



A NEW PATAGONIAN SPECIES OF *CRICOSAURUS* (CROCODYLIFORMES, THALATTOSUCHIA): FIRST EVIDENCE OF *CRICOSAURUS* IN MIDDLE–UPPER TITHONIAN LITHOGRAPHIC LIMESTONE FROM GONDWANA

by YANINA HERRERA*, ZULMA GASPARINI and MARTA S. FERNÁNDEZ

División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, W1900FWA La Plata, Argentina; e-mails: yaninah@fcnym.unlp.edu.ar, zgaspari@fcnym.unlp.edu.ar, martafer@fcnym.unlp.edu.ar

*Corresponding author.

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Abstract: Upper Jurassic (Tithonian) deposits in north-western Patagonia, Argentina, have yielded rich and taxonomically diverse assemblages of marine reptiles. These assemblages are also remarkable by their quality of preservation and are represented by ichthyosaurs, plesiosaurs, turtles and crocodyliforms. Despite the abundant crocodyliform record, only two metriorhynchid taxa have been identified: *Cricosaurus araucanensis* and *Dakosaurus andiniensis*. Here we described a new species of *Cricosaurus*, which represents the second species of *Cricosaurus* in the Tithonian of the Neuquén Basin, and the first metriorhynchid found in lithographic limestone from Gondwana. Furthermore, this specimen has the most complete postcranial remains of any metriorhynchid from South America. The new species is characterized by a short distance

between the premaxilla and the nasal, a relatively narrow interorbital width, 23–25 mandibular teeth, bicarinated teeth with fine apicobasally aligned ridges, interalveolar spaces between the first seven teeth approximately 1.5 times longer than the anteroposterior diameter of the respective alveoli. To test the assignment of the new species to *Cricosaurus*, we carried out two phylogenetic analyses. In both analyses, *Cricosaurus lithographicus* sp. nov. is nested with other species referred to this genus. This new species has peculiar enamel ornamentation, characterized by numerous, fine apicobasally aligned ridges, when compared to other species of the genus.

Key words: Metriorhynchidae, Upper Jurassic, Neuquén Basin, Argentina.

IN Gondwana, Jurassic marine reptiles are scarce except for those exhumed from the south-oriental margin (i.e. Argentina and Chile) of this megacontinent. Tithonian (Late Jurassic) marine reptiles from northwest Patagonia (Neuquén Basin, Argentina) are one of the most taxonomically diverse assemblages of this age. The Patagonian assemblages are also remarkable by their quality of preservation, and comprise ichthyosaurs, plesiosaurs, turtles and crocodyliforms (Gasparini and Fernández 2005, 2011). This diversity is significant to compare with the Late Jurassic marine reptiles from Laurasia, and allows the analyses of the diversity and significance of marine reptiles of Gondwana.

Unlike the thalattosuchian fossil record from Laurasia, which comprises both teleosaurids and metriorhynchids, the presence of teleosaurids in Gondwana is uncertain (Chong Diaz and Gasparini 1972; Fara *et al.* 2002). However, there is an abundant metriorhynchid fossil record,

particularly along the southern margins of Oriental Gondwana.

Metriorhynchids are the only archosaurian group that can be defined as completely adapted to a pelagic marine life. Their skeletons exhibit unique modifications such as a streamlined skull and body; loss of bony armour; osteoporotic lightening of skull, femora and ribs; reduced pectoral and pelvic girdles; short and paddle-like forelimbs and hypocercal tail (Fraas 1902; Andrews 1913, 1915; Hua 1994; Hua and de Buffrenil 1996).

The fossil record along the southern margins of Oriental Gondwana increased the knowledge of metriorhynchid diversity and furthermore allowed to explore palaeobiological aspects of these peculiar crocodyliforms. Exceptionally preserved natural snout casts of *Cricosaurus araucanensis* (Gasparini and Dellapé, 1976) recovered from the Tithonian levels of the Vaca Muerta Formation (Neuquén Basin) revealed the presence of enlarged

cephalic glands (salt glands) crucial in the successful adaptation of metriorhynchids to marine life (Fernández and Gasparini 2000, 2008), as well as modifications in the paranasal sinus system associated with the internalization of the antorbital cavity and the development of a neomorphic opening for salt glands drainage (Fernández and Herrera 2009). Likewise, one to three-dimensionally preserved metriorhynchid skull from the Oxfordian of northern Chile allowed the first detailed description of the external and internal braincase in this group of crocodyliforms (Fernández *et al.* 2011).

The phylogenetic affinities of Thalattosuchia constitute one of the major unsolved problems in crocodyliform systematic (Pol and Larsson 2011). Some phylogenetic analyses support thalattosuchians as basal mesoeucrocodylians (Buckley *et al.* 2000; Sereno *et al.* 2001; Tykoski *et al.* 2002; Larsson and Sues 2007; Sereno and Larsson 2009; Young and Andrade 2009), whereas other authors find them nested within Neosuchia and related to other longirostrine neosuchians such as pholidosaurids and dyrosaurids (Clark 1994; Wu *et al.* 1997, 2001; Larsson and Gado 2000; Brochu *et al.* 2002; Gasparini *et al.* 2006; Jouve 2009; Pol and Gasparini 2009; Leardi *et al.* 2012). In both hypotheses, the thalattosuchians are recovered as a monophyletic group but the internal relationships are variable. Increasing taxon sampling and/or increasing character sampling, may help to resolve these conflicts.

Of particular interest in the analyses of the diversity of metriorhynchids in Gondwana seas by the end of the Jurassic is the genus *Cricosaurus* Wagner, 1958, as most of the Patagonian metriorhynchids are referred to this genus. Recently, Young and Andrade (2009) proposed that all species traditionally assigned to *Geosaurus* Cuvier, 1824, except for the type species *G. giganteus* (von Sömmerring, 1816), must be reassigned to *Cricosaurus* (including the genus *Enaliosuchus* Koken, 1883). Furthermore, they referred the Tithonian species *G. gracilis*, which reverts back to the genus *Rhacheosaurus* von Meyer, 1831.

Cricosaurus is widely distributed, and its evolutionary history spans from the middle-late Oxfordian (Gasparini and Iturralde-Vinent 2001) to the late Valanginian (Koken 1883; Karl *et al.* 2006). According to recent revisions (Young and Andrade 2009; Young *et al.* 2010; Young *et al.* in press) this genus has nine valid species: *C. elegans* (Wagner, 1852) Wagner, 1858; *C. medius* Wagner, 1858; *C. gracilis* (Philips, 1871); *C. macrospondylus* (Koken, 1883); *C. suevicus* (Fraas, 1901); *C. schroederi* (Kuhn, 1936); *C. araucanensis* (Gasparini and Dellapé, 1976); *C. vignaudi* (Frey *et al.*, 2002), and *C. saltillense* (Buchy *et al.*, 2006). Most of the specimens recovered from Tithonian levels of the Vaca Muerta Formation are referable to *C. araucanensis*. Other Upper Jurassic metriorhynchids recovered from the Neuquén Basin include: *Metriorhynchus* sp. (Pol and Gasparini 2007) (= *Purranisaurus potens*

Rusconi, 1948; Young *et al.* 2010) from the upper Tithonian of the south of Mendoza province (Gasparini 1973); and *Dakosaurus andiniensis* Vignaud and Gasparini, 1996 from the upper Tithonian – lower Berriasian of Neuquén and Mendoza provinces (Pol and Gasparini 2009).

Here we describe a new species of Metriorhynchidae found at Los Catutos (38°47'40"S, 70°10'05"W), in Neuquén province, Argentina. The bearing level of the new taxon corresponds to Los Catutos Member (Vaca Muerta Formation), a homogeneous unit composed of lithographic limestone intercalated with marl and shale (Leanza and Zeiss 1990). Based on their tabular geometry, thin bedding and fossil preservation, the limestone in which the new species has been preserved can be considered as lithographic (Leanza and Zeiss 1992; Scasso *et al.* 2002; Scasso *et al.* 2005). The lithographic limestone of Los Catutos Member deposited in a marine environment during late early to middle late Tithonian (biozone of *Aulacosphinctes proximus* and *Windhausenicerias internispinosum*; Leanza and Zeiss 1990; Scasso and Concheyro 1999). The lithographic limestone is significant as it is the only known worldwide from the middle-upper Tithonian and is the only lithographic limestone unit known from Gondwana. In contrast to other Upper Jurassic lithographic limestone units of Laurasia (e.g. Kimmeridgian assemblages from Cerin, France and Solothurn, Switzerland, and early Tithonian from Solnhofen, Germany), the Los Catutos assemblage is composed only by marine forms (Gasparini *et al.* 1995) while the herpetofauna recovered from lithographic limestone of the western Tethys has yielded a mixed assemblage of marine and continental reptiles (Billon-Bruyat *et al.* 2005).

The skull and jaw of the holotype designated as a new species of *Cricosaurus* (MOZ-PV 5787) were briefly mentioned and illustrated. However, the specimen has never been described nor had its postcranial elements been figured. The new species described herein is the second species of *Cricosaurus* recognized for the Tithonian of the Neuquén Basin.

Institutional abbreviations. BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; GPIT, Institut für Geowissenschaften Biogeologie, Tübingen, Germany; MLP, Museo de La Plata, La Plata, Argentina; MOZ, Museo Juan Augusto Olsacher de Zapala, Neuquén, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Anatomical abbreviations. an, angular; ar, articular; as, astragalus; bo, basioccipital; bsp, basisphenoid; ca, calcaneum; ca.v, caudal vertebra; co, coracoid; cor, coronoid; c.r, cervical rib; cr. B, crest B; d, dentary; d.r, dorsal rib; d.v, dorsal vertebra; en, external nares; eo, exoccipital; fe, femur; fi, fibula; fm, foramen magnum; fr, frontal; h, humerus; il, ilium; j, jugal; la, lacrimal; ls, laterosphenoid; mc, metacarpal; mt, metatarsal; mx, maxilla; mef, medial eustachian foramen; na, nasal; oc, occipital condyle;

pa, parietal; ph, phalanx; pl, palatine; pmx, premaxilla; po, post-orbital; poz, postzygapophysis; pref, preorbital fossa; prez, prezygapophysis; pfr, prefrontal; pt, pterygoid; pu, pubis; q, quadrate; r, radius; ra, radiale; r.ar, retroarticular process; san, surangular; sdg, surangular-dentary groove; so, supraoccipital; sof, suborbital fenestra; sq, squamosal; stf, supratemporal fenestra; s.v, sacral vertebra; ti, tibia; u, ulna; ul, ulnare; v, vertebra.

SYSTEMATIC PALAEOLOGY

Superorder CROCODYLORPHA Walker, 1970

Order CROCODYLIFORMES Hay, 1930

Infraorder THALATTOSUCHIA Fraas, 1901

Family METRIORHYNCHIDAE Fitzinger, 1843

Genus CRICOSAURUS Wagner, 1858

Type species. *Cricosaurus elegans* (Wagner, 1852) Wagner, 1858.

Emended generic diagnosis. Metriorhynchid thalattosuchian with teeth with little to no lateromedially compression; cranial bones smooth, lacking conspicuous ornamentation; acute angle formed by the posterolateral and posteromedial processes of the frontal; orbit as large as the supratemporal fenestra at least in mature individuals; surangular and angular well developed, extending rostrally beyond the orbits; symphyseal part of the mandible low, only about 15 mm high; lateral margin of the prefrontals rounded; external nares bifurcated by premaxillary septum, and terminating at the end of the second maxillary alveoli; deltopectoral crest reduced or absent; calcaneum tuber absent or vestigial; proximal end of metatarsal I greatly enlarged (modified from Young and Andrade 2009).

Cricosaurus lithographicus sp. nov.

Figures 1–4

1995 *Geosaurus* sp. Gasparini, de la Fuente and Fernández, pp. 82–83, fig. 1.

Holotype. MOZ-PV 5787 (Figs 1–4); a complete skull with articulated lower jaws, dorsal, sacral and caudal vertebrae, pectoral girdle element, incomplete forelimb, pelvic girdle elements and an incomplete hind limb.

Diagnosis. A member of *Cricosaurus* characterized by the following combination of characters (autapomorphic characters are indicated by an asterisk): distance between the posterior margin of the premaxilla and the anterior margin of the nasal equivalent to the extension of 3–4 pairs of maxillary alveoli*; nasal process of the frontal extending far behind the anterior margin of the prefrontal; interorbital width narrower than the width of the supratemporal fossa*;

participation of the parietal in the interfenestral crest of 50 per cent; mandibular symphysis in adults approximately 35 per cent of mandible length*; number of teeth in each mandibular ramus ranges from 23 to 25; bicarinated teeth with fine apicobasally aligned ridges that vanish towards the smooth apex; interalveolar spaces between the first seven teeth approximately 1.5 times longer than the antero-posterior diameter of the alveoli.

Derivation of name. *Lithographicus* refers to the lithographic limestone of El Ministerio Quarry (Los Catutos Member, Vaca Muerta Formation).

Type locality. El Ministerio Quarry, Los Catutos Area (38°47'40"S, 70°10'05"W), Zapala Department, Neuquén province, Argentina.

Stratigraphic range. Vaca Muerta Formation, Los Catutos Member (biozone of *Aulacosphinctes proximus* and *Windhausenicerias intenispinosum*), upper lower – middle upper Tithonian, Upper Jurassic (Leanza and Zeiss 1990).

DESCRIPTION

General preservation. MOZ-PV 5787 is preserved in five slabs. Slab 1 contains the skull and mandible, and is dorsoventrally crushed. However, most of the bones remain in their natural arrangement (Fig. 1). Due to deformation, the occipital table is crushed and mainly exposed in dorsal view so that the ventral portion of both parietal and squamosal, as well as the exoccipital and the supraoccipital are visible in this view. The mandible is partially preserved. The right mandibular ramus is exposed in dorsal view while the left one is exposed in ventral view and partially covered by matrix (Fig. 1).

The postcranium is included in 4 slabs, numbered from 2 to 5. Slab 2 contains five vertebrae that may be the last cervicals and the first dorsal, one cervical rib and partially preserved dorsal ribs (Figs 2A, 3A). This slab has a joint with slab 3 that contains one coracoid, the incomplete right forelimb, incomplete vertebrae, ribs, one chevron bone and a few unidentified elements, one of this can be the ischium (Figs 2B, 3B). Slab 4 contains isolated ribs (Fig. 2C). Slab 5 is the biggest of the series and contains incomplete sacral and caudal vertebrae, ribs, pelvic girdle elements and the incomplete right hind limb (Figs 2D, 3C).

Cranial openings

External nares. The external nares of MOZ-PV 5787 are elongated, divided by an osseous septum and posterodorsal retracted (Fig. 1A–B). This septum is not complete and only the anterior and posterior tips are preserved. In MOZ-PV 5787, the external nares begin posterior to the third premaxillary alveolus and the posterior margin ends beyond the third maxillary alveolus (Fig. 1E).

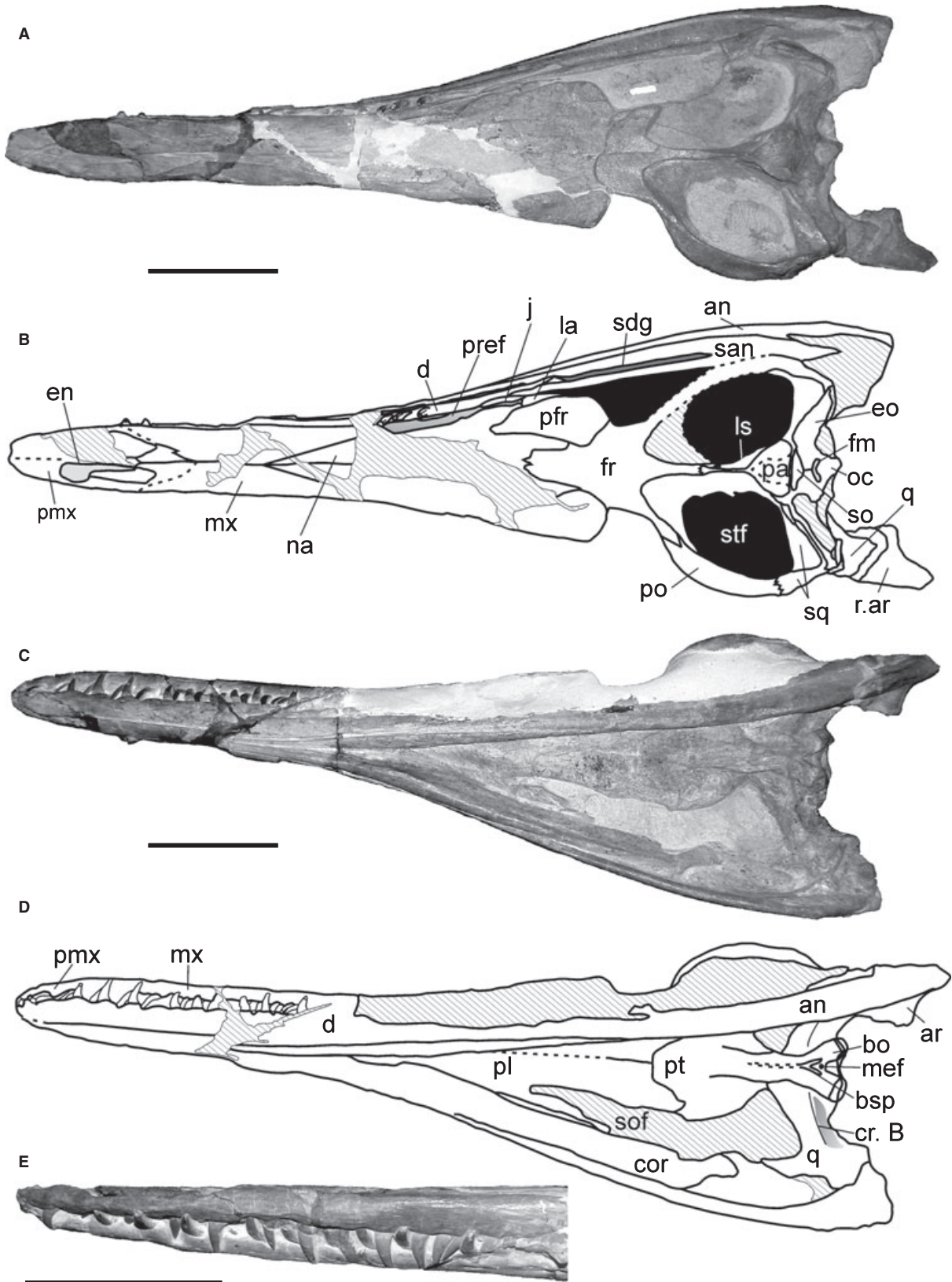


FIG. 1. *Cricosaurus lithographicus* sp. nov., MOZ-PV 5787, skull and mandible. A–B, dorsal view. A, photograph; B, drawing. C–D, ventral view; C, photograph; D, drawing. E, snout in left lateral view. All scale bars represent 100 mm.

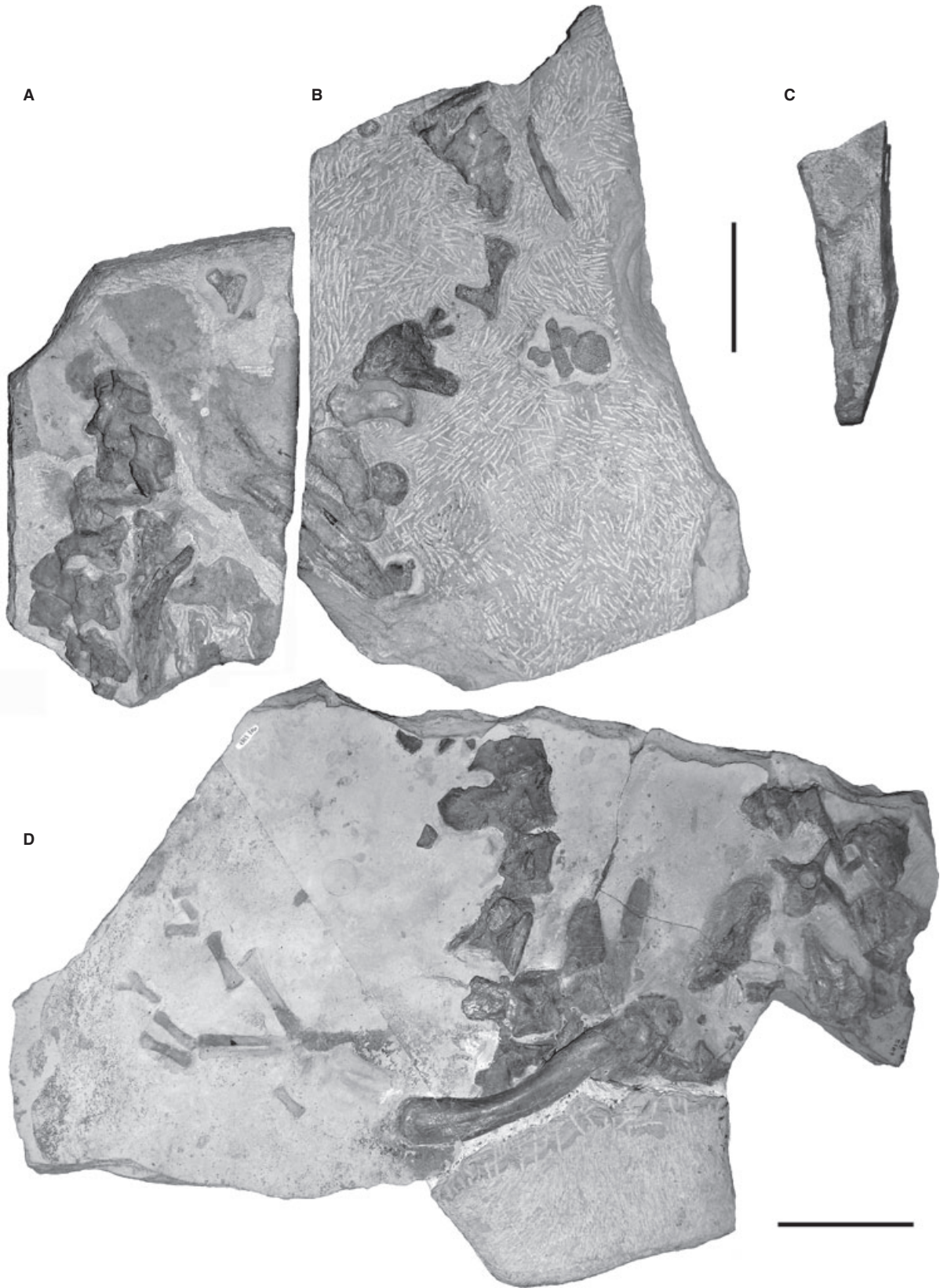


FIG. 2. *Cricosaurus lithographicus* sp. nov., MOZ-PV 5787, postcranial elements preserved in four slabs. A, slab 2. B, slab 3. C, slab 4. D, slab 5. All scale bars represent 100 mm.

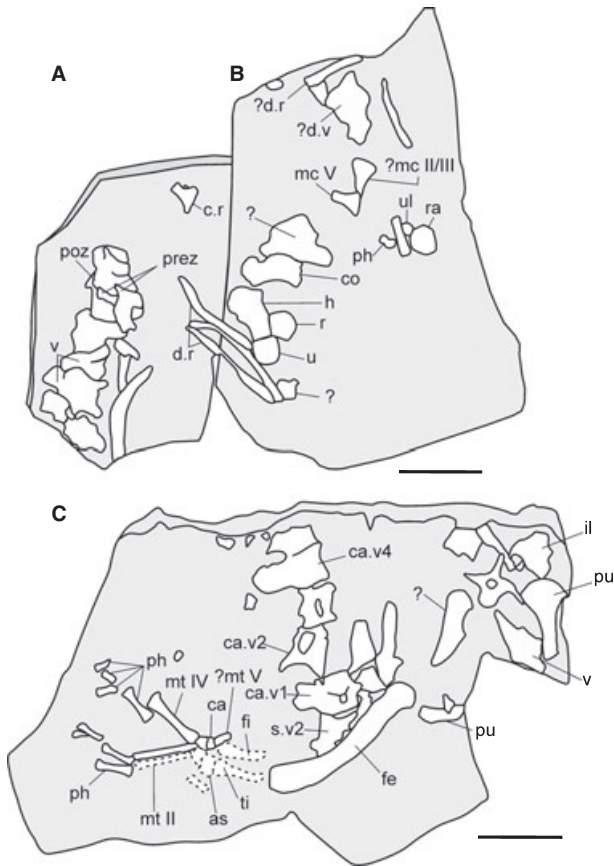


FIG. 3. *Cricosaurus lithographicus* sp. nov., MOZ-PV 5787, postcranial elements. A, drawing of slab 2. B, drawing of slab 3. C, drawing of slab 5. All scale bars represent 100 mm.

Preorbital fossa and preorbital opening. These structures are poorly preserved in MOZ-PV 5787; except for the right preorbital fossa. It is low and elongated with the major axis orientated obliquely, being its anterior end more dorsally than its posterior end. As in *Cricosaurus araucanensis*, the dorsal margin of the preorbital fossa is formed by the maxilla and nasal, its posterior margin is formed by the lacrimal, whereas its ventral margin is formed by the maxilla and jugal (Fig. 1A–B). The preorbital openings of both sides are completely obliterated by deformation.

Orbit. Due to compression both orbits are obliterated but it is still evident that these openings face laterally as in all metriorhynchids.

Supratemporal fossa and fenestra. Only the left supratemporal fossa and fenestra are complete preserved. The supratemporal fossa is large, longer than wider and oval in outline. The supratemporal fenestra is sub-circular in outline. The anterior margin is formed by the frontal and postorbital, laterally by the postorbital and squamosal. The posterior margin is formed by the squamosal and parietal and the medial margin by the frontal and parietal (Fig. 1A–B).

Suborbital fenestra. This structure is partially preserved on the right side only. The suborbital fenestra is narrow and anteroposteriorly elongated, with a rounded anterior margin. This margin is narrower than the posterior one. The medial margin is formed by the palatines; the anterior and lateral margins are formed by the maxilla (Fig. 1C–D). Due to preservation it cannot be determined whether the pterygoid forms part of the posteromedial margin of the suborbital fenestra. The ectopterygoids are not preserved.

Secondary choana. The secondary choana is widely opened. The anterior margin is formed by the palatines and the lateral and posterior margins by the pterygoids (Fig. 1C–D). The anterior portion of the secondary choana has not an osseous septum, whereas on the posterior one there is a subtle pterygoid fold, anteroposteriorly directed. Posteriorly, this fold is overlain by a crest formed by the basisphenoid. The ventral surface of the pterygoid is flat; this feature is most likely due to deformation.

External mandibular fenestra. As in all metriorhynchids, the external mandibular fenestra is absent (Vignaud 1995; Hua and Buffetaut 1997; Pol and Gasparini 2009; Young and Andrade 2009; Fig. 1A–D).

Skull

Premaxilla. As in most metriorhynchids, the medial margins of both premaxillae are in contact with each other enclosing the external nares. The posterior margin of the premaxilla contacts the anterior margin of the maxilla through an irregular suture that forms a posteriorly pointed ‘V’-shaped suture (Fig. 1A–B). The premaxilla bears three alveoli. The interalveolar spaces are 1.5 times the size of the respective alveoli. The ventral margin of the premaxilla is slightly festooned (Fig. 1E). However, we cannot determine with accuracy if this feature is due to diagenesis.

Maxilla. Both maxillae are completely preserved; however, their palatal face is covered by the mandible. The maxillae meet along the midline of the skull through a short suture extending between fifth to eighth maxillary alveoli. Posteriorly, it is sutured with the nasals through a ‘V’-shaped suture anteriorly directed (Fig. 1A–B). The external surface is smooth with some isolated elliptical/sub-circular pits. In lateral view, there are a few neurovascular foramina above the tooth row. The posterior margin of the maxilla contacts the nasal, dorsal to the preorbital fossa. Ventrally, the maxilla is overlapped by the jugal (Fig. 1A–B). The maxilla forms the anterior and the ventral margins of the elongated preorbital fossa, and extends medially forming their anterior and ventral walls. In MOZ-PV 5787, the maxillary teeth are interlocked with the mandibular teeth. As the premaxilla, the alveolar margin is slightly festooned (Fig. 1E), but as we said above, we cannot determine whether it is a natural feature.

Nasal. The nasal is elongate and narrow with a triangular outline in dorsal view. As in most metriorhynchids, the anterior end is acute and does not reach the premaxilla. The distance between nasal and premaxilla comprises 3–4 pairs of alveoli

(Fig. 1A–B). The posteromedial processes of the nasal are shorter and stouter than in *C. araucanensis* (MLP 72-IV-7-1, MLP 72-IV-7-4). Posteriorly, on the dorsal surface of the skull, the nasal is sutured to the frontal and prefrontal. In MOZ-PV 5787, the caudal margin of the posteromedial process of the nasal does not reach the level of the external angle of the prefrontal. The posterolateral process of the nasal forms the dorsal margin as well as the internal wall of the preorbital fossa. The posterior margin of the posterolateral process dorsally contacts the prefrontal (Fig. 1A–B).

Lacrimal. Only the right lacrimal is preserved. Due to deformation, the lacrimal is exposed in dorsal view, lateral to the prefrontal and medial to the mandible (Fig. 1A–B). Despite its dorsal exposition the lacrimal faces laterally, character common in metriorhynchids. The lacrimal forms the ventral portion of the orbital anterior margin and extends anteriorly reaching the preorbital fossa.

Jugal. Only the most anterior part of the right jugal is preserved, forming the ventral margin of the preorbital fossa. In this region, the jugal overlaps the maxilla (Fig. 1A–B).

Prefrontal. The right prefrontal is completely preserved, whereas the left is incomplete and partially reconstructed (Fig. 1A–B). As in other metriorhynchids, the prefrontals are enlarged and well-developed mediolaterally, overhanging the anterodorsal portion of the orbit. The prefrontal forms the anterior half of the dorsal margin of the orbit. In dorsal view, the prefrontal is about twice as long as broad. Its anterior margin contacts the nasal and its posteromedial one contacts the frontal (Fig. 1A–B). As in other *Cricosaurus*, the lateral margin is rounded (Frey *et al.* 2002; Young and Andrade 2009). The prefrontal has no conspicuous ornamentation bearing some isolated elliptical/sub-circular pits.

Frontal. As in all adult mesoeucrocodylians, the frontal is a single element (Clark 1994). The anterior process of the frontal extends anteriorly between the posteromedial processes of the nasal, forming an irregular suture (Fig. 1A–B). This anterior process is broader than in *C. araucanensis* (MLP 72-IV-7-1; MLP 72-IV-7-2; MLP 72-IV-7-4) and does not reach the anterior margin of the prefrontal. The posterolateral postorbital processes form an angle of 45 degrees with the sagittal plane, used to define the *Cricosaurus* genus (Frey *et al.* 2002; Young and Andrade 2009). These posterolateral postorbital processes of the frontal contact the postorbital through a 'V'-shape suture directed posteriorly. The interorbital region is narrower than in *C. araucanensis* (MLP 72-IV-7-1; MLP 72-IV-7-2; MLP 72-IV-7-4). Posteriorly, the frontal enters the supratemporal fossa and fenestra extensively, and forms the anterior floor as well as the anterior and anterolateral margin of the fossa. The dorsal surface of the frontal, between the supratemporal fossae, is well preserved. This surface is narrow and flat, and contacts the parietal through a serrated suture (Fig. 1A–B).

Parietal. As in all crocodylomorphs, the parietals are completely fused into a single element. Anteriorly, between the supratemporal fossae, this element has an elongated, flat and narrow dorsal

surface tapering posteriorly to form a crest. This crest widens posteriorly and forms a broad triangular surface. The parietal participates in the occipital surface of the skull, above the supraoccipital; however, due to compression, the occipital region of the parietal is dorsally exposed. At its posterior end, the parietal forms the posteromedial margins of the supratemporal fenestra, where it contacts the squamosal through a 'V'-shaped suture. In dorsal view, the parietal forms more than 50 per cent of the interfenestral bar. The lateral surface of the parietal extends ventrally as a vertical wall towards the medial margins of the supratemporal fenestra. In lateral view, inside the supratemporal fossa, the fronto-parietal suture is directed more posteriorly than in dorsal view (Fig. 1A–B), unlike *C. araucanensis* (MLP 72-IV-7-1).

Postorbital. Only the left postorbital is incompletely preserved. This element forms the posterior half of the dorsal margin of the orbit. Posteriorly, along the temporal region, the sharp dorsal margin of the postorbital forms the lateral margin of the supratemporal fossa. Anteriorly, it is sutured to the frontal and posteriorly to the squamosal; this latter is serrated (Fig. 1A–B).

Squamosal. Both squamosals are completely preserved but deformed. Because of this they are extensively exposed in dorsal view. The contribution of the squamosal to the supratemporal arch is approximately 30 per cent. As in other metriorhynchids (e.g. *Cricosaurus araucanensis*; *Dakosaurus andiniensis*, Pol and Gasparini 2009), in MOZ-PV 5787, lateral to the distal end of the paroccipital process, the squamosal has a distinct subcircular surface facing posterolaterally (Fig. 1A–B).

Supraoccipital. Due to deformation the supraoccipital is exposed in dorsal view. It is sub-rhomboidal in outline with rounded margins and contacts dorsolaterally the parietal and ventrally the exoccipital (Fig. 1A–B). The supraoccipital does not contact the foramen magnum (Fig. 1A–B).

Exoccipital. The exoccipitals have a wide contact along the occipital midline and form the dorsal and lateral margins of the foramen magnum. The right paroccipital process is crushed and dorsolaterally covered by the squamosal (Fig. 1A–B). We cannot determine whether the exoccipitals contribute to the formation of the occipital condyle.

Basioccipital. This element is partially preserved and mainly exposed in dorsal and ventral views (Fig. 1A–D). The occipital condyle is poorly preserved (Fig. 1A–B). In ventral view, the large and pendulous basioccipital tubera are well preserved (Fig. 1C–D). The basioccipital tubera are separated by a transverse, convex bony bridge (Fig. 1C–D).

Basisphenoid. This bone is incompletely preserved and only exposed in ventral view. Its ventral surface is distorted. Ventrally, the basisphenoid is narrow and triangular in outline, anterior to the medial eustachian foramen. Its anterior portion is a narrow crest that overlaps the pterygoids and approximately reaches the posterior half of the secondary choana (Fig. 1C–D).

Palatine. The palatine is partially exposed in ventral view. Its most anterior portion is overlain by the mandible; therefore, the suture with the maxilla cannot be traced. The palatine participates in the anterior and anterolateral margins of the secondary choana (Fig. 1C–D). Posteriorly, it is sutured to the pterygoid by a lateral protrusion.

Pterygoid. The pterygoid is crushed and deformed. Anteriorly, it contacts the palatine and participates in the posterolateral and posterior margins of the secondary choana. Inside the secondary choana, the pterygoid forms a subtle fold (Fig. 1C–D) not identified in *C. araucanensis*.

Quadrate. Both quadrates are completely preserved. However, the left quadrate is covered by the mandible while the right one is exposed in ventral view (Fig. 1C–D). In thalattosuchians (e.g. *Cricosaurus araucanensis*, *Metriorhynchus* cf. *M. westermanni*, *Dakosaurus andiniensis*, *Pelagosaurus typus*), on the anterior margin of the pterygoid branch there is a blunt crest ('crest B' of Iordansky 1964, 1973) that extends parallel to this margin. The 'crest B' was recognized in MOZ-PV 5787, *C. araucanensis* (MLP 72-IV-7-1, MLP 72-IV-7-2, MLP 72-IV-7-4) and other thalattosuchians (Holliday and Witmer 2009; Jouve 2009; Fernández *et al.* 2011). Due to deformation, the orbital process of the quadrate is hidden under the pterygoid, the basioccipital and the basisphenoid, and we cannot determinate if it remains free of bony attachment like in *C. araucanensis*, *M. cf. M. westermanni*, *D. andiniensis*, *Teleosaurus cadomensis* and *P. typus* (Holliday and Witmer 2009; Jouve 2009; Fernández *et al.* 2011).

Mandible

The mandibular rami slightly diverge posteriorly following the narrow outline of the skull and, as in the longirostrine species they are low and gracile. The posterior-most portion of the right mandibular ramus is distorted, laterally displaced and exposed in dorsal view while the left one is partially preserved and exposed in ventral view (Fig. 1A–B).

Dentary. Both dentaries are partially preserved (Fig. 1C–D). The dentary is elongated with straight dorsal and ventral margins. The anterior-most region of the dorsal margin is slightly festooned (Fig. 1E), like in the premaxilla and maxilla this festooning may result from diagenetic deformation. The dentaries form approximately 60 per cent of the mandibular symphysis. Posteriorly, the dentary is sutured to the surangular and angular, denoting the absence of external mandibular fenestra (Fig. 1A–D). On its lateral surface, the dentary bears a deep groove in its posterodorsal portion that is continuous with the groove present in the surangular (Fig. 1A–B). This groove is present in other thalattosuchians (e.g. *Cricosaurus elegans*, BSPG AS I 504; *C. medius*, BSPG AS VI 2; *C. suevicus*, SMNS 9808; *Pelagosaurus typus*, BSPG 1890 I 5; *C. vignaudi*, Frey *et al.* 2002; *Dakosaurus andiniensis*, Pol and Gasparini 2009; Mr Leeds' specimen, Young *et al.* in press).

Surangular. Only the right surangular is preserved and exposed in dorsal view. Anteriorly, the surangular contacts the dentary through an irregular suture, which ends at the level of the posterior margin of the preorbital fossa. Ventrally, the surangular contacts the angular in a straight suture. Its contact with the coronoid cannot be determined. The groove mentioned for the dentary continues on the surangular (Fig. 1A–B).

Angular. The right angular is exposed in dorsal view while the left one is distorted and exposed in ventral view. Posteriorly, the angular forms the ventral edge of the mandibular ramus (Fig. 1A–D). Its ventral margin is straight and curves dorsally towards the articular (Fig. 1C–D). Its dorsal margin is sutured to the surangular, anterodorsally it contacts the ventral edge of the dentary, and medially it contacts the splenial (Fig. 1A–B).

Splenial. Both splenials are exposed. The participation of the splenials on the mandibular symphysis is extensive (approximately 40 per cent). Anteriorly, the splenial contacts the dentary through a 'V'-shaped suture that ends at the level to the 10–11 mandibular alveoli (Fig. 1C–D).

Coronoid. The left coronoid is completely covered by the left mandibular ramus. The right one is partially exposed and disarticulated from the mandible. This element is long, thin and curves dorsally (Fig. 1C–D).

Articular. Only the left articular is incompletely preserved. The articular extends posteriorly in a long retroarticular process (Fig. 1A–D). The process curves posterodorsally; however, due to deformation the degree of curvature cannot be determined. A transverse crest separates the articular fossa from the retroarticular process (Fig. 1A–B). Dorsally, the retroarticular process is subtriangular in outline.

Dentition

The left premaxilla bears three partially preserved teeth (Fig. 1E). On the right premaxilla, only the alveoli are preserved. The two first teeth preserve the basal section of the root; while the last tooth is complete. The teeth are curved posteriorly.

In the left maxillary, 11 teeth are exposed (Fig. 1E) while in the right one only partially fragmentary teeth are preserved. The maxillary series was estimated by examining both sides, the tooth maxillary count would have ranged between 20 from 22. Their crowns are slightly curved posterior and lingually, being the lingual surface more convex than the labial one (Fig. 4A). The interalveolar spaces between the first seven teeth are approximately 1.5 times the anteroposterior diameter of the respective alveoli (Fig. 1E).

We estimate that the dentary had 19 teeth, although we may be underestimating the number. The first three teeth are the smallest of the series while the fourth tooth is the largest. All crowns are slightly curved posterior and lingually.

The teeth are slightly mediolaterally compressed. No constriction is present at the crown/root junction. All teeth have conspicuous longitudinal ridges that run across the crown

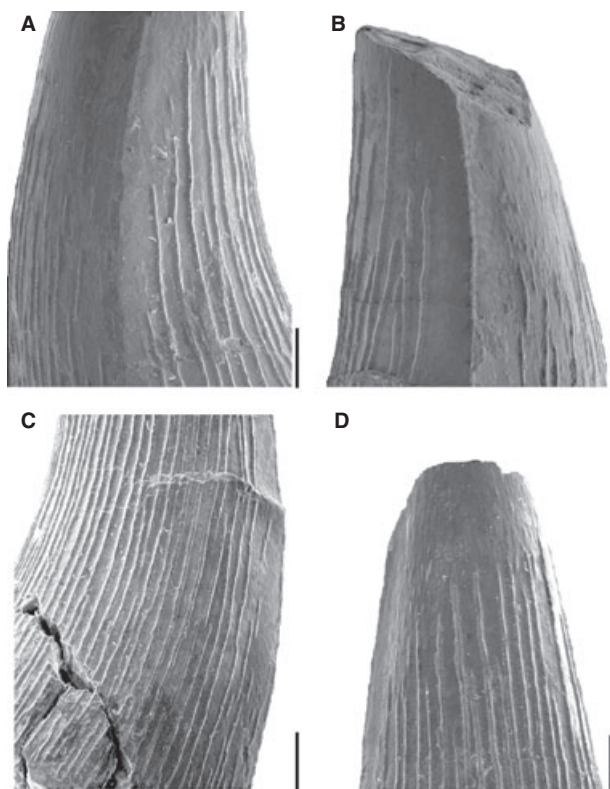


FIG. 4. *Cricosaurus lithographicus* sp. nov., MOZ-PV 5787, posterior dentary tooth. A, carina in distal view. B, carina in mesial view. C, crown in lingual view. D, apex in lingual view. All scale bars represent 1 mm.

(Fig. 4A–C), except the apical region which is smooth (Fig. 4D). These longitudinal ridges are better defined on the lingual surface (Fig. 4C). The SEM analysis presented here shows that the longitudinal ridges are not continuous along the length of the crown (Fig. 4). The teeth are bicarinated with a smooth carina on the mesial and distal margins, without evidences of serration (Fig. 4A–B).

Postcranial

Vertebra. On the slab 2, there are five vertebrae poorly preserved and partially articulated (Figs 2A, 3A). Due to the poor preservation it is not possible to determine accurately if these vertebrae correspond to the cervical or the dorsal series. The first two vertebrae are exposed in dorsal view while the other three are in right lateral view. The prezygapophysis of the second vertebra are well developed and separated in the midline by a wide and deep fossa. As in other metriorhynchids (e.g. *Cricosaurus suevicus*, *Metriorhynchus superciliosus*), the neural spine is square, low and wide (Figs 2A, 3A). The slab 3 contains an incomplete vertebra, preserved in lateral view. In the slab 5, both sacral and four articulated caudal vertebrae are preserved. All vertebrae are exposed in right lateral view. Two other vertebrae are poorly preserved (Figs 2D, 3C). The second sacral vertebra is the most

complete of the series. The vertebral body length is 47 mm. The neural spine is high and wide, although the dorsal edge is broken. The vertebral body of the most complete caudal vertebra is approximately 40 mm in length. The transverse processes of caudal vertebrae are represented only by the proximal portion, which is positioned anteriorly on the vertebral body. The only preserved neural spine of caudal vertebrae is high and broad, and the distal end is convex, feature also present in *Cricosaurus suevicus* (GPIT/43/97/3-4).

Pectoral girdle. The only preserved element of the pectoral girdle is the right coracoid (Figs 2B, 3B). The proximal region of this element is partially preserved while the distal region is covered by an unidentified bone. The coracoid has the typical fan-like shape present in other metriorhynchids (e.g. *Cricosaurus araucanensis*, *C. suevicus*, *Metriorhynchus superciliosus*), with the proximal and distal regions expanded and the medial region constricted. The proximal region is less expanded than the distal region (Figs 2B, 3B).

Forelimb. The right forelimb is preserved although incomplete, and exposed in ventral view. Their elements are disarticulated and displaced, with the exception of the humerus which is articulated with the radius and ulna. However, the articulation between the radius and ulna is slightly displaced from their natural position. Two proximal carpals are preserved disarticulated and displaced. Due to their proportions we inferred that they correspond to the radiale and ulnare (Figs 2B, 3B). Two metacarpals and one phalanx are preserved (Figs 2B, 3B).

Humerus. The right humerus is eroded. It is 64 mm in length; the proximal articular head is 42 mm wide, while the distal articular region is 26 mm wide. In MOZ-PV 5787, the proximal region is more expanded than the distal region (Figs 2B, 3B), and as in *C. araucanensis* (MLP 72-IV-7-1), the humeral head is anteroposteriorly convex and the articular region is anteroposteriorly wide (Figs 2B, 3B). On its anterior margin, there is a knob that corresponds to an extremely reduced deltopectoral crest (Figs 2B, 3B). This crest is also reduced in *C. araucanensis* (MLP 72-IV-7-1). The distal articular surface occupies the distal margin and continues on the anterior margin (Figs 2B, 3B). The distal articular surfaces form an angle of 45 degrees (Figs 2B, 3B).

Radius. As in other metriorhynchids, the radius is flattened and discoidal (Figs 2B, 3B). In MOZ-PV 5787, the radius is antero-posteriorly shorter than in *C. araucanensis*. The proximal-distal axis is longer than the antero-posterior axis. The radius has a strongly convex anterior margin. The articular surfaces with the humerus, ulna and radiale are straight. The articular surfaces with the humerus and radiale are longer than the articular surface with the ulna (Figs 2B, 3B).

Ulna. This bone is subcircular in outline with a convex posterior margin. The ulna is slightly larger than the radius. All articular surfaces are straight. The ulna-humerus articular surface is the longest, the ulna-radius is the shortest, and the ulna-ulnare is intermediate in length (Figs 2B, 3B).

Radiale. This is the largest element of the proximal carpus. It is subcircular, with two straight articular surfaces for the articulation with the radius and the ulna. The articular surface for the radius is longer than the articular surface for the ulna (Figs 2B, 3B).

Ulnare. The ulnare is disarticulated from the zeugopodium. In MOZ-PV 5787, the ulnare is the smallest bone of the distal carpus, it is sub-pentagonal in outline, with three straight articular surfaces (Figs 2B, 3B).

Metacarpal. There are two metacarpals preserved. One of them is a long and slender bone 45 mm in length; with the distal end expanded (Figs 2B, 3B). Based on the proportions and in comparison with *Cricosaurus araucanensis* (MLP 73-II-27-1), this element would correspond to metacarpal II or III. The other metacarpal has the distal portion strongly expanded in relation with the shaft (Figs 2B, 3B). Based on this expansion, and in comparison with *C. araucanensis* (MLP 73-II-27-1), we interpreted that this bone corresponds to the metacarpal V. The metacarpal V is shorter than metacarpal II or III.

Phalanx. Only one phalanx is preserved. It is small and short, 17 mm in length and 11 mm in width. It is sub-rectangular in outline and slightly constricted in the middle region (Figs 2B, 3B).

Pelvic girdle. Both pubic bones are incompletely preserved, being the right ilium exposed in medial view (Figs 2D, 3C).

Ilium. As in other metriorhynchids (Fraas 1902; Andrews 1913; Young *et al.* in press), the outline of the ilium is subtriangular. On the dorsal region, there is a rugose surface that corresponds to the articular region of the sacral vertebrae. The dorsal margin of the ilium is quite straight. The short, thin and slightly ventrally curved preacetabular process is projected anteriorly. This process reaches the anterior margin of the ilium.

Pubis. The right pubis is the most complete and preserves only the distal expansion, while the shaft and proximal region are preserved as an impression on the matrix. The pubic shaft is rod-shaped and the distal region is expanded. Along the distal region there is a nearly straight area that may represent the pubic symphysis (Figs 2D, 3C). The right pubis is 97 mm in length, and 55 mm wide at the distal expansion. The left pubis, represented only by a proximal region, is in contact with the left femur (Figs 2D, 3C).

Hind limb. The left hind limb is completely preserved but disarticulated. The left femur is exposed in medial view. The other elements are disarticulated and, in some cases (e.g. zeugopodial elements), preserved as impressions on the matrix (Figs 2D, 3C). The astragalus and calcaneum are the elements preserved of the proximal tarsus, and two tarsals are preserved of the distal tarsus (Figs 2D, 3C).

Femur. The left femur is a robust bone with the sigmoidal shape seen in other metriorhynchids (Fraas 1902; Andrews 1913; Wil-

kinson *et al.* 2008; Young *et al.* in press; Figs 2D, 3C). The femur is 205 mm in total proximal-distal length, with a width of 43 mm for the proximal head and 33 mm for the distal head. The distal end is more expanded and flat than the proximal end. The distal articular surfaces form an angle of 45 degrees (Figs 2D, 3C), as in *Cricosaurus suevicus* (SMNS 9808).

In the last descriptions of metriorhynchids (Wilkinson *et al.* 2008; Young and Andrade 2009; Young *et al.* 2010, in press), the absence of fourth trochanter *sensu stricto* is considered a character shared by all metriorhynchids. However, these authors described a flattened rugose surface in the area where the fourth trochanter is located in other crocodyliforms. Buffetaut (1982) and Hua and Buffetaut (1997) mentioned that the reduction of fourth trochanter in metriorhynchids is related to a reduction on caudofemoralis musculature. In MOZ-PV 5787, there is a very rough area, slightly protruded in the proximal-posterior region in medial view. This structure has been identified in *Cricosaurus araucanensis* (MLP 72-IV-7-1), *Metriorhynchus superciliosus* (SMNS 10116) and *Metriorhynchus sp.* (GPIT/RE/0302) and is here interpreted as a reduced fourth trochanter.

Tibia. The tibia has an estimated length of 56 mm (Figs 2D, 3C). It is stouter than the fibula, character shared with *Gracilineustes leedsi* (= *Metriorhynchus laeve* in Andrews 1913) and *Cricosaurus suevicus* (SMNS 9808).

Fibula. The distal end and the shaft are well defined (Figs 2D, 3C). We inferred a length of 55 mm.

Astragalus. The astragalus is preserved as an impression on the matrix. Its medial and distal margins are well defined, while the lateral and proximal are not defined. We inferred a sub-quadrangular outline for this bone (Figs 2D, 3C).

Calcaneum. The calcaneum is sub-quadrangular and is preserved in contact with the fibula and the metatarsal IV. On the proximalateral margin, it superimposes another bone, which would correspond to the metatarsal V (Figs 2D, 3C). We cannot identify the calcaneum tuber.

Distal tarsal. One of the distal tarsals is in contact with the astragalus; it is a subcircular impression on the matrix with only the medial margin straight. The other tarsal is quadrangular and contacts the calcaneum and metatarsal IV (Figs 2D, 3C).

Metatarsal. Only four metatarsals are preserved and correspond to metatarsals II, III, IV and V. The IV metatarsal contacts the calcaneum and is the longest (Figs 2D, 3C). As in *Cricosaurus suevicus* (Fraas 1902) and *Gracilineustes leedsi* (Andrews 1913), the length of these bones increases from metatarsal II to metatarsal IV. The distal end of the IV metatarsal is more expanded than the proximal end. The V metatarsal is superimposed over the calcaneum (Figs 2D, 3C).

Phalanx. Three proximal phalanges are preserved, which correspond to digits II to IV. The phalanx IV is the largest and its proximal end is more expanded than the distal end. The phalanx that corresponds to digit III is shorter than the phalanx IV and

their expansions are subtle. In the phalanx that corresponds to digit II, the proximal region is more expanded than the distal region (Figs 2D, 3C). Other five disarticulated phalanges are preserved.

PHYLOGENETIC ANALYSES

To test the phylogenetic relationships of the new species within Metriorhynchidae, two cladistic analyses were performed: the one used by Pol and Gasparini (2009) with the modifications and incorporation of new morphological characters proposed by Leardi *et al.* (2012); and the data set of Young *et al.* (in press; see Supporting Information). Based on new information, minor modifications of character scoring in some species of Thalattosuchia were included in both data sets (Supporting Information). *Purranisaurus potens* Rusconi, 1948 was removed from the data set of Young *et al.* (in press) as the holotype, and only known specimen deserves further preparation and it is currently under revision.

Both data sets were analysed using TNT 1.1 (Goloboff *et al.* 2003). A heuristic tree STR search strategy was conducted by performing 1000 replicates of Wagner trees (using random addition sequences) followed by tree bisection-reconnection branch swapping (holding 10 trees per replicate). Nodal support was evaluated using non-parametric bootstrapping with 1000 replicates, using traditional searching, and Bremer support index.

The analysis based on the data set of Pol and Gasparini (2009) resulted in a three equally most parsimonious trees (MPTs) with a length of 897 steps (ensemble Consistency Index, CI = 0.359; ensemble Retention Index, RI = 0.717; rescaled consistency Index, RC = 0.257). The topology of the strict consensus is consistent with the one reported by Pol and Gasparini (2009; Fig. 5A), and depicts *Cricosaurus lithographicus* sp. nov. nested with the other two species of *Cricosaurus*, although the inter relationships of *Cricosaurus* species is not resolved. *Cricosaurus* clade is supported by: external nares facing anterolaterally or anteriorly, dorsally separated by premaxillary bar (character 6) and external nares divided by a septum (character 66). Support found for *Metriorhynchus* + *Dakosaurus* + *Cricosaurus* clade is bootstrap = 95 per cent, Bremer support = 2. On the other hand, lowest support was found for *Cricosaurus* (bootstrap = 24 per cent, Bremer support = 1).

The analysis carried out, based on the data set of Young *et al.* (in press), resulted in a 48 MPTs with a length of 493 steps (ensemble Consistency Index, CI = 0.556; ensemble Retention Index, RI = 0.856; rescaled consistency Index, RC = 0.480). The topology of the strict consensus is consistent with that of Young *et al.* (in press; Fig. 5B). However, our analysis found *C. schroederi* as the sister taxon of *C. macrospondylus* + *C. araucanensis* +

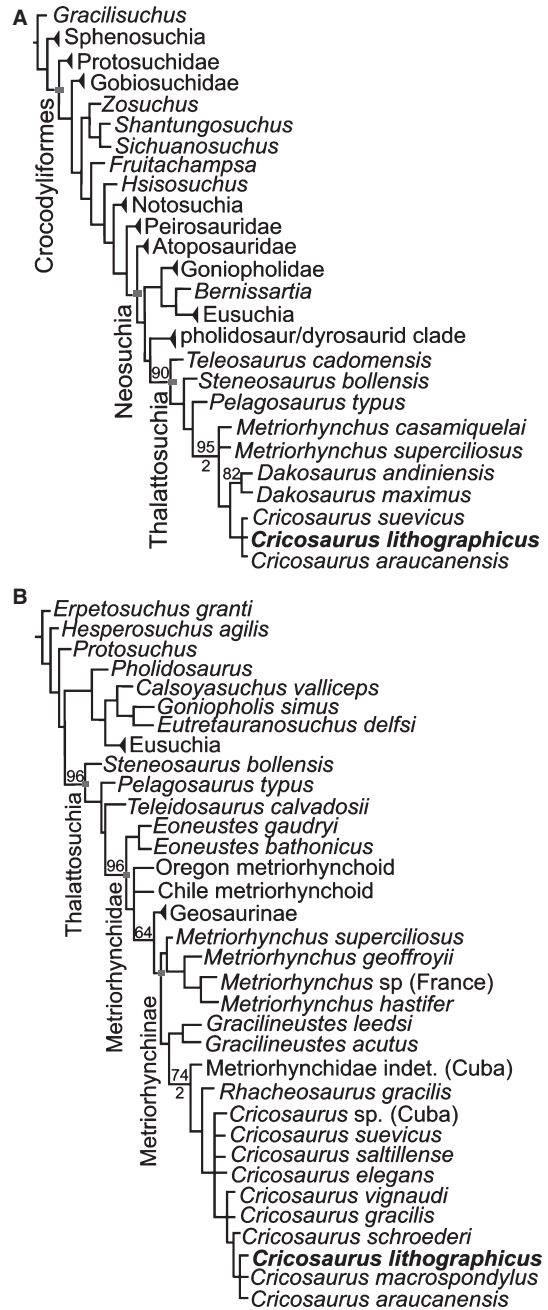


FIG. 5. A, strict consensus topology of the first phylogenetic analysis (based on data set of Pol and Gasparini 2009). B, strict consensus topology of the second phylogenetic analysis (based on data set of Young *et al.* in press).

C. lithographicus sp. nov. (Fig. 5B). As in the case of the analysis based on the data set of Pol and Gasparini (2009), the new species is nested with *Cricosaurus* clade. The clade formed by *C. macrospondylus* + *C. araucanensis* + *C. lithographicus* sp. nov. is supported by uncarinated and bicarinated teeth while the clade formed by *C. schroederi* + *C. macrospondylus* + *C. araucanensis* + *C. lithographicus* sp.

nov. is supported by the nasal contact with the prefrontal, in dorsal view is a smooth curve with a concavity directed posterolaterally (character 11) and the nasal-prefrontal suture has a posteriorly directed 'V'-shape (character 45). The support found for Metriorhynchidae indet. + *Rhachosaurus* + *Cricosaurus* is bootstrap = 74 per cent, Bremer support = 2.

DISCUSSION

Comparative palaeontology

The new species is referred to *Cricosaurus* on the basis of the following combination of features: the cranial bones are smooth, lacking conspicuous ornamentation; the external nares are posterodorsally retracted, elongated and divided by an osseous septum; the lateral margin of the prefrontals is rounded; the posterolateral postorbital process of the frontal form a 45 degrees angle with the interfenestral crest; the angular and surangular are well developed anteriorly and extend beyond the orbit, and the mandibular symphysis is low.

The other diagnostic characters of the genus (Vignaud 1995; Frey *et al.* 2002; Young and Andrade 2009), such as the size of the orbit in comparison with the supratemporal fenestra, could not be identified due to preservation. Vignaud (1995) and Frey *et al.* (2002) used as diagnostic character for *Cricosaurus*, the dorsal margin of the supratemporal arcade lower than the parietal crest. However, this character is also present in *Metriorhynchus casamiquelai* and *M. westermanni*.

Within the genus, *Cricosaurus lithographicus* sp. nov. shows a unique combination of features supporting the erection of a new species. In *Cricosaurus lithographicus*, the external nares are more retracted and located posterior to the level of the third premaxillary alveolus and their posterior margin ends beyond the third maxillary alveolus (Fig. 1E; feature shared only with *C. araucanensis* and *C. macrospondylus*). The distance between the posterior margin of the premaxilla and the anterior margin of the nasal is noticeably shorter, with a length equivalent to 3–4 pairs of maxillary alveoli in *C. lithographicus* sp. nov. while in *C. araucanensis* the distance equals to 10–11 pairs. In the new species, the nasal process of the frontal is far behind the anterior margin of the prefrontal, a feature shared with *C. macrospondylus*, *C. vignaudi* and *C. elegans*. In *C. araucanensis*, this process reaches the level of the anterior margin of the prefrontal. In *C. lithographicus* sp. nov., the interorbital region is narrower than the supratemporal fossa, a feature not observed in any *Cricosaurus* but present in *Neptunidraco ammoniticus* (Cau and Fanti 2011). In *C. lithographicus* sp. nov., the participation of the parietal in the interfenestral bar is of

50 per cent while it is weaker in *C. araucanensis* and *C. vignaudi*. In *C. lithographicus* sp. nov., the fronto-parietal suture in lateral view is posterior to this suture in dorsal view, while in *C. araucanensis* the position is opposite. On the posterior-most margin of the pterygoid of the new species, inside the secondary choana, there is a subtle fold in the midline. This fold has not been identified in *C. araucanensis*. The mandibular symphysis in *C. lithographicus* sp. nov. is approximately 35 per cent of the mandibular length, in *C. araucanensis*, *C. vignaudi* (Frey *et al.* 2002), *C. elegans*, and *C. suevicus* the symphysis is 40 per cent of the mandible length or even more. Contrasting with most species of *Cricosaurus*, in *C. lithographicus* sp. nov. teeth crowns are bicarinated and have fine apicobasal aligned ridges that vanish towards the smooth apex. Carinated tooth crown with striations has also been reported in *C. macrospondylus* (Hua *et al.* 2000), and bicarinated but smooth tooth crown in *C. araucanensis*.

Cricosaurus lithographicus sp. nov. is characterized by a moderate number of maxillary teeth (20–22 teeth) with the interalveolar spaces between the first seven teeth approximately 1.5 times the anteroposterior diameter of the respective alveoli (Fig. 1E), conditions that contrast with the other species of *Cricosaurus* of the Neuquén Basin (i.e. *C. araucanensis*) with more than 30 maxillary teeth and with the interalveolar spaces even smaller than the anteroposterior diameter of the alveoli.

The phylogenetic analyses carried out are consistent with the inclusion of the new species within the genus *Cricosaurus*. It is worthy to remark that in both analyses, although they are based on different data sets, the inclusion of *Cricosaurus lithographicus* sp. nov. does not change previous proposals of the internal metriorhynchids topology.

Cricosaurus is in the analyses with more exhaustive taxon sampling (Young *et al.* in press), the richest genus of metriorhynchids, and also the clade internally less resolved. While consistently found as a monophyletic group, internal topology depicts three polytomies. When *Cricosaurus lithographicus* sp. nov. is scored in Young *et al.* (in press) data set, all the MPTs recovered form a clade with *C. macrospondylus* and the other *Cricosaurus* from the Neuquén Basin, *C. araucanensis*. The resolution of the internal topology of *Cricosaurus* clade seems to be more related to character sampling than to taxon sampling, particularly those of the postcranial skeleton. Quite interesting is that the main peculiarity of metriorhynchids is that it is the only group of crocodyliforms completely adapted to a pelagic lifestyle. A general trend among reptiles secondarily adapted to the marine realm is the strong modification of the postcranial skeleton. In ichthyosaurs and plesiosaurs, two unrelated groups considered as the paradigm of Mesozoic marine reptiles, phylogenetic signal

of postcranial features is strong. In the data sets used in two seminal papers for the resolution of the phylogeny of ichthyosaurs (Motani 1999) and plesiosaurs (O'Keefe 2001), the major proportion of characters corresponds to the postcranium (72 and 62 per cent respectively). In the case of the data sets used in phylogenetic analysis of metriorhynchids, this proportion is significantly lower (15 per cent in Pol and Gasparini 2009, and 27 per cent in Young *et al.* in press).

Most of the metriorhynchid taxa are represented solely by skulls and/or disarticulated and incomplete postcranial skeleton; therefore, this part of the skeleton is still poorly known or even unknown for many metriorhynchids. Consequently, there is a low proportion of postcranial features in data sets, and isolated postcranial elements are currently non-diagnostic at generic level. Recent revisions of metriorhynchids improved the knowledge on postcranial material of these crocodyliforms (Wilkinson *et al.* 2008; Herrera *et al.* 2009; Young *et al.* 2011b; Young *et al.* in press). In this sense, although the present contribution does not improve significantly the phylogenetic resolution of *Cricosaurus*, the description herein provides information of the postcranial skeleton representing a putative source of characters.

Morphological diversity of metriorhynchids from the Neuquén Basin

Although Tithonian–Berriasian metriorhynchid records recovered from the Neuquén Basin are not taxonomically diverse, as they are represented by four taxa (*Cricosaurus araucanensis*, *C. lithographicus* sp. nov., *Dakosaurus andiniensis* and *Purranisaurus potens*), they are significant in terms of morphological diversity. Busbey (1995) proposed three categories of crocodylian rostra shape using the ratio of rostral length versus basal skull length: long (the rostrum contributes 70 per cent or more to basicranial length), normal (between 70 and 55 per cent) and short (less than 55 per cent). Most metriorhynchids fall in an intermediate condition (or mesorostrine) with the exception of only three longirostrine taxa (*Gracilisuchus acutus*, *G. leedsi* and *Rhacheosaurus gracilis*) and one brevirostrine (*D. andiniensis*) (Young *et al.* 2010). Within morphological variations, Tithonian–Berriasian metriorhynchids from Neuquén fall in two different morphotypes: mesorostrine morphotype, *Cricosaurus araucanensis* and *C. lithographicus* sp. nov., and brevirostrine morphotype, *Dakosaurus andiniensis*. Patagonian metriorhynchid taxa not only differ in craniofacial morphology but also depict variation in dental morphology suggesting different feeding habits and eventually niche partitioning (Pierce *et al.* 2009; Young *et al.* 2010; Young *et al.* 2011a). During the Jurassic and Early Cretaceous metriorhynchids diversified

including large super-predators and piscivores/teuthophages forms (Young *et al.* 2011a). Within this variety of ecological and morphological types, Tithonian–Berriasian records recovered from the Vaca Muerta Formation indicate that the southern margins of the palaeopacific (Neuquén Basin palaeogulf) were inhabited by super-predators like *D. andiniensis* and piscivores/teuthophages forms (*Cricosaurus araucanensis* and *C. lithographicus* sp. nov.). Even more, both species of *Cricosaurus*, although sharing bicarinate teeth, they have different dental morphology characterized by a relatively high number of smooth maxillary teeth (*C. araucanensis*) versus fewer more robust and striated teeth (*C. lithographicus* sp. nov.). These differences could respond to different prey preferences.

At present *Cricosaurus lithographicus* sp. nov. is the only metriorhynchid recorded in El Ministerio Quarry (late early to middle late Tithonian) while *Cricosaurus araucanensis* (late Tithonian) has been recorded in many localities of the Neuquén Basin. *Cricosaurus lithographicus* sp. nov. allows us to confirm that the taxonomic and morphological diversity of the Tithonian metriorhynchids of the Neuquén Basin has been underestimated.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

Appendix S1. Data matrix used in the phylogenetic analysis based on Pol and Gasparini (2009) and Leardi *et al.* (2012).

Appendix S2. Data matrix used in the phylogenetic analysis based on Young *et al.* (in press).

REFERENCES

- ANDREWS, C. W. 1913. *A descriptive catalogue of the marine reptiles of the Oxford Clay*, 2. British Museum (Natural History), London, 206 pp.
- 1915. Note on a fore-paddle of *Metriorhynchus* from the Oxford Clay of Peterborough. *Geological Magazine*, **2**, 444–447.
- BILLON-BRUYAT, J.-P., LÉCUYER, C., MARTINEAU, F. and MAZIN, J.-M. 2005. Oxygen isotope compositions of Late Jurassic vertebrate remains from lithographic limestones of western Europe: implications for the ecology of fish, turtles, and crocodylians. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **216**, 359–375.
- BROCHU, C. A., BOUARE, M. L., SISSOKO, F., ROBERTS, E. M. and O'LEARY, M. A. 2002. A dyrosaurid crocodyliform braincase from Mali. *Journal of Paleontology*, **76**, 1060–1071.
- BUCHY, M.-C., VIGNAUD, P., FREY, E., STINNESBECK, W. and GONZÁLEZ GONZÁLEZ, A. H. 2006. A new thalattosuchian crocodyliform from the Tithonian (Upper Jurassic) of northeastern Mexico. *Comptes Rendus Palevol*, **5**, 785–794.
- BUCKLEY, G. A., BROCHU, C. A., KRAUSE, D. W. and POL, D. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature*, **405**, 941–944.
- BUFFETAUT, E. 1982. Radiation évolutive, paléoécologie et biogéographie des crocodyliens mésosuchiens. *Mémoires de la Société Géologique de France*, **142**, 1–88.
- BUSBEY, A. B. 1995. The structural consequences of skull flattening in crocodylians. 173–192. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge, 277 pp.
- CAU, A. and FANTI, F. 2011. The oldest known metriorhynchid crocodylian from the Middle Jurassic of North-eastern Italy: *Neptunidraco ammoniticus* gen. et sp. nov. *Gondwana Research*, **19**, 550–565.
- CHONG DIAZ, G. and GASPARINI, Z. 1972. Presencia de Crocodylia marinos en el Jurásico de Chile. *Revista de la Asociación Geológica Argentina*, **27**, 406–409.
- CLARK, J. M. 1994. Patterns of evolution in Mesozoic Crocodyliformes. 84–97. In FRASER, N. C. and SUES, H.-D. (eds). *In the shadows of dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press, Cambridge, 435 pp.
- CUVIER, G. 1824. Sur les ossements fossiles de crocodiles, 5. 143–160. In DUFOUR, G. and D'OCCAGNE, E. (eds). *Recherches sur les ossements fossiles*, Second édition. Dufour and d'Occagne, Paris, 548 pp.
- FARA, E., OUAJA, M., BUFFETAUT, E. and SRARFI, D. 2002. First occurrences of thalattosuchian crocodiles in the Middle and Upper Jurassic of Tunisia. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **8**, 465–476.
- FERNÁNDEZ, M. and GASPARINI, Z. 2000. Salt glands in a Tithonian metriorhynchid crocodyliform and their physiological significance. *Lethaia*, **33**, 269–276.
- 2008. Salt glands in the Jurassic metriorhynchid *Geosaurus*: implications for the evolution of osmoregulation in Mesozoic marine crocodyliforms. *Naturwissenschaften*, **95**, 79–84.
- and HERRERA, Y. 2009. Paranasal sinus system of *Geosaurus araucanensis* and the homology of the antorbital fenestra of metriorhynchids (Thalattosuchia: Crocodylomorpha). *Journal of Vertebrate Paleontology*, **29**, 702–714.
- PAULINA CARABAJAL, A., GASPARINI, Z. and CHONG DÍAZ, G. 2011. A metriorhynchid crocodyliform braincase from northern Chile. *Journal of Vertebrate Paleontology*, **31**, 369–377.
- FITZINGER, L. 1843. *Systema Reptilium*. Braumüller and Seidel, Vienna, **128** pp.
- FRAAS, E. 1901. Die Meerkrokodile (Thalattosuchia n.g.), eine Sauriergruppe der Juraformation. *Jahreshefte des Vereins für Vaterländische Naturkunde Württembergs*, **57**, 409–418.
- 1902. Die Meer-Krocodylier (Thalattosuchia) des oberen Jura unter specieller Berücksichtigung von *Dacosaurus* und *Geosaurus*. *Paleontographica*, **49**, 1–72.
- FREY, E., BUCHY, M.-C., STINNESBECK, W. and LÓPEZ-OLIVA, J. G. 2002. *Geosaurus vignaudi* n. sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodylians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences*, **39**, 1467–1483.
- GASPARINI, Z. 1973. Revisión de “*Purranisaurus potens*” Rusconi, 1948 (Crocodylia, Thalattosuchia). Los Thalattosuchia como un nuevo Infraorden de los Crocodylia. *Actas V Congreso Geológico Argentino*, **3**, 423–431.
- and DELLAPÉ, D. 1976. Un nuevo cocodrilo marino (Thalattosuchia, Metriorhynchidae) de la Formación Vaca Muerta (Jurásico, Titoniano) de la provincia de Neuquén. *Actas I Congreso Geológico Chileno*, **1**, C1–C21.
- 2005. Jurassic marine reptiles of the Neuquén Basin: records, faunas and their palaeobiogeographic significance. 279–294. In VEIGA, G. D., SPALLETTI, L. A., HOWELL, J. A. and SCHWARZ, E. (eds). *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics*. Geological Society, London, Special Publications 252, 336 pp.
- 2011. Reptiles marinos mesozoicos. 529–538. In LEANZA, H. A., ARREGUI, C., CARBONE, O., DANIELA, J. C. and VALLÉS, J. M. (eds). *Relatorio del XVIII Congreso Geológico Argentino, Neuquén*. Asociación Geológica Argentina, Buenos Aires, 893 pp.
- and ITURRALDE-VINENT, M. 2001. Metriorhynchid crocodyles (Crocodyliformes) from the Oxfordian of Western Cuba. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2001**, 534–542.
- DE LA FUENTE, M. S. and FERNÁNDEZ, M. S. 1995. Sea reptiles from the lithographic limestones of the Neuquén Basin, Argentina. *II International Symposium on Lithographic Limestones*. Universidad Autónoma de Madrid, Madrid, Spain, 81–84.
- POL, D. and SPALLETTI, L. A. 2006. An unusual marine Crocodyliform from the Jurassic–Cretaceous boundary of Patagonia. *Science*, **311**, 70–73.
- GOLOBOFF, P. A., FARRIS, J. S. and NIXON, K. 2003. TNT: tree analysis using new technologies. Program and documentation available from the authors and at <http://www.zmuc.dk/public/phylogeny>.

- HAY, O. P. 1930. *Second Bibliography and Catalogue of the Fossil Vertebrata of North America, Vol II*. Carnegie Institute of Washington Publication No. 390. Carnegie Institute of Washington, Washington, DC, 1074 pp.
- HERRERA, Y., FERNÁNDEZ, M. S. and VARELA, J. A. 2009. Morfología del miembro anterior de *Geosaurus araucanensis* Gasparini y Dellapé, 1976 (Crocodyliformes: Thalattosuchia). *Ameghiniana*, **46**, 657–667.
- HOLLIDAY, C. M. and WITMER, L. M. 2009. The epipterygoid of crocodyliforms and its significance for the evolution of the orbitotemporal region of eusuchians. *Journal of Vertebrate Paleontology*, **29**, 715–733.
- HUA, S. 1994. Hydrodynamique et modalités d'allègement chez *Metriorhynchus superciliosus* (Crocodylia, Thalattosuchia: implications paléocéologiques). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **193**, 1–19.
- and BUFFETAUT, E. 1997. Crocodilia. 357–374. In CALLAWAY, J. M. and NICHOLLS, E. L. (eds). *Ancient Marine Reptiles*. San Diego Academic Press, California, 501 pp.
- and de BUFFENIL, V. 1996. Bone histology as a clue in the interpretation of functional adaptations in the Thalattosuchia (Reptilia, Crocodylia). *Journal of Vertebrate Paleontology*, **16**, 703–717.
- VIGNAUD, P., ATROPS, F. and CLEMENT, A. 2000. *Enaliosuchus macrospondylus* Koken, 1883 (Crocodylia, Metriorhynchidae) du Valanginien de Barret le Bas (Hautes Alpes, France): un cas unique de remontée des narines externes parmi les crocodiliens. *Géobios*, **33**, 467–474.
- IORDANSKY, N. N. 1964. The jaw muscles of the crocodiles and some relating structures of the crocodilian skull. *Anatomischer Anzeiger*, **115**, 256–280.
- 1973. The skull of Crocodilia. 201–261. In GANS, C. and PARSONS, T. S. (eds). *Biology of the Reptilia*. Academic Press, London 4, 539 pp.
- JOUVE, S. 2009. The skull of *Teleosaurus cadomensis* (Crocodylomorpha; Thalattosuchia), and phylogenetic analysis of Thalattosuchia. *Journal of Vertebrate Paleontology*, **29**, 88–102.
- KARL, H.-V., GRÖNING, E., BRAUCKMANN, C. and KNÖTSCHKE, N. 2006. Revision of the genus *Enaliosuchus* Koken, 1883 (Archosauromorpha: Metriorhynchidae) from the Early Cretaceous of Northwestern Germany. *Studia Geologica Salmanticensia*, **42**, 49–59.
- KOKEN, E. 1883. Die reptilian der norddeutschen unteren Kreide. *Zeitschrift Deutschen Geologischen Gesellschaft*, **35**, 735–827.
- KUHN, O. 1936. *Crocodylia. Fossilium Catalogus I: Animalia* 75. Gracenhage, Junk, 144 pp.
- LARSSON, H. C. E. and GADO, B. 2000. A new Early Cretaceous crocodyliform from Niger. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **217**, 131–141.
- and SUES, H.-D. 2007. Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society*, **149**, 533–567.
- LEANZA, H. and ZEISS, A. 1990. Upper Jurassic lithographic limestones from Argentina (Neuquén Basin): stratigraphy and fossils. *Facies*, **22**, 169–186.
- — 1992. On the ammonite fauna of the Lithographic Limestones from the Zapala region (Neuquén province, Argentina), with the description of a new genus. *Zentralblatt für Geologie und Paläontologie*, **1**, 1841–1850.
- LEARDI, J. M., POL, D. and FERNÁNDEZ, M. S. 2012. The antorbital fenestra of Metriorhynchidae (Crocodyliformes, Thalattosuchia): testing its homology within a phylogenetic framework. *Journal of Vertebrate Paleontology*, **32**, 490–494.
- MEYER, C. E. H. VON 1831. Neue fossile Reptilien aus der Ordnung der Saurier. *Nova Acta Academiae Leopoldino-Carolinae Curios*, **15**, 173–184.
- MOTANI, R. 1999. Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology*, **19**, 473–496.
- O'KEEFE, F. R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica*, **213**, 1–63.
- PHILIPS, J. 1871. *Geology of Oxford and the Valley of the Thames*. Clarendon Press, Oxford, 523 pp.
- PIERCE, S. E., ANGIELCZYK, K. D. and RAYFIELD, E. J. 2009. Shape and mechanics in thalattosuchian (Crocodylomorpha) skulls: implications for feeding behaviour and niche partitioning. *Journal of Anatomy*, **215**, 555–576.
- POL, D. and GASPARINI, Z. 2007. Crocodyliformes. 116–142. In GASPARINI, Z., SALGADO, L. and CORIA, R. A. (eds). *Patagonian Mesozoic Reptiles*. Indiana University Press, Indiana, 374 pp.
- — 2009. Skull anatomy of *Dakosaurus andiniensis* (Thalattosuchia: Crocodylomorpha) and the phylogenetic position of Thalattosuchia. *Journal of Systematic Paleontology*, **7**, 163–197.
- and LARSSON, H. C. E. 2011. 1st Symposium on the evolution of crocodyliforms. *Zoological Journal of the Linnean Society*, **163**, S1–S6.
- RUSCONI, C. 1948. Nuevo plesiosaurio, pez y langosta del mar jurásico de Mendoza. *Revista del Museo Historia Natural de Mendoza*, **2**, 3–12.
- SCASSO, R. and CONCHEYRO, A. 1999. Nanofósiles calcáreos, duración y origen de ciclos caliza-marga (Jurásico tardío de la Cuenca Neuquina). *Revista de la Asociación Geológica Argentina*, **54**, 290–297.
- ALONSO, M. S., LANÉS, S., VILLAR, H. J. and LIPPAI, H. 2002. Petrología y geoquímica de una ritmita de margacaliza del Hemisferio Austral: el Miembro Los Catutos (Formación Vaca Muerta), Tithoniano Medio de la Cuenca Neuquina. *Revista de la Asociación Geológica Argentina*, **57**, 143–159.
- — — — and LAFFITTE, G. 2005. Geochemistry and petrology of a Middle Tithonian limestone-marl rhythmite in the Neuquén Basin, Argentina: depositional and burial history. 207–229. In VEIGA, G. D., SPALLETTI, L. A., HOWELL, J. A. and SCHWARZ, E. (eds). *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics*. Geological Society, London, Special Publications 252, 336 pp.
- SERENO, P. C. and LARSSON, H. C. E. 2009. Cretaceous crocodyliforms from the Sahara. *ZooKeys*, **28**, 1–143.
- — — — SIDOR, C. A. and GADO, B. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, **294**, 1516–1519.

- SÖMMERRING, S. T. VON 1816. Ueber die *Lacerta gigantea* der Vorwelt. *Denkschriften der Königlichen Akademie der Wissenschaften zu Münch 6: Classe der Mathematik und Naturwissenschaften*, 37–59 pp.
- TYKOSKI, R. S., ROWE, T. B., KETCHAM, R. A. and COLBERT, M. W. 2002. *Calsoyasuchus valliceps*, a new crocodyliform from the Early Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **22**, 593–611.
- VIGNAUD, P. 1995. Les Thalattosuchia, crocodiles marins du Mésozoïque: systématique, phylogénie, paléobiologie, biochronologie et implications paléogéographiques. Unpublished PhD thesis, Université de Poitiers, Poitiers, 265 pp.
- and GASPARINI, Z. B. 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences Paris*, **322**, 245–250.
- WAGNER, A. 1852. Neu-aufgefundene saurier-veberreste aus den lithographischer Schiefen ind den obern Juralke. *Abhandlungen der Mathemat.-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften*, **6**, 661–710.
- 1858. Zur Kenntniss der Sauier aus den lithographischen Schiefen. *Abhandlungen der Mathemat.-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften*, **8**, 415–528.
- WALKER, A. D. 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society London, Series B*, **257**, 323–372.
- WILKINSON, L. E., YOUNG, M. T. and BENTON, M. J. 2008. A new metriorhynchid crocodile (Mesoeucrocodylia: Thalattosuchia) from the Kimmeridgian (Upper Jurassic) of Wiltshire, UK. *Palaontology*, **51**, 1307–1333.
- WU, X., SUES, H.-D. and DONG, Z.-M. 1997. *Sichuanosuchus shuhanensis*: a new Early Cretaceous protosuchian (Archosauria: Crocodyliformes) from Sichuan (China), and the monophyly of Protosuchia. *Journal of Vertebrate Paleontology*, **17**, 89–103.
- RUSSELL, A. P. and CUMBAA, S. L. 2001. *Terminonaris* (Archosauria: Crocodyliformes): new material from Saskatchewan, Canada, and comments on its phylogenetic relationships. *Journal of Vertebrate Paleontology*, **21**, 492–514.
- YOUNG, M. T. and ANDRADE, M. B. 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. *Zoological Journal of the Linnean Society*, **157**, 551–585.
- BRUSATTE, S. L., RUTA, M. and ANDRADE, M. B. 2010. The evolution of Metriorhynchidea (Mesoeucrocodylia, Thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity and biomechanics. *Zoological Journal of the Linnean Society*, **158**, 801–859.
- BELL, M. A. and BRUSATTE, S. L. 2011a. Craniofacial form and function in Metriorhynchidae (Crocodylomorpha: Thalattosuchia): modelling phenotypic evolution with maximum-likelihood methods. *Biology letters*, **7**, 913–916.
- — ANDRADE, M. B. and BRUSATTE, S. L. 2011b. Body size estimation and evolution in metriorhynchid crocodylomorphs: implications for species diversification and niche partitioning. *Zoological Journal of the Linnean Society*, **163**, 1199–1216.
- ANDRADE, M. B., BRUSATTE, S. L., SAKAMOTO, M. and LISTON, J. in press. The oldest known metriorhynchid super-predator: a new genus and species from the Middle Jurassic of England, with implications for serration and mandibular evolution in predacious clades. *Journal of Systematic Palaeontology*.