

Article

Integrative Taxonomic Assessment of Two *Atractus* (Serpentes: Dipsadidae) from Mérida Andes, Venezuela

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Abstract

Recently, the nominal species *Atractus meridensis* was considered a junior synonym of *Atractus erythromelas*, both species being endemic to the cordillera de Mérida in Venezuela. Here, its taxonomic status is resolved through the examination of the original descriptions, available type specimens, and an extensive comparison of additional museum material. In this review, we provide a new morphological–phylogenetic approach regarding its diagnosis and description for each species, including a model of its current distribution, which demonstrates its allopatric distribution. Both sleepyhead snakes are considered mimetic, but *A. erythromelas* exhibits a polymorphic color pattern with at least five known morphs, while *A. meridensis* is dichromatic with only two known color patterns. According to the IUCN, both taxa should be included in the Vulnerable category according to criteria B2abi,ii,iii,iv.

Keywords: systematics; taxonomic status; sleepyhead snakes; Venezuelan Andes



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1. Resumen

Recientemente, la especie nominal *Atractus meridensis* fue considerada un sinónimo menor de *Atractus erythromelas*, ambas especies endémicas de la cordillera de Mérida, Venezuela. Aquí su estatus taxonómico es resuelto mediante el examen de las descripciones originales, especímenes tipo disponibles y una comparación extensa de material museístico adicional. En esta revisión, proporcionamos un nuevo enfoque morfológico-filogenético con relación a su diagnóstico y descripción para cada especie, incluyendo una modelización de su actual distribución, que demuestra su distribución alopatrica. Ambas serpientes dormilonas se consideran miméticas, pero *A. erythromelas* exhibe un patrón de coloración polimórfico con al menos cinco morfos conocidos, mientras que *A. meridensis* es dicromática

con solo dos patrones de coloración conocidos. De acuerdo con la IUCN, ambos taxones deben ser incluidos en la categoría Vulnerable según los criterios B2abi,ii,iii,iv.

Palabras clave: sistemática, estatus taxonómico, serpientes dormilonas, Andes venezolanos

2. Introduction

Although they originated in the Old World and later dispersed to South America [1], dipsadines snakes exhibit a spectacular ecological and phenotypic diversity as a result of adaptive radiation, with fossorial habits clearly differentiating them from other groups [2]. If we consider that dipsadines diversity reaches at least ~806 species [1], it is remarkable from both an evolutionary and ecological perspective that the ground or sleepyhead (During field activities conducted in 2021 in the Andes of Mérida, we had the opportunity to interact with inhabitants from several localities. In this region, these snakes are commonly referred to as “sleepyhead” because they are usually found coiled on the ground or beneath logs and rocks, remaining almost motionless. Our observations frequently confirmed this behavior, particularly in montane areas above 1500 m in altitude.) snakes of the genus *Atractus* Wagler, 1828, account for 18.6% of all known dipsadines [3]. Moreover, *Atractus* represents the dominant group in mid- to high-elevation environments across northern South America. In Venezuela, it is the most diverse snake genus, with 30 recognized species [4,5].

Recently, Passos et al. [6] reviewed several species of *Atractus* from northern South America (Colombia and Venezuela), recognizing five new species from Colombia and proposing the synonymy of five species from Venezuela. While their work represents a step forward in the study of these snakes, some of their comparative criteria raise concerns and leave open questions regarding species boundaries. Here, we present the results of research that integrates molecular and morphological data from Venezuelan Andean populations, which not only support the distinct status of these taxa but also provide evidence for the recognition of additional new species.

Within the framework of multiple sources of evidence [7], the taxonomy of *A. erythromelas* and *A. meridensis*, both endemic species of the cordillera de Mérida and exhibiting a distinctive allopatric pattern, is reorganized. In addition, the conceptual ideas of species, diagnostic characters, variability, geographic limits, and biogeographic scenarios are explored. Without a doubt, this theoretical exercise provides a coherent, comparative, and explanatory frame of reference to understand the core of the actions and assessments that were published in relation to the *Atractus* species in the Venezuelan Andes (see [6]). Although we acknowledge the status of other Andean species, such as *A. eriki*, *A. micheleae*, *A. ochrosetrus*, *A. tamaensis*, and *A. mijaresi* [8,9], here, we clearly demonstrate that *A. meridensis* represents a distinct taxon, closely related to a new species of sleepyhead (sympatric along its distribution), and that both diverged from *A. erythromelas* during the late Miocene [10]. Also, a comparative table of *Atractus* species is provided, along with a biogeographical discussion and conservation status.

3. Materials and Methods

3.1. DNA Extraction, Amplification, and Sequencing

DNA was extracted from intercostal muscles, liver, and heart tissues of specimens collected by Luis Felipe Esqueda (LFE) and preserved in 95% ethanol. The specimens were later transferred to 75% ethanol and deposited in the Zoology Museum of the University of Concepción, Chile (MZUC). Additional tissues, preserved using the same protocol, were provided from sources like MHNLS, Venezuela. Extractions and amplifications followed the Wizard® SV Genomic DNA Purification System protocol (PROMEGA, Wisconsin, United States) at the Herpetozoa laboratory, University of Concepción. Two mitochondrial genes (Cytb and ND4) and two nuclear genes (NT3 and RAG-1) were amplified using the

primers and PCR conditions detailed in Supplementary Material Table S1. DNA quality was assessed on 1.5% agarose gels stained with SYBR® Vitrogen. Sequencing was performed by MACROGEN (Seoul, Republic of Korea), and chromatograms were verified using BioEdit 7.0.9.0 [11]. Open reading frames were checked in Mega v.11 [12]. Heterozygous nuclear DNA sequences were identified visually for double peaks in chromatograms, and individual alleles were reconstructed using DnaSP v.6.12 [13] with two independent runs. Alignments showed no gaps in mitochondrial sequences, and sequences for other species were sourced from GenBank (Supplementary Material Table S2), ensuring the amplified loci were from single voucher specimens to avoid “terminal chimeras”.

3.2. Phylogenetic Analyses

The new sequences generated in this study were combined with sequences downloaded from GenBank. Additionally, 20 specimens representing 18 species were used as outgroups (highlighted in yellow, Supplementary Table S2). Five gene fragments were obtained, corresponding to three mitochondrial amplicons, namely, long 16S ribosomal RNA (525 bp), cytochrome b (897 bp), and NADH dehydrogenase ND4 subunit IV (713 bp), and two nuclear amplicons, namely, neurotrophin-3 gene NT3 (516 bp) and recombination activator RAG-1 (879 bp). Substitution saturation of each locus was assessed using the software DAMBE v.5 [14]. We also assessed congruence among gene phylogenies by running individual gene tree analyses and calculating gene (gCF) and site (sCF) concordance factors in IQtree v.2 [15].

The authenticity of the obtained sequences and the homology of the specific mtDNA and nuDNA markers were evaluated with a BLAST v2.7 search in the NCBI genetic database (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>, accessed on 15 December 2024). The consensus sequences for each locus were aligned using MAFFT [16], contained in Jalview v. 2.11.1.4 [17], the L.INS-i option, with the following parameters: gap: 1.53 and gap: 0.123, BLOSUM62 and 200PAM/k = 2 (except region 16S aligned with the E.INS-i option). Only 16S mtDNA alignments that exhibited nucleotide positions with high entropy and may have had misaligned or incongruent regions were refined with BMGE v.1.12, with a BLOSUM62 matrix, a minimum block size of 20, a maximum entropy threshold of 0.5, and a rate limit gap of 0.65 [18], available on the web service <https://ngphylogeny.fr/>, accessed on 15 December 2024 [19]. Finally, the concatenation of all alignments was performed with Mesquite v3.6 [20]. Given the use of coding genes, all nucleotide sequences were translated into amino acids to evaluate the reading frame and ensure the absence of premature stop codons or other nonsense mutations [21].

Two methods of phylogenetic analysis were used for all datasets, and their results were compared. Firstly, we used maximum likelihood (ML) analysis to obtain the optimal tree topology of the concatenated dataset. The best partition and substitution models were automatically selected using ModelFinder [22] and then implemented in IQ-TREE v.2 software [15] under the Bayesian information criterion (BIC), where the best-fitting substitution models were TIM + F + I + G4 (transition model with unequal nucleotide frequencies). The best ML tree was selected from 10,000 iterations, and the confidence of the branches in the best ML tree was evaluated with the ultrafast bootstrap method using 10,000 bootstrap pseudoreplicates [23]. Posteriorly, we ran 20 individual runs to avoid possible local optima using the following configuration: `Iqtree2 -s myfile -m TESTMERGE -ninit 200 -nstop 1000 -pers 0.2 -ntop 100 -nbest 20 -rcluster 30 -alrt 1000 -bb 10,000`. Previously, we performed runs for each locus on the web-server Iqtree (<http://iqtree.cibiv.univie.ac.at/>, <https://ngphylogeny.fr/>, accessed on 15 December 2024 [24]), where branch support was calculated using the ultrafast bootstrap approximation (UFBS) [23] and the Shimodaira–Hasegawa approximate likelihood ratio test

(SH-aLRT) [25], with 1000 replicas. The consensus tree was visualized in FigTree [26]. Nodes with bootstrap values ≥ 70 were considered strongly supported, and the nodes with 95% were considered highly supported.

In the second instance, we used Bayesian inference (BI) analysis using the Bayesian framework implemented in BEAST 2.7.5 software, assuming the Yule speciation model, where all tips were sampled at the same time [27]. The matrix was partitioned by genes, with coding loci such as Cytb and ND4 treated separately, forming non-coding loci like 16S, except nuclear markers NT3, RAG-1, and CMOS, where we applied a linked strategy to avoid overparameterization, implementing the “bModelTest “allreversible” option to estimate mutation rates for all genes evaluated. In addition, we used bModelTest switches between substitution models during the Metropolis coupled MCMC (MC3, [28–30]), with a temperature of 0.02 and two chains, established in three independent runs of 50 million generations, saving the parameters and trees every 5000 generations (10,000 trees/runs). The convergence of the runs, effective sample size (ESS) values, and optimal burn-up values were verified using Tracer v1.7 [31]. The runs were combined with LogCombiner v2.7.5 [32]. Tree distribution and the estimated parameters were summarized on the maximum clade credibility tree with common ancestor heights and 10% burn-in using TreeAnnotator 2.7.5 [33] implemented on the CIPRES Science Gateway online platform (<https://www.phylo.org/>) [34].

Finally, we also calculated the uncorrected genetic distance (p-distance) using MEGA v.11.0 [35] for mitochondrial Cytb and ND4, respectively.

3.3. Ecological Niche Modeling

To understand the distribution and habitat in the biogeographic context, we generated species distribution models (SDMs) to predict and compare the potential geographic ranges of *A. erythromelas* and *A. meridensis* using correctly identified records (including material not yet entered into the MZUC museum by LFE). Therefore, the records that could be downloaded from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>) and iDigBio (www.idigbio.org) databases that we could not verify were discarded, totaling 109 specimens between both verified taxa (see Supplementary Table S3).

3.4. Input Data (Records and Environmental Variables)

Each record’s coordinates were obtained via Google Earth, converted to decimal degrees, and saved in CSV format. We used 20 bioclimatic variables as environmental predictors in the current scenario (1970–2000), WorldClim v.2.1 [36], with a spatial resolution of ~5 km (2.5 arc minutes). These variables encompassed 19 climate-related factors (temperature and precipitation) and elevation as a topographic variable. Additional environmental layers were sourced from EarthEnv (<http://www.earthenv.org>), including continuous topographic variables with ~5 km resolution [37]. After modeling in MaxEnt, we used the vegetation map of Venezuela made by Huber and Oliveira-Miranda [38] to calculate the surface area (km²) predicted, excluding areas inconsistent with the species’ ecological preferences. Protected area maps, downloaded as shapefiles from Provita (<https://geoportal.provita.org.ve/>), were also used to determine the overlap between predicted distributions and conservation areas. Environmental layers were processed into raster format using QGIS v.3.28 [39].

3.5. Approach to Predictive Models (Habitat Suitability)

To explore habitat suitability using a unique model (SDM), given the limited and spatially concentrated occurrence data [40], our first approach was based on a unique maximum entropy model to predict the distribution range of the species (MaxEnt v.3.4; [41]). This algorithm is highly effective in inferring species suitability from presence-only

data, even with small sample sizes, due to its ability to estimate probabilities based on maximum entropy principles [41–43]. In the first instance, doubtful information and duplicate records were removed. To reduce collinearity among bioclimatic variables, we performed a Pearson [44] correlation analysis in R (v.4.3) using ENMTools (Supplementary Table S4; [45]), discarding variables with $r^2 > 0.8$ [46], resulting in seven bioclimatic variables in the present scenery (Supplementary Table S5). In MaxEnt, we disabled Extrapolate and Do clamping to avoid overfitting [42]. Because we had fewer than 50 records per species, we used Crossvalidate for stable evaluation, with a convergence limit of 0.00001, default prevalence of 0.65, 10 percentile training presence rules, and a max of 5000 iterations. We randomly selected 65% of the sites for training and 25% for testing [41]. The Jackknife test was used to estimate the contribution and response of each variable [47].

To understand changes in habitat suitability that presumably led to historical isolation or not during restriction to shared refugia, we retrospectively projected the current MDS onto Pleistocene and Pliocene climate data available in the PaleoClim database (<http://www.paleoclim.org/>, [48]). Later, the projections were used for the mid-Pliocene warm period, between 3264 and 3025 Myr [49], and Last Maximum Glacial (LGM, 21 Kya) [50]. It should be noted that not all bioclimatic variables are represented in these projections, so we generated SDMs with a subset of variables represented in paleoclimate datasets (BIO_1, BIO_3, BIO_4, BIO_12, BIO_13, BIO_17, and BIO_18) using the same approach as the current models and predicted habitat suitability with the predictive function in MaxEnt v.3.4 [41].

3.6. Evaluation Index and Visualization

The accuracy of the models in the single-approach framework was evaluated as follows: (1) In the single approach, model outputs were manually inspected, and the model exhibiting the highest area under the curve (AUC) was selected. AUC values range from 0.5 (random prediction) to 0.8–0.9 (good fit) and above 0.9 (excellent fit) [51]. The logistic output provides a probabilistic suitability index, ranging from 0 to 1, with values closer to 1 indicating optimal conditions for a species. Although the AUC metric is widely used in species distribution models (e.g., MaxEnt), its reliability has been questioned because it does not account for true absences, potentially leading to uncertain predictions [52]. To avoid biases, additional statistical metrics, including the Z value, were used to assess the significance of the predictions [53]. The True Skill Statistic (TSS) compares sensitivity and specificity, providing a robust, prevalence-independent metric, with values close to 1 indicating excellent predictive capacity [54]. Before running MaxEnt, we optimized the model configuration using the ENMeval library [55] in R v.4.3 [56], selecting the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Supplementary Table S6). Using selected multipliers and feature types (e.g., linear, quadratic), we compared models based on a threshold-dependent approach and evaluated omissions and significance rates. Models with better predictions showed low omission and performed statistically better than random predictions [41]. Although we performed 10 replicas to calibrate our present model, only the best-fitted model ultimately ran above the critical values of TSS (>0.4) and AUC (>0.7).

The analysis of the niche was carried out separately for each species of *Atractus* using the R ecospat library [57]. The ecological space (E-space) was evaluated using an ambient PCA environment (PCA-env hereafter) framework and an ordination approach. Climatic variables were transformed into three-dimensional spaces defined by their main components. The superposition of niches between *A. erythromelas* and *A. meridensis* was calculated using Schoener's D statistics directly on the ecological niche space and modified Hellinger distances [58,59]. The value of D varies between 0, when the species do not

overlap in the ambient space, and 1, when the species compete within the same ambient space. We evaluated the conservation of niche (alternative = major, is decided, the superposition of a niche is more equivalent/similar than random) and niche divergence (alternative = smaller, i.e., niche overlap is less equivalent/similar than random) [57,60]. For each hypothesis, 1000 permutations were made. All these analyses were executed in R v.4.3 [56].

To account for the actual suitability of the habitat, we used vegetation cover data collected by Chacón-Moreno and Moral [61]. Next, we recalculated the resulting output of the models in each area, which were filtered in QGIS v.3.28 for values < 0.15 , and the potential distribution was refined in R v.4.3 [56] using the raster, sf, and dplyr libraries by excluding areas with unsuitable vegetation or land use. Finally, we used all available sighting records of the taxon to determine its extent of occurrence (EOO; minimum convex polygon encompassing all known occurrences, excluding inconsistencies) and area of occupancy (AOO; re-count of 2 km² grid cells identified with sighting records or with suitable habitat encircled by grid cells with sighting records within the EOO, [62]). Comparatively, we used the geospatial conservation evaluation tool to calculate the EOO and AOO metrics, which allowed us to evaluate the status of the focal species according to IUCN (geocat, <https://geocat.iucnredlist.org/> accessed on 8 March 2025) [63]. This open-source online tool is a web-based application developed by the IUCN Red List, allowing the visualization of georeferenced species data through a Google Maps interface [64].

3.7. Sample Source

We reviewed 292 specimens collected in the field during 2021 north of the Orinoco River, with scientific hunting permits and access to genetic resources processed and approved by the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under N° DGBD/2021/0095 to Luis Felipe Esqueda (LFE). The specimens were posteriorly deposited in the Museum of Zoology of the University of Concepción, Chile (MZUC). We also examined material deposited in the following collections: Laboratorio de Biogeografía, universidad de Los Andes, Mérida, Venezuela (ULABG); Museo de vertebrados de la universidad de Los Andes, Mérida, Venezuela (CVULA); Museo de la Estación Biológica Rancho Grande, Maracay, Aragua, Venezuela (EBRG); Museo de Ciencias Naturales de Caracas, Venezuela (MCNC); Museo de Historia Natural La Salle, Caracas, Venezuela (MHNLS); British Museum Natural History, London, United Kingdom (BMNH); Museum of Comparative Zoology, Cambridge, USA (MCZ); and American Museum of Natural History, New York, USA (AMNH).

3.8. Morphometric and Morphological Data

Previously, all available information about Venezuelan species was reviewed [5,6,8,9,65–79], as well as information about other related species from Colombia [80–84], Ecuador [85–89], and Brazil [90–93].

For each specimen evaluated, including the related species (e.g., *Atractus nemosophis*) [10], detailed descriptions of meristic and morphological traits were compiled across five informative categories: (1) scutellation of the head and body; (2) body and tail measurements, along with selected cephalic scutellation metrics; (3) coloration in life and/or preservation; (4) hemipenial morphology and diagnostic features; and (5) cranial osteology, with emphasis on the maxilla and dentition. The last three categories depended on the availability of material, although hemipenial and osteological data were included whenever possible.

With respect to scutellation, the terminology for head shields and dorsal, ventral, and subcaudal counts for the genus *Atractus* follows that indicated by Dowling [94], Savage [95], Hoogmoed [96], Myers [97], and Natera-Mumaw et al. [5].

Due to their taxonomic importance in the genus, some characters are defined as follows. The rostral scute in dorsal view can be defined as three states: condition (A), it is barely visible from above, with the apex of the scale contacting the internasals being narrow, rounded, or forming an obtuse angle, below the imaginary straight line between nostrils; the apical width is less than the distance between nostrils. Condition (B), something is visible from above, where the distal portion of the scale exceeds the imaginary line, generally narrow; the apical width is less than or equal to the distance between the nostrils, but does not exceed the internasal suture and condition (C), it is clearly visible, with the scale measured between its supralabial contacts, always forming an obtuse angle and above the imaginary straight line between the nostrils; the apical width is >0.5 times the distance between the nostrils, always greater than or equal to the internasal suture. Additional details, such as the presence or absence of a medial projection, vary from these three conditions of the rostral and are of taxonomic importance. The region that includes the snout has two conditions, weak or strongly compressed, which can be quantitatively verified if compared with the interocular distance and nostril between distance.

Contact between the first supralabial and the rostral in lateral view is classified as short to moderate when the contact length is less than or equal to the height of the supralabial and as ample when it exceeds half the height of the supralabial. Eye–loreal contact is considered narrow when it measures less than half the suture length between the prefrontal and postnasal and wide when it equals or exceeds half of that suture, approaching the width at the contact with the postnasal. Eye–prefrontal contact is classified as narrow when shorter than the prefrontal–postnasal suture and extensive when equal to or exceeding half of that suture length.

Here, we follow the proposal made by Natera-Mumaw et al. [5] for loreal scales. A short loreal (condition A) occurs when its length is less than HED and it is always in contact with two supralabials (e.g., *A. elaps*, *A. latifrons*, and *A. steyermarki*, [77,95,98]). A moderate loreal (condition B), occurs when its length is greater than HED, but ≤ 1.5 times HED; it may be in contact with two or three supralabial scales. In addition, there are two conditions: the first occurs when the loreal and supralabial margin that it contacts previously are less than the height of the loreal measured at the angle between the supralabial. The other state occurs when ALO is greater than the margin between the loreal and anterior supralabial in contact. Finally, an elongated loreal (condition C) occurs when its length is greater than 1.5 times HED; it is frequently in contact with three supralabials, and the margin between the loreal and anterior supralabial is greater than ALO (e.g., *A. torquatus*, *A. ochrosetrus*, and *A. heyeri*, [6]). However, exceptions exist with an elongated loreal: only two supralabials are in contact, similar to *A. emigdioi* and *A. multidentatus* (also see species from Ecuador; [88,89]). In each case mentioned, we can find that the margin between the loreal and anterior supralabial can be less or greater than ALO, and regarding condition B, there may be exceptional individuals with a loreal in contact with three supralabials (e.g., *A. ventrimaculatus*, LFE unpublished data).

Regarding the count of infralabial scales, they are considered infralabial up to the labial commissure, in contact with the last supralabial in lateral view. We do not consider small adjacent scales as infralabial; sometimes, one or two are in contact with the supralabial when the mouth is closed in lateral view. Therefore, this defines how many infralabials are in contact with the upper labials. Other case is sublabial scales have gone unnoticed and are confused in their descriptions. These scales have two states: no contract with each other or when in contact with each other, they separate the middle gular from the posterior contact with the genials. In the past, some authors have considered them a second pair of genials. In fact, many species in the genus *Geophis* often have this characteristic [97,99].

There are two scale types that are often problematic and whose definition remains unclear (we have personally observed intraspecific variability): gulars and preentrals. In the anterior ventral arrangement of the head, the genials are followed posteriorly by the gular rows, with the first gular contacting the genials and sublabials. These are followed by the preentrals, which are narrower than the ventrals, in the strict sense, and in lateral contact with the first dorsal rows behind the parietals. The remaining dorsal and ventral scales are well defined and counted according to established standards. Melo-Sampaio and Venegas [100], when describing a new species from Peru, reported the presence of apical pits, a feature absent in all other species known to us. Further detailed analyses (e.g., electron microscopy) will be necessary to confirm this observation, as it may represent a preservation artifact. All measurements and descriptions of cephalic scutellation were taken on the right side of the head, but they were verified on both sides.

Morphometric measurements and meristic counting were carried out through scaled images and using Image J v.1.54d software, as follows: **TL**, total length from the snout to the tip of the tail; **TaL**, tail length; **HL**, head length from the tip of the snout to the end of the parietal suture; **HW**, head width measured between labial commissures in dorsal view; **FL**, frontal length; **FW**, frontal width measured from the anterior portion between the eyes; **PSL**, parietal suture length; **PrSL**, prefrontal suture length; **ISL**, suture length between the internasals; **FRD**, distance between the frontal and rostral; **ID**, interocular distance; **IND**, internostril distance; **HED**, horizontal eye diameter; **END**, eye–nostril distance; **LOL**, loreal length; **HLO**, height of the loreal measured at the angle between two supralabials; **TEL**, first temporal length; **SupL**, length of the first supralabial in contact with the ocular orbit; **SLG**, suture length between the genials; **RoW**, rostral scale width measured between the supralabials; **RoDW**, distal width of the rostral measured between the nostrils; and **WMB**, width at the middle of the body.

Here, we considered dorsal and ventral coloration in life as the first distinguishing option among *Atractus* since some details are lost during preservation. The dorsal body pattern is divided into three sections: vertebral, paravertebral, and dorsolateral. Here, we differentiated dots or blotches arranged on the dorsum of the body, where dots occupy less than three dorsal scales and blotches extend to more than three scales; the presence of a cream border on dots or blotches is called margination. Regarding the transverse bands or stripes, these can be narrow (<dorsal scale) or wide (>dorsal scale), continuous or discontinuous, and arranged in any section of the dorsal region. If we consider the previous arguments, there are three basic patterns with variations: one uniform without spots, dots, or lines/bands, with one to three differentiated dorsal rows (clear in the preserved species and reddish, yellowish, or cream in the live species); another with spots or dots, where the spots or dots can be circumscribed, marginalized, or not; and one with one or more bands/bands along the body. The ventral surface of the body and tail consists of three patterns and their variants. The first is considered immaculate and may sometimes have small scattered dots or blotches, which do not occupy 15% of the scale surface. The second one has spots or dots arranged horizontally on each ventral scale, giving the impression of one or several discontinuous lines/stripes. This detail may be slightly evident toward the anterior part and intensifies toward the cloaca. The third one presents interspersed or irregular spots, forming blocks that occupy at least 60% of the scale. Sometimes, a wide line is observed in the medial part, and finally, the ventral region is completely stained, which is less common than in the other patterns.

The maxillary bone of one or several specimens was extracted (left sides) and posteriorly cleaned using KOH 3% for 10 min and distilled water for 10 h. Then, scale photos were taken using an Olympus E620 camera (Olympus, Tokyo, Japan) fixed to a brand stereo-

scopic magnifying glass. In the remaining specimens examined; after cleaning the maxillary bone of tissue, the arranged teeth or sockets were counted to eliminate the erroneous count.

The extraction and preparation of the hemipenial organs followed the procedures described by Manzani and Abe [101], as modified by Pesantes [102] and Zaher [103] for snakes. Passos et al. [104] replaced the KOH indicated in Pesantes [102] with distilled water. Here we applied both procedures, but in different ways, which allowed for a better extension of the organ according to its condition. First condition, when the hemipenes are not everted partially or totally at the time of specimen preservation, but are instead fixed with formaldehyde or ethanol. In this case, the organ offers much more rigidity, depending on the amount of formaldehyde injected; generally, many museum specimens were not injected (personal observation, LFE); the other condition is that the hemipenes were everted during the preservation of the specimen. Recovering the elasticity of the organ is the most important step because, later on, using a burnisher with a spherical tip, the tissue can be moved until its maximum extension is achieved. For this reason, three immersion stations were established as follows: the first with distilled water at 60 °C for 2–3 min, the second with 3% KOH for one minute, and the third with distilled water at room temperature for 10–30 min. If the timing was appropriate, the organ could be observed with a transparent amber coloration; otherwise, steps 1 and 3 were repeated. Before using the burnisher to extend the tissue, it is recommended to inject a glycerin–water solution into the tissue at the base connected to the muscle. This ensures that, upon introduction of the burnisher, smooth lubrication allows retraction movements, facilitating full observation of hemipenial eversion. Once eversion was achieved, we applied vaseline or glycerin–water, secured the base, and immersed the organ in a solution of 70% ethanol with alizarin red or a suitable dye for approximately 10 min. Finally, we stored the specimen in an Eppendorf tube with glycerin. With respect to the calcareous structure’s ornamentation, we followed Uzzell [105] and Harvey and Embert [106]. The qualitative and quantitative descriptions of the hemipenial characters followed Zaher [103], Passos et al. [104], Uzzell [105], Dowling and Savage [107], Schargel and Castoe [108], Myers and Cadle [109] Zaher and Prudente [110], Myers and McDowell [111]. Although the term “diastema” has been considered in the past for this group of snakes, it is a distinctive character [81–83]. We will discuss space and/or reduction between the last teeth, following that indicated by Oliveira et al. [112], who recognized that goo-eating dipsadines do not present diastema.

3.9. Statistical Processing (Comparative Data and Geometric Morphometrics)

To evaluate the specific status of *A. erythromelas* and *A. meridensis*, including the existence of cryptic species using morphological–morphometric evidence and coloration, we defined four OTUs (Operational Taxonomic Units), previously obtained from our phylogenetic analyses: OTU 1 = *A. erythromelas*, populations limited to the middle-upper basin of the Chama River, at the level of the city of Mérida and its surroundings between the Sierra Nevada and the Sierra de la Culata (right–left margin); OTU 2 = *A. erythromelas*, populations limited to the middle-upper basin of the Chama River, at the level of the town of Mucurubá and its surroundings; OTU 3 = *A. meridensis*, populations from the Santo Domingo River basin; and OTU 4 = *A. meridensis*, populations from the Boconó and Motatán-Carache river basins, Trujillo state.

We used the statistical environment R v. 4.3.1 [56] and Excel software XLSTAT v. 2019 2.2 [113] to perform all statistical analyses. To this end, we defined five procedures: P1 = the range of variations (minimum and maximum), mean ($\bar{X}$), and standard deviation (SD) were calculated for each OTU specimen. We checked and removed outliers from our data using the dplyr library in the R environment [114]. P2 = statistical analysis of differences between OTUs and sexes, evaluating through normality tests (Kolmogorov–Smirnov)

or checking the data normality by the Shapiro–Wilk test to determine whether a parametric (ANOVA) or nonparametric (Kruskal–Wallis) analysis should be applied. Subsequently, Levene’s test was used to verify the homogeneity of variances between sexes [115]. Depending on the results of these tests, the appropriate analysis was selected to compare the differences between sexes within each species. Finally, to explore differences between species and sexes, an analysis of variance (ANOVA) with the interaction between species and sex was performed, followed by a Tukey post hoc test to identify significant differences between species and sex combinations. Finally, P3 = a discriminant analysis (DFA, [116]) to evaluate the separability of OTUs by calculating Mahalanobis distances [117]. We used the following characters in the statistical analyses: ventral scale count, subcaudal scale count, total length of the body (TL), tail length (TaL), internasal suture length (INTL), broad apical margin of the rostral between the nostrils (BMAros), loreal length (LOL), loreal height (LOA), height of the first supralabial (HSup), frontal length (FL), and ventral pattern of the body (VP).

Without previously defined OTUs for *A. erythromelas* and *A. meridensis*, we built two-dimensional surface models of the head using 41 specimens out of the 109 examined (many were excluded because of missing data, juvenile status, or head damage; see Supplementary Table S3). We aimed to quantify aspects of the head shape in dorsal view, from the frontal to the rostral scute (*A. erythromelas*, $n = 21$; *A. meridensis*, $n = 21$; Supplementary Table S7), as well as the proportionality and extension of the rostral (*A. erythromelas*, $n = 14$; *A. meridensis*, $n = 22$; Supplementary Table S7), using a geometric morphometric approach with the geomorph package in R [118]. All scale photographs were taken with an Olympus E620 camera (Olympus, Tokyo, Japan) mounted on a Leica-brand stereoscopic microscope (Leica, Wetzlar, Germany). Anatomical landmarks were placed at the junctions of the scales using ImageJ v1.54f. Coordinates were organized in Excel into individual CSV files per specimen, and TPS files were generated using geomorph v4.1 in R v4.3 [56]. The landmarks defined here are optimal for detecting differences in the proportionality and extension of the frontal, internasal, and rostral scales, which had not been evaluated in *Atractus* before. Size and shape data were obtained from the Cartesian coordinates of the landmarks using Procrustes-based geometric morphometrics [119,120]. The procedure for separating shape from size data is known as Procrustes superimposition [121,122]. Size was estimated as centroid size (CS), which is the square root of the sum of squared distances from each landmark to the centroid. Shape data were obtained in three steps: (A) standardization of size by dividing the landmark coordinates by the centroid size of each specimen; (B) removal of translational variation by superimposing all specimens; and (C) minimization of rotational differences via least-squares minimization of the sum of squared distances between corresponding landmarks [122]. All procedures were performed using the geomorph package in R v4.3 [56].

To detect shape differences related to sex, we performed a multivariate Procrustes analysis of variance (Procrustes ANOVA) using the `procD.lm()` function. This analysis evaluates the effect of sex on shape using random permutations (usually 999 or more), allowing robust statistical inference even under non-parametric distributions of morphological data [123–125]. We also conducted a morphological disparity analysis to compare Procrustes variances between the sex categories, using the `morphol.disparity()` function, and a phenotypic trajectory analysis to describe, compare, and visualize differences between the species [126]. A principal component analysis (PCA) was applied to the aligned coordinates to explore overall morphological variation among individuals and visualize potential groupings by sex or species [127]. Mesh deformations and deformation vectors (warp grids) were also used to graphically represent shape change patterns. Additionally, a canonical variates analysis (CVA) was performed to graphically represent interspecific variation,

as this technique assumes similar variance–covariance structures between groups and generates canonical axes (LDs) to facilitate visualization and statistical evaluation of morphological segregation [126,128]. Finally, Mahalanobis distances between group centroids in morphometric space were calculated—this robust multivariate measure accounts for both variance and covariance and is widely used to assess morphological separation [129,130]. To test the significance of these distances, a permutation test ($n = 10,000$) was conducted, comparing observed distances to a randomly generated null distribution.

4. Results

4.1. Phylogenetic Approach

The final concatenated molecular dataset consists of 3535 bp corresponding to three mitochondrial genes (136 sequences in 16S: 525 bp, 130 informative sites, 45 singleton, 350 conserved sites, missing data 0.76–30%; 97 sequences in Cytb: 897 bp, 425 informative sites, 71 singleton, 401 conserved sites, missing data 0–34%; and 111 sequences in ND4: 713 bp, 363 informative sites, 44 singleton, 323 conserved sites, missing data 0–29%) and two nuclear genes (79 sequences in NT3: 521 bp, 91 informative sites, 50 singleton, 375 conserved sites, missing data 0–25%; 63 sequences in RAG-1: 879 bp, 90 informative sites, 95 singleton, 694 sites preserved, missing data 0–18%). It includes 172 samples/terminals of *Atractus* and 19 samples/terminals as outgroups (Boidae = 2 spp., Viperidae = 4 spp., Colubridae = 5 spp. and Dipsadidae = 8 spp.).

The molecular phylogenetic trees resulting from the ML (Figure 1) and BI (Figure 2) analyses are consistent and similar in topology, suggesting that the data provide a robust phylogenetic signal recognized by both methods. The monophyly of *Atractus* was well supported in the ML analysis, where it was divided into two major lineages, while in the BI topology, it resulted in moderate support (>0.8). Our Bayesian analysis generally showed moderate or strong support within the nodes in *Atractus*, except for some that had low support (<0.5). Differences in support between ML and IB may stem from the way these methods handle uncertainty and evolution models [131–133]. Here, posterior probability values above 0.95 were considered strongly supported, values between 0.7 and 0.95 were moderately supported, and values below 0.7 were weakly supported.

In our phylogeny, the mimetic clade of Andean sleepyheads, *Atractus erythromelas*, was recovered as the sister species of *A. meridensis* and *Atractus nemosophis*, with strong support in both ML (100%) and BI ($pp = 0.94$) analyses. Although *A. ochrosetrus* and *A. ventrimaculatus* are sister species (ML = 100% and BI = 0.95) from the cordillera de Mérida, both are found nested with *A. trilineatus*, a species from the eastern stretch of the cordillera de la Costa and south of the Orinoco River (ML = 100% and BI = 0.93). However, the Mérida–Trujillo Andean clade was recovered as monophyletic, with strong support in ML (100%) and moderate support in BI (0.89), constituted by *A. emigdioi*, *A. taphorni*, *A. mariselae*, *A. mijaresi*, *Atractus xaxi*, *A. erythromelas*, *A. meridensis*, and *Atractus nemosophis*.

Uncorrected interspecific genetic p-distances are presented for Cytb (Supplementary Tables S8 and S9) and ND4 (Supplementary Tables S10 and S11). In the case of Cytb, mean genetic distances of the Venezuelan mimic species range from 0.072887 ± 0.009654 (*A. erythromelas* vs. *A. meridensis*) to 0.078595 ± 0.009556 (*A. erythromelas* vs. *Atractus nemosophis*) and 0.059436 ± 0.009067 (*A. meridensis* vs. *Atractus nemosophis*). The sister species *A. ochrosetrus* and *A. ventrimaculatus* possess a mean genetic distance range from 0.050887 ± 0.008151 . Meanwhile, the uncorrected p-distances between each taxon/lineage within *Atractus* range from 1.05% (*A. snethlageae* vs. *A. pachacamac*) to greater than 17% (*A. esepe* vs. *A. carrioni*). For ND4, the mean genetic distances vary from 0.05393 ± 0.00933 (*A. erythromelas* vs. *A. meridensis*) to 0.06073 ± 0.01055 (*A. erythromelas* vs. *A. nemosophis*) and 0.04197 ± 0.00896 (*A. meridensis* vs. *Atractus nemosophis*); in *A. ochrosetrus* and

A. ventrimaculatus, the average is 0.06851 ± 0.01075 . At the genus level, the mean genetic distances average 1.1% (*A. snethlageae* vs. *A. pachacamac*) and 17% (*A. ventrimaculatus* vs. *A. vittatus*).

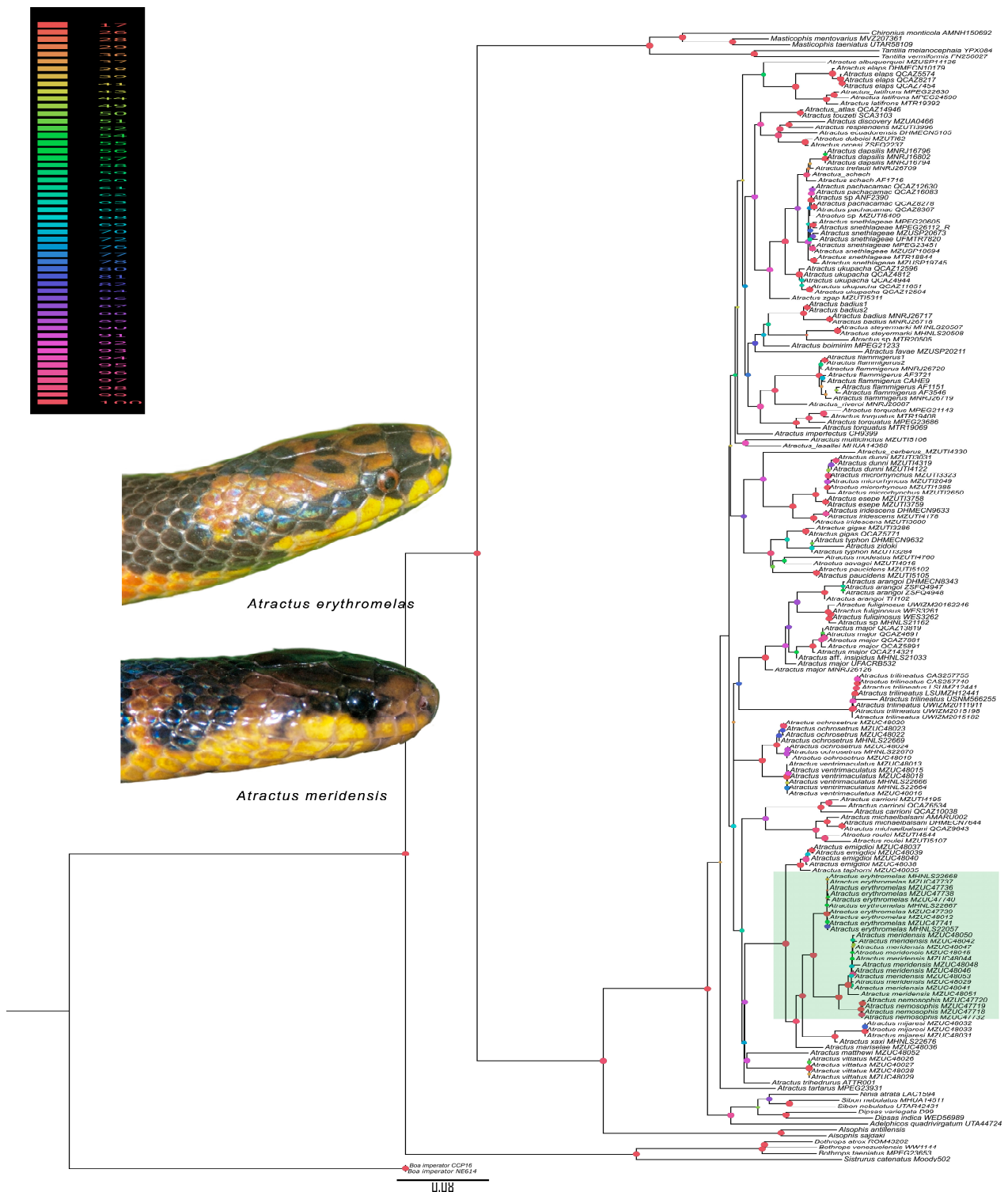


Figure 1. Maximum likelihood (ML) tree estimated with Iqtree, showing the relationships among some South American species of *Atractus*. Information on bootstrap values >70% in ML is shown on the left side. The green box delimits the species under discussion.

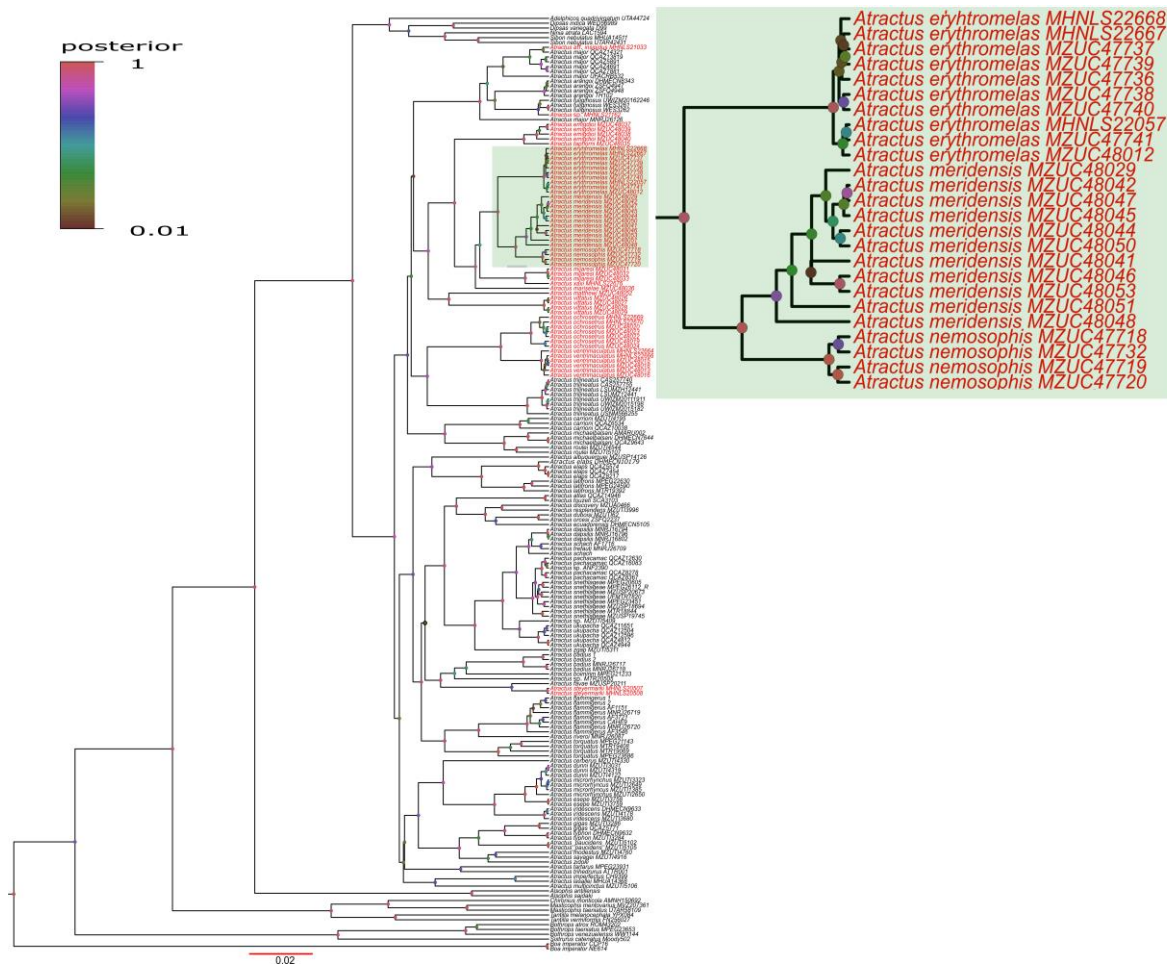


Figure 2. Bayesian inference tree using Metropolis-coupled MCMC for estimation under the topology. Best posterior probability values symbol >0.95 (legend). Bars on nodes represent the 95% credibility interval of divergence times. Terminals in red refer to the material incorporated by us. Highlighted green square species under discussion.

4.2. Ecological Approach

According to the consistency and quality of environmental modeling for the species studied, the final ROC curve of the model for each of the scenarios showed AUC values between 0.985 and 0.988 for the training data and between 0.905 and 0.908 for the test data (Supplementary Table S12), indicating that the Maxent model effectively predicted the distribution with highly suitable environments for *A. erythromelas* (Figure 3A) and *A. meridensis* (Figure 3B). In comparison, according to the statistics of True Skills (TSS) and the operational characteristics of reception (ROC), they obtained values above 0.72–94 and 0.73–0.5, respectively (Supplementary Table S13). The projection for both taxa for the LGM 21 Kya climate indicated that the distribution of adequate environments for this species could have been more limited at the time (Figure 3C,D), unlike the Pliocene, 3.2 Myr, during which an expansion of their distribution area is observed (Figure 3D,E). In the current scenario, *A. erythromelas* occupies an area of 2126.8 km² and is mostly distributed in the montane rainforest of the Northern Andes and intervening areas, with a suitable area of 1074 km² (Supplementary Table S14). Meanwhile, *A. meridensis* occupies an area of 3029.1 km² and is mostly distributed in the montane rainforest of the Northern Andes, with a suitable area of 1503.8 km² (Supplementary Table S14). Our sorted and verified data suggest that the altitudinal range of *A. erythromelas* varies between 1160 and 2684 m (494.1 km² would correspond to moderate-high suitability areas between 2000 and

2500 m asl), and *A. meridensis* occurs between 1077 and 3275 m (666 km² would correspond to moderate–high suitability areas between 1500 and 2500 m asl).

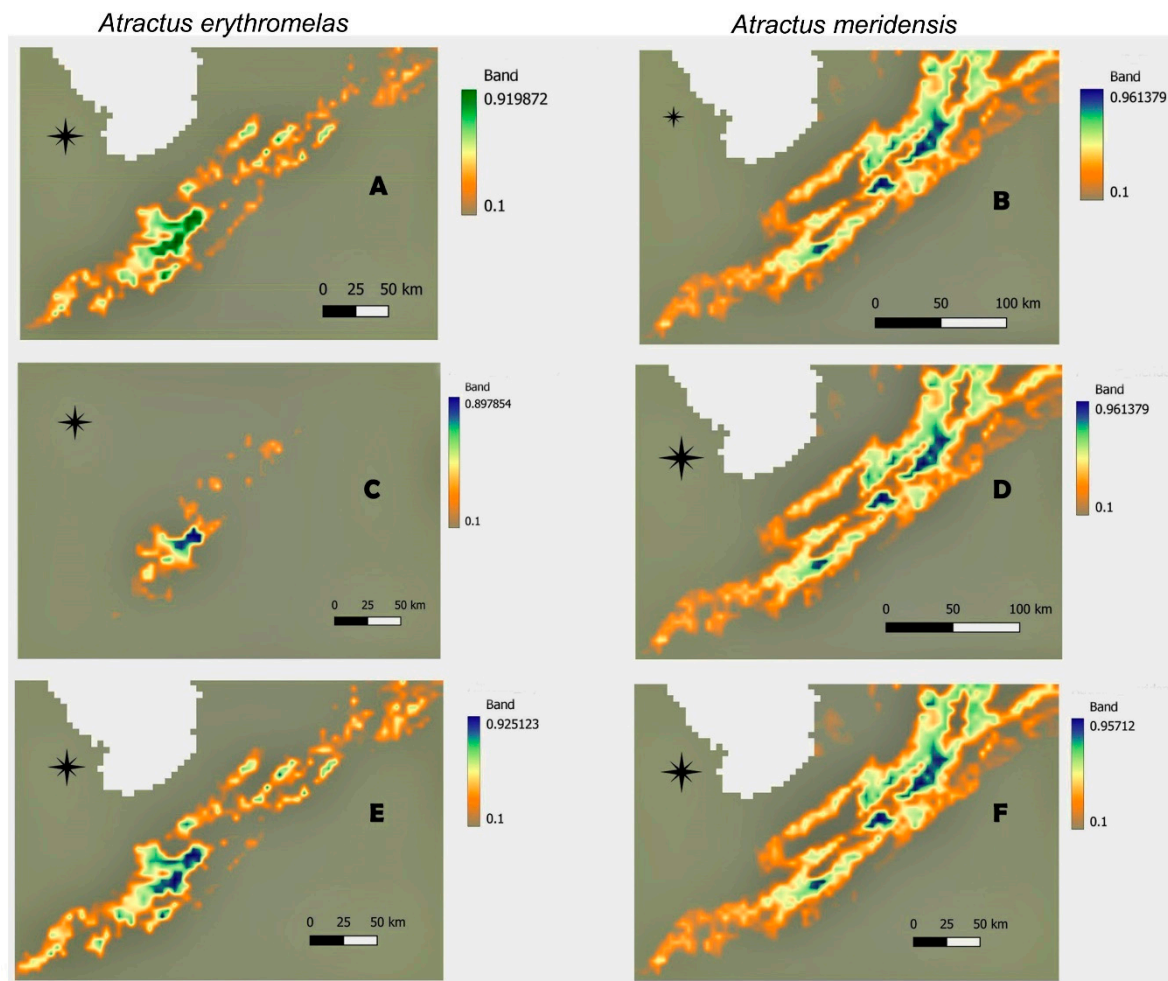


Figure 3. Geographic projection of the ecological niche model built for *A. erythromelas* and *A. meridensis* in the climatic scenarios explored. (A,B) Present scenery; (C,D) LGM scenery, 21 Kya, and (E,F) Pliocene scenery, 3.2 Myr. The environmental suitability predicted is depicted without a defined umbral.

In the Maxent model for each scenario, the Jackknife method was used, and the results show the weight of different environmental factors that affect the suitability of the habitat for *A. erythromelas* and *A. meridensis* (Supplementary Table S15). On the other hand, one of the main determining environmental factors in the potential distribution in the three scenarios was the Bio_1 variable, in *A. erythromelas* with 48.1–65.9% (Supplementary Table S16) and in *A. meridensis* with 60.9–66.9% (Supplementary Table S16).

The principal component analysis (PCA) revealed that the first three components together explain more than 90% of the variation in the bioclimatic variables across all predicted scenarios (Figure 4). Regarding the three climatic scenarios, no significant differences in the ecological niche were found between the present and the Pliocene, whereas significant differences were detected under the LGM scenario (PERMANOVA p -value = 0.001; Supplementary Table S17). The Schoener's D and Hellinger's I indices indicate a high degree of niche overlap under present-day conditions, a moderate overlap during the Pliocene, and a marked niche divergence during the LGM. The overlap calculated between the ellipses for each scenario confirms that during the LGM, only ~10–14% of the climatic volume was shared between taxa. This divergence is further supported by a Jaccard index

of 0, suggesting completely dissimilar niche occupancy (Supplementary Table S18). Moreover, the ellipse constructed from the observed climatic distribution data of *A. meridensis* is notably larger, suggesting a broader climatic niche compared to that of *A. erythromelas*. For the LGM scenario specifically, the climatic space occupied by *A. meridensis* is primarily influenced by variables associated with mean annual temperature and precipitation during the warmest quarter (Supplementary Table S18).

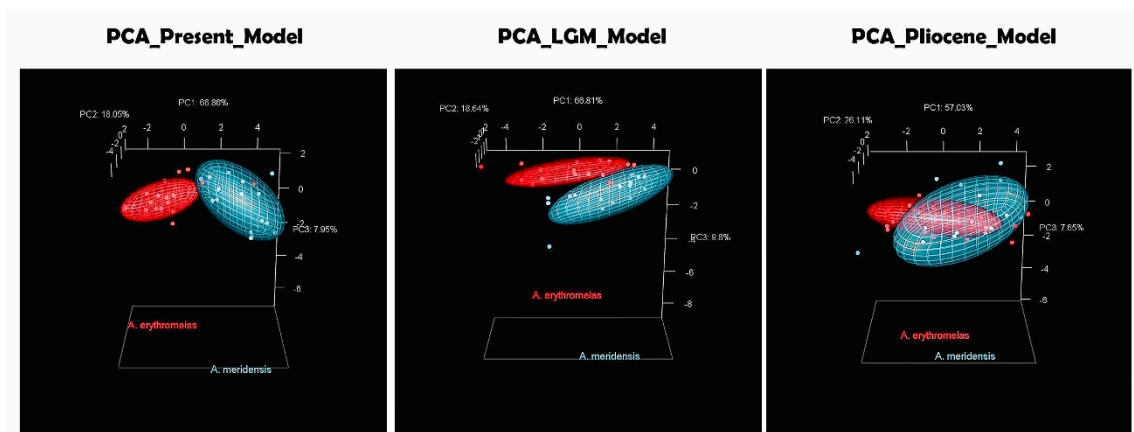


Figure 4. The orthogonal projection of the first three principal components constructed from climatic characterizations of the geographic distribution of *A. erythromelas* and *A. meridensis* for each of the modeled scenarios. The points correspond to the localities characterized based on 6–7 bioclimatic variables, and the ellipses correspond to the volumes built from the climatic niches of *A. erythromelas* (red ellipse) and *A. meridensis* (blue ellipse). The percentage of explained variance accounted for by each principal component is depicted.

According to our ENM for the current scenario, *A. erythromelas* has an EOO of 466.979 km² and an AOO of 116 km² (geocat EOO = 469.755 km² and AOO = 120 km² to 2 km; Supplementary Table S19), while *A. meridensis* has an EOO = 3093.19 km² and an AOO = 68 km² (geocat EOO = 3113.344 km² and AOO = 76 km² to 2 km; Supplementary Table S19).

4.3. Morphological–Statistical Approach

For *A. erythromelas*, the ventral scale count showed a significant difference between sexes (ANOVA, $p < 0.001$), indicating sexual dimorphism. Subcaudal scales also differed significantly between sexes (Kruskal–Wallis, $p = 0.00011$). In contrast, total length (TL) did not show a significant difference (ANOVA, $p = 0.06725$), nor did tail length (TaL) (Kruskal–Wallis, $p = 0.39377$). For *A. meridensis*, the ventral scale count showed a significant difference between sexes (ANOVA, $p < 0.001$), as did the subcaudal scales (ANOVA, $p < 0.001$). TL showed no significant difference between sexes (ANOVA, $p = 0.10212$), whereas TaL was significantly different (ANOVA, $p < 0.001$), with males having longer tails. When comparing *A. meridensis* and *A. erythromelas*, differences in these meristic characters were not significant overall (ANOVA, $p = 0.784$), suggesting that species alone did not explain the variation. However, the interaction between sex and species was highly significant ($p = 3.14 \times 10^{-5}$), indicating that sexual dimorphism varies between species. In particular, tail length in *A. meridensis* males was significantly greater than in *A. erythromelas* males ($p = 0.0038$), suggesting this trait may be taxonomically informative (boxplot; Supplementary Table S20).

Our evaluation found differences between sexes for the species *A. erythromelas* and *A. meridensis* in some morphometric variables, such as the ventral and subcaudal scales, where the p -value was significant. However, there were no significant differences in variables such as TL and TaL for some species. The differences were not uniform be-

tween species. In *A. erythromelas*, there were differences in almost all variables, while in *A. meridensis*, some variables showed differences, while others did not. So, there were significant differences between the sexes within the species, but the magnitude and presence of these differences varied according to the species and the morphometric variable (Boxplot, Supplementary Table S20).

Our analysis revealed significant sexual dimorphism in *A. erythromelas* and *A. meridensis* for certain morphometric traits, particularly the ventral and subcaudal scale counts. However, not all variables showed significant differences, and the patterns varied between species. In *A. erythromelas*, most variables displayed sexual differences, while in *A. meridensis*, the differences were limited to specific traits. This indicates that while sexual dimorphism is present in both species, the extent and nature of this dimorphism depend on the species and the specific morphometric variable being considered.

Discriminant analyses performed for *A. erythromelas* (seven variables, n males = 12, n females = 9) and *A. meridensis* (seven variables, n males = 9, n females = 20) (Supplementary Table S21) showed that the taxa differ. The first two linear discriminants accounted for 94.35% (46.47% and 47.88%, respectively) of the total variance (Figure 5A). In addition, the disjunctive set of populations of both species (OTU) overlap, which is less evident between the OTU3 and OTU4 populations corresponding to *A. meridensis* (Figure 5B).

4.3.1. Spatial Morphometry

For both *A. erythromelas* (MA₁ and MA₂) and *A. meridensis* (MA₁ and MA₂), the measurement error was assessed using a Procrustes ANOVA on all landmarks from five individuals per species, each digitized twice (i.e., two replicates per individual). The analysis yielded significant *p*-values (*p* = 0.002997 ** for *A. erythromelas* and *p* = 0.000999 *** for *A. meridensis*), indicating that within-species variance was minimal compared to the variance between individuals. Specifically, 96.2% of the shape variation in *A. erythromelas* and 97.1% in *A. meridensis* was attributed to differences among individuals. Similarly, the repeatability values [126] were high, at *R* = 0.9385 for *A. erythromelas* and *R* = 0.9546 for *A. meridensis*, supporting the accuracy and reliability of our landmark configuration in capturing true biological shape variation. In contrast, the sexual dimorphism analysis showed no statistically significant differences in head and rostral shape between males and females in either species. However, the result for *A. erythromelas* may suggest a potential trend, although it was not statistically significant (Supplementary Table S22).

Our geometric morphometric analysis of dorsal head scalation (MA₁) and rostral scute projection in frontal view (MA₂) revealed significant morphological differences between *A. erythromelas* and *A. meridensis* (Figure 6). A principal component analysis (PCA) was used to explore overall shape variation, which revealed a clear separation between the two species along the first two principal axes, explaining the majority of the variation (59.06% in MA₁ and 78.61% in MA₂). Although some degree of overlap was present, the centroid positions of each species occupied distinct regions of the morphospace, suggesting consistent differences in head shape. These interspecific differences were statistically confirmed by a PERMANOVA, which detected significant variation between species (*p* < 0.05), indicating that head shape differences are systematic rather than due to random variation (Supplementary Table S23). Additionally, ANOVAs on the principal components revealed significant differences in specific shape variables between the two taxa. Morphological disparity analysis (based on Procrustes variance) showed that *A. erythromelas* exhibited greater intraspecific shape variation than *A. meridensis*, with an absolute difference of 0.00118864 in morphological variance. This difference was statistically significant (*p* = 0.03996), suggesting a higher degree of head shape diversity within *A. erythromelas* (MA₁). A Canonical Variate Analysis (CVA) further emphasized the separation between the species, achieving

high classification accuracy. The canonical axes demonstrated that head shape effectively discriminates between *A. erythromelas* and *A. meridensis*, supporting the presence of diagnostic morphological patterns (differences reflected in frontal, internasal, and rostral). Finally, the Mahalanobis distance between species was high and statistically significant, reinforcing the notion of clear interspecific divergence. This measure, which accounts for covariation among shape variables, confirms that the observed differences reflect true morphological divergence rather than stochastic variation (Supplementary Table S23). Consequently, the shape and extent of the internasals and the rostral are distinctive characteristics in both species. In fact, the extent of contact between the rostral and the first supralabial is broader in *A. meridensis* than in *A. erythromelas*.

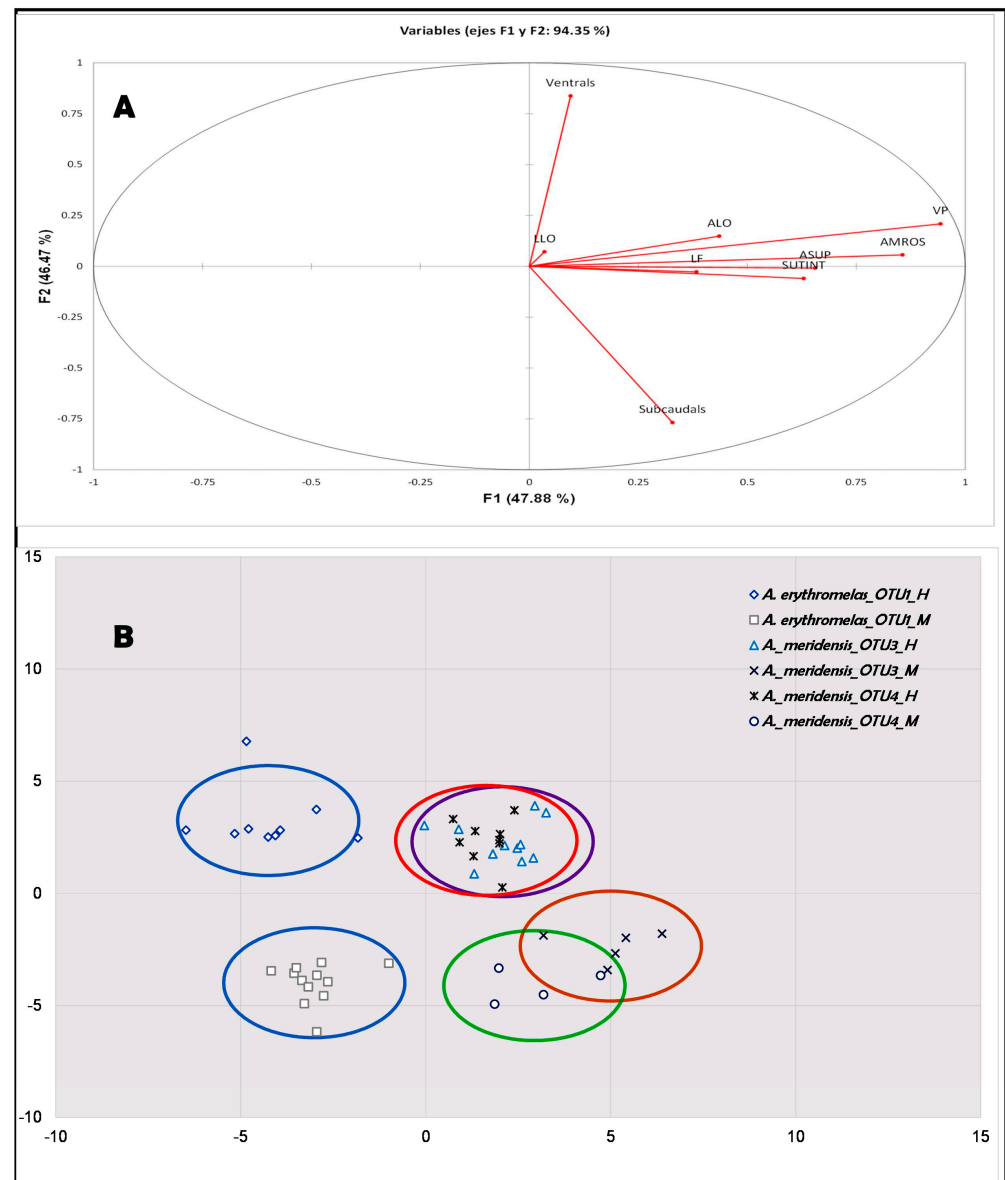


Figure 5. (A) Contribution of each variable to the first two principal coordinates: ventrals, subcaudals, VP = ventral pattern, AMROS = maximum width of the rostral between the nostrils, Asup = height of the first supralabial, SUTINT = long internasal suture, LF = long frontal, ALO = height of the loreal measured anteriorly, and LLO = length of the loreal. (B) Discriminant analysis scatter diagram (DA), produced using XLSTAT software, for *A. erythromelas* and *A. meridensis*. In OTU, H = female and M = male.

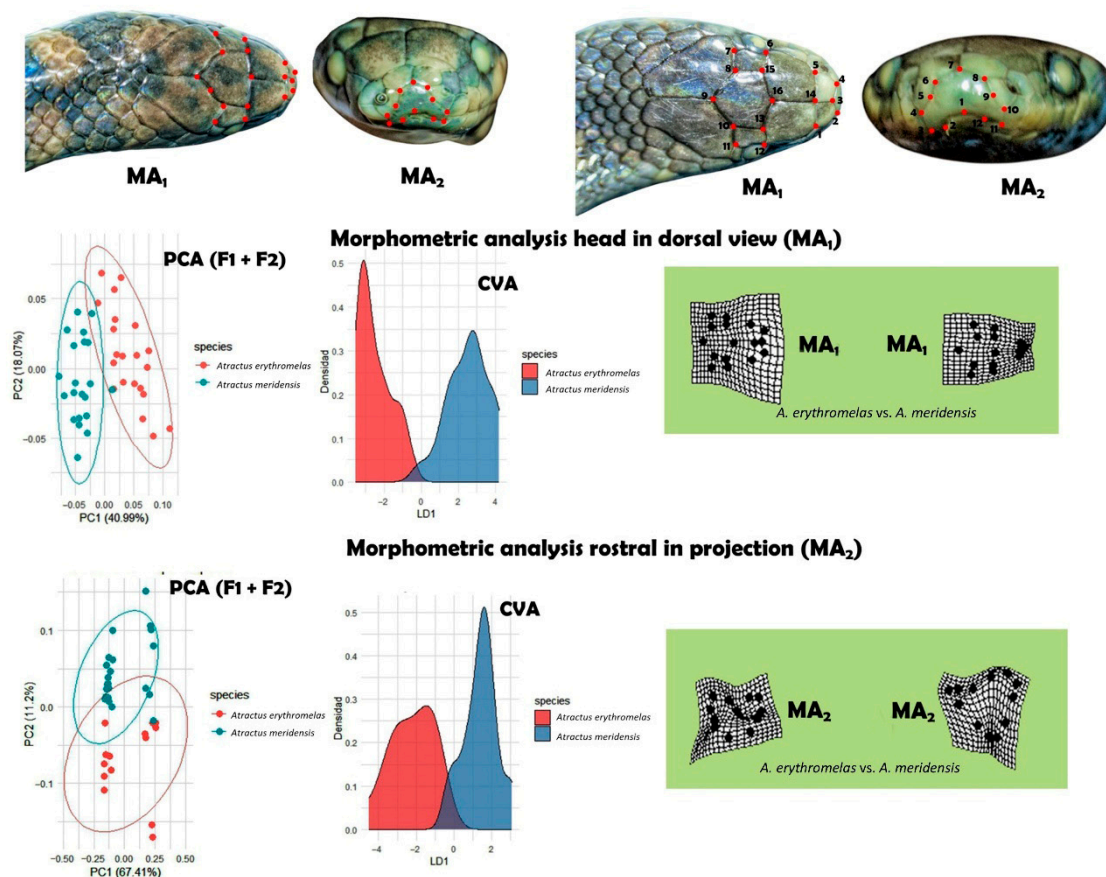


Figure 6. Projections of adult individuals of *A. erythromelas* (red dots) and *A. meridensis* (turquoise blue dots) on the two PCA variation axes and on a single CVA axis, using morphometric measurements. MA1, morphospace based on cephalic scales in dorsal view (frontal to rostral); MA2, extension and projection of the rostral scale in frontal view.

4.3.2. Systematic Overview

Historical background between *Atractus erythromelas* Boulenger, 1903, and *A. meridensis* Esqueda and La Marca, 2005.

Without defining a type (syntype material, [134] (p. 73.2)), Boulenger [65] (pp. 483–484) described *A. erythromelas* from “Merida, Venezuela, at an altitude of 1600 m”. His original description indicates the following: small rostral, just visible from above; seven supralabials, the third and fourth in contact with the eye orbit; three infralabials in contact with geneials; scales in 17 rows (obviously referring to the dorsal ones); 159–168 ventral scales in males and 171–186 in females; 28–31 subcaudal scales in males and 23–25 in females; and highly variable coloration. Roze ([66] (p. 106)) refers to the species, noting its variable color pattern consisting of black and red transverse bands, but included it among the species with 15 dorsal scale rows at midbody, posteriorly indicated by Roze ([67] (pp. 80–81)) and Peters and Orejas-Miranda [135], respectively. In their review of *Atractus* from the cordillera de Mérida, Esqueda and La Marca [8] considered that all the specimens examined with 15 dorsal scale rows at midbody from the city of Mérida and its surroundings corresponded to *A. erythromelas*. Although these latter authors did not mention Boulenger’s original description, they did refer to Roze [66], who apparently reviewed the material from the British Museum. However, in that same work, the authors described *A. meridensis*, whose type locality is described as “a 1 Km del puente sobre el río Santo Domingo en la vía principal desde La Mitisús hasta Santo Domingo, y a 500 m del cruce de acceso a la Población de Las Piedras; 08°52′45″ N, 70°39′09″ W”.

Recently, Passos et al. [6] redescribed *A. erythromelas*, noting that the species may present 17 or 15 dorsal scale rows at midbody. Based on this variation, and assuming the absence of diagnostic differences in *A. meridensis*, the authors proposed its synonymy with *A. erythromelas*. However, this decision lacks both morphological and molecular support. Moreover, their study did not include sufficient material from populations near the type localities (particularly for *A. meridensis*), nor did it consider diagnostic coloration patterns in life. Additional issues arise from their treatment, which require clarification. For instance, Passos et al. ([6] (p. 23)) designated a lectotype as the “adult female specimen, BMNH 1946.1.716, collected by S. Briceño in the municipality of Mérida (08°36′ N, 71°09′ W; ca. 1600 m), state of Mérida, Venezuela”. However, this lectotype designation presents several issues. First, Boulenger did not explicitly designate a type but provided measurements (“total length 430 mm; tail 40 mm”) for a single specimen among the syntypes. The specimen illustrated by Passos et al. [6]: Figure 14A, measures 351 mm in total length and 40 mm in tail length, with no scale provided, making verification difficult. Additionally, the museum labels were removed, limiting specimen recognition. Second, the original description refers to “Mérida, Venezuela,” which, at the time, could indicate either the city or the state, and Passos et al. [6] incorrectly cited the “municipality of Mérida” instead of the Libertador municipality [136]. According to ICZN [134] (p. 74.4, 74.7); recommendations 74A, C, E, these points suggest that the lectotype assignment was not strictly correct. While the stability of *A. erythromelas* is unaffected, the synonymy of *A. meridensis* proposed by Passos et al. [6] lacks sufficient justification, and the removal of the museum label contravenes Recommendation 74C.

Currently, the taxonomic status of *A. erythromelas* is well established [134] (p. 75.2). In contrast, the possible resurrection of *A. meridensis* as a distinct species requires further clarification regarding the distribution and geographic boundaries of both taxa, as well as a better understanding of the historical and current biogeographic patterns from their type localities. Passos et al. [6] designated one of the syntypes from Boulenger’s description as a lectotype (BM 1946.1.715), which establishes its type locality following [134] (p. 76.2). However, this decision also highlights a potential ambiguity: the locality “Mérida” [65] may refer either to the city of Mérida (founded in 1558) or to the state of Mérida (created in 1861 and officially recognized in 1874) [137]. Given this uncertainty, the most coherent and practical step to clarify the geographic distribution of this taxon would be the designation of a neotype under articles 75.3.1, 75.3.5, and 75.3.6 of the [134].

Atractus erythromelas BOULENGER, 1903

(Figures 7–10)

Atractus erythromelas—Boulenger [65]; *Annals and Magazine of Natural History* 11: 483.

Atractus erythromelas—Passos et al. [6]; *South American Journal of Herpetology*, 32 (Special Issue): 1–123.

Lectotype—Adult female, BMNH 1946.1.716, collected by S. Briceño at the municipality of Mérida (08°36′ N, 71°09′ W; ca. 1600 m asl), state of Mérida, Venezuela, by present designation (Figures 14A,B and 15) [6].

Paralectotypes—Adult male (BMNH 1946.1.715) and female (BMNH 1946.1.717; Figures 14C,D and 16) with the same data as the lectotype [6].

Neotype—Adult female, MZUC 47736 (field number LFE 145). Collected by Luis Felipe Esqueda, Santos Bazó, and Alexis Peña, 4 July 2021, deposited in the Zoology Museum of the Faculty of Natural and Oceanographic Sciences, University of Concepción, Chile (MZUC). Nearly Truchicultura Monterrey, El Valle-La Culata road, Mérida, Mérida state, Venezuela; altitude 2250 m asl; 8°40′27.94″ N and 71°6′47.15″ W.

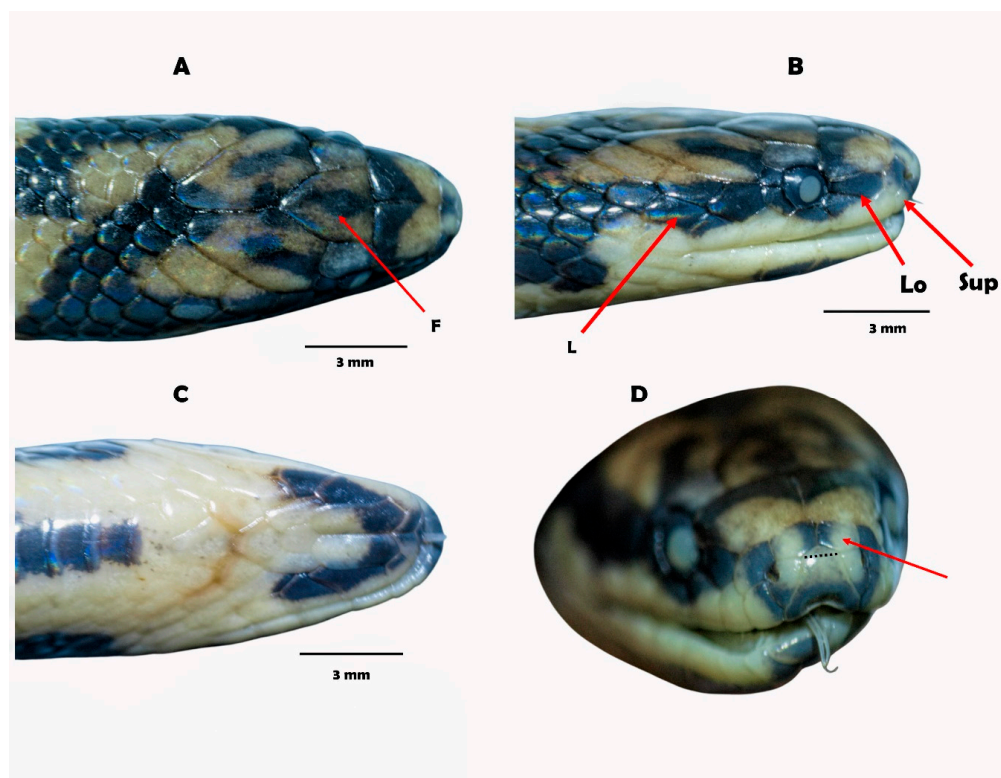


Figure 7. Adult female *A. erythromelas* individual, MZUC 47736. Dorsal view (A), lateral view (B), and ventral view of the head (C). Finally, frontal view of the rostral scale (D). Lo= loreal scale; Sup = first supralabial.

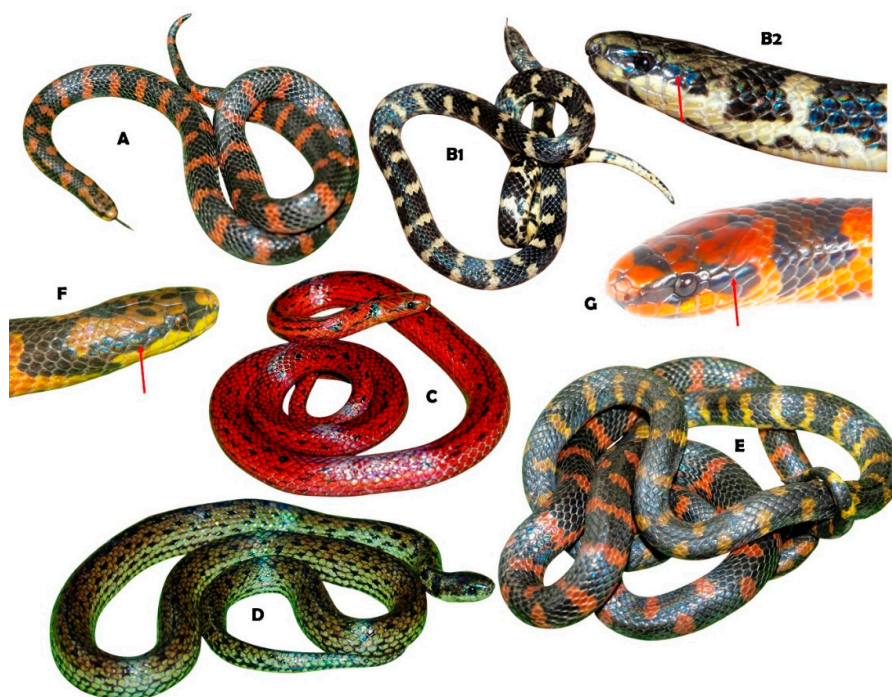


Figure 8. Dorsal patterns in life of *A. erythromelas*. (A,B) Bicolor, red-or-white and black crossbands along the body; (C) not bicolor, crossbands absent; (D) not bicolor, hazelnut or yellowish-hazelnut background; (E) bicolor, yellowish-green and black crossbands along the body; (F,G) black horizontal band behind the eyes present. Photos ©Luis Felipe Esqueda (LFE).

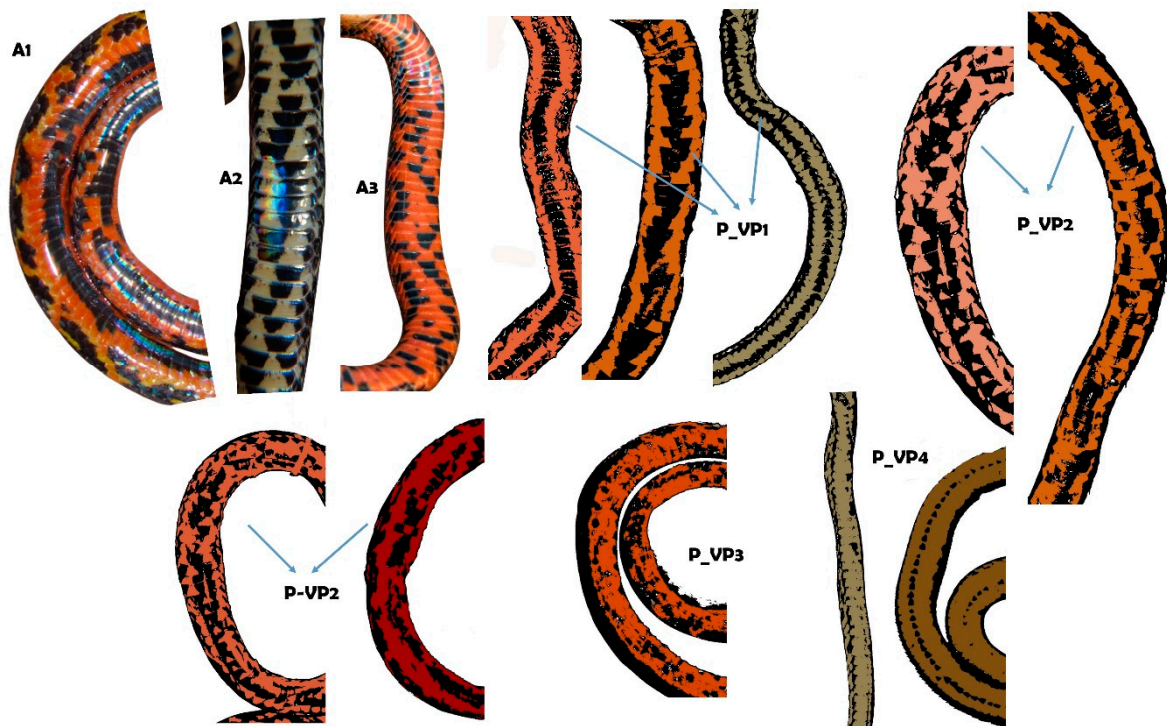


Figure 9. Ventral pattern (VP) in life of *A. erythromelas*, A1–3. The other patterns were constructed from field data of the specimens (Preserved Ventral Pattern, P_VP). P_VP1, reddish or whitish background, with black spots on each scale; P_VP2, reddish or whitish background, with black spots on each scale; P_VP3, reddish or whitish background, with black spots on each scale; and P_VP4, called tabby, reddish or yellowish ventral background.

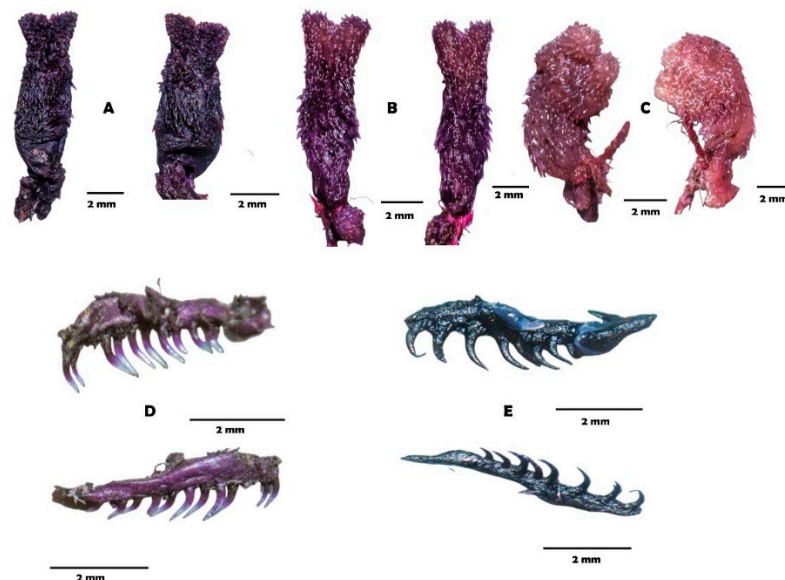


Figure 10. Hemipenes and maxillary dentition of *A. erythromelas*. (A) Sulcate and asulcate region of the hemipenis in specimen CVULA 7374; (B) sulcate and asulcate region of the hemipenis in specimen CVULA 7400; (C) sulcate and asulcate region of the hemipenis in specimen MHNLS22668. Maxillary dentition extracted from specimen MZUC 47737 (D) and CVULA 7395 (E).

Definition—(1) A total of 15 or 17 scale rows dorsal to midbody, with or without reduction in two scales in those individuals with 17 scales at midbody; (2) maximum total length in males 338.11 mm, 449.57 mm in females; (3) rostral barely or slightly visible from above, in frontal view, wider than tall, apical margin short-moderate (<0.5 distance between

the nostrils) and slightly or not exceeding an imaginary straight line between the nostrils; (4) internasals small-moderate, quadrangular, usually suture 2.8–5.9 times PrSL in males and 2.9–7.3 in females; (5) ventral scale count, 151–169 in males and 169–179 in females; (6) subcaudal scale count, 26–35 in males and 16–27 in females; (7) polychromatic dorsal pattern, the most common being interspersed red or white and black bands; adults have red or white crossbands, not margined of black, frequently widened dorsolaterally. Then, we have the pattern with an intense reddish or ochre-yellow background, with scattered black spots, giving the impression of a tabby pattern, and, finally, an emerging pattern consisting of interspersed yellowish-green and black bands, the yellowish-green ones not bordered by black, 2–3 scales and widened dorsolaterally, frequently the light crossbands joined at vertebral level; (8) horizontal line behind and before the eye present; (9) seven supralabials, the first small or moderate, taller than it is wide, with protrusion between the postnasal–prenasal; (10) short to moderate supralabial–rostral contact; (11) moderate loreal, in contact with two supralabials; (12) first temporal scale not elongated, 1–1.9 times than END; (13) frontal hexagonal or subhexagonal, usually longer than wide and with straight or slightly straight edges, 83.3% of the individuals examined males and 77.7% in females; (14) eye–prefrontal contact; (14) 8–10 maxillary teeth, lateral process of the palatine well developed and located between the 5 and 6th tooth; (15) hemipenis slightly bilobed, semicapitate and semicalyculate.

Description of the series examined—TL 251.91–338.11 mm in males ($\bar{x} = 304.8 \pm 22.77$; $n = 12$) and 256.75–449.57 mm in females ($\bar{x} = 338.4 \pm 51.23$; $n = 11$); maximum tail length 46.62 mm in males ($\bar{x} = 36.4$ mm; 18.46 – 46.62 mm ± 7.68 ; $n = 12$), 48.82 mm in females ($\bar{x} = 35.9$ mm; 23.35 – 48.82 mm ± 8.11 ; $n = 11$); HL 7.84–9.68 mm in males ($\bar{x} = 8.6$ mm ± 2.55 ; $n = 12$) and 6.98–10.23 mm ($\bar{x} = 8.6$ mm ± 0.89 ; $n = 11$) in females. In dorsal view, the head is slightly differentiated from the neck, oblong, the snout is relatively short, not compressed or barely compressed, with a rounded edge (ID and IND reduction in the head 12.5–49.5% in males and 23.5–54.7% in females). In lateral view, the snout is usually rounded or subacuminate; the rostral is barely or slightly visible from above (condition A–B). In frontal view, the subtrapezoidal is as wide as high or slightly wider (Figure 7D), with its lateral margins straight or slightly concave; the apical edge of the is scale short-moderate (<0.5 of the distance between nostrils) and barely exceeding the imaginary straight line between the nostrils or in the same arrangement; two internasals, usually longer than wide, and others quadrangular (less common wider than long); no sinastria, suture 2.8–5.9 times PrSL in males ($\bar{x} = 4.4 \pm 0.82$), 2.9–7.3 in females ($\bar{x} = 5 \pm 1.27$); two prefrontals, projecting laterally, suture longer than FL and XX times in relation to SPL; frontal hexagonal or subhexagonal, usually longer than wide (Figure 7A) and with straight or slightly straight edges (83.3% of the individual examined males and 77.7% of the females); two supraoculars, elongated and posteriorly wider; two parietals, PSL 0.26–0.39 times head length. Eye oval, HED moderate, 0.51–0.69 times END in males and 0.45–0.75 in females; eye–prefrontal contact greater than eye–loreal contact ($n = 15$) but shorter than prefrontal–postnasal contact; loreal generally moderate (sometimes short), irregularly pentagonal, narrower or equal to anterior end towards eye (Figure 7B), in contact with second and third supralabials; margin between loreal and anterior supralabial slightly shorter than LOL; first supralabial small-moderate, pentagonal, taller than wide, protrusion present between postnasal–prenasal; short or moderate rostral contact; 7(3–4) supralabials, third supralabial elongated, third and fourth horizontal length 1.06–1.31 times shorter than END in males, 1.01–1.41 in females (condition in 90% of the specimens examined in males and 66.6% in females); two postoculars, the lower one mostly vertically extended; temporal formula 1 + 2, first temporal as long as tall, 1.1–1.9 times END in males and 1–1.6 in females, posterior supratemporal definite or not (variable between sexes). Mental scute subtriangular, wider than long; six infralabials,

three in contact with geneials (Figure 7C); a single pair of geneials, suture 0.76–1.47 times END in males and 0.7–1.29 in females; sublabials or pseudo-chinshields elongate, separated from each other by the gular scale, its width greater than the suture of the single pair of infralabials; three gulars; 1–2 prefrontals. Ventral scale count: 151–169 in males ($\bar{x}$ = 160.8; n = 15) and 169–179 in females ($\bar{x}$ = 174.8; n = 13); cloacal scale entire, subcaudals divided, counting 26–35 in males ($\bar{x}$ = 31.6; n = 15) and 16–27 in females ($\bar{x}$ = 24.08; n = 13).

Coloration information (in life)—This species exhibits a polychromatic dorsal pattern, consisting of at least five detected morphs: (A) bicolor, red-or-white, and black crossbands along the body, intercalated, light bands not marginate of black, usually extending to the first dorsal row, and may be divided or fused at the vertebral level (Figure 8A,B1). Red or white bands widened dorsolaterally, 2–3 dorsal scales (more evident at midbody). The dorsal background of the head is similar to the body; a black line behind and in front of the eye is well defined (Figure 8B2,G). This pattern has been observed in the city of Mérida and its surroundings, which includes the middle part of the Chama River basin, between 1000 and 1800 m asl, where the red crossband is more frequent than the white crossband (Figure 8A); (B) not bicolor, crossbands absent, reddish background along the body, with just small to moderate black spots forming stretch marks on the paravertebral–vertebral region of the body, sometimes constituting a small narrow line. The dorsal background of the head is similar to the body; laterally, a black line behind the eye and in front is found, which is poorly defined (Figure 8C); (C) not bicolor, hazelnut or yellowish-hazelnut background with black blotches, variable in size and irregularly dispersed, 1–3 dorsal rows, sometimes forming a longitudinal black line that is not perfectly continuous along the body. The dorsal color of the head is similar to the body, although darker, without a black line behind and in front of the eye (Figure 8D); (D) bicolor, yellowish-green and black crossbands along the body, intercalated, 2–3 scales and widened dorsolaterally, continuous or discontinuous medially, light crossbands not marginate of black (Figure 8E). The dorsal background of the head is yellowish-brown (Figure 8F); a black line behind and in front of the eye is well defined (Figure 8F,G). Geographically, the emerging and rare B and C patterns have been observed in the city of Mérida between the Chama and Albarregas River basins, while populations with pattern D are geographically circumscribed within the middle-upper part of the Chama River basin, in the direction of Mucurubá. This pattern has been found in other individuals with pattern A. The northernmost record of this distribution corresponds to specimen MHNLS 22057, collected at 2980 m altitude.

The ventral pattern is variable but subject to the dorsal pattern; four patterns are defined, VP. Individuals with dorsal patterns A and D exhibit the following: (A) VP1, reddish or whitish background, with black spots on each scale, trapezoidal or rectangular; usually, part of its extension is aligned at the midventral level; they can occupy between 30 and 60% of the surface of each scale (Figure 9A1,P_VP1); (B) VP2, reddish or whitish background, with black spots on each scale, trapezoidal or rectangular, intercalated or not, arranged irregularly, occupying more than 50% of the surface of each scale (Figure 9A2,P_VP2); and (C) VP3, reddish or whitish background, with black spots on each scale, rectangular and arranged in two lateroventral rows, they can occupy less 50% of the surface of each scale (Figure 9A3,P_VP3). When dorsal pattern B is present, the ventral surface is always reddish, uniform or with a black line, similar to patterns A and D. Finally, VP4, which we call tabby, has a reddish or yellowish ventral background, with black dots or small spots, arranged at a midventral level and occupying less than 30% of the surface of each scale; sometimes, the pattern is almost immaculate (Figure 9P_VP4). Sometimes, these dots are replaced by a black line, similar to that observed in dorsal patterns A and D.

Regarding the ventral surface of the tail, in almost all cases, it is spotted black, either on a reddish (ventral pattern VP1), yellowish (dorsal pattern VP4), or cream (pattern A)

background. In many of the observed cases, the tongue is reddish; this also occurs in the pupil of the eye, which can be reddish or reddish-brown. The background of the supralabials can vary from reddish, yellowish, to whitish, depending on the dorsal patterns.

Hemipenis (everted organs $n = 3$)—In specimens CVULA 7375 and CVULA 7400 (Figure 10A,B), the hemipenis is slightly bilobed, semicapitate, and semicalyculate; capitulum lobes are defined and more or less similar in size, clavate, and with a rounded apical edge; its length varies between 6.3 and 6.4 mm from the base to the apex of the lobe. The capitulum is clearly defined, located above or just above the bifurcation of the sulcus spermaticus; its extension varies between 25% and 42% of the length of the hemipenis. The capitated region is composed of spinulate calyces, which are progressively replaced by papillae towards the apex of the lobes; sulcus spermaticus bifurcates in the middle of the organ, with each branch oriented centrifugally, reaching the tips of the lobes; margins of sulcus spermaticus smooth and laterally expanded, bordered by spinules from its base to the apices of the lobes; body of the hemipenis somewhat globular, narrow above the sulcus spermaticus, with calcified hooked spines; large spines restricted to the lateral surfaces of the organ; naked basal pocket absent, longitudinal folds indefinite. In specimen MHNLS 22668 (Figure 10C), the ornamentation of the hemipenis is similar to the previous specimens, although the capitulum situated above the bifurcation of the sulcus spermaticus tends to be wider than the body of the hemipenis; it has clearly defined lobes situated above the capitulum, subcylindrical, with an apical rounded edge. In all specimens, the asulcate region is covered by calcified spines, which are progressively replaced by spinulate calyces and papillae towards the lobes.

Maxillary bone—The maxillary bone varies from 3.9 to 3.1 mm in length ($n = 10$), with the anterior third arched and posteriorly depressed; the palatine process is projected and well developed, located between the fifth and sixth teeth; 8–10 maxillary teeth, acute, curved and decreasing posteriorly, the last two tending to be smaller; the space between the teeth is short; the posterior projection is defined (Figure 10D,E).

Distribution and natural history—Towards the middle Chama River basin, which includes the city of Mérida and its surroundings, the species inhabits the Andean montane semideciduous forest and the ecotone towards the cloud forest between 1200 and 2400 m asl; towards the middle-upper Chama River basin, it extends between 1700 and 2980 m asl, occupying the Andean montane semideciduous forest, cloud forest, and Andean high-montane scrublands [61,138] (Figure 11).

The species was observed to be active at the end of the afternoon and during the night in zones belonging to the University of the Andes (LFE, unpublished data). On the other hand, we collected specimens under rocks on the way to Valle to La Culata, Finca La Hermita, an area with anthropized vegetation dominated by Kikuyu grass for livestock (LFE, unpublished data 2021). We also found individuals under rocks or dry material in decomposition towards Mucurubá, where the only other species reported was *A. mijaresi*. Although the species seems to be sympatric with *A. ventrimaculatus* towards the city of Mérida (MHNLS 22668 and MHNLS 22666–67), our field observations suggest that *A. ventrimaculatus* occupies the cloud forest and *A. erythromelas* the Andean montane semideciduous forests, except those populations from the medium-high Chama River basin (sector Mucurubá), whose vegetation exhibits a strong conversion, being a mixture of altimontane arbustals, relicts of Andean montane semideciduous forests, and agricultural and/or grassland areas for high livestock. Instead, other populations detected towards the Mucuy would occupy the Andean montane semideciduous forests and the cloud forest, the latter being best preserved because it is within the limits of the Sierra Nevada National Park.

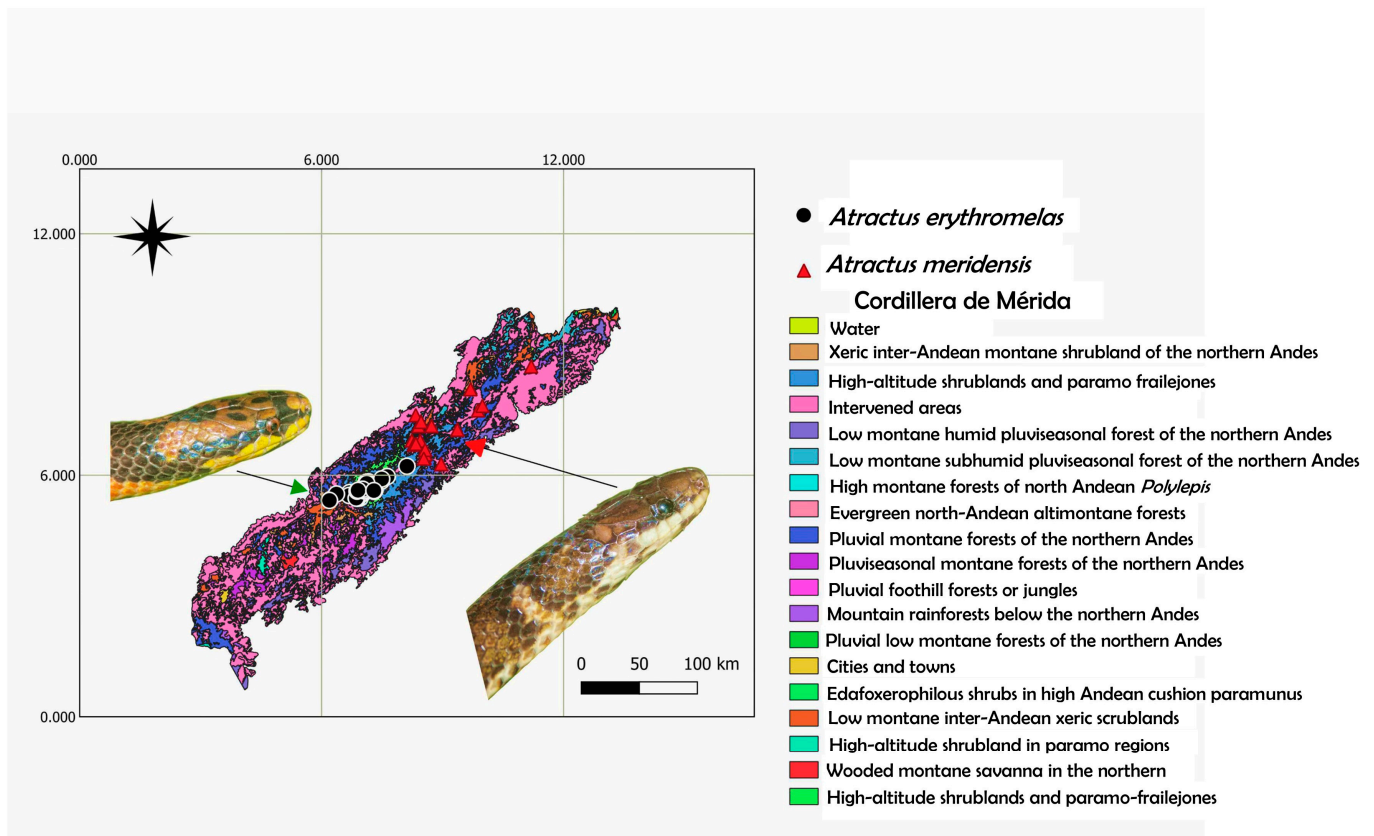


Figure 11. Map of the cordillera de Mérida showing the distribution of *A. erythromelas* and *A. meridensis*. Base vegetation map; ©Eulogio Chacón Moreno.

An adult female MZUC 45655 (LFE269) contained three well-developed oviductal eggs, collected under a rock, attempting to bury herself in the ground, after the Cacute curve, El Molinero restaurant, 3.37 km S of the town of Mucurubá, Mérida state, Venezuela, on July 31, 2021, at 2: 43 PM ($8^{\circ}41'27.00''$ N and $70^{\circ}59'48.75''$ W, 2204 m asl, notes LFE).

Conservation status—Niche modeling using MaxEnt yielded a predicted suitable distribution area for the species of 2126.8 km², consisting mostly of montane rainforests of the northern Andes (558.6 km²). According to the IUCN, an area of 466.979 km² comprises EOO (geocat 469.755 km²) and 116 km² comprises AOO (geocat 120 km² to 2 km²). The city of Mérida constitutes the topotypic area of the species, which is located at an average altitude of 1630 m asl (1000–2400 m), on a quaternary plateau in the Venezuelan Andes flanked by two mountainous chains: the Sierra Nevada to the east and the Sierra de la Culata to the northwest. The city occupies an extension of 55 km², the main water courses being the Chama and Albarregas rivers. The native vegetation corresponds to the Andean montane semicaducifolious forest [138], but most of it has been transformed, and now only wooded remnants persist within the boundaries of the city. Although the species seems to be frequent in anthromes [139], this group has a diet specialized in worms, whose ecological requirements can be affected by the conversion of the habitat [140,141], which could have effects on the population dynamics of these snakes (e.g., *Atractus lasallei* in Colombia, [142]).

Here, we demonstrate that the extent of presence and area of occupancy of the species are well reduced, along with a continuous decline in habitat quality due to the conversion of semideciduous and cloud forests for agricultural activities, high-altitude pastures for livestock, and urban–rural development. So far, we detected two disjunct populations with little area under protection (e.g., surroundings of Mérida, Sierra de la Culata National Park). In this sense, the species could be classified as “Vulnerable” according to criteria B2abi,ii,iii,iv. Previously, Esqueda and La Marca [143] recognized it as a Vulnerable species.

Atractus meridensis ESQUEDA & LA MARCA, 2005
Resurrection.
(Figures 12–16).

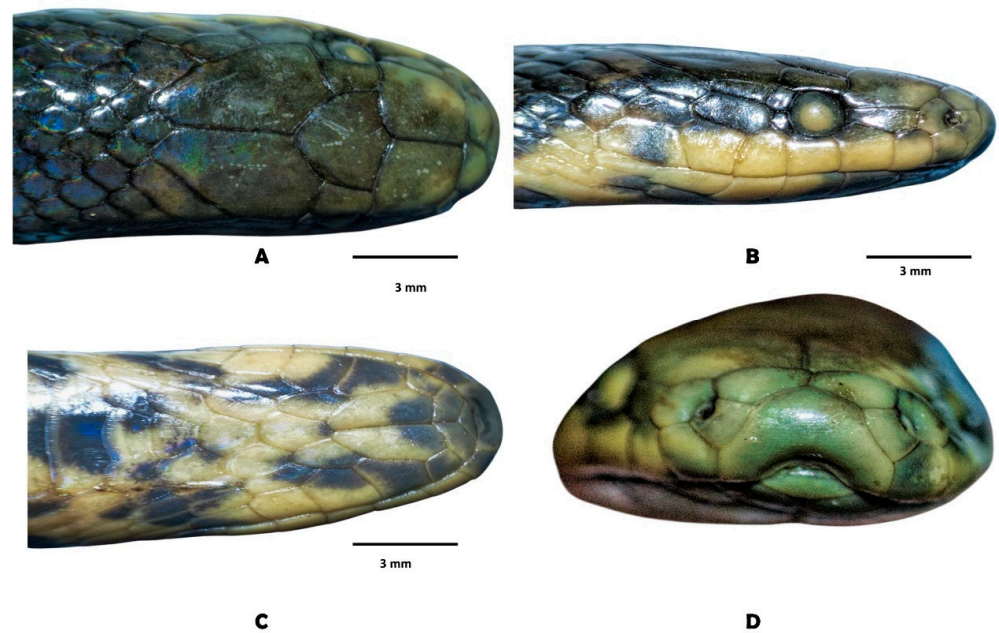


Figure 12. Adult male *A. meridensis* individual, MZUC 48051: dorsal view (A), lateral view (B), and ventral view of the head (C) and frontal view of the rostral scale (D).



Figure 13. Dorsal coloration pattern in life of *A. meridensis*. Bicolor pattern, intercalated red-or-reddish-orange and black crossbands (A–D) and bicolor pattern, intercalated white-or-whitish and brown-black crossbands (E,F). Juvenile specimen without marginalization of the white or cream crossbands (G). Correspond to specimens of *Atractus micheleae* from Boconó, Trujillo, with a pattern of intercalated red-white and black crossbands, but which begin from the third dorsolateral row (H1–H3). Images © Luis Felipe Esqueda.

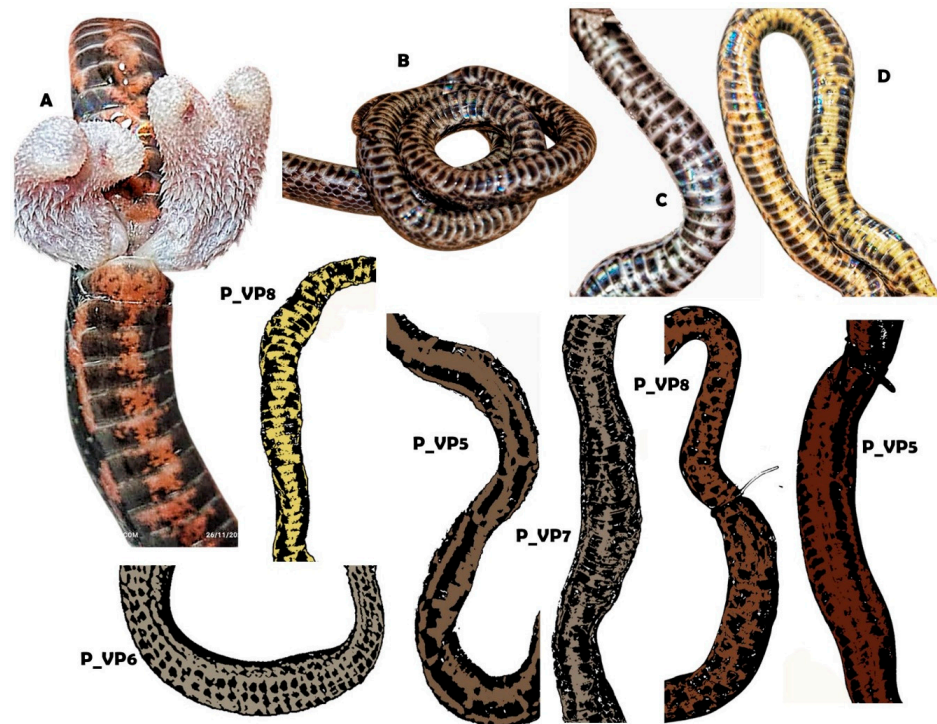


Figure 14. Ventral pattern (PV) in life of *A. meridensis*, (A–D). The other patterns were constructed from field data of the specimens (Preserved Ventral Pattern, P_VP). P_VP5, reddish, whitish, or pale-yellow background ((A,D) and P_VP5); P_VP6, reddish or whitish background; P_VP7, reddish or whitish background ((B,C) and P_VP7); and P_VP8, whitish background.

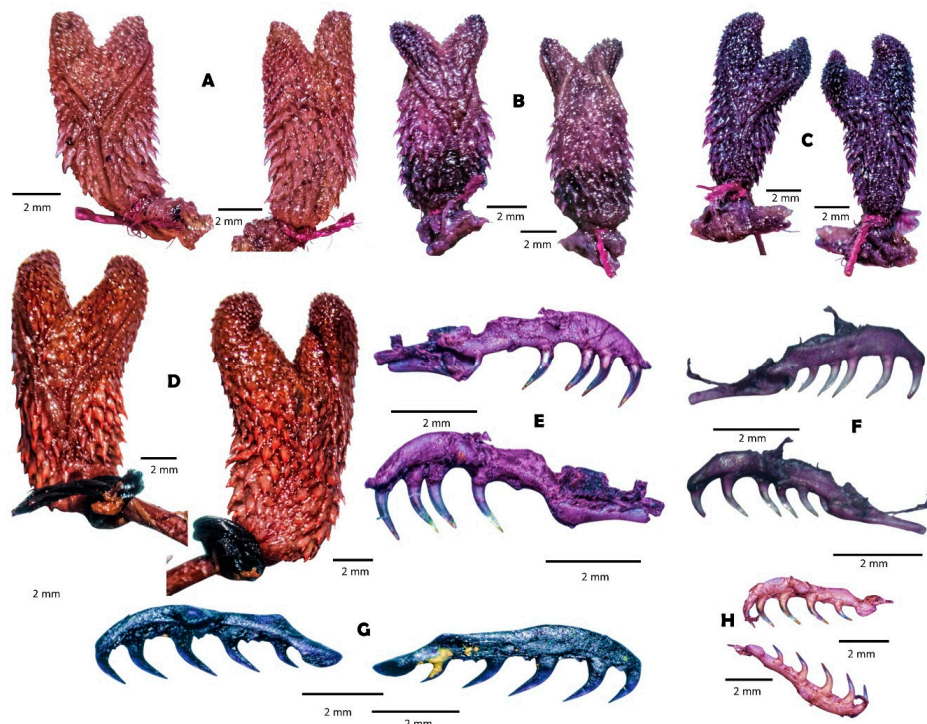


Figure 15. Hemipenes and maxillary dentition of *A. meridensis*. (A) Sulcate and asulcate region of the hemipenis in specimen MZUC 45660; (B) sulcate and asulcate region of the hemipenis in specimen MZUC 45661; (C) sulcate and asulcate region of the hemipenis in specimen MZUC 45662; and (D) sulcate and asulcate region of the hemipenis in specimen MZUC 45663. Maxillary dentition: (E) = specimen MZUC 48043; (F) = specimen MZUC 45662, (G) = specimen MZUC 48054, and (H) = specimen MZUC 45671.



Figure 16. Natural history records of *A. meridensis*. (A) Adult individual with a reddish-black bicolor pattern found under a rock next to another specimen of *A. emigdioi* on a road to Tabó, near Niquitao, Trujillo state, Venezuela; (B) sighting of an aggregation of many *A. meridensis* in a rural area in La Puerta, Trujillo state, Venezuela; (C) specimen MZUC 48050, found active while crossing a dirt road on the way to Tabó, near Niquitao, Trujillo state, Venezuela; and (D) a partially digested earthworm found in the digestive tract of juvenile specimen MZUC 45656.

Atractus meridensis—Esqueda and La Marca [8]; *Herpetotropicos*, 2(1): 10–14.

Atractus meridensis.—Passos et al. [6]; *South American Journal of Herpetology*, 32(Special Issue): 1–123.

Holotype—Adult male, ULABG 4341, coleccionado por Enrique La Marca el 22 de marzo de 1997, depositado en la Colección de Anfibios y Reptiles, Laboratorio de Biogeografía, de la Universidad de Los Andes, Mérida, Venezuela (Esqueda and La Marca [8] (pp. 10–14). Espécimen colectado a 1 Km del puente sobre el río Santo Domingo en la vía principal desde La Mitisús hasta Santo Domingo, y a 500 m del cruce de acceso a la Población de Las Piedras; 08°52′45″ N, 70°39′09″ W.

Definition—(1) A total of 17 dorsal scale rows around the body, without reduction anteriorly and posteriorly; (2) maximum total length 433.68 mm in males and 406.46 mm in females; (3) rostral distinctly visible from above, apical margin broad (>0.5 distance between the nostrils); (4) two moderate internasals, often wider than long and suture 2.4–5.2 times PrSL in males and 2.2–4.4 in females; (5) ventral scale count, 156–173 in males and 160–180 in females; (6) subcaudal scale count, 27–39 males and 21–35 females; (7) dorsal pattern bicolor–dichromatic, red or white crossbands interspersed with brown or black crossbands; adults have red or white crossbands margined with black in life, often not widened dorsolaterally; (8) horizontal black line behind eyes absent or weakly defined; (9) seven supralabials, first enlarged, without protrusion between the postnasal

and prenasal; (10) ample supralabial–rostral contact; (11) moderate loreal; (12) first temporal scale elongated, 1.1–1.7 shorter than END; (13) hexagonal frontal scute, often as wide as long or wider, 77.7% in males and 65% in females; (14) usually wide eye–prefrontal contact; (15) 5–6 maxillary teeth, palatine process projected and well developed, located between the fourth and fifth teeth; (16) hemipenis moderately bilobed to bilobed, semicapitate and semicalyculate.

So far, in the cordillera de Mérida, only three species show a mimetic–bicolor pattern of light and dark crossbands: *A. erythromelas*, *A. meridensis*, and *A. micheleae* (Table 1).

Table 1. Comparative attributes among the mimetic species present in the cordillera de Mérida, Venezuela. (Information built by us). Cordillera de Mérida (CM).

Morphology, Coloration and Geography	<i>A. meridensis</i>	<i>A. erythromelas</i>	<i>Atractus nemosophis</i>	<i>A. micheleae</i>
Geographic Distribution (CM, Venezuela)	Isolated populations to the northeast of the state of Mérida and Trujillo, in the river basins Motatán, Boconó and Santo Domingo	Medium-high basin of the Chama River, from the city of Mérida to beyond Mucurubá, Mérida state	Isolated populations northeast of the Trujillo–Mérida state, in the river basins Motatán, Boconó and Santo Domingo	Southwest isolated populations of the state Táchira and the Boconó River Basin, Trujillo state
Altitudinal range	1160–2684 m asl	1077–3275 m asl	1864–2404 m asl	900–1500 m asl
Habitat (natural)	Andean montane semicaducifolious forest and cloud forest	Andean montane semicaducifolious forests and cloud forest	Andean montane semicaducifolious forest and cloud forest	Andean submontane forest and Andean montane semicaducifolious forest
Maximum Total Length (SVL + TaL)	433.68 mm males and 406.46 mm in females	338 mm in males and 449.57 mm in females	419 mm in males and 470 mm in females	324.74 mm in males and 405 mm females
Rows of dorsal scales at midbody	17 (always)	15 or 17	17 (always)	17
Ventral scale (count)	156–173 males and 160–180 females	151–169 males and 169–179 females	158–177 males, 173–190 females	152–159 males and 162–172 females
Subcaudal scale (count)	27–39 males and 21–35 females	26–35 males and 16–27 females	36–41 males and 23–31 females	32–35 males and 23–28 females
Supralabials	7–8 (3,4)	7 (3,4)	7 (3,4)	8(4,5) or 8 (3,4)
Infralabials	6 (3–4)	6 (3)	6 (3), rarely four	7(4)
Supralabials in contact with Loreal	Two	Two	Two	Three
Eye-Prefrontal contact	Greater than eye-loreal contact	Greater than eye-loreal contact	Usually shorter than eye-loreal contact	Greater than eye-loreal contact
Rostral (dorsal view)	Distinctively visible from above (condition C)	Slightly visible or barely visible from above (frequent)	Distinctively visible from above (condition C)	Barely visible from above
Prenasal	Longer than tall, small or similar than postnasal	Taller than long, usually smaller than postnasal	Taller than long, smaller than postnasal	Higher than long, slightly larger than postnasal
Eye-Loreal contact	Distinctively narrow, less than the anterior margin of the loreal–postnasal	Usually narrow or similar that the anterior margin of the loreal–postnasal	Distinctively narrow, less than the anterior margin of the loreal–postnasal	Distinctively narrow, less than the anterior margin of the loreal–postnasal
Supralabial-rostral contact	Ample, supralabial scale pentagonal but does not form an angle, that is, protrusion between postnasal and prenasal. Enlarged supralabial	Short-moderate, usually the supralabial scale is pentagonal, taller than wide, forming an angle, that is, postnasal and prenasal project. Small or moderate supralabial	Ample, supralabial scale pentagonal but does not form an angle, protrusion between postnasal and prenasal. Enlarged supralabial	Short, supralabial scale pentagonal, taller than wide, protrusion between postnasal–prenasal. Small supralabial
Posterior supratemporal (elongated)	Absent, less frequent present	Absent, less frequent present	Present (frequent)	Present (frequent)
Internasals	Usually longer than wide, moderate-long suture	usually quadrangular, short-moderate suture	Longer than wide, moderate-long suture	Usually longer than wide, short-moderate suture
Frontal scute	Usually so wide than long or wider	Usually longer than wide	Usually so wide than long or wider	Usually so wide than long or wider
Head in lateral view, snout	Forming an oblique angle	Rounded or subacuminate	Forming an oblique angle	variable, rounded or subacuminate
Head in view dorsal (forms)	Oblong, snout not compressed	Oblong, snout not compressed	Oblong, snout not compressed	Subtriangular, snout slightly compressed

Table 1. Cont.

Morphology, Coloration and Geography	<i>A. meridensis</i>	<i>A. erythromelas</i>	<i>Atractus nemosophis</i>	<i>A. micheleae</i>
Snout (lateral view)	Slightly truncated	Rounded	Rounded	Rounded
Maxillary and lateral process	Well-developed palatine lateral process, located between the fourth and fifth tooth	Well-developed palatine lateral process, located between the six and seven tooth	Well-developed palatine lateral process, located between the third and fourth tooth	Well-developed palatine lateral process, located between the third and fourth tooth
Maxillary teeth	5–6	9–10	5–6	5–8
Hemipenis	Semicapitate, semicalyculate, moderate bilobed or bilobate, subcylindrical lobes and rounded apex	Semicapitate, semicalyculate, slightly bilobed, clavate lobes and rounded apex	Semicapitate, semicalyculate, moderate bilobed, cylindrical lobes and plane apex	Semicapitate, semicalyculate, moderate bilobed, cylindrical lobes and plane apex
Dorsal pattern in life	Dichromatic-bicolor, red-white, and black crossbands, interspersed, light bands margined of black	Polymorphic, there are bicolor individuals with red-white and black bands, interspersed, clear non-marginalized bands; another pattern is brown or yellow brown with irregular black stains (tabby); reddish background, almost immaculate, with few spots that form an occasionally	A pattern frequent is the grayish-brown dorsum, without a vertebral line but with small dark spots scattered irregularly along the body; another reddish or reddish-brown pattern uniform or with a vertebral black (less than one scale) and another observed is grayish brown with irregularly scattered spots, being able to also be uniform	Dichromatic-bicolor, red-white and black-brown crossbands, interspersed, lights crossbands not margined of black
Dark line behind and in front of the eyes	Usually absent, rarely defined	Present both and conspicuous, rarely absent	Absent	Absent
Light band behind the parietals	Present, wel defined	Present, well defined	Present, inconspicuous in adults	Absent

Description of the series examined—TL 254.03–433.68 mm in males ($\bar{x}$ = 356.45 mm $\pm$ 51.47; n = 9) and 245.98–406.46 mm in females ($\bar{x}$ = 324.6 mm $\pm$ 44.72 n = 20); maximum tail length 59.28 mm in males ($\bar{x}$ = 48.2 mm; 34.9–59.28 mm $\pm$ 8.4; n = 9) and 45.31 mm in females ($\bar{x}$ = 30.7 mm; 19.27–45.31 mm $\pm$ 6.32; n = 20); HL 8.38–11.62 mm ($\bar{x}$ = 10.1 $\pm$ 1.18; n = 9) in males and 7.21–11.8 mm ($\bar{x}$ = 9.5 $\pm$ 1.2; n = 20) in females. In dorsal view, the head is slightly distinct from the neck, oblong; the snout is appreciably short, not compressed or barely compressed, with a slightly truncated margin (ID and IND reduction in head: 27.7–44.8% in males and 15.53–51.4% in females). In lateral view, frequently, the snout forms an oblique angle; rostral distinctly visible from above (condition C) (Figure 12D), trapezoidal, slightly wider than high, prominent medial projection, concave lateral margins, apical margin broad (>0.5 distance between the nostrils) and exceeds the imaginary straight line; prominent lingual notch; two moderate internasals, usually wider than long (rarely quadrangular or more long than wider), sinastria or not, internasal suture 2.4–5.2 times PrSL in males ($\bar{x}$ = 3.4 $\pm$ 0.99; n = 11) and 2.2–4.4 in females ($\bar{x}$ = 3.5 $\pm$ 0.6; n = 13); FRD equal to or slightly shorter than PSL; hexagonal frontal scute, often as wide as long or wider (77.7% in males and 65% in females), and the anterior margins are frequently convex (Figure 12A); two moderate prefrontals, widened posteriorly; two parietals, parietal suture longer than frontal length, 0.29–0.38 times HL. Eye oval, HED moderate, 0.47–0.65 times END in males and 0.44–0.65 in females; eye–prefrontal contact greater than eye–loreal contact (n = 25) and similar to or slightly shorter than prefrontal–postnasal contact; loreal irregularly pentagonal, frequently moderate (less common short), usually narrowing towards the eye and in contact with the second and third supralabials (Figure 12B), margin between the loreal and anterior supralabial shorter than LOL; postnasal irregularly heptagonal, higher than wide, proportionally larger than prenasal; the latter is rectangular and usually longer than high; seven supralabials, with the third and fourth in contact with the eye orbit; first supralabial

enlarged, pentagonal, without protrusion between the postnasal and prenasal; horizontal length of the third and fourth 1.01–1.14 times longer than END in males and 0.98–1.16 in females (66.6% in males and 63.3% in females); ample supralabial–rostral contact; snout rounded in lateral view; two postoculars, with the lower one slightly more extended; temporal formula 1 + 2, elongated supratemporal present, rarely indefinite; first temporal elongated, 1.1–1.7 times END. Mental shield frequently expanded, subtriangular and wider than long (Figure 12C); six infralabials, with three in contact with geneials; geneial suture 0.77–1.08 times END in males and 0.7–1.19 in females; sublabials or pseudo-chinshields separated by median gular, their width greater than the suture of a single pair of infralabials; three gulars; 1–2 prementals. Ventral scale count: 156–173 in males ($\bar{x}$ = 163.4; n = 11) and 160–180 in females (n = 172.9; n = 20); cloacal scale entire; subcaudals divided, counting 27–39 in males ($\bar{x}$ = 34.5; n = 11) and 21–35 in females ($\bar{x}$ = 27.1; n = 20).

Coloration information (in life)—This taxon, unlike *A. erythromelas*, exhibits a dichromatic pattern: (A) Bicolor pattern, intercalated red-or-reddish-orange and brownish-black crossbands. The reddish crossbands narrow (one scale), infrequently widened medially, continuous, or discontinuous medially, and always margined with black (Figure 13A,B,D). (B) Bicolor pattern, intercalated white-or-whitish and brown-black crossbands, narrow (one scale), not widened medially, continuous, or discontinuous medially and margined with black (Figure 13C,E,F). In both dorsal patterns, the head is light brown, differentiated from the body, and less commonly dark brown. A black line behind and in front of the eye is absent or poorly defined. Juvenile individuals do not have the light bands margined with black, which is more evident in pattern B (Figure 13G). On the other hand, towards the Boconó River basin, in the town of Boconó and its surroundings heading towards Biscucuy, Portuguesa state, we detected a population where juveniles and adults do not have the reddish-white crossbands margined with black, but have morphological characters and hemipenes distinct; we recognize this population as *A. micheleae* (Figure 13H1–H3).

Regarding the ventral surface (midventral), we find at least four variations, i.e., VPs. (A) VP5, reddish, whitish, or pale-yellow background, with black spots on each scale, rectangular, arranged in two lateroventral lines, they can occupy a space between 30% and 60% (Figure 14A,D and P_VP5). (B) VP6, reddish or whitish background, with black spots on each scale, rounded, mottled or rectangular, arranged in three lines; the medioventral one is usually smaller. The space varies considerably, but it can be above 50% of the surface on each scale (Figure 14P_VP6). (C) VP7, reddish or whitish background, with black spots on each scale, rounded, mottled, or rectangular, arranged horizontally to the scale. The space varies, but it can be above 50% to 100% (Figure 14B,C and P_VP7). (D) VP8, whitish background, with black spots on each scale, rectangular, arranged irregularly (they do not form a line); they can occupy 30% to 50% of the space on each scale (Figure 14P_VP6).

In all specimens with life coloration data, the background of the supralabials varies from cream, yellowish cream, or reddish, depending on the dorsal pattern. The cloacal plate may be cream, yellowish cream, or reddish, usually lightly pigmented black; the background of the subcaudals is similar to the ventral patterns, but it is heavily pigmented black.

Hemipenis (everted organs n = 4)—The hemipenis organ is moderately bilobed (Figure 15A–C) to bilobed (Figure 15D), semicapitate, semicalyculate; well-defined lobes, similar in size and located towards the distal portion of the capitulum, can vary from sub-cylindrical to cylindrical, with a rounded apex. Lobes and capitulum covered by spinulate calyces, progressively replaced by papillae towards the tips of the lobes. Capitulum located above the sulcus spermaticus, longer than the body of the hemipenis; capitular groove not definite; the beginning of the bifurcation of the sulcus spermaticus varies between ~26% (Figure 15C,D) and 42–50% (Figure 15A,B) with respect to the length of the hemipenis, arranged centrifugally; margins of the sulcus spermaticus are smooth, expanded laterally

and bordered by spinules from its base apical to the lobes; the body of the hemipenis is medially wider than its base, subcylindrical, covered with medium-sized, hooked spines, developed and grouped from the bifurcation of the sulcus spermaticus towards the base of the hemipenis; basal region of the hemipenis covered by spinules and laterally by calcified spines; basal naked pocket absent. In sulcate view, the hemipenial body is covered by spines, which decrease towards the base, while towards the lobes, they are progressively replaced by spinulate calyces and papillae towards the tips of the lobes.

Maxillary bone—The maxillary bone size varies from 3.1 to 5.47 mm in length ($n = 6$), with the anterior third barely arched and weakly depressed posteriorly; the palatine process is projected and well developed, located between the fourth and fifth teeth; 5–6 maxillary teeth, acute, curved, and decreasing posteriorly, the last one is very small; the space between the teeth is short except between the fourth and fifth teeth or fifth and sixth teeth, where a notable space is appreciated; defined posterior projection (Figure 15E–H).

Distribution and natural history—Currently, its distribution is restricted to isolated populations in the northeast of Mérida and Trujillo states, Venezuela, between 1077 and 3275 m asl (Figure 11). Its type locality is found within the limits of the upper Santo Domingo River basin, with an altitudinal range that varies from 1600 to 4906 m asl and a predominant vegetation of paramo (35%), scrubland (32%), Andean montane semideciduous forests (10.5%), and intervened areas destined for agricultural crops (16%) [144]. Other detected populations come from the basin of the Motatán rivers (middle-upper part between 1000 and 2700 m asl) and Boconó (upper part between 1700 and 2340 m asl). Our data from both basins indicate that the species occupies the Andean montane semideciduous forest between 1000 and 2000 m asl and the cloud forest below 2500 m asl, although many of the areas where the species was collected now correspond to high-altitude cattle pastures above 1500 m asl (e.g., African grasslands, *Pennisetum clandestinum* Hochst. ex Chiov. and *Melinis minutiflora* Beauv., [145–147]. This taxon is sympatric with *Tantilla palamala* in its type locality. Esqueda et al. [148], the authors mistakenly typed and labelled the specimens 74711, 74712, and 74713, when they are actually 47711, 47712, and 47713, as correctly noted elsewhere in the article and Supplementary Material).

This taxon is found in sympatry with *A. emigdioi* (Figure 16A) and *Atractus nemosophis*, recently described [10], previously referred to as *A. meridensis* by Esqueda and La Marca [8] (specimen ULABG 4694) and also indicated by Passos et al. [6]. Although gregarious behavior is known in vermivorous snakes [149], here, we report the first known case of *Atractus meridensis* in Venezuela. The anecdotal sighting occurred in La Puerta, Trujillo state, Venezuela, while an excavation was being carried out on an abandoned lot, covered with herbaceous plants (Figure 16B, dat. ined. Santos Bazó 2022).

Two adult females, MZUC 45651 (LFE281) and MZUC 45652 (LFE286), contained three and two oviductal eggs, respectively. They were collected inactive under rocks in Las Piedras, La Quinta sector, Mérida state, Venezuela, on 1 August 2021, at 1:16 p.m. (8°54'8.65" N and 70°38'53.42" W, 1925 m asl, notes LFE 2021). Another adult female MZUC 48050 (LFE 080) contained three well-developed oviductal eggs, which was collected while crossing a dirt road in the Mibó sector, near Niquitao, Trujillo state, Venezuela, on 3 June 2021, at 2:14 p.m., with 70 % measured humidity and a temperature of 23.5 °C (9° 5'51.35" N and 70°24'18.54" W; Figure 16C).

So far, it is believed that vermivorous snakes of the genus *Atractus* exhibit cathemeral activity [150–152], although their foraging occurs more frequently at night due to their diet (earthworms). Although specimen MZUC 48050 (LFE 080) was found active during the day, it is possible that its activity could be associated with other factors unrelated to its natural activity period (e.g., thermoregulation). In fact, juvenile specimen MZUC 45657 was observed active at night on a dirt road near a rural house, La Quebrada, El Monte

sector, Trujillo state, Venezuela (9°7′42.34″ N and 70°36′29.62″ O, 1863 m, 17 June 2021, at 10:00 p.m., temperature 22 °C and 70% measured humidity, LFE 2021).

Juvenile specimen MZUC 45656 (LFE 083, Figure 16D) contained a partially digested worm in its digestive tract, probably from the Rhinodriliidae family, although it is very likely that other introduced worms exist in the area (Sam James 2025 comm. pers.).

Conservation status—Niche modeling using MaxEnt yielded a predicted suitable distribution area for the species of 3029.1 km², consisting mostly of montane rainforests of the northern Andes (1117 km²). According to the IUCN, an area of 3093.19 km² comprises EOO (geocat EOO = 3113.344 km²), and 68 km² comprises AOO (76 km² to 2 km²). The new field data and analysis demonstrate that the species exhibits isolated but abundant populations in the sampled localities. However, much of its area, which includes Andean montane semideciduous forests and Andean cloud forests, is highly fragmented and/or converted to high-altitude agrosilvopastorals systems, a situation that significantly impacts the water dynamics of these ecosystems [153]. This ecogeographical scenario, together with the fact that these snakes feed exclusively on earthworms, can directly affect its diversity and population dynamics due to deforestation and conversion of their environments because it promotes inadequate edaphic conditions, such as alkaline pH, fertility, quality of organic matter, and alteration of soil properties, such as physical–chemical [154], particularly in tropical mountain ecosystems that exhibit high rates of endemism in relatively small areas [155]. As a consequence, considering the IUCN conservation criteria [64] and the vulnerability index of reptile species (IVER, [143]), *Atractus meridensis* must be included in the Vulnerable category according to criteria B2abi,ii,iii,iv.

5. Discussion

5.1. Species Limits and Taxonomy

Although we acknowledge the contribution of Passos et al. [6], the treatment of species from the Venezuelan Andes leaves several questions open and presents inconsistencies that warrant further clarification. This is particularly the case where the authors, by not comparing the types of both species, significantly obscure important interspecific characters, such as the shape and extension of the rostral and/or the coloration pattern in life, which is usually lost during preservation (e.g., red-white crossbands margined with black in adults). Boulenger [65], in his description, indicated that *A. erythromelas* had 17 dorsal scale rows at midbody, but, in contrast, Roze [66,67] reported 15 rows at midbody. This discrepancy led Esqueda and La Marca [8], without having reviewed Boulenger syntypes, to consider that the species has 15 rows at midbody rather than 17. Passos et al. [6] recognized that *A. erythromelas* may have either 15 or 17 dorsal scale rows at midbody, with some specimens exhibiting a reduction of 2 rows toward the neck and tail. However, the series of specimens assigned to *A. meridensis* from the Santo Domingo River basin and surrounding areas has 17 scale rows at midbody without any reduction, a condition overlooked by Passos et al. [6] in their comparative analysis. Additionally, the lack of data from live specimens in their study prevents the recognition that *A. erythromelas* is more polymorphic, with at least five morphs identified (e.g., the most common being the bicolor, crossbanded type), whereas *A. meridensis* displays a dichromatic pattern (also the bicolor, crossbanded type).

The delimitation of species is often challenging in recently diverged groups (e.g., *Atractus*; [156]), particularly when morphology is highly conserved. Although not an absolute rule, recent conceptual advances in systematic biology support the view that distinct allopatric lineages are best regarded as evolutionary species. In mountainous systems, the diversification of such organisms is frequently obscured by traditional or overly convenient taxonomic practices that fail to integrate multiple lines of evidence

(e.g., Passos et al. [6]). Based on the totality of evidence presented here, particularly our mitochondrial and nuclear DNA sequence data, together with a comprehensive morphological assessment grounded in a larger series of specimens for both taxa, we recognize *A. meridensis* as a valid taxon, closely related to *A. nemosophis* and distinct from *A. erythromelas*. Thus, both species are endemic to the cordillera de Mérida but display an allopatric distribution pattern, contrary to what was previously suggested [8].

Passos et al. [6] considered five species from the cordillera de Mérida as synonyms. However, in their vague and reserved discussion, they suggest that this stance might not hold true in light of new evidence. To better understand this practice, we must first examine similar cases involving other South American *Atractus* species in which the first author, Paulo Passos, has also been involved. (1) Prudente and Passos [157] described *A. hoogmoedi*, noting that the only difference in *A. zidoki* was the condition of the hemipenis: either single or bifurcated. They interpreted this as evidence of cryptic species that are morphologically indistinguishable. However, from a taxonomic and ecological perspective, the term “cryptic species” implies that, although morphologically similar, they should be genetically distinct, which these authors did not confirm, as no phylogenetic analysis was performed. (2) *Atractus medusa* was described based on a single male specimen and distinguished from *A. boulengerii* by having 133 ventrals, a single postdiastemal tooth, and a posteriorly black venter, versus 180–189 ventrals in males, two postdiastemal teeth, and an immaculate creamish-white venter [158]. In Figure 10, the belly of *A. medusa* is only slightly spotted compared to the specimen of *A. boulengerii* in Figure 1, unlike the strongly spotted vs. immaculate subcaudals (a possible lapsus mentalis). Both species are geographically close in the Colombian Pacific (~160 km in a straight line, below 200 m elevation). (3) Melo-Sampaio et al. [159] described *A. pachacamac* from the western Brazilian Amazon, distinguishing it by ≥ 158 ventrals, ≥ 39 subcaudals, and >320 mm SVL in males vs. ≤ 155 ventrals, ≤ 34 subcaudals, and <300 mm SVL in males in *A. snethlageae*. In their ML phylogeny, both species are closely related, and our ML and BI phylogenies confirm this. However, the genetic divergence we calculated using the Cytb and ND4 markers is low ($<1.2\%$). In their discussion, Melo-Sampaio et al. [159] recognized *A. snethlageae* as a complex but, curiously, did not address the fact that both taxa overlap geographically and are morphologically very similar. (4) Passos et al. [6] described *A. pearti* from the Serranía de Perijá in Colombia. According to their data, this taxon has 169–179 ventrals in females, 156 in males; 25–28 subcaudals in females, 30 in males; and a tail length of 9.4–10.9% SVL in females and 13.1% SVL in males. In contrast, *A. turikensis* shows 166 ventrals in females; 20–23 subcaudals in females and 24–27 in males; and a tail length of 5.0% SVL in females and 9.0–10.3% in males. The authors also noted that *A. turikensis* is more closely related to *A. indistinctus*, which occurs parapatrically in the Perijá range. Later in the article, curiously, in the diagnosis of *A. turikensis*, they state that this taxon and *A. indistinctus* usually have an irregular vertebral stripe connected to the paravertebral mark and a belly with lateral margins of the ventrals pigmented black (Passos et al. [6], Figure 90). This coloration pattern is strikingly similar to *A. pearti*, yet completely overlooked (it could be that several species were lumped together in their description). In fact, Montes-Correa et al. [79] reported *A. turikensis* from the Colombian Perijá range based on two specimens from the type locality of *A. pearti*, which are morphologically similar to the individuals now under discussion.

All the species from the cordillera de Mérida that Passos et al. [6] synonymized are valid taxa, and their definitive recognition will be explained in various forthcoming articles [10]. For example, new data soon to be published allows the recognition of *A. pearti* as a synonym of *A. turikensis*, found on both slopes of the Serranía de Perijá, occurring parapatrically with *A. indistinctus*. Although Passos et al. [6] synonymized *A. eriki* with *A. indistinctus*, their interpretations are inconsistent. According to these latter authors,

Esqueda et al. [9] stated that *A. eriki* has a uniform dorsal coloration, yet they described and illustrated a vertebral line. However, this statement is not correct and what was really mentioned was “A simple vista, la superficie dorsal de la cabeza y dorso del cuerpo es uniformemente pardo-oscura” and “Al examinar el ejemplar bajo la lupa, las escamas dorsales presentan el borde pardo-oscuro, mientras que la región central es más clara (más evidente en las primeras hileras dorsolaterales en el holotipo”; while the specimen ULABG 6710 has “las escamas que comprenden la región dorsal del cuerpo en su mayoría son de color pardo oliváceo, aunque al nivel de la tercera hilera dorsoventral son pardo oscuras y tienden a formar una línea longitudinal. Entretanto, la región dorsovertebral es pardo oscura, aunque no en todas las escamas”. Nowhere do the authors refer to a vertebral line, as seen in *A. indistinctus* (see Passos et al. [6], Figures 52–54). On the contrary, they refer to dorsal rows 1–3 as immaculate (pale yellow in life; LFE, pers. data). Moreover, a detail not mentioned by Passos et al. [6] refers to the hemipenial morphology: moderately bilobed in *A. indistinctus* vs. slightly bilobed in *A. eriki*. Likewise, the specimen from Cerro Las Tetas, Zulia state (MBUCV, uncatalogued), observed by those authors, shows a fairly uniform coloration, clearly lacking lines (Figure 51A), a point that was also not discussed. While we recognize the specific status of *A. eriki*, a reexamination with multiple sources of evidence is necessary. The same applies to *A. ochrosetrus*, *A. mijaresi*, *A. tamaensis*, and *A. micheleae* (Esqueda et al., in prep.).

Except for the Venezuelan species included here, our ML and BI phylogeny is generally consistent with previous studies on the phylogenetic relationships within the genus *Atractus* [88,89,93,159–161]. Recently, Gonzalez et al. [162] proposed that genetic distances of 3–4% can serve as a useful indicator for species delimitation in the genus *Boa*, incorporating various sources of phenotypic evidence, even in the presence of apparent high polymorphism. In our case, the genetic divergence between *A. erythromelas* and *A. meridensis* exceeds 7% in Cytb and 5% in ND4, and distinction through a set of morphological, meristic, morphometric, and coloration characters supports the recognition of both taxa as distinct species. Therefore, the synonymization proposed by Passos et al. [6] is unjustified, even considering the broader context of their other publications. In contrast, *A. pachacamac* and *A. snethlageae* exhibit very low genetic divergence, and the diagnostic characters used to differentiate them may reflect clinal variation or a degree of polymorphism not yet well defined. Previously, Prudente and Passos [157] recognized that populations of *A. torquatus* from the Amazon Basin (west of Rio Negro, south to Rio Amazonas) correspond to a single species. Interestingly, the geographic pattern exhibited by *A. torquatus* is notably similar to that of *A. snethlageae* (see [159], Figure 6).

A comparable situation is found in the recent proposal by Arteaga et al. [163] to recognize several new species of *Bothriechis* in South America, which was later rebutted by Reyes-Velasco [164], who argued that the genetic differences interpreted as species boundaries may actually reflect clinal variation rather than independent evolutionary lineages (methods and delimitation are inconsistent, [165]). Although hybridization and introgression are evolutionary processes that may play important roles in speciation [166], their historical and geographic contexts in shaping species complexes are only beginning to be understood (e.g., *Bothriechis*, [167]; *Crotalus*, [168]; Schield et al., [169,170]).

5.2. Biogeographical Interpretation and Conservation Status

The results obtained here regarding niche modeling under different paleoclimatic scenarios (Present, LGM 21 Kya, Pliocene 3.2 Myr) suggest that *Atractus erythromelas* and *A. meridensis* have experienced marked geographical differentiation without substantial divergence in their environmental preferences, supporting a scenario of allopatric speciation and niche conservatism [171,172]. The greater niche overlap in the Pliocene could reflect

more stable or broader climatic conditions, which allowed for greater ecological matching between the species. In contrast, the minimum overlap during the LGM ($D = 0.098$) suggests that climatic restrictions intensified ecological segregation and reduced connectivity between populations, thus favoring divergence, although this may have been a passive response to environmental change rather than an adaptive divergence [173,174]. Currently, although a moderate overlap is observed ($D = 0.538$), PERMANOVA tests and niche equivalence indicate significant differences between the species, which reinforces the idea of an ecological separation maintained over time where, despite sharing similar niches, their distribution remains restricted to separate mountainous blocks (e.g., slopes separated by rivers and/or climatic barriers such as extensive semi-arid valleys), probably due to topographic barriers (e.g., topographic complexity) and low vagility, typical of fossorial–cryptic organisms of specialized microhabitats, especially in mountains [88].

For the moment, this dynamic aligns with the idea that non-climatic barriers, such as mountain ranges, deep valleys, or rivers, have played a more significant role than ecological conditions per se in the separation of these mimicry snakes [171,175]. Consequently, the microendemism observed in this group could be explained by a combination of niche conservatism [171], paleoclimatic history (spatial heterogeneity leading to paleoendemism and neoendemism), and topographic complexity (a continuous history of geological changes, [176,177]), rather than active ecological divergence processes [178]. Incorporating more molecular data from Venezuelan Andean species and/or phylogeographic analyses, to the extent possible, would allow us to test alternative hypotheses and refine our understanding of the underlying mechanisms driving diversification in this lineage of snakes, whose diversity in the mountainous systems of the northern Andes is evident [6,8,88,89]. For example, a calibrated phylogeny shows that the mimetic snake group with *A. erythromelas*, *A. meridensis*, and *Atractus nemosophis* diverged from other sleepyhead snakes of the Venezuelan Andes 10.8 Myr ago during the Late Miocene, while *A. erythromelas* diverged from *A. meridensis* and *Atractus nemosophis* 7.61 Myr ago [10]. Today, it is known that low extinction rates are correlated with greater climatic buffering in mountainous regions [179], which would favor both paleoendemism–neoendemism, where museum or cradle hypotheses could explain the diversity of snakes with a narrow distribution like *Atractus* in the Venezuelan Andes (Esqueda et al., in prep.).

Particularly, the cordillera de Mérida comprises a basal uplift ~100 km wide that extends in a NE–SW direction for about 400 km, which does not maintain geomorphological relationships with the eastern cordillera of the Colombian Andes [180], as it was formed from a complex geodynamic interaction between the Caribbean plate, the Panama Arc, the South American plate, and the Maracaibo continental block [181]. It is considered a doubly vergent orogen, with the wetter wedge of the Lake Maracaibo basin on the northwest side and the drier basin and wedge of Barinas on the southeast side [182]. Although it covers an area of ~4.3% of the country, it is more complex than any other nearby mountain system. The pattern is determined by its extensive and variable altitudinal gradient and the presence of two different climatic regimes between both slopes, which directly influence the landscapes of the intramontane valleys [61]. Another finding that corroborates the above is *Tantilla palamala*, an Andean snake that diverged from the other species of the *T. melanocephala* group about 8.09 Myr ago, which exhibits a biogeographic pattern similar to that found by us for *A. meridensis* [148]. In fact, this timing is consistent with Boschman [183], who suggested that the cordillera de Mérida had elevations between 3500 and 4000 m 7 Myr ago, based on the discovery evidence of paramo vegetation in the sediments of the Lake Maracaibo basin.

A. erythromelas and *A. meridensis* are a reflection of strictly vicariant speciation due to geographical isolation, and niche conservation is expected (see [173]). While climatic niche

divergence may be a widespread mechanism of speciation in terrestrial vertebrates [184], vicariant allopatric speciation can precede niche divergence [185,186]. In cases where, for example, two populations isolate themselves in allopatric but environmentally similar habitats, the lineages can adapt in parallel, and speciation can occur through factors unrelated to niche divergence [186]. Unlike anurans, the distribution of lizards and snakes in tropical mid-highlands is related to the plasticity of their thermal physiology and their evolutionary history (e.g., *Anadia*, [187,188]). Therefore, mountain species with small distributions follow aggregated geographical patterns (e.g., birds, [189]) derived from high spatial and temporal variation in climate and habitat [190,191], emerging narrow climatic niches [192], and/or climatic niche breadth [193]. Our still incipient data suggest that *Atractus* exhibits this pattern, although we can establish a macroevolutionary interpretation regarding speciation and the underlying mechanisms that drive it, which would be a key question to be evaluated [10].

Our field data accumulated over several years suggest that the sleepyhead snakes of the cordillera de Mérida tend to be locally common and gregarious in response to a variety of signals, such as reproductive or thermal [194], but with a reduced habitat breadth (<20,000 km²), and they frequently occur in highlands [195], similar to other Neotropical snakes (e.g., viperids, [196]). Although the ecology of this South American genus remains discrete, compared to its diversity (>150 spp., Uetz et al. [3]), various studies show that these snakes exhibit a specialized diet of earthworms [151,152,197]. Until now, all environments above 1500 m in altitude in the cordillera de Mérida have been seriously affected by anthropogenic activities [146,198,199]. During 2021, we had the opportunity to visit the Mucuyupu–Tafallé population, Trujillo state, Venezuela, between 2000 and 2500 m, where, according to the locals, *Atractus* was a very commonly observed snake. However, we only managed to find a single juvenile specimen of *A. meridensis* and an adult female of *A. emigdioi* (still uncatalogued). The area has been subjected to intense periods of agricultural activities, and we did not observe any worms. Although the abundance and population dynamics of earthworms can be affected by anthropogenic activities [200,201], if we consider the optimal foraging theory [202], it is possible that the spatial and temporal dimensions of habitat disturbance could affect specialist reptiles like vermivorous snakes, but there are no studies demonstrating this in *Atractus*. Balestrin et al. [152] suggested that the abundance of *A. reticulatus* in anthromes is due to the adaptation to new prey (introduced earthworms). We are aware that there are more questions than answers, but it is well known that twenty percent of Neotropical reptile species are threatened, with the same proportion catalogued as Data-Deficient [203].

To conclude, it is highlighted that the integrative review of *A. erythromelas* and *A. meridensis* first resolves their taxonomic status and then recognizes their allopatric and highly fragmented distribution due to the gradual deterioration of their environments, and, although locally abundant, they exhibit a narrow breadth. Therefore, the recognition according to IUCN criteria as Vulnerable provides a solid foundation necessary to reevaluate the biodiversity and conservation status of Andean reptiles. Although the Andes of Venezuela are among the five critical hotspots of biodiversity [204], the political–social crisis of recent decades has decimated any research efforts in that direction (see [205]). In fact, if we consider that Oliveira-Miranda et al. [206] published information regarding the vulnerability situation of the ecosystems in the country and that we are unaware of the effect of the crisis due to a lack of data (e.g., extraction of wood from Andean forests), the current outlook could be concerning for many reptile species, in particular specialists like *Atractus*.

Supplementary Materials: <https://www.mdpi.com/article/10.3390/d17100725/s1>, Table S1: PCR. Refs. [207–210] are cited in the supplementary materials; Table S2: Specimens Genbank, Table S3: Specimens_Museum, Table S4: Pearson Corr, Table S5: Bioclimatic Variables, Table S6: Models ENMVAL, Table S7: Geometric_Morphometric, Table S8: CYTB Distance, Table S9: Cytb Group, Table S10: ND4 Distance, Table S11: ND4 Distance Group, Table S12: AUC Maxent, Table S13: TSS Metric, Table S14: Vegetation_MaxEnt, Table S15: Jackknife_MaxEnt, Table S16: Bio_Variables_MaxEnt, Table S17: PCA climatic niche, Table S18: Variables_PCA niche, Table S19: EOO and AOO, Table S20: Analyses Morph, Table S21: DFA, Table S22: ANOVA_Species_PCA, Table S23: PERMANOVA_Mala_Di_PCA.

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