A M E G H I N I A N A

Revista de la Asociación Paleontológica Argentina

Volume XVI July 1979 No. 1-2

DISCOVERY OF THE FIRST NEST OF TRIASSIC DINOSAURS (SAURISCHIA, PROSAUROPODA), FROM THE UPPER TRIASSIC OF PATAGONIA, ARGENTINA*

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ORIGINAL ENGLISH ABSTRACT: Several incomplete skeletons of juvenile Prosauropoda and two eggs were recovered from Upper Triassic beds of southern Patagonia. The specimens are referred to a new genus and species, *Mussaurus patagonicus*, showing a mixed picture of anatomical affinities. The forelimbs, pelvis and hindlimb are typically prosauropod; the short cervical vertebrae resemble those of the Middle Triassic thecodont *Lagosuchus*, and some characters of the skull suggest relationships with both Prosauropoda and Sauropoda. Tentatively a new family of prosauropods is proposed to include this new species.

INTRODUCTION

In the course of a paleontological expedition organized by the Universidad Nacional de Tucumán and the Fundación Miguel Lillo, with the support of the National Geographic Society, we reaped the benefits of a notable paleontological discovery, unique in its kind by corresponding to the Upper Triassic. It is seven juvenile individuals of prosauropod dinosaurs found in direct association and nearby two fossil eggs. The small size of these dinosaurs (total estimated length 20 cm) , besides the juvenile characters shown by the skull, make conclude that it is a very juvenile collection of these reptiles which still living in their nest, near two eggs.

These materials were found in the El Tranquillo Formation, in north-central Santa Cruz province, in the same beds which produced diverse specimens of *Plateosaurus* sp., exhumed by the Museo de La Plata between 1962 and 1968 (Casamiquela 1977).

* Original reference: Bonaparte, J. F. and M. Vince. 1979. El hallazgo del primer nido de dinosaurios triasicos, (Saurischia, Prosauropoda), Triásico superior de Patagonia, Argentina. *Ameghiniana* 16(1-2):173-182.

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In the present work is given to know the discovery, including a brief description and comparison of the most complete specimen. An analysis of the biological significance of this material, which suggests certain type of brooding care between these primitive dinosaurs, is reserved for the future. Likewise, in the future will be understood, from the ontogenetic perspective, the peculiar anatomical characters which these small prosauropods show.

SPECIMENS THAT COMPRISE THE "NEST"

In total there are seven juvenile prosauropod specimens recovered, and two eggs of distinct size. It is probable that originally the components of the "nest" were more numerous than those recovered, since erosion has had strong effects in the place from the time to be destroyed.

1. Holotype specimen, PVL 4068, composed of most of a skeleton (Fig. 1).
2. Specimen PVL 4208, composed of a skull and mandibles, cervical vertebrae, scapular blade, incomplete forelimbs, incomplete pelvis and incomplete hindlimbs.
3. Specimen PVL 4209, composed of part of a skull and mandible, vertebrae and numerous disarticulated postcrania.
4. Specimen PVL 4210, composed of a skull and mandibles, cervical and dorsal vertebrae, scapular blade and articulated forelimbs, pelvis and articulated hindlimbs.
5. Remains of a specimen that include skull and incomplete mandibles and most of the disarticulated postcranium, PVL 4211.
6. Partially articulated postcranial skeleton, PVL 4212.
7. Diverse grouped postcranial remains, PVL 4213.
8. Most of a bone of approximately 60 mm greater diameter and 45 mm lesser diameter, PVL 4214.
9. Most of a bone of 20 mm greater diameter and 16 mm lesser diameter, PVL 4215.

All the specimens are of similar size, with the skull approximately 30 mm and with a length of approximately 16 cm from the snout to the posterior end of the pelvis; with the tail holding one 20 cm. It is estimated that the specimens were some weeks old when buried because the largest of the collected bones could not harbor an embryo of the size of the specimens collected.

The disparity of size of the discovered bones can be interpreted as corresponding to two distinct species. Nevertheless, by lack of other evidence we think tentatively that the smallest bone, with external appearance similar to the largest bone, would be a bone of aberrant size of the same species.

DESCRIPTION OF SPECIMEN PVL 4068

Infraorder: *PROSAUROPODA*

Family: *MUSSAURIDAE* nov.

Genus: **MUSSAURUS** nov.

Type species: *Mussaurus patagonicus* nov. sp.

Etymology: *Mus*: rat; *saurus*: lizard; *patagonicus*: from Patagonia. In reference to the rat size of this dinosaur, coming from Patagonia.

Locality and age: La Colorada lake, Cañadon Largo farm, north-central Santa Cruz province, Patagonia, Argentina. Upper section of the El Tranquillo Formation, upper Coloradian, top part of the Upper Triassic.

Diagnosis: short and high skull, with elongate frontals and parietals, very short snout. Antorbital fenestra short and high, placed very near the orbit. Long teeth, very rounded. Lower jaw with thick symphysis. Cervical vertebrae short and high as in the thecodont *Lagosuchus*. Dorsal vertebrae, pelvis and hindlimbs of prosauropod type.

Skull: It is short and high, with large orbits, and the short snout, features that indicate its juvenile character. The maxilla and premaxilla are very high and short axially, recalling the skull type of the sauropod *Camarasaurus*. The antorbital fenestra likewise recalls this genus, with its major axis directed dorsoventrally. The temporal fenestrae are of the type present in Prosauropoda, with the triradiate postorbital in a shape similar to that of *Anchisaurus* (Fig. 2) and *Plateosaurus.* The quadrate is inclined backwards as in *Anchisaurus* (Galton 1976) and other sauropod. The frontals and particularly the parietals are more elongated than in known prosauropods, including Anchisaurus.

The lower jaw has a thick symphysis that coincides more with this feature in Camarasaurus thn with the weak symphysis of the Prosauropoda.

The dentition of the specimen described consists of more cylindrical and proportionally longer teeth than in the Prosauropoda. In other specimens these features are less marked, approaching a more typically prosauropod morphology, with somewhat laterally compressed teeth and with some indentations on the edges. There are 4 teeth in the premaxilla and six teeth preserved in the incomplete row of maxillary teeth, which must have consisted of 10 to 12 elements.

Vertebrae: The cervicals are proportionally short and tall, 7 mm from the ventral border of the vertebral centrum to the dorsal end of the neural spine, and only 4 mm along the axial length of the vertebral centrum (Fig. 4). From the 3rd vertebra forwards, the cervicals have well developed zygapophyses. The neural spines are short and axially short. The lateral face of the cervicals has very reduced parapophyses and diapophyses, which are encountered well defined from the eighth cervical forwards.

The dorsal vertebrae show increases in length of the vertebral centrum towards the sacrum, with a length of 4.5 mm for the 9th vertebra and 6 mm for the 22nd. The dorsals show prominent diapophyses, pronounced zygapophyses, short neural spines and

laterally concave vertebral centra. The evidence indicates that there were 3 sacrals comparable to the last dorsals.

The morphology of the cervical vertebrae is comparable to that of the thecodont *Lagosuchus talampayensis* Romer, from the Middle Triassic of La Rioja.. It is considered as a probable ancestor of the Saurischia (Bonaparte 1975), and in turn distinct from that of known Prosauropoda. In them (Anchisauridae, Plateosauridae and Melanorosauridae), the cervical vertebrae are always low and elongated, especially in the anterior half of the neck, becoming more gracile closer to the skull. Among the Sauropoda, *Camarasaurus* has relatively short and high vertebrae only in the anterior cervical region, although its general morphology, and prominent para- and diapophyses are very distinct from the simple morphology of the vertebrae of *Mussaurus patagonicus*. The dorsal vertebrae are comparable to those of Prosauropoda.

Scapular blade: The scapula is long, gracile (Fig. 3) and longer than that of known prosauropods, whereas the coracoids match morphologically with them.

Forelimb: Both humeri, ulnae, and radii are preserved. Their morphology coincides well with the prosauropod type. In specimen PVL 4210 metacarpals I, II, III and IV are preserved, showing the characters and proportions typical of prosauropods. The size relation between the fore and hindlimbs is somewhat different, with the humerus proportionally longer than in known prosauropods.

Pelvis: The pelvis is not well preserved in this specimen, although its principal characters are present. The ilium is low, of prosauropod type, with a pronounced posterior projection; the pubic peduncle elongate and the ischial short. Lamentably the anterior iliac projection is not preserved. The preserved part of the pubis includes most of the distal elongations, laminar and long as in Prosauropoda. The characters of the ischia are likewise comparable to those of prosauropods, but proportionally longer. The pelvis of this species corresponds well with the type present in Prosauropoda.

Hindlimb: The morphology of the femur matches with thatof Prosauropoda except in the lack of a well developed articular head which could be the result of the juvenile condition of the specimen. The tibia and fibula are shorter than the femur (femur 30 mm, tibia 27 mm). Both tarsals are relatively well preserved, except the calcaneum is lacking probably due to deficient ossification. The general morphology of the astragalus, distal tarsals and metatarsals (Fig. 4) coincide well with Prosauropoda, *e.g. Riojasaurus* or *Plateosaurus.* The elongate metatarsals are not similar to that of any known Sauropoda.

AFFINITIES OF *MUSSAURUS PATAGONICUS*

As much the great proportional size of the orbits as the short snout of this species well could be the result of the juvenile condition of the available specimens. With respect we must hold on account that certain ontogenetic changes would have occurred during the growth.

Excluding the form of the antorbital fenestrae, the long teeth, and the thick mandibular symphysis, the remaining postorbital and mandibular characters are clearly shared with Prosauropoda, although they are not identifiable with any known species.

The cervical vertebrae exhibit a primitive morphology, because they are short and high, with more dorsally positioned zygapophyses, characters not registered currently in any Sauropodomorpha (Prosauropoda and Sauropoda), but present in the Middle Triassic thecodont *Lagosuchus*. The cervical vertebrae of *Mussaurus patagonicus* may represent the retention of an unspecialized vertebral type that probably is present in the more primitive (unknown) prosauropods. In great measure our systematic position before these juvenile specimens has its fundamental in the peculiarity of the characters of the cervical vertebrae, which impede its assignment to any of the known families of Prosauropoda.

The pectoral girdle does not offer indications of the affinities of this small dinosaur, at least in the preliminary form in which we have analyzed here.

The forelimb suggests clear affinities with Prosauropoda because the morphology and proportions of its distinct bony segments is basically the same as in *Plateosaurus* (Huene 1907-08) and *Riojasaurus* (Bonaparte 1971).

The pelvis and hindlimb likewise coincide in showing strong affinities with Prosauropoda, particularly in the morphology of the tarsus and pes.

In summary, most of the skeleton of *Mussaurus patagonicus* shows clear affinities with Prosauropoda, the infraorder within which we place this species. Some cranial characters recall the type present in the sauropod *Camarasaurus*, while those of the cervicals suggest pre-Sauropodomorph affinities (Thecodontia). Both groups of characters are significant and can have implications as much for relative aspects to the origin of Prosauropoda as with respect to the phylogenetic relationships among them and Sauropoda.

The picture of the affinities of *Mussaurus patagonicus* indicates that it is a prosauropod, although of a distinct family from those known due to the collection of primitive (cervical) and advanced (cranial) characters it presents. Nevertheless it is admitted that a wide ontogenetic analysis of these specimens added to the consideration of ontogenetic evidences in some living reptiles and birds could indicate very distinct *systematic* conclusions, including that it could belong to young of the genus *Plateosaurus*, present in the same beds of the El Tranquillo Formation.

From the Upper Triassic of Germany is known a small archosaur specimen, *Elachistosuchus huenei* Janensch (1949), Walker (1966), of which specimen he could to observe in the Museum für Naturkunde in Berlin, which was the object of additional preparation (Jaeger, pers. comm.). Some characters of the dentary as well as the enormous orbit that it possesses, makes one think that it could belong to a very juvenile prosauropod comparable to *Mussaurus patagonicus*.

THE JUVENILE CONDITION OF *MUSSAURUS PATAGONICUS*

The specimen described and the remaining specimens included in this prosauropod "nest" are undoubtedly juveniles. The ossification, although in general it shows good articular caps on the ends of long bones, exhibits deficiencies in the union of the neural arches with the vertebral centra, an irregular surface, with striations, in the shaft of some

long bones of the limbs, and thinner bones in the skull roof. Nevertheless, it results very difficult to estimate how juveniles were the specimens of *Mussaurus patagonicus*. We can admit that the proportional size of the orbit suggests that the specimens must have lived more than 2 turns of size that they present, and eventually reaches the size of a large prosauropod.

In relation to the magnitude of the ontogenetic changes that would have occurred in this species we can only obtain some inferences based on the changes that occur in crocodilians (Kalin 1955; Dodson 1975), the observations available in the lepidosaur *Tanystropheus* (Wild 1973) and the pterosaur *Pterodactylus* (Wellnhofer 1970). In general, the ontogenetic changes that we have consulted indicate that the modifications have affected different parts of the skeleton in a different manner, but without alterations so large as to produce a basically different morphology in the adult state.

Considering the cited evidences it seems little probable that the short and high skull of *Mussaurus patagonicus* could produce a long and low skull, similar to that of *Anchisaurus* or *Plateosaurus.* Less probable still would be to suppose that the short and high cervical vertebrae of *M. patagonicus* could vary ontogenetically enough to give place to low and long vertebrae, typical of the three known families of Prosauropoda. These morphological aspects of the described species have led us to propose a new family of Prosauropoda, because in the current state of understanding of ontogenetic changes among reptiles has resulted for us very difficult to justify the inclusion of *M. patagonicus* in any of the three prosauropod families already established.

ORIGIN OF SAUROPODA

Various authors have reasonably expressed that Prosauropoda could include forms ancestral to Sauropoda. This was noted by Romer (1956) and Huene (1956), citing the family Melanorosauridae as firm evidence for linking Prosauropoda with Sauropoda. This statement, was followed without significant modifications by Colbert (1964), Romer (1966, 1968), Charig *et al.* (1965), and Raath (1972), gaining general acceptance.

Nevertheless, Reig (1970) suggested that Melanorosauridae could in reality have been sauropods, and that they probably originated in the erythrosuchid Proterosuchia at the end of the Lower Triassic.

With respect to the first part of this statement we must record that the known osteology of Melanorosauridae is basically the same as that of Plateosauridae and Anchisauridae. In the same manner, if as suggested by this author, Melanorosauridae is considered as Sauropoda, there are no anatomical reasons for maintaining Anchisauridae and Plateosauridae in a distinct infraorder. Or it would be, that if we follow this proposal, the three families of Prosauropoda become part of Sauropoda...while to the second part of this proposal, the different osteologies between erythrosuchid Proterosuchia and melanorosaurid Prosauropoda are so great that the descendence of this latter from the Erythrosuchidae is only a conjecture.

Romer (1972) suggested, with great doubt, that the erythrosuchid or prestosuchid Proterosuchia could have changed during the Triassic and been converted into the ancestors of Sauropoda. The suggestion is interesting, and distinct from the former, but at present there exists no explanation or evidence to demonstrate this possibility.

Thulborn (1975) refers to "a fairly strong consensus of opinion" that Sauropoda originated during the Triassic, probably from proterosuchian ancestors. It is probable that both concepts are not correct and that such a consensus of opinion does not exist. Proterosuchia, by its primitive condition, could be ancestral to Crocodylia, Pterosauria, Ornithischia, Carnosauria, etc. In reality it is a basal group of Archosauria, but the morphological distance between it and sauropoda is so serious and enormous that to consider them ancestors of these latter is a generality that does not signify any advance in clarifying which was the near ancestor (not distant) ancestor, which had originated Sauropoda.

Although the theme of the origin of Sauropoda cannot be treated here extensively, we confirm the idea that Prosauropoda is an adequate group to consider as a potential ancestor to them. Nevertheless, although basically correct, the statement must be considered with some reservation. Some doubtful points that offer this possibility (see Charig *et al.* 1965), consist of certain morphological differences from the osteology of Sauropoda, without intermediate stages known (for now), as *e.g.* the vertebral morphology, the shape of the ilium, the proportions of the metacarpals and metatarsals, etc., that are in reality little compared with the quantity of similar features.

Prosauropoda is known as a fairly uniform infraorder, with very similar osteology in its three traditional families. To reconsider a melanorosaurid as a large plateosaurid it is necessary to dispose of a good part of the skeleton and yet also doubts could persist. perhaps the different proportions between the fore- and hindlimbs would be one of the few distinctive characters. The shapes of the gracile pes and robust pes recognized by Galton (Galton and Cluver 1976) is useful for distinguishing between Anchisauridae and Plateosauridae, which on the other hand present very similar postcranial osteologies.

The new genus and species described, *Mussaurus patagonicus*, and the new family proposed, Mussauridae, corroborate the suggestion that Prosauropoda must have had a great morphological diversity. It is possible that the knowledge of this infraorder does not represent the totality of the adaptive radiation operated among Prosauropoda, and that future discoveries will show a group more varied in its constitution. Yet while we do not consider that the described species would be ancestral to Sauropoda, especially because from the Liassic of India (Kota Formation), Jain *et al.* (1975) have documented good evidence of large sauropods, it is important to note that the Patagonian species shows for the first time a prosauropod with some cranial characters that are similar to those of certain Jurassic sauropoda (*e.g. Camarasaurus*).

The sauropod characters that *Mussaurus patagonicus* possesses in the skull, mandibular symphysis, and teeth, added to its juvenile condition, suggest the possibility that Sauropoda differentiated from Prosauropoda due to the persistence of some juvenile characters in the adult state (neoteny) in some of the families of this infraorder.

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FIGURE CAPTIONS

Fig. 1. – Holotype specimen of **Mussaurus patagonicus** in a woman's hands.

Fig. 2. – Above, lateral view of the skull and mandible of **Mussaurus patagonicus**, reconstructed on the basis of preserved features on both sides of the specimen. Below, skull and mandible of the prosauropod Anchisaurus polyzelus in lateral view, for comparison with **M. patagonicus**; after Galton.

Fig. 3. – Holotype skeleton of **Mussaurus patagonicus** as preserved. Hatched areas indicate reconstruction.

Fig. 4. – Above, the first three cervical vertebrae of **Mussaurus patagonicus** in lateral view. Below, left tarsus and metatarsus of the same species in plantar view.