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

by

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**Abstract.** - The stratigraphy and the dinosaurs of the Middle Jurassic (Callovian of Cerro C6ndor) of west-central Chubut province (Patagonia, Argentina) are briefly described.

*Piatnitzkysaurus floresi* Bonaparte (1979) is an allosaurid carnosaur known from a large part of the skeleton. The basicranium of this species is different from that of *Allosaurus fragilis*, *Ceratosaurus nasicornis*, *Acrocanthosaurus atokensis*, *Piveteausaurus divesensis* and *Dilophosaurus wetherilli* and shows some similarities to that of *Eustreptospondylus oxoniensis*. The postcranial skeleton has similarities to that of *Allosaurus fragilis*, although it has many plesiomorphic characters relative to the North American species: the pubis has a completely closed obturator foramen and a less developed distal process; the femur is directed anteromedially at its head and not medially as in *A. fragilis*; the tibia is more gracile and the cnemial crest less developed in *Piatnitzkysaurus floresi*. Many elements of the postcranial skeleton are hollowed by pneumatic cavities.

*Patagosaurus fariasi* Bonaparte (1979) is a cetiosaurid sauropod represented by several incomplete specimens, providing considerable information about the postcranial skeleton.

In the discussion and comparisons, it is reminiscent of a group of "primitive" pre-Upper Jurassic sauropods: *Barapasaurus*, *Vulcanodon*, *Cetiosaurus*, *Lapparentosaurus*, *Rhoetosaurus*, *Amygdalodon*, *Volkheimeria*, *Patagosaurus*, with more primitive dorsal vertebrate than the Upper Jurassic sauropods *Diplodocus*, *Camarasaurus*, *Haplocanthosaurus*, *Brachiosaurus*, *Dicraeosaurus*, etc.

*Volkheimeria chubutensis*, another sauropod from Cerro C6ndor, is also represented by an incomplete skeleton. It differs from *Patagosaurus fariasi* in the anatomy of the posterior dorsal and sacral vertebrae, which have lower neural arches and flatter neural spines, are rectangular in section, and lack a bladelike expansion. The vertebral anatomy of *V. chubutensis* is more plesiomorphic than that of *P. fariasi* and more comparable to that of *Lapparentosaurus* of Madagascar. The axial and appendicular skeletons show some differences compared to *Patagosaurus fariasi*, which are difficult to understand from an evolutionary point of view.

From the vertebral anatomy of the sauropods described and that of the other cetiosaurids, three levels of organization can be distinguished among the pre-Upper Jurassic sauropods: a) *Vulcanodon* is more primitive, with prosauropod-type caudal and sacral (in part) vertebrae and a sauropod-type appendicular skeleton; b) *Lapparentosaurus* and *Volkheimeria*, with relatively low neural arches, and posterior dorsal and sacral neural spines that are rectangular in section and lack bladelike expansions; c) *Barapasaurus*, *Cetiosaurus* and *Patagosaurus*, with more derived neural arch characters, such as greater height, an axial neural cavity below the neural canal, and high neural spines that are X-shaped in transverse section through the development of bony blades.

The affinities of the known carnosaur and sauropods of the Lower and Middle Jurassic from India, Africa, Australia, Europe, North and South America reveal a global distribution without endemism, which is interpreted as the result of the dominant paleogeographic situation at that time, which allowed migrations of tetrapods between the different continents.

The family Cetiosauridae, in addition to its large geographic and chronologic distribution, shows that its members possessed distinct levels of vertebral organization, attesting to the complex character of this family. The possibility that this character was ancestral for the Upper Jurassic sauropods is discussed.

## INTRODUCTION

The discovery and excavation of two important Middle Jurassic (Callovian) localities in Patagonia has brought to light the very complete remains of carnosaur and sauropod dinosaurs and permitted the development of significant studies on the vast theme of Jurassic dinosaurs, which at present are reserved nearly exclusively for the paleontology of the Northern Hemisphere.

Fortunately, the age of the materials collected in Chubut province corresponds to a very poorly known period in the history of carnosaur and sauropods, which brings a very particular significance to this material.

Dr. Angel Cabrera (1947) discovered the first remains of Jurassic sauropods in Argentina, found in the same west-central region of Chubut where we worked, although he worked in more ancient beds, probably Liassic. The studies that Cabrera made on this material, on which he founded the species *Amygdalodon patagonicus*, led us to begin the exploration of the region. After a fruitless visit to the site of *Amygdalodon* in 1976, our search was crowned with success the following year (1977) thanks to information published by Tasch and Volkheimer and their associates.

The present study follows a short note (Bonaparte, 1978) in which I made known the new genera *Piatnitzkysaurus*, *Patagosaurus* and *Volkheimeria*. The quantity of material recovered is so large that it exceeds my current abilities to study them integrally, and as a result I have chosen to make known only the most prominent aspects of the group. The work realized here is neither a short note nor a complete study. In the future, it remains to study in detail all material, in particular where the young appear, which could bring forth information on the ontogenetic development of sauropods.

## FIELD WORK

In the summer of 1977, a group of paleontologists from the Fondacion Lillo, CONICET and the Universidad Nacional de Tucumán visited the Cerro Cóndor region to look for vertebrate fossils in the Cañadón Asfalto Formation, under the project title "Jurassic and Cretaceous continental vertebrates of South America," funded by the aforementioned organizations and the National Geographic Society.

The explorations allowed the discovery of an important dinosaur locality containing well-preserved carnosaur and sauropods, partly discovered in 1977 and situated on the face of Cerro Cóndor. In 1978, based on information from villager Ricardo Farias, we worked on another

locality, 5 km north of Cerro Cóndor, which we named Cerro Cóndor North, and on which we concentrated our efforts during the summers of 1978, 1979, 1980 and, in part, 1982.

The end of the 1982 season and that of 1983 were dedicated to the goal of exploring the locality of Cerro Cóndor situated to the west of the Farias store. At the end of 1979, expeditions were organized under the Museo Argentino de Ciencias Naturales in Buenos Aires with the National Geographic Society and CONICET. Many people participated in diverse field activities, often accomplishing difficult tasks.

Participants were: technicians M. Vince, J. C. and J. Leal, driver T. H. Fasola, geologist J. H. Powell, and botanists S. Halloy and O. Coria from the Fundación Lillo and the Universidad Nacional de Tucumán; O. A. Gutierrez and technician J. C. Lopez from the Museo Argentino de Ciencias Naturales in Buenos Aires. Temporary personnel were also invited to accompany me: students F. Novas, N. and M. Rougier, A. Antucci, A. Tello, A. Bonaparte, R. Semerano, R. Gutierrez, and also my wife Reyna Carrasco and my son Juan José. I express here my gratitude to all of them for their helpful collaboration.

## THE LOCALITIES OF THE CERRO CÓNDOR REGION

We worked on two fossil localities that were very rich in dinosaurs, both from the Cañadón Asfaltón Formation.

One of the two, although noted long ago by Feruglio (1949), had never been excavated: “In the banks on the right of the river, 15 km to the west of the Farias farm... rocky tuff beds with flint containing male and female dinosaurs.”

We worked in this region in 1977, 1982 and 1983, recovering 2 *Piatnitzkysaurus floresi*, 5 incomplete specimens of different sizes of *Patagosaurus fariasi* and 1 very incomplete skeleton of *Volkheimeria chubutensis*. This locality (fig. 1, no. 5) covers a certain surface area; it is very well exposed, without sedimentary cover, in a bed of arenaceous tuff inclined 15°N and corresponding to deposits of medium-energy water flow.

Within another exposed surface, some completely disarticulated specimens were found, indicating weak dispersal, and two sauropods, articulated but incomplete due to recent erosion.

The stratigraphic position of this locality within the Cañadón Asfaltón Formation is less clear because of the strong folding and faulting present in the outcrops in this region. Nonetheless, it is situated in the lower third of the Cerro Cóndor section.

The other locality, situated 5 km to the north of Cerro Cóndor and called Cerro Cóndor North (fig. 1, no. 6), produced 4 incomplete skeletons of *Patagosaurus fariasi* (1 juvenile and 3 adults of different sizes which are the holotype PVL 4170). The 4 specimens were disarticulated and dispersed over an area 15 m long by 5 m wide. The approximate arrangement of the principal

bony elements is represented in figure 2. The fossiliferous bed is a finely layered calcareous tuff, and is part of a sedimentary package formed by very fine deposits, beds containing carbonized plant remains, and fine sands; the setting corresponds to that of a very wet floodplain.

This site was found by Ricardo Farias, who allowed us to access it.

Regarding the stratigraphic position of this locality within the Cañadón Asfaltón Formation, according to our observations it is located in the lower third of the section outcropping in this area, perhaps a little lower than the aforementioned locality.

## GEOLOGY OF THE CERRO CÓNDOR REGION

The region around Cerro Cóndor is characterized by the presence of Mesozoic continental geologic groups.

a) The Lonco Tapial Group, or Sierra de Olte Complex, containing principally Middle Jurassic age fossils, is formed of vulcanites, was very affected by Araucana-phase tectonism (Stipanovic *et al.*, 1968), and has a depth that varies between 180 and 400 m.

b) The Chubut Group is represented principally by the subhorizontal tuffs, sands, and clear-colored conglomerates of the Los Adobes Formation (Stipanovic *et al.*, 1968), equivalent to the Gorro Frigio Formation (Chebli *et al.*, 1976). The date is essentially Lower Cretaceous, (Albiano Musacchio, 1972); it lies unconformably on the preceding Middle Jurassic deposits.

Geographically, the Cretaceous deposits surround the Middle Jurassic outcrops and are very expanded, dominating the landscape that extends to the NE, E and SE in the Cerro Cóndor region.

The Jurassic outcrops of Cerro Cóndor have been studied in particular by Piatnitzky (1936), Feruglio (1949), Flores (1948), Stipanovic *et al.* (1968), Tasch and Volkheimer (1970), and Lesta *et al.* (1980). However they did not supply a detailed, synthesized geologic study providing reliable data on the regional correlations of the units now presented. There also exist some very different opinions from those of these authors, such as those of Stipanovic *et al.* and Volkheimer who accept that these units correspond to the Sierra de Olte Complex of Feruglio (1938), rather than Lesta *et al.* (1980: 1350) who feel that one of them, the Cañadón Asfalto Formation, does not correspond to the Lonco Tapial Group (Rubbiani 1971) present in the region, since it lies unconformably on this bed.

For my part, I think that the position of Feruglio, Stipanovic *et al.* and Volkheimer is reasonable, considering that the Middle Jurassic outcrops of the middle Rio Chubut, otherwise known as the Pampa de Agnia and Cañadón Asfalto Formations, should be combined in the same geologic unit, which in this case should be the Sierra de Olte Group, or the more commonly used term Lonco Tapial Group, if that is preferred.

In the Cerro Cónдор area, the geologic landscape is composed of hills on both sides of the Rio Chubut, with many traces of vulcanites from the Pampa de Agnia Formation particularly on the left bank of the river, and abundant deposits of fine yellow sediments from the Cañadón Asfalto Formation on the right bank, all folded and covered unconformably by the deposits of the Los Adobes Formation, representing the Lower Cretaceous.

Stipanovic *et al.* (1968: 86) distinguished vulcanite beds intercalated with yellow tuffs under the name Pampa de Agnia Formation, which corresponds to the lower section of the outcrop near Cerro Cónдор, exposed mainly on the left bank of the river.

The Cañadón Asfalto Formation lies, probably unconformably, on this stratigraphic unit, characterized in this region by a succession of marine calcareous tuffs, arenaceous clay tuffs, calcareous flint nodules and a conglomerate, which are together a yellowish to grayish color with the enhancement of the marine calcareous beds (Tasch and Volkheimer, 1970), and exposed throughout the length of the right bank of the Rio Chubut. The Cañadón Asfalto Formation contains a paleoflora studied by Frenguelli (1949) and collected by Flores in the Cañadón Lahuinco, where the following species were identified:

- *Sphenopteris patagonica* Halle
- *Sphenopteris hallei* Frenguelli
- *Scleropteris* cf. *furcata* Halle
- *Pagiophyllum divaricatum* (Bumby)
- *Pagiophyllum feistmanteli* Halle
- *Athrotaxis ungeri* (Halle) Florin
- *Cladophlebis grahami* Frenguelli Seward
- *Araucarites cutchenthis* Feistmantel
- *Palissya conferta* (Oldhan) Feistmantel
- *Palissya jabalpurensis* Feistmantel
- *Equisetites aproximatus* Nathorst.

In addition to indeterminate marine forms, there were also gastropods, pelecypods, and several conchostracans of the genus *Cyzicus*, described by Tasch and Volkheimer (1970).

Therefore, as has already been noted, the stratigraphic position of the dinosaur localities of Cerro Cónдор and Cerro Cónдор North is within the lower third of the Cañadón Asfalto Formation, with Cerro Cónдор North at a slightly lower level.

Regarding the oft-cited fish of the Cañadón Asfalto Formation, it is probable that they are found in subjacent beds, entirely distinct from this formation but beneath the Los Adobes Formation. According to our interpretation, the fish beds of the Colan Conhué stream (fig. 1, no. 7), which are comparable to those of Almada, correspond to a distinct stratigraphic unit of the Cañadón Asfalto Formation, either affected by the same Araucana-phase orogeny or older than the Los Adobes Formation. The lithologic characters of the bed containing fish and body fossils are complex and very different from those of the Cañadón Asfalto Formation. In this work, we

designate it by the informal name “indeterminate formation” (fig. 1, no. 3) and wait for it to be specifically characterized.

Order *SAURISCHIA* Seeley 1888

Suborder *THEROPODA* Marsh 1881

Infraorder *CARNOSAURIA* Huene 1920

Family *Allosauridae* Marsh 1878

*Piatnitzkysaurus floresi* Bonaparte 1979

*Holotype*. - PVL 4073, representing the greater part of a medium-sized adult and comprising: the occipital region, braincase, left frontal and maxilla, anterior part of two mandibles; 13 presacral vertebrae including the axis, anterior and posterior cervicals, and dorsals, the majority incomplete; incomplete sacrum with 4 vertebrae, two anterior caudals; proximal fragments of dorsal ribs. Two scapulae and coracoids, right humerus, left ulna; fragments of the ilia, the majority of the pubes and ischia, two femora, tibiae and fibulae.

*Hypodigm*. - MACN-CH 895, a specimen represented by an incomplete right maxilla, right humerus, proximal part of the two pubes; an ischium, left tibia; left metatarsals II, III, IV; incomplete sacrum with 4 vertebrae; two posterior dorsal vertebrae and two dorsal vertebral bodies.

*Geographic and stratigraphic position*. - About 1 km west of the Farias store, Cerro Cónдор. Lower third of the Cañadón Asfalto Formation, Callovian.

*Diagnosis*. - Allosaurid with deep depressions between the basioccipital condyle and the opisthotic process; braincase similar to that of *Eustreptospondylus* but with more pronounced lateral basisphenoid depressions and alar process of the laterosphenoid. Most postcranial characters comparable to those of *Allosaurus*, but with a shorter scapula and a coracoid not expanded but subcircular. Pubis with an obturator foramen totally enclosed by an bony lamina and forming a modest neck; ischium less reduced ventrally than that of *Allosaurus*. Ulna, tibia and femur more slender than in *Allosaurus*, but proportionally a little more massive than in *Dilophosaurus*.

## DESCRIPTION

### SKULL

A large part of the occipital region, braincase, left frontal and an incomplete left maxilla are preserved in the holotype skull.

The mandible is represented by the anterior end of the left mandibular ramus.

### ***Basicranium***

The basicranial region (fig. 3 and 4) is formed by the two paroccipital processes (broken at their ends), the occipital condyle, most of the basioccipital process, the 2 basipterygoid processes, the 2 prootics, the laterosphenoids (incomplete anteriorly), the 2 parietals and the nearly complete supraoccipital.

In posterior view, the occipital condyle is low and wide, with a neck that is well-marked on the ventral and lateral faces but does not extend beyond the dorsal edge of the exoccipitals. These border the majority of the foramen magnum and are firmly fused to the basioccipital and the paroccipital processes. The preserved part of these processes shows that they are relatively thin, bladelike, have shallower depressions on their posterior face, and are directed towards the exterior, backwards, and ventrally.

Between the ventral projection of the paroccipital process and the occipital condyle there is a large, deep depression that is well defined and noticeably stronger than in the other carnosaurs *Allosaurus*, *Ceratosaurus* and *Piveteausaurus*, but very similar to that of an undescribed carnosaur found in the same beds as *Dilophosaurus*, said to be Lower Jurassic and kept in the collections of the Museum of Paleontology at Berkeley (U.S.A.).

Directly beneath the condyle there is an axial depression that connects with the large medioventral fossa of the basisphenoid or sphenoid sinus. The basipterygoid processes are proportionally small and very close to the sagittal plane, in contrast to *Allosaurus* where they are more developed and more expanded.

Laterally, the posteroventral region of the laterosphenoid has a robust alar process, or basisphenoid wing according to Taquet and Welles (1977), that projects near the base and the rear, robust in appearance, and a little expanded at the edges of the cranial wall formed by the basisphenoid. This process must serve for the insertion of the temporal muscles.

Beneath the laterosphenoid process, the basisphenoid is strongly constricted; a kind of sagittal wing spreads out ventrally in the direction of the basipterygoid processes.

The fenestra ovale occupies a large space between the posterior edge of the prootic and the opisthotic.

In the anterior region of the prootic, one finds a large indentation that joins the foramen for the trigeminal nerve. On the ventral and posterior border of the prootic, near its suture with the laterosphenoid and the dorsal expansion of the basisphenoid, there is a foramen that could be that for nerve VII. The dorsal basisphenoid projections that form the lateral and inferior faces of



the basicranium are more or less ossified, with two openings on the right side that are totally closed off from the left side.

*Comparison.* - The basicranium of *Piatnitzkysaurus floresi* is characterized by marked sinuses or depressions between the condyle and the ventral projections of the opisthotics, the basisphenoid constriction above the basipterygoid processes, and the weak separation between these processes and the robust laterosphenoid processes.

Comparisons with *Allosaurus*, *Ceratosaurus*, *Acrocanthosaurus* (at Salt Lake City), an undescribed form from the Kayenta Formation, and *Dilophosaurus* (at Berkeley) suggest the following:

a) The basicranium of *Piatnitzkysaurus* differs noticeably from that of *Allosaurus* in the region near the occipital condyle, the proportions and the position of the basipterygoid processes, the morphology of the basisphenoid, and the orientation of the basioccipital processes.

b) There are also profound differences with *Ceratosaurus* posteriorly, since this genus does not possess the remarkable cavities between the opisthotic and the basioccipital condyle. Further, *Ceratosaurus* has a thick sagittal septum beneath the condyle, while *Piatnitzkysaurus* has a strong depression.

c) *Acrocanthosaurus* from the Lower Cretaceous of North America shows remarkable similarities with the general morphology of the basicranium of *Piatnitzkysaurus*, notably in the occipital region and the constriction of the basisphenoid in the dorsal region and in front of the basipterygoid processes. Nonetheless, the separation between these processes is greater in *Acrocanthosaurus*, and the sinus proportionally more developed.

d) *Piveteausaurus divesensis* (Taquet and Welles, 1977) of the upper Callovian of France is distinguished by an occipital region devoid of the strong depressions observed in *Piatnitzkysaurus*. In ventral view one notes that the basioccipital canals are proportionally larger and the basisphenoid body more expanded anteroposteriorly in the Patagonian genus. Laterally, the position of the alar process of the laterosphenoid relative to the different foramina (except the fenestra ovale) are equally different.

e) An undescribed form from the Lower Jurassic Kayenta Formation (Welles, pers. comm.) in the collection of the Museum of Paleontology in Berkeley offers notable similarities with the basicranium of *Piatnitzkysaurus*, except the depressions between the occipital condyle and the opisthotics, which are less pronounced in the Argentine genus.

f) Comparison with the remains of *Eustreptospondylus* of the upper Callovian of England, kindly communicated by Dr. Welles, also suggest important similarities in the lateral and posterior aspects; nevertheless in the latter, the depressions between the occipital condyle and the opisthotics are more marked than in the Argentine genus.

Laterally, after the same remains, *Eustreptospondylus* has depressions in the basisphenoid, but they are less pronounced than in *Piatnitzkysaurus*. The well-developed and strong alar process of the laterosphenoid in the Argentine genus is more reduced in *Eustreptospondylus*.

Finally, these comparisons suggest a stronger affinity with older forms than with those of the Upper Jurassic, and particularly with *Eustreptospondylus*.

### ***Frontal***

A large part of the left frontal is preserved (fig. 5), showing the posterior part that articulates with the parietal.

Ventrally and sagittally there are strong longitudinal indentations for the passage of the olfactory nerve. The nasal is widened to form a vast depression that must have been occupied by part of the olfactory lobe.

The region corresponding to the orbit shows an important concavity on the ventral face of the frontal.

### ***Maxilla***

The 2 known maxillae of *Piatnitzkysaurus* are those of the holotype (fig. 6).

The latter has a gently sinuous alveolar border with 18 alveoli. The interdental plates are not fused between them: these same show a clear separation up to the foramen for the tooth germ.

Externally, in the anterior region of the orbital cavity, there is a supplementary opening as in *Allosaurus*, but closed off internally. In this case the basal region of the nasal process, although completely hollowed, is closed medially, while in *Allosaurus* it is pierced by 2 large internal openings.

It is difficult to suppose that an olfactory organ was lodged in this cavity, as suggested by Madsen (1976), because it communicates only with the exterior region.

Two smaller depressions are exposed on the rear of the nasal process.

In the anterior region, the medioanterior maxillary process is strong and covered with marked striations.

The teeth preserved are relatively fragile, and very laterally compressed.

### ***Mandible***

The mandible is represented only by the anterior part of the left dentary (fig. 7). The surface of the mandibular symphysis is small, and the absence of a defined plane of contact suggests a mobile articulation.

The external face is significantly higher than the internal, because the alveoli are partially open sagittally. A number of supplying foramina open externally; most are oriented ventrally and are arranged in 2 rows in the dorsal area of the bone, while there is a series of small foramina in the inferior area.

## VERTEBRAL COLUMN

The presacral and sacral vertebrae are well represented: 15 presacrals that are basically complete and 5 sacrals, which are the more anterior, showing signs of coossification.

### *Axis*

This well-preserved vertebra is relatively light and fragile, with a narrow vertebral centrum that is laterally compressed, in contrast to that of *Allosaurus* (Madsen, 1976) which is significantly more robust. The vertebral centrum is a little larger in *Piatnitzkysaurus*. The diapophysis is a little more prominent, and does not show a pleurocoel in contrast to *Allosaurus*. The epiphyses project far in front of the postzygapophyses (fig. 8).

Overall the axis is the same type as that of *Allosaurus* but with some significant differences.

### *Presacral vertebrae*

*4th and 5th vertebrae.* The determination of the exact location of these vertebrae in the vertebral column, as with the other presacrals, is conjectural, but the range of error is about one vertebra.

While the 4th vertebra (fig. 9) is incomplete, the 5th is nearly intact. Compared with the vertebrae of *Allosaurus*, they are proportionally larger and have lower zygapophyses. The bodies of these two vertebrae are hollowed by deep lateral depressions, and the ventral face, lacking a keel, is robust in appearance with a very apparent opisthocoel. On the fourth vertebra, there is a small orifice in front of the parapophysis that connects with the large cavities of the vertebral centrum. The 5th vertebra lacks this, but one can see that the vertebral centrum is equally hollowed by large cavities like that of the anterior vertebra.

The parapophysis is well developed, with a distinct lateral projection on the lateroinferior border of the centrum.

The diapophyses are large, thin, and present a dorsoventrally oriented edge on the internal face that forms a septum. This delimits two strong concavities at the contact of the vertebral centrum, which could have communicated with those of the neural arch (fig. 10). The prezygapophyses and epipophyses terminate in large projections; the neural spine is flat, without true relief for insertion of the intervertebral ligaments. The zygapophyses are enlarged transversely, the prezygapophyses a little less so than the others.

The *7th presacral vertebra* (fig. 11), very incomplete, shows the essential characters of its structure and the disposition of the pneumatic cavities. The vertebral centrum is low, widened, strongly opisthocoelous and significantly larger than those of the anterior vertebrae. The central dorsolateral part, that is to say medially relative to the diapophysis, is deeply depressed and connects with the other cavities of the vertebra. On its side, the typical pleurocoel is situated very close to the parapophysis, in the anterior third of the vertebral centrum. It is a little larger in size than that of the 4th vertebra and it communicates with a large cavity of the vertebral centrum (fig. 11, c1). It also differs from the preceding vertebrae in the strong depression situated in front of the postzygapophysis and bordered laterally by the diapophyseal-postzygapophyseal lamina.

This deep depression does not seem to connect with the pneumatic cavities.

The *10th presacral vertebra* (fig. 12 and 13), probably the first dorsal, possesses a significantly more voluminous vertebral centrum; the opisthocoel is less marked. The transverse processes are large and the neural spine is short. Its general morphology is comparable to that of *Allosaurus* (Madsen, 1976, 1 pl. 15) in spite of a large size difference. The opisthocoel is more apparent in the North American genus; the system of cavities has been more developed in *Piatnitzkysaurus*, the diapophyseal-postzygapophyseal lamina shows a strong indentation in *Allosaurus* that is lacking in the Argentine genus; the neural spine is proportionally more elevated in *Piatnitzkysaurus*. In posterior view, there are also differences in the presence of two small, deep depressions between the neural canal and the inferior part of the postzygapophysis, which are lacking in *Allosaurus* according the illustrations of Madsen.

The postzygapophyses are widened dorsoventrally. The transverse processes expand far laterally and are comprised of a system of bony laminae that demarcate large lacunae. The anterior and posterior lacunae connect with the system of pneumatic cavities of the neural arch and of the dorsal part of the vertebral centrum by fenestrae.

The vertebral centrum shows a very evident ventral keel in its anterior part, where it is widened and participates in the bony formation that extends between the two parapophyses. These are robust, and are situated near the ventrolateral and anterior edges of the vertebral centrum.

The pleurocoel, in exterior view, has been more developed than in the anterior vertebrae. On the right lateral face, there is a supplementary fenestra that probably communicates with the system of internal cavities but it is lacking on the opposite side.

The *11th vertebra* is incomplete; it is lacking the transverse processes and the neural arch is in two pieces. It is similar to the preceding vertebra but shorter axially, opisthocoelous, and with the parapophyses in a more dorsal position than on the 10th. It also has an important ventral keel and the openings of the pleurocoels are larger than on the 10th vertebra. The postzygapophyses are of comparable size and shape to those of the 10th but they are more expanded and the neural spine is larger. The broken neural arch allows a view of the disposition of the pneumatic cavities within the vertebra. Two of these cavities are situated at the base of the neural spine; separated by a median septum, they communicate with the exterior via a fenestra in front of the postzygapophysis, visible in lateral view. Another cavity is hollowed at the base of the posterior infradiapophyseal blade, opening by a large foramen behind its base.

The *13th presacral vertebra* (fig. 14) is nearly intact. The centrum is more laterally compressed, and shows a thin and prominent keel, a weak opisthocoel, and larger pleurocoels. The neural arch is higher, the neural spine longer, and the transverse processes oriented laterodorsally. The base of the neural arch is similarly shorter in the longitudinal direction. Laterally, the distal thirds of the anterior and posterior infradiapophyseal laminae are fused. Near the base of the neural arch, these laminae are less expanded than on the preceding vertebrae.

The vast anterior and posterior cavities of the transverse processes connect with the pneumatic cavities of the neural arch by large openings. The one in-between is situated below and laterally relative to the prezygapophysis, while the other is below and in front of the postzygapophysis. Both are visible laterally. The differences with the same vertebrae of *Allosaurus* are minimal (Madsen, 1976, pl. 17), except that the opisthocoel is clearly more developed in the latter genus. The rugose surface for the insertion of the intervertebral ligaments is also more extensive in *Allosaurus*. Finally, the zygapophyses of the Argentine genus have a greater inclination towards the sagittal plane.

The *14th presacral vertebra* is incomplete; the vertebral centrum is practically complete; it bears the base of the neural arch. A neural spine, found isolated, is referred with reservation to this vertebra.

The vertebral centrum is lacking a ventral keel. The parapophysis reaches almost to the distal edge of the centrum, and the pleurocoel, despite its moderate depth, does not penetrate to the interior of the centrum as on the thirteenth vertebra. A good part of the hyposphene is also preserved along with the neural arch fragment. It is probably from around the first dorsal

vertebra, since this element also seems to be present in the successive vertebrae. On the dorsal spine, one notes the indications of a moderate sagittal elongation. Although widened here, it is notable that the area of insertion for the intervertebral ligaments does not reach as dorsal a position as in *Allosaurus*.

The *16th vertebra* was divided dorsoventrally in the transverse plane. Nonetheless, several characters are still observable. The centrum, according to its posterior face, must be amphiplatyan. The transverse process has a slightly posterodorsal orientation. In contrast to the fourteenth vertebra, the 16th has only the posterior diapophyseal lamina, which is also the principal lateral support of the transverse process.

The neural area is as high as those of the anterior vertebrae. It is flattened transversely with a sagittal expansion. Here as well, the reliefs for the intervertebral ligaments do not reach as dorsal a level as in *Allosaurus*.

Thanks to a break, the presence of a pneumatic cavity can be detected situated dorsally relative to the neural canal (fig. 15, c1), and another laterally, both opening in front of the postzygapophysis. Posteriorly, the postzygapophyses are very close together and in a subhorizontal position. Part of the hyosphene is preserved above the neural canal.

Of the *17th vertebra* (fig. 16), there remains the vertebral centrum and the incomplete inferior part of the neural arch. The centrum is so compressed laterally that the anterior and posterior faces have very prominent lateral and ventral edges. The vertebral centrum is of an amphiplatyan type, with a very strong dorsoventral concavity.

The parapophysis is higher than the center and shows a slight lateral projection. Although the zygapophyses are not preserved, the hypantrum and hyosphene still remain.

Above the neural canal there are two cavities, separated from each other by a bony septum (fig. 16), which connect in front and behind via a pair of orifices that are identical to those of the 16th vertebra.

The *19th vertebra* is exceptionally complete and not deformed. The vertebral centrum is identical to that of the 17th vertebra but smaller. The neural spine is tall and flat, with the anterior and posterior edges showing relief for ligamentous insertions that does not extend up to the dorsal extremity. In the inferior part of the spine, the two edges are very concave, particularly the anterior which bears remarkable supraprezygapophyseal laminae. The subhorizontal zygapophyses are very close together and are accompanied by the hyosphenes and the very differentiated zygosphenes.

The parapophyses project a certain distance laterally from the dorsal edge of the vertebral centrum. A bony lamina detaches from the parapophysis and connects to the

prezygapophyseal-diapophyseal blade, defining the entrance of the pneumatic cavities located above the neural canal (fig. 17 and 18).

The transverse process, expanded ventrolaterally, has a well-developed infradiapophyseal lamina. In front of this lamina, there is a deep fossa that reaches very close to the sagittal plane. Behind the lamina and the postzygapophysis, there is a deep fossa that also connects to the aforementioned pneumatic cavities.

The *20th and 21st vertebrae*, mostly preserved, are of the same type as the 19th, with slightly larger vertebral bodies.

Of the *22nd vertebra* there remains only a fragment of the centrum and the base of the neural arch. The postzygapophyses are expanded axially, and the bodies of the zygosphenes seem more robust than in the preceding vertebrae.

The *23rd vertebra* is represented essentially by the neural arch, the vertebral centrum having been broken. The neural spine is a thin blade, less expanded than that of the 19th vertebra, while the transverse processes are shorter and more robust. There is no parapophysis, perhaps because of its dorsal migration and reduction.

The *24th vertebra* has a very developed vertebral centrum, particularly on the posterior face where there are traces of its suturing to the sacrum. The neural arch, also strong, has slightly expanded transverse processes, and parapophysis in a very dorsal position, situated at the level of the prezygapophysis.

### *Sacrum*

The sacrum of the holotype includes the first four sacral vertebrae (fused), while that of specimen MACN-CH 895 is formed by vertebrae 2 to 5. One can thus deduce that the sacrum of *Piatnitzkysaurus* was composed of 5 vertebrae. The bodies of the two anterior ones were laterally compressed, with prominent edges in the anterior and posterior regions and strong, distinct transverse processes. The other three vertebrae have less compressed bodies and are strongly coossified with the sacral ribs. The transverse processes of the 3rd and 4th sacrals have aliform expansions that insert strongly on the ilium. Those of the 5th vertebra are less developed.

The neural spine of the first sacral vertebra is relatively narrow relative to the following, wider ones. They differ from those of *Allosaurus* (Madsen, 1976) in not being fused together.

The two sacra show very advanced fusion of the vertebral bodies and neural arches. The four first vertebral bodies are fused, while the limits between the neural arches persist.

### *Caudal vertebrae*

In the holotype, two proximal caudal vertebrae are preserved, probably the second and fourth. The second is very robust, with a centrum that is procoelous anteriorly and platycoelous posteriorly. It is barely laterally compressed, and the edges of the anterior and posterior faces are thicker than on the posterior dorsal vertebrae. The transverse process is fat; directed both a little towards the rear and the top, but narrowing near the distal border.

The fourth caudal vertebra is a little smaller but is constructed on the same plan as the preceding vertebra. The postzygapophyses are preserved. They are oriented ventrolaterally, forming an angle of about 35° relative to the sagittal plane. The postzygapophyses meet ventrally to form a pseudohyposphene. Towards the rear, there is a deep indentation that partially cuts into the posterior border of the neural spine.

### **RIBS**

The ribs are represented by three proximal fragments with the articular region, two with the tuberculum and a part of the costal body, and one corresponding to a part of the proximal moiety of another rib. They are all located in the dorsal region and are characterized by their slender construction.

A weak thickening marks the location of the capitulum and tuberculum on the three fragments of the proximal region. The blade uniting the two apophyses is thin (2 to 4 mm), as is the larger part of its extension near the costal body. Proximally there is a hollowed (anterior?) concave face, and another slightly convex or flatter. Distally relative to the tuberculum, and on the supposed anterior face, a strong existing concavity is expanded on the opposite face, but less pronounced. It follows a T in section, which fades distally.

### **COMPARISON OF THE AXIAL SKELETON**

The axial skeleton is considered, both in its entirety and in the different parts and in the morphological variations between each region, to closely resemble that of *Allosaurus fragilis* (Madsen, 1976), apart from the differences of robustness or proportions that do not affect all the similarities.

In contrast, comparison with the skeleton of *Ceratosaurus nasicornis* (Marsh, 1876) shows very significant differences that are seen on all the vertebrae figured by the author, such



that the two taxa are completely distinguished from one another. The vertebrae of *Acrocanthosaurus* (Stovall and Langston, 1950) from the Lower Cretaceous of Oklahoma, are in the same situation. The cervicals have long neural spines and expanded shafts, while the caudals have elongated bodies and long spines as well.

Comparison with *Dilophosaurus* from the Lower Jurassic of Arizona, made possible by the grace and kindness of Dr. Welles (Museum of Paleontology, Berkeley), shows some interesting similarities. According to all the characters together, the vertebrae are of a similar construction and belong to the same type. But there are also significant differences. Thus the bodies of the cervical vertebrae are proportionally longer in *Dilophosaurus*, and their neural spines are shorter and less developed, than in *Piatnitzkysaurus*. The sacral vertebral centra of *Dilophosaurus* are less fused to the sacral ribs, the neural spines are more separated, and fewer vertebrae are implicated in the formation of the sacrum than in *Piatnitzkysaurus*.

### PECTORAL GIRDLE

The two scapulae of the holotype are practically complete. The right lacks the distal extremity and the left has lost a part of the acromial region.

The right coracoid has a broken posterior process. On the left, the same process is complete but a large part of the coracoid blade is missing.

In posterior view, the entire scapulocoracoid is quite curved, evoking the convexity of the thorax. Laterally (fig. 19), the scapula of *Piatnitzkysaurus* has a dorsal expansion that is moderate but more prominent than in *Allosaurus*. The anterior edge is elongated and terminates at the relatively strong acromial process. Between this process and the glenoid cavity, a well-defined depression expands that is both more distinct and dorsoventrally deeper than in *Allosaurus*. The scapular blade is thickened inferiorly.

The coracoid as seen on its face is larger, subcircular in shape, widened anteroposteriorly, strongly convex near the exterior, and bears a marked posterior process. The coracoid foramen is relatively large. It opens from the internal side, at some distance from the edge of the bone and in front of the preglenoid expansion. The glenoid cavity of the scapula is well-defined by a rolled edge on the lateral, dorsal, and internal faces. The coracoid part of the glenoid cavity is also bordered by a thickening. The glenoid cavity is clearly situated in a lateral and posteroventral plane, facilitating all the movements of the forelimb.

The scapulocoracoid unit of *Piatnitzkysaurus* is the same type as that of *Allosaurus* in spite of some minor differences. Among these, we have noted that the scapula of *Allosaurus* is proportionally longer and thinner.

Comparison with *Ceratosaurus* shows that its scapula is larger, lacks a dorsal expansion, and is very widened in the region of the coracoid and acromial depression.

Comparison with the scapulocoracoid of *Dilophosaurus* (Lower Jurassic, U.S.A.) shows a very similar morphology to that of *Piatnitzkysaurus* in the acromial, glenoid and (partially) the coracoid regions. However, an important difference appears in the scapular blade, which is short and large in *Dilophosaurus*.

It is possible that the enlargement and the slenderness of the scapular blade of the Argentine genus, still a little more developed in *Allosaurus*, is a derived character relative to the condition seen in *Dilophosaurus*.

*Dimensions.* - Maximal length of the left scapula of the holotype: 48 mm. Anteroposterior length of the coracoid of the holotype: 170 mm.

## FORELIMB

This part of the skeleton is represented by the right humerus and left ulna of the holotype and the right humerus of specimen MACN-CH 895. No element of the hand of *P. floresi* was recovered.

### *Humerus*

The humerus (fig. 20) is, on the whole, comparable to that of *Allosaurus fragilis* (Madsen, 1976, pl. 42), but proportionally more slender. The internal tuberosity is better defined and more separated from the humeral head. The radial condyle projects less externally, and the inferior end of the deltoid crest bears numerous strong traces of muscular insertions while the crest *sensu stricto* is ventrally prominent and elongated.

On the lateral face, barely visible in dorsal view (fig. 20), there is a foramen about 3 mm in diameter that connects with the internal cavity of the humerus. This pneumatic foramen is situated at the same point in *Allosaurus* (Madsen, 1976, p. 42).

The distal part has undergone a large torsion relative to the proximal plane. It differs from that of *Allosaurus* by a larger extension of the internal side and a prominent entepicondylar area, so that the widening of the external side is more modest.

On the dorsal face and the dorsal end, there is a large depression that is slightly deep and expanded on the proximal side, so that one also finds a large supracondylar depression on the ventral side that is very clear but less extended.

This humerus offers some striking similarities with that of *Allosaurus*. Regarding the differences noted above, in my opinion, they point to a less specialized state in *Piatnitzkysaurus*.

Comparison with the humerus of *Dilophosaurus* reveals a less sigmoid shape, smaller internal tuberosity, and simpler deltoid crest in the Kayenta genus. However, the torsion

between the two ends is comparable, the deltoid crest occupies the same relative position, and the distal parts of the humerus has a closely resemblance. On the whole, the humerus of *Piatnitzkysaurus* is more robust and more specialized than that of *Dilophosaurus*, but probably the two genera belong to very close lineages.

*Dimensions.* - Maximal length of the humerus of the holotype: 286 mm.

### *Ulna*

The left ulna is complete (fig. 21). The olecranon is more proximally developed and the articulation for the humerus is deeper than in *Allosaurus*. Similarly, the distal expansion is proportionally more pronounced in the Argentine genus. Laterally, the anterior border of the ulna is very curved along a continuous line, while its anterodorsal projection reaches the dorsal extremity. The posterior border is sigmoid. Posteriorly, the proximal region of the ulna is much flatter and larger, becoming more rounded on the distal side. The internal face is relatively flattened and a little concave proximally. It has two processes for ligamentous insertions, well-developed distally.

In general, the ulna of *Piatnitzkysaurus* is comparable to that of *Allosaurus*, but it also differs in the morphology of the distal region of the olecranon process and the proximal region where it articulates with the radius. By comparison, *Dilophosaurus* has a considerably more gracile ulna with less enlarged proximal and distal regions, although certain morphologic details of the distal region are comparable to those of *Piatnitzkysaurus*.

*Dimensions.* - Maximal length of the ulna of the holotype: 218 mm.

## **PELVIC GIRDLE**

This part of the skeleton is well represented. The major part of the left ilium, a fragment of the posterior region of the right iliac blade, most of the two pubes, and the left ischium are preserved in the holotype. The distal part of the left ischium, the proximal parts of the right, and the right pubis were recovered from specimen MACN-CH 895. These diverse fragments provide enough complementary information on those proximal regions of the ischium and pubis that are missing in the holotype.

### *Ilium*

The ilium is very similar to that of *Allosaurus fragilis* (Madsen, 1976, pl. 46) in spite of some differences, among which is the presence of a deep depression on the lateral face of the iliac blade that divides the dorsoventral edge (fig. 22). This character is not observed in *Allosaurus* but, in contrast, it is present in *Stokesosaurus* (Madsen, 1974) and in *Iliosaurus* (Huene, 1932; Galton and Jensen, 1979), although it is clearly less developed in these two genera.

*Allosaurus* and *Piatnitzkysaurus* are equally different in the morphology and orientation of the much deeper pubic peduncle and the more posterior projection of the ischial peduncle in the Argentine genus. This placement probably reflects a different position of the acetabulum in the two genera. Finally, the supraacetabular crest is clearly more marked laterally and ventrally in *Piatnitzkysaurus*, as in *Dilophosaurus*, so much so that the roof of the acetabulum cannot be observed in lateral view because of the canopy that forms this crest.

The ilium of the Argentine genus has two pneumatic foramina, one in the dorsal part of the pubic peduncle below the iliac blade, and the other in the inferior part above the acetabulum. Curiously, the internal structure of the iliac blade shows well-developed pneumatic cavities and bony macrocellules, the function of which is discussed later.

In spite of these noted differences, the ilium of the Argentine genus has the greatest similarities to that of *Allosaurus*, although comparison with *Dilophosaurus* suggests that *Piatnitzkysaurus* possesses some characters intermediate between the two North American genera. On this subject, the similarities in the acetabulum, ischial peduncle, and posteromedial blade of *Piatnitzkysaurus* and *Dilophosaurus* are significant.

*Dimensions.* - Height of the ilium of the holotype between the pubic peduncle and the dorsal border: 270 mm. Anteroposterior length preserved: 430 mm.

### ***Pubis***

The pubis is very different and in general less specialized than that of *Allosaurus*. In the proximal region, *Piatnitzkysaurus* has a well-developed lamina that borders the obturator foramen ventrally. The same blade is vestigial in *Allosaurus* (Madsen, 1976).

Regarding the posterior border of the pubis, it is practically rectilinear, with a weak anterior projection in its more dorsal part, and at the dorsal end recalls the more primitive condition of *Torvosaurus* (Galton and Jensen, 1979) rather than the more evolved state of *Allosaurus*.

Regarding the posterior part, it has a more modest posterior expansion and a very short anterior projection, very slightly specialized characters compared to *Allosaurus*, in which the two elements are very developed, but more specialized than in *Dilophosaurus* of the Lower Jurassic, where the “foot” of the pubis is barely defined.

Further down the length of the bone, on the lateral face, there is a bony process that could correspond to the insertion of the *ambiens* muscle (fig. 23).

It appears from the evident facts that the pubis of *Piatnitzkysaurus* is at an intermediate evolutionary stage between that of *Dilophosaurus* (primitive) and the specialized state of *Allosaurus*. Perhaps this element of the postcranial skeleton is one of the more noticeable changes surveyed in this lineage, since it is easily to perceive differences, which are much less marked in the case of the ilium.

*Dimensions.* - Length of the right pubis of the holotype: 450 mm.

### ***Ischium***

(fig. 24)

The reconstruction of the ischium is entirely reliable because it is based on adequate material. The proximal part is preserved in MACN-CH 895. The medial surface is flat from the ventral blade almost up to its distal extremity, and hence there is an expanded ischial symphysis. The ventral blade has a long anteroposterior expansion that becomes slender distally. On the lateral face of the body, there is a process that could have served for the insertion of the *ischio-femoralis* muscle. Proximally, the ventral blade continues almost to the pubic peduncle and shows some sign of reduction, as in *Allosaurus* (Madsen, 1976, p. 48). However, the orientation of the peduncle is different: it is directed towards the front in *Allosaurus*, while more dorsally in *Piatnitzkysaurus*.

The great resemblances are very significant in the proximal ischium, particularly in the details of the ventral blade, the pubic peduncle, the form of the posteroproximal edge, etc. and suggest the existence of ties between *Piatnitzkysaurus* and *Allosaurus*, in spite of the presence of varied and important primitive characters.

*Dimensions.* - Length of the restored ischium of the holotype: 423 mm.

## **HINDLIMB**

The femur, tibiae and fibulae are preserved, basically complete, in the holotype. The left tibia and left metatarsals II, III, and IV are present in specimen MACN-CH 895.

### ***Femur***

The femur is fundamentally the same type as that of *Allosaurus*, with a nearly straight shaft that is subcircular in section for most of its length. The distal enlargement is moderate on all sides except the posterior, where the condyles are very apparent (fig. 25).

The three condyles are globular in shape, as in *Allosaurus*, and present a distinct intercondylar depression on the posterior face that extends weakly distally and posteriorly. In the proximal region, the femoral head has an expanded dorsal plane with a slightly larger greater trochanter that forms a straight angle with the long axis of the femur. The femoral head does not project completely internally as in *Allosaurus* (Madsen, 1976, pl. 50), but is directed anteromedially.

However, the hind limb has not reached the level of functional organization of *Allosaurus* and retains the “primitive” disposition of prosauropods.

The lesser trochanter is an expanded blade, situated in a more dorsal position. The morphology of the fourth trochanter is nearly identical to that of *Allosaurus*, but is in a more dorsal position.

In summary, the femur of *Piatnitzkysaurus* is morphologically very close to that of *Allosaurus*, although a little less specialized in the orientation of the femoral head and the more dorsal position of the fourth trochanter. Comparison with the femur of *Dilophosaurus* shows the robustness, larger size of the very delimited femoral head, and very slight development of the lesser trochanter of *Piatnitzkysaurus*.

*Dimension.* - Length of the femur of the holotype: 552 mm.

### ***Tibia*** (fig. 26)

The tibia is a little shorter than the femur, with a tibia:femur ratio of 1:1.12. Proportionally, the tibia of *Piatnitzkysaurus* is more spindly than that of *Allosaurus*, with a less developed cnemial crest, more dorsal alar process for the fibula, less developed internal expansion of the dorsal extremity, and slightly weaker torsion between the two ends. The proximal region is robust with the internal border of the articular facet for the femur more dorsal than lateral in position. The external part of the femoral articulation is beginning to be differentiated. It forms a globular articular condyle that is separated from the rest of the articulation by a posterior indentation. In *Allosaurus* this differentiation is more marked. The lateral region of the cnemial crest is grooved by the depressions accompanying the rugosities for the insertion of the extensor muscles. In the distal region the articular area for the astragalus (fig. 26) is large, with an anterodorsal depression that is deep laterally. The distal extremity is thin, except in the internal section, which is a little more expanded than the external; it is hollowed by a distal depression in

the posterior angle. Although this region is more developed in *Allosaurus*, it shows practically the same general morphology. In *Ceratosaurus*, the cnemial crest is well-developed and the lateral process for the fibula reaches a more dorsal position than in *Piatnitzkysaurus*. In *Dilophosaurus*, the tibia is less specialized; the cnemial crest is less important, and the articular area for the astragalus is more expanded.

*Dimensions.* - Length of the tibia of the holotype: 492 mm.

### ***Fibula***

The fibula is proportionally longer and thinner than that of *Allosaurus*. It has an important proximal expansion, in large part at the expense of the posterior edge. The anterolateral process is barely visible and is located on the proximal third of the shaft. The distal end has a modest expansion, with a process on its inferolateral edge. The internal face is covered by a weak but perceptible concavity, a kind of groove that is widened in the proximal internal region. It disappears near the distal end, and the internal region becomes convex. The distal end has a convex articular surface for the calcaneum.

*Dimension.* - Length of the fibula of the holotype: 470 mm.

### ***Metatarsals***

The left metatarsals II, III and IV of the holotype (fig. 27) are well preserved. Although they present the same morphologic characteristics as those of *Allosaurus*, they are clearly more gracile than those figured by Madsen (1976, pl. 53 and 55), in spite of comparable proportions according to the table of measurements. It is notable that the differences in specific proportions between the various skeletal elements of *Piatnitzkysaurus* and *Allosaurus* could probably be explained, for the most part, by the difference in size between the compared specimens.

*Dimensions.* - Length of the metatarsals: met. II: 253 mm; met. III: 290 mm; met. IV: 252 mm.

Metatarsal II is the most robust of the three, with an expanded proximal end and a flat articular facet for the third metatarsal, so that the opposite (internal) side is very convex. The distal end has a strong internal expansion, and another externally that affects essentially the ventral/posterior region. The articular facet for the first phalanx is continued on the anterior and

distal part, but it is hollowed by a strong furrow on the ventral/posterior face, directed obliquely near the exterior.

Metatarsal III is the largest, slightly curved, and with large contact surfaces for metatarsals II and IV in the proximal region. The latter is very enlarged obliquely, anteroexternoposterointernal. The shaft is rather subcircular in section, and basically regular. There is a marked transverse expansion at the distal end, forming an articular facet for the expanded first phalanx. This facet is particularly well defined by a depression on the proximal side. Laterally, the distal end is rounded and presents a distinct central depression on the distal side. There are deep depressions for muscular insertions on these two sides.

Metatarsal IV has the same length as the second but is still more curved, thus bringing its inferior end into a very lateral position. The shaft is rather trapezoidal in section, with the internal and external sides subequal, so that the posterior edge is distinctly larger than the slightly convex anterior edge. The distal region has a dorsoventral expansion; the internal face is concave with a depression for muscular insertions. The posterior facet is narrow and very curved; it rejoins a depression in the anterior/ventral region.

Neither the tarsals nor any other bones of the foot were recovered, with the exception of the distal part of a phalanx bearing a large articular pulley.

Comparison of the metatarsals of different species demonstrates notable similarities between *Piatnitzkysaurus* and *Dilophosaurus*, particularly concerning the size and proportions, in spite of some differences in the shape of the distal expansions. It seems that the proximal regions, though fundamentally comparable, are more different in *Allosaurus*. In *Ceratosaurus*, the proportions are entirely distinct, such that for an equal length of metatarsal II, that of *Ceratosaurus* is approximately 1.6 times more robust than that of the Argentine genus.

## PNEUMATIC CAVITIES

Throughout the description of the postcranial skeleton of *Piatnitzkysaurus*, brief allusions were made to the existence of pneumatic cavities in most presacral vertebrae, some bones of the girdles, and those of the limbs. In the vertebral column, the number and volume of these cavities culminate in the cervical vertebrae (fig. 9 and 11), but they decrease from front to back. The placement of these cavities in the cervical vertebrae belies a definite organization. They are developed at the points where the bony mass is sufficiently narrow. In the seventh vertebra (fig. 11), they are observed in the vertebral body, at the junction of the body and the base of the neural arch, on both sides of the neural canal, and finally in the neural canal itself, almost into the zygapophyses. In the tenth vertebra (fig. 13), there is a large opening (f) that communicates with the cavities of the neural arch. In the thirteenth vertebra, there are similar openings (fig. 14, f) under the pre- and postzygapophyses. The sixteenth vertebra is hollowed by a large axial cavity



beneath the neural canal, and by another part at the base of the transverse process. In the seventeenth vertebra, the axial cavity is partially divided by a partition with large orifices of connection (between or through?) in front and behind. The interior of these cavities is covered with very compact bone tissue, apparently identical to the periosteum that covered the external face of the vertebrae.

The openings of the vertebral cavities, between or through, are of substantial size. They can be interpreted as playing a dynamic role. Ultimately, the existence of a regular system to contain the cavities could have acted at determined moments by rapidly filling or emptying.

On the ilium, there are two small foramina (fig. 22, fp) that connect with the internal cavities of the (rather thin) iliac blade and pubic peduncle. The shafts of the femur, tibia and metatarsals are equally hollowed with large cavities. On the tibia (fig. 26, f), a small foramen connects this cavity with the exterior. The humerus has an analogous foramen on its internal face. Madsen (1976) also reported foramina on the femur, tibia and humerus of *Allosaurus fragilis*, in a very similar position to those of the Argentine species. In the appendicular skeleton, the cavities are limited by very compact bone, comparable to the periosteum. Different authors (Ostrom, Madsen...) have interpreted these bony cavities in theropods as anatomical solutions, or adaptations, tending to reduce the weight while maintaining a particular size. We adopt the same point of view, since the large distribution of these cavities in all the postcranial bones represents a considerable volume compared to the total volume of the skeleton, and makes this alleged function plausible. The fact that the cavities are more frequent in the predatory bipedal forms is congruent with the need to reduce weight in order to allow rapid locomotion.

This scenario is a little uncertain because of the presence of an enormous tail that represents a very heavy expense, not compensated by the pneumatization in the rest of the skeleton, and that must be explained otherwise.

## COMPARISONS

All the similarities noted throughout the description of the skeleton of *Piatnitzkysaurus floresi* establish that this species is anatomically close to *Allosaurus fragilis*, in spite of some more primitive characters allied to the other clearly different taxa. Among these, note the morphology of the occipital region, in particular the deep depressions between the occipital condyle and the edge of the opisthotic, the strong sagittal constriction of the region near the basiptyergoid processes, and the presence of a remarkably robust alar process on the laterosphenoid. The precise interpretation of these differences is not simple and only a general study of the Jurassic carnosaur could estimate their importance. However, the marked resemblances in the basicranial region between *P. floresi* and an undescribed species from the

Lower Jurassic Kayenta Formation, and *Eustreptospondylus* of the Callovian, suggest that these characters should be considered slightly specialized compared to *Allosaurus fragilis*. Certainly these grades of specialization do not correspond to the organization of the braincase or basicranium in relation to encephalic capacity, but instead to details of the muscular system that, fitting into this region, would assure the movements of the cranium relative to the neck and the mandible.

Would it perhaps be more appropriate to mention only the more or less greater difference in the structure of the basicranium relative to that acknowledged in the older species, rather than to interpret it in terms of specialization? In that case, if some of the criteria were considered, *P. floresi* could be closer to the primitive condition of *Allosaurus fragilis*. The same observations stand out in the comparative study of the postcranial skeleton: profound affinities with *A. fragilis*, and differences interpreted as proof of a slight specialization of the Argentine species. This is the case with the pubis, where the distal process is less developed, and with the proximal region of the tibia, where the external femoral condyle is more distinct and convex in *Allosaurus fragilis*, whereas it is more integrated into the internal articular surface in the Argentine species. The same is true for the femoral head, which is clearly anteriointernal and not internal as in *A. fragilis*.

In summary, in spite of the differences between the basicrania of *P. floresi* and *A. fragilis*, I think that the similarities noted throughout postcranial skeleton demonstrate a familial affinity.

Regarding the significant differences with *Piveteausaurus* (Taquet and Welles, 1977) mentioned in the comparison of the braincase of *P. floresi*, in my opinion, they indicate that a type of adaptive radiation was in the process of being realized during the Middle Jurassic, and that it would eventually produce distinct types distributed into several families. This is why the distinction of *Piveteausaurus* from the other known genera by Taquet and Welles is entirely justified, and it is possible that this taxon represents its own family.

For the moment, it would be difficult to propose a valid synthesis of relationships between the different carnosaurian genera. This situation is at risk of continuing as long as we do not have more information on the postcranial skeleton of this group of dinosaurs. Under these conditions, I think it necessary to recall that, in spite of important differences in the basicranium and the braincase between *P. floresi* and *A. fragilis* that could be interpreted as the mark of a separation into distinct lineages, the many resemblances in the postcranial skeleton indicate, in contrast, phyletic closeness. We are able then to suppose that in reality the two taxa belong to the same family.

In contrast, when comparing *P. floresi* to *Ceratosaurus* and *Torvosaurus*, it seems that the significant differences force their placement in different families. Among the Jurassic carnosaur genera whose cranial material was compared to *Piatnitzkysaurus*, three lineages or families can be distinguished by the very evident distinctive characters:

Allosauridae

*Dilophosaurus*

*Piatnitzkysaurus*

*Eustreptospondylus*

*Allosaurus*

*Acrocanthosaurus*

Ceratosauridae

*Ceratosaurus*

Torvosauridae

*Torvosaurus*

*Megalosaurus* is not included in the above list because, having had the occasion to compare it directly, I consider that this genus is insufficiently known to determine its affinities.

## FIGURE CAPTIONS

FIG. 1. - Geologic sketch of the Cerro C ndor region on both sides of the Rio Chubut (west-central Chubut Province). 1, Pampa de Agnia Formation, Bajocian; 2, Ca nad n Asfalto Formation, Callovian; 3, "indeterminate formation"; 4, Los Adobes Formation, Albian; 5, sauropod and carnosaur locality of Cerro C ndor; 6, sauropod locality of Cerro C ndor North; 7, fish locality of Arroyo Col n Cohu  (map after Volkheimer, 1970).

FIG. 2. - Diagram of the distribution of the different skeletal remains of *Patagosaurus fariasi* of Cerro C ndor North, corresponding to the lower third of the Ca nad n Asfalto Formation.

FIG. 3. - Posterior view of the basicranium of *Piatnitzkysaurus floresi*. *bo*, basioccipital; *bsf*, basisphenoid; *exo*, exoccipital; *opst*, opisthotic; *pbpt*, basipterygoid process; *soc*, supraoccipital; *tbsf*, basisphenoid tuberosities.

FIG. 4. - Lateral view of the basicranium and braincase of *Piatnitzkysaurus floresi*. Abbreviations as in figure 3 and: *aso*, unossified area; *ce*, encephalic cavity; *fo*, foramen ovale; *lse*, laterosphenoid; *proot*, prootic; *ssf*, sphenoid sinus; *st*, sella turcica.

FIG. 5. - Dorsal and ventral views of the left frontal of *Piatnitzkysaurus floresi*. *cno*, canal for the olfactory nerve.

FIG. 6. - Internal view of the left maxilla of *Piatnitzkysaurus floresi*. *fgd*, foramen for the tooth germ.

FIG. 7. - Lateral and internal views of the anterior dentary fragment of *Piatnitzkysaurus floresi*.

FIG. 8. - Lateral and anterior views of the axis of *Piatnitzkysaurus floresi*. *dp*, diapophysis; *ep*, epiapophysis; *ia*, intercentrum of axis; *pp*, parapophysis; *prz*, prezygapophysis; *pz*, postzygapophysis.

FIG. 9. - Lateral view of the 4th cervical vertebra of *Piatnitzkysaurus floresi* showing the distribution and form of the pneumatic cavities: *c1*, *c2*, *c3* in the neural arch (top).

FIG. 10. - Lateral and anterior views of the 5th cervical vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in fig. 8 (center and bottom).

FIG. 11. - Lateral view of the 7th cervical vertebra of *Piatnitzkysaurus floresi*, with the bone partly broken to show the pneumatic cavities in the vertebral centrum and neural arch. *c*, pneumatic cavity; *c1*, principal pneumatic cavity of the vertebral centrum; *cn*, neural canal.

FIG. 12. - Lateral view of the 10th vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in fig. 8 and: *q*, keel.

FIG. 13. - Anterior view of the 10th vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in fig. 8 and: *f*, fenestra for communication between the cavities.

FIG. 14. - Anterior and lateral views of the 13th vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in figure 8 and: *ili*, insertion for intervertebral ligaments; *lifa*, anterior infradiapophyseal blade; *lifp*, posterior infradiapophyseal blade.

FIG. 15. - Anterior view of the 16th vertebra of *Piatnitzkysaurus floresi* sectioned to show the pneumatic cavities, c1 and c2 of the neural arch. Abbreviations as in the preceding figures and: *rii*, region for insertion of intervertebral ligaments.

FIG. 16. - Lateral view of the 17th vertebra of *Piatnitzkysaurus floresi* showing the detail of the network of pneumatic cavities. Abbreviations as in the preceding figures and: *ce*, external communication of the pneumatic cavity; *hi*, hypophene; *hy*, hypantrum; *s*, septum separating the cavities in the sagittal plane.

FIG. 17. - Lateral view of the 19th vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in the preceding figures and: *lp*, parapophyseal blade.

FIG. 18. - Anterior view of the 19th vertebra of *Piatnitzkysaurus floresi*. Abbreviations as in the preceding figures and: *lspz*, supraprezygapophyseal blade.

FIG. 19. - Right scapula and coracoid of *Piatnitzkysaurus floresi* in lateral view. *cg*, glenoid cavity; *fc*, coracoid foramen; *pa*, acromial process; *ps*, process for the triceps.

FIG. 20. - Right humerus of *Piatnitzkysaurus floresi* in dorsal view. *cd*, deltoid crest; *cu*, ulnar condyle; *cr*, radial condyle; *fp*, pneumatic foramen; *ti*, internal tuberosity.

FIG. 21. - Left ulna of *Piatnitzkysaurus floresi* in lateral (A) and internal (B) views. *po*, olecranon process; *pl*, process for ligamentous insertion.

FIG. 22. - Left ilium of *Piatnitzkysaurus floresi* in lateral view, dotted lines indicating missing parts. *cs*, supraacetabular crest; *fp*, pneumatic foramen; *lpm*, posteromedial blade; *pp*, pubic peduncle; *pi*, ischial peduncle.

FIG. 23. - Left pubis of *Piatnitzkysaurus floresi* in lateral view. Dotted lines indicate missing parts. *a*, acetabular region; *fi*, articular surface for the ilium; *i*, articular surface for the ischium; *fo*, obturator foramen; *pa*, process for the ambiens muscle; *pp*, pubic foot.

FIG. 24. - Left ischium of *Piatnitzkysaurus floresi* in lateral view. *e*, distal expansion; *lv*, ventral blade; *pi*, iliac peduncle; *pif?*, process for the ischio-femoralis muscle?; *pp*, pubic peduncle. Drawn after the two incomplete ischia.

FIG. 25. - Right femur of *Piatnitzkysaurus floresi* in dorsal view. *dsc*, supracondylar depression; *tm*, lesser trochanter; *tmy*, greater trochanter.

FIG. 26. - Left tibia of *Piatnitzkysaurus floresi* in lateral view, and the distal part of the same in anterior view. *a*, zone of contact with the dorsal process of the astragalus; *cl*, lateral condyle for the fibula; *f*, pneumatic foramen; *el*, lateral expansion of the tibia; *pf*, fibular process.

FIG. 27. - Left metatarsals of *Piatnitzkysaurus floresi* in dorsal view. *ca*, articular facet for the phalanx; *f*, articular facet; *fl*, fossa for ligamentous insertion; *pl*, process for the external ligament.

FIG. 28. - Skeletal reconstruction of *Piatnitzkysaurus floresi*.