A new specimen of *Cricosaurus saltillensis* (Crocodylomorpha: Metriorhynchidae) from the Upper Jurassic of Mexico: evidence for craniofacial convergence within Metriorhynchidae

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Abstract - Here we describe a new specimen of the metriorhynchid crocodylomorph *Cricosaurus saltillensis*. Furthermore, we amend the specific epithet to use the masculine suffix rather than the neuter suffix (i.e., change *saltillense* to *saltillensis*). The new specimen, like the holotype, is from the Tithonian (Upper Jurassic) La Caja Formation of Gomez Farías, Mexico. Based on this new specimen, *C. saltillensis* had proportionally the shortest snout and the shortest maxillary and dentary tooth rows of any member of the subfamily Metriorhynchinae. Furthermore, while the teeth are poorly preserved, carinae are visible (a rare morphology within *Cricosaurus*). The enlarged intratemporal flanges (anteromedial corners of the supratemporal fossae) demonstrate that the fibre length of the supratemporal adductor muscles were increased in *C. saltillensis*, this would have increased the medial component of the force vectors thereby stabilising the skull against torque. The reduced tooth count and carinated teeth, and a skull adapted to better resist torque suggest *C. saltillensis* was better suited to feeding on large-bodied prey than other members of the genus *Cricosaurus*.

Key words: *Cricosaurus*, Jurassic, Metriorhynchidae, Mexico, Rhacheosaurini, Tithonian.

INTRODUCTION

Investigation of the marine outcrops of the La Casita and La Caja Formations (Kimmeridgian to Berriasian) in north-east Mexico, as well as studies of specimens held in collections, has yielded a rich assemblage of marine reptiles (see a review in Buchy 2007, 2008a, b, 2010a, in press; Buchy & López Oliva, 2009; research financed by Deutsche Forschungsgemeinschaft and Consejo Estatal de Ciencia y Tecnología over the past decade). Although excavation and study are ongoing, metriorhynchid crocodylomorphs are the most abundant marine reptile group from these formations (Frey *et al.*, 2002; Buchy *et al.*, 2006b, c, 2007; Buchy, 2007, 2008a, b). Metriorhynchids are a highly aberrant clade of crocodylomorphs, which evolved numerous adaptations to a pelagic lifestyle, including a complete loss of their osteoderm armour, hydrofoil-like forelimbs, a hypocercal tail and large salt glands (Fraas, 1902; Andrews, 1913; Fernández & Gasparini, 2000, 2008; Fernández & Herrera, 2009; Young *et al.*, 2010).

One section of the La Caja Formation of particular interest is early Tithonian in age and is close to Gomez Farías in the State of Coahuila (Buchy *et al.*, 2006c). This section is a 1.5 m thick coquina layer considered a concentration Lagerstätte due to its richness of marine vertebrates (Buchy *et al.*, 2006a). It has yielded hundreds of remains of marine vertebrates (most held in the Museo del Desierto, Saltillo), many of which are awaiting preparation and/or study. Most unpublished thalattosuchian remains are still on loan at the Staatliches Museum für Naturkunde Karlsruhe, Germany. Although systematic statistical study of the composition of the Gomez Farías assemblage is still wanting, metriorhynchids represent the majority of marine reptile remains from the Gomez Farías assemblage (MCB pers. obs.). Following preliminary observations, Buchy *et al.* (2006a) suggested that the coquina was deposited in a shallow, subtidal, mud bottom environment below the storm wave base. This was suggested as the coquina shows a reduced rate of sedimentation and condensation, possibly due to transgression (see also Velasco Segura, 2005, 2007). However, a proper taphonomical study of the vertebrate remains is still needed (see Buchy *et al.*, 2006a; Buchy, 2010a).

Currently, only one species of metriorhynchid is known from the Gomez Farías site: *Cricosaurus saltillensis*

(Buchy *et al*., 2006c). Here we describe another specimen of *C. saltillensis* from the type locality, show that this specimen and species had a craniodental morphology convergent with geosaurine metriorhynchids, and finally we correct the suffix of the specific epithet from *saltillense* to *saltillensis*.

Institutional abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; CPC, Colección Paleontológica de Coahuila at MUDE; GLAHM, Hunterian Museum, Glasgow, United Kingdom; MUDE, Museo del Desierto, Saltillo, Coahuila, Mexico; NHMUK, Natural History Museum, London, United Kingdom; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

SYSTEMATIC PALAEONTOLOGY

Crocodylomorpha Hay, 1930 *sensu* Walker, 1970
Thalattosuchia Fraas, 1901 *sensu* Young & Andrade, 2009
Metriorhynchidae Fitzinger, 1843 *sensu* Young & Andrade, 2009
Geosaurinae Lydekker, 1889 *sensu* Young & Andrade, 2009
Rhacheosaurini Young *et al*., 2011a
Cricosaurus **Wagner, 1858**

Type species. *Stenosaurus elegans* [sic] Wagner, 1852. This follows Recommendation 67B of the Code of the International Commission on Zoological Nomenclature (ICZN).

Etymology. "Ring lizard". *Crico*- is derived from the Ancient Greek for ring (for the sclerotic ring within the orbit). While *–saurus* is the Latinised version of *sauros*, the Ancient Greek for lizard.

Emended diagnosis. Metriorhynchid crocodylomorph with the following unique combination of characters (autapomorphic characters are indicated by an asterisk*): procumbent dentition with a range of mediolateral compression; cranial bones generally smooth, lacking conspicuous ornamentation; acute angle formed by the lateral and medial processes of the frontal; dorsal margin of the supratemporal arcade lower than the medial process of the frontal*; orbit as large as the supratemporal fenestra*; surangular and angular well-developed, proceeding anteriorly beyond the orbit*; symphysial part of the mandible low*; lateral margin of the prefrontals rounded*; external nares is divided along the skull midline by premaxillary septum; external nares terminates level to the second maxillary alveoli or further posteriorly*; calcaneum tuber absent or vestigial*; proximal end of metatarsal I greatly enlarged* (modified from Young & Andrade, 2009).

Cricosaurus saltillensis **(Buchy *et al*., 2006c) Young & Andrade, 2009**
v* 2006c. *Geosaurus saltillense* sp. nov. – Buchy *et al*., p. 1571, figures 2-3.

Holotype. MUDE CPC 218: poorly preserved skull (lacking snout) with atlas-axis and several cervical vertebrae. Note the accession number of this specimen was formerly MUDE CEP 1823 (see Buchy *et al*., 2006c).

Etymology. 'Ring lizard from Saltillo municipality'.

Type Locality and Horizon. Early Tithonian (Upper Jurassic) section of the La Caja Formation at the Sierra El Jabalí (sometimes erroneously referred to as Sierra de Buñuelos), near Gomez Farías, Municipio de Saltillo, Coahuila, Mexico.

Referred specimen. MUDE CPC 487: Partial cranium and mandible with teeth, atlas-axis and four cervical vertebrae and ribs (from the type locality).

Emended diagnosis. Metriorhynchid crocodylomorph within the genus *Cricosaurus* with five autapomorphic characters: 1) foreshortening of the rostrum relative to basicranial length, with a resultant reduction in maxillary (maximum of 17 teeth per maxillae) and dentary teeth (approximately 15 teeth per dentary ramus); 2) frontal excluded from the centre of the dorsal margin of the orbit by the prefrontal; 3) anterior portion of the supratemporal fossae (intratemporal flange) are large and enter the minimum interorbital distance; 4) supratemporal fossae extremely long: maximum length approximately 2.5 times the posterior width; 5) the intertemporal bar is uniformly narrow in dorsal view, except at the anterior end of the parietal contribution which is transversely expanded. Note, the teeth are still poorly prepared, but based on an initial examination, the tooth crowns have a blunt apex and mesial and distal carinae (bicarinate dentition). Future work will be necessary to confirm this observation.

Correction of name. The spelling of *C. saltillense* is hereby corrected to *C. saltillensis*. This amendment of the specific epithet is based on using the masculine suffix rather than retaining the neuter suffix (i.e., *–sis* instead of *–se*). In accordance with the ICZN Code, Article 30.1.3 the gender of the generic and epithet name must match (if the epithet is adjectival). As *Cricosaurus* is masculine, the correct epithet suffix is *–sis*.

Preservation and taphonomy

The specimen was collected in March/April 2004 (field number GF31). Mechanical preparation was initiated at MUDE in October 2009 by Z.M. Casas Garcías, mostly done by A.I. Oyervides Salazar and completed by MCB.

The posterior and right edges of the specimen correspond to recent breaks that had weathered away recently, as did the posterior part of the ventral face (Figs. 1-3). The plaster jacket however encompassed whatever was left around the visible specimen of the bone-bearing level, resulting in an almost meter-wide jacket. No further remains were encountered, however there are difficulties associated with the Gomez Farías site: its vertical outcrop, remote location and poor contrast between bone and matrix (these are discussed fully by: Buchy *et al*. 2006a, c; Buchy, 2010a). The specimen comprises the dorsoventrally compressed (Fig. 4) complete left half of the skull, incomplete intertemporal bar and occip-
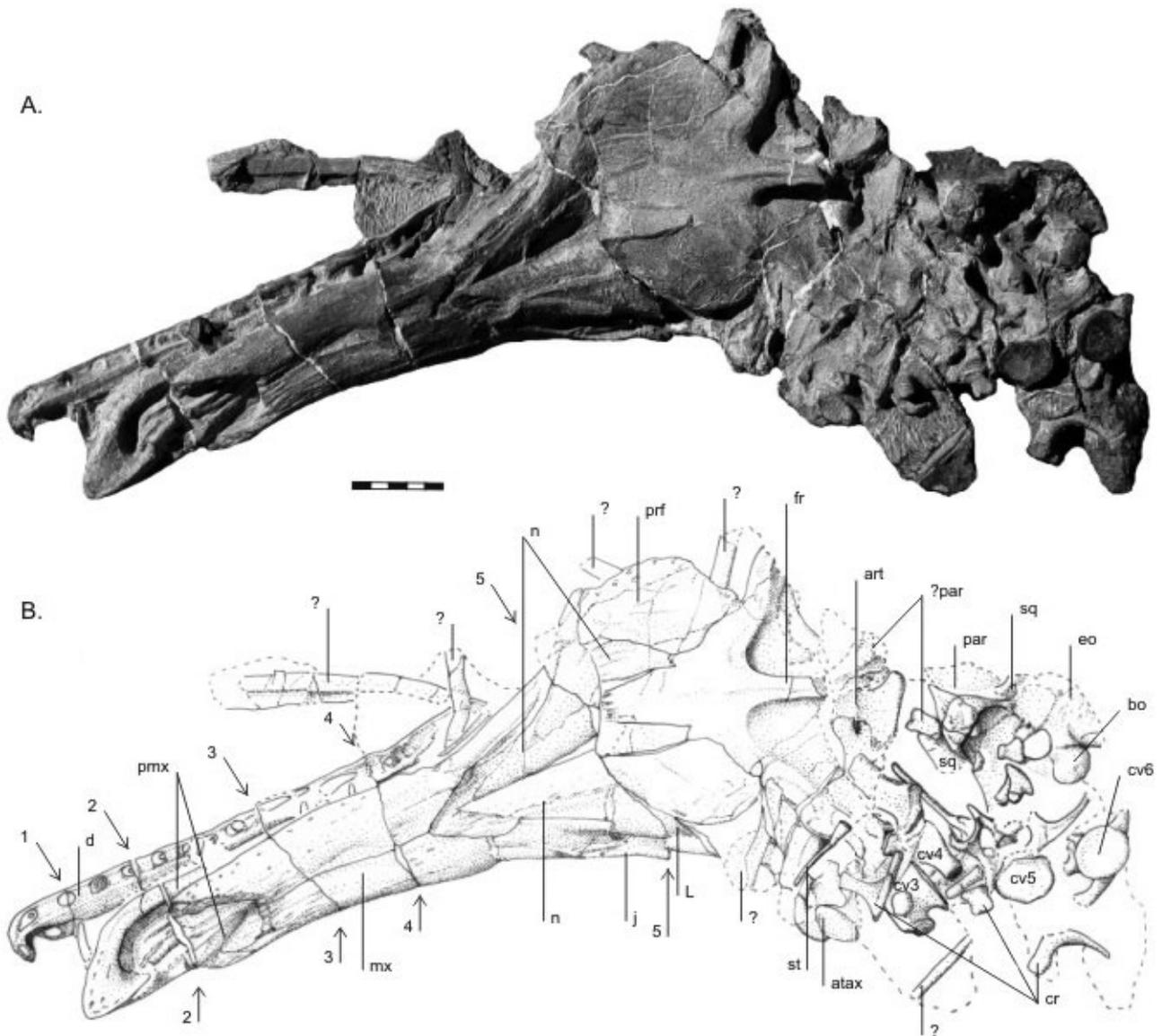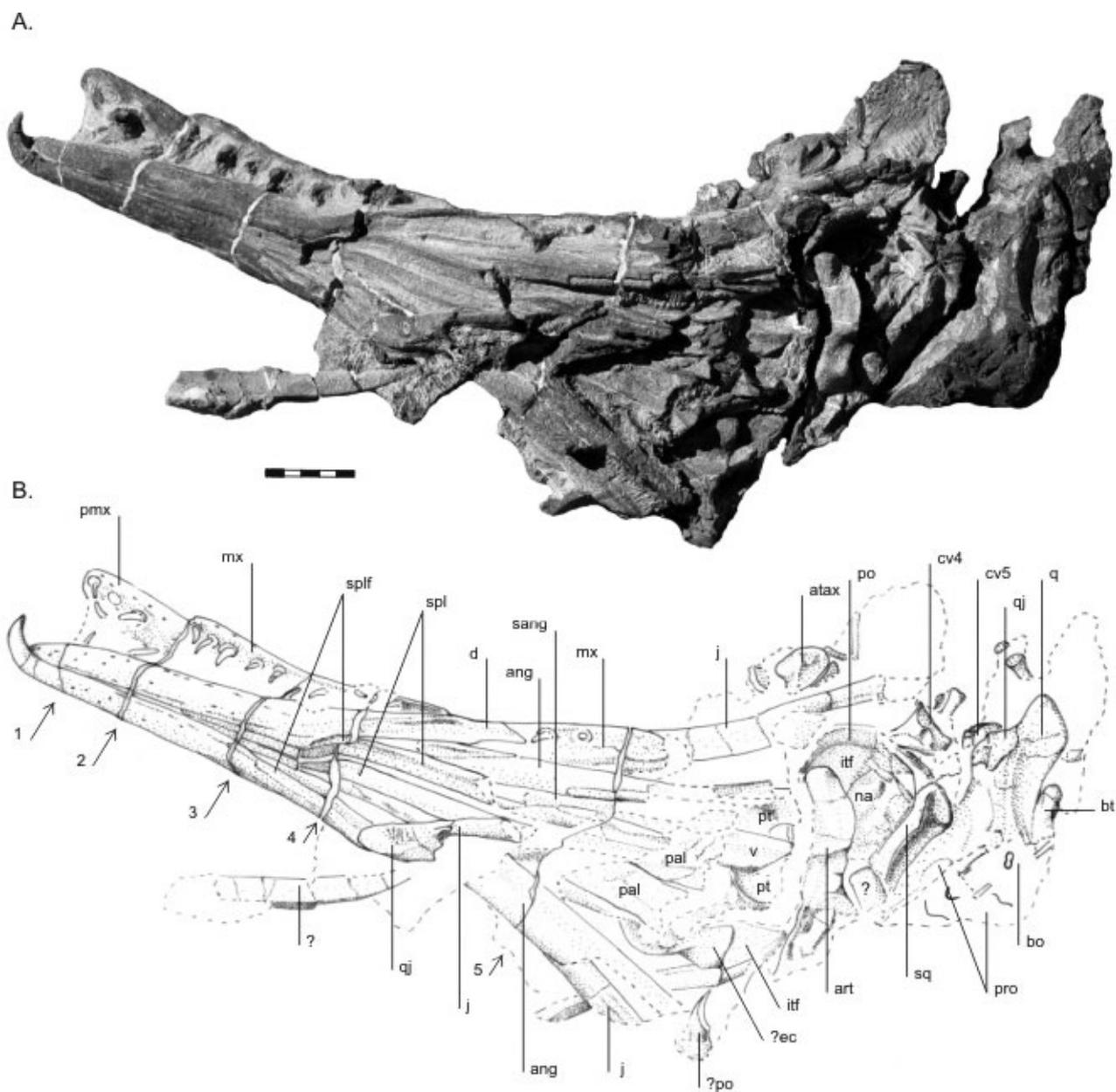
Fig. 1 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. A./ Dorsal view of the specimen; B./ interpretative drawing. Scale 50 mm.
Abbreviations: ang: angular; art: articular; atax: atlas-axis; bs: basisphenoid; bo: basioccipital; bo*: portion of the basioccipital exposed due to damaged quadrate; bt: basal tuber; cor: coronoid; cr: cervical rib; cvx: cervical vertebra *x*; d: dentary; ec: ectopterygoid; eo: exoccipital; fm: foramen magnum; fr: frontal; itf: intratemporal flange; j: jugal; L: lacrimal; me: cavity for the medulla elongata; mef: median eustachian foramen; mx: maxilla; n: nasal; na: neural arch; orb: orbit; pal: palatine; par: parietal; pca: posterior carotid artery; pmx: premaxilla; po: postorbital; pp: paroccipital process; prf: prefrontal; prfp: prefrontal pillar; pro: proötic; pt: pterygoid; ptf: posttemporal fenestra; q: quadrate; qc: quadrate condyle; qj: quadratojugal; rs: rhomboidal sinus; sang: surangular; scc: semicircular canal; so: supraoccipital; spl: splenial; splf: splenial facet on the dentary; sq: squamosal; st: stapes; tc: tympanic cavity; v: vomer; XII: foraminae for cranial nerve XII. Numbered arrows locate the sections illustrated in Figure 5.

ital surface whose ventral portion is weathered away. The posterior-most part of the right jugal and articulated partial quadratojugal is preserved ventral to the posterior portion of the right tooth row, which hints at some disarticulation prior to recent weathering, as does the posterior portion of the right mandible preserved transversely oriented just posterior to the pterygoids. The partial vertebral column (atlas-axis, cervical centra three [C3] to six [C6] with articulated neural arches and ribs) is resting over the left supratemporal fenestra and occiput. The right mandibular ramus slid anteriorly against the left one (as witnessed by the relative position of visible alveoli on both rami); subsequently, the anterior-most part of the right ramus bent medially. This type of preservation is reminiscent of the ophthalmosaur MUDE CPC 238 from the same site, and hints at at-least partial vertical embedding in a soft substrate prior to winnowing (Buchy,
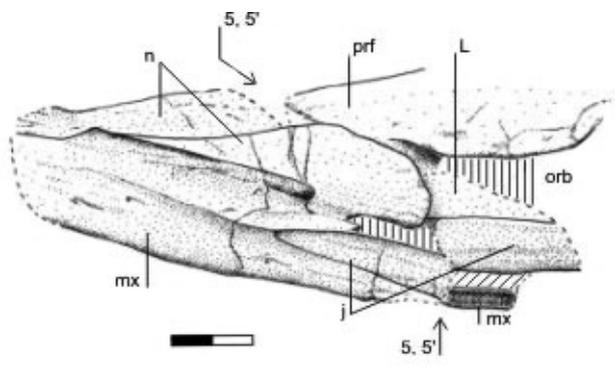
Fig. 2 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. A./ Ventral view of the specimen; B./ interpretative drawing. Scale 50 mm. Abbreviations as in Figure 1.

2010a). The premaxilla was disarticulated from the maxilla, its posterior portion having rotated rightward and/or its anterior portion leftward, so that the posterior-most portion of the left premaxilla now rests within the external nares and the same portion of the right premaxilla is pressed against the lateral anterior-most part of the right maxilla. The maxillary rostrum also curved leftward and broke, whereas the whole preorbital portion is rotated leftward compared to the prefrontal-postorbital portion. This last movement was not accompanied by extensive breakage (except of the posterior processes of the nasals); instead, it exposed the grooved overlapping surface contacts (Fig. 1). This hints at an incompletely ossified specimen, as do the very clear sutures com-

pared to the condition of other specimens from the same site (Buchy, 2007, 2010a). Similarly, the various elements of the mandibular rami posterior to the mandibular symphysis are disarticulated without breakage, and close to their original position. Transverse breaks allowed a view of the inner anatomy of the specimen: these are numbered from 1 and 1' to 5 and 5' (1 for the anterior aspect of break 1, 1' for its posterior counter-aspect, etc.), illustrated in Figure 5 and discussed below. Damaged sections were documented photographically, studied, and then restored, to prevent damage and loss of material during future curation. The type of epoxy resin is unlikely to prevent computed-tomography (CT) scanning of the specimen in the future (Liston pers. com., 2009).
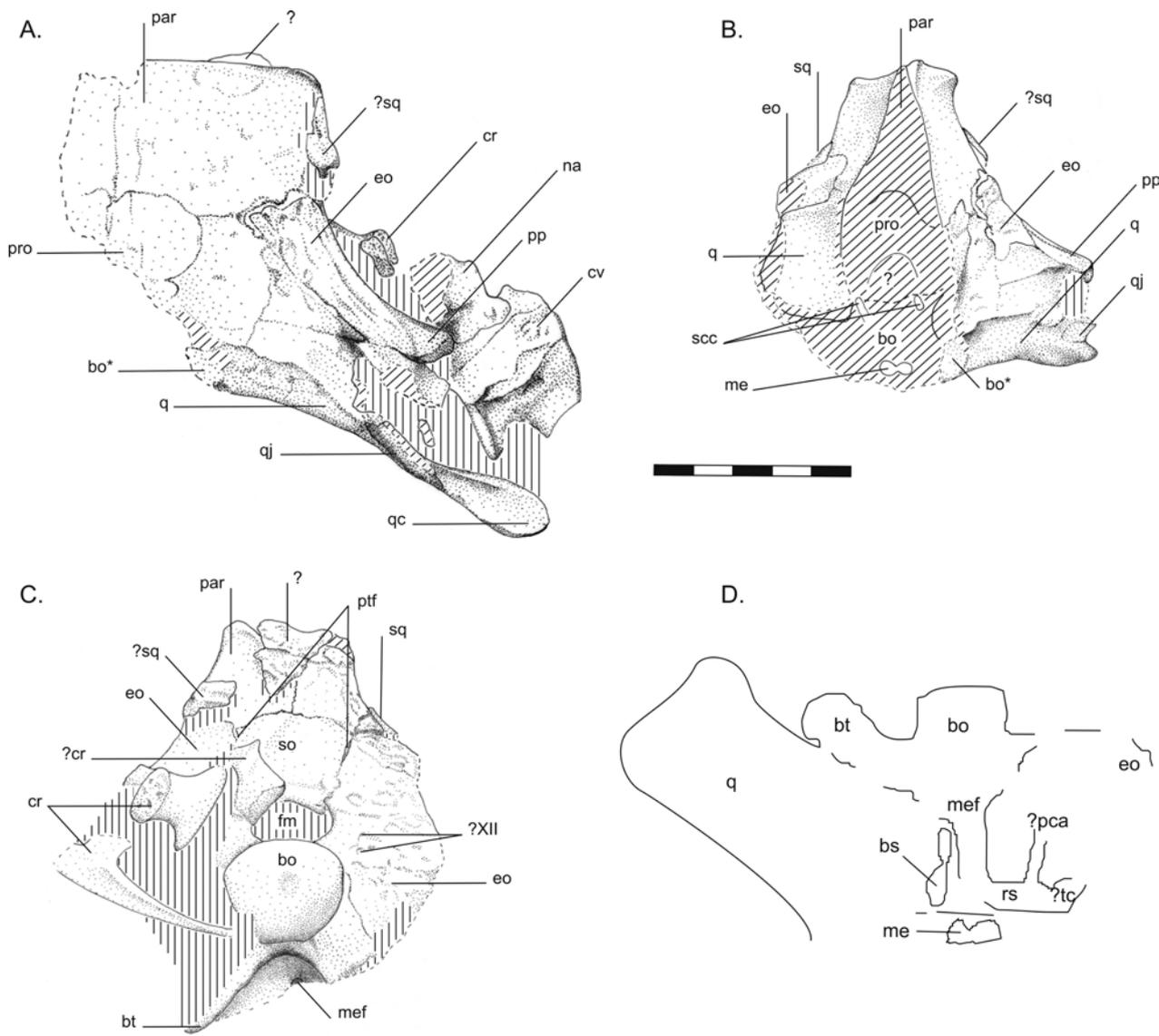
Fig. 3 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. Interpretative drawings of occipital portion in A./ left lateral; B./ anterior; and C./ occipital (= posterior) views. D./ Sketch of the occipital portion in ventral view (this face is extremely weathered). Scale 50 mm. Abbreviations as in Figure 1.
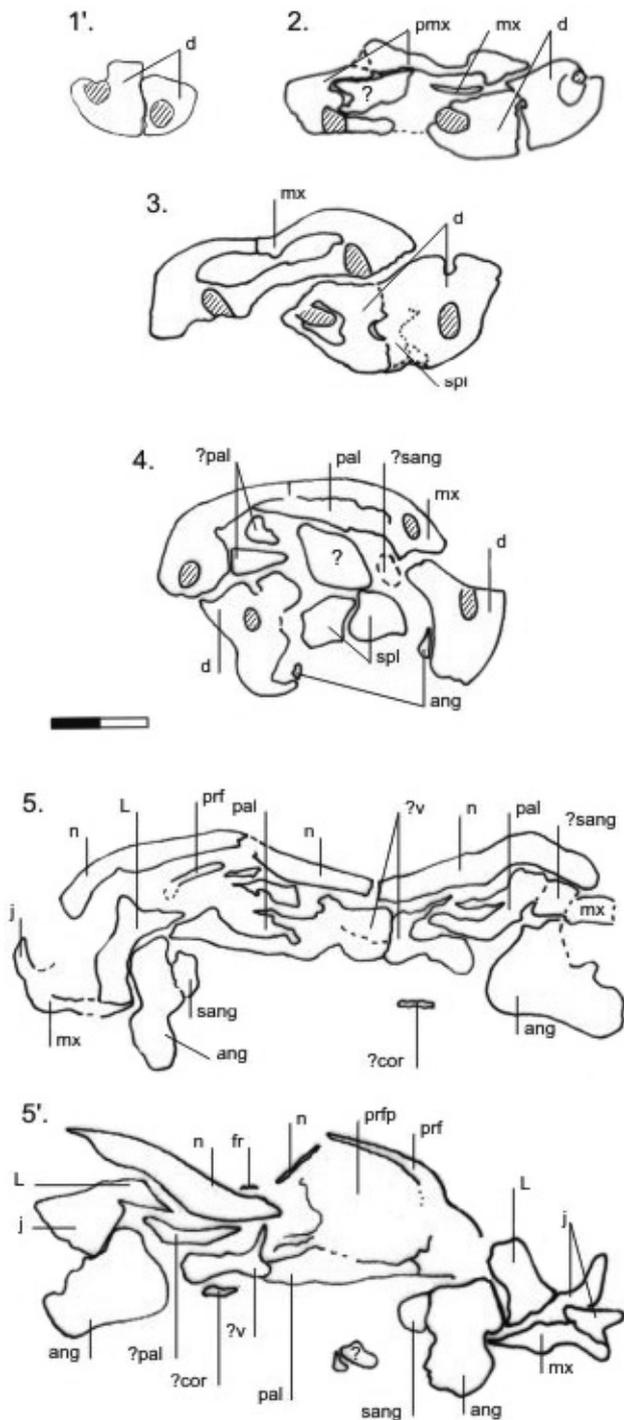

Fig. 4 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. Interpretative drawing of the left preorbital fenestra area. Scale 20 mm. Abbreviations as in Figure 1.

Several fossilized wood fragments were preserved with the specimen. Some unidentified elements, visible on sections 2 and 4 (Fig. 5), may represent further of these. Wood is generally abundant from the site, from where specimens collected may reach up to several decimetres in length.

Mechanical preparation could not adequately expose the enamel of the teeth (Fig. 6). This appears a general problem for the Late Jurassic Mexican sites, one that remains unexplained (Buchy, 2007). Some teeth were left unprepared so that taphonomical studies may indicate a preparation technique that would yield better results, and to leave the possibility of CT scanning.
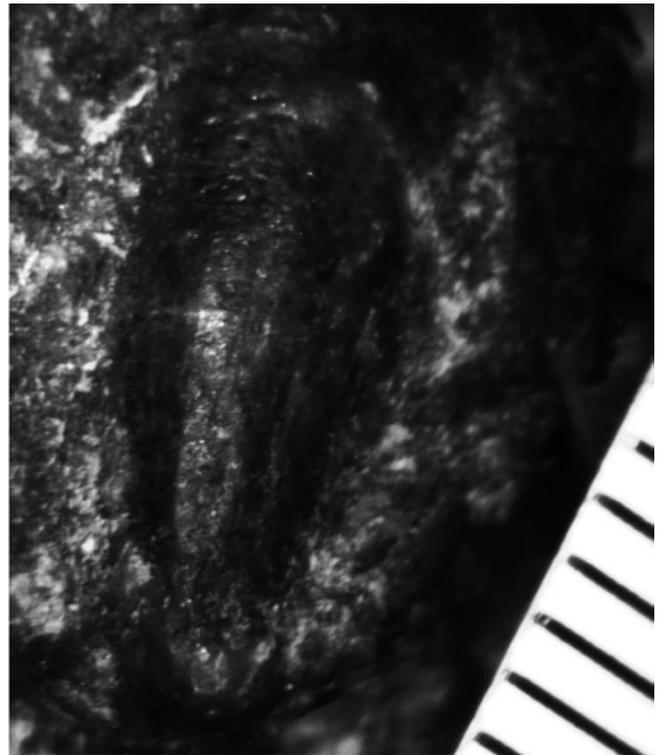
Ontogenetic stage and body length estimate

The progression of vertebral centrum-neural arch fusion has often been used as an indicator of ontoge-

Fig. 6 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. Photograph of one of the visible right maxillary teeth. Scale in mm.

Fig. 5 - *Cricosaurus saltillensis* referred specimen MUDE CPC 487. Cross-sections through the rostrum as numbered on Figures 1 and 2, interpretative drawings. Scale 20 mm. Abbreviations as in Figure 1.

netic stage in fossil crocodylomorphs (Brochu, 1996). The sequence of neurocentral suture closure in the crocodylian vertebral column follows a consistent pattern: caudal to cranial, with fusion of the cervical neurocentral sutures occurring in morphologically mature specimens (Brochu, 1996). The caudocranial pattern has been observed in Early Juras-

sic thalattosuchians (Delfino & Dal Sasso, 2006) and Middle Jurassic metriorhynchids (see Young *et al*., in press).

The neurocentral sutures of the cervical vertebrae are not fused in MUDE CPC 487 (Fig. 1). As such, this individual is not a morphologically mature individual. However, without the rest of the vertebral column we cannot exactly determine ontogenetic stage of the individual. The basicranial length of MUDE CPC 487 is conservatively estimated to be 500 mm, which using the body estimation method outlined by Young *et al*. (2011b) gives a total length of 2.67 m. With such a basicranial length, MUDE CPC 487 is a medium-sized cricosaur (see Table 1).

Skull

Premaxilla. Each premaxilla has three tooth alveoli. A short diastema follows posteriorly (section 2, Fig. 5). Ventrally, the premaxilla is obscured by matrix and teeth; as such, the contact with the maxilla could not be determined. The interpremaxillary suture was not exposed dorsally by preparation, most likely due to the thinness of the structures. The premaxilla appears to be gently constricted between alveoli one and two, and to expand posterolaterally, although this may be due to preservation. Anteriorly, the premaxillae unite to form a midline septum dividing the external nares. Bone fragments within the external nares are likely part of the premaxillae that were compressed and broken post-mortem (section 2, Fig. 5).

Table 1 - Alveoli count of selected metriorhynchine species. In all species the premaxillary tooth count is invariant at three.

Species	Age	Skull length (cm)	Maxilla	Dentary	Carinae
Metriorhynchus superciliosus GLAHM V985, GLAHM V987, GLAHM V1009; SMNS 10115, SMNS 10116; Andrews, 1913; Eudes-Deslongchamps, 1869; Lepage *et al.*, 2008	Middle – Late Callovian	61-83	23-28	20-22	Bicarinate
Gracilineustes leedsi NHMUK PV R3014, NHMUK PV R3015, NHMUK PV R3540; Andrews, 1913	Middle Callovian	48-58	~34	~34	Bicarinate
Cricosaurus araucanensis Gasparini & Dellapé, 1976	Early Tithonian	60	27/28	29	No
Cricosaurus elegans BSPG AS I 504; Wagner 1852, 1858	Early Tithonian	~35	20+	20+	No
Cricosaurus macrospondylus Hua *et al.*, 2000	Late Valanginian	~85	up to 18	?	Unicarinate
Cricosaurus saltillensis	Early Tithonian	~50	up to 17	~ 15	Bicarinate?
Cricosaurus suevicus SMNS 9808; Fraas 1901, 1902	Late Kimmeridgian	39	26	24	No
Cricosaurus vignaudi Frey *et al.*, 2002	Tithonian	49.5	?	15 visible, up to 20	No

Maxilla. In dorsal view, the premaxilla-maxilla sutural contact is a 5-7 mm long surface of anteroposteriorally oriented grooves and ridges (with the premaxilla overlapping the maxilla). Posteriorly, the maxilla overlapped the nasal. Along the skull midline, the maxilla solely forms the dorsal margin of the rostrum over a length equivalent to the total length of the premaxilla. Due to dorsoventral compression, the anatomy of the preorbital fenestra/fossa region is unclear (Fig. 4; sections 5, 5', Fig. 5). The maxilla appears to form the floor of the preorbital groove and the anterior margin of the fenestra (see Fernández & Herrera, 2009 for a discussion on the homology of the metriorhynchid preorbital fenestra and the archosaurian antorbital fenestra). Dorsal to the groove, the maxilla also forms a sharp crest, which abruptly terminates at the suture with the nasal, possibly due to ventral compression of the nasal part of the crest (as appears to indicate section 5, Fig. 5).

The interalveolar spaces are irregular in length, from a few millimetres in length to more than 10 mm (Fig. 2). Consequently, the number of maxillary teeth is difficult to estimate (also due to the material being left to be prepared in the future). The exact number of alveoli in the left maxilla is unclear, but it is possible that 12 are preserved. Where the dentary obscures the alveolar surface of the left maxilla (Fig. 2), a maximum of five more alveoli could have been housed. The maxilla terminates about 20 mm posterior to section 5 (Fig. 5) as a millimetre-thin lamina of bone ventral to the jugal, the maxillary tooth row terminates about 20 mm anterior to that section.

Lacrimal. The left lacrimal is better visible on sections 5 and 5' (Fig. 5). In that view it is quadrangular in shape, however it is unknown how much of it was actually exposed laterally.

Jugal. The anterior-most portion of the jugal forms the lateral margin of the preorbital groove (Fig. 4). Posteriorly (section 5, Fig. 5) the jugal enlarges medially and ventrally to form a massive bar that formed the ventral margin of the orbit. The contact with the postorbital is not visible. The jugal narrows posterior to the orbit, with its width being approximately half that of its width beneath the orbit. The cross-sectional shape of the orbital portion cannot be determined. Posteriorly, the jugal is a dorsoventrally-orientated oval in cross-section until it contacts the quadratojugal. The suture with the quadratojugal is indistinct, except in ventral view. Here the suture orientated anteromedially - posteriolaterally.

Quadratojugal. The posterior-most margin of the right quadratojugal is gently rounded and millimetre-thin. Further anteriorly, the bone is somewhat thicker, where it was wedged between the jugal and the quadrate. In this area, the sutural contact surface with the quadrate is marked by subvertical grooves and ridges (Fig. 2). A small portion of the left quadratojugal is still articulated with the quadrate, approximately level with the distal-most extremity of the paroccipital process (Fig. 3).

Postorbital. The left postorbital (Figs 1, 2) is preserved below the partial vertebral column and is mostly visible in ventral view. It forms the ventrally sharp, semicircular lateral margin of the supratemporal fenestra (that may be partially formed by the frontal anteriorly, and the squamosal posteriorly, but these sutures cannot be identified). The right postorbital has suffered recent weathering, but there is no indication that it had been distorted by overlying elements. As the anterior-most portion of both the left and right postorbitals is similar in dorsal view, they may be close to their in vivo position. The anterolateral margin of both supratemporal bars are gently rounded in dorsal aspect.

Nasal. The anterior portion of the nasal is triangular in shape, and contacts the maxillae in along its lateral margins (Fig. 1). Assuming little of the posterior-most part of the left nasal was lost when it rotated against the prefrontal, the nasolacrimal suture was gently rounded (Fig. 4). Anteriorly, the suture between the frontal and the posterior process of the nasal is straight as far as can be determined. However, it forms an acute angle laterally so that the posterior-most margin of the nasal posterior process is actually lateroanteriorially oriented. Medially, the nasal appears to have overlapped the frontal (Fig. 1). The lateral margin of the posterior process of the nasal (its contact with the prefrontal) is slightly convex.

Prefrontal. The anterior extremities of both prefrontals are damaged and their original extent cannot be determined (Fig. 1). The lateral margin of the prefrontal is gently rounded. Shallow pitting is preserved on the lateral-most edge of the right prefrontal, but hardly visible on the left one. The rest of the visible portions of the bones are smooth.

Frontal. The dorsal surface of the frontal is smooth as well, except for a low median crest that emerges level with the centre point of the orbit and continues posteriorly on the intertemporal bar (Fig. 1). The angle between the lateral and median processes of the frontal is about 50 degrees. However the anterior margin of the supratemporal fossa is wide and gently rounded. The intratemporal flange is mostly formed by the frontal itself in its visible portions; although the contact with the postorbital cannot be identified. The frontal part of the intertemporal bar is quadrangular in transverse section, and as preserved terminates as a subvertical transversely oriented surface of rounded pits and humps that resembles more a sutural surface with the parietal than a break. Should this actually represent the frontoparietal suture, then the frontal would have represented a maximum of one third of the intertemporal bar. Interestingly, the frontal is largely excluded from the dorsal margin of the orbit by the prefrontal, much like in the holotype of *Cricosaurus saltillensis* (Buchy *et al*., 2006c).

Parietal. The anterior-most portion of the parietal may be preserved close to its original position (Fig. 1), but this cannot be confirmed. We cannot determine how much of the intertemporal bar is missing. Therefore, the original dimension of the supratemporal fenestra are also is unknown (the left postorbital bar and squamosal appear close to their original position). About 30 mm anterior to the posttemporal bar, the parietal is triangular in cross-section, its dorsal margin forming a sharp crest that enlarges lateroposteriorly to form the triangular (in dorsal view) skull table which is obscured by unidentified overlying bone fragments (Figs 1, 3). At the level of the cross-section, the inverted U-shaped ventral margin of the parietal contacts the proötic. In lateral view, the parietal contacts the proötic, the quadrate for a short straight distance, then at the level of the posttemporal bar, the exoccipital. The contact between parietal and exoccipital is only visible because the squamosal was disarticulated (see that section). Either the parietal did not participate in the posttemporal bar, or its participation was restricted to a millimetre thin lateral flange that covered dorsally the proximal part of the exoccipital (Figs 1, 3) and contacted the squamosal laterally. On the occipital face, a subvertical, median interparietal suture is visible.

Squamosal. The squamosal formed the dorsal part of the posttemporal bar, contacting the parietal medially and the postorbital laterally. The bone is reduced to an approximately 2 mm thin transversely elongate lamina, which 'wraps' the exoccipital anterodorsally (Figs 1, 3). This becomes evident due to the disarticulation of the poorly ossified specimen.

Exoccipital. The surface of the exoccipital in the (dorsal) portion where it was covered by the squamosal presents irregular proximodistally oriented grooves, whereas posterolaterally the surface of the paroccipital process is smooth. On the occipital face, only the right occipital is adequately visible, and its surface is poorly preserved. The posttemporal fossa is tentatively identified at the dorsal-most point of the exoccipitosupraoccipital suture (Fig. 3). A pair of millimetric foraminae located one above the other at the level of the base of the foramen magnum and about 10 mm lateral to its lateral margin may represent the foraminae for the cranial nerves XII1 and XII2 (Wenz, 1968; Vignaud, 1995). Other foramina classically recognized on the occipital face cannot be identified with certainty. The exoccipitals may exclude the supraoccipital from the dorsal margin of the foramen magnum. However the area is obscured and slightly distorted. In addition, the interexoccipital suture is not visible.

Supraoccipital. As noted above, the ventral margin of the supraoccipital (and whether or not it participated in the dorsal margin of the foramen magnum) is not identified (Fig. 3). The lateral suture with the exoccipital is dorsolaterally oriented, while the dorsal margin of the bone (its contact with the parietal) is slightly convex.

Proötic. Only the posterior-most portion of the proötic is preserved. In lateral view (Fig. 3) its posterior margin is gently rounded, contacting the parietal dorsally and the

quadrate ventroposteriorally. As is visible in cross-section (Fig. 3), the lateral-most portion of the ventral margin of the proötic contacts the basioccipital (see that section). Medially, its ventral margin draws an inverted U that contacts a bone wedged between the proötic and the basioccipital; this bone may represent a anterior process of the exoccipital or a posterior process of the alisphenoid.

Stapes. The proximal-most portion of one stapes is preserved over the left postorbital bar and axis neural arch (Fig. 1). It appears slightly curved, subcircular in cross-section and proximally enlarged.

Basioccipital. The basioccipital forms alone the occipital condyle and the median part of the floor of the foramen magnum (Fig. 3). The preserved left basal tuber is posteroventrally directed, it borders the quadrate medially (but the suture is indistinct) and reaches about half the length of the articular ramus of the latter bone; its distal extremity is gently rounded.

Further anteriorly, as is visible along the weathered break (Fig. 3), the basioccipital encloses completely the dumb-bell-shaped cavity for the medulla oblongata. It contacts the quadrate laterally and ventroposteriorally (the basioccipital is also exposed laterally on the left side where the quadrate is damaged). Dorsal to the cavity for the medulla oblongata is a pair of posteroventrally directed lateral canals (as can be deduced from the level and irregular orientation of the section). From their size, form and location, these are interpreted as being the posterior semicircular canals. They appear to be mostly enclosed by the basioccipital except for their dorsal-most margin (at least at the level of the section) which is located on the proöticobasioccipital suture. The dorsal margin of the basioccipital between the canals is subhorizontal.

On the weathered ventral surface (Fig. 3), a portion of the eustachian tube system is likely visible, being filled with a whitish mineral, presumably calcite. From the median eustachian foramen situated ventral to the occipital condyle (Fig. 3), the posterior median eustachian tube runs anterodorsally, and then bifurcates. The right portion of the system is visible in the weathered area: shortly further laterally the tube enlarges, presumably for the rhomboidal sinus (Colbert, 1946), from which a posteriorally directed tube emerges, presumably for the posterior carotid artery. Following the first sinus, another enlarged area filled with calcite may represent the infill of the tympanic cavity.

Basisphenoid. Only a small portion of the basisphenoid appears preserved ventrally, bordering laterally the posterior median eustachian tube and contacting the quadrate laterally (Fig. 3).

Quadrate. The ventral face of the quadrate is gently concave. Its dorsal face is not exposed. In lateral view (Fig. 3), the quadrate contacts the proötic, the parietal and the exoccipital (this latter suture as visible differs between the right and left sides, depending on the extent and pattern of weathering).

Palatal area. Palatines, pterygoids, vomer and possibly the right ectopterygoid can be identified (Fig. 2).

However, due to preservation, nothing can be said about the original margins of the bones, and individual bones cannot be identified with certainty on the cross-sections (Fig. 5).

Mandible

Dentary. The dentary has approximately 15 alveoli (Fig. 1). A depression on the ventrolateral face of the dentary starting level with the tenth dentary alveolus likely housed the splenial where it emerged in lateral view. In its posterior-most portion, the dentary (as visible on the exposed left side) must have been L-shaped in cross-section, with a subhorizontal, tooth bearing portion, and a subvertical lateral flange covering the angular, now horizontal due to compression. The dentary terminates approximately level with the anterior-most point of the nasal. The mandibular symphysis is poorly fused.

Splenial. The splenial emerges in ventral view level with dentary tooth eight (Fig. 1). The posterior-most part of both splenials weathered away recently.

Other mandibular elements. Of the other elements of the mandible, most were identified thanks to the cross-sections (Fig. 5), and little can be deduced about what was originally exposed of them on the lateral and medial faces of the mandibular ramus. The angular extends further anteriorally than section 4 (Figs 1, 5). It likely emerged in lateral view from the dentary flange that wrapped it laterally. The exposed dentary-angular contact must have been posterodorsally oriented as described in the Oxford Clay Formation metriorhynchids *Metriorhynchus superciliosus* and "*Metriorhynchus*" *brachyrhynchus* (see Andrews, 1913). The retroarticular process is about twice as long as the glenoid itself. The respective participation of the angular, articular, surangular and possibly prearticular to the area cannot be determined.

Dentition

All visible crowns are circular in basal cross-section, slightly recurved, and likely sub-circular in cross-section until the apex (Fig. 6). Preliminary observation of the teeth indicates the presence of cutting structures at the crown edges, but their distribution (distal and mesial margins) and exact morphology remains unclear. Unfortunately, the current state of preparation of the teeth precludes identification of carinae on both margins. Currently we cannot determine whether MUDE CPC 487 has unicarinate or bicarinate dentition, however denticles were not observed during preparation. The labial and lingual crowns surfaces appear to be ornamented with faint apicobasally aligned subparallel ridges, with little or no anastomosis.

Cervical vertebrae

The atlas-axis and cervical vertebrae correspond to what has been described for other metriorhynchid species (e.g. Andrews, 1913; Wilkinson *et al.*, 2008), when distortion is taken into account. The atlas/axis complex morphology closely resembles that described for other species of *Cricosaurus* (e.g. *C. suevicus* and *C. vignaudi*; Fraas, 1902,

Frey *et al*., 2002). The axis neural arch appears to be higher than the height of its centrum, as are the neural arches of the remaining cervical vertebrae compared to their respective centrum. The articular faces of the cervical vertebrae are oval to circular and moderately concave. In C3 to C6, the parapophyseal processes are situated anteriorly, near the ventral margin of the centrum, possibly without protruding beyond the bottom of the centra (however all elements in this area are distorted). The parapophyses are short and at the outer end they bear an articulation surface for attachment with the capitulum of the cervical ribs. The diapophyseal process in these four vertebrae is associated with the neural arch, very small, and angled downwards. Again these processes bear articulation surfaces for union with the tubercle, similar to those on the parapophyses.

DISCUSSION

Referral of MUDE CPC 487 to *Cricosaurus* and *C. saltillensis*

Based on our description of MUDE CPC 487 we refer the specimen to the species *Cricosaurus saltillensis*. The referral of MUDE CPC 487 to the genus *Cricosaurus* is supported by presence of the following autapomorphies and unique combination of characters:

1. External nares are subdivided by a midline 'premaxillary septum'

2. External surface of the cranial bones are smooth and unornamented

3. Angle between the medial and lateral processes of the frontal is approximately 45 degrees or more acute

4. The external nares terminate level to, or further posteriorly than, the second maxillary alveoli

5. The surangular and angular proceed anteriorly beyond the orbit

Buchy *et al*. (2006c) listed three autapomorphic characteristics that define *Cricosaurus saltillensis*:

1. Frontal excluded from the centre of the dorsal margin of the orbit by the prefrontal;

2. Supratemporal fossae extremely long: maximum length approximately 2.5 times the posterior width;

3. The intertemporal bar is uniformly narrow in dorsal view, except at the anterior end of the parietal contribution which is transversely expanded

However, MUDE CPC 487 does not preserve the entire intertemporal bar (in particular the parietal contribution), nor does it preserve the shape and extent of the supratemporal fossae. As such, characteristics two and three cannot be examined. This leaves characteristic one. While the frontal is not completely excluded from the orbital dorsal margin in MUDE CPC 487, the prefrontal greatly restricts the frontals contribution to this margin (see Fig. 1). As such, MUDE CPC 487 shares the same autapomorphic prefrontal-frontal morphology as the holotype of *C. saltillensis*.

Furthermore, there is no morphological evidence to support a distinction between both the type of *C. saltillensis* and MUDE CPC 487. As they are from the same locality and horizon, we confidently refer MUDE CPC 487 to *C. saltillensis*.

Comparative palaeontology

Currently there are two described species of *Cricosaurus* from the Tithonian (Upper Jurassic) of the Mexican Gulf. Apart from *Cricosaurus saltillensis*, there is *Cricosaurus vignaudi* (Frey *et al*., 2002) from the 'mid' Tithonian of the La Pimienta Formation. *Cricosaurus saltillensis* MUDE CPC 487 differs from the holotype and only known specimen of *Cricosaurus vignaudi* (Frey *et al*., 2002) in: 1) the absence of the ventral deflection of the dentary, 2) lower tooth count (see Table 1) and 3) teeth have carinae.

Interestingly, a recent re-evaluation of the holotype of *Plesiosaurus mexicanus* Wieland, 1910 has shown that it too is a metriorhynchid (Buchy, 2008). "*Plesiosaurus*" *mexicanus* was provisionally included within the genus *Cricosaurus* (see Young *et al*., 2010). The dental and rostral morphology of "*P*". *mexicanus* is consistent with *Cricosaurus*: procumbent, uncompressed crowns with fine apicobasally aligned ridges; with a tubular snout; the dentary and maxilla parallel; and lacking denticulated carinae. It is worth noting that "*P*". *mexicanus* may be the senior subjective synonym of either described Mexican species. However, until more complete remains are discovered this issue cannot be resolved.

Feeding ecology

Within Metriorhynchinae, *Cricosaurus saltillensis* is unique, as it has the shortest maxillary and dentary tooth rows (Table 1; Fig. 7). This reduction in tooth row length is convergent with basal geosaurines (e.g. "*Metriorhynchus*" *brachyrhynchus*, NHMUK PV R3804; see Andrews, 1913). The supratemporal fossae of *C. saltillensis* are greatly enlarged compared to other metriorhynchines, being only comparable to *Cricosaurus schroederi* (Karl *et al*., 2006) and the geosaurines *Dakosaurus maximus* and *D. andiniensis* (Fraas, 1902; Pol & Gasparini, 2009; Young *et al*., 2012). In these four species the anteromedial corner of the supratemporal fossae (= infratemporal flange of Buchy, 2008) are enlarged and enter into the minimum interorbital distance (see Fig. 1). This morphology is analogous to the 'anterior terraces' of the temporal fenestrae observed in Triassic ichthyosaurs.

The convergence between *C. saltillensis* and *Dakosaurus* (Fraas, 1902; Pol & Gasparini, 2009; Young *et al*., 2012) is intriguing as not only do they share the anterior extension of the intratemporal flange, but they have the proportionally shortest tooth rows in their respective subfamilies. This reduction of the tooth rows is a consequence of foreshortening the rostrum. Treating the skull of *C. saltillensis* as a third-class lever system, 1) the foreshortening of the rostrum indicates a reduction in the length of the out-lever (i.e. the distance between the fulcrum, the jaw joint, and
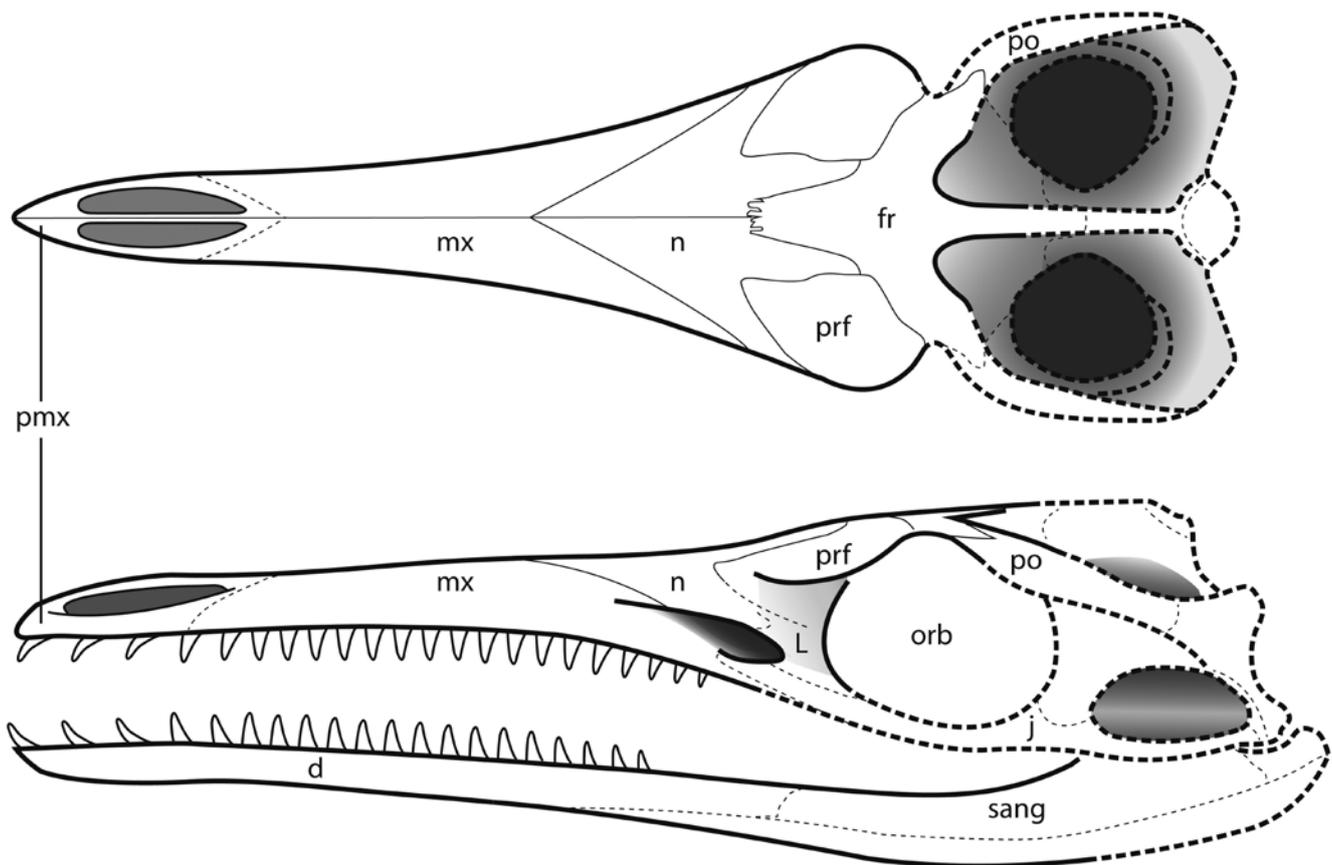
Fig. 7 - Hypothetical reconstruction of the skull of *Cricosaurus saltillensis* in dorsal (top) and lateral (bottom) views, based on the holotype MUDE CPC 487 and other well known *Cricosaurus* species (e.g. *Cricosaurus araucanensis*). Dashed lines represent unknown structures/ sutures, or elements that were highly deformed and flattened. Shaded areas represent fossae. Dentition reconstructed on the basis of distribution of visible alveoli and the tooth crown in Figure 6. Abbreviations as in Figure 1.

point of resistance, the bite point), while 2) the in-lever (i.e. the distance between the fulcrum and the point of applied force, adductor musculature attachment on the mandible) remains unchanged. As such, overall cranial biomechanics is convergent with geosaurines, as in that clade reduction in out-lever length increased the mechanical advantage of the adductor musculature (Young *et al*., 2010). If we treat *Cricosaurus* skulls simply in terms of lever-mechanics, during occlusion the skull of a typical *Cricosaurus* species (e.g. *C. araucanensis*, *C. vignaudi*) had higher velocity and acceleration of the mandible than *C. saltillensis*; while, *C. saltillensis* would have delivered higher bite forces. However, the enlargement of the intratemporal flange in *C. saltillensis* is interesting. Buchy (2008a) demonstrated that an enlarged intratemporal flange would have increased the fibre length of the supratemporal adductor muscles (thereby increasing jaw-closure velocity), and increased the medial component of the force vectors (thereby stabilising the skull against torque). It can be hypothesised that the anterior enlargement of the intratemporal flange in *C. saltillensis* compensated for the foreshortening of the snout, and the resultant decrease in jaw-closure velocity (a convergent adaptation observed in

Dakosaurus; see Pol & Gasparini, 2009; Young *et al*., 2012). The foreshortened snout and a skull better suited to resisting torque suggest *C. saltillensis* would have been adapted to predate larger prey-items than other *Cricosaurus* species. Future studies using three-dimensional biomechanical modelling will be needed to quantitatively test these hypotheses.

The reduced tooth count and carinated teeth, and a skull adapted to better resist torque suggest *C. saltillensis* was better suited to feeding on large-bodied prey than other members of *Cricosaurus*. The long snout (with 25+ teeth per upper jaw) and lack of true dental carinae suggest most species of *Cricosaurus* were specialised predators of small aquatic prey (Young *et al*., 2010).

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