

# ON THE PALAEOBIOLOGY OF THE SOUTH AMERICAN HORNED THEROPOD CARNOTAURUS SASTREI BONAPARTE

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ABSTRACT: Some palaeobiological traits of the horned carnivorous dinosaur *Carnotaurus* BONAPARTE are assessed. Its body mass and indicator of athletic capabilities are estimated. A model of the jaw mechanics is proposed, including the analysis of the cranial kinesis. Further, the strength of the horns, head and neck muscles are studied. It is concluded that *Carnotaurus* was an agile theropod, with a somewhat fast rather than strong bite, and that it must have used the horns in intraspecific fights or even in hunting.

RESUMO: Neste trabalho, discutem-se alguns aspectos paleobiológicos do dinossáurio carnívoro com cornos *Carnotaurus* BONAPARTE. Sua massa corporal e a sua capacidade atlética foram estimados. Propõe-se um modelo da mecânica mandibular, incluindo uma análise da cinética do crânio. Além disto, a resistência dos cornos, cabeça e pescoço é estudada. Conclui-se que *Carnotaurus* era um terópode ágil, com uma mordida mais rápida do que forte e que deve ter usado seus cornos para lutas intraespecíficas ou mesmo para a caça.

#### INTRODUCTION

*Carnotaurus sastrei* BONAPARTE, 1985, is a very interesting and unusual theropod from the Cretaceous of South America. In spite of the fact that some theropods are known to have bony structures on the skull (like longitudinal crests as in *Dilophosaurus* WELLES and *Syntarsus* RAATH or a single nasal horn as in *Ceratosaurus* MARSH and *Proceratosaurus* HUENE), this is the only example described of a horned carnivore with a pair of stout frontal horns, either among dinosaurs or mammals.

*Carnotaurus* is based on an exceptionally well preserved and almost complete skeleton with all of the bones perfectly articulated, and at present is the best known theropod from the Gondwanian continents (BONAPARTE, 1996). This remarkable speci-

men was collected in the lower section of La Colonia Formation (ARDOLINO & DELPINO, 1987), Lower-Upper Cretaceous, Chubut Province, Argentina. Although the skull shows very different proportions from those of Abelisaurus comahuensis BONAPARTE & NOVAS, 1985, it bears diagnostic characters of the Abelisauridae such as the large infratemporal fenestra, the elongated quadrate, the quadratojugal fused with the quadrate, the contact of lachrimal and postorbital above the orbit, the reduced preantorbital fenestra, the posteriorly directed squamosal with a ventral, rod-like process, and the narrow dorsal process of the maxilla (NOVAS, 1989). Following BONAPARTE, NOVAS & CORIA (1990), these shared cranial features suggest that both Carnotaurus and Abelisaurus belong to the same family, Abelisauridae, as defined by BONAPARTE & NOVAS (1985). The

lower jaw of Carnotaurus shows a very weak contact between dentary and postdentary bones, forming a large mandibular fenestra. The cervical vertebrae present derived characters, such as reduced neural spines and large and high epipophyses. The forelimbs are extremely reduced and the hindlimbs are long and slender. Unique features of Carnotaurus are the wide, short, and high jugal, and the conspicuous horns made by a short and stout laterodorsal expansion of each frontal (NOVAS, 1989; BONAPARTE, NOVAS & CORIA, 1990; BONAPARTE, 1996). Also, it was noted that there are strong differences between it and the Cretaceous theropods from the northern continents, especially in the skull, axial skeleton, and in the striking reduction of the forelimbs. The marked anatomical differences of the Abelisauridae, to which Carnotaurus was referred, in comparison with theropods from the Northern Hemisphere, have been interpreted by BONAPARTE (1985, 1986) and BONAPARTE & NOVAS (1985) to be the result of the long geographic isolation of the Laurasia and Gondwana supercontinents. Very large titanosaurid sauropods like Argentinosaurus huinculensis BONA-PARTE & CORIA, Chubutisaurus insignes DEL CORRO 1975, and Andesaurus delgadoi CALVO & BONA-PARTE lived on Patagonia during the Cretaceous, and they were probably contemporary (at least some of these species) of Carnotaurus.

Palaeobiological studies of South American dinosaurs are scarce (CASAMIQUELA, 1978). In this paper, some aspects of the palaeobiology of this horned hunter are assessed, using approaches previously applied to other dinosaurs and extinct mammals (ALEXANDER, 1985; SMITH & REDFORD, 1990; FARIÑA, 1995).

## MATERIAL AND METHODS

The skeleton cast mounted at the exhibition of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" and other material kept at the same institution, labelled MACN-CH 894, were used for this study.

The mass of *Carnotaurus* was calculated using geometric approximation. In doing that, width and height of the skeleton were measured at regular intervals from the snout to the tip of the tail. Then, using a specifically designed software, each pair of measurements were assumed to be the larger and lesser diameters of an ellipse. The outer surface of successive ellipses were smoothed so as have a continuous outline of the body. An overall density of 1000 kg.m<sup>-3</sup> was assumed for the body, although other values have been proposed for dinosaurs by PAUL (1988) and FARLOW, SMITH & ROBINSON (1995).

The indicator of strength was calculated according to ALEXANDER (1983, 1985). Leg bones are particularly vulnerable to forces that impose bending moments on them (RUBIN & LANYON, 1982). The most important components of the bending moments are components about transverse axes (AL-EXANDER, 1985).

When a bone has to withstand a force exerted at its distal end at right angles to its long axis, its strength is directly related to its section modulus for bending in a parasagittal plane (*Z*), obtained from its cross section (ALEXANDER, 1983), and inversely related to the bone length and to the force exerted. This force is proportional to the fraction (*a*) of the weight (*mg*) of the animal the corresponding pair of limbs supports. Thus, a strength indicator is built, expressed as *Z/amgx*, where *x* is the distance from the distal end where the section is taken, usually half way along the bone, or near it, if a large process for muscle attachment was present in this precise place (see ALEXANDER, 1985, for further explanations).

Cross-sections of femora were measured directly with the aid of a profile gauge at distances *x* from the distal end in *Carnotaurus sastrei*. All these bones were assumed to have a material composition typical of tetrapods, so that comparisons could be directly made. A similar procedure was applied to the horns and head.

The neck muscles were reconstructed following the scars left on the bones and by comparison with modern crocodiles and birds. To estimate this muscle mass, muscles in the form of a truncated cone were assumed, whose volume was calculated accordingly and its density assumed to have been the same as that observed in the striated muscles of modern mammals, i.e., 1060 kg.m<sup>-3</sup> (MÉNDEZ & KEYS, 1960).

In studying the jaw mechanics and the cranial kinesis, a geometric model was build (ALEXANDER, 1983). Jaw muscles were reconstructed by comparison to crocodiles, following SCHUMACHER (1985). The moment arms of the reconstructed musculature were estimated following the approach applied to mammals by SMITH & REDFORD (1990).

A shape analysis method, Resistant Fit Theta Rho Analysis (RFTRA), was applied for the comparison of the cranial morphology of *Ceratosaurus* and *Carnotaurus*. RFTRA provides graphical results that include superimposed constellations of landmarks, vectors indicating the direction of change of each landmark between specimens, and a distance coefficient representing an estimate of the morphological distance between the two specimens being studied based on the landmarks used (for detailed discussion of this method, see SIEGEL & BENSON, 1982). The mentioned comparison was used as an

#### TABLE I

Values of body mass (in metric tonnes), the fraction of the body weight supported by the hind limbs ( $a_{hind}$ ), and of the indicator of athletic capability (Z/amgx, in GPa<sup>-1</sup>) for femora of fossil and modern animals. Data for *Carnotaurus* and *Piatnitzkysaurus* are new, others from FARIÑA, VIZCAINO & BLANCO (1997) and references therein.

Taxon	Body Mass 10 <sup>3</sup> kg)	a <sub>hind</sub>	Z/amgx femur (GPa <sup>-1</sup> )
Carnotaurus sastrei BONAPARTE	1.5	1	29
Piatnitzkysaurus floresi BONAPARTE	0.45	1	29
Apatosaurus sp. MARSH	33.5	0.70	9
Tyrannosaurus rex OSBORN	7.7	1.00	9
Triceratops horridus MARSH	6.4	0.52	19
Stegosaurus ungulatus GILLMORE	4.0	0.7	12
Ankylosaurus magniventris BROWN	5.0	0.6	6
Struthio camelus LINNAEUS	0.04	1	44
Loxodonta africana (BLUMENBACH)	2.5	0.42	7
Ceratotherium simum (BURCHELL)	0.75	0.40	26
Syncerus caffer (SPARRMAN)	0.5	0.40	22
Glyptodon clavipes OWEN	2.00	0.60	22

exploratory basis for analysing cranial differences within the framework of a functional analysis of the feeding mechanisms of *Carnotaurus*. For this case, drawings of crania of the two genera provided in BONAPARTE, NOVAS & CORIA (1990: fig. 2, 7F) were used. Twenty eight landmarks were identified on the lateral views of the crania, consisting mostly of triplejunction contacts between cranial bones or fenestrae, but also including contacts between sutures and the limits of the lateral profiles. The landmarks chosen are illustrated on a simple lateral view of the *Carnotaurus* cranium in Figure 1. Because of the exploratory nature of this comparison, detailed discussions of landmark choices and polygonal figure selection and development will not be given.

## RESULTS

# MASS ESTIMATION AND LIMB BONE STRENGTH

These results can be seen in TABLE I, where the figures obtained for *Carnotaurus* are compared with those of other tetrapods (see FARIÑA, VIZCAÍNO & BLANCO, 1997 and references therein). According to our estimations, *Carnotaurus* reached a mass of 1500 kg, which can be considered modest in comparison with such giants as *Tyrannosaurus* and (probably) *Giganotosaurus*. Its femoral strength is 29 GPa<sup>-1</sup>.

## HORNS, HEAD AND NECK

The horns of *Carnotaurus* may have been used as weapons in intraspecific combats, much in the way rams do, as suggested by NOVAS (1989). A deer-styled fight seems less likely, as there is no evidence of interlocking structures. As can be seen in TABLE II, if the blow was frontal, and hence absorbed by the epaxial musculature, *Carnotaurus* would have had approximately the same ratio epaxial musculature mass/body mass as the rhinoceros (which is known to fight with the head).

#### JAW MECHANICS

Following SCHUMACHER (1985), according to its relation to the Nervus trigeminus, the Musculus adductor mandibulae is subdivided in sauropsids in M.a.m. externus, M.a.m. posterior, and M.a.m. internus. The latter is a complex of muscles including both the M. pseudotemporalis and the M. pterygoideus. In adition to the portions mentioned, the crocodilians have a large M. intramandibularis as another important division of the M.a.m. internus. The bulk of the jaw adductors in crocodilians is formed by the M. pterygoideus (subdivided in that group into M. pterygoideus anterior and M. pterygoideus posterior). In order to keep the model as simple as possible, and taking into account that in crocodiles the M.a.m. internus is considerably stronger than the rest of the jaw adductors, in this first approach to the jaw mechanics of theropods we will focus our analysis on it, particularly on the anterior and posterior pterygoid muscles. In theropods, the fibres of the *M. pterygoi*deus anterior might have originated from the dorsal surface of the palate onto the rostrum, at the level of the antorbital fossa. In this place, they would have attached to a mandibular adductor tendon horizontally situated and connected to the dorsomedial face of the surangular, to a Cartilago transiliens, possibly situated adjacent to the surangular, and also to the medial face of the angular. On the other hand, the M.

Species	BODY MASS (kg)	EPAXIAL MUSCULATURE MASS (kg)	Ratio
<i>Carnotaurus sastrei</i> BONAPARTE	1500	200	0.13
<i>Rhinoceros unicornis</i> LINNAEUS	1300	150	0.12
<i>Hippopotamus amphibius</i> LINNAEUS	1200	75	0.06

TABLE II Epaxial musculature mass in several tetrapods (see text).

*pterygoideus posterior* probably would have bulged behind the retroarticular process of the lower jaw. The muscle fibres arising from the ventral surface of the pterygoid would have reached a tendon aponeurosis attached to the posterior part of the lower jaw.

The fibres of the *M. pterygoideus* anterior would have developed a strong protraction component, which opposes the strong retraction component developed by *the M. pterygoideus* posterior. The simultaneous contraction of both muscles would have resulted in a strong adduction component, acting in a vertical direction.

Thus, assuming a crocodilian-like disposition for the model of the jaw muscles in theropods, the main line of action of the adductor muscles is on the vertical direction (Fig. 2), i.e., between the ventral margin of the adductory fossa and the *Cartilago transiliens*. The *M. depressor mandibulae* was also considered. Other branches of the adductor muscles would have shown a very complex disposition and will be the matter of future contributions.

The results of our analysis, compared to *Cerato-saurus* and *Tyrannosaurus*, are summarised in TA-BLE III. The figures for the *M. pterygoideus* indicate that, despite differences in size, the jaw design of



Fig. 1 - Lateral view of the *Carnotaurus* BONAPARTE, 1985 cranium with the landmarks used in the RFTRA.

*Carnotaurus* makes it able of fast movements rather than strong ones. This feature is shared with *Tyrannosaurus*, while *Ceratosaurus* is better designed for stronger bite throughout the whole mandibular length. On the other hand, *Carnotaurus* shows a longer lever arm of the *M. depressor mandibulae*, which might be related to the cranial kinesis (see below).

#### **CRANIAL KINESIS**

According to Novas (1989) and BONAPARTE, NO-VAS & CORIA (1990), both the skull and lower jaws have loose sutures between some bones that suggest a kinetic structure. Although this condition was not unusual in the skull of theropods (BAKKER, 1986), Carnotaurus presented apparently much more mobile joints than the rest of the known dinosaurs, including Allosaurus MARSH (see NOVAS, 1989). The posterodorsal skull region (conformed by the frontals, parietals, supraoccipitals, opisthotics, postorbitals and squamosals bones) is strongly fused with the basicranium, probably in relation to the presence of horns, in order to establish a resistant basis for impact transmission. This relatively compact region contrast with the apparently high kinesis of the rest of the skull and lower jaws. The suture between the frontal and nasal bones is straight and transverse, and forms a conspicuous hinge joint (known as "prokinetic" in the terminology of FRAZZETTA, 1962) between the muzzle and the posterior part of the skull roof. Also, the nasals show weak sutures with the premaxillae and lachrymals, suggesting mobility. However, the union of the nasals with the maxillae, although not fused, suggests that it was less mobile than those cited above. The postorbital has a wide contact with the frontal horn. Its suture with the dorsal process of the jugal is weak, suggesting that movement is possible. The ventral projection of the squamosal is rod-like, with a short contact with the quadratojugal. This projection probably had the function as a stop for the movement of the quadrate. The squamosal has a shallow ventral notch for the quadrate head, forming a probably mobile joint. Mobility of the quadrate at this joint is referred to as streptostyly. The development of a mobile joint between the dorsal extremity of the



Fig. 2 - Moment arms of the pterygoideus (Mp) and the posteriormost bite point (Mb) in the lower jaw of *Carnotaurus* BONAPARTE, 1985.

quadrate and the squamosal, like in lizards and snakes, suggests an important improvement, in view that it appears to be a major factor in the successful of these modern reptiles (SMITH, 1980). The quadrate and quadratojugal are fused to one another and show a movable contact with the jugal. The jugal shows a rigid suture with the maxilla, whereas those with the lachrymal, postorbital, and quadratojugal are weak, suggesting once again that kinesis was possible. The quadrate is dorsoventrally long, with the lower condyles well defined in medial view and less so in lateral view. The lower jaw shows an articular region low and elongated in lateral view. It has a large mandibular fenestra and, behind it, on the medial side, a wide adductory fossa. The connection between the dentary-splenial and the postdentary bones is extremely weak. It is reduced to only two mobile contact points, above and below the mandibular fenestra. The dorsal joint is between the surangular and dentary and bears a well-developed condyle and socket respectively, and the ventral joint occurs between the angular and a rod-like projection of the dentary, the former sliding on the latter. The glenoid has two concave facets for the quadrate condyles, with the main axis directed anteromedially. Both lower jaws are loosely connected (probably by elastic ligaments) at the mobile symphysis and are hinged to the quadrates.

The posterior part of the skull roof, the quadrates, the palate, the premaxillae and the nasals form a five-bar crank chain mechanism (some of the bars are duplicated in that they are bilaterally paired). If, for instance, the posterior part of the skull roof is held stationary and the quadrates are moved, the muzzle must move in a particular way. If the ventral ends of the quadrates are pushed forwards, the muzzle and then the nasals swing up. If they are pushed back, the muzzle swings down.

If the pterygoid connected to the quadrate, both bones must have moved together. The distal end of the pterygoid would swing forward when the quadrate did the same. This push the palate region forward, making the snout rotate upwards at the prokinetic joint.

The dentary-surangular connection is a ball-andsocket joint allowing three degrees of freedom of movement whereas the dentary-angular connection is a sliding and hinge joint allowing two degrees of freedom. The jaw joints allow two degrees of freedom of movement between the jaw and the cranium. Thus, the mouth can be opened and closed and the lower jaw can rotate outward.

The quadrate bone, which connected the lower jaw to the braincase, shared a hinge joint with the top rear corner of the skull. When this bone swung outward, it splayed out the jaw to the sides. Even the lower jaw was loosely constructed of two sections. The front section carried the teeth, the rear housed the muscles and joint of the jaw. The front and rear complexes met along a quite loose ligamentous junction. At the mandibular symphysis, the right and left lower jaws met at yet another very weak joint held together by ligaments. The head of snakes are in general similarly designed to those of the dinosaurs with kinetic skull; snakes have a central, tightly knit braincase, which acts as the core for the loosely attached jaws, snout, cheek bones, and palate (FRAZZETTA, 1966; BAKKER, 1986). Snakes also possess backwardly curved teeth, another similarity. When a snake starts to swallow large prey, the jaw muscles pull these teeth into the prey's body and all the loose joints swing apart so that the snake gullet can accommodate a very large body. The skull of Carnotaurus must have functioned very much in the same way. When Carnotaurus swallowed a large chunk of meat, its capacity would have increased as each loose joint flexed and bowed outward.

In *Carnotaurus*, like in birds, the prokinetic hinge is anterior to the orbits, and consequently the posi-



Fig. 3 - Results of the RFTRA of theropod crania using *Ceratosaurus* MARSH (base specimen; discontinuous line) and *Carnotaurus* BONAPARTE, 1985 (continuous line). Diagram of superimposed figures with landmarks and vectors. Distance coefficient is 0.3571.

	Carnotaurus sastrei	Ceratosaurus nasicornis	Tyrannosaurus rex
Moment arm of <i>M. pterygoideus</i>	35	55	40
Moment arm of (and ratio muscle to) posterior bite	62 (0.56)	79 (0.70)	74 (0.54)
Moment arm of (and ratio muscle to) mid-bite	92 (0.38)	105 (0.52)	100 (0.40)
Moment arm of (and ratio muscle to) anterior bite	124 (0.28)	132 (0.42)	128 (0.31)
Moment arm of depressor	18	9	12

TABLE III Comparison of the moment arms of the jaw muscles and bite points in several theropods.

tion of that portion of the skull which houses the eyes did not change with the movement of elevation or depression of the upper jaws. Thus, if the sight of *Carnotaurus* was fixed on its potential prey, the movements of the jaws did not displace the prey from the line of sight.

#### SHAPE ANALYSIS

The results of the RFTRA of the twenty eight landmarks used in the comparison of the cranial morphology of Ceratosaurus (base specimen) and Carnotaurus in lateral view are given in Figure 3. However, a dorsal cranial view or analysis of other elements may indicate a much higher level of difference. The results presented in Figure 3 can be summarised as follows. For the landmarks, the changes tend to be general and not localised in a specific region. However, a major trend is apparent in the whole skull. The overall cranium appears to have a much lower degree of dorso-ventral vaulting in Ceratosaurus than in Carnotaurus. This is indicated by vector directions in the dorsal direction for the landmarks in the frontoparietal area, vectors in the anterior and ventral direction for the jugal, quadratojugal and guadrate landmarks, and vectors in the posterior and dorsal direction for the rostral area landmarks.

The vertical components of the vectors are in general greater, indicating a dorso-ventral expansion rather than a shrinking of the *Carnotaurus*'s skull. This is consistent with the rapid bite hypothesis; if the cranium had evolved by shortening, that would have implied a selection for a greater mechanical advantage of the jaw adductor musculature. On the other hand, if the cranium remained long, but became higher, the jaw adduction would have remained fast, rather than powerful. The aforementioned major trend would have implications regarding to the forces that could be generated by the jaws and the feeding mode suggested for *Carnotaurus*.

#### DISCUSSION

#### LOCOMOTION

The figures obtained for the femur of *Carnotaurus* are very high when compared to those for the large *Tyrannosaurus* (9 GPa<sup>-1</sup>). Also, they are the same as for the femur of the medium sized theropod *Piatnitzkysaurus* (29 GPa<sup>-1</sup>). These values can be compared to living mammals (ALEXANDER, 1985, 1989). Values above 20 are shown by animals able to gallop such as the buffalo (*Syncerus*, 22 GPa<sup>-1</sup>) and the white rhinoceros (*Ceratotherium*, 26 GPa<sup>-1</sup>). On the other hand those animals not able to gallop show low values, for instance the African elephant (*Loxodonta*, 7 GPa<sup>-1</sup>).

According to this results, *Carnotaurus* and *Piatnitzkysaurus* would have been able to run fast. On the other hand, *Tyrannosaurus* has values that are similar to those of the African elephant. Therefore, *Tyrannosaurus* could not have been able to run very fast, although using a different approach based on limb bone proportions a rather different view has been offered by HOLTZ (1994; see also FARLOW, SMITH & ROBINSON, 1995), who has proposed that tyrannosaurids must have been more agile than other theropods of similar size. In that view, it is conceivable that *Tyrannosaurus* might have preyed upon slower prey, or might have driven away faster, smaller predators after they had captured a prey.

#### FIGHTING OR HORN-HUNTING Carnotaurus

According to the results obtained, the epaxial musculature could have had the same shock absorbing function in *Carnotaurus* as in those mammals used for comparison. Therefore, the possibility of a shock-absorbing function is not refuted. A lateral blow could have been absorbed by only one side of the musculature, although not only the epaxial mus-

culature might have been involved, but the whole of the side musculature.

Also, a more precise calculation can be done, an approach developed by Alexander (pers. comm., 1997), who kindly let us use it before it has been published in a different species. The energy of the impact between two animals ramming to each other is absorbed in the same proportion by each of the competitors. This energy can be absorbed by neck muscles. Consider a muscle that is forcibly stretched, exerting a stress of 500 kPa (ALEXANDER, 1983). If it is extended by 25% of its length, the work absorbed is 500 x 0.25 = 125 kJ.m<sup>-3</sup> or about 120 J.kg<sup>-1</sup>. Therefore, the epaxial musculature of the neck and back of Carnotaurus could have absorbed 24 kJ. If the energy of each animal is  $\frac{1}{2}$  m.v<sup>2</sup>, and the mass *m* is 1500 kg, the muscle mass we have calculated would have been enough to absorb the shock produced by each animal running at 5.7 m.s<sup>-1</sup>. This is about the speed recorded by ALEXANDER & POND (1992) for a white rhinoceros, which has similar indicators of athleticism.

The structure of the *Carnotaurus*'s horns is not very different in appearance from the horn cores present in bovids (e.g., domestic cattle), although they are certainly not identical. The horns may have had a keratinous covering, which would have made the horns longer during the animal's life (BONA-PARTE, NOVAS & CORIA, 1990).

Although the horn cores are rather blunt in *Carnotaurus*, the corneous horns might have had the same form as in bovids (i.e., with the characteristic open "U" shape), and therefore they might have been used as weapons to kill or to injure severely small preys. If this hypothesis were correct, it would represent the only known or inferred case of the use of horns to kill prey.

#### MANDIBULAR MOVEMENTS

In the case of *Carnotaurus*, we suggest that their cranial kinesis is probably an adaptation for increasing the oral gape (and consequently the volume of the mouth) and also for maintaining an unchanging orientation of the eye with respect to prey. *Carnotaurus* skull differ from those of lizards in that the orbits are not located in the movable upper jaws section (i.e., the muzzle region) so that the eyes were not to be moved along with the elevation and depression of the muzzle. Thus it seems that the kinetic skull of *Carnotaurus* was well adapted for preserving the visual orientation between the eye and the prey since their kinetic movements themselves would have not a tendency to disrupt this orientation.

Moreover, the rotatory movements of the upper and lower jaws change the orientation of the tooth tips with respect to the prey. Possibly, when the jaws struck the food, the teeth were projected forward to impale the prey, and as the muzzle was rotated downward and at the same time the anterior portion of the mandible was rotated upward, the tooth tips were turned caudally to restrict escape movements of the prey. In this interpretation, cranial kinesis had an important function in regard to the carnivorous habits of *Carnotaurus*.

The snout of *Carnotaurus* was transversely compressed to clear its field of vision, and its eyes faced forward to provide some overlap between visual fields from the right and left eyes. That would have permitted stereoscopic vision, although not so marked like that proposed for *Tyrannosaurus* (BAK-KER, 1986).

#### CONCLUSIONS

*Carnotaurus sastrei* seemed to have been well equipped for fast running, and had a fast (rather than powerful) bite. Also, it had a highly kinetic skull. All this features are consistent with a predator that chased and swallow whole fast, small preys. The horns and neck are well designed as shockabsorbing structures, and might have been used in intraspecific fights.

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