

The Miocene La Venta Biome (Colombia): A century of research and future perspectives

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ABSTRACT

The La Venta deposits (Colombia) record one of the most fossil-rich regions in tropical South America and offers an exceptional opportunity to study the effect of the Miocene climatic changes and the evolution of extinct and extant clades in a low-latitude ecosystem. Land and freshwater vertebrates, and less commonly plants and invertebrates, constitute most of the La Venta fossils. The mammal record has been used to define the Laventan Age/Stage *c.* 13.5-11.8 million years old. La Venta has been studied for nearly a century, but the last major collecting efforts were done several decades ago. Recently, Colombian and international researchers have begun studies at La Venta, with the valuable participation of the local community. The joint efforts resulted in the establishment of a new La Venta natural history museum (*Museo de Historia Natural La Tatacoa*). This new wave of paleontological and geological studies has resulted in an improved stratigraphy of La Venta and new paleobiological and evolutionary hypotheses of several vertebrate groups, and in the museum's educational and outreach activities. Here, we review the current geological and paleontological knowledge of La Venta, identify knowledge gaps, and discuss future research directions. A century after the first paleontological expedition, La Venta's fossil record continues to illuminate the evolution of the South American tropical biodiversity during the Miocene.

RÉSUMÉ

Le biome miocène de La Venta (Colombie) : un siècle de recherche et des perspectives d'avenir.

Les dépôts de La Venta, en Colombie, fournissent l'un des assemblages fossiles les plus riches de l'Amérique du Sud tropicale et offrent une occasion exceptionnelle d'étudier l'effet des changements climatiques du Miocène et l'évolution des clades éteints et actuels dans un écosystème de basse latitude. Les vertébrés terrestres et d'eau douce, et plus rarement les plantes et les invertébrés, constituent la plupart des fossiles de La Venta. Le registre des mammifères a été utilisé pour définir l'âge laventien, *c.* 13.5-11.8 millions d'années. La Venta est étudiée depuis près d'un siècle, mais les dernières collectes importantes ont eu lieu il y a plusieurs décennies. Récemment, des chercheurs colombiens et internationaux ont entamé des études à La Venta, avec la participation précieuse de la communauté locale. Ces efforts conjoints ont abouti à la création d'un nouveau Musée d'histoire naturelle à La Venta (*Museo de Historia Natural La Tatacoa*). Cette nouvelle vague d'études paléontologiques et géologiques a permis d'améliorer la connaissance de la stratigraphie de La Venta et de formuler de nouvelles hypothèses paléobiologiques et évolutives pour plusieurs groupes de vertébrés. Nous faisons ici le point sur les connaissances géologiques et paléontologiques actuelles de La Venta, identifions les lacunes de connaissances et discutons des orientations futures de la recherche. Un siècle après la première expédition paléontologique, les archives fossiles de La Venta continuent d'éclairer l'évolution de la biodiversité tropicale sud-américaine au cours du Miocène.

RESUMEN

El bioma mioceno de La Venta (Colombia): un siglo de investigación y perspectivas para el futuro.

En los depósitos fosilíferos de La Venta, en Colombia, se registra una de las biotas fósiles más ricas de la porción tropical de Suramérica, lo que representa una oportunidad excepcional para estudiar los efectos de los cambios climáticos del Mioceno y la evolución de clados existentes y extintos en un ecosistema de latitudes bajas. Los vertebrados terrestres y acuáticos son los fósiles mayormente representados; mientras que registros de plantas e invertebrados son menos comunes. Se destaca, dentro de los grupos de vertebrados, una diversa comunidad de mamíferos, la cual ha sido usada para definir el Piso Laventense *c.* 13.5-11.8 Ma. A pesar que La Venta ha sido estudiada por cerca de un siglo, los últimos grandes esfuerzos de colecta se dieron hace varias décadas. Recientemente investigadores colombianos y extranjeros, junto con la comunidad local, han llevado a cabo nuevas expediciones, que han dado como fruto el establecimiento de un nuevo museo de historia natural, el *Museo de Historia Natural de La Tatacoa*. Esta nueva ola de investigación en la geología y paleontología de La Venta ha llevado a una mejora del registro estratigráfico, al desarrollo de nuevas hipótesis sobre la evolución de varios grupos de vertebrados y al crecimiento y la mejora de las actividades de divulgación y educación del museo. En este trabajo presentamos una revisión de la información geológica y paleontológica de La Venta, identificamos vacíos en el conocimiento y discutimos direcciones de investigación en el futuro. Un siglo después de la primera expedición paleontológica en La Venta, su registro fósil continúa esclareciendo la historia evolutiva de la biodiversidad tropical de Suramérica en el Mioceno.

INTRODUCTION

A major challenge in studying the past climatic and biotic changes in tropical South America is the lack of adequate

sampling, as there are few well-sampled fossil sites (Carrillo *et al.* 2015). The Miocene fossil site of La Venta, in the region known as La Tatacoa Desert in Colombia, is one of the most studied fossil assemblages of the continent (Fig. 1)

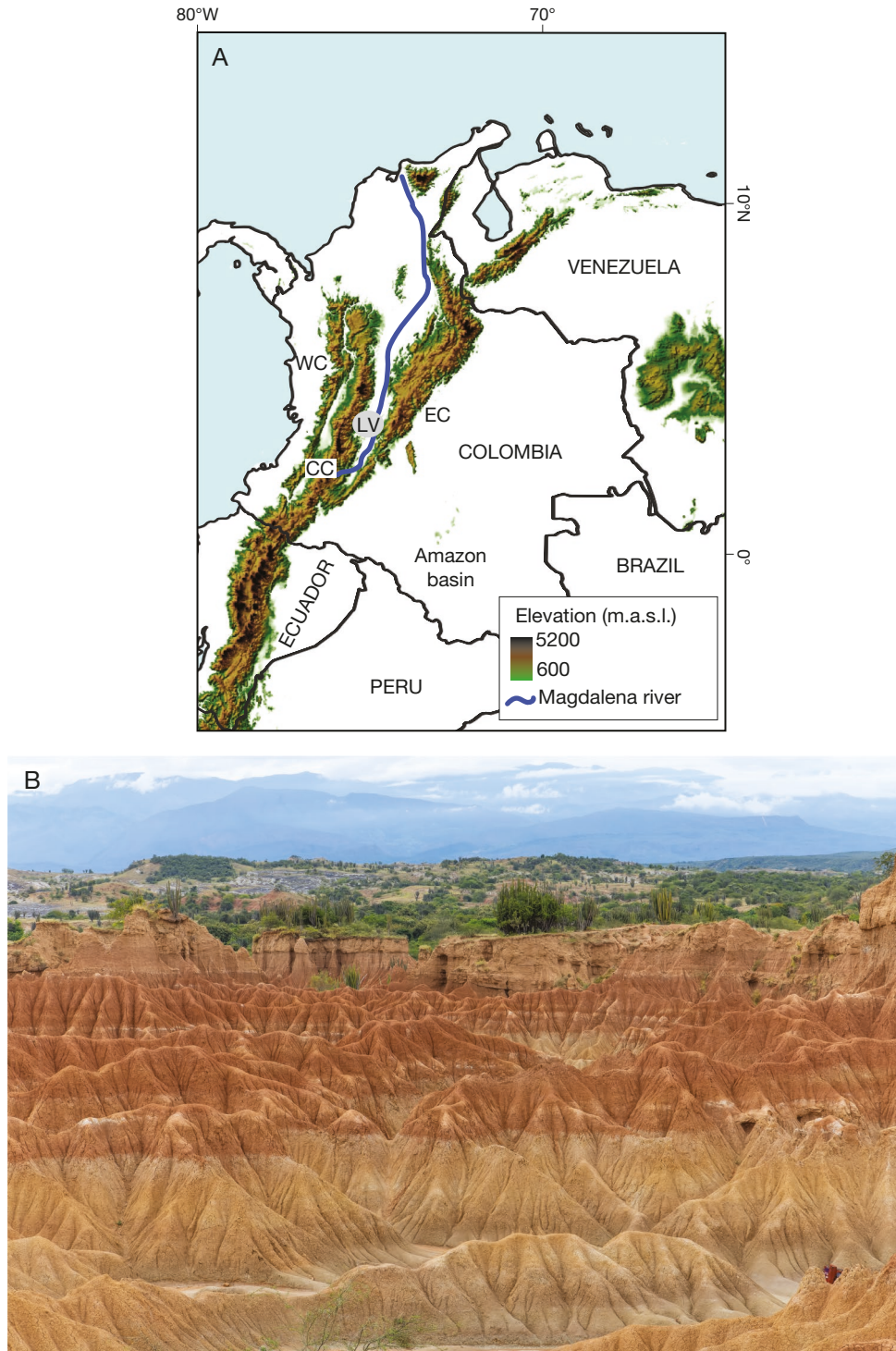


FIG. 1. — Location and landscape of La Tatacoa Desert, Colombia: **A**, geographic location of La Venta fossil site in the Magdalena Valley, Colombia. Modified from Zapata *et al.* (2023); **B**, badlands of La Tatacoa Desert. Abbreviations: **WC**, Western Cordillera; **CC**, Central Cordillera; **EC**, Eastern Cordillera; **LV**, La Venta. Photo by C. Ziegler.

(Kay *et al.* 1997; Croft 2016; Defler 2019; Jaramillo & Oviedo 2023). La Venta offers an exceptional opportunity to study the effect of the Miocene climatic and environmental changes on the evolution of tropical diversity and to assess how tropical ecosystems fared during times warmer than the pre-Industrial revolution. The site represents an ancient

tropical ecosystem (Kay & Madden 1997a, b; Spradley *et al.* 2019) with an exceptionally rich fossil record that includes plants, invertebrates, freshwater fishes, amphibians, squamates, birds, turtles, crocodyliforms, and mammals (Kay *et al.* 1997), which has been used to define the Laventan Age/Stage (Madden *et al.* 1997a).

La Venta has a century of paleontological research. The first scientific report of fossils from the region, by the Catholic priests and naturalists Brothers Ariste Joseph (Maurice Rollot) and Nicéforo María (Antoine Rouhaire) was in 1923 (Ariste Joseph & Nicéforo María 1923; Madden *et al.* 1997b; Rodríguez 2002). Since then, numerous paleontological surveys were conducted by Colombian and international institutions (Madden *et al.* 1997b; Oviedo *et al.* 2023). However, participation and publication of scientific results by Colombian researchers have been limited during the last century (Fig. 2), partly because there have historically been fewer professional paleontologists in Colombia than in other South American countries (e.g., Brazil and Argentina).

The last major fossil collections in La Venta were made during the 1980's and 1990's (Madden *et al.* 1997b). In recent years, several Colombian and international researchers have resumed fossil collecting efforts at La Venta, in close collaboration with the local community and the local non-governmental organisation “*Vigías del Patrimonio Paleontológico La Tatacoa*” (Villavieja, Colombia; VPPLT). The joint efforts resulted in the establishment of a new local museum, the *Museo de Historia Natural La Tatacoa* (Oviedo *et al.* 2023), which now has the largest collection of fossils from La Venta (> 4000 specimens), including exceptionally complete and well-preserved specimens (Figs 3; 4), many of which still need to be studied.

The resulting thematic publication (Carrillo 2023) presents the most recent advances in the study of La Venta. It is the product of close collaboration among the researchers, *Vigías*, and the *Museo de Historia Natural La Tatacoa*, and another local museum, the *Museo La Tormenta*. In this work, we review the current geological and paleontological knowledge of La Venta, identify knowledge gaps, and discuss future research directions.

TECTONOSTRATIGRAPHY OF THE HONDA GROUP AND THE MIOCENE PALEOGEOGRAPHY OF THE NORTHERN ANDES

The Miocene sedimentary rocks of the La Venta site provide crucial insights into the tectonic and paleogeographic evolution of the northern Andes. La Venta is located in the Upper Magdalena Valley, a hinterland basin bounded by the Central Cordillera in the west and the Garzón Massif in the east (Fig. 1). La Venta fossils are preserved within the Honda Group, which consists of the Victoria and Villavieja formations, two clastic sedimentary successions deposited in fluvial and alluvial systems during the Middle Miocene (Villarreal *et al.* 1996; Anderson *et al.* 2016; Mora-Rojas *et al.* 2023). Previous studies revealed that the Honda Group marks a regional shift in sedimentation, transitioning from Early Miocene lacustrine to Middle Miocene fluvial and alluvial sedimentation, which is characterized by high sedimentation rates, the appearance of reworked volcanoclastic materials, and syn-sedimentary deformation (Wellman 1970; Montes *et al.* 2021; Mora-Rojas *et al.* 2023; Zapata *et al.* 2023). Maximum depositional ages obtained from zircon U-Pb data exhibit a

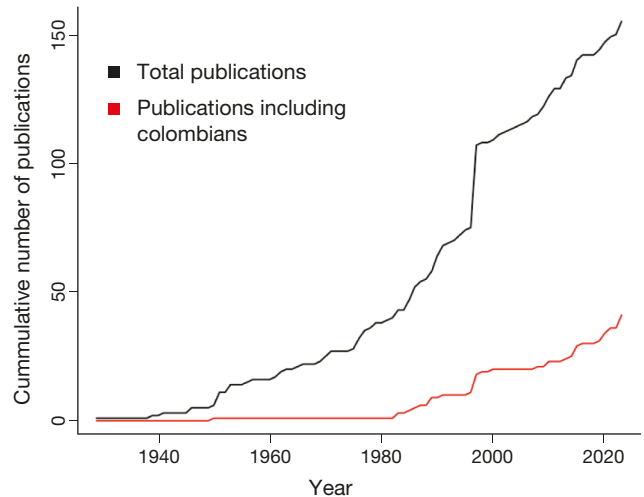


FIG. 2. — Cumulative number of publications from the La Venta fossil site during a century of paleontological research. The results are derived from a compilation of all the publications produced in La Venta that were compiled in a database (see Appendix 2).

pattern of decreasing age towards the top of the sedimentary succession, which together with Ar-Ar and fission-track ages from pyroclastic rocks indicate sediment deposition between *c.* 16 Ma and 10.5 Ma (Flynn *et al.* 1997; Anderson *et al.* 2016; Mora-Rojas *et al.* 2023; Zapata *et al.* 2023).

The Miocene accumulation of the Honda Group was contemporaneous with major landscape and tectonic reconfigurations that shaped the Northern Andes. Miocene magmatism in the Upper Magdalena Basin, data from extinct and living species, and thermochronological data indicate that the uplift of the Garzón Massif did not occur before 10 Ma, and the Miocene fragmentation of the Central Cordillera suggests a continuous fluvial connection among the western Colombian Andes, the Upper Magdalena Basin, and the Pebas system in western Amazonia (Lundberg & Chernoff 1992; Montes *et al.* 2021; Rodríguez-Muñoz *et al.* 2022; Zapata *et al.* 2023), a connection that no longer exists, as these regions are separated by the Central Cordillera and the Garzón massif.

Further research is necessary to better understand the timing and mechanisms that uplifted the sections of the Central Cordillera and the southern part of the Eastern Cordillera (e.g., Garzón massif). The La Venta site presents an opportunity to elucidate the relationships of the flora and fauna to orography, soil composition, and sediment supply. We require a better understanding of the biomes that occupied the landscape of La Venta. Was La Venta a landscape dominated by savannas with riparian forests along the water bodies, or a forest with a closed canopy occupying the entire landscape? What sort of connection existed with the Pebas system? Did the marine incursion into western Amazonia affect the La Venta region? And finally, the lack of proper taphonomic studies leaves us with a poor understanding of the fossilisation process that led to such excellent fossil preservation. These various lines of research represent the next steps in enhancing our knowledge of the La Venta fossil site and of the evolution of the Northern Andes landscape and ecosystem.

GEOCHEMISTRY, PALEOENVIRONMENT AND PALEOBIOLOGY IN LA VENTA

Remains of organisms such as bone and tooth biominerals record the chemical signal of the environment in which the organisms lived (Ben-David & Flaherty 2012). This signal is often retained even after fossilisation, and isotopes have been widely used as tracers of ecological, environmental, climatic, and physiological information (Higgins 2018). However, to our knowledge, no isotopic work has been done on the extensive collection of La Venta fossil remains. Carbon, oxygen, nitrogen, and strontium isotope studies of sediments and fossils could unlock a wealth of information. Carbon isotope analysis of fossil tooth enamel could provide dietary information, whereas nitrogen isotopes could provide insights into diet and trophic position (Higgins 2018). Carbon and nitrogen isotopes analyses on aquatic mammals (cetaceans and sirenians) could elucidate habitat and foraging preferences. Oxygen isotopes in fish otoliths, turtles, and crocodylians could be used to reconstruct water temperature and salinity (e.g., Gou *et al.* 2022). Clump isotope analysis of paleosols could help assess paleotemperature (e.g., Garzzone *et al.* 2014) as well as brGDGTs (e.g., Häggi *et al.* 2023). Strontium isotope analyses on rocks, soils, water, plants together with strontium isotope data on fossil remains could provide information on animals migration routes and habitat ranges (e.g., Wallace *et al.* 2019). In short, state-of-the-art paleontology uses a large battery of geochemistry analyses that could be of critical importance for understanding the climate and environmental changes in the tropics during the middle Miocene.

PALEOBOTANY IN LA VENTA

There are no published palynological studies from La Venta (Plata-Torres *et al.* 2023), and the only reports of a few pollen grains derived from three palynological samples in an unpublished PhD dissertation (Muñoz Saba 2018), but the sample locations are unknown. We have processed palynological samples at many different localities and stratigraphic levels, which have yielded no organic matter. This is a common feature in dry landscapes, where intense modern weathering and/or oxidation destroys the organic matter. In similar regions, such as the Guajira desert in northern Colombia, outcrop samples are also sterile, but samples from the same stratigraphic levels taken from oil wells have yielded abundant recovery of organic matter and palynomorphs (Jaramillo *et al.* 2020). The possibility of large-scale palynological studies therefore remains to be explored, but from well samples rather than outcrops.

Phytoliths, microscopic opaline silica particles deposited in or around plant cells, are emerging as a powerful tool for reconstructing the structure of vegetation in deep time (Dunn *et al.* 2015; Strömberg *et al.* 2018). Phytoliths can be classified broadly by their morphology into the main categories of grassland or forest indicators, and their relative proportions are used to interpret fossil assemblages as representatives of different grass- or forest-dominated environments (Strömberg 2004, 2011; Strömberg *et al.* 2018). Often, phytoliths are preserved in highly oxidized, fine-grained sediments of

terrestrial origin, such as those in La Venta, where the preservation of other organic plant remains, including macrofossils or pollen, is limited (Retallack 1983; Strömberg *et al.* 2018). However, despite extensive sampling of the sediments of the La Victoria and Villavieja formations for phytolith extraction, we recovered no interpretable phytolith assemblages. In similar vertebrate rich localities, phytoliths have been recovered from scrapings of preserved dental calculus (Strömberg *et al.* 2018). This approach has not been attempted in La Venta.

Taking into account that many tropical grasses and trees contain abundant silica (Strömberg *et al.* 2018), we believe the absence of phytoliths in the deposits at La Venta is due primarily to factors related to phytolith taphonomy and preservation rather than low phytolith production. The degree to which phytoliths are dissolved or preserved in soils or sediment depends on specific chemical conditions, which include pH, the prevalence of other sources of easily dissolvable silica, the presence of organic material, and oxide coating of phytoliths (Madella & Lancelotti 2012; Song *et al.* 2016; Strömberg *et al.* 2018). Under pH > 7 (especially > 8.5) and in the presence of organic molecules, which form silica-organic complexes even at neutral pH, rates of phytolith dissolution increase (Bennett & Siegel 1987; Strömberg *et al.* 2018). Conversely, phytolith preservation is enhanced in sediment with abundant volcanic glass or opal A in the form of diatoms, and by Al- and Fe-oxyhydroxide grain coatings (Kendrick 2006; Song *et al.* 2016).

Our hypothesis of poor preservation is borne out by geological evidence (Guerrero 1993, 1997; Montes *et al.* 2021) from La Venta, which indicates higher soil pH during sediment deposition and pedogenesis. Specifically, pedogenic carbonates, which tend to form at high pH (Zamanian *et al.* 2016), are abundant in the La Victoria and Villavieja formations (Guerrero 1993, 1997). In addition, deposits at La Venta are not highly volcanoclastic, except for discrete ash-rich layers, and lack the abundant volcanic glass often associated with well-preserved fossil phytolith assemblages, such as in the Cenozoic of southern Argentina and the Great Plains of North America (Strömberg 2004; Zucol *et al.* 2010; Strömberg *et al.* 2013, 2018).

Up to date, no leaf or other plant compression/impression fossils have been formally described from the La Tatacoa region. The deep weathering profile observed in this tropical site is highly problematic when scouting for consolidated, fossiliferous beds. Only a handful of fossil-containing lenses have been found in the La Victoria and Villavieja formations. These include *c.* 5 cm-thick lenses of bluish-grey mudstones and claystones interspersed between red paleosol deposits. Highly fragmented plant remains have been retrieved and include identifiable impressions of floating ferns (*Salvinia* sp.), minutely toothed, pinnate fern fronds with possible affinities to Blechnaceae (identified by two of us, MC and FH), and other unidentifiable leaf remains. The presence of these ferns in lenses indicates the development of temporal freshwater water bodies within the pedogenic column.

The plant fossil record from La Venta is represented mostly by petrified wood (Fig. 5). This type of fossil material has been widely known by the local and the scientific community for



Fig. 3. — Paleontological research and outreach in La Victoria, Colombia: **A, B**, Images of the exhibit *Fossil Territory, Living Stories* at the *Museo de Historia Natural La Tatacoa (MHNT)* (Oviedo et al. 2023); **C**, researchers working at the MHNT; **D**, the Vanegas brothers, Rubén (left) and Andrés (right), who manage the MHNT and founders of *Vigías*; **E**, celebration event in La Victoria organized by the MHNT on the occasion of the 100 years of paleontological research in the region; **F**, César Perdomo, fossil collector and founder of the *Museo La Tormenta* prospecting for fossils; **G**, researchers, students, journalists and members of *Vigías* that participated in the fieldwork in 2023. All the photos were taken during the fieldwork in May 2023 by C. Ziegler.

more than 50 years; it is abundant and consists of trunks that can reach up to 8 m long. Permineralization and replacement of La Venta wood has resulted from silica deposition. Despite its abundance and good preservation, only three reports have been formally described from the Honda Group: *Goupioxylon stutzeri* Schönfeld, Goupiaceae, has been collected from Los Mangos and La Ceibita localities (Pons 1970, 1983); *Terminalioxylon portae* Mirioni, Combretaceae and *Leguminoxylon dindense* Pons, Fabaceae, were collected from El Dinde locality (Pons 1983), and the description of each one was based on a single specimen. The pioneering work from Pons demonstrates the high potential that this fossil material has for reconstructing the past ecosystem; however, both the geological interpretations and the taxonomic affinities should be revised in light of new stratigraphic information (Montes *et al.* 2021; Mora-Rojas *et al.* 2023), and broader sampling is needed, as some taxonomic affinities could be misleading due to poor preservation of some fossil samples.

Preliminary field observations support the idea that fossil wood is present and abundant in both the La Victoria Formation (San Alfonso, Cerro Gordo, Chunchullo, Tatacoa beds) and the Villavieja Formation (Cerbatana and Cardon beds); more than fifty samples have been collected. In all sampled beds we found a very common morphotype that resembles *Leguminoxylon dindense*. Undergoing investigations aim to reconstruct the past ecosystem of the Honda Group, using floristic composition and climate estimations based on wood functional characters.

TRACE FOSSILS IN LA VENTA

Although little work has focused on the trace fossil assemblages of the La Victoria and Villavieja formations, rhizoliths and non-specific bioturbation are reportedly abundant throughout La Venta, in addition to vertebrate coprolites and burrows (Guerrero 1993, 1997). Describing the occurrence and composition of trace fossil assemblages in La Venta could provide a new perspective on its sedimentary and paleoecological dynamics. In fluvial floodplain deposits, trace fossil diversity and abundance are variable and may be highly specific to their sub-environment (e.g., channel, sandbar, crevasse splay, pond) (Buatois & Mángano 2011). The degree and intensity of bioturbation in fluvial settings are dictated mainly by the colonization window between depositional events and soil development, which in turn are linked to basin processes and climate (D'Alessandro *et al.* 1987; Buatois & Mángano 2004; Buatois *et al.* 2007; Buatois & Mángano 2011).

Trace fossil assemblages in channel and channel-adjacent sediments are often not diverse or well preserved (Buatois & Mángano 2011). However, paleosol ichnofacies have increasingly been shown to be controlled by the climate under which the soils developed. Climate is among the most important factors driving paleosol ichnofacies (Genise *et al.* 2010; Buatois & Mángano 2011). In Miocene fluvial floodplains akin to La Venta, when integrated with a sedimentological, stratigraphic, and paleontological framework, trace fossils have been used to interpret ecosystem stability and primary productivity (D'Alessandro *et al.* 1987; Genise *et al.* 2000; Buatois *et al.* 2007; Catena *et al.* 2016, 2017).

CRAB AND MOLLUSC FOSSILS IN LA VENTA

To date, the fossil record of invertebrates in the Honda Group in La Venta is restricted to freshwater crab remains. These remains correspond mostly to isolated claw fingers (dactyli and pollices) and, to a lesser extent, to claw palms (propodi) with the fingers articulated (Fig. 6A-D), which have been found across a dozen localities spanning the La Victoria and Villavieja formations, ranging roughly between 15 and 11 Ma (see Mora-Rojas *et al.* 2023). All of those fossil remains have been referred to crabs of the superfamily Trichodactyloidea, which, together with Pseudothelphusoidea, are the only superfamilies of true freshwater crabs in the Americas (Luque *et al.* 2023 and references therein). Rodríguez (1997) was the first to report the fossil trichodactyloids from La Venta and assigned them to an extant species, *Sylviocarcinus pyriformis* (Pretzmann 1968), which is the only freshwater crab species that lives in the area today. However, this systematic placement is problematic, as Luque *et al.* (2017) indicated. First, most species last for 1-3, not 11-15, million years, casting doubts on the specific affinities of the incomplete fossil material. Second, preservation of complete male individuals, ideally with their sexual apparatuses (gonopods), is usually needed to tell freshwater crab species and even genera apart. Thus, crab claw fragments alone might not provide sufficient systematic resolution. Lastly, the Miocene sedimentary succession of the Honda Group records a very heterogeneous landscape, shifting between meandriform fluvial systems (upper La Victoria Formation – lower Villavieja Formation) and an anastomosed fluvial system (upper part of Villavieja Formation) as a result of tectonic and climatic changes in the basin (Mora-Rojas *et al.* 2023). The constantly changing topography and drainage systems in the area may have enhanced reproductive isolation in crab species (or genera), facilitating speciation. In fact, it is the geological history of Colombia and its aquatic ecosystems richness that make it the second most diverse country for freshwater crabs, with >100 species, more than 80% of which are endemic (Campos & Lasso 2015). Therefore, following Luque *et al.* (2017), we retain the fossil crabs from La Venta within the genus *Sylviocarcinus* but with no species affinity. Future prospective efforts in more stratigraphic intervals across the La Venta site, and the excavations of small trenches to find the crabs *in situ* before eroding, might yield more complete specimens that will allow us to better assess their generic and specific systematic affinities.

No written reports about Miocene molluscs in the La Venta region exist. However, the collection stored at the Museum national d'Histoire naturelle (Paris) and sampled by Robert Hoffstetter (unknown coordinates and surveying dates), contains freshwater bivalve and gastropod fossil remains (Fig. 6E-H). The label of the collection says 'Rio Cabrera – San Alfonso', which is in the northwestern part of the La Venta (Hoffstetter 1971; Guerrero 1997; Montes *et al.* 2021). We searched for that specific locality without success during the 2019 and 2023 expeditions. One possibility is that this collection might be stratigraphically assigned to the Barzalosa Formation, which is overlain by the Honda Group (Oligocene-Miocene?; De Porta 1974). Finding the locality of these freshwater bivalves



FIG. 4. — Selection of fossils from La Tatacoa Desert housed at the *Museo de Historia Natural La Tatacoa*, including some specimens featured in this thematic issue: **A**, *Lepidosiren paradoxa* (VPPLT 1483); **B**, parieto-supraoccipital frontal fragment of *Phractocephalus* sp. (VPPLT 1272; Carrillo-Briceno *et al.* 2023); **C**, skull of *Purussaurus neivensis*; **D**, skeleton of Caimaninae; **E**, skull of *Caninemys tridentata* Meylan, Gaffney & de Almeida Campos, 2009 (VPPLT-1720; Cadena *et al.* 2021); **F**, shell of *Podocnemis tatacoensis* Cadena & Vanegas, 2023 (VPPLT 1727; Cadena & Vanegas 2023); **G**, skull of *Miocochilius anomopodus* Stirton, 1953 (VPPLT 1512); **H**, skull of “*Prodolichotis*” *pridiana* Fields, 1957 (VPPLT 1614); **I**, skull of *Anachlysis gracilis* Goin, 1997 (VPPLT 1612; Suarez *et al.* 2023); **J**, partial mandible of *Megadolodus molariformis* McKenna, 1956 (VPPLT 974; Carrillo *et al.* 2023); **K**, skull of *Cebupithecia sarmiento* Stirton & Savage, 1950. Abbreviation: VPPLT, Vigias del Patrimonio Paleontológico La Tatacoa. Specimens are not shown to scale. Photos by C. Ziegler.

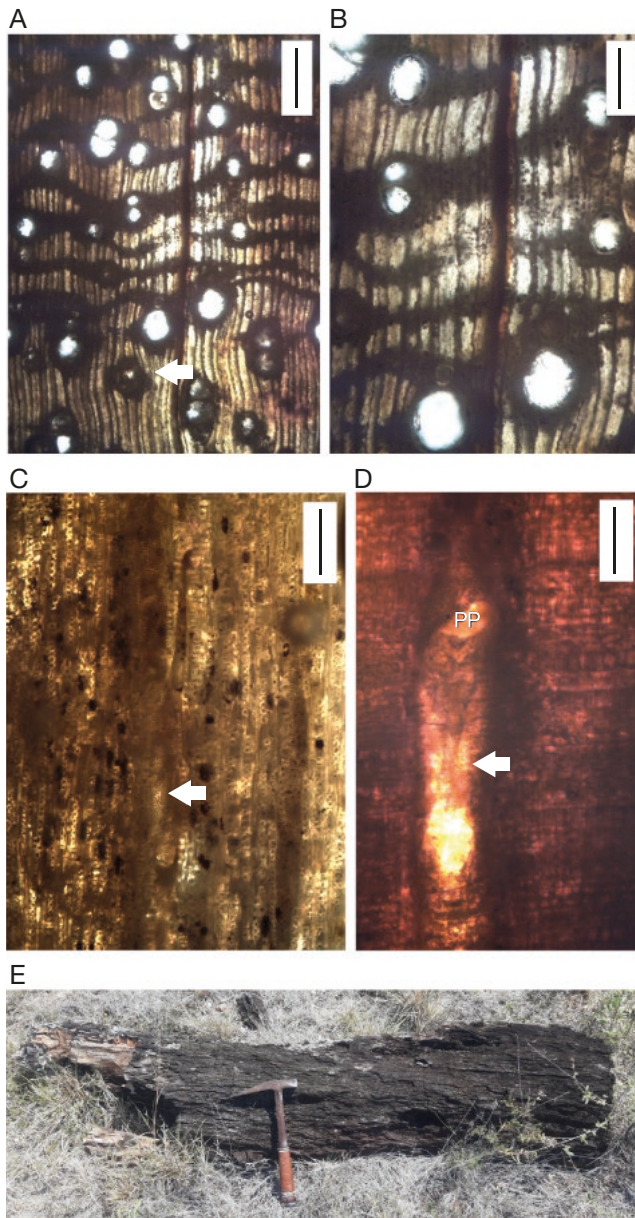


Fig. 5. — Fabaceae fossil wood from La Venta (VPPLT 008): **A**, diffuse porous wood, solitary vessels and in radial multiples of two vessels, aliform parenchyma (arrow); **B**, banded parenchyma in tangential lines; **C**, intervascular pits (arrow), uniseriate rays and non-septate fibers; **D**, vessel-ray parenchyma pits similar to intervessel pits (arrow), simple perforation plates (PP) and weakly heterocellular rays (RLS); **E**, fossil wood of Fabaceae (VPPLT 008) in the Cerro Gordo Beds. Scale bars: A, 500 µm; B-D, 200 µm.

will be essential for determining the depositional system of Barzalosa and the paleotemperatures of the La Venta region during the Miocene.

VERTEBRATE FOSSILS IN LA VENTA

Ichthyofauna

The paleoichthyofauna from La Venta is one of the best-studied Miocene freshwater fish assemblages from the ancient Amazonas hydrographic system (Lundberg 1997; Ballen & Moreno-Bernal 2019; Carrillo-Briceño *et al.* 2021a, b, 2023; Ballen *et al.* 2022; Schwarzahans *et al.* 2022). Fish are also the most abundant and

diverse vertebrate group in the La Venta fauna, with at least 23 taxa of chondrichthyans and bony fishes reported from at least 71 localities from La Victoria and Villavieja formations (Carrillo-Briceño *et al.* 2023). Chondrichthyans are represented exclusively by a single taxon of a freshwater stingray (*Potamotrygon*), whereas bony fishes are represented mainly by 14 South American families of dipnoids, characiforms, cichlids, siluriforms, and osteoglossiforms. The La Venta palaeoichthyofauna has a typical tropical-freshwater composition, with extant representatives that inhabit a wide range of environments such as lakes, swamps, streams, rivers, ponds, seasonal floodplains, and inundated forests (Van der Sleen & Albert 2018), thus supporting the great variety of freshwater environments proposed for the Honda Group (Mora-Rojas *et al.* 2023). The Tatacoa Desert today is located in the upper Magdalena River Valley, which drains into the Caribbean (Fig. 1). The La Venta paleoichthyofauna is characterized by taxonomic and biogeographic affinities with living counterparts among the taxa of the modern Orinoco and Amazonas rivers. It is likely that changes in the hydrographic configuration of the region due to the uplifting of the Northern Andes (see section Tectonostratigraphy of the Honda Group and the paleogeography of the Northern Andes) greatly affected fish populations by reducing both habitat size and faunal turnover. Among other large fishes from the La Venta Fauna (e.g., *Arapaima*, *Brachyplatystoma*), one classic example is the Redtail catfish *Phractocephalus*, a taxon well adapted to fluvial conditions whose fossil record in the Guajira Peninsula (Ballen *et al.* 2022), Falcón state in Venezuela (Lundberg & Aguilera 2003), and Amazon (Aguilera *et al.* 2008; Tejada-Lara *et al.* 2015) shows marked reduction in its geographical distribution (Van der Sleen & Albert 2018). Although the fish paleodiversity of the La Venta is likely underestimated as result of a bias in the fossil record, it sheds new light on the evolutionary history of the Neotropical fishes.

Turtles

Turtles represent one of the most abundant fossil vertebrate finds in the La Venta fauna, including nearly complete specimens or shell fragments from various localities and stratigraphic horizons throughout the entire region (Wood 1997). To date, both major groups of extinct and living turtles – the cryptodirans or hidden-necked, and the pleurodirans or side-necked turtles – have been recorded (Wood 1997; Cadena *et al.* 2020a, b, 2021, 2023; Cadena & Vanegas 2023). Currently, a revision based on new specimens of *Chelonoidis* is underway, as well as the description of a new genus and species of podocnemid, showing that our knowledge of the paleodiversity of turtles that inhabited this region during the Middle Miocene is far from complete. Additionally, the fossil turtles from La Venta have shown exceptional preservation not only macroscopically, but also in the preservation of their bone microstructural components, such as osteocyte cells, blood vessels, and potentially remains of their original biomolecular components (Cadena 2020). Future research on these fossil turtles should be focused on better understanding their paleoecology and bone histology, with the aim of addressing paleophysiological and paleobiological questions.

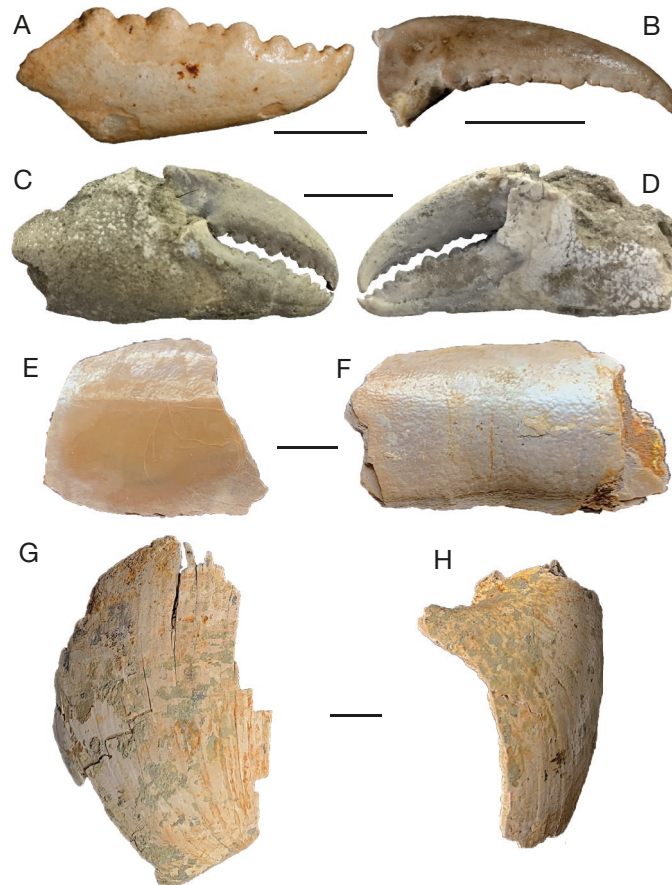


FIG. 6. — Miocene Freshwater invertebrates from La Venta, Huila, Colombia: **A–D**, trichodactylid freshwater crab remains, assigned to *Sylviocarcinus* sp., from La Victoria and Villavieja formations (Honda Group); **A**, fixed finger (pollex) of right cheliped (claw), specimen VPPLT-0954; **B**, mobile finger (dactylus) of right cheliped, specimen VPPLT-1306; **C, D**, articulated right cheliped, outer (**C**) and inner (**D**) views, showing details of the dactylus, propodus and pollex, specimen IGM 89-499, Colombian Geological Survey; **E, F**, freshwater bivalves, tentatively assigned to *Anodontites* Bruguière, 1792; **G, H**, gastropods. The bivalves and gastropods are possibly from the Barzalosa Formation, surveyed at locality Río Cabrera (La Venta region), from the Hoffstetter's collection housed by Muséum national d'Histoire naturelle, Paris. Scale bars: A, 5 mm; B–H, 10 mm.

Crocodyliforms

Crocodyliforms include the crown clade Crocodylia and their early relatives (*sensu* Sereno *et al.* 2001). These reptiles attained an extreme diversification in La Venta during the Middle Miocene fluvial-influenced Andean slopes of the proto-Amazonian Pebas System. Non-crocodylian crocodyliforms of putative terrestrial habits are represented by two taxa of Sebecidae: the gracile medium-sized *Sebecus huilensis* Langston, 1965 (synonym of *Langstonia huilensis*; Paolillo & Linares 2007), and an enigmatic larger and more robust form (Langston 1965; Langston & Gasparini 1997). Members of the Crocodylia in La Venta (Caimaninae; Longirostres *sensu* Harshman *et al.* 2003; Gavialidae) were all semiaquatic, ranging from small (total body length *c.* 170 cm) to large (*c.* 618 cm; Pujos & Salas-Gismondi 2020) species with a broad array of snout shapes. Among the caimanines, large species with distinct ecological roles have been identified, such as *Purussaurus neivensis* (Mook 1941; macro-generalist) and *Mourasuchus atopus* (Langston 1965; filter feeder). *Balanerodus logimus* Langston, 1965 is now considered an invalid species, because its conspicuous teeth with bulb-shaped crowns correspond to the posterior dental pieces of *Purussaurus* (Salas-Gismondi *et al.* 2015). Small caimanines are not fully identified, and as of now

these are referred to *Eocaiman* sp., *Caiman* sp., and *Kuttanacaiman iquitosensis* Salas-Gismondi, Flynn, Baby, Wesselingh & Antoine, 2015 (Langston 1965; Moreno-Bernal *et al.* 2018). The Longirostres clade comprises a large gavialid, *Gryposuchus colombianus* Langston 1965, and a slender-snouted taxon of uncertain affinities, *Charactosuchus fieldsi* Langston 1965, known only from fragmentary pieces of the jaw and characterized by deeply emarginated interalveolar notches.

This conservative taxonomic review reveals that the crocodyliform richness of La Venta encompasses at least nine species (Appendix 1). Our knowledge of *Purussaurus neivensis* and *Gryposuchus colombianus* is grounded on well-preserved specimens, yet the anatomy, ecology, phylogenetic relationships, and even the precise identity of most other taxa remain obscure. Since the last comprehensive study of Langston & Gasparini (1997), new crocodyliform material has been discovered and is stored at the Museo de Historia Natural de la Tatacoa. This collection comprises finely preserved remains of taxa previously recognized at La Venta, but also presumably new forms, including cranial material of the large sebecid and the most complete skeleton of a small caimanine known so far (Fig. 4D). Studies are being carried out to characterize the anatomy and affinities of this small

caiman species and to reassess the fossil crocodyliforms from La Venta by using traditional and new techniques to decipher their phylogenetic relationships and functional roles as predators in the proto-Amazonian ecosystems.

Snakes

In La Venta, fossil snakes have been found in many localities and stratigraphic horizons throughout the La Victoria and Villavieja formations (Alfonso-Rojas 2023). The fossils represent different taxa, such as "scoleophidians" (Hecht & LaDuke 1997), "anilioids", boids, and colubroids (Hoffstetter & Rage 1977; Hecht & LaDuke 1997). Although most of the recovered fossils consist of isolated vertebrae, which usually do not provide enough taxonomic information (Smith & Georgalis 2022), three species have been described to date. *Eunectes stirtoni* (Hoffstetter & Rage 1977), considered the oldest record of anacondas, was described on the basis of skull bones associated with vertebral remains. Additionally, two species of the enigmatic "anilioid," *Colombophis portai* (Hoffstetter & Rage 1977) and *Colombophis spinosus* (Hsiou *et al.* 2010), have been described, and their diagnoses were recently updated by Alfonso-Rojas *et al.* (2023). Currently, several research projects are being conducted, including the description of a boid with preserved fragments of the skull, the description of a potential new taxon, and the analysis of the fossilized skull reported by Hecht & LaDuke (1997), which will shed light on the taxonomic affinities and ecology of *Colombophis*. Published research indicates a collection bias, as most of the described fossils are relatively large, but colubroids and blind snakes, which usually have small bones, are not common. Additional fieldwork focused on screen-washing or sieving could improve our understanding of the snake paleodiversity in La Venta.

Birds

Although birds are highly diverse in tropical South America today, they are one of the less abundant fossil vertebrates in the La Venta biota. The only published materials are of cranial remains of an extinct hoatzin, *Hoazinoides magdalenae* (Opisthocomiformes) (Miller 1953), and postcranial remains referred to the families Anhingidae (Suliformes), Galbulidae (Piciformes), Aramidae (Gruiformes), and Ciconiidae (Ciconiiformes) (Rasmussen & Kay 1992; Rasmussen 1997). One of the anHINGA fossils comes from the lower part of the Villavieja Formation, and the rest from different sections of the La Victoria Formation. The fossil of an extinct hoatzin (no. 42823 UCMP Locality V 4517) is a single partial skull placed in the family Opisthocomidae (Miller 1953). The only extant hoatzin species lives in the Amazon and Orinoco basins (Cherrie 1909), which makes the La Venta hoatzin taxonomically and paleogeographically significant. The anHINGID material comprises a cervical vertebra (possibly a 12th or 13th, IGM 183549) and a distal end of a left ulna (IGM 183485), both referred to as *AnHINGA* cf. *A. grandis* (Rasmussen & Kay 1992). This anHINGA specimen is the first fossil record of the family AnHINGidae (Suliformes) in South America, providing evidence of aerial faunal interchange with other continents during the Miocene (Rasmussen & Kay 1992). Another undescribed anHINGID postcranial specimen

was found in Laventan beds in Tamshiyacu (near Iquitos, Peru) (P.-O Antoine, personal communication, November 10, 2023). The bird material from the La Victoria Formation includes *Galbula hylochoreutes* (IGM 250565; Galbulidae, Galbuliformes), a proximal end of a right humerus, reported from above the Chunchullo sandstone beds; *Aramus paludigrus* (UNC 29-IV-8-4; Aramidae, Gruiformes), an entire left tibiotarsus, reported from below the Chunchullo sandstone beds; and *Jabiru* aff. *J. mycteria* (IGM 184266; Ciconiidae, Ciconiiformes), a distal end of a left tibiotarsus with unknown locality. The presence of these avian groups in La Venta suggests a diversity of environments present in this ecosystem, from swamps and bogs to deeper water and much larger environments suitable for many bird groups. Currently, new avian fossils from the Honda Group are being described. Two samples correspond to distal ulnae of two individuals of different sizes and unknown taxonomic affinities. A third sample corresponds to a proximal tarsometatarsal fragment of a larger individual possibly referable to the family Gruidae (cranes), whose extant species are apparently absent from South America and Antarctica (Olsen 2009). A distal fragment of a tibiotarsal of a gruiform bird was identified in an Early Miocene locality (MD-61) in southern Peru (Marivaux *et al.* 2012). The potential presence of crane bird fossils at La Venta would add evidence to the presence of certain crane lineages in South America during the Miocene. Additional material includes several fragmentary specimens corresponding to isolated long bones, distal tarsometatarsi, two humeral diaphyses, a carpometacarpus, a distal coracoid, and possibly sternum remains, all from separate individuals of unknown taxonomic affinities. A large set of other bird bone occurrences are currently being investigated, including material from both local museums in La Venta. The description of these fossils will increase our knowledge of avian diversity in the Neotropics. By the Neogene, most neoavian families would have radiated after their rapid diversification during the K-Pg transition (Claramunt & Cracraft 2015); thus, we would expect the bird diversity and abundance in La Venta to be significantly higher. Investigating the influence of taphonomic and sampling biases on the diversity and abundance of the fossil birds in La Venta is also highly needed. Other relevant questions that remain unexplored are how the bird occurrences of La Venta could be integrated to bird time-calibrated phylogenies, and how climatic factors during the Miocene may have influenced the dispersion, diversification, and evolution of Neotropical birds.

Metatherians

The metatherian mammals include the marsupials and related extinct taxa (Goin *et al.* 2016). Owing to their metabolic and reproductive characteristics, metatherians have been highly affected by global climate changes. Some of the main diversification events of this group could be a consequence of global warming pulses (Goin 2021). The metatherian fossil assemblage from La Venta is one of the most diverse in South America (Goin 1997; Suarez 2019), and its high diversity could be related to the Miocene Climatic Optimum (Suarez 2019).

Four metatherian orders are represented in La Venta: Sparassodonta, Didelphimorphia, Paucituberculata, and Micro-

biotheria. Other specimens might be referred to metatherian lineages whose affinities are still far from clear (Suarez *et al.* 2016; Suarez 2019). In total, 11 species have been formally reported (Marshall 1976, 1977; Takai *et al.* 1991; Dumont & Bown 1997; Goin 1997; Czaplewski *et al.* 2003; Suarez 2019) (Appendix 1). If we included the preliminarily described but still-unnamed species, however, there would be at least 22 species (Goin 1997; Suarez 2019), most of them only recorded in La Venta, though some of the genera are present in other South American fossil assemblages (e.g., *Lycopsis*, *Pachybiotherium*, and *Pitheculites*; Ameghino 1902; Cabrera 1927; Goin 1997; Forasiepi *et al.* 2003; Suarez *et al.* 2016; Stutz *et al.* 2022). A specimen from the Late Miocene of Peru (MUSM 4018) was referred to *Thylamys* cf. *T. colombianus* by Stutz *et al.* 2022, a taxon present in La Venta. However, MUSM 4018 shows some plesiomorphic characters (e.g., a posterior cingulid) which are present in other taxa (*Marmosopsis* and *Monodelphopsis*) and absent *Thylamys*, which suggest additional specimens are needed to confirm the presence of *Thylamys* in the Late Miocene of Peru.

The carnivore niche is the best represented among La Venta metatherians. However, it apparently does not include "bone breakers", and small carnivores (e.g., hathiacyinids) are underrepresented (Goin 1997; Suarez 2019). The absence of large didelphines is also remarkable; perhaps their ecological role was performed by other taxa, similar in habits and morphology (e.g., small sparassodonts; Suarez 2019). The didelphimorphians from La Venta had omnivore diets, mainly insectivorous or faunivorous, with a tendency to carnivory (Suarez 2019). Small arboreal frugivores (e.g., paucituberculatans and *Pachybiotherium*) are the least represented, possibly because this niche was shared with some eutherian taxa, such as primates (Suarez 2019).

The sparassodonts are the most important metatherian group in the La Venta fossil assemblage in terms of diversity and number of specimens collected. Some are represented by complete materials, preserving cranial and postcranial elements. Recent fieldwork in La Venta led to the discovery of the most complete skeleton of the thylacosmilid *Anachlysictis gracilis* ever found and one of the most complete for Sparassodonta (Suarez *et al.* 2023).

The didelphimorphians represent the second most abundant group (in diversity and specimens collected) in the La Venta metatherian assemblage. The presence of the oldest representatives of extant didelphid genera points to this assemblage as the origin of a Neogene radiation (Goin 1997; Suarez 2019). This fact contrasts with the presence of a basal didelphimorph in the same assemblage, confirming La Venta as an example of simultaneous "cradle" and "museum" of diversity.

Other metatherians with unclear affinities are reported in La Venta (Suarez 2019). Some of these specimens have plesiomorphic morphologies that could be related to taxa from older South American assemblages, such as Itaborai (Itaboraian SALMA, early Eocene from Brazil; Suarez 2019). One example is *Kiotomops lopezi* (Takai *et al.* 1991); originally described as a molossid chiropteran, it was later excluded from this group owing to the presence of diagnostic metatherian characters

(Czaplewski *et al.* 2003; Suarez 2019). This species shares characters with the "ameridelphians" Sternbergiidae (Suarez 2019).

Xenarthrans

Despite a possible origin of *Xenarthra* at low latitudes in South America (Gaudin & Croft 2015), La Venta is one of the few fossil sites in tropical South America that has provided a remarkable diversity of this group. The cingulates (armadillos and glyptodonts) from La Venta include taxa that belong to clades that are recorded in Patagonia only during the Paleogene and the earliest Miocene (e.g., *Astegotheriinae*), as well as taxa representing the earliest members of clades that diversified during the Late Miocene-Pliocene (e.g., *Glyptodontinae*, *Pachyarmatheriidae*, *Pampatheriidae*, *Dasypodinae*, and *Tolypeutinae*). Interestingly, among all these members of *Cingulata*, the presence of supposedly plesiomorphic characters is common (e.g., pentagonal to hexagonal osteoderms, with polygonal central figure against posterior margin, or lageniform; anterior teeth with incipient lobulation; not all the dorsal vertebrae completely fused into a tube; metacarpals without marked reduction) (Carlini *et al.* 1997). The phylogenetic relationships of the *Cingulata* from La Venta (e.g., *Boreostemma gigantea*, *B. acostae*, *Neoglyptatelus originalis*, *Scirrotherium hondaensis*, *Anadasypus hondanus*, *Nanoastegotherium prostaticum*, *Pedrolypeutes praecursor*, among others), have been treated in varying depth by various authors (e.g., Carlini *et al.* 1997, 2008a, 2013; Theodor & Edmund 1997; Zurita *et al.* 2013, 2018; Castro 2014; Castro *et al.* 2014; Fernicola *et al.* 2017).

The works of Hirschfeld (1976, 1985) and McDonald (1997) are the basis of our knowledge about the high diversity *Pilosa* (sloths and anteaters) from La Venta, the alpha-taxonomy of which needs to be reviewed (see Carlini *et al.* 2006a, b, 2008b; Rincón & McDonald 2020; Miño-Boilini & Brandoni 2023). In these contributions, at least eight different *Pilosa* taxa are recognized as belonging to the clades *Mylodontidae* (*Mylodontinae* and *Scelidotheriinae*), *Megalonychidae*, *Megatheriidae*, *Nothrotheriidae*, and *Myrmecophagidae* (*Vermilingua*, anteaters) (Appendix 1). The species *Pseudopreopotherium confusum* (Hirschfeld 1985) was recently assigned to the new genus *Magdalenabradys*, with the new combination *Magdalenabradys confusum* (Rincón & McDonald, 2020). However, following the International Code of Zoological Nomenclature (ICZN 1999: art. 34.2), the correct combination is *Magdalenabradys confusum* (Hirschfeld 1985) (Appendix 1). Regarding the phylogenetic relationships, the sloths from La Venta may have some affinities with Patagonian lineages, although the phylogenetic relationships of Miocene-Pliocene fossil sloths from northern South America are not fully understood (Carlini *et al.* 2006a, b, 2008b).

From a paleoenvironmental perspective, the xenarthran taxa described to date suggest certain regional environmental heterogeneity. It is likely that these different environmental scenarios were not necessarily synchronous, but rather they may have been successive/alternating. The *Glyptodontinae*, *Pampatheriidae*, *Megatheriidae*, large *Mylodontidae* and *Vermilingua* may have occupied partially open areas; the

Astegotheriini, Dasypodini, small Megalonychidae, and Nothrotheriidae may have inhabited more closed forested areas; and the Dasypodini, Tolypeutinae, perhaps the Pachyarmatheriidae, Scelidotheriinae, and small Mylodontinae may have occupied ecotonal areas (Carlini *et al.* 1997).

Further study of the Xenarthra would allow a reinterpretation of the cladogenesis of this characteristic group of South American mammals given the geographic location of the La Venta deposits. As for the native ungulates (see below), the study of the internal cranial anatomy of La Venta xenarthrans may also deliver new characters informative for the reconstruction of phylogenetic relationships in the group (e.g., Le Verger *et al.* 2021). This is of considerable importance given that phylogenetic reconstructions using morphological data have been strongly challenged by molecular phylogenetics (Delsuc *et al.* 2016, 2019; Mitchell *et al.* 2016; Presslee *et al.* 2019) and could thus benefit from scrutiny of new morphological data.

Cetaceans and Sirenians

Modern South America is home to the Amazon River dolphin, *Inia geoffrensis*, and the La Plata dolphin, *Pontoporia blainvillei*. These, along with other ‘river dolphins’, belong to non-related groups of toothed cetaceans (odontocetes) with a scant fossil record. Tracking the evolutionary history of these animals in South America has been difficult, as only a few isolated remains have been found in Argentina (Gutstein *et al.* 2014), Brazil (Cozzuol 1993), Peru (Bianucci *et al.* 2013), and Venezuela (Aguirre-Fernández *et al.* 2017). Surprisingly, isolated ear bone fossils from La Venta (Colombia) and the Fitzcarrald arch (Peru) indicate the presence of platanistoids (relatives of the South Asian river dolphin *Platanista*) in continental South America during the Middle Miocene (Bianucci *et al.* 2013; Benites-Palomino *et al.* 2020). Based on these fragmentary findings, the phylogenetic reconstructions indicate a strong relationship between the two morphotypes and the extant genus *Platanista*. Given the systematic information retained in ear bones, however, no further biogeographic or evolutionary inferences can be made. Nevertheless, the findings from Colombia and Peru suggest that platanistoids invaded continental waters in South America before the relatives of *Inia* and *Pontoporia* in an independent invasion event, possibly triggered by the ecological pressure from more crownward odontocetes or the successive marine transgressions in the Miocene (Benites-Palomino *et al.* in press).

Sirenians are the only lineage of fully aquatic, herbivorous mammals. Sirenians evolved from terrestrial ancestors and colonized both freshwater and shallow marine environments in tropical and subtropical waters (Domning 2001). The oldest fossil records of sirenians are prorastomids from the middle Eocene of Jamaica, Senegal, and other sirenians of uncertain affinities from the early-middle Eocene of Tunisia and middle Eocene of Spain (Savage *et al.* 1994; Domning 2001; Hautier *et al.* 2012; Benoit *et al.* 2013; Díaz-Berenguer *et al.* 2018). Sirenia includes the extant families Dugongidae and Trichechidae, and their fossil relatives (Domning 2000, 2018; Velez-Juarbe & Wood 2019; Díaz-Berenguer *et al.* 2020). The

only sirenian reported for La Venta is the trichechid *Potamosiren magdalenensis* Reinhart 1951 (Reinhart 1951; Kellogg 1965; Domning 1982, 1997; Suarez *et al.* 2021). One of the remarkable characters of *Potamosiren* is the bunodont dentition with thick enamel. Domning (1997) considered this character an adaptation for munching soft, mostly non-abrasive aquatic vegetation. This diet would differ from that of the trichechids of the extinct genus *Ribodon* and the extant genus *Trichechus*, which have continuously erupting cheek teeth adapted for diets based on siliceous grasses (Domning 1997). However, the thickened enamel could also be interpreted as an adaptation to counter a new, more abrasive diet (Suarez *et al.* 2021). Re-adaptation of sirenians to life in freshwater environments marked a shift in dietary preferences from seagrasses to other groups of aquatic-adapted macrophytes, including true grasses (which contain phytoliths) (Domning 1982). Despite the good preservation and high diversity of vertebrates in La Venta, *P. magdalenensis* is represented only by a few, fragmentary remains (e.g., Reinhart 1951; Domning 1982, 1997). Additional exploration efforts to find new specimens are crucial for better understanding this species’ anatomy, paleobiology, and paleoecology.

South American native ungulates

The term South American native ungulates (SANUs) refer to several clades of hoofed placental mammals that radiated in South America during the Cenozoic (Croft *et al.* 2020). During the Miocene, SANUs were represented by three clades, Astrapotheria, Litopterna, and Notoungulata, all of which are recorded in La Venta (Defler 2019). The documented diversity of Laventan SANUs is high, with three species of astrapotheres (Johnson 1984; Johnson & Madden 1997; Vallejo-Pareja *et al.* 2015; Carrillo *et al.* 2018), at least five taxa of litopterns (McKenna 1956; Hoffstetter & Soria 1986; Cifelli & Guerrero 1997; Cifelli & Villarroel 1997; McGrath *et al.* 2020a, b; Carrillo *et al.* 2023), and three species of notoungulates (Stirton 1953; Villarroel & Guerrero 1985; Madden 1997; Villarroel & Danis 1997; Carrillo *et al.* 2018) (Appendix 1).

All the described SANU species from La Venta have been included in phylogenetic studies, providing important insights into the biogeography and evolution of SANUs in South America. For example, La Venta records the last representatives of Astrapotheria (Johnson & Madden 1997; Croft *et al.* 2020). These belonged to the clade Uruguaytheriinae, which is mostly composed of tropical taxa that survived until the Middle Miocene (Laventan Stage/Age; Kramarz 2009; Goillot *et al.* 2011; Vallejo-Pareja *et al.* 2015; Carrillo *et al.* 2018). The drivers and causes of the extinction of Astrapotheria are still not fully understood (Goillot *et al.* 2011), but it is possibly related to the demise of the Pebas megawetland system (Hoorn *et al.* 2010; Jaramillo *et al.* 2017). Sedimentological and bone microstructure evidence suggests that astrapotheres may have had semiaquatic habits (Houssaye *et al.* 2016; Carrillo *et al.* 2018).

In the case of the litopterns, the taxa from La Venta include four species traditionally recognized as proterotheriids and

one macraucheniid (Cifelli & Guerrero 1997; McGrath *et al.* 2020a, b). Recent discoveries provided important information for reevaluating the interrelationships within Litopterna and closely related taxa. In particular, they enabled the recognition of Megadolodinae, an exclusively tropical clade of bunodont litopterns during the Miocene (Cifelli & Villarroel 1997; Carrillo *et al.* 2023). This clade includes *Megadolodus molariformis*, a species with traits that resemble living suids (Cifelli & Villarroel 1997), a morphotype not seen in other Miocene SANUs. Finally, the three Laventan notoungulate species represent the main subclades Toxodontia and Typotheria and have also helped clarify the systematics of their clades (Vera 2015; Forasiepi *et al.* 2015; Cerdeño & Vera 2015; Carrillo *et al.* 2018; Vera *et al.* 2019; Ferrero *et al.* 2021).

Despite the important recent advances in the systematics of SANUs, there remain major challenges to elucidating the phylogenetic relationships among and within SANU clades (Croft *et al.* 2020; Kramarz & MacPhee 2022). The study of the internal cranial anatomy of the La Venta SANUs through the use of computed tomography might help clarify their phylogenetic relationships and paleobiology (e.g., MacPhee *et al.* 2021).

SANUs were an important component of the South American mammal palaeocommunities, as they filled the ecospace of ungulate herbivores in the continent. Geochemical analyses on the stable isotopes of bone and tooth biominerals of SANUs from La Venta can provide important information for palaeoecological studies and paleoenvironmental reconstructions (see Geochemistry, paleoenvironment and paleobiology in La Venta section). In addition, SANUs are suitable for ecometric studies. Ecometrics is the quantitative study of the relationship between functional traits and environment across time and space (Eronen *et al.* 2010a, b; Polly & Head 2015). Ecometric studies of living ungulates (Artiodactyla and Perissodactyla) have identified dental morphological traits that vary across climatic and environmental gradients and can be used to reconstruct palaeoenvironments by using fossil teeth (Fortelius *et al.* 2002; Eronen *et al.* 2010a, b; Short *et al.* 2021). These ecometric approaches have been used in the study of extinct ungulates from North America, Eurasia, and Africa, but to date they have not been tested on SANUs. The abundant SANU fossil material from La Venta would provide an opportunity to incorporate ecometrics into the study of paleoenvironmental evolution in tropical South America. Complementarily, the presence of abundant ontogenetic series for various SANU taxa at La Venta (e.g., *Miocochilius*, *Pericotoxodon*) could enable the coupling of ecometric approaches with ontogenetic ones to gain more knowledge on the life history and specializations of these extinct herbivores (Gomes Rodrigues *et al.* 2017).

Rodents

Caviomorphs are a lineage of hystricognath rodents endemic to the Americas and are the only group of rodents present in La Venta. Their fossil record suggests they have been on the continent at least since the late Eocene-early Oligocene

(Antoine *et al.* 2012; Arnal *et al.* 2022; Campbell *et al.* 2021). Since then, they have become one of the most important groups of mammals in terms of abundance and diversity in South America (Vucetich *et al.* 2015). In La Venta, the four main caviomorph clades (Cavioidea, Chinchilloidea, Erethizontoidea, Octodontoidea) are represented by abundant material recovered from different stratigraphic levels (Walton 1997; Mora-Rojas *et al.* 2023) (Appendix 1).

Our current understanding of caviomorphs of La Venta derives primarily from the seminal studies of Fields (1957) and Walton (1997). Fields was the first to provide detailed descriptions of the rodent species from this locality and an initial interpretation of their paleoenvironmental context. Walton (1997) described additional taxa and observed morphological differences among those species previously described by Fields (1957), suggesting that the rodent assemblage could be richer than previously thought. Walton (1997) established several open taxonomic categories (Appendix 1) to identify cases where a reevaluation and redescription of the species was necessary.

In recent years, using material coming from a Laventan locality from the Miocene of Peru (Tar-31 Locality) and dental material from La Venta, Boivin and collaborators (2021) provided detailed descriptions and validated four species previously described by Walton (1997): including the erethizontoid *Microsteiromys jacobsi*, the octodontoid *Ricardomys longidens*, and the chinchilloids *Microscleromys paradoxalis* and *M. cribriphilus*. More recently, Urrea-Barreto *et al.* (2023) redescribed and revalidated the cavioid *Neoreomys huilensis* Fields, 1957, on the basis of previously described and recently collected materials from La Venta. However, most of the alpha taxonomy remains unresolved.

The most abundant taxa (genera “*Scleromys*” and “*Olenopsis*”; sensu Walton 1997) are related to lineages that more closely resemble the modern Pacarana (*Dinomys branikii*), a forest-dwelling species inhabiting the western margins of lowland Amazonian rainforest to upper montane tropical forest on the Andean slopes (Patton 2015). Additional taxa are possible forest-dwelling or arboreal/semi-arboreal species, such as the octodontoids or erethizontoids. Nonetheless, other morphologies, such as those exhibited by “*Prodolichotis*” *pridiana* (sensu Pérez *et al.* 2020), suggest more open environments, such as grasslands or scrubs (Walton 1997).

Our current efforts are focused on reevaluating taxonomic diversity of Laventan rodents through detailed analyses of anatomical features (e.g., craniomandibular, dental, postcranial characters, and postnatal ontogeny). By resolving the taxonomic uncertainties, we aim to establish the phylogenetic relationships among the four lineages and to determine the biogeographical implications of the caviomorphs from La Venta in the evolutionary history of the group.

Bats

The La Venta site holds one of the most diverse assemblages of extinct bats in South America (Czaplewski 1997). Although Savage first reported the presence of Chiroptera at La Venta in 1951, most fossil bats have been found after intensive



Fig. 7. — Reconstitution of the La Venta biome (Colombia). Illustration by Guillermo Torres. Banco de Imágenes Ambientales (BIA). Instituto de Investigaciones de Recursos Biológicos Alexander von Humboldt.

sieving and screen-washing that took place during the 1980's and early 1990's (Czaplewski 1997; Czaplewski *et al.* 2003). Overall, 14 bat taxa have been described from the Middle Miocene site of La Venta (Appendix 1), including many of the oldest records for extant bat families in South America, as well as a few species that remain indeterminate (Czaplewski *et al.* 2003). Many of the fossil bat teeth are missing their enamel, possibly after passing through the digestive system of predators (e.g., crocodylians; Fisher 1981), they still preserve the underlying dentine layer.

Although nowadays South America has the highest continental bat diversity, and many South American localities have unparalleled bat species richness (e.g., Yasuni in Ecuador has over 100 sympatric bat species), the bat fossil record of South America is strikingly poor (Lim 2009). La Venta stands out as an important locality for the study of extinct bats, although most taxa are known from only a few specimens with teeth, mandibular and maxillary fragments, and very few postcranial elements (Czaplewski 1997). Even with these limitations, the bat fossils from La Venta have provided important insights into the evolution of South American bats. La Venta has the earliest record of a plant-visiting bat, with nectar and insects being the inferred diet of *Palynephyllum antimaster* (Glossophaginae) (Yohe *et al.* 2015). Also, La Venta had phyllostomine

bats, such as *Notonycterix magdalenensis*; these are related to some of the largest extant bats in South America (*Vampyrus* and *Chrotopterus*), which are also the most animalivorous (López-Aguirre *et al.* 2022).

Additional efforts to recover bat fossils from both known and unexplored localities are needed. Since 2020, these efforts have resumed at La Venta with the use of sieving. Analyses of dental topology of Laventan bats may yield additional evidence of their dietary niches.

Primates

The Miocene deposits of La Venta have yielded one of the most diverse extinct primate assemblages (Stirton & Savage 1950; Stirton 1951; Luchterhand *et al.* 1986; Kay *et al.* 1987; Setoguchi & Rosenberger 1987; Rosenberger *et al.* 1991; Fleagle *et al.* 1997; Kay & Meldrum 1997; Takai *et al.* 2001), akin to the most primate-rich areas of South American today. As one of the few tropical localities with platyrrhine fossils in South America, with at least 12 taxa described (Appendix 1), La Venta is key to understanding the evolutionary history of this group. The primate assemblage includes species that may be closely related to extant platyrrhine lineages, though the evolutionary relationships of other species are not fully understood (Fleagle *et al.* 1997).

One of the striking features of Laventan primates is that they might represent early members of crown Platyrrhini (Kay 2015; Beck *et al.* 2023). Primate fossils from La Venta include species closely related to all four major platyrrhine clades: Atelidae, Pitheciidae, Cebidae, and Callitrichidae. For example, Beck *et al.* (2023) have proposed that *Stirtonia* is closely related to howler monkeys (genus *Alouatta*), *Neosaimiri* and *Laventiana* to squirrel monkeys (genus *Saimiri*), and *Cebupithecia* and *Nuciraptor* to Pitheciinae. Other smaller taxa have been suggested to group closely to Callitrichidae. Nonetheless, the evolutionary relationships of other fossil primates from La Venta remain unresolved, mainly due to the fragmentary and incomplete fossil record.

Although a few taxa are relatively well known from cranial and postcranial evidence (e.g., *Cebupithecia* and *Neosaimiri*), most are known only from fragmentary mandibles or maxillae (e.g., *Stirtonia*), or even from isolated teeth (e.g., *Micodon*). The incompleteness of the neotropical fossil record, including La Venta, leaves many aspects of primate paleobiology poorly understood.

During the last decade, a few important primate fossils have been found in La Venta, and the description of these specimens, as well as studies on the evolution of dietary adaptations in platyrrhines, are currently underway.

CONCLUSION

After a century of paleontological research, La Venta is one of the better-known fossil sites in tropical South America. Nonetheless, La Venta is still in the early phases of study, and many areas and stratigraphic levels have been barely explored and sampled. To more fully understand the relationship between climatic/environmental change and biotic evolution in the tropics, we estimate that several decades of further exploration and a range of taxonomic, geochemical, paleobiological, taphonomic, biogeographic, macroevolutionary, and diversification studies will be necessary.

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APPENDIX 1. — Biotic taxonomic list of the Honda Group (Middle Miocene) in the La Venta fossil site in the Magdalena Valley, Colombia. ?, unknown.

Higher rank	Family or Subfamily	Taxa	La Victoria Fm	Villavieja Fm	References	
Polypodiopsida	Salvinales	Salviniaceae	<i>Salvinia</i> sp.	×	×	This work
Magnoliopsida	Malpighiales	Goupiaceae	<i>Goupioxylon stutzeri</i>	–	×	Pons 1970, 1983
		Combretaceae	<i>Terminalioxylon portae</i>	–	×	Pons 1983
Magnoliopsida	Fabales	Fabaceae	<i>Leguminoxylon dindense</i>	–	×	Pons 1983
Malacostraca	Decapoda	Trichodactylidae	<i>Sylviocarcinus</i> sp.	×	×	Rodríguez 1997; Luque <i>et al.</i> 2017
Chondrichthyes	Myliobatiformes	Potamotrygonidae	<i>Potamotrygon</i> sp.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023
Osteichthyes	Dipnoi	Lepidosirenidae	<i>Lepidosiren paradoxa</i>	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023
	Characiformes	Anostomidae	cf. <i>Leporinus</i> sp.	×	×	Lundberg 1997
		Characidae	cf. Tetragonopterinae indet.	–	×	Lundberg 1997
		Erythrinidae	<i>Hoplias</i> sp.	?	?	Lundberg 1997
		Cynodontidae	<i>Hydrolycus</i> sp.	×	×	Lundberg 1997
			cf. <i>Hydrolycus</i> sp.	×	×	Carrillo-Briceño <i>et al.</i> 2023
		Serrasalminidae	<i>Colossoma macropomum</i>	–	×	Lundberg 1997
			? <i>Colossoma</i> or ? <i>Piaractus</i> sp.	×	×	Carrillo-Briceño <i>et al.</i> 2023
			? <i>Pristobrycon</i> / <i>Pygocentrus</i> / <i>Serrasalmus</i> sp.	–	×	Lundberg 1997
Cichliformes	Cichlidae		cf. <i>Astronotus</i> sp.	×	–	Carrillo-Briceño <i>et al.</i> 2023
			cf. <i>Cichla</i> sp.	×	–	Carrillo-Briceño <i>et al.</i> 2023
			Cichlidae indet.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023
Siluriformes	Ariidae	<i>Sciades maldonadonis</i>	×	–	Carrillo-Briceño <i>et al.</i> 2023	
		Ariidae indet.	–	×	Lundberg 1997	
	Callichthyidae	<i>Hoplosternum</i> sp.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023	
	Doradidae	<i>Oxydoras</i> sp.	–	×	Carrillo-Briceño <i>et al.</i> 2023	
		Doradidae indet.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023	
	Loricariidae	cf. <i>Acanthicus</i> sp.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023	
		cf. <i>Hypostomus</i> sp.	×	×	Lundberg 1997	
	Pimelodidae	<i>Brachyplatystoma</i> cf. <i>vallantii</i>	–	×	Lundberg 1997	
		<i>Brachyplatystoma promagdalenae</i>	–	×	Lundberg 1997	
		<i>Brachyplatystoma</i> sp.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023	
<i>Phractocephalus</i> sp.		×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023		
	cf. <i>Pimelodus</i> sp.	×	×	Lundberg 1997; Carrillo-Briceño <i>et al.</i> 2023		
Osteoglossiformes	Arapaimidae	<i>Arapaima</i> sp.	–	×	Lundberg 1997	
		Arapaimidae indet.	×	×	Carrillo-Briceño <i>et al.</i> 2023	
	Acregoliathidae	<i>Acregoliath rancii</i>	×	×	Ballen & Moreno-Bernal 2019; Carrillo-Briceño <i>et al.</i> 2023	
Reptilia	Testudines	Podocnemididae	<i>Podocnemis pritchardi</i>	×	–	Wood 1997
			<i>Podocnemis medemi</i>	–	–	Wood 1997
			<i>Podocnemis tatacoensis</i>	×	–	Cadena & Vanegas 2023
			<i>Stupendemys geographica</i>	×	–	Cadena <i>et al.</i> 2020b, 2021
			<i>Caninemys tridentata</i>	×	–	Cadena <i>et al.</i> 2021
		Chelidae	<i>Chelus colombiana</i>	–	–	Wood 1997; Cadena <i>et al.</i> 2023
			<i>Mesoclemmys vanegasorum</i>	×	–	Cadena <i>et al.</i> 2020a
			<i>Chelonoidis hesterna</i>	–	–	Wood 1997
		Testudinidae	<i>Chelonoidis</i> sp.	–	–	Wood 1997
Crocodyliformes	Sebecidae	<i>Sebecus huilensis</i>	×	×	Langston 1965; Busbey 1986	
		Sebecidae indet.	×	?	This work	
	Caimaninae	<i>Purussaurus neivensis</i>	×	×	Mook 1941; Langston 1965	
		<i>Mourasuchus atopus</i>	×	×	Langston 1965, 1966; Langston & Gasparini 1997	

Appendix 1. — Continuation.

Higher rank	Family or Subfamily	Taxa	La Victoria Fm	Villavieja Fm	References	
Reptilia (continuation)	Crocodyliformes (continuation)	Caimaninae (continuation)	<i>Eocaiman</i> sp.	–	×	Langston 1965; Moreno-Bernal <i>et al.</i> 2018
			<i>Caiman</i> spp.	×	×	Langston 1965; Moreno-Bernal <i>et al.</i> 2018
			<i>Kuttanacaiman iquitosensis</i>	×	–	Moreno-Bernal <i>et al.</i> 2018
		Gavialidae	<i>Gryposuchus colombianus</i>	×	×	Langston 1965; Langston & Gasparini 1997
		? Crocodylidae	<i>Charactosuchus fieldsi</i>	×	×	Langston 1965
	Squamata	Boidae incertae sedis	<i>Eunectes stirtoni</i> <i>Colombophis portai</i> <i>Colombophis spinosus</i>	– ×	×	Hoffstetter & Rage 1977 Hoffstetter & Rage 1977; Alfonso-Rojas <i>et al.</i> 2023 Hsiou <i>et al.</i> 2010; Alfonso-Rojas <i>et al.</i> 2023
Aves	Opisthocomiformes	Opisthocomidae	<i>Hoazinoides magdalenae</i>	–	×	Miller 1953
	Suliformes	Anhingidae	<i>Anhinga</i> cf. <i>A. grandis</i>	×	×	Rasmussen & Kay 1992
	Piciformes	Galbulidae	<i>Galbula hylochoreutes</i>	×	–	Rasmussen & Kay 1992
	Gruiformes	Aramidae	<i>Aramus paludigrus</i>	×	–	Rasmussen & Kay 1992
	Ciconiiformes	Ciconiidae	<i>Jabiru</i> aff. <i>J. mycteria</i>	×	–	Rasmussen & Kay 1992
Mammalia						
Metatheria	Sparassodonta		<i>Hondadelphys fieldsi</i>	×	×	Marshall 1976; Suarez 2019
			<i>Hondadelphys</i> sp. 1	×	–	Suarez 2019
			<i>Hondadelphys</i> sp. 2	×	–	Suarez 2019
			<i>Lycopsis longirostris</i>	×	×	Marshall 1977; Goin 1997; Suarez 2019
			<i>Duckecynus magnus</i>	–	×	Goin 1997; Suarez 2019
			Thylacosmilidae	<i>Anachlysictis gracilis</i>	×	–
		Hathliacynidae	Thylacosmilidae gen. 1 sp. 1 Hathliacynidae indet.	×	–	Goin 1997; Suarez 2019 Suarez 2019
	Didelphimorphia	Didelphidae	<i>Marmosa laventica</i>	×	×	Marshall 1976
			<i>Marmosa</i> sp. 1	–	×	Suarez 2019
			<i>Thylamys colombianus</i>	–	×	Goin 1997
			<i>Thylamys minutus</i>	–	×	Goin 1997
			Marmosini cf. <i>Tlacuatzin</i>	–	×	Suarez 2019
			incertae sedis	Didelphimorphia gen. 1 sp. 1 Didelphimorphia gen. 1 sp. 2	–	×
	Paucituberculata	Palaeothentidae	<i>Hondathentes cazador</i>	–	×	Dumont & Bown 1997
		Abderithidae	<i>Pitheculites chenche</i> Palaeothentoidea indet.	×	–	Dumont & Bown 1997 Suarez (2019)
			Microbiotheriidae	<i>Pachybiotherium minor</i>	–	×
	incertae sedis		<i>Kiotomops lopezi</i>	–	×	Takai <i>et al.</i> 1991; Czaplewski <i>et al.</i> 2003; Suarez 2019
			“Ameridelphia” indet.	?	?	Suarez (2019)
			Indet.	Metatheria indet. 1 Metatheria indet. 2	?	?
	Xenarthra	Cingulata	Glyptodontidae	<i>Boreostemma gigantea</i>	×	–
<i>Boreostemma acostae</i>				×	×	Villarroel 1983; Zurita <i>et al.</i> 2013
<i>Neoglyptatelus originalis</i>				–	×	Carlini <i>et al.</i> 1997
Pampatheriidae Dasypodidae			<i>Scirrotherium hondaensis</i>	×	×	Edmund & Theodor 1997
			<i>Anadasypus hondanus</i>	×	×	Carlini <i>et al.</i> 1997
			<i>Nanoastegotherium prostatum</i> <i>Pedrolypeutes praecursor</i>	×	×	Carlini <i>et al.</i> 1997 Carlini <i>et al.</i> 1997
Phyllophaga		Mylodontidae	<i>Nematherium</i> sp.	×	×	Hirschfeld 1985; Miño-Boilini & Brandoni 2023
			<i>Neonematherium flabellatum</i>	×	×	McDonald 1997
			<i>Brievabradys laventensis</i>	×	×	Hirschfeld 1985; McDonald 1997; Villarroel 2000
			<i>Magdalenabradys confusus</i>	×	×	Hirschfeld 1985; McDonald 1997; Rincón & McDonald 2020

Appendix 1. – Continuation.

Higher rank		Family or Subfamily	Taxa	La Victoria Fm	Villavieja Fm	References	
Xenarthra (continuation)	Phyllophaga (continuation)	Megalonychidae	Megalonychidae indet. (large morphotype)	×	×	McDonald 1997	
			Megalonychidae indet. (small morphotype)	×	–	McDonald 1997	
		Megatheriidae	<i>Huilabradys magdalenensis</i>	–	×	Villarroel 1998	
			<i>Eucholoeops</i> aff. <i>E. fronto</i>	×	–	Villarroel 1998	
			<i>Hapalops</i> sp.	×	–	Villarroel 1998	
			Nothrotheriinae indet. (large morphotype)	×	×	McDonald 1997	
			Nothrotheriinae indet. (small morphotype)	×	×	McDonald 1997	
			Megatheriinae indet.	×	×	McDonald 1997	
Vermilingua	Myrmecophagidae	<i>Neotamandua borealis</i>	–	×	Hirschfeld 1976		
Sirenia	Trichechidae	<i>Potamosiren magdalenensis</i>	×	×	Reinhart 1951; Domning 1997; Suarez <i>et al.</i> 2021		
Cetacea	Odonticeti	Platanistidae	Platanistinae indet.	–	×	Benites-Palomino <i>et al.</i> 2020	
		cf. Platanistidae	cf. Platanistidae indet.	×	×	Benites-Palomino <i>et al.</i> 2020	
Astrapotheria		Uruguaytheriinae	<i>Granastrapotherium snorki</i>	×	×	Johnson & Madden 1997	
			<i>Xenstrapotherium kraglievichi</i>	×	×	Johnson & Madden 1997	
			<i>Hilarcotherium castanedaii</i>	×	–	Vallejo-Pareja <i>et al.</i> 2015	
Litopterna		Protheroheriidae	<i>Megadolodus molariformis</i>	×	×	McKenna 1956; Cifelli & Villarroel 1997; Carrillo <i>et al.</i> 2023	
			<i>Neodolodus colombianus</i>	×	×	Hoffstetter & Soria 1986; Cifelli & Guerrero Díaz 1989; McGrath <i>et al.</i> 2020a; Carrillo <i>et al.</i> 2023	
			<i>Mesolichthium sanalfonense</i>	×	×	Cifelli & Guerrero 1997; McGrath <i>et al.</i> 2020a	
			<i>Villarroelia totoyoi</i>	×	–	Cifelli & Guerrero 1997	
		Protheroheriidae indet.	×	–	Cifelli & Guerrero 1997		
		Macrauchenidae	<i>Theosodon</i> sp.	×	×	Cifelli & Guerrero 1997	
		Notoungulata	Toxodontia	Leontiniidae	<i>Huilatherium pluriplicatum</i>	×	×
Toxodontidae	<i>Pericotoxodon platignathus</i>			×	×	Madden 1997	
Typotheria	Interatheriidae		<i>Miocochilius anomopodus</i>	×	×	Stirton 1953	
Rodentia	Cavioidea		<i>Neoreomys huilensis</i>	×	×	Fields 1957; Walton 1997; Urrea-Barreto <i>et al.</i> 2023	
			<i>Prodolichotis pridiana</i>	×	×	Fields 1957; Walton 1997	
			Dolichotinae indet. (large morphotype)	×	×	Walton 1997	
			Dolichotinae indet. (small morphotype)	×	×	Walton 1997	
	Erethizontoidea			<i>Microsteiomys jacobsi</i>	–	×	Walton 1997; Boivin <i>et al.</i> 2021
				? <i>Steiromys</i> sp.	×	×	Fields 1957
	Chinchilloidea			“ <i>Scleromys</i> ” <i>colombianus</i>	×	×	Fields 1957; Walton 1997
				“ <i>Scleromys</i> ” <i>schurmanni</i>	×	×	Stehlin 1939; Walton 1997
				<i>Microscleromys cribriphilus</i>	–	×	Walton 1997; Boivin <i>et al.</i> 2021
				<i>Microscleromys paradoxalis</i>	–	×	Walton 1997; Boivin <i>et al.</i> 2021
				“ <i>Olenopsis</i> ” sp. <i>small</i>	×	–	Walton 1997
				“ <i>Olenopsis</i> ” sp. <i>large</i>	×	×	Walton 1997
	Octodontoidea			<i>Acarechimys minutissimus</i>	–	×	Walton 1997; Boivin <i>et al.</i> 2021
				<i>Ricardomys longidens</i>	–	×	Walton 1997; Boivin <i>et al.</i> 2021
				Echimyidae indet.	–	×	Walton 1997; Boivin <i>et al.</i> 2021
Echimyidae indet. (small morphotype)				–	×	Walton 1997; Boivin <i>et al.</i> 2021	
Chiroptera		Emballonuridae	<i>Diclidurus</i> sp.	–	×	Czaplewski 1997	
		Emballonuridae indet.	–	×	Czaplewski <i>et al.</i> 2003		
		Noctilionidae	<i>Noctilio albiventris</i>	–	×	Czaplewski 1997	

Appendix 1. — Continuation.

Higher rank		Family or Subfamily	Taxa	La Victoria Fm	Villavieja Fm	References	
Chiroptera (continuation)		Phyllostomidae	<i>Notonycteris magdalenensis</i>	–	×	Savage 1951; Czaplewski 1997; López-Aguirre <i>et al.</i> 2022	
			<i>Notonycteris sucharadeus</i>	–	×	Czaplewski <i>et al.</i> 2003	
			<i>Tonatia</i> or <i>Lophostoma</i> sp. indet.	–	×	Czaplewski 1997; Czaplewski <i>et al.</i> 2003	
			<i>Palynephyllum antimaster</i>	–	×	Czaplewski <i>et al.</i> 2003; Yohe <i>et al.</i> 2015	
		Thyropteridae	<i>Thyroptera lavalii</i>	–	×	Czaplewski <i>et al.</i> 2003	
			<i>Thyroptera robusta</i>	–	×	Czaplewski 1997	
			<i>Thyroptera</i> cf. <i>T. tricolor</i>	–	×	Czaplewski 1997	
		Molossidae	<i>Mormopterus colombiensis</i>	–	×	Czaplewski 1997	
			<i>Eumops</i> sp.	–	×	Czaplewski 1997; Czaplewski <i>et al.</i> 2003	
				<i>Potamops mascahehenes</i>	×	–	Czaplewski 1997
				Molossidae indet.	–	×	Czaplewski <i>et al.</i> 2003
			?Vespertilionidae	?Vespertilionidae indet.	–	×	Czaplewski <i>et al.</i> 2003
Primates	Platyrrhini	Atelidae	<i>Stirtonia victoriae</i>	×	–	Kay <i>et al.</i> 1987	
			<i>Stirtonia tatacoensis</i>	–	×	Stirton 1951; Setoguchi 1985; Kay <i>et al.</i> 1987	
		Callitrichinae	<i>“Aotus” dindensis</i>	–	×	Setoguchi & Rosenberger 1987	
			<i>Lagonimico conclucatus</i>	×	–	Kay 1994	
			<i>Mohanamico hershkovitzi</i>	–	×	Luchterhand <i>et al.</i> 1986	
			<i>Micodon kiotensis</i>	–	×	Setoguchi & Rosenberger 1985	
			<i>Patasola magdalenae</i>	×	–	Kay & Meldrum 1997	
		Cebinae	<i>Neosaimiri annectens</i>	–	×	Rosenberger <i>et al.</i> 1991; Kay <i>et al.</i> 1997	
			<i>Neosaimiri fieldsi</i>	–	×	Stirton 1951	
		Pitheciidae	<i>Cebupithecia sarmientoi</i>	×	×	Stirton & Savage 1950	
			<i>Miocallicebus villaviejai</i>	×	–	Takai <i>et al.</i> 2001	
			<i>Nuciruptor rubricae</i>	–	×	Meldrum & Kay 1997	

APPENDIX 2. — Supplementary material (xml file with BibTex citation style) with the compilation of all paleontological publications (224) related with La Venta (Colombia). https://doi.org/10.5852/geodiversitas2023v45a26_s1