NOTES ON THE FIRST SKULL AND JAWS OF *RIOJASAURUS INCERTUS* (DINOSAURIA, PROSAUROPODA, MELANOROSAURIDAE) OF THE LATE TRIASSIC OF LA RIOJA, ARGENTINA[†]

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ORIGINAL ENGLISH ABSTRACT: *NOTES ON THE FIRST SKULL AND JAWS OF* RIOJASAURUS INCERTUS *(DINOSAURIA, PROSAUROPODA, MELANOROSAURIDAE) OF THE LATE TRIASSIC OF LA RIOJA, ARGENTINA*. An almost complete skull and jaws of *Riojasaurus incertus* demonstrates that the melanorosaurid skull is the most primitive among prosauropod dinosaurs. The preorbital depression and opening are large, placed anterior to a vertical lacrimal; the jaw articulation is in line with the alveolar plane of the maxilla; the basicranial region does not show a step between the basioccipital and basisphenoid; and the teeth are rather conical, not leaf shaped. The position of the lacrimal and the preorbital depression suggests that sauropods may be derived from Melanorosauridae and not from prosauropods with a backwardly inclined lacrimal and a preorbital opening that is placed partially below it. The origin of the Prosauropoda is briefly discussed and some shared derived characters between *Riojasaurus* and *Coelophysis* appear consistent with the assumption that Triassic Ceratosauria and Melanorosauridae possibly had a near common ancestor - not Herrerasauridae - from which both evolutionary lines split.

INTRODUCTION

The Prosauropoda represent the first and successful manifestation of the herbivorous type among saurischian dinosaurs. Their origins have not been analyzed until the present, although it is probable that these lie within the clade Ceratosauria. Their geographical distribution has been documented in diverse continents and their biochron extended from the Upper Triassic (approximately from the Carnian-Norian limit) until the Lower Jurassic (Toarcian) (Galton, 1990).

Their diversity is significant since the existence of six families has been recognized (Galton, 1990), although the majority of these have a basic structural plan of the postcranial skeleton which is without major differences except those related to size. Representatives of one

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[†] Original reference: Bonaparte, J. F. and Pumares J. A. 1995. Notas sobre el primer craneo de *Riojasaurus incertus* (Dinosauria, Prosauropoda, Melanosauridae) del Triasico superior de La Rioja, Argentina. Ameghiniana 32:341-349.

of these families, the Melanorosauridae, have been registered in South Africa, Europe, and South America, but cranial material has never been discovered for this family of prosauropods. Galton (1990) has equivocally illustrated and cited the skulls *Massospondylus* and *Lufengosaurus* as corresponding to the Melanorosauridae, but in reality they correspond to Massospondylidae (Galton, 1990:339) and Plateosauridae (Galton, 1990:340), respectively.

During an paleontological exploratory trip in 1986 to the La Esquina locality, near Pagancilla in La Rioja Province (Figure 1) organized by the Museo Argentino de Ciencias Naturales and the Universidad Provincial de La Rioja, an almost complete skeleton of the melanorosaurid *Riojasaurus incertus* Bonaparte 1967 was discovered with the better part of the skull and lower jaws. The presence of this skull gives us the opportunity to discover fundamental characters of its anatomy, and to evaluate the generalized idea that this family was the origin of the Sauropoda (Colbert, 1964; Charig et al., 1965; Romer, 1968; Gauthier, 1986).

It is very probable that the Sauropoda were differentiated from one (or eventually more than one) species of the Prosauropoda, particularly because of the presence of comparatively derived anatomical characters within prosauropods which suggest ancestor-descendent relations, as in the case of increasing complexity and enlargement of the cervical vertebrae, the ventral displacement of the jaw articulation, the tendency towards gigantism associated with the attainment of straight femora, and the comparative small size of the head, among others.

At the same time, there exist other characters in prosauropods which make them difficult to consider as ancestors of the Sauropoda, especially those of the hand with digits reduced progressively towards the fifth, or those of the foot with a reduced metatarsal V. In both cases, they pertain to a set of characters more derived than in the Sauropoda.

SYSTEMATICS AND DESCRIPTION

Order SAURISCHIA Seeley, 1887

Suborder SAUROPODOMORPHA Huene, 1932

Infraorder PROSAUROPODA Huene, 1920

Family MELANOROSAURIDAE Huene, 1929

Genus RIOJASAURUS Bonaparte, 1967

Type Species *Riojasaurus incertus*

Riojasaurus incertus Bonaparte 1967

Figs. 2-5

Holotype: PVL 3808, corresponding to a large part of a postcranial skeleton which lacks the skull, mandibles, 6 presacral vertebrae, diverse caudals, both scapulae, the ischia, and the bones of the hand.

Hypodigm: In addition to that indicated by Bonaparte (1972:130-131), an articulated individual with skull and lower jaws, ULR 56 (Figs. 2-5).

Extended diagnosis: Melanorosaurid with the cranium provided with an wide preorbital opening, larger than in other prosauropods and with a vertically oriented lacrimal bar. Maxilla long and straight with 24 conical, subcylindrical teeth; mandibular articulation in the line of the alveolar plane of the maxilla, with osseous crests in the axial plane and anterior of the premaxillae and dentaries. Cervical vertebrae in general more robust than in *Coloradisaurus* or *Plateosaurus*, without ventral keel and with neural spines shorter axially in cervicals 7 to 10. Tall dorsal vertebrae, with well developed hyposphene-hypantrum and neural spine laminae low and axially extensive; three sacral vertebrae of which the two anterior are intimately fused. Pectoral girdle comparable to that of *Plateosaurus-Lufengosaurus*. Pelvic girdle comparable to these two genera but with shorter preacetabular processes and taller acetabulum. Humerus proportionally large and robust, with strong deltopectoral crest. Femur and tibia comparable to those of *Melanorosaurus*, but less robust. Astragalus and calcaneum of the type present in *Plateosaurus* and *Massospondylus*; characters of the hand and foot similar to *Plateosaurus-Lufengosaurus*. Disparity between fore and hindlimb less than in those genera. The humerus and radius represent

67% the length of the femur and tibia; the humerus is 80% the length of the femur; the tibia and astragalus represent 90% the length of the femur.

DESCRIPTION OF THE SKULL AND MANDIBLES

Skull

The described specimen has been identified as *Riojasaurus incertus* on the basis of the comparisons of the cervical and dorsal vertebrae, the pectoral and pelvic girdles, and the bones of the extremities with the holotype of the species, although it pertains to an individual approximately 35% smaller than the holotype.

The skull of *Riojasaurus incertus*, which is studied preliminarily in this paper, measures 25cm in length, equal to the length of the first four cervical vertebrae (atlas, axis, and cervicals 3 and 4 in articulation). Its general aspect coincides with the typical cranial morphology of the prosauropods, but possesses some more primitive characters, and is lower and more elongate than *Thecodontosaurus*, *Coloradisaurus*, *Massospondylus*, and *Yunnanosaurus* (Galton, 1990), particularly in the preorbital region. In lateral view (Figure 3A) its highest point is located in front of the parietals and frontals, becoming lower posteriorly to the squamosal-opisthotic. From this highest point forward, its height diminishes in an almost straight line; this generally convex profile is different than that of other prosauropods.

The preorbital depression is markedly wider than that of other prosauropods, probably representing a primitive feature, with a broad exposure of the lacrimal laminae dorsoposterior of the above mentioned depression and the anterior half of the maxilla. The preorbital opening, which is much smaller than the depression, is located on the ventral and posterior borders of this depression. The reduced anterior extension of the jugal participates in the border of this portion of the preorbital opening. The external nares have a broad ventral base as in *Plateosaurus*, and are proportionally larger than in *Yunnanosaurus*, *Thecodontosaurus* (juvenile) and *Anchisaurus* (Galton, 1990).

The orbit has an anteroposterior diameter which is approximately 28% the total length of the skull, proportionally much larger than in *Plateosaurus*, and smaller than in *Anchisaurus*, *Thecodontosaurus* (juvenile individual), and *Coloradisaurus*.

The temporal region of the skull of *Riojasaurus* presents several primitive features, such as the well defined parietal crest and the infratemporal fenestra without the posteroventral expansion present in *Plateosaurus*, *Lufengosaurus*, or *Coloradisaurus*.

The jaw articulation is located at the level of the alveolar row of the maxilla, a difference from *Plateosaurus* and the majority of prosauropods which in differing degrees are much lower.

In the occipital region (Figure 4), it is seen that the quadrates are transversely narrow and oriented vertically, with the internal condyle in a position more ventral than the external, but not as medially projecting as in *Plateosaurus* (Galton, 1990). There is no quadrate foramen. The occipital condyle is almost completely formed by the basioccipital. The opisthotics have a concave ventral border and their distal extreme, which is exposed in lateral view behind the squamosal, is located above the dorsal margin of the foramen magnum. Between the supraoccipital and the axial and posterior portion of the parietals exists a window, or unossified area, which is visible in dorsal and posterior views.

The ventral region of the basicranium has basal tubera which are separate, but less divergent than in *Plateosaurus* and *Lufengosaurus*, and in a more anterior position. The basipterygoid processes of the basisphenoid are distally expanded, and with a broad axial fossa below the supposed position of the parasphenoids (which were not preserved), representing a derived character with respect to Herrerasauridae, Ornithosuchidae, and Euparkeriidae. The basipterygoid processes are near the level of the occipital condyle, representing a primitive character when compared to *Plateosaurus* and *Coloradisaurus*, which have them at a level much lower than the condyle.

In dorsal view (Figure 3B) the skull of *Riojasaurus* is, among prosauropods, probably one of the most narrow, comparable to *Yunnanosaurus* Young (1942). In this view, the posterior profile of the skull shows the opisthotic and squamosal projecting posteriorly, slightly outward, and sharp distally. The supratemporal opening is narrow and has its major axis oriented

anteroposteriorly. It is not possible to recognize the suture between the frontals and nasals; in contrast it is very clear in between the parietals and frontals, extending between the two postorbitals.

In the most anterior region of the skull, the premaxilla shows a slight lateral expansion, well defined by a dorsoventrally oriented border, in front of which is a surface which was probably covered by a horny material, forming a sort of beak. This particular morphology corresponds to comparable feature of the symphysial region of the lower jaw, which eventually also had a horny covering.

Lower Jaw (Figure 3A)

The lower jaw is low, with subparallel inferior and superior borders. The tooth row is situated on the internal side of the jaw, and its external border, or cheek, extends to the anterior portion of the dentary, which suggests the presence of thick lips. Galton (1976:90) suggested that this trait was not common in prosauropods, although he has remarked (1990:326) that cheeks are developed to variable degrees in all prosauropods. The state of this character in *Riojasaurus* is undoubtedly derived.

The dorsal projection of the surangular is very modest, and the articular region is at the level of or below the alveolar margin, as indicated by the position of the lower jaw in Figure 3A. The retroarticular process is massive, with an equal participation of the posterior section of the angular. The mandibular fenestra is proportionally small, possibly smaller than that of other prosauropods.

Teeth

Five subequal alveoli are observed in the premaxilla. The dentition of *Riojasaurus*, as has been remarked above, is not of the type present in *Plateosaurus* or other prosauropods which have transversely flattened teeth in the form of a leaf and with a constriction between crown and root. They are more subcylindrical, slightly concave, and with very small denticles - ones which can be observed in some of the maxillary teeth. This tooth type is also recorded in

Thecodontosaurus (Galton, 1990, fig. 15.4D) although those in *Riojasaurus* are larger and more rounded. It is probable that the dentition of *Riojasaurus* could be more primitive, or closer to the ancestral condition than that of other prosauropods.

COMPARISONS

With the aim of demonstrating morphological differences between *Riojasaurus* and *Coloradisaurus* Bonaparte, 1978 the skull, lower jaws, and necks of these prosauropods from the superior levels of the Los Colorados Formation, in the region of La Esquina, La Rioja have illustrated (Figure 5). In the case of *Riojasaurus*, the skull articulated with the neck and first three dorsals have been illustrated, in the case of *Coloradisaurus*, the skull is shown with the anterior and middle cervicals (with one of the vertebral segments reconstructed).

Apart from the very apparent differences in the skull, especially that of the position of the jaw joint, the form of the preorbital opening and diverse characters of the lower jaw, significant differences in the morphology of the cervical vertebrae can be appreciated.

The atlas of *Riojasaurus* has both halves of its neural arch broad, both it terms of its dorsal and lateral extent, with a broad region for the postzygapophyses. The atlas of *Coloradisaurus*, for its part, is styloform, dorsoventrally and transversely reduced.

The available cervicals, and those which can be compared, indicate that those of *Riojasaurus* are of a more robust morphology and do not possess the well defined and large ventral keel present in the middle cervicals of *Coloradisaurus*. It is probable that the neck of *Riojasaurus* was noticeably more robust than in *Coloradisaurus* since the middle and posterior cervicals are more robust and less cervicalized than that of *Plateosaurus*, probably representing a plesiomorphic feature.

In this way, the differences between the skull and cervicals in these genera from the upper level of the Los Colorados Formation are eloquent, and justify that the two correspond to different families: Plateosauridae (*Coloradisaurus*) and Melanorosauridae (*Riojasaurus*).

We have restricted the comparison of the skull of *Riojasaurus* to those genera which have the jaw articulation at or slightly below the level of the maxillary tooth row. The character of the

relatively high position of the mandibular articulation defines, in our opinion, a primitive grade very distinct from those with the articulation below the maxillary tooth row - which represent a more derived evolutionary level, one which signifies the ventral displacement of diverse cranial structures in the temporal region and evident modifications of muscles which close the jaw.

Attridge et al. (1985) suggested that the ventral displacement of the jaw joint corresponds to a variation in size, an interpretation which is not confirmed in the case of *Mussaurus* (Bonaparte and Vince, 1979), which with only 3cm long skulls have a very ventrally located jaw articulation, comparable to *Plateosaurus*, *Lufengosaurus*, and *Coloradisaurus*.

Within the genera which have the jaw articulation only slightly above the tooth row, such as *Massospondylus*, *Yunnanosaurus*, and *Anchisaurus* (Attridge et al., 1985; Galton, 1990) which approximate the condition in *Riojasaurus*, we note an important difference which involves the lacrimal and the preorbital region. In these prosauropods, the lacrimal bar is noticeably more inclined forward and downward and the preorbital depression and opening are relatively small and located below this bar. In the skull of *Riojasaurus* the situation is different since the depression and opening are large and the lacrimal bar is very close to a vertical position. This difference is significant and can be of phylogenetic interest, since in the skulls of sauropods (McIntosh, 1990), barring errors of orientation, the lacrimal bar is not oriented forward and the preorbital opening is located in front of the lacrimal. The vertical or subvertical preorbital depression and opening within prosauropods may correspond to a primitive state which distinguishes derived levels among prosauropods, and which eventually were retained in sauropods. In contrast, the prosauropods which have the derived characters cited above could be distant from the ancestral group of Sauropoda (e.g. *Anchisaurus*, *Thecodontosaurus*, *Coloradisaurus*, *Massospondylus*, *Yunnanosaurus*, *Mussaurus*). In this way, the set of primitive characters in the skull and jaws of *Riojasaurus* (high position of the jaw articulation, large preorbital depression and fossa, subvertical preorbital bar, conical and subcylindrical teeth) which were surpassed by other prosauropods, serve to differentiate the skull of *Riojasaurus* from the rest of Prosauropoda. As in the cited cranial characters, the unspecialized nature of the

middle and posterior cervical vertebrae indicates levels of organization more primitive in *Riojasaurus* than in other prosauropods.

ORIGIN OF PROSAUROPODS

The origin of the Prosauropoda is an interesting theme which still has not been analyzed, and which have been cited only as outgroups for their evaluation of characters. Galton (1990) considered the outgroups of *Herrerasaurus*, *Staurikosaurus*, *Lagosuchus*, and *Euparkeria* (only the skull), to conclude that *Thecodontosaurus* is the most primitive prosauropod. Nonetheless, as has been explained above, the skull of *Riojasaurus* presents characters perceivably more primitive then *Thecodontosaurus*, which can favor the search of its possibilities as an ancestor.

It is probable that the Prosauropoda are, as has been suggested above, the first manifestation toward the herbivore type within the clade Saurischia. It is also probable that this adaptive differentiation has occurred as a grade of derived forms slightly more advanced than *Lagosuchus* Romer 1971; 1972 (Bonaparte, 1975) in the characters of the dorsal vertebrae, and partially more primitive than in this Middle Triassic genus, although its pubis is more derived.

The anatomical condition of the pelvis and vertebral column of the Herrerasauridae (*Herrerasaurus* and *Staurikosaurus*, Benedetto, 1975; Novas, 1992) unites derived characters which impede their consideration as ancestral to Prosauropoda. Among these are included the transversely narrow pubis (in its distal extreme) and with an axial expansion; dorsal vertebrae with neural spines axially short; scapular blade reduced; ilium with a reduced postacetabular lamina; and hand with a very derived reduction of external digits.

For its part, the skeletal characters of *Coelophysis*, although in general more derived than the Prosauropoda, seem to hold certain coherence for accepting that *Coelophysis* and the Prosauropoda had a close common ancestor. The arguments for this hypothesis are based on the following characters:

1. The generalized skull of *Riojasaurus* shows suggestive similarities with that of *Coelophysis* in the extensive preorbital region, the height and elongation of the skull, the morphology of the temporal opening and surrounding bones, the relatively straight alveolar line,

the anterior section of the jugal participating in the preorbital opening; even though the size of the preorbital depression and opening of *Coelophysis* correspond to characters more derived than in *Riojasaurus*. In dorsal and occipital views of the cranium, and in ventral view of the basicranium, we can appreciate diverse common characters in the two genera. In spite of the fact that many of the similarities are primitive, there are others which are shared derived traits if we take as references the more primitive taxa Herrerasauridae, Ornithosuchidae, and Euparkeridae: (a) marked reduction of the anterior extreme of the jugal which participates in the preorbital opening; (b) reduction of the dorsal exposure of the lacrimal; (c) dorsal processes of the quadratojugal and squamosal reduced in size, styloform; (d) narrow and elongate skull, with a relation of a length of more than two times height; (e) reduction of the postemporal opening; (f) transversely reduced quadrate, quadratojugal, and quadrate foramen; (g) development of laterally and distally expanded basipterygoid processes; (h) basal tubera well developed and located well below the occipital condyle.

2. The vertebral column of *Coelophysis* show significant affinities with that of *Riojasaurus* both in the general characters of the types of vertebrae as well as in other details of comparative interest. The six vertebrae posterior to the axis of *Coelophysis* are low, elongate, provided with very low, neural spine laminae, and with a lateral depression in the vertebral centra which extends forwards between the parapophysis and the diapophysis. In *Riojasaurus*, these derived features are only manifest in the fourth vertebra after the axis, representing a plesiomorphic state in the distribution of these features in the cervical region. In *Coelophysis* (Colbert, 1989) the last two cervical and first two dorsal vertebrae show a shortening in anteroposterior length of the neural spine and the vertebral body, these last two being the shortest dorsal vertebrae. Comparable derived characters are manifest in *Riojasaurus*, but the shortest dorsals are 2 and 3. In *Coelophysis*, the middle and posterior dorsals have laminate neural spines which are relatively low (although noticeably taller than the anterior and middle cervicals) and with ample interspinal separation. The vertebral centra are slightly elongate, and concave laterally and ventrally. In *Riojasaurus*, the middle and posterior dorsals coincide with

the characters cited in *Coelophysis*. Nonetheless, the strong differences of size make the vertebrae of *Riojasaurus* seem proportionally more robust.

3. The hand of *Riojasaurus* (Bonaparte, 1972) and those of other prosauropods (Galton, 1990) reveal a primitive state which has been surpassed by *Coelophysis* (Colbert, 1989), *Herrerasaurus* (Sereno and Novas, 1992) and *Dilophosaurus* (Welles, 1984). But the plan of the hand is the same, and they all show the same tendency of reduction of digits IV and V. If we have in mind the distinct function of the hand in the primitive theropods, which are principally bipedal predators, and in prosauropods, which are principally quadrupedal herbivores, it can be conceived that the common plan they present is a good indication of their close phylogenetic affinities.

For the characters discussed above, we consider that the Prosauropoda and *Coelophysis* (Ceratosauria *sensu* Rowe and Gauthier, 1990) could well have possessed a close common ancestor, equal to that which had effected an evolutionary dichotomy, differentiating the Triassic prosauropods and ceratosaurs.

It is probable that *Herrerasaurus* was not phylogenetically very close to the ancestral clade to the prosauropods and that the derived characters in the presacral vertebrae, the narrow scapular lamina, the ventral torsion of the pubis, and its distal expansion suggest that it had taken a very divergent evolutionary path, eventually without descendants.

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FIGURE 1. Map of the location of the discovery of the specimen described here, in the vicinity of the Triassic beds of Ischigualasto-Villa Unión, and originating from the upper sector of the Los Colorados Formation (reproduced from Bonaparte, 1972).

FIGURE 2. Schematic diagram of the position in which the mostly articulated skeleton of ***Riojasaurus incertus*** (ULR 56) was discovered. The skull and neck are discussed in this work. Scale bar 50cm.

FIGURE 3. ***Riojasaurus incertus*** (ULR 56). Skull and jaws in left lateral view; and skull in dorsal view. The missing portions are represented by dashed lines. Abbreviations: **a**, angular; **bo**, basioccipital; **d**, dentary; **eo**, exoccipital; **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **op**, opisthotic; **p**, parietal; **pm**, premaxilla; **po**, postorbital; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **soc**, supraoccipital; **sq**, squamosal.

FIGURE 4. ***Riojasaurus incertus*** (ULR 56). A, occipital view of the skull; B, ventral view of the basicranium. The missing pieces are represented by dashed lines. Abbreviations as in Figure 3, as well as **bs**, basisphenoids

FIGURE 5. A, ***Riojasaurus incertus*** (ULR 56) with articulated skull, mandible, cervicals and four anterior dorsals. B, ***Coloradisaurus brevis*** (ULR 3967) with articulated skull, mandible, and seven cervicals. C, lateral view of the preatlas and atlas of the right side of ***Riojasaurus incertus*** (ULR 56); D, restoration in dorsal view of the preatlas and atlas shown in C. E, lateral view of the atlas arch and intercentrum of ***Coloradisaurus brevis*** (ULR 3967). F, dorsal view of the arch shown in E. Scale bars for A and B 10cm, for C-F 1cm.