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Non-invasive imaging reveals new cranial element of the basal ornithischian dinosaur *Laquintasaura venezuelae*, Early Jurassic of Venezuela

Imágenes no invasivas revelan nuevo elemento craneal del dinosaurio ornitisquio basal *Laquintasaura venezuelae*, Jurásico Temprano de Venezuela

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ABSTRACT

We report and describe the new left premaxillary bone of the basal ornithischian *Laquintasaura venezuelae* coming from a bonebed of the La Quinta Formation in the Andes of Venezuela. Previous dating of the bonebed based on U-Pb zircon analysis suggested an earliest Jurassic (Hettangian) maximum age. To our knowledge, for the first-time high-resolution computer tomography scanning was applied to rocks of this site to search for fossils, leading to the discovery reported here and the promise of this method to cope with unprepared blocks from the same site. We created a three-dimensional model of the fossil and show that the left premaxilla of *L. venezuelae* presents the unusual characteristic of a seven dental grooves count. This number is known only in other two basal thyreophorans such as *Huayangosaurus taibaii* and *Gargoyleosaurus parkpini*. This is consistent to the general trend reported for ornithischian evolution to lose premaxillary teeth, which suggests that *Laquintasaura* represents the plesiomorphic state of the character, with a high tooth count. Only with new anatomical data on *Laquintasaura* can we generate robust hypothesis of its evolutionary relationships, which address some of the earliest history of dinosaurs and their occurrence in the otherwise poorly documented equatorial areas of the globe.

Keywords: Andes, premaxilla, computer tomography, anatomy.

RESUMEN

Se registra y describe un nuevo hueso premaxilar izquierdo del ornitisquio basal *Laquintasaura venezuelae* proveniente de un lecho fosilífero de la Formación La Quinta en los Andes de Venezuela. La datación previa de este lecho fosilífero, basada en el análisis de circón U–Pb, sugirió una edad máxima del Jurásico temprano (Hettangiana). Por primera vez se aplicó una tomografía computarizada de alta resolución a las rocas de este sitio, lo que llevó al descubrimiento que se informa aquí, ratificando las potencialidades de este método para hacer frente a bloques no preparados y a la identificación de fósiles. Hemos creado un modelo tridimensional del fósil y mostramos que el premaxilar izquierdo de *L. venezuelae* presenta la característica inusual de un recuento de siete surcos dentales. Este número se conoce sólo en otros dos tireóforos basales, tales como *Huayangosaurus taibaii* y *Gargoyleosaurus parkpini*. Este descubrimiento es consistente con la tendencia general observada en la evolución de los ornitisquios a perder los dientes premaxilares, lo que sugiere que *Laquintasaura* representa el estado plesiomórfico del carácter, con un alto recuento de dientes. Sólo con nuevos datos anatómicos sobre *Laquintasaura* podemos generar hipótesis sólidas de sus relaciones evolutivas, que aborden parte de la historia más temprana de los dinosaurios y su aparición en las áreas ecuatoriales del mundo, mismas que de otro modo estarían mal documentadas.

Palabras clave: Andes, premaxila, tomografía computarizada, anatomía.

INTRODUCTION

Understanding the early diversification of dinosaurs benefits from new discoveries of fossils and investigations of their palaeobiology (Sereno 1999, 2010, Irmis 2011, Baron *et al*. 2017, Langer *et al*. 2010, 2017, Padian 2017, and references therein). Their fossil record suggests that this clade dates back to the Triassic (Sereno 1999, Sereno *et al*. 1993, Nesbitt & Sues 2020, Tanner *et al*. 2004), with a geographical origin in Laurasia (Baron *et al*. 2017) and/or in Gondwana (Lee *et al*. 2018). The oldest known dinosaur *Nyasasaurus parringtoni*, of an African provenance (Tanzania), supports a southern Pangaean origin (Nesbitt *et al*. 2013). The appearance of dinosaurs in the Triassic was an important event in the history of life, marking the onset of a faunal diversification that dominated worldwide terrestrial ecosystems for almost 230 Myr. (Langer *et al*. 2010, Nesbitt *et al*. 2013). The phylogenetic relations within members of the three major Dinosauria clades Theropoda, Sauropodomorpha, and Ornithischia, have been a subject of debate (Baron *et al*. 2016, 2017, Padian 2017, Langer *et al*. 2017). The early evolution of the Ornithischian clade is critical in this regard. The exclusion of *Pisanosaurus mertii* from Ornithischia (Agnolín & Rozadilla 2017, Baron *et al*. 2019) implies the absence of members of this group during the Triassic, which raises questions regarding the origin of the clade (Baron 2019). For example, Baron (2019) proposed that the solution to the gap in the fossil record of ornithischians might be solved through a reinterpretation of their phylogenetic position as being nested within Theropoda or Sauropodomorpha.

Laquintasaura venezuelae, as the earliest securely dated representative of the ornithischians (Barrett *et al*. 2014), finds itself in the middle of the debate. Previous studies suggested that at the Triassic-Jurassic boundary ecosystems near the palaeoequatorial region were inhospitable for early dinosaurs (Tanner *et al*. 2004, Irmis 2011, Ezcurra 2010). Nevertheless, the geographic location where *L. venezuelae* was found challenged this idea (Barrett *et al*. 2014), being congruent with the hypothesis that the earliest diverging ornithischian lineages (e.g., heterodontosaurids, *Laquintasaura* and *Lesothosaurus*) occurred in Gondwanan (Lee *et al*. 2018). The phylogenetic position of *L. venezuelae* falls in a polytomy at the base of the ornithischian tree according to Barrett *et al*. (2014), more recently resolved to a higher definition at the base of the Thyreophora group, as a sister taxon to *Scutellosaurus* (Baron *et al*. 2016, Raven & Maidment 2017). Presence of premaxillary teeth, convergently reduced in many derived forms of the inner clades, is consistent with a basal position of *Laquintasaura* on the ornithischian tree of life (Nabavizadeh & Weishampel 2016). Details of premaxillary anatomy would further provide relevant anatomical information.

Here we describe a new premaxillary bone attributable to *L. venezuelae*, which comes from a sandy siltstone block collected in 1993, housed in the collection of the University of Zulia (Maracaibo, Venezuela). For the first time CT scan and a 3D model was carried out in remains of the *L. venezuelae*. The presence of recognizable apomorphies sheds new light on the anatomy of *L. venezuelae*, and its potential significance in understanding its phylogenetic position.

MATERIALS AND METHODS

Referred material

The new premaxillary bone MBLUZ P-4882 described herein, and other hundreds of new postcranial elements (currently under study), including all the specimens referred in Barrett *et al*. (2008, 2014), come from a sandy siltstone block collected by MRSV and collaborators in December 1993 from a single bonebed (see below section) of the La Quinta Fm. (Fig. 1). The specimens reported here are housed at the Museo de Biología de la Universidad del Zulia (MBLUZ P-). Thanks to the permissions issued by the authorities of the MBLUZ, and the Instituto del Patrimonio Cultural de Venezuela (IPC, certificates N° 002/15, and 071/15), rock blocks were brought on loan to the University of Zurich (Switzerland) for preparation and study. The fossil preparation ended in 2017, and it resulted in abundant disarticulated skeletal remains, most of them still embedded in the block matrix. This is the case of the premaxillary bone MBLUZ P-4882, which we have scanned using a Nikon XT H 225 ST at the University of Zurich. A 3D model of the maxillary bone was performed using the image segmentation software Mimics (Materialise NV, Leuven, Belgium, 1992-2015). Due to the lack of contrast between the bones and the surrounding sediment, the segmentation was performed layer by layer, differentiating the bone from the matrix by hand.

Geological settings and the "bonebed findings"

The La Quinta Formation consists mainly of continental red beds and volcanic rocks that where deposited in a series of restricted tectonic basins associated with the breakup of Pangaea during the early Mesozoic and in the Andes of Venezuela (Schubert *et al*. 1979, Maze 1984, Schubert 1986). The dinosaur bonebed is located on the right bank of the Río La Grita, near the Sector Llano de Cura, close to a road cut between the towns of La Grita and

Figure 1. The La Quinta Fm. bonebed and its geographical location. **a)** Location map. **b-c**). Outcrop of the bonebed. In the picture (**c**), Marco Badaracco, Cathy Villalba and Sylvia Lim in the bonebed in 1993 (photo by MRSV).

Seboruco, Táchira state (Fig. 1). This bonebed is characterized by a medium to poorly sorted sandy siltstone with angular to sub-angular clast and pebbles (Moody 1997). The bonebed section is located directly opposite the type section of the La Quinta Fm. (Schubert *et al*. 1979, Schubert 1986), possibly separated by one or more faults (Russell *et al*. 1992, Moody 1997, Barrett *et al*. 2008). Because of this faulting, precise stratigraphic placement of the bonebed has been difficult, with interpretations ranging likely from the middle to upper portion of the La Quinta Fm. (Barrett *et al*. 2008). Dating based on U-Pb zircon analysis suggests an earliest Jurassic (Hettangian) maximum age for the bonebed (Barrett *et al*. 2014, Langer *et al*. 2014).

A couple of French paleontologists discovered the bonebed and first dinosaur remains from Venezuela in the 1980s. These specimens were originally attributed to *Lesothosaurus* sp. based on the similarities of few cranial elements (Russell *et al*. 1992). These first remains where represented by a premaxillary and a maxillary tooth, and a left quadrate bone fragment (Russell *et al*. 1992, fig. 4). For many years these remains described by Russell *et al*. (1992) were housed in Paris, and in the late 1990s under the co-

ordination MRSV, all the specimens returned to Venezuela and were deposited the at the Museo de Biología de la Universidad del Zulia (MBLUZ) (see acknowledgments section in Barrett *et al*., 2008). Oblivious to the previous work by the French team, and due to the potentialities of the La Quinta Fm., MRSV carried out a reconnaissance trip in 1989 to locate vertebrate material visiting the type section of this unit together with the Venezuelan geologist Oscar Odreman, whom he had met at the Latinamerican herpetological congress that took place in Mérida that year. Vertebrate fossils could not be found. Posteriorly in 1992 and 1993, MSRV organized three expeditions (Sánchez-Villagra & Clark 1994). The first in early 1992 resulted in the relocation of the bonebed first discovered by the French team, thanks to the good eye and expertise of James Clark, a dinosaur expert who visited Venezuela and recognized fossils where Marcelo Sánchez would have not. They collected some plaster jackets, one of which was transported by Marcelo Sánchez to Buenos Aires to learn and conduct preparation of it there, under the kind supervision of Dr. Guillermo Rougier and his team; there first contacts with Fernando Novas were made. Work during three months resulted in different blocks with exposed fossils that were transported back to Venezuela, to the Laboratorio de Paleobiología of Omar Linares at the Universidad Simón Bolívar (USB-PB), where Sánchez-Villagra had conducted his Licenciatura thesis. These fossils housed have remained since then without being studied to our knowledge. Another trip was coordinated by MRSV in the company of Omar Linares from the Universidad Simón Bolívar, which ended up a failed attempt to reach La Quinta outcrops, as in the middle of the way to Táchira from Caracas the car loaned by MRSV' father broke down (total loss, see acknowledgments section in Barrett *et al*. 2008). Before starting doctoral studies in the USA, MRSV learned that he could not have access to the materials he had collected and prepared in Buenos Aires before (housed in the Universidad Simón Bolívar), and given the commitment to SVP and the need to report to them, he had to coordinate a whole new expedition. In the December 1993, MRSV invited Marco Tulio Badaracco, Cathy Villalba and her US-American friend Sylvia Lim to travel from Caracas to Táchira. This team collected abundant rock blocks from the fossiliferous bonebed (Fig. 1b-c), which were deposited in the MBLUZ, in coordination with John Moody. Preparation anew of fossils from one of the blocks resulted in the report at SVP by Sánchez-Villagra and Clark (1994). The premaxillary bone MBLUZ P-4882 described herein, all the specimens described in Sánchez-Villagra and Clark (1994), Barrett *et al*. (2008, 2014), and Barrett and Sánchez-Villagra (2012), as well as hundreds of new specimens under study, come from this 1993 expedition, which includes to-date still unprepared blocks in the MBLUZ collections. In 2000, Fernando Novas and MRSV obtained a grant from the Jurassic Foundation to study the materials in Maracaibo, which was started with a visit by Fernando Novas to the collection in LUZ. Eventually, this project could be brought to completion in 2008 with the publication led by Paul Barrett from the Natural History Museum in London, where MRSV was based when the project was reactivated in 2005 (Barrett *et al*. 2008). Further studies led to the description of *Laquintasaura* in 2014 by Barrett *et al*.

In 1994, John Moody from MBLUZ led an expedition to La Quinta Fm. that resulted in the collection of abundant rock blocks from the bonebed section, which led to the first report of an indeterminate theropod dinosaur in the unit (Moody 1996, 1997). Additional theropod materials (a partial femur and two partial teeth) from the La Quinta type locality, were also collected in 1996 by geologists of the Instituto Universitario de Tecnología de Maracaibo (IUTM). These specimens were loaned and prepared by John Moody in MBLUZ, and posteriorly returned to the collections of the IUTM (Moody, personal communication). Posteriorly, Langer *et al*. (2014) described the theropod *Tachiraptor admirabilis* based on specimens coming also from the bonebed.

The only remain of dinosaurs in Venezuela that has not been collected in the bonebed or in the type locality of the La Quinta Fm. is a leg bone fragment been attributed to a dinosaur of big size (see Sachs 1991); although the remain was considered not diagnostic enough to explain in more detail its phylogenetic position. This specimen was collected by the geologist Oscar Odreman in the surrounding of the La Fundación town (Táchira state), in an outcrop of the La Quinta Fm. (Sachs 1991); however, no other precise stratigraphic a location information exist about. The fossil was donated by Odreman to MSRV, who deposited it in 1992 in the Universidad Simón Bolívar, Laboratorio de Paleobiología (USB-PB).

TAXONOMIC DESCRIPTION

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
Laquintasaura venezuelae Barrett *et al*., 2014

Description and remarks

The specimen MBLUZ P-4882 (Fig. 2b-g) corresponds to a left premaxilla of approximately 38 mm in length (from the anterior most part of the bone until the posterolateral process), attached to the vomer, which is

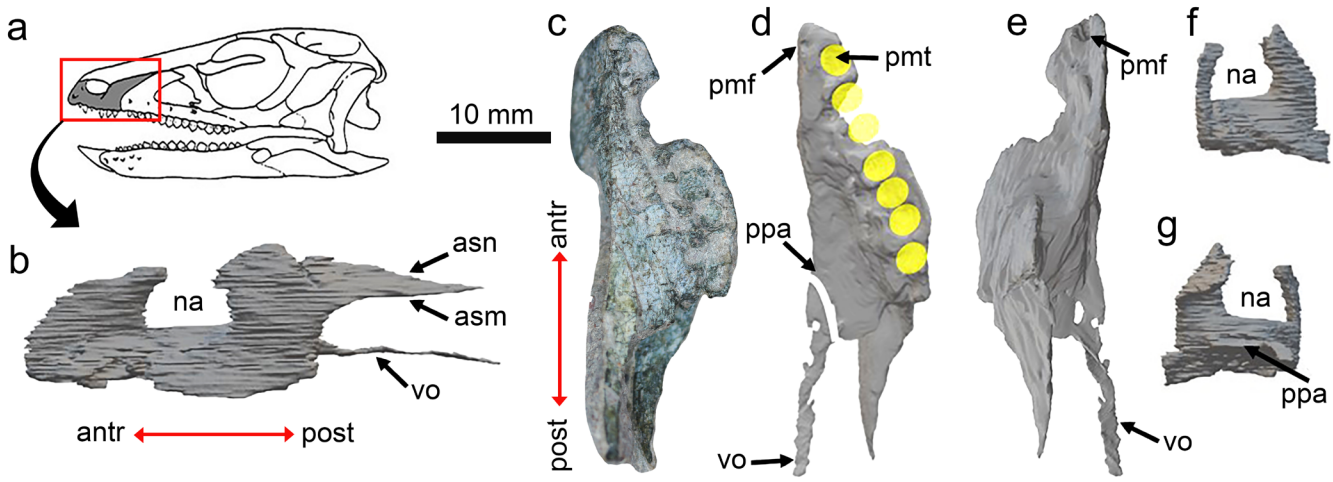

Figure 2. a-g) Original (**c**) and 3D model (**b, d-g**) of the left premaxilla MBLUZ P-4882 of *Laquintasaura venezuelae*. Drawing of skull (**a**) based on *Lesothosaurus*, and modified after Crompton & Attride (1986). Abbreviations: antr (anterior), asm (articular surface of the maxilla), asn (articular surface of the nasal), na (nares), ppa (premaxillary palate), pmf (premaxillary foramen), pmt (premaxillary teeth grooves), post (posterior), vo (vomer). Views: anterior (**f**), dorsal (**e**), left lateral (**b**), posterior (**g**), ventral (**c-d**).

dorsoventrally flattened and anteroposteriorly elongated, attached to the premaxilla by a diagonal suture. MBLUZ P-4882 is still embedded in the block matrix, and it is only observable in ventral view (Fig. 2c). The rostral premaxillary border is rugose in the midline, a characteristic that is diagnostic of Ornithischia (Weishampel *et al*. 2007). A premaxillary foramen is present, perforating the premaxilla from the ventral surface, anterior to the first premaxillary tooth alveoli, to the dorsal surface, anterior most part of the bone (Fig. 2d-e). The external naris size is small and entirely overlying the premaxilla, as opposed to nares extending over the maxilla. The posterolateral process of the premaxilla contacts only with the nasal and maxilla. The premaxillary palate is horizontal and connected to the vomer by a diagonal suture. As in other ornithischians, it is flat and extends caudally passed the last premaxillary tooth. No signs of a fossa-like depression positioned on the premaxilla-maxilla boundary is found.

Seven dental grooves are well preserved in MBLUZ P-4882 (Fig. 2c-d). This figure contrasts with that of other basal ornithischians, which are characterized by fewer teeth, for example five in *Scelidosaurus* (Norman 2020) and *Emausaurus* (Weishampel *et al*. 2007), six in *Lesothosaurus* (Sereno 2010, Porro *et al*. 2015) and *Scutellosaurus* (Weishampel *et al*. 2007). Only the basal stegosaurid *Huayangosaurus taibaii* from the Middle Jurassic, and the ankylosaurid *Gargoyleosaurus parkpini* from the Upper Jurassic are found to have a premaxillary tooth count of seven (Sereno & Zhimin 1992, Carpenter *et al*. 1998). The prosauropod *Plateosaurus* is reported to have four or five premaxillary teeth (Prieto-Márquez & Norell 2011), and none of the silesaurids are observed to have more than four premaxillary teeth (Müller & García 2020). In MBLUZ P-4882, the first premaxillary tooth is positioned adjacent to the symphysis (Fig. 2d).

DISCUSSION AND CONCLUSIONS

Premaxillary dentition is a trait commonly observed in basal thyreophorans (Nabavizadeh & Weishampel 2016). The common number of teeth observed in this group is five or six, as seen in basal ornithischians *Scelidosaurus harrisonii* (Norman 2020), *Emausaurus* (Weishampel *et al*. 2007), *Lesothosaurus diagnosticus* (Sereno 2010, Porro *et al*. 2015), and *Scutellosaurus* (Weishampel *et al*. 2007). Given the phylogenetic position of *Laquintasaura* at the base of the thyreophoran tree, it is of interest to understand how the premaxillary tooth count evolved in the group. The premaxillary dentition is also present in the basal stegosaur *Huayangosaurus taibaii* (tooth count seven) (Sereno & Zhimin 1992), and nodosaurids such as *Silvisaurus* (tooth count eight or nine) (Eaton 1960), *Pawpawsaurus* (tooth count six) (Lee 2010), *Gargoyleosaurus parkpini* (tooth count seven) (Carpenter *et al*. 1998, Kilbourne *et al*. 2005), *Tatankacephalus cooneyorum* (Parsons & Parsons 2009) and *Sauropelta* (Lee 2010). In contrast, other derived nodosaurids such as *Edmontonia, Panoplosaurus*, and ankylosaurids lack premaxillary teeth (Lee 2010, Nabavizadeh & Weishampel 2016). The same is true for *Stegosaurus* and other derived stegosaurids (Sereno & Zhimin 2010, Nabavizadeh & Weishampel 2016).

In ornithischians the premaxillary dentition has been convergently lost in the derived taxa in each subclade. This has been attributed either to the development of an elongate diastema in some groups, or to the development of a much broader oral margin of the premaxilla with a denticulate edge of its own (Nabavizadeh & Weishampel 2016). The information provided by the study of MBLUZ P-4882 suggests that *L. venezuelae* presents the plesiomorphic characteristic of a high premaxillary tooth count (7), coherent with the narrow oral margin and lack of premaxillary-maxillary diastema. This makes *Laquintasaura* the oldest genus to have this characteristic, which, given its position at the base of the Thyreophora clade, implies that this is the plesiomorphic state from which the lesser premaxillary tooth count of evolved. This morphological trend may relate to the evolution of new feeding mechanisms (Nabavizadeh & Weishampel 2016).

The bonebed of the La Quinta Fm. offers to date the only known dinosaur remains from the earliest Jurassic of the region. Despite the disarticulated nature of the remains and the granularity of the sandy sediments where those are embedded, some bones have been preserved, including some fragile structures, such as the vomer found in the premaxilla of MBLUZ P-4882. These remains are of interest to understand the evolution of early dinosaurs. As described, the presence of the seven-tooth count on the premaxilla is congruent with other discoveries that indicate that the presence of premaxillary teeth is common among basal ornithischians (Nabavizadeh & Weishampel 2016). Knowledge of the general morphology of a dinosaur as *L. venezuelae* helps understanding the early evolution and diversification of ornithischian and offers another data point with which to analyse the history of the group.

From the La Quinta Fm. bonebed, two dinosaur species have been named, *Laquintasaura venezuelae* (Barrett *et al*. 2014), and the small theropod *Tachirraptor admirabilis* (Langer *et al*. 2014). The remains attributable to *L. venezuelae* are abundant in the bonebed, especially postcranial elements. Barrett *et al*. (2008, 2014) referred few cranial bones of la *L. venezuelae*. Among these a right premaxilla (MBLUZ P-5014) missing all teeth was mentioned but not described or illustrated (Barrett *et al*. 2014, electronic supplementary material). The left premaxilla MBLUZ P-4882 (Fig. 2b-g) described herein sheds new light on the anatomy of the Venezuelan basal ornithischian.

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