



Taphonomic attributes of the holotype of the lambeosaurine dinosaur *Latirhinus uitstlani* from the late Campanian of Mexico: Implications for its phylogenetic systematics

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ABSTRACT

Latirhinus uitstlani represents one of the most emblematic dinosaurs from Mexico. This hadrosaurid, originally described as a member of the Saurolophinae by Prieto-Márquez and Serrano-Brañas in 2012, was re-evaluated as a lambeosaurine by Ramírez-Velasco et al. (2021). In addition, these authors stated that the description of the 2012 holotype was based on a chimeric skeleton and designated a new holotype (a different concept for the composition of essentially the same individual). The composition of their 2021 holotype was based on the size, association and similar mode of preservation of the bones within the quarry. Notably, no details were provided regarding such mode of preservation. However, the fact that the type locality of *L. uitstlani* is an attritional bonebed where other similar-sized individuals were also present calls into question the criteria used by Ramírez-Velasco et al. (2021) in the composition of their holotype. We address this shortcoming by describing the taphonomic signature of the skeletal elements in the *L. uitstlani* holotype of Ramírez-Velasco et al. (2021), as well as that of other bones discussed collected from this species' type locality and other sites of the late Campanian Cerro del Pueblo Formation. Our observations show different taphonomic attributes among the bones of the 2021 holotype, indicating that it is likely a chimera of different specimens. Such taphonomic attributes support a holotype for *L. uitstlani* consisting of the original elements listed in Prieto-Márquez and Serrano-Brañas (2012), with exclusion of the IGM 12712 jugal and a right scapula. We concur in that IGM 12712 is actually a fragmentary jugal, which represents an unusually large hadrosaurid specimen. We also tested the referral of *L. uitstlani* to Lambeosaurinae via a cladistic parsimony analysis that confirmed that this specimen belongs to that major clade of hadrosaurids; however, its relationships with other lambeosaurines remain unresolved. Finally, we re-evaluated the diagnostic utility of the characters used by Ramírez-Velasco et al. (2021) for referring other specimens to different hadrosaurid clades, concluding that several of them can only be referred to Hadrosauridae indeterminate.

1. Introduction

In 1988, a team of paleontologists from the Instituto de Geología of the UNAM led by Luis Espinosa-Arrubarrena, René Hernández-Rivera and Shelton P. Applegate discovered, collected and assembled the remains of a hadrosaurid dinosaur from the late Campanian Cerro del Pueblo Formation, Coahuila, northern Mexico. Nearly a quarter-century later, Prieto-Márquez and Serrano-Brañas (2012) described many of these remains and erected a new taxon for this animal, *Latirhinus uitstlani*, based on a holotype (IGM 6583) that they referred to

Saurolophinae. Recently, Ramírez-Velasco et al. (2021) presented a revised description and taxonomy of *L. uitstlani*. These authors stated that the holotype described by Prieto-Márquez and Serrano-Brañas (2012; henceforth the 2012 holotype) is a chimera consisting of six different hadrosaurids (Ramírez-Velasco et al., 2021: Fig. 2). Furthermore, they concluded that this species is actually a member of Lambeosaurinae.

The thorough revisionary work by Ramírez-Velasco et al. (2021) contributed to clarify the systematics of *Latirhinus uitstlani*, adding value to the documentation of its anatomy. However, these authors did not

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consider in their study the taphonomic attributes of the bones. Here we address this shortcoming by documenting the taphonomic signature of the skeletal elements in the holotype of *L. uistlani* presented by Ramírez-Velasco et al. (2021; henceforth the 2021 holotype), as well as that of other bones discussed in that study collected from the *L. uistlani* type locality and other sites of late Campanian Cerro del Pueblo Formation cropping out in the state of Coahuila. We then use this data to re-evaluate the skeletal composition of the holotype of *L. uistlani*; we also discuss the diagnostic utility of the characters used by Ramírez-Velasco et al. (2021) for referring several specimens to various hadrosaurid clades, and test the referral of *L. uistlani* to Lambeosaurinae via a cladistic parsimony analysis. Finally, we address an aspect that was overlooked in Ramírez-Velasco et al. (2021), the gigantism likely achieved by one of the specimens in the bone assemblage.

Institutional abbreviations. AMNH FARB, American Museum of Natural History, Fossil Amphibian, Reptile and Bird collection, New York City, New York, USA. CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada. Coah, field numbers from uncatalogued materials collected in various localities (including the type locality of *Latirhinus uistlani*) of the Cerro del Pueblo Formation, state of Coahuila, northern México. IGM, Colección Nacional de Paleontología, Instituto de Geología, UNAM, México City, México. LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA. MOR, Museum of the Rockies, Bozeman, Montana, USA. ROM, Royal Ontario Museum, Toronto, Ontario, Canada. UNAM, Universidad Nacional Autónoma de México, México City, México. UTEP, Centennial Museum at the University of Texas El Paso, Texas, USA.

2. Taphonomic documentation of the 2021 holotype of *Latirhinus uistlani* and other hadrosaurid specimens from the cerro del Pueblo Formation

Bone modification features provide valuable information regarding the taphonomic history of a fossil site, aiding in deciphering the different types of physical, chemical and biological processes affecting a fossil assemblage (Binford, 1981; Shipman, 1981; Fiorillo, 1991). Here, we describe the distinct taphonomic imprints on the bones that were collected at the SPA-88-9 quarry, particularly in relation to the skeletal composition of the 2021 holotype of *L. uistlani*. Because no taphonomic data have been released for the SPA-88-9 quarry since its discovery (such as bonebed area, spatial density, spatial arrangement, sample size, relative abundance of the elements, etc.), a full taphonomic study (Behrensmeyer, 1991; Eberth et al., 2007; Blob and Badgley, 2007) cannot be conducted yet. Still, some taphonomic attributes of the bones can be directly described and measured, revealing to some extent the modifications that these remains experienced during the genesis of the site, informing on which elements belong to which individual at the SPA 88-9 quarry. The latter is based on two premises: 1) if the bones of the 2021 holotype of *L. uistlani* belong to the same individual, they must have similar taphonomic attributes; and 2) the taphonomic attributes of such holotype should differ from those of the other hadrosaurids collected from the same quarry.

2.1. Bone assemblage data

2.1.1. Number of individuals

Based on the previous work by Serrano-Brañas (2006), who examined the skeletal remains of the different hadrosaurids collected from this quarry, it was possible to determine a total number of 61 identifiable bones that had been previously prepared since 1988 (Table 1). Within these elements are the remains of the 2012 holotype of *Latirhinus uistlani*, as well as the elements from the scapular and pelvic girdle described by Ramírez-Velasco et al. (2021). It is important to highlight that part of the most fragmentary bones that were originally collected within the SPA-88-9 quarry still need to be prepared (Ramírez-Velasco et al., 2021), so this material was not included in our analysis. If one

follows the conclusions of Ramírez-Velasco et al. (2021), there is a minimum of seven individuals in this quarry (IGM 6583, IGM 12712, IGM 12713, IGM 12714, Coah 14-1/2, Coah 14-1/4 and Coah 14-1/5). However, our present study considers IGM 6583, IGM 12713 and IGM 12714 as part of the same individual, resulting in a minimum number of individuals represented by these specimens of only five.

2.1.2. Body size

Ramírez-Velasco and collaborators provided several measurements of the skeletal remains of their holotype of *Latirhinus uistlani* estimating that this hadrosaurid was 8.72 m in length (see supplemental information in Ramírez-Velasco et al., 2021). Although no complete skeletons were recovered, it is possible to compare the length of different bones from individuals not belonging to IGM 6583 with the ones of other hadrosaurids previously published elsewhere (including 2021 holotype of *L. uistlani*) in order to have some clues about their possible body size. For example, the length of the distal ventral expansions of the two other ischia preserved in the SPA-88-9 quarry show that they are similar in size to the ones in the 2021 holotype: these processes in the ischia assigned to the 2021 holotype have a length of 195 mm for the right ischium (Fig. 1a) and 203 mm for the left ischium (Fig. 1b), whereas in Coah 14-1/4 (right ischium; Fig. 1c) and Coah 14-1/5 (left ischium; Fig. 1d) they are 198 mm and 205 mm in length, respectively. These measurements indicate that they are consistent in size with large lambeosaurine individuals (e.g. Lull and Wright, 1942; Prieto-Márquez et al., 2012; Godefroit et al., 2003; Ramírez-Velasco et al., 2021). Also, Ramírez-Velasco et al. (2021) referred IGM 12712 (right jugal), IGM 12713 (dorsal vertebrae) and IGM 12714 (left and right metatarsi and phalanges) to large saurolophine hadrosaurids due to their relative size (see supplemental information in Ramírez-Velasco et al., 2021). Finally, the length of Coah 14-1/2 (230 mm) indicates that this dentary belongs to a much smaller hadrosaurid (e.g., compared to the dentary of the large saurolophine PASAC-1 (680 mm, also collected in the state of Coahuila, Mexico; Kirkland et al., 2006). Therefore, most of the identified hadrosaurids in the SPA-88-9 quarry correspond to large individuals, with the exception of Coah 14-1/2.

2.1.3. Degree of bone disarticulation

According to Luis Espinosa-Arrubarrena et al. (1989), who participated in the original excavation of *Latirhinus uistlani* in 1988, the SPA-88-9 quarry was the closest thing to a “bone junkyard”, a place where all the disarticulated skeletal remains of the hadrosaurids preserved in this quarry were dragged and deposited by a fluvial system. This description of the quarry possibly allows for disassociation not to be ubiquitous, which is compatible with the varying taphonomic histories of the individuals in it. Ramírez-Velasco et al. (2021) stated that the remains of *L. uistlani* were found associated in the same spot within the SPA-88-9 quarry, which is also possible, as the elements of a skeleton may be disarticulated, but still associated.

2.1.4. Skeletal parts (Voorhies Groups)

We evaluated the skeletal representation or bone frequency in the SPA-88-9 quarry, using Voorhies groups, which is fundamental for recognizing sorting processes on the thanatocoenosis (Voorhies, 1969; Behrensmeyer, 1991). The observed value of this taphonomic attribute for the SPA-88-9 quarry compared to the theoretical value (THV) of Voorhies grouping of a complete hadrosaurid skeleton (sensu Horner et al., 2004 and Bell and Campione, 2014), shows a slightly higher percentage of bones pertaining to Voorhies Group I (52.46%), although Voorhies groups II (44.26%) and III (3.28%) are also represented (Fig. 2 and Table 2). In addition, the maximum lengths of all 61 bones range from 81 to 1030 mm.

2.2. Bone modification

We evaluate bone modification through the different stages of

Table 1

Taphonomic attributes of the identified bones from the SPA-88-9 quarry. Abbreviations: Complete bones (CO), incomplete bones (IN), not applicable (NA), number of identifiable bones (NISP), partially complete bones (PC), and bones to which the criterion of 'most advance stage covering more than 1 cm² was applied (*).

TYPE OF BONE	SIDE	NISP	Weathering	Abrasion	Breakage	Scoring Marks
Jugal (IGM 12712)	Right	1	3	1	IN	Absent
Dentary (Coah 14-1/2)	Right	1	2*	1	PC	Absent
Thoracic Vertebrae (IGM 12713)	NA	10	3*	0	PC	Absent
Caudal Vertebrae (IGM 6583)	NA	14	3*	0	PC	Absent
Coracoid (IGM 6583)	Left	1	3	0	PC	Absent
Scapula (IGM 6583)	Left	1	3	0	IN	Absent
Scapula (IGM 6583)	Right	1	0	1	IN	Absent
Humerus (IGM 6583)	Right	1	3	0	CO	Absent
Humerus (IGM 6583)	Left	1	3*	0	CO	Absent
Ulna (IGM 6583)	Right	1	3	0	CO	Absent
Ulna (IGM 6583)	Left	1	3	0	PC	Absent
Metacarpal III (IGM 6583)	Right	1	3	0	CO	Absent
Metacarpal IV (IGM 6583)	Right	1	3	0	CO	Absent
Manual Ungual (IGM 6583)	Right	1	3	0	CO	Absent
Ilium (Pecacetabular Process; IGM 6583)	Left	1	3*	0	IN	Absent
Ilium (Body; IGM 6583)	Left	1	0	1	IN	Absent
Ilium (Body; IGM 6583)	Right	2	0	1	IN	Present
Ilium (Postacetabular Process; IGM 6583)	Right	1	0	1	IN	Present
Ischium (Shaft; IGM 6583)	Right	1	0	1	PC	Absent
Ischium (Shaft; IGM 6583)	Left	1	0	1	IN	Absent
Ischium (Distal process; IGM 6583)	Right	1	0	1	IN	Present
Ischium (Distal process; IGM 6583)	Left	1	0	1	IN	Present
Ischium (Distal process; Coah14/1-4)	Right	1	0	1	IN	Present
Ischium (Distal process; Coah 14/1-5)	Left	1	0	1	IN	Present
Femur (IGM 6583)	Right	1	3	0	CO	Absent
Femur (IGM 6583)	Left	1	3*	0	CO	Absent
Tibia (IGM 6583)	Right	1	3	0	CO	Absent
Tibia (IGM 6583)	Left	1	3*	0	CO	Absent
Fibula (IGM 6583)	Right	1	3	0	IN	Absent
Fibula (IGM 6583)	Left	1	3*	0	CO	Absent
Astragalus (IGM 6583)	Left	1	3	0	CO	Absent
Metatarsal III (IGM 12714)	Right	1	3	0	CO	Absent
Metatarsal III (IGM 12714)	Left	1	3	0	PC	Absent
Metatarsal IV (IGM 12714)	Right	1	3	0	CO	Absent
Metatarsal IV (IGM 12714)	Left	1	3	0	CO	Absent
Phalanx II-1 (IGM 12714)	Left	1	3	0	CO	Absent
Phalanx III-1 (IGM 12714)	Right	1	3	0	CO	Absent
Phalanx III-1 (IGM 12714)	Left	1	3	0	CO	Absent

Total number of specimens = 61.

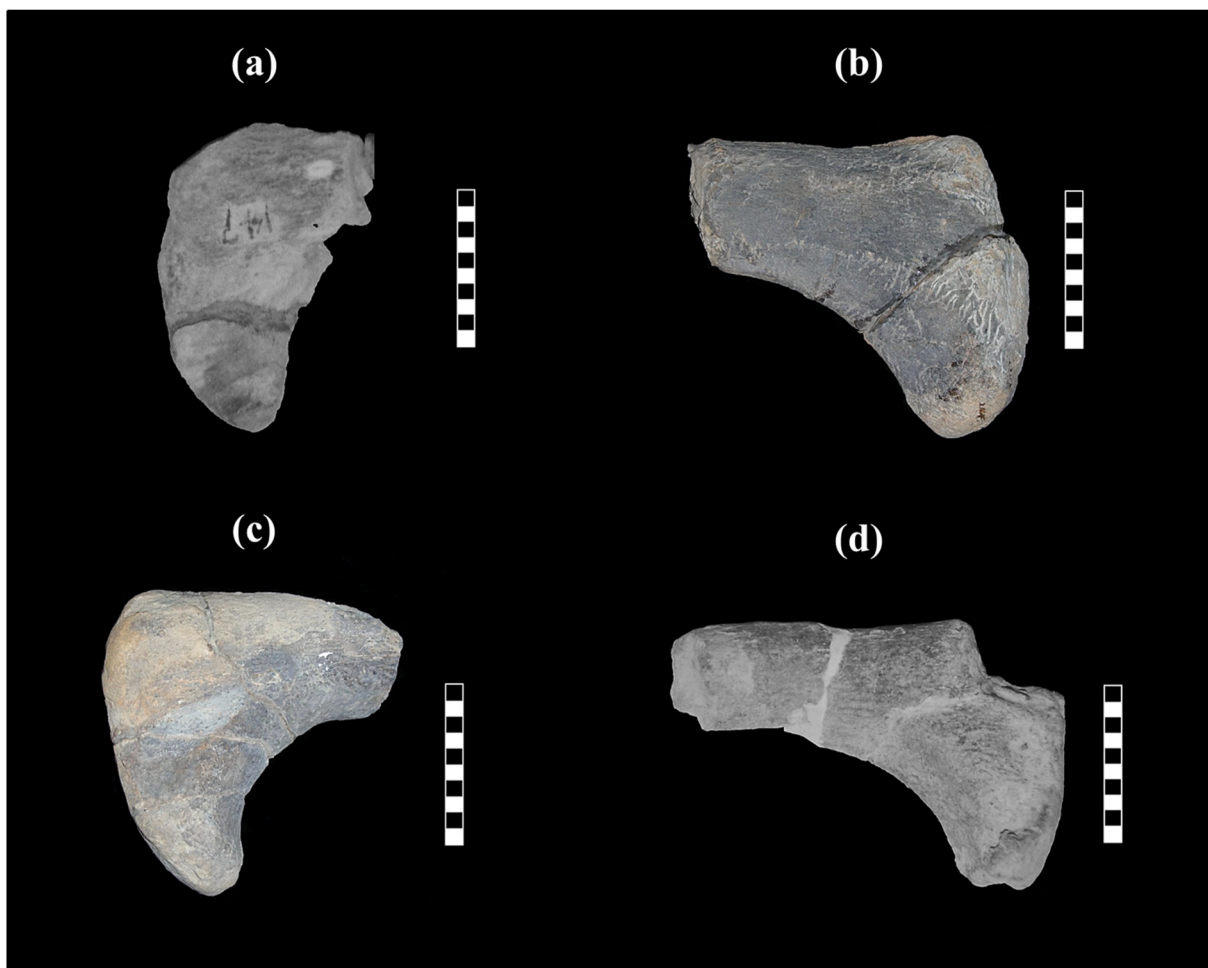


Fig. 1. Ischiadic distal processes from the lambeosaurine hadrosaurids collected from the SPA-88-9 quarry: (a) IGM 6583, right distal process; (b) IGM 6583, left distal process; (c) Coah 14-1/4, right distal process; (d) Coah 14-1/5, left distal process. Scale bar = 10 cm.

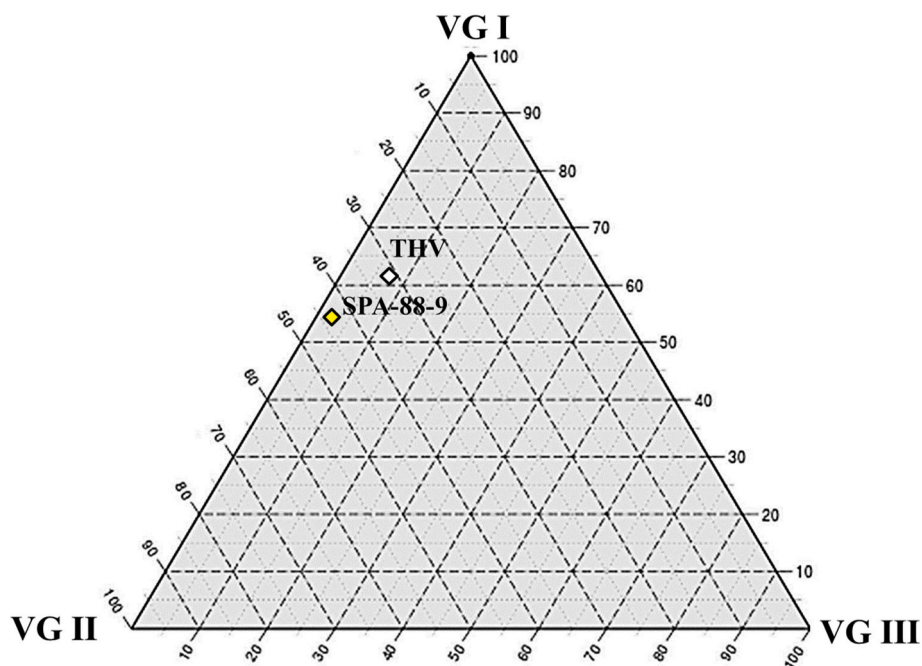


Fig. 2. Ternary diagram of Voorhies group distribution of the skeletal elements from the SPA-88-9 quarry calculated from Table 1, compared with the theoretical value of a complete hadrosaurid skeleton. Abbreviations: THV: theoretical value; VG: Voorhies groups.

Table 2

Bone frequency of all recognizable bones from the SPA-88-9 bonebed measured using Voorhies (1969) Groups.

Voorhies Group I	No.	Voorhies Group II	No.	Voorhies Group III	No.
Dorsal Vertebrae	10	Coracoids	1	Jugal	1
Caudal Vertebrae	14	Humeri	2	Dentary	1
Ulnae	2	Pelvis	11		
Scapulae	2	Femora	2		
Phalanges	4	Tibiae	2		
		Fibulae	2		
		Astragali	1		
		Metapodials	6		
Total	32		27		2
Percent Assemblage	52.46%		44.26%		3.28%

breakage, abrasion, weathering, and scoring marks on bone surface (i.e., trampling marks) for all 61 bones from the SPA-88-9 quarry, according to the methodologies proposed by Behrensmeyer (1978), Myers et al. (1980), Shipman (1981), Fiorillo (1988, 1991) and Bell and Campione (2014). A summary of these results is shown in Table 1.

2.2.1. Breakage

The SPA-88-9 quarry produced complete, partially complete and identifiable fragmented bones. Of these, complete elements represent 29.51% of the total bones collected. Partial and identifiable fragmented

bones correspond to the 47.54% and 22.95%, respectively. In particular, complete elements are represented by left and right humeri, right ulna, right metacarpals III and IV, left and right femora and tibiae, left fibula, left astragalus, right metatarsal III, both left and right metatarsi IV and all phalanges (Table 1). Partial bones correspond to the right dentary, dorsal and caudal vertebrae, left coracoid, left ulna, right ischium shaft, and left metatarsal III (Table 1). Finally, identifiable fragmented bones are represented by the right jugal, scapulae, the preacetabular process of the left ilium, fragments of the left and right iliac bodies, shaft of the left ischium, the postacetabular process of the right ilium, two left and two right ischia distal processes and the right fibula (Table 1). Transverse fractures in the majority of the bones suggest that breakage occurred after the alteration of the original bone material during the taphocoenosis (e.g. Fig. 3a, b, c and d) (Myers et al., 1980; Shipman, 1981; Fiorillo, 1988; Araújo-Junior and Marinho, 2013).

2.2.2. Abrasion

78.69% of the elements from the SPA-88-9 quarry do not show any sign of abrasion, corresponding to rank 0 (bone edges and processes still sharp and well defined; see Fiorillo, 1988) (Fig. 3a and b; Table 1). Only the right jugal (IGM 12712), right dentary (uncatalogued; field designation Coah 14-1/2), right scapula (Ramírez-Velasco et al., 2021: Fig. 4C-E) and elements of the pelvic girdle (with the exception of the left preacetabular process; Fig. 3c-f) are slightly abraded, corresponding to rank 1 (some edges and processes of the bones are slightly rounded or polished; see Fiorillo (1988)); these elements represent 21.31% of the sample (Table 1).

2.2.3. Weathering

80.33% of the studied bones from the SPA-88-9 quarry are

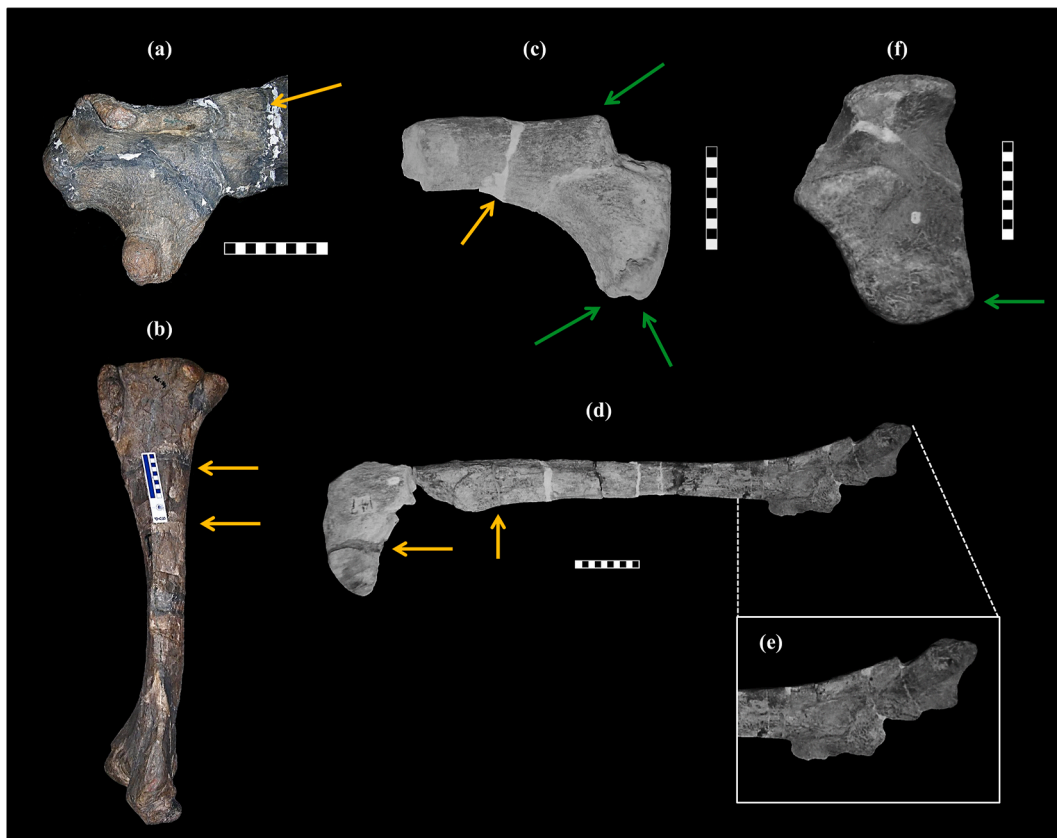


Fig. 3. Examples of breakage and abrasion attributes found in different bones from the SPA-88-9 quarry. Non-abraded bones are (a) left scapula (IGM 6583) and (b) left tibia (IGM 6583). Slightly abraded bones are (c) distal process of a left ischium (Coah 14-1/5), (d) right ischium (IGM 6583), (e) cranial end of the right ischium (IGM 6583), and (f) fragment of a right iliac body (IGM 6583). Green arrows indicate abraded surfaces and yellow arrows show transversal fractures on the bones. Scale bar = 10 cm.

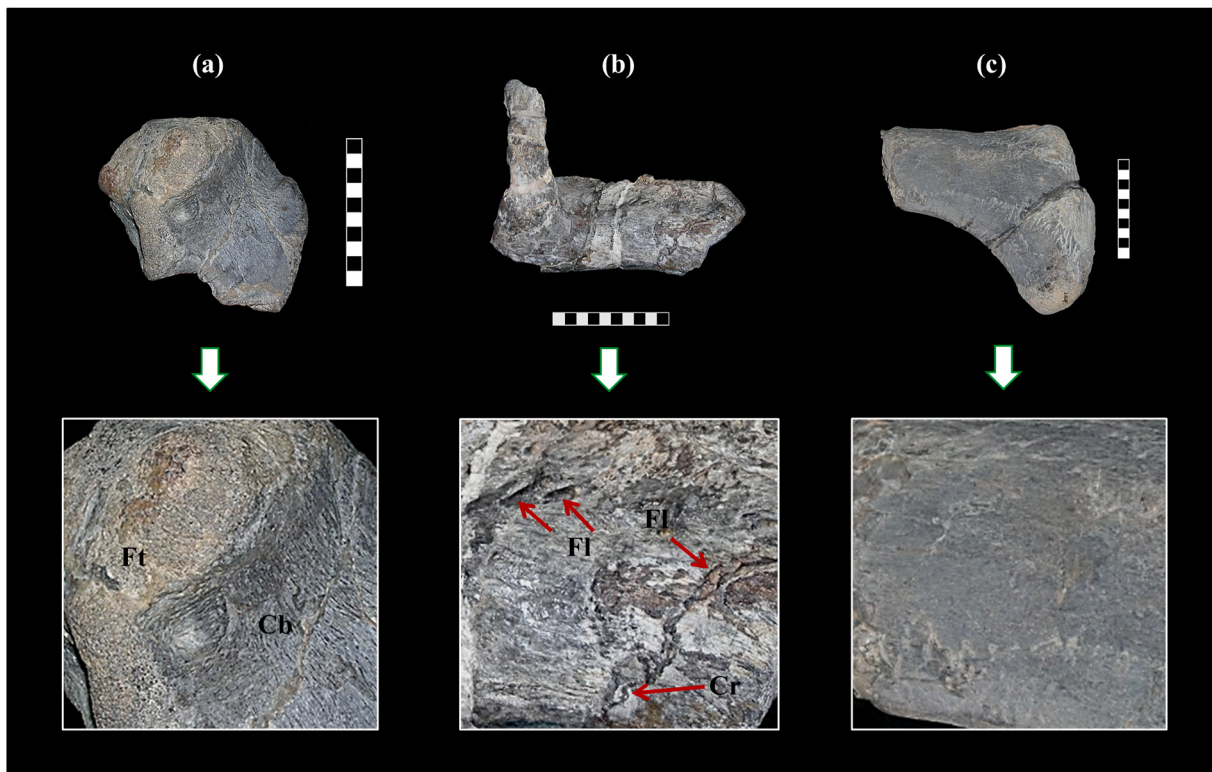


Fig. 4. Weathering stages found in various elements from the SPA-88-9 quarry: (a) weathered (rank 3) left coracoid, IGM 6583, in lateral view]; (b) slightly weathered (rank 2) right dentary, Coahuila 14-1/2, in lateral view]; (c) non-weathered (rank 0) distal process of left ischium, IGM 6583, in lateral view. Abbreviations: Fibrous texture (Ft), cortical bone (Cb), flacking (Fl), crack (Cr). Scale bar = 10 cm.

weathered according to rank 3 (bone surface characterized by the presence of patches of rough and homogeneously weathered compact bone resulting in a fibrous texture, with bone fibers being still firmly attached to each other) (Behrensmeier, 1978; Fiorillo, 1988) (Fig. 4a). 1.64% of the elements are slightly weathered (rank 2: bone surface shows flacking, usually associated with cracks; Behrensmeier, 1978; Fiorillo, 1988) and 18.03% are non-weathered bones (rank 0: bone surface lacking any sign of cracking or flacking; Behrensmeier, 1978; Fiorillo, 1988) (Fig. 4b and c).

Weathered bones are represented by the right jugal, dorsal and caudal vertebrae, left and right humeri and ulnae, left coracoid, left scapula, right metacarpals III and IV, the preacetabular process of the left ilium, left and right femora, tibiae and fibulae, left astragalus, left and right metatarsi III and IV and all phalanges including the ungual (Table 1). Prieto-Márquez and Serrano-Brañas (2012) reported abrasion in the aforementioned coracoid; however, re-examination of the surface texture of the element indicates weathering rather than abrasion. The term ‘abrasion’ in Prieto-Márquez and Serrano-Brañas (2012) was not used with precision, but instead it was improperly used in a broader sense to include other forms of taphonomic damage, like weathering.

Slightly weathered elements are only represented by a right dentary (Table 1). Finally, non-weathered bones correspond to the right scapula, all fragments of the left and right iliac bodies, left and right shafts of the ischia, the postacetabular process of the right ilium and four ischiadic distal processes (Table 1). Differences in weathering stages from all 61 sampled bones suggest that these bones had distinct times of subaerial exposure on the ground before they were finally buried. Specifically, non-weathered bones were probably exposed less than a year, slightly weathered bones between two and six years, and weathered bones between four and more than 15 years (following Behrensmeier, 1978 and Fiorillo, 1988). According to Behrensmeier (1978) and Behrensmeier and Miller (2012), the presence of non-weathered, slightly weathered and weathered bones indicate that the genesis of the SPA-88-9 quarry

corresponds to an attritional bone assemblage, where different carcasses were continually added over time.

In addition, it is important to highlight that some elements such as the left humerus, left femur, left tibia, left fibula and some dorsal and caudal vertebrae exhibit various weathering stages, where most of their surfaces show no sign of weathering and only some bone patches were weathered (corresponding to rank 3; Behrensmeier, 1978; Fiorillo, 1988) (Fig. 5 and Ramírez-Velasco et al., 2021: Fig. 19B and C). Such variation was probably due to the fact that these bones were initially semi-buried and only some parts were left exposed, as it happens with some animal remains today (e.g. bones from the Amboseli Basin in Behrensmeier, 1978). When bones with these weathering characteristics are found, the criterion of ‘most advanced stage covering more than 1 cm²’ should be applied in order to assess their final weathering stage (Behrensmeier, 1978), and we applied this criterion in such cases (Table 1).

2.2.4. Scoring marks on bone surfaces

Most elements from the SPA-88-9 quarry do not have scoring marks (90.16%), with exception of six pelvic elements (9.84%) (Table 1). The latter correspond to the largest fragment of the right iliac body (Ramírez-Velasco et al., 2021: Fig. 9B and D), the right postacetabular process and the four ischiadic distal processes. Scoring marks correspond to parallel striae that were likely derived when these bones were pressed against a coarser substrate (e.g. sandy substrate) causing the surface to be abraded (Behrensmeier et al., 1986; Fiorillo, 1988, 1989; Bell and Campione, 2014). In some cases, the striae are localized on the flat surfaces from both medial and lateral sides of the bones (e.g., the postacetabular process of the right ilium of IGM 6583; Fig. 6a and b; see also Ramírez-Velasco et al., 2021: Fig. 9D), or they can commonly be located on only one side (e.g., Coah 14-1/4; Fig. 6c).

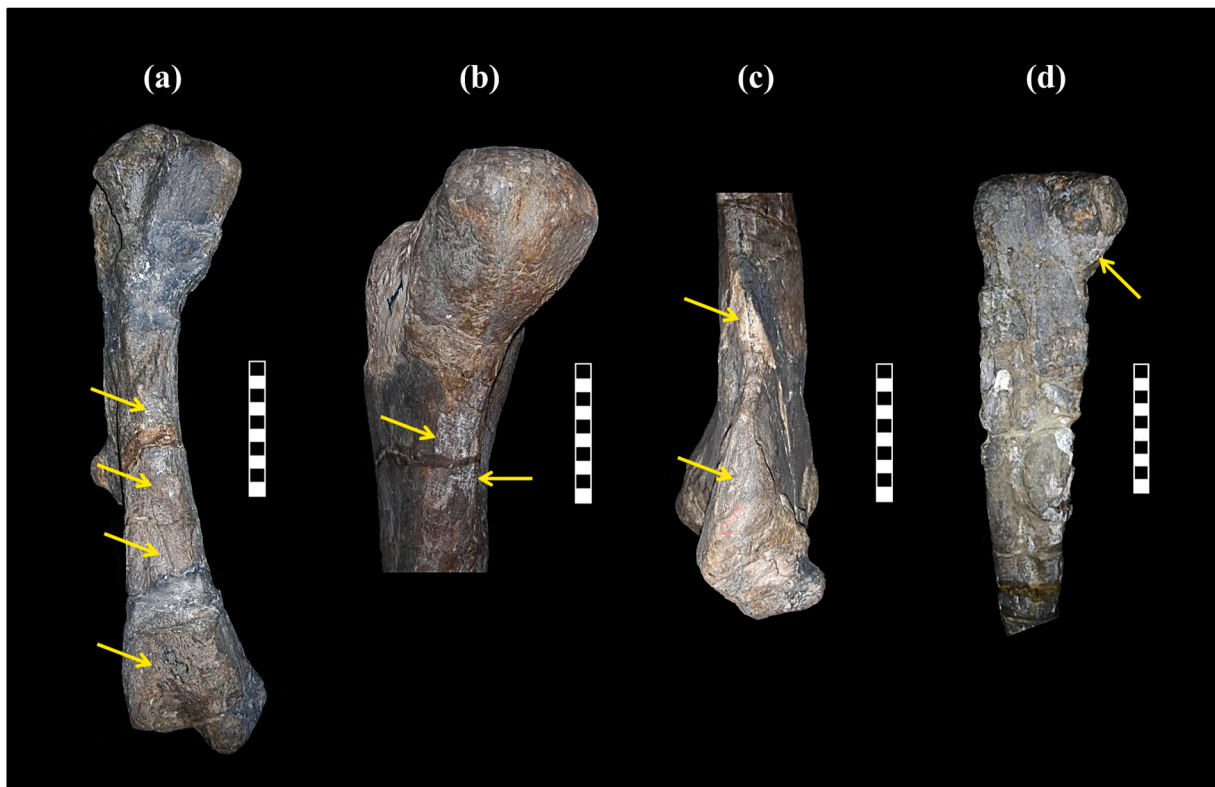


Fig. 5. Variation of weathering stages in some bones from the SPA-88-9 quarry, where the yellow arrows point to the most weathered (rank 3) surface patches: (a) left humerus, IGM 6583, in posterior view; (b) proximal end of left femur, IGM 6583, in medial view; (c) distal end of left tibia, IGM 6583, in lateral view; (d) proximal end of left fibula, IGM 6583, in lateral view. Scale bar = 10 cm.

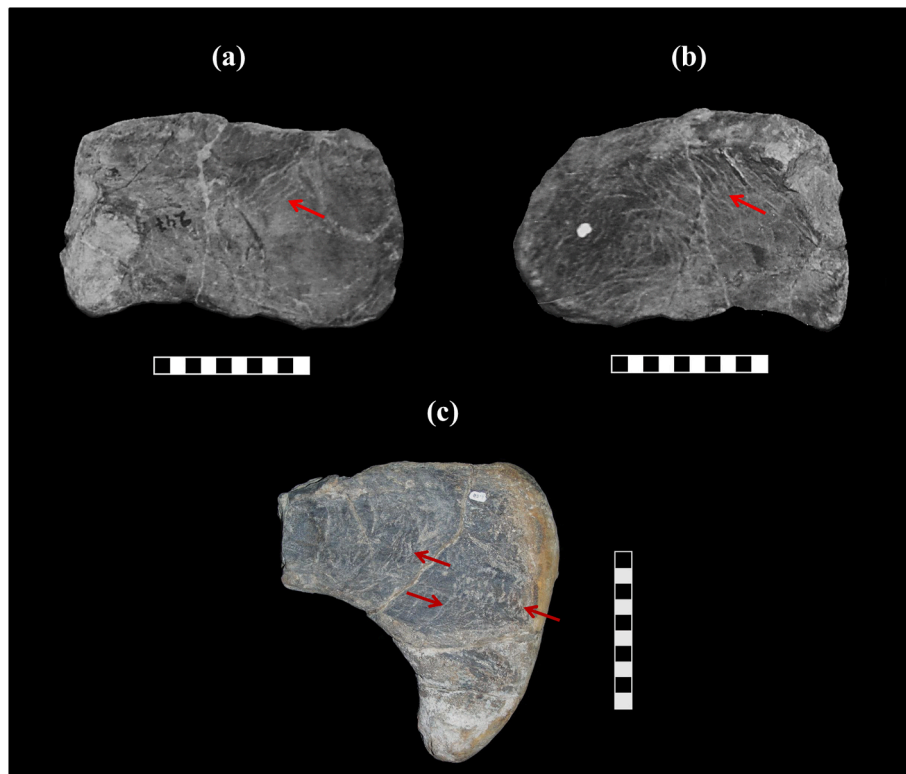


Fig. 6. Scoring marks present in some bones from the SPA-88-9 quarry: (a) Parallel striae located on the medial side of the postacetabular process of the right ilium, IGM 6583; (b) parallel striae located on the lateral side of the postacetabular process of the right ilium, IGM 6583; (c) parallel striae located on the medial side of the right distal process of the ischium, Coah 14-1/4. Red arrows point to the parallel striae. Scale bar = 10 cm.

2.3. Taphonomic attributes of the 2021 holotype of *Latirhinus uitstlani*

These taphonomic observations show a clear discrepancy regarding the skeletal unity of the 2021 holotype of *Latirhinus uitstlani* (IGM 6583) because the included elements display different taphonomic attributes. The skeleton of that holotype lacks a homogeneous degree of weathering. Instead, it shows both non-weathered (rank 0, represented by the new scapular and pelvic bones; Fig. 7a–e and Ramírez-Velasco et al., 2021: Fig. 4C–E and 9A–D, G and H) and weathered (rank 3, corresponding to the 70% of the original skeleton described by Prieto-Márquez and Serrano-Brañas, 2012: Fig. 8) bones (Table 1). This implies that the time of exposure differ among these bones (<1 year vs 4–15+ years). It is important to note that the right scapula and new pelvic bones added by Ramírez-Velasco et al. (2021: Fig. 4C–E and 9A–D, G) do not show any evidence of bone patches with different stages of weathering, suggesting that these bones remained exposed for less than a year.

The 2021 holotype of *Latirhinus uitstlani* consists of elements with different stages of breakage and abrasion, displaying also scoring marks. 70% of the skeleton originally described by Prieto-Márquez and Serrano-Brañas (2012) consists mostly of complete and partially complete bones, since only the left scapula, right fibula and left pre-acetabular iliac process are fragmented (Table 1). The lack of abrasion (rank 0) suggests that these bones experienced limited transportation (Hunt, 1978; Fiorillo, 1988; Holland et al., 2021). The absence of scoring marks (measured on the surfaces that still preserved the cortical bone; Table 1) indicate that these bones were either not trampled or that the

sediment where they were deposited did not produce surficial marks (e.g., such sediment contained no sand; see Fiorillo, 1991). In contrast, the new bones added by Ramírez-Velasco et al. (2021) to their *L. uitstlani* holotype are mostly represented by fragments (e.g., right scapula, both ilia, left ischiadic shaft and two ischiadic distal processes) and only one partial element (right ischiadic shaft). The latter bones are slightly abraded (rank 1), indicating some sort of transportation (e.g., hydraulic transportation). At least six of these elements display parallel striae on their surfaces, suggesting biogenic modification by trampling in a coarser sediment (e.g., sandy substrate) (Table 1; see Behrensmeier et al., 1986; Fiorillo, 1991; Holland et al., 2021).

Therefore, given the aforementioned taphonomic attributes, we conclude that the holotype of *L. uitstlani* presented by Ramírez-Velasco et al. (2021) is likely a chimera of different specimens.

2.4. Taphonomic attributes of the 2021 holotype of *Latirhinus uitstlani* compared to those of other hadrosaurids from the SPA-88-9 quarry

Comparison of the taphonomic attributes of the skeletal remains from the other hadrosaurids collected in the SPA-88-9 quarry (IGM 12712, IGM 12713, IGM 12714, Coah 14-1/2, Coah 14-1/4 and Coah 14-1/5) with those of the new holotype of *Latirhinus uitstlani* described by Ramírez-Velasco et al. (2021) exposes four clear patterns. First, 70% of the original skeleton (Fig. 8) exhibits taphonomic attributes that are identical to those in IGM 12713 (dorsal vertebrae) and IGM 12714 (left and right metatarsi and phalanges). All these bones were part of the *L. uitstlani* holotype in Prieto-Márquez and Serrano-Brañas (2012),

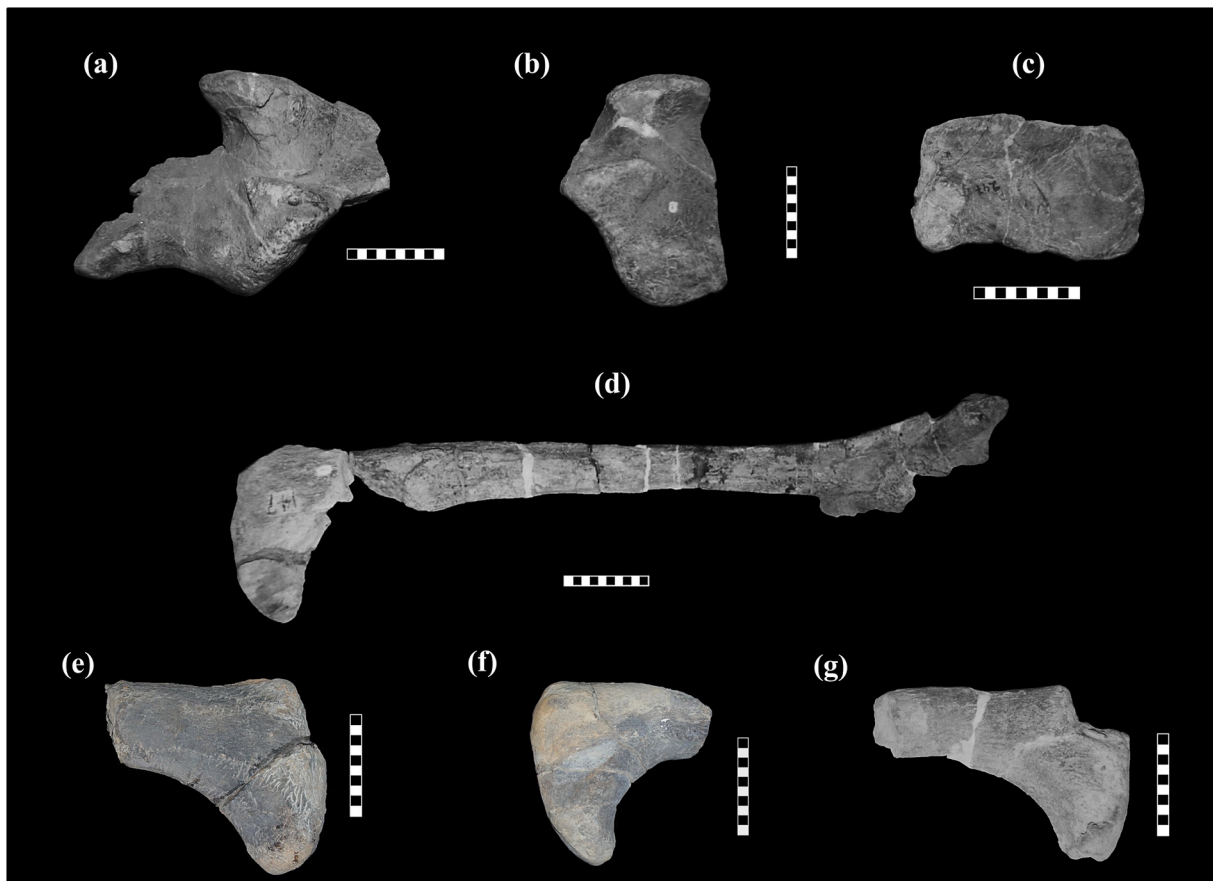


Fig. 7. Non-weathered (rank 0) pelvic bones from the new holotype of *Latirhinus uitstlani* (IGM 6583) described by Ramírez-Velasco et al. (2021) and from other bones found in the SPA-88-9 quarry (Coah 14-1/4 and Coah 14-1/5): (a) fragment of left iliac body, IGM 6583, in lateral view; (b) fragment of right iliac body, IGM 6583, in lateral view; (c) postacetabular process of right ilium, IGM 6583, in medial view; (d) right ischium, IGM 6583, in lateral view; (e) distal process of left ischium, IGM 6583, in lateral view; (f) distal process of right ischium, Coah 14-1/4, in lateral view; (g) distal process of the left ischium, Coah 14-1/5, in lateral view. Scale bar = 10 cm.



Fig. 8. Examples of weathered (rank 3) bones from 70% of the original holotype of *Latirhinus uitstlani*, IGM 6583, found in the SPA-88-9 quarry: (a) Proximal end of the left scapula, IGM 6583, in lateral view; (b) left coracoid, IGM 6583, in lateral view; (c) right humerus, IGM 6583, in medial view; (d) right ulna, IGM 6583, in lateral view; (e) right metacarpals III and IV, IGM 6583, in dorsal view; (f) preacetabular process of the left ilium, IGM 6583, in lateral view; (g) left astragalus, IGM 6583, in dorsal view; (h) right femur, IGM 6583, in posterior view; (i) right tibia, IGM 6583, in medial view; (j) right fibula, IGM 6583, in medial view; (k) left manual ungual II, IGM 6583, in dorsal view. Scale bar = 10 cm.

which supports the hypothesis that all of these non-overlapping elements belonged to the same individual (Fig. 9a–c; Table 1). Furthermore, the taphonomic information provided by all of these bones as part of the same skeleton suggests that the original *Latirhinus uitstlani* holotype (Prieto-Márquez and Serrano-Brañas, 2012) represents a parautochthonous hadrosaurid, whose remains experienced limited transportation indicated by the lack of abrasion and when deposited, remained exposed for a prolonged period of time (4–15+ years).

A second and third taphonomic pattern were observed in the right jugal of IGM 12712 (Fig. 9d and e) and in the right dentary of Coah 14-1/

2 (Fig. 10). The presence of these dense bones belonging to the Voorhies group 3 and the fact that they are only slightly abraded (rank 1) indicate that these elements probably came from distinct areas (Table 2; Voorhies, 1969; Fiorillo, 1988; Behrensmeyer, 1991) and were subsequently deposited at different times with the original *Latirhinus uitstlani* holotype. Once in the depositional site, IGM 12712 was also exposed on the surface for a prolonged period of time (4–15+ years; rank 3), as in the case of the type specimen of *L. uitstlani*. Coah 14-1/2 only was exposed on the surface for approximately two to six years before burial, a time window suggested by its slightly weathered surface (rank 2).

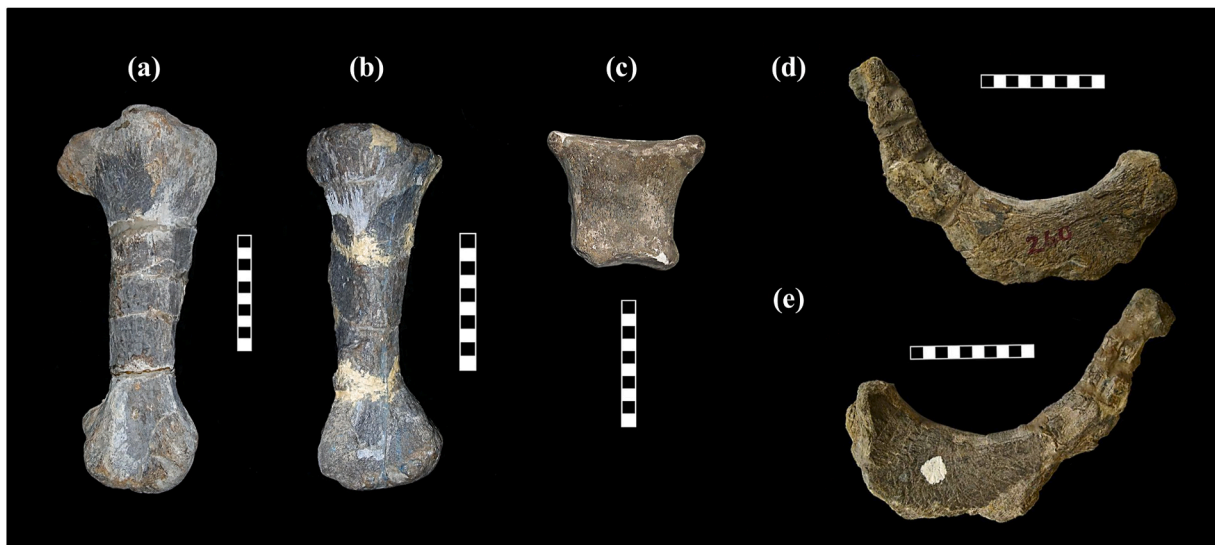


Fig. 9. Examples of weathered (rank 3) bones from IGM 12712 and IGM 12714 found in the SPA-88-9 quarry: (a) left metatarsal III (IGM 12714) in lateral view; (b) right metatarsal IV (IGM 12714) in lateral view; (c) right pedal phalanx III-1 (IGM 12714) in dorsal view; (d) fragment of right jugal (IGM 12712) in lateral view; (e) fragment of right jugal (IGM 12712) in medial view. Scale bar = 10 cm.

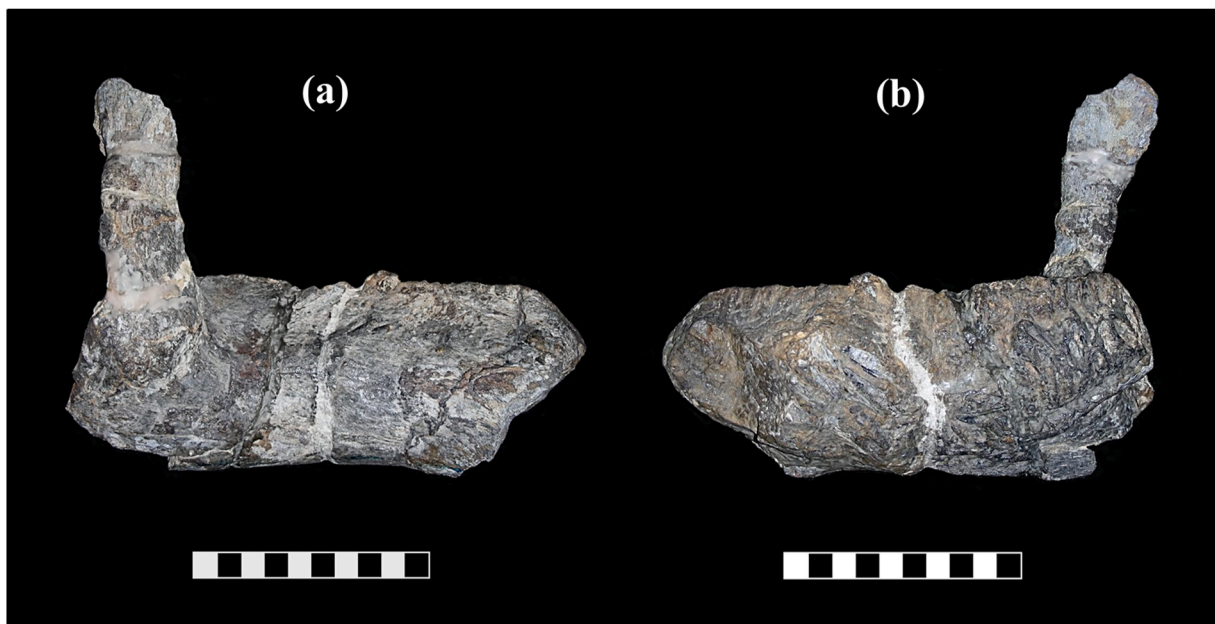


Fig. 10. Slightly weathered right dentary (Coah 14-1/2) displaying rank 2 in (a) lateral and (b) medial views. Scale bar = 10 cm.

Finally, a fourth taphonomic pattern is seen in the new bones added to the holotype by Ramírez-Velasco et al. (Fig. 7a–e and Ramírez-Velasco et al., 2021: 4C–E, 9A–D, G and H), which display identical taphonomic attributes to the two lambeosaurines (Coah 14-1/4, Fig. 7f; Coah 14-1/5, Fig. 7g) collected also from the SPA-88-9 quarry (Table 1). This indicates that the taphonomic history of these lambeosaurines differs from that of the original *Latirhinus uitstlani* holotype (IGM 6583, Prieto-Márquez and Serrano-Brañas, 2012) and the undetermined hadrosaurids IGM 12712 and Coah 14-1/2. Because these lambeosaurine overlapping elements (two right and two left ischiadic distal processes; Figs. 1 and 7d–7g, respectively) exhibit the same taphonomic attributes and belong to individuals of similar size, it is not possible to determine which girdle bones correspond to which individual, and could indeed represent four different specimens. Furthermore, referral of the right and left pelvic girdles to the new holotype of *L. uitstlani*

(Ramírez-Velasco et al., 2021; Fig. 9) is not warranted, since these bone fragments could belong to any of the lambeosaurines collected from the SPA-88-9 quarry.

The homogenous weathering signature across several individuals from a bonebed can be used as an indicator of both autochthony and relatively sudden mortality of a group of animals (Behrensmeyer, 1991). Accordingly, these lambeosaurines probably died during the same event in a different area that had relatively coarser sediments (e.g., sandy substrate), where their non-weathered remains were at some point trampled and disarticulated, before being buried in less than 1 year. Subsequently, their remains were selectively removed from the original depositional site, indicated by the sorting of bones from Voorhies groups I and II (Table 2; Voorhies, 1969; Behrensmeyer, 1991), probably by the action of a hydraulic flux, where they became slightly abraded (Table 1). Finally, the bones were transported until they were deposited together

with the remains of the original holotype of *Latirhinus uitstlani* (Prieto-Márquez and Serrano-Brañas, 2012) and the undetermined hadrosaurids IGM 12712 and Coah 14-1/2 (Behrensmeyer, 1988). In this way, it is possible to conclude that the sedimentation rate at the final burial site was characterized by a non-depositional period that allowed all the attritional remains to accumulate, followed by a period of rapid sedimentation that finally buried this attritional bone-rich horizon (Behrensmeyer, 1988).

3. Assessment of the phylogenetic relationships of *Latirhinus uitstlani*

We evaluated the purported lambeosaurine affinities of *Latirhinus uitstlani* by means of a parsimony cladistic analysis. The taxonomic sample included 75 iguanodontian taxa, including 54 hadrosaurid species of which 26 are lambeosaurines. Only the skeletal elements of the holotype of *L. uitstlani* presented in this study, as informed by their similar taphonomic signature, were scored. The data set consisted of 291 discrete morphological characters (208 cranial and 83 postcranial; Supplementary Data 1 and 2). Multistate characters containing states that are not mutually exclusive, following a natural morphocline, were ordered. A traditional search of 10,000 replicates using random additional sequences was conducted in TNT version 1.5 (Goloboff and Catalano, 2016). Bremer support (Bremer, 1988) was assessed by computing decay indices (Donoghue et al., 1992) using TNT. Bootstrap proportions (Felsenstein, 1985) were also calculated using TNT, setting the analysis for 5000 replicates using heuristic searches, in which each search was conducted using random additional sequences with branch-swapping by subtree pruning and regrafting and 25 replicates.

The phylogenetic analysis resulted in 154 most parsimonious trees of 1198 steps each (C.I. = 0.41, R.I. = 0.76), a best score hit 684 times out of the 10,000 replicates. *Latirhinus uitstlani* was positioned within Lambeosaurinae, confirming the referral of Ramírez-Velasco et al. (2021), although its relationship with other members of the clade remains unresolved (Fig. 11). Characters supporting the lambeosaurine affinities of *L. uitstlani* are the anterodorsal orientation of the acromion process of the scapula (convergent in *Brachylophosaurus canadensis*) and the short medial platform of the astragalus.

4. Systematic paleontology

Dinosauria Owen, 1842.

Ornithischia Seeley, 1888

Hadrosauridae Cope, 1869.

Referred material. IGM 12712, fragment of right jugal; IGM 12715, partial right fibula; IGM 12716, three sacral centra.

Locality and horizon. IGM 12712 comes from the SPA-88-9 quarry in the Ejido Presa San Antonio, Parras de la Fuente Municipality, state of Coahuila, northern Mexico (note: the SPA-88-9 quarry is also known as Coah 14-1 in Serrano-Brañas, 2006). IGM 12715 was collected at Quarry 2 of the Cerro de los Dinosaurios in the Ejido Rincón Colorado, General Cepeda Municipality, Coahuila, northern Mexico. IGM 12716 was collected at Quarry Coah 14-2, also in the Ejido Presa San Antonio, Parras de la Fuente Municipality, state of Coahuila, northern Mexico. These localities correspond to the late Campanian strata of the Cerro del Pueblo Formation.

Remarks. A key element in the original diagnosis of *Latirhinus uitstlani* by Prieto-Márquez and Serrano-Brañas (2012) was the interpretation of an arcuate bone fragment as part of a partial nasal. In their review, Ramírez-Velasco et al. (2021) identified this element (currently labeled as IGM 12712) as a fragment of right jugal corresponding to the region that underlies the orbit. These authors correctly pointed out that the medial surface of the nasal in (saurolophine) hadrosaurids is typically concave to form the internal wall of the nasal cavity. As preserved, the medial surface of IGM 12712 certainly lacks a pronounced concavity that would be expected in a saurolophine nasal, such as for example, that

of *Gryposaurus latidens* (e.g., AMNH FARB 5465). The medial surface of IGM 12712 does show a slight medial curvature (that can be seen in Ramírez-Velasco et al., 2021: Fig. 18C), but this is certainly far from the deeper concavity present in saurolophine nasals. Thus, we concur with Ramírez-Velasco et al. (2021) in that the anatomy of IGM 12712 best conforms to that of a fragmentary jugal. We also agree with these authors in that the bone preserves the base of the lacrimal process. The slightly raised anterior margin of the medial surface of the fragment would correspond to the separation between the articular surface for the maxilla that forms most of the medial surface of the anterior process of the jugal, from the medial side of the area ventral to the orbit. Both the facet for the palatine and the maxilla occur on the medial side of the anterior process in hadrosaurids. However, because the anterior process is missing in IGM 12712, no remnants of the actual articular facets appear to be present in this element. The parts of these facets labeled in Ramírez-Velasco et al. (2021: Fig. 18B') are here interpreted as fractured surfaces exposing the inner parts of those facets rather than actual articular surfaces.

Ramírez-Velasco et al. (2021) referred IGM 12712 to Saurolophinae. However, no characters were provided as a basis for this referral. The limited extent of the anatomy preserved in this element, where practically no taxonomically informative elements can be recognized, does not allow referring IGM 12712 to any clade beyond Hadrosauridae. The preserved anterior region of the fragment indicates that this area was probably relatively deep, as in hadrosaurids (Prieto-Márquez, 2010).

The partial fibula IGM 12715 was also referred to Saurolophinae by Ramírez-Velasco et al. (2021). They primarily based this referral on the relatively poorly developed hemimalleolus. Indeed, Prieto-Márquez (2010) reported that relatively less developed hemimalleoli are found in saurolophines in comparison with that of lambeosaurines. However, more recent updates of the phylogenetic hypothesis of hadrosaurid relationships by this author and collaborators (e.g., Prieto-Márquez et al., 2019) have excluded this condition from taxonomically or phylogenetically informative characters. This is because more exhaustive comparative anatomical observations of this region of the fibula revealed the presence of prominent hemimalleolus also among Saurolophinae (e.g., *Edmontosaurus annectens*, LACM 23502, or *Gryposaurus latidens*, AMNH FARB 5465), blurring what once seemed like a distinctive pattern of variation allowing distinction of the two major clades of hadrosaurids.

Finally, Ramírez-Velasco et al. (2021) referred IGM 12716, a fragmentary sacrum collected at Quarry Coah 14-2 consisting of three centra, to Lambeosaurinae on the basis of the oblique orientation of the sacral laminae. However, this is not exclusive of lambeosaurines. It can also be observed in at least some saurolophines, such as *Brachylophosaurus canadensis* (e.g., MOR 1071), *Gryposaurus latidens* (e.g., AMNH 5465) and *Edmontosaurus regalis* (e.g., CMN 2289). These examples also show that the inclination of the sacral laminae varies within a single sacrum.

Lambeosaurinae Parks, 1923

Referred material. IGM 6583 (in part): partial central plate of left ilium, and partial central plate and postacetabular process of right ilium (Ramírez-Velasco et al., 2021: Fig. 9A–D); partial left and right ischia (Ramírez-Velasco et al., 2021: Fig. 9G–H).

Locality and horizon. SPA-88-9 quarry; late Campanian strata of the Cerro del Pueblo Formation.

Remarks. These elements are excluded from the holotype of *Latirhinus uitstlani* because they exhibit different taphonomic attributes (i. e., weathering stage 0, abrasion stage 1 and similar degree of breakage; see Table 1) (Fig. 7a–e). The presence of a distal process in the ischia, a condition present in all lambeosaurines, allows referring these pelvic elements to the latter clade of hadrosaurids.

Latirhinus uitstlani Prieto-Márquez and Serrano-Brañas (2012).

Holotype. IGM 6583 (in part), consisting of 14 caudal vertebrae, left coracoid, proximal fragment of left scapula, both humeri and ulnae, right metacarpals III and IV, left manual phalanx II-1, preacetabular process of left ilium, both femora, tibiae, and fibulae, left astragalus;

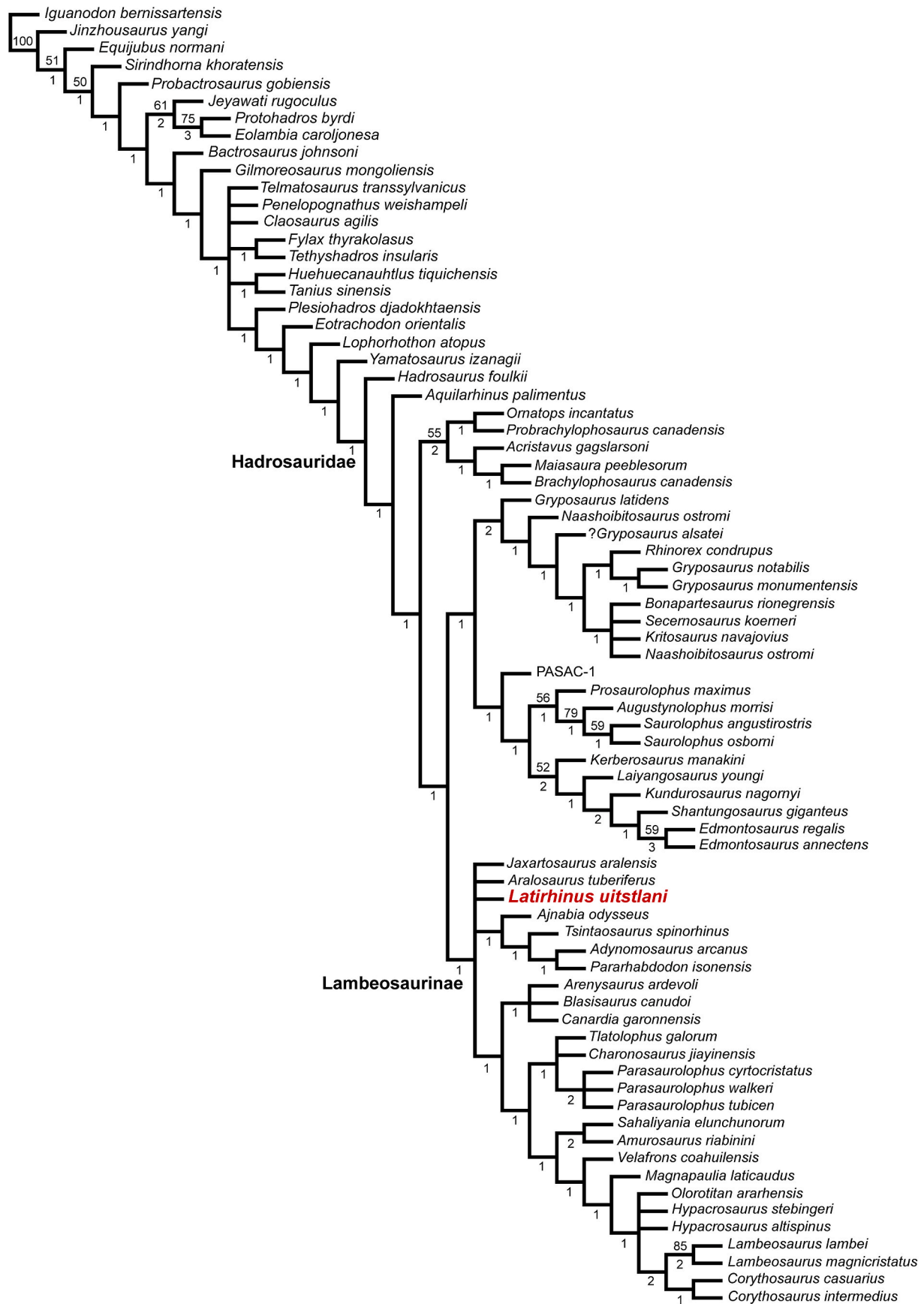


Fig. 11. Strict consensus tree showing the position of *Latirhinus uitstlani* within lambeosaurine hadrosaurids. Numbers above branches indicate bootstrap proportions, whereas those below are decay indices.

IGM 12713, ten associated partial dorsal vertebrae; IGM 12714, left and right metatarsal III, left and right metatarsal IV, both proximal phalanges III-1, and a left proximal pedal phalanx II-1 (Fig. 12).

Locality and horizon. SPA-88-9 quarry; late Campanian strata of the Cerro del Pueblo Formation.

Revised diagnosis. Lambeosaurine hadrosaurid characterized by the following unique combination of characters: coracoid oval in shape and poorly developed laterally, with elongate biceps tuberosity, rounded dorsal margin in medial view (convergent in basally branching hadrosauroids), well developed and medially pronounced subcoracoid tuberculum, low sternal process (convergent in basally branching hadrosauroids), and rounded slightly anteroposteriorly compressed bump in scapular glenoid process; trapezoid lateroventral corner of humeral deltopectoral crest abruptly expanded anteriorly, consisting of two lobes protruding medially and laterally.

Remarks. We excluded two characters that Ramírez-Velasco et al. (2021) included in their diagnosis of *Latirhinus uitstlani*. One of them is a deltopectoral crest where the proximal half is thin and the distal half becomes relatively thicker; a distally thicker deltopectoral crest is commonly found in all hadrosaurid humeri (e.g., saurolophines like *Brachylophosaurus canadensis* MOR 794, *Edmontosaurus annectens* AMNH 5886, *Gryposaurus notabilis* TMP 80.22.1, *G. latidens* AMNH 5465, or *Prosaurolophus maximus* TMP 84.1.1; and lambeosaurines such as *Amurosaurus riabinini* AEHM 1/278, *Canardia garonnensis* MDE-Ma3-20, *Corythosaurus intermedius* ROM 845, *Hypacrosaurus altispinus* CMN 8501, *Magnapaulia laticaudus* LACM 17715, or *Olorotitan ararhensis* AEHM 2/845, to name a few). The other excluded character is the strong development and ventral deflection of the preacetabular process, because such condition is present in nearly all lambeosaurines (see Supplementary Data 2).

The holotype of *Latirhinus uitstlani* proposed by Ramírez-Velasco et al. (2021) included several elements from the original holotype by Prieto-Márquez and Serrano-Brañas (2012) under the IGM 6583 catalog number: the 14 caudal vertebrae, partial left scapula, both humeri and ulnae, left coracoid, right fused metacarpals III and IV, left manual ungual II, the preacetabular process of a left ilium, both femora, tibiae and fibulae, and a left astragalus. Elements from the 2012 holotype that were excluded by Ramírez-Velasco et al. (2021) include the fragmentary jugal IGM 12712, ten dorsal vertebrae, and both metatarsals III, both metatarsals IV, both proximal phalanges III-1, and a left proximal pedal phalanx II-1. Then, Ramírez-Velasco et al. (2021: Figs. 2 and 3) added to their holotype a fragment of right proximal scapula and two partial ilia and ischia. These authors claimed that because the bones in their revised holotype were found associated in the same spot within the SPA-88-9 quarry, are proportionally similar in size and display the same mode of preservation, they must have belonged to the same individual (Ramírez-Velasco et al., 2021: Fig. 3). However, there is substantial uncertainty in using size for assigning specific bones to an individual when other partial skeletons or even scattered bones are preserved nearby within the same depositional site (e.g. Ayer, 2000; Wiersma-Weyand et al., 2021). This may become particularly complicated by the presence of two or more disarticulated specimens of the same taxon with

similar body sizes (Wiersma-Weyand et al., 2021). Notably, at least two more lambeosaurine individuals of similar size were also found at the SPA-88-9 quarry (Fig. 1; see also section 3.1). Furthermore, Ramírez-Velasco et al. (2021) did not describe the mode of preservation of the fossil bones and how it differs from that of other hadrosaurids within the same quarry.

Ramírez-Velasco et al. (2021) stated that the 2012 holotype (IGM 6583) of *Latirhinus uitstlani* is actually a chimera was based first on the finding of two misplaced bones mixed with the holotype. These elements consist of an incomplete right fibula (IGM 12715, see section 4: Hadrosauridae) from a different locality (Ramírez-Velasco et al., 2021: Fig. 21) and a fragmentary sacrum (Coah-2/1, now re-labeled as IGM 12716, see section 4: Hadrosauridae; Ramírez-Velasco et al., 2021: Fig. 21). Originally, *L. uitstlani* was housed at the Museo de Geología of the Universidad Nacional Autónoma de México (UNAM), where it was stored in a series of drawers designated for this holotype. Because of an error that occurred long after the formal publication of the holotype (Prieto-Márquez and Serrano Brañas, 2012), both the incomplete right fibula (IGM 12715) and the partial sacrum (IGM 12716) were stored together with the skeletal remains of *L. uitstlani*. Subsequently, all the bones that were in these drawers were transported to the Instituto de Geología of UNAM in order to be incorporated into the National Collection of Paleontology and unfortunately, IGM 12715 and 12716 were also included. However, none of these two elements were used in the original description of *L. uitstlani*. The sacrum IGM 12716 was collected in a different quarry (Coah 14-2) within the Presa San Antonio area, so it was never considered part of the original skeleton (Serrano-Brañas, 2006; Prieto-Márquez and Serrano Brañas, 2012; Ramírez-Velasco et al., 2021). The description of the fibula of *L. uitstlani* was solely based on the original complete left element that was collected at the SPA-88-9 quarry (in the Ejido Presa San Antonio, Parras de la Fuente Municipality, state of Coahuila) along with the rest of the bones of the holotype (Prieto-Márquez and Serrano Brañas, 2012: Fig. 9E).

We agree with Ramírez-Velasco et al. (2021) in that the iliac peduncle of right ischium is in fact a proximal fragment of right scapula. However, this element was removed from the holotype of *Latirhinus uitstlani* because it exhibits different taphonomic attributes (i.e., weathering stage 0, abrasion stage 1 and its highly broken; see Table 1).

Ramírez-Velasco et al. (2021) referred to Saurolophinae IGM 12713 (ten associated dorsal vertebrae) and IGM 12714 (consisting of left and right metatarsal III, left and right metatarsal IV, both proximal phalanges III-1, and a left proximal pedal phalanx II-1 that they consider part of the same individual). IGM 12713 was referred to Saurolophinae on the basis of the rectangular and vertical morphology of the neural spines, while according to Ramírez-Velasco et al. (2021) in lambeosaurines the neural spines of anterior dorsal vertebrae are acicular-shaped as in *Latirhinus uitstlani*. These authors cite Prieto-Márquez (2010) as a reference for these presumably diagnostic characters, although this study deals with the distribution of the height of the neural spines, not their geometry. Actually, the width of the neural spines of anterior-most dorsals decreases distally in both saurolophines and lambeosaurines. Posteriorly along the dorsal series, in

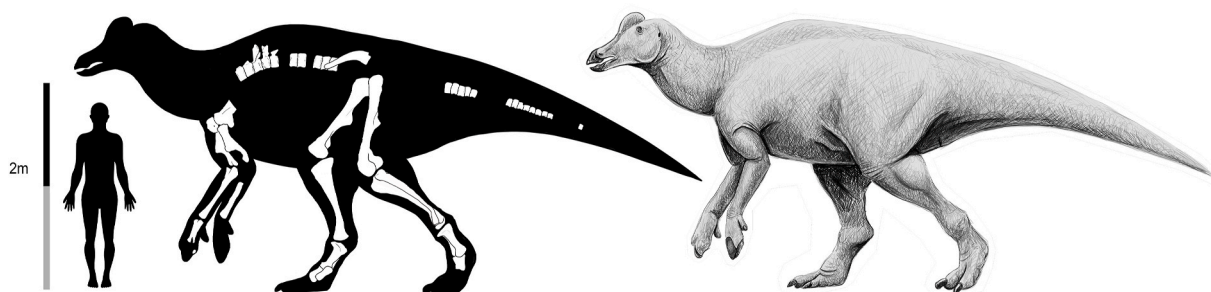


Fig. 12. Idealized lambeosaurine silhouette showing the elements preserved of the holotype of *Latirhinus uitstlani*, accompanied by a life rendition of the specimen.

both hadrosaurid clades the dorsal neural spines become rectangular (e.g., *Hypacrosaurus stebingeri* MOR 549). Thus, the shape of these neural spines is not a reliable character to diagnose this material as saurolophine.

Regarding IGM 12714, Ramírez-Velasco et al. (2021) reported that the metatarsals III display distinctly elongate proportions, which would support the saurolophine affinities of this material given that such proportions are only shared with saurolophines *Augustynolophus morrissi* and UTEP P37.7.34 (an unnamed hadrosaurid from Campanian strata of Big Bend National Park in Texas), the former would probably represent a saurolophine. However, there are also instances of lambeosaurine taxa showing metatarsals III with similarly elongate proportions, such as *Amurosaurus riabinini* (Godefroit et al., 2004: Fig. 17C) and the unnamed form from the Basturs Poble bonebed (e.g., MCD 4707). Ramírez-Velasco et al. (2021) also noted that in the right metatarsal III of IGM 12714, the mediodorsal corner of the proximal end forms an unusual conical process. As pointed out by these authors, one specimen of *A. morrissi*, LACM CIT 2760, displays a conical crista dorsalis (sensu Ramírez-Velasco et al., 2021). However, it is worth noting that LACM CIT 2760 is heavily distorted, having experienced substantial dorsoventral compression. Aside from this occurrence, a similarly prominent crista dorsalis is present in the right metatarsal III of ROM 845, an exemplar of *Corythosaurus intermedius*. These exemplars, along with the tendency of this region of metatarsal III to appear variably eroded among hadrosaurids, suggest caution in using the development or morphology of the crista dorsalis as a diagnostic character. Additionally, IGM 12713 and 12714 exhibit identical taphonomic attributes than IGM 6583, supporting inclusion of the former in the holotype of *Latirhinus uitstlani*.

5. Comments on the size of IGM 12712

Using the scale provided by Ramírez-Velasco et al. (2021: Fig. 18A and B) for the fragmentary jugal IGM 12712, we measured the distance from the mid-width of the dorsal margin of the postorbital process to the mid-width of the preserved anterior margin in 22 cm. This implies that the complete jugal outline represented in Ramírez-Velasco et al. (2021: Fig. 18D) would be approximately 60 cm in length. Assuming a shorter apex for the anterior process and anteroposteriorly less elongate proportions (Fig. 13), it is still the case that IGM 12712 is an exceedingly

large jugal, easily reaching 50 cm in total length (measured from the tip of the anterior process to the posterior margin of the quadratojugal flange). In turn this indicates an unusually large individual. In order to provide a basis for comparison with other known hadrosaurids, we conducted regression analyses for predicting skull length from jugal length (Fig. 13), using measurements from a sample of articulated skulls of saurolophine and lambeosaurine hadrosaurid species (Fig. 13 and Supplementary Data 3). Skull length was measured from the oral margin of the premaxilla to the posterior margin of the quadrate. Using a rough estimate for the jugal of 50 cm in length, these regressions provided estimations for the skull length of IGM 12712 of approximately 125 cm in the case of it being lambeosaurine and 140 cm in the scenario of it being a saurolophine. If IGM 12712 is a saurolophine, these estimations place IGM 12712 in the size range of *Shantungosaurus giganteus*, the largest known species of hadrosaurid (Hone et al., 2014) from middle-late Campanian strata of the Xingezhuang and Hogtuya formations of Shandong Province, China (Xing et al., 2014). No complete jugal exists, to our knowledge, for *S. giganteus*; however, previous studies show reconstructed skulls exceeding 140 cm in length (Hu, 1973).

If IGM 12712 is a lambeosaurine, this may be the largest recorded member of this clade, growing to a size well beyond that of other species of these 'hollow-crested' hadrosaurids for which the complete skull is known (Fig. 13; see also Supplementary Data 3). To illustrate this point, the longest lambeosaurine skull in our sample, that of the *Corythosaurus casuarius* specimen AMNH 5240, is only 74 cm in length (based on measurements by Brown, 1914). However, the Mexican lambeosaurine record includes *Magnapaulia laticaudus*, a remarkably large species from the late Campanian El Gallo Formation of Baja California that may have reached a size (e.g., LACM 17712; see Prieto-Márquez et al., 2012: Fig. 2B) comparable to that of IGM 12712. For all we know, it is not beyond the realm of possibility that IGM 12712 could be a *M. laticaudus* individual. The available cranial material for *M. laticaudus* is limited to the few elements preserved in the holotype LACM 17715, including a nearly complete jugal (Prieto-Márquez et al., 2012). LACM 17715 is, however, a much smaller individual of the species (Prieto-Márquez et al., 2012: Fig. 2A), the jugal measuring only 17.8 cm in length. The fragmentary state of IGM 12712 prevents any informative comparison with LACM 17715. Yet, the size of IGM 12712 indicates an animal that is probably larger than the holotype of *Latirhinus uitstlani*, supporting removal of this jugal fragment from IGM 6583.

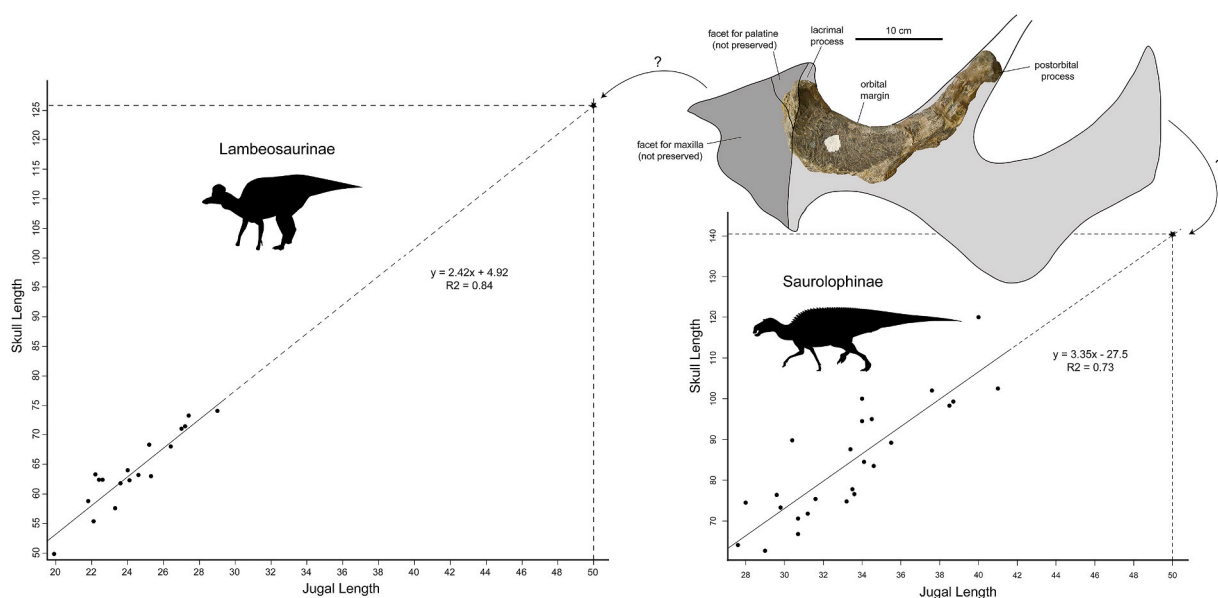


Fig. 13. Bivariate regression plots of skull length vs jugal length for a sample of saurolophine and lambeosaurine hadrosaurids, with a tentative reconstruction of the medial view of the jugal IGM 12712 based on the jugal of a common hadrosaurid such as *Gryposaurus notabilis* (e.g., CMN 2278). The values along the 'x' and 'y' axes of the regression plots are in cm.

6. Conclusions

We concur with the revisionary work of Ramírez-Velasco et al. (2021) that *Latirhinus uitstlani* is a lambeosaurine hadrosaurid and that the arched bone that we previously identified as a nasal is more likely a fragmentary jugal. However, the taphonomic attributes of the bones support a holotype of this species consisting of the original elements listed in Prieto-Márquez and Serrano-Brañas (2012), with exclusion of the jugal and the right scapula. This jugal is too fragmentary to allow referral beyond Hadrosauridae indeterminate. However, it is worth noting that it represents an unusually large hadrosaurid specimen approaching or even rivaling in size to some of the largest known species of the clade. The iliac and ischiadic fragments belong to other lambeosaurine individuals, perhaps also *L. uitstlani*, although at this juncture no characters permit such assignation. All other bones from the type and other localities in the late Campanian Cerro del Pueblo are referable to Hadrosauridae indeterminate.

CRedit authorship contribution statement

Albert Prieto-Márquez: Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they do not have any conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jsames.2021.103689>.

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