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Carnotaurus Sastrei Bonaparte, The Horned, Lightly Built Carnosaur from the Middle Cretaceous of Patagonia

J. F. Bonaparte, F. E. Novas, and R. A. Coria
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ABSTRACT. Carnotaurus sastrei Bonaparte, 1985, is known from Cretaceous deposits referred to the Gorro Frigio Formation (Albian or Cenomanian) of Chubut Province, Patagonia, Argentina. It is an unusual theropod, with two short, stout frontal horns; a very weak contact between dentary and postdentary bones; cervical vertebrae quite derived, with small neural spines and very pronounced epipophyses; forelimbs extremely reduced; and long, slender hindlimbs. Carnotaurus sastrei shares several derived and primitive characters with Abelisaurus comahuensis Bonaparte and Novas, 1985, from the Allen Formation, Maastrichtian of Patagonia, Argentina: maxilla short and high in its anterior half, a small maxillary fenestra, nasals strongly decorated, wide contact between postorbital and lachrymal above the orbit, elongate quadrate, and ventral branch of the squamosal ventrally directed. These features suggest that both species belong to the same family, Abelisauridae Bonaparte and Novas, 1985.

The Noasauridae, represented by Noasaurus leali Bonaparte and Powell, 1980, from the Lecho Formation, Maastrichtian, northwestern Argentina, appears to be related to the Abelisauridae because the contained species have a similar type of cervical vertebrae, i.e., with reduced neural spines and well-developed, spine-like epipophyses. Comparative analyses suggest that Abelisauridae and Noasauridae share more characters with Ceratosauridae than with any other Theropoda. Two superfamilies are recognized: Ceratosaurioidea (including Ceratosauridae, Abelisauridae, and Noasauridae) and Tyranynosauroidae (including Allosauridae and Tyrannosaurus).

RESUMEN. Carnotaurus sastrei Bonaparte, 1985, proveniente de depósitos Cretácicos referidos a la Formación Gorro Frigio (Albiano o Cenomaniano) de la Provincia del Chubut, Patagonia, Argentina, es un usual terópodo con dos cortos y robustos cuernos frontales; mandíbula con díbil contacto entre los elementos dentarios y postdentarios; vértebras cervicales especializadas, con espinas neuronales pequeñas y epipófisis muy pronunciadas; miembros anteriores sumamente reducidos; y miembros posteriores largos y gráciles. Carnotaurus sastrei comparte una serie de caracteres derivados y primitivos con Abelisaurus comahuensis Bonaparte y Novas, 1985, de la Formación Allen, Maastrichtiano de Patagonia, Argentina: maxilar corto y alto en su sector anterior, fenestra maxilar pequeña, nasales fuertemente decorados, postorbital y lacrimal con amplio contacto por encima de la órbita, cuadrado largo, y escamoso con rama ventral dirigida ventralmente. Estos caracteres sugieren que ambos taxones pertenecen a la familia Abelisauridae Bonaparte y Novas, 1985.

La familia Noasauridae, representada por Noasaurus leali Bonaparte y Powell, 1980, de la Formación Lecho, Maastrichtiano, NW de la Argentina, parece estar relacionado a la familia Abelisauridae, debido a que presenta un tipo similar de vértebras cervicales, con espinas neuronales reducidas y epipófisis desarrolladas. Las comparaciones efectuadas sugieren que Abelisauridae y Noasauridae comparten más caracteres con los Ceratosauridae que con otros terópodos conocidos. Se reconocen dos superfamilias: Ceratosaurioidea (que incluye a Ceratosauridae, Abelisauridae, y Noasauridae) y Tyranynosauroidae (que incluye a Allosauridae y Tyrannosaurus).

INTRODUCTION

During fieldwork of the 8th Paleontological Expedition to Patagonia, within the project "Jurassic and Cretaceous Terrestrial Vertebrates of South America" sponsored by the National Geographic Society, the skeleton of a theropod of rather great size was excavated. It was in a good state of preservation, with all of the preserved bones perfectly articulated. Skin impressions were found in the area of its right side, perhaps the first recorded among the carnivorous dinosaurs. However, weathering had affected the central and distal parts of the tail, most of the tibiae, both fibulae, and the hind feet. The remainder of the skeleton was complete, articulated, and with some lateromedial deformation that was more pronounced in the skull.

Carnotaurus sastrei was briefly described by Bonaparte (1985). It was noted that there are strong differences between it and the Cretaceous carnivorous from the northern continents, especially in the skull, axial skeleton, and in the striking reduction of the forelimbs. Bonaparte and Novas (1985) recognized that Abelisaurus comahuensis represented a new family of the Carnosauria, Abelisauridae, to which C. sastrei was referred. This family is clearly defined by characters of the skull: large infratemporal fenestra; elongated quadrate; posteriorly directed squamosal with a ventral, rod-like process; and a small maxillary fenestra located very near the preorbital opening.

The marked anatomical differences of this family of Patagonian theropods, in comparison with theropods from the Northern Hemisphere, have been interpreted by Bonaparte (1985, 1986b) and Bonaparte and Novas (1985) to be the result of the long geographic separation of the Laurasian and Gondwanian supercontinents. According to the paleogeographic evidence (Bonaparte, 1986b), the isolation occurred from the late Middle Jurassic to the Late Cretaceous (Campanian).

The following abbreviations are used in this paper: AMNH, American Museum of Natural History; MACN-CH, Museo Argentino de Ciencias Naturales "B. Rivadavia," Colección Chubut; and USNM, United States National Museum of Natural History.

SYSTEMATICS AND PALEONTOLOGY

Order Saurischia Seeley, 1888
Suborder Theropoda Marsh, 1881
Infraorder Carnosauria Huene, 1920
Family Abelisauridae
Bonaparte and Novas, 1985
Genus *Carnotaurus* Bonaparte, 1985
Type species *Carnotaurus sastrei*
Bonaparte, 1985

**HOLOTYPE.** MACN-CH 894. Almost complete skeleton, with skin impressions, lacking medial and distal parts of the tail, central and distal parts of the tibiae, both fibulae, and hind feet.

**LOCALITY.** Estancia Pocho Sastre, near Bajada Moreno, Department of Telsen, Province of Chubut, Patagonia, Argentina (Fig. 1).

**HORIZON AND AGE.** Near the top of the Gorro Frigio Formation, Cretaceous (Albian or Cenomanian).

**REVISED GENERIC DIAGNOSIS.** Abelisaurid carnivore, with skull shorter and higher than in *Abelisaurus* and other theropods, and with deep snout and prominent frontal horns. Orbit divided into two parts: an upper, rounded section anterolaterally projected for the eyes, with a pronounced posteroventral orbital wall, and a lower, dorsoventrally elongated section. Supratemporal opening small, with parietal and squamosal forming a high posterior wall and having a low, lateral border. Infratemporal and preorbital openings smaller than in *Abelisaurus*. Quadrates very high, and squamosal having a short, rod-like ventral projection. Loose contact between dentary and prefrontal bones, forming a large mandibular fenestra. Cervical vertebrae behind the axis with reduced neural spines and high, well-developed epipophyses. Sacrum with seven fused vertebrae. Forelimbs reduced, with extremely short and stout radius and ulna, both provided with large, convex distal ends. Ilium long and square-shaped. Pubes, ischia, and femora long and slender.

**CRANIAL SKELETON**

**Skull**

The skull of *Carnotaurus sastrei* (Figs. 2-5) was somewhat laterally compressed in fossilization, mainly around the temporal and orbital openings. It is short and high, with two robust frontal horns. Both the skull and lower jaws have loose sutures between some bones that suggest slight motion. Most of the lateral and dorsal surfaces of the skull have sharp rugosities, canals, and small foramina. But the occipital region, the quadratojugal, the supra-occipital region, and the occipital crest are smooth. These areas of the skull were covered by a muscular mass, whereas in the rugose areas the soft covering possibly was horny.

The *premaxilla* is thick and massive, with the narial opening in a high position. The posteroventral process is not exposed. Below the external nares there is a wide depression of smooth bone, very different from the rest of the muzzle. It may have been the position of a salt gland comparable to that of some herbivorous dinosaurs (Osmolska, 1979).

The *maxilla* is very short and high, with one maxillary fenestra that is dorsoventrally elongated, anteroposteriorly short, and located very near the anterior border of the preorbital opening. The latter opening is also higher than long, quite different from the situation in tyrannosaurs (Fig. 7) and dromaeosaurids.

The *lachrymal* has only a small anterior projection that contacts the nasal (Fig. 2). The ventral projection is posteriorly convex, as in *Abelisaurus* (Bonaparte and Novas, 1985); fig. 7.

The *jugal* is very short and high, with the anterior projection dorsoventrally thick. The suture with
the maxilla is rigid, whereas those with the lachrymal, postorbital, and quadratojugal are weak, suggesting that kinesis was possible.

The postorbital is proportionally large, with a conspicuous anteroventral process that defines the lower rim of the orbit and closely approaches the lachrymal. The postorbital has a wide contact with the frontal horn. The sutures with the squamosal and the dorsal process of the jugal are weak, suggesting that movement was possible.

The squamosal is relatively small, with little participation of the supratemporal fenestra. The ventral projection is rod-like, with a short contact with the quadratojugal. The cavity for the quadratojugal is not deep, and the posteroventral projection is modest.

The quadratojugal and quadratojugal are fused to one another and show a movable contact with the jugal. The quadratojugal is dorsoventrally long, with the lower condyles well defined in medial view and less so in lateral view. The anteromedial projection is high, and it is most easily distinguished at the contact with the quadratojugal branch of the pterygoid. In occipital view (Fig. 4) the quadratojugal is dorsoventrally long and wide, showing a rather sharp border running down from near the paraoccipital process, separating the posterolateral surface from the posteroventral one.

The nasals show more pronounced rugosities than do other parts of the skull. They are transversely convex and almost straight anteroposteriorly. The anteroventral process is pronounced. The sutures of the nasals with the frontals, the premaxillae, and lachrymals are weak, suggesting mobility. But the union of the nasals with the maxillae, although not fused, suggests that it was more rigid than those cited above.

The frontals are fused with the anterior part of the parietals, but the sutures with the lachrymals and postorbitals are loose. The horns of this species
are formed by the frontals. They project laterdorsal and are relatively short and very thick, with the dorsoposterior surfaces rather flat (Figs. 3, 4, 5B). They show a system of shallow grooves, lateromedially directed, that make the surface very different from the rugose nature of the muzzle. The structure of the horns is not very different in appearance from the horn cores present in bovids, although they are certainly not identical to the latter. The horns may have had a cornaceous covering, which would have made the horns much longer in life.

The parietals are fused to the frontals. Anteriorly, they are wide, forming a flat dorsal region. Centrally, the sagittal crest is thin and projects abruptly dorsad to form a posterodorsal process. This is axially thick and transversely wide, with a posterior projection extending over the conspicuous medial crest of the supraoccipital. From here, the supraoccipital crest extends ventrad to the squamosals. As a result, the supratemporal fenestra have low, lateral borders, whereas medially they have elevated borders. The anterolateral side of the parietals diverge outward, forming a strong basal structure for the horns and at the same time forming the posterior orbital wall.

The supraoccipital has a prominent posterior projection.

The occipital crest is transversely broad, although not as broad as the paraoccipital processes. The squamosals and parietals contribute to the high occipital crest, which in posterior view makes a continuous subcircular dome.

The paraoccipital processes are rather thin, directed partially towards the rear and a little downward, with the lateral projections modestly expanded.

The occipital condyle is robust, subspherical, with a marked ventral neck, and with the exoccipitals dorsolaterally directed, although no sutures are seen.
Lower Jaws

Both lower jaws (Figs. 2, 3) are completely preserved with all their teeth. Unfortunately some teeth were fragmented when the jaws were being separated from the skull.

The lower jaw is low and elongated (Figs. 2, 3), with the articular region and retroarticular process low and elongated in lateral view. It has a large mandibular fenestra and, behind it, on the internal side, a wide abductory fossa.

externally, the postdentary bones have a smooth surface, whereas the dentary shows rugosities in the lower half, below the row of nutrient foramina. Above the foramina, the bone surface is rather smooth.

The connection between the dentary-splenial and the postdentary bones is extremely weak. It is reduced to only two contact points, a dorsal one between the dentary and surangular, and a ventral one between a rod-like projection of the dentary and the angular (Fig. 2).

The dentary bears 13 teeth and 2 empty alveoli. The area of the jaw occupied by teeth is rather long. The posterior area of the dentary is bifurcate, bordering a large mandibular fenestra. The posterodorsal projection of the dentary has a notch for an anterodorsal projection of the surangular.

The splenial is very near its original position against the right dentary (Fig. 3) and a bit moved relative to the left dentary. It is elongated and low, with the lower border progressively thicker towards the rear, where it forms most of the lower border of the jaw. The dorsal border is thin and fits into a special depression of the dentary. The anterior extension of this bone, which is dorsoventrally short, has an indentation that is related to the Meckelian cartilage. The posterior margin of the splenial is concave. The Meckelian foramen is present near the ventral border of this bone.

The angular is relatively small, forming the ventral border of the mandibular fenestra.

The surangular borders the mandibular fenestra dorsally and posteriorly. Its dorsal border is convex in lateral view. Posteriorly, near the angular, it has a 6-mm foramen, the "posterior surangular foramen" indicated for Allosaurus (Madsen, 1976: pl. 8). The posterior area of the surangular is low and elongated.

The prearticular is large, with the characteristic open "U" shape (Fig. 3B) defining an opening between its anterodorsal projection and the splenial. Its posterior projection, which is rather low, reaches the end of the retroarticular process.

The articular bears a well-developed medial projection. The quadrate condyles, with the axis directed anteromedial. The internal portion of the articular is larger and more defined than the external portion, and a clear longitudinal crest separates them. Posterior to the articular facet the dorsal portion of the retroarticular process is transversely concave. There is a postglenoid fossa between the articular and the dorsal area of the retroarticular process (Fig. 3B).

The coronoid is a small, elongate bone placed against the medial side of the surangular above the prearticular. Its dorsal border is transversely wide, and it has a lateral depression where the posterodorsal projection of the dentary inserts (Figs. 2, 3B).

Hyoid Apparatus

Three pieces of the hyoid arch (Fig. 6) were found articulated between and within the lower jaws.

Anteriorly there is a corpus (see Romer and Parsons, 1978), which is flat, trapezoidal, and dorsally concave. On its posterior area there are two articular facets for the ceratobranchials (Ostrom, 1961). These are elongate, dorsally concave, and laterally convex.

Comparisons of Skull and Lower Jaws

Comparison with Tyrannosauridae. The general plan of the skull and lower jaws of Carnotaurus is very different from that of the Laurasian Cretaceous carnosaurs. The genera Tarbosaurus (Mai, 1955), Daspletosaurus and Albertosaurus (Russell, 1970), and Tyrannosaurus (Osborn, 1912) have the skull proportionally long and low, with the infratemporal fenestra reduced by an anterior projection of the squamosal and quadratejugal. The region of the preorbital vacuity in these genera is anteroposteriorly large (Fig. 7K). In comparison, the skull of Carnotaurus is proportionally short and
very high, with a wide infratemporal fenestra. The preorbital vacuity is reduced anteroposteriorly, and the skull has well-developed frontal horns.

The lower jaws of *Carnotaurus* have large mandibular fenestrae, the retroarticulars are long and low, and the contacts between the dentary and the postdental bones are limited.

These major differences between the *Carnotaurus* skull and jaws and those of the Tyrannosauridae suggest that two basically different adaptative models existed within the role of great predators. In detail, the main differences with the Tyrannosauridae are as follows:

- a) Tyrannosaurids lack frontal horns.
- b) The lachrymal of *Carnotaurus* does not have the pronounced anterior projection wedged between the maxilla and the nasal found in most of the Tyrannosauridae.
- c) The lachrymal of *Carnotaurus* is posteriorly convex, not anteriorly convex as in the Tyrannosauridae.
- d) The postorbital of *Carnotaurus* has a very short posterior projection, whereas in the Tyrannosauridae it is long.
- e) The postorbital of *Carnotaurus* has a conspicuous anteroventral process that is very near the

Figure 5. *Carnotaurus sastrei*. Skull in lateral (A), dorsal (B), posterior (C), and anterior (D) views. Scale = 10 cm.
Table 1. Measurements (in millimeters) of the skull of *Carnotaurus sastrei*.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of the skull from extremity of premaxilla to distal end of quadrate</td>
<td>596</td>
</tr>
<tr>
<td>Height of the skull from dorsal border of occipital crest to ventral border of jugal</td>
<td>425</td>
</tr>
<tr>
<td>Height of the skull from tip of the horn to ventral border of jugal</td>
<td>434</td>
</tr>
<tr>
<td>Distance from distal end of quadrate to top of parietal crest</td>
<td>416</td>
</tr>
<tr>
<td>Distance between tip of the frontal horns</td>
<td>346</td>
</tr>
<tr>
<td>Greatest expanse of paraoccipital processes</td>
<td>245</td>
</tr>
<tr>
<td>Greatest expanse of parietal crest</td>
<td>185</td>
</tr>
<tr>
<td>Transverse diameter of occipital condyle</td>
<td>50</td>
</tr>
<tr>
<td>Preorbital opening height</td>
<td>172</td>
</tr>
<tr>
<td>Preorbital opening length</td>
<td>98</td>
</tr>
<tr>
<td>Orbit height</td>
<td>50</td>
</tr>
<tr>
<td>Orbit length</td>
<td>80</td>
</tr>
<tr>
<td>Greatest length of quadrate</td>
<td>221</td>
</tr>
</tbody>
</table>

Jaw

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length of the jaw</td>
<td>595</td>
</tr>
<tr>
<td>Dentary length</td>
<td>337</td>
</tr>
<tr>
<td>Height of the jaw from dorsal border of surangular to ventral border of angular</td>
<td>125</td>
</tr>
</tbody>
</table>

lachrymal, defining the ocular cavity and forming a well-defined opening.

f) The jugal of *Carnotaurus* does not have the typical anterior projection present in the Tyrannosauridae.

g) The squamosal and quadratojugal of *Carnotaurus* do not have the pronounced anterior projection (always present in the Tyrannosauridae) that virtually divides the infratemporal fenestra into two parts. In contrast, the squamosal of *Carnotaurus* has a rod-like ventral process that touches the anterior edge of the quadrate.

h) In *Carnotaurus* the quadrate is fused to the quadratojugal, and there is no indication of the quadrate foramen.

i) The development of the frontal horns resulted in strong modifications of the frontals, representing derived characters not developed within the Tyrannosauridae.

j) The pronounced axial crest of the supraoccipital, which dorsally contacts the doro-posterior process of the parietals in *Carnotaurus*, is not present in the Tyrannosauridae.

k) The paraoccipital processes of *Carnotaurus* are long and slender, whereas in the Tyrannosauridae they are massive and robust (Fig. 7M).

l) The lower jaw of *Carnotaurus* has a large mandibular fenestra and only a weak contact between the dentary and postdental bones. These are very different than those present in the Tyrannosauridae.

m) The posterior region of the *Carnotaurus* lower jaw is low and elongated, with the retroarticular process well defined and slender. These characters are very different from those of the Tyrannosauridae, where the lower jaw is high and the retroarticular process short and heavy.

**Comparison with Deinonychosauria.** The anatomical differences between *Carnotaurus* and Deinonychosaurus skulls are significant and readily apparent; however, we will discuss some of them in detail as *Carnotaurus* and deinonychosaur were contemporaneous theropods.

The infraorder Deinonychosauria is composed of the families Dromaeosauridae (Colbert and Russell, 1969), with the genera *Dromaeosaurus*, *Deinonychus* (Ostrom, 1969), and *Velociraptor*; and Troodontidae (Currie, 1987), with the genera *Saurornithoides* and *Troodon*. Both families, in spite of good anatomical differences that support their systematic validity (Osmolska, 1982), show a number of common characters.

A comparison of *Carnotaurus* with the Dromaeosauridae and Troodontidae shows outstanding differences in the skull and jaw. The more striking differences are as follows:

a) The deinonychosaurian skull is low and elongate, very different from that of *Carnotaurus*.

b) The parietal crest of deinonychosaur is rather generalized, with plesiomorphic characters in its
thickness in linear projection. In *Carnotaurus* the parietal crest shows derived characters in the dorsal projection of its posterior area, reduction of its axial length, and anterolateral expansion as a result of the frontal horns.

c) The frontals of deinonychosaurids do not have any indication of osseous crests or horns.
d) In deinonychosaurids, the posterodorsal process of the premaxilla contacts the nasal, the anterior projection of the jugal borders the preorbital
depression, and the anterior projection of the lachrymal has a long contact with the nasal and maxilla. None of these characters are present in Carnotaurus.

c) The condition of the quadrate and quadratojugal is pleiomorphic in deinonychosaurus as they are not fused and retain the quadrate foramen. In Carnotaurus such bones have the apomorphic condition of being fused, and the quadrate foramen is concealed.

There are more differences between deinonychosaurus and Carnotaurus. We consider those listed above sufficient to demonstrate that the skull of Carnotaurus is structurally and morphologically very different from that of the Deinonychosauria.

**Comparison with Ceratosauridae.** The comparison with Ceratosaurus (Gilmore, 1920), from the Upper Jurassic of North America, the only known genus of the family Ceratosauridae, results in an interesting picture of similarities. However, at least in reference to the skull, we do not interpret such similarities as indicators of an ancestor-descendant relationship, but rather as suggesting some degree of phylogenetic relationship. The more significant similarities are as follows:

a) The Carnotaurus premaxilla has a deep sub-narial body, and the posterodorsal projection is reduced or absent, as in Ceratosaurus.

b) The additional preorbital opening in Ceratosaurus (according to Gilmore, 1920; pl. 18) is small and lies quite near the preorbital opening, as in Carnotaurus.

c) The infratemporal fenestra and the quadrate of Ceratosaurus and Carnotaurus are dorsoventrally large and do not show the typical anterior projections of the quadratojugal and squamosal of other theropods.

d) In Gilmore (1920; fig. 53), a dorsal projection of the parietals is seen that resembles the more derived condition of Carnotaurus.

These similarities are accompanied by significant differences, such as the proportions in the length and height of the skull of each genus, the absence in Carnotaurus of any nasal crest, and the absence in Ceratosaurus of any indication of a frontal or prefrontal osseous prominence. Also, in Ceratosaurus, the quadratojugal is not fused to the quadrate, and there is a well-developed quadrate foramen, whereas the opposite is true for Carnotaurus. The contact between the mandibular bones of the dentary and postdental areas is rather firm in Ceratosaurus, but it is extremely weak in Carnotaurus, in which the mandibular fenestra is larger than the former.

**Comparison with Allosauridae.** There are a few similarities with Allosaurus (Madsen, 1976), the best known genus of the family Allosauridae. The most significant of these are as follows:

a) The deep premaxilla below the external nares.

b) The dorsal development of the posterior region of the parietals.

The differences are better expressed than the similarities. One very significant difference is that the squamosal, paroccipital process, quadrate, and quadratojugal all show several derived characters not present in Carnotaurus. The squamosal of Allosaurus projects downward, the lateral end of the paroccipital process is lower, and the quadrate is relatively shorter. Such morphological differences suggest that they represent very different adaptive types, although they may share a common ancestor older than Late Jurassic.

In the lower jaw, the differences between Carnotaurus and Allosaurus are very prominent because the mandibular fenestra is almost absent in the latter genus (Madsen, 1976; pl. 1).

**Comparison with Abelisauridae.** Abelisaurus comahuensis Bonaparte and Novas, 1985 (Fig. 7D, E), the type genus of the family Abelisauridae, from the Allen Formation, Lower Maastrichtian of Río Negro Province, Argentina, is a rather large theropod, with a skull of some 85 cm in total length. Although the skull of Carnotaurus has different proportions than the skull of Abelisaurus (short and high in the former, low and elongated in the latter), there are several common features that support allocation to the same family. They are the following:

a) The squamosal is very similar, especially in the shape and orientation of the ventral process, but with some differences in the posterior process.

b) The quadrate in both genera is long and fused to the quadratojugal.

c) The postorbital almost meets the lachrymal underneath the ocular cavity, although there are morphological differences in the anterior process of this bone between the genera.

d) The lachrymal is dorsoventrally convex towards the rear in each genus, and it contacts the postorbital above the orbit.

e) The shape and location of the additional preorbital opening is the same in both genera.

f) The premaxilla is deep below the narial opening in both genera.

g) The nasals show rugosities along most of the dorsal and lateral sides in both genera.

h) The posterior region of the parietal crest is elevated, and the supraoccipital bears a large dorsal keel in the axial plane, in both genera.

i) In dorsal view, the shape of the parietal crest is narrow posteriorly, widening anteriorly in both genera.

Of the common characters listed above, we consider that b, c, d, e, g, and i are synapomorphies of the family Abelisauridae. Abelisaurus and Carnotaurus are thus placed together in this family.

**AXIAL SKELETON**

**Vertebral Column**

The vertebral column of specimen MACN-CH 894 is complete and articulated from the atlas through the 6th caudal. The posterior caudals were de-
stroyed by weathering, except the 12th, which is incomplete.

In general terms, the sequence of vertebrae is characterized by opisthocoelous cervicals with very reduced neural spines and very large epipophyses, and most of the dorsals are subamphiplatyan. The sacrum has seven fused vertebrae, and the anterior caudals have transverse processes projecting dorsolaterally.

**Cervical Vertebrae.** The *atlas* (Fig. 8A) has the intercentrum almost complete, and it is fused to the atlantal arches. The articular facet for the occipital condyle spreads onto most of the dorsal articular area and projects upward and forward. It does not show the articular facet for the odontoid as is seen in *Deinonychus* (Ostrom, 1969: fig. 26) but resembles the characters of *Ceratosaurus* (Gilmore, 1920: pl. 19) and *Allosaurus* (Madsen, 1976: pl. 11). In the ventral side of the intercentrum there are two processes (one on each side) for muscular attachments. On the posterior face the articular area for the axis intercentrum, which has a good suture with the centrum of the axis, is transversely wide, resembling the condition in *Ceratosaurus* and to a lesser extent that in *Allosaurus*. The atlantal arch is fused to the intercentrum and shows no indication of articulation with a proatlas, which may not have existed in *Carnotaurus*. The posterior projection is incomplete; the postzygapophysis is small. In posterior view the lower side of the roof made by the atlantal arches has a subcircular cavity for the passage of the spinal chord. Mobility between the atlas and axis appears to have been small in this genus.

The *axis* (Fig. 8A, B) is complete and shows little deformation. The centrum and intercentrum are relatively elongated, but with rather modest transverse and dorsoventral diameters.

In anterior view the continuous surface for articulation with the atlas and the odontoid articulation for the occipital condyle are seen. The posterior face of the centrum is very concave, with the lower area projected posteriorly. In ventral view the axis bears a poorly defined, rather vestigial keel. In lateral view two small pleurocoels are present in the upper half of the centrum. A well-defined cavity, subdivided into two, lies behind and a bit dorsal to the diapophyses, and two depressions with foramina are located above and behind the prezygapophysis. The depressions with foramina that penetrate the axis probably correspond to a system of pneumatic cavities as in *Platanystylopus floresi* (Bonaparte, 1986a).

The prezygapophysis is small, whereas the postzygapophysis is large with the longest axis transversely placed. The parapophysis is not defined, although it may correspond to the suture between the intercentrum and the centrum. The diapophysis is rather small.

The blade of the neural spine is large with the dorsal border convex in lateral view, as in *Ceratosaurus* (Gilmore, 1920: pl. 19). This border is slightly forked at the postero dorsal end in dorsal view. Below it a division follows to the epipophy-
seal area. In posterior view there is a deep depression with foramina in the axial plane below the neural spine and a wide, deep depression with foramina above the neural canal. The axis is markedly different in almost all details from that of *Tyrannosaurus* (Osborn, 1917). It is, however, very similar to that of *Ceratosaurus* and, to a lesser degree, *Allosaurus* (Madsen, 1976: pl. 11).

The third cervical (Fig. 9) is complete and, like the remaining cervicals, is characterized by a significant reduction of the neural spine and hypertrophy of the epipophysis.

In lateral view the anterior face of the centrum makes a sharp angle with the anteroposterior plane, indicating the limits of the dorsoventral flexion of the neck.

There are two small pleurocoels on the rather flat lateral side of the centrum. The lower border of the centrum is almost straight. Behind and above the diapophysis there is a large depression and a foramen passing into the neural arch. Anterior to the diapophysis there is a modest foramen. Both the parapophysis and diapophysis are of modest size. The epipophysis is strongly developed, and a lamina connects it to the prezygapophysis. This lamina sharply delimits the lateral and dorsal areas of the neural arch. In lateral view, the neural spine is a bit lower than the epipophysis. The prezygapophyses are well separated from one another, each having the major axis transversely directed and each inclined towards the axial plane.

In posterior view a large cavity is exposed that leads into the neural arch. In the axial area there is a rugose zone for insertion of intervertebral ligaments. The posterior concavity of the centrum is deep, with its geometric center moved to the upper half. In dorsal view this vertebra is rather flat with wide laminar surfaces.

The fourth cervical is basically the same as the 3rd cervical, but larger. The ventral border of the centrum is more curved, the parapophysis better defined, and the diapophysis thicker. The cavities and foramina for the pneumatic system are similar, except that the one behind the diapophysis is larger.
The postzygapophyses are larger and the epipophyses are axially longer, with a posteriorly defined process and an incipient anterior process. In anterior view the neural spine is more reduced than in the 3rd cervical. There is a depression on the dorsal surface in front of the reduced neural spine and another one between the neural spine and the dorsal projection of the epipophysis.

The fifth cervical is larger than the 4th cervical, especially in the volume of the centrum. The diapophysis is more robust, and the epipophysis has the anterior and posterior processes more defined. Also, the lamina that extends between the epipophysis and prezygapophysis is higher and more laterally placed. The system of depressions and foramina of the pneumatic cavities is similar to that of the 4th cervical.

The sixth cervical (Figs. 10, 11) is a little larger than the 5th cervical. In the centrum the inclinations of the anterior and posterior faces are more pronounced. The epipophyses are better developed anteroposteriorly, and the postzygapophyses are well separated.

The seventh cervical is essentially the same as the 6th cervical, although more robust. The postzygapophysis is larger, with the larger dimension transversely placed and the articular facet directed obliquely ventromedially. In posterior view the wide depression behind the neural spine has two rather large fenestrae that lead into the neural arch. Posteriorly, the centrum is subcircular and less concave than in the 6th cervical.

The eighth cervical vertebra is more voluminous and higher than the 7th cervical. The centrum is
slightly concave on its ventral side, as in the preceding ones, and it lacks a keel. In the area of the pleurocoel there is a depression and three foramina penetrate the centrum. The neural spine is almost nonexistent, and the epiphysis is more elevated than in the 7th cervical. The diaphysis is a little higher, and the opisthocoelia is less pronounced.

The ninth cervical (Fig. 12) is larger than the 8th cervical, although it shows generally the same morphology. In comparison, however, the opisthocoelia is less pronounced, the diaphyses are more elevated and stronger, and the neural spine is a little more developed. The system of depressions, foramina, and pneumatic cavities appears to be the same, but with larger foramina. A ventral, rounded keel is present on the centrum, with slight depressions on each side of it.

The tenth cervical (Fig. 13) has a centrum with the anterior and posterior articulations at a right angle with respect to the horizontal axis. A modest keel exists on the ventral border. The diaphysis is more elevated, more robust, and longer than in the 9th cervical. The neural spine is also higher, although it remains lower than the epiphysis. The latter shows some reduction, with the anterior and posterior processes very reduced. On the posterior side of the neural spine there are strong rugosities for the attachment of interspinous ligaments.

Dorsal Vertebrae. The first dorsal vertebra was affected by a small fault in the rock that produced some displacement and deformation in its neural arch. The centrum is almost the same, except for a larger “pleurocoelus depression,” and the parapophysis is more dorsally placed.

In the neural arch the changes in relation to the last cervical are abrupt. There is no epiphysis, the neural spine is the highest dorsal element of the vertebra, and the robust transverse process is at the level of the zygapophyses. However, the morphology and orientation of the zygapophyses are similar to those of the cervicals. The total height of the vertebra is greater than the 10th cervical. Comparatively, the shallow opisthocoelia of the last cervical and first dorsal are very different to the marked opisthocoelia of the same vertebrae of Allosaurus (Madsen, 1976: pl. 15).

The second dorsal (Fig. 14) has the transverse process more elevated and robust than in the 1st dorsal, and the neural spine is a little larger. The zygapophyses are nearer to the axial plane, in particular the postzygapophyses, which show an incipient hypophyseal. In lateral view, the borders are present on the ventral side of the transverse process: the anterior and posterior infradiaphyseal laminae. A noticeable depression penetrating into the neural arch is present between the anterior infradiaphyseal lamina and the prezygapophysis.

The third dorsal is like the 2nd dorsal, but the neural spine is longer and more robust and the transverse process longer. The zygapophyses are less inclined, particularly the postzygapophysis, which is almost horizontal. Below the postzygapophysis is a well-developed hypophyseal. Underneath the prezygapophysis there is a column-like process, which borders laterally a large depression that communicates with the neural arch.

The fourth dorsal (Fig. 15) has a longer neural spine than the 3rd dorsal, which is also anteroposteriorly flat and posteriorly inclined. The prezygapophysis is subhorizontal and projects anteriorly. The postzygapophysis is horizontal, and the lateral border is directed downward. The hypophyseal of this vertebra is well developed and forms a wide body that reaches the roof of the neural canal. The parapophysis is dorsal to the vertebral body.

In the fifth dorsal (Fig. 16) the parapophysis is in a very different position—approximately in the middle of the neural arch and projecting laterad. The parapophysis borders a large cavity that penetrates into the neural arch, in contrast with the condition in the 4th dorsal. The neural spine is large, in part laterally compressed, and with a dorsal expansion. The centrum is almost amphiplatyan.

In the sixth dorsal, and to a degree in the 5th dorsal, below the prezygapophysis there is a lower, anterior projection. The parapophysis is more dorsally placed, and it has a long, laterally projecting stem. Between the parapophysis stem and the diaphysis there is a very large fossa communicating into the neural arch. In dorsal view the transverse process has a wide, flat surface. The centrum of this vertebra has a lateral depression oriented anteroposteriorly just below the union of the centrum with the neural arch. Two conspicuous foramina are located there. Along most of its perimeter the posterior border of the centrum is pathologically hypertrophied.

The seventh, eighth, and ninth dorsals (Figs. 17, 18) are of similar morphology. The 7th dorsal is a bit taller than the 6th dorsal, and the process below the prezygapophysis persists. The postzygapophysis is transversely concave. In the neural spine, there are strong osseous processes for the attachment of
tendons. In the 8th dorsal, the dorsal surface of the transverse processes is larger than in the 7th dorsal, and it is even more so in the 9th.

The tenth and eleventh dorsals (Figs. 19, 20) have centra of greater diameter than the preceding vertebrae. The parapophysis, very dorsal in position, tends to become part of the dorsal lamina of the diapophysis. The parapophysis, is larger anteroposteriorly than in previous vertebrae, increasing its surface posteriorly. The neural spine of the 10th dorsal does not show the conspicuous osseous rugosities for attachment of tendons, but they are present in the 11th. The prezygapophysis of the 11th dorsal is reduced and suggests that the movements between the 10th and 11th vertebrae were very restricted.

Sacral Vertebrae. The sacrum of Carnotaurus is almost complete, except for the system of plate-like sacral ribs that was not well preserved. The sacrum consists of seven vertebrae, of which the 1st sacral is fused only in the vicinity of the postzygapophysis and the following six are intimately fused (see Fig. 20). The 1st sacral preserves most of the characters of the last dorsals, but the transverse processes are reduced, both in length and width. The neural spine is axially reduced, and the lateral cavities of the neural arch are concealed.

The 2nd to 7th sacral vertebrae are strongly fused, both through the centra and through the neural arches. The neural spines, especially distally, form a continuous ossification. The co-ossified centrum, in lateral view, a dorsally convex arch. In ventral view, the centra in the middle of the sacrum (sacrals 3, 4, and 5) are transversely reduced, particularly the 4th sacral. There is thus a marked reduction of volume in the vertebral bodies of the sacrum.

The lateral projections of the sacrum are short,
indicating that the pelvis of *Carnotaurus* was narrow. The main connection between the sacrum and the ilia was through the transverse processes. The sacral ribs are incomplete, but appear to be very short. From the 3rd sacral distal they are rather thick in cross section.

Caudal Vertebrae (Figs. 21–23). Only six proximal, articulated caudals are preserved, with some of them showing effects of weathering. Also preserved is an isolated centrum with part of the neural arch, possibly the 12th caudal.

The first two caudals are very large and robust. The caudals rapidly decrease in size posteriorly to the 5th, and the centrum of each is amphicoelous. Elongation of the vertebral bodies is apparent, and the centra show only slight lateral depressions.

The dorsolaterally projecting transverse processes reach a level very near the top of the neural spine, suggesting a derived condition. The lower surface of the transverse process faces ventrolaterally. Another curious, derived character seen in the available caudals is the expanded distal end of the transverse process. This feature is present in the six proximal caudals, whereas in the 12th caudal it is not preserved.

Comparison of Vertebral Column. The presacral vertebrae of *Carnotaurus sastrei* correspond well with the general model present in the Theropoda, particularly in the Carnosauria. However, they bear several derived characters that readily distinguish them from the known theropods, except perhaps *Noasaurus leali* (Bonaparte and Powell, 1980).

The cervicals of *Carnotaurus*, posterior to the axis and up to the 10th, show a strong reduction of the neural spine and a strong dorsal development of the epipophyses, which form a paired row of neural spine-like processes. This model of cervical vertebrae was undoubtedly adapted for quite a new arrangement of the muscular system, related to better functional control of neck and cranial movements. It resembles in part the neck morphology of the Ornithomimidae, in which the neural spine is vestigial and bears dorsolateral processes higher than the neural spine.

In *Allosaurus fragilis* the 4th and 7th cervicals show the lateral lamina connecting the epipophysis.
with the prezygapophysis, and the 5th cervical shows good dorsal development of the epipophysis (Madsen, 1976: pl. 13), although it is less developed than in *Carnotaurus*. However, the anatomy of these vertebrae of *Allosaurus* suggests that, at least in part, the unique anatomy of the cervicals of *Carnotaurus* were roughly outlined in *Allosaurus*.

The dorsal vertebrae are significantly different in the lateral structure of the neural arch from those of the Tyrannosauridae, Allosauridae, Ceratosauridae, and Deinonychidae. The differences relate to the higher position of the parapophyses in *Carnotaurus*, which increases from the 5th dorsal posteriorly to reach their highest point in the 10th and 11th dorsals, in which diapophyses and parapophyses are very near one another in the horizontal plane. Thus, the dorsal migration of the parapophyses of *Carnotaurus* led to several autopomorphies of the Patagonian form, *i.e.*, anteroposteriorly wide transverse processes, presence of a discrete fossa between the parapophyses and the infradiapophyso-lamina, and presence of a well-defined lamina between the parapophysis and dorsolateral border of the centrum.

In contrast to the similarities of the skull and axis discussed previously, no shared derived characters have been seen in the presacral vertebrae of *Carnotaurus* and *Ceratosaurus*.

The count of seven sacral vertebrae and the presence of a six-vertebrae synsacrum represent significant derived characters not recorded, as far as we know, in other Carnosauria. However, a comparable number of sacrals is present in some small theropods, such as *Sauornithoides* (Barsbold, 1974). Osborn (1917) recognized five sacral vertebrae in *Tyrannosaurus*, although from the figure
of the pelvis and sacrum in lateral view we suspect that the 13th dorsal may very well be the first functional sacral because of its position "within" the ilia, even though it is not fused to the remaining sacrals. In Osborn's paper (1917: fig. 19) one can see that the sacrum of *Tyrannosaurus* is proportionally shorter than that of *Carnotaurus*, and it is wider at both ends. Also, it is possible to see that it has neither the dorsal arching along the ventral border of the centra nor along the row of sacral ribs. Even though the co-ossified dorsal end of the neural spines is a common character for *Tyrannosaurus* and *Carnotaurus*, the arching of the centra and the line of union between the sacrum and ilia (see Fig. 20), as well as the strong co-ossification of the centra and their reduced thickness, represent a set of derived characters not present in *Tyrannosaurus*. This suggests that the sacrum of the Patagonian genus is more derived than that of the tyrannosaurids. *Piatnitzkysaurus* and *Allosaurus* clearly have more primitive sacra (Gilmore, 1920; Madsen, 1976; Bonaparte, 1986a), each with five vertebrae that are not completely fused.

*Ceratosaurus* shows similarities in the general plan and in several derived characters. The sacrum is composed of five fused vertebrae (Gilmore, 1920), which are well co-ossified, as in *Carnotaurus*. In addition, in *Ceratosaurus* reduction of the thickness of the fused centra is also similar to the situation in *Carnotaurus*. Gilmore considered the sacral vertebrae of *Ceratosaurus* to number five, taking into account only the fused ones. In our opinion the functional sacral vertebrae of this North Amer-
ican Morrison Formation genus includes seven and possibly eight vertebrae, including the last two presacra and possibly the first caudal of Gilmore. The seven sacral vertebrae of Carnotaurus, with the 1st sacral “recently” incorporated from the dorsals (note the intermediate morphology of this vertebra and its partial fusion with the posterior sacra [see Fig. 20]), suggest that general organization of the sacrum is rather similar to that of Ceratosaurus. The similarities in the sacrum of these two genera strongly suggest a common trend of specialization that may reflect a close phylogenetic relationship.

Concerning the caudal vertebrae, we are not aware of comparable characters in other theropods. It suggests that both uncinate processes and laterally elevated transverse processes may represent an autapomorphy of Carnotaurus.

Ribs

The complete series of cervical ribs and most of the dorsal ribs are preserved. The atlantal rib (Fig. 24A) has an articular head with a slightly flat expansion, but without indication of a separate capitulum or tuberculum. The stem is long, rather flat, and reaches the 4th cervical vertebra.

The second rib is larger and has a more defined proximal area. The shaft is rather flat until the 3rd vertebra, behind which it extends stelliform to the 5th cervical vertebra.

The third cervical rib (Fig. 24B) shows a well-defined capitulum and tuberculum. The latter forms an expanded dorsal process. A short anterior process that increases in size in the following ribs is present. The shaft of this rib is very long, almost
reaching the 7th cervical vertebra. The proximal area of the shaft is laterally convex and continues distad as a subcylindrical rod of constant diameter.

The fourth cervical rib (Fig. 24C) is similar to the previous one, but the proximal laminar area is larger, followed posteriorly by an elongate and delicate stilet.

The shape of the 4th cervical rib is repeated up to the 9th cervical rib (see Fig. 24D, E). The anterior process remains conspicuous, and each rib possesses a well-defined capitulum and tuberculum.

In the tenth cervical rib a lamina connects the capitulum and tuberculum. The anterior process is abruptly reduced, and there is no distinction in the shaft between the proximal and distal portions. The shaft of this rib is relatively short and thick.

The first dorsal rib (Fig. 25A, B) is much longer and thicker, and it has a large capitulum and robust
tuberculum. The second dorsal is similar, but larger, with a larger and stronger proximal process. The third and fourth dorsal ribs (Fig. 25C, D and E, F, respectively) increase in size. The size of the proximal region of each rib decreases posteriorly, and the shaft of the capitulum becomes shorter because of the dorsal migration of the parapophysis. The last dorsal, the 11th (Fig. 25I, J), is short and in the living animal would have almost touched the anterior border of the ilia.

Gastralia

Because of weathering and the nature of the excavation process, the gastralia, which were in their original position, were not properly recovered. They were positioned from very near the anterior border of the pubis forward and consisted of rather long, subcylindrical rods, lying transversely very near one another.

Haemal Arches

The anterior haemal arches (Fig. 26) are represented by natural molds and bone fragments (one with the proximal part preserved and another one complete). They are proportionately long and slender, with a relatively wide proximal articulation and the haemal canal enclosed dorsally. The articular facets and the shape of the haemal canal suggest that the haemaphyses had a more posterior than ventral orientation.

In the anterior part, the haemal canal has a lateral expansion, whereas posteriorly the canal shows a deep distal depression. These features indicate that the haemal canal had an oblique position relative to the long axis of the shaft of the haemaphysis. These features suggest that natural position of the haemaphysis was far from perpendicular to the axis of the tail and that it more probably formed a very acute angle with it. It also means that the tail of Carnotaurus was probably dorsoventrally flattened.

### Table 2. Measurements (in millimeters) of presacral, sacral, and caudal vertebrae of Carnotaurus sastrei.

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a = approximate.
‡ = from dorsal border of epipophysis to posteroventral border of the centrum.

APPENDICULAR SKELETON

Pectoral Girdle and Forearm

Scapulo-Coracoid and Sternal Plates. Both scapulo-coracoids are completely preserved. The cor-
acoid and the proximal part of the scapula are rather large compared with the modest scapular blade (Fig. 27). The latter has a constant width from a little above the glenoid cavity to the distal end, where there is no expansion as in *Tyrannosaurus* (Osborn, 1917) or other carnosaurs.

The anterior border of the scapula passes gradually to the acromial area, resembling the condition of *Deinonychus*, whereas it is more angular in *Tyrannosaurus*, *Allosaurus*, and *Ceratosaurus*.

The scapula and coracoid are strongly fused. The coracoid is large, with the distal border making a wide, continuous curvature, from near the posterolateral process of the coracoid up to the scapulo-coracoid suture on the anterior border. The position of the posterolateral process is near the glenoid cavity, a character we have not seen in other Carnosauria. In this area there are rugosities suggesting strong muscular attachment, probably of the m. biceps.

At the level of the glenoid cavity there is a large subacromial depression, located below a border of

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**Figure 19. Carnotaurus sastrei.** Tenth dorsal vertebra in dorsal (A), lateral (B), and anterior (C) views. Abbreviations as in previous figures.
the scapula that may be the acromial process. The coracoid foramen is large and perforates the coracoid with a slight inclination.

The glenoid cavity is well defined, with well-developed supra- and infraglenoid processes that enlarge the articular region dorsally and ventrally. The shape is subspheric, except in the posterior section of the coracoid where the cavity between the processes is flat.

Near the area of the glenoid cavity in both scap-
ulo-coracoids there is an ossification on the inner side of the bones (about 50 mm in diameter), the function of which is unknown to us.

In life, the scapular blade was probably almost parallel with the row of dorsal vertebrae. On the internal side of the coracoid there are marks of dorsal ribs, indicating that they were parallel to the long axis of the coracoid.

The clavicle (Fig. 27C) may be represented by a slightly curved, rod-like bone with a modest, proximal expansion. It was lying on the anterolateral portion of the right coracoid, in front of the sternal plates. Because of its position and morphology we interpret it as the right clavicle, although some portion of it may be missing.

The sternal plates (Fig. 27C) are preserved nearly complete. They were found close behind the coracoids. The right humerus was lying on the lateral surface of the right sternal plate. They are nearly flat and oval in outline, with a short ventral projection and two rib processes projecting posterodorsad and separated by a concavity.
The position of the sternal plates as found, i.e., touching the medial border of the coracoids, may not have been too far from their natural position.

Forelimbs. The two forelimbs are almost complete, articulated, and with both humeri within the glenoid cavity. Unfortunately, the forefeet are not completely articulated, and some bones are not easy to interpret.

The forelimbs of Carnotaurus have significant derived characters, particularly in the epipodial bones, which are strongly reduced and appear to be a functional part of the hand. In this, the Patagonian genus shows derived characters not recorded in other Theropoda.

The humerus (Fig. 28) is robust and relatively short. Its dorsal region is transversely convex, and the internal side is concave proximodistally, as is common in the Carnosauria, and the opposed side is convex in the same direction. This means that in dorsal view the humerus is curved distally and internally, and in lateral view relatively straight.

The humeral head is well defined and subspheric, with similar length axes in the dorsoventral and lateromedial direction. A well-defined, but short, neck is present. These characters suggest that the humeral movements were pronounced in all directions, although the anteroposterior component was probably greater. The internal tuberosity is well developed, although proportionally smaller than in Piatnitzkysaurus (Bonaparte, 1986a) or Allosaurus (Madsen, 1976). The deltopectoral crest is massive, with the distal area most pronounced. Distally, the articulations for radius and ulna are dorsoventrally large and relatively flat, suggesting that the forelimb bones did not rotate on them significantly and that movements were probably restricted to the anteroposterior plane. Several typical characters of the theropod humerus have been strongly modified in the distal area of the Carnotaurus humerus: a) the large supracondylar depression on the dorsal face was replaced by a convexity of the bone; b) the intercondylar depression on the ventral side was also modified, and this area is convex; c) the articular condyles were modified from subspheric to flat and dorsoventrally large; and d) the proximodistal torsion of the humerus is notably reduced.

The radii and ulnae (Figs. 29A-C, 30) are complete, and in articulation with the humeri and each other. They are very short, each only ⅔ the length of the humerus. The ulna has a large, concave articular facet for the humerus, with the posterior area elevated and transversely wide. The anterior part of the facet is narrow and in a lower position than the posterior. In proximal view, the articular facet is triangular, with the apex anterior. The distal articulation is a wide condyle, convex in both directions, with the longest axis directed anteroposteriorly. A marked neck lies between the distal articulation and the short diaphysis.

The radius is slightly shorter than the ulna. It has a large, rather flat, proximal articular facet. It articulates with the ulna via a convex area near its proximal end. The distal articulation is large and wide in both directions, but less convex than that of the ulna. There is not as great a difference between the size of the shaft and the ends of the bone as seen in the ulna. A well-defined osseous process, whose function is unknown, is found on the lateral side of the diaphysis and in the middle of its length.

Large parts of both the right and left manus have been preserved, although we do not have a definitive interpretation of the distribution or relationship of the different pieces of their carpi and digits of the Carnotaurus. The reconstruction is tentative (Fig. 29C); however, we observe the following:

a) There is a group of carpal bones, of unknown number, below the ulna.

b) Four metacarpals are present. Metacarpal I is short, similar in length to metacarpal III; metacarpal II is the largest, morphologically similar to I, but ½ longer in size, with a large proximal articulation; metacarpal III is shorter than II, but transversely wider than metacarpals I and II, with the proximal area anteroposteriorly large and the distal area smaller; metacarpal IV is atypical, with a very large articulation for the large condyle of the ulna.

c) The first row of phalanges was limited to digits I, II, and perhaps III. The second row of phalanges is represented only by a proximal fragment of the second phalanx of digit II.

Comparisons of Pectoral Girdle and Forelimb. A comparison of the scapulo-coracoid of Carnotaurus with that of the genera of the families Allosauridae, Tyrannosauridae, and Ceratosauridae shows strong differences. The weakly developed acromial region of Carnotaurus differs greatly from that in the cited families, in which this region is well developed. Also, in Carnotaurus the postero-lateral process of the coracoid is very near the glenoid cavity.
The scapular blade resembles more of the dromaeosaurid type of scapula, particularly that of Deinonychus, with the parallel anterior and posterior borders and the modest acromial expansion. However, differences with the coracoid of Deinonychus are strong enough to minimize any phylogenetic or systematic interpretations based on the similarities of the scapular blade.

The humerus of Carnotaurus is very similar to that of Tyranosaurus (Osborn, 1917: fig. 21) and Albertosaurus (Lambe, 1917: fig. 31), although there are clearly differences in details, such as a more reduced deltopectoral crest, a more developed internal tuberosity, and a more derived distal region in the humerus of Carnotaurus.

The megalosaurid Torvosaurus (Galton and Jensen, 1979) has a different model of humerus with respect to Carnotaurus in the development of the
deltoplectoral crest and humeral head. *Carnotaurus* has radii and ulnae proportionally shorter than *Tyrannosaurus*.

In the manus, the morphology and proportion of the several bones observed, and the characters of the distal end of the radius and ulna, are not typical for a carnosaur. The hand shows a group of plesiomorphic (e.g., four digits) and apomorphic (e.g., metacarpal IV with a very large articulation for the distal condyle of the ulna) characters, whose association has not been reported in other Theropoda, except in *Ceratosaurus* where Gilmore (1920: figs. 60, 62) illustrated four digits with short phalanges.

We believe that the strong modification in the forelimbs of *Carnotaurus*, among them the almost total lack of torsion of the humerus and the parallel position of radius and ulna, resulted in a complete

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**Figure 24.** *Carnotaurus sastrei*. Left cervical ribs: 1st (A), 3rd (B), 4th (C), and 5th (D) in dorsal view and 8th (E) in dorsomedial view. ca, capitulum; e, anterior spine; pa, aliform process; tu, tuberculum.

**Figure 25.** *Carnotaurus sastrei*. Proximal ends of right dorsal ribs. 1st rib (A, B), 2nd rib (C, D), 4th rib (E, F), 9th rib (G, H), 11th rib (I, J) in ventral (A, C, E, G, I) and dorsal (B, D, F, H, J) views.

**Figure 26.** *Carnotaurus sastrei*. Fourth haemal arch (A–C) and 10th haemal arch (D–F) in dorsal (A, D), lateral (B, E), and ventral (C, F) views. hc, haemal canal.

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change of the original position of the hand. If this is true, the palmar side moved to a dorsal position, with digit I assuming a lateral position and digit IV an internal position.

Table 3. Measurements (in millimeters) of the shoulder girdle of *Carnotaurus sastrei.*

<table>
<thead>
<tr>
<th></th>
<th>Right</th>
<th>Left</th>
</tr>
</thead>
<tbody>
<tr>
<td>Greatest length of scapula and coracoid measured along curve of outside</td>
<td>905</td>
<td>900</td>
</tr>
<tr>
<td>Maximum length of scapula</td>
<td>645</td>
<td>610</td>
</tr>
<tr>
<td>Maximum breadth of scapular blade (at level of tubercle for <em>m. triceps</em>)</td>
<td>128</td>
<td>133</td>
</tr>
<tr>
<td>Greatest transverse expanse of glenoid fossa</td>
<td>63</td>
<td>70</td>
</tr>
<tr>
<td>Greatest proximodistal expanse of glenoid fossa</td>
<td>80</td>
<td>95</td>
</tr>
<tr>
<td>Greatest length of coracoid</td>
<td>430a</td>
<td>430a</td>
</tr>
<tr>
<td>Greatest depth of coracoid</td>
<td>290</td>
<td>290</td>
</tr>
<tr>
<td>Anteroposterior expanse of sternal plate</td>
<td>180</td>
<td>—</td>
</tr>
</tbody>
</table>

a = approximate.

Table 4. Measurements (in millimeters) of the forelimb and manus of *Carnotaurus sastrei.*

<table>
<thead>
<tr>
<th></th>
<th>Right</th>
<th>Left</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humerus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>285</td>
<td>284</td>
</tr>
<tr>
<td>Distal transverse width</td>
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<td>93</td>
</tr>
<tr>
<td>Proximal transverse width</td>
<td>95</td>
<td>100</td>
</tr>
<tr>
<td>Transverse width of humeral head</td>
<td>76</td>
<td>75</td>
</tr>
<tr>
<td>Anteroposterior width of humeral head</td>
<td>70</td>
<td>73</td>
</tr>
<tr>
<td>Least transverse width of shaft</td>
<td>53</td>
<td>55</td>
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<tr>
<td>Ulna</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>78</td>
<td>85</td>
</tr>
<tr>
<td>Greatest distal transverse width</td>
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<td>55</td>
</tr>
<tr>
<td>Greatest proximal transverse width</td>
<td>50</td>
<td>56</td>
</tr>
<tr>
<td>Greatest anteroposterior distance of proximal end</td>
<td>66</td>
<td>71</td>
</tr>
<tr>
<td>Least diameter of shaft</td>
<td>22</td>
<td>26</td>
</tr>
<tr>
<td>Radius</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>73</td>
<td>80</td>
</tr>
<tr>
<td>Greatest distal transverse width</td>
<td>63</td>
<td>58</td>
</tr>
<tr>
<td>Greatest proximal transverse width</td>
<td>47</td>
<td>48</td>
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<tr>
<td>Least diameter of shaft</td>
<td>30</td>
<td>31</td>
</tr>
<tr>
<td>Radiale</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length (proximodistal)</td>
<td>10</td>
<td>—</td>
</tr>
<tr>
<td>Transverse width</td>
<td>25</td>
<td>—</td>
</tr>
<tr>
<td>Ulnare</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>18</td>
<td>—</td>
</tr>
<tr>
<td>Transverse width</td>
<td>24</td>
<td>—</td>
</tr>
<tr>
<td>Metacarpal I</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>30</td>
<td>—</td>
</tr>
<tr>
<td>Proximal transverse width</td>
<td>23</td>
<td>—</td>
</tr>
<tr>
<td>Distal transverse width</td>
<td>23</td>
<td>—</td>
</tr>
<tr>
<td>Metacarpal II</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>37</td>
<td>36</td>
</tr>
<tr>
<td>Proximal transverse width</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Distal transverse width</td>
<td>23</td>
<td>—</td>
</tr>
<tr>
<td>Metacarpal III</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>29</td>
<td>31</td>
</tr>
<tr>
<td>Proximal transverse width</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Distal transverse width</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Metacarpal IV</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Length</td>
<td>84</td>
<td>—</td>
</tr>
</tbody>
</table>

Pelvic Girdle and Hindlimb

The pelvic bones were articulated to each other, the sacrum, and the femora. The farmer who found the specimen, Mr. Sastre, removed some marginal rock containing the distal part of both ischia. The length of the ischium (Fig. 31) is, therefore, an estimate, and a few centimeters could possibly be added between the preserved parts.

Pelvic Girdle (Fig. 31). The ventral bones of the
Carnotaurus pelvis are proportionately long, slender, and straight, and the distal end of the ischium is expanded into a foot. The acetabulum is large and open medially, and all three pelvic bones contribute to it.

The ilium (Figs. 20, 31) is long and low, with the dorsal border rounded and axially straight, except its anterior area where it bends ventrad. The ventral border behind the acetabulum is parallel with the dorsal border. The iliac blade has a high posterior border and is concave in its central area. The anterior projection of the ilium is dorsoventrally large, and it projects ventrad more than in Tyrannosaurus (Osborn, 1917) or Allosaurus (Madsen, 1976), resembling the condition of Ceratosaurus (Gilmore, 1920).

The precise union between the pubis and the ilium is hard to locate. A series of rugosities may correspond to that union, as tentatively indicated in Figure 31. The pubic pedicel is wide and short.

The pubis (Fig. 31) has a large contact with the ischium, and the obturator foramen is largely encircled by bone. The shaft is almost straight, with a well-developed foot and a long, fused symphysis. Proximal to the distal foot, both pubes are separated by an elongate aperture.

The ischium (Fig. 31) is long and proportionally thicker than the pubis. Both ischia are fused for most of their length. Ventrally, the fused area is present from the distal end up to the middle of the ventral laminae. Dorsally, the fused area is shorter, and before the level of the ventral laminae is reached distad, both ischia begin to separate along their dorsal edge. Proximally, the ventral laminae are separated and form a wide acetabular concavity. The union with the pubis is laminar via a strong fusion. The posterior pedicel of the ilium shows a partial fusion with the ischium. In the proximolateral region, almost on its dorsal border, there is an obvious osseous process for muscular attachment, possibly for the m. flexor tibialis internus. According to Gregory and Camp (1918) this is a character present in Ceratosaurus and Tyrannosaurus, but not in Allosaurus or Deinonychus.

In the distal area the ischia are intimately fused and show an anteroposterior, foot-like expansion. As the distal portions of the ischia are not in clear contact with the proximal portions, as indicated above, we do not know the actual length of these bones.

Hindlimb (Figs. 32, 33). The hindlimbs are represented only by the femora and the proximal third of both tibiae. Unfortunately, erosion destroyed the rest of both hindlimbs, including the feet. However, there is sufficient information from other re-
from Patagonia that permits restoration of the hindlimbs, except for the tarsals and digits.

In general terms, *Carnotaurus* had long and slender hindlimbs, not very different from those of *Bahariasaurus* (Stromer, 1915). They show both primitive and derived characters that distinguish them from *Tyannosaurus* and, to a lesser degree, from *Allosaurus*.

The left femur (Fig. 32) is reasonably complete, with the central portion restored after a natural mold. Its total length is 103 cm, and the average diameter of the diaphysis is 11 cm, a good indication of its slender condition. D. Russell (pers. comm.) suggests that the size of the femur indicates that the total weight of this *Carnotaurus sastrei* specimen was about 1,350 kg.

The distal end of the femur has a modest transverse expansion, to 19 cm, and the proximal end has a length to the major anteromedial axis of 22 cm. The diaphysis is subcylindrical and proximodistally convex on the anterior side. In the distal internal region, a sharp mediodistal crest originates and ends near the inner tibial condyle. This crest separates the concave dorsal surface from the medial side, which is also concave. The inner tibial condyle projects strongly posterior, but it is transversely narrow, whereas the outer condyle is transversely wider but less pronounced posteriorly. The major axis of the fibular condyle projects upward and outward.

At the proximal end the femoral head has a convex continuity with the major trochanter. The femoral head is, therefore, anteroposteriorly narrow and not subspheric as in *Tyannosaurus*. Nor does it project medially as in *Tyannosaurus* and *Allosaurus*, but instead it projects anteromedial. The lesser trochanter is well developed, but proximally

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**Figure 30.** *Carnotaurus sastrei*. Right humerus, radius, and ulna in anterior (A), posterior (B), medial (C), and lateral (D) views. Scale = 10 cm.

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**Figure 31.** *Carnotaurus sastrei*. Pelvis in lateral view. ilio-pubic suture suggested by dashed line. ab, anterior blade; ac, acetabulum; il, ilium; isq, ischium; ob, obturator foramen; pb, posterior blade; pft, process for the *m. flexor tibiialis internus*; pub, pubis.
Table 5. Measurements of pelvic bones and hindlimb of *Carnotaurus sastrei*.

<table>
<thead>
<tr>
<th>Bone</th>
<th>Right</th>
<th>Left</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ilium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest length</td>
<td>970</td>
<td></td>
</tr>
<tr>
<td>Height above middle of acetabulum</td>
<td>235</td>
<td></td>
</tr>
<tr>
<td>Ischiium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest expanse from ventral border of obturator process to posterior border of iliac pedicle</td>
<td>250</td>
<td></td>
</tr>
<tr>
<td>Pubis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest length along anterior border</td>
<td>880</td>
<td></td>
</tr>
<tr>
<td>Greatest length of distal “foot”</td>
<td>252</td>
<td></td>
</tr>
<tr>
<td>Greatest length of distal “foot”</td>
<td>106</td>
<td></td>
</tr>
<tr>
<td>Greatest transverse width at center of combined shaft of both pubes</td>
<td>157</td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greatest length</td>
<td>—</td>
<td>1030</td>
</tr>
<tr>
<td>Greatest diameter of head</td>
<td>—</td>
<td>206</td>
</tr>
<tr>
<td>Distal width</td>
<td>197</td>
<td>198</td>
</tr>
<tr>
<td>Tibia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proximal width</td>
<td>120</td>
<td>134</td>
</tr>
<tr>
<td>Greatest anteroposterior expanse</td>
<td>245a</td>
<td>245a</td>
</tr>
</tbody>
</table>

*a* = approximate.

It reaches to only slightly below the femoral head. Both *Tyrannosaurus* and *Allosaurus* have dorsally higher lesser trochanters. The internal, or 4th, trochanter is not well preserved, but its relative position appears to be somewhat higher than in *Tyrannosaurus*.

The *tibiae* (Fig. 33A, B) are represented only by their proximal parts. The articular surface for the femur is inclined outward and downward. The outer facet is in a posterior position, near the posterior border of the tibia. The articulation for the fibula is anteroposteriorly convex. The eurycnial crest is not complete, but it appears to have been well developed, although perhaps less so than in *Allosaurus*. The crest for a ligamentous union with the fibula is dorsally placed, and it lies slightly anterior to the fibular condyle.

**Reconstruction of Tibia-Fibula-Tarsus of *Carnotaurus***. Recently, some associated remains of *Carnosaurus* were described by Martínez et al. (1986). The material includes incomplete vertebrae and a complete femur, tibia, fibula, and tarsus, on which *Xenotarsosaurus bonapartei* Martínez, Giménez, Rodríguez, and Bochatey from the Upper Cretaceous of Patagonia was based.

The similarities of the preserved vertebrae and limb bones of this theropod with those of *Carnotaurus* are so marked that its familial indentification is unquestionable, as Martínez et al. (1986) recognized. The generic differences are based on the vertebral morphology, where some differences exist. But the morphology of the femora strongly suggests that the hindlimbs of both forms were probably basically the same.

On this basis we estimate that the tibiae of *Carnotaurus* were slightly shorter than the femora, possibly about 97 cm in length. It is possible that the distal region of the tibia had a moderate transverse expansion and that it might have been fused to the astragalus and calcaneum, as in *Xenotarsosaurus*, forming a rigid unit. The fibula was probably not fused to its neighboring bones, as in *Xenotarsosaurus*.

**Comparisons of Pelvic Girdle and Hindlimb**. The pelvis of *Carnotaurus* is typically carnosaursian, with similarities to *Ceratosaurus nasicoernis*. We see little indication of phylogenetic affinities with *Deinonychus* or *Coelurosauria*. There are strong differences in the morphology of the tyrannosaurid ischia, which lack a distal expansion, and the tyrannosaurid pubis, which is transversely wide and robust and lacks an obturator foramen.

The general plan of the sacrum and pelvis is comparable to that of *Ceratosaurus*, with an axially extended ilium, an elongated, slender pubis with an obturator fenestra encircled by bone, and a wide, laminar contact between the pubis and ischium. The ischium is elongated and rather slender, and it has a distal foot-like expansion in both genera (Marsh, 1896: pl. 10, fig. 1; Gilmore, 1920: 108). *Carnotaurus* shows derived characters, relative to
Ceratosaurus, in having the dorsal border of the ilium straight and parallel to the ventral postacetabular border, which forms a right angle with the high posterior border of the ilium, and in having the pubo-ischiatic symphysis more reduced. We believe the similarities are sufficient to consider the two genera to be closely related.

The hindlimb of Carnotaurus has very slender proportions, which suggests that it may have been a more agile form than other carnivores, except for the African forms described as Babariasaurus and cf. Spinosaurus (Stromer, 1934: pls. 1, 3). However, the hindlimb shows significant plesiomorphic characters relative to Allosaurus and Tyrannosaurus, including a) femoral head projecting antero-medial; b) femoral head slightly lower than the major trochanter, with a convexity between them; and c) lesser trochanter with a modest dorsal projection. These differences suggest that the Allosauridae and Tyrannosauridae are quite distinct from the Abelisauridae, which includes Carnotaurus.

The Ceratosaurus femur (Gilmore, 1920: fig. 64) is similar to Carnotaurus in the following features: a) morphology and relative position of the femoral head and the major trochanter; b) characters of the lesser trochanter in its dorsal expression; c) characters of the distal end, including the relative position and morphology of the tibial and fibular condyles; and d) the position and characters of the anteromedial crest that separate the medial from the anterior face of the dorsal side in this part of the femur.

The similarities with the African Cenomanian forms (Stromer, 1915, 1931, 1934) are significant, but some differences are present. The region of the femoral head-major trochanter is the same, but the lesser trochanter is more developed. In the distal end of the femur there are several peculiar characters in the African forms. In the proximal end of the tibia, the fibular condyle is not near the posterior border as in Carnotaurus, but rather it is in a more anterior position.

**Skin**

Several fragments of skin impressions were found underneath the right side of the skeleton. They correspond to several parts of the body. One fragment is from the anterior cervical region, and it is associated with the anterior cervical ribs. Another fragment is from the scapular area near the glenoid cavity. Two fragments are from the thoracic region, and they are associated with the mid-proximal area of the ribs. The largest available skin impression corresponds to the lower area of the proximal part of the tail. There appears to be little variation among the different fragments. The surface of the skin is made of rather low, conical protuberances of about 4 to 5 cm in diameter (Fig. 37), each with a modest keel and separated from one another by about 8 to 10 cm. The surface between the protuberances is rough, with rather rounded, low, and small granules about 5 mm in diameter that are separated from one another by narrow furrows.

**GENERAL COMPARISONS**

We consider Carnotaurus sastrei to represent a new, previously unknown, adaptive type within the Theropoda that has many derived skeletal characters. These derived characters may give us a wider perspective of the adaptive potentialities of this group of dinosaurs, and we believe that the unique anatomical characters of Carnotaurus must be considered in developing the systematics of the Carnosauria.

It is necessary, perhaps, to overcome an interpretation of the 1970's in which the biogeography of the Gondwanan dinosaurs was only superficially considered, e.g., Charig (1973: 351): "...it may be that the congeneric dinosaurs found in the various Gondwanaland regions (if indeed congeneric) were merely the remnants of populations, once widely distributed, which have been driven south by various agencies into the already isolated peninsulas of the Southern Hemisphere." The biogeographic history of the Cretaceous dinosaurs of Gondwana was probably completely different from that implied by Charig's statement.

**Is Carnotaurus sastrei a Carnosaur?**

Typical members of the Carnosauria are represented by the Jurassic and Cretaceous families Megalosauroid-
dae, Allosauridae, Ceratosauridae, and Tyrannosauridae. In addition, the families Dryptosauridae, Spinosauridae, and Abelisauridae are very probably members of the Carnosauria. All of these families represent a relatively homogeneous group of predators of considerable size, in which a progressive reduction of the forelimbs is documented. These families are also characterized by long pubes with a distal foot and with femora slightly longer than the corresponding tibiae. These characters, in association with other more generalized ones of the skull, ilium, scapulo-coracoid, and foot, distinguish the different taxa of the Carnosauria.

The inclusion of Carnotaurus sastrei among the Carnosauria is fairly conclusive because the outstanding reduction of the forelimbs, with the strong humerus, and the characters of the sactrum, pelvis, and femur point to a relationship with Ceratosaurus. All of these arguments clearly demonstrate that it is a carnosaurs with several derived characters. We do not believe it is necessary to make comparisons with other groups of the Theropoda such as Deinonychosaurus, Oviraptorosaurus, Ornithomimosauria, Segnosauria, and Therizinosauridae (fide Russell, 1984).

Comparison with Jurassic and Cretaceous Carnosaurs of South America

All of the significant specimens of South American carnosaurs are from Argentina. The known remains from Brasil (Price, 1960) are isolated teeth. Likewise, taxa described by del Corro (1966, 1974) as Megalosaurus inexpectatus and Megalosaurus chubutensis lack diagnostic characters and should be considered as nomen dubia.

Piatnitzkysaurus floresi Bonaparte (1979, 1986a) is an allosaur from the Middle Jurassic, Callovian, of Patagonia, showing some pleiosorphic characters relative to Allosaurus fragilis. The comparison of Carnotaurus with the Middle Jurassic form does not provide more information than the comparison with Allosaurus. However, the more primitive condition of Piatnitzkysaurus suggests that it is nearer to the common ancestry of Ceratosauridae-Abelisauridae than Allosaurus.

Genyodectes serus Smith-woodward, 1901, is based on the anterior part of a skull and jaws, and these show significant similarities with Carnotaurus. However, it lacks sufficient diagnostic characters to identify it with, or differentiate it from, C. sastrei. In addition, the geographic and stratigraphic provenance of Genyodectes serus is so imprecise that we are unable to determine if the type specimen came from Jurassic or Cretaceous deposits, much less from Middle or Upper Cretaceous deposits. We do not have the necessary stratigraphic or anatomical data for comparison. There is some doubt as to the validity of the taxon Genyodectes serus.

Unquillosaurus ceibali Powell (1979) is based on most of a left pubis, bearing a “foot” and an anterolateral proximal canal. The obturator foramen is open, which is more derived than in Carnotaurus sastrei. Although Unquillosaurus ceibali is based on incomplete material, there are sufficient differences to distinguish it from Carnotaurus.

Xenotarsosaurus bonapartei (Martinez et al. 1986) is from the Bajo Barreal Formation, southern Chubut Province, Patagonia, probably Senonian in age. This species is based on two incomplete vertebrae associated with the femur, tibia, and tarsus of the right side. Martinez et al. (1986) recognized some significant differences between Xenotarsosaurus and Carnotaurus vertebrae as the depressions of the vertebral centra are more marked, the parapophyses are larger, and the cavities underneath the prezygapophysis are more developed in Xenotarsosaurus. These characters suggest Xenotarsosaurus is a distinct genus.

A comparison of what is preserved of the hindlimb of Carnotaurus with the limb bones of Xenotarsosaurus is very useful, the similarities showing that both genera are in the same family. Characters of the femora of both genera are similar, except that the Carnotaurus femur is relatively longer and more slender. A comparison of the proximal part of the tibia shows common characters in the posterior position of the external tibial condyle, the morphology of the enimal crest, and the relative position of the fibular crest. Xenotarsosaurus shows some differences from Carnotaurus in the verte-
brae, but the characteristics of the hindlimbs show that both genera belong to the Abelisauridae.

*Abelisaurus communensis* Bonaparte and Novas, 1985, is based on an incomplete skull from the Allen Formation, Maastrichtian, of Rio Negro province, Patagonia. Even though the proportions of the skull are very different from the short, high skull of *Carnotaurus*, the two genera share several diagnostic features at the family level. In the temporal region of *Abelisaurus*, pleiomorphic characters exist in the squamosal and the general shape of the infratemporal opening. In the orbit, the postorbital almost encloses the orbit ventrally, and the lacrimal is posteriorly convex, as in *Carnotaurus*. The preorbital opening is large, but with different proportions than that of *Carnotaurus*. The position and small size of the maxillary fenestra, which is slightly separated from the main preorbital opening but is still within the same general depression, is similar in both genera. In the supratemporal region of both genera there are shared characters in the parietal crest and in the proportions of the openings. Finally, the ornamentation of the nasals with rugosities suggests a corneous covering in both genera. Although *Abelisaurus*, with its elongated skull, represents an adaptive type different from *Carnotaurus*, it is evident that they correspond to the same family.

*Noasaurus leali* Bonaparte and Powell, 1980, is a small theropod represented by only a few, but diagnostic, pieces from the Lecho Formation, Maastrichtian, of Salta Province, northwestern Argentina. The authors recognized a different family, Noasauridae, which, with some doubt, they referred to the Coelurosauria. Considering what is presently known of the anatomy of *Abelisaurus* and *Carnotaurus*, the original systematic interpretation may be subject to change.

The maxilla of *Noasaurus* (Fig. 7H) is relatively short and high, suggesting that the general shape of the skull was probably short. The preorbital opening resembles the condition in *Abelisaurus* and *Carnotaurus*.

The squamosal of *Noasaurus* (Fig. 7I) has a ventral process without a forward inclination. In this character it resembles *Abelisaurus* and *Carnotaurus*, although there are significant differences in other characters of the bone. The quadrate of *Noasaurus* (Fig. 7G) is long, in agreement with *Abelisaurus* and *Carnotaurus*.

The neural arch of the cervical vertebra of *Noasaurus* (Fig. 34C, F) shows characters similar to those of *Carnotaurus* (Fig. 34B, E). The outstanding development of the epipophysis and the reduced neural spine, which was assumed to be lacking by Bonaparte and Powell (1980), correspond to characters of the peculiar type of cervical neural arch of *Carnotaurus*. The cervical ribs of *Noasaurus* are very different from those of *Carnotaurus*.

Fundamental characters of the maxilla, squamosal, and quadrate, and especially the structure of the cervical neural arch of *Noasaurus* and *Carnotaurus*, suggest that although the two genera represent different families, they may belong to a common major taxon, possibly a superfamly.

Comparisons with Tyrannosauridae

The comparisons with this family of Carnosauria are primarily made with *Tyrannosaurus* because it is generally considered very representative of the family.

The design of the *Tyrannosaurus* skull (Fig. 7K, L, M) corresponds to a long, low model, with a massive lower jaw in lateral view, with a reduced mandibular fenestra. *Carnotaurus* has a short, high skull, and the lower jaw is slender with a large mandibular fenestra. The significant differences of the infratemporal opening, orbital and preorbital region, characters of the jugal, lacrimal, and other bones have been pointed out in the description.

The general anatomy of the vertebrae posterior to the axis shows fundamental differences from that of *Tyrannosaurus* because of the hypertrophy of the epipophysis and atrophy of the neural spines in *Carnotaurus*, which are derived characters not
present within the Tyrannosauridae. The forelimb shows derived characters in the outstanding reduction of the forearm and the degree of humeral torsion, characters different from those found in Tyrannosauridae (Fig. 34). In the manus, the general plan of the digits is quite different in Carnotaurus and tyrannosauroids. In the pelvic girdle (Fig. 35), strong differences are seen in the morphology of the pubis and ischium, as the obturator foramen is encircled by bone and the ischium is expanded distally in Carnotaurus. In the hindlimb, the femur of Carnotaurus is relatively longer and more slender, the femoral head is medioanteriorly rather than medially projected, the lesser trochanter has a lower position, the 4th trochanter is more dorsally placed, and the fibular condyle has a different orientation.

The indicated differences between Carnotaurus and members of Tyrannosauridae make it clear that Carnotaurus does not belong to this family. The differences between Tyrannosauridae and Abelisauridae are actually more obvious and better defined than between the Tyrannosauridae and the other families of Carnosauria (Allosauridae, Megalosauridae, and Ceratosauridae).

Comparison with Allosauridae

The differences between Allosaurus and Carnotaurus are significant and present throughout the skeleton. In general terms we may consider Allosaurus as a potential ancestor to the Tyrannosauridae because of several derived characters that persist or are more fully developed in the Cretaceous family (i.e., the anteroventral projection of the squamosal, the short quadrate, the near absence of mandibular fenestra, the medial projection of the femoral head, and the well-developed pubis). None of these characters are typical of Carnotaurus, in which the plesiomorphic condition prevails. Carnotaurus has several apomorphic characters not recorded in Allosaurus, including the high, short skull, frontal horns, a weak contact between the dentary-splenial and postdentary bones, hypertrophy of epipophyses and atrophy of the neural spines of the cervicals (Fig. 34), strong fusion and size reduction of the sacral centra, unique uncinate processes of the anterior caudals, and the extreme reduction of the forearm bones (Fig. 34G, l).

We consider these differences sufficient to demonstrate that the Allosauridae and Abelisauridae are separate taxonomic entities, widely separated by their morphology. They diverged from an evolutionary stage prior to Allosaurus, perhaps not far from Piatnitzkysaurus of the Middle Jurassic.

Comparison with Ceratosauridae

The Ceratosauridae is a monotypic family of the Late Jurassic that, because of its peculiar anatomy, stimulated the interest of several workers (Marsh, 1884; 1896; Gilmore, 1920; Huene, 1926). Ceratosaurus nasicornis Marsh, from the Morrison
Formation, Fremont County, Colorado, has several distinctive characters upon which the family Ceratosauridae Marsh was based. According to Gilmore (1920), the poor definition of the family was the main reason for the rejection of the new family by paleontologists of the time. However, Gilmore (1920) restudied Ceratosaurus and reaffirmed the validity of the family. 

If, as indicated by Gilmore (1920), Ceratosaurus has several pleiomorphic characters that identify it as one of the more primitive post- Triassic Theropoda, it is also true that it bears several derived characters that show specialized features of its anatomy. We do not believe the derived characters of the sacrum and ilia were ever evaluated in Ceratosaurus, and we think that these characters reveal specialized features not recorded in contemporaneous Carnosauria. The number of vertebrae forming the synsacrum, the degree of ossification, and the secondary reduction in size of the five fused centra represent a suite of derived characters not recorded in other Jurassic or Cretaceous Carnosauria of the Northern Hemisphere. The synsacrum of Ceratosaurus includes two anterior vertebrae that serve a sacral function ("presacraals 22 and 23") and a posterior sacral, indicated as "caudal 1" (Gilmore, 1920: pl. 21). Such a specialized sacrum fits between the extended ilia of Ceratosaurus, which are relatively more developed and derived than in Allosaurus. The ratio between the lengths of the radius and femur of Ceratosaurus and Allosaurus also illustrates the degree of limb disparity; the ratio is more derived in Ceratosaurus than in Allosaurus. The radius of Ceratosaurus is 24% the length of the femur, whereas in Allosaurus (USNM 4734) it is 28%. This may be a good indication, when considered with the other characters cited above, that Ceratosaurus was not the most primitive of the post-Triassic theropods, but an adaptive type characterized by a mix of pleiomorphic and apomorphic characters that followed a different evolutionary path than did the Allosauridae-Tyranosaurus line.

In spite of the different ages of Ceratosaurus (Late Jurassic) and of Carnotaurus (Middle or Late Cretaceous) and the presence in both genera of very different characters, we believe that they share a common ancestor. Both represent a comparable adaptive level based on the pleiomorphic and apomorphic characters they share.

We shall consider first the similarities and then the differences. In addition to the skulls being similar in the height of the premaxilla in the nasal region, they have: a small maxillary fenestra located near the preorbital opening; a jugal that lacks an anterior projection overlying the maxilla and which does not border the preorbital opening; a large infratemporal opening, without an anterior projection of the quadratojugal and squamosal; a dorsoventrally long quadrate; and a squamosal with a slender, rod-like ventral projection, not oriented anteroventrally.

There are many similarities in the postcranial skeleton: the centra are well fused in the sacrum and secondarily reduced; the pubis (Fig. 35A, B) is axially elongated; the pubis has the obturator foramen surrounded by bone; there is a large laminar contact between pubis and ischium; the ischium has a distal expansion; the femoral head is lower than the major trochanter and directed anteromedially; the lesser trochanter is poorly developed dorsally; and digits of the manus have short phalanges. The more significant differences between the genera include three premaxillary teeth in Ceratosaurus and four in Carnotaurus; an absence of nasal horn or lachrymal protuberances in Carnotaurus; an absence of frontal horns in Ceratosaurus; skull short and high in Carnotaurus; lachrymal posteriorly convex in Carnotaurus; anterior projection of postorbital absent in Ceratosaurus; a very wide jugal in Carnotaurus; more developed mandibular fenestrae in Carnotaurus; cervical vertebrae that are basically different, being much more derived in Carnotaurus (Fig. 34D, B); anterior caudal vertebrae more derived in Carnotaurus; and major differences in the humerus (Galton and Jensen, 1979: fig. 31) and in the forearm bones.

Some of these differences rule out the possibility that Ceratosaurus was in an ancestral position to Carnotaurus. These include the nasal and lachrymal protuberances and the presence of only three teeth in the premaxilla. Other important characters, such as the peculiar morphology of the cervical and caudal vertebrae of Carnotaurus, do not have any morphological similarities in Ceratosaurus, preventing us from relating these two genera directly.

Finally, the similarities, even ignoring those that are pleiomorphic characters, are broad enough to suggest a significant, close phylogenetic relationship between Ceratosaurus and Carnotaurus. At present it is not easy to define such a relationship, but it is obviously closer than with any other family of Carnosauria. This means that in spite of several good differences at the family level, Ceratosauroidea and Abelisauridae appear to be related, and they may belong in the same superfamily. Such an arrangement may be useful to unite them and, at the same time, distinguish them from the remaining families of Carnosauria.

Comparison with Theropods from Egypt and India

The theropod remains from the Cenomanian of Bahariya, Egypt, include significant remains of Carnosauria. They correspond to Spinosaurus aegyptiacus Stromer, 1913, Carcharodontosaurus saharicus Stromer, 1931, and Bahariasaurus ingens Stromer, 1934. According to Stromer, these three genera are characterized by elongate, slender appendicular bones, without large expansions in the distal end of the femur. In the case of Bahariasaurus, there are pleiomorphic characters in the proximal region of the femur, with the femoral
head projecting medioanteriori and lower than the major trochanter.

The possibility of comparison between the African forms and the Abelisauridae (Abelisaurus, Carnotaurus, and Xenotarsosaurus) are limited because of the fragmentary condition of the former, by the notable derived characters of the Spinosaurus vertebrae, and in part, too, because the African
specimens were damaged or destroyed during World War II. But, in spite of the limitations, there are anatomical features that suggest more similarities between Carnotaurus (Abelisauroidea) and the African forms than between Abelisauroidea and Tyrannosauridae. For example, there are indications that the basic characters of the hindlimb of Carnotaurus and the African forms are very similar and differ markedly from those of the Tyrannosauridae. Characters of the latter include a robust femora, with the proximal head projecting mediad and higher than the major trochanter and with the lesser trochanter more dorsally developed.

We do not have sufficient information to evaluate the validity of the Spinosauroidea; however, the vertebral characters and the features of the lower jaw and teeth appear to be sufficiently derived to recognize it as valid.

From a paleobiogeographic approach, it has been considered that the Spinosauroidea and Abelisauroidea would be endemic families for the Cretaceous of Gondwana (Bonaparte, 1968a), whereas the Tyrannosauridae appear to be endemic to Laurasia. If this interpretation, based on paleogeographic events of great magnitude, such as the separation of Laurasia and Gondwana before the end of the Jurassic, is correct, we can hypothesize that the few similarities cited between the African and South American Middle and Late Cretaceous Carnosauria result from a common biogeographic history.

The carnosaur from the Upper Cretaceous of India, Indosuchus mattleyi (Huene and Mattley, 1933), and Indosuchus raptorius (Huene and Mattley, 1933), were reviewed by Walker (1964) and by Chatterjee (1978). The latter described new material of Indosuchus stored at the AMNH. Chatterjee agreed with Walker's interpretation that Indosaurus is a megalosaurid (=Allosauridae) and that Indosuchus is a tyrannosaurid. The assignment of Indosuchus to the Tyrannosauridae appears without basis, primarily because the maxilla of Indosuchus lacks the typical maxillary fenestra of the tyrannosaurids.

Our interpretation of Indosuchus is that it represents a different family than the Tyrannosauridae, possibly corresponding to the Abelisauroidea, in which the maxillary fenestra exists in a reduced form within the main preorbital vacuity.

We do not have enough information for a full systematic evaluation of Indosuchus; however, we call attention to the imprecise suggestion that it is a "megalosaur" (Chatterjee, 1978: 573), which means less than to say "carnosaur." This assignment was based on fragments discovered in latitudes very distant from where Jurassic megalosaurus are recorded. Lacking the necessary evidence, we believe it is better to suggest that Indosuchus may represent a new, unknown family rather than force geography and chronology by identifying it with European or North American forms.

Summary
Comparisons of Carnotaurus sastrei with other species of Carnosauria allow the following interpretations:

1. The cranial characters of Carnotaurus sastrei are good indicators of familial affinities with Abelisauroidea comahuensis, type species of the family Abelisauroidea Bonaparte and Novas, 1983. This permits reference, without doubt, of C. sastrei to that family of Carnosauria.

2. As indicated in the description and in comparisons with Cretaceous theropods of Laurasia, the Abelisauroidea have a suite of characters that distinguish them from the other theropod families of that supercontinent, especially the Tyrannosauridae.

3. The phylogenetic relationship between the
Abelisauridae and Noasauridae, based on the morphology of the maxilla, quadrate, squamosal, and cervical neural arch, appear convincing in view of the following synapomorphies: significant reduction of the additional preorbital opening, reduction of the cervical neural spines, strong anterior development of the epipophyses, and the lateral crest from the epipophyses. We interpret these characters as suggesting a monophyletic relationship for the two families.

4. Theropods from the Cenomanian of Egypt resemble the Abelisauridae more than the Tyrannosauridae, at least in the hindlimb organization.

5. Comparisons between C. sastrei and Jurassic theropods suggest that the Abelisauridae, and probably Noasauridae, may be phylogenetically related to the Ceratosauridae, but we cannot clearly define this relationship at present. The phylogenetic relationship may be one of common ancestry at the familial level, based on the common possession of several apomorphic characters, such as sacrum with several fused vertebrae with reduced centrae, anteroposteriorly elongated ilium with extended supra-acetabular crest, the ischia distally expanded as a “foot,” and a very slender pubis shaft. Several plesiomorphic characters, e.g., a large infratemporal opening, manus with four digits, obturator foramen enclosed by bone, poor development of the lesser trochanter, femoral head medioanteriorly projected, have also been noted.

**DISCUSSION**

The comparisons of *Carnotaurus sastrei* with other theropods have permitted us to recognize similarities and differences at different levels, with taxa from South America and other continents.

The phylogenetic relationship between the Allosauridae and Tyrannosauridae that is recognized by some authors (Paul, 1984; Gauthier, 1986) appears well based, and it seems to represent one of the main lineages of the Carnosauria. Another lineage, of similar importance, is formed by the Ceratosauridae-Abelisauridae-Noasauridae. We hypothesize that from Jurassic ancestors of Pangean distribution two vicariant groups developed, leading to the Cretaceous families Tyrannosauridae in Laurasia and Abelisauridae in Gondwana.

Following the results of the comparisons detailed above, we believe it is convenient to recognize a
systematic entity at the superfamily level—the Ceratosauroida—to contain the Ceratosauridae, Abelisauridae, and Noasauridae, whose main radiation and Cretaceous evolution was in Gondwana.

The systematic interpretation of this hypothesis may be stated as:

Superfamily Tyrannosauroidea
  Family Allosauridae
  Family Tyrannosauridae

Superfamily Ceratosauridae
  Family Ceratosauridae
  Family Abelisauridae
  Family Noasauridae

This interpretation presents us with the novel opportunity of interpreting as carnivores a family—
the Noasauridae—to date known only from small-sized species such as Noasaurus leali, which has a skull approximately 10 to 12 cm long. The interpretation is based on the synapomorphies of the maxilla and peculiar characters of the cervical neural arch. The presence of Noasauridae among the Carnosauria, an infraorder normally characterized by large predators, may relate to the long isolation of the Gondwana continents through the Cretaceous (Bonaparte, 1986b) and the apparent absence of Coelurosauria in the Cretaceous of Gondwana. The Cretaceous isolation of both supercontinents would have provided an opportunity for the Gondwanian Carnosauria to occupy the ecological niches of small predators.

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