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Over a century later, new records of *Oroperipatus balzani* (Camerano, 1897; Onychophora: Peripatidae) from Sara Ana Research and Training Center (Bolivian Yungas, La Paz, Bolivia), with a checklist of the species known from the country

Jaime Sarmiento[1,2,*], Soraya Barrera[1,2], Alberto Mariscal[3] and Stéphane Saj[4]

[1] Museo Nacional de Historia Natural, Calle 26 Cota Cota, La Paz, Bolivia

[2] Colección Boliviana de Fauna, Calle 27 Cota Cota, Campus Universitario, La Paz, Bolivia

[3] Independent Researcher

[4] Research Institute of Organic Agriculture (FiBL), Department of International Cooperation, Switzerland

[*] Corresponding author, e-mail: jsarmientotavel@gmail.com

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Abstract

After over a hundred and twenty years, we here report a new record of Oroperipatus balzani (Camerano, 1997) in western Bolivia's lower Yungas of La Paz department. Six specimens of this species, first collected in 1891 by the Italian explorer L. Balzan, were observed at the Sara Ana Station (15°27′36″S, 67°28′17″W; 390 m above sea level) within both secondary forests and agricultural systems between October 2018 and December 2021. *Oroperipatus balzani* come from a mid-altitude forest of the eastern Andean slopes, and the specimen here reported was found at less than 500 m s.n.m., representing a notable altitude extension of the known range. The current record marks only the second documented occurrence of this species in Bolivia. Currently, three species (*Oroperipatus*, *balzani*, *O. intermedius*, and *O. soratanus*) are known in the country. All three species correspond to the Andean clade of Neotropical Onychophora. A checklist from Bolivia was updated. Furthermore, we discuss the distribution of Onychophora species in Bolivia.

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Keywords *Oroperipatus balzani*, Andean velvet worms, Velvet worm distribution, Bolivian Yungas, Anthropogenized systems, Agroforestry

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1. Introduction

Species of phylum Onychophora, commonly known as velvet worms or peripatus, are often referred to as 'living fossils' due to their ancient lineage (Barquero-González et al., 2016). These enigmatic yet charismatic creatures have captured the interest of researchers across various fields, including historical biogeography, conservation biology, and evolution (Allwood et al., 2010; Murienne et al., 2014; Giribet et al., 2018). As one of the oldest terrestrial groups with limited dispersal abilities, such the well-known Tardigrada (water bears), some enigmatic groups of millipede-like arthropods (Myriapoda), a number of different arachnids (including mites and pseudoscorpions), and primitively flightless hexapods (sprigtails and silverfish) (Garwood and Edgecombe, 2011) , they play a pivotal role in understanding the Panarthropoda evolution (Monge-Nájera, 1995; Sampaio-Costa et al., 2009; Murienne et al., 2014; Contreras-Félix et al., 2018). The Onychophora exhibits characteristics reminiscent of both 'worm-like' Nematoda and Nematomorpha (segmentation, worm-like body, layered musculature, paired waste-elimination organs, simple constructed brain and eyes), and arthropods with which they share the chitinous exoskeleton, open blood system and posterior tubular heart, perivisceral and pericardial cavities, tracheal breathing, segmentation and two body appendages per segment (Grimaldi & Engel, 2005; Barquero-González et al., 2016). Their extraordinary biology includes unique features such as the only known placenta in an invertebrate and the production of a particular hunting adhesive weapon (Concha et al., 2015; Barquero-González et al., 2016).

Almost all species of Onychophora reproduce sexually. Although at least one species from Guyana, which lacks males, reproduces by parthenogenesis. Interestingly, females of many species are fertilized only once, and copulation occurs before females fully develop. All species studied to date have internal fertilization. However, there is a high diversity in the modes of sperm transfer, ranging from dermal insemination to the use of specialized head structures in the male. Oviparity occurs solely in the Peripatopsidae from Australia and New Zealand, often in regions with unsettled climates. Most species are ovoviviparous: the embryos remain in the mother's uterus and feed on the yolk contained in the eggs (lecithotrophy). Live-bearing species occur mainly in tropical regions. The embryos develop and nourish in their mother's uterus (matrotrophy). Most Neotropical species develop a genuine tissue connection between the epithelium of the uterus and the embryo (known as the placenta), and nourishment is supplied exclusively in this way (placentotrophic viviparity). The gestation period can be up to 15 months, and females can have between 1 and 23 offspring (Mayer et al., 2015; Glime, 2017).

To date, 237 species of velvet worms have been described, distributed across two extant subgroups: Peripatidae (92 species) and Peripatopsidae (140 species), and five fossil species with unclear relationships to extant taxa. Among the 237 species, 216 are accepted as valid and, due to significant taxonomic inconsistencies, at least 21 species are considered *nomina dubia*. Many valid species require revision, particularly the fossil taxa (Monge-Nájera & Xianguang, 1999; Contreras-Félix et al., 2018; Oliveira, 2023). The Neotropical Onychophora (Peripatidae) are traditionally classified into two distinct groups: Andean and Caribbean peripatids (Chagas-Júnior & Costa, 2014). Despite their predominantly Gondwanan distribution, estimates of divergence time suggest that onychophorans were once widely distributed throughout the ancient supercontinent of Pangaea (Murienne et al., 2014). Peripatidae species are primarily found in tropical regions (Mexico, the Neotropics, West Africa, and South Asia), while Peripatopsidae species exhibit a southern temperate distribution (Chile, South Africa, and Oceania) (Monge-Nájera, 1995). Several species are known from only a few specimens, limiting knowledge of their distribution, ecology, natural history, and taxonomy (Vasconcellos et al., 2004, 2006; Brito et al., 2010). They inhabit rainforests in tropical and temperate regions, dwelling under rotten trees, stones, moss, leaf litter, soil crevices, and near water sources, including termite and ant mounds (Grimaldi & Engel, 2005; Vasconcellos et al., 2006; Barrett et al., 2016; Barquero et al., 2016; Glime, 2017). Additionally, they are found in deciduous forests and various anthropogenic environments, such as suburban areas and agroforestry plantations (Barrett et al., 2016; Monge-Nájera, 2018).

Human activities significantly influence soil biodiversity, impacting its vast diversity and critical role in ecosystem functioning and delivery of ecosystem services. Many threats to soil biodiversity and function stem directly from human-induced changes in land use cover (FAO et al., 2020). Deforestation in the Neotropics, driven by activities such as conversion of tropical forests for cattle ranching, mechanized cultivation (particularly soybean pro-

duction), and small-scale agriculture, represents a significant challenge. This issue is critically important in Bolivia, as it leads to changes in soil's physical and chemical characteristics that disrupt habitat suitability and result in the loss of specialized species, such as onychophorans (FAO et al., 2020; Boillat et al., 2022). Agroforestry systems, in contrast to monocultures, have been found to support higher diversity and abundance of wildlife, sometimes rivaling that of forests (Nijmeijer et al., 2019; Bos et al., 2007), thus serving as important biodiversity reservoirs. The long-term experimental site established in Sara Ana, Bolivia, in 2009 presents a unique opportunity to study soil communities across various cacao production systems and secondary forests over time.

This study unveils new records of *Oroperipatus balzani* from the Experimental Station of Sara Ana, Bolivia. Additionally, we provide a critical review of the knowledge, geographic data, and current information regarding the distribution and status of the three species currently documented in Bolivia. Our findings contribute to a comprehensive list of Bolivian velvet worm species, drawing from literature, museum specimens, and firsthand observations.

2. Study area

The study area is located within the Alto Beni Municipality of the La Paz department in northeastern Bolivia. Situated in the Bolivian Yungas ecoregion, it forms a part of South America's Andean Mountain Forest and Valleys Bioregion. Characterized by geological diversity, the region comprises several parallel low hill ranges and broad valleys, serving as a transitional zone between the Amazonian lowlands and the highland Puna.

Ecologically, the Alto Beni municipality encompasses a wide array of ecosystems, ranging from humid tropical forests to high-altitude prairies. The natural vegetation of the Alto Beni region consists of a medium to tall seasonal evergreen rainforest, characterized by a continuous canopy reaching heights of 15 to 20 m, with sporadic emergent trees exceeding 30 m (Navarro et al. 2003). Renowned for its rich biodiversity and high level of endemism, this ecoregion has been highlighted for its significance by OneEarth (2023) and Ripa et al. (2021). The soils in the area predominantly stem from sandstone, shales, tertiary conglomerates, and alluvial deposits along the rivers (Elbers 1995, Ripa et al. 2021). These mineral-rich and well-drained soils provide a fertile substrate for agriculture, fostering diverse crops such as coffee and cacao.

The study site is precisely located in the experimental station Sara Ana, at 15°27′36″S and 67°28′17″W. The landscape of Sara Ana consists of secondary humid forests, riparian forests, and cocoa orchards cultivated under organic agroforestry systems (Marconi et al. 2021). The climate is humid tropical with dry winters. The mean annual temperature is 26 °C, and the mean annual rainfall is 1535 mm. The field site spans approximately 9 hectares, with loamy soil structure and predominating soil types being lixisols and luvisols (Ripa et al., 2021). Sara Ana is not designated as a protected area per se, but it falls within the Vilcabamba-Amboró Conservation Corridor (VACC), including 16 protected areas spanning Peru and Bolivia. This corridor represents a binational initiative aimed at conserving the Tropical Andes Hotspot, recognized as one of the planet's most biologically, ecologically, and culturally diverse area. Adjacent to Sara Ana, two subnational status protected areas—Municipal Park and Natural Integrated Management Area (MP-NIMA) Mayaya and MP-NIMA Alto Beni—have been established to enhance connectivity between protected areas.

3. Methods

During field expeditions for soil macro-invertebrate studies, we collected Onychophora specimens by actively searching within and beneath fallen trees, partially decomposed logs, and under leaf litter (Brito et al., 2010; Oliveira et al.. 2010; Barquero-González et al., 2016). All collected specimens were preserved in 75% ethanol and stored in the invertebrate collection of the Colección Boliviana de Fauna (Bolivian Fauna Collection, CBF) (Museo Nacional de Historia Natural - Instituto de Ecología Universidad Mayor de San Andrés; MNHN-IE).

Sampling occurred biannually, during both the rainy and drought seasons, in 2018, 2020, and 2021. A consistent approach was maintained across all sampling periods. Two team members (always the same), conducted searches for macroinvertebrates for one hour in the central area (20 × 20 m2) of 20 cacao cropping plots, avoiding border effects (see Schneider et al, 2017 for details on cropping and trial design). Considering the low detectability of velvet worms, sampling took place during the daylight hours. We conducted the same sample effort every time on two secondary forest

plots nearly 50 and 200 m from the nearest cocoa plot.

We compiled data from literature sources and primary databases housed in museums, the Global Biodiversity Information Facility (GBIF), and others. Additionally, we carefully reviewed all Onychophora specimens in the CBF collections.

We alphabetically organized the Bolivian Onychophora checklist, detailing the author and year for each taxon name. For each species, we provide comprehensive information, including synonyms, details on types and type localities, specimen locations, the language of original description, and a synthesis of relevant taxonomic characteristics (Oliveira et al., 2012a; Barquero-González et al., 2016). All available data on Onychophora localities in Bolivia, including visual records, are depicted in a map (Figure 1).

Species identification follows Bouvier (1905), with generic classification aligned with Peck (1975). We gathered locality data from gazetteers to identify collection sites precisely and carefully reviewed Balzan's and Günther's expedition reports to Bolivia. Each specimen's locality record was incorporated into a database and subsequently exported to Q-GIS for map visualization.

Figure 1. Specimens of Onychophora from the Sara Ana Station

4. Results

New records of Oroperipatus balzani from Bolivia

During macro-invertebrate field sampling conducted at the Sara Ana research and training center, situated in the Alto Beni region of the La Paz Department, Bolivia (15°27′36″S, 67°28′17″W; 390 m a.s.l.), between October 2018 and December 2021, we either collected or recorded seven specimens belonging to the phylum Onychophora (Figure 1). Following morphological examination, we assigned these specimens to the genus Oroperipatus and provisionally identified them as belonging to the species *Oroperipatus balzani* (Camerano, 1897). The research center site encompasses five cocoa crop schemes, each replicated four times. These include two full-sun monocultures under conventional and organic agriculture, two agroforestry systems employing conventional and organic farming practices, and one highly diverse agroforestry system (Figure 2). Surrounding the experimental area are patches of secondary forest (Durot et al., 2023). The mean annual temperature in the area is 26.9 ± 0.4 °C. The mean yearly rainfall is 1645 ± 244 mm with the dry season (average monthly precipitation of less than 100 mm) spanning from May to September and the rainy season between December and March (Durot et al., 2023).

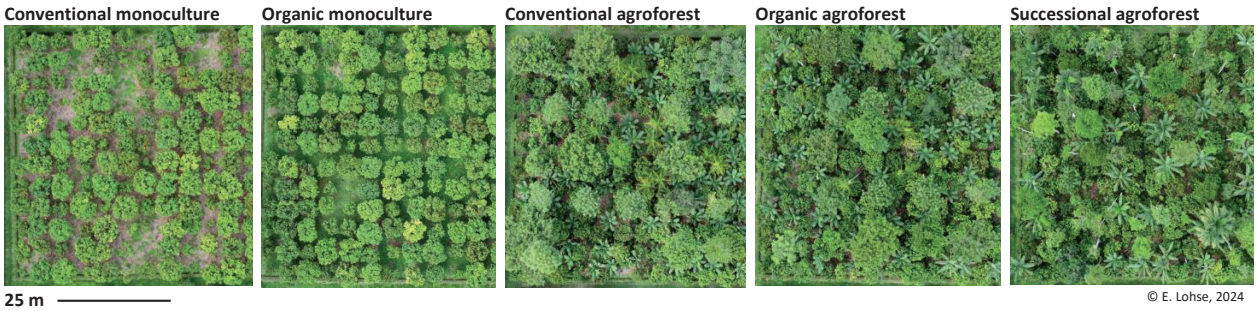

Figure 2. Cocoa production plots in the Sara Ana Station.

Velvet worm specimens were discovered within the experimental area and in the adjacent secondary forest during fieldwork in October 2018, February 2020, and December 2021. One individual was found in conventional monoculture, two in organic monoculture, and one in organic agroforestry cocoa plots, where they were moving under leaf litter and often associated with partially decomposing logs. Additionally, we found three other individuals within decaying logs in the secondary forest near the plots where the others were encountered.

Furthermore, another specimen of *Oroperipatus balzani* was collected from a location in a primary forest near the town of Chirca, within the Municipality of Chulumani in the Sud Yungas province of the La Paz Department (16°23′54″S, 67°35′1″W; 1690 m a.s.l.; Figure 3). This locality is near the putative collection site of the specimen used to describe *O. balzani*, approximately 6 km northeast of Chulumani and 27 km south of Coroico.

Additionally, we report two visual records of velvet worms from Bolivia, made more than ten years ago. The first record originates from Coroico, one of the reference localities for the specimens collected by Balzan. This specimen was observed over riparian vegetation near a small mountain stream. The second record is from the Zongo Valley, approximately 35 km northeast of Coroico (Figure 3).

Identification

Based on the presence of two anterior and two posterior distal foot papillae, at least four spinous pads, and nephridial tubercles inserted in the third creeping pad on leg (Bouvier, 1905; Peck, 1975; Oliveira et al., 2012b), we assigned the specimens to the genus *Oroperipatus*. Following the original description by Camerano (1897) and the morphological characters used by Bouvier (1905), the species fit *Oroperipatus balzani* (Camerano, 1897). However, the species is known only of the two specimens collected in 1891, and the descriptions do not agree with the nomenclature and today‘s standards. Hence, accurate taxonomic determination of Bolivian specimens requires detailed morphological revision and proper description according to recent terminology.

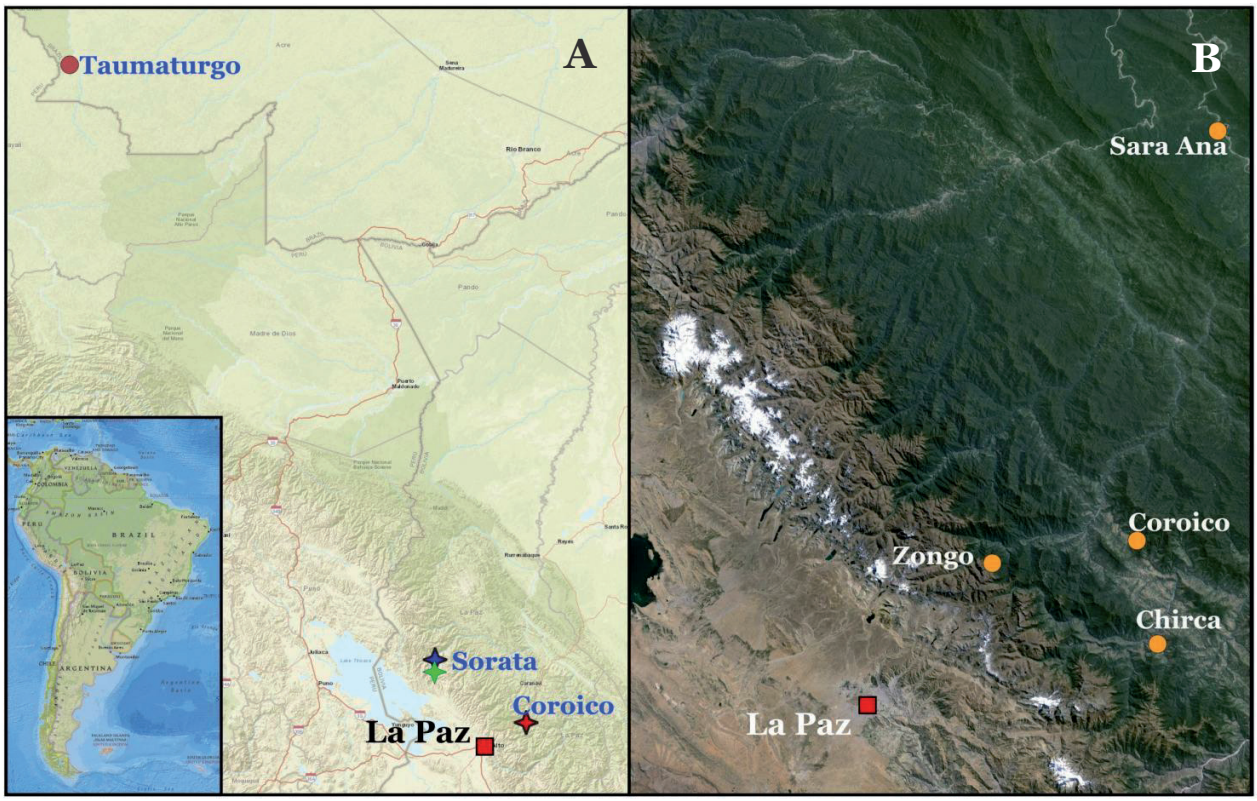

Figure 3. A. Type localities for Bolivian Onychophora: Oroperipatus balzani (red star); O. soratanus (blue star); O. intermedius (green star), including one record of O. balzani from the State of Amazonas in Brazil (red dot). B. Bolivian localities for Oroperipatus balzani.

Checklist of the species of Onychophora from Bolivia

Three species of velvet worms are presently documented in Bolivia: *Oroperipatus balzani* (Camerano 1897), *O. intermedius* (Bouvier 1901), and *O. soratanus* (Bouvier 1901) (Oliveira et al., 2012). However, knowledge about these species remains rudimentary, with only a handful of specimens known, most of which were collected over a century ago and require thorough revision (Oliveira et al., 2012). The first Onychophora species described from Bolivia dates back to the late nineteenth century (1891) when the Italian zoologist Luigi Balzan collected two specimens during his expedition to the *Misiones Mosetenes* region in northeastern Bolivia (Balzan, 1891; Camerano, 1897; López-Beltrán, 2008). These specimens were obtained from an unspecified locality between the Municipalities of Coroico and Chulumani ("cantoni di Coroico e Chulumani, Yungas"), at an elevation of nearly 1600 meters (Camerano, 1897).

Our knowledge of these species is preliminary, as it relies on brief descriptions hindered by outdated taxonomy and lack of data regarding their distribution. Two species (*O. soratanus* and *O. intermedius*) are solely known from their type locality and have not been encountered since their original collections.

Checklist

ONYCHOPHORA Grube, 1853
PERIPATIDAE Evans, 1901
Type genus: *Peripatus Guilding*, 1826
Oroperipatus (Cockerell, 1908)
Type species: *Oroperipatus lankesteri* (Bouvier, 1899), by original designation (Cockerell 1908: 620).
Remarks: Initially introduced as a subgenus of *Peripatus* (see Cockerell 1908: 620), *Oroperipatus* was elevated to genus status by Clark (1913) (Oliveira et al., 2012a).

1. Oroperipatus balzani (Camerano, 1897)

Synonyms:
Peripatus balzani as originally designated (Camerano 1897: 14)
Peripatus balzani (Bouvier 1905: 149)

Oroperipatus balzani (Clark 1913: 16)
Oroperipatus balzani (Peck 1975: 347)
Oroperipatus balzani (Sampaio-Costa et al. 2009: 558)

Holotype: Not designated.
Type locality: BOLIVIA, Yungas, between Chulumani and Coroico, at 1,600 m a.s.l. (Camerano 1897).
Distribution: Bolivia (La Paz Department) and Brazil (Acre State).
Specimen localization: Museo Civico di Storia Naturale di Genova. MZT, MHNG (Sampaio-Costa et al., 2009).
Language of species description: Italian.
Taxonomic characteristics: Females are chocolate-brown dorsally, with light spots over papillae and a darker median longitudinal stripe; legs paler than the back; 26-27 paired legs; outer mandible three-toothed, inner mandible with four large teeth (Camerano 1897).
Remarks: Described from two specimens (Camerano 1897), this species requires thorough revision. Initially considered a pair of females by Camerano, they were later identified as two males by Bouvier (1905). Until recently, it was only known from the type locality. However, a recent report documented *Oroperipatus balzani* from a specimen collected in the State of Acre, Brazil, nearly 1000 km north of the type locality. This specimen is housed at the Museu Nacional de Rio de Janeiro (MNRJ) (Sampaio-Costa et al., 2009). Nevertheless, we treat this record cautiously due to the commonly accepted restricted distribution of most Onychophora.

2. Oroperipatus intermedius (Bouvier, 1901)

Synonyms:
Peripatus intermedius as originally designated (Bouvier 1901: 168);
Peripatus intermedius (Bouvier 1905: 154)
Oroperipatus intermedius (Clark 1913: 16)
Oroperipatus intermedius (Peck 1975: 347)

Holotype: Preserved at the Natural History Museum of Lübeck, Lübeck, Germany.
Type locality: BOLIVIA, La Paz, Sorata.
Distribution: Known solely from the type locality.
Specimen localization: Natural History Museum of Lübeck, Lübeck, Germany.
Language of species description: French.
Taxonomic characteristics: Requires thorough revision.
Remarks: Described by Bouvier (1901) from a female specimen collected in Bolivia and housed at the Natural History Museum of Lübeck, Germany. The museum was severely damaged during World War II, and the collection material, including type material, was destroyed. We could not ascertain the survival of the type specimen for *O. intermedius*. Nevertheless, obtaining new collections to elucidate taxonomic and biological information about this species is imperative.

3. Oroperipatus soratanus (Bouvier, 1901)

Synonyms:
Peripatus soratanus, as originally designated (Bouvier 1901: 168);
Peripatus soratanus (Bouvier 1905: 143)
Oroperipatus soratanus (Clark 1913: 16)
Oroperipatus soratanus (Peck 1975: 348)
Holotype: Not designated.
Type locality: BOLIVIA, La Paz, Sorata.
Distribution: Known solely from the type locality.
Specimen localization: Natural History Museum of Lübeck, Lübeck, Germany.
Language of species description: French.
Taxonomic characteristics: Requires thorough revision.
Remarks: Like *O. intermedius*, Bouvier (1901) described *O. soratanus* from a female specimen collected in Bolivia and housed at the Natural History Museum of Lübeck. Consequently, the specimen may also be missing, underscoring the importance of acquiring new samples to enhance understanding of this species‘ taxonomy and natural history.

5. Discussion

Currently, the precise number of Onychophora species remains uncertain. Approximately 230 species have already been described (Oliveira et al., 2012; Contreras-Félix et al., 2018, Oliveira, 2023). However, this count likely underestimates the true diversity of Onychophora, as evidence suggests a considerable number of not described and cryptic species within both Peripatidae and Peripatopsidae (Reid, 1996; Daniels et al., 2009; Brito et al., 2010; Lacorte et al., 2011; Oliveira et al., 2011, 2012; McDonald and Daniels, 2012; McDonald et al., 2012). Recent evidence also highlights hidden diversity and a prevalence of endemics confined to relatively small areas (Trewick, 1998; Daniels et al., 2009; Oliveira et al., 2011, 2012a). Consequently, it is anticipated that several new Onychophora species will be discovered and described in the Neotropic region, including Bolivia. Given Bolivia‘s expansive territorial area and the limited number of localities where Onychophora have been collected, it is reasonable to assume that the total diversity of these creatures is much greater than currently recognized. Thus, there is

an urgent need for additional collection efforts, especially considering that many old localities face intense human pressure, posing an escalating risk of extinction.

We collected four Onychophora specimens from the Sara Ana station and identified them as *Oroperipatus balzani*. However, as Oliveira et al. (2012a, 2023) suggested, we stress the urgency for morphological revision and molecular characterization of all three Bolivian species. Morphological uniformity, low character variation, and intraspecific variability obscure species differentiation. Additionally, recent studies indicate that the taxonomic classification of Peripatidae is challenging both morphologically (Oliveira et al., 2012b, 2013, 2015) and molecularly. Therefore, taxonomic delineation and species diagnosis have transitioned from solely morphological to multi-methodological approaches, with molecular techniques gaining prominence as standard procedures (Oliveira, 2023). Consequently, the application of molecular techniques could aid in the accurate differentiation of Onychophora species. Moreover, geographic references provided for Bolivian material are imprecise. For instance, the locality for *O. balzani* is an unspecified location between the localities of Coroico and Chulumani. Although these localities are only 32 km apart (in a straight line), their climatic and vegetation characteristics vary from humid and hyper-humid in Coroico to drier conditions in Chulumani (Navarro & Maldonado 2005).

The other two species (*O. soratanus* and *O. intermedius*) were described from specimens collected by M. Günther in Sorata, northern Bolivia, in the late 1800s (Bouvier, 1901). M. Ernest Günther, a German citizen, was involved in prominent enterprises that exported quina bark (Cinchona spp.), the primary treatment for malaria at that time. While Sorata served as the operational base, the cinchona bark originated from the more humid forests of Tipuani and Mapiri, located approximately 50 km north and at lower altitudes. Hence, it is plausible that the specimens collected by M. Günther originated from the moister region of Tipuani-Mapiri, as this species has never been reported from Sorata region yet.

Bolivia represents the southernmost distributional boundary, particularly for the Andean lineage of Onychophora (genus *Oroperipatus*). Only three species are known from the country, with records and collections limited to small areas around Sorata, Coroico, and Chulumani, within a large area of humid forests on the eastern slope of the Andes. Since knowledge of Bolivian Andean Onychophora diversity is crucial for understanding the southern extension distribution patterns of velvet worms in South America, exploring this region to document Onychophora diversity thoroughly is imperative. Furthermore, like other animal groups, especially invertebrates, phylogenetic and biogeographic studies face a significant data gap concerning Bolivia. Recent studies, such as Giribet et al. (2018), do not incorporate samples from Peru and Bolivia, relying primarily on samples from northern South America and Trans Andean species to analyze the genus *Oroperipatus*.

Conservation efforts for the nearly 200 recognized species of velvet worms are scarce, despite the concern that they are at risk due to their small populations and high vulnerability to habitat alteration (Wells et al., 1983; Mesibov & Ruhberg, 1991; New, 1995; Vasconcellos et al., 2006; Morera-Brenes et al., 2019). Compounding this issue, numerous species are morphologically indistinguishable (Costa et al., 2018), making them elusive and challenging to locate even in their known habitats (New, 1995). The International Union for Conservation of Nature (IUCN) lists several species from various regions as critically endangered, endangered, or vulnerable due to habitat loss (Oliveira et al., 2014; IUCN, 2018). Bolivian species, documented solely from their type localities outside protected areas, lack sufficient data to assess their conservation status accurately.

Effective conservation strategies require taxonomic identification and comprehensive data on distribution and life history characteristics, posing significant challenges for Bolivian species due to the near absence of information within the country‘s borders. Nevertheless, considering their confined distributions, small populations, and susceptibility to disruption, velvet worms should be included in conservation programs. Their charismatic appeal to scientists and the public could enhance community engagement and support for conservation efforts.

Until recently, researchers studying onychophorans primarily associated them with primary forest habitats. However, records from exotic plantations, harvested forests, and urban habitats suggest their ability to thrive can survive in modified habitats (Morera-Brenes et al. 2019). Specimens discovered in Sara Ana came from cocoa plots managed under different techniques, from full-sun monoculture plots exposed to high solar radiation to agroforestry plots and secondary forests shaded by canopy trees. The presence of onychophorans in full-sun plots challenges the notion that reduced humidity would necessarily preclude their survival, indicating that the management practices employed in Sara Ana may support the persistence of velvet worm. We hypothesize that the management practices developed in the Alto Beni region for cocoa production, such as periodic pruning and litter accumulation fostering refuge and small moist areas, could create modified habitats conducive to conserving sensitive invertebrates, particularly Onychophora. Furthermore, this suggests that such habitats could play a vital role alongside conventional protected areas in shaping conservation corridors, effectively enhancing biodiversity conservation efforts.

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7. Additional information

Conflict of interest
The authors declare that no competing interests exist.

Ethical statement
No ethical statement is reported.

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Author contributions
Conceptualization: JS, SB. Data curation: JST. Investigation: JS, SB. Writing – original draft: JS, SB, SS. Writing – review and editing: JS, SB, SS, AM. English language check: SS.

Author ORCIDs
Jaime Sarmiento https://orcid.org/0000-0002-5588-5956
Soraya Barrera https://orcid.org/0000-0002-7043-4440
Stéphane Saj https://orcid.org/0000-0001-5856-5459

Data availability
All data supporting this study findings are available in the main text.

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