

A PROBABLE THEROPOD (SAURISCHIA) FROM THE ISCHIGUALASTO FORMATION (UPPER TRIASSIC), SAN JUAN, ARGENTINA*

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ABSTRACT

Frenguellisaurus ischigualastensis n. gen., n. sp. is a medium-sized carnivorous archosaur from the Ischigualasto Fm., characterized by a short and tall maxilla with a convex ventral margin, supplied with three robust "canines", and distal caudal vertebrae with elongated prezygapophyses that overlap the posterior half of the preceding vertebra. These and other characters permit differentiating it from known families of thecodonts. Caudals with such elongated prezygapophyses have not been recorded in thecodonts and quadrupedal saurischians, but have in various theropod saurischians (obligatorily bipedal cursors). Assuming that this vertebral pattern is related to advances in the locomotor apparatus, *Frenguellisaurus* is considered to be a dinosaur of the suborder Theropoda. *Frenguellisaurus* and *Herrerasaurus* are considered representatives of the oldest radiation of medium-sized carnivorous bipedal archosaurs.

INTRODUCTION

In the course of an exploratory paleontological trip undertaken in 1975 to the Hoyada de Ischigualasto, San Juan prov., remains of a new archosaur were encountered in layers of the Ischigualasto Fm. The discovery was made by Messrs. Gargiulo and Oñate from the Museo de Ciencias Naturales de San Juan.

Knowledge of the oldest saurischians was restricted to only three incompletely known genera, *Staurikosaurus*, *Herrerasaurus* and *Ischisaurus*, from the upper Middle Triassic to lower Upper Triassic of South America. The new discovery improves the knowledge of the adaptive types developed in the

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early stages of saurischian evolution. The anatomical characteristics of these dinosaurs, which were difficult to locate satisfactorily within the saurischian groups of the latter time, suggest that they represent archaic lineages, close to the first stages of the evolution of the group.

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ABBREVIATIONS USED

MACN: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”.
PVL: Paleontología de Vertebrados Instituto “Miguel Lillo”.
PV-UNSJ: Paleontología de Vertebrados – Universidad Nacional de San Juan.

SYSTEMATICS

Frenquellisaurus gen. nov.

Etymology

In honor of Dr. Joaquín Frenquelli, who realized an important paleontological and geological work in the Triassic Ischigualasto-Villa Unión Valley.

Type species

Frenquellisaurus ischigualastensis sp. nov.

Distribution

Lower section (close to the Middle Triassic) of the Ischigualasto Fm. Ischigualastian Reptile Age, principally of the Upper Triassic, San Juan, Argentina.

Diagnosis

Medium-sized carnivorous dinosaur, with low and long skull (56 cm); maxilla distinct from those of Ornithosuchidae and Rauisuchidae, and comparable to that of *Dilophosaurus* in its anterior section with convex ventral margin, provided with strong “canines”; below the antorbital fenestra the maxilla is lower than in this genus. Antorbital fenestra smaller and with a wider anterior

section than in *Dilophosaurus* and the representatives of the families cited. Tall jugal, with ventral border more inclined posteriorly and ventrally, such that the maxilla and jugal form a pronounced sinuosity, greater than in *Dilophosaurus*. Short dentary, representing half the length of the mandible. Specialized posterior caudal vertebrae, similar to those of *Allosaurus*, with longer prezygapophyses that surpass the posterior half of the centrum of the preceding vertebra. The prezygapophyses are reinforced laterally by a thick edge; on the lateral face of the centrum and the base of the neural arch exist horizontal “crests” and “prominences” for muscular insertions.

Frenguellisaurus ischigualastensis sp. nov.

Etymology

Ischigualastensis, from Ischigualasto, locality where the described material was discovered.

Holotype

PV-UNSJ 53. Most of a skull including the right premaxilla, both maxillae, left jugal, and temporal, occipital and basicranial regions; both mandibular rami; axis, part of one anterior cervical and twenty-five distal caudals.

Stratigraphic and geographic provenance

Lower section (close to the Middle Triassic) of the Ischigualasto Fm., left bank of the La Chilca River, about 12 km before the Puerta de La Chilca, NW sector of the Hoyada de Ischigualasto, Valle Fértil dept., San Juan prov.

Diagnosis.

The same as for the genus.

DESCRIPTION

Skull

The skull, somewhat incomplete, preserves elements of sufficient diagnostic value to allow its reconstruction. The temporal region shows lateral flattening and breakage that do not greatly alter the proportions and morphology of its constituent bones.

The skull is long and low, 56 cm long. The premaxilla, mostly broken, is robust and has an ascending ramus to contact the extensive and laterally compressed maxilla. The maxilla has a tall, wide anterior sector whose ventral margin is strongly convex; in this region the interdental plates reach their greatest size; these characters correspond to the presence of three large “canines”, laterally compressed and with serrated edges; the estimated length of the largest of these would be 6 cm. Below the antorbital fenestra the maxilla is low; somewhat in lateral view the maxilla ends at the height of the lacrimal, medially it reaches further posteriorly, ending below the orbit. A recess of poorly defined

contours precedes the antorbital fenestra. This latter is proportionally short axially and has a widely concave anterior margin, bordered anteriorly and ventrally by a slight antorbital fossa.

The jugal is slender and tall, such that the orbital fenestra occupies an elevated position relative to the infratemporal fenestra. The inferior margin of the maxilla and jugal is markedly sinuous.

The parietal crest is relatively long. The supra- and infratemporal fenestrae are extended axially. The squamosal shows a ventral ramus not totally preserved but with indications that it had a certain anteroventral projection. The quadrate is long and has a mobile articulation with the squamosal; the posterior face has the quadrate foramen.

The mandible is tall relative to the skull. The dentary, very laterally compressed, represents half the length of the mandible. The splenial exceeds the posterior end of the dentary ventrally in both hemimandibles. The glenoid cavity is deep and transversely extensive. The retroarticular process is tall, wide and short anteroposteriorly.

The occiput is exposed posterodorsally and presents a triangular contour. The occipital condyle is subspherical, and the paroccipital processes are very long and have expanded distal ends.

Vertebrae

The axis, an anterior cervical in a bad state of preservation, and 25 distal caudal vertebrae are available.

The axis has a centrum longer than tall, provided with a ventral keel; the odontoid process is large. The neural spine, axially extensive, increases its height and thickness posteriorly. A deep basin affects the posterior part of the neural spine.

The anterior cervical is incomplete, but indicates that it is a vertebra with a tall neural arch and a centrum relatively low and somewhat elongated.

The preserved caudal vertebrae possibly correspond to the interval between caudals 14 and 51. In all of them the centrum is longer than tall, and except the most distal ones, the vertebral centrum presents its middle part very constricted and its ends bulky. There are marked structures related to tendinous insertions, consisting of longitudinal "prominences" and "crests" developed on the lateral face of the vertebral centrum and the base of the neural arch. The prezygapophyses, crossed laterally by a conspicuous rim, experience a notable elongation in the distal half of the tail; in caudals 28? to 35? they overlap the posterior half of the preceding vertebra, and in the last caudals (44? to 51?) they come to surpass the posterior two-thirds of the preceding vertebra.

COMPARISONS

The comparisons of the skull will be restricted to thecodonts of medium to large size with representatives in the Ischigualasto Fm. (Rauisuchidae and Ornithosuchidae), pseudosuchians considered ancestral to dinosaurs

(Euparkeriidae and Lagosuchidae), and some carnivorous saurischians. Then comparisons are made of the caudal vertebrae with thecodonts and saurischians in general.

Rauisuchidae

Thecodonts of quadrupedal and plantigrade habit, that include the largest carnivores of the Middle and Upper Triassic (Bonaparte, 1984). In the Ischigualasto Fm. they are represented by *Saurosuchus galilei* (Sill, 1974), whose skull has an approximate length of 70 cm. Different from *Frenquellisaurus*, the rausuchids possess: tall maxilla, antorbital fenestra with low anterior margin, jugal low (*Saurosuchus*, *Heptasuchus*, *Luperosuchus*) or relatively low (*Prestosuchus*); ventral margin of the maxilla and jugal rectilinear or somewhat sinuous, but not as markedly so as in *Frenquellisaurus*. In none of the rausuchids is there a recess anterior to the antorbital fenestra. The dentary is longer than the postdentary elements. The retroarticular process is very robust, clearly individualized and moved away from the glenoid cavity.

Ornithosuchidae

A family represented by the genera *Venaticosuchus* (Ischigualasto Fm.; Bonaparte, 1975a), *Ornithosuchus* ("Lossiemouth Beds", Scotland; Walker, 1964) and *Riojasuchus* (Los Colorados Fm., La Rioja, Argentina; Bonaparte, 1975a). They are clearly different from *Frenquellisaurus* in the following features: maxilla with rectilinear or slightly convex inferior margin, continuous with that of the jugal; jugal without ventral expansion; dentary robust and long (*Ornithosuchus*) or short and with a concave ventral margin (*Venaticosuchus*, *Riojasuchus*); retroarticular process very tall (*Ornithosuchus*) or very low and small (*Venaticosuchus*, *Riojasuchus*).

Euparkeriidae

Thecodonts of small size from the Lower Triassic (Ewer, 1965). Different from *Frenquellisaurus* in possessing a long maxilla of rectangular shape and with a rectilinear ventral margin; the anterior ascending process of the maxilla is axially short. The jugal is low. The mandible has a low and long retroarticular process.

Lagosuchidae

Thecodonts of small size from the Middle Triassic of Argentina. Only the basicranium and maxilla are known from the skull of *Lagosuchus* (Bonaparte, 1975b). This latter is long, styliform below the antorbital fenestra, and has a rectilinear ventral margin. The teeth do not show a marked size disparity.

Herrerasauridae

Carnivorous saurischians that include the genera *Herrerasaurus* and *Ischisaurus* (both from the Ischigualasto Fm.; Reig, 1963) and, eventually, *Staurikosaurus* (Colbert, 1970; Galton, 1977) from the Santa María Fm. (Zone associated with Rhynchocephalia), Brazil.

Only the two mandibular rami are known from the skull of *Staurikosaurus*, both affected by deformation. It differs from *Frenguellisaurus* in the morphology of the articular region, with the internal laminar process in a more posterior position, continuous with the posteroventral end of the mandible.

The holotype material of *Ischisaurus* (MACN 18.060) includes dentaries, splenials and articular regions. In both mandibular rami the splenial is exposed ventrolaterally, as in *Frenguellisaurus*. The articular region has a laminar projection directed posterodorsally that limits the glenoid cavity. This notable specialization allows *Ischisaurus* to be differentiated not only from *Frenguellisaurus* but also from the rest of the dinosaurs.

Reig (1963, figure 1) illustrated a dentary that he attributed to the genus *Herrerasaurus*. This specimen (PVL 2558) includes portions of the femur and tibia that are assignable to Herrerasauridae, and posterior dorsal vertebrae and a pubis that decidedly do not pertain to the genus *Herrerasaurus*. It is evident that this specimen unites pieces of two (or more) individuals corresponding to distinct taxa. Faced with the impossibility of deciding to which of these the cranial material pertains, it is not considered representative of the genus *Herrerasaurus*.

Upper Triassic–Lower Jurassic Theropods

Dilophosaurus, from the Kayenta Fm. (Upper Triassic–Lower Jurassic) of the U.S.A., has a skull of comparable size and shape to that of *Frenguellisaurus*. Different from the latter, it has an antorbital fenestra extended in its ventral section, with a low anterior margin, not preceded by a recess; an anteroposteriorly shorter infratemporal fenestra; a mandible with a longer dentary and comparatively small medial laminar process.

Syntarsus (Forest Sandstone, Zimbabwe), *Coelophysis* (Chinle Fm., U.S.A.), *Liliensternus* (Knollenmergel, Germany; Welles, 1984), *Procompsognathus* (Stubensandstein, Germany), all from the Upper Triassic, present marked differences with *Frenguellisaurus* in the morphology and proportions of the skull, making any comparison unnecessary.

With respect to the caudal vertebrae, it must be decided that there are few genera of thecodonts where the distal caudals are known. Among those are counted *Ticinosuchus* (Krebs, 1965), *Postosuchus* (Chatterjee, 1985) and *Lagosuchus*, which lack elongated prezygapophyses as in *Frenguellisaurus*. Better documented is the morphology of the distal caudals in dinosaurs. Among these, caudal vertebrae with very long prezygapophyses are frequent and almost exclusive to the suborder Theropoda. Specimens of this are *Staurikosaurus*, *Ischisaurus*, *Ornitholestes*, *Allosaurus*, tyrannosaurs, ornithomimids (Osborn, 1917), *Deinonychus*, etc. Nevertheless, some representatives of the group do not have such a specialization, as for example *Compsognathus* and *Dilophosaurus*. Structures for tendinous insertions similar to those observable in *Frenguellisaurus* are shown particularly in *Allosaurus* (Madsen, 1976, pl. 34).

The previous comparisons allow differentiating *Frenguellisaurus* from the known families and genera of thecodonts and dinosaurs. I now intend to establish to which of these archosaur orders it pertains.

Recently, Paul (1984) intended to distinguish the characters of thecodonts and dinosaurs. For the majority of thecodonts the following characters were found in the skull: 1) jugal robust, tetra-radiate; 2) lacrimal short and wide; 3) quadrate inclined backward and down; 4) maxilla tall and rectangular. *Frenguellisaurus* presents characters 1), 3) and presumably 2). Following this author, primitive theropods, prosauropods and generalized ornithischians have the following characters that distinguish them from thecodonts: 1) skull with long and low profile; 2) quadrate tall and vertical; 3) jugal small, tri-radiate; 4) maxilla low and triangular; 5) lacrimal wide. The skull of *Frenguellisaurus* would be found, therefore, closer to the thecodont parentage than that of the dinosaurs.

The anatomy of the caudal end of *Frenguellisaurus*, similar to that of advanced theropods, thus as the absence of this morphological type in thecodonts and other quadrupedal dinosaurs suggests, on the contrary, greater affinities with the former.

In summary: some of the cranial morphology of *Frenguellisaurus* recalls in certain aspects the thecodont parentage, the morpho-functional advances of the dinosaur grade that the tail implies, it is included among the latter group. Since the dinosaurs on which Paul (op. cit.) based his study are from the Upper Triassic, it is probable that in more archaic forms, from the Ischigualastian age (close to the thecodont condition), the skull maintained primitive characters like those observed in *Frenguellisaurus*.

From the functional point of view, caudal vertebrae with long prezygapophyses seem to hold a narrow relationship with bipedalism and cursoriality (nevertheless, bipedal progression does not necessarily imply the development of such structures). Thus to suggest the fact to be so spread out among theropods (of those that are not doubted, were obligatory bipeds, the majority cursorial) and in addition to not be recorded in thecodonts and other quadrupedal dinosaurs. The elongated prezygapophyses restrict the possibilities for lateral flexion at the caudal end, in the manner that the same act as a single body, composing the moments of inertia of each vertebral segment into a single one (Ostrom, 1969). The tail functioned as a dynamic stabilizer during running, when the animal achieved rapid and irregular movements.

CONCLUSIONS

Although *Frenguellisaurus* possesses a skull with primitive characters for a saurischian, the morphology of the maxilla, jugal, dentary and the presence of large "canines" constitute derived characters compared to those of thecodonts and dinosaurs, suggesting a more specialized mechanism of the buccal apparatus for the capture of prey.

The presence of distal caudals with elongated prezygapophyses in *Frenguellisaurus* and *Staurikosaurus* permits affirming that this character, related to bipedal locomotion, had developed early in saurischians eventually not directly ancestral with typical theropods from the Triassic.

The existing fossil record permits considering *Frenguellisaurus* and *Herrerasaurus* as representatives of the oldest radiation of medium-sized, carnivorous, bipedal archosaurs (approximate total length: 4m), occurred at the beginning of the Upper Triassic (Ischigualastian). The rapid increase in body size and the reinforcement of adaptations related to locomotion, permitted the members of the Lagosuchidae-*Staurikosaurus-Herrerasaurus* lineage to participate in trophic levels each time higher in the course of the Triassic, than in the Ischigualastian had been occupied only by raiusuchid thecodonts.

The radiation of these primitive carnivorous saurischians precedes that of typical Upper Triassic theropods (Coelophysidae, Procompsognathidae, Halticosauridae) provided with major advances in the locomotor apparatus (dolichoiliac ilium, major tibia-astragalus connection, tridactyly).

BIBLIOGRAPHY

- BARBERENA, M. 1978. A huge thecodont skull from the Triassic of Brazil. *Pesquisas*, 9:62-75.
- BONAPARTE, J. F. 1975a. The family Ornithosuchidae. *Coll. Intern. CNRS*, 218:485-502.
- , 1975b. Nuevos materiales de *Lagosuchus talampayensis* Romer...—*Acta Geol. Lilloana*, 13, 1:5-90.
- , 1984. Locomotion in raiusuchid thecodonts. *Journ. Vert. Pal.*, 3(4):210-218.
- CHATTERJEE, S. 1985. *Postosuchus*, a new thecodontian reptile...—*Phil. Trans. R. Soc. London*, (B) 309:395-460.
- COLBERT, E. H. 1970. A saurischian dinosaur from the Triassic of Brazil. *Amer. Mus. Novit.*, 2405:1-39.
- EWER, R. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. *Phil. Trans. R. Soc. London*, (B) 248:379-435.
- GALTON, P. 1977. On *Staurikosaurus pricei*, an early saurischian dinosaur...—*Palaeont. Z.*, 51(3/4):234-245.
- KREBS, B. 1965. *Ticinosuchus ferox* nov. gen., nov. sp. Ein neuer Pseudosuchier...—*Palaont. Abh.*, 81:1-140.
- MADSEN, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geol. Min. Survey Bull.*, 109:1-163.
- OSBORN, H. F. 1917. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, and *Tyrannosaurus*...—*Bull. Amer. Mus. Nat. Hist.*, 35:753-771.
- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod...—*Bull. Peabody Mus. Nat. Hist.*, 30:1-165.
- PAUL, G. S. 1984. The segnosaurian dinosaurs...—*Journ. Vert. Pal.*, 4(4):507-515.
- REIG, O. A. 1963. La presencia de dinosaurios...—*Ameghiniana*, 3(1):3-20.
- SILL, W. D. 1974. The anatomy of *Saurosuchus galilei*...—*Bull. Mus. Comp. Zool. Harvard*, 146(7):317-362.
- WALKER, A. D. 1964. Triassic reptiles from the Elgin area...—*Phil. Trans. R. Soc. London*, (B) 248:53-134.
- WELLES, S. P. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda)...—*Palaeontogr.*, (A) 185(4-6):85-180.

PLATE I, *Frenguellisaurus ischigualastensis* n. gen., n. sp.

- A. Skull in lateral view (right temporal region reversed).
- B. Caudal vertebra 14(?) (the neural spine is based on that of caudal 18?).
- C. Caudals 27-28-29 (?)/
- D. The same vertebrae in dorsal view.
- E. Caudals 46-47-48 (?).

Abbreviations

c: "crest"; **d**: dentary; **e**: splenial; **mx**: maxilla; **p**: "prominence"; **pmx**: premaxilla; **po**: postorbital; **pos**: postzygapophysis; **prz**: prezygapophysis; **q**: quadrate; **qy**: quadratojugal; **r**: lateral edge of the prezygapophysis; **sq**: squamosal; **y**: jugal.

Scale of skull: 10 cm.

Scale of vertebrae: 1 cm.