

First abelisaurid bone remains from the Maastrichtian Marília Formation, Bauru Basin, Brazil

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Abstract

Bones of abelisaurid theropods from the Upper Cretaceous (Maastrichtian) Marília Formation, Bauru Basin, Brazil, are here described. They are a dorsal vertebra, the distal part of a femur, and a pedal phalanx corresponding to three specimens found in different fossil sites of Uberaba County, Minas Gerais State. These specimens are the first abelisaurid bones from Uberaba County and thus verify the presence of these theropods, previously indicated only by isolated teeth. The new discoveries, together with that of the abelisaurid *Pycnonemosaurus* found elsewhere in the Bauru Basin, indicate that these theropods were the most common large predatory dinosaurs in South America during the Cretaceous. The assemblage of abelisaurid theropods and titanosaurid sauropods in the Maastrichtian beds of Brazil is congruent with that documented in same-aged beds of Patagonia.

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1. Introduction

Abelisaurid theropods constitute a distinctive lineage of predatory dinosaurs that were abundant and diverse on the Gondwanan continents during most of the Cretaceous period. As far as South America is concerned, abelisaurid remains have frequently been discovered in Patagonia (southern

Argentina), providing the most complete source of anatomical and biostratigraphical data on the phylogeny of the clade (e.g., Novas et al., 2004).

In contrast, the record of these theropods in other regions of South America has remained poor until recently: excavations in the Cretaceous beds of different localities of the Bauru Basin, southeastern Brazil, have resulted in the discovery of several bones and teeth which not only extend the geographical distribution of abelisaurids within South America, but also increase the taxonomic diversity of the group. Reports of abelisaurids from Brazil currently consist of isolated occurrences in two sedimentary units of the Bauru Group, namely the Adamantina (Turonian–Santonian) and Marília (Maastrichtian) formations. The first mention of an abelisaurid from the Bauru

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Basin was by Bertini (1996), who announced the discovery of a fragmentary premaxilla and an isolated tooth collected in São Paulo State, in beds of the Adamantina Formation, but without offering detailed images and descriptions of this material. From an undifferentiated unit of the Bauru Group (either the Adamantina or Marília formations), cropping out at Mato Grosso State, Kellner and Campos (2002) (see also Bittencourt and Kellner, 2002) described the first named abelisaurid from Brazil, *Pycnonemosaurus nevesi*, on the basis of several skeletal elements (i.e., teeth, tibia, pubis, caudal vertebrae). Teeth referred to Abelisauridae have been reported by Candeiro (2002) and Candeiro et al. (2004, 2006a,b) from different localities in the Bauru Basin.

Thanks to the efforts of the late Llewellyn Ivor Price, and more recently due to the sustained work carried on by the personnel of the Centro de Pesquisas Paleontológicas, Peirópolis, abundant and well preserved reptile remains have been collected in Peirópolis, Minas Gerais State. This area has yielded large numbers of titanosaurid bones, some found in partial articulation (e.g., Powell, 2003; Campos et al., 2005; Kellner et al., 2005), as well as beautifully preserved crocodyliforms (Carvalho et al., 2004, 2005) and turtles (França and Langer, 2005). Nevertheless, theropod bones and teeth are much less abundant and more incomplete than other members of this faunal assemblage. From the Peirópolis fossil site we have recently reported an isolated ungual of a maniraptoran theropod resembling elmisaurids (Novas et al., 2005). Here we describe three abelisaurid bones discovered in different quarries in the vicinity of Peirópolis, thus enlarging the list of dinosaur taxa recorded in this area. Aside from being the first abelisaurid bones from Peirópolis, these specimens reveal interesting anatomical details not identified or considered in depth in previous papers on these theropod dinosaurs.

Institutional abbreviations: CPP, Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”, Peirópolis; GSI, Geological Survey of India, Kolkata; MACN, Museo Argentino de Ciencias Naturales, Chubut Collection, Buenos Aires.

Systematic nomenclature: Following Padian et al. (1999), Rauhut (2003), Wilson et al. (2003), and Sereno et al. (2004), we employ the term Ceratosauria for the stem-grouping of all neotheropods more closely related to *Ceratosaurus* than to Neornithes, thus Ceratosauria includes the Abelisauoidea. Furthermore, we follow Holtz (1994) and Rauhut (2003) in considering Abelisauoidea as the stem-based clade that includes all ceratosaurs more closely related to *Carnotaurus* than to *Ceratosaurus*, thus *Elaphrosaurus bambergi* is a member of this clade (Rauhut, 2003). Following Wilson et al. (2003) and Sereno et al. (2004), Coelophysoidea is considered the sister group of Ceratosauria + Tetanurae (= Spinosauoidea + Coelurosauria + Carnosauria).

2. Geology and palaeoenvironmental setting

The Bauru Basin comprises an area of 370,000 km², partially covering the Brazilian states of São Paulo, Paraná,

Mato Grosso do Sul, Minas Gerais and Goiás (Fig. 1). The basin developed during the rifting apart of South America and Africa in the Late Cretaceous, and was infilled by fluvial and lacustrine deposits which overlay the basalts of the Serra Geral Formation (Fernandes and Coimbra, 1996, 1999).

The age of the Bauru Basin sediments (Caiuá Group and Bauru Group) ranges from Aptian to Maastrichtian (Fig. 2; Fulfaro et al., 1994). The Bauru Group was divided by Fernandes and Coimbra (1996) into three formations which from bottom to top are Adamantina, Uberaba and Marília. The Adamantina Formation (Turonian-Santonian age; Castro et al., 1999; Dias-Brito et al., 2001) is a sequence of fine sandstones intercalated by mudstones, siltstones and clayish sandstones (recently, the lowermost part of this unit was redefined as the Araçatuba Formation by Batezelli et al., 1999). The overlying Uberaba Formation (Coniacian–Santonian) is composed of fine greenish sandstones interbedded by siltstones, coarse sandstones, mudstones and volcanoclastics. The uppermost Marília Formation is made up of a sequence of coarse to conglomeratic sandstones, mudstones and carbonate layers (e.g., Soares et al., 1980). Based on microfossils, the age of the Marília Formation is considered to be Maastrichtian (Dias-Brito et al., 2001).

In the Uberaba region (Minas Gerais State), the Marília Formation is subdivided into the Ponte Alta and Serra da Galga members. The Ponte Alta Member is made up of coarse sandstones, conglomerates and breccias associated with impure carbonates. The Serra da Galga Member is composed of fine to coarse-grained sandstones, associated with conglomerates in fining-upwards cycles. Carbonate cements sometimes produce caliche levels in both units. The fossils found in the Marília Formation are charophyte gyrogonites, pteridophyte sporocarps, freshwater molluscs (gastropods and bivalves), conchostracans, invertebrate ichnofossils, dinosaur eggs, coprolites, and a variety of vertebrate remains such as fish scales, frog bones, turtles, lizards, crocodylomorphs and dinosaurs (Petri, 1955; Price, 1955; Estes and Price, 1973; Báez and Perí, 1989; Mezzalana, 1980; Campanha et al., 1992; Senra and Silva e Silva, 1999; Magalhães Ribeiro and Ribeiro, 1999; França and Langer, 2005; Carvalho et al., 2004, 2005; Campos et al., 2005; Kellner et al., 2005; Novas et al., 2005).

The theropod fossils described herein were excavated in the municipality of Uberaba, in the Serra da Galga Member of the Marília Formation. They were discovered adjacent to the National Road BR-050 and at the Serra do Veadinho outcrops. On outcrops lying on the side of National Road BR-050 we discovered an isolated abelisaurid vertebra (CPP 893). From one fossil locality at Serra do Veadinho (“outcrop 1”) an abelisaurid pedal phalanx (CPP 692) was found in association with remains of the crocodylomorphs *Itasuchus jesuinoi*, *Peirosaurus tormini*, and *Uberabasuchus terrificus* (Price, 1955; Carvalho et al., 2004), the titanosaurid sauropods *Trigonosaurus pricei* and *Baurutitan britoi* (Campos et al., 2005; Kellner et al., 2005), and a manual ungual phalanx of an elmisaurid-like maniraptoran (Novas et al., 2005). Another fossil locality on the same hill (“outcrop 2” of Serra do Veadinho) yielded a partial abelisaurid femur (CPP 174) found in the same level

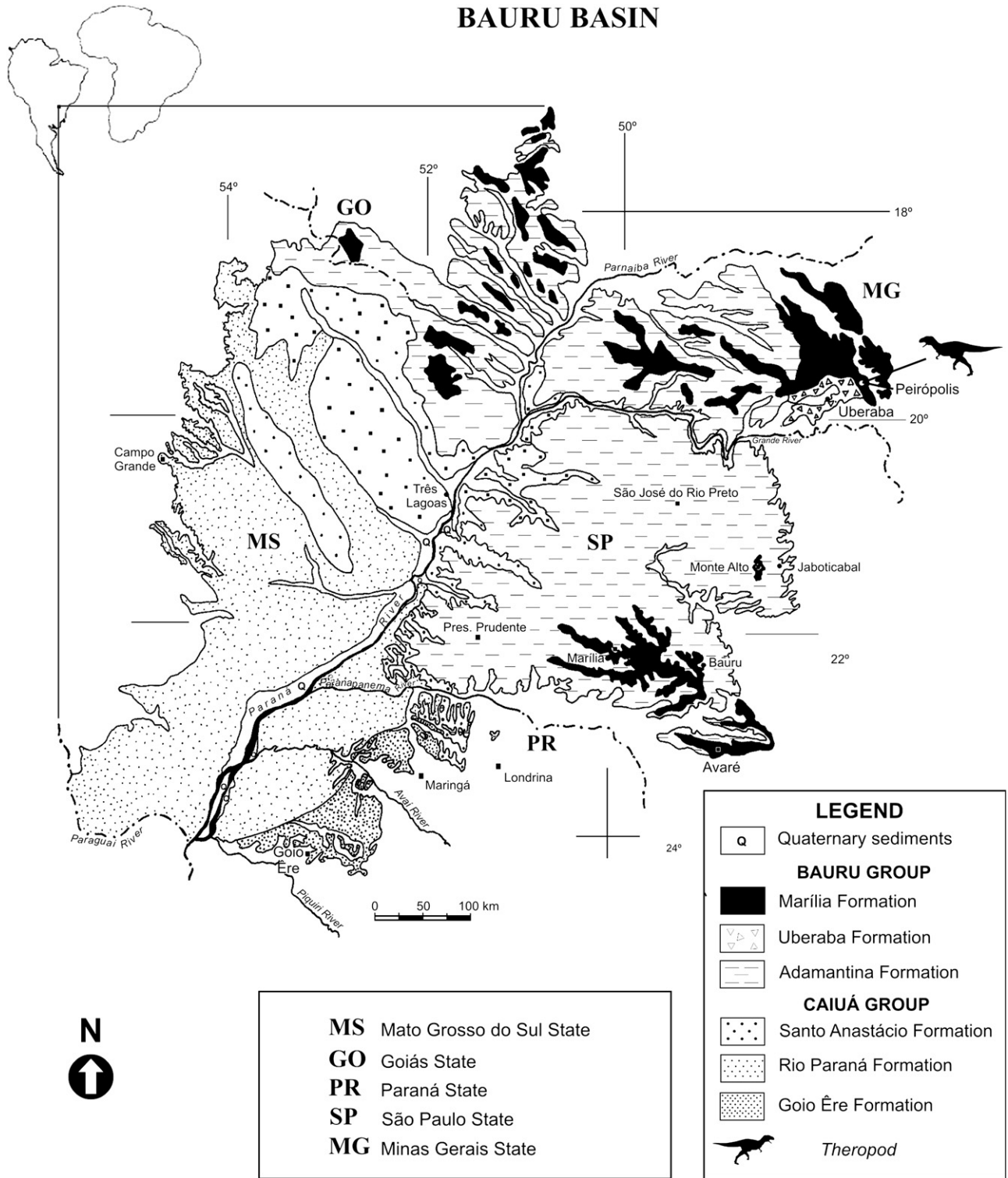


Fig. 1. Geological map of the Bauru Basin with the location area of Peirópolis, Uberaba County (modified from Fernandes and Coimbra, 1996).

as the turtle *Cambaremys langertoni* (França and Langer, 2005).

The Serra da Galga deposits exposed both at Serra do Veadinho and National Route BR-050 are composed of carbonate-rich sandstones associated with impure limestones, overlain by coarse to conglomeratic sandstones and fine sandstones interbedded with clayish sandstones. The dominant geometry of

the strata is tabular, although cross-bedding and planar cross-stratification are also common. There are fining-upwards cycles finished by fine quartz-rich sandstones with planar cross-stratification. Interbedded are pelites, clayish sandstones and coarse sandstones, with mud intraclasts. The fossils found in these successions generally consist of non-articulated bones and bone fragments, which are associated with mud intraclasts

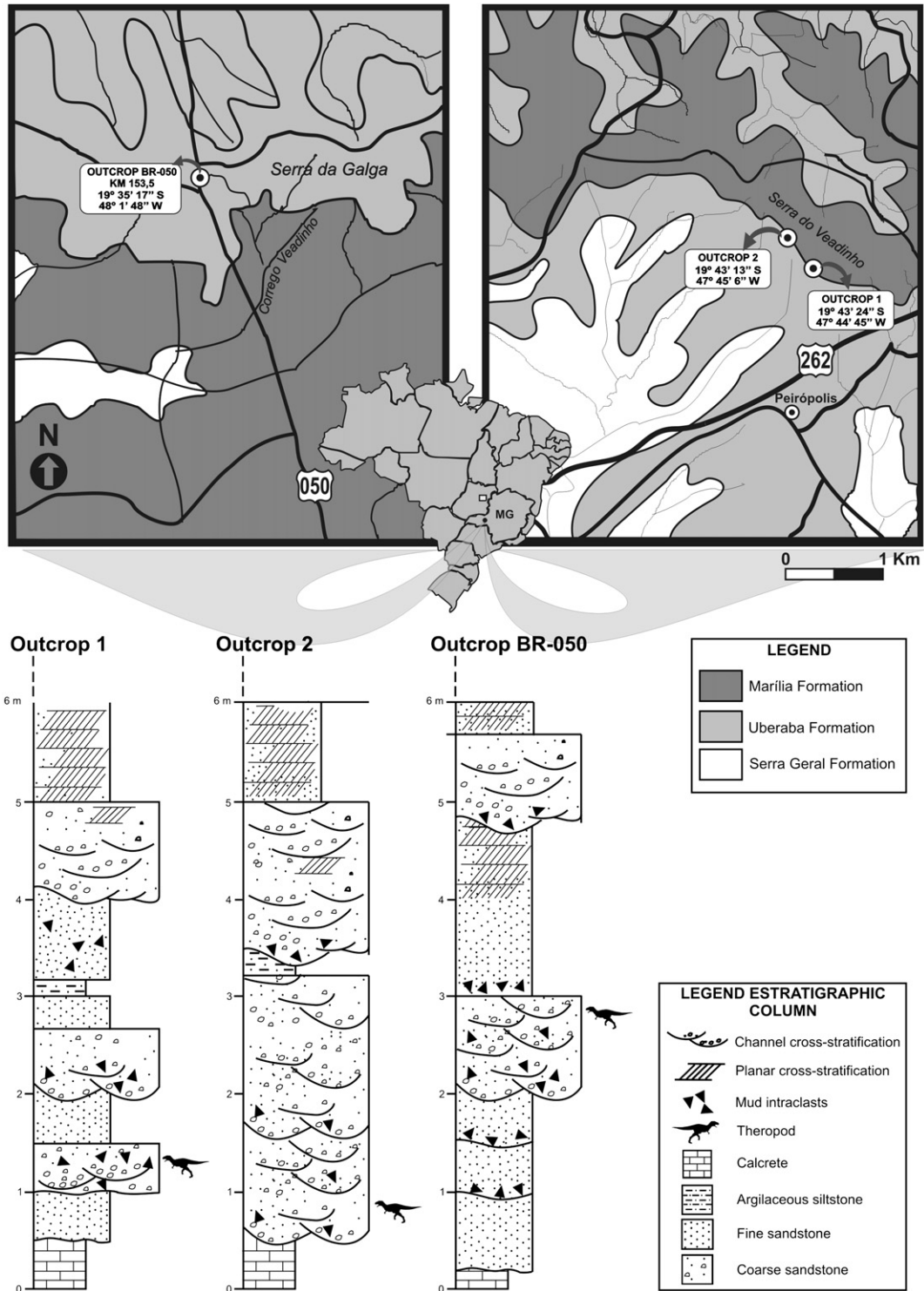


Fig. 2. Location map and stratigraphic context for the theropod occurrences at Uberaba County, Bauru Basin.

and caliche fragments. These levels are here interpreted as probable flash-flood deposits that reworked previously exposed soil sediments (caliche), in the context of a seasonally arid environment.

Garcia et al. (1999) argued that, for the Uberaba region, the palaeoclimatic conditions became more arid during the Maastrichtian. This aridity was considered by Goldberg and Garcia

(2000) to reflect global climatic conditions and was enhanced by the topographic height of the region, thus allowing the development of a dry microclimate. A more humid climate was present in the surrounding mountains that acted as geographic barriers to the entry of humid winds. The climatic seasonality was marked by longer dry intervals interrupted by periods of heavy rains, when small lakes and temporary ponds (relatively

deep during the flood periods; Senra and Silva e Silva, 1999) supported an abundant and diverse flora and fauna.

The theropod remains described here were found in coarse sandstones, probably deposited during sudden floods over the alluvial plains. The flash floods during the rainy seasons represented episodic events that allowed the fossilization of non-articulated specimens, such as the theropods described herein.

Systematic Palaeontology

Theropoda Marsh, 1881

Abelisauroidea (Bonaparte and Novas, 1985) Bonaparte, 1991

Abelisauridae Bonaparte and Novas, 1985

3. Description

The following elements (i.e., a dorsal vertebra, the distal part of a femur, and a pedal phalanx) were collected at different localities corresponding to the Serra da Galga Member of the Marília Formation.

Dorsal vertebra (CPP 893). This element is well preserved, with some parts broken, but preserving interesting details of its surface, that allow the recognition of delicate ridges and grooves that may correlate with muscular, ligamental, tendinal and cartilage attachments. Such details are difficult to recognize in other abelisauroid specimens (e.g., *Carnotaurus sastrei* – MACN 865) (Fig. 3). It corresponds to the cranial half of the dorsal column, being closely similar to dorsal vertebra 5 of *Carnotaurus* (Bonaparte et al., 1990). Nomenclature for vertebral laminae follows that of Wilson (1999).

The vertebra measures 18 cm in height and has a maximum transverse width of 22 cm. The centrum is long (8 cm), low (6.5 cm) and transversely narrow (6.2 cm). Though resembling D5 of *Carnotaurus*, it belongs to a smaller animal (the maximum height of D5 in *Carnotaurus* is 29 cm, and its maximum width is 29 cm, taken at the level of the diapophyses). Based on the holotype skeleton of *Carnotaurus*, CPP 893 may have measured 4–5 m in total length.

Both the cranial and caudal surfaces of the centrum of CPP 893 are concave and decorated with radially oriented rugosities. A small pit is present on the articular surfaces. An elliptical pneumatic opening of modest size (0.7–1 cm long) is located on the cranioventral margin of a wide and shallow depression present on both sides of the centrum.

The neural arch is fused to the centrum. It is wide and deep, but narrow at its base. The cranial pedicles of the neural arch exhibit an oblique lip on their cranial surfaces (Fig. 3A). The caudal pedicles, instead, project above the lateral surface of centrum, forming a tongue-like process (Fig. 3C). The neural canal is elliptical, being taller than wide. A deep, longitudinal furrow runs along the roof of the neural canal. The parapophysis (only the left one is preserved) is prominent and located high on the neural arch, as is usual among ceratosaurian theropods. It is laterally expanded into a button-like articular surface (oriented laterally, caudally and ventrally) to attach to the

tuberculum. A centroparapophyseal lamina buttresses the parapophyses ventrally. A rounded ridge extends from the parapophyses towards the prezygapophyses on the cranial surface of the neural arch (this may constitute the prpl (prezygoparapophyseal lamina) in dorsals 4–5 of *Majungasaurus*; O'Connor, 2007). This ridge ventrally bounds the infraprezygapophyseal fossa. Such a ridge is present in D5 of *Carnotaurus*, but the centroparapophyseal lamina is deeper in *Carnotaurus* than in CPP 893. This ridge is not visible in *Majungasaurus*. The diapophysis projects outward forming a wing-like, laterodorsally oriented process, with the cranial margin strongly convex and the caudal one concave, as seen from above (Fig. 3D). At its lateral tip, the diapophysis ends in an elliptical, convex surface to articulate with the capitulum. Dorsal to this articular surface, the diapophysis exhibits three craniocaudally oriented scars (sc; Fig. 3D), the middle one being the most prominent of the three. As is the case in other abelisauroids, the cranial surface of the diapophysis is dorsoventrally deep, in part due to the dorsal migration of the parapophysis (Fig. 3A). A sharp parapodiapophyseal lamina connects both structures (pdl; Fig. 3C). Well developed pneumatic features (pnc; Fig. 3) are associated with the diapophyses: a deep and narrow cavity exists on the base of its cranial surface, immediately behind the prezygapophysis; a pair of large depressions are present below the diapophysis, one being delimited by the conjunction of the paradiapophyseal lamina, the posterior centroparapophyseal lamina (cdl; Fig. 3C), and by a lamina connecting these two laminae; another pair of small cavities are present on the caudal surface of the diapophysis. The prezygapophyses are finger-like processes, the articular surfaces of which are subcircular in dorsal view, flattened, and with concentric rings (Fig. 3D). The internal surfaces of both prezygapophyses form vertical walls which bound the hypantrum. Such vertical walls are ventrally prolonged through pendant processes below the prezygapophyses (Fig. 3A, C). A transverse scar (ts; Fig. 3D), contiguous with the cranial margin of the diapophysis, serves as a caudal limit of the pedicle of both prezygapophyses, separating them from the prespinal cavity. The articular surfaces of the postzygapophyses are transversely concave and ventrally and very slightly medially oriented. As a consequence of this shape and orientation, the external margins of the postzygapophyses are prominent. The hyposphene (hyf; Fig. 3B,C) is a deep, cone-shaped structure located ventral to the intersection of both postzygapophyses.

The neural spine is robust, being craniocaudally long (4 cm) and transversely thick (2.4 cm). Both pre- and postspinal cavities excavate the base of the spine. At the bottom of the prespinal cavity, two asymmetrically located, elliptical excavations are present (pnc; Fig. 3E). Both sides of the neural spine show a shallow groove running obliquely from the craniodorsal corner of the spine towards the postzygapophyses (ogr; Fig. 3F), the anatomical significance of which is unknown. The top of the neural spine ends in a table, triangular in dorsal view, made distinct from the rest of the spine by the craniocaudal orientation of its osseous fibres (Fig. 3D). Ligament scars are well developed along both cranial and caudal surfaces of the neural spine. They describe an eye-shaped,

vertically oriented structure (ls; Fig. 3A,B). The cranial ligament scar is ventrally V-shaped, ending between the pair of previously mentioned elliptical excavations located at the bottom of the prespinal cavity (Fig. 3E). The dorsal tip of the caudal ligament scar projects between the caudal ends of the spine table, forming a small but well defined cone above the dorsal surface of the neural spine (Fig. 3B,D). The external margins of both cranial and caudal ligament scars are represented by protruding polygonal structures, decorated with horizontal grooves perpendicular to the vertical axis of the spine (Fig. 3F). These polygonal structures are separated from the rest of the lateral surface of the neural spine by a delicate, sub-vertical groove (gr; Fig. 3F).

Comparisons of dorsal vertebra. Dorsal vertebrae almost equivalent in position to that inferred for CPP 893 have been illustrated for *Carnotaurus sastrei*, *Ilokelesia aguadagrandensis* (both from the Upper Cretaceous of Patagonia; Bonaparte et al., 1990; Coria and Salgado, 1998), *Majungasaurus crenatissimus*, from the Maastrichtian of Madagascar (O'Connor, 2007), and *Rajasaurus narmadensis* (Wilson et al., 2003). Dorsal vertebrae are also known for *Spinostropheus gautieri*, a close relative of abelisauroids from the Hauterivian of Niger (Sereni et al., 2004).

CPP 893 looks more elongate than D5 of *Carnotaurus*, and the diapophyses are orientated less dorsally than in the Patagonian taxon. The available dorsal vertebra of *Ilokelesia*

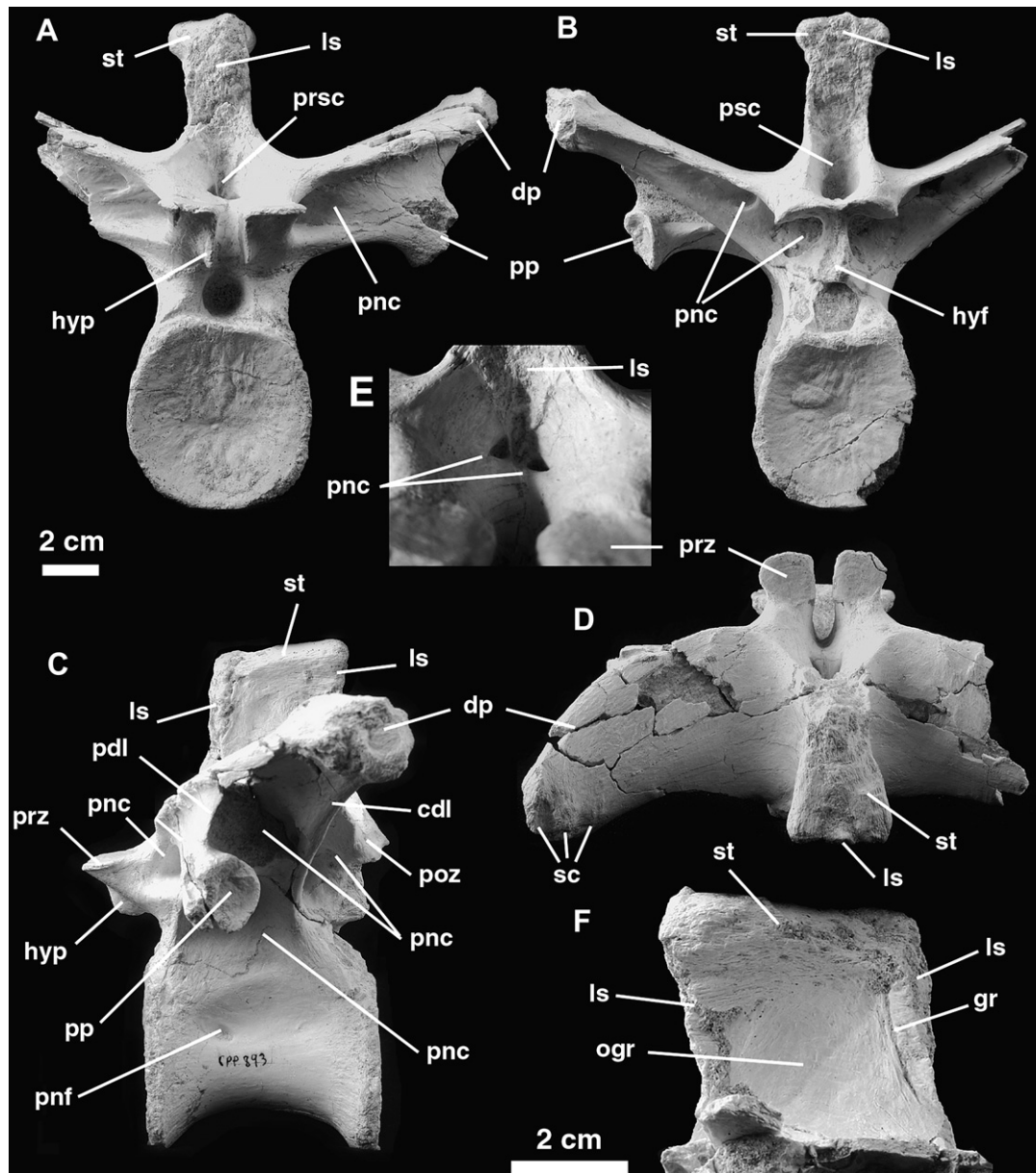


Fig. 3. Abelisauroid dorsal vertebra CPP 893 in cranial (A), caudal (B), left lateral (C) and dorsal (D) views. Detail of prespinal cavity in craniodorsal view (E), and detail of neural spine in right lateral view (F). Abbreviations: **cdl**, centrodiapophyseal lamina; **dp**, diapophysis; **gr**, groove; **hyf**, hyposphene; **hyp**, hypanthrum; **ls**, ligament scar; **ogr**, oblique groove; **pdl**, paradiapophyseal lamina; **pnc**, pneumatic cavity; **pnf**, pneumatic foramen; **poz**, postzygapophysis; **pp**, parapophysis; **prsc**, prespinal cavity; **prz**, parazygapophysis; **psc**, postspinal cavity; **sc**, scar; **st**, spine table.

(probably corresponding to a more caudal position than CPP 893) is proportionally lower and longer than in the Brazilian form. The parapophyses project laterally and occupy a high position on the neural arch, close to the diapophyses, a feature that is present in *Ceratosaurus* (Gilmore, 1920; Madsen and Welles, 2000), *Spinostropheus* (Sereno et al., 2004) and the remaining abelisauroids (e.g., *Ilokelesia*, *Carnotaurus*, *Majungasaurus*). However, in CPP 893 the paradiapophyseal lamina is well developed (i.e., laterally projected), as is the case in other abelisauroids (e.g., *Carnotaurus*, *Majungasaurus*), and in contrast to more remote outgroups (e.g., *Ceratosaurus*, *Spinostropheus*; Madsen and Welles, 2000; Sereno et al., 2004) in which a deep notch separates (in cranial view) the diapophysis from the prominent parapophysis.

In *Carnotaurus* the cranial ligament scar is more prominent cranially than it is in CPP 893, but it does not reach the spine table, thus describing a step in lateral view. In congruence with the lower position of the cranial ligament scar, the caudal one does not reach the dorsal end of the spine either. CPP 893 retains the primitive condition (e.g., ligament scars reaching the top of the neural spine) present in, for example, *Majungasaurus*, *Spinostropheus*, *Sinraptor*, *Allosaurus* and *Tyrannosaurus*, among others.

The spine table of CPP 893 is similar to that of D5 of *Carnotaurus*. In contrast, in dorsal vertebrae of *Majungasaurus* (O'Connor, 2007), the spine table is poorly developed or absent.

Dorsals 5 to 7 of *Carnotaurus* exhibit a pair of pneumatic depressions in the bottom of the prespinal cavity, as in CPP 893.

In *Carnotaurus* the entire neural arch looks deeper than it is in CPP 893, as is obvious in the taller proportions of both the prezygapophyses and the cranial surfaces of the diapophyses.

In *Carnotaurus* each prezygapophysis looks like an inverted cone (as seen from the side), due to its lateral surface being transversely convex, and because of the ventral notch that separates the prezygapophysis from the base of the neural arch. In CPP 893 the prezygapophyses are not cone-shaped as in *Carnotaurus*, but their lateral surfaces are transversely sinuous, thus distinguishing them from the ventrally directed tongue formed by the hypantral projections of the prezygapophyses. This tongue is better defined with respect to the lateral surfaces of the prezygapophysis (in *Carnotaurus* the prezygapophysis is transversely more rounded). The articular surface of the prezygapophyses of CPP 893 are dorsally and slightly medially projected, in contrast to the more caudal dorsals (i.e., caudal to D6–7) of *Carnotaurus*, *Ilokelesia*, and *Majungasaurus* in which the articular surfaces are dorsolaterally oriented (Bonaparte et al., 1990; Coria and Salgado, 1998; O'Connor, 2007).

The hyposphene in *Carnotaurus* (dorsals 3 to 8) and *Rajasaurus* (an isolated cranial dorsal; Wilson et al., 2003) is very prominent, extending beyond the caudal level of the postzygapophyses in lateral view. In this regard, CPP 893 (as does the abelisauroid *Majungasaurus*; P.O'Connor, pers. comm.) retained the primitive theropod condition as represented by *Ceratosaurus*, *Sinraptor*, *Tyrannosaurus*, and *Deinonychus*, for

example (Ostrom, 1969; Currie and Zhao, 1993; Madsen and Welles, 2000; Brochu, 2003), in which the hyposphene is much less projected caudally than are the postzygapophyses.

CPP 893 bears a pneumatic foramen on each side of the centrum, as is the case in *Carnotaurus* (in which pleurocoels are present along the entire dorsal series), but in contrast to the equivalent dorsals of other abelisauroids (e.g., *Ilokelesia*, *Rajasaurus*, *Majungasaurus*) and more remote sister taxa (e.g., *Spinostropheus*, *Ceratosaurus*, *Sinraptor*) in which the foramen is absent in dorsals that are caudal to D3–D4.

The pattern of pneumatic cavities in CPP 893 is closely similar to that of *Majungasaurus* and *Carnotaurus* in the presence of an infraprezygapophyseal fossa, a pair of large infradiapophyseal fossae, and an infrapostzygapophyseal fossa excavated on the caudal surfaces of the diapophysis. Nevertheless, such pneumatic excavations are not exclusive to Abelisauridae since they are also present in *Ceratosaurus*, *Sinraptor*, and *Spinostropheus*, among others, although in a somewhat different shape and development. Notably, CPP 893, *Majungasaurus*, *Ilokelesia*, *Carnotaurus*, and *Spinostropheus* lack “anterior infraprezygapophyseal fossae” (Coria and Currie, 2006) below and between the prezygapophyses. Because such excavations are present in *Ceratosaurus* and basal tetanurans (e.g., *Sinraptor*, *Allosaurus*, Carcharodontosauridae), we interpret the absence of “anterior infraprezygapophyseal fossae” as synapomorphic of Abelisauroida plus *Spinostropheus*.

On the basis of these few comparisons, we conclude that CPP 893 is phylogenetically closer to *Carnotaurus* than to the less derived abelisauroid *Ilokelesia*. In sum, CPP 893 apparently constitutes a derived member of the abelisauroid family Abelisauridae.

Femur (CPP 174). The specimen consists of the distal two thirds of a left femur (27 cm long as preserved), with a maximum transverse width of 10.2 cm. The preserved portion is almost the same size and proportions as the femur of the Patagonian abelisauroid *Xenotarsosaurus bonapartei* (Martínez et al., 1986), suggesting a complete femoral length of around 57 cm. Extrapolations taken from the holotype skeleton of *Carnotaurus sastrei* indicate that CPP 174 corresponded to an animal about 3–4 m in total length.

The femoral shaft is curved in lateral view (Fig. 4), and, viewed cranially, it looks slightly curved medially, in part due to the presence of a laterally protruding prominence that confers a sinuous contour to the external surface of the femoral shaft (Fig. 4A, lp). The shaft is triangular in cross section (it measures approximately 5 cm, both transversely and cranio-caudally), but becomes more quadrangular towards its distal end.

The caudal surface of the femoral shaft is almost flattened, and is separated from the lateral surface by a sharp edge (the linea intermuscularis caudalis; Figs. 4B, 5B lip) extending along the central third of the shaft. This intermuscular ridge, widely present among archosaurs (Hutchinson, 2001), marks the boundary between the areas of origin of the M. femorotibialis externus (cranio-laterally) and the M. adductor femoris (caudomedially) (Hutchinson, 2001). The linea

intermuscularis caudalis of CPP 174 is represented by a strongly rugose and straight edge that bifurcates distally into two curved scars: an external one (that ends in the laterally protruding prominence mentioned above), and another one running in a more medial position that extends toward the popliteal fossa. This last ridge is probably homologous with the adductor ridge (Hutchinson, 2001), which forms a low but highly rugose area on the caudal surface of the shaft.

The caudal surface of the femoral shaft ends distally in the popliteal fossa, laterally bounded by the tibiofibular condyle, medially by the tibial condyle, distally by a ridge connecting these two articular condyles, and proximomedially by the ridge connecting the tibial condyle with the convex area of the adductor ridge cited above.

As usual among ceratosaurians and basal tetanurans, a well developed crest is present along the craniomedial margin of the distal part of the shaft, approximately occupying the distal 14 cm of the femur. As seen in cranial view, this crest is medially convex. The craniomedial distal crest cranially bounds a deep fossa (the “abductor fossa” of Novas, 1997; but see Hutchinson, 2001, for a different interpretation of this feature), which is developed on the distal third of the femoral shaft. The “abductor fossa” is also limited distally by the raised and strongly rugose surface of the tibial condyle.

Proximal to the craniomedial crest there is an interesting anatomical feature not previously reported among dinosaurs: a smooth, longitudinal furrow (Figs. 4A and 5A, lf) limited by two sharp, collateral ridges, the more lateral of which is

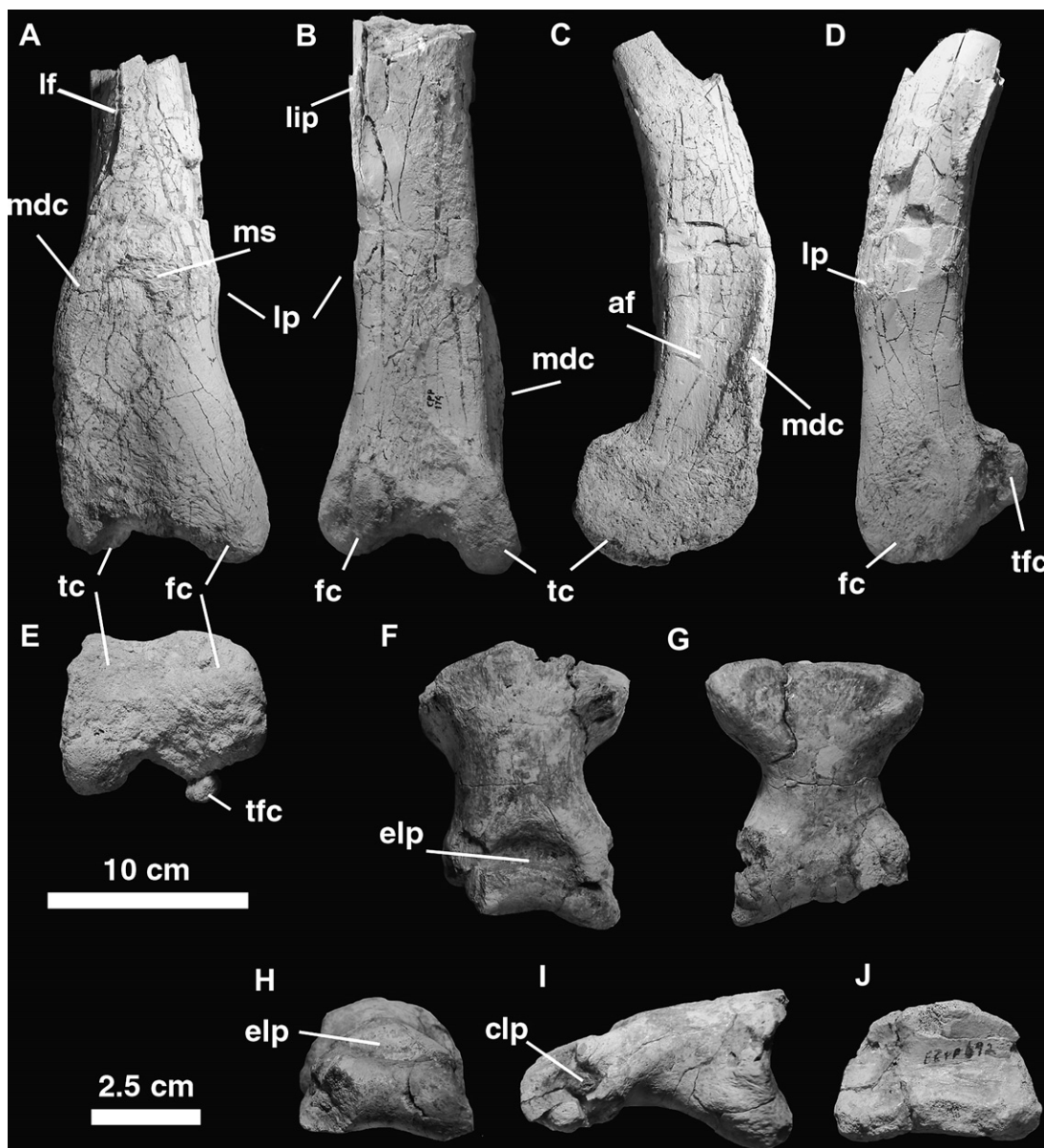


Fig. 4. A–E, Abelisauroid left femur CPP 174 in cranial (A), caudal (B), medial (C), lateral (D) and distal (E) views. F–J, Abelisauroid pedal phalanx (presumably phalanx 2.III) in dorsal (F), plantar (G), distal (H), lateral (I), and proximal (J) views. Abbreviations: **af**, abductor fossa; **clp**, collateral ligament pit; **elp**, extensor ligament pit; **fc**, fibular condyle; **lf**, longitudinal furrow; **lip**, linea intermuscularis caudalis; **lp**, lateral prominence; **mdc**, mediolateral crest; **ms**, muscle scar; **tc**, tibial condyle; **tfc**, tibiofibular condyle.

formed by a low but prominent, cranially projected crest. Both collateral ridges are decorated by perpendicular grooves and ridges. We interpret these parallel crests as being homologous with the linea intermuscularis cranialis (Hutchinson, 2001) seen in other members of Archosauria, but in a much less developed condition. The linea intermuscularis cranialis constitutes the border between the origins of the Mm. femorotibialis externus and internus (Hutchinson, 2001).

The cranial surface of the distal shaft of the femur exhibits a distinct elliptical muscle scar, located close to the craniomedial distal crest described above. This muscle scar is more prominent in its proximolateral region, where the fibers exhibit a horizontal orientation. We interpret this elliptical scar as marking the origin of the distal portion of the M. femorotibialis externus (Currie and Zhao, 1993; Novas, 1994; Hutchinson, 2001).

The distal portion of the cranial surface of the femoral shaft is transversely concave, with a shallow extensor groove, lacking the deeply incised condition present in the tetanuran theropods *Sinraptor*, *Allosaurus* and *Baryonyx*, for example. Distally, the femur ends in a transversely narrow tibial condyle (being 8 cm long craniocaudally, and 3 cm wide transversely), and a rounded fibular condyle. The tibiofibular condyle is rectangular in lateral view. Proximal to the fibular condyle, there are muscle scar on both cranial and lateral surfaces of the femoral shaft.

Comparisons of femur: The laterally protruding prominence of the femur is a feature documented in CPP 174, *Carnotaurus sastrei* (MACN-CH 894), *Ekrixinosaurus novasi* (MUCPv-294), and *Quilmesaurus curriei* (Coria, 2001), and probably also in the basal Jurassic abelisauroid *Elaphrosaurus bambergi* (Janensch, 1920). Thus, the presence of this prominence may constitute a synapomorphy of Abelisauroidea (*sensu* Rauhut, 2003). *Ekrixinosaurus novasi* (MUCPv-294) exhibits the same pattern of rugosities and intermuscular lines on both cranial and caudal surfaces of the distal shaft of the femur, thus reinforcing the referral of CPP 174 to Abelisauroidea. CPP 174 is congruent with other abelisauroids in the presence of a well developed craniomedial distal crest, a feature that is widely distributed among ceratosaurians and basal tetanurans.

Pedal non-ungual phalanx (CPP 692). Based on its axial symmetry, proportions in dorsal aspect, and dorsoventral depth, we interpret this element (Fig. 4I–J) as probably belonging to phalanx 2 of digit III (its morphology matches well the shape of this pedal phalanx in *Allosaurus*; Madsen, 1976). It is well preserved, lacking some parts of the distal ginglymus. The phalanx is robust, being transversely wide (5 cm) in respect to its maximum length (6 cm). However, the phalanx is dorsoventrally compressed (the maximum depth at the proximal articular end is 3.2 cm). Phalanx CPP 692, however, is proportionally more robust than the corresponding phalanges of *Sinraptor* (Currie and Zhao, 1993), *Allosaurus* (Madsen, 1976) and *Ilokelesia* (Coria and Salgado, 1998), resembling more the short and robust proportions of an isolated abelisauroid phalanx from India (GSI K27/653; Novas et al., 2004).

As previously noted, the phalanx looks robust, mainly due to the transverse expansion of its proximal end. It flares to both

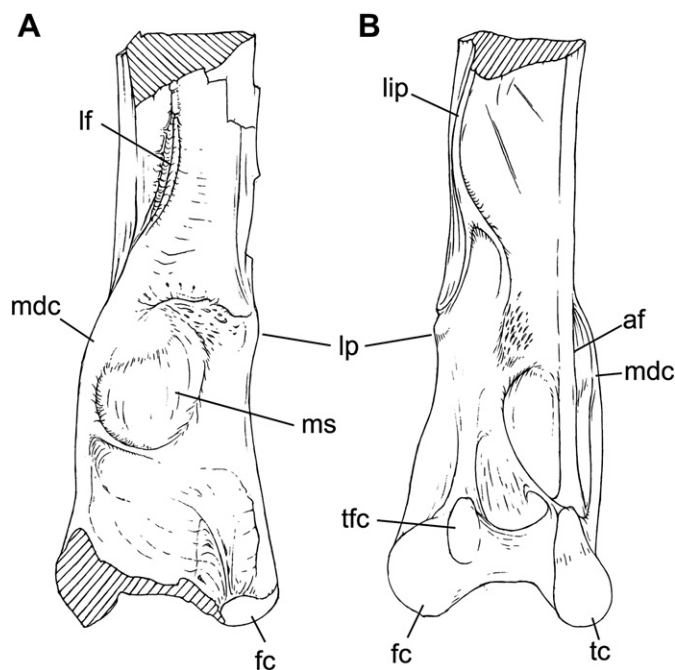


Fig. 5. Line drawing of the abelisauroid left femur CPP 174 in cranial (A) and caudal (B) views depicting rugosities and muscle scars. Abbreviations: af, abductor fossa; fc, fibular condyle; lf, longitudinal furrow; lip, linea intermuscularis caudalis; lp, lateral prominence; mdc, mediolateral crest; ms, muscle scar; tc, tibial condyle; tfc, tibiofibular condyle.

sides, contrasting with the transverse diameter of mid-shaft (2.7 cm). Its proximal articular surface is kidney-shaped and smooth, devoid of a median vertical ridge, thus indicating that the distal ginglymus of the preceding proximal phalanx (i.e., ph 1-III) was also smooth, lacking the slight dorsoventral groove seen in ph 1-III of *Allosaurus* and *Sinraptor*, for example. Moreover, the morphology of CPP 692 suggests that its corresponding ph 1-III (not found) had its distal ginglymus low, wide, and devoid of dorsoventral grooving, features that are present in the pedal phalanges of the abelisauroid *Ilokelesia* (Coria and Salgado, 1998). The ventral surface of CPP 692 shows a distinct subtriangular area, which is slightly concave and decorated with ridges and furrows. Distally, the phalanx ends in a saddle-shaped, dorsoventrally shallow, transversely wide distal ginglymus. It is proximodorsally bounded by a deep extensor pit, and on both sides of the distal ginglymus a well excavated collateral ligament pit is present.

The phalanx can be distinguished from the corresponding elements of *Sinraptor* (Currie and Zhao, 1993) and *Allosaurus* (Madsen, 1976) in that the distal ginglymus is dorsoventrally shallower and does not surpass the dorsal level of the rest of the bone. The condition present in CPP 692 is also present in the basal abelisauroid *Ilokelesia* (Coria and Salgado, 1998). On the basis of overall similarities of CPP 692 with abelisauroid pedal phalanges (including a smooth and kidney-shaped proximal articular surface, devoid of a median vertical ridge, and distal ginglymus dorsoventrally shallow, not surpassing the dorsal level of the rest of the bone), we tentatively refer this bone to this group of theropod dinosaurs.

4. Conclusions

We report the first abelisaurid bone remains from the Peirópolis area, a much studied region of the Bauru Basin that has yielded abundant remains of titanosaurid sauropods. Abelisaurid theropods were already documented by numerous isolated teeth found in the Bauru Basin, including the Peirópolis fossil site (Bittencourt and Kellner, 2002; Candeiro, 2002). Discoveries made in the Peirópolis area demonstrate that abelisaurids lived alongside elmsaurid-like maniraptorans (Novas et al., 2005) and presumably also with carcharodontosaurid carnosaurs (Candeiro et al., 2006a,b), although the evidence in support for the presence of this latter group is far from conclusive.

The isolated bones described above are referable to Abelisauroida, and on the basis of their size (all of them correspond to individuals no less than 5 m long), are almost probably referable to the family Abelisauridae. Because the bones come from different points within the basin, they almost certainly represent three different individuals. It can thus be concluded that abelisaurids were the most numerous theropods in the Bauru Basin, in congruence with discoveries in Matto Grosso as well as with other parts of Gondwana (Patagonia, Madagascar, India).

No autapomorphies were identified in the available elements that might allow us to diagnose a new genus and species within Abelisauridae.

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