

NOTES ON THE EVOLUTION OF VERTEBRAE IN THE SAUROPODOMORPHA

by

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Abstract. EVOLUTION OF THE PRESACRAL VERTEBRAE OF THE SAUROPODOMORPHA. The presacral vertebrae of the pre-dinosaur *Marasuchus* and the prosauropods *Riojasaurus* and *Plateosaurus* are redescribed and discussed. A new genus and species, *Lessemsaurus sauropoides*, diagnosed by tall neural arches and infrapostzygapophyseal constriction in the posterior cervicals, is described; the vertebral morphology of the cetiosaurid sauropods *Volkheimeria*, *Lapparentosaurus* and *Patagosaurus* is discussed and compared; as well as that of *Diplodocus*, *Apatosaurus*, *Brachiosaurus brancai*, *Camarasaurus*, *Dicraeosaurus*, *Haplocanthosaurus*, the Titanosauridae s. str., *Saltasaurus*, and a Titanosaurinae indet. from Brazil. Other incompletely known Titanosauria and *Opisthocoelicaudia* are discussed more briefly.

This study demonstrates that the presacral vertebrae represent a rich source of information for understanding the evolution and systematics of sauropodomorphs. In the basal dinosauro-morph *Marasuchus*, three morphological types of vertebrae are recognized, a condition further developed by sauropodomorphs. Within Prosauropoda, the melanorosaurid *Riojasaurus* shows the most primitive condition in the number and organization of the cervical vertebrae: it has 9 cervicals, the first 5 of which exhibit the cervical morphological type, whereas the last 4 correspond to the dorsal morphological type. *Plateosaurus* is more derived than *Riojasaurus* in characters of the neck. The primitive sauropod-type vertebrae is more advanced than the typical prosauropod-type vertebrae, but it shows more primitive characters than the cetiosaurid type. It is considered that the cetiosaurid-type presacrals correspond to an evolutionary stage that might have made gigantism possible, triggering the adaptive radiation recorded in the Upper Jurassic of North America, Africa and Asia. In diplodocids the presacrals show clear relationships to the cetiosaurid type, but there are a high number of cervicals, and opisthocoely of centra is more developed. Significant differences in the cervical vertebrae of *Apatosaurus* with respect to those of *Diplodocus*, *Camarasaurus* and other sauropods suggest that *Apatosaurus* should be placed in a family of its own: Apatosauridae nov.

Presacrals of *Brachiosaurus* type are examined only in *Brachiosaurus brancai* because the generic identity of *Brachiosaurus altithorax* is doubtful, possess several

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characters, such as opisthocoely extending to the last dorsal, that are more advanced than in *Patagosaurus* and *Diplodocus*. Other characters of the *Brachiosaurus* type of vertebrae are more primitive than those in *Diplodocus*, thus suggesting origin from a condition more primitive than that exemplified by the cetiosaurid type.

Restudy of camarasaurid-type presacrals does not confirm previous interpretations of these vertebrae as primitive; furthermore, several features are more derived than in *Diplodocus*. Also, it is proposed that the dicraeosaurid type might have evolved independently of other presacral types, the cetiosaurid type probably representing the ancestral condition. Presacrals of *Haplocanthosaurus* have a distinct morphology; thus this genus is included in Haplocanthosauridae nov. Titanosaurs exhibit several morphological types of presacrals, indicating several levels of organization. Distinctive features are present in the cervical region of members of Titanosauridae s. str., e.g. a unique design of the infrapostzygapophyseal constriction, reduced distance between the centrum and the zygapophyses, and the near absence of the neural spine. In general, *Malawisaurus*, *Andesaurus* and *Argentinosaurus* are of more primitive organization than Titanosauridae s. str. Tentative interpretation of the significance of several complex characters involving presacral vertebrae, such as the sigmoid neck, the dorsoventral extension of the dorsals, the transversely wide neural spines, the relation between the number of cervicals and dorsals, the pleurocoels, and the supraneural cavity are discussed. In addition, a new prosauropod genus, *Lessemsaurus sauropoides*, is erected, diagnosed by its high neural arches and the infrapostzygapophyseal constriction of the posterior cervicals.

KEY WORDS: Evolution. Presacral vertebrae. Sauropodomorpha.

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INTRODUCTION

The marked process of gigantism documented among the sauropodomorph dinosaurs has been intimately related to the development of very particular adaptations in the spine, especially in the presacral and sacral vertebrae. Although the skeleton of the girdles and limbs also suffered very evident changes (McIntosh, 1990), it is probable that the modifications of the presacral vertebrae are more remarkable, and that the knowledge of their complexity contributes to better understanding the evolutionary phenomenon that created these big Mesozoic quadrupeds.

Although it is usually pointed out that the sauropods were ancient herbivorous dinosaurs, provided with proportionally very small brains, and little efficiency of the masticatory system and locomotion (Dodson, 1990:402), it is worthwhile to point out that the evolutionary marvels of the sauropods, like those of any other organism, are not appreciated by means of arbitrary comparative parameters, but in the observation and evaluation of their own derived characters and the biological organization and functional resultants of them. In such a sense, the incredible sizes of these Mesozoic giants, their extensive biocron, and their estimated individual longevity are the result of a complex and amazing evolutionary history in which a great number of biological and physical factors have been involved, which does not seem to support Dodson's appreciations.

The evolutionary history of sauropod neural spines, which constituted the support for their long necks and heavy thoracic cavities, is showed to us as revealing only one aspect of the remarkable adaptive capacity and interesting morphofunctional aspects developed among these dinosaurs. In this work I try to emphasize the variable organization of the vertebral column of some sauropodomorphs, advancing functional interpretations of different bony characters and their probable relationships with the axial musculature. I recognize the uncertainty of most of the relationships between the details of the bony morphology and certain muscular packages, but I consider beyond doubt that the vertebral complexity of the sauropods was completely linked to a very specialized system of axial muscles for support and control of movements, and not to a system of lightening the weight of the bones as is frequently hypothesized (Janensch, 1947, 1950; McIntosh, 1990).

Collection Abbreviations: AMNH: American Museum Natural of History; DNPM: Nacional Direçao do Produçao Mineral, Rio de Janeiro; ISIC: Indian Statistical Institute, Calcutta; BAD: Southern Methodist University, Dallas; MLP: Museo Nacional de La Plata; PVL: Paleontological Collection of the Instituto-Fondacion Lillo; MCZ, Museum of Comparative Zoology, Harvard University; MBR: Museum für Naturkunde, Berlin; UPLR, Paleontological Collection of the Universidad Nacional de La Rioja; ZPAL: Zaklad Paleobiologii, Warsaw.

OBJECTIVES AND APPROACH TO THE TOPIC

The study of the anatomy and function of sauropodomorph vertebrae is a task that greatly exceeds the author's abilities, because of the evolutionary historical projection that inevitably should be analyzed in detail, and the variety in Jurassic and Cretaceous forms to be considered. Because of this, the objective of this work is only to intrude in the study of the presacral vertebrae of the well-represented taxa, with the intention of analyzing and interpreting some important aspects that demonstrate the remarkable wealth of the topic and its potential phylogenetic and systematic significance.

Perhaps it would be opportune to refer here to the systematic value of the presacral vertebrae among tetrapods. Both for reptiles or mammals, the vertebrae have not been very useful tools to identify, at generic level, their owners. At the family level their identification is, in most of the cases, still uncertain, and newly at the ordinal level a reliable identification can be arrived at in certain cases, doubtful in others. For example, among crocodiles (living archosaurs), it is very strange when starting from a sequence of presacral vertebrae to recognize a taxon to Eusuchia or to "Mesosuchia". Among mammals presacral vertebrae do not differ clearly among arctiodactyls and perissodactyls, although by the way certain differences are appreciated when we stop in their observation. Nevertheless, among *Tapirus* (Ceratomorpha) and *Equus* (Hippomorpha) the difference in the cervicals is evident but within a common plan among the Perissodactyla.

The reason for the limited use of the axial skeleton in recognizing taxa is that the type or types of presacral vertebrae in most tetrapods are notably conservative (except partly in labyrinthodonts and ophidians), differing presumably only in punctual details that are difficult to appreciate. But in sauropodomorphs the reality is different. The diversity of vertebral types is notably high, in particular among sauropods, but also, although to a smaller degree, among prosauropods.

If we looked for an explanation to this novel situation we can argue, not without doubts by the way, that the genetic control linked to the development of the axial skeleton and its musculature, so conservative between reptiles and therapsids-mammals, would have suffered alterations in the archosaur group linked to the origin of Sauropodomorpha, probably during Middle Triassic times, facilitating the differentiation of this great group that, for particular genetic qualities (that we do not know), caused morphological changes in their presacral vertebrae leading to an novel gigantism among the terrestrial tetrapods.

It is probable that, in certain way, the vertebral types of sauropods have also been conservative, but with diverse taxa giving place to family-level groupings.

If we adopted the opposite approach, in which the different vertebral types did not have systematic significance beyond the generic level, we would be propagating approaches that are not applied in the classification of other groups of vertebrates. The different presacral vertebrae types that have their expression in sauropod families, satisfactorily characterized and represented by adequate materials, are sufficiently different as to demonstrate their diagnostic qualities. The presacral vertebrae of *Brachiosaurus brancai* Janensch (1914), *Diplodocus* Marsh 1878, or of *Camarasaurus* Cope 1877 exhibit different morphological types. This situation is useful so that, when we recognize a new morphologic type of presacral vertebrae, it allows us to consider that we are in front of a different family grouping, independently whether they have the same dental type or the same proportions among whichever limb bone. This would imply that in the Sauropoda the hierarchy of vertebral characters is of more importance than the characters of the teeth or the girdle and limb bones.

The most primitive references that I have taken are the presacral vertebrae of the dinosauromorph *Marasuchus* Sereno and Arcucci, 1994, from the Middle Triassic of Argentina, as one that obviously develops the anatomical character of the presence of an S-shaped neck. This feature was an initial, basic acquisition in the evolutionary history of saurischians (Bonaparte, 1975), and it was among sauropodomorphs where it was developed at extreme specialization levels.

Among prosauropods, besides the melanorosaurid *Riojasaurus* Bonaparte (1969), I have paid special attention to an individual of *Plateosaurus* Meyer (1837) from Germany, from the collections of the Museum für Naturkunde, Berlin, that has preserved remarkable features linked to ligaments and muscular insertions. Their cervical vertebrae show a

remarkable organization that reveals a more primitive stage than that of primitive sauropods.

I have also analyzed to another melanorosaurid prosauropod with very derived vertebrae, of the primitive sauropod type (see respective chapter), corresponding to a new genus and species from the Los Colorados Formation, Upper Triassic of La Rioja province, Argentina that is described later on.

Among sauropods the availability of exceptional materials of the cetiosaurid *Patagosaurus* Bonaparte (1979, 1986) from the Middle Jurassic of Patagonia, and the observations made on the holotype of *Barapasaurus tagorei* Jain et al. (1977), deposited in the Indian Statistical Institute, Calcutta, have allowed me to illustrate an initial stage in the vertebral organization of sauropods, morphologically previous to that of the Upper Jurassic sauropods.

Diplodocus Marsh (1878), *Apatosaurus* Marsh (1877), *Camarasaurus* Cope (1877), *Dicraeosaurus* Janensch (1914), *Amargasaurus* Salgado and Bonaparte (1991), *Brachiosaurus brancai* Janensch (1914), and *Haplocanthosaurus* Hatcher (1903), based on direct observations in the Carnegie Museum of Pittsburgh, Museum für Naturkunde, Berlin, Museo Argentino de Ciencias Naturales of Buenos Aires, and Cleveland Museum of Natural History, I have taken as evidence of the remarkable adaptative radiation that is manifest in the presacral vertebral anatomy of sauropods from the Upper Jurassic and Lower Cretaceous. Finally, the titanosaurians *Andesaurus* and *Argentinosaurus*, and the titanosaurids s. str. *Saltasaurus* Bonaparte and Powell (1980) and an exceptional individual from the Upper Cretaceous of Peirópolis, Brazil (Powell, 1987) were consulted directly. They are part of one very derived evolutionary line, with remarkable anatomical acquisitions in their presacral vertebrae.

In this work I use the term Titanosauridae following the proposal of Powell (1986) for recognizing this taxonomic entity integrated by the subfamilies Titanosaurinae, Saltosaurinae, Antarctosaurinae, and Argyrosaurinae. I believe it convenient to express Titanosauridae s. str. to define the reach of this taxon that is frequently used involving more primitive forms (McIntosh, 1990; Jacobs et al., 1993).

Although not very attractive, the use of a particular terminology is of fundamental importance to defining characters, evaluating them, and relating them. Without the handling and distinction of these characters, it would be very difficult to understand the evolution of sauropod vertebrae, like trying to understand the evolution of Theria while ignoring what is a protocone or a hypoconulid.

If through this work it was demonstrated that the evolution of the presacral region of the spine of sauropodomorphs is an important source of information for evaluating the evolutionary dynamics of these herbivores, and that its study is just as or more fascinating than the study of the evolution of the limbs of the theropods, then the objective of this work will have been fulfilled.

METHODOLOGY AND CHARACTER EVALUATION

To try to organize the evaluation of the characters of the vertebrae under study, I have arbitrarily divided the cervical and dorsal vertebrae into anterior, middle and posterior. The anterior dorsals show, since the primitive stage of the evolution of Prosauropoda, the more remarkable morphological changes, probably linked to the support and handling of a neck that ended up having incredible dimensions among certain sauropods such as *Mamenchisaurus* Young (1954). Nevertheless, the posterior dorsals, more conservative in their morphology, also offer very useful information for understanding, at least partly, the changes suffered by sauropod presacral vertebrae.

All the figures included in this work show the vertebrae in right posterior view to

facilitate their observation and comparison. For this reason it has been necessary to change the orientation of numerous figures published by other authors, and these are included, redrawn, in this work.

In figure 1, corresponding to a posterior cervical of *Patagosaurus fariasi* (Bonaparte 1979, 1986) from the Middle Jurassic, 10 areas were distinguished for evaluating the most obvious changes that the vertebrae of sauropodomorphs have undergone. They are:

- 1 – Anterior area of the vertebral centrum. It is the area corresponding to the articulation between the vertebral centra that brings modifications from the condition present in *Marasuchus* Sereno and Arcucci (1994), as in prosauropods and sauropods.
- 2 – Lateral area of the vertebral centrum. It is the region of the vertebral centrum that shows the most evident modifications. The area is limited below by the diapophyses, which are not included, although the parapophyses are.
- 3 – Ventral area of the vertebral centrum. It is a complex region that shows numerous morphological changes.
- 4 – Zone anterolateral to the postzygapophyses. It is the area located below the lamina that runs forward from the postzygapophyses and includes the most inferior sector of the neural arch.
- 5 – Zone posterolateral to the prezygapophyses. It is the zone opposite the one mentioned in 4, located (in sauropods) below the lamina that connects the prezygapophyses with the diapophyses.
- 6 – Dorsolateral zone. It is the whole posterior area of the neural arch from the diapophyses toward the neural spine, and opposes areas 4 and 5 (in sauropods between the diapophysial-postzygapophyseal and diapophysial-prezygapophyseal laminae).
- 7 – Prespinal area. It is the area exposed in anterior view between the neural spine and the prezygapophyses.
- 8 – Anterior circumneural area. It is the area located in both sides of the neural canal below the prezygapophyses.
- 9 – Postspinal area. It is the area exposed in posterior view between the neural spine and the internal faces of the postzygapophyses.
- 10 – Neural spine area. It is the specific area of the dorsal part of the neural spine.

These 10 areas present, in author's opinion, a heterogeneous anatomical significance, as much functional as evolutionary, although a comparative evaluation has not been attempted either to determine which would be more important in functional or phylogenetic terms. Rather morphologic information has been obtained from them that the author has tried to interpret in terms of progressive changes in order to evaluate levels of derivation.

In my interpretation, the vertebral morphological changes in sauropodomorphs have been concomitant with the development of an increasingly complex axial muscular system that on the one hand was able to provide the support and necessary flexibility for the heavy thorax-abdomen, and on the other to sustain and manage in varied ways the necks that ended up being several meters long and weighing more than 1 ton (Alexander, 1989). For it, the incursion in some aspects of the musculature has been unavoidable, particularly when trying to recognize the significance of the epaxial and hypaxial muscular systems with the observed bony characters, although tentative, but with the support of the rather conservative condition and general distribution shown by this musculature among diverse tetrapods groups (Romer, 1956; Frey, 1988).

To reconstruct the complex axial musculature that sauropods should have is not, of course, within the reaches of this work, still some basic interpretations are included, although

not without serious reservations. A good work in this sense would be for an experienced team of paleontologists and physiologists.

I believe that the methodologies of paleontological investigation, particularly in vertebrates, should be from the evolutionary school practiced for distinguished scientists such as Simpson, Romer, Parrington, Charig, Bown, etc., or from the phylogenetic systematics school, at the moment of very diffused use, especially in the English-speaking countries, as the two are neither contradictory nor antagonistic in their searches and results. On the contrary, I consider that they are supplemental and not mutually exclusive. For that reason I have not wanted to sign up formally in one or another school, but rather have used those postulates of both that I consider valid.

I have analyzed the characters in some detail and interpreted their probable primitive or derived condition, and I have considered these as significant testimonies to the groups to interpret their evolution, still whether they could be monophyletic. I believe that this paradigm of phylogenetic systematics, today accepted by a great number of paleontologists, will have, as many scientific paradigms, a transitory validity in the continuous improvement of methodology and scientific interpretation, to be perfected or replaced by new enunciations and methods.

I have tried to analyze the vertebral characters and their changes in a historical perspective, with a view toward understanding the basic aspects and novelties of those characters. The analyzed characters, even superficially, and the recognition of their different stages that I have kept in mind to try to understand the evolution of these vertebrae, are listed in Appendix I:

THE PRESACRAL VERTEBRAE OF THE DINOSAUROMORPHS *MARASUCHUS* ("LAGOSUCHUS") AND *LAGERPETON*

It is probable that these genera from the Middle Triassic of Los Chañares, Argentina, are not direct ancestors of the Saurischia or Ornithischia, because of diverse very derived anatomical details that they show and are pointed out later. But probably they were part of the adaptive radiation that begat the Saurischia (Bonaparte, 1975). *Marasuchus* is clearly more derived in its organization level than *Euparkeria* (Ewer, 1965), especially in the clear differentiation of the presacral vertebrae into three morphological types, and in the development of the neck into the S-shape that characterizes these basal dinosauromorphs.

Recently, Sereno and Arcucci (1994) considered *Lagosuchus talampayensis* as a *nomen dubium*, an unacceptable interpretation because the holotype contains a great number of characters in its vertebrae, forelimbs, and hind limbs. In my opinion, the genus and species *Lagosuchus talampayensis* based on the holotype UPLR 09 (former MLP-64-XI-14-11) are valid.

Nevertheless, the material studied by Bonaparte (1975) and referred by this author to *Lagosuchus talampayensis* differs in the proportions among the fore- and hind limbs from those presented by the holotype of that species, and for that reason the proposal made by Sereno and Arcucci (1994) for recognizing a new genus and species, *Marasuchus lilloensis*, is accepted in this work, not without recognizing that we are ignoring the range of interspecific and individual variation of that genus and species for the time being.

In the dinosauromorph *Marasuchus*, represented by specimens PVL 3870, PVL 3871, PVL 3872, PVL 4672 and MCZ 4116 (described by Bonaparte, 1975 as *Lagosuchus talampayensis*), from the Middle Triassic of Los Chañares, Argentina, an evolutionary stage is observed in the evolution of the presacral vertebrae that is primitive compared with that of Prosauropoda, but very derived compared with that of other thecodontians such as *Euparkeria* (Ewer, 1965), *Ornithosuchus* (Walker, 1964) or *Riojasuchus* (Bonaparte, 1969).

In *Marasuchus* three types of presacral vertebrae are very clearly differentiated: a) anterior cervicals; b) anterior cervicals and posterior dorsals; and c) middle and posterior dorsals. This zonation probably had to do with the beginning of the lengthening of the neck, within a general 'S'-shaped plan, that would have conditioned the great versatility in that part of the skeleton of these archosaurs, possibly linked to or resultant from the bipedal posture that was already at an advanced stage in *Lagosuchus* and *Marasuchus*.

DESCRIPTION

The presacral vertebrae of *Marasuchus* mentioned by Bonaparte (1975, figures 5-7), illustrated here in figure 2, show the following morphological types: 1) anterior cervical vertebrae somewhat higher than long, with a marked angle at the ends of the vertebral centra, and anteriorly extensive prezygapophyses; 2) relatively short, tall posterior cervical and anterior dorsals, and axially short and anteriorly bowed neural spines; and 3) middle and posterior dorsals with vertebral centra somewhat lengthened, not very anteriorly extended prezygapophyses; laminar and axially-extended neural spines, with an anteroposterior constriction at their base, and little separation between the spines of contiguous vertebrae.

The anterior and posterior sides of the cervical vertebral centra are mainly amphiplatyan in *Marasuchus*, contrary to the Prosauropoda that are markedly amphicoelous, a topic of interest that is discussed later.

The first vertebral type of *Marasuchus* corresponds to the anterior cervical vertebrae, (figure 2A). They measure about 7 mm long and present the extensive posterior fossa of the vertebral centra clearly behind the area occupied by the diapophyses-parapophyses, and at the level of or below the diapophyses. This position of the posterior fossa of the vertebral centrum suggests that it would have been occupied by hypaxial musculature, probably the *m. longus capitis* and *m. longus colli*.

Still, although the posterior fossa of the cervical vertebral centrum of *Marasuchus* is comparable to that present in prosauropods, functionally its position relative to the diapophyses and parapophyses is different, as is its dorsoventral development. Whereas in prosauropods the cited fossa is between the diapophyses and the parapophyses, from the anterior border of the centrum until near the posterior border, and is dorsoventrally low, in *Marasuchus* the fossa is behind the diapophyses and parapophyses, high dorsoventrally, and begins far from the anterior border of the centrum.

These differences suggest that *Marasuchus* possesses cervical centra with different characters than those present in prosauropods, and that it possibly does not represent a potential ancestor of them. This interpretation seems to be confirmed by the forward inclination that the neural spines of *Marasuchus* show in cervicals 7 and 8 (Sereno and Arcucci, 1994), a primitive character registered among Prosauropoda.

The second vertebral type of *Marasuchus* includes cervicals 7 and 8 and the two anterior dorsals. They are anteroposteriorly short, high and with axially brief neural spines, that is to say morphologically adapted so that the neck carries out wide dorsoventral movements. In the anterior dorsals it is possible to observe an incipient infradiapophyseal fossa, probably the central one. A type of functionally comparable vertebra, although of more derived morphology, is in cervical 10 and dorsals 1-3 of *Plateosaurus*, and cervical 9 and dorsals 1 and 2 of *Riojasaurus*, which could indicate that the region of the base of the neck moved back in the prosauropods starting from a situation comparable to that in *Marasuchus*.

The mid and posterior dorsals of *Marasuchus*, which correspond to the third vertebral morphotype mentioned above, are proportionately low, somewhat lengthened, and have an axially extensive neural spine. This last character would limit the dorsoventral flexion of that

region of the spine. In *Plateosaurus* and *Riojasaurus*, starting from number 7-8 the laminar neural spine begins to have an approximate extension of 80-85% of the length of the vertebral centrum, exceeding 90% in some individuals of *Riojasaurus*, and in *Marasuchus* it is bigger still. In such a way we can conclude that *Plateosaurus*–*Riojasaurus* has reduced the axial extension of the neural spine relative to the existing proportions in *Lagosuchus*, which would have conferred greater dorsoventral flexibility to the dorsal region of the spine.

In *Marasuchus* the centra of the dorsal vertebrae are laterally concave, with a more depressed region of that surface, a condition comparable to that observed in Prosauropoda.

For the neural arch of the dorsals of *Marasuchus*, only in the two more anterior is an incipient central infradiapophyseal fossa appreciated, lacking the remaining fossae that are characteristic of *Plateosaurus* (Huene, 1907-1908). In the mid and posterior dorsals of *Marasuchus* infradiapophyseal fossae are not observed. In *Riojasaurus* the three infradiapophyseal fossae are present only in the first dorsals, and the prezygapophyseal-diapophyseal lamina are lacking toward the mid and posterior dorsals. On the other hand, in *Plateosaurus* the three fossae are present in all the dorsals, except in just the last two. They are: a central, which is the most primitive, an anterior one, and another posterior one, representing a group of characters markedly more derived than in *Marasuchus*. Here it is important to point out that the condition in the melanorosaurid *Riojasaurus* is more primitive than in *Plateosaurus*, because only it shows the central and posterior infradiapophyseal fossae in most of the dorsals, due to the lack of development of the prezygapophyseal-diapophyseal lamina, which defines to the anterior infradiapophyseal fossa.

I consider that the vertebral anatomy of *Marasuchus* is significant for this study for the morphological references that it gives, and that they illustrate an ancestral stage of vertebral organization.

As for the presacral vertebrae of *Lagerpeton* Romer (1971), we know very little of them. Sereno and Arcucci (1994) referred 9 posterior dorsal vertebrae to *Lagerpeton* but they did not describe them or figured them in detail, although they mentioned that they possess anteriorly bowed neural spines.

For what is appreciated in Sereno's schematic reconstruction (Sereno and Arcucci, 1994, figure 5A) are proportionally short and dorsoventrally high vertebrae, with the neural arch approximately twice the height of the vertebral centrum. The neural spines seem to be laminar, anteriorly bowed, and have parallel anterior and posterior borders. It seems clear that the posterior dorsals of *Lagerpeton* possess very derived spines, with wide surfaces for the insertion of the epaxial muscles.

Obviously *Lagerpeton* is more derived than *Marasuchus* in its dorsal vertebrae, and as Sereno and Arcucci have pointed out (1994), it presents an unique vertebral model among Triassic archosaurs. The great difference in the morphological type of the mentioned vertebrae of *Lagerpeton* and *Marasuchus* suggests that besides representing very different adaptative types, these taxa correspond very probably to different dinosauiromorph families.

If we summarize the information of the presacral vertebrae of these basal dinosauiromorphs, we see that in the case of *Marasuchus*, the oldest appearance of three vertebral morphotypes is manifest in the presacrals of an archosaur. This derived condition is associated with diverse primitive characters of the neural spines of the mid and posterior dorsals, as is its great anteroposterior development and its laminar character, as well as the incipient beginning of some of the infradiapophyseal fossae, present only in the two more anterior dorsals. In such a way, the morphologic distance between *Marasuchus* and prosauropods is very marked, in some aspects with more primitive characters, such as the inclination of the neural spines in the cervicals (Sereno and Arcucci, 1994), and the different position and relationships of the posterior fossa in the centra of the above-mentioned

vertebrae, suggesting that *Marasuchus* would not have been directly linked to the origin of prosauropods.

THE PRESACRAL VERTEBRAE OF *RIOJASAUROS* AND *PLATEOSAURUS*

The vertebral type of Prosauropoda is not uniform, because it is possible to recognize three organization levels previous to the sauropod condition. The most primitive is present in the melanorosaurid *Riojasaurus* Bonaparte (1969), continues to the level of organization present in *Plateosaurus* Meyer (1837), and finally to the case of *Lessemsaurus* gen. nov., from the Los Colorados Formation, which it is described and compared further on. I should point out that it has not been possible to acquire useful information for studying the presacral vertebrae of the primitive prosauropods of the families Thecodontosauridae and Anchisauridae (Galton, 1973, 1976, 1990), still this author has presented good illustrations, although of isolated or incomplete regions of the spine.

The remaining interpretation regarding the 3 organization levels mentioned is based on the presence of 9 cervicals in *Riojasaurus* and 10 in *Plateosaurus*. Also, there are differences in the number of vertebrae of the cervical morphological type present in one or another genus. In *Riojasaurus* only 6 vertebrae of the cervical type are observed, as the remaining 3 cervicals are more similar to the dorsal type. On the other hand in *Plateosaurus* 9 vertebrae of the cervical morphological type are observed, and only the last one coincides more with the dorsal type. Also the presence or absence of the prezygapophyseal-diapophyseal lamina in these genera suggests that *Riojasaurus* is more primitive than *Plateosaurus*, because in the first one the development of that lamina is very incomplete and the anterior infradiapophyseal fossa is not defined.

Finally in *Lessemsaurus* gen. nov. is observed, among other details, a great development of the neural spine of the dorsals, which is a more derived condition than in *Riojasaurus* and *Plateosaurus*. In such a way the three levels of vertebral organization are represented, progressively, by *Riojasaurus*, *Plateosaurus* and *Lessemsaurus*.

PRESACRAL VERTEBRAE OF *RIOJASAUROS*.

The holotype of *Riojasaurus incertus* Bonaparte (1969, 1972) possesses a great part of the presacral vertebrae, for which the description was based mainly on that individual, but aided by a specimen of the Museo de la Universidad Nacional de La Rioja, MPLR 56, that possessed most of the presacral vertebrae articulated to each other and with the skull (Bonaparte and Pumares, 1995).

I have referred to other individuals from the Fundacion-Instituto M. Lillo, collected by the author and assistants between 1965 and 1975.

Differences in proportions are appreciated among the vertebrae of the different individuals studied, partly because they correspond to individuals of different sizes and partly due to allometric phenomena in ontogenetic development. It is not unlikely that certain heterocronic phenomena have differentially influenced the ontogenetic development of the presacral vertebrae of *Riojasaurus*, which we could understand in the mature individuals such as the holotype, the neural arch of the anterior dorsals is sensibly lower than the vertebral centrum. On the other hand in a smaller individual, MPLR 56, the mentioned relationship is inverted, presenting a neural arch higher than the vertebral centrum. This is probably a derived character present in immature individuals that gets lost in the mature state, which is known as peramorphic phenomenon (McKinney and McNamara, 1991).

On the contrary, the proportional length of the cervical vertebrae is greater in the holotype of *R. incertus* than in smaller individuals of the same species, suggesting that the derived condition of this character was accentuated in the mature state, which would be the

well-known process of hypermorphosis (McKinney and McNamara, 1991)

The total number of presacral vertebrae in *Riojasaurus* was estimated as 25 by Bonaparte (1972), but there is not certainty in this respect. Recent observations indicate us that it possessed 9 cervicals, excluding the preatlas.

Cervicals. In specimen UPLR 56 the complete sequence of cervical vertebrae was present, from the preatlas to the first dorsal (sadly lost by a robbery in 1991). We see in this way that the number of cervicals is 9 and that the morphological type of axially long and lower vertebrae is present only in the axis and the 3 successive vertebrae, and from there back cervicals 6-9 are proportionally higher than long, that is to say more similar to the dorsal type.

In the holotype of *Riojasaurus*, assuming that it possessed 9 cervicals, the morphological type of low cervical is present up to the 6th cervical inclusive, that is to say one vertebra more than in UPLR 56.

Anterior cervicals. In the holotype (figure 6A-C) these vertebrae are low, lengthened, “amphicoelous”, with modest manifestation of the diapophyses and parapophyses, and a posterior fossa on the not very marked centrum. Up to the 5th cervical the diapophyses do not possess a hanging lamina, neither do infradiapophyseal laminae or fossa exist.

Mid- cervicals. The 6th cervical preserves the low and lengthened morphological type (figure 7A) and shows the beginning of development of the not very apparent diapophyseal lamina, without infradiapophyseal laminae.

Posterior cervicals. The 8th and 9th cervicals (figure 7B-C) show proportions of the dorsal type, of length equal to (8th) or greater than height (9th). They are of “amphicoelous” type, with marked posterior fossa of the centrum, with a hanging diapophyseal lamina, but they do not possess infradiapophyseal laminae. In the 9th cervical the diapophyseal-postzygapophyseal lamina is defined, and also partially the diapophyseal-prezygapophyseal lamina.

The cervicals of *Riojasaurus* are more derived than those of *Marasuchus* as evidenced by the long, low type of cervical vertebrae, as well as by the posterior fossa of the centrum, the definition of the diapophyseal lamina, and the infrapostzygapophyseal fossa. But they are less derived than those of *Plateosaurus* by the lesser definition of the diapophyseal lamina, the lack of an infradiapophyseal lamina, the smaller number of cervical vertebrae, and the smaller transverse development in the upper part of the neural spine.

Dorsals. For the description and evaluation of the dorsals I have taken those of the holotype specimen, also with the comparative aid of other existing individuals in the collection of the Fundacion-Instituto M. Lillo of Tucumán. Regrettably we do not know the exact number of these vertebrae in *Riojasaurus*, but in a small individual of the mentioned collection, PVL s/n (of collection), it presents 14 dorsals.

Anterior dorsals. In the holotype the first dorsal is complete. It possesses a very low neural arch (figure 7D), only representing 2/5 of the total height of the vertebra. In *Plateosaurus* the neural arch of this vertebra occupies more than the height of the vertebra.

The diapophyses are strong, and possess the two infradiapophyseal laminae up to the 5th. In a small individual, with a first dorsal 6 cm long, the infradiapophyseal laminae are present from the 1st to the 6th, which suggests a reversal of that character in mature individuals.

The neural spine of the 1st is anteroposteriorly brief and presents a transverse expansion in its dorsal end, with 4 different places for ligament insertions, comparable to what is observed in *Plateosaurus* (figure 10E).

Mid- and posterior dorsals. In these vertebrae the neural arch is proportionally

higher than in the anterior dorsals, occupying somewhat more than half of the total height of each vertebra (figure 8). In the 5th the neural spine is already laminar, and somewhat more extensive anteroposteriorly than dorsoventrally.

The diapophyses possess the two infradiapophyseal laminae, but the diapophyseal-prezygapophyseal lamina does not reach the prezygapophyses. In the 9th the laminar neural spine is more extensive anteroposteriorly. The general aspect of the posterior dorsals indicates that they are of heavier and more solid construction than in *Plateosaurus*, with less posteriorly excavated centra, and less marked laminae and fossae of the neural arch.

Comparisons and possible origin of prosauropods. In general the presacral vertebrae of *Riojasaurus* differ clearly from those of *Plateosaurus* in having various more primitive characters, pointed out above. In this sense it seems certain that the Melanorosauridae represents an earlier evolutionary stage than the Plateosauridae, as much for the evidence that we analyze here, as for the cranial anatomy (Bonaparte and Pumares, 1995).

The comparison of the presacral vertebrae of *Riojasaurus* with those of *Coelophysis bauri* (Cope, 1889; Colbert, 1989) offers some interesting hints if we try to look for a possible ancestral morphological type. The cervicals of *Coelophysis* possess more derived characters such as the presence of hanging diapophyses on the anterior cervicals, a defined posterior fossa of the vertebral centrum, defined infraprezygapophyseal and infrapostzygapophyseal fossae, and a greater number of cervical morphotype vertebrae. But the situation is different for the anterior and posterior dorsals.

In *Coelophysis* the anterior dorsals (Colbert, 1989, figure 53) are basically similar to those of *Riojasaurus*, with a low neural arch, two infradiapophyseal laminae, and poorly-defined prezygapophyseal-diapophyseal and diapophyseal-postzygapophyseal laminae, less developed than in *Riojasaurus*.

In the posterior dorsals, those of *Coelophysis* are more primitive than those of *Riojasaurus* in the total absence of infradiapophyseal laminae, and the lack of a wide infrapostzygapophyseal fossa. Still, although the centra of these dorsals are longer in *Coelophysis*, the structure of the neural arch and the characters of the ventral border of the centrum are more derived in *Riojasaurus* than in this primitive ceratosaur. I believe that it is an interesting possibility that primitive Triassic ceratosaurs were involved in the differentiation of primitive prosauropods.

PRESACRAL VERTEBRAE OF *PLATEOSAURUS*

The study of the presacral vertebrae of *Plateosaurus* Meyer (1837) was carried out on an exceptionally well-preserved specimen in the paleontological collections of the Museum für Naturkunde, Humboldt Universität, Berlin, MBR.2090 that came from the proximity of Albertstadt, Germany.

In *Plateosaurus* a notable development of the cervical vertebral morphotype of the of the neck is observed, with length-height ratios of 2:1 up to the 7th cervical, and the presence of 10 cervical vertebrae. Besides the strong changes in the proportions of the cervicals, we also see remarkable changes in their morphology when we compare them with the pattern present in *Riojasaurus*, and still more with that of *Marasuchus*.

Cervicals. In the anterior and posterior area of the vertebral centrum a wide amphicoely has been developed, not present in *Lagosuchus*, and that could with difficulty be considered a plesiomorphic feature or a reversion to a primitive character. My interpretation of this character is that it is incipient opisthocoely in which the posterior face of the vertebral centrum shows a wide cavity for articulation, and the anterior, less concave face harbored a cartilaginous condyle that fit snugly into the preceding vertebra. This interpretation includes

up to the last cervical, where there are good indications of this.

In the posterior area of the vertebral centrum, besides the lengthening of the centra, the development of a longitudinal fossa is manifest starting from the axis (figure 9) and increasing back. In the axis it is only a shallow furrow, well framed by edges; in the 3rd vertebra the fossa is located between parapophyses and diapophyses, very near the anterior border of the centrum. In the 5th vertebra it is rather larger and has moved to a somewhat more dorsal position. In the 7th (figure 10), the width of this posterior fossa is noticeably greater and extends dorsally below the hanging diapophyses. In the 9th cervical the fossa diminishes in its posterior extension, and in the 10th it is very diminished by the very dorsal position of the parapophyses; in the 1st dorsal it is practically nonexistent.

This posterior fossa is developed above the parapophyses and below the diapophyses, which differs markedly from *Marasuchus* in which the fossa is behind those processes and has a strong dorsoventral development. These differences could be significant enough to exclude *Marasuchus* from an ancestral position.

The mentioned fossa probably corresponded to places for the origination and insertion of the musculature that contributed to the posterior movements of the neck and skull. Their virtual disappearance in the 1st dorsal (figure 10E) suggests that it would have been fundamentally cervical musculature, and their position partly below the cervical ribs allows hypothesizing that it would have corresponded to a package of hypaxial muscles, possibly the system of the *m. longus capitis*.

It is evident that the lengthening of the cervical vertebrae among prosauropods was accompanied by an increase in the hypaxial musculature (and naturally epaxial) that conditioned the development of the posterior and ventral fossae of the vertebral centrum in the cervicals.

The ventral face of the cervical vertebral centra is very concave in *Plateosaurus* and show, among cervicals 4-9, an anteroposterior concavity located medially to the parapophyses. In *Coloradisaurus* (Bonaparte, 1978, 1984) a very defined ventral keel is present. Probably the ventral fossa of the cervicals, like the mentioned concavity and keel, was occupied by musculature of the *m. longus capitis* system for producing ventral movements of the neck and head.

In the posterior area ahead of the postzygapophyses, *Plateosaurus* shows a particular elaboration starting from cervical 9 back, in which a modest small fossa is manifest posterior on (figure 10C). In cervical 10 the small fossa is wide enough and penetrates forward below the base of the diapophyses. This character is wide in the dorsal vertebrae and constitutes the posterior infradiapophyseal fossa that is present in all the dorsals. It is a feature characteristic of the dorsals and begins, reduced, in cervical 9. In sauropods this character progresses to reach the axis cranially, and gave place to the formation of the diapophyseal-postzygapophyseal lamina.

Marasuchus shows the primitive condition because this central infradiapophyseal fossa is not defined in the dorsals, whereas in *Riojasaurus* it is manifest in the 1st dorsal. It seems logical to suppose that this fossa was occupied by musculature, and that it would connect that region of the vertebrae with the anteroposterior region of the subsequent vertebra, located behind. When placing the vertebrae of *Plateosaurus* in articular sequence, that relationship is presented as very probable. The musculature involved in this character extended for all the dorsals of *Plateosaurus* and would have ended at cervical 9. But because the character extends up to the axis as in sauropods, I believe that the interpretation that the musculature and the bony feature extended forward starting from a similar condition to that of *Plateosaurus* is reasonable.

In the posterior area behind the prezygapophyses a development has occurred parallel

to that exposed in the anterior area, because in cervical 9 (figure 10C) a small fossa appears from behind of the base of the prexygapophyses that increases in size in cervical 10 and is prolonged back until number 8. In *Riojasaurus* the character is present but with less development, because it is not observed in the mid and posterior dorsals.

The mentioned character is present in *Diplodocus* (Hatcher, 1901) and other sauropods up to cervical 3, and their historical development has probably been the same as that for the anterior character, that is to say it advances cranially starting from its fundamentally dorsal position in prosauropods. The functional relationship of these characters is evident, and I believe that the same epaxial musculature would have been involved, possibly the *m. longissimus* system.

In the posterior area we see that the development of the hanging diapophyseal lamina that one observes clearly starting from cervical 7 of *Plateosaurus* (figure 10A) has given place to the formation of a posterodorsal surface, which increases in size until the last cervical. That surface was accompanied by the definition of the diapophyseal-prezygapophyseal and diapophyseal-postzygapophyseal laminae, which acquired great development in sauropods.

Also starting from cervical 7 of *Plateosaurus* a dorsoventrally depressed area is manifest in the vicinity of the neural spine that defines, in cervicals 9 and 10, a dorsally-exposed plane that is distinguished from the dorsolateral diapophyseal surface. Both planes are limited by an edge that runs from the prezygapophyses back (figure 10C-D) up to the dorsal area of the postzygapophyses. It is probable that both areas were occupied by two epaxial muscular packages, one of dorsal position for dorsal movements of the neck and the remaining one for posterior movements. Their clear manifestation in the last 4 cervicals of *Plateosaurus* could be the result of the existence of a very marked musculature in the basal section of the neck, which diminished in volume in association with the occipital region of the skull.

In dorsals 1, 2 and following, the diapophyseal surface is smaller and is not exposed dorsolaterally but dorsally.

In the cervicals of *Plateosaurus* very marked changes are manifest in the morphology of the neural spines, related to the functional aspects of a neck of remarkable length and surely of efficient maneuverability.

In *Marasuchus* the neural spines are also of varied morphology, but with marked differences from Prosauropoda. In the anterior cervicals they are somewhat lengthened anteroposteriorly and inclined back, whereas in the posterior cervicals they are short and bowed forward. There are appreciable differences, partly corresponding to different adaptations, partly to different degrees of derivation. Truly the cervicals of *Marasuchus* do not support the hypothesis of its ancestry to prosauropods, which can be intended according to the morphology of the mid and posterior dorsals, or starting from some characters of the pelvis, or especially for the organization of the hind limb.

Up to cervical 7 of *Plateosaurus* the neural spines are laminar, low, anteroposteriorly lengthened, and located on the posterior half of the vertebral centrum, that is to say with quite a greater distance between the spine and the anterior border of the vertebral centrum than between the spine and the posterior border of the centrum. Their height increases gradually back, from 1 cm in cervical 3 to 2 cm in cervical 7. From cervical 8 to 10 (figure 10B-D) the neural spine shows an anteroposterior reduction at the same time as it achieves greater height and width in its superior end.

As seen in figure 10, the dorsal view of the spine reveals the presence of four areas of ligamentous insertion that, starting from cervical 8, decrease anteroposteriorly and expand transversely, achieving its maximum expression in cervical 10 and dorsal 1. Back from this

point the character reverts gradually to laminar spines.

These morphological changes of the neural spines of *Plateosaurus* are, probably, developments of certain functional aspects that I consider of importance. The distance among the neural spines is, generally, greater than the length of one of them, which suggests the presence of long interspinal ligaments, and consequently the capacity for good extension and contraction. The transverse development of the upper part of the spine and their four areas of subequal muscular insertion in the posterior cervicals and dorsal 1, suggests a good capacity for posterior movements next to dorsoventral. The posterior movements should also exist in the anterior part of the neck, but the musculature involved would have been smaller than in its basal region, simply to be in that more graceful region.

The prespinal area is very well defined in the cervicals of *Plateosaurus*, forming a triangular space with its vertex at the anterior base of the neural spine, and its posterior borders formed by the posterior edges that unite the spine with both prezygapophyses. The area of the vertex of this space is located somewhat below the anterior border of the spine where a fossa is formed. Their dorsoventral extension is appreciable, limited ventrally by the roof of the neural canal. This prespinal area is very developed in all the cervicals posterior to the axis, but decreases in cervicals 9 and 10, and more obviously starting from dorsal 4 back. The fossa was probably occupied by intervertebral epaxial musculature, bound by the postspinal region of the preceding vertebra. In the Cetiosauridae and more derived sauropod groups this fossa achieves a very marked development.

In the anterior circumneural region, *Plateosaurus* shows an initial development with the incipient formation of a circular fossa to each side of the neural canal. In sauropods, strong depressions or fossae are manifest in this region, e.g. in an anterior cervical of *Barosaurus africanus* from the collection of the Museum für Naturkunde, Berlin (figure 39C) that shows two wide, deep, subcircular posterior fossae dorsal to the neural canal, or in cervical 3 of *Brachiosaurus brancai* Janensch (1914) (figure 39D) that possesses these oblong fossae, diverging dorsally from the vicinity of the neural canal. These fossae could have harbored epaxial musculature of the *m. longissimus* system, possibly part of the *m. intertransversarii*.

The postspinal area forms a triangular space, with the vertex located forward, surpassing the posterior border of the neural spine. Its posterior limit forms the suprapostzygapophyseal laminae which unite to form the neural spine. In *Plateosaurus* it is present from the axis until the last cervical (figures 9 and 10). In the anterior cervicals it is less dorsoventrally deep than in the posterior ones. In dorsals 4, 5 and more posterior their volume decreases markedly. In *Marasuchus* the postspinal space is very reduced, perhaps representing the primitive condition. In Cetiosauridae and more derived sauropods this space is proportionally large where strong musculature would have been located. In *Plateosaurus* and sauropods, it marks where that musculature would have been bound to the prespinal region of the subsequent vertebra.

Dorsals. The dorsals of *Plateosaurus* are, in general, of relatively constant morphology, although remarkable changes are appreciated in detail. Among them the variation shows that in dorsals 1-3 the neural spines are transversely thick, with a wide dorsal end where 4 subequal areas are manifest for insertions (figure 10D-y). Further back, they increase their anteroposterior extension, reducing their transverse thickness to the point that in dorsals 7-8 they are laminar (figure 12), rectangular in posterior view, with the dorsal part of the spine axially extensive. The variation in the spine was probably conditioned to the different functions in which it participated. In the anterior dorsal region the flexibility of the spine would have been produced by multiple movements of the neck, whereas in the central and posterior dorsal regions it would have had less flexibility, possibly only movements

linked to locomotory undulations and other less frequent ones such as those of rising in the hind limbs.

With the most dorsal position in the diapophyses (and parapophyses) in dorsal 1, the two infradiapophyseal laminae are exposed very well in posterior view, which in turn form, next to the zygapophyseal laminae, three deep fossae that vary along the dorsals. In dorsal 4 the central infradiapophyseal fossa is observed, which is a primitive character present in diverse archosaurs. It is constant in all the dorsals of *Plateosaurus* but with detailed modifications, especially in the place occupied by the diapophyses, moving slightly forward as it approaches the sacrum.

From behind that fossa is the posterior infradiapophyseal fossa which is also a primitive character; that fossa is deep and located in front of the postzygapophyses. Along the dorsals this fossa shows a certain reduction toward the sacrum.

Finally, in the anterior region of these vertebrae is the anterior infradiapophyseal fossa which is a derived character of prosauropods that is observed from dorsal 7, in which it is small, until dorsal 1, in which it is large, up to cervical 9, in which is very reduced.

In table 1 I have schematized the distribution of these infradiapophyseal fossae, probably used for epaxial (the anterior and posterior infradiapophyseal fossae) and hypaxial (central infradiapophyseal fossa) musculature, probably of varied function (e.g. to tie neighboring vertebrae (or not) to each other, to cooperate to the posterior movements, undulatory movements during the locomotion, and possibly breathing by means of movements of the ribs). Naturally that these fossae have a evolutionary meaning, representing a condition sensibly more derived than in *Marasuchus*, which practically does not possess either infradiapophyseal laminae or fossae. But the rauisuchid thecodontians, such as *Fasolasuchus* Bonaparte (1981) and *Saurosuchus* Reig (1959; Sill, 1974), possess two infradiapophyseal laminae in the posterior cervicals and anterior dorsals, but not the prezygapophyseal-diapophyseal lamina which defines the anterior infradiapophyseal fossa.

The infradiapophyseal fossae of *Plateosaurus*, well defined by the different laminae, suggest in their distribution along the spine that they were places for muscular insertion and origination. The same ones were increased in sauropods, as we see later on, to the greatest relative height in the posterior wall of the neural arch, as a result of greater muscular requirements imposed by the greater size.

The vertebral centra of the dorsals are compressed transversely, with a marked posterior fossa in the dorsal half of the centrum. The diameters of the anterior and posterior faces of the centrum are quite larger than the radius of the vertebral centrum, originating a wide fossa in the posterior and ventral faces where the musculature would have fit comfortably.

CHARACTERIZATION OF THE VERTEBRAE OF *PLATEOSAURUS*

The vertebrae of *Plateosaurus* can be characterized, in general terms, in the following manner. For the presacral vertebrae in their entirety:

1 – presacral vertebrae with 3 types well differentiated morphological: a) cervical anterior and low, lengthened stockings; with neural spines low, extensive laminar axially; b) posterior cervical and anterior dorsals as long as high; with neural spines axially brief and high, transversely expanded in their dorsal end; c) slightly higher posterior dorsals that you release (ratio 7/5), with laminar neural spine shorter than the vertebral centrum. The following things can be pointed out in more detail:

Anterior and mid-cervicals. Low and lengthened vertebrae, with width/height ratio at 2/1. Vertebral centra with posterior fossa vestigial in cervical 2, to very developed in cervical 7 and posterior. Lamina of the diapophyses vestigial in cervical 5, increasing their development toward cervical 10. Neural spines laminar, very low until cervical 4, and

increase of height until cervical 10.

Posterior cervicals. Increment of height and reduction anteroposterior among cervicals 7 and 10. Strong ventral and posterior concavity of the centrum. Increase in the posterior surface of the lamina of the diapophyses, and of the infradiapophyseal fossa. Definition of 4 areas for inserts in the dorsal end, expanded transversely, of the neural spine. Definition of an exposed surface dorsally in the posterior base of the neural spine.

Anterior dorsals. Slightly longer vertebral centra that high, forming an angle between the posterior face and the most ventral points in the centrum of approximately 78°. Posterior and ventral depressions of the marked centrum. Arch same or slightly higher neural than the vertebral centrum. Lamina exposed diapophyseal dorsally. Infradiapophyseal fossae (anterior, central and posterior) very defined by thick laminae. Neural spine anteroposteriorly brief, it lowers, with transverse expansion in the upper end in number 1 that decreases toward the mid dorsals.

Mid- and posterior dorsals. Size relationship between the centrum and the neural arch like in the anterior dorsals, but with an angle of approximately 90° between the faces of the centrum and its lower borders; amphiplatyan. The anterior infradiapophyseal fossa decreases in number 7 and disappears 10 due to dorsal migration of the parapophyses. Its neural spine is laminate, lower (less than 1/3 of the total height of the vertebra), and anteroposteriorly extensive (7/8 to 6/7 of the length of the centrum).

PRIMITIVE SAUROPOD-TYPE VERTEBRAE

We consider vertebrae from the primitive sauropod type of sauropodomorphs to have overcome the condition of *Plateosaurus* in the ratio between the height of the neural arch: height of the vertebral centrum, but that they are less derived than in the "cetiosaurid" type. They are characterized as presenting a higher neural arch than in *Plateosaurus*, with neural spines markedly higher than long, still laminar or sublaminar in the mid and posterior dorsals but with dorsoventral furrows.

The recognition of this level of vertebral organization is based on a series of materials coming from 1) the upper part of the Los Colorados Formation, Upper Triassic, of the Prov. of La Rioja, 2) the Bathonian of Madagascar, and 3) the Cañadón Asfalto Formation, Callovian of Chubut Prov. These materials correspond to the holotype of *Lessemsaurus sauropoides* gen. et sp. nov., PVL 4822, that it is described in this work, to the holotype of *Lapparentosaurus madagascariensis* (Bonaparte, 1986b), and to the holotype of *Volkheimeria chubutensis* (Bonaparte, 1979, 1986a) respectively.

SPECIMEN PVL 4822

This is a group of materials corresponding to 3 prosauropod specimens of considerable size, but with size differences among them that allows me to infer which vertebrae correspond each one of them. These materials include cervical vertebrae, dorsals, sacrals and caudals, as well as various bones of the girdles, fore- and hind limbs, even pieces of the mani and pedes that leave no doubts as to their prosauropod ownership. They were collected in 1971 during a paleontological expedition carried out by the Fundación M. Lillo of Tucumán and financed by CONICET, directed by the author and with the participation of technicians Messrs. M. Vince, J. C. Loyal and T. H. Fasola. They come from the same levels from which abundant materials of aetosaurs, ornithosuchids, melanorosaurid and plateosaurid prosauropods (Bonaparte, 1972; 1978), rauisuchids (Bonaparte, 1981), turtles (Rougier et al., 1995) and theropods (Bonaparte, 1972; Arcucci and Coria, 1997) have been found. Two vertebrae corresponding to individuals included in PVL 4822 were mentioned and figured by Bonaparte (1986b), to illustrate a primitive stage in the development of sauropod vertebrae.

The smaller individual of the three mentioned above (PVL 4822-1) is described and compared next, in order to formalize this Triassic taxon which represents a systematically very derived evolutionary stage in the evolution of the morphological types of vertebrae between prosauropods and sauropods.

Prosauropoda Huene 1920

Melanorosauridae Huene 1929

Lessemsaurus gen. nov.

Etymology. In honor of Donald Lessem, founder of The Dinosaur Society, from the USA.

Diagnosis. Prosauropod larger than *Riojasaurus*, with the mid and posterior cervical vertebrae and available dorsals with higher neural arches than in other prosauropods. Mid and posterior cervicals with strong transverse infrapostzygapophyseal constriction, deep postspinal fossa, and high infrapostzygapophyseal fossa. Mid and posterior dorsals with neural spines higher than wide, with a ratio of 1.5-2 (height) to 1 (width).

Lessemsaurus sauropoides sp. nov.

Etymology. *sauropoides*, like sauropods, to stress that the morphology of its presacral vertebrae recalls that of primitive sauropods.

Holotype. PVL 4822-1, a group of presacral vertebrae and sacrals represented by 3 cervical neural arches and 3 separate cervical vertebral centra; 14 dorsal neural arches; 2 sacral neural arches, and numerous dorsal vertebral centra. This material is probably associated with some elements of the girdles or appendicular skeleton that it has not been possible to identify, for the time being, among the group of 3 individuals of different sizes numbered PVL 4822.

Diagnosis. The same as for the genus.

Locality and Age. Paraje la Esquina, Dept. Independencia, southwest La Rioja, Argentina, in the environment of the Upper Triassic of Ischigualasto-Villa Union, about 8 km west of provincial route 26, km 142. Upper part of the Los Colorados Formation, about 150 meters below the contact of that unit, Coloradian Reptile Age, (Bonaparte, 1973), approximately equivalent to upper Norian.

DESCRIPTION

Posterior cervicals. There are two neural arches corresponding to posterior cervicals, and a third that I interpret with doubts as from the last one cervical. The first ones are proportionally high (figure 13A, B), with the zygapophyses in a high position, far from the union between the neural arch and the vertebral centrum. This high position of the zygapophyses gives place to the presence of a wide infrapostzygapophyseal space where a marked supraneural constriction is defined in posterior view (figure 13A1, B1), characteristic of diverse sauropods (*Patagosaurus* Bonaparte (1979), *Diplodocus* Marsh (1878), *Camarasaurus* Osborn and Mook, (1921) etc.) but not registered among typical prosauropods such as *Plateosaurus* Meyer (1837) and *Riojasaurus* Bonaparte (1969). This constriction, less marked than in the cervicals of sauropods, represents the beginning of an important character in the evolution of the cervical vertebrae.

The neural spine is high and vertical in its anterior face, with marked, high postspinal laminae that unite the spine with the postzygapophyses, forming a wide postspinal fossa. These big postspinal laminae are also characteristics of Jurassic sauropods, whereas in prosauropods they are invariably less developed. In the diapophyses of these neural arches the two infradiapophyseal laminae clearly present in *Plateosaurus* are not observed. The lack

of these characters, present only in the first dorsals, seems to be a good argument for considering *Lessemsaurus* more closely linked to the melanorosaurid *Riojasaurus*, a genus that also shows a poor development of these laminae, than to the plateosaurid *Plateosaurus*.

Anterior dorsals. The first dorsal (figure 14A), which possibly could also be the 2nd dorsal, shows a strong, horizontally-directed diapophysis. It possesses the two infradiapophyseal laminae, thick and blunt, besides the diapophyseal-postzygapophyseal laminae and a brief diapophyseal-prezygapophyseal lamina. The infrapostzygapophyseal fossa is wide and high, with the postzygapophyses in a very high position, a character that is different from typical prosauropods.

The neural spine is high and transversely thick, with a wide interpostzygapophyseal fossa. The height of this neural spine is, surely, greater than the height of the vertebral centrum, which represents proportions common among the diverse Jurassic sauropods, whereas among typical prosauropods it is the inverse. These neural arches of *Lessemsaurus* are more derived than in typical prosauropods by their greater posteroventral development of the infradiapophyseal part of the arch, the wide fossa posteroventral to the infrapostzygapophyseal region, and the increase in the thickness and height of the neural spine.

Surprisingly, in these anterior dorsals there is a full development of the prezygapophyseal-diapophyseal laminae, is a character not observed that is present in *Plateosaurus* between dorsals 1 and 7. The poor development of that character, which happens also in *Riojasaurus*, suggests that it is a primitive feature of the Melanorosauridae and *Lessemsaurus*. This would represent a mosaic evolution of the neural arch, in which derived characters in *Plateosaurus* (diapophyseal-prezygapophyseal lamina) took place in primitive neural arches (provided with low neural spines); whereas in *Lessemsaurus* high neural arches were developed but with the mentioned lamina not very apparent.

Mid- and posterior dorsals. In these vertebrae (figures 15 and 16) the marked posteroventral development of the neural arch remains, as much the infradiapophyseal region as in the neural spine.

The diapophyses goes somewhat dorsally, in such a way that in posterior view its ventral region is observed. The infradiapophyseal laminae remain, but the anterior one is affected by the very dorsal position of the parapophyses. In the mid-posterior dorsals, due to the dorsal and anterior displacement of the parapophyses, the anterior infradiapophyseal lamina decreases in length and raises to a more dorsal position, changes that seem to already affect to the reduced prezygapophyseal-diapophyseal lamina, which atrophies and disappears (figure 16).

The neural spine is laminar, extensive, and axially wide dorsoventrally, slightly briefer axially than the vertebral centrum. As can be appreciated, although the dorsoventral extension is a derived character, in *Lessemsaurus* it is associated with the plesiomorphic feature of marked axial extension, not less than 90% of the length of the vertebral centrum. The postzygapophyses are mostly horizontal and present well-developed hyposphenes.

In the two remaining individuals of *Lessemsaurus sauropiodes* included in PVL 4822, diverse mid and posterior dorsal vertebrae have been preserved, as well as complete sacra, that allow us to appreciate their proportions completely. All are high vertebrae, provided with laminar spines higher than long, without a prezygapophyseal-diapophyseal lamina, with appreciable extension of the neural arch below the diapophyses (see figure 16), and vertebral centra with marked posterior and ventral fossae.

The ratio of the height of the centrum to the height of the neural arch is 1:2 in *Lessemsaurus*, whereas in *Plateosaurus-Riojasaurus* it is from 1:1 to 1:1.2.

LAPPARENTOSAURUS BONAPARTE, 1986

The holotype material of *Lapparentosaurus madagascariensis* Bonaparte (1986b), (figure 17C) consists of 2 neural arches of posterior dorsals that, although basically comparable to those described for *Lessemsaurus* gen. et sp. nov. in the proportions and characters of their neural arches, they include some derived characters that are not present in that Upper Triassic material. *L. madagascariensis* is from the Bathonian, and it shows the well-developed prezygapophyseal-diapophyseal lamina, and consequently the anterior infradiapophyseal fossa is present; the suprapostzygapophyseal laminae are very developed in the posterior view of the neural spine; this forms a wide dorsoventral fossa in each of their posterior faces, which would correspond to a derived character not present in *Lessemsaurus* gen. nov., and finally the neural spine is thick and sublaminar, not laminar as in that genus.

VOLKHEIMERIA BONAPARTE, 1979

Regrettably cervical vertebrae are not known in the very conservative *Volkheimeria* Bonaparte (1979, 1986a) from the Callovian of Patagonia, but complete dorsal neural arches are (figure 17A, B). In these an extensive neural spine is observed with two dorsoventral fossae in each of the posterior faces, and a marked edge between both fossae, with a modest widening. This spine model is more derived morphologically than in *Lessemsaurus* gen. nov., and somewhat more derived relative to *Lapparentosaurus*, suggesting a previous morphological stage to the cross-section of the spine of the “cetiosaurid” type. As for the sector of the neural arch below the zygapophyses, it is comparable to that of *Lapparentosaurus*, that is to say comparable also to that shown in *Lessemsaurus*, but less developed dorsoventrally than in *Patagosaurus* (“cetiosaurid”-type). *Volkheimeria* has a well-developed prezygapophyseal-diapophyseal lamina, with a deep anterior infradiapophyseal fossa.

It is evident that *Lessemsaurus* gen. nov., *Lapparentosaurus* and *Volkheimeria* show similar proportions in the dorsoventral development of the neural spine and in the region of the neural arch below the zygapophyses, which suggests that the volume of the epaxial and hypaxial musculature would have been comparable in these three taxa. Nevertheless, the great derivation in the neural spine and the presence of the prezygapophyseal-diapophyseal lamina in *Lapparentosaurus* and *Volkheimeria* indicate that mainly the epaxial muscles would have been more developed in these Jurassic genera than in *Lessemsaurus* from the Upper Triassic. On the other hand, the primitive sauropod type of vertebrae is obviously more derived than in *Plateosaurus*.

CHARACTERIZATION OF THE “PRIMITIVE SAUROPOD” MORPHOTYPE

Since regrettably we do not have anterior cervicals, the characterization of this type of vertebrae begins with the posterior cervicals.

Posterior cervicals. The neural arch is higher than in Melanorosauridae-Plateosauridae, with a marked infrapostzygapophyseal constriction. The postzygapophyses are located more dorsally, and the postspinal laminae that connect with the postzygapophyses are more dorsally extended than the supraprezygapophyseal laminae.

Anterior dorsals. The neural arch is higher than the vertebral centrum, approximately 2/3 of the total height of the vertebra, and brief anteroposteriorly, with the prezygapophyses and postzygapophyses next to each other. The neural spine is high, with a high, planar anterior face, and a posterior face with wide suprapostzygapophyseal laminae. They show a larger infrazygapophyseal space dorsoventrally than in Melanorosauridae-Plateosauridae.

Posterior dorsals. The neural arch is higher than in Melanorosauridae-

Plateosauridae, with the neural spine higher than long, with a widened transverse process, and incipient formation of dorsoventral furrows that begin to define a prespinal lamina.

These vertebral characters are obviously more derived than in Melanorosauridae-Plateosauridae (and probably than in all prosauropods except *Lessemsaurus* gen. nov.), and at the same time more primitive than in Cetiosauridae. Their complexity suggests the existence of adaptations for a more voluminous and complex epaxial musculature than in *Plateosaurus*. The dorsoventral widening of the posterior dorsal neural spines suggests the beginning of the morphological complexity present in the neural spines of the cetiosaurid level that is discussed later.

McIntosh (1990:348 and 383) considered *Volkheimeria* a brachiosaurid in his systematic list and text. The differences between the dorsal vertebrae of *Brachiosaurus* and those of *Volkheimeria* are of such magnitude that only considering that the vertebral types are capricious products, without systematic and phylogenetic meaning can these two genera meet in one family. It is enough to point out that all the dorsals of *Brachiosaurus* are strongly opisthocoelous, whereas in *Volkheimeria* they are amphiplatyan, and that the neural spines of *Brachiosaurus* have a +-shaped cross-section with a solid dorsal end, whereas in *Volkheimeria* they are laminar with a dorsoventral thickening, and without dorsal expansion.

The origin and small quantity of the materials on which the primitive sauropod type is based or recognized are not very satisfactory, especially because materials from the Upper Triassic and Lower Jurassic are gathered together. Nevertheless they are coherent in showing a specialization level intermediate between *Riojasaurus-Plateosaurus* and Cetiosauridae, at the same time that they are well differentiated from each of them.

It is possible that the vertebral morphology of typical prosauropods such as *Riojasaurus-Plateosaurus* have been an obstacle for the development of larger species, the reason for which prosauropods usually show medium sizes. Functionally, the explanation for this case is that the weak height of the neural arch could not harbor the necessary axial musculature for support of a thorax-abdomen of the volume present in primitive sauropods such as the Cetiosauridae.

The primitive sauropod morphological type seems to show the intermediate or transitional adaptative stage, with the development of higher neural arches, with a ratio of length:height in the posterior dorsal vertebrae of approximately 1:2.5, instead of the ratio of approximately 1:1 that characterizes the posterior dorsals of melanorosaurid-plateosaurid prosauropods.

“CETIOSAURID”-TYPE VERTEBRAE

The vertebrae of the “cetiosaurid” morphological type present a varied group of basic specialized characters that are retained, with modifications, in most of the more derived sauropods such as Diplodocidae, Camarasauridae, Brachiosauridae, Titanosauridae, etc., which in turn have developed their own characters in each case, overcoming the “cetiosaurid”-type in different manners, and reaching markedly giant sizes.

Besides the characters of vertebral morphology that define the “cetiosaurid”-type and represent a notable advance regarding the primitive sauropod type, there is an important derived character in the number of cervical vertebrae. This is 12-13 in *Patagosaurus* Bonaparte (1986a), and a similar number was probably present in *Barapasaurus* Jain et al., (1977), and *Cetiosaurus* Owen (1841), although we do not have evidence in this respect. This number of cervicals in *Patagosaurus* reveals a increase of 2-4 with regard to *Plateosaurus* and the melanorosaurid *Riojasaurus*, a phenomenon that corresponds to a progressive cervicalization of the dorsals among Sauropoda that, in the case of *Mamenchisaurus* Young (1954), has reached extreme values.

PATAGOSAURUS BONAPARTE 1979

Anterior cervicals. These vertebrae have an opisthocoelous centrum, low and lengthened (figure 18A), with a deep posterior fossa in the anterior part that ends abruptly at a certain distance from the anterior border, diminishing gradually toward the posterior border. The ventral face is anteroposteriorly concave, and between the parapophyses it is transversely concave with a deep point.

The neural arch is generally very fused to the centrum, relatively low (centrum height:neural arch height ratio approximately 1:1.5), with a wide diapophyseal lamina that connects to the zygapophyses; well developed epiphysis. The neural spine is rather high, with moderate anteroposterior extension, continuing back by means of the suprapostzygapophyseal laminae. They possess the three well-developed infradiapophyseal fossae. In posterior view the neural arch shows a strong transverse constriction above the neural canal along almost its entire length, forming the infrapostzygapophyseal constriction.

Posterior cervicals. They possess centra and neural arches sensibly higher than the anterior ones (figure 18B), with the centrum height:neural arch height ratio approximately 1:1.8. Except for their greater robustness, the centra do not show differences with the anterior ones. The neural arch possesses the highest, transversely wide and anteroposteriorly brief spine. The three infradiapophyseal fossae and their corresponding four laminae are present.

Anterior dorsals. They are short and high (figure 18C), with centra of the cervical type (opisthocoelous, with deep posterior fossa), but short, and the parapophyses are located in the dorsal part of the centrum. The neural arch is very short and high (centrum height:neural arch height ratio approximately 1:1.8), with the zygapophyses more fence among if that in the posterior cervicals. The neural spine has a high, dorsoventrally convex, transversely planar, and anteroposteriorly brief anterior border. Postzygapophyses and suprapostzygapophyseal laminae of high position, forming a great postspinal fossa. They do not possess the transverse constriction above the neural canal that are marked in the cervicals. They show the three fossae and four infradiapophyseal laminae.

Posterior dorsals. They are shorter and higher than the anterior dorsals. The centra are amphiplatyan (figure 18E), with a marked posterior fossa that shows its deeper part in the anterodorsal region, without pleurocoels. The neural arch is high with the height of the centrum:height of the neural arch ratio approximately 1:2. Below the zygapophyses the neural arch is relatively high, transversely wide, with a wide supraneural fossa (figure 18D, E) above the neural canal; a posterior fenestra in the central infradiapophyseal fossa communicates with the mentioned fossa. The three infradiapophyseal fossae are clearly developed.

The neural spine is of square cross-section in its dorsal part, and is massive. From there a wide posterior concavity extends downward up to the upper part of the transverse process. This posterior fossa is limited anteriorly by the supraprezygapophyseal lamina, and posteriorly by the suprapostzygapophyseal lamina. The cross-section of this part of the spine is in form of X.

Discussion on this vertebral type. A significant character of the cervicals of the “cetiosaurid” type is that the central, posterior and anterior infradiapophyseal fossae have advanced from the cervical region up to cervical 3, whereas in *Plateosaurus* two of those fossae do not extend past cervical 9, and the remaining one (central infradiapophyseal fossa) does not extend past cervical 6.

In cervical 2 of the “cetiosaurid” type, the posterior and central infradiapophyseal fossae are very defined. The posterior fossa of the axial vertebral centrum is as limited by an

abrupt edge in the anterior part as in the posterior one. These are derived characters with regard to *Plateosaurus*, and suggest the existence of backward-directed muscular insertion packages in the anterior sector, whereas in the posterior sector they should be directed toward the occipital region of the skull.

The presence of the three very defined infradiapophyseal fossae and the edges that limit them in the cervicals of the “cetiosaurid” type are typical features of the neural arch that characterizes sauropods. The transversely wide neural spine in the posterior cervicals is a derived character present in this vertebral type, the same as the marked infrapostzygapophyseal constriction (figure 40B).

In *Patagosaurus* the first two dorsals show several cervicalization characters: a) the posterior fossa of the centrum is abruptly limited anteriorly, and b) the suprapostzygapophyseal lamina is continuous with the dorsal end of the neural spine.

The presacral vertebrae of the “cetiosaurid” type are present in *Cetiosaurus oxionensis* Phillips (1871), *Barapasaurus tagorei* Jain et al. (1975), and *Patagosaurus fariasi* Bonaparte (1979) etc., mostly from the Lower Jurassic, and they can be characterized in this manner:

Cervical and more anterior dorsal vertebrae opisthocoelous; and mid and posterior dorsals amphiplatyan. Cervical vertebrae (even axis) with wide posterior fossae in the vertebral centrum, abruptly defined near the anterior border where they are deeper and, except the axis, they gradually diminish in depth toward the posterior border. Occasionally, in a few cervicals from the various available individuals of *Patagosaurus*, a differentiation is observed between the anterior and posterior parts of the posterior fossa of the centrum by means of a dorsoventral edge, giving the anterior sector greater vicinity to the axial plane. There are prominent parapophyses and a deep ventral interparapophyseal fossa.

Strong infrapostzygapophyseal constriction of the neural arch (in posterior view), above the neural canal. The epiphysis extends back to the postzygapophyses. Posterior cervicals with the neural arch sensibly higher than the vertebral centrum. Neural spine strongly connected to the prezygapophyseal and postzygapophyseal laminae, which in turn define wide prespinal and postspinal fossae. Wide posterior exhibition of the diapophyseal lamina that shows continuity with the neural spine.

High anterior dorsals, with width:height ratio 1:2.6; opisthocoelous centrum, with posterior fossa of the type present in the posterior cervicals, but of smaller anteroposterior extension, with marked ventral fossa. Neural arch almost twice the height of the centrum, with high neural spine in the anterior face that is planar and dorsoventrally extensive. Posterior face of the concave spine, together with high suprapostzygapophyseal laminae. Zygapophyses of high position, far from the vertebral centrum. Transverse process anteroposteriorly brief, curved down.

Mid and posterior dorsal vertebrae very high, amphiplatyan, without pleurocoels but with a marked anteroposterior fossa; total centrum:height ratio 1:4 to 1:4.5; with a wide supraneural fossa with fenestra in the posterior wall of the neural arch, below the transverse process (figure 18D, E).

Long, thin posterior infradiapophyseal lamina, directed toward the ventrolateral border of the neural arch. Diapophyseal-parapophyseal lamina extensive and thin, of similar characteristic to the diapophyseal-prezygapophyseal lamina. In the central infradiapophyseal fossa an exposed opening is present posteriorly that communicates with the supraneural fossa illustrated in figure 19. The posterior infradiapophyseal fossa is reduced.

High neural spines, with X-shaped cross-section and with a solid dorsal end, without further expansions. Very exposed, wide supraprezygapophyseal laminae in anterior view. Wide posterior fossa, extensive dorsoventrally, limited anteriorly for the

supraprezygapophyseal lamina and posteriorly on for the suprapostzygapophyseal lamina.

The presence in the anterior cervicals of the infradiapophyseal fossae and the laminae that limit them, demonstrates a progression toward the cranial region of the characters present in cervical 10 of *Plateosaurus*, basically with the same distribution (see figure 10C).

Among the most evident changes in the mid and posterior dorsal vertebrae of the “cetiosaurid” morphological type relative to the primitive sauropod type, we have the dorsoventral lengthening of the lower part of the neural arch, and the development of the neural spine made up of four laminae that are arranged in an X. In transverse section this is two complex changes, because the first gave place to the appearance of the supraneural fossa (figure 19), of uncertain function, and the second to a novel model of neural spine in the clade Sauropodomorpha.

The first of the mentioned changes probably propitiated the development of an higher neural arch to harbor more hypaxial musculature below the transverse process. The second of the changes, in the neural spine, corresponds to the development of a more complex axial musculature, with muscular packages more different in their insertion and origination sites, according to the crests (four) and the posterior hollows that these spines possess. Also, the thickening of the dorsal end of the spine, with wide, rough surfaces for insertions on its posterior, anterior, and dorsal faces, suggests the existence of intervertebral ligaments with differentiated functions, because each one of the mentioned faces is defined more or less by angular edges.

“DIPLODOCID”-TYPE VERTEBRAE

The vertebrae of *Diplodocus* Marsh, 1878 are broadly well known, thanks to the detailed, very well read, works of Hatcher (1901, 1903), Osborn (1899), and Gilmore (1932), as well as the diffusion of the anatomy of this sauropod generated by the worldwide distribution of casts of the complete skeleton of *Diplodocus carnegiei*. Because of this, the descriptive treatment of this vertebral type will be briefer; not therefore the comments that it generates.

The vertebrae of *Diplodocus* are more derived than those of the “cetiosaurid” morphotype in several important aspects of their structure, remarkable changes being appreciated. The most significant refer to the increase in the number of cervicals, the bifurcation of the neural spines in most of the presacral vertebrae and partially in the anterior caudals. The marked bifurcation of the neural spines or only a strong notch in their dorsal end, would be evidence of the existence of an elastic ligament (Alexander, 1989) that helped muscular efforts for dorsoventral movements. This organ probably originated in the sacrals, extending forwards until cervical 3 (which shows evidence of bifurcation) or even more posterior, and back to an uncertain point in the column.

Also the pleurocoels present in all dorsals, and the system of small fossae and laminar edges present in the mid and posterior cervicals, represent derived characters relative to the “cetiosaurid” type.

The lengthening of the neck and increase in size were probably concomitant with the development of a more complex, strong musculature that originated or inserted in the pleurocoels, fossae and laminar edges mentioned above. In the “cetiosaurid” type the morphological and muscular limitations would have been important conditions that controlled the mobility and size of these primitive sauropods.

DESCRIPTION AND COMMENTS

Anterior cervicals. Cervicals 2-6 (figure 20A, B) are relatively simple, not much more derived than the anterior cervicals of *Patagosaurus*. Nevertheless, in *Diplodocus* the

presence of a deep pleurocoel is appreciated in the posterior face of the centrum, along with the reduction of the condyle to articulate with it. In the case of the pleurocoel its functionality would have been linked to the origin or insertion of hypaxial muscles, more differentiated than in the “cetiosaurid”-type. The small size of the condyle suggests that it corresponds to an adaptation for further movement between each next anterior cervical to the skull.

Mid- and posterior cervicals. In these vertebrae of *Diplodocus* (figure 20C-E), a growing complexity of the structure of the posterior face of the vertebral centrum is manifest between cervicals 7 and 11. In this last one, the complex structure of the vertebral centrum shows three well differentiated areas: a) an anterior, transversely deep area, with six small hollows separated by clear edges; b) a wide central area that is prolonged medial and ventral to the diapophyseal lamina, with three deep, sharply defined hollows; c) a posterior and ventral area with two very marked hollows. This complex region of the vertebral centrum is located below the diapophyses, which would be occupied by hypaxial musculature. This musculature would have reached its greatest complexity in cervical 11 of *Diplodocus*, and the morphology described of the posterior face of the vertebral centrum would be a good indication of the complexity of that musculature. From cervical 11 to 15, the topography of the area described is simplified, but acquires a greater surface, suggesting that the musculature did not diminish its volume posteriorly.

In the neural arch of *Diplodocus*, a growing complexity is observed from cervical 11 back. Cervicals 14 and 15 show a depressed, deep area at the base of the neural spine and the beginning of the process that culminates in the prezygapophyses. Particularly in cervical 14 four bony edges are manifest in posterior view, on the posterior face of the neural spine, which define wide fossae. These features of the neural arch represent derived characters that are not present in the posterior cervicals of the “cetiosaurid” type. In *Patagosaurus* this region of the neural arch is smoothly concave on its entire surface, exposed mainly in posterior view. In *Diplodocus* it is deep, with bony edges, exposed anterolaterally and dorsally. This region of the neural arch would have probably been occupied by epaxial musculature, markedly more developed and complex than in *Patagosaurus*.

Anterior dorsals. The four anterior dorsals of *Diplodocus* are markedly opisthocoelous (figure 21A, B, C), with the vertebral centrum lengthened and lower in dorsals 1 and 2, comparable to the cervical type. The wide posterior fossa, anteroposterior, and deep pleurocoel of the vertebral centrum of dorsal 1 diminishes until it almost disappears in dorsal 4, which can be interpreted as a reduction of the surface for origination and insertion of the hypaxial muscles. Nevertheless, the dorsal migration of the diapophysis conditions a bigger dorsoventral space in dorsals 3 and 4 that would compensate the mentioned reduction. The surfaces exposed anteriorly, posteriorly and dorsally in the area of the neural spine decrease progressively until dorsal 4 which possesses the very defined morphotype of dorsal vertebra, with the high, vertical neural spine. The two infradiapophyseal laminae are clearly developed in these anterior dorsals, defining the three diapophyseal fossae (anterior, central and posterior) that on the whole is a primitive character.

The transverse processes of dorsals 1-4 increase their thickness and development, not only to stop a strong union with the thick ribs, but also to accommodate part of the musculature of the base of the neck, implicated in posterior movements.

Mid- and posterior dorsals. From dorsal 5 to 10 (figure 21D-G) the vertebral centra are practically amphiplatyan, with some tendency to develop opisthocoely. The pleurocoels are large, especially in dorsals 8-10. The function of the pleurocoels should have been to accommodate muscles and ligaments that strongly held together the vertebral centra, in this manner avoiding the tendency toward separation imposed by the great weight of the

abdomen. The widespread interpretation that the pleurocoels would have been to alleviate the weight of the bony skeleton seems not very probable when we calculate that the weight saved in individuals weighing 25-30 tons would have been only about 20-30 kg.

The neural arch is high, as much relative to the space between the transverse process and the base of the neural arch as between the transverse process and the dorsal end of the neural spine. These proportions that we consider derived in *Patagosaurus* relative to the primitive sauropod type, are considered primitive *Diplodocus* because they are present in Cetiosauridae.

Diplodocus possesses a supraneural cavity comparable to that of *Patagosaurus*, which added to other characters in common allows recognizing a probable phylogenetic relationship with *Diplodocus* (Bonaparte, 1986b).

In the dorsals 1-7 of *Diplodocus* the two infradiapophyseal laminae are observed which form the anterior, central and posterior fossae, a primitive character present very clearly in all the dorsals of *Patagosaurus*. But in dorsals 8-10 the anterior infradiapophyseal lamina has disappeared and only the central and posterior fossae are present, which is a derived feature. The tendency to lose the mentioned lamina is generalized, as we will see when treating other sauropods. In dorsals 5-10 of *Diplodocus* is observed the presence of one or two (according to the vertebrae) bony edges directed obliquely down and behind from the parapophyses, toward the dorsal and posterior border of the vertebral centrum. It is a derived character not observed among the Cetiosauridae (figure 21D-G).

The neural spine is high, provided with a dorsal and posterior region with rugosities for ligament insertion comparable to that of *Patagosaurus*. Nevertheless, the posterior dorsals, not affected by bifurcation of the spine, show more derived structures than in *Patagosaurus*: a) the supraprezygapophyseal laminae are practically united, forming a prespinal lamina; b) a conspicuous supradiapophyseal lamina in dorsals 7-10; c) presence of a postspinal lamina, of variable development, in the last dorsals.

In sum, we note that the presacral vertebrae of *Diplodocus* show the following derived characters relative to “cetiosaurid”-type vertebrae: 1 – opisthocoely reaches to dorsal 4 (15 cervicals plus 4 dorsals); 2 – bifurcation of the neural spines between dorsal 6 and cervical 3; 3 – posterior fossa of the centrum of cervicals 7-15 with deep hollows and edges; 4 – strong supradiapophyseal fossa; hollows and bony edges in the posterior face of the neural spine of cervicals 11-15; 5 – pleurocoels present in all the dorsals; 6 – edges projected obliquely back and below from the parapophyses in the posterior dorsals; 7 – strong fossae in the posterior and inferior faces of the neural spine and the base of the process for the prezygapophyses; 8 – presence of the prespinal lamina and supradiapophyseal lamina in dorsals 7-10.

“APATOSAURID”-TYPE VERTEBRAE

The presacral vertebrae discussed in this chapter are very different from those of *Diplodocus*, to the point that merits attention by placing these sauropods genera in their own family.

Initially and for many years, *Apatosaurus* was considered to be a camarasaurid (Marsh, 1883, 1891; White, 1958; etc.), whereas Holland (1915) considered it a diplodocid, an approach maintained at the present time (Berman and McIntosh, 1978; McIntosh, 1990). The history of the changes in the interpretations of the relationships of *Apatosaurus* has been commented on in detail by McIntosh and Berman (1975) and Berman and McIntosh (1978). After these works the interpretation that *Apatosaurus* and *Diplodocus* are members of the same family was firmly ingrained, objectionable as it will be appear below.

In several aspects of their structure and proportions, the presacral vertebrae of *Apatosaurus* are not only different from those of *Diplodocus* but also differ markedly from

those of other sauropods.

CERVICAL VERTEBRAE

The group of the cervical vertebrae of *Apatosaurus*, excluding the atlas and axis, illustrated by Gilmore (1936, 24 and 31) from *A. louisae* and *A. excelsus*, shows that the morphological complexity in all the cervicals is very similar, such that in cervicals 3 and 4 all the structural characters of the posterior cervicals are present, except the differences in proportions, as the relatively low and lengthened cervicals become short and high in the posterior cervicals, with an approximate ratio of 1:2, excluding the cervical rib.

In *Diplodocus* (Hatcher, 1904) the group of cervical vertebrae (axis excluded) shows a growing complexity starting from cervical 7, reaching its greatest expression in cervical 14, to the point that if we compare cervical 4 with 14 very strong differences can be observed. In *Apatosaurus* the situation is different, as it is pointed out above.

In *Camarasaurus* (Osborn and Mook, 1921) the sequence of cervicals shows that those anterior have a degree of morphological complexity not very different from the posterior cervicals, but with different proportions, that is to say they go from being rather low in the anterior region to being relatively short and high in the posterior, resembling the proportions of these vertebrae in *Apatosaurus*. Nevertheless, the morphological characters of both genus are definitely different, as is shown below.

Anterior cervicals. To compare these vertebrae, I have arbitrarily considered the anterior cervicals as vertebrae 3-6. In *Apatosaurus* (figure 22A, B) the vertebral centra have two large pleurocoels. The parapophyses are long, projected posteroventrally, and provided with a long capitulum and tuberculum for the cervical rib, thoroughly extending past the ventral level of the centrum. The neural arch possesses a high, very defined neural spine, and the posterior diapophyseal lamina is very concave, and exposed dorsally by the presence of a strong fossa that occupies a great part of that lamina. In *Diplodocus* the vertebral centra possess less developed pleurocoels. The parapophyses are modest until cervical 5 and pronounced in cervical 6. The next cervical rib is at the ventral level of the centrum. The neural arch possesses a less well defined, lower neural spine than in *Apatosaurus*. The diapophyseal lamina is slightly concave and exposed mostly in posterior view. In *Camarasaurus* the vertebral centra have 2-3 pleurocoels. The parapophyses are short and projected posteriorly, except in cervical 6 where they project ventrolaterally. The neural arch has a low, not very well-defined spine. The diapophyseal lamina is not very exposed posteriorly, and oriented anterodorsally. The high diapophyseal-postzygapophyseal lamina has an indentation near the diapophyses.

Mid- cervicals. Also for these vertebrae, I consider arbitrarily the mid cervicals as vertebrae 7-12 of *Apatosaurus* and *Diplodocus*, and 7-10 of *Camarasaurus*. In *Apatosaurus* the vertebral centra maintain 2-3 simple pleurocoels of modest size (figure 22C, D). The parapophyses increases their size back to the point of occupying (in cervicals 9-12) one-third of the total length of the centrum. They are long and projected posteroventrally; and the ribs possess an enormous capitulum and tuberculum. In the neural arch the forked spines are very well-defined, with a concave anterior border for a strong retraction of the supraprezygapophyseal lamina. The diapophyseal lamina is strongly depressed, with a wide fossa toward the base of the spine, and a marked edge formed by the diapophyseal-postzygapophyseal lamina. The infrapostzygapophyseal fossa is wide but relatively simple.

In *Diplodocus* the complexity of the pleurocoels of the vertebral centra increases backward, to the point that in cervical 11 three areas with pleurocoels are appreciated: one located posteromedial to the parapophyses, with several subdivided pleurocoels; another on the posterior face of the centrum, with 3 pleurocoels separated by bony partitions; and the

third in the posterior and ventral part of the same posterior face, with 2 pleurocoels. The parapophyses remain moderate in size, not reaching one-fourth of the total length of the centrum, and they do not extend much past the ventral border of the centrum. The cervical ribs possess a modest capitulum and tuberculum.

In the neural arch the spine is well-defined and forked, and the supraprezygapophyseal lamina that forms its anterior border is less concave than in *Apatosaurus*. The diapophyseal lamina is exposed mostly in posterior view, and to a lesser degree dorsally. It presents a strong fossa at the base of the neural spine in cervicals 11 and 12, although not in the preceding ones. In cervicals 11 and 12 a marked edge is observed that travels on the posterior face of the spine, which is not present in *Apatosaurus*. The infrapostzygapophyseal fossa possesses modest pleurocoels.

In *Camarasaurus* the vertebral centra have these pleurocoels with few changes. The modest parapophyses are projected more posteriorly than ventrally. In the neural arch the spines are low, and in cervical 10 the anterior border forms a marked concavity in the supraprezygapophyseal lamina. The diapophyseal lamina and the diapophyses are located in a very anterior position, and the prezygapophyses thoroughly exceed the anterior border of the centrum. The diapophyseal-postzygapophyseal lamina of the cervicals show a strong indentation near the diapophyses. An appreciable distance exists between the prezygapophyses and the anterior border of the spine, a character that *Apatosaurus* does not possess. The infrapostzygapophyseal fossa is prolonged anteriorly much more than in *Apatosaurus*, and it shows 1-2 pleurocoels.

Posterior cervicals. I consider posterior cervicals as vertebrae 13-15 in *Apatosaurus-Diplodocus*, and 11-13 in *Camarasaurus*. In *Apatosaurus* the 3 last cervicals become progressively shorter, higher, and wide posteriorly. The vertebral centra possess a wide posterior fossa, possibly with small pleurocoels. The parapophyses decrease toward the last cervical, but the cervical ribs maintain a hypertrophied capitulum and tuberculum.

In the neural arch the lower portion is higher, there being a greater distance between the upper border of the centrum and the zygapophyses. The neural spine becomes very high and vertical in two last cervicals, very short anteroposteriorly, with a deep fossa in its posterior face, upward from the level of the zygapophyses.

In *Diplodocus* the posterior cervicals have inverse proportions to those of *Apatosaurus*; they are longer than high. The vertebral centra have complex pleurocoels, and the cervical ribs possess a rather fragile capitulum and tuberculum, not hypertrophied as in *Apatosaurus*. In the neural arch the spine has continuity back by means of the very high suprapostzygapophyseal lamina, almost horizontal in cervicals 13 and 15 as illustrated by Hatcher (1904, plate 3), whereas in *Apatosaurus* that lamina is subvertical in cervicals 14 and 15 (Gilmore, 1936, plate 24). The morphology of the prezygapophyseal processes and the orientation of the zygapophyses are also very different in the two genera.

In *Camarasaurus* the 3 last cervicals are shortened anteroposteriorly as in *Apatosaurus*, but the vertebral morphology is very different. In the vertebral centrum the posterior fossa of *Camarasaurus* is irregular, with wide pleurocoels in cervicals 11 and 12, and markedly smaller in cervical 13.

In the neural arch the neural spine is brief, rising little above the zygapophyses. In *Camarasaurus*, the zygapophyses are more fenced off from one another in posterior view than in *Apatosaurus*. The disposition of the diapophyses and the infradiapophyseal laminae are elevated in *Camarasaurus* in such a way that both infradiapophyseal laminae are observed, and the fossae that are perfectly limited in posterior view. On the other hand in *Apatosaurus* they have a more ventral position and cover the mentioned features in posterior view.

Synthesis of the cervicals. As derived from the comparisons, the general morphological type of the cervicals of *Apatosaurus* includes the following derived characters that differentiate it from those of *Diplodocus* and *Camarasaurus*, taking the cetiosaurid *Patagosaurus* from the Middle Jurassic of Patagonia (Bonaparte, 1979; 1986a) as a reference or ancestral group:

1 – progressive posterior reduction of the last 4 cervicals (in *Camarasaurus* it includes 3, and in *Patagosaurus-Diplodocus* all of them); 2 – hypertrophy of the parapophyses; 3 – neural arch proportionally very high, representing three-quarters of the total height of cervicals 14 and 15 (in *Diplodocus* it is two-thirds, and in *Camarasaurus* less than two-thirds in cervicals 11 and 12, and two-thirds in cervical 13); 4 – hypertrophied capitulum and tuberculum.

On the other hand, *Camarasaurus* presents, among other things, a remarkable derived character that differentiates it from *Apatosaurus* and *Diplodocus*, consisting of the extremely extensive transverse processes or diapophyses in its last four cervicals.

Finally *Diplodocus* shows two complex derived characters that differentiate it from *Apatosaurus* and *Camarasaurus*:

1 – posterior vertebral centra of the cervicals with very numerous pleurocoels separated by laminae; 2 – posterior neural arch of the cervicals provided with numerous pleurocoels, with laminar edges, and the suprapostzygapophyseal lamina is subhorizontal in the cervicals.

DORSAL VERTEBRAE

The comparison of the dorsal series of *Apatosaurus* with *Diplodocus* and *Camarasaurus* also shows very marked differences. In general terms I wish to point out that the first two dorsals of *Apatosaurus* are of the dorsal, that is to say high, type and are anteroposteriorly brief, as in *Camarasaurus*, but different from those of *Diplodocus*, which are closer to the cervical pattern, with long centra and an appreciable distance between the pre- and postzygapophyses. But as for the dorsoventral length of the neural spine, the dorsals of *Apatosaurus* are more similar to *Diplodocus* than to *Camarasaurus*, because in this genus they are notably short.

Anterior dorsals. I have considered the first 4 dorsals as such. In *Apatosaurus* (figure 23B) the vertebral centra vary in being opisthocoelous in the first two vertebrae, semi-opisthocoelous in dorsal 3, and amphiplatyan in the dorsal 4 (according to Gilmore, 1936, plate 25); with small pleurocoels in first two that are markedly larger in dorsals 3 and 4.

In the neural arch the infradiapophyseal laminae are present until dorsal 3; in dorsal 4 they are only observed in the posterior infradiapophyseal lamina. The supradiapophyseal lamina forms the anteroposterior border of the neural spine in dorsals 1-4, and the suprapostzygapophyseal lamina forms the posterior border of the spine.

In *Diplodocus* the first 4 dorsals have centra with very clear opisthocoely. The centrum of dorsal 1 is long and that of dorsal 4 is approximately only 55% of its length. The pleurocoelous area in the posterior face of the centrum decreases markedly up to dorsal 4.

In the neural arch the infradiapophyseal laminae are present in the anterior dorsals, which is continued up to dorsal 7. The supradiapophyseal lamina is nonexistent in these four dorsals. As in *Apatosaurus*, the suprapostzygapophyseal lamina forms the posterior border of the neural spine.

In *Camarasaurus* the vertebral centra are highly opisthocoelous, with pleurocoels that increase in size posteriorly. The neural arch is anteroposteriorly brief, recalling the condition in *Apatosaurus* and differing from that of *Diplodocus*. The infradiapophyseal laminae are present in their typical position up to dorsal 3, and have an atypical disposition in dorsal 4.

The supradiapophyseal lamina has a very modest dorsal expression and connects to the posterior border of the neural spine, that is to say to the inverse of the condition in *Apatosaurus* in which this lamina forms the anteroposterior border of the spine.

As for the height of the neural spines, an increase in height is not observed between dorsals 1 and 4 according to the detailed figures of Osborn and Mook (1921), on the contrary dorsal 1 has its (forked) neural spine higher than in dorsals 3 and 4, measured from the superior and medial part of the transverse processes. The morphology of the neural spine shows its dorsal end reverted posteriorly, differing of *Apatosaurus* and *Diplodocus* in which it is more vertical.

Mid- and posterior dorsals. In general terms these vertebrae are, at first sight, similar or comparable in *Apatosaurus* and *Diplodocus*, and different from those of *Camarasaurus*. But a quick analysis demonstrates that there are three different morphological types. The bifurcation of the spine, clear or incipient, reaches to dorsal 6 in *Apatosaurus*, to dorsals 6-7 in *Camarasaurus*, and to dorsals 8-9 in *Diplodocus*.

In *Apatosaurus* (figure 23C-D) these vertebrae are high, practically straight in anterior (or posterior) view, with a good space below the transverse processes and semi-opisthocoelous vertebral centra, because the condyle of the centrum is not very apparent. The pleurocoels are evenly large.

The neural arch is high with the transverse processes directed horizontally. The two infradiapophyseal laminae are present only in dorsal 6 (Gilmore 1936, plate 25). In the remaining dorsals it reappears in imprecise form in dorsal 9. In dorsal 7 of *A. louisae*, and in dorsals 6-9 of *A. excelsus* (Gilmore 1936, plates 25 and 32), an edge or thick lamina is observed in posterior view that connects the parapophyses with the ventral portion of the neural arch.

In the neural spine, formed by the axial prespinal and postspinal laminae, and the lateral laminae disposed transversely, it is observed that the prespinal is formed by the supraprezygapophyseal laminae which fuse for most of their course. The posterior laminae are formed by the bifurcation of the supradiapophyseal and suprapostzygapophyseal laminae. Finally, in dorsals 7-9 the postspinal lamina is formed by the medial bifurcation of the suprapostzygapophyseal lamina, which unites to the opposite one in the axial plane for almost all its course, whereas in 5-6 they are separated in their lower half.

In *Diplodocus* these vertebrae are high, as they increase their height posteriorly as in *Apatosaurus*. They present a semi-opisthocoelous condition in the centra as in the mentioned genus, but contrary to *Apatosaurus* the pleurocoels increase in size posteriorly and have a different contour.

The transverse processes are directed horizontally, with the distal part somewhat twisted ventrally. The infradiapophyseal laminae are present up to dorsal 7. In dorsals 5-9 an edge (occasionally two) is observed in posterior view that connects the region of the parapophyses with the ventral and posterior end of the neural arch.

The neural spines of *Diplodocus*, in particular those of the last 3 dorsals, have a similar aspect to those of *Apatosaurus*, but with different structures. In dorsals 5 and 6 the supradiapophyseal lamina is very reduced and does not contribute to the structure of the spine. In fact a posterior lamina does not exist in these dorsals, as is the case in *Apatosaurus*. In the dorsal 7 and subsequent dorsals the supradiapophyseal lamina newly forms the posterior lamina, but without the suprapostzygapophyseal lamina, as is the case in *Apatosaurus*. The prespinal lamina is formed by the supraprezygapophyseal laminae, which fuse to each other in the last 3 dorsals and remain separated in the remaining dorsals. Finally, the postspinal lamina, very defined from dorsal 7 posteriorly, is formed by the suprapostzygapophyseal lamina, which is not divided as in *Apatosaurus*.

In *Camarasaurus* dorsal vertebrae 5 to 10-11 are lower than in *Apatosaurus* and *Diplodocus*, the transverse processes pass dorsolaterally, the vertebral centra are highly opisthocoelous until the last dorsal, and the neural spines are very low, expanded posteriorly, and lack pre- or postspinal laminae.

The centra show a progressive reduction posteriorly. They have pleurocoels of similar size to the dorsals. In the neural arch, the extreme dorsoventral brevity of the neural spines and their strong posterior expansion from dorsal 7 back are derived characters of this genus that are not present in *Diplodocus* or *Apatosaurus*. But, as in *Apatosaurus*, it possesses a suprapostzygapophyseal lamina with a medial continuation that does not reach the axial plane, and another posterior one that forms the posterior border of the spine.

RESULTS OF THE COMPARISONS

In the comparisons of the cervical vertebrae we see that *Apatosaurus* has several derived characters that differentiate it from *Camarasaurus* and *Diplodocus*, for which it cannot be included in Camarasauridae or Diplodocidae.

As for the anterior dorsal vertebrae, those observed also indicate that they are three different taxa, which should differ at the family level. The following derived characters suggest this:

Apatosaurus: 1 – presence of supradiapophyseal lamina that forms the anteroposterior border of the neural spine; 2 – absence of the anterior infradiapophyseal lamina in dorsal 4; 3 – presence of postspinal lamina in dorsal 4.

Diplodocus: 1 – dorsals 1 and 2 of the cervical type.

Camarasaurus: 1 – neural spines reduced in height, with thick dorsal end and reverted posteriorly; 2 – transverse processes of dorsal 4 directed posteriorly and dorsally; 3 – transversely very wide hyposphenes.

In turn the mid and posterior dorsal vertebrae show the following derived characters:

Apatosaurus: 1 – absence of the anterior infradiapophyseal lamina, except in the last dorsal; 2 – symmetrical position of the prespinal, postspinal, and posterior laminae along the whole length of the neural spine; 3 – bifurcation of the suprapostzygapophyseal lamina participating in the posterior lamina, and fused to the postspinal lamina.

Diplodocus: 1 – oblique edges on the posterior face of dorsals 5-9, between the posterodorsal border of the centrum and the posteroventral border of the parapophyses; 2 – pleurocoels of the posterior dorsals dorsally extensive, extending past the dorsal border of the centrum.

Camarasaurus: 1 – neural arches of the dorsals very low, with the spine shorter than the height of the centrum; 2 – neural spine with marked posterior borders.

To facilitate the reader's understanding of the anatomical references that I consider important for excluding the genus *Apatosaurus* from the family Diplodocidae, the following list, with comments, will be useful:

1 – in *Diplodocus* the first two dorsals are of the cervical pattern, whereas in *Apatosaurus* the last two cervicals (except for the ribs) recall more the dorsal type, especially in the pattern of the neural spine. Here it is different evolutionary models that include the dorsals in *Diplodocus* with the more anterior cervical type, whereas in *Apatosaurus* the cervical pattern disappears before finishing the cervical sequence. Naturally these bony differences would have meant great differences in the constitution of the axial muscular system.

2 – in *Apatosaurus* cervical vertebrae 3-13 present the same characters with very little variation in their proportions, but vary in their absolute size. In *Diplodocus* the situation is very different, with anterior cervicals simpler than the posterior ones, and these being very

complex ones. It can be admitted that the muscular plan of the neck of *Apatosaurus* had a certain homogeneity throughout its length, whereas in *Diplodocus* the complexity of the muscular mass and the number of insertions in the vertebrae increased considerably posteriorly.

3 – the progressive reduction (anteroposterior) of the last three cervicals of *Apatosaurus* contrasts with the situation in *Diplodocus*, in which the length stays practically the same in the last four cervicals.

4 – the neural arches of the mid and posterior cervicals of *Apatosaurus* are markedly higher than in *Diplodocus*, and functionally should have accommodated a more voluminous epaxial musculature.

5 – the hypertrophy of the parapophyses and of the cervical ribs shown in *Apatosaurus* is much more developed than in *Diplodocus*.

6 – the posterior vertebral centra of the cervicals of *Diplodocus* possess numerous pleurocoels separated by laminae, indicating an intricate system of muscular insertions. In *Apatosaurus* the posterior fossa of the vertebral centra is simple.

7 – the posterior neural arches of the cervicals of *Diplodocus* show numerous fossae and laminar edges, surely linked to areas of muscular origination and insertion. In *Apatosaurus* only a great fossa exists at the base of the neural spine.

8 – in *Apatosaurus* the supradiapophyseal lamina forms the anteroposterior border of the spine in dorsals 1-4, whereas in *Diplodocus* this lamina is not present in those dorsals, newly appearing in dorsal 7.

9 – *Apatosaurus* shows an almost symmetrical disposition of the four laminae that form the neural spine, throughout practically its whole length, especially in the last three dorsals. In *Diplodocus* the symmetry is less appreciable because the posterior laminae are wider than the axial ones, and these in turn differ from each other in width, because the postspinal is narrower than the prespinal.

10 – in *Apatosaurus* the suprapostzygapophyseal lamina is forked whereas in *Diplodocus* it forms the postspinal lamina (odd numbered) in the last four dorsals.

11 – in *Apatosaurus* the bifurcation of the neural spine, still incipient, extends between cervical 6 and dorsal 6, and in *Diplodocus* between cervical 3 and dorsals 8-9.

These differential characters can be interpreted as indications of different families. In any family of theropods, crocodiles, thecodonts or therapsid-mammals such a magnitude of differences is manifest in the structure of its vertebrae. For this reason, I consider that *Apatosaurus* deserves an *ad hoc* status family, but still considered phylogenetically closer to Diplodocidae than to Camarasauridae. With this last family the relationships are, in my opinion, very distant.

“BRACHIOSAURID”-TYPE VERTEBRAE

The type of presacral vertebrae characterizing this group is based on the materials of *Brachiosaurus brancai* Janensch (1914;1950) that, although incomplete, possess more information than the specimen represented by the materials of *Brachiosaurus altithorax* Riggs (1903; 1904). On the other hand differences exist among the posterior dorsals of the latter species, which probably represents a different genus (already observed by Paul, 1988), with characters more derived in *B. altithorax*, especially for the greater development in the structures of the hyposphene and of the infradiapophyseal fossae. In order to achieve a more coherent definition of this vertebral type, for the time being we have omitted information from *B. altithorax*, although it is certain that its vertebrae are of the “brachiosaurid” morphotype.

This type of vertebrae shows the development of opisthocoely up to the last dorsal,

relatively lengthened dorsal vertebral centra, and neural spines of the posterior dorsals proportionally low and wide, all them derived characters when compared with the situation present in *Patagosaurus* Bonaparte (1979; 1986) and *Diplodocus* Hatcher (1901; 1903). But at the same time it shows primitive characters in the presence of infradiapophyseal laminae, limited number of cervical vertebrae, and lack of bifurcation of the neural spine.

Obviously it is a vertebral type adapted for quadrupedal forms with the anterior dorsal region higher than the sacral, which would have resulted in the neural spines being progressively lower toward the sacral region.

DESCRIPTION AND COMMENTS

Anterior cervicals. The anterior cervicals are relatively simple up to the sixth vertebra (figure 24A-C). Nevertheless, the neural arch shows some derived structures not present in *Patagosaurus-Diplodocus*, such as the hollows in the anterodorsal region of the diapophyseal lamina, and below that lamina in the region anterior to the postzygapophyses.

The posterior fossa of the centrum shows hollows and edges characteristic of sites for strong muscular insertions. The neural spines are low and transversely narrow, suggesting a primitive condition.

Mid- and posterior cervicals. From the seventh cervical the development of a special topography is manifest in the mainly posterior face of the diapophyseal lamina and its continuation on the posterior face of the neural spine (figure 24D, E). This consists of edges and marked depressions that occupy almost the entirety of the mentioned surface, whose projection is posterior in the eighth cervical and not dorsolateral as is the case in *Diplodocus*. That is to say the cervical epaxial musculature of *Brachiosaurus* would be mostly in a posterior position, and in a smaller proportion in the dorsal position.

The structure of the posterior fossa of the centrum of the mid and posterior cervicals does not possess the complexity present in *Diplodocus*. It is a simpler morphotype, surely resulting from the high forward position of the dorsal part of the spine, which made the neck a kind of gradual continuation of the anterior dorsals. In *Diplodocus* and other sauropods with forelimbs shorter than the hind limbs, the neck was a structure abruptly differentiated from the thorax and more pendant than in *Brachiosaurus*.

The mid- and posterior cervicals of *Brachiosaurus brancai* are low, with low, transversely narrow neural spines, partly more derived than in *Patagosaurus*, but in a direction different from *Diplodocus*. In this genus the spines remain high as in *Patagosaurus*, with the ensemble of the bifurcation and other diverse characters noted above. In *Brachiosaurus brancai* the spines reduced their height and conserved the primitive character (at least until cervical 8) of being transversely narrow.

Anterior dorsals. In *B. brancai* only the vertebral centra of the dorsals 1 and 2 are known (Janensch, 1950, figs. 49 and 50), providing little information except that an abrupt reduction takes place between the last cervicals and the first dorsals.

Mid- and posterior dorsals. The anterior dorsals of *B. brancai* with the most information is the 4th (Janensch, 1950, figs. 53 and 54) (figure 25A). This vertebra possesses parapophyses in a very high position, and it could be the 5th. Of the available dorsals of *B. brancai* (figure 25), as much the material in Berlin as the material in the British Museum, this dorsal is the one that possesses the higher and relatively thinner neural spine relative to the remaining well-known dorsals.

In general, and in spite of some effects of deformation, the vertebral centra are relatively low, transversely wide, and axially lengthened, which would be a character characteristic of this genus. These centra are very different very different from the dorsal centra of *Patagosaurus-Diplodocus*, and also from *Brachiosaurus altithorax* Riggs (1903).

The neural arch has a reduced extension between the upper part of the vertebral centrum and the emergence of the transverse process. A comparable reduction is observed in the neural spine, which is dorsoventrally reduced in the last three dorsals (figure 25C, D).

The supraprezygapophyseal laminae are very close to each other and unite in the upper third of the last dorsals, forming an incipient prespinal lamina. In more anterior dorsals these laminae do not unite to each other. In the posterior view of the neural spine, the suprapostzygapophyseal laminae remain separate, and a very defined postspinal lamina is prolonged ventrally from the dorsal thickening.

In the posterior dorsals (Janensch, 1950, fig. 62), the two infradiapophyseal laminae are noted which contain the central infradiapophyseal fossa, and they limit the anterior and posterior infradiapophyseal fossae, which is a primitive character, but it is not present in the most anterior dorsal. The supradiapophyseal laminae are well developed and unite dorsally to the ventral and posterior continuation of the rugose expansion of the dorsal part of the spine.

In the dorsals of *B. brancai* existing in the collection of the Museum für Naturkunde, Berlin, or in the individual in the British Museum, the derived structures posteroventral to the hyposphene possessed in the anterior dorsals of *B. altithorax* (Riggs, 1904, pl. 72, figs. 6 and 7) are not in evidence. The neural spine of *B. brancai* is formed posteriorly by the supraprezygapophyseal and suprapostzygapophyseal laminae, as in *Patagosaurus*, with participation of the supradiapophyseal laminae, with a transverse widening.

In sum, we see that the vertebrae of *B. brancai* present various specialized characters with regard to the vertebrae of *Patagosaurus*:

1 – greater elaboration of the surface of the diapophyseal lamina, with hollows and edges that increase in the mid and perhaps the posterior cervicals; 2 – greater elaboration of the posterior face of the cervical vertebral centra (without reaching the level of *Diplodocus*); 3 – reduction of the height of the cervical neural spines; 4 – development of opisthocoely up to the last dorsal; 5 – pleurocoel development in all the dorsal centra; 6 – reduction of the space between the superior border of the centrum and the base of the transverse processes (reversal?); 7 – reduction of the height of the neural spine (possible reversal) in the posterior dorsals; 8 – widening of the neural spine in the posterior dorsals, with transverse development of the supradiapophyseal lamina at their dorsal end, and wide pre- and postspinal thickenings.

On the other hand, primitive characters are manifest, such as: a) lack of bifurcation of the spine in the whole presacral series; b) cervical neural spines with very little transverse expansion; c) presence of 3 infradiapophyseal fossae (and laminae) in the posterior dorsals; d) preponderance of the suprazygapophyseal laminae in the neural spine; e) little axial development of the pre- and postspinal laminae.

This panorama of characters, several of them more derived than in *Patagosaurus*, others more primitive than in *Diplodocus*, and finally a group of characters plesiomorphic or more primitive than in *Patagosaurus*, makes think of two alternative phylogenies that can be produced: a) that the differentiation of the morphological type of the Brachiosauridae began in a stage prior to that of *Patagosaurus*; b) that the differentiation of the latter mentioned adaptive type was at the level of Cetiosauridae, giving place to the development of diverse reversals. The first alternative is more in agreement with the information and does not require the aid of reversals for its acceptance.

“CAMARASAURID”-TYPE VERTEBRAE

The work of Osborn and Mook (1921) includes a great amount of information on the vertebrae of *Camarasaurus* Cope (1877), of these that practically all are known from all their

components, still certain doubts exist on the real sequence of the cervicals and dorsals, because those authors gathered them in the best possible form starting from incomplete information.

Osborn and Mook (1921) pointed out the most primitive conditions in *Camarasaurus* relative to *Diplodocus* (Hatcher 1901; 1903), including the smaller number of cervical vertebrae, the smaller development of the bifurcation of the neural spine, and their more robust condition. Nevertheless, although these characters were evaluated very well by those authors, they are only a few characters within a larger group of characters. When we evaluate them in a wider perspective, with the aid of some information on the evolution of the vertebral characters in the sauropodomorphs, they reveal that although some of them are primitive, many others are derived. In general terms the presacral vertebrae of this genus show characters sensibly more derived than in *Patagosaurus-Diplodocus*, such as the reduction of the height of the neural spine from the mid cervicals up to the sacrals, and the development of opisthocoely in all the dorsals. The same thing is also suggested by the disappearance of the anterior infradiapophyseal fossa in the mid and posterior dorsals, and the anteroposterior reduction of the posterior dorsals.

It is not unlikely that the number of cervicals was estimated by Osborn and Mook (1921), and that in fact it is somewhat smaller. This observation arises from the remarkable robustness of the transverse processes in the last four cervicals illustrated in plates 67 and 69.

DESCRIPTION AND COMMENTS

Anterior cervicals. Until the sixth cervical *Camarasaurus* shows more derived characters than *Patagosaurus-Diplodocus*. In the neural arch the diapophyseal lamina of *Camarasaurus* is not exposed posteriorly, but rather it is exposed partly dorsally, by the development of a marked fossa between the neural spine and the postzygapophyses. The diapophysis has a higher position; the diapophyseal-postzygapophyseal lamina is also higher and more concave. In the anterior vertebral cervical centra the posterior region is more elaborated in *Camarasaurus*, with two or three pleurocoels in the posterior fossa.

Mid- and posterior cervicals. These vertebrae of *Camarasaurus* are proportionally shorter and higher than in *Diplodocus*, which can be interpreted as a derived character if in fact *Patagosaurus* and *Diplodocus* represent the primitive condition, an interpretation that we find reasonable.

In mid cervicals approximately 7-10, the neural spines are low, the prezygapophyses are very anteriorly projected, and the diapophyses are in a very anterior position. The diapophyseal-postzygapophyseal laminae are very concave at their posterior border, which reduces the surface of the lamina. The posterior fossa of the vertebral centrum does not increase its complexity visibly with regard to the anterior cervicals. As much in the mid cervicals as in the posterior ones, the complexity of the neural arch and of the vertebral centrum is smaller than in *Diplodocus*, but markedly more derived than in *Patagosaurus*.

In the posterior cervicals of *Camarasaurus* the neural spine and the diapophyses spread to become defined and rise (although of little volume), and the the structure of the posterior fossa of the centrum becomes simplified. A sequence of comparable changes is observed in *Diplodocus*, but in *Camarasaurus* it is more marked. For example, in cervicals 12 and 13 of *Camarasaurus*, the infradiapophyseal laminae are well exposed in posterior view, with the three fossae very exposed posteriorly. These characters are less developed dorsoventrally in *Diplodocus* and *Patagosaurus*, as a result of which I interpret that *Camarasaurus* possesses the derived condition because they have a more dorsal position in those characters. The vertebral centra of the last cervicals (according to the interpretation of Osborn and Mook, 1921) are notably robust if we compare them with the condition in

Patagosaurus or *Diplodocus*. Possibly it could represent a feature characteristic of *Camarasaurus*. The bifurcation of the neural spine is manifest from cervical 7 posteriorly, whereas in *Diplodocus* this character is more derived because it is observed starting from cervical 3.

Anterior dorsals. The anterior dorsals of *Camarasaurus* show an interesting derived character that contributes to recognizing its evolutionary level. It is a strong reduction in the height of the neural spine that is of totally different proportions from those in *Patagosaurus-Diplodocus*. In the 5 anterior dorsals the region of the neural spine located above the transverse process represents approximately one-fifth of the total height of those vertebrae. In *Patagosaurus-Diplodocus* that ratio is very close to 1:2, with slightly lower values in *Patagosaurus*. Undoubtedly *Camarasaurus* is derived relative to *Diplodocus* in this character.

In contrast, a group of primitive characters is observed in these anterior dorsals, as noted in plate 71 in Osborn and Mook (1921). This plate shows the presence of the two infradiapophyseal laminae that define the three fossae. A similar situation, with some variation, is present in *Diplodocus*, *Patagosaurus* and *Plateosaurus*.

In *Camarasaurus* the hyposphenes of dorsals 3-5 have a strong posterior development next to the presence of some posteroventrally-guided columnar “supports”, called infrapostzygapophyseal laminae. In *Diplodocus* there is something that recalls this condition, but in *Camarasaurus* the character is more derived.

Posterior dorsals. The bifurcation of the neural spine does not occur on posterior dorsal 6, which represents a primitive character relative to *Diplodocus*. In the posterior dorsals, up to the last dorsal the characters of low, transversely wide, neural spines and strong posterior development of the supradiapophyseal lamina remain. At least in the posterior dorsals of *Camarasaurus*, it is observed that the reduction of the height of the neural spine was not accompanied by reduction of the height of the neural arch between the zygapophyses and the dorsal border of the centrum. This distance is not visibly decreased relative to the proportions present in *Patagosaurus-Diplodocus*. This means that only the spine decreased, involving a reduction in the volume of the epaxial musculature, whereas the region occupied by hypaxial musculature remained stable.

In *Brachiosaurus* the decrease affected both areas of the posterior dorsals, because both the height of the spine and the infrazygapophyseal fossa are very reduced.

The anterior infradiapophyseal fossa seems not to be present in the posterior dorsals of *Camarasaurus*, on the other hand this fossa is very defined in *Patagosaurus*, *Diplodocus* and *Brachiosaurus*.

Finally, the posterior dorsals, opisthocoelous as has already been pointed out, are very short axially, perhaps as an adaptation to reduce the length of the abdomen. In sum, we can recognize the following derived characters in *Camarasaurus*:

- 1 – reduction of the height of the neural spine from the mid cervicals back to the last dorsal;
- 2 – development of opisthocoely up to the last dorsal;
- 3 – reduction of the anterior infradiapophyseal fossa in the mid and posterior dorsals;
- 4 – anterior cervicals with the diapophyseal lamina exposed dorsally;
- 5 – low neural spines in the mid cervicals and reduced diapophyseal-postzygapophyseal lamina, with a concave posterior border;
- 6 – more derived infrapostzygapophyseal constriction than in *Diplodocus*, with thicker infrapostzygapophyseal laminae;
- 7 – dorsals with a strong reduction of the neural spine;
- 8 – supradiapophyseal lamina projected posteriorly in the last dorsals;
- 9 – very developed hyposphenes of the anterior dorsals, with columnar “supports” guided posteroventrally;
- 10 – anteroposterior reduction of the last 3 dorsals.

On the other hand the following primitive characters are manifest: a) – limited

number of cervicals, and limited bifurcation of the neural spine (from cervical 7 to dorsal 6); b) – presence of 2 infradiapophyseal laminae in dorsals 1-5; c) – presence of the supraneural fossa in the posterior dorsals (Bonaparte, 1986b); d) – absence of prespinal and postspinal laminae; e) – suprazygapophyseal laminae developed far from the axial plane (as in *Patagosaurus*).

“DICRAEOSAURID”-TYPE VERTEBRAE

This type of presacral vertebrae is very well represented by complete sequences in two genera: *Dicraeosaurus* Janensch (1914) from the Upper Jurassic of Tanzania, and *Amargasaurus* Salgado and Bonaparte (1991) from the Upper Neocomian of Argentina, in both cases with cranial remains from the temporal region that serve to better evaluate the differences or similarities of the vertebrae in a better measure of anatomical references.

It has sometimes been said (McIntosh, pers. comm.) that the vertebral morphology of sauropods is so varied that two neighboring vertebrae within a single taxon can show marked differences. It is worthwhile to remember here that in a mammal the differences between M2 and M3 can be so marked that if considered as isolated elements they can cause serious confusions to those who are not familiar with its anatomy. This topic, discussed later on, is in *Dicraeosaurus-Amargasaurus* a fortunate demonstration that the variation exists, but internal types are well defined and morphologically stable. It could not be otherwise, because the vertebral types would have been controlled instead in their development by a conservative origination in each group or sauropod clade. Still, when this is not known experimentally, it can be inferred starting from what is observed in the most diverse groups of living tetrapods, which show stable, constant vertebral types within the diverse genera and species that form a larger group.

Primitive characters persist in the vertebrae of *Dicraeosaurus-Amargasaurus*. They are: pleurocoels absent in the mid and posterior dorsals; little or no elaboration of the posterior fossa of the cervical vertebral centra; posterior (and not dorsal) exhibition of the diapophyseal lamina of the cervicals; relatively low number of cervical vertebrae (10 in *Dicraeosaurus*, 12 in *Amargasaurus*); and little development of opisthocoely, involving more presacral vertebrae than in *Patagosaurus* but less than in the Upper Jurassic sauropods that are commented on in this work.

On the other hand, derived characters are present in the extra development of the neural spines of the cervicals (*Dicraeosaurus*), or cervicals and anterior dorsals (*Amargasaurus*), the great lengthening of the neural arch of the dorsals relative to the vertebral centrum, the wide development of the posterior lamina in the upper half of the neural spine of the posterior dorsals, and the absence in almost all the dorsals of the anterior infradiapophyseal fossa, giving this vertebral type a mosaic of derived and primitive characters not registered in other sauropods, which can contribute to elucidating its phylogenetic position among those sauropodomorphs.

DESCRIPTION AND COMMENTS

Anterior cervicals. Cervicals 2-4 not only have neural spines that are dorsoventrally hypertrophied, but also are located very posterior relative to the vertebral centrum. The diapophyseal lamina is exposed posteriorly and is continuous with the neural spine (starting from the 4th in *Dicraeosaurus*). There are no special features in these anterior cervicals, such as small pleurocoels or edges, that suggest special muscle insertions. In the 3rd and 4th cervicals, the bifurcation of the neural spine is deep, especially in the 4th.

Mid- and posterior cervicals. The number of cervicals would not have included more than 10 vertebrae, as deduced from the volume of the diapophyses, which is a low

number for sauropods. In all these vertebrae of *Dicraeosaurus* the neural spines are inclined forward, whereas in *Amargasaurus* they are more normal, that is to say bowed back or vertical, but hypertrophied. In cervicals 7-10 it is observed that the diapophyseal lamina, exposed posteriorly, possesses a very marked, deep depression next to the base of the neural spine, which diminishes in depth anteriorly. In *Amargasaurus* this depression is more marked and elaborated than in *Dicraeosaurus*. The vertebral centra do not show more derived characters than those present in *Patagosaurus* Bonaparte (1986a).

Anterior dorsals. The first two dorsals only possess the vertebral centra, which both resemble the cervical centra, having very defined pleurocoels. Posteriorly the pleurocoels are less marked, reaching up to the 4th and continuing back as only a weak fossa.

From dorsal 4 back the very high dorsal vertebrae are manifest, with a ratio between the height of the neural arch and the vertebral centrum of 4 to 1, with slight variations. In the neural arch, the bifurcation of the spine is deep in the first three dorsals, diminishing posteriorly. The anterior infradiapophyseal fossa is present in the first two dorsals, having disappeared in the following vertebrae, which is a derived character. The central infradiapophyseal fossa is wide, being prolonged forward up to the prezygapophyses. In their posterior face this fossa shows a deep depression that I have not observed in other sauropods, and that was probably the insertion site for the hypaxial musculature, possibly for interconnecting the dorsals, perhaps paralleling the function of the absent pleurocoel in these vertebrae.

Mid- and posterior dorsals. In the following dorsals, between the 5th and 8th, the general structure is as for the anterior dorsals except that the vertebral centra do not possess pleurocoels, and the neural spines are somewhat longer. The decrease in the bifurcation of the spine is marked, to the point that in the 8th it only impacts half of the spine. In this vertebra each half of the neural spine is made more laminar, being transitional to the structure of the posterior dorsals that have a transversely wide, laminar spine, the upper region expanded relative to the inferior one, and well-developed pre- and postspinal laminae, all derived characters relative to *Patagosaurus-Diplodocus*.

The transverse processes are fairly high in practically all these vertebrae, delineating a wide space for the hypaxial muscles.

In *Dicraeosaurus* the last 5 dorsals are not affected by bifurcation of the spine, on the other hand in *Amargasaurus* only the 3 last lack evidence of bifurcation.

In summary, the vertebrae of the “dicraeosaurid” morphotype show derived and primitive characters whose association characterizes them very well. Their construction is light and high, with proportionally small vertebral centra, and a reduced number of cervical vertebrae. The derived characters relative to the condition in *Patagosaurus-Diplodocus* are the following: 1 – neural spines of the cervical vertebrae lengthened dorsoventrally, reduced anteroposteriorly; 2 – marked posterior depression in the posterior diapophyseal lamina of the cervicals and first dorsals (in *Diplodocus* the depression is dorsal, see figures 20 and 21); 3 – strong posterior depression in the central infradiapophyseal fossa of the anterior dorsals; 4 – very high dorsal vertebrae, with centra proportionally small (ratio of the total height of the dorsal vertebrae to the height of the vertebral centrum: 4 to 1); 5 – absence of the anterior infradiapophyseal fossa from 3rd dorsal back; 6 – pre- and postspinal laminae well developed starting from dorsal 10 in *Dicraeosaurus* and dorsal 12 in *Amargasaurus*; 7 – posterior (not supradiapophyseal) laminae less developed in the upper half of the neural spine in those posterior dorsals affected by bifurcation.

The most prominent primitive characters are: a) – little elaboration of the posterior fossa of the cervical vertebral centra; b) – pleurocoels absent in the vertebral centra starting from dorsal 5 back (condition comparable to *Patagosaurus*); c) – presence of 10 to 12

cervical vertebrae (a low number among sauropods); d) – little development of opisthocoely, until dorsals 4-5.

Dicraeosaurus-Amargasaurus conserve diverse primitive characters that prevent linking them with any one of the sauropod groups from the Upper Jurassic, such as Diplodocidae, Brachiosauridae, Camarasauridae, or *Haplocanthosaurus*. Their phylogenetic position seems to correspond to the level of *Patagosaurus* or perhaps even more primitive. For a different interpretation, it would be necessary to think of various concomitant, interrelated reversals (such as the reduced number of cervicals, the lack of elaboration of the posterior depression of the centrum of the cervicals, pleurocoels lacking in most of the dorsals, modest fossae of the well-known individuals). I do not believe that this group of characters reasonably can be interpreted as reversals.

“HAPLOCANTHOSAURID”-TYPE VERTEBRAE

The presacral vertebrae of *Haplocanthosaurus* (Hatcher 1903) are very well known thanks to that author’s very cultured works. Hatcher (1903) described the species *H. priscus* and *H. utterbacki*, and concluded that although *Haplocanthosaurus* and *Cetiosaurus* Owen (1841) are generically different, they could well correspond to the same family (Hatcher, 1903:54). From then until now, it has been considered that *Haplocanthosaurus* is a primitive member of Cetiosauridae (McIntosh, 1990). Nevertheless Bonaparte (1986b) pointed out some important differences between the vertebrae of the cetiosaurids *Patagosaurus* Bonaparte (1979; 1986b) and *Barapasaurus* Jain et al. (1975) and those of *Haplocanthosaurus*, concluding that those types with different vertebrae should correspond to different sauropod families.

If, as is postulated in this work, the presacral vertebrae of sauropods gather characters firmly diagnosing different taxonomic categories, the differences among the presacral vertebrae of *Patagosaurus* (Cetiosauridae) and those of *Haplocanthosaurus* that are markedly greater than between *Patagosaurus* and *Diplodocus* Marsh (1878) inevitably lead to the recognition that *Haplocanthosaurus* corresponds to a different family of sauropods. *Haplocanthosaurus* is markedly more derived than the genera of Cetiosauridae (*Cetiosaurus*, *Patagosaurus*, *Barapasaurus*), as it is more derived than *Diplodocus* in some important characters of the presacrals, which can be appreciated in the following discussion of its vertebral anatomy.

The cervical number of 15 interpreted by Hatcher (1903) seems considerably overestimated, as McIntosh has remarked (1990). Nevertheless, for lack of direct observations on the material needed to infer the number of cervicals, I do not have information to alter Hatcher’s interpretation. For this reason, I accept the number of 15 cervicals with a query.

The presacral vertebrae of *Haplocanthosaurus* are characterized by a certain homogeneity in their cervical and dorsal type, in such a way that I retain 4-5 vertebrae as involved in the cervico-dorsal transition, the remaining cervicals on the one hand and the dorsals on the other not showing marked changes from one other.

DESCRIPTION AND COMMENTS

Anterior cervicals. In *Haplocanthosaurus* only cervical 4 and a small part of cervical 3 are known of the anterior cervicals. In the vertebral centrum the posterior depression possesses two wide and deep pleurocoels separated by a clear vertical edge. In *Patagosaurus* and *Volkheimeria* Bonaparte (1979), the posterior depression of the centrum is less elaborated, generally just by a wide depression, sometimes deep in its more anterior part. Only occasionally in some cervicals of *Patagosaurus* a modest edge appears that spreads out

to define two fossae.

In the neural arch of *Haplocanthosaurus* we see some derived characters relative to *Patagosaurus*: a) the neural spine is not individualized in posterior view by a greater development of the suprapostzygapophyseal lamina connecting the neural spine with the epipophysis. This type of neural spine is also present in cervical 3, incomplete in *Haplocanthosaurus* (Hatcher 1903, Pl. II, 4), representing a derived condition relative to *Patagosaurus* and *Diplodocus*; b) a deep posterior fossa in the diapophyseal lamina, limited medially by a marked edge formed by the supraprezygapophyseal lamina. Comparable characters do not exist in the cervicals of *Patagosaurus*, whereas in *Diplodocus* there are similar features in the posterior cervicals. In such a way it is interpreted that the anterior cervicals of *Haplocanthosaurus* are more clearly derived than in *Patagosaurus* and, to a lesser degree, are also more derived than in *Diplodocus*.

Posterior cervicals. The posterior cervicals of *Haplocanthosaurus* maintain the differences mentioned for the anterior cervicals relative to *Patagosaurus*. That is to say that: a) the neural spine is continuous with the border that connects with the epipophysis; b) the diapophyseal lamina shows a deep depression limited medially by a marked edge; and c) in the vertebral centrum the fossa is occupied by two very defined pleurocoels, separated by a dorsoventral edge. All the characters of the neural arch are derived with regard to *Patagosaurus*.

Compared with *Diplodocus*, only the continuity between the superior border of the spine and the epipophysis shows that *Haplocanthosaurus* is more derived. In the rest of the characters a greater elaboration is easily appreciated in the posterior cervicals of *Diplodocus*. This genus has developed other possibly comparable but more complex characters, as is the case of the structure of the posterior fossa of the vertebral centrum.

It calls attention to the small relative size of the vertebral centra of these cervicals in *Haplocanthosaurus*, which probably represents a derived character.

Anterior dorsals. A remarkable similarity is observed between the particular orientation of the neural spines of dorsals 2, 3 and 4 of *Haplocanthosaurus* and *Diplodocus*, which in turn differ from the orientation of those spines in *Patagosaurus*.

The derived characters relative to *Patagosaurus* that are shown in these vertebrae are: a) diapophyses of high position, b) zygapophyses of high position, c) large pleurocoels, d) vertebral centra of small size in the first dorsals.

In *Haplocanthosaurus* the two infradiapophyseal laminae are present in the anterior dorsals, up to dorsal 5, although starting from dorsal 3 back the anterior infradiapophyseal lamina shows a strong reduction.

Among the primitive characters that are observed in the anterior dorsals of *Haplocanthosaurus* we point out the following: a) neural spines not reduced, b) high neural arch, and c) presence of both infradiapophyseal laminae until the 5th.

Mid- and posterior dorsals. In the mid and posterior dorsals of *Haplocanthosaurus* (from the 6th dorsal) important derived characters are observed that reveal the evolutionary degree reached by this genus in its presacral vertebrae. They are: a) disappearance of the anterior infradiapophyseal lamina starting from the 6th; b) deep and wide axially-positioned fossae below the zygapophyses, with a transverse bony partition that separates the anterior fossa from the posterior one, forming an H in cross-section; c) parapophyses and diapophyses of high position; d) presence of prespinal and postspinal laminae from dorsals 6-7 back; e) large pleurocoels; f) short neural spines; g) union of the suprapostzygapophyseal and supradiapophyseal laminae from dorsals 7-8 back; h) deep posterior depression under the diapophyses and before the infradiapophyseal lamina, from dorsals 6-7 back.

The significance of these derived characters allows us to interpret that the mid and

posterior dorsals are, in general, more derived than in *Patagosaurus* and *Diplodocus*. For example, the supraneural cavity that is present in Cetiosauridae, *Diplodocus*, and *Camarasaurus* Osborn and Mook (1921) is nonexistent in *Haplocanthosaurus* as a result of an anteroposterior process of reduction that has affected that cavity (Bonaparte, 1986b).

Other characters are more derived than in *Camarasaurus* and *Brachiosaurus brancai* (Janensch 1914), like the very dorsal position of the zygapophyses, the greater distance between the vertebral centrum and the transverse processes, and the proportional reduction of the vertebral centra.

The presence of certain primitive characters next to those derived ones mentioned above, force the admission of a different systematic position for *Haplocanthosaurus* relative to other sauropods. Among them: a) vertebrae amphiplatyan from dorsal 8 back; b) non-forked neural spines; and c) high number of dorsal vertebrae.

In synthesis, the presacral vertebrae of *Haplocanthosaurus* represent a different morphological type from that of other sauropod families, and it should be recognized as such. The similarities with Cetiosauridae are almost nonexistent when it is compared to them in detail. Obviously *Haplocanthosaurus* is more derived than *Cetiosaurus*, *Patagosaurus*, and *Barapasaurus* in important characters.

There are some similarities in the orientation of the neural spine of the last cervicals and first dorsals with the morphotype present in *Diplodocus*. These similarities can be interpreted as a result of certain taxonomic vicinity, or as parallel development. But in most of the characters commented on above there are very marked differences that coincide in indicating a more derived state for *Haplocanthosaurus*. Because of the aforementioned ideas the recognition of the family Haplocanthosauridae nov is proposed.

“TITANOSAURID”-TYPE VERTEBRAE

The vertebrae of “titanosaurid”-type that are discussed here correspond to some genera included in Titanosauridae according to the systematic interpretation of Powell (1986; 1987). I consider that the concept of Titanosauridae presented by Salgado et al. (1997:20) is too inclusive, including in that family genera with very diverse vertebral characters. The interpretation of Upchurch (1995) is similar to that of Powell.

Only in some Titanosauridae s. str., such as *Saltasaurus* (Bonaparte and Powell, 1980) and two individuals of Titanosaurinae indet. from the Upper Cretaceous of Brazil studied by Powell (1987), are there series of presacral vertebrae useful for study and comparison. Other genera of Titanosauridae s. str., such as *Neuquensaurus* (Powell, 1986) and *Argyrosaurus*, only have some presacral vertebrae but complete sequences are not known. Other genera like *Antarctosaurus* Huene (1929) and *Aeolosaurus* Powell (1986) do not have vertebrae useful for study.

The few available presacral vertebrae of *Andesaurus* (Calvo and Bonaparte, 1991) and *Argentinosaurus* (Bonaparte and Coria, 1993), titanosaurs referred to the family Andesauridae by the last mentioned authors, although discussed later on, cannot be analyzed comparatively until more complete materials are available.

Finally, what we have of the presacral vertebrae of Titanosauridae *sensu* Powell (1986) seems sufficiently clear for defining their morphological type and carrying out basic comparisons with other families of Sauropoda. We can point out the presacral vertebrae of this family in order to gather a series of very derived characters relative to the “cetiosaurid”-type and different from those of other derived families, to the point that it would be very doubtful, for the time being, to trace their possible relationships with other sauropods families.

The series of presacral vertebral series is composed of 13 cervicals and 10 dorsals, all

opisthocoelous according to the observations of Powell (1987) on articulated sequences of Titanosaurinae indet. from Brazil. This number of vertebrae could be a primitive condition for the first number of cervicals, comparable to that present in *Patagosaurus* (Bonaparte 1986a). Nevertheless, it could also be a regression due to the great temporal distance between the times of occurrences of these and other sauropods.

Also the total absence of bifurcation of the neural spine in well-known titanosaurs, not only of Titanosauridae, points out another primitive condition, which does not mean that the general morphology of the presacral vertebrae of titanosaurs can be considered primitive. On the contrary, and especially in the cervicals, the derived condition is manifest in a very different manner from that of the Jurassic sauropods considered above.

SALTASAURUS AND TITANOSAURINAE INDET.

Anterior and mid-cervicals. *Saltasaurus* Bonaparte and Powell (1980) possesses some complete anterior cervicals (figure 30A, B). In the axis, the vertebral centrum and neural arch are proportionally short and high, differing from the rest of the cervicals. The neural spine is thick and very wide in its posterior sector, especially due to a posterior expansion that occupies the dorsal part. The robustness of the axis is exceptional, especially for the bony mass of the neural arch, which is much bigger than the vertebral centrum. Functionally it might be thought that such a solid and proportionally tall structure would be linked to very strong movements of the skull. As much as it is possible, comparison of the proportions and morphology of the axis of *Saltasaurus* are exceptional among sauropods. In *Patagosaurus* and *Diplodocus* (Hatcher 1901) the axis is generally lengthened, approximately similar in proportions to the anterior cervicals. In *Saltasaurus* the situation is different, and it is probably the same, with some variation, in other Titanosauridae, according to what is indicated by a Titanosaurinae indet. axis from Peirópolis, Brazil, figured by Powell (1986, pl. 13, 1a and 1b). This interpretation has against it the relative morphological perseverance of the cervicals known in *Saltasaurus*, the articulated materials of Brazil (Powell, 1987), as well as an isolated, incomplete and uncertain cervical of Titanosauridae.

In an anterior cervical of *Saltasaurus*, probably the 3rd or 4th, and in the 4th cervical of the articulated series from Peirópolis, the following derived characters are observed relative to *Patagosaurus*: a) virtual disappearance of the neural spine, not observable in posterior view; b) horizontal, robust postzygapophyses located approximately at the level of the location of the neural spine; c) modified diapophyseal lamina, forming a wide, deep, and complex depression (figure 32B) between the base of the neural spine and the prezygapophyseal processes, particularly in *Saltasaurus*. It is a significant derived character that is present in all the cervicals of *Saltasaurus* and to a lesser degree in the mentioned cervicals from Peirópolis, Brazil; d) prezygapophyseal processes well separated from the neural spine; e) presence of an interprezygapophyseal lamina, oriented transversely and connecting both prezygapophyses; f) strong modification of the infrapostzygapophyseal constriction (figure 37E); g) reduction of the pre- and postspinal cavities; h) vertebral centrum low and wide, with not very deep posterior fossae and lacking the edge that limits them anteriorly; i) vertebral centrum relatively planar on its ventral surface.

These derived characters remains in the mid-cervicals with some appreciable modifications, such as the prezygapophyseal processes guided dorsally, and the development of an extra lamina behind the prezygapophyseal lamina, between the posteromedial part of the prezygapophyseal processes and the dorsomedial part of the diapophyseal depression.

In the Titanosaurinae indet. cervical series (series A, Powell, 1986; 1987) from the Baurú Group of Peirópolis, Minas Gerais, Brazil, is observed that although they are coincident in general with the cervicals of *Saltasaurus*, differences are appreciated that

suggest a less derived condition than in the *Salta* genus. They are:

a) The axis of Titanosaurinae indet. it is proportionally lower and more lengthened than in *Saltasaurus*; b) the surface of the diapophyseal lamina is less concave and more exposed posteriorly than in *Saltasaurus*; c) the postzygapophyseal processes are somewhat lower than the dorsal border of the neural spine; d) the infrapostzygapophyseal constriction is more marked; e) the parapophyses are more ventrally directed than in *Saltasaurus*.

All these characters are coincident in indicating that the Titanosaurinae indet. cervicals from Peirópolis (Powell, 1986; 1987) are more primitive than those of *Saltasaurus*. Nevertheless, they share the mentioned derived characters whose association differentiates them from the cervicals of *Patagosaurus* and other sauropods.

Posterior cervicals. Among the numerous materials of *Saltasaurus* Powell (1986), some cervicals posterior are recognized, with which the available information of the cervical sequence of this sauropod is broadened. These vertebrae are also present in the series corresponding to Titanosaurinae indet. from Brazil (Powell, 1987), which offers information for comparing and evaluating their characters.

The posterior cervicals are basically similar to the vertebrae that precede them, although they can be characterized by the wide vertebral centrum, with a strong posterior projection of the parapophyses, which continue in the ventral plane of the centrum posteriorly. The posterior face of the centrum is very reduced ventrally back, with a very limited posterior depression and occasionally with small pleurocoels.

The neural arch shows a lack of progressive development of the neural spine toward the posterior, although it is slightly higher on these vertebrae than the postzygapophyses.

Perhaps the more remarkable feature of the cervicals of *Saltasaurus* and the series from Peirópolis (Powell, 1986) is the markedly posterior position of the pre- and postzygapophyses, reaching a more posterior position than that of the vertebral centrum. This derived character is more marked in the posterior cervicals, but it is present with variations in all the cervicals. The anterior region of the neural arch does not possess the cavity between both prezygapophyses, because these pass posteriorly, which conforms to a group of derived characters of these vertebrae of *Saltasaurus*.

In this genus the diapophyseal lamina possesses a deep concavity toward the base of the neural spine, limited anteriorly by a rather thick bony edge that corresponds to the prezygapophyseal lamina. In the posterior sector, the cavity is limited by another edge that corresponds to the postzygapophyseal lamina.

The comparison of these posterior cervicals with those of *Patagosaurus* gives cause to recognizing the following derived characters: a) neural arch, including the spine, of reduced height; b) deep exposed posterior concavity in the base of the neural spine above the diapophyses; c) transversely extensive diapophyses, directed posteriorly; d) posterior fossae of the vertebral centra less deep and poorly defined; e) very modified infrapostzygapophyseal constriction (figure 40E); f) absence of the anterior fossa located between the prezygapophyseal processes; g) prezygapophyseal processes projected posteriorly.

Comparison of *Saltasaurus* and *Diplodocus* shows that in the Morrison genus the complexity of its characters has been developed without altering the basic plan present in *Patagosaurus*, whereas in *Saltasaurus* and other Titanosauridae a novel morphotype has been developed, with the virtual disappearance of the neural spine, the prezygapophyses directed posteriorly, the vertebral centrum low and wide with very reduced spaces for the pleurocoels, reduction of the infrapostzygapophyseal constriction, etc.

The diverse origination and insertion areas for muscles and tendons that can be inferred in *Saltasaurus* are very different from the structure seen in *Diplodocus*. We interpret that such differences are the result of the development of fundamentally different adaptive

types. An important difference that can endorse this supposition is that the neural spines of the cervicals of *Diplodocus* are very apparent in the whole cervical series, with an increase in size and posterior surface in the 14th and 15th cervicals, whereas in Titanosaurinae indet. (Powell, 1987) the spines are weakly manifest in the last 3 cervicals, reflecting a basically different plan and volume of epaxial muscles: very derived in *Diplodocus*, possibly starting from the plan present in *Patagosaurus*; and very also derived in Titanosaurinae indet. starting from a muscular plan for which currently we have no osteological antecedent.

Anterior dorsals. The most anterior dorsals, 1st and 2nd, of *Saltasaurus* (figure 30) are characterized by a higher vertebral centrum than in the cervicals, with a modest pleurocoel in the posterior face and a concave inferior border.

The neural arch is high, with the neural spine long in its anterior part, and wide for the well-developed transverse processes, angled slightly up. The prezygapophyses are far from the axial plane (as in the posterior cervicals), and there is a wide bony depression between the prezygapophyses that continues back up to the base of the neural spine.

The neural spine is anteriorly almost planar, with slight indications of a rudimentary prespinal lamina. A slight transverse concavity is appreciated that forms a continuous surface with the dorsomedial plane of the transverse processes. In other words, a wide cavity or depression exists limited by the neural spine and posteriorly by the transverse processes, with an exposed floor dorsally that is not much above the neural canal. This wide cavity seems an important adaptative novelty.

The prezygapophyses, very separate from each other, show two bony “pillars” for support, very defined and vertical in position, with a brief fossa between them.

In posterior view, the postzygapophyses are very separate from each other, oriented ventrolaterally, with the ventral sector being part of the posterior surface of the neural arch. An incipient postspinal lamina is appreciated.

As for the high position of the transverse processes and the brevity of the neural spine in their posterior view, it seems clear that the hypaxial musculature had a greater development than the epaxial, a situation that is appreciated more clearly in the mid and posterior dorsals.

In the anterior dorsals of the Peirópolis series illustrated by Powell (1986, 1987), an increase is appreciated in the length of the neural spine (figure 32A, B) and the neural arch, but seemingly the spine does not have the flat anterior surface as is the case in the 2nd or 3rd of *Saltasaurus*.

Mid- and posterior dorsals. The mid and posterior dorsals are relatively uniform (figure 32E, F), with not very evident morphological changes, but with appreciable differences between those of *Saltasaurus* and those from Peirópolis (figure 34D). The posterior vertebral centrum is rather subcylindrical and lengthened, markedly opisthocelous, with a concave ventral border and moderate pleurocoel.

The neural arch is relatively high, with the transverse processes directed posterodorsally in such a way that in posterior view its ventral face is appreciated. The neural spine is short and thick, overcoming the height of the transverse process slightly in *Saltasaurus* and in a greater proportion in the series from Peirópolis. The neural spine is oriented somewhat back, and it is proportionally robust, presenting its extensive anterior face dorsoventrally, whereas its posterior face is very reduced for a posterior diapophyseal lamina that passes back. Actually it is a lamina between the anteroposterior border of the neural spine and the posterior border of the diapophyses. It seems to be a different structure from that called supradiapophyseal lamina, thus representing a characteristic feature of this vertebral morphotype. The spines have a prespinal lamina, extensive dorsoventrally, of little height in *Saltasaurus* but prominent in the series from Peirópolis. The presence of edges or

small laminae is observed in the neural spine of *Saltasaurus*. One of them, of anteroposterior position, unites to the posterior part of the diapophyses, and another, posterior, corresponds to the suprapostzygapophyseal lamina.

In the posterior dorsals, the neural spine is of very posterior position, especially in the series from Peirópolis, recalling the condition present in some Jurassic sauropods such as *Diplodocus*, *Patagosaurus*, etc.

The posterior infradiapophyseal lamina is very modified relative to the condition present in e.g. *Patagosaurus-Diplodocus*. It is a simple lamina, very blunt in its dorsal sector and more laminar in the ventral sector where it unites with, or forms, the posterior border of the neural arch, defining a deep cavity, angled downward. In the articulated series from Peirópolis a pronounced fossa is observed in the centrum on the posterior face of the neural arch, limited posteriorly by the posterior infradiapophyseal lamina, and anteriorly by the infrapapophyseal lamina. In *Saltasaurus* it only exists as a depression, less deep and imprecisely defined.

The most significant derived characters in the posterior dorsals of *Saltasaurus* and the series from Peirópolis that we have been able to distinguish are the following: 1) diapophyses directed dorsolaterally with a lamina that connects their posterior border with the anterolateral sector of the neural spine; 2) neural spines with posterior faces very brief dorsoventrally, whereas the anterior face is extensive in that direction, with a brief prespinal lamina; 3) greater space for the hypaxial musculature and smaller space for the epaxial muscles; 4) deep fossa formed by the ventral sector of the posterior infradiapophyseal lamina and the posterior border in the neural arch; 5) absence of the anterior infradiapophyseal lamina or strut; 6) marked fossa or depression in the posterior face of the neural arch formed between the infradiapophyseal and infrapapophyseal laminae; 7) presence of a space limited by the anterior border of the neural spine and the internal faces of the transverse processes that should harbor musculature linked to the intervertebral connections, and that corresponds to part of the space that accommodates the posterior region of the spine of the preceding vertebra; 8) great development of the macrocellular system in all the dorsals.

ARGYROSAURUS LYDEKKER 1893

Although only a few presacral vertebrae are known of this Titanosauridae, I consider it important to describe and illustrate them in order to have wider information of this sauropod family. Following Powell (1986) we consider this genus as a Titanosauridae s. str. We have 3 dorsal vertebrae of *Argyrosaurus*. The opisthocoely is still marked in the available posterior dorsals. Contrary to *Saltasaurus*, the transverse processes pass more posteriorly, giving greater individuality and length to the neural spine. In an anterior dorsal vertebra (figure 33A) it is observed in posterior view the existence of an infradiapophyseal lamina that forks ventrally, forming an anterior lamina and another posterior lamina. It is a primitive character that I have not observed in other titanosaurs, but that is present in prosauropods (figure 11), *Patagosaurus* (figure 18), *Diplodocus* (figure 21), *Brachiosaurus* (figure 25), etc.

In the half-dorsal of *Argyrosaurus* (figure 35B) a very defined lamina arises from the base of the infradiapophyseal lamina and is oriented dorsoposteriorly to finish more anteriorly than the postzygapophyses. This lamina is not present in *Saltasaurus*, and together with the infradiapophyseal lamina forms a large, deep, angular fossa, with the vertex down. Behind and medial to the mentioned lamina is the infrapostzygapophyseal lamina that also forms another angular fossa with the vertex down. In anterior view, this vertebra presents, at the height of the prezygapophyses, a wide fossa with high posterior borders that form a wide semicircular space jointly with the base of the neural spine. A similar, but not identical,

character was illustrated by Powell (1992, fig. 10) for the 2nd or 3rd dorsal of *Saltasaurus*. It is a derived feature, possibly present in all Titanosauridae.

A posterior, quite complete, opisthocoelous dorsal (figure 35C) is observed to possess a proportionally larger and deeper pleurocoel than in other titanosaurs. Also in this vertebra the infradiapophyseal lamina forks ventrally into an anterior lamina and another posterior one, delimiting a modest fossa.

As the parapophyses has a high position, almost at a level with the diapophyses, it possesses an extensive infrapapophyseal lamina that limits the anterior border of the neural arch. Between this lamina and the anterior infradiapophyseal lamina, a wide subtriangular space exists that becomes more narrow ventrally. In the superior half of that space exists a fossa or cavity, ventrally angular, deep, and oriented medially, that possibly communicated with a supposed internal cavity, in which case it would be a primitive character present in *Patagosaurus* and *Diplodocus* (Bonaparte, 1986c).

The diapophyses is not oriented dorsally as in *Saltasaurus*, but mainly posteriorly. From their posterior end the thick and wide supradiapophyseal lamina unites to the extended neural spine. The width of this lamina makes a very wide concave surface that is observed in anterior view, amphitheater-shaped, deep dorsoventrally, located behind the prezygapophyses. In the axial plane of this wide concavity the modest but extensive prespinal lamina is located.

In the region of the postzygapophyses the typical structures of the hyposphene are not observed, absent in Titanosauridae s. str., but posteroventral bony edges are observed that can be interpreted as being derived from the hyposphene, as is present in *Argentinosaurus* (Bonaparte and Coria, 1993), although regrettably they are not very well enough preserved in these vertebrae to interpret them appropriately.

Discussion. In sum, we can point out that the presacral vertebrae of the “titanosaurid”-type, exemplified by those corresponding to *Saltasaurus* (Saltosaurinae) and the vertebral series from Peirópolis studied by Powell (1986, 1987) corresponding to a Titanosaurinae, show the following derived characters relative to *Patagosaurus-Diplodocus*: a) – extreme reduction of the neural spine in the anterior and mid-cervicals, and neural spines very low in the posterior ones; b) – very low cervical neural arches, with the postzygapophyses adjacent to the vertebral centrum; c) – long, thick postzygapophyseal processes, without the prominent suprapostzygapophyseal lamina; d) – prezygapophyseal processes of very low position; e) – vertebral centra with faint posterior fossae and sometimes with modest pleurocoels; f) – spongy fabric of all the presacrals formed by bony macrocells; g) – infrapostzygapophyseal constriction extremely modified relative to that of Upper Jurassic sauropods; h) – diapophyses directed dorsolaterally.

I consider that due to the lack of more or less complete cervical and dorsal series in non-Titanosauridae s. str. titanosaurs it is not very wise to try and summarize the derived characters that characterize the Titanosauria. It is necessary to wait to have more information from enough genera like *Andesaurus*, *Argentinosaurus* and *Malawisaurus* that are discussed below, and that seem to be more primitive than Titanosauridae s. str. such as *Saltasaurus* and the Titanosaurinae indet. from Peirópolis (Powell, 1986; 1987).

PRESACRAL VERTEBRAE OF OTHER TITANOSAURIA

In other Titanosauria the readiness of information is not enough to have a wide panorama of the morphology of the presacral vertebrae. Nevertheless, I believe it is useful to include the available information that is important to more broadly evaluate the morphological diversity of the presacral vertebrae of Titanosauria.

ANDESAURUS BONAPARTE AND CALVO 1991

Of this genus 4 posterior dorsal vertebrae are known that were described, along with other postcranial material, by Calvo and Bonaparte (1991). The dorsals, one of which is illustrated in figure 36C, includes very different characters from those present in *Saltasaurus* and other Titanosauridae s. str., which encouraged the mentioned authors to propose the family Andesauridae (for anatomical characters to see the mentioned work).

The posterior dorsals of *Andesaurus* are slightly opisthocoelous, almost amphiplatyan. The neural spine is high, almost vertical, with a prominent prespinal lamina, and a smaller, but well-developed postspinal lamina. The transverse processes, up to what it is possible to infer, would have projected posteriorly.

Perhaps the most remarkable character in these vertebrae, and which is different from those of the Titanosauridae, is the presence of well developed hyposphenes, lingering posteroventrally by means of a lamina that unites it to the base of the neural arch. Undoubtedly it is a derived condition relative to *Patagosaurus* Bonaparte (1986) and *Diplodocus* Hatcher (1901), in which the hyposphene is hanging. But at the same time it is primitive when compared with the additional articulations present in *Argentinosaurus* Bonaparte and Coria (1993), or with their absence in Titanosauridae s. str.

The vertebrae of *Andesaurus* are lacking the mentioned wide, amphitheater-shaped cavity that is observed in *Argyrosaurus*, exposed behind the prezygapophyses in anterior view.

ARGENTINOSAURUS BONAPARTE AND CORIA 1993

Of this gigantic titanosaurian (figure 36 A, B, D, E) three anterior and three posterior dorsal vertebrae are known, besides other materials that form the holotype of *A. huinculensis* (Bonaparte and Coria, 1993). These vertebrae are incomplete, although they offer broad, significant information.

The anterior dorsals (figure 36 A, B) possess horizontally-oriented transverse processes. The neural spine is transversely wide and axially brief, with a very modest prespinal lamina, and a still less evident postspinal lamina, which seems to correspond to a characteristic feature of this genus. In posterior view a marked depression is visible behind of the diapophyses and the area of the postzygapophyses. In this depression a wide foramen exists that communicates with the interior of the neural arch. Another foramen of appreciable size is dorsal to this, in the posterior face of the neural spine. In both cases these openings are also observed in posterior view, and are possibly characteristic features of *Argentinosaurus*.

In posterior view of the posterior dorsals (figure 36D), it is observed that the infradiapophyseal lamina is not forked, and that it would represent the only dorsoventral structure present in this view. In front of that lamina and up to the parapophyses, a wide depression exists with a large foramen that connects with the interior of the neural arch.

In anterior view (figure 34E), the region of the prezygapophyses, transverse processes and base of the spine form a wide and robust structure, with wide and complex hypantra that, together with the hyposphenes, form the extra articulations. These complex articulations are considered a derived character for the dorsals of *Argentinosaurus*.

In the posterior dorsals the character of the infradiapophyseal lamina remains the dominant dorsoventral structure, partly by the great dimension of the fossae located in front of and behind that lamina, which evidently is a remarkable derived character of *Argentinosaurus*, (figure 36D) shared partly by the series from Peirópolis.

The diapophysis is oriented posterodorsally, and the infrapapophyseal lamina unites ventrally with the base of the infradiapophyseal lamina, skirting ventral to the anterior fossa

mentioned above. The accessory articulations formed by the posterior continuations of the hypantrum and hyposphene are very clear as seen in figure 36D.

MALAWISAURUS JACOBS ET AL. 1993

Jacobs et al., (1993) described material from Malawi that they referred to *Malawisaurus dixeyi* (Haughton 1928) comb. nov. Those authors assigned *Malawisaurus* to the family Titanosauridae. In my opinion *Malawisaurus* is morphologically distant from any Titanosauridae s. str. It is more primitive and requires placement in a different family, perhaps Andesauridae, although regrettably we still do not know the details of the dorsal vertebrae of *Malawisaurus*. Nevertheless, the cervical vertebra illustrated by those authors provides important information for comparing it with other titanosaurs.

The cervical vertebra is rather large, almost 38 cm long and 41 cm high (figure 37). A significant character that distinguishes this vertebra from that of any other titanosaurian is the primitive morphology of the neural spine. In *Saltasaurus* (Bonaparte and Powell, 1980; Powell, 1992) and Titanosaurinae indet. from Peirópolis (Powell, 1986; 1987), the neural spines are extremely reduced (figures 32, 33) to the point that their height barely exceeds the height of the zygapophyses. In *Malawisaurus* the dorsoventral extension of the neural spine is approximately half the total height of the vertebra.

Other characters, also primitive and probably related to the height of the spine, are manifest in the morphology of the pre- and postzygapophyseal processes. Invariably in Titanosauridae the postzygapophyseal processes are subcylindrical, dorsoventrally low, and have a subhorizontal position. In *Malawisaurus* the postzygapophysis is connected to a dorsally-directed bony lamina and is oriented anteriorly toward the peak of the neural spine.

Also as to the prezygapophyseal process, we see that in Titanosauridae there is an inflection (very marked in *Saltasaurus*) where this process begins, a character that is not observed in the figured cervical referred to *Malawisaurus*. Nevertheless, the morphology of the vertebral centrum, with absent or almost absent pleurocoels or posterior depressions, coincides with what is known of titanosaurs. It also offers similar information regarding the region located in front of the postzygapophyses, which is reduced dorsoventrally and probably wide transversely. In summary, this cervical referred to *Malawisaurus* (Jacobs et al., 1993) probably corresponds to Titanosauria (Bonaparte and Coria, 1993), but not to Titanosauridae (Powell, 1986, 1992; Bonaparte and Coria, 1993), with which it exhibits very marked differences.

OPISTHOCOELICAUDIA BORSUK-BIALYNICKA, 1977

This interesting sauropod genus from the Upper Cretaceous of Mongolia was described and illustrated by Borsuk-Bialynicka (1977), and considered as Camarasauridae, although that author recognized diverse similarities with “Titanosaurinae” (at the present time Titanosauridae, or of greater systematic breadth Titanosauria). The study of its dorsal vertebrae starting from the descriptions and illustrations presented by that author does not confirm its similarity with Camarasauridae, whereas it indicates with more probability its membership in Titanosauria (sensu Bonaparte and Coria, 1993), a conclusion also proposed by Upchurch (1995) and Salgado et al. (1997).

In the first place, the dorsals of *Opisthocoelicaudia* show a very reduced space between the vertebral centrum and the location of the zygapophyses, such that there is no place for the wide supraneural cavity that *Camarasaurus*, *Diplodocus*, *Patagosaurus* and other sauropods of the Middle and Upper Jurassic possess. The lack of that space is a derived character observed in *Saltasaurus* and a Titanosaurinae indet., both from the Upper Cretaceous (Powell, 1986; 1987), which are discussed in this chapter, but that I have not

observed in other sauropods, even primitive titanosaurs such as *Andesaurus* (Calvo and Bonaparte, 1991) or *Argentinosaurus* (Bonaparte and Coria, 1993).

Anterior dorsals. In posterior view, the incomplete dorsal 1 of *Opisthocoelicaudia* shows an edge or posterior infradiapophyseal lamina, oriented back and below, in a form very similar to that present in dorsal 1 of a Titanosaurinae indet. individual (see figure 34). At the same time, it is very different from the characters of the more anterior dorsals of *Camarasaurus*, *Diplodocus*, *Brachiosaurus*, *Dicraeosaurus* or *Haplocanthosaurus*. The hyposphene-hypantrum absence that Borsuk-Bialynicka points out (1977) is a derived feature shared with Titanosauridae s. str.

Mid-dorsals. Also in posterior view, dorsal 6 of *Opisthocoelicaudia* shows characters similar to those of a number of Titanosauridae such as *Saltasaurus*, including an infradiapophyseal lamina; presence of the postdiapophyseal lamina that connects with the neural spine (in posterior view); presence of an infrapapophyseal edge; and other morphological details that can be appreciated in figure 32E. On the other hand, the mid-dorsals of Camarasauridae are basically different, in general and in detail, from dorsal 6 of *Opisthocoelicaudia*, particularly in posterior view. In anterior view there are certain general similarities, but they retain strong differences: a) the orientation, size and bony morphology of the prezygapophyses; b) the distance between the dorsal border of the centrum and the prezygapophyses; c) the morphology of the neural spine; d) the relative position of the diapophyses relative to the rest of the neural arch. With *Diplodocus* and other sauropods of the Upper Jurassic the differences are greater still.

Posterior dorsals. Dorsal 10 of *Opisthocoelicaudia* also compares with the posterior dorsals of Titanosauridae s. str. Here we see that in both forms the posterior diapophyseal lamina that connects with the anterolateral border of the neural spine is present. This shared derived character has not been observed in other sauropods. In *Camarasaurus* the mentioned posterior diapophyseal lamina is connected with the posterior border of the spine.

In the posterior dorsals of *Opisthocoelicaudia* the presence of a hyposphene-hypantrum is not clear according to the mentioned author. Probably, as in the anterior dorsals, these vertebrae did not possess those structures, which would identify it more thoroughly with Titanosauridae s. str.

In synthesis, the similarity of the dorsals of *Opisthocoelicaudia* are clearly more evident with genera of Titanosauridae s. str. from the Upper Cretaceous than with any sauropod from the Upper Jurassic. The bifurcation of the neural spines of *Opisthocoelicaudia*, which has not been registered among the Titanosauria, perhaps can be interpreted as a characteristic feature of the genus, that is to say a late development, convergent with the bifurcation of the spine that occurred in other sauropod lineages from the Upper Jurassic and Lower Cretaceous. It does not necessarily indicate a relationship with sauropods provided with forked spines, because this character is one among the many that the presacral vertebrae possess. As for the opisthocoelous condition, so remarkable and unique, of the 15 anterior caudal vertebrae, I believe that it should be interpreted with a certain amplitude of criterion, so it overcomes the simple morphological comparison and keeps in mind the existence of genetic and ontogenetic factors that could be responsible for the development of that character, without affecting the rest of the anatomical features of the caudal vertebrae.

Borsuk-Bialynicka points out (1977:15) that the first 15 vertebral centra are opisthocoelous in different degrees; centra 16-27 are amphiplatyan; and centra 28-34 are biconvex. Such a heterogeneous panorama in the condition of the vertebral caudal centra can well be a response to a very special ontogenetic development in that lineage, rather than a condition bound firmly to the phylogeny of *Opisthocoelicaudia*. With it alone I want to point

out that the ontogenetic development, as other many mechanisms of the vertebrate organism, is exposed to alterations that can appear at individual levels, and possibly at specific levels. This interpretation, which can seem to be lacking foundation, has a mark of non-worthless references at least, in the great similarity of the dorsal vertebrae, the scapular girdle, the forelimb, etc., that are observed when comparing *Opisthocoelicaudia* with Titanosauridae s. str. from the Upper Cretaceous of South America.

Diverse and significant differences are also naturally observed, e.g. the extreme ventral position of the 4th trochanter (and the trochanter located posteriorly to the 4th tr.) in the femur. Nevertheless, a general mark of similarity that suggests phylogenetic vicinity with Titanosauridae exists. My opinion is that *Opisthocoelicaudia* deserves an ad hoc family status, for which I propose the term Opisthocoelicaudidae nov that is part of a larger grouping alongside Titanosauridae and Andesauridae: Titanosauria (Bonaparte and Coria, 1993; Bonaparte, 1996).

“REBBACHISAURID”-TYPE VERTEBRAE

The inclusion of the rebbachisaurid type in this work only fulfills the purpose of pointing out that we have a type morphologically different in the presacral vertebrae, but which we do not still have the necessary elements to study with certain detail. Very little has been published until the present of *Rebbachisaurus* Lavocat 1954, but the existence of a practically complete dorsal vertebra of *R. garasbae* Lavocat 1954 in the Institute de Paléontologie of Paris, the recent description of great part of a skeleton of *R. tessonei* Calvo and Salgado (1995) from the Albian-Cenomanian of Patagonia, and the existence of some isolated material from the Neocomian of Neuquén, enlarge somewhat the availability of evidence on this novel grouping of sauropods.

Anterior cervical. Calvo and Salgado (1995) only illustrated an anterior cervical of *Rebbachisaurus tessonei* in posterior view, showing the derived character of a high neural spine, showing on the posterior half of the vertebral centrum. Only in *Apatosaurus* (Gilmore, 1936) and in *Dicraeosaurus* (Janensch, 1914) is an anterior cervical with a high neural spine observed, although of a different morphology from that present in *R. tessonei*.

Posterior cervicals. A posterior cervical of *R. tessonei* illustrated by Calvo and Salgado (1995, figure 8B) shows the high neural spine on the anterior half of the centrum, a character frequent among sauropods, e.g. *Patagosaurus*, *Diplodocus*, *Apatosaurus*, *Dicraeosaurus*, and *Haplocanthosaurus*. In the neural arch it shows a lamina that those authors called “accessory suprapostzygapophyseal lamina”, which has not been observed in other sauropods. The mentioned lamina, and another less extensive lamina located ventrally to the anterior one on the surface of the diapophyseal lamina, seem to represent derived characteristic features of these vertebrae. The vertebral centrum shows two wide pleurocoels separated by a dorsoventral edge, a character that indicates a condition more derived than in the “cetiosaurid”-type, and comparable to what is shown in some posterior cervicals of *Haplocanthosaurus* (Hatcher, 1904). In general terms, the posterior cervical illustrated in posterior view by the mentioned authors does not show significant derived characters, except the mentioned laminae which mostly do not impact on their general morphology.

Anterior dorsal. Calvo and Salgado (1995) illustrated an anterior dorsal of *R. tessonei* that, up to where it is possible to infer, also presents very widespread characters. The neural spine is of vertical position, the neural arch anteroposteriorly brief and proportionally high because it is 2.5 times higher than the vertebral centrum. The neural spine is formed by the four suprazygapophyseal laminae “that are connected dorsally” (Calvo and Salgado, 1995:20), which is a primitive character already present, with variations, in *Patagosaurus* Bonaparte (1986a).

Posterior dorsal. A practically complete posterior dorsal of *R. garasbae* exists. It is a very light vertebra, formed by very thin laminae in the neural arch, an extensive neural spine, and an amphicoelous to amphiplatyan vertebral centrum, provided with a wide pleurocoel.

The neural spine is very long, somewhat more than 4 times the posteroventral length of the vertebral centrum, considering it from a little above the postzygapophyses up to the more preserved dorsal part. The posterior borders of the spine are subparallel, with the dorsal part of the spine wider than the rest. The spine is formed by the prespinal and postspinal laminae, thin, of axial position, and only forking toward the zygapophyses in the ventral part. The posterior laminae of the spine, also thin, correspond to the supradiapophyseal laminae.

The transverse processes are projected posterodorsally, with a marked dorsal cavity that converges axially to a wide angular cavity, formed by the diapophyseal-postzygapophyseal and suprapostzygapophyseal laminae. Posteriorly, the ventral sector of the neural arch, between the transverse process and the dorsal border of the vertebral centrum, presents a wide posterior cavity defined anteriorly by the infraprezygapophyseal lamina, and posteriorly by the posterior infradiapophyseal lamina.

It does not possess a hyposphene, but does have two short infrapostzygapophyseal laminae. The vertebral centrum is not opisthocelous, although its posterior face is more concave than the anterior one. It possesses a wide and deep pleurocoel in the centrum along the length of the vertebral centrum.

The posterior dorsal illustrated by Calvo and Salgado (1995) is comparable to that of *R. garasbae*, but it is useful to point out that it does not correspond to the holotype of *R. tessonei* but to specimen MUCPv 206, referred by those authors to *R. tessonei*.

Comments. The posterior dorsals are probably those that better characterize this vertebral type. We can provisionally characterize it as presenting anterior cervicals with long neural spines, located on the posterior half of the vertebral centrum; posterior cervicals and very widespread anterior dorsals with few characters derived relative to *Patagosaurus*; and posterior dorsals formed by very thin laminae and deep depressions in the base of the neural spine, and in the posterior face of the neural arch below the transverse process. Vertebral centrum with large, very defined and deep pleurocoels. Hyposphene absence. Long neural spine, with subparallel posterior borders, somewhat divergent toward the dorsal end, and formed by 4 thin laminae: two spinal of axial position and two supradiapophyseal of posterior position.

Although some characters can recall the condition of *Dicraeosaurus-Amargasaurus*, others are very different, such as the formation of the neural spine, the fine laminae and strong hollows present in the neural arch, and likewise the marked pleurocoels.

Due to the lack of more information from associated individuals, I tentatively interpret that the type of presacral vertebrae, especially the posterior dorsals, present only in *Rebbachisaurus garasbae*, is very different from that registered in other groups of Sauropoda.

EVOLUTIONARY PANORAMA OF THE PRESACRAL VERTEBRAE

Of the description and discussion of the presacral vertebrae included in this study, partial interpretations are suggested that seem clear when they pertain to a determined taxon, or when we try to interpret certain characters isolated in a sequence. But the situation is more problematic when we try to interpret the possible phylogenetic relationships of sauropodomorphs starting from that analyzed in this work. There are two important restrictive factors that block this task. One is that semi-complete or complete presacral vertebrae are preserved particularly in a reduced number of genera that would only represent a fraction of the real existing diversity in Middle-Upper Jurassic and Lower-medial

Cretaceous times. A second factor is that, starting from the vertebral type of cetiosaurids or possibly before, a strong adaptive radiation would have taken place among sauropods, giving rise to the diversity registered in the Upper Jurassic of the Morrison, Tendaguru and China, and of which we do not have—as far as I know—sauropods with transitional or intermediate vertebral types, except in the case of *Patagosaurus-Diplodocus* where very clear linkings are observed.

In the case of titanosaurs we meet with a similar situation in that we do not have the smallest idea of their possible ancestors. Surely an increase in the availability of new appropriate materials, such as better access to the variety registered in the last 20 years in China, will enlarge the interpretive possibilities regarding the phylogenetic relationships among the different vertebral morphotypes. Nevertheless, we can point out some observations that could generate some hypotheses on the evolution of the vertebrae in sauropodomorphs. They are:

- 1 – the lengthening of the neck in sauropodomorphs was probably a characteristic inherited from their carnivorous ancestors, eventually more primitive ceratosaurs such as *Coelophysis*, and that formed a feature common to all them. The melanosaurid *Riojasaurus* represents the most primitive stage, and *Mamenchisaurus* Young and Zhang, 1972 represents the most derived one, that makes us admit that that tendency reached its maximum expression in the Upper Jurassic.
- 2 – the evident complexity of the muscular and tendinous insertions in the posterior cervicals and anterior dorsals of *Plateosaurus* reveal that the quality of managing long necks was more developed than in *Riojasaurus*, and that it would have been a quality progressively developed until overcoming the level of Cetiosauridae, with extreme manifestations in certain lineages (*Mamenchisaurus*).
- 3 – the dorsoventral lengthening of the dorsal vertebrae began to appear in very derived prosauropods such as *Lessemsaurus sauropoides* gen. et sp. nov. during the Upper Triassic, and in primitive sauropods such as *Lapparentosaurus-Volkheimeria*. This character would have conditioned by, or concomitant with, the beginning of gigantism among sauropods.
- 4 – the achievement of the infrapostzygapophyseal constriction appeared starting from prosauropods more derived than the typical Melanosauridae-Plateosauridae (e.g. *Lessemsaurus sauropoides* gen. et sp. nov. from the Los Colorados Formation), being differentially developed in diverse families from the Upper Jurassic-Lower Cretaceous, and reaching a very derived, extreme condition in Titanosauridae *s. str.*
- 5 – the deep depressions and fossae of the presacral vertebrae of sauropods, developed to their maximum expression in the region that includes the posterior cervicals and anterior dorsals, would have been linked to a complex axial muscular system, partly committed to handling of the neck, and not to a process of lightening the bony weight.
- 6 – the bifurcation of the neural spines would have been related to the derived condition of the insertion sites for the strong elastic ligament (Alexander, 1989), which originated in the sacral region and extended in both directions, cranial and caudal. This derived condition was only developed in some lineages, after overcoming the level of Cetiosauridae. Probably this ligament, less developed, was present already in prosauropods, which it is possible to infer from their presence of the intersegmental ligaments in *Alligator* (Frey, 1988).
- 7 – the opisthocoely incipiently developed in the cervicals of prosauropods, and clearly present in the cervicals and anterior dorsals of cetiosaurids, only overcame this stage in some lineages by including all the dorsals.

DISCUSSION OF SOME IMPORTANT CHARACTERS

Here I consider in comparative form some characters that can guide the interpretation of the direction of evolutionary changes, in certain cases starting from primitive archosaurs such as *Euparkeria* (Ewer, 1965) and *Fasolasuchus* (Bonaparte, 1981) or the basal dinosauromorph *Marasuchus* (Bonaparte, 1975; Sereno and Arcucci, 1994). The sequence of these subsequent characters is arbitrary, and does not indicate that a given character preceded to the following one.

Sigmoid neck. I have already pointed out above that the sigmoid development of the cervical series would have been an initial, basic achievement in the evolutionary history of saurischians. This character, very complex because of the development of the same one involved the morphologic differentiation of the two types of cervico-dorsal vertebrae, is already present in *Marasuchus* (Bonaparte, 1975; Sereno and Arcucci, 1994), but it is not observed in more primitive forms such as *Euparkeria* (Ewer, 1965), *Ornithosuchus* (Walker, 1964), *Riojasuchus* (Bonaparte, 1972), *Pseudhesperosuchus* (Bonaparte, 1972), *Gracilisuchus* (Romer, 1972), and *Fasolasuchus* (Bonaparte, 1981).

Dorsoventral lengthening of the dorsal vertebrae. In sauropodomorphs it is observed that the dorsals of typical prosauropods such as *Plateosaurus*, *Anchisaurus*, (Galton, 1973), and *Riojasaurus* (Bonaparte, 1972) are relatively low, with similar dorsoventral extensions of the vertebral centrum and the neural arch, with a ratio of approximately 1:1. In the prosauropod *Lessemsaurus sauropoides* gen. et sp. nov. from the Los Colorados Formation (figures 13-16), it is observed that the neural arch is markedly higher, with the neural spine prolonged dorsally, having a ratio between the height of the centrum and the height of the neural arch of 1:1.9, which represents a notable increase of the space to accommodate mainly the epaxial musculature. This ratio, visibly different from that of typical prosauropods, seems to mark the beginning of the very widespread characteristic among sauropods of possessing high dorsal vertebrae, with ratios of 1:2 in *Volkheimeria*, 1:2.2 in *Patagosaurus*, 1:3 in *Diplodocus*, 1:3.3 in an anterior dorsal of *Brachiosaurus*, 1:2 in a posterior dorsal of *Brachiosaurus*, 1:2 in *Camarasaurus*, 1:3.3 in *Dicraeosaurus*, 1:2 in *Haplocanthosaurus*, and 1:2 in *Saltasaurus*.

In *Marasuchus*, the basal dinosauromorph from the Middle Triassic of La Rioja, the dorsal vertebrae are low and primitive, with a ratio of 1:1.3, very similar to that of typical prosauropods.

This dorsoventral lengthening of the dorsals was not an exclusive character of sauropodomorphs because in some rauisuchians such as *Fasolasuchus* the ratio is 1:1.5, and in *Saurosuchus* it is 1:1.4.

As pointed out above, the difference in the ratios between typical prosauropods and primitive sauropods makes suggests that the proportional increase of the height of the neural arch would have been concomitant with a greater achievement of size than those of the mentioned prosauropods.

Infradiapophyseal fossae. The infradiapophyseal fossae are defined by the diapophyseal-prezygapophyseal, anterior infradiapophyseal, posterior infradiapophyseal, and diapophyseal-postzygapophyseal laminae. These four laminae, when they are present, define three fossae: the anterior, central, and posterior infradiapophyseal fossae.

It is these fossae where muscles probably originated and inserted, mainly part of the hypaxial system. The depth of the fossae and the height of the laminae would have offered greater areas for the origination and insertion of those muscles. If we ignore the specific function of each one of these fossae we cannot interpret whether the development of the same fossae was interrelated or whether they differed in independent form.

In *Marasuchus* the condition of the infradiapophyseal fossae is very primitive because the central infradiapophyseal fossa alone is observed in the posterior cervicals and supposedly in the most anterior dorsals. In the subsequent dorsals infradiapophyseal fossae limited by edges do not exist, but only a wide undifferentiated depression, located below the diapophyses.

If the small size of *Marasuchus* did not impact in the definition of the infradiapophyseal fossae, it should be admitted that this Middle Triassic genus presents the most primitive condition among the dinosauromorphs that we know. In some rauisuchians such as *Saurosuchus* and *Fasolasuchus* a very derived condition is observed. The posterior infradiapophyseal fossa is present in all the dorsals, whereas the central infradiapophyseal fossa is present alone in the 4 anterior dorsals, and the anterior infradiapophyseal fossa only in the anterior and mid-dorsals. If the condition in rauisuchians represents the approximate primitive condition for sauropodomorphs, and keeping in mind the condition present in *Marasuchus*, we can interpret that these infradiapophyseal fossae originated in the region of cervico-dorsal transition and thst from there they expanded through the entire, or almost entire (according to the case), cervical and dorsal region.

In *Riojasaurus* and *Plateosaurus* the distribution of these fossae is very similar, with the central and posterior infradiapophyseal fossae distributed from cervical 5-7 until the last dorsal. On the other hand, the anterior infradiapophyseal fossa is present in more vertebrae of *Plateosaurus* than *Riojasaurus*. In such a manner *Plateosaurus* is more derived in this character.

As we can see in Table 1, in *Patagosaurus* from the Middle Jurassic up to *Brachiosaurus* and *Diplodocus* from the Upper Jurassic, the maximum development of these fossae is observed, being clearly more derived than the prosauropods. In diverse lineages from the Upper Jurassic a partial reduction operated on that complex character. It is probable that the absence of the anterior infradiapophyseal fossa in some vertebrae, observed in *Camarasaurus* or *Dicraeosaurus* relative to *Patagosaurus*, represents a reversal to an authentic primitive character. This possible reversal only partly affected the anterior infradiapophyseal fossa of the dorsal vertebrae, because the remaining fossae did not revert.

From the analysis of the distribution of these fossae the following interpretation arises: 1) prosauropods present a greater number of vertebrae with these fossae relative to *Marasuchus*; 2) *Patagosaurus* developed a condition very derived relative to prosauropods, whereas the condition of *Patagosaurus*, with few variations, was conserved by *Diplodocus* and *Brachiosaurus* from the Upper Jurassic; 3) in *Camarasaurus*, *Haplocanthosaurus*, *Dicraeosaurus* and *Mamenchisaurus* a retraction operated on the anterior infradiapophyseal fossa in the region of the dorsal vertebrae, which is interpreted as a reversal.

Opisthocoely. In the Table 2 of the comparative development of opisthocoely among sauropodomorphs, some facts of interest are appreciated. In the first place we have the case of prosauropods, which do not show bony evidence of opisthocoely, but which possess characters in their cervical centra suggesting the existence of that character which, in their greatest part, would have been cartilaginous. In this manner we see that: 1) the cervical vertebral centra possess two concave ends that with difficulty represents a primitive condition. Rather it seems to correspond to an initial adaptation of opisthocoely in which the anterior condyle would have been formed by cartilage in order to accommodate the posterior end of the preceding vertebra; 2) the posterior concavity is well ossified along its entire perimeter, and its diameter is generally somewhat greater than that of the anterior end; 3) the anterior concavity does not possess a well-ossified border, and it shows a perimeter in its posterior and ventral faces where the cartilaginous would have been noticed.

Although the incipient opisthocoelous condition of prosauropods is no more than a

tentative interpretation, it seems probable that the amphiplatyan condition of primitive archosaurs has reverted to amphicoely in prosauropods provided with long necks. It is more probable that prosauropods had a condition previous to the opisthocoelous of sauropods.

Another important aspect of this Table on opisthocoely is that invariably this condition is present in sauropods starting from the axis throughout the cervicals. Opisthocoely, which would have been developed from the cervicals back, reaches to the first 2 or 3 dorsals in *Patagosaurus*, on the other hand it reaches up to the 5th in *Diplodocus*.

In *Haplocanthosaurus* and *Dicraeosaurus* opisthocoely reaches to the 7th and 8th dorsals respectively, and in *Mamenchisaurus* to dorsal 8. In *Camarasaurus* and *Brachiosaurus* opisthocoely reaches the last dorsal, as in Titanosauridae s. str.

It is evident that the maximum distribution of opisthocoely in the presacrals of sauropods was reached in the Upper Jurassic, in genera such as *Camarasaurus* and *Brachiosaurus*, and more belatedly in Titanosauridae s. str. and *Opisthocoelicaudia*.

Transversely wide neural spines. The panorama of the presacral neural spines, axially extensive and laminar, is present in the diverse Triassic archosaurs, which represents the primitive condition. The mid and posterior dorsals of *Herrerasaurus* (Novas, 1994) are modified, representing a substantially derived, but possibly sterile, morphotype. Evidently axially extensive neural spines is the ancestral condition that shows marked changes in *Plateosaurus* where we see a widening of dorsal end of the last cervicals and the first dorsals, in fact between the 2nd and 7th cervicals 7th inclusive. Functionally the mentioned widening would have been linked to muscle insertions for cooperating in the posterior movements of the neck.

In *Patagosaurus* the axially brief and transversely wide neural spines are present between cervical 6 and the last dorsal inclusive, with variations along the way.

In *Diplodocus* the widening of the spine reached the axis, besides covering all the cervicals and dorsals, a condition that is also observed in *Camarasaurus* and *Haplocanthosaurus*. In *Dicraeosaurus* the expansion of the spine begins at cervical 5, reaching up to the sacrals. In *Brachiosaurus* the available cervicals do not show signs of posterior expansion, but all the dorsals do. This unique condition would have been related, supposedly, to the high and non-pendant position of its long neck. In such a case, and keeping in mind the ancestral condition of cetiosaurids, one can interpret it as a reversal. Nevertheless, there is room for an alternative explanation, in the case that the adaptive type of an erect neck was already present in a level preceding that of cetiosaurids.

Relationship between the number of cervical and dorsal vertebrae. The primitive number of cervical vertebrae, present in *Marasuchus*, *Fasolasuchus*, *Riojasuchus* and other Triassic archosaurs, is 7-8. In prosauropods, although we see different degrees of cervicalization of the neck vertebrae, a cervical number of 9-10 seems widespread.

In *Patagosaurus* the cervicals reach 13, a number that is also present in *Camarasaurus* and *Brachiosaurus*. *Diplodocus* and *Haplocanthosaurus* possess 15 cervicals, and *Mamenchisaurus* with 19 cervicals shows the highest number among sauropods.

Dicraeosaurus and *Amargasaurus* possess 10 and 12 cervicals respectively, which is a primitive character that, if we associate it rather with the primitive type of neural spine up to the 5th cervical of *Dicraeosaurus*, next to the limited opisthocoely, and the pleurocoels lacking in almost all the dorsals, allows us to recognize that the dicraeosaurids from the Upper Jurassic retained important primitive characters from level preceding Cetiosauridae. This situation is less evident in *Amargasaurus*, from the Neocomian of Argentina.

Infrapostzygapophyseal constriction. The infrapostzygapophyseal constriction is an outstanding feature that characterizes the cervical vertebrae of sauropods. It is a character that results from the very high position of the postzygapophyses and the strong

infrapostzygapophyseal fossa. In posterior view (figure 40) this constriction is manifest immediately above the neural canal, from which point it is enlarged transversely up to the postzygapophyses and ventrally toward the vertebral centrum. Probably the maximum vicinity to the axial plane of this constriction was linked to origination areas for muscles guided obliquely back and out, involved in posterior movements of the neck. Tentatively we interpret that some of the muscles originated in the area of the mentioned constriction would have inserted on the cervical rib of the subsequent vertebra. In *Riojasaurus* and *Plateosaurus* I have not observed this constriction, but in the melanorosaurid *Lessemsaurus* gen. nov. a very significant initial stage is manifest (figure 40). In *Patagosaurus* the mentioned constriction is very well defined throughout the cervicals, although in the last one it begins to become enlarged transversely, and in the dorsals it is not present.

In some cervicals a short vertical lamina is occasionally observed (infrapostzygapophyseal lamina, Osborn and Mook, 1921) that adds to or arises from the posterior border of the constriction, which recalls the condition of *Diplodocus* and is commented on below.

In *Diplodocus* the constriction is present in all the cervicals, but cervicals 9-10 begin to show a dorsoventrally brief lamina that, mediating a brief space or fossa is added posteriorly (figure 40C), transversely enlarging the area of the constriction. This character is accentuated toward cervical 15 where the mentioned lamina (infrapostzygapophyseal lamina) reaches a very posterior position and is relatively far from the axial plane. Although the beginning of the development of laminae are occasionally seen in some cervicals of *Patagosaurus*, I believe that its perseverance in cervicals 12-15 of *Diplodocus* represents a derived character for this genus.

In *Camarasaurus* the constriction is simple until cervicals 5-6. But from the 7th back the presence of very defined infrapostzygapophyseal laminae is observed (figure 40D), forming two fossae separated from the axial plane for a bony strut that would have represented the primitive position of the maximum constriction.

In the posterior cervicals the mentioned laminae have become two robust bony processes that connect the inferior and posterior regions of the postzygapophyses with the vertebral centrum (figure 40D). In this character it seems *Camarasaurus* very undoubtedly is more derived than *Diplodocus*.

In *Brachiosaurus brancai* it can be observed up to the 8th cervical, remaining because the cervicals are incomplete. The infrapostzygapophyseal laminae are present from the 3rd cervical back. In the 8th cervical they are present but modest, thin, and do not alter the width of the constriction too much. In such a way it is possible to observe that in this character *Brachiosaurus* is less derived than *Camarasaurus*.

In *Dicraeosaurus* the infrapostzygapophyseal laminae are present from the 5th cervical back and show a good development, to the point that they seem to be as derived as in *Camarasaurus*, but less robust, perhaps due to the marked size difference. *Amargasaurus*, whose presacral series is complete, shows a stage that seems to be more derived than in *Dicraeosaurus*, and in consequence still more derived than in the sauropods mentioned above. The infrapostzygapophyseal laminae are more developed, reaching a more posterior position than the original laminae of the constriction.

In *Haplocanthosaurus* a notable development of the infrapostzygapophyseal laminae is observed in the last cervicals, but the axial partition is maintained, which would be a relict of the axial structure of the constriction.

Among titanosaurs only one has available information, because *Saltasaurus* possesses some complete cervicals. It has not been possible to make observations on the Titanosaurinae from Peirópolis (Powell 1987).

In *Saltasaurus* the derived condition is very remarkable because the infrapostzygapophyseal laminae, thick and low, form the entirety of the connection (in posterior view) between the neural arch and the centrum (figure 40). In posterior view it is observed that the diapophyseal-postzygapophyseal lamina has united or connected to the infrapostzygapophyseal lamina, which seems to be a derived character of *Saltasaurus* and possibly of Titanosauridae that distinguishes them from the remaining sauropods that we have compared. In such a way, the condition of the infrapostzygapophyseal constriction of *Saltasaurus* is the most derived among sauropods.

Pleurocoels. The pleurocoels of the presacral vertebrae seem to have two developmental stages. One of them is in the cervical vertebrae, which show an initial, incipient state in the case of prosauropods, and which later on in cetiosaurid sauropods is manifest in notorious form, forming a deep cavity that usually reaches the axial plane, with the anterior limit abrupt and the posterior one gradual.

In the more anterior dorsals of cetiosaurids, diverse characters of the cervical type are manifest, showing the pleurocoel reduced anteroposteriorly, which disappears in the mid- and posterior dorsals, where only a weak, moderately deep posterior depression exists, but no pleurocoel.

In most Upper Jurassic sauropods except *Dicraeosaurus*, the development of the pleurocoels ended up including the entirety of the dorsals. It seems evident that the development of pleurocoels in the cervicals preceded that of the vertebrae of the dorsal region which possibly would have been developed from the anterior dorsals back, although I do not know any intermediate example that shows this stage. The limitation of the pleurocoels to the first 2-3 dorsals presented by *Dicraeosaurus* and *Amargasaurus* indicates a primitive character for these taxa.

In titanosaurs the posterior fossa of the cervical centra is generally not very well defined, and low dorsoventrally, which could be a secondary reduction starting from the condition present in Cetiosauridae. The pleurocoels of the dorsals are small and located inside a lenticular fossa that is rarely observed in other sauropods. If we compare them with the wide, very defined pleurocoels of Upper Jurassic sauropods, the condition of titanosaurs could represent a partial reversal of that character, before supposing an independent origin of the same character starting from the condition present in cetiosaurids, which, on the other hand, would not be impossible.

Supraneural cavity. The supraneural cavity is an important morphological feature that would have originated due to the posteroventral lengthening of the neural arches of the dorsal vertebrae, specifically in the space between the base of the neural arch and the ventral part of the transverse processes (figure 41). The characters and evaluation of this cavity were already treated by the author in a previous work (Bonaparte, 1986b), but I believed their inclusion in this work useful in order to supplement derived appreciations of other observations. The function of this cavity is ignored for the time being.

In prosauropods, even *Lessemsaurus* gen. nov., I have not observed the supraneural cavity, and neither is it present among the available material of *Volkheimeria* or *Lapparentosaurus* (Bonaparte, 1986a), which suggests that this wide cavity is manifest starting from the level of *Patagosaurus-Cetiosaurus* (Phillips, 1871; Owen, 1875), which possesses a posterior opening in the space between the anterior infradiapophyseal and posterior infradiapophyseal laminae (figures 18D, E and 19). Observations on this character indicate that the most primitive condition was present in *Patagosaurus*. In this cetiosaurid the cavity occupies the whole transverse space in a region immediately above the neural canal. The anterior and posterior walls are thin, rather symmetrical, and the posterior ones something thicker. In *Diplodocus* (figure 41C), which also possesses a wide cavity, a

reduction is appreciated by the forward displacement on the centrum of the posterior wall.

In *Camarasaurus* (figure 41B) the cavity is somewhat more reduced anteroposteriorly and it presents a bony septum. Finally, in *Haplocanthosaurus* the cavity would have been obliterated completely, originating a thick transverse lamina.

In such a way, starting from the condition of *Patagosaurus* which is derived relative to sauropodomorphs, *Lessemsaurus*, *Volkheimeria* and *Lapparentosaurus*, and primitive with regard to *Diplodocus*, *Camarasaurus* and *Haplocanthosaurus*, we see a progressive reduction of the cavity that culminates in *Haplocanthosaurus*, a genus in which all the dorsals present a strong anterior depression that occupies the place of this cavity.

Anterior circumneural area. In this region, located below the prezygapophyses of the mid and posterior cervicals and the most anterior dorsals, two cavities are presented, one to each side of the neural canal (figure 42). In different genera, the morphology of these cavities varies, representing a useful character for understanding the development of the presacral vertebral morphology of the sauropodomorphs that we consider better. In the prosauropods *Riojasaurus* and *Plateosaurus* they are an incipient feature, hardly defined in some cervical vertebrae. In *Lessemsaurus* both are not very deep, and small cavities are observed in the last cervical, but in the 2nd they are an outstanding feature (figure 42A). In *Patagosaurus* (figure 42B) the cavities are quite larger and deeper in the mid and posterior cervicals. In *Barosaurus* (figure 42C) both large cavities are observed, partly above the neural canal and reaching the axial plane. In *Brachiosaurus* (figure 42D) the cavities reach a very dorsal position, and they are dorsally divergent from the axial plane.

In the titanosaurid *Saltasaurus* they are not present, probably due to a process of reduction, perhaps representing the derived condition.

APPLICATION TO SYSTEMATICS

The present study does not enable us to make a broad and constructive systematic revision of Sauropodomorpha, but it does permit us to develop some partial comments on the existing classification of this great group, and to propose some isolated interpretations.

Although it is certain that classifications are hypotheses elaborated by investigators and that they are influenced by impermanent concepts, it is no less certain that it is a significant part of those enunciated theories to understand the studied objects better. It is with these concepts that I am brought to a theme as inevitable as attractive.

The group Sauropodomorpha was recently treated in detail and in character revision and synthesis by Galton (1990) for Prosauropoda, and by McIntosh (1990) for Sauropoda. The first author recognized a division into 7 families: Thecodontosauridae, Anchisauridae, Massospondylidae, Yunnanosauridae, Plateosauridae, Melanorosauridae, and Blikanasauridae. McIntosh, on the other hand, distinguished 6 families among Sauropoda: Vulcanodontidae, Cetiosauridae, Brachiosauridae, Camarasauridae, Diplodocidae and Titanosauridae.

The characters mentioned by Galton (op. cit.) to diagnose or characterize each of those families seem insufficient for that taxonomic level. For example, for Massospondylidae he mentions only one derived character: the dorsal process of the maxilla centrally located on the maxilla and projected almost vertically. A similar situation is the case for Blikanasauridae, in which he points out only the robust condition of the hind limb and the more internal position of the distal tarsals, which allow a contact between the calcaneum and metatarsal IV. In Thecodontosauridae he points out the very clear bipedal condition, in fact not very distant from that of *Plateosaurus*, and that does not confirm satisfactorily to his figure 15-1; and similar derived characters such as the long retroarticular process of the jaw and the obliterated interpterygoid vacuity.

In my opinion, several family groups can be distinguished among prosauropods, but regardless they should exhibit significant and varied differences to be compactly-based entities. What I have been able to carry out in the presentwork on the presacral vertebrae shows very clear differences between Melanorosauridae and Plateosauridae regarding the presacral vertebral morphology (see the respective comparisons in chapter V), but it has not been possible to include other prosauropod families.

The classification of Sauropoda presented by McIntosh (1990) offers interesting family characters, with some references to the axial skeleton, although without the coherence that could arise from the numerous differential features of the presacral vertebrae. An example of this is the inclusion of *Barapasaurus* (Jain et al., 1975) in the family Vulcanodontidae, next to *Vulcanodon* (Raath, 1972). Yet although Vulcanodontidae could well be a valid family for its own notable characteristics that it possesses that African genus, as the characters of the metatarsuses, associated to astragalus and pubis of type sauropod, it is evident that the available material is insufficient to characterize to that family. McIntosh (1990) it included *Barapasaurus* in the family Vulcanodontidae, but the likeness of the posterior dorsal vertebrae (Jain et al., 1975, fig. 101) are very clear with those of *Patagosaurus* (Bonaparte, 1986, fig. 42), a member of the family Cetiosauridae something more derived than *Barapasaurus*. In such a way, the vertebral anatomy (cervical and dorsals), it links *Barapasaurus* closely with the family Cetiosauridae. The inclusion of the Hindu genus in Vulcanodontidae does not have important anatomical arguments.

In the analysis of Cetiosauridae, McIntosh (1990) included the genus *Haplocanthosaurus* in that family, an interpretation that does not have any support based on the anatomy of the presacral vertebrae. *Haplocanthosaurus* (treated more later) is so different from the diverse genera of Cetiosauridae that it deserves to be considered a representative of a different family: Haplocanthosauridae, as is argued in chapter XIII of this work.

In the study of the family Brachiosauridae attention is drawn to the fact that McIntosh (op. cit.) included the genera *Lapparentosaurus* and *Volkheimeria* in it, apparently only for the presence of low neural spines in the posterior dorsal and sacral vertebrae. I believe that such brief arguments are not enough to refer any genus to a certain family, particularly in this case where the neural spines of the two genera are of primitive morphology, as is described and discussed in chapter X, whereas the neural spines of the brachiosaurid morphotype in the posterior dorsals and sacrals are really very derived.

On the other hand the assignment of *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) to Camarasauridae does not find arguments against justification in the anatomy of the dorsal vertebrae (the cervicals of the Mongolian genus are not known), as explained in detail in the respective chapter. *Opisthocoelicaudia* shows very significant likeness with titanosaurs, not only in the anatomy of the available presacral vertebrae, but also in the bones of the girdles and limbs (Upchurch, 1995; Salgado et al., 1997). In my opinion this genus from Mongolia constitutes a good argument for admitting that Titanosauria is an complex suprafamilial entity, with a diversity of families: Andesauridae, Opisthocoelicaudidae, and Titanosauridae, and possibly another family for the primitive cervical vertebrae of *Malawisaurus* (Jacobs et al., 1993).

As has been done in recent years, McIntosh (1990) included *Apatosaurus* in the family Diplodocidae, although its cervical vertebra and dorsals have little to do with those of *Diplodocus*, as I have tried to demonstrate above. In a similar situation *Dicraeosaurus-Amargasaurus* are considered by McIntosh (1990) to be diplodocids, whereas in this work (to see XII chapter) I consider them as Dicraeosauridae, in agreement with Salgado and Bonaparte (1991) and Salgado and Calvo (1992).

Rebbachisaurus garasbae (Lavocat, 1954) was considered of uncertain systematic position by McIntosh, although this author included it within the Diplodocidae in his Table 16.1 (Sauropoda) as in the "Systematics" chapter. According to the anatomy of the posterior dorsal of *Rebbachisaurus* in the collections of the Institute of Paléontologie of Paris (figure 39A, B), their likeness with the well-known Sauropoda families are very remote, and it deserves an ad hoc family status, Rebbachisauridae.

McIntosh (op. cit.) included the genus "*Tornieria*", in fact *Janenschia* (Wild, 1991), in the family Titanosauridae. The type material of *Janenschia* is a hind limb, whereas the material assigned to that genus, two anterior dorsal vertebrae and a practically complete tail, come from towns very distant from that of the type material, and they are not identifiable with the holotype. In such a situation it is not possible to evaluate their systematic position starting with material assigned without the necessary anatomical justifications (Bonaparte et al., in press), still more when the assigned anterior caudal vertebrae are procoelous. The character of anterior caudal procoely does not have systematic significance, as is recognized in Bonaparte et al. (in press).

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Appendix I:

- 1 – Height of the neural arch in relation to the total height of the dorsal vertebrae.
 - State 1 -: 1/2 of the height; in typical Prosauropods such as *Anchisaurus*, *Riojasaurus* and *Plateosaurus*.
 - State 2 -: 2/3 of the height, in *Lessemsaurus* gen. nov., *Volkheimeria* and *Lapparentosaurus*.
 - State 3 -: 4/5 of the height, in *Patagosaurus*, *Diplodocus* and *Dicraeosaurus*, *Haplocanthosaurus*, *Brachiosaurus* (part).
 - State 4 -: 2/3 of the height (interpreted as a reversal), in *Camarasaurus*, *Brachiosaurus* (part) and Titanosauridae s. str.

- 2 – Pleurocels in the dorsal centra, degree of development.
 - State 1 -: Absent initially, in *Patagosaurus*, *Dicraeosaurus*.
 - State 2 -: Present but little developed, in *Brachiosaurus*, Titanosauridae s. str.
 - State 3 -: Very developed and deep, in *Camarasaurus*, *Diplodocus*, *Haplocanthosaurus*.

- 3 – Opisthocoely, degree of development.
 - State 1 -: Inferred in the cervicals, in Prosauropoda.
 - State 2 -: Present in the cervicals and the first two or three dorsals, in *Patagosaurus*, *Barapasaurus*.
 - State 3 -: Up to the middle dorsals inclusive, in *Diplodocus*, *Haplocanthosaurus*, *Dicraeosaurus*.
 - State 4 -: Up to the sacrals, in *Camarasaurus*, *Brachiosaurus*, Titanosauridae s. str.

- 4 – Posterior depression in the cervical centra and their degree of complexity.
 - State 1 -: light and simple depression, in Prosauropoda.
 - State 2 -: Well defined, with abrupt anterior border, in *Patagosaurus*, *Dicraeosaurus*, *Haplocanthosaurus*.
 - State 3 -: Well defined, with some pleurocoels: *Camarasaurus*, *Brachiosaurus*.
 - State 4 -: Very complex, with laminae and pleurocoels, in *Diplodocus*.
 - State 5 -: Dorsoventrally very reduced, in Titanosauridae s. str.

- 5 – Infrapapophyseal fossa in the cervical centra.
 - State 1 -: Only in the posterior cervicals and not very deep, in Prosauropoda.
 - State 2 -: In all the cervicals and very deep, in *Patagosaurus*, *Diplodocus*, *Camarasaurus*, etc.
 - State 3 -: Not very deep (interpreted as a probable reversal), in Titanosauridae s. str.

- 6 – Number of cervical vertebrae.
 - State 1 -: 9-10, in Prosauropoda, *Dicraeosaurus*.
 - State 2 -: 11-13, in *Amargasaurus*, *Patagosaurus*, *Brachiosaurus*, *Camarasaurus*, *Saltasaurus*.
 - State 3 -: 15, in *Diplodocus*, *Haplocanthosaurus*.
 - State 4 -: 19, in *Mamenchisaurus*.

- 7 – Laminae and infradiapophyseal fossae.
 - State 1 -: The three fossae in the posterior cervicals and anterior dorsals, in Prosauropoda.
 - State 2 -: In most of the cervicals and the anterior dorsals, in *Camarasaurus*,

Haplocanthosaurus, Dicraeosaurus, Mamenchisaurus.

State 3 -: In practically all the presacrals, in *Patagosaurus, Barapasaurus, Diplodocus, Brachiosaurus.*

8 – Length of the dorsal neural arch below the zygapophyses.

State 1 -: 1/2 of the height of the vertebral centrum, in Prosauropoda.

State 2 -: 3/4 to 4/5 of the height of the vertebral centrum in *Lessemsaurus, Volkheimeria, Lapparentosaurus, Haplocanthosaurus.*

State 3 -: 1/1 or more than the height of the vertebral centrum, in *Patagosaurus, Diplodocus, Camarasaurus.*

9 – Supraneural cavity.

State 1 -: Anteroposteriorly wide, in *Patagosaurus, Diplodocus.*

State 2 -: In the process of being reeduced anteroposteriorly, in *Camarasaurus.*

State 3 -: Obliterated, with transverse partition, in *Haplocanthosaurus.*

10 – Posterior infradiapophyseal fenestra.

State 1 -: Absent, in Prosauropoda, *Volkheimeria, Lessemsaurus, ?Lapparentosaurus.*

State 2 -: Present, in *Patagosaurus, Camarasaurus, Dicraeosaurus, Amargasaurus.*

11 – Transverse processes development angle.

State 1 -: Approximately perpendicular to the dorsoventral plane, in Prosauropoda, *Patagosaurus, Diplodocus.*

State 2 -: Arising somewhat dorsally, in *Dicraeosaurus, Brachiosaurus, Camarasaurus.*

State 3 -: Dorsally very high, in *Haplocanthosaurus, Titanosauridae.*

12 – Fossa in the posterodorsal extension of the diapophyseal lamina.

State 1 -: Absent, in Prosauropoda.

State 2 -: Not very marked, in *Patagosaurus, Haplocantosaur, Dicraeosaurus, Camarasaurus, Brachiosaurus.*

State 3 -: Deep, in *Diplodocus, Saltasaurus.*

13 – Circumneural depressions in cervicals.

State 1 -: Incipient, in Prosauropoda (part).

State 2 -: Small, in *Lessemsaurus.*

State 3 -: Deep, in *Patagosaurus, Diplodocus, Camarasaurus, Brachiosaurus, etc.*

14 – Infrapostzygapophyseal constriction in cervicals.

State 1 -: Not very defined, in *Lessemsaurus.*

State 2.: Very defined, in *Patagosaurus.*

State 3 -: With infrapostzygapophyseal laminae, in *Diplodocus, Camarasaurus.*

State 4 -: With thick infrapostzygapophyseal process and zygapophyseal inter-horizontal laminae, in Titanosauridae s. str.

15 – Pleurocoels in the neural arch of the cervical vertebrae.

State 1 -: Absent, in Prosauropoda, *Patagosaurus, Dicraeosaurus, Haplocanthosaurus.*

State 2 -: Present, in *Diplodocus, Brachiosaurus, Camarasaurus, Saltasaurus.*

16 – Type of neural spine in the dorsal vertebrae.

State 1 -: Lower and laminar, in Prosauropoda.

State 2 -: High, laminar or thick, in *Lessemsaurus*, *Volkheimeria*.

State 3 – High, and in X or + section, in *Patagosaurus*, *Diplodocus*, *Camarasaurus*, *Brachiosaurus*, *Haplocanthosaurus*, Titanosauridae s. str.

17 – Neural spine transversely wide in the posterior cervical and anterior dorsals.

State 1 -: Incipient, in *Plateosaurus*.

State 2 -: Very defined, in *Patagosaurus*, *Diplodocus*, ?*Brachiosaurus*, *Camarasaurus*, etc.

FIGURE LEGENDS:

Figure 1. Posterior cervical vertebra of the sauropod *Patagosaurus*, MACN-CH 934. A, anterior; B, posterior; and C, posterior views, with indication of the recognized areas for its study: 1, anterior portion of the centrum; 2, posterior portion of the centrum; 3, ventral area of the centrum; 4, area anteroposterior to the postzygapophyses; 5, area posterior to the prezygapophyses; 6, posterodorsal area; 7, prespinal area; 8, anterior circumneural area; 9, postspinal area; 10, area of the neural spine.

Figure 2. Presacral vertebrae of *Marasuchus*, PVL 3870, showing the three vertebral morphotypes present in this Middle Triassic pre-dinosaur from La Rioja. A, anterior cervical morphotype; B, anterior dorsal morphotype; and C, median and posterior dorsal morphotype. Abbreviations in page...

Figure 3. Presacral vertebrae of *Marasuchus*, PVL 3870.; A, cervical 3 ,B, cervical 5; C, cervical 7. Note some backwards direction of the neural spine of cervical 3, while in the cervical 7 is in opposite direction. ; D, dorsal 6 or 7 , E, dorsal 3 or 4. Note in these dorsal vertebrae the absence of the infradiapophyseal laminae; and F, three posterior dorsals in normal position, showing a virtual contact between the neural spines. Abbreviations in page...

Figure 4. Cervical vertebrae of the melanosaurid prosauropod *Riojasaurus*, UPLR 56, corresponding to a juvenile-adult individual. A-F, cervicals 3 to 8. Note that the cervicals 7-8 bear a transitional morphology between the cervical and the dorsal model in figure 5. Abbreviations in page...

Figure 5. Vertebrae of the melanosaurid prosauropod *Riojasaurus*, UPLR 56.A, cervical 10; B-C-D, dorsals 1, 2, and 3. Abbreviations in page...

Figure 6. Cervical vertebrae of the melanosaurid prosauropod *Riojasaurus incertus* holotype, adult specimen, PVL 3808. A-D cervicals 2 to 5. Abbreviations in page...

Figure 7. Vertebrae of the melanosaurid prosauropod *Riojasaurus incertus*, holotype specimen, adul, PVL 3808. A-C, cervicals 6, 8 and 9; D, dorsal 1. Compare the height of the neural arch of cervical 9 and dorsal 1 of the juvenile-adult specimen of figure 5. Abbreviations in page...

Figure 8. Dorsal vertebrae of the melanosaurid prosauropod *Riojasaurus incertus*, holotype, adult specimen, PVL 3808. A, dorsal 4; B, dorsal 8. Note the reduced diapophyseal-prezygapophyseal lamina. Abbreviations in page...

Figure 9. Vertebrae of the plateosaurid prosauropod *Plateosaurus*, MBR 2090. A-E, cervicals 2 to 6. Note the diapophyseal fossa present from cervical 6 backwards. Stippled lines indicate diapophysial, postspinal and prespinal cavities. Abbreviations in page...

Figure 10. Presacral vertebrae of the plateosaurid *Plateosaurus*, MBR 2090. A-D, cervicals 7 to 10; E – F, dorsal 1 and 2. Some views of the top of the neural spines show their transversal width, and the four insertion areas for ligaments. Note that in cervical 9 are

present the infrazygapophyseal cavities and their laminae, not observed in more anterior cervicals. Note that the last cervical shows a morphotype similar to that of the anterior dorsals. Abbreviations in page...

Figure 11. Presacral vertebrae of the plateosaurid prosauropod *Plateosaurus*, MBR 2090. A-C, dorsals 3-5, with dorsal views of the neural spines. The maximum width of the top of the spine is in dorsal 1 (figure 10), decreasing backwards. Abbreviations in page...

Figure 12. Presacral vertebrae of the plateosaurid prosauropod *Plateosaurus*, MBR 2090. A-C, dorsal 6 to 8, with a dorsal view of each neural spine. Note the absence of the anterior infradiapophyseal lamina in dorsal 8. Abbreviations in page...

Figure 13. *Lessemsaurus sauropoides* gen. et sp. nov. Part of the type material, PVL 4822-1. A and A1, neural arch of cervical 7? in posterior and posterior views; B and B1, neural arch of cervical 8? in posterior and posterior views; C, neural arch of dorsal 1 in posterior view. Abbreviations in page...

Figure 14. *Lessemsaurus sauropoides* gen. et sp. nov. Part of the type material, PVL 4822-1. A, B, and C, neural arches of the dorsals 2, 3 and 4 in posterior views. Abbreviations in page...

Figure 15. *Lessemsaurus sauropoides* gen. et sp. nov. Part of the type material, PVL 4822-1. Two neural arches of posterior dorsals, possibly 7 and 8. Abbreviations in page...

Figure 16. Two median posterior dorsals referred to *Lessemsaurus sauropoides* gen. et sp. nov., from Los Colorados Fm., La Rioja, Argentina, PVL collection without number. Note the dorsoventral length of the neural arches is near twice that of the centra. Abbreviations in page...

Figure 17. Neural arches of the “primitive sauropod” morphotype. A, median dorsal of *Volkheimeria*, and B, anterior dorsal, PVL 4077, both of them in posterior and anterior views; C, neural arches of two median dorsals of *Lapparentosaurus*, MNHN MAA 91-92, in posterior and anterior views. Note the deep anterior fossa dorsally placed to the neural canal, which may represent an anterior condition to the development of the supraneural cavity recorded in *Patagosaurus*, *Diplodocus*, *Camarasaurus*. Redrawn from Bonaparte, 1986. Abbreviations in page...

Figure 18. Vertebrae of the cetiosaurid sauropod *Patagosaurus fariasi*, holotype specimen, PVL 4170. A, anterior cervical; B, posterior cervical; C, dorsal 1; D, median anterior dorsal; E, posterior dorsal. The posterior cervical bears the neural spine transversely wide. The median and posterior dorsals bear a large posterior fenestra connecting to the supraneural cavity. Redrawn from Bonaparte, 1986. Abbreviations in page...

Figure 19. Transverse section of an anterior dorsal vertebra of *Patagosaurus*, PVL 4170, just above the neural canal, to illustrate the characters of the supraneural cavity. Redrawn from Bonaparte, 1986. Abbreviations in page...

Figure 20. Presacral vertebrae of the diplodocid sauropod *Diplodocus*, CM 84. A, cervical 5; B, cervical 7; C, cervical 11; D, cervical 14; and, E cervical 15. Redrawn from

Hatcher, 1901. Abbreviations in page...

Figure 21. Presacral vertebrae of the diplodocid sauropod *Diplodocus*, CM 84. A-C, dorsals 1 – 3; D-G, dorsals 6-9. The infrapapophyseal rims, ventrally and posteriorly directed, are derived characters for this genus. Redrawn from Hatcher, 1901. Abbreviations in page...

Figure 22. Cervical vertebrae of *Apatosaurus*, CM 3018. A-F, cervicals 3, 4, 7, 8, 14 and 15. Inverted and redrawn from Gilmore, 1936. Abbreviations in page...

Figure 23. Dorsal vertebrae of *Apatosaurus*, CM 3018. A-D, dorsals 1, 2, 8, and 9. Inverted and redrawn from Gilmore, 1936. Abbreviations in page...

Figure 24. Cervical vertebrae of the brachiosaurid *Brachiosaurus brancai*, collection MBR. A-E, cervicals 3, 4, 5, 7 and 8. Note the complex morphology of the surface of the diapophyseal lamina of cervical 8, probably for muscular insertions of the episomatic muscles. Redrawn from Janensch, 1950. Abbreviations in page...

Figure 25. Dorsal vertebrae of the brachiosaurid *Brachiosaurus brancai*, collection MBR. A-D, dorsals 3?, 7?, 10?, and 12?-13?. Probably dorsal 7? (*sensu* Janensch, 1950) is actually dorsal 2 or 3, according to the position of the parapophyseal-diapophyseal lamina. Redrawn from Janensch, 1950. Abbreviations in page...

Figure 26. Presacral vertebrae of the camarasaurid *Camarasaurus*, AMNH Cope Collection 5760-5761. A-D, cervicals 5, 7, 8, and 13 respectively; E-H, dorsals 2, 3, 4, and 10 respectively. Note the pronounced indentation in the diapophyseal-postzygapophyseal laminae of the cervicals. Redrawn from Osborn and Mook, 1921. Abbreviations in page...

Figure 27. Presacral vertebrae of the dicraeosaurid *Dicraeosaurus*, collection MBR. A-D, cervicals 3, 5, 9, and 10 respectively; E-G, dorsals 9, 11, and 12. Note the presence of only one infradiapophyseal lamina, the posterior one, in all the dorsals except perhaps in dorsal 1. Redrawn from Janensch, 1929. Abbreviations in page...

Figure 28. Presacral vertebrae of the dicraeosaurid *Amargasaurus cazau*, MACN-N 15 in posterior view. A, atlas and axis; B, cervical 4; C, cervical 10; D, dorsal 4; and E, dorsal 11. Scale bar: 10 cm. Redrawn from Salgado and Bonaparte, 1991. Abbreviations in page...

Figure 29. Presacral vertebrae of the dicraeosaurid *Amargasaurus cazau*, MACN-N 15, in anterior view. A, cervical 4; B, cervical 10; C, dorsal 4; D, dorsal 10; and E, dorsal 11. Scale bar: 10 cm. Redrawn from Salgado and Bonaparte, 1991. Abbreviations in page...

Figure 30. Presacral vertebrae of *Haplocanthosaurus*, CM 879. A-B-C-D-E, cervicals 4, 8, 10, 12, and 14 respectively; F, dorsal 1. Note in the cervicals the type of depression, with pronounced borders, on the diapophyseal lamina, and the large, simple pleocoels of the centra. Redrawn from Hatcher, 1904. Abbreviations in page...

Figure 31. Dorsal vertebrae of *Haplocanthosaurus*, CM 879. A-E, dorsals 3, 5, 6, 7, and 13

respectively. The presence of only one infradiapophysial lamina from dorsal 6 backwards is a derived character, as well as the obliteration of the supraneural cavity and other characters cited in the text. Redrawn from Hatcher, 1904. Abbreviations in page...

Figure 32. Presacral vertebrae of the titanosaurid *Saltasaurus*, PVL 4017. A, axis; B, anterior cervical; C, dorsal 1 or eventually the last cervical; D, E, and F, anterior, median, and posterior dorsals respectively. Note the absence of the diapophysial-postzygapophysial lamina in the anterior and median dorsals, and the absence of the anterior infradiapophysial laminae in all the dorsals. E, and F, redrawn from Powell, 1986; C, and D, redrawn from Bonaparte and Powell, 1980. Abbreviations in page...

Figure 33. Cervical vertebrae of a Titanosauridae, Titanosaurinae indet. from Peirópolis, Brazil, DNPM Serie B. A, cervical 7; B, cervical 4; C, cervical 13; and D, cervical 10. Redrawn from Powell, 1987. Abbreviations in page...

Figure 34. Dorsal vertebrae of a Titanosauridae, Titanosaurinae indet., of Peirópolis, Brazil, DNPM Serie B. A-D, dorsals 1, 4, 6, and 8. Note the absence of the infradiapophysial anterior laminae, and of the diapophysial-postzygapophysial laminae, except in dorsal 1. Redrawn from Powell, 1987. Abbreviations in page...

Figure 35. Dorsal vertebrae of the titanosaurid cf. *Argyrosaurus*, MACN-CH 217. A, anterior dorsal; B, anterior median dorsal; and C, posterior dorsal. In the anterior dorsal the two infradiapophysial laminae are present, but the diapophysial-postzygapophysial lamina is not. In the posterior dorsal the posterior infradiapophysial lamina is ventrally splitted in two. Abbreviations in page...

Figure 36. Presacral vertebrae of the titanosaurs *Argentinosaurus*, PVPH 1, and *Andesaurus*, MUCPv 132. A, posterior dorsal of the holotype of the andesaurid *Andesaurus delgadoi*, bearing a large prespinal lamina; B, C, anterior and posterior views of the neural arch of an anterior dorsal of *Argentinosaurus*; D, anterior view of a posterior median dorsal of *Argentinosaurus* with the complex development of the hyposphene; and E, two posterior dorsals of *Argentinosaurus* showing a large posterior fossa between parapophysis and diapophysis. A, redrawn from Calvo and Bonaparte, 1991; B, C, D, and E, redrawn from Bonaparte and Coria, 1993. Abbreviations in page...

Figure 37. Cervical vertebrae of titanosaurs with different level of derivation. A, *Malawisaurus* from Africa, MAL 89-78; B, *Saltasaurus*; and C, Titanosaurinae indet. from Peirópolis, Brazil, DNPM series B. In *Malawisaurus* note the primitive condition of the neural spine, with large subvertical laminae connecting to the zygapophyses. However, the centrum, slightly excavated posteriorly, fit well with the morphology present in titanosaurs. A, redrawn from Jacobs et al., 1993; B, redrawn from Bonaparte and Powell, 1980; and C, redrawn from Powell, 1987. Abbreviations in page...

Figure 38. Upper row: dorsal vertebrae of *Opisthocoelicaudia*, ZPAL MgD-I/48, and lower row, dorsal vertebrae of titanosaurid for comparison. A-C, dorsals 1, 6, and 10 respectively of the Mongolian genus; D, and E, dorsals 1 and 4 of Titanosaurinae indet. from Peirópolis, Brazil, DNPM series B; and F, posterior dorsal of *Saltasaurus*, PVL 4017. A-C redrawn from Borsuk-Bialynicka, 1977; D-F, redrawn from Powell, 1986.

Abbreviations in page...

Figure 39. Posterior dorsal of the sauropod *Rebbachisaurus garasbae*, collection MNHN, Paris. A, posterioroposterior view; B, posterior view. Abbreviations in page...

Figure 40. Posterior view of the median posterior cervicals to show details of the infrapostzygapophysial constriction. A, *Lessemsaurus*, PVL 4822-1; B, the cetiosaurid *Patagosaurus*, PVL 4170; the diplodocid *Diplodocus*, CM. 84, showing development of the infrapostzygapophysial processes; D, the camarasaurid *Camarasaurus*, AMNH Cope Collection 5760-5761, with robust infrapostzygapophysial processes; and E, the titanosaurid *Saltasaurus*, PVL 4017, showing the greatest level of derivation. Not to scale. Abbreviations in page...

Figure 41. The supraneural cavity in some genera of sauropods and indications of possible relationships. A, in the cetiosaurid *Patagosaurus*, PVL 4170; B in the camarasaurid *Camarasaurus*, CM 11338 (Ba, anterior dorsal; Bb, posterior dorsal); C, posterior dorsal of *Diplodocus*, CM 84; and D, posterior dorsal of *Haplocanthosaurus*, CM 572. Not to scale. Reproduced from Bonaparte, 1986. Abbreviations in page...

Figure 42. Anterior views of posterior cervicals to show the circumneural region. A, the prosauropod *Lessemsaurus*, PVL 4822-1; B, the cetiosaurid *Patagosaurus*, PVL 4170; C, the diplodocid *Barosaurus*, MBR collection; and D, the brachiosaurid *Brachiosaurus*, MBR collection. Not to scale. Abbreviations in page...

Abbreviations:

CA, angular cavity
CASN, anterior supraneural cavity
DC, cervical rib
CN, neural canal
CCN, circumneural cavity
CD, infradiapophyseal fossa
CID, central infradiapophyseal fossa
CIDA, anterior infradiapophyseal fossa
CIDP, later infradiapophyseal fossa
CIZ, infrapostzygapophyseal constriction
CLC, posterior cavity of the centrum
CPE, postspinal fossa
CPRE, prespinal fossa
DIPOZ, infrapostzygapophyseal depression
DLD, depression of the diapophyseal lamina
DLLD, posterior depression of the diapophyseal lamina
DP, diapophysis
EN, neural spine
ENTA, transversely wide neural spine
ENTN, transversely narrow neural spine
EP, epipophysis
F, foramen
FCSN, foramen of the supraneural cavity
FPP, postparapophyseal fossa
HY, hyposphene
HYP, hypantrum
LD, diapophyseal lamina
LDP, lateral diapophyseal lamina
LDPOZ, diapophyseal-postzygapophyseal lamina
LDPRZ, diapophyseal-prezygapophyseal lamina
LI, infradiapophyseal lamina
LIA, anterior infradiapophyseal lamina
LIP, later infradiapophyseal lamina
LIPRZ, infraprezygapophyseal lamina
LIDP, later infradiapophyseal lamina
LPOS, postspinal lamina
LPS, prespinal lamina
LPSA, accessory prespinal lamina
LSD, supradiapophyseal lamina
LSPO, suprapostzygapophyseal lamina
LSPRZ, supraprezygapophyseal lamina
PIPOZ, infrapostzygapophyseal process
POZ, postzygapophysis
PP, parapophysis
PPOZ, postzygapophyseal process
PRZ, prezygapophysis
RAEN, anterior edge of the neural spine

RIP, infrapapophyseal edges

RLN, posterior edge of the neural spine

RPS, prespinal edge

TABLE LEGENDS:

Table 1 – The distribution of the three infradiapophysial fossae in some selected sauropodomorphs are indicated. A) distribution of the central infradiapophysial fossa; B) distribution of the posterior infradiapophysial fossa; and C) distribution of the anterior infradiapophysial fossa. The question mark indicates doubt whether the character extends more than indicated. See the text for evaluation of these characters.

Table 2 – The distribution of opisthocoely in the presacral vertebrae of *Marasuchus*, *Coelophysis*, and select sauropodomorphs is indicated. In *Coelophysis*, *Riojasaurus*, and *Plateosaurus* it is indicated by a dotted line because opisthocoely is only inferred. See the text for evaluation of these characters.

Table 3 – The distribution of transversely wide neural spines in select sauropodomorphs is indicated. *Plateosaurus* exhibits the initial condition of this character. See the text for evaluation of this character.

Table 4 – The number of cervical and dorsal vertebrae in the rauisuchid *Fasolasuchus*, the dinosauiromorph *Marasuchus*, and select sauropodomorphs are indicated. The question mark indicates that the number of presacral vertebrae is not known exactly. See the text for evaluation of this character.