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A NEW TRIASSIC ORNITHISCHIAN DINOSAUR (*PISANOSAURUS MERTII*; ORNITHOPODA) FROM THE ISCHIGUALASTO FORMATION, ARGENTINA[†]

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ORIGINAL ENGLISH ABSTRACT: Some illustrative skeletal remains of a small reptilian form from the Triassic Ischigualasto Formation, San Juan Province, Argentina, are studied. After a short general introduction to the problem, the new form is described and, especially on the morphology of jaws and dentition, to a very primitive representative of the Ornithischia finally assigned.

I. INTRODUCTION

1. GENERALITIES

Months ago José Bonaparte, vertebrate paleontologist of the Instituto Miguel Lillo in Tucumán, placed in my hands the valuable, substantial object of the analysis in this work. It was unearthed in 1962 personally by him, Herbst and the preparators Vince and Scaglia, from a new locality in the Ischigualasto Formation[1], already classic in the literature of the Universal Triassic and on which brief references are given *below* in this chapter. And not only collected, but in reality anticipated, because Bonaparte, without having made a special analysis of the matter, was inclined to consider it as pertaining to a true ornithischian.

To make room for it in my own currently overloaded work plan, given its exceptional interest, I nevertheless have to indicate a certain limitation to its study; thus, aspects such as the origin of this new form, elucidation of the state of the formation

[†] Original reference: Casamiquela, R. M. 1967. Un nuevo dinosaurio ornitisquio triasico (*Pisanosaurus mertii*; Ornithopoda) de la formacion Ischigualasto, Argentina. *Ameghiniana* 4(2):47-64. Translated by Matthew T. Carrano, University of Chicago, 1997.

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bearing it and others will only be discussed here superficially. From any manner, I continue the study of Argentine dinosaurs with the present contribution (*vide* Casamiquela, 1963; 1964).

Therefore, I give deep thanks to Bonaparte for his kindness; to Scaglia and Vince for the excellence of preparation and to the Laboratorio de Fotografía of the Facultad de Ciencias Naturales y Museo for photographs of the materials; finally, to Rosendo Pascual, Chief of the Division Paleontología de Vertebrados of this Facultad, where the work was developed, for his bibliographic and critical assessment.

2. THE ISCHIGUALASTO FORMATION

The lithological knowledge and stratigraphic relationships of this formation are based fundamentally on the fieldwork of De la Mota (unpublished thesis, 1946) and Frenguelli (1948). Groeber and Stipanicic (1952) and presently Stipanicic (1957) framed these reports and others within the whole Triassic; Romer ultimately (1962) gave another panorama of the geology of the area. Meanwhile, the paleontological understanding rests on the works of Archangelsky (plants), Huene (tetrapod footprints), Cabrera, Reig, Bonaparte, Casamiquela, Romer and Cox (tetrapods). Bonaparte and Pascual are currently occupied with the chronological conclusions that grew out of this vertebrate paleontological panorama, so that—except for not sufficiently managing the significance of some elements—I prefer not to enter into a parallel analysis of the problem in this work.

Therefore, with the help of Groeber and Stipanicic on the fundamentals, I will only provide some data about the Ischigualasto Formation, and finally give my own brief opinion as to its age.

To begin, there used to be the Ischigualasto-Ischichuca Triassic "series" in our country. In it, or rather in this profile, Frenguelli recognized four "sections" that are, in ascending order, the "Ischichuca," "Los Rastros," "Ischigualasto," and "Gualo" strata. Nowadays he has replaced this last name with "Los Colorados" on the suggestion of De la Mota, and tacitly, or expressly, given a functional category to each of the four named units.

The "series" in question includes about 2000 km^2 "between the southern Famatina, the mountains of Valle Fértil and the Cerro de Villa Unión" (southwest of the Province of San Juan and the contiguous portion of La Rioja); "it is very extensive and arranged in the form of a flat-bottomed barrel, almost planar, with somewhat straightened edges or wings" (Stipanicic, 1957).

The Ischigualasto Formation, with its own lithologic characteristics that are clearly differentiable from those of the subjacent and suprajacent formations (both apparently discordant), was defined ("Ischigualasto Strata") by Groeber and Stipanicic in the following manner (1952, 89): "correspond to the 2nd Level or 'Jurassic' of Bodenbender, and thus constitute a homogeneous complex that reaches a maximum extent of 555 meters, a superior section is recognized where partly or totally interbedded sandstones predominate, which sometimes get to be coarse sands that are entirely clear grey or greenish grey in color; in the median part clear grey calcareous tufas with plant fossils predominate, and simultaneously sandstones, coarse sands and mineral fragments newly abound in the inferior part. In the Los Colorados-Cerro Morado region, De la Mota found near them, within this complex and around its base, two layers of melaphyres that have produced metamorphism in the sediments that support them." Its thickness varies between 500 and 600 meters; "Los Rastros" totals 400 m (sandstones and arkoses with layers of intercalated basalt), and "Los Colorados" 1000 m (sandstones and conglomerates in the base).

This last formation, reputedly sterile from a vertebratological point of view, has provided a great quantity of materials, fundamentally "sauropodomorphs" (*sensu* Charig, Attridge and Crompton, 1965) of Upper Triassic affinities, to the investigators of the Instituto Miguel Lillo in Tucumán, headed by Bonaparte.

These data, united into their own faunal list of the underlying (that is, Ischigualasto) formation, permits assigning a BASAL **Upper Triassic** age to it, therefore somewhat younger than that held by the consensus (Romer, Reig), which fixed it within the upper Middle Triassic. For me, the decisive element in this assignment is provided by stagonolepid pseudosuchians of the family Aetosauridae (*vide* Casamiquela, 1961 and MS 1). It will be necessary to add the material analyzed in this work to them, because of its clear ornithischian affiliation. As is learned—and we will see in the next chapter—ornithischians known from the Triassic worldwide are very rare, and come entirely from the more superior part of this period.

II. ANTECEDENTS, PHYLOGENY AND SYSTEMATICS

The origin of ornithischians is obscure. All that the currently described forms can affirm is that, yes, this origin is older than had previously been accepted, and in this sense the form under study speaks so eloquently, being already perfectly differentiated during a period as early as that proposed above. I believe that in the present state of things we will have to turn on the *a priori* that prevented, in greater measure, acceptance of the interpretations of Huene (1931) regarding the footprints of *Rigalites ischigualastianus*, originating fortuitously from the Los Rastros Formation, below the Ischigualasto Formation as we saw, and interpreted by the same author, with great audacity, as of ornithischian extraction. If this was real[2] *Rigalites* would be the oldest[3] representative of this group in the entire world.

The oldest, but not the only Triassic, although the known remains can be counted on the the fingers of a single hand: *Geranosaurus atavus*, from the Karroo; *Lycorhinus angustidens*, from the "Red Beds", formerly taken to be an ictidosaur (Therapsida) but with all probability an ornithischian (*fide* Crompton and Charig, 1962); and *Heterodontosaurus tucki* (id), from the "Cave Sandstone"—all these Upper Triassic. The fourth will be *Pisanosaurus mertii* described here...if this extraction is not for *Poposaurus gracilis*, from the Upper Triassic of Wyoming, postulated as such by Nopsca (1921; 1928) and Huene (1950, 1956). Recently Colbert (1961) rebuffed this interpretation and assigned it to the Theropoda; presumably it is treated, by him, as an aberrant carnosaur. Nevertheless, the notable feature in the axial anatomy cited by Colbert, that is, the presence of a pair of bars to reinforce the lateral apophysis of the dorsal vertebrae, also

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[2] Personally I do not believe it. Here I can study with a certain detachment these prints and I am inclined to look for to their author among the pseudosuchians.

[3] Remains reevaluated as the ichno-form **Anomoepus** Hitchcock, from the Triassic of Connecticut (cf. Lapparent and Lavocat, 1955, 830).

appears in *Pisanosaurus*, and therefore—if this is a true ornithischian—I believe that it will be necessary to reconsider the controversial evidence of *Poposaurus* (especially the problem of the ilium, a left according to Colbert and a right according to the remaining authors); see *below* on this topic.

And with this rapid glance the information that I have with respect to the presence of ornithischians in the Triassic is exhausted. On the other hand, the group holds fast and individualizes from the Liassic; in fact already then—and even in the Triassic—the principal **lineages** that constitute it were differentiated. I said this last, that is, the possibility of a differentiation so much older than the Triassic, to mention the judgement of Huene, who (*cf.* 1956), with enough audacity, placed *Geranosaurus* in the origin of the lineage of his suborders Ornithopoda (which comprises hypsilophodontids, psittacosaurids, pachycephalosaurids, camptosaurids, iguanodontids, and the group "Hadrosauria") and Ponderopoda ("ceratopsoids"), and *Poposaurus* in the lineage of his suborder Thyreophora (which includes Stegosauridae and Apraedentalidae, this is acanthopholines and nodosaurines[4] *auctorum*).

Both lineages meet below, at an unnamed point, that translates our ignorance about the origin of the group (in the stem of the Thecodontia).

I proceed, in passing, to indicate that Huene's classification coincides in its fundamentals with that of Lapparent and Lavocat (on which I rely), who speak of three units—equivalent—of the superfamily hierarchy: iguanodontoids (or ornithopods), ceratopsoids, and stegosauroids.

The evidence is that, with *Scelidosaurus* from the Liassic of Great Britain, we are certainly securely within this latter group (Thyreophora or Stegosauria), that is, we are before a form already specialized in a certain manner; and the same follows with the three remaining known Liassic forms. And from there fortuitously the investigators do not hesitate to reject the possible significance of a chronologic inversion of such magnitude by having the small Hypsilophodontidae, from the Lower Cretaceous (Wealden) of the Isle of Wight, as the most primitive group of post-Triassic ornithischians.

In one of my preceding works (1964), dedicated to the description of a Patagonian hadrosaurid, I gave a small list—isolated bones or plates—of classified Argentinian materials (by Huene, 1929) that would turn out to belong to ceratopsids and "acanthopholids." Obviously, the hadrosaurid mentioned added the Ornithopoda (Iguanodontoidea) to the South American representations of Ornithischia, with which it can be said that the three great groups that form this order were present there. Perhaps, therefore, it is not a mere defect of collection that we do not know them better.

Now, with the discovery of *Pisanosaurus mertii* in layers as old as those of the Ischigualasto Formation, the paleontological significance of the group gains in interest considerably. Moreover, from the concretely phylogenetic point of view, if one recalls that this form has been determined—although provisionally— to be a primitive member of the Ornithopoda. We pass on to its description.

III. ANALYSIS OF THE MATERIAL

1. REVIEW OF THE MATERIAL

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[4] However in the phylogenetic frame of page 567 these categories are elevated to families.

The limited material recovered has a relatively good state of preservation, although poor in the axial portions, and consists of a fragment of right maxilla with teeth; an incomplete right mandible, also with teeth; an obscure fragment of left mandible; portions of three caudal vertebrae; nine incomplete dorsal vertebrae (lumbars); a rib and a pair of fragments probably attributable to ribs; a complete right tibia and fibula with the articulated astragalus and calcaneum; a small bone of the second distal tarsal united to a metatarsal; two metatarsals with corresponding incomplete and articulated digits; a problematic fragment of long bone.

2. DESCRIPTION, No. P.V.L.[5] 2577.

SKULL. (*Vide* plate I.) — Only the inferior portion of the right maxilla is preserved, fortunately equipped with several teeth, with a typical state of preservation. The most significant feature of the element is fortuitously the reciprocal arrangement of the dental series and the supradental portion, forming a dihedral angle slightly more than straight (with vertex facing outwards and aperture facing inwards). This arrangement arises from the implantation of the teeth in the bone, forming a type of interiorly-directed palisade whose masticatory surface becomes superimposed on those of the mandibular teeth. In other words—if the separation of both elements, articulated in the original discovery, did not affect the morphology of such surfaces—the occlusal faces of the teeth form a more or less continuous surface, bevelled from top to bottom and externally, and subparallel to the interior bone surface. Anyway, the supraalveolar region is somewhat inclined towards the interior and swells rapidly upwards. This enlarging, which gives a wheel shape to the rest of the preserved bone, can be well appreciated on the internal side because at this height the external side is somewhat affected by destruction. In some way, a transverse narrowing of the aforementioned wheel, or bar, is visible in concordance with the reduction in size of the teeth, of which apparently even the last are preserved. Externally, the bone is smoothly concave in the longitudinal direction.

11 visible teeth and the probable root of a 12th (the most anterior) are preserved, inferable by the presence—doubtful—of a ---CULO in the bone. As stated, the tooth row forms a sort of palisade, more compact in inferoexternal view, from which the subperpendicular elements are distributed like a keyboard. Nevertheless, from this view it can be appreciated that is extended distally, which makes that—the “crowns” contacting together—there exists a small basal separation between tooth and tooth. Finally, there is a kind of bending external to these that contributes fundamentally to the obliqueness in the direction of the aforementioned masticatory surfaces. Now in inferointernal view, note that these surfaces, or “crowns”, are bevelled inwards and upwards from the infero-external coronal border. Each tooth is inserted into a particular alveolus, and it can be appreciated that the emergent cross-section is subcylindrical, and in some cases a light is visible between the—emergent—bases of two contiguous teeth. It is even possible that the germ of a replacement tooth is present in a small fossa on the internal side, between the 5th and 6th teeth; but this is highly doubtful. On the other hand, I venture to say very little about the morphology of the fairly deteriorated occlusal tooth surface, and that is destined—as stated—to be superimposed on the corresponding mandibular teeth. The tooth cross-section at the level of the “crowns” is variable: subcircular to subelliptical, in this last case with a somewhat diagonal major axis. In the 10th and 11th elements (from back to front) a coronal dilation is noted that corresponds to an internal buttress. The “crown” is bilobate, in the form of an 8, with the internal lobe smaller.

In the robust and elongated right mandibular ramus, the most characteristic feature observed in superior or lateral external view is the presence of a kind of wide base, or buttress, that is developed from approximately the 9th tooth (counted from back to front) and even comes to form a smooth furrow contiguous with the tooth row.

It is precisely the widening of the element in this region that gives its longitudinal cross-section an elongated S-shape, because the line of the dentition is hardly curved, with the concavity towards the exterior. This elongation corresponds to the dentary, although it is impossible to delimit the articulation of this bone with the remaining mandibular elements. Towards the front—still in external view—this buttress is fairly brusquely attenuated to the height of these teeth, but in any case does not disappear, and

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[5] Laboratorio de Paleontología de Vertebrados of the Instituto Miguel Lillo in Tucumán.

thus the tooth series is always maintained against the internal border of the bone and yields a small, rounded margin, free from the external side up to the preserved end (which is the presumed dentary-predentary articulation line).

Still in the same external view, it is possible to note, that the ramus gains rapidly in height towards the front, and that the buttress or thickened border is elevated parallel to the elevation of the tooth row and becomes wheel-shaped towards the back, that is, it delimits a more planar, and even depressed, surface below and back, corresponding to the surangular-angular region, elements not differentiated (nor in their articulation with the dentary). A small "fenestra" present in the medial part of this caudal region of the mandibular ramus is, in my judgement, merely the product of breakage owing to the extreme delicacy of the bony lamina at this point. The lamina is equally truncated above, but it is possible to infer that its coronoid process was not very well developed.

On the other hand, attention is drawn to the length of this postdentary portion of the ramus relative to the other, hardly longer, preserved part.

Finally, the articular region of the element is robust, enlarged into a kind of tubercle, and gives off the retroarticular process as a rounded caudal projection.

In infero-internal view a smooth longitudinal cavity is evident, and a rapid descent of the border towards the half of the tooth row preserved, which comes to form an anteroposterior convexity. Apically (in the preserved part) it rises again abruptly, and one cannot avoid the impression that it must be forming a kind of beak. Seemingly the bone is broken approximately coincident with the dentary-predentary suture, although of course this is only a presumption with little basis.

In internal view, it may be noted first that the tooth row forms a palisade that is directly continuous with the internal face of the mandibular ramus (that is, it has no internal base). It is not possible to distinguish here the manner in which the dentary articulates with the splenial or other mandibular bones, however I believe that the splenial occupied the entire inferior length of the ramus. The internal wall is slightly inclined towards the interior in the anteriomedial region, verticalizes towards the center of the tooth row, and is inclined towards the exterior more backwards. At the level of the last teeth, a small fossa is delimited against the inferior border, anterior to the prominence supposedly formed by the prearticular and which in turn delimits the deeper and apparently ellipsoidal mandibular fossa (adductor fossa) in front. As stated, in the depth of the fossa the wall (of the surangular) is so thin that it has been perforated. This fossa is bordered ventrally by a strong bar (caudal portion of the prearticular?) that ends, very enlarged, at the caudal mandibular ramus as a massive tubercle from which the well-differentiated retroarticular process descends. Between them the wide articular fossa, strongly angled towards the inside, is disposed. There remains to mention an apparently displaced pillar-like element that delimits the adductor fossa anterosuperiorly, and that must correspond to a very wide coronoid.

As for the tooth row, it consists of 15 teeth, of which the 5th and 8th appear to be the best preserved with respect to the masticatory surface. I have the impression that the first tooth preserved is the true first of the series, because no traces of an alveolus in the small preserved anterior portion can be distinguished. In this manner, I believe that the possible presence of a "canine," in the manner of that present in *Geranosaurus, Heterodontosaurus*, and *Lycorhinus*, is absolutely dismissable.

As stated, it is possible that a predentary exists, having the form of the particular curve that has been produced by the anterior section of the bone, and that could coincide approximately with the sutural line.

The teeth are lodged in individual alveoli and are subcylindrical in the basal part, widening somewhat asymmetrically in the crown. I will say that the cross-section of the "crowns" oscillates between ellipsoidal (with the major axis clearly anteroposterior) to subpentagonal or the like. The 8th is the largest and the others diminish in size gradually towards both ends.

The morphology of the masticatory surfaces is as follows: the 5th (from the front) is bevelled towards the exterior and slightly backwards, and its transverse cross-section is smoothly concave. The 8th shows an elevated lingual border, a strong external overhang and an anterior platform or buttress with a rear overhang. The 9th shows attenuation of this arrangement, but the overhang is towards the front. The size of the "crowns" increases towards the ninth tooth and the others decrease gradually towards the rear.

It is impossible to decide if this morphology is natural (that is, in every case produced by wear) or in certain places produced by artificial modifications (fossilization and preparation, because, as stated, the mandible and maxilla were in position in the original). Either—lamentably—prevents me from saying anything as to the presence or absence of enamel. I cannot fail to mention, finally, that the entire row gains height in parallel with the elevation of the ramus, and that therefore the surface formed by the crowns altogether is longitudinally concave.

VERTEBRAL COLUMN. (*Vide* plate II.) I attribute an articulated group of 7 centra to the dorsal region (lumbar), arched with an inferior convexity and fairly poorly preserved. In it the very thick (although perhaps somewhat squashed) centra are spool-shaped, however the inferior arch—in lateral view—is somewhat rigid. The articular surfaces appear planar (or concave).

In lateral view a pair of buttresses of the transverse processes, in the manner of reinforcing "tendons", separate and decend fairly symmetrically from the base of the aforementioned apophyses to disappear towards the anterior and posterior limits of the vertebral face respectively. In some centra the presence of a third segment is visible, here longitudinal and placed mesially on this surface, which contacts those of the other two bars by its ends; the whole thing thus forms a true triangle.

The transverse processes, which are directed upwards and forwards, are robust relative to this reinforcement system, which is completed with a last tendon or bar standing out below and (in appearance) anteriorly from each transverse process, and which accompanies it along its length, without exaggeration.

The neural spines look bad; only the root of a pair of them are preserved, apparently restricted in anteroposterior development to the caudal 3/4 of the centrum.

At the end of one of the transverse processes, the tuberculum of one rib may have been preserved.

A pair of fused, well broken centra pertain to the lumbar region. They are equally thick and their articular faces look smoothly concave. The reinforcing bars cannot be seen and this give the impression that the transverse processes—damaged by breakage—originated in a plane above that of the dorsal vertebrae.

I identify fragments of three articulated vertebrae as caudals. The following elements can be individualized from a global observation of them: the centra are spool-shaped, long, thick, medially depressed (for the inferior face) and their very expanded articular surfaces appear to be fused.

From the apparent absence of chevrons (in the only centrum preserved)—in addition to their size—it can be inferred that the group pertains to the proximal portion of the tail.

Laterally, a notable mesio-superior excavation can be seen on the centra. This excavation causes the transverse process—hardly incipent—to become blurred with a bony bar that is extended forwards and outwards, and directed diagonally forwards and up. Fortuitously, it is the anterior end of the supposed bar that articulates externally with the articular pulley, which is directed caudodorsally towards the outside from the postzygapophysis of the previous centrum. The group gives the impression of a series of little headless men taken by the shoulders. The "decapitation" alludes specifically to the near total absence of the destroyed neural spines (even having produced a fossa in their place).

Moreover a group of incomplete impressions of six vertebral centra are preserved. They permit observing the notable lateral constriction of the centra and at least in one case the width of the transverse processes, located on one of the halves of the vertebra (posterior?). On the opposite side the fragment of matrix shows a pair of impressions of apparently contralateral elements that could correspond to pelvic bones (?). This interpretation depends on the depth of the region of the column to which the vertebral elements pertain.

RIBS. (*Vide* plate II.) At least one left rib is preserved, clearly curved ventrally and crossed by a distinct longitudinal groove on its anterior face. It is a delicate element with a narrow cross-section, and expands proximally by giving origin to a clearly separated capitulum and tuberculum—although unfortunately not preserved, just as the distal end. For this reason (differentiation of the proximal elements) I think that it is an anterior rib of the dorsal series.

I also attribute to ribs, with much reservation, three similar fragments of suboval cross-section and with a kind of rounded laminar keel on one of the edges (*vide* intermediate figure, below, plate II), which could correspond to the site of bending of the ribs.

PROBLEMATICUM. A fragment of sharp bone of roughly ellipsoidal or flattened cross-section rests in this category. It could be from a rib *sui generis*, but it is also not possible to discard assimilation with another region of the skeleton (pelvis).

FORELIMB. The inferomedial portion of the left scapula (*vide* left figure, above, plate III) is a delicate bone, that much reminds me of the same bone in aetosaurids. It shows an enlargement—a kind of edge—along the concave anterior border, an edge that thickens inferiorly. On the posterior side the border is straight and only starts to bend upwards by forming an edge in the inferior portion (preserved). The internal surface, clearly concave longitudinally, shows a kind of tuberculum towards the middle of the preserved part, against the anterior border.

I interpret as a mesial portion of the right ulna (?) a fragment that includes slightly less than half of this bone, which lacks even the proximal end. It is a crudely prism-shaped element with an enlarged head, strong body, and elliptical cross-section (with a transverse major axis). In the superior-internal portion it shows a deep, internally situated articular fossa—if the attribution of this bone to a right ulna is correct—limited above by the rapid slope of the head of the bone, and below by an edge and crest situated mesially with respect to the shaft, which nevertheless crosses by a space of some millimeters. Externally the element is smoothly convex in both directions. (*Vide* middle figure, left, plate III).

HIND LIMB. The mesiodistal portions of both femora are preserved, lamentably in poor condition, both affected by a *peeling* that has notably reduced the thickness of the shaft; by this it is evident that it was massive. In spite of the poor preservation, it is possible to state that the femora were long, gracile, and turned, I would say on the model of stagonolepoids. In posterior view a distal cavity clearly delimits a pair of articular condyles for the tibia. (*Vide* lower figure, left, plate III.)

The right tibia and fibula (*vide* plates III and IV) are preserved in original articulation and remain connected, one to the astragalus and the other to the calcaneum. The group impresses by its length and gracility, nevertheless not free from robustness. Viewed from its anterior face, the tibia in position (and dispensing with the eventual post-mortem deformations) shows a superior longitudinal crest that is lateralized (in the internal direction), and fades away towards almost the midshaft of the bone by giving room to a superficial convexity that continues to the distal end, slightly slanted in a direction descending from outside to inside. The bone is, then, flattened in its superior portion, and a subcylindrical to quadrangular prism distally. A left-concave curvature mesial to the shaft is due to artificial deformation. Correlated with the superior crest, the internal face of the bone is planar and somewhat slightly depressed superiorly, and is only rounded from the midshaft. The inferior border is convex; the head is thrust forwards (perhaps by breakage) and in a correlated fashion it widens backwards, like a point.

On the posterior face, this point resolves into two blunt pillars separated by a deep furrow; this is attenuated immediately and the rest of this face of the bone is convex. The line of the inferior end that separates the tibia and astragalus now becomes concave.

The external (or fibular) face remains. On this face the smooth depression leaving this superior portion is repeated, in addition to the caudal elongation of the head. The body soon becomes convex and turns to become flat and somewhat depressed distally. Here the distal morphology is notable, because the articular line with the astragalus immediately rises abruptly to form a caudal projection, in order to mark a deep recess.

In superior view, the cross-section is subtriangular, with apex anterior. The inferior is described indirectly.

The fibula is a long and slender bone, although robust, and slightly curved externally by artificial deformation. The internal face is flat and somewhat depressed at both ends, and widened more than the superior. The distal end is convex, and the proximal end is straight but inclined backwards. The external face is convex (in both directions). The distal line, which delimits the articulation with the calcaneum, now becomes completely concave.

In superior view the bone, very slender and arched, is convex externally and concave internally.

In addition, there is a pair of tiny fragments that could have corresponded to the shaft of a tibia and fibula, respectively.

TARSUS. (*Vide* plate IV.) The morphology of the astragalus and calcaneum is partially indicated by the described bones of the leg. The astragalus is very robust, asymmetrical in anterior view, and formed by two lobules (of exactly inverse form) of which that placed on the right is more elevated and dull below, and the other is descended and pointed inwards and forwards. It is this “lobule” that is attenuated in anterior view to form a type of calcified edge. The face of the small bone is directed outwards smoothly in the caudal direction, and in posterior view again shows an asymmetrical profile of attenuated lobulation. As was indirectly stated, the bone gains abruptly in height on its external face and forms a subpentagonal face, deeply encased in the lateral depression of the tibia. It is this face of the bone that is destined to articulate with the internal face of the calcaneum for at least 3/4 of its surface (inferior part).

In basal view, the noted asymmetrical lobules, separated by an anteroposterior and convex groove, are clearly appreciated.

The calcaneum is considerably smaller and wider, semilunar in shape on its internal face and ellipsoidal (axis diagonal and descending backwards) on the external. Basally, a deep anteroposterior groove delimits two regions (asymmetrical, the external much greater).

The third small tarsal bone preserved (*vide* plate IV) could be the 4th of the following row, which suggests, in correlation, accepting that the metatarsal to which it is attached is also the 4th. It is a subquadrangular element, wider than long (at least if the preservation is good), and articulates on the **free** portion of the 4th metatarsal, since the rest of this bone, a bevelled face, is destined for its lateral articulation with the anterior metatarsal (3rd).

In addition I have a flat bone of irregular shape and depressed on one of its faces that I assign to a left astragalus.

I pass on to the metatarsal region. Both preserved metapodials (*vide* plate IV) are affected by artificial deformation. They are long but generally robust, I would say on the theropod model, and relative to the appearance of the zeugopodium suggest an agile runner (certainly bipedal). The metatarsal interpreted as the 4th is, of course, weaker and shorter than the supposed 3rd, and offers a bevelled, flat, and slightly depressed internal face for the connection (overlapping) of the corresponding region of the 3rd. It follows that yet a fifth element would have existed, still more reduced (according to comparison with *Plateosaurus*, for example) judging by the scarce development of the anteroinferior face of the bone. This face is depressed proximally and is continued with a groove almost to the midshaft of the element; afterwards the bone is subelliptical in cross-section (with major axis diagonally inferior-superior) towards the front. The internal face is flattened towards the front and depressed terminally; in contrast the external face is convex and more enlarged.

As stated, the other preserved metatarsal (3rd) is superimposed on this along its flat or depressed basal portion, in the manner of two overlapping roof tiles. For this articulation this entire basal part is diagonalized and in this way delimits a new planar and slightly concave articular surface by the superior-left face, destined in turn for the 2nd metatarsal. The inferior face continues depressed and flat towards the front, the same as the superior, which only fades away after the midshaft of the bone. The rest forms a more dorsally planar and somewhat ventrally enlarged segment that ends in a strong, expanded epiphysis, convex on the articular surface for the corresponding phalanx (also preserved). The general curvature of both bones in position is left-convex, but a balance is reestablished because the distal shafts have a certain turn towards the inside, which in the 3rd metatarsal comes to direct slightly towards the inside the articular surface.

Finally, the proximal portion (*vide* lower figure, plate IV) of the presumed 2nd metatarsal is preserved, flattened and depressed on both faces.

There remains to mention the elements preserved from the digits: namely the 3 articulated proximal phalanges of III (missing the ungual), and 4 articulated distal phalanges of IV, if not in error (here the absence is the proximal, if the attribution of the group to digit IV is correct). These elements are short and very robust, especially the proximal; they are as a group fairly weaker. In all ways, the foot of the specimen under study was certainly solid and generalized; in agreement with this the only ungual phalanx preserved is very sharp, although straight, like a point. (*Vide* plate IV, right.)

3. MORPHOLOGICAL BALANCE

In agreement with the descriptive analysis of the material, the following provisional balance of morphological elements can be established in *Pisanosaurus mertii*: I. In the skull, (a) the dentition is a palisade, from the morphological point of view, and the teeth have alveoli and are subcylindrical, but in contrast have differentiated “crowns” and an occlusal mechanism. There is a small probability that the tooth replacement was of ornithischian type; apparently it did not have a differentiated “canine”; (b) the mandible is primitive (on the generalized pseudosuchian model) in the following characters: length of the postdentary portion; presence of a well developed adductor fossa; presumed limited height of the coronoid process; inferred relation of the bones that form the mandibular ramus. And it is evolved in the ornithischian sense in the following: descended position of the “fulcrum” or articulation (with respect to the line of the tooth alveoli); presumed presence of a predentary; presence of a clear lateroexternal base; disposition of the articular fossa. II. In the postcranial skeleton, (a) the vertebral column that recalls *prima facie* that of *Poposaurus*, and (b) the hindlimb evidently having a generalization in light of a dinosaurian interpretation with the rules of running (it is said to presage the problem of the presumed bipedal habit of the form; *cf.* Casamiquela MS 2).

In summary, it is a very small bipedal “dinosaur”, a good runner and therefore generalized from this focus, consistent with the presence of certain primitive features in the skull, but already on the way along the ornithischian direction in agreement with the morphology of other characters of the mandible and dentition.

4. AFFINITIES

Something different establishes the formal affinities. In agreement with everything stated, it seems evident to me that *Pisanosaurus* completely lacks the "specializations" that could establish a **ceratopsoid** or **stegosauroid** affiliation (*sensu* Lapparent and Lavocat); in contrast nothing opposes considering it a good representative, although very primitive, of the Ornithopoda.

Within this group a consensus exists that considers—weighing the temporal inversion that is a supposed fact, as already stated—the hypsilophodontids of the Cretaceous as the most primitive forms of the entire post-Triassic. And from there Romer (1956) and Huene (1956) included *Geranosaurus* in the family Hypsilophodontidae. *Poposaurus*, interpreted as an ornithischian by Nopsca (1928) and recently as a stegosaurid by Huene (1950, 1956), was, as stated, recently reinterpreted as a saurischian, more concretely a **carnosaur**—which certainly does not disqualify it from the comparison.

While *Nanosaurus* (or *Nannosaurus*), a camptosaurid according to Huene (1956) and a hypsilophodontid according to Romer (1956), is uncertain (down to the age) according to Lapparent and Lavocat (1955), but equally I have to mention it here—to discard it immediately afterwards. But we plunge into the subject:

Of the confused Triassic forms, in this part or *above*, *Lycorhinus* (*cf.* Haughton, 1924) is discarded by the presence of a robust caniniform in the mandible, neither observable nor inferable in *Pisanosaurus*, and the same feature discards *Geranosaurus* (Broom, 1911). The morphology of the dentition, which does not form a palisade, equally permits eliminating *Nanosaurus* (Huene and Lull, 1908) and finally *Heterodontosaurus*, which, as said in the name, presents a marked dental differentiation (*vide* Crompton and Charig, 1962) in addition to a strong mandibular caniniform.

Curiously, *Poposaurus*—of which no known cranial elements have been recovered—bears well a first comparison with *Pisanosaurus*, as also said, in particular on the basis of the vertebral morphology, because the dorsal centra in this form have a large lateral constriction and the particular buttresses noted in the Argentine genus; in such a way this was one of the features that conveyed Colbert to think it was within the Saurischia. We recall this.

As Colbert noted, *Hypsilophodon* (and *Camptosaurus*) have already lost the lateral constriction of the centra, a feature for which alone—apart from that of the dentition and the considerable difference in age—disqualifies it from the comparison. And I believe that the last argument is decisive as to an eventual comparison with the remaining forms of hypsilophodontids.

The conclusion of this entire series, briefly, is that *Pisanosaurus mertii* can be classified as a very primitive ornithopod, with all probability represents an *ad hoc* family, and that alone of all the primitive forms of known (or suspected) ornithischian affinities it resists the comparison—perhaps thanks to the incompleteness of the material—with *Poposaurus*, an Upper Triassic form from North America paradoxically assigned as a primitive saurischian carnosaur...(which in all ways obliges us to reconsider this last reinterpretation).

5. DIAGNOSIS

Order **Ornithischia**
Suborder **Orthopoda**
Superfamily **Ornithopoda**
Family **Pisanosauridae** *nova*

GENUS: *Pisanosaurus*[6] n. gen.

Small, presumably bipedal ornithopod, separable from all other known forms of pseudosuchians, ornithischians and saurischians by its unique combination of generalized and specialized features; among them, namely, the presence of an adductor fossa on the mandible; the length of the postdentary portion with respect to the dentary in the mandibular ramus; the vertebral and hindlimb morphology. Among these, the descended position of the articular condyle of the mandible; the morphology of the dentary (with a strong base); and the homogeneity and distribution in the palisade of the dentition, in addition to the form of occlusion.

Pisanosaurus mertii[7] sp. n.

The generic diagnosis corresponds to the species.

PROVENANCE: "Agua de las Catas," in front of km 461 on National Route no. 40. Province of La Rioja.

HORIZON AND AGE: Ischigualasto Formation (middle part). Lower Upper Triassic?

IV. SIGNIFICANCE

1. From a paleozoogeographic point of view, the description of an ornithopod dinosaur with the characteristics of *Pisanosaurus mertii* in Argentina is entirely a surprise, especially in light of the paucity of remains of representatives of the Ornithischia throughout the entire geologic column in South America. Lack of Jurassic material in general in this part of the world, makes it impossible for me for the moment, lamentably, to complete the recent news with presumptions about the later history of the group until the Cretaceous (Upper Cretaceous), a moment in which we return to find it, although as I said more poorly represented, and already integrated by entities common to other regions, particularly North America (*cf.* Casamiquela, 1965).

2. In contrast, with the phylogenetic focus it is possible to gather some complementary considerations. The first is that *Pisanosaurus* constitutes a good morphological "link" between the pseudosuchian stem and the Ornithopoda *sensu stricto* of the Jurassic and Cretaceous. The second is that, in a correlated fashion, its particular morphology confirms the idea that in the stem of the great group of Ornithischia in general very different evolutionary potentials had to have coexisted. The third is that with all certainty the moment of differentiation of the ornithischians (and saurischians) was before that classically considered and had occurred by at least the latest of the Middle Triassic. And the fourth, finally, is that the Triassic of South America had to have a correspondingly equally large role—and I think not islolated geographically—in this differentiation.

TABLE OF MEASUREMENTS (in millimeters)

Mandibles

Maximum measured length	107

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[6] In honor of paleontologist Juan Pisano, work companion in the Facultad de Ciencias Naturales and the Museo de La Plata, recently deceased.

[7] In honor of Araucanian naturalist Carlos Merti, recently departed.

Maxmimum width in the middle part of the bone in the dentary region	11.5
Height of same (without counting the teeth)	11
Length of the dental series MEDIBLE	50

Vertebrae	*Dorsals*	*Lumbars*	*Caudals*
Measured length of the centra (front to back)	?; 8.4; 9; 10.2; 10.3; 10.9; 11	15.8	18
Width of articular faces	6.2 (last)	9.6	
Height of articular faces	8.7 (last)	12.6	
Minimum width of centra (front to back)	?; 5.5; 5; 4.8; 4.8; 5.2	5.5	5.7

Vertebrae (impressions):

Length of centra	16.5; 17; 17.3 respectively
Width of transverse apophyses, base (in one)	9.6

FORELIMB:

Scapula.

Minimum width	12.5
Mimimum thickness	3.8
Maxmimum length	+70.0

Ulna.

Width of head	13.7
Thickness of head	6.6
Minimum width of shaft (preserved)	10.0
Thickness of same	6.0

HINDLIMB:

Femur.

Width (reconstructed) of terminal portion	25.0
Thickness of same	23.0

					Phalanges						
	Tibia	*Fibula*	*Metat.*	*Metat.*	*Digit III*			*Digit IV*			
			3rd	4th	1st	2nd	3rd	1st	2nd	3rd	4th
Length	160.7	158.7	95.0	81.8	24.6	18.6	14.6	16.0	11.0	10.8	11.0
Min. width of body	10.5	5.5	5.4	6.2	6.4	5.26.0					
Min. thickness of body	12.5	7.5	7.2	6.4	6.0	5.04.0					
Thickness of distal epiphysis	16.0	8.8	10.4	10.6	8.7	6.45.0					
Width of same	11.2	5.5	12.3	6.8	10.9	8.15.8					
Thickness of head	35.8	22.0	11.8	9.7	10.4	9.07.4					
Width of head	12.3	4.2	8.6	6.7	12.6	10.08.2					

BIBLIOGRAPHY

BROOM, R. 1911. On the dinosaurs of the Stormberg, South Africa. *Ann. S. Afr. Mus.*, 7: 291-322.

CASAMIQUELA, R. M. 1961. Dos nuevos estagonolepoideos argentinos (de Ischigualasto, San Juan). *Rev. Asoc. Geol. Arg.*, 16 (3-4): 143-203.

— 1963. Consideraciones acerca de *Amygdalodon* Cabrera (Sauropoda, Cetiosauridae) del Jurásico Medio de la Patagonia. *Ameghiniana, Rev. Asoc. Pal. Arg*., (3) 3: 79-92.

— 1964. Sobre un dinosaurio hadrosáurido de la Argentina. *Ameghiniana, Rev. Asoc. Pal. Arg*., (3) 9: 285-308.

— MS 1. Materiales adicionales y reinterpretación de *Aetosauroides scagliai* (Pseudosuchia, Aetosauridae), de Ischigualasto, San Juan. (In press in *Rev. Mus. La Plata*).

— MS 2. Algunas consideraciones teóricas sobre los andares de los dinosaurios saurisquios. Implicaciones filogenéticas. (In press in *Ameghiniana*).

COLBERT, E. H. 1961. The Triassic reptile, *Poposaurus*. *Field. Geol*., (14) 4: 59-78.

CROMPTON, A. W. and A. J. CHARIG. 1962. A new ornithischian from the Upper Triassic of South Africa. *Nature*, 196 (4859): 1074-1077.

CHARIG, A. J., J. ATTRIDGE and A. W. CROMPTON. 1965. On the origin of the sauropods and the classification of the Saurischia. *Proc. Linn. Soc. Lon.*, 176 (2): 197-221.

DE LA MOTA, H. F. 1946. Estudios geológicos en el Cerro “Bola” al sur de Villa Unión, Dpto. Gral. Lavalle, Prov. de La Rioja. I y II. (*Unpublished thesis, Facultad de Ciencias Naturales y Museo de La Plata*).

FREGUELLI, J. 1948. Estratigrafia y edad del llamado Rético en la Argentina. *Gaea*, 8: 159-309.

GROEBER, P. and P. N. STIPANICIC. 1952. Triásico, pp. 13-141 *in* Geografía de la República Argentina, *Gaea*, 2 (1): 1-541. Bs. Aires.

HAUGHTON, S. H. 1924. The fauna and stratigraphy of the Stormberg Series. *Ann. S. Afr. Mus*., 12: 323-498.

HUENE, F. 1929. Los saurisquios y ornitisquios del Cretáceo Argentino. *Ann. Mus. La Plata* (2), 3: 1-194.

— 1931. Die fossilen Fahrten im Rhät von Ischigualasto in Nordwest-Argentinien. *Paleobiol.*, 4: 99-112.

— 1950. Die Entstehung der Ornithischia schon früh in der Trias. *N. Jahr. Geol. Pal. Mon. B,* 2: 53-58.

— 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. Stuttgart.

HUENE, F. and R. S. LULL. 1908. Neubeschreibung des Originals von *Nanosaurus agilis* Marsh. *N. Jahr. Min. Geol. Pal.*, 1: 134-144.

LAPPARENT, A. F. and R. LAVOCAT. 1955. Dinosauriens, *in Traité de Paléontologie* (J. Piveteau), Paris: 785-962.

MEHL, M. G. 1915. *Poposaurus gracilis,* a new reptile from the Triassic of Wyoming. *J. Geol.,* 23: 516-522.

OSBORN, H. F. 1924. *Psittacosaurus* and *Protiguanodon*: two Lower Cretaceous iguanodonts from Mongolia. *Amer. Mus. Nov.,* 127.

OSTROM, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bull. Am. Mus. Nat. Hist.,* 122 (2): 33-186.

ROMER, A. S. *Osteology of the Reptiles*. The Univ. Chicago Press.

— 1962. The fossiliferous Triassic deposits of Ischigualasto, Argentina, pp. 1-8 *in* Romer, A. S. and C. B. Cox, The fossiliferous Triassic deposits of Ischigualasto, Argentina, and preliminary description of *Ischigualastia*, a new genus of dicynodont. *Breviora*, 156.

STERNBERG, C. M. 1940. *Thescelosaurus edmontonensis*, n. sp., and classification of the Hypsilophodontidae. *J. Pal.*, 14 (5): 481-494.

STIPANICIC, P. N. 1957. El sistema triásico en la Argentina. *Congr. Geol. Intern. XXª Sesión, México, 1956. II, El Mesozoico del Hemisfero Occidental y sus correlaciones mundiales*: 73-112.

EXPLANATION OF PLATES

PLATE I

First row: left, right maxilla in external view; right, same in internal view. Second through fourth rows: right mandible, in external, internal, and superior views. Fifth row: left maxilla in inferior-internal view. Sixth row: right mandible in superior-external view.

PLATE II

First through third rows: dorsal vertebrae in left, right, and basal views. Fourth row: caudal vertebrae in left lateral view. Fifth row: lumbar vertebrae in left lateral view. At left: left rib. At center: supposed rib fragment.

PLATE III

At center: right tibia and fibula (with attached astragalus and calcaneum) in right lateral view. To the tight: the same bones in left lateral view. At left: above, mesial-inferior portion of the left scapula; center, proximal portion of the right ulna (?); below, distal portion of the femur in internal view.

PLATE IV

At left: right tibia and fibula (with attached astragalus and calcaneum) articulated in anterior view. At center: the same bones articulated in posterior view. At right: 4th (with a small tarsal bone attached) and 3rd metapodials with elements of the corresponding digits (in the former the first phalanx is missing and in this the last). Below: both metapodials articulated; proximal portion of 2nd.