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A NEW SPECIES OF *BAURUSUCHUS* (CROCODYLIFORMES, MESOEUCROCODYLIA) FROM THE UPPER CRETACEOUS OF BRAZIL, WITH THE FIRST COMPLETE POSTCRANIAL SKELETON DESCRIBED FOR THE FAMILY BAURUSUCHIDAE

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ABSTRACT

The present work describes a new species of Baurusuchidae from Upper Cretaceous sediments of the Bauru Basin, and provides the first complete postcranial description for the family. Many postcranial features observed in the new species are also present in other notosuchian taxa, and are thus considered plesiomorphic for the genus. These are: long cervical neural spines; robust deltopectoral crest of the humerus; large proximal portion in the radiale that contacts the ulna; ulnare anterior distal projection; supra-acetabular crest well developed laterally; post-acetabular process posterodorsally deflected; presence of an anteromedial crest in the femur; fourth trochanter of femur posteriorly positioned; tibia with a laterally curved shaft; calcaneum tuber posteroventrally oriented; osteoderms ornamented with grooves and imbricated in the tail. On the other hand, we found the following sacral and carpal features to be unique among all mesoeucrocodylians analyzed: transverse processes of sacral vertebrae dorsolaterally deflected; presence of a longitudinal crest in the lateral surface of sacral vertebrae; pisiform carpal with a condyle-like surface. The majority of these cited features corroborates a cursorial locomotion for the new species described in the present study, suggesting that members of the family Baurusuchidae were also cursorial species.

KEYWORDS: Upper Cretaceous; Baurusuchidae; *Baurusuchus*; Morphology; Postcranium.

INTRODUCTION

The family Baurusuchidae was originally erected by Price (1945) to allocate *Baurusuchus pachecoi*, a crocodile known by a partially preserved skull from the Upper Cretaceous Adamantina Formation of Brazil. A second species, *Baurusuchus salgadoensis*, was recently described by Carvalho *et al.* (2005), based on an almost complete skull found near the city of

General Salgado, on the upper northwestern part of the State of São Paulo, also in sediments of the Adamantina Formation.

Stratiosuchus maxhechti (Campos *et al.*, 2001; Pinheiro *et al.*, 2008) and *Pabwehshi pakistanensis* (Wilson *et al.*, 2001) represent two other Upper Cretaceous large terrestrial, and probably cursorial, crocodiles that are commonly referred to the family Baurusuchidae. *Pabwehshi pakistanensis* (Wilson *et al.*, 2001)

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was recently allocated in the Baurusuchidae by Nascimento & Zaher (*in prep.*). Although Larsson & Sues (2007) and Riff (2007) reject a close affinity between *Pabwehshi* and the Baurusuchidae, suggesting instead that its affinities lie with the Peirosauridae, we here follow the phylogenetic hypothesis given by Turner & Calvo (2005), Nascimento (2008), and Nascimento & Zaher (*in prep.*) in which *Pabwehshi* appears deeply nested within the Baurusuchidae. Two additional Upper Cretaceous South American terrestrial crocodiles, *Cynodontosuchus rothi* (Woodward, 1896) and *Wargosuchus australis* (Martinelli & Pais, 2008), were tentatively allocated in the Baurusuchidae by most authors (Price, 1959; Gasparini, 1981; Martinelli & Pais, 2008). However, their very fragmentary nature does not allow a more accurate evaluation of their phylogenetic position within the notosuchian radiation of South American mesoeucrocodylians.

In recent phylogenies, the family Baurusuchidae has been consistently found to be nested within Notosuchia (Ortega *et al.*, 2000; Sereno *et al.*, 2003; Pol, 2003; Pol & Norell, 2004; Pol & Apesteguía, 2005; Gasparini *et al.*, 2005; Zaher *et al.*, 2006; Andrade & Bertini, 2008), a clade originally erected by Gasparini (1971) to accommodate the small-sized terrestrial fossil crocodyliforms from South America. The genera *Cynodontosuchus*, *Stratiotosuchus*, and *Wargosuchus*, commonly included in the family Baurusuchidae, share with *Baurusuchus* the following features: presence of theropodomorph teeth; reduction of tooth number; maxilla with a hypertrophied tooth; dentary with a hypertrophied tooth which fits in the premaxilla-maxilla notch; maxillae verticalized; enlarged third premaxillary tooth overhanging the dentary; high mandibular symphysis (Gasparini, 1981, Campos *et al.*, 2001).

Although the cranial anatomy of the family Baurusuchidae is well known (*e.g.*, nearly complete skulls were described for *Baurusuchus pachecoi*, *B. salgadoensis*, and *Stratiotosuchus maxhechti*), the postcranial anatomy is virtually unknown. Even postcranial descriptions of notosuchian taxa are scarce, the most relevant one being that of *Notosuchus terrestris* (Pol, 1999, 2005). Postcranial elements of *Uruguaysuchus aznarezzi* (Rusconi, 1933), *Chimaerasuchus paradoxus* (Wu & Sues, 1996), *Malawisuchus mwakayasyunguti* (Gomani, 1997), *Mahajangasuchus insignis* (Buckley & Brochu, 1999), *Adamantinasuchus navae* (Nobre & Carvalho, 2006), and *Stratiotosuchus maxhechti* (Riff, 2007) are also available for comparison. However, the overall scarcity of detailed descriptions still hinders any attempt to accurately define the specialized postcranial anatomy of the family Baurusuchidae

(Bertini *et al.*, 1991, 1999; Manzini *et al.*, 1996; Brandt-Neto *et al.*, 1992; Arruda *et al.*, 2004; Avilla *et al.*, 2004).

Here we describe a new species of the genus *Baurusuchus* represented by a fragmentary skull and an almost complete postcranial skeleton, representing the first detailed postcranial description for the family Baurusuchidae.

MATERIAL AND METHODS

We analyzed Crocodyliform material from the following institutions (acronyms given in parenthesis): Museu de Zoologia da Universidade de São Paulo (MZSP); Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro (DGM); Museu de Paleontologia de Monte Alto (MPMA); Museo Argentino de Ciencias Naturales, Buenos Aires (MACN); Museo Paleontológico Carlo Ameghino, Cipoletti (MPCA); Museo de La Plata (MLP); Museo Professor Juan Olsacher, Zapala (MOZ); Museo de La Universidad de Comahue, Neuquén (MUC).

The following taxa were analyzed and compared with our material: *Araripesuchus patagonicus* (MUC-PV 269, MUC-PV 270, MUC-PV 283), *Araripesuchus buitreaensis* (MPCA-PV 235), *Baurusuchus pachecoi* (DGM 299-R), *Baurusuchus salgadoensis* (MPMA 62-0001-02), *Comahuesuchus brachybuccalis* (MUC-PV 202, MACN-N 30, MACN-N 31, MOZ 6131P), *Cynodontosuchus rothi* (MLP 64-IV-16-25), *Dakosaurus andiniensis* (MOZ 6146P), *Stratiotosuchus maxhechti* (DGM 1477-R), *Lomasuchus palpebrosus* (MOZ 4084 PV), *Marilia-suchus amarali* (MZSP-PV 50-51), *Geosaurus araucanensis* (MACN-N 95, MACN-N 64), *Notosuchus terrestris* (MLP 64-IV-16-1, MLP 64-IV-16-5, MLP 64-IV-16-6, MLP 64-IV-16-10, MLP 64-IV-16-11, MLP 64-IV-16-12, MLP 64-IV-16-13, MLP 64-IV-16-23, MACN-RN 1037, MACN-RN 1040, MACN-RN 1041, MACN-RN 1042, MACN-RN1043, MACN-RN 1044, MUC-PV 287, MPCA-PV 249, MPCA-PV250), *Peirosaurus tormini* (MOZ 1750 PV), *Caiman niger* (MZSP 2269), *Caiman crocodylus* (MZSP 2063), *Caiman yacare* (MZSP 2140), *Caiman latirostris* (MZSP 2137), *Gavialis gangeticus* (MZSP 2244).

Muscle terminology follows: Cleuren & De Vree (2000) and Schumacher (1973) for cranial and cervical musculature, Frey (1982) for the posterior axial musculature, Meers (2003) for the anterior appendicular musculature, and Romer (1923) and Haughton

(1865) for the posterior appendicular musculature. Osteological terminology follows: Iordansky (1973) and Romer (1956) for cranial bones, Romer (1956), Hoffstetter & Gasc (1973), Mook (1921), and Tarsitano (1982) for poscranial bones. As in Pol (2005), vertebral count was made considering the atlas as the first vertebra. Following Parrish (1987; see also Pol, 2005), positional terms used for the description of the appendicular skeleton refer to a vertical orientation of limb elements. For the sake of clarity in comparisons, the same terminology was used to describe the limbs of extant crocodiles.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Clark, 1986
MESOEUCROCODYLIA Whetstone &
Whybrow, 1983
BAURUSUCHIDAE Price, 1945
Baurusuchus Price, 1945
Baurusuchus albertoi sp. nov.

Holotype: Museu de Zoologia da Universidade de São Paulo, Vertebrate Paleontology collection (MZSP-PV) 140, the right posterior portion of a skull with mandible, part of the hyoid apparatus (*Cornu branchiale* I), a complete postcranium lacking only the 12th, 17th, and terminal caudal vertebrae, and parts of left appendicular skeleton.

Horizon and locality: The specimen was collected in August 2004, in an outcrop of the Boa Esperança farm (20°34'014"S, 50°27'498"W), located in the district of Prudêncio e Morais, near the city of General Salgado, state of São Paulo. The outcrops belong to the Adamantina Formation, Bauru Group, northwestern part of the Bauru Basin, possibly of Campanian to Maastrichtian age (Santucci & Bertini, 2001; Pires-Domingues, 2005).

Diagnosis: Jugal with a triangular and rugose ventrolateral projection in the anterior portion, more ventrally developed than in other Baurusuchidae; jugal infratemporal bar dorsoventrally slender, and anteroposteriorly as long as the inferior edge of the orbit; retroarticular process lateromedially flattened and vertically oriented, with a posterodorsal expansion; lateral projection of the vertical portion of the squamosal posteriorly concave; well developed ventromedial crest of the quadrate, dividing the descendent body of the quadrate in medial and anterior surfaces.

Etymology: The specific name, a noun in the genitive case, honors Dr. Alberto Barbosa de Carvalho for his contribution to the Paleontology of the state of São Paulo.

Description

Cranial elements

Except for a fragment of the left pterygoid flange, only the right posterior portion of the skull is preserved, including the squamosal, postorbital, posterior palpebral, quadratojugal, jugal, ectopterygoid, quadrate, fragments of the otooccipital, basioccipital, pterygoid and anterior palpebral (Fig. 1). Also preserved are the posterior half of the right mandible, formed by the angular, surangular, articular and a fragment of a dentary, and part of the hyoid apparatus represented by both elements of the *Cornu branchiale* I.

The infratemporal fenestra has a triangular shape, formed by the postorbital, jugal and quadratojugal. The external mandibular fenestra has a parallelogram shape and is delimited by the angular, surangular, and dentary (Fig. 1).

Dorsal and temporal regions

The squamosal forms the posterolateral limit of the skull. Its posteromedial portion is missing. Laterally, it forms the dorsal and posterior borders of the otic recess and otic cavity. The posterior half of the squamosal is almost vertical, a characteristic condition of Baurusuchidae (Riff, 2003; Nascimento, 2008). However, the lateral process of this vertical portion of the bone is medially convex and laterally concave, different from other Baurusuchidae in which it is laterally convex and medially concave. The lateral process extends ventrally, forming a free ending, posteriorly directed extremity.

The postorbital contacts the squamosal anteriorly, the quadratojugal and possibly the quadrate posteroventrally, the jugal anteroventrally, and the posterior palpebral anterodorsally. The anteromedial portion of the postorbital is missing. The lateral border of the postorbital forms (along with the squamosal) a deep external otic recess that overhangs both quadrate and quadratojugal. The medial postorbital wall is badly damaged making it difficult to visualize the postorbital-quadratojugal suture. The suture with the squamosal is shaped as an inverted "C", when

observed in lateral view. The descending postorbital ramus is smooth and cylindrical.

Two palpebrals are present in *B. albertoi*, an anterior (only partially preserved) and a posterior one. The preserved portion of the anterior palpebral is "D"-shaped and dorsally convex. The posterior

palpebral shows an almost triangular shape in dorsal view, being convex dorsally and slightly concave ventrally. The posterior palpebral is positioned as to cover the orbit dorsally.

The anterior ramus of the jugal is mediolaterally flat and dorsoventrally developed, being more

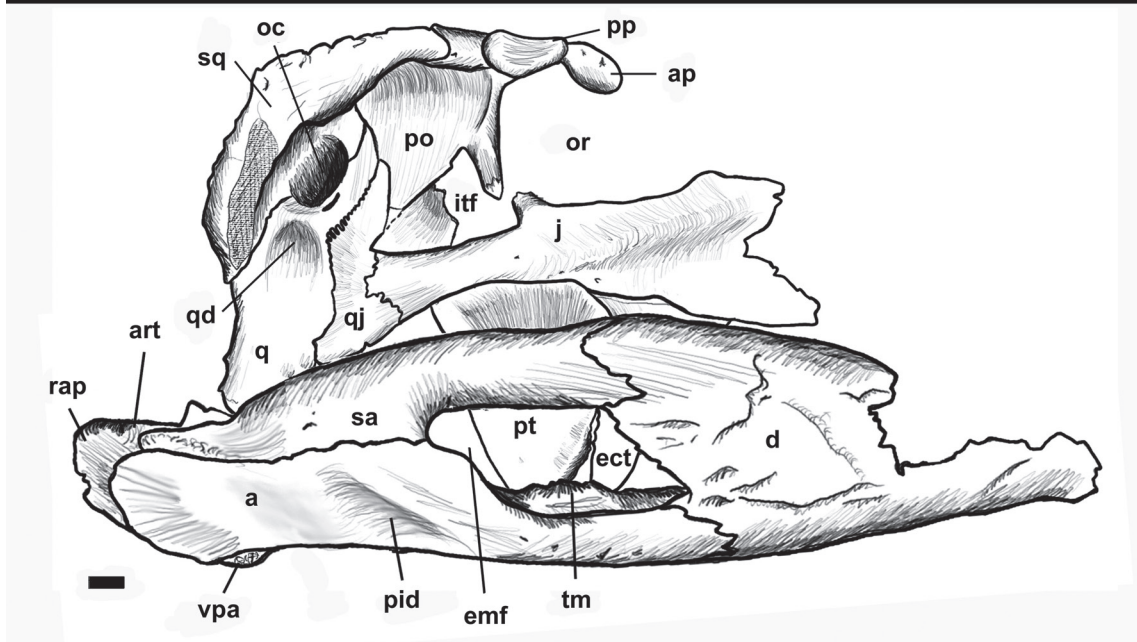


FIGURE 1: Skull and mandible of *Baurusuchus albertoi* in right lateral view. Abbreviations: a, angular; ap, anterior palpebral; art, articular; d, dentary; ect, ectopterygoid; emf, external mandibular fenestra; itf, infratemporal fenestra; j, jugal; oc, otic cavity; or, orbit; pid, depression of *M. pterygoideus* posterior insertion; pp, posterior palpebral; po, postorbital; pt, pterygoid; q, quadrate; qd, quadrate depression; qj, quadratojugal; rap, retroarticular process; sa, surangular; sq, squamosal; tm, torose margin; vpa, ventral process of the articular. Scale bar = 1 cm.

than twice as high as the posterior ramus. The dorsal edge that forms the inferior border of the orbit is smooth and concave. The ascending process of the jugal is slightly directed medially. The posterior portion of the jugal is rod-shaped, slender, and as long as the inferior border of the orbit. Additionally, the anterolateral surface shows a triangular depression, that broadens anteriorly, as in Baurusuchidae (Riff, 2003) and *Sphagesaurus huenei* (Pol, 1999). This depression is continuous, ending in the ventral limit of the jugal.

The quadratojugal broadly contacts the postorbital dorsally and the quadrate posteriorly. Its lateral surface is striated.

The quadrate is highly vertical. There is a wide and rounded concavity on the dorsolateral surface of the quadrate, typical of Baurusuchidae (Riff, 2007; Pinheiro *et al.*, 2008). Its ventromedial surface has a pronounced crest that runs from the anterior edge of the medial mandibular condyle to the basioccipital. This crest is very distinct in other Baurusuchidae. The two mandibular condyles are well defined, separated by a developed groove. Only one pneumatic foramen is present.

Braincase

Only the lateral portion of the paroccipital process of the right otooccipital is preserved in *B. albertoi*. The paroccipital process contacts the quadrate ventrally and the squamosal dorsolaterally. The right paroccipital process is dorsoventrally wide and slightly narrower laterally. The process forms two distinct surfaces delimited by a poorly developed, transversely oriented ridge.

Only a fragment of the basioccipital is preserved, corresponding to its rugose posterolateral corner. This fragment is exposed posteroventrally, and contacts the quadrate laterally.

Palate

The ectopterygoid lacks the anterior part. The contact with the jugal is wide and elliptical, restricted to the anterior portion. Ventrally to this area, the ectopterygoid has a constriction that ends medially in a broken surface. The ventral portion of the ectopterygoid forms a pointed posteroventrally oriented tip that contacts the pterygoid flange posteriorly.

There are many preserved fragments of the pterygoids of *B. albertoi*. One of these fragments is a tiny piece that contacts the anteroventral portion

of the quadrate. Both pterygoid flanges are preserved, being “U”-shaped and flattened lateromedially, and highly rugose anteriorly. Another preserved part corresponds to a middle portion, ventral to the braincase and dorsal to the pterygoid flanges. This part has very thin walls and an elliptical shape dorsally that narrows lateromedially to form the pterygoid wings.

Mandible

The preserved part of the mandible is formed by the dentary anteriorly, the angular posteroventrally, the surangular posterodorsally, and the articular posteromedially. The anterior portion of the dentary is not preserved in *B. albertoi*. The dentary is straight and lateromedially narrow.

The angular is “U”-shaped. The posterior portion of the angular is lateromedially flat and has a rounded outline. The lateral surface of the surangular retains a well-developed depression behind the mandibular fenestra that corresponds to the area of attachment of a greatly developed *M. pterygoideus posterior*, a diagnostic feature of Baurusuchidae (Nascimento, 2008).

The surangular is an elongated element. Its suture with the dentary is mostly “S”-shaped in lateral view. The lateral wall of the surangular is lower than that of the angular. Ventrally, the surangular possesses a thin prolongation that fits between the angular (laterally) and the articular (medially). The posterior extremity of the surangular is deflected dorsally, forming a small, rugose and funneled projection.

The articular is a triradiate element. The anteroventral portion is an acute tip, and has a middle longitudinal crest. The glenoid fossa possesses two concavities divided by a middle prominence. The retroarticular process of *B. albertoi* differs from other Baurusuchidae, being verticalized, lateromedially flattened and dorsally rounded. Posteriorly, the transition of the glenoid fossa to the retroarticular process is very abrupt. This transition is gentle in the other species of *Baurusuchus*. The retroarticular process has a ventral expansion that forms a small, rounded and rugose projection that is anteromedially deflected.

Hyoid apparatus

Both *Cornua branchiale* I of the hyoid apparatus of *B. albertoi* were found, semi-articulated to the skull. The two elements are 9 and 10 centimeters long and are bow-shaped.

Axial elements

The axial skeleton of *B. albertoi* is almost completely preserved and articulated. Atlas and axis are present, despite the fact that the basicranial remains lack any vestige of an occipital condyle (Fig. 2A). The other cervical and thoracic vertebrae are preserved articulated, but suffered compressions and breaks due the fossilization process. The left side of the sacral vertebrae did not resist weathering that resulted from

a long postdiagenetic period of exposure. The right side, however, is perfectly preserved. The caudal vertebrae are almost complete, except for the 12th, 17th, and an unknown number of terminal vertebrae. The 12th vertebra was damaged during removal of the specimen from the field. The total length of the specimen is estimated to be two meters. All vertebrae of *B. albertoi* are amphicoelic, and include an atlas, axis, six cervical vertebrae (Vertebrae III-VIII), 16 dorsal vertebrae (Vertebrae IX-XXIV), three sacral vertebrae

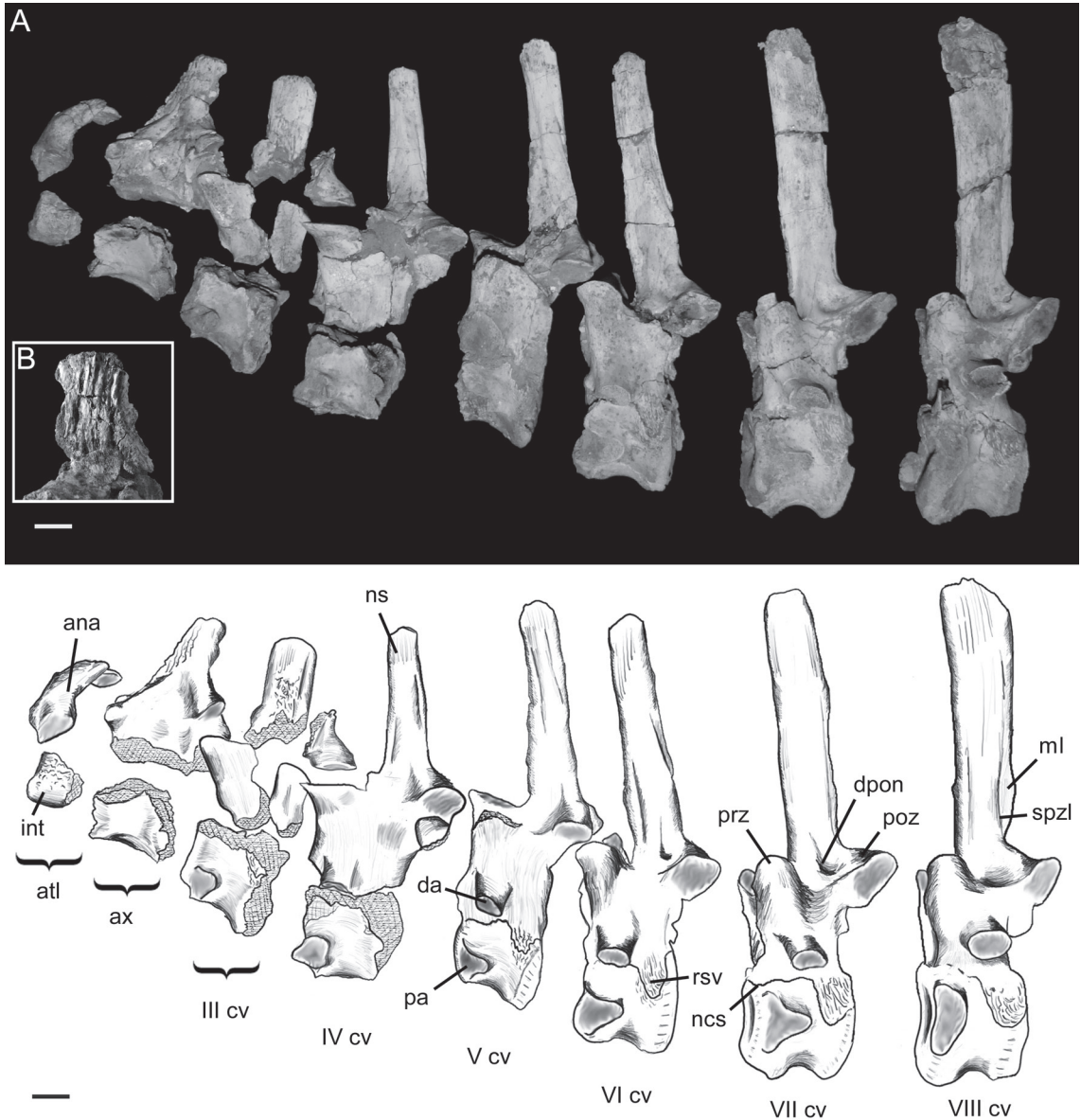


FIGURE 2: A, cervical vertebrae of *Baurusuchus albertoi* in left lateral view; B, detail of the neural spine of the axis in right lateral view. Abbreviations: ana, atlas neural arch; atl, atlas; ax, axis; da, diapophysis; dpon, depression between postzygapophysis and neural spine; int, atlas intercentrum; ml, medial lamina; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; spzl, suprapostzygapophyseal lamina; rsv, rugosity of lateral surface of vertebra. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

(Vertebrae XXV-XXVII), and 35 preserved caudal vertebrae (Vertebrae XXVIII-LXII).

Atlas

Both halves of the neural arch and intercentrum were found disarticulated, but associated to the occipital region of the skull (Figs. 3A-B). The intercentrum is damaged in its posterior portion, making it impossible to define whether it was anteroposteriorly elongated (as in *Caiman*), short (as in *Crocodylus* and *Gavialis*), or if it had a distinct shape. Anteriorly, the intercentrum has a cotyle-shaped concavity for the articulation of the inferior portion of the occipital condyle (Fig. 3B). The neural arch elements are narrow and bow-shaped, forming together a dorsally-opened neural canal. Anterodorsally, the neural arch shows an anteriorly deflected process (also present in *Notosuchus terrestris*; Pol, 2005) with a small notch located ventrolaterally to it. This notch corresponds to the passage of the first spinal nerve in Crocodylia (Hoffstetter & Gasc, 1973) (Fig. 3A). Posterodorsally, the neural arch bends medially, forming two postzygapophyseal surfaces that articulate with the axis. These dorsoventrally flat postzygapophyses delimit dorsally the neural canal and have a rounded outline in dorsal view. Laterally, there is a posteriorly directed

process, separated from both postzygapophyses by a notch, which is also present in living crocodiles. A second and larger notch can be observed in the posterior region, below the postzygapophysis, and corresponds to the passage of the second spinal nerve (Hoffstetter & Gasc, 1973). The same notch is also present in *Notosuchus* (Pol, 2005). Anteroventrally, there is a flat surface that contacts the occipital condyle, and posteroventrally, a concave surface that contacts the odontoid process of the axis.

Axis

The axis was found broken in two pieces: a dorsal one (with the neural spine, postzygapophyses and dorsal part of the neural canal) and a ventral one (with the ventral part of the neural canal and vertebral centrum); the odontoid process is not preserved (Fig. 3C). The neural spine of the axis is posteriorly directed and dorsoventrally shorter than any other neural spine present in the presacral vertebrae of *B. albertoi* (Fig. 2A). It is also narrow anteroposteriorly, with an almost quadrangular outline. Its shape is very similar to that of *Notosuchus terrestris*, *Sphagesaurus huenei* (Pol, 2005), and *Chimaerasuchus paradoxus* (Wu & Sues, 1996). Both sides of the neural spine are ornamented by a large number of grooves that are

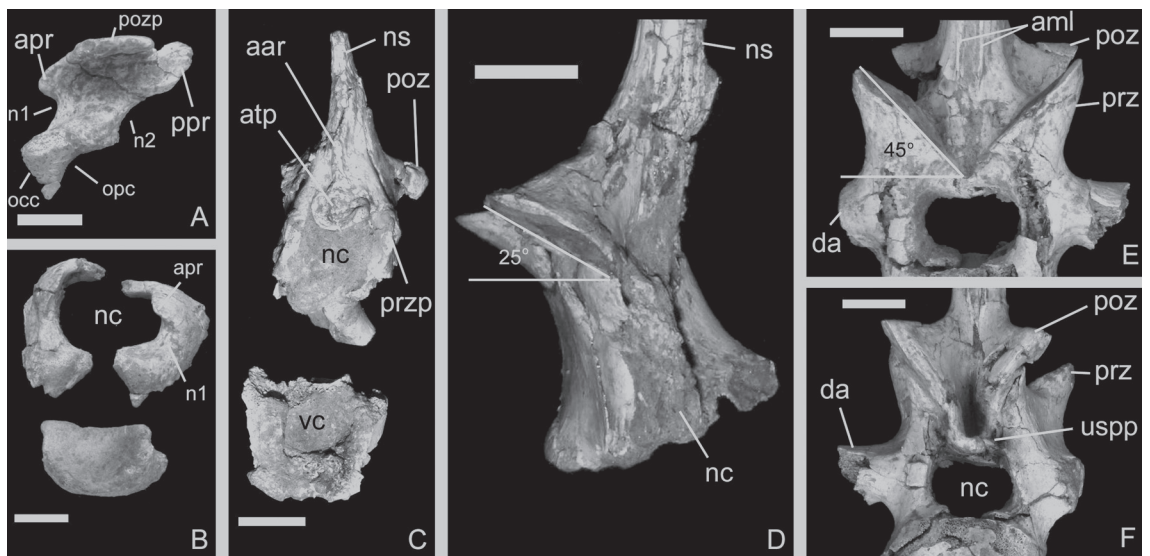


FIGURE 3: Atlas, axis and cervical vertebrae IV and VIII of *Baurusuchus albertoi*. A, medial view of the right neural arch pedicel of the atlas; B, anterior view of the atlas; C, anterior view of the axis; D, posterior view of cervical vertebra IV; E, anterior view of cervical vertebra VIII; F, posterior view of cervical vertebra VIII. Abbreviations: aar, axis anterior ridge; aml, anterior medial lamina; apr, atlas anterior process; atp, anterior tongue-like process of the axis; da, diapophysis; n1, atlas notch to the first cranial nerves; n2, atlas notch second cranial nerves; nc, neural canal; ns, neural spine; occ, occipital condyle contact area; opc, odontoid process contact area; poz, postzygapophysis; pozp, postzygapophyseal process; prz, prezygapophysis; przp, prezygapophyseal process; uspp, “U” shaped process between postzygapophyses; vc, vertebral centrum. Scale bar = 1 cm.

dorsoventrally oriented, defining an area of muscle attachment (Cleuren & De Vree, 2000) (Fig. 2B). These grooves are not present in *Notosuchus* or in living forms. A mid-anterior narrow ridge runs through the neural spine to reach the anteriormost portion of the axis, widening at the anterior end and forming an anterior “tongue-shaped” projection, which is flattened dorsoventrally (Fig. 3C). This structure is absent in other known crocodyliforms. The rounded prezygapophyses arise anteriorly from the dorsolateral portion of the neural canal. As in *Notosuchus*, there is no connection between prezygapophyses and the neural spine (Pol, 2005). The prezygapophyses are separated from the middle “tongue-shaped” projection by a deep groove. The neural arch enlarges posterolaterally and ventrally to the neural spine, forming the postzygapophyses. Dorsally the rounded postzygapophyses are curved and slightly continuous with the neural arch. Ventrally, the surface is flattened. *Baurusuchus albertoi* lacks the triangular depression present between the neural spine of the axis and the postzygapophyses, known to occur in *Notosuchus* (Pol, 2005). The vertebral centrum is “U” shaped in an anterior view (Fig. 3C). Ventrally, there is a tiny longitudinal crest that is slightly broader posteriorly than anteriorly.

Cervical vertebrae (Vertebrae III to VIII)

Although usually difficult to determine in crocodiles, the last cervical vertebra is distinguished from the first dorsal vertebra according to its position in respect to the sternum (Romer, 1956; Hoffstetter & Gasc, 1973). Since the sternum of *B. albertoi* was not preserved, here we consider the eighth vertebra as the last cervical one, following the count given by Hoffstetter & Gasc (1973) for extant crocodiles. In general view, the cervical vertebrae of *B. albertoi* are very similar to those of *Stratiotosuchus* (DGM 1477-R).

The third and fourth cervical vertebrae, as the axis, are broken in two pieces. The dorsal portion of the third vertebra is extremely incomplete (Fig. 2). The neural spine was found isolated, and is larger and higher than that of the axis. It shows a rectangular shape, with the dorsal surface slightly convex, unlike *Notosuchus* in which the neural spine of the third vertebra is clearly trapezoidal (Pol, 2005). The dorsoventral grooves originated from muscle scars are evident (see axis description). The neural spine of the fourth vertebra is longer, its anteroposterior length is almost half than that of the third vertebra, and is located very posteriorly in the neural

arches, with the postzygapophyses projected posteriorly beyond the posterior limit of the vertebral centrum. This condition contrasts with the one present in extant crocodiles, in which the neural spines are placed more centrally in the dorsal area of the neural arches. In *Notosuchus* (Pol, 2005), the neural spines are also placed posteriorly, but not so posteriorly as in *B. albertoi*. From the fourth vertebra back, the neural spines become gradually higher and anteroposteriorly longer (Fig. 2A), with the maximum height proportion present in the seventh and eighth vertebra, where the neural spine represents more than half of the total height of vertebrae. There is also a gradual transition of the neural spine position, from a more posterior position at the level of the fourth vertebra to a central position at the level of the eighth cervical vertebra. The neural spine of the eighth cervical vertebra is narrower at the base and broader at the top, a pattern that is distinct from the other cervicals, but similar to the more posterior dorsal vertebrae. The suprapostzygapophyseal laminae are high, starting from approximately the middle of the neural spine. This structure is also present in *Notosuchus*, *Malawisuchus*, *Uruguaysuchus*, *Mariliasuchus*, and *Araripesuchus* (Pol, 2005). Between the two suprapostzygapophyseal laminae there is a sagittal lamina, the medial lamina (Pol, 2005), which is broken or damaged in all vertebrae of *B. albertoi*, but is clearly a robust and well developed lamina. These laminae become more prominent in the posterior cervical elements. The medial lamina of *Notosuchus* is much thinner than the one present in *B. albertoi*. A deep groove separates the suprapostzygapophyseal laminae from the medial lamina. A medial lamina is also recognizable on the anterior limit of the neural spines of the cervical vertebrae. These laminae are broken in all vertebrae, but clearly they were sagittally bifid. This condition is unknown for the other crocodyliforms. There is a depression lateral to the suprapostzygapophyseal laminae, also present in *Notosuchus* (Pol, 2005), which is shallow in the sixth vertebra and deeper in the posterior ones (Fig. 2A).

Only the left zygapophyses are preserved in the third vertebra, and both possess a rounded shape in ventral view, being the postzygapophysis articulation facet almost twice larger lateromedially than that of the prezygapophysis. Along the cervical column there is a gradual increase of the zygapophyseal dorsal inclination in relation to the horizontal plane, from about 25° in the fourth vertebra to 45° in the eighth vertebra (Fig. 3E). Ventrally, the postzygapophyses contact each other through a thin “U”-shaped protuberance that bridges them (Fig. 3F). The length of the neural arches and vertebral centra gradually

decrease anteroposteriorly along the cervical column, more abruptly than in living crocodiles (Hoffstetter & Gasc, 1973). Similar to *Notosuchus* (Pol, 2005), the diapophysis varies along the cervical column, being anteriorly positioned and ventrolaterally oriented in the fourth vertebra while it changes to a more posterior position with a lateral orientation in the eighth vertebra. Additionally, the diapophysial shape is elliptical in the fourth vertebra and almost circular in the eighth vertebra.

Anteriorly, the vertebral centra of the cervical vertebrae are laterally compressed, with an elliptical shape. All presacral vertebrae possess a convex and rugose surface dorsal to the neurocentral suture and posterodorsal to the vertebral centra, which probably represents the site of origin for the fibers of the *M. longissimus capitis superficialis* (Cleuren & De Vree, 2000) (Fig. 2A). The parapophyses appear anteriorly in the lateral surface of the vertebral centra, also varying gradually along the cervical column, being more

ventral in the third vertebra while more dorsal in the eighth vertebra. The parapophyses from the third to the seventh vertebrae are very similar, being subtriangular and elongate anteroposteriorly. The eighth vertebral parapophysis is very different, kidney-shaped and elongated dorsoventrally. Ventrally, the vertebral centra possess a very small sagittal keel, which is more prominent in the fifth vertebra and less developed in the other ones. Contrary to the condition present in living crocodiles, there is no evidence of cervical hypapophyses (Hoffstetter & Gasc, 1973).

First dorsal vertebra (vertebra IX)

As in living crocodiles (Mook, 1921), the first dorsal vertebra is very similar to the last cervical one, the neural spine being more than half the total height of the vertebra and possessing a *medial lamina*. However, it is shorter anteroposteriorly than a cervical,

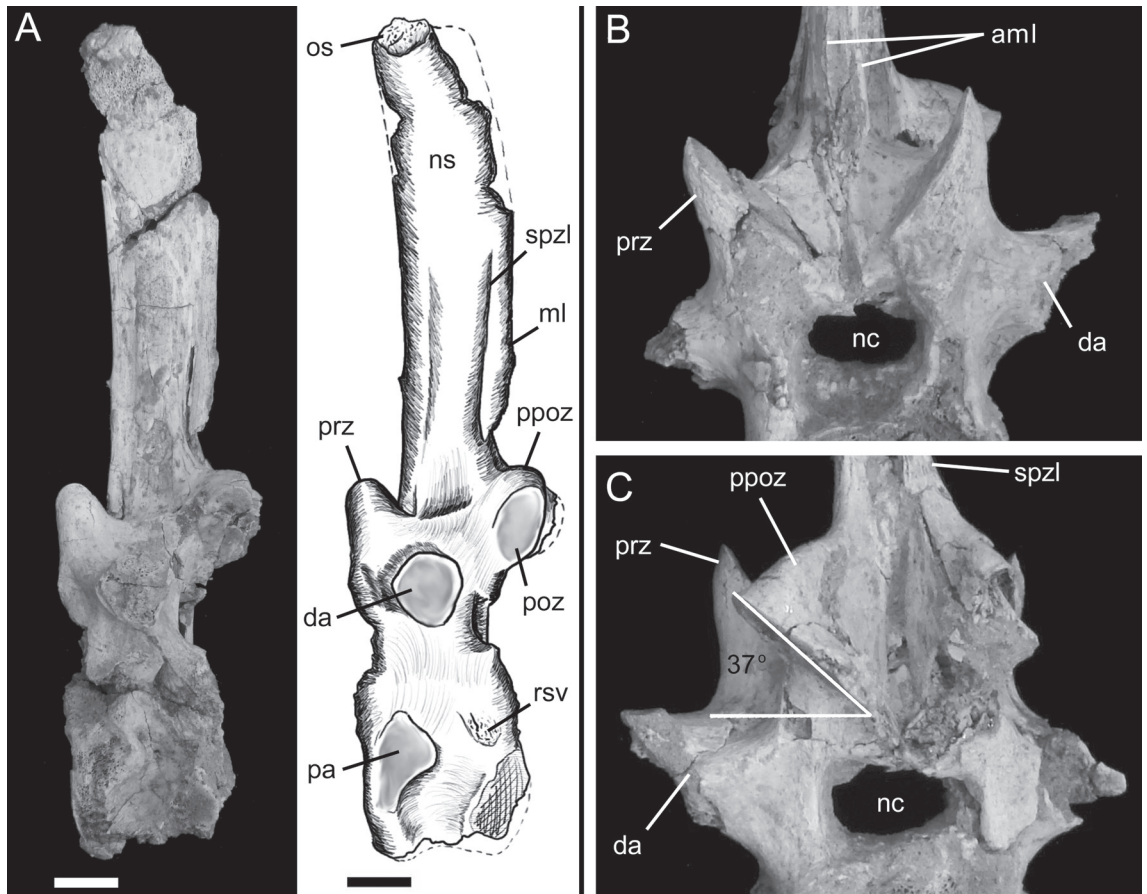


FIGURE 4: First dorsal vertebra (Vertebra IX) of *Baurusuchus albertoi*. A, left lateral view; B, detail of the neural arches in anterior view; C, detail of the neural arches in posterior view. Abbreviations: aml, anterior medial lamina; da, diapophysis; ml, medial lamina; nc, neural canal; ns, neural spine; os, osteoderm; pa, parapophysis; poz, postzygapophysis; ppoz, protuberance of the postzygapophysis; prz, prezygapophysis; rsv, rugosity of lateral surface of vertebra; spzl, suprapostzygapophyseal lamina. Scale bar = 1 cm.

and the prezygapophyses are anteroposteriorly narrower and less dorsally deflected (Fig. 4). Ventral to the suprapostzygapophyseal laminae, the dorsal outline of postzygapophyses is highly convex (Fig. 4). This peculiar shape is absent in the cervical vertebrae (Figs. 3F, 4C). One of the anterior dorsal vertebrae of *Stratiotosuchus maxbechti* (DGM 1477-R) also possesses this peculiar postzygapophyseal shape, being more marked than in *B. albertoi*. The diapophyses are more dorsal than in the cervicals, being placed slightly dorsal to the neural canal. The parapophyses are kidney-shaped.

Second to sixteenth dorsal vertebrae (Vertebrae X to XXIV)

The other dorsal vertebrae are not as well preserved than the first one. The second dorsal vertebra is poorly preserved, being broken in several pieces that are concealed under the humerus and the left scapula, only its neural spine visible. The remaining more posterior dorsal vertebrae are also broken, incomplete, or with parts that are still not visible after preparation. However, the gradual varying characteristic of the serial structures forming the dorsal column is still visible through the second to the last vertebrae (Figs. 5-8). The neural spines of the fifth, ninth, tenth, and twelfth dorsal vertebrae were partly or completely lost. Although not preserved, it is possible to conclude that the neural spines become gradually elongated anteroposteriorly, with a base that is anteroposteriorly shorter than the top, all anteroposteriorly centered in relation to the neural arches. The neural spine of the third dorsal vertebra is slightly posteriorly deflected. Following the dorsal column, the neural spines gradually deflect anteriorly and, in the sixth dorsal vertebra, the neural spine is aligned vertically with the vertebral centrum. At the level of the eleventh dorsal vertebra, the neural spines become slightly anteriorly deflected. The suprapostzygapophyseal laminae are clearly distinguishable only in the first and third dorsal vertebrae, while in *Notosuchus* they are present in almost all vertebrae (Pol, 2005). It is impossible to confirm the presence of a medial lamina in these dorsal vertebrae. The zygapophyseal surfaces of articulation are nearly horizontal, a condition also observed in *Notosuchus* (Pol, 2005) and *Chimaerasuchus* (Wu & Sues, 1996), but distinct from the condition of extant forms where the zygapophyseal articulations are dorsally deflected. The prezygapophyses are laterally projected in all dorsal vertebrae, contrary to the condition present in *Notosuchus* (Pol, 2005) and in *Malawisuchus* (Gomani,

1997) where they are projected anteriorly. The strongly curved dorsal outline of the postzygapophyses is still present in the third and fourth dorsal vertebrae (Fig. 5). The postzygapophyses are posteriorly directed until the fifth dorsal vertebra. After that, the orientation of the postzygapophyses becomes gradually lateral, reaching a completely lateral orientation in the ninth dorsal vertebra. After the tenth dorsal vertebra, the postzygapophyses revert again to a more posteriorly oriented condition (Fig. 6). This differs from *Uberabasuchus*, in which apparently all the postzygapophyses are laterally deflected (Vasconcellos, 2006). As in extant crocodiles (Hoffstetter & Gasc, 1973), the parapophyses and the diapophyses migrate gradually to a more dorsal position towards the posterior region of the dorsal series. The diapophyses project laterally, aligning dorsoventrally with the zygapophyses. The parapophyses migrate dorsally until they reach an anterior position in respect to the diapophysis. Both diapophysis and parapophysis fuse to form the transverse process of the seventh dorsal vertebra, contrasting with the condition present in *Crocodylus niloticus* where this fusion occurs in the fourth dorsal vertebra (Hoffstetter & Gasc, 1973). The transverse processes fuse with the prezygapophyses from the seventh dorsal vertebra on, being separated from each other by just a small prezygapophyseal inclination. This kind of connection between the transverse process and the prezygapophysis is present in the posterior dorsal vertebrae of *Stratiotosuchus* (DGM 1477-R) and *Notosuchus* (Pol, 2005). In *Mahajangasuchus* (Buckley & Brochu, 1999) and in extant crocodiles (Mook, 1921; Hoffstetter & Gasc, 1973) this union is not so conspicuous. The transverse processes are slightly posteriorly deflected in almost all dorsal vertebrae. The neural canal of the dorsal vertebrae is always ventral to the zygapophyses and, almost always, ventral to the transverse processes. The overall form of the vertebral centra is spool-shaped, like in *Notosuchus* (Pol, 2005) and *Chimaerasuchus* (Wu & Sues, 1996). In anterior view, the vertebral centra are elliptical and laterally compressed, without hypapophyses or ventral keels.

Sacral vertebrae

Some features can be observed in the sacral vertebrae, despite the fact that this part is poorly preserved in *Baurusuchus albertoi*. There are three sacral vertebrae as in *Stratiotosuchus* (Riff, 2007), in contrast with living crocodiles, that have only two. The vertebral centra are preserved only on the right side, and show flattened lateral and ventral surfaces

that are separated by a crest, as in *Mariliasuchus*. This crest is more evident in the second sacral vertebra, but almost absent in the third vertebra that is more rounded. The vertebral centra are disposed ventrally to the ilium. The third sacral vertebra possesses a very robust transverse process, laterodorsally deflected (present only in Baurusuchidae) and strongly sutured to ventral portion of the posterior process of the ilium (Fig. 9).

Caudal vertebrae

The tail of *Baurusuchus albertoi* was collected in two sections: an anterior one with the first 12 articulated vertebrae (with the 12th damaged), and a posterior one with 16 articulated vertebrae and several fragments of other 7 vertebrae (Figs. 10-14). The 17th vertebra is too fragmented to be reconstructed. The terminal vertebrae are missing.

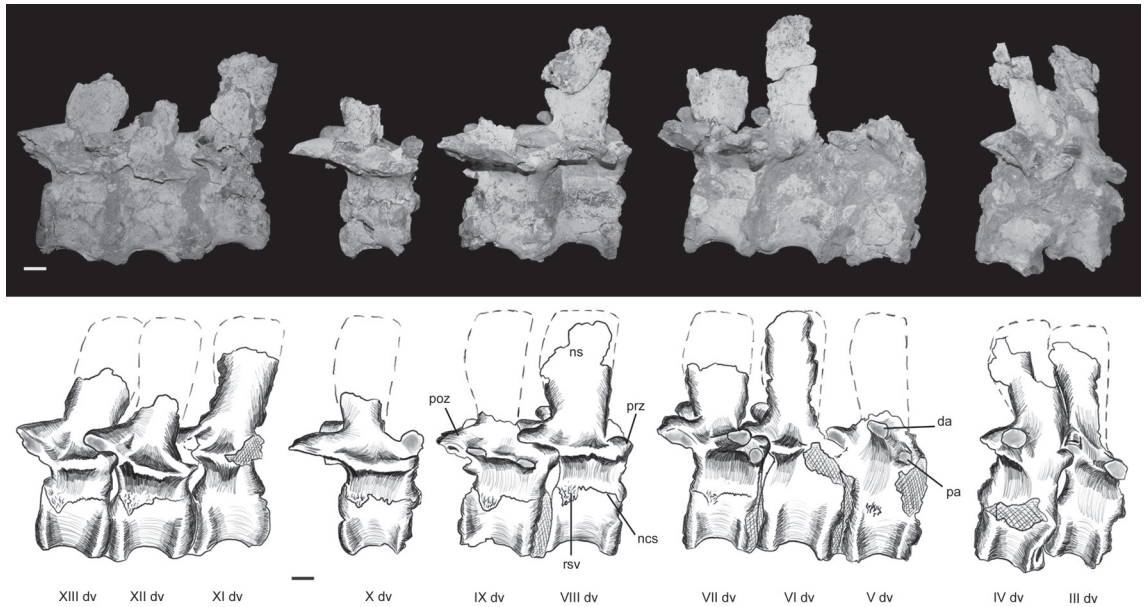


FIGURE 5: Third to 13th dorsal vertebrae of *Baurusuchus albertoi* in right lateral view. Abbreviations: da, diapophysis; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; rsv, rugosity of lateral surface of vertebra. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

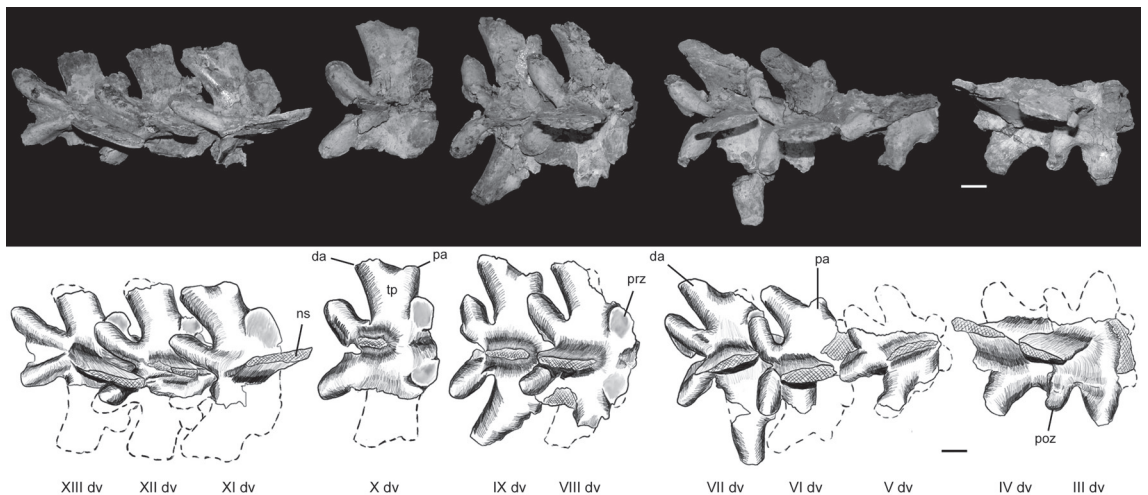


FIGURE 6: third to 13th dorsal vertebrae of *Baurusuchus albertoi* in dorsal view. Abbreviations: da, diapophysis; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

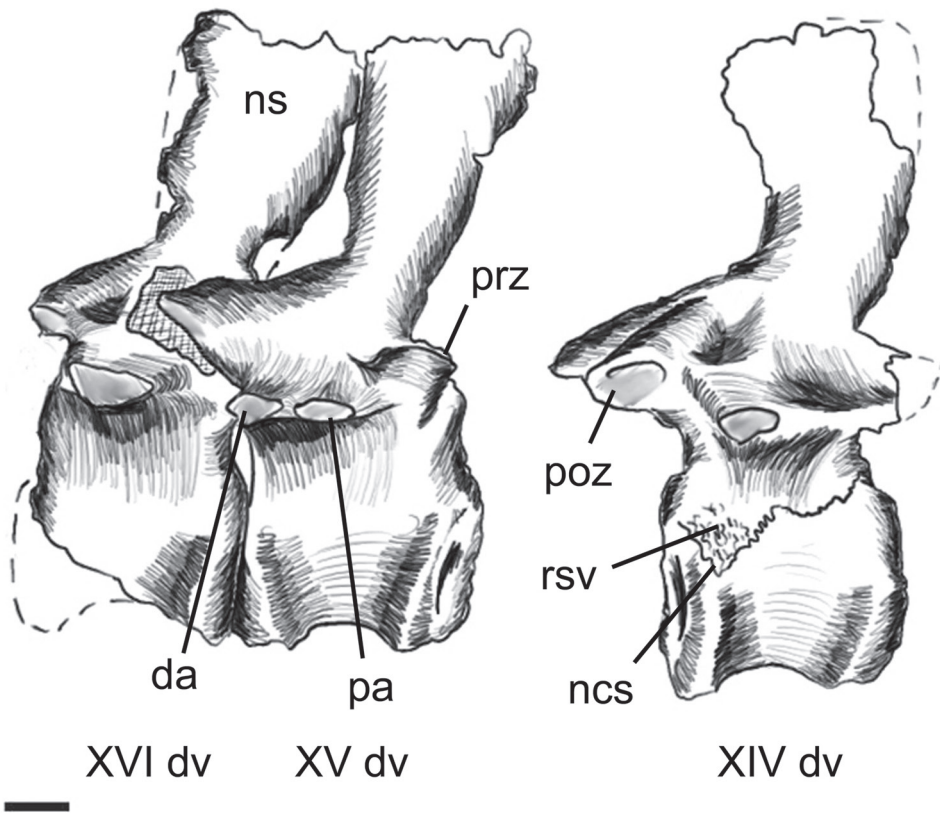
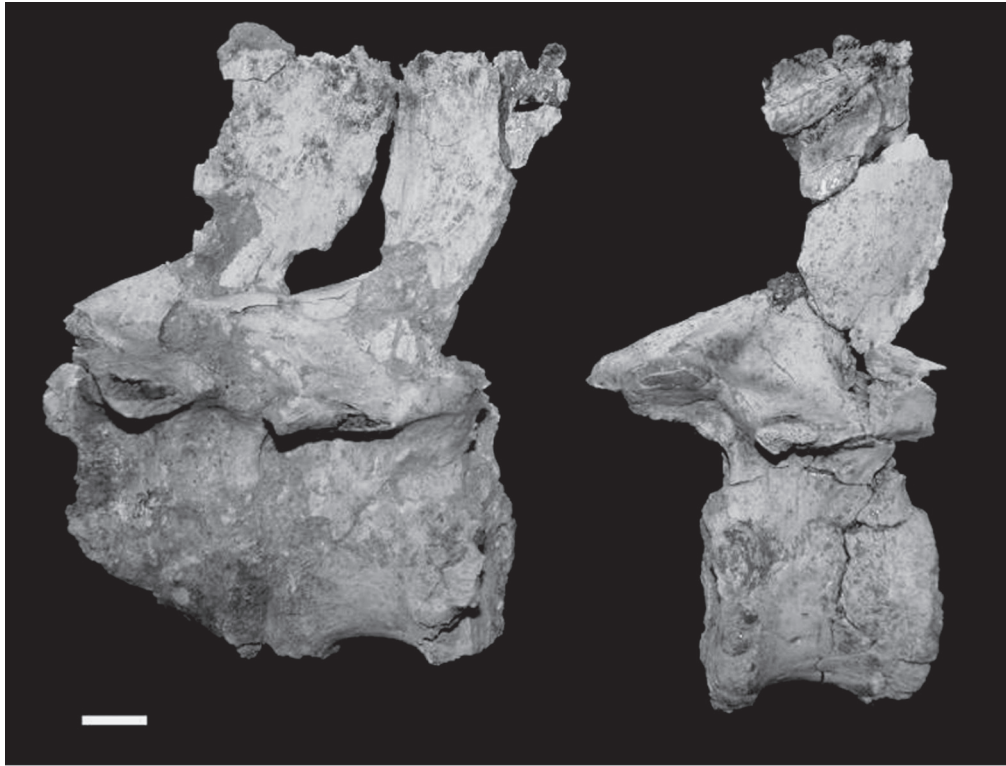


FIGURE 7: “Lumbar” vertebrae of *Baurusuchus albertoi* in right lateral view. Abbreviations: da, diapophysis; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; ncs, neurocentral suture; rsv, rugosity of lateral surface of vertebra. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

The neural spines decrease in size gradually along the tail. This decrease is more conspicuous dorsoventrally than anteroposteriorly. The neural spines of the anterior caudal vertebrae are very high

and narrow anteroposteriorly (in contrast to members of the Crocodylia). Near the base, the neural spine expands anteriorly, forming a very thin keel (Figs. 10-12). The neural spines of the last caudal

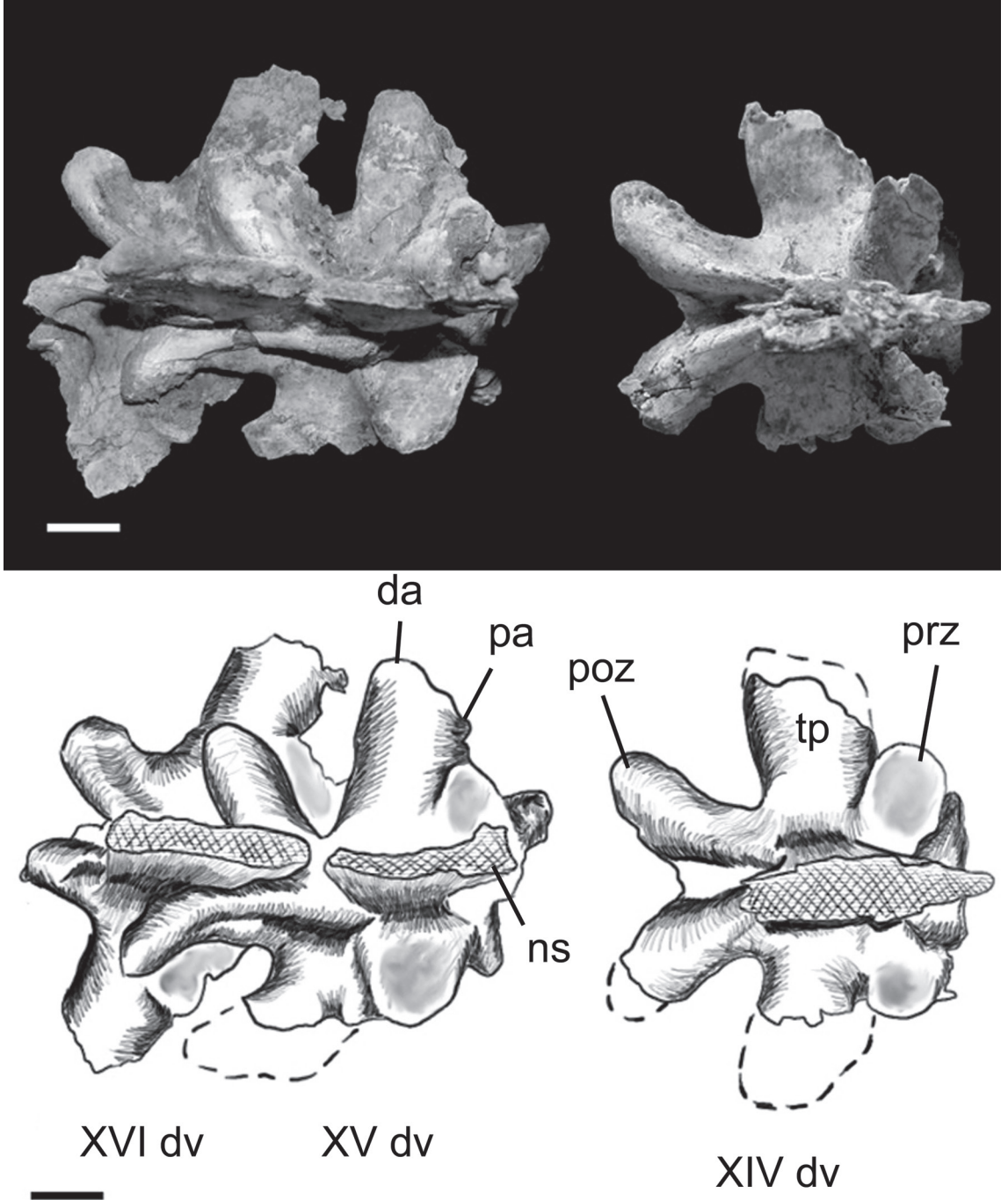


FIGURE 8: “Lumbar” vertebrae of *Baurusuchus albertoi* in dorsal view. The roman numerals indicate the number of the vertebral count. Abbreviations: da, diapophysis; ns, neural spine; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

vertebrae possess an almost square shape that reduces into a small keel in the 35th and last caudal vertebra, the last one preserved. The caudal zygapophyses of *B. albertoi* are slightly dorsally deflected in the first four vertebrae, becoming horizontal in all the others. This condition differs from *Notosuchus* (Pol, 2005) and extant forms, in which all the zygapophyses possess a strong dorsal inclination. The caudal vertebrae of the first half have thin transverse processes posterolaterally oriented and dorsally deflected, that are at the same horizontal level of the zygapophyseal articular surfaces and dorsal to the neural canal. This condition differs from that of *Crocodylia*, where the transverse processes are horizontal, and are ventral to the zygapophyses and the neural canal. A rugose protuberance is present in the middle portion of the anterior edge of the transverse processes, being more visible on dorsal surface (Fig. 15A). The transverse processes decrease in size gradually along the tail, to reach a vestigial size in the 25th caudal vertebra and disappear in the 26th vertebra. The vertebral centra are laterally compressed, contrary to the *Crocodylia* in which they are cylindrical. Ventrally there are two posterior, parallel and longitudinal keel-like processes that form an area of articulation that receives the hemal arches. These keels are more developed in

B. albertoi than in *Notosuchus* (Pol, 2005), *Mahajangasuchus* (Buckley & Brochu, 1999), and *Crocodylia* (Mook, 1921).

Ribs

Almost all ribs of *B. albertoi* were found, but none of them are well preserved, the majority being broken or fragmented. The right cervical ribs preserved correspond to those of the atlas, axis (fragmented), fourth, fifth, sixth (fragmented), and seventh vertebrae, while the left preserved cervical ribs were those belonging to the atlas, axis (fragmented), third, fourth, sixth and eighth vertebrae. The atlas ribs have a sword shape, with only one contact surface. The cervical ribs, from the axis to the seventh vertebra, have a conservative archosaurian morphology (Mook, 1921; Romer, 1956; Hoffstetter & Gasc, 1973). The tubercular process is pointed dorsally, and the capitular one is medially directed. Each rib shows an anterior process, ventral to the tubercular process, which fits in the posterior portion of the anterior rib, being funneled anteriorly and slightly concave medially (Fig. 16). Such anterior process is present in all crocodyliforms and related forms (Pol, 2005). As in

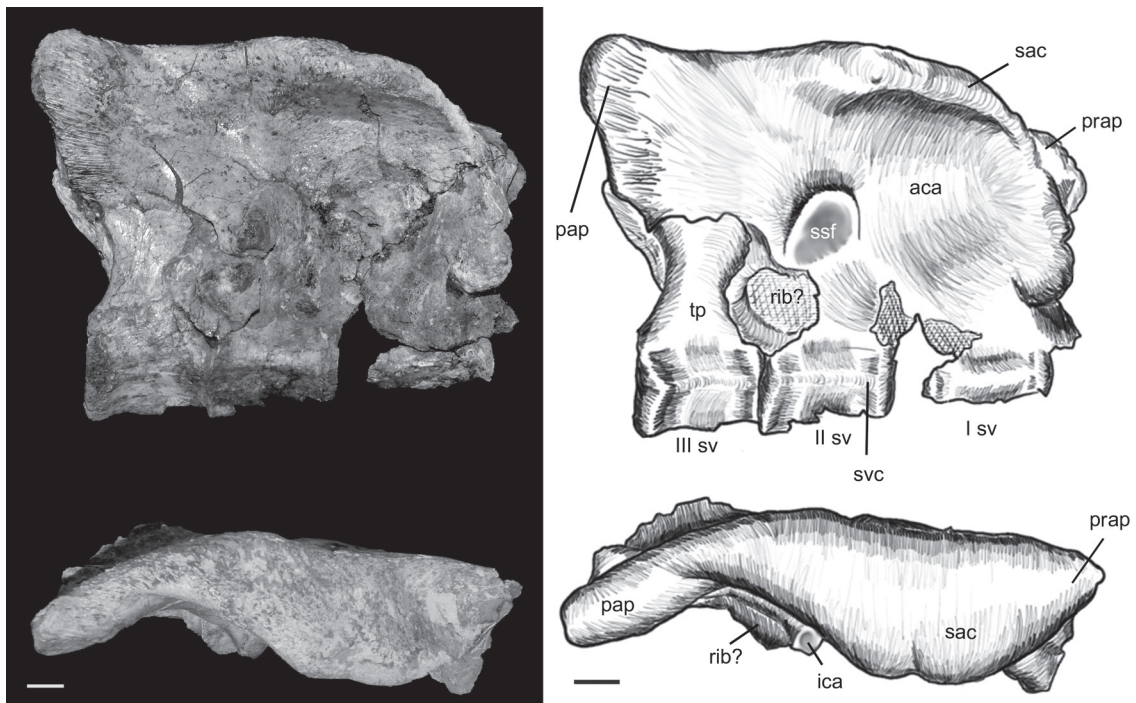


FIGURE 9: Ilium and sacral vertebrae of *Baurusuchus albertoi* in right lateral view (above) and ilium in dorsal view (below). Abbreviations: prap, preacetabular process; aca, acetabular area; pap, posteroacetabular process; sac, supraacetabular crest; ssf, smooth surface to femur contact; sv, sacral vertebra crest; tp, transverse process. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

living crocodiles, the eighth ribs are elongated, lateromedially flattened, and smaller than the first dorsal ribs.

Almost all dorsal ribs were preserved in the specimen (ten on the right side and 13 on the left side). The three last dorsal vertebrae lack ribs, an absence that could characterize a “lumbar” region (Romer, 1956). The dorsal ribs are very fragmented, but their shape is very similar to that of the eighth

cervical rib, which is bow-shaped, elongated dorsoventrally, narrow anteroposteriorly, and compressed lateromedially. Following the vertebral column there is a gradual increase in the curvature of the rib and decrease in its size (Fig. 16). The articulation areas show the same pattern present in living crocodiles, with the tubercular area placed more dorsally. However, the capitular area is more anteroventrally positioned, tending to a more dorsal position along the

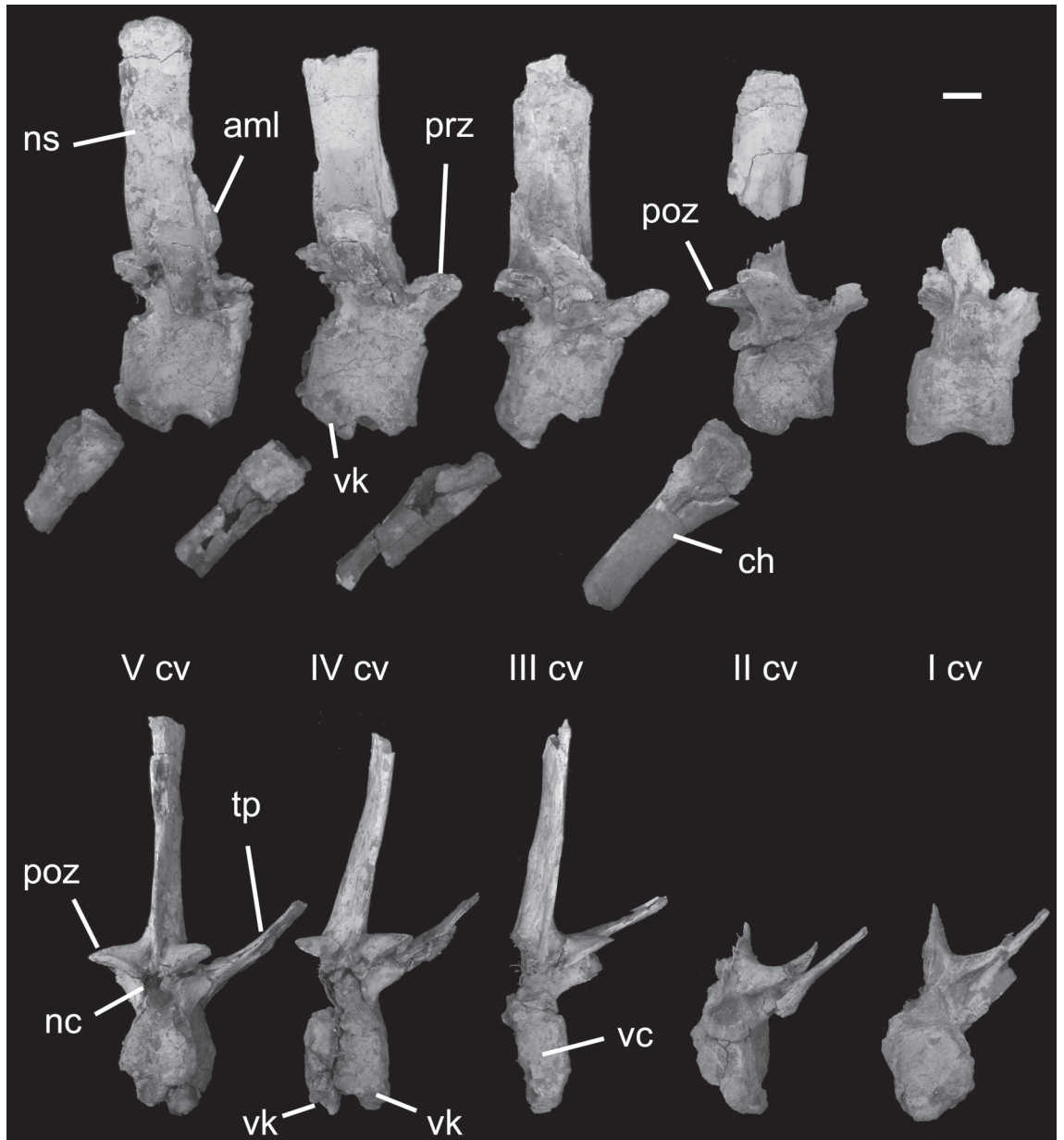


FIGURE 10: First to fifth caudal vertebrae of *Baurusuchus albertoi* in right lateral view (above, with chevrons) and posterior view (below). The roman numerals indicate the number of the vertebral count. Abbreviations: aml, anterior medial lamina; ch, chevron; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vc, vertebral centrum; vk, ventral keel for chevron attachment. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

dorsal column, while following the gradual migration of the parapophyses.

Haemal arches

Thirty-three haemal arches were found in *B. albertoi*, the first one articulating with the second caudal vertebra and each haemal arch gradually decreasing in size along the tail (Figs. 10-14). The haemal arches articulate in the posteroventral region of the centrum of the caudal vertebrae. The latter projects posteroventrally, conferring a concave shape to the centrum in lateral view. Articular facets are well-differentiated in all haemal arches and do not join to form a proximal "crus," like the condition seen in extant crocodiles (Fig. 15B). The haemal arches are formed by two deeply divided proximal rami that unite to form a single distal ramus. The division between rami extends for one-third the full length of the bone, forming a narrow "V", while

the distal part extends the other two-thirds of the haemal arch and is transversely compressed, anteroposteriorly expanded and blade-like distally.

Gastralia

Only some small pieces from the gastralia were found in *B. albertoi*. At least four lines of gastralia could be distinguished during the preparation process. The pieces were found between the sacral vertebrae and the posterior half of the trunk. The small fragments are elongated and elliptical.

Appendicular elements

The right appendicular skeleton is perfectly preserved in *B. albertoi* while the left one is fragmented and weathered.

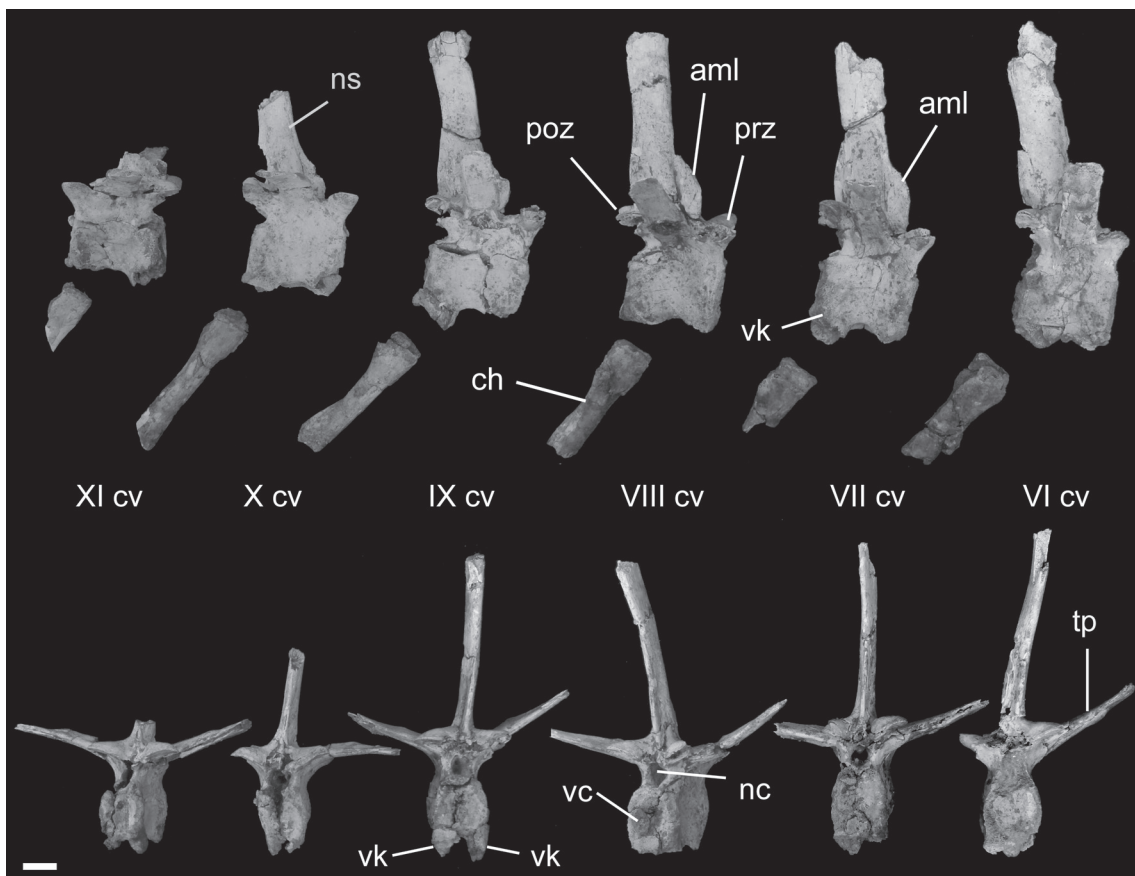


FIGURE 11: Sixth to 11th caudal vertebrae of *Baurusuchus albertoi* in right lateral view (above, with chevrons) and posterior view (below). Roman numerals indicate the number of the vertebral count. Abbreviations: aml, anterior medial lamina; ch, chevron; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vc, vertebral centrum; vk, ventral keel for chevron attachment. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

Coracoid

The ventral expansion is damaged on both coracoids, but a part of the posteroventral process is visible in the right coracoid (Fig. 17). The poor preservation of the coracoid extremities could be evidence of its cartilaginous nature, as in living crocodiles. The area of contact between the coracoid and scapula is a straight surface, immediately anterior to the glenoid surface, as in other crocodylomorphs (Wu & Chatterjee, 1993; Wu & Sues, 1996; Mook, 1921). The concave glenoid surface is posterolaterally oriented. The large coracoid foramen is located just anterior

to the glenoid surface, approximately in the middle of the dorsal expansion of the coracoid. Posteroventrally to the glenoid surface, on the proximal aspect of the shaft, there is a dorsoventrally expanded groove (Fig. 17). In anterior view the shaft of the coracoid is concave medially.

Scapula

Both scapulae are damaged, with many clefts and missing parts. Nevertheless, an approximated outline could be inferred (Fig. 18), and it is basically

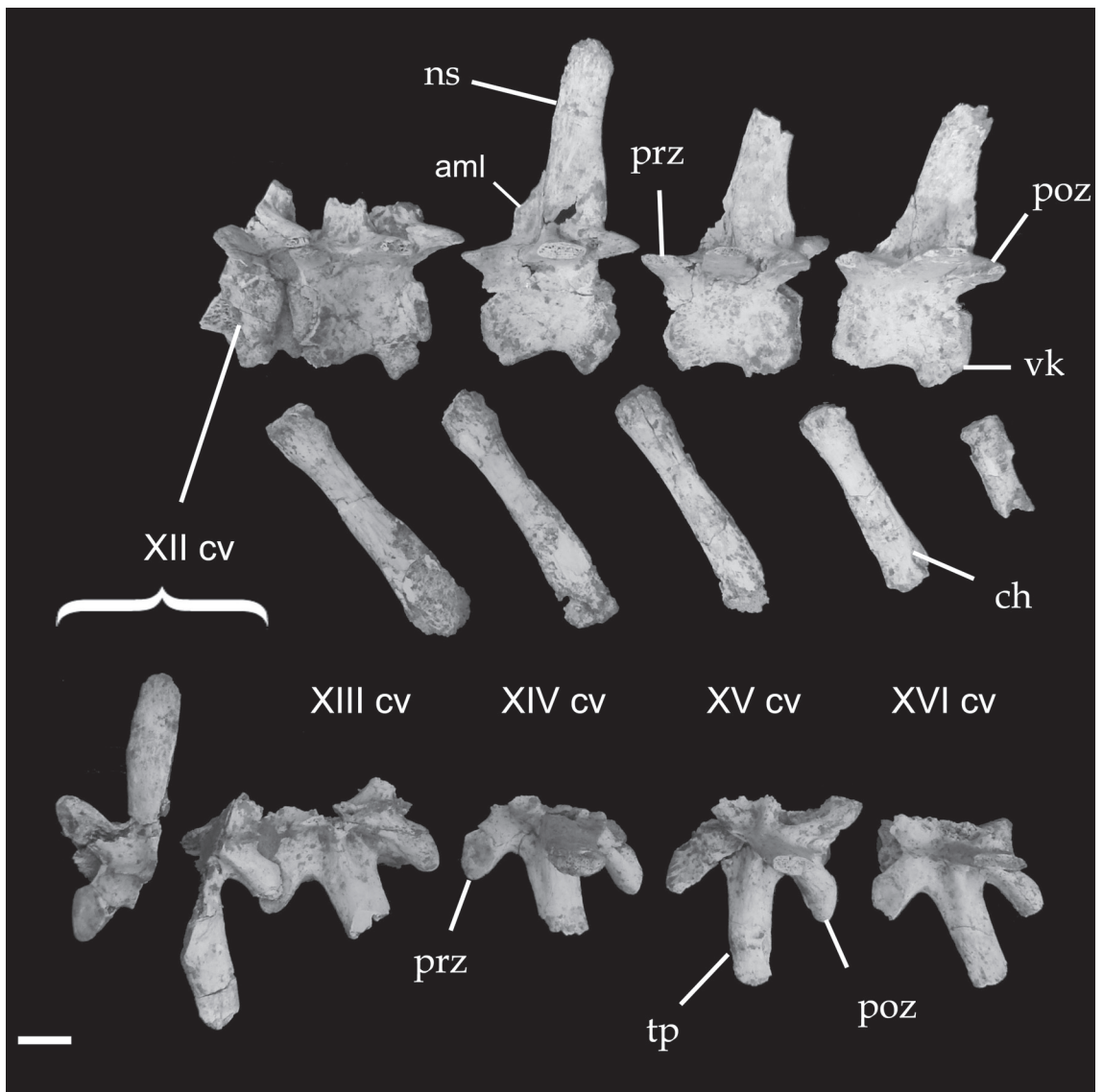


FIGURE 12: 12th to 16th caudal vertebrae of *Baurusuchus albertoi* in left lateral view (above, with chevrons) and dorsal view (below). Abbreviations: aml, anterior medial lamina; ch, chevron; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vk, ventral keel for chevron attachment. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

equal to that of *Mariliasuchus* (MZSP-PV 50). As in all Crocodylomorpha, the scapula is formed by a dorsal and a ventral expansion, separated by a constriction (Pol, 2005). However, the scapula of *B. albertoi* is very different from the pattern present in living crocodiles (Mook, 1921; Meers, 2003) and basal Crocodylomorpha (Colbert, 1952; Wu & Chatterjee, 1993), being much more anteroposteriorly expanded. The dorsal expansion of the scapula is a very thin lamina. A posterodorsal tip divides the dorsal edge from the posterior one. The anterior and dorsal edges form a continuous and convex outline, while the posterior edge is slightly convex, being almost straight. This condition contrasts with the one seen in *Notosuchus*, where an anterior tip and a posterior one form a well-delineated dorsal edge. The middle constriction is well marked anteriorly, contrasting with the condition present in *Notosuchus*. The ventral portion of the scapula is more lateromedially robust, and forms the dorsal part of the glenoid cavity posteriorly. Dorsally to the glenoid surface there is a deep longitudinal groove (Fig. 18). Anterior to the glenoid cavity there

is a flat surface for the coracoid contact, as in most Crocodylomorpha (Wu & Chatterjee, 1993, Wu *et al.*, 2001, Meers, 2003; Pol, 2005). On the lateral side of the right scapula there is an anteriorly placed smooth, convex shallow crest. *Notosuchus* (Pol, 2005) and *Terminonaris* (Wu *et al.*, 2001) show a poorly developed acromial crest, but its presence is not clear in *B. albertoi*.

Humerus

The right humerus of *B. albertoi* is fully preserved, with few signs of compression and fracture. The left humerus lacks the distal end, and the medial portion of the proximal end is damaged in both humeri. The humeri of *B. albertoi* possess the pattern of Archosauria (Romer, 1956), being long and slender, with widening ends, especially the proximal one. In lateral view, the humerus presents a sigmoid shape, since its proximal end is slightly curved backwards and its distal portion directed anteriorly, as in *Notosuchus*

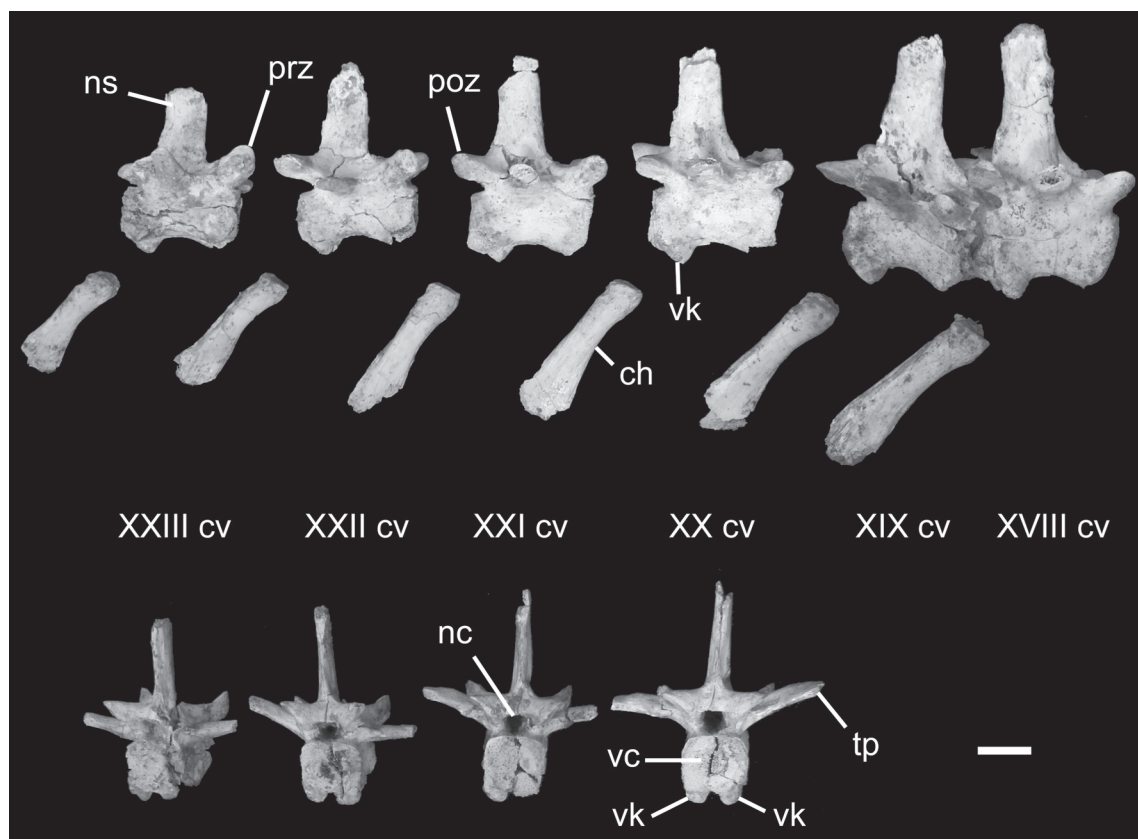


FIGURE 13: 18th to 23rd caudal vertebrae of *Baurusuchus albertoi* in right lateral view (above, with chevrons) and in posterior view (below, except the 19th and 18th vertebrae). Abbreviations: ch, chevron; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vc, vertebral centrum; vk, ventral keel for chevron attachment. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

(Pol, 2005) (Fig. 19). The articulation surface with the glenoid cavity is a marked convexity, lateromedially elongated (as in fossil and living crocodyliforms; Romer, 1956). In posterior view, below the proximal edge of the bone, there is a well-developed circular depression. This depression is present in *Notosuchus*, in *Uruguaysuchus* (Pol, 2005), and in *Chimaerasuchus* (Wu & Sues, 1996), but not as developed in recent crocodiles. The deltopectoral crest is located in the dorso-lateral corner of the humerus (Romer, 1956). The crest expands anteriorly and is lower and more robust lateromedially than in living crocodiles, a condition also present in *Mariliasuchus* (MZSP-PV 50). Distally,

the crest gradually curves medially, disappearing at half of the shaft. The medial surface of the deltooid crest is concave, and the lateral face is convex, rounded, and covered with scars from muscular insertion (Meers, 2003). There is a shallow longitudinal depression posterior to the deltooid crest (Fig. 19) that is absent in living crocodiles. Two small ridges are present in the middle of the shaft: one arising from the ventral edge of the deltooid crest, and the other from the ventral edge of the lateral depression. These ridges are, respectively, the origin ridge to *M. triceps brevis cranialis* and the *linea intermuscularis* between *M. humeroradialis* and *M. brachialis*. Both ridges meet ventrally (Meers, 2003)

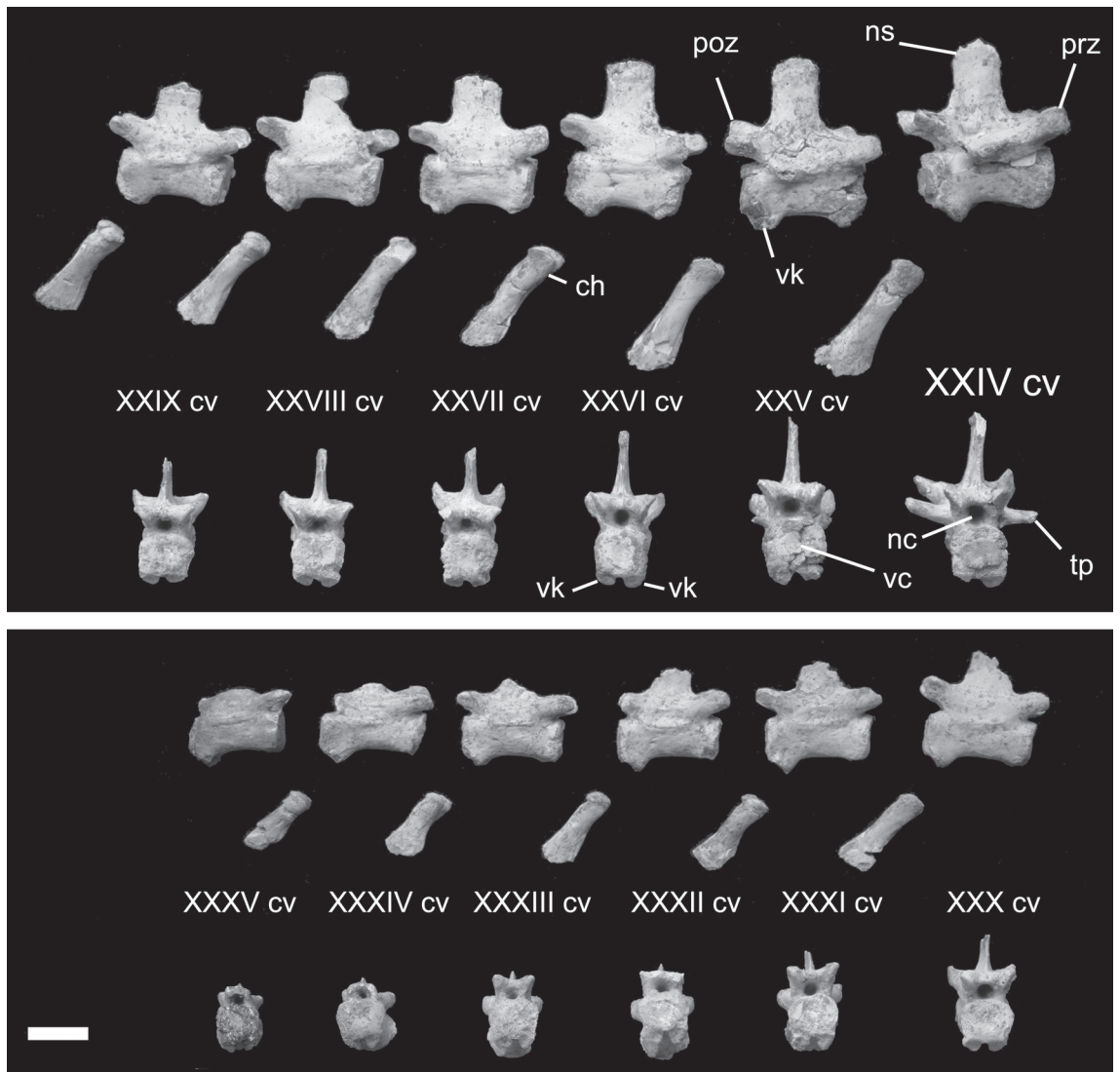


FIGURE 14: 24th to 35th caudal vertebrae of *Baurusuchus albertoi* in right lateral view (above, with chevrons) and in posterior view (below). Abbreviations: ch, chevron; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; vc, vertebral centrum; vk, ventral keel for chevron attachment. Roman numerals indicate the number of the vertebral count. Scale bar = 1 cm.

(Fig. 19). The distal end has a marked anterior concavity, as in living crocodiles. The lateral and medial surfaces of the distal end are broad and flat. The distal end is concave posteriorly, with many longitudinal scars corresponding to muscle attachment, as in *Notosuchus* (Pol, 2005). Despite deformation, the distal end of the humerus of *B. albertoi* is less expanded lateromedially than the same region in living crocodiles. The distal surface is formed by two epicondyles, a posterolateral (*capitellum* – Romer, 1956) and an anteromedial one. The epicondyles are convex, and separated by an intercondylar concavity (*trochlea*).

Ulna

The right ulna of *B. albertoi* is very well preserved, except for the diagenetic medial

compressions present in the proximal end. The lateral shape of the ulna is slightly sigmoid, with the proximal end being anteriorly deflected while the distal end is posteriorly deflected (Fig. 20), a very conservative condition among *Crocodylomorpha* (Mook, 1921; Colbert, 1952; Wu & Sues, 1996; Buckley & Brochu, 1999; Pol, 2005; Vasconcelos, 2006). The proximal region of the ulna is anteroposteriorly expanded and lateromedially compressed, with flat lateral and medial surfaces. The proximal articular surface is concave, and presents a near triangular shape, due to an anterolateral expansion that forms a short and rounded protuberance (Fig. 20) also present in *Caiman niger*. The posterior portion of the proximal end possesses a convex shape, and a bulging lateral morphology, at the attachment of the *M. triceps*. Along the shaft there is a transition from a flat morphology of the lateral and

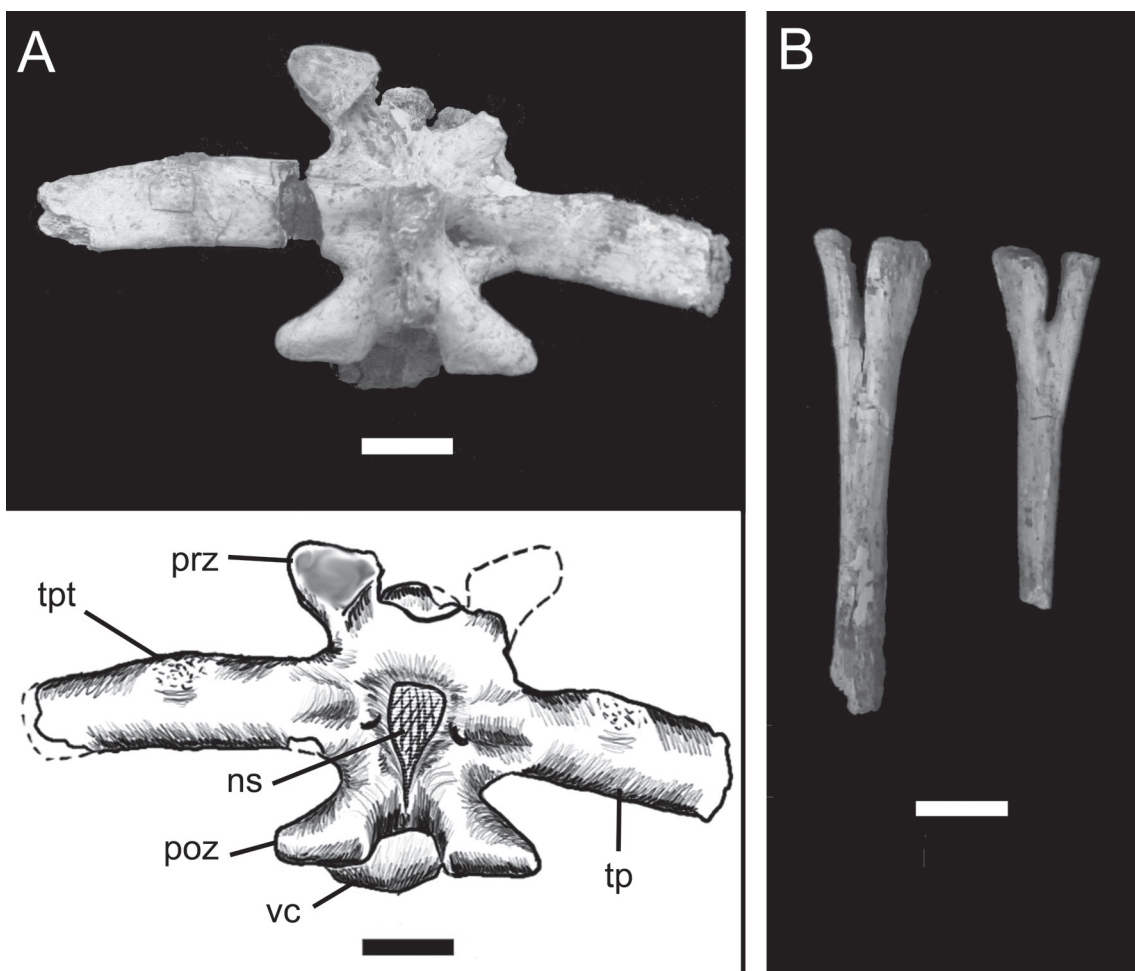


FIGURE 15: 11th caudal vertebra and chevron of *Baurusuchus albertoi*. A, 11th caudal vertebra in dorsal view; B, chevrons from 12th (left) and 15th (right) caudal vertebrae in anterior view. Abbreviations: ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; tpt, transverse process thickness; vc, vertebral centrum.

medial surfaces at the level of the proximal region towards an almost cylindrical cross section at the distal end. The shaft suffers a slightly clockwise rotation in relation to the proximal end. The distal extremity is not perfectly preserved. As in *Notosuchus*

(Pol, 2005), the ulna of *B. albertoi* possesses an anterolateral protuberance at the distal end that fits in the posterodistal concavity of the radius. The distal surface is strongly damaged. Both ulnare and radiale contact the ulna.



FIGURE 16: Ribs of *Baurusuchus albertoi*. From left do right above: left ribs from third and fourth vertebrae. From left to right below: left rib from eighth dorsal vertebrae, left rib from fifth dorsal vertebra, left rib from seventh dorsal vertebra, right rib from ninth dorsal vertebra, and left rib from tenth dorsal vertebra. Abbreviations: apcr, anterior process of cervical ribs; c, capitular area; t, tubercular area. Scale bar = 1 cm.

Radius

The right radius of *B. albertoi* is perfectly preserved. Its general shape is quite similar to that of *Notosuchus* (Pol, 2005) and to the preserved portion (distal) of that of *Chimaerasuchus* (Wu & Sues, 1996). It is an elongated bone with expanded extremities, the diameter of which increases slightly distally (Fig. 21). The proximal end expands lateromedially, as in most Crocodyliformes (Pol, 2005), forming two projections: one anteromedially directed (more proximal), and the other posterolaterally directed (more distal). Below the posterolateral expansion there is a thin longitudinal crest running along the posterior surface of the bone. This crest disappears before the beginning of the shaft, where the anterior portion of the proximal end of the ulna fits. On the anterior surface, immediately ventral to the proximal end, there is a muscle scar, probably from the *M. humeroradialis* insertion (Meers, 2003). The shaft is nearly cylindrical. In distal view, the bone possesses a triradiate shape, with lateral, medial (a little more narrow and longer than the lateral), and anterior projections. Posteriorly, there is a strong concavity, which fits in the anterolateral protuberance of the ulna. The distal articular surface is not perfectly preserved, but it is clear that it was a convex surface fitting in the proximal concavity of the radiale.

Carpals

Baurusuchus albertoi shows the same carpal pattern present in Crocodylia, with three ossified proximal carpals (ulnare, radiale and pisiform) and a distal one (Figs. 22-23) (Mook, 1921; Müller & Alberch, 1990; Rieppel, 1993; Buscalioni *et al.*, 1997). The ulnare and radiale are elongated bones, a synapomorphic condition to Crocodylomorpha (Benton & Clark, 1988) (Fig. 22), being constricted between the enlarged proximal and distal ends.

The proximal end of the radiale is more robust than the distal one. The radiale proximal surface is concave, the articulation area to the radius distal end. The lateral portion of the proximal radiale possesses a big concave and elliptical facet which contacts the ulna. There is no lateral widening, forming a surface to contact the ulnare in *B. albertoi*, opposite to the condition present in *Notosuchus* and many other taxa (*Montsecosuchus*, *Orthosuchus*, *Chimaerasuchus*, and *Sunosuchus*, *apud* Pol, 2005). Nevertheless, this structure is also absent in Crocodylia (Mook, 1921) and in *Sichuanosuchus* (Wu *et al.*, 1997). There is a well marked crest that divides the anterior face longitudinally, as present in *Notosuchus* (Pol, 2005). In *B. albertoi* this crest is wider and more robust than that of *Notosuchus*. The radiale distal end also possesses an elliptical concavity,

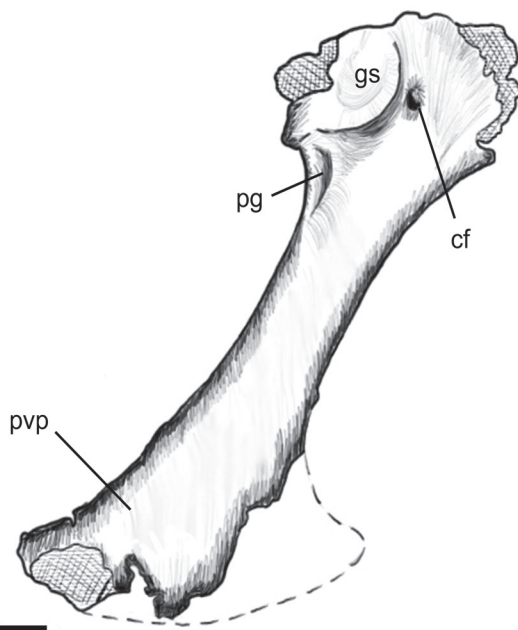


FIGURE 17: Right coracoid of *Baurusuchus albertoi* in lateral view. Abbreviations: cf, big coracoid foramen; gs, glenoid surface; pg, posterior groove; pvp, posteroventral process. Scale bar = 1 cm.

which contacts the proximal ends of metacarpals I and II.

The ulnare is one-third shorter than the radiale, and is significantly more constricted between the proximal and distal expansions in comparison with the radiale. The distal end is more expanded than the proximal end, as in *Notosuchus* (Pol, 2005),

Sichuanosuchus shubanensis (Wu *et al.*, 1997) and in most non-crocodylian crocodyliforms (Pol, 2005). Its proximal extremity contacts the ulna, in a rounded articulation. The distal portion of the ulnare contacts the distal carpal. The distal extremity of the ulnare has a triangular shape due to a narrow anterior prolongation, as in *Uberabasuchus* (Vasconcellos, 2006).

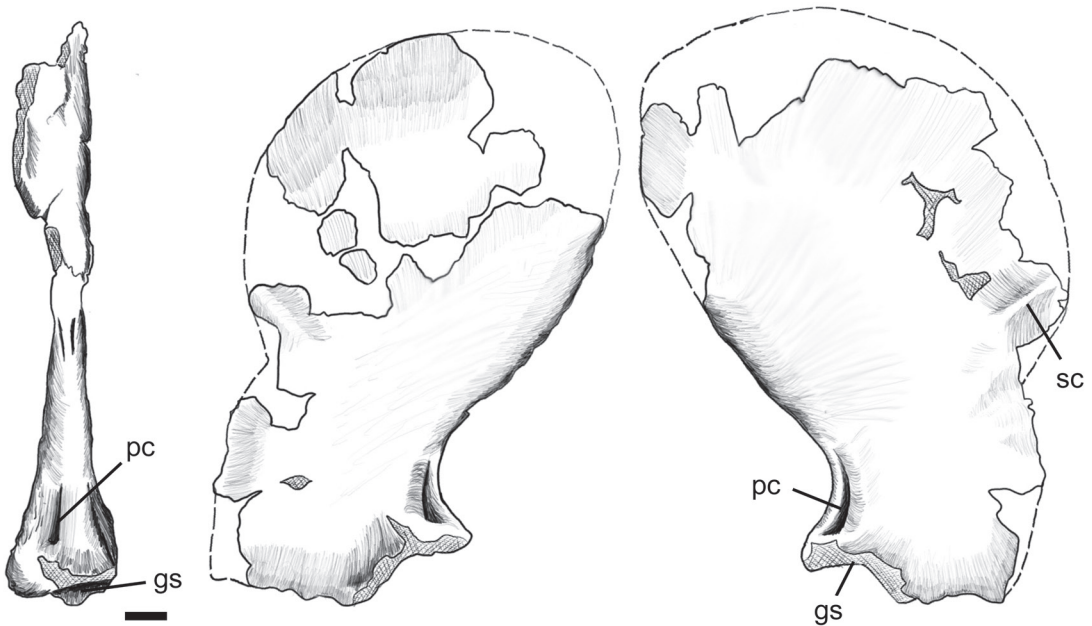
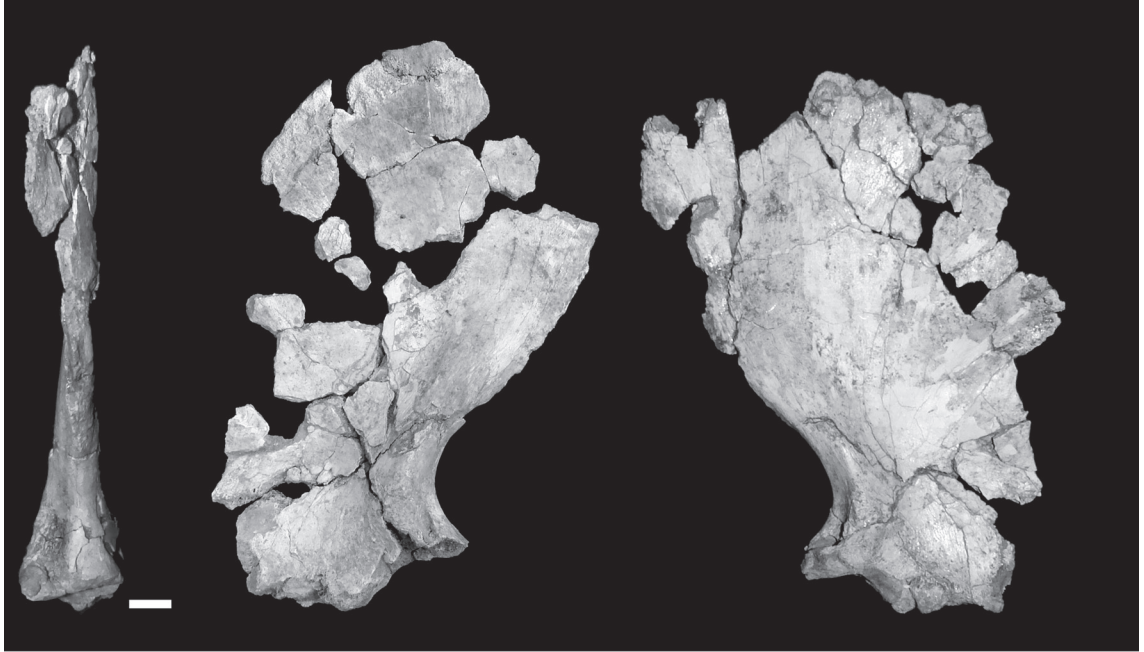


FIGURE 18: Right scapula of *Baurusuchus albertoi* in anterior view (left), left scapula in lateral view (middle) and right scapula in lateral view (right). Abbreviations: gs, glenoid surface; pc, posterior concavity; sc, shallow crest. Scale bar = 1 cm.

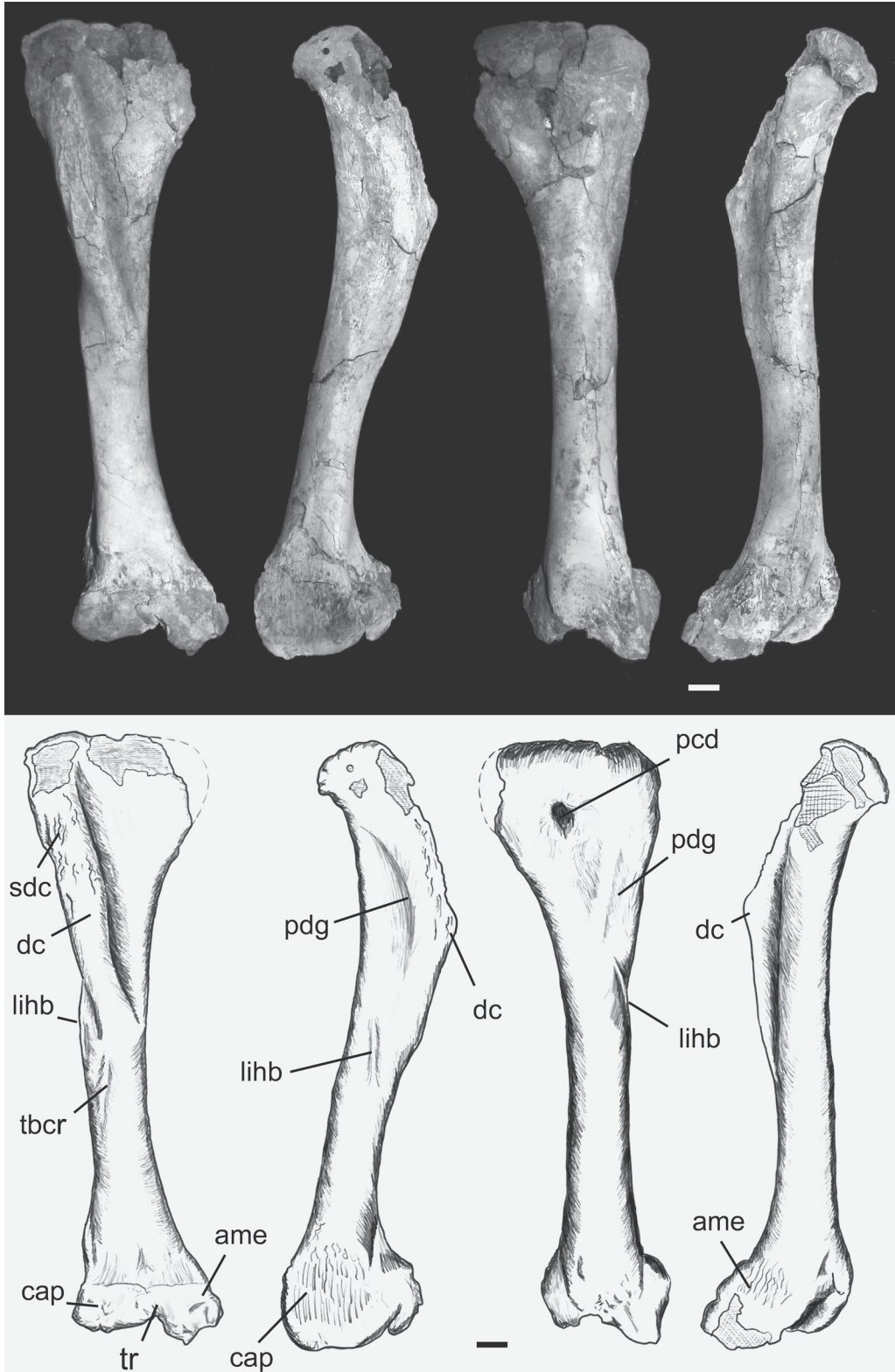


FIGURE 19: right humerus of *Baurusuchus albertoi*, from left to right, in anterior view, lateral view, posterior view and medial view. Abbreviations: ame, anteromedial epicondyle; cap, capitulum (posterolateral epicondyle); dc, deltopectoral (or deltoid) crest; lihb, *linea intermuscularis* between *M. humeroradialis* and *M. brachialis*; pcd, posterior circular depression; pdg, posterior deltoid groove; sdc, scars of *M. deltoideus clavicularis*; tbcrc, *M. triceps brevis cranialis* origin ridge; tr, trochlea. Scale bar = 1 cm.

The bone identified as a pisiform is poorly preserved, probably due its partial cartilaginous nature. It was found contacting the ulnare laterally. The pisiform of *B. albertoi* is compressed lateromedially, which is very distinct from the shape shown by *Caiman crocodylus* (Fig. 23A). Anteriorly, it possesses a surface that resembles a condyle, a feature that is absent in *Crocodylia* (Fig. 23B) and has not been reported in literature yet.

The distal carpal of *B. albertoi* is an oval piece, small and without projections. Its articulation surface with the ulnare is rounded, while its articulation surface with metacarpals possesses three slight concavities: a lateral, a posteromedial, and an anteromedial one. The distal carpal contacts the third, fourth and fifth metacarpals. This tiny bone is almost equal to the one present in *Crocodylia* (Figs. 23C-D). Pol



FIGURE 20: Right ulna of *Baurusuchus albertoi* in lateral view (left) and anterior view (right). Abbreviations: ale, anterolateral expansion; alr, anterolateral protuberance that contacts the radius; ti, triceps insertion area. Scale bar = 1 cm.

(2005) reported the presence of two distal carpals in *Notosuchus*. As in *B. albertoi*, *Protosuchus*, *Alligatorium meyeri*, *Steneosaurus bollensis*, and *Eusuchia* show

only one ossified distal carpal (Colbert & Mook, 1951; Müller & Alberch, 1990; Buscalioni *et al.*, 1997).

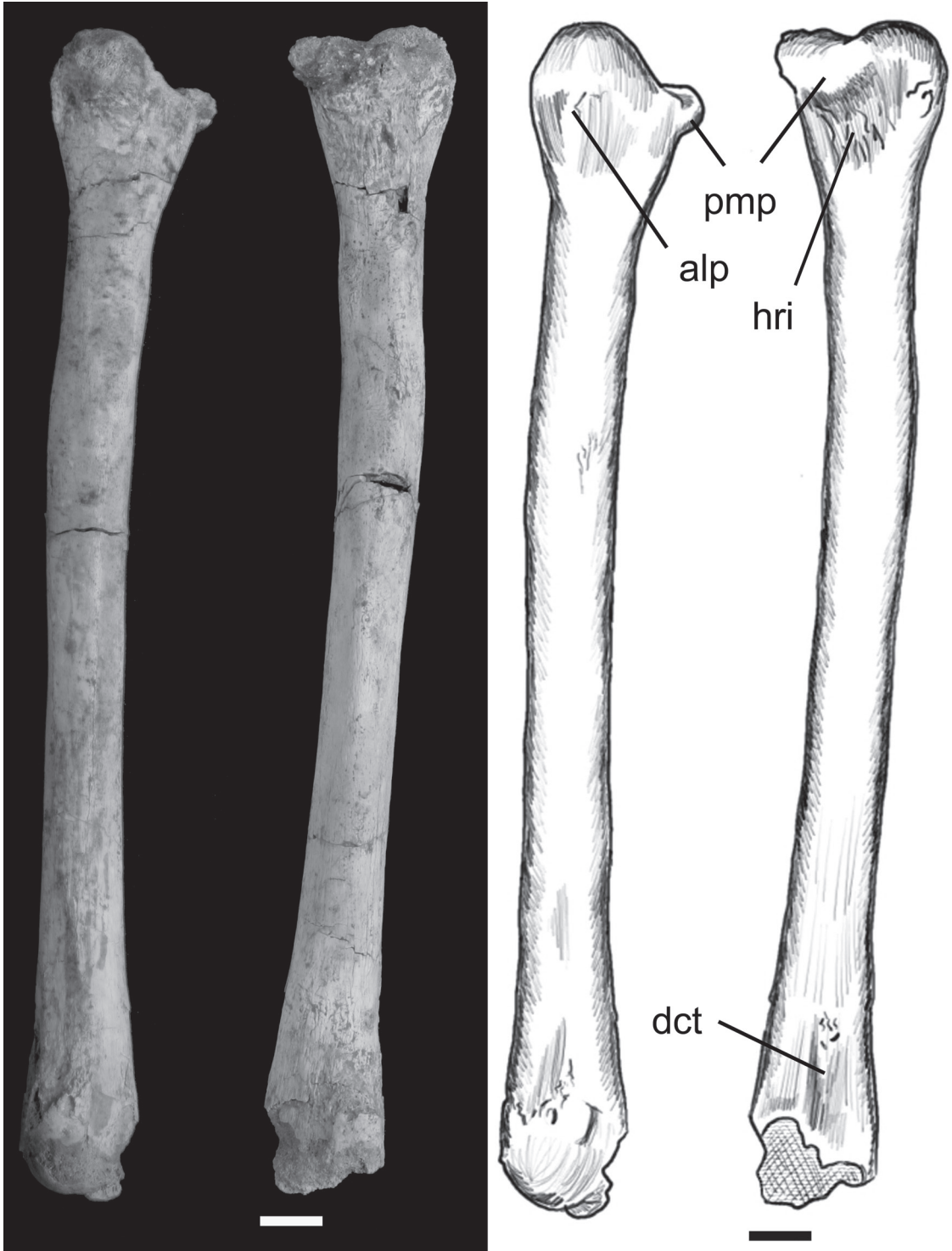


FIGURE 21: Right radius of *Baurusuchus albertoi* in anterior view (left) and in posterior view (right). Abbreviations: alp, anterolateral process; dct, distal concavity to tibia contact; hri, *M. humeroradialis* insertion; pmp, posteromedial process. Scale bar = 1 cm.

Manus

As most Amniota, *Baurusuchus albertoi* maintains five digits in the manus (Romer, 1956) (Fig. 24A). All metacarpals and non-distal phalanges possess a distal widening that forms the area of articulation with the proximal phalanges. This area has a convex surface that is more expanded ventrally than dorsally, and divided in two sections by a dorsoventral groove, a primitive condition in reptiles (Romer, 1956). A circular depression is present laterally and medially to the articular surface, at the attachment of the aponeurosis of *M. interossei (interosseus)* (Meers, 2003) (Fig. 24B).

The metacarpals of *B. albertoi* present an increase in length and a decrease in thickness from the

first to fourth element, being expanded proximally (Romer, 1956). The proximal expansion of the first to fourth metacarpals overlaps the proximal end of the immediately lateral metacarpal. The first metacarpal has a straight medial surface. The fourth metacarpal has a very incipient proximal expansion that is dorsally directed, as in the third metacarpal. Contrary to the other three metacarpals, the fourth stays under the proximal widening of metacarpal V. The fifth metacarpal is thinner and shorter than the others. Its proximal surface is dorsoventrally flat and very wide lateromedially.

The phalangeal formula of the manus of *B. albertoi* is 2-3-4-4-3, the same as in living crocodiles. In the latter, the fourth and fifth digits possess a distal cartilaginous phalanx (Müller & Alberch, 1990).



FIGURE 22: Radiale (left) and ulnare (right) of *Baurusuchus albertoi*. Radiale: A, anterior view; B, lateral view; C, posterior view; D, medial view. Ulnare: E, anterior view; F, lateral view; G, posterior view; H, medial view. Abbreviations: alr, anterior longitudinal ridge; rca, radius contact area; uap, ulnare anterior projection; uca, ulna contact area. Scale bar = 1 cm.

However, the presence of a distal cartilaginous phalanx in *B. albertoi* could not be confirmed. As occurs with the metacarpals, there is a gradual decrease in thickness of the phalanges from the first to the fifth

digit that is more abrupt in the fourth and fifth digits. There is also a decrease in phalangeal length from the proximal to the distal ones. All phalanges (except unguals) present a middle constriction that confers a

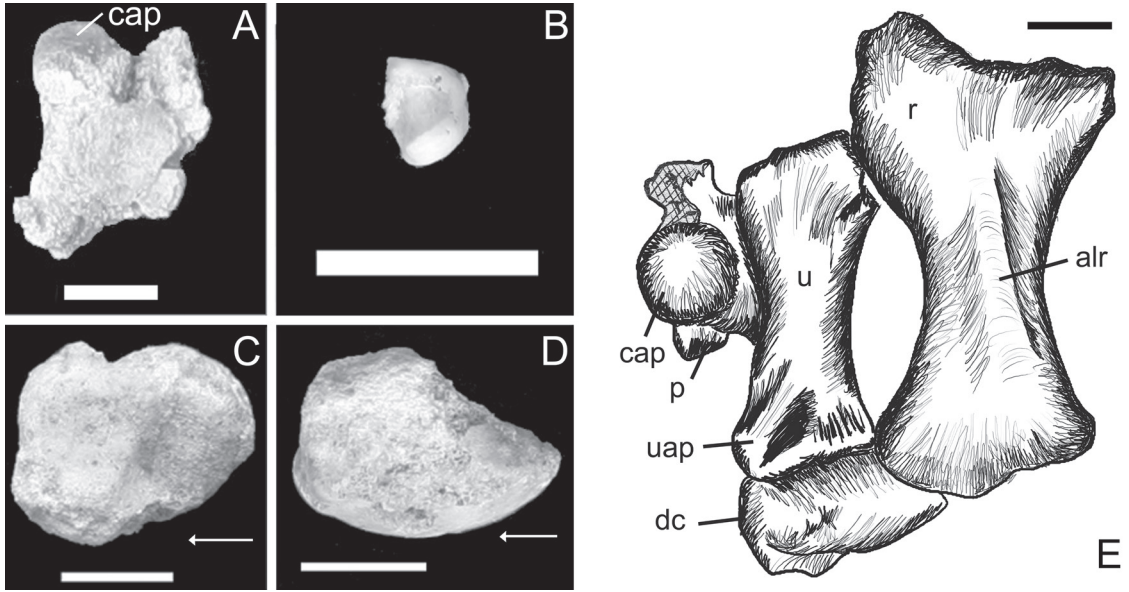


FIGURE 23: Carpal region. A, pisiform of *Baurusuchus albertoi* in medial view; B, pisiform of *Caiman crocodylus* (MZSP 2063) in medial view; C, distal carpal of *Baurusuchus albertoi* in distal view; D, distal carpal of *Baurusuchus albertoi* in ventral view; E, reconstitution of the carpal area of *B. albertoi* in anterior view. Abbreviations: alr, anterior longitudinal ridge of radiale; cap, condylar area of pisiform; dc, distal carpal; p, pisiform; r, radiale; u, ulnare; uap, ulnare anterior projection. Arrows point in anterior direction. Scale bar = 1 cm.

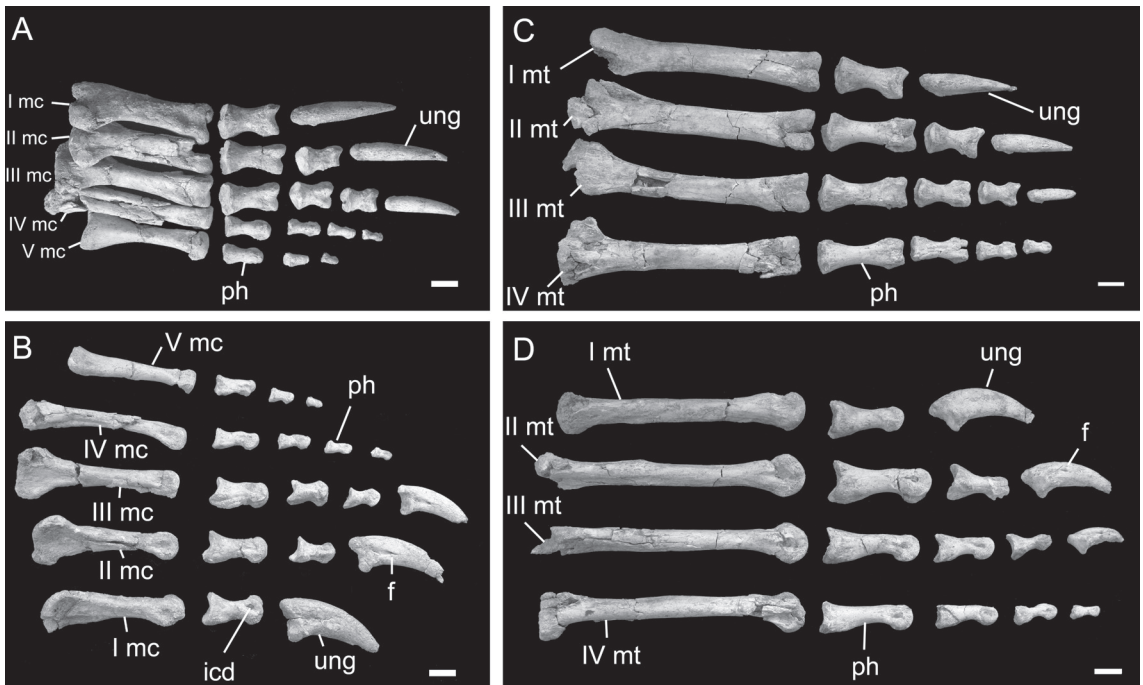


FIGURE 24: Manus and pes of *Baurusuchus albertoi*. A, manus in dorsal view, with metacarpals; B, manus in lateral view; C, pes in dorsal view; D, pes in lateral view. Abbreviations: f, foramen; icd, *M. interossei* circular depression; mc, metacarpal; mt, metatarsal; ph, phalanx; ung, unguinal phalanx. Scale bar = 1 cm.

log-glass shape to these bones. The proximal articulation of all phalanges (except those from fourth and fifth digits, and unguals) form two concavities separated by a dorsoventral crest. This crest is more developed ventrally than dorsally, forming a beak-like structure that limits the ventral digit abduction. The phalanges of the fourth and fifth digits possess simple convex distal surfaces. The first phalanx of the second digit is longer than the same phalanx of the other digits, in contrast with the condition present in *Notosuchus* (Pol, 2005). The terminal phalanges of the fourth and fifth digits are much reduced, with a rounded distal end.

The first three digits possess an unguual phalanx, differing from the condition of *Chimaerasuchus* that has an unguual in the fourth digit (Wu & Sues, 1996). The unguals are lateromedially compressed, ventrally curved, and decrease in size from first to third digits. They possess the articulation surface compound by a middle concave surface, and are limited dorsally and ventrally by convexities. According to Vasconcellos *et al.* (2004), the unguals of Baurusuchidae are more ventrally curved than the ones of Peirosauridae, being very similar to those of living crocodiles and large extant lizards of the genus *Varanus*. The three unguals possess a lateral foramen in their more proximal surface (Fig. 24B). There is a narrow canal that runs from the foramen to the proximal end of the unguual. This canal is very shallow in the first digit unguual.

Pelvic girdle

Only the right ilium and fragments of the right pubis are recognizable in *B. albertoi*. The ilium has a short preacetabular process, a feature that is considered a synapomorphy of Mesoeucrocodylia (Benton & Clark, 1988) (Fig. 9). This part of the ilium is badly preserved, but it is clear that it becomes shorter dorsoventrally, and probably would form an articulation area for the pubis, as in living crocodiles. Posteriorly, there is a wide lateral, deflected supraacetabular crest, that is very developed, as in *Notosuchus* (Pol, 2005) and *Mariliasuchus* (MZSP-PV 50). This wide deflected crest is also present (but less developed) in *Protosuchus* (Colbert & Mook, 1951) and *Mahajangasuchus* (Buckley & Brochu, 1999), but is absent in *Chimaerasuchus* (Wu & Sues, 1996). The supraacetabular crest is dorsally directed in extant forms. The dorsal surface of the ilium is flat, rugose, and lateromedially wide, as in *Notosuchus* (Fig. 9). The acetabular concavity is deep, forming an acetabular roof (as in *Notosuchus*) with many furrows and scars that correspond to the

area of origin of the *M. ilio femoralis* (Romer, 1923). There is a smooth, half-circle shaped surface posterior to the acetabular concavity to contact the femur. This same structure is ventrally deflected in living crocodiles instead of being lateral as in *B. albertoi*. The posteroacetabular process is larger than the anterior one, and bends posterodorsally (as in living crocodiles, but contrary to the condition present in other fossil taxa), forming a robust and nearly spatulated projection that is slightly laterally deflected. This structure is densely grooved and furrowed longitudinally, for muscular attachment connecting the ilium and the tibia (Romer, 1923). These furrows are present in Crocodylia, but not as conspicuous as in *B. albertoi*. Ventrally, the postacetabular process is strongly sutured to the transverse process of the third sacral vertebra. Medially, the ilium is flat and vertical.

The pubis fragment consists in a long cylindrical bone, expanded in one of the extremities (probably the proximal one) and flattened in the other.

Femur

The femur of *B. albertoi* has the typical crocodyliform shape (Romer, 1956), being sigmoidally curved, with the proximal end being anteriorly deflected while the distal end is posteriorly deflected (Fig. 25). The proximal articular surface is convex. The proximal end is compressed lateromedially, with flattened anterolateral and posteromedial surfaces. The medial portion of the proximal end is convex, and forms an articular surface with the acetabular area of the ilium. Below this medial convexity there is a deep concavity with broken edges, probably a diagenetic artifact. The anterolateral facet of the proximal end has many longitudinal grooves formed by the attachment of a well-developed *M. pubo-ischio-femoralis internus* (Fig. 25). Posterior to these scars there is a longitudinal crest, the “largest trochanter” (Riff, 2007), which divides the anterolateral face from the posterolateral one. This crest extends until the first third part of the shaft, when it slightly deflects posteromedially and disappears. The same crest has a much more posterior position in living crocodiles. Beneath the proximal end, there is an abrupt constriction of the shaft. Below this constriction, there is a very developed anterior trochanter, called cranium-medial crest by Riff (2007). This trochanter is rugose, dorsoventrally long and is medially concave (Fig. 25) (see discussion). Posteriorly to this trochanter, in the posteromedial surface, there is a large rugose and convex structure with a middle concavity which corresponds to the area of attachment

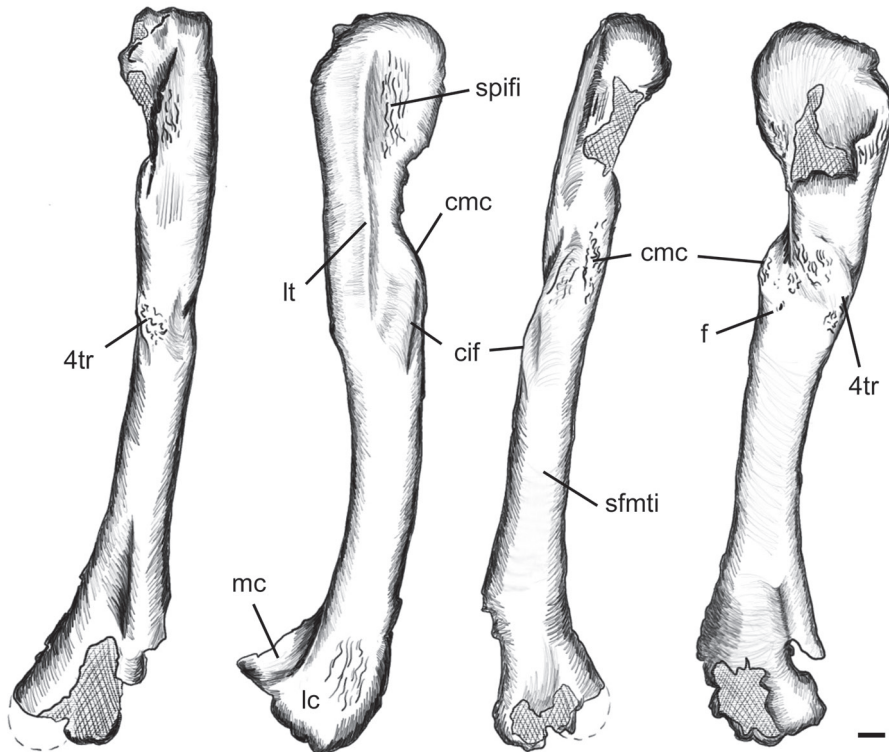
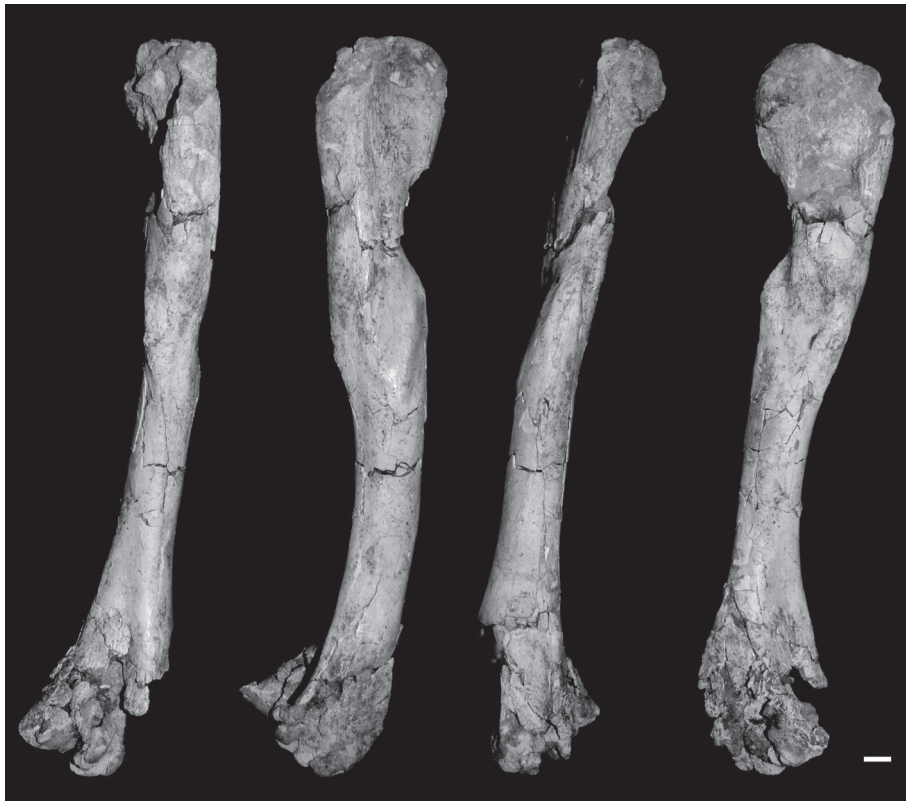


FIGURE 25: Right femur of *Baurusuchus albertoi*, from left to right, in posterior, lateral, anterior and medial views. Abbreviations: 4tr, fourth trochanter; cif, crest for *M. ileo-femoralis* attachment; cmc, cranium-medial crest; f, foramen; lc, lateral condyle; lt, largest trochanter; mc, medial condyle; sfmti, surface to *M. femoro-tibialis internus* attachment; spifi, surface to *M. pubo-ischio-femoralis internus*. Scale bar = 1 cm.

of the *M. caudifemoralis longus*. The fourth trochanter is positioned posteroventrally to this structure, corresponding to an Archosauria synapomorphy (Benton & Clark, 1988). The fourth trochanter is placed more posteriorly in *B. albertoi* than in living crocodiles (Parrish, 1987). A longitudinal crest is present laterally to the fourth trochanter. This crest is more laterally placed, shorter and more robust than the same structure in living crocodiles (Fig. 25). The distal end of the bone has a small counter-clockwise torsion in relation to the proximal end. This torsion orients this portion of the bone in an anteroposterior direction. The distal end is strongly compressed laterally due the diagenetic process, preventing any observation of a fibular condyle, typical of erect forms (Parrish, 1987). There are two distal condyles, with a longitudinal concavity between them (intercondylar fossa).

Tibia

The tibia of *B. albertoi* is a long and medially curved element (Fig. 26). This “bow-shaped” feature occurs in *Mariliasuchus* (MZSP-PV 50) and

Stratiotosuchus (Riff, 2007), but differs from Crocodylia, in which the tibia shaft is straight. The tibia has expanded ends, being the proximal end much more expanded than the distal one. The proximal end is lateromedially compressed, contrasting with the condition found in living crocodiles. The tibia has a long longitudinal crest, the *linea intermuscularis* (Riff, 2007), placed in the proximal portion of the shaft (Fig. 26). This crest is well developed and has a rugose surface, being also present in *Stratiotosuchus* and in *Caiman*. The distal end of the tibia is lateromedially expanded, with an almost cylindrical shape. The anterior and posterior surfaces of the distal end are nearly flat, forming a small lateral projection. The distal articular surface is not preserved. The fibula fits posteriorly into the *linea intermuscularis* of the tibia.

Fibula

The fibula of *B. albertoi* is three times thinner than the tibia and expanded in the extremities (Fig. 27). The proximal end is lateromedially flat, developed in a posteromedial direction, but not as



FIGURE 26: Right tibia of *Baurusuchus albertoi* in posterior view (left), lateral view (middle) and anterior view (right). Abbreviations: li, *linea intermuscularis*. Scale bar = 1 cm.

curved posteriorly as in *Stratiotosuchus* (Riff, 2007). A large, rugose, prominent and dorsoventrally elongated trochanter is evident on the lateral surface of the anterior portion of the proximal end. This structure is called “tuberositas” by Hutchinson (2002), and represents the insertion point of the *M. iliofibularis*. This structure is present in *Mariliasuchus* (MZSP-PV 50) and in living crocodiles, but apparently absent in *Hesperosuchus* (Colbert, 1952). The shaft is cylindrical and slightly compressed lateromedially. The fibular main axis has a slightly developed clockwise torsion near the distal end (as occurs in *Crocodylus acutus*, Mook 1921). The distal end is less expanded than the proximal one, and, as in the tibia, is poorly preserved. The distal end of the fibula contacts the calcaneum and, probably, the astragalus.

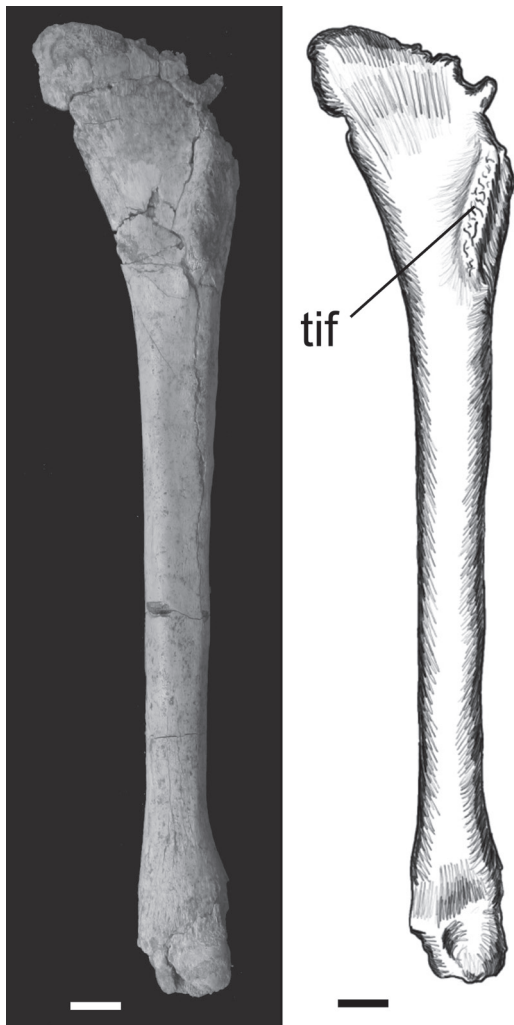


FIGURE 27: Right fibula of *Baurusuchus albertoi* in lateral view. Abbreviations: tif, “tuberositas” to *M. iliofibularis* insertion. Scale bar = 1 cm.

Tarsals

Only the proximal tarsals (astragalus and calcaneum) of *B. albertoi* are described below since the distal tarsals are mostly destroyed. Both calcaneum and astragalus of *B. albertoi* are very similar to that of other Crocodyliformes, with a “normal crocodylian-like” articulation, *i.e.*, with a calcaneum “socket” that articulates with an astragalus “peg-like” structure (Tarsitano, 1982) (Fig. 28). The calcaneum (or fibulare) possesses an anteroposterior constriction in its middle portion. Dorsoanteriorly to this constriction, the calcaneum shows a nearly arrow-point shape. The anterior portion of this “arrow-point” is a flat surface for the articulation with the fourth distal tarsal. Medially to this surface there is a calcaneum “socket”. Posteroventrally to the socket, ventrally limited by the middle constriction, there is a tongue-like projection, which helps in the articulation with the astragalus. Ventrally to the middle constriction the calcaneum expands to form the “tuber”, a big posteroventral projection (considered a crocodylotarsal synapomorphy by Benton & Clark, 1988), that ends in an anteroposteriorly expanded surface, with a very deep longitudinal middle groove. This surface receives the tarsal aponeurosis that connects with the pes flexor muscles and with the distal insertion of *M. gastrocnemius* (Haughton, 1865, Brinkman, 1980). The *B. albertoi* calcaneum tuber is more posteriorly directed than in living crocodiles, making a straight lateral surface, and not concave as in the latter.

The astragalus has approximately the same size of the calcaneum, and possesses an anterior, large, drop-shaped structure similar to a condyle. Its surface is smooth, and forms the articulation area with third distal tarsal and with first and second metatarsals. Dorsally to this structure, there is a concave surface to the tibia contact. Ventrolaterally, there is the “peg-like” structure that articulates with the calcaneum socket. Medially to the “peg-like” process, there is the astragalar trochlea that contacts the calcaneum tongue. Dorsally to the trochlea there is a concave surface, smooth and with two diminute nutrient foramina (Gower, 1996), probably associated to the perforating artery (Serenó, 1991). Immediately dorsal to this articulation structure, there is a deep notch, separating it from a laterodorsal process with a nearly cubic-shaped. The ventral portion is damaged.

Pes

The first four metatarsals are very similar, being longer than the metacarpals. As in metacarpals,

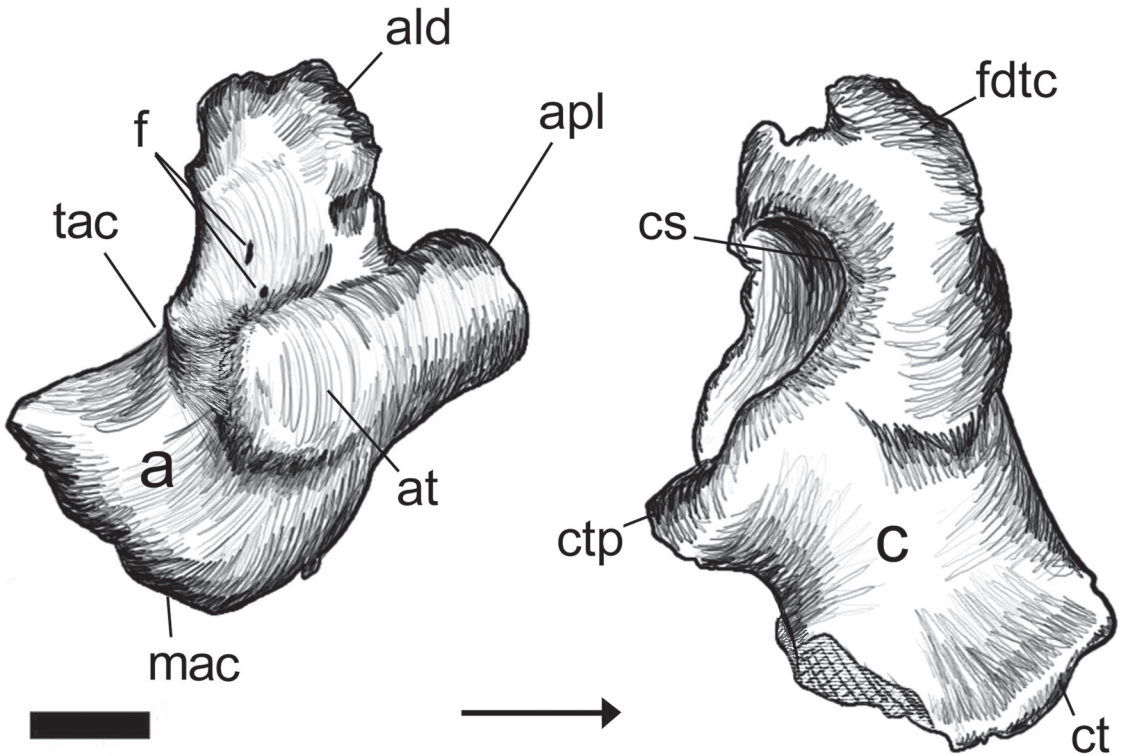
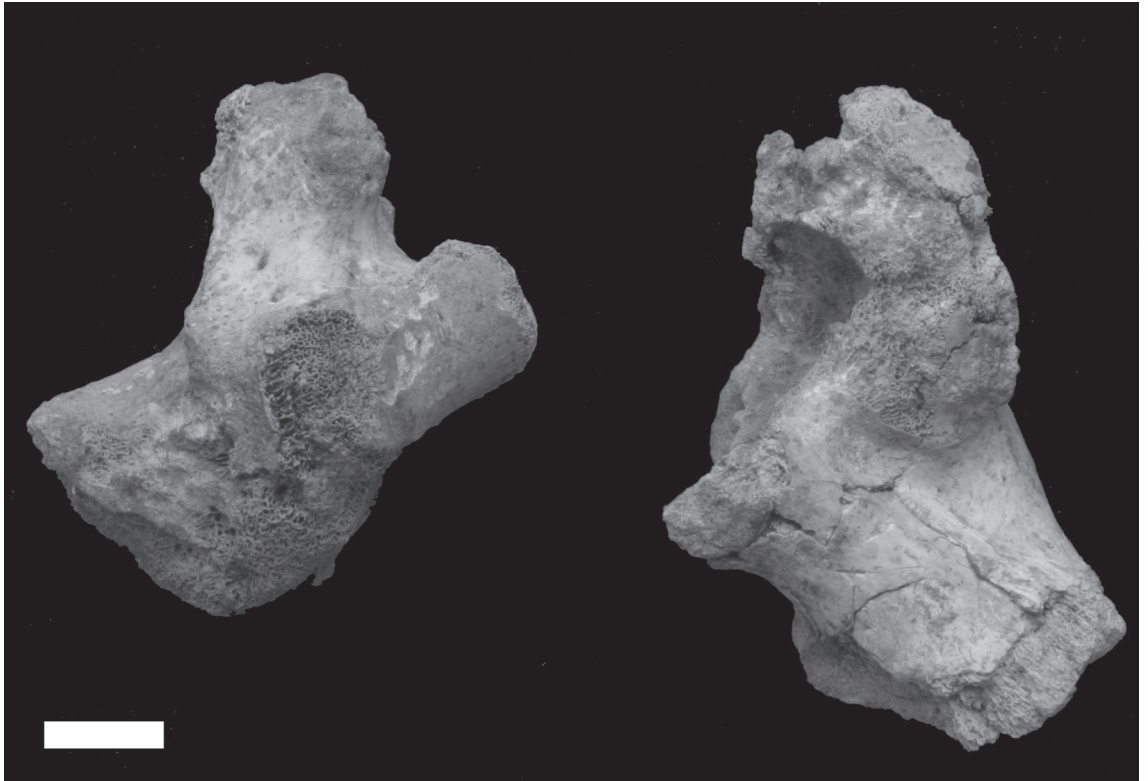


FIGURE 28: Proximal tarsals of *Baurusuchus albertoi*, with the astragalus in anterodorsal view and the calcaneum in anteroventral view. Abbreviations: a, astragalus; ald, astragalus laterodorsal process; apl, astragalus peg-like projection; at, astragalus trochlea; c, calcaneum; cs, calcaneum socket; ct, calcaneum tuber; ctp, calcaneum tongue process; f, foramen associated to perforating artery; fdtc, fourth distal tarsal contact; mac, metatarsals-astragalus contact; tac, tibia-astragalus contact. Arrow points in lateral direction. Scale bar = 1 cm.

the proximal ends are flat and wide, with the lateral widening always overlapping the medial widening of the next metatarsal. The first metatarsal lacks the proximomedial expansion. The metatarsal shaft is elliptical in cross section. Many furrows are present in the distal end, representing scars from the digital flexors and abductor muscles (Haughton, 1865). The metatarsals decrease in thickness from the first to the fourth. The second and third metatarsals are longer than the others (Figs. 24C-D). Only a fragment from metatarsal V was found in *B. albertoi*. The fifth metatarsal is highly modified, as in all Archosauria (Benton & Clark, 1988).

The pes possesses a phalangeal formula of 2-3-4-4-0, as in living crocodiles (Mook, 1921). Living forms also possess a fifth cartilaginous phalanx in the fourth digit (Müller & Alberch, 1990) that cannot be inferred in *B. albertoi*. The fifth digit lost the phalanx in living crocodiles (Brinkman, 1980), and also in *Protosuchus*, *Orthosuchus*, and *Hallopus* (Parrish, 1987). The proximal phalanges are longer than the same phalanges of the manus. The first phalanx of the first digit is shorter than the same phalanx of the other digits. The other phalanges (except unguals) reduce gradually in size and width mediolaterally. The phalanges that contact the unguals possess distal ends with different articulations, these being lateromedially wider and with more gentle convexities than in other phalanges. The terminal phalanx of the fourth digit is small, with a rounded distal end.

The first three digits of the pes possess unguual phalanges that are quite similar to those of the manus, also decreasing in size from the first to the third digit. The articulation is also very similar to those of manus, being slightly stronger laterally. They are very curved claws, with a robust base. The lateral surface of the unguals of the pes also possesses a tiny foramen, as in the unguals of the manus (Fig. 24D). However, these foramina are much reduced in the pes and without the evident posterior canal. The foramen of the first unguual is almost invisible, probably due to diagenetic alterations.

Dermal armor

Two parasagittal rows of osteoderms are present in *B. albertoi*. Many osteoderms were fragmented by diagenesis. Their shape and size vary significantly along the vertebral column. The cervical osteoderms are very tiny, one centimeter long, with dorsal grooves (Figs. 4A, 29). The osteoderms posterior to the scapula are significantly larger than the cervical ones, about three centimeters wide and two centimeters high, growing gradually in size and without imbrication. These osteoderms are elliptical, with a central sagittal crest, which also increases in height gradually, following the vertebral column. The sagittal crest in each osteoderm of *B. albertoi* is very similar to the one present in the osteoderms of the midtrunk of

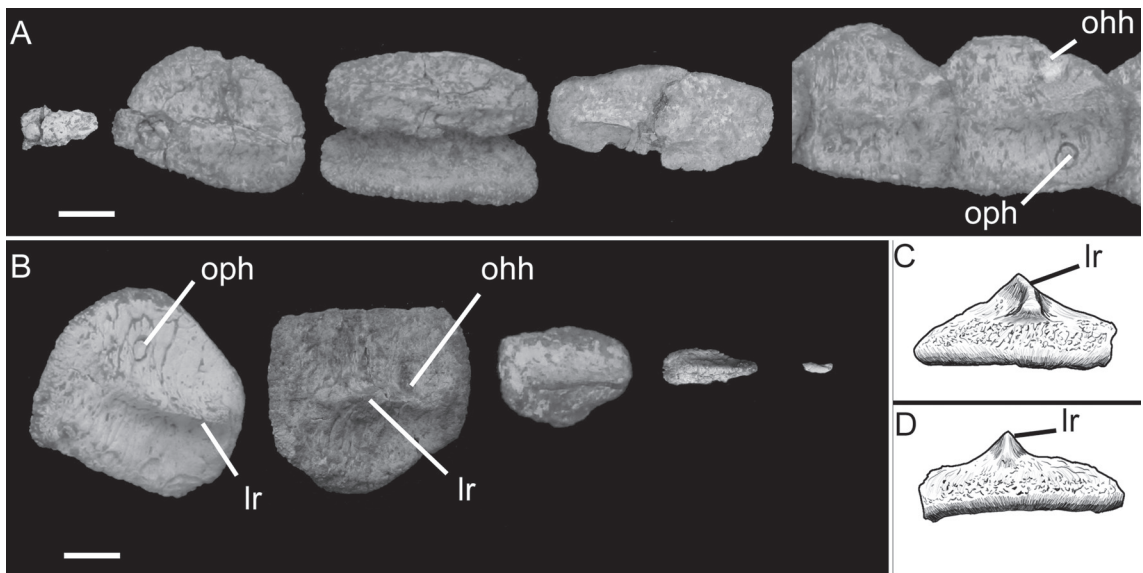


FIGURE 29: Osteoderms of *Baurusuchus albertoi*. A, from left to right, the scapular osteoderm, an anterior trunk osteoderm, a posterior trunk osteoderm, a sacral osteoderm, and two anterior caudal osteoderms, showing imbrications; B, from left to right, caudal osteoderms, showing decrease in size. The rightmost one is the last osteoderm found; C, caudal osteoderm in anterior view; D, the same osteoderm in posterior view. Abbreviations: lr, longitudinal ridge; ohh, osteoderm with an unfilled hole; oph, osteoderm with a filled hole. Scale bar = 1 cm.



FIGURE 30: Gastrolith. Scale bar = 1 cm.

Alligator mississippiensis (Hill & Lucas, 2006) and to the few osteoderms known from *Notosuchus* (Pol, 2005). The caudal osteoderms are clearly the larger and thicker ones in the dermal armor of *B. albertoi* (Figs. 29C-D). They are imbricated, with each osteoderm being overlapped by the preceding one (Fig. 29), as in *Notosuchus* (Pol, 1999) and most crocodyliforms. This condition does not occur in *Marilia-suchus* (MZSP-PV 50). The shape of the caudal osteoderms forms a “D” in the first caudals, changing to an almost pentagonal shape in the posterior half of the tail. In the more posterior portion of the tail, the osteoderms begin to decrease in size, maintaining a sagittal crest. The most posterior osteoderm found is one-half centimeter wide. Ventrally, all osteoderms are straight or slightly concave. The dorsal and ventral surfaces of the osteoderms have a micro-texture interlaced as a mesh, similar to that present in some fossil Eusuchia (Hill & Lucas, 2006) or anchilosaurid dinosaurs (Scheyer & Sander, 2004). The dorsal ornamentation of the osteoderms is also made of many transversally oriented irregular furrows. This pattern of furrows is very similar to the one present in *Notosuchus* (Pol, 2005) and *Marilia-suchus*, but very different from the condition found in the Peirosauridae

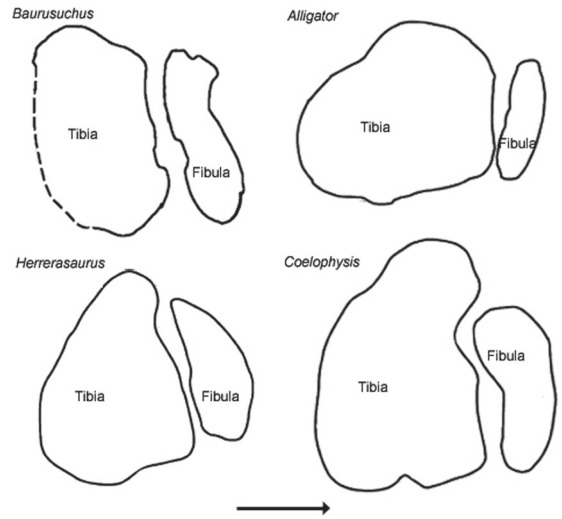


FIGURE 31: Tibia and fibula of *Baurusuchus albertoi*. A, tibia and fibula in proximal view from *Baurusuchus albertoi*, *Alligator*, *Herrerasaurus*, and *Coelophysis* (modified from Hutchinson, 2002). Arrow points to lateral direction. Scale bar = 1 cm.

and neosuchians, in which furrows are substituted by deep pits (Vasconcellos, 2006).

Several caudal osteoderms show rounded cavities in their dorsal surface (Fig. 29), with some filled by osteological material (Fig. 29). Avilla *et al.* (2004) suggested that these cavities could represent bite marks due to predation or intraspecific competition, as observed in living crocodiles.

Gastrolith

A small, smoothed gastrolith was found associated with *B. albertoi*. It is about 1,5 to 3 centimeters in length, gray, and has a distinct constitution from that of the surrounding sedimentary matrix (Fig. 30). This stone, quite similar to a river pebble, was found immediately anterior to the pubis, ventrally to dorsal vertebrae XII and XIII. Ventrally to this stone, were some gastralia fragments. Vasconcellos *et al.* (2008) noticed the occurrence of gastroliths in other crocodile fossils from General Salgado, showing that *B. albertoi* is not an isolated case.

DISCUSSION

Several authors already stressed the marked differences in the locomotion pattern of living crocodiles and their extinct relatives (Colbert & Mook, 1951; Parrish, 1987; Carrano, 1999; Hutchinson, 2002; Pol, 2005; Riff, 2007). One of the most conspicuous

distinctions relates to body posture, with baurusuchids showing several morphological features that suggest an erect posture. The long cervical neural spines of *B. albertoi* are noticeable when compared to the relatively short condition of Crocodylia. This feature is also present in *Notosuchus* (Pol, 2005), *Mahajangasuchus* (Buckley & Brochu, 1999) and *Mariliasuchus* (MZSP-PV 50), but in *Baurusuchus* the cervical neural spines are more elongated in relation to the body vertebrae. A similar condition to the one present in *Baurusuchus* is also visible in *Dibothrosuchus elaphros* (Wu & Chatterjee, 1993). The combination of elongated cervical neural spines, enlarged zygapophyses, and separated prezygapophyses would allow for marked dorsoventral cervical movements (Pol, 2005), suggesting that *B. albertoi* must have had an upright way of life, with the head far up from the ground. Another peculiar feature of the Baurusuchidae, present in *B. albertoi*, is the laterodorsal orientation of the sacral transverse processes. This feature corresponds to the presence of a unique type of muscle attachment, not seen in living and other fossil forms, and might be associated with the presence of an erected posture. However, more comparative and biomechanical analyses are needed in order to clarify this point of Baurusuchidae anatomy.

The deltopectoral crest of the humerus of *B. albertoi* is quite distinct from the one present in Crocodylia. The wide lateral and medial surfaces of the deltopectoral crest of extant crocodiles receive several muscles responsible for the adduction and abduction of the humerus (Meers, 2003). On the other hand, this type of supination of the forelimbs in Crocodylia was not so relevant in Baurusuchidae, as suggested by the wider anterior and straighter lateral and medial surfaces of the humerus of *B. albertoi*, being indicative of a constant erect walk in the latter.

The presence of a laterally developed supra-acetabular crest of the ilium in *B. albertoi* also corroborates a parasagittal position of the hindlimbs. According to Parrish (1987), a supra-acetabular crest is present only in taxa that retain an erect position (e.g., *Protosuchus*, *Notosuchus*, *Mahajangasuchus*), by providing a different point of attachment to the muscles *Mm. ilio femoralis* and *ilio tibialis*.

Additional evidence indicating a cursorial way of life is also present in the femur of *B. albertoi*. Its femur possesses a more posteriorly positioned 4th trochanter that increases the use of the caudofemoralis muscles responsible for pulling it back, in addition to a well developed cranio-medial crest (Riff, 2007) for the *M. pubo-ischio-femoralis internus* that maintains the medial portion of the femur near the body.

The proximal end of the tibia is expanded anteroposteriorly instead of being rounded as in extant crocodiles (Hutchinson, 2002), a morphology comparable to the condition found in the cursorial theropod dinosaurs (Fig. 31).

The calcaneum tuber of *B. albertoi* is posterolaterally deflected, being similar to other cursorial forms of Archosauria that possess a calcaneum tuber parallel to the limb axis and perpendicular to the vertebral column (Parrish, 1987).

All the postcranial features listed above support the view that *Baurusuchus albertoi* had an erect posture, suggesting also that all members of the family Baurusuchidae were more cursorial than other Crocodyliformes. More detailed studies of the postcranial anatomy of other Crocodyliformes would certainly help clarify the paleoecological role of the Baurusuchidae and other Gondwanic Cretaceous crocodiles.

RESUMO

O presente trabalho descreve uma espécie nova de Baurusuchidae proveniente de sedimentos do Cretáceo Superior da Bacia Bauru, no Estado de São Paulo, fornecendo a primeira descrição de um esqueleto pós-craniano completo para a família. Muitas características pós-cranianas da nova espécie estão presentes em outros táxons de Notosuchia gondwânicos e são, desta forma, consideradas plesiomórficas para o gênero. Entre estas se destacam: espinhas neurais cervicais muito longas; três vértebras sacrais; crista deltopectoral do úmero robusta; porção proximal do radiale com grande área de contato para a ulna; ulnare com projeção anterior distal; crista supra-acetabular bem desenvolvida lateralmente; processo pós-acetabular póstero-dorsalmente direcionado; presença de uma crista crânio-medial no fêmur; quarto trocânter do fêmur em uma posição posterior; diáfise da tibia lateralmente curvada; tubérculo do calcâneo orientado póstero-ventralmente; osteodermas ornamentados com sulcos e imbricados na região caudal. Contudo, alguns caracteres são inéditos, sendo ausentes nas demais famílias de Crocodyliformes. Estes são: processos transversos das vértebras sacrais direcionados dorsolateralmente; presença de uma crista longitudinal na superfície lateral das vértebras sacrais; presença de uma superfície semelhante a um côndilo no carpal pisiforme. A maioria destas características corrobora um padrão de locomoção cursorial para a espécie descrita neste trabalho, e para a família Baurusuchidae.

PALAVRAS-CHAVE: Cretáceo Superior; Baurusuchidae; *Baurusuchus*; Morfologia; Pós-crânio.

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