

CRANIAL MECHANICS AND FUNCTIONAL INTERPRETATION OF THE HORNED CARNIVOROUS DINOSAUR *CARNOTAURUS SASTREI*

GERARDO V. MAZZETTA,^{*,1} ADRIÁN P. CISILINO,² R. ERNESTO BLANCO,³ and NÉSTOR CALVO⁴

¹Departamento de Paleontología, Facultad de Ciencias, Universidad de la República, Iguá 4225, (11400) Montevideo, Uruguay, mazzetta@fcien.edu.uy

²División Soldadura y Fractomecánica, INTEMA, Facultad de Ingeniería, Universidad Nacional de Mar del Plata – Consejo Nacional de Investigaciones Científicas (CONICET), Av. Juan B. Justo 4302 (7600) Mar del Plata, Argentina, cisilino@fi.mdp.edu.ar

³Instituto de Física, Facultad de Ingeniería, Universidad de la República, Julio Herrera y Reissig 565, CC: 30, (11000) Montevideo, Uruguay, blanco@fing.edu.uy

⁴Centro Internacional de Métodos Computacionales en Ingeniería (CIMEC), Universidad Nacional del Litoral – Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Güemes 3450 (3000) Santa Fe, Argentina, ncalvo@ceride.gov.ar

ABSTRACT—Three-dimensional finite element analyses were performed on the cranium of the horned theropod *Carnotaurus sastrei* to assess how it would have performed mechanically during biting and frontal butting. This technique proved to be an effective tool to provide a better understanding of the cranial functional morphology of *C. sastrei*. The analyses indicated that the jaw-closing musculature of *C. sastrei* would have played a key role in diminishing the stress level on the cranium during biting, particularly for the braincase. Force analyses show that *C. sastrei* would have had a comparatively weak (and faster than *Allosaurus fragillius*) muscle-driven bite. The finite element analyses also provide quantitative evidence to suggest that the cranium of *C. sastrei* could have withstood high velocity impacts to its teeth resulting from a hypothetical hatchet-like biting mode, but could not have endured severe, rapid frontal blows during agonistic encounters.

INTRODUCTION

The theropod *Carnotaurus sastrei* from the Cretaceous of Patagonia is distinctive for its strikingly unusual skull (Fig. 1). Although several theropods are known to possess cranial ornamentation (e.g., the dome in *Majungatholus*, the longitudinal crests in *Syntarsus*, *Dilophosaurus* and *Cryolophosaurus*, or the single nasal horn in *Ceratosaurus* and *Proceratosaurus*), *Carnotaurus* is unique among theropods in possessing two large horns emerging latero-dorsally from the frontal bones (Bonaparte, 1985; Novas, 1989; Bonaparte et al., 1990). In fact, this species is the only known example of a bipedal carnivorous vertebrate having frontal horns.

The functional significance of the horns, as well as the performance of the skull as a whole, have undergone preliminary examinations through comparative and biomechanical approaches (Novas, 1989; Mazzetta et al., 1998; Mazzetta, 2002). Although the frontal horns may have played a role in intraspecific displays, as suggested for the horns of ceratopsians (Farlow and Dodson, 1975), it is also possible that, like the horns of many modern ungulates, they may have been used in combat. The functional demands of combat would be expected to have been quite severe, potentially subjecting these structures (and the rest of the skull) to high magnitude tensile and compressive loads.

Evaluation of the forces and stresses to which the bones of extinct animals are exposed is a complicated undertaking, because recordings cannot be collected directly from the animals, as is possible for living species. However, the development of finite element (FE) modeling provides an opportunity to address such functional questions in a quantitative manner. In this study,

we constructed three-dimensional FE models of the cranium of *Carnotaurus* to evaluate how it performed mechanically under loads associated with biting and frontal butting. We then compare its performance and the loads involved in such life situations to those determined for other extinct and living species in order to gain insight into its likely behavior. This study constitutes the first quantitative attempt to analyze the potential of *Carnotaurus* extraordinary robust frontal expansions as shock-absorbing structures, as previously suggested by Novas (1989). Precedents to other aspects of this work can be found in the studies of the biting performance of the dinosaurs *Allosaurus fragillius* (Rayfield et al., 2001) and *Tyrannosaurus rex* (Rayfield, 2004), based on three- and two-dimensional FE analyses of cranial models, respectively.

METHODS

Geometric Reconstruction and Finite Element Discretization

A life-sized resin cast of the cranium of *Carnotaurus sastrei* from the holotype specimen MACN-CH 894 was subjected to computerized tomography (CT) scanning using a *General Electric, Prospeed Hilight* model, helicoidal tomographer. CT scanning the original was dismissed as a viable option because of significant risks of specimen damage during shipping and scanning. The cast does not reproduce the internal cavities and pneumaticity of the actual cranium. Nonetheless, it is suitable for the purposes of our study, as beam theory analyses of generalized skull shapes indicate similar stress responses in solid and hollow models subjected to bending (G.V.M.; personal observation). The use of a skull cast precluded a proper representation of cranial sutures in our analyses. However, FE analyses of biting and tearing carried out in “fused” (without sutures) and “mobile”

*Corresponding author.

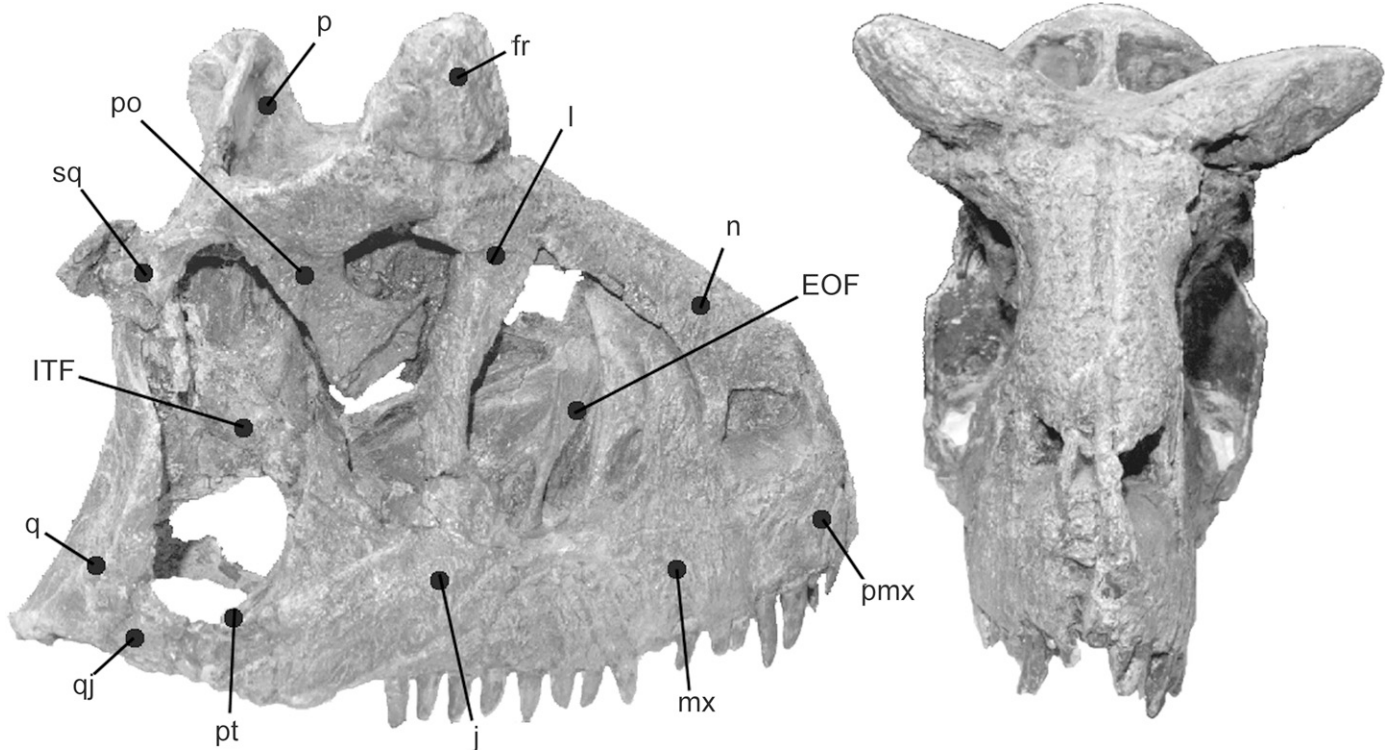


FIGURE 1. Cranium of *Carnotaurus sastrei* (anterior and lateral views): Abbreviations: **AOF**, antorbital fenestra; **ITF**, infratemporal fenestra; **fr**, frontal; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sq**, squamosal.

cranial models of another carnivorous dinosaur show very similar stress distribution patterns among them (Rayfield, 2004), which allow us to be confident on the representativeness of our models.

A series of 130 transaxial images (CT scans) spaced at intervals of 5 mm were obtained for the cranium. The images were converted to a bitmap format and manually edited in order to reconstruct missing parts and to correct for small morphological distortions due to diagenetic processes. The edited cranial images were then used to obtain cross-sectional silhouettes. A regular grid was superimposed on each of the silhouettes to determine the coordinates of the nodes. These coordinates were set at the intersections between the vertical and horizontal grid lines located within the silhouettes, and at the intersections of the grid lines (either horizontal or vertical) with the boundary of the silhouettes. The grid interval was set to 2.76 mm (6 pixels), which is approximately half the separation between consecutive CT scans. The process generated 98,375 nodes.

A mesh of tetrahedral elements was built from the nodal positions using an Extended Delaunay Tessellation algorithm (Calvo et al., 2003; Idelsohn et al., 2003). The resultant discretization produced 488,444 elements, a sufficiently high resolution to account for most of the details in the cranial geometry. The bilateral symmetry of the skull allowed us to construct a model of the cranium from only one half of the skull geometry, substantially reducing the amount of data required in the analyses. The discontinuities in the model geometry caused by abrupt transitions between successive cross-sectional images were fixed by applying a Laplacian smoothing algorithm to the surface nodes (Freitag and Ollivier-Gooch, 1997). Since the smoothing process tends to eliminate geometric details from the model, the number of smoothing iterations that was chosen resulted from a compro-

mise between the improvement of the discretization topology and the loss of accuracy in relation to the geometric representation of the cranium. After qualitative comparisons of the resulting model geometry to those of the actual skull components, it was concluded that the best result was that obtained after two smoothing iterations. The smoothing process yielded a good quality FE mesh. An element distortion analysis measuring the element aspect ratio (Cook, 1995) showed that only 1.5% of the elements presented high distortion ratios (>10). These highly distorted elements were mostly confined to the discretization of the teeth. A rendered image of the model is shown in Figure 2.

The obtained model was imported in DXF format into the FE modeling and analysis package Algor (Version 12, Algor Inc., PA, USA). The accuracy of the stress computations for the FE model was assessed by performing an error estimate analysis. This was calculated from the normalized maximum difference method for the von Mises equivalent stresses (Cook, 1995) and it resulted in an estimate average stress error of about 3%.

Material Properties

Histologically, the bone of carnivorous dinosaurs shares many similarities with that of fast-growing bovines, because both are composed of secondarily remodeled Haversian bone with primary compact bone restricted to the surface (Reid, 1996). It was assumed that similar histology indicates broadly similar material properties. Consequently, and following Rayfield et al. (2001), the material properties of bovine Haversian bone studied by Reilly and Burstein (1975) were assigned to the cranial model of *Carnotaurus* (Young's modulus = 10 GPa, shear modulus = 3.6 GPa, and Poisson's ratio = 0.4). More detailed consideration

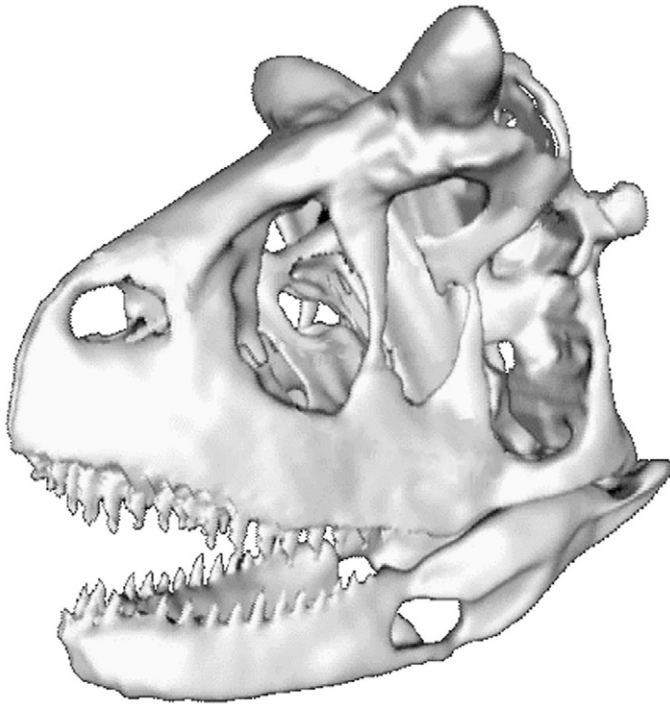


FIGURE 2. Renderized image of the skull of *Carnotaurus sastrei*. FE models of the cranium and mandible are shown after the smoothing process. The model of the mandible was not included in the FE analyses, but is shown for the sake of completeness.

of compact bone material properties could influence our results, but CT scans of the actual cranium would be needed to evaluate the extent of such effects. The material response was considered linearly elastic, homogeneous and isotropic, since the lack of information regarding these properties in dinosaur bone precluded us in using a more refined approach. The yield stress of bone was taken from Currey (2002) as 132 and -196 MPa, in tension and compression, respectively.

Muscular Forces

The restoration of the jaw musculature of *Carnotaurus* was based upon the examination of the scars left by its muscles on the bones of the cranium and mandible of the specimen MACN-CH 894, and homologies in their positions with extant crocodylians and lizards. The jaw muscles were grouped into three functional units as follows: 1, adductor posterior (MAMP); 2, temporal region group (TRM; comprising the adductor externus and pseudotemporalis); and 3, pterygoideus group (MPT; consisting of the pterygoideus anterior and posterior). These muscle units were restored in clay on a life-sized cast of *Carnotaurus* skull, and then incised in their widest part. The cross-sectional surfaces thus obtained were measured digitally on Scion Image (version Beta 3b, Scion Image Corporation, MD, USA). Muscle forces were calculated from cross-sectional area measurements and a maximum isometric stress of 392 kPa (Thomason et al., 1990). It was assumed that all adductor muscles were contracting maximally and simultaneously at the time of the bite to assess the maximal values of skull stress. This is a reasonable assumption since studies carried out in crocodylians by Cleuren et al. (1995) do show the biological feasibility of such a situation.

Initially, all jaw muscles were assumed parallel-fibered (model 1) to allow for a meaningful, direct comparison of bite force results with those published for other theropods (e.g., Rayfield et al., 2001;

Mazzetta et al., 2004). Unfortunately, the great variability of jaw muscle architecture exhibited by extant archosaurs (see examples of specific cases in Beecher, 1951, 1978; Zweers, 1974; van Drongelen and Dullemeijer, 1982; Busbey, 1989)—particularly among birds (Bühler, 1981), or when it comes to birds compared with crocodylians (Holliday and Witmer, 2007)—reduces confidence in such an assumption. Therefore, we considered an alternative, less simplistic model of the cranium (model 2), in which the MPT and MAMP were assumed pinnate-fibered as in modern crocodylians (Schumacher, 1973; van Drongelen and Dullemeijer, 1982; Busbey, 1989).

Our clay restoration of the jaw musculature implies that muscle volume is a fixed quantity regardless of the muscle architecture considered. Therefore, the force exerted by the pinnate muscles of our alternative model can be calculated as $F(L/L_p)\cos\alpha$, where F is the force developed by a parallel-fibered muscle, L and L_p are the lengths of parallel and pinnate fibers, respectively, and α is the pinnation angle. The cosine of the latter quantity was assumed equal to 1 (that is, as it would occur in parallel fibers) for the sake of simplicity, since there is a paucity of reliable data for the pinnation angle of jaw muscles in crocodylians (Busbey, 1989); this produced maximal estimates of muscle force. Values for the ratio L/L_p of the MPT (1.9) and MAMP (2.4) were based on average length data obtained from specimens of *Caiman crocodylus* scaled to the same size (data published by Sinclair and Alexander, 1987, and taken from personal measurements, G.V.M.).

Model 2 also took into account other uncertain features related to the MPT, as unequivocal evidence of the size and orientation of its anterior portion was not found. Such uncertain features are its cross-sectional area (assumed 10% greater than the area measured for model 1), and the direction of its line of action (taken as 16° higher). The actual bite force, condylar force and peak stresses developed during a muscle-driven bite lie somewhere within the range of values calculated for both the initial and the alternative models. This provided a basic sensitivity analysis whereby we were able to determine the extent to which our conclusions depend on the muscle restoration and muscle architecture we adopted.

Forces calculated for the adductor muscles were applied to the FE model of the cranium as point loads acting on the nodes located at the attachment sites of the muscles. The lines of action of these forces make angles θ_i ($i = 1, 2, 3$, indicating the muscular unit considered) with the line connecting the tip of the anterior-most tooth and the contact region between the cranium and mandible at the jaw joint (Fig. 3).

Load Cases

Our analyses assume that the cranial models of *Carnotaurus* are in equilibrium and consequently behaving as lever systems for force transmission. They also assume that the dinosaur is biting or head-butting symmetrically (bilaterally), so that no forces are transmitted across its skull between the left and right sides. The cranial models were anchored at their occipital surfaces, on the attachment points of the neck muscles (Fig. 4, black crosses), and appropriate symmetry boundary conditions were set on their sagittal planes. The models were solved using static, linear-elastic FE analyses.

Two modes of biting as well as hypothetical situations involving biting or head-butting were analyzed through loads applied to the models. Load case A corresponded to the physiologic loads exerted on the cranium during static biting. It was assumed that the mouth is closed against a food item. In doing so, a line of nodes coincident with the jaw joint was fixed in order to model this articulation as a simple hinge joint, and a restriction of displacement was applied at the tip of the teeth in the direction determined by their central axes. Bite forces for selected posi-

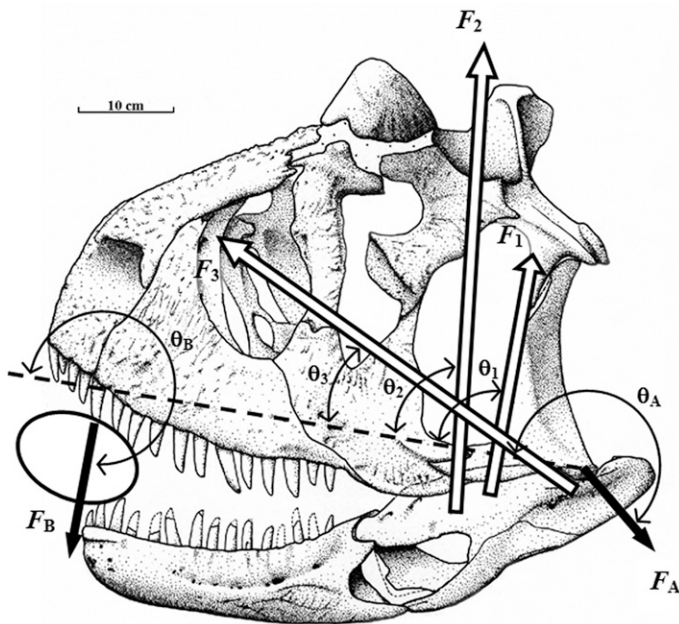


FIGURE 3. Free-body diagram showing the forces acting on the skull of *Carnotaurus sastrei* during biting (load case A; see text). The arrows represent the lines of action of the forces exerted by F_A , the jaw joint; F_B , the prey item; F_1 , adductor posterior; F_2 , temporal region group; F_3 , pterygoideus group. The angles θ_i represent corresponding force directions. (Sketch of the skull modified from Bonaparte et al., 1990.)

tions along the tooth row (anterior, central, and posterior bite points) were computed as the sum of the reaction forces at the tip of three contiguous teeth on each half of the cranium (Fig. 4). Load case B is almost identical to A, except that in B (only modeled for biting at the anterior teeth) an anteriorly directed force representing the tug of a prey was also taken into account. The force magnitude of the tug represents the maximum force that can be applied to the cranium before yielding.

Load case C was employed to assess the functional effect of the adductor musculature on the stresses developed on the cranium during biting (Fig. 5). In doing so, the jaw-closing muscles were considered quiescent, and simulated dorsally directed forces (equivalent to calculated bite forces for load case A) were applied to the teeth at corresponding positions. Moreover, this load case proved to be useful to explore the feasibility of a hypothetical high velocity impact delivered by the upper jaw of *Carnotaurus* onto its prey, such as that inferred for *Allosaurus* by Rayfield et al. (2001).

Load case D studied the effect that a frontal blow with the horns would have on the cranium. Such a blow was simulated through a vertically directed force applied bilaterally at the cranial model on the dorsodistal surface of the horns (Fig. 6). The magnitude of the blow force was assumed equal to that causing the maximum stress on the cranium before yielding. By doing so, we were able to determine the feasibility of the head-butting scenario using a simple analogy with the style of combat seen in bighorn sheep (Kitchener, 1988).

RESULTS

Bite Force Results

The forces exerted by each of the adductor muscles of *Carnotaurus* under model 1 were compared with those estimated by Rayfield et al. (2001) for *Allosaurus* (Table 1). Although the adductor muscles are of similar proportions in *Carnotaurus* and

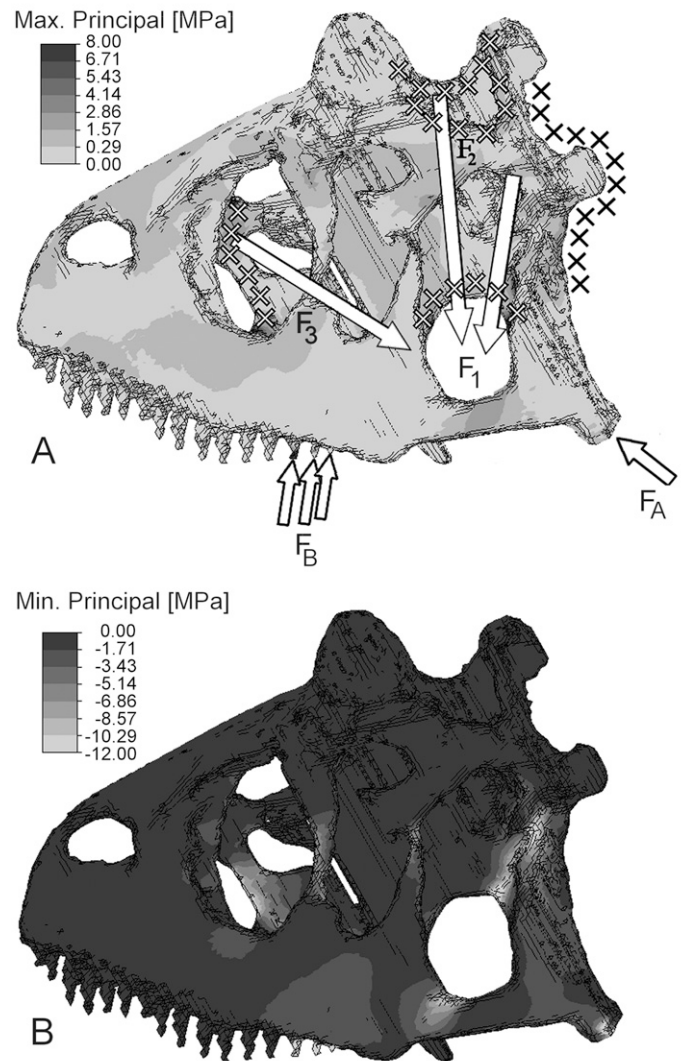


FIGURE 4. Distribution patterns of maximum (A) and minimum (B) principal stresses on the cranium of *Carnotaurus sastrei* during bilateral static bite at the posteriormost teeth. The FE model shows applied loads and reactions at the teeth and jaw joint (abbreviations as in Fig. 3). Black crosses indicate displacement boundary conditions (anchorage points) at the occiput; white crosses indicate the muscle attachment points. (Note: The sign convention used indicates that tensile stress magnitudes are positive, and compressive stress magnitudes are negative. The stresses shown on the teeth are artificial.)

Allosaurus, the forces exerted by *Carnotaurus* are consistently lower. However, higher forces than those for *Allosaurus* can be estimated from model 2 for the MAMP and MPT of *Carnotaurus*, which are 1,066 and 5,079 N, respectively. The maximum bite force is exerted at the posteriormost teeth of *Carnotaurus* (3,341 N; Table 2). When we allow for muscle pinnation and the other features accounted for in model 2, the resultant maximum bite force (5,274 N) and condylar force (11,190 N) are 58% and 88% higher than those calculated for model 1, respectively. However, the direction of the condylar force shows an increase of only 6 degrees.

The velocity of jaw adduction is mechanically determined by the muscle group closer to the jaw joint, that is, the MPT of *Carnotaurus* and *Allosaurus* (Table 1). The moment arms for anterior bites are 0.54 m for *Carnotaurus* and 0.81 m for *Allosau-*

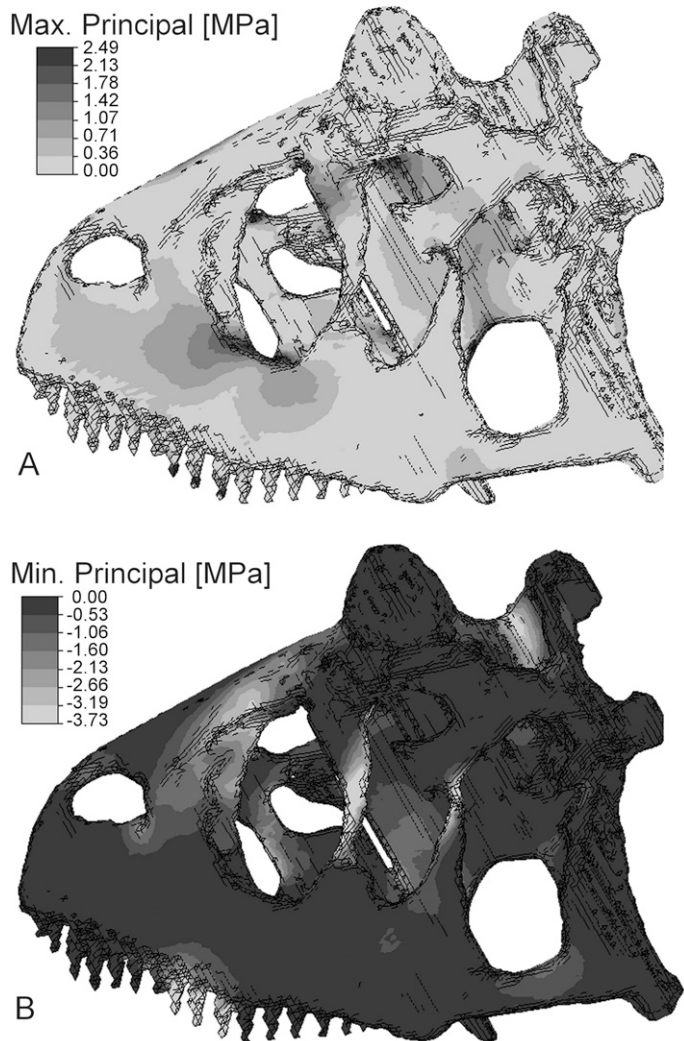


FIGURE 5. Distribution patterns of maximum (A) and minimum (B) principal stresses on the cranium of *Carnotaurus sastrei* when a dorsally directed force (2,485 N) is applied to the central teeth; an inactive adductor musculature is considered. (Sign convention as in Fig. 4. The stresses shown on the teeth are artificial.)

rus, so their velocity ratios are 0.056 and 0.081, as computed from their corresponding moment arms for the MPt. This implies that *Carnotaurus* would have been better equipped to deliver a faster bite than *Allosaurus*. In fact, the velocity ratio of *Carnotaurus* is closer to that in extant crocodylians such as *Caiman crocodylus* (0.041; ratio computed from information published by Sinclair and Alexander, 1987) than it is to *Allosaurus*.

TABLE 1. Maximum forces exerted by the adductor muscles of *Carnotaurus sastrei* and *Allosaurus fragilis*.

Taxon	MAMP			TRM			MPt		
	L_1 (m)	F_1 (N)	θ_1	L_2 (m)	F_2 (N)	θ_2	L_3 (m)	F_3 (N)	θ_3
<i>C. sastrei</i>	0.097	444	90	0.218	2,082	86	0.030	2,430	24
<i>A. fragilis</i>	0.092	610	101	0.132	3,130	93	0.066	3,601	28

Abbreviations: θ_i , force directions; F_i , force magnitudes; L_i , moment arms of muscle forces; **MAMP**, adductor posterior; **TRM**, temporal region group; **MPt**, pterygoideus group. Force magnitudes referred to one side of the head only, with directions (in degrees) indicated with respect to the horizontal. Data corresponding to *Allosaurus fragilis* taken from Rayfield et al. (2001).

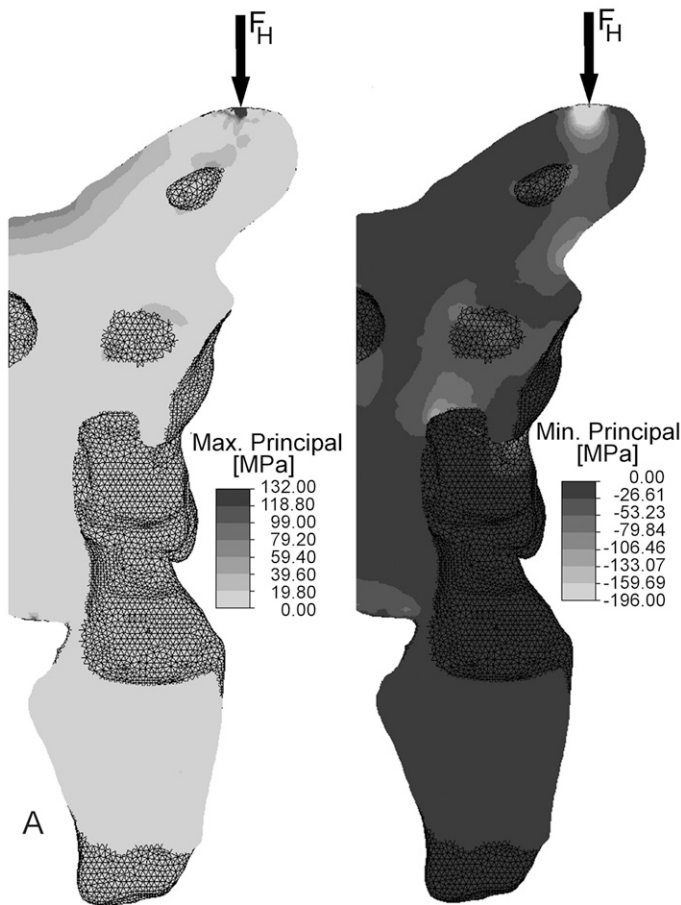


FIGURE 6. Left half of the cranium of *Carnotaurus sastrei* shown across a section coincident with the distal end of the frontal horn. The FE model shows the distribution of maximum (A) and minimum (B) principal stresses produced during a hypothetical head-butting contest. The arrow represents the line of action of F_h , the force exerted by the blow. (Sign convention as in Fig. 4.)

On the whole, the adductor musculature of *Carnotaurus* exerts a force of 8,503 N (model 1). As the bite force exerted at the anteriormost teeth is 1,959 N (Table 2), its mechanical advantage for this bite position is 0.230, which is higher than those in *Allosaurus* (0.160) and *Caiman* (0.225), as calculated from data published by Rayfield et al. (2001), and Sinclair and Alexander (1987). For a posterior bite, the feeding apparatus of *Carnotaurus* is also mechanically more advantageous (0.393) than those in *Allosaurus* (0.330) and *Caiman* (0.270).

On the other hand, the condylar force (F_A) in *Carnotaurus* is 2.61 times higher than its bite force (F_B) at the central teeth

TABLE 2. Maximum reaction forces exerted by a bilateral static bite.

Taxon	Bite position	L_B [m]	F_B [N]	F_A [N]	θ_A [degree]
<i>Carnotaurus sastrei</i>	Anterior	0.538	1,959	6,862	226
	Central	0.413	2,485	6,498	222
	Posterior	0.283	3,341	5,962	216
<i>Allosaurus fragilis</i>	Central	0.581	2,148	10,443	236

Abbreviations: θ_A , direction of the condylar force; F_A , magnitude of the condylar force; F_B , magnitude of the bite force; and L_B , moment arm of the bite force. The bite force was vertically directed ($\theta_B = 90^\circ$) at the indicated positions. Data corresponding to *Allosaurus fragilis* taken from Rayfield et al. (2001).

(Table 2). This force ratio is nearly twice as large in *Allosaurus*, (4.86; after data published by Rayfield et al., 2001). A comparison with data for *Caiman* (reported by Sinclair and Alexander, 1987) shows even greater differences in terms of mechanical “waste”; condylar forces are 3.50 and 7.81 times higher than corresponding bite forces, for anterior bites in *Carnotaurus* and *Caiman*, respectively. Nonetheless, the difference is less substantial for posterior bites (1.78 and 3.08 times higher). These results show that, mechanically, the jaw design of *Carnotaurus* is at least 42% more efficient (less wasteful) than that observed in extant crocodylians such as *Caiman*. The bite force of *Carnotaurus* (model 1) appears to be comparatively weak in relation to those reported for other theropods and living carnivorous vertebrates (Table 3). A bite force computed from model 2 (5,274 N; see above) does not alter radically the conclusion extracted from this comparison, even though its consideration would make *Carnotaurus* a stronger biter than living lions and hyenas.

Cranial Stress Results

Under a simple, static bite (load case *A*; model 1), the stress distribution patterns shown by the model of the cranium are similar for the three bite positions selected along the upper jaw. The highest stresses are restricted to the central and posterior parts of the palatal region and the arrangement of bones that support the braincase. They do not affect (with the exception of the anteriormost portion of the premaxillae on a bite at the anterior teeth) the rostrum nor the braincase (Fig. 4). In those regions, peak stresses range from 16 to 20 MPa (tensile), and -15 to -16 MPa (compressive), becoming higher as the bite situates more posteriorly. Model 2 reveals almost identical stress distribution patterns for this load case, though higher peak stresses can be found that range from 40 to 60 MPa (tensile), and -40 to -55 MPa (compressive). Moreover, model 2 shows higher peak stresses as the bite situates more anteriorly, which is contrary to the tendency indicated by model 1. Regardless of the model used, the peak stresses on the cranium (in both tension and compression) are not critical when compared with the corre-

sponding yield stresses. The peak stresses generated are $132/20 = 7$ times (posterior bite; model 1) or $132/60 = 2$ times (anterior bite; model 2) lower than those required to initiate yielding.

Interestingly, the action of prey tugging during biting (load case *B*) produces a stress distribution pattern very similar to that shown in the previous load case. Moreover, this case indicates that the cranium of *Carnotaurus* could have resisted a static tug of up to 45,464 N (or 38,520 N if model 2 is considered) before yielding. However, the actual force magnitude on which the cranium yields could be markedly reduced if the dynamic effect of tugging in life situations is taken into account. It would be interesting to calculate the forces involved in dynamic tugging, but the data required are not currently available.

The model of the cranium shows a major change in the stress distribution pattern when simulated forces are only applied to the cranial teeth (load case *C*). In this case, new regions of stress concentration were identified in addition to the those previously pointed out for load case *A*. Maximum tensile stresses, ranging from 1.7 to 2.5 MPa, are now also located at the anteroventral portion of the braincase, the quadrate branch of the pterygoids, and various places along the lateral face of the upper jaws and jugals (Fig. 5a); other regions located on the lacrimals and post-orbitals are also affected when the simulated bite force is applied to the posterior teeth. The zones now identified with the highest compressive stresses (-2.0 to -3.7 MPa) also involve the dorsal regions of the rostrum and braincase, as well as the regions at the jugal-lacral and jugal-postorbital contacts (Fig. 5b).

The most severe situation along the tooth row occurs when a force of 2,485 N is applied to the central teeth (Fig. 5). Nonetheless, the stresses are seven times (tensile) and four times (compressive) lower than those produced by a central bite (load case *A*; model 1). The much lower stresses (in relation to corresponding yield stresses) produced in load case *C* suggests that the cranium of *Carnotaurus* would have been much better prepared to withstand the stresses involved in a hypothetical hatchet-like biting mode.

Head-butting in *Carnotaurus* (load case *D*) was tentatively considered as analogous to that observed in intraspecific combats of bighorn sheep. Our FE analysis shows that the cranium of *Carnotaurus* could have resisted forces of up to 225 kN, statically applied on the dorsodistal surfaces of the frontal horns. The strong fusion between the frontals and parietals (Bonaparte et al., 1990) renders an appropriate design to withstand compressive loads. The resultant stresses would have been rapidly dissipated at the skull roof and, thus, not affect the bony elements which accommodate the brain (Fig. 6).

The clashing force delivered in head-butting contests with comparable size conspecifics (F_h) can be approximately estimated as $F_h = mv^2/2d$, where m and v are the body mass and speed of the contestant, and d is the deformation of the clashing structure (Alexander, 1989). We assumed that the factor d could be conservatively estimated as 0.2 m in *Carnotaurus*, as the overall morphology of its cervical skeleton (as shown by Bonaparte et al., 1990) would allow for such a retrocession of the clashing horns. The body mass of *Carnotaurus* was estimated

TABLE 3. Bite forces reported for some theropods and extant vertebrates. (a) bilateral static bite at the posteriormost teeth; (b) unilateral quasistatic bite at a posterior tooth; (c) unilateral snapping bite at the posteriormost teeth. 1, Rayfield et al. (2001); 2, Mazzetta et al. (2004); 3, Erickson et al. (1996); 4, Erickson et al. (2003); 5, Binder and Van Valkenburgh (2000); 6, Thomason (1991).

Taxon	Bite Force (N)	Bite Type	Reference
<i>Carnotaurus sastrei</i>	3,341	(a)	This study
<i>Allosaurus fragilis</i>	3,573	(a)	1
<i>Giganotosaurus carolinii</i>	13,258	(a)	2
<i>Tyrannosaurus rex</i>	13,400	(b)	3
<i>Alligator mississippiensis</i>	9,452	(c)	4
<i>Crocota crocuta</i>	4,500	(c)	5
<i>Panthera leo</i>	4,168	(a)	6

The force magnitudes were estimated, except for *Alligator* and *Crocota*, where they were measured.

to be 1,500 kg (Mazzetta et al., 1998). Consequently, assuming a ramming speed of only 3 ms^{-1} for *Carnotaurus* specimens (similar to that observed during frontal ramming in bighorn sheep), a clashing force of 33.8 kN can be calculated. The safety factor (*sensu* Alexander, 1981) for this hypothetical low-motion clash would be lower than that computed from the ratio $225 \text{ kN}/33.8 \text{ kN} = 6.7$; unfortunately, we are not able to calculate the corresponding ratio for the situation hypothesized since the extent of the dynamic effect on the forces involved in frontal ramming is unknown. This effect is probably quite important as it is the case in many brisk activities. Nonetheless, the calculated safety factor implies that scenarios involving head blows at greater (than modeled) speeds can likely be ruled out for *Carnotaurus*. Frontal pushing events, which do not involve large accelerations, would constitute perhaps a better interpretation for a hypothetical agonistic behavior in *Carnotaurus*.

DISCUSSION

Bite force is an important aspect in the ecology of carnivorous vertebrates, with the potential to shed light on the evolution of community structure and prey size in extinct species (Meers, 2002; Vizcaíno and de Iuliis, 2003; Mazzetta et al., 2004; Rayfield, 2004; Wroe et al., 2005). As an upper restriction on niche, a predator's maximal prey size is a significant component of its ecology and is likely to be strongly influenced by its biomechanical constraints (Wroe et al., 2005). Our analyses show that *Carnotaurus* probably relied heavily on the speed of jaw closure for prey capture. In this sense, observations in modern crocodylians show that jaw speed is much more important than bite force in capturing small prey (Iordansky, 1964; Endo et al., 2002). The unremarkable bite force computed for *Carnotaurus* could be, then, explained in the light of those observations, which allow us to infer a comparable feeding preference for *Carnotaurus*. However, the capacity of the skull to endure high loads during static tugging suggests that larger prey were also accessible to this species.

The mechanical advantage of *Carnotaurus* jaws is very much the same as in normal-to-long snouted (*sensu* Busbey, 1995) crocodylians such as *Caiman crocodylus* (0.23 in both cases; see results). This means that their jaws are equally proportionate in relation to the ratio of the moment arm of the force applied by the adductor musculature to that applied by the bite. However, such equality does not correspond to an identical ratio of bite to joint forces (F_B/F_A). In fact, the latter ratio in *Carnotaurus* is higher than that of equally proportionate, normal-to-long-snouted crocodylians, which reflects a more efficient (less wasteful) mechanical design of its jaws. The differences in efficiency are accounted for the oreinostral (highly vaulted) design of *Carnotaurus* skull, which allows for a different arrangement of the adductor muscles in terms of force magnitudes and moment arms.

In a study investigating size-related variables crucial to successful predation in animals, Meers (2002) presented a least squares regression equation predicting maximum bite force from body mass for extant predatory amniotes. For a predator having the same body mass as *Carnotaurus* (1,500 kg, according to Mazzetta et al., 1998), Meers' equation predicts a bilateral bite force of 66 kN, or about twelve times the maximum bite force calculated in the present study (model 2). Despite being the result of an extrapolation, the bite force predicted looks reliable enough as the largest animal in Meers' data sample (*Alligator mississippiensis*) has a mass nearly an order of magnitude less than that in a hypothetical *Carnotaurus*-sized predator. Nonetheless, it would not have been possible for a 1,500-kg *Carnotaurus* to attain such a bite force because of the constraint imposed by its unremarkable cranial strength (see below). Our stress results for model 1 (where a bite force of about 3.3 kN generates a tensile stress of 20 MPa) show that a bilateral bite force of only 22 kN

(or even less if model 2 results are considered) should be enough to induce yielding in *Carnotaurus* cranium. Consequently, this would set a limit on the reliability of bite force inferences for an extinct animal (such as that presented by Meers, 2002) based on extrapolation from the biomechanics of extant predators.

The relationship between bite force, muscle force output, and patterns of stress in the cranium was assessed by applying FE analyses. Under load case A, regions developing peak stresses are placed mostly away from the roof of the skull, the anteroventral portion of the braincase, the dorsal and lateral regions of the rostrum, the cheek region, and the quadrate branch of the pterygoids; conversely, those are the regions more affected when the adductor muscles are inactive (load case C), particularly in relation to the neurocranium. This indicates that, during biting, the jaw-closing musculature of *Carnotaurus* would have played a key role in diminishing the stress level on the aforementioned cranial regions.

As described above (see results), the stress distribution pattern on the cranium during biting and simultaneous tugging (load case B) does not differ considerably from that caused by a simple bite, and consequently their similarity will be even greater as the force generated by the tug becomes weaker. The same applies to the cranial stress distribution produced by the retractive forces of the neck musculature during tearing and slicing of prey, as this situation is symmetrical in relation to prey tugging. The similarity in stress responses to simple biting and tearing may not be unusual in carnivorous dinosaurs as it was also observed in *Tyrannosaurus rex* by Rayfield (2004).

The overall strength of a biological structure such as the cranium can be estimated by considering its safety factor. This is a term used in engineering that can be defined as the ratio of the strength of an animal body component, to the maximum load it is expected to withstand during life (Alexander, 1981). Mammalian cranial bone is known to operate at factors of safety ranging from 1.8 to 11 (Thomason and Russell, 1986). This is totally consistent with our findings, as the safety factor for *Carnotaurus* cranium during static biting was estimated to lie in the range 2 to 7. Nonetheless, this seems to be quite incompatible with a similar study carried out on the cranium of another theropod; FE analyses and bite force ratios based on comparisons between different biting modes have been used to suggest that the cranium of *Allosaurus* is "overengineered" (Rayfield et al., 2001). However, those ratios are not a good proxy for the safety factor of the cranium; a more appropriate estimate is obtained from the ratio of yielding stresses of bone to the stresses developed on the cranium during each particular mode of biting. On the other hand, if we assumed an inactive jaw musculature, the static forces at the teeth required to initiate cranial yielding in both *Carnotaurus* and *Allosaurus*, are 131 kN (this study) and 55 kN (Rayfield et al., 2001), respectively. This shows a stronger cranial design in *Carnotaurus* than *Allosaurus*, but does not imply over-engineering, because its corresponding safety factor for static biting is quite unremarkable. Rayfield et al. (2001) concluded that *Allosaurus* may have applied a high-impact hatched-like bite to kill prey. Our results (load case C) do not rule out this possibility in *Carnotaurus*, but we argue against the conclusion that a strongly built skull would have been needed to allow for such a hypothetical killing technique to occur.

Although analogies of head-butting combats in *Carnotaurus* with those of living ungulates have been suggested on morphological grounds (Novas, 1989), quantitative functional assessments of this hypothesis have not been attempted previously. We modeled a "worst-case" head-butting scenario, in the sense that the impact force would be strictly localized at the distal ends of the frontal horns. Nonetheless, the horns of *Carnotaurus* are flat on their posterodorsal surfaces (Bonaparte et al., 1990), providing a broad contact surface for the distribution of the impact force during frontal clashes with conspecifics. Moreover,

the possibility that the horns may have had a corneous covering (Novas, 1989; Bonaparte et al., 1990), which would have provided them with further cushion to absorb shocks, was not taken into account. Although our constrained model may lead to an underestimation of the safety factor calculated for this activity, the uncertainties regarding the dynamic effect in head-butting combats discouraged us from using more favorable assumptions. Our mechanical analyses support the use of head-butting, provided that they consisted of low-motion, or even quasi-static, contests. Moreover, the strong fusion between frontals and parietals (Bonaparte et al., 1990) should effectively dissipate stresses on the cranium of *Carnotaurus*, providing increased protection against brain damage during low-motion head-butting contests. If combat did occur, the laterally divergent frontal horns probably engaged such that the contest was settled in most cases by shoving. Such confrontational encounter would have been reminiscent to those seen in bovids as *Bos* and *Bison*, but probably did not involve wrestling given the unfavorable orientations of *Carnotaurus* horns.

Although the specific function of *Carnotaurus* horns cannot be conclusively demonstrated, some indication of the likelihood of suggested functions has been obtained through a FE analysis. Microscopic examination of fossilized bone tissue from the frontals, as well as reliable experimental data (not presently available) on the clashing forces delivered by ramming ungulates would help to further refine our analyses. Moreover, complementary mechanical analyses considering alternative combat scenarios such as head-to-head lateral blows or flank butting, could provide additional insight into the potential for agonistic behavior in this species.

ACKNOWLEDGMENTS

We wish to express our thanks to J. F. Bonaparte and C. Muñoz, who kindly supplied the fossil material and cast used in this study, to R.A. Fariña (Universidad de la República), E. J. Rayfield (University of Cambridge), I. Jenkins (University of Bristol), J. D. Currey (University of York), and T. G. Bromage (City University, New York) for their useful suggestions. Two anonymous referees made a careful reading and provided constructive criticism on an earlier draft of the manuscript. We are also grateful to F. Dalla Torre, and the staff of Clínica Radiológica “Dr. Pedro Moguillansky”, Neuquén, Argentina, for CT scanning the cast. Eduardo López took the photographs of the fossil cranium and E. Agbevev edited the English version of the manuscript. This research was partially supported by Programa de Desarrollo de las Ciencias Básicas (PEDECIBA), Uruguay (GVM), and by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica (PICT 12-14114), Argentina (APC and NC).

LITERATURE CITED

- Alexander, R. M. 1981. Factors of safety in the structure of animals. *Science Progress*, Oxford 67:109–130.
- Alexander, R. M. 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. Columbia University Press, New York, 167 pp.
- Beecher, W. J. 1951. Adaptations for food-getting in the American blackbirds. *Auk* 68:411–441.
- Beecher, W. J. 1978. Feeding adaptations and evolution in the starlings. *Bulletin of the Chicago Academy of Science* 11:268–297.
- Binder, W. J., and B. Van Valkenburgh. 2000. Development of bite strength and feeding behaviour in juvenile spotted hyenas (*Crocuta crocuta*). *Journal of Zoology*, London 252:273–283.
- Bonaparte, J. F. 1985. A horned Cretaceous carnosaur from Patagonia. *National Geographic Research* 1:149–151.
- Bonaparte, J. F., F. E. Novas, and R. A. Coria. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Contributions in Science* 416:1–42.
- Bühler, P. 1981. Functional anatomy of the avian jaw apparatus; pp. 439–468 in A. S. King, and J. McLelland (eds.), *Form and Function in Birds*. Volume 2. Academic Press, New York.
- Busbey, A. B., III. 1989. Form and function of the feeding apparatus of *Alligator mississippiensis*. *Journal of Morphology* 202:99–127.
- Busbey, A. B., III. 1995. The structural consequences of skull flattening in crocodylians; pp. 173–192 in J. J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge.
- Calvo, N., S. R. Idelsohn, and E. Oñate. 2003. The Extended Delaunay Tessellation. *Engineering Computations* 20:5–6.
- Cleuren, J., P. Aerts, and F. De Vree. 1995. Bite and joint force analysis in *Caiman crocodilus*. *Belgian Journal of Zoology* 125:79–94.
- Cook, R. D. 1995. *Finite Element Modeling for Stress Analysis*. John Wiley & Sons, New York, 336 pp.
- Currey, J. D. 2002. *Bones: Structure and Mechanics*. Princeton University Press, Princeton, 436 pp.
- Drongelen, W. Van, and P. Dullemeijer. 1982. The feeding apparatus of *Caiman crocodilus*; a functional-morphological study. *Anatomischer Anzeiger* 151:337–366.
- Endo, H., R. Aoki, H. Taru, J. Kimura, M. Sasaki, M. Yamamoto, K. Arishima, and Y. Hayashi. 2002. Comparative functional morphology of the masticatory apparatus in the long-snouted crocodiles. *Anatomia, Histologia, Embryologia* 31:206–213.
- Erickson, G. M., A. K. Lappin, and K. A. Vliet. 2003. The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology*, London 260:317–327.
- Erickson, G. M., S. D. Kirk, J. Su, M. E. Levenston, W. E. Caler, and D. R. Carter. 1996. Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature* 382:706–708.
- Farlow, J. O., and P. Dodson. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution* 29:353–361.
- Freitag, L. A., and C. Ollivier-Gooch. 1997. Tetrahedral mesh improvement using swapping and smoothing. *International Journal for Numerical Methods in Engineering* 40:3979–4002.
- Holliday, C. M., and L. M. Witmer. 2007. Archosaur adductor chamber evolution: Integration of musculoskeletal and topological criteria in jaw muscle homology. *Journal of Morphology* 268:457–484.
- Idelsohn, S. R., N. Calvo, and E. Oñate. 2003. Polyhedrization of an arbitrary 3D point set. *Computer Methods in Applied Mechanics and Engineering* 192:2649–2667.
- Iordansky, N. N. 1964. The jaw muscles of the crocodiles and some relating structures of the crocodylian skull. *Anatomischer Anzeiger* 115:256–280.
- Kitchener, A. 1988. An analysis of the forces of fighting of the blackbuck (*Antilope cervicapra*) and the bighorn sheep (*Ovis canadensis*) and the mechanical design of the horns of bovines. *Journal of Zoology*, London 214:1–20.
- Mazzetta, G. V. 2002. *Mecánica locomotora y mandibular de dinosaurios saurisquios de América del Sur*. Ph.D. dissertation Universidad de la República, Montevideo, Uruguay, 227 pp.
- Mazzetta, G. V., R. E. Blanco, and A. P. Cisilino. 2004. Modelización con elementos finitos de un diente referido al género *Giganotosaurus* Coria y Salgado, 1995 (Theropoda: Carcharodontosauridae). *Ameghiniana* 41:619–626.
- Mazzetta, G. V., R. A. Fariña, and S. F. Vizcaíno. 1998. On the palaeobiology of the South American horned theropod *Carnotaurus sastrei* Bonaparte; pp. 185–192 in B. P. Pérez-Moreno, T. R. Holtz, Jr., J. L. Sanz, and J. J. Moratalla (eds.), *Aspects of Theropod Paleobiology*. Gaia 15.
- Meers, M. B. 2002. Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior. *Historical Biology* 16:1–12.
- Novas, F. E. 1989. *Los dinosaurios carnívoros de la Argentina*. Ph.D. dissertation Universidad Nacional de La Plata, La Plata, Argentina, 510 pp.
- Rayfield, E. J. 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proceedings of the Royal Society B* 271:1451–1459.
- Rayfield, E. J., D. B. Norman, C. C. Horner, J. R. Horner, P. M. Smith, J. J. Thomason, and P. Upchurch. 2001. Cranial design and function in a large theropod dinosaur. *Nature* 409:1033–1037.
- Reid, R. E. H. 1996. Bone histology of the Cleveland-Lloyd dinosaurs and the dinosaurs in general. *Brigham Young University Geology Studies* 41:25–71.

- Reilly, D. T., and A. H. Burstein. 1975. The elastic and ultimate properties of compact bone tissue. *Journal of Biomechanics* 8: 393–405.
- Schumacher, G.-H. 1973. The head muscles and hyolaryngeal skeleton of turtles and crocodylians; pp. 101–200 in C. Gans (ed.), *Biology of the Reptilia*. Volume 4. Academic Press, New York.
- Sinclair, A. G., and R. M. Alexander. 1987. Estimates of forces exerted by the jaw muscles of some reptiles. *Journal of Zoology* 213: 107–115.
- Thomason, J. J. 1991. Cranial strength in relation to estimated biting forces in some mammals. *Canadian Journal of Zoology* 69: 2326–2333.
- Thomason, J. J., and A. P. Russell. 1986. Mechanical factors in the evolution of the mammalian secondary palate: a theoretical analysis. *Journal of Morphology* 189:199–213.
- Thomason, J. J., A. P. Russell, and M. Morgelli. 1990. Forces of biting, body size and masticatory muscle tension in the opossum *Didelphis virginiana*. *Canadian Journal of Zoology* 68:318–324.
- Vizcaíno, S. F., and G. de Iuliis. 2003. Evidence for advanced carnivory in fossil armadillos (Mammalia Xenarthra, Dasypodidae). *Paleobiology* 29:123–138.
- Wroe, S., C. McHenry, and J. Thomason. 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society B* 272:619–625.
- Zweers, G. A. 1974. Structure, movement, and myography of the feeding apparatus of the mallard (*Anas platyrhynchos* L.): A study in functional anatomy. *Netherlands Journal of Zoology* 24:323–467.

Submitted July 21, 2008; accepted October 23, 2008.