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THE DINOSAURS
(CARNOSAURS, ALLOSAURIDS,
SAUROPODS, CETIOSAURIDS)
OF THE MIDDLE JURASSIC OF CERRO CÓNDOR
(CHUBUT, ARGENTINA)

by

J. F. BONAPARTE*

translated by Matthew T. Carrano, Dept. of Anatomy
University of Chicago, October 1995

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* CONICET MACN, Museo "B. Rivadavia", Avenida Angel Gallardo 470, 1405 Buenos Aires,
Argentina. Translation: B. Lange-Badre.

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Order SAURISCHIA Seeley 1888

Suborder SAUROPODOMORPHA Huene 1932

Infraorder SAUROPODA Marsh 1878

Family Cetiosauridae Lydekker 1888

Patagosaurus fariasi Bonaparte 1979

Holotype. - Specimen PVL 4170 corresponds to an adult of large size. It includes 4 anterior cervical vertebrae, 3 posterior cervical vertebrae, 3 anterior dorsals articulated to the last cervical, 5 mid- and posterior dorsals, 2 dorsal bodies, the complete sacrum of 5 vertebrae, 6 proximal caudals, a collection of 12 mid- and distal caudals, some incomplete ribs, several haemal arches, the right ilium, 2 ischia partly fused but broken in their proximal regions, the right pubis, the proximal part of the right scapula associated with the broken coracoid, the proximal part of the right humerus, and the right femur.

Hypodigm. - It is composed of the less complete specimens PVL 4615, PVL 4616, PVL 4171, and PVL 4172; these are temporarily deposited in the Museo Argentino de las Ciencias Naturales in Buenos Aires (MACN-CH 935, 932, 933, Chubut collection).

MACN-CH 935, of comparable size to the holotype, includes 4 mid-dorsal vertebral neural arches, 3 dorsal centra, 4 sacral vertebrae with their ribs, 1 sacral vertebral body, 2 fused sacral neural arches, 1 sacral neural arch with the neural spine, 1 proximal caudal vertebral body, 6 mid- and distal caudal vertebrae, 2 incomplete neural spines, 3 haemal arches, 6 proximal sections of dorsal ribs, a fragment of ilium with the acetabular cavity, the right pubis and the 2 ischia.

MACN-CH 932 corresponds to an individual of small to medium size. It includes 2 cervical vertebral bodies, an anterior dorsal body, 6 neural arches and 8 bodies of dorsals, a sacral neural arch, 3 vertebral bodies, 2 sacral ribs, the right scapula, coracoid, humerus, radius and ulna, a pubis, 3 metatarsals, 2 phalanges and an ungual phalanx.

MACN-CH 933, a juvenile individual, is represented by an incomplete left mandible, 2 cervical vertebral bodies, one anterior dorsal body, 4 neural arches and 3 bodies of dorsals, a sacral neural arch, a pubis, a fragment of ilium, and a right femur and tibia.

Other collected material. - Specimen PVL 4076 from Cerro C6ndor is an adult of large size. It includes 5 mid-cervical vertebrae, the left premaxilla, 2 incomplete posterior cervical vertebrae, 4 dorsal bodies, an anterior dorsal neural arch, a dorsal body with part

of the neural arch, various fragments of dorsal ribs, 17 mid- and mid-proximal caudal vertebrae, the incomplete right pubis, and the right femur and tibia.

Specimen PVL 4075, also from Cerro C ndor, is an adult of considerable size, which includes 3 dorsal vertebral bodies, a scapula, the left humerus, a proximal fragment of ischium, and a left femur.

PVL 4617, still from Cerro C ndor, is represented by 6 incomplete caudal vertebrae, a cervical rib, a scapula, a coracoid and an ungual phalanx.

MACN-CH 934 includes both maxillae, 5 dorsal neural arches, an ilium, a pubis, an ischium and several appendicular elements of a young individual, also found at Cerro C ndor.

Geographic and stratigraphic location. - The holotype and hypodigm were found in Cerro C ndor North, located 5 kilometers to the north of Cerro C ndor and 100 meters west of the route that connects Cerro C ndor to Paso del Sapo (Paso de Indios Department, Chubut Province, Argentina). They were all found in the same locality and bed of layered pebbles and calcified cement, corresponding to the lower third of the Ca nadon Asfalto Formation (Callovian, Middle Jurassic).

The collected material was recovered from an area 1 kilometer west of the Farias farm (Cerro C ndor locality) in fluviatile beds with rounded, slightly sorted calcareous pebbles, corresponding to the lower third of the Ca nadon Asfalto Formation.

Diagnosis. - Cetiosaurid of large size, with tall dorsal vertebrae; posterior dorsals with elevated neural arches and well-developed neural spines, formed from 4 divergent laminae and with a massive dorsal region; dorsoventrally-oriented neural spine cavities, more expanded than in *Barapasaurus*. Anterior and lateral regions of the neural arch similar to that of *Cetiosaurus* and *Barapasaurus*. Sacrum with 5 vertebrae, elevated neural spines, and a large dilation of the neural canal forming a neural cavity. Pelvis with pubis showing distal and proximolateral expansions, more developed than in *Barapasaurus*, and a less expanded pubic symphysis than in *Amygdalodon*. Ischium slightly transversely compressed, with a ventromedial ridge of sublaminar type, and with a clear distal expansion. Ratio of tibia-femur lengths from 1:1.5 in juveniles, reaching 1:1.7 in adults. Mandible with weak medial torsion. Spatulate teeth with occlusal traces.

DESCRIPTION

SKULL

The description of the skull of this species relies fundamentally on the hypodigm, except for the premaxilla, the two maxillae, and the axis, which are part of the collected material.

The available cranial material includes the left premaxilla of a very large individual, both maxillae (left and right) of a slightly smaller individual, and the incomplete mandible of a juvenile.

Premaxilla

The incomplete left premaxilla which we prepared (fig. 29) was found associated with a group of cervical vertebrae and some limb bones not described in this work (such as a femur 1.50 m long) that all pertain to the collection of the Fondacion Miguel Lillo, PVL 4076.

This is a robust, thickened, dorsoventrally convex element, a little taller than wide, and with proportions recalling those of *Camarasaurus* (Ostrom and McIntosh, 1966). The very thickened symphyseal region in the upper part (35 mm) permits orientation of this piece to a reasonable approximation, indicating that the skull should be proportionally short and wide, very different from the type in Diplodocidae. The characteristics of this premaxilla and the orientation of the sagittal plane suggest that the width of the skull at the level of the union with the maxilla should be about 18 cm. The surface of the union with the maxilla is very much straight dorsoventrally, but angled in the transverse direction, with a lateral edge that superimposes on the maxilla. It is probable that the union between the two premaxillae would have been rigid.

In the dorsal region, observe a large depression that must correspond to the anteroventral portion of the external naris, with a clearly different morphology from that of other Upper Jurassic sauropods with wide premaxillae like *Camarasaurus* or *Brachiosaurus*. The alveolar region shows an external border lower (25 mm) than the internal, which probably corresponds to a derived character, tied to the cutting and tearing function of the anterior teeth.

The 4 alveoli are large, subcircular, the fourth including a tooth in the process of erupting.

Measurements: Mesiodistal length of the long alveolar border: 101 mm.

Mesiodistal length of the upper third: 84 mm.

Maximal preserved length in the symphyseal plane: 122 mm.

Maximal thickness in the symphyseal plane: 41 mm.

Mesiodistal diameter of each alveolus: 20 mm.

Maxilla

The two maxillae probably belong to a young *Patagosaurus fariasi*, MACN-CH 934.

These pieces are from the very thickened and robust alveolar and supra-alveolar regions, while the nasal process and its posterior projections for the lacrimal and jugal are fragile and blade-like. The anteromedial process is also fragile. The external surface of the maxillary body is convex backwards near the bottom, with various nutrient foramina and dorsoventral depressions which suggest the existence of a good muscular covering. The depression for the external naris is deep (25 mm), particularly in its lower part, at the level of the anteromedial process.

The nasal process is high, directed backwards in its inferior part then near the top. The inferior border of the antorbital opening is higher than the lower part of the nasal depression, different from the Upper Jurassic sauropods *Camarasaurus* and *Brachiosaurus*. The region of the alveolar border on the better preserved right maxilla shows a backwards-ascending curve, or in other words a ventrally convex border. On the interior side, observe a deep (25 mm) depression that surrounds the antorbital opening and extends dorsally on the internal side of the nasal process of the maxilla.

The tooth alveoli, like those of the premaxilla, possess an external wall which is more ventral than the internal. The interdental plates are fused together and separated by a clear projection from the rest of the maxilla. In this projection, the foramina for the germ teeth are found. Each maxilla holds 12 teeth.

Mandible

Of the mandible, two fragments of the left dentary of a juvenile are available, MACN-CH 933, coming from the Cerro Cónдор North locality.

The anterior fragment (fig. 33) corresponds to the symphyseal region and contains six tooth alveoli, of which two contain broken functional teeth and two are in eruption. The posterior fragment contains four alveoli of which two are with teeth in the process of erupting. Consequently, the total number of teeth estimated from the alveoli is 13.

The two fragments show that the mandible was notably tall in the symphyseal region, and also in the posterior region. The reconstruction of the dentary indicates that it had a non-negligible curvature in the anterior region, although it was not abruptly turned

as in the Diplodocidae. In the symphyseal region, the alveolar border is elevated to form an angle of less than 90° with the anterior border of the dentary. The inferior border is curved slightly towards the bottom, and also the anterior region is more dorsoventrally extended than the central region of the dentary. The characters and orientation of the symphysis suggest that the angle between the two mandibular rami must have been approximately 40° relative to the axial plane, with a slight medial inflexion of each dentary near its anterior end. The external alveolar border is clearly more elevated than the internal as in the premaxilla and maxilla.

DENTITION

Only some large teeth are available, which are attributed to adult individuals, and those pointed out in the description of the incomplete mandible interpreted as having belonged to a juvenile. Fundamentally, the large teeth are of the type seen in *Camarasaurus* or *Brachiosaurus*, in other words spatulate teeth with a clear separation between the crown and base (fig. 34). The teeth described and figured by Cabrera (1947) of *Amygdalodon patagonicus*, a cetiosaurid from the Bajocian-Bathonian of Patagonia, are very similar or identical to these which are attributed to *Patagosaurus fariasi*.

The external part of the crown is dorsoventrally and anteroposteriorly convex with a dorsoventral groove near one of the edges. The lingual face is concave in both directions and covered dorsoventrally by two grooves. Most of these teeth show clear occlusal traces, with a wear mark on the apical edge that habitually shows a curved neck on each side for each tooth to occlude with the opposing tooth.

The enamel shows abundant striations and small rugosities. The base of the rare large teeth recovered is rather conical up to its end.

On their side, the mandibular teeth of the juvenile individual show some differences worthy of being mentioned. The crown is considerably higher and less spatulate than in the adults, and a collar is not observed between the crown and base. One of the teeth of this mandible, broken at the level of the crown, shows its large cylindrical base which recalls that of Diplodocidae.

VERTEBRAL COLUMN

The vertebral column is well enough represented by the group of material used in this description.

Axis

The only axis which is available belongs to specimen MACN-CH 936 (fig. 35). It was associated with a large number of presacral vertebrae not included in this description.

This nearly complete axis is well preserved. It lacks only the most anterior part of the neural spine and the region of the prezygapophyses. The vertebral body is very widened, with a continuous and expanded lateral depression, deeper in the anterior and posterior regions than in the central part. It is opisthocoelous and its anterior end is fused to the intercentrum and the odontoid process.

The ventral face is very flat in the transverse direction with a clear projection ventral and axial to its anterior end. In posterior view, the body of the axis is subcircular.

The neural arch is closely fused to the vertebral body. The postzygapophyses are wide, subcircular and ventrally oriented. Immediately in front of the prezygapophyses, there is a vast, ventrolaterally oriented depression, which is also found in other sauropods such as *Camarasaurus* (*Morosaurus grandis* Marsh, 1877) and in a more reduced form in *Diplodocus* (Hatcher, 1901).

The diapophysis is wide, including a very considerable part of the neural arch. Underneath, there is a substantial, slightly deep conical depression. The neural spine is robust, wide, and low in the posterior part, slimming abruptly towards the front and showing a strong lateral indentation in the anterior region. In posterior view, the maximal width between the postzygapophyses exceeds the width of the vertebral body (as in other sauropods), while the maximal width of the neural spine above the postzygapophyses is comparable to that of the vertebral body. The posterior region of the neural spine is very concave between the two zygapophyses, showing a deep depression possibly for the insertion of interspinous ligaments. The epiapophyses project slightly more backwards than the zygapophyses, and one can note the beginning of the formation of hyposphenes.

The principal measurements of this vertebra are:

Maximal length in the sagittal plane: 240 mm.

Width of the posterior face of the body: 105 mm.

Maximal width between the postzygapophyses: 140 mm.

Maximal dorsoventral height: 240 mm.

Anterior cervical

(fig. 36)

This vertebra from the holotype is very likely the 5th cervical. It differs from the axis by its larger size, the strong anterodorsal projection of the prezygapophyses, and the central position of the neural spine. The vertebral body is strongly opisthocoelous, with the parapophysis situated at the level of the ventral border, and a deep lateral depression of pleurocoel type in its anterior region which slowly diminishes towards the rear, becoming lost near the posterior border.

Along the sagittal plane and in lateral view, the ventral face of the vertebral body describes a sigmoid shape, with a concave region in the anterior part and a concave region in the posterior part. In the concave zone, a distinct axial ventral keel exists which diminishes towards the convex region.

The neural arch of this cervical vertebra, and the others excepting the axis, has a general morphology formed essentially by a complete ensemble of bony laminae which give the impression of composing a resistant but light structure. The union of the neural arch and the vertebral body is very closed with a clear fusion. The diapophysis is pendant and connects in front to the prezygapophysis at the middle of a large lamina (diapoprezygapophyseal lamina) and in back with the postzygapophysis by another lamina (diapopostzygapophyseal lamina). A third lamina which rejoins the diapophysis is from the medial direction (infradiapophyseal lamina); it delimits all at once an anterior cavity and a posterior cavity, covered laterally by the diapophysis.

The zygapophyses are wide, subcircular, and inclined from 30 to 35°, with epiapophyses on the postzygapophyses, and the prezygapophysis not only joined to the diapophysis but also connected to the vertebral body by the infraprezygapophyseal lamina, and to the base of the neural spine by the supraprezygapophyseal lamina. On their sides, the postzygapophyses are joined to the diapophyses and the neural spine by a strong lamina in the dorsal position (suprapostzygapophyseal lamina) and by another in the dorsal region of the roof of the neural canal (infrapostzygapophyseal lamina).

The neural spine proper of this vertebra is laterally compressed, somewhat lamellar and axially extended. The anterior face of the spine is concave with projecting lateral borders, indicating the dorsal continuation of the supraprezygapophyseal lamina. The posterior edge of the spine, invisible in lateral view (indicated by dashes in figure 36) is dorsoventrally oriented; it is concave in posterior view, and the suprapostzygapophyseal laminae are joined together in its dorsal region. The collection of bony laminae of these vertebrae, disposed in distinct planes and directions, bring about the formation of several cavities which were partly occupied by muscles. In dorsal view, note two large cavities; one is situated behind the neural spine, limited laterally by the

suprapostzygapophyseal laminae, and ventrally by the V-shaped union of two infrapostzygapophyseal laminae above the neural canal.

In front of the neural spine, there exists another cavity bordered laterally by the supra- and infraprezygapophyseal laminae and ventrally by the dorsal edge of the anterior region of the vertebral body. This cavity, opening anterodorsally, is very large in anterior view.

In lateral view, note the large cavity situated under the diapostzygapophyseal lamina. Medial to the diapophyseal lamina, the infradiapophyseal lamina separates two comparatively small but deep cavities, communicating laterally with the large lateral cavity (pleurocoel) of the vertebral body.

In anterior view, above the neural canal and under the neural spine, there exists a more or less vertical bony structure, with a dorsoventral crest which separates two depressions. We see further that it persists with variations in practically all the presacral vertebrae.

The principle measurements of these vertebrae are:

Maximal length: 375 mm.

Maximal height: 322 mm.

Maximal width in the posterior region of the vertebral body: about 145 mm.

Posterior cervical

(fig. 37)

This vertebra belonging to the holotype is probably the penultimate. Its structure is fundamentally the same as that of the cervical described above, but it differs in some details and in its proportions. The vertebral body is a little more robust, the prezygapophyses are better delimited by a sort of neck, and there are more differentiated epiapophyses. The postzygapophyses seem a little more ventral, immediately under the edge which forms the diapostzygapophyseal lamina. But the most remarkable consists of the thickening of the neural spine and its practically flat, transversely oriented aspect, with wide, flat surfaces that are very visible in anterior and posterior views. Also note a change in the proportions of this posterior cervical vertebra relative to the anterior ones which, likewise longer than wide, become clearly taller than long. The cervical vertebrae of *Patagosaurus fariasi* are very similar or identical to those of *Cetiosaurus oxoniensis* from the Bathonian of Rutland, England (Jones, 1969-70). Four complete and two incomplete cervical vertebrae are known from this species, which I had the opportunity to compare at the Leicester Museum. The general plan and the principal details of the

two species reveal a remarkable morphological proximity. Also note the great resemblances with the anterior cervical of *Barapasaurus tagorei* Jain *et al.*, 1977 from the Liassic of Deccan, India, due to a similar level of organization.

In contrast, comparison with the cervicals of Upper Jurassic sauropods, either from the Morrison Formation in North America (*Diplodocus*, *Camarasaurus*, *Barosaurus*, *Haplocanthosaurus*), or from the Tendaguru beds in East Africa (*Brachiosaurus*, *Dicraeosaurus*), invariably reveals strong differences which denote a greater specialization of the Upper Jurassic forms. Thus in *Diplodocus*, *Camarasaurus*, *Barosaurus*, and *Brachiosaurus*, the development of pleurocoels is much more important than in *Patagosaurus*, while the neural arch and spine are clearly larger, with bifurcated spines. *Patagosaurus*, *Barapasaurus* and *Cetiosaurus* possess common characters at the level of their cervical vertebrae, revealing a clearly more primitive stage than that represented by Upper Jurassic sauropods.

Anterior dorsal

(fig. 38)

This vertebra, belonging to the holotype, is probably the first dorsal. The morphology is very modified between this vertebra and the last cervical before it (fig. 37), although intermediate characters are observed between one region of the vertebral column and the other.

It is a proportionally short and tall vertebra, with a notable reduction in the length of the vertebral body and consequently the neural arch. The vertebral body is clearly opisthocoelous, with a very excavated posterior face that has a markedly larger diameter than that of the anterior.

The ventral edge of the body presents a clear transverse indentation; the lateral face bears a deep, widely open depression. The parapophysis has migrated dorsally and is situated in the upper part of the vertebral body. On the neural arch, note the preponderance of the neural spine, which is relatively anteroposteriorly flat, elongated transversely in the dorsal region, and straighter in the lower part. The prezygapophyses do not reach beyond the anterior edge of the body, and the postzygapophyses project beyond the posterior edge. The diapophyses are pendant, situated low on the vertebral body, and anteroposteriorly straight. Note an important reduction in the diaprezygapophyseal lamina, an increase of the infraprezygapophyseal lamina which is very visible in lateral view, and a substantial modification in the position of the diapostzygapophyseal lamina which has a subvertical orientation.

The height of the neural arch places the postzygapophyses at a great distance from the vertebral body, but retains the morphology of the cervical vertebrae. The suprapostzygapophyseal lamina is short, and note a clear edge of the epiapophysis.

Since no dorsal vertebra of a cetiosaurid has been described or figured, it is not possible to make comparisons. There exist very clear differences with the Upper Jurassic species, and a distinct grade for each case. Nevertheless, invariably in the different families of these sauropods there exists a changing morphology, appreciable in the first dorsals which noticeably modify their proportions, passing from relatively elongate and low to short and tall.

Mid-dorsals

(fig. 39)

They are represented by four nearly complete neural arches of consecutive vertebrae in the mid-dorsal region of specimen MACH-CH 935, which is a little smaller than the holotype (and found in the same locality). Between these four neural arches (successive vertebrae) note the gradual changes which are manifest principally in the anteroposterior straightening and height of the neural spine. These neural arches are tall, relatively axially short, and provided with remarkable transverse processes, projecting a little dorsally. In general the structures are light and lamellar, with internal and external cavities.

The region of the neural arch under the transverse processes is roughly quadrangular, with closed anterior and posterior faces, while the lateral faces possess a large opening (fig. 39) which communicates with a vast neural cavity, and of which the transverse cross-section situated immediately above the neural canal is illustrated in figure 40. To be precise, there are two cavities separated by a thin partition, which is not always preserved. These are important cavities which extend from the extreme base of the neural arch to the region of the origin of the neural spine. Their walls are thin except in the angles. These cavities were noted by Jain *et al.* (1977) in *Barapasaurus* from the Liassic of India with very similar characteristics to those of *Patagosaurus*, are encountered with marked variations and modifications in the majority of Upper Jurassic sauropods, and have particular value in understanding the phylogenetic relationships of sauropods (Bonaparte MS).

In anterior view, this part of the neural arch is very concave transversely, with lateral borders projecting forwards. Above the neural canal, a vertical edge in the axial

position separates the two large depressions which occupy the major part of the anterior concavity.

In posterior view, this region of the neural arch is a little more dorsoventrally extended since the postzygapophyses are slightly taller than the prezygapophyses. In general, the posterior face is much straighter dorsoventrally, with an axial plane which continues towards the base of the hyposphene, slightly projected towards the rear. In the dorsal portion of this large posterior face, and at a certain distance from the axial plane, there exists an opening on each side which communicates with the interior of the neural arch cavity.

In lateral view, there is also a large opening, situated between the parapophyseal-diapophyseal and infradiapophyseal laminae, which communicates with the neural arch cavity and which varies in relative size and position towards the rear.

The prezygapophyses are very robust, a little inclined towards the axial plane, transversely convex, and with additional articulations (hypantrum) on their prolonged medial border. The postzygapophyses are wide, transversely concave, and are preceded by a sort of indentation.

Towards the axial plane the hyposphenes, which have a strong ventral projection towards the axial plane, are confluent with the additional articulations. The transverse processes are wide and slightly dorsally oriented. Their cross-section is roughly triangular, with the anterior angle corresponding to the prezygapophyseal-diapophyseal lamina, the posterior angle to the connection with the postzygapophyseal region, and the ventral angle to where the two paradiapophyseal and infradiapophyseal laminae detach.

The neural spine of this vertebra, like the other dorsals, is formed from four divergent laminae (fig. 39) which converge towards the central region and which emerge from the pre- and postzygapophyses (supraprezygapophyseal and suprapostzygapophyseal laminae).

Thus they delimit two lateral supradiapophyseal laminae, and further one anterior and one posterior. Towards the dorsal end of the spine, these cavities disappear and are replaced by the massive body, rugose in the dorsal region of the spine.

The vertebral bodies corresponding to these neural arches are proportionally elevated and slightly elongated longitudinally, with the diameter of the anterior face a little straighter than that of the posterior, and a slightly deep lateral depression in the posterior region.

Posterior dorsal

(fig. 42)

In order to illustrate the morphological type of the posterior dorsals, a very well preserved complete vertebra from the holotype PVL 4170 will be described.

The vertebral body is amphiplatyan, a little taller than long, with projecting edges and a weak lateral depression.

The neural arch is practically the same type as that of the mid-dorsals. It presents the following variations. The lower part is taller. The pre- and postzygapophyses are situated lower in the same way as the parapophyses and the diapophyses. The prezygapophyseal-diapophyseal lamina is horizontal and the parapophyseal-diapophyseal lamina is subhorizontal. The lateral opening of the neural cavity is proportionally smaller and placed clearly lower than on the mid-dorsals.

In anterior view, the concavity of the neural arch is wide and extends to the lower part of the anterior region of the neural canal. The transverse processes are more horizontally placed than on the mid-dorsals. The neural spine is very similar to that of the mid-posterior dorsals, although the base of the suprapostzygapophyseal laminae projects more towards the rear.

Sacrum

(fig. 43 and 44)

The sacrum of the holotype includes five practically intact vertebrae. The first sacral vertebra is of the posterior dorsal type, and suggests a recent incorporation into the sacrum. The 2nd and 3rd sacrals are clearly fused from the dorsal end of the spines up to the base of the vertebral body (in other words for their entire height). The 4th and 5th have characters of caudal vertebrae, notably their neural spines. The 5th sacral is not fused to those preceding.

In general, these are tall vertebrae, with long, proportionally thin neural spines and wide bony laminae for the attachment of the ilium. The vertebral bodies of the end vertebrae are large or normal and transversely narrow in the 2nd, 4th and above all the 3rd (fig. 44).

The sacrum of *Patagosaurus* possesses a remarkable globular expansion of the neural canal of around 2,500 cm². This expansion is manifest particularly in the 3rd sacral but it continues in the 2nd while the first offers but slight traces. It is lacking in the 4th. In the 3rd, the walls of the expansion are concave and form a well-delimited cavity.

The system of bony laminae of the sacral ribs is comparable to that seen in some Upper Jurassic sauropods like *Haplocanthosaurus* (Hatcher, 1903) or *Camarasaurus*

(Osborn and Mook, 1921) but with differences in the details. The laminae, numbering four for each rib, extending from the emplacement corresponding to the diapophyses, to the parapophyses situated approximately at mid-height of the vertebral body. These diapophyses are well defined from the 2nd to the last sacral vertebra, each being wide in its contact with the ilium. Up to the 4th sacral, the three parapophyses form a horizontal series, but the 5th projects much more dorsally. The number of parapophyses and diapophyses connected to the bony laminae is four, because the first shows only the beginning of the development of a lamina on the parapophysis, while the diapophysis preserves numerous characters of the posterior dorsals though being entirely smaller. The 1st and 2nd sacrals enter into contact by the rudimentary zygapophyses, which indicate the "recent" incorporation of this vertebra into the sacrum. In this aspect *Patagosaurus fariasi* reveals primitive characters relative to the condition of four vertebral sacrals in *Barapasaurus* (Jain *et al.*, 1977).

Dimensions of the sacrum:

Height of the 1st sacral vertebra: 840 mm.

Height of the 2nd sacral vertebra: 800 mm.

Sagittal length of the ventral face: 920 mm.

Dorsal sagittal length along the neural spines: 540 mm.

Caudal vertebrae

The caudal vertebrae are well represented by the holotype, the hypodigm and the other specimens referred to this species.

The anterior caudals are proportionally large, with a tall neural spine and very short centrum. In contrast the distal caudals possess low neural spines and elongate vertebral bodies.

The data are lacking to determine approximately the number of caudal vertebrae.

Anterior caudal

(fig. 45a)

The neural spine is flat laterally, a little taller than the centrum, and with very short prezygapophyses and slightly prominent postzygapophyses, oriented in a V and separated by a notch. The transverse processes are short and slightly dorsoventrally compressed.

Mid-caudal

(Fig. 45b)

The body of this vertebra is also amphiplatyan; it is also longer than tall with projecting edges. The neural spine is flat laterally; the prezygapophyses project in front of the anterior end of the body and the postzygapophyses are less prominent and oriented in a V. The short transverse processes have a round cross-section close to the centrum.

Distal caudal

This vertebra comes from the proximal part of the distal region of the tail. The vertebral body is noticeably longer than tall, its edges being clearly in relief. The body is a little compressed laterally and ventrally. The neural spine is very inclined towards the rear. It looks like a proportionally tall and long blade. The prezygapophyses do not go beyond the centrum and the postzygapophyses are poorly defined.

RIBS

The cervical ribs (fig. 46 A, B, C), sometimes fused to the vertebrae, present a dorsolateral surface on the external face bearing the tuberculum, and a ventrolateral face with the capitulum. The two surfaces are united in a type of external edge, extended forwards anteroposteriorly by a distinct anterior process.

The internal face is very concave, with a longitudinal groove along its median line, which disappears from the start of the costal body. The surface of the capitulum is a little larger than that of the tuberculum.

Based on these observations, the cervical ribs were relatively frail up to the 7th or 8th vertebra, from which point they thicken considerably.

The ribs of larger size correspond to the anterior mid-dorsals (fig. 47). They are wide, flat in their proximal region, and with a long capitulum and a fairly short tuberculum, both fairly thick. On these flat ribs, the torsion in the anterior or transverse plane relative to the lateral or external plane occurs more distally than in the less flat ribs.

The other ribs have an especially marked proportionally thicker capitulum, forming a variable angle relative to the body of the rib. The wide tuberculum also has variable orientations compared with the different positions of the para- and diapophyses of the dorsal vertebrae.

The characters of the dorsal ribs, and the placement of their articular surfaces with the vertebrae, give supposition that the thorax and abdomen of these large dinosaurs must have been essentially straight and long, from the proportions surely higher than the ratio of width: 1, length: 1.6.

Haemal arches

The haemapophyses of *Patagosaurus fariasi* are proportionally robust, with the proximal processes solidly fused and forming a transverse expansion in this region. The lower part is generally flat while the proximal region is transversely wide. On the anterior face, the opening of the haemapophyses shows the dorsal and ventral elongation of a marked depression which does not exist on the posterior face.

PECTORAL GIRDLE

The holotype includes the entire left scapula and coracoid, and the right scapula articulated with the coracoid, both incomplete.

The right scapula and coracoid are available in specimens PVL 4172 and MACN-CH 932, of small and medium sizes.

Scapula

The scapula of the holotype is large, robust, proportionally thick in the posteroventral region or near to the glenoid, and with a strong anterior expansion in the acromial region. The scapular blade is medially flat and with a convex external border of which the curvature diminishes progressively and disappears near the dorsal border. Its expansion is moderate and attains its largest dimension in the anterior region. The entire anterior border is curved and the lower portion shows a robust acromial process. Between the glenoid cavity and the acromial process extends a wide depression, very well delimited dorsally and which forms a progressive passage for the coracoid.

The posterior border of the scapula is quite straight, with a distinct posterior supraglenoid projection. The glenoid cavity is transversely wide in the posterior region and very thick (23 cm) near the coracoid. From the glenoid cavity to the front, the contact with the coracoid slims noticeably until it has a thickness of less than 2 cm. The glenoid cavity is visible throughout in posterior view, in such a way that it is barely apparent on the external side.

Measurements:

Maximal length: 1240 mm.

Maximal length of the dorsal expansion: 420 mm.

Minimal width of the scapular blade: 205 mm.

Maximal width glenoid cavity - acromial process: 640 mm.

In the young specimen, note the differences in the lesser form and development of the dorsal expansion, in the less distinct manifestation of the acromial process, and in other minor details, while the proportions and general morphology are coincident with those of the holotype.

Measurements:

Maximal length: 765 mm.

Maximal length of the dorsal expansion: 126 mm.

Minimal width of the scapular blade: 126 mm.

Maximal width between the
posterior border–glenoid cavity–alveolar process: 220 mm.

Coracoid

(fig. 50 and 51)

The coracoid is a robust, subcircular element, convex on the external side, without an edge limiting the planes defined on the external face. In review, there is a clear border in front of the glenoid cavity towards the contact surface with the scapula.

Measurements:

Maximal anteroposterior length:

Maximal dorsoventral length: 560 mm.

Maximal thickness in the glenoid region: 190 mm.

The coracoid of the juvenile differs clearly from that of the holotype. Its contour is oval, with a very enlarged anterior region, and a coracoid foramen in the posterior region and not in the middle as in the holotype. This proportionally robust coracoid presents, from this coracoid process, a slight border or an elevated surface that separates the anteromedial region from the posteroexternal, characters not found in the holotype and which are interpreted as juvenile features of the coracoid of *Patagosaurus fariasi*.

Measurements:

Maximal length: 330 mm.

Maximal width: 200 mm.

Maximal thickness in the glenoid region: 110 mm.

The general morphology of the scapula and coracoid of *Patagosaurus fariasi* is comparable to that of *Barapasaurus tagorei* (Jain *et al.*, 1973, fig. 73) (neither measurements nor comparisons could be made from the schematic drawing of this species) and to that of *Cetiosaurus* (Phillips, 1871, fig. 99). With *Camarasaurus*, note the differences such that its scapula is proportionally shorter and the blade of the acromial depression is more ventrally reduced.

Diplodocus and *Apatosaurus* generally have a more slender scapular blade, with a less marked dorsal expansion. The acromial region has a different contour than that of *Patagosaurus*. In *Brachiosaurus*, the scapula presents a strong constriction at the base of the scapular blade following an important dorsal expansion.

With the coracoid the anteroventral contour forms a continuous curvature in *Patagosaurus*, a character shared in part with *Camarasaurus* but distinct from that of other Upper Jurassic sauropods, where it tends to form an angle at the anteroventral end.

PELVIC GIRDLE

The pelvic girdle is well represented by elements found from specimens of all ages. The two ilia and the pubis of the holotype are complete; the ischia are fused, but they lack their proximal regions. The pubes, ilia and ischia of other individuals are well preserved.

Ilium

(fig. 52)

This pelvic element has a pubic peduncle, very large and straight, with a dilated lower end. The ischial peduncle is short and in large part masked by the development of the iliac blade. The acetabular cavity is large, its most dorsal extension is located in the anterior moiety. The acetabulum is widely open on the internal side as in *Barapasaurus* (Jain *et al.*, 1977, fig. 93 and 94). The iliac blade presents a convex dorsal border, and anterior and posterior borders thick with rugosities for cartilaginous insertions. The anterior projection extends anterolaterally and the most depressed region of the blade is located above the most elevated part of the acetabulum. The anterior projection is wide, a

little more than that of *Barapasaurus*. The contour of the iliac blade varies a little from one ilium to the other.

Measurements:

Maximal length: 1010 mm.

Maximal height: 710 mm.

Maximal width of the acetabular cavity: 390 mm.

Maximal height of the acetabular cavity: 250 mm.

Pubis

(fig. 53, 54 and 55)

This is a massive, robust element, especially in the adults such as the holotype (fig. 53). The lateral border of the pubis is very concave in anterior view, in such a way that the proximal end which unites to the ilium projects strongly laterally and to a lesser degree anterodorsally, the two projections being the prolongation of one from the other. The distal end, of similar form, shows wide lateral, anterior and posterior projections forming a robust inferior end. The body of the pubis is relatively flat in anterior view and transversely convex in posterior view. The medioproximal blade of the pubis pierced by the obturator foramen shows a strong torsion, such that its principle orientation is backwards, in a subhorizontal plane. In the axial region of this blade, note a thickening for the pubic symphysis.

The comparison of the pubis of *Patagosaurus fariasi* with those of other sauropods, especially *Barapasaurus* of the Indian Lias (Jain *et al.*, 1977) and *Lapparentosaurus* (Bonaparte, in press) of the Bathonian of Madagascar (Ogier, 1975), shows that there is a greater affinity with this last genus and to a lesser degree with the Indian species, particularly in the development of proximal and distal projections as well as in the external separation between the two pubes in the proximal region (fig. 54), which constitute a group of derived characters which clearly differentiate it from *Barapasaurus*. On this point, the pubes of *Patagosaurus* and *Lapparentosaurus* are morphologically closer to *Camarasaurus* or *Diplodocus* than to *Barapasaurus*.

Ischium

(fig. 56, 57 and 58)

This is a considerably more gracile bone than the pubis, with more modest expansions at its ends. That of the holotype is at the same time deformed hence an

abnormal curvature, and incomplete in its proximal part. As a consequence, the ischium of PVL 4616, practically without deformation, is more representative. In the proximal region, the acetabular area is very dorsally projected, forming a marked angle with the external face of the bone. Above the acetabular region is found the iliac peduncle which is robust, transversely thickened, and a little laterally projected. Below the same region, there is the bony process for the pubis which is relatively short but with an extended and robust articular area.

The dorsal end possesses a moderate dilation with a dorsoventrally enlarged cross-section, while it is of modest size transversely. The rather wide dorsal border of the ischium forms a large curve, while the rather lamellar ventral border is hardly incurved in its middle part.

This ischium appears developed on the same morphological plan as that of the two diplodocids *Diplodocus* and *Apatosaurus* (McIntosh, 1981), while the differences with that of *Camarasaurus* abundantly illustrated by Osborn and Mook (1921) indicate the presence of diverse derived characters in this genus, such as the remarkable development of the proximal region accompanied by a strong dorsal projection, the reduction in height by two-thirds, and the virtual disappearance of the distal thickening. Also note that the type of ischium in *Patagosaurus fariasi* essentially matches that primitive for Diplodocidae. Figures 57 and 58 illustrate the reconstruction of the pelvis of *Patagosaurus fariasi* and the juvenile specimen MACN-CH 934, respectively.

FORE LIMB

The fore limb of *Patagosaurus* is not totally represented because no remains of the manus are available. A well-preserved humerus, radius and ulna correspond to MACN-CH 932. Another humerus belongs to PVL 4075, referred to this species.

Humerus (fig. 59)

This bone has a slender shape, with a relatively elongate shaft and modest proximal and distal expansions. The proximal region is very convex on its dorsal face, with a prominent central region that extends in the central part of the bone from the articular head up to beneath the region of the shaft. The internal tuberosity is slightly prominent and poorly defined but well separated from the humeral head by a groove. The deltoid crest, unfortunately incomplete, has a large width and probably a projection on

the ventral or posterior side, although we do not know the importance and location of its maximal ventral (or anterior) extension.

In the distal region, the epicondyles are very reduced. On the dorsal face, there is a modest supracondylar depression. On the ventral face, there is a convex region probably corresponding in part to the poorly delimited radial and ulnar condyles. The torsion between the two ends of the humerus is on the order of 15-20°.

Radius

(fig. 60)

A right radius is available, belonging to a large juvenile individual. This is also a slender element with moderately enlarged ends. The proximal region shows a modest posterior expansion, while on the other faces the expansions are minimal. The articular surface for the humerus (with wide reliefs for cartilaginous insertions) is rather rectangular with the major axis oriented anteroposteriorly. On the distal end, the articular facet is oval, subcircular, with the major axis oriented approximately transversely (mediolaterally).

In the lower third of the radius and on the posterior face, note a well-defined bony process which continues dorsally, forming a ridge up to the region near the shaft. This process corresponds to the insertion area for the radioulnar ligaments.

Ulna

(fig. 60)

This belongs to the same individual as the humerus and radius. It is complete but covered by a pair of sediment-filled breaks which leave doubts as to the original shape of the element. Its proximal region presents three planes, each very clearly separated by a ridge. One of these planes (convex) corresponds to the internal face, while the two others are concave. One of the two corresponds to the posterolateral face. The ridge which divides these two concave faces is prominent and sharp; it disappears near the middle of the shaft.

In the distal region, the ulna has a subcircular cross-section and presents a clear anterior expansion.

The comparison of the fore limb of *Patagosaurus* with that of other Jurassic sauropods, *Camarasaurus*, *Apatosaurus*, etc., shows important differences in proportions because all have considerably thicker and heavier arm bones. In contrast,

there are more similarities with the type of fore limb in *Diplodocus* with proportionally gracile bones. For all that, this does not signify a strong phylogenetic connection between one or another of the Upper Jurassic sauropods, but rather that the morphological similarities could be the result of comparable locomotor adaptations.

The similarities of the fore limb of *Patagosaurus* are more evident with *Lapparentosaurus* from the Bathonian of Madagascar, studied by Ogier (1975), with which very clear resemblances are noted.

HIND LIMB

The hind limbs of *Patagosaurus* are represented essentially by femora and tibiae, and by very few elements of the pes. The right femur of the holotype is flattened anteroposteriorly and the left anteromedially. The remains of the right femur and tibia of the juvenile specimen MACN-CH 933, the right femur and tibia in the material collected from specimen PVL 4076, the left femur of specimen PVL 4075, and the recently collected left femur and tibia of another, are also represented.

Femur

(fig. 61 and 62)

The femora from two adult specimens show some differences from that of the juvenile in figure 62. They are in general straighter or more columnar, and the shaft cross-sections more oval. In anterior view, note that the largest part of the shaft preserves a constant width, with the medial and lateral sides subparallel. The proximal expansion is abrupt near the internal side since the femoral head is well projected.

The femoral head is well-defined, except the internal side which produces the greater trochanter. This latter is convex from front-to-back, forming a well-defined plane suggesting an articular function.

The distal expansion is rather symmetrical in posterior view, forming two condylar surfaces of similar size, separated by a wide intercondylar depression which continues a little towards the anterior face, forming a short supracondylar depression. In posterior view, the two tibial condyles project widely towards the rear, and the internal, of greater volume, is well separated by the intercondylar depression. The fibular condyle is large and clearly separated from the external tibial condyle by a dorsoventral depression.

The fourth trochanter is located on the posterior face of the femur, oriented obliquely from the top/interior to the bottom/exterior. It is relatively well-defined in its distal part, diminishing near the top. It is situated on the proximal region of the femur, although a short part of the trochanter overflows the proximal region of the femur distally.

The femur of the juvenile specimen (fig. 62) is slightly concave on its posterior face and a little sigmoid on its medial face. The cross-section of the shaft is subcircular. The more pronounced fourth trochanter is completely situated in the proximal part of the femur.

Tibia

(fig. 63)

The tibia is short and robust, with a well-defined cnemial crest. The proximal region is thickened, very convex on its medial face, with a weak depression behind the cnemial crest on its lateral face. On this same face, observe that the anterior border of the tibia is incurved while the posterior is rather rectilinear. On the distal end, the articular surface for the astragalus is broken down into two parts, one anterior and elevated, the other posterior and depressed.

The ratio between the lengths of the femur and tibia show slight variations. In the juvenile, the ratio is: tibia = 1, femur = 1.5; in an adult where the femur measures 1.32 m in length, the ratio is: tibia = 1, femur = 1.65; and in PVL 4076 where the length of the femur is 1.55 m, the ratio attains: tibia = 1; femur = 1.72. Thus note that as the specimens get larger, the tibia gets proportionally smaller. Comparisons of these bones with those of other sauropods give results that are a little weak and difficult to materialize, perhaps because there are few variations between the different Upper Jurassic sauropods. Nevertheless one can underline the clearer similarities with *Cetiosaurus* (Phillips, 1871) and *Lapparentosaurus* than with the species from the Morrison Formation or the Tendaguru Beds of the terminal Jurassic.

COMPARISONS

Two parts are distinguished in the comparisons of *Patagosaurus* with other sauropods. One bears on the sauropods prior to the end-Jurassic such as *Barapasaurus*, *Vulcanodon*, *Cetiosaurus*, *Lapparentosaurus*, *Rhoetosaurus*, *Amygdalodon*, with the aim of partially understanding the primitive stage in the evolution of the group. The other

deals with the end-Jurassic sauropods, essentially from the Morrison and Tendaguru Formations. The distinction of these two parts is justified by the evolutionary grade and entirely distinct differentiation that separates the end-Jurassic sauropods from those prior. They are so different that one can qualify the latter (Eosauropods) as relatively primitive, generalized and little varied at the family level, while the former reflect the effects of a marked adaptive radiation with the appearance of at least four families characterized by anatomical characters well-differentiated in the skull and vertebrae, but less marked in the appendicular skeleton. To this group of evolved sauropods one can award the name Neosauropods, with the sole valuable connotation of an evolutionary grade considerably distinct from that of Eosauropods.

We do not enter into a comparison with Cretaceous sauropods because those which are known from this period show differences and gaps so significant that we do not consider it useful to attempt a similar work in the current state of knowledge.

Sauropods prior to the end-Jurassic, or Eosauropods

These sauropods are relatively few in number, and are essentially represented in Gondwana and Europe. The species which are sufficiently diagnostic to be compared to *Patagosaurus fariasi* are the following:

Vulcanodon karibaensis Raath, 1972. Rhaeto-Hettangian, Lac Kariiba, Rhodesia.

Barapasaurus tagorei Jain et al., 1975. Liassic, Pranhita-Godovari Valley, India.

Ohmdenosaurus liasicus Wild, 1978. Toarcian, Holzmaden, Germany.

Amygdalodon patagonicus Cabrera, 1947. Liassic?-Bajocian, Chubut, Argentina.

Rhoetosaurus brownei Longman, 1926. Dogger?, Queensland, Australia.

Volkheimeria chubutensis Bonaparte, 1972. Bathonian-Callovian, Chubut, Argentina.

Lapparentosaurus madagascariensis (Lydekker, 1895; Bonaparte, in press). Bathonian, Madagascar.

Cetiosaurus oxoniensis Phillips, 1871. Rutland, England.

Vulcanodon karibaensis

We interpret this remarkable species from the Triassic-Jurassic boundary as a sauropod, but the carnivorous teeth figured by Raath (1972, pl. VII) as teeth of

Vulcanodon do not belong to this taxon. It is well known that in practically all the localities of remains associated with sauropods, Jurassic or Cretaceous, theropod teeth are nearly always found, evidence of predatory action or scavenging of carnivores.

The principal skeletal characters of *Vulcanodon* clearly indicate its sauropod condition, especially the pubis (Raath, 1972, fig. 5) which suggests a more evolved stage than that of *Barapasaurus* (Jain *et al.*, 1977, fig. 97B). The length and morphology of the metacarpals, characters of the astragalus, and in a certain sense the ischium, clearly indicate its membership among sauropods.

The pubis of *Patagosaurus fariasi* is more laterally extended in the proximal region than that of *Vulcanodon karibaensis*, which appears derived relative to the Patagonian species. As for the ischium, note such similarities between the two species as the reduction of the ventral blade and the shape of the distal expansion, though it is difficult to evaluate some particular traits.

The incomplete sacral and caudal vertebrae of *Vulcanodon*, of which it is possible to take measurements from the illustrations of Raath, have clearly marked similarities with prosauropods, and at the same time evident differences with *Patagosaurus* and *Barapasaurus*. Thus the association of prosauropod-type vertebrae with a sauropod-type pubis, ischium, astragalus, and metacarpals shows evidence of the important differences not only with the aforementioned genera but also with cetiosaurids among sauropods.

As a consequence, I think Cooper's (1984) proposition, to establish a new family for this species which would be the most primitive of all sauropod families, is adequate, with the reservations imposed by the available material. However there is no reason to include *Barapasaurus*, which is a cetiosaurid according to its vertebral anatomy.

Barapasaurus tagorei

The similarities presented by this species with that previously described are particularly highly significant, although they are seen here as different genera. The cervical vertebrae, according to the schematic figures of Jain *et al.* (1977, pl. 98A), and also the mid- and posterior dorsals, are fundamentally identical to those of *Patagosaurus fariasi*. The structure of the neural spine, of the transverse processes, the lateral fenestra of the neural cavity, the deep anterior depression below the prezygapophyses and between the parapophyses, the type of vertebral body, etc., are many characters common to the two species.

The similarities of the vertebrae are extended to the scapula and coracoids, whose proportions and shapes are practically identical in the two species. Meanwhile, the pubis of *Barapasaurus tagorei* is more primitive, with a proportionally smaller amplitude between the two lateral borders of the proximal region. From this point of view, the relatively much wider and shorter pubis of *Patagosaurus fariasi* is closer to the arrangement presented by some end-Jurassic sauropods. Also note that the acetabular cavity of the ilium of *Barapasaurus tagorei* presents a well-developed medial wall. This is a primitive character relative to *P. fariasi*, where the acetabulum is very open on the medial side.

The inclusion of *Barapasaurus tagorei* in the cetiosaur family is indisputable, based on clear similarities with two cetiosaurid species from England, notably the level of the vertebral, scapular, and pelvic morphologies. As a consequence, we do not doubt that *B. tagorei* was a more primitive and relatively more ancient species than *P. fariasi*, and yet corresponds to the same family of sauropods, the cetiosaurids.

Cetiosaurus oxoniensis*, *Cetiosaurus leedsii

For practical reasons, it is convenient to compare the genus *Cetiosaurus* to *Patagosaurus* since the distinctions between the species of *Cetiosaurus* are not clear.

Phillips (1871, fig. 86) figured a mid-dorsal vertebra of *Cetiosaurus* that, although deformed, shows characters with many similarities to those of *Patagosaurus*. Among these are the structure of the neural spine with wide lateral depressions, the general morphology and orientation of the transverse processes, and the vast anterior depression below the prezygapophyses and between the parapophyses. On the two dorsal vertebral bodies of *Cetiosaurus* in the British Museum (N.H.), the lateral depressions are identical to those of *Patagosaurus*. Regarding the scapulae figured by the author, we remark on the similarities in the form and characteristics of the scapular blade, in the region of the glenoid cavity and the expansion which ends in the acromial region, to the point that we do not see any significant differences here.

The humerus is also very similar, except that the proximal and distal expansions are less marked in the juvenile *Patagosaurus* (fig. 59). The proximal expansion of the right humerus, PVL 4075, 1.05 m in length, which well resembles that of *Cetiosaurus*, is noticeably larger than that of the juvenile. There are equally notable similarities between the pelvic bones of the two genera. In the collections of the British Museum (N.H.), there is a pubis and ischium labeled "*Cetiosaurus*" that are practically identical in detail to those of *Patagosaurus*.

In summary, the anatomical plan of different bony parts of the English genus is fundamentally identical, and we observe generic differences only in some parts of the skeleton, for example in the more slender humeral shaft of *Patagosaurus* (PVL 4075), and possibly the form of the acetabulum. Meanwhile, it is necessary to add the important morphological difference in the mediodistal haemal arches figured by Smith Woodward (1905, fig. 46) under the name *Cetiosaurus leedsii*, of bifurcate type as seen in *Diplodocus* and not *Patagosaurus*.

Ohmdenosaurus liasicus

This Liassic species from Germany is represented by an incomplete hind limb that, in our opinion, is not diagnostic enough to show evidence for eventual relationships with *Patagosaurus*. When the anatomy of the hind limb of Jurassic sauropods is better known, one could determine, at least in part, the significance of that of *Ohmdenosaurus liasicus* and also compare it to *Patagosaurus*.

Amygdalodon patagonicus

This species was defined by Cabrera (1947) and Casamiquela (1963), based on fragmentary material belonging to two individuals of different sizes.

The dorsal vertebrae, quite incomplete, show the evident fact that the anatomical characters of the vertebral body and neural arch of *Amygdalodon* and *Patagosaurus* are identical. It is the same for the teeth of the two genera. However, the medial blade of the pubis is more elongate in *Amygdalodon*, whence a more extended symphysis. For this reason and in spite of restrictions imposed the use of a unique character, we think that *Amygdalodon* is more primitive, which is confirmed in part by its clearly more ancient stratigraphic position than *Patagosaurus*. In effect, the recent studies of Musacchio, in the region of Pampa de Agnia (personal communication) confirm the ideas of Piatnitzky (1936), according to whom the beds of *Amygdalodon* in the Cerro Carnero Formation interpenetrate and are superimposed on the marine Liassic of the region. That is to say that if *Amygdalodon* is not already Liassic, it is not very far removed. In contrast, *Patagosaurus* is considered to be Callovian or perhaps Bathonian, which by all facts signifies a difference of 6 ma with *Amygdalodon*.

In summary, *Amygdalodon patagonicus* is considered a little more primitive than *Patagosaurus fariasi*, although the two species are morphologically very close, and without doubt form part of the family Cetiosauridae.

Rhoetosaurus brownei

At present this species is known from very incomplete and fragmentary facts, since the material which would be diagnostic was figured without preparation by Longman (1929, pl. 2). As a consequence, in admitting that *Rhoetosaurus brownei* could be a cetiosaurid, sufficient anatomical elements to affirm this are not available, and still fewer to try to compare it to *Patagosaurus fariasi*.

Volkheimeria chubutensis

This species is based on a specimen that is incomplete but includes diagnostic material, among them the femur, tibia, pelvis, and cervical, dorsal, sacral and caudal vertebrae, all well preserved (Bonaparte, 1979). The characteristic elements on which the genus and species are founded are essentially characters of the mid- and posterior dorsal vertebrae, whose neural spines show a structure distinct from that of *Patagosaurus fariasi*. In *Volkheimeria*, the neural spine is relatively flat in lateral view, with straight anterior and posterior borders of the axial lamina. In *Patagosaurus*, the neural spine in the presacral region is tetroradiate (fig. 42) with a deep depression in the axial plane from front to back.

This important vertebral morphological difference is considered to have a generic significance that unfortunately is not also manifest clearly in the other parts of the skeletons of the two genera.

Without doubt, the vertebrae of *Volkheimeria* represent a more primitive state than those of *Patagosaurus*, *Barapasaurus* and *Cetiosaurus* in which the neural spine is formed from four laminae which converge near the axial plane. Nevertheless, and in spite of the preceding doubts, *Volkheimeria* is included among the Cetiosauridae, and considered as a primitive representative due to its vertebral structure.

Bothriospondylus madagascariensis

The genus *Bothriospondylus*, created by Owen (1875) for the type species *B. suffosus*, was founded on four dorsal centra from the Kimmeridgian of England. Lydekker attributed various vertebral bodies found in Narinda Bay (northwest Madagascar) to the same genus, and founded the species *B. madagascariensis* on a dorsal vertebral body (Lydekker, *op. cit.*, fig. 3) characterized by deep pleurocoels separated by a thin septum.

The generic determination is very doubtful, just as is the choice of a new species, because the mentioned characters correspond to individual variability, and besides are also found in species of clearly distinct origin.

Thevenin (1907) brought to light different incomplete sauropod remains from Narinda Bay, from the environs of Analabara, recovered in beds reported as Bathonian by Lemoine and assigned to the species *B. madagascariensis*.

The reported specimens of this species may or may not correspond to Owen's genus since they are based mostly on fragmentary material whose principal characters agree with those of the Cetiosauridae, but in truth do not permit valuable comparisons at the generic level.

Recently, A. Ogier (1975) studied new materials assigned to *Bothriospondylus* sp. also from the Bathonian of Madagascar. This material was reinterpreted by Bonaparte (in press) and served as the basis for the new genus *Lapparentosaurus*, species *L. madagascariensis*. It was from a young specimen with a humerus 0.50 m long and a femur 0.60 m long, which can be compared with the juveniles of *Patagosaurus fariasi*. Some of the remarkable morphological affinities are observed in the scapula, humerus, pubis and femur and also perhaps in the ilium, but there are visible differences in the ischium, especially at the level of the haemal arches figured by Ogier. The ischium of the Malagasy species has a very flattened shaft with a marked torsion of such degree that its distal end is turned nearly 90° relative to the proximal plane, which differentiates it from *P. fariasi*.

But it is chiefly between the neural arches of the posterior dorsal and sacral vertebrae of the two species that more clear differences can be observed. In *L. madagascariensis*, the neural arch is low, with a reduced space between the zygapophyses and the base of the neural arch, and a neural spine of rather lamellar type without divergent laminae. Thus *L. madagascariensis* is clearly distinguished from *P. fariasi* by the structure of the neural arch and the characters of the ischium, and shows more similarities with *Volkheimeria chubutensis*.

Comparisons with end-Jurassic sauropods, or Neosauropods

Most of the end-Jurassic sauropods are found in the rich localities of the Morrison Formation (U.S.A.) and the Tendaguru region (Tanzania). It is necessary here to add the contemporary specimens from Chile, although they are not included in the comparison because of insufficient information.

The different sauropods from the Morrison and Tendaguru Formations, belonging to several families, invariably show apomorphic characters relative to Cetiosauridae. They are Camarasauridae, Brachiosauridae, Diplodocidae, Dicraeosauridae and Atlantosauridae. The genus *Haplocanthosaurus*, often referred to Cetiosauridae or Cetiosaurinae (Romer, 1966; McIntosh, 1981), possesses derived characters at the level of the dorsal vertebrae, which clearly differentiates it from other Cetiosauridae (Bonaparte, in press) and which bring it partly closer to *Dicraeosaurus*.

In a study of probable phyletic relationships among Jurassic sauropods and their origin among the prosauropods (Bonaparte, in press), I have given particular attention to the anatomical characters of the presacral vertebrae of these giant tetrapods, in order to construct the phylogenetic scheme reproduced in figure 65. As can be verified, Upper Jurassic sauropods correspond to well differentiated adaptive types, resulting in notable variations probably from Cetiosauridae. For this reason, research of their relationships to other kin has been greatly facilitated by the study of taxa structurally and chronologically more primitive than the cetiosaurids from the Callovian of Patagonia.

Note that, in large part, the total confusion reigning in the systematics and phylogeny of Jurassic sauropods, well summarized by A. S. Ron (1968, p. 138: "It will be a long time, if ever, before we obtain a grand comprehensive picture of sauropod classification and phylogeny") has as its origin the ignorance of the general anatomy of ancestral forms such as Lower and Middle Jurassic cetiosaurids.

The many basic attempts on the relationships of Morrison and Tendaguru are met with very serious difficulties in the mosaic of common and distinctive characters encountered in diverse adaptive types, which are impossible to interpret without the aid of the anatomy of ancestral forms.

Camarasauridae

Generally, the presacral vertebrae of *Camarasaurus* (Osborn and Mook, 1921) show an ensemble of derived characters which differentiate them clearly from those of *Patagosaurus*. The presacral vertebrae of *Camarasaurus* are lower and particularly wide due to the development of large, strong transverse processes.

Also, frequently the neural canal is entirely delimited by the ventral and medial development of the neural arch pedicels, according to an arrangement never observed in *Patagosaurus*.

On most of the dorsals, the anterior face of the neural arch below the zygapophyses shows a wide, deep depression which is very distinct from the cavity

encountered in *Patagosaurus*, although this arrangement and those of Cetiosauridae in general could have been ancestral.

The neural spines of *Camarasaurus* are strongly modified since they are low and bifurcate up to the seventh dorsal and beyond, whence they are low but without bifurcation.

Finally the bodies of all presacral vertebrae of *Camarasaurus* show an clear opisthocoely, while in *Patagosaurus* this condition is only realized in the mid-dorsals.

Brachiosauridae

The very evident differences between *Patagosaurus* and *Brachiosaurus* (Riggs, 1904; Janensch, 1950) are observed practically throughout the skeleton. The proportions between the fore and hind limbs and the relative length of the cervical vertebrae are so distinct from one genus to another that they represent distinct adaptive types with, further, a great number of apomorphic characters in *Brachiosaurus*.

The hypertrophied cervical vertebrae of *Brachiosaurus* are very cavernous. The neural arch of the dorsals is very longitudinally extended with low spines on the last dorsals and sacrals, which clearly differentiate them from those of *Patagosaurus*. The opisthocoely is also much more developed in *Brachiosaurus*, where it reaches all the vertebrae, than in *Patagosaurus*.

As to the dentition, note that it is fundamentally comparable to that of *Patagosaurus* and *Camarasaurus*. Thus it should be admitted that the adaptive types, also different between those that represent Cetiosauridae, Camarasauridae and Brachiosauridae, had a comparable basal type of dentition in common, which does not indicate that they had identical feeding regimes. On the contrary, we suspect that the spatulate teeth of these sauropods are sufficiently ubiquitous to have been able to confront diverse regimes.

Diplodocidae

In a discussion of this family (Bonaparte, in press) including the Jurassic genera *Diplodocus*, *Barosaurus*, *Apatosaurus*, probably *Cetiosauriscus* and *Mamenchisaurus* (Berman and McIntosh, 1978), I noted the inconvenience of including the genus *Dicraeosaurus* among the diplodocids as certain authors would entrust it.

Diplodocus is probably the least specialized genus of this family, which permits interesting phylogenetic comparisons with *Patagosaurus*.

The vertebrae of *Diplodocus* and *Patagosaurus* are comparable; in the second genus, the pleurocoels are more pronounced and a system of trabeculae is developed, which can be interpreted as derived characters.

The dorsal vertebrae of *Diplodocus* show many characters in common with *Patagosaurus*.

Among the first, note the proportions (height and anteroposterior breadth), the system of bony laminae which connect the diapophyses to different parts of the neural arch, the general morphology of the neural arch beneath the transverse process, the neural cavity situated below the neural canal, and the principal components of the neural spine.

Among the derived characters of *Diplodocus*, note the development of the supradiapophyseal lamina incorporating the lateral region of the spine, the bifurcation of the neural spine, and the development of pleurocoels.

In summary, the vertebral morphology of *Diplodocus* very likely is derived from that of Cetiosauridae and as a consequence from *Patagosaurus*, although that by no means implies that the Argentine genus is the direct ancestor of *Diplodocus*.

As to the dentition of *Diplodocus*, it is undoubtedly more specialized than that of *Patagosaurus* and the cetiosaurids. Nevertheless on the mandible of the juvenile *Patagosaurus* (fig. 53), the teeth show a limited expansion of the crown and as a result the absence of differentiation between the neck and the crown, that is to say the previous stage to the formation of the cylindrical teeth shown in the diplodocids.

Dicraeosauridae

In agreement with von Huene (1956), we consider that this family is known only from *Dicraeosaurus* Janensch (1929) from Tendaguru.

It is a genus whose cranial morphology and dentition show certain affinities with diplodocids, but the presacral vertebrae possess very derived characters which clearly distinguish it from *Patagosaurus* and other cetiosaurids.

The dorsal vertebrae have very large neural spines, which are deeply bifurcated in anterior view, except the last. The neural arch is tall and very reduced transversely, and the anterior and posterior faces are very deep under the zygapophyses to the point that the separation between the two anterior and posterior cavities is reduced to a bony lamina. This arrangement is fundamentally distinct from that of *Patagosaurus*, *Barapasaurus*, etc. It constitutes a remarkable apomorphy of the genus *Dicraeosaurus*. Regarding the neural spines of the last dorsals (not bifurcated), they have a structure radically distinct from that in *Patagosaurus*, since the axial laminae of the spines are

formed by a remarkable development of the insertion area for the intervertebral ligaments. In *Patagosaurus*, this part of the spine is not developed axially. As a consequence, the cross-section of the neural spine of *Dicraeosaurus* is entirely distinct from that of *Patagosaurus*.

The lateral concavities of the vertebral bodies of *Patagosaurus*, which can occasionally resemble pleurocoels, are completely closed or absent in *Dicraeosaurus*. This is why I consider this absence of lateral depressions on the posterior dorsal vertebral bodies, so widespread in the cetiosaurids, as another derived character of the African genus.

Haplocanthosaurus

This genus from the Morrison Formation (Hatcher, 1903) has frequently been interpreted as a cetiosaurid (Huene, 1956; Berman and McIntosh, 1978). However the analysis of its vertebral structure shows that it presents a number of derived characters. The inferior part of the neural arch is very reduced transversely, with strong depressions on the anterior and posterior faces, similar to those of *Dicraeosaurus* and separated by a transverse septum. The neural spine also possesses derived characters relative to *Patagosaurus* since the axial laminae for the intervertebral ligaments shows a large development, and since the lateral laminae originate from the supradiapophyseal laminae, in general very little developed in cetiosaurids.

Thus the resemblances between *Haplocanthosaurus* and cetiosaurids, which led them to be considered as playing a part in this family (absence of bifurcation of the neural spine and very well developed "pleurocoels" in the dorsal vertebrae) lose all significance before the remarkable derived characters of the different parts of the neural arch, which have attained an entirely distinct grade of specialization from that of cetiosaurids including *Patagosaurus*.

***Volkheimeria chubutensis* Bonaparte 1979**

This species was made the object of a short description by the author, accompanied by a brief discussion of its differences with *Patagosaurus*, *Haplocanthosaurus* and *Cetiosaurus*. Here, we propose to define its characters and affinities more clearly.

Holotype. - PVL 4077 includes an incomplete cervical vertebra, two posterior dorsal vertebrae, an incomplete dorsal neural arch, two incomplete sacral vertebrae, two incomplete ilia, an ischium, a pubis, and the left femur and tibia.

Geographic and stratigraphic position. - Collected from Cerro Cóndor, from 1000 m around the Farias store (Department of Paso de Indios, Province of Chubut, Argentina), in a fluvial bed of unsorted pebbles, corresponding to the lower third of the Cañadon Asfalto Formation, Callovian, Middle Jurassic.

Diagnosis.- Cetiosaurid of smaller size than *Patagosaurus fariasi*, with femur measuring 63 cm in length. Posterior dorsal vertebrae with lower neural arch than *Patagosaurus*; laterally flattened neural spine with rectangular basal cross-section, lacking the divergent laminae present in *Patagosaurus*, comparable to *Lapparentosaurus madagascariensis*. Iliac blade turned back to project anteriorly, ischium with subcircular shaft and without lamellar tendency, more gracile and elongate pubis than in *Patagosaurus* or *Lapparentosaurus madagascariensis*.

DESCRIPTION

The material on which *Volkheimeria chubutensis* is founded is less abundant but includes sufficiently diagnostic elements, such as the neural arch from the posterior dorsals, the ischium, the pubis, and the anterior projection of the ilium, to justify the proposed generic distinction (Bonaparte, 1979).

VERTEBRAL COLUMN

Cervical vertebra

The cervical vertebra, reduced to the major part of the vertebral body and the very damaged neural arch, does not offer any particular interest. The centrum is opisthocoelous as in other sauropods.

Dorsal vertebrae

In contrast, the posterior dorsal vertebrae reveal interesting diagnostic characters (fig. 66, 67 and 68). The neural arch in this group is relatively tall; its inferior part up to

the transverse processes is also proportionally low if one compares it to that of *Patagosaurus fariasi*. Nevertheless, there are not morphological differences between them. They show the same prezygapophyseal-diapophyseal, parapophyseal-diapophyseal and infradiapophyseal laminae delimiting two large cavities, and the same opening with the neural cavity placed above the neural canal, mentioned by Jain *et al.* (1977) in *Barapasaurus*.

In anterior view, the region between the two parapophyses and enclosing the neural canal is less excavated than that of *P. fariasi*. It does not have the dorsoventral crest present in *P. fariasi*, since the neural canal is near the top (fig. 39 and 41). In posterior view, note the existence of a strong medial lamina since the postzygapophyses are near the base where the large hyosphenes are found.

The neural spine of the posterior dorsals of *V. chubutensis* present particular characters which clearly differentiate them from those of *P. fariasi*. These spines are relatively flat, of moderate width, and elongated sagittally. On the anterior and posterior edges, subparallel from top to bottom, note rugosities for the insertions of intervertebral ligaments. These edges are clearly observed in lateral view since they represent the extreme anteroposterior limit of the neural spine, while in *Patagosaurus* the areas of ligamentous insertion are not visible because they are covered by the laminar expansions.

The lateral surface of the neural spine presents a regular depression from top to bottom, near the posterior border, and underlined anteriorly by a modest thickening which we interpret as playing a part in the suprapostzygapophyseal lamina since it detaches from the postzygapophysis. In *P. fariasi*, this same character is much more marked. It is the same for the supraprezygapophyseal lamina. The greatest part of the lateral surface of the spine is slightly concave, especially in the upper third where the concavity is transformed into a depression. The most dorsal part of the spine is thicker than the rest (fig. 66 and 67).

This type of neural spine, very different from that of *P. fariasi* thus corresponds to a different muscular organization in the two species. Nevertheless the arrangement of *P. fariasi* is very probably derived from that of *V. chubutensis* by hypertrophy of the supraprezygapophyseal laminae.

Comparison of the dorsal vertebrae of *V. chubutensis* with those of *Lapparentosaurus madagascariensis* permits recognition that the two species present a comparable level of vertebral organization with relatively flat neural spines.

Sacral and caudal vertebrae

The available sacral vertebrae do not permit understanding the number of vertebrae in the sacrum. The very dorsoventrally flattened neural arch (fig. 69), probably from the last sacral, indicates that it possessed lower spines than the posterior dorsals, with a clear dorsal expansion of the spine. There are two vertebral bodies, each bearing a sacral rib (fig. 70), probably the last of the sacrum.

They are much thicker, providing a robust rib which projects ventrolaterally. There is no evidence of fusion between the vertebral bodies or between the centra and the neural arches or the sacral ribs. In *Patagosaurus fariasi*, the adult specimens, of large size, do not present any more than traces of coossification in the sacral vertebrae.

A caudal neural arch (fig. 71) shows marks of strong intervertebral insertions on its interior and posterior borders. The spine is relatively short, and the zygapophyses subvertical and very near the sagittal plane.

PELVIC GIRDLE

Ilium

Of the two incomplete ilia, neither permits a good detailed study. The general shape (fig. 72) is of the type seen in *Patagosaurus*, with a very long pubic peduncle while that for the ischium is less apparent. Meanwhile, the anterior projection of the iliac blade of the two ilia shows a remarkable dorsolateral torsion, also observed on the different ilia of *Patagosaurus*. The internal projection of the acetabular region is also much more pronounced than the external, such that the iliac blade is located above the external portion of the acetabulum. This character is less marked in *Patagosaurus*, but most of the morphological traits are observed in *Lapparentosaurus madagascariensis* from the Middle Jurassic of Madagascar.

Ischium

The right ischium is preserved in a satisfactory fashion (fig. 73A). Like the pubis, it is a gracile element, narrow and long, with modest proximal expansions, especially for the process for union with the pubis. The shaft is subcircular in cross-section, with the plane of the symphysis relatively reduced, except near its distal end where the element thickens ventrally.

There are therefore clear differences with the ischium of *Patagosaurus*, which normally is more flattened in lateral view, and shows a greater development of the

proximal part of the ventral lamina. It also differs from the ischium of *L. madagascariensis* whose shaft and distal end are very flattened and nearly lamellar.

Figure 74 gives a reconstruction of the pelvis of *V. chubutensis*.

Pubis

The left pubis (fig. 73B) is sufficiently complete although the central part is a little deformed. It is proportionally longer and straighter than that of *Patagosaurus*, with a much less marked dorsolateral projection. The distal end presents a dorsoventral thickening less apparent laterally. This type of pubis is comparatively more gracile than that of *L. madagascariensis*, which more resembles that of *Patagosaurus*.

HIND LIMB

Femur

The femur (fig. 75) is complete. Its shaft is subcircular in cross-section, with the greater part of the fourth trochanter in the proximal part. The distal condyles are particularly prominent towards the posterior face and have the smallest proportions near the internal face.

The internal projection of the femoral head is moderate, less than in *Patagosaurus* or *Lapparentosaurus*.

Tibia

The left tibia is complete (fig. 76). It is relatively large and robust in the proximal region, with a modest cnemial crest and a notable fibular condyle. At its distal end, the posteroventral process is less marked. In general, it seems more gracile than that of *Patagosaurus*. The ratio of its length to that of the femur is 1 to 1.65.

COMPARISONS

V. chubutensis is clearly characterized by the relatively flat structure of the neural spines of its posterior dorsal vertebrae, lacking the system of four divergent laminae characteristic of the other cetiosaurids, *Cetiosaurus*, *Barapasaurus* or *Patagosaurus*.

This plesiomorphy totally separates *Volkheimeria* from all the cetiosaurids, joining it to *Lapparentosaurus madagascariensis*.

In the object of making the comparison with this species precise, I must underline that recently (Bonaparte, in press), after having analyzed the systematic stature of "*Bothriospondylus* sp.", I have proposed the genus *Lapparentosaurus* and the species *L. madagascariensis* for the material described by Ogier (1975) found in the Middle Jurassic of Madagascar. The comparable organization of the neural spines of the posterior dorsals of *Volkheimeria* and *Lapparentosaurus* permit recognizing two groups within the family Cetiosauridae. One includes the species with relatively flat neural spines in the transverse direction (*Volkheimeria*, *Lapparentosaurus*), and the other unites forms with a derived arrangement of the neural spine formed by four divergent laminae (*Cetiosaurus*, *Barapasaurus* and *Patagosaurus*). Nevertheless, the similarities of the neural spines of the species from Madagascar and that from Patagonia do not appear sufficient to establish a generic identity when the pubes and ischia are so different. The ensemble justifies to our eyes the distinction of two genera.

CONCLUSIONS

The comparisons of *Patagosaurus fariasi* and *Volkheimeria chubutensis* with the pre-end-Jurassic sauropods (Morrison and Tendaguru faunas) permits extricating three conclusions which contribute to the interpretation of the phylogenetic position of the Patagonian species and their systematic relationships within the group of sauropods.

1) *Vulcanodon karibaensis* Raath (1972) represents the most primitive stage of sauropods. Associated with typical derived characters of sauropods such as the morphology of the pubis and ischium, the morphology and proportions of the metacarpals and astragalus, one finds primitive characters of the sacral vertebrae and proximal caudals which correspond very well with the model prosauropods *Plateosaurus* (Huene, 1920) or *Riojasaurus* (Bonaparte, 1971). It is considered that the above-cited characters of *Vulcanodon* reveal a more primitive organization than that known in sauropods, notably relative to *Patagosaurus* and other similar genera.

2) A second stage of organization is recognized among the primitive sauropods with *Lapparentosaurus madagascariensis* (Bonaparte, in press) and *Volkheimeria chubutensis* (Bonaparte, 1979). It is characterized by the relatively low neural arches of the posterior dorsal, sacral, and anterior caudal vertebrae, by the short distance separating

the zygapophyses at the base of the neural arch, and by the more or less rectangular cross-section of the posterior dorsal and sacral neural spines without development of lateral laminae. It is more sauropod-like than the prosauropods, that is to say the girdles and limbs are clearly of sauropod type and that the vertebral anatomy (in our opinion, having an entirely diagnostic value in sauropods) indicates an intermediate stage between the Plateosauridae-Melanorosauridae prosauropods and cetiosaurids such as *Barapasaurus*, *Cetiosaurus* and *Patagosaurus*.

3) The vertebral structure of *Barapasaurus*, *Cetiosaurus* and *Patagosaurus* is in a still more specialized state than those of primitive sauropods such as *Lapparentosaurus* and *Volkheimeria*. The posterior dorsal and sacral vertebrae of the former are tall, indeed very tall. A great distance separates the zygapophyses and the base of the neural arch of the posterior dorsals. On the anterior face, near the neural canal, they bear a vast depression limited laterally by the anterior edges of the parapophyses. On the wide lateral faces, the neural cavity opens by a modest aperture beneath the transverse process. The four principal laminae forming the neural spine (fig. 42) rejoin the slightly voluminous centrum; they delimit the anterior and posterior lateral cavities, which disappear from the dorsal region when the spine becomes massive.

The differences between the specialized states and those of primitive sauropods are clearly observed in the organization of the vertebrae, since the derived characters fundamentally characteristic of the girdles and the appendicular extremities of sauropods were developed to a very advanced state from their beginnings, perhaps in response to gigantism which, at the end of the Triassic, was manifest widely in different genera of prosauropods, notably in the South African and South American Melanorosauridae. In figure 65, the phylogenetic relationships of Eosauropoda, Prosauropoda and Neosauropoda are represented.

On the one hand, according to the data currently available on pre-Upper Jurassic sauropods, it is possible that sauropods, especially the eosauropods, originated in the southern hemisphere of Pangaea. The numerous remains of melanorosaurids noted in Africa (Haughton, 1924) and South America (Bonaparte, 1971) in the same way as the presence of *Vulcanodon* in the Liassic(?) beds of Zimbabwe, are many elements in favor of the appearance of eosauropods in the southern hemisphere. On the other hand, the census of Liassic sauropods from India (Jain *et al.*, 1977), Patagonia (Cabrera, 1947; Piatnitzky, 1936) and Africa (Raath, 1972), and from the Middle Jurassic of Patagonia, North Africa (Taquet, pers. comm.) and Australia (Longman, 1926) show a proliferation of the group from its beginnings on the southern continents.

From the Toarcian or before, eosauropods are known from a Pangaeian distribution, as evidenced by the presence of *Ohmdenosaurus* in the Toarcian of Holzmaden (Wild, 1978), *Cetiosaurus* from the Middle Jurassic of England (Phillips, 1871) and the contemporary Chinese genera *Datousaurus* and *Shunosaurus* (Dong and Tang, 1984; Zhang et al., 1984).

The remarkable geographic distribution of eosauropods agrees perfectly with the paleogeographic data from the greater part of the Jurassic (Smith *et al.*, 1973; Hallam 1983), an epoch in the course of which the connections between the different continental masses were firm and wide. But the beginning of the opening of the North Atlantic permitted only occasional exchanges of terrestrial faunas between North American and Europe until about the Middle Jurassic.

FIGURE CAPTIONS

Fig. 29. - Left premaxilla of adult *P. fariasi* in internal view (at left) and lateral view (at right). *ps*, symphysial plane; *de*, tooth in eruption.

Fig. 30. - Left maxilla of juvenile *P. fariasi* in external view. *apo*, preorbital opening; *de*, tooth in eruption; *pn*, nasal process.

Fig. 31. - Left maxilla of juvenile *P. fariasi* in internal view. *fd*, dentary foramina; *pam*, anteromedial process.

Fig. 32. - Right maxilla of juvenile *P. fariasi* in internal view. Abbreviations as in other figures.

Fig. 33. - Anterior fragment of left dentary of juvenile *P. fariasi* in lateral and internal views. *ps*, symphysial plane.

Fig. 34. - Internal view of three teeth of *P. fariasi*.

Fig. 35. - Axis of *P. fariasi* in lateral view. *dp*, diapophysis; *en*, neural spine; *ep*, epiapophysis; *hy*, hyposphene; *pod*, odontoid process; *pp*, parapophysis; *pz*, postzygapophysis.

Fig. 36. - Anterior cervical vertebra of *P. fariasi* in lateral view. Abbreviations as in figure 35; *cn*, neural canal; *ldprz*, diapophyseal-prezygapophyseal lamina; *liprz*, infraprezygapophyseal lamina; *lipz*, infrapostzygapophyseal lamina; *lspz*, supraposzygapophyseal lamina; *lsprz*, supraprezygapophyseal lamina; *prz*, prezygapophysis.

Fig. 37. - Posterior cervical vertebra of *P. fariasi* in lateral view. Abbreviations as in other figures.

Fig. 38. - Anterior dorsal vertebra (probably 1st dorsal) of *P. fariasi* in lateral view. Abbreviations as in other figures.

Fig. 39. - Middle anterior dorsal vertebra of *P. fariasi* in lateral and anterior views. Abbreviations as in other figures; *hyp*, hypantrum; *lsdp*, supradiapophyseal lamina; *rsn*, supraneural border.

Fig. 40. - Schematic transverse section of the neural arch of *P. fariasi*, immediately above the neural canal, showing the two vast cavities separated by a thin septum. These cavities have a lateral opening (*an*) visible in figures 41 and 42.

Fig. 41. - Middle posterior dorsal vertebra of *P. fariasi* in lateral and anterior views. Abbreviations as in other figures; *al*, lateral opening; *lpp-dp*, parapophyseal-diapophyseal lamina.

Fig. 42. - Posterior dorsal vertebra of *P. fariasi* in lateral and anterior views. Abbreviations as in other figures; *clen*, lateral cavity of the neural spine.

Fig. 43. - Sacrum of *P. fariasi* in lateral view. Abbreviations as in other figures; *cs*, sacral rib.

Fig. 44. - Ventral view of the sacrum.

Fig. 45. - Three caudal vertebrae of *P. fariasi* in lateral view. a, posterior caudal; b, mid-caudal; c, distal caudal.

Fig. 46. - Cervical ribs of *P. fariasi*. A and B, proximal region of the anterior cervical in dorsal and anterior views. C, lateral view of a middle cervical. *c*, capitulum; *pa*, anterior projection; *t*, tuberculum.

Fig. 47. - Proximal region of different dorsal ribs of *P. fariasi*.

Fig. 48. - Haemal arches of *P. fariasi* in posterior and lateral views.

Fig. 49. - Left scapula of *P. fariasi* in lateral anterior view. *pa*, acromial process; *cg*, glenoid cavity.

Fig. 50. - Scapula and coracoid of juvenile *P. fariasi* in lateral and internal views. Abbreviations as in figure 49; *fc*, coracoid foramen; *ppc*, posterior coracoid process.

Fig. 51. - Coracoid of *P. fariasi* in lateral anterior view. Abbreviations as in other figures; *csc*, contact surface with the scapula; *rsg*, supraglenoid border.

Fig. 52. - Lateral view of right ilium of *P. fariasi*. *pan*, anterior projection; *pis*, ischial peduncle; *ppo*, posterior projection; *ppu*, pubic peduncle.

Fig. 53. - Pubis of *P. fariasi* in lateral and anterior views. *a*, acetabular region; *ai*, contact zone with the ilium; *ci*, contact zone with the ischium; *pap*, anterodistal projection of the pubis; *pa*, anterior projection; *ppp*, posterodistal projection of the pubis; *pl*, proximolateral projection; *plp*, laterodistal projection.

Fig. 54. - Reconstructed anterior view of the two pubes of *P. fariasi* showing their considerable proximolateral projection.

Fig. 55. - Pubis of a young *P. fariasi* in anterior, internal and posterior views.

Fig. 56. - Right ischium of *P. fariasi* in lateral anterior view. *a*, acetabulum; *pil*, contact zone for the iliac peduncle; *pup*, contact zone for the pubis; *ed*, distal expansion.

Fig. 57. - Reconstruction of the pelvis of *P. fariasi*, holotype.

Fig. 58. - Pelvis of juvenile *P. fariasi* in lateral view.

Fig. 59. - Right humerus of *P. fariasi* in dorsal (posterior) and ventral (anterior) views.

Fig. 60. - Right radius and ulna of juvenile *P. fariasi*. Anterior (A), posterior (B), internal (C) and posterior (D) views.

Fig. 61. - Restored right femur of *P. fariasi*, holotype, in internal view. *ti*, 4th trochanter.

Fig. 62. - Right femur of juvenile *P. fariasi* in anterior (A), internal (B) and posterior (C) views. *ci*, internal tibial condyles; *ce*, external tibial condyles; *cf*, fibular condyle; *ti*, fourth trochanter; *tm*, greater trochanter.

Fig. 63. - Right tibia of juvenile *P. fariasi* in anterior (A), internal (B) and lateral (C) views. *a*, articular surface of the astragalus; *cf*, fibular condyle; *cn*, cnemial crest.

Fig. 64. - Skeletal reconstruction of *P. fariasi*.

Fig. 65. - Possible phylogenetic relationships of cetiosaurids.

Fig. 66. - Lateral and anterior views of the neural arch of a posterior dorsal vertebra of *Volkheimeria chubutensis*. Abbreviations as in figures 35 and 36; *lipd*, infradiapophyseal lamina; *lpp-dp*, parapophyseal-diapophyseal lamina; *lpr-dp*, prezygapophyseal-diapophyseal lamina.

Fig. 67. - Lateral and anterior views of the neural arch of another posterior dorsal vertebra of *V. chubutensis*. Abbreviations as in figure 66.

Fig. 68. - Left lateral view of a middle or posterior dorsal centrum of *V. chubutensis*.

Fig. 69. - Lateral and anterior views of the neural arch of posterior sacral vertebra of *V. chubutensis*. *pz*, postzygapophysis.

Fig. 70. - Posterior view of a sacral vertebral body and a sacral rib of *V. chubutensis*. Abbrev.: *cn*, neural canal; *cs*, sacral rib.

Fig. 71. - Lateral and anterior views of the neural arch of caudal vertebra of *V. chubutensis*. *prz*, prezygapophysis; *pz*, postzygapophysis.

Fig. 72. - Left ilium of *V. chubutensis*. Restored parts are in dashes; *pal*, anterolateral projection; *pp*, pubic peduncle; *pi*, ischial peduncle.

Fig. 73. - Lateral view of the right ischium (A) and left pubis of *V. chubutensis*. *fo*, obturator foramen; *plp*, lateral process of the pubis; *pp*, pubic peduncle; *lv*, ventral lamina.

Fig. 74. - Reconstruction of the pelvis of *V. chubutensis*.

Fig. 75. - Left femur of *V. chubutensis* in posterior view. *cf*, fibular condyle; *ct*, tibial condyle; *ti*, broken 4th trochanter.

Fig. 76. - Left tibia of *V. chubutensis* in lateral view. *fa*, facets for the astragalus; *cn*, cnemial crest.