ABELISAURUS COMAHUENSIS, N. G., N. SP., CARNOSAURIA FROM THE LATE CRETACEOUS OF PATAGONIA.^{*}

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ABSTRACT: An almost complete skull of a carnosaur from the Allen Formation (Maastrichtian of Río Negro Province) is described as the holotype of *Abelisaurus comahuensis*. It is a high skull with a broad interorbital roof, a huge antorbital fenestra, squamosal nearly horizontal with the quadratojugal process ventrally directed, very wide lower temporal fenestra, very long quadrate, large orbital fenestra with almost closed orbits. The differences with Tyrannosauridae and other Cretaceous carnosaur families appear so significant as to propose a new family, Abelisauridae, probably of Gondwanan distribution.

INTRODUCTION

Knowledge of South American Cretaceous carnosaurs is quite fragmentary, indeed nearly nonexistent, since only *Genyodectes serus* has been reported (Smith Woodward, 1901), represented by cranial and mandibular fragments with teeth, and whose provenance is so doubtful that it is not even known with any certainty if it was found in Cretaceous beds. Other records of this group consist of isolated dentary pieces (Del Corro, 1966, 1974). Powell (1979) discovered the carnosaur *Unquillosaurus*, based on an isolated pubis from the Campanian-Maastrichtian of northern Argentina, which serves to document the presence of this group, although not to clarify the basic relationships of South American carnosaurs.

Curiously, the numerous Argentine, and even South American, Cretaceous localities that have presented so many frequent and significant remains of sauropods do not produce any illustrative or diagnostic evidence of the large predators which must have accompanied them.

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Knowledge of Cretaceous carnosaurs is based fundamentally on evidence from North America (Osborn, 1905, 1912; Ostrom, 1969; Russell, 1970; and others) and Asia (Kurzanov, 1976; Maleev, 1955, 1964; Rozhdestvensky, 1965); this knowledge has been strengthened in recent years by the works of Barsbold (1976, 1977), Barsbold and Perle (1980) and Osmólska and Roniewicz (1970). The discoveries from Gondwana (Chatterjee, 1978; Molnar *et al.*, 1980, 1981; Stromer, 1915) are hardly clear, to the point that, even with *Spinosaurus*, we are not provided with an elemental picture of the characteristics of this group in the Southern Hemisphere. Regarding this, the recent discovery of the large part of a skull in Maastrichtian beds of northern Patagonia (carried out by the Director of the Museo de Cipolleti, Prof. Roberto Abel) has permitted us to recognize the existence of a lineage of large Carnosauria, whose anatomy suggests adaptive characters distinct from those recognized in Laurasia.

This discovery, besides making possible a major understanding of the evolution of Cretaceous carnosaurs, presents the opportunity to better understand the character of the associations of large tetrapods in the Cretaceous of South America.

SYSTEMATICS AND DESCRIPTION

Order SAURISCHIA Seeley, 1888 Suborder THEROPODA Marsh, 1881 Infraorder CARNOSAURIA von Huene, 1920 Family ABELISAURIDAE nov.

Abelisaurus gen. nov.

DERIVATION OF NAME: in honor of Prof. Roberto Abel, Director of the Museo de Cipolleti and author of the discovery.

TYPE SPECIES: *Abelisaurus comahuensis* sp. nov.

KNOWN DISTRIBUTION: Lower part of the Allen Formation, early Maastrichtian of Río Negro, Argentina.

DIAGNOSIS: Carnosauria of large size, with high, narrow, widely fenestrated skull with prominent rugosities on the nasals. With antorbital fenestra proportionally larger than in Tyrannosauridae and in the remaining Cretaceous and even Jurassic carnosaurs; small accessory antorbital fenestra located on the anterior border of the antorbital fossa.

Interorbital region wider than in other carnosaurs, and with lateral contact external to the lacrimal and postorbitals, forming a type of orbital overhang. Orbital fenestra very tall, with a low jugal, and with the orbit as mentioned very marked for the postorbital and lacrimal, forming a circumference hardly open ventrally, partly recalling the condition seen in *Tyrannosaurus rex*. Squamosal projecting nearly backwards, almost horizontally, with its process for the quadratojugal directed ventrally and not as forwards as in Tyrannosauridae, recalling the condition of *Ceratosaurus*, and to a lesser degree that of *Allosaurus*. Quadrate notably longer than in Tyrannosauridae, comparable to *Ceratosaurus*. Lower temporal fenestra very wide in both directions, notably larger than in Tyrannosauridae, recalling that seen in *Ceratosaurus*. Upper temporal fenestrae shorter axially. Extended horizontal ramus of the maxilla, provided with thick teeth, very laterally compressed. Braincase comparable to that of *Piatnitzkysaurus* in the conspicuous aliform processes of the laterosphenoids, and in the marked transverse constriction of the basisphenoids.

Abelisaurus comahuensis sp. nov.

ETYMOLOGY: *comahuensis*, referring to the Comahue region, where the material described here was discovered.

HOLOTYPE: Museo de Cipolleti, No. 11098, corresponding to a large part of the skull, lacking the right maxilla, jugal, quadratojugal, and squamosal, as well as the major part of the palate.

STRATIGRAPHIC AND GEOGRAPHIC LOCATION: Lower part of the Allen Formation, Lago Pellegrini stone quarries, Department of General Rocas, Province of Río Negro.

DIAGNOSIS: the same as for the genus.

DESCRIPTION

Abelisaurus comahuensis has a large skull, 85 cm in maximal length, provided with wide lower temporal, antorbital, orbital and nasal fenestrae. With robust cranial roof in the interorbital region and profusely rugose nasals, even with irregular prominences in the form of small sharp points.

Premaxilla: the premaxillae are fused together: they are tall, strong, without anteroposterior reduction, and provided with four alveoli on each side. The nasal process of the premaxilla is stout, although its extent is not known due to fracture. In the symphysial region the premaxillae have some rugosities of the type present on the nasals. The union between the premaxillae and maxillae is firm and had movement with difficulty.

Maxilla: both maxillae were incomplete, although the left preserves its anterior region. This bone was provided with an small accessory antorbital fenestra, especially in the axial direction, located on the more anterior border of the antorbital fossa, and limited in back by a narrow bony bridge. The maxilla is tall in its anterior region, with a very ascendant suture between the nasal and maxilla, prolonged backwards and above for half of a narrow bony blade that reaches more backwards into the nasals. The anterior region of the maxilla possesses 7 alveoli and eventually would be complemented by 5-6 alveoli more, totaling 12-13 alveoli in sum.

Nasals: they have a wide and firm contact with the maxillae; they are very convex transversely, expanded backwards in the direction of the lacrimals. The contact with the frontals is crudely notched and located towards the anterior third of the orbit. Dorsally it presents two deep grooves, in the axial direction, from the frontals forwards, bordered by rugosities and separated between them by 4 cm in one, and of another 16 cm in width. They show a marked constriction in the direction of the accessory antorbital fenestra. The nasals are the only bones that show prominent rugosities.

Lacrimals: they have a wide dorsal expression, convex in both directions, sutured crudely from the external border to the frontals. The ventral expression of the lacrimals consists of an anteriorly and posteriorly convex extended rod, which is united with the jugal in the lower third of the orbital fenestra. The posterior border of this rod is convex, thus differentiating it from the character seen in Tyrannosauridae. The anterior projection of the lacrimal which is connected to the nasals is not preserved.

Prefrontals: the evidence of the prefrontal is not clear, although apparently it constitutes a small ossification limited by the nasals, lacrimals, and frontals.

Postorbitals: present an wide, transversely convex dorsal manifestation, and which is composed with the lacrimal and frontal, forming together an wide rugose prominence that eventually had some major expression in the life of the animal.

The overhang formed by the postorbital and lacrimal has a clearly more external position than the origination of the ventral processes of both bones. The ventral process is wide, laminar in its anteroventral end, stout in the rest and forming a well-marked semicircle posterior to the orbit proper. The posterior projection of the postorbital covers the squamosal laterally, although without recognizing clear sutures between them.

Squamosal: the squamosal is triradiate, with an anterior projection covered laterally by the posterior ramus of the postorbital, a ventral projection directed below and partially backwards to contact with the quadratojugal, and finally the posterior projection which forms a definite otic surface ventrally where the quadrate condyle articulates. There is a dorsomedial process in the dorsal region of the squamosal which eventually would have united with the occipital crest. Behind this process it has a step which affects to the posterior projection of the squamosal and the lateral region of the paroccipital process.

Quadratopterygoids: a large part of the left quadrate is preserved, with articular marks for the squamosal and basipterygoid process, which indicates its approximate original position. The quadrate is proportionally wide, rather more than in Tyrannosauridae, with a transversely wide distal articular region, with the internal border rather lower than the external. The pterygoid ramus of the quadrate is extended, it is very fused to the pterygoids, since sutures cannot be recognized. The contact of the quadratopterygoid with the basipterygoid process is wide, with a surface which forms a very clear concave region.

Quadratojugal: it is very incomplete, with its posteroventral region very fused to the quadrate. The dorsal projection of this bone is not known. The anteroventral projection of the quadratojugal is complete enough, preserving a vestige of the jugal sutured to it.

Jugal: the incomplete left jugal was preserved, including the ascending ramus which contacts with the postorbital. The anterior prolongation of the jugal is broken and did not contact the maxillae. The preservation of the jugal indicates that it was dorsoventrally low.

Frontals: the axial region of the frontals constitute a depressed area, with good sutures with the nasals, although poorly defined with the parietals. The suture with the postorbitals, seen on the left side, indicates that the lateral projection of the frontals is wide and participates in the supraorbital protuberance cited above. The frontals demarcate the anterior depression of the upper temporal fenestra.

Parietals: they are axially short. In the posterior region is integrated an elevated area that bifurcates on both sides into the rudimentary occipital crest.

Supraoccipital: the supraoccipital projects backwards in the axial plane, forming a projection that surpasses the position of the occipital condyle. In posterior view note a thin crest in the axial direction, and a minor crest in the lateral plane to each side.

Paroccipital processes: they are directed backwards and outwards, culminating in a lateral expression that surrounds the squamosal, and contributing in the formation of the otic surface. Towards the axial plane the ventral border of these processes merges into the basioccipital tuberae.

Basioccipital: it has well separated tuberae and forms an wide concave surface exposed in posterior view. The condyle is subhemispherical, more defined in its ventral region than in the dorsal plane, where the surface of the foramen magnum exists. The condyle shows a well-defined neck in the ventral region and part of the lateral regions, a character that disappears near the region of the exoccipitals.

Basipterygoid processes: they are widely separated from each other and relatively near the tuberae. The articular surface with the pterygoids is convex, and its major axis is directed downwards, outwards and backwards. They form a body curved backwards and downwards.

Laterosphenoids: the braincase shows wide aliform processes in the laterosphenoids, with rugosities on their surface, constituting probable areas of insertion of the mandibular muscles, of the same type as those of *Piatnitzkysaurus floresi* (Bonaparte, 1979) from the Middle Jurassic of Patagonia.

Ethmoids-sphenethmoids-parasphenoids: a medial ossification that is widely united to the ventral face of the frontals, passes ventrally to an axial lamina. A cavity for nerve I is presented in the posterodorsal region that exits facing forwards, to the end of the ossification, of the type present in *Tyrannosaurus* (Osborn, 1912, fig. 8). There are other structures in the basicranium, incomplete, that will be studied in a more detailed work.

COMPARISONS

The good understanding we have of *Tyrannosaurus*, *Albertosaurus*, *Daspletosaurus* and other genera that comprise the family Tyrannosauridae is important in the comparison of this form from the Upper Cretaceous of Patagonia, which we make in the first place with this family, of such wide distribution in the Upper Cretaceous.

In the first place, the general adaptive type of the cranial morphology is at first glance comparable to that of Tyrannosauridae. So we note that the extended antorbital region and the rugosities of the nasals are common characters. Nevertheless, a comparative analysis of the cranial anatomy of *Abelisaurus* reveals components that differentiate it radically from Tyrannosauridae.

A) Interorbital region: The wide interorbital space of Abelisaurus is the result of the lateral contact of the lacrimal and postorbital, forming an orbital overhang, while in the distinct genera of Tyrannosauridae, such as Albertosaurus and Daspletosaurus, there is a surface that reduces the interorbital width. This same character is present in more primitive forms such as Ceratosaurus (Gilmore, 1920) and Allosaurus (Madsen, 1976) from the Upper Jurassic, and probably Acrocanthosaurus (Stovall and Langston, 1950) from the Lower Cretaceous.

B) Lower temporal region: Another notable difference with Tyrannosauridae refers to the characteristics of the lower temporal fenestra and in particular to the bones that border the posterior region of this fenestra, especially the squamosal, quadrate and quadratojugal. This we hold that this fenestra in *Abelisaurus* is extremely wide with a notable extension of the horizontal rod of the jugal and quadratojugal, which exceeds notably the same character of Tyrannosauridae. Yet since the proximal region of the quadratojugal is lacking, the characteristics of the ventral process of the squamosal that unites with the quadratojugal, shows that the lower temporal fenestra of *Abelisaurus* did not show the notable indentation that in Tyrannosauridae forms the union of the squamosal and quadratojugal. In such manner the difference in proportions and form of this fenestra between *Abelisaurus* and Tyrannosauridae is more marked and implies a distinct morphology of the bones that encircle it in the posterior region. On the contrary, and obviously, note the similarities with *Ceratosaurus* (Gilmore, 1920) in the general aspects of the temporal region of the skull.

The squamosal of *Abelisaurus* projects backwards in an approximately horizontal plane, forming a pronounced otic surface for half of a wide opisthotic process. From this manner, the cavity for the articulation of the quadrate head is located in a very elevated plane, and the quadrate is a notably wide bone. The distinct genera of Tyrannosauridae, on the contrary, are uniform in showing that: a) the squamosal projects posteroventrally; b) the

opisthotic process is very short; c) the process for the quadratojugal is approximately horizontal and directed forwards; and e) the quadrate is visibly shorter than in *Abelisaurus*.

C) Orbital region: the orbital region in *Abelisaurus* is very tall, since the jugal, in the corresponding region, is low and also because the skull of *Abelisaurus* in the temporal region is proportionally taller than in Tyrannosauridae. The configuration of the inferior region of the postorbital tends to demarcate the orbit proper in its inferior region, a character that recalls that of *Tyrannosaurus rex* (American Museum of Natural History no. 5027). Beneath this ventral process of the postorbital the orbital fenestra continues widely. The lacrimal of *Abelisaurus* has a convex posterior border that contributes to demarcating the orbit proper and the slightly concave anterior border, the inverse of Tyrannosauridae in which invariably the lacrimal shows concave posterior and convex anterior borders.

Another difference of the lacrimal consists in that its ventral projection is short and would require a dorsal prolongation of the jugal for its contact, a character not present in Tyrannosauridae, *Ceratosaurus* and *Allosaurus*.

D) **Antorbital region**: a notable difference between *Abelisaurus* and Tyrannosauridae is manifest in the magnitude of the antorbital fenestra. In the Patagonian form it is notably large, to the point that the space between the anterior end of this fenestra and the external naris is very reduced, while in the distinct forms of Tyrannosauridae exists invariably a distance as great as the same anteroposterior diameter of the antorbital fenestra. The accessory antorbital fenestra has an elliptical shape with the major axis directed dorsoventrally and separated from the antorbital fenestra by a narrow rod, characters not observed in Tyrannosauridae.

COMPARISON WITH OTHER CRETACEOUS FORMS

A group of carnivorous forms from the Late Cretaceous of Laurasia shows distinct evolutionary tendencies, which motivated novel taxonomic appreciations (Barsbold, 1976a; Barsbold and Perle, 1980). Some of these forms are represented principally by postcranial remains, such as *Segnosaurus* (Barsbold and Perle, 1980; Perle, 1979), *Deinocheirus* (Osmólska and Roniewicz, 1970) and *Therizinosaurus* (Barsbold, 1976b), which impede comparisons with the skull described in this work, except *Erlikosaurus* (Barsbold and Perle, 1980), a segnosaur with very distinct specializations from those of *Abelisaurus*, to the point that prevents supposing some near relationship between segnosaurs and the Patagonian form. With respect to the Upper Cretaceous carnosaurs from India (von Huene and Matley, 1933; Chatterjee, 1978) which are based on very fragmentary materials, we can note that there are some indications of affinities with *Indosaurus*, with a wide interorbital region, and *Indosuchus*, with a antorbital region apparently comparable to that of *Abelisaurus*. These probable affinities cannot be supported systematically until such time as direct comparisons can be made with the fragmentary materials from India.

With respect to Dromaeosauria, taking *Dromaeosaurus albertensis* as a point of reference (Matthew and Brown, 1922; Colbert and Russell, 1969), besides the size note very strong differences in the interorbital, antorbital, and upper and lower temporal regions that prevent any possible close systematic relationship.

CONCLUSIONS

Comparison with *Erlikosaurus andrewsi* (Segnosauria) reveals they represent distinct adaptive types (compare C with E, fig. 3), while comparison with Dromaeosauria also reveals substantial differences that are expressed as distinct infraorders.

From comparison with Tyrannosauridae, a picture follows of such marked differences as to justify the conclusion that *Abelisaurus* does not belong to this family.

In summary, we consider that *Abelisaurus* is a carnosaur of a particular family, representing an adaptive type comparable to Tyrannosauridae, yet with diverse characters that unite it with Jurassic forms such as *Piatnitzkysaurus* and *Ceratosaurus*.

Because of the display we propose to recognize the family Abelisauridae nov., probably of Gondwanan distribution, that paralleled Northern Hemisphere Tyrannosauridae.

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Manuscript received 10 April 1984. Revised manuscript received 25 June 1984. Published 24 June 1985. FIG. 1: - *Abelisaurus comahuensis*. 1: skull in lateral view; 2: dorsal view. Restored portions indicated by dotted lines and broken areas indicated by hatching. BOC: occipital condyle; E: ethmoids-sphenethmoids; F: frontal; L: lacrimal; MX: maxilla; N: nasal; P: parietal; PF?: prefrontal (possibly); PPO: paroccipital process; PS: parasphenoids; PT: pterygoids; Q: quadrate; QY: quadratojugal; SOC: supraoccipital; SQ: squamosal; Y: jugal; I: exit for the optic nerve. The scale represents 10 cm.

FIG. 2: Skull of *Abelisaurus* (C) compared with various genera of carnosaurs to show their principal differences. (A) *Tyrannosaurus rex*; (B) *Ceratosaurus nasicornis*; (D) *Dromaeosaurus albertensis*; (E) *Erlikosaurus andrewsi*. The scale represents 10 cm.