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ARTICLE

A NEW PROTOSUCHID CROCODYLIFORM (PSEUDOSUCHIA, CROCODYLOMORPHA) FROM THE NORIAN LOS COLORADOS FORMATION, NORTHWESTERN ARGENTINA

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ABSTRACT—Protosuchids are known from the Late Triassic to the Early Cretaceous and form a basal clade of Crocodyliformes. We report here a new protosuchid crocodyliform, *Coloradisuchus abelini*, gen. et sp. nov., from the middle Norian Los Colorados Formation, La Rioja, northwestern Argentina. Our phylogenetic analysis recovers *Coloradisuchus abelini* within Protosuchidae, as the sister group of the clade formed by *Hemiprotosuchus* and two species of *Protosuchus* (*P. richardsoni* and *P. haughtoni*). The new protosuchid *C. abelini* increases the diversity of crocodyliforms in the Late Triassic and, together with *H. leali* from the same stratigraphic levels of the Los Colorados Formation, shows that the diversification of basal crocodyliforms was probably faster and/or older than thought previously.

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INTRODUCTION

Protosuchidae (Brown, 1934) is a clade of basal crocodyliforms known from the Late Triassic to the Early Cretaceous (Bonaparte, 1971; Busbey and Gow, 1984; Clark, 1986; Sues et al., 1996; Gow, 2000; Pol et al., 2004). The youngest record is *Edentosuchus tienshanensis* (Young, 1973; Pol et al., 2004), which is known from two specimens from the Lower Cretaceous beds of the Tugulu Group in China. The Lower Jurassic record of Protosuchidae is the most diverse. It includes three species of *Protosuchus*, the protosuchid genus with the widest geographic distribution, and an unnamed taxon from the Lower Jurassic Kayenta Formation of Arizona (Clark and Fastovsky, 1986; Sues et al., 1994; Osi, 2013). Among *Protosuchus*, *P. haughtoni* is known from several specimens, all from the Upper Elliot Formation in the Stormberg series of southern Africa (Busbey and Gow, 1984; Gow, 2000). Several complete skulls of *P. richardsoni* were discovered from the Moenave Formation of North America (Brown, 1933; Colbert and Mook, 1951; Crompton, 1980; Clark, 1986), making it probably the best-known protosuchid. Finally, *P. micmac* from the McCoy Brook Formation of Nova Scotia, Canada (Sues et al., 1996), is the most poorly known species of *Protosuchus* and is based on several specimens consisting of a small number of isolated cranial elements.

The only known Triassic record of Protosuchidae is *Hemiprotosuchus leali*, from the upper levels of the middle Norian Los Colorados Formation (Bonaparte, 1971; Kent et al., 2014), and a putative, unnamed protosuchid from the late Norian–Rhaetian Quebrada del Barro Formation (Martínez et al., 2015), both from northwestern Argentina. *Hemiprotosuchus leali* has been considered to be a close relative of *Protosuchus* (Clark, 1986, 1994). The material of *H. leali* includes an almost complete but badly preserved skull and partial postcranial remains.

The upper section of the Los Colorados Formation, which includes the topotype horizon of *H. leali*, is very well known for its unusual tetrapod assemblage, consisting of a mixture of taxa typical of the Upper Triassic, such as non-crocodylomorph paracrocodylomorphs, aetosaurs, and ornithosuchids, with taxa typical of the Lower Jurassic such as protosuchids and tritylodontids, and other taxa with Triassic–Jurassic affinities such as 'sphenosuchians,' basal neotheropods, diverse basal sauropodomorphs, and stem testudinatans (Arcucci and Coria, 2003).

We report here a new protosuchid crocodyliform collected from the upper levels of the middle Norian Los Colorados Formation (Kent et al., 2014), in the eastern Ischigualasto–Villa Unión Basin.

Institutional Abbreviations—**BPI**, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa; **CRILARPV**, Centro Regional de Investigaciones La Rioja, La Rioja, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **PVL**, Instituo Miguel Lillo, Tucumán, Argentina; **UCMP**, University of California Museun of Paleontology, Berkeley, California, U.S.A.

GEOLOGICAL SETTING

The holotype specimen of the new taxon (CRILARPV 301) was found in the Los Colorados Formation in the year 2003

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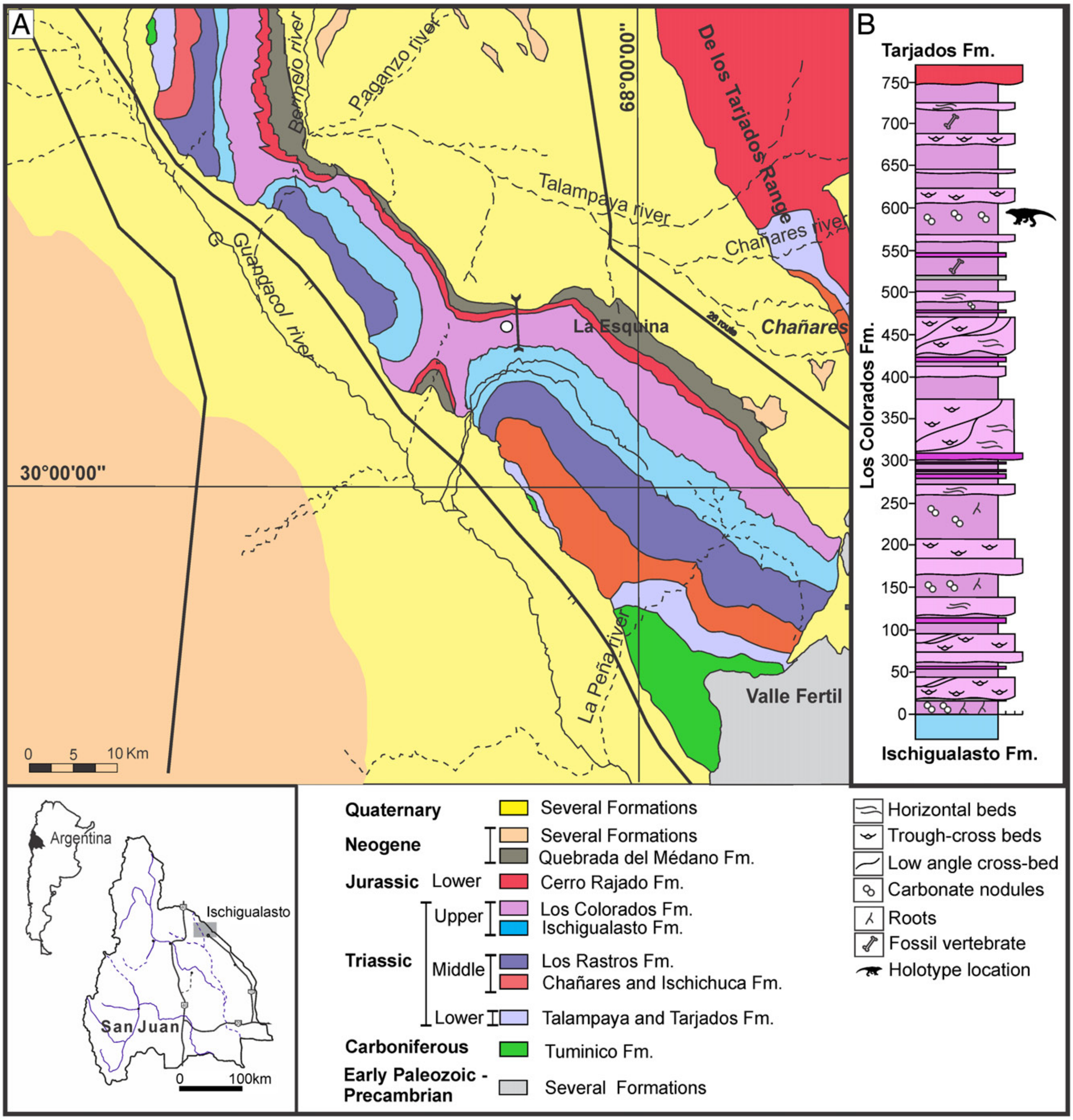

FIGURE 1. Location and geology of the Ischigualasto–Villa Unión Basin. **A**, geological map of the Ischigualasto–Villa Unión Basin. **B**, stratigraphic section of the Los Colorados Formation. Black circle indicates the type locality of *Coloradisuchus abelini* CRILARPV 301; black line indicates the location of the stratigraphic section. Modified from Martínez (1994).

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during field work carried out by the Instituto y Museo de Ciencias Naturales of the Universidad Nacional de San Juan. The Los Colorados Formation crops out in northwestern Argentina and forms part of the continental Triassic Ischigualasto–Villa Unión Basin (Fig. 1).

The continental Ischigualasto–Villa Unión Basin is one of the extensional basins developed during the Lower Mesozoic along the southwestern edge of Pangaea (Spalletti, 1999). The stratigraphy of the basin comprises, from bottom to top, the Talampaya (Permian–Lower Triassic), Tarjados (Middle Triassic), Chañares (Ladinian–earliest Carnian), Los Rastros (Carnian), Ischigualasto (Carnian–Norian), and Los Colorados (Norian) formations. The Los Colorados Formation conformably overlies the Ischigualasto Formation, with variable thickness from ca. 600 to 750 m (Caselli et al., 2001; Arcucci et al., 2004). The unit is composed of channel sandstones facies and overbank sandstones and mudstones deposited by high-sinuosity fluvial systems. The age of the Los Colorados Formation has been magnetostratigraphically determined to lower–middle Norian (Kent et al., 2014). The type locality is located 5 km west of the classic locality of La Esquina, well known for its fossiliferous richness. The specimen was found in the upper section of the unit, 580 m above the base, in a depositional interval characterized by high-sinuosity channels with mature calcisols in the floodplains (Fig. 1B).

MATERIALS AND METHODS

Terminology—We use the term 'basal' for the earliest-diverging branches of a lineage with respect to the later-diverging branches, which are often anatomically more derived. We employ traditional, or 'Romerian,' anatomical and directional terms (Romer, 1956) over veterinarian alternatives. 'Anterior' and 'posterior,' for example, are used as directional terms rather than the veterinarian alternatives 'rostral' or 'cranial' and 'caudal.'

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Clark in Benton and Clark, 1988
PROTOSUCHIDAE Brown, 1934 sensu Clark, 1986
COLORADISUCHUS ABELINI, gen. et sp. nov.

Diagnosis—Protosuchid characterized by the following combination of characters (an asterisk indicates an autapomorphy): anteroposteriorly long, elliptical lateral notch between the premaxilla and maxilla to receive the hypertrophied mandibular tooth*; maxillary contribution to the antorbital fossa extending ventrally to the entire ventral rim of the antorbital fenestra, reaching its maximum depth along its posterior half; low maxillary superficial surface between the alveolar margin and the antorbital fossa; thin and slender anterior ramus of the jugal; elongated trough running ventrally to the jugal ridge extending along the suborbital region of the jugal*; large infratemporal fenestra bordered by a narrow ascending process of the quadratojugal; anteroposteriorly long external mandibular fenestra; and mandibular ramus posterior to the mandibular fenestra approximately 3 times longer than high.

Holotype—CRILARPV 301, small skull (58 mm long) with lower jaws in occlusion, lacking skull roof and most of left part of the suspensorium. Partial articulated cervical vertebrae and osteoderms.

Horizon and Locality—Upper Los Colorados Formation (Ischigualasto Basin; Upper Triassic: Norian). La Esquina locality, Parque Nacional Talampaya, La Rioja Province, Argentina. Universal Transverse Mercator (UTM) coordinates: 19 J 586976, 6695479. The specimen was found scattered in several pieces within a radius of 2 m in a reddish silty sandstone from floodplain deposits located 580 m above the bottom of the unit (Fig. 1).

Etymology—*Coloradi*, from the Los Colorados Formation; *suchus*, Greek for crocodile; and *abelini* for Diego Abelin, technician of the Museo de Ciencias Naturales de San Juan who discovered and prepared the type specimen.

DESCRIPTION

Skull

Preservation—The skull with the lower jaws in occlusion is incomplete (Figs. 2–4). It was found in several scattered pieces, and some fragments are missing. Due to diagenetic pressure exerted from the right dorsolateral surface towards the left ventrolateral side, the skull and lower jaws have suffered a shear-type deformation effect, slightly rotating the lateral surfaces of the skull and lower jaws with respect to the horizontal plane, counterclockwise on the left side and clockwise on the right side. Thus, the right lateral side of the skull is more dorsally exposed, whereas the left side is more ventrally exposed. Despite this rotation, the plastic deformation of the specimen did not produce a marked deformation of the height and shape of the individual bones and most features are consistent on the left and right sides. The skull roof is eroded from the anterior border of the antorbital fenestra to its posterior end, although the jugal, quadratojugal, quadrate, and squamosal from the right side were preserved. The braincase has been partially preserved, but it is obscured because of poor preservation and the natural lightness and high pneumaticity of this area of the skull. The palatal complex is partially exposed dorsally and ventrally.

General Features—The skull has a narrow rostral region, as in more basal crocodylomorphs (e.g., *Sphenosuchus acutus*; Walker, 1990), but the region posterior to the orbit has a broad expansion typical of most crocodyliforms (e.g., *Gobiosuchus kielanae*; Osmólska, 1972).

Premaxilla—The premaxilla is a triangular bone that forms the anterior border of the rostral notch and the ventrolateral border of the external nares (Figs. 2–4). Both premaxillae meet anteriorly at the midline, forming the floor of the narial passage. The ascending internarial process is broken at its base and missing. Dorsally, it contacts the lateral border of the anterior process of the nasal (Fig. 2A, B). The premaxilla has an incipiently sculptured dorsal surface. The sculpturing of the premaxilla, as in the other sculpted bones, consists in a densely distributed, small, and shallow subcircular pit. Posteriorly, it contacts the maxilla inside a deep and wide rostral notch, which receives the lower caniniform tooth (Figs. 2, 4). This notch in *C. abelini* is similar, but significantly anteroposteriorly wider, than the ones in *P. haughtoni* and *P. richardsoni* and many other basal crocodyliforms. This contrasts with the condition in *H. leali*, which lacks a ventrally opened notch for receiving a hypertrophied mandibular tooth. The ventral region of the notch of *C. abelini* is partially closed by a posteriorly oriented process of the premaxilla.

Maxilla—The facial portion of the maxilla is trapezoidal and forms most of the lateral surface of the rostrum (Figs. 2–4). The anterior margin of the maxilla contacts the premaxilla medially and dorsally to the rostral notch. Posteriorly, it contacts the jugal and the lacrimal, whereas dorsomedially it contacts the nasal. The maxilla bears weak sculpturing on most of its dorsolateral surface, whereas within the antorbital fossa and inside the rostral notch it is smooth (as in the corresponding area of the premaxillae). Ventrally to the antorbital fossa, both maxillae have lost most of their external surface so that the presence of sculpture above the alveolar margin cannot be determined. The maxilla forms the anterior and ventral rims of the antorbital fenestra (Fig. 4). Below the ventral border of the antorbital fenestra, the maxilla forms the medial wall of a deep and anteroposteriorly elongated antorbital fossa. This antorbital fossa of the maxilla is more developed along the ventral margin than along its anterior margin, differing from the condition in *P. richardsoni* (MCZ 6727). Additionally, the ventral margin of the antorbital fossa (running dorsally to the alveolar margin of the maxilla) is deeper and dorsoventrally higher in its posterior half than along its anterior region, differing from the condition in *H. leali*. In both *Coloradisuchus* and *Hemiprotosuchus*, the ventral region of the antorbital fossa is approximately as dorsoventrally high as the lateral surface of the maxilla (extending between the maxillary alveolar margin and the ventral margin of the antorbital fossa), whereas in *P.*

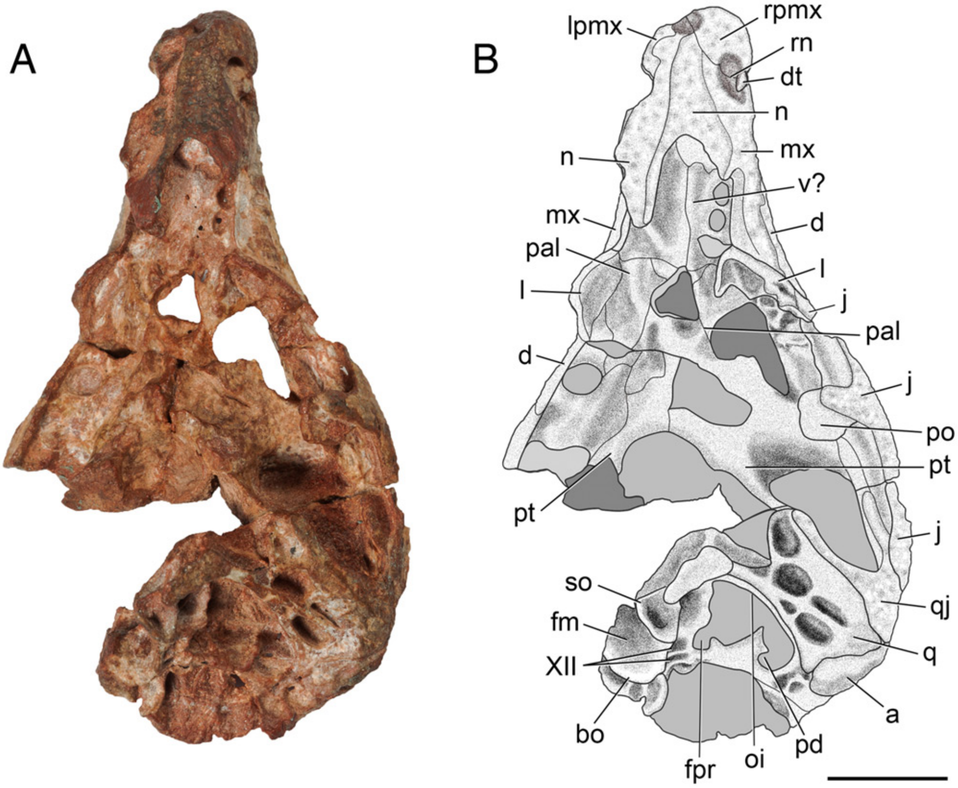

FIGURE 2. *Coloradisuchus abelini*, CRILARPV 301, skull in dorsal view. **A**, photograph; **B**, interpretive line drawing. Dark gray indicates broken surfaces; light gray indicates matrix. **Abbreviations**: **a**, articular; **bo**, basioccipital; **d**, dentary; **dt**, dentary tooth; **fm**, foramen magnum; **fpr**, fenestra pseudorotunda; **j**, jugal; **l**, lacrimal; **lpmx**, left premaxilla; **m**, maxilla; **n**, nasal; **oi**, otic incisure; **pal**, palatine; **pd**, prootic depression; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rn**, rostral notch; **rpmx**, right premaxilla; **so**, supraoccipital; **sq**, squamosal; **v**, vomer; **XII**, exit for XII nerve. Scale bar equals 1 cm.

richardsoni and *P. haughtoni* the lateral surface of the maxilla ventral to the antorbital fossa is deeper than the ventral region of the antorbital fossa. *Coloradisuchus abelini* lacks the large lateral concavity along the posterior half of the maxilla present in *P. haughtoni* (BPI/1/4770; Gow, 2000). The lateral surface of the maxilla lacks visible neurovascular foramina, but this could be due to superficial damage of the surface of this element.

Nasal—The anterior end of the nasals is not complete, but the preserved part forms the anterior dorsal surface of the rostrum. The external surface is sculpted, and, as preserved, it seems to be the bone of the skull with the coarsest sculpted surface. The contact with the premaxilla is fairly clear and shows what is interpreted here as an overlapping contact of the premaxilla over the nasal. The sutural details of the ventrolateral border of the nasal are not clear, but the nasal-maxilla suture seems to be straight and posterolaterally oriented (Figs. 2, 4). The anterior end of the nasals forms the posterodorsal border of the external naris.

Lacrimal—Only the ventral ends of both lacrimals have been preserved. This portion lacks sculpturing and is anterodorsally oriented, lying between the antorbital fenestra and the orbit. The anteroventral border overlaps the maxilla, and posteriorly the lacrimal is sutured to the jugal, excluding the maxilla from the orbital border (Fig. 4).

Postorbital—Only the ventral end of the jugal ramus of the right postorbital is preserved (Figs. 2, 4). It is flattened in transverse section, and laterally it is sutured with the medial surface of the postorbital ramus of the jugal, as in other protosuchids.

Jugal—Most of the left jugal is missing, but the right one is almost completely preserved, except for a small section ventral to the orbit. The lateral surface of the jugal is slightly sculpted (Fig. 4A, B). The jugal forms the ventral border of the orbit and the anteroventral border of the infratemporal fenestra. The anterior end of the jugal is acute and does not enter in the antorbital fossa. The thin anterior process of the jugal is sutured to the maxilla and lacrimal, resembling the condition in *P. micmac*. In contrast, the infraorbital region of the jugal of *H. leali* is dorsoventrally higher, whereas in *P. richardsoni*, *P. haughtoni*, and *Edentosuchus tienshanensis* this region is remarkably high and deeply sculpted (Clark, 1986; Gow, 2000; Pol et al., 2004). The long posterior process extends back and contacts the ventral border of the quadratojugal, a condition also observed in *H. leali* (PVL 3829) and *P. richardsoni* (UCMP 130860).

The dorsal ramus of the jugal is superficial, flattened in transverse section, and positioned at the anteroposterior midpoint of this bone. Its base is anteroposteriorly wide as in *P. richardsoni* and *P. haughtoni*, and wider than in *H. leali*. The lateral surface of the jugal bears a well-developed ventrolateral keel, which starts along the suborbital region and ends 3 mm before the posterior border of the jugal (Figs. 3A, B, 4A, B, 6). A similarly extensive keel is present in *P. haughtoni* (BPI/1/770), but in the latter the keel is much thicker and heavily sculpted. In H. leali, however, this keel is thin as in C. abelini but it is restricted to the infratemporal region of the jugal. A unique feature of *C. abelini* is that it bears an elongated trough

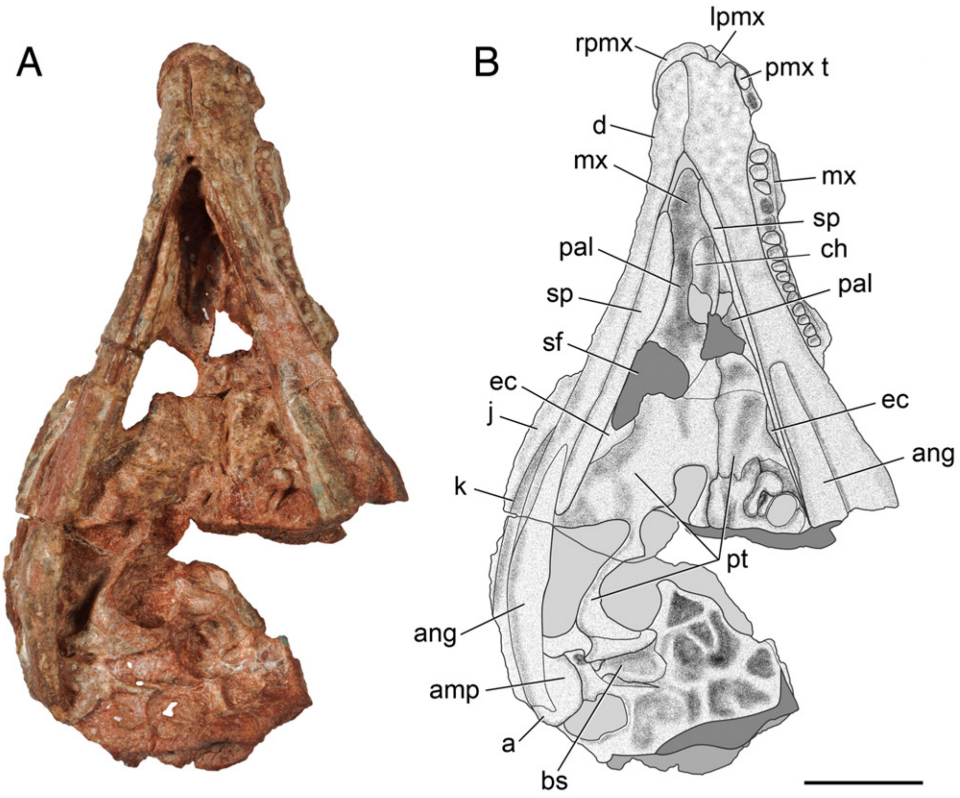

FIGURE 3. *Coloradisuchus abelini*, CRILARPV 301, skull in ventral view. **A**, photograph; **B**, interpretive line drawing. Dark gray indicates broken surfaces; light gray indicates matrix. **Abbreviations**: **a**, articular; **amp**, articular medial process; **ang**, angular; **bs**, basisphenoid; **ch**, choana; **d**, dentary; **dt**, dentary tooth; **ec**, ectopterygoid; **j**, jugal; **k**, jugal lateromedial keel; **lpmx**, left premaxilla; **m**, maxilla; **pal**, palatine; **pmx t**, premaxillary tooth; **pt**, pterygoids; **rpmx**, right premaxilla; **sf**, suborbital fenestra; **sp**, splenial. Scale bar equals 1 cm.

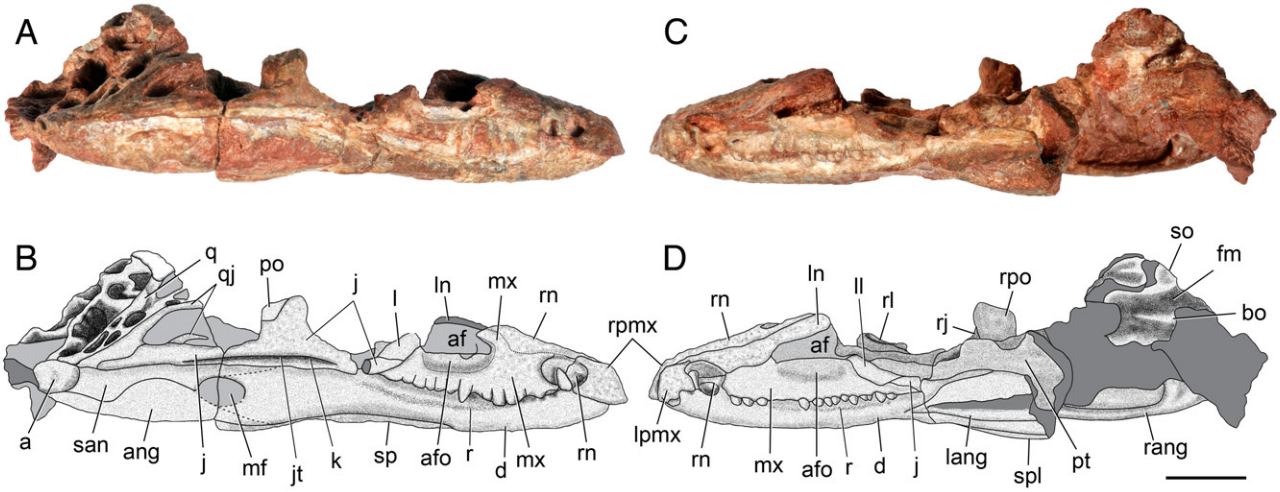

FIGURE 4. *Coloradisuchus abelini*, CRILARPV 301, skull in right (**A**, **B**) and left (**C**, **D**) lateral views. **A**, **C**, photographs; **B**, **D**, interpretive line drawings. Dark gray indicates broken surfaces; light gray indicates matrix. **Abbreviations**: **a**, articular; **af**, antorbital fenestra; **afo**, antorbital fossa; **ang**, angular; **bo**, basioccipital; **d**, dentary; **fm**, foramen magnum; **j**, jugal; **jt**, jugal trough; **k**, keel; **l**, lacrimal; **lang**, left angular; **ln**, left nasal; **lpmx**, left premaxilla; **m**, maxilla; **mf**, external mandibular fenestra; **n**, nasal; **pal**, palatine; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **rang**, right angular; **rn**, rostral notch; **rpmx**, right premaxilla; **rpo**, right postorbital; **san**, surangular; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal. Scale bar equals 1 cm.

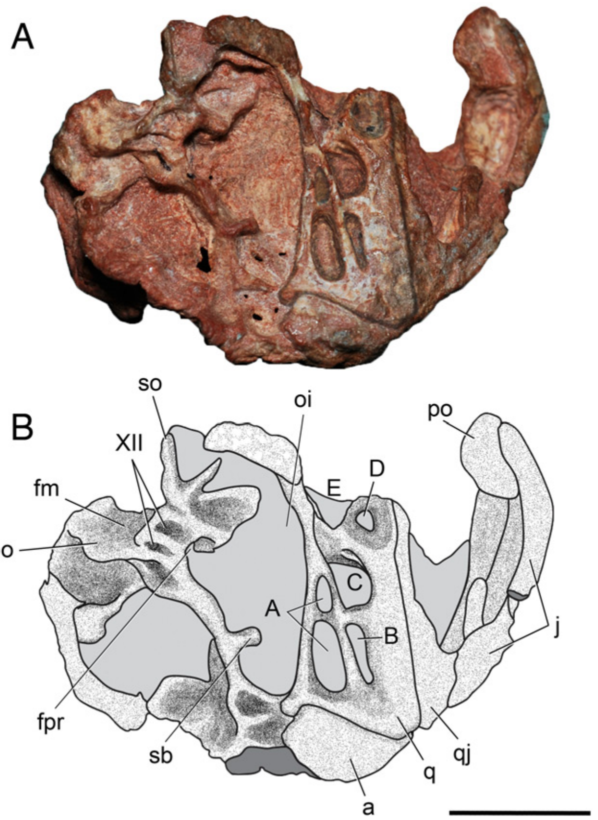

FIGURE 5. *Coloradisuchus abelini*, CRILARPV 301, skull in posterolateral view. **A**, photograph; **B**, interpretive line drawing. **Abbreviations**: **a**, articular; **A–E**, quadrate fenestrae; **bo**, basioccipital; **fm**, foramen magnum; **fpr**, fenestra pseudorotunda; **j**, jugal; **oi**, otic incisure; **po**, postorbital; **q**, quadrate; **qj**, quadratojugal; **sb**, strut of the basisphenoid; **so**, supraoccipital; **sq**, squamosal; **XII**, exit for XII nerve. Scale bar equals 1 cm.

running ventral to the keel, which faces ventrally and is deepest at the level of the posteroventral corner of the orbit.

Quadratojugal—This element forms the posterodorsal border of the infratemporal fenestra, where it is incipiently sculpted (Figs. 2A, B, 4A, B). The posteroventral end of the quadratojugal ends close to the quadrate condyles but does not participate in the craniomandibular articulation. The ascending process of the quadratojugal slopes anteromediodorsally and faces posterodorsolaterally, and its posterior border is sutured to the anterior edge of the quadrate. The ascending process is extremely narrow, anteriorly concave, and borders a broad infratemporal fenestra. This contrasts with the remarkably broad ascending process of the quadratojugal in *P. richardsoni* and *P. haughtoni*, which reduces the infratemporal fenestra to a narrow vertically oriented slit (Gow, 2000; Clark, 1986). In *H. leali*, the ascending process of the quadratojugal is narrower than in *Protosuchus* spp., but not as much as in *C. abelini* (and lacks the anteriorly concave margin of the infratemporal fenestra). The anterodorsal end of the quadratojugal is missing, so its relationship with the postorbital is unknown.

Quadrate—The quadrate is a large and flat bone that is anteriorly inclined and faces posterolaterodorsally. The anterolateral border is overlapped by the quadratojugal. The dorsal end of the quadrate is missing; thus, its contact with the squamosal and the postorbital cannot be determined. The distal end of the quadrate forms the articular condyle for the mandible, which in posterior view has a visible concavity separating a medial and a more protruding lateral condyle (Fig. 4A, B). The medial and internal portions of the quadrate are not visible, so the relationships with the braincase and the palate are unknown. The lateral surface of the quadrate forms a broad otic region as in most protosuchids (Fig. 5). The lateral surface of the quadrate in the otic region is smooth and heavily fenestrated. The quadrate presents five fenestrae (subtympanic foramina sensu Montefeltro et al., 2016) distributed like those in *P. richardsoni* (Hecht and Tarsitano, 1983), although in *C. abelini* they are larger and different in shape (Fig. 5). The most ventromedially located one (fenestra A, following the nomenclature used by Hecht and Tarsitano, 1983) is oblong and subdivided by a bony strut as in *P. richardsoni*, but it is dorsoventrally longer and reaches closer to the articular condyles. Lateral and parallel to this fenestra, fenestra B is a large and oblong aperture, much longer than in *P. richardsoni*. Fenestra C is a large subcircular opening located dorsolateral to fenestra A. Fenestra D is smaller and subtriangular, with its long axis dorsoventrally oriented and entirely included within the quadrate, differing from the condition in *P. richardsoni* in which this fenestra is anteriorly bordered by the quadratojugal (Clark, 1986). Fenestra E (topologically equivalent to the siphoneal foramen or single subtympanic foramen of most mesoeucrocodylians) is the largest and most dorsally located. Posterior to these fenestrae, the quadrate forms the anterior margin of the large otic incisure, which is long, gently concave, and not closed posteriorly (Fig. 5) as in protosuchids and most basal crocodyliforms (e.g., *Gobiosuchus*).

Palatal Complex

The palatal complex of *C. abelini* is poorly preserved, and although most of its elements are visible, the majority of their contacts are obscure. The occluded lower jaws preclude determination of the participation of the premaxillae and most of the maxillae in the palatal complex. The posteromedial region of the palatal shelf of the right maxilla shows that the maxillae meet along the midline and form the anterior margin of the choanal opening (Fig. 3), as in all basal crocodyliforms, where known.

Palatine—Both palatines are partially preserved, but their relationship with most of the secondary palate is somewhat imprecise (Figs. 2, 3). The posteromedial edge of the palatine underlies the pterygoid as in *P. richardsoni* (Clark, 1986). The lateral and anterior edges contact the maxilla, and the anteromedial border probably contacted the vomer. The posterior edge borders the suborbital fenestra. The left suborbital fenestra is not visible, although the right one is partially preserved, enough to infer an anteroposteriorly elongated shape that extends for most of the anteroposterior extension of the orbit (Fig. 3A, B). The lateral and anterior borders of the choana are preserved on the right side and are bounded by the palatine and the maxilla, respectively. The lateral borders are almost straight, and the anterior margin is concave (Fig. 3A, B).

Pterygoid—Along the posterior portion of the palate, the pterygoids meet at the midline (Fig. 3A, B) but are not fused to each other, in contrast to the condition in mesoeucrocodylians. The palatal surface is practically flat and smooth, in contrast to the condition in *P. richardsoni* and *P. haughtoni* in which it is gently convex and sculpted (Clark, 1986). Most of the posterior portion was eroded, so the posterior contact with the basisphenoid is not very clear. The lateral flanges are broad, and laterally they reach the medial surface of the mandible, as in all crocodyliforms. The lateral portion of the anterior border contacts the ectopterygoids. The quadrate ramus is sutured with the basisphenoid posteromedially, extending onto

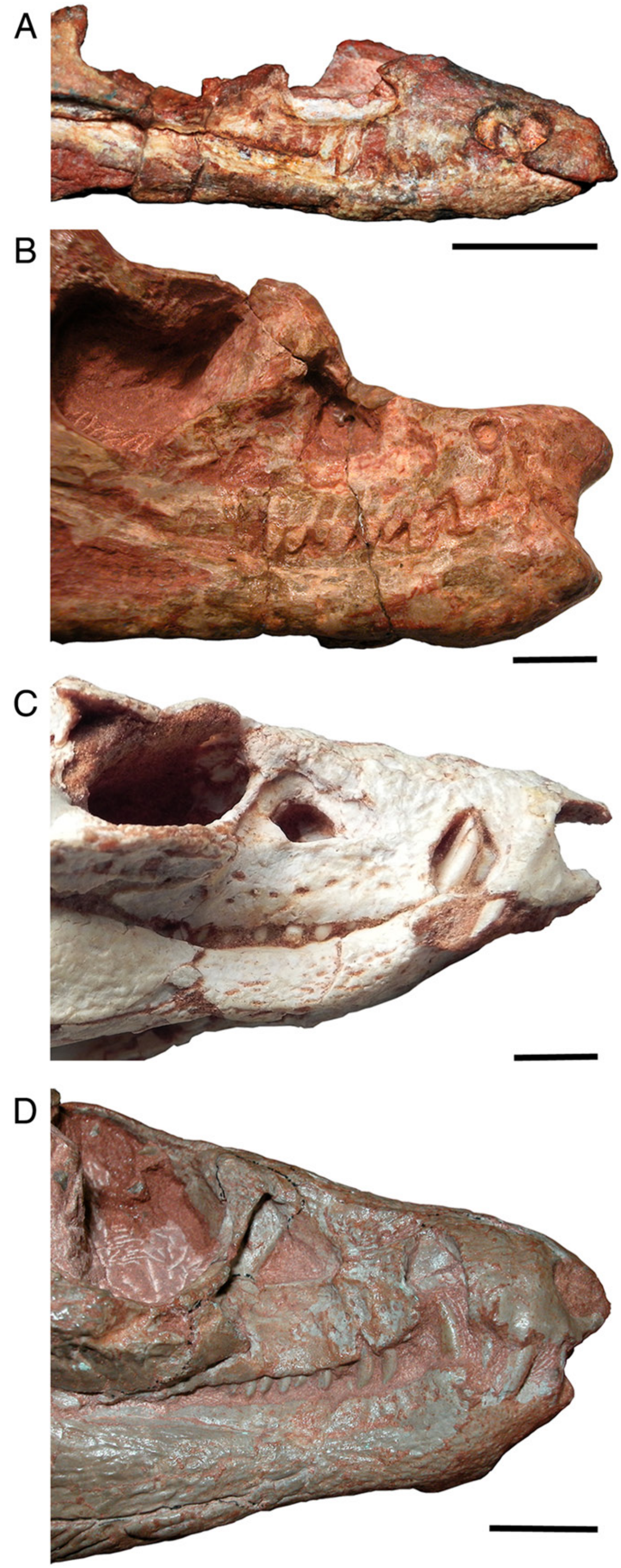

FIGURE 6. Comparative anatomy of protosuchid rostra in right lateral view. **A**, *Coloradisuchus abelini*, CRILARPV 30. **B**, *Hemiprotosuchus leali*, PVL 3829. **C**, *Protosuchus richardsoni*, MCZ 6727. **D**, *Protosuchus haughtoni*, BPI/1/4770. Scale bars equal 1 cm.

the ventral surface of the braincase, and the quadrate posterolaterally (Fig. 3A, B). Dorsally, the pterygoids form an interorbital ridge along the midline. Unfortunately, the loss of most of the posterodorsal area of the pterygoids, as well as the dorsal portion of the braincase, precludes describing its relationships with the basisphenoid rostrum and the laterosphenoids.

Ectopterygoid—Both ectopterygoids are preserved, although the right one is better exposed. It is slender and directed laterally (rather than anteriorly as in *E. tienshanensis*) and contacts the pterygoid flange posteromedially and the jugal laterally. The concave anterior edge forms the posterior border of the suborbital fenestra (Fig. 3A, B).

Braincase

Due to the small size of the specimen and the very delicate nature of the bony structure of the otic region, preparation of the braincase was extremely difficult and in some regions proved impossible. All of the left half of the braincase is missing and the right half is poorly preserved, but enough is present to observe its highly pneumatic nature, as in other protosuchids and other basal crocodyliforms. The sutural relationships between all the preserved bones are not visible, so our description will focus on the pneumatic cavities and on comparison with other basal crocodyliforms.

Parts of the supraoccipital, the otoccipital, and the basioccipital are partially preserved, especially the portions around the foramen magnum (Figs. 2A, B, 4C, D, 5A, B). The occipital condyle is lost, as is the entire ventral portion of the basioccipital, so its relationship with the basisphenoid is not visible. Ventrolateral to the foramen magnum, two small foramina are visible, probably the exits for both branches of N. hypoglossus (cranial nerve XII). Lateral to these foramina, a ventrolateral expansion that almost reaches the right quadrate condyle represents a strut of the basisphenoid. A notch within this expanded area may represent the internal course of the A. carotis interna. In ventral view (Fig. 3), remains of a partially preserved basisphenoid show that this element was highly expanded and pneumatic, as in *P. richardsoni* (Clark, 1986).

Mandible

Both mandibular rami are partially preserved. The right ramus is almost complete but lacking the retroarticular process, and the left ramus is missing from the level of the posterior border of the lateral mandibular fenestra (Figs. 3, 4). The lateral and ventral surfaces of the mandible are sculpted with a series of grooves, ridges, and pits, as in other protosuchids. Deficient preservation does not allow precise recognition of the limits of the mandibular fenestra. This opening, however, seems to be longer than high (Fig. 4A, B), a feature common among more advanced crocodyliforms such as the mesoeucrocodylians (*Zosuchus davidsoni* Pol and Norell, 2004; *Araripesuchus*), but contrasting with the anteroposteriorly short and subvertically oriented mandibular fenestra in *P. richardsoni* and *P. haughtoni*. The condition in *H. leali* unfortunately cannot be determined. A major difference between the mandibular ramus of *C. abelini* and that of other protosuchids is the proportion of the region posterior to the mandibular fenestra (Fig. 7). In *C. abelini*, the mandibular ramus is low and elongated (at least 3 times longer than high), but in other protosuchids the posterior region of the mandibular ramus is proportionately shorter and higher (ranging from 1.5 times in *H. leali* to approximately subequal in *P. haughtoni*) (Fig. 7).

Dentary—The dentary forms the anterior part of the mandible and is more than half the length of the mandible. The anterior external portion shows an incipiently sculpted surface

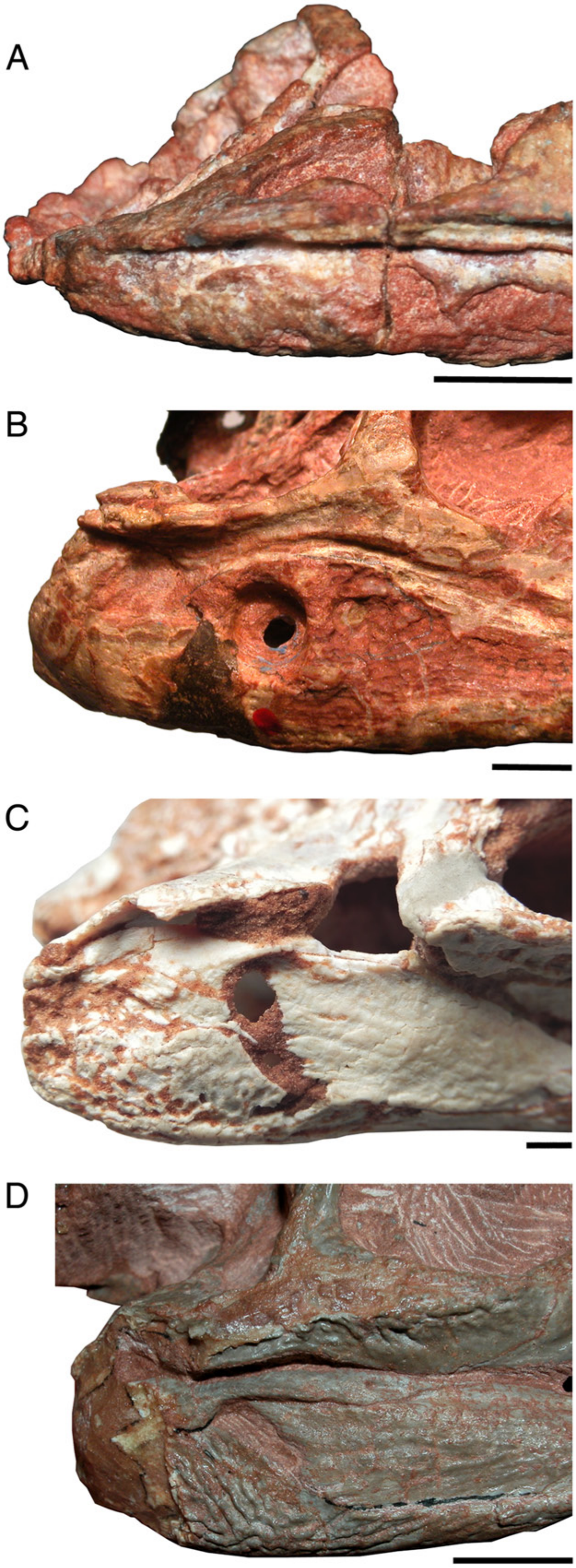

FIGURE 7. Comparative anatomy of protosuchid posterior mandibular rami in right lateral view. **A**, *Coloradisuchus abelini*, CRILARPV 301. **B**, *Hemiprotosuchus leali*, PVL 3829. **C**, *Protosuchus richardsoni*, MCZ 6727. **D**, *Protosuchus haughtoni*, BPI/1/4770. Scale bars equal 1 cm.

characterized by small protuberances uniformly distributed along the surface. The symphysis is relatively long and extends backwards, passing the level of the hypertrophied mandibular tooth (Fig 3A, B, 4). The symphyseal area is the stoutest part of the mandible, similar to the condition in *P. richardsoni* and *P. haughtoni*, although dorsoventrally lower and less robust than in *H. leali*. Anteriorly, the lateral surface of the dentary protrudes laterally in the position of the root of the enlarged mandibular teeth (Figs. 3A, B, 4A, B). Just posterior to the symphysis, the mandibular ramus is the narrowest part of the mandible. The lateral surface of the dentary bears an anteroposterior ridge that runs from the level of the hypertrophied mandibular tooth to the posterior end of the tooth row. The lateral surface of the alveolar margin of the dentary is inset with respect to the dentary ridge. In *C. abelini*, this ridge is more developed than in *Protosuchus* spp., especially along its anterior half. Posteriorly, the dentary extends along the dorsal border of the external mandibular fenestra, where it must have contacted the surangular (but the preservation is not good enough to determine this suture).

Splenial—The splenial is a broad sheet of bone covering the medial surface of the dentary (Fig. 3A, B). Anteriorly, it ends posterior to the symphysis, as in other basal crocodyliforms. The posterior end reaches the level of the anterior half of the mandibular fenestra. The ventral border extends further posteriorly than does the dorsal one.

Angular—The angular forms the ventral half of the posterior part of the mandible and probably the ventral border of the external mandibular fenestra. The erosion of the ventral surface of the dentary exposes the full length of the angular, which extends anteriorly to the level of the last maxillary teeth (Fig. 4C, D). Posterolaterally, the angular contacts the articular and the surangular.

Surangular—The surangular forms the dorsal half of the lateral surface of the mandible and posteriorly contacts the articular. Because the lower jaw is in occlusion, the dorsal border is not entirely visible. As in *P. richardsoni* and *P. haughtoni*, the surangular is slightly arched dorsally so that the posterior half of the mandible is approximately twice as tall as the anterior half (Fig. 4A, B). The surangular extends anteriorly along the dorsal edge of the dentary above and possibly anterior to the mandibular fenestra. Possibly due to the different anteroposterior length of the fenestra, *C. abelini* lacks the long anterior ramus of the surangular present in *P. richardsoni* and *P. haughtoni.* Posterior to the mandibular fenestra, the surangular contacts the angular ventrally.

Articular—The articular is a large bone firmly fused to the surangular and the angular. It forms the articulation with the quadrate and the insertion area for the M. depressor mandibulae. The posterior end of the articular is broken but seems to be similar to the extremely short and low retroarticular process present in *P. richardsoni* and *P. haughtoni*. The articular has a long medial process (Fig. 3), resembling the condition in other protosuchids, but the relationship with the otoccipital is not clear because of poor preservation (Fig. 2A, B).

Dentition—Although dentaries, maxillae, and premaxillae are preserved, the occluded and inset lower jaw precludes determining the exact dental formula of *C. abelini*. The only exposed premaxillary tooth is preserved in the left premaxilla. Judging from its location with only one more alveolus posterior to it, and the relationship between its mesiodistal length and the length of the alveolar margin of the premaxilla, this probably corresponds to the third premaxillary tooth. Following this criterion, *C. abelini* may have four premaxillary teeth, as in *P. haughtoni* (Gow, 2000) and *P. richardsoni* (Clark, 1986). The tooth is broken at the base of the crown, but the size of the section demonstrates that this premaxillary tooth was much larger than any maxillary teeth (Fig. 3A, B).

Both sides of the maxillary dentition are exposed, although the left side is the most complete and well preserved. The left maxilla holds 15 alveoli, of which the fourth and the fifth are empty. The right maxilla, although superficially damaged, and preserving just the impression of most of the teeth, seems to bear the same number of teeth, allowing us to confirm with complete confidence that this is its maxillary dental formula (Figs. 2A, B, 4A–C). Among the other Protosuchidae, *H. leali* and *P. haughtoni* have 14 maxillary teeth, the largest individual of *P. richardsoni* has 12, and *E. tienshanensis* has five (Pol et al., 2004). All maxillary teeth are closely packed, with a bulbous labial surface and without a basal constriction of the crowns. As in most basal crocodyliforms, the maxillary teeth are of approximately the same size, lacking the one or two waves of size variation present in many mesoeucrocodylians. They seem to lack mesial or distal serrations, although the poor preservation precludes determining this with confidence. The crowns are mesiodistally symmetrical, robust and short (the longest preserved crown is 1.8 times longer than mesiodistally wide), and perpendicular to the alveolar margin. These features of the maxillary teeth are similar to those in *H. leali* (Bonaparte, 1971), but different from the proportionally longer, slightly posteriorly directed and serrated teeth of *P. richardsoni*, *P. haughtoni*, and the Kayenta crocodyliform (Clark, 1986; Gow, 2000; Sues et al., 1994), as well as the multicuspidate teeth of *E. tienshanensis* (Pol et al., 2004).

The only completely visible dentary tooth is the large right caniniform, which lies inside the rostral notch. In the left dentary, an empty alveolus marks the position of the left hypertrophied mandibular tooth, but an anterior one is partially covered by the left premaxilla (Fig. 4). The hypertrophied mandibular tooth occludes within the large and wide notch formed by the premaxilla and the maxilla. The right dentary hypertrophied mandibular tooth is oriented almost perpendicular to the alveolar margin. It is at least twice as large as any of the maxillary teeth, and is possibly similar in size (judging by its mesiodistal length) to the partially preserved premaxillary tooth. It is labiolingually flat, with a slightly convex mesial border and slightly concave distal border. It lacks serrations, as in the other teeth, although this can be a preservational artifact. The preserved left dentary tooth is incomplete, lacking its apical part. It is slightly anterodorsally directed. The distal border is concave and lacks serrations. Considering the size of the preserved part of the crown, it seems to be larger than the right caniniform (Fig. 4).

PHYLOGENETIC ANALYSIS

The phylogenetic relationships of *Coloradisuchus abelini* were tested through a parsimony analysis using a data set of Crocodyliformes (Supplementary Data 1), based on Pol et al. (2014) and using the subsequent modifications introduced by Leardi et al. (2015) and Fiorelli et al. (2016). One additional character describing the anatomy of the maxillary contribution to the antorbital fossa has been added to this data set (see Supplementary Data 2). The equally weighted parsimony analysis conducted in TNT (Goloboff et al., 2008a, 2008b) resulted in 58,988 most parsimonious trees of 1695 steps (consistency index [CI] = 0.312, retention index [RI] = 0.742), all of which show the same topology for basal crocodyliforms. In the strict consensus (Fig. 8) *Coloradisuchus* is placed within Protosuchidae (sensu Clark, 1986), the most basal clade of Crocodyliformes. Other taxa included in this clade are *Protosuchus*, *Hemiprotosuchus*, *Edentosuchus*, and an undescribed crocodyliform from the Kayenta Formation (Clark, 1986, 1994). This clade is diagnosed by six unambiguous synapomorphies (see Supplementary Data 2), three of which can be scored in *Coloradisuchus*: presence of a long medial process of the articular (which contacts the otoccipital and basisphenoid in the well-preserved members of this clade; char. 73.2), mandibular symphysis shallow and tapering anteriorly in lateral view (char. 103.0), and dorsoventrally high maxillary contribution to the antorbital fossa (char. 441.1; reversal in *Protosuchus*). Within Protosuchidae, *Coloradisuchus* is the sister taxon of the clade formed by *Hemiprotosuchus* and the two included species of *Protosuchus* (*P. richardsoni* and *P. haughtoni*). This clade including *Coloradisuchus* is supported by two unambiguous synapomorphies: the skull expands abruptly at the orbits (char. 2.1) and the presence of a longitudinal ridge on the lateral surface of the jugal below the infratemporal fenestra (char. 216.1). *Coloradisuchus* is placed basal to the *Hemiprotosuchus* + *Protosuchus* clade given the absence of a sculpted palatal surface of the pterygoids, which diagnoses this clade (char. 40.1). Finally, the two species of *Protosuchus* share three features absent in other protosuchids: anterior part of the jugal twice as deep as the posterior part (char. 17.1), presence of large and aligned neurovascular foramina on the lateral maxillary surface (char. 138.1), and maxillary contribution to antorbital fossa tapering posteriorly (char. 411.0). Support values within Protosuchidae are relatively low, indicating that the relationships presented here may easily change with the addition of new data. The Bremer support (Bremer, 1994) value for Protosuchidae is 3 and for all of its internal clades it is 2, except for the clade formed by *Hemiprotosuchus* + *Protosuchus*, which has minimal Bremer support value (Fig. 8). Similarly, bootstrap and jackknife frequencies are low for most nodes within Protosuchidae (Fig. 8). Placing *Coloradisuchus* as the sister group of the rest of the protosuchids or in a more derived position within Protosuchidae implies only two or one extra step, respectively. Nevertheless, placing *Coloradisuchus* more basally or more apically among Crocodyliformes implies at least four extra steps, indicating that its inclusion in Protosuchidae is moderately well supported.

Protosuchidae is depicted in our analysis as the most basal clade of Crocodyliformes, in accordance with most previous phylogenetic studies of the group (e.g., Benton and Clark, 1988; Clark, 1994; Pol and Norell, 2004; Pol et al., 2014). Recently, however, Wilberg (2015) suggested that Thalattosuchia could be positioned as the most basal group of Crocodyliformes. Although this problem falls outside the scope of the present paper, a constrained search on our data set forcing Thalattosuchia to be the sister group of all other crocodyliforms still places *Coloradisuchus* with Protosuchidae. These constrained topologies are markedly suboptimal (13 extra steps) and show that the protosuchid affinities of *Coloradisuchus* are robust to the phylogenetic placement of this family.

DISCUSSION

Coloradisuchus abelini exhibits several features that allow it to be distinguished from other protosuchids: (1) anteroposteriorly long elliptical lateral notch between the premaxilla and the maxilla to receive the lower caniniform tooth, different from the smaller and dorsoventrally wider notch present in *P. richardsoni* and *P. haughtoni* (Fig. 6); (2) maxillary contribution to the antorbital fossa extending below the entire ventral rim of the antorbital fenestra (Fig. 6); (3) thin and slender anterior ramus of the jugal, contrasting with the high and robust ramus present in *P. richardsoni* and *P. haughtoni* (Fig.

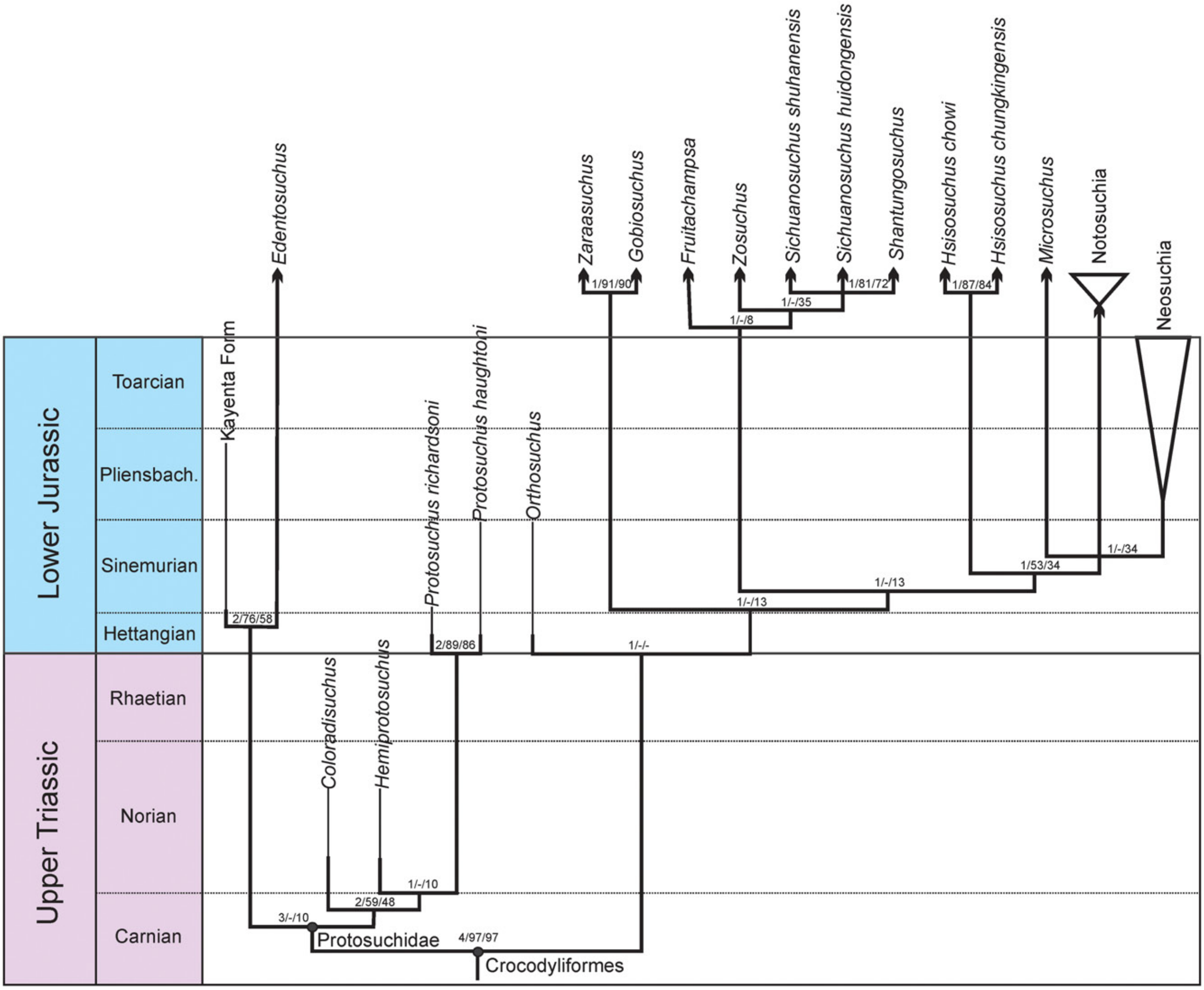

FIGURE 8. Phylogenetic position of *Coloradisuchus abelini* among basal Crocodyliformes. Numbers above the nodes represent the Bremer support values, followed by the bootstrap absolute and GC frequencies (Goloboff et al., 2008a). See Supplementary Data 2 for further details.

6); (4) deep trough running ventral to the jugal ridge from the infratemporal to the suborbital process; (5) large infratemporal fenestra bordered by a narrow ascending process of the quadratojugal, in contrast to the narrow, vertically oriented slit present in *P. richardsoni* and *P. haughtoni*; (6) anteroposteriorly long external mandibular fenestra (Fig. 7); and (7) low and anteroposteriorly long mandibular ramus posterior to the mandibular fenestra (Fig. 7).

This combination of characters (e.g., thin and slender anterior ramus of the jugal; large infratemporal fenestra bordered by a narrow ascending process of the quadratojugal) together with autapomorphies (e.g., anteroposteriorly long, elliptical lateral notch between premaxilla and maxilla to receive the hypertrophied mandibular tooth; elongated trough running ventrally to the jugal ridge extending along the suborbital region of the jugal) allows us to distinguish *C. abelini* from other protosuchids. Furthermore, although *C. abelini* and *H. leali* are from similar stratigraphic levels of the Los Colorados Formation and share protosuchid traits that place them phylogenetically close to each other, the new taxon can be further distinguished from *H. leali* by other characters: (1) presence of a ventrally open notch between the premaxilla and the maxilla, whereas in *H. leali* these elements contact each other along the alveolar margin (Fig. 6); (2) mandibular symphysis seems to be dorsoventrally lower and less robust than the deep symphysis of *H. leali*, although the anterior-most region of its symphysis may be missing (Fig. 6); (3) ventral region of antorbital fossa deepest along posterior half and lacking a dorsal projection along anterior margin of antorbital fenestra, whereas in *H. leali* the posterior depression is not present and the maxilla contributes to a broad anterior region of the antorbital fossa (Fig. 6); (4) jugal ridge extending along the suborbital region dorsal to the longitudinal trough, whereas in *H. leali* the jugal ridge is present only along the infratemporal region and disappears at the level of the ascending process of the jugal (and the jugal lateral surface lacks the trough below the orbit; Fig. 7); (5) 15 maxillary teeth in a smaller skull than the 14 present in the *H. leali* type material; and (6) mandibular ramus posterior to the external mandibular fenestra much longer than high, whereas in *H. leali* it is higher than long (Fig. 7).

Protosuchids are the most basal clade of Crocodyliformes, and this clade represents the first radiation of the group.

Although the inclusion of *Coloradisuchus* in Protosuchidae does not extend the temporal range of the clade, it increases its diversity in the Late Triassic. More importantly, the occurrence of this new taxon in the same stratigraphic level as the oldest protosuchid known so far (*H. leali*) shows that the diversification of basal crocodyliforms was probably faster and/or older than previously thought. *Coloradisuchus abelini* and *H. leali* are the oldest known records of Crocodyliformes and, together with the putative unnamed taxon from Quebrada del Barro Formation (Martínez et al., 2015), are the only known Triassic crocodyliforms. Strengthening the inference of a fast diversification of Crocodyliformes is the presence of the oldest known record of Crocodylomorpha, *Trialestes romeri* (Bonaparte, 1982), in the underlying Ischigualasto Formation (upper Carnian–lower Norian; Martínez et al., 2011), temporarily separated from *C. abelini* by no more than 15 million years.

The current record of the early diversification of Crocodyliformes, provided by the oldest records from Los Colorados Formation, suggests that this group was restricted to southwestern Pangea up to the end of the Triassic. Only after the end-Triassic mass extinction, during the earliest part of the Early Jurassic, did crocodyliforms (including Protosuchidae) significantly increase their diversity and expand their geographic distribution (as well as their morphological disparity; Stubbs et al., 2013; Toljagic and Butler, 2013). This diversification is documented by the protosuchids through their records from the Lower Jurassic of North America (*P. richardsoni*, *P. micmac*, Kayenta crocodyliform; Clark, 1986) and southern Africa (*P. haughtoni*). Finally, the youngest record of this group is known from the Cretaceous of Asia (*E. tienshanensis*), which extends the stratigraphic range of this group for more than a hundred million years and denotes the success of this clade of small basal crocodyliforms.

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