



The first crocodyliform from the Chubut Group (Chubut Province, Argentina) and its phylogenetic position within basal Mesoeucrocodylia

Juan Martín Leardi^{a,c,*}, Diego Pol^{b,c}

^aLaboratorio de Paleontología de Vertebrados, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Pabellón II, Universidad de Buenos Aires, Intendente Güiraldes 2160, Ciudad Universitaria (C1428EGA), Buenos Aires, Argentina

^bMuseo Paleontológico Egidio Feruglio, Avenue Fontana 140 (9100), Trelew, Chubut, Argentina

^cCONICET- Consejo Nacional de Investigaciones Científicas y Técnicas, Avenue Rivadavia 1917, Buenos Aires, Argentina

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ABSTRACT

A new crocodyliform specimen is presented here found in the Cerro Castaño Member of the Cerro Barcino Formation (Chubut Group). The material consists of cranial and postcranial remains that represent a new taxon that has strong affinities with Peirosauridae, but also shares derived features present in *Araripesuchus*. The phylogenetic relationships of this new taxon were tested through a cladistic analysis depicting it as a member of the Peirosauridae. The inclusion of *Barcinosuchus* within this clade of basal mesoeucrocodylians is supported by the presence of hypapophyses up to the third or fourth dorsal vertebrae, anterolateral facing edge on postorbital, quadrate dorsal surface divided in two planes by a ridge; mandibular symphysis tapering anteriorly in ventral view, lateral surface of dentary convex anterior to mandibular fenestra, distal body of quadrate well developed, anteroposteriorly thin and lateromedially broad. The new specimen broadens the temporal and geographical distribution of Peirosauridae during the Cretaceous of Gondwana, representing the southern-most and the most ancient record of the group in Patagonia. The new material also provides insights on the postcranial anatomy of peirosaurids, a group that has been so far studied almost exclusively from cranial material.

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1. Introduction

The Cretaceous fossil record of vertebrates from Patagonia is among the best known from the southern hemisphere. However, most of our knowledge is centered on taxa found in Upper Cretaceous beds of the Neuquén basin, northwestern Patagonia (Gasparini et al., 2007). Fossils from other stages of the Cretaceous and other regions of Patagonia are not as common, although an increasing amount of evidence has been collected from central and southern Patagonia in recent years (Novas et al., 2004, 2005a, b, 2008; Martínez et al., 2004; Martínez and Novas, 2006).

The Chubut Group has extensive outcrops of Cretaceous age located in central Patagonia, Chubut Province (Page et al., 1999) and its vertebrate content was originally limited to the sauropod *Chubutisaurus insignis* (Del Corro, 1975), but recent findings have greatly increased the known diversity of this unit, including

theropods (*Tyrannotitan chubutensis*, Novas et al., 2005b; Rauhut et al., 2003), sauropods (Rauhut et al., 2003), turtles (*Chubutemys copelloi*, Gaffney et al., 2007), and eilenodontine sphenodontians (Apesteguía and Carballido, 2008). Fossil crocodyliforms, however, were so far unknown in the Chubut Group as the only known remains from Patagonia came from the Neuquén Basin (Pol and Gasparini, 2007), with the exception of fragmentary material from central Patagonia briefly reported by Lamanna et al. (2003).

In this paper we present remains of a new crocodyliform taxon found in the Cerro Barcino Formation (Chubut Group) that shows close affinities with Peirosauridae, a group of Cretaceous crocodyliforms that was abundant and widely distributed in the Cretaceous of Gondwana. The new material represents not only the first record of Crocodyliformes in the Chubut Group but also one of the earliest and southernmost records of Peirosauridae.

2. Systematic paleontology

CROCODYLOMORPHA Hay, 1930 (sensu Walker, 1970)

CROCODYLIFORMES Hay, 1930 (sensu Clark, 1986)

MESOEUCROCODYLIA Whetstone and Whybrow, 1983

PEIROSAURIDAE Gasparini, 1982

* Corresponding author. Laboratorio de Paleontología de Vertebrados, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Pabellón II, Universidad de Buenos Aires, Intendente Güiraldes 2160, Ciudad Universitaria (C1428EGA), Buenos Aires, Argentina.

E-mail address: juanmartinleardi@gmail.com (J.M. Leardi).

Barcosuchus gradilis, nov. gen. et sp.

Holotype: The specimen of *Barcosuchus* (MPEF-PV 3095) consists of skull, mandible, and postcranial remains found closely associated but not in articulation (with the exception of the four anterior cervical vertebrae and the mandible that were found articulated).

Etymology: *Barcino*, from the Formation where the specimen was found; *suchus*, from the Greek *Souchos* that refers to the Egyptian crocodile god; and *gradilis*, from the Latin that means to have steps, in reference to the particular anterior cervical hypapophyseal morphology (see Axial skeleton).

Horizon and locality: The holotype was found on the east face of Sierra de la Cicutá, near El Escorial village (34°05'46"S 68°33'28"W), Chubut Province, Argentina. The fossiliferous horizon is assigned to the lower part of the Cerro Castaño Member from the Cerro Barcino Formation (Chubut Group; Codignotto et al., 1978). The age of this unit is poorly constrained, although it has been generally regarded as Aptian-Albian (Musacchio, 1972; Musacchio and Chebli, 1975; Geuna et al., 2000; Novas et al., 2005b).

Diagnosis: *Barcosuchus* represents a new crocodyliform taxon diagnosed by the following unique combination of characters (autapomorphic characters are marked with an asterisk): spool shaped vertebrae; hypapophyses of the two first postaxial cervical vertebrae transversely elongated and tabular shaped (forming a distinct step in lateral view)*; small knob-shaped hypapophyses on anterior dorsal vertebrae; deep ellipsoidal depressions with vascular foramen above parapophysis in anterior cervical centra*; well developed epipophyses*; quadratojugal does not participate on the cranio-mandibular joint, but reaches the quadrate condyles; longitudinal crest on the posterodorsal surface of distal body of the quadrate; frontal takes part of the supratemporal fenestrae; presence of ziphodont, pseudoziphodont, and smooth carinated teeth; medially displaced deltoid crest on the humerus.

3. Description

The cranial and postcranial remains were described following the osteological nomenclature proposed by Mook (1921), Romer (1956), and Hoffstetter and Gasc (1973). For the appendicular muscles we followed Romer (1923) and Meers (2003). The ligament insertions on the axial skeleton were identified following the nomenclature applied by Frey (1988). Finally, the terminology applied for the structural and functional description of the denticles of the teeth was the one established by Currie et al. (1990), Abler (1992), and Buscalioni et al. (1997).

3.1. Skull

The frontal is unpaired as in all mesoeucrocodylians. Its dorsal surface is flat and heavily ornamented with subcircular to irregular pits. The orbital margins are not elevated in contrast to the condition of derived neosuchians. The posterior edge of the frontal shows a narrow notch interpreted here as the anterior margin of the supratemporal fenestra (Fig. 1A). The frontal participates from the margin of this fenestra as in *Trematochampsia taqueti* (Buffetaut, 1976), *Lomasuchus palpebrosus* (Gasparini et al., 1991), *Araripesuchus tsangatsangana* (Turner, 2006) and *Araripesuchus buitreaensis* (Pol and Apesteguía, 2005); whereas in *Hamadasuchus rebouli* (Larsson and Sues, 2007), *Araripesuchus patagonicus* (Ortega et al., 2000) and *Araripesuchus gomesii* (Pol and Apesteguía, 2005) the frontal takes part of the supratemporal fossa but fails to reach the fenestra. The sutural contacts with the parietal and nasal have not been preserved, although part of the right postorbital is present attached to the ventral surface of the frontal. Anteriorly, this surface

bears two parallel crests identified here as the *crista cranii* (Iordansky, 1973).

The distal body of the quadrate is lateromedially broad and anteroposteriorly flattened, contrasting with the robust quadrate of most notosuchians (including *Araripesuchus*). Its lateral surface has an extensive facet for the quadratojugal that reaches the level of the quadrate condyles. The dorsal surface of the quadrate bears a sharp crest that runs along the major axis of the bone dividing this surface in two planes, a lateral and medial one (Fig. 1B). The dorsal crest widens towards the condyles and serves for the insertion of the mandibular adductor muscles (Colbert, 1946). A similar crest on the dorsal surface of the quadrate is observed in peirosaurids, like *Hamadasuchus rebouli* (Larsson and Sues, 2007) and *Lomasuchus* (MCF-PVPH-160), *Trematochampsia taqueti* (Buffetaut, 1976), sebecids (e.g. *Sebecus icaeorhinus* –Colbert, 1946–), *Pristichampsus vorax* (Langston, 1975) and *Notosuchus terrestris* (Gasparini, 1971). The articular condyles of the quadrate are horizontally aligned and subequal to each other, being the medial one slightly larger. This resembles the condition of *Trematochampsia taqueti* (Buffetaut, 1976), *Lomasuchus* (MCF-PVPH-160), *Hamadasuchus rebouli* (Larsson and Sues, 2007), *Araripesuchus tsangatsangana* (Turner, 2006) and neosuchians but contrasts with that of notosuchians, in which the condyles differ in size and are aligned diagonally. The ventral surface of the quadrate bears a long crest for the insertion of the mandibular adductor muscles, which runs parallel to the suture with the quadratojugal and corresponds to the location of crest A (Iordansky, 1973). Near its distal end, a distinct bulge extends medially, resembling the crest D (Fig. 1C) present in some crocodylians (Iordansky, 1973). *Trematochampsia taqueti* (Buffetaut, 1976) and *Hamadasuchus rebouli* (Larsson and Sues, 2007) have the crests A and B, while *Lomasuchus* bears the crest A and one that is difficult to identify (MCF-PVPH-160). *Araripesuchus patagonicus* has no crests on the ventral surface of the quadrate (Ortega et al., 2000). Only the posteroventral end of the quadratojugal has been preserved, which bears a strong ornamentation composed by subcircular pits. Its posterolateral edge extends as a wedge-like smooth process that overlaps the lateral surface of the quadrate lateral condyles, as in notosuchians. This wedge-like process does not form a condyle, precluding the participation of the quadratojugal in the cranio-mandibular joint. The jugal is only represented by fragments of the infratemporal bar, which is ovoid in cross section and ornamented by irregular pits on its lateral surface.

The basisphenoid is exposed ventrally (Fig. 1D) as in all non-eusuchian mesoeucrocodylians. This surface is triangular in outline, being bordered by two crests that run parallel to the suture with the quadrate process of the pterygoids. The ventral surface of the basisphenoid also has a single sagittal crest that expands at the median eustachian foramen, which is preserved only partially in cross section. On the dorsal surface part of the *sella turica* has been preserved, and lateral to it the two *foramina caroticum arteriosum* (with posterior grooves interpreted as the passage of the internal carotids). The pterygoids are represented by very fragmentary remains, only preserving medium and distal part of the pterygoid flanges. These fragments are laminar and do not show signs of pneumaticity as seen in *Araripesuchus gomesii* and *Araripesuchus patagonicus* (Pol and Apesteguía, 2005).

3.2. Mandible

The preserved mandibular remains include isolated articulars, the third part of the left mandibular ramus and the almost complete right mandibular ramus (Fig. 2). The symphyseal region tapers mediolaterally ending in an acute apex. The mandibular symphysis has a moderate anteroposterior development, reaching

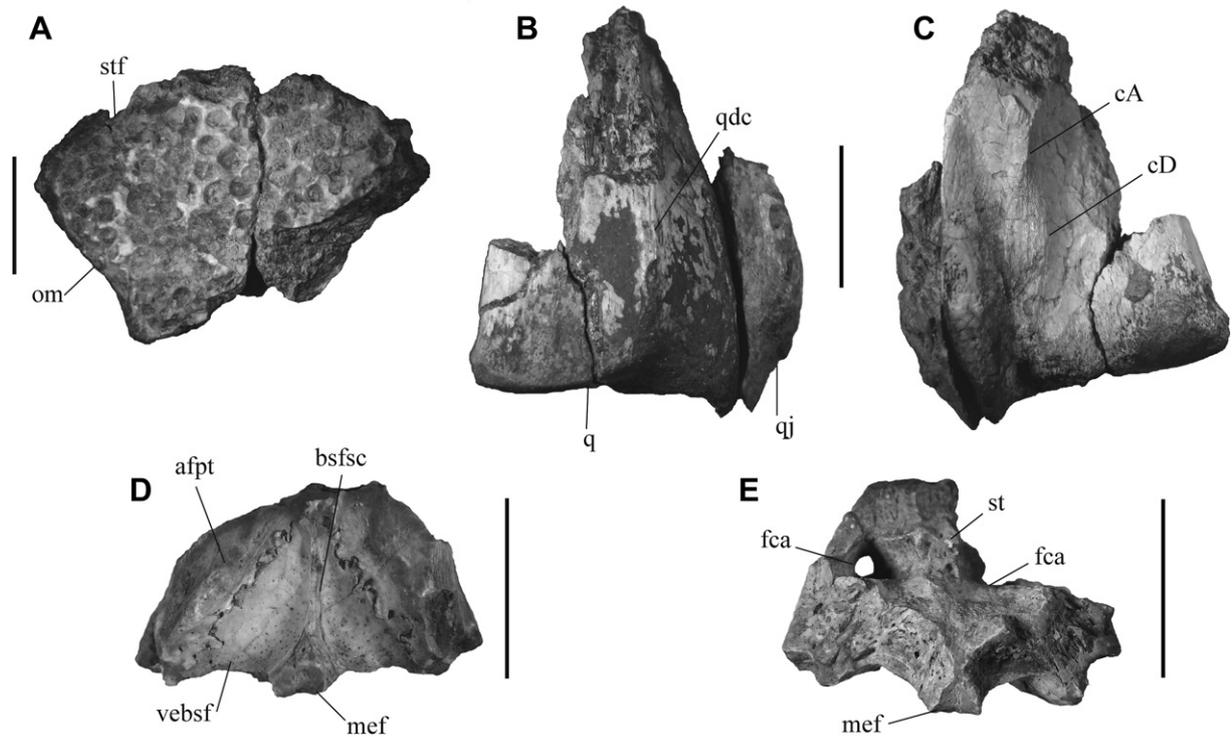


Fig. 1. Skull remains of MPEF-PV 3095. Frontal in dorsal view (A), quadrate and quadratojugal in dorsal (B) and ventral (C) views, basisphenoid in ventral (D) and posterior (E) view. Scale bars equals 1 cm. Abbreviations: bsfsc, sagittal crest of the basisphenoid; cA, crest A; cD, crest D; fca, foramen caroticum arteriosum; q, quadrate; qdc, dorsal crest of the quadrate; qj, quadratojugal; st, sella turica; stf, supratemporal fenestra; vebsf, ventral exposure of the basisphenoid.

up the third or fourth mandibular tooth, as in *Araripesuchus*. Other mesoeucrocodylians have either a shorter symphysis (e.g., *Mahajangasuchus insignis* –Buckley and Brochu, 1999–) or longer symphysis (e.g. *Hamadasuchus rebouli* –Larsson and Sues, 2007–). The dorsal surface is severely damaged, precluding the recognition of sutures. The ventral surface of the mandibular symphysis shows a small participation of the splenial, as in most basal mesoeucrocodylians. The lateral surface of the dentary is ornamentated

with few elongated grooves oriented anteroposteriorly. These grooves are also present along the ventral edge of the dentary, unlike modern crocodylians that progressively show subcircular pits toward the mandibular ventral surface. The dentary increases in height posterior to the mandibular symphysis, but its dorsal surface does not show the abrupt step present in *Araripesuchus gomesii*, *Sebecus icaeorhinus*, and *Comahuesuchus brachybuccalis* (Pol and Apesteguía, 2005).

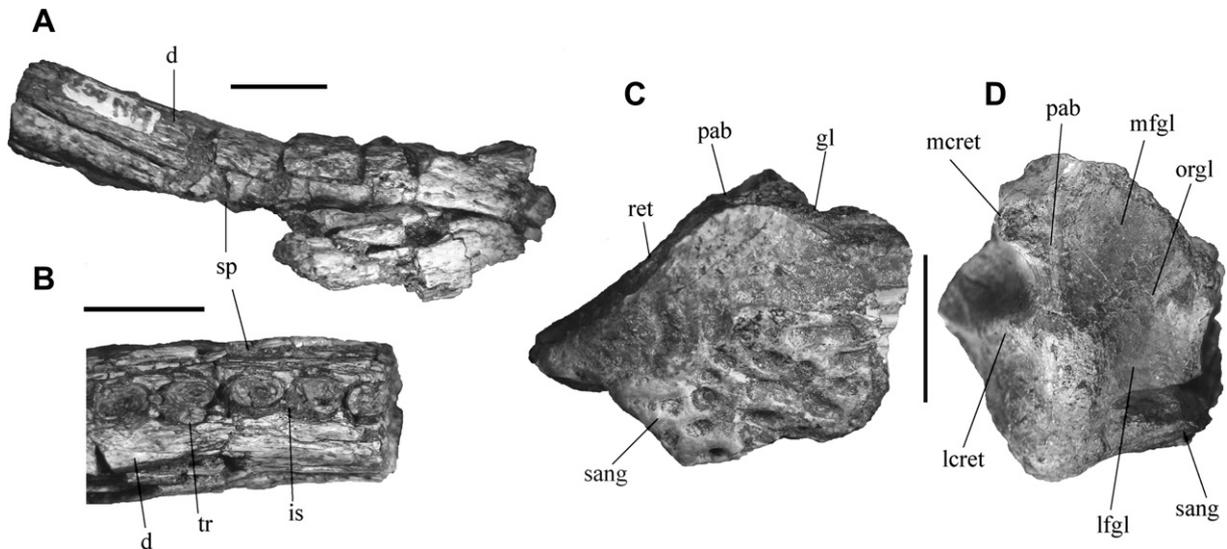


Fig. 2. Mandibular remains of MPEF-PV 3095. Mandibular symphysis in ventral view (A), detail of posterior mandibular alveoli (B), right articular and surangular in lateral (C) and dorsal (D) view. Scale bars equals 1 cm. Abbreviations: d, dentary; gl, glenoid fosa; is, interdenticular septum; lcret, lateral crest of the retroarticular process; lfgl, lateral fosa of the glenoid fosa; mcret, medial crest of the retroarticular process; mfgl, medial fosa of the glenoid fosa; orgl, oblique ridge of the glenoid fosa; pab, posterior glenoid ridge; ret, retroarticular process; sang, surangular;; sp, splenial; tr, tooth root.

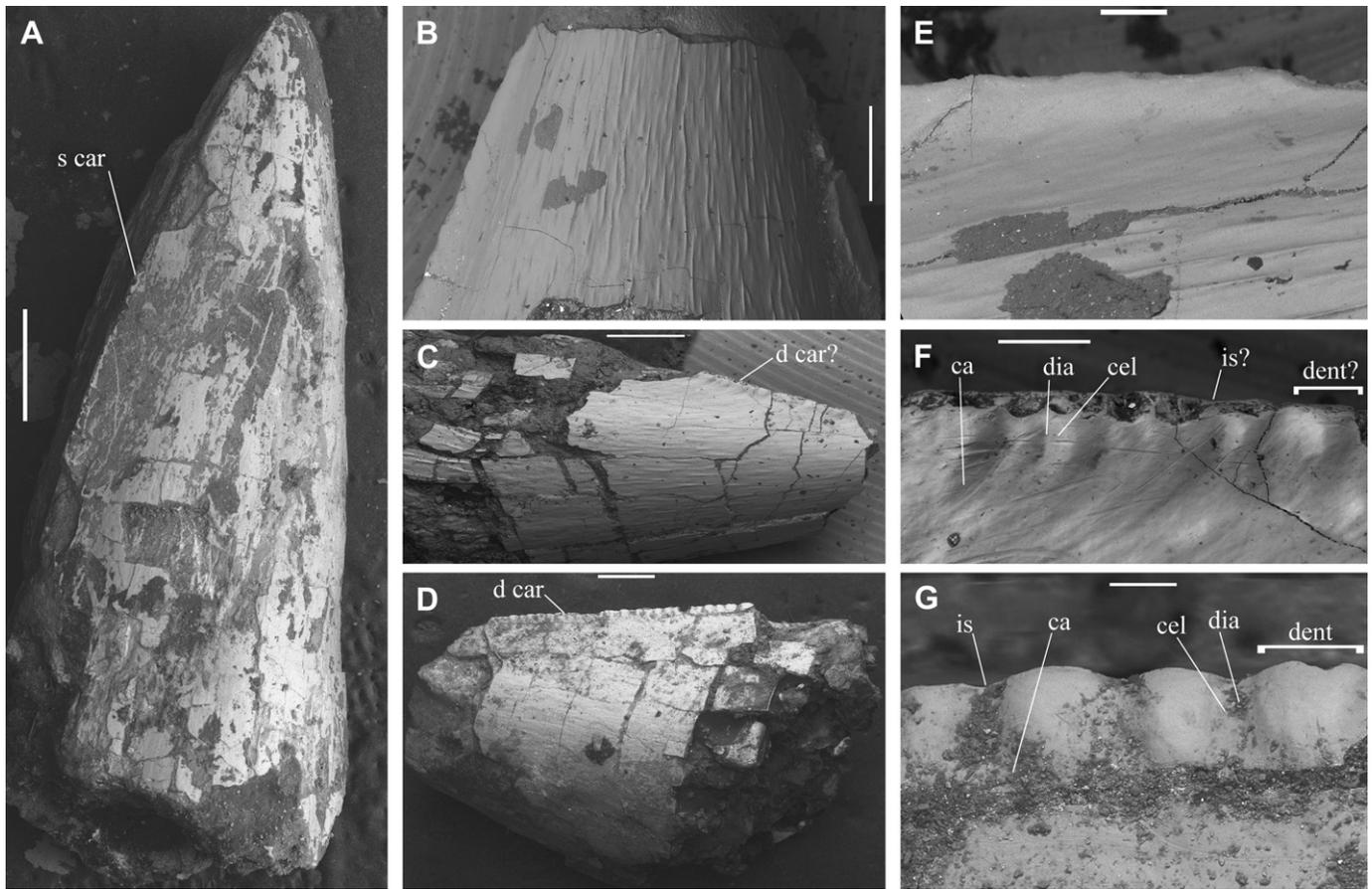


Fig. 3. SEM images of A) smooth keeled tooth MPEF-PV 3095/19, B) replacement tooth MPEF-PV 3095/61, C) pseudozipodont tooth MPEF-PV 3095/17, D) zipodont tooth MPEF-PV 3095/18, E) close up of the keel of MPEF-PV 3095/61, F) close up of denticles of MPEF-PV 3095/17 and G) close up of denticles of MPEF-PV 3095/18. Scale bars equals 500 μm (A, B, C and D), 100 μm (E and F) and 50 μm (G). Abbreviations: ca, cauda; cel, cella; d car, denticulated tooth carina; dent, denticle; dia, diaphysis; ids, interdenticular slits; s car, smooth tooth carina.

The ventral surface of the splenial forms a V-shaped process along the symphysis (Fig. 2A) as in most mesoeucrocodylians, but contrasting with the U-shaped process present in *Araripesuchus buitreaensis*, *Notosuchus terrestris* and *Comahuesuchus brachybuccalis* (Pol and Apesteguía, 2005). Posterior to the mandibular symphysis the splenial is dorsoventrally high and extends onto the ventral surface of the mandibular ramus, where it forms half of the width of this surface. The medial surface is slightly convex as in most crocodylians, except in *Araripesuchus gomesii*. The splenial forms the medial edge of the alveoli.

Twelve alveoli are present in the preserved portion of the right mandibular ramus, but due the complete tooth count was probably higher (possibly reaching up to 18 mandibular teeth). All alveoli are limited mesially and distally by complete septa (Fig. 2B), contrasting with the continuous alveolar groove in which the posterior mandibular teeth are set in all species of *Araripesuchus* (except *A. tsangatsangana*) and some basal mesoeucrocodylians (e.g. *Fruita* form, *Notosuchus*, *Simosuchus*, *Uruguaysuchus*). All alveoli are similar sized, and there are no signs of a hypertrophied tooth in the posterior region of the mandibular ramus, as in *Araripesuchus tsangatsangana* (Turner, 2006).

Both articulars were preserved isolated. The right one also has part of the surangular attached to its lateral surface. The prearticular process is preserved on its posterior part, and presents a triangular fossa on the lateral half of its dorsal surface. The lateral surface of the prearticular process is flat and the medial one is concave. The glenoid fossa is wider than long (Fig. 2D), as in

peirosaurids and neosuchians, and is limited anteriorly and posteriorly by two sinusoidal crests, contrasting to the absence of these crests in notosuchians, *Mahajangasuchus insignis* (UA 8654) and *Araripesuchus tsangatsangana* (Turner, 2006) or with the presence of only the posterior glenoid wall in *Lomasuchus palpebrosus* (MCF-PVPF-160) and most eusuchians. The fossa is divided by an oblique crest in two halves, a medial and a lateral one. This division of the glenoid fossa is seen also in other taxa, including *Araripesuchus tsangatsangana* (Turner, 2006) and *Lomasuchus* (MCF-PVPH-160). The retroarticular process is almost completely preserved. This process is short and broad and lacks a dorsal upturn present in Crocodylia and *Lomasuchus* (MCF-PVPH-160). The surface for the insertion of the *M. depressor mandibulae* is oriented posterodorsally and is divided by a longitudinal sigmoid crest, which separates the medial and lateral halves. The medial region also bears an accessory crest that is interrupted by a broken section of the articular bone (Fig. 2D).

The surangular contacts the articular laterally (Fig. 2C and D), covering the major part of the lateral surface, contrasting with the condition seen in *Araripesuchus gomesii* (Ortega et al., 2000) where it covers the dorsolateral region of the retroarticular process. The surangular forms the lateral wall of the glenoid fossa, in contrast with many basal mesoeucrocodylians in which it forms part of the craniomandibular articulation (*Trematochampsia taqueti* -Buffetaut, 1976-, *Lomasuchus* -MCF-PVPH-160-, *Araripesuchus gomesii*, and *Sebecus icaeorhinus* -Colbert, 1946-). The lateral surface is ornamented by subcircular pits, and this ornamentation disappears

prior to the contact with the glenoid fossa. Extant crocodylians also have a smooth surface that serves for the insertion of the *M. pterigoideus posterior* (Adams, 1919; Colbert, 1946), although it is more dorsoventrally expanded in this new specimen.

3.3. Dentition

The mandibular teeth preserved on the posterior region of the right mandibular ramus have only preserved the basal part of the crowns, except for a small replacement tooth located on the sixth preserved alveolus. This tooth was extracted and studied under SEM along with three other isolated tooth crowns that were found on the matrix surrounding the mandibular remains. The isolated teeth are only moderately compressed labiolingually with the base of their crowns subcircular in cross section, as in the South American *Araripesuchus* and many of the preserved teeth of *Lomasuchus*. These elements have distal keels, and MPEF-PV 3095/19 bears keels also on its mesial edge. The keeled margin of different teeth varies from smooth to fully denticulated (see below).

The smooth keeled tooth MPEF-PV 3095/19 (Fig. 3A) is the only element that preserves the general shape of the teeth. This conical tooth is slightly curved lingually and has slightly marked keels on its mesial and distal surfaces. Unlike the rest of the teeth, the replacement tooth MPEF-PV 3095/61 (Fig. 3B) is strongly compressed labiolingually and has a triangular shape in buccal or lingual view. It bears mesial and distal keels with an undulated margin, with very subtle convexities and shallow concavities (Fig. 3E). The outer buccal and lingual surface of the crown bears apicobasally oriented ridges. These ridges are thin, sinuous, and discontinuous, and seem to be formed only by a folding of the enamel coat.

The MPEF-PV 3095/17 tooth (Fig. 3C) can be described as pseudoziphodont (sensu Prasad and de Broin, 2002) or incipiently ziphodont, since the enamel bears oblique ridges respect to the apicobasal axis of the keel and the denticles (and their interdenticular slits) are barely individualized or absent. Between the

denticles, the *cellae*, *diaphysis*, and *cauda* (sensu Buscalioni et al., 1997) are well developed. The *cellae* and *diaphysis* disappear before reaching the distal margin of the keel and the *cauda* form an angle of 30° with the *cellae*. The mesial and buccal surface of the crown also bears thin and discontinuous apicobasal ridges, as in the replacement tooth described above.

MPEF-PV 3095/18 is a fully ziphodont tooth (Fig. 3D) and has a denticle density of 11 or 12 denticles per millimetre, the denticle height varies between 100 and 125 µm, and their width varies between 85 and 90 µm. The denticles are chisel-like and show very shallow and broad interdenticular slits, *diaphysis*, *cellae* and *cauda* (Fig. 3G). The interdenticular slits represent less than a seventh of the denticle height, while the *cellae* extend up to the half of the height of the denticles and the *diaphysis* reach the distal half or third of the *cellae*. The *cauda* (or blood groove) are mildly developed and are oblique with respect to the major axis of the denticles, at an angle of 45° oriented posteriorly. The buccal and lingual surface of the crown lacks the thin apicobasal ridges present in the teeth described above.

3.4. Axial skeleton

A total of 12 vertebrae were preserved, providing a good sample of the elements of the cervicodorsal region. These elements were found disarticulated, with the exception of the four anteriormost cervical vertebrae that were in articulation and associated with the mandible. The vertebrae are mainly represented by their centra and the base of their neural arches (except for the anterior dorsals that have more complete neural arches). Other disarticulated fragments of the neural arches have been found in close association to this specimen.

The vertebrae of this new specimen are spool-shaped, as in neosuchians and contrasting with the more cylindrical vertebrae of the notosuchians. All vertebral centra are longer than high and their articular surfaces are amphicoelous, as in most no-eusuchian mesoeucrocodylians.

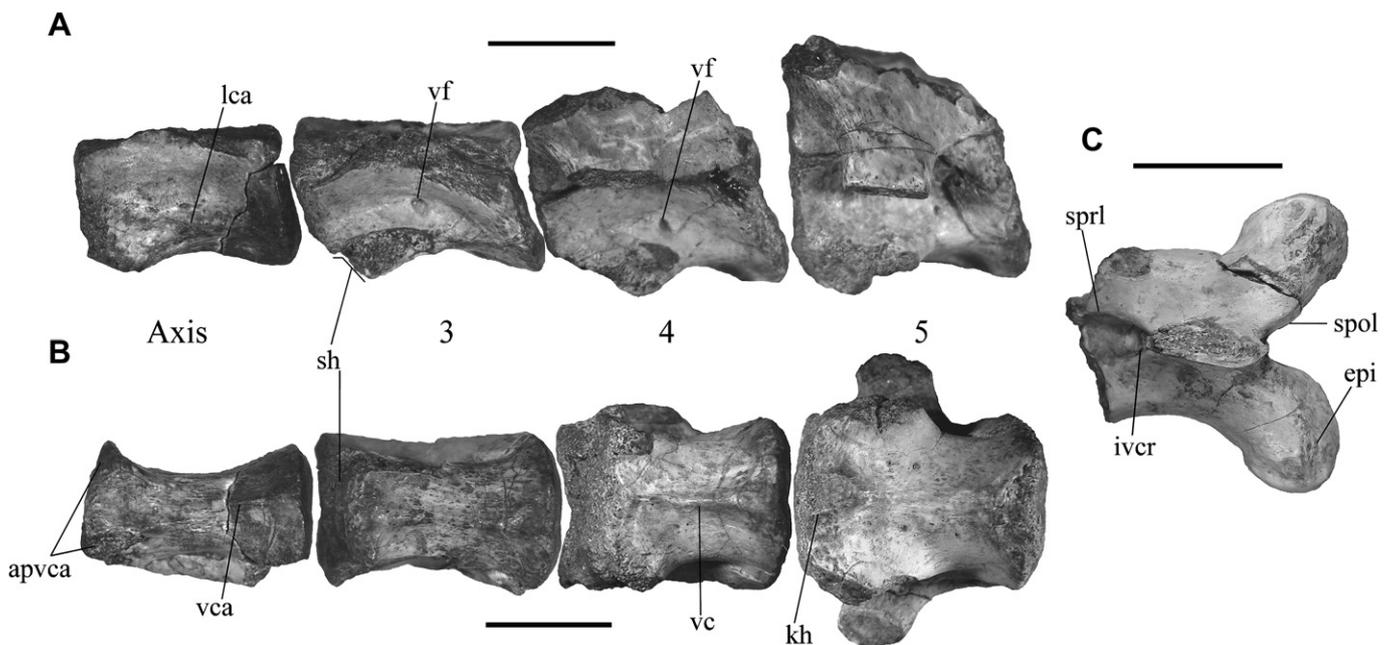


Fig. 4. Cervical vertebrae of MPEF-PV 3095. A) axis, 3, 4, and 5 in lateral and B) ventral views. C) cervical neural arch in dorsal view. Scale bars equals 1 cm. Abbreviations: apvca, anterior process of the ventral crest of the axis; epi, epipophyses; ivcr, incisura vertebralis cranealis; kh, knob-like hypapophyses; lca, lateral crest of the axis; sh, step-like hypapophyses; spol, suprapostzygapophyseal lamina; sprl, supraprezigapophyseal lamina; vca, ventral crest of the axis; vf, vascular foramen.

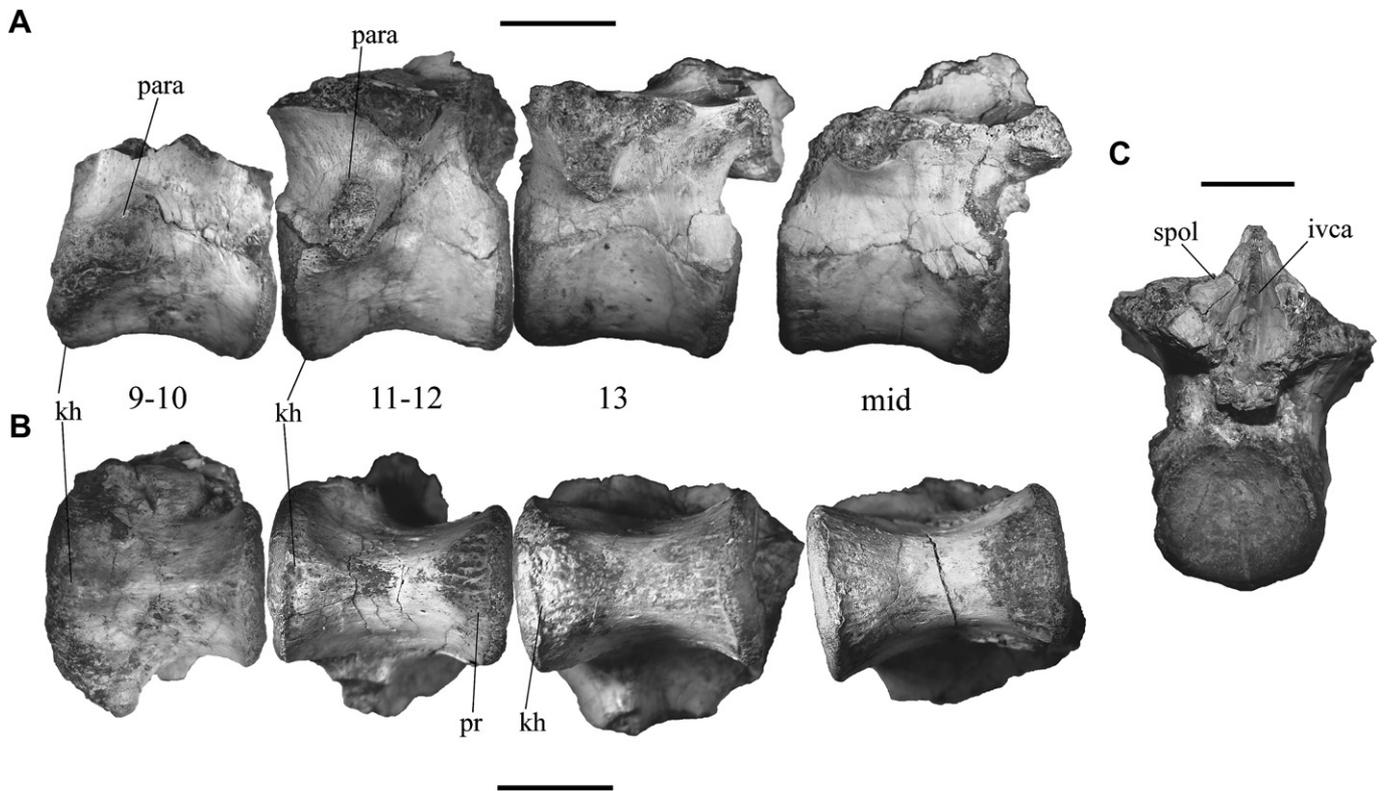


Fig. 5. Dorsal vertebrae of MPEF-PV 3095. A) anterior (9–10, 11–12 and 13) and mid dorsal vertebrae in lateral and B) ventral views. C) mid dorsal vertebra in posterior view. Scale bars equals 1 cm. Abbreviations: ivca, incussura vertebralis caudalis; para, parapophyses; pr, posterior rugosities; other abbreviations in Fig. 4.

3.4.1. Axis

The axis has a concave posterior articular facet and a flat rugose anterior articular facet that represents the suture with the odontoid process, which has not been preserved. The ventral surface bears a sagittal crest that bifurcates toward the anterior half (Fig. 4B). The bifurcated crest projects anteroventrally but fails to reach the anterior margin of the centrum. A similar but shallower crest is present on the ventral half of the lateral surface of the centrum (Fig. 4A). The ventral branch of the each lateral crest merges with the bifurcated ventral crest, whereas the dorsal ramus attenuates before reaching the anterior edge of the lateral surface. The neural canal is narrow, particularly on the anterior edge, and has two elongated foramina on the dorsal surface of the axis.

3.4.2. Postaxial cervical vertebrae

Almost the complete postaxial cervical series has been preserved, having represented the 3, 4, 5, 6/7 and 8 vertebrae of this specimen. As mentioned before the cervical centra are longer than high, contrasting with the cervical centra of *Mahajangasuchus insignis* (UA 8654) which are higher than long.

All postaxial cervical vertebrae show hypapophyses as in *Trematochampsia taqueti* (Buffetaut, 1976) and in *Mahajangasuchus insignis* (Buckley and Brochu, 1999), contrasting to the absence of these processes in *Araripesuchus tsangatsangana* (Turner, 2006). The hypapophyses of the third and fourth cervical vertebrae are tabular and transversally elongated, forming a distinct step, while in the posterior cervicals the hypapophyses are reduced and knob-shaped (Fig. 4B). Small knob-shaped hypapophyses on the cervicals are also present in *Mahajangasuchus insignis* (UA 8645). A sagittal undivided crest is also present on the ventral surface of the centrum of all cervical centra, which is posteriorly expanded and

rugose and probably served for the insertion of the *L. discocapitulare* (Frey, 1988). These ventral crests are also present in *Araripesuchus tsangatsangana* and in the posterior cervical vertebrae of *Mahajangasuchus insignis* (UA 8654).

The lateral surface of the anterior and mid cervical vertebrae (from 3 to 4) show marked ellipsoidal depressions between the parapophyses and the base of the neural arches, where large vascular foramina are present (Fig. 4). These foramina decrease in size and move posteriorly from the anterior to mid cervical vertebrae. The parapophyses are located anteroventrally on the centra and gradually migrate posterodorsally, as in extant crocodylians (Mook, 1921), reaching the neurocentral suture along their dorsal edge on the last (8) cervical. The parapophyses show a posterior crest that fades posteriorly not reaching the posterior articular surface, although this crest is absent in the last cervical. The diapophyses are preserved on the fourth, fifth and sixth/seventh cervicals and project ventrally, having their anteroposterior axis oriented obliquely.

The neural canal is wide, with its anterior end broader than its posterior end. In all cervical vertebrae the neurocentral suture is clearly seen, suggesting this specimen is not a fully mature individual (Brochu, 1996).

Partial remains from the neural arches were preserved isolated. The best preserved element is the dorsal half of a neural arch lacking the prezygapophyses that probably belong to an anterior cervical vertebra (Fig. 4C). The neural spine is mediolaterally compressed and is located on the posterior half of the neural arch. The posterior surface of the spine bears an interspinous medial lamina (sensu Frey, 1988). The *incissura vertebralis cranialis* is drop-shaped and is limited laterally by well developed supraprezygapophyseal laminae, whereas the *incissura vertebralis caudalis* is rhomboidal. Suprapotzygapophyseal laminae are present but poorly developed and

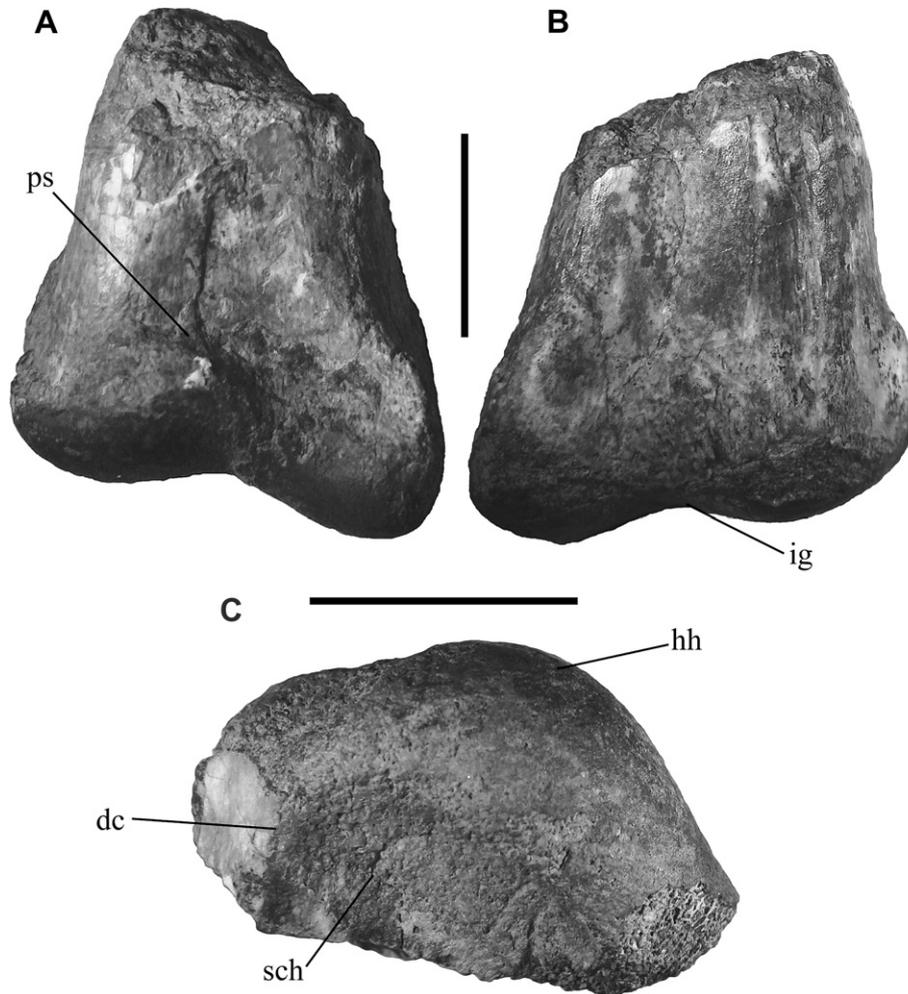


Fig. 6. Appendicular remains of MPEF-PV 3095. A) distal femur in posterior and B) anterior views. C) proximal humerus in anterior view. Scale bars equals 1 cm. Abbreviations: sch, shallow concavity on the posterior humeral surface; dc, deltoid crest; hh, humeral head; ig, intercondylar groove; ps, popliteal space.

extend briefly from the posterior edge of the neural spine to the dorsal surface of the postzygapophyses, finishing well before their posterior border. The posterior region of the dorsal surface of the postzygapophyses bear well developed epipophyses, a character also present in isolated postzygapophyses of this specimen.

An isolated left cervical rib has been preserved. The posterior process is elongated and shows the typical U-shaped depression seen in crocodyliforms for the articulation with the anterior process of the preceding vertebra (Mook, 1921; Colbert and Mook, 1951; Hoffstetter and Gasc, 1973). The posterior process does not have the postdorsally projecting spine described for *Araripesuchus tsangatsangana* and *Mahajangasuchus insignis* (Turner, 2006).

3.4.3. Dorsal vertebrae

The vertebrae preserved are three anterior (9/10; 11/12 and 13), two mid and three posterior dorsals. Only the two posteriormost anterior dorsal and the anteriormost mid dorsal have well preserved neural arches; while the other dorsals only have preserved the pedicels of the neural arches.

As mentioned before, all centra are longer than high, as in most crocodyliforms but differing from the anterior dorsals of *Mahajangasuchus insignis* (UA 8654) and *Lomasuchus* (MCF-PVPH-160) in which the height of their centra is larger than their length. The ventral surface of the anterior and mid dorsals bears a rugose area for the insertion of the *L. discocapitulare* (Frey, 1988). The anterior

dorsals have hypapophyses, being only slightly developed in the third/fourth dorsal (Fig. 5B). This condition resembles that of Crocodylia and some other basal mesoeucrocodylians such as *Mahajangasuchus insignis* (UA 8654) or *Araripesuchus gomesii* (AMNH 24450), which bear hypapophyses up to the third dorsal. The hypapophyses are small and knob-shaped as in the posterior cervicals, resembling the condition present in *Mahajangasuchus insignis* (UA 8654) and *Lomasuchus* (MCF-PVPH-160), but contrasting with the pointed or laminar hypapophyses of other crocodyliforms (including *A. gomesii*). The lateral surface of the dorsal centra lack the large vascular foramina present on the lateral surface of the cervicals (Fig. 4A). Except for the anteriormost dorsal, the parapophyses are completely located on the neural arch, forming synapophyses on the third/fourth dorsal (Fig. 5A). This fusion occurs in the sixth dorsal in *Araripesuchus tsangatsangana* (Turner, 2006) and in the posterior dorsals in *Mahajangasuchus insignis* (Buckley and Brochu, 1999).

The neurocentral suture is open in the anterior and mid dorsals, while is completely closed in the posterior ones. The neural canal of the anterior dorsals is wider than higher. The remains of diapophyses, prezygapophyses and postzygapophyses are partial, mainly represented by their bases. The neural spines on the anterior dorsals are mediolaterally narrow and anteroposteriorly long, extending along almost the complete dorsal surface of the neural arch. Anteriorly to the neural spine a conspicuous drop shaped

incisura vertebralis cranealis is present, but is not bordered by supraprezygapophyseal laminae as in the cervicals. The posterior surface of the neural spine bears a rhomboidal and deep *incisura vertebralis caudalis*. Suprapostzygapophyseal laminae seem to be more developed than in the cervical vertebrae (Fig. 5C), but they are also restricted to the anterior region of the dorsal surface of the postzygapophyses. The presence of suprapostzygapophyseal laminae is shared with several basal mesoeucrocodylians, such as *Notosuchus terrestris* (Pol, 2005), *Lomasuchus* (MCF-PVPH-160), *Malawisuchus* (Gomani, 1997), *Uruguaysuchus* (Rusconi, 1933), and *Araripesuchus* (Pol, 2005; Turner, 2006).

3.5. Apendicular skeleton

The forelimb remains are fragmentary and only part of the right humeral head was preserved, as well as small fragments that may represent the ulna, radius, ulnare, and proximal regions of the scapula and coracoid. Ventrally to the humeral head, the posterior surface of the humerus bears a shallow concavity as in *Lomasuchus* (MCF-PVPH 160), but not as deep as in *Notosuchus terrestris* (Pol, 2005), *Chimaerasuchus paradoxus* (Wu and Sues, 1996), *Uruguaysuchus aznarezi* (Rusconi, 1933), and *Araripesuchus gomesii* (AMNH 24450). The base of the deltoid crest is displaced medially with respect to the lateral surface of the humerus (Fig. 6C), as in *Araripesuchus tsangatsangana* (Turner, 2006), *Lomasuchus* (MCF-PVPH-160), *Mahajangasuchus insignis* (UA 8654) and *Notosuchus terrestris* (Pol, 2005).

The hindlimb is presented only by three fragments of the right femur and a small fragment of the fibula. The proximal and mid sections of the femur are badly damaged by erosion but the distal end (Fig. 6A and B) of the femur is better preserved. This region has two condyles with similar anteroposterior and mediolateral development, being the medial one only slightly larger, in contrast to the condition of *Araripesuchus tsangatsangana* (Turner, 2006)

and *Mahajangasuchus insignis* (UA 8654) in which the lateral condyle is more developed than the medial one. The intercondylar groove continues on the anterior surface of the femur as a shallow groove that projects up to the mid region of the shaft. The posterior surface of the femur bears a triangular popliteal space located above the intercondylar groove. The lateral fibular articular surface is crescent-shaped, and is separated from the posterior surface by a strongly developed crest. An oblique but more faintly developed crest is also observed on the medial surface.

3.6. Osteoderms

The osteoderms are abundant but fragmentary. None of the elements preserved have remains of the anterolateral processes present in the basal crocodyliforms and their dorsal surface is strongly ornamented with subcircular pits. Most osteoderms are flat although one of them bears a large, thick dorsal keel located close to its lateral edge (Fig. 7B and C). The flat osteoderms are slightly bowed, having a slightly concave ventral surface. The anterior edge of these osteoderms have an extensive and slightly bent articular surface for the preceding osteoderms (Fig. 7A). Based on the fragmentary nature of these remains, it is not possible to determine at the moment if the keeled osteoderm belong to the parasagittal row of osteoderms (being part of the nuchal shield) or if this specimen actually had more than two rows of dorsal osteoderms.

4. Phylogenetic relationships

Given the anatomical similarities of *Barcosuchus* and several groups of basal mesoeucrocodylians, including *Araripesuchus* spp. and peirosaurids, we have tested its phylogenetic affinities through a cladistic analysis including the new specimen in the dataset of Gasparini et al. (2006). In addition to the original 257 characters of

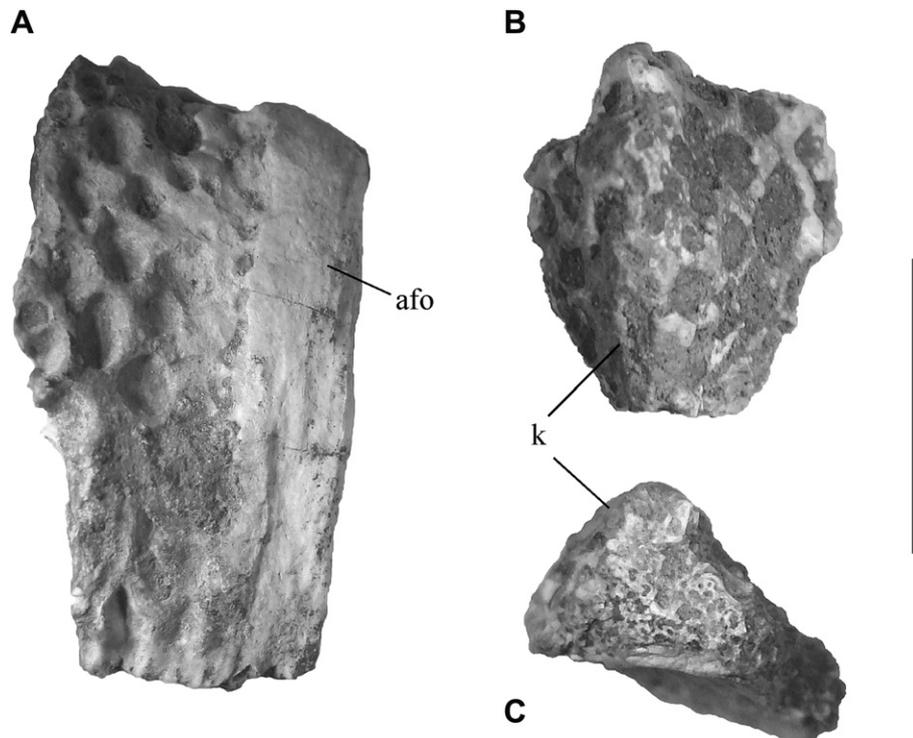


Fig. 7. Osteoderms of MPEF-PV 3095. A) flat osteoderm in dorsal view, B) keeled osteoderm in dorsal and C) anterior view. Scale bars equals 1 cm. Abbreviations: afo, articular facet for the preceding osteoderm; k, keel.

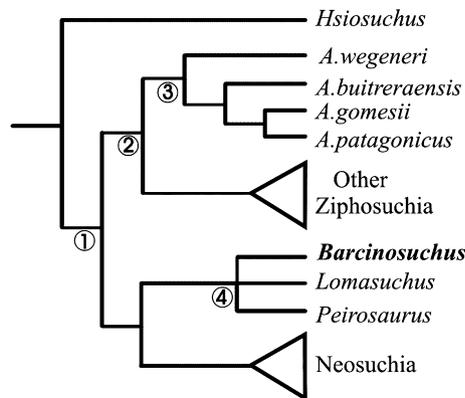


Fig. 8. Phylogenetic position of *Barcinosuchus* within the context of basal mesoeucrocodylians. This tree represents a summarized topology of the single most parsimonious tree. Numbered nodes: 1, Mesoeucrocodylia; 2, Notosuchia; 3, *Araripesuchus*; and 4, Peirosauridae.

this data matrix, we have added two characters from Turner (2006) and a new character (see Appendix 1). An equally weighted parsimony analysis was conducted through heuristic searches in TNT (Goloboff et al., 2008a,b) consisting of 1000 replicates of RAS + TBR. The search yielded a single most parsimonious tree (Fig. 8) of 865 steps (found in 85% of the replicates). This topology depicts *Barcinosuchus* nested within Peirosauridae, forming a polytomy with *Lomasuchus palpebrosus* and *Peirosaurus torminni*.

The position of *Barcinosuchus* within Peirosauridae is supported in this analysis by the presence of a single unambiguous synapomorphy: the presence of hypapophyses up to the third or fourth dorsal vertebrae (char. 91: states 3 or 4; paralleled in *A. gomesii* and eusuchians). Several other characters of *Barcinosuchus* also provide support to this position, as they indicate that the new specimen (as peirosaurids) is more basal than neosuchians (e.g., anterolateral facing edge on postorbital [char 29: state 1], quadrate dorsal surface divided in two planes by a ridge [char 150: state 1]; mandibular symphysis tapering anteriorly in ventral view [char 154: state 0]) but more derived than to notosuchians, including *Araripesuchus* (e.g., spool-shaped vertebrae [char 113: state 1], lateral surface of dentary convex anterior to mandibular fenestra [char 160: state 1], distal body of quadrate well developed ventral to otoccipital contact [char 197: state 0] and anteroposteriorly thin and lateromedially broad [char 192: state 0], dentaries below alveolar margin continuous with rest of lateral surface of the dentaries [char 193: state 0]).

The lack of described postcranial remains of other peirosaurids and the fragmentary nature of the cranial remains of *Barcinosuchus* precludes both the resolution of the peirosaurid polytomy obtained in this analysis and a robust phylogenetic placement of the specimen reported here. For instance, the only exclusive synapomorphy of the Peirosauridae (presence of a wedge-like process of the maxilla on the lateral surface of the premaxilla-maxilla suture; char. 213: state 1) is currently unknown in *Barcinosuchus*. Other characters that are ambiguous synapomorphies of peirosaurids are also unknown in the new specimen (absence of the contact between nasals and lacrimals [char. 11: state 1], presence of a hypertrophied tooth on the dentary at the level of premaxilla-maxilla contact [char. 80: state 1], palpebrals extensively sutured between each other and to the lateral margin of the frontals [char. 214: state 1]).

The lack of robust support for the phylogenetic position of *Barcinosuchus* in this analysis is also reflected in the suboptimal

trees of one step longer in which *Barcinosuchus* is depicted at the base of the clade formed by Neosuchia + Peirosauridae or nested with the South American members of the genus *Araripesuchus* in suboptimal trees with two additional steps. These results are attributed to a combination of lack of cranial information (missing entries) and the presence of conflictive characters in *Barcinosuchus* (such as unsculpted region in dentary below toothrow). Furthermore, the uncertainty on the position of *Barcinosuchus* is also affected by the poorly supported position of Peirosauridae within basal Mesoeucrocodylia, as shown by the conflictive results on its monophyly in recently published analyses (Larsson and Sues, 2007; Turner and Buckley, 2008). In sum, based on the available evidence, *Barcinosuchus* is most parsimoniously interpreted as a member of Peirosauridae, although further material of this taxon (and of other peirosaurids) are needed to provide a more robust assessment of its phylogenetic position, as well as to resolve more clearly the relationships of Peirosauridae within Mesoeucrocodylia.

5. Conclusions

The new specimen reported in this paper represents the first record of a crocodyliform from the Chubut Group and the first Cretaceous member of this group known from Central Patagonia, with the possible exception of the fragmentary remains briefly mentioned by Lamanna et al. (2003). This material is also important as it broadens the known temporal and geographical distribution of Peirosauridae during the Cretaceous of Gondwana, given that it represents the southern-most record of the group in South America and the earliest record of the group in Patagonia (if the age of the Cerro Barcino Formation is indeed Aptian-Albian). Furthermore, the new material represents one of the first records of postcranial material assigned to Peirosauridae, increasing the anatomical knowledge on this group.

Further anatomical and phylogenetic studies on this group of basal mesoeucrocodylians are needed in order to obtain better-supported hypotheses on its internal relationships and its affinities with other clades. Such studies would be important given that, as previously noted (Pol and Gasparini, 2007), peirosaurids are widely distributed in Lower and Upper Cretaceous beds of the southern hemisphere and therefore have the potential of providing critical information to understand the biogeographical relationships of the major land-masses during the break-up of Gondwana.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.cretres.2009.08.002.

Appendix 1

List of modified characters of Gasparini et al. (2006) used in the phylogenetic analysis:

Character 137 (modified from Pol, 1999: char. 151): Compressed crown of maxillary and posterior mandibular teeth: oriented parallel to the longitudinal axis of skull (0), or obliquely disposed (1).

Character 140 (modified from Pol, 1999: char. 154 and Ortega et al., 200: char. 104): Maxillary and posterior mandibular teeth: not compressed laterally (0), or compressed laterally (1).

List of characters added to the data matrix:

Character 258 (new char.): Hypapophyses of the anterior dorsal vertebrae: dorsoventrally deep and projecting ventrally from the vertebral centrum (0), or reduced knob-shaped hypapophyses (1).

Character 259 (Turner, 2006: char. 128): Proximal-most portion of fibular head straight to weakly developed posteriorly (0) or very sharply projecting posteriorly, forming distinct flange (1).

Character 260 (Turner, 2006: char. 129): Posterior process of shaft in the posterior cervical ribs lacks (0) or possesses (1) a posterodorsally projecting spine at the junction with the tubercular process.

Appendix 2

Scorings used in the phylogenetic analyses for:

Lomasuchus

201????1211?00?11000101111??110001022?1010001??12??1?100??1??1??3?21?
???00??0[12]11??????[234]????????1????00??00??00??00??1?110?00?
??00011?0??1?0??????0?????10000?0??10????00?0?00??0?0?01?10?10??
01?10000??11000??0??0??0?0?0?100?0??0000?0??00100?001??

Barcosuchus

2????????????????1001????1?0??11??0????1?????1?0????????????
1?0??1???0????1??[01]400?[12]0?0?0?00????????1?????1[01]????????????
???0?00??1????1???010?00100?????00????????0?????0?0010?00??00??
0?????0?0?????0?00?0?0????????????????????????????1?????1?0

Appendix 3

List of institutional acronyms used in this study

- AMNH, American Museum of Natural History, New York, USA
- MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina
- MCF, Museo Carmen Funes, Plaza Huincul, Argentina
- UA, University of Antananarivo, Antananarivo, Madagascar