# Diversidad Taxonómica De Los Onicóforos (Onychophora: Peripatidae) Presentes En El Flanco Occidental De La Cordillera Oriental De Los Andes, Departamento De Santander.

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#### Dedicatoria

A Dios por bendecir mi carrera con experiencias enriquecedoras a nivel personal y profesional, por iluminar mi mente y fortalecerme en los momentos difíciles.

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#### Resumen

TÍTULO: DIVERSIDAD TAXONÓMICA DE LOS ONICÓFOROS (ONYCHOPHORA: PERIPATIDAE) PRESENTES EN EL FLANCO OCCIDENTAL DE LA CORDILLERA ORIENTAL DE LOS ANDES, DEPARTAMENTO DE SANTANDER. \*

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PALABRAS CLAVE: ONYCHOPHORA, PERIPATIDAE, ONICÓFOROS NEOTROPICALES, MORFOLOGÍA, FILOGENIA, DISTANCIA GENÉTICA, SIMPATRÍA,

ESPECIACIÓN CRIPTICA.

Los onicóforos o gusanos aterciopelados pertenecen al phylum Onychophora, este cuenta con aproximadamente 210 especies, agrupadas en dos familias. Peripatidae es nuestra familia de interés y presenta una distribución Ecuatorial con 85 especies actualmente descritas. Sin embargo, varios autores indican una subestimación de su diversidad debido a especiación críptica y la falta de muestreo. En Colombia los registros de onicóforos datan de más de un siglo, estos carecen de los métodos científicos empleados actualmente. En este trabajo, se realizó un muestreo en el flanco occidental de la cordillera oriental de los Andes, Departamento de Santander, explorando la fauna de onicóforos. Para explorar las relaciones filogenéticas corrimos analices de Máxima Verosimilitud e Inferencia Bayesiana (con genes COI, 12S rRNA y 16S rRNA) de los onicóforos muestreados con otras especies de Peripatidae. Adicionalmente, calculamos la distancia genética e hicimos un análisis descubrimiento por código de barras automático (GAP) para las secuencias de ADN de cada gen. Nuestros resultados nos permiten inferir que los onicóforos del área de estudio i) están presentes en hábitats intervenidos y conservados. ii) viven en microhábitats previamente descritos, incluso el más reciente, briosfera arbórea. iii) tienen una distribución altitudinal desde 1220-3000 m. iv) muestran una alta diversidad de especies, donde algunas reportan baja variación genética, a pesar de su amplia distribución. v) el análisis filogenético reveló cinco clados monofiléticos incluyendo un nuevo género para Colombia. vi) caracteres morfológicos únicos soportan la descripción del nuevo género y tres especies relacionadas. Resaltamos el hallazgo de una especie candidata con dimorfismo sexual, tres especies simpátricas y otra especie candidata con una amplia distribución y dos morfotipos de coloración. Nuestros resultados sugieren que la taxonomía de los onicóforos requiere de múltiples datos para una correcta delimitación de especies. Este trabajo es pionero en el estudio de la diversidad de onicóforos en Colombia.

<sup>\*</sup> Trabajo de grado.

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#### Abstract

**TITLE:** TAXONOMIC DIVERSITY OF THE ONYCHOPHORANS (ONYCHOPHORA: PERIPATIDAE) PRESENT IN THE WESTERN SLOPE OF THE EASTERN ANDEAN MOUNTAINS, SANTANDER DEPARTMENT. \*

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**KEYWORDS:** ONYCHOPHORA, PERIPATIDAE, NEOTROPICAL ONYCHOPHORANS, MORPHOLOGY, PHYLOGENY, GENETIC DISTANCE, SYMPATRY, CRYPTIC SPECIATION.

Onychophorans or velvet worms belong to the phylum Onychophora, which has approximately 210 species, grouped into two families. The family Peripatidae has an Equatorial distribution with 85 species described. However, some authors have pointed out an underestimated diversity due to cryptic speciation and lack of sampling. In Colombia, published records date for more than a century and were not taken under contemporary scientific standards. In this work, we sampled the western Slope of the Eastern Andean Mountains, Santander Department, exploring the onychophoran fauna. To explore the phylogenetic relationships, we ran a Maximum likelihood and Bayesian inferences (COI, 12S rRNA and 16S rRNA genes) of Colombian onychophorans with other species described of Peripatidae. Additionally, we calculate genetic distances using genetic pairwise and species Automatic Barcode GAP Discovery analyses. Taken together, our results reveal that colombian onychophorans from the study area i) reside in both intervened and conserved habitats; ii) occupy typical microhabitats describe, even the recently describe, arboreal bryosphere. iii) are distributed in a broad altitudinal range from 1220-3000 m. iv) species exhibit high diversity, although, some show low genetic variation despite their broad distribution. v) phylogenetic analysis showed five monophyletic clades, including a new genus for Colombia. vi) morphology revealed unique character combination for the description of the new genus and three related species. We highlight the finding of a candidate species with sexual dimorphism, three sympatric species and two color morphotypes for another candidate species. Our results suggest that onychophoran taxonomy requires an integration of multiple evidence for accurate species delimitation. This work is pioneer in the study of onychophoran biodiversity in Colombia.

<sup>\*</sup> Master's thesis.

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#### Introduction

Onychophorans also known as velvet worms are charming soft-bodied, terrestrial and carnivorous macroinvertebrates. They usually display cryptic behavior, low dispersal capacity and preference for wet habitats, to avoid desiccation and light stimuli (Beckmann et al., 2015; Clusella-Trullas & Chown, 2008; Daniels & Ruhberg, 2010; Kirwan et al., 2018; Mcdonald & Daniels, 2012; Ruhberg, & Daniels, 2013; J Monge-Nájera et al., 1993; J Monge-Nájera & Xianguang, 1999; Rockman et al., 2001; Ruhberg & Daniels, 2013; Woodman et al., 2007). These organisms occupy a wide variety of microhabitats with high humidity such as: moist soil, wet mosses, in or under rotten log, under stones, caves, epiphytes, and the recently described arboreal bryosphere (Espinasa et al., 2015; Hamer et al., 1997; Monge-Nájera & Alfaro, 1995; Peck, 1975; Vasconcellos et al., 2006; Zitani et al., 2018). Since onychophorans exhibit a preference for these microhabitats, they are considered members of the community of saproxylic organisms, which are susceptible to habitat disturbance. Given their charismatic appearance, onychophorans have been chosen as umbrella taxa, to protect other species from the saproxylic community and their surrounding habitat (Daniels et al., 2009; Myburgh & Daniels, 2015; New, 1995; Oliveira et al., 2014; Ruhberg & Hamer, 2005).

Onychophorans share characteristics with both annelids and arthropods and their body plan has remained unchanged since the carboniferous, according to a fossil embedded in Ambar (Bouvier, 1904; Garwood et al., 2016; Ghiselin, 1984; Oliveira et al., 2016; Poinar, 2000; Wright, 2012). For these reasons, this group has been useful to answer questions in evolution, phylogenetic position in Panarthropod, developmental biology, reproduction mechanisms, morphology, molecular and species diversity, among others (Brockmann et al., 2001; Eriksson & Budd, 2000; Eriksson et al., 2003; Eriksson et al., 2009; Frase & Richter, 2013; Hogvall et al., 2014; Martin et al., 2017; Mayer, 2007; Mayer et al., 2004; Mayer & Whitington, 2009b, 2009a; Oliveira & Mayer, 2017; Oliveira et al., 2018; Oliveira et al., 2014; Roeding et al., 2007; Sedgwick, 1884; Storch & Ruhberg, 1990; Strausfeld et al., 2006; Sunnucks et al., 2000; Walker & Tait, 2004). Thanks to the broadcast in 2005 of the BBC series Life in the Undergrowth, onychophorans got the attention from a broad general audience, that found exceptionally the way they hunt insects with a sticky solution ejected by special organs in their head (Julián Monge-Nájera & Morera-Brenes, 2015).

The phylum Onychophora comprise nearly 210 species currently recognized, divided into two families, Peripatopsidae and Peripatidae (Oliveira et al., 2012, 2013, 2014, 2018); Oliveira & Mayer, 2017). The former displays a circumaustral distribution, contrasting with the Equatorial distribution of the latter. Peripatidae is our group of interest; it contains 12 genera and 85 species described until now. However, Oliveira et al., 2011, 2012 Daniels et al., 2017 have pointed out an underestimated diversity of the group due to cryptic speciation and insufficient sampling. The use of scanning electron microscopy (SEM) has showed a hidden character diversity for species taxonomy (Oliveira et al., 2012, 2014). Additionally, the use of molecular tools has helped access DNA data from various species of Peripatidae (Murienne et al., 2013). Nevertheless, the lack of a morphological examination in sequenced species or rather correspond to a new and yet undescribed species or genus. Thus, the need for a revision and species description using an integrative approach is crucial to unravel the taxonomy of this group.

In Colombia there are five onychophoran species described, Epiperipatus vespucci (Brues, 1914), Oroperipatus bimbergi (Fuhrmann, 1913), Oroperipatus multipodes (Fuhrmann, 1913),

Oroperipatus tuberculatus (Bouvier, 1898) and Peripatus bouvieri (Fuhrmann, 1913). Although, the diversity of these soft-body invertebrates in the country is poorly known since the previous species descriptions date from over 100 years ago, type localities are not clear and there are no paratypes in national museums, limiting taxonomic studies to the original descriptions. In 2009, Jerez-Jaimes & Bernal-Pérez studied the thermal and physical properties of the onychophoran slime; also, they tried to include a taxonomic examination of the collected specimens. However, the characters used have a low taxonomic resolution and ended in the misidentification of the specimens (Oliveira et al., 2012). In this study, we explored the western slope of the Eastern Colombian Andes, in search for onychophorans within an altitudinal range, covering a rich variety of habitats and microhabitats. We employed an integrative taxonomic approach by using morphological, molecular and ecological data to expand current knowledge of the unexplored onychophoran fauna in the country.

#### 1. Objectives

#### 1.1 Main objective

• The principal objective of my thesis was to characterize the onychophoran fauna present in the Eastern Colombian Andes, Santander Department.

#### **1.2 Specific objectives**

- Collect onychophoran specimens in different localities within the western flank of the Eastern Colombian Andes.
- Classify taxonomically the collected onychophoran specimens based on their morphological characteristics.
- Classify taxonomically the collected onychophoran specimens based on the analysis of nucleotide sequences of the mitochondrial cytochrome oxidase I (COI) and the ribosomal subunit 12S rRNA.
- Integrate the morphological and molecular results in the species diagnosis of the onychophorans present in the study area.
- Delimit the geographic distribution of the onychophoran species discovered in the study area.

#### 2. Materials and methods

#### 2.1. Collection of specimens

The specimens were collected between 2016-2017, during the rainy and dry seasons, in 23 localities on the western slope of the Eastern Andes, Santander Department, Colombia (Figure 2; Table 1). The sampling method consisted on searching in all possible microhabitats available. The specimens were transported in cloth bags filled with leaves, soil and pieces of rotten logs. These bags were moistened frequently until they arrived to the laboratory, where velvet worms were transferred to plastic boxes and maintained at 17-25 °C, following Oliveira et al., (2012) and Baer & Mayer, (2012). The specimens were collected with the authorization from Autoridad Nacional de Licencias Ambientales (Resolución 0047-2015 and Resolución 0260-2016) and the ethics endorsement of the Comité de Ética en Investigación Científica (CEINCI) of Universidad Industrial de Santander.

#### 2.2 Morphological data

Living specimens were photographed under daylight. Euthanasia was carried out using an overdose of topical lidocaine and immersion in 4% liquid lidocaine. Specimens were fixed with an injection of paraformaldehyde (4% PFA), immersed in the same solution for about 1 h, and preserved in 70% ethanol. To create Scanning Electron Microscopy (SEM) images, specimens were dehydrated in an ethanol series according to Oliveira et al., (2012). Finally, specimens were cut into small pieces and dried in a critical point dryer (E3100, Quorum technologies, Lewes, United Kingdom), coated with gold in a Cressington 108 sputter coater (Watford, United Kingdom) and viewed in a Quanta microscope FEG 650 (FEI, Oregon, United States). Terminology of morphological features was based on Oliveira et al., (2010, 2012).

#### 2.3 Molecular data

Total DNA was extracted from dissected legs (~ 25 mg), fixed in absolute ethanol using the DNeasy Blood & Tissue kit (Oiagen®, #69506), according to the manufacturer's protocol. Three partial mitochondrial gene fragments, cytochrome c oxidase subunit I (COI), the large ribosomal subunit RNA (16S rRNA) and the small ribosomal subunit RNA (12S rRNA), were amplified by using primer pairs LCO1490 & HCO2198 (Folmer et al., 1994), 16Sar & 16Sb (Edgecombe et al., 2002) and 12S\_PH\_F & 12S\_PH\_R (Oliveira et al., 2012), respectively. We redesigned COI difficult primers to amplify some samples: Ony COU F 5'-TTTCTACTAATCATAAGGATATTGG-3' and Ony COU Rd 3'-TAAACCTCWGGRTGWCCAAAAAACCA -5'. PCR amplifications were performed in 25 µL with 40 ng of DNA, TopTaq Buffer 1x (Qiagen®), 2 mM MgCl2, 0.2 µM dNTPs, 0.18 µM primers, 1x Q-solution (Qiagen®) and 1 U TopTaq DNA polymerase (Qiagen®). The PCR program consisted of a first denaturation step at 94 °C for 5 min, followed by a standard three step protocol of 35 cycles of denaturation at 94 °C for 45 s, annealing at 59 °C for 45 s, and extension at 72 °C for 1 min. A final elongation step consisted of 72 °C for 5 min. The 12S and 16S programs only varied in the annealing temperature, which was at 54 °C and 56 °C, respectively. Amplicon purification and sequencing of both strands were performed by capillary electrophoresis (MACROGEN Inc., Seoul, South Korea). COI, 16S and 12S rRNA sequences were checked for quality, edited and assembled using Geneious 9.1.6 (Kearse et al., 2012).

#### 2.4 Phylogenetic analyses

Homologous sequences from other Onychophorans were collected from National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov/), Barcode Of Life Data Systems database (BOLDSYSTEMS, http://www.boldsystems.org/index.php) and compared with our molecular data (see Table 2). We performed a multiple alignment of non-coding mitochondrial sequences of the 12S and 16S rRNA genes by applying the Q-INS-i algorithm (Katoh & Toh, 2008) implemented in MAFFT version 7.304 (Katoh & Standley, 2013), which considers information of the RNA secondary structure. For protein-coding COI sequences we computed a multiple alignment using default parameters in MAFFT and then confirmed alignment and gap placement by translating them into amino acid sequences using Mesquite 3.31 (Maddison & Maddison, 2018). The phylogenetic analyses were performed with the concatenated dataset, which includes information from 52 samples (23 species) for the 12S rRNA gene, 27 samples (15 species) for the 16S rRNA gene, and 51 samples (26 species) for the COI gene. For the latter gene, the sequences KC754638, KC754639, KC754640, and KC754644 were excluded from the analyses because they were amplified from a different region of the COI gene. We inferred the best-fit partition scheme along with the best-fit models of evolution using the greedy heuristic algorithm in PartitionFinder version 2.1.1 (Lanfear et al., 2017) under the Bayesian Information Criterion (BIC). We conducted a maximum likelihood (ML) phylogenetic analysis on IQ-TREE 1.5.3 (Nguyen et al., 2015); running 10,000 ultrafast bootstrap pseudoreplicates for internal node support (Minh et al., 2013). We also performed a Bayesian Inference (BI) phylogenetic reconstruction in MrBayes 3.2.6 (Ronquist et al., 2012) with all parameters left at default. We calculated uncorrected genetic distances among species for COI, 12S and 16S genes separately (Tables 2 and 3), using Kimura, (1980) 2-parameter (K2P) model with 1000 bootstrap replicates using MEGA7 (Kumar et al., 2016).

#### 2.5 GAP analyses

We performed a barcode GAP analysis to calculate the overlap between intra and inter-specific genetic data for the three genes COI, 12S rRNA and 16S rRNA using simple distances with the

ABGDsoftware(Puillandreetal.,2012).(http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html).

#### 2.6 Distributional range

We created distributional maps for the species here described using the minimum convex polygon (MCP) approach with Quantum GIS software (QGIS development team, 2018). For this, we used the Convex Hull Function to create the smallest convex polygon enclosing all occurrence sites. Finally, we calculated the area of the range polygon of the species as a proxy for the extent of occurrence of the species by summing the pixels within the final MCP.

#### 3. Results

#### 3.1 General features of the habitat and microhabitat

Field expeditions were performed from 2016 to 2017, covering different habitats (e.g., native and secondary forests, grasslands, and agroecosystems) and microhabitats in the wet and dry seasons. Interestingly, onychophorans were present in the 23 surveyed localities (Table 1). The velvet worms were found inactive during daylight, in solitary or in groups of specimens in different life stages. Hidden in humid, fresh and shadowed microhabitats such as the rhizosphere, leaf litter, epiphytes, and sulcate petioles in species of Araceae, decaying logs and under stones. During night surveys, the individuals were observed in solitary, perching on the fronds of ferns, plant leaves, bryophytes and the trunk of trees near small streams (Figure 1). We did not register any of them feeding or hunting. The onychophorans found ranged from 1220 to 3000 m of elevation (Figure 2). In addition, we had access to specimens collected in Cundinamarca (Eastern Andes) and Amazonas Departments that were donated to our project. We typically collected from 1 to 12 specimens per locality.

#### 3.2 Molecular and phylogenetic analyses

To study the genetic diversity of the collected onychophorans we used three mitochondrial genes 16S rRNA, 12S rRNA and COI. Amplicons of these genes had approximate sizes of 463-491, 410-486 and 519-698 bp, respectively. We included collected specimens from each locality in the analysis, excluding sequences with 100% identity. Translated COI sequences did not show internal stop codons; thus, they correspond to a functional coding sequence. Although, the alignment of the COI sequences revealed a codon deletion at positions 160-162 in the specimens Epiperipatus biolleyi and Cerradopatus sucuriuensis.

A preliminary phylogenetic (ML) and genetic distance (p-distance) analyses was run; the result showed a strong relationship (99 and 0.98, respectively) between the COI sequence U62429 from the NCBI, named as Oroperipatus corradoi, and the outgroup (Peripatopsidae members). A BLASTN search revealed a sequence identity and query cover of 100% with Euperipatoides rowelli; for this reason, we excluded this sequence from the molecular analyses.

The best partition scheme (LnL=-21,944.90, BIC=45,210.83) for the concatenated genes 16S rRNA, 12S rRNA and COI includes five subsets, each with an evolutionary model (16S GTR+G) (12S TVM+I+G) (COI pos1: TIM+I+G; pos2: K81UF+I+G; pos3: TIM+G). The family Peripatidae was monophyletic with high nodal support values (UFB = 100, PP = 1.00). Monophyly was strongly supported for six described genera within this family: Cerradopatus (UFB = 100, PP = 1.00), Eoperipatus (UFB = 98, PP = 1.00), Macroperipatus (UFB = 96, PP = 0.95), Mesoperipatus (UFB = 98, PP = 1.00), Oroperipatus (UFB = 100, PP = 1.00), and Principapillatus (UFB = 100, PP = 1.00). However, monophyly was not supported for two of the described genera: Epiperipatus and Peripatus. This phylogeny includes 8 of the 12 genera currently recognized for the Peripatidae family, except Heteroperipatus, Plicatoperipatus,

Speleoperipatus and Typhloperipatus, for which there is no molecular data available. In addition, we recovered 10 monophyletic lineages (Figure 3, Clades A-J) and the new genus Andinopatus gen. nov. (UFB=100, PP=1.00).

Sequences without a taxonomic classification at the genus level were treated as unnamed taxa in our phylogeny (Figure 3, Clades A-J). This included: DNA104978-79 and DNA103556 of Murienne et al., (2013), identified as Peripatidae, here grouped in clades A and J; linages A, B and C from Cunha et al., (2017), here recovered as the monophyletic clades F, G and H, respectively. Finally, the sequence BCMS40812 (BOLD Systems) from Brazil identified by Livia Cordeiro Borghezan as order Euonychophora, here recovered in clade I as a member of the Peripatidae. The sequence CTM20513 (BOLD Systems) from Mexico, was also identified as Euonychophora by Leon Ibarra Garibay. However, our phylogenetic and genetic pairwise analyses showed this sequence grouped with Oroperipatus sp., from Belize with a genetic distance of 0.047(COI); for this reason, we renamed it to Oroperipatus sp2. Likewise, the sequence DNA103689 classified by Murienne et al., (2013) as Epiperipatus biolleyi, is grouped with Principapillatus hitoyensis in our phylogenetic tree with a genetic distance of 0.047 (12S); given this, we treated this sequence as Principapillatus sp.

Our phylogenetic analyses of the Colombian onychophoran fauna led to the discovery of a new genus, Andinopatus gen. nov., that differs from other existing genera of Peripatidae, forming a distinct monophyletic clade recovered as a sister group of Oroperipatus (UFB=84). The new genus is composed of three species and two candidate species. The rest of the Colombian sequences were assigned to 4 clades (Figure 2 B-E), for which there was not enough material for a formal species description. Despite this, a preliminary examination of their gross morphology suggests that our samples from clade B should be considered as a candidate genus

(see Figure 9 B and Table 3). Mean genetic pairwise values for members of clade D, 0.033 (COI), 0.015 (12S) and 0.058 (16S), and gross morphology examination suggest that this clade might constitute a candidate genus (Figure 9 D; Tables 4, 5 and 6). Additionally, sequences from Colombia of Murienne et al., (2013) were assigned to Epiperipatus and Macroperipatus without a specified criterion. The authors did not mention how they classified these specimens and the locality records are not clear; thus, we put these taxa inside quotation marks given the uncertainty of their taxonomic identity.

Genetic pairwise distances were calculated using p-distance and K2P for the three genes. We found little difference between the two parameters ( $\approx 0.022$ ); though, we performed the analyses with the p-distance values as recommended by other authors (Srivathsan & Meier, 2012). Andinopatus gen. nov. shows a low mean genetic distance among the five species in the clade (see appendix 2-6); the lowest distance was 0.039 (12S), for the other genes the mean values were 0.067 (16S) and 0.089 (COI). Additionally, we performed a barcode gap analysis using p-distance. Our results from the gap analyses for the different genes and datasets (COI, 51 taxa; 12S, 52 taxa and 16S, 27 taxa) showed a similar grouping as the clades in our phylogenetic tree (see appendix 7-9).

#### 3.3 Morphological characteristics of the new genera and species.

**3.3.1. Genus etymology.** The name Andinopatus refers to the Andean mountains, the word Andes is believed to derivate from the Quechua word anti which means east, while Andino means inhabitant or native to the Andes, where these species live. The termination patus, is derived from the Greek peripatos or "walking about"; the latter is typically used to name genera for the phylum Onychophora. We chose this combination because it would translate "walking about the Andes".

3.3.1.2. Genus description. Andinopatus gen. nov. Specimens of Andinopatus can be distinguished from other Peripatidae genera by an exclusive combination of characters. Antennas with 46 rings from the base to the top. Mouth with eighteen external lips and around twelve to fourteen internal lips (Figure 3 D). Both mandibles with a single accessory tooth; inner jaw blade with a diastema and a variable number of denticles ranging from 8 to 11 (Figure 3 F). Dorsally, there are 12 plicae: 2 incomplete, 10 are complete, where 7 plicae extend dorsolaterally, crossing between the legs (Figure 3 C). Primary papillae conical with rounded bases; apical piece conical with 2-3 scales bearing a short bristle (Figure 8); one species with more than one type of primary papillae (Figure 8 D, E). Accessory papillae small, variable in number and distribution between pairs of primary papillae (Figure 7). Legs with eight transverse rings in dorsal view composed of primary and accessory papillae intercalated with thinner rings showing only accessory papillae (Figure 3 G). The distal foot papilla consists of two anterior and one posterior papillae (Figure 3 H); the setiform ridge below the claws bears more than one bristle in ventral view (Figure 9 A, F). In the legs, the number of spinous pads ranged from four to five (Figure 3 E, Figure 9). In some specimens, the last spinous pad is small, incomplete or rudimentary (Figure 9); the last pair of legs with only two spinous pads (Figure 3 H). Nephridial tubercles are present in the fourth and fifth leg pairs between the third and fourth spinous pads (Figure 3 E; 9 B, D and F); usually in these legs, the last spinous pad appears rudimentary. The coxal vesicle at the base of the leg is well-developed. The ovary is paired, endogenous and covered with a thin epithelium. The ascendant or proximal portion of the uterus has embryos in different developmental stages; the descendant or distal portion of the uterus has fetuses in different pigmentation and developmental stages.

Coloration. The specimens of this genus exhibit a uniform body coloration in life (Figures 2 B-D; 3 A). Dorsally the body appears greyish-brown with a dark dorsal midline. There is another pattern, a rhombic shape along the dorsal midline, observed in individuals with paled coloration. Ventrally, the coloration is light-brown with white dots. The coloration of specimens preserved in 80% ethanol retains the original pattern, however sometimes the color tends to fade.

#### 3.3.2. Andinopatus sublapis gen. et sp. nov.

**3.3.2.1.Holotype.** OHL-182 (Figure 2 d), an adult female from vereda La Mina (6.283812, -72.994207; 1919 m asl), municipality of Coromoro, Santander department, Colombia. Collected by O.Y. Hernández-Lagos, C. Hernández-Jaimes, S. Porras-Lemus and S. Cote on October 2017.

**3.3.2.2. Paratypes.** OHL-183, 187 and 197 (adult female), with the same data as the holotype, collected at 1,919 and 1,987 m in elevation, respectively. OHL- 135, 138 (adult female), from vereda La Herrerita (6.291115, -73.190419; 1744 m asl), municipality of Charalá, Santander department, collected on March 2017. OHL-121 (adult female), from vereda Las Flores (6.34473, -73.3092; 1282 m in elevation), municipality of Guapotá, Santander department, collected on November 2016. OHL-133 (female) and OHL-134 (male) (6.446512, -73.11268; 1489 m in elevation; 6.443084, -73.096899; 1636 m in elevation) municipality of Valle de San José, Santander department, collected on March 2017.

**3.3.2.3. Etymology.** The name sublapis is derived from the Latin sub (=under) and lapis (=stone). This name was chosen because the species was found mainly under stones in the type locality.

**3.3.2.4. Species diagnosis.** The plicae shows a typical arrangement of primary and accessory papillae (Figure 7). The dorsomedian furrow is bordered by three accessory papillae on each side, followed by primary papillae, and then accessory papillae, at the periphery of the plicae there are a major amount of short accessory papillae (Figure 7 A). The specimens of Andinopatus sublapis differ from other species of the family by the nucleotide sequence of the COI, 12S rRNA and 16S rRNA genes (Table 1, Accession numbers).

**3.3.2.5. Description.** Coloration: specimens in vivo vary from dark to light-brown with a lighter rhomboid pattern along the black dashed midline, antennae and head region with the same coloration. Laterally, above the legs, the coloration is pale forming a longitudinal band on each side of the body. Shining primary papillae are distributed in the ventral surface of the body, standing out from the dark background color (Figure 2 d). After fixation, some specimens lost their coloration and became pale brown with purple at the tips of the legs. Head: Each antenna bears 46 rings; the antennal sensory field begins at the third complete ring from the base to the top and extends for approximately nineteen rings (Figure 3 B, 6 A). The spindle-shaped sensilla bear three scales and end in a short bristle; these sensilla are bigger than the type II sensilla (Figure 6 B). Chemoreceptors and type I sensilla present in the antennal tip; there are also type II sensilla a few rings behind the antennal tip. Eyes well-developed, present laterally behind the antennae. Mouth composed of two rows of lips; the external row exhibits eighteen lips and the internal row twelve lips (Figure 5 A). Slime papillae is compose of conical primary papillae, which is covered with seven or eight scales, apical piece with three scales and finally a long bristle (Figure 5 B). Mandibles with outer and inner jaw blades, both with one principal and one accessory tooth; inner blade with eleven denticles. Body: Dorsally, there are 12 plicae: 2 incomplete, 10 are complete, where 7 plicae extend dorsolaterally, crossing between the legs.

The plicae shows a typical arrangement of primary and accessory papillae (Figure 7). The dorsomedian furrow is bordered by three accessory papillae on each side, followed by primary papillae, and then accessory papillae, at the periphery of the plicae there are a major amount of short accessory papillae (Figure 7 A). There is one type of primary papillae with conical form covered with 5-6 scales the apical piece is conical with 2-3 scales with a decentered short bristle (Figure 8 A). Two kinds of accessory papillae, the biggest in the middle of two primary papillae, the smallest at the periphery of the plicae (Figure 8 B) Type II crater-shaped papillae with sixteen scales in the apical collar (Figure 8 C). First pair of legs with four spinous pads; last pair of legs reduced in size bearing only two spinous pads and the penultimate pair with three pads; the remaining legs exhibit four spinous pads (Figure 9 A), some of them with a fifth rudimentary pad. Dorsally, the legs show eight transverse rings composed of primary and accessory papillae alternated with thinner rings with only accessory papillae; two anterior and one posterior distal foot papillae located below the claws, laterally to the leg. The ventral surface of the foot bears two proximal and two distal bristles relative to the setiform ridge. The number of legs overlaps between males and females. The genital pore is located between the penultimate leg pair in females and males (Figure 10). In both sexes, the genital pore is covered with primary papillae from the periphery to the center, in females the opening is cross-shaped, contrasting with the males, which exhibit a longitudinal opening (Figure 10 A, B). Males exhibit a pair of crural tubercles in two pair of legs before the genital pore, and a pair of anal gland opening anterior outer border of the anus (Figure 10 B).

**3.3.2.6. Distribution.** This species is known from the type locality vereda La Mina (6.283812, -72.994207; 1,919-1,987 m asl), municipality of Coromoro. Additional locality records include: vereda La Herrerita (6.291115, -73.190419, 1744 m asl), municipality of Charalá; vereda Las

Flores (6.34473, -73.3092; 1282 m asl), municipality of Guapotá and municipality of Valle de San José, in Santander department, Colombia (6.446512, -73.11268; 1489-1636 m asl) (Figure 2 C). The species was registered from 1,489 to 1,987 m of altitude.

**3.3.2.7. Ecology and natural history.** The specimens from the type locality were found always under stones in a grassland used for cattle ranching and within riparian vegetation next to a big forest patch. In the other localities, the specimens were found in a cacao plantation (Guapotá); inside rotten logs next to a coffee-shade plantation (Valle de San José); in low vegetation and the base of tree trunks in the streamside of a secondary forest (Charalá). In the latter locality, the specimens were found in sympatry with another less-abundant undescribed species from a candidate genus, here included in Clade C (Figure 2 e; 3).

#### 3.3.3. Andinopatus saproxylicus sp. nov.

**3.3.3.1. Holotype.** OHL-115 (Figure 2 b), an adult female from vereda Vegas del Quemado (7.200922, -73.011648, 1,710 m asl), municipality of Tona, Santander department, Colombia. Collected by O.Y. Hernández-Lagos and C. Hernández-Jaimes, on March 2016.

**3.3.3.2. Paratypes.** OHL-107 (female) OHL-stub (Male), with the same locality data as the holotype, collected at 1667 and 1710 m in elevation, respectively. OHL-109-110 (female), from municipality of Suratá (7.372070, -72.989880; 1933 m asl), Santander department, collected on November 2016.

**3.3.3.3. Etymology.** The name saproxylicus comes from the Greek saprós (=rotten, decaying) and the prefix xyl- (xúlon=wood). This name was chosen because onychophoran species are usually found in saproxylic microhabitats.

**3.3.3.4. Species diagnosis.** The plicae shows a typical arrangement of primary and accessory papillae. The dorsomedian furrow is bordered by a single accessory papilla on each side, followed by primary papillae, and then accessory papillae, at the periphery of the plicae there are minor and short accessory papillae (Figure 7 B). In addition, the bristle in the spindle-shaped sensilla is larger compared with the other two species described in this study, and the general shape of the spindle-shape sensilla is smaller, covered with two scales (Figure 6 D). The specimens of Andinopatus saproxylicus differ from other species of the family by the nucleotide sequence of the COI, 12S rRNA and 16S rRNA genes (Table 1, Accession numbers).

3.3.3.5. Description. Coloration: The coloration in vivo varies from dark to light brown and some specimens have gravish coloration uniformly along the body until it reaches the ventral side where the color turns lighter. Light body colored specimens have a visible rhomboid pattern along the dashed midline along the body (Figure 2 b). After fixation the original pigment is preserved, although sometimes it turns darker. Head: Each antenna bears 46 rings; the sensory field starts at the third ring and extends for nineteen rings (Figure 3 B; 6 C). The spindle-shaped sensillum is covered with two scales and ends in a long bristle, this sensillum is the shortest of the three species described in this study; the type II sensilium is shorter than the spindle-shaped sensillum (Figure 6 D); chemoreceptors and type I sensillum are present in the antennal tip. The eye is well-developed and is located posterolateral to the antenna. The mouth is composed of eighteen external and fourteen internal lips (Figure 5 C); the mandibles are composed of an inner and outer blades, both with one principal and one accessory tooth; the inner blade bears ten denticles. The slime papillae is compose of primary papillae, the latter is conical, the base is covered with six scales and the apical piece two scales, ending in a short bristle (Figure 5 D). Body: Dorsally, there are 12 plicae: 2 incomplete, 10 are complete, where 7 plicae extend

dorsolaterally, crossing between the legs. The dorsomedian furrow is bordered by a single accessory papilla on each side, followed by primary papillae, and then accessory papillae, at the periphery of the plicae there are minor and short accessory papillae (Figure 7 B). There are two types of primary papillae that differ in the number of scales, the first type bears six rows of scales while the smaller type is covered with four scales; the apical piece is composed of three scales and ends in a short bristle (Figure 8 D, E). There are also two types of accessory papillae, the bigger one consists of six rows of scales and is located between the primary papillae, while the smaller type is covered by four rows of scales and is at the periphery of the plicae (Figure 8) F). Type II crater-shaped papillae with approximately 8-10 scales in the apical collar (Figure 8 G). First leg pair with four spinous pads; last pair of legs with two spinous pads, sometimes a third rudimentary pad; penultimate leg pair with three pads; the remaining legs exhibit four spinous pads, although in some legs a fifth rudimentary pad is visible (Figure 9 C). In the fourth and fifth leg pairs, the nephridial tubercle is present between the third and fourth spinous pads (Figure 9 D). Dorsally, the legs are compose of eight transverse rings as depicted above in the previous species description. Also, two anterior and one posterior distal foot papillae. The ventral region of the foot exhibits two bristles in the distal and proximal regions of the setiform ridge. The bristles on the spinous pads appear to be the largest from the species described here (Figure 9). The genital pore is located and bears the same arrangement for primary papillae as previously described (Figure 10). In females, the opening of the genital pore is longitudinal, different from males that exhibit a cross-shaped opening (Figure 10 C, D). Males exhibit the same number and distribution of the crural tubercles and anal gland openings as previously described (Figure 10 D).

**3.3.3.6. Distribution.** This species is known from the type locality vereda Vega Del Quemado (7.196265, -73.015337, 1,659 m asl), municipality of Tona. Additional locality records include: municipality of Suratá (7.372070, -72.989880; 1933 m asl), in Santander department, Colombia. The species was registered from 1,659 to 1,933 m of altitude (Figure 2 C).

**3.3.3.7. Ecology and natural history.** The specimens from the type locality were found under stones, within and under decaying wood in grasslands, a fruit plantation and inside a riparian forest. In the latter habitat, the species was found sympatrically with another undescribed species from a candidate genus, here included in Clade D (Figures 2 a; 3). In the locality of Suratá, the specimens were observed under fallen logs next to a stream surrounded by grasslands and shrubs.

#### 3.3.4. Andinopatus xerira sp. nov.

**3.3.4.1. Holotype.** OHL-085 (Figure 2, c) an adult female from vereda El Carrizal (6.860180, -73.046970; 1,652 m asl), municipality of Los Santos, Santander department, Colombia. Collected by O.Y. Hernández-Lagos and C. Hernández-Jaimes on November 2016.

**3.3.4.2. Paratypes.** OHL-083 (female) and OHL-070 (male), with the same locality data as the holotype, collected at 1,626 and 1,658 m in elevation, respectively. OHL-154,156 (female), from vereda El Tabacal (6.853965, -72.844433; 1,893 m asl), municipality of Guaca, Santander department, collected on June 2017. OHL-095, 097 (female), from vereda Esparta (7.013607, -72.897394; 2,266 m asl), municipality of Santa Bárbara, Santander department, collected on November 2017. OHL-023 (female), from vereda Las Amarillas (6.973111 -73.016778; 1,495 m asl), municipality of Piedecuesta, Santander department, collected on December 2016.

**3.3.4.3. Etymology.** The name xerira refers to the territory of the Cacique Guanentá, maximum leader or chief of the indigenous tribe that originally inhabited the type locality of Los Santos, Santander department, in the pre-Columbian era.

**3.3.4.4. Species diagnosis.** The plicae show a typical arrangement of primary and accessory papillae. The dorsomedian furrow bordered by accessory papillae each side; however, the size of these papillae varies in some plica. There are two assembling in the plica after the dorsomedian accessory papillae, i) two accessory papillae, followed by a primary papilla, then three accessory papillae and again a primary papilla, ii) a primary papilla, followed by three accessory papillae, then a primary papilla (Figure 7 C). In addition, the bristle in the spindle-shaped sensilla is smaller and with a thicker appearance than the other two species previously described; the general shape of the spindle-shaped sensilla is tall and conical covered with three scales. The specimens of Andinopatus xerira differ from other species of the family by the nucleotide sequence of the COI, 12S rRNA and 16S rRNA genes (Table 1, Accession numbers).

**3.3.4.5. Description.** Coloration: The coloration in vivo is dark brown to grayish; in young juveniles, the color is lighter and a pale brown line is noticeable along the dorsomedian furrow. Depending on the coloration, a dashed line is visible in the middle of the dorso (Figure 2 c). After fixation, some specimens turned into a lighter color and others went purple. Head: Antennae with 46 rings, the sensory field starts at the third ring and extends for nineteen rings (Figure 3 B; 6 E); the spindle-shaped sensillum is covered with three scales and ends in a short and thick bristle; the type II sensillum is shorter, covered with two scales and ends in a long thinner bristle (Figure 6 F). The tip of the antenna bears chemoreceptors and both types of sensilla. The eye is well-developed and located posterolaterally to the antenna. The mouth is composed of eighteen external and fourteen internal lips (Figure 5 E); the mandibles are

composed of an inner and outer blades, both showing one principal and one accessory tooth; the inner blade exhibits eight denticles. Slime papillae covered with conical primary papillae, which bears four scales in the base and two in the apical piece, ending in a concentrical bristle. Body: Dorsally, there are 12 plicae: 2 incomplete, 10 are complete, where 7 plicae extend dorsolaterally, crossing between the legs. The dorsomedian furrow bordered by accessory papillae each side; however, the size of these papillae varies in some plica. There are two assembling in the plica after the dorsomedian accessory papillae, i) two accessory papillae, followed by a primary papilla, then three accessory papillae and again a primary papillae, ii) a primary papillae, followed by three accessory papillae, then a primary papillae. There is one type of primary and accessory papillae; the former with conical form, which bears six scales in the base and two or three in the apical piece (Figure 8 H); the latter is composed with five scales (Figure 8 I). Type II crater-shaped papillae bears ten scales in the apical collar (Figure 8 H). The first leg pair as described in the previous species. The last leg pairs with two spinous pads and penultimate leg pair with three; the remaining legs with four spinous pads, although, in some legs there is a rudimentary pad (Figure 9 E); the nephridial tubercle is located between the third and the fourth spinous pads in the fourth and the fifth leg pairs (Figure 9 F). Dorsally, the legs have eight transverse rings as described previously. Distal foot papillae consist of two anterior and one posterior papillae. Ventrally, there are two bristles in the distal and proximal regions of the setiform ridge. The genital pore is located as previously described (Figure 10). The genital pore exhibits primary papillae at the periphery in both sexes. Additionally, Females and males exhibit a longitudinal opening (Figure 10 E, F). Males display the same number and distribution of the crural tubercles and anal gland openings as previously described (Figure 10 **F**).

**3.3.4.6. Distribution.** This species is known from the type locality vereda El Carrizal (6.860180, -73.046970; 1,652 m asl), municipality of Los Santos. Additional locality records include: vereda El Tabacal (6.853965, -72.844433; 1,893 m asl), municipality of Guaca; vereda Esparta (7.013607, -72.897394; 2,266 m asl), municipality of Santa Bárbara and vereda Las Amarillas (6.973111 -73.016778; 1,495 m asl), municipality of Piedecuesta, in Santander department, Colombia (Figure 2 C). The species was registered from 1,495 to 2,266 m of altitude.

**3.3.4.7. Ecology and natural history.** The specimens from the type locality were found in an organic coffee-shade plantation in humid microhabitats such as the rhizosphere covered with leaf litter under coffee plants, under decaying logs and beneath the rhytidome of fallen trees. In the other localities, the specimens were observed within rotten logs, near an ant nest, and under stones in a grassland near a riverside, or in the leaf litter and fallen epiphytes in a plantation of shade-grown coffee (Guaca); under stones in a ranch field (Santa Bárbara) and in the sulcated petiole of Araceae plants (Piedecuesta) (Figure 2 C). In the type locality the specimens were found in sympatry with another less-abundant species of Andinopatus, here name as A. candidate species 1 (Figure 3).

#### 3.3.5. Differences between Andinopatus gen. nov. and other Andean genera.

Considering the morphological characters observed under the stereomicroscope and Scanning Electron Microscopy (SEM), we found that the morphology of the Andean species of onychophorans is highly conserved (See Table 2). The new species of the described genus Andinopatus gen. nov. show four characteristics that differ among them: i) arrangement and morphology of the primary and accessory papillae in the plica (Figure 7). ii) number of scales in the primary and crater-shaped papillae (Figure 8). iii) number of scales of the primary papillae

in the slime papillae (Figure 5, B, D, F). iv) number of scales of the spindle-shaped papillae (Figure 6).

Morphological differences between the species of Andinopatus gen. nov. and the other Andean species include coloration patterns, position of the nephridial tubercle and the appearance of primary and accessory papillae. The specimens from municipality of Florián, represented in the phylogeny by OH\_071\_CO from Clade C (Figures 2 h; 3) exhibited a unique coloration pattern. Males present a yellow body coloration with white legs and a dorsomedian dark rhomboid pattern; the head is red, bearing white antennae with purple antennal tips; females show a dark red coloration dorsally and light red color ventrally. According to the genetic pairwise distance and preliminary phylogenetic analyses including ten sequences from the same locality, these specimens correspond the same species with 100% identity. This constitutes the first report of sexual dichromatism for the family Peripatidae. In general, the legs bear five spinous pads and sometimes a sixth rudimentary pad is visible; the nephridial tubercle is located between the third and fourth spinous pads, in the fourth and fifth leg pairs (Figure 11C). The primary and accessory papillae appear globular. Additionally, the crural tubercles in males show a different appearance than that of Andinopatus gen. nov. species. The specimen OH 132 CO, also a member of clade C (Figures 2 e, 3), presents a different coloration pattern, as follows: the body is light red, a white horizontal band is present dorsally behind the eyes covering most of the head; the antennae is dark-red from the base to the top. The morphology of the crural tubercles seems globular. The number of spinous pads and the position of the nephridial tubercle is similar to other specimens described above (Figure 11 A).

The specimens from Clade E (Figures 2 a, 3) exhibit a relatively broad geographic distribution (Figure 2 B); despite this, the coloration pattern remains similar. The body appears dark-yellow

to light brown, there is a black dorsomedian rhomboid pattern bordered by a yellow pattern with pairs of shiny papillae running on opposite sides; laterally, there is a pale black band along the body, below this band and above the legs there are a prominent number of shiny papillae. In one locality we found a different color variation, the body is black and the yellow rhomboid pattern is less distinct; the shiny papillae as described above (Figures 2 a). The legs have four spinous pads; the nephridial tubercle is located centrally between the third and fourth spinous pads, in the fourth and fifth leg pairs (Figures 11 D). The phylogenetic and genetic distance analyses revealed that these two morphotypes belong to the same species.

The specimens OH\_103\_CO and OH\_104\_CO from Clade B (Figure 3, clade B) are most different from all the Andean species. These specimens are distributed in the Amazon region from southern Colombia (Figures 2 A, i). The body coloration of specimen OH\_103\_CO in vivo is pale-brown with a dashed black line in the dorsomedian furrow; the antennae is dark-brown with a yellow band of primary papillae above the legs. The other specimen (OH\_104\_CO) is dark brown with a black dashed line in the midline of the body, and a longitudinal light-brown line above the legs, running throughout the body (Figure 2 i). The legs have four spinous pads; the nephridial tubercle is located between the second and third spinous pads in the fourth and fifth leg pairs (Figure 11 B). Additionally, the number and distribution of distal foot papillae differ from Andinopatus gen. nov.: in specimen OH\_103\_CO there are two anterior and two posterior distal foot papillae, while specimen OH\_104\_CO exhibits three distal foot papillae on each side of the leg.

#### 4. Discussion

This study is the first phylogenetic assessment of Neotropical onychophorans in Colombia. Based on molecular and morphological data from specimens, we propose a new genus, Andinopatus gen. nov., and four candidate genera grouped in clades B-E (Figure 3). We described three new species, A. sublapis, A. saproxylicus and A. xerira, which exhibit a broad and sympatric distribution in the study area. As a novelty, we found a candidate species in one locality, which displays color dimorphism between males and females. Additionally, we found a distinct candidate species with a broad distribution with two color morphotypes.

Onychophorans are known to live in habitats with high humidity, within a variety of microhabitats like burrows in moist soil, mosses, inside or under rotten logs, under stones and in caves, among others. In the course of our exploration, we found onychophorans in the typical microhabitats described in the literature. Recently, Zitani et al., (2018) reported the discovery of a novel microhabitat, the arboreal bryosphere, where the branches and trunks are covered with bryophytes and epiphytes (see appendix 1). During night surveys, the onychophorans were found standing still in the low vegetation. Some authors have regarded onychophorans as active foragers (Monge-Nájera & Morera-Brenes, 2015; Read & Hughes, 1987). However, based on our observations, we consider that onychophorans display a sit-and-wait strategy, which is supported by reports of low vision, spectral sensitivity, low vagility, and water loss in this group (Beckmann et al., 2015; Clusella-Trullas & Chown, 2008; Kirwan et al., 2018; Monge-Nájera & Morera-Brenes, 1994; Woodman et al., 2007).

Interestingly, we report the sympatry of the three new species of Andinopatus gen. nov., described herein with other candidate species from clades C and D as well as A. candidate sp1 (Figure 3). Hitherto, sympatry has been reported only in members of the family Peripatopsidae: Peripatoides sympatrica, P. kawekaensis and P. morgani, Euperipatoides leuckartii and Cephalofovea tomahmontis from New Zealand and Australia (S R Daniels et al., 2009; S R Daniels & Ruhberg, 2010; Leishman & Eldridge, 1990; Sherbon & Walker, 2004; Trewick,

1998). Nevertheless, the use of advanced molecular and morphological techniques have revealed the existence of cryptic speciation in both onychophoran families. Cunha et al., (2017) reported a case of three sympatric species in the Amazon basin; however, this study was based exclusively on molecular data, lacking sufficient taxonomic evidence for the correct classification at the species level. According to the current standards shown herein a morphological description is strictly required to suggest a new species.

The unique combination of morphological characters observed in Andinopatus gen. nov. led us to propose a new genus out of the already accepted 12 described Peripatidae genera (Oliveira et al., 2014; Oliveira et al., 2012). In contrast with representatives of Eoperipatus (Evans, 1901a), Typhloperipatus (Kemp, 1913) and Heteroperipatus (Zilch, 1954), the new genus displays a different arrangement of the distal foot papillae. Eoperipatus and Typhloperipatus show one anterior and one posterior distal foot papillae, while Heteroperipatus exhibits three anterior and one posterior foot papillae. On the contrary, Andinopatus bears two anterior and one posterior distal foot papillae. Oroperipatus (Cockerell, 1908) has a distinctive nephridial tubercle in the third spinous pad while in Andinopatus it is located between the third and fourth spinous pads. In the same way, the new genus cannot be assigned to Peripatus (Guilding, 1826) or Cerradopatus (Oliveira et al. 2014), because of the presence of crural tubercles in more than two pregenital legs. This is in contrast with Andinopatus, where males exhibit only a pair of crural tubercles in only two pregenital legs. Mesoperipatus (Evans, 1901a) shows three spinous pads per leg and a common anal gland opening, while Andinopatus bears four spinous pads, sometimes a fifth rudimentary pad, and separate anal gland openings. Plicatoperipatus (Clark, 1913), exhibits 24 plicae per segment versus 12 plicae present in Andinopatus. Primary papillae have quadrangular bases in Macroperipatus (Clark, 1913) and rounded bases in Andinopatus.

Speleoperipatus (Peck, 1975) lacks pigmentation in the body and eyes, while Andinopatus exhibits well-developed pigmented eyes and body. Furthermore, Epiperipatus (Clark, 1913) and Principapillatus (Oliveira et al. 2012) lack the arrangement of primary and accessory papillae per plica seen in the new genus. Besides these morphological characteristics, the new genus is well supported as monophyletic by the results from the phylogenetic and genetic distance analyses.

Our phylogenetic results showed supported monophyly for the family Peripatidae, similar to other studies (Murienne et al., 2013; Oliveira et al., 2012, 2013, 2014). Likewise, the nonmonophyly of Epiperipatus (Cunha et al., 2017; Oliveira et al., 2012, 2013, 2014) and Peripatus (Murienne et al., 2013) were also revealed in our phylogenetic analysis. This is congruent with our results from the genetic distance and gap analyses, which showed high distance within Epiperipatus and Peripatus. These genera were described in 1826; at this time, the use of advanced techniques like Scanning Electron Microscopy (SEM), Molecular Biology tools and karyotyping were not available (Oliveira, 2012; Oliveira et al., 2010). Hence, Peripatus and Epiperipatus need a thorough taxonomic revision. Similarly, we suggest: i) an exhaustive revision of genera from Peripatidae that are described morphologically but lack molecular data, like Heteroperipatus, Plicatoperipatus, Speleoperipatus, Typhloperipatus and Eoperipatus. ii) the urgent need to collect specimens of type species in their type localities, to update their taxonomic status based on newly obtained morphological and molecular data. Without this information we cannot be certain of the taxonomic classification of DNA sequences deposited in public databases, which may correspond to undescribed taxa (e.g., Murienne et al. 2013). iii) the use of primers that amplify the same region of the target genes, unlike Murienne et al., (2013), where sequences of the COI gene were obtained from a different region than published
data, impeding their comparison with existing DNA data. iv) the examination of morphological characters to unravel the diversity of new molecular lineages.

We found that the three new species of Andinopatus gen. nov., exhibit a relatively broad distributional range, with some localities separated by more than 40 linear km. A. sublapis was registered in five localities, exhibiting the broadest distribution of the three species. A. xerira is distributed in four localities divided by the Chicamocha canyon. On the other hand, A. saproxylicus is so far known from only two localities separated by 20 linear km and a mountain chain. Some authors suggest a narrow distribution for Brazilian onychophoran species, proposing that specimens separated by more than 20 km might correspond to different species (Oliveira et al., 2011; Oliveira et al., 2014). Indeed, onychophoran species generally exhibit high endemism rates (Daniels et al., 2009; Reid, 1996; Trewick, 1998, 1999). Although some species of Peripatopsidae were previously thought to have a wide distribution, the use of molecular tools have revealed the existence of cryptic speciation (Daniels et al., 2009; Daniels & Ruhberg, 2010; Daniels et al., 2017), meaning that more than one species can occur in a single location. Cryptic speciation and high endemism rates have also been reported in Peripatidae species, especially in Brazil (Lacorte et al., 2011; Oliveira et al., 2011; Oliveira et al., 2014).

During our field explorations we found onychophoran species in different habitats, from riparian forests to grasslands; in the latter, onychophorans where confined to refugia like underneath rocks or rotten logs with humid and low temperature conditions away from direct sunlight. There have been reports, that in highly intervened areas, the onychophorans use the available refugia (Oliveira et al., 2014). Distribution, habitat and microhabitat conditions represent important data to determine the conservation status of species. Only 11 species of

onychophorans are categorized in the IUCN red list of threatened species. Among them, the species Cerradopatus sucuriuensis, was suggested as critically endangered given their low distribution area, and other criteria from the IUCN guidelines (Oliveira et al., 2014). We hope that the data presented here for the Andinopatus species could help assess their conservation status soon, thereby contributing to the conservation of these species. Additionally, in 1995 New suggested that onychophorans are "charismatic members" of the saproxylic community, and that, given their high susceptibility to habitat disturbance and dehydration, they should be considered as umbrella or flagship taxa in conservation programs in order to protect the diversity of this particular type of microhabitats (Clusella-Trullas & Chown, 2008; Monge-Nájera et al., 1993; New, 1995; Oliveira et al., 2014; Pereira & Bicudo, 1986; Ruhberg & Hamer, 2005; Storch, 1984; Weldon, Daniels, Clusella-Trullas, & Chown, 2013). So far, there is a unique case of a natural reserve, the Estação Ecológica do Tripuí in Brazil of 3.92 km2, created according to the data of the onychophoran species, Epiperipatus acacioi in Brazil (Oliveira et al., 2014).

We found that the candidate species from Florian in clade D (Figure 2 h; 3) exhibits sexual dichromatism, which is a form of sexual dimorphism; this constitutes the first report of color dimorphism for the family Peripatidae. Sexual dimorphism has been reported in several species of Peripatopsidae family, where the species have developed structures and coloration patterns to differentiate females from males (Mayer, 2007; Norman & Tait, 2008; Rockman et al., 2001; Tait & Briscoe, 1990). Species of the family Peripatidae exhibit sexual dimorphism in the following characters: presence of crural tubercles in males (Clark, 1913; Lacorte et al., 2011; Oliveira et al., 2012 2013, 2014, 2010;; Peck, 1975). Body size, where females are usually bigger than males (Ghiselin, 1984; Havel, Wilson, & Herbert, 1989; I D S Oliveira, Franke, et

al., 2012) and number of legs (Chagas-júnior & Costa, 2014; Costa & Giribet, 2016; Oliveira et al., 2011, 2012, 2013, 2014). However, these dimorphic characters represent some difficulties; for instance, crural tubercles are not distinguished by naked eye, body size and there could be an overlap in the number of legs in young females, and between females and males.

#### 5. Conclusions

This work represents the rediscovery of a biodiverse onychophoran fauna in Colombia, which remained unexplored for more than a century (Bouvier, 1898; Brues, 1914; Fuhrmann, 1913). Our results suggest that the Andes Mountains house a high diversity of onychophoran species, waiting to be discovered. Our explorations were carried out in a perimeter of around 600 km2, leading to the discovery of a new genus with five species new to science and approximately five more candidate species. We highlight the need for more explorations in Colombia to answer new questions about species diversity in low and highland regions, patterns of diversification in the Andes mountain ranges, natural history, reproductive biology, karyotype diversity of Colombian species, the use of non-invasive tools for species identification, phylogeography and genetic population studies, among many others. We also hope that our work will encourage other researchers in the country to begin study this unexplored and biodiverse group in Colombia.

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Figures



**Figure 1**. Habitat and microhabitats where onychophorans were found. (A-C) different types of habitats. A Shadowed-coffee Plantation, type locality of Andinopatus xerira. B) Stream inside a riparian forest. C) Grassland near to a riparian forest. D-E microhabitat in the localities occupy by onychophorans. D rotten logs and leaf litter near to the shadowed-coffee plantation. E Rotten logs where the onychophorans live inside. F Rock covered with vegetation in the grassland landscape. G-I onychophorans in different microhabitats. G *A. xerira* under leaf litter. H *A. saproxylicus* inside a rotten log. I *A. sublapis* above vegetation near to a stream.



**Figure 2.** Distributional map of the Colombian onychophorans and their localities. (A-B) records from different localities across the country and the area of the study. A Geographical map of Colombia with the altitude in green scale. B Localities studied from the western slope of the eastern Andes in Santander Department. C Maximum convex polygon analysis for the new sps gen. nov.



**Figure 3.** Morphological features of Andinopatus gen. nov.. A Dorsal general view of an onychophoran from the new genus, this photograph has insets with a dashed line showing the other images from the figure. B number of the antennal rings. C number of dorsal plica per segment. D. number of mouth lips external and internal rows. E Fourth leg showing the spinous pads and the nephridial tubercle. F Outer and inner jaw blades, the denticles are numbered. G number of leg rings (dorsal view). H Ventral view of the posterior region.



**Figure 4**. Phylogenetic relationships of the species studied. Maximum likelihood and Bayesian topology combining three mitochondrial gene COI, 12S, 16S. Five species of the family Peripatopsidae where used as outgroup taxa. Ultra-fast bootstrap (UFB) and a posteriori probability (PP) values are provided above or under the branches. Bootstrap values below 90 are not indicated. Clades A-J represent unnamed taxa. Photographs of the species described are located in the clade Andinopatus gen. nov.



**Figure 5**. Mouth and slime papillae details of the three new species of Andinopatus gen. nov. Blue dots located in the internal row lips and paled yellow triangles the external row lip. Note the opening of the slime gland (blue arrowheads) primary papillae in the surface (paled-yellow asterisks). (A-B) A. sublapis. (bC-D) A. saproxylicus. (E-F) A. xerira. Abbreviations: sp, slime gland; af, antennal sensory field; m, mandibles; ul, unpaired lip. Scale bar is 100  $\mu$ m.



**Figure 6**. Sensory structures in the antenna of Andinopatus gen. nov. Blue asterisk indicate type I sensillum paled yellow arrowheads indicate spindle-shaped sensillum t. (A-B) *A. sublapis*. (C-D) *A. saproxylicus*. (E-F) *A. xerira*. Scale bar is 100 µm.



**Figure. 7.** Arrangement of the primary and accessory papillae in the dorsal plicae of Andinopatus gen. nov. accessory dorsomedian papillae red colored primary papilla with purple, big accessory papillae blue colored, smallest accessory papilla at the periphery of the plicae (orange colored). (A) A. sublapis. (B) A. saproxylicus. (C) A. xerira. Scale bar is 100 µm.



**Figure 8**. Morphology of the dorsal primary and accessory papillae, and the ventrally crater-shaped papillae. Colored primary and accessory papillae with purple and red, respectively. Arrowhead point the crater-shaped papillae located ventrally between two leg pairs. A-C A. sublapis. Conical primary papillae covered with 5-6 scales, apical piece with two to three scales, ending a decentered short bristle. Two types of accessory papillae one bigger with four scales and the small accessory with three. Crater-shaped papillae with sixteen scales. D-G A. saproxylicus. Two types of primary and accessory papillae. Primary papillae with six and four scales at the base, apical piece with three scales. Crater-shaped papillae with 8-10 scales. H-J A. xerira one type or primary and accessory papillae. The former with six scales at the base and three in the apical piece. The latter with five scales. Crater-shaped papillae with 10 scales. Scale bar 50 µm



**Figure 9**. Leg morphology and nephridial tubercle distribution of the Andinopatus gen. nov. rudimentary spinous pad highlighted with dashed line. Arrowhead point to distal foot papillae. Asterisk point bristles in the setiform ridge. Leg with four spinous pads or plus a rudimentary one. Nephridial tubercle between the third and fourth spinous pad A, B A. sublapis. C, D A. saproxylicus. E, F A. xerira. Abbreviations nt, nephridial tubercle; no, nephridial opening. Scale bar 200 µm



**Figure. 10.** Genital pore of female and males. Males present crural tubercles in the pregenital legs and a pair of anal gland opening located in the anterior outer border of the anus A-B Andinopatus sublapis. Genital pore opening with cross-shaped form in females and longitudinal in males C-D A. saproxylicus. Genital pore opening longitudinal in females and cross-shaped in males. E-F A. xerira Genital pore opening longitudinal for both sexes. Scale bar 200 µm



**Figure 11**. Leg morphology and nephridial tubercle distribution in the other Andean and non-Andean onychophoran species. A, C) specimens from clade C. B) specimen from the Amazonian. D) Specimen from clade D scale bar 200 µm

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**Table 1**. List of the species used for the phylogenetic and genetic pairwise analysis with corresponding accession number GenBank and BOLD system (sequences from our study have been submitted to GenBank). Voucher, localities and reference.

Species		Accessions		Voucher	Locality	Reference				
	128	<b>16S</b>	COI							
Eoperipatus totoro	KC139083	N/A	KC139082	N/A	Vietnam, Cát Tien National Park	Oliveira et al., 2013				
Eoperipatus sp. 1	KC754471	KC754519	KC754636	DNA103566	Malaysia, Pulau Perhentian	Murienne et al., 2014				
Eoperipatus sp. 2	JX568982	N/A	JX569005	N/A	Thailand	Oliveira et al., 2012				
Epiperipatus acacioi	HQ404923	N/A	HQ655618	ONY-ITA004/Tripui31	Brazil, Ouro Preto	Unpublished/Lacorte et al., 2011				
Epiperipatus acacioi	HQ404921	N/A	HQ655635	ONY-TRI008/Tripui48	Brazil, Ouro Preto	Unpublished/Lacorte et al., 2011				
Epiperipatus adenocryptus	HQ236139	N/A	HQ236113	CS6	Brazil, Minas Gerais, Córrego dos Ferreiras	Oliveira et al., 2011				
Epiperipatus adenocryptus	HQ236134	N/A	HQ236108	CS1	Brazil, Minas Gerais, Córrego dos Ferreiras	Oliveira et al., 2011				
Epiperipatus biolleyi	KC754474	N/A	KC754640	DNA103689	Costa Rica	Murienne et al., 2014				
Epiperipatus biolleyi	NC009082	NC009082	NC009082	N/A	Costa Rica	Podsiadlowski et al., 2007				
Epiperipatus diadenocryptus	HQ236120	N/A	HQ236094	MS2	Brazil, Minas Gerais, RPPN Mata do Sossego	Oliveira et al., 2011				
Epiperipatus edwardsii	HG531961	HG531962	HG531958	N/A	French Guiana, Cayenne	Murienne et al., 2014				
Epiperipatus machadoi	HQ236116	N/A	HQ236090	FM2	Brazil, Minas Gerais, RPPN Feliciano Miguel Abdala	Oliveira et al., 2011				
Epiperipatus paurognostus	HQ236131	N/A	HQ236105	ME8	Brazil, Minas Gerais, Mata do Eremitério	Oliveira et al., 2011				
Epiperipatus sp.	KC754475	KC754524	KC754641	DNA104980	Colombia	Murienne et al., 2014				
Cerradopatus sucuriuensis	KM095124	N/A	KM095118	ONY-MTS04	Brazil, Mato Grosso do Sul	Oliveira et al., 2014				
Macroperipatus torquatus	N/A	KC754522	N/A	DNA104657	Trinidad & Tobago	Murienne et al., 2014				
Macroperipatus sp. 1	N/A	KC754527	KC754644	DNA104651	Colombia, Cundinamarca	Murienne et al., 2014				
Macroperipatus sp. 2	N/A	N/A	KC754638	DNA104807	Jamaica, Saint Catherine	Murienne et al., 2014				
Mesoperipatus tholloni	KC754478	KC754528	KC754645	DNA104625	Gabon, Middle Ogooué	Murienne et al., 2014				
Oroperipatus corradoi	N/A	N/A	U62429	N/A	Ecuador, Sucumbíos, Cuyabeno	Gleeson et al.,1998				
Oroperipatus sp.	NC015890	NC015890	NC015890	N/A	Belice, Toledo	Segovia et al. (2011)				
Peripatus dominicae	KC754479	N/A	KC754646	DNA104977	Republica Dominicana, La Vega	Murienne et al., 2014				
Peripatus juanensis	N/A	KC754523	N/A	DNA104654	Puerto Rico	Murienne et al., 2014				
Peripatus solorzanoi	KM095128	N/A	KM095130	PE11	Costa Rica, Guayacán de Siquirres	Morera-Brenes & Monge- Nájera, 2010				
Plicatoperipatus jamaicensis	N/A	N/A	KC754639	DNA104808	Jamaica, Portland Parish	Murienne et al., 2014				
Principapillatus hitoyensis	JX568977	KC754525	JX569000	N/A	Costa Rica, Limón	Oliveira et al., 2012				

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Peripatidae sp. 1	N/A	N/A	BCMS408- 12	N/A	Brazil, Mato Grosso do Sul	Livia Medeiros Cordeiro Borghezan, Unpublished
Peripatidae sp. 2	N/A	N/A	CTM205- 13	N/A	Mexico, Campeche	Leon Esteban Ibarra Garibay, Unpublished
Peripatidae sp. 3	KC754472	KC754520	KC754637	DNA104978	Ecuador, Napo	Murienne et al., 2014
Peripatidae sp. 4	KC754477	KC754526	KC754643	DNA104979	Ecuador, Napo	Murienne et al., 2014
Peripatidae sp. 5	KC754473	KC754521	N/A	DNA103556	Mexico, Chiapas	Murienne et al., 2014
Peripatidae Linage A	N/A	KX394458	KX394478	OTI43	Brazil, Pará, Ilha de Outeiro	Cuhna et al., 2016
Peripatidae Linage B	N/A	KX394467	KX394494	BRG63	Brazil, Pará, Braganca	Cuhna et al., 2016
Peripatidae Linage C	N/A	KX394456	KX394482	OTI52	Brazil, Pará, Ilha de Outeiro	Cuhna et al., 2016
Peripatidae G1sp1	*	N/A	N/A	OHL 103	Colombia, Amazonas, Leticia, Reserva El Zafire	This work
Peripatidae G1sp2	*	*	N/A	OHL 104	Colombia, Amazonas, Leticia, Reserva El Zafire	This work
Peripatidae G2sp3	*	*	*	OHL 132	Colombia, Santander, Charalá, Reserva Los Aguacos	This work
Peripatidae G2sp4	*	*	*	OHL 71	Colombia, Santander, Florián	This work
Peripatidae G2sp5	*	N/A	*	OHL 19	Colombia, Santander, Piedecuesta, Vereda Holanda	This work
Peripatidae G2sp5	*	*	*	OHL 25	Colombia, Santander, Floridablanca, Cerro La Judía, Reserva Los Maklenkes	This work
Peripatidae G2sp5	*	N/A	*	OHL 99	Colombia, Santander, San Vicente de Chucurí, Vereda La Colorada	This work
Peripatidae G2sp5	*	N/A	*	OHL 140	Colombia, Santander, Tona, Vereda Vegas del Quemado	This work
Andinopatus candidate species 1	*	*	*	OHL 27	Colombia, Santander, Charalá	This work
Andinopatus candidate species 1	*	N/A	N/A	OHL 75	Colombia, Santander, Charalá	This work
Andinopatus candidate species 1	*	N/A	*	OHL 93	Colombia, Santander, Los Santos, Vereda El Carrizal, Hacienda El Roble	This work
Andinopatus candidate species 1	*	N/A	*	OHL 175	Colombia, Santander, Paramo, Reserva Juan Curí	This work
Andinopatus sublapis	*	N/A	*	OHL 60	Colombia, Santander, Curití, Vereda Irapire	This work
Andinopatus sublapis	*	N/A	*	OHL 137	Colombia, Santander, Charalá, Reserva Los Aguacos	This work
Andinopatus sublapis	*	N/A	*	OHL 165	Colombia, Santander, Coromoro, Vereda La Mina	This work
Andinopatus sublapis	*	*	*	OHL 121	Colombia, Santander, Guapotá, Vereda Las Flores	This work
Andinopatus sublapis	*	N/A	N/A	OHL 144	Colombia, Santander, Guapotá	This work

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Andinopatus sublapis	*	N/A	*	OHL 133	Colombia, Santander, Valle de San José	This work
Andinopatus saproxylicus	*	*	*	OHL 109	Colombia, Santander, Suratá	This work
Andinopatus saproxylicus	*	N/A	N/A	OHL 110	Colombia, Santander, Suratá	This work
Andinopatus saproxylicus	*	N/A	*	OHL 142	Colombia, Santander, Tona, Vereda Vegas del Quemado	This work
Andinopatus candidate species 2	*	*	*	OHL 30	Colombia, Santander, San Gil, Vereda San José	This work
Andinopatus xerira	*	N/A	*	OHL 23	Colombia, Santander, Piedecuesta, Vereda Las Amarillas	This work
Andinopatus xerira	*	N/A	*	OHL 32	Colombia, Santander, Los Santos, Vereda El Carrizal, Hacienda El Roble	This work
Andinopatus xerira	*	N/A	*	OHL 33	Colombia, Santander, Los Santos, Vereda El Carrizal, Hacienda El Roble	This work
Andinopatus xerira	*	*	*	OHL 146	Colombia, Santander, Guaca, Vereda El Tabacal	This work
Andinopatus xerira	*	N/A	*	OHL 95	Colombia, Santander, Santa Bárbara	This work
Peripatidae G4sp11	*	*	*	JPR 31	Colombia, Cundinamarca, Machetá	This work
Peripatidae G5sp12	*	N/A	*	OHL 94	Colombia, Santander, Guaca, Vereda Quebradas, El Término	This work
Peripatidae G6sp13	*	*	*	OHL 26	Colombia, Santander, Floridablanca, Finca El Carajo	This work
Euperipatoides rowelli	AF338016	KC754532	U62425		New South Wales, Australia	Murienne et al., 2014; Rockman et al., 2001; Gleeson et al., 1998
Metaperipatus inae	EF624055	KC754541	EF624055		Chile	Braband et al., 2010; Murienne et al., 2014
Opisthopatus cinctipes	NC014273	KC754556	NC014273		South Africa	Braband et al., 2010; Murienne et al., 2014
Peripatopsis moseleyi	EU855469	KC754569	EU855276		South Africa	Daniels et al., 2009; Murienne et al., 2014
► Phallocephale tallagandensis	AF338015	KC754571	PTU62407		New South Wales, Australia	Rockman et al., 2001; Murienne et al., 2014; Gleeson et al., 1998

**Table 2.** Morphological features of Colombian onychophorans.

Species/ characters	Dorsal plica	# legs	Primary Papillae	Apical Piece	Accessory Papillae	Spinous pads	Nephridial tubercle	Inner Jaw Blade	Outer Jaw Blade	Distal Foot Papillae
Epiperipatus vespucci	10-11 dorsal plicae per segment. there are incomplete plicae near the legs	30-34	Small and conical	Cylindrical poorly developed (nipple shape)	Few in number, located at the edges of the plicae alone or in pairs	four	In the fourth and fifth leg between the third and fourth pad. The tubercle does not interrupt the fourth pad	One large accessory tooth and nine denticles		2 anterior, 1 posterior
Oroperipatus bimbergi	12 dorsal plica per segment with 3 incomplete	24-28	Rounded	rounded	Rounded, three between Primary Papillae	Four to five	In the third pad, it separates the pad.	One principal tooth, 2 accessory teeth and 11-14 denticles	One principal tooth and three accessory teeth	2 anterior, 2 posterior
Oroperipatus multipodes	12 dorsal plica per segment with 2 incomplete	33	Two rounded types	rounded	Rounded and few	five, the last poorly developed	In the third pad. It divides the pad in two.	One principal tooth, 2 accessory teeth and eight to nine denticles	One principal and accessory tooth	2 anterior, 2 posterior
Oroperipatus tuberculatus	12 dorsal plica per segment with 2 incomplete	37	Three kinds, one big-size , one medium- size with a cylindrical cone isolated, one small-size cylindrical	?	Conical and few	Six , the fifth divided and the last one incomplete	In the third pad diving into two.	One principal tooth, three accessory teeth and seven denticles	One principal tooth, three accessory teeth	2 anterior, 2 posterior
Peripatus bouvieri	12 dorsal plica per segment	28-29	Two kinds, one big-size rounded and one medium- size rounded	?	Rounded, one or two between Primary Papillae	Five, fourth and fifth thinner than the rest. In legs fourth and fifth the last pad is incomplete	Between the third and the fourth pad.	One principal tooth, two accessory teeth and seven to eight denticles	One principal and accessory tooth	2 anterior, 1 posterior

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**Table 3.** Morphological features of the Colombian onychophorans from this work. Abbreviations a= anterior, p=posterior, r=rudimentary.

MORPHOLOGICAL FEATURES /GENUS OR CLADE	ANDINOPATUS GEN. NOV.	CLADE B	CLADE C	CLADE D	CLADE E
NUMBER OF SPINOUS PADS PER LEG	4 or 4+r	5	4	5 or 5+r	4
POSITION OF THE NEPHRIDIAL TUBERCLE	Between 3rd and 4th	Between 2 <sup>nd</sup> and 3 <sup>rd</sup>	Between 3rd and 4th	Between 3rd and 4th	Between 3rd and 4th
NUMBER OF DISTAL FOOT PAPILLAE	(3) 2a +1p	(6) 3a + 3p	(4) 2a +2p	(3) 2a +1p	(3) 2a +1p
LEGS WITH CRURAL TUBERCLES	2	?	2	2	?
NUMBER OF ANTENNAL RINGS	46	44	44-46	46	42
NUMBER OF SPINOUS PADS IN THE 4TH AND 5TH LEG	4 or 4+r	4	5	4 or 4+r	?
NUMBER OF SPINOUS PADS IN THE PENULTIMATE LEG PAIR	3 or 3+r	?	4	4+r	?
NUMBER OF SPINOUS PADS IN THE LAST LEG PAIR	2	?	4	3+r	?
NUMBER OF LEG PAIRS	26-34	26	?	34	27
POSITION OF THE ANAL GLAND OPENINGS	Paired in front of the	?	Paired in front of	Paired in front of the	?
	anus		the anus	anus	
INNER JAW BLADE	1 accessory tooth and 9-11 denticles	?	1 accessory tooth and 4 denticles	?	?
OUTER JAW BLADE	Single accessory tooth	?	?	?	?
INCOMPLETE OR BIFURCATED DP IN THE SPACE BETWEEN TWO LEGS					
DORSAL PRIMARY PAPILLAE SHAPE	rounded	Quadrangular	rounded	rounded	?
RING LEGS	8	8	8	8	8
1 OR MORE BRISTLE ON EACH SETIFORM RIDGES	+	+	+	+	+
POSITION OF CRURAL TUBERCLES IN MALES					
NUMBER OF DORSAL PLICAE PER SEGMENT	12	12	12	12	12
CONICAL ACCESSORY PAPILLAE SMALLER THAN THE DDIMARY DADIL LAE	+	+	+	+	+
WELL DEVELOPED COVAL VESICLE		4	4	4	+
WELL-DEVELOI ED COXAL VESICLE	+ 	+	+	+	+ 
UTERINE EMBRYOS OF DIFFERENT ACE	1 	1	, т	1 	, 
OVARIES SEPARATED INTO TWO DIFFERENT		1 +	+	1 +	, +
CAVITIES		ľ	·	,	ľ
ARRANGEMENT OF DORSAL PRIMARY AND ACCESSORY PAPILLAE	One to three accessory papillae between primary papillae	?	?	?	?

Appendix

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Appendix A. Sampling and different microhabitat uses of onychophorans. A Principal Investigator searching for onychophorans. B specimen in wet moss. C specimen in the recently describe arboreal bryosphere.

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Appendix B.Genetic Pairwise 16S. Below the diagonal, genetic distance. Upper diagonal standard deviation.

SPECIMEN													V	ALUE	s												
A_SAPROXYLICUS_OH109_CO		0.013	0.010	0.015	0.010	0.021	0.020	0.020	0.017	0.017	0.015	0.018	0.018	0.014	0.017	0.015	0.017	0.018	0.016	0.022	0.018	0.019	0.015	0.021	0.016	0.017	0.017
A_SP1_OH27_CO	0.067		0.013	0.015	0.013	0.021	0.020	0.020	0.016	0.016	0.015	0.018	0.018	0.015	0.017	0.015	0.016	0.017	0.016	0.023	0.015	0.019	0.015	0.021	0.015	0.016	0.017
A_SP4_OH30_CO	0.044	0.076		0.014	0.008	0.021	0.020	0.020	0.017	0.017	0.016	0.018	0.018	0.014	0.017	0.015	0.016	0.018	0.016	0.022	0.017	0.018	0.016	0.021	0.016	0.016	0.017
A_SUBLAPIS_OH121_CO	0.087	0.087	0.085		0.014	0.022	0.022	0.022	0.018	0.018	0.018	0.020	0.020	0.016	0.019	0.017	0.017	0.019	0.018	0.023	0.018	0.018	0.018	0.022	0.018	0.018	0.019
A_XERIRA_OH146_CO	0.041	0.067	0.029	0.087		0.020	0.020	0.020	0.016	0.017	0.016	0.018	0.018	0.015	0.017	0.015	0.017	0.018	0.016	0.022	0.017	0.018	0.016	0.021	0.016	0.016	0.017
CLADEA_DNA104978_EC	0.201	0.198	0.213	0.213	0.204		0.014	0.020	0.019	0.020	0.019	0.022	0.022	0.020	0.021	0.021	0.021	0.022	0.022	0.021	0.023	0.022	0.022	0.020	0.021	0.021	0.022
CLADEA_DNA104979_EC	0.192	0.184	0.201	0.216	0.195	0.082		0.019	0.019	0.019	0.018	0.020	0.020	0.019	0.021	0.020	0.020	0.021	0.021	0.021	0.021	0.022	0.020	0.021	0.020	0.020	0.021
CLADEB_OH_104_CO	0.195	0.192	0.178	0.245	0.198	0.195	0.181		0.020	0.020	0.019	0.020	0.020	0.019	0.020	0.019	0.021	0.021	0.021	0.022	0.021	0.021	0.021	0.020	0.020	0.021	0.021
CLADEC_MA_SP_DNA104651_CO	0.122	0.114	0.122	0.140	0.120	0.178	0.160	0.198		0.009	0.012	0.016	0.016	0.014	0.016	0.017	0.016	0.018	0.016	0.022	0.017	0.019	0.016	0.021	0.015	0.016	0.018
CLADEC_OH_132_CO	0.125	0.105	0.128	0.137	0.125	0.181	0.163	0.204	0.032		0.012	0.016	0.016	0.014	0.016	0.017	0.016	0.018	0.016	0.022	0.017	0.019	0.015	0.021	0.016	0.016	0.018
CLADEC_OH_71_CO	0.102	0.090	0.117	0.140	0.111	0.166	0.152	0.178	0.058	0.052		0.015	0.015	0.014	0.016	0.017	0.016	0.018	0.016	0.022	0.017	0.019	0.015	0.021	0.015	0.016	0.017
CLADED_OH_19_CO	0.146	0.134	0.149	0.178	0.149	0.204	0.184	0.207	0.105	0.108	0.087		0.000	0.017	0.019	0.019	0.019	0.020	0.019	0.023	0.017	0.021	0.018	0.021	0.018	0.018	0.018
CLADED_OH_25_CO	0.146	0.134	0.149	0.178	0.149	0.204	0.184	0.207	0.105	0.108	0.087	0.000		0.017	0.019	0.019	0.019	0.020	0.019	0.023	0.017	0.021	0.018	0.021	0.018	0.018	0.018
CLADEE_JPR_31_CO	0.093	0.087	0.096	0.111	0.099	0.175	0.155	0.184	0.076	0.082	0.076	0.117	0.117		0.015	0.015	0.015	0.016	0.014	0.021	0.015	0.017	0.015	0.021	0.014	0.015	0.016
CLADEE_OH_26_CO	0.131	0.120	0.128	0.143	0.137	0.204	0.195	0.195	0.111	0.111	0.117	0.149	0.149	0.087		0.017	0.017	0.018	0.016	0.022	0.017	0.017	0.015	0.020	0.017	0.017	0.017
CLADEF_OTI52_BR	0.105	0.096	0.099	0.122	0.108	0.195	0.166	0.187	0.128	0.128	0.125	0.152	0.152	0.087	0.120		0.017	0.017	0.017	0.021	0.016	0.017	0.016	0.021	0.016	0.016	0.017
CLADEG_BRG63_BR	0.128	0.105	0.131	0.131	0.131	0.198	0.187	0.222	0.111	0.105	0.111	0.157	0.157	0.093	0.120	0.114		0.016	0.016	0.023	0.017	0.017	0.016	0.022	0.015	0.017	0.016
CLADEH_OTI43_BR	0.152	0.134	0.146	0.166	0.152	0.219	0.192	0.213	0.131	0.134	0.140	0.184	0.184	0.111	0.143	0.117	0.111		0.018	0.023	0.017	0.018	0.017	0.022	0.017	0.017	0.018
CLADEJ_DNA103556_MX	0.114	0.111	0.111	0.128	0.111	0.213	0.187	0.216	0.096	0.096	0.105	0.152	0.152	0.085	0.096	0.114	0.114	0.134		0.023	0.016	0.018	0.015	0.021	0.016	0.014	0.016
EO_SP1_DNA103566_MY	0.251	0.242	0.251	0.262	0.248	0.210	0.216	0.245	0.236	0.239	0.251	0.259	0.259	0.210	0.236	0.222	0.251	0.251	0.242		0.022	0.022	0.022	0.022	0.022	0.022	0.024
EP_BIOLLEYI_NC009082_CR	0.125	0.093	0.125	0.137	0.125	0.219	0.195	0.192	0.125	0.122	0.114	0.134	0.134	0.093	0.117	0.105	0.122	0.140	0.102	0.233		0.019	0.016	0.022	0.016	0.016	0.014
EP_EDWARDSII_GF1803_GF	0.160	0.155	0.146	0.146	0.155	0.216	0.210	0.201	0.149	0.149	0.149	0.190	0.190	0.114	0.128	0.117	0.131	0.134	0.137	0.251	0.155		0.018	0.021	0.018	0.018	0.020
MA_TORQUATUS_KC754522_T	0.114	0.108	0.117	0.149	0.122	0.195	0.178	0.204	0.105	0.102	0.105	0.146	0.146	0.090	0.096	0.114	0.117	0.134	0.096	0.227	0.117	0.149		0.021	0.016	0.014	0.017
ME_THOLLONI_DNA104625_GA	0.224	0.216	0.219	0.251	0.224	0.219	0.210	0.192	0.227	0.230	0.216	0.254	0.254	0.219	0.207	0.204	0.236	0.251	0.222	0.248	0.222	0.233	0.227		0.022	0.021	0.022
OR_SP_NC_015890_BZ	0.120	0.099	0.108	0.140	0.102	0.195	0.181	0.195	0.099	0.099	0.096	0.128	0.128	0.087	0.122	0.105	0.102	0.128	0.105	0.233	0.096	0.140	0.111	0.239		0.015	0.016
PE_JUANENSIS_KC754523_PR	0.125	0.105	0.117	0.134	0.111	0.190	0.178	0.210	0.111	0.114	0.108	0.146	0.146	0.090	0.117	0.111	0.114	0.131	0.090	0.227	0.105	0.149	0.096	0.227	0.093		0.017
PR_HITOYENSIS_DNA103564_CR	0.137	0.120	0.131	0.152	0.131	0.207	0.184	0.204	0.128	0.125	0.125	0.152	0.152	0.114	0.120	0.108	0.114	0.146	0.114	0.262	0.076	0.169	0.125	0.227	0.108	0.125	

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Appendix C. Genetic Pairwise 12S. Below the diagonal, genetic distance. Upper diagonal standard deviation.

SPECIMEN												1	VALUES												
A saproxylicus OH109 CO		0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A saproxylicus OH110 CO	0.00		0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A saproxylicus OH142 CO	0.00	0.00		0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A Sp1 OH175 CO	0.05	0.05	0.04		0.00	0.00	0.00	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A Sp1 OH27 CO	0.05	0.05	0.04	0.00		0.00	0.00	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A Sp1 OH75 CO	0.05	0.05	0.04	0.00	0.00		0.00	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A Sp1 OH93 CO	0.05	0.05	0.04	0.00	0.00	0.00		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A Sp4 OH30 CO	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.01	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A sublapis OH121 CO	0.07	0.07	0.06	0.08	0.08	0.08	0.08	0.07	0.02	0.01	0.01	0.00	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03
A sublapis OH133 CO	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.03		0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A sublapis OH137 CO	0.03	0.03	0.03	0.05	0.05	0.05	0.05	0.05	0.04	0.01		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A sublapis OH144 CO	0.07	0.07	0.06	0.08	0.08	0.08	0.08	0.07	0.00	0.03	0.04		0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03
A sublapis OH165 CO	0.05	0.05	0.04	0.06	0.06	0.06	0.06	0.05	0.03	0.00	0.01	0.03		0.00	0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A sublapis OH60 CO	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.03	0.00	0.01	0.03	0.00		0.01	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A xerira OH146 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.07	0.04	0.04	0.07	0.04	0.04		0.01	0.01	0.01	0.00	0.03	0.03	0.03	0.03	0.03	0.03
A xerira OH23 CO	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.03	0.07	0.04	0.04	0.07	0.05	0.04	0.01		0.01	0.00	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A xerira OH32 CO	0.04	0.04	0.03	0.04	0.04	0.04	0.04	0.03	0.07	0.04	0.04	0.07	0.05	0.04	0.01	0.01		0.00	0.01	0.03	0.03	0.03	0.03	0.03	0.03
A xerira OH33 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.07	0.04	0.04	0.07	0.04	0.04	0.01	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.03	0.03	0.03
A xerira OH95 CO	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.07	0.03	0.03	0.07	0.04	0.03	0.00	0.01	0.01	0.00		0.03	0.03	0.03	0.03	0.03	0.03
Ce sucuriuensis ONYMTS04 BR	0.19	0.19	0.18	0.21	0.21	0.21	0.21	0.20	0.18	0.20	0.19	0.18	0.19	0.20	0.19	0.19	0.20	0.20	0.19		0.03	0.03	0.03	0.03	0.03
CladeA DNA104978 EC {Gp 6}	0.31	0.31	0.31	0.32	0.32	0.32	0.32	0.31	0.31	0.31	0.31	0.31	0.31	0.31	0.29	0.30	0.30	0.30	0.30	0.28		0.02	0.03	0.03	0.03
CladeA DNA104979 EC	0.29	0.29	0.29	0.31	0.31	0.31	0.31	0.29	0.29	0.30	0.30	0.29	0.30	0.30	0.29	0.30	0.30	0.29	0.29	0.26	0.09		0.03	0.03	0.03
CladeA OH 103 CO	0.30	0.30	0.30	0.32	0.32	0.32	0.32	0.29	0.29	0.30	0.30	0.29	0.30	0.30	0.29	0.29	0.30	0.29	0.29	0.29	0.22	0.23		0.03	0.03
CladeA OH 104 CO	0.32	0.32	0.31	0.32	0.32	0.32	0.32	0.31	0.32	0.32	0.32	0.32	0.32	0.32	0.31	0.31	0.32	0.32	0.31	0.33	0.25	0.25	0.19		0.03
CladeC OH 132 CO	0.21	0.21	0.21	0.22	0.22	0.22	0.22	0.21	0.22	0.21	0.21	0.22	0.21	0.21	0.20	0.20	0.21	0.21	0.20	0.25	0.29	0.27	0.26	0.31	
CladeC OH 71 CO	0.21	0.21	0.21	0.22	0.22	0.22	0.22	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.20	0.26	0.30	0.29	0.28	0.32	0.12
CladeD OH 140 CO	0.19	0.19	0.19	0.20	0.20	0.20	0.20	0.19	0.17	0.19	0.20	0.17	0.19	0.19	0.18	0.17	0.18	0.18	0.18	0.22	0.29	0.28	0.25	0.29	0.17
CladeD OH 19 CO	0.20	0.20	0.20	0.21	0.21	0.21	0.21	0.20	0.18	0.20	0.21	0.18	0.20	0.20	0.19	0.18	0.19	0.19	0.19	0.22	0.29	0.29	0.26	0.29	0.18
CladeD OH 25 CO	0.19	0.19	0.19	0.20	0.20	0.20	0.20	0.19	0.17	0.19	0.20	0.17	0.19	0.19	0.18	0.17	0.18	0.18	0.18	0.22	0.29	0.28	0.25	0.29	0.17
CladeD OH 99 CO	0.20	0.20	0.19	0.21	0.21	0.21	0.21	0.20	0.17	0.19	0.20	0.17	0.19	0.19	0.19	0.18	0.19	0.18	0.18	0.23	0.29	0.29	0.26	0.29	0.18
CladeE JPR 31 CO	0.24	0.24	0.24	0.27	0.27	0.27	0.27	0.25	0.24	0.26	0.26	0.24	0.25	0.26	0.23	0.23	0.23	0.23	0.24	0.20	0.26	0.23	0.29	0.32	0.25
CladeE OH 26 CO	0.19	0.19	0.19	0.20	0.20	0.20	0.20	0.18	0.17	0.19	0.20	0.17	0.19	0.19	0.18	0.19	0.18	0.18	0.18	0.16	0.29	0.27	0.29	0.33	0.23
CladeE OH 94 CO	0.15	0.15	0.15	0.17	0.17	0.17	0.17	0.15	0.17	0.17	0.17	0.17	0.16	0.17	0.15	0.15	0.15	0.15	0.15	0.14	0.25	0.25	0.28	0.31	0.20
CladeJ DNA103556 MX	0.18	0.18	0.17	0.21	0.21	0.21	0.21	0.20	0.21	0.21	0.20	0.21	0.21	0.21	0.18	0.18	0.18	0.18	0.18	0.19	0.27	0.26	0.30	0.31	0.26
Eo_sp_LH2012_TH	0.35	0.35	0.35	0.36	0.36	0.36	0.36	0.35	0.35	0.36	0.36	0.35	0.36	0.36	0.34	0.34	0.35	0.35	0.34	0.33	0.29	0.29	0.31	0.31	0.31
Eo sp1_DNA103566_MY	0.34	0.34	0.34	0.36	0.36	0.36	0.36	0.33	0.34	0.34	0.35	0.34	0.35	0.34	0.33	0.34	0.34	0.34	0.34	0.33	0.30	0.29	0.33	0.31	0.34
EO_TOTORO_ZMMU_VN	0.32	0.32	0.33	0.34	0.34	0.34	0.34	0.33	0.33	0.33	0.34	0.33	0.34	0.33	0.32	0.33	0.33	0.33	0.32	0.35	0.27	0.29	0.32	0.30	0.31
EP_ACACIOI_ONYITA004_BR	0.21	0.21	0.20	0.21	0.21	0.21	0.21	0.21	0.21	0.21	0.22	0.21	0.22	0.21	0.20	0.20	0.21	0.21	0.20	0.16	0.29	0.25	0.29	0.33	0.26
Ep_adenocryptus_CS1_BR}	0.19	0.19	0.19	0.21	0.21	0.21	0.21	0.20	0.21	0.21	0.21	0.21	0.22	0.21	0.19	0.20	0.20	0.20	0.19	0.15	0.26	0.24	0.30	0.31	0.25
Ep_adenocryptus_CS6_BR	0.19	0.19	0.18	0.21	0.21	0.21	0.21	0.20	0.21	0.21	0.21	0.21	0.21	0.21	0.18	0.19	0.19	0.19	0.19	0.15	0.26	0.24	0.29	0.30	0.25
Ep_biolleyi_NC009082_CR	0.14	0.14	0.13	0.15	0.15	0.15	0.15	0.15	0.14	0.15	0.14	0.14	0.15	0.15	0.14	0.14	0.14	0.14	0.13	0.15	0.29	0.28	0.29	0.29	0.21
Ep_diadenocryptus_MS2_BR	0.19	0.19	0.18	0.21	0.21	0.21	0.21	0.19	0.20	0.21	0.20	0.20	0.21	0.21	0.19	0.18	0.19	0.19	0.18	0.16	0.26	0.23	0.29	0.30	0.25
Ep_edwardsii_GF1803_GF	0.18	0.18	0.18	0.20	0.20	0.20	0.20	0.17	0.18	0.19	0.19	0.18	0.19	0.19	0.17	0.18	0.18	0.18	0.17	0.14	0.27	0.23	0.27	0.32	0.21
Ep_machadoi_FM2_BR	0.19	0.19	0.19	0.21	0.21	0.21	0.21	0.20	0.21	0.21	0.21	0.21	0.22	0.21	0.19	0.19	0.20	0.20	0.19	0.16	0.25	0.21	0.27	0.30	0.22
Ep_paurognostus_ME8_BR	0.18	0.18	0.18	0.20	0.20	0.20	0.20	0.19	0.20	0.21	0.20	0.20	0.21	0.21	0.18	0.19	0.19	0.19	0.18	0.14	0.26	0.23	0.30	0.30	0.25
Ep_sp_DNA104980_CO	0.29	0.29	0.29	0.30	0.30	0.30	0.30	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.28	0.29	0.25	0.24	0.15	0.25	0.29
Me_tholloni_DNA104625_GA	0.33	0.33	0.32	0.32	0.32	0.32	0.32	0.33	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.32	0.33	0.33	0.32	0.29	0.32	0.33	0.28	0.30	0.31
Oroperipatus_sp_NC_015890_BZ	0.14	0.14	0.13	0.15	0.15	0.15	0.15	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.13	0.13	0.14	0.13	0.13	0.14	0.27	0.25	0.25	0.30	0.20
PE_DOMINICAE_DNA104977_DO	0.16	0.16	0.16	0.18	0.18	0.18	0.18	0.15	0.16	0.17	0.17	0.16	0.17	0.17	0.16	0.15	0.15	0.15	0.15	0.14	0.26	0.24	0.26	0.30	0.18
PE_SOLORZANOI_PE11	0.16	0.16	0.16	0.19	0.19	0.19	0.19	0.18	0.16	0.17	0.16	0.16	0.17	0.17	0.16	0.17	0.17	0.17	0.16	0.17	0.28	0.24	0.30	0.31	0.23
Pr_hitoyensis_DNA103564_CR	0.16	0.16	0.16	0.18	0.18	0.18	0.18	0.18	0.15	0.16	0.16	0.15	0.16	0.16	0.16	0.15	0.16	0.16	0.15	0.16	0.26	0.24	0.29	0.30	0.21
Principapillatus_sp_KC754474_CR	0.18	0.18	0.18	0.20	0.20	0.20	0.20	0.19	0.15	0.17	0.17	0.15	0.17	0.17	0.18	0.17	0.18	0.18	0.17	0.16	0.26	0.24	0.30	0.32	0.21

SPECIMEN													VALU	IES												
A_saproxylicus_OH109_CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A_saproxylicus_OH110_CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A_saproxylicus_OH142_CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A Sp1 OH175 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03
A Sp1 OH27 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03
A Sp1 OH75 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03
A Sp1 OH93 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03
A Sp4 OH30 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03
A sublapis OH121 CO	0.03	0.02	0.02	0.02	0.02	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A sublapis OH133 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A sublapis OH137 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A sublapis OH144 CO	0.03	0.02	0.02	0.02	0.02	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A sublapis OH165 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A sublapis OH60 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A xerira OH146 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A xerira OH23 CO	0.03	0.02	0.03	0.02	0.02	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.02
A xerira OH32 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A xerira OH33 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
A xerira OH95 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
Ce sucuriuensis ONYMTS04 BR	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.03	0.03	0.02	0.02	0.03	0.02
CladeA DNA104978 EC {Gp 6}	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeA DNA104979 EC	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeA OH 103 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03
CladeA OH 104 CO	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeC OH 132 CO	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03
CladeC OH 71 CO	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeD OH 140 CO	0.15	0.02	0.01	0.00	0.01	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02
CladeD OH 19 CO	0.16	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02
CladeD OH 25 CO	0.15	0.00	0.01	0.01	0.01	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02
CladeD OH 99 CO	0.16	0.02	0.02	0.02	0.01	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeE_IPR_31_CO	0.29	0.02	0.24	0.23	0.24	0.00	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeE OH 26 CO	0.22	0.20	0.21	0.20	0.20	0.18	0.01	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
CladeE_OH_94_CO	0.22	0.16	0.16	0.16	0.20	0.16	0 14	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.02
Clade L DNA103556 MY	0.22	0.10	0.72	0.10	0.22	0.10	0.14	0.18	0.05	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.03	0.03	0.02	0.02	0.02	0.02
Fo sn LH2012 TH	0.34	0.31	0.32	0.31	0.33	0.33	0.34	0.33	0.36	0.05	0.03	0.03	0.03	0.02	0.03	0.02	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.02	0.02	0.02
Eo_sp1_DNA103566_MV	0.32	0.32	0.33	0.32	0.33	0.30	0.31	0.31	0.35	0 15	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
	0.32	0.32	0.33	0.32	0.33	0.35	0.34	0.33	0.35	0.13	0 19	0.00	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
	0.25	0.32	0.33	0.32	0.33	0.35	0.10	0.55	0.00	0.32	0.10	0.36	0.05	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
En adenocryptus CS1 BP\	0.25	0.21	0.22	0.21	0.21	0.13	0.15	0.16	0.20	0.32	0.30	0.33	0.00	0.02	0.02	0.03	0.02	0.03	0.02	0.02	0.03	0.03	0.02	0.02	0.03	0.03
Ep_adenocryptus_CS6_BP	0.20	0.22	0.23	0.22	0.23	0.10	0.13	0.16	0.10	0.33	0.32	0.33	0.03	0.00	0.00	0.03	0.02	0.03	0.02	0.01	0.03	0.03	0.02	0.02	0.03	0.03
Ep_adenocryptus_030_DR	0.20	0.21	0.25	0.21	0.22	0.10	0.10	0.10	0.10	0.32	0.31	0.33	0.03	0.00	0.18	0.00	0.02	0.02	0.02	0.00	0.03	0.03	0.02	0.02	0.03	0.03
En diadenocryptus MS2 BD	0.20	0.17	0.10	0.17	0.10	0.23	0.10	0.15	0.13	0.32	0.33	0.34	0.22	0.13	0.10	0.18	0.05	0.02	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
Ep_ulauenocryptus_M32_DR	0.23	0.13	0.21	0.15	0.20	0.17	0.15	0.15	0.20	0.32	0.31	0.34	0.07	0.00	0.07	0.10	0.17	0.05	0.01	0.02	0.03	0.03	0.02	0.02	0.03	0.02
Ep_edwaldsi_GF1605_GF	0.23	0.22	0.23	0.22	0.22	0.10	0.10	0.15	0.10	0.23	0.30	0.32	0.10	0.10	0.17	0.15	0.05	0.17	0.03	0.03	0.03	0.03	0.02	0.02	0.02	0.02
Ep_machador_1 m2_DR	0.24	0.13	0.21	0.13	0.20	0.17	0.20	0.10	0.21	0.33	0.21	0.33	0.10	0.03	0.00	0.20	0.00	0.17	0.00	0.02	0.03	0.03	0.02	0.03	0.03	0.03
Ep_paulogiloslus_NEO_DR	0.20	0.21	0.22	0.21	0.22	0.10	0.15	0.10	0.10	0.33	0.31	0.33	0.09	0.01	0.00	0.10	0.00	0.10	0.05	0.20	0.03	0.03	0.02	0.02	0.03	0.03
Ep_sp_DNA104500_CO	0.30	0.24	0.23	0.24	0.20	0.23	0.30	0.20	0.30	0.33	0.33	0.34	0.23	0.30	0.30	0.20	0.20	0.20	0.23	0.29	0.20	0.05	0.03	0.03	0.03	0.03
Orenerinatus en NC 015200 B7	0.33	0.30	0.31	0.30	0.31	0.34	0.33	0.32	0.35	0.35	0.30	0.30	0.32	0.30	0.30	0.33	0.33	0.32	0.32	0.29	0.30	0.24	0.05	0.03	0.03	0.03
	0.21	0.19	0.19	0.19	0.19	0.21	0.10	0.15	0.10	0.30	0.33	0.32	0.14	0.10	0.15	0.14	0.14	0.15	0.15	0.10	0.27	0.31	0.42	0.02	0.02	0.02
	0.19	0.17	0.10	0.17	0.10	0.20	0.17	0.14	0.15	0.32	0.33	0.32	0.10	0.10	0.10	0.14	0.14	0.10	0.17	0.15	0.25	0.31	0.12	0.44	0.02	0.02
PE_SULUKZANUL_PE11	0.24	0.22	0.22	0.22	0.22	0.21	0.18	0.15	0.16	0.33	0.32	0.31	0.20	0.19	0.18	0.10	0.19	0.14	0.20	0.18	0.27	0.32	0.16	0.14	0.00	0.02
Pr_nitoyenSIS_DNA103564_CR	0.21	0.18	0.18	0.18	0.18	0.21	0.17	0.16	0.15	0.30	0.32	0.29	0.20	0.18	0.18	0.09	0.17	0.13	0.19	0.17	0.28	0.32	0.12	0.11	0.08	
## ONYCHOPHORAN DIVERSITY IN THE ANDEAN MOUNTAINS

Appendix D. Genetic Pairwise COI. Below the diagonal, genetic distance. Upper diagonal standard deviation.

SPECIMEN												VALI	ES											
		0.00	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SAPROXILICUS_OH142_CO	0.01	0.00	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SP1 0H175 CO	0.13	0.13	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SP1 0H27 CO	0.13	0.13	0.00	0.00	0.00	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SP1 0H93 CO	0.13	0.13	0.00	0.00	0.00	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SP4 OH30 CO	0.10	0.10	0.15	0.00	0.15	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
	0.08	0.08	0.12	0.12	0.12	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.07	0.02
A SUBLARIS OH133 CO	0.00	0.00	0.12	0.12	0.12	0.00	0.04	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SUBLARIS OH137 CO	0.09	0.09	0.11	0.13	0.11	0.10	0.04	0.04	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SUBLARIS OH165 CO	0.08	0.08	0.12	0.12	0.12	0.09	0.03	0.02	0.04	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A SUBLAPIS OHEO CO	0.08	0.08	0.12	0.12	0.12	0.10	0.04	0.00	0.04	0.02		0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A XERIRA OH146 CO	0.07	0.07	0.11	0.11	0.11	0.09	0.08	0.09	0.09	0.09	0.09	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A XERIRA OH23 CO	0.08	0.08	0.13	0.13	0.13	0.10	0.09	0.11	0.11	0.00	0.11	0.06	0.01	0.01	0.00	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A XERIRA OH32 CO	0.08	0.08	0.12	0.12	0.12	0.09	0.09	0.10	0.10	0.09	0.10	0.05	0.01		0.00	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A XERIRA OH33 CO	0.08	0.08	0.12	0.12	0.12	0.09	0.09	0.11	0.10	0.09	0.10	0.05	0.01	0.00		0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
A XERIRA OH95 CO	0.07	0.07	0.12	0.12	0.12	0.09	0.09	0.10	0.10	0.00	0.10	0.05	0.03	0.03	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CE SUCURIUENSIS ONYMITS04 BR	0.12	0.12	0.14	0.14	0.14	0.13	0.12	0.13	0.13	0.12	0.13	0.12	0.12	0.11	0.12	0 11	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CLADEA DNA104978 EC	0.13	0.14	0.13	0.13	0.13	0.15	0.12	0.14	0.12	0.13	0.14	0.14	0.13	0.13	0.13	0.13	0.15	0.02	0.01	0.02	0.02	0.02	0.02	0.02
CLADEA DNA104979 EC	0.12	0.13	0.17	0.17	0.17	0.14	0.11	0.14	0.13	0.12	0.13	0.12	0.12	0.12	0.12	0.13	0.14	0.10		0.02	0.02	0.02	0.02	0.02
CLADEC OH 132 CO	0.15	0.15	0.16	0.16	0.16	0.13	0.14	0.15	0.13	0.14	0.15	0.13	0.14	0.14	0.14	0.14	0.14	0.15	0.14		0.02	0.02	0.02	0.02
CLADEC OH 71 CO	0.15	0.15	0.14	0.14	0.14	0.15	0.13	0.15	0.15	0.14	0.15	0.15	0.15	0.14	0.14	0.15	0.14	0.14	0.15	0.12		0.02	0.02	0.02
CLADED OH 140 CO	0.15	0.15	0.15	0.15	0.15	0.13	0.13	0.15	0.14	0.14	0.14	0.15	0.14	0.13	0.14	0.13	0.13	0.15	0.15	0.13	0.14		0.01	0.00
CLADED OH 19 CO	0.14	0.15	0.15	0.15	0.15	0.13	0.13	0.15	0.14	0.14	0.14	0.14	0.14	0.13	0.13	0.14	0.13	0.15	0.14	0.13	0.14	0.02		0.01
CLADED OH 25 CO	0.15	0.15	0.15	0.15	0.15	0.14	0.13	0.15	0.14	0.14	0.15	0.15	0.14	0.14	0.14	0.14	0.13	0.15	0.15	0.14	0.14	0.00	0.02	
CLADED OH 99 CO	0.15	0.15	0.16	0.16	0.16	0.13	0.13	0.14	0.14	0.14	0.14	0.15	0.15	0.14	0.14	0.14	0.12	0.15	0.14	0.15	0.13	0.05	0.05	0.06
CLADEE_JPR_31_CO	0.15	0.15	0.16	0.16	0.16	0.14	0.13	0.15	0.14	0.14	0.15	0.13	0.14	0.14	0.14	0.14	0.13	0.15	0.13	0.14	0.15	0.12	0.12	0.12
CLADEE_OH_26_CO	0.14	0.15	0.15	0.15	0.15	0.14	0.13	0.14	0.15	0.14	0.14	0.14	0.15	0.15	0.14	0.15	0.12	0.14	0.13	0.14	0.14	0.12	0.12	0.12
CLADEE_OH_94_CO	0.16	0.16	0.15	0.15	0.15	0.15	0.13	0.14	0.14	0.14	0.14	0.16	0.15	0.16	0.15	0.15	0.13	0.14	0.14	0.13	0.14	0.12	0.13	0.13
CLADEF_OTI52_BR	0.14	0.15	0.14	0.14	0.14	0.14	0.14	0.15	0.14	0.13	0.14	0.14	0.15	0.14	0.14	0.14	0.12	0.15	0.14	0.15	0.15	0.12	0.12	0.13
CLADEG_BRG63_BR	0.12	0.13	0.11	0.11	0.11	0.12	0.10	0.12	0.11	0.10	0.12	0.11	0.12	0.10	0.11	0.11	0.09	0.12	0.13	0.13	0.12	0.10	0.10	0.11
CLADEH_OTI43_BR	0.14	0.14	0.15	0.15	0.15	0.14	0.14	0.15	0.14	0.13	0.14	0.12	0.12	0.12	0.12	0.12	0.12	0.15	0.15	0.14	0.15	0.14	0.14	0.14
CLADEI_BCMS40812_BR	0.15	0.15	0.16	0.16	0.16	0.16	0.14	0.16	0.15	0.15	0.16	0.14	0.14	0.13	0.13	0.13	0.11	0.15	0.16	0.15	0.15	0.13	0.13	0.13
EO_SP_LH2012_TH	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.21	0.20	0.20	0.21	0.18	0.18	0.17	0.18	0.18	0.18	0.18	0.17	0.18	0.20	0.17	0.16	0.17
EO_SP1_DNA103566_MY	0.20	0.20	0.18	0.18	0.18	0.19	0.18	0.20	0.18	0.19	0.20	0.19	0.19	0.19	0.20	0.20	0.18	0.16	0.16	0.20	0.19	0.18	0.18	0.18
EO_TOTORO_ZMMU_VN	0.18	0.18	0.20	0.20	0.20	0.18	0.16	0.18	0.17	0.18	0.18	0.19	0.19	0.19	0.20	0.20	0.20	0.17	0.18	0.17	0.20	0.18	0.18	0.19
EP_ACACIOI_TRIPUI31_BR	0.12	0.13	0.14	0.14	0.14	0.14	0.12	0.13	0.13	0.12	0.13	0.13	0.13	0.12	0.12	0.12	0.01	0.15	0.13	0.14	0.14	0.13	0.13	0.13
EP_ADENOCRYPTUS_C\$1_BR	0.15	0.16	0.16	0.16	0.16	0.16	0.16	0.17	0.16	0.16	0.17	0.15	0.15	0.14	0.15	0.14	0.09	0.16	0.16	0.15	0.16	0.15	0.15	0.15
EP_ADENOCRYPTUS_CS6_BR	0.14	0.14	0.14	0.14	0.14	0.15	0.13	0.15	0.14	0.14	0.14	0.13	0.14	0.13	0.13	0.12	0.06	0.14	0.14	0.13	0.14	0.13	0.13	0.14
EP_BIOLLEYI_NC009082_CR	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.17	0.16	0.16	0.17	0.15	0.16	0.15	0.16	0.16	0.17	0.16	0.14	0.15	0.18	0.15	0.14	0.15
EP_DIADENOCRYPTUS_MS2_BR	0.14	0.14	0.15	0.15	0.15	0.15	0.14	0.16	0.15	0.14	0.16	0.14	0.14	0.14	0.14	0.13	0.08	0.15	0.15	0.14	0.14	0.13	0.13	0.13
EP_EDWARDSII_GF1803_GF	0.15	0.15	0.16	0.16	0.16	0.16	0.15	0.16	0.16	0.16	0.16	0.15	0.15	0.15	0.15	0.15	0.12	0.15	0.14	0.16	0.15	0.14	0.14	0.14
EP_MACHADOI_FM2_BR	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.16	0.15	0.14	0.15	0.13	0.13	0.13	0.13	0.12	0.09	0.15	0.14	0.14	0.15	0.13	0.13	0.13
EP_PAUROGNOSTUS_ME8_BR	0.15	0.15	0.16	0.16	0.16	0.15	0.15	0.16	0.15	0.15	0.16	0.15	0.15	0.14	0.15	0.14	0.10	0.16	0.16	0.15	0.15	0.14	0.14	0.14
EP_SP_DNA104980_CO	0.14	0.14	0.14	0.14	0.14	0.13	0.12	0.13	0.11	0.11	0.13	0.14	0.14	0.13	0.13	0.14	0.14	0.11	0.12	0.15	0.15	0.13	0.12	0.13
ME_THOLLONI_DNA104625_GA	0.17	0.17	0.18	0.18	0.18	0.15	0.16	0.17	0.17	0.16	0.16	0.16	0.17	0.16	0.16	0.15	0.16	0.16	0.15	0.18	0.18	0.15	0.14	0.15
OROPERIPATUS_SP1_BZ	0.12	0.12	0.12	0.12	0.12	0.11	0.10	0.12	0.12	0.10	0.12	0.11	0.11	0.10	0.11	0.11	0.10	0.12	0.12	0.12	0.13	0.11	0.10	0.11
DRUPERIPATUS_SPZ_MX	0.13	0.13	0.13	0.13	0.13	0.13	0.12	0.13	0.12	0.11	0.12	0.12	0.12	0.11	0.12	0.12	0.11	0.13	0.13	0.14	0.14	0.12	0.12	0.12
PE_DUMINICAE_DNA1049//_DO	0.12	0.12	0.14	0.14	0.14	0.13	0.12	0.14	0.13	0.12	0.14	0.13	0.12	0.12	0.12	0.12	0.10	0.14	0.13	0.14	0.15	0.10	0.11	0.11
PE_SOLORZANOI_PE11_CR	0.14	0.14	0.16	0.16	0.16	0.14	0.13	0.15	0.13	0.14	0.15	0.14	0.14	0.14	0.14	0.14	0.16	0.11	0.14	0.16	0.15	0.13	0.13	0.13
PR_HITOYENSIS_DNA103564_CR	0.14	0.14	0.16	0.16	0.16	0.15	0.13	0.14	0.13	0.13	0.14	0.15	0.15	0.14	0.14	0.15	0.13	0.12	0.13	0.15	0.15	0.13	0.12	0.13

SPECIMEN													VALUES												
A_saproxylicus_OH109_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02
A_saproxylicus_OH142_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02
A_Sp1_OH175_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02
A_Sp1_OH27_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02
A_Sp1_OH93_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02
A_Sp4_OH30_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
A_sublapis_OH121_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
A_sublapis_OH133_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
A_sublapis_OH137_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
A_sublapis_OH165_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.01	0.02	0.02
A_sublapis_OH60_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
A_xerira_OH146_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02
A_xerira_OH23_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02
A_xerira_OH32_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.01	0.02	0.02
A_xerira_OH33_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.01	0.02	0.02
A_xerira_OH95_CO	0.02	0.02	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01	0.02
Ce_sucuriuensis_ONYMTS04_BR	0.01	0.02	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.02	0.02	0.00	0.01	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02
CladeA_DNA104978_EC	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.01
CladeA_DNA104979_EC	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02
CladeC_OH_132_CO	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CladeC_OH_71_CO	0.01	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CladeD_OH_140_CO	0.01	0.02	0.01	0.01	0.01	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02
CladeD_OH_19_CO	0.01	0.02	0.01	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02
CladeD_OH_25_CO	0.01	0.02	0.02	0.01	0.01	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02
CladeD_OH_99_CO		0.02	0.01	0.02	0.01	0.01	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.01	0.01	0.01	0.02
CladeE_JPR_31_CO	0.13		0.01	0.01	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CladeE_OH_26_CO	0.12	0.10		0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CladeE_OH_94_CO	0.14	0.12	0.12		0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
CladeF_OTI52_BR	0.12	0.13	0.14	0.13		0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02
CladeG_BRG63_BR	0.10	0.11	0.12	0.12	0.09		0.01	0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02
CladeH_OTI43_BR	0.15	0.13	0.14	0.15	0.13	0.11		0.01	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.02	0.02
Cladel_BCMS40812_BR	0.13	0.12	0.13	0.13	0.13	0.10	0.12		0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.01	0.02	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.02
Eo_sp_LH2012_TH	0.16	0.18	0.18	0.20	0.17	0.16	0.15	0.16		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Eo_sp1_DNA103566_MY	0.18	0.17	0.17	0.19	0.17	0.16	0.17	0.16	0.16		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Eo_totoro_ZMMU_VN	0.19	0.18	0.19	0.17	0.18	0.17	0.19	0.19	0.19	0.17		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Ep_acacioi_Tripui31_BR	0.12	0.13	0.12	0.13	0.12	0.09	0.12	0.12	0.18	0.18	0.20		0.01	0.01	0.02	0.01	0.02	0.01	0.01	0.02	0.02	0.01	0.01	0.01	0.02
Ep_adenocryptus_CS1_BR	0.15	0.15	0.16	0.15	0.15	0.12	0.14	0.13	0.19	0.20	0.24	0.10		0.01	0.02	0.01	0.02	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02
Ep_adenocryptus_CS6_BR	0.13	0.12	0.14	0.13	0.13	0.10	0.12	0.11	0.17	0.18	0.21	0.06	0.04		0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.02
Ep_biolleyi_NC009082_CR	0.16	0.15	0.16	0.16	0.16	0.13	0.16	0.16	0.18	0.17	0.18	0.16	0.19	0.17		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Ep_diadenocryptus_MS2_BR	0.13	0.15	0.14	0.12	0.13	0.10	0.12	0.11	0.17	0.18	0.20	0.07	0.08	0.07	0.16		0.02	0.01	0.01	0.02	0.02	0.01	0.02	0.01	0.02
Ep_edwardsii_GF1803_GF	0.14	0.14	0.16	0.14	0.14	0.12	0.12	0.15	0.18	0.19	0.20	0.12	0.16	0.13	0.17	0.14		0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
Ep_machadoi_FM2_BR	0.13	0.14	0.13	0.12	0.12	0.09	0.12	0.11	0.15	0.18	0.20	0.08	0.11	0.09	0.16	0.05	0.13		0.01	0.02	0.02	0.01	0.02	0.01	0.02
Ep_paurognostus_ME8_BR	0.14	0.15	0.15	0.14	0.14	0.11	0.12	0.13	0.18	0.17	0.22	0.10	0.07	0.06	0.18	0.04	0.15	0.09		0.02	0.02	0.01	0.02	0.01	0.02
Ep_sp_DNA104980_CO	0.12	0.13	0.13	0.14	0.14	0.11	0.14	0.14	0.16	0.16	0.18	0.14	0.15	0.13	0.15	0.14	0.14	0.14	0.14		0.01	0.01	0.01	0.02	0.02
me_tholloni_DNA104625_GA	0.15	0.14	0.14	0.17	0.16	0.14	0.16	0.16	0.18	0.21	0.21	0.16	0.18	0.17	0.17	0.16	0.17	0.15	0.17	0.13		0.02	0.02	0.02	0.02
Oroperipatus_sp1_BZ	0.11	0.12	0.11	0.13	0.12	0.09	0.10	0.10	0.16	0.15	0.19	0.10	0.12	0.10	0.13	0.11	0.14	0.12	0.11	0.10	0.14		0.01	0.01	0.02
Oroperipatus_sp2_MX	0.12	0.14	0.14	0.15	0.13	0.10	0.12	0.11	0.16	0.15	0.19	0.11	0.14	0.12	0.13	0.13	0.15	0.13	0.13	0.12	0.15	0.05		0.01	0.01
Pe_dominicae_DNA104977_DO	0.11	0.14	0.14	0.12	0.12	0.09	0.12	0.11	0.17	0.16	0.18	0.10	0.13	0.10	0.14	0.10	0.14	0.10	0.11	0.13	0.15	0.10	0.10		0.02
Pe_solorzanoi_PE11_CR	0.13	0.15	0.15	0.13	0.14	0.12	0.14	0.13	0.18	0.17	0.18	0.16	0.16	0.14	0.11	0.15	0.16	0.14	0.16	0.13	0.16	0.12	0.12	0.13	
Pr_hitoyensis_DNA103564_CR	0.12	0.14	0.14	0.15	0.15	0.13	0.14	0.14	0.17	0.18	0.19	0.13	0.13	0.12	0.14	0.14	0.15	0.14	0.15	0.12	0.16	0.12	0.13	0.13	0.11

ONYCHOPHORAN DIVERSITY IN THE ANDEAN MOUNTAINS **Appendix E**. GAP Analysis COI gene.



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## ONYCHOPHORAN DIVERSITY IN THE ANDEAN MOUNTAINS **Appendix F.** GAP Analysis 12S rRNA gene.



0.04

ONYCHOPHORAN DIVERSITY IN THE ANDEAN MOUNTAINS **Appendix G.** GAP Analysis 16S rRNA gene.



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