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ON A NEW TITANOSAUR SAUROPOD FROM THE BAURU GROUP, LATE CRETACEOUS OF BRAZIL [1]

(With 28 figures)

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ABSTRACT: Four field seasons (1998, 2000, 2001 and 2002) organized by the Paleovertebrate Sector of the Museu Nacional at Campina Verde – Prata road, at a site known as Serra da Boa Vista some 45km west to the Prata town, Minas Gerais State resulted in the discovery of a medium sized titanosaur sauropod dinosaur, with an estimated length of 13m. *Maxakalisaurus topai* n.gen., n.sp. consists of a partial skeleton found in fine to medium grained sandstones of the Adamantina Formation (Late Cretaceous), Bauru Group, and is the fifth unequivocal titanosaur species described from Brazil. It has the anterior and middle caudal vertebrae with dorsoventrally compressed centra, the midposterior caudal vertebrae have the lateral surface of the centrum strongly concave (spool-shaped), and show at least one biconvex element. *Maxakalisaurus topai* is also distinguished by having a metacarpal IV about 12% shorter than metacarpal II, among other features. The compressed anterior and most middle caudal vertebrae suggest that the new species is in close relationship with the Saltasaurinae, a hypothesis that needs further testing.

Key words: Dinosauria. Sauropoda. Titanosauria. Cretaceous. Brazil.

RESUMO: Um novo saurópodo titanossauro do grupo Bauru, Neocretáceo do Brasil.

Quatro expedições (1998, 2000, 2001 e 2002), organizadas pelo Setor de Paleovertebrados do Museu Nacional, na rodovia Campina Verde – Prata, na localidade conhecida como Serra da Boa

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Vista, situada a cerca de 45km a oeste da cidade de Prata, estado de Minas Gerais, resultaram na descoberta de um dinossauro saurópodo titanossauro de médio porte, com comprimento estimado em 13m. *Maxakalisaurus topai* n.gen., n.sp. consiste de um esqueleto parcial encontrado em arenitos finos a médios da Formação Adamantina (Neocretáceo), Grupo Bauru, representando a quinta espécie inequívoca de titanossauro descrito para o Brasil. A cauda apresenta vértebras caudais anteriores e médias com o centro comprimido dorsoventralmente, caudais mesoposteriores com a superfície lateral do centro fortemente côncava (forma de carretel) e pelo menos um elemento biconvexo. *Maxakalisaurus topai* também é diagnosticado por ter o metacarpal IV cerca de 12% mais curto do que o metacarpal II, entre outras feições. A conformação comprimida dorsoventralmente das vértebras caudais anteriores e da maioria das médias, sugere que a nova espécie está proximamente relacionada aos Saltasaurinae, uma hipótese que ainda necessita de comprovação.

Palavras-chave: Dinosauria. Sauropoda. Titanosauria. Cretáceo. Brasil.

INTRODUCTION

The dinosaur record in Brazil is very poor and despite numerous localities, the majority of the material consists of incomplete specimens or isolated bones (Kellner & Campos, 2000). The most common dinosaurs recorded so far are sauropods that can be attributed to the Titanosauria. Up to date, there are four accepted titanosaur species from Brazil: *Gondwanatitan faustoi* Kellner & Azevedo, 1999; *Baurutitan britoi* Kellner, Campos & Trotta, 2005; *Trigonosaurus pricei* Campos, Kellner, Bertini & Santucci 2005, and *Adamantisaurus mezzalirai* Santucci & Bertini, 2006 (Kellner & Azevedo, 1999; Kellner *et al.*, 2005; Campos *et al.*, 2005; Santucci & Bertini, 2006). All were found in the Bauru Group that comprises mainly siliciclastic sediments deposited in fluvial conditions (e.g., Bertini *et al.*, 1993; Fernandes & Coimbra, 1996). The upper part of the Bauru Group comprises the Adamantina and the Marília formations, whose age is disputed: Turonian-Santonian (Dias-Brito *et al.*, 2001) or Campanian-Maastrichtian (Gobbo-Rodrigues *et al.*, 1999).

Over 10 years ago, Goldberg *et al.* (1995) have reported the occurrence of dinosaur remains in outcrops of the Adamantina Formation at the Serra da Boa Vista, situated on the Campina Verde - Prata road, some 45km west to the Prata town, Minas Gerais State (Fig.1). Four field seasons (1998, 2000, 2001 and 2002) were organized by the Paleovertebrate Sector of the Museu Nacional and resulted in the recovery of a medium sized titanosaur sauropod. This specimen was briefly mentioned in the literature (Henriques *et al.*, 1998; Henriques *et al.*, 2002) and is fully described here.

Besides the Brazilian titanosaur taxa mentioned before, the new species is also compared with the following titanosaur sauropods: *Aeolosaurus rionegrinus* Powell, 2003; *Aeolosaurus sp.* (Salgado & Coria, 1993); *Aeolosaurus sp.* (Salgado *et al.*, 1997b); *Alamosaurus sanjuanensis* Gilmore, 1922; *Andesaurus delgadoi* Calvo & Bonaparte, 1991; *Antarctosaurus wichmannianus* Huene, 1929 (Powell, 2003); *Argyrosaurus superbus* Lydekker, 1893 (Powell, 2003) *Epachthosaurus sciuttoi* Powell, 1990 (Martínez *et al.*, 2004); *Isisaurus colberti* (Jain & Bandyopadhyay, 1997) (Wilson & Upchurch, 2003); *Lirainosaurus astibiae* Sanz *et al.*, 1999; *Malawisaurus dixeyi* (Haughton, 1928) (Jacobs *et al.*, 1993); *Mendozasaurus neguyelap* González Riga, 2003; *Neuquensaurus australis* (Lydekker, 1893); *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977; *Pellegrinisaurus powelli* Salgado, 1996; *Rapetosaurus krausei* Curry Rogers & Forster,

2001; *Rinconsaurus caudamirus* Calvo & González Riga, 2003; *Saltasaurus loricatus* Bonaparte & Powell, 1980; and *Titanosaurus araukanicus* (Huene, 1929). The data from most of the mentioned titanosaur taxa was obtained from the original description and complemented with other papers among which GILMORE, (1946), CORIA *et al.* (1998), POWELL (1992, 2003), BONAPARTE (1996), SALGADO *et al.* (1997a), LEHMAN & COULSON (2002), and GONZÁLEZ RIGA (2005).

TAPHONOMIC ASPECTS

Maxakalisaurus topai was found in an area of 40m² in a fine to medium grained reddish sandstone above a thin conglomeratic layer. Sedimentological studies indicate that those rocks were formed in a fluvial depositional environment where semi-arid condition, with dry and wet alternate periods predominated (GOLDBERG & GARCIA, 2000). Fossils were not collected in adjacent areas.

Fig.1- Map of South America, showing the southwestern part of the Minas Gerais State (Brazil), with the outcrops of the Marilia and Adamantina formations (partially based on FERNANDES & COIMBRA, 1996). The star indicates the outcrop at the Serra da Boa Vista where the dinosaur specimen was collected.

The assemblage comprises disarticulated bones, but the cervicals and three caudals were found partially articulated. Among the recovered elements are an incomplete jaw with the last five preserved alveoli, the first four of which still bearing teeth, sternal plates, vertebrae, transverse processes, chevrons, ribs and limb bones (Fig.2). Except for two extra sternal plates, and a distal end of a right scapula, that belong to a second animal attributed to *Maxakalisaurus topai*, and one caudal vertebra that may or may not pertain to this species (see discussion), the bones recovered were closely associated. In the lack of more evidence, we consider those bones as belonging to the same individual (MN 5013-V). As far as comparison is possible, there is no size discrepancy among the recovered elements. Some isolated vertebral centra and neural arches suggest that this was a still young animal at time of death, with bones relatively more fragile.

Maxakalisaurus topai bones were recovered along with several isolated theropod and crocodylomorph teeth, turtle elements and some small non-dinosaurian hollow bones. Bioturbation is present in several levels, sometimes in close connection with the dinosaur elements.

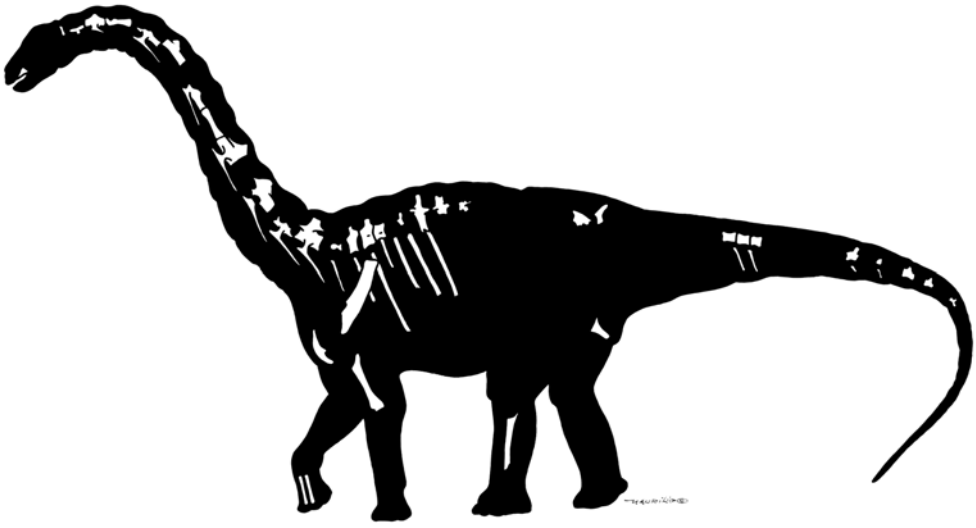


Fig.2- Outline showing the remains of *Maxakalisaurus topai* n.gen.; n.sp. (MN 5013-V) recovered.

All bones show essentially the same preservational condition and, the majority of them, some degree of breakage. Weathering features were mostly observed as external crackled surface and longitudinal fractures, which is an indicative of prolonged subaerial exposure. Some bones show signs of limited compression. There is no taphonomic evidence for water transport, fossil sorting and or preferred orientation of bones in the fossil bed. Also, the edges of the broken bones were sharp and with no degrees of rounding, indicating that the studied assemblage consists of associated and autochthonous remains restricted to a single horizon.

LYMAN (1994) compiled data about the study of dispersal according to the disposition of elements on horizontal and inclined surfaces, relating the last ones to trampling. At least two steeply inclined elements were found in the Prata Site, as the preserved portion of the scapula found above the dorsal vertebrae, which suggests that trampling occurred to some extent. According to VARRICCHIO (1995:312) "the non preservation of articulated elements implies an absence of trampling activity or a consolidated substrate during the period of complete disarticulation". Trampling in a soft muddy substrate can explain the inclined elements found. Disarticulation was caused not only by the prolonged subaerial exposure but also by the action of carrion feeders or "opportunistic" scavengers, like some theropods, whose teeth were also recovered from this deposit and is further indicated by the presence of tooth-marked elements (Fig.3). Those features suggest that the carcass was scavenged, besides being also partially trampled.

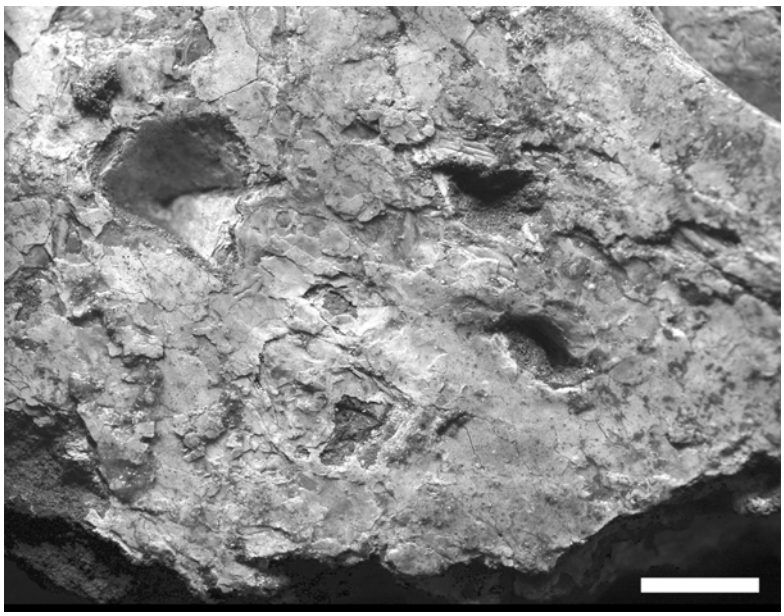


Fig.3- Tooth marks in *Maxakalisaurus topai* n.gen.; n.sp. (MN 5013-V) bone. Scale bar: 10mm.

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley, 1888
Sauropodomorpha Huene, 1932
Sauropoda Marsh, 1878
Titanosauria Bonaparte & Coria, 1993
Maxakalisaurus new genus

Type species – *Maxakalisaurus topai* new species, type by monotypy.

Etymology – The generic name is formed by *Maxakali*, from one of the Macro-jê stock language, honoring the Maxakali ethnic group that is present in the Minas Gerais State where this dinosaur was found, and *saurus*, which is the Greek word for lizard, commonly assigned to fossil reptiles.

Diagnosis – The same as for the species.

Maxakalisaurus topai n.sp.

Holotype – Partial skeleton composed of an incomplete right maxilla (with teeth), the remains of 12 cervical vertebrae (including several cervical ribs), part of seven dorsals (and ribs), one sacral neural spine, one sacral centrum, six caudals, several hemal arches, part of both scapulae, both sternal plates, the distal portion of a left ischium, both humeri, the second and forth right metacarpals, incomplete fibula, one osteoderm, and several

unidentified bones. This specimen (MN 5013-V) is housed at the Museu Nacional of the Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Figs.2-27).

Etymology – The specific name also derives from a Maxakali word *Topa* which is a tribal god worshiped by the Maxakali ethnic group.

Type locality – MN 5013-V was collected about 45km west of the Prata town, at the Prata – Campina Verde road, in a region called Serra da Boa Vista, Minas Gerais State, Brazil.

Geological setting – The specimen was collected in a fine to medium grained reddish sandstone that has been regarded as part of the Adamantina Formation, Bauru Group, Upper Cretaceous (Goldberg *et al.*, 1995; Dias-Brito *et al.*, 2001; Gobbo-Rodrigues *et al.*, 1999).

Diagnosis – Titanosaur dinosaur characterized by the following combination of features: tail composed of anterior and midposterior caudal vertebrae with the anterior (and posterior) surface of the centrum dorsoventrally compressed; midposterior caudal vertebrae with the lateral surface of the centrum strongly concave (spool-shaped); dorsal margin of neural spine in midposterior caudal vertebrae inclined anteriorly; presence of at least one midposterior caudal with biconvex centrum; metacarpal IV about 12% shorter than metacarpal II; sacral centrum with keel-shaped ventral surface.

Associated material – The distal end of a right scapula (MN 7048-V) and two sternal plates (MN 7049-V and MN 7050-V) of a second animal attributed to *Maxakalisaurus topai*, one caudal vertebra (MN 7051-V) that may or not pertain to this species, and crocodylomorph and theropod teeth.

DESCRIPTIONS AND COMPARISONS

The material of *Maxakalisaurus topai* consists of a partial skeleton with most elements broken. Some bones show signs of limited compression. The main part of this skeleton consists of cervical and dorsal vertebrae (including several ribs) that were found partially articulated. Humeri, metacarpals and other elements were found associated with this vertebral column. All material was collected in an area of 10 by 4 meters. Except for the sternal plates (four of which were collected), and the proximal end of one scapula, there is no further duplicity in bones. Therefore we regard the majority of the bones collected at this site as beloging to one individual.

Maxilla and teeth

A partial right maxilla – the first recorded from a Brazilian sauropod – was collected (Figs.4A-D). It is a fragile element, a common condition of the cranial bones in titanosaur sauropods (e.g., Curry Rogers & Forster, 2004). It has five alveoli that decrease in size posteriorly, with the last one less than half the diameter of the first. The first four preserved alveoli still bear teeth, with the first and second including one replacement tooth.

The preserved portion of the maxilla gently curves inward, suggesting that the anterior part of the skull of *Maxakalisaurus topai* was rounded, as observed in other titanosaurs whose skulls are known (e.g., Curry Rogers & Forster, 2004).

The teeth show the general pencil-like condition found in other titanosaurs. The teeth show anterior and posterior carinae which are not normally found in other titanosaurid

teeth, including those recovered from the outcrops of the Marília Formation (Bauru Group) at the famous localities of the Peirópolis region (KELLNER, 1996). Titanosaur teeth with defined carinae were reported in *Rinconsaurus* (CALVO & GONZÁLEZ RIGA, 2003) and *Rapetosaurus* (CURRY ROGERS & FORSTER, 2004).

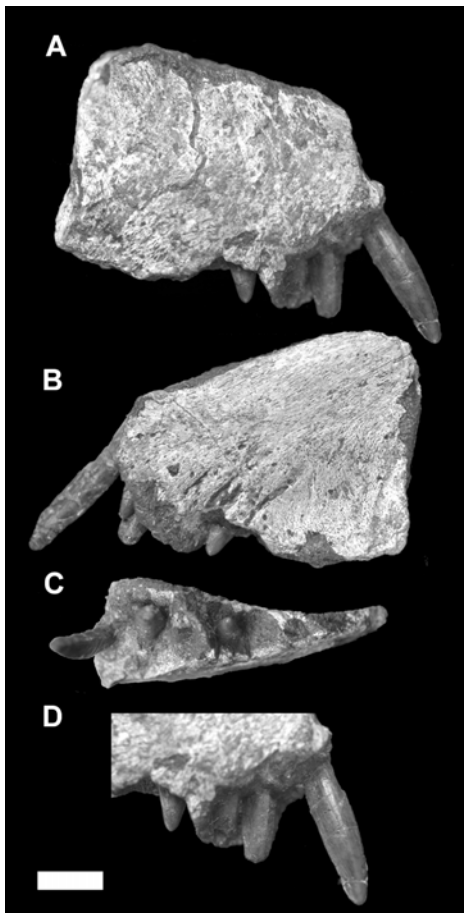


Fig.4- *Maxakalisaurus topai* n.gen.; n.sp. (MN 5013-V): maxila (A) lateral view; (B) mesial view; (C) oclusal view; (D) teeth in detail. Scale bar: 10mm.

CERVICAL VERTEBRAE AND RIBS

The remains of 12 cervical vertebrae (besides cervical ribs - see below) were collected: the third, some elements of the middle series (possibly cervical vertebrae 7-10) and one posterior (possibly cervical vertebra 12). As far as comparisons are possible, all are opisthocoelous, a general condition among titanosaurs. No pleurocoels were found in the preserved elements and the neural spines are single (e.g., not bifid).

Cervical vertebra 3 has the centrum partially damaged (Fig.5). The neural spine is low and anteroposteriorly elongated, with the dorsal margin inclined anteriorly. Prezygapophyses are well developed and inclined anterodorsally, slightly surpassing the anterior articulation surface of the centrum. The articulation surfaces face dorsomedially. Postzygapophyses are stronger and directed posterodorsally. The articulation surfaces face ventrally and are slightly twisted laterally.

The cervical vertebrae from the middle part of the neck are more elongated (with the anteroposterior length/height of the posterior articulations surface more than 3), have undivided centroprezygapophyseal lamina, and display a comparatively high neural spine but are still longer than high (Fig.6). The tip of the neural spine is blunt and transversally thickened. Prezygapophyses are directed forward, only slightly surpassing the articulation surface of the centrum. The posterior cervical vertebrae are less elongated and laterally more expanded, giving them a comparatively more robust appearance. Except for the region close to the articulations, the ventral surface is concave. In posterior cervical vertebrae the spinoprezygapophyseal laminae are only preserved in the 10th cervical vertebra, being comparatively thin (Fig.7). Deep pre- and postspinal fossae are present. The last preserved cervical (possibly cervical 12) is the shortest of all, with the cervical centrum wider than tall. Pre- and postzygapophyses are robust and short and display large articulation surfaces. All middle and mid-posterior cervical vertebrae show a deep lateral depression on the base of the neural spine.

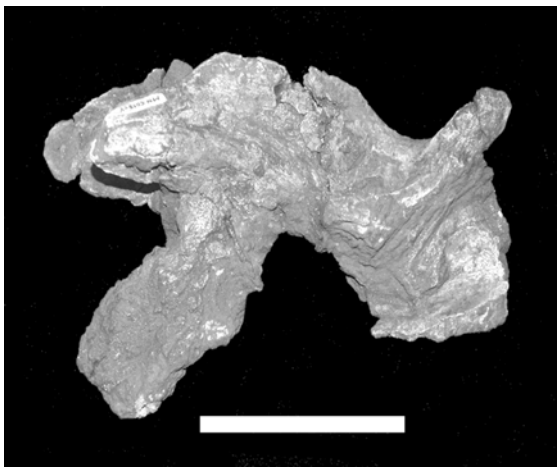


Fig.5- *Maxakalisaurus topai* n.gen.; n.sp. (MN 5013-V): 3rd cervical vertebra in right lateral view. Scale bar: 100mm.

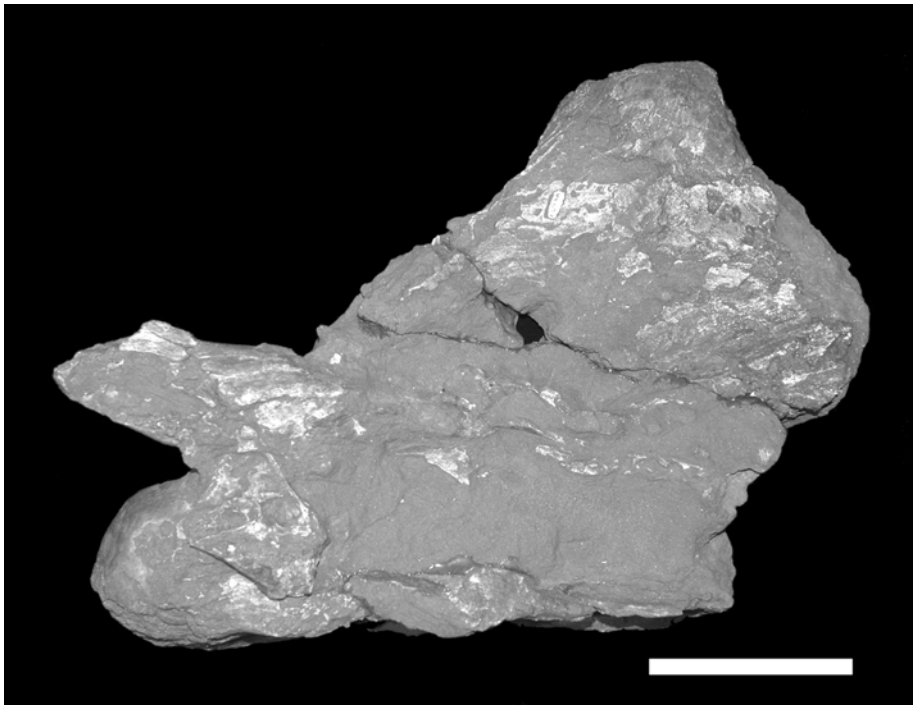


Fig.6- *Maxakalisaurus topai* n. gen.; n. sp. (MN 5013-V): midcervical vertebra (possible the 7th) in left lateral view. Scale bar: 100mm.

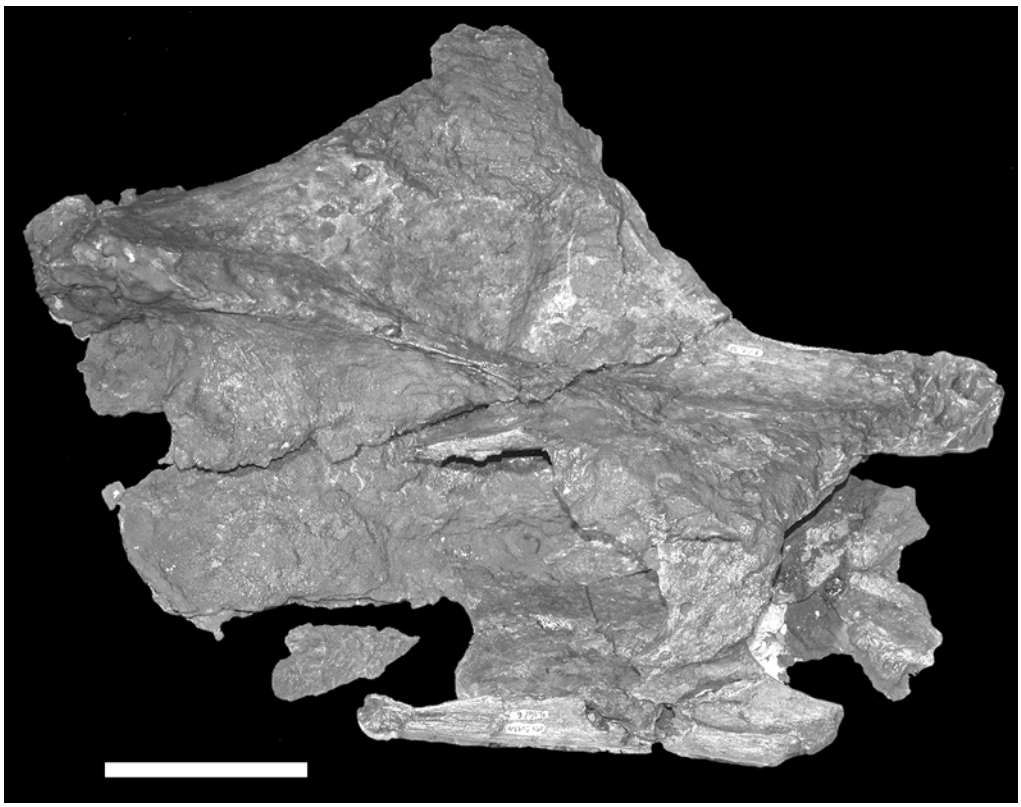


Fig.7- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): midposterior cervical vertebra (possible the 10th) in right lateral view. Scale bar: 100mm.

There are only a few titanosaur taxa whose cervical vertebrae are known that can be compared with *Maxakalisaurus topai*. Some titanosaur taxa show elongated cervical vertebrae while in others they are reduced. *Maxakalisaurus topai* falls in the category of elongated cervical vertebrae, therefore differing from the condition observed in *Isisaurus* and *Mendozasaurus*, both having a taller neural spine (JAIN & BANDYOPADHYAY, 1997; GONZÁLEZ RIGA, 2005). *Isisaurus colberti* further differs from *Maxakalisaurus topai* by having pleurocoels on the centrum. *Mendozasaurus neguyelap* has the neural spine laterally expanded in posterior cervicals (GONZÁLEZ RIGA, 2005), a condition also absent in the new Brazilian taxon.

The sole mid-posterior cervical reported from *Malawisaurus dixeyi* is also higher than in *Maxakalisaurus topai* and has the ventral margin straighter (JACOBS *et al.*, 1993). *Rinconsaurus caudamirus* differs from *Maxakalisaurus topai* by having a long anterioposterior depression on the cervical centra that bear small pleurocoels (CALVO & GONZÁLEZ RIGA, 2003). *Alamosaurus sanjuanensis* differs by having a smaller neural spine and shorter postzygapophyses (LEHMAN & COULSON, 2002).

The cervical vertebrae of the Saltasaurinae *Saltasaurus loricatus* also displays a quite distinct morphology of those preserved in *Maxakalisaurus topai* by being shorter, having short prezygapophyses that are dorsally inclined with the articular facets near the level of the diapophyses (a sinapomorphy of the Saltasaurinae), the peculiar posteriorly extended postzygapophyses, low neural spine and deep pleurocoels perforating the centrum (SALGADO *et al.*, 1997a; POWELL, 2003).

Regarding the titanosaur sauropods known from Brazil, cervical vertebrae are only known for *Gondwanatitan* and *Trigonosaurus*. The cervical series of *Gondwanatitan faustoi* is incomplete and comparisons with *Maxakalisaurus topai* are limited. The main difference is the presence of a ventral depression on the centrum, separated by a bony ridge (KELLNER & AZEVEDO, 1999), not observed in *Maxakalisaurus*. Compared to *Trigonosaurus pricei*, *Maxakalisaurus topai* has proportionally higher midcervical vertebrae with shorter prezygapohyses. Both taxa have similar lateral depression on the base of the neural spine.

Several cervical ribs were preserved fused or in close association to the corresponding cervical vertebrae but oddly enough, some were found isolated and possibly belong to cervical vertebrae that have not been recovered. The cervical ribs have a short anterior and a longer posterior process, a common feature in sauropod dinosaurs. They are double-headed and fused with the diapophysis and parapophysis. Those found isolated were clearly broken off from the corresponding cervical vertebra (e.g., Figs.8-9). The cervical ribs of the mid-cervical vertebrae tend to be more elongated (Fig. 8) whereas those associated with more posterior elements tend to be shorter and deeper (Figs.5, 9), possible related to the size of the cervical centrum. The anterior projection surpasses the centrum and levels with the prezygaphophysis. The posterior projection clearly extends beyond the anterior margin of the centrum and possible reaches the middle part of the succeeding cervical vertebra.

Fig.8- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): isolated cervical rib from middle cervical vertebra. Scale bar: 100mm.

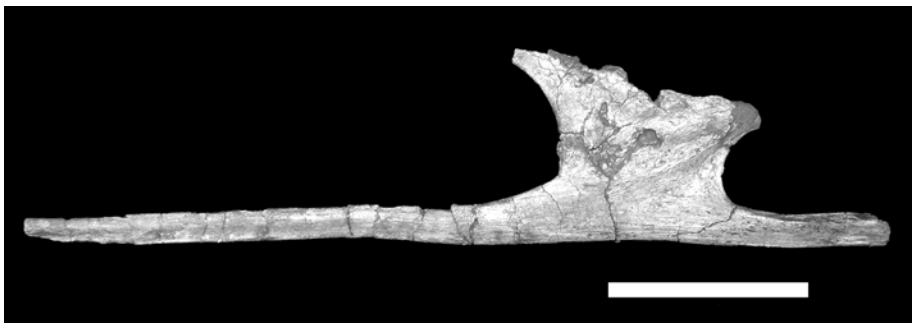


Fig.9- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): isolated cervical rib from midposterior cervical vertebra. Scale bar: 100mm.

Comparisons with other cervical ribs from titanosaur sauropods are very limited since those elements are either not preserved or have not been described. *Isisaurus* differs from *Maxakalisaurus* by having short cervical ribs that do not reach the succeeding element (JAIN & BANDYOPADHYAY, 1997). This condition might also have been the case for *Mendozasaurus* which, like *Isisaurus*, also displays short cervical vertebrae (GONZÁLEZ RIGA, 2005). In a cervical series found in Peirópolis (POWELL, 1987, 2003), the general shape of the cervical ribs is similar to the condition observed in *Maxakalisaurus topai*.

DORSAL VERTEBRAE AND RIBS

The remains of about 7 dorsal vertebrae of *Maxakalisaurus topai* have been collected, but most elements are fragmentary. Among the best preserved element is the neural arch of one anterior dorsal vertebra (Figs.10-11). Together with two centra (that lack most of the neural arches), this element provides most of the anatomical information of the dorsal series for the new taxon. The neural arch has a short base (Fig.10), indicating that the dorsal vertebrae were comparatively short, which is confirmed by the two other preserved centra. The lateral surface of the centrum is slightly concave. A well-developed triangular cavity can be observed below the prezygapophyses.

The neural spine has a subtriangular shape in anterior view and is bordered by well-developed spinodiapophyseal lamina. It is tall and inclined posteriorly. The preserved portion indicates that it was single and not bifid.

The diapophysis is long and directed dorsolaterally. It shows a well-developed spinodiapophyseal lamina that is smaller and less pronounced than the centrodiapophyseal laminae on the posterior side (Fig.11). Small opening is present on the ventrolateral surface of the diapophysis. The prezygapophyses are short with the articulation surface facing dorsomedially. The postzygapophyses are well developed and placed in close contact to each other. They are elliptical, with the longest axis directed mediolaterally. The postzygapophyses have thick columnar spinopostzygapophyseal laminae that form a deep dorsoventrally elongated fossa behind the neural spine. No evidence of hyposphene-hypantrum is observed.

There are two partial centra of the dorsal series preserved, lacking most of the neural arch, both being partially compressed. They are opisthocoelic with the anterior condyle well developed and a circular and deep posterior articulation. A small depression is located in the lateral surface, indicating the presence of a pleurocoel.

The dorsal vertebrae of *Maxakalisaurus topai* are less elongate and possess smaller pleurocoels than *Epachthosaurus*, *Trigonosaurus*, *Gondwanatitan* and *Saltasaurus* (KELLNER & AZEVEDO, 1999; POWELL, 2003; MARTÍNEZ *et al.*, 2004; CAMPOS *et al.*, 2005). The neural spine is less inclined than in *Rinconsaurus* and *Trigonosaurus* (CALVO & GONZÁLEZ RIGA, 2003). The dorsal vertebrae of the new species further lack the hyposphene-hypanthrum observed in *Epachthosaurus* and basal titanosaurs. The new taxon differs from *Opisthocoelicaudia skarzynskii* by lacking bifurcated neural spines (BORSUK-BIALYNICKA, 1977). The latter also has the centrum twice as wide than high, similar to *Pellegrinisaurus* (SALGADO, 1996), which differs from the more rounded condition observed in *Maxakalisaurus*.

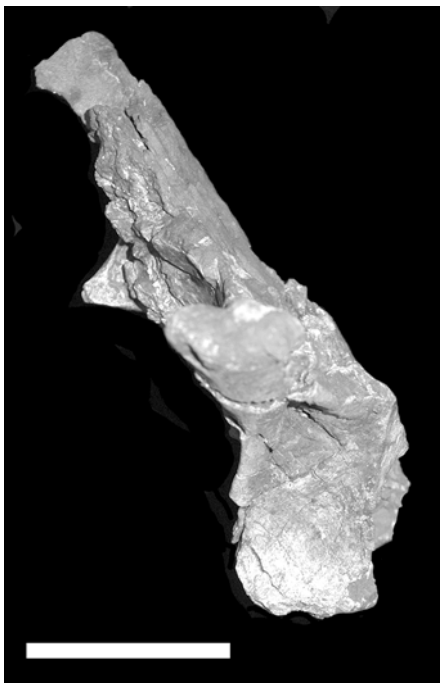


Fig.10- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): anterior dorsal vertebra in right lateral view. Scale bar: 100mm.

Several dorsal ribs are preserved, but most are incomplete. The more anterior ones tend to be smaller and more massive, whereas the more posterior ones are larger and anteroposteriorly flattened. All preserved proximal parts have the posterior margin pierced by pneumatic foramina, which tend to be larger in the largest ribs.

Ribs are not usually described in titanosaur dinosaurs. Those foramina are present in several titanosaur ribs (AWAK personal observation) but are not commonly reported. *Gondwanatitan faustoi* also has such pneumatic foramina (KELLNER & AZEVEDO, 1999), but are not as well developed as in *Maxakalisaurus topai*. No pneumatic foramina were reported in the ribs of *Epachthosaurus* (MARTÍNEZ *et al.*, 2004).

SACRAL VERTEBRAE

The sacrum is poorly preserved in this specimen. There are only two remains - one partial neural arch and one isolated centrum. The neural arch was clearly broken off a centrum (not preserved). It bears a laminar neural spine that is elongated anteroposteriorly. It is pierced by several foramina and openings, a common feature in titanosaur sacral vertebrae.

The isolated sacral centrum is amphiplatyan and clearly was not fused with other sacral elements. Due to its shape, it is here interpreted as the fifth sacral. Among the most important features, this element has the ventral surface of the centrum compressed, a feature not reported in any other titanosaur sauropod where the sacrum is known (Fig.12).

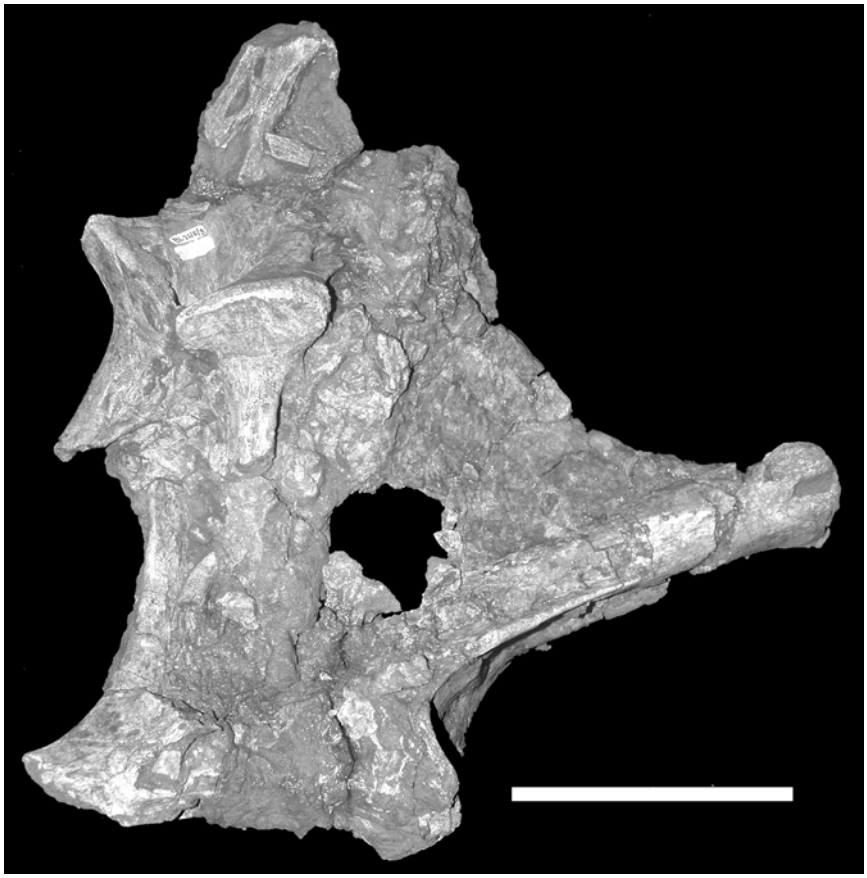


Fig.11- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): same anterior dorsal vertebra of figure 9, in posterior view. Scale bar: 100mm.

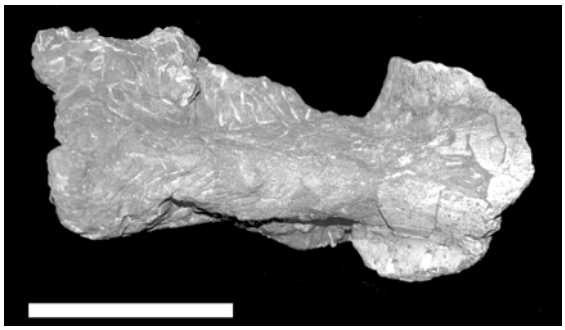


Fig.12- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): fifth sacral vertebra in ventral view. Scale bar: 100mm.

ANTERIOR CAUDAL VERTEBRAE

Six caudal vertebrae are preserved, showing the morphology of the anterior, middle and middle-posterior portion of the tail. Compared to *Baurutitan britoi*, one of the few titanosaurs where a partial tail is preserved in anatomical sequence (KELLNER *et al.*, 2005), we interpret the preserved elements as possible caudals 5-7, 15, 18 and 21. For descriptive and comparison purposes, we discuss the anterior and middle caudal elements separately.

All three anterior caudal vertebrae are known only by their centra. They are strongly procoelous with well-developed articulation surfaces for the chevrons. The two most anterior elements (5^{th}-6^{th}?) were broken and only the ventral half of the centrum is preserved. The 7^{th} (?) caudal has a complete centrum and provides most of the information for the anterior caudal vertebrae of *Maxakalisaurus topai* (Figs.13-14).

The neural arch is not preserved and it is clear that it was unfused with the centrum. It occupied great part of the centrum, placed near the rim of the anterior margin. Although not complete, the lower portion of the neural canal marked on the dorsal surface of the centrum (Fig.14) indicates that this canal was wide and likely very large. Only the left transverse process is complete. It is a stout and short element that sits on a broad base and is deflected distally.

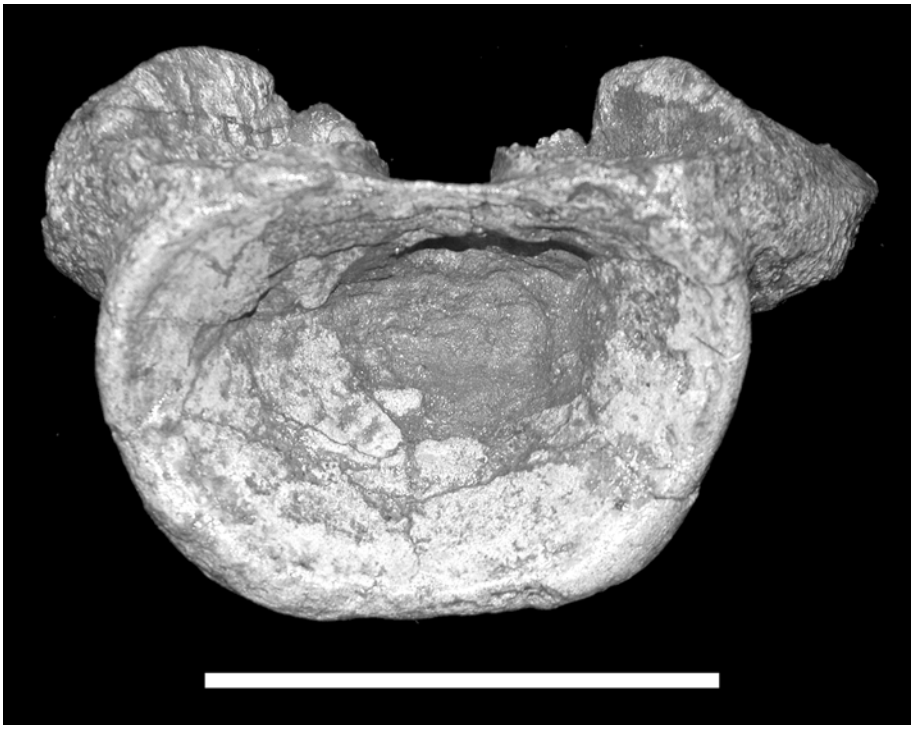


Fig.13- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): anterior caudal vertebra (7^{th}?) in anterior view. Scale bar: 100mm.

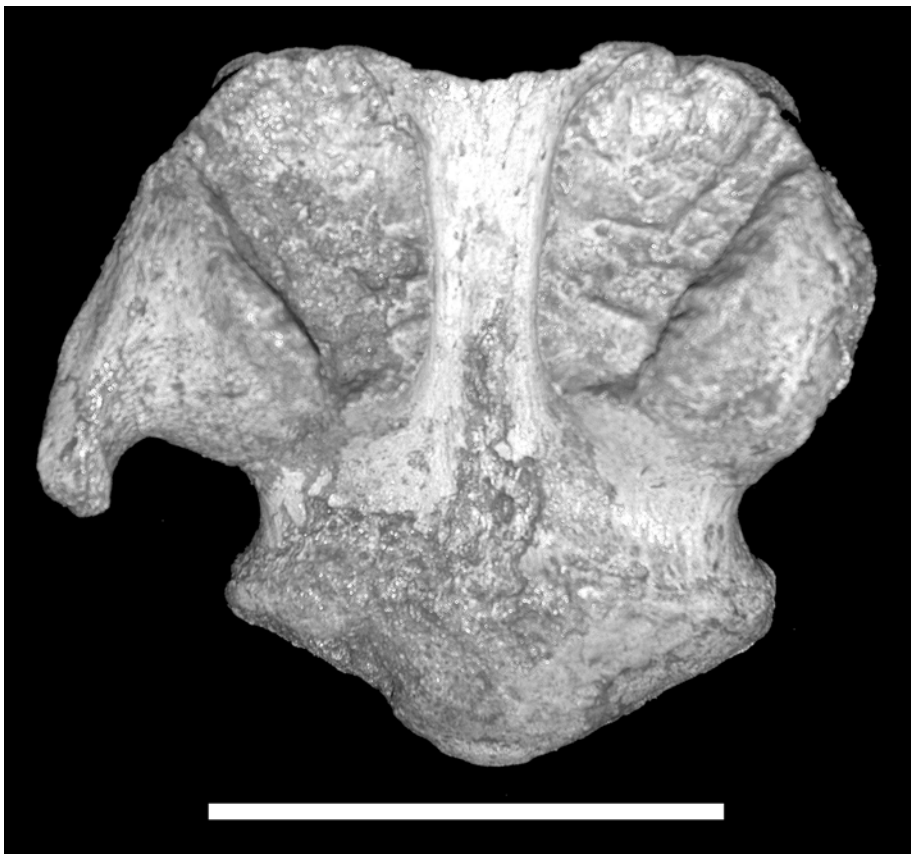


Fig.14- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): anterior caudal vertebra (7th?) in dorsal view. Scale bar: 100mm.

The centrum is wider than high (105 x 75mm in anterior cotyle), having convex lateral walls. The anterior cavity is strongly procoelous (almost 40mm deep) with the deepest point displaced upwards. The cotyle is bordered by a thick rim of bone, except at the dorsal part anterior to the base of the neural canal, where it is very thin. In lateral view, the centrum is longer than high. The condyle is well developed and the ventral surface is concave, and the ventral length of the centrum is shorter than the dorsal one (85mm). The distal condyle is well developed and protuberant, being dorsally displaced. In posterior view, it is wider than high, being comparatively more depressed than the anterior cotyle. The ventral part of the centrum is constricted and the articular surfaces for the chevrons are separated by a shallow concavity.

The comparisons between the anterior caudal vertebrae of *Maxakalisaurus topai* are limited by the absence of the neural arch. Several anatomical differences between the new taxon and some other titanosaurs allow an easy distinction. This is the case of

Opisthocoelicaudia skarzynskii that shows an opisthocoelous condition, shorter centra and rounded outline of the anterior and posterior surfaces (BORSUK-BIALYNICKA, 1977). *Opisthocoelicaudia skarzynskii* apparently shows a ventral concavity bordered by ventrolateral ridges throughout the caudal series, which are absent in *Maxakalisaurus*. The bases of the neural spines of caudal 2-7 of *Opisthocoelicaudia skarzynskii* are set over the distal half of the respective centra (BORSUK-BIALYNICKA, 1977: pl.4, figs.1b, 2a; pl.5, fig.2a) and not on the anterior half like in *Maxakalisaurus*. Another difference is observed in the transverse processes, which in *Opisthocoelicaudia skarzynskii* are rudimentary, heavy blunt knobs, less developed than in the new Brazilian taxon.

The presence of hyposphene-hypantrum articulations in the anterior (and middle) caudal vertebrae in *Epachthosaurus sciuttoi* (MARTÍNEZ *et al.*, 2004) can also easily separate this titanosaur from *Maxakalisaurus topai*. The centrum of the new taxon is more dorsoventrally compressed, shows a straight dorsal margin and has the ventral portion slightly compressed. *Epachthosaurus* further differs from *Maxakalisaurus* in having an unusually large condyle (MARTÍNEZ *et al.*, 2004: fig.7).

The main difference between the anterior caudals of *Maxakalisaurus topai* and the remaining titanosaur taxa is the anterior and posterior outline of the centrum. *Alamosaurus sanjuanensis* and *Rinconsaurus caudamirus* have the centrum higher than wide (GILMORE, 1922, 1946; CALVO & GONZÁLEZ RIGA, 2003) while in *Lirainosaurus astibiae*, *Isisaurus colberti* and *Mendozasaurus neguyelap* the caudal centra have subcircular articular outline (JAIN & BANDYOPADHYAY, 1997; SANZ *et al.*, 1999; GONZÁLEZ RIGA, 2003). *Pellegrinisaurus powelli* differs from *Maxakalisaurus topai* by having the centrum of the anterior caudals more compressed and the lateral surfaces convex (SALGADO, 1996). *Saltasaurus loricatus* also has the centrum of the anterior vertebrae more compressed dorsoventally than *Maxakalisaurus topai* (POWELL, 2003).

From the titanosaur sauropods recorded in Brazil, *Maxakalisaurus topai* differs from *Adamantisaurus mezzalirai* by having the centra of the anterior caudal vertebrae more dorsoventrally compressed, with a straight dorsal margin of the cotyle (SANTUCCI & BERTINI, 2006). *Gondwanatitan faustoi*, *Trigonosaurus pricei* and *Baurutitan britoi* also show anterior caudals with centra that are wider than high (KELLNER *et al.*, 2005; CAMPOS *et al.*, 2005) and the anterior surface is therefore similar to *Maxakalisaurus topai*. The main difference is observed in the posterior surface, where *Maxakalisaurus* is more compressed dorsoventrally. It further differs from the more "heart-shaped" posterior articulation surface observed in *Gondwanatitan* and *Trigonosaurus*. *Trigonosaurus* further differs by having the transverse processes more developed than the new species.

MIDDLE AND MIDPOSTERIOR CAUDAL VERTEBRAE

The middle caudal vertebrae of *Maxakalisaurus topai* are represented by two vertebrae, interpreted as being the 15th and 18th.

The 15th (?) caudal vertebra is fairly complete and well preserved (Fig.15A). This caudal has an almost complete neural arch, with a complete left prezygapophysis and an incomplete right one. The right side of the centrum is preserved, as well as most of the distal articular condyle. The body of the centrum is long (almost 2 times longer than high), and depressed dorsoventally, but not to the same degree as in the anterior caudals (and also in the middle posterior elements – see below). The lateral

wall of the centrum is concave, giving the vertebra a spool-shaped appearance. The neural arch is placed on the anterior half of the centrum, not reaching the anterior margin. An anteroposteriorly-oriented ridge is observed on the lateral surface. The neural canal (in posterior view) is round. The neural spine is low and elongated anteroposteriorly, with the dorsal margin slightly inclined anteriorly. The most anterior part of the neural spine levels with the anterior half of the vertebra whereas the posterior tip levels at the base of the condyle. The prezygapophyses are well developed, long and thick. The prezygapophyseal articulation surfaces are rounded, subvertically oriented and face medially. The postzygapophyses are small, but still individualized in this vertebra, being slightly detached from the neural spine.

The 18th (?) caudal vertebra is incomplete, lacking pre- and postzygapophyses (Fig.15B). Nevertheless it shows the same basic morphology as the 15th (?) caudal vertebra, having a long centrum (e.g., 2 times longer than high), and the spool-shaped appearance with slightly convex lateral walls but differs by being biconvex. The anterior condyle is more projected than the posterior one, both showing a rounded concavity in the middle. The neural arch is placed on the anterior half of the centrum and has a rounded neural canal.

The last preserved caudal vertebra is here tentatively regarded as the 21st, making it a midposterior element (Fig.15C) It is complete lacking only the tip of the left prezygapophysis and a small portion of the ventral rim of the cotyle. Its basic shape is very similar to the other middle caudal vertebra by being procoelous, but differs in having a lower and less pronounced neural spine, the lateral surfaces less concave and the condyle comparatively less developed. The anterior and posterior articulations are a bit wider than long, having slightly convex lateral walls. The ventral surface is concave. An outstanding feature of this vertebra is the presence of a ventral projection placed on the anteroventral corner of the centrum, close to the rim of the cotyle. This ventral projection apparently represents the articular surface for a chevron that should be attached to the anterior part of the centrum, rather than to the posterior, that lacks any projections for the chevrons. The neural arch is placed over the anterior half of the centrum, at some distance from

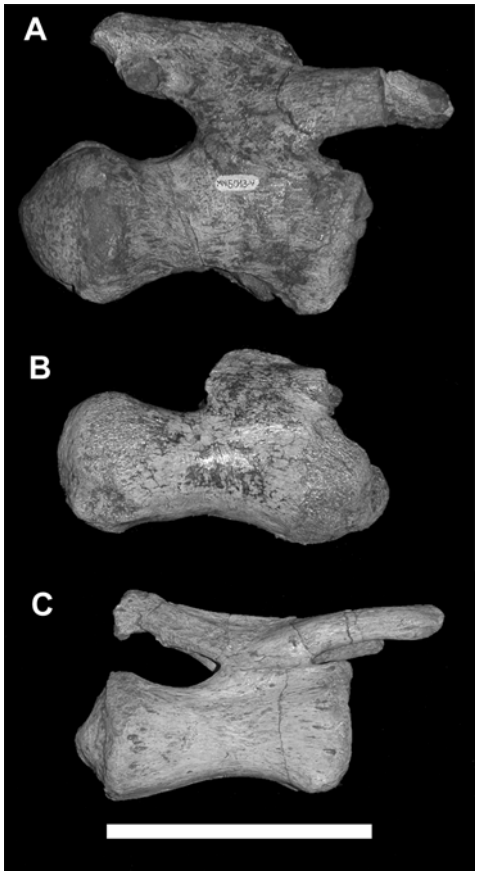


Fig.15- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): middle (A)15th?; (B)18th? and midposterior (C) 21th? caudal vertebrae in right lateral view. Scale bar: 100mm.

the anterior margin. The neural canal is rounded. The lateral base of the neural arch displays an anteroposterior ridge. This ridge is sharp and well pronounced. Just below the ridge, the surface of the centrum is slightly concave. The neural spine is reduced, being represented as a posterior projection that extends almost to the distal border of the centrum and has the dorsal margin inclined anteriorly. A sharp prespinal lamina runs over the dorsal margin of it. The distal tip of the neural spine is blunt and expanded dorsoventrally, having an elliptical cross section. The prezygapophyses are long and slender. A dorsal rugose knob between the bases of the prezygapophyses, close to the base of the prespinal lamina is observed. Postzygapophyses are absent. In lateral view, the posterior margin of the neural arch merges with the ventral margin of the neural spine forming a ridge. There is another ridge on the lateral surface of the neural spine itself.

As the anterior caudal vertebrae, the middle caudal vertebrae of *Maxakalisaurus topai* can easily by distinguished from *Opisthocoelicaudia skarzynskii* by not being opisthocoelous or amphiplatyan (Borsuk-Bialynicka, 1977). The new taxon also lacks the ventral concavity bordered by ventrolateral ridges reported for this taxon. The strong procoelous condition of the middle caudals further differentiates *Maxakalisaurus topai* from the more primitive titanosaurs like *Andesaurus* and *Malawisaurus* (Salgado *et al.*, 1997a) *Epachthosaurus sciuttoi* differs by the presence of hyposphene-hypantrum articulations in the caudals 8-14. *Alamosaurus sanjuanensis*, *Mendozasaurus neguyelap* and *Isisaurus colberti* have the outline of the centrum more rounded. *Isisaurus colberti* further differs by having the condyle very projected anteroposteriorly ("cone-like"; Jain & Bandyopadhyay, 1997). *Saltasaurus loricatus* and *Neuquensaurus australis* have an anteroposteriorly-elongated depression, divided by a sagittal crest on the ventral surface of the centra (Powell, 2003), which is not recorded in *Maxakalisaurus topai*.

The middle caudal vertebrae of *Rinconsaurus caudamirus* show bony processes separating the articular faces of the postzygapophyses from the neural spine (Calvo & González Riga, 2003), absent in *Maxakalisaurus topai*. Among the middle and distal caudal vertebrae of *Rinconsaurus caudamirus*, there is a series (MRS-Pv 29) with unusual centra, showing a procoelous plus amphicoelous plus biconvex articulation (Calvo & González Riga, 2003: pl.3, fig.A). A biconvex caudal vertebra was also found in *Maxakalisaurus* and it is possible that also this taxon shows a similar variation, which was also reported in an unnamed caudal sequence from the Bauru Group (Trotta *et al.*, 2002).

Besides those differences, *Maxakalisaurus topai* differs from all other titanosaur taxa by the anteriorly directed dorsal margin of the neural spine.

As observed in *Alamosaurus*, *Gondwanatitan* and *Baurutitan*, *Maxakalisaurus* also possesses a lateral ridge on the middle caudal vertebrae. In *Baurutitan britoi* this process corresponds to the tuberosity present in more anterior elements and is not homologous with the transverse process. Whether this is also the case for *Maxakalisaurus topai* cannot be established at present.

Besides the six elements described above, another caudal vertebra (MN 7051-V) was found with the holotype (Fig.16). It shows a quite distinct morphology from all others. Since the remains of other individuals were also found together with the holotype (as

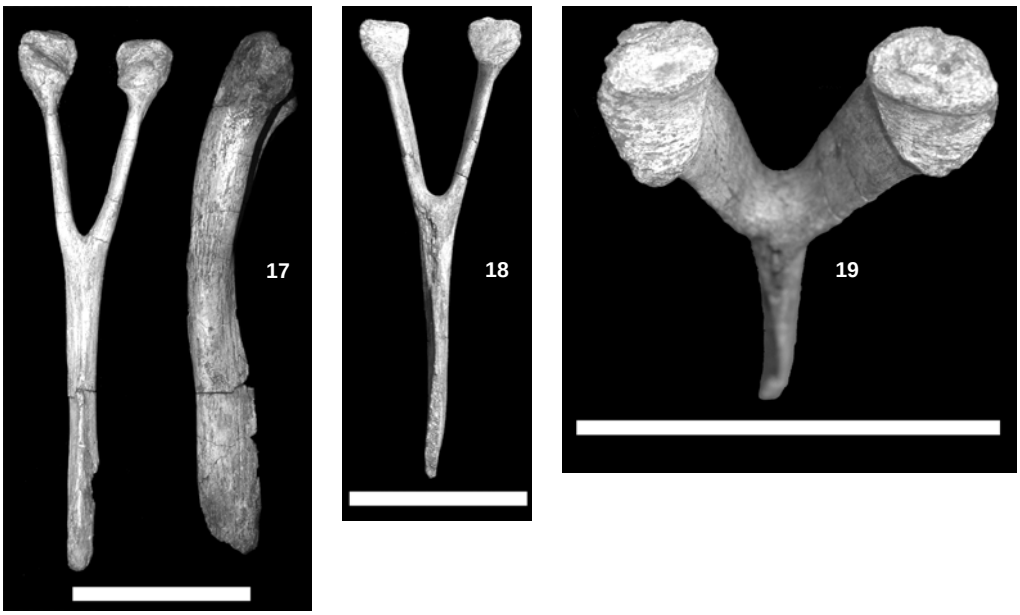
indicated by the extra sternal plates and scapula), it is uncertain wether this vertebra belongs or not to the same taxon. Although the bone surface is not very well preserved, this element is almost complete, lacking the neural spine and the postzygapophyses. It is procoelous and has the centrum higher than wide, with almost vertical lateral walls (differing from the remaining caudal vertebrae of this taxon). The anterior cotyle is not as deep and the condyle is less projected compared to the other caudals. Below the condyle there is a well-developed projection for the attachment of the chevron. Transverse processes are reduced to a rounded bony protuberance. The neural canal is elliptical, wider than high. An interprezygapophyseal fossa is well developed in between the basal portion of the prezygapophyses, placed just above the neural canal.

Fig.16- MN 7051-V: caudal vertebrae in anterior view. Scale bar: 100mm

CHEVRONS

There are three very well preserved chevrons or hemal arches and the remains of some more (Figs.17-18). They are open dorsally and have a typical Y-shape, with dorsal processes that attach to the caudal vertebra and a ventral process. In the preserved elements, those processes are always less than half the total length of this bone and the hemal canal is wide. In lateral view, the ventral part of the chevron forms a distal anteroposteriorly expanded bony blade. Anterior and posterior longitudinal ridges are present on this part of the bone.

In all titanosaur taxa the chevrons are open dorsally, a feature that is also present in *Maxakalisaurus topai*. In the new species, the proximal articulation (Fig.19) is expanded and divided into two well distinct surfaces, a feature also reported in *Mendozasaurus* and *Aeolosaurus* (GONZÁLEZ RIGA, 2003). The anterior one is slightly convex, whereas the posterior one is larger and concave. Besides this feature, the hemal arches of *Maxakalisaurus topai* differ from *Baurutitan*, *Adamantisaurus*, *Alamosaurus, Mendozasaurus* and *Aeolosaurus* by having the arms that unite ventrally forming the hemal spine more laterally compressed. They further differ from *Adamantisaurus mezzalirai* by being less expanded anteroposteriorly (SANTUCCI & BERTINI, 2006).



Maxakalisaurus topai n.gen., n.sp. (MN 5013-V): fig.17- chevron in posterior view; fig.18- chevron in posterior view; fig.19- chevron in proximal view. Scale bar: 100mm.

STERNUM

Both sternal plates were found. They are not complete, but it is clear that they have a semilunar outline (Fig.20), a common feature in titanosaurs (SALGADO *et al.*, 1997a; CALVO & GONZÁLEZ RIGA, 2003). The sternum is essentially a compressed plate of bone that meets its counterpart at the midline. From the anterior view, the lateral margin is thicker and concave while the medial margin is thinner and convex.

The right sternal plate has a ventral ridge still preserved, but lacks part of the medial side. The left sternal plate lacks the anterior portion, but has a better preserved medial side. The lateral side is gently curved, differing from the strong curved condition observed in *Aeolosaurus sp.* (SALGADO *et al.*, 1997b), *Alamosaurus sanjuanensis*, *Opisthocoelicaudia*, and *Saltasaurus.* Except for *Alamosaurus sanjuanensis* and *Saltasaurus*, *Maxakalisaurus* can also be distinguished from the previous mentioned species by having an antero-ventral ridge. It can further be distinguished from *Alamosaurus sanjuanensis, Malawisaurus dixeyi* and *Mendozasaurus neguyelap* by not having a truncated distal end. Among titanosaurids that have a less curved lateral margin of the sternal plate are *Lirainosaurus astibiae* and *Rinconsaurus caudamirus. Maxakalisaurus* can be distinguished at least from *Lirainosaurus astibiae* by having the antero-ventral ridge less developed. The information regarding *Rinconsaurus caudamirus* does not allow any further comparisons.

ISCHIUM

Only the distal part of the left ischium is preserved (Fig.21). The anterior border is thin,

blade-like, while the posterior border is thick and convex. The entire piece is about 35cm long, bearing a 23cm long distal process, which is expanded at the distal end. The width of this process varies from 9cm at the proximal base to 12cm at the distal end, with a minimum width of about 7.5cm. Therefore, the average width of this piece ranges from about one half to one third of its total length.

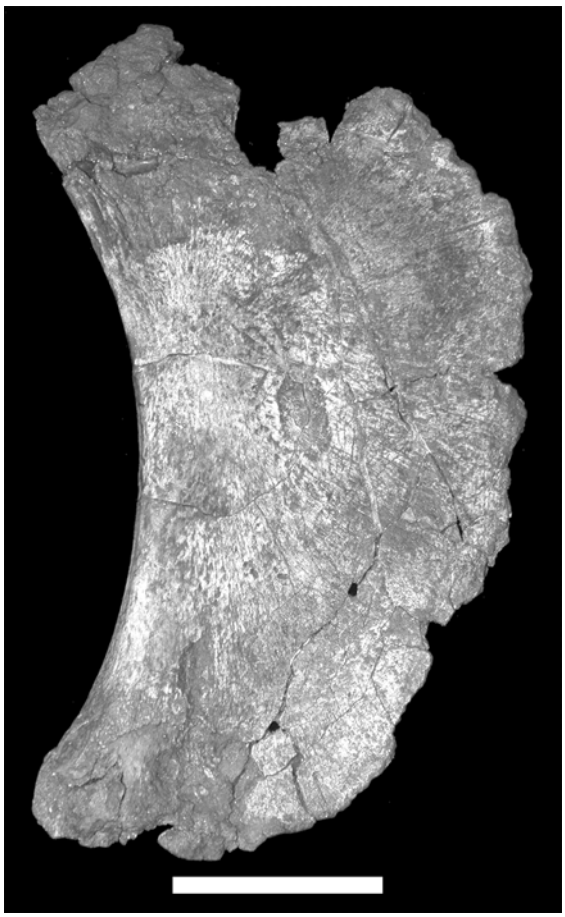


Fig.20- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): sternal plate. Scale bar: 100mm.

The ischium in Titanosauria generally bears a short distal process, with a relatively wide blade, that merges proximally with the pubic peduncle (e.g. *Andesaurus*, *Malawisaurus*, *Alamosaurus*, *Isisaurus, Saltasaurus*, *Neuquensaurus*). *Epachthosaurus sciuttoi* (Martínez *et al.*, 2004) and *Rinconsaurus caudamirus* show a less wide distal process (Calvo & González Riga, 2003), but those are still comparatively wider than in *Maxakalisaurus.* The figured ischium of *Opisthocoelicaudia skarzinskii* (Borsuk-Bialynicka, 1977) shows a long and narrow distal process, being similar to *Maxakalisaurus.*

The ischium of *Aeolosaurus rionegrinus* has a long distal process which lacks the anterior border, thus hindering estimations of its width in respect to length. Nevertheless, the ischium of *Aeolosaurus rionegrinus* seems to be similar to *Maxakalisaurus* by having an expanded distal end (Powell, 2003). Another ischium attributed to *Aeolosaurus sp.* is also similar to *Maxakalisaurus* by displaying a long and narrow distal process whose width at the distal end is about one half of the total length. Meddially and proximaly, however, it seems to be even narrower in the Argentinean specimen (Salgado & Coria, 1993).

From all other Titanosaurids described in Brazil so far, only *Gondwantitan faustoi* has ischial elements. Although incomplete, they appear to be comparatively wider than in *Maxakalisaurus*.

Humerus

Both humeri are preserved, lacking the proximal part. It is a slender bone, with a constricted shaft and expanded articulations (Fig.22). It is clear from the preserved part

Maxakalisaurus topai n.gen., n.sp. (MN 5013-V): Fig.21- ischium in right lateral view; fig.22- humerus in anterior view. Scale bar: 100mm.

that the proximal articulation is wider than the distal one. The midshaft cross section is D-shaped, with the posterior surface more convex. The deltopectoral crest is incomplete in both, but the preserved part suggests it had a broad base and was well developed.

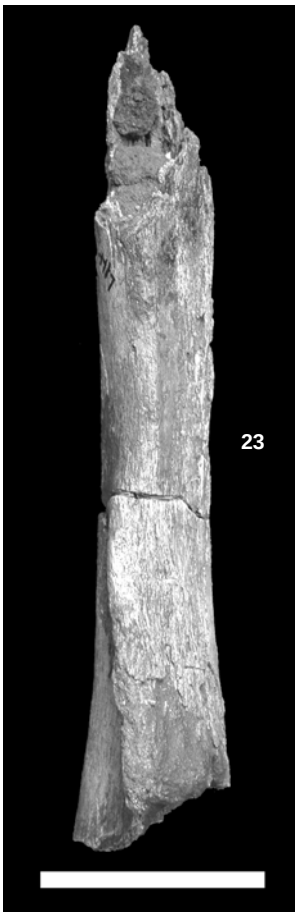
There are two general types of humerus in titanosaur sauropods - a more slender and elongate one and a more robust and shorter one. The humerus of *Maxakalisaurus topai* falls into the first category, differing therefore from *Opisthocoelicaudia*, *Argyrosaurus*, *Neuquensaurus*, and *Saltasaurus*. It is also slender than the humerus of *Epachthosaurus* and differs from *Andesaurus* that, according to the reconstruction presented by Calvo & Bonaparte (1991), has the slenderest humerus among all titanosaurs. The humerus of *Maxakalisaurus* differs from *Gondwanatitan* (the only Brazilian species for which the humerus is known) by having the deltopectoral crest less extended down the shaft.

FIBULA

Only a medial portion, close to the distal articulation of the left fibula is preserved (Fig.23), indicating that it is a robust element, similar to the condition observed in *Opisthocoelicaudia*, *Aeolosaurus*, *Alamosaurus*, *Epachthosaurus*, *Mendozasaurus* and the Saltasaurinae. The anteromedial corner has a rougth expansion bordering a medial depression, which is absent in *Alamosaurus* (LEHMAN & COULSON, 2002). A similar depression is observed in some isolated fibulae from the Peirópolis region (MNFT pers. observation).

METACARPALS

Two metacarpal bones were collected close to each other and, based on comparisons with *Epachthosaurus* were identified as metacarpal II and IV from the right side



Maxakalisaurus topai n.gen., n.sp. (MN 5013-V): fig.23- fibula in anterior view; fig.24- (A) metacarpal IV and (B) metacarpal II in anterior view. Scale bar: 100mm.

(Figs.24A-B). The proximal articulation in both is subtriangular with the point of the triangle directed interiorly. The proximal part of metacarpal IV is more compressed laterally, resulting in a comparatively more elongated proximal articulation surface. In both this surface is rugose (Figs.25 A-B). Distally those elements become subrectangular, with the anterior part broader than the posterior (= internal) one. The shaft in metacarpal II is more sigmoid, contrasting to the more compressed and straighter shaft of metacarpal IV. In terms of size, metacarpal IV is about 12 % shorter than metacarpal II.

Metacarpal elements have not been often reported in titanosaur sauropods. With the exception of *Epachthosaurus*, there is no complete manus of a titanosaur described so far, although some exist (CALVO, personal communication 2006). *Epachthosaurus* also has the metacarpal II longer than the metacarpal IV, which, according to the published measurements of MARTÍNEZ *et al.* (2004) varies between 4 and 9%, but in *Maxakalisaurus* this difference is higher.

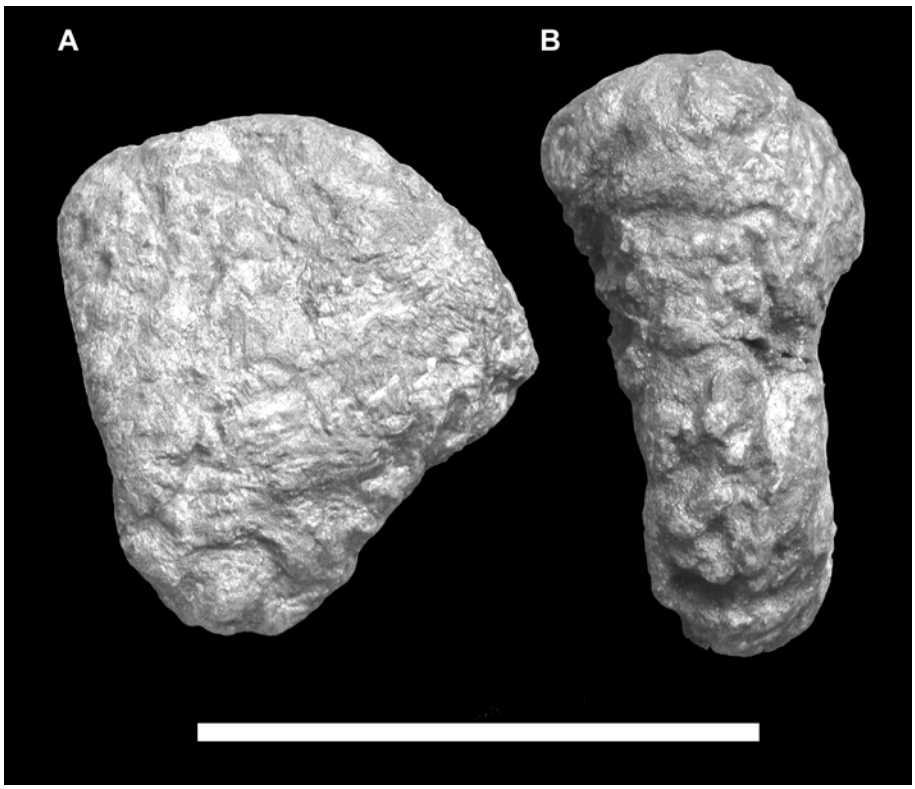


Fig.25- *Maxakalisaurus topai* n.gen, n.sp. (MN 5013-V): (A) metacarpal II and (B) metacarpal IV in proximal view. Scale bar: 100mm.

OSTEODERM

One isolated element was identified as an osteoderm (Fig.26). Although not complete, it is about 105mm long and 84mm wide, with a thicknes of about 62mm. The element is ellipsoid in outline. The dorsal side is strongly convex, with the medial line set higher. It bears ornamentation in the form of intercalated tiny bumps and pits. The ventral side is comparatively less convex, and bears a rough surface, not strongly ornamented. Internally, the osteoderm is filled by bone of spongy texture (Fig.27).

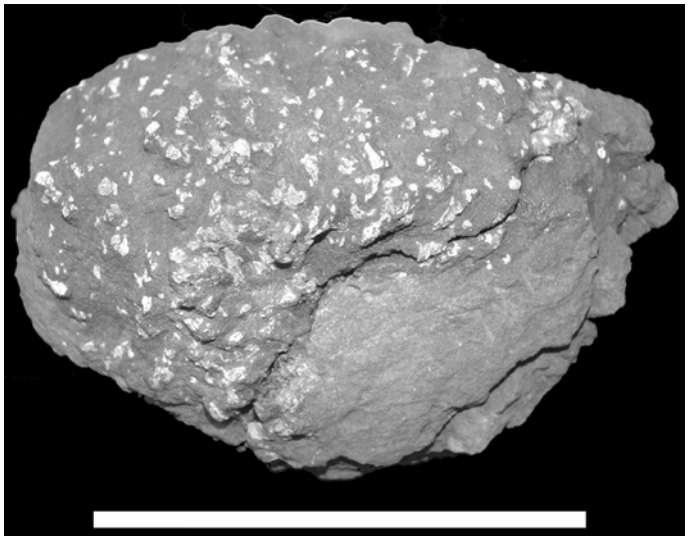


Fig.26- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): osteoderm. Scale bar: 100mm.

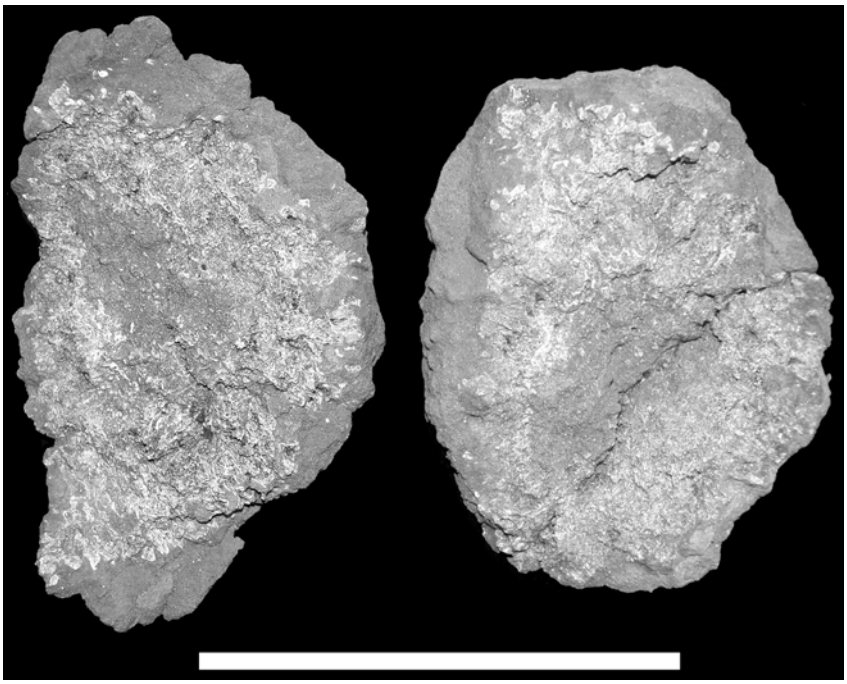


Fig.27- *Maxakalisaurus topai* n.gen., n.sp. (MN 5013-V): osteoderm in internal view. Scale bar: 100mm.

Only one isolated osteoderm was described from Brazil so far, collected in the Marilia Formation (AZEVEDO & KELLNER, 1998), and differs by being smaller and more dorsoventally compressed. The new specimen also lacks the ridge and the canals observed in the former. The osteoderms of *Saltasaurus loricatus* differ from this element by being subcircular in outline, and by bearing a ventral ridge on the internal side (POWELL, 2003).

DISCUSSION

Most titanosaur taxa are incomplete what hampers the establishment of their phylogenetic relationships. Unfortunately *Maxakalisaurus topai* is also not an exception to this rule and despite the fact that several elements of its skeleton were recovered, crucial parts are unknown. Among those are the skull, the hindlimbs and well-preserved dorsal vertebrae.

Nevertheless *Maxakalisaurus topai* can be distinguished from all four Brazilian titanosaurs presently known, even those known based on incomplete specimens. The new taxon differs from *Adamantisaurus mezzalirai* (known only by six anterior caudal vertebrae and two hemal arches) by having the centra of the anterior caudal vertebrae dorsoventrally compressed, with a straight dorsal margin of the cotyle. The chevrons described for *Adamantisaurus* are also more expanded anteroposteriorly and lack the particular articulation sufaces present in *Maxakalisaurus*. *Gondwanatitan faustoi* has a completely different shaped centrum of the anterior and medial caudal elements. The centra of the anterior and middle caudal vertebrae of *Baurutitan britoi* (known by the last sacral and 18 articulated caudal vertebrae and hemal arches) are also quite distinct from *Maxakalisaurus topai* in being more rectangular and less compressed dorsoventrally. *Trigonosaurus pricei* also differs from the new taxon by several features, including cervical vertebrae with comparatively smaller neural spines and shorter prezygapophyses, the longer dorsal vertebrae, middle caudals with well-developed transverse processes and sacral that is not constricted ventrally. *Trigonosaurus pricei* shares at least one important feature with *Maxakalisaurus topai* - the presence of a deep depression on the lateral surface of the cervical vertebrae close to the base of the neural spine. Although this could be regarded as a potential synapomorphy uniting those taxa, it should be noted that a lateral depression was also reported on a distantly related titanosaur, *Mendozasaurus neguyelap* (GONZÁLEZ RIGA, 2005), and therefore the phylogenetic signal of this feature must still be evaluated.

Besides those differences, *Maxakalisaurus topai* differs from all other titanosaur taxa by the following combination of characters: dorsoventrally compressed caudals (intermediate between Saltasaurinae and *Alamosaurus*), strongly "spool-shaped" midposterior caudals, and the dorsal margin of the neural spine in midposterior caudals inclined anteriorly, at least one sacral centrum with keel-shaped ventral surface, and metacarpal IV about 12% shorter than metacarpal II. *Maxakalisaurus* further shows the presence of at least one midposterior caudal vertebra with biconcave centrum, which is also unusual, and has been reported only in *Rinconsaurus caudamirus* (CALVO & GONZÁLEZ RIGA, 2003) and an unnamed caudal sequence from Brazil (TROTTA *et al.*, 2002). Based on comparisons with more complete titanosaurs (e.g., *Epachthosaurus sciuttoi* and *Gondwanatitan faustoi*) *Maxakalisaurus topai* reached a length of about 13m (Fig.28).

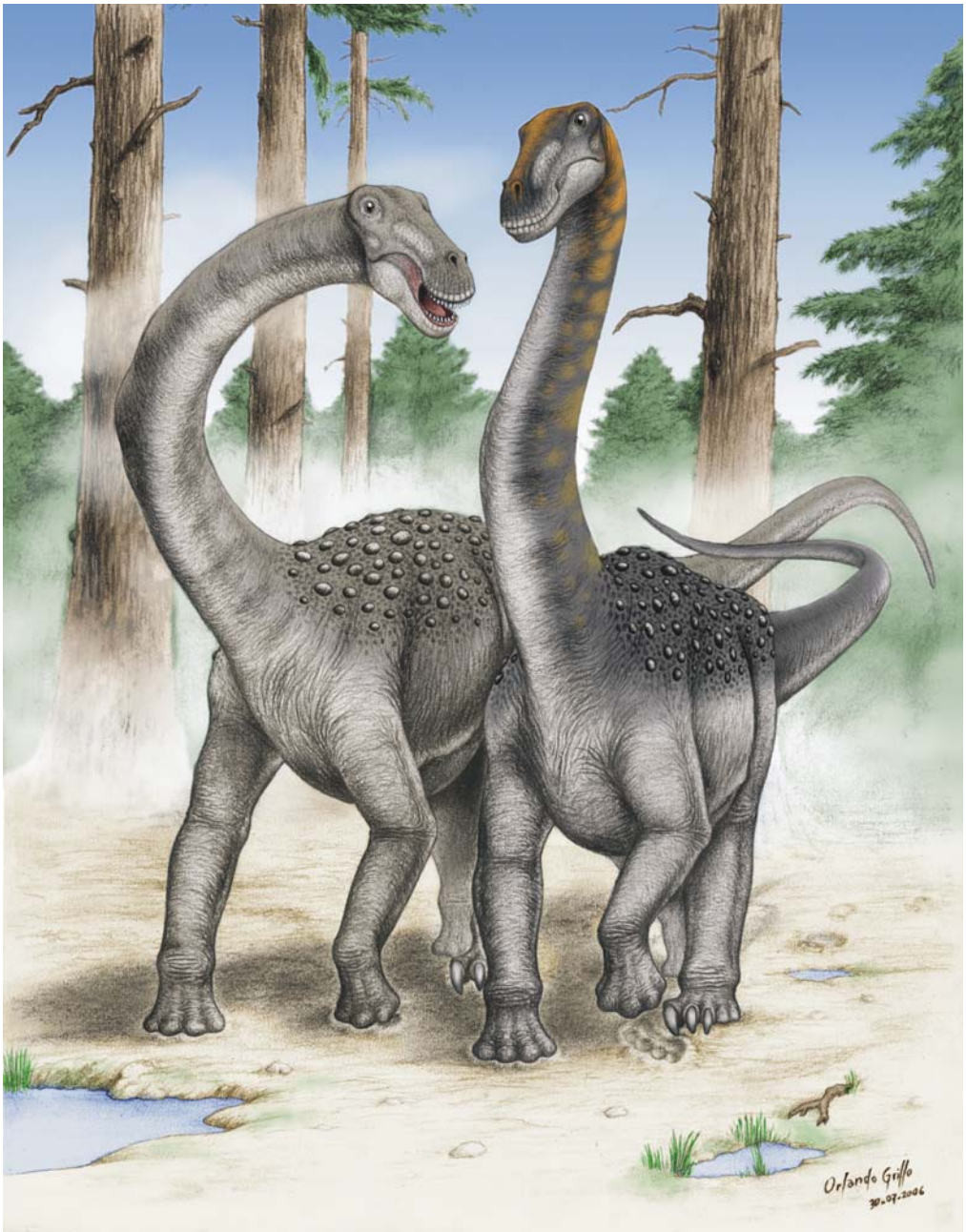


Fig.28- Life-reconstruction of *Maxakalisaurus topai* n.gen., n.sp.

Caudal vertebra MN 7051-V was excluded from the holotype because the presence of a caudal element with high centrum in *Maxakalisaurus topai* would suggest an odd configuration of the mid-caudal vertebrae, by having some elements with centra higher than wide in a sequence where the majority of the vertebrae are dorsoventrally compressed. Such a configuration was never reported in any titanosaur where almost complete portions of the tails are known. In *Alamosaurus sanjuanensis* the anterior and middle caudal vertebrae have centra which are higher than wide, with depressed elements appearing only in the distalmost portion of the tail. In *Saltasaurus loricatus*, the whole caudal sequence is made of elements with depressed centra. Despite the available data, however, we cannot exclude the possibility that such unusual configuration may exist, but only with the discovery of new, more complete material this hypothesis could be confirmed.

The phylogenetic position of *Maxakalisaurus topai* is still complex to be determined. The caudal vertebrae clearly indicate that the new Brazilian species is not a primitive member of the Titanosauria. The cervical vertebrae, not known for most titanosaurs, suggests that *Maxakalisaurus* is more derived than *Isisaurus* and *Mendozasaurus* but not a member of the consensually accepted more derived titanosaur clade named Saltasaurinae. Nevertheless *Maxakalisaurus* has the centrum of the anterior and most middle caudal vertebrae depressed, a feature also observed in the Saltasaurinae. Therefore the new Brazilian taxon is tentatively regarded as a sister group to Saltasaurinae, pending a rigorous phylogenetic analysis of the Titanosauria (which is beyond the scope of this paper).

Lastly, it is worth to mention that complete manus of titanosaur sauropods remains basically unknown. One exception is *Epachthosaurus* that shows no manual phalanges except for a vestigial element fused to the metacarpal V (MARTÍNEZ *et al.*, 2004). *Ophisthocoelicaudia* also lacks manual phalanges, which lead to the supposition that the manual phalanges in titanosaur sauropods were strongly reduced, unossified or absent (e.g., SALGADO *et al.*, 1997a). The comparatively large difference in *Maxakalisaurus topai* appears to indicate that one small phalanx might have been present in the manual digit IV. This suspicion can only be confirmed with more complete material.

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