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First record of a mosasaurid (Squamata: Mosasauridae) from the Upper Cretaceous of Ecuador

Primer registro de un mosasaurido (Squamata: Mosasauridae) del Cretácico Superior de Ecuador

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Abstract: We report the first Upper Cretaceous marine reptile fossil in Ecuador, identified as an incomplete right maxilla from the Mosasauridae family. The remains were unearthed from marine marlstones and limestones within a karstic cave in the Tamia Yura indigenous community, situated northeast of Tena in the central Subandean Zone of the Ecuadorian Amazon. Morphological analysis reveals seven preserved teeth conical in shape. Stratigraphic analysis suggests the remains belong to the Middle Napo Fm., Oriente basin, indicating a presence from the Turonian to the end of the Coniacian. This discovery offers new insights into the study of Cretaceous marine reptiles in South America.

Resumen: Reportamos el primer fósil de un reptil marino del Cretácico Superior en Ecuador, identificado como un maxilar derecho incompleto de la familia Mosasauridae. Los restos fueron desenterrados de margas y calizas marinas dentro de una cueva kárstica en la comunidad indígena Tamia Yura, ubicada al noreste de Tena en la Zona Subandina central de la Amazonía ecuatoriana. El análisis morfológico revela 7 dientes con forma cónica. El análisis estratigráfico sugiere que los restos pertenecen a la Formación Napo Medio, cuenca Oriente, indicando una presencia desde el Turoniense hasta el final del Coniaciense. Este descubrimiento proporciona nuevas perspectivas sobre el estudio de reptiles marinos del Cretácico en Sudamérica.

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INTRODUCTION

During the Late Cretaceous, oceans were dominated by large marine reptiles such as mosasaurids. These enormous marine varanoid reptiles are known exclusively from the Upper Cretaceous deposits, particularly in strata ranging from the Turonian to the Maastrichtian ages. Turonian mosasaurids remains generally consist of only fragmentary material (Páramo-Fonseca, 2000). Mosasaurids spread throughout Earth's major oceans during a geological period of approximately 25–30 My. Mosasaurids suddenly disappeared at 65.5 My due to the Cretaceous–Paleogene mass extinction event, which also wiped out non-avian dinosaurs all over the Earth (Polcyn *et al.*, 2014). In South America, mosasaurids remains have been reported from Chile, Colombia, Argentina, Venezuela, Brazil, and Peru. Table 1 presents a list of mosasaurids fossils found in South America. All these records of Mosasaurids have been published in peer-reviewed journals where the systematic attribution of each fossil has been developed for each record.

The records showed at Table 1 are classified according to their corresponding subdivision of the Late Cretaceous between 100.5 and 66.0 million years. The table also provides information for each occurrence, including the country and location of the discovery, geological setting, lithology, age of the fossil, taxonomy, fossil parts, and coordinates of the discovery. From the records, it is possible to identify that most of the discoveries are in Chile (8 records) and Colombia (7 records), followed by Brazil and Argentina (4 records each), Peru with one fossil, and Ecuador with one fossil, which corresponds to our study. The findings from the

Table 1. Mosasaurid records in South America, including references, country, paleobiogeography, and basin. Additional reports, geographic coordinates, stratigraphic units, age, lithology, and taxonomy are provided in the appendix. Abbreviations: **GTS,** Geological Time Scale; **CrMa,** Maastrichtian (72.1–66.0 My); **CrCa,** Campanian (83.6–72.1 My); **CrSa,** Santonian (86.3–83.6 My); **CrCo,** Coniacian (89.8–86.3 My); **CrTu,** Turonian (93.9–89.8 My); **CrCe,** Cenomanian (100.5–93.9 My).

Cod	GTS [My]	References	Country	Paleobiogeography	Basin
1	CrMa	Price (1957), Bardet *et al.* (2008).	NE Brazil	Southern Atlantic	Pernambuco-Paraíba
2		Price (1957), Bardet *et al.* (2008)	NE Brazil	Southern Atlantic	Pernambuco-Paraíba
3		Bardet *et al.* (2008)	NE Brazil	Southern Tethys (Southern Tethys) (20°N - 20°S)	Unknown
4		Otero (2021)	Central Chile	Eastern Pacific	Shallow marine platform
5		Jiménez-Huidobro *et al.* (2015)	Central Chile	Eastern Pacific	Shallow marine platform
6		Soto-Acuña *et al.* (2015), Jiménez-Jiménez-Huidobro *et al.* (2015)	Southernmost Chile	Southern Atlantic, from the Weddellian Biogeographic Province.	Magallanes
7		Jiménez-Huidobro *et al.* (2015)	Central Chile	Eastern Pacific	Quiriquina
8		Jiménez-Huidobro *et al.* (2015)	Capentral Chile	Eastern Pacific	Quiriquina
9		Jiménez-Huidobro *et al.* (2015)	Central Chile	Eastern Pacific	Quiriquina
10		Jiménez-Huidobro *et al.* (2015)	Central Chile	Eastern Pacific	Quiriquina
11		Jiménez-Huidobro *et al.* (2015)	Central Chile	Eastern Pacific	Shallow marine platform
12		Fernández *et al.* (2008)	South Argentina	Southern Atlantic	Marine platform
13		Leuzinger *et al.* (2023)	South Argentina	Southern Atlantic	Marine platform
14		Gasparini *et al.* (2001)	South Argentina	Atlantic transgressions	SE Neuquen
15	CrCa	Páramo-Fonseca (2012, 2013, 2015)	Central Colombia	Cretaceous interior sea	TolimaWiffen
16		Wiffen (1980, 1990), Christiansen and Bonde (2002).	No available information		
17		Novas *et al.* (2019)	South Argentina	Marine-influenced paleoenvironment	Austral
18		Martin and Fernández (2007), Kear *et al.* (2008).	No available information		
19		Consoli and Stilwell (2009).	No available information		
20	CrSa	Lundelius and Warne (1960), Kear *et al.* (2005)	No available information		
21		Konishi *et al.* (2010)	Central Peru	Cretaceous interior sea	Ucayali
22		Garzón *et al.* (2024, this article)	SAZ Ecuador	Cretaceous interior sea	Oriente
23		Páramo-Fonseca (2015)	Central Colombia	Cretaceous interior sea	Middle - Upper Magdalena Valley
24	CrCo	Camacho and De Porta (1963), Páramo-Fonseca (2015)	Central Colombia	Cretaceous interior sea	Tolima
25		Páramo-Fonseca (2012, 2015)	Northern Colombia	Cretaceous interior sea	Upper Magdalena Valley
26	CrTu	Bengtson and Lindgren (2005)	NE Brazil	Southern Atlantic	Sergipe
27		Páramo-Fonseca (1994, 2015)	SW Colombia	Cretaceous interior sea	Upper Magdalena Valley
28		Páramo-Fonseca (1997, 2000, 2012, 2015)	SW Colombia	Cretaceous interior sea	Cauca Valley
29		Páramo-Fonseca (1997, 2012, 2015)	Central Colombia	Cretaceous interior sea	Upper Magdalena Valley
30	CrCe	Vilas Bôas and Carvalho (2001)	NNE Brazil	Southern Atlantic	Sao Luis

northern part of South America (Colombia and two from Brazil) are the oldest fossils of Mosasauridae found in the region, followed by the findings from the central region (Peru), while the findings from the southernmost part of the continent (Chile and Argentina) are relatively recent. Figure 1 illustrates the geographic distribution of Mosasauridae found in the literature across South America.

This paper aims to report the first mosasaurid fossil discovered within clastic and calcareous marine sediments sub-cropping in the central-eastern Sub-Andean Zone of the Amazon region of Ecuador. We provide a detailed description of the locality in which the fossil specimen was found, including a description of the geological context. This is the first record of a Cretaceous marine reptile in Ecuador. The discovery can potentially lead to a better understanding of the paleoenvironment, paleoceanography, and paleobiogeography evolution in the Amazon during the Cretaceous period. Understanding the possible environmental conditions in which mosasaurids lived allows us to gather information about the development of the Amazon region into its present-day environmental state.

GEOLOGICAL SETTING

The Sub-Andean Zone (**SAZ**) of Ecuador is comprised of the Upper Jurassic volcanic arc (Misahualli Fm.) basement and Cretaceous (Lower Hollin, Napo, M1, and Tena stratigraphic units) to Paleogene sedimentary cover. Farther east, the Oriente Basin, which is part of the Upper Amazon Basin, has a Neo-Proterozoic cratonic basement (Teixeira *et al.*, 1989), belonging to the South American plate, and Paleozoic to Cenozoic cover (see Fig. 2).

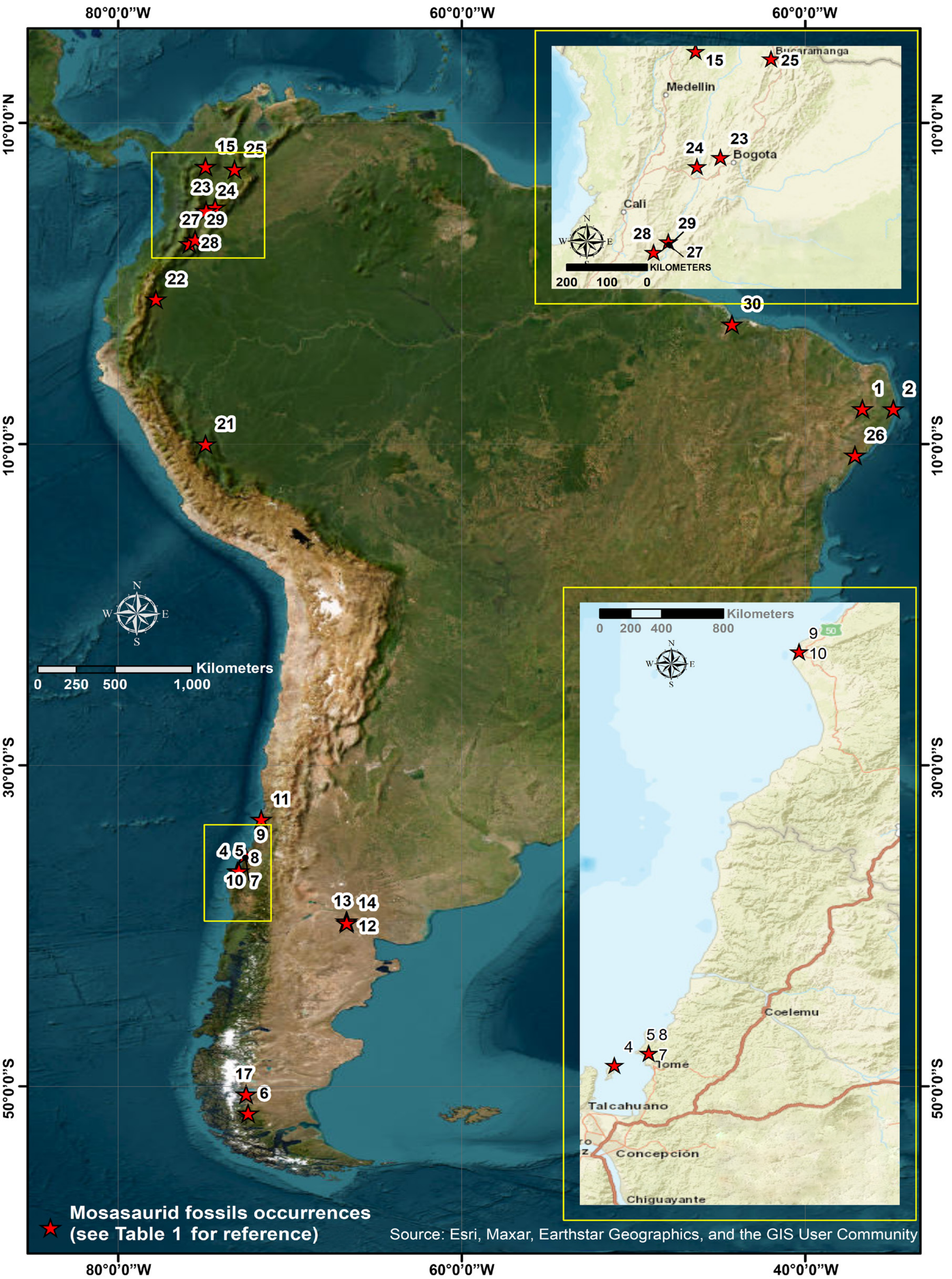

Figure 1. Geographic distribution of Mosasauridae Fossils Occurrences in South America. Scale provided in the map. Data for the main map from Esri. (2019). World Imagery. Retrieved from https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9. Data for the inset maps from Esri. (2024). World Topographic Map. Retrieved from https://www.arcgis.com/home/item.html?id=30e5fe3149c34df1ba922e6f5bbf808f.

Jaillard *et al*. (1997) refined the Cretaceous stratigraphy and ages of the Oriente Basin, proposing a succession from the continental clastic Lower Hollin Fm. (Aptian to Albian in age) at the base, followed by the clastic and calcareous Napo Group (composed by four units: Basal Napo, Lower Napo, Middle Napo, and Upper Napo formations, from lower Albian to Late Santonian), mainly marine, and the clastic continental Tena Fm. (Maastrichtian to Paleocene) at the top.

In the Central SAZ of Ecuador (see Fig. 2), Wasson and Sinclair (1927) reported three fossiliferous sites, with all fossils identified after Reeside (1932), pointing out the interval from middle Albanian to Turonian. The sites are closely located to the east of the Tamia Yura community: 1) 5 km to the Southeast of Archidona city, on the Misahualli river, 3.2 km upstream of the confluence with the Tena river, in which they found one middle Albian ammonite; 2) on the Misahualli river, between the junctions with the Tena river and the Hollin river, where they were found Cenomanian to Turonian species of bivalves, and middle Albian ammonites; and 3) 8 km to the SE of Archidona city, in which they identified Albian species of bivalves, ammonites, and Turonian species of bivalves.

Within calcareous core samples from Basal Napo Fm. cut in the Pungarayacu-30 well, drilled East of Tena city, Jaillard *et al*. (1997) reported the middle to Late Middle Albian ammonite.At the Latas stream, South of Tena city, Vera (2013) reported the Turonian to Santonian echinoderm *Hemiaster texanus*.

At the Misahualli river section, east to NE of Puerto Napo county, Jaillard *et al*. (1997) found several species of early Upper Albian ammonites in shales, marlstones and limestones; all of them within the Basal Napo Fm.; and three species of *Mortoniceras* sp., from middle Upper Albian in the Lower Napo Fm. All of these species range from basal to middle Upper Albian. Moreover, in central to southern SAZ of Ecuador, at the Upano river section, Jaillard *et al*. (1997) reported several ammonite species, from basal to late middle Albian to basal to early Upper Albian, within shales and limestones from the Basal Napo Fm.

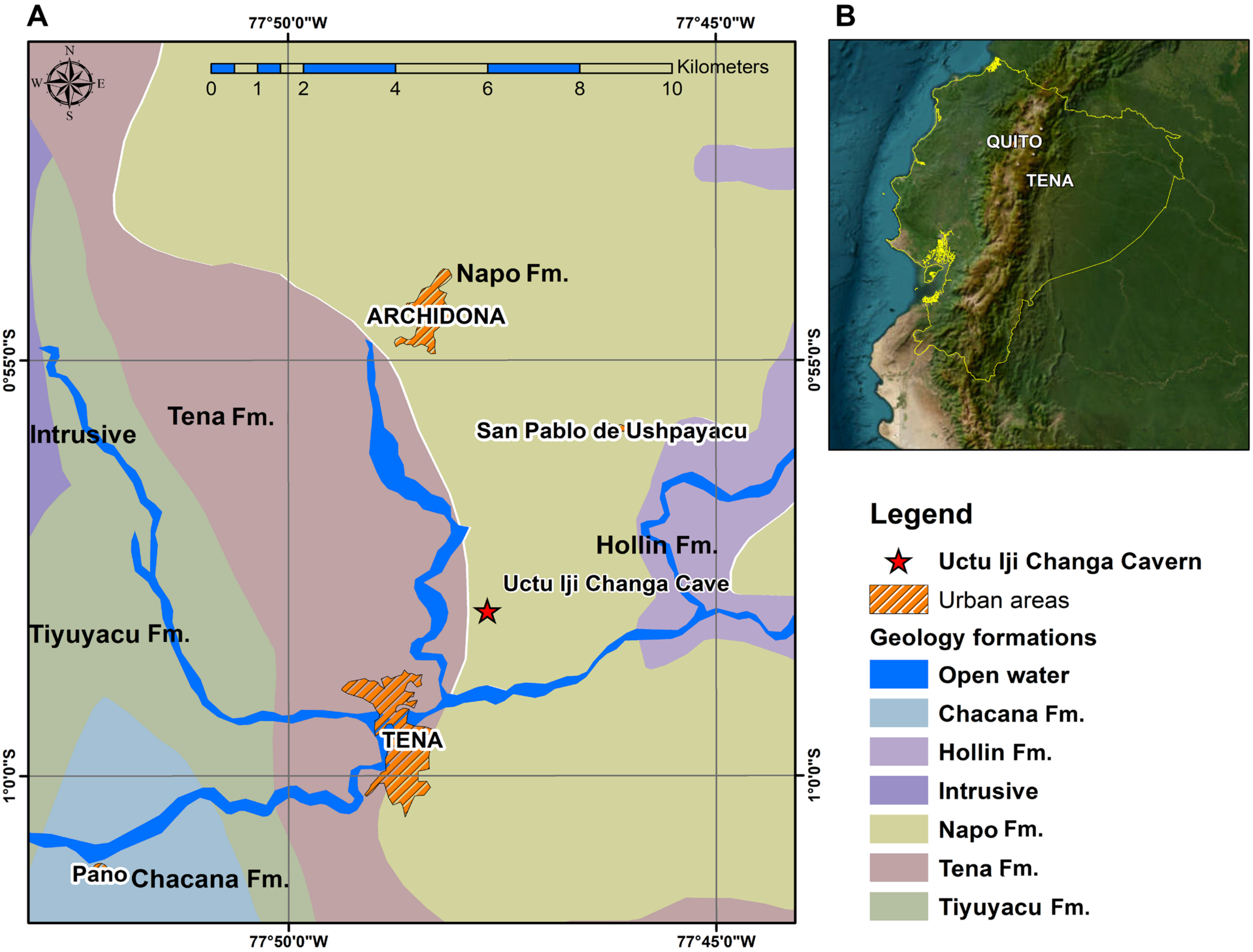

Figure 2. A, Detailed Location of the Uctu Iji Changa Cave, including Geological Formations and Major urban areas; **B,** map of Ecuador, highlighting the capital, Quito, and Tena, the closest city to the Uctu Iji Changa Cave. Data for the main map from INIGEM (2017). Geological Map of Ecuador, scale 1:1,000,000. Quito. Data for the inset map from Esri. (2019). World Imagery. Retrieved from https://www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9.

REGIONAL AND LOCAL GEOLOGY

The study site is located in the central SAZ, in the north-south oriented uplifted area of the Amazonian foreland basin.

The area (Fig. 3), including the Misahualli river section to the south, and to the southeast, the sediments, the sediments are marine clastic (shaly, silty, and fine-grained sandy) and calcareous (fossiliferous marlstones and limestones) (White *et al.*, 1995; Jaillard *et al*., 1997; Shanmugam *et al.*, 2000)

The study site is characterized by black shales, gray limestones to black and calcareous sandstones. Inside the Uctu Iji Changa (**UIC**) cave, macrofossils of bivalves, gastropods, and a few corals were found. These findings coincide with fossil reports in deposits connected to the Oriente Basin (Jaillard *et al.*, 2005). Daily rainfalls seep and collect in the cave floor generating fluctuations of the subterranean stream flow level. The force of the streams erodes and dissolves calcareous walls and floors, causing oval-shaped carbonate concretions to detach from the cave walls.

A Mosasaurid jaw was identified inside one carbonate concretion, and although it was determined that other fossils were embedded in the walls (see Fig. 4A and 4B), it was only possible to extract the jaw that was exposed by erosion and weathering.

Considering the taphonomic processes that acted on this fossil specimen remains, it is highly probable that more skeletal fragments rest trapped inside of the cave's rocks. The fact that only a fragment of an maxilla was found at UIC implies the original organism (a mosasaurid) followed a taphonomic sequence, starting with the dead organism until fossilization, including: dismembering and fragmentation before burial, scavenging, dissolution, erosion and transport by marine currents, isolation and mineralization of bones, compaction and preservation inside calcareous sediments (Rich & Zambito, 2022).

The partial right maxilla was found in the UIC cave inside a carbonate concretion, after which the electric tomography confirmed its exact location. The cave was measured, and identification points were left to identify the specific places; the structure of the code was 17-N, where the first two digits represent the year, and N represents the control point. The fossil was found at the identification point 17-057, which corresponds to 765 m from the entrance. The rest of the fossil is still localized almost at the cave's end, where human access is still possible.

PALEONTOLOGICAL SITE

The Ucti Iji Changa cave belongs to the Amazon Karst System (**AKS**). It results from the active percolation of acidic waters through calcareous rocks, dissolving them. Karst drainages use the lithological contacts between limestones and underlying shales as cave inception horizons developed within the softer shales

Figure 3. Details of clastic and calcareous sediments of the Napo Group outcropping south of the study site, 1 km west of Puerto Napo parish. **A,** Outcrop composed of horizontally interbedded gray to pale-gray massive limestones, and black shales and silty-shales; vertical transit signal for scale = 1 m; **B,** detail of the outcrop composed of beds of calcareous concretions at the bottom; beds of gray limestones (just below the hammer); and horizontally laminated black silty-shales (above the hammer); geologist hammer for scale = 30.0 cm.

(Constantin *et al.*, 2019). We measured the length of the cave over 1250 meters; after that, human access became difficult. It has a maximum interior height of 5.4 m and a mean height of 2.6 m, a maximum width of about 7.9 m and a mean width of 1.8 m. Using electric resistivity tomography (**ERT**) tests, based upon resistivity contrasts between air voids in the cave and

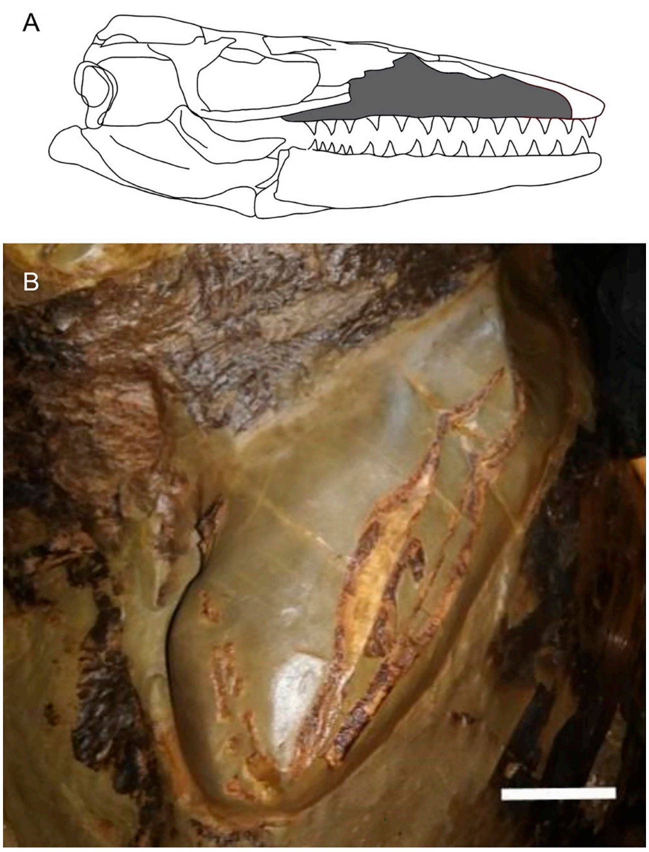

Figure 4. A, Incomplete right maxilla in lateral view. Skull mosasaurid drawing modified from Russell (1967); **B,** calcareous concretion containing the fossil specimen in the Ucti Iji Changa cave. Fossil bone and tissue remains are a different color from the pale brown mudstone calcareous concretio; scale bar = 5 cm.

bedrock and between limestones, marlstones, and shales, Chamba (2020) defined the general stratigraphic framework along the cave in which he established three sub-horizontal layers (see Fig. 5) with beddings between 5° and 15° composed of: 1) Cave base: the cave floor, composed of bivalve-rich, dark gray, well-cemented massive packstones to grainstones, interpreted as bioclastic limestones; 2) Cave void or the cave *s.s.*: the 2–6 m high cave passage composed of light gray marlstones with 1–10 cm diameter carbonate sub-spherical to ellipsoidal concretions and interbedded with brown moderately consolidated mudstones at its base; and 3) Cave ceiling: 2–12 m thick, composed of bivalve-rich dark gray massive well-cemented packstones to grainstones, interpreted as bioclastic limestones.

MATERIALS AND METHODS

The measurement of the cave was done following the methodology of Butcher (1950). After collecting the fossil in the cave, computed tomography (**CT**) studies were performed to verify that the bone section was indeed a maxilla (see Fig. 6). The CT allowed us to observe characteristics such as interdental ridges, and the teeth before the cleaning process.

The CT showed that the morphology of the maxilla (Luan *et al.*, 2009) coincides with that of the mosasaurids group. Cleaning of fossil fragments was done with pneumatic tips to remove the rock's exterior and an acid treatment (hydrochloric acid and hydrogen peroxide) to clean up the surface due to the solubility of calcium carbonate and the insolubility of bone phosphate in acids, following the protocol by Toombs and Rixon (1959).

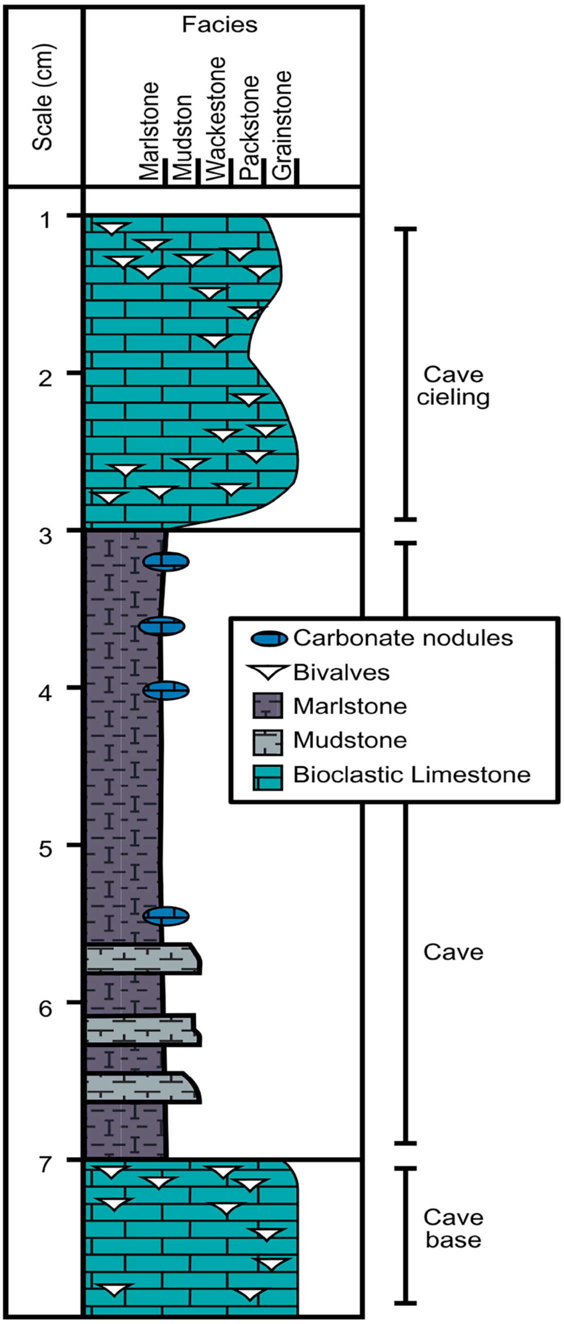

Figure 5. Graphic log representing the stratigraphy at the Uctu Iji Changa cave, NE of Tena city (Modified from Chamba, 2020).

SYSTEMATIC PALEONTOLOGY

The material studied herein is housed in the School of Earth Sciences, Energy and Environment at Yachay Tech University. It has been classified as the following taxa:

Order SQUAMATA Oppel, 1811
Family MOSASAURIDAE Gervais, 1853
Subfamily MOSASAURIDAE indet.

Referred Specimen. Incomplete right maxilla, No. 17-057 stored at the School of Earth Sciences, Energy and Environment, Yachay Tech University, Imbabura, Ecuador.

Locality. Sampled at the Uctu Iji Changa (UIC) cave, Tamia Yura Community, NE of Ecuador.

Stratigraphic precedence. Napo Group, Middle Napo formation, Turonian to Coniacian, as defined by Tschopp (1953) and Jaillard *et al*. (1997).

Collectors and Storage. The fossil was discovered by the members of the first Rikuna project expedition in 2018 and the indigenous leader Carlos Cerda. The fossil was stored and studied by researchers at Yachay Tech University under the permission of the Ecuadorian National Institute of Cultural Heritage (**INPC**).

Description. The maxillary fragment is 30 centimeters long. It has preserved 7 teeth. Since the maxilla is incomplete, it is not possible to know the exact number of total teeth or the relationship of the fossil to the rest of the skull. The teeth are pale brown to brown in color; the tooth roots are almost completely exposed in lingual view, there is no marked distance between the teeth and they appear to be inserted in a shallow fossa that gives the appearance of pleurodontic insertion (see Fig. 7). The crowns are conical, subcircular, and relatively robust, with no swelling at the base. Because the crowns are incomplete, it is not possible to distinguish any type of curvature. The tooth enamel is smooth, with a polished appearance, but gives the appearance of faint longitudinal striations. The apices of the teeth are broken and do not show worn ends. The roots of these teeth are strongly consolidated within the mandibular structure, with an exposed basal width of between 16–20 mm. The crown heights of the remaining teeth range from 17–25 mm. The labial and lingual surfaces appear to be more U-shaped than V-shaped. The lateral roof of the maxilla has subparallel to wavy longitudinal striae.

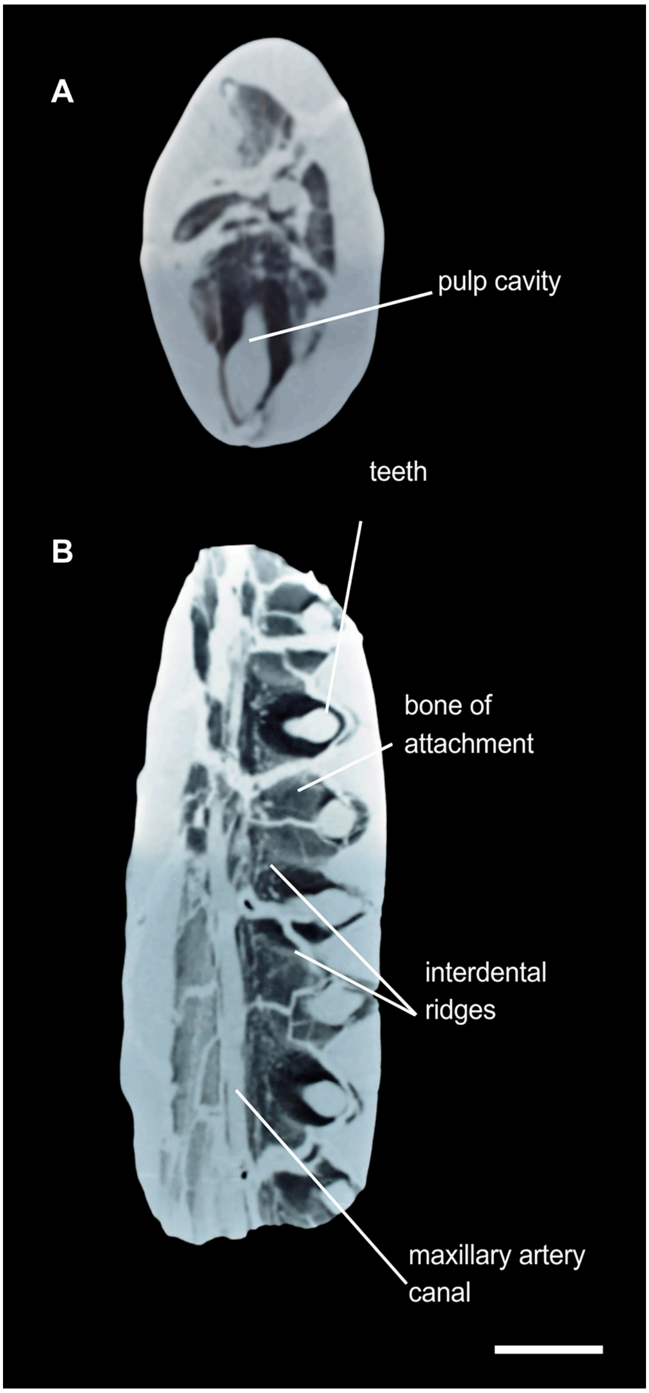

Figure 6. Computed tomography of the incomplete right maxilla (No. 17-057). **A,** Posterior views; **B,** lateral views. (Morphological elements on: Rieppel & Kearney, 2005); scale bar = 5 cm.

DISCUSSION AND CONCLUSIONS

This article presents the discovery of the first marine reptile fossil from the Upper Cretaceous in the central Subandean Zone of Ecuador. The study identifies the find as a Mosasaurid fossil, based on its distinctive tooth shape and size, the root structure in the jaw, the geological structure of the region, and the specific stratigraphy of the cave where it was discovered. As previously described, the stratigraphy corresponds to the Napo Group, specifically the Middle Napo Formation, which ranges from the Turonian to the Coniacian stages, as defined by Tschopp (1953) and Jaillard *et al*. (1997). According to prior studies in the region, all ages supported by ammonite determinations from the surrounding area–in shales, marlstones, and limestones, from the south (Upano river section, Misahualli river section, Latas stream) to near and

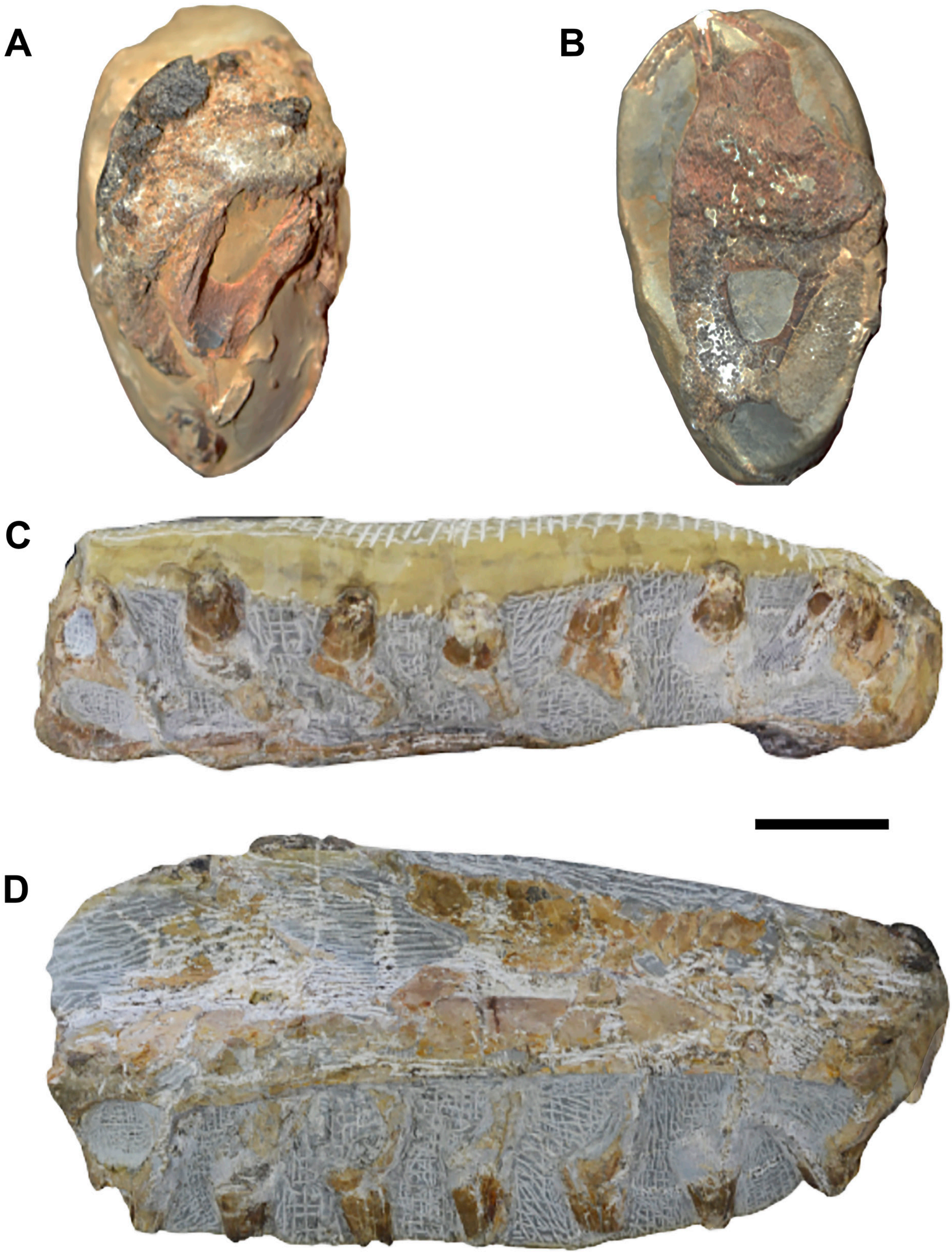

Figure 7. Fragment of the right maxilla (No.17-057) in different views. **A,** Posterior view; **B,** anterior view; **C,** ventral; **D,** medial view; scale bar = 5 cm.

north of the study site (Puerto Napo county, 5 km and 8 km southeast of Archidona city, and upstream of the Misahualli river near the Hollin river) —indicate a minimum age of basal to early Middle Albian and a maximum age of Turonian.

Note that the study site is located in the region toward the top of the Napo anticline, in the upper structure, cut by deep West-dipping reverse faults, central SAZ, in which appears metric bivalve-rich horizontally-bedded limestones, interbedded with shales, mudstones, wackestones and packstones, more probably similar to the shales and limestones occurring in the Middle Napo Fm. found in the Oriente basin in core samples. Hence, the age for the sediments in the UIC cave—in which the mosasaurid's skull fragment was found—would more probably belong to the Middle Napo Fm., Turonian to Coniacian in age.

The specimen is composed of a fragment of a right maxilla of a Mosasauridae, with dentary teeth typically numbering between fourteen to seventeen. These teeth have a polished appearance and exhibit robust crowns that are roughly circular when viewed in cross-section. They possess conical shapes, are relatively stout, and lack any notable swelling at their bases. Moreover, there are no discernible ridges or other structures that would suggest the presence of serrated edges, and there is no evidence of curvature in these teeth.

Assuming similarity with some groups recorded in neighboring regions, it is estimated that the fossil of our study (No. 17-057) from the Turonian of the late Cretaceous is comparable to the Colombian species *Eonatator coellensis* (Páramo-Fonseca, 2013) found in the Campanian rocks for the late Cretaceous. Assuming approximately similar proportions of the bodies from the two reptiles, we estimated the cranium and total length as follows:

1) considering the ratio between the lengths of the jaw to the total cranium of the *Eonatator coellensis* is about 0.76, the mosasaurid's cranium length at the UIC site would be approximately 90.2 cm.

2) considering the ratio between the lengths of the cranium to the skeleton (from the first cervical vertebrate to the last caudal vertebrate) of the *Eonatator coellensis* is about 0.15, and this ratio is similar to the the mosasaurid in the UIC, then its skeleton total length would be 608.7 cm.

Considering the type of cemented matrix involving this partial maxilla fossil, we can infer that it is highly probable that more skeletal fragments rest trapped inside of the cave's rocks. The partial right maxilla of the mosasaur, was found encapsulated within a carbonate calcium concretion located within the UIC cave. Despite its incomplete state, this fossilized maxilla provides invaluable geological insights into the morphology and characteristics of this ancient marine reptile. It is crucial to note that the fossil was exposed due to natural geological processes such as erosion and weathering, raising the tantalizing possibility of additional skeletal fragments concealed within the cave's sedimentary rocks. We can expect to find more mosasaurids fragments of specimens and species throughout this zone since these reptiles spread rapidly in major oceans 25–30 My (Lingham-Soliar, 1995; Díaz & Ortega, 2007), in particular along the interior sea (Scotese *et al.*, 1988) that flooded north and northwestern, and central South America during the Upper Cretaceous subperiod. In addition, mosasaurid specimens are likely to be found in regions with a high concentration of belemnites, ammonites, or foraminifera (Driscoll *et al.*, 2019), as occurs in the Tena region (Jaillard *et al.*, 1997; Ordoñez *et al.*, 2006), and in particular at the UIC cave. Regarding the presence of mosasaurids in the Middle Napo Fm, Oriente basin, that shows was present from Turonian until the end of the Coniacian, in a shallow marine paleoenvironment, with low oxygenation, evidenced by the presence of Heterohelicids, this discovery of the first mosasaurid opens a new field of study of marine reptiles in the Amazon region of Ecuador.

IMPORTANCE & PERSPECTIVES

The present discovery of the first Cretaceous marine reptile in Ecuador is of great geological importance for the region. This finding represents the first documented occurrence of such a reptile in this region, shedding light on the ancient marine fauna that once inhabited these waters. The study site is situated within the Sub-Andean Zone of Ecuador, a geological setting characterized by an intricate history that includes an Upper Jurassic volcanic basement overlain by sedimentary deposits ranging from the Cretaceous to the Paleogene.

The UIC cave, a prominent feature of the Amazon Karst System, plays a pivotal role in this discovery. This cave system is notable for its considerable length, dimensions, and well-defined stratigraphic framework, which includes distinct layers. These layers comprise the cave ceiling, cave void, and cave base, each of which contributes to the overall geological architecture of the cave.

The unearthing of a Cretaceous marine reptile in Ecuador is a momentous geological revelation. It not only enriches our understanding of the paleobiogeography of this region but also underscores the vital role of paleontological research in deciphering Earth's ancient ecosystems. The distinctive geological context of the UIC cave offers a glimpse into the environmental conditions that prevailed during the Cretaceous period in this part of the world, providing an invaluable source of data for geologists and paleontologists alike.

Supplementary information. This article has no additional data.

Authors Contributions. DNG led the research and was involved in the expeditions, choosing the site of study, identification of the fossil, analysis of the fossil, and writing the manuscript. PA was involved in the writing and analysis of both the fossil and the geological site, as well as funding. JTA assisted in writing the manuscript and analyzing the fossil and geological site. JLRC participated in the writing and fossil analysis. JEO, PA, CMO, PA, MO and AV were involved in the expeditions, cleaning of the fossil, analysis of the fossil, and writing the manuscript. NMJO contributed to the writing and geological site analysis.

Competing interest. The authors declare no competing interests.

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