Full article

Revista Actualidades Biológicas

Actual. Biol. 47(122): e4705, 2025 | Jan-Jun | Medellin | DOI:10.17533/udea.acbi/v47n122a05

Phylogenetic analysis of colombian populations of the genus *Tamandua* (Pilosa: Myrmecophagidae)

Análisis filogenético de las poblaciones colombianas del género *Tamandua* (Pilosa: Myrmecophagidae)

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Abstract

The genus *Tamandua* is made up of two species of anteaters, both with distributions in Colombia; *Tamandua mexicana* in the trans-Andean region and *Tamandua tetradactyla* in the Cisandina region. There is a sympatry zone in the center of the country, where individuals with intermediate phenotypes have been found and are classified as *Tamandua mexicana* despite not having the complete phenotype of this species. In this study, a genetic characterization of *Tamandua* individuals was carried out through a phylogenetic reconstruction by maximum likelihood and a Bayesian analysis, based on the mitochondrial markers Ribosomal RNA 16S (rRNA 16S), Cytochrome Oxidase I (COI), and the Hypervariable Region I of Mitochondria. The results show genetic differentiation between *T. mexicana* and *T. tetradactyla* individuals, which supports the existence of two species for the genus. Individuals with the intermediate phenotype do not show a tendency to form an isolated clade within the group of *T. mexicana*. These results are consistent with the current taxonomic classification of the genus, and do not support any further evolutionary process.

Keywords: hybridization, intermediate phenotype, mitochondrial markers, *Tamandua mexicana*, *Tamandua tetradactyla*

Resumen

El género *Tamandua* se encuentra conformado por dos especies de hormigueros, ambas con distribución en Colombia. *Tamandua mexicana* se encuentra en el noroccidente del país, y *T. tetradactyla* en el suroriente. Sin embargo, existe una zona de simpatría en el oriente de la Cordillera Central, colindando con la Amazonía y los Llanos Orientales, extendiéndose hacia el norte en la Cordillera Oriental, en donde se han encontrado individuos con fenotipos intermedios, que han sido clasificados como *T. mexicana*, a pesar de no tener el fenotipo completo de esta especie. En este estudio se realizó una caracterización genética de algunos individuos del género *Tamandua*, mediante una reconstrucción filogenética por máxima verosimilitud y un análisis bayesiano, a partir de los marcadores mitocondriales ARN ribosomal 16S (ARNr 16S), Citocromo Oxidasa I (COI), y la Región Hipervariable de la Mitocondria I. Los resultados evidencian una diferenciación genética entre los individuos de *T. mexicana* y *T. tetradactyla*, lo cual soporta la existencia de dos especies para el género; los individuos con el fenotipo intermedio no muestran ninguna tendencia a formar un clado aislado dentro del grupo de *T. mexicana*. Estos resultados son consistentes con la clasificación taxonómica actual del género.

Palabras clave: fenotipo intermedio, hibridación, marcadores mitocondriales, *Tamandua mexicana*, *Tamandua tetradactyla*

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Received: February 16, 2024; accepted: August 1, 2024; published: February 11, 2025.

INTRODUCTION

The superorder Xenarthra (Gardner, 2008) is composed of the orders Cingulata (armadillos) and Pilosa. Pilosa in turn contains the suborders Folivora (sloths) and Vermilingua (antbirds), the latter with Myrmecophagidae as the only family that makes up the suborder, with the genera *Cyclopes*, *Myrmecophaga* and *Tamandua*. The genus *Tamandua* consists of the species *T. mexicana* (Saussure, 1860) and *T. tetradactyla* (Linnaeus, 1758).

Both species are common and widely distributed: *T. mexicana* is distributed from southern Mexico to northwestern Peru and northwestern Venezuela, from zero to 2700 m a.s.l. (Rojano & Plese, 2016), while *T. tetradactyla* occurs in the eastern Andes from Colombia, Venezuela, Trinidad and the Guyanas (French Guiana, Guyana and Suriname), and south to northern Uruguay and Argentina, from zero to 1600 m a.s.l. (Hayssen, 2011).

These two species differ mainly in their distribution, with *T. mexicana* considered to be from Central America and *T. tetradactyla* from South America (Hayssen, 2011), although in some areas of Colombia, both occur in sympatry (Navarrete & Ortega, 2011). Morphologically, the main difference between these species is that *T. mexicana* presents a "black vest" pattern on the dorsum, which flanks and belly against a pale yellow background (Figure 1), while *T. tetradactyla* presents a uniform pale yellow or golden coloration without the "vest" pattern, or uniform black (Rojano & Plese, 2016). However, morphotypes have been reported, considered subspecies of *T. tetradactyla* that present a dorsal black coloration, as is the case of *T. tetradactyla* quichua (Thomas, 1927) and *T. tetradactyla* nigra (Geoffroy St.-Hilaire, 1803) which are distributed in Peru (Rojano et al., 2014). Other morphological differences are the size of the ears, which measure between 40 and 46 mm (millimeters) in *T. mexicana*, and between 50 and 54 mm in *T. tetradactyla*, in addition to some cranial characteristics, such as the shape of the infraorbital foramen and the number of orbital holes (Hayssen, 2011).

In Colombia, *T. mexicana* is distributed in the north, center and west; *T. tetradactyla* is found in the southeast of the country. The sympatric zones for these species are in the center of the country, ending in the Andean region, in the departments of Huila, Cundinamarca, Caldas, Quindío and Valle del Cauca. Additionally, individuals have been found with an intermediate phenotype in their coloration pattern, which makes their taxonomic identification as one of the Tamandua species difficult (Alzate-Gaviria et al.,

Figure 1. The common phenotype of a *Tamandua mexicana* individual. Photograph: Tinka Plese, Fundación AIUNAU, Colombia.

2016; T. Plese, personal communication, 2019). This phenotype consists of a marbled-yellowish coloration of the vest pattern; sometimes only the vest shape is present at the base of the skin, and the fur is yellowish (Figure 2). This suggests that a hybridization phenomenon may be occurring between the two *Tamandua* species, and that individuals with intermediate phenotypes belong to a previously undescribed species, or that there is only one species for the genus (Katiehutchin, 2021). In Colombia, most of the studies conducted with *Tamandua* have to do with their diet or ectoparasites (Alzate-Gaviria et al., 2016), genetic studies have also been conducted within the family Myrmecophagidae (Ruiz-García, 2021), and recently a study of coloration variation within the genus was published in Brazil (Cotts et al., 2023).

In this sense, it is necessary to expand the state of knowledge of these species, since it is essential to have accurate information on the status of their populations, since conservation efforts can be affected by lack of information (DeSalle & Amato, 2004). Thus, the purpose of this study was to carry out a phylogenetic analysis of some individuals from Colombian populations of the genus *Tamandua*, in order to contribute to their taxonomic characterization, and thus expand the state of knowledge about them.

Figure 2. *Tamandua* sp. individual with an intermediate phenotype. Photograph: Tinka Plese, Fundación AIUNAU, Colombia.

MATERIALS AND METHODS

The geographical coverage of the study was taken at the departmental level, since the precise, or georeferenced, origin of the sampled individuals was not available (Figure 3).

A total of 24 samples were analyzed, distributed as follows: 22 belonged to *T. mexicana* (of which five had an intermediate phenotype) and 2 to *T. tetradactyla*. As for their origin, five of them were supplied by the Biological Collections of the CES University (CBUCES)-sub collection of animal tissues; 17 by the AIUNAU foundation, derived from animals rescued in different parts of Colombia with known origin; and two samples were sampled in the Los Ocarros biopark. Of these 24 samples, 22 came from buccal swabs and two from muscle. Oral mucosa sampling was performed by experienced personnel. This procedure consisted of introducing a sterile applicator into the mouth of the fasting animal, allowing it to chew it (Gallina & López, 2011; Moscoso et al., 2021), trying to have minimal contact with the individual. Muscle samples were obtained from animals that died during the rehabilitation process.

To conduct this study, permission was obtained from the Institutional Committee for the Care and Use of Animals - CICUA of CES University, in addition to the Framework Permit for the Collection of Specimens from the Biological Collections of CES University - CBUCES, granted by Resolution of the National Environmental Licensing Authority - ANLA No. 0790 of 2014, modified by Resolution No. 01510 of 2021.

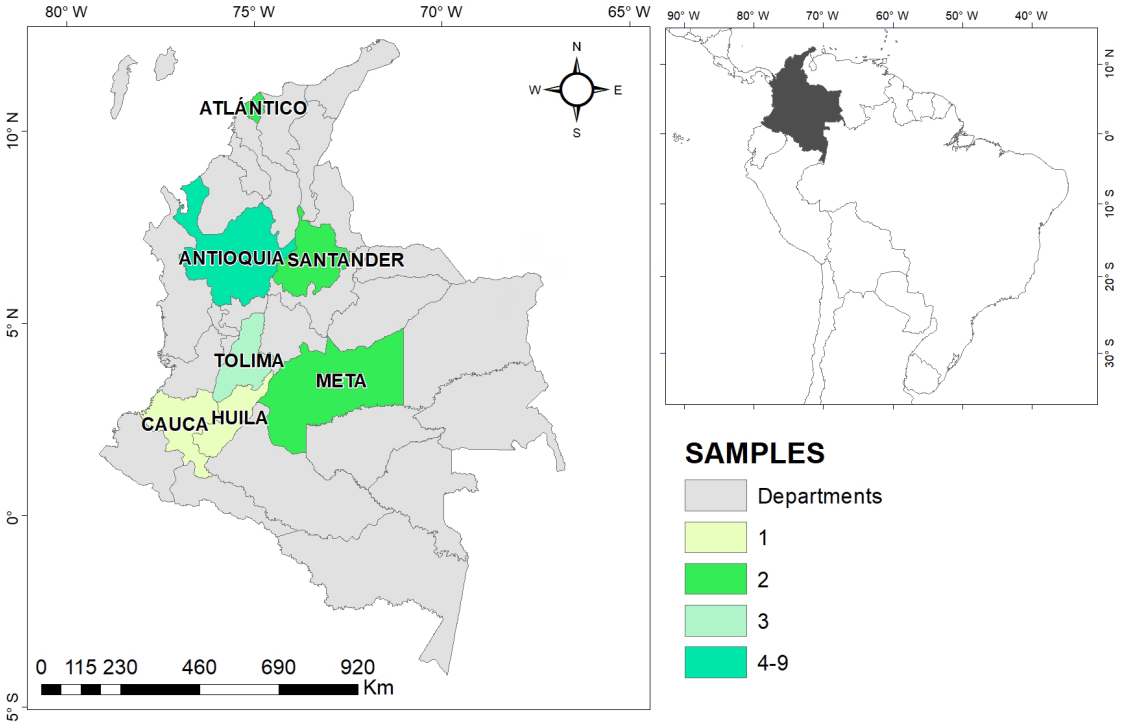

Figure 3. Departmental provenance map of *Tamandua* sp. samples used for this study.

DNA was extracted from samples from the AIUNAU foundation and Los Ocarros biopark using the GeneJET™ genomic DNA purification kit (cat. K0722) (Thermo Fisher Scientific, Waltham, Massachusetts, USA), following the manufacturer's recommendations. Genetic material from samples from CBUCES biological collections had been extracted previously using the GeneJETTM and PrepFilerTM purification kit (Thermo Fisher Scientific, Waltham, Massachusetts, USA).
Subsequently, the quantity and purity of the genetic material was determined by spectrophotometry using a Nanodrop 2000 (Thermo Fisher Scientific Inc., USA). Samples that underwent a DNA extraction process for this project were entered into the CBUCES biological collections.

The samples were then amplified specifically for the COI and 16S rRNA genes, in addition to the *Hypervariable Region I of Mitochondria* (HVI). For this, *in silico* primer design was performed using Primer3 software version 4.1.0 (Kõressaar et al., 2018; Untergasser et al., 2012). Standardization of the hybridization temperature for each primer was carried out by a PCR gradient using a temperature between 50 °C and 60 °C. Through verification by 1.5% agarose gel electrophoresis, the temperature that produced the highest amount of amplified product was identified and used in all PCR assays. This standardization process was performed independently for each of the markers. The hybridization temperature and other primer conditions are shown in table 1.

Regarding amplification conditions, 35 thermal cycles were used for all assays, with an initial denaturation phase at 95 °C for two minutes, followed by a denaturation phase at 95 °C for 30 seconds; an extension phase at 72 °C for one minute and a final extension at 72 °C for ten minutes. Hybridization temperature was gene specific and is shown in Table 1. The DNA concentration used in all PCR assays was 5 to 10 ng/uL. PCR amplification was verified by agarose gel electrophoresis at a concentration of 1.5% and with a 100 bp molecular weight marker.

Genes were sequenced by MACROGEN Company (Seoul, South Korea), using Sanger methodology (Sanger et al., 1977). Positive and negative controls were used for all PCR assays. For the positive control, sample TS012 (*T. mexicana* TOLIMA 2) was used, as it had been successfully amplified in all PCR gradient assays, so it was standardized as a control sample. This allowed comparing and verifying the efficiency of amplification in the other samples. For the negative control, all PCR components were used without a target sequence, which would serve to detect possible contamination in the reagents or samples.

Table 1. Physicochemical conditions of the primers designed for the amplification of the markers selected for this study.

PCR primer conditions designed for PCR

Primer name	Sequence	Primer size (bp)	Amplicon size (bp)	% G-C	Hybridization T (°C)
T16S-F	ACCTTTCTCTCCACgCACAAgT	20	931	50	59.77
T16S-R	ggCTCTCTgCCACCTTAACAAA	20		50	60.25
TCOI-F	CCCggggTAAgCTTAACCTACTACTACTC	24	1,000	50	58.89
TCOI-R	CTCAAACgATAAAgCCCAAg	20		45	57.52
THVI-F	TTCCgACCACACTAAgCCAACT	20	804	50	59.73
THVI-R	CCATAgCTgAgTCgATgCAACCATAgCTgAgTCgATgCAA	20		50	59.97

bp: base pairs; **%G-C**: guanine-cytosine percentage; **Hybridization T. (°C)**: hybridization temperature in degrees Celsius.

For the analysis of the genetic data, alignments were performed for each gene using the parameters of the MAFFT algorithm (Katoh & Standley, 2013). A concatenated matrix with the three alignments was then obtained with the Mesquite® program (Maddison & Maddison 2021). Using the Bayesian information criterion (Nei & Kumar et al., 2000; Tamura et al., 2021), the nucleotide substitution model for each of the alignments was selected. Finally, phylogenetic reconstructions were performed using the maximum likelihood method by the RaxML algorithm and by the Bayesian inference method, both implemented in the CIPRES portal version 3.3 (Miller et al., 2010).

RESULTS

DNA extraction was successful for all 19 buccal swab samples. Considering that five samples previously submitted to extraction were already available, a total of 24 DNAs were available for PCR assays. After performing electrophoresis to verify PCR amplification of 16S rRNA, COI and HVI markers, three samples were discarded because amplification was not achieved for some of the genes (Table 2). The other amplified products were of the expected size (Figure 4).

The best nucleotide substitution model for the 16S rRNA marker was HKY (model proposed

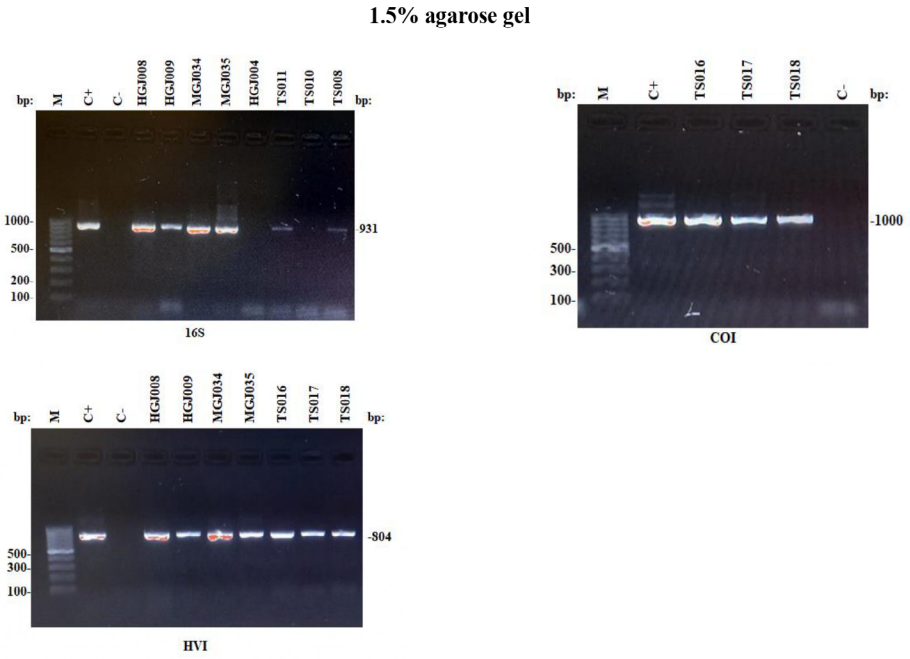

Figure 4. Electrophoresis result on 1.5% agarose gels to visualize PCR amplification of the mitochondrial markers 16S rRNA, COI and HVI. **M**: 100 bp molecular weight marker. **C+**: positive control. **C-**: negative control.

Table 2. Results for each sample of the DNA extraction processes and PCR assays for 16S rRNA, COI and HVI markers.

PCR assay results for DNA extracts						
Sample code	CBUCES Collection Code	Location	DNA extraction result	PCR assay result		
				16S rRNA	IOC	HVI
TS001	CBUCESL1004	Antioquia	Positive	Positive	Positive	Positive
TS003	CBUCESL1006	Antioquia	Positive	Positive	Positive	Positive
TS004	CBUCESL1007	Antioquia	Positive	Positive	Positive	Positive
TS005	CBUCESL1008	Chocó	Positive	Positive	Positive	Positive
TS008	CBUCESL1011	Antioquia	Positive	Positive	Positive	Positive
TS009	CBUCESL1012	Tolima	Positive	Positive	Positive	Positive
TS012	CBUCESL1015	Tolima	Positive	Positive	Positive	Positive
TS011-2	CBUCESL1014	Antioquia	Positive	Positive	Positive	Positive
TS013	CBUCESL1016	Antioquia	Positive	Positive	Positive	Positive
TS014	CBUCESL1017	Antioquia	Positive	Positive	Positive	Positive
TS015	CBUCESL1018	Huila	Positive	Positive	Positive	Positive
TS016	CBUCESL1019	Antioquia	Positive	Positive	Positive	Positive
TS017	CBUCESL1020	Antioquia	Positive	Positive	Positive	Positive
TS018	CBUCESL1021	Atlantic	Positive	Positive	Positive	Positive
HGJ008	CBUCESHGJ008	Santander	Not applicable	Positive	Positive	Positive
HGJ009	CBUCESHGJ009	Santander	Not applicable	Positive	Positive	Positive
MGJ034	CBUCESMGJ034	Tolima	Not applicable	Positive	Positive	Positive
MGJ035	CBUCESMGJ035	Atlantic	Not applicable	Positive	Positive	Positive
N01	CBUCESL1024	Cauca	Positive	Positive	Positive	Positive
N02	CBUCESL1022	Goal	Positive	Positive	Positive	Positive
N03	CBUCESL1023	Goal	Positive	Positive	Positive	Positive
TS002	CBUCESL1005	Tolima	Positive	Negative	Negative	Negative
TS010	CBUCESL1013	Quindío	Positive	Negative	Negative	Positive
HGJ004	CBUCESHGJ004	Santander	Not applicable	Negative	Negative	Negative

Samples HGJ008, HGJ009, MGJ034 and MGJ035 were not subjected to DNA extraction in this study, as this process had already been performed previously.

by Hasegawa, Kishino and Yano), with a CIB (Bayesian Information Criterion) value of 2490.53; for the COI and HVI genes, the best model was HKY+I (HKY + invariant sites), with a CIB of 2210.35 for both.

The maximum likelihood and Bayes trees yielded similar results (Figures 5 and 6). Both recover two main groups, one composed of *T. mexicana* specimens and the other of *T. tetradactyla* specimens. A differentiation is also shown between the specimen of *T. mexicana* named ANTIOQUIA 2 and the others of this species. No clear grouping is evident among the taxa within the *T. mexicana* group.

Nucleotide sequences were published in GenBank with accession numbers ranging from PP929896 to PP929914, from PP930407 to PP930423, and from PP946328 to PP946345.

DISCUSSION

The use of molecular markers in conservation genetics has allowed studies to evaluate the degree of genetic isolation between species (Ripperger et

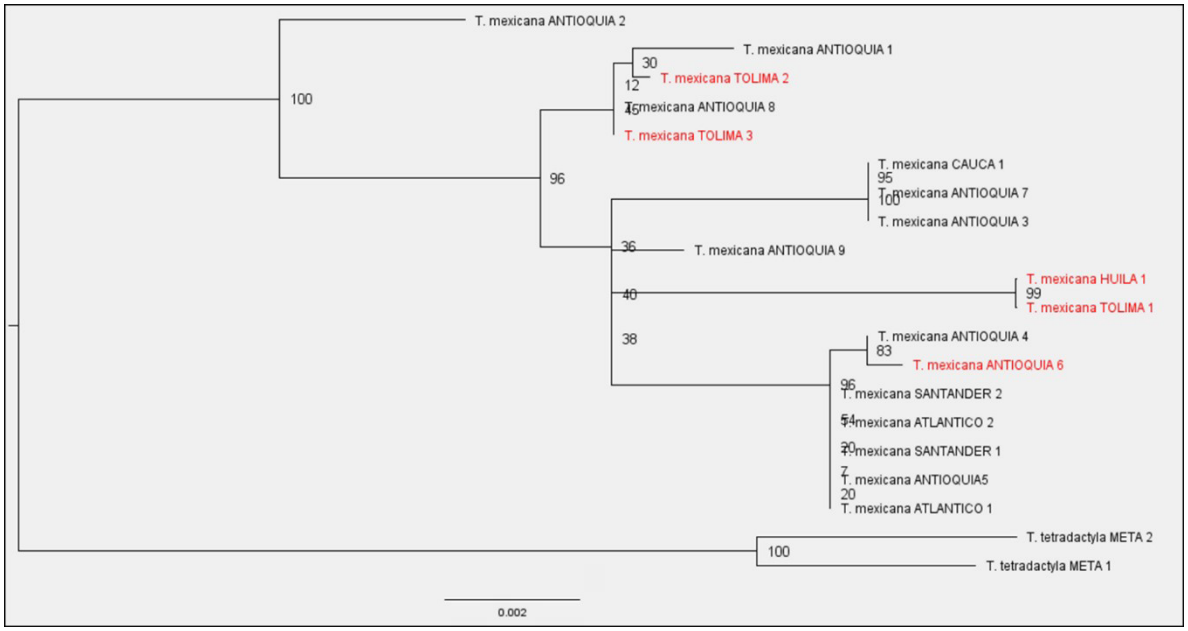

Figure 5. Phylogenetic reconstruction by maximum likelihood with Bootstrap supports. Taxa marked with red color were reported as individuals with intermediate phenotype or possible hybrids.

al., 2012). In addition, molecular markers serve both to recognize the regions of origin of rescued individuals and to consider their application in their reintroduction (Ruiz-García et al., 2009).

The phylogenies obtained through this study show a clear differentiation between *T. mexicana* and *T. tetradactyla*, which supports the current taxonomy of the genus (Figures 5 and 6). However, in 2021, a mitogenomic study was published on Myrmecophagidae, in order to resolve the number of taxa within the family (Ruiz-García et al., 2021), for which 74 samples of *Tamandua* sp. from specimens from several Central and South American countries were analyzed. In this study, the length of the mitochondrial DNA sequences was 16,543 bp, where three haplogroups were detected for the genus *Tamandua*, all intermixed with specimens of both *T. mexicana* and *T. tetradactyla*, suggesting that only one species should be considered within the genus (Ruiz-García et al., 2021). It is important to note that the individuals found intermixed, for

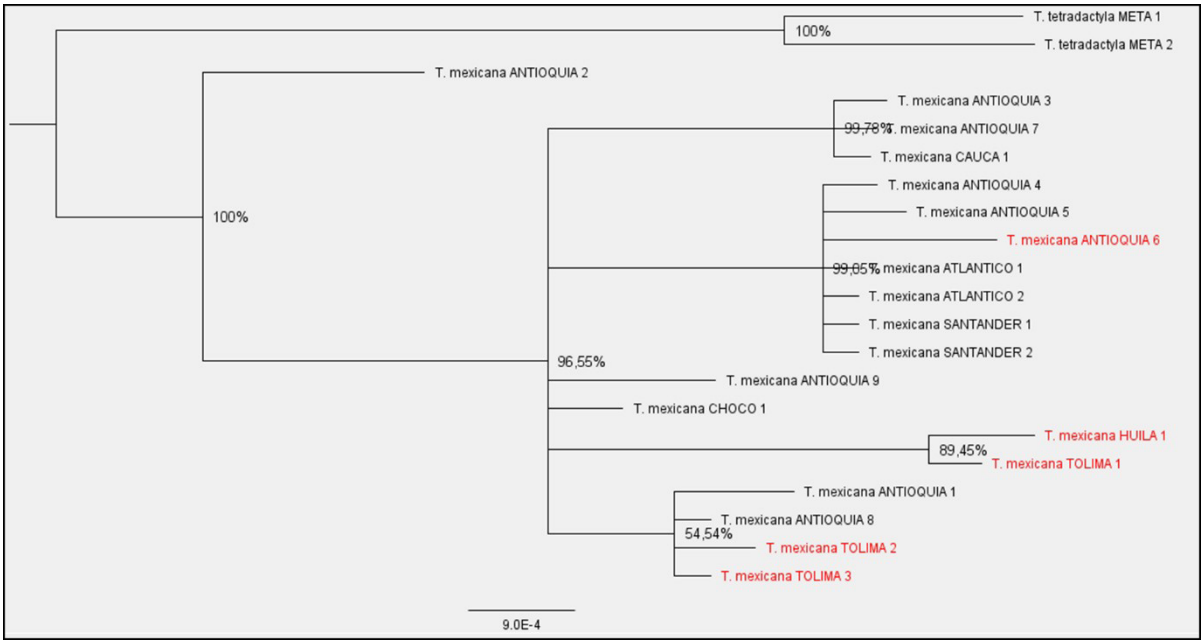

Figure 6. Phylogenetic reconstruction by Bayesian inference. Taxa marked with red color were reported as individuals with intermediate phenotype or possible hybrids.

which it is suggested that only one species should be considered for the genus, have a distribution corresponding to a potentially sympatric zone, so there may have been a misidentification of the specimen, so there is insufficient evidence to affirm that there is only one species. It should also be noted that, unlike Ruiz-García et al. (2021), who used the complete mitochondrial genome and had a wider geographical coverage, only three markers were analyzed (COI, 16S and HVI) in this research, and only samples from Colombia were used, with different analysis methodologies that generate differences in the findings.

With the present results, there is no evidence of genetic structuring in the Colombian populations of *T. mexicana*, as it shows a polytomy, which is not clear in terms of the grouping of taxa. This may be due to the processes of fauna release, given that on many occasions the wildlife care centers (CAV) reintroduce individuals into natural populations, but not in the same area where they come from, which influences the populations, generating mixing among them as a consequence of anthropic activity.

The specimens from Huila, Tolima, and the one named as Antioquia 6, presented an intermediate phenotype in the "vest" coloration pattern, but there was no evidence of a tendency of these individuals to group together (Figures 5 and 6), so it can be inferred that the phenotype described does not have sufficient resolution to indicate a speciation process, and that this is a phenotypic variation within *T. mexicana*. In agreement with these results, Ruiz-García et al. (2021) concluded that coloration patterns in *Tamandua* species, in addition to body size and other morphological characteristics, may be variable among populations, and therefore have no phylogeographic or systematic value.

For future studies, the inclusion of nuclear markers, expanded sampling and more precise identification of the origin of individuals are recommended. This could provide clues about the microevolutionary trends of these species at the population level.

ACKNOWLEDGMENTS

We thank the Directorate of Research and Innovation of the CES University for funding the resources for the realization of this project. We also thank the CES University for its administrative support and for providing the space for the execution of the research, and the laboratory personnel for their constant accompaniment. We also thank the AIUNAU Foundation and the Biopark Los Ocarros for providing the biological samples. Finally, we thank the teacher Juan Camilo Arredondo for his observations for the improvement of the manuscript and the biologist Esteban Restrepo for his help with the elaboration of the distribution map.

AUTHOR CONTRIBUTION

Juliana Martínez-Garro contributed in the elaboration of the research idea, methodological orientation and analysis of the results, in addition to the administrative management for obtaining the financial resources for the execution of the project. The author Fabián Mejía-Franco accompanied the entire methodological process, data analysis and interpretation of the results. Sara Alzate-Velásquez performed the experiments, edited the sequences, ran the data analysis and wrote the manuscript. All authors reviewed and approved the final version of the manuscript.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

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