



ON A SEQUENCE OF SACROCAUDAL THEROPOD DINOSAUR VERTEBRAE FROM THE LOWER CRETACEOUS SANTANA FORMATION, NORTHEASTERN BRAZIL¹

(With 14 figures)

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ABSTRACT: Besides being rare, most theropod remains from fossil deposits of Brazil are incomplete. Up to date the Romualdo Member (Aptian/Albian) of the Santana Formation yielded six theropod specimens. To those we add the description of a sequence of three posterior sacral and six anterior caudal vertebrae with three chevrons (MN 4743-V). Differences between MN 4743-V and members of the major theropod clades such as Ceratosauria, Allosauroida and Coelurosauria do not allow its assignment to one of those groups. Instead, MN 4743-V is referred to the Spinosauroida (Spinosauridae plus Torvosauridae), based on the presence of three robust laminae below the transverse process of the anterior caudals, which delimit three fossae. The lack of paired processes on the chevrons suggest that within Spinosauroida MN 4743-V is a member of the Spinosauridae. This is congruent with previous findings of spinosaurids in the Romualdo Member. MN 4743-V differs from the remaining specimens that present sacrocaudal elements indicating the co-existence of at least five theropod species in this deposit.

Key words: Spinosauroida, Dinosauria, Santana Formation, Lower Cretaceous, Brazil.

RESUMO: Sobre uma seqüência de vértebras sacrocaudais de um dinossauro terópode da Formação Santana, Cretáceo Inferior, Nordeste do Brasil.

Restos de terópodes de depósitos fossilíferos brasileiros são raros, sendo a maioria dos espécimens incompletos. O Membro Romualdo (Aptiano/Albiano) da Formação Santana forneceu até então seis exemplares. Somando-se a estes é descrito uma seqüência de seis vértebras sacrais posteriores, seis anteriores com três chevrons (MN 4743-V). Diferenças marcantes entre MN 4743-V e alguns táxons dos principais grupos de Theropoda, como Ceratosauria, Allosauroida e Coelurosauria não permitem que este material seja associado a algum destes clados. Por outro lado, MN 4743-V apresenta uma semelhança marcante com os Spinosauroida (Spinosauridae+Torvosauridae), que é a presença de duas lâminas robustas sob o processo transversal, delimitando três fossas. A ausência de processos pareados na parte proximal do chevron sugere que, dentro de Spinosauroida, MN 4743-V seja um membro de Spinosauridae, o que é congruente com achados prévios de espinossaurídeos no Membro Romualdo. MN 4743-V difere dos demais exemplares com elementos sacro-caudais encontrados no Membro Romualdo, indicando a presença de pelo menos cinco espécies de terópodes neste depósito.

Palavras-chave: Spinosauroida, Dinosauria, Formação Santana, Cretáceo Inferior, Brasil.

INTRODUCTION

Theropod remains from fossil deposits of Brazil are rare and most specimens are fragmentary. Besides *Staurikosaurus pricei* Colbert, 1970 from the Late Triassic strata of the Santa Maria Formation (COLBERT, 1970) and *Pycnonemosaurus nevesi* Kellner & Campos, 2002 from the Late Cretaceous Bauru Group (KELLNER & CAMPOS, 2002), only three other non-avian theropod taxa were described, all from the Early Cretaceous

(Aptian-Albian) Romualdo Member of the Santana Formation (see KELLNER, 1998; KELLNER & CAMPOS, 2000, for a review): *Irritator challengeri* Martill, Cruikshank, Frey, Small & Clarke, 1996, *Angaturama limai* Kellner & Campos, 1996, and *Santanaraptor placidus* Kellner, 1999.

Irritator challengeri, known from the posterior end of a skull, was first regarded as a maniraptoran dinosaur (MARTILL *et al.*, 1996) and latter referred to the Spinosauridae (KELLNER, 1996), what was

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followed by other authors (CHARIG & MILNER, 1997; SERENO *et al.*, 1998; SUES *et al.*, 2002; TAQUET & RUSSEL, 1998). *Angaturama limai*, also a spinosaurid, is based on the anterior end of a skull (KELLNER & CAMPOS, 1996), and the much smaller tyrannoraptoran *Santanaraptor placidus* is based on an incomplete pelvis, caudal vertebrae, and hind limbs (KELLNER, 1999). Other theropod remains from the Romualdo Member include an undetermined sacrum with fragments of the right ilium (FREY & MARTILL, 1995), a partial skeleton of a small coelurosaurian theropod (MARTILL *et al.*, 2000), and a large pelvis with segments of the vertebral column and limbs, figured (CAMPOS & KELLNER, 1991; KELLNER, 2001) but not described yet. To this we add the description of a series of sacral and caudal vertebrae, housed at the Museu Nacional/ UFRJ (MN 4743-V), which is the seventh theropod specimen from the Araripe basin known so far. This material was briefly mentioned in the literature (CAMPOS & KELLNER, 1991; BITTENCOURT & KELLNER, 2002; KELLNER & CAMPOS, 1999), and is fully described here.

GEOLOGICAL SETTING

The Santana Formation is the most fossiliferous lithostratigraphic unit of the Araripe Basin (see MAISEY, 1991, for a review). It was divided by BEURLIN (1971) in three members, respectively from base to top: Ipubi, Crato, and Romualdo.

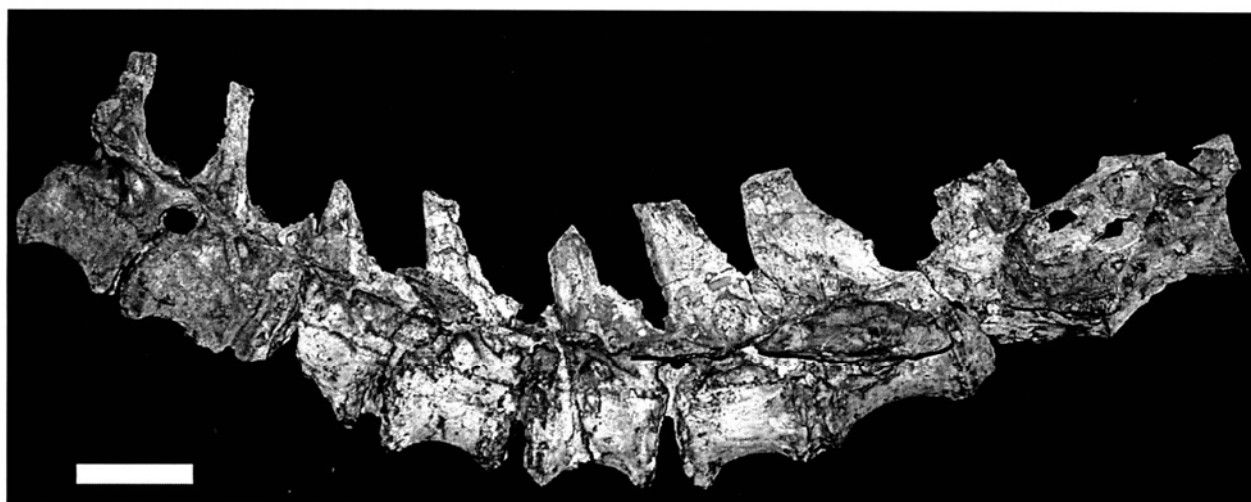
The Romualdo Member, where the specimen MN4743-V was found, is composed of shales and

marls, with locally coarser sediments such as siltstones and fine-grained sandstones (CAVALCANTI & VIANA, 1990). The famous Santana-nodules, widely known for the exquisitely preserved fossils, are found within the shales and marls. The fossil vertebrate record is extensive, comprising a large diversity of fishes and pterosaurs. Turtles, crocodylomorphs, and more rarely dinosaurs are found too (*e.g.*, KELLNER & CAMPOS, 1999). Based on palynomorphs an Aptian-Albian age is suggested for this fossil *lagerstätte* (PONS, BERTHOUE & CAMPOS, 1990).

The outcrops of the Santana Formation are situated in the states of Ceará, Pernambuco, and Piauí. The specimen MN 4743-V was possible collected in the surroundings of Santana do Cariri City, southern Ceará State, where most of the nodules from the Santana Formation are collected (KELLNER & CAMPOS, 2000; KELLNER & TOMIDA, 2000).

DESCRIPTION

The specimen MN 4743-V comprises nine articulated vertebrae: three posterior sacrals and six anterior caudals, that were preserved in an upward curvature (Figs. 1-13). Three chevrons are also preserved: one of them complete, another lacking its ventral end and the last presenting only its basal part. Overall the material is well preserved, without any major sign of distortion. The neural arches of some elements are incomplete and in some parts the vertebrae were broken, possible during the collecting activity. The specimen was prepared mainly with



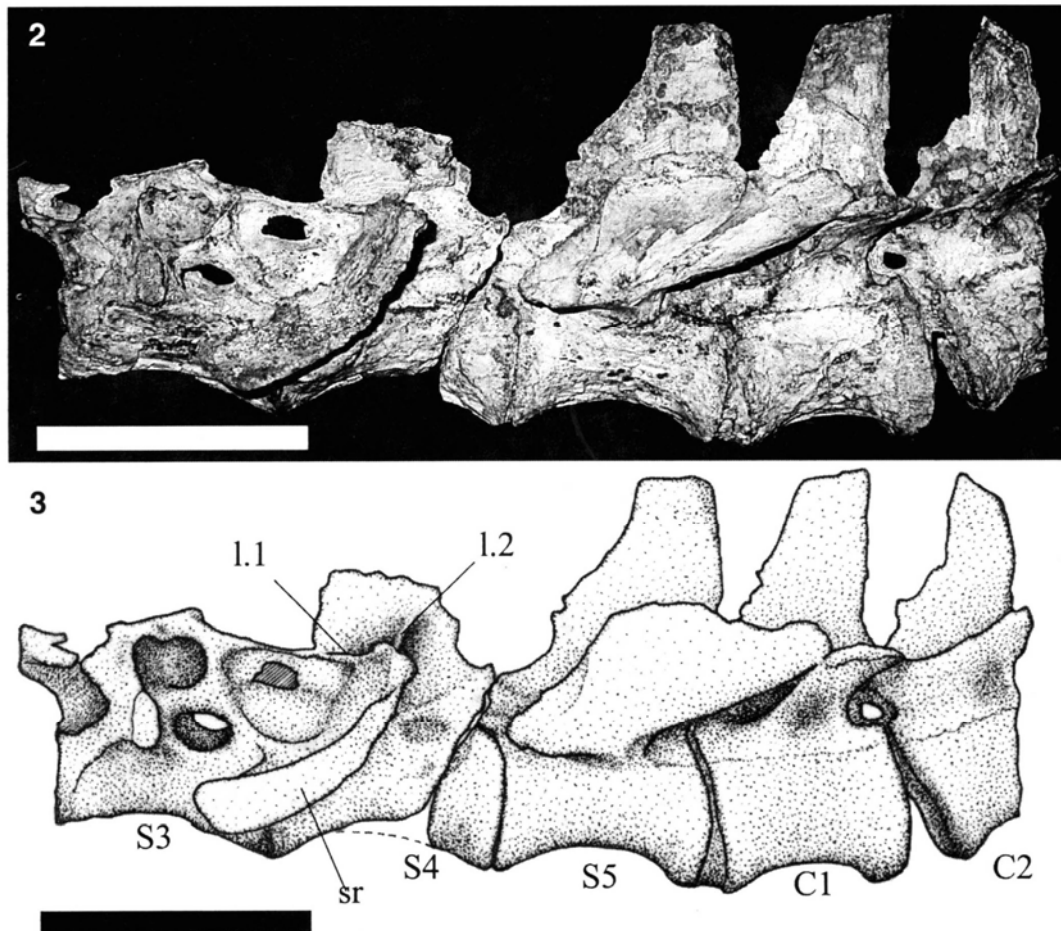
MN 4743-V: fig. 1- photograph of the sacral and caudal vertebrae (right lateral view), in natural position. Scale bar = 5cm

acid, following a method developed for tetrapods preserved in calcareous nodules from the Santana Formation (KELLNER, 1995).

All vertebral centra are amphicoelous and spool-shaped, with concave lateral and ventral surfaces. The neural canal is broad and decreases in size from the first to the ninth vertebra. The suture of the neural arch and the centrum is visible in all elements, indicating that MN 4743-V does not represent a completely mature animal.

Despite being closely connected, none of the centra of the three sacrals are fused to each other. With few exceptions (*e.g.*, Herrerasauridae and some ceratosaurs) the non-coelurosaurian theropod sacrum is composed of five vertebrae. Since it is very unlikely that MN 4743-V represents a coelurosaur (see Discussion), we interpret that the preserved

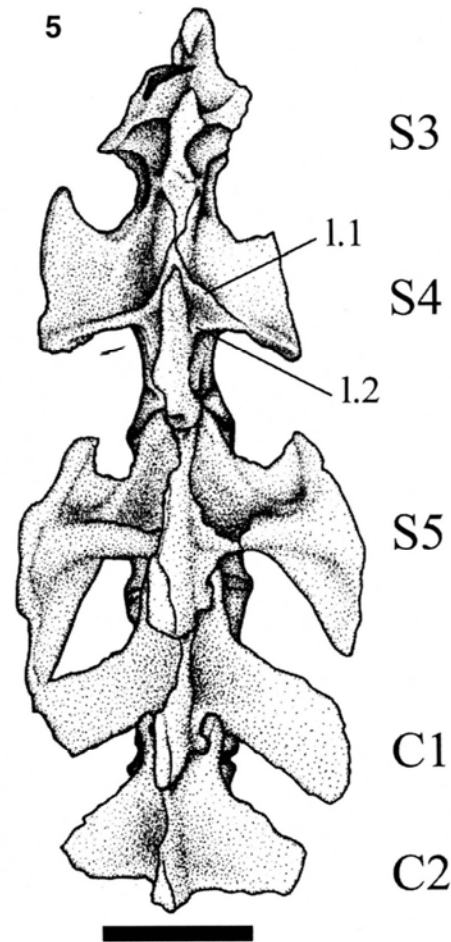
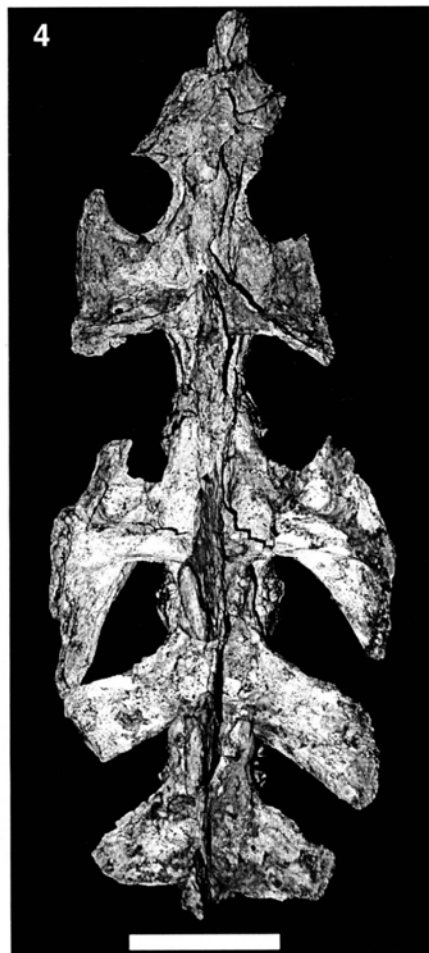
sacrals of MN 4743-V represent the third, fourth and fifth sacral vertebrae. The first preserved sacral (sacral 3) is partially broken, particularly the neural arch (Figs.2-3). The attachment surface for the sacral rib is visible on the right side and is positioned at the contact surface of the centrum and the neural arch. On the left side, part of the sacral rib is preserved. A deep rounded fossa is present on the neural arch, above the parapophysis, which is better preserved on the left side (Figs.2-3). A well developed oval foramen, the intervertebral foramen, is present at the contact surface between the neural arch and the centrum and connects with the neural canal. The centrum is elongated anteroposteriorly and has a rounded outline (differing from the elliptic condition observed in the caudals).



MN 4743-V, the sacral and caudal vertebrae 1 and 2, in left lateral view: fig.2- photograph; fig.3- drawing. (S3-S5) presumed sacral vertebrae 3, 4 and 5, (C1-C2), caudal vertebrae 1 and 2, (l.1) lamina 1, (l.2) lamina 2, (sr) sacral rib. Scale bar = 5cm.

The second preserved sacral (sacral 4) is tightly connected with the first. The neural spine forms a thin bony blade that is elongated anteroposteriorly; its exact height cannot be established since the dorsal portion is not preserved (Figs.2-3). The transverse process forms a thin expanded lamina which, in lateral view, is posteriorly inclined relative to the horizontal plane. Dorsally the transverse process sends a thin lamina that extends over the basal part of the lateral surface of the neural spine (Fig.2-5). A second lamina, directed anteriorly, is present at the base of the former (Figs.2-5). The intersection of both laminae and the base of the neural spine forms a shallow depression. As in the preceding sacral, a fossa is present on the lateral surface of the neural arch posterior to the transverse

process, differing by being more elongated and less uniform, with two marked depressions. A rounded and smaller intervertebral foramen is also present. The anterior surface of the transverse process shows a well developed concavity close to its ventral margin (Figs.4-5). The parapophysis is large and placed on the anterior part of the vertebra, occupying a lower position compared to the first preserved sacral (Figs.2-3). The suture between the parapophysis and the sacral rib is not closed. The sacral rib is stout and connects with the transverse process, forming a bony lamina. The suture between the transverse process and the sacral rib is still open and runs from the laterodorsal to the ventromedial corner of this of bony lamina. Distally, the sacral rib is expanded and forms the articular surface for the



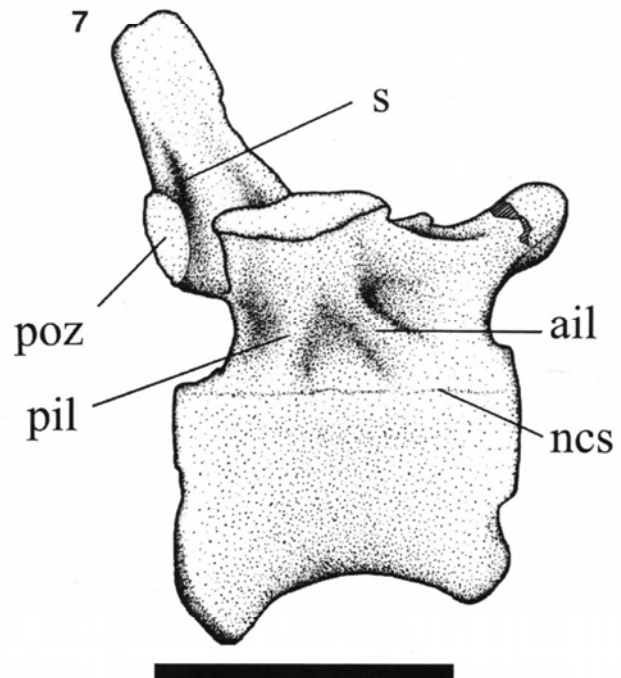
MN 4743-V, the sacral and caudal vertebrae 1 and 2, in dorsal view: fig.4- photograph; fig.5- drawing. (S3-S5) presumed sacral vertebrae 3, 4 and 5, (C1-C2), caudal vertebrae 1 and 2, (l.1) lamina 1, (l.2) lamina 2. Scale bar = 5cm.

ilium, getting broader ventrally. The centrum is similar to the preceding vertebra by being elongated anteroposteriorly and showing an rounded outline. It differs from the other sacrals by having the anterior articular surface wider than the posterior one.

The third preserved sacral (sacral 5) is the best preserved one (Figs.2-5). The neural spine is blade-like, anteroposteriorly expanded, broader on the base than on the top, and, in lateral view, shows an anterior projection (Figs.2-3). The transverse process is broad and robust, and has the dorsal margin forming a right angle with the neural spine. The anterior lamina, uniting the transverse process with the neural spine is less developed than in the preceding sacral. A dorsally projected crest, uniting the transverse process and the neural spine is also observed. The concavity at the base of the transverse process observed in the preceding sacral is also present here, but much more developed. Compared to the preceding sacral, the parapophysis is located more posteriorly (reaching the middle portion of the centrum) and occupies a higher position (Figs.2-3). The sacral rib is fused with the transverse process

and forms a stout, anteroposteriorly expansion that contacts the ilium (Figs.2-5). The centrum shows the basic morphology of the preceding sacrals, and, like the first preserved one, has the posterior articular surface wider than the anterior one (differing from the second preserved one).

The caudal series is formed by six anteriormost vertebrae that decrease in size posteriorly (Fig. 1). All are very similar in their general morphology. The neural spines are tall, broader on the base and inclined backward (Figs.6-7). A shallow groove for the interspinous ligament is observed on the posterior part, between the postzygapophyses (Figs.8-9). A well marked dorsoventrally depression is present on the posterior portion of the neural spine, anterior to the postzygapophyses (Figs.6-7). In each caudal, the transverse processes are directed lateroposteriorly, with a slight inclination upward (Figs.2-3, 6-7). The distal end is slightly broader than the proximal one. On the dorsal surface, close to the base of the neural spine, a deep and rounded supradiapophyseal fossa is observed.

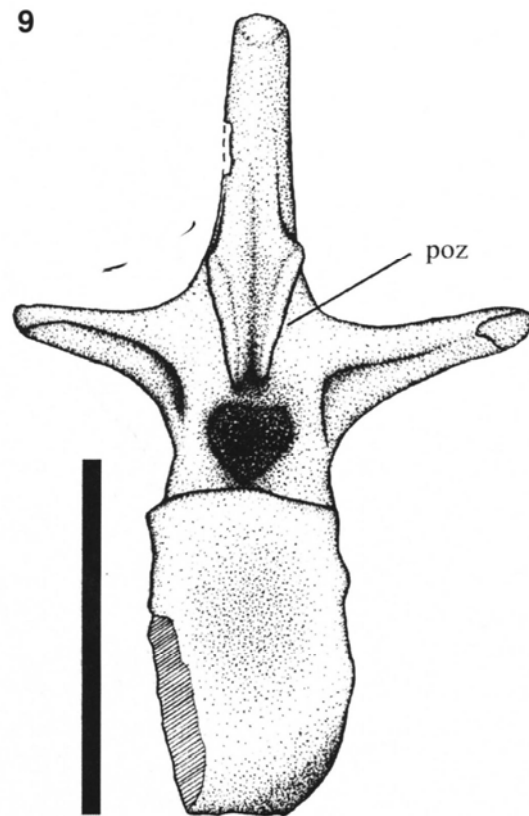
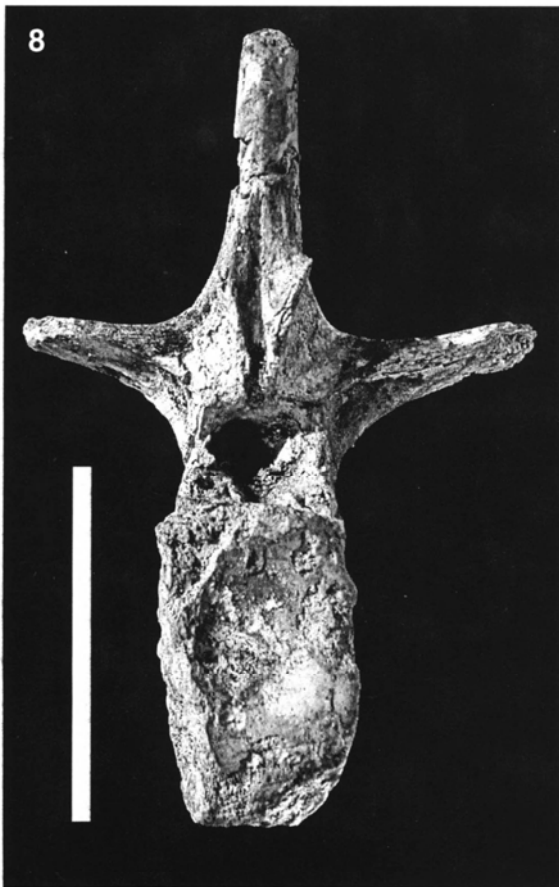


MN 4743-V, right lateral view, the caudal vertebrae 5 and 6: fig.6- photograph; fig.7- drawing. (ail) anterior infradiapophyseal lamina, (ncs) neurocentral suture, (pil) posterior infradiapophyseal lamina, (poz) postzygapophyses, (s) sulcus. Scale bar = 8cm.

The ventral region of the transverse process shows a complex morphology, with two infradiapophyseal buttresses separating three different fossae (Figs.6-7). In the first caudal, the anterior region of the transverse process has two components. The dorsal one forms a horizontal bony shelf (the prezygapophyseal lamina), linking the transverse process to the prezygapophysis, while the ventral one forms the anterior buttress. This anterior buttress gets gradually more separated from the prezygapophyseal laminae in the subsequent caudal vertebrae. The posterior infradiapophyseal buttress is more robust and occupies essentially the same position in all preserved elements.

The most anterior fossa is delimited dorsally by the prezygapophyseal lamina and posteroventrally by the infradiapophyseal buttress (Figs.6-7). In the first caudal vertebra this opening is well developed, being

larger than the other two fossae, but in the subsequent caudals it is comparatively smaller. The intermediate fossa is bordered anteriorly and posteriorly by both buttresses and dorsally by the main part of the transverse process. In the first caudal this opening is comparatively small, has a rounded shape and shows a sharp ventral margin formed by a bony ridge. Starting at the second caudal, the intermediate fossa gets comparatively larger, with the ventral margin less marked. The posterior fossa, limited by the posterior infradiapophyseal buttress and the posterior margin of the transverse process is the smallest of the three and gets shallower in the posterior caudals (Figs.6-7). The prezygapophysis is long and pointed in lateral view, directed forward and upward. The postzygapophysis, observable in detail only on the sixth caudal (Figs.6-9), is formed by two distinct elliptical areas faced laterally and downward,



MN 4743-V, the caudal vertebrae 6, in posterior view: fig.8- photograph; fig.9- drawing. (poz) postzygapophyses. Scale bar = 5cm

separated by the groove of interspinous ligament. The centra are taller than wide, a condition that is accentuated in subsequent vertebrae, which are laterally more compressed (Figs.8-9). The ventroposterior margin of all preserved elements is ventrally projected relative to the anterior one (Figs.1, 6-7). The ventral margin of the posterior articular surface is bevelled and shows a pair of small keels for the articulation of the chevron (Figs.10-11). The ventral surface is concave and lacks any groove along its midline. All preserved caudal vertebrae lack lateral foramina or pleurocoels.

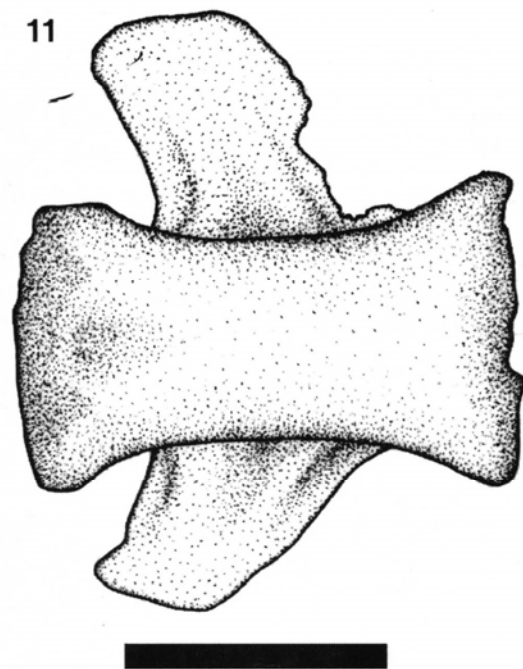
The three preserved chevrons belong to anterior segment of the tail, but their exact position on the caudal series can not be asserted. They differ in size, with the largest comprising only the proximal part, the second lacking only the distal part and the third (and smallest one) being complete. The better preserved one is dorsoventrally elongated and laterally compressed on its distal part (Figs.12-13). The haemal canal is higher than wide, delimited dorsally by a bony bridge (Figs.14-15). The articulation surface with the centrum is concave. All lack any anterior or posterior process close to the base, as found in some theropods (*e.g.*, BRITT,

1991). In lateral view, the shaft of the chevron curves posteriorly; this curvature gets less accentuated posteriorly. The posterior surface bears a dorsoventrally oriented sulcus.

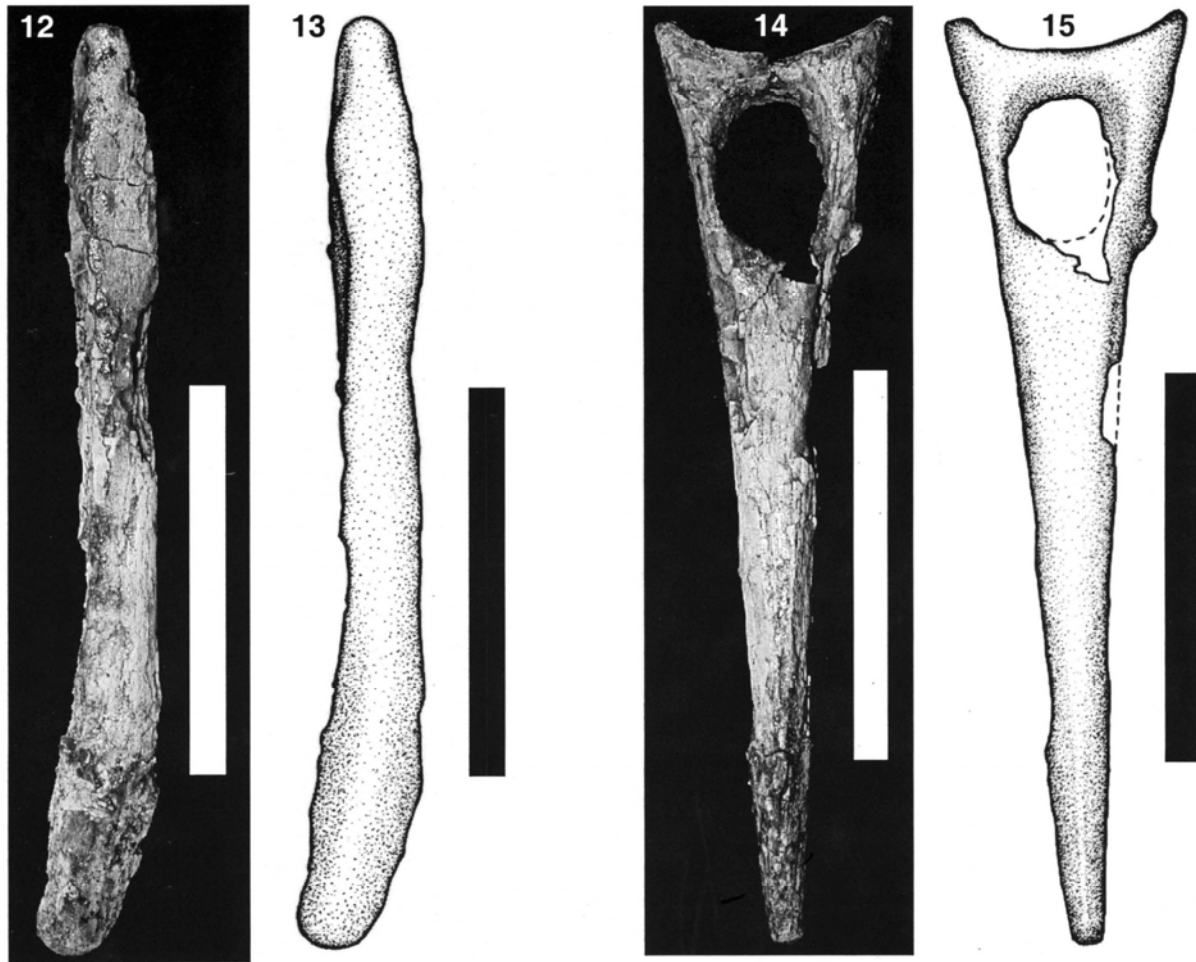
DISCUSSION

The caudal vertebral centra of MN 4743-V are taller than wide, a feature commonly found in Theropoda (MAKOVICKY, 1997) allowing its assignment to this dinosaur clade. The establishment of the relationships of the new specimen to other theropod groups, however, is more complicated. Despite the large amount of characters used in the phylogeny of theropod dinosaurs, synapomorphies based on sacral or caudal elements are scarce (GAUTHIER, 1986; SERENO, 1999) or highly homoplastic (HOLTZ, 2000). Below, we discuss the sacrocaudal synapomorphies of some theropod clades based on matrices available in the literature (CURRIE & CARPENTER, 2000; HARRIS, 1998; HOLTZ, 2000; NORELL, CLARK & MAKOVICKY, 2001; SERENO, 1999), in order to clarify the phylogenetic position of MN 4743-V.

Although there are several conflicts regarding



MN 4743-V, the caudal vertebra 3, in ventral view: fig.10- photograph; fig.11- drawing. Scale bar = 3cm.



MN 4743-V: fig.12- photograph of the posteriormost preserved chevron in lateral view; fig.13- drawing of the caudal vertebra 6 in posterior view; fig.14- photograph of the posteriormost preserved chevron in anterior view; fig.15- drawing of the photograph of the posteriormost preserved chevron in anterior view. Scale bar = 5cm.

published theropod phylogenies, most agree in dividing the Theropoda into the following clades: Ceratosauria (including the Abelisauria), Spinosauroida, Allosauroida, and Coelurosauria (including Maniraptora).

The Ceratosauria has been largely recognized as a natural group (GAUTHIER, 1986; HOLTZ, 2000; SERENO, 1999), although some authors have questioned its monophyly (RAUHUT, 1998; FORSTER, 1999). HOLTZ (2000) assigned two synapomorphies to Ceratosauria based on caudal and sacral vertebrae: the fusion of sacral vertebrae forming a synsacrum in adults and the presence of a shallow sulcus in the ventral margin of the anterior caudal vertebrae. Regarding the synsacrum, although it is true that most

ceratosaurs display this feature, *Dilophosaurus wetherilli* (Welles, 1970) (HOLTZ, 2000) and some specimens of *Coelophysis bauri* (Cope, 1889) (COLBERT, 1989) lack a synsacrum. In any case, MN 4743-V also lacks a synsacrum.

The second ceratosaurian synapomorphy presented by HOLTZ (2000) is more problematic: a sulcus on the ventral margin of the caudal vertebrae is present in several non-ceratosaurian theropod taxa as *Allosaurus fragilis* Marsh, 1877 (MADSEN, 1993), *Sinraptor dongi* Currie & Zhao, 1993 (CURRIE & ZHAO, 1993; HARRIS, 1998), *Acrocanthosaurus atokensis* Stovall & Langston, 1950 (CURRIE & CARPENTER, 2000; HARRIS, 1998;), *Torvosaurus tanneri* Galton & Jensen, 1979 (BRITT, 1991), and

in many maniraptorans (NORELL, CLARK & MAKOVICKY, 2001; NORELL & MAKOVICKY, 1997; MAKOVICKY & SUES, 1998). The ventral margin of the anterior caudals of MN 4743-V are smooth and do not present any sulcus.

Within Ceratosauria, there is one group that shows several Gondwanic taxa: the Abelisauria (BONAPARTE, 1996; BONAPARTE & NOVAS 1985; BONAPARTE, NOVAS & CORIA, 1990; KELLNER & CAMPOS, 2002; NOVAS, 1991, 1997; SAMPSON *et al.*, 1996, 1998; SAMPSON, CARRANO & FORSTER, 2001). CORIA & SALGADO (1998) suggested that the presence of caudal transverse processes distally expanded is a synapomorphy of the Abelisauria, what was confirmed by latter studies (KELLNER & CAMPOS, 2002). Although the distal end of caudal transverse processes of MN 4743-V tends to be broader than the proximal, this condition is distinct from that of abelisaurids. Therefore MN 4743-V lacks any feature that diagnoses the Ceratosauria (including the Abelisauria) and is not a member of this clade.

Another large and widespread theropod group is the Allosauroidae (*sensu* SERENO *et al.*, 1996). Although no synapomorphy was found in the sacra or caudals that diagnoses this clade, the sacrocaudal anatomy is well known for at least one of its members (*e.g.*, *Allosaurus* Marsh, 1877), while for others such as *Acrocanthosaurus* Stovall & Langston, 1950 and *Sinraptor* Currie & Zhao, 1993, the available information is limited. A feature present on these three species is a midline groove along the ventral face of the anterior caudals (CURRIE & ZHAO, 1993; HARRIS, 1998; MADSEN, 1993). Furthermore, both *Acrochontosaurus* and *Allosaurus* bear pleurocoels on sacral centra. None of those characters are seen in the specimen described in this paper, suggesting that MN 4347-V is not an allosauroid. An additional difference between MN 4743-V and *Allosaurus* is that, in the former, the transverse process and sacral rib are fused to each other in sacral 4, while in the latter, they are not. In *Acrochontosaurus* and *Sinraptor*, the material is too fragmented to verify the condition of this character. *Sinraptor* further differs other theropods (including MN 4743-V) by having the ventral margin of the posterior articular facet of the sacral and caudal centra strongly offset above anterior one (CURRIE & ZHAO, 1993).

The taxonomic composition of Coelurosauria is debatable, since some authors regard the Tyrannosauridae as a member of that clade (HOLTZ, 2000; SERENO, 1999), while others do not (GAUTHIER, 1986; NORELL, CLARK & MAKOVICKY, 2001). The synapomorphies of the Coelurosauria

proposed by SERENO (1999) and HOLTZ (2000) are based on characters that require more complete material, such as the number of sacral vertebrae, the transition point in the tail and the anatomy of the posterior chevrons, none of which can be verified in MN 4743-V. More recently, NORELL, CLARK & MAKOVICKY (2001) proposed two sacrocaudal sinapomorphies for the Coelurosauria (without Tyrannosauridae): ventral surface of the posterior sacral centra flattened, sometimes presenting a shallow sulcus, and proximal end of chevrons of anterior caudals elongated anteroposteriorly, flattened and platelike. None of these are observed in the MN 4743-V, suggesting that it is not a coelurosaur *sensu* NORELL, CLARK & MAKOVICKY (2001).

Regarding Tyrannosauridae, the only synapomorphic sacrocaudal character proposed by NORELL, CLARK & MAKOVICKY (2001) for this clade is the presence of pleurocoels on the anterior sacra, which cannot be verified in MN 4743-V (which has only the last three sacra preserved). HOLTZ (2000) raised the possibility of a close relationship between Tyrannosauridae and Ornithomimosauria, forming the Arctometatarsalia. The only sacrocaudal synapomorphy raised by him that can be evaluated in MN 4743-V is the fusion of the sacral neural spines forming a lamina (HOLTZ 2000), a condition not displayed by the material described here.

The remaining group of theropods with which MN 4743-V is compared are the Spinosauroidae. Regarded as a clade of basal Tetanurae, it is formed by the Spinosauridae and Torvosauridae, which share several features of the skull, jaws and forearms (SERENO, 1999; SERENO *et al.*, 1998). Unfortunately, most spinosauroid species lack detailed information regarding the sacral and caudal vertebrae. The only species in which sacro-caudal material is available are *Suchomimus tenerensis* Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson & Wilson, 1998 and *Baryonyx walkeri* Charig & Milner, 1986. Based on the published reconstruction of *Suchomimus tenerensis* (SERENO *et al.*, 1998: fig.3), there are some sacral vertebrae (undescribed) that apparently bear comparatively large neural spines. Although the neural spines in MN 4743-V are tall, they apparently did not reach the same proportions as in this taxon. All caudal vertebrae referred to *Suchomimus tenerensis* are from the middle or posterior region of the tail and cannot be directly compared with MN 4743-V. The only anterior caudal vertebrae described for *Baryonyx walkeri* shows a strongly laterally compressed centrum (an autapomorphic feature of this species according to

Concerning the previous record of theropods in the Santana Formation, there are four specimens that comprise postcranial material that apparently belong to different taxa: the comparatively small coelurosaurs *Santanaraptor placidus* and SMNK 2349 PAL; the incomplete sacrum and ilium of unknown affinities (SMNS 58203); and the complete pelvis with segments of the vertebral column and limbs (MN 4802-V) representing an indeterminate spinosaurid. The new material described here (MN 4743-V) differs from all, indicating the presence of five different theropod species co-existing in the stratigraphic horizon of the Romualdo Member.

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LITERATURE CITED

- BEURLEN, K., 1971. As condições ecológicas e fisiológicas da formação Santana na chapada do Araripe (Nordeste do Brasil). **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, **43**:411-415.
- BITTENCOURT, J.S. & KELLNER, A.W.A., 2002. New theropod remains from the Romualdo Member, Santana Formation (Aptian-Albian), Northeastern Brazil. In: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 3., Rio de Janeiro. **Livro de Resumos...**, Rio de Janeiro: UERJ, p.18.
- BONAPARTE, J.F., 1985. A horned Cretaceous carnosaur from Patagonia. **National Geographic Research**, Washington, **1**:149-152.
- BONAPARTE J.F., 1996. Cretaceous tetrapods of Argentina. **Münchner Geowissenschaft Abhandlungen (A)**, München, **30**:73-130.
- BONAPARTE, J.F. & NOVAS, F.E., 1985. *Abelisaurus comahuensis*, n.gen., n.sp., Carnosauria del Cretácico tardío de Patagonia. **Ameghiniana**, Buenos Aires, **21**(2-4):259-265.
- BONAPARTE, J.F.; NOVAS, F.E. & CORIA, R.A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. **Contributions in Science**, Los Angeles, **416**:1-41.
- BRITT, B.B., 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. **Brigham Young University Geology Studies**, Utah, **37**:1-72.
- CAMPOS, D.A. & KELLNER, A.W.A., 1991. Dinosaurs of the Santana Formation with comments on other Brazilian occurrences. In: MAISEY, J.G. (Ed.) **Santana fossils: an illustrated atlas**, Neptune: T.F.H. p.372-375.
- CAVALCANTI, V.M.M. & VIANA, M.S.S., 1990. Faciologia dos sedimentos não-lacustres da formação Santana (Cretáceo Inferior da bacia do Araripe, Nordeste do Brasil). In: SIMPÓSIO SOBRE A BACIA DO ARARIPE E BACIAS INTERIORES DO NORDESTE, 1., Crato. **Atas...**, Crato: URCA/SBP, p.193-207.
- CHARIG, A.J. & MILNER, A.C., 1986. *Baryonyx walkeri*, a remarkable new theropod dinosaur. **Nature**, London, **324**:11-70.
- CHARIG, A.J. & MILNER, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. **Bulletin of the Natural History Museum of London (Geol)**, London, **53**(1):11-70.
- COLBERT, E.H., 1970. A saurischian dinosaur from the Triassic of Brazil. **American Museum Novitates**, New York, **2405**:1-39.
- COLBERT, E.H., 1989. The Triassic dinosaur *Coelophysis*. **Museum of Northern Arizona Bulletin**, Flagstaff, **57**:1-160.
- CORIA, R.A. & SALGADO L., 1998. A basal Abelisauria Novas, 1992 (Theropoda-Ceratosauria) from the Cretaceous of Patagonia, Argentina. **Gaia**, Lisboa, **15**:89-102.
- CURRIE, P.J. & CARPENTER, K., 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. **Geodiversitas**, Paris, **22**(2):207-246.
- CURRIE, P.J. & ZHAO, X.J., 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xingjiang, People's Republic of China. **Canadian Journal of Earth Sciences**, Dartmouth, **30**(10-11):2037-2081.
- FORSTER, C.A. 1999. Gondwana dinosaur evolution and biogeographic analysis. **Journal of African Earth Sciences**, Amsterdam, **28**(1):169-185.
- FREY, E. & MARTILL, D.M., 1995. A possible oviraptorosaurid theropod from the Santana Formation (Lower Cretaceous, ?Albiano) of Brazil. **Neues Jahrbuch für Geologie und Paläontologie Monatshefte**, Stuttgart, **1995**(7):397-421.
- GAUTHIER, J., 1986. Saurischian monophyly and the origin of birds. **Memoirs of the California Academy of Sciences**, San Francisco, **8**:1-55.
- HARRIS, J., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status and paleobiogeographic implications, based on a new specimen from Texas. **New Mexico Museum National History Bulletin**, Albuquerque, **13**:1-75.

- HOLTZ, T.R., 2000. A new phylogeny of the carnivorous dinosaurs. **Gaia**, Lisboa, **15**:5-61.
- KELLNER, A.W.A., 1995. Técnica de preparação para tetrápodes fósseis preservados em rochas calcárias. **A Terra em Revista**, Rio de Janeiro, **1**(0):24-31.
- KELLNER, A.W.A., 1996. Remarks on Brazilian dinosaurs. **Memoirs of the Queensland Museum**, Brisbane, **39**(3):611-626.
- KELLNER, A.W.A., 1998. Panorama e Perspectiva do Estudo de Répteis Fósseis do Brasil. **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, **70**(3):647-676.
- KELLNER, A.W.A., 1999. Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian), Northeastern Brazil. **Boletim do Museu Nacional, Nova Série, Geologia**, Rio de Janeiro (49):1-8.
- KELLNER, A.W.A., 2001. New information on the theropod dinosaurs from the Santana Formation (Aptian-Albian), Araripe Basin, Northeastern Brazil. **Journal of Vertebrate Paleontology**, Illinois, **21**(supp.3):67A.
- KELLNER, A.W.A. & CAMPOS, D.A., 1996. First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. **Neues Jahrbuch für Geologie und Paläontologie Abhandlungen**, Stuttgart, **199**(2):151-166.
- KELLNER, A.W.A. & CAMPOS, D.A., 1999. Vertebrate paleontology in Brazil- a review. **Episodes**, Beijing, **22**(3):238-251.
- KELLNER, A.W.A. & CAMPOS, D.A., 2000. Brief review of dinosaur studies and perspectives in Brazil. **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, **72**(4):509-538.
- KELLNER, A.W.A. & CAMPOS, D.A., 2002. On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. **Arquivos do Museu Nacional**, Rio de Janeiro, **60**(3):163-170.
- KELLNER, A.W.A. & TOMIDA, Y., 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), Northeastern Brazil. **National Science Museum Monographs**, Tokyo, **17**:1-135.
- MADSEN, J.H., 1993. *Allosaurus fragilis*: a revised osteology. **Bulletin of Utah Geological Survey**, Utah, **109**:1-163.
- MAISEY, J.G. (Ed.), 1991. **Santana fossils: an illustrated atlas**. Neptune: T.F.H. 459p.
- MAKOVICKY, P., 1997. Postcranial axial skeleton, comparative anatomy. In: CURRIE, P.J. & PADIAN, K. (Eds.) **Encyclopedia of dinosaurs**. San Diego: Academic Press. p.579-590.
- MAKOVICKY, P.J. & SUES, H.D., 1998. Anatomy and Phylogenetic Relationships of the Theropod Dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. **American Museum Novitates**, New York, **3240**:1-27.
- MARTILL, D.M.; CRUICKSHANK, A.R.I.; FREY, E.; SMALL, P.G. & CLARKE, M., 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. **Journal of the Geological Society of London**, London, **153**(1):5-8.
- MARTILL, D.M.; FREY, E.; SUES, H.D.; CRUICKSHANK, A.R.I., 2000. Skeletal remains of a small theropod dinosaur with associated soft structures from the Lower Cretaceous Santana Formation of Northeastern Brazil. **Canadian Journal of Earth Sciences**, Dartmouth, **37**:891-900.
- NORELL, M.A.; CLARK, J.M. & MAKOVICKY, P.J., 2001. Phylogenetic relationships among coelurosaurian theropods. In: GAUTHIER, J. & GALL, L.F. (Eds.) **New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom**. New Haven: Peabody Museum of Natural History. p.49-66.
- NORELL, M.A. & MAKOVICKY, P.J., 1997. Important features of the dromaeosaur skeleton: information from a new specimen. **American Museum Novitates**, New York, **3215**:1-28.
- NOVAS, F.E., 1991. Relaciones filogenéticas de los dinosaurios teropodos ceratosaurios. **Ameghiniana**, Buenos Aires, **28**(3-4):410.
- NOVAS, F.E., 1997. Abelisauridae. In: CURRIE, P.J. & PADIAN, K. (Eds.) **Encyclopedia of dinosaurs**. San Diego: Academic Press. p.1-2.
- PONS, D.; BERTHOUS, P.Y. & CAMPOS, D.A., 1990. Quelques observations sur la palynologie de l'Aptien Supérieur et de l'Albien du bassin d' Araripe (N.E. du Brésil). In: SIMPÓSIO SOBRE A BACIA DO ARARIPE E BACIAS INTERIORES DO NORDESTE, 1., Crato. **Atas...**, Crato: URCA. p.141-152.
- RAUHUT, O., 1998. *Elaphrosaurus bambergi* and the early evolution of theropod dinosaurs. **Journal of Vertebrate Paleontology**, Illinois, **18**(supp.3):71A.
- SAMPSON, S.D.; CARRANO, M.T.; FORSTER, C.A., 2001. A bizarre predatory dinosaur from the Late Cretaceous of Madagascar. **Nature**, London, **409**:504-506.
- SAMPSON, S.D.; KRAUSE, D.W.; DODSON, P. & FORSTER, C.A., 1996. The premaxilla of *Majungasaurus* (Dinosauria: Theropoda) with implications for Gondwanan paleobiogeography. **Journal of Vertebrate Paleontology**, Illinois, **16**(4):601-605.
- SAMPSON, S.D.; WITMER, L.M.; FORSTER, C.A.; KRAUSE, D.W.; O'CONNOR, P.M.; DODSON, P. & RAVOAVY, F., 1998. Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. **Science**, Washington, **280**:1048-1051.
- SERENO, P.C., 1999. The evolution of dinosaurs. **Science**, Washington, **284**:2137-2147.
- SERENO, P.C.; BECK, A.L.; DUTHEIL, D.B.; GADO, B.; LARSSON, H.C.E.; LYON, G.H.; MARCOT, J.D.; RAUHUT, O.W.M.; SADLEIR, R.W.; SIDOR, C.A.; VARRICCHIO, D.D.; WILSON, G.P. & WILSON, J.A., 1998. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. **Science**, Washington, **282**:1298-1302.
- SERENO, P.C.; DUTHEIL, D.B.; IAROCHE, M.; LARSSON, H.C.E.; LYON, G.H.; MAGWENE, P.M.; SIDOR, C.A.; VARRICCHIO, D.J. & WILSON, J.A., 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. **Science**, Washington, **272**:986-991.
- SUES, H.D.; FREY, E.; MARTILL, D.M. & SCOTT, D.M., 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. **Journal of Vertebrate Paleontology**, Illinois, **22**(3):535-547.
- TAQUET & RUSSEL, 1998. New data on spinosaurid dinosaurs from the Early Cretaceous of the Sahara. **Compte Rendues Academie des Sciences**, Sciences de la terre et des planètes, Paris, **327**:347-353.