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¿ARE THE VENEZUELAN ANDES A SPECIES PUMP FOR *ATRACTUS* SNAKES (SERPENTES: DIPSADIDAE)? CONTRASTING THE EVOLUTIONARY AND BIOGEOGRAPHICAL HISTORY IN THREE BIOREGIONS OF VENEZUELA

TESIS PARA OPTAR AL GRADO DE DOCTOR EN SISTEMÁTICA Y BIODIVERSIDAD

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DEDICATION

I am a multidimensional being living a physical experience, and thanks to the immeasurable love of Luis Ramón Esqueda and Luisa Elena González Gómez, I exist on this existential plane... In their memory forever!!!

"Rise again and again until the Lambs become Lions". CHARLES DICKENS…

Resist, persist and do not stop! "We are the ones we have been waiting for". HOPI INDIANS…

"Triumph and failure are opposite sides of the same coin; you must live both in every existence". LFE 2023…

ACKNOWLEDGEMENTS

Throughout my university journey, I have had to face various obstacles and setbacks that, thanks to the wisdom and help of hundreds of people, I have been able to overcome with persistence, dedication, and conviction. Although I cannot name them all, I carry them in my heart as an imprint. With reference to academics and research, I wish to immensely thank the professors: Enrique La Marca, Jorge Durán Pulido, Dario Garay Jerez, Irma Guillen, Ceres Boada, and Henry Rodríguez Carrasquero, who believed in me unconditionally, providing their support to reach the academic pinnacle. Their humanism, academic sense, and values have been exceptional in my journey as a ULA student; to Enrique La Marca, a mentor, colleague, and friend, equally enamored as I am with the diversity of reptiles and amphibians in Venezuela, especially those unique to the Andes of Venezuela; the research I have achieved so far bears a significant imprint of his influence. Not all setbacks tend to have a bitter taste; they can be positive or vary in their effect, but in the end, we must face them. Between 2010 and 2015, after the death of my great friend Marco Natera, I had to bravely take on his unfinished project, "The Snakes of Venezuela," which I managed to publish with the immeasurable help of my wife Marisol Díaz. Although she was not present during the final phase of my doctorate, as she decided to separate, I cannot forget that her support and love while she was there were the driving force to continue pursuing this goal.

In the context of the doctorate, I must first express my gratitude with great humility and heartfelt recognition to the University of Concepción and the committee of the PhD in Systematics and Biodiversity, Faculty of Natural and Oceanographic Sciences, for this opportunity. During a phase of the doctorate, I had to go through a difficult personal situation; however, the support from Professor Juan Carlos Ortiz and Claudio Correa has been unwavering, always providing encouragement to successfully complete this project.

Since I had the idea, this ambitious and unprecedented project has involved enormous contributions and assistance from many people and institutions. On a personal level, my mentors have believed in the idea and have been consistent in dealing with the unexpected vicissitudes, which have been managed under a complex scenario. Regarding the field activities, the start of the project received immeasurable support

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RESUMEN

La diversidad de especies puede variar considerablemente entre grupos taxonómicos y a lo largo del tiempo en un mismo linaje. Comprender estos procesos y mecanismos en relación con su diversificación en el Neotrópico constituye siempre un tema abierto en la biología evolutiva, sobre todo en las serpientes que han experimentado momentos explosivos de innovación trófica a lo largo de su historia evolutiva. Dentro de los dipsadinos, *Atractus* Wagler, 1828 representan una radiación de ~150 especies distribuidas por el Nuevo Mundo, desde el sur de Panamá hasta Argentina. El interés en este enigmático grupo de serpientes continúa creciendo debido, en parte, a su bioecología y distribución dominante en montañas, brinda una excelente oportunidad para investigar los patrones desde una perspectiva biogeográfica y evolutiva. Para examinar la diversificación y los patrones biogeográficos en este grupo de serpientes, reunimos un conjunto de datos multilocus ~3500 pb que abarca dos loci nucleares (NT-3 and RAG-1) y tres mitocondriales (16S, Cytb and ND4). Se implementaron análisis filogenéticos calibrados con fósiles y análisis de la tasa de diversificación subsiguiente mediante máxima verosimilitud e inferencia bayesiana para examinar su historia evolutiva y la dinámica temporal de la diversidad. Con base a esta idea, investigamos la dinámica de diversificación mediante la integración de múltiples enfoques filogenéticos y macroevolutivos (42 % de su diversidad). Los gráficos de linaje a través del tiempo (LTT) y las métricas de la tasa de diversificación (DR) indicaron una acumulación heterogénea de linajes, con cambios asociados a los eventos orogénicos andinos. Los modelos de diversificación dependiente de la densidad (DDD) sugirieron que la acumulación de linajes puede estar restringida por límites ecológicos, con evidencia que favorece los escenarios dependientes de la diversidad sobre los modelos de tasa constante. Los modelos dependientes del estado revelaron un papel de la geografía en la conformación de la diversificación: los análisis BiSSE respaldaron las diferencias en especiación y extinción vinculadas a las regiones andinas versus no andinas, mientras que los modelos ClaSSE destacaron la influencia de estados distribucionales complejos y procesos cladogenéticos. Complementariamente, los análisis BAMM detectaron heterogeneidad en la tasa de diversificación, identificando aceleraciones de la tasa en clados montanos. MEDUSA corroboró cambios significativos en la tasa a lo largo de la filogenia, en consonancia con una radiación en áreas topográficamente complejas. En

conjunto, estos enfoques complementarios revelan que la diversificación de *Atractus* ha sido determinada por una combinación de oportunidades geográficas, limitaciones ecológicas y radiaciones impulsadas por las montañas (e.g, levantamiento de los Andes centrales y septentrionales). Hasta este momento, encontramos apoyo para el aumento de las tasas de especiación y extinción asociadas con los linajes Andinos vs. No Andinos, lo que respalda la hipótesis de que los Andes pudo haber funcionado como cuna o bomba de especies, debido a la heterogeneidad de paisajes y complejidad topográfica que favoreció la especiación alopátrica. Mientras, los análisis biogeográficos sugieren un origen en los Andes septentrionales hacia el Pacífico, alrededor de 22 Myr durante el Mioceno temprano, indicando una rápida radiación temprana seguida de una reciente disminución de la tasa de especiación. Finalmente, reevaluamos la sistemática del género en Venezuela por medio de una robusta delimitación de especies, con la ayuda de múltiples fuentes de evidencia, describiendo nuevas especies y evaluando su estatus de conservación. Este estudio proporciona un marco combinado de hipótesis evolutiva-biogeográfica, taxonómica y de conservación para entender la riqueza de estos dipsadinos y el papel del levantamiento andino en su diversificación y patrón biogeográfico.

ABSTRACT

Species diversity can vary considerably between taxonomic groups and over time within the same lineage. Understanding these processes and mechanisms in relation to their diversification in the Neotropics is always an open topic in evolutionary biology, especially in snakes that have experienced explosive moments of trophic innovation throughout their evolutionary history. Within the dipsadines, *Atractus* Wagler, 1828 represent a radiation of ~150 species distributed across the New World, from southern Panama to Argentina. Interest in this enigmatic group of snakes continues to grow, partly due to their bioecology and dominant distribution in mountains, providing an excellent opportunity to investigate patterns from a biogeographical and evolutionary perspective. To examine the diversification and biogeographic patterns in this group of snakes, we gathered a multilocus dataset of ~3500 bp encompassing two nuclear loci (NT-3 and RAG-1) and three mitochondrial loci (16S, Cytb, and ND4). Phylogenetic

analyzes calibrated with fossils and subsequent diversification rate analyzes using maximum likelihood and Bayesian inference were implemented to examine their evolutionary history and the temporal dynamics of diversity. Based on this idea, we investigated the dynamics of diversification by integrating multiple phylogenetic and macroevolutionary approaches (42% of their diversity). The lineage-through-time (LTT) plots and diversification rate (DR) metrics indicated a heterogeneous accumulation of lineages, with changes associated with Andean orogenic events. Density-dependent diversification (DDD) models suggested that lineage accumulation may be restricted by ecological limits, with evidence favoring diversity-dependent scenarios over constant-rate models. State-dependent models revealed a role of geography in shaping diversification: BiSSE analyzes supported differences in speciation and extinction linked to Andean versus non-Andean regions, while ClaSSE models highlighted the influence of complex distributional states and cladogenetic processes. Complementarily, BAMM analyzes detected heterogeneity in the diversification rate, identifying rate accelerations in montane clades. MEDUSA corroborated significant changes in the rate throughout the phylogeny, in line with a radiation in topographically complex areas. Overall, these complementary approaches reveal that the diversification of *Atractus* has been determined by a combination of geographical opportunities, ecological limitations, and mountain-driven radiations (e.g., the uplift of the central and northern Andes). So far, we have found support for the increase in speciation and extinction rates associated with Andean vs. Non-Andean lineages, which supports the hypothesis that the Andes may have functioned as a cradle or species pump, due to the landscape heterogeneity and topographic complexity that favored allopatric speciation. Meanwhile, biogeographic analyzes suggest an origin in the northern Andes toward the Pacific, around 22 Myr during the early Miocene, indicating a rapid early radiation followed by a recent decline in the speciation rate. Finally, we reevaluated the systematics of the genus in Venezuela thru a robust species delimitation, with the help of multiple sources of evidence, describing new species and assessing their conservation status. This study provides a combined framework of evolutionary-biogeographic, taxonomic, and conservation hypotheses to understand the richness of these dipsadines and the role of the Andean uplift in their diversification and biogeographic pattern.

OVERVIEWS OF CONCLUSIONS

Origin and diversification linked to the Andean uplift: suggests an Andean-Pacific origin of the genus *Atractus* during the Miocene (~22 Ma), followed by a colonization towards the northern Andes during its early-middle uplift phase in the Pliocene. This reinforces the hypothesis that the uplift of the Andes was a key driver in the diversification of the group.

Diversity concentrated in mountainous areas with high endemism: although the systematics of the genus remains an open topic, here with 42% of the known *Atractus* species evaluated, a marked concentration of diversity above 1000 m in the central and northern Andes is demonstrated. In particular, the species of the cordillera de Mérida reflect historical events of geographical isolation, distribution changes due to climatic fluctuations, and recent population expansion.

Niche conserved in allopatric species: ecological analyses show consistent patterns of niche conservation among Andean species (Venezuela), with high similarity in the use of climatic space. This indicates that speciation occurred without substantial changes in the niche, supporting the hypothesis of allopatric speciation driven by geographic isolation rather than adaptive divergence.

The Andes as a driver and receiver of evolutionary diversity: The applied models reveal that the Andes not only promote high rates of speciation and extinction (the "species pump" hypothesis) but also act as a biogeographic magnet ("species attractor"), with high rates of colonization from non-Andean areas (at least the central Andes). Then the Andes stands out as a dynamic hotspot of evolution, favored by its topography, isolation, and ecological stability.

Conservation implications: all Andean species of *Atractus* in Venezuela inhabit cloud forests above 2000 m, ecosystems in severe decline due to anthropogenic transformation. Although a broader assessment is still required, preliminary data indicate that all these species should be considered Vulnerable under the IUCN criteria A2 and B2, highlighting the urgency of their protection.

AUTORIZATION

To whom it may concern, Luis Felipe Esqueda González, rut 22.413.699-4, student of the Doctorate program in Systematics and Biodiversity, taught by the Faculty of Natural and Oceanographic Sciences, of the University of Concepción, I declare that I am the author of the thesis project titled "Are the Venezuelan Andes a Species Pump for *Atractus* snakes (Serpentes: Dipsadidae)? Contrasting the Evolutionary and Biogeographic History in three Bioregions of Venezuela. In this sense, I grant the right of publication, communication to the public, and reproduction to the University of Concepción, becoming an integral part of the collection of physical or digital material in any of the libraries of the University of Concepción and its institutional repository. This authorization is free of charge, without prejudice to your unpublished information that must be subsequently published as required by the academic and scientific institutional bodies. In such a way, its reproduction and dissemination are for academic purposes and for national and international dissemination. For the subsequent purposes, I finally declare that this thesis project does not infringe any copyright of third parties, nor does it constitute plagiarism or unauthorized use of unpublished information.

On the twenty-one day of June 2025,

Luis Felipe Esqueda González

BACKGROUND

1.1 Biogeographic synthesis from Venezuela

Venezuela is located on the northern coastal of South America, between the equator and 12° north and the western meridians 60° and 74°. It is bounded to the north by the Caribbean Sea and to the northeast by the Atlantic Ocean. It borders Brazil to the south, Guyana to the east, and Colombia to the west. Likewise, it has a continental area equivalent to 916,445 km^2 and a coastline of 4,261 km. The landscape of Venezuela is the result of intense past geological activity that shaped the current coastlines (Caribbean coast) and the formation or depression of mountain chains or mountain ranges such as the Andean and the Coastal. Likewise, the emergence of sedimentary land formations ("Los Llanos") is due to changes on the course of the Orinoco River (Gamero 1995) and the ancestral influence of the Guiana Shield and Pantepui (Rod 1981; Hoorn et al. 1995). Thus, here we find diverse landscapes of Andean mountains, Caribbean mountains and islands, tepuis, Amazonian shade forests and jungles, gallery forests and jungles, mangroves and other marine-coastal ecosystems, continental wetlands, savannahs, and xeric shrubs, among others. As for the current climate of Venezuela, it is tropical, with an isothermal temperature regime, and with two main rainfall patterns: one with a single peak and another with two annual rainfall maximums. Below 1,000 m elevation there are warm and very warm climates, while in the middle-highlands there is a wide variability of topoclimates (La Marca 2012). In this sense, four of the largest biogeographic regions located in South America converge in Venezuela: Guiana, the Amazon, the Caribbean and the Andes.

MARN (2001) divided Venezuela into ten main bioregions according to climatic and vegetation characteristics. Although, the serranía de Perijá and the cordillera of Mérida are considered separate bioregions, these make up what we know as Venezuela Andes. If well the Pantepui could be a separate bioregion, here preferred to leave that area as the bioregion of the Venezuelan Guiana Shield (McDiarmid and Donnelly 2005; Rodríguez et al. 2010). Then, for biogeographic purposes with respect to the sleepyhead snakes of *Atractus* genus, we are only going to treat three bioregions where the greatest diversity of this group is found so far: cordillera of Mérida, cordillera de la Costa (central and eastern stretch), and Guiana Shield to the South of the Orinoco River (Delta Amacuro, Bolivar and Amazonas states).

1.1.2. Cordillera de la Costa

In the central north and towards the northeast of Venezuela there is a series of mountain ranges with the Caribbean climatic influence, caused by the tectonic interaction between the South American plate and the Caribbean plate (La Marca 2012). The Coastal Mountain Range, formed during the Tertiary period, is older than the Andes. This began to be uplifted by tectonic movement during the Late Cretaceous period, and reached its current configuration with an orientation from west to east (Steyermark 1979). It is separated from the Andes (cordillera of Mérida) by the Yaracuy depression, and from the southern forests of the floristic province of Guiana by the extensive Llanos. The montane forests are isolated from each other by extensive xeric vegetation. Isolation and a great variety of physiographic settings have created an extraordinary richness of species and strong speciation processes that are manifested in a relatively high level of endemism in plants and animals. According to Huber (1997), this bioregion includes three types of forests: evergreen transitional forests, evergreen montane cloud forests, and upper montane dwarf forests. Transitional evergreen forests, ranging from 600 to 900 m, form a narrow belt between lower montane semideciduous forests and upper montane forests, or evergreen montane cloud forests. Phytogeographically, the cordillera de la Costa shows a stronger affinity with Mesoamerica and the Caribbean regions more than with the flora of northern Andes (Huber 1997) and components of the flora of Guiana (Steyermark 1979).

1.1.3. Venezuela Andes (cordillera de Mérida + serranía de Perijá + Tamá massif)

The northern Andes, which are located north of the Huancabamba deflection at 6° S (Gansser 1973), differ from other segments of the Andes due to the presence of oceanic material accretion and a transpresional deformation regime during the construction of the Cenozoic Mountain (Ramos and Alemán 2000; Taboada et al. 2000; Trenkamp et al. 2002). The Venezuelan Andes constitute an extension of the eastern mountain range of Colombia, which bifurcates in the Pamplona Nude, in what we know as the Perijá mountain range and the cordillera of Mérida. The latter is separated by the Tamá massif, at the northern end of the eastern part of the mountain range, by the so-called Táchira depression. The cordillera de Mérida extends over 400 km long and 80 km wide in a northeasterly direction to the Carora (Lara state) and Yaracuy (Yaracuy state)

depressions, in an area of approximately 32,500 km^2. It creates a large division between the watersheds of the Orinoco tributaries in the southeast, and the Lake Maracaibo drainage to the northwest. It can be divided into three main sections: southwest, center and northeast. The southwestern section is dominated by the Paramo of Batallón at 3913 m, the slightly lower Zumbador and La Negra massifs, and the Sierra de Tovar, which culminates in the Paramo de Nariño at 3517 m. The central section is the highest, with two parallel ranges separated by the Chama River valley, the Sierra Nevada with the highest elevation in Venezuela, Pico Bolívar at 5007 m, and several peaks exceeding 4500 m, extending towards the northeast of the Sierra of Santo Domingo, and the Paramo of the Culata with the highest elevation in the Paramo of Piedras Blancas at 4729 m, which extends to the Sierra of Trujillo, with the highest elevation in the Teta de Niquitao at 4003 m. The northern section is formed by the Guaramacal massifs and its northern extension is the Paramo Cendé at 3650 m. The Tama massif is a geological and biogeographic extension of the Eastern cordillera of Colombia that penetrates the Venezuelan states of Tachira and Apure. The area of the Andean-Llanos foothills (Tachira and Mérida states) has recently been proposed as a different zoogeographic unit based on the vegetation, which has been considered different from both that of the Llanos and the rest of the region. Previously, the Andean foothills of Táchira state, especially Doradas River valley, had been proposed as an inlet for western Amazonian fauna (La Marca 2012). One of the most interesting distribution patterns of the herpetofaunistic richness of the cordillera of Mérida is the presence of Amazonian elements, or Amazonian affinities, on the Andean-plain slopes of this mountain system. This is the youngest mountain range of Venezuela, reaching its present landscape configuration just 1 Myr, during Pleistocene. Biogeographic affinities are markedly Caribbean, and have been assigned to the Costa Venezolana biogeographic province Morrone (2001).

1.1.4. Guiana Shield (Escudo de Guayana o Escudo Guayanés)

The Guayana Shield region, and the area of north-eastern South America extending between the Orinoco River to the North and the Amazon River to the South (8°N to 1° S). The region that includes Venezuela it occupies almost half of the national territory. It is made up of the remains of formations from the pre-Cambrian period, which contains the oldest rocks on the planet (~1.7 billion years old). The Guayana region is surrounded by the Caribbean and Amazon regions and is subdivided into four

provinces: the province of Eastern Guayana, the province of Western Guayana, the province of Central Guayana, and the province of Pantepui. Present-day montane landscape characterized by the numerous, up to 3000-m high table mountains (tepuis), which are surrounded by wide uplands, deep valleys and extensive premontane glacis, one of the oldest geological areas in South America (Rull et al. 2019). This area is a geological unit that comprises approximately 13 % of South America (1, 800, 000 km^2) This region is environmentally, hydrologically and topographically complex, mostly covered by a highly diversified mosaic of tropical lowland and upland forest types, with the spectacular flat-topped sandstone mountains known locally as tepuis that rise abruptly above the surrounding highlands and lowlands, constituting its most distinctive physiographic feature, and with a diversity of fauna and flora notable, but even more striking is its level of endemism (Berry and Riina 2005; Hollowell and Reynolds 2005; Naka 2011). Pantepui has been defined as a discontinuous biogeographic province of Guayana (Rull et al. 2019), ranging between 1500 and 3014 meters above sea level (Huber 1988), with a composite area of approximately 6,000 km^2 (Nogué et al. 2009), which represents a small proportion (<1 %) of the total area of the entire Guayana Shield (Huber 1995). While the Orinoco Delta supports a vast, largely undeveloped mosaic of tropical wetlands and shallow aquatic ecosystems within the coastal plain of eastern Venezuela (Warne et al. 2002), marked by its own climatic, geological, and biological patterns, which have been subject of great controversy and multiple proposals of biogeographic hypotheses regarding its diversity and classifications of its natural areas (Pérez-Hernández and Lew 2001).

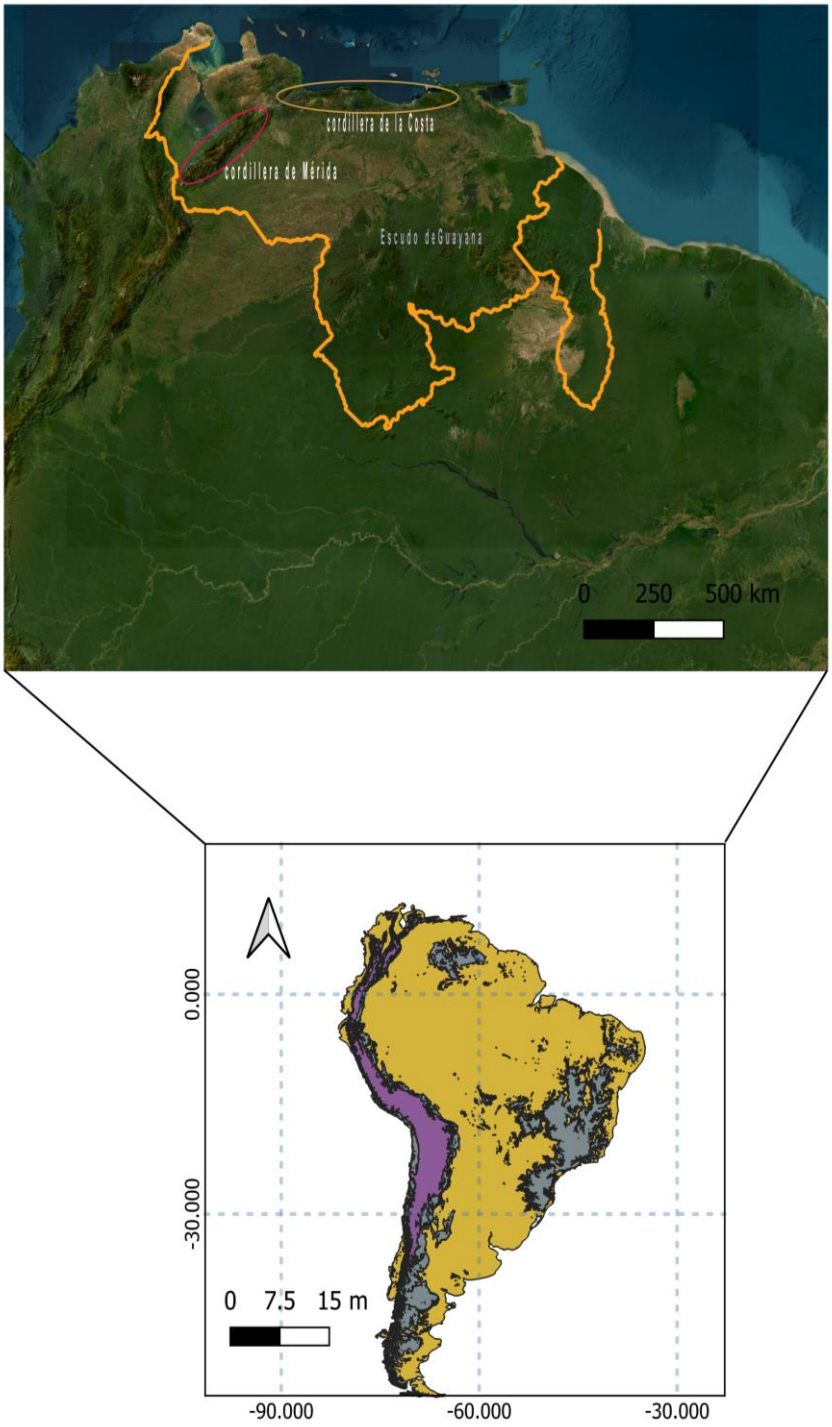

FIGURE 1. Location of Venezuela in South America. Highlighted areas include the study areas, with special emphasis on the cordillera de Mérida, which presents the greatest diversity of *Atractus* in the country.

1.2 Squamata, the most diverse reptiles

1.2.1. Origin and diversification of reptiles

Among the fascinating tetrapods, the current reptiles that comprise the order Squamata Oppel, 1811 (moon lizards and snakes) are among the most diverse radiations of

terrestrial vertebrates. Squamata includes more than 10,000 species and 2,700 subspecies, organized into 92 families and 1,220 genera (Uetz et al. 2023). Although uncertainty remains regarding clade relationships in Squamate, Sauria is best defined as all lepidosaurs that are more closely related to snakes than to Sphenodon (Townsend et al. 2004; Vidal and Hedges 2005; Sánchez-Martínez et al. 2007; Conrad 2008). However, the first radiation must have occurred between the Late Triassic and Middle Jurassic. Many Jurassic-Early Cretaceous taxa of Squamate are basal members of the major clades, but Squamata fossils from the Middle Cretaceous demonstrate greater morphological diversity and provide the first records of modern families (see Evans et al. 2006).

This diversity makes reptiles the largest group of vertebrates after fish (~25,000 species) and birds (~10,000 species). The rate of new species descriptions shows no signs of slowing down, with a record 168 new species described in 2012 (Uetz et al. 2018), higher than the highest annual rates of the 18th and 19th centuries, for example, 118 species in 1758 and 144 in 1854, respectively were described. Biogeographically, Squamate are found on all continents except Antarctica and the Indian Ocean and exhibit diverse dietary ecology and body forms adapted to different environments, from limbless fossorial to aquatic. In South America, Squamate constitutes >22 % of all the diversity known in the rest of the world. When referring to snakes, Dipsadidae is the most ecologically and morphologically diverse family of snakes (Cadle and Greene 1993). Although its origin in the past has been contradictory due to different positions (Cadle 1985), recent studies support the clade's Asian origin 50 Myr ago and the subsequent dispersal towards North America (Serrano et al. 2023), probably through the Beringian Bridge, a land bridge that connected the Palearctic and Nearctic realms during the Eocene approx. 33-55 Myr (Wolfe 1975; Baskin and Baskin 2016) and that favored the dispersal of ectothermic organisms (Graham 2018), due to the presence of a mosaic of vegetation types adapted to mesic and arid conditions such as forests, shrublands and associations of steppes (Young 1982; Elias and Crocker 2008). Other examples in Squamata are consistent with this idea, where at least three independent dispersal events of lizards from Asia to North America occurred (Macey et al. 2006); even current members of the Lampropeltini tribe of North America are a consequence of the dispersal of an ancestor from Asia in the late Eocene (Burbrink and Lawson 2007). Another idea relatively consistent with the available data suggests a Central

American origin for the Dipsadidae snakes of the subfamilies Dipsadinae and Xenodontinae, with their subsequent dispersal to South America. Although a large part of the lineages Xenodontinae diversified outside of Central America, Dipsadinae did not, and they experienced dispersal to South America several times during their diversification (Serrano et al. 2023) and before the formation of the Isthmus of Panama, where there was expansion to and from Central America of these snakes, consistent with two significant increases in migration rate (Bacon et al. 2015). In Viperidae, *Bothrops asper* related to *B. atrox* and *B. venezuelensis* (Carrasco et al. 2023) invaded Mesoamerica several times during its complex history, involving at least two events before closing the Isthmus of Panama (Saldarriaga-Córdoba et al. 2017). Previously, the idea was supported by Savage (2002) to explain the differential distribution of taxa of South American origin in Mesoamerica. Regarding the dipsadids, Serrano et al. (2023) propose a Central American ancestor for the *Geophis* + *Atractus* clades and that the latter, like other members of Dipsadines diversified in South America during the early Miocene (~23 Myr). 25 Myr ago, the western mountain range of the Colombian Andes was at no more than half of its modern elevation, while the eastern mountain range of Colombia reached 25-30 % of its modern elevation in 20 Myr; and no more than half of its modern elevation in 10 Myr (Gregory-Wodzicki 2000). On the other hand, the cordillera of Mérida had a significant elevation starting 2000 m about 5-2 Myr (van der Hammen et al. 1973. Initially, this scenario is consistent with dispersal, but to the extent that mountain building (northern Andes) during the Middle Miocene (~12 Myr) and Early Pliocene (~4 Myr) led to vicariant events resulting in a diversification pattern Cis-Andean and Trans-Andean for many clades of dipsadid snakes, the most distinctive example of which is *Atractus* with more than 151 species (~100 spp. Cis-Andean).

In recent decades, molecular studies have focused on exploring different hypotheses to explain the origin of this vast, enormous and poorly understood South American diversity (Haffer 1969; Terborgh et al. 1990; Molino and Sabatier 2001; Leite and Rogers 2013; Crouch et al. 2019). Most of these studies have used genetic genealogies to infer the timing and geographic location of divergence across taxa, and have primarily linked patterns of evolutionary relationships to vicariant events generated by Pliocene/Miocene landscape changes (e.g. Andean orogeny, connection of the Isthmus of Panama, drainage changes of large rivers, and marine transgressions) or climatic oscillations during the Pleistocene (glacial-interglacial cycle) (Rull 2011; Turchetto-

Zolet et al. 2013). However, recent meta-analyses have shown that such generalizations do not justify everything; consequently, the origin and maintenance of existing Neotropical biodiversity seem to respond to a complex phenomenon. From this follows the dependence on synergistic environmental drivers that have operability and are, therefore, tied to different spatial and temporal scales (Rull 2008; Turchetto-Zolet et al. 2013; Antonelli et al. 2018).

1.2.2 *Atractus* as a model in the northern of South America

Both reptiles and amphibians collectively comprise much of the diversity of known tetrapods on the planet. The order Squamata Oppel, 1811, includes by far the greatest diversity of reptiles in the world, and is the largest and most diverse radiation of terrestrial vertebrates. Within Squamate, snakes are a group consisting of ~3,793 spp. (Uetz et al. 2023), where the Caenophidia clade corresponds to a lineage of advanced alethinophidia snakes that radiated mainly during the Neogene (Zaher et al. 2019). On the other hand, within the Caenophidia, Dipsadidae *sensu lato* constitutes a monophyletic lineage exclusive to the Neotropics and currently comprises around 700 distributed species (Cadle and Greene 1993); the family is defined both by morphological characters, such as the presence of elongated lateral spines and two distinctly ornamented regions of lobes on the hemipenes (Zaher 1999) and molecular data (Vidal et al. 2000; Zaher et al. 2009; Pyron et al. 2013; Grazziotin et al. 2012; Zaher et al. 2019). Meanwhile, the subfamily Dipsadinae (Zaher 1999) is made up of 24 genera and approximately ~350 species of snakes of diverse habits (Ferrerazi 1994; Fernandes 1995; Zaher 1999), making the genus *Atractus* the most ecologically diverse and rich in species. It currently includes over 151 recognized species (Uetz et al. 2023).

The genus *Atractus* Wagler, 1828 called tierreras or sleepyhead, comprises a member of the subfamily Dipsadinae, with a wide distribution in South America, from the eastern region of the Isthmus of Panama (Myers 2003) to northern Argentina (Savage 1960; Roze 1966; Peters and Orejas-Miranda 1970; Pérez-Santos and Moreno 1988; Giraudo and Scrocchi 2000). Unlike other clades of South American ophidians, information about their biology and ecology remains incompletely resolved. Among the small dipsadid species that may have secondarily acquired slow catching behavior are many species of *Atractus*. These species all appear to eat earthworms, presumably in the same

way, but show extraordinary variation in the cervicomandibularis muscle with yet unexplained functional relevance (Cundall and Irish 2008). Although scarce, analyses of the available diet of some *Atractus* suggest a diet predominantly of worms (Martins and Oliveira 1999; Balestrin et al. 2007; Camper and Zart 2014; Perrella and Francisco 2016; Passos et al. 2018; Murphy et al. 2019), compatible with the anatomy of the gnathic complex (*sensu* Cundall and Greene 2000). This dietary specialization is also shared by other snakes of similar habits such as *Carphophis*, *Diadophis*, *Geophis*, *Ninia*, *Storeria*, *Virginia* and semiaquatic snakes *Gomesophis*, *Sordellina* and *Thamnophis* (Pisani 2009). These curious snakes are small to medium, usually not exceeding 500 mm, but some species reach 1000 mm (Passos et al. 2018); they are diurnal or nocturnal snakes, and to a lesser extent cathemeral, exclusive in terms of their microhabitat and secretive behavior, so published data from observations have suggested that they may be terrestrial, cryptozoic and semifossorial. With thin bodies and a different head, not the neck, and clear differences between the species that suggest clear adaptations to their environment and not their diet, they have a small head that passes imperceptibly into the body and a short to long tail (sexual dimorphism usually occurs). Small eye with a round pupil. The scales are mostly smooth, rarely keeled (Hoogmoed 1980a,b; Martins and Oliveira 1993; Prudente and Passos 2010), apical pits are absent in most cases (Martins and Oliveira 1993). Dorsal scales on the body without reduction, arranged in 15 or 17 rows. Loreal scale present in all species, in contact into orbit, separating prefrontals and supralabials. Preocular absent, except sometimes in *A. favae* (Savage 1960). Temporal scale formula usually 1 + 2. A single pair of geneial shields, except for some species such as *A. vittatus* and *A. favae* (Roze 1966; Savage 1960). Cloacal plate entire, subcaudals divided. Maxillary teeth vary between 4-8, without diastema. Bilobed or single hemipenis, differentiated or not, hemipenes are structures that, unlike others, do not have an obvious correlation with the ecology, feeding or locomotion of the animal, therefore, they provide better information on genealogical relationships between taxa than characters correlated with the habitat, especially at levels inferior to family (Zaher 1999).

This increase in the number of Squamate species in the last decade is the direct result of an intensification of phylogenetic research in the group, with greater effort dedicated to including not only more species in the analyses, but also new molecular markers of rapid evolution (Uetz et al. 2021). At a hierarchical level, Zaher et al. (2009) presented a

molecular phylogenetic analysis of xenophidian snakes, using sequences of two mitochondrial genes (12S and 16S rRNA) and one nuclear gene (c-mos), (1681 total base pairs) and 131 terminal taxa sampled from all over of the planet, mainly xenophidian lineages, but focusing on neotropical xenodontines. Grazziotin et al. (2012) performed a phylogenetic analysis of New World dipsadids based on an expanded data matrix including 246 terminal taxa, of which 196 are dipsadids, sampled for eight genes (12S, 16S, cytb, nd2, nd4, bdnf, c-mos, rag2). Likewise, Pyron et al. (2013) presented the first large-scale phylogenetic estimate for Squamata, the estimated phylogeny contains 4,161 species, representing all currently recognized families and subfamilies. The analysis was based on up to 12,896 database pairs of sequence data per species (average = 2,497 bp) from 12 genes, including seven nuclear loci (Bdnf, c-mos, Nt3, Pdc, R35, Rag-1 and Rag-2) and five mitochondrial genes (12S, 16S, cytochrome b, Nd2 and Nd4), where *Geophis* seems paraphyletic with respect to the genus *Atractus* and corroborated by a more recent study with a greater number of species (Pyron et al. 2013; Zaher et al. 2019). The first phylogenetic analysis of *Atractus* in a strict and broad sense was presented by Arteaga et al. (2017), who generated a molecular phylogeny of the genus (a single molecular marker), whose sampling included 21.4 % of the 140 species currently recognized at that time. The phylogenetic tree supports the existence of at least three new species in the Pacific lowlands and the adjacent Andean slopes of the Ecuadorian Andes. Previously, Oliveira and Hernández-Ruz (2016), using a mitochondrial marker, made another phylogeny with the relationship to *Atractus tartarus*. The tendency to use the genus as a biogeographic study model is beginning to be vital to understanding the phylogeographic and phylogenetic patterns of its diversification, even though ~27 % of the known species have not yet been reached (Melo-Sampaio et al. 2019, 2021; Murphy et al. 2019).

The first taxa of *Atractus* were described by Boie (1827), who described three species and mentioned the name of a fourth under the generic name *Brachyorrhos*. Due to the problems involved with the type specimen of *Atractus trilineatus* and the previous names *Brachyorrhos* Kuhli Schlegel, 1826 and *Brachyura* Kuhl & Van Hasselt, 1822, it was decided to keep the name *Atractus* described by Wagler (1828) as valid because a name change would be very inconvenient (Hoogmoed 1982). Regarding our knowledge of the species of the genus *Atractus* in Venezuela, it has grown with variation during the last 61 years, but its diversity is still far from being well known (Natera-Mumaw et al.

2015) and significantly underestimated if we consider the number of species valid until now in neighboring countries such as Colombia with >50 spp. and Brazil with >30 spp. (Uetz et al. 2023). Of the 31 recognized species, 24 are considered endemic to the country (Natera-Mumaw et al. 2015). The first species reported was under the name "*Coluber fuliginosus* from 200 miles from Caracas (Hallowell, 1845); later, Jan (1862) described another species for "Caracas" under the name "*Rhabdosoma univittatum*". A review of both types and additional material allowed us to demonstrate that the latter is a synonym (Natera-Mumaw et al. 2015). At the end of the 18th century, *Atractus vittatus* was described from the cordillera of the Coast by Boulenger (1894); At the beginning of the 19th century, *Atractus erythromelas* and *Atractus ventrimaculatus* from the city of Mérida were described by Boulenger (1903, 1905). After this last author, there was a gap in information about this genus equivalent to almost four decades until Schmidt (1932) reported *Atractus lasallei* for the Turimiquire mountain range, Venezuela; material that was later identified by Roze (1961, 1966) as *Atractus fuliginosus*. Sometime later, Beebe (1946) recorded *Atractus trilineatus* for the first time in Venezuela (Caripito, Monagas state). Later, material from the museum of Caracas was identified as "*Atractus badius*" by Marcuzzi (1950); *Atractus lancinii* was later described by Roze (1961). Although for a long time and with poor identifications the name *Atractus badius* remained reported for the country, consistently Natera-Mumaw et al. (2015) demonstrated the lack of a reliable record of this species in southern Venezuela and that the populations north of the Orinoco River correspond to other endemic mimetic species. Similarly, it occurs with the record of *Atractus latifrons* for Venezuela by Almeida et al. (2014) (pers. comm. Paulo Passos), who continue to carry the error pointed out by Martins and Oliveira (1993). Between 1958 and 1961 other species of *Atractus* were described in southern Venezuela: *A. steryermarki*, *A. duidensis*, *A. insipidus* and *A. riveroi* (Roze 1958, 1961). This last snake was originally described based on two specimens from Cerro Duida (1800 meters above sea level) and Cerro Marahuaka (1300 m asl) in Amazonas, Venezuela. Fifty-one years after the original description, the species was redescribed based on the type series and an additional specimen from Sierra Parima (980 m) in Venezuela (Passos et al. 2013), and then a range extension of the species was documented for the Amazon rainforest on the Brazilian side of the Pantepui region, in the extreme northern part of Brazil (Fraga et al. 2017). After Roze (1966), *Atractus mariselae* and *Atractus emigdioi* were described from the cordillera of Mérida, specifically Boconó, Trujillo state (Lancini 1969;

González-Sponga 1971). Another information gap occurs regarding the diversity of the group in the country until the description of *Atractus taphorni* endemic to Mérida (Schargel and García-Pérez 2002). Subsequently, Esqueda and La Marca (2005) published the first compendium of the group in the cordillera of Mérida with the description of several species (*A. meridensis*, *A. mijaresi*, *A. tamaensis*, *A. ochrosetrus* and *A. micheleae*). Successively, other species have been described to date, *A. tamessari* (Kok 2006), *A. eriki* (Esqueda et al. 2007), *Atractus acheronius* and *A. multidentatus* (Passos et al. 2009), *A. ayeush* (Esqueda 2011), *A. heyeri* (Esqueda and McDiarmid 2015). Sánchez et al. (2004) and Marchezich and Barrio-Amorós (2004) described *A. nororientalis* and *A. matthewi*, respectively, but with similar specimens in which the valid species was the latter (Kok et al. 2007). Many of these species with a distribution towards the south of Venezuela were little known or, in most cases, lacked detailed descriptions, which is why they were intuitively and pertinently redescribed by Passos et al. (2013). Finally, in their book on the snakes of Venezuela Natera-Mumaw et al. (2015) updated the available information, including new data and photographic information on the species.

1.3 Pragmatic approach to species and integrative taxonomy

If species are groups of actually or potentially interbreeding natural populations that are also reproductively isolated from other similar groups, then speciation is the process by which reproductive isolation evolves between populations. However, the idea of speciation without allowing gene flow is often untrue because of its dimensionality, allowing for exciting avenues of research to understand a more complex view of species evolution, unrestricted by unrealistic notions of what species should be (Burbrink and Ruane 2021). Hence, species delimitations using any method under any concept are merely hypotheses (de Queiroz 2005). Rannala and Yang (2020) suggested that species delimitation must include an evidence-based approach that adequately examines the genetic structure integrated with additional data to better understand the time of origin, gene flow and degrees of introgression.

While the evolution of reproductive isolation is typically a gradual process that occurs along a gradient, starting from a single variable and continuous population to differentiated populations that are still connected by gene flow and can ultimately lead to distinct species and reproductive isolation (speciation continuum), movement along the speciation continuum is clearly bidirectional (Curie 2012; (Schluter 2009). From the

ecological perspective, divergent niches could drive geographic isolation, eventually leading to genetic and morphological differentiation (Pyron and Burbrink 2009; Wooten and Gibbs 2012; Zhang et al. 2014).

Hence, explaining variation in species richness among clades, over time, and among geographic regions constitutes a major challenge for ecology and evolutionary biology (Rabosky 2013). What constitutes a distinct species? This historical question has been the catalyst for one of the most debated topics at the scientific level, encouraged especially in taxonomy by a basic disagreement in concepts (De Queiroz 2007; Wiens 2007; Padial et al. 2010; Frankham et al. 2012). While it is generally accepted that a species represents a separately evolving metapopulation lineage, the crux of the debate has centered on what point in the evolutionary history of this lineage is the species that delimits the drawn boundary (De Queiroz 2007, 2020; Padial et al. 2010; Frankham et al. 2012). However, in cases where populations are close or have experienced recent divergence, it is difficult to establish their boundaries due to subtle differences in morphology, coloration pattern, incomplete reproductive isolation, or incomplete lineage sorting (Maddison and Knowles 2006; de Queiroz 2007). Apparently, depending on the species, the limits of the concept used can be drawn based on haplotype variation, reproductive isolation, ecological divergence or morphological distinction (De Queiroz 2007; Padial et al. 2010; Frankham et al. 2012). However, relying on just one of these criteria seems problematic, since they do not arise in any clearly defined order or at any given time. In recent years, species delimitation studies have begun to use multiple lines of evidence to determine whether conspecific lineages are units that evolve separately (De Queiroz 2007; Will et al. 2005; Padial et al. 2010), although it has yet to produce a definition of universally accepted species, and it is for this reason that the debate continues to this day (Gómez and Dawson 2019).

Indeed, different methods and species definitions can produce different results when applied to a set of taxa (Camargo et al. 2010). Although the advent of genomic sequencing methods, along with associated analytical approaches (e.g., coalescence-based species delimitation; Fujita et al. 2012), has provided new tools for uncovering diversity and delimiting species. These advances have led to important findings on patterns and processes of genetic variation and how hybridization and introgression between divergent populations affect species boundaries (Morando et al. 2004; Grummer et al. 2018; Olave et al. 2018; Billerman et al. 2019).

The last decade has seen a renewal of taxonomy, illustrated by the increasing number of published articles that seek to reevaluate the idea of traditionally defined species and subspecies, the methodology of species delimitation, and its application (Raxworthy et al. 2007; Rissler and Apodaca 2007; Yeates et al. 2011; Soto-Centeno et al. 2013). In Neotropical reptiles, for example, the integrative taxonomic approach has been operationally used to evaluate the systematics of many taxa, including lizards and amphisbaenids (Sturaro et al. 2018; Kok et al. 2018) and snakes (Kok et al. 2018; Streicher and Meik 2018; Entiauspe-Neto et al. 2020; Melo-Sampaio et al. 2021).

1.4 Concretizing the idea

Species-level systematics is still marked by theoretical and empirical tensions between the desires to identify geographic lineages, delimit species, and estimate their relationships. Beyond divergent opinions, its concept is ineluctably the central unit of biological, biogeographical, ecological and conservation analyses (de Queiroz 2007; Sterner 2017; Hillis 2019). Detecting and understanding species distribution patterns, drivers and the processes involved necessarily involves understanding the evolutionary history of organisms, their past and their ecological or environmental limitations throughout their distribution. Then, it is understood why species are hypotheses, since the name of a species is no longer a reference to a particular hypothesis. However, guidance on species delimitation has largely focused on morphology and reproductive isolation patterns (Mayr 1942; Coyne and Orr 2004; Nosil 2012), although with the inclusion of molecular techniques, they are increasingly used to clarify species boundaries (Kuchta 2007). For example, using molecular markers, many morphologically cryptic taxa have been identified, and deep divergences between allopatric components have been quantified (Gottscho et al. 2014). In this sense, species formation is a long-term process, potentially including the sorting of incomplete lineages, introgressive hybridization, the anastomosis of previously isolated lineages, and the development of complex patterns of population structure between separated lineages incomplete (Kuchta and Wake 2016). Therefore, the parameter space relevant to species delimitation is large and complex. It is now possible to identify phylogeographic lineages, delimit species using molecular and morphological data and estimate their relationships in a single coherent set of analyses, which is not what we mean by the integrative or multiple evidence approach.

Various studies have shown that the evolutionary history of the biota and fauna throughout South America has been influenced by different geological processes and climatic events such as the Andean orogeny, marine introgressions, drainage reversals and glaciations (Moritz et al. 2000; Rull 2008; Hernández et al. 2005; Hoorn et al. 2010; Turchetto-Zolet et al. 2013; Mendoza-Henao and García-R 2021). In northern South America, within snakes, a model clade to develop studies of a micro and macroevolutionary nature is the genus *Atractus* Wagler, 1828. Currently, 150 cryptozoic-semifossorial species are known, of which more than 75 % occur in mountain systems above 1000 meters above sea level and in different habitats, with numerous allopatric and sympatric species, without there yet being a more detailed review at the level of speciation and evolutionary history. However, to achieve this purpose, a consistent taxonomy is imperative, but most of these taxa have remained poorly defined with few museum specimens, in addition to an uncertain geographic distribution and unknown phylogenetic relationships. Therefore, my central objective is to carry out a comprehensive and consistent analysis of the morphological and genetic variation of hundreds of field and museum samples through an integrative approach, using modern methods and concepts that allow the delimitation of species, in addition to constructing and comparing the diversity of the genus and its evolutionary history throughout three biogeographic regions of Venezuela (cordillera of Mérida, cordillera de la Costa and Guiana Shield).

This dissertation provides for the first time a holistic view of the diversity of a group of Neotropical snakes of the family Dipsadidae. Hence, my thesis is divided into two parts, although the second is organized into several scientific articles because it deals with the description of new species.

Concerning **chapter I**, the central idea underlies that *Atractus* exhibits a particularly high species richness in the northern Andes (>70 %), mainly in environments above 1000 m asl and in comparison, with other Neotropical regions. A singular scenario glimpses a causal relationship between the construction of mountains and their diversification via isolation due to elevation and topographic complexity, thus favoring the generation of new species (neoendemism, rapid diversification) or the accumulation of species through dispersion in a region that is environmentally complex, as could happen with the cordillera of Mérida (paeloendemism). Under this scenario, assembled the most comprehensive time-calibrated molecular data set of *Atractus* (42 % known

species) to investigate the phylogenetic relationships and diversification dynamics of these cryptozoic-fossorial and with a diet specialized in oligochaetes. In this way, combining historical analysis of biogeography, time- and trait-dependent diversification, we test according to the above framework if the cordillera of Mérida (northern Andes) acts as a "species pump" to explain Andean species richness, without being to be strictly hypothesis not mutually exclusive of others that have been previously proposed (e.g., museum, species attractor; Chazot et al. 2016). Therefore, this scenario would indicate that relict diversity coexists with a more recently evolved diversity, where its endemic lineages exhibit restricted distributions (microendemism) and cryptic diversity could be relevant, unlike other neotropical environments such as the Amazonia where endemic lineages are appreciated with broader distributions and cryptic diversity apparently has a weak role, although not fully evaluated (e.g., reptiles) (Azevedo et al. 2019).

While **chapters** II, III, and IV evaluated the systematics and species delimitation of the cordillera de Mérida, through the idea of multiple sources of evidence or integrative taxonomy that includes morphological, ecological, and molecular data. Subsequently, this review allowed for the description of two new species for science and consolidates the idea that the cordillera de Mérida should be recognized as a hotspot area for *Atractus*, exhibiting the highest endemism and diversity known in Venezuela (see Myers et al. 2000 for others groups of organisms).

In this integrative approach, which combines systematics, historical biogeography, and diversification rate evolution, fundamental questions arise for the understanding of *Atractus* snakes (Dipsadidae), a cryptic and predominantly montane group from northern South America: (1) What are the phylogenetic relationships among *Atractus* species and their implications in the systematics and taxonomy, considering the possible existence of cryptic or undescribed lineages? (2) What role did the Andean uplift play in the speciation of *Atractus*, and what mechanisms such as vicariance, altitudinal expansion-retraction, or dispersal could have been involved? (3) What divergence dates and spatial patterns allow the delimitation of lineages based on biogeographic regions such as the Mérida Andes, the Guiana Shield, and the cordillera de la Costa? (4) Is the cordillera de Mérida an ancestral area that marks the direction of diversification towards other geographical units such as the Guiana Shield and the cordillera de la Costa? (5) Do Andean *Atractus* lineages show faster diversification rates compared to those in

non-Andean regions, as evidence of the effect of the uplift of the central-northern Andes during the Neogene, and then the impact of climatic oscillations during the Pliocene-Pleistocene? (6) If niche conservatism is common in Atractus species, what would be its implications in the face of climate change and anthropogenic alterations, and what conservation strategies arise from this scenario?

Answering these questions allows to shed light on the evolutionary and biogeographical history of the group, within a context where the Andean topographical complexity, along with pulses of habitat isolation and reconnection, has promoted complementary mechanisms of speciation. Consequently, evaluating non-mutually exclusive hypotheses provides a robust pathway to understand the underlying macroevolutionary processes. The articulation between phylogenetic analyses, biogeographic reconstructions, and diversification rate models reinforces the value of taxonomy as an interpretive framework for evolutionary history, integrating evidence from multiple sources to understand the dynamics of generation and conservation of Neotropical diversity.

GENERAL OBJECTIVE

Determine and understand the main drivers of the biogeographical history and diversification patterns of the genus *Atractus*, integrating molecular, morphological, ecological, and geographical evidence for species delimitation and the recognition of macroevolutionary processes associated with its radiation.

SPECIFIC OBJECTIVES

- Evaluate the current validity of *Atractus* species with the new results by integrating morphological and molecular data as species delimitation.
- Reconstruct the phylogenetic relationships of the species of *Atractus* Wagler, 1828.
- Test the identity of natural groups within the genus using hemipenial morphology and the phylogenetic hypothesis.
- Visualize and analyze the variation in speciation, extinction, and diversification rates over time for different clades, allowing the identification of periods of evolutionary acceleration or decline.
- Explore the diversification patterns of the genus *Atractus* using comparative and state-dependent phylogenetic models, with an emphasis on mountainous regions of northern South America.
- Estimate the divergence times and the reconstruction of the ancestral area of the genus *Atractus* in three bioregions of the country to elucidate the main biogeographical events that could explain its current diversity and geographical pattern.
- Model the potential distribution of species of the genus *Atractus* using ecological niche tools and machine learning, to identify patterns of environmental suitability, endemism, and degree of conservatism in the species of the cordillera de Mérida.
- Evaluate the potential conservation status of *Atractus* species based on their modeled geographical distribution, restricted ranges, and ecological contexts, considering microendemism and environmental threats.

HYPOTHESIS

In this thesis, a set of non-mutually exclusive hypotheses is proposed and evaluated, addressing the diversity of the genus *Atractus* from three complementary levels: taxonomic, evolutionary-biogeographical, and conservation. The taxonomic hypothesis is based on the premise that the current species boundaries may be underestimated due to a poorly understood diversification history, especially in montane environments above 1000 m asl, so the integration of molecular, morphological, and geographical data would allow for the delimitation of independent evolutionary lineages (de Queiroz 2007; Padial et al. 2010). In the evolutionary context, it is evaluated whether the diversification of *Atractus* has been modulated by the geological-climatic history of the Andes, particularly if the Andes of Venezuela has functioned as a species pump, which suggests that certain clades may experience intense pulses of diversification in response to the availability of niches or geographical isolation (especially in topographically complex regions like the northern Andes), accompanied by non-negligible extinction, multiple transition events between regions, and, most importantly, a mosaic of neoendemism and paleoendemism reflected in young clades coexisting with deeply divergent lineages (see Rangel et al. 2018; Hoorn et al. 2010). Finally, the conservation hypothesis proposes that many lineages of *Atractus*, highly endemic and with restricted distributions, could be threatened by habitat loss, climate change, or lack of taxonomic recognition, thus their conservation status requires reevaluation under an integrative approach of niche modeling and phylogeography (see Guisan et al. 2013; Loyola et al. 2014). Therefore, this proposed holistic approach allows for a deeper understanding of the processes that have shaped the current diversity of the group and provides fundamental tools for its conservation.

Taxonomic hypothesis: It is proposed that the populations of *Atractus* distributed in the Venezuelan Andes (cordillera de Mérida) constitute distinct species and form a monophyletic lineage, as a consequence of an isolation event promoted by the Andean uplift during the Middle Miocene (~8–2 Ma). This geographical separation would have favored genetic and morphological divergence, accompanied by a signal of high speciation followed by stagnation or net decline, as detected in evolutionary rate analyses. Although this clade is mostly associated with montane environments, some lowland endemic species show affinities with Andean lineages and not with the Guiana

Shield, which reinforces their recognition as independent taxonomic units under a context of allopatric speciation.

Hypothesis on the evolutionary and biogeographical history: Given that the Andean uplift has historically been one of the main drivers of neotropical biota diversification (Hoorn et al. 2010; Rangel et al. 2018), we propose that the diversification patterns of *Atractus* respond to non-mutually exclusive scenarios, described as (1) Montane Species Pump model hypothesis. Following Valentine (1967), the high topographic heterogeneity combined with repeated cycles of connectivity and isolation would have promoted allopatric radiations, resulting in persistent lineages and localized endemism; (2) Montane Cradle model hypothesis. early colonization of regions or habitats facilitates greater richness because there is more time for in situ speciation and species accumulation; (3) Montane Museum model hypothesis. These mountainous regions could have acted as climatically stable refuges, allowing the persistence of ancient lineages with low extinction rates (Rangel et al. 2018); (4) Species-Attractor model hypothesis. The availability of new montane ecosystems would have generated multiple events of independent colonization from neighboring regions (e.g., Amazonia, Guiana Shield; Chazot et al. 2016) and (5) Time of speciation hypothesis. The greater antiquity of colonization events in the Andes would allow for a greater accumulation of species compared to other regions (Chazot et al. 2016).

Conservation hypothesis: If the Andean uplift has played a dominant role in their diversification and the Venezuelan Andes (Mérida cordillera) have mostly functioned as a species pump, then the current richness of *Atractus* in these mountainous systems is explained by historical processes of rapid speciation and endemism. However, this richness now faces severe vulnerability: deforestation, climatic change, niche conservatism (Guisan et al. 2013; Wiens and Graham 2005), a specialized diet (earthworms), and narrow distribution ranges. All of this suggests a high vulnerability to current and future environmental changes, which could lead to a population collapse if these species are not recognized as priority conservation units (Loyola et al. 2014).

PREDICTIONS

Species Pump	Montane musem	Species-Attractor
Higher diversification rate in the Andes compared to other evaluated bioregions, signs of extinction or contraction of	Determined by evolutionary time rather than speciation rate in the configuration of the observed mid-high elevation	Diversification rates and speciation times identical between bioregions (e.g., Andean vs. non-Andean). More recent

populations, and isolated in remnants of optimal areas called	richness pattern, "time-speciation effect, although the latter holds that Andean lineages (colonization are ancient vs. non-Andes)."	speciation in the Andes compared to non-Andean bioregions, with a slowdown in diversification.
The Andean regions would act as centers of rapid speciation and extinction, generating a high turnover of lineages (neoendemism + paleoendemism), promoted by the rugged topography and pulses of isolation and reconnection (e.g., Miocene-Pleistocene events).	Andean lineages have suffered lower extinction rates at a medium-high level compared to non-Andean regions. Moderate or low speciation rates do not fully fit because extinction is relevant.	Higher rates of dispersion and colonization in the Andes than in other bioregions, due to the availability of newly formed ecosystems (ecological niches). The Andes, due to their recent formation and ecological variety, would attract multiple independent lineages, functioning as a "magnet" for biodiversity.
Andean clades with patterns of explosive diversification followed by deceleration (observed in Rate Through Time, LTT curves).	Constant diversification over time, without explosions (not observed in Rate Through Time, LTT curves).	High colonization rates towards the Andes (in diversification models evaluated as ClaSSE).

Table 1. Three defined hypotheses with three predictions each, not mutually exclusive.

GENERAL PREDICTION

Ancestral reconstruction and divergence time estimation predict at least three independent biogeographic disjunctions among montane lineages: the Andes, the Guiana Shield, and the cordillera de la Costa. These regions originated as historically separate units, with specific and independent transitions between the Guiana Shield and the Venezuelan Andes, and between the Guiana Shield and the cordillera de la Costa.

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CHAPTER I

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IN AND OUT OF MOUNTAINS: MOLECULAR PHYLOGENY AND HISTORICAL BIOGEOGRAPHY OF THE DORMILONAS SNAKES OF *ATRACTUS GENUS* (SERPENTES: DIPSADIDAE) IN VENEZUELA

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ABSTRACT

Within the South American dipsadids, the genus *Atractus* (sleepyhead) constitutes one of the most diverse groups of cryptic snakes, with a marked affinity for mountainous ecosystems. Their diversity at high altitudes is comparable only to that of the *Liolaemus* lizards in the central-southern Andes. To explain the extraordinary Andean diversity, three hypotheses have been proposed: the Andes as a "museum" of persistent lineages, as a "cradle" of recent species, or as a "species pump," acting as an epicenter of dispersal to adjacent lowlands. Based on molecular, morphological, and distribution data from 63 species, we evaluated the diversification patterns and biogeography of the genus. Phylogenetic analyzes with weak support the monophyly of *Atractus* and suggest an Andean origin in the early Miocene (~22.6 Ma). Our macroevolutionary results indicate that the diversification rate was initially high in montane clades, followed by deceleration and persistence, in accordance with museum scenarios. BAMM and MEDUSA detected significant rate changes, including diversification peaks associated with the uplift of the northern Andes, while ClaSSE supported the cradle and museum, and BiSSE leaned toward cradle and cradle–museum scenarios. Overall, the evidence indicates that the diversity of *Atractus* responds to a mosaic dynamic: the Andes acted as a cradle and pump of species during the Miocene, with subsequent museum effects in certain clades. The complex topography and environmental heterogeneity, especially in young systems like the Mérida Andes, explain the unique diversity and endemism pattern of the genus.

KEY WORDS. – phylogeny, speciation, extinction, cordillera de Mérida, cordillera de la Costa, Guiana Shields

RESUMEN

Dentro de las dipsádidos suramericanos, el género *Atractus* (dormilonas) constituye uno de los grupos más diversos de serpientes criptozoicas, con una marcada afinidad por ecosistemas montañosos. Su diversidad en altura es comparable solo con la de los lagartos *Liolaemus* en los Andes centro-sur. Para explicar la extraordinaria diversidad andina se han propuesto tres hipótesis: los Andes como "museo" de linajes persistentes, como "cuna" de especies recientes o como "bomba de especies", actuando como epicentro de dispersión hacia tierras bajas adyacentes. Con base en datos moleculares, morfológicos y de distribución de 63 especies, evaluamos los patrones de diversificación y biogeografía del género. Los análisis filogenéticos respaldan con débil soporte la monofilia de *Atractus* y sugieren un origen andino en el Mioceno temprano (~22.6 Ma). Nuestros resultados macroevolutivos indican que la tasa de diversificación fue inicialmente alta en clados montanos, seguida por desaceleración y persistencia, en concordancia con escenarios de museo. BAMM y MEDUSA detectaron cambios significativos de tasa, incluyendo picos de diversificación asociados a la elevación de los Andes septentrionales, mientras que ClaSSE apoyó la bomba y el museo, y BiSSE se inclinó por escenarios de cuna y cuna–bomba. En conjunto, la evidencia señala que la diversidad de *Atractus* responde a una dinámica mosaico: los Andes actuaron como cuna y bomba de especies durante el Mioceno, con efectos posteriores de museo en ciertos clados. La topografía compleja y la heterogeneidad ambiental, especialmente en sistemas jóvenes como la cordillera de Mérida, explican la singular diversidad y el patrón de endemismo del género.

PALABRAS CLAVE. – filogenia, especiación, extinción, cordillera de Mérida, cordillera de la Costa, escudo de Guayana

INTRODUCCIÓN

Since Darwin, understanding the richness and distribution of organisms has been central in evolutionary biogeography (Morrone 2001). Mountains, in particular, are ideal systems to study diversification processes (e.g., northern Andes uplift and the Amazon effect; Hoorn 1995). They cover around 12 % of Earth's land surface (Körner et al. 2017), and about 70% of the 36 global biodiversity hotspots are mountainous regions (Myers et al. 2000; Mittermeier et al. 2011). These areas are recognized as centers of

endemism, likely due to higher speciation and lower extinction rates (Hoorn et al. 2013). Although the link between mountain formation and radiations is still debated (Antonelli et al. 2010, 2018), several hypotheses highlight the role of ecological gradients, habitat heterogeneity, and reduced competition in driving rapid diversification (Graham et al. 2004; Brumfield and Edwards 2007; Caro et al. 2013; Grytnes and McCain 2007; Haffer 2008; Mendoza-Henao and García-R 2021). In South America, geological and climatic events, especially the Andean orogeny have shaped biodiversity over the last 60 Myr (Hernández et al. 2005; Hoorn et al. 2010; Turchetto-Zolet et al. 2013). Explaining current diversity patterns is challenging due to this complex history and the lack of resolution at local and regional scales (e.g., Guiana Shield tepuis; Marshall et al. 2018).

Northern South American mountain ranges host some of the highest reptile diversity, with lineages showing distinct evolutionary histories (e.g., *Anolis*, *Gonatodes*, Mabuya, *Loxopholis*, *Anadia*, *Tantilla*, *Chironius*, *Atractus*). Traditionally, allopatric speciation via geographic isolation (vicariance) has been considered the main mechanism behind this diversification (Wüster et al. 2005; Guarnizo and Bermingham 2009; Nascimento et al. 2018; Nogueira et al. 2021). Still, vicariance alone cannot fully explain current richness and distributions, leading to alternative hypotheses like niche conservatism, vicariance-disturbance, refugia, river barriers and vertical displacement, among others (Nores 1999; Wiens and Graham 2005; Smith et al. 2007; Wiens et al. 2007; Haffer 2008; Leite and Rogers 2013).

In the evolutionary context, three main processes shape species richness in a region: speciation, extinction, and dispersal (Ricklefs 1987). In mountainous systems, three non-exclusive hypotheses have been proposed to explain elevated diversity: MONTANE *SPECIES PUMP*, referring to changes in speciation and extinction rates due to contractions and expansions of distribution areas (see original idea Valentine 1967); CRADLE, which highlights increased speciation, and *MONTANE MUSEUM*, where older lineages persist over time (Stephens and Wiens 2003; Smith et al. 2007; Wiens et al. 2007). The latter suggests that richness at mid-high elevations results from longer periods of accumulation since early colonization, rather than higher speciation rates. Building on this, another recently evaluated option is the *species attractor* hypothesis emphasizes higher colonization rates into certain regions (Chazot et al. 2016, 2018). However, this view may overlook the role of major barriers, such as the vast fluvio-lacustrine system

active between 24-10 Myr, which likely impeded dispersal between the Andes and the Amazon (Shephard et al. 2010; Hutter et al. 2017).

A key area to test these hypotheses is the Venezuelan Andes, particularly the cordillera de Mérida. This mountain system is geologically distinct, formed through a complex interaction among the Caribbean, South American, and Panama plates with the Maracaibo block (Audemard and Audemard 2002; Bermúdez et al. 2010). It represents a doubly vergent orogen flanked by contrasting basins—humid to the northwest (Maracaibo) and dry to the southeast (Barinas) (Erikson et al. 2012). Although it covers only ~9.5% of Venezuela, its position between the Andes and Amazon separated by the Llanos along with at least two uplift events between 8-2 Myr, shaping historical patterns of isolation and diversification, what has favored a high richness and endemism (Hazzi et al. 2018).

Snakes show ancient and geographically structured lineages, reflecting complex diversification scenarios and repeated shifts in diet and prey use traits that have facilitated their success across Neotropical environments (Grundler and Rabosky 2014, 2021). Among them, *Atractus* Wagler, 1828 stands out as a prime model for evolutionary and biogeographic studies (Myers and McDowell 2014; Hamdan et al. 2017; Azevedo et al. 2019; Torres-Carvajal and Terán 2021). This genus is exclusively South American, composed of ~150 cryptozoic or semifossorial species (Martins and Oliveira 1993, 1999), over 60 % of which inhabit mountainous areas above 1000 m asl, often in allopatry or sympatry but with limited historical study. Similarly, as ectotherms with low vagility and high sensitivity to local conditions (Navas 2002), being excellent indicators of environmental and geographic influences on biodiversity. The most species show narrow distributions shaped by ecological and geographic barriers. In fact, *Atractus* is ideal for studying inter-ecoregional dynamics due to its exceptional diversity, since ~70 % of species occurring in Tropical Andes and Guiana Shield ecosystems, two major biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2011).

Focusing on the cordillera de Mérida, Venezuela and other bioregions of South America, our study explores the phylogenetic, biogeographic relationships, and diversification patterns in cryptozoic-semi-fossorial snakes of the genus *Atractus*, with the greatest known diversity in Venezuela (Esqueda and La Marca 2005; Natera-Mumaw et al. 2015; Esqueda et al. 2025). Their current diversity seems to be framed

within complex biogeographic scenarios (paleo and neoendemism), without an integrative hypothesis so far. We address key questions such as: (1) What are the phylogenetic relationships within *Atractus* and what implications do they have for its systematics? (2) Did the Andean uplift drive speciation in the group, and what mechanisms were involved? (3) What divergence dates and delineated biogeographic lineages can be estimated? Do they coincide with climatic events of the Pliocene-Pleistocene? (4) Can the cordillera de Mérida be considered an ancestral area, given its position between the Guiana Shield and the cordillera de la Costa? (5) Was diversification more accelerated in Andean lineages compared to non-Andean ones, in response to pulses of dispersion and contraction linked to recent climatic changes?

MATERIALS AND METHODS

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. 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, USA) at the Herpetozoa laboratory, University of Concepción. Two mitochondrial genes (Cytb and ND4) and two nuclear genes (NT3 and RAG–1) were amplified using primers and PCR conditions detailed in Supplementary_1_1, DNA quality was assessed on 1.5 % agarose gels stained with SYBR® Vitrogen. Sequencing was performed by MACROGEN (Korea), and chromatograms were verified using BioEdit 7.0.9.0 (Hall 1999). Open reading frames were checked in Mega v.11 (Tamura *et al.* 2021). Heterozygous nuclear DNA sequences were identified visually for double peaks in chromatograms, and individual alleles were reconstructed using DnaSP v.6.12 (Librado and Rozas 2009) with two independent runs. Alignments showed no gaps in mitochondrial sequences, and sequences for other species were sourced from GenBank (Supplementary_1_2), ensuring amplified loci were from single voucher specimens to avoid "terminal chimeras."

Phylogenetic analyses

The new sequences generated in this study were combined with sequences downloaded from GenBank. Additionally, 20 specimens representing to 18 species were used as outgroups (highlighted in yellow, Supplementary_1_2). Five gene fragments were obtained, corresponding to three mitochondrial amplicons, long 16S ribosomal RNA (525 bp); cytochrome b (897 bp); and NADH dehydrogenase ND4 subunit IV (713 bp) and two nuclear amplicons, neurotrophin–3 gene NT3 (516 bp); recombination activator RAG–1 (879 bp). Substitution saturation of each locus was assessed using the software DAMBE v.5 (Xia 2013). 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 (Nguyen *et al.* 2015).

The authenticity of the obtained sequences and the homology of the specific mtDNA and nuDNA markers were evaluated with a BLAST search in the NCBI genetic database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The consensus sequences for each locus were aligned using MAFFT (Katoh and Standley 2013) contained in Jalview v. 2.11.1.4 (Waterhouse *et al.* 2009), 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 exhibit nucleotide positions with high entropy and may have misaligned or incongruent regions were refined with the BMGE software: a BLOSUM62 matrix, a minimum block size of 20, a maximum entropy threshold of 0.5, and a rate limit gap of 0.65 (Criscuolo and Gribaldo 2010), available on the web service https://ngphylogeny.fr/ (Lemoine *et al.* 2019). Finally, the concatenation of all alignments was done with Mesquite v3.6 (Maddison and Maddison 2021). 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 (Triant and Dewoody 2007).

Here, we used maximum likelihood (ML) analysis to obtain the optimal tree topology of the concatenated data set. The best partition and substitution models were automatically selected using ModelFinder (Kalyaanamoorthy *et al.* 2017) and then implemented in IQ–TREE v.2 software (Nguyen *et al.* 2015) under the Bayesian information criterion (BIC). The best ML tree was selected from10,000 iterations and the confidence of the branches of the best ML tree was evaluated with the ultrafast bootstrap method using 10,000 bootstrap pseudoreplicates (Minh *et al.* 2013). 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/, Trifinopoulos *et al.* 2016), where branch support was calculated using the ultrafast bootstrap approximation (UFBS) (Minh *et al.* 2013) and the Shimodaira–Hasegawa approximate likelihood ratio test (SH–aLRT) (Anisimova *et al.* 2011), with 1,000 replicas. The consensus tree was visualized in FigTree (Rambaut 2014). Nodes with bootstrap values ≥ 70 were considered strongly supported and those nodes with 95 % were considered highly supported.

Divergence time estimation and calibration points

We estimated divergence times of sleepyhead snakes of the genus *Atractus* using the Bayesian framework implemented in the BEAST 2.7.5 software (Bouckeart and Drummond 2017). For all analyses, the matrix was partitioning by genes, 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. Unlike previous analyses with maximum likelihood (ML) and Bayesian inference (BI), where the best partition schemes and molecular evolution models were defined using ModelFinder and Partition Finder in the integrated PhyloSuite platform (Zhang *et al.* 2020). Here, the BEAST 2.7.5 software implements the "bModelTest "allreversible" option to estimate mutation rates for all genes evaluated. When implemented, bModelTest switches between substitution models during the Metropolis coupled MCMC (MC3), inferring and marginalizing site models, thus averaging the uncertainty about those models (Bouckaert and Drummond 2017), except for partitions that were defined by PartitionFinder because bModelTest does not incorporate substitution models average site over partitions from alignment. While Bayesian relaxed clock methods may produce more correct estimates when using multiple loci (mtDNA + nuDNA) (Battistuzzi *et al.* 2010), it is unclear how using faster–evolving mitochondrial genes (animals) may influence dating by divergence in relation to the use of nuclear loci that have a slower rate of evolution (Zheng *et al.* 2011). Here, the likelihood ratio test (LRT) implemented in Mega v.11 software (Kumar *et al.* 2018) rejected strict clock evolution models, favoring the lognormal relaxed clock

model for all partitions. Although the classic uncorrelated relaxed clock (Drummond *et al.* 2006) works well when rates and branch lengths are not highly correlated, on the contrary, it is poor, so here we will use the "optimized relaxed clock" model according to Douglas *et al.* (2021) which works well in both scenarios. On the other hand, we will apply a birth–death speciation model (Kendall 1948) as opposed to the Yule model (Yule 1925), since this assumes zero extinction rates and it is commonly known that extinction is extremely significant in the diversification of species (Sarver *et al.* 2019). Other antecedents were set to their default values, except the birth rate, which had an exponential distribution (lower 0.1 and upper 10).

Phylogenetic analyses often involve data sets comprising sequences from multiple loci. A common practice is to partition the data set, for example, by gene or by codon position, and assign separate substitution models to subsets of the data (Yang and Kumar 1996). In molecular clock analyses, the simplest approach is to apply a single model of rate variation between lineages to the entire sequence alignment. However, this approach does not account for heterogeneity between genes, which may have evolved under very different conditions. For instance, multilocus data sets may include combinations of markers from mitochondrial, chloroplast, and nuclear genomes. An ideal scenario for calibrating phylogenetic trees is when they are obtained from well–dated fossils; however, the incomplete or imperfect nature of the fossil record often only provides evidence of the minimum age of a clade, potentially leading to overestimation divergence time (Lukoschek *et al.* 2012). In fact, fossils rarely represent specific nodes but rather points along a branch (Lee 1999; Conroy and van Tuinen 2003).

On the other hand, multiple underlying factors can contribute to inaccurately calibrated clocks (e.g., patterns of evolution, saturation, and/or combinations of genes that evolve more rapidly vs. others that evolve more slowly). In snakes, the Caenophidia group contains the greatest diversity of extant snakes (> 2500 spp., Uetz *et al.* 2024) and includes acrochordids, xenodermids and all colubriforms (Pyron *et al.* 2013), a group with a controversial fossil record (Head 2015; Head *et al.* 2016). Considering the countless setbacks that persist in obtaining ultrametric trees (Lukoschek *et al.* 2012), there is greater consensus on using multiple independent calibrations of fossils (Ho and Phillips 2009). In our case, the calibration points of the nodes were defined based on the available fossil record (one corresponding to Colubridae and four positioned in the external groups), using ages and interpretations of fossils similar to those described in

Zaher et al (2018; 2019) and García-Sotelo *et al.* (2021) (Supplementary_1_3). We use Metropolis coupled MCMC (MC3, Atchadé *et al.* 2011; Maturana-Russel *et al.* 2018; Müller and Bouckaert 2019), with a temperature of 0.03 and four chains, established in three independent runs of 50 million generations, saving the parameters and trees every 10,000 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 (Rambaut *et al.* 2022). Combining the runs was done with LogCombiner v2.7.5 (Drummond *et al.* 2012). After performing a 10 % burning, the maximum credible tree was obtained by using TreeAnnotator 2.7.5 (Rambaut and Drummond 2016) implemented on the CIPRES Science Gateway online platform (https://www.phylo.org/) (Miller *et al.* 2010).

Ancestral geographic range estimation

The geographic distribution, elevation range, and vegetation type of each of the species to be studied were compiled primarily from specimens collected by us, specimens preserved in national and foreign museums (data exclusively from Venezuelan species), and occurrence records available based on online digital data BGIF (https://www.gbif.org/) and VertNet (http://vertnet.org/), as well as what is available in the literature (non-Venezuelan species), supported with museum material, and whose record is coherent to avoid the use of misidentified specimens (e.g. see discussion Arteaga et al. 2017, 2022 and Passos et al. 2022).

A priori, there are different methods for defining biogeographic areas, considering different spatial-temporal scales, geological-climatic events, composition, endemism and distribution of organisms (Ferrari 2018). Understanding the diversification/speciation histories of areas based on different groups of animals and plants implies the integration of multiple evidences, although vicariant events have been a classic descriptor of such patterns (Guedes et al. 2014). Current patterns of the distribution of species essentially express an interaction of ecological and evolutionary processes, undoubtedly linked to a complex and historically contingent environment. In fact, no defined biogeographic framework is usually optimal for all groups of organisms (Whittaker et al. 2014).

Our study covers ~42 % of the known *Atractus* species, skewed towards northern South America (Ecuador, Colombia, Brazil and Venezuela occur ~90 % spp.). Furthermore, being a group with few museum samples and a high degree of endemism, we have barely been revealing its geographical and phylogenetic pattern. In this context and combining previous criteria (e.g. bioregions of Venezuela, MARN 2001; amphibians, Godinho et al. 2014 and snakes, Guedes et al. 2014), as well as main geological and climatic events (Hoorn et al. 2010; Condamine et al. 2012; Lewis et al. 2015), for which we defined a total of 13 biogeographic areas (Supplementary_1_4): (A) Andes of Venezuela, which includes the cordillera of Mérida, the Tamá massif and the Perijá mountain range, northwest of the Orinoco River, **AVzla**; (B) Cordillera de la Costa in its central and eastern stretch, north of the Orinoco River, **CC**; (C) Guayana Shield south of the Orinoco River, which includes the lowlands and the Pantepui, **EG** and (D) Tropical and riparian forests of the western, central and eastern Llanos of Venezuela and the eastern Llanos of Colombia, **BLLVC**; (E) Central Andes of Colombia, **ACCO**; (F) Andes of Ecuador-Colombia in the direction to the Amazon, **AE**; (G) Western Andes toward Pacific slope of Ecuador and Colombia, **ROECCO**; (H) East from Andes of Peru and Bolivia, **APB**; (I) Northern region of the Amazon basin from Brazil, **NRCAM**; (J) Central-Southern region of the Amazon basin from Brazil, **CSRCAM**, (K) Western region of the Amazon basin, **WRCAM**; (L) Tropical forests of the Guianas, **TFG** and (M) Lowland and mountain environments adjacent to the Pacific of Colombia and Central America (**LMPCC**).

We define “lowlands” as the altitudinal distribution between 0-250 m altitude, above which it is considered piedmont up to 500 m. The only Venezuelan species whose distribution corresponds to lowlands and foothills are *Atractus fuliginosus*, which occupies environments on the Andean slope towards Los Llanos (cordillera of Mérida) and the cordillera de la Costa in its central-eastern section; *A. trilineatus*, whose distribution includes lowlands of the cordillera de la Costa in its eastern stretch (e.g., Cumanacoa, 200 m asl) and *Atractus major*, which exhibits disjunct populations on the Andean-Llanera slope (cordillera of the Coast) and the Guayana shield (Bolívar and Amazonas states). The remaining species known in the country (26 spp., Natera-Mumaw et al. 2015) have a distribution restricted to one of the three Venezuelan biogeographic areas mentioned above. With respect to the total of species evaluated (Venezuela + other countries), only 35.9 % cover what we define as lowlands.

To infer the potential influence of biogeographic characteristics on the diversification of 63 *Atractus* species (including 4 putative species in description or redefinition), we performed ancestral range reconstruction (ARR) analysis using RASP v4.2 (Yu et al. 2019). These programs can determine the probability of an ancestral range at a node by averaging over a posterior set of trees and thus accounting for phylogenetic uncertainty (Bryson et al. 2013). We use our credibility tree obtained in the BEAST 2.7.5 analysis (Bouckeart and Drummond 2017). Outgroups were removed using the option available in the software. The consensus tree used to map the ancestral distribution at each node was obtained with the "Compute Condense" option in RASP v4.2., considering 25 % of the trees obtained in BEAST, that is, 7,500 random trees related to the consensus tree of maximum credibility (using R , library APE and TREEIO). Although the occurrences of the species were coded within 13 areas, more than 80 % of the species only occupy one area, except for those lowland species present in the foothills of some mountain systems, so we restricted the ranges to encompass at most three different areas at each node. This software allows customizing matrices of dispersal rates and temporal stratification events, as well as inferring areas between the following historical biogeographic frameworks: **(1)** statistical dispersal-vicariance S-DIVA (Yu et al. 2010), which predicts ancestral ranges by giving extinction and dispersal events a higher cost than vicariance events, considering phylogenetic uncertainty. S-DIVA was carried out using 7,500 trees randomly sampled from the input trees, allowing reconstruction with default parameters for the final tree and **(2**) Bayesian Binary Monte Carlo analysis (BBM) (Yu et al. 2010), executed under the fixed state frequency model F+81+G (Felsenstein), a temperature of 0.1, with a variation of 5,000,000 generations, 10 chains each and sampling every 100. Once the analysis is complete, we check its tracking and consider a burn-in of 25 %, since low values tend to give inaccurate results. We set the maximum number of ancestral ranges at three, which represents the largest number of units spanned by any species in our analyses.

Diversification analysis

To conduct our diversification analysis incorporating phylogenetic uncertainty, we randomly sampled 10 and 100 trees with the highest posterior probability relative to the maximum credibility tree obtained from the BEAST run (dataset of 30,000 trees). Before conducting the diversification analyses, we used the drop.tip function from the

library (Paradis et al. 2004) in R software v.4.3 (R Core Team 2020) to remove the set of species corresponding to the outgroup and retain only *Atractus*. After the routine verification of the trees, we proceeded to generate the csv file corresponding to the states "Andes=1" and "No Andes=0" for each of the terminals of our calibrated phylogeny (data necessary for BiSSE and ClaSSE models). Having the necessary files, our strategy consisted of three approaches to evaluate the dynamics of the diversification rate within the phylogeny of the sleepyhead snakes, considering a 0.42 % sampling of the known species (Uetz et al. 2024).

Strategy 1, using the Ape, phytools, lmtest library in R software v.4.3 (R Core Team 2020) to create lineage-through-time (LTT) plots for the maximum credibility tree under a simulation following the script available where is adjusting the speciation and extinction models (script available at http://blog.phytools.org/). Next, we used LASER v.2.4 (Rabosky 2006) to calculate the γ statistic (Pybus and Harvey 2000) based on the MCC tree to test deviations from the constancy of the diversification rate and the likelihood ratio test (LRT) (Pagel 1999). Significance was evaluated using the mccrTest in LASER, consisting of 5,000 replicates and assuming an incompletely sampled phylogeny (63 spp.). Later, we used the diversification rate (DR) metric as a proxy for the speciation rate at the tree tips. This is calculated as the sum of the reciprocals of the distances from each tip to the root (terminals), which gives greater weight to recent branching (Jetz et al. 2012). This allows us to evaluate the nodes of interest with respect to the speciation-extinction rate (Supplementary_1_5).

Strategy 2, we fitted four diversification models to the 10 previously obtained ultrametric phylogenetic trees to test whether diversification rates in the group are better explained by constant or diversity-dependent processes. The models implemented were: (1) BD, Birth-Death model: a constant-rate model where speciation (λ) and extinction (μ) rates remain constant over time and independent of lineage diversity. This serves as a null hypothesis for diversification dynamics. (2) PBD, Proportional Birth-Death model: a model in which λ and μ may vary over time or with diversity but maintain a proportional relationship (e.g. $\mu = \varepsilon\lambda$). This allows for flexible changes in rates while maintaining their ratio; (3) DDL+E, Diversity-Dependent Linear model with Extinction: a diversity-dependent model where speciation rate (λ) decreases linearly with increasing diversity (number of lineages), and extinction rate (μ) is also estimated. This model includes a parameter K (clade-level carrying capacity), representing the diversity at

which λ equals μ, i.e., net diversification becomes zero. It reflects niche saturation or ecological limits to diversification and (4) DD, Diversity-Dependent model with μ = 0: A variant of the diversity-dependent model in which extinction is assumed to be zero (μ = 0). Only λ and K are estimated, assuming that extinction plays a negligible role. This is useful when extinction estimates are unstable or when the fossil record suggests low extinction. These models were implemented using the DDD package in v.4.3 (R Core Team 2020), which allows for maximum-likelihood estimation of diversification parameters under various diversity-dependent scenarios (Etienne et al. 2014).

Strategy 3, To test whether diversification dynamics in our focal clade are influenced by the current distribution of species across distinct biogeographic regions (e.g., Andean vs. non-Andean areas), we implemented the Binary State Speciation and Extinction (BiSSE) model using the diversitree package in R (FitzJohn 2012). This model allows estimation of speciation (λ), extinction (μ), and transition (q) rates as a function of a binary character—in our case, species presence in the Andes (state = 1) versus outside the Andes (state = 0). We first constructed a BiSSE likelihood function using the make.BiSSE function based on the maximum credibility tree and a binary-coded state vector. This likelihood function was optimized using maximum likelihood estimation (find.mle) to obtain point estimates of the six BiSSE parameters: λ_0, λ_1: speciation rates for state 0 and 1; μ_0, μ_1: extinction rates for state 0 and 1 and q_{01}, q_{10}: transition rates between states. Subsequently, we performed Bayesian MCMC sampling (mcmc) to estimate the posterior distributions of the parameters, using exponential priors based on initial ML estimates. Chains were run for 100,000 generations with a burn-in of 10 %, and convergence was visually assessed via trace plots and effective sample size (ESS). This allowed us to evaluate the uncertainty around estimates and infer whether diversification rates are significantly different between Andean and non-Andean species. All analyses followed the recommended practices for BiSSE (FitzJohn et al. 2009; Maddison et al. 2007), and the results were later compared with ClaSSE outputs to assess consistency in geographic state-dependent diversification.

Strategy 4, To corroborate our hypothesis that the Venezuelan Andes act as a "species pump", we arbitrarily defined the diversity of *Atractus* by non-Andean and Andean regions, where test if (h1) speciation-extinction rate increases in the Andes in different periods due to contractions and expansions of the distribution areas; (h2) speciation-extinction rate increases in the Andes, it acts as a "cradle"; (h3) a lower extinction rate

in the Andes, acts as a "museum"; (h4) high colonization rate of the Andes, acts as a "species attractor". We used the state-dependent speciation and extinction model "ClaSSE" (Golberg and Igic 2012), implemented in the DIVERSITREE package in R (FitzJohn 2012) in R software v.4.3 (R Core Team 2020), instead of the geographic state speciation-extinction model "GeoSSE" because all species of *Atractus* from meso-altimontane lands of each bioregion are not in another, except for the lowland (0-250 m) and premontane (250-500 m) species. ClaSSE extends the BiSSE model to accommodate multiple discrete geographic states and allows for both anagenetic (within-lineage) and cladogenetic (lineage-splitting) state transitions. We classify the species as Andean or Non-Andean, based on their currently known distributions and those previously established. Specifically, this model allows for character changes that are both cladogenetic (at the nodes) and anagenetic (along the branches). For a two-state character, the model considers up to six speciation rates, two extinction rates (μ2, μ1), and two anagenetic transition rates (q12, q21). Two speciation rates explain the speciation events without a change in character state (λ222, λ111). Two other rates explain speciation accompanied by a change in character state of one of the two descendant species (λ112, λ212), and the last two speciation rates account for cases where speciation involved a change in character state of both descendant species (λ122, λ211). (changes in the cladogenetic characters in the last two cases (Goldberg and Igic 2012; Rolland et al. 2014 2014).

We fitted 10 alternative ClaSSE models to 100 posterior phylogenies to test explicit diversification scenarios inspired by Chazot et al. (2016), each differing in which parameters were allowed to vary (e.g., speciation in Andean vs. non-Andean regions, extinction constraints, state transitions). Model comparison was based on the corrected Akaike Information Criterion (AICc), and models were ranked and classified according to their support. The table below summarizes each model, its key characteristics, and the biological hypothesis it tests (Supplementary_1_Table 6). All models were fitted across 100 trees from the posterior distribution to account for phylogenetic uncertainty. For each run, we extracted log-likelihoods, AICc scores (Burnham and Anderson 2002), and parameter estimates (λ, μ, q). We then selected the best-supported model(s) per tree ($\Delta AICc \leq 2$), and summarized the frequency of support for each hypothesis.

Strategy 5, using MEDUSA, constant diversification rates over time are assumed to detect rate variations in lineages based on a maximum likelihood approach. It is

implemented in the R package Geiger (Alfaro et al. 2009; Pennell et al. 2014) to detect changes in the selection of the 100 random trees of the posterior distribution and in the "MCC" tree, using as a second step the method indicated by Morlon et al. (2011). Following these last authors, six diversification models will be considered: constant speciation without extinction, time-dependent speciation without extinction, constant speciation with constant extinction, time-dependent speciation and constant extinction, constant speciation and time-dependent extinction, and speciation time-dependent and time-dependent extinction. The time dependence will be modeled using an exponential function. The models will be compared using the Akaike information criterion "AIC". The root of the tree will be excluded from the analysis. Because the phylogeny does not include all known species, a sampling fraction other than 1 must be set (sampling equals ~42 % of known species).

Strategy 6, using BAMM considers variation in diversification rates over time and among lineages using transdimensional Markov chain (reversible jump) Monte Carlo (rjMCMC) (Rabosky 2014). For this method, we applied tree MCC, in which the event data was 20,000.000 generations, and a burnin based on visual inspection of the log-likelihood trace of the MCMC output and the effective rate where the size of the sample (ESS $\geq$ 200), which were calculated using the R Coda library in R Studio (R Core Team 2020). Prior distributions were set according to the setBAMMPriors function of the BAMMtools package in R (Rabosky et al. 2014), ensuring that the prior density on relative velocity changes across the tree is invariant at the scale of the tree. The parameter "globalSamplingFraction" was set 0.42 after sampling coverage of the current phylogeny considering incomplete sampling. Finally, we processed the output data using BAMMtools to obtain summary statistics after removing a 10 % burn-in and to plot the diversification rate over time in our tree. Other parameters in the control file were modified: numberOfGenerations (set to 20,000,000, we increased the number of generations to achieve better exploration of the parameter space and allow a higher probability of MCMC convergence), expectedNumberOfShifts (set to 2.0 or 3.0, this parameter was adjusted to reflect the hypothesis that there may be multiple independent events of acceleration or deceleration of diversification, for example in the Mérida Mountain Range (Andes)), lambdaInitPrior and muInitPrior (manually specified, values from previous analyses (BISSE/ClaSSE) were used to establish more informed priors, helping to reduce convergence time and avoid unrealistic areas of the parameter space).

Finally, phylogenetic signal (PS) testing provides a simple means to quantify correlations between evolutionary history and traits such as elevational distribution. A statistical measure of the nonindependence of trait values of taxa due to evolutionary relatedness, where PS quantifies the tendency for closely related taxa to be more similar than taxa drawn randomly from a phylogeny (Felsenstein 1985; Losos 2008; Revell et al. 2008). So, isolation driven by topography increases speciation rates in mountainous areas (Steinbauer et al. 2016), under the rationale that isolation mediated by elevation necessarily implies understanding that areas become smaller and more remote, effectively acting as islands (e.g., northern Andes, Hutter et al. 2013), which would be defined a predictor of microendemism. Although speciation and endemism are not automatically linked, the latter, due to topographic complexity in mountains, can broadly reflect gradients of speciation.

To further evaluate the evolution of the altitudinal pattern in sleepyhead snakes, we used the MrBayes mechanism for discrete trait ASR that uses continuous-time Markov modeling against topology (Ronquist et al. 2012) and branch lengths of a tree to provide a statistical estimate of character states at ancestral tree nodes (MBSAR, Heritage 2021), with the MCMC coupled consensus tree obtained from the BEAST analysis. For each ancestral state reconstruction, a Markov chain Monte Carlo (MCMC) simulation was performed for 1,000,000 generations (MBASR, n.samples=10,000) with a sample taken every 100 generations. MBASR automatically sets burn-in to discard samples whose log-odds score below the 25% upper threshold. All executions were carried out as "disorderly." Here is the R script (R Core Team 2020), both the input tree file and the input feature TXT file of the altitude information to replicate each run. We prefer to keep all terminals in our topology, because certain records of specimens constitute populations that have not been fully studied (e.g. *Atractus major or Atractus* sp.). For each species, information was available on its altitudinal, ecological and biogeographic range (areas previously mentioned above) considering articles and verifiable museum specimens. In this particular, six altitudinal patterns were defined: (1) environments corresponding to lowlands between 0-500 m asl; (2) lowlands contiguous to Cis-Andean or Trans-Andean premontane regions, between 0 and ≤1200 m asl; (3) lowlands to Trans-Andean meso-montane-montane regions, between 0 and ≤2600 m asl; (4) premontane to meso-montane-montane Cis-Andean regions, >500 and ≤3000 m asl; (5) meso-montane to Cis-Andean or Trans-Andean montane regions, >1000 and ≤2800 m

asl and (6) meso-montane to intramontane montane regions, between 1500 and ≥3000 m asl.

RESULTS

Phylogenetic information

Here we present a multilocus phylogenetic estimate for the sleepyhead snakes of the genus *Atractus* based on the largest sampling known to date (~63 species and 191 specimens). The final concatenated molecular data set 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 % and 63 sequences in RAG-1: 879 bp, 90 informative sites, 95 singleton, 694 sites preserved, missing data 0-18 %). 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 (Fig. 1) and BI (Fig. 2) analyses are consistent and similar in topology, suggesting that the data provide a robust phylogenetic signal recognized by both methods. Any differences in support between ML and IB may stem from the way these methods handle uncertainty and evolution models (Alfaro et al. 2003; Holder and Lewis 2003; Yang and Rannala 2012). In our study, posterior probability values above 0.95 were considered strongly supported, values between 0.7 and 0.95 was moderately supported, and below 0.7 as weakly supported. Although the monophyly of *Atractus* was weakly supported, it is divided into two major lineages (ML and BI).

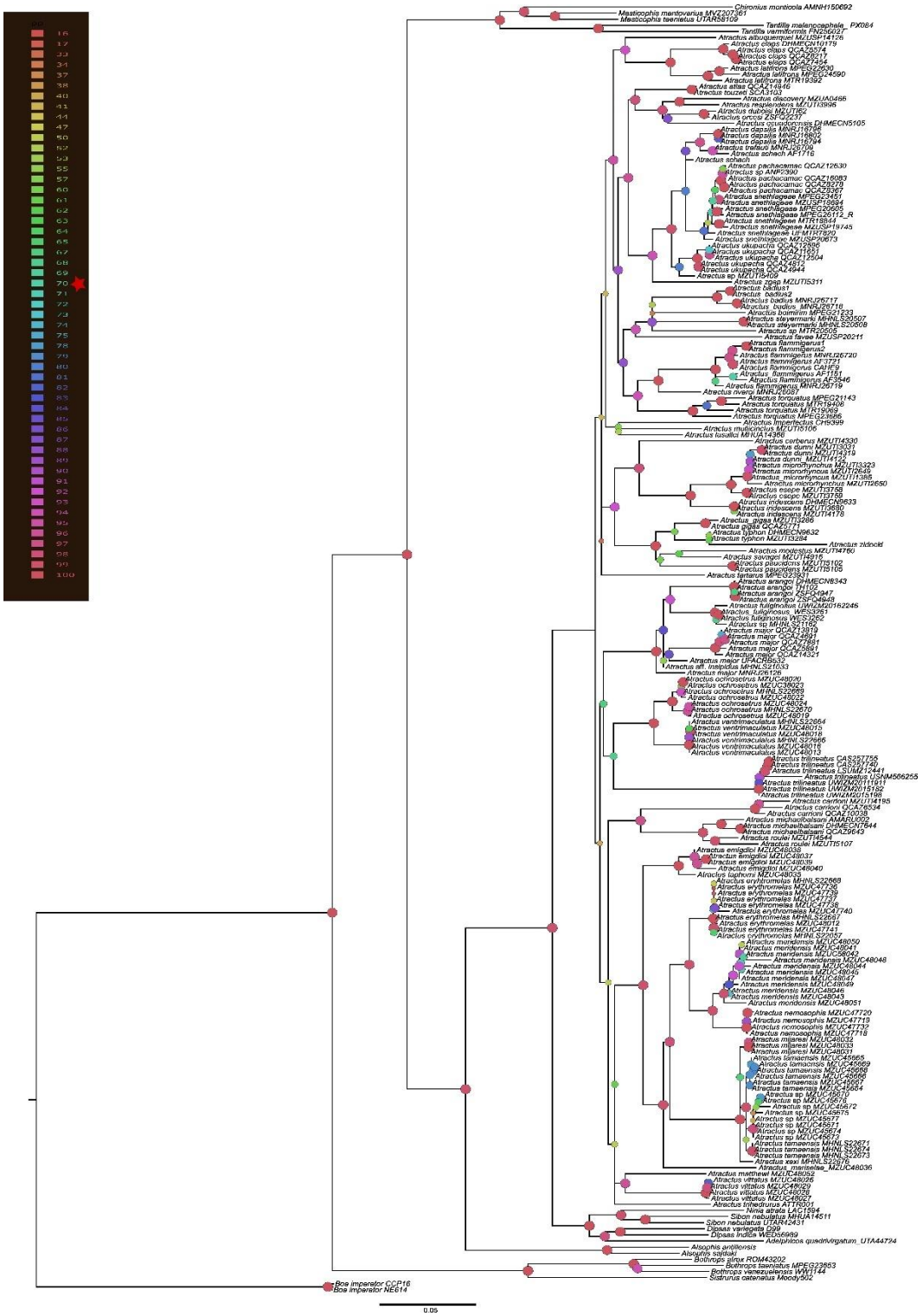

FIGURE 1. MAXIMUM LIKELIHOOD (ML) TREE WAS ESTIMATED OF IQTREE, SHOWING THE RELATIONSHIPS AMONG SOME SOUTH AMERICAN SPECIES OF *ATRACTUS*. INFORMATION ON BOOTSTRAP VALUES >70 % IN ML ARE SHOWN, LEFT SIDE.

Divergence time

Our time-calibrated phylogeny recovered estimates the most recent common ancestor (TMRCA) of *Atractus* at 22.63 Myr during the Early Miocene (95 % HDP = 18.93-26.84). **Lineage A**: TMRCA of 21.87 Myr (95% HDP = 18.5-25.7) are includes: clade of *A. multicinctus*, *A. imperfectus* and *A. lasallei* with a TMRCA age of 16.9 (95 % HDP = 10.2-22.14), clade of *A. albuquerquei*, *A. elaps* and *A. latifrons* with a TMRCA age of 16.46 Myr (95 % HDP = 12.7-20.43), clade of *A. badius*, *A. favae* and *A. steyermarki* with a TMRCA age of 14.8 Myr (95 % HDP = 11.51-18.35) and clade of *A. ukupacha* + *A. atlas*, *A. touzeti*, *A. discovery*, *A. resplendens*, *A. ecuadorensis*, *A. duboisi* and *A. orcesi* + *A. zgap*, *A.* cf. *schach*, *A. dapsilis*, *A. schach* and *A. trefauti* + *A. pachacamac* and *A. snethlageae* with a TMRCA age of 15.31 (95 % HDP = 12.28-18.59) and clade of *A. riveroi*, *A. flammigerus* and *A. torquatus* with an age TMRCA of 14.73 Myr (95 % HDP = 11.6-17.97). **Lineage B:** TMRCA of 20.53 Myr (95 % HDP = 17.23-24.15), comprising of clade *A. ochrosetrus* and *A. ventrimaculatus* + *A. trilineatus* with a TMRCA age of 17.16 Myr (95 % HDP = 13.47-20.98); clade of *A. matthewi* + *A. vittatus* with a TMRCA age of 15.4 Myr (95 % HDP = 11.12-19.64); Venezuelan Andean clade of *A. emigdioi* and *A. taphorni* with a TMRCA age of 3.4 Myr (95 % HDP = 1.89-5.3); Ecuadorian Pacific clade of *A. roulei*, *A. michaelbalsani* and *A. carrioni* with a TMRCA age of 14.52 Myr (95 % HDP = 11.17-18.21); Venezuelan Andean clade of *A. mariselae*, *A. xaxi*, *A. mijaresi*, *A. tamaensis* and *A.* sp + *A. erythromelas*, *A. meridensis* and *Atractus nemosophis* with a TMRCA age of 10.47 Myr (95 % HDP = 7.98-13.11); and clade of *A. major*, *A. arangoi*, *A. fuliginosus*, *A.* aff. *insipidus* and *A. sp*. with a TMRCA age of 9.62 Myr (95 % HDP = 6.44-13.49).

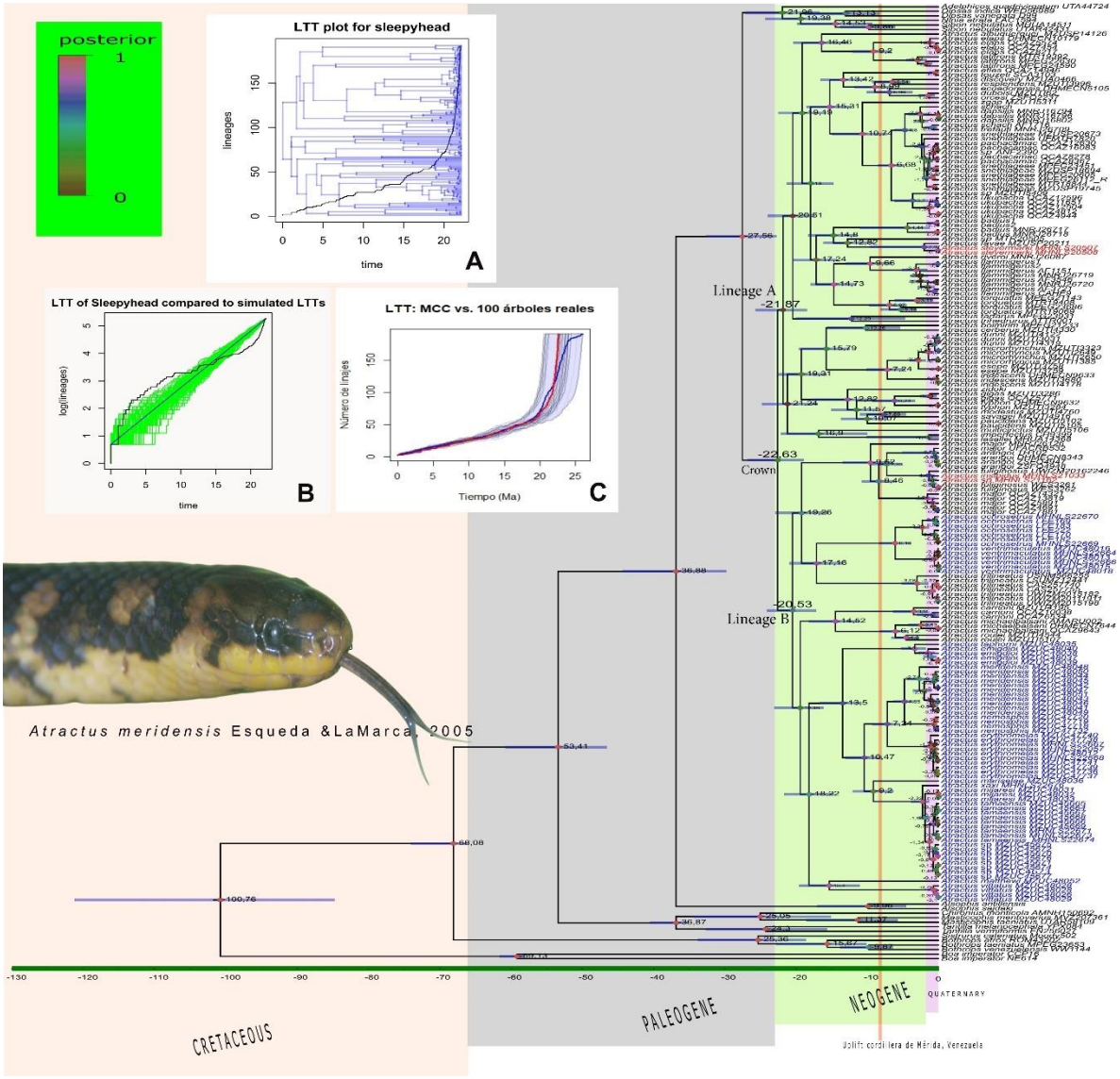

FIGURE 2. BAYESIAN INFERENCE TREE ALONG WITH DIVERGENCE TIME ESTIMATION UNDER THE TOPOLOGY. BEAST POSTERIOR PROBABILITY VALUES SYMBOL >0.95 (COLOR CIRCLES, SEE LEGEND). BARS ON NODES REPRESENT THE 95% CREDIBILITY INTERVAL OF DIVERGENCE TIMES. LINEAGE-THROUGH-TIME (LTT) PLOT WITH THE HIGHEST 95% POSTERIOR DENSITY INTERVALS (GRAY) SIMULATED AND 100 TREES EXTRACTED FROM THE BEAST FILE AND THE MAXIMUM CREDIBILITY TREE OF THE CLADE (RED LINE, A; BLACK LINE, B; RED AND BLUE-MEDIAN LINE, C).

Reconstruction of ancestral areas

The reconstructions of ancestral areas based on S-DIVA and BBM analyses were largely similar with some minor differences (Fig. 3), evidencing two major lineages, one fundamentally Andean and the other Andean-Amazonian. Based on both methods, ancestral state estimation for the MRCA of *Atractus* up to this moment, it remains ambiguous. The support of node 381 varies between 2.24 % and 21.25 % and

preliminarily suggests at least three areas as primary centers of diversification: the first would be between the central Andes and the Andean slope towards the Pacific of Colombia-Ecuador; the second would be the Pacific between Colombia and Ecuador, and the last would be the Andes of Venezuela and the Pacific. Both S-DIVA and BMM suggest a complex biogeographical history where dispersal and vicariance have been vital in shaping the current distribution pattern in *Atractus*. S-DIVA and BMM identified 173 and 176 dispersals, with the Andes of Venezuela and the Andes towards the Pacific of Colombia-Ecuador being the biogeographical zones with the highest dispersal-speciation within areas. Both also identified 25 vicariance events, and 6 to 2 extinction events, respectively. With reference to node 373, which corresponds to the sleepyhead snakes of the Andes of Venezuela, except for *Atractus ochrosetrus* and *A. ventrimaculatus*, the ancestral range would correspond to the cordillera de Mérida with a marginal probability of 100 % or 97 %, respectively. While node 380, which includes species from the Andes of Venezuela + Andes towards the Pacific and Andes towards the western Amazon, its center of origin would be the Andes of Venezuela with a marginal probability ranging from 83.5 % to 93 %, respectively. In contrast, node 252, which mainly includes species with an Amazonian distribution, has its center of origin in the northern region of the Amazon, which encompasses Brazil, Venezuela, and Colombia, with a marginal probability of 70.7 % and 93.8 %, respectively.

The sleepyhead snakes exhibit an altitudinal range between 0-3200 m, although at least 60 % of the known species occur above 1000 m asl. According to the reconstructed ancestral elevation, the most recent common ancestor of *Atractus* was a lowland species below 500 m asl with at least 75 % probability (Fig. 4). Likewise, the reconstruction of the ancestral altitudinal preferences corresponding to the lineage A and B, the most recent common ancestor it would correspond to lowlands; while for clade from the Andes of Venezuela, with high probability the most recent ancestor corresponds to meso-montane to intramontane montane regions, between 1500 and ≥3000 m asl.

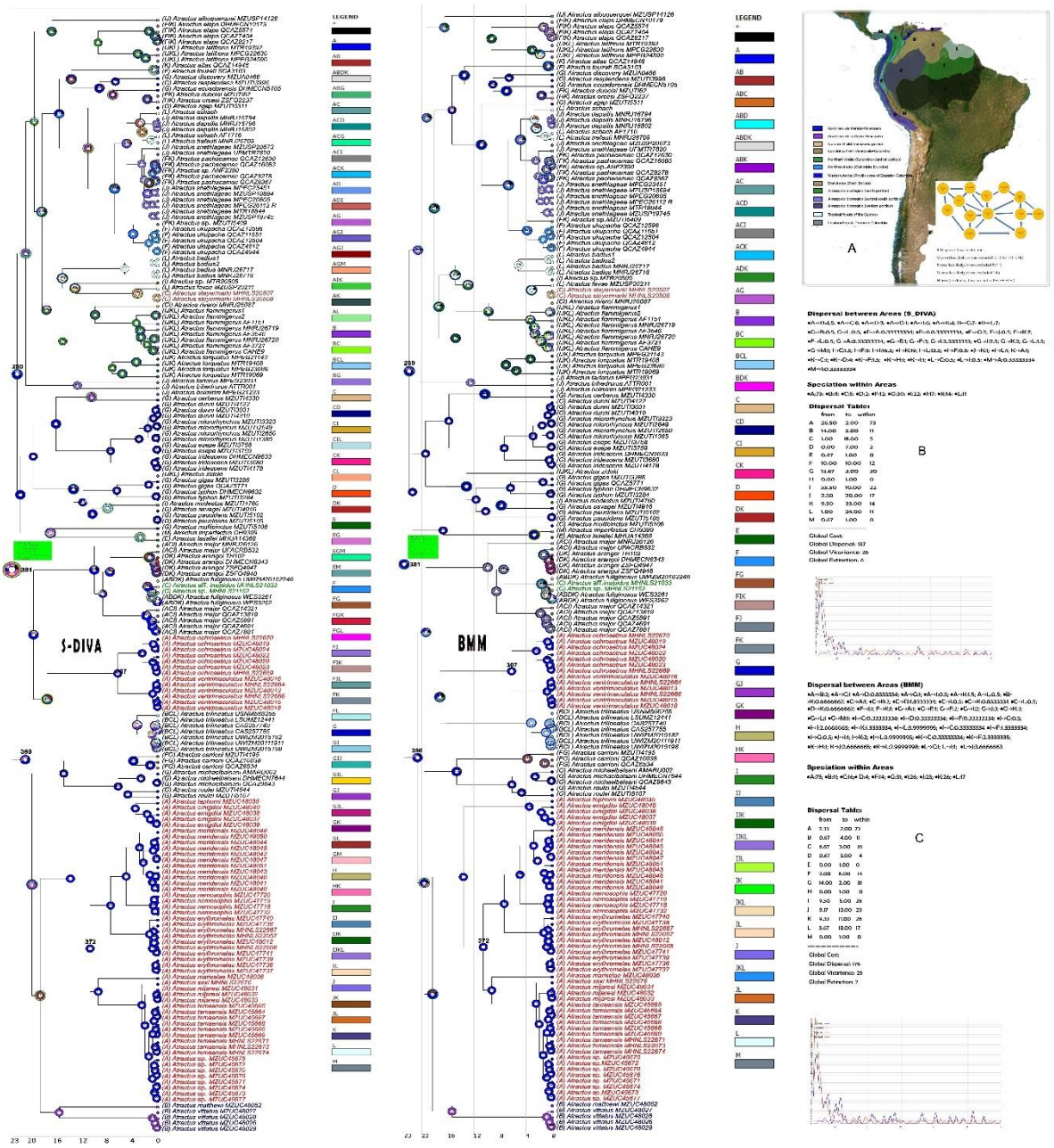

FIGURE 3. TIME-CALIBRATED TREE OF THE SLEEPYHEAD SNAKES OF THE GENUS *ATRACTUS*. ON THE LEFT, THE MOST PROBABLE ANCESTRAL AREAS INFERRED USING THE S-DIVA MODEL ARE REPRESENTED, WHILE ON THE RIGHT, THE PROBABILITIES USING THE BMM MODEL ARE SHOWN, BOTH IMPLEMENTED IN THE RASP V.4.2 SOFTWARE. THE PIE CHARTS SHOW THE SUM OF THE MARGINAL PROBABILITY OF EACH INFERRED BIOGEOGRAPHIC STATE. THE SAMPLED LOCALITIES ARE COLOR-CODED TO MATCH THE PREVIOUSLY DEFINED BIOGEOGRAPHIC REGIONS. LEFT SIDE, A = 13 BIOGEOGRAPHIC AREAS IN SOUTH AMERICA WHERE THE GREATEST DIVERSITY OF *ATRACTUS* IS DISTRIBUTED. LIKEWISE, THE POSSIBLE DISPERSALS AND RESTRICTIONS BETWEEN AREAS ARE ALSO AVAILABLE. LEFT SIDE, B = RESULTS OF THE S-DIVA MODEL AND LEFT SIDE, C = RESULTS OF THE BMM MODEL.

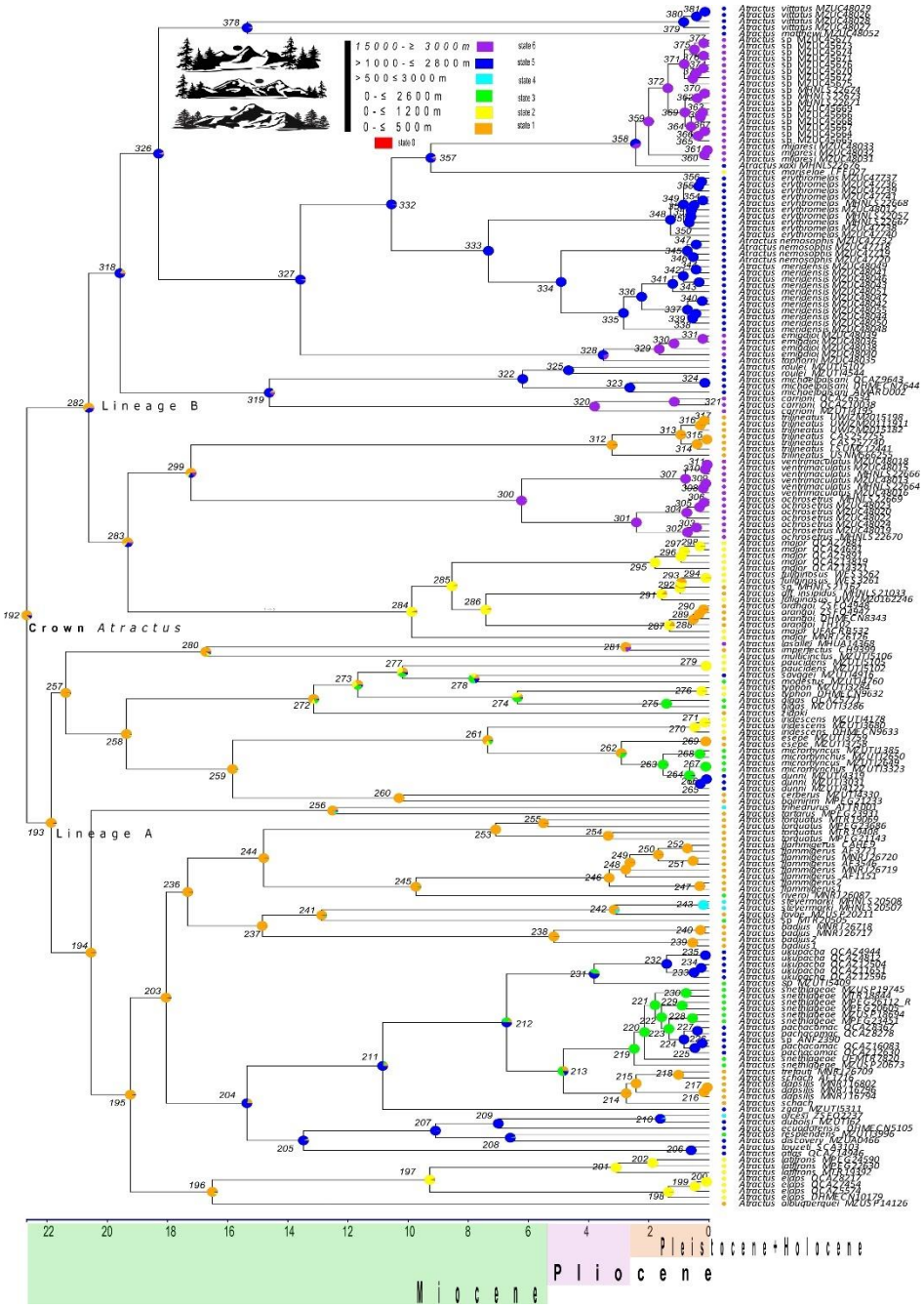

Figure 4. RECONSTRUCTION OF THE ANCESTRAL STATE FOR ALTITUDE USING THE MBASR LIBRARY IN R V.4.1. SIX ALTITUDINAL STATES WERE DEFINED, THE CIRCULAR GRAPHS SHOW THE SUM OF THE MARGINAL PROBABILITY OF EACH INFERRED BIOGEOGRAPHIC STATE.

Time-dependent diversification

The lineages through time (LTT) plots showed a recent decline in the rate of lineage accumulation towards the present (Fig. 2), suggesting a non-constant pattern of speciation. Using the MCC tree, a value of $\gamma = -5.13$ was calculated. From this value, we simulated a null distribution of γ under a pure birth model (Yule), with 1000

replicas, assuming a phylogeny with incomplete sampling (ρ = 0.42). The Monte Carlo test (mccrTest) implemented in the LASER package yielded a critical value of γ = –4.80, indicating that the empirical value of γ was significantly lower than expected under a constant rate model (p = 1.0), supporting a recent decline in the diversification rate. Likewise, the calculation of γ was repeated for a sample of 100 trees after the burn-in of the posterior distribution, obtaining an average value of γ = 9.09 ± 0.24. In all cases, the empirical values of γ were significantly lower than the critical threshold (γ-critical = –4.80, $p < 0.01$), suggesting that heterogeneity in the diversification rate is a robust characteristic of the evaluated group. On the other hand, when comparing simple diversification models, the birth-death (BD) model showed a significantly better fit than the Yule (pure birth) model, with log-likelihood values of 392.30 and 299.81, respectively. The likelihood ratio test (LRT) yielded a value of LR = 184.98, $p < 2.2e-16$, indicating that extinction has been a key process in the evolutionary history of the group. These results were consistent with the estimates made in diversitree, which reported similar values of λ ≈ 1.75 and μ ≈ 1.70 for the BD model, reaffirming that the turnover of lineages has been high, possibly reflecting processes of microendemism, geographical isolation, and recurrent contraction-expansion events in montane environments.

With the idea of comparing the nodes of interest, we applied the DR (diversification rate) metric to the 100 trees. Our topology yielded two lineages A (node 193, Fig. 5) and B (node 282, Fig. 5). In this particular case, both nodes (lineages) show statistically significant differences in speciation and extinction rates, with p-values < 0.001 in both Wilcoxon tests (Fig. 5A-B). This suggests that species associated with exclusively Andean mountainous environments (node 282) exhibit more intense evolutionary dynamics compared to node 193, which includes species with broad altitudinal gradients from the Andes and non-Andean regions (e.g., Amazonia). To another level of our phylogeny, the comparison of speciation rates (Lambda), extinction (Mu), and net diversification (TD) among the four main nodes reveals heterogeneous patterns associated with geography. Node 257, corresponding to Ecuadorian species from the Pacific Andes, exhibits the highest and sustained speciation rate, with a high TD, consistent with a cradle pattern, where local radiation seems to drive diversification. In contrast, node 327, formed by Andean species from Venezuela, exhibits a moderate TD and intermediate λ, along with significant extinction, suggesting a pattern closer to

pump, where diversification would be mediated by dispersal to or from other mountainous regions. Node 194, which groups Ecuadorian Andean and Amazonian species, shows intermediate values λ and μ, with moderate TD, reflecting the combination of lowland and mountainous lineages; its dynamics point to a mixed node, with limited local speciation and connectivity between regions. Finally, node 283, which includes Andean species from Venezuela, the Coastal Range, and the Amazon, constitutes a transitional node, where lowland species predominate, but some isolated Andean lineages could be related to mountain lineages in Colombia; its average Lambda and TD indicate moderate diversification, while μ suggests some vulnerability of the mountain lineages. Overall, these results demonstrate that geography and elevation modulate speciation and extinction rates, generating nodes with clearly differentiated dynamics between cradle, pump, and mixed or transient nodes.

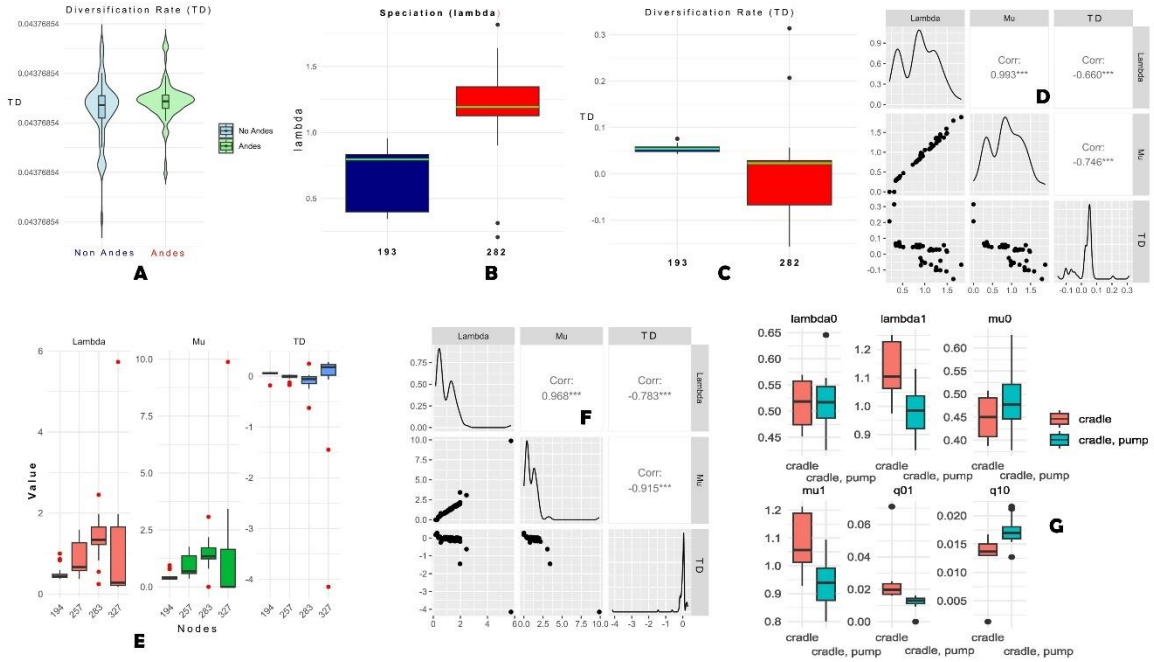

FIGURE 5. A = DR MODEL FOR NON-ANDES AND ANDES SPECIES; B-D = DR MODEL FOR LINEAGE A (NODE 193) AND LINEAGE B (NODE 282); E-F = SPECIATION, EXTINCTION AND DIVERSIFICATION RATE USING DR MODEL FOR NODES 194, 257, 283 AND 327, AND G= BOXPLOT BISSE MODEL.

Macroevolutionary models applied to *Atractus* phylogenies reveal consistent patterns of diversity-dependent diversification (Supplementary_1_7). Comparing constant speciation-extinction models (BD), protracted models (PBD), and density-dependent models (DD), we found that the DD simple model (linear diversity dependence with extinction) was the best fit in 100 % of the evaluated trees (10 out of 10), with the

lowest AIC values (average AIC = 817.5). This model represents a scenario where both speciation and extinction are regulated by the number of existing lineages, reflecting a possible ecological limit or niche saturation, which is consistent with a "museum" type diversification pattern. That is, the accumulation of species could be strongly influenced by the maintenance of lineages over time in stable environments, rather than by a rapid and recent radiation. In contrast, neither the BD model (cradle hypothesis: rapid speciation without limits) nor the PBD model (pump hypothesis: delay in post-speciation diversification) were selected as the best for any tree. This suggests that neither a recent adaptive radiation nor prolonged speciation processes adequately explain the diversification of the group. Moreover, the DD model without extinction was discarded due to its consistently high AIC values (average ≈ 950). Overall, these results support the idea that *Atractus* diversified under a regime of moderate ecological turnover in montane systems, likely influenced by microendemism, ecological specialization (e.g., vermivory), and limited dispersal. The coexistence of speciation and local extinction processes is further supported by the shape of the lineage-through-time (LTT) curves. In summary, diversity-dependent models provide strong evidence for a long-term, stable diversification scenario, reinforcing the museum hypothesis as the main explanatory framework for *Atractus* diversity.

The binary state-dependent diversification models (BiSSE) indicated consistent patterns of differential speciation between lineages distributed in the Andes (state = 1) and those outside this region, non-Andes (state = 0) (Supplementary_1_8). In the 100 trees analyzed (100 + MCC), speciation rates were consistently higher in the Andean lineages (λ_1 = 0.84–1.25) compared to the non-Andean ones (λ_0 = 0.42–0.64). This difference could suggest strong support for the "species pump" hypothesis of diversification in the Andes, where new lineages would have originated more frequently. However, extinction rates were also slightly higher in Andean lineages (μ_1 = 0.79-1.21) compared to non-Andean ones (μ_0 = 0.37-0.62), although the difference was less pronounced than in speciation rates. This could reflect a dynamic equilibrium of high turnover in mountainous areas, possibly influenced by ecological and paleoclimatic factors. In contrast, the transition rates between states were generally low (q_{01} = 3.10493E-07-0.071002391; q_{10} ≈ 0.001320717- 0.021611718), indicating that the dispersion between Andean and non-Andean regions was limited over evolutionary time. In particular, the transition rate from the Andes to other regions (q_{10}) was almost null in most trees,

suggesting a pattern of phylogeographic retention in Andean environments and possible ecological conservatism. Overall, these results support an Andes-centered diversification history, characterized by high speciation rates, relatively balanced extinction, and limited geographical transitions. Thus, the detected pattern could be consistent with a mountain scenario as a "species pump" under specialized ecological conditions, such as the niche conservatism observed in this group. Although trees 83, 90, and 97 showed the best AICc values (Supplementary_1_7), supporting the "cradle" hypothesis (5G).

After running the ClaSSE models on 100 phylogenetic trees, ten diversification models were evaluated, representing different hypotheses about the evolutionary dynamics of *Atractus* in neotropical regions. Of these, five models were consistent with the "species pump" hypothesis (speciation-extinction in the Andes with transitions), three models with the "museum" hypothesis (low extinction in the Andes), and two with the "attractor species" hypothesis (preferential colonization towards the Andes). No models were identified that fit the "cradle" or "time for speciation" hypotheses. The descriptive analysis showed that the models classified as "species pump" presented, on average, a higher speciation rate ($\lambda = 1.72$) and a low extinction rate ($\mu = 0.016$). On the other hand, the "museum" models also showed low extinction rates ($\mu = 0.028$) but with slightly lower speciation rates ($\lambda = 1.48$), which is consistent with a scenario of linear lineage accumulation. Meanwhile, the "attractor species" models showed even lower values of speciation and extinction, suggesting a more conservative pattern. The statistical tests did not indicate significant differences in most of the evaluated parameters, except for the speciation rate (λ), where the Kruskal-Wallis's test showed marginally significant differences between hypotheses ($p = 0.042$). The post-hoc analysis (Dunn test) indicated that the comparisons between "pump species" and "museum" were not statistically significant after Bonferroni correction, but did show a relevant trend (adjusted $p = 0.0787$). Overall, the results suggest that the Andes could be functioning as a "species pump" or "museum" system, where the high diversity of *Atractus* can be explained both by speciation-extinction rates and by the persistence of ancient lineages. This underscores the complexity of the processes that regulate diversity in tropical mountainous regions.

With relation BAMM, a Bayesian framework for modeling and visualizing speciation and extinction rates that uses the transdimensional reversible jump Markov chain Monte

Carlo (RJMCMC) which allows exploring a vast state space of candidate diversification models (Fig. 6). The rate analyses at key nodes of the phylogenetic tree revealed interesting variations in the diversification processes. In particular, nodes 194, 257, 283, and 327 showed relatively high speciation (λ) and extinction (μ) rates, with average values close to 2.2. However, the net diversification rate ($r = \lambda - \mu$) was low or even negative in most of the nodes, indicating that extinction has been equal to or slightly higher than speciation in these lineages. Node 257 was the only one that showed a positive net rate ($r \approx 0.078$), suggesting a slight increase in the diversification of that particular clade. In contrast, the other nodes showed negative or near-zero net rates, implying that those lineages might be experiencing a decline or stagnation in the number of species due to the high extinction rate. These results suggest that the diversification dynamics within the group are heterogeneous, with some clades possibly in decline or in equilibrium, while others still show some growth in diversification. This pattern could reflect complex ecological and geographical processes, such as recurrent events of isolation and extinction in mountainous environments, which differentially affect the various subregions and lineages within the studied group.

The analysis of net diversification rates from the configurations sampled in BAMM revealed a consistent pattern of recent deceleration in group diversification. Initially showed positive diversification rates towards the basal nodes, with maximum values reaching between 0.35 and 0.57, followed by a marked decrease towards the terminal branches, where the net rates become negative (between -0.21 and -0.12).

This pattern supports the hypothesis of a "cradle" model where mountainous regions promoted accelerated speciation in early stages, followed by a reduction in diversification possibly associated with ecological saturation effects or geographical constraints in recent stages. Likewise, the decrease in the net rate towards the terminals could reflect local extinction processes or a decrease in colonization, which is consistent with the "museum" (diversity retention) and "species-attractor" (species attraction) hypotheses in certain mountainous regions. Overall, these results suggest that the diversification dynamics of the group have been heterogeneous in time and space, with episodes of early high speciation followed by decelerations associated with environmental and biogeographical factors.

The analysis using MEDUSA identified two significant shifts in diversification rates ($\Delta AICc > 6.25$) along the phylogeny (Fig. 7A). The first shift occurred at node 192,

which represents the root of the clade, with a net diversification rate of r = 0.0828, and a relative extinction rate of ε = 0.7761. A second shift was detected at node 282 (r = 0.0345, ε = 0.9716), suggesting a substantial slowdown in diversification, likely associated with microendemic Andean lineages. These two clades showed non-overlapping confidence intervals, indicating statistically distinct dynamics. The presence of this secondary shift corresponds to one of the major Andean lineages previously identified using ClaSSE (Fig. B) and BAMM, reinforcing the hypothesis of a regionally constrained diversification process.

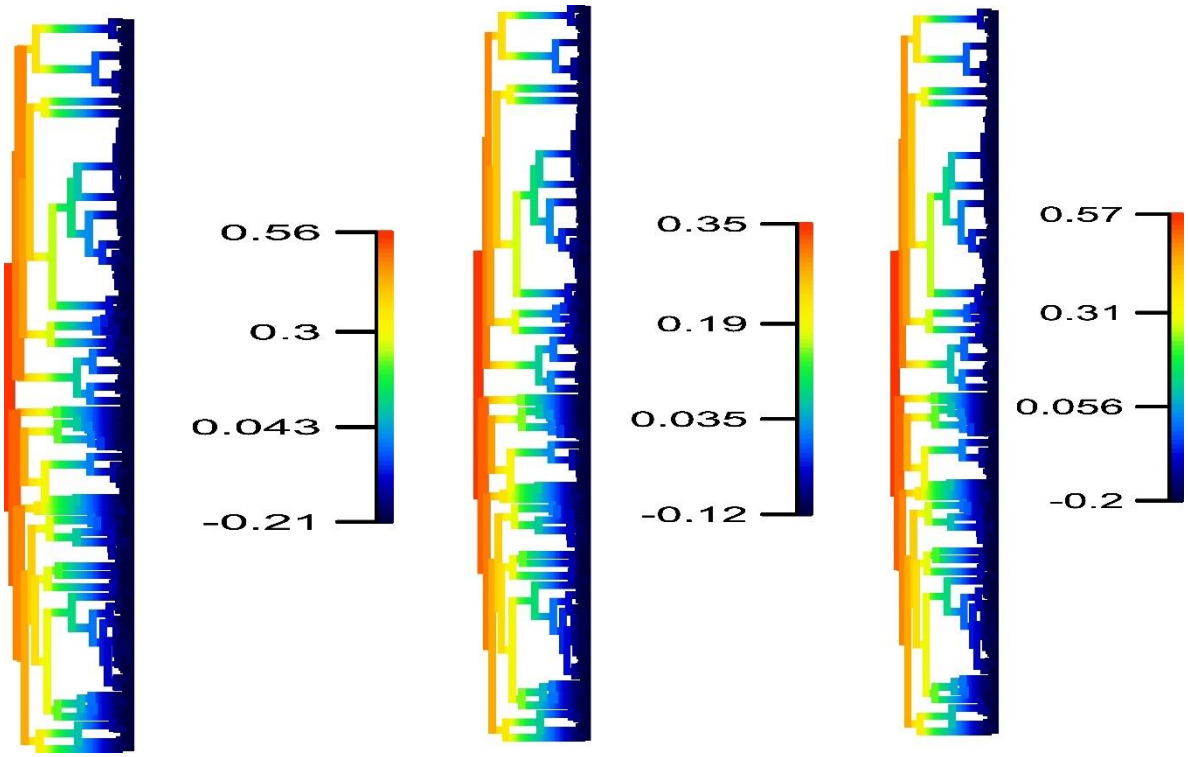

FIGURE 6. IB PHYLOGENY OF SLEEPYHEAD SNAKES *ATRACTUS*, WITH BAMM ESTIMATES OF SPECIATION RATE (LAMBDA, A), EXTINCTION (MU, B), AND NET DIVERSIFICATION RATE (C).

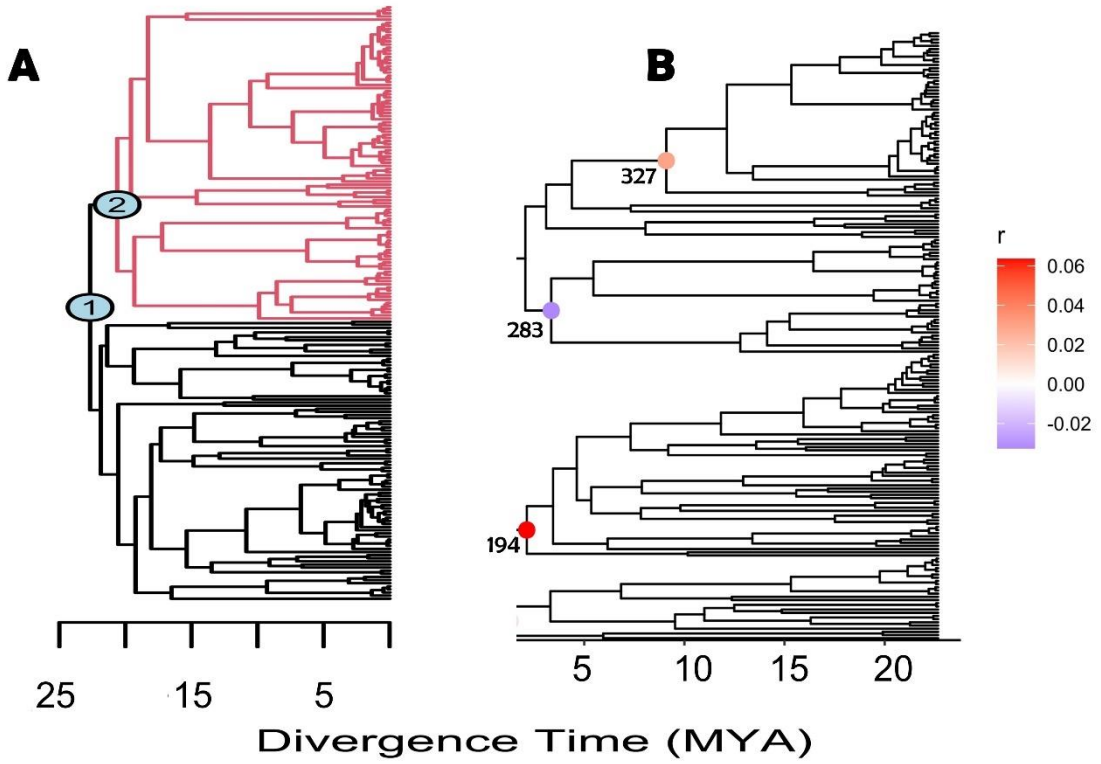

FIGURE 7. (A) DIVERSITY TREE OF ATRACTUS SLEEPY SNAKES USING MEDUSA, THE CLADES WITH CHANGES IN DIVERSIFICATION RATES ARE INDICATED WITH NUMBERS AND (B) TREE CONSTRUCTED WITH CLASSE SHOWING THE DIVERSIFICATION RATE AT NODES 194, 283, AND 327.

DISCUSSION

Within the South American dipsadids, *Atractus* undoubtedly constitutes a remarkably diverse and particularly relevant group of snakes, especially considering that their greatest diversity is associated with the orogenesis in northern South America. For this reason, we believe that sleepyhead snakes have the potential to be the most important model system for comparative snake biology and particularly equivalent to other reptile groups such as *Liolaemus* (Esquerré et al. 2019). This study represents a first step in this direction by providing a calibrated multilocus phylogenetic estimate based on ~63 spp. (22 spp. from Venezuela), provides important baseline information about the history of these snakes, especially those inhabiting the Andes of Venezuela. However, we are aware of our limitations regarding the available sampling to evaluate their diversification and biogeographic pattern (e.g., limited sampling of taxa, 42 % of the known species; support for basal nodes).

Our results are contingent upon the phylogenetic hypothesis we used, which consists of the most complete phylogenies available at this time and our data on Venezuelan species, and in general, they are consistent with other studies (Arteaga et al. 2017, 2022; Melo-Sampaio et al. 2019, 2021; Murphy et al. 2019; Passos et al. 2022). In this sense, our divergence time estimates support an origin in the early Miocene around 22.63 Myr for the sleepyhead snakes of *Atractus* genus, being consistent with Serrano et al. (2023).

In this temporal context, in the early Neogene (~23 Myr), the Andes consisted of a more or less continuous mountain range, although significantly smaller in width and height compared to the present day (Boschman 2021). At this time, high elevations (i.e., close to modern ones) were present only in the Patagonian Andes (Colwyn et al. 2019) and in the western range of the Central Andes (Quade et al. 2015; Sundell et al. 2019). By that time, the region corresponding to the Eastern Andes and the Altiplano of the Central Andes would be at altitudes between 1000-2000 m (Leier et al. 2013; Garzione et al. 2014; Florella et al. 2014; Sundell et al. 2019). Although the northern Andes during that period still had low elevations of less than 2000 m (Anderson et al. 2015, 2016), the Middle Miocene uplift of the eastern cordillera (~12 Myr) and the Late Miocene uplift of the Mérida Andes (~8 Myr) constitute key orogenic scenarios in the distribution and diversification of South American biota. Due to the uplift of both mountain systems, the wetland environments of Pebas disappeared and were replaced by a landscape dominated by rivers, also known as the Acre phase (Hoorn et al. 2010), which then between the Late Miocene and the Holocene (~11.5 Myr–10 ka) would favor the intersection of the Andes with the lowlands of western Amazonia. Further north, the dry region of La Guajira between Colombia and Venezuela (Caribbean coast) once harbored a humid tropical rainforest that turned into a desert sometime between the Miocene and the Pliocene (17.3 and 3 Myr) (Jaramillo et al. 2020).

In this study, we estimate divergence times and reconstruct the ancestral geographic distributions of the sleepyhead snakes of the genus *Atractus* in South America. Our analyses suggest a complex history involving repeated colonizations of several broadly defined biogeographic areas. These events have occurred over a long period of time, what it suggests that a series of factors may have influenced the evolution of modern species diversity. Next, we discuss the general patterns recovered and their possible explanations.

Although our phylogeny represents about 42 % of the known diversity, preliminary data already allow us to identify patterns consistent with an Andean "species pump" and a possible attractor dynamic in that region. These results underscore how topographic complexity (microendemism) and climatic fluctuations in mountainous systems may have favored multiple mechanisms of diversification. Evaluating non-exclusive hypotheses within this framework offers a solid pathway for future studies on the evolution of reptiles in the northern Andes.

Phylogenetic and macroevolutionary analyses applied to the genus *Atractus* have revealed patterns, at least preliminary, that allow for the testing of non-mutually exclusive hypotheses of Andean diversification. The LTT (Lineage Through Time) curves, obtained from trees calibrated with BEAST, show a constant increase in lineages towards the Pliocene-Pleistocene, coinciding with significant Andean uplift events and climatic oscillations, what reinforces a correspondence with the uplift of the central and northern Andes regarding the diversification of sleepyhead snakes. This aligns with previous studies that have highlighted the importance of Andean orogeny as a generator of diversity, either through high speciation rates or the prolonged conservation of ancient lineages (Hughes and Eastwood 2006; Rull 2011). This signal is particularly noticeable in the species distributed in the Andes of Venezuela (cordillera de Mérida), where diversification rates increase sharply during this interval. In contrast, state-dependent models, especially BiSSE and ClaSSE, revealed patterns consistent with the "species pump" hypothesis, showing high rates of both speciation and extinction in Andean areas. In particular, the ClaSSE models that fit best were those that allowed transitions between combined areas and specific speciation rates for Andean lineages, which suggests that unstable and intramontane environments acted as dynamic centers of diversification, driving both the formation and extinction of species. The "species pump" hypothesis suggests that diversification is driven by high speciation linked to topographic complexity, Andean ecological changes, and periods of extinction and subsequent transitions, which can be seen in different groups, including plants and amphibians (Madriñán et al. 2013; Antonelli et al. 2018). The trend towards a significantly higher speciation rate in our "species pump" models reaffirms this pattern.

Additionally, strong support was found for the "attractor species" hypothesis, given that the transition parameters (q) in ClaSSE and BiSSE indicated a high colonization rate towards the Andean regions from non-mountain areas. This pattern is reinforced by the

high proportion of dispersal events inferred in the ancestral state analyses (S-DIVA: 176 dispersals vs. 25 vicariance; BMM: 137 dispersals vs. 25 vicariance), which suggests that the mountains acted as ecological sinks. The role of transitions to and from the Andes in generating diversity necessarily requires expanding the analysis to include *Atractus* species from the Andean foothills, especially in Colombia and Venezuela. Although in other Andean organisms, transitions were frequent with significant impacts on their diversity (Birds, Sedano and Burns 2010; Beckman et al. 2015. Frogs, Hutter et al. 2013; Castroviejo-Fisher et al. 2013; Muñoz-Ortíz et al. 2015; Mendoza-Henao et al. 2021), in others like hummingbirds it was independent, with an extraordinarily significant diversification in the northern Andes and a South American origin dating back to the early Miocene around 23 Myr (McGuire et al. 2014) and similar to the origin of *Atractus*. Understanding the pattern of altitudinal transitions in relation to speciation and underlying processes in this group could be a puzzle not yet well understood. For the moment, we believe they are independent, at least for the cordillera de Mérida, where the greatest diversity of *Atractus* occurs at the montane level and not towards the slopes.

On the other hand, the "museum" hypothesis received little support, given that the estimated extinction rates for the Andean areas were similar or even higher than in lowland areas. The "cradle hypothesis" has partial support, as high speciation rates were observed in montane lineages, but these were not homogeneous across all of the Andes (more intense in Venezuela than in Ecuador-Colombia). Although Chazot et al. (2016) discussed Valentine (1967) species pump hypothesis, they did not include it in their analyses, so their results regarding a higher speciation rate in the Andes are consistent with the cradle hypothesis. While their reasoning is understandable, here we prefer to separate both hypotheses, understanding the role of extinction in the Andes, especially if we consider that the ecological characteristics and distribution of this group would indicate vulnerability to climate changes, primarily during the asynchronous uplift (e.g., cordillera de Mérida; Audemard and Audemard 2002; Bermúdez et al. 2011) and then the contractions-expansions due to climate oscillations during the Pliocene-Pleistocene (McCain y Coldwell 2011). Finally, the strong niche conservatism (restricted to cloud forests and a vermivorous diet) and the limited vagility of *Atractus* could support the "time for speciation" hypothesis, where the ecological stability of certain montane gradients allowed for the accumulation of lineages over long periods. Although our

ancestral reconstruction models failed to significantly determine the origin of the basal node in *Atractus*, the emerging option could be somewhere in the northern Andes between Colombia and Ecuador toward the Pacific. And although the cordillera de Mérida exhibits a significant rate of speciation, it is ruled out as the center of origin of the group.

Although Weir (2006) found in birds a suggestive pattern of species accumulation indicating that lowland and highland regions were affected differently by recent climatic fluctuations. Our results are consistent with idea that suggested that average diversification rates of Andean taxa were higher than those of non-Andean taxa (e.g., Amazonia). Similarly, consistent with studies that highlight the Andes as a stable refuge for ancient lineages during adverse climatic periods (Hoorn et al. 2010; Antonelli et al. 2009). The absence of models fitting as "time for speciation" hypotheses may reflect that for *Atractus*, the evolutionary history is more influenced by dynamic processes in speciation and lineage retention than by a simple increase in colonization time or origins within the region. In summary, these findings emphasize the need to approach diversification in mountainous regions from multiple perspectives, integrating complex ecological and evolutionary processes that cannot be explained by a single hypothesis.

In fact, results from BAMM and MEDUSA evidence of temporal heterogeneity in diversification: the pattern of early high speciation and subsequent deceleration suggests that diversification was not constant, supporting non-equilibrium models of diversification. Thus, the high net rates at basal nodes suggest that mountains functioned as centers for the rapid generation of new species, that is, the "cradle" hypothesis. While the reduction of net diversification towards the terminals could indicate a conservation effect or species attraction that limits current diversification (e.g., "museum"). If this future scenario with increased sampling persists, what biogeographical implications are there? For example, the slowdown in diversification may reflect ecological saturation, local extinctions, or geographical barriers that reduce colonization and recent speciation. These snakes have a diet specialized in worms and are cryptozoic-semi-fossorial, which would be relevant in relation to microendemism and the Andean uplift that has been asynchronous, with changes in climatic dynamics (e.g., slopes with different rainfall regimes) and affected by the climatic oscillations of the Pliocene-Pleistocene. Such observed patterns coincide with recurrent processes of geographical isolation, budding, and climatic fluctuations that favor alternating episodes

of speciation and extinction, which could fit more with the idea of a species pump, where extinction would play a role by favoring a rate in the regime of change that would drive speciation (e.g., cordillera de Mérida at the intramontane level).

Under this previous scenario, our analyzes integrating various macroevolutionary approaches allow us to conclude that the diversification of *Atractus* has followed a complex pattern, where phases of rapid radiation are combined with processes of lineage saturation and persistence. The greatest diversity of the genus is concentrated in mountainous systems above 1000 m asl, where no species are shared between biogeographic areas, except in certain lowland clades that show more transient and mixed dynamics. The results of BAMM and DDD agreed in indicating a slowdown in diversification rates, consistent with the "museum" hypothesis, where niche saturation and lineage persistence explain much of the evolutionary dynamics. However, state-dependent models (BiSSE and ClaSSE) suggest additional processes: while BiSSE supported "cradle" and "cradle–radiation" scenarios, ClaSSE revealed an important role of cladogenetic events and supported "species pump" and "museum" hypotheses, showing how topography and geography have shaped speciation in the group. For their part, DR analyzes confirmed the coexistence of "cradle" patterns in certain Andean clades, "museum" in lineages with rapid expansions, and mixed scenarios in other nodes. The cordillera de Mérida represents an emblematic case: despite being a relatively young mountain system (≈8 Ma), its complex geological history generated intramontane heterogeneity and a unique topography that favored microendemism and accelerated diversification. Overall, the results support a mosaic view of evolution in Atractus, where the mountains act both as a "cradle" for new lineages in scenarios of rapid speciation and as a "museum" by retaining diversity in intricate and environmentally stable landscapes. Thus, the interaction between the geological history of the Andes, the topographic complexity, and the biogeographic boundaries explains the unique diversity and the pattern of endemism that characterize the genus.

A first evolutionary insight into the sleepyhead snakes of the genus *Atractus* in a changing climate and landscape due to the uplift of the northern Andes: key points

1. Our data indicate up to this point two major lineages, whose origin and diversification have hypothetically followed the uplift of the central and northern Andes, which favored new habitats that could be colonized by isolating organisms

on both sides of the mountains (e.g., diversity of the cordillera de Mérida). Due to incomplete sampling, there remains uncertainty regarding the ancestral origin of the group, but given the geological and climatic scenarios during the Neogene, the most recent ancestor likely had to be from lowlands between the northern Andes towards the Pacific. Although there is a possibility that the decreasing rates of species accumulation towards the tip of the tree may be partly artifactual, resulting from incomplete sampling, we currently believe that the decreasing rates of diversification over time in *Atractus* may also reflect fewer opportunities for diversification as the mountains reached their modern elevations in the Late Pliocene (Gregory-Wodzicki 2000) or the reduction of the potential for repeated cycles of allopatric speciation due to infrequent range expansions (Moen and Morlon 2014).

2. The specific responses of the clade to environmental changes show the need to emphasize the complexity of the system instead of generalizing. For example, the Andes of Venezuela, specifically the cordillera de Mérida, can be recognized as both a species pump and cradle. The available evidence suggests that the diversification of *Atractus* in the northern Andes has been mostly allopatric. In the cordillera de Mérida, the coexistence of species along altitudinal gradients reflects secondary contact after allopatric divergence (e.g., *Atractus meridensis*, *A. emigdioi*, and *Atractus* sp., Esqueda et al. in prep.). This implies that the geographical ranges of the species must have been dynamic over evolutionary time, regardless of whether the species are currently limited by dispersal.
3. An outstanding characteristic of these snakes is their high degree of endemism and restricted altitudinal ranges, like other organisms with similar patterns (Muñoz-Ortíz et al. 2015). Most species are associated with cloud forests above 2000 m asl, both in Colombia (cordillera of Eastern) and the Andes of Venezuela (cordillera de Mérida). Andean montane forests are distributed along a highly fragmented system of "sky islands" with predominantly homogeneous climatic conditions, where niche conservation seems to be the rule. For example, theoretical and empirical studies have shown that the geographical distribution and ecological and morphological breadth of species that originate from adaptive or non-adaptive radiations can be very different. In fact, when divergence is primarily driven by adaptive factors, the species will be more environmentally and morphologically diverse than the taxa derived from non-adaptive processes (Muschick et al. 2014).

Although our Andean sleepyhead snakes from Venezuela have shown little or no climatic niche differentiation (Esqueda et al. in prep.), their morphological differences fit within a framework of geographic isolation, suggestive of a non-adaptive species radiation (Rundell and Price 2009). This would be strongly supported as a result of an interaction between the intrinsic traits of these organisms, a diet specialized in earthworms (Martins and Oliveira 1993, 1999), and a low dispersal capacity, which makes them prone to speciation, and the history and topography of the region they inhabit (e.g., Mérida Andes). Thus, the dynamics and topographical heterogeneity of the northern Andes likely provided ample geographical opportunities for population expansion and subsequent isolation that led to allopatric speciation. Similar patterns of non-adaptive radiations have been reported in other taxa restricted to montane ecosystems, such as land snails in the Pacific (Parent and Crespi 2009), freshwater fishes in Central America (Seehausen 2006), and amphibians and reptiles in the tropical Andes (Castroviejo_Fisher et al. 2013; Esquerré et al. 2019). In these systems, the combination of limited dispersal, ecological conservatism, and strong topographic complexity fosters lineage diversification without substantial ecological divergence. Our findings thus contribute to the growing evidence that mountain systems can act not only as arenas for adaptive radiations driven by ecological opportunity but also as cradles of non-adaptive radiations fueled by geographical isolation and intrinsic biological constraints.

4. Our analyses indicate that the Andean uplift did not create a uniform scenario of diversification, but rather a mosaic of evolutionary histories associated with different ecological and altitudinal contexts, which aligns with the asynchronous condition of the uplift of the central and northern Andes (Bermúdez et al. 2011). Under this scenario, we identify two major configurations: the intramontane regions and the mountain slopes or foothills, each with distinct responses to the geoclimatic dynamics. In the intramontane regions such as the mid-high basin of the cordillera de Mérida, it is likely that the environmental conditions were more unstable, subject to contractions-expansions of habitats, for example, during the Pliocene-Pleistocene. This context may have promoted high rates of speciation, but also extinction, leading to multiple transitions between states, reflecting the temporal and spatial complexity of these areas. These fluctuations may have favored cycles of isolation and reconnection, shaping a pattern of diversification linked to

mountain processes, but mediated by events of ecological fragmentation. On the other hand, the Andean slopes, particularly those in contact with cloud forests, seem to have offered more stable conditions, functioning as persistent refuges during periods of climate change. This pattern is consistent with the ecological stability model, where habitat continuity favors the persistence of lineages and in situ diversification without major displacements.

The evidence of niche conservatism (Wiens and Graham 2005) in *Atractus*, with a diet specialized in earthworms and cryptozoic-semi-fossorial habits, reinforces this idea. The species do not appear to have evolved into new ecological niches, but rather have maintained their requirements over time, suggesting that their diversification has been more linked to geography than to ecological innovation. Moreover, our ancestral altitudinal reconstruction data reveal that the origin of the clade must have been lowland, but the species of the clade from the Venezuelan Andes show a clear montane origin, unlike the lineages from the western Andes (Ecuador-Colombia towards the Pacific), where the altitudinal ranges are broader (0-3000 m asl). This asymmetry suggests an altitudinal polarity in diversification, possibly associated with the historical stability of the cloud forest in the Venezuelan Andes, in contrast to the greater vertical connectivity in the western Andes, which aligns with the "flickering connectivity" hypothesis proposed by Flantua et al. (2018) in which the Páramos situated above the cloud forest experienced dynamic contractions and expansions, causing them to descend along with the cloud forests (e.g., during the Pleistocene in the Andes, Hooghiemstra and van der Hammen 2004; van der Hammen and Cleef 1986). Although in Venezuela we still do not have evidence of *Atractus* sightings in Páramos, we do have them in the ecotone with the cloud forest (e.g., *Atractus ochrosetrus* and *A. ventrimaculatus*; Esqueda et al. in prep.), they would have been indirectly affected, acting as core zones of stability or reconnection.

Overall, this evidence suggests that the current diversity of *Atractus* in the Andes is the result of a combination of: conserved ecological specialization, differential geoclimatic dynamics between regions, and progressive geological uplift, which allowed for both isolation and expansion at key moments in its history.

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Author contributions

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Data availability

All data generated or analyzed during this study are included in this published article (see supplementary information files in format xlsx, except unpublished data that are not yet public until the time of their publication in the repository GENBANK). All unpublished specimens are not listed on the IUCN Red List of Threatened Species Index and met the standards required by the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE). All data generated or analyzed during this study are included in this published article (including supplementary information files).

Declarations

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CHAPTER II

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INTEGRATIVE TAXONOMIC ASSESSMENT OF TWO *ATRACTUS* (SERPENTES: DIPSADIDAE) FROM MÉRIDA ANDES, VENEZUELA

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ABSTRACT

Recently, the nominal species *Atractus meridensis* Esqueda & La Marca, 2005 was considered a junior synonym of *Atractus erythromelas* Boulenger, 1903, both species 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 modeling 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.

KEY WORDS. – Systematics, taxonomic status, sleepyhead snakes, Venezuelan Andes

RESUMEN

Recientemente, la especie nominal *Atractus meridensis* Esqueda & La Marca, 2005 fue considerada un sinónimo menor de *Atractus erythromelas* Boulenger, 1903, 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 diagnosis y descripción para cada especie, incluyendo una modelización de su actual

distribución, que demuestra su distribución alopátrica. 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

INTRODUCTION

Although they originated in the Old World and later dispersed to South America (Zaher et al. 2019), dipsadines snakes exhibit a spectacular ecological and phenotypic diversity as result of adaptive radiation, and where snakes with fossorial habits clearly differentiate themselves from other groups (Pandelis et al. 2023). If we consider that dipsadines diversity reaches at least ~806 species (Zaher et al., 2019), it is remarkable from both an evolutionary and ecological perspective that the ground or sleepyhead[1] snakes of the genus *Atractus* Wagler, 1828, account for 18.6% of all known dipsadines (Uetz et al., 2024). 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 (Rivas et al., 2012; Natera-Mumaw et al., 2015).

Recently, Passos et al. (2024) 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 integrate 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 (Padial et al. 2010), 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 idea of species, diagnostic characters, variability, geographic limits, and biogeographic scenarios is explored. Without a doubt, this theoretical exercise allows 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 Passos et al. 2024). Although we acknowledge the status of other Andean species such as *A. eriki*, *A. micheleae*, *A. ochrosetrus*, *A. tamaensis* and *A. mijaresi* (Esqueda and La Marca 2005; Esqueda et al. 2007), 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 of *A. erythromelas* during the late Miocene (Esqueda et al. 2025). Also, a comparative table between *Atractus* species is provided, along with a biogeographical discussion and conservation status.

[1]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 1,500 meters in altitude.

MATERIALS AND METHODS

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. 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, USA) at the Herpetozoa laboratory, University of Concepción. Two mitochondrial genes (Cytb and ND4) and two nuclear genes (NT3 and RAG-1) were amplified using primers and PCR conditions detailed in supplementary material_1_Table 1. DNA quality was assessed on 1.5 % agarose gels stained with SYBR® Vitrogen. Sequencing was performed by MACROGEN (Korea), and chromatograms were verified using BioEdit 7.0.9.0 (Hall, 1999). Open reading frames

were checked in Mega v.11 (Tamura et al. 2021). Heterozygous nuclear DNA sequences were identified visually for double peaks in chromatograms, and individual alleles were reconstructed using DnaSP v.6.12 (Librado and Rozas 2009) with two independent runs. Alignments showed no gaps in mitochondrial sequences, and sequences for other species were sourced from GenBank (supplementary material_1_Table 2), ensuring amplified loci were from single voucher specimens to avoid "terminal chimeras."

Phylogenetic analyses

The new sequences generated in this study were combined with sequences downloaded from GenBank. Additionally, 20 specimens representing to 18 species were used as outgroups (highlighted in yellow, supplementary_1_Table 2). Five gene fragments were obtained, corresponding to three mitochondrial amplicons, long 16S ribosomal RNA (525 bp); cytochrome b (897 bp); and NADH dehydrogenase ND4 subunit IV (713 bp) and two nuclear amplicons, neurotrophin-3 gene NT3 (516 bp); recombination activator RAG-1 (879 bp). Substitution saturation of each locus was assessed using the software DAMBE v.5 (Xia 2013). 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 (Nguyen et al. 2015).

The authenticity of the obtained sequences and the homology of the specific mtDNA and nuDNA markers were evaluated with a BLAST search in the NCBI genetic database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The consensus sequences for each locus were aligned using MAFFT (Katoh and Standley 2013) contained in Jalview v. 2.11.1.4 (Waterhouse et al. 2009), 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 exhibit nucleotide positions with high entropy and may have misaligned or incongruent regions were refined with the BMGE software: a BLOSUM62 matrix, a minimum block size of 20, a maximum entropy threshold of 0.5, and a rate limit gap of 0.65 (Criscuolo and Gribaldo 2010), available on the web service https://ngphylogeny.fr/ (Lemoine et al. 2019). Finally, the concatenation of all alignments was done with Mesquite v3.6 (Maddison and Maddison 2021). 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 (Triant and Dewoody 2007).

Two methods of phylogenetic analysis were used for all data sets and their results were compared. Firstly, we used maximum likelihood (ML) analysis to obtain the optimal tree topology of the concatenated data set. The best partition and substitution models were automatically selected using ModelFinder (Kalyaanamoorthy et al. 2017) and then implemented in IQ-TREE v.2 software (Nguyen et al. 2015) 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 from10,000 iterations and the confidence of the branches of the best ML tree was evaluated with the ultrafast bootstrap method using 10,000 bootstrap pseudoreplicates (Minh et al. 2013). 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/, Trifinopoulos et al. 2016), where branch support was calculated using the ultrafast bootstrap approximation (UFBS) (Minh et al. 2013) and the Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT) (Anisimova et al. 2011), with 1,000 replicas. The consensus tree was visualized in FigTree (Rambaut 2014). Nodes with bootstrap values ≥ 70 were considered strongly supported and those nodes with 95 % were considered highly supported.

In the second instance, we used bayesian inference (BI) analysis using the Bayesian framework implemented in the BEAST 2.7.5 software, and assuming the Yule speciation model, where all tips are sampled at the same time (Bouckaert and Drummond 2017). The matrix was partitioning by genes, 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, implements the “bModelTest “allreversible” option to estimate mutation rates for all genes evaluated. In addition, we use bModelTest switches between substitution models during the Metropolis coupled MCMC (MC3, Atchadé et al. 2011; Maturana-Russel et al. 2018; Müller and Bouckaert 2019), with a temperature of 0.02 and two chains, established in three independent runs of 50 million generations, saving the parameters and trees every 5,000 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 (Rambaut et al. 2022). Combining the runs was done with LogCombiner

v2.7.5 (Drummond et al. 2012). 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 (Rambaut and Drummond 2016) implemented on the CIPRES Science Gateway online platform (https://www.phylo.org/) (Miller et al. 2010).

Finally, we also calculated the uncorrected genetic distance (p-distance) using MEGA v.11.0 (Kumar et al. 2018) for mitochondrial Cytb and ND4, respectively.

Ecological niche modeling

To understand the distribution and habitat in the biogeographic context, we generated species distribution models (SDM) 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, those 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, being in total 109 specimens between both taxa verified.

Input data (records and environmental variables)

Each record's coordinates were obtained via Google Earth, converted to decimal degrees, and saved in CSV format. Environmental predictors included 20 bioclimatic variables representing the current scenario (1970–2000) from WorldClim v.2.1 (Fick and Hijmans 2017), 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 (Amatulli et al. 2018). After modeling in MaxEnt, the vegetation map of Venezuela by Huber and Oliveira-Miranda (2010) was used to calculate the surface area (km^2) predicted by the model and to exclude 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 (QGIS Development Team 2024).

Approach to predictive models (habitat suitability)

Exploring habitat suitability using a unique model (SDMs): given the limited and spatially concentrated occurrence data (Hernández et al. 2006), Our first approach was based on a unique maximum entropy model to predict the distribution range of the species (MaxEnt v.3.4; Phillips et al. 2006). This algorithm is highly effective for inferring species suitability from presence-only data, even with small sample sizes, due to its ability to estimate probabilities based on maximum entropy principles (Phillips et al. 2006; Elith et al. 2011; Warren and Seifert 2011). In the first instances, doubtful information and duplicate records were removed. To reduce collinearity among bioclimatic variables, we performed a Pearson (Pearson 1900) correlation analysis in R (v.4.3) using ENMTools (supplementary_1_Table 3; Warren et al. 2021), discarding variables with r^2 >0.8 (Dormann et al. 2013), resulting in seven bioclimatic variables in the present scenery (supplementary_1_Table 4). In MaxEnt, we disabled Extrapolate and Do clamping to avoid overfitting (Elith et al. 2011). Due to fewer than 50 records by 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 5,000 iterations. We randomly selected 65 % of sites for training and 25 % for testing (Phillips et al. 2006). The Jackknife test was used to estimate the contribution and response of each variable (Shcheglovitova and Anderson 2013).

To understand changes in habitat suitability that presumably led to historical isolation or not during restriction to shared refugia, we retrospectively projected current MDS onto Pleistocene and Pliocene climate data available in the PaleoClim database (Brown et al. 2018, http://www.paleoclim.org/). Later, projections were used for the mid-Pliocene warm period, between 3,264-3,025 Myr (Downset et al. 2010) and Last Maximum Glacial (LGM, 21 Kya; Karger et al. 2017). 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 current models and predicted habitat suitability with the predictive function in MaxEnt v.3.4 (Phillips et al. 2006).

Evaluation index and visualization

The accuracy of the models in the single-approach framework was evaluated as follows: (1) 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) (Thuiller et al. 2003). The logistic output provides a probabilistic suitability index, ranging from 0 to 1, with values closer to 1 indicating optimal conditions for the 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 (Peterson and Nakazawa 2008). To avoid biases, additional statistical metrics, including the Z value, were used to assess the significance of the predictions (Manly 2006). The True Skill Statistic (TSS) compares sensitivity and specificity, providing a robust, prevalence-independent metric, with values close to 1 indicating excellent predictive capacity (Allouche et al. 2006). Before running MaxEnt, we optimized the model configuration using the ENMeval library (Muscarella et al. 2014; supplementary_1_Table 5) in R v.4.3 (R Core Team 2020), selecting the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc). 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 (Phillips et al. 2006). 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 is carried out separately for each species of *Atractus* using the R ecospat library (Di Cola et al. 2017). The ecological space (E-space) is evaluated using an ambient PCA environment (PCA-env hereafter) framework and an ordination approach. Climatic variables transform 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 (Schoener 1968; Warren et al. 2008). The value of D varies between 0, when the species do not overlap in the ambient space, and 1, when the species compare within the same ambient space. We evaluate the conservation of niche (alternative = major, is decided, the superposition of niche is more

equivalent/similar than random) and niche divergence (alternative = smaller, i.e., niche overlap is less equivalent/similar than random) (Broennimann et al. 2012; Di Cola et al. 2017). For each hypothesis, 1,000 permutations were made. All these analyses were executed in R v.4.3 (R Core Team 2020).

To account for the actual suitability of the habitat, we used vegetation cover data made by Chacón-Moreno and Moral (2020). Next, we recalculated the resulting output of the models in each, which were filtered in QGIS v.3.28 for values <0.15, and the potential distribution was refined in R v.4.3 (R Core Team 2020) using 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-km^2 grid cells identified with sighting records or with suitable habitat encircled by grid cells with sighting records within the EOO; IUCN 2022). Comparatively, we use the geospacial conservation evaluation tool to calculate the metrics EOO and AOO, that allow us to evaluate the status of focal species according to IUCN (geocat, http: //geocat.kew.org/, accessed March 8, 2025) (Bachman et al. 2011). This open-source online tool is a web-based application developed from the IUCN Red List, allowing the visualization of georeferenced species data through a Google Maps interface (IUCN 2012).

Sample Source

We reviewed 292 specimens collected in the field during 2021 north of the Orinoco River, whose scientific hunting permits and access to genetic resources were processed and approved by the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE) and 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).

Morphometric and morphological data

Previously, all available information about Venezuelan species were reviewed (Boulenger 1903; Roze 1961, 1966; Lancini 1969; González-Sponga 1971; Barros 2000; Schargel and García-Pérez 2002; Markezich and Barrio-Amorós 2004; Sánchez et al. 2004; Esqueda and La Marca 2005; Kok 2006; Myers and Schargel 2006; Esqueda et al. 2007; Passos et al. 2009b, 2013; Esqueda 2011; Natera-Mumaw et al. 2015; Montes-Correa et a. 2017; Passos et al. 2024) and other related species from Colombia (Pérez-Santos y Moreno 1988; Passos et al. 2009a,c; Passos et al. 2010; Meneses-Pelayo et al. 2019), Ecuador (Schargel et al. 2013; Salazar-Valenzuela et al. 2014; Arteaga et al. 2017, 2022) and Brazil (Cuhna and Nascimento 1983; Martins and Oliveira 1993; Passos et al. 2005, 2010, 2022).

For each specimen evaluated, including related species (e.g., *Atractus nemosophis*; Esqueda et al. 2025), 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, dorsal, ventral and subcaudal counts for the genus *Atractus* follows that indicated by Dowling (1951), Savage (1960), Hoogmoed (1980), Myers (2003) and Natera-Mumaw et al. (2015).

Due to their taxonomic importance in the genus, some characters are defined as follows: rostral scute in dorsal view, there can be defined as three states: condition A, 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; apical width is less than the distance between nostrils. Condition B, something visible from above, where the distal portion of the scale exceeds the imaginary line, usually narrow toward its distal portion; apical width less or equal than the distance between nostrils, but does not exceed the internasal suture and (C) distinctly visible, with the scale measured between its supralabial contacts, always forming an obtuse angle and

above the imaginary straight line between nostrils; apical width > 0.5 than the distance between 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 which can be quantitatively verified if compared with the interocular 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. (2015) for loreal scale, a short loreal (condition A), occurs when its length is less than HED and always in contact with two supralabials (e.g., *A. elaps*, *A. latifrons*, and *A. steyermarki*, Savage 1960; Passos et al. 2013; Almeida et al. 2014); moderate loreal (condition B), occur when its length is greater than HED, but ≤ 1.5 times HED, 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 contacts previously are less than the height of loreal measured at the angle between supralabial and another state occurs when ALO is greater than the margin between loreal and anterior supralabial in contact. Finally, elongated loreal (condition C), occurs when its length is greater than 1.5 times HED, frequently in contact with three supralabials, the margin between loreal and anterior supralabial is greater than ALO (e.g. *A. torquatus*, *A. ochrosetrus* and *A. heyeri*; Natera-Mumaw et al. 2015). However, exist exceptions where with an elongated loreal, only two supralabials are in contact, just as it happens with *A. emigdioi* and *A. multidentatus* (see also species from Ecuador; Arteaga et al. 2017, 2022). In each case mentioned, we can find that the margin between loreal and anterior supralabial can be less or greater than ALO, and relating to condition B, there may be exceptionally individuals with loreal in contact with three supralabial (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 there are one or two in contact with the supralabial when the mouth is closed in lateral view, therefore, it is defined how many infralabials are in contact with the greats. Sublabial scale, has gone unnoticed but is confused in the descriptions, this scale has two states, in contact with each other, it occurs when separating the middle gular from the posterior contact with the geneials; some authors in the past have considered it a second pair of genials. In fact, in the genus *Geophis*, many of its species often have this characteristic (Downs 1967; Myers 2003).

There are two scale types that are often problematic and whose definition remains unclear (we have personally observed intraspecific variability): gulars and preventrals. 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. Then come the preventrals, 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 (2023), 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 verified on both sides.

Morphometric measurements and meristic counting were carried out through scaled images and using software Image J v.1.54d, as follows: **TL**, total length from snout to the tip of the tail; **TaL**, tail length; **HL**, head length, from tip of snout to end of parietal suture; **HW**, head width measured between labial commissures in dorsal view; **FL**, frontal length; **FW**, frontal width measured from in the anterior portion between the eyes; **PSL**, parietal suture length; **PrSL**, prefrontal suture length; **ISL**, suture length between internasals; **FRD**, distance between 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 geneials; **RoW**, rostral scale width measured between supralabials; **RoDW**, distal width of the rostral measured between nostrils; **WMB**, width at the middle of the body.

Here, we consider 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 differentiate 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 longitudinal lines or stripes, these can be narrow (< a dorsal scale) or wide (> a dorsal scale), continuous or discontinuous and arranged in any section of the dorsal region. If we consider the previous arguments, exist three base patterns with variants: one uniform without blotches, dots, or lines-stripes, with 1-3 differentiated dorsal rows (light in preserved and reddish, yellowish, or cream in life); blotched or dotted, where the blotches or dots may or may not be circumscribed, marginalized or not and with one or more lines-stripes an along the body. The ventral surface of the body and tail, consist of three patterns and their variants, the first is considered immaculate, and may sometimes have small scattered dots or blotches but which do not occupy 15 % of the scale surface; blotches or dots disposed horizontally on the scale, giving the impression of one or varies discontinuous lines-stripes, it may be little evident anteriorly and intensifies towards the cloaca; interspersed or irregular blotches, forming blocks that occupy at least 60 % of the scale, sometimes a wide line is observed medially and finally the ventral region is completely stained, less common than the other patterns.

The maxillary bone of one or several specimens was extracted (left sides) and posteriorly cleaned using KOH 3 % by 10 minutes and distilled water for 10 hours. Then scale photos were taken using an Olympus E620 camera fixed to brand stereoscopic 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 (1988), modified by Pesantes (1994) and Zaher (1999) for snakes. Passos et al. (2016) replaced the KOH indicated in Pesantes (1994) with distilled water. We adopted both procedures, but in a different way, which was a successful way to achieve organ extension. The most common is that the hemipenes have not been previously partially or totally extracted at the time of conservation of the specimen, being fixed with formaldehyde and/or ethanol, where the first option exists

much more rigidity and mostly the tail could have been fixed with little formaldehyde (pers. obs. LFE). 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 emersion stations were established, the first with distilled water at 60 ºC for 2-3 minutes, the second with 3 % KOH for one minute and the third with distilled water at room temperature for 10-30 minutes. If the timing is appropriate, the organ can be observed with a transparent amber coloration; otherwise, repeat steps 1 and 3. 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 is achieved, apply Vaseline or glycerin-water, secure the base, and immerse the organ in a solution of 70 % ethanol with alizarin red or a suitable dye for approximately 10 minutes. Finally, store the specimen in an Eppendorf tube with glycerin. With respect to the calcareous structure's ornamentation, we follow to Uzzell (1973) and Harvey and Embert (2008). Qualitative and quantitative description of hemipenial characters follows Dowling and Savage (1960), Uzzell (1973), Zaher (1999), Schargel and Castoe (2003); Myers and Cadle (2003); Zaher and Prudente (2003); Myers and McDowell (2014) and Passos et al. (2016). Although the term "diastema" has been considered in the past for this group of snakes, being a distinctive character (e.g. Passos et al. 2009a,c, Passos and Lynch 2010). We will talk about space and/or reduction between the last teeth, following the indicated by Oliveira et al. (2023), who recognize that goo-eating dipsadines do not present diastema.

Statistical processing (comparative data and geometric morphometric)

Under the idea of evaluating 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 (R Core Team 2020) and the excel software XLSTAT v. 2019 2.2 (Addinsoft 2025) to perform all statistical analyses. To this end, we defined five procedures: P1= the range of variations (minimum and maximum), mean (*X*), and standard deviation (SD) were calculated for each OTU specimen. We checked and removed outliers from our data using the dplyr library in R environment (Wickham et al. 2023); P2 = statistical analysis of differences between OTUs and sexes, evaluating through normality tests (Kolmogorov-Smirnov) or the data normality checked 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 (Zar 1999). 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, Fisher 1936) to evaluate separability of OTUs, calculating Mahalanobis distances (Mahalanobis 1936). We used the following character in the statistical analyses: ventral scales count; subcaudal scales count; total length of the body (TL); tail length (TaL); internasal suture length (INTL); broad apical margin of the rostral between nostrils (BMARos); loreal length (LOL); loreal height (LOA); height of the first supralabial (HSup); frontal length (FL) and ventral pattern of the body (PV).

Not based on 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 due to missing data, juvenile status, or head damage; see Supplementary_1_Table 6). We aimed to quantify aspects of head shape in dorsal view, from the frontal to the rostral scute (*A. erythromelas*, n = 21; *A. meridensis*, n = 21; Supplementary_1_Table 7A), as well as the proportionality and extension of the rostral (*A. erythromelas*, n = 14; *A. meridensis*, n = 22; supplementary_1_Table 7B)), using a geometric morphometric approach with the geomorph package in R (Adams and Otárola-Castillo 2013). All scale photographs were taken with an Olympus E620 camera mounted on a Leica-brand stereoscopic microscope. 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 (R Core Team 2020). 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 (Adams et al. 2004, 2013). The procedure for separating shape from size data is known as Procrustes superimposition (Rohlf 1990; Rohlf and Slice 1990). 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 (Rohlf and Slice 1990). All procedures were performed using the geomorph package in R v4.3 (R Core Team 2020; script_1_1).

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 (Klingenberg and McIntyre 1998; Klingenberg et al. 2002, 2013). 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 (Zelditch et al. 2012). 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 (Zelditch et al. 2004). 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 (Rohlf 2002; Zelditch et al. 2012). 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 (Claude 2008; Bookstein 1991). To test the significance of these distances, a permutation test (n = 10,000) was conducted, comparing observed distances to a randomly generated null distribution.

RESULTS

Phylogenetic approach

The final concatenated molecular data set 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 % and 63 sequences in RAG-1: 879 bp, 90 informative sites, 95 singleton, 694 sites preserved, missing data 0-18 %). 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 (Fig. 1) and BI (Fig. 2) analyses are consistent and similar in its 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 a moderate support (> 0.8). Our Bayesian analysis generally showed a moderate or strong support within the nodes in *Atractus*, except for some that were low support (<0.5). Differences in support between ML and IB may stem from the way these methods handle uncertainty and evolution models (Alfaro et al. 2003; Holder and Lewis 2003; Yang and Rannala 2012). Here, posterior probability values above 0.95 was considered strongly supported, values between 0.7 and 0.95 was moderately supported, and below 0.7 was weakly supported.

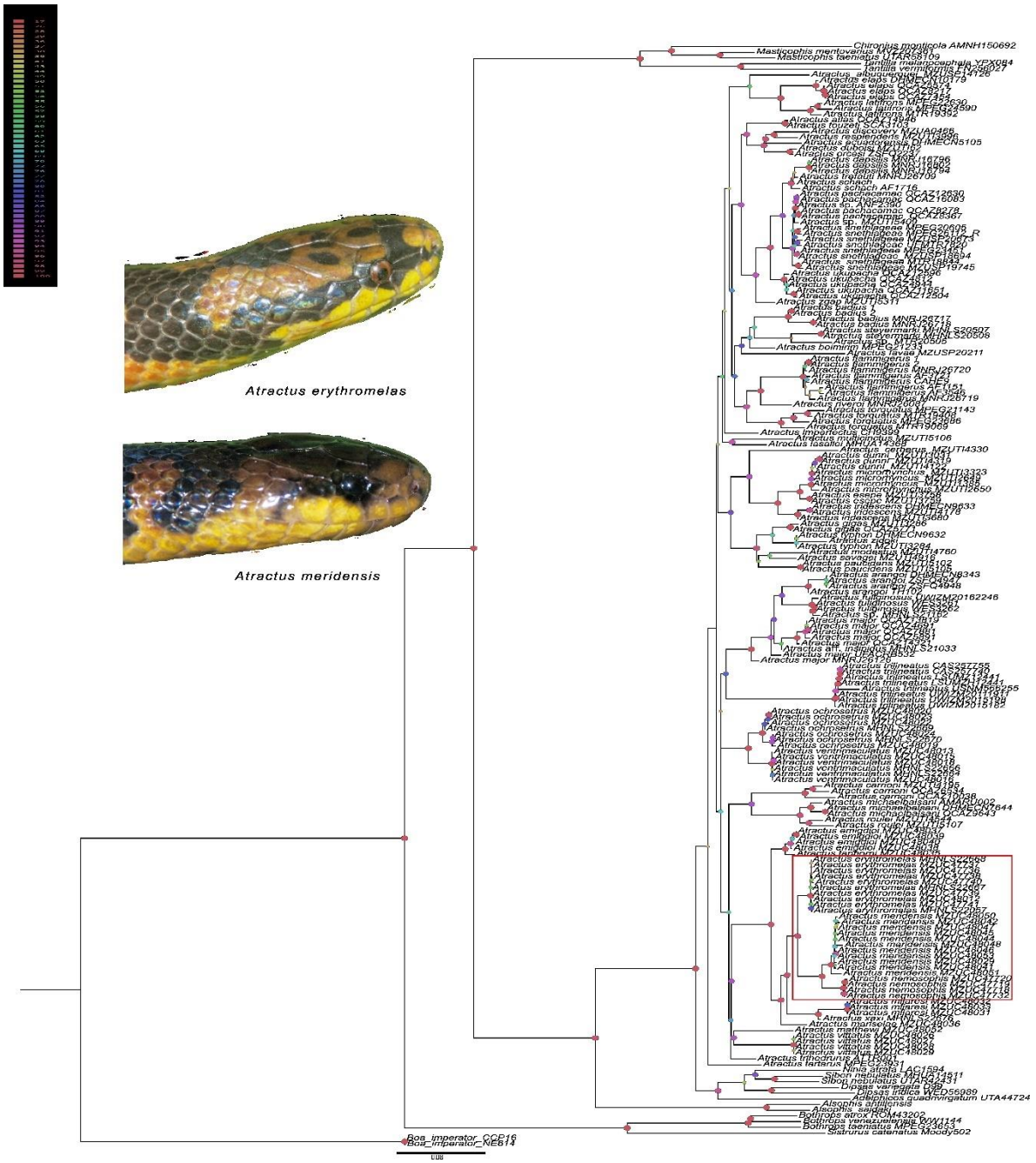

FIGURE 2. Maximum likelihood (ML) tree was estimated of Iqtree, showing the relationships among some South American species of *Atractus*. Information on bootstrap values >70 % in ML are shown, left side. Purple box delimits the species under discussion.

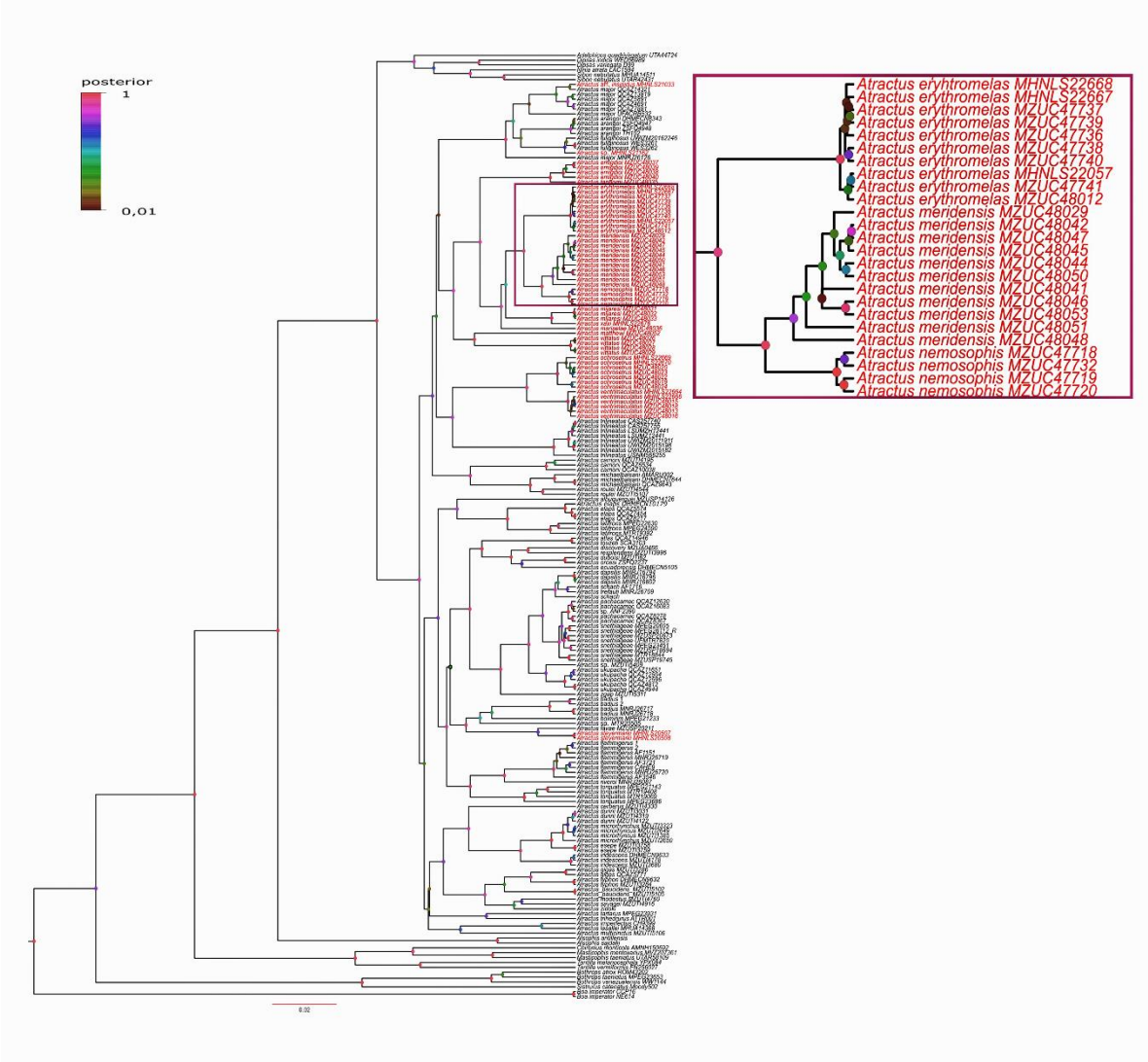

FIGURE 3. Bayesian inference tree using Metropolis coupled MCMC for estimation under the topology. Beast posterior probability values symbol >0.95 (legend). Bars on nodes represent the 95 % credibility interval of divergence times. Terminals in red refer to the material incorporated by us. Purple box delimits the species under discussion.

In our phylogeny, 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), both from the cordillera de Mérida, 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, 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*. (new species, LFE in press), *A. erythromelas*, *A. meridensis* and *Atractus* sp. (new species, LFE in press).

Uncorrected interspecific genetic p-distances are presented for Cytb (supplementary_1_Table 8-9) and ND4 (supplementary_1_Table 10-11). In the case of Cytb, mean genetic distances of the Venezuelan mimic species range of 0.072887 ± 0.009654 (*A. erythromelas* vs. *A. meridensis*), 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 mean genetic distance range from 0.050887 ± 0.008151. Meanwhile, 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, mean genetic distances varied from 0.05393 ± 0.00933 (*A. erythromelas* vs. *A. meridensis*), 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* average 0.06851 ± 0.01075. At the genus level, mean genetic distances average 1.1 % (*A. snethlageae* vs. *A. pachacamac*) and 17 % (*A. ventrimaculatus* vs. *A. vittatus*).

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 0.985-0.988 for the training data and 0.905-098 for the test data (supplementary_1_Table 12), indicating that the Maxent model effectively predicted the distribution with highly suitable environments for *A. erythromelas* (Fig. 3A) and *A. meridensis* (Fig. 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_1_Table 13). 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 (Fig. 3C-D), unlike the Pliocene 3.2 Myr, during which an expansion of their distribution area is observed (Fig. 3D-E). In the current scenario, *A. erythromelas* occupies an area of 2,126.8 km^2 and is mostly distributed in the montane rainforest of the Northern Andes and intervening areas, with a suitable area of 1,074 km^2 (Supplementary_1_Table 14). Meanwhile, *A. meridensis* occupies an area of 3,029.1 km^2 and is mostly distributed in montane rainforest of the Northern Andes, with a suitable area of 1,503.8 km^2 (Supplementary_1_Table 14). Our sorted and verified data suggest that the altitudinal range of *A. erythromelas* varies between 1160-2684 m (494.1 km^2 would correspond to

moderate-high suitability areas between 2000-2500 m asl) and *A. meridensis* occurs between 1077-3275 m (666 km^2 would correspond to moderate-high suitability areas between 1500-2500 m asl).

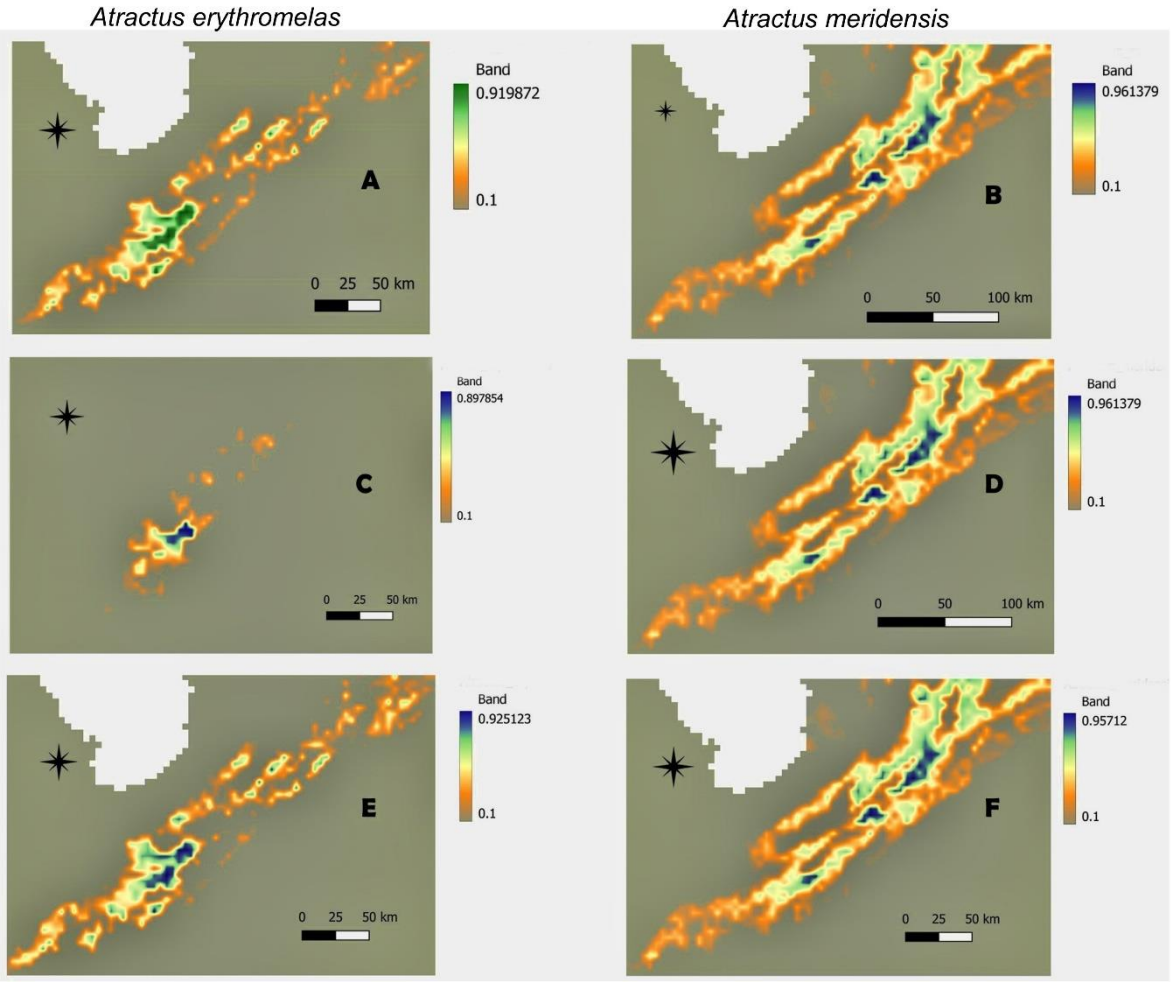

Figure 4. Geographic projection of the ecological niche model built for *A. erythromelas* and *A. meridensis* into the climatic scenarios explored. (A-B) Present scenery; (C-D) LGM scenery, 21 Kya and (E-F) Pliocene scenery, 3.2 Myr. The environmental suitability predicted is depicted without umbral defined.

In the Maxent model for each scenario, the Jackknife method was used, and the results may show the weight of different environmental factors that affect the suitability of the habitat for *A. erythromelas* and *A. meridensis* (supplementary_1, Table 15). On the other hand, one of the main determining environmental factors in the potential distribution in the three scenarios was Bio_1 variable, in *A. erythromelas* with 48.1-65.9 % (supplementary_1, Table 16) and *A. meridensis* with 60.9-66.9 % (supplementary_1, Table 16).

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 (Fig. 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_1_Table 17). 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_1_Table 18). 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_1_Table 18).

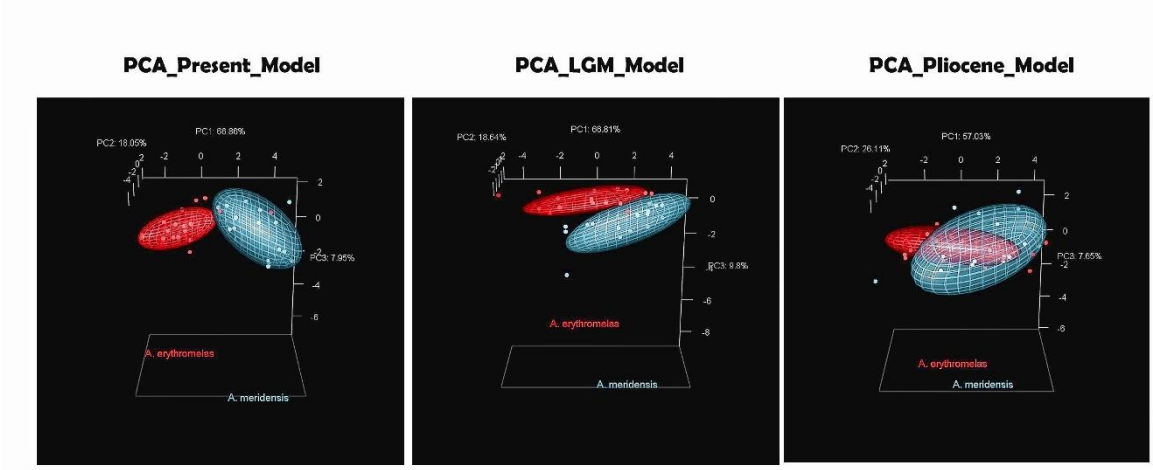

FIGURE 5. The orthogonal projection of the first three principal components constructed from climatic characterizations of the geographic distribution from *A. erythromelas* and *A. meridensis* for each of the modeled scenarios. The points correspond to the localities characterized based on 6-7 bioclimatic variables and the ellipses correspond to the volumes built from the climatic niches of *A. erythromelas* (red ellipse) and *A. meridensis* (blue ellipse). 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 km^2 and AOO of 116 km^2 (geocat EOO = 469.755 km^2 and AOO= 120 km^2 to 2 km;

supplementary_Table 19A), while *A. meridensis* has an EOO= 3,093.19 km^2 and AOO= 68 km^2 (geocat EOO= 3,113.344 km^2 and AOO= 76 km^2 to 2 km; supplementary_Table 19B).

Morphological-Statistical approach

For *A. erythromelas*, 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*, ventral scale count showed a significant difference between sexes (ANOVA, $p < 0.001$), as did 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, $p = 0.784$), reinforcing that species alone did not explain the variation. However, the interaction between sex and species was highly significant ($p = 3.14e{-}05$), 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_1_Table 20).

Our evaluation found differences between the sexes in the species *A. erythromelas* and *A. meridensis* in some morphometric variables, such as ventral and subcaudal scales, where the P value is significant. However, there are no significant differences in variables such as TL and TaL for some species. Differences are not uniform between species. In *A. erythromelas*, there are differences in almost all variables, while in *A. meridensis*, some variables show differences, while others do not. So, there are significant differences between the sexes within the species, but the magnitude and presence of these differences varies according to the species and the morphometric variable (Boxplot, Supplementary_1_Table 20).

Our analysis revealed significant sexual dimorphism in *A. erythromelas* and *A. meridensis* for certain morphometric traits, particularly 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*, 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_1_Table 21) showed first that the taxa differ, then the disjunctive set of populations of both species (OTU) overlap, less evident between them the OTU3 and OTU4 populations corresponding to *A. meridensis*. The first two linear discriminants accounted for 94.35 % (46.47 % and 47. 88%, respectively) of the total variance (Fig. 5).

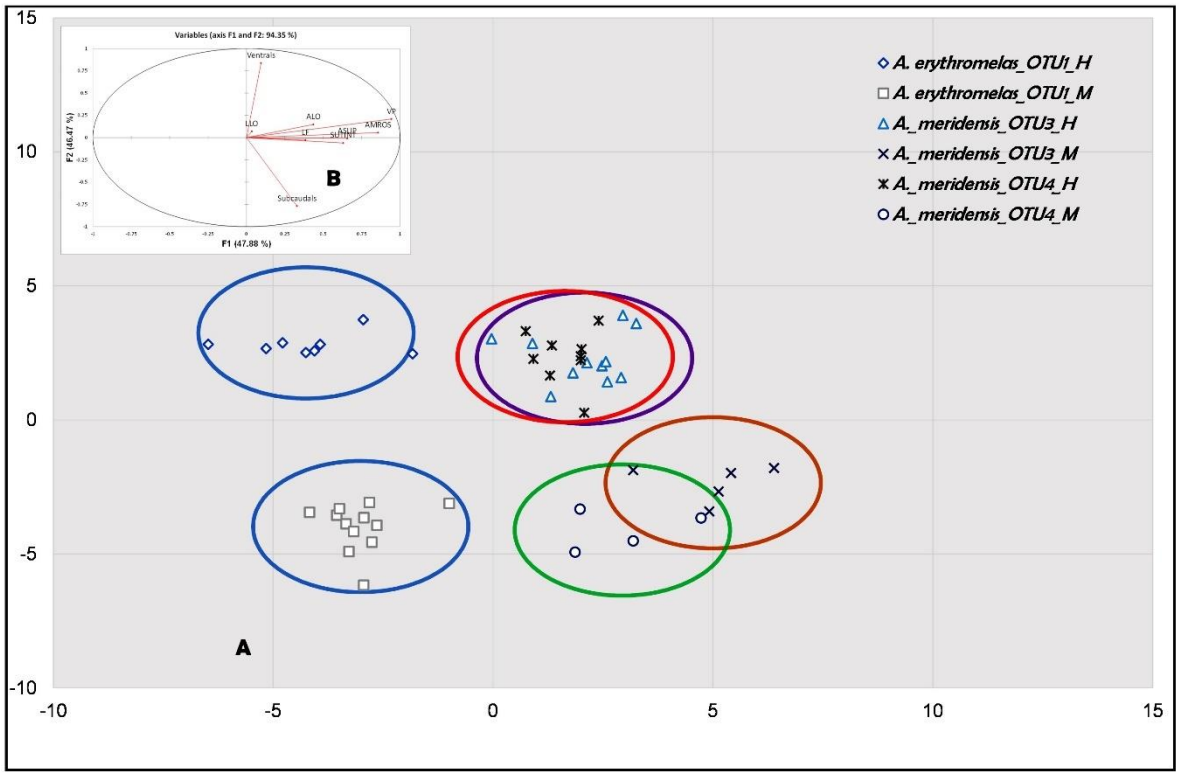

Figure 6. (A) Discriminant analysis scatter diagram (DA) using software XLSTAT for *A. erythromelas* and *A. meridensis*; (B) contribution of each variable to the first two principal coordinates: ventrals, subcaudals, VP= ventral pattern, AMROS= maximum width of the rostral between nostrils, Asup= height of the first supralabial, SUTINT= long internasal suture, LF= long frontal, ALO= height of loreal measured anteriorly and LLO= long of loreal. In OTU, H= female and M= male.

Spatial morphometry

For both *A. erythromelas* (MA_1 and MA_2) and *A. meridensis* (MA_1 and MA_2), 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 (Zelditch et al. 2012) were high: 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 in *A. erythromelas* may suggest a potential trend, although it was not statistically significant (Supplementary_1_Table 22).

Our geometric morphometric analysis of dorsal head scalation (MA_1) and rostral scute projection in frontal view (MA_2) revealed significant morphological differences between *A. erythromelas* and *A. meridensis*. Principal Component Analysis (PCA) was used to explore overall shape variation and revealed a clear separation between the two species along the first two principal axes, which explained the majority of variation (59.06 % in MA_1, Fig. 6A; 78.61 % in MA_2, Fig. 6B). Although some degree of overlap was present, the centroid positions of each species occupied distinct regions of 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_1_Table 23). 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* (MA_1). 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_1_Table 23).

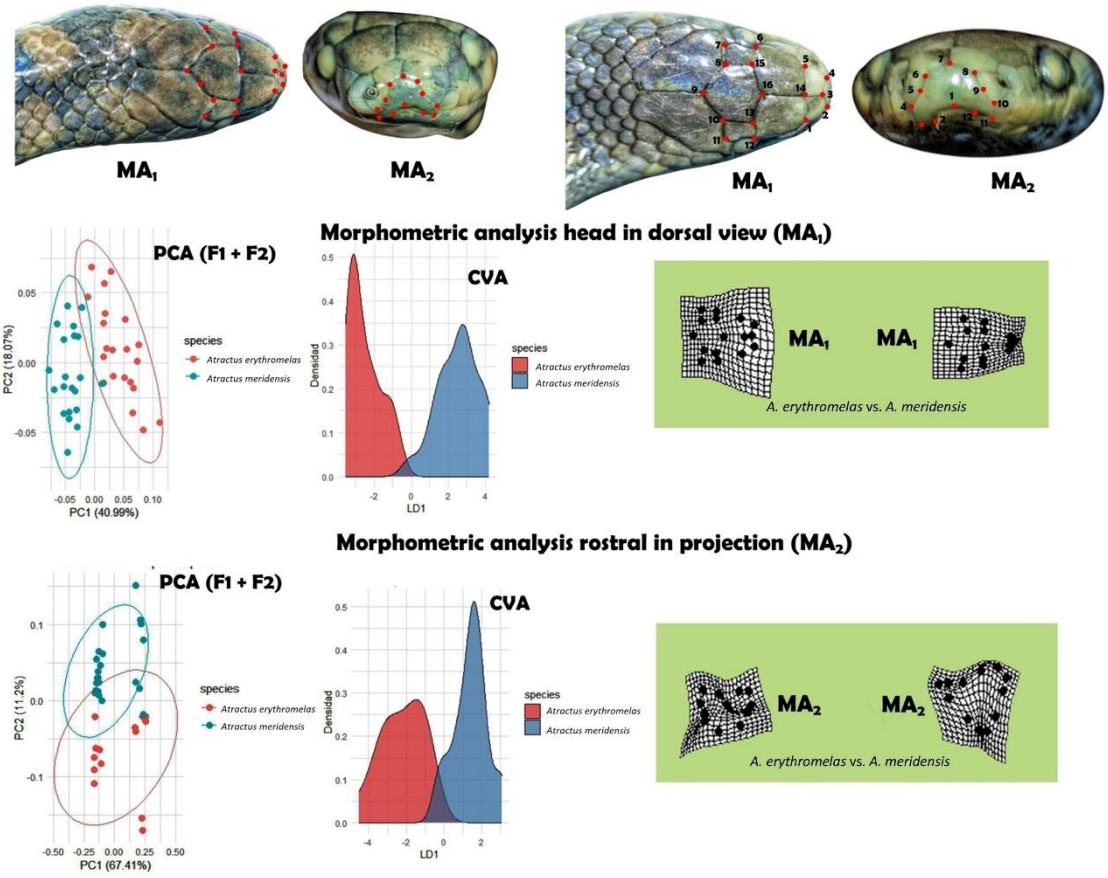

FIGURE 7. Projections of adult individuals of *A. erythromelas* and *A. meridensis* on the two PCA variation axes and on a single CVA axis, using morphometric measurements. MA1, morphospace based on cephalic scales in dorsal view (frontal to rostral); MA2, extension and projection of the rostral scale in frontal view.

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

Without defining a type (syntype material, ICZN 1999, art. 73.2), Boulenger (1903: 483-484) described *A. erythromelas* from "Merida, Venezuela, at an altitude of 1600 meters". In his original description indicate 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 (1961: 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 (1966: 80-81) and Peters and Orejas-Miranda (1970), respectively. In their review of the *Atractus* from the cordillera de Mérida, Esqueda and La Marca (2005) 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 they did not mention Boulenger original description, but if to Roze (1961), who had revised the material from the British Museum. However, in that same work the authors described *A. meridensis*, whose type locality is "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; 08º52'45'' N, 70º'39'09'' W", presenting 17 rows of dorsal scales at midbody and sympatric populations with *A. erythromelas*.

Recently, Passos et al. (2024) 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. (2024: 23) designated as lectotype the "adult female specimen, BMNH 1946.1.716, collected by S. Briceño in the municipality of Mérida (08°36′N, 71°09′W; ca. 1,600 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. (2024, fig. 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. (2024) incorrectly cited the "municipality of Mérida" instead of Libertador municipality (INE 2013). According to ICZN (1999, arts. 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. lacks sufficient justification, and the removal of the museum label contravenes Recommendation 74C.

Currently, the taxonomic status of *A. erythromelas* is well established (see ICZN 1999, art. 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. (2024) designated one of the syntypes from Boulenger's description as lectotype (BM 1946.1.715), which establishes its type locality following ICZN (1999, art. 76.2). However, this decision also highlights a potential ambiguity: the locality "Mérida" (Boulenger 1903) 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) (Monzón-Briceño 2005). 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 ICZN (1999).

Systematic overview

ATRACTUS ERYTHROMELAS BOULENGER, 1903

(Figs. 7-10)

Atractus erythromelas. - Boulenger, 1903; Annals and Magazine of Natural History 11: 483.

Atractus erythromelas. - Passos et al. 2024; South American Journal of Herpetology, 32(Special Issue): 1-123.

Lectotype. - Adult female, BMNH 1946.1.716, collected by S. Briceño at municipally of Mérida (08°36′N, 71°09′W; ca. 1,600 m), state of Mérida, Venezuela by present designation (Figs. 14A-B, 15) (Passos et al. 2024).

Paralectotypes. - Adult male (BMNH 1946.1.715) and female (BMNH 1946.1.717; Figs. 14C-D, 16) with same data as the lectotype (Passos et al. 2024).

Neotype. – Adult female, MZUC 47736 (field number LFE 145). Collected by Luis Felipe Esqueda, Santos Bazó and Alexis Peña, July 4, 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.

Definition. - (1) 15 or 17 scale rows dorsal to midbody, with or without reduction of 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 nostrils) and slightly or not exceeding imaginary straight line between 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 marginated 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 5-6th tooth; (15) hemipenis slightly bilobed, semicapitate and semicalyculate.

Description of the series examined. - TL in males 251.91-338.11; mm ($\bar{x}$= 304.8 ± 22.77; n= 12) and in 256.75-449.57 mm in females ($\bar{x}$= 338.4 ± 51.23; n= 11); maximum tail length in males 46.62 mm ($\bar{x}$= 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 in males 7.84-9.68 mm ($\bar{x}$= 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, snout relatively short, not compressed or barely compressed and with a rounded edge (ID and IND reduction of head 12.5-49.5 % in males and 23.5-54.7 % in females). In lateral view, usually snout rounded or subacuminate; rostral barely or slightly visible from above (condition A-B), in frontal view subtrapezoidal, as wide as high or slightly wider (Fig. 7D), with its lateral margins straight or slightly concave, apical edge of the scale short-moderate (< 0.5 of the distance between nostrils) and barely exceeding the imaginary straight line between 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 ± 0.82), 2.9-7.3 in females ($\bar{x}$= 5 ± 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 (Fig. 7A) and with straight or slightly straight edges (83.3 % of the individuals examined males and 77.7 % in 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 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 (Fig. 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 specimens examined in males and 66.6 % in females); two postoculars, the lower one mostly vertically extended; temporal formula 1+2, first temporal so long so 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 (Fig. 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; 3 gulars; 1-2 preventrals. 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).

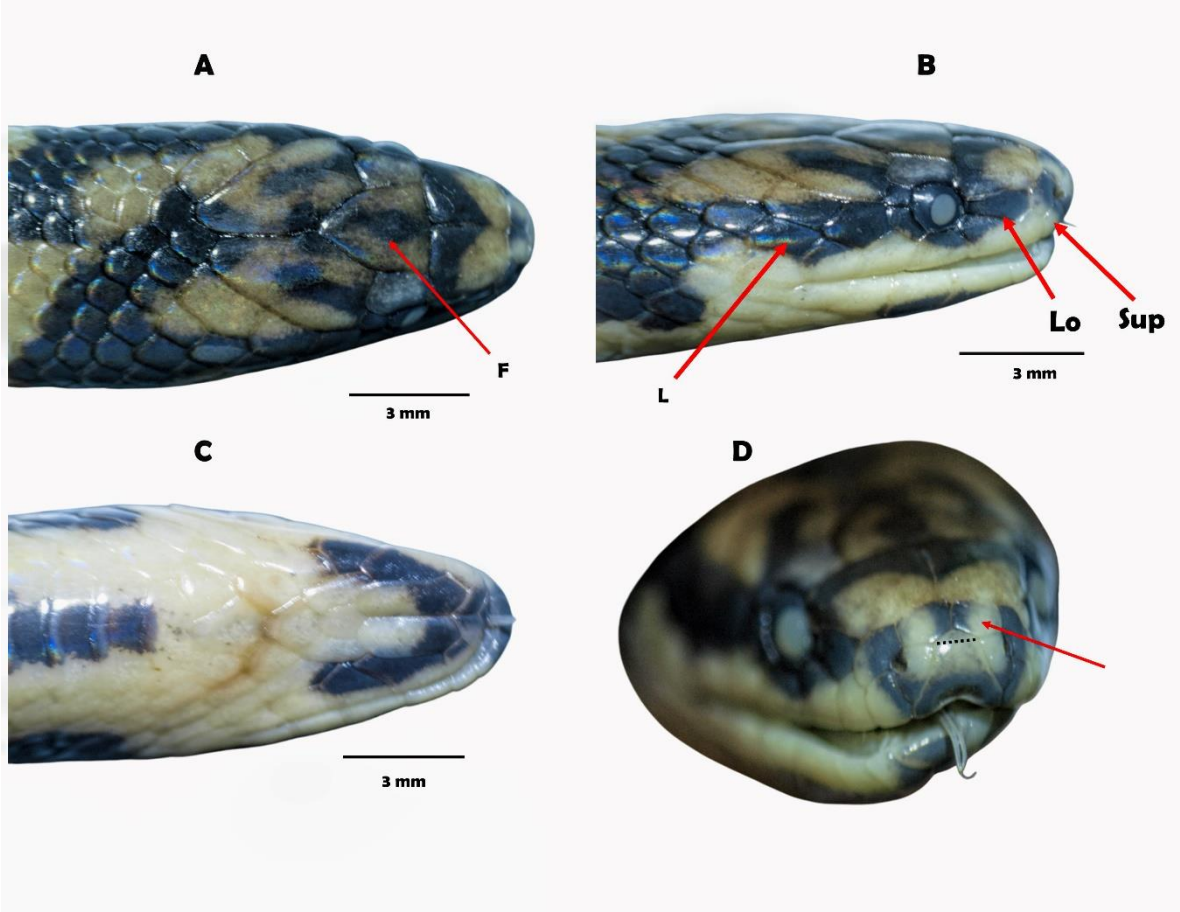

FIGURE 8. Adult female individual of *A. erythromelas* (MZUC 47736). Dorsal view (A), lateral view (B), and ventral view of the head (C). Finally, frontal view of the rostral scale (D). Lo= loreal scale; Sup= first supralabial.

Information of coloration (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 (Fig. 8A-B1). Red or white bands widened dorsolaterally, 2-3 dorsal scales (more evident at midbody). Dorsal background of the head similar to the body, a black line behind and in front of the eye is well defined (Fig. 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 1000-1800 m asl, being red crossband more frequent than white crossband (Fig. 8A); (B) not bicolor, crossbands absent, reddish background along the body, with just small to moderate black spots forming stretch marks on paravertebral-vertebral region of the body, sometimes constitutes a small narrow line. The dorsal background of the head similar to the body, laterally black line behind the eye and in front is found poorly defined (Fig. 8C); (C) not bicolor, hazelnut or yellowish-hazelnut background with black blotches, variable in size and irregularly dispersed, 1-3 dorsal row, sometimes forming a longitudinal black line not perfectly continuous along the body. The dorsal colour of the head is similar to the body, although darker, without a black line behind and in front of the eye (Fig. 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 (Fig. 8E). The dorsal background of head yellowish-brown (Fig. 8F); black line behind and in front of the eye well-defined (Fig. 8F-G). Geographically, the emerging and rare patterns B and C have been sighted 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 direction to Mucurubá. This pattern has been found with other individuals that have pattern A. The northernmost record of this distribution corresponds to a specimen MHNLS 22057, collected at 2980 m altitude.

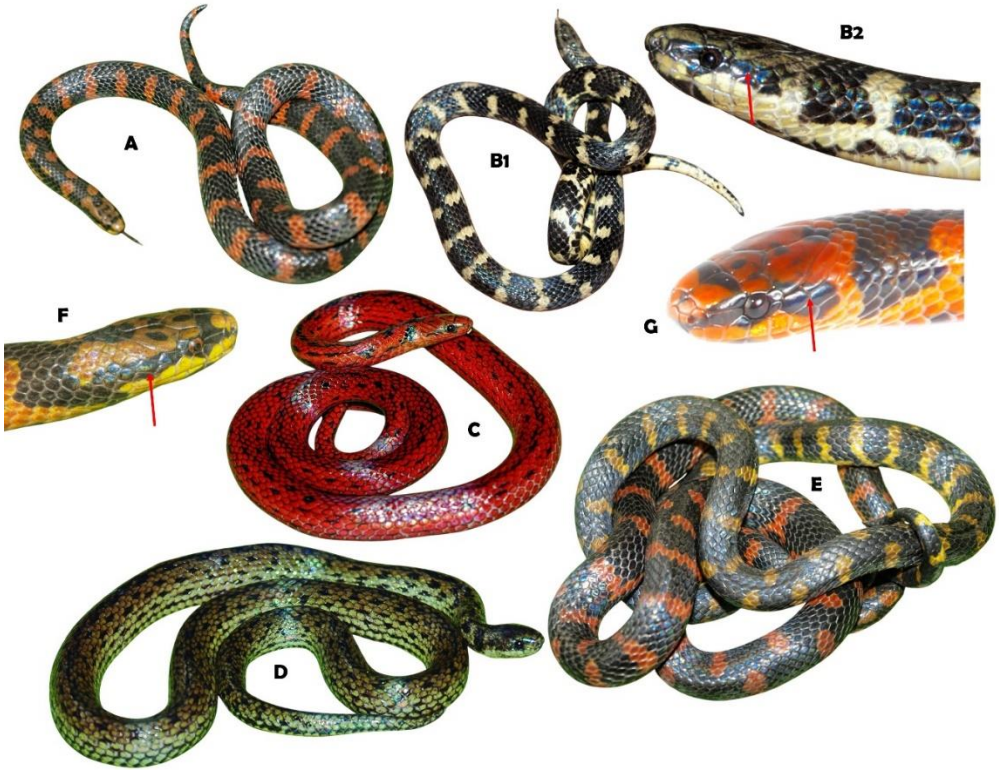

FIGURE 9. Dorsal patterns in life of *A. erythromelas*. (A-B) bicolor, red-or-white and black crossbands along the body; (C) not bicolor, crossbands absent; (D) not bicolor, hazelnut or yellowish-hazelnut background; (E-F) bicolor, yellowish-green and black crossbands along the body. Photos ®Luis Felipe Esqueda (LFE).

The ventral pattern is variable but subject to the dorsal pattern, four patterns are defined, VP. Individuals with dorsal pattern A and D exhibit: (A) VP1, reddish or whitish background, with black spots on each scale, trapezoidal or rectangular; usually part of its extension is aligned at midventral level, they can occupy between 30-60 % of the surface of each scale (Fig. 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 (Fig. 9A2, P_VP2); (C) VP3, reddish or whitish background, with black spots on each scale, rectangular and arranged in two latero-ventral rows, they can occupy less 50 % of the surface of each scale (Fig. 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 that we call tabby, has a reddish or yellowish ventral background, with black dots or small spots, arranged at a mid-ventral level and occupying less than 30 % of the surface of each scale; sometimes the pattern is almost immaculate (Fig. 9P_VP4). Sometimes

these dots are replaced by a black line similar to those 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 background (ventral pattern VP1), yellowish (dorsal pattern VP4) or cream (pattern A). In many of the observed cases, the tongue is reddish, similarly occurs with the pupil of the eye which can be reddish or reddish-brown. The background of the supralabials can vary from reddish, yellowish, or whitish and depends on the dorsal patterns.

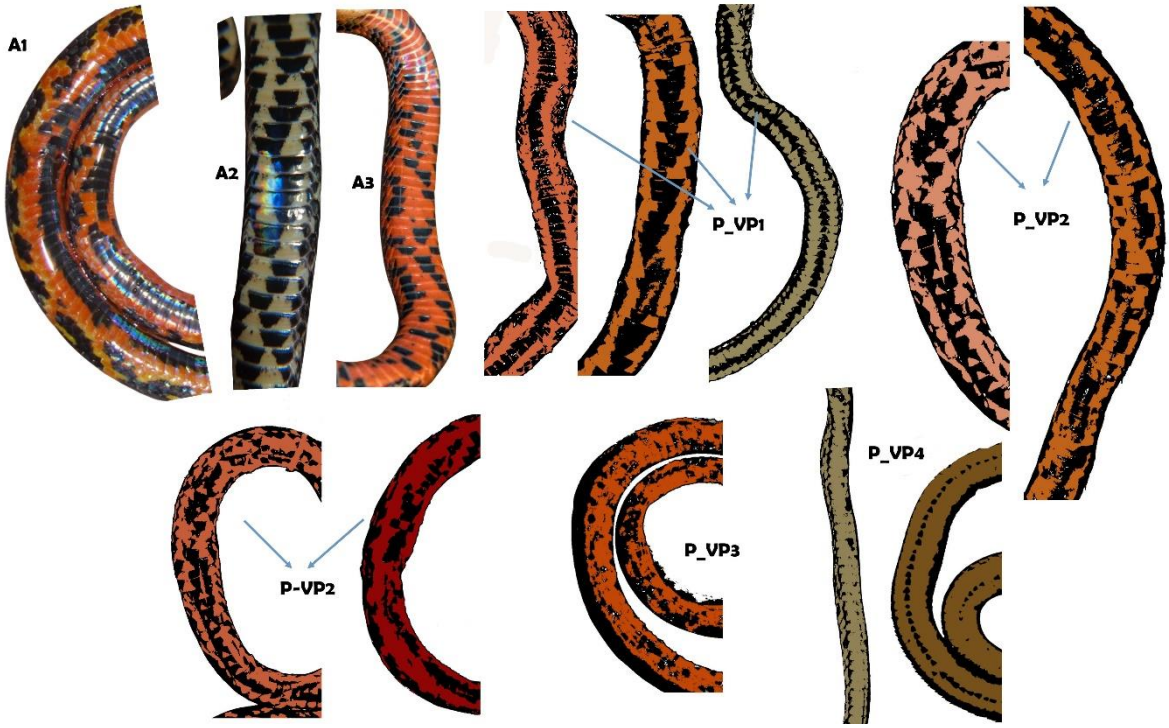

FIGURE 10 Ventral pattern (VP) in life of *A. erythromelas*, A1,2,3. Moreover, other patterns were constructed from field data of the specimens (Preserved Ventral Pattern, P_VP). VP1, reddish or whitish background, with black spots on each scale; VP2, reddish or whitish background, with black spots on each scale; VP3, reddish or whitish background, with black spots on each scale and VP4, call tabby, has a reddish or yellowish ventral background.

Hemipenis (everted organs n= 3). – Specimens CVULA 7375 and CVULA 7400 (Fig. 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 6.3-6.4 mm from the base to the apex of the lobe. The capitulum is clearly defined, located above or just above the bifurcation of 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 of sulcus spermaticus, with calcified hooked spines; large spines restricted to the lateral surfaces of the organ; naked basal pocket absent, longitudinal folds indefinite. In the specimen MHNLS 22668 (Fig. 10C), the ornamentation of hemipenis is similar to the previous specimens, although the capitulum situated above the bifurcation of sulcus spermaticus tends to be wider than the body of the hemipenis; clearly defined lobes, situated above the capitulum, subcylindrical and 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.

Maxillar bone. – The same varies from 3.9-3.1 mm in length (n= 10), with the anterior third arched and posteriorly depressed; palatine process 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; space between the teeth is short; posterior projection defined (Fig. 10D-E).

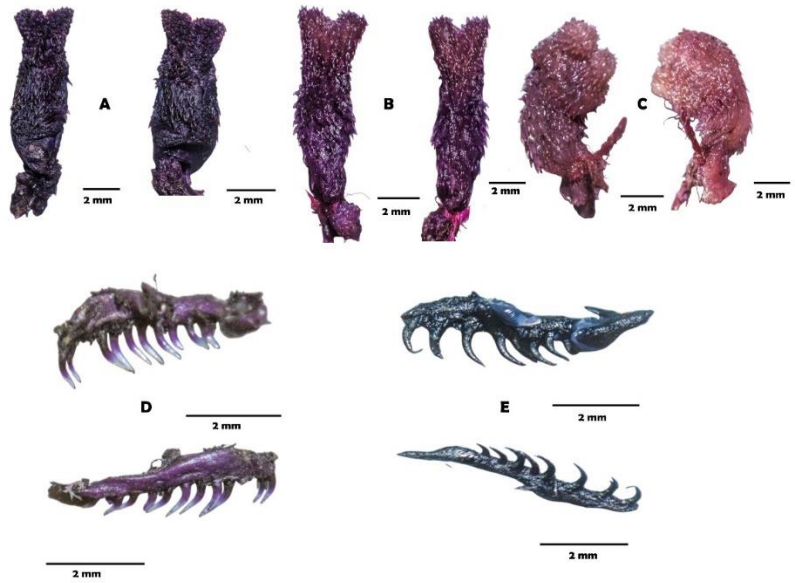

FIGURE 11. Hemipenes and maxillary dentition of *A. erythromelas*. (A) sulcate and asulcate region of the hemipenis in specimen CVULA 7374; (B) sulcate and asulcate region of the hemipenis in specimen CVULA 7400; (C) sulcate and asulcate region of the hemipenis in specimen MHNLS22668. Maxillary extracted from specimen MZUC 47737 (D) and CVULA 7395 (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 semi-deciduous forest and the ecotone towards the cloud forest between 1200-2400 m asl; while towards the middle-upper Chama River basin it extends between 1700-2980 m asl, occupying the Andean montane semideciduous forest, cloud forest and Andean high-montane scrublands (Ataroff and Sarmiento 2004; Chacón-Moreno and Moral 2020) (Fig. 11).

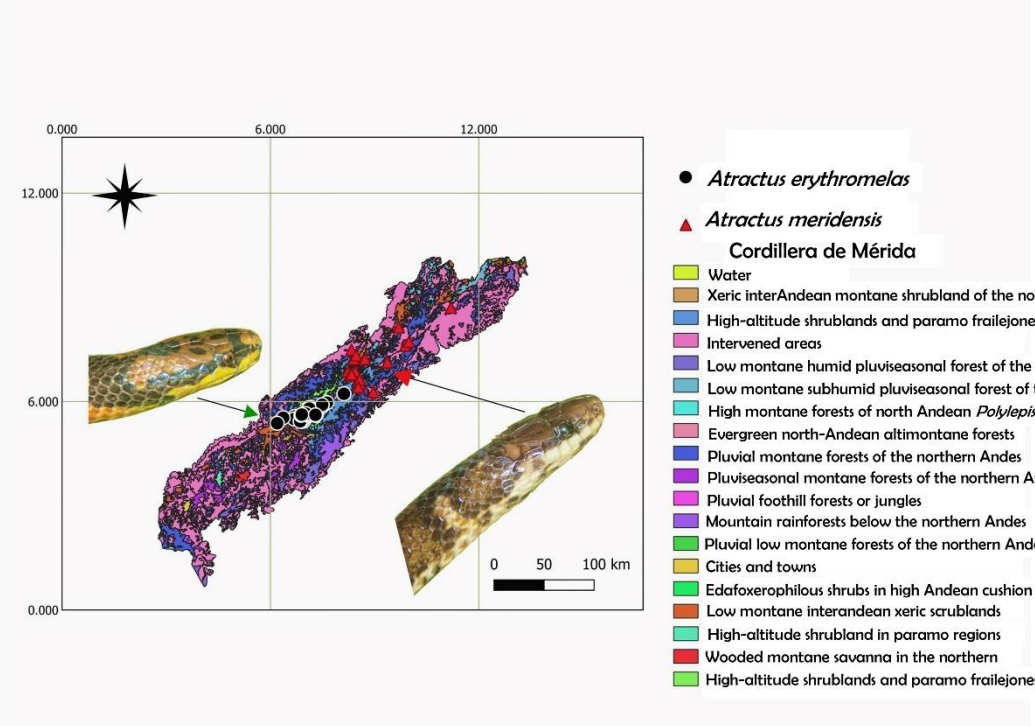

FIGURE 12. Map of the cordillera de Mérida showing the distribution from *A. erythromelas* and *A. meridensis*. Base vegetation map ®Eulogio Chacón Moreno.

The species was observed 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 have collected specimens under rocks on the way the Valle to La Culata, Finca La Hermita, an area with anthropized vegetation dominated by Kikuyu grass for livestock (LFE, unpublished data 2021). We have also found individuals under rocks or dry material in decomposition towards Mucurubá, where the only other species reported has been *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 suggests that *A. ventrimaculatus* would occupy 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 be occupying the Andean montane semideciduous forests and the cloud forest, the latter best preserved because it is within the limits of the Sierra Nevada National Park.

An adult female MZUC 45655 (LFE269) contained 3 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°41'27.00"N and 70°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 2,126.8 km^2, consisting mostly of montane rainforests of the northern Andes (558.6 km^2). According to IUCN, an area of 466.979 km^2 comprises EOO (geocat 469.755 km^2) and 116 km^2 AOO (geocat 120 km^2 to 2 km). 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), being in 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 km^2, the main water courses being the Chama and Albarregas River. The native vegetation corresponds to the Andean montane semicaducifolious forest (Ataroff and Sarmiento 2004), 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 (Ellis et al. 2010), this group has a diet specialized in worms, whose ecological requirements can be affected by the conversion of the habitat (Johnston et al. 2015; Maggi and Tang 2021), which could have effects in the population dynamics of these snakes (e.g., *Atractus lasallei* in Colombia, Cruz-Arroyave et al. 2024).

Here we demonstrate that the extent of presence and the area of occupancy of the species are well reduced, along with a continuous decline in habitat quality due to the conversion of semi-deciduous and cloud forests for agricultural activities, high-altitude pastures for livestock, and urban-rural development. So far, we have 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

Morphological details, coloration and geographical	*A. meridensis* Esqueda & La Marca, 2005	*A. erythromelas* Boulenger, 1903	*Atractus* sp. nov (in press)	*A. micheleae* Esqueda & La Marca, 2005
Geographic distribution in cordillera de Mérida, 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
Type od 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 Lenght (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	always 17	15 or 17	always 17	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)	distintivly visible from above (condition C)	slightly visible or barely visible from above (frecuent)	distintivly 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, the supralabial scale is pentagonal but does not form an angle, that is, proruction 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, the supralabial scale is pentagonal but does not form an angle, that is, proruction between postnasal and prenasal. Enlarged supralabial	short, the suppthalabial scale is pentagonal, taller than wide, proitruption 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 quandragular, 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)	oblog, snout not compressed	oblong, snout not compressed	oblong, snout not compressed	subtriagular, snout slightly compressed
In lateral view, snout	slightly truncated	roudend	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 count	five or six	nine to ten	five or six	five to eight
Hemipenis	semicapitate, semicalyculate, moderate bilobed or bilobate, subcylindrical lobes and roudend 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 croosbands, interspersed, ligth bands marginated of back	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 crossbans not marginated 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

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

"Vulnerable", according to criteria B2abi,ii,iii,iv. Previously, Esqueda y La Marca (2015) recognized it as vulnerable species.

ATRACTUS MERIDENSIS ESQUEDA & LA MARCA, 2005

Resurrection

(Figs. 12-16)

Atractus meridensis Esqueda and La Marca 2005; Herpetotropicos, 2(1): 10-14.

Atractus meridensis Passos et al. 2024: 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 2005: 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; 08º52'45'' N, 70º''39'09'' W.

Definition.- (1) 17 dorsal scale rows around the body, without reduction anteriorly and posteriorly; (2) maximum total length in males 433.68 mm and 406.46 mm in females; (3) rostral distinctly visible from above, apical margin broad (> 0.5 distance between 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 of 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-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 eye-prefrontal

contact wide; (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 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).

Description of the series examined. - TL in males 254.03-433.68 mm ($\bar{x}$= 356.45 mm ± 51.47; n= 9) and 245.98-406.46 mm in females ($\bar{x}$= 324.6 mm ± 44.72 n= 20); maximum tail length in males 59.28 mm ($\bar{x}$= 48.2 mm; 34.9-59.28 mm ± 8.4; n= 9) and 45.31 mm in females ($\bar{x}$= 30.7 mm; 19.27-45.31 mm ± 6.32; n= 20); HL in males 8.38-11.62 mm ($\bar{x}$= 10.1 ± 1.18; n= 9) and 7.21-11.8 mm ($\bar{x}$= 9.5 ± 1.2; n= 20) in females. In dorsal view, head slightly distinct of the neck, oblong; snout appreciably short, not compressed or barely compressed and with a slightly truncated margin (ID and IND reduction of head 27.7-44.8 % in males and 15.53-51.4 % in females). In lateral view, frequently snout forms an oblique angle; rostral distinctly visible from above (condition C) (Fig. 12D), trapezoidal, slightly wider than high, prominent medial projection, concave lateral margins, apical margin broad (> 0.5 distance between 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 ± 0.99; n= 11) and 2.2-4.4 in females ($\bar{x}$= 3.5 ± 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 frequently convex (Fig. 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 (Fig. 12B), margin between loreal and anterior supralabial shorter than LOL; postnasal irregularly heptagonal, higher than wide, proportionally larger than prenasal, the latter rectangular and usually longer than high; seven supralabials, third and fourth in contact with the eye orbit; first supralabial enlarged, pentagonal, without protrusion between the postnasal-prenasal; horizontal

length of 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, 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 (Fig. 12C); six infralabials, 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 suture of single pair of infralabials; three gulars; 1-2 preventrals. 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).

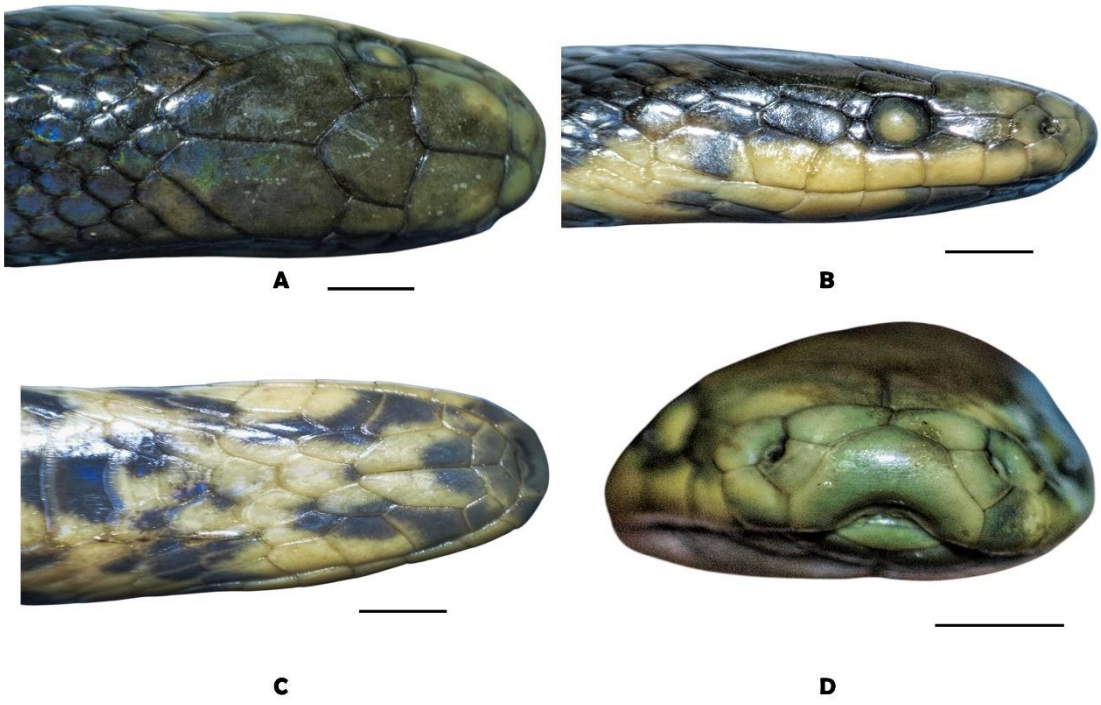

FIGURE 13. Adult male individual of *A. meridensis* (MZUC 48051), dorsal view (A), lateral view (B), and ventral view of the head (C). Finally, frontal view of the rostral scale (D).

Information of coloration (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 of black (Fig. 13A, B, D) and (B) bicolor pattern, intercalated white-or-whitish and brown-black

crossbands, narrow (one scale), not widened medially, continuous, or discontinuous medially and margined of black (Fig. 13C, E, F). In both dorsal patterns, the head is light brown, differentiated of the body, less commonly dark brown. A black line behind and in front of the eye is absent or poorly defined. Juvenile individuals not have the light bands marginate of black, more evident in pattern B (Fig.13G). On the other hand, towards the Boconó River basin, in the town of Boconó and its surroundings heading towards Biscucuy, Portuguesa state, we have detected a population where juveniles and adults do not have the reddish-white crossbands margined of black, but having morphological characters and hemipenes distinct and we recognize as *A. micheleae* (Fig. 13H1-3).

FIGURE 14. 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). G = juvenile specimen without marginalization of the white or cream crossbands. H1-H3 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. Images ®Luis Felipe Esqueda

As for the ventral surface (midventral), we find at least four variations, VP: (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 % (Fig. 14A, D; P_VP5); (B) VP6, reddish or whitish background, with black spots on

each scale, rounded, mottled or rectangular, arranged in three lines, the medio-ventral one is usually smaller; the space varies considerably, but can be above 50 % of the surface on each scale (Fig. 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 % (Fig. 14B-C, P_VP7) and (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 (Fig. 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. 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 heavily pigmented black.

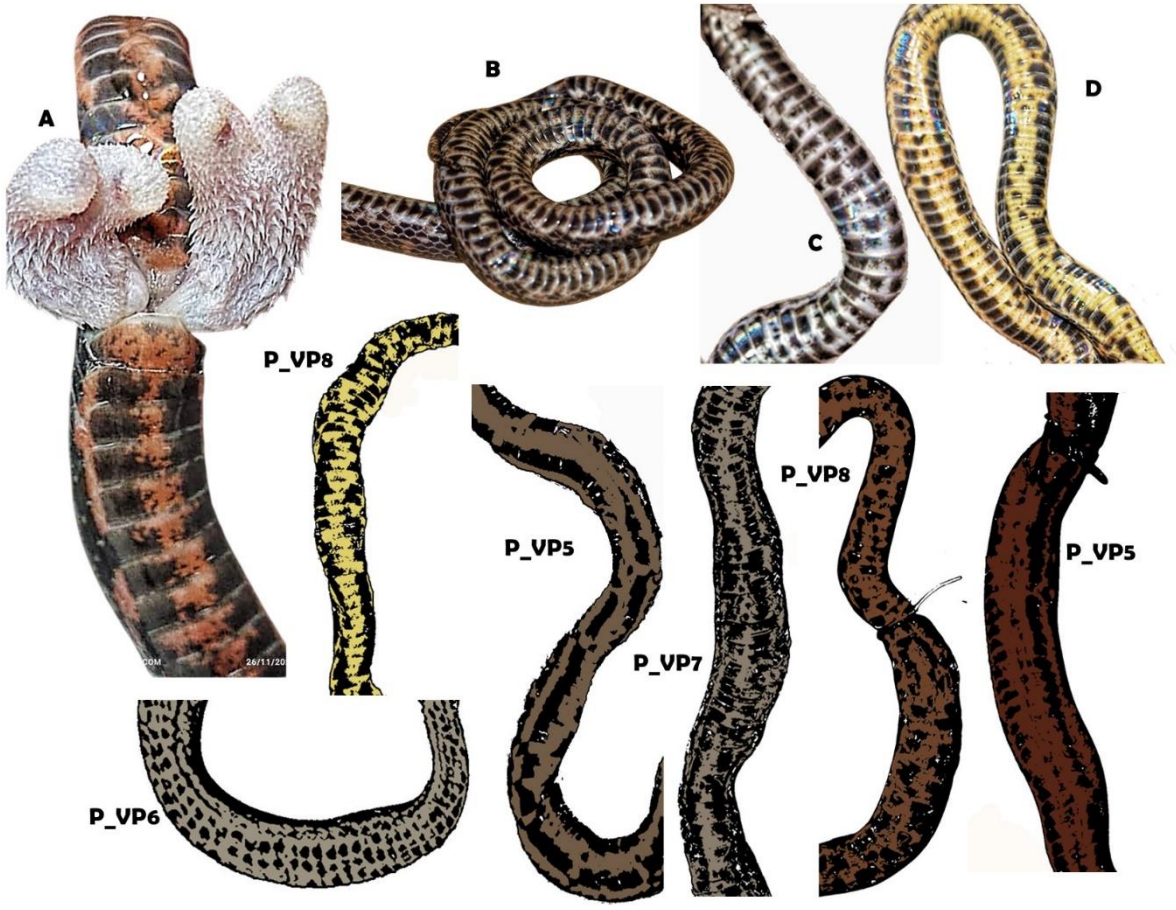

FIGURE 15. Ventral pattern (PV) in life of *A. meridensis*, A_D. Moreover, other patterns were constructed from field data of the specimens (Preserved Ventral Pattern, P_VP). VP5, reddish, whitish or pale-yellow background (A, D; P_VP5); VP6, reddish or whitish background (P_VP6); VP7, reddish or whitish background (B-C, P_VP7) and VP8, whitish background (P_VP6).

Hemipenis (everted organs n= 4). – Organ moderately bilobed (Fig. 15A-C) to bilobed (Fig. 15D), semicapitate, semicalyculate; well-defined lobes, similar in size and located towards the distal portion of the capitulum, can vary of subcylindrical to cylindrical and 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 sulcus spermaticus varies between ~26 % (Fig. 15C-D) and 42-50% % (Fig. 15A-B) with respect to the length of the hemipenis, arranged centrifugally; margins of sulcus spermaticus are smooth, expanded laterally and bordered by spinules from its base apical of the lobes; body of the hemipenis medially wider than its base, subcylindrical, covered with medium-sized, hooked spines, developed and grouped from the bifurcation of 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 asulcate 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.

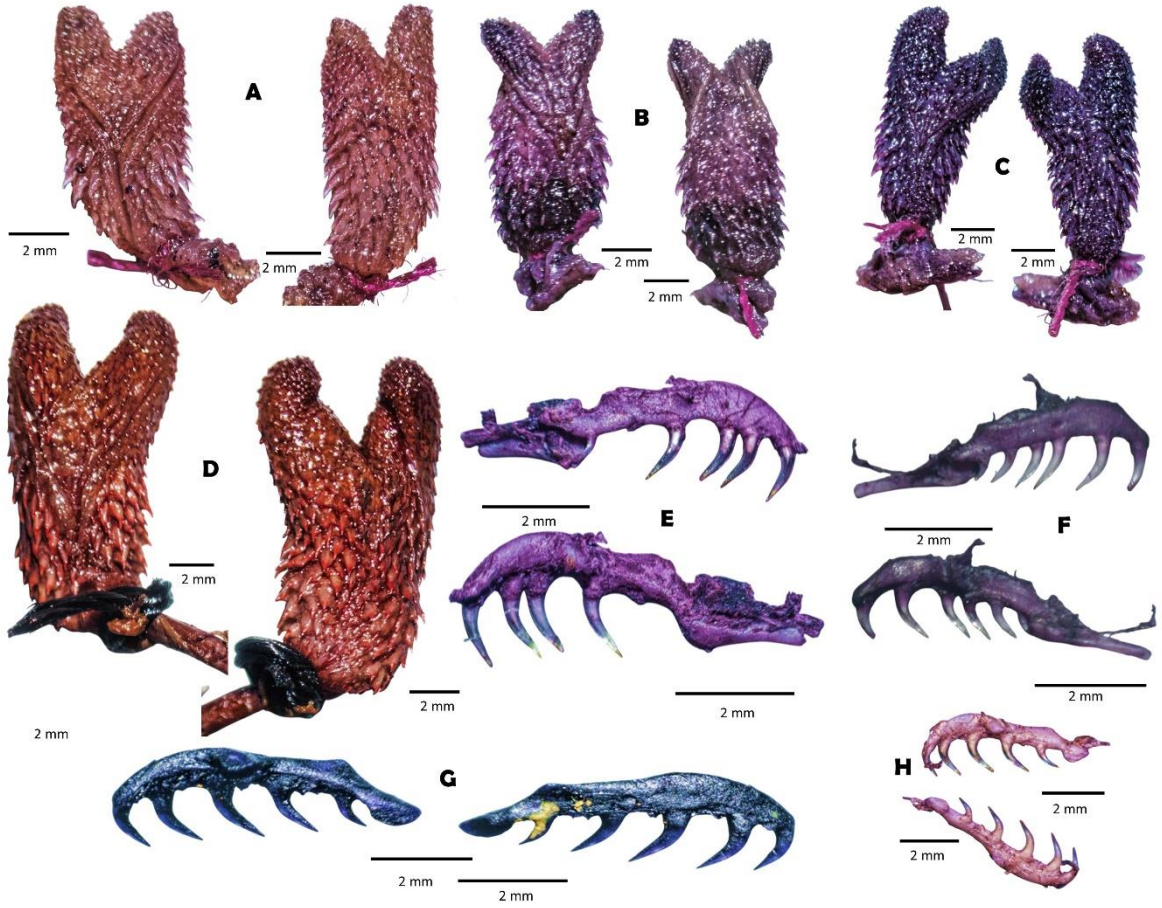

FIGURE 16. Hemipenes and maxillary dentition of *A. meridensis*. (A) sulcate and asulcate region of the hemipenis in specimen MZUC 45660; (B) sulcate and asulcate region of the hemipenis in specimen MZUC 45661; (C) sulcate and asulcate region of the hemipenis in specimen MZUC 45662 and (D) sulcate and asulcate region of the hemipenis in specimen MZUC 45663. Maxillary dentition, E= specimen MZUC 45666; F= specimen MZUC 45662, G= specimen MZUC 45664 and H= specimen MZUC 45665.

Maxillar bone. – Its size varies from 3.1-5.47 mm in length (n= 6), with the anterior third barely arched and weakly depressed posteriorly; palatine process projected and well developed, located between the fourth and fifth teeth; 5-6 maxillary teeth, acute, curved and decreasing posteriorly, the last one 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 (Fig. 15E-H).

Distribution and natural history. – Currently, restricted to isolated populations in the northeast of Mérida and Trujillo states, Venezuela, between 1,077 and 3,275 m asl (Fig. 11B). Its type locality is found within the limits of the upper Santo Domingo River basin, with an altitudinal range that varies from 1,600 to 4,906 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 %) (Osorio et al.

2009). Other detected populations come from the basin of the Motatán rivers (middle-upper part between 1000-2700 m asl) and Boconó (upper part between 1700-2340 m asl). Our data from both basins indicate that the species would occupy the Andean montane semideciduous forest between 1000-2000 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, Ataroff 2001; Ataroff and Rada 2000; Cavelier et al. 2001). This taxon is sympatric with *Tantilla palamala* in its type locality. (Esqueda et al. 2025, the authors mistakenly typed labelled the specimens 74711, 74712, and 74713, when they are actually 47711, 47712, and 47713 but correctly noted elsewhere in the article and supplementary material).

This taxon is found in sympatry with *A. emigdioi* (Fig. 16A) and *Atractus nemosophis* recently described (Esqueda et al. 2025), previously referred to as *A. meridensis* by Esqueda and La Marca 2005 (specimen ULABG 4694) and also indicated by Passos et al. (2024). Although gregarious behavior is known in vermivorous snakes (Gray 2013), here we report the first known case for Venezuela in *Atractus meridensis*. 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 (Fig. 16B, dat. ined. Santos Bazó 2022).

Two adult females MZUC 45651 (LFE281) and MZUC 45652 (LFE286) contained 3 and 2 oviductal eggs, respectively. They were collected inactive under rocks in Las Piedras, way La Quinta sector, Mérida state, Venezuela, on August 1, 2021, at 1:16 PM (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 3 well-developed oviductal eggs, which was collected while crossing a dirt road in the Mibó sector, near Niquitao, Trujillo state, Venezuela, on June 3, 2021, at 2:14 PM with 70 % measured humidity and a temperature of 23.5 ºC (9° 5'51.35"N and 70°24'18.54"W; Fig. 16C).

FIGURE 17. 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 the 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) finding of a partially digested earthworm in the digestive tract of the juvenile specimen MZUC 45656.

So far, it is believed that vermivorous snakes of the genus *Atractus* exhibit cathemeral activity (Silva and Valdez 1985; Martins and Oliveira 1999; Balestrin et al. 2007), although their foraging occurs more frequently at night due to their diet (earthworms). Although the 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, a juvenile specimen MZUC 45657 was observed active of 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, June 17, 2021, at 10:00 PM, temperature 22 ºC and 70 % measured humidity, LFE 2021).

A juvenile specimen MZUC 45656 (LFE 083, Fig. 16D) contained a partially digested worm in its digestive tract, probably from the Rhinodrilidae 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 3,029.1 km^2, consisting mostly of montane rainforests of the northern Andes (1,117 km^2). According to IUCN, an area of 3,093.19 km^2 comprises EOO (geocat EOO= 3,113.344 km^2) and 68 km^2 AOO (76 km^2 to 2 km). 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 (Ataroff and Naranjo 2009). This eco-geographical 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 (Hendrix et al. 2008), particularly in tropical mountain ecosystems that exhibit high rates of endemism in relatively small areas (Lavelle and Lapied 2003). In consequence, considering the IUCN conservation criteria (IUCN 2012) and the vulnerability index of reptile species (IVER, Esqueda and La Marca 2015), *Atractus meridensis* it must be included in the Vulnerable category according to criteria B2abi,ii,iii,iv).

DISCUSSION

Species limits and taxonomy

Although we acknowledge the contribution of Passos et al. (2024), 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 (1903), in his description, indicated that *A. erythromelas* had 17 dorsal scale rows at midbody, but in contrast, Roze (1961, 1966) reported 15 rows at midbody. This discrepancy led Esqueda and La Marca (2005), without having reviewed Boulenger syntypes, to consider that the species

has 15 rows at midbody rather than 17. Passos et al. (2024) recognized that *A. erythromelas* may have either 15 or 17 dorsal scale rows at midbody, with some specimens exhibiting a reduction of two rows toward the neck and tail. However, the series of specimens assigned to *A. meridensis* from the Santo Domingo River basin and surrounding areas have 17 scale rows at midbody without any reduction, a condition overlooked by Passos et al. (2024) 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 bicolor, crossbanded type).

The delimitation of species is often challenging in recently diverged groups (e.g., *Atractus*; Serrano et al. 2024), 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. 2024). 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 (Esqueda and La Marca 2005).

Passos et al. (2024) 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 (2010) described *A. hoogmoedi*, noting that the only difference of *A. zidoki* was the condition of the hemipenis: either single or bifurcated. They interpreted this as evidence of cryptic species, 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 test, 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 (Passos et al. 2009d). In their 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. (2020) described *A. pachacamac* from the western Brazilian Amazon, distinguishing it by ≥158 ventrals, ≥39 subcaudals, and >320 mm SVL in males versus ≤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 Cytb and ND4 markers is low (<1.2 %). In their discussion, Melo-Sampaio et al. (2020) recognized *A. snethlageae* as a complex but, curiously, did not address the fact that both taxa overlap geographically and are morphologically very similar and (4) Passos et al. (2024) 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 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 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. 2024, Fig. 90). A coloration pattern strikingly similar to *A. pearti*, yet completely overlooked (could it be that several species are being lumped together in their description?). In fact, Montes-Correa et al. (2017) 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. (2024) synonymized are valid taxa, and their definitive recognition will occur in various forthcoming articles

(Esqueda et al. 2025). 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. (2024) synonymized *A. eriki* with *A. indistinctus*, their interpretations are inconsistent. According to those authors, Esqueda and La Marca (2007) stated that *A. eriki* has a uniform dorsal coloration, yet they describe and illustrate a vertebral line. This statement is not correct. What was actually 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 oscuro, aunque no en todas las escamas". Nowhere do the authors refer to a vertebral line as seen in *A. indistinctus* (see Passos et al. 2024, 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. (2024) refers to hemipenial morphology: moderately bilobed in *A. indistinctus* vs. slightly bilobed in *A. eriki*. Likewise, the specimen from Cerro Las Tetas, Zulia state (MBUCV, uncataloged), observed by those authors, shows a fairly uniform coloration, clearly lacking lines (Fig. 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 (Murphy et al. 2019; Arteaga et al. 2017, 2022; Melo-Sampaio et al. 2019, 2020; Passos et al. 2022). Recently, Gonzalez et al. (2024) 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,

support the recognition of both taxa as distinct species. Therefore, the synonymization proposed by Passos et al. (2024) 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 (2012) 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 Melo-Sampaio et al. 2021: fig. 6).

A comparable situation is found in the recent proposal by Arteaga et al. (2024) to recognize several new species of *Bothriechis* in South America, which was later rebutted by Reyes-Velasco (2024), who argued that the genetic differences interpreted as species boundaries may actually reflect clinal variation rather than independent evolutionary lineages (methods and delimitation inconsistent, Cartens et al. 2013). Although hybridization and introgression are evolutionary processes that may play important roles in speciation (Taylor and Larson 2019), their historical and geographic contexts in shaping species complexes are only beginning to be understood (e.g., *Bothriechis*, Mason et al. 2019; *Crotalus*, Myers 2021; Schield et al. 2017, 2019).

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 (Wiens 2004; Kozak and Wiens 2006). 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 (Peterson et al. 1999; Martínez-Meyer et al. 2004). 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 that, 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 (Arteaga et al. 2017).

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 (Wiens 2004; Cadena et al. 2012). Consequently, the microendemism observed in this group could be explained by a combination of niche conservatism (Wiens 2004), paleoclimatic history (spatial heterogeneity leading to paleoendemism and neoendemism and topographic complexity (a continuous history of geological changes; (Jetz and Rahbek 2002; Antonelli et al. 2018), rather than active ecological divergence processes (Schluter 2009). To the extent that we can incorporate more molecular data from Venezuelan Andean species and/or phylogeographic analyses, it 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 northern Andes is evident (Esqueda and La Marca 2005; Arteaga et al. 2017, 2022; Passos et al. 2024). For example, a calibrated phylogeny shows that the mimetic snake group *A. erythromelas*, *A. meridensis*, and *Atractus* sp. diverged from other sleeping 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 (Esqueda et al. 2025). Today it is known that low extinction rates are correlated with greater climatic buffering in mountainous regions (Azevedo et al. 2020), which would favor of both paleoendemism-neoendemism and where museum or cradle hypotheses could explain the diversity of snakes with a narrow distribution like *Atractus* in 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, and that does not maintain geomorphological relationships with the Eastern cordillera of the Colombian Andes (Audemard and Audemard 2002), 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 (Bermúdez et al. 2011). 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 (Erikson et al. 2012). Although it covers an area of ~9.5 % of the country, it is more complex than any other nearby mountain system. Said 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 (Chacón-Moreno and Moral 2020). Another finding that corroborates the above is *Tantilla palamala*, an Andean snake that diverged from the other species of the *T. melanocepahala* group about 8.09 Myr ago and that exhibits a biogeographic pattern similar to that found by us in *A. meridensis* (Esqueda et al. 2025). In fact, this timing is consistent with Boschman (2021), who suggested that the cordillera de Mérida had elevations between 3500-4000 m 7 Myr ago due to the discovery evidences of paramo vegetation in the sediments of the Lake Maracaibo basin.

A. erythromelas and *A. meridensis* reflect strictly vicariant speciation due to geographical isolation, and niche conservation is expected (see Peterson 1999). While climatic niche divergence may be a widespread mechanism of speciation in terrestrial vertebrates (Hernández-Hernández et al. 2021), vicariant allopatric speciation can precede niche divergence (Aguilée et al., 2018; Anderson and Weir 2022). In cases where, for example, two populations isolate themselves in allopatric but environmentally similar habitats, the lineages can adapt in parallel and speciation occurs through factors unrelated to niche divergence (Anderson and Weir 2022). Unlike anurans, the distribution of lizards and snakes in tropical mid-highlands would be related to the plasticity of their thermal physiology and their evolutionary history (e.g., *Anadia*, Navas 2006; Angilleta 2009). Therefore, mountain species with small distributions follow aggregated geographical patterns (e.g. Birds, Rahbek et al. 2006) derived from high spatial and temporal variation in climate and habitat (Lagomarsino et al. 2016; Quintero and Jetz 2018), emerging narrow climatic niches (Thom et al. 2021) and/or climatic niche breadth (Moreira et al. 2024). Our still incipient data suggest that *Atractus* exhibits this pattern, although being able to establish a macroevolutionary interpretation regarding speciation and its underlying mechanisms that drive it would be a key question to be evaluated (Esqueda et al. 2025).

Our accumulated field data over several years tell us 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 (Aubret and Shine 2009), but with a reduced habitat breadth (< 20,000 km²) and frequently occurs in highlands (Böhm et al. 2017), such as other Neotropical snakes (e.g. viperids; Birskis-Barros et al. 2019). Although the ecology of this South American genus remains discrete, comparatively to its diversity (> 150 spp., Uetz et al. 2024), various studies exist showing that these snakes exhibit a specialized diet in earthworms. (Martins and Oliveira 1999; Balestrin et al. 2007; Ferreira-Silva et al. 2019). Until now, all environments above 1500 meters in altitude in the cordillera de Mérida have been seriously affected by anthropogenic activities (Ataroff and Rada 2000; Llambí 2015; Chacón-Moreno et al. 2021). During 2021, we had the opportunity to be in Mucuyupu-Tafallé population, Trujillo state, Venezuela, between 2000-2500 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 (Miglani et al. 2019; Singh et al. 2019). If we invoke the optimal foraging theory (Perry and Pianka 1997), it is possible to think that the spatial and temporal dimension of habitat disturbance could affect specialist reptiles like vermivorous snakes, but there are no studies demonstrating this in *Atractus*. Balestrin et al. (2007) are of the opinion 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 (Böhm et al. 2013).

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 is among five critical hotspots biodiversity (Myers et al. 2000), the

political-social crisis of recent decades has decimated any efforts in that direction (see de Sousa 2023). In fact, if we consider that Oliveira-Miranda et al. (2010) 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 lack of data (e.g., extraction of wood on Andean forests), the current outlook could be concerning for many reptile species, in particular specialist those like *Atractus*.

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Data availability

All data generated or analyzed during this study are included in this published article (see supplementary information files in format xlsx, except unpublished data that are not yet public until the time of their publication in the repository GENBANK). All unpublished specimens are not listed on the IUCN Red List of Threatened Species Index and met the standards required by the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE). All data generated or analyzed during this study are included in this published article (including supplementary information files).

Competing interests

The authors declare no competing interests.

Declaration of ethics

Not applicable

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CHAPTER III

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UNRAVELING THE DIVERSITY OF *ATRACTUS* (SERPENTES: DIPSADIDAE) IN THE VENEZUELAN ANDES

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ABSTRACT

Today among the recognized species of *Atractus* in Venezuela, the nominal taxa *A. ochrosetrus* Esqueda & La Marca, 2005 and *A. mijaresi* Esqueda & La Marca, 2005, were recently considered a junior synonym of *A. ventrimaculatus* Boulenger, 1905 and

A. pamplonensis Amaral, 1937, respectively. However, based on new morphological (coloration pattern, scalation, dentition, hemipenes and morphometrics), phylogenetic (topology using Maximum Likelihood + Bayesian Inference and genetic distance) and geographic (ecological niche modeling) evidence, *A. ochrosetrus* and *A. mijaresi*, both endemic species of the cordillera de Mérida, are revalidated and redescribed. The first is restricted to a series of mountain ranges southwest of the Chama River basin, between the states of Mérida and Táchira; while *A. mijaresi* occurs between Mucurubá and Capaz east of the Chama River basin, Mérida state. *A. ochrosetrus* and *A. ventrimaculatus* closely related species diverged in the Late Miocene 6.67 Myr ago (95 % HPD = 4.4–9.02), coinciding with the uplift of the northern Andes between 8–5 Myr. While *A. mijaresi* would be related to *Atractus* sp. yet to be described and that its diversification occurred during the end of the Pliocene and the beginning of the Pleistocene 2.85 Myr ago (95 % HPD = 0.87–5.21). Finally, we record the second specimen from Betania, Táchira state, which we provisionally designate as *Atractus* aff. *pamplonensis*. According to the IUCN, *A. ochrosetrus*, *A. ventrimaculatus* and *A. mijaresi* should be included in the Vulnerable category according to criteria A2 and B2 (i,ii,iii,iv).

KEY WORDS. – Systematics, taxonomic status, sleepyhead snakes, cordillera de Mérida

INTRODUCTION

If well they originated in the Old World and later dispersed to South America (Zaher *et al.* 2019), dipsadines snakes exhibit a spectacular ecological and phenotypic diversity as result of adaptive radiation, and where snakes with fossorial habits clearly differentiated themselves from other groups (Pandelis *et al.* 2023). If we consider that the diversity of dipsadines reaches at least ~806 spp. (Zaher *et al.* 2019), it is notable from the evolutionary and ecological point of view that the snakes called ground or sleepyhead snakes of the genus *Atractus* Wagler, 1828 comprises 18.6 % of all dipsadines known (Uetz *et al.* 2024), clearly establishing itself as the dominant group in the middle–high mountain environments toward northern South America. In the case of Venezuela constitutes the most diverse dipsadid genus with 30 recognized species (Rivas *et al.* 2012; Natera–Mumaw *et al.* 2015).

Recently, some species of the genus were revised by Passos *et al.* (2024) for northern South America (Colombia and Venezuela), with the recognition of five new species for Colombia and the synonymy of five species for Venezuela. Although its article is considered a progress in the knowledge of these snakes, their criteria such as the adequacy of the data at a comparative level are dubious, erroneous, incoherent, altered, hidden, and intentionally ordered to show a complex and overlapping situation that would justify their non–taxonomic recognition, but in their discreet and convenient discussion they suggest that a possible phylogenetic hypothesis or other evidence could change said taxonomic action. Although the taxonomy and systematics of this group have made significant advances in recent decades (e.g., increase in its diversity, Uetz *et al.* 2024), the incorporation of molecular biology has allowed for the recognition that the diversity of the group may be greater, and that, in some cases, multiple sources of evidence are required for its recognition (Arteaga *et al.* 2017, 2022; Melo–Sampaio *et al.* 2019, 2021; Passos *et al.* 2022).

In their monograph, Passos *et al.* (2024) have overlooked, evaded, or tangled fundamental criteria in understanding species formation and differentiation. From the systematic John Ray (Ray 1686), through the theory of evolution (Darwin 1859; Darwin & Wallace 1859) to current advances in molecular biology, the definition of species has evolved, shifting from a morphological approach, considered today as a weak criterion for delimiting true species, towards a more integrative and dynamic vision (Wiens and Servedio 2000). Speciation, understood as a complex and discrete process (Rabosky *et al.* 2013), does not always produce clear boundaries between species (Walker *et al.* 2024), which has led to the acceptance that these can be temporary segments of lineages in stabilization. If a lineage is a sequence of ancestors/descendants of populations or metapopulations (e.g., unified species criterion, de Queiroz 2007), then the species can be considered, synergistically speaking, as a segment of that lineage; Although phenotypic discontinuities between groups of organisms may reflect only selective advantages of particular trait combinations, in the context of speciation, species constitute temporary fragments of stabilized lineages (Dupré 2024).

Within this framework, polymorphism, particularly in coloration, serves as an excellent model for studying ecological and evolutionary processes, as different morphologies, maintained by genetic mechanisms, can reflect adaptations to local selective pressures. Polymorphism is then considered the appearance of two or more clearly different and

genetically determined morphologies or forms that occur at the intrapopulation level, with interbreeding (Forsman 2016; McLean & Stuart–Fox 2016; White & Kemp 2016) and whose frequencies are relatively high (> 1%). In addition, geographic variants that suppose a level of isolation that could lead to allopatric speciation are excluded, plus polymorphisms strictly occur in panmictic populations, and rare variations or mutations are excluded as polymorphisms. It is important to distinguish between polymorphism with at least two known morphs (dichromatism) from those involving multiple morphs that are usually more common in nature (polychromatism). Notably, distinct colour morphs are not necessarily genetically determined, but can be induced by environmental cues or depend on the developmental stage of an organism (so–called polyphenosms, Mayr 1963; Pfenning & McGee 2010). Polymorphisms are also often associated with species radiations, whereby multiple closely related species harbor similar intraspecific morphs (Enbody *et al.* 2021; Gray & McKinnon 2007; Hugall & Stuart–Fox 2012; Jamie & Meier 2020).

Building on the speciation–polymorphism idea, phenomena such as melanism, subject to natural and sexual selection can be see affect its selection and frequency (Prince 2003), potentially leading to adaptive responses that eventually accumulate significant genetic differences, triggering speciation events. This pattern is observed, for example, in species of the genus *Atractus* from mountainous environments, where differences in pigmentation seem to be associated with geographical isolation and potential events of diversification recent, which have not yet been fully studied.

The coadaptation hypothesis suggests that there is a correlation of multiple characters within a species, so that morphology (e.g., body shape, coloration, among others), thermoregulation of behavior and thermal sensitivity of performance can evolve together (Huey & Bennett 1987; Bauwens *et al.* 1995; Angilletta *et al.* 2002). Thus, dark coloration may lead to greater heat absorption and be advantageous in cold climates (middle–upper mountain floors, Bogert's rule, Bogert 1949; Clusella–Trullas *et al.* 2007), but it may also occur in lowland organisms (Glober's rule, Glober 1833; Rensch 1929). Although such a condition suggests of possible adaptive responses, little is known about the underlying mechanisms that regulate this relationship and how frequent it would be in the population context, particularly regarding taxonomic significance and how these patterns in populations respond to local selective pressures, resulting in distinctive traits and genetic adaptations (Mimura *et al.* 2017). Beyond this,

its seems plausible that the establishment of genetically based geographic variation (genetic accommodation, West–Eberhard 2003) and species differences in melanin patterns may be favored by environmental effects on both the intensity and pattern of melanin, as observed in *A. taphorni* vs. *A. emigdioi* and *A. ventrimaculatus* vs. *A. ochrosetrus*, closely related species that occur allopatrically in medium–high mountain environments of the cordillera de Mérida (unpublished data LFE 2021).

Herein, we re–evaluate and re–validate the taxonomy of *A. ochrosetrus* vs. *A. ventrimaculatus* and *A. mijaresi* vs. *A. pamplonensis* integrating morphological and molecular data that had not been done previously. All endemic are species of the cordillera de Mérida, except *A. pamplonensis*, whose presence in the country it is based on a single specimen identified by Schargel & García–Pérez (2002), notably not evaluated by Passos *et al.* (2024). Here, we formally incorporate the description of a second specimen from the same locality, but defining its status as *A.* aff. *pamplonensis*.

Although we recognized the status of other Andean species such as *A. eriki*, *A. micheleae*, *A. meridensis* and *A. tamaensis*, the same is being redescribed in other articles (Esqueda and col. in publ.).

MATERIALS AND METHODS

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. 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, USA) at the Herpetozoa laboratory, University of Concepción. Two mitochondrial genes (Cytb and ND4) and two nuclear genes (NT3 and RAG–1) were amplified using primers and PCR conditions detailed in Supp._1_1, DNA quality was assessed on 1.5 % agarose gels stained with SYBR® Vitrogen. Sequencing was performed by MACROGEN (Korea), and chromatograms were verified using BioEdit 7.0.9.0 (Hall 1999). Open reading frames were checked in Mega v.11 (Tamura *et al.*

2021). Heterozygous nuclear DNA sequences were identified visually for double peaks in chromatograms, and individual alleles were reconstructed using DnaSP v.6.12 (Librado & Rozas 2009) with two independent runs. Alignments showed no gaps in mitochondrial sequences, and sequences for other species were sourced from GenBank (Supp._1_2), ensuring amplified loci were from single voucher specimens to avoid "terminal chimeras."

Phylogenetic analyses

The new sequences generated in this study were combined with sequences downloaded from GenBank. Additionally, 20 specimens representing to 18 species were used as outgroups (highlighted in yellow, Supp._1_2). Five gene fragments were obtained, corresponding to three mitochondrial amplicons, long 16S ribosomal RNA (525 bp); cytochrome b (897 bp); and NADH dehydrogenase ND4 subunit IV (713 bp) and two nuclear amplicons, neurotrophin–3 gene NT3 (516 bp); recombination activator RAG–1 (879 bp). Substitution saturation of each locus was assessed using the software DAMBE v.5 (Xia 2013). 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 (Nguyen *et al.* 2015).

The authenticity of the obtained sequences and the homology of the specific mtDNA and nuDNA markers were evaluated with a BLAST search in the NCBI genetic database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The consensus sequences for each locus were aligned using MAFFT (Katoh and Standley 2013) contained in Jalview v. 2.11.1.4 (Waterhouse *et al.* 2009), 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 exhibit nucleotide positions with high entropy and may have misaligned or incongruent regions were refined with the BMGE software: a BLOSUM62 matrix, a minimum block size of 20, a maximum entropy threshold of 0.5, and a rate limit gap of 0.65 (Criscuolo & Gribaldo 2010), available on the web service https://ngphylogeny.fr/ (Lemoine *et al.* 2019). Finally, the concatenation of all alignments was done with Mesquite v3.6 (Maddison & Maddison 2021). 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 (Triant & Dewoody 2007).

Here, we used maximum likelihood (ML) analysis to obtain the optimal tree topology of the concatenated data set. The best partition and substitution models were automatically selected using ModelFinder (Kalyaanamoorthy *et al.* 2017) and then implemented in IQ–TREE v.2 software (Nguyen *et al.* 2015) under the Bayesian information criterion (BIC). The best ML tree was selected from10,000 iterations and the confidence of the branches of the best ML tree was evaluated with the ultrafast bootstrap method using 10,000 bootstrap pseudoreplicates (Minh *et al.* 2013). 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/, Trifinopoulos *et al.* 2016), where branch support was calculated using the ultrafast bootstrap approximation (UFBS) (Minh *et al.* 2013) and the Shimodaira–Hasegawa approximate likelihood ratio test (SH–aLRT) (Anisimova *et al.* 2011), with 1,000 replicas. The consensus tree was visualized in FigTree (Rambaut 2014). Nodes with bootstrap values ≥ 70 were considered strongly supported and those nodes with 95 % were considered highly supported.

Divergence time estimation and calibration points

We estimated divergence times of sleepyhead snakes of the genus *Atractus* using the Bayesian framework implemented in the BEAST 2.7.5 software (Bouckeart & Drummond 2017). For all analyses, the matrix was partitioning by genes, 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. Unlike previous analyses with maximum likelihood (ML) and Bayesian inference (BI), where the best partition schemes and molecular evolution models were defined using ModelFinder and Partition Finder in the integrated PhyloSuite platform (Zhang *et al.* 2020). Here, the BEAST 2.7.5 software implements the "bModelTest "allreversible" option to estimate mutation rates for all genes evaluated. When implemented, bModelTest switches between substitution models during the Metropolis coupled MCMC (MC3), inferring and marginalizing site models, thus averaging the uncertainty about those models (Bouckaert & Drummond 2017), except for partitions that were defined by PartitionFinder because bModelTest does not incorporate substitution models average site over partitions from alignment. While

Bayesian relaxed clock methods may produce more correct estimates when using multiple loci (mtDNA + nuDNA) (Battistuzzi *et al.* 2010), it is unclear how using faster–evolving mitochondrial genes (animals) may influence dating by divergence in relation to the use of nuclear loci that have a slower rate of evolution (Zheng *et al.* 2011). Here, the likelihood ratio test (LRT) implemented in Mega v.11 software (Kumar *et al.* 2018) rejected strict clock evolution models, favoring the lognormal relaxed clock model for all partitions. Although the classic uncorrelated relaxed clock (Drummond *et al.* 2006) works well when rates and branch lengths are not highly correlated, on the contrary, it is poor, so here we will use the "optimized relaxed clock" model according to Douglas *et al.* (2021) which works well in both scenarios. On the other hand, we will apply a birth–death speciation model (Kendall 1948) as opposed to the Yule model (Yule 1925), since this assumes zero extinction rates and it is commonly known that extinction is extremely significant in the diversification of species (Sarver *et al.* 2019). Other antecedents were set to their default values, except the birth rate, which had an exponential distribution (lower 0.1 and upper 10).

Phylogenetic analyses often involve data sets comprising sequences from multiple loci. A common practice is to partition the data set, for example, by gene or by codon position, and assign separate substitution models to subsets of the data (Yang & Kumar 1996). In molecular clock analyses, the simplest approach is to apply a single model of rate variation between lineages to the entire sequence alignment. However, this approach does not account for heterogeneity between genes, which may have evolved under very different conditions. For instance, multilocus data sets may include combinations of markers from mitochondrial, chloroplast, and nuclear genomes. An ideal scenario for calibrating phylogenetic trees is when they are obtained from well–dated fossils; however, the incomplete or imperfect nature of the fossil record often only provides evidence of the minimum age of a clade, potentially leading to overestimation divergence time (Lukoschek *et al.* 2012). In fact, fossils rarely represent specific nodes but rather points along a branch (Lee 1999; Conroy & van Tuinen 2003).

On the other hand, multiple underlying factors can contribute to inaccurately calibrated clocks (e.g., patterns of evolution, saturation, and/or combinations of genes that evolve more rapidly vs. others that evolve more slowly). In snakes, the Caenophidia group contains the greatest diversity of extant snakes (> 2500 spp., Uetz *et al.* 2024) and includes acrochordids, xenodermids and all colubriforms (Pyron *et al.* 2013), a group

with a controversial fossil record (Head 2015; Head *et al.* 2016). Considering the countless setbacks that persist in obtaining ultrametric trees (Lukoschek *et al.* 2012), there is greater consensus on using multiple independent calibrations of fossils (Ho & Phillips 2009). In our case, the calibration points of the nodes were defined based on the available fossil record (one corresponding to Colubridae and four positioned in the external groups), using ages and interpretations of fossils similar to those described in Zaher et al (2018; 2019) and García–Sotelo *et al.* (2021) (Supp._1_3). We use Metropolis coupled MCMC (MC3, Atchadé *et al.* 2011; Maturana–Russel *et al.* 2018; Müller and Bouckaert 2019), with a temperature of 0.03 and four chains, established in three independent runs of 50 million generations, saving the parameters and trees every 10,000 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 (Rambaut *et al.* 2022). Combining the runs was done with LogCombiner v2.7.5 (Drummond *et al.* 2012). After performing a 10 % burning, the maximum credible tree was obtained by using TreeAnnotator 2.7.5 (Rambaut & Drummond 2016) implemented on the CIPRES Science Gateway online platform (https://www.phylo.org/) (Miller *et al.* 2010).

Finally, we also calculated the uncorrected genetic distance (p–distance) using MEGA v.11.0 (Kumar *et al.* 2018) for mitochondrial CYTb and ND4, respectively.

Ecological niche modeling

To understand the distribution and habitat in the biogeographic context, we generated species distribution models (SDM) to predict and compare the potential geographic ranges of *A. ochrosetrus* and *A. ventrimaculatus* using correctly identified records (including material MZUC museum by LFE). Therefore, those 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, being in total 49 records/specimens between both taxa verified (Supp._1_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. Environmental predictors included 20 bioclimatic variables representing the current scenario (1970–2000) from WorldClim v.2.1 (Fick &

Hijmans 2017), 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 (Amatulli *et al.* 2018). After modeling in MaxEnt, the vegetation map of Venezuela by Huber and Oliveira–Miranda (2010) was used to calculate the surface area (km²) predicted by the model and to exclude 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 (QGIS Development Team 2024).

Approach to predictive models (habitat suitability)

Exploring habitat suitability using a unique model (SDMs): given the limited and spatially concentrated occurrence data (Hernandez *et al.* 2006), Our first approach was based on a unique maximum entropy model to predict the distribution range of the species (MaxEnt v.3.4; Phillips *et al.* 2006). This algorithm is highly effective for inferring species suitability from presence–only data, even with small sample sizes, due to its ability to estimate probabilities based on maximum entropy principles (Phillips *et al.* 2006; Elith *et al.* 2011; Warren and Seifert 2011). In the first instances, doubtful information and duplicate records were removed. To reduce collinearity among bioclimatic variables, we performed a Pearson (Pearson 1900) correlation analysis in R (v.4.3) using ENMTools (Supp._1_5; Warren *et al.* 2021), discarding variables with r^2 >0.8 (Dormann *et al.* 2013), resulting in seven bioclimatic variables in the present scenery (Supp._1_6). In MaxEnt, we disabled Extrapolate and Do clamping to avoid overfitting (Elith *et al.* 2011). Due to fewer than 50 records by 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 5,000 iterations. We randomly selected 65 % of sites for training and 25 % for testing (Phillips *et al.* 2006). The Jackknife test was used to estimate the contribution and response of each variable (Shcheglovitova and Anderson 2013).

To understand changes in habitat suitability that presumably led to historical isolation or not during restriction to shared refugia, we retrospectively projected current MDS onto Pleistocene and Pliocene climate data available in the PaleoClim database (Brown *et al.*

2018, http://www.paleoclim.org/). In this particular, projections were used for the mid–Pliocene warm period, between 3,264–3,025 Myr (Downset *et al.* 2010) and Last Maximum Glacial (LGM, 21 Kya; Karger *et al.* 2017). 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 current models and predicted habitat suitability with the predictive function in MaxEnt v.3.4 (Phillips *et al.* 2006).

Evaluation index and visualization

The accuracy of the models either in the single approach was evaluated as follows: (1) single approach: the model outputs were manually checked, and the model with the largest area under the curve (AUC) was selected. AUC values range from 0.5 (random model) to 0.8–0.9 (good fit) and above 0.9 (excellent fit) (Thuiller *et al.* 2003). The logistic output indicates a probabilistic similarity index, with values from 0 to 1, where values closer to 1 represent ideal conditions for the species. While the AUC test is commonly used in species distribution models (e.g., MaxEnt), its validation has been questioned for not accounting for true absences, leading to uncertain models (Peterson & Nakazawa 2008). To avoid biases, additional statistical metrics, including the Z value, were used to assess the significance of the predictions (Manly 2006). The True Skill Statistic (TSS) compares sensitivity and specificity, providing a robust, prevalence–independent metric, with values close to 1 indicating excellent predictive capacity (Allouche *et al.* 2006). Before running MaxEnt, we optimized the model configuration using the ENMeval library (Muscarella *et al.* 2014; Supp._1_7) in R v.4.3 (R Core Team 2020), selecting the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc). 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 (Phillips *et al.* 2006). 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 is carried out separately for each species of *Atractus* using the R ecospat library (Di Cola *et al.* 2017). The ecological space (E–space) is evaluated

using an ambient PCA environment (PCA–env hereafter) framework and an ordination approach. Climatic variables transform into three–dimensional spaces defined by their main components. The superposition of niches between *A. ochrosetrus* and *A. ventrimaculatus* was calculated using Schoener's D statistics directly on the ecological niche space and modified Hellinger distances (Schoener 1968; Warren *et al.* 2008). The value of D varies between 0, when the species do not overlap in the ambient space, and 1, when the species compare with in the same ambient space. We evaluate the conservation of niche (alternative = major, is decided, the superposition of niche is more equivalent/similar than random) and niche divergence (alternative = smaller, i.e., niche overlap is less equivalent/similar than random) (Broennimann *et al.* 2012; Di Cola *et al.* 2017). For each hypothesis, 1,000 permutations were made. All these analyses were executed in R v.4.3 (R Core Team 2020).

To account for the actual suitability of the habitat, we used vegetation cover data made by Chacón–Moreno & Moral (2020). Next, we recalculated the resulting output of the models in each, which were filtered in QGIS v.3.28 for values <0.15, and the potential distribution was refined in R v.4.3 (R Core Team 2020) using 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–km^2 grid cells identified with sighting records or with suitable habitat encircled by grid cells with sighting records within the EOO; IUCN 2022). Comparatively, we use the geospacial conservation evaluation tool to calculate the metrics EOO and AOO, that allow us to evaluate the status of focal species according to IUCN (geocat, http: //geocat.kew.org/, accessed 8 March, 2025) (Bachman *et al.* 2011). This online tool type open source is an application based on the web of the IUCN red list by laying georeferenced data on the species by Google Maps interface (IUCN 2012).

Sample Source

This study includes the review of 292 specimens collected in the field during 2021 north of the Orinoco River, whose scientific hunting permits and access to genetic resources were processed and approved before the Ministerio de Ecosocialismo y Aguas (MINEC–Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE). Not all the material has been formally deposited in the museum yet (Museum of Zoology of

the University of Concepción, Chile, MZUC). Examined material is in the following museum institutions: 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).

Morphometric and morphological data

Previously, all available information about Venezuelan species were reviewed (Boulenger 1903; Roze 1961, 1966; Lancini 1969; González–Sponga 1971; Barros 2000; Schargel & García–Pérez 2002; Markezich & Barrio–Amorós 2004; Sánchez *et al.* 2004; .Esqueda & La Marca 2005; Kok 2006; Myers & Schargel 2006; Esqueda *et al.* 2007; Passos *et al.* 2009b, 2013; Esqueda 2011; Prudente & Passos 2012; Natera–Mumaw *et al.* 2015; Montes–Correa et a. 2017; Passos *et al.* 2024) and other related species from Colombia (Pérez–Santos y Moreno 1988; Passos *et al.* 2009a,c,d; Passos *et al.* 2010; Meneses–Pelayo *et al.* 2019), Ecuador (Schargel *et al.* 2013; Salazar–Valenzuela *et al.* 2014; Arteaga *et al.* 2017, 2022) and Brazil (Cuhna & Nascimento 1983; Martins and Oliveira 1993; Passos *et al.* 2005, 2010, 2022).

For each specimen of the species evaluated, including candidate species, detailed descriptions of meristic and morphological characters were available, defined in five informative categories: (1) scutellation, encompassing the head and body; (2) measurements of total length and tail, along with certain cephalic scutellation measurements; (3) coloration in life and/or preserved; (4) structure and systematic characteristics of the hemipenis, and (5) cranial osteology, particularly regarding the maxillary bone and teeth. The latter three depends on items the availability of information, although hemipenial and osteological data were included whenever possible.

With respect to scutellation, the terminology for head shields, dorsal, ventral and subcaudal counts for the genus *Atractus* follows that indicated by Dowling (1951), Savage (1960), Hoogmoed (1980), Myers (2003) and Natera–Mumaw *et al.* (2015).

Due to their taxonomic importance in the genus, some characters are defined as follows: rostral scute in dorsal view, there can be defined as three states: condition A, 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; apical width is less than the distance between nostrils. Condition B, something visible from above, where the distal portion of the scale exceeds the imaginary line, usually narrow toward its distal portion; apical width less or equal than the distance between nostrils, but does not exceed the internasal suture and (C) distinctly visible, with the scale measured between its supralabial contacts, always forming an obtuse angle and above the imaginary straight line between nostrils; apical width > 0.5 than the distance between 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 which can be quantitatively verified if compared with the interocular distance.

Contact between the first supralabial and rostral scute in lateral view; can be short–moderate its contact, occurs when less than or equal the height of the supralabial and ample contact, it happens when it exceeds half the height of the supralabial. Eye–Loreal contact narrow, when it is less than half of the suture between prefrontal and postnasal and wider; when its width is at least half or more of the width of prefrontal suture and postnasal, so it is similar to its width towards the contact with the postnasal. Eye–Prefrontal contact is narrow, smaller than the prefrontal–postnasal suture and extensive when it is greater than half, equal to or larger than the prefrontal–postnasal suture.

Here, we follow the proposal made by Natera–Mumaw *et al.* (2015) for loreal scale, a short loreal (condition A), occurs when its length is less than HED and always in contact with two supralabials (e.g.,, *A. elaps*, *A. latifrons*, and *A. steyermarki*, Savage 1960; Passos *et al.* 2013; Almeida *et al.* 2014); moderate loreal (condition B), occur when its length is greater than HED, but ≤ 1.5 times HED, 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 contacts previously are less than the height of loreal measured at the angle between supralabial and another state occurs when ALO is greater than the margin between loreal and anterior supralabial in contact. Finally, elongated loreal (condition C), occurs when its length is greater than 1.5 times HED, frequently in contact with three supralabials, the margin between loreal and anterior

supralabial is greater than ALO (e.g., *A. torquatus*, *A. ochrosetrus* and *A. heyeri*; Esqueda 2015; Natera-Mumaw *et al.* 2015). However, exist exceptions where with an elongated loreal, only two supralabials are in contact, just as it happens with *A. emigdioi* Sponga, 1971 and *A. multidentatus* Passos, Rivas-Fuenmayor & Barrio-Amorós, 2009 (see also species from Ecuador; Arteaga *et al.* 2017, 2022). In each case mentioned, we can find that the margin between loreal and anterior supralabial can be less or greater than ALO, and relating to condition B, there may be exceptionally individuals with loreal in contact with three supralabial (e.g., *A. ventrimaculatus*, LFE unpublished data). On the other hand, we consider three types of snouts in dorsal view: one short with an FRD equal to or less than 1.5 times END, moderate between 1.5–2 times END, and long greater than 2.5 times END.

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 there are one or two in contact with the supralabial when the mouth is closed in lateral view, therefore, it is defined how many infralabials are in contact with the greats. Sublabial scale, has gone unnoticed but is confused in the descriptions, this scale has two states, in contact with each other, it occurs when separating the middle gular from the posterior contact with the geneials; some authors in the past have considered it a second pair of genials. In fact, in the genus *Geophis*, many of its species often have this characteristic (Downs 1967).

There are two scales that tend to be conflictive and whose usefulness has not been clearly defined (we have personally observed intraspecific variability), gulars and preventral (s). In the first order of ventral arrangement of the head, genials is arranged along the head, posteriorly begins the gular rows and between sublabials (first gular that contacts with geneials). Next, there are several preventral ones, less wide than the ventral ones in the strict sense, in lateral contact with the first dorsal rows behind the parietal ones. The remaining scales of the body, both dorsally and ventrally, have a definition and count that follow what was previously known. Melo–Sampaio and Venegas (2023) when describing a new species from Peru, pointed out the presence of apical pits, an attribute absent in all the other species that we know. Later, it will be necessary for an exhaustive analysis (electron microscopy) to corroborate or not, which makes us assume that it could be more of a conservation artifact. For all measurements and descriptions of cephalic scutellation they are strictly based on the right side of the head but verified on both sides.

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

Here, we consider 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 differentiate 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 longitudinal lines or stripes, these can be narrow (< a dorsal scale) or wide (> a dorsal scale), continuous or discontinuous and arranged in any section of the dorsal region. If we consider the previous arguments, exist three base patterns with variants: one uniform without blotches, dots, or lines–stripes, with 1–3 differentiated dorsal rows (light in preserved and reddish, yellowish, or cream in life); blotched or dotted, where the blotches or dots may or may not be circumscribed, marginalized or not and with one or more lines–stripes an along the body. The ventral surface of the body and tail, consist of three patterns and their variants, the first is considered immaculate, and may sometimes have small scattered dots or blotches but which do not occupy 15 % of the scale surface; blotches or dots disposed horizontally on the scale, giving the impression of one or varies discontinuous lines–stripes, it may be little evident anteriorly and intensifies towards the cloaca; interspersed or irregular blotches, forming blocks that occupy at least 60 % of the scale, sometimes a wide line is observed medially and finally the ventral region is completely stained, less common than the other patterns.

The maxillary bone of one or several specimens was extracted (left sides) and posteriorly cleaned using KOH 3 % by 10 minutes and distilled water for 10 hours. Then scale photos were taken using an Olympus E620 camera fixed to brand stereoscopic 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 (1988), modified by Pesantes (1994) and Zaher (1999) for snakes. Passos *et al.* (2016) replaced the KOH indicated in Pesantes (1994) with distilled water. We adopted both procedures, but in a different way, which was a successful way to achieve organ extension. The most common is that the hemipenes have not been previously partially or totally extracted at the time of conservation of the specimen, being fixed with formaldehyde and/or ethanol, where the first option exists much more rigidity and mostly the tail could have been fixed with little formaldehyde (pers. obs. LFE). 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 emersion stations were established, the first with distilled water at 60 ºC for 2–3 minutes, the second with 3 % KOH for one minute and the third with distilled water at room temperature for 10–30 minutes. If the time is right, you will be able to see the organ in a transparent amber color, otherwise, do stations 1 and 3 again. Before starting to use the burnisher to extend the tissue, it is advisable to inject glycerin + water into the tissue from the base that connects with the muscle. This procedure guarantees that when the burnisher is introduced, it can move due to lubrication, with retraction movements that allow the extension of the hemipenis to be observed. Once the extension of the hemipenis has been achieved, vaseline or glycerin + water is injected and the base is tied, then it is immersed in a solution of 70 % ethanol and alizarin red or candle color for about 10 minutes, and finally it is stored in an Eppendorf with glycerin. With respect to the calcareous structure's ornamentation, we follow to Uzzell (1973) and Harvey and Embert (2008). Qualitative and quantitative description of hemipenial characters follows Dowling and Savage (1960), Uzzell (1973), Zaher (1999), Schargel & Castoe (2003); Myers & Cadle (2003); Zaher and Prudente (2003); Myers & McDowell (2014) and Passos *et al.* (2016). Although the term "diastema" has been considered in the past

for this group of snakes, being a distinctive character (e.g., Passos *et al.* 2009a,c, Passos & Lynch 2010). We will talk about space and/or reduction between the last teeth, following the indicated by Oliveira *et al.* (2023), who recognize that goo–eating dipsadines do not present diastema.

RESULTS

Phylogenetic approach

The final concatenated molecular data set 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 % and 63 sequences in RAG–1: 879 bp, 90 informative sites, 95 singleton, 694 sites preserved, missing data 0–18 %). 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 (Fig. 1) and BI (Fig. 2) analyses are consistent and similar in topology, suggesting that the data provide a robust phylogenetic signal recognized by both methods. However, the node support within *Atractus* was generally <0.5 in for BI. Differences in support between ML and IB may stem from the way these methods handle uncertainty and evolution models (Alfaro *et al.* 2003; Holder & Lewis 2003; Yang and Rannala 2012). In our study, posterior probability values above 0.95 were considered strongly supported, values between 0.7 and 0.95 was moderately supported, and below 0.7 as weakly supported. The monophyly of *Atractus* was well–supported in the ML analysis, where it was divided into two major lineages (ML and BI).

Our time–calibrated phylogeny recovered estimates the most recent common ancestor (TMRCA) of *Atractus* at 22.54 Myr during the Early Miocene (95 % HDP = 19.08–26.23). **Lineage A**, that included clade constitutes by *A. multicinctus* (Jan, 1865), *A.*

lasallei Amaral, 1931 and *A. imperfectus* Myers, 1903. **Lineage B** has a TMRCA of 21.54 Myr (95% HDP = 18.09–24.78) are includes: clade of *A. cerberus* Arteaga et al., 2017, *A. iridescens* Peracca, 1896, *A. esepe* Arteaga et al., 2017, *A. microrhynchus* (Cope, 1868) and *A. dunni* Savage, 1955 with a TMRCA of 15.19 Myr age (95% HDP = 11.89–16.64); clade of *A. zidoki*, *A. savage* and *A. modestus* (Boulenger, 1894) + *A. paudicens* Depax, 1910, *A. typhon* Passos, Mueses-Cisneros, Lynch & Fernandes, 2009 and *A. gigas Myers &* Schargel, 2006 with TMRCA of 13.05 Myr age (95% HDP = 9.04–17.67). All of these diverged 19.46 Myr ago (95 % HDP = 16.44–22.68) of clade constitutes for *A. albuquerquei* Cunha & Nascimento, 1983, *A. elaps* Günther, 1858 and *A. latifrons* Günther, 1868 with a TMRCA age of 16.76 Myr (95 % HDP = 13.22–20.61), clade of *A. riveroi* Roze, 1961, *A. flammigerus* (Boie, 1827) and *A. torquatus* Duméril, Bibron & Duméril, 1854 with a TMRCA of 14.66 Myr (95 % HDP = 11.55–17.86), clade of *A. steyermarki* Roze, 1958 *and A. favae* (De Filippi, 1840)+ *Atractus* sp., *A. boimirin* Passos, Prudente & Lynch, 2016 and *A. badius* (Boie, 1827) with a TMRCA age of 15.29 Myr (95 % HDP = 12.22–16.62) and the clade with a TMRCA of 14.94 Myr ago (95 % HDP = 12.09–18.01) constitutes for *A. atlas* Passos, Scanferla, Melo-Sampaio, Brito, & Almendariz, 2018 and *A. touzeti* Schargel et al., 2013 + *A. ecuadorensis* Savage, 1955, *A. orcesi* Savage, 1955 and *A. duboisi* (Boulenger, 1880) + *A. discovery* Arteaga et al. 2022 and *A. resplendens* Werner, 1901, and that diverged of clade *A. zgap* Arteaga, Quezada, Vieira & Guayasamín, 2022 + *A. ukupacha* Melo-Sampaio, Passos, Prudente, Venegas & Torres-Carvajal, 2021 and *Atractus* sp. + *A. snethlageae* Cunha & Nascimento, 1983, *A. pachacamac* Melo-Sampaio, Passos, Prudente, Venegas & Torres-Carvajal, 2021 and *Atractus* sp. + *A. schach* (Boie, 1827), *A. trefauti* Melo-Sampaio, Passos, Fouquet, Costa-Prudente & Torres-Carvajal, 2019 and *A. dapsilis* Melo-Sampaio, Passos, Fouquet, Costa-Prudente & Torres-Carvajal, 2019. **Lineage C:** TMRCA of 20.18 Myr (95 % HDP = 16.92–23.53), where the clade *A. major* Boulenger, 1894, *A. arangoi* Prado, 1940, *A. fuliginosus* (Hallowell, 1845), *Atractus* aff. *insipidus* and *Atractus* sp. diverged 19.26 Myr ago (95 % HDP = 16.1–22.86) of the clade that includes *A. ochrosetrus* and *A. ventrimaculatus* + *A. trilineatus* Wagler, 1828 with a TMRCA age of 17.18 Myr (95% HDP = 13.61–20.87); while all of these diverged 20.18 Myr ago (95% HDP = 16.92–23.53) of clade *A. roulei* Despax, 1910, *A. michaelbalsani* and *A. carrioni* + *A. taphorni* and *A. emigdioi* + *A. vittatus* and *A. matthewi* + *A. erythromelas*, *Atractus* sp. and *A. meridensis*. With Venezuelan Andean clade of *A. emigdioi* and *A. taphorni* with a TMRCA age of 3.59 Myr (95 %

HDP = 1.92–5.47); Venezuelan Andean clade of *A. mariselae*, *Atractus* sp. and *A. mijaresi* + *A. erythromelas*, *Atractus* sp. and *A. meridensis* Esqueda & La Marca, 2005 with a TMRCA age of 9.55 Myr (95 % HDP = 1.1–12.16); Ecuadorian Pacific clade of *A. roulei*, *A. michaelbalsani* Arteaga et al., 2022 and *A. carrioni* Parker, 1930 with a TMRCA age of 14.31 Myr (95 % HDP = 10.96–17.75).

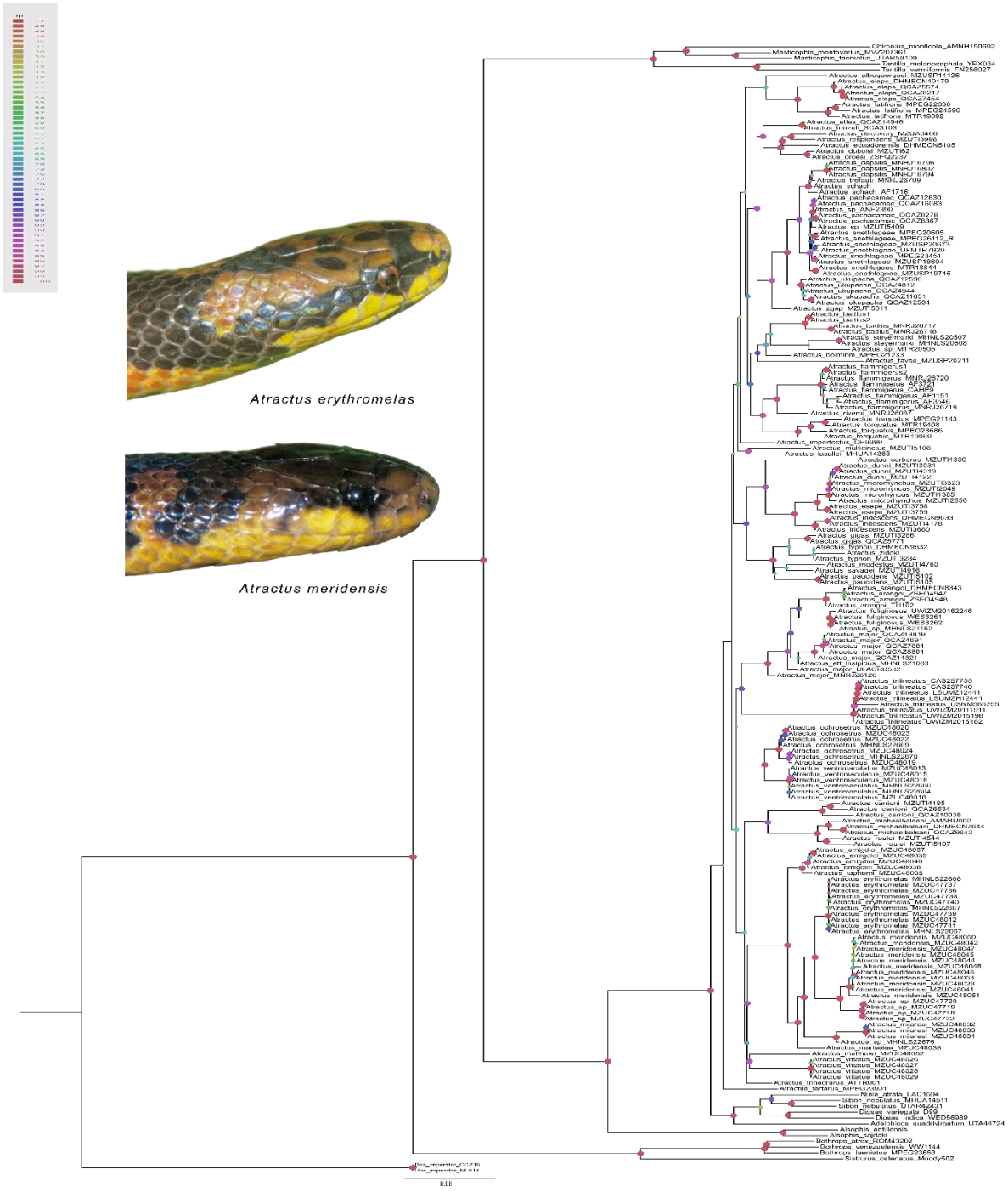

FIGURE 18. Maximum likelihood (ML) tree was estimated of Iqtree, showing the relationships among some South American species of *Atractus*. Information on bootstrap values >70 % in ML are shown, left side.

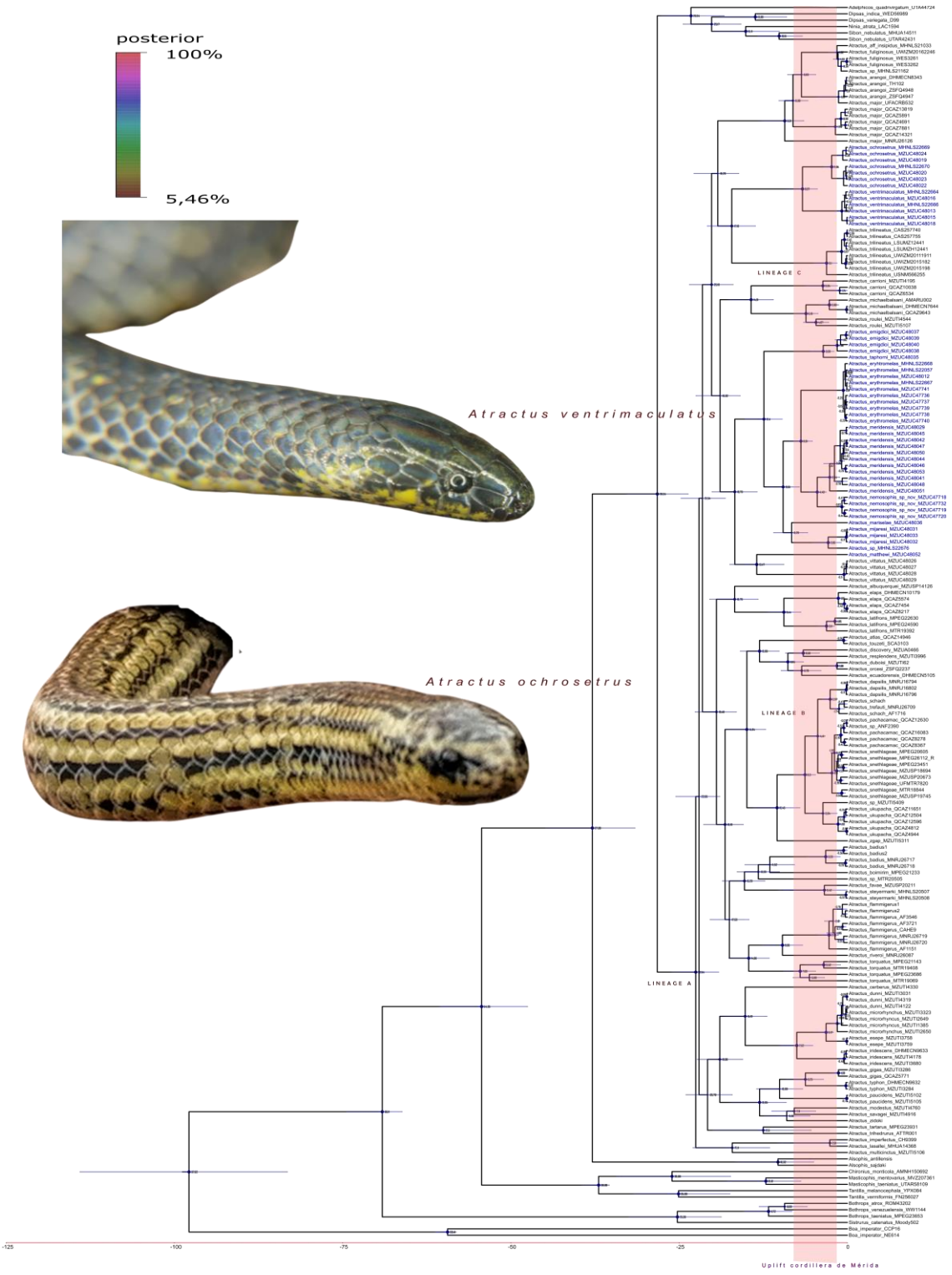

FIGURE 19. Bayesian inference tree along with divergence time estimation under the topology. Beast posterior probability values symbol >0.95 (color circles, see legend). Bars on nodes represent the 95% credibility interval of divergence times.

Uncorrected interspecific genetic p–distances are presented for Cytb (Supp._1_8–9) and ND4 (Supp._1_10–11). In the case of Cytb, mean genetic distances of the Venezuelan mimic species range of 0.072887 ± 0.009654 (*A. erythromelas* vs. *A. meridensis*), 0.078595 ± 0.009556 (*A. erythromelas* vs. *Atractus* sp.) and 0.059436 ± 0.009067 (*A. meridensis* vs. *Atractus* sp.). The sister species *A. ochrosetrus* and *A. ventrimaculatus* possess mean genetic distance range from 0.050887 ± 0.008151. Meanwhile, 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, mean genetic distances varied from 0.05393 ± 0.00933 (*A. erythromelas* vs. *A. meridensis*), 0.06073 ± 0.01055 (*A. erythromelas* vs. *A. meridensis*) and 0.04197 ± 0.00896 (*A. meridensis* vs. *Atractus* sp.); in *A. ochrosetrus* and *A. ventrimaculatus* average 0.06851 ± 0.01075. At the genus level, mean genetic distances average 1.1 % (*A. snethlageae* vs. *A. pachacamac*) and 17 % (*A. ventrimaculatus* vs. *A. vittatus*).

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 0.99 for the training data and 0.97–099 for the test data (Supp._1_12), indicating that the Maxent model effectively predicted the distribution with highly suitable environments for *A. ochrosetrus* and *A. ventrimaculatus* for the three scenarios (Fig. 3). In comparison, according to the statistics of True Skills (TSS) and the operational characteristics of Reception (ROC), they obtained values above 0.72–96 and 0.58–1, respectively (Supp._1_13). In the current scenario (Fig. 3A), *A. ventrimaculatus* occupies an area of 2,212.749 km^2 and is mostly distributed in the montane rainforest of the Northern Andes and intervened areas, with a suitable area of 494.109 km^2 (Suppl._1_14). Meanwhile, *A. ochrosetrus* occupies an area of 751.905 km^2 and is mostly distributed in montane rainforest of the Northern Andes, with a suitable area of 429.66 km^2 (Supp._1_14). 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 (Fig. 3B), unlike the Pliocene 3.2 Myr, during which an expansion of their distribution area is observed (Fig. 3C). Our sorted and verified data suggest that the altitudinal range from *A. ventrimaculatus* varies between 1160–2684 m (494.1 km^2 would correspond to moderate–high suitability areas between 2000–2500 m

a.s.l.) and *A. ochrosetrus* occurs between 1077–3275 m (666 km^2 would correspond to moderate–high suitability areas between 1500–2500 m a.s.l.).

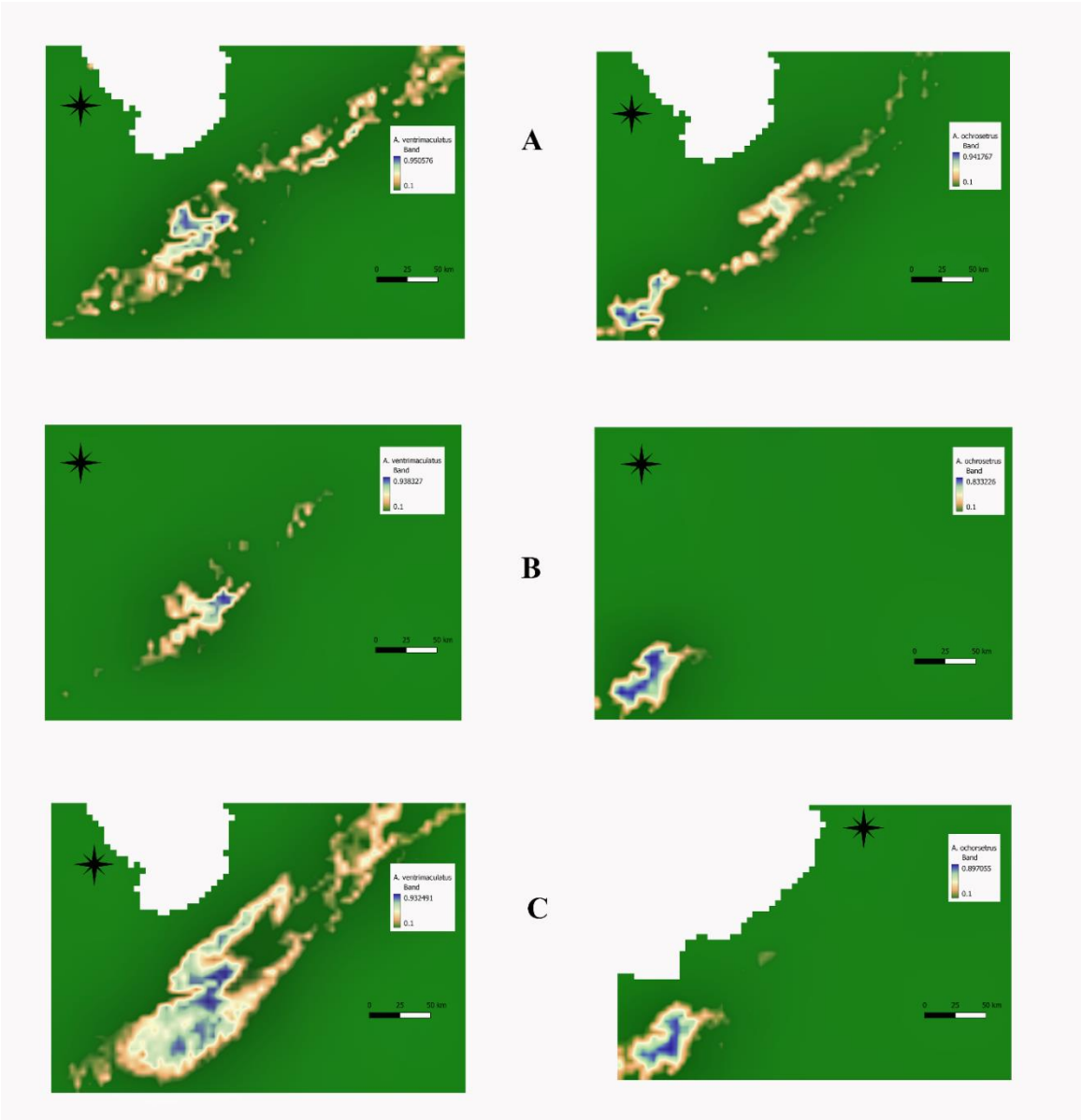

FIGURE 20. Geographic projection of the ecological niche model built for *A. ochrosetrus* and *A. ventrimaculatus* into the climatic scenarios explored. (A) Present scenery; (B) LGM scenery, 21 Kya and (C) Pliocene scenery, 3.2 Myr. The environmental suitability predicted is depicted without umbral defined.

In the Maxent model for each scenario, the Jackknife method was used, and the results may show the weight of different environmental factors that affect the suitability of the habitat for *A. ochrosetrus* and *A. ventrimaculatus* (Supp._1_15). On the other hand, one of the main determining environmental factors in the potential distribution in the three

scenarios was Bio_1 variable, in *A. ochrosetrus* with 49.7-62.2 % (Supp._1_16) and *A. ventrimaculatus* with 46.5-69.7 % (Supp._1_16).

Principal Component Analysis (PCA) revealed that the first three components together explain more than 86–98 % of the variation in the bioclimatic variables across all predicted scenarios. In the current scenario (Fig. 4A), moderate overlap between the niches was observed (D = 0.68, I = 0.77). The PERMANOVA test showed significant differences between the niche centroids (R^2 = 0.14, p = 0.005) (Supp._1_17). The equivalence (p = 0.0139) and similarity tests reveal asymmetry: *A. ochrosetrus* cannot occupy the niche of *A. ventrimaculatus* (p = 0.0024), while the opposite is not significant (p = 0.175). The variables that contribute most to the segregation are the precipitation of the wettest month (BIO13), the annual mean temperature (BIO1), and the temperature seasonality (BIO4) (Suppl._1_18). During the LGM (Fig. 4B), the overlap was null (D ≈ 0, I ≈ 0), and the differences were highly significant (R^2 = 0.68, p = 0.001) (Supp._1_17). The equivalence (p ≈ 2.9e–09) and similarity tests suggest that the niches were completely divergent, with a slight possibility of reciprocal occupation only by *A. ventrimaculatus* (p = 0.0047). During this period, the niche was primarily structured by BIO13, BIO17 (precipitation of the driest quarter), and BIO12 (annual precipitation) (Supp._1_18). While during the Pliocene (Fig. 4C), low overlap was also observed (D = 0.04, I = 0.04) with significant differences (R^2 = 0.49, p = 0.001) (Supp._1_17). The dominant variables were BIO1, BIO13, and BIO4, reflecting a segregation associated with both temperature and water availability (Supp._1_18). These results suggest a historical divergence in the use of climatic space, possibly influenced by differential adaptation to past climates and ecological constraints.

According to our ENM for the current scenario, *A. ochrosetrus* had an EOO of 273.19 km^2 and AOO of 28 km^2 (geocat EOO = 274.454 km^2 and AOO= 40 km^2 to 2 km; Supp._1_19A), while *A. ventrimaculatus* had an EOO= 157.31 km^2 and AOO= 36 km^2 (geocat EOO= 158.232 km^2 and AOO= 48 km^2 to 2 km; Supp._1_19B).

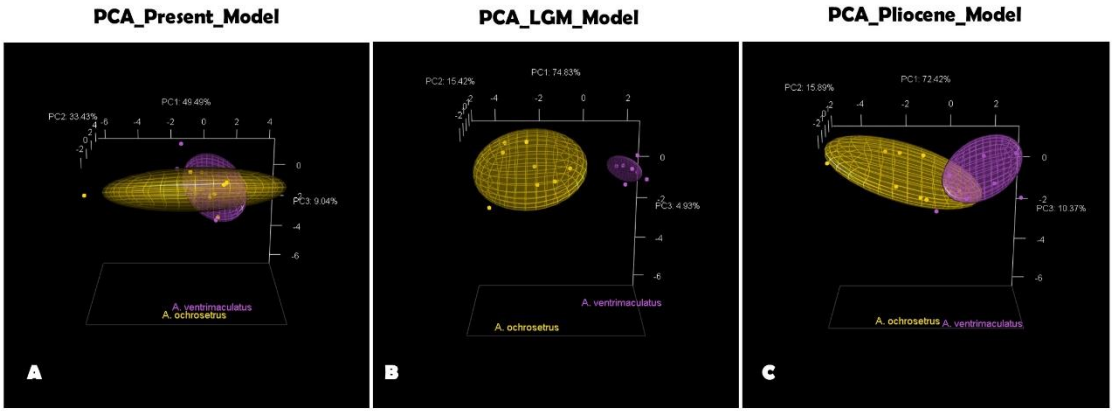

Figure 21. The orthogonal projection of the first three principal components constructed from climatic characterizations of the geographic distribution from *A. erythromelas* and *A. meridensis* for each of the modeled scenarios. The points correspond to the localities characterized based on 6–7 bioclimatic variables and the ellipses correspond to the volumes built from the climatic niches of *A. ochrosetrus* (yellow ellipse) and *A. ventrimaculatus* (violet ellipse). Percentage of explained variance accounted for by each principal component is depicted.

Morphological approach

Historical background between *A. pamplonensis* Amaral, 1937 and *Atractus mijaresi* Esqueda & La Marca, 2005

The species was described base on six specimens and formally accepted in publication as Amaral (1937) (Passos *et al.* 2024: 57). It was later mentioned by Peters and Orejas–Miranda (1970) and Pérez–Santos and Moreno (1988), both of whom noted that the species exhibits a ventral scale count in males >170–183 and in females >170–184 and which corresponds to the original description (Amaral 1937: 220). Meanwhile, *A. mijaresi* was described by Esqueda & La Marca (2005: 16–17, Fig. 15) starting from an adult female of Mucurubá, Mérida state. Conveniently, Passos *et al.* (2024: 57) consider this latter species a synonym of *A. pamplonensis*. Even though their discriminant analysis clearly identifies differences in the ventral scale count in males, they argue that overlap in other characters justifies said decision. However, in light of new evidence molecular (DNAm and DNAn), morphology of the hemipenis and coloration in life allows for the clear distinction of these populations restricted to the northwest of the middle–high basin of the Chama River as a valid taxon, being sufficient arguments to understand that its nomenclatural decision lacks support and was clearly premature.

In fact, some comparative examples in the genus: *A. hoogmoedi* was described by Prudente and Passos (2010), being the only distinctive character with respect to *A. zidoki* Gasc & Rodrigues, 1979, the bifurcation of the spermaticus sulcus and some details in the hemipenial ornamentation. Moreover, they consider such evidence of a cryptic condition, but there is no phylogenetic analysis to support it. When comparing *A. boulengerii* Peracca, 1896 with *A. medusa* Passos, Mueses-Cisneros, Lynch & Fernandes, 2009, the most distinctive character is the ventral count in males 133 vs. 176–189 and geographically close (Passos *et al.* 2009e). When comparing *A. multidentatus* (Fig. 10M) with *A. emigdioi*, the only clear difference is the maxillary teeth count (Passos *et al.* 2009b; Passos *et al.* 2024). When comparing *A. ronnie* Passos, Fernandes & Borges-Nojosa, 2007 with *A. natans* Hoogmoed & Prudente, 2003, the one distinctive character that sets her apart is venter uniformly creamish white vs. venter with a wide central black stripe of irregular width (Passos *et al.* 2007). When comparing *A. gaigeae* (Savage, 1955) with *A. alphonsehogei* Cunha & Nascimento, 1983 and *A. collaris* Peracca, 1897, the only distinguishing feature is the ventral count 200–214 in females and 184–198 in males vs. 163–176 in females and150–162 in males, and 167–186 in females and 145–178 in males, respectively (Passos *et al.* 2018)

On the other hand, Schargel & García–Pérez (2002) indicated as *Atractus* sp. a material from La Carbonera, Mérida state (MCNG R–1898–1904), not mentioned by Passos *et al.* (2024), but in their examined material indicated other material from the same area as *A. pamplonensis,* but deposited in CVULA (here recognized as *A. mijaresi*).

Historical background between *Atractus ventrimaculatus* Boulenger, 1905 and *A. ochrosetrus* Esqueda & La Marca, 2005

A. ventrimaculatus was described by Boulenger (1905) based on several specimens deposited in the British Museum, although in his description the author only indicated a measurement of total length and tail, there was no designation of the holotype or lectotype, so these specimens constitute syntypes (ICZN 1999, art. 72.3). Regarding the type locality, the author indicated “Several specimens from Merida (1630 m.) and Fuqueros (2500 m.), Venezuela, collected by Mr. Briceño”. Although the “Fuqueros” locality has been mentioned for *Anadia bitaeniata* (Harris & Ayala 1987) and *Bolitoglossa orestes* Brame &Wake, 1962 (Fermin *et al.* 2012), its veracity can be difficult to verify so far. Meanwhile, in 1904 the districts that made up the Venezuelan federation had come together to form several states, including Mérida, so the locality

"Merida" indicated by Boulenger (1905) is also considered ambiguous due to the extension or precision of the data, since it cannot be demonstrated whether it refers to the city or the state already consolidated at that time (Monzón-Briceño 2005). Recently, Passos *et al.* (2024: 37) erroneously indicated "Fugueros" instead of "Fuqueros" for the lectotype BMNH 1946.1.7.7 (BMNH 1905.5.31.74; Wallach *et al.* 2014), designated according to them by Roze (1961: 108). When reviewing this last author, he only noted "We have examined the type of this species in BM 1905. 5. 31. 74", which should be considered an assignment of the lectotype (ICZN 1999, art. 74.5). Then the type locality of the species would be the one determined by the lectotype (ICZN 1999, art. 76.2), in this case "Fuqueros", not indicated by Roze (1961: 108), but if Roze (1966: 90). However, this locality is considered uncertain, being difficult to locate geographically and despite the fact that there is a suggestion to select the lectotype based on the verification of its locality for assignments after 1999 and not before (ICZN 1999, art. 74.7., recommendation 74E); Without an option to invalidate a lectotype with a doubtful locality, the remaining syntypes become paralectotypes (see Passos *et al.* 2024). Consequently, only the assignment of a neotype (ICZN 1999, art. 75.3.1) remains to stabilize the type locality of the species, allowing the establishment of a coherent distribution pattern and geographic limits with additional data. Specimen BM 1946.1.5.15 was indicated by Passos *et al.* (2005: 218) as the paratype, later by Passos *et al.* (2009d: 403) as the holotype, and subsequently by Natera–Mumaw *et al.* (2015: 126); This action is erroneous, since the recognition of the holotype can only be established by the author in its original description (ICZN 1999, art. 73.1.3 and art. 74.6). While Wallach *et al.* (2014: 83) indicated this taxon for the state of Zulia based on the record made by Rojas–Runjaic *et al.* (2007), Natera–Mumaw *et al.* (2015: 126) consider it erroneous and retain the endemic status of the species for the state of Mérida; and although Montes–Correa *et al.* (2017: 36) continued to indicate *A. ventrimaculatus* for the serranía of Perijá, in Passos *et al.* (2024: 43) they did not even mention it. On the other hand, these last authors erroneously identify specimen CVULA 7381 as this species, when in fact it corresponds to an undescribed species with 17 dorsal scales at midbody (Esqueda and col. in prep.); they also point out three specimens from Manzano Alto and Tapa Azul slope corresponding to a private collection "CBA", without giving further details, and we assume they refer to César Barrio Amorós (I consider such records doubtful until evidence exists to the contrary); they also misspelled the locality

"Humbo Peak: (EBRG 4052)", its correct locality being Humboldt Peak, Sierra Nevada National Park.

Otherworldly and disconcerting, the amount errors referred to toponymy, identities of specimens, scientific names and locality indicated in the article of Passos *et al.* (2024). With reference to the comparison of *A. ventrimaculatus* and *A. ochrosetrus*, the following: .Esqueda & La Marca (2005) described *A. ochrosetrus* whose type locality is VENEZUELA: Mérida State: Tovar Municipality: on the road from Bailadores to "La Y", El Delgadito, approx. 2600 m.a.s.l., 08°13'06"N, 71°52'26" W (see ICZN 2012, art. 76.1); erroneously indicated as "from the Tovar-Guaraque Highway, municipality of Tovar, sate of Mérida, Venezuela" by Passos *et al.* (2024: 37, p. 122); similarly, specimen ULABG 2409 indicated as *A. ventrimaculatus* and coming from "Táchira: Betania" (Passos *et al.* 2024: 40 and 122), its correct locality is Betania, between El Molino and La "Y" via Estanques–Canaguá, Mérida state, Venezuela (ULABG database, where Luis Felipe Esqueda was Ad Honorem curator of the collection for several years); It is curious but Enrique La Marca, director of the ULABG collection and who in all my years in the collection never provided an incorrect location, does not appear in the acknowledgments.

According to Passos *et al.* (2024) *A. ochrosetrus* should be considered a synonym of *A. ventrimaculatus* due to a misinterpretation of the character states: (1) they point out that the maxillary teeth of the holotype and paratype in Esqueda & La Marca (2005) are 12–14 and not eight as previously stated. We have examined six specimens from the topotypic locality and they present 8–10 maxillary teeth, last tooth reduced (see Fig. 8C–D), while we have examined five specimens of *A. ventrimaculatus* that present 12 maxillary teeth (Fig. 5F–H); (2) these authors point out that the pattern in *A. ventrimaculatus* is highly variable and that the coloration of *A. ochrosetrus* is an oversimplification of the polychromatic one in *A. ventrimaculatus*, based on the interpretation of preserved material and not information on coloration in life. Then, this unsupported argument, not is true: (A) information from Boulenger (1905) and Roze (1966) regarding coloration is based on preserved material. The authors point out the frequency of a dark vertebral line, continuous or discontinuous, but in none of the cases two dark, continuous dorsolateral lines, 1 ½ scales wide, a detail present in all the *A. ochrosetrus* adults that we have observed and notable in the holotype (Esqueda & La Marca 2005: 19, Fig. 19), but not discussed by Passos *et al.* (2024); (B) in *A.*

ventrimaculatus there is frequently a melanic dorsal pattern in life, with the dorsal region being uniformly black, sometimes with small yellow spots, but without a vertebral line being appreciated (absent or not visibly in life, unpublished data LFE 2021; see also La Marca and Soriano 2004: 95, Fig. 42). Another less common pattern consists of a brown to greyish–brown background, without a vertebral line, but with narrow, discontinuous, paravertebral yellow lines bordered by black (Natera–Mumaw *et al.* 2015: 150, Fig. 148), or there may be a brown background with dark and light stretch marks arranged longitudinally (Lancini 1979; Esqueda & La Marca 2005). A third pattern presents a dark brown or greyish–brown back with dark spots, irregularly dispersed, without a defined design. Finally, we found a male specimen with a yellowish–brown back, with scattered dark spots (unpublished data, LFE 2021); (3) in accordance with Passos *et al.* (2024), the information on the hemipenes of both species given by Esqueda & La Marca (2005) is wrong, although they conveniently forget to point out the information provided by Esqueda *et al.* (2007: 92), who correct it and point out some additional details. When reviewing the article by Passos *et al.* (2024: 42), an anecdotal detail reiterated in other descriptions is the absence of a voucher regarding the description of the hemipenis. On the other hand, its description has similar and/or different details to the description indicated by Schargel & Castoe (2003) for *A. ventrimaculatus*, as follows: (A) both descriptions point out the slightly bilobed condition, especially noticeable in the drawing provided by Schargel & Castoe (2003). Although this information is not entirely certain (see later in their redescriptions), the important thing is that the image provided by Esqueda *et al.* (2007: 92, Fig. 5) of the only hemipenis available in *A. ochrosetrus* and that demonstrate its unicapitate condition (see for interpretation of hemipenis, Dowling and Savage 1961; Zaher 1999), conveniently not discussed by Passos *et al.* (2024); (B) although Schargel & Castoe reported the hemipenis as unicapitate in *A. ventrimaculatus*, Passos *et al.* (2024) recognized it as semicapitate, without providing any record of the specimen or drawings or photos; (C) Schargel & Castoe (2003) noted that the organ is bare towards the basal region, a detail omitted in the description of Passos *et al.* (2024); (D) according to Passos *et al.* (2024), *A. ventrimaculatus* would have a capitulum located proximal to sulcus spermaticus bifurcation with similar length as hemipenis body, while the drawing provided by Schargel & García–Pérez (2002: 720, Fig. A) shows a capitulum with greater extension than the body of the hemipenis and would start a little below the bifurcation of the spermatic sulcus, although the rounded shape of the capitulum and the

spinulate fringes are not observed in *A. ochrosetrus* (Esqueda *et al.* 2007: 92, Fig. 5), evenly not discussed by Passos *et al.* (2024).

SPECIES ACCOUNT

***Atractus ventrimaculatus* Boulenger, 1905**

(Figs. 6A–C)

Atractus ventrimaculatus. – Boulenger, 1905; Annals and Magazine of Natural History 15: 455.

Atractus ventrimaculatus. – Passos *et al.* (2024, 32: 1–123).

LECTOTYPE. Adult male, BMNH 1946.1.7.7, (formerly BMNH 1905.5.31.74; Wallach *et al.*, 2014), collected by S. Briceño at locality of Fugueros (not traced, ca. 2,500 m a.s.l.), state of Mérida, Venezuela. Lectotype designated by Roze (1961:108). **Note:** Boulenger indicated "fuqueros", and in no case "Fugueros" as mentioned Passos *et al.* (2024) (see Roze 1966).

PARALECTOTYPES. Five specimens (as stated in the BMNH database): 1946.1.5.12−15, all collected by S. Briceño at municipality of Mérida (08°36′N, 71°09′W; ca. 1,500 m a.s.l.), state of Mérida, Venezuela (Figs. 29–30 in Passos *et al.* 2024). **Note:** In the original description, only appears "Several specimens from Merida (1630 m.) and Fuqueros (2500 m.), Venezuela, collected by Señor Briceño".

NEOTYPE. Adult female, MZUC 48014 (field number LFE 140). Collected by Luis Felipe Esqueda, Santos Bazó and Alexis Peña, July 4, 2021, deposited in the Zoology Museum of the Faculty of Natural and Oceanographic Sciences, University of Concepción, Chile (MZUC). 1.6 km N from Truchicultura Monterrey, El Valle–La Culata road, Mérida, Mérida state, Venezuela, altitude 2477 m a.s.l., 8°41'4.61"N and 71°7'56.51"W.

Definition and diagnosis. – (1) 15 scale rows dorsal to midbody, without reduction; (2) maximum total length 402.37 mm in males and 413.62 in females; (3) sublabials or pseudo–chinchields separate with each other, the distance is greater than the suture of the first pair of infralabials; (4) unilobed, unicapitate, semicalyculate hemipenis; (5) 11–12 maxillary teeth, the last one not reduced; usually a weakly defined lateral process,

arranged horizontally to the maxilla and situated between the 6th to 9th teeth; (6) supralabial in contact with anterior temporal and postocular is wider, with its upper margins asymmetrical; (7) 8(4,5) or 7(3,4) supralabials; (8) seven infralabials, four in contact with geneials; (9) postnasal similar in size to prenasal; (10) rostral slightly visible from above; in frontal view sub–trapezoidal, as high as wide or wider, narrow apical edge, < 0.5 distance between nostrils and concave lateral margins; (11) first supralabial small, higher than wide, short–moderate supralabial–rostral contact; (12) loreal moderate–long, in contact with three o two supralabials; (13) frontal scute irregularly hexagonal, usually longer than wide; (14) moderate internasals, longer than wide, two or less of the prefrontal suture; (15) moderate– snout, frontal–rostral distance 1.93–3.44 mm; (16) head indifferent from the neck, strongly compressed in dorsal view, being subtriangular and with a rounded snout, relation AEE–AEN 43.2–58.9 % in females, 37.4–52.6 %; (17) in life, very frequently the dorsal pattern observed has a melanistic background, in which the black vertebral line is indistinguishable, only present or absent in preserved specimens. Other patterns have a light brown, grayish–brown, and yellowish–brown dorsal background, with dark spots sometimes bordered in black and distributed longitudinally, a black vertebral line is not noticeable. In none of the detected patterns are there one or more dorsolateral lines; only in certain individuals are there two narrow yellow paravertebral lines; (18) in life, ventral surface has an intense yellowish background, with extensive black spots that almost cover the entire surface on certain sides; (19) usually yellow stretch marks on the dorsocaudals, ventral surface of the tail yellow, moderate or strongly stained with black; (20) thick tail, short–moderate and ends in a blunt tip, 11–15.7% SVL in males and 4.7–11.4% SVL in females; (21) 138–153 ventrals in males, 147–161 in females; (22) 18–22 subcaudals in males, 13–20 in females.

Description on museum material. – Maximum total length in males 402.37 mm and in 413.62 mm in females (SVL 246.68–364.778 in males and 282.3–382.6 in females); tail length 28.43–42.29 mm (n= 10) and 17.87–36.44 (n=10); head length in males 8.43–12.04 (n=10, $\bar{x}$= 10.37 ± 1.4159) in males and 7.12–12.04 (n=10, $\bar{x}$= 10.01 ± 1.5244) in females; head width 6.59–9.95 mm (n=10, $\bar{x}$= 8.11 ± 1.17) and 5.78–8.9 mm (n=10, $\bar{x}$= 7.75 ± 0.98097) in females. Head in dorsal view: longer than wide, undifferentiated from the neck, compressed (ID/IND relation 40.1–52.6 % in males and 37.4–58.9 % in females; rounded snout. Rostral slightly visible from above, in frontal view sub–

trapezoidal, as wide as high or slightly wider, concave lateral margins, narrow apical edge (< 0.5 times END) and exceeds the imaginary straight line between the nostrils (Fig. 5D); two internasals, higher than wide, internasal suture 2.4–4.7 times in relation to the prefrontal suture, no sinastria; two prefrontals, frontal–rostral distance shorter than frontal length, prefrontal–postnasal contact shorter than the eye–prefrontal contact; frontal scute irregularly hexagonal, longer than wide (n=15) or wider than long (n=5) (Fig. 5A); supraoculars tetragonal, much wider posteriorly; two parietals, parietal suture 0.29–0.34 of HL in males and 0.29–0.41 of HL in females. In lateral view: circular eye, 1.26–1.85 mm HED in males and 0.97–1.64 mm in females; elongated snout, END 2.38–3.55 mm in males and 2.27–3.43 mm in females; prenasal and postnasal more or less similar in size, nostril situated above the prenasal edge; postnasal–loreal contact wider than eye–loreal contact; loreal elongated, higher anteriorly, in contact with two or three supralabials (usually three); two postoculars, the upper quadrangular and widened, the lower elongated (Fig. 5B); temporal formula 1+2, the first temporal well elongated, almost equal to END, short first postocular–temporal contact and wide second postocular contact; 8(4,5), 8 (3,4) or 7(3,4) supralabials; first supralabial higher than wide, barely differentiated in size compared to the second, short or moderate supralabial–rostral contact; supralabial that contacts with anterior temporal and pentagonal postocular usually widened, with its upper margins asymmetrical. Ventrally, mental subtriangular, wider than long; seven infralabials, four in contact with the pair of geneials (Fig. 5C); sublabials or pseudo–chinschields separated, spacing greater than or equal to the suture of the first pair of infralabials; geneials elongated, suture 0.64–0.95 times longer than END in males and 0.44–0.9 times longer than in females (less common, shorter than END); 4–5 gulars; 1–3 preventrals; 138–153 ventrals in males (n=11, $\bar{x}$= 147.27 ± 4.7768) 147–161 in females (n=10, $\bar{x}$= 152.7 ± 4.9187); 18–22 subcaudals in males (n=10, $\bar{x}$= 20.2 ± 1.5491) and 13–20 in females (n=10, $\bar{x}$= 15.88 ± 2.7131).Thick tail, 4–8 dorsocaudals at the level of the sixth subcaudal; entire cloacal scale, 1.76–4.02 mm long in males and 2.52–4.26 mm in females. 15 dorsal scales at the midbody, without reduction; body thickness at the midbody 10.5–15.87 mm in males (n=10, $\bar{x}$= 11.7 mm ± 2.0377) and 8.76–16.09 in females (n=10, $\bar{x}$= 12.5 mm ± 2.1328).

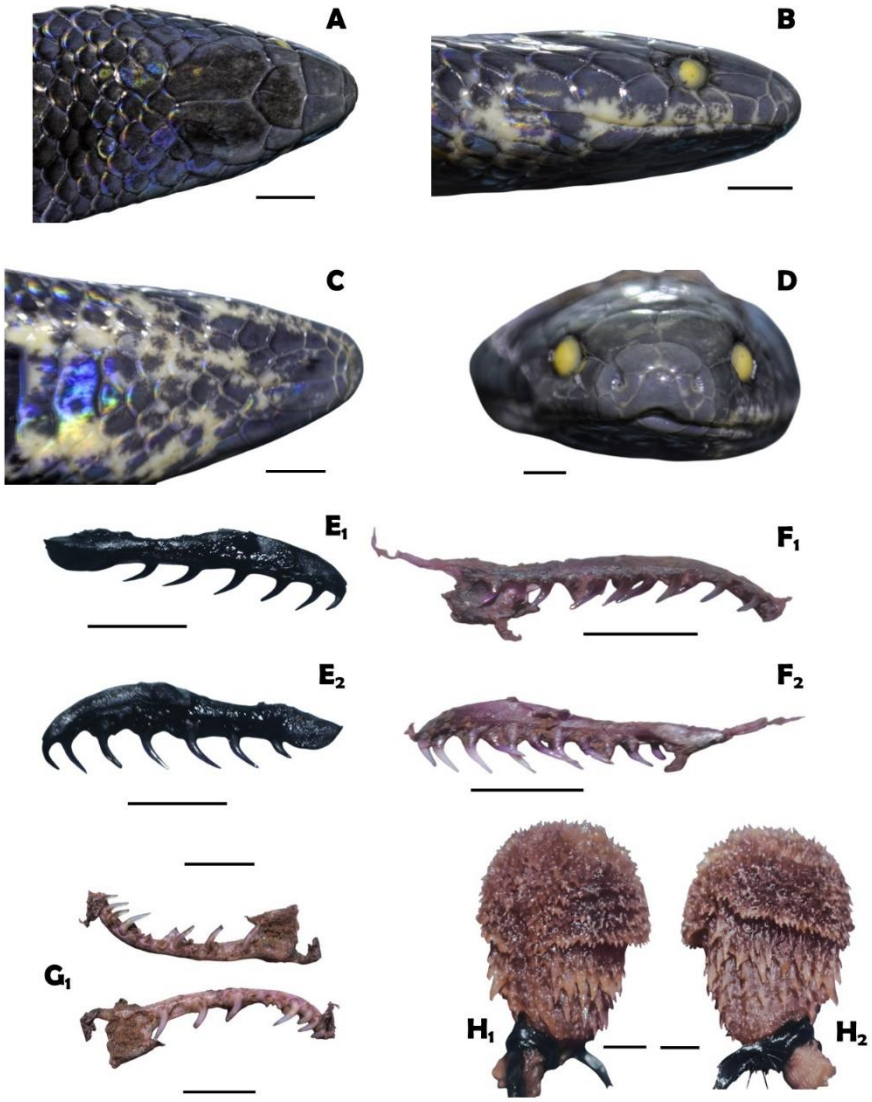

Figure 22. Morphological details related to *Atractus ventrimaculatus*. Specimen MZUC 48014, (A) dorsal view of head; (B) lateral view of head; ventral view of head and (D) frontal view of the frontal scale. Specimen MZUC 48013, internal and external view of the maxilla (E1–E2). Specimen MZUC 48015, internal and external view of the maxilla (F1–F2) and Specimen MZUC 48016, internal and external view of the maxilla (G1–G2). Specimen MZUC 48013, sulcate and asulcate view of hemipenis (H_1–H_2).

Maxillar bone. – Between teeth 1–2 narrow, then it can be somewhat or well arched; 4.49–5.4 mm long; lateral process moderately defined or pronounced, but horizontally arranged with respect to the bone, located between the seventh and ninth tooth (Fig. 5E–G); 11–12 maxillary teeth (n=5), curved, the last slightly more spaced (not reduced).

Hemipenis (everted organs n= 1, MZUC 48013). – Unilobed, unicapitate and semicalyculate organ (Fig. 5H). Well–defined capitulum, extensively larger than the rest

of the hemipenis, completely encircled by spinulate flounces. Body of the hemipenis provided with rows of long spines, with insertions of small spines; capitular groove definite (in sulcate and asulcate region); bifurcation of sulcus spermaticus occurs on the capitulum. Asulcate region covered with the same pattern of long and small spines, but with a higher frequency of long spines. The base of the hemipenis is nude, with only small spinules insertions; basal naked pocket not defined.

Coloration in life. – The information described by Boulenger (1905) and Roze (1966) is based on preserved specimens. La Marca and Soriano (2004, fig. 42) indicated that the dorsal coloration is uniform, dark brown or almost black, and the belly is yellow with numerous dark brown spots. Whereas Esqueda & La Marca (2005) noted the belly as yellow with black spots. This taxon frequently exhibits a melanistic pattern on the dorsal side of the body and head (Fig. 6A), an inconspicuous or absent black vertebral line (observable in preserved specimens); sometimes, towards the dorsocaudal region, some yellow striated spots are observed (Fig. 6B).The ventral surface of the body has a bright yellow background, heavily spotted with black; immaculate or weakly laterally spotted cloacal scale; yellow subcaudals, weakly or heavily spotted with dark brown or black. A pattern that had not yet been observed in life, the preserved specimens exhibit a dorsum adorned with dark brown spots, irregularly dispersed, conspicuous, cream–margined, and sometimes concentrated laterally or towards the vertebral region (see Esqueda & La Marca 2005: fig 24; Passos *et al.* 2024: fig 29). Dorsal coloration of the head similar to the body background, the supralabials intense yellow, with a wider spot behind the eye (Fig. 6C). In certain individuals, yellow stretch marks have been observed in life towards the dorsocaudal region (Natera–Mumaw *et al.* 2015: fig. 148), similar to those observed in *Atractus matthewi* Barrio-Amorós & Markezich, 2004 (LFE unpublished data 2021).

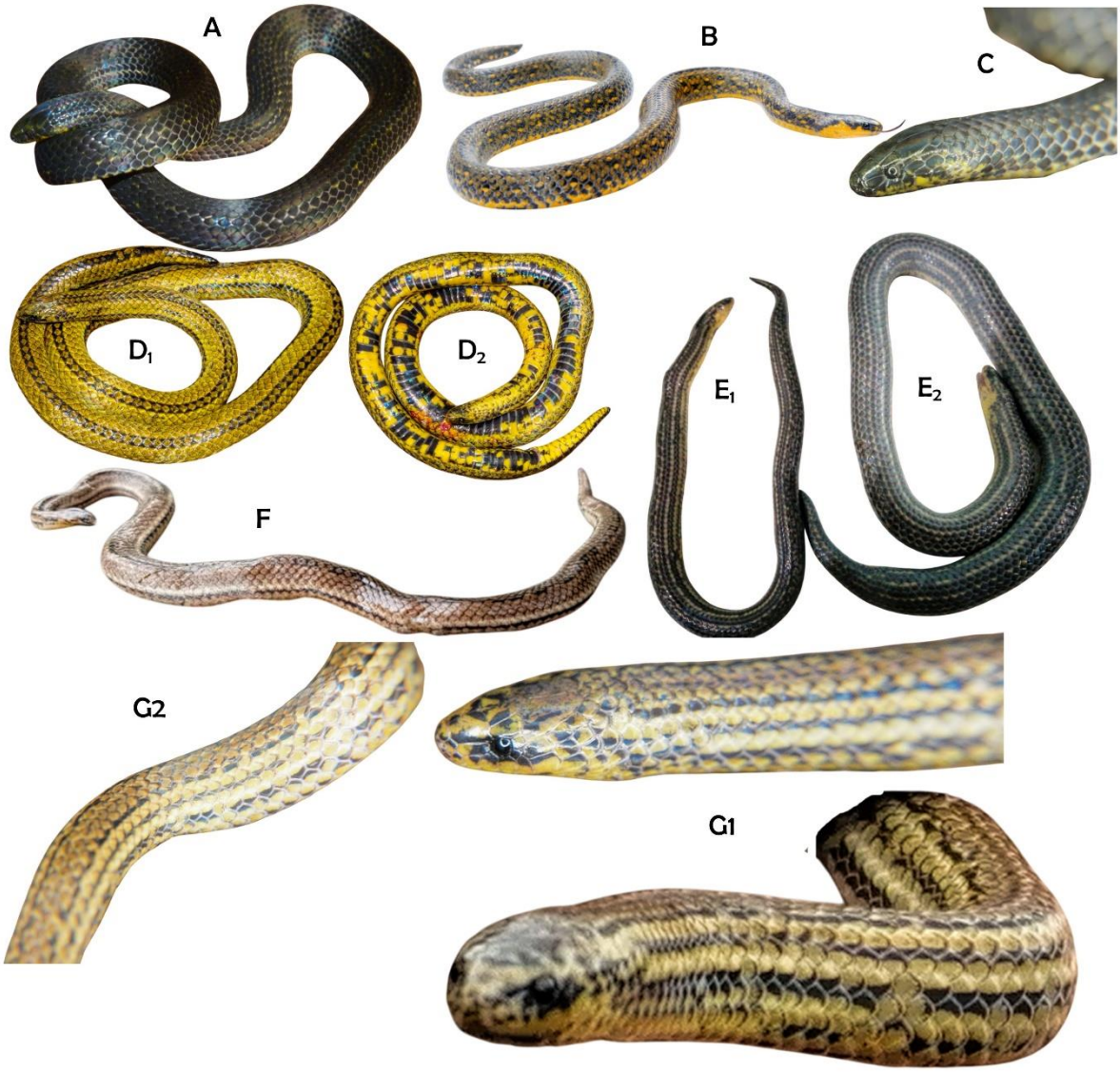

FIGURE 23. Details of the coloration in life of *A. ventrimaculatus*: (A) specimen MZUC 48018, posterior to the Truchicultura Monterrey, way El Valle–La Culata, Mérida state, Venezuela. Dorsal view of the body and head showing the melanic pattern. ® Luis Felipe Esqueda; (B) adult individual s/n, city of Mérida, with the brown–yellowish pattern, without lines and with scattered spots by Daniel Quihua; (C) specimen MZUC 48015, dorsal view of head showing the contact of supralabials with loreal by Luis Felipe Esqueda. Details of the coloration in life of *A. ochrosetrus*: (D_1–D_2) adult female collected 9.3 km on the EL Zumbador–Queniquea road. Dorsal and ventral views of body and head by Enrique La Marca; (E_1–E_2) specimens MZUC 48020–21, collected in La M (curve), after Bailadores near of the road way Las Porqueras, Mérida state, Venezuela. Dorsal and ventral view of the body and head by Luis Felipe Esqueda; (F) individual s/n, found dead on the road near the Páramo Batallón y La Negra National Park, Táchira state. Dorsal view shows the presence of dorsolateral lines by Jairo Rodríguez; (G_1–G_2) specimen MZUC 48022, collected in Potrero Grande, after the M (curve), way Las Porqueras,

Mérida state, Venezuela. Lateral view of body and view of head and anterior third of body, the presence of dorsolateral and paravertebral lines is observed. ® Luis Felipe Esqueda.

Distribution and natural history. – This taxon is considered endemic to the cordillera de Mérida. It is found in sympatry with *A. erythromelas* Boulenger, 1903 along the middle basin of the Chama River, heading towards La Culata from Jají, passing through the city of Mérida (Chorros de Milla and Santa Rosa above) and El Valle; then it exhibits some disjunct populations towards La Mucuy high towards the Sierra Nevada Park (Fig. 7). Altitudinally, it occupies the montane semideciduous forest floor and the Andean cloud forest, between 1700 and 3250 m. Here we define that the reference locality with respect to its topotypical area, but avoiding erroneous or very general localities, is the region that includes El Valle, specifically towards Truchicultura San Javier and its surroundings, and that varies in altitude from 2000 to 2500 m a.s.l.

So far, we have not observed any individuals active during the day. Our findings have been under moderately sized rocks (>20 kg), in anthropized environments, consisting of high–altitude grasslands (e.g., kikuyu). Near the San Javier Trout Farm, El Valle, Mérida state (2477 m a.s.l., 8°41'4.61"N and 71° 7'6.51"W), we found two specimens together MZUC 48017–48018 during the day under a rock (collected July 4, 2025). Another individual MZUC 48013 was found around an egg communal nest of *Anadia bitaeniata* Boulenger, 1903.

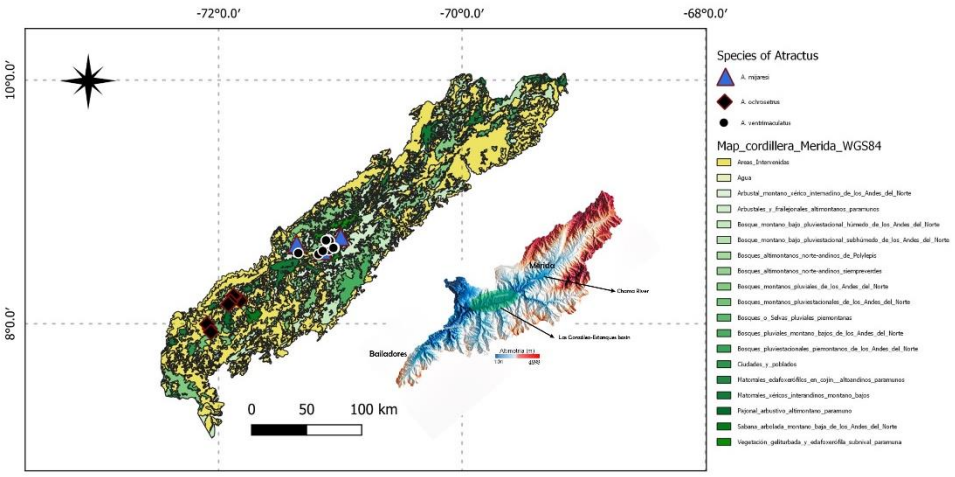

FIGURE 24. Map of the cordillera de Mérida showing the distribution from *A. ochrosetrus*, *A. ventrimaculatus* and *A. mijaresi*. Base vegetation map ® Eulogio Chacón Moreno.

Conservation status. – Niche modeling using MaxEnt yielded a predicted suitable distribution area for the species of 2,212.749 km^2, consisting mostly of montane rainforests of the northern Andes (494.109 km^2) and intervened areas (515.592 km^2) (Supplementary_1_Table 14). Our calculations in R according to IUCN, indicate an area EOO of 157.31 km^2 (geocat EOO =158.232 km^2) and AOO of 36 km^2 (geocat AOO= 48 km^2), https://geocat.iucnredlist.org/ (Supplementary_1_Table 19B). 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 (Ataroff & Naranjo 2009). This eco–geographical 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 (Hendrix *et al.* 2008), particularly in tropical mountain ecosystems that exhibit high rates of endemism in relatively small areas (Lavelle & Lapied 2003). In consequence, considering the IUCN conservation criteria (IUCN 2012) and the vulnerability index of reptile species (IVER, Esqueda & La Marca 2015), *Atractus ventrimaculatus* it must be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv).

Atractus ochrosetrus Esqueda & La Marca, 2005 comb.nov.

(Figs. 8D–G)

Atractus ochrosetrus.– Esqueda & La Marca (2005: 18).

Atractus ventrimaculatus.– Passos *et al.* (2024: 37).

HOLOTYPE. Adult male, ULABG 4698, coleccionado por Enrique La Marca el 12 de enero de 1999, depositado en la Colección de Anfibios y Reptiles, Laboratorio de Biogeografía, de la Universidad de Los Andes, Mérida, Venezuela (Esqueda & La Marca 2005).

Definition and diagnosis

(1) 15 scale rows dorsal to midbody, without reduction; (2) maximum total length 376.75 mm in males and 421.65 in females; (3) usually sublabials or pseudo–chinchields in contact with each other, when separate the width does not exceed the suture of the first pair of infralabials; (4) unilobed, semicapitate, semicalyculate hemipenis, capitular groove defined; (5) 8–10 maxillary teeth, usually last reduced; well–defined lateral process, disposed obliquely and located at the level of the 5–8 teeth; (6) normally supralabial in contact with anterior temporal and postocular is narrow, with its upper margins symmetrical; (7) frequently 8(4,5) supralabials, less common seven; (8) seven infralabials, four in contact with geneials; (9) postnasal enlarged compared to prenasal; (10) rostral barely visible from above; in frontal view subtrapezoidal, taller than wide and slightly concave lateral margins; normally its apical edge is wide, > 0.5 the distance between nostrils and exceeds the imaginary straight line between nostrils; (11) first supralabial small, short supralabial–rostral contact; (12) loreal moderate–long, usually in contact with three supralabials; (13) frontal subtriangular or subhexagonal, longer than wide, convex anterior margins; (14) moderate internasal, longer than wide, two or less than prefrontal suture; (15) short–moderate snout, frontal–rostral distance 1.61–2.97 mm; (16) head indifferent from the neck, compressed in dorsal view, being subtriangular and with a rounded snout, relation ID–ND 38.4–44.3 % in females and 36.6–44.6 % in males; (17) in life, dorsal background frequently chestnut–yellow, less observed yellowish–brown or melanic, but with dorsolateral lines always visible. Black dorsolateral lines between the 3th to 5th dorsal row. Dark vertebral line defined, sometimes narrow and discontinuous and at other times wide and continuous. Apart from the dorsolateral lines, there may be narrow, continuous or discontinuous black paravertebral lines, and sometimes bordered with cream; (18) pale or intense yellow ventral background of the body, heavily spotted with black, forming large intercalated spaces, rectangular and that sometimes occupy completely the scale in life. Yellow subcaudals, immaculate or weakly pigmented of black; (19) thick tail, short–moderate and ends in a blunt tip, 10.6–13.2 SVL in males and 6.6–9.1 SVL in females; (21) 144–152 ventrals in males, 146–156 in females; (22) 21–20 subcaudals in males, 14–18 in females.

The only species with certain similar attributes that inhabit the cordillera de Mérida are A. taphorni and *A. emigdioi*, but they are differentiated by both having a non–capitate

(differentiated) and slightly bilobed hemipenis; usually seven supralabials and two in contact with the loreal vs. *A. ochrosetrus* which has a unicapitate (differentiated) and non–bilobed hemipenis; eight supralabials and three in contact with the loreal. On the other hand, our phylogenetic analysis suggests that the sister species of *A. ochrosetrus* is *A. ventrimaculatus*, which is differentiated by a usually melanic life pattern, with the vertebral line absent or inconspicuous in life (if exists, visible in preserved), without dorsolateral lines; sublabials or pseudo–chinchields separated from each other and usually the subcaudals are moderately to heavily pigmented black (other comparative details, see Table 1).

Description on museum material

Maximum total length in males 376.75 mm and in 421.65 mm in females (SVL in males 288.6–340.57 mm and in females 290.71–370.87 mm); tail length 33.4–39.85 mm in males (n=4) and 19.27–35.09 mm in females (n=5); head length in males 8.06–11.12 mm (n=4) and 7.73–11.9 mm in females (n=5); head width in males 7–8.51 (n=4) and 5.75–8.36 mm in females (n=5). Head in dorsal view: longer than wide, undifferentiated from the neck, compressed (ID/IND relation 36.6–37.9 % in males and 38.4–43.6); rounded snout. Rostral barely visible from above, subtriangular or subtrapezoidal in frontal view, as high as wide, straight lateral margins, narrow apical edge that internasals (< 0.5 END) and well exceeding the imaginary straight line between nostrils (Fig. 8A_4–B_4); two internasals, longer than wide, internasal suture two or less than prefrontal suture, no sinastria; two prefrontals, widest posteriorly, frontal–rostral distance shorter than frontal length, prefrontal–postnasal contact shorter than eye–loreal contact (unusually similar); frontal shield subtriangular (Fig. 8A_1–B_1), with anterior margins straight or slightly convex, usually slightly longer than wide; two parietals, parietal suture longer than frontal length; two supraoculars elongate (~0.75 END). In lateral view: anteriorly arched or slightly arched, with a slightly rounded snout; frequently 8(4,5) supralabials (n=12), less common 7(3,4) (n=3); first supralabial small, supralabial–rostral contact short; supralabial in contact with anterior temporal and narrow postocular, with its upper margins symmetrical (Fig. 8A_2–B_2); postnasal irregularly hexagonal and vertically arranged, enlarged relative to prenasal; loreal elongate, slightly or more high anteriorly, irregularly hexagonal and in contact with three supralabials (less common two); two postoculars, first rectangular, second the same or just slightly taller; temporal formula 1+2, without distinct supratemporals, 1st

temporal elongated (~0.85 DON). Ventrally: mental subtriangular, wider than long; seven infralabials, four in contact with genials; frequently sublabials or pseudo–chinchields in contact with each other (n=8, Fig. $8A_3$–B_3), rarely separate, but their width does not exceed the suture of the single pair of infralabials (n=6); 1–3 gulars and 1–3 preventrals; ventrals in males 144–152 (n=6, $\bar{x}$= 147.6 ± 3.7815) and 146–156 (n=7, $\bar{x}$= 152.5 ± 4.1352) in females; subcaudals divided, count in males 20–22 (n=6, $\bar{x}$= 21 ± 0.707) and 14–26 (n=7, $\bar{x}$= 17.6 ± 4.3204) in females. Thick tail, 6.6–9.1 % in females and 10.6–13.2 % in males; eight dorsocaudals at the level of the sixth subcaudal; cloacal scale entire, 1.43–2.35 mm in males and 2.32–3.89 mm in females. 15 rows of dorsal scales in the middle of the body, without reduction towards the neck and tail.

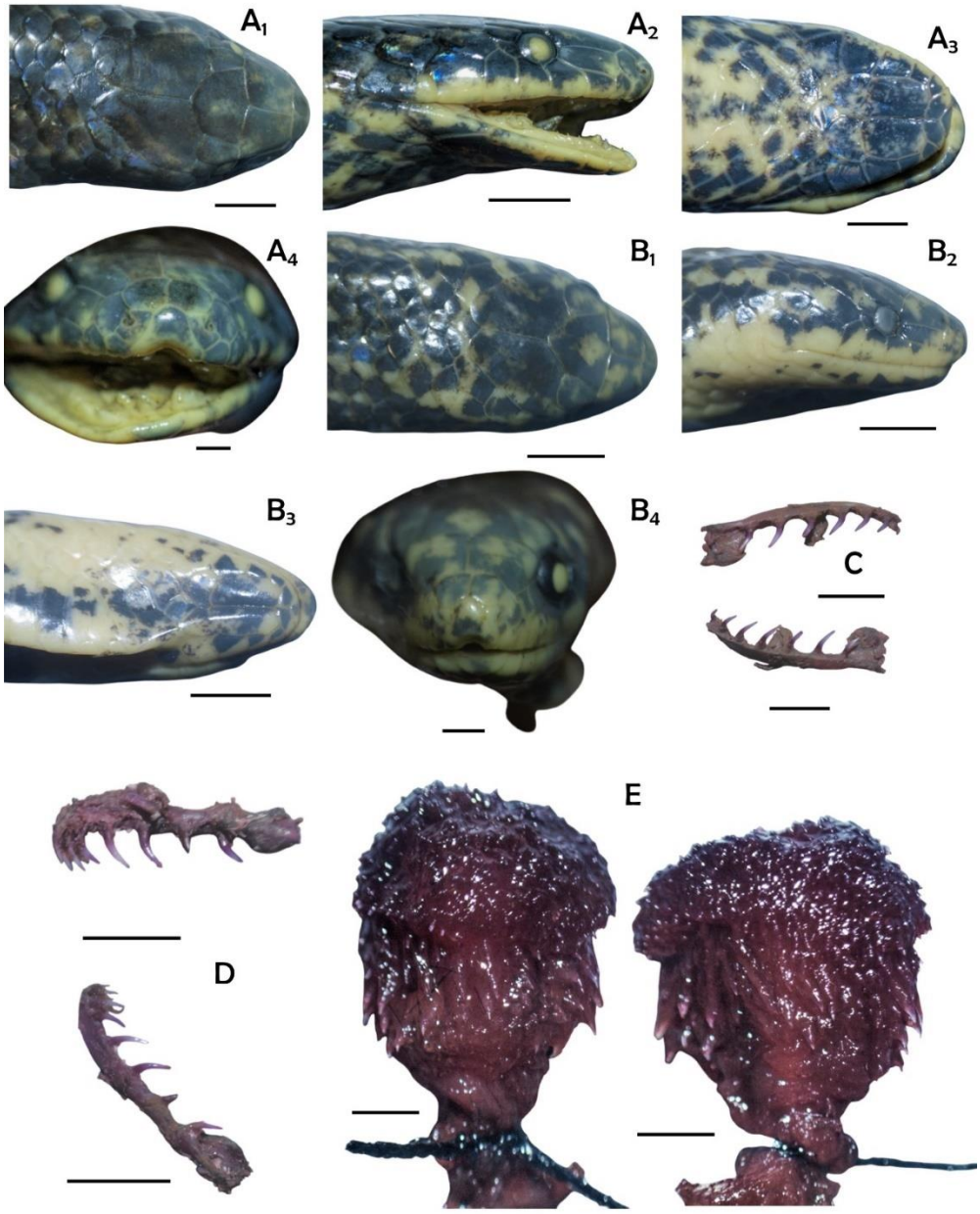

FIGURE 25. Morphological details related to *Atractus ochrosetrus*. Specimen MZUC 48014, (A) dorsal view of head; (B) lateral view of head; ventral view of the and (D) frontal view of the frontal scale. Specimen MZUC 48013, internal and external view of the maxilla (F_1–F_2). Specimen MZUC 48015, internal and external view of the maxilla (G_1–G_2) and Specimen MZUC 48016, internal and external view of the maxilla (H_1–H_2). Specimen MZUC 48013, sulcate and asulcate view of hemipenis (I_1–I_2).

Maxillar bone

Weakly arched, at the level of the widened lateral process; 3.8–4.7 mm in length; well–developed lateral process, situated between the sixth and eighth tooth, arranged

obliquely with respect to the bone. 8–10 maxillary teeth, the last one reduced in size (Fig. 8C–D). Posterior projection visible.

Hemipenis (everted organs n= 1, MZUC 48023)

Unilobed, unicapitate, and semicalyculate organ. Well–defined capitulum, no longer than the body of the hemipenis, completely encircled by spinulate flounces (Fig. 8E). capitular groove definite (sulcate and asulcate sides); bifurcation of sulcus spermaticus occurs on the capitulum. Body of the hemipenis provided with rows of long spines, with insertions of small spines; nude basal region, except for a few small spinules and visible transverse plicae. Asulcate region covered of long spines, interspersed and decreasing in size towards the hemipenial base.

Information of coloration (in life)

The dorsal pattern in common life observed in most of the collected specimens has a chestnut–yellow background with three longitudinal black lines. A vertebral stripe less than one scale wide, generally continuous to the end of the tail. On each side of the body, exist a wide black stripe (at least equivalent to a scale), situated between the second–third or third–fourth dorsal rows, being able to be marginalized or not, on both sides, by a whitish line and that extends until the tail (Figs. 6D_1, F). In other individuals, we can observe two additional longitudinal black lines on the paravertebral region, continuous (Fig. 6E_1–E_2) or discontinuous (Fig. 6G_1–G_2), and that extend until the tail. The specimen ULABG 6745 (Fig. 6D_1), adult female, exhibits the common chestnut–yellow pattern with three longitudinal black lines, but the vertebral line between scales 7–9 is partitioned into continuous triangular strokes on the sides and the middle scale chestnut–yellow (here defined as a rhomboidal vertebral line with black lateral strokes and chestnut–yellow center). The specimen MZUC 48023 present a more melanistic coloration, although the dorsolateral lines are notably visible. Dorsal background of the head similar to the body; supralabials yellow with black spots above (Fig. 6G_1). The ventral region of the body is yellowish, heavily stained black, forming blocks of spots, irregularly interspersed, and sometimes covering the entire scale (Fig. 6D_2); cloacal shield yellowish, being able to be immaculate (n= 5) or spotted with black (n=7). The yellowish subcaudals, usually immaculate or weakly speckled of black (n= 8), although less common can be a pattern moderate or strongly spotted of black (n= 4). The head is

yellowish ventrally, with the first four infralabials, mental and geneials strongly spotted with black.

Distribution and natural history

Like *A. ventrimaculatus*, it is an endemic species of the cordillera de Mérida. It extends southeast from the cordillera de Mérida, corresponding to the upper basins of the Uribante, El Valle, La Grita, and Mocoties rivers, Táchira and Mérida states, respectively (Fig. 7). Its altitudinal range varies between 2000–3000 m a.s.l., corresponding to the Andean cloud forest, which has largely been converted into grasslands for high–altitude livestock farming. It is very likely that the elfin cloud forest also inhabits the drier slopes between 2000–2700 m a.s.l. and the upper limit of the montane Andean semideciduous forest between 1500–2000 m a.s.l. (Ataroff and Sarmiento 2004).

The species is found in sympatry with *A. tamaensis* and another *Atractus* sp., currently under study (Esqueda *et al.* in prep.), although less frequently. Although the material collected by us was under rocks, an adult female specimen ULABG 6745 was recently found run over in the morning, in a cloud forest, 9.3 km on the El Zumbador to Queniquea road (2705 m, 7°57'28.7"N and 72°4'21"W). Therefore, it is likely that the species is cathemeral, being active during the day or night.

Conservation status

Niche modeling using MaxEnt yielded a predicted suitable distribution area for the species of 751.905 km^2, consisting mostly of montane rainforests of the northern Andes (429.66 km^2) and intervened areas (85.932 km^2) (Supplementary_1_Table 14). According to IUCN, an area EOO 273.19 (geocat EOO 274.454 km^2) and AOO 28 km^2 (geocat AOO= 40 km^2), https://geocat.iucnredlist.org/editor (Supplementary_1_Table 19A). 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 (Ataroff & Naranjo 2009). This eco–geographical 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 (Hendrix *et al.* 2008), particularly in tropical mountain ecosystems that exhibit high rates of endemism in relatively small areas (Lavelle & Lapied 2003). In consequence, considering the IUCN conservation criteria (IUCN 2012) and the vulnerability index of reptile species (IVER, Esqueda & La Marca 2015), *Atractus ochrosetrus* it must be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv).

***Atractus mijaresi* Esqueda & La Marca, 2005** comb.nov.

(Figs. 10A–D)

Atractus mijaresi.– Esqueda & La Marca (2005: 16–17).

Atractus pamplonensis.– Passos *et al.* (2024: 51).

HOLOTYPE. Adult female, ULABG 4697, coleccionada por Néstor Jáuregui el 5 de mayo de 1997, depositada en la Colección de Anfibios y Reptiles, Laboratorio de Biogeografía, de la Universidad de Los Andes, Mérida, Venezuela (Esqueda & La Marca 2005).

TYPE LOCALITY. "Mucurubá, Mérida state".

Definition and diagnosis

(1) 17 scale rows dorsal to midbody, without reduction; (2) maximum total length 331.9 mm in males and 377.8 in females; (3) rostral barely visible from above; subtrapezoidal frontal view, wider than high; short–moderate apical edge, < 0.5 END, equal or barely exceeding the imaginary margin between nostrils; (4) first supralabial enlarged, moderate–ample supralabial–rostral contact; (5) head in dorsal view slightly differentiated from the neck, broad anteriorly and with the snout usually truncate, rarely rounded, and in lateral view with the snout subacuminate; (6) frontal hexagonal or subhexagonal, anterior margins slightly convex or straight, usually longer than wide; (7) loreal moderate, narrowed towards the eye and in contact with two supralabials; (8) 7(3,4) supralabials; (9) six infralabials, three scales in contact with geneials; (10) eye–prefrontal contact wide and < than prefrontal–postnasal contact; (11) sublabials or pseudo–chinchields well separated, as wide as the suture of the single pair of

infralabials; (12) 4–5 gular scales; (12) 145–160 ventral in males and 157–170 in females; (13) 27–31 subcaudal in males and 24–30 in females; (14) in life the head is dorsally brown or uniformly olive–brown, with a lighter snout; dorsal background brown, copper–brown or uniform olive–brown, with barely distinguishable dark spots, circumscribed to the scale and irregularly arranged; (15) in life the ventral region has a pale yellow, pinkish or yellowish–orange background, lateroventrally spotted with brown or black, although the spots are not well defined; tail yellow, strongly mottled brown or black, cloacal scale yellow, weakly mottled; (16) six o seven dorsocaudals to sixth subcaudal scale; (17) thin tail, 9–11.3 % in females and 12.3–14.1 % in males; (18) moderately bilobed, semicapitate, semicalyculate hemipenis, subcylindrical lobes, capitular groove undefined and body of the hemipenis globular, where the capitulum is narrower; (19) 6–8, usually six maxillary teeth, well–developed lateral process, arranged horizontally to the bone between 5–6 teeth, last tooth visibly reduced in relation to the previous one.

Although geographically separated, but closest within the cordillera de Mérida, only *A. eriki*, *A. tamaensis* and *A. mariselae* share similarities, but differs from these in having a moderately bilobed, semicapitate hemipenis, subcylindrical lobes, capitulum narrower than the body of the hemipenis and capitular groove undefined vs. non–bilobed to poorly bilobed, with a wide capitulum in *A. tamaensis*; slightly bilobed hemipenis, not subcylindrical lobes and capitular groove defined in *A. eriki* and slightly bilobed, not capitate hemipenis, not subcylindrical lobes and capitular groove undefined in *A. mariselae*. In the case of *A. pamplonensis*, this taxon has a slightly bilobed hemipenis, clavate lobes with a rounded apical edge and capitular groove defined (Passos *et al.* 2024). Other distinguishing characteristics between the species are listed in Table 1.

Description on museum material

Total maximum length in males 331.9 mm and in 377.9 in females (SVL in males 230.1–290.9 mm and in females 265.2–344.2 mm); tail length 31.2–41.05 mm in males (n=5) and 24.5–33.7 mm in females (n=5); head length in males 7.8–9.3 mm (n= 5) and 7.9–9.6 mm (n= 5) in females; head width in males 5.06–7.06 (n= 5) and 5.85–7.78 mm (n= 5) in females. Head in dorsal view longer than wide, slightly distinct from the neck; short, slightly truncated, or rounded and weakly compressed snout (ID–IND relation 27.1–40.9 % in males and 28.1–55.2 % in females). Rostral barely visible from above, in frontal view subtrapezoidal, wider than high, lateral margins usually concave; apical

edge short (<0.5 END, Fig. 9A_4–B_4) and just reaching the imaginary straight line between nostrils; two internasals, variable in shape, but more commonly longer than wide or quadrangular, internasal suture 2 or 2 ½ times prefrontal suture, not sinastria; two prefrontals, slightly wider posteriorly; frontal shield hexagonal or subhexagonal, longer than wide, with convex or slightly convex anterior margins (Fig. 9A_1–B_1); small supraoculars (< 0.75 END), irregularly pentagonal and wider posteriorly; two parietals, parietal suture 2.34–3.42 mm in males and 2.21–2.99 mm in females, longer than frontal length. In lateral view, head slightly arched after eye, snout truncated; 7(3,4)/7(3,4) supralabials, first supralabial moderate or elongated, higher than wide, short–moderate supralabial–rostral contact; two supralabials in contact with loreal (Fig. 9A_2–B_2); first supralabial in contact with the ocular orbit, its edge is smaller than the eye–frontal contact + eye–loreal contact; postnasal irregularly heptagonal, more or less similar in proportion to prenasal, prefrontal–postnasal contact wider than eye–prefrontal contact; loreal moderate, eye–loreal contact less than eye–prefrontal contact and loreal–postnasal contact; eye oval, 0.55–0.81 in males and 0.51–0.56 in females END; two postoculars, first enlarged, second elongated; temporal formula 1+2, supratemporal elongated usually present, first temporal enlarged. Mental subtriangular, wider than long; six infralabials, three in contact with geneials (Fig. 9A3–B3); sublabials or pseudo–chinchields separated from each other, width greater than suture of single pair of infralabials; 3–4 gulars, two preventrals; 145–160 ventrals in males (n=5, $\bar{x}$= 150.4 ± 5.6391) and 157–170 in females (n= 5, $\bar{x}$= 154.8 ± 5.5856); cloacal shield entire; subcaudals divided, count in males 27–31 (n= 5, $\bar{x}$= 28.6 ± 1.5165) and 24–30 (n= 5, $\bar{x}$= 25,6 ± 2.8809) in females. Thin tail, 9–11.3 % in females and 12.3–14.1 % in males. 17 rows of dorsal scales in the middle of the body, without reduction towards the neck and tail.

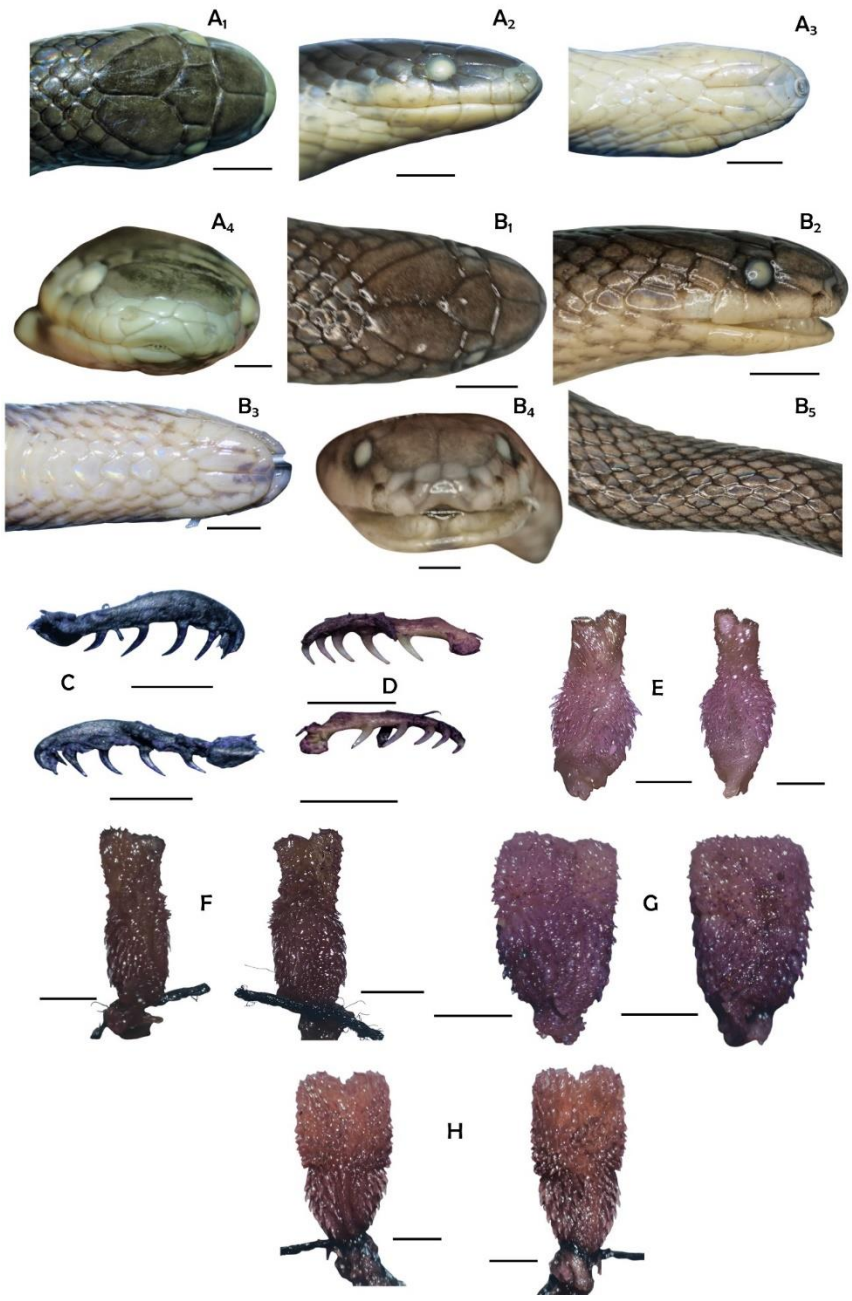

FIGURE 26. Morphological details related to *Atractus mijaresi*. Specimen MZUC 48032, (A_1) dorsal view of head; (A_2) lateral view of head; ventral view of the and (A_3) frontal view of the frontal scale (A_4). Specimen CVULA 7410, (B_1) dorsal view of head; (B_2) lateral view of head; ventral view of head (B_3), frontal view of the frontal scale (B_4) and lateral view of body (B_5). Specimen CVULA 7410, internal and external view of the maxilla (C). Spécimen MZUC 45678, internal and external view of the maxilla, designated as *A. tamaensis* (D). Specimen MZUC 45679 as *A. mijaresi*, sulcate and asulcate view of hemipenis (E). Specimen MZUC 45680 as *A. mijaresi*, sulcate and asulcate view of hemipenis (F). Specimen MZUC 45678 as *A. tamaensis*, sulcate and asulcate view of hemipenis (G) and Specimen MZUC 45680 as *Atractus* sp., sulcate and asulcate view of hemipenis (H).

Maxillar bone

Arched in lateral view, well–developed lateral process, arranged horizontally to the bone between 5–6 teeth. 6–8 maxillary teeth (n= 5, Fig. 9C–D), but normally six; the first three with a narrow spacing, while the subsequent ones have a spacing that varies between 1½ to 2 times in relation to the previous ones. The last tooth visibly reduced in relation to the previous one. Posterior projection visible.

Hemipenis (everted organs n= 2)

Moderately bilobed, semicapitate, and semicalyculate organ; subcylindrical lobes with a rounded apical edge, differentiated from the capitulum and a third or more of the hemipenial body (Fig. 9E–F). Lobes and capitulum covered with concentrate spinulate calyces; capitular groove undefined on asulcate and sulcate sides of hemipenis; capitulum located just above bifurcation of sulcus spermaticus, slightly shorter than body of the hemipenial body, and shorter in size to lobes. Sulcus spermaticus bifurcated right in the middle portion of the hemipenial body; body hemipenial globular, wider than the capitulum, extensively covered with hooked spines that are more noticeable towards the periphery, while decrease in size towards the border of the sulcus spermaticus and the basal portion.

Information of coloration (in life)

In general, we have detected at least three dorsal patterns, which can be brown, coppery brown and olive–brown, all with the body mostly uniform (Fig. 10A, E) or with small dark spots, circumscribed to the scales and irregularly arranged (Fig. 10B_2, C_2). Head dorsally is uniform, not differentiated of body, but with a lighter snout; supralabials usually pale yellow, weakly pigmented of black (Fig. 10C_1), less common a reddish–yellow hue (Fig. 10B_1); rostral in frontal view pigmented of olive–brown, coppery brown or light brown. The ventral region of the body with the background pale yellow, pinkish (Fig. 10A) or yellowish–orange (Fig. 10B_2, D), all with dark spots arranged laterally on each ventral scale; cloacal shield immaculate or pigmented of dark brown, subcaudals strongly blemished brown or black; head with the background ventrally cream, pale yellow or yellowish–orange, with the infralabials and genials weakly pigmented black. Pupil dark brown or coppery brown.

FIGURE 27. Details of the coloration in life of *A. mijaresi*, all the images derive of the material collected in Capaz, Mérida state, Venezuela. Specimen MZUC 48032, uniform brown dorsal

pattern and pink belly (A). Specimen MZUC 45682, reddish–brown dorsal pattern, yellowish supralabials, and orange belly (B_1–B_2). Specimen LFE 106, light brown dorsal pattern with small dark spots, pale yellow supralabials, and belly (C_1–C_2). Specimen MZUC 45679, orange ventral surface and strongly dark brown–spotted subcaudals (D). Specimen MZUC 48031, uniform dark brown dorsal pattern (E). Specimen MZUC 45669, dorsal and ventral view of *A. tamaensis* (F). *Atractus* sp., that comes from Las Porqueras and El Triunfo, estado Táchira, Venezuela (G–I). *A. eriki*, that comes from Escuque, Trujillo state, Venezuela by Santos Bazó (J). *A. mariselae*, uncatalogued, coming from Boconó, Trujillo state by Luis Felipe Esqueda (K). *A. multidentatus*, holotipo CVULA IV–7080 and *Atractus* aff. *pamplonensis*, specimen MCNC 8269 que proviene de Betania, estado Táchira, Venezuela (M).

Distribution and natural history

Middle–high basin of the Chama River between 1600–2450 m and the upper basin of the Capaz River between 1900–2300 m a.s.l., both regions corresponding to the Sierra de la Culata, Mérida state, Venezuela (Fig. 7). The type locality "Mucurubá" (Esqueda & La Marca 2005) exhibits strong precipitation seasonality (less than 1000 mm year), which is why the natural vegetation corresponds to the montane dry evergreen forest that varies between 2000–2700 m a.s.l. On the other hand, the towns of Mérida and Capaz correspond to the montane Andean semideciduous forest and the cloud forest, respectively (Ataroff & Sarmiento 2004). Although they have not been found together, it is likely that it shares habitat with *A. taphorni* in the upper basin of the Capaz River (MZUC 48034–35 collected 5.84 km NW in cloud forest, LFE 2021).

In Capaz via San Rafael del Macho, 8°39'15.51"N and 71°21'30.28"W, 2031 m a.s.l., 29 specimens were collected (not all yet entered into the Zoology Museum of the University of Concepción, LFE). The site constitutes a fallow land of grasses, ferns, and some trees that seem to be part of the cloud forest. Abrupt terrain and soil with mounds of compacted earth where specimens were found, others by digging or under rocks and accumulated vegetation debris. A few minutes from the site, there was a more or less intact stretch of the cloud forest, with many rocks; some were lifted, and we found more specimens (field data LFE 2021).

A specimen MCZ R–1784 comes from Mérida, which suggests that the species would be present in the montane Andean semideciduous forest, currently very fragmented. Esqueda & La Marca (2005) noted *A. taphorni* for the city of Mérida, which corroborates the sympatric condition of both species.

Specimens MZUC 45684–85, adult females contained four oviductal eggs, respectively; while MZUC 48687 and MZUC 45686 contained thee–two oviductal eggs.

Conservation status

Due to the number of localities, we did not conduct an ecological niche modeling. However, according to IUCN (https://geocat.iucnredlist.org/editor) this taxon would have an EOO of 201.904 km² (extent of occurrence) and an AOO of 12 km² (area of occupancy). Our data indicate that this taxon has disjunct populations, and in these localities, there is a significant conversion of its natural habitat. For example, towards the upper basin of the Capaz River, cloud forest lower montane showed a negative balance, with a net loss of 38.9 % between 1952–1997, replaced by grasslands for high–altitude livestock grazing and agricultural crops (Rodríguez–Morales *et al.* 2009). This conversion pattern is similar for the semideciduous forest and the dry evergreen forest towards the other previously mentioned locations (Buitrago *et al.* 2011). Due to its specialized diet and the direct effects resulting from the dynamics of the original vegetation cover, we believe that this taxon meets the IUCN conservation criteria (IUCN 2012) it must be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv) (see Esqueda & La Marca 2015).

Morphological details, coloration and geographical	*A. ventrimaculatus*	*A. ochrauetrus*	*A. mijaresi*	*A. pamplonensis*	*A. tamaensis*	*Atractus* sp.	*A. marisolae*
Geographic distribution in cordillera de Mérida, Venezuela	Restricted to the middle-high basin of the Chama River, Mérida state	Restricted to the middle-upper basin of the Mocoties River, Mérida and Táchira states	It is restricted to the middle–upper basin of the Chama River, towards La Culata (intramontane-lacustrine slope), Mérida state, from Mucurubá, the city of Mérida, and Capaz (upper basin).	So far, two specimens that match the original description and come from Betania, Táchira state have been identified.	type series comes from Betania, Táchira state, new identified populations come from Bailadores (Las Pleitas-Las Minas), middle-upper basin of the Mocoties River	Restricted to Jají and its surroundings, Mérida state	Boconó and its surroundings, Trujillo state; the species has not been found towards Niquitao, the outermost part of the Boconó River.
Altitudinal range m asl	1700-3250	2000-3000	1900-2300	1200-2500 in Colombia ***, ~2400 in Venezuela	1900-2000	1800	1200-1300
Type of habitat (natural), according to Ataroff and Sarmiento (2004)	cloud forest	cloud forest, elfin cloud forest, Andean montane semideciduous forest	cloud forest, Andean montane semideciduous forest	cloud forest	Andean montane semideciduous forest	Andean montane semideciduous forest	Andean montane semideciduous forest
Maximum Total Lenght (SVL + TaL)	372 mm males and 413 mm females	376 mm males and 421 mm females	348 mm males and 377 mm females	273 mm male in holotype *** and 459 mm female, specimen comes from Betania, Táchira state, Venezuela	283 mm males and 305 mm females	390 mm females ****	325 mm males and 395 mm females ****
Tail with relation SVL	thick tail, 4.7-8.9 % females and 10.3-15.7 % in males	thick tail, 6.6-9.1 % in females and 10.6-13.2 % in males	thin tail, 9-11.3 % in females and 12.3-14.1 % in males	thin tail, 8.4-12 % in females and 15.5 % in males	thin tail, 6.6-9.1 % in females and 10.6-13.2 % in males	thin tail, 11 % in females	thin tail, 6.6-9.1 % in females and 10.6-13.2 % in males
Wide at the middle of the body (WMB)	> 9 mm	> 9 mm	≤ 9 mm	≤ 9 mm	≤ 9 mm	≤ 9 mm	≤ 9 mm
Rows of dorsal scales at midbody	15	15	17	17	17	17	17
Ventral scale count	138-153 males and 147-161 females	144-152 males and 146-156 females	145-160 males and 157-170	167-169 males and 174-193 females. In Passos et al. (2024) it is not defined from the examined sample whether the Venezuelan material was included, so we took the averages: 167 is males and 177 in females	145-152 males and 160-165 males ****	168-169 females	168-171 females and 157-162 males ****
Subcaudal scale count	18-22 males, 13-20 females	21-20 males, 14-18 females	27-31 males, 24-30 females	24-35 males and 18-29 females. In Passos et al. (2024): 24-34 males and 19-28 females	26-28 males and 21-23 females ****	28-35 females	31-33 females and 36-39 males ****
Supralabials	usually 8(4,5)	usually 8(4,5)	7(3,4)	7(3,4) ***	7(3,4)	8(3,4)	8(3,4), rare seven
Infralabials	7(4)	7(4)	6(3)	7(3–4) ***	6(3)	7(4)	7(4-5)
Sublabials or Pseudo-Chinshields	separated from each other	usually in contact	separated from each other	separated from each other	separated from each other	separated from each other	separated from each other
Supralabials in contact with Loreal	three, less common two	three, but is frecuently specimens with two	two	two	two	three	three, rare two
1st supralabial	small, short-moderate rostral-supralabial contac	small, short-moderate rostral-supralabial contac	enlarged, moderate rostral-supralabial contac	S/D	enlarged, moderate rostral-supralabial contac	small, short-moderate rostral-supralabial contac	small, short-moderate rostral-supralabial contac
Eye-prefrontal contact	> than prefrontal-postnasal contact	> than prefrontal-postnasal contact	< than prefrontal-postnasal contact	< than prefrontal-postnasal contact	< than prefrontal-postnasal contact	< than prefrontal-postnasal contact	< than prefrontal-postnasal contact
Rostral (frontal view)	subtriangular, usually higher than wide or as high as wide, lateral margins slightly concave or straight, moderate-ample apical margin, situated above the straight line between the nostrils, > 0.5 END	subtriangular, usually as wide as high or as high as wide, straight or barely concave lateral margins, short-moderate apical margin, above the straight line between the nostrils, ≤ 0.5 END	subtrapezoidal, wider than high or as high as wide, concave lateral margins, short apical margin, ≤ 0.5 END, barely crosses the straight line between the nostrils	In specimens examined, the scale slightly visible from above. Although we did not have the material to verify its shape in frontal view, it does not suggest that it could be taller than wide, with a moderate apical margin.	subtrapezoidal, wider than high or as high as wide, concave lateral margins, short apical edge, ≤ 0.5 END, barely crosses the straight line between the nostrils	subtriangular, as high as wide or slightly higher, straight lateral margins, short-moderate apical edge (<0.5 END), just above the straight line between the nostrils	subtrapezoidal, wider than high or as high as wide, straight lateral margins, moderate apical egde, ≤ 0.5 END, barely crosses the straight line between the nostrils
Elongated posterior supratemporal	absent	absent	frequently present	variable ***	frequently present	absent	frequently present
First supralabial in contact with the eye	small, higher than wide; short supralabial-rostral contact	small, higher than wide; short supralabial-rostral contact	enlarged, supralabial-rostral contact usually moderate-wide	enlarged, short supralabial-rostral contact	small, taller than wide, short supralabial-rostral contac	small, higher than wide, short supralabial-rostral contact	small, taller than wide, short supralabial. rostral contac
Suture internasal			short, three times prefrontal suture; internasals longer than wide	short, three times prefrontal suture; internasals wider than long	short, three times suture prefrontal; internasals wider than long, less common quadrangulars	moderada, 2 ½ veces la sutura prefrontal; internasals wider than long	short, almost three times prefrontal suture; internasals longer than wide
Frontal scute	usually longer than wide, hexagonal or subhexagonal	usually as long as wide, subtriangular	normally as long as wide, hexagonal	longer than wide, hexagonal, anterior margins convex	slightly longer than wide or as long as wide, hexagonal, with the anterior margins convex or slightly convex	hexagonal, wider than long, shorter than the parietal suture and with the anterior margins medially forming a triangle-shaped notch	longer than wide, subhexagonal, anterior margins slightly convex
Supraocular	long, subtrapezoidal, posterior edge in parietal contact at least twice as wide as the anterior edge	long, subtrapezoidal, posterior edge in parietal contact at least twice three times than anterior edge	short-moderate, usually subtrapezoidal, less common subrectangular, posterior edge in parietal contac barely 1 ½ times anterior edge	short-moderate, subrectangular, posterior edge in parietal contac at least just wider than anterior edge	short-moderate, usually subrectangular, less common subtrapezoidal, posterior edge in parietal contact at least just wider than anterior edge	long, subrectangular, barely posterior edge in parital contac wider than anterior edge	long, subtrapezoidal, posterior edge in parietal contact at least twice than anterior edge
Maxilla and lateral posterior process	arched, lateral process moderately defined or pronounced, horizontally arranged with respect to the bone, located between the seventh and ninth tooth	weakly arched, lateral process well-defined, disposed obliquely with respect to the bone, located between the sixth and eighth tooth	arched and short, well-developed lateral process, arranged horizontally to the bone between 5-6 teeth; defined posterior process	arched anteriorly in dorsal view, medially flattened toward its posterior end; maxilla with nine teeth arranged fwcafy, teeth 1-2 larger and little spaced; teeth 3-7 smaller than first teeth, moderately spaced; last two teeth small (holotype) ***	arched and short, well-defined lateral process, arranged obliquely; defined posterior process	arched, well developed lateral process, located between the fifth and sixth teeth	data not available
Maxillary teeth count	10-14 ***, here 11-12, the last one tooth not reduced	8-10, the last one tooth reduced	5-8 maxillary teeth, usually six	frequently 8-9 teeth ***	5-7 teeth	8 teeth	8-9 teeth
Hemipenis	unilobed, semicapitate, semicalyculate; capitular groove undefined	unilobed, semicapitate, semicalyculate, capitular groove undefined	moderately bilobed, semicapitate, semicalyculate;subcylindical lobules with a rounded apical border; body of the hemipenis globular, extensively longer than lobules; capitular groove not defined in both sides (sulcate-asulcate)	slightly bilobed, semicapitate, semicalyculate; clavate lobules with round apices; capitulum extensively wider than body of the hemipenis; capitular groove indistinct on sulcate face, barely defined at asulcate side of organ ***	poorly defined or slightly bilobed, semicapitate, semicalyculate; lobes with straight apices; capitulum wider than body of the hemipenis, capitular groove undefined (asulcate-sulcate)	Information on hemipenis unknown	slightly bilobed, no capitate, semicalyculate, capitulum no wider than the body of the hemipene; capitular groove undefined (asulcate-sulcate) ****
Dorsal pattern in life	the most commonly observed pattern is melanic, with or without an undefined vertebral line; another pattern consits of light brown, grayish, or yellowish, with black spots (which may or may not be bordered in yellow), discontinous and arranged linearly on the body. Another rarely observed pattern is a dark brown background with two narrow yellow lines, paravertebral and partially discontinuous, with no visible black vertebral line.	the pattern often observed has a light brown background, a continuous black vertebral line, and two continuous black lines, narrow or wide (one on each side); another pattern has a similar background but with paravertebral, dorsolateral lines, and a discontinuous narrow vertebral line, with a well-defined cream band between the paravertebral and dorsolateral lines; finally, there are specimens with a melanistic pattern, but the dorsolateral lines are well-defined and bordered with cream. There are individuals that exhibit a yellowish background, with a wide and continuous vertebral line, while the black dorsolateral lines are well-defined and not bordered by cream.	variable, light brown, grayish brown, or reddish brown, it can be uniform or with small dark spots bordered by the scale and arranged irregularly	body reddish brown with black marks (dots, spots, or blotches) ***	light brown or reddish-brown, uniform or with small dark spots arranged regularly over the paravertebral region. These small spots, no larger than a scale, can gradually decrease in size and eventually disappear in some individuals.	black uniform, no visible stains	light brown, dark brown, or olive brown; it can be uniform or have small dark spots irregularly dispersed
Ventral pattern in life	intense yellow background, with blocks of rectangular black spots, some covering the entire scale; pattern normally moderately to heavily spotted	intense yellow background, with blocks of rectangular black spots, some covering the entire scale; moderately to heavily spotted normal pattern	pale yellow, pink, or orange background, weakly speckled with black or with rectangular black spots on each side of the ventral scale (its extent does not cover 50% of the surface)	intense yellow, usually with black spots on each side of the ventral scale (covering more than 50% of the surface)	pale yellow, usually immaculate or barely speckled with small black spots on each side of the ventral scale (less than 50 % of the surface)	whitish, with black spots arranged horizontally on each scale	whitish or cream, weakly speckled with irregular black or with poorly defined spots arranged horizontally
Ventral surface of the tail	usually moderately to heavily stained black with a yellow background	usually immaculate or faintly stained with black and with a yellowish background	weakly or moderately to strongly stained black with a pale yellow, orange, or pink background	usually moderately to heavily stained black and with an intense or pale yellow background	a pale yellow background, immaculate or faintly stained with black	moderately to heavily stained black and the background similar to the belly	usually moderately to heavily stained black and the background similar to the belly
Light band or spot behind the parietals	absent	absent	absent	incomplete light band and inconspicuous in some adults, juveniles with a band conspicuous	no light band, light spot bordered in black in some adults, more common in juveniles	absent	absent

Data defined by us based on examined material (without asterisk); data defined by Passos et al. (2024) (***); Data from other authors (****): Lancini 1969; Esqueda and La Marca 2005; Natera-Mumaw et al. 2015

Note: although Passos et al. (2024) had a considerable sample of *A. pamplonensis* specimens (Colombia), they mixed the data with Venezuelan specimens, making a coherent analysis impossible. For that reason, it is not considered, except for the average in males and females provided by these authors.

Table 1. Comparative morphology in the species of *Atractus* from Venezuela (in discussion)

Atractus aff. *pamplonensis*

Atractus pamplonensis.– Schargel & García–Pérez (2002: 400)

Atractus pamplonensis.– Passos *et al.* (2024: 51).

Description on museum material

Adult female with total length 459.18 mm (SVL= 413.15 mm); tail length 46.03 mm; head length 11.58; head width 6.89 mm. Head in dorsal view: distinctly longer than wide, somewhat differentiated from the neck, weakly compressed (ID/IND relation 34.9 %); snout slightly truncated; rostral slightly visible from above; two internasals, wider than long, internasal suture 0.84 mm (three times prefrontal length); two prefrontals,

longer than wide, prefrontal–postnasal contact 0.85 mm, wider than eye–prefrontal contact (0.63 mm); frontal shield longer than wide (3.67 mm and 3.33 mm), anterior edges convex; two supraoculars, elongated and irregularly pentagonal; two parietals, parietal suture 2.97 mm, shorter than FL. Head in lateral view: snout sub–acuminated; eye sub–oval, 1.61 mm (36.1 % less than HED), eye–nostril distance 2.52 mm; prefrontal–eye contact greater or equal than loreal–eye contact; loreal moderate, pentagonal, loreal–postnasal contact similar or greater than loreal–eye contact (2.16 mm LOL, 0.81 mm HLO), in contact with two supralabials; postnasal irregularly heptagonal, higher than wide, similar in size to the prenasal and obliquely arranged, well–defined nostril; two postoculars, the first irregularly pentagonal, longer than wide, wide temporal–1st postocular contact, second postocular small, dorsally in contact with the fifth supralabial and separated from the fourth supralabial; temporal formula 1+2; anterior temporal enlarged; posterior supratemporal elongated not defined (only right side); 7(3,4)/7(3,4) supralabials, first supralabial moderate–enlarged, moderate or ample supralabial–rostral contact; horizontal distance between supralabials in contact with ocular orbit 3.17 (20.5 greater than END). Head in ventral view: subtriangular mental, wider than long; six infralabials, three in contact with geneials; a pair of geneials, 3.38 mm long (26 % greater than END); two sublabials or pseudo–chinchields, separated from each other (0.692 mm), just greater than suture of the first pair of infralabials (0.631 mm); three gulars and two preventrals; 178 ventrals; entire cloacal scale, 29/29 subcaudals. Thin tail, 11. 1 %. Dorsal scales disposed in 17–17–17 rows.

Coloration of the specimen MCNC 8269 (preservative)

There are no details on the coloration in life. The preserved specimen presents the dorsal background of the body in chocolate brown, with two lines of dark brown spots at the paravertebral level (Fig. 10M$_1$), then at the dorsolateral level, faintly other rows of irregular dark spots are observed, rows 1–3 dorsal similar to the body, not bordered by cream or yellow. Dorsal background of the head uniform, similar to the dorsal background of the body. At the ventral level, the body background is ochre yellow, heavily mottled with black; generally, the dark brown spots are rectangular, arranged horizontally on each ventral scale and forming two continuous lateroventral lines (between the third and middle of the belly, the spots extend over almost the entire surface of the scale, Fig. 10M$_2$). Ventral surface of the cloaca weakly mottled with dark brown towards the sides; subcaudals yellow with the same ventral pattern as the body.

Head with an ochre yellow background, more subdued, with the mental, infralabials, and genials strongly mottled with dark brown.

Distribution and natural history

Population of Betania, Táchira state, Venezuela (2442 m a.s.l., 7°27' 7"N and 72° 26' 28"W), which corresponds to the Tamá massif. According to this data, this taxon would be occupying the Andean cloud forest. A specimen from the same locality recognized as *A. pamplonensis* was reported by Schargel & García–Pérez (2002).

DISCUSSION

Biogeography, species limits and taxonomy

Similar to *Liolaemus* (Esquerré *et al.* 2019), *Atractus* constitutes a lineage that has diversified explosively in the mountains of South America, dominating the middle–high environments between 1000–3200 m a.s.l. (e.g., north and central Andes). Serrano *et al.* (2023) proposed that during the Early Miocene, the movement of dipsadines from Central America to South America involved different processes, dating back to approximately 20–25 Myr, whereas the genera *Geophis* + *Atractus* are around 22 Myr, with their Central American ancestors first expanding their distribution to South America and subsequently experiencing vicariance. Our calibrated phylogeny constructed estimated the divergence of *Atractus* with respect other dipsadines around 22.54 Myr (95 % HDP = 19.08–26.23). By way of comparison, the common ancestor of hummingbirds in South America occurred 22 Myr ago, where a substantial proportion of hummingbird diversification took placed in conjunction with the uplift of the Andes, around 140 spp., and where Coquettes and Brilliants completed the great majority of their speciation took place over the last 10 Myr in the context of the rapidly rising Andes (McGuire *et al.* 2014).

At that time, the scenario concerning the central and northern Andes was particularly fundamental for understanding the dispersion, colonization, and diversification of these snakes. In fact, the Andean orogeny is considered one of the most important events regarding the diversity of South American biota (e.g., amphibians, Hutter *et al.* 2013). Events to consider in our analysis: (1) during the Miocene, 26–6 Ma, the eastern cordillera began its uplift and the Magdalena River valley formed as a lowland corridor,

whose habitat was primarily arid (Egbue & Kellogg 2012), what could have driven the dispersion and colonization in mountain slopes (foothills). During 15.3–23.8 Myr, the transgression of shallow seas into the northern Andes constituted a barrier to the east and a historical connection between the Amazon basin and the Chocó (Hoorn 1994), which must have favored the dispersion between both biogeographic regions. In our phylogeny, with moderate support, we found *A. trilineatus* related to *A. ochrosetrus* and *A. ventrimaculatus*, with a divergence that occurred 17.18 Myr ago, suggesting an ancestor whose dispersion it must have been from the western Amazon basin. On the other hand, although our phylogeny does not encompass 50 % of the known species, at least three clades (Andean spp. + Andean–Amazonian spp. and Andean–Central American spp.) are visualized with weak support; (2) during most of the early and middle Miocene, the upper Amazon region was covered by the great Pebas wetland (Wesselingh & Salo 2006; Hoorn *et al.* 2010); (3) the role of the Táchira depression as a barrier between the eastern cordillera of Colombia (Magdalena River valley) and the cordillera de Mérida (Andean slope towards Los Llanos and intramontane regions); (4) origin, continuity, and distribution of the cloud forests to the north of the Andes, understanding the dynamics of species between the eastern cordillera of Colombia and the Mérida cordillera. Of the species known in the cordillera de Mérida (Natera–Mumaw *et al.* 2015), *A. ochrosetrus, A. ventrimaculatus, A. taphorni* and *A. emigdioi* are intramontane species that occupy an altitudinal range comprising the Andean cloud forest between 1800–3000 m (Ataroff & Sarmiento 2004). Species of the Andean cloud forests exhibit a mosaic of evolutionary histories and rapid diversification rates (Pérez–Escobar *et al.* 2023), and many of these radiations occurred from the Early Miocene, when the formation of the cloud forest is believed to have happened (Sempere *et al.* 2005). (5) climatic oscillations during the Pliocene–Pleistocene in the cordillera de Mérida. These climatic fluctuations and the extensive glaciations of the late Pliocene and Pleistocene may have contributed to the expansion and diversification of their distribution area in many organisms through temporary dispersal corridors through suitable habitats, followed by fragmentation into refuges (e.g., birds, Chaves *et al.* 2011) or the contraction of environments at the intramontane level that favored isolation (e.g., mammals, Quiroga–Carmona 2021; plants, Flantua & Hooghiemstra 2018).

Our dating indicates that the divergence of *A. ochrosetrus* and *A. ventrimaculatus* must have occurred at some point during the Late Miocene, coinciding with the uplift of the

northern Andes between 8–5 Myr (Pérez–Escobar *et al.* 2022) and in line with what was stated by Boschman (2021), who suggested that the cordillera de Mérida had elevations between 3500–4000 m 7 Myr ago due to the discovery evidences of paramo vegetation in the sediments of the Lake Maracaibo basin, and that other recently described species suggest the same scenery (e.g., *Tantilla palamala*, Esqueda *et al.* 2025) The cordillera de Mérida is considered a double–vergent orogen with the wetter basin and wedge of the Lake Maracaibo basin on the northwest side and the drier basin and wedge of Barinas on the southeast side (Erikson *et al.* 2012), creating a pattern 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 (Chacón–Moreno and Moral 2020). Hence, *A. ochrosetrus* and *A. ventrimaculatus* are separated by an extensive dry valley known as the González basin, in the middle–lower basin of the Chama River (León 1999). On the other hand, our phylogeny strongly supports that *A. taphorni* and *A. emigdioi* are sister species, whose divergence occurred 3.59 Myr ago (HDP= 1.92–5.47), while *A. mijaresi* and *Atractus* sp. would be related but separated of *A. mariselae*, a species that occupies a lower altitudinal zone (1200–1300 m), although in the same area that *A. emigdioi* (1800–2300 m, LFE data 2021). Passos *et al.* (2024: 81) erroneously consider that both species are very similar, with the possibility that both taxa are conspecific. Furthermore, these authors in their manuscript arbitrarily and without concrete evidence incorrectly use the term "parapatric species" (no phylogenetic evidence to support it). Far from reality, both taxa have distinct histories and absolutely indisputable morphological differences, in addition to relationships with Andean taxa. So far, our data corroborate that the intramontane region of the cordillera de Mérida exhibits the greatest diversification of the genus, strongly related to the Andean uplift and climatic oscillations during the Pliocene–Pleistocene. The cordillera de Mérida is a unique orogen that features an extensive intramontane region, characterized by deep valleys and variations in altitude that act as a geographical barrier, favoring genetic drift and the differentiation of high–montane lineages (e.g., birds in other mountainous regions, Chaves *et al.* 2011). *Atractus* could be a typical example of the "sky island" effect in montane reptiles. Our analyses showed that these two species have very similar and restricted niches, which is consistent with recent speciation influenced by topography and climate. However, despite their phylogenetic divergence, both species have retained their ancestral niche (niche conservatism, Wiens & Graham 2005), possibly due to physiological or

ecological constraints. Under this preliminary scenario, it is suggestive to think that these snakes exhibit high speciation rates in mountains and are consistent with the cradle hypothesis, which posits that Andean lineages have higher speciation rates compared to other regions in South America (Esqueda *et al.* in prep.).

Despite the accumulated progress in the last 10 years regarding the taxonomy of *Atractus*, we are far from understanding its diversity and relationships (e.g., only 43 % of the species are available at the phylogenetic level). Although we recognize the contribution of the article by Passos *et al.* (2024), we don't agree with the treatment of the species from the Venezuelan Andes. This reticence has been driven largely by two distinct, interrelated instances: (1) a long–standing disagreement over species concepts, facilitating erroneous and convenient interpretations that do not follow a biogeographic and phylogenetic conceptualization; (2) it is true that many species require an evaluation due to the little that is known, but that does not imply that the current comparisons are based on convoluted criteria, conveniently used for some species and not for others, including incorrect identifications of specimens and/or localities. Therefore, far from resolving the issue, is markedly biased and riddled with inconsistencies that urgently need clarification.

– *A. ochrosetrus* vs. *A. ventrimaculatus*: both closely related species diverged in the Late Miocene 6.67 Myr ago (95% HPD = 4.4–9.02). Our combined study data offer an opportunity to examine the importance of these geographic discontinuities and test whether the patterns of intraspecific differentiation are related to differences in niche space (in terms of altitudinal zonation and habitat preference). Both mitochondrial and nuclear DNA data, when comparing both taxa in terms of their patterns of geographic subdivision, degree of genetic differentiation, and inferred demography, consistently demonstrate their taxonomic recognition.

Passos *et al.* (2024: 43) pointed out that Esqueda & La Marca (2005) mistakenly interpreted the condition of the hemipenis of *A. ventrimaculatus*. Is well is true this information, conveniently Passos *et al.* (20024) overlooked what was indicated by Esqueda *et al.* (2007), those who had the opportunity to correct and highlight some distinct attributes of the hemipenes between *A. ochrosetrus* and *A. ventrimaculatus*. In fact, if we review the information on the hemipenis of *A. ventrimaculatus* provided by Passos *et al.* (2024: 42), these authors noted “slightly bilobed, semicapitate, semicalyculate; lobes similar in size, clavate with round apices, weakly distinct from

capitulum", inclusive these authors do not indicate which specimen their description is based on (v. Schargel & Castoe 2003). Our information about the hemipenis of *A. ventrimaculatus* contradicts that indicated by these authors, as we consider that the hemipenis is unilobed, not clavate, and with rounded edges, with the remaining attributes similar to what was previously known for the species. Although the use of hemipenial characters in systematic studies of *Atractus* has been fundamental and necessarily defined in modern descriptions, if possible (Passos *et al.* 2018), its variability has not yet been fully tested. However, evidence does not suggest that hemipenial morphology in snakes is highly conserved intraspecifically, but it is poorly documented (e.g., *Siphlophis*, Zaher *et al.* 1999; *Oxyrhopus clathratus*, Bernardo *et al.* 2012). In the future, it will be necessary to evaluate more hemipenes of this taxon, but since Passos *et al.* (2024) did not provide an illustration or photograph and Schargel & Castoe (2003) only provided an illustration, we prefer to think that it might have been an error since the hemipenis not was fully expanded or at least, is to have indicated when using instrumentation, if they tried to move it distally during its mounting. Consequently, we recognize that the hemipenis of *A. ventrimaculatus* as unilobed, semicapitate, semicalyculate and capitular groove well–defined. Compared to *A. ochrosetrus*, the ornamentation is generally similar, with some difference in the extension of the capitulum, shorter in *A. ochrosetrus* than in *A. ventrimaculatus*, and the body of the hemipenis wider in *A. ochrosetrus* than in *A. ventrimaculatus*. In our calibrated phylogeny, both species are related to *A. trilineatus*, a species of the cordillera de la Costa, whose divergence occurred 17.18 Myr ago (95 % HDP = 13.61–20.87); while *A. vittatus* + *A. matthewi*, both species of the cordillera de la Costa, Venezuela, diverged from the Andean clade where *A. mijaresi*, and *A. mariselae* are found 16.73 Myr ago (95 % HPD = 13.36–20.16). Unlike the Andean species *A. ochrosetrus* and *A. ventrimaculatus*, *A. trilineatus* exhibits a non–capitate and slightly bilobed hemipenis.

The original description of *A. ochrosetrus* consisted of three specimens, one adult male and two juveniles. The juvenile ULABG 3007 presents a coloration without lines on the back, and according to the authors, the "back is dark gray, the belly is light gray, and the tail and throat are washed yellowish." In contrast, the juvenile specimens examined by us, MHNLS 22669–70, near the type locality of the species, clearly exhibit dorsolateral lines, just like the juvenile MZUC 48020 (Fig. 6E1). Passos *et al.* (2024: fig. 31E–F)

incorrectly indicated the collection locality of the adult female specimen ULAB 2409 as "Betania, state of Táchira, Venezuela," when in reality it comes from Betania, between El Molino and "La Y," via Estanques–Canaguá, 2350 m, Pinto Salinas municipality, Mérida state, collected on April 12, 1989, by Enrique La Marca (LFE was an ad Honorem curator for six years of the collection). The only specimens that come from Betania, Táchira state, correspond to *Dendrosophus pelidna*, collected by Enrique La Marca, Juan Elías García, Abraham Mijares, and Maricela Sosa in 1987. Regarding the status of specimen ULABG 2409, it is located to the southwest of the Las González–Estanques basin, which geographically separates it from the sensu populations of *A. ventrimaculatus*. We prefer to keep its definition on hold due to new data that is being evaluated.

Although Passos *et al.* (2024: 43) did not have live specimens to corroborate the coloration pattern in *A. ventrimaculatus* and *A. ochrosetrus*, the authors stated "The color differences between the above species mentioned by Esqueda & La Marca (2005) are the result oversimplification of the polychromatic *A. ventrimaculatus*". The first mistake is not considering available live photographs of both species (e.g., La Marca and Soriano 2004; Natera–Mumaw *et al.* 2015). Coloration patterns in life are lost during preservation, although sometimes they can be retained through formalin treatment (e.g., specimen MCNC 8269 of *Atractus* aff. *pamplonensis*, Fig. 10M). However, there are taxa that can exhibit melanism in their pattern, such as *A. ventrimaculatus*, and some details like the vertebral line would be undefined (not visible). Until now, the information available on the living *A. ventrimaculatus* does not confirm a wide or narrow black vertebral line on the back of the body, except in some preserved specimens that were examined. In fact, Boulenger in his original description noted "a black vertebral sometimes present", while in another part of the writing it gives the impression that the common pattern is "olive to blackish brown above, uniform or with dark and light spots". Also, Roze (1966) noted "gray to grayish–brown above, with a black vertebral line that is often reduced to a series of longitudinal black spots". Usually, melanism in the context of polymorphism occurs that inhabit highlands reptiles, as seen in other *Atractus* collected such as *A. taphorni* and *A. emigdioi* (both found in the cloud forest). Bogert (1949) suggests that darker individuals warm up more quickly under solar radiation, which increases their thermoregulatory efficiency in cold or humid environments (thermal hypothesis), such as the Andean cloud forests. In our

ecological niche models (ENM) for *A. ventrimaculatus* and *A. ochrosetrus*, the variable with the highest contribution was the precipitation of the wettest quarter and general humidity, associated with the cloud forest in their distributions (Clusella–Trullas *et al.* 2007). So, melanism could represent an adaptive response, facilitated by phenotypic plasticity, the gradient of humidity, and temperature in their habitats (West–Eberhard 2003). If so, it could have been maintained in ancestral populations as an adaptive strategy in high–altitude environments. On the other hand, in *A. ventrimaculatus* climatic oscillations of the Pliocene–Pleistocene (e.g., the Mérida glaciation, Shubert and Clapperton 1990) may have favored melanism due to the contraction and expansion of the cloud forest (v. Hooghiemstra and Van der Hammen 2004), unlike *A. ochrosetrus* which mostly occupies more seasonal environments (Mocoties River basin, León 1999; Rivas *et al.* 2009). Although we found individuals of this taxon with melanism (MZUC 48023, Supp._1_20), the dorsolateral lines are clearly distinguishable. Therefore, the presence of dorsolateral lines in the dorsal region of the body is a distinguishing attribute between both taxa and not oversimplification of the polychromatic. Although the role of polymorphism as a driver of speciation is an open topic in polymorphic and altimontane species (Gray & McKinnon 2007; Pizzato 2012), the more plausible explanation here is that vicariance facilitated the fragmentation of populations and subsequent differentiation in an ancestral species. Under this geographical scenario where the cordillera de Mérida arose diachronically between both slopes (the lacustrine slope rose faster than the one towards Los Llanos; Audemard 2003; Bermudez *et al.* 2011), as a hypothesis, it is possible that *A. ochrosetrus* constitutes the ancestral species and that *A. ventrimaculatus* could have arisen by budding–off (Coyne and Orr 2004), and subsequently, melanism increased due to the climatic oscillations of the Pliocene–Pleistocene.

– *A. mijaresi* vs. *A. pamplonensis*: according to our data, *A. mariselae* diverged from *A. mijaresi* and *Atractus* sp. during the Late Miocene 8.29 Myr ago (95% HPD = 5.85–11.01), while *A. mijaresi* diverged from *Atractus* sp (Esqueda *et al.* in press) most likely during the end of the Pliocene and the beginning of the Pleistocene 2.85 Myr ago (95% HPD = 0.87–5.21). Despite the geographical distance and distinctive barriers (e.g., semiarid enclave, Las González basin and Táchira depression), Passos *et al.* (2024) arbitrarily considered that *A. mijaresi* as a synonym of *A. pamplonensis*, despite a clear difference in the count of ventral scales, lacking information on the hemipenis and

coloration in life. Morphologically Passos *et al.* (2009a) relates *A. pamplonensis* with *A. sanctamartae* Dunn, 1946, *A. Macondo* Passos, J.D. Lynch & Fernandes, 2009, *A. crassicaudatus* (Duméril, Bibron & Duméril, 1854, *A. nigriventris* Amaral, 1933 and *A. variegatus* Prado, 1942 for having a set of characters, in which it stands out hemipenis with a lateral depression in the lobe apices (curiously not indicated in the description of the hemipenis in Passos *et al.* 2024), capitulum broader than hemipenial body (both characters absent in *A. mijaresi*). Although there is still no molecular information on *A. pamplonensis*, *A. mijaresi* would be related to *Atractus* sp. geographically close (actually in description, Esqueda *et al.* in press), and contrary to the information indicated by Passos *et al.* (2024), our morphological data confirm a set of differences between both taxa (Table 1). On the other hand, populations detected in Táchira state (middle–high basin of the Mocoties River), here for us assigned as *A. tamaensis* and *Atractus* sp. (actually in description by Esqueda and col. in prep.), although they present capitulum broader than hemipenial body, they do not have lateral depression on lobe apices (Fig. 8G–H).

Schargel & García–Pérez (2002) identified a specimen MCNG–R 5877 from Betania, Táchira state, a border locality with Colombia and constituting the Tamá massif as *Atractus pamplonensis*. Neither Passos *et al.* (2024) nor we were able to check that specimen. However, we found a series of specimens in the Natural Sciences Museum of Caracas (MCNC) that we provisionally assigned as *Atractus* aff. *pamplonensis*, and their definitive evaluation will be in another article (Esqueda *et al.* in prep.). However, here we describe specimen MCNC 8269 for comparative purposes with the information provided by Schargel & García–Pérez (2002). Although both records share attributes with the information on *A. pamplonensis* provided by Passos *et al.* (2024), these authors point out another population in Colombia as *Atractus* aff. *pamplonensis* (MHUA–R 4867), whose hemipenial morphology can be very different from that defined for *A. pamplonensis* (v. fig 45 A and B, p. 55). Although this hemipenis is stained red, there is an extraordinary similarity with the hemipenis of *A. paisa* (Passos *et al.* 2009c: fig. 2B, p. 428). On the other hand, there are several strange entanglements in that description that warrant discussion: the description is based on a series of specimens, but upon observing and comparing figure 4 (MHUA 14274) and figure 5 (MHUA 14236), they are actually two distinct species. The first specimen presents a completely dark uniform coloration and comes from a locality in the central cordillera of Colombia (eastern

slope, Magdalena basin), about 312 km in a straight line from the type locality of *A. pamplonensis*, which would be in the oriental cordillera (western slope). Although Passos *et al.* (2009c) indicated that *A. paisa* would have 17 vs. 15 in *A. lasallei*, it is necessary to reevaluate its status. In fact, the holotype assigned to *A. paisa* Passos, Arredondo, Fernandes & Lynch, 2009 is ICN 10698, but in its description, there is information about the coloration in life that corresponds to the specimen MHUA 14236 (fig. 5, p. 430). Although the authors illustrate the holotype (fig. 6, p. 431), the provided lateral view v.ms very similar to the paratype MHUA 14274. In the same article, there is another error in the character state when describing *A. titanicus* Passos, Arredondo, Fernandes & Lynch, 2009, where the holotype (fig. 7, p. 432) clearly has a uniform dorsal coloration, while the specimen ICN 10697 has a banded dorsal pattern (fig. 8, p. 432), but curiously in their species definition they indicate "banded color pattern, with alternate dark and light dorsal rings (three scales wide)".

Conservation status

Our accumulated field data over several years tell us 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 (Aubret & Shine 2009), but with a reduced habitat breadth (< 20,000 km²) and frequently occurs in highlands (Böhm *et al.* 2017), such as other Neotropical snakes (e.g., viperids; Birskis–Barros *et al.* 2019). Until now, all environments above 1500 meters in altitude in the cordillera de Mérida have been seriously affected by anthropogenic activities (Ataroff & Rada 2000; Llambí 2015; Chacón–Moreno *et al.* 2021).

If we invoke the optimal foraging theory (Perry & Pianka 1997), it is possible to think that the spatial and temporal dimension of habitat disturbance could affect specialist reptiles like vermivorous snakes, but there are no studies demonstrating this in *Atractus*. Balestrin *et al.* (2007) are of the opinion 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 (Böhm *et al.* 2013). In fact, earthworms are considered ecosystem engineers, have been part of ecosystems for over 400 million years (Maggi &Tang 2021). In this sense, climate change, particularly extremes of drought and flooding, has been shown to directly affect earthworm communities by altering their activity, abundance, and

biomass. In addition, the indirect effects of anthropogenic activities on these communities remain poorly studied. Then said activities, which often result in soil contamination, also negatively affect epigean biota (Miglani *et al.* 2019; Singh *et al.* 2019), potentially affecting the abundance and distribution of *Atractus* in mountains where preexisting barriers are limiting.

In light of new evidence, we can conclude that *A. ochrosetrus* and *A. mijaresi* are valid species, that exhibit an allopatric and highly fragmented distribution due to the gradual deterioration of their environments; and although are 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 is among the five critical hotspots (Myers *et al.* 2000), the political–social crisis of recent decades has decimated any efforts in that direction (see de Sousa 2023). In fact, if we consider that Oliveira–Miranda *et al.* (2010) 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 lack of data (e.g., extraction of wood on Andean forests), the current outlook could be concerning for many reptile species, in particular specialist those like *Atractus* (e.g., *Urotheca multilineata*, Esqueda *et al.* in prep.).

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Data availability

All data generated or analyzed during this study are included in this published article (v. supplementary information files in format xlsx, except unpublished data that are not yet public until the time of their publication in the repository GENBANK). All unpublished specimens are not listed on the IUCN Red List of Threatened Species Index and met the standards required by the Ministerio de Ecosocialismo y Aguas (MINEC–Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE). All data generated or analyzed during this study are included in this published article (including supplementary information files).

Competing interests

The authors declare no competing interests.

Declaration of ethics

Not applicable

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CHAPTER IV

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A FIRST PHYLOGENETIC AND TAXONOMIC APPROACH TO SLEEPYHEAD SNAKES FROM VENEZUELA (DIPSADIDAE: *ATRACTUS*), WITH THE DESCRIPTION OF TWO NEW ANDEAN SPECIES

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ABSTRACT

This study constitutes the first evolutionary investigation that adds Venezuelan species of sleepyhead snakes of the genus *Atractus*, the most diverse and with the largest number of species with a restricted distribution area above 1000 m asl, whose estimated divergence occurred 21-22 MY. In this context, phylogenetic analyses using a combination of mitochondrial (16S, Cytb, ND4) and nuclear (RAG1, NT3) markers within the framework of Maximum Likelihood and Bayesian models, as well as morphological and meristic data, support the recognition of two new species that inhabit montane semideciduous forests and cloud forests between 1800-2200 m asl: *A.* sp. nov. a polymorphic species related to *A. meridensis*, instead, *A.* sp. nov. exhibits a uniform dorsal pattern very closely with *A. mariselae* and *A. mijaresi*, respectively. Finally, we provide new data on the diversity and distribution of the *Atractus* from the cordillera de Mérida, including a dichotomous key and a novel perception of their conservation status when considered the most diverse and dominant snakes of the Andean Mountain landscapes. *Atractus* sp. nov. and *Atractus* sp. nov. should be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv).

KEY WORDS. - Cryptozoic and semifossorial snakes, northern Andes, cordillera de Mérida, montane semideciduous forests and cloud forests, taxonomy and conservation

RESUMEN

Este estudio constituye la primera investigación a nivel evolutivo que agrega especies venezolanas de serpientes dormilonas del género *Atractus*, el más diverso y con el mayor número de especies de área de distribución restringida por encima de 1000 m snm, cuya divergencia estimada ocurrió hace 21-22 MA. En este contexto, los análisis filogenéticos utilizando una combinación de marcadores mitocondriales (16S, Cytb, ND4) y nucleares (RAG1, NT3) en el marco de modelos de Máxima Verosimilitud y Bayesiano, así como datos morfológicos y merísticos respaldan el reconocimiento de dos nuevas especies habitantes de los bosques semicaducifolios montanos y bosques nublados entre 1800-2200 m snm: *A.* sp. nov. una especie polimórfica relacionada con *A. meridensis*, en cambio, *A. xaxi* sp. nov. exhibe un patrón dorsal uniforme muy cercana con *A. mariselae* y *A. mijaresi*, respectivamente. Finalmente, proporcionamos nuevos datos acerca de la diversidad y distribución de la *Atractus* de la cordillera de Mérida, incluyendo una clave dicotómica y una percepción novel acerca de su estatus de conservación al considerarse las serpientes más diversas y dominantes de los paisajes montañosos andinos. *Atractus* sp. nov. y *Atractus* sp. nov. deberían incluirse en la categoría Vulnerable según los criterios IUCN Ac y B2(i,ii,iii,iv).

PALABRAS CLAVE. – serpientes criptozoicas y semifosoriales, Andes septentrionales, cordillera de Mérida, bosques semicadufolios montanos y bosques nublados, taxonomía y conservación

INTRODUCTION

The Neotropical region, with its 19 million km^2, is home to one of the highest levels of biodiversity on the planet, encompassing 36 "hotspot" areas where at least 70 % of the surface corresponds to mountainous regions (Myers et al. 2000; Mittermeier et al. 2011). This variety of ecosystems in both lowlands and mountains has acted as a museum or cradle of life due to a rich and complex paleogeographic and climatic history as an effect of the interaction of continental masses and associated island systems (Rull 2011; Hughes et al. 2013; Sonne et al. 2022; Vasconcelos et al. 2022). An example of this is the northern Andes, consisting of several mountain chains and drainages in Ecuador, Colombia and Venezuela. Paleo-elevation estimates suggest a tectonic history different from that of the Central Andes, with crustal deformation and collisions, allowing the northern mountain range to reach higher elevations (Gregory-Wodzicki 2000). However, the idea of rapid uplift during the Miocene or gradual uplift since the Eocene is still debated (Pérez-Escobar et al. 2022), although a recent reconstruction with paleo-altimetry data supports the idea that the uplift of the Andes has been a large diachronic process, with time and uplift rates varying significantly throughout its range (Boschman 2021).

In this orogenic context, a particular and unique case is the Mérida Andes or cordillera de Mérida, which includes a basal uplift ~100 km wide that extends in a NE-SW direction for about 400 km. Although it is located in the northeast extension of the Eastern cordillera of Colombia, it does not maintain a geomorphological relationship with it (Audemard and Audemard 2002; Audemard 2003), 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 (Bermúdez et al. 2011). It is considered a doubly vergent orogen with the wetter basin and wedge of the Lake Maracaibo basin on the northwest side and the drier basin and wedge of Barinas on the southeast side (Erikson et al. 2012). Although it covers an area of ~9.5 % of the country, it is more complex than any other nearby mountain system. Said 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 (Chacón-Moreno and Moral 2020). This complexity, includes at least two cycles of uplift between 8 and 5-2 Myr that allowed for different historical scenarios of isolation and diversification (vicariance + dispersion) over time, driving its

richness and endemism (Hazzi et al. 2018). For example, in *Atractus* their histories fit both paleo- and neoendemic models, suggesting increased climatic buffering has favored speciation in mid-high montane landscapes in northern South America, especially the northern Andes of Ecuador, Colombia, and Venezuela that harbor more than 50 % of known species. The general understanding of speciation is based on the idea that species arise from geographically isolated populations of the same ancestral species, with montane diversity being a typical example due to the topographic complexity and niche conservatism exhibited by many organisms, favoring opportunities for allopatric speciation.

Within reptiles, snakes comprise a global radiation that represents more than 10 % of the diversity of terrestrial vertebrates, exhibit high levels of speciation and endemism in the Neotropical region, and represent more than a third of all known species, especially driven by mountain environments (Bonaccorso and Guayasamin 2013; Roll et al. 2017; Guedes et al. 2018). In Caenophidia, the families Dipsadidae (Bonaparte, 1838), show one the most rapid rates of dietary change, with more than 700 known species (Grazziotin et al. 2012; Zaher et al. 2019). Among them, *Atractus* Wagler, 1828 is the most diverse genus, with 150 spp. known (Uetz et al. 2024), distributed from Panama to Argentina (Myers and Schargel 2006; Giraudo and Scrocchi 2000), and occupying different environments between 0-3200 m above sea level, with notable predominance in mountainous systems (~70 % of their diversity lives above 1000 m, unpublished data LFE 2024). Despite biogeographic uncertainty and descriptive generalities of its taxonomy in the past, at least in more than 70 % of the described taxa (Savage 1960; Roze 1966; Peters and Orejas-Miranda 1970; Pérez-Santos and Moreno 1988; Giraudo and Scrocchi 2000), in the last 13 years, important advances have been made in resolving the systematics of ground or sleepyhead snakes, especially by combining multiple evidences (Passos et al. 2010, 2012, 2016, 2018, 2022; Melo-Sampaio et al. 2019, 2021). On the other hand, this explosive interest in studying these snakes has allowed us to consolidate the idea of multiple scenarios that have favored a complex diversification where cryptic diversity and microendemism become increasingly evident with the advent of genomics (Melo-Sampaio et al. 2019, 2021; Arteaga et al. 2022). Although Passos et al. (2024) synonymized five species from the Venezuelan Andes, their criteria are insufficient and inconsistent, with errors in localities, misidentifications, and the absence of a phylogenetic analysis, which is why we

continue to maintain the recognition of 30 species of *Atractus* in Venezuela and 17 in the cordillera de Mérida (see Natera-Mumaw et al. 2015; Rivas et al. 2012). However, a more extensive response based on a review of ~400 specimens, with unpublished data in life and new approaches is being developed (Esqueda in prep.).

Combining multiple sources of evidence, such as mitochondrial and nuclear genetic data and morphological, we have discovered two new endemic species from the cordillera de Mérida. These species differ from all other species know by a unique combination of morphological characters and coloration patterns. The primary aim of this study is their taxonomic recognition and description based on diagnostic and comparative characters. Additionally, the recent discovery of these taxa in areas characterized by a mosaic of natural landscapes and novel environments knows as anthromes (Ellis et al. 2010) facilitates the assessment of their conservation status according to IUCN extinction risk categories. This assessment is based on habitat characterization and bioecological data, with a focus on microendemism and cryptic diversity.

MATERIALS AND METHODS

DNA extraction, amplification and sequencing

Regarding the specimens collected in the field (Luis Felipe Esqueda 2021, LFE), DNA was extracted in situ from different tissues such as intercostal muscles, liver and heart and preserved in 95 % ethanol. Additionally, each specimen was preserved in 95 % ethanol and later transferred to individual bottles whose ethanol concentration consisted of ~75 %. Other woven items conserved under the same protocol were provided as supplementary support to the project (e.g. MHNLS conserved material, Venezuela). DNA extractions and amplifications were carried out in the Laboratory of Systematics and Conservation of Herpetozoa (Lab SyCoH), Faculty of Natural and Oceanographic Sciences, University of Concepción, following the protocol defined by the PROMEGA USA kit (Wizard® SV Genomic DNA Purification System). The primers and PCR conditions used for the amplification of all defined genetic fragments are summarized in supplementary_1_Table 1. DNA amplifications and their concentrations were evaluated on 1.5 % agarose gels, stained with SYBR® Vitrogen and observed in a chamber UV transilluminator (MajorScience). The sequencing and purification of the amplifications

were generated by the company MACROGEN (Korea). Later, we verified the chromatograms and assembled the contings using Sequencher 4.7 (Gene Codes, Corp.) and manually with BioEdit 7.0.9.0 (Hall 1999), in addition, an open reading frame was verified for each gene (Mega v.11, Tamura et al. 2021). Since the DNA samples are diploid, the identification of haplotypes can be ambiguous, especially in regions where heterozygous individuals are observed (Audigeos et al. 2010). First, heterozygous sequences were identified visually by checking for double peaks (point mutations) in the chromatograms. Then, the inference of individual alleles (haplotypes) from nuclear sequences (RAG-1 and NT3) was reconstructed for each sequence-specimen item using DnaSP v 6.12 with 100 iterations, 1 thinning interval, 100 burning and a recombination modeling option (Librado and Rozas, 2009) by performing two independent runs. Alignments were unambiguous, with no intermediate gaps present in any of the mitochondrial genes for any of the *Atractus* in this study. Likewise, sequences corresponding to other species were available through the GenBank repository (supplementary_1_Table 2) and they complied with the rule that all amplified loci were obtained from a single specimen (a voucher deposited in a museum) to avoid "terminal chimeras".

Phylogenetic analyses

The new sequences generated in this study were combined with sequences downloaded from GenBank. Additionally, 20 specimens representing to 18 species were used as outgroups (highlighted in yellow, supplementary_1_Table 2). Five gene fragments were obtained, corresponding to three mitochondrial amplicons, long 16S ribosomal RNA (525 bp); cytochrome b (897 bp); and NADH dehydrogenase ND4 subunit IV (713 bp) and two nuclear amplicons, neurotrophin-3 gene NT3 (516 bp); recombination activator RAG-1 (879 bp). Substitution saturation of each locus was assessed using the software DAMBE v.5 (Xia 2013). 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 (Nguyen et al. 2015).

The authenticity of the obtained sequences and the homology of the specific mtDNA and nuDNA markers were evaluated with a BLAST search in the NCBI genetic database (http://blast.ncbi.nlm.nih.gov/Blast.cgi). The consensus sequences for each locus were aligned using MAFFT (Katoh and Standley 2013) contained in Jalview

v.2.11.1.4 (Waterhouse et al. 2009), 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 exhibit nucleotide positions with high entropy and may have misaligned or incongruent regions were refined with the BMGE software: a BLOSUM62 matrix, a minimum block size of 20, a maximum entropy threshold of 0.5, and a rate limit gap of 0.65 (Criscuolo and Gribaldo 2010), available on the web service https://ngphylogeny.fr/ (Lemoine et al. 2019). Finally, the concatenation of all alignments was done with Mesquite v3.6 (Maddison and Maddison 2021). 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 (Triant and Dewoody 2007).

The identification of the boundaries between the evaluated taxa began by calculating the average inter-intraspecific and distance using k_2P genetic distances for each of the mitochondrial genes in MEGA software v.11 (Kumar et al. 2018). In these methods, we use a parameter "d" (Transitions + Transversions), assuming uniform rates between sites and homogeneous patterns between lineages, while considering the proportional differences (p) between nucleotide sites where the two compared sequences differ. This was inferred by dividing the nucleotide differences by the total number of nucleotides (Tamura et al. 2021). Each run was performed with a bootstrap of 1,000. Although the p-distance model is popular, we alternatively chose the mutational models of Kimura 2 parameters (Kimura 1980; Kumar et al. 2018) and Tamura and Nei 3 parameters (Tamura 1992; Tamura and Kumar 2002) because they consider variable substitution rates between sites, unequal nucleotide frequencies, and different frequencies of transition and transversion events. These issues are particularly important when dealing with variation at the interspecific level, where simpler methods may tend to underestimate true divergence (Tamura and Nei 1993).

Firstly, we used maximum likelihood (ML) analysis to obtain the optimal tree topology of the concatenated data set. The best partition and substitution models were automatically selected using ModelFinder (Kalyaanamoorthy et al. 2017) and then implemented in IQ-TREE v.2 software (Nguyen et al. 2015) under the Bayesian information criterion (BIC). The best ML tree was selected from10,000 iterations and the confidence of the branches of the best ML tree was evaluated with the ultrafast bootstrap method using 10,000 bootstrap pseudoreplicates (Minh et al. 2013).

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/, Trifinopoulos et al. 2016), where branch support was calculated using the ultrafast bootstrap approximation (UFBS) (Minh et al. 2013) and the Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT) (Anisimova et al. 2011), with 1,000 replicas. The consensus tree was visualized in FigTree (Rambaut 2014). Nodes with bootstrap values ≥ 70 were considered strongly supported and those nodes with 95 % were considered highly supported.

Divergence time estimation and calibration points

We estimated divergence times of sleepyhead snakes of the genus *Atractus* using the Bayesian framework implemented in the BEAST 2.7.5 software (Bouckaert and Drummond 2017). For all analyses, the matrix was partitioning by genes, 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. Unlike previous analyses with maximum likelihood (ML) and Bayesian inference (BI), where the best partition schemes and molecular evolution models were defined using ModelFinder and Partition Finder in the integrated PhyloSuite platform (Zhang et al. 2020). Here, the BEAST 2.7.5 software implements the "bModelTest "allreversible" option to estimate mutation rates for all genes evaluated. When implemented, bModelTest switches between substitution models during the Metropolis coupled MCMC (MC3), inferring and marginalizing site models, thus averaging the uncertainty about those models (Bouckaert and Drummond 2017), except for partitions that were defined by PartitionFinder because bModelTest does not incorporate substitution models average site over partitions from alignment. While Bayesian relaxed clock methods may produce more correct estimates when using multiple loci (mtDNA + nuDNA) (Battistuzzi et al. 2010), it is unclear how using faster-evolving mitochondrial genes (animals) may influence dating by divergence in relation to the use of nuclear loci that have a slower rate of evolution (Zheng et al. 2011). Here, the likelihood ratio test (LRT) implemented in Mega v.11 software (Kumar et al. 2018) rejected strict clock evolution models, favoring the lognormal relaxed clock

model for all partitions. Although the classic uncorrelated relaxed clock (Drummond et al. 2006) works well when rates and branch lengths are not highly correlated, on the contrary, it is poor, so here we will use the "optimized relaxed clock" model according to Douglas et al. (2021) which works well in both scenarios. On the other hand, we will apply a birth-death speciation model (Kendall 1948) as opposed to the Yule model (Yule 1925), since this assumes zero extinction rates and it is commonly known that extinction is extremely significant in the diversification of species (Sarver et al. 2019). Other antecedents were set to their default values, except the birth rate, which had an exponential distribution (lower 0.1 and upper 10).

Phylogenetic analyses often involve data sets comprising sequences from multiple loci. A common practice is to partition the data set, for example, by gene or by codon position, and assign separate substitution models to subsets of the data (Yang and Kumar 1996). In molecular clock analyses, the simplest approach is to apply a single model of rate variation between lineages to the entire sequence alignment. However, this approach does not account for heterogeneity between genes, which may have evolved under very different conditions. For instance, multilocus data sets may include combinations of markers from mitochondrial, chloroplast, and nuclear genomes. An ideal scenario for calibrating phylogenetic trees is when they are obtained from well-dated fossils; however, the incomplete or imperfect nature of the fossil record often only provides evidence of the minimum age of a clade, potentially leading to overestimation divergence time (Lukoschek et al. 2012). In fact, fossils rarely represent specific nodes but rather points along a branch (Lee 1999; Conroy and van Tuinen 2003).

On the other hand, multiple underlying factors can contribute to inaccurately calibrated clocks (e.g., patterns of evolution, saturation, and/or combinations of genes that evolve more rapidly vs. others that evolve more slowly). In snakes, the Caenophidia group contains the greatest diversity of extant snakes (> 2500 spp., Uetz et al. 2024) and includes acrochordids, xenodermids and all colubriforms (Pyron et al. 2013), a group with a controversial fossil record (Head 2015; Head et al. 2016). Considering the countless setbacks that persist in obtaining ultrametric trees (Lukoschek et al. 2012), there is greater consensus on using multiple independent calibrations of fossils (Ho and Phillips 2009). In our case, the calibration points of the nodes were defined based on the available fossil record (one corresponding to Colubridae and four positioned in the external groups), using ages and interpretations of fossils similar to those described in

Zaher et al (2018; 2019) and García-Sotelo et al. (2021) (supplementary_1_Table 3). We use Metropolis coupled MCMC (MC3, Atchadé et al. 2011; Maturana-Russel et al. 2018; Müller and Bouckaert 2019), with a temperature of 0.02 and four chains, established in three independent runs of 50 million generations, saving the parameters and trees every 10,000 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 (Rambaut et al. 2022). Combining the runs was done with LogCombiner v2.7.5 (Drummond et al. 2012). After performing a 10 % burning, the maximum credible tree was obtained by using TreeAnnotator 2.7.5 (Rambaut and Drummond 2016) implemented on the CIPRES Science Gateway online platform (https://www.phylo.org/) (Miller et al. 2010).

Sample Source

This study includes the review of 292 specimens collected in the field during 2021 north of the Orinoco River, whose scientific hunting permits and access to genetic resources were processed and approved before the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE) and posteriorly deposited in the Museum of Zoology of the University of Concepción, Chile (MZUC). Also, we examine specimens deposited in the Colección de Vertebrados de la Universidad de Los Andes, Mérida, Venezuela (CVULA); Museo de la Estación Biológica de Rancho Grande, Aragua, Venezuela (EBRG); Laboratorio de Biogeografía, Universidad de Los Andes, Mérida, Venezuela (ULABG); Museo de Ciencias Naturales de Caracas, Venezuela (MCNC); Museo de Ciencias Naturales La Salle, Caracas, Venezuela (MHNLS); Museo de Biología de la Universidad Central de Venezuela (MBUCV); Museo de Zoología de la Universidad del Zulia (MBLUZ); Museum Comparative of Zoology, University of Harvard, USA (MCZ) and Field Museum Natural History, University of Chicago, USA (FMNH). Information on collected and/or museum specimens examined for each species is provided in supplementary_1_Table 4.

Morphometric and morphological data

Previously, all available information about Venezuelan species (Boulenger 1903; Roze 1961, 1966; Lancini 1969; González-Sponga 1971; Barros 2000; Schargel and García-Pérez 2002; Markezich and Barrio-Amorós 2004; Sánchez et al. 2004; Esqueda and La

Marca 2005; Kok 2006; Myers and Schargel 2006; Esqueda et al. 2007; Passos et al. 2009b, 2013; Esqueda 2011; Natera-Mumaw et al. 2015) and other related species from Colombia (Pérez-Santos y Moreno 1988; Passos et al. 2009a, 2009e; Passos et al. 2010; Meneses-Pelayo and Passos 2019), Ecuador (Schargel et al. 2013; Salazar-Valenzuela et al. 2014; Arteaga et al. 2017, 2022) and Brazil (Cuhna and Nascimento 1983; Martins and Oliveira 1993; Passos et al. 2005, 2009d, 2010, 2022) were reviewed.

For each specimen of the species evaluated, including candidate species, detailed descriptions of meristic and morphological characters were available, defined in five informative categories: (1) scutellation, encompassing the head and body; (2) measurements of total length and tail, along with certain cephalic scutellation measurements; (3) coloration in life and/or preserved; (4) structure and systematic characteristics of the hemipenis, and (5) cranial osteology, particularly regarding the maxillary bone and teeth. The latter three depends on items the availability of information, although hemipenial and osteological data were included whenever possible.

With respect to scutellation, the terminology for head shields, dorsal, ventral and subcaudal counts for the genus *Atractus* follows that indicated by Dowling (1951), Savage (1960), Hoogmoed (1980), Myers (2003) and Natera-Mumaw et al. (2015). Due to their taxonomic importance in the genus, some characters are defined as follows: rostral scute in dorsal view, there can be defined as three states: condition A, 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; apical width is less than the distance between nostrils. Condition B, something visible from above, where the distal portion of the scale exceeds the imaginary line, usually narrow toward its distal portion; apical width less or equal than the distance between nostrils, but does not exceed the internasal suture and (C) distinctly visible, with the scale measured between its supralabial contacts, always forming an obtuse angle and above the imaginary straight line between nostrils; apical width > 0.5 than the distance between 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 which can be quantitatively verified if compared with the interocular distance.

Contact between the first supralabial and rostral scale in lateral view, can be short-moderate contact, occurs when less than or equal the height of the supralabial (see figures of new species) and ample contact, it happens when it exceeds half the height of the supralabial (see figures of new species). Eye-Loreal contact, being narrow, when it is less than half of the suture between prefrontal and postnasal and wider; when its width is at least half or more of the width of prefrontal suture and postnasal, so it is similar to its width towards the contact with the postnasal. Eye-Prefrontal contact narrow, smaller than the prefrontal-postnasal suture and extensive when it is greater than half, equal to or larger than the prefrontal-postnasal suture.

Here, we follow the proposal made by Natera–Mumaw *et al.* (2015) for loreal scale, a short loreal (condition A), occurs when its length is less than HED and always in contact with two supralabials (e.g.,, *A. elaps*, *A. latifrons*, and *A. steyermarki*, Savage 1960; Passos *et al.* 2013; Almeida *et al.* 2014); moderate loreal (condition B), occur when its length is greater than HED, but ≤ 1.5 times HED, 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 contacts previously are less than the height of loreal measured at the angle between supralabial and another state occurs when ALO is greater than the margin between loreal and anterior supralabial in contact. Finally, elongated loreal (condition C), occurs when its length is greater than 1.5 times HED, frequently in contact with three supralabials, the margin between loreal and anterior supralabial is greater than ALO (e.g., *A. torquatus*, *A. ochrosetrus* and *A. heyeri* Esqueda, 2015; Natera–Mumaw *et al.* 2015). However, exist exceptions where with an elongated loreal, only two supralabials are in contact, just as it happens with *A. emigdioi* Sponga, 1971 and *A. multidentatus* Passos, Rivas-Fuenmayor & Barrio-Amorós, 2009 (see also species from Ecuador; Arteaga *et al.* 2017, 2022). In each case mentioned, we can find that the margin between loreal and anterior supralabial can be less or greater than ALO, and relating to condition B, there may be exceptionally individuals with loreal in contact with three supralabial (e.g., *A. ventrimaculatus*, LFE unpublished data). On the other hand, we consider three types of snouts in dorsal view: one short with an FRD equal to or less than 1.5 times END, moderate between 1.5–2 times END, and long greater than 2.5 times END.

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 there are one or two in contact with the

supralabial when the mouth is closed in lateral view (see figures of new species), therefore, it is defined how many infralabials are in contact with the greats. Sublabial scale, has gone unnoticed but is confused in the descriptions, this scale has two states, in contact with each other, it occurs when separating the middle gular from the posterior contact with the geneials; some authors in the past have considered it a second pair of genials; in fact, in the genus *Geophis*, many of its species often have this characteristic (see Downs 1967). Two scales that tend to be conflictive and whose usefulness has not been clearly defined (we have personally observed intraspecific variability), are the gulars and preventral (s). In the first order of ventral arrangement of the head, genials is arranged along the head, posteriorly begins the gular rows and between sublabials (first gular that contacts with geneials). Next, there are several preventral ones, less wide than the ventral ones in the strict sense, in lateral contact with the first dorsal rows behind the parietal ones. The remaining scales of the body, both dorsally and ventrally, have a definition and count that follow what was previously known. Melo-Sampaio and Venegas (2023) when describing a new species from Peru, pointed out the presence of apical pits, an attribute absent in all the other species that we know. Later, it will be necessary for an exhaustive analysis (electron microscopy) to corroborate or not, which makes us assume that it could be more of a conservation artifact. For all measurements and descriptions of cephalic scutellation they are strictly based on the right side of the head but verified on both sides.

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

Here, we consider dorsal and ventral coloration in life as the first distinguishing option among *Atractus*, since some details are lost during preservation. Dorsal body pattern is divided into three sections, vertebral, paravertebral, and dorsolateral. Here we differentiate 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 longitudinal lines or stripes, these can be narrow (< a dorsal scale) or wide (> a dorsal scale), continuous or discontinuous and arranged in any section of the dorsal region. If we consider the previous arguments, exist three base patterns with variants: one uniform without blotches, dots, or lines-stripes, with 1-3 differentiated dorsal rows (light in preserved and reddish, yellowish, or cream in life); blotched or dotted, where the blotches or dots may or may not be circumscribed, marginated or unmarginated, and with one or more lines-stripes an along the body. The ventral surface of the body and tail, consist of three patterns and their variants, the first is considered immaculate, and may sometimes have small scattered dots or blotches but which do not occupy 15 % of the scale surface; blotches or dots disposed horizontally on the scale, giving the impression of one or varies discontinuous lines-stripes, it may be little evident anteriorly and intensifies towards the cloaca; interspersed or irregular blotches, forming blocks that occupy at least 60 % of the scale, sometimes a wide line is observed medially and finally the ventral region is completely stained, less common than the other patterns.

The maxillary bone of one or several specimens was extracted (left sides) and posteriorly cleaned using KOH 3 % by 10 minutes and distilled water for 10 hours. Then scale photos were taken using an Olympus E620 camera fixed to brand stereoscopic 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 (1988), modified by Pesantes (1994) and Zaher (1999) for snakes. Passos et al. (2016) replaced the KOH indicated in Pesantes (1994) with distilled water. We adopted both procedures, but in a different way, which was a successful way to achieve organ extension. The most common is that the hemipenes have not been previously partially or totally extracted at the time of conservation of the specimen, being fixed with formaldehyde and/or ethanol, where the first option exists

much more rigidity and mostly the tail could have been fixed with little formaldehyde (pers. obs. LFE). 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 emersion stations were established, the first with distilled water at 60 ºC for 2-3 minutes, the second with 3 % KOH for one minute and the third with distilled water at room temperature for 10-30 minutes. If the time is right, you will be able to see the organ in a transparent amber color, otherwise, do stations 1 and 3 again. Before starting to use the burnisher to extend the tissue, it is advisable to inject glycerin + water into the tissue from the base that connects with the muscle. This procedure guarantees that when the burnisher is introduced, it can move due to lubrication, with retraction movements that allow the extension of the hemipenis to be observed. Once the extension of the hemipenis has been achieved, vaseline or glycerin + water is injected and the base is tied, then it is immersed in a solution of 70 % ethanol and alizarin red or candle color for about 10 minutes, and finally it is stored in an Eppendorf with glycerin. With respect to the calcareous structures ornamentation, according to Uzzell (1973) and Harvey and Embert (2008), the qualitative and quantitative description of hemipenial characters follows Dowling and Savage (1960), Uzzell (1973), Zaher (1999), Schargel and Castoe (2003); Myers and Cadle (2003); Zaher and Prudente (2003); Myers and McDowell (2014) and Passos et al. (2016). Although the term “diastema” has been considered in the past for this group of snakes, being a distinctive character (e.g. Passos et al. 2009a,c, Passos and Lynch 2010). Hence, we will talk about space and/or reduction between the last teeth, following the indicated by Oliveira et al. (2023), who recognize that goo-eating dipsadines do not present diastema.

RESULTS

PHYLOGENETIC INFORMATION

The final concatenated molecular data set 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 % and 63 sequences in RAG-1: 879 bp, 90 informative sites, 95 singleton, 694 sites preserved, missing data 0-18 %). 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 (Fig. 1) and BI (Fig. 2) analyses are consistent and similar in topology, suggesting that the data provide a robust phylogenetic signal recognized by both methods. However, the node support within *Atractus* was generally <0.5 in for BI. Differences in support between ML and IB may stem from the way these methods handle uncertainty and evolution models (Alfaro et al. 2003; Holder and Lewis 2003; Yang and Rannala 2012). In our study, posterior probability values above 0.95 were considered strongly supported, values between 0.7 and 0.95 was moderately supported, and below 0.7 as weakly supported. The monophyly of *Atractus* was well-supported in the ML analysis, where it was divided into two major lineages (ML and BI).

Our time-calibrated phylogeny recovered estimates the most recent common ancestor (TMRCA) of *Atractus* at 22.29 Myr during the Early Miocene (95% HDP = 17.8-25.79). **Lineage A:** TMRCA of 20.57 Myr (95% HDP = 17.15-23.89), comprising of clade *A. ochrosetrus* and *A. ventrimaculatus* + *A. trilineatus* with a TMRCA age of 17.36 Myr (95% HDP = 13.56-21.28); clade of *A. matthewi* + *A. vittatus* with a TMRCA age of 15.71 Myr (95% HDP = 10.74-19.78); Venezuelan Andean clade of *A. emigdioi* and *A. taphorni* with a TMRCA age of 3.87 Myr (95% HDP = 1.92-6.34); Venezuelan Andean clade of *A. mariselae*, *A. xaxi* sp. nov. and *A. mijaresi* + *A. erythromelas*, *A. meridensis* and *A. nemosophis* sp. nov. with a TMRCA age of 10.88 Myr (95% HDP = 8.81-13.58); Ecuadorian Pacific clade of *A. roulei*, *A. michaelbalsani* and *A. carrioni* with a TMRCA age of 14.63 Myr (95% HDP = 10.6-17.69) and clade of *A. major*, *A. arangoi*, *A. fuliginosus*, *A. insipidus* and *A. sp*. with a TMRCA age of 9.84 Myr (95% HDP = 6.77-13.85). The **lineage B** has a TMRCA of 21.22 Myr (95% HDP = 17.8-22.57) are includes: clade of *A. multicinctus*, *A. imperfectus* and *A. lasallei* with a TMRCA age of 17.05 (95% HDP = 17.8-22.57) , clade of *A. albuquerquei*, *A. elaps* and *A. latifrons* with a TMRCA age of 16.61 Myr (95% HDP = 12.68-20.23), clade of *A. riveroi*, *A. flammigerus* and *A. torquatus* with an age TMRCA of 14.83 Myr (95%

HDP = 11.68-17.54), clade of *A. badius*, *A. favae* and *A. steyermarki* with a TMRCA age of 15.5 Myr (95% HDP = 11.6-18.22) and clade of *A. ukupacha* + *A. atlas*, *A. touzeti*, *A. discovery*, *A. resplendens*, *A. ecuadorensis*, *A. duboisi* and *A. orcesi* + *A. zgap*, *A.* cf. *schach*, *A. dapsilis*, *A. schach* and *A. trefauti* + *A. pachacamac* and *A. snethlageae* with a TMRCA age of 15.28 (95% HDP = 12.12-18.27).

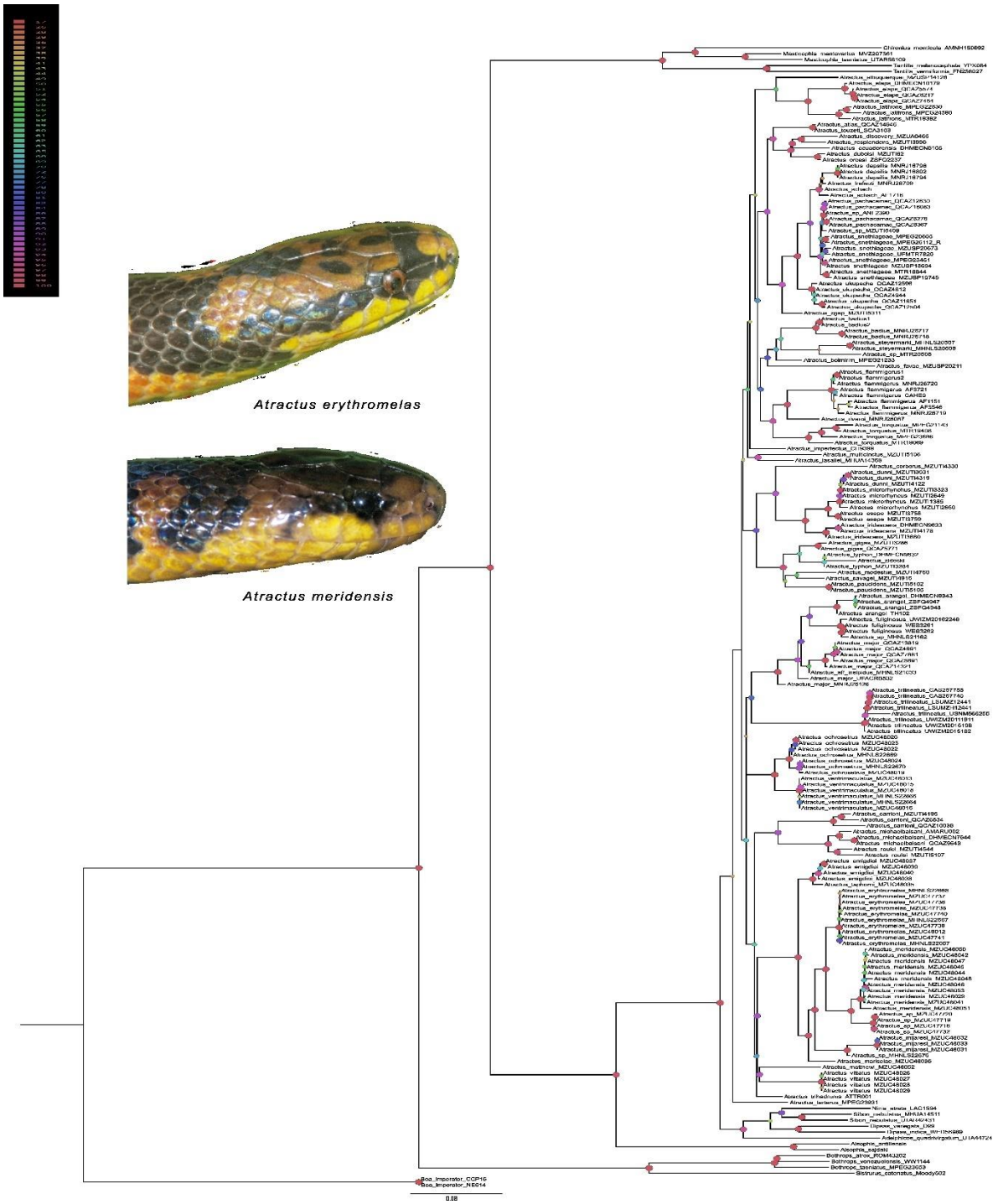


FIGURE 28. Maximum likelihood (ML) tree was estimated of Iqtree, showing the relationships among some South American species of *Atractus*. Information on bootstrap values >70 % in ML are shown, left side.

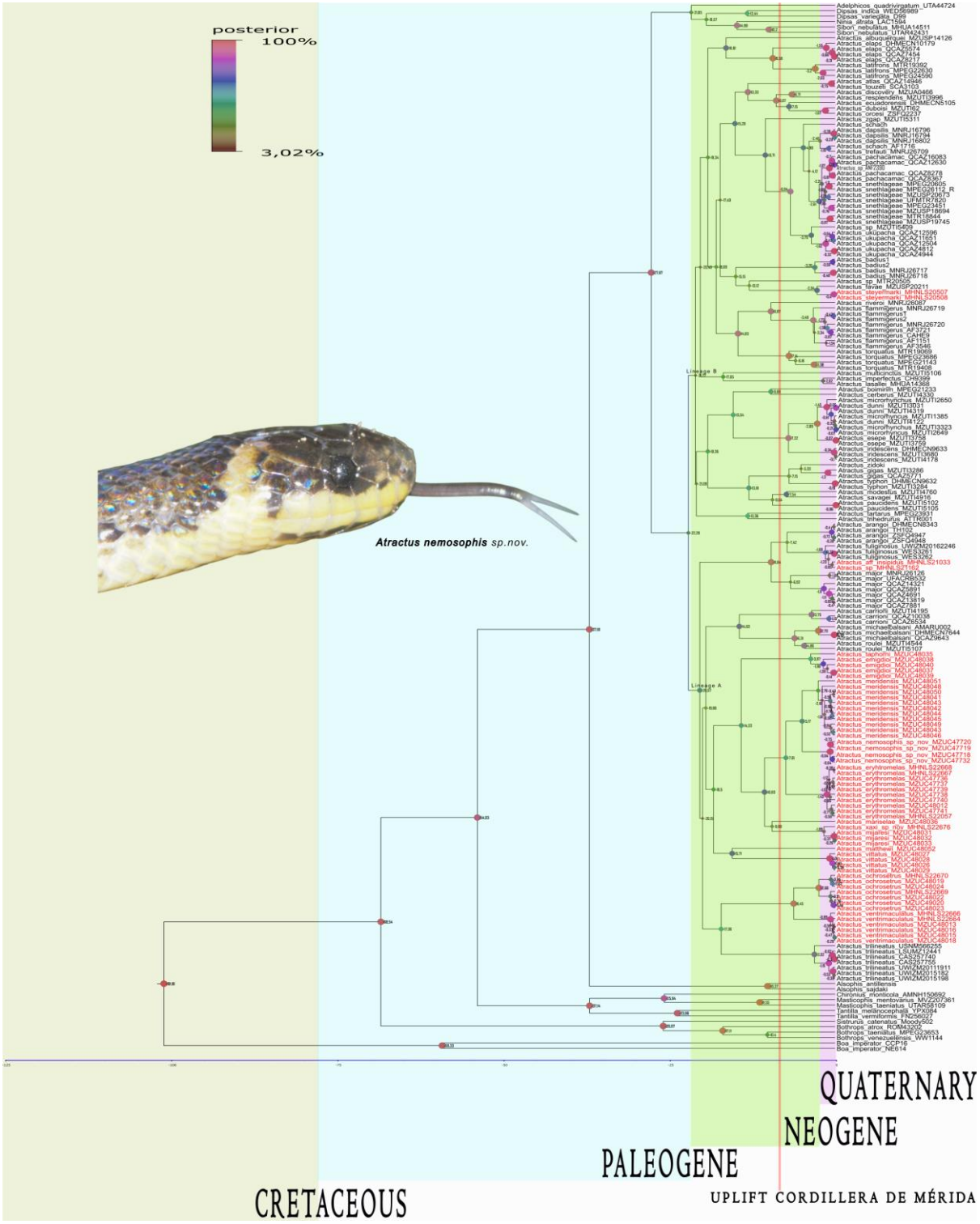


FIGURE 29. Bayesian inference tree along with divergence time estimation under the topology. Beast posterior probability values symbol >0.95 (*). Bars on nodes represent the 95% credibility interval of divergence times.

SYSTEMATICS

Taxonomic decision

Here we adopt the idea of the general concept of species lineage, referring to species as unique lineages of metapopulations that have evolved separately (de Queiroz 1998; 2007). This approach considers different lines of evidence (operational criteria) relevant to evaluating the separation of the lineage, although phenotypic discontinuities between groups of organisms reflect only selective advantages of particular trait packages (e.g. speciation), species constitute temporary fragments of stabilized lineages (Dupré 2024). Therefore, agreement is sought between the topology of the molecular hypothesis derived from the relevant methods and the phenotypic evidence of discrete and continuous characters, defined as descriptors that are not correlated with each other and that represent independent evidence of robust limits between species. In this sense, we support the idea of integrative taxonomy for species delimitation, where one or more characters are used to define putative species (Padial et al. 2010).

Atractus nemosophis sp. nov. Esqueda, Rojas-Runjaic, Prudente, Bazó, Navarrete, Camargo-Sillet, Ortiz, Correa, Guerrero & Urra

ZooBank LSID urn:lsid:zoobank.org:act:D6982B35-FA9C-4322-ADE2-C865DF0DF896

Holotype. - Adult female, MZUC 47720 (field Nº LFE237), collected under a rock, being a place intervened with remnants of a semicadufolious forest and the incorporation of grassland for livestock (Anthromes), next to the road that goes from Alto Tomón to Monte Carmelo, 9°12'42.32" N and 70°44'0.16"O, 1890 m, Trujillo state, Venezuela. Obtained by Luis Felipe Esqueda and Héctor García, at 12:12 p.m. on 21 June 2021.

Paratypes (type locality). – Five adult males, MZUC 47718-19 (field Nº LFE 238-239); MZUC 47725 (field Nº LFE 410), MZUC 47729 (field Nº LFE 413), MZUC 47730 (field Nº LFE 417) and subadult male MZUC 477722 (field Nº LFE 241); four adult females, MZUC 47724 (field Nº LFE 409), MZUC 47727 (field Nº LFE 414), MZUC 477128 (field Nº LFE 412), MZUC 47731 (field Nº LFE 418); three juveniles,

MZUC 47721 (field Nº LFE 240); MZUC 47723 (field Nº LFE 242, probably female) and MZUC 47726 (field Nº 411).

Paratypes. - One adult male, MZUC 47732 (field Nº LFE 257), collected under rocks piled next to a cultivation area in the La Quebrada sector, 9°7'42.34"N and 70°36'29.62"W, 1864 m altitude, Trujillo state, Venezuela. Obtained by Santos Bazó and Luis Felipe Esqueda on 22 June 2021 at 12:00 p.m.; three juveniles, MZUC 47733 (field Nº LFE 259) and MZUC 47734 (field Nº LFE 436), collected under some rocks on the edge of the road that leads from La Quebrada to Montero, 9° 7'29.52"N and 70°36'46.26 "W, 2014 m altitude, Trujillo state, Venezuela. Obtained by Luis Felipe and Santos Bazó 21 June 2021 at 10:25 p.m. and MZUC 47735 (field Nº LFE 404), collected under a rock on the edge of the road that leads from La Montañita to Tuñame, 9°3'42.05"N and 70°39'12.43"W, 2404 m altitude, Trujillo state, Venezuela. Obtained by Luis Felipe Esqueda and Santos Bazó 2 October 2021 at 11:30 a.m.

Etymology. - The specific name is an adjective derived from the Greek words "NEMOS, which means forest or wood with pasture for cattle, and OPHIS m., which means snake" (Brown 1956), to refer to the place where it was found, which originally corresponds to a semicaducifolious forest Andean montane (Ataroff and Sarmiento 2004), but currently they have been transformed, giving rise to new novel landscapes called anthromes (Ellis et al. 2010).

Definition and diagnosis. - (1) 17-17-17 dorsal scales, smooth and without apical pits; (2); moderated and pentagonal loreal, narrow towards the eye, lower margin form a convex angle between the second and third supralabial; (3) supralabial-rostral contact wide, ≥ than the eye-loreal contact; (4) hexagonal frontal shield, slightly longer than wide and often 80-90 % of the prefrontal suture; (5) frequently posterior supratemporal is elongated and there is always one side with the extension; (6) rostral visible from above and trapezoidal, distal margin well above the imaginary straight line between nostrils; (7) moderate-wide prefrontal-eye contact, as long as loreal-eye contact; (8) frequently internasals are wider than long, sutured 2 or 2 ½ times with respect to the prefrontal suture; (9) 7(3,4)/7(3,4) supralabials and third elongated, slightly longer than the horizontal diameter of the eye; (10) 6(3)/6(3) infralabials; (11) 158-177 ventral scales in males and 190-173 in females; (12) 41-36 subcaudal scales in males and 31-23 in females; (13) 5-6 maxillary teeth and lateral process well developed; (14) moderately bilobed, semicapitate, semicalyculate hemipenis; lobes of similar size, centrifugally

oriented, distinct and restricted to distal portion of capitulum, subcylindrical with flattened apices; (15) an incomplete light transversal band behind parietals conspicuous in juveniles, adults weakly defined; (16) polymorphic dorsal pattern, the most common being reddish or reddish brown, with or without a black vertebral line. Another frequent pattern is the grayish-brown dorsum, without a vertebral line but with small dark spots scattered irregularly along the body and a third less frequent pattern is the uniform grayish brown dorsum. In the last two patterns, on third dorsal row there are cream small spots forming a discontinuous line; (17) background color is always cream, except in specimens with the reddish-brown or reddish dorsal pattern, which have a reddish background and black spots that become more pronounced towards the cloaca. The spots have regular shapes and dispositions, usually they are aligned horizontally, others there may be a mid-ventral line of spots visible in their anterior portion; (18) ventral coloration of the head is similar to the body, but all specimens have spots on the infralabials and mental that together constitute a black horseshoe-shaped spot; (19) subcaudals black in life, few light spaces; (20) anterior third of tongue cream or grayish; (21) maximum total length in males 419.9 mm and 470.1 in females.

We currently know that the different species of *Atractus* evaluated in terms of their phylogenetic relationships and that occupy mountain environments exhibit diversification in situ (data in preparation and publication LFE 2024). In this sense, the different coloration patterns that we found are the result of evolutionary convergence, so our species exhibits a set of characters that, until now, were not observed in mountain species north of the Orinoco River, Venezuela. However, it is separated from *Atractus ochrosetrus*, *A. ventrimaculatus*, *A. taphorni*, *A. vittatus* and *A. trilineatus* because they have 15 dorsal scales in the middle of the body vs. 17 dorsal scales (Roze 1966; Esqueda et al. 2005; Natera-Mumaw et al. 2015); a yellow ventral coloration with or without dark spots, rostral barely visible from above and short supralabial-rostral contact is distinctive of *A. fuliginosus*, *A. turikensis*, *A. pamplonensis* and *A. matthewi* vs. reddish or cream, with well-defined dark spots, usually arranged horizontally, rostral visible from above and wide supralabial-rostral contact. The presence of 8 supralabial scales, loreal in contact with three supralabials, short supralabial-rostral contact, four infralabials in contact with geneials are distinguishable attributes of *A. mariselae*, *A. heyeri*, *A. micheleae* and *A. lancinii* vs. 7 supralabials, loreal in contact with two supralabials, wide supralabial-rostral contact and three infralabials in contact with

geneials. < 170 ventrals in females, rostral barely visible from above, frontal subtriangular and subcaudals weakly stained are distinctive characters of *A. acheronius* vs. > 170 ventrals in females, rostral visible from above, frontal hexagonal and subcaudals strongly stained. Therefore, it differs from *A. multidentatus* because it has a triangular rostral, rostral barely visible from above, short supralabial-rostral contact, compressed and slightly obtuse snout in dorsal view and 8 supralabials vs. hexagonal rostral, rostral visible from above, wide supralabial-rostral contact, snout wide and rounded in dorsal view and 7 supralabials. A mimetic and polymorphic species is *A. erythromelas*, whose frequent pattern consists of interspersed red-black or white-black bands, less common is an emerging pattern consisting of yellowish-black bands and the back is uniformly reddish but without lines and which is distinctive with respect to the new species that does not have bands and when the color is reddish, it exhibits a dark vertebral line. Regarding to the block of *Atractus* distributed towards the southwest of the cordillera de Mérida, which are *A. pamplonensis* and *A. tamaensis*, they have a yellow venter in life, weakly spotted subcaudals, rostral barely visible from above, short supralabial-rostral contact vs. ventral surface reddish or cream-grayish with or without dark spots, subcaudals strongly pigmented black, rostral visible from above and supralabial-rostral contact wide. In *Atractus mijaresi*, a species distributed in the cordillera de Mérida, since it has a rostral barely visible from above, < 175 ventral scales in females, short supralabial-rostral contact, and ventral surface in life pink or light yellow with dark spots arranged laterally and forming a dashed line vs. rostral visible from above, > 175 ventral scales in females, wide supralabial-rostral contact, and ventral surface reddish or cream-grey, but dark spots arranged horizontally on the scale. While *A. ayeush* has four infralabials in contact with the genials, rostral barely visible from above and light band behind the parietals absent vs. three infralabials in contact with the genials, rostral visible from above and a light band present in juveniles (Esqueda 2011). Finally, throughout the distribution that we have detected the new species, it is in sympatry with *Atractus eriki, A. emigdioi and A. meridensis*. In the case of *A. eriki* and *A. emigdioi*, is differentiated because they have the rostral scale barely visible from above, without a clear transverse band behind the parietals in adults and juveniles, short supralabial-rostral contact, less than 175 ventral scales in females and light or intense yellow, pink or orange background on the ventral surface vs. rostral scale visible from above, a light transverse band behind the parietals present, broad supralabial-rostral contact, more than 175 ventral scales in females and cream or reddish

background on the ventral surface. Finally, *A. meridensis* is distinguished by having the body alternating with light and dark bands or bars, without a light band behind the parietals in juveniles, hemipenis with subcylindrical and distally flat lobes and bifurcation of the spermatic sulcus is located in the distal part of the body hemipenial vs. dorsal pattern variable, may be uniform, with small spots, with a dark mid-dorsal longitudinal line and a light longitudinal line between the third and fourth row of dorsal scales; light transverse band behind the parietals present in juveniles, poorly defined in adults; hemipenis with attenuated and clavate lobes, bifurcation of the spermatic sulcus situated in the middle or lower of the hemipenial body.

Description of the holotype. - Adult female (Fig. 3). Total length 470.1 mm; tail length 39.7 mm; relation TaL/TL 0.08; head length 11.9 mm; head width between commissures 6.32 mm; parietal suture length 3.8 mm; frontal shield length 3.8 mm; previously measured frontal shield width 3.3 mm; prefrontal suture length 2.3 mm; internasal suture length 0.7 mm; distance between frontal and rostral 3.1 mm; distance between eye 4.6 mm; distance between nostrils 2.9 mm; first temporal scale length 2.4 mm; horizontal eye diameter 1.78 mm; loreal scale length 2.23 mm; eye-nostril distance 3.2 mm; length of the first supralabial in contact with the ocular orbit 1.6 mm; suture length between geneials 3.83 mm; rostral scales width, measured at the base that contacts the supralabial 2.28 mm; distal width of the rostral measured between nostrils 1.5 mm; width at the middle of the body 10.91 mm.

Head differentiated of the body, longer than wide, snout not compressed in dorsal view, truncate and relation ID/ND 0.62 (>50 %, is considered wide); frontal shield slightly longer than wide (Fig. 3A), same as parietal suture, with anterior margins slightly convex; FRD/HL ratio 0.26, almost a third of the head so it is considered an elongated snout; rostral well visible from above, in frontal view trapezoidal, wider than tall; two prefrontals, contact with the ocular orbit 0.4 mm and just shorter than the eye-real contact 0.5 mm; two internasals, wider than long, with a suture 3.3 times shorter than the prefrontal suture; two elongated supraoculars, wider posteriorly. Eye moderate, snout slightly rounded in lateral view; moderated loreal scale, narrow towards the eye, in contact with the second and third supralabial scales (Fig. 3B-C); postnasal arranged vertically, irregularly hexagonal and taller than wide; nostril located above the prenasal that is subtriangular; first supralabial enlarged, its contact with the rostral wide (> 0.5 HED) (Fig. 3D); two elongated postoculars, similar in proportion; 1+2 temporals, first

temporal elongated, 1.35 longer than the horizontal diameter of the eye; 7(3,4)/7(3,4) supralabials, elongated third supralabials, 0.9 with respect to HED; mental scale small and subtriangular; 6(4)/6(3) infralabials; a single pair of geneials (Fig. 3E), suture 1.2 to the NBD; 1/1 sublabial, separated from each other by a wide gular scale; three gular and one preventral; 181 ventral scales; subcaudal scales 23; 17-17-17 dorsal scales, smooth and without apical pits, nine dorsocaudals around the fifth-sixth subcaudal. Right maxillary bone extracted (Fig. 3F), anteriorly over the second tooth widened, giving the impression of being slightly arched upwards in lateral view, narrower backwards, curved inwards and almost flattened; space not defined, five angular teeth decreasing in size towards backward and spaced, being the last one small and hidden; lateral process poorly developed and situated at level the second tooth.

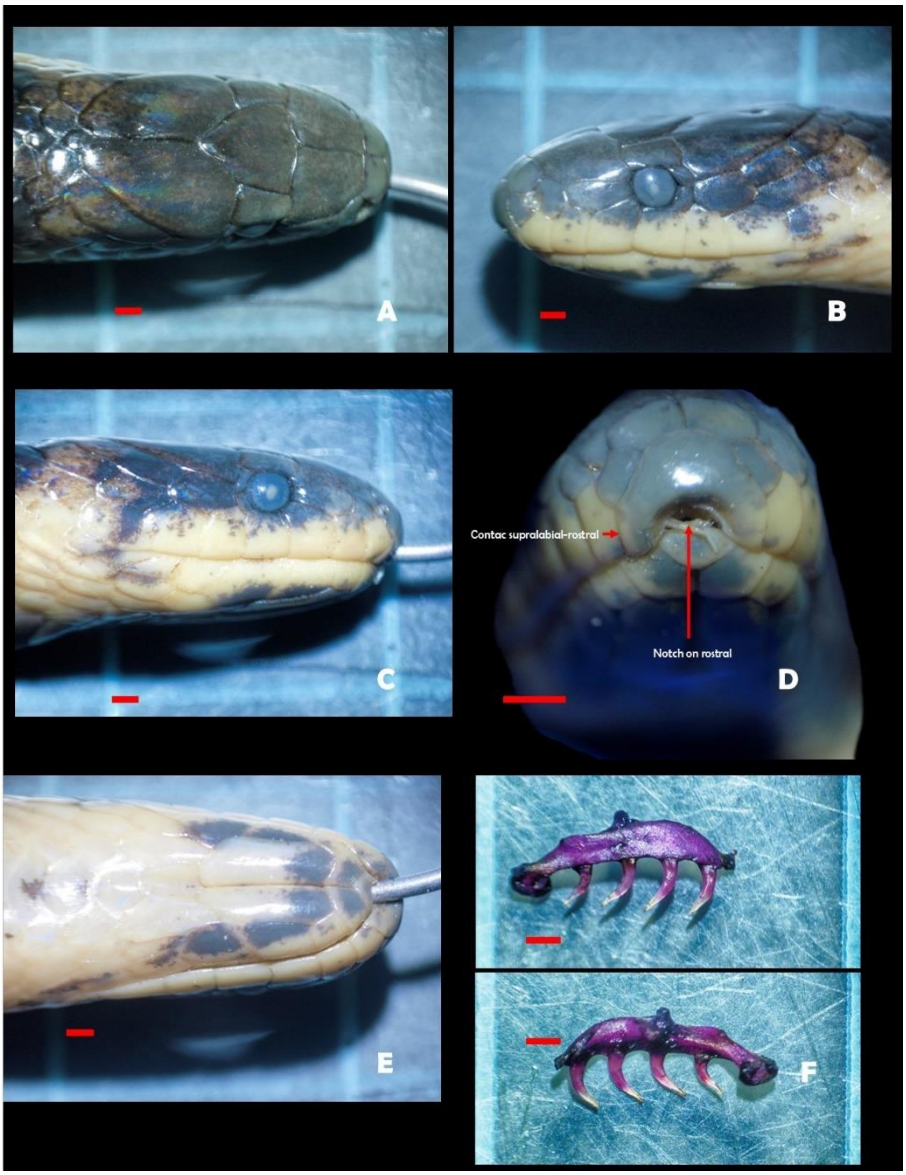


FIGURE 30. Preserved holotype (MZUC 47720, field Nº LFE237): Dorsal view of the head (A); lateral views of the head, right and left sides (B-C); frontal view of the head (D), highlighting the supralabial-rostral contact, a distinctive character of the species; ventral view of the head (E); anterior and posterior views of the right maxillary bone (F). Scale: 1 mm.

Color in life (notes LFE 2021): head dark brown dorsally and with the supralabial region slightly reddish with cream spaces, differentiated from the dorsal pattern of the body, which has a reddish-brown background with black spots arranged on the vertebral region, giving the impression of a not completely continuous line; Other small black spots are arranged irregularly along the dorsolateral region; those located on dorsal rows one and two they form a discontinuous line. Ventral surface of the body is reddish with three longitudinal rows of dark brown spots, discontinuous to the cloaca and the medial less conspicuous; cloacal plate is reddish, subcaudals reddish, faintly dotted with black;

Ventrally the head is reddish, but with a black horseshoe-shaped spot that occupies the infralabials and the mental (Fig. 4A-B).

Figure 31. Images of *Atractus nemosophis* sp. nov. in life. Holotype MZUC 47720: dorsal view of the body and head, showing the black vertebral line and a very attenuated light band behind the parietals; ventral view of the body and tail, displaying a reddish pattern with three spots on each scale, forming incomplete longitudinal lines (A-B). MZUC 47729: dorsal view of the body and head, exhibiting a greyish-brown pattern with an interrupted white line between the 1st and 3rd dorsal scale rows and a whitish surface heavily pigmented with black (C-D). MZUC 47726 and MZUC 47718: reddish pattern with a black vertebral line and a strongly pigmented orange

belly (E-G). MZUC 47735: olive-brown pattern with a black vertebral line, with supralabials and the ventral surface of the head showing a yellowish hue (H). Image of *Atractus xaxi* sp. nov. in life: head and dorsum of the body entirely black (© Daniel Quihua).

Color in preservative: dorsal region of head uniform grayish brown, distinguishable of the body, laterally varies between dark brown and grayish; supralabials and infralabials cream, weakly dotted with dark brown; a cream transverse band behind the parietals, somewhat diffuse and interrupted medially. Ventrally the head has is cream, with a horseshoe-shaped dark brown spot, that covers the mental, first four infralabials and anterior portion of the geneials; rostral almost completely grayish. Cream ventral scales with three dark brown spots, two lateral and one middle, arranged in three discontinuous lines to the cloaca; At the level of the body and tail, the tone of the dorsal background varies from light to dark brown, except for a dark spot on the vertebral region that forms a continuous line in the first third of the body, later on becomes discontinuous and disappears before the cloaca (Fig. 7A-B).

Variation of the type series (Figs. 5-6). - TL= 419.9-249.2 (X=312 n=7) mm in males, 325-269.9 (X=348.2 n=6) in females; TaL= 57.9-21.9 (X=38.6 n=7) mm in males, 39.7-29.5 (X=34.4 n=6) in females; relation TaL/TL= 0.15-0.09 (X=0.12 n=7) in males, 0.10-0,11 (X=0.10 n=6) in females; HL= 10.61-8.42 (8.92 ± 1.07 n=7) in males, 9.2-8.48 (9.81 ± 1.45 n= 6) in females; HW= 7.29-5.23 (6.06 ± 0.66 n=7) in males, 6.67-5.63 (6.63 ±1.39 n=6) in females; PSL= 3.14-2.35 (2.73 ± 0.28 n=7) in males, 2.49-2.69 (3.06 ± 0.46 n=6) in females; FL= 3.46-2.63 (2.94 ± 0.3 n=7) in males, 3.94-2.39 (3.07 ± 0.65 n=6) in females; FW= 2.85-2.23 (2.51 ± 0.2 n=7) in males, 3.52-2.06 (2.66 ± 0.6 n=6) in females; FRD= 3.3-2.38 (2.76 ± 0.36 n=7) in males, 3.47-2.3 (2.85 ± 0.42 n=6) in females; PrSL= 2.5-1.48 (2.08 ± 0.39 n=7) in males, 2.44-1.5 (2.09 ± 0.34 n=6) in females; INSL= 0.99-0.66 (0.83 ± 0.14 n=7) in males, 0.89-0.45 (0.76 ± 0.19 n=6) in females; ID= 4.64-3.53 (4.03 ± 0.42 n=7) in males, 4.2-3.64 (4.24 ± 0.76 n=6) in females; ND= 2.8-2.06 (2.47 ± 0.26 n=7) in males, 2.9-2.06 (2.39 ± 0.42 n=6) in females; TEL= 1.77-1.47 (1.58 ± 0.11 n=7) in males, 1.74-1.55 (1.93 ± 0.36 n=6) in females; HED= 1.49-1.31 (1.46 ± 0.17 n=7) in males, 1.7-1.18 (1.46 ± 0.24 n=6) in females; END= 2.94-2.05 (2.45 ± 0.36 n=7) in males, 3.6-2.35 (2.72 ± 0.57 n=6) in females; LL= 2.12-1.39 (1.61 ± 0.32 n=7) in males, 2.3-1.36 (1.8 ± 0.4 n=6) in females; SupL= 1.38-0.91 (1.12 ± 0.15 n=7) in males, 1.8-1.22 (1.49 ± 0.23 n=6) in females; SLG= 2.68-1.72 (2.21 ± 0.41 n=7) in males, 2.7-2.41 (2.66 ± 0.61 n=6) in females;

RoW= 2.45-1.57 (1.98 ± 0.36 n=7) in males, 3.2-1.74 (2.24 ± 0.58 n=6) in females; RoDW= 1.4-1.1 (1.24 ± 0.14 n=7) in males, 1.7-1.1 (1.49 ± 0.85 n=6) in females.

Regarding the cephalic scalation, very little variation was observed, except for the following: specimen MZUC 47718 presents the loreal scale divided towards the eye, whose portion is narrow; not elongated posterior supratemporal (right side) in specimens MZUC 47718, MZUC 47732, MZUC 47733, and MZUC 47729; specimen MZUC 477128 presents the loreal very narrow towards the eye (right side) and the posterior supratemporal not elongated (left side); 177-158 (170 ± 6.62 n=7) ventral scales in males, 190-173 (181 ± 5.71 n=6) in females; 41-36 (39 ± 2.07 n=7) subcaudal scales in males, 31-23 (29 ± 3.5 n=6). Hemipenis moderately bilobed, capitate and semicalyculate; lobes of similar size and form, centrifugally oriented, subcylindrical with flattened apices and restricted to distal portion of capitulum; lobes uniformly covered with spinulate calyces; papillae progressively replaced by spinules toward base of capitulum, this last located well above sulcus spermaticus bifurcation occurring a little above the middle of the hemipenial body; capitulum longer than hemipenial body; sulcus spermaticus branches centrifugally oriented, running to apices of lobes; margins of sulcus spermaticus well-defined, bordered with spinules at the level of the hemipenial body and capitulum; hemipenial body globular and broader than capitulum, uniformly covered by medium-size hooked spines, large spines concentrated on the median portion of asulcate and lateral portions of sulcate side; basal naked pocket restricted to basal region of hemipenial body (n: 3, Fig. 6C-F). Maxilla in its anterior third arched, without space, 5-6 teeth, with irregular spaces between them, except for the first two that almost touch each other; decreasing in size towards posteriorly, being the last small; robust at the base and narrowed on the apices, angular in cross-section; lateral process of the maxilla well developed, situated in the middle of the bone; defined posterior projection (n: 3, Fig. 6A-B).

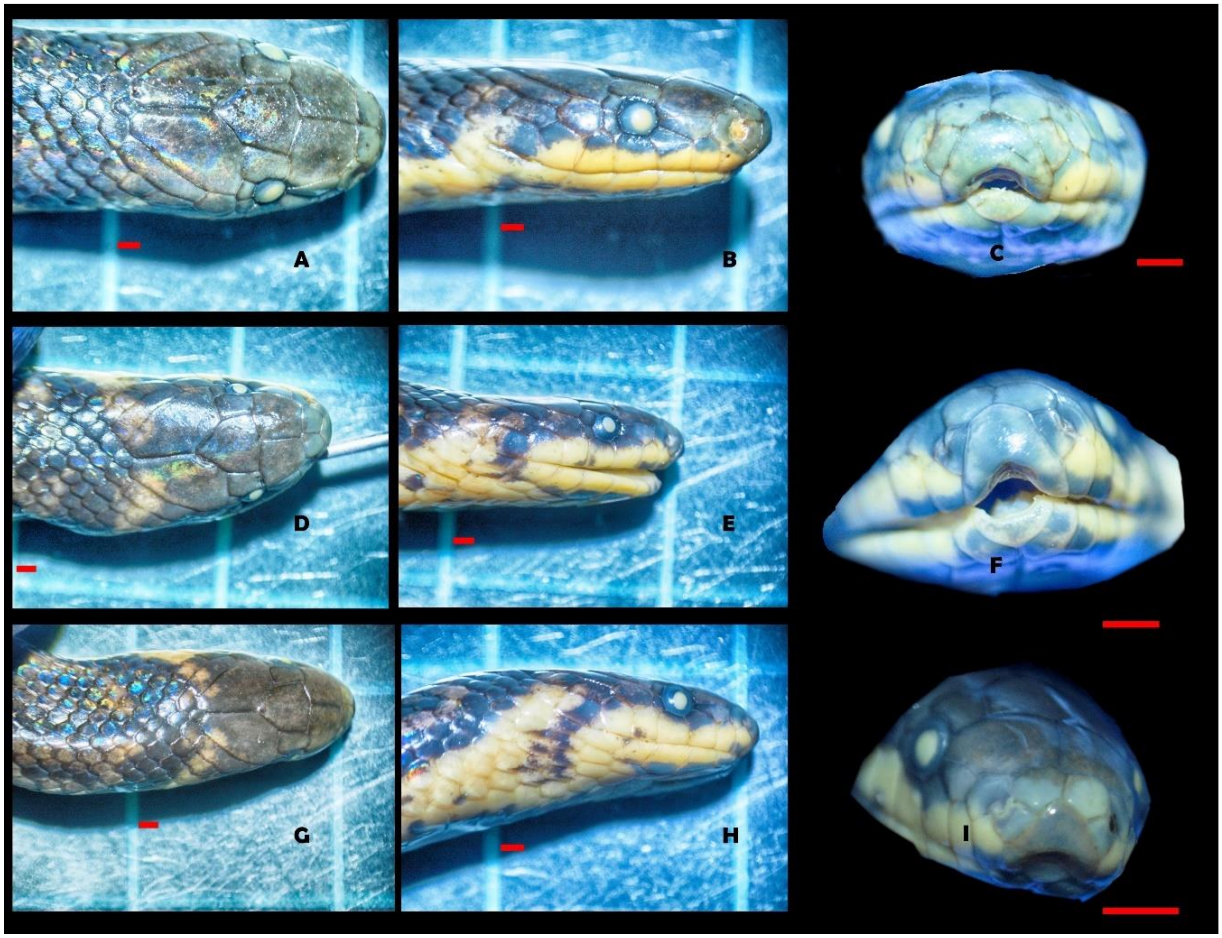


Figure 32. Dorsal, lateral and frontal views of rostral scale, type series: MZUC 47719, field Nº LFE239 (A-B), MZUC 47727, field Nº LFE414 (C-D) and MZUC 47726, field Nº LFE411 (E-F). Scale bar 1 mm.

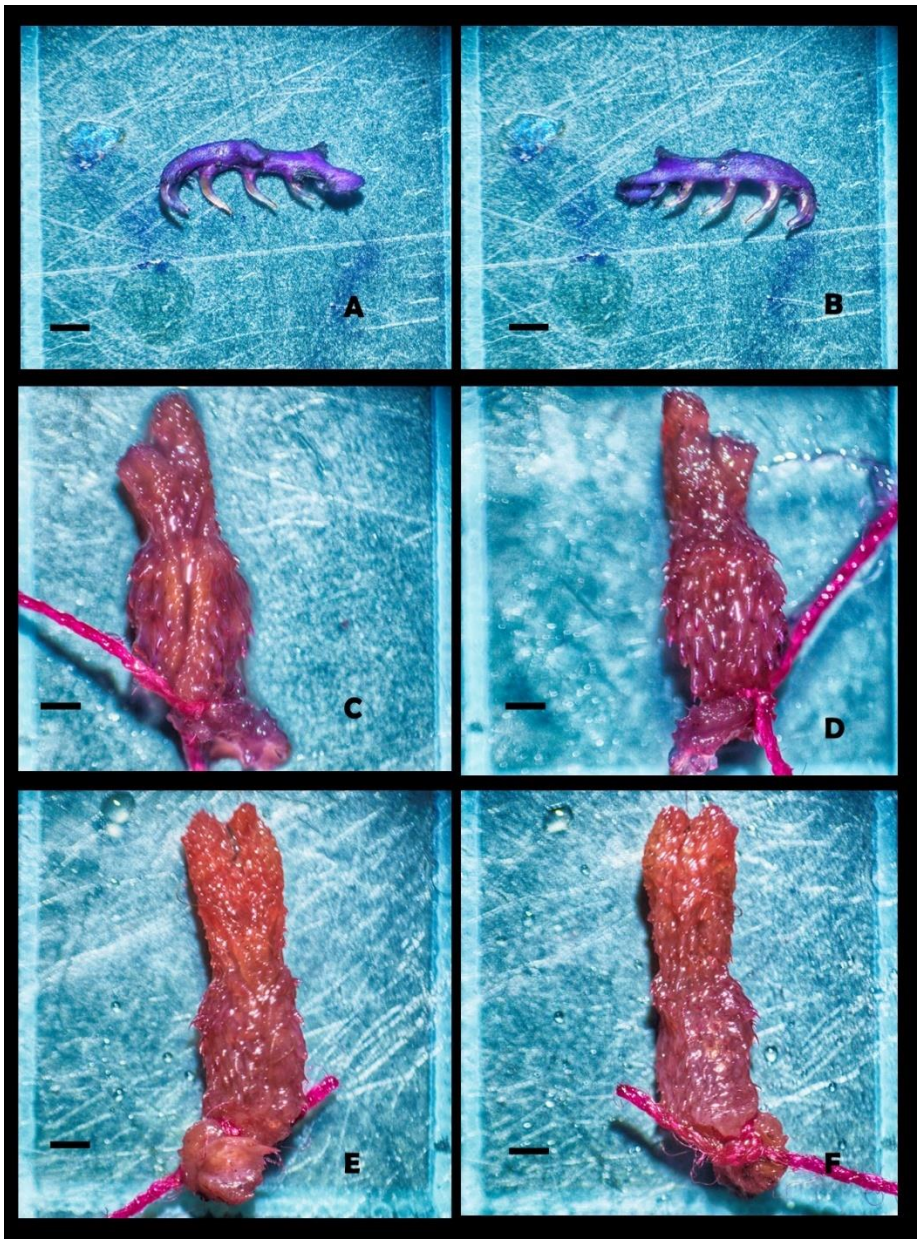


Figure 33. Right maxilla of *Atractus nemosophis* sp. nov., male MZUC 47718 (A-B). Hemipenis, sulcate and asulcate view: male MZUC 47725 (A-B) and male MZUC 47730 (C-D).

Regarding to coloration in life, we have found three morphs: the first has a reddish-brown dorsum of the body, with orange iridescence towards the first dorsal rows, there is a black vertebral line somewhat diffuse in its first third and slightly discontinuous, the rest of the body is well-defined. On the background you can see small spots restricted to the scale that are irregular, in some parts they join the black vertebral line; ventral surface orange with black spots arranged horizontally on each scale; subcaudals with the same pattern (Fig. 4F). In some juvenile or adult specimens with this pattern, only the intensity of spots on the ventral surface of the body and tail varies; exceptionally there

is an olive-brown emerging dorsal pattern with a yellow belly and lips. The second and most common pattern observed presents the body as light brown to grayish brown, with a less evident and continuous black vertebral line in contact with a transverse cream band behind the parietals; laterally at the level of the third dorsal row, there is a whitish, discontinuous line that begins behind the last supralabial and continues to the cloaca; ventrally the background is grayish white with black spots arranged horizontally on the scale; olive brown head dorsally, darker than the body; in lateral view, the supralabials are cream with small black spots (Fig. 4C-D). The third pattern detected exhibits a reddish-brown back, but more uniform, without dark spots restricted to the scale; there is also a well-defined black vertebral line along the body and in contact with a transverse reddish band that has been marginated in black posteriorly; dorsally, the head is dark brown lighter towards the snout and ventrally cream with some reddish towards the gulars; ventral surface of the body is reddish with black spots; supralabials are reddish or yellow, sparsely dotted with black (Fig. 4H). In preserved specimens (adults and juveniles), they show a brown dorsal pattern with a dark line, a light band behind the parietals more evident in juveniles that adults and a ventral design with dark spots (Fig. 7C-F).

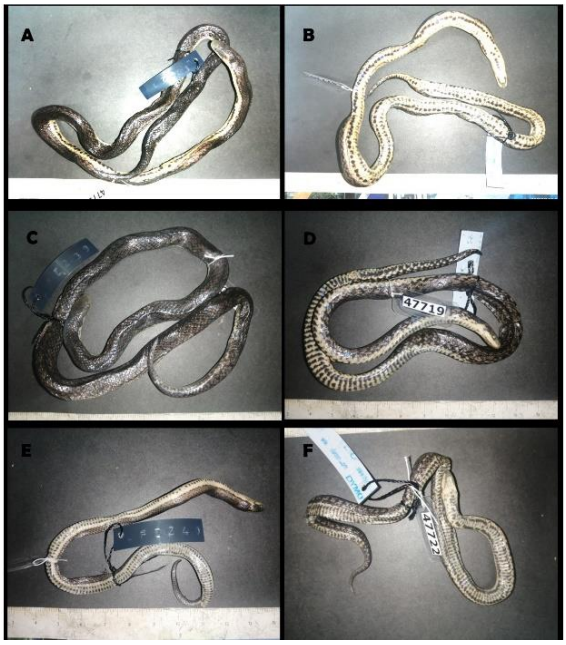


FIGURE 34. Dorsal and ventral view of the body of *Atractus nemosophis* sp. nov., holotype MZUC 47720; Dorsal and ventral view of the body MZUC 47719; ventral view of juvenile MZUC 47721 and subadult male MZUC 47722.

Ecogeographical pattern and natural history. – *Atractus nemosophis* sp. nov. is endemic to the Trujillo state that inhabits the upper limit of the semideciduous montane forest between 1500-2000 m above sea level and the lower limit of the cloud forest between 2000-2500 m above sea level in the direction to the Maracaibo basin slope (Fig. 8A). The conversion of forest ecosystems into mountains due to different anthropogenic activities such as agriculture and/or grasslands for high-altitude livestock farming are currently frequent landscapes, and we can define them as anthromes (Ellis 2010), where the species has been frequently observed (Fig. 8B). Although field observations did not detect signs of direct activity in the collected individuals, what we know so far is that snakes of this genus preferentially feed on oligochaetes (Balestrin et al. 2007; Camper and Zart 2014). In these cases, earthworms are very sensitive to bright light, so their activity at ground level occurs at night or in periods of very little light, being considered crepuscular (Duriez et al. 2006). A visited farm, located in the La Quebrada a Montero sector, a juvenile female of *A. meridensis* was collected around 9:00 p.m., active at ground level (not yet entered the museum, field data LFE 261). Then, about 200 meters from the site, on the edge of the paved road and under some small rocks, two juveniles corresponding to the new species (MZUC 47733 and MZUC 47734) were found, moving energetically when lifting the rock. There are still no studies about the circadian rhythm in this very diverse group, but such data suggest that the new species must be nocturnal and/or crepuscular; in fact, a specimen of *A. ochrosetrus* was captured while crossing a paved road, at 13:45 p.m., on a cloudy day, with winds and no rain (Esqueda and La Marca 2005).

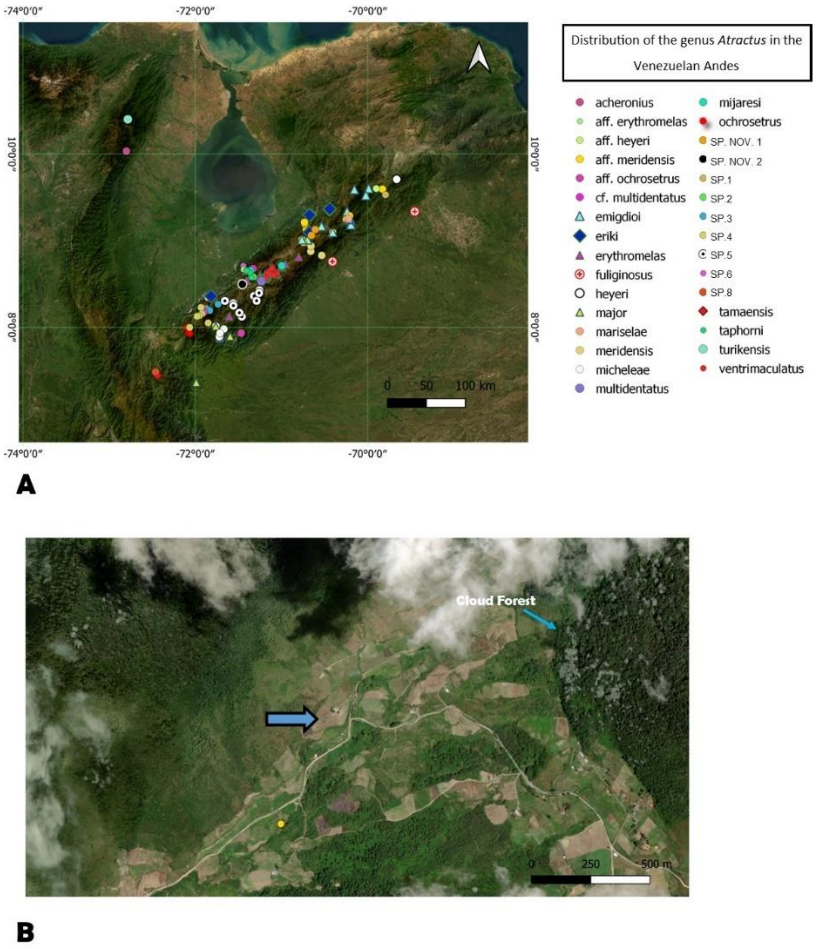


FIGURE 35. Geographic distribution of *Atractus* species in the cordillera de Mérida (A) and type locality of *A. nemosophis* sp. nov., Alto Tomón, to 1:20 hrs. from the city of Valera, Trujillo state (B). Map created using the software QGIS v.3.28.

Conservation status. – Trujillo state has an area of 7,400 km^2, of which 1,000 km^2 constitute montane forests. According to the localities detected, we have defined its topotypical area around to ~800 km^2, situated in the Motatán River basin that drainage begins in Timotes, Trujillo state. In addition, earthworms, which are their exclusive food, can be directly affected in their diversity and population dynamics due to deforestation and conversion of their environments by promoting inadequate edaphic conditions such as alkaline pH, fertility, quality of organic matter and alteration of soil properties such as physical-chemical (Hendrix et al. 2008), particularly in tropical mountain ecosystems that exhibit high rates of endemism in relatively small areas (Lavelle and Lapied 2003). Consequently, considering the IUCN conservation criteria (IUCN 2012) and the vulnerability index of reptile species (IVER, Esqueda and La

Marca 2015), *Atractus nemosophis* sp. nov. it must be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv). In our field trips, we had the opportunity to explore an area where according to the residents, it was very common to find *Atractus* 10 years ago (Mucuyupu-Tafalle, 2595 m above sea level, 9° 0'44.71"N and 70°45'39.32"W); however, our effort yielded only two specimens, a juvenile of *A. meridensis* and another adult female of *A. emigdioi* (not yet entered the museum, LFE 482-83). The low presence of worms was verified in situ, even though the area would be fallow, but in the past, it was intensely subjected to the use of agrochemicals and insecticides to production of crops such as potatoes, carrots, and vegetables. Scientific evidence shows that the use of xenobiotic compounds can cause significant effects on the diversity and dynamic populations of earthworms immediately (e.g. mortality and reproduction by reducing fertility and individuals' growth) and with lasting effects over time (Johnston et al. 2015; Miglani et al. 2019; Maggi y Tang 2021).

Atractus xaxi sp. nov. Esqueda, Rojas-Runjaic, Prudente, Bazó, Navarrete, Camargo-Sillet, Ortiz, Correa, Guerrero & Urra

ZooBank LSID urn:lsid:zoobank.org:act:8E492BDD-C6A9-4FF4-8EE8-083BCAA5EF8C

Holotype. - Adult female, CVULA 7381, material coming from Jají, Mérida state, Venezuela, at 1781 m altitude the town of Jají is located, 8° 34'14" N and 71°20'40" W.

Paratype. - Adult female, MHNLS 22676, collected in the surroundings of Jají (specific location unknown), Mérida state, Venezuela.

Etymology. - The word "xaxi" is a toponym of the first indigenous settlers of the area (the Chamas tribes) and that, with the arrival of the Spanish people, was transformed morphologically to be known today as "Jají" (Gordones-Rojas and Meneses-Pacheco 2004). The town is one of the oldest in Mérida state, Venezuela, founded in 1580.

Definition and diagnosis. - (1) 17-17-17 dorsal scales, smooth and without apical pits; (2) elongated and hexagonal loreal, narrow towards the eye, in contact with three supralabials; (3) supralabial-rostral contact short, < than the eye-loreal contact; (4) frontal hexagonal, wider than long, shorter than the parietal suture and with the anterior margins medially forming a triangle-shaped notch; (5) rostral barely visible from above,

subtriangular, distally forming an obtuse angle and barely exceeding the straight line between nostrils; (6) elongated, hexagonal loreal and in contact with three supralabials; (7) 8(4,5) supralabials, last elongated; (8) 7(4) infralabials; (9) 168-169 ventral scales; (10) 28-35 subcaudal scales; (11) eight maxillary teeth, lateral process well developed and located between the fifth and sixth teeth; (12) uniform chocolate brown dorsal pattern in preservative, black uniform in life; (13) ventral surface of the body is cream, with three irregular brown spots, may be separated or merged forming an irregular spot on the basis of each ventral scale and that is accentuated towards the middle of the body where they can occupy more than 60 % of the surface; (14) ventral region of head cream, strongly pigmented black, especially the geneials and first four infralabials.

Among all the Venezuelan Andean species, *Atractus xaxi* sp. nov. differs from *A. ochrosetrus*, *A. ventrimaculatus* and *A. taphorni* because they have 15 dorsal scales in the middle of the body vs. 17 dorsal scales. On the other hand, the presence of seven supralabial and three infralabial scales in contact with geneiales is distinctive of *A. eriki*, *A. meridensis*, *A. erythromelas*, *A. tamaensis*, *A. mijaresi*, *A. major*, *A. pamplonensis* and *A. fuliginosus* vs. eight supralabials and four infralabials in contact with greats. Meanwhile, *A. multidentatus* and *A. emigdioi* are distinguished by having longitudinal lines along the body and less than 165 ventral scales in females vs. uniform body without line, black in life and more than 165 ventral scales in females. Regarding two species from the Perijá mountain range, *A. acheronius* and *A. turikensis*, are distinguished because the first has a width in the middle of the body >10 mm, two supralabial scales in contact with the loreal and a total length of 536 mm in the only female known vs. width in the middle of the body 7-8 mm, three supralabial scales in contact with the loreal and a total length 389 mm in females; while it differs from *A. turikensis* because it has 7 supralabial scales, usually elongated posterior supratemporal and subtriangular frontal scale vs. 8 supralabial scales, indefinite posterior supratemporal and hexagonal frontal scale. *Atractus xaxi* sp. nov. differs from *A. micheleae* because the latter has light transverse bars on a dark background at the dorsal level of the body, dorsal coloration of the head differentiated of the body, elongated posterior supratemporal scale and generally prefrontal-postnasal contact ≤ than eye-prefrontal contact vs. uniform dorsal region, coloration dorsal of the head undifferentiated of the body, indefinite posterior supratemporal and prefrontal-postnasal contact > than eye-prefrontal contact. The most similar species is *A. mariselae* (in

parentheses), but the new species differs in having the ventral surface of the head strongly pigmented dark brown, especially the geneials; ventral surface cream, with three horizontally arranged dark spots on each scale, together forming three lines of dark spots (ventral region of head weakly pigmented; ventrals cream, which may be weakly spotted with dark spots or have one more or less continuous spot horizontally on each scale).

Description of the holotype. - Adult female (Fig. 9). Total length 390 mm; tail length 43.4 mm; relation TaL/TL 0.11; head length 9.6 mm; head width between commissures 7.4 mm; parietal suture length 3.2 mm; frontal shield length 2.9 mm; previously measured frontal shield width 3.1 mm; prefrontal suture length 2.4 mm; internasal suture length 0.6 mm; distance between frontal and rostral 3.1 mm; distance between eyes 4.4 mm; distance between nostrils 2.2 mm; first temporal scale length 2.3 mm; horizontal eye diameter 1.4 mm; loreal scale length 2.1 mm; eye-nostril distance 2.7 mm; length of the first supralabial in contact with the ocular orbit 1.2 mm; geneial suture length 2.7 mm; rostral scales width, measured at the base that contacts the supralabial 1.7 mm; distal width of the rostral measured between nostrils 0.7 mm; width at the middle of the body 8.7 mm.

Head with barely distinct cervical, longer than wide, snout relatively short (0.29 HL), slightly compressed in dorsal, barely truncate and with a relation DBE/DBN 0.50 (50 %, is considered wide); frontal shield wider than long, same as parietal suture, with anterior margins slightly straight (Fig. 9A), medially forming an inverted V; rostral barely visible from above, subtriangular in frontal view, wider than tall, with the distal end forming an obtuse angle and just above the imaginary straight line between nostrils; two prefrontals, contact with the ocular orbit shorter than eye-loreal contact; two internasals small and more or less quadrangular, with a suture 3.8 times shorter than the prefrontal suture; two elongated supraoculars, wider posteriorly. Eye moderate, snout slightly subacuminate in lateral view; loreal scale hexagonal and elongated, lateral edges with similar width and in contact with three supralabials (Fig. 9B); postnasal irregularly heptagonal, arranged vertically, taller than wide and prefrontal-postnasal contact greater than eye-loreal contact; circular nostril, disposed medially between postnasal and prenasal, this last similar to postnasal; first supralabial narrow but tall, its contact with the rostral is short (< 0.5 DBE) (Fig. 9C); two postoculars, the first quadrangular and smaller than the second; 1+2 temporals, first temporal elongated, 1.6

times longer than the horizontal diameter of the eye; 8(4,5)/7(4,5) supralabials, elongated four and eight supralabials; mental scale small and subtriangular; 7(4)/6(4) infralabials; a single pair of geneials, suture similar to the FRD; 1/1 sublabial, separated from each other by a wide gular scale (Fig. 9D); three gular and one preventral; 168 ventral scales; 23 subcaudal scales; 17-17-17 dorsal scales, smooth and without apical pits, seven dorsocaudals around the fifth-sixth subcaudal. Right maxillary bone extracted and cleaned (Fig. 9E-F): maxilla in its anterior third arched, 8 teeth, with irregular spaces between them, except for the first two that almost touch each other; decreasing in size towards posteriorly starting from the 4-5 tooth; robust at the base and narrowed on the apices, angular in cross-section; lateral process of the maxilla well-developed, situated between the fifth and sixth tooth; defined posterior projection.

Color of holotype in preservative. - Body and tail dorsally uniform chocolate brown, with irregular spaces attenuated in color giving the impression of small spots restricted to the scale, although it seems to us more like the conservation of the specimen; ventrally cream with a horizontal series of three irregular spots, dark brown and arranged slightly apart or fused forming a spot extending at least more than 50 % of the scale surface (plus light spaces between the first 20 ventral scales); entire cloacal scale, almost completely stained by this series of spots; subcaudals completely stained dark brown. The head dorsally is similar to the dorsal background of the body (Fig. 9G), ventrally it is cream with small and scattered spots towards the gular region (Fig. 9H), while the mental, first infralabials in contact with genials and anterior portion of the genials stained dark brown. Cream supralabial scales, slightly barred irregularly dark brown.

Variation of the paratype. - TL= 328 mm; TaL= 37.4 mm; relation TaL/TL= 0.11; HL= 8.28 mm; HW= 7.18; PSL= 3 mm; FL= 2.51 mm; FW= 3 mm; FRD= 2.5 mm; PrSL= 1.97 mm; ISL= 0.5; DBE= 4.6 mm; DBN= 2.4 mm; TEL= 2.27 mm; HED= 1.3; END= 3.1; LL= 2.3; SupL= 1.5; SLG= 2.7; RoW= 2.3; RoDW= 0.8. Exist very little variation at the level of the cephalic squamation, only in this specimen the eye-prefrontal contact is clearly greater than the eye-loreal contact, but less than the prefrontal-postnasal contact; loreal similarly hexagonal, but the margin that contacts the fourth supralabial is longer and the eye-loreal contact is shorter than the loreal-postnasal contact; 169 ventral scales; 35/35 subcaudal scales. In preservative, the coloration pattern is similar to the holotype. A photo probably of the specimen shows that the back

is uniformly black, with some paravertebral scales stained with white and the first dorsal row stained with white on at least 50 % of the surface. Ventral surface white with black spots arranged horizontally on the scale. Head dorsally black, with the supralabials and infralabials whitish (Fig. 4H).

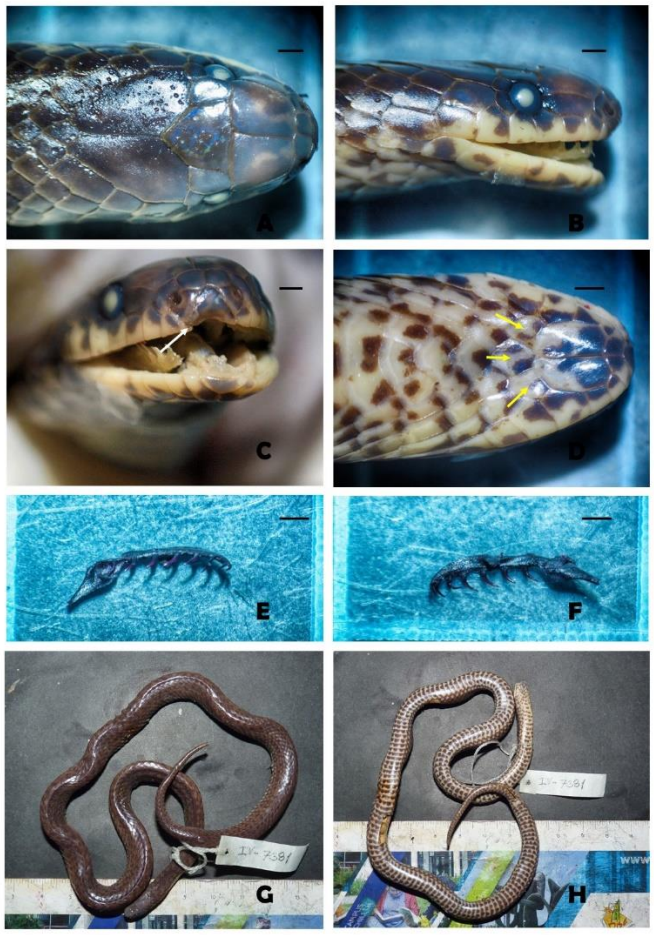


FIGURE 36. Preserved holotype (CVULA 8151): Dorsal view of the head (A); lateral view of the head, right side (B); frontal view of the head, showing supralabial-rostral contact and the shape and arrangement of the rostral (C); ventral view of the head, with sublabials and the middle gular in posterior contact with the genials, indicated by a yellow arrow (D); anterior and posterior views of the right maxillary bone (E-F); dorsal and ventral views of the body (G-H). Scale: 1 mm.

Ecogeographical pattern and natural history. – Until now, the new species is known from a single locality that is located east of the Chama River basin in the intramontane region of the cordillera de Mérida, Mérida state (Fig. 8A). Bioclimatically, it corresponds to the humid pluviseasonal limit (Chacón-Moreno and Moral 2020), with an altitudinal variation of the topotypical area between 1700-2000 m above sea level

whose vegetation includes the upper limit of the montane semideciduous forest and the beginning of the cloud forest (Ataroff and Sarmiento 2003). Both female specimens did not contain eggs or food remains in their digestive tracts.

Conservation status. – Combining the topography and vegetation, we defined a topotypical area using Google Earth Pro software that comprises ~9.8 km^2 (1.1 % of the Mérida state surface), where the natural vegetation has undergone a strong conversion by different anthropogenic activities. Furthermore, a large part of the extension between 1500-2000 m in an east-west direction and vice versa from the town of Jají is not protected as a National Park or Natural Monument. For this reason, we consider that *Atractus xaxi* sp. nov. it should be included in the Vulnerable category according to the IUCN Ac and B2(i,ii,iii,iv) criteria (IUCN 2012).

Key to *Atractus* species from the cordillera de Mérida

1A.- 15 dorsal scales in the middle of the body, without a dorsal pattern with transverse bands, reddish, white or olive brown with scattered dark spots, but dorsolateral lines present ……...……. 2

1B.- 17 dorsal scales in the middle of the body, when there are 15 scales it is always associated with a dorsal pattern with transverse bands, reddish, white or olive brown with scattered dark spots y/or dark lines ……...…….……...……..…….. 4

2A.- 7 (3,4) supralabial scales; two supralabial scales in contact with loreal (Fig. K1, C); two continuous paravertebral lines, marginated of whitish color ……..… *A. taphorni*

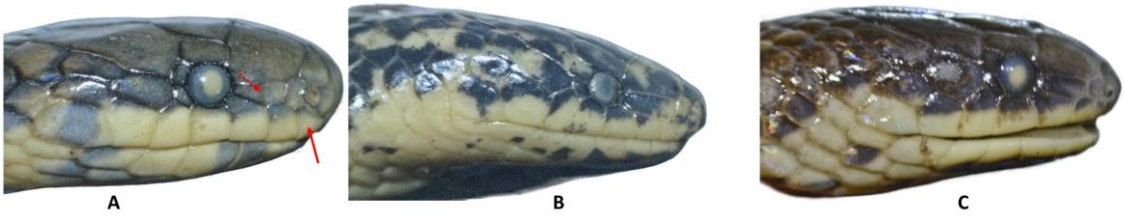


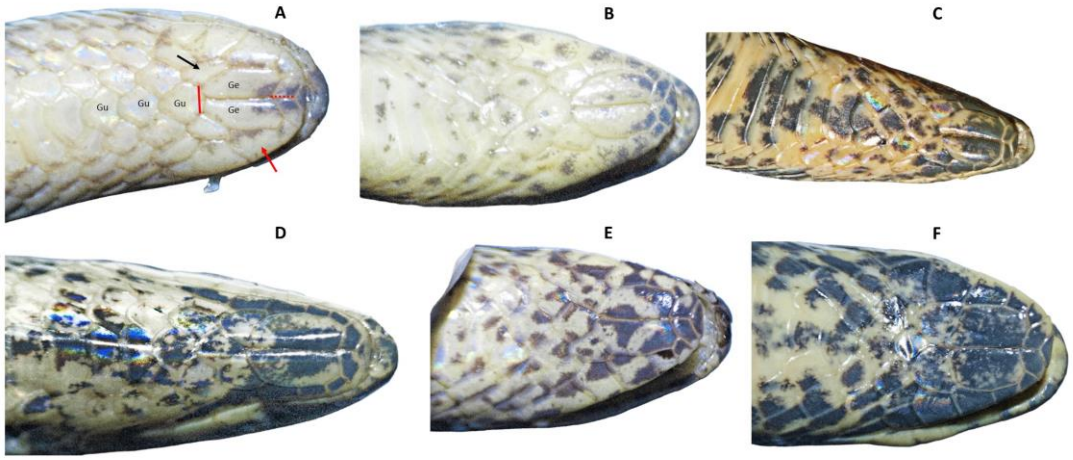
Figure K1. A= *A. meridensis (*LFE288, uncatalogued, Las Piedras, way Pueblo Llano sector La Quinta, Santo Domingo basin, Mérida state, Venezuela; B= *A. ochrosetrus* (MZUC 48020, La M, way Las Porqueras from Bailadores, Mérida state, Venezuela) and C= *A. taphorni* (CVULA1838, Mérida state).

Solid red arrow indicates enlarged first supralabial scale; dashed red arrow indicates loreal scale, with two or three supralabials and narrow, moderate and wide eye-loreal contact with respect to loreal-postnasal contact and/or prefrontal-postnasal contact.

2B.- Frequently 8 (3,4) supralabial scales; three supralabial scales in contact with loreal (Fig. K1, B); when there are paravertebral lines, they are discontinuous, unmarginated ……..…….... 3

3A.- Without dark dorsolateral lines; usually a dark vertebral line visible in the yellowish-brown pattern, but in melanistic specimens it is not distinguishable in life; sublabial scales separated (pseudo-chinchields), rarely in contact, but its width is similar to the suture of the first pair of supralabials (Fig. K2, C); postnasal proportional in size to the prenasal ……..……... *A. ventrimaculatus*

3B.- A continuous dark dorsolateral line present on both sides of the body, in some specimens there are discontinuous paravertebral lines and in specimens with a yellowish or dark brown back (melanistic) there may be a dark vertebral line, with light rhombuses; frequently sublabial scales in contact (pseudo-chinchields), when separated, the width is less than the suture of the first pair of infralabials (Fig. K2, D and F); usually postnasal differentiated of the prenasal



……..……..……. *A. ochrosetrus*

Figure K2. A= *Atractus eriki* (LFE uncatalogued, Trujillo city, Venezuela); B= *A. mariselae* (LFE 052, uncatalogued, Boconó, Trujillo state, Venezuela); C= *A. ventrimaculatus* (BMNH 1908.5.29.141, "Mérida"); D= *A. ochrosetrus* (MZUC 48022, La M, way Las Porqueras from Bailadores, sector Potrero

Grande, Mérida state, Venezuela); E= *A. xaxi* sp. nov. (MHNLS22676, Jají, Mérida state, Venezuela) and F= *A. ochrosetrus* (MZUC 48023, Sector Amarillito, right intersection of Páramo del Zumbador, Táchira state, Venezuela). Ge= Geneial; Gu= Gular. Width between sublabials, solid red line; width of the suture of the first pair of infralabials, dotted red line; sublabials, black arrow; infralabial, red arrow.

4A.- Head subtriangular, snout compressed in dorsal view and slightly arched in lateral view; paravertebral lines present ……...……. 5

4B.- Not like the previous ones ……...……...…6

5A.- 18 maxillary teeth ……...……..…….... *A. multidentatus*

5B.- ≤14 maxillary teeth ……..…….,…… *A. emigdioi*

6A.- Usually eight supralabial scales; three supralabials in contact with loreal …….... 7

6B.- Seven supralabial scales, rarely eight but always with two supralabial scales in contact with loreal ……..…….... 9

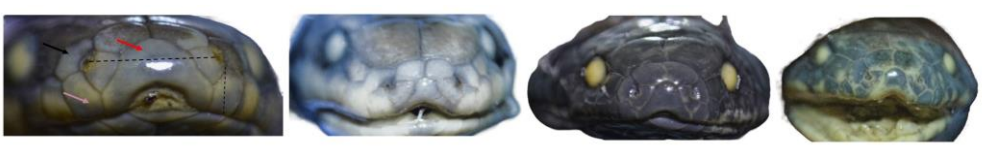
7A.- Dark dorsum with light transverse bars; head dorsally differentiated from the dorsal background of body …..…….……...……. *A. micheleae*

7B.- Uniform dark dorsum, sometimes some iridescent dorsal scales and/or small dark spots on a brown or olive-brown dorsal background; head indistinguishable from the dorsal background of the body ……....… 8

8A.- Ventral region of head weakly pigmented; ventral surface of body cream, varying to sparsely spotted or spotted horizontally on each scale (Fig K6, B)…...……. *A. mariselae*

8B.- Ventral region of head strongly pigmented, especially the genials; ventral surface cream, with three dark spots arranged horizontally and tending to form three lines of discontinuous spots (Fig. K6, A) ……...… *A. xaxi* sp. nov.

9A.- Hemipenis moderately bilobed and/or bilobed; wide supralabial-rostral contact;



rostral well visible from above (Fig. K3, A) ……..…….. 10

Figure K3. A= *A. meridensis* (MZUC 48051, Las Piedras, way Pueblo Llano sector La Quinta, Santo Domingo basin, Mérida state, Venezuela); B= *A. erythromelas* (CVULA 7395, Manzano Alto, Mérida city, Mérida state); C= *A. ventrimaculatus* (MZUC 48018, Posterior to the Truchicultura Monterrey, way El Valle-La Culata, Mérida city, Mérida state, Venezuela) and D= *A. ochrosetrus* (MZUC 48022, La M, way Las Porqueras from Bailadores, sector Potrero Grande, Mérida state, Venezuela). Distance between nostrils, indicated by horizontal dashed line; height of first supralabial, indicated by vertical dashed line. Red arrow indicates rostral scale; violet arrow indicates contact between first supralabial and rostral scale; black arrow indicates postnasal scale in relation to prenasal scale.

9B.- Hemipenis slightly bilobed or poorly defined lobes of capitulum; usually short supralabial-rostral contact; rostral barely visible from above (Fig. K3, B) …… 12

10A.- Dorsum reddish brown, with brown spots on more than three dorsal scales, arranged transversely and marginated of cream; subcaudals immaculate or weakly pigmented with dark; width at midbody >10 mm ……..……. *A. major* (populations Mérida-Táchira state, Venezuela)

10B.- Dorsal pattern variable, being uniform, with lines, bicolour bands and/or with small, unmarginated dark spots; subcaudals strongly pigmented; width at midbody less than 10 mm ……..……..…… 11

11A.- Dichromatic dorsal pattern, consisting of brown-black and red bands and/or brown-black and white bands, but light bands edged with black; sulcus spermaticus bifurcates at middle of organ or less (Fig. K5, B and C) ……..……..... *A. meridensis*

11B.- Dorsal pattern not constituted by bands, there may be specimens with a reddish or reddish-brown dorsal background with a dark vertebral line and also a discontinuous black line on the first dorsal row, in other cases, the dorsum is grayish brown or dark brown but a dark vertebral line and a light discontinuous dorsolateral line are also maintained; capitulum situated just above sulcus spermaticus bifurcation ……*A. nemosophis* sp. nov.

12A.- Mimetic polymorphic dorsal pattern, usually bicolour of red-white and black bands, uniformly reddish or small irregular dark spots (brindle), less common a

yellowish-brown back with scattered dark spots (brindle) (Fig. K4, A-B); ventral surface in life is always reddish, rarely yellowish, but always heavily spotted with black and which form continuous or discontinuous blocks…….…. *A. erythromelas*

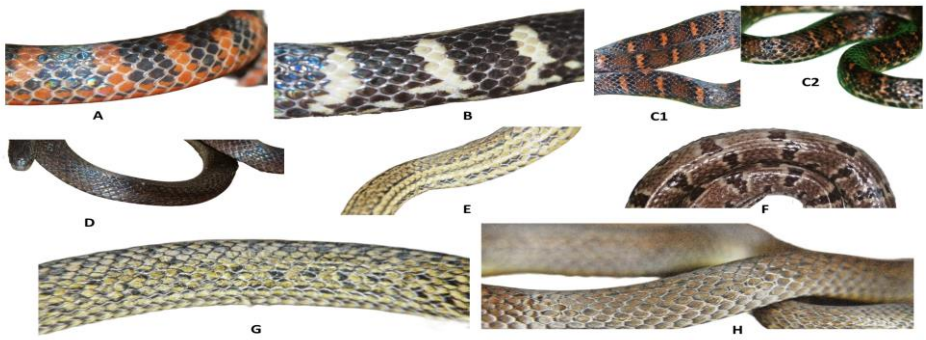


Figure K4. A= *Atractus erythromelas*, pattern with reddish and black bands on body and not margined (MZUC 47736); B= *A. erythromelas*, pattern with black and white bands, not margined (MZUC 47738); C= *A. meridensis*, pattern with reddish and brownish bands, clearly margined with black (C1= MZUC 48057, C2= MZUC 48051); D= *A. mijaresi*, uniform dorsal pattern with small spots restricted to the scale (MZUC 48032); E= *A. ochrosetrus*, light brown dorsal pattern with paravertebral and dorsolateral lines (MZUC 48022); F= *A.* aff. *major*, dorsal pattern with dark spots, margined with cream (CVULA 4317); G= *Atractus* sp., dorsal pattern with a yellowish-brown background, with small black spots irregularly scattered and not marginated (uncatalogued LFE); H= *A. tamaensis*, uniform reddish-brown pattern, with small black spots, restricted to the scale and distributed more frequently over the paravertebral region (LFE 161, uncatalogued).

12B.- Not like the previous one ……..…… 13

13A.- Males subcaudals 36-40 (except *A. fuliginosus*), cloacal scute and subcaudal scales completely stained dark brown in preserved and black in life ……...……. *A. eriki*

13B.- Males subcaudals ≤ 31, cloacal scale and subcaudals immaculate or faintly blotched with dark brown ……..… 14

14A.- Ventral surface of head, body and tail immaculate, rarely small dark spots in the middle of each ventral scale and subcaudals; frequently a black vertebral line extending behind the parietals to the tip of the tail, sometimes there are dark spots occupying the vertebral and paravertebral region, continuous or discontinued and marginalized or not with cream on a reddish-brown background.…… *A. fuliginosus*

14B.- Not like the previous one ……..…… 15

15A.- Discontinuous light band behind the parietals in juveniles; >175 ventral scales in females, usually 180-191 and >165 in males; space present towards the posterior teeth, 9-12 maxillary teeth; hemipenis with a lateral depression on the lobes apices, dark blotches on the dorsal region with cream margins and lobes of hemipenis clavate and with rounded apex (Fig. K5, D) ……..……...…… *A.* aff. *pamplonensis*

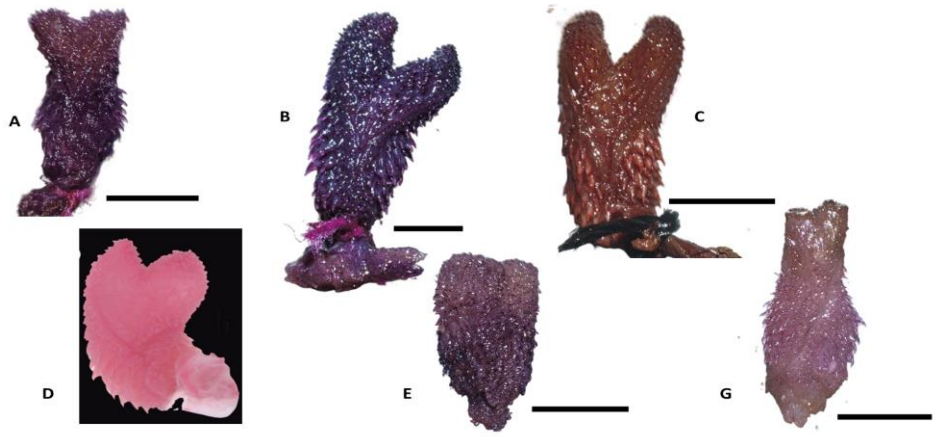
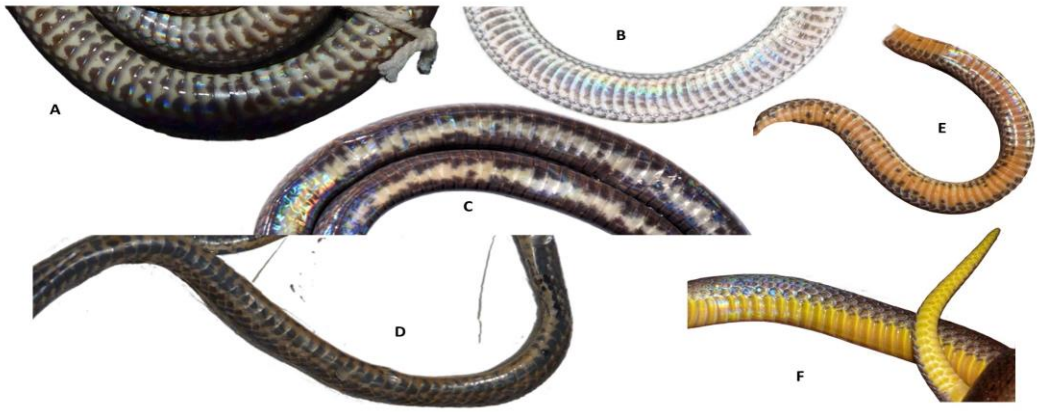


Fig. K5. A= *Atractus erythromelas*, hemipenis semicapitate, semicalyculate and slightly bilobed. Lobes clavate, similar in size and with rounded apex (CVULA 7400); B-C= *A. meridensis*, hemipenis semicapitate, semicalyculate and moderately bilobed to bilobed, with rounded apex of the lobes (LFE 420 and LFE 412, uncatalogued, La Puerta and Alto Tomón, Trujillo state, Venezuela); D= *A. pamplonensis*, hemipenis semicapitate, semicalyculate and slightly bilobed, lobes clavate and with rounded apex (data provided by Passos et al. 2024); E= *A. tamaensis*, hemipenis semicapitate, semicalyculate and poorly bilobed, lobes broad and with flattened apex (LFE 161, uncatalogued, coming from Las Playitas, ULA,

Mérida state, Venezuela) and G= *A. mijaresi*, hemipenis semicapitate, semicalyculate and moderately bilobed, lobes subcylindrical and with flattened and/or rounded apex (MZUC 47707, LFE119, Capaz, Mérida state, Venezuela). Scale 3 mm

15B- Without any character in coloration that suggests ontogeny; ventral scales in females ≤ 170 and ≤ 165 in males; space not defined towards the posterior teeth, 5-8 maxillary teeth and lobes of hemipenis with flattened apex



……..…….. 16

Figure K6. A= *Atractus xaxi* sp. nov. (MHNLS22676, Jají, Mérida state, Venezuela); B= *A. mariselae* (LFE 052, uncatalogued, Boconó, Trujillo state); C= *A. pamplonensis* (MHUA R-14164); D= *A.* aff. *pamplonensis* (MCNC 8269, Betania, Táchira state, Venezuela); E= *A. mijaresi* (MZUC 48032, Capaz, Mérida state, Venezuela) and F= *A. tamaensis* (LFE 160, uncatalogued, Las Playitas, Mérida state, Venezuela).

16A.- Hemipenis with lobes poorly defined, as wide as the capitulum (Fig. K5, E); frontal pentagonal, with anterior margins straight or slightly straight; narrow loreal towards the eye, wide eye-prefrontal contact (≥ postnasal-prefrontal contact); rostral above the straight line between nostrils; intense yellow belly in life ……..…….. *A. tamaensis*

16B.- Hemipenis moderately bilobed, subcylindrical and differentiated of the capitulum (Fig. K5, F); hexagonal frontal, anterior margins concave; usually eye-loreal contact similar to loreal-postnasal contact, eye-prefrontal contact ≤ prefrontal-postnasal contact; rostral located on the straight line between nostrils; yellow-orange or pale-yellow belly in life..… ……..... *A. mijaresi*

Note: In the key we include *A. pamplonensis*= *A. aff. pamplonensis* because of the record made by Schargel and García-Pérez (2002), but the populations of that region require a separate evaluation, although its presence in Venezuela is referred in the discussion.

DISCUSSION

Calibrated phylogeny of *Atractus* in the Neotropics

The taxonomy and possible relationships of *Atractus* from Venezuela are based exclusively on morphological characters (Roze 1966; Barros 2000; Schargel and García-Pérez 2002; Esqueda et. al. 2005, 2007; Kok 2006; Passos et al. 2009b, 2013; Esqueda 2011). For the first time, molecular information is available in *Atractus* species restricted to Venezuela, particularly in the cordillera de Mérida, which harbors the greatest known diversity so far (Natera-Mumaw et al. 2015). Serrano et al. (2023) proposed that during the Early Miocene, the movement of dipsadines from Central America to South America involved different processes, dating back to approximately 20-25 Myr, whereas the genera *Geophis* + *Atractus* are around 22 Myr, with their Central American ancestors first expanding their distribution to South America and subsequently experiencing vicariance. Our calibrated phylogeny constructed using different methods estimated the divergence of *Atractus* with respect other dipsadines around 22.29 Myr (95 % HDP = 18.58-25.79).

Since Savage (1960), who proposed three groups within *Atractus* (*A. badius*, *A. elaps*, and *A. trilineatus*), other groups have been established with various modifications and/or reassignments (Passos et al. 2009d, 2013, 2016; Arteaga et al. 2017), including their rejection when found to be non-monophyletic, as in the case of the *A. flammigerus* group (Melo-Sampaio et al. 2019). Therefore, considering the most recent molecular phylogenies, which include approximately 30 % of the total known diversity, as well as discussions regarding the correct assignment of museum specimens and the validity of certain species (Arteaga et al. 2022; Passos et al. 2009c,d,e), it seems premature to construct hypotheses without at least a supporting synapomorphy (e.g., *Atractus iridescens* group, Arteaga et al. 2017).

To date, our time-calibrated phylogeny, which includes 59 taxa (~40 % of the total diversity), reveals two well-structured *Atractus* lineages. The younger lineage, Lineage A, is estimated to be around 20.57 Myr old (95 % HPD = 17.15-23.89) and comprises

22 species with a predominantly cis-Andean distribution, including the cis-Andean regions of the cordillera de Mérida, the cordillera de la Costa, the Llanos of Venezuela and Colombia, and western Amazonia (Colombia and Ecuador). Additionally, this lineage includes a clade consisting of *A. michaelbalsani* and (*A. roulei* + *A. carrioni*), which is distributed in the southern Andes of Ecuador and parts of Peru, on the western slope at elevations between 880 and 2,890 m asl (these species are trans-Andean). In contrast, lineage B is estimated to be 21.22 Myr old (95 % HPD = 17.43-22.57) and consists of 36 species, primarily cis-Andean.

The only calibrated phylogeny prior to ours is that provided by Murphy et al. (2019), who found *A. trilineatus* to be the sister species of the remaining ones. This species is distributed in the eastern section of the cordillera de la Costa in its eastern section, Trinidad and the Guiana Shield (sampling 21.7 %); here this species is nested with *A. ochrosetrus* and *A. ventrimaculatus*, both endemic to cordillera de Mérida and which share 15 rows of dorsal scales in the middle of the body. Although Arteaga et al. (2022) proposed that cis-Andean species would be more closely related to others with similar distribution and vice versa for trans-Andean species, many trans-Andean species in their study, as well as in our topology, lack nuclear gene data. It is known that rapidly evolving genes can artificially shorten branch lengths, leading to overestimated divergence times. While mitochondrial relationships remain consistent (Townsend 2004), nuclear genes are less prone to such effects (Lukoschek et al. 2012). We believe that in the future, the incorporation of species from Colombia along the Andes may determine the balance in favor of an idea at least addressed here that suggests unique clades in each mountain system in the northern Andes and is clearly separated from those species distributed towards the Guyana shield and the Amazon basin, with elements dispersed east of the Andes from Peru to Colombia and then connected with the Andean-Llanero piedmont of the cordillera de Mérida, which remains a poorly sampled area and requires efforts in the future. For example, Esqueda and La Marca (2005) reported for the *A. major* slope, a species with wide distribution and disjunct populations east of Ecuador and northern Amazonia (Natera-Mumaw et al. 2015). However, the recognition of *A. arangoi* with respect to *A. major* (Arteaga et al. 2022), whose distribution occurs further northeast in the Ecuadorian and Colombian Andes, and which probably has contact zones with another species with a similar dorsal pattern, such as *A. punctiventris* limited to the eastern slope of Colombia on its eastern slope and

which could be in Venezuela (Passos et al. 2016). This hints at unresolved evolutionary relationships between these mountain systems that warrant further investigation.

Although our study lacks samples that could clarify relationships between the aforementioned mountain systems, the phylogenetic topologies derived from maximum likelihood and Bayesian Inference analyses provided strong support for recognizing *Atractus nemosophis* and *Atractus xaxi* as full species and for determining their relationships with other endemic species from the cordillera de Mérida. In this context, *A. nemosophis* appears to be phylogenetically closer to *A. meridensis*, sharing key morphological traits such as the presence of a loreal scale, rostral-supralabial contact, and the shape of the rostral scale in dorsal view. However, their sympatric populations exhibit highly distinct hemipenial structures. *A. nemosophis* possesses a semicapitate, semicalyculate, moderately bilobed hemipenis with a subcylindrical shape, straight lobes at the apex, and a sulcus spermaticus that bifurcates towards the distal region of the hemipenial body. In contrast, *A. meridensis* presents a semicapitate, semicalyculate, bilobed or moderately bilobed hemipenis, and a sulcus spermaticus bifurcation located at the middle or near the base of the hemipenial body. We consider *A. meridensis* to represent a species complex currently under evaluation (data LFE 2024). Regarding *A. xaxi*, our results suggest it is more closely related to *A. mijaresi* and *A. mariselae*. However, hemipenial data for the new species are not yet available. *A. mijaresi* exhibits a semicapitate, semicalyculate, moderately bilobed hemipenis with subcylindrical lobes, a flat apex, and a sulcus spermaticus bifurcation towards the distal region of the hemipenial body (unpublished data, LFE 2021). In contrast, *A. mariselae* possesses a non-capitate, non-calyculate, slightly bilobed hemipenis with a sulcus spermaticus bifurcation occurring at the middle region of the hemipenial body (Schargel and Castoe 2003).

We fully agree with Passos et al. (2018) that hemipenial morphology is essential for species recognition and the identification of putative populations within this group of snakes, particularly in cases where external morphological traits are ambiguous or have not been thoroughly evaluated through extensive sampling and interspecific comparisons. Although our field observations suggest that certain species are locally abundant and appear to thrive in anthropogenically modified habitats, such as grasslands used for high-altitude livestock farming, others are not favored by such

environmental changes. This disparity affects the resolution of comparative morphological analyses at an interspecific level.

Taxonomically, we are in an era of expansion driven by genomics, yet biogeographic and ecological aspects remain poorly defined. In fact, the cordillera de Mérida harbors a remarkable diversity of *Atractus* species, suggesting a pattern of multiple species coexisting within the same geographical area, yet occupying clearly differentiated niches (e.g., habitat, microhabitat, and/or circadian cycle; unpublished data, LFE 2021).

The allopatric speciation model predicts that secondary contact between sister or closely related species occurs only after they have undergone significant genetic or niche differentiation (Weir and Price 2011). Consequently, under this model, the probability or extent of secondary contact tends to increase with divergence times between species (Barraclough and Vogler 2000; Phillimore et al. 2008; Weir and Price 2011). In such divergence scenarios, populations may have been initially isolated in disjunct habitat patches that were once connected, with isolation triggering and promoting speciation in allopatry. If these montane habitats were later reconnected, for example, due to Pliocene-Pleistocene climatic oscillations (Knowles 2001; Flantua and Hooghiemstra 2018). The newly emerged species could have expanded their ranges and come into secondary contact. This, in turn, could have accelerated the establishment of reproductive isolation, a key factor for diversification and community assembly (Price et al. 2014).

Thus, the relatively short timeframes required for secondary contact to occur after allopatric divergence between closely related species could plausibly explain the high richness and endemism of *Atractus* in montane environments (Steinbauer et al. 2016). Moreover, certain traits, such as hemipenial morphology, may be subject to strong sexual selection pressures, as observed in *A. nemosophis*, which is geographically associated with *A. meridensis*, *A. eriki*, and *A. emigdioi*, all species exhibiting distinct hemipenial characteristics (Schargel and Castoe 2003; Esqueda et al. 2007; unpublished data LFE 2021).

Checking the taxonomy of *Atractus* in the Andes from Venezuela

Recently, Passos et al. (2024) "conducted a morphological review of the species distributed in the cordillera de Mérida, considering five synonyms. However, they suggest that a subsequent phylogenetic analysis would validate all species. Also, their

interpretations are erroneous due to the lack of extensive information, all of which were based on limited museum material from Venezuela, including key morphological traits such as scalation, hemipenial morphology, and coloration patterns. Additionally, their study presents errors in specimen identification, erroneous geographic data, and a lack of understanding of the biogeography of the Venezuelan Andes, due to the absence of phylogenetic analyses. In this sense, we maintain the validity of the species, constituting so far 17 species for this region of Venezuela (*A. emigdioi*, *A. eriki*, *A. erythromelas*, *A. fuliginosus*, *A. major*, *A. mariselae*, *A. meridensis*, *A. micheleae*, *A. mijaresi*, *A. multidentatus*, *A. ochrosetrus*, *A. tamaensis*, *A. taphorni*, *A. ventrimaculatus*, *A. nemosophis* sp. nov. and *A. xaxi* sp. nov.) and the momentary record of *A. pamplonensis* (Schargel and García-Pérez 2002). Since the purpose of this article is the description of two species and a first phylogenetic approximation of the Venezuelan species, we will only address specific data, although several separate articles are being prepared in response to this article (Esqueda in prep.).

In reference to the diversity of the cordillera de Mérida, Natera-Mumaw et al. (2015) considered the record of Rojas-Runjaic et al. (2007) to be uncertain for the serranía of Perijá of *A. ventrimaculatus*, a species mainly restricted to the north of the city of Mérida in intramontane valleys between 2000-3250 m altitude, making it one of the Andean species with the highest altitudinal range. However, this geographical record persists arbitrarily, without a discussion supported by direct specimen verification (Montes-Correa et al. 2017) and not even pointed out by Passos et al. (2024), probably assuming what was pointed out by Natera-Mumaw et al. (2015). Through the curator Gilson Rivas of Museum of Biology of the University of Zulia (MBLUZ), kindly provided us with photographs of the specimen MBLUZ-R-0390 (information in parentheses), an adult female with TL=530 mm, TaL=31 mm and 15 dorsal scales to the midbody" → "an adult female (TL = 530 mm, TaL = 31 mm), with 15 dorsal scales at midbody, and which differs from *A. ventrimaculatus* because the latter snout rounded in dorsal view, two supralabials in contact with the eye orbit, rarely one; usually 4-5 gulars, four infralabials in contact with chinchields, eight supralabials and three in contact with loreal (snout truncated in view dorsal, one supralabial in contact with the eye orbit, two gulars, three infralabials in contact with chinchields and seven supralabials and two in contact with loreal). Another distinctive indication is the

collection area of this specimen “Ayajpaina, Negro River basin, Machiques de Perijá Municipality, Sierra de Perijá” which is located at an altitude of 1168 m asl.

On the other hand, Esqueda and La Marca (2005) identified a juvenile specimen, ULABG 2398, from 30.8 km S of Estanques way El Molino, to the south of Mérida city (2500 m altitude), as *A. ventrimaculatus*. However, these populations are currently geographically separated from the topotypical populations of *A. ventrimaculatus* by semiarid environments corresponding to Gonzalez-Estanques basin between 1000-1300 m on intramontane valleys of the central Andes of the cordillera de Mérida (Audemard 2003), whose exhumation suggests an uplift around 10-4 Myr during the Late Miocene-Pliocene (Bermudez et al. 2011), and geographically closer with *A. ochrosetrus*, although this last in our analysis would be related to *A. ventrimaculatus* and diverged 6.45 Myr ago (95 % HDP = 4.12-8.77; Fig. 8). This timing is consistent with Boschman (2021), who suggested that the cordillera de Mérida had elevations between 3500-4000 m 7 Myr ago due to the discovery evidences of paramo vegetation in the sediments of the Lake Maracaibo basin. In this context, Passos et al. (2024: 40,122) provided an erroneous locality such as “Betania, Táchira state” for specimen ULABG 2409, when in reality it is Betania, between El Molino and La "Y" via Estanques-Canaguá, Mérida state, collected on April 12, 1989, by Enrique La Marca, Juan Elías García and Ricardo Casart (Reviewed by LFE, curator ad Honorem of the museum during the period 1999-2006).

Schargel and García-Pérez (2002) indicated the presence of *A. pamplonensis* in Venezuela based on a specimen (MCNG R-5877 name correct, these authors mistyped it “MCNC”) from the “Páramo de Tamá, Táchira state,” also referenced by Esqueda and La Marca (2005). However, this record could not be verified by us. Instead, we examined a specimen (MCNC 8269), an adult male from Betania, Junín municipality, Táchira state, collected by A.R. Lacini in 1976. This specimen particularly agrees with the details of the one reported by Schargel and García-Pérez (2002). While Passos et al. (2024) provided a more extensive description of *A. pamplonensis* with specimens from Colombia, they did not review additional Venezuelan specimens, except for the referred material of *A. tamaensis* and *A. mijaresi* (see Esqueda and La Marca 2005), which they considered synonyms of *A. pamplonensis*. In contrast to these authors, whose data were imprecise and insufficient, our morphological and molecular data demonstrate a

complex of populations along the Andean-Llanera slope of the cordillera de Mérida (Esqueda et al. in prep.).

For the moment, we consider it pertinent to note:

1. Dorsal pattern differences. - Passos et al. (2024: 52) provided images of the holotype of *A. pamplonensis*, clearly showing that the dorsal spots occupy more than one scale in width, are margined with cream, and arranged in at least two rows (as a reticulated pattern according to them). The material from Colombia reviewed by Natera-Mumaw et al. (2015: 123) exhibits the same dorsal pattern. However, the holotype of *A. mijaresi* shows dark spots on the dorsum, but these are not margined, do not occupy more than two scales, and are irregularly arranged. In the case of *A. tamaensis*, the dorsal pattern consists of two rows of scales, unmarginated, and in most cases, occupying only one dorsal scale.

2. Light band behind parietals. - The holotype of *A. pamplonensis* displays a subtle and incomplete light band behind the parietals, a character noted by Natera-Mumaw et al. (2015), who indicated that this light band is conspicuous in juveniles, while it can be either conspicuous or inconspicuous in adults. In contrast, juveniles, and adults of *A. mijaresi* and *A. tamaensis* lack this characteristic (Esqueda in prep.).

3. Ventral pattern. - Passos et al. (2024) did not discuss or reference the record of *A. pamplonensis* made by Schargel and García-Pérez (2002), which corroborates the sympatry of *A. pamplonensis* and *A. tamaensis*. According to Schargel and García-Pérez, *A. pamplonensis* exhibits a black ventral region bordered laterally by white with a discontinuous white medioventral line. However, this description does not match our observations of *A. pamplonensis*, where the venter is cream-colored with two rows of dark rectangular spots (one on each side of each ventral scale, occupying ~40 % of the width). While *A. mijaresi* has dark lateroventral spots, they are found on a pale-yellow or yellowish-orange background in life, unlike *A. pamplonensis*, which has an intense yellow venter and dark brown-pigmented subcaudals (Passos et al. 2024: 54). In contrast, *A. tamaensis* may or may not have dark ventral spots, with a light-yellow background, and its subcaudals are immaculate. Images of living specimens in

the IUCN conservation sheet for *A. pamplonensis* align with our observations (Caicedo et al. 2017).

Following Passos et al. (2009a), who did not define a distinct group, they suggested that *A. sanctaemartae*, *A. macondo*, *A. nigriventris*, *A. pamplonensis*, and *A. variegatus* share a set of characters, including 9-12 maxillary teeth and a diastema (or space between posterior teeth, see Passos et al. 2024), as well as a dorsal pattern that is reticulate, banded, or variegated, and a ventral region strongly pigmented with black.

Currently, we are analyzing material collected along the mountains that extend from Bailadores to La Grita, Mérida and Táchira states, at elevations above 1700-2300 m asl (Esqueda et al. in prep.). This material exhibits a variable dorsal pattern ranging from uniform brown to one with small scattered dark spots (reticulate). The specimens show an intense yellow venter in life, with two rectangular black spots on each side of the ventral scales. These individuals have fewer than nine maxillary teeth and lack a "diastema." Although Passos in previous articles acknowledged the term "diastema," Passos et al. (2024) recognized a possible error in its application to this group. These observations suggest that the record of *A. pamplonensis* for Venezuela requires extensive review, particularly in light of an additional examination of individuals from Tamá, where *A. tamaensis* also occurs. Furthermore, Passos et al. (2024) recognized material very close to the type locality of *A. pamplonensis*, which they referred to as *A.* aff. *pamplonensis*. This material was noted to have a ventral count of 132-142 in males and 136-142 in females. In contrast, *A. tamaensis* has a ventral count of 145-152 in males and 160-165 in females (Esqueda and La Marca 2005), while the record of *A. pamplonensis* reported by Schargel and García-Pérez (2002) shows 189 ventrals in the only known female. We examined a specimen (MCNC 8269), an adult male from the same locality, which has 178 ventrals.

Finally, *A. multidentatus* was described by Passos et al. (2009b) based on a single specimen, CVULA 7080. According to Passos et al. (2009b), the only species that resembles it is *A. emigdioi*, which is geographically distant and would have 7-12 maxillary teeth compared to the 18 maxillary teeth of *A. multidentatus*. As far as is known in the Andes, no *Atractus* species possesses such a large number of maxillary teeth, except for *A. heliobelluomini*, which is distributed in the Colombian Amazon and

has 21-22 maxillary teeth, according to these authors. Could this be a lapsus mentalis on the part of the authors? When reviewing the appendix of examined specimens, there is no reference to this species. Additionally, the original description does not provide information on the maxillary teeth of the only known specimen, which has a well-defined vertebral line (Silva-Haad 2004), contrary to the description by Passos et al. (2009b) who indicated three longitudinal lines. Passos et al. (2024: 87, 90) revised the comparative diagnosis and now recognize the similarity with *A. emigdioi*. In our phylogenetic analysis, *A. taphorni* is related to *A. emigdioi* and diverged from the latter 3.87 million years ago (95 % HDP = 1.92–6.32, Fig. 8). According to Schargel and García-Pérez (2002) and Esqueda and La Marca (2005), *A. taphorni* would have a distribution suggesting contact with *A. multidentatus*, although there is no data on hemipenes for either species. In *A. emigdioi*, the hemipenis is not capitate, unicalyculate, and poorly bilobed (Schargel and Castoe 2003; unpublished data LFE 2021). Our biogeographic understanding of *Atractus* assemblages in the Venezuelan Andes indicates that species with similar patterns do not coexist in the same environments.

To date, *A. erythromelas* is the only species exhibiting 15 or 17 dorsal midbody scales (with a higher frequency of 15 in males, Esqueda in prep.), unlike *A. meridensis*, which only has 17 dorsal midbody scales. Passos et al. (2024) arbitrarily considered *A. meridensis* a synonym of *A. erythromelas*, despite the significant differences between the two species (unpublished data LFE). Our calibrated phylogenetic tree indicates that *A. erythromelas* diverged 7.61 million years ago (95 % HDP = 5.41-9.46) from *A. meridensis* and *A. nemosophis* (sister species). With improved morphological and phylogenetic data, we have determined that *A. meridensis* and *A. nemosophis* are sympatric across much of their distribution, sharing a unique and distinct morphological trait, the development and extension of the rostral scale. This feature is absent in populations of *A. erythromelas*, which exhibits an allopatric distribution relative to *A. meridensis* (Esqueda in prep.).

While a more extensive discussion of the errors and misinterpretations made by Passos et al. (2024) is warranted, it falls outside the scope of this work. For instance, the divergence of Andean species in Venezuela from those in the cordillera de la Costa and the Venezuelan Amazon is evident in our phylogenetic data. In fact, Passos et al. (2024) incorrectly consider *A. micheleae* a synonym of *A. lancinii*, to justify the presence of

this species in the Andes of Venezuela (Esqueda in prep.). This divergence is also reflected in the genus *Tantilla* in the Venezuelan Andes (Esqueda et al. in press). Similarly, Bonaccorso and Guayasamin (2013) found a stronger relationship between the *Aulacorhynchus* toucans of the cordillera de la Costa and Pantepui (southern Venezuela), where the Andes constitute an ancestral area, diverging at the end of the Miocene.

At present, this phylogenetic information is particularly relevant as new taxonomic assessments may highlight speciation potential, genetic diversification, and endemism in the Mérida Andes, a system with a particularly unique climatic and geological history. This history is reflected in species exhibiting reduced geographic ranges (e.g., microendemism), one of the criteria used to determine species conservation status.

Conservation status

The current resolution regarding the taxonomy of *Atractus* remains a subject of ongoing debate, with discussions on its diversity continually evolving (Melo-Sampaio and Venegas 2022; Passos et al. 2022; Passos et al. 2024). For the first time, Esqueda and La Marca (2015) evaluated the conservation status of *Atractus* species from Venezuela using the IUCN criteria, supplemented by an additional set they defined as IVER. According to their assessment of 30 species (excluding *A. guerreroi*; see Natera-Mumaw et al. 2015), 10 species were categorized as Least Concern, 7 as Near Threatened, 9 as having Insufficient Data, and 4 as Vulnerable. Our analysis expands upon this work by adding two endemic species from the cordillera de Mérida, *A. nemosophis* and *A. xaxi* to the Vulnerable category. Both species inhabit the medium-high altitudes of the cordillera de Mérida, where they face significant threats from various anthropogenic activities. A similar situation is observed in the cordillera de la Costa, where *A. lancinii* and *A. vittatus* are found. While parts of their distributions are within protected areas (e.g., National Parks), these species also experience pressures from human activity. Specifically, *A. lancinii* has an altitudinal range of 700-1700 m asl, while *A. vittatus* is occurs between 1500 and 2000 m asl.

A fundamental yet scarcely studied issue in reptile conservation is the susceptibility of cryptozoic-fossorial snakes to indirect anthropogenic threats, particularly those impacting their prey populations (Böhm et al. 2013). *Atractus* is currently considered a group of dipsadid snakes with a specialized diet primarily consisting of earthworms

(Balestrin et al. 2007; Oliveira et al. 2023). While it is not always the case that specialized feeding strategies arise from more generalist ancestors, this idea can be explored by examining the relationship between maximum ecological changes and phenotypic optima. Vermivorous snakes serve as a distinctive example of ecological independence in almost all snake lineages, having evolved this feeding strategy since the Cretaceous. It is considered one of the most evolutionary and ecologically accessible feeding strategies (Grundler and Rabosky 2021). This is especially true in mountain environments, where earthworm diversity is high (Edwards and Arancon 2022), a condition seen in these Neotropical snakes.

Globally, studies show that the conversion of natural environments into human-dominated land uses has significantly impacted earthworm diversity and status. Earthworms, considered ecosystem engineers, have been part of ecosystems for over 400 million years (Maggi and Tang 2021). Additionally, climate change, particularly extremes of drought and flooding, has been shown to directly affect earthworm communities by altering their activity, abundance, and biomass. However, the indirect effects of anthropogenic activities on these communities remain poorly studied. These activities, which often result in soil contamination, also negatively affect epigean biota (Miglani et al. 2019; Singh et al. 2019).

These relatively small, cryptozoic-semifossorial snakes with specialized diets are a source of concern due to their dominance in the mountainous landscapes of the northern Andes. In particular, we view them as an ideal model for both micro and macroevolutionary studies. Given their endemism and bioecological characteristics, they can also be defined as bioindicators of site quality. Although this study represents the first comprehensive attempt to understand the relationships of these snakes in Venezuela and reinforces their systematics, we are still far from fully understanding their diversity and distribution. The Venezuelan Andes remain an underexplored region, and we hope to continue contributing to its knowledge. With this in mind, we would like to highlight some important points based on our field experience, which should serve as a snapshot of the current state of these snakes, following Böhm et al. (2013).

1. Understanding Population Stability. - Due to their apparent restricted distribution and specialized diet, it is crucial to understand the role of mixed environments in the stability of their populations (Esqueda in prep.). While the highest observed abundance of *Atractus* has been in anthromes, areas that were

previously abundant with these snakes, such as mountainous landscapes in Trujillo state, have seen a significant decline in their presence. These areas have been strongly impacted by intense agricultural activities and the use of agrochemicals, leading to major contractions and conversions in the landscape.

2. Microendemism and Cryptic Diversity. - Our research over many years has led us to recognize that *Atractus* is a distinctive component of medium-high environments in the Venezuelan Andes. However, microendemism and cryptic diversity in these species have yet to be evaluated. This aspect is crucial for establishing a coherent baseline for assessing the risk levels of species whose bioecological characteristics make direct monitoring challenging. Our preliminary data suggest that the geological-climatic history of the cordillera de la Costa and ecological details of this group such as a specialized diet, limited dispersal, and habitat preference (>1500 m asl) have allowed a spatial mosaic of populations with a strong hierarchical genetic structure at geographic scales, without being fully evaluated (microendemism). While this hypothesis is attractive, it will require further future studies (Esqueda et al. in prep.), but suggests that the formation of barriers during uplift events in this mountain system reduced dispersal and facilitated diversification in high altitude environments (e.g. *A. ventrimaculatus* vs. *A. ochrosetrus*; *A. erythromelas* vs. *A. meridensis*; *A. mariselae, A. mijaresi* and *A. xaxi* sp. nov.).

3. Impact of Anthropogenic Activities. - Our understanding of the cause-effect relationship between anthropogenic activities and the decline of reptile species remains incomplete, particularly in tropical environments. We believe that raising awareness locally about the need to preserve fragments of natural habitats, as opposed to fully converted areas like grasslands or crop systems, could help mitigate risks to these populations. Although we lack immediate data, it is evident that the conversion of natural landscapes has destroyed a significant portion of primary habitats, making it increasingly difficult to detect the microendemic ranges of these cryptozoic-fossorial snakes.

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Author contributions

Writing-original draft preparation, L.F.E.; Writing and data, L.F.E., F.R.R. and A.P.; data L.F.E., S.B., L.F.N. and E.C.S.; review, writing and funding, L.F.E., J.C.O., C.C. and P.G.; funding F.U. All authors have read and agreed to the published version of the manuscript.

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Data availability

All data generated or analyzed during this study are included in this published article (see supplementary information files in format xlsx, except unpublished data that are not yet public until the time of their publication in the repository GENBANK). All unpublished specimens are not listed on the IUCN Red List of Threatened Species Index and met the standards required by the Ministerio de Ecosocialismo y Aguas (MINEC-Venezuela) under Nº DGBD/2021/0095 to Luis Felipe Esqueda (LFE). All data generated or analyzed during this study are included in this published article (including supplementary information files).

Declarations

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CONCLUSIONS (SYNTHESIS OF ALL CHAPTERS)

The dataset gathered here constitutes a first approximation with ~42 % of the known species to begin understanding the diversification and biogeographical history of the sleepyhead snakes of the genus *Atractus* and that their greatest diversity occurs in mountain environments above 1000 m asl in the central and northern Andes. Although these snakes exhibit a high degree of endemism in the middle-highlands of the Andes, the information obtained here provides evidence of the link between the chronological uplift of the Andes and the diversification of sleepyhead snakes. Our divergence estimates and ancestral biogeographic reconstructions suggest an Andean or Andean-Pacific origin during the Miocene (~22 Myr), followed by the subsequent colonization of the northern Andes during its early to mid-Pliocene uplift phase, and consistent with others results previously obtained in the Dipsadidae family (Serrano et al. 2023). From there, the following aspects can be highlighted:

(1) despite still having a significant number of species from Colombia, two major clades are discernible: the first mostly with Andean species and the other including Andean species and those from the Amazon basin, which suggests the idea of a connection zone in the past between western Amazonia and the Andes towards the Pacific (see Boschman and Condamine 2021).

(2) the clade of sleepyhead snakes from the cordillera de Mérida, some species align with its uplift between 8-5 Myr, while other species seem to have experienced changes and contractions in their distribution area influenced by climatic fluctuations during the Pliocene-Pleistocene, followed by population expansion in more recent times. Although we have not evaluated all Andean species at the level of their ecological pattern, those that have been evaluated reveal a consistent pattern of niche conservatism. In both cases, the overlap metrics (Schoener's D and I) showed high values, and the statistical tests did not reveal significant differences in the occupation of the available climatic space, suggesting that these species maintain similar environmental conditions despite their phylogenetic divergence. This finding is consistent with the hypothesis that, in mountainous environments like the Andes of Venezuela, ecological constraints and physiological specialization can limit the ability of species to ecologically diversify. Thus, allopatric speciation appears to have occurred without drastic changes in the climatic niche, reinforcing the notion that geographic isolation and complex topography

have been key drivers in the diversification of the group, rather than adaptive divergence in the niche;

(3) until now, the role of the Andes in the diversification of these cryptic-fossorial snakes, mostly South American, had not been tested, where different biogeographic scenarios have been evaluated. Our analyses of state-dependent diversification, applying BiSSE and ClaSSE models under a comparative approach between lineages distributed in and outside the Andes, reveal patterns consistent with complex speciation scenarios linked to geography. First, found strong support for the species pump hypothesis, characterized by high rates of speciation and extinction in Andean regions, suggesting that these mountainous environments function as dynamic engines of diversification with accelerated evolutionary turnover. Then, the models that best fit the empirical pattern also support the hypothesis of species attraction to the Andes, evidenced by high transition (dispersal) rates from non-Andean areas to the Andean regions. This result is consistent with a central role of the Andes not only as a source of diversification but also as a preferred evolutionary destination, where new species tend to establish themselves. Overall, the results suggest that the Andes have functioned as areas of high evolutionary dynamics, where the combination of complex topography, geographical isolation, niche conservatism, and ecological attractiveness has promoted both the formation and accumulation of species in this biodiversity hotspot (Myers et al. 2000). Although it has not been fully evaluated, all Andean species in Venezuela occur in cloud forests that appear from an altitude of 2000 m, and these environments have been subjected to significant conversion in recent decades, so a broader study is necessary to categorize all the species. For the moment, our data suggest that all species should be considered to be included in the Vulnerable category according to criteria Ac and B2 (i,ii,iii,iv) (IUCN 2012).