                  | Atlantic rainforest            |
| Oliveira et al., 2011         |                                                                                |                                |
| *Epiperipatus edwardsi*       | French Guiana, Cayenne                                                        | Atlantic rainforest            |
| 1 (Blanchard, 1847)           |                                                                                |                                |
| *Epiperipatus machadoi*       | Brazil, MG, Caratinga, RPPN Feliciano Miguel Abdala                           | Atlantic rainforest            |
| Oliveira & Wieloch, 2005      |                                                                                |                                |
| *Epiperipatus ohausi*         | Brazil, RJ, Petrópolis                                                        | Atlantic rainforest            |
| (Bouvier, 1900)               |                                                                                |                                |
| *Epiperipatus paurognostus*   | Brazil, MG, Piedade de Caratinga, Mata do Eremitério                          | Atlantic rainforest            |
| Oliveira et al., 2011         |                                                                                |                                |
| *Epiperipatus simoni*         | Venezuela, Caracas                                                             | Amazon rainforest*             |
| 2 (Bouvier, 1899b)            |                                                                                |                                |
| *Epiperipatus tucupi*         | Brazil, PA                                                                    | Amazon rainforest              |
| 2 (Froehlich, 1968)           |                                                                                |                                |
| *Macroperipatus geayi*        | Brazil, AP, high Calçoene                                                     | Amazon rainforest              |
| 2 (Bouvier, 1899c)            |                                                                                |                                |
| *Oroperipatus balzani*        | Bolivia, Yungas, Chulumani, near Coroico                                      | Amazon rainforest**            |
| 1 (Camerano, 1897)            |                                                                                |                                |
| *Oroperipatus eisenii*        | Mexico, Nayarit, outskirts of Tepic                                            | Amazon rainforest**            |
| 1 (Wheeler, 1898)             |                                                                                |                                |
| *Peripatus evelinae* Marcus,  | Brazil, GO, environs of Nova Roma                                             | Cerrado (savannah)             |
| 1937                          |                                                                                |                                |
| *Peripatus heloisae* Carvalho,| Brazil, MT, left border of Tapirapé river, next to its confluence with the   | Cerrado (savannah)             |
| 1941                          | river Araguaia                                                                 |                                |

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1Putative misidentification in Brazil (see Oliveira et al., 2011). 2Nomen dubium (see Oliveira, Read & Mayer, 2012). "See Peck (1975)." **See Sampaio-Costa, Chagas-Junior, and Baptista (2009)."
published karyotype and biochemical information (Baer, Oliveira, Steinhagen, Beck-Sickinger, & Mayer, 2014; Jeffery, Oliveira, Gregory, Rowell, & Mayer, 2012), to describe the new species studied and assign it to a new genus based on its unique set of morphological characters. Five years of study in situ (2007–2011) revealed that this species is most likely restricted to four small, unprotected areas in the state of Mato Grosso do Sul. These fragments of forest are being continuously impacted by human activities and this species might quickly go extinct if urgent conservation actions are not implemented.

**Materials and methods**

**Specimens**
The specimens studied were collected between May 2007 and November 2011 in four adjacent fragments of forest near the Pequena Central Hidrelétrica (=PCH) Porto das Pedras [small hydroelectric power plant Porto das Pedras] situated along the Sucuriú River, municipality of Chapadão do Sul, Mato Grosso do Sul state (Figs 1, 2; centre of the largest fragment at 52°32′33″W, 19°28′44″S, 420 m). The animals were either preserved according to Oliveira, Wieloch, and Mayer (2010) and placed in the scientific collection of the Department of Zoology at the Universidade Federal de Minas Gerais, Brazil (=DZUFMG) (n=18) or kept in culture in Leipzig, Germany (n=24), as previously described (Baer & Mayer, 2012; Oliveira, Franke, et al., 2012). All specimens were collected under the Brazilian federal license (ICMBio) number 10432/3 and exported under the federal license (ICMBio) number 113141.

**Morphological studies**
Living specimens were photographed with a Nikon D7000 camera under daylight. Specimens preserved in 70%
ethanol were analysed and photographed with a stereomicroscope (Wild M10, Leica Microsystems, Wetzlar, Germany), equipped with a digital camera (PCO AG SensiCam, Kelheim, Germany). For scanning electron microscopy, specimens of both sexes and different ages, including dissected embryos, were fixed and preserved according to Oliveira, Franke, et al. (2012). After dehydration in an ethanol series, specimens were cut into smaller parts, dried in a critical point dryer (K850, Emitech Ltd., Kent, UK), coated with gold in a SCD 050 Sputter Coater (BALZERS UNION, Balzers, Liechtenstein), and examined with the scanning electron microscope EVO 50 (Carl Zeiss, Jena, Germany). Intra-specific character variation was assessed by comparing the data obtained from specimens of different ages and both sexes (n=20). For the terminology of morphological features and embryonic staging used, see Oliveira, Franke, et al. (2012), Oliveira & Mayer (2013), Oliveira et al. (2010) and Walker and Campiglia (1990), respectively.

Nomenclatural acts
The present work and its nomenclatural acts have been registered in ZooBank, which is the online registration system for the ICZN, and the ZooBank LSIDs (Life Science Identifiers) can be resolved through any web browser by appending the LSID to the prefix ‘http://zoobank.org/’. The LSID for this publication is: urn:lsid:zoobank.org:pub:10D0762E-7842-428B-8ABB-9096BED10F65.

Molecular studies
Genomic DNA was extracted from small body pieces (~25 mg) of six freshly dissected specimens from different fragments of forest, including embryos found within gravid females, using the DNeasy Tissue Kit (Qiagen, Hilden, Germany) according to the manufacturer’s protocol. DNA sequences of the mitochondrial genes cytochrome c oxidase subunit I (COI) and the small ribosomal subunit RNA (12S rRNA) were amplified using the primers COI5584 and COI6174 from Lacorte, Oliveira and Da Fonseca (2011) and SR-J-14233 and SR-N-14588 from Simon et al. (1994), respectively. PCR amplifications were performed in 20 μl reaction volumes containing 40 ng of genomic DNA, Buffer 1B (Phoneutria®, Belo Horizonte, Brazil: 1.5 mM MgCl₂, 10 mM Tris-HCl, 50 mM KCl, 0.1% Triton X-100), 0.8 μM dNTPs, 0.3 μM primers, 1% bovine serum albumin (BSA) and 1 unit of Taq polymerase (Phoneutria®). After an initial denaturing step for 5 min at 94°C, the PCR conditions for the COI and 12S rRNA fragments followed a standard three-step protocol, with 27 cycles of (1) denaturing for 45 s at 94°C, (2) annealing for 45 s at 56°C (COI primers) or 54°C (12S rRNA primers), and (3) extension for 1 min at 72°C, followed by a final extension step for 5 min at 72°C. The PCR products were purified using a solution of 20% polyethylene glycol 8000 and 2.5M NaCl according to Sambrook and Russel (2001). After purification, the PCR products were sequenced in both directions using the BigDye Terminator Kit v3 (Applied Biosystems, Foster City, USA) and an ABI3100® automated sequencer (Applied Biosystems, Foster City, CA, USA). Sequences were aligned using the online version of MAFFT (http://mafft.cbrc.jp/alignment/server/) for 12S rRNA sequences, applying the FFT-NS-i strategy, and TranslatorX (http://translatex.co.uk) for COI sequences, using the Invertebrate Mitochondrial Codon Table (code no. 5). The obtained sequences were placed in GenBank with specific accession numbers (Table 2).

Phylogenetic analyses
The Maximum Likelihood inference method was used for phylogenetic analyses using the combined 12S rRNA and COI datasets as described previously (Oliveira, Franke, et al., 2012; Oliveira, Schaffer, et al., 2013). Twenty-nine additional sequences from 12 species of Peripatidae (ingroup), including all taxa available from Brazil, and five species of Peripatopsidae (outgroup) were obtained from GenBank and from the literature and included in the phylogenetic analyses (Table 2). Translated amino acid alignments were verified a priori using TranslatorX (http://translatex.co.uk). The Maximum Likelihood analysis was conducted using RAxML 8.0.19 PTHREADS-SSE3 (Stamatakis, 2014), selecting the substitution models GTR+G for nucleotides and MTART+G for amino acids. The latter was derived from PROTEST3 (Abascal, Zardoya, & Posada, 2005) according to the Akaike information criterion (Akaike, 1974). Node support was calculated using 1000 bootstrap pseudoreplicates (Felsenstein, 1985).

Image processing
Light and scanning electron micrographs were processed with Adobe (San Jose, CA, USA) Photoshop CS5.1. Final panels were designed with Adobe Illustrator CS5.1 and exported in the Tagged Image File Format.

Results
A new onychophoran from the Brazilian savannah
The onychophoran species studied was first discovered in January 2007 during a faunal assessment and further investigated periodically in situ until 2011. Morphological and molecular analyses of the obtained material revealed that this species is new to science and exhibits a unique
Table 2. COI and 12S rRNA gene sequences used for phylogenetic analyses, with corresponding GenBank accession numbers and references.

| Species name | Accession number (COI) | Reference (COI) | Accession number (12S rRNA) | Reference (12S rRNA) |
|--------------|------------------------|-----------------|-----------------------------|----------------------|
| Peripatidae (ingroup) | | | | |
| Cerradopatus sucuriuensis gen. et sp. nov. | KM095116–095121 | Present work | KM095122–095127 | Present work |
| Eoperipatus sp. | JX569005 | Oliveira, Franke, et al., 2012 | JX568982 | Oliveira, Franke, et al., 2012 |
| Eoperipatus totoro Oliveira, Schaffer, et al., 2013 | KC139082 | Oliveira, Schaffer, et al., 2013 | KC139083 | Oliveira, Schaffer, et al., 2013 |
| Epiperipatus acacioi (Marcus & Marcus, 1955) | HQ404902–404905 | Lacorte et al., 2011 | HQ404920–404923 | Lacorte et al., 2011 |
| Epiperipatus adenocryptus Oliveira et al., 2011 | HQ236113, 236114 | Oliveira et al., 2011 | HQ236139, 236140 | Oliveira et al., 2011 |
| Epiperipatus bollyei (Bouvier, 1902) | NC_009082 | Podsiadlowski, Braband & Mayer, 2008 | NC_009082 | Podsiadlowski et al., 2008 |
| Epiperipatus bollyei (Bouvier, 1902) | HM600781 | Rota-Stabelli et al., 2010 | HM600781 | Rota-Stabelli et al., 2010 |
| Epiperipatus diadenoproctus Oliveira et al., 2011 | HQ236095–236097 | Oliveira et al., 2011 | HQ236121–236123 | Oliveira et al., 2011 |
| Epiperipatus machadoi (Oliveira & Wieloch, 2005) | HQ236092, 236093 | Lacorte et al., 2011 | HQ236115, 236116 | Lacorte et al., 2011 |
| Epiperipatus psurognotus Oliveira et al., 2011 | HQ236104–HQ236106 | Oliveira et al., 2011 | HQ236130–236132 | Oliveira et al., 2011 |
| Mesoperipatus tholloni (Bouvier, 1898) | KC754645 | Murienna et al., 2014 | KC754478 | Murienna et al., 2014 |
| Oroperipatus sp. | NC01589 | Segovia, Pett, Trewick & Lavrov, 2011 | NC015890 | Segovia et al., 2011 |
| Peripatus solorzanoi Morera-Brenes & Monge-Nájera, 2010 | KM095130, 095131 | Present work | KM095128, 095129 | Present work |
| Principapillatus hitoyensis Oliveira, Franke, 2012 | JX568985, 568995 | Oliveira, Franke, et al., 2012 | JX568962, 568972 | Oliveira, Franke, et al., 2012 |
| Peripatopsidae (outgroup): | | | | |
| Euperipatoides rowelli Reid, 1996 | KC754650 | Muntenne et al., 2014 | AF338016 | Rockman, Rowell & Tait, 2001 |
| Metaperipatus inae Mayer, 2007 | EF624055 | Braband, Podsiadlowski, Cameron, Daniels & Mayer, 2010 | EF624055 | Braband, Podsiadlowski, et al., 2010 |
| Opisthopatus cinctipes Purcell, 1899 | NC014273 | Braband, Cameron, Podsiadlowski, Daniels & Mayer, 2010 | NC014273 | Braband, Cameron, et al., 2010 |
| Peripatopsis moseleyi (Wood-Mason, 1879) | EU855276 | Daniels et al., 2009 | EU855469 | Daniels et al., 2009 |
| Phallocephale tallagandensis Reid, 1996 | U62407 | Gleeson, Rowell, Bricoe, Tait & Higgins, 1998 | AF338015 | Rockman et al., 2001 |

*Sequences originally obtained from Morera-Brenes & Monge-Nájera (2010) and deposited in GenBank for the present paper.*
combination of characters inconsistent with the diagnosis of the described genera of Peripatidae (see Oliveira, Franke, et al., 2012; Peck, 1975; Read, 1988). Hence, a new genus of Peripatidae is raised herein for the new species and both the species and the genus are described below according to the provisions of the International Code of Zoological Nomenclature (ICZN, 1999).

*Cerradopatus* gen. nov.

urn:lsid:zoobank.org:act:FF9AC26C-B4A5-4E61-974D-39CBE5F5A4FC

**Type species:** Cerradopatus sucuriuensis gen. et sp. nov., by monotypy.

**Genus etymology:** Cerradopatus is derived from the name of the Brazilian savannah (=Cerrado), the biome in which the species occurs, in combination with patus, a suffix extracted from Peripatus and traditionally used for composing the names of onychophoran genera.

**Genus diagnosis:** Three pairs of separate, rounded interpedal structures per segment, varying in size and shape and covered with a finely structured cuticle (Figs 3–5); interpedal structures absent in segments posterior to the first pregenital leg pair (Fig. 3); female genital pad large, densely covered with modified scales, which appear smaller than those covering dermal papillae (Figs 6, 7); dermal papillae of the female genital pad few in number and mostly restricted to its periphery (Figs 3, 6, 7); irregular fields of modified scales present along the ventral midline between the genital pad and the anus (Figs 3, 6); males lacking modified scales in the genital pad and posterior body region (Figs 3, 8).

![Fig. 3. Simplified diagrams of the posterior body region of a female and a male of Cerradopatus sucuriuensis gen. et sp. nov. showing the position of structures studied. Anterior is up. Abbreviations: au, anus; cf, coxal furrow; cv, coxal vesicle; dp, dermal papilla; fm, fields of modified scales; ft, foot; go, genital opening; is, interpedal structures; lg, leg; no, nephridial opening; pa, spinous pad; pv, pre-ventral organ; vo, ventral organ; vr, ventral row of crater-shaped papillae.](image-url)
Figs. 4–8. Diagnostic characters of the genus *Cerradopatus* gen. nov. Scanning electron micrographs. Anterior is up in all images. 4. The three pairs of interpedal structures (dotted lines) found ventrally in all pregenital leg-bearing segments. 5. Detail of a single interpedal structure, which is covered with a finely sculptured cuticle. 6. Ventral view of the female posterior body region. Arrows point to preventral organs, whereas arrowheads indicate ventral organs. Note the modified scales covering the genital opening and forming irregular fields (dotted lines) posterior to it. 7. Detail of the modified scales covering the genital opening and forming irregular fields (dotted lines) posterior to it. 8. Genital opening of a male, which is instead covered with regular dermal papillae. Abbreviations: au, anus; dp, dermal papilla; go, genital opening; is, interpedal structure; vo, ventral organ. Scale bars: 50 μm (4, 7), 10 μm (5), 150 μm (6) and 100 μm (8).
Cerradopatus sucuriuenensis gen. et sp. nov.

urn:lsid:zoobank.org:act:DB4A2B4--5DC7-4D50-A60D-1B57B35F4839

Previously referred to as ‘Epiperipatus sp.’ (Baer et al., 2014; Jeffery et al., 2012), and ‘Epiperipatus sp. 2’ (Oliveira, Tait, Strübing, & Mayer, 2013).

Holotype: UFMG 193 (male, October 2013; born in culture from a female collected in November 2011 at the type locality, I.S. Oliveira col.).

Paratypes: UFMG 168, 169, 194 (two females, I.S. Oliveira, A.P.L. Giupponi & C. Sampaio-Costa col., November 2008; one male born in culture from a female collected in November 2011 at the type locality, I.S. Oliveira col.).

Additional material: UFMG 025–36, 170–173 (two females from 52°32′27″W, 19°28′31″S, Oliveira, I.S. Col., May 2007; seven females from 52°33′10″W, 19°28′26″S, I.S. Oliveira, A.P.L. Giupponi & C. Sampaio-Costa col., November 2007 to November 2008; five females from the type locality, I.S. Oliveira, A.P.L. Giupponi & C. Sampaio-Costa col., November 2007 to November 2008; two females from 52°31′40″W, 19°28′57″S, I.S. Oliveira, A.P.L. Giupponi & C. Sampaio-Costa col., November 2008).

Type locality: Brazil, Mato Grosso do Sul State, municipality of Chapadão do Sul, small fragment of gallery forest (0.67 km²) in the environs of the PCH (=small hydroelectric power plant) Porto das Pedras at the river Sucuriú (centre of the largest fragment at 52°32′33″W, 19°28′44″S, 420 m; Figs 1, 2).

Additional localities: Brazil, Mato Grosso do Sul State, municipality of Chapadão do Sul, two small fragments of gallery forest in the environs of the PCH (=small hydroelectric power plant) Porto das Pedras at the river Sucuriú: (i) 0.47 km², centre at 52°33′15″W, 19°28′34″S, 436 m; (ii) 0.54 km², centre at 52°31′35″W, 19°29′04″S, 414 m (see Fig. 2).

Etymology: The species is named in reference to its type locality, which is situated along the banks of the river Sucuriú. The name Sucuriú might be derived from a ritual dance of the indigenous people who lived along this river (unconfirmed information). The common name ‘Sucuriú’ or ‘Sucuri’ is also used for anaconda snakes (Eunectes spp.), which are commonly found in that region.

Species diagnosis: Characteristic colour pattern (Figs 9–11); three classes of dermal papillae in the dorsal integument: primary, accessory, and the herein named peripheral accessory papillae (Figs 12, 13); primary papillae similar in size; accessory papillae largely varying in size; peripheral accessory papillae numerous, bud-like, pigmented and situated marginally in the anterior and posterior borders of the plicate (Figs 12, 13). Crural tubercles paired and present in three pregenital leg pairs of males (Figs 3, 14, 15); paired anal gland openings of males inconspicuous, separated from each other and evidenced as small furrows on the latero-anterior anal region (Figs 3, 16, 17). Flexed-stage embryos bearing smooth foot projections on the distal leg portions (Figs 18, 19). Males with 28 or 29 leg pairs, females with 30–32. Karyotype 2n=22, including six pairs of acrocentric and five pairs of metacentric/submetacentric chromosomes; heteromorphic sexual chromosomes absent (Fig. 4 in Jeffery et al., 2012, p. 501). Slime protein profiling in sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) composed of 12 bands in regions of large (4 bands), mid-sized (2 bands) and small (6 bands) proteins (Fig. 5 in Baer et al., 2014, p. 269). COI and 12S rRNA sequences as each in the six specimens sequenced (Table 2).

Description

The following description complements the data presented in the genus and species diagnoses.

Measurements. Maximum body size after preservation in 70% ethanol: length 71.8 mm, width 5.6 mm, height 4.7 mm.

Colour pattern. Dorsal integument in vivo brown (Fig. 9); large primary papillae appearing as bright spots, forming bright lines along the main body axis (Fig. 9); dorsal midline darker than surrounding integument (Figs 9, 10); head reddish orange (Fig. 9); antennae and ocular region dark brown with a bright, diamond-shaped spot in the interocular regions; the dark ring around each eye continuous with the dorsal midline, forming a dark Y-shaped pattern on the head (Figs 9, 10). Ventral body surface pale (Fig. 11); repeated bright spots along the ventral midline corresponding to the ventral + preventral organs and to the interpedal structures (Fig. 11).

Antennae. Antennal tip composed of a terminal button and 12 rings; 8th, 10th and 12th rings thinner than others (Fig. 20); antennal body composed of additional 27–30 rings. Type I sensilla (sensu Oliveira, Franke, et al., 2012) occurring in the whole antennae; type II sensilla restricted to antennal tip (Fig. 20). Chemoreceptors roundish, numerous and arranged in anterior rows on each ring of antennal tip, except for thinner rings that lack chemoreceptors altogether (Fig. 20); few chemoreceptors found dorso-laterally on alternating rings of proximal antennal portion. Spindle-shaped sensilla oval in shape and with long, pointed bristles (Fig. 21).

Head. Arrangement of dermal papillae on the head (=head pattern) irregular (Fig. 22). Eyes pigmented, with ~120 μm in diameter (Fig. 22). Frontal organs present. Mouth composed of an anterior unpaired lip papilla followed posteriorly by eight pairs of lip papillae (Fig. 23). Outer and inner jaw blades with one principal and one
Figs. 9–13. Diagnostic characters of the species *Cerradopatus sucuriuensis* gen. et sp. nov. Photographs (9–11) and light (12) and scanning electron micrographs (13). Anterior is up in 11–13. 9, 10. Living specimen (~85 mm) and detail of its head. Note the specific colour pattern consisting of a reddish cephalic region contrasting with the dark brown trunk, antennae and ocular region. Also note the diamond-shaped bright spot between the antennae and the dark Y-shaped pattern on the head (arrowheads in 10). 11. Mid-body of an anaesthetized specimen in ventral view. Note the repeated bright spots along the ventral midline, which correspond to the interpedal structures (dotted circles) and to the ventral and preventral organs (arrows). 12. Light micrograph of the dorsal integument, which is composed of three classes of dermal papillae: primary, accessory and peripheral accessory papillae (arrowheads). Arrow points to the dorsal midline. Note the high number of peripheral accessory papillae compared with the other two classes of papillae. 13. Scanning electron micrograph of the dorsal integument. Note the position of the numerous peripheral accessory papillae (artificially coloured in orange) and the variation in size of accessory papillae. Abbreviations: ap, accessory papilla; pe, peripheral accessory papilla; pp, primary papilla. Scale bars: 250 µm (11, 12) and 50 µm (13).
Figs. 14–19. Diagnostic characters of the species *Cerradopatus sucuriuensis* gen. et sp. nov. Scanning electron micrographs. Anterior is up in 14–17 and left in 18 and 19. 14. Posterior body region of a male in ventral view showing the distribution of crural tubercles (arrowheads) in three pregenital leg pairs. 15. Detail of the paired crural tubercles on a male pregenital leg. 16. Ventral view of the anal region of a male showing paired, inconspicuous anal gland openings (arrows). 17. Detail of an anal gland opening of a male. 18, 19. Distal leg portion of a flexed-stage embryo showing the embryonic foot projections, which in this species appear smooth (detail in 19). Abbreviations: ag, anal gland opening; au, anus; ct, crural tubercle; cv, coxal vesicle; fp, embryonic foot projections; ft, foot; gp, genital pad; lg, leg. Scale bars: 200 μm (14), 50 μm (15, 16, 18) and 10 μm (17, 19).
Figs. 20–24. Cephalic structures in *Cerradopatus sucuriuensis* gen. et sp. nov. Scanning electron micrographs (20–23) and light micrograph (24). Anterior is up in 20–23. 20. Proximal portion of the antennal tip in dorsal view. Note the distribution of the two types of antennal sensilla and the lack of chemoreceptors on thinner rings, which are numbered according to their position in the antennal tip. 21. Spindle-shaped sensillae of the antennal ventral basis. 22. The irregular pattern of dermal papillae on the dorsal head region. Arrow points to the eye. 23. Mouth in ventral view illustrating the arrangement of oral lips. Note the unpaired, anterior-most lip papilla followed by eight pairs of posterior lip papillae (numbered). 24. Dissected jaw blades. Arrows point to the accessory tooth of the inner and outer jaw blades. Note that the apodeme associated with the inner jaw blade has been removed. Abbreviations: an, antenna; as1, type I antennal sensilla; as2, type II antennal sensilla; cr, chemoreceptors; dt, denticles; ib, inner jaw blade; mo, mouth; ob, outer jaw blade; pt, principal tooth; ss, spindle-shaped sensilla; ul, unpaired anterior-most lip papilla. Scale bars: 50 μm (20), 20 μm (21), 200 μm (22, 23) and 100 μm (24).
accessory tooth (Fig. 24); inner jaw blade with 6–9 denticles; principal and accessory teeth sickle-like (Fig. 24).

Dorsal integument. Twelve complete plicae per segment, seven of which pass between adjacent leg pairs to ventral side. Dorsomedian furrow distinct along entire body length (Fig. 12); paired, rounded hyaline organs present in each plical furrow along the dorsal midline. Primary and accessory papillae distributed in a repeated, alternated pattern along the dorsal midline: plicae with one accessory papilla and one primary papilla on each side of the dorsomedian furrow are followed by plicae with three accessory papillae and one primary papilla flanking the dorsomedian furrow (Fig. 12). Dorsal primary papillae similar in shape and size, cylindrical and with apical and basal pieces separated by a constriction (Figs 13, 25). Basal piece cylindrical, larger than apical piece and with five to 10 antero-posterior and four to eight lateral scale ranks (Fig. 25). Asymmetrical apical pieces covered with scales arranged in five to six anterior and two or three posterior scale ranks; symmetrical apical pieces showing three or four scale ranks (Fig. 25). Sensory bristle of apical pieces thorn-shaped; varying in size, centred in symmetrical and shifted posteriorly in asymmetrical apical pieces (Figs 13, 25). Peripheral accessory papillae more numerous than accessory papillae, which are more numerous than primary papillae (Figs 12, 13); usually one to three accessory papillae between each two primary papillae; peripheral accessory papillae less numerous in the head region than in the trunk, usually hidden inside plical furrows and hardly visible in contracted specimens (Figs 12, 13, 25).

Ventral integument. Type I crater-shaped papillae (sensu Oliveira, Franke, et al., 2012) absent; type II crater-shaped papillae with elongated bases, seven to nine scales in apical collar and lacking rudimentary apical pieces (Fig. 26); type II crater-shaped papillae arranged in regular ventral and ventro-lateral rows of six papillae between subsequent leg pairs, except between the penultimate and last leg pairs, where their number varies between three and four crater-shaped papillae in a row (Fig. 3). Ventral organs roundish, preventral organ reduced and hardly visible (Appendix S1, online supplemental material, which is available from the article’s Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2014.985621); ventral and preventral organs separated by genital pad in genital segment (Fig. 6). Paired interpedal structures aligned respectively to the fourth, fifth and sixth type II crater-shaped papillae (from anterior to posterior) of the corresponding segment (Fig. 3).

Legs. First leg pair and last two leg pairs reduced in size; legs of last pair not rotated posteriorly. Dorsal leg surface with eight transverse rings; bean-shaped papilla found on the dorsal leg surface, lying in a pouch formed by two conspicuous tegumental folds, which may appear nearly closed in some specimens (Fig. 27). Four spinous pads per leg, nearly straight, increasing proximally in size and occupying an area of approximately half the leg length (Fig. 28); fifth, fragmented pad present in few, random legs of the mid-body; only three pads in the last two leg pairs (Fig. 3). Nephridial tubercle in fourth and fifth leg pairs attached to the third spinous pad, but opening proximally to it, strongly indenting the fourth pad, which might appear divided into two parts (Fig. 29). Spines on spinous pads densely distributed, needle-shaped and with textured basis (Fig. 30). Eversible coxal vesicles present in all legs, except for fourth and fifth leg pairs (Fig. 28). Three or four distal foot papillae per foot, i.e. two anterior and one or two posterior (Figs 31, 32). One bristle on proximal and three on distal setiform ridges (Fig. 33).

Posterior region. Genital pad of both sexes situated between penultimate leg pair (Fig. 3); genital opening appearing as a longitudinal slit in both sexes (Figs 6, 8); male genital pad surrounded by numerous, regular dermal papillae (Fig. 8). Crural tubercles covered by six or seven ranks of flat scales; crural gland opening smooth (Fig. 15). Anal gland openings of males not situated on modified anal gland papillae (arrows in Fig. 16). Anal cone well-developed in both males and females; anus terminal (Fig. 6).

Remarks on reproduction: Females kept in culture in Leipzig (Germany) give birth between October and April, a period that corresponds to the wet season at the type locality of the species. Similar seasonality has been reported for *Epiperipatus acacioi*, a species from the Brazilian Atlantic rainforest that reproduces between December and July (Lavallard & Campiglia, 1975). The ratio of males and females born in culture is approximately 50/50, in contrast to the ratio of collected animals, which was female-biased with males rarely found in nature. A comparable situation has been reported from other onychophoran species (Barclay, Rowell, & Ash, 2000; Monge-Nájera, 1995; Oliveira, Franke, et al., 2012; Scott & Rowell, 1991; Sunnucks et al., 2000).

Distinction from other peripatid species: To date, only three nominal species of Onychophora have been reported from the Brazilian Cerrado: *Peripatus evelinae*, *P. heloisae* and *Cerradopatus sucuiriensis* gen. et sp. nov. (Table 1). These three species differ from the remaining taxa described from the Brazilian Amazon and Atlantic rainforests by the presence of crural tubercles in more than two pregenital leg pairs of males, although the corresponding character state remains unknown in *Epiperipatus cratensis* Brito et al., 2010. Among the species from the Cerrado, *Cerradopatus sucuiriensis* gen. et sp. nov. is distinguishable by the number of leg pairs, the distribution of crural tubercles in males and the specific colour pattern. It shows 28 or 29 leg pairs in males and 30–32 in females, while *P. heloisae* males have 28–32 and females 31–34 leg pairs. The number of leg pairs reported for *P. evelinae* is controversial: two females with 32 and 34 leg pairs were originally described (Marcus, 1937), but a re-examination of the type material instead revealed a male with 33 and a female with 35 leg pairs.
Figs. 25–30. Scanning electron micrographs of additional features in *Cerradopatus sucariuensis* gen. et sp. nov. Lateral is left in 25 and 26, anterior is right in 27–30. 25. A primary papilla of the dorsal integument. White dots and white dots with black centre indicate the scale ranks in the posterior and lateral region of the basal piece respectively, whereas black dots with white centre indicate those in the posterior region of the apical piece. 26. Crater-shaped papilla of the ventral integument. Black dots with white centre indicate the number of scales composing the apical collar. 27. Bean-shaped papilla of the dorso-distal leg portion. 28. Spinous pads (numbered) of mid-body legs in ventral view. Note the eversible coxal vesicle at the basis of each leg. 29. Fifth leg in ventral view. Note that the forth pad (dotted lines) is indented and split into two parts by the nephridial tubercle. 30. Detail of the spines covering a spinous pad. Abbreviations: ap, apical piece; be, bean-shaped papillae; bp, basal piece; cv, coxal vesicle; ft, foot; nt, nephridial tubercle; pe, peripheral papilla; sb, sensory bristle. Scale bars: 25 μm (25, 27), 10 μm (26, 28), 50 μm (29) and 200 μm (30).
(Froehlich, 1968). In either case, *P. evelinae* also exceeds the number of leg pairs observed in *Cerradopatus sucuriuensis* gen. et sp. nov. Moreover, the male crural tubercles appear in up to 10 pregenital leg pairs in *P. evelinae* (Froehlich, 1968) but only in three pregenital leg pairs in *P. heloisae* and *Cerradopatus sucuriuensis* gen. et sp. nov. The latter two species show distinct colour patterns: *P. heloisae* has a dark-brown body and antennae contrasting with an unpigmented white head (see Carvalho, 1942), whereas the cephalic region of *Cerradopatus sucuriuensis* gen. et sp. nov. appears pigmented and reddish-orange. The in vivo colour pattern of *P. evelinae* is unknown (Marcus, 1937).

Finally, the great distance between the type localities of these three species (lying over 800 km apart) suggests that they are not conspecific, considering the point endemism observed in most onychophoran species (Oliveira et al., 2012).

**Molecular analyses and phylogenetic relationship**

The results of molecular analyses combining the mitochondrial COI and 12S rRNA sequences are in line with
morphological data, supporting *Cerradopatus sucuriuensis* gen. et sp. nov. as a new taxon. The final alignment of 12S rRNA and COI mitochondrial gene sequences used for phylogenetic analyses consisted of 365 and 627 nucleotide positions respectively. Sequences of both genes are A+T biased and COI sequences show no stop codons when translated into amino acids, suggesting that these belong to functional mitochondrial protein-coding genes. The number of parsimony informative nucleotide positions in the molecular matrix combining 12S rRNA and COI sequences varied from a maximum of 433, including all nucleotides, to a minimum of 277 excluding the third codon position of COI sequences. The final alignment of COI sequences excluding the third codon position contained 783 nucleotides.

Phylogenetic Maximum likelihood analyses reveal similar topologies, irrespective of whether all nucleotides, only the first and second codon positions, or translated amino acid sequences of COI are analysed in combination with 12S rRNA sequences (Fig. 34; Appendices S2, S3, see supplemental material online). In all analyses, *Cerradopatus sucuriuensis* gen. et sp. nov. is retrieved as a well-supported, monophyletic sister group to a major clade containing the *Epiperipatus* lineages from Brazil (Fig. 34; Appendices S2, S3, see supplemental material online). *Cerradopatus sucuriuensis* gen. et sp. nov. is retrieved as the sister group of *Epiperipatus accacioides* in analyses combining all nucleotides of COI and 12S rRNA sequences (Appendix S2, see supplemental material online). However, this relationship could not be recovered in additional analyses after excluding the third codon position or translating COI sequences into amino acids (Fig. 34; Appendix S3, see supplemental material online), suggesting that the relationship between these two species is most likely an artefact caused by the saturation of the third codon position in COI sequences. The long internal

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**Fig. 34.** Maximum likelihood topology combining the 12S rRNA nucleotide sequences and the translated amino acid sequences of COI. Five species of Peripatopsidae were used as outgroup taxa. Bootstrap values indicated above the branches correspond to analyses combining 12S rRNA and translated amino acids of COI, those beneath the branches to analyses combining 12S rRNA and COI nucleotide sequences excluding the third codon position. Asterisks indicate maximum bootstrap support values (=100) and dashes indicate that the clade was not retrieved in the respective analysis. Abbreviations at terminal branches correspond to the accession numbers of COI sequences in GenBank.
branch separating Cerradopatus sucuriuensis gen. et sp. nov. from the remaining ingroup taxa observed in all analyses suggests great genetic distance between these species, thus supporting the designation of the new genus and species herein.

**Distribution, habitat and immediate threats**

*Cerradopatus sucuriuensis* gen. et sp. nov. is known only from its type locality, which are the environs of the small hydroelectric power plant Porto das Pedras at the river Sucuriú (Figs 1, 2). Attempts to infer the distribution of the species covered numerous areas along ∼38 km of the river Sucuriú (from 19°20’09”S, 52°40’21”W to 19°29’22”S, 52°31’34”W), yet *Cerradopatus sucuriuensis* gen. et sp. nov. was only recorded in four small fragments of forest adjacent to each other (Fig. 2). The restricted distribution of this species is further supported by the fact that no onychophoran has ever been reported from along the river Sucuriú despite exhaustive sampling in recent years for different plant and animal taxa, including arachnids commonly found together with onychophorans (see Pagotto & Souza, 2006). The areas where *Cerradopatus sucuriuensis* gen. et sp. nov. occurs consist of dense patches of forest, which contrast with the surrounding savannah/pasture vegetation (Fig. 35). The interior of these fragments appears heterogeneous, showing dry areas with sparse canopy and small humid spots, usually associated with shady banks of small watercourses. Within the fragments, *Cerradopatus sucuriuensis* gen. et sp. nov. is confined to these humid spots and commonly inhabits the leaf litter, although it can also be found within or under rotted logs, under stones and in soil cavities. These animals are mostly found during the wet season (October to April), whereas they become extremely difficult to find in the dry period (May to September). Two specimens found during the dry season inhabited a small hole in a ravine, suggesting that this species might migrate deep in the soil during this part of the year.

Between 2007 and 2011, it was observed that human activities such as logging, selective cut, opening of trails and cattle breeding have destroyed habitats with which *Cerradopatus sucuriuensis* gen. et sp. nov. is associated. During the construction of the hydroelectric power plant Porto das Pedras, one of the fragments where this species had been previously recorded was substantially logged (Figs 35–38) and despite repeated efforts over four years, no onychophoran has subsequently been found in the residual patch of forest. In the remaining three areas, it was observed that the selective cutting of trees and opening of trails also affected the microhabitats colonized by *Cerradopatus sucuriuensis* gen. et sp. nov., in particular the humid spots where this species occurs (Figs 39–42). Although the real effects of such activities have not been quantified, onychophorans became more difficult to find or were even absent in impacted humid patches, which appeared to be drier after human activities (Fig. 41, 42). Likewise, opened trails allow the cattle from the surrounding pasture to access the interior of the fragments, degrading the leaf litter and compressing the soil, the two main microhabitats that *Cerradopatus sucuriuensis* gen. et sp. nov. inhabits.

**Discussion**

Morphological analyses of the new onychophoran species described in the present work, *Cerradopatus sucuriuensis* gen. et sp. nov., revealed hitherto undescribed characters and character states for Peripatidae. These include a high number of interpedal structures per segment, modified scales in the female genital pad and posterior body region and a third class of dermal papillae in the dorsal integument. To date, interpedal structures have only been described from four species of Peripatidae: *Principapilla tus hitoyensis* and *Eoperipatus biolleyi*, which show a single pair of interpedal structures per segment (Oliveira, Franke, et al., 2012), and two representatives of *Eoperipatus*, which instead show irregular fields of modified scales in the corresponding area of the integument (Oliveira, Schaffer, et al., 2013). Neither case is comparable to the three pairs of interpedal structures per segment found in *Cerradopatus sucuriuensis* gen. et sp. nov. On the other hand, the modified scales on the female genital and posterior body region have not been reported from any other species of Peripatidae thus far. Interestingly, the occurrence of accessory papillae on the edges of the plicae is also reported from other species of Peripatidae (see Bouvier, 1905), e.g. *Oroperipatus balzani* (Camerano, 1897), *O. soratanus* (Bouvier, 1901), *Epiperipatus imthurni* (Sclater, 1888) and *E. edwardsii* (Blanchard, 1847). However, it is unclear whether or not these ‘accessory papillae’ correspond to the peripheral accessory papillae described herein, which are clearly different from regular accessory papillae lying on the ridge of the plicae, i.e. they are smaller in size and are composed of fewer scales (see Fig. 13; Appendix S4, see supplemental material online). It is worth mentioning that the morphology of many known peripatids remains largely unexplored and the importance of these findings is still uncertain, as comparative data are missing from most described species (see discussion by Oliveira, Franke, et al., 2012). However, the variation already observed, at least for the interpedal structures, suggests that these features are of high taxonomic/systemic value.

A comparison between our remaining morphological data and information available in the literature revealed that *Cerradopatus sucuriuensis* gen. et sp. nov. cannot be consistently assigned to any of the 11 described genera of
Peripatidae (Oliveira, Franke, et al., 2012; Oliveira et al., 2012). Notably, it differs from representatives of Eoperipatus Evans, 1901a, Epiperipatus (Clark, 1913), Macroperipatus (Clark, 1913), Mesoperipatus Evans, 1901a, Oroperipatus (Cockerell, 1908), Plicatoperipatus (Clark, 1913), Principapillatus Oliveira, Franke, et al., 2012, and Typhloperipatus Kemp, 1913, by the presence of crural tubercles in three, rather than two pregenital leg pairs of males (Bouvier, 1905; Evans, 1901a, 1901b; Kemp, 1913; Oliveira, Franke, et al., 2012; Oliveira, Schaffer, et al., 2013; Peck, 1975). A similar arrangement of crural tubercles, i.e. in more than two pregenital leg pairs, has also been reported from species of Peripatus Guilding, 1826 (Bouvier, 1905; Peck, 1975), but in contrast to representatives of this genus, the dorsal primary papillae in Cerradopatus sucuriuensis gen. et sp. nov. do not vary greatly in size, nor is the apical piece more developed than the basal piece (Oliveira, Franke, et al., 2012; Peck, 1975). Therefore, it cannot be assigned to Peripatus either. Likewise, Cerradopatus sucuriuensis gen. et sp. nov. cannot be allocated into the remaining two genera of Peripatidae, because it shows two rather than three anterior distal foot papillae, as in Heteroperipatus Zilch, 1954, and its body is pigmented and bears well-developed eyes, contrasting with the unpigmented and blind caver-nicolous genus Speleoperipatus Peck, 1975 (Peck, 1975; Zilch, 1954). Since attempts to assign the new species to any described genus would result in inconsistencies, we

Figs. 35–38. Progressive destruction of natural habitats in areas where Cerradopatus sucuriuensis gen. et sp. nov. occurs. Photographs from the same area (different perspectives) prior (35), during (36, 37) and after (38) the establishment of a small power plant in the river Sucuriú. Note that the fragment of forest in this area was completely logged within a month (36, 37).
have raised a new genus of Peripatidae for the investigated species based on a set of putative derived characters. While onychophorans have recently been described or reported from the Atlantic and the Amazon rainforests in Brazil (Table 1; Brito, Pereira, Ferreira, Vasconcellos, & Almeida, 2010; Chagas-Júnior & Costa, 2014; Lacorte et al., 2011; Oliveira et al., 2011; Oliveira & Wieloch, 2005; Sampaio-Costa et al., 2009; Vasconcellos, Almeida, & Eloy, 2004; Vasconcellos, Almeida, & Souza, 2006), Cerradopatus sucuriuensis gen. et sp. nov. is only the third onychophoran species described from the Brazilian savannah, the previous one having been documented over 70 years ago (Carvalho, 1941; Marcus, 1937). However, numerous undescribed species collected in different regions and placed in scientific collections (Lacorte et al., 2011; Sampaio-Costa et al., 2009) suggest that the onychophoran diversity has not been explored sufficiently in the Cerrado. These records, as also observed for Cerradopatus sucuriuensis gen. et sp. nov., correspond to small gallery forests that form along watercourses in the Cerrado (Oliveira-Filho & Ratter, 2002), indicating that the occurrence of Onychophora in the savannah is sparse and restricted to these humid areas, given the dry savannah environment and the high susceptibility of onychophorans to desiccation (Reid, 1996; Ruhberg & Mayer, 2013). Furthermore, it also suggests that the point endemism of

Figs. 39–42. Selective cut within the fragments of forest where Cerradopatus sucuriuensis gen. et sp. nov. occurs. Comparative photographs from the same areas in similar perspectives. Arrows point to the same tree used as a landmark in all images. The images were taken during the wet season (October to April) without artificial light. Note that habitats previously humid (39, 40) became drier and showed stronger incidence of light after selected trees had been removed (41, 42).
onychophoran species might be even more pronounced in the Cerrado than, for example, in the Brazilian rainforests, where the permanently humid environment enables species to have a wider range (Lacorte et al., 2011; Oliveira et al., 2012; Oliveira et al., 2010; Sampaio-Costa et al., 2009).

Since the predominantly dry vegetation of the Cerrado constitutes a dispersal barrier for onychophorans, species currently inhabiting gallery forests most likely represent remnants of ancient populations that colonized these areas prior to the savannah formation. This assumption is in line with recent palynological findings, which suggest that the Cerrado was previously covered with forests (Ledru, 2002). The earliest record of savannah vegetation in Brazil dates back to 32 000 years ago, but vegetation resembling the present-day Cerrado might have only expanded ca. 7000 years ago, when the progressive increase of seasonality and temperature led to a strong contraction of forest areas to the current gallery forests (Ledru, 2002). On the other hand, Onychophora is a very old animal group, representatives of which were most likely distributed throughout the entire ancient supercontinent of Pangea (~360 My ago), and modern species might have diverged prior to the late Oligocene, approximately 23 My ago (Murienne, Daniels, Buckley, Mayer, & Giribet, 2014). Therefore, it is reasonable to assume that species currently occurring in the Cerrado, like Cerradopatus sucuriuensis gen. et sp. nov., endured past climate and vegetation changes during the Pleistocene/Holocene (Oliveira-Filho & Ratter, 2002; Zuo, Smith, & Charnov, 2013), and their descendants, as well as those of other forest taxa (see Ledru, 2002), became confined to the only remaining humid areas.

Although this evidence supports the previous assumption that onychophorans should be the focus of conservation efforts due to their point endemism, restriction to habitats susceptible to disturbance, small populations and low density (New, 1995; Reid, 1996; Wells et al., 1983), several species of Onychophora have nevertheless become endangered or even extinct in recent years (Brinck, 1957; Daniels, Picker, Cowlin, & Hamer, 2009; Hamer, Samways & Rubberg, 1997; Jackson & Taylor, 1994; Rubberg, 1985; Rubberg & Hamer, 2005) because effective conservation policies could not be enacted as fast as their habitats disappeared. Accordingly, habitat losses due to logging and/or agriculture (including cattle breeding), as described herein, are reported from many parts of the world (e.g. in Australia; see Mesibov, 2004) as being the main threat to the terrestrial invertebrate fauna (Gerlach et al., 2012). Regarding the Cerrado specifically, these activities are extremely profitable and unfortunately expected to continuously expand at a fast pace rather than decrease or at least stabilize (Klink & Machado, 2005). Meanwhile, several species might become endangered or even extinct (e.g. Diniz-Filho et al., 2008; Durigan, Siqueira, & Franco, 2007; Klink & Machado, 2005), whereas only the almost negligible portion of this biome (1.4%) that corresponds to effectively protected areas (CI, 2014) might be saved from direct anthropogenic activities.

The scenario described herein for Cerradopatus sucuriuensis gen. et sp. nov. clearly exemplifies how fast endemic species may disappear along with their habitats in the Cerrado (cf. Figs 35–38). Based on morphological and molecular similarities found among specimens from the different areas sampled, we can assume that this species inhabited a continuous, large patch of forest in the past, and its current restriction to only three small fragments of gallery forest most likely resulted from intensive human activities in the area. While it is difficult to pinpoint when and why this fragmentation occurred, it is reasonable to assume that it took place recently, since archaeological evidence (~9000 years ago) suggests the presence of only hunter-gatherer or forager cultures occupying the biome in the past (Klink & Moreira, 2002). On the other hand, the agriculture and cattle grazing activities that began between 1920 and 1930 with the first economic boom in the Cerrado have increased continuously in the area (Klink & Moreira, 2002) and are most likely the reason for the actual fragmentation.

It is important to stress that the fragments of forest inhabited by Cerradopatus sucuriuensis gen. et sp. nov. (cf. Fig. 2) are mainly owned by farmers and do not constitute legally protected areas. Therefore, they are still susceptible to human activities that directly affect the populations of this species (cf. Figs 35–42). The most extreme example occurred during the construction of a small hydroelectric power plant, for which one fragment was substantially logged. No onychophorans were found in the remaining patch of forest during the 4 years of monitoring that succeeded the logging. On the one hand, it would still be important to continuously monitor this fragment to verify whether or not the population will recover, but on the other hand, it seems unlikely, as the remaining fragment no longer holds suitable conditions for onychophorans (see Figs 2 and 35–38) and the fragmentation prevents new colonization of a re-established forest. This whole scenario, together with the peculiar biology of onychophorans, e.g. the low reproduction rates of neotropical peripatids (see Lavallard & Campiglia, 1975; Oliveira, Franke, et al., 2012), led us to assess the threatened status of this species. According to the IUCN Red List categories and criteria (2012, 2014), Cerradopatus sucuriuensis gen. et sp. nov. might be considered a Critically Endangered (CR) species since: (i) it occurs in areas smaller than 10 km² (occupancy area), (ii) its total distribution (extent of occurrence) is estimated to be less than 100 km², and (iii) its habitat is severely fragmented and vulnerable to continuing decline. Based on our observations, we agree that this species is prone to an ‘extremely high risk of extinction in the wild’ (IUCN, 2012) if urgent conservation measures are not implemented and,
therefore, we suggest its inclusion as a Critically Endangered (CR) species in the IUCN Red List.

The conservation of invertebrates is challenging and sometimes more effectively promoted if habitats or ecosystems are targeted, rather than single species (Lewinsohn et al., 2005). However, flagship species alone might justify the preservation of habitats regardless of the species richness of the area. Among the few examples worldwide, in which reserves have been created based on a single flagship invertebrate species, we may cite the Myers Allotment in UK (0.072 km²) created for the High Brown Fritillary, the Breton Blue Butterfly Reserve in South Africa (0.015 km²), the Mahoenui Giant Weta Reserve in New Zealand (2.4 km²), the Estação Ecológica do Triupi in Brazil (3.92 km²) created for the onychophoran E. acacioi, and the Monarch Butterfly Biosphere Reserve in Mexico (562.59 km²). Following these examples, Cerradopatus sucuriuensis gen. et sp. nov. could be used as a flagship species for the legal protection of its habitat. This would constitute a reserve of at least 1.68 km² that, in our view, might be enough to ensure the survival of this species, although no study has ever stipulated the minimum area required for keeping a viable onychophoran population long term.

Moreover, according to the Brazilian law (MMA 09/2007; Silva, 2007), such a reserve could be established by justifying the biological importance of these areas to relevant authorities, yet immediate actions would be still required, as legal processes usually demand considerable time. A putative, short-term solution for protecting Cerradopatus sucuriuensis gen. et sp. nov. would be to fence these areas and educate the locals about the biological importance of the fragments, which could at least reduce the selective cutting of trees, opening of trails and presence of cattle within the fragments. At the same time, relevant authorities must be contacted to initiate the legal procedures required to protect the species and the areas in which it occurs.

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Supplemental data

Supplemental data for this article can be accessed here.

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