

THE PRESENCE OF SAURISCHIAN DINOSAURS  
IN THE "ISCHIGUALASTO BEDS"  
(UPPER MIDDLE TRIASSIC) OF THE PROVINCES  
OF SAN JUAN AND LA RIOJA (ARGENTINE REPUBLIC)\*

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## 1. INTRODUCTION

Successive Argentine expeditions to the Ischigualasto Triassic vertebrate locality, carried out principally for the Laboratorio de Vertebrados Fósiles of the Instituto Miguel Lillo at the Universidad de Tucumán, with resources supplied in major part by the Consejo Nacional de Investigaciones Científicas y Técnicas of the Argentine Republic, and which represented the common effort of the aforementioned Tucumán institution, the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, the Museo de La Plata and the Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata, has allowed the assembling of an extraordinary collection of lower tetrapods. This study is offering data of singular interest, and is establishing new problems whose elucidation could require some important modifications in the generally accepted picture of the evolution of Triassic terrestrial vertebrate faunas.

It is one of these problems which concerns us in this note: the confirmation of the existence of saurischian dinosaurs with the typical Middle Triassic association of cynodonts and rhynchosaurs. Until now, the total known Triassic sequences in which the presence of saurischian dinosaurs had been confirmed were restricted to the start of the Upper Triassic, following the extinction of the cynodont therapsids, whose last representatives reach up to the Middle Triassic, a period characterized by the association of gomphodont cynodonts and rhynchosaurs. Although the remains of dinosaurs have been cited in the Middle Triassic deposits of Tanganyika and Brazil (Huene, 1939, 1936-1942), these fragmentary and exceptional remains were noted with reservation, and Charig (following Romer, 1960) believed it was very probable that they belonged to thecodonts.

It will be understood, then, the great interest in a review that has confirmed the discovery of the presence of a variety of saurischians in the "Ischigualasto Beds", having been discovered in the same beds - and in various cases in clear association - with the remains of traversodont cynodonts, rhynchosaurs and other typical Middle Triassic elements. In reality, it was hoped that at some time it would yield incontestable remains of dinosaurs older than those known from the Keuper. The saurischians which appear in the Upper Triassic already show a grade of evolution and a diversity which requires thinking that the origin of the order must go back to older epochs within the Triassic, perhaps to near the Lower Triassic.

The list of saurischians which are brought to light in this work support this last possibility. They are representatives which are already well differentiated within the order, and in some cases of a fairly advanced evolutionary level. At the current level of understanding, it is not possible to say whether they are more primitive animals than their neighboring relatives from the Upper Triassic. Thus an adequate evaluation of their phylogenetic importance can only be realized after a reevaluation of the all Triassic saurischians; a task of considerable practical difficulties, because

of the dispersion of the collections and the fragmentary nature of the remains of these lower Mesozoic dinosaurs.

The author wishes to state his appreciation to his friend and collaborator Galileo J. Scaglia, responsible for the overwhelming majority of the discoveries realized by our expeditions in Ischigualasto, and to whom went the duty of cleaning and restoring of the material. And to give thanks to the perseverance and ability of José F. Bonaparte, responsible for the organization of the final work in the locality.

Dr. Noemí V. Cattoi is offered our gratitude, for his understanding and support which facilitated our work in the Museo Argentino de Ciencias Naturales.

## 2. ANTECEDENTS

During the months of May and June 1961, Galileo J. Scaglia and José F. Bonaparte made their third visit to the Ischigualasto locality, with members of the Laboratorio de Vertebrados Fósiles of the Instituto Miguel Lillo. Along with technician Martín Vince and guide and collector Victorino Herrera, in such an opportunity these colleagues collected fairly complete and very significant specimens of undoubtedly saurischian dinosaurs, together with new remains of cynodonts, dicynodonts and rhynchosaurs.

Afterwards, in a final trip that took place in May 1962, Scaglia and Bonaparte, along with Rafael Herbst, found new localities of Triassic tetrapods coeval with those of the Ischigualasto Valley in the province of La Rioja. In one of these, Las Lajas Valley (around the Cerro Bola Valley, Villa Unión zone), Scaglia obtained a partial skeleton of a small saurischian, in proximity to which were exhumed a few remains of rhynchosaurs and the traversodontid *Exaeretodon*.

In reality, during the previous expeditions of 1959 and 1960, remains had already been discovered which attested to the presence of saurischians in the Ischigualasto Valley, associated with therapsids, rhynchosaurs, and thecodonts. These materials have still not been extracted from their matrix. In our determinations from the field and laboratory preparations, we had assigned them as pertaining to thecodonts or archosaurs *sensu lato*, proceeding with a certain skepticism on the possibility that the remains of true dinosaurs could be found in Ischigualasto. In this spirit, Bonaparte brought to light (1960) a large portion of a femur found in the Los Colorados Beds, immediately underlying the Ischigualasto Beds, which he referred to an ornithosuchid thecodont, and which he compared with two nearly complete hindlimbs (specimen No. PVL 2054 in the collection of the Instituto Miguel Lillo) produced by the typical Ischigualasto Beds. Bonaparte referred a few of these latter remains to a representative of the superfamily Ornithosuchoidea, saying that "it pertains evidently to a representative... of the order Thecodontia" (p. 183). In reality, proof of such a thing does not exist, and both the femur from Los Colorados and the two

limbs from the Ischigualasto Beds constitute remains of typical saurischian dinosaurs, referable with all probability to the same genus - the new genus *Herrerasaurus* - which is diagnosed below.

It was these discoveries realized by the 1961 expedition that convinced us of the existence of true dinosaurs in the Triassic of Ischigualasto, encouraging us to give priority to the study of other remains of previously discovered archosaurs, some of which as a result likewise pertained to this group of reptiles. Summing up the materials collected by the successive expeditions of 1959, 1960, 1961 and 1962, we counted at present the abundant remains of more or less eleven individuals, assignable to four distinct types of saurischian dinosaurs: a carnosaur of medium size, a coelurosaur the size of *Coelophysis*, a much smaller coelurosaur, and another animal the size of *Massospondylus* with entirely uncertain affinities <sup>(1)</sup>. In this work we will supply the preliminary diagnosis of three of these dinosaurs, since one of them - the much smaller coelurosaur, which was found in the Las Lajas Valley - has still not been adequately prepared at this moment. The entirety of the material will be brought to light in monographic form in the near future. This study offers great difficulties, which follow especially from the vagueness and lack of systematics in the current knowledge of Triassic saurischians, many *taxa* of which suffer from a fairly defective systematic *status*.

### 3. DIAGNOSIS, LIST OF MATERIAL, AND DISCUSSION OF NEW TAXA

#### 3.1 *HERRERASAURUS*, n. gen. <sup>(2)</sup>

DIAGNOSIS. - A carnosaur of slightly smaller size than *Gryponyx africanus*; robust, high premaxilla with three teeth; tall maxilla with eight teeth; robust, wide teeth surrounded by rounded alveoli. Antorbital fossa apparently very withdrawn from the nares. Dentary with twelve teeth; mandibular symphysis strong and taller than the rest of the alveolar ramus. Sacrum with three vertebrae. Short, tall ilium with very robust anterior spine, similar to *Plateosaurus*. Pubis almost as long as the tibia, nearly perpendicular to the vertebral axis, expanded at its distal end forming an extensive "foot" similar to that of *Antrodemus*. Ischium shorter than the pubis, similar to that of *Plateosaurus*. Gracile femur, slightly curved in the form of an S, with very clear greater trochanter and

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<sup>(1)</sup> The possibility exists that we must recognize the presence of five distinct *taxa* of saurischians in Ischigualasto, since there is also a complete tibia (PVL 2469) the size of the aforementioned carnosaur, that does not match in morphology with that of the latter. This tibia, 44 cm in length, could belong to a fifth genus entirely poorly represented.

<sup>(2)</sup> In honor of Don Victorino Herrera, settler of the Ischigualasto zone, guide and experienced collector, who was converted into an irreplaceable collaborator of the scientific undertakings developed in these pages.

very distinct, aliform fourth trochanter more proximally located, in the upper 2/5 of the bone. Humerus longer than half the femur. Robust tibia, shorter than the femur (tibia/femur index: 87). Wide astragalus without ascending process; very small calcaneum. Foot similar to that of the plateosaurids; however, as in *Ammosaurus*, the central metatarsals are more elongate (3rd Mt./femur index: 45), and lateral metatarsals are slender and elongate; the first is more than 2/3 the length of the second, and the fifth is 2/3 the length of the fourth.

TYPE SPECIES:

***Herrerasaurus ischigualastensis*, n. sp.**

(Figures 1, 2, 3 and 4A)

HOLOTYPE. - Complete series of vertebrae from the third anterior to the sacrum up to the last caudals; both ilia and ischia, nearly complete right pubis and portions of the left; nearly complete right hindlimb; left astragalus. Fossils very well preserved, without deformation, discovered by Victorino Herrera in May 1961 in the Ischigualasto Valley, a few Km. ESE of the Aguada de La Peña, in the lower beds of the Ischigualasto Beds. The specimen was prepared by Galileo J. Scaglia in the laboratories of the Instituto Miguel Lillo and the Museo Argentino de Ciencias Naturales. It was deposited in the collections of the first institution, and labeled with No. PVL 2566. <sup>(3)</sup>

HYPODIGM. - Apart from the holotype, we refer the following specimens to this species which, together with those mentioned, constitute the hypodigm:

PVL 2558. Proximal and distal portions of two femora, of two tibiae and fibulae; terminal portions of both humeri; portions of the ilium, the proximal portion of both pubes; various presacral vertebrae, some caudals; portions of the ulna and radius, portions of the metatarsals, proximal phalanges of the pes, unguis phalanx of the first manual digit; right premaxilla, both incomplete maxillae, the better part of both dentaries, articular portion of the right mandible. It is basically the remains of a skeleton disintegrated by weathering, and of which remains this collection of very significant fragments, in a very good state of preservation and without deformation. Apart from the mentioned materials, other small pieces of the tibiae and other long bones show that originally there existed the skeletons of two associated individuals. The remains were discovered by Galileo J. Scaglia in May 1961, about 3000 meters ESE of the Aguada de La Peña, Ischigualasto Valley, in the lower beds of the Ischigualasto Beds.

PVL 2045. The greater part of both femora, both tibiae and fibulae, and both hind feet, fragments of gastralia and both pubes. These remains were discovered by O. A. Reig in April 1959, about 6000 meters WNW of the Aguada de La Peña, about 200 meters to the right of the dry river bed of the Arroyo de la Pintada. They were

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<sup>(3)</sup> PVL, abbreviation characterizes the collections of the Laboratorio de Vertebrados Fósiles of the Instituto Miguel Lillo, of the Universidad de Tucumán.

found in the middle beds of the Ischigualasto Beds, and associated with both mandibular rami and loose cranial teeth from a cynodont of the genus *Exaeretodon*. About fifty meters from this specimen, and in the same beds, were exhumed the skull of a rhynchosaur and two skulls of *Exaeretodon*.

MLP <sup>(4)</sup> 61-VII-2-2. Both incomplete pelvises, articulated, in a poor state of preservation. Ischigualasto Valley, intermediate beds of the "Ischigualasto Beds". Discovered during the 1960 expedition.

PVL 2264. Incomplete left femur. Discovered by Galileo J. Scaglia in June 1960 in the Los Colorados Beds, about 3000 meters N of the Aguada de La Peña. Bone strong, flattened anteroposteriorly, recovered from hard matrix. Figured by Bonaparte (1960) as a femur from an ornithosuchid thecodont.

PROVENANCE AND AGE. - Ischigualasto Valley, department of Valle Fértil, province of San Juan, Argentina. "Ischigualasto Beds" and "Los Colorados Beds" of the "Ischigualasto-Ischichuca" Series. Upper Middle Triassic.

DIAGNOSIS. - As for the genus.

DISCUSSION. - *Herrerasaurus* can be attributed to the infraorder Carnosauria without much doubt; however it offers a fairly confusing view with regard to its closest relations. The form of the pelvis, with the pubis expanded distally to form a "foot" as in Allosauridae and Tyrannosauridae from the Jurassic and Cretaceous, is different from that of all known Triassic carnosaur. The reduced number of the teeth in the maxilla and lower jaw is another character of advanced evolution that is difficult to resolve in so ancient a carnosaur. The foot is also unusual, having metatarsal proportions recalling more those of *Ammosaurus* than those of teratosaurids and gryponychids. At the same time, in vertebral morphology, the sacrum, the form of the ilium and ischium, and the morphology of the astragalus, it has features typical of Triassic pachypodosaur. It is without doubt curious to have a megalosaur of fairly specialized characters, like this taxon, associated with cynodonts. It is a discovery that does not agree with the data collected up to now on carnosaur evolution. The phylogenetic appraisal of *Herrerasaurus* could require modifying the accepted alignment of evolutionary sequence in the megalosaurs, which would indicate, as Welles suspected (1954), a certain regularity in the progressive changes of the skeletal structure from the oldest forms at the base of the Upper Triassic to *Tyrannosaurus* of the Upper Cretaceous. *Herrerasaurus*, which in certain characters indicates having reached the evolutionary level of *Megalosaurus* and in others that of *Antrodemus*, in spite of its great

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<sup>(4)</sup> MLP, abbreviation indicates the collections of the División de Paleontología de Vertebrados of the Museo de La Plata.

antiquity and retention of primitive traits in other characters presents the possibility that from its origins the carnosaur stock had a plural differentiation, having definite lineages with distinct evolutionary rates. For now, and until we have not given up on the possibility of a direct comparison with known Triassic and Jurassic carnosaur - which would also permit deciding on the familial assignment of *Herrerasaurus* - there is no other alternative left to us than to leave the problem as it is.

### 3.2. *ISCHISAURUS*, n. gen. <sup>(5)</sup>

DIAGNOSIS. - A saurischian of moderate size, comparable to that of *Massospondylus carinatus*; premaxilla with four large, laterally compressed, backwards-inclined teeth. Gracile, slender dentary with fifteen teeth of narrow and elongate cross-section, the same as those of the maxilla; low maxilla. Relatively short cervical vertebrae without ventral keel, similar to those of *Thecodontosaurus*, the same as in the trunk. Gracile femur, lightly curved into an S, with fourth trochanter located on the upper third of the bone; gracile tibia, a little shorter than the femur (T/Fe index: 89), with laterally shortened proximal end. Short humerus, a third of the length of the femur; gracile, with prominent lateral process. Ulna with a typical olecranon. Foot similar to that of *Herrerasaurus*, the same for the astragalus; however the calcaneum is larger. Short coracoids with rounded borders, similar to those in Plateosauridae.

TYPE SPECIES:

*Ischisaurus cattoi*, <sup>(6)</sup> n. sp.

(Figure 5)

HOLOTYPE. - Left femur, both tibiae, elements of both hind feet, both humeri, fragments of forearm and forefoot, fragments of pelvis, two cervical vertebrae, various dorsal and caudal vertebrae, most of both mandibles, right premaxilla and portion of right maxilla; other cranial fragments. This specimen was found by Galileo J. Scaglia on the expedition funded by the Instituto Miguel Lillo, Museo Argentino de Ciencias Naturales, Museo de La Plata and Museo Municipal de Ciencias Naturales de Mar del Plata, carried out in 1960. It was collected about 3700 meters ESE of Aguada de La Peña, in the lower beds of the Ischigualasto Beds. Its preparation was done by Scaglia in the laboratories of the MACN <sup>(7)</sup>. It belongs to the collections of this last institution, where it was catalogued with No. 18.060 in the Colección del Departamento de Paleontología.

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<sup>(5)</sup> From *Ischi*, first part of the word Ischigualasto, and the component *Saurus*, used in the generic names of dinosaurs.

<sup>(6)</sup> I dedicate this species to Dr. Noemi V. Cattoi, in recognition of his repeated collaboration in the development of our activities in the Museo Argentino de Ciencias Naturales.

<sup>(7)</sup> MACN, abbreviation indicates the Museo Argentino de Ciencias Naturales and the collection of its Departamento de Paleontología.

HYPODIGM. - Apart from the holotype, specimen MLP 61-VIII-2-3, which includes a complete right femur, various elements of the right hind foot, both humeri, fragments of the forearm, fragments of vertebrae, coracoids, and fragments of maxilla, other cranial elements, and the mandibular rami. Found by Victorino Herrera in the same region as the holotype, about 4000 meters ESE of Aguada de La Peña. Like the holotype, found in the lower beds of the Ischigualasto Beds.

PROVENANCE AND AGE. - Ischigualasto Valley, department of Valle Fértil, province of San Juan, Argentina. "Ischigualasto Beds" of the "Ischigualasto-Ischichuca" Series. Upper Middle Triassic.

DISCUSSION. - Comparison of *Ischisaurus* with other Triassic dinosaurs does not allow us to get very clear precision on its relationships for now. In the course of our work we had suggested the hypothesis that the remains we now attribute to *Ischisaurus cattoi* represent juvenile specimens of *Herrerasaurus ischigualastensis*, or another smaller species of this same genus. This possibility was established by the great similarity existing in the forms of the femur, astragalus and metatarsals. The marked differences that exist between other skeletal elements in both forms could be attributed, under this hypothesis, to factors of age or deformation, frequent in fossils of great antiquity. However this hypothesis cannot be validated by a closer observation, since we noticed differences that cannot be attributed to the alluded factors, such as the number of teeth and their morphology, the presence of an olecranon on the ulna, the relative height of the maxilla, the relative development of the calcaneum, the form of the proximal end of the tibia, etc.

Another possibility that can be discarded is that the remains which we attribute to *Ischisaurus* could pertain to *Spondylosoma* (see Huene, 1936-1942), the genus of saurischian which was found in the approximately coeval fauna of Santa Maria, Brazil. There exists similarities in size and relative length of the cervical vertebrae with this genus. However, those of *Ischisaurus* differ from those of the Brazilian genus in the absence of a keel on the inferior border of the centrum, and in the relative positions of the zygapophyses. The humerus attributed by Huene to *Spondylosoma*, for another thing, differs essentially from that of *Ischisaurus*.

That *Ischisaurus* is not a thecodontosaurid can be demonstrated by the shape of the femur, which in the San Juan genus is more gracile, incurved and has a more elevated fourth trochanter than in the known members of the aforementioned family. At the same time, the relative size of the forelimb, with the humerus alone half the length of the femur, and the particular possession of an ulna with a typical olecranon (exceptional for a saurischian), coincide to exclude *Ischisaurus* from the Thecodontosauridae. This last character has been confirmed in the ulnae of the known individuals, because its presence in this form excludes all doubt. Comparison with other families does not allow obtaining more positive results. The proportions between the femur, tibia and

metatarsals match those of certain Triassic pachypodosaur, and not those of coelurosaur. Nevertheless, the foot retains certain affinities with that of *Ammosaurus* (see Huene, 1906; Lull, 1915); however, *Ischisaurus* differs from this genus in having the tibia shorter than the femur, by the marked character of the olecranon, and in various other traits. The form of the femur, and above all the proportions between the humerus and femur, also suggest looking for its relations among the coelurosaur. Perhaps we are in the presence of a primitive form which includes primitive characters of pachypodosaur and coelurosaur, and which represents a moment in saurischian evolution in which both groups had not entirely differentiated. However any conclusion on the relationships and significance of *Ischisaurus* is entirely premature; clarification will require new materials and direct comparisons.

### 3.3. *TRIASSOLESTES*, <sup>8)</sup> n. gen.

DIAGNOSIS. - A podokesaurid the size of *Coelophysis longicollis*, with large, rounded orbit; antorbital fossa very large, tall, twice the diameter of the orbit, with rounded anterior border; maxilla with convex alveolar border, with fifteen teeth of unequal size, the anterior ones larger; maxilla elongate behind the tooth row in a slender expansion that reaches the level of the posterior border of the orbit. Very slender mandible, low dentary, with its superior border concave and its inferior convex, with twelve teeth of unequal size, of which the first third are the largest and have a caniniform aspect. Teeth sharp, long, laterally compressed, recurved. Foot gracile, with the three central metatarsals elongate and the first and fifth metatarsals present, the first functional, however narrow and much less than the second metatarsal; astragalus of rectangular shape without heel; cervical vertebrae long, narrow, a little shorter than those of *Coelophysis*; pubis similar to that of the latter genus.

TYPE SPECIES:

*Triassolestes romeri*, <sup>9)</sup> n. sp.

(Figures 4B and 6)

HOLOTYPE. - Incomplete skull with mandibles, laterally flattened, associated with four fairly complete cervical vertebrae, the centrum of another cervical and a collection of twelve vertebral centra, apparently all caudal vertebrae. This specimen was discovered by Galileo J. Scaglia in May of 1961, about 4200 meters ESE of Aguada de La Peña, in the lower beds of the Ischigualasto Beds. In its proximity was encountered, in the same beds, various specimens of rhynchosaurs and cynodonts. The remains were closely associated with a scapula, humerus,

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<sup>8)</sup> *Triasso-*, in allusion to the Triassic age of the genus, and *-lestes*, from the Greek ληστης, thief, robber, in allusion to its probable carnivorous habits.

<sup>9)</sup> I dedicate this species to Dr. Alfred Sherwood Romer, notable investigator of lower tetrapods and leader of the first great expedition to the Ischigualasto locality from Harvard University and the Museo Argentino de Ciencias Naturales, from May-June of 1958.

ulna, radius, basipodium, and the proximal end of a metapodial. Before its cleaning, we supposed that these last remains pertained to the same individual; however afterwards we noticed that the forelimb pertained to a typical crocodile, with the carpal structure characteristic of the order. These remains, associated with the skull and vertebrae of *Triassolestes*, confirm the presence of crocodiles in the Ischigualasto locality, advanced by me through the assignment of the genus *Proterochampsa* to this order (Reig, 1959). It is very probable that the forelimb could be referable to this same crocodile. It is deposited in the collection of the Instituto Miguel Lillo, where it is figured with No. PVL 2561.

**HYPODIGM.** - The holotype specimen and PVL 2559: right third metatarsal and portions of the first, second and fourth; various phalanges, right astragalus, centrum of a posterior trunk vertebra, proximal portion of the fibula and other fragments. This specimen was found by Galileo J. Scaglia in May 1961, about 3500 meters ESE of Aguada de La Peña, in the middle third of the "Ischigualasto Beds".

**PROVENANCE AND AGE.** - Ischigualasto Valley, department of Valle Fértil, province of San Juan, Argentina. "Ischigualasto Beds" of the "Ischigualasto-Ischichuca" Series. Upper Middle Triassic.

**DIAGNOSIS.** - As for the genus.

**DISCUSSION.** - The attribution of this coelurosaur to the family Podokesauridae seems to rely on the greatest number of probabilities, above all, on the nearness it presents with the genus *Coelophysis* <sup>(10)</sup>. The general morphology of the skull, with a large orbit and a very elongate antorbital fossa; the elongation of the maxilla underneath the level of the orbit, and the morphology of the known remains of the hindlimb, certainly indicate this proximity. The anterior end of the pubis also matches that of *Coelophysis* (see Colbert & Baird, 1958). Without reservation, we must admit that the definition of the family Podokesauridae and its contents are somewhat vague, since all the families of Triassic coelurosaurs are also placed in a vague grouping. And so it requires entirely revising them in order to be able to specify with more security the familial assignment of *Triassolestes*; which does not mean that excessive doubts are justified about its pertaining to a group of coelurosaurs, and that among these it represents an animal as advanced as those assigned to the family Podokesauridae, known until now only from the Upper Triassic.

#### 4. THE AGE OF THE ISCHIGUALASTO FAUNA

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<sup>(10)</sup> The comparison with *Coelophysis* was made enormously easy thanks to the kindness of Dr. Colbert, who sent us excellent photographs of extraordinary specimens, some not described, of this genus discovered in New Mexico (see sites in Colbert, 1947).

The age of the Ischigualasto Beds of the "Ischigualasto-Ischichuca" Series have been the object of differing opinions. Stelzner (1885) considered that the entire Series (from which today we denominate the Ischichuca Beds at the base, up to the Los Colorados Beds, before the Gualo Beds at the top) corresponded to the Rhaetian, while Bodenbender (1911) judged the Los Rastros Beds (below the Ischigualasto Beds) to be this age, attributed the Ischigualasto to the Jurassic, and those we now distinguish as Los Colorados Beds to the "Andean Upper Cretaceous". Freguelli (1948), to whom we owe the current stratigraphic scheme of the Series, restricted his "Gualo Beds" (= Los Colorados Beds) to the Rhaetian, and attributed to the Keuperian age the Los Rastros Beds (lower Keuper) and the Ischigualasto (upper Keuper). Maintaining the Los Colorados in the Rhaetian with a certain hesitation, Groeber & Stipanovic (1952) homologized some of the Los Rastros, such as the Ischigualasto, with the upper "Norian"; that is, with the uppermost part of the Keuper.

All these datings are based on the requirements of the regional geology - that is, they have the character of generalizations of the second grade - or on the paleophytological contents of the formations. Dr. Archangelsky insisted to me recently (pers. comm.) that the remains of plant fossils do not constitute, to the current state of our understanding, an important aid for fixing correlations within the Argentine Triassic; of such a manner that paleobotanists are seen to obtain the precise conclusions of vertebrate paleontologists, to try to arrange a geochronological scheme of our Triassic. In this sense, and in that which we refer to the Ischigualasto Beds, it is worthwhile to record the brief notes made by Romer (1962: 5): "The vertebrate remains suggest a lower position, although full discussion should be postponed until the fauna has been more thoroughly studied".

In a previous work, Romer (1960a: 1291) pointed out the following: "These beds (the Ischigualasto beds) appear to be definitely pre-Norian and probably pre-Carnian, for dinosaurs are absent, and flourishing reptile groups are cynodonts and rhynchosaurs - groups that flourished in the Middle Triassic and are almost entirely unknown in beds in the northern continents equated with the Carnian or later Triassic stages". In the 1962 article this author completed the same argument thus (page 5): "The Norian stage is one in which is found the typical Upper Triassic dinosaurian fauna; the Ischigualasto is, on the contrary, one in which there is little evidence of dinosaurs, and in which gomphodont-cynodonts and rhynchosaurs are dominant. The Ischigualasto formation is essentially comparable to the Santa Maria beds of Brazil and the Manda beds of Tanganyika. It is surely pre-Norian and not improbably pre-Carnian; the gomphodont-rhynchosaur faunas would appear to be essentially Middle Triassic in age".

With the confirmation of the existence of an entire list of dinosaurs in the Ischigualasto fauna, one may think that the plan of Romer has been harmed. And especially we add to this fact

the verification of the existence of aetosaurid thecodonts (Casamiquela, 1960; Reig, 1961) and true crocodiles (Reig, 1959 and the present article) in the same fauna. The Aetosauridae (see last revision of Walker, 1961) have been found up to now only in the Keuper of the Northern Hemisphere, and the more ancient crocodiles that were known before the discovery of *Proterochampsia* have been found in the uppermost Triassic of South Africa and North America.

However, there remains standing a fundamental fact: the dominant element of the Ischigualasto fauna is constituted - a fact very well noted by Romer - by gomphodont cynodonts (Traversodontidae) and rhynchosaurs, and this association is not known in any Upper Triassic fauna in the world apart from the Ischigualasto Beds, excluding the Santa Maria Formation (Brazil) and the "Manda Beds" of Tanganyika. The affinity between these three faunas is also extended by the fact that in them are encountered representatives of the thecodont family Raulisuchidae (see Reig, 1959, 1961). And both the fauna from Brazil and the one from Tanganyika are considered typical Middle Triassic faunas; a conclusion that seems validated by the recent discovery of a traversodontid in the Capas de Molteno, which occupies an intermediate position between the Capas with *Cynognathus* (upper Eotriassic) and the "Red Beds" of the Stormberg Series (lower Neotriassic) (see Crompton & Ellenberger, 1957) in the classic South African Karroo Sequence.

We believe, then, that the Ischigualasto fauna is somewhat paradoxical in uniting elements of typical Middle Triassic facies with other, less preponderant, elements that characterize the Neotriassic. If not for the fact that these distinct elements are found in the same beds and are frequently associated, it could be thought that we are in the presence of two faunas: one older and one more modern. However this suspicion can be completely discarded by the repeated verification of the marked conditions of the discoveries. To the best of our knowledge, these facts can only be explained by admitting that the Ischigualasto fauna represents a more modern age than that of the Brazilian and Tanganyikan faunas; however, at the same time, it is older than oldest known Keuper faunas.

In reality, when we speak of the Middle Triassic, it must be noted that we are referring to an epoch that lasted many millions of years, during which it had to have produced significant changes in the terrestrial vertebrate faunas. This possibly great duration of the Middle Triassic can be seen as confirmed by the following facts: the lower beds of the Capas de Molteno furnish remains of a therapsid (*Cynidiognathus longipes*) equal to one of the *Cynognathus* biozone (see Boonstra, 1947), while the upper beds of the same Capas produce a traversodontid (*Scalenodontoides macrodontes*) more advanced than those of Tanganyika or Brazil. It is very possible that the formations which we have mentioned from these two latter countries represent lower or middle beds of the Middle Triassic, upper Anisian or lower Ladinian, while the "Ischigualasto Beds" and the "Upper Molteno Beds" represent upper Ladinian; that is, the highest Middle Triassic.

On the greater youth of the Ischigualasto Beds with respect to the "Manda Beds" and the Santa María Formation within the Middle Triassic, other facts also speak in favor of this. The traversodontids of Ischigualasto (*Exaeretodon* and other entirely undescribed genera) are of a more advanced type than those of the other two faunas (see Bonaparte, 1962); and the same can be verified with raiisuchid thecodonts (Reig, 1961). Within the character of probable approximations that these generalizations can have, perhaps entirely premature since we have noted the fragmentary nature of the knowledge on the Triassic faunas of the world, the conclusion closest to the truth seems to be that a highest Middle Triassic age be recognized for the Ischigualasto fauna. And this requires us to admit the necessity of carrying back the biochron of saurischian dinosaurs, aetosaurid thecodonts and crocodiles to an older epoch within the Triassic, which will be generally admitted.

## 5. CONCLUSIONS

The fauna of the Ischigualasto Beds, whose dominant elements are constituted by the association of gomphodont cynodonts (family Traversodontidae) and rhynchosaurs, and in which dicynodonts and raiisuchid thecodonts also abound, also includes saurischian dinosaurs of a distinct type, and other elements characteristic of the Upper Triassic such as aetosaurid thecodonts and crocodiles. In this the association of dinosaurs with cynodonts can be verified without objection for the first time.

The remains of about eleven individuals of saurischian dinosaurs are recognized, which correspond to at least four distinct genera, both in the type locality of the Ischigualasto Beds (Ischigualasto Valley) and in the new locality of Las Lajas Valley (Villa Unión zone, province of La Rioja), recently discovered by Scaglia, Bonaparte and Herbst. At the same time, the presence of a saurischian in the "Los Colorados Beds" of the Ischigualasto Valley has been confirmed, on the basis of remains previously attributed by Bonaparte to an ornithosuchid thecodont.

One of these four dinosaurs represents a small coelurosaur from the Las Lajas Valley, which has not been entirely prepared and which is not described here. Of the other three, one (*Triassoolestes romeri*, n. gen., n. sp.) is a typical coelurosaur assignable to the family Podokesauridae and near enough to *Coelophysis*; the second (*Ischisaurus cattoi*, n. gen., n. sp.) is an animal the size of *Massospondylus carinatus* and of doubtful affinities, which has some characters of a coelurosaur and others of a pachypodosaur; the third (*Herrerasaurus ischigualastensis*, n. gen., n. sp.) is a typical carnosaur the size of *Gryponyx africanus*, except that in certain characters it shows a level of evolution apparently more advanced than that of other known Triassic carnosaurs.

The presence of elements from Neotriassic facies in the Ischigualasto fauna (saurischians, aetosaurids and crocodiles), together with the typical Middle Triassic association of cynodonts and rhynchosaurs, creates the problem of the age and correlation of this fauna. It is supported that it is somewhat more modern than the typical Middle Triassic faunas of Santa María (Brazil) and Tanganyika, which are tentatively assigned in this work to the upper Anisian or lower Ladinian. The fauna of the Ischigualasto Beds then represents the highest Middle Triassic, equivalent to the upper Ladinian and probably to the "Upper Molteno Beds" of South Africa.

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## FIGURE CAPTIONS

**Figure 1.** Large part of the right dentary of *Herrerasaurus ischigualastensis*, n. gen., n. sp. Specimen No. PVL 2558. - A: Internal view; B: Superior view; C: External view (x 2/3). - Reig-Pérsico *del.*

**Figure 2.** Right lateral view of the ilium, pubis, and ischium of *Herrerasaurus ischigualastensis*, n. gen., n. sp. Holotype, No. PVL 2566 (x 1/4). - Reig-Pérsico *del.*

**Figure 3.** *Herrerasaurus ischigualastensis*, n. gen., n. sp. Holotype specimen, No. PVL 2566. A: Posterior view, right femur. B: Posterior view of right tibia, fibula, astragalus, and calcaneum. C: Lateral internal view of right tibia and astragalus. D: Anterior view of right femur. (All figures, x 1/4). - Reig-Pérsico *del.*

**Figure 4.** A: Right foot (partially reconstructed) of *Herrerasaurus ischigualastensis*, n. gen., n. sp. Holotype, No. PVL 2566. Antero-dorsal view. - B: Right foot (reconstructed) of *Triassolestes romeri*, n. gen., n. sp., No. PVL 2559. Antero-dorsal view. (Both figures, reduced according to scale). - Reig-Pérsico *del.*

**Figure 5.** *Ischisaurus cattoi*, n. gen., n. sp. Femur and humerus of the holotype specimen. No. MACN 18.060. - A: Left femur, external lateral view. B: Left humerus, posterior view. C: Left femur, posterior view. (All figures, x 1/3). - Reig-Pérsico *del.*

**Figure 6.** Right lateral view of skull and mandible (partially reconstructed) of *Triassolestes romeri*, n. gen., n. sp., No. PVL 2561 (x 1/2).. - Reig-Pérsico *del.*

TABLE I

Principle measurements of selected elements of the postcranial skeleton of *Herrerasaurus ischigualastensis*, *Ischisaurus cattoi*, and *Triassoolestes romeri*. All measurements are given in centimeters (*a*, approximate; *c*, calculated; *i*, left; *d*, right).

TAXON	HERRERASAURUS			ISCHISAURUS		TRIASSOLESTES
	ISCHIGUALASTENSIS			CATTOI		ROMERI
SPECIMEN NO.	PVL	PVL	PVL	MACN	MLP	PVL
MAGNITUDES	2566	2054	2558	18.060	61-VII-2-3	2559
Total femur length	47.3	<i>a</i> 38.5	<i>c</i> 44.0	28.6	33.5	—
Maximum distal femur diameter	9.7	<i>a</i> 7.2	8.0	5.0	6.5	—
Total tibia length	41.1	32.7	—	28.0	—	—
Maximum proximal tibia diameter	12.5	—	10.0	5.9	—	—
Total 3rd metatarsal length	22.3	17.6	—	<i>c</i> 13.4	<i>a</i> 15.6	12.3
Max. distal diameter 3rd metatarsal	4.9	—	—	<i>c</i> 2.1	—	1.7
Max. (transverse) diameter astragalus	<i>d</i> 8.0	—	—	4.3	—	3.1
Anteroposterior astragalus diameter	<i>d</i> 5.7	—	—	3.0	—	2.2
Ilium A/P diameter on iliac spine	23.8	—	—	—	—	—
Ilium height on iliac spine	<i>a</i> 18.0	—	—	—	—	—
Maximum pubis length	40.9	—	—	—	—	<i>a</i> 28.0
Maximum A/P diameter of distal end of pubis	19.0	—	—	—	—	3.2
Maximum ischium length	33.0	—	—	—	—	—
Total humerus length	—	—	<i>c</i> 25.0	19.7	—	—
Transverse diam proximal end humerus	—	—	7.7	4.3	—	—
Centrum length of a mid-cervical vertebra	—	—	—	3.6	—	4.7
Centrum length of an anterior trunk vertebra	—	—	4.3	2.7	—	—
Centrum length of a posterior trunk vertebra	4.7	—	4.5	—	—	—
Centrum length of second sacral vertebra	5.7	—	—	—	—	<i>a</i> 5.1

TABLE II

Principle measurements of skull and mandibles of *Herrerasaurus ischigualastensis*, *Ischisaurus cattoi*, and *Triasolestes romeri*. All measurements are given in centimeters (*a*, approximate).

TAXON	HERRERASAURUS ISCHIGUALASTENSIS	TRIASOLESTES ROMERI	ISCHISAURUS CATTOI
SPECIMEN NO.	PVL 2054	PVL 2561	MACN 18.060
MAGNITUDES			
Total skull length (calculated)	29.0 ± 2.0	22.0 ± 1.0	25.0 ± 1.0
Antorbital fossa length	—	8.0	—
Skull height at level of anterior border of orbit (calculated)	—	6.9	—
Height of orbit (calculated)	—	4.7	—
Anteroposterior orbit diameter	—	<i>a</i> 4.7	—
Total mandible length (calculated)	30.0 ± 1.0	22.5 ± 1.0	25.5 ± 1.0
Space occupied by maxillary teeth	11.7	9.8	—
Space occupied by mandibular teeth	13.9	7.3	<i>a</i> 10.8
Dentary height at symphysis	3.9	1.6	2.3
Minimum dentary height	3.2	1.4	1.9
Maximum mandibular height at level of mandibular fenestra	—	4.1	—
Anteroposterior diameter of third mandibular tooth	1.5	0.7	0.5
Transverse diameter of third mandibular tooth	1.3	0.35	—
Anteroposterior diameter of fourth mandibular tooth	1.0	—	0.3
Transverse diameter of fourth mandibular tooth	0.7	—	—