Equatorial pliosaurid from Venezuela marks the youngest South American occurrence of the clade

Dylan Bastiaans1, Daniel Madzia2*, Jorge D. Carrillo-Briceño1 & Sven Sachs3

Pliosaurids were the dominant macropredators in aquatic environments at least since the Middle Jurassic until their extinction in the early Late Cretaceous. Until very recently, the Cretaceous record of Pliosauridae has been poor and difficult to interpret from the taxonomic and phylogenetic perspective. Despite that the knowledge of Cretaceous pliosaurids improved in recent years, numerous aspects of their evolutionary history still remain only poorly known. Here, we report the first pliosaurid material from Venezuela. The taxon is most likely earliest Cenomanian in age, thus representing the youngest occurrence of Pliosauridae from South America. The Venezuelan taxon is based on a well-preserved tooth crown whose morphology and outer enamel structural elements appear to resemble especially those observable in the giant pliosaurid Sachicasaurus vitae from the Lower Cretaceous of Colombia. The new discovery extends the pliosaurid record on the continent by more than 10 million years and likely marks the southernmost Upper Cretaceous occurrence of Pliosauridae, worldwide. We also briefly discuss the affinities of the enigmatic Venezuelan elasmosaurid Alzadasaurus tropicus and highlight similarities to elasmosaurids from the Western Interior Seaway.

With the appearance of the Thalassophonea, possibly around the Early-Middle Jurassic transitional interval¹, pliosaurids became the dominant macropredators in the aquatic environments. They played an important role as apex predators in marine ecosystems until their extinction possibly around the middle Turonian (early Late Cretaceous) (e.g.,¹–⁶). While Jurassic thalassophoneans have been intensively studied, especially those from the fossil-rich provenances in Europe (e.g.,²,⁷–¹¹), the Cretaceous representatives have long been neglected; and were based on patchy occurrences (e.g.,¹²–²³) with largely unexplored phylogenetic affinities (see, e.g.,²⁵). Recent studies, including establishments of new taxa from the Lower Cretaceous of Colombia²⁴–²⁶ and Russia²⁷,²⁸ and from the Upper Cretaceous of the United States³, reports of newly discovered, isolated pliosaurid material²⁵,²⁹–³³ as well as reassessment of historical material¹⁴,³¹,³⁴, led to a better understanding of pliosaurid phylogeny (e.g.,¹,²,⁶,²⁶–²⁸,³⁵,³⁶) and enabled some initial inferences of the divergence times and rates of their Cretaceous lineages¹.

Despite that the knowledge of the Cretaceous thalassophonean pliosaurids has improved in recent years, still considerable efforts are necessary to obtain an accurate perception of the clade’s diversity, disparity, and dispersal patterns during the final tens of millions of years of their evolutionary history.

Here, we report the first pliosaurid material from Venezuela. The new specimen originates from the mid-Cretaceous succession of the La Luna Formation, Candelaria Municipality, Trujillo state, western Venezuela (Fig. 1)³⁷–⁴⁰. This find is significant because it represents the youngest record of Pliosauridae from the South American continent: younger by more than 10 million years than the late Aptian (late Early Cretaceous) ‘Kronosaurus’ boyacensis, the second youngest South American record³¹. It is also very likely the southernmost Upper Cretaceous occurrence of the clade, worldwide. The pliosaurid specimen also marks only the second plesiosaur record known from Venezuela. A partial elasmosaurid skeleton from the eastern part of the country (the affinities of which are discussed below) has been described in 1949 by Colbert⁴¹ and named Alzadasaurus tropicus.

The Venezuelan pliosaurid material described herein is a valuable addition to the scarce plesiosaur record of the mid-Cretaceous—i.e., Aptian–Albian to Cenomanian–Turonian—of South America (Fig. 2). Plesiosaurs, in general, are extraordinarily rare in the mid-Cretaceous of South America. They are often represented by...
isolated fragmentary material, with the notable exception of the taxa originating from the upper Aptian (Lower Cretaceous) of the Paja Formation in Colombia\textsuperscript{15,36,43}, and are not diagnostic beyond larger clades (Table 1). Despite that the new material is represented by an isolated tooth crown, its excellent preservation allows for a detailed description of its morphology and the outer enamel structural elements. Through comparisons with other Cretaceous pliosaurids, and by using multivariate analyses of pliosaurid dental features that have recently become available\textsuperscript{5}, it is possible to determine its taxonomic affinities and an approximate phylogenetic placement.

**Institutional abbreviations.** AMNH, American Museum of Natural History, New York, USA; CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge, Cambridge, UK; DMNS, Denver Museum of Nature and Science, Denver, USA; FMNH, Field Museum of Natural History, Chicago, USA; GFMSU, Geological Faculty of Lomonosov Moscow State University, Museum at the academic base named after Prof. A. A. Bogdanov, Bakhchisaray district, Crimea; MCNC, Museo de Ciencias Naturales de Caracas, Caracas, Venezuela; MWGUW, Stanislaw Józef Thugutt Geological Museum, Warsaw, Poland; UNSM, University of Nebraska State Museum of Natural History, Lincoln, USA.

**Geological and stratigraphic setting.** The specimen MCNC-1830 originates from the La Aguada Member of the La Luna Formation at the “Cementos Andinos” quarry, where calcareous rocks are mined for cement production. The quarry is located in the Andes range (Cordillera de Mérida), east of Lake Maracaibo, 10 km to the northeast of Monay city, Candelaria Municipality, Trujillo state, western Venezuela (Fig. 1A). MCNC-1830 was collected in situ in 2014 by one of the authors (JDCB), at the top of the quarry (9° 36′ 52″ N, 70° 24′ 3″ W), in the same outcrop of the La Aguada Member shown by\textsuperscript{37} (Fig. 3A in\textsuperscript{37}) (Fig. 1).

The La Luna Formation is the most prolific petroleum source rock in western Venezuela and part of eastern Colombia\textsuperscript{54–57}, and represents a marine sequence deposited under anoxic–dysoxic conditions along the passive margin of northern South America during the Cenomanian–Campanian\textsuperscript{57}. The La Luna Formation is an extensive geological unit that spans the foreland of the southern Caribbean Ridge, including a large part of northwest Venezuela (Sierra de Perijá to the Mérida Andes) and to Colombia, and gradually transitions east into the contemporaneous Rio Querecuál Formation (eastern Venezuela) which is equivalent in facies\textsuperscript{55}. These concretions range from a few centimeters to well over a meter in length (e.g.,\textsuperscript{37}, Fig. 3C,D). In the southeast of the Maracaibo basin in the Lara and Trujillo states, the La Luna Formation is divided into three members (Fig. 1B):
Figure 2. Distribution of mid-Cretaceous (Aptian-Turonian) plesiosaurs in South America. The new pliosaurid from the La Luna Formation is highlighted. (1) Jaén area, Romirón Fm., Peru; (2) Villa de Leiva, Paja Fm., Colombia; (3) Cementos Andinos Quarry, La Luna Fm., Venezuela; (4) Altigracia de Orituco area, Querecual Limestone, Venezuela; (5) Near Sao Luís, Alcântara Fm., Brazil; (6) Santa Cruz Province, Mata Amarilla Fm., Argentina. See Table 1 for details and references (map provided with permission by PD Dr. Torsten M. Scheyer; modified by Dylan Bastiaans using Adobe Illustrator & Photoshop [v2021.25.0]).

Table 1. Locality information and literature references on the mid-Cretaceous plesiosaurs of South America. Welles14,44, Hampe15, Páramo-Fonseca et al.26,36,43, Colbert41, Carpenter45, Jaillard et al.49, Carvalho et al.50, O’Gorman and Varela52, Ameghino53, Jaimes and Parra46, Goñi and Gasparini47, Bôas and Carvalho51, Meza-Velez and O’Gorman48. Note that Pliosauroida?/Pliosauridae? indet.48 may represent the same material as that of49. aAptian, C Cenomanian, T Turonian, l lower, u upper. bLeast inclusive clade. cThis study.

| Original taxonomic assignment | Locality | Country | Unit | Stage | Material | Current taxonomic assignment | LIC | Original taxonomic assignment | Locality | Country | Unit | Stage | Material | Current taxonomic assignment | LIC |
|------------------------------|----------|---------|------|-------|----------|--------------------------------|-----|-----------------------------|----------|---------|------|-------|----------|--------------------------------|-----|
| Alzadasaurus colombiensis14  | Villa de Leiva | Colombia | Paja Formation | uA    | Several skeletons and skeletal remains | Callawaytsaurus colombiensis14-46 | Elasmosauridae | Alzadasaurus colombiensis14  | Villa de Leiva | Colombia | Paja Formation | uA    | Several skeletons and skeletal remains | Callawaytsaurus colombiensis14-46 | Elasmosauridae |
| Lovunastes bernardoi15,36    | Villa de Leiva | Colombia | Paja Formation | uA    | Anterior half of the skull | As original | Elasmosauridae | Lovunastes bernardoi15,36    | Villa de Leiva | Colombia | Paja Formation | uA    | Anterior half of the skull | As original | Elasmosauridae |
| Kronosaurus boyacensis15     | Villa de Leiva | Colombia | Paja Formation | uA    | Largely complete skeleton | Kronosaurus boyacensis15 | Brachaschinenae | Kronosaurus boyacensis15     | Villa de Leiva | Colombia | Paja Formation | uA    | Largely complete skeleton | Kronosaurus boyacensis15 | Brachaschinenae |
| Pliosauroida?/Pliosauridae? indet.48 | Jaén area | Peru | Romirón Formation | uC–IT | Two vertebrae | Plesiosauria indet. | Plesiosauria | Pliosauroida?/Pliosauridae? indet.48 | Jaén area | Peru | Romirón Formation | uC–IT | Two vertebrae | Plesiosauria indet. | Plesiosauria |
| Elasmosauridae indet.48      | Jaén area | Peru | Romirón Formation | uC–IT | 5 cervical vertebrae | As original | Elasmosauridae | Elasmosauridae indet.48      | Jaén area | Peru | Romirón Formation | uC–IT | 5 cervical vertebrae | As original | Elasmosauridae |
| Plesiosauria indet.46         | Near Sao Luis | Brazil | Alcântara Formation | C | Teeth | As original | Plesiosauria | Plesiosauria indet.46         | Near Sao Luis | Brazil | Alcântara Formation | C | Teeth | As original | Plesiosauria |
| Alzadasaurus tropicus41       | Near Altigracia de Orituco | Venezuela | Querecual limestone | C–T | Partial postcranial skeleton | Elasmosauridae indet.46 | Elasmosauridae | Alzadasaurus tropicus41       | Near Altigracia de Orituco | Venezuela | Querecual limestone | C–T | Partial postcranial skeleton | Elasmosauridae indet.46 | Elasmosauridae |
| Elasmosauridae indet.52      | Near Tres Lagos | Argentina | Mata Amarilla Formation | C–S | Teeth, vertebrals, pro- podal | As original | Elasmosauridae | Elasmosauridae indet.52      | Near Tres Lagos | Argentina | Mata Amarilla Formation | C–S | Teeth, vertebrals, pro- podal | As original | Elasmosauridae |
| Polyptychodon patagonicus53   | Santa Cruz Province | Argentina | Mata Amarilla Formation | ? | Teeth | Plesiosauria indet.52 | Plesiosauria | Polyptychodon patagonicus53   | Santa Cruz Province | Argentina | Mata Amarilla Formation | ? | Teeth | Plesiosauria indet.52 | Plesiosauria |
Xiphactinus is a genus of bony fish with narial and postcranial remains of a wide variety of bony fish remains have been uncovered, including scales, isolated and semi-articulated cranial and generally nutrient-rich surface waters and a stratified water column seem to have been present40,55. The La Luna Formation (presence and abundance of globigerinid and a scarcity of globotruncanid foraminifera) with oxygenated (less than ~ 60–70 cm thick), intercalated by compact and laminated black/dark-grey shales, and abundant calcareous concretions. MCNC-1830 derives from a black shale horizon that has produced ichnofossils, molluscs, chondrichthyans48, abundant osteichthyans59, and a marine snake67. The base of the La Aguada Member at the “Cementos Andinos” quarry overlays a fossiliferous dark-grey sandy limestone (personal observation, Fig. 1C) that has been identified as the top of the upper Albian Maraca Formation in the Andes of Trujillo and Lara states38. Other authors (e.g., 61,62) have used the term the ‘La Puya member’ to refer to a thin section (< 30 m) at the top of the Peñas Altas Formation in the Andes of Lara and Trujillo (Fig. 1). Therefore, the discrepancy between the use of the Maraca Formation or the ‘La Puya Member’ for the thin sequence under the La Aguada Member is still unresolved37.

The precise age of the La Aguada Member and its corresponding sections across Venezuela and Colombia remains uncertain, ranging from Albian–Cenomanian35,37,43–45, lower–upper Cenomanian59,63–69 and even Cenomanian–Santonian40. Most relevant, perhaps, is the dating of the La Peña/San Felipe Sections by 55, located in the eastern part of the Maracaibo Basin on the eastern edge of the village of Chejendé, Trujillo, which is less than 10 km from the “Cementos Andinos” quarry. Based on ammonofossils, the La Aguada Member of Chejendé was deposited no earlier than in the latest Albian to middle Cenomanian interval35. However, only the base of the La Aguada Member was exposed, thus strongly suggesting an earliest Cenomanian age for MCNC-1830 that was recovered much higher in the section (55, p. 352 and Fig. 3A). Despite the debate on the exact age of the base of the La Luna Formation east of Lake Maracaibo (e.g., La Aguada Member), it seems that, based on the ammonite record, it becomes progressively younger westward63–65. For a detailed discussion on the age of the La Aguada Member see Supplementary Information 1.

Paleoenvironment and other vertebrates. During much of the Early Cretaceous, what is today Venezuela was covered by an epicontinental sea that rapidly transgressed during the latest Albian and Cenomanian towards the craton followed by a period of re-oxygenation84. The La Aguada Member has often been considered to cover a transitional environment between the shallow water conditions of the Maraca Formation (La Puya Member) and the pelagic low energy conditions of the La Luna Formation; however, water depths never exceeded 50 m48,40,55,57. The La Aguada Member has intervals rich in organic matter which have been suggested to be of algal origin40. Sedimentological and vertebrate (micro)fossil proxies indicate a shallow water environment (presence and abundance of globigerinid and a scarcity of globotruncanid foraminifera) with oxygenated and generally nutrient-rich surface waters and a stratified water column seem to have been present40,55. The La Luna Formation is associated with an outer shelf/upper slope paleoenvironment with a high diversity of medium to large marine vertebrates (see Supplementary Table 1) that would have served as ample food resources for opportunistic predators37. Nonetheless, the vertebrate record of the La Aguada Member remains fairly limited. A wide variety of bony fish remains have been uncovered, including scales, isolated and semi-articulated cranial and postcranial remains of Xiphactinus48, other ichthyodectiforms, enchodontids, and small indeterminate fishes48,64. A high diversity of lamniform sharks (at least 12 taxa in five clades, eight of which are anacoracids), have been described from the La Luna Formation, representing active pelagic predators and scavengers of large vertebrates and small nektobenthic predators feeding on small bony fish and invertebrates65. The new plesiosaur specimen adds to the diversity of large marine reptiles from the La Luna Formation and represents the largest predator described from the strata so far (Fig. 3, Supplementary Table 1).

Bottom water conditions were predominantly anoxic or suboxic, as indicated by the scarcity of benthic invertebrates with only rare occurrences of small bivalve moulds in the limestones (and undetermined ammonites), and some inoceramids in the calcareous concretions and a lack of reworking by bioturbation and/or high-water energy conditions (for more details see the Supplementary Information 1,40,65). It seems that anoxic sedimentation, possibly related to upwelling along the northwestern coast of South America, was widespread across the Venezuelan and Colombian platform and possibly even spanning a major part of northern South America and the southern Caribbean during the Cenomanian–Santonian55. Towards the top of the Chejendé Member oxygen and nutrient conditions improve and pelycypods and ammonites are more frequent in the concretion-rich portion of the section55.

Material and methods

Material. The study is based on an isolated tooth crown belonging to a brachauchenine pliosaurid of probable early Cenomanian (early Late Cretaceous) age. The specimen originates from the La Aguada Member of the La Luna Formation, Candelaria Municipality, Trujillo state, western Venezuela. It is housed at the Museo de Ciencias Naturales de Caracas in Caracas, Venezuela (MCNC) under the catalog number MCNC-1830 (Fig. 3).

The specimen (MCNC-1830) was found as part of a larger collection of fossil vertebrates at the “Cementos Andinos” quarry with the support of the authorities of the mining company. Legal authorization was issued by the Instituto del Patrimonio Cultural de Venezuela (IPC) through the collection permit No. 000327/2013, and through permission for mobilization and study No. 071/2015.

Multivariate analyses. To further assess the taxonomic affinities of MCNC-1830 and to explore its morphospace occupation among thalassophonean pliosaurs, we performed cluster and principal coordinates analyses using the dataset of 55. This dataset was constructed to collectively summarize the dental morphological
features present in Thalassophonea. The Venezuelan taxon (MCNC-1830) and Sachicasaurus vitae from the upper Barremian of Sáchica, Colombia, were added to this dataset. The former was scored based on personal observations and the latter based on discussions with Cristian David Benavides-Cabra (Universidad Nacional de Colombia, Bogotá, Colombia). We further modified the carinal score (character 3) for GFMSU h-216 (0 → 2), hereafter termed the ‘Crimean pliosaurid’, that was miss-scored in the original version of the dataset as lacking the carinae, while, in fact, the crown has two carinae. See Supplementary Information 1 for the matrix.

We replicated the protocol of; we applied a 50% completeness threshold to remove the influence of taxa based on insufficiently complete/preserved material, scaled the data to equal variance and a mean of zero through subtraction of the mean value for each character and then divided it by the standard deviation. A distance matrix was created using the Gower metric, that is well suited for datasets that comprise both continuous and discrete variables. We used the cluster v2.1.0 package in the R statistical environment (RStudio Version 1.2.5033); from the resulting distance matrix a cluster dendrogram analysis using the stats base package and the Ward.D2 method was produced.

The same matrix was used to explore the dental morphospace occupation of particular thalassophonean taxa through a principal coordinates analysis, using ape v5.3. We again used the Gower metric and applied the Cailliez correction for negative eigenvalues. See Supplementary Information 2 for the R code.

The terminology of tooth crown orientation and morphology. We follow the crown orientation terminology of: apical, toward the crown apex; basal, toward the cervix dentis; distal, away from the tip of the snout; labial, toward the lips; lingual, toward the tongue; mesial, toward the tip of the snout. The morphological traits exposed on the outer enamel surface are described using the nomenclature as adopted by: apicobasal ridges, longitudinally running enamel ridges of variable apicobasal extent that can be developed around the entire crown circumference and are approximately semicircular or triangular in cross-section; ridglets, subtle apicobasally-expressed enamel structures that are often developed between adjacent apicobasal ridges or on an unridged enamel surface; the ridglets may be very indistinct as well as produce a distinct vermicular pattern (see: Fig. 7).

Systematic paleontology.

Plesiosauria
Pliosauridae
Thalassophonea
Brachaucheninae
Brachaucheninae indet.

Material. MCNC-1830, an isolated tooth crown (height of the preserved part = ~ 30 mm).

Occurrence. (Most likely) lower Cenomanian, Upper Cretaceous from the La Aguada Member, La Luna Formation (see ‘Geological and stratigraphic setting’ for detailed information with respect to the stratigraphic context).
Description and comparisons. The apicalmost part of MCNC-1830 is broken off and the basal section is slightly compressed in labiolingual direction. Linguodistally, part of the crown is crushed near the base. The crown is conical (subcircular in cross-section), as in Acostasaurus pavachoquensis25, Brachauchenius lucasi20,22, 'Kronosaurus' boyacensis15, Kronosaurus queenslandicus82, Megacephalosaurus eulerti6, 'Polyptychodon' hudsoni, Sachicasaurus vitae26, and the element-rich assemblage collectively assigned to 'Polyptychodon interrumpus' reappraised by4 as probably belonging to multiple taxa, but differing from Luskhan itilensis28, Makhaira rossica27, Stenorhynchosaurus munozi24, and the 'Crimean pliosaurid'29 that possess trihedral (M. rossica), sub-trihedral (L. itilensis, S. munozi), and trihedral-to-'trapezoid' (the 'Crimean pliosaurid') cross-sectional shapes of their tooth crowns. No carinae/cutting edges are present, unlike the condition observable in L. itilensis, M. rossica, S. munozi, and the 'Crimean pliosaurid', which are characterized by the presence of one (L. itilensis, S. munozi), two (the 'Crimean pliosaurid'), and three (M. rossica) carinae. The apicobasal ridges in MCNC-1830 are approximately semicircular in cross-section and are developed around the entire circumference though they are most densely packed linguodistally. All of the ridges appear to reach the apex though due to the lack of the apical part, this cannot be confirmed. Some of the ridges are approaching each other on the linguodistal part of the crown, around the mid-section, but no ridges have been observed to branch, unlike in Brachauchenius lucasi, 'Polyptychodon' hudsoni, and Megacephalosaurus eulerti that typically show clear branching ridges around the mid-sections of tooth crowns. Mesiolabially, the enamel surface exposed between the apicobasal ridges shows well-pronounced ridglets, forming a vermicular pattern, similar to the state observable in Sachicasaurus vitae and some specimens from the 'Polyptychodon' assemblage, such as CAMSM B 75754.

Assessment through multivariate analyses. The results of our multivariate analyses are broadly similar to those of5. The principal coordinates analysis (PCoA) as well as the cluster analysis recognize the presence of two general tooth crown ‘morphogroups’ in pliosaurids, one comprising the crowns with a conical shape (subcircular cross-section) and the other one including those with the trihedral/subtrihedral morphology (triangular/sub-triangular cross-section) (Fig. 4). As in5, PCoA largely separates the two ‘morphogroups’ by the first principal coordinate axis (Fig. 4A). The specimen MCNC-1830 is placed on the positive sides of the first and second axis, in close proximity to Sachicasaurus vitae and the ‘Polyptychodon’ type 1, a tooth morphotype from the middle to upper Albian Gault Formation and the lowermost Cenomanian Cambridge Greensand Member of the West Melbury Marly Chalk Formation (late Albian in age), represented by a number of tooth crowns of differing sizes that are characterized especially by their arrangements of apicobasal ridges (11, Figs. 3A, 4A, and 5). These crowns differ from MCNC-1830 in that their enamel surface is smoother than in MCNC-1830 and do not include well-pronounced ridglets.

A similar result, to that of the PCoA, was obtained through the cluster analysis that placed MCNC-1830 in a cluster with S. vitae and further with ‘Polyptychodon’ type 1 and Megacephalosaurus eulerti (Fig. 4B), within the ‘conical’ part of the cluster dendrogram.
Discussion

Dental disparity of the Cretaceous pliosaurids. The results of our multivariate analyses differ in some aspects from those of^{2}, which warrants some discussion. The addition of the late Barremian brachyuranine *Sachicasaurus vitae* expands the crown morphospace occupation of the pre-Aptian taxa towards the positive side of the second coordinate axis, further supporting the hypothesis that the late brahmauchines experienced a substantial decrease in their dental disparity.

The most significant difference is the placement of GFMSU h-216 (‘Crimean pliosaurid’) within the ‘trihedral’ cluster. The analysis of^{2} placed the specimen among the conical-toothed taxa, in a cluster together with the Callovian (Middle Jurassic) taxon ‘Pliosaurus’ Andrewesi and the Cenomanian (Late Cretaceous) specimen MWGUW 009761 (‘Anopol pliosaurid’), none of which is particularly reminiscent of the trihedral-to-‘trapezoid’ morphology of GFMSU h-216. It is worth noting that MWGUW 009761 shows a cross-section somewhat resembling a triangular shape, and may thus be characterized as being gently trihedral^{34}. However, considering its overall morphology and its enamel character state distribution, we did not alter any scores for this specimen in the current version of the dataset.

The difference in the placement of GFMSU h-216 between^{2} and our study clearly stems for the correction of the carinal score for the specimen (0 → 2). ‘Pliosaurus’ Andrews and MWGUW 009761 still cluster together among the conical-toothed pliosaurids.

Remarks on the Venezuelan elasmosaur *Alzadasaurus tropicus*. The most complete pliososaur find from Venezuela is a partial postcranial skeleton (AMNH 6796) that was discovered by a Venezuelan oil company near the vicinity of Altacraga de Orituco, eastern Venezuela and established as *Alzadasaurus tropicus* by Colbert^{41}. Preserved are the posteriormost cervical vertebra, four pectoral and eight dorsal vertebrae, parts of associate ribs, the left scapula, a nearly complete left and parts of the right coracoid, a left humerus as well as parts of the left radius, ulna and carpus (^{41}, p. 4). *A. tropicus* was considered a ‘nomen vanum’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by vertebrae with round centra and rather high, compressed, neural spines; scapula that has a broad dorsal process and a fairly broad ventral plate, lacking a pectoral bar, is a condition reminiscent of *Alzadasaurus tropicus* was considered a ‘nomen dubium’ by^{44} (p. 54), a taxon that was adequately described but lacks sufficient diagnostic characters (nomen dubium of current use). Following Colbert’s (^{41}, p. 5) diagnosis for *A. tropicus*, the taxon is characterized by verteba...
representing a caudal and a sacral or proximal caudal centrum, has not been supplemented with detailed comparisons of contemporary taxa. A morphometric analysis of the specimens placed them outside the Elasmosauridae, which led to the conclusion that pliosaurids are the most plausible group. However, similar proportions and a similar morphology (centra that are wider than long/high and higher than long, having amphicoelous articular faces) are also known for coeval early Late Cretaceous polypterygians (see e.g. 53). This group was not considered in the comparisons by Meza-Velez and O’Gorman 48. For that reason, and owing to the apparent homoplasy in plesiosaur vertebral characters (e.g., 94), the taxonomic assignment is questionable. Pending more detailed assessment of the material and vertebral character distribution within Plesiosauria, the vertebrae are probably best interpreted as Plesiosauria indet.

Conclusions

With the notable exception of the pliosaurid and elasmosaurid specimens originating from the upper Aptian (Lower Cretaceous) strata of the Paja Formation in Colombia, the pliosaur record from the mid-Cretaceous (approximately encompassing the Aptian-Turonian interval) of South America is based on fragmentary remains of indeterminate phylogenetic affinities.

Here, we report the first pliosaurid material from Venezuela. The specimen originates from the La Aguada Member of the La Luna Formation in the Andes range (Cordillera de Mérida), east of Lake Maracaibo, 10 km to the northeast of Monay city, Candelaria Municipality, Trujillo state, western Venezuela. It was discovered in strata most likely deposited in the early Cenomanian (earliest Late Cretaceous). Despite comprising a single tooth crown, the preservation of the specimen allows for a detailed description, comparisons to teeth of other Cretaceous pliosaurids, and an assessment through multivariate analyses of data that have become available recently.

The overall morphology of the Venezuelan specimen and the distribution of its outer enamel structural elements indicate affinities to late-diverging braucheninines and appear to resemble especially those observable in Sachicasaurus vitae, a recently described giant pliosaurid from the upper Barremian (Lower Cretaceous) of Boyacá, Colombia.

The most complete plesiosaur material from Venezuela described to date includes a partial postcranial specimen, established as the type of Alzadasaurus tropicus. The taxon is usually considered to lack diagnostic features and is treated as a nomen dubium. Our preliminary assessment of the specimen concurs with this though we have also observed characters that are shared with the middle Cenomanian (lower Upper Cretaceous) elasmosaurid Thalassomedon hanningtoni from the midwestern USA.

In turn, the Venezuelan pliosaurid represents the youngest South American representative of the clade, over 10 Ma younger than the second youngest South American record (‘Kronosaurus’ boyacensis). Additionally, if the early Cenomanian age for the deposition of the fossil-bearing strata proves correct, the newly described specimen also marks the southernmost Upper Cretaceous occurrence of Pliosauridae, worldwide. Regardless, the Venezuelan pliosaurid represents a significant addition to the scarce record of the mid-Cretaceous plesiosaurs of South America and is another indicator of the potential and abundance of marine vertebrates from the Cretaceous of Venezuela.

Received: 27 March 2021; Accepted: 13 July 2021
Published online: 29 July 2021

References

1. Madzia, D. & Cau, A. Estimating the evolutionary rates in mosasauroiids and pliosaurids: Discussion of niche occupation in Late Cretaceous seas. PeerJ 8, e8941 (2020).
2. Benson, R. et al. A giant pliosaurid skull from the Late Jurassic of England. PLos ONE 8, e65989. https://doi.org/10.1371/journal.pone.0065989 (2013).
3. Schumacher, B. A., Carpenter, K. & Everhart, M. J. A new Cretaceous pliosaurid (Reptilia, Plesiosauria) from the Carlile Shale (middle Turonian) of Russell County, Kansas. J. Vertebrate Paleontol. 33, 613–628 (2013).
4. Madzia, D. A reappraisal of Polyptychodon (Plesiosauria) from the Cretaceous of England. PeerJ 4, e1998 (2016).
5. Zverkov, N. G., Fischer, V., Madzia, D. & Benson, R. B. J. Increased pliosaurid dental disparity across the Jurassic–Cretaceous transition. Palaeontology 61, 825–846 (2018).
6. Madzia, D., Sachs, S. & Lindgren, J. Morphological and phylogenetic aspects of the dentition of Megacephalosaurus eulerti, a pliosaurid from the Turonian of Kansas, USA, with remarks on the cranial anatomy of the taxon. Geol. Mag. 156, 1201–1216 (2019).
7. Tarlo, L. B. A review of the Upper Jurassic pliosauroiids. Bull. Br. Mus. (Nat. Hist.) Geol. Lond. 4(5), 145–189 (1960).
8. Nop, L. F. A taxonomic and functional study of the Callovian (Middle Jurassic) Pliosauridae (Reptilia, Sauropterygia), PhD thesis, University of Derby, 616 pp (2001).
9. Ketchum, H. F. & Benson, R. B. J. The cranial anatomy and taxonomy of Peloneustes philarchus (Sauropterygia, Pliosauridae) from the Peterborough member (Callovian, Middle Jurassic) of the United Kingdom. Palaeontology 54(3), 639–665 (2011).
10. Knutsen, E. M. A taxonomic revision of the genus Pliosaurus (Owen, 1841a) Owen, 1841b. Norw. J. Geol. 92, 259–276 (2012).
11. Knutsen, E. M., Druckenmiller, P. S. & Hurum, J. H. A new species of Pliosaurus (Sauropterygia: Plesiosauria) from the Middle Volcanic of central Spitsbergen, Norway. Norw. J. Geol. 92, 235–258 (2012).
12. Williston, S. W. North American plesiosaurs. Field Columbian Museum, Pub. 73, Geological Series 2, 1–79 (1903).
13. Williston, S. W. The skull of Brachiauchenis, with special observations on the relationships of the plesiosaurs. US Natl. Museum Proc. 32, 477–489 (1907).
14. Welles, S. P. & Slaughter, B. H. The first record of the plesiosaurian genus Polyptychodon (Pliosauridae) from the New World. J. Paleontol. 37, 131–133 (1963).
15. Hampe, O. Ein großwüchsiger Pliosauride (Reptilia: Plesiosauria) aus der Unterkreide (oberes Aptium) von Kolumbien. Courier Forschungs-Institut Senckenberg 145, 1–32 (1992).
16. Carpenter, K. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jb. Geol. Paläontol. Abh. 201, 259–287 (1996).
17. VonLoh, J. P. & Bell, G. L. Jr. Fossil Reptiles from the Late Cretaceous Greenhorn Formation (Late Cenomanian-Middle Turonian) of the Black Hills Region, South Dakota. Dakoterra 5, 28–38 (1998).
18. Kear, B. P. Cretaceous marine reptiles of Australia: A review of taxonomy and distribution. Cretac. Res. 24, 277–303 (2003).

19. Hampe, O. Considerations on a Brachauchenius skeleton (Pleurosauroidea) from the lower Paja Formation (late Barremian) of Villa de Leyva area (Colombia). Fossil Record 8, 37–51 (2005).

23. Ketchum, H. F. & Benson, R. B. J. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. Biol. Rev. 85, 361–392 (2010).

27. Fischer, V. Peculiar macrophagous adaptations in a new Cretaceous pliosaurid. J. Vertebr. Paleontol. 25, 37–51 (2005).

28. Fischer, V. P. & Ketchum, H. F. Plasticity and convergence in the evolution of short-necked plesiosaurs. Curr. Biol. 27, 1667–1676.e3 (2017).

30. Zverkov, N. G. On a typically Late Jurassic pliosaur from the Lower Cretaceous of Crimea. The International Scientific Conference on the Jurassic/Cretaceous boundary, Samara, Russia, 89–94 (2015).

31. Madzia, D. & Machalski, M. Isolated pliosaurid teeth from the Albian-Cenomanian (Cretaceous) of Annopol, Poland.

32. Lukeneder, A. & Zverkov, N. G. First evidence of a conical-toothed pliosaurid (Reptilia, Sauropterygia) in the Hauterivian of the Northern Calcareous Alps, Austria. Palaeontogr. Abt. A 210, 5–42 (2017).

36. Páramo-Fonseca, M. E., Benavides-Cabra, C. D. & Gutiérrez, I. E. A new species of elasmosaurid from the Paja Formation, Villa de Leiva, Colombia. Cretaceous Res. 99, 30–49 (2019).

40. Guinot, G. & Carrillo-Briceño, J. D. Lamniform sharks from the Cenomanian (Upper Cretaceous) of Venezuela.

43. Páramo-Fonseca, M. E., O’Gorman, J. P. First evidence of a conical-toothed pliosaurid (Reptilia, Sauropterygia) in the Lower Cretaceous of the Palaeontogr. Abt. A 393–403 (2017).

44. Welles, S. P. A new species of elasmosaur from the Aptian of Colombia, and a review of the Cretaceous pliosauridae. Univ. California Publ. Geol. Sci., 1–96 (1962).

45. Carpenter, K. Revision of North American elasmobranchs from the Cretaceous of the Western Interior. Palaeobiology 12, 367–377. https://doi.org/10.1038/s41598-021-94515-8 (2021).

46. Jaillard, E., Cordova, A., Mazin, J.-M. & Mourier, T. La transgression du Cénomanien supérieur-Turonien inférieur dans le région de Jaén (Nord du Pérou): donnés sédimentologique et stratigraphiques: Découverte du premier saurien marin du Pérou, Série II. C. R. Acad. Sc. Paris 301(20), 1429–1432 (1985).

47. Carvalho, I., Velas Bóas, I. & Bergqvist, L. Plesiosauos da regiao equatorial Brasileira Bacia de Sao Luiz (Cretáceo Superior) Brazil. Acta Geológica Leopoldina 23(51), 533–541 (2000).

48. O’Gorman, J. P. & Varela, A. N. The oldest lower Upper Cretaceous pliosaur (Reptilia, Sauropelgia) from southern Patagonia, Argentina. Ameghiniana 47, 447–459 (2010).

49. Meza-Vélez, I. & O’Gorman, J. E. registro fósil de plesiosaurios (Diapsida, Sauropelgia) en el Perú. Rev. Per. Biol. 28(1), 1–8 (2021).

50. Jaillard, E., Cordova, A., Mazin, J.-M. & Mourier, T. La transgression du Cénomanien supérieur-Turonien inférieur dans le région de Jaén (Nord du Pérou): donnés sédimentologique et stratigraphiques: Découverte du premier saurien marin du Pérou, Série II. C. R. Acad. Sc. Paris 301(20), 1429–1432 (1985).

51. Carvalho, I., Velas Bóas, I. & Bergqvist, L. Plesiosauos da regiao equatorial Brasileira Bacia de Sao Luiz (Cretáceo Superior) Brazil. Acta Geológica Leopoldina 23(51), 533–541 (2000).

52. O’Gorman, J. P. & Varela, A. N. The oldest lower Upper Cretaceous pliosaur (Reptilia, Sauropelgia) from southern Patagonia, Argentina. Ameghiniana 47, 447–459 (2010).

53. Meza-Vélez, I. & O’Gorman, J. E. registro fósil de plesiosaurios (Diapsida, Sauropelgia) en el Perú. Rev. Per. Biol. 28(1), 1–8 (2021).
Fonseca (Universidad Nacional de Colombia, Bogotá, Colombia) and two anonymous reviewers for their collaboration. Finally, we would like to thank Cristian David Benavides-Cabra (Universidad Nacional de Colombia, Edwin Chávez-Aponte (Museo de Ciencias Naturales de Caracas) are further thanked for their valuable collaboration. We would like to express our gratitude to Engelberth Montilla, Crisanto Silva, Norelis Valera, and Cementos Andinos CA., for assistance during the fieldwork. We would also like to thank the authorities at the Instituto del Patrimonio Cultural de Venezuela for the permissions to collect and study the specimen. Hyram Moreno and Edwin Chávez-Aponte (Museo de Ciencias Naturales de Caracas) are further thanked for their valuable collaboration. Finally, we would like to thank Cristian David Benavides-Cabra (Universidad Nacional de Colombia, Bogotá, Colombia) for information on the dental anatomy of Sachicasaurus vitae and Maria Eurdice Páramo-Fonsca (Universidad Nacional de Colombia, Bogotá, Colombia) and two anonymous reviewers for their constructive and helpful comments that have improved this manuscript.
**Author contributions**
D.B. and D.M. designed the project. D.B. prepared Fig. 2, Supplementary Fig. 1, and Supplementary Table 1. D.M. compiled data for multivariate analyses, carried out the analyses, and prepared Figs. 3 and 4. J.D.C.-B. prepared Fig. 1. S.S. prepared Table 1. All authors participated to the writing process and gave final approval for publication.

**Funding**
DB was partially funded through the Swiss National Science Foundation (Grant no. 31003 A_179401 to T. Scheyer).

**Competing interests**
The authors declare no competing interests.

**Additional information**

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1038/s41598-021-94515-8.

**Correspondence** and requests for materials should be addressed to D.M.

**Reprints and permissions information** is available at www.nature.com/reprints.

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2021