

A Deinosuchus riograndensis (Eusuchia: Alligatoroidea) from Coahuila, North Mexico

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ABSTRACT

Diagnostic remains of *Deinosuchus* have been discovered in the Aguja Formation (Late Cretaceous, late Campanian) near the town of La Salada (northwestern Coahuila, Mexico) and are described here for the first time. The material comprises six teeth and tooth fragments that were found associated with postcranial material such as two osteoderms and a cervical and caudal vertebra and is referred here to *D. riograndensis*. The association with a variety of herbivorous dinosaurs and trionychid turtles suggest a predator-prey interaction, which is confirmed by the occurrence of a vertebra with a *Deinosuchus* bite mark. The *Deinosuchus* remains from La Salada represent the southernmost occurrence of the genus known to date.

Key words: *Eusuchia*, *Alligatoroidea*, *Deinosuchus*, paleobiogeography, paleoecology, Late Cretaceous, Coahuila, Mexico.

RESUMEN

Restos diagnósticos de *Deinosuchus* han sido descubiertos por primera vez en la Formación Aguja (Cretácico Tardío, Campaniano tardío) cerca del poblado de La Salada (Noroeste de Coahuila, México), y se describen aquí por primera vez. El material abarca seis dientes y material postcranial como dos osteoderms y una vértebra cervical y una caudal referidas aquí a *D. riograndensis*. La asociación con una variedad de dinosaurios herbívoros y tortugas trionychidas sugiere una interacción depredador-presa, la cual es confirmada por la presencia de una vértebra con la mordida de un *Deinosuchus*. A la fecha, los restos de *Deinosuchus* de La Salada representan la ocurrencia más sureña del género.

Palabras clave: *Eusuchia*, *Alligatoroidea*, *Deinosuchus*, Coahuila, paleobiogeografía, paleoecología, Cretácico Tardío, México.

INTRODUCTION

Fossil remains of Mesozoic crocodyliforms are scarce in Mexico. Some material assigned to *Thalattosuchia* has been recently described for the marine Late Jurassic of Puebla (*Geosaurus vignaudi* Frey et al., 2002), Nuevo León (Velasco-Segura, 2007) and Coahuila (*Geosaurus saltillense* Buchy et al., 2006). A few Cretaceous crocodyliforms have been discovered in northern Coahuila. Two fragmentary skulls of dyrosaurids have been shown to two of us (EF and WS) by private collectors at Sabinas, and material referable to dyrosaurid crocodylians was collected at Las Aguilas but not yet been published. Recently, fragments of the giant alligatoroid *Deinosuchus* have been described from the Late Cretaceous (Campanian) San Carlos Formation in northern Chihuahua, south of Ojinaga (Westgate et al., 2006; Brown et al., 2004). Rivera-Sylva et al. (2009b) mentioned a tooth referred to cf. *Deinosuchus* from a new fossil site located near the border region between the Mexican states of Chihuahua and Coahuila (Figure 1). Further evidence for *Deinosuchus* came from the Aguja Formation (Late Cretaceous, late Campanian) near the town of La Salada in northwestern Coahuila, Mexico (Rivera-Sylva et al., 2008; Figure 1). These discoveries expanded the occurrence of *Deinosuchus* some 60 km further to the south than was previously known. However, the material was undiagnostic to species level. The material described in this paper represents the first record of skeletal elements diagnostic for *Deinosuchus riograndensis* (Eusuchia, Alligatoroidea). All fragments presented here likely come from the same individual with the exception of one vertebra. The speci-

mens were collected from the lower section of the Aguja Formation near La Salada (Figure 2). This discovery not only represents the first record of *Deinosuchus riograndensis* for Coahuila, but also it is the southernmost record of *Deinosuchus riograndensis* to date.

The Aguja Formation is Campanian in age and was deposited under deltaic conditions, representing marsh, lagoonal, and eu littoral to shallow marine environments (Hopkins, 1965; Weide et al., 1972; Lehman, 1982). These environments may have been the preferred habitat of *Deinosuchus* (Schwimmer, 2002; Lucas et al., 2006).

ABBREVIATIONS

CPC: Colección Paleontológica de Coahuila, housed at the Museo del Desierto. INEGI: Instituto Nacional de Estadística, Geografía e Informática.

SYSTEMATIC PALAEOLOGY

Crocodyliformes Benton and Clark, 1988
 Suborder Eusuchia Huxley, 1875
 Family Alligatoroidea Gray, 1844
 Genus *Deinosuchus* Holland, 1909

Deinosuchus riograndensis Colbert and Bird, 1954

Deinosuchus riograndensis Colbert and Bird, 1954, fig. 5

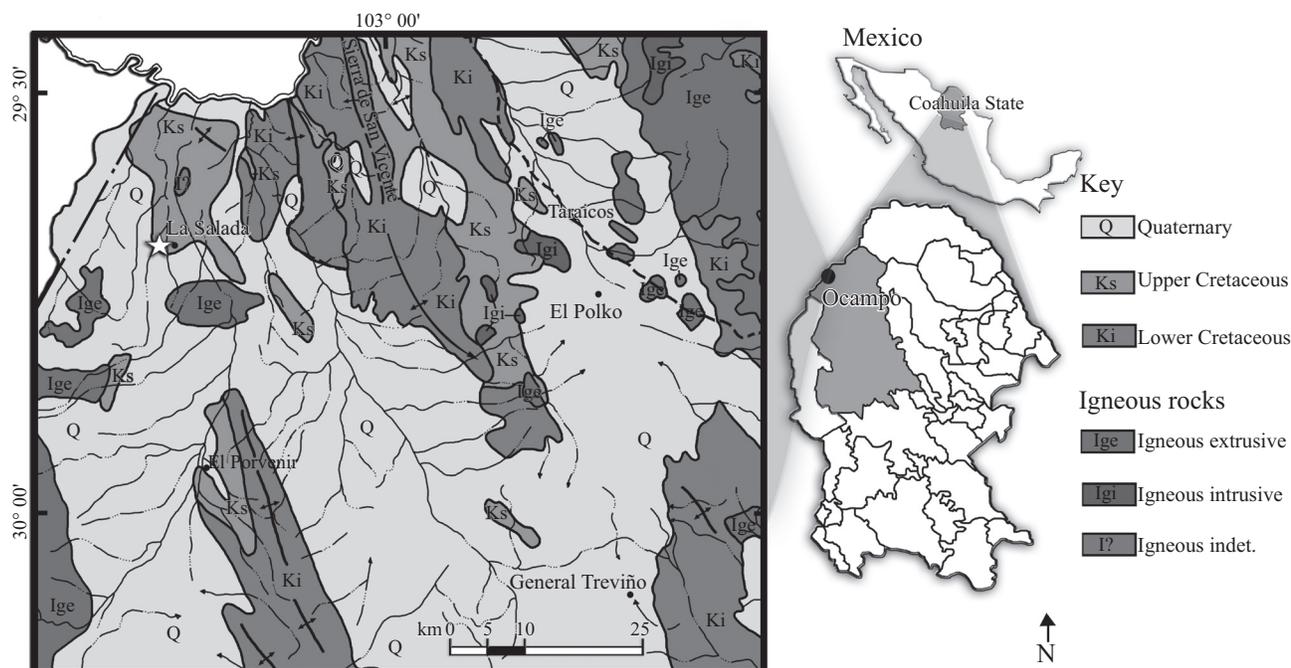


Figure 1. Geographical map of the La Salada locality; star indicates the *Deinosuchus* collection site.

Diagnosis. The robustness of the teeth and tooth fragments, combined with the extraordinary thickness of the enamel are diagnostic for the genus *Deinosuchus* (Figure 3; Colbert and Bird, 1954). The two procoelous vertebrae with preserved remnants of a circumference for the annulus fibrosus (Figure 4 a-l; Salisbury and Frey, 2000) are indicative for Eusuchia (Huxley, 1875).

The osteoderms are exceedingly massive compared with their size and show a coarsely pitted and wrinkled external surface, which is also diagnostic for *Deinosuchus* (Figure 4m-4s; Holland, 1909; Brochu, 1999; Lucas *et al.*, 2006).

Following Brochu (2003), Rivera-Sylva *et al.* (2008) assumed that the specimens from Coahuila were likely conspecific with *Deinosuchus riograndensis*, which had been described by Colbert and Bird (1954) from the Aguja Formation, Big Bend National Park, Texas (Colbert and Bird, 1954).

Material. The material described here is housed at the palaeontological collection of the Museo del Desierto (MUDE), Saltillo, Coahuila and is accessible under the collection number CPC 484. It comprises six teeth and tooth fragments (CPC 484/1; CPC 484/2; CPC 484/3; CPC 484/4; CPC 484/5; CPC 484/6; Figure 3), a sixth or seventh cervical vertebra (CPC 484/7; Figure 4 a-f), a caudal vertebra (CPC 484/8; Figure 4 g-l), an accessory cervical left osteoderm (CPC 484/9; Figure 4 p-s), and a ventral osteoderm from the gulothoracic area (CPC 484/10; Figure 4 m-o).

Distribution. Lower member of the Aguja Formation (Late Cretaceous, late Campanian) in the La Salada, Ocampo district, northwestern Coahuila, Mexico (Figures 1, 2).

Description. Teeth. The six tooth crowns show only chips of the enamel (CPC 484/5 and CPC 484/6; Figure 3 s-u) and are identified as belonging to *Deinosuchus* considering the thickness of the enamel as the only diagnostic character. Two specimens (CPC 484/3 and CPC 484/4; Figure 3 m-r) represent fragments of tooth crowns. One of them (CPC 484/4; Figure 3 p-r) lacks the apex and base. The second (CPC 484/3; Figure 3 m-o) lacks the apex and a section of the basolingual enamel, but the dentine core is preserved to the base of the crown. The crown height is reconstructed to about 40 mm with a basal diameter of about 20 mm. The tooth crowns CPC 484/1 (Figure 3 a-f) and CPC 484/2 (Figure 3 g-l) are complete with the enamel preserved to the apex. At the crown base, chips of the enamel have flaked off and the dentine core is exposed there. Crown CPC 484/2 (Figure 3 g-l) lacks the entire root and a bit of the crown base. The crown height is 49 mm with a maximum basal diameter of 29.3 mm and a minimum one of is 26.9 mm. On the labial face, a chip of enamel is missing. Crown CPC 484/1 (Figure 3 a-f) is the most complete of the six specimens, because the apical fourth of the root is preserved. With a crown height of 48.6 mm it is the largest of crowns. The diameter at the crown base is 29 mm, it is circular in cross section. Both teeth show one (CPC 484/1) or two cracks (CPC 484/2) respectively, that run from the

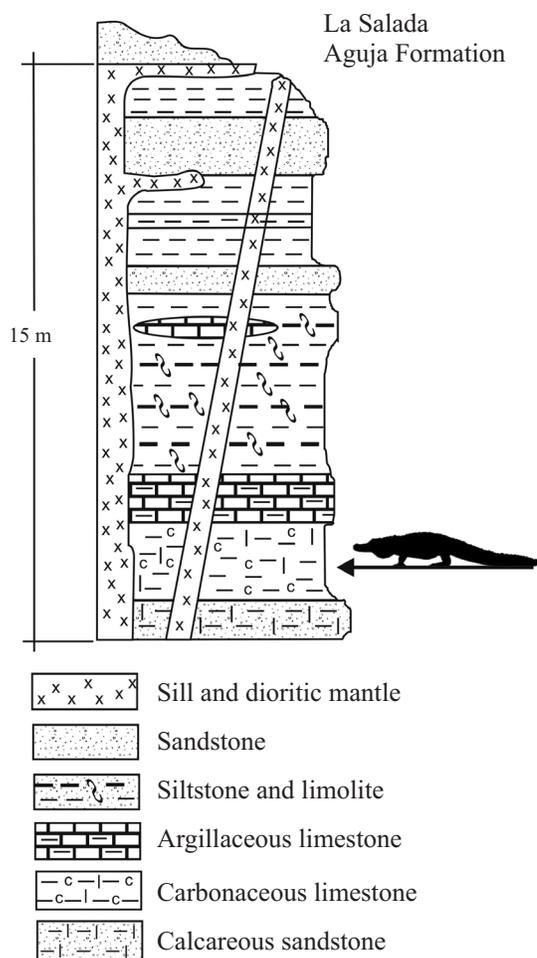


Figure 2. Stratigraphic section of the Aguja Formation at the La Salada locality.

basal end of the tooth fragment to almost the apex of the crown. The enamel surface is finely striated, the striation is more dense and pronounced around the base of the crowns (Figure 3 a-o). Lingually, several pronounced carinae almost reach the otherwise smooth apex, which does not show any traces of wear. The carinae on the labial face are much less expressed. While the dentine core of CPC 484/2 (Figure 3 g-j) shows no zoning, the root fragment CPC 484/1 (Figure 3 a-d) consists of two concentric cores. The crack only affects the external core and then curves into the border between the internal and external dentine layer. In all three teeth where the base of the crown is preserved, the apex of the pulp cavity is visible (Figure 3 f, l, o). Because there is no trace of resorption inside the pulp cavity, the teeth most likely fell off the jaws of a *Deinosuchus* carcass (Frey and Mooninger, 2010). The cracks occurred as a consequence of post-mortem desiccation. Similar desiccation cracks are found in extant crocodylians (EF pers. obs.).

Vertebrae. Both vertebrae are procoelous, which is consistent with the eusuchian type of vertebrae (Figure 4 a-l; see above). In both vertebrae only the centrum is preserved. One of the two (CPC 484/8; Figure 4 g-l),

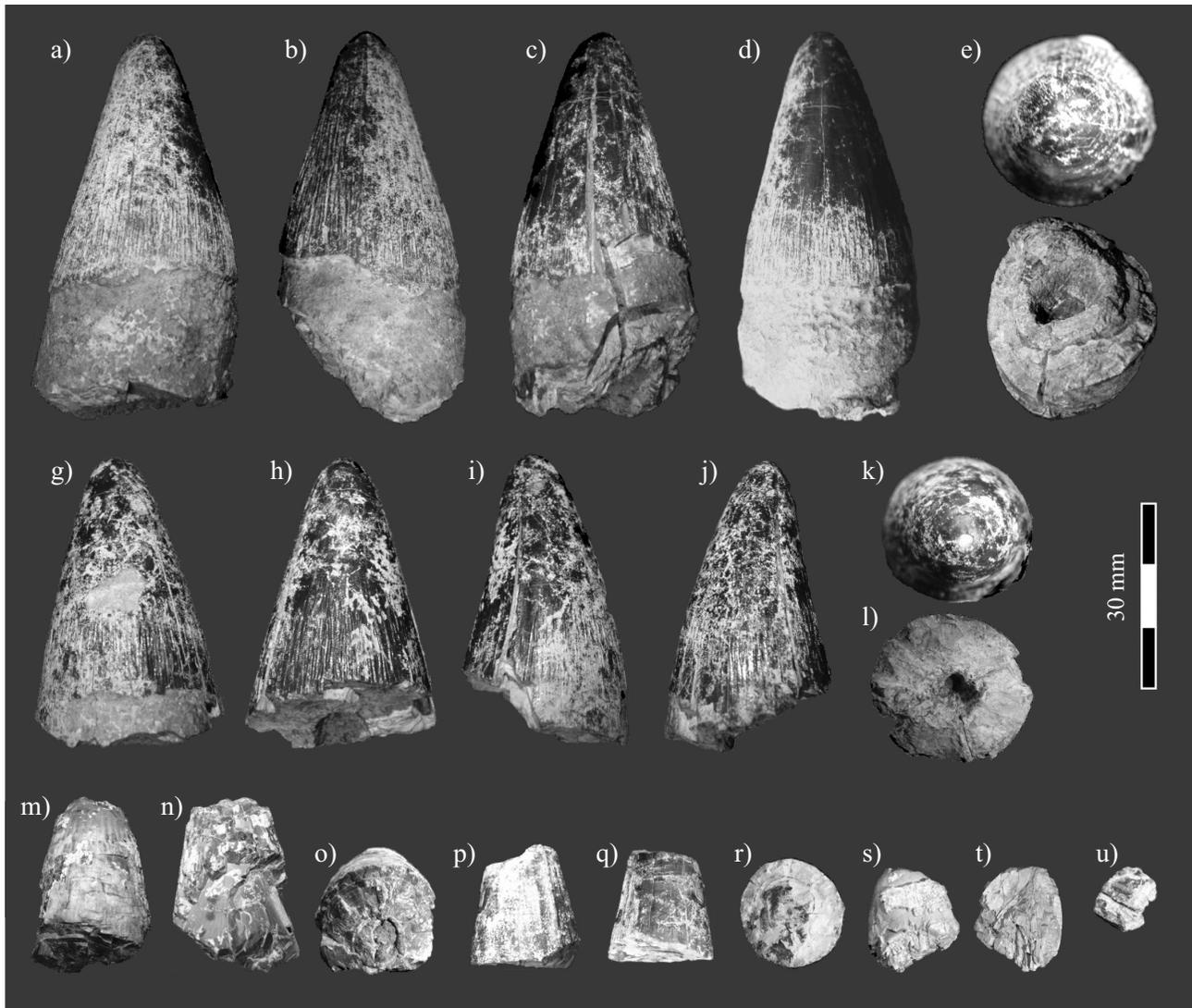


Figure 3. *Deinosuchus rugosus*, teeth. a-f: CPC 484/1; a: labial view, b: lingual view, c: cranial view, d: caudal view, e: apical view, f: radical view. g-l: CPC 484/2; g: labial view, h: lingual view, i: cranial view, j: caudal view, k: apical view, l: radical view. m-o: CPC 484/3; m: labial view, n: lingual view, o: radical view. p-r: CPC 484/4. p: labial view, q: lingual view, r: radical view. s-t: CPC 484/5; s: labial view, t: lingual view. u: CPC 484/6; fragment.

which shows surface abrasion due to transport, presents a transverse oval cross section and a wide floor of the canalis neuralis. The badly worn facets of the sutura neurocentralis are orientated dorsolaterally at an angle of approximately 45° with the horizontal plane. The cranial articular facet is transverse oval in outline, 43 mm wide and 35.7 mm high. The articular condyle is regularly convex in all directions and shows surface weathering. Its caudal extension is half the length of the centrum. A pair of long oval parapophyses protrudes from the lateral face of the centrum. They are badly worn and face ventrolaterally at an angle of about 120° as can be judged from the left parapophysis which is the better preserved. The right one has broken off at its base. The ventral face of the centrum shows two depressions where the parapophyseal peduncles merge with the centrum. Along the ventral median line of the centrum there is a low

but sharp keel, which represents the remnant of an almost completely weathered hypapophysis. The transverse oval cross section, the presence of a parapophysis on the lateral face of the centrum and the presence of a hypapophysis are typical features for vertebrae from the cervical and prothoracic series (Frey, 1988b). Based on comparison with the skeleton of an extant *Alligator mississippiensis* we conclude that the vertebral corpus most likely represents the sixth or seventh vertebra of the cervical series, especially due to the position and length of the parapophysis.

The second vertebra (CPC 484/7; Figure 4 a-d) has a maximum length of 98.84 mm, a height of 59.1 mm and a width of 48.94 mm, which makes it high oval in cross section. The neural canal is about 4 mm wide. The sutura neurocentralis is orientated almost horizontally. Ventral to the sutura neurocentralis there is a shallow depression,

which extends along almost the entire lateral face of the centrum. The centrum bears a single blunt ventral keel, which is indicative for a caudal vertebra of the terminal third of the tail. The terminal extension of the vertebral condyle is half the length of the centrum and the cranial articular facet partially preserves the circumferential flange for the annulus fibrosus (Salisbury and Frey, 2000). Compacta is only preserved on the lateral faces, the ventral keel and the cranial articular facet of the centrum.

Osteoderms. The material comprises two isolated osteoderms. One of the two (CPC 484/10; Figure 4 m-o) is irregularly hexagonal. Breakage occurred along two opposing margins, but little substance is missing. The osteoderm has a maximum diameter of 67.9 mm measured between two intact corners. Its thickness ranges from 10 mm up to 19 mm, resulting in a thickness coefficient ($\text{diameter}^{\text{max}} / \text{thickness}^{\text{max}}$) of approximately 3.5, which falls within the range of a ventral osteoderm of *Deinosuchus*. The external surface is sculptured with 16 subcircular pits, which are widely spaced and randomly scattered (Figure 4m). Their diameters range from 3 mm to 10 mm. Otherwise the external face of the osteoderm is smooth and slightly vaulted in all directions. The internal face shows faint radial striations along the margins and a lattice work in the centre (Figure 4o). The striae do not penetrate the basal plate and therefore represent the insertion places of connective tissue within the corium (Salisbury and Frey, 2000). It presents three nutritious foramina with a diameter of about 2 mm, perforating the basal plate in one half of the internal surface, which is slightly convex in one direction. All intact margins are irregular and strongly serrated. The broken surfaces show a transverse oval medullar cavity separating the basal plate from the external cortex. The medullar cavity is filled with the same yellow-red sediment, in which the specimen was embedded. The sculptured external surface lacking a keel, the polygonal outline and the serrated margins make it likely that the osteoderm comes from the ventral armour probably from the gulothoracic area, where most polygonal osteoderms occur.

The second osteoderm is nearly complete and (CPC 484/9; Figure 4 p-s) has an irregular long oval outline. The length is 55.6 mm, with a width of 46 mm, that makes a length-width ratio of 1.2. The external face of the osteoderm bears a blunt keel that runs at an angle of about 20° to the long axis of the bone (Figure 4p). The terminus of the keel slightly overlaps the margin of the osteoderm and marks its caudal end. The very tip of the keel is missing. Cranially the keel merges with the rest of the osteodermal surface, which is irregularly wrinkled and covered with scratch marks from an earlier preparation attempt. There are twelve circular pits scattered randomly over the flanks of the keel. Furthermore, the surface of the osteoderm presents scratch marks, resulting from the attempt of an amateur to clean the specimen (see above). The margin bears numerous blunt protrusions which become more pronounced cranially (Figure 4p). The cranial margin shows a pair of symmetrical blunt convexities

separated by a sharp median recess. The internal surface of the osteoderm is smooth and slightly convex in all directions (Figure 4q). A faint radial striation arranged in concentric circles marks the insertion places of the corium connective tissue. There is one nutritious foramen. Due to its margin free of sutures, the osteoderm was a floating osteoderm within a keratinous scale. Such osteoderms occur in the dermis of the flanks of tail and body, of the neck (accessory osteoderms), but also of legs and arms (Frey, 1988a). The inclination of the keel as well as its shape and shortness identify the osteoderm as coming most likely from left side of the neck. All other accessory osteoderms from the body show a more symmetrical orientation of the keel, are flatter, and the keel does not protrude over the margin of the osteoderms (Frey, 1988a). The osteoderms in the extremities are mostly restricted to the keel of the scale and thus show no basal plate.

DISCUSSION

In the vicinity of the *Deinosuchus* finds at La Salada we collected fossil remains of a diverse tetrapod assemblage, including lepisosteid scales, osteoderms of a trionychid turtle, and dinosaur remains referred to Hadrosauridae and Ceratopsidae, including a hadrosaurian vertebra with a bitemark applied by a *Deinosuchus* (Rivera-Sylva *et al.*, 2007; Rivera-Sylva *et al.*, 2009a). Foraminifers associated with the vertebrate fossils belong to the genus *Heterohelix* and suggest a Late Cretaceous Campanian to Maastrichtian age for the sediment. This interval falls within the time frame of the North American specimens of *Deinosuchus*. Sedimentological data at La Salada suggest a deltaic river system with frequent incursions of sea water. A similarly brackish regime was suggested as habitat for *Deinosuchus* in other regions of North America, especially for the coastal areas of the Western Interior Seaway (WIS; Schwimmer, 2002). Previously specimens of *Deinosuchus* have been reported from Alabama, Georgia, Mississippi, Montana, New Jersey, New Mexico, North Carolina, Texas, Utah, and Wyoming (Titus *et al.*, 2008). In 2006, the first Mexican specimen of *Deinosuchus* consisted of an isolated osteoderm from the San Carlos Formation of Coahuila, close to the border with Texas (Westgate *et al.*, 2006), indicating that the giant alligators also inhabited the coastal plains of the ancient Gulf of Mexico (Westgate *et al.*, 2006, Lucas *et al.*, 2006). The present finds provide further evidence that *Deinosuchus* inhabited the deltaic river systems that drained into the ancient Gulf of Mexico. This view is consistent with the assumption of Anglen *et al.* (2000) that *Deinosuchus* preferred stagnant brackish environments (see also Schwimmer, 2002). The finds of *Deinosuchus* reported here as coming from evidently deltaic deposits, less than ten kilometres from shore, indicate that *Deinosuchus*, could tolerate brackish or even marine environments at least for some time but likely inhabited freshwater as well. This hy-

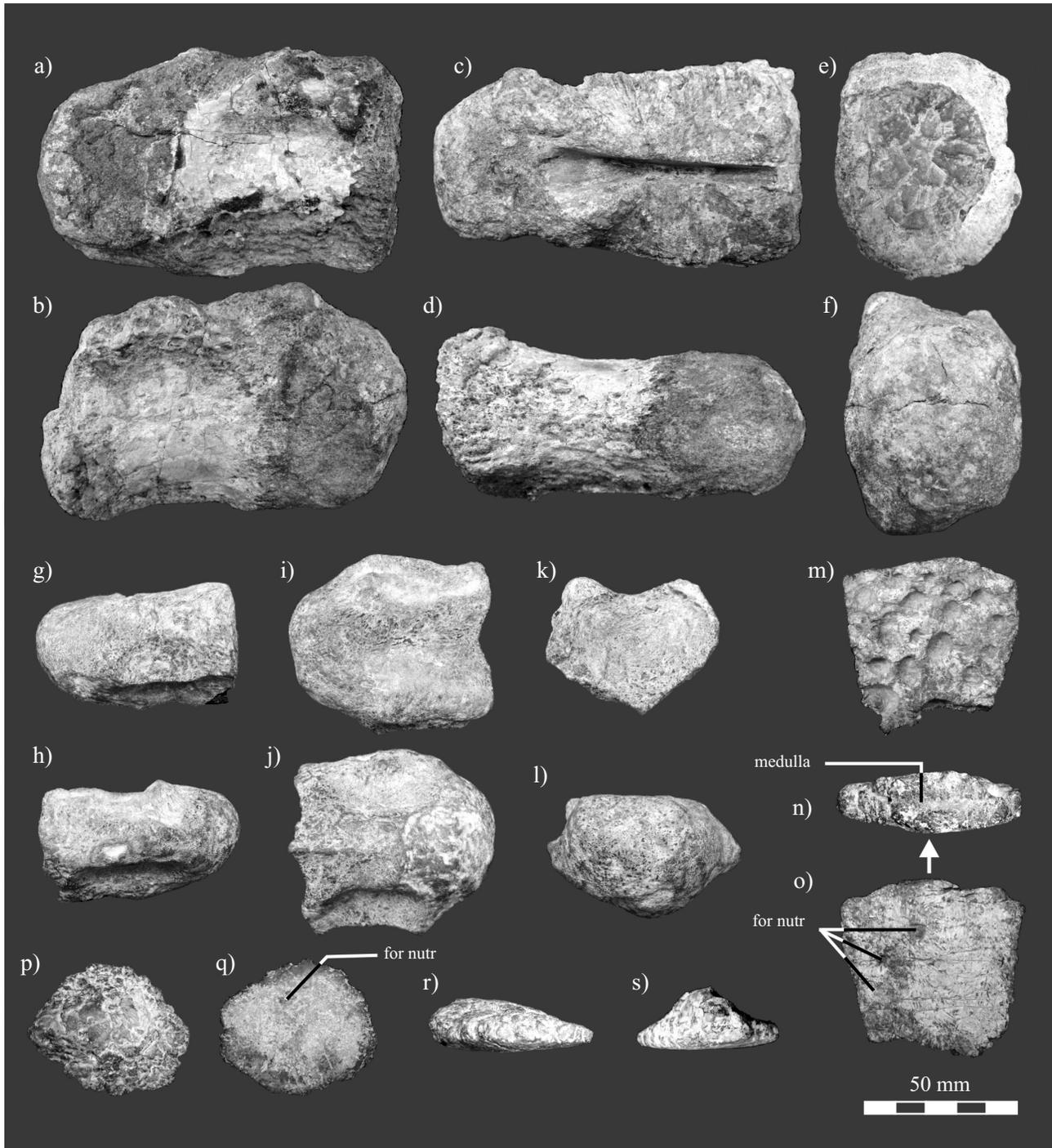


Figure 4. *Deinosuchus rugosus*, postcranial material. a-f: Caudal vertebra CPC 484/7; a: right view, b: left view, c: dorsal view, d: ventral view, e: cranial view, f: terminal view. g-l: cervical vertebra CPC 484/8: g: right view, h: left view, i: dorsal view, k: cranial view, l: terminal view. m-o: ventral osteoderm CPC 484/10: m: external view, n: section, o: internal view. p-s: accessory left cervical osteoderm CPC 484/9: p: external view, q: internal view, r: lateral view, s: cranial view.

pothesis is supported by the occurrence of large specimens of tryonychid turtles that survive brackish habitats but never invade marine environments (Böhme, 2002). Besides this, none of the extant alligatorid Eusuchia is known to have effective salt glands in contrast to some crocodylids like *Crocodylus porosus*, *C. niloticus* and *C. acutus*, and they are

thus unable to spread along coast lines or invade offshore islands. It cannot be excluded that *Deinosuchus* being an alligatoroid may have been more salt tolerant than extant alligatoroids and could invade the coastal sea. This would explain the occurrence of *Deinosuchus* remnants in marine deposits.

Desiccation cracks in the tooth specimens CPC 484/1 (Figure 3 a-f) and CPC 484/2 (Figure 3 g-l) indicate that the carcass was exposed to the sun for a long time and thus must have rested on land. Likely, the crocodylian died somewhere upstream in the water and was washed upon a sand bar where it decayed, or it died on this sand bar. After the carcass had completely decomposed the bones were washed back into the river system, where they were buried. With the exception of cervical vertebra CPC 484/8 (Figure 4 g-l), none of the specimens shows traces of abrasion. This indicates that they were embedded after a short distance of travel. Given the rarity of *Deinosuchus* bones in the area, the close assemblage of these specimens in the same state of preservation and coming from a crocodylian of similar dimensions suggest that they may derive from a single individual. In cervical vertebra CPC 484/7 (Figure 4 g-l) the surface appears to be polished. Corners and processes are degraded and barely visible. This bone was transported over a longer distance than the rest of the material collected and thus originated from upstream.

The size of the animal is estimated to a total length of about eight metres (Lehmann pers. comm. 2010) and thus represents a near adult specimen of *Deinosuchus*.

CONCLUSIONS

The new *Deinosuchus* material from northwest Coahuila, Mexico, represents the southernmost evidence for the occurrence of this animal known to date and shifts the distribution of this crocodylian 60 kilometres further to the south. During the Campanian-Maastrichtian, the coastline was less than ten kilometres away to the south and the landscape resembled that of the Everglades in Florida (U.S.A.). The presence of planctic foraminifers (*e.g.*, *Heterohelix*) indicates marine influence, but the occurrence of large trionychids suggests that it never became fully marine. The absence of *Deinosuchus* in the approximately coeval deposits of the Parras Basin (Coahuila, Mexico), about 300 kilometers south of La Salada indicates the presence of a geographical or an ecological barrier south of La Salada. Even after 15 years of thorough survey in the Parras Basin, *e.g.*, Las Aguilas, no trace of the presence of *Deinosuchus* was discovered. At Las Aguilas near the village of Jalpa de Zaragoza, a rhythmical sequence of sandstones and siltstones suggest deposition under brackish conditions, as indicated by oyster banks, shallow marine environments with abundant bivalves and gastropods, but also sharks, mosasauroids, dyrosaurid crocodylians and ammonites, and continental to brackish conditions, as indicated by characean oogonids, vascular plants, shell fragments of trionychid turtles and goniopholid crocodylians and dinosaurs (*e.g.*, Rodríguez-de la Rosa, 2007, Meyer *et al.*, 2008). Thus, there must have been a demarcation area between La Salada and Las Aguilas. The absence of *Deinosuchus* in the Parras Basin may be explained by the regional palaeogeography.

During the late Campanian, large wave-dominated delta lobes developed west of Piedras Negras, including the La Salada area, as well as around Monclova and towards the south in the Parras basin. Deposition in these areas was cyclical and consisted of alternating prodelta, delta front, delta plain and fluvial sediments. In the region between the two delta lobes, a contemporaneous large bay extended in the Muzquiz – Nueva Rosita – Sabinas area and sublittoral to marine sedimentation prevailed (McBride, *et al.* 1975, *fide* Arenas Partida *et al.*, 1986). We suggest that *Deinosuchus* was not able to cross the Sabinas marine embayment to the south probably due to a restricted saltwater tolerance. This could hint to an absence of salt glands in this giant alligatoroid and thus a limited saltwater tolerance.

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