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A new Triassic carnivorous dinosaur from Argentina

Andrea B. ARCUCCI[1] and Rodolfo A. CORIA[2]

Abstract. A new Triassic theropod, *Zupaysaurus rougieri* is described from La Rioja Province and its phylogenetic relationships amongst Theropoda are discussed. *Zupaysaurus* shares with Tetanurae several features that include the presence of a tooth row that is anterior to the orbit, a pneumatized lacrimal, and a tibia with a posterolaterally concave and transversely expanded distal end. Features shared with some ceratosaurs, like the presence of a longitudinal alveolar ridge on the maxilla, a large antorbital fenestra, and a fused astragalus-calcaneum, are either homoplasies with some ceratosaurs or plesiomorphic features within Neotheropoda. Based on relative stratigraphical position, *Zupaysaurus* is regarded as Late Triassic in age, which makes it the oldest record of Tetanurae. *Zupaysaurus* provides data about the early evolution of theropods, strengthening the assumption about the origin of tetanurans in the Late Triassic, and indicating their simultaneous record with the oldest coelophysids (i.e. *Coelophysis* and *Liliensternus*)

Resumen. NUEVO DINOSAURIO CARNÍVORO TRIÁSICO DE ARGENTINA. Se describe un nuevo terópodo triásico de la provincia de La Rioja, *Zupaysaurus rougieri*, y se discuten sus relaciones filogenéticas dentro de los Theropoda. *Zupaysaurus* comparte con Tetanurae varios caracteres que incluyen la presencia de una hilera dental por delante de la órbita, un lagrimal pneumatizado y una tibia con extremo distal posterolateralmente cóncavo y expandido lateralmente. Caracteres compartidos con algunos ceratosaurios, tales como la presencia de una cresta alveolar longitudinal en el maxilar, una fenestra antorbital grande, y astrágalo y calcáneo fusionados, son considerados homoplásicos o caracteres plesiomórficos dentro de los Neotheropoda. En base a la posición estratigráfica relativa de los niveles en donde se encontró el holotipo, se considera que *Zupaysaurus* es de edad Triásica tardía, lo que lo convierte en el registro más antiguo de Tetanurae. *Zupaysaurus* provee información acerca de la evolución temprana de los terópodos, fortaleciendo la hipótesis del origen de los tetanuros en el Triásico Superior, e indicando su registro simultáneo con los celofísidos más antiguos (*p.e. Coelophysis* y *Liliensternus*).

Key words. Theropoda. Triassic. Los Colorados Formation. Phylogeny.

Palabras clave. Theropoda. Triásico. Formación Los Colorados. Filogenia.

Introduction

Late Triassic theropod dinosaurs are scarce worldwide, with a few reports from South America, North America and Europe (Huene, 1934; Bonaparte, 1971; Colbert, 1989; Carpenter, 1997; Heckert and Lucas, 2000; Rauhut and Hungerbühler, 1998). These records include primitive carnivorous forms, such as *Eoraptor* (Sereno *et al.* 1993), *Herrerasaurus* (Reig, 1964) and coelophysids (Rowe and Gauthier, 1990), that show important stages in the origin and evolution of theropods. These genera allow workers to build a phylogenetic scenario of the evolution of the Theropoda. Moreover, they have been useful as successive outgroups to polarize the character states within the more derived and diversified Tetanurae (including *Allosaurus*, *Tyrannosaurus* and birds; Gauthier, 1986), which have a significantly more abundant fossil record throughout the Mesozoic (Gauthier, 1986; Novas, 1989; Holtz, 1994; Sereno, 1997). Interestingly, Triassic theropods have not yet included forms that could be assigned to tetanurans, whose earliest record is from the Early Jurassic (*Cryolophosaurus*; Hammer and Hickerson, 1994).

A new carnivorous dinosaur, *Zupaysaurus rougieri* gen. et sp. nov., is described here, which contributes significantly to the theropod record of the Argentinian Late Triassic Los Colorados Formation (Arcucci and Coria, 1997, 1998), from which only a poorly preserved small specimen of uncertain affinities was formerly known (Bonaparte, 1971). This new taxon increases information about the oldest dinosaurs in one of the most diverse Triassic terrestrial vertebrate assemblages from South America (Bonaparte, 1971, 1982; Marsicano *et al.*, 2001), and shows that tetanuran theropods were already present during the Late Triassic. It is represented by one skeleton that includes an almost complete skull with articulated mandibles, the neck, anterior dorsal vertebrae, and other associated postcranial remains.

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[1] Universidad Nacional de San Luis, Area de Zoología. Chacabuco 914, 5700 San Luis, Argentina.

[2] Dirección Provincial de Cultura, Museo Carmen Funes, Av. Córdoba 55, 8318 Plaza Huincul, Neuquén, Argentina.

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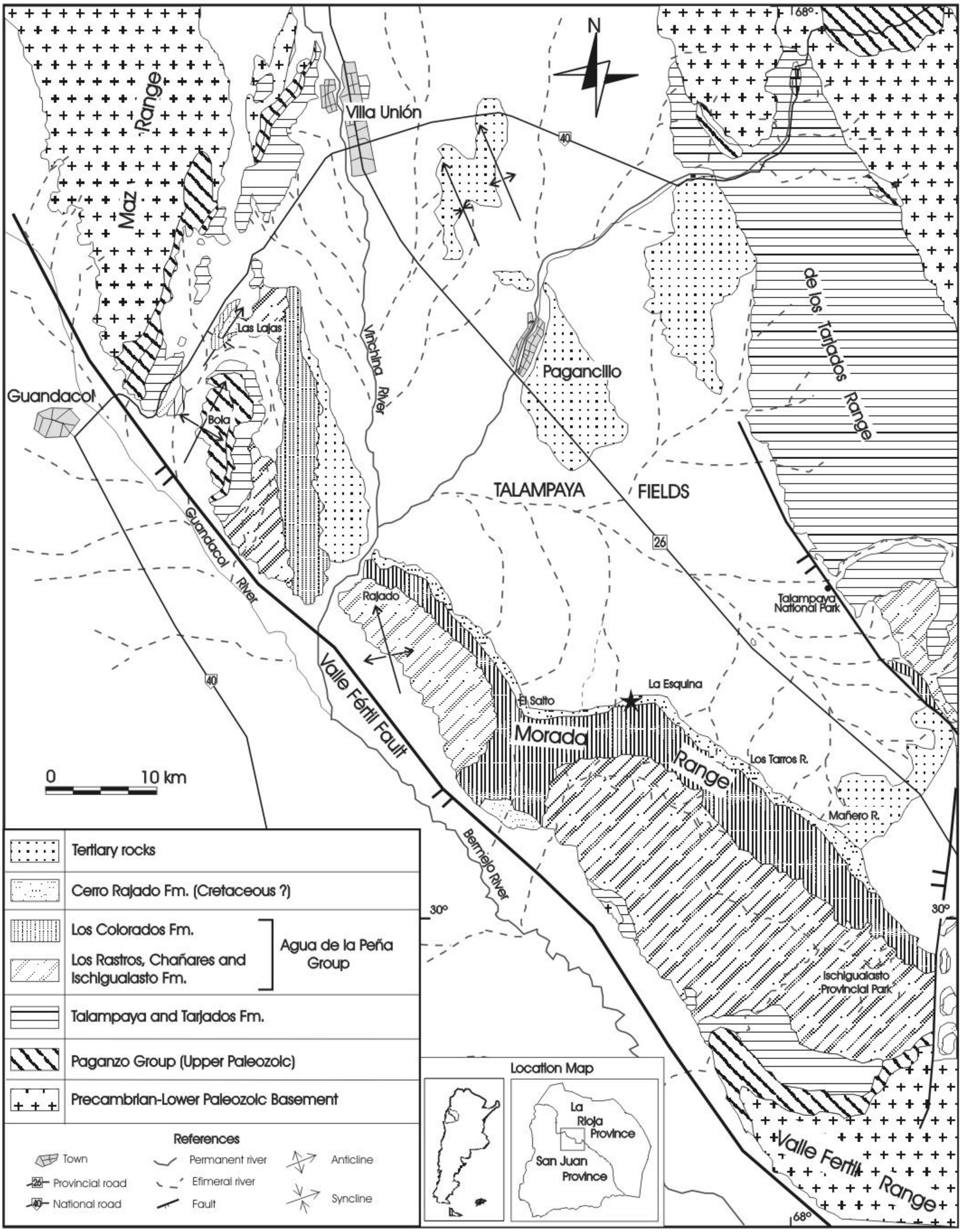

Figure 1. Location map showing the area where the holotype of *Zupaysaurus rougieri* was found (modified from Caselli, 1998 and Caselli *et al.*, 2001). / *Mapa de ubicación mostrando el área donde se encontró el holotipo de* Zupaysaurus rougieri *(modificado de Caselli, 1998 y Caselli* et al., *2001)*.

With an estimated total skull length of 45 cm (figure 2), *Zupaysaurus rougieri* gen. et sp. nov. is a larger animal than other Triassic theropods such as *Coelophysis* (Colbert, 1989), *Liliensternus* (Huene, 1934), *Eoraptor* (Sereno *et al.* 1993) and *Herrerasaurus* (Reig, 1964), but is similar in size to *Goijirasaurus* (Carpenter, 1997). *Zupaysaurus* also adds to the poorly-known diversity of Triassic theropods. In spite of the high number of individuals of *Coelophysis* and *Syntarsus* (Colbert, 1989; Raath, 1990) collected, there is limited anatomical information due to either the preservation of the fossils or the low number of other taxa recorded from the same age.

Institutional abbreviations: BPI, Bernard Price Institute, Johannesburg, South Africa; MUNC-CH, Museo de la Universidad Nacional del Comahue, Colección El Chocón, Neuquén, Argentina; PULR, Paleontología, Universidad Nacional de La Rioja.

Systematic paleontology

SAURISCHIA
THEROPODA
TETANURAE
Zupaysaurus rougieri gen. et sp. nov.
Figures 2 and 3

Etymology. *Zupaysaurus*, from Quechua native language *zupay*, devil, and saurus (Greek), lizard; *rougieri*, in acknowledgment of Dr. Guillermo Rougier, under whose direction the specimen was found and collected.

Holotype. PULR-076 (Paleontología, Universidad de La Rioja). The specimen includes the skull, which lacks only the premaxillae, articulated posterior cervical and anterior dorsal vertebrae, two incomplete, fused sacral vertebrae, the proximal end of the right scapula and coracoid, the distal ends of the right tibia and fibula, the fused right astragalus and calcaneum, and proximal parts of two pedal unguals.

Locality and horizon. Quebrada de los Jachaleros, 7 km West of National Route 126, La Rioja Province, Argentina (figure 1). Upper levels of Los Colorados Formation, Upper Triassic (Caselli *et al.*, 2001).

Diagnosis. *Zupaysaurus rougieri* is distinguished by having an oval, anteroventrally oriented antorbital fenestra; two parasagittal crests on the snout formed by the nasals; anterior process of lacrimal longer than the ventral; main body of the maxilla with parallel dorsal and ventral borders; tibial-astragalar articulation locked medioposteriorly by astragalar process in posteriorly open tibial notch.

Associated material. The holotype specimen was found associated with a fused left scapulo-coracoid, left ilium, the distal end of a right femur, all of which belong to a smaller individual of uncertain affinities that is not included in the description.

Description

Skull. The skull of *Zupaysaurus* (PULR-076) is almost complete, lacking only the premaxillae (figure 2). The specimen has a long, narrow and low skull. The preserved skull length, from the anterior end of the maxilla up to the quadrate distal articulation is 38 cm. Its height from the top of the supraoccipital crest to the ventral border of the quadratojugal is 13.5 cm (figures 2.A, 2.E) and the width between the postorbitals is 12.5 cm (figures 2.C-D). The skull has suffered some distortion, mainly on its left side where there are indications of weathering (figure 2.B).

This contribution is focused on the rostral, orbital and temporal regions of the skull, and does not include the description of bones that are part of the braincase (*e.g.* skull roof and occiput), which are being described elsewhere.

The maxilla, lacrimal and jugal have been displaced anteriorly. The left nasal seems to have collapsed into the skull and it was also exposed on the right side after preparation (figures 2.A and 2.B). The orbit is oval, unlike the round orbit of *Coelophysis* (Colbert, 1989) and *Syntarsus* (Rowe, 1989), and lacks the intraorbital projection of the postorbital recorded in some large theropods like *Giganotosaurus* (Coria and Salgado, 1995), some tyrannosaurids (Molnar *et al.*, 1990) and *Carnotaurus* (Bonaparte, 1991).

The maxilla is long (26 cm) and low (3 cm at level of the horizontal process). Laterally, it has an alveolar ridge that extends from the anterior edge of the antorbital fossa to the distal end of the bone at its contact with the jugal, resembling the condition reported for *Eoraptor* (Sereno *et al.*, 1993, fig. 1), *Coelophysis*, *Syntarsus* and *Liliensternus* (Rowe and Gauthier, 1990) (figure 2). The well-defined antorbital fossa has a tall internal lamina that is widely exposed in front of the anterior margin of the antorbital fenestra, and extends up onto the wide ascending process of the maxilla (figures 2.A and 2.E). The anterior end of the maxilla has a conspicuous step, with a vertical edge that anteriorly encloses the antorbital fossa. Both maxillary fenestra and promaxillary fenestra are present (figures 2.A and 2.E). The base of the ascending process is anteroposteriorly broad above the maxillary fenestra. It projects posterodorsally, thinning and forking distally. The dorsal edge is angular, unlike the ventral edge, which is concave. Such an angularity is determinated by an elongate, narrow notch, positioned above the promaxillary fenestra, likely for the anterior end of the nasal. The horizontal process of the maxilla is a long bar of bone, with parallel dorsal and ventral borders, unlike the condition of *Syntarsus*, *Coelophysis*, *Ceratosaurus*, *Carnotaurus*, *Allosaurus* and most theropods, in which the process clearly tapers posteriorly (Madsen, 1976;

Colbert, 1989; Rowe, 1989; Bonaparte *et al.*, 1990; Madsen and Welles, 2000) (figure 2.A).

The antorbital fenestra is not as large as in the coelophysids *Coelophysis* and *Syntarsus* (Rowe and Gauthier, 1990), resembling in contrast the condition present in *Ceratosaurus* (Gilmore, 1920), *Carnotaurus* (Bonaparte *et al.*, 1990), *Allosaurus* (Madsen, 1976) and more advanced tetanurans. The anterior border of the fossa extends forward approximately to the position of the ninth or tenth maxillary tooth in *Zupaysaurus*. In contrast, the anterior border of the antorbital fossa is at the seventh or eight tooth in *Coelophysis* (Colbert, 1989) and the fifth or sixth one in *Syntarsus kayentakatae* (Rowe, 1989).

Unlike most archosaurs, in which the antorbital fenestra has a distinct triangular outline, *Zupaysaurus* exhibits apomorphically an oval antorbital fenestra, with an anteroventrally inclined greater axis with the highest point at the dorsoposterior corner at the level of the lacrimal fossa. This corner is behind the base of the vertical process of the lacrimal (figures 2.A and 2.E).

There are fifteen preserved maxillary teeth, with an estimated total number of twenty three or twenty four. At the anterior end of the maxilla, the fourth tooth seems to be the largest of the dental row, measuring 3 cm high and 1 cm wide. Most of the preserved teeth have been weathered, making it impossible to identify characteristics of the enamel and the serrations. The last tooth is levelled with the anterior margin of the orbit, as all tetanurans. *Zupaysaurus* has one of the highest numbers of maxillary teeth ever recorded in theropods more primitive than coelurosaurs, and is only surpassed by some individuals of *Coelophysis* (Colbert, 1989) (see table 1).

The nasals in *Zupaysaurus* form a pair of thin crests on the dorsal margins of the snout. The right nasal has been preserved in natural position (figure 2.A), but the left is broken and was found inside the snout during preparation (figure 2.B). The roughly 1 mm thick nasal crests seem to have met on the midline above the anterior part of the antorbital fenestra along the internasal suture (figure 2.D). Each side of the crest seems to have projected dorsolaterally and diverged posterolaterally to contact the lacrimal and prefrontal. There was no participation of the lacrimals in the crest, unlike *Syntarsus kayentakatae* (Rowe, 1989), *Cryolophosaurus* (Hammer and Hickerson, 1994) and *Dilophosaurus* (Welles, 1984).

The jugal has little participation in the ventral margin of the antorbital fenestra as in *Herrerasaurus*, *Sinraptor*, and abelisaurs (Currie and Zhao, 1993; Sereno and Novas, 1993; Bonaparte, 1991) (figures 2.A, 2.E). In lateral view, it wedges between maxilla and lacrimal, contacting both bones with flat and straight sutural surfaces. This anterior process extends forward on the maxilla above the last six maxillary teeth. The postorbital process is broad based, tapers abruptly dorsoposteriorly, and contacts the posterior border of the jugal process of the postorbital. Below the mid point of the orbit, the posterior process forks into two slender and long processes for contact with the quadratojugal. The ventral process extends almost to the back of the quadratojugal. The anterior and ventral margins of the infratemporal fenestra meet in a roughly right angle formed by the jugal. The ventral margin of the infratemporal fenestra is flat and straight as in *Eoraptor* (Sereno *et al.*, 1993), *Herrerasaurus* (Sereno and Novas, 1993) and most ceratosaurs.

The lacrimal forms about 50% of the total margin of the antorbital fenestra (figures 2.A, 2.E). The anterodorsal process, which contacts both nasal and maxilla, is dorsally convex and is longer than the ventral process. A rugose and laterally projected ridge roofs the antorbital fossa posterodorsally. A well developed lacrimal fossa is present, pierced by two deep foramina, but is not as strongly developed as in *Allosaurus* (Madsen, 1976) or *Giganotosaurus* (Coria and Salgado, 1995). The lacrimal fossa is enclosed ventrally by a convex expansion that projects anteriorly in lateral view, similar to those in *Allosaurus* (Madsen, 1976), *Giganotosaurus* (MUNC-CH-1) and *Cryolophosaurus* (Hammer and Hickerson, 1994; Rich *et al.*, 1997). The ventral process is broad ventrally as in *Allosaurus* and *Sinraptor* (Madsen, 1976; Currie and Zhao, 1993), and is deeply excavated laterally as in *Syntarsus kayentakatae* (Rowe, 1989) and *Cryolophosaurus* (Hammer and Hickerson, 1994; Rich *et al.*, 1997).

As in most theropods, the postorbital is a T-shaped bone that borders the dorsoposterior corner of the orbit. It is involved in almost half of the total outline of this fenestra (figures 2.A, 2.E). The anterior process is dorsally convex and extends forward to the midpoint of the dorsal margin of the orbit. The ventral process for the jugal projects anteroventrally, and is thin, slender, and concave anteriorly as in

Figure 2. Skull of *Zupaysaurus rougieri* in right lateral (A), left lateral (B) and dorsal (C) views, and a reconstructed dorsal (D) and right side (E) views of the skull based on the original material. Abbreviations: a, angular; d, dentary; j, jugal; l, lacrimal; m, maxilla; mf, mandibular fenestra; mxf, maxillary fenestra; n, nasal; oc, occipital condyle; p, parietal; pf, prefrontal; po, postorbital; prmf, promaxillary fenestra; q, quadrate; qf, quadratic foramen; qj, quadrate-jugal; s, squamosal; sa, surangular; soc, supraoccipital crest. / *Cráneo de* Zupaysaurus rougieri *en vistas lateral derecha (A), izquierda (B) y dorsal (C); y vistas reconstruídas dorsal (D) y lateral (E) del cráneo basadas en el material original. Abreviaturas: a, angular; d, dentario; j, yugal; l, lagrimal; m, maxilar; mf, fenestra mandibular; mxf, fenestra maxilar; n, nasal; oc, cóndilo occipital; p, parietal; pf, prefrontal; po, postorbital; prmf, fenestra promaxilar; q, cuadrado; qf, foramen cuadrático; qj, cuadradoyugal; s, escamosal; sa, surangular; soc, cresta supraoccipital.*

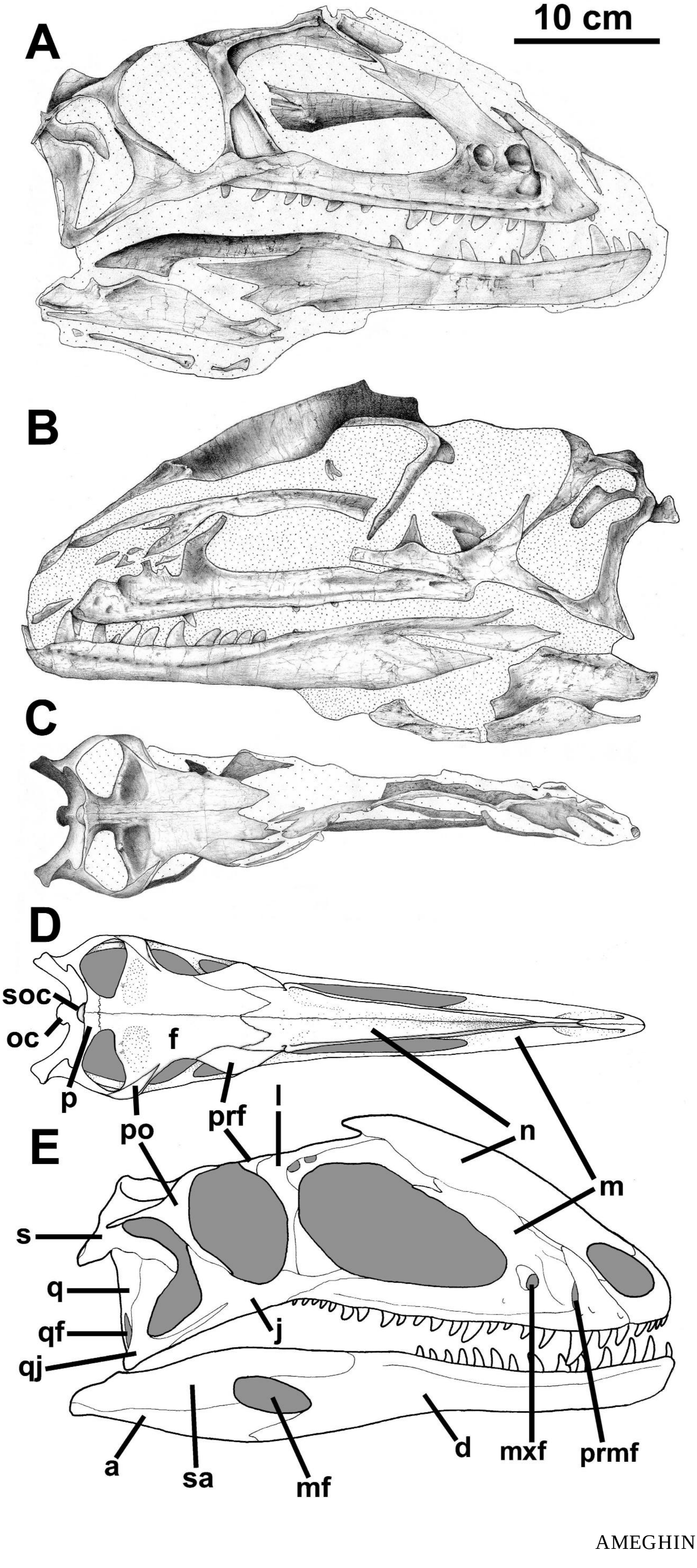
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Table 1. Measurements regarding the length of the maxillary fenestra and number of teeth of different theropods. / *Medidas referidas al largo de la fenestra maxilar y el número de dientes de diferentes terópodos.*

	Total number of maxillary teeth	Number of teeth in front of maxillary fenestra	Number of teeth behind the maxillary fenestra	Number of dentary teeth	Maxillary fenestra / maxillar lenghts (%)	Maxillary fenestra / cranial lenghts (%)
Eoraptor	18	7	11	-	37	15
Herrerasaurus	16	6-7	9-10	19?	42	21
Coelophysis	22-26	7-8	14-18	25-27	50	27~43
Syntarsus rhodesiensis Raath	19-20	5-6	14?	25?	-	-
Syntarsus kayentakatae Rowe	18	7	12	25?	46	26
Ceratosaurus	15	7	8	16-17	40	22
Carnotaurus	12	6	6	15	33	17
Zupaysaurus	23-24	9-10	14	15?	61	37
Allosaurus	14-16	8	8	15	45	20
Tyrannosaurus	12	7	5	14	33	20

Eoraptor (Sereno *et al.*, 1993), *Herrerasaurus* (Sereno and Novas, 1993), *Coelophysis* (Colbert, 1989), *Syntarsus* (Rowe, 1989), *Ceratosaurus* (Gilmore, 1920) and *Allosaurus* (Madsen, 1976). It lacks the intraorbital projection seen in *Giganotosaurus* (Coria and Salgado, 1995), *Carnotaurus* (Bonaparte *et al.*, 1990), *Ilokelesia* (Coria and Salgado, 1998) and tyrannosaurids (Molnar *et al.*, 1990). The contact with the jugal is extensive, separating most of the jugal from the posterior margin of the orbit.

The quadratojugal is fused to the quadrate to such a degree that it is not possible to distinguish one bone from the other. It forms approximately 50% of the posterior margin and a small part of the ventral margin of the infratemporal fenestra. The processes for the quadrate and jugal form a sharp angle in the posteroventral corner of the fenestra. The dorsal process for the quadrate projects anterodorsally as in most theropods other than *Coelophysis* (Colbert, 1989) and *Carnotaurus* (Bonaparte *et al.*, 1990). The dorsal ramus of the quadratojugal extends along the entire lateral side of the quadrate. It expands dorsally into a laminar process that has a wide, anteroposteriorly oriented contact with the squamosal (figures 2.A and 2.E).

The quadrate, as previously mentioned, is completely coossified with the quadratojugal as in *Carnotaurus* (Bonaparte *et al.*, 1990) and mature tyrannosaurids. It has a long ascending process, and the condyle at its upper end articulates within a socket on the ventral surface of the squamosal. The quadrate is distinctly broader than those of most ceratosaurs. In posterior view, there is a relatively large quadratic foramen, slightly located medially, and presumably completely surrounded by the quadrate, although the suture quadrate-quadratojugal is completely obliterated.

The squamosal has a distinct ventral process with a sigmoidal curvature. It extends anteroposteriorly along its contact with the quadratojugal, expanding widely into the infratemporal fenestra. Thus, the infratemporal fenestra of *Zupaysaurus* is keyhole-shaped like those of *Coelophysis* (Colbert, 1989), *Syntarsus* (Rowe, 1989), basal tetanurans (i.e. *Allosaurus* and *Giganotosaurus*, Madsen, 1976; Coria and Salgado, 1995) and tyrannosaurids (Molnar, 1991), but unlike those of *Ceratosaurus* (Rowe and Gauthier, 1990), *Dilophosaurus* (Welles, 1984) and abelisaurids (Bonaparte, 1991).

The frontals are solidly fused with each other and with the parietals (figure 2.C). The contacts with the prefrontals and postorbitals are only barely discernible. In dorsal view, it is possible to observe that each frontal has little participation in the orbit rim, wedged between prefrontal and postorbital (figures 2.C-D). There is no evidence of any ossification connecting the postorbital and prefrontal as there is in carcharodontosaurids and some abelisaurids, and which has been interpreted as the palpebral (Coria and Currie, 2002). Each frontal has a triangular outline, with its base positioned posteriorly and its apex oriented anteriorly towards the nasal contact, in a W-shaped contact like most theropods (figures 2.C-D).

The prefrontal is dorsally flat and rhomboid-shaped, with its greater axis oriented anteroposteriorly. It forms most of the anterior part of the dorsal margin of the orbit (figures 2.C-D). Posteriorly, it does not reach the postorbital, but contacts the lacrimal anterolaterally and the frontal medially. At the posterior point of the lacrimal-prefrontal contact, the prefrontal expands laterally, forming the lesser axis of the rhomboid shape. Each prefrontal forms almost one third of the skull roof above the orbit, similar to *Coelophysis* (Colbert, 1989), but unlike *Syntarsus* (Colbert, 1989), *Allosaurus* (Madsen, 1976), and most other theropods.

Mandibles: Both mandibular rami have remained articulated with each other on the symphysial contact. They kept a close natural position with respect to the skull, although there is 3 cm separating the quadrates and the articulars. The right mandible is preserved best (figure 2.A), and is 44 cm long.

The dentary is approximately 30 cm long from the symphysis to the distal end of the dorsal process for the surangular. Both dentaries have fifteen teeth, although it is uncertain if the dental row extended beyond the last preserved tooth. The symphysial end is blunt with no indication of dorsoventral expansion as in *Dilophosaurus* (Welles, 1984). The dentigerous ramus is straight, slender and fragile. Its dorsal margin is parallel to the ventral margin until approximately the position of the 15th tooth. Behind that point, the dentary expands dorsoventrally. In lateral view, there is a shallow, longitudinal groove with associated foramina for the alveolar vessels and nerves. At the anterior end, there is an enlarged tooth, likely the 4th, positioned in front of the anterior end of the maxilla. The presence of such an enlarged tooth suggests the existence of a premaxillary-maxillary diastema or subnarial gap in *Zupaysaurus*.

The dentary shows weak contacts with the postdentary bones, suggesting a significantly mobile intramandibular joint. The posterior end of the dentary forms the anterior margin of a laterally open mandibular fenestra positioned beneath the orbit. The size of the fenestra compares with those of most ceratosaurs, but seems to be proportionally smaller than in *Herrerasaurus* (Sereno and Novas, 1993) and *Carnotaurus* (Bonaparte *et al.*, 1990).

The surangular borders the mandibular fenestra dorsally and posteriorly. It has a long, transversely convex shelf-like process that extends forward, overlapping the dentary approximately 3 cm anterior to the anterior margin of the mandibular fenestra. This feature has been regarded as an ancestral archosauriform condition retained by ceratosaurs (Rowe and Gauthier, 1990).

The angular forms much of the lower border of the external mandibular fenestra, as well as the lower border of the mandibular ramus. Anteroventrally, it is covered by the ventral distal process of the dentary.

Axial skeleton. Only ten presacral vertebrae are preserved with the skull. Although they are articulated, their state of preservation is poor. Most of the neural arches are preserved as natural casts. The atlas and axis are slightly dislocated from the occiput of the skull. The axis is approximately 11 cm long, with a wide, anteroposteriorly extensive neural spine. The cervical centra are long, low, and are constricted at mid length. Most of the neural arches are not preserved. The neural spines appear to be reduced and posteriorly positioned. The cervical ribs are thin, long, and are fused to the neural arches. The dorsal centra are constricted at mid-length and are amphyplatian. The transverse processes of the two proximal dorsals preserved are laterally extensive.

Only the proximal end of the right scapula is preserved, and it does not seem to have been fused to the coracoid. The coracoid has a strong lateral process as in some coelophysids (Rowe and Gauthier, 1990, fig. 5.4) and basal Dinosauromorpha such as *Lewisuchus* (PULR-06; A.B.A., pers. obs.). The glenoid cavity is relatively deep and transversely narrow.

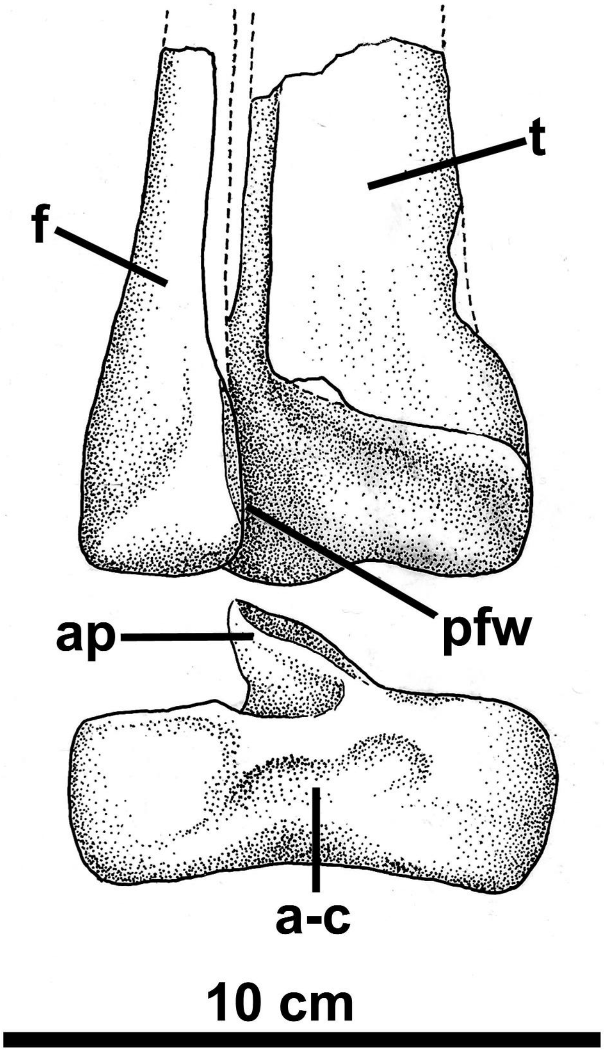

Figure 3. Right tibio-tarsal joint of *Zupaysaurus rougieri* in anterior view. Abbreviations: a-c, astragalus-calcaneum; ap, ascending process; fi, fibula; pfw, postfibular wing; t, tibia. Scale: 10 cm./ *Huesos de la articulación tibio-tarsal de* Zupaysaurus rougieri *en vista anterior. Abreviaturas: a-c, astrágalo-calcáneo; ap, proceso ascendente; fi, fíbula; pfw, ala postfibular; t, tibia. Escala: 10 cm.*

The distal end of the femur lacks the anterior intercondylar groove as does *Herrerasaurus*, but in contrast with most other theropods. The mediodistal crest seems to have projected strongly medially.

The tibia has a transversally expanded distal end as in tetanuran theropods (Sereno, 1997) (figure 3). The postfibular wing (Novas, 1989) is wide and projects laterally. The facet for the ascending process of the astragalus is well developed. In posterior view, there is a distinct ridge separating medial and lateral sides, the latter being slightly concave as in basal tetanurans like *Allosaurus* (Madsen, 1976), *Giganotosaurus* (Coria and Salgado, 1995) and *Sinraptor* (Currie and Zhao, 1993), rather than planar or convex as in *Dilophosaurus* (Welles,

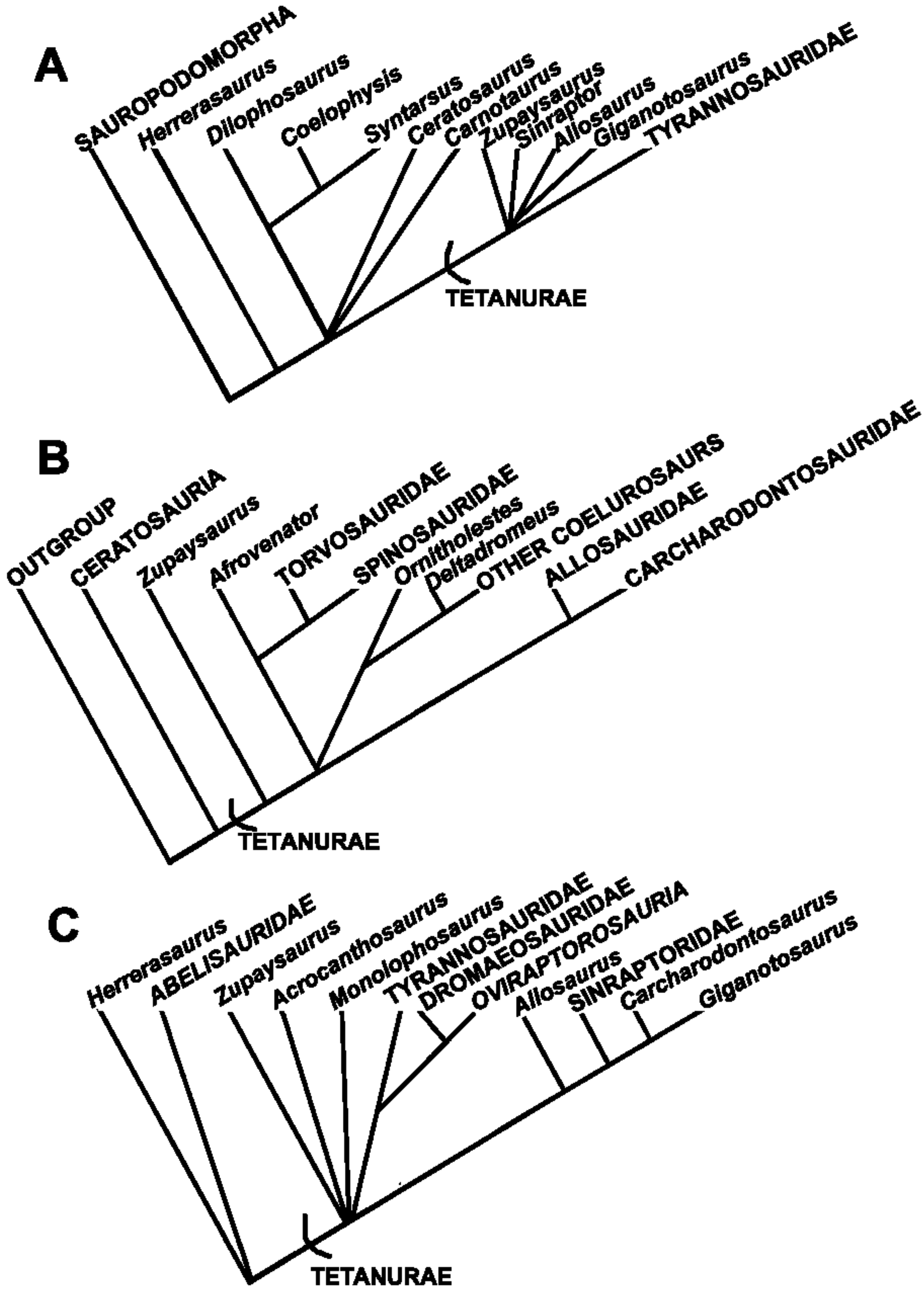

Figure 4. Cladograms depicting the phylogenetic relationships of *Zupaysaurus rougieri* according the character matrix published by (A) the present contribution (Appendix II), (B) Sereno *et al*., 1994, and (C) Currie and Carpenter, 2000. / *Cladogramas indicando las relaciones filogenéticas de* Zupaysaurus rougieri *según las matrices de caracteres publicadas por (A) la presente contribución (Apéndice II), (B) Sereno* et al.*, 1994, y (C) Currie y Carpenter, 2000.*

1984) and *Herrerasaurus* (Novas, 1989). The tibia extends slightly behind the fibula as in most tetanurans. In contrast, the fibula does not overlap the ascending process of the astragalus anteriorly.

The astragalus and calcaneum are co-ossified (figure 3). The astragalus has a well-developed posteromedial process that articulates with a conspicuous notch at the distal end of the tibia. This notch is proportionally deeper than the one present in *Allosaurus* (Madsen, 1976), *Giganotosaurus* (Coria and Salgado, 1995) and *Sinraptor* (Currie and Zhao, 1993), and is open posteriorly. The ascending process is well developed, laterally inclined, and twists slightly upward and forward. Its base is anteroposteriorly narrower than in *Dilophosaurus* (Welles, 1984), but is not as laminar as in more derived tetanurans (i.e. *Allosaurus*; Madsen, 1976).

Phylogenetic analysis

Neotheropoda has been defined as the theropod group that includes *Coelophysis*, Neornithes, their most recent common ancestor and all descendants (Sereno, 1998). Among Neotheropoda, two major clades of theropods are recognized, Ceratosauria and Tetanurae (Gauthier, 1986; Holtz, 1994; Coria and Salgado, 1995, 1999; Sereno, 1997). The monophyly of Ceratosauria, although widely accepted (Gauthier, 1986; Rowe and Gauthier, 1990; Coria and Salgado, 1998), has been discussed and its possible condition as a paraphyletic entity has been suggested by several authors (Currie, 1995; Carrano and Sampson, 1999).

To analyze the phylogenetic relationships of *Zupaysaurus* within Neotheropoda we included ten taxa in the cladistic analysis: *Dilophosaurus*, *Coelophysis*, *Syntarsus*, *Ceratosaurus*, *Carnotaurus*, *Zupaysaurus*, *Allosauridae*, *Giganotosaurus* and Coelurosauria. *Herrerasaurus* and Sauropodomorpha were used as more distant successive outgroups. The anatomical information given by *Zupaysaurus* was scored in a data matrix of 19 cranial and postcranial characters (see Appendix I). The data matrix was analyzed with Hennig86 version 1.5 using the implicit enumeration option. Twelve most parsimonious trees were obtained, with *Zupaysaurus* invariably nested among a monophyletic Tetanurae. By using the NELSEN option, a consensus tree of 27 steps resulted, with a consistency index of 0.70 and a retention index of 0.83. This consensual analysis maintains the same phylogenetic position of *Zupaysaurus* in relation to Tetanurae and Neotheropoda (figure 4.A).

In order to test the results of our analysis, we used the data matrices published by Sereno *et al.* (1994) and Currie and Carpenter (2000) in their analysis of *Carcharondontosaurus* and *Acrocanthosaurus* respectively (figures 4.B and 4.C). The consensus trees obtained in all cases show *Zupaysaurus* as the closest theropod to the more derived allosaurids, tyrannosaurs and other tetanuran theropods. In other words, *Zupaysaurus* remains within Tetanurae, with ceratosaurs and *Herrerasaurus* as the more plesiomorphic successive sister taxa.

Tetanurans exhibit derived characters (Gauthier, 1986; Sereno, 1997), many of which are present in *Zupaysaurus*. These include the presence of both promaxillary and maxillary openings in the antorbital fossa; a reduced and key-hole shaped lateral temporal fenestra; a maxillary tooth row that ends anterior to the orbit; the presence of a lacrimal pneumatic recess; a lacrimal horn developed as a low crest or ridge; transversely expanded distal end of tibia; a fibula with the distal end expanded almost double the shaft width; and an anteriorly positioned ascending process of the astragalus.

On the other hand, the sibling theropod taxon of Tetanurae, the Ceratosauria, has been defined in reference to a stem-based lineage that includes *Ceratosaurus nasicornis* and its closest relatives amongst the Theropoda (Gauthier, 1986; Rowe and Gauthier, 1990). In this regard, the Ceratosauria are diagnosed by the presence of two pairs of pleurocoels in the cervical vertebrae, the perforation of the pubic plate by two fenestra, the fusion of sacral vertebrae and ribs in adults, the fusion of the astragalus and calcaneum in adults, and the presence of a flange on the distal end of the fibula that flares medially to overlap the ascending process of the astragalus anteriorly.

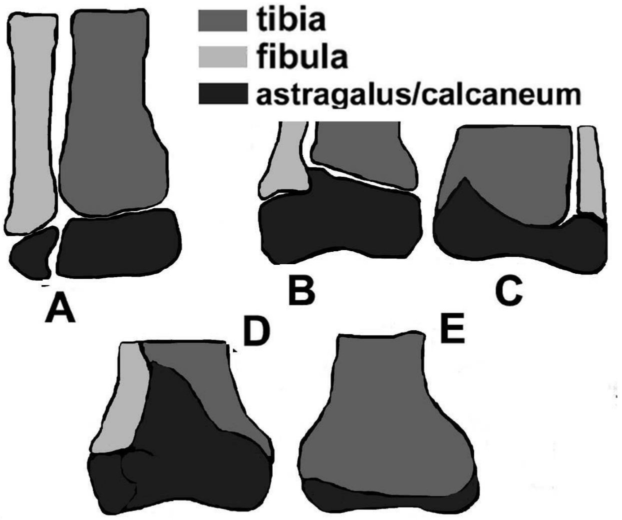

Figure 5. Comparative scheme indicating the morphological changes occurred in the theropod tibia-fibula-tarsus joint: (A) *Herrerasaurus*, (B) *Zupaysaurus*, (D) *Allosaurus* in anterior views, (C) *Zupaysaurus* and (E) *Allosaurus* in posterior view. Not to scale./ *Esquema comparativo indicando los cambios morfológicos ocurridos en la articulación tibio-fibulo-tarsal de terópodos: (A)* Herrerasaurus, *(B)* Zupaysaurus, *(D)* Allosaurus *en vista anterior, (C)* Zupaysaurus y *(E)* Allosaurus *en vista posterior. Los dibujos no están a escala.*

Ceratosauria is composed of two clades, Coelophysoidea (*Dilophosaurus* + coelophysids) and Neoceratosauria (*Ceratosaurus* + [*Elaphosaurus* + abelisaurids]) (Holtz, 1994). The presence of a maxilla with an alveolar crest has been proposed as the single synapomorphic character to erect a node-based taxon to include all coelophysids (*Liliensternus*, *Coelophysis* and *Syntarsus*; [Node 3, Rowe and Gauthier, 1990]). Moreover, Rowe (1989) proposed a close relationship between *Coelophysis* and *Syntarsus* based on the presence of an antorbital fossa that is more than 25% of the total skull length, elongate cervical ribs, and a sharp caudal rim on the iliac fossa.

Zupaysaurus has a co-ossified astragalus and calcaneum, but they are not fused to the tibia. More inclusively, the South American form shares with the Node 3 of Rowe and Gauthier (1990) the presence of a maxilla with with an alveolar ridge. Finally, *Zupaysaurus* exhibits the apomorphic condition of an antorbital fossa greater than 25% of the skull length that diagnoses the node-based taxon proposed for *Coelophysis* and *Syntarsus* (Node 4, Rowe, 1989). The presence of that maxilla alveolar ridge, a subnarial gap (inferred by the presence of a fang-like tooth in the dentary) and a coracoid with a lateral process are here considered, in the light of the current phylogenetic analysis, primitive features amongst Theropoda. These characters are retained in this new Triassic theropod (figure 4).

Cranial ornamentation is widely distributed amongst theropods, as has been noted elsewhere (Zhao and Currie, 1993). However, the anatomical details of these structures vary greatly (i.e. the ceratosaurs *Dilophosaurus* and *Syntarsus kayentakatae*; and the basal tetanurans *Cryolophosaurus* and *Monolophosaurus*; Welles, 1984; Rowe, 1989; Hammer and Hickerson, 1994; Zhao and Currie, 1993). The skull of *Zupaysaurus* displays parasagittal crests exclusively formed by the nasals, unlike the nasolacrimal complex present in the coelophysoids.

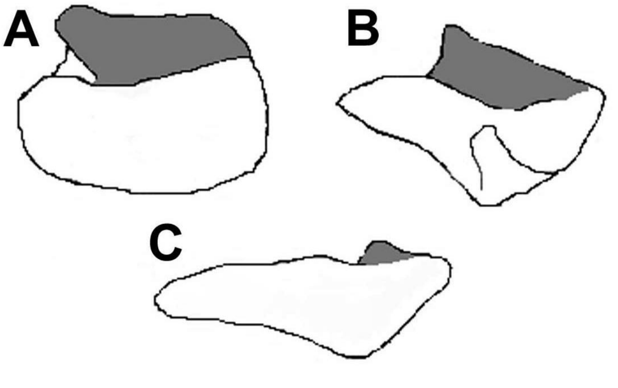

Figure 6. Comparative scheme indicating the morphological changes occurred in the distal articular surface of the theropod tibia. Shaded areas indicate articular contact of the tibia for the ascending process of the astragalus. (A) *Herrerasaurus*, (B) *Zupaysaurus*, (C) *Allosaurus*. Not to scale. / *Esquema comparativo de los cambios morfológicos ocurridos en la superficie articular distal de la tibia de los terópodos. Áreas sombreadas indican el contacto articular de la tibia con el proceso ascendente del astrágalo. (A)* Herrerasaurus, *(B)* Zupaysaurus, *(C)* Allosaurus. *Los dibujos no están a escala.*

The tarsus of *Zupaysaurus* exhibits an intermediate morphology between basal theropods (*Herrerasaurus* and ceratosaurs) and more derived tetanurans (Coria and Arcucci, 1999). This condition allows us to propose a sequence of evolutionary changes, inferred from the phylogenetic hypothesis proposed in this contribution. These changes occurred in the lateral expansion of the distal end of the tibia and its relationship to the position of the fibula. In basal theropods, the fibula is clearly positioned lateral to the tibia (i.e. *Herrerasaurus*, figure 5.A). In *Zupaysaurus*, in contrast, the distal end of the fibula is slightly overlapped by the tibia in posterior view (figure 5.B). In more derived tetanurans such as *Allosaurus*, the distal end of the fibula is completely in front of the lateral maleolous of the tibia (figure 5.C).

Another character that shows important changes is the facet of the tibia for the ascending process of the astragalus. In primitive theropods, this facet is robust and is larger than the posterior process of the tibia, with subequal transverse and craniocaudal axes (figure 6.A). In *Zupaysaurus*, both the facet and the posterior process are about the same size, and in distal view, the profile is broader transversely (figure 6.B). In more derived tetanurans (i.e. *Allosaurus*), the facet is reduced and the transverse width is almost twice the anteroposterior length (figure 6.C).

Other changes are seen in the ascending process of the astragalus. In primitive forms, the astragalus is pyramidal in shape, dorsocaudally oriented, and has no contact with the fibula (figure 5.A). In *Zupaysaurus*, the process has parallel anterior and posterior sides, and has a dorsal articular surface for the tibial facet that is clearly located on the cranial side of the astragalus and has contact with the fibula (figure 5.B). In more derived tetanurans, the ascending process is a thin plate-like process, overlapped slightly laterally by the fibula (figure 5.C).

The Tetanurae, defined as all theropods closer to birds than to Ceratosauria (Gauthier, 1986) includes the major diversity of carnivorous dinosaurs. It has an assumed temporal range from Early Jurassic to recent, because no tetanurans had been previously been recorded from any Triassic locality around the world. Phylogenetic analysis (figure 4) indicates that *Zupaysaurus* is the most primitive tetanuran theropod known, and suggests that the divergence of the two major clades of meat-eating dinosaurs (Ceratosauria and Tetanurae) (Gauthier, 1986) occurred not long after the basal split of Dinosauria into ornithischian and saurischian lineages in the Carnian (Sereno, 1997).

Zupaysaurus as the oldest tetanuran

The phylogenetic interpretation of *Zupaysaurus* as a tetanuran implies that this animal is the oldest representative of this clade, having been collected from approximately the middle of the upper part of the Los Colorados Formation. This formation is the upper part of the Agua de la Peña Group in the Ischigualasto-Villa Union Basin in western Argentina. This sequence is characterized by sandstones and mudstones deposited by moderately sinuous fluvial systems that interfinger laterally and grade into horizontally bedded flood-plain deposits (Caselli *et al.*, 2001). The Los Colorados Formation yields a great abundance of tetrapods that includes basal archosaurs, prosauropods, cynodonts and turtles (Bonaparte, 1971; Rougier *et al.*, 1995, Marsicano *et al.*, 2001). The age of the Los Colorados Formation has been widely considered as Norian, according to both biostratigraphic and chronostratigraphic analysis. Recently Heckert and Lucas (2000) have referred the Los Colorados Formation to the Rhaethian, basing this statement upon correlations of other tetrapod genera, mainly aetosaurs. This kind of chronostratigraphical correlation based on co-generic comparisons needs great understanding of the phylogenetic relationships, which is not available at present. Moreover, recognition of the existence of the Rhaethian, a European stage typical of marine facies, is difficult in this predominantly terrestrial South American Triassic basin.

With this caveat, and in spite of the lack of independent evidence to provide a precise age for this level, there is a wide consensus that this South American basin represents the upper part of the Late Triassic (Bonaparte, 1982, 1997; Olsen and Sues, 1986; Shubin and Sues, 1991; Heckert and Lucas, 1998; Caselli *et al.*, 2001). Consequently, we consider the age of the Los Colorados Formation as the latest part of the Late Triassic because of its faunal composition and its relative stratigraphic position with the underlying formations.

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Appendix I

List of characters used in the cladistic analysis. Sauropodomorpha and *Herrerasaurus* were used as the outgroups. *Herrerasaurus* was considered a basal theropod in agreement with current hypothesis (Novas, 1996, Sereno and Novas, 1993; Sereno *et al.* 1993).

Cranium

1. Crescentic naso-lacrimal crests.
2. Hanging premaxilla (apparently mobile).
3. Alveolar crest on maxilla.
4. Antorbital fossa larger than 25% skull length.
5. Nasal fenestra.
6. Antorbital maxillary teeth.
7. Pneumatized lacrimal and jugal.
8. Absence of fang-like tooth in dentary.
9. Large maxillary fenestra and posteriorly positioned.
10. Well developed parietal crest.
11. Prefrontal reduced or absent.

Postcranium

12. Two pairs of pleurocoels in the cervical vertebrae.
13. Transverse processes of dorsal vertebrae strongly backturned and triangular when view from above.
14. Astragalus and calcaneum fused to each other and to the tibia.
15. Ascending process of astragalus directed vertically, subparallel to the tibial shaft, and largely overlapped by the fibula.
16. Deep sulcus along the lateral border of the base of the tibiofibular crest.
17. Loss of axial diapophysis.
18. Elongated cervical ribs.
19. Tibia transversely expanded.

Appendix II

Character matrix. Distribution of character states used for phylogenetic analysis of *Zupaysaurus rougieri*.

Sauropodomorpha	00000	00?00	00000	0000
Herrerasaurus	00000	00000	00000	0000
Carnotaurus	00000	1?100	010??	100?
Allosauridae	00000	11110	00000	0001
Ceratosaurus	00000	10100	01011	1000
Dilophosaurus	11100	00000	01111	1100
Coelophysis	01111	00000	01111	1110
Syntarsus	11111	00000	01111	1110
Zupaysaurus	0?110	11010	0?0?0	0??1
Coelurosauria	00000	11111	10000	0110