PALÆO VERTEBRATA

ARTICLE

Terrestrial vertebrate paleocommunities from the Cerro del Pueblo Formation (Late Cretaceous; Late Campanian) at Las Águilas, Coahuila, Mexico

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This paper is in memory of the French Palaeontologist Jean-Claude Rage, who for a long period of time coined the science of vertebrate palaeontology in Europe and the world. He unexpectedly died end of March 2018.

Abstract: The Las Águilas site near Porvenir de Jalpa, Coahuila, Mexico, is extremely rich in tetrapod remains comprising both bones and trackways of several dinosaur taxa of late Campanian age. Within a 50 m thick section we identified at least nine layers with dinosaur bone assemblages. In one of these the dinosaur bones are associated with remnants of eusuchian crocodilians, turtles, plesiosaurs, pterosaurs, tyrannosaurids, dromaeosaurids, parksosaurids, hadrosaurids, ceratopsids, and ankylosaurs. This layer is also rich in coprolites of turtles, crocodilians and likely theropods, thus providing evidence for the wealth of Late Cretaceous vertebrate life in the area.

Keywords: Cerro del Pueblo Formation, Campanian, dinosaurs, vertebrates, Coahuila, Mexico

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INTRODUCTION

The Las Águilas fossil site was discovered in the late 1990s by Jose Lopez-Espinoza “Pato”, then a preparator of the Museo del Desierto (MUDE), Saltillo, north of the Cerro de Angostura, 4.2 km East of the hamlet Porvenir de Jalpa and about 50 km West of Saltillo, Coahuila, north-eastern Mexico (Fig. 1).

The potential of finding dinosaur bones and trackways in this area is enormous and was first brought to scientific attention in 1996, when Rodriguez de la Rosa (1996) published a brief catalogue on vertebrate remains from Las Águilas comprising dinosaurs, crocodilians, turtles and pterosaurs, among other fossils. Subsequently, the locality was mentioned by Kirkland *et al*. (2000), Brinkman *et al*. (2002), and Eberth *et al*. (2003). In 2003, the first dinosaur trackway was described by Rodriguez de la Rosa *et al*. (2003). The authors referred the track to hadrosaurs but a revision by Meyer *et al*. (2008) concluded that they were produced by tyrannosaurids, with the exception of one single footprint of an ornithomimid theropod (Rivera-Sylva *et al*., 2017). Parallel to the tyrannosaurid tracks, there are the trackways of numerous hadrosaurs. The best of these were removed without taking measurements, and their context is now destroyed. One trackway in the riverbed near Cerro de Angostura was described as an “unusual ornithopod trackway” (Rodriguez de la Rosa, 2007; Rodriguez de la Rosa *et al*., 2004; 2005), but turned out to have been produced by a large dromaeosaurid (Meyer *et al*., 2008), although the size of this animal may have been exaggerated (Rivera-Sylva *et al*., 2017).

Even though abundant and diverse dinosaur material was discovered in the vicinity of the trackways at Las Águilas and has partially been collected by the palaeontology work group of the Secretaría de Educación Pública de Coahuila, Mexico, only a handful of monographic descriptions of testudines (e.g. Brinkman & Rodríguez de la Rosa, 2006; Brinkman, 2014) and dinosaurs (e.g. Lowen *et al*., 2010) has been published. The dinosaur bone clusters at Cerro de Angostura and vicinity remained virtually untouched until now. While geological, stratigraphical and palaeoecological details of the Las Águilas section have recently been presented by Vogt *et al*. (2016), we here present a first overview on the vertebrate diversity of the locality, and more specifically of a new site termed LA 14 (for Las Águilas). This site is located about 1.5 km west of the Cerro de Angostura site, in which abundant surface material has weathered out of a fine-grained green to buff-coloured siltstone.

Institutional Abbreviations: CPC- Colección Paleontológica de Coahuila, Saltillo, Coahuila, Mexico; CNA- Consejo Nacional de Arqueología, Mexico; IEUH- Institute of Earth Sciences, Heidelberg University, Germany; INAH- Instituto Nacional de Antropología e Historia, Mexico; MUDE- Museo del Desierto, Saltillo, Coahuila, Mexico; SMNK- State Museum of Natural History, Karlsruhe, Germany; SGM- Servicio Geológico Mexicano, Pachuca, Mexico.

GEOLOGICAL SETTING AND PALEOENVIRONMENT

The Difunta Group represents an extended foreland to the Sierra Madre Oriental fold and thrust belt and is located in the northeastern Mexican states of Chihuahua, Coahuila, and northeastern Nuevo León. The sediment sequence is Late Campanian to Eocene in age (e.g. Vega-Vera *et al*., 1989; Soegaard *et al*., 2003; Ifrim *et al*., 2010) and was deposited under deltaic conditions, representing marsh, lagoonal, and eulittoral to shallow marine environments (Hopkins, 1965; Weidie, 1961; Lehman, 1982). The delta drained into the ancient Gulf of Mexico to the East.

The Cerro del Pueblo Formation represents the basal unit of this sequence and was dated to the Late Campanian (McBride 1975; Soegaard *et al*., 2003; Eberth *et al*., 2003; Vogt *et al*., 2016). The strata at Las Águilas are assigned to the Cerro del Pueblo Formation based on abundant and diverse vertebrate, invertebrate and plant assemblages (e.g., Eberth *et al*., 2004), as well as strontium isotope data (Vogt *et al*., 2016).

The depositional setting at Las Águilas was influenced by cyclically fluctuating paleoenvironments of intermittent shallow-marine, brackish to fresh water or even subaerial conditions. The abundance of oysters throughout the measured section displays the permanent mixing of salt- and freshwater, generating intermittent brackish environmental conditions with changing salinities (Vogt *et al*., 2016).

MATERIALS AND METHODS

Fossils were collected at Las Águilas during extensive surface survey by a joint team from MUDE, SMNK, IEUH, and the SGM. All fossils are stored in the Museo del Desierto (MUDE), Saltillo. Locality information is on file at that institution. The specimens were photographed using a Olympus E 620, with an Olympus Zuiko standard lens (14-42 mmf/3,5-5,6), an Olympus Zuiko macro lens (35 mm, f/3,5), and a Canon EOS Rebel T2i with a Canon 18-55mm 1:3.5-5.6 IS II lens.

The fossils of this report were collected during several field seasons in 2014. All materials are catalogued in the collections of the MUDE and were collected with permission from the INAH through its CNA [Oficio 401.B(4)19.2013/36/1862].

Figure 1. Locality map of Las Águilas (red star), near the town of Porvenir de Jalpa, Coahuila, Mexico.

SYSTEMATIC PALEONTOLOGY

Superclass Osteichthyes Huxley, 1880
Osteichthyes indet.

Referred specimens – CPC 1843 a,b, 2 amphicoelus vertebra (Fig. 2 E-H, M).
Locality – LA14
Description –The preserved margin is irregularly striated and pitted. The articular face shows concentric sculpturing. There is no trace of a notochordal perforation. CPC 1843a is 15.5 mm wide and 6.6 mm in length. CPC 1843b is 10.6 mm wide and 3.2 mm in length.
Discussion – The partial vertebra is referred to Osteichthyes because of its external structure. Otherwise the bone is undiagnostic.

Order Lepisosteiformes Hay, 1929
Family Lepisosteidae Cuvier, 1825
Lepisosteidae indet.

Referred specimens – CPC 1844, 1 opisthocoelous vertebra (Fig. 2 A-D); CPC 1845, 3 scales (Fig. 2 I-L).
Locality – LA14
Description – The vertebra is about 1.5 times longer than its diameter. The dorsal surface of the centrum is flat, with a few transverse grooves and a shallow longitudinal sulcus, which represents the floor of the neural canal (Fig 2 C). A sharp ridge extends along the midline of the ventral surface, which is bordered by two longitudinally oval pleurocoels (Fig 2 D). The bases of a pair of stout transverse processes extend laterally from the cranial half of the lateral face of the vertebra (Fig 2 B-D). Caudal to the base of the transverse processes there is a shallow depression bordered by low ridges that diverge caudally and terminate at the cranial margin of the circumference of the caudal intervertebral articulation (Fig 2 B). The depression is deepest in its cranial half. The vertebra is 36.4 mm long, has a transverse diameter of 31.7 mm and a dorsoventral one of 27.1 mm.

Only portions of the scales are preserved, which present the characteristic glossy ganoin-coated surface (Fig. 2 I-L).
Discussion – The vertebra is diagnostic for Lepisosteidae, compared with material documented by Sankey (2008) and Carr & Seitz (2015), as is the ganoid scale.

Class Reptilia Laurenti, 1768
Order Testudines Linnaeus, 1758

Family Pleurosternidae Cope, 1868
Genus *Compsemys* Leidy, 1856
***Compsemys* sp.**

Referred specimens – CPC 1853 a,b,c (Fig 3 N-P)
Locality –LA 14
Description – There are fragments of carapace with a sculpture pattern that consists of compactly arranged, low tubercles. Their size ranges from 29.8 mm to 13.7 mm.

Discussion – The sculpture pattern is a characteristic of *Compsemys* (Brinkman, 2014).

Family Chelydridae Gray, 1831
Chelydridae indet.

Referred specimens–CPC 1846 a,b,c,d,e (Fig. 3 C, D, E-I)
Locality – LA 14
Description – There are numerous thick marginal osteoderms with prominent ridges running parallel to the osteoderm margin. Their size ranges from 28.5 mm to 23.3 mm.
Discussion – The sculpture resembles that seen in chelydrid turtles, e.g. *Macroclemys*.

Family Dermatemydidae Gray, 1870
Genus *Hoplochelys* Hay, 1908
***Hoplochelys* sp.**

Referred specimens – CPC 1854 a-f (Fig. 3 B)
Locality –LA 14
Description – There is a prominent midline keel with two lower lateral keels on the dorsal face of the neuralia. The ventral face is also marked by prominent ridges. The size of the fragments ranges from 25.5 mm to 16.8 mm.
Discussion – The morphology of the neuralia is diagnostic of *Hoplochelys* based on Brinkman (2014).

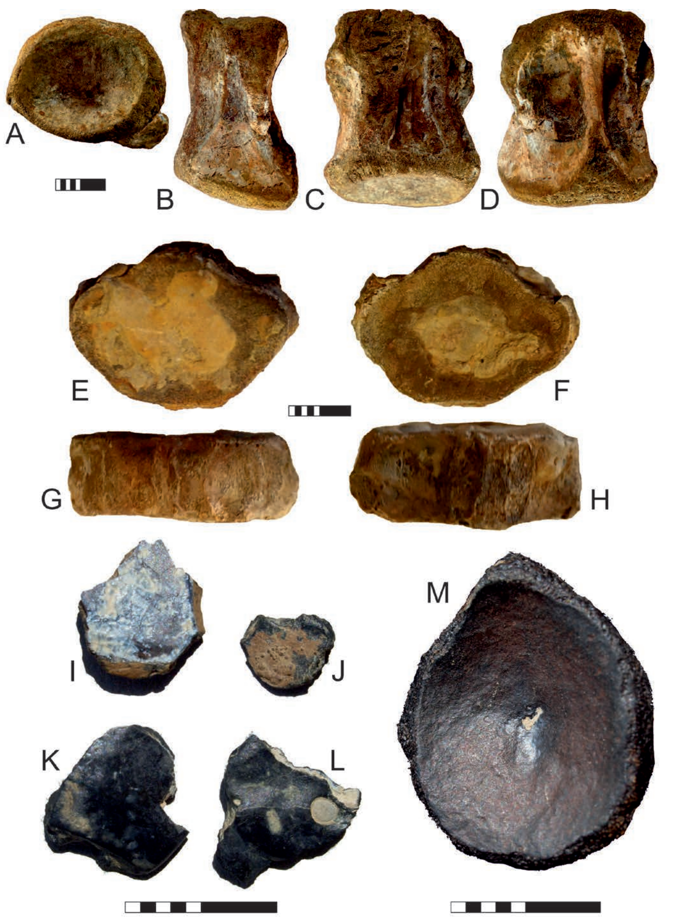

Figure 2. A-D. Vertebra of a lepisosteid (CPC 1844) in: A. cranial, B. left lateral, C. dorsal, and D. ventral views. **E-H, M**. Amphicoelous vertebrae of fishes (CPC 1843a) in: E, M. cranial, F. caudal, G. ventral, and H. dorsal views; **I-L**. Lepisosteiformes scales (CPC 1843) in dorsal views. Scale bar = 10 mm.

Family Adocidae Cope, 1870
Genus *Adocus* Cope, 1868
***Adocus* sp.**

Referred specimen – CPC 1860 (Fig. 3 A)
Locality –LA 14
Description – This is a fragment of a carapace of 20.7 mm x 15.6 mm in diameter.
Discussion – The sculpture pattern is characteristic of the genus *Adocus* (Brinkman, 2014).

Family Trionychidae Fitzinger, 1826
Trionychidae indet.

Referred specimens – CPC 1847 a,b,c,d (Fig 3 J-M)
Locality – LA 11, LA 14
Description – There are abundant fragments of costal and neural osteoderms with densely pitted external surfaces. The internal surface of the osteoderms is smooth. The costalia may show rib fragments and the neuralia remnants of the articular facet with the neural spine. Their size ranges from 24.5 mm to 11.7 mm.
Discussion – Significant size variation of pit diameters on the external face suggests the presence of different sizes classes, probably representing different ontogenetic stages, but possibly also separate species. Trionychids must have been extremely abundant in the delta plain environment of Las Águilas. Modern trionychids inhabit both fresh and brackish water bodies and tolerate even short periods of salt water ingression.

Figure 3. Testudines carapace fragments. **A.** *Adocus* sp. (CPC 1860); **B.** *Hoplochelys* sp. (CPC 1854 a-f); **C, D, E-I.** Chelydridae indet. (CPC 1846 a-e); **J-M.** Trionychidae indet. (CPC 1847 a-d); **N-P.** *Compsemys* sp. (CPC 1853 a-c). Scale bar = 10 mm.

Clade Lepidosauromorpha Benton, 1983
Lepidosauromorpha indet.

Referred specimens – CPC 1848, jaw fragment, likely from the maxilla (Fig. 4 A).
Locality – LA 11
Description – The maxilla fragment bears two horizontally broken tooth bases exposing a circular cross-section level with the root-crown transition. The bone itself is badly damaged. Where exposed, the compacta is smooth. The implantation type of the teeth cannot be securely identified, but appears to be thecodont. Measurements: length of 28.8 mm, width of 14.6 mm, height of 22.9 mm, with a diameter of the tooth base between 9.7-10.2 mm.
Discussion – The smooth compacta excludes Osteichthyes, Lepisosteiformes and Crocodilia, where the compacta is striated or pitted. The circular shape of the tooth in cross-section and the lack of carinae excludes it from the clade Dinosauria known from the study area. The density of the spongiosa and the thickness of the compacta precludes Pterosauria as origin for the maxilla fragment. The only sauropsids that have such a combination of features and that are known from the area are Mosasauroidea and Plesiosauria, both belonging to Lepidosauromorpha.

Order Plesiosauria Blainville, 1835
Plesiosauria indet.

Referred specimens – CPC 1849 a-d, four isolated phalanges (Fig. 4, B,C).
Locality – LA 14
Description – The phalanges are rounded hexagonal or pentagonal. The flat surfaces, which represent the palmar/ plantar or dorsal faces, show a faint concentric striation converging to a central fovea commonly seen in juveniles. The cortex is irregularly rugose. The lengths of the phalanges vary between 17.9 mm and 19.8 mm.
Discussion – The polygonal outline, the radial sculpturing and the central fovea are diagnostic for Plesiosauria phalanges. Size and thickness of the phalanges suggest basal phalanges. An identification beyond Plesiosauria is not possible. The estimated length of the respective animal would have ranged between 1.5 and 2 meters.

Clade Crocodyliformes Hay, 1930
Clade Eusuchia Huxley, 1875
Eusuchia indet.

Referred specimens –CPC 1851 a-e, five jaw fragments; CPC 1856 a-e, five almost complete procoelous vertebrae; CPC 1861, one first caudal vertebra; CPC 1852, one claw; and CPC 1862 one osteoderm.

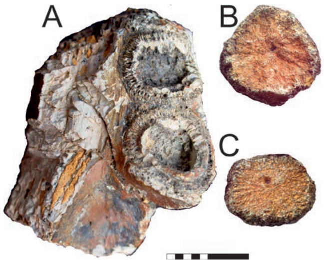

Figure 4. Lepidosauromorpha indet. **A.** Jaw fragment (CPC 1848); **B-C.** Plesiosauria indet. isolated phalanges (CPC 1849 a and b) in dorsal views. Scale bar = 20 mm.

Locality – LA 14: the five procoelous vertebrae, claw, osteoderm, and all jaw fragments (Fig. 5 A-G); LA 11: one biconvex vertebra (Fig 6 F,G).
Description – CPC 1851a (Fig. 5 A,B) is the middle part of a dentary with six circular alveoli. The diameter difference of these is very small but suggests anisodonty. The labial and ventral cortex is sculptured with wrinkles and pits. The lingual face is smooth with the exception of two longitudinally running concavities. The labial one is bordered by two sharp ridges that converge rostrally. The rostral distance between the two ridges is half the caudal one. The ventral concavity is bordered by the ventral ridge of the dorsal concavity, while a broken ridge that protrudes from the ventrolabial corner of the dentary runs parallel to the dorsal border of the concavity. Likely, the lingual area was covered by the splenial, which would explain the presence of the longitudinal concavities as attachment places. Lingual of the tooth row there is a near horizontal and rostrally diverging shelf which reaches the same transverse expansion as the alveolar area. The outline of the rostral break is rounded triangular, while that of the caudal break is rounded rectangular. Measurements: height of 9.9 mm, length of 20.7 mm, and a width of 6.9 mm; the diameter of the alveoli ranges between 1.9 to 2.9 mm.

CPC 1851b (Fig 5 C,D) is the fragment of a right premaxilla. Only the rostral margin is preserved. The curvature of the wrinkled dorsorostral face is regular. On the ventral face there are four alveoli with circular margins. Three of them are of equal diameter. The diameter of the lateral-most alveolus is one third smaller suggesting anisodonty. Measurements: height: 8.4 mm, length: 26.3 mm, width 11.9 mm; the diameter of the alveoli ranges from 4.8 mm to 6.9 mm.

CPC 1851c and d are two small fragments of a dentary, each with one weathered tooth in place. Measurements: CPC 1853

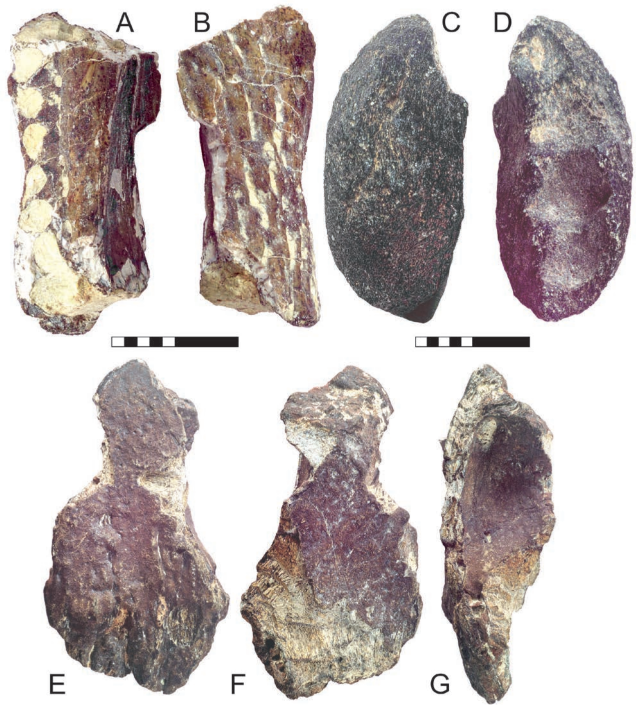

Figure 5. Eusuchia indet. **A-B.** dentary (CPC 1851a) in: A. dorsal and B. left lateral views. **C-D**. Right maxilla (CPC 1851b) in: C. cranial and D. caudal views. **E-G.** Left surangular (CPC 1851e) in: E. left lateral, F. right lateral, and G. dorsal views. Scale bar in A-D = 10 mm. Scale bar in E-G = 50 mm.

length: 11.9 mm, width: 7.7 mm, height: 16.6 mm; CPC 1854 length: 8.3 mm, width: 7.0 mm, height: 13.4 mm.

The fragment CPC 1851e (Fig. 5 E-G) is identified as coming from a left surangular of a larger individual likely exceeding a length of one meter, estimated from the mandibular glenoid fossa. The transversely striated, rugose face of the surangular-coracoid suture lies rostrally. Here, the caudal process of the coronoid contacted the surangular. The rostral process that formed the caudodorsal margin of the mandibular fenestra has broken off. The external face is deeply and irregularly pitted. Measurements: height: 51.3 mm, length: 97.2 mm, width: 29.8 mm.

CPC 1856a (Fig. 6 H-J) is a cervical vertebra that presents a transverse oval cross-section. The articular condyle is regularly convex in all directions. A pair of long oval parapophyses protrudes from the lateral face of the centrum. They face ventrolaterally at an angle of about 120°. The ventral face of the corpus shows a depression where the parapophyseal peduncles merge with the corpus. Along the ventral median line of the corpus there is the remnant of a hypapophysis.

CPC 1856 b-e (Fig. 6 A-E) are four caudal vertebrae with the pair of ventral ridges. They cranially and caudally terminate in the articular facet for the hemal arches.

CPC 1861 (Fig. 6 F, G) is a first caudal vertebra with the biconvex vertebral body typical for Eusuchia. Measurements: height: 7.4 mm, length: 15.3 mm, width: 10.9 mm.

CPC 1852 (Fig. 6 K-M) is an ungual which cannot be referred to any digit. Measurements: length: 16.3 mm; height: 8.5 mm; width: 8.7 mm.

CPC 1862 is a square osteoderm with widely spaced nearly circular pits that likely comes from the dorsal shield of an eusuchian. Measurements: height: 5.7 mm, width 13.2 mm, width: 14.4 mm.

Discussion – The vertebrae indicate to the presence of small Eusuchia, as is indicated by their procoely or biconvexity in the case of the first caudal vertebra (CPC 1861). The size of the vertebrae suggests that these animals reached maximum lengths of about one meter. Crocodilians must have been rare, probably due to the presence of theropods, but they evidently inhabited the area. Rivera-Sylva *et al*. (in press) had identified *Brachychampsa* from the Cerro del Pueblo Formation, but none of the specimens from Las Águilas can be attributed to this taxon.

Figure 6. Eusichia indet. **A-E.** vertebra (CPC1856 b) in: A. right lateral, B. cranial, C. ventral, D. caudal, and E. dorsal views. **F-G.** First caudal vertebra (CPC 1861) in: F. ventral and G. dorsal views. **H-J**. Cervical vertebra (CPC 1856a) in: H. ventral, I. dorsal, and J. lateral views. **K-M.** Ungual (CPC 1852) in: K. ventral, L. dorsal, and M. left lateral views. Scale bar = 10 mm.

Order Pterosauria Kaup, 1834
Pterosauria indet.

Referred specimens – CPC 1863, long bone fragment (Fig. 7 A-C).
Locality – LA 14
Description – The long bone fragment has a 0.5 mm thick compacta. The medular cavity is mostly filled with sediment. There is no trace of a spongiosa, which suggests that the bone was extremely pneumatic. The bone is almost circular in cross-section. It is 19.8 mm long and 9.3 mm wide.
Discussion – Until now, only one long bone section of an ornithocheroid pterosaur has been reported from Las Águilas by Rodríguez de la Rosa & Cevallos-Ferríz (1998). The fragment comes from the shaft of a tibia or the mid-shaft of a radius and could also be referred to a nyctosaurid. The earliest of these occurred in the Coniacian (Frey *et al*. 2006). The compacta of CPC 1863 is much thinner than that of a Cretaceous bird or a dromaeosaur and thus characteristic for Pterosauria. The rarity of pterosaur material may be due to a taphonomy bias, because pneumatic bones are transported more easily than massive ones. They also degrade very rapidly.

Order Archosauria Cope, 1869
Suborder Theropoda Marsh, 1881
Theropoda indet.

Referred specimens – CPC 1859, manual phalanx (Fig. 9, A-D).
Locality – LA 14
Description – CPC 1859 corresponds to an isolated distal half of a manual phalanx of a theropod (Fig. 9 A-D) and shows well defined contralateral fossae. The dorsal face is smooth without the presence of the extensor fossa. The ventral face is weathered and shows the left condyle, while the right condyle is completely weathered. The bone measures 20 mm in length and 7 mm width.

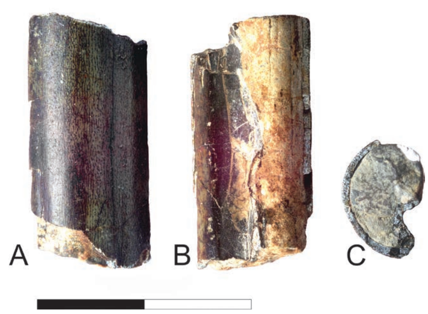

Figure 7. Pterosauria indet. long bone (CPC 1863) in : A. left lateral, B. right lateral, and C. cranial views. Scale bar = 20 mm.

Discussion – Because of the slenderness of the specimen, it is identified as a manual phalanx. The weathered nature of the specimen makes it difficult to determine to which side it belongs.

Family Tyrannosauridae Osborn, 1906
Tyrannosauridae indet.

Referred specimens – CPC 1864 a-o, fifteen isolated teeth (Fig. 8, A-W).
Locality – LA 14
Description - CPC 1864g (Fig. 8 U-W) is a small faintly recurved premaxillar tooth, 15.8 mm high, with a rounded cross-section and no denticles on the labial carina. The longitudinal basal length is 7.4 mm, the basal width 5.0 mm. CPC 1864 n-o, CPC 1864 q (Fig. 8 A-T). The fragments come from large to medium-sized recurved conical teeth with serrated mesial and distal carinae. The crown tips are missing. The tooth cross-section varies from oval to a D-shape (Fig. 8 E,F,K,L,Q,T). The denticles are chisel-shaped, with a basal diameter of 0.5 mm in mesiodistal and 0.6 mm in labiolingual direction. The interdenticular space measures 0.2 mm. The serration density is two denticles per mm. The height of the tooth crowns reaches from 14.1 mm to 60.8 mm, with a basal mesiodistal length of between 9.0 mm and 27.4 mm, and a labiolingual length of 5.2 mm to 16.9 mm.
Discussion – The serration density is diagnostic for tyrannosaurids (Farlow & Brinkman, 1987; Currie *et al*., 1990; Abler, 1997; Sankey, 2001; Holtz, 2004). This identification is supported by the spatulate outline of the denticles and the tooth morphology in general (Sankey, 2001).

Family Ornithomimidae Marsh, 1890
Ornithomimidae indet.

Referred specimens – CPC 1865 a,b,c, pedal unguals (Fig. 9 H-Q)
Locality – LA 14
Description – CPC 1865a, b, c, are three pedal unguals with the tip and proximal articular surface missing. They are triangular in cross-section with an almost flat plantar surface. The flexor depression is seen more clearly in CPC 1865a than in CPC 1865b. In lateral view, the unguals are straight, with deep sulci on both the lateral and medial faces. Measurements: CPC 1865a: length 12.7 mm, height 6.1 mm, width of 6.8 mm. CPC 1865b: length 23 mm, height 12 mm, width 11.2 mm. CPC 1865c: length 80 mm, height 45 mm, width 45 mm.
Discussion – According to Makovicky *et al*. (2004), the pedal

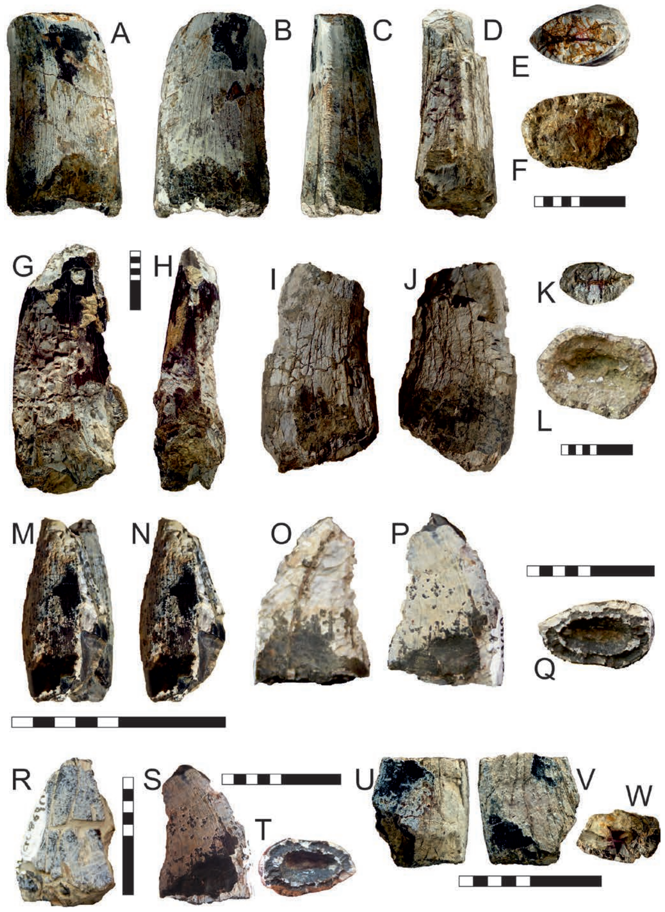

Figure 8. Theropoda: Tyrannosauridae indet. teeth: **A-F.** CPC 1864b in: A. lingual, B. labial, C. cranial, D. caudal, E. dorsal, and F. cross-section at base views; **G-H.** CPC 1864o in: G. lingual and H. labial views; **I-L.** CPC 1864c in: I. lingual, J. labial, K. dorsal, and L. cross-section at base views; **M-N.** CPC 1864a in: M. right lateral and N. left lateral views; **O-Q.** CPC 1864q in: O. left lateral, P. right lateral, and Q. cross-section at base views; **R-T.** CPC 1864n in: R. left lateral, S. right lateral, and T. cross-section at base views; **U-W.** CPC 1864g in: U. left lateral, V. right lateral, and W. dorsal views. Scale bar = 10 mm.

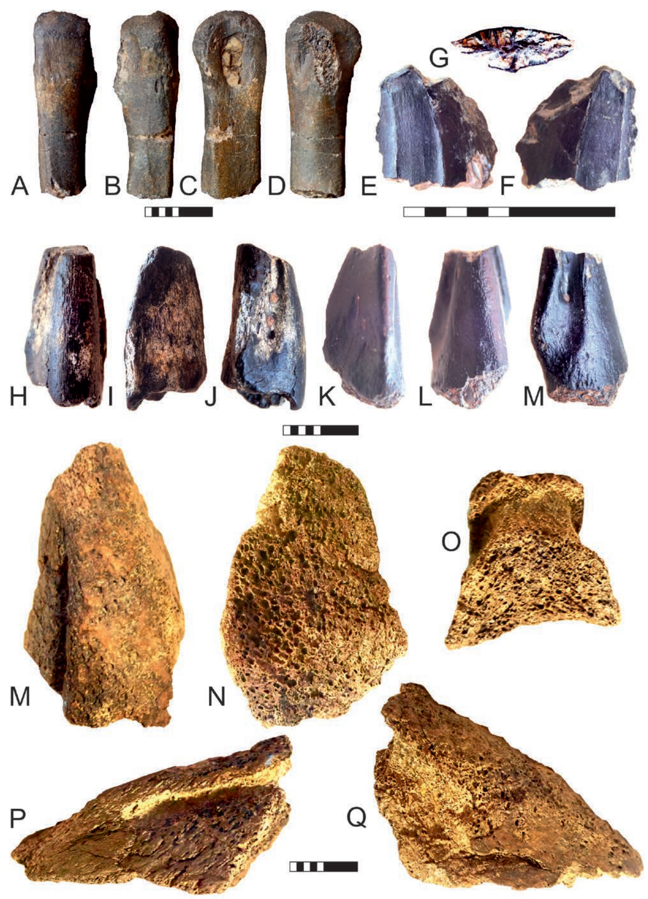

Figure 9. A-D. Theropod metatarsal (CPC 1859) in: A. dorsal, B. ventral, C. left lateral, and D. right lateral views; **E-G.** Dromaeosaurid tooth (CPC 1855) in: E. lingual, F. labial, and G. cross-section at base views. Ornithomimid unguals **H-J.** CPC 1865a in: H. dorsal, I. ventral, and J. left lateral views; **K-M.** CPC 1865b in: K. ventral, L. dorsal, M. left lateral; **N-R.** CPC 1865c in: N. dorsal, O. ventral, P. caudal, Q. left lateral, and R. right lateral views. Scale bar = 10 mm.

unguals of ornithomimidae typically show a triangular cross-section, which is diagnostic for the group. Evidence that the animals inhabited the area also comes from footprints, which were discovered on the large trackway site at Las Águilas associated with tracks of large theropods and hadrosaurs (Rivera-Sylva *et al*., 2017). Based on CPC 1865c, gigantic ornithomimids must have populated the Campanian Las Águilas area.

Family Dromaeosauridae Matthew and Brown, 1922
Dromaeosauridae indet.

Referred specimens – CPC 1855, tooth (Fig. 9 E-G)
Locality – LA 14
Description – CPC 1855 is a small tooth fragment, with a preserved crown height of 10.5 mm, a basal length of 9.7 mm, and a basal width of 3.7 mm. It is labiolingually compressed. The basal cross-section thus forms a laterally compressed ellipse. There are two prominent vertical carinae on the mesial and distal face of the tooth. The denticle-bearing carina is lost as is the tip of the tooth.
Discussion – The tooth differs from *Paronychodon*, because the cross-section is labiolingually compressed. The teeth of *Paronychodon* have one plain side while the other is convex. Although fragmentary, the specimen shares similarities with teeth of *Zapsalis*. Even though, it cannot be attributed to either of these taxa because of a different stratigraphic and geographic range (Larson & Currie, 2013). It should therefore be considered as a new taxon. The presence of a large Dromaeosauridae in Las Águilas is evidenced by trackways (Meyer *et al*. 2008; Rivera-Sylva *et al*., 2017).

Order Ornithischia Seeley, 1887
Suborder Ornithopoda Marsh, 1881
Family Ankylosauridae Brown, 1908
Ankylosauridae indet.

Referred specimens – CPC 1867, an osteoderm (Fig. 10, A-D)
Locality – LA 14
Description – CPC 1867 was described in detailed by Rivera-Sylva *et al*. (2018a) as the cranial fragment of an ankylosaur osteoderm, which is transversely broken in the middle. The lateral margin is broken, too. The coarsely pitted and wrinkled external face bears a medial blunt longitudinal keel. The ventral surface is smooth and deeply concave. The maximum length of the fragment is 57.1 mm, the maximum width 64.1 mm. The maximum thickness is 26.4 mm. The compacta is exceedingly thin measuring only 2 mm. The large medular cavity is filled with a foamy irregular spongiosa.
Discussion – Because of the thin-walled compacta, the foamy spongiosa and the deeply concave internal face, the osteoderm is referred to Ankylosauridae (Carpenter, 2004).

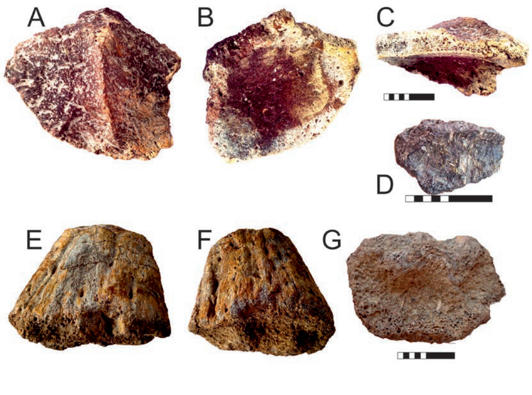

Figure 10. Ornithischia: **A-D.** Ankylosauridae indet. osteoderm (CPC 1867) in: A. dorsal, B. ventral, C. lateral, D. caudal views. **E-G.** Ceratopsidae indet. horncore (CPC 1888) in: E. right lateral, F. left lateral, and G. ventral views. Scale bar = 10 mm.

Family Parksosauridae Bucholtz, 2002
Parksosauridae indet.

Referred specimens – CPC 1872, tooth (Fig. 11 A-B), CPC 1866 a, posterior dorsal vertebra (Fig. 11 C-H).
Locality – LA 14
Description – CPC 1872 (Fig. 11 A-B) was identified as a premaxillary tooth crown from Parksosauridae by Rivera-Sylva *et al*. (2018b). It is slightly mediolaterally compressed and slightly constricted at its base; the crown has a blunt tip. Serrated carinae are missing, and the enamel is smooth. The crown height is 5 mm, and the basal maximum diameter is 3 mm.

CPC 1866 (Fig. 11 C-H) is a posterior thoracic vertebra of Parksosauridae according to Rivera-Sylva *et al*. (2018b), and is amphicoelous and spool-shaped in ventral aspect. In caudal aspect the centrum is transversely rounded triangular in outline, with the dorsal face being flat, while the lateral faces are slightly convex. On its dorsal surface, there are deep transverse striations and the floor of the neural canal is hourglass shaped in dorsal aspect. The ventral face is constricted in the middle with no special feature. The caudal face of the centrum has a concave area separated by a dorso-medial ridge. Measurements: length of 48 mm, height of 42 mm and a width of 31 mm.

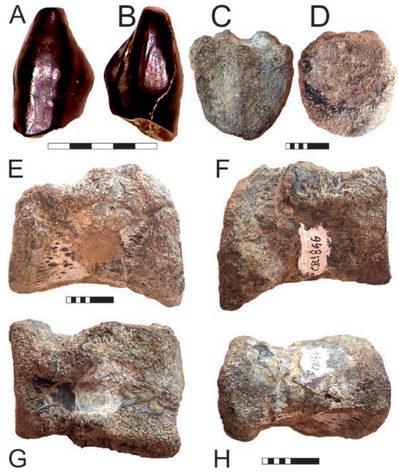

Figure 11. Parksosauridae indet. **A-B.** tooth (CPC 1872) in: A. labial and B. lingual views; **C-H.** vertebra (CPC 1866) in: C. cranial, D. caudal, E. left lateral, F. right lateral, G. dorsal, and H. ventral views. Scale bar in A-B = 5 mm. Scale bar in C-G = 10 mm.

Figure 12. Lambeosaurinae indet. ischium (CPC 1871) in: A. left lateral and B. right lateral views. Scale bar = 10 mm.

Discussion – The tooth shows the characters described by Boyd (2014) as diagnostic for Parksosauridae. The spool shaped centrum and almost platycoelous intervertebral joint are diagnostic for a dorsal vertebra of this group (Brown et al., 2013). The concave area on the caudal face of the centrum separated by a dorso-medial ridge identifies this vertebra as the caudal-most dorsal vertebra (Galton, 1974) and much resembles those illustrated by Carr & Seitz (2015: 107) for *Thescelosaurus*.

Family Hadrosauridae Cope, 1869
Hadrosauridae indet.

Referred specimens – CPC 1868 a-p, 16 teeth (Fig. 13 A-B); CPC 1869 a-e five jaw fragments (Fig. 13 C-J; Fig. 14); CPC 1870 a-j, 10 vertebrae (Fig. 15; Fig. 16 A-I), CPC 1871 ischium (Fig. 12), CPC 2613 pedal phalanx (Fig. 16 L-M); CPC 1873 a,b pedal unguals (Fig. 16, J-K)
Locality – LA 11, LA 9, LA 14
Description – Fifteen teeth from hadrosaurs were discovered, five of them with worn crowns. All of them bear prominent middle ridges on the enamel. The largest tooth is 30.7 mm high, the smallest 8.9 mm (Fig. 13 A-B).

Five jaw fragments (CPC 1869 a-e, Fig. 13 C-J; Fig. 14) were collected. One lacks teeth and the tooth channels are exposed (CPC 1869 c). The fragment is 243.5 mm long and 104.7 mm high. The tooth channels have an average width of 6.4 mm. The other jaw fragment (CPC 1869b, Fig. 13, E-H) has 4 teeth lacking the crowns. As preserved, they are 98 mm long and 120 mm high.

CPC 1870a (Fig. 15 A-D) is an almost complete opisthocoelous anterior dorsal vertebra, with a centrum that is slightly concave ventrally. It has a vertically orientated neural spine. The centrum is 84 mm long and 85 mm high. The total height including the neural spine is 310 mm, and the total width including the transverse processes is 66 mm.

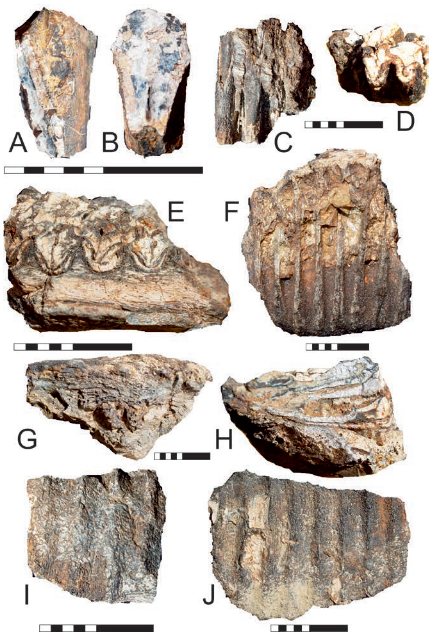

Figure 13. Hadrosauridae indet. **A-B.** tooth (CPC 1868a) in: A. labial and B. lingual views; **C-D.** jaw fragment (CPC 1869c) in: C. labial and D. dorsal views; **E-H.** jaw fragment (CPC 1869b) in: E. dorsal, F. labial, G. ventral, and H. cranial views; **I.** jaw fragment (CPC 1869d) in lingual view; and **J.** jaw fragment (CPC 1869a) in lingual view. Scale bar = 10 mm.

CPC 1870b (Fig. 15 J) is the lateral half of a centrum of a caudal vertebra of a hadrosaur. The specimen is 798.9 mm long and 841.0 mm high. A set of three bite marks pierce the lateral face of the vertebra (Fig. 15 J, yellow circles). The anterior-most bite mark is rounded and has a diameter of 8.3 mm and a depth of 7.4 mm. The two others are elongate oval, with the middle bite mark being 13.3 mm long and 5.0 mm wide, and the third 8.8 mm long and 4.9 mm wide. The distance between the centre of the first and the central bite mark measures 27.5 mm, that between the central and the third is 46.8 mm.

CPC 1870c – 1870f (Fig. 15 E-I) are platycoelous caudal centra, from different positions in the series, but with similar morphologies. The centra are as wide as high and, in cross-section, show the hexagonal outline diagnostic for Hadrosauria. The centra likely come from juvenile individuals and range in length between 13.2 mm and 20 mm, between 11.7 mm – 19.5 mm in height and between 14.5 mm and 26.7 mm in width.

CPC 1871 (Figure 12) is a fragmentary lambeosaurine ischium identified by the expanded distal knob. The bone fragment, as preserved, is 60.6 mm long, and 42.1 mm in maximum height at the peduncle.

CPC 2613 corresponds to a pedal phalanx (Fig. 16 L-M). It is dorsoventrally compressed and higher than wide. CPC 2613 has a length of 85 mm and a maximum width of 74 mm, with a maximum height of 76 mm.

CPC 1873 a,b corresponds to two fragments of proximal manual unguals. They are dorsoventrally compressed and short. CPC 1873a has a length of 30 mm and a maximum width of 32 mm, with a maximum height of 12 mm. CPC 1873b (Fig. 16, J-K) has a length of 41 mm with a maximum width of 40 mm and with a maximum height of 15 mm.
Discussion – Numerous hadrosaur remains are known from the Las Águilas site, mainly adults with an average length of about 9-10 meters. Their hadrosaurian nature is evidenced by platycoeleous vertebrae with a hexagonal outline, and a lack of pleurocoels. Remnants of numerous juveniles have also been recovered, the smallest with an estimated length of less than one meter. Most of the individuals range between two and six meters (Vogt *et al*. 2016). The largest remains may come from individuals exceeding a length of 10 meters.

Though abundant, the fragmentary nature of the hadrosaurian material is evident, mostly consisting of disarticulated bone assemblages. Many bones show wear traces indicating the decay of the hadrosaur carcasses upstream, followed by a subsequent transport downstream, or reworking prior to final deposition (Vogt *et al*., 2016). The different age stages of the individuals hint to the presence of family groups that either inhabited the area or migrated through it along the river banks, which must have been rich in vegetation.

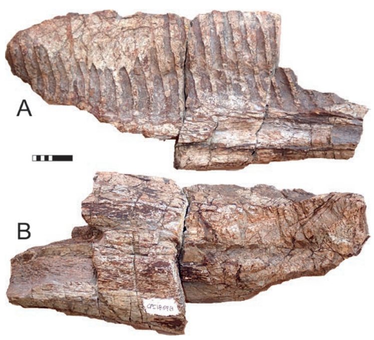

Figure 14. Hadrosauridae indet. jaw fragment (CPC 1869a) in: A. lingual and B. labial views. Scale bar = 20 mm.

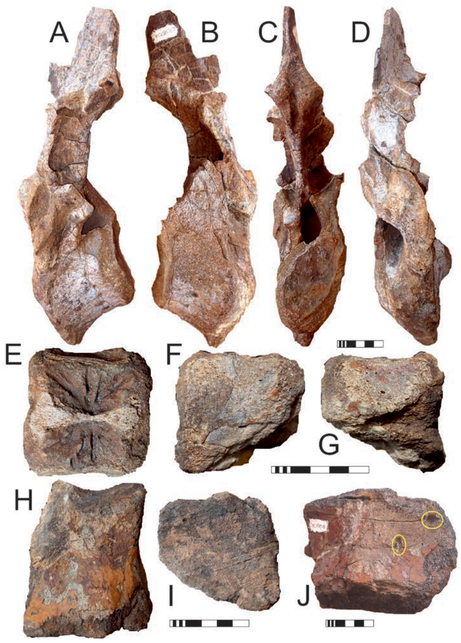

Figure 15. Hadrosauridae indet. **A-D.** anterior dorsal vertebra (CPC 1870a) in: A. left lateral, B. right lateral, C. caudal, and D. cranial views; **E-I.** caudal vertebra (CPC 1870c); **J.** caudal vertebra (CPC 1870b) in lateral view, yellow circles show bite marks. Scale bar = 50 mm.

The theropod predation is evidenced by bite marks on CPC 1870a (Fig. 15 J, yellow circles). They are referred to a tyrannosaurine theropod based on their size, shape and spacing. The morphology of the bite marks is almost identical to other bite marks that have been referred to large tyrannosaurines (e.g., Fowler & Sullivan, 2006; Hone & Watabe, 2010). During the Late Cretaceous of North America, only tyrannosaurines reached body sizes large enough to explain the diameter of bite marks in CPC 1870a. The bite marks described here represent the first record of tyrannosaurine bite marks from the Cerro del Pueblo Formation. The bites must either have been applied post-mortem or were the result of a lethal attack, because there is no evidence of callus formation. However, the bite marks are located on the lateral face of the centrum. Here, bites can only be applied when the animals are dead and dismembered. In the case of CPC 1870a it cannot be said if bites were applied while dismembering a fresh kill or to an animal that died of other causes.

Family Ceratopsidae Marsh, 1888
Ceratopsidae indet.

Referred specimens – CPC 1874, nasal horn core (Fig. 10 E-G)
Locality – LA 9
Description – The nasal horn core is conical with a rounded tip and a long-oval cross section at its base. The surface is extremely vascularised and rugose. The horn core is 44.8 mm long and 38.5 mm high with a maximum basal diameter of 30.3 mm.
Discussion – The specimen is identified as a nasal horn core of a ceratopsian based on a thick cortical layer combined with a small core of spongiosa (Carpenter, pers. comm. to HRS, 2016). The morphology of the horn core resembles that of *Coahuilaceratops*, *Arrhinoceratops*, *Anchiceratops*, *Agujaceratops* and *Pentaceratops*, but cannot be referred to any of these genera because it likely comes from a juvenile, as is indicated by its reduced size and stubby appearance.

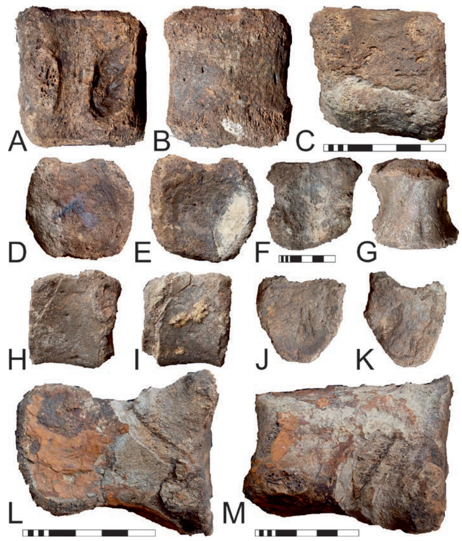

Figure 16. Hadrosauridae indet. **A-E.** vertebra (CPC 1870c) in: A. dorsal, B. ventral, C. lateral, D. cranial, and E. caudal views; **F-I.** vertebra (CPC 1870d) in: F. dorsal, G. ventral, H. left lateral, and I. right lateral views; **J-K.** ungual (CPC 1873b) in: J. ventral and K. dorsal views; **L-M.** pedal phalanx (CPC 2613) in: L. right lateral and M. dorsal views. Scale bar = 50 mm.

ENVIRONMENTAL IMPLICATIONS OF THE VERTEBRATE ASSEMBLAGE

The vertebrate fossils found at Las Águilas comprise both aquatic (freshwater, brackish and marine) and terrestrial elements (Vogt *et al*., 2016). This combination of assemblages is similar to other coeval localities to the north, in the United States and Canada (e.g. Sankey *et al*., 2002; Sankey, 2008; Sankey, 2010). The presence of trionychid turtles and lepisosteid fishes provides evidence for an extensive and partially deep fresh to brackish water fluvial system with low kinetic energy. The presence of deep oxbows and blind river arms is more than likely. Trionychid turtles tolerate brackish and even saline waters but need sandy riverbanks with shallow sections for breeding (Plummer, 1977). As in extant species, trionychids and lepisosteids from Las Águilas may have preyed on a variety of invertebrates but predominantly on fishes and possibly other small vertebrates, although the presence of the latter still needs to be verified. The other two types of turtles may have been much less salt-water tolerant than trionychids, but were omnivorous or carnivorous, too. Turtles represent the second-most abundant vertebrate group (28 %), With the exception of Trionychidae, the cryptodires occurring in Las Águilas are mainly aquatic and nonmarine. They form the most diverse and abundant group, suggesting that the inferred environment is consistent with the sedimentary model of a meander belt depositional system in an outer delta environment (Vogt *et al*., 2016). Channels of meandering streams with sandy or muddy grounds and shallow banks are favoured by trionychid turtles, remnants of which are the most abundant Testudines of Las Águilas.

Dinosauria is the dominant taxon found at Las Águilas (39 %) consisting of ornithomimosaurids, dromaeosaurids, tyrannosaurids, ankylosaurids, ceratopsians, parksosaurids, and hadrosaurids. Lepidosauromorphs, crocodilians, and pterosaurs form the rest of the Las Águilas fossil vertebrate assemblage. Although generally scarce, crocodilians (5 %) are mainly represented by teeth, jaw fragments and osteoderms, indicating that they must have been common, but not abundant.

Lepidosauromorpha (5 %) are represented by a single skull element and several phalanges. No matter if mosasauroid or plesiosaur, they may have invaded the delta from the sea side on the search of food, or their decaying carcasses were washed into the outer delta and there milled up by the tide.

Theropoda and Hadrosauridae are terrestrial elements of the assemblage. Nothing can be said about the habits of the theropods because of their scarcity in the present fossil record and the extreme fragmentation of their remnants. One could speculate that these terrestrial predators only occasionally entered the river system on their search for prey, however their tracks are presented at Las Águilas and tell a different story (Rivera-Sylva *et al*., 2017).

Most of the tyrannosaurid teeth are small shed teeth, likely deriving from juveniles. The abundance of teeth of juvenile tyrannosaurids and the presence of numerous juvenile hadrosaurs supports the idea that juvenile tyrannosaurids may have preferably preyed on juvenile hadrosaurs, or fed on hadrosaurian carcasses which were periodically washed up in large quantities on the river banks during high energy flash floods (Vogt *et al*., 2016).

According to the vast number of body fossils, hadrosaurs appear to have been the most abundant faunal element of the terrestrial tetrapod assemblage. The presence of small individuals of less than one meter length suggests the presence of family groups. A breeding area close by is indicated by a very small specimen of less than one meter estimated length (pers. obs. EF, WS), which suggests a post-hatchling juvenile. However, due to the lack of egg shells, the assumption of a nesting site in close vicinity of the locality would be speculative. The depositional environment of the studied area as inferred by sedimentological features (Vogt *et al*., 2016), is consistent with the habitat types postulated for the present type of vertebrate assemblage. The freshwater system was located on a coastal plain, which drained into the Paleogulf of Mexico (Vogt *et al*., 2016). Further survey will certainly yield more fossils, especially plant material, for a more detailed reconstruction of the habitat type represented in the area, as well as the geographic range of the system within the palaeogeographical context of that time period.

The dominance of isolated and fragmentary bones suggests that many dinosaur carcasses decayed upstream, were subsequently reworked and transported as isolated bones or partial carcasses prior to final burial. Both sediments and fossils further indicate that the likely agent of reworking and transport were at least periodically high energy alluvial channels (Vogt *et al*., 2016).

The taphonomy of the taxonomically diverse Las Águilas dinosaur site resembles that of almost coeval late Campanian localities of Alberta (Eberth & Currie, 2005) and Texas (Sankey, 2010), with a wide range of preservation types including worn and milled bone fragments to unworn dinosaur teeth and bones. This situation suggests a variety of taphonomic histories for the Las Águilas dinosaur specimens, the cause of which is under study. From what we know now, the typical sequence of events would include: (1) death of an animal (natural, drowning, predation); (2) scavenging and dismembering of the carcasses by tyrannosaurids and other theropods; (3) periodical flash flood events sweeping the remains into fluvial channels; (4) final deposition with sediment on the lee sides of channels. However, the partially articulated skeleton of a juvenile individual (Fig. 12) suggests that the death of animals in the outer delta was rare.

CONCLUSIONS

The late Campanian vertebrate assemblage of the Las Águilas site in Coahuila, significantly improves our knowledge of the terrestrial and littoral fauna that inhabited the extreme southern margin of continental North America. Non-marine terrestrial environments at Las Águilas are dominated by a diverse assemblage of saurischian and ornithischian dinosaurs, turtles, crocodilians, and fresh water fishes, in a hitherto unknown diversity.

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