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VERTEBRATE SUCCESSION IN THE ISCHIGUALASTO FORMATION

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ABSTRACT—The Upper Triassic (Carnian–Norian) Ischigualasto Formation has yielded a diverse vertebrate fauna that records the initial phase of dinosaur evolution. Radioisotopic dates from ash layers within the formation provide a chronostratigraphic framework, and stratigraphic and sedimentological studies have subdivided the formation into four members and three abundance-based biozones. We describe two new basal dinosauriforms, an unnamed lagerpetid and a new silesaurid, *Ignotosaurus fragilis*, gen. et sp. nov., which increase to 29 the number of vertebrates in the Ischigualasto fauna. We provide a census of 848 fossil specimens representing 26 vertebrate taxa logged to stratigraphic intervals of 50 m. This temporally calibrated census shows that abundance and taxonomic diversity within the Ischigualasto Formation does not change suddenly but rather appears to gradually decline in response to climatic deterioration. The only abrupt shift in faunal composition occurs at the end of the second of three biozones, when the abundant cynodont *Exaeretodon* is replaced by the rare dicynodont *Jachaleria*.

RESUMEN—La Formación Ischigualasto del Triásico Superior (Carniano–Noriano) ha producido una diversa fauna de vertebrados que registra la fase inicial de la evolución de los dinosaurios. Edades radioisotópicas obtenidas de capas de ceniza constituyen un marco cronoestratigráfico y estudios estratigráficos y sedimentológicos permitieron subdividir la formación en cuatro miembros y tres biozonas de abundancia. Describimos dos nuevos dinosauriformos basales, un lagerpétido indeterminado y un nuevo silesáurido, *Ignotosaurus fragilis*, gen. et sp. nov., que aumentan a 29 el número de vertebrados conocidos en la fauna de Ischigualasto. Ofrecemos un censo de 848 especímenes fósiles que representan 26 taxones de vertebrados relevados a intervalos estratigráficos de 50 m. Este censo calibrado temporalmente muestra que la abundancia y la diversidad taxonómica dentro de la Formación Ischigualasto no cambian de repente, sino que parecen disminuir gradualmente en respuesta al deterioro climático. El único cambio abrupto en la composición de la fauna se produce al final de la segunda de las tres biozonas, cuando el abundante cinodonte *Exaeretodon* es sustituido por el escaso dicinodonte *Jachaleria*.

INTRODUCTION

The Upper Triassic Ischigualasto Formation is broadly exposed in a 50-km-long valley within the Ischigualasto-Villa Unión Basin in northwestern Argentina (San Juan Province) (Fig. 1). Reaching a thickness of up to 700 m, the Ischigualasto Formation comprises an alternating combination of fluvial and floodplain sandstones and overbank mudstones rich in fossil remains (Currie et al., 2009). Unlike other fossiliferous Late Triassic deposits from southern Pangaea, the Ischigualasto Formation includes volcanic ash layers that have yielded ⁴⁰Ar/³⁹Ar radioisotopic dates (Rogers et al., 1993; Martínez et al., 2011b). The ages near the bottom and top of the formation (231.4 ± 0.3 and 225.9 ± 0.9 Ma, respectively) suggest that it was laid down over a period of approximately 6 million years during the late Carnian to early Norian (Martínez et al., 2011b; Walker et al., 2013).

Although vertebrate fossils from the Ischigualasto Formation first came to light 70 years ago (Cabrera, 1943), intensive collection of fossil vertebrates began in the late 1950s, led by American paleontologist A. S. Romer and Argentine paleontologists O. Reig and J. F. Bonaparte. In the late 1980s and early 1990s, a second phase of intensive work was initiated by several of us (O.A.A., R.N.M., P.C.S.) and continued for over a dozen years with volunteers and financial assistance from the Earthwatch Institute (Brightsmith et al., 2008). The resulting fossil collection includes thousands of specimens housed principally at the Instituto

y Museo de Ciencias Naturales of the Universidad Nacional de San Juan, with smaller but important collections at the Instituto “Miguel Lillo” in San Miguel de Tucumán, the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” in Buenos Aires, and the Museum of Comparative Zoology at Harvard University in Cambridge, Massachusetts, U.S.A.

Scientific and public attention has focused on the extraordinary record of the earliest dinosaurs, which now includes representatives from each of the three principal dinosaurian subgroups—Ornithischia, Sauropodomorpha, and Theropoda. *Pisanosaurus mertii*, the least well known of these basal dinosaurs, remains to date the earliest-known ornithischian (Casamiquela, 1967a; Bonaparte, 1976; Irmis et al., 2007a; Sereno, 2012). The basal sauropodomorphs *Eoraptor lunensis* (Sereno et al., 1993), *Panphagia protos* (Martínez and Alcober, 2009), and *Chromogisaurus novasi* (Ezcurra, 2010) collectively revamp knowledge of the early evolution of Sauropodomorpha (see Martínez et al., 2013b; Sereno et al., 2013). Finally, *Herrerasaurus ischigualastensis* (Reig, 1963), *Sanjuansaurus gordilloi* (Alcober and Martínez, 2010), and *Eodromaesus murphi* (Martínez et al., 2011b) document early evolution within Theropoda.

The vast majority of the fossil remains from the Ischigualasto Formation, nonetheless, belong to non-dinosaurian tetrapods, including temnospondyl amphibians, basal archosauromorphs and archosauromorphs, crurotarsans, early dinosauriforms, dicynodonts, and non-mammalian cynodonts. In this paper, we describe two new basal dinosauriforms based on fragmentary, although diagnostic, remains. The first is a lagerpetid (Fig. 2; Appendix 1),

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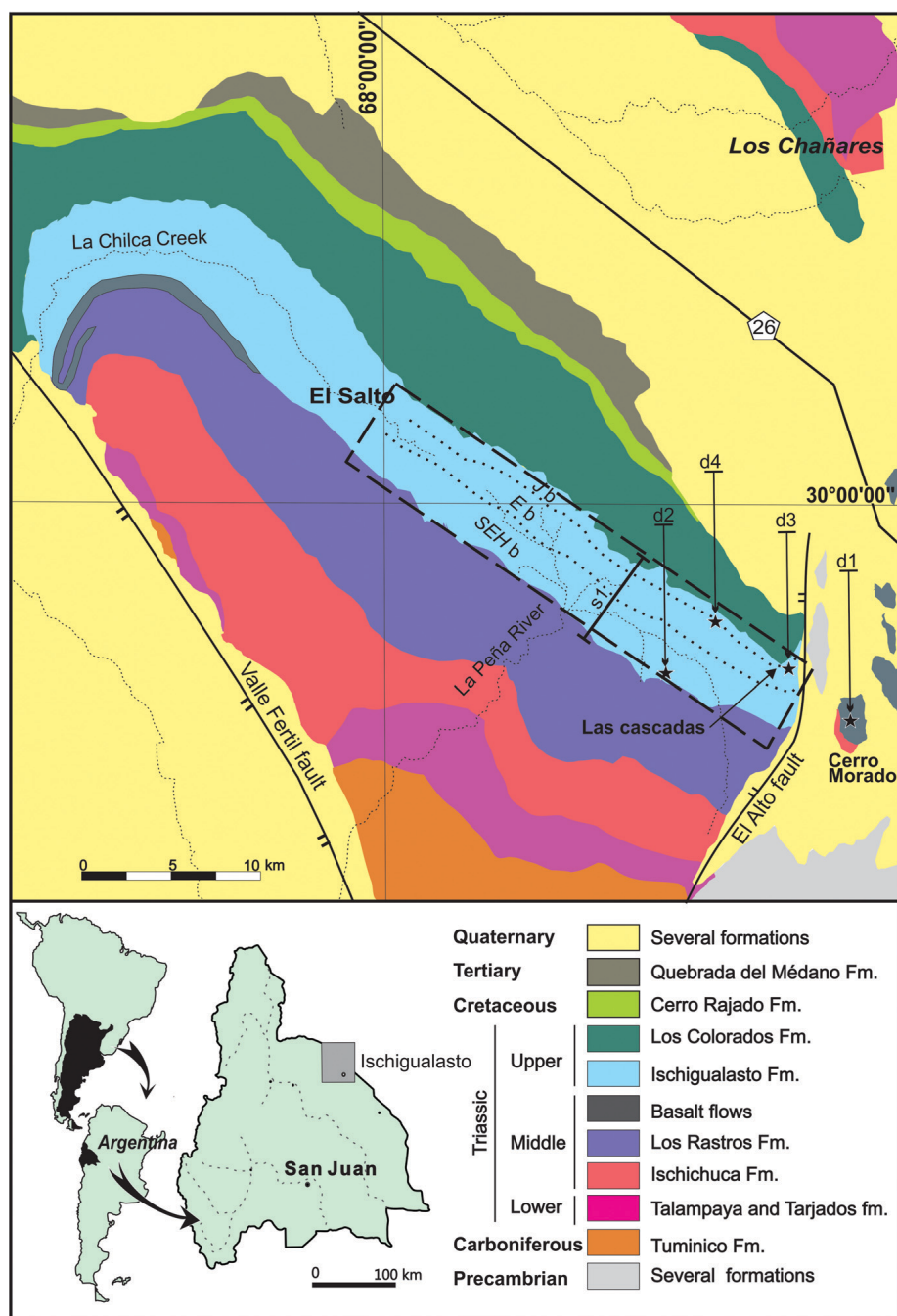


FIGURE 1. Geographic and geologic maps of the southern portion of the Ischigualasto-Villa Unión Basin, which straddles the border between San Juan and La Rioja Provinces in Argentina. Black stars indicate the location of four available radioisotopic dates within the Ischigualasto Formation; a black dashed rectangle surrounds the fossiliferous outcrop that has been intensively prospected; bold black dotted lines indicate the approximate boundaries between biozones; gray dotted lines indicate drainages; and black lines indicate major fault zones and paved roads. **Abbreviations:** d1–4, location of ashbed samples yielding radioisotopic dates d1–4; **E b**, *Exaeretodon* biozone; **J b**, *Jachaleria* biozone; **s1**, reference stratigraphic section; **SEH b**, *Scaponyx-Exaeretodon-Herrerasaurus* biozone.

which extends the temporal range of these small-bodied, lanky bipeds in southern Pangaea from the pre-dinosaurian Middle Triassic horizon of the Chañares Formation into the mid-Upper Triassic of the Ischigualasto Formation. The second is a silesaurid, *Ignotosaurus fragilis* (Fig. 3; Appendix 1), which documents the presence of this small-bodied, quadrupedal clade in the Ischigualasto assemblage. Both of these taxa provide additional evidence of the global distribution of basal dinosauroforms in association with the earliest dinosaurs during the Late Triassic (Irmis et al., 2007b; Fig. 4).

We then turn our attention to the vertebrate succession within the Ischigualasto Formation. In a preliminary account of fossil vertebrate distribution, three successive biozones were recognized

within the formation (Martínez et al., 2011b). In this initial analysis, the extinction of once-dominant non-dinosaurian herbivores and carnivores does not appear to be correlated with dinosaurian diversity or abundance, but this result was based on only 19 of 29 known vertebrate taxa. The temporal distribution of taxa, in addition, was registered only by biozone. In this paper, we update the known faunal composition of the Ischigualasto Formation (Appendix 2), summarize the geologic and paleoclimatologic setting of the Ischigualasto Formation, outline current evidence for its age and duration within the Late Triassic period, and discuss the succession of vertebrates within the formation. We summarize the temporal distribution of 848 vertebrate specimens in a spindle diagram (Fig. 5; Table 2). Finally, we discuss the nature of the

relationship between the observed waxing and waning of vertebrate diversity and abundance and major climatic and geologic events.

Institutional Abbreviations—MACN, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina; MCP, Museo de Ciencias e Tecnología, Porto Alegre, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; PVL, Paleontología de Vertebrados, Instituto “Miguel Lillo,” San Miguel de Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; UFSM, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

METHODS

Specimen Photography

To remove color distraction, fossil specimens were coated with neutral gray acrylic paint prior to photography.

Anatomical Orientation

We employ traditional, or ‘Romerian,’ directional terms over veterinarian alternatives (Wilson, 2006). ‘Anterior’ and ‘posterior,’ for example, are used as directional terms rather than the veterinarian alternatives ‘rostral’ or ‘cranial’ and ‘caudal.’

Taxonomic Terms

Autapomorphies, or character states that are uniquely derived for a single taxon, constitute the evidential basis for recognition of taxa in this study. Features that are not derived but only ‘differentiate’ a taxon from others are also listed but clearly designated as differential.

We organize the tetrapod species from the Ischigualasto Formation in an unranked suprageneric taxonomy, following Gauthier et al. (1989) and Sereno (2005) for suprageneric taxonomy within Tetrapoda and Archosauria, respectively.

Phylogenetic Analysis—We added the new lagerpetid and silesaurid to the data matrix in Nesbitt et al. (2010), an analysis that includes currently known lagerpetids and silesaurids (Appendix 1). We followed the original analysis in our choice of outgroups: *Erythrosuchus* was constrained as the outgroup, *Pseudolagosuchus* and *Lewisuchus* were combined as a single terminal taxon. All characters were equally weighted, and 15 multistate characters were ordered (characters 21, 78, 89, 98, 116, 142, 159, 169, 175, 177, 195, 200, 227, 250, 281). The new data set was analyzed with TNT (version 1.1; Goloboff et al., 2008) with equally weighted parsimony, a heuristic search algorithm involving 1000 replicate analyses, and branch swapping. Support for each branch was estimated by performing Bootstrap replications (1000) for each minimum-length tree and calculating decay indices.

Census

The area of the Ischigualasto Formation chosen for the census of vertebrate remains includes most outcrop south of a locality called El Salto (Fig. 1). We chose this area because of the excellent preservation and abundance of fossils. In this area, the outcrops are well exposed from the bottom to the top of the unit. Sampling was done by the authors with the same level of detail over the entire area, minimizing sampling bias.

The census is composed of specimens housed in the Instituto y Museo de Ciencias Naturales of the Universidad Nacional de San Juan collection (‘PVSJ collection’) as well as uncollected specimens to avoid biases that may play a role in determining which taxa or specimens are collected. All specimens in the PVSJ collection were recovered in the last 25 years in field efforts led by several of the authors (R.N.M., O.A.A., P.C.S.) and are associated

with stratigraphic horizon and geographic coordinate data. The stratigraphic position of vertebrate specimens was determined in relation to three stratigraphic sections across the census area. We included only those specimens that could be identified taxonomically with confidence.

The stratigraphic sampling interval was based on the abundance of fossils. We used a 50-m interval in the specimen-rich lower 300 m of the formation and a 60-m interval for the less fossiliferous upper strata.

The stratigraphic distribution and relative abundance of 26 of the 29 known vertebrate taxa is summarized in a range chart with statistical confidence bars (Fig. 5). Three taxa were omitted from the census, because they were collected prior to our field work and their stratigraphic position is poorly constrained: the ornithischian *Pisanosaurus*, the ornithosuchid *Venaticosuchus*, and the non-mammalian cynodont *Ischnathus*.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869
DINOSAURIFORMES Benton, 1985
LAGERPETIDAE Arcucci, 1986
Gen. et sp. indet.
(Fig. 2A–F; Table 1)

Material—PVSJ 883, distal end of the left femur.

Locality and Horizon—S30°08'14", W 67°52'39", Valle Pinado in Ischigualasto Provincial Park, San Juan Province, Argentina. The holotype was discovered 40 m above the base of the Ischigualasto Formation, in the upper portion of the La Peña Member (sensu Currie et al., 2009) and lower portion of the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Fig. 5). The single known specimen (PVSJ 883) was found intermixed with the holotype (PVSJ 882) of the basal sauropodomorph *Panphagia protos* (Martínez and Alcober, 2009) and an unnamed advanced eucynodont (Martínez et al., 2011a).

Age—Late Carnian on the basis of a radioisotopic date near the base of the Ischigualasto Formation in the vicinity of the type locality (Rogers et al., 1993) (Figs. 1, 5). This date was recently recalibrated to 231.4 ± 0.3 Ma (Martínez et al., 2011b; Walker et al., 2013).

Description—The material of PVSJ 883 is limited to a single specimen comprising the distal end of the left femur (Fig. 2A–F). Maximum transverse width of the distal end (25.1 mm; Table 1) suggests that the complete femur measured approximately 109–139 mm, as estimated from the ratio between the distal width

TABLE 1. Measurements (in mm) of the lagerpetid PVSJ 883 and the silesaurid *Ignotosaurus fragilis*, gen. et sp. nov. (PVSJ 884).

Measurement	PVSJ 883	PVSJ 884
Ilium		
Iliac blade, length	—	59.1
Iliac blade, depth dorsal to acetabulum	—	33.1
Acetabulum, depth	—	15.2
Pubic peduncle, transverse width	—	12.4
Preacetabular process, length from acetabular rim	—	32.7
Postacetabular process, length from acetabular rim	—	41.0
Femur		
Length	(109–139)	—
Femoral head, maximum length	—	—
Head to apex of fourth trochanter	—	—
Fourth trochanter, length	—	—
Shaft, minimum transverse diameter	—	—
Distal end, maximum transverse width	(25.1)	—
Distal end, maximum anteroposterior depth	(16.1)	—

Parentheses indicate estimated measurement or measurement range.

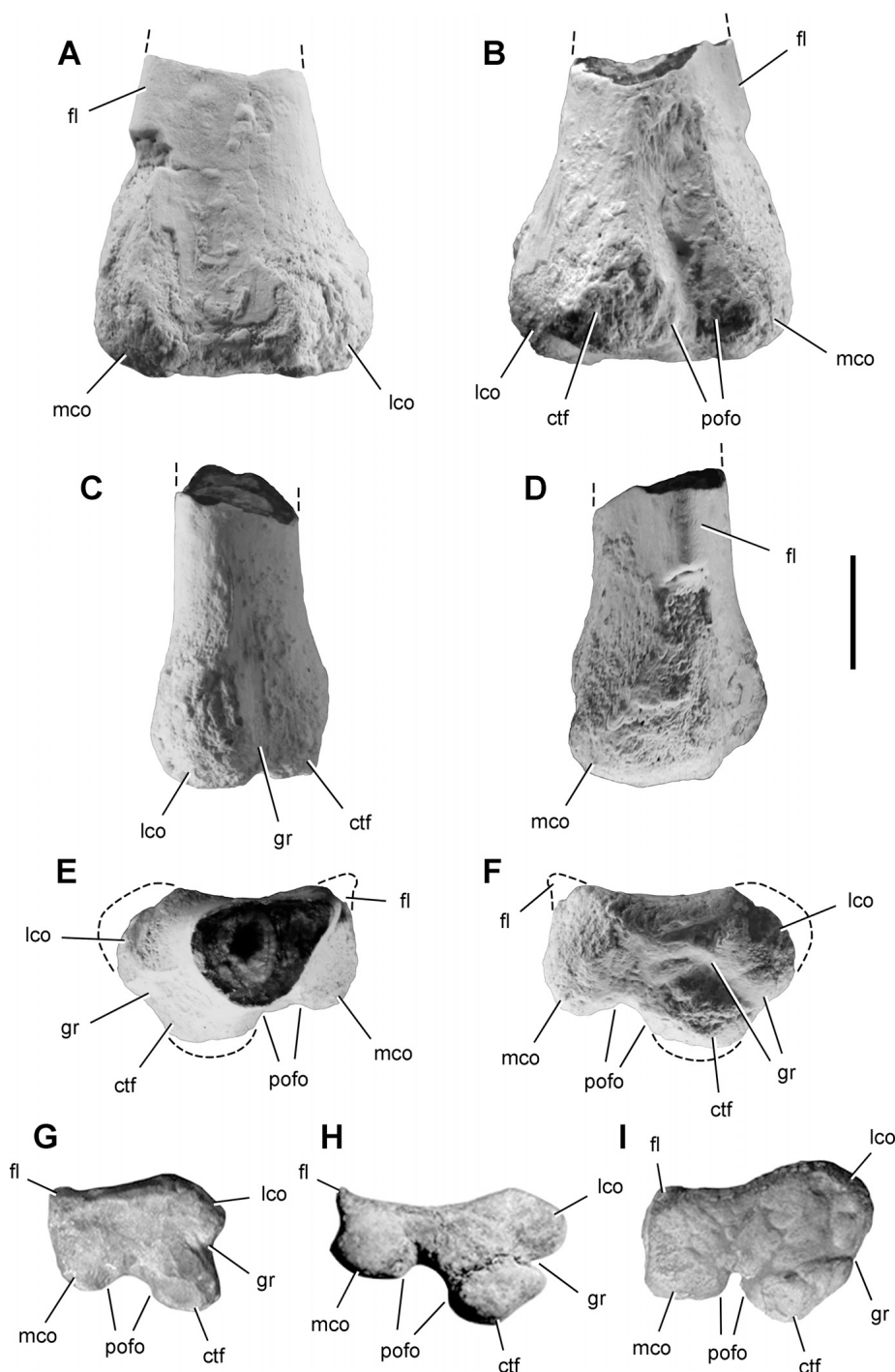


FIGURE 2. Distal end of the femur in Lagerpetidae. Distal end of the left femur of PVSJ 883 from the Ischigualasto Formation in anterior (A), posterior (B), lateral (C), medial (D), proximal (E), and distal (F) views. Distal view of the left femur (anterior toward top of page) of *Lagerpeton chanarensis* (G), *Dromomeron romeri* (H), and *Dromomeron gregorii* (I) (from Nesbitt et al. (2009)). **Abbreviations:** ctf, crista tibiofibularis; fl, flange; gr, groove; lco, lateral condyle; mco, medial condyle; pofo, popliteal fossa. Dashed line indicates a missing margin. Scale bar equals 1 cm.

and length of complete femora in *Lagerpeton chanarensis* and *Dromomeron gregorii* (Fig. 2G–I). The femoral shaft is hollow in cross-section, with a medullary cavity occupying approximately one-half the volume of the shaft (Fig. 2E). Some abrasion of the edges of the distal condyles has occurred (Fig. 2E, F).

In lagerpetids, the distal end of the femur is diagnostic in several regards (Fig. 2F–I). The distal condyles are transversely broad relative to their maximum depth, and the anterior margin is transversely concave. Both of these features are present in PVSJ 883 (Fig. 2F).

In distal view, the crista tibiofibularis (fibular condyle) is proportionately large, its transverse width approximately 50% of the maximum width of the distal end of the femur (Fig. 2B, F), as in the two species of *Dromomeron* (Fig. 2H, I). The crista tibiofibularis is proportionately narrower in *Lagerpeton*, measuring approximately 38% of the width of the distal end of the femur. In PVSJ 883, a shallow groove or trough separates the crista tibiofibularis from the lateral distal condyle (Fig. 2F). This groove is intermediate in form between the narrow slit in *Dromomeron gregorii* and the deeper, 'V'-shaped notch in *Dromomeron romeri* (Fig. 2H, I).

As in *Lagerpeton* and *Dromomeron romeri*, the medial distal condyle is rounded (Fig. 2G, H), in contrast to the subquadrate condyle in *Dromomeron gregorii* (Fig. 2I). The anterior edge of the medial condyle has a characteristic shape in lagerpetids; it protrudes to a varying degree as a sharp lip or flange (Irmis et al., 2007b). In PVSJ 883, this flange is present but is broken at the distal end (Fig. 2E, F). In PVSJ 883, the anterior and medial surfaces that delimit the flange meet at an acute angle of 45°, similar to the condition in *Dromomeron romeri* (Fig. 2D, E, H). In *Lagerpeton* (Fig. 2G) and *Dromomeron gregorii* (Fig. 2I), in contrast, these surfaces meet at nearly a 90° angle.

The lateral distal condyle is subequal in width to the crista tibiofibularis and medial distal condyle in PVSJ 883. In *Dromomeron gregorii*, in contrast, the lateral distal condyle is more rounded and swollen anteriorly (Fig. 2I). The popliteal fossa broadly separates the posterior aspect of the medial distal condyle and crista tibiofibularis (Fig. 2F). This notch is broader in *Dromomeron romeri* (Fig. 2H).

DINOSAURIFORMES Novas, 1992

SILESAURIDAE Nesbitt, Sidor, Irmis, Angielczyk, Smith, and Tsuji, 2010

IGNOTOSAURUS FRAGILIS, gen. et sp. nov.
(Fig. 3A–E; Table 1)

Etymology—From the Latin ‘ignotus,’ unknown; from the Greek ‘sauros,’ lizard; from the Latin ‘fragilis,’ fragile. The generic name ‘unknown lizard’ is in reference to the previously unknown presence of silesaurids in the well-sampled Ischigualasto Formation. The specific name is in reference to the extremely thin central portion of the blade of the ilium and gracile proportions of the femur.

Holotype—PVSJ 884, right ilium.

Type Locality and Horizon—S30°06'51", W67°54'14", situated along the northern edge of Cancha de Bochas, Ischigualasto Provincial Park, San Juan, Argentina, approximately 95 m above the base of the Ischigualasto Formation in the lower portion of the Cancha de Bochas Member (sensu Currie et al., 2009), and the lower portion of the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Fig. 5).

Age—Late Carnian on the basis of a radioisotopic date (⁴⁰Ar/³⁹Ar) from and ashbed located near the type locality. The original date (Rogers et al., 1993) has been recalibrated to 231.4 ± 0.3 Ma (Martínez et al., 2011b; Walker et al., 2013).

Diagnosis—Small silesaurid dinosauriform characterized by the following autapomorphies: iliac preacetabular process anteroposteriorly compressed and oriented at 90° to the iliac blade (Fig. 3A, C); iliac postacetabular process broadening distally and with a squared distal end in dorsal view (Fig. 3B, C).

Description—The right ilium of *Ignotosaurus fragilis*, which is missing only the central portion of the iliac blade (Fig. 3A–E), has the saddle-shaped lateral profile characteristic of silesaurids (Dzik, 2003). The ilium is longer anteroposteriorly than deep dorsoventrally, as in *Silesaurus* (Dzik, 2003) and many basal saurischians (e.g., *Eoraptor*, Sereno et al., 1993; *Panphagia*, Martínez and Alcober, 2009; *Chromogisaurus*; Ezcurra, 2010). In other basal dinosauriforms, such as *Marasuchus* (Sereno and Arcucci, 1994a), *Asilisaurus* (Nesbitt et al., 2010), and *Lagerpeton* (Sereno and Arcucci, 1994b), the ilium is proportionately deeper than long.

A ventral flange provides a back wall to the acetabulum, closing an articular socket with its contact with the ischium and pubis along its ventral edge, as in *Silesaurus* (Fig. 3A, B, D). The flange is deepest ventral to the pubic peduncle and has gently arched articular edges anteriorly and posteriorly. The middle portion of the iliac blade is extremely thin (ca. 1 mm), as in *Silesaurus* (Dzik, 2003). Also as in the latter, the dorsal edge of the iliac blade is slightly concave and tipped anteroventrally, from the postacetabular to the preacetabular process (Fig. 3A, B).

The supraacetabular crest is prominently oriented laterally, arching away from the pubic peduncle to form the lateral half of the articular surface for the femur (Fig. 3D). In lateral view (Fig. 3A), the crest only slightly overhangs the acetabular socket, as in *Silesaurus* and less so than in *Eoraptor*. Midway along the supraacetabular crest, a ridge rises from its dorsal surface and joins the lateral edge of the preacetabular process (Fig. 3A, E), as in *Silesaurus* (Fig. 3F), *Sacisaurus* (Ferguson and Langer, 2007), and *Asilisaurus* (Nesbitt et al., 2010).

The preacetabular process is flattened, with planar surfaces facing posterodorsally and anteroventrally (Fig. 3A–C, E). A plane through the process angles anterodorsally, its lateral margin coincident with the ridge descending to the acetabular crest. The preacetabular process projects anterodorsally nearly as far as the anterior margin of the pubic peduncle, as in *Silesaurus* (Fig. 3F). In *Marasuchus*, the preacetabular process is proportionately shorter (Fig. 3G). In *Ignotosaurus*, as in *Silesaurus*, the end of the process is marked by a rugose tuberosity (Fig. 3A, F). In *Silesaurus*, the tuberosity extends across the entire distal end of the process, whereas it is more limited in *Ignotosaurus*. The preacetabular process is directed anterolaterally, forming an angle of approximately 90° to the anteroposterior axis of the iliac blade (Fig. 3A, C), which is very different than in *Marasuchus* (Fig. 3G). The long postacetabular process is directed posterodorsally and has a well-developed brevis fossa on its ventral aspect (Fig. 3A, D), as in the dinosauriform *Silesaurus* (Fig. 3F) and most basal dinosaurs (e.g., *Eoraptor*, *Panphagia*, *Eodromaeus*). The brevis fossa is absent in other basal dinosauriforms such as *Lagerpeton* and *Marasuchus* (Fig. 3G). The end of postacetabular process is symmetrical with medial and lateral blades of equal width (Fig. 3D). The end of the postacetabular process is thickened and rectangular in cross-section. The lateral aspect of the distal end has a rugose area, which tapers anteriorly (Fig. 3A, C). A rugosity is present in a similar position in *Silesaurus* (Fig. 3F).

The pubic peduncle is long and stout as in *Silesaurus* (Fig. 3A, F). The dorsal margin of the process is prominent, giving the process a subtriangular cross-section (Fig. 3D). The articular surface is roughly concave with protruding dorsolateral and dorsomedial edges (Fig. 3E). The rounded ischial peduncle is anteroposteriorly elongate, with a ventrally and slightly posteriorly facing articular surface for the ischium (Fig. 3A, B, D). The distal articular surface forms a narrow triangle, the short side facing the acetabulum (Fig. 3D).

Phylogenetic Affinities of PVSJ 883 and *Ignotosaurus*

We scored PVSJ 883 and *Ignotosaurus* (Appendix 1) and included them in a phylogenetic analysis based on the data matrix in Nesbitt et al. (2010). Nine most parsimonious trees were generated with a length of 741 steps (consistency index, 0.467; retention index, 0.710) (Fig. 4). The indices and strict consensus tree are similar to those in the original analysis (Nesbitt et al., 2010). Implicit enumeration and branch support were estimated by performing 1000 bootstrap replications and calculating decay indices for each node (Fig. 4).

In the strict consensus tree, PVSJ 883 is positioned within Lagerpetidae as the sister taxon to the two species of *Dromomeron*, *D. romeri* and *D. gregorii*. This position is supported by the presence of a deep groove between the lateral condyle and crista tibiofibularis on the distal surface of the femur (character 221.1) and an acute anteromedial corner of the distal end of the femur (character 226.1). The decay index for this node is 2 and the bootstrap frequency of 66%, which is the most support that any node receives within the generally poorly known basal dinosauriform clades (Fig. 4). The enlarged crista tibiofibularis (much larger than the medial condyle) is an unambiguous synapomorphy uniting Lagerpetidae (Nesbitt et al., 2009). PVSJ 883 lacks two

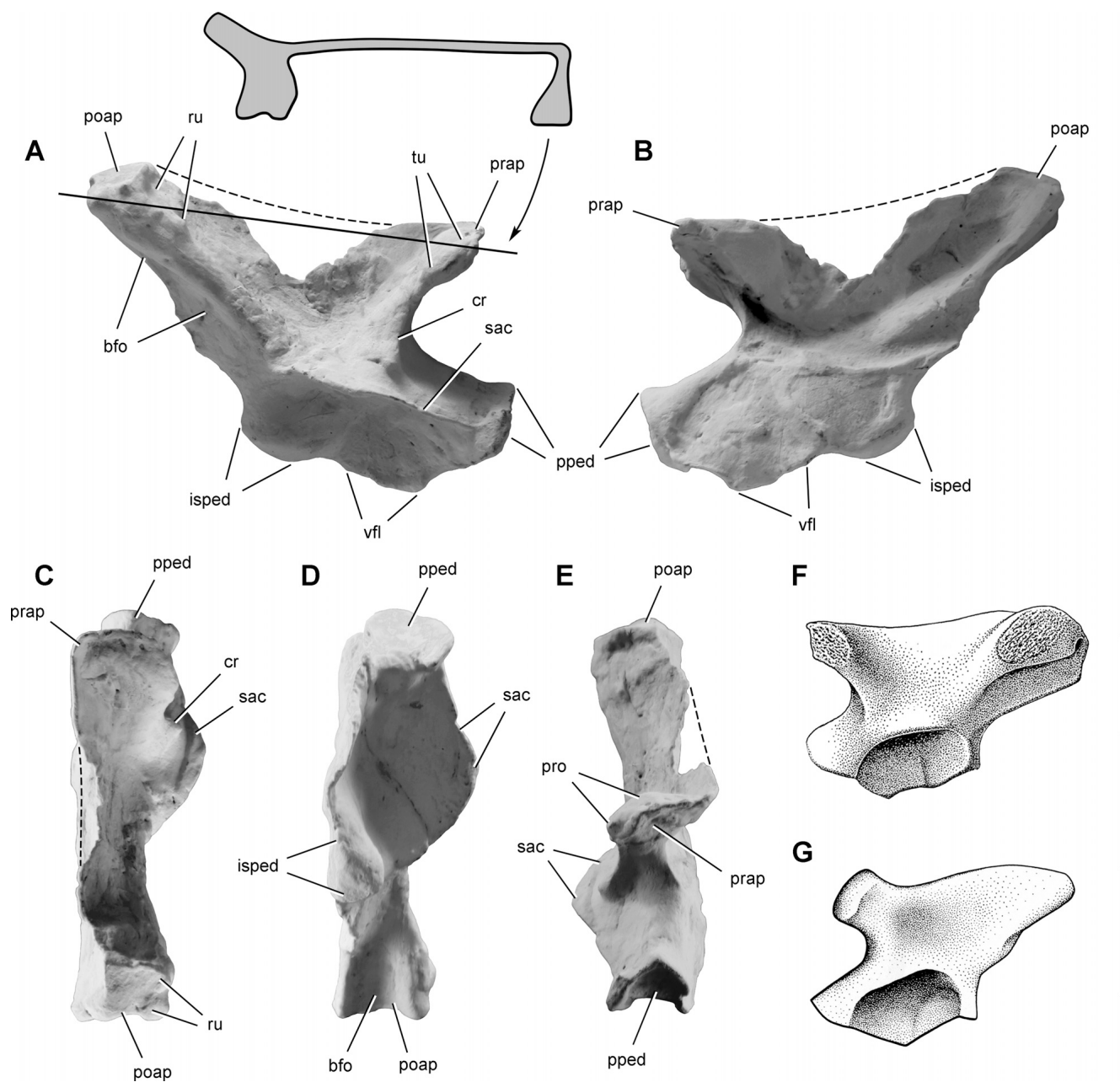


FIGURE 3. Ilium in Silesauridae and the basal dinosauriform *Marasuchus lilloensis*. Right ilium (PVSJ 884) of *Ignotosaurus fragilis*, gen. et sp. nov., from the Ischigualasto Formation in lateral (A), medial (B), dorsal (C), ventral (D), and anterodorsal (E) views. Horizontal cross-section of the ilium of *Ignotosaurus* (A). Left ilium in lateral view of the silesaurids *Silesaurus opolensis* (F) (from Dzik, 2003) and *Marasuchus lilloensis* (G) (from Sereno and Arcucci, 1994b). **Abbreviations:** bfo, brevis fossa; cr, crest; isped, ischial peduncle; poap, postacetabular process; pped, pubic peduncle; prap, preacetabular process; pro, protuberance; ru, rugosity; sac, supraacetabular crest; tu, tuberosity; vfl, ventral flange. Dashed line indicates a missing margin. Scale bar equals 2 cm in A–E, 3 cm in F, and 1 cm in G.

synapomorphies that diagnose *Dromomeron*—the concave posterolateral surface of the crista tibiofibularis and presence of distinct scar on the anterior surface of the distal end of the femur (Nesbitt et al., 2009).

Ignotosaurus fragilis is positioned within Silesauridae, joining a basal polytomy with *Lewisuchus* and other silesaurids (Fig. 4). Silesauridae is supported by three synapomorphies: presence of a distinct fossa in the ilium for the attachment of the m. caudifemoralis brevis (177.1); fossa trochanteric of the femur at level with greater trochanter (215.0); and lateral condyle of the tibia at

level with the medial condyle at its posterior border (230.1). Because only the first of these is preserved in *Ignotosaurus*, its inclusion is poorly supported (decay index of 1; bootstrap frequency below 50%) (Fig. 4).

GEOLOGIC AND PALEOCLIMATIC SETTING

The evolution of the Ischigualasto-Villa Unión basin during the Late Triassic has long generated considerable interest as a key field area for understanding Triassic tectonics and paleoclimate (e.g., Stipanovic and Bonaparte, 1972; Milana and

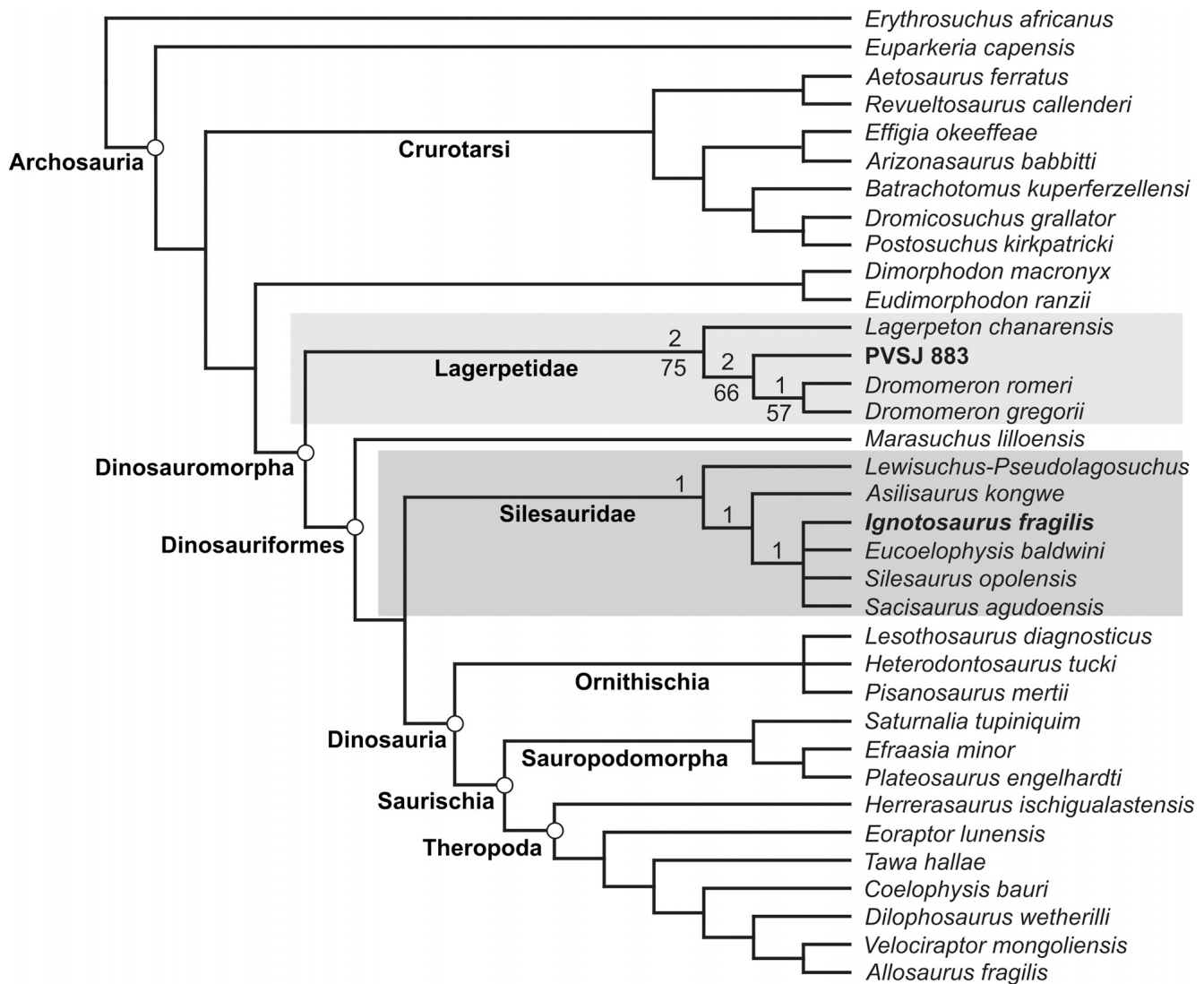


FIGURE 4. Strict consensus tree for basal archosaurs generated from maximum parsimony analysis of a data matrix modified from Nesbitt et al. (2010). Nine minimum-length trees have a length of 741 steps (consistency index, 0.467; retention index, 0.710). Lagerpetids including PVSJ 883 and silesaurids including *Ignotosaurus fragilis*, gen. et sp. nov., are shaded (see Appendix 1 for scorings). Nodal support (decay indices above, bootstrap frequencies greater than 50% below) is given at nodes within Lagerpetidae and Silesauridae.

Alcober, 1994; Spalletti et al., 1999; Shipman, 2004; Tabor et al., 2006; Colombi, 2007; Colombi and Parrish, 2008; Currie et al., 2009). These studies focus on sediment architecture, paleosols, paleobotany, and taphonomy and permit an overview of climatic and tectosedimentary (geomorphic) evolution. The vertebrate fauna described and tabulated below entered the fossil record through this taphonomic and climatic filter.

The Ischigualasto Formation is an almost exclusively fluvial succession deposited in the last stage of the extensional opening of the Ischigualasto-Villa Unión Basin (Milana and Alcober, 1994). The fluvial architecture and paleosols vary in a characteristic manner within the formation, which has allowed recognition of four lithostratigraphic members. From the base to the top, these include the La Peña (ca. 50 m), Cancha de Bochas (ca. 130 m), Valle de la Luna (ca. 450 m), and Quebrada de la Sal members (ca. 60 m) (Currie et al., 2009). Plant (Colombi and Parrish, 2008) and vertebrate (Colombi et al., 2013) preservational features vary, mirroring these stratigraphic divisions.

The division into distinctive members has been seen as a reflection of the accommodation space, or degree of confinement, of the basin during opening of a structural rift in combination with local and global climatic change (Milana and Alcober, 1994; Colombi and Parrish, 2008; Colombi et al., 2010, 2011). An abrupt increase in accommodation space occurred at the beginning of Ischigualasto deposition (ca. 231.6 Ma), when rifting changed the depositional setting from a lacustrine to an open fluvial basin. A second interval (ca. 231.1 Ma) is characterized by intermittent rifting and seasonal aridity, as evidenced by variation in aggradation rates, calcic soils, absence of root traces, and calcic permineralization of vertebrate fossils. A third interval (ca. 230.2 Ma) records the gradual increase in the humidity, as evidenced by standing water in thicker floodplain deposits, transition to argillisol, abundant plant remains including cuticles and palynomorphs, and rare vertebrate fossils characterized by hematitic permineralization. The last interval (ca. 226 Ma) represents transitional facies to the overlying redbeds of the Los Colorados Formation.

CHRONOSTRATIGRAPHY

With the exception of a Jurassic age assigned to the Ischigualasto Formation by Bodenbender (1911), authors have historically regarded the Ischigualasto Formation as late Middle (Ladinian) to Late (Carnian–Norian) Triassic in age prior to evidence generated by radioisotopic dating (Romer, 1960a, 1960b; Reig, 1963; Bonaparte, 1973, 1982; Sereno and Novas, 1992). The age of the Ischigualasto Formation was originally based on regional geologic criteria (Stelzner, 1885; Bodenbender, 1911; Frenguelli, 1948; Groeber and Stipanovic, 1952). With the discovery of vertebrate fossils (Cabrera, 1943), that age was revised using vertebrate biostratigraphic correlations to other units in South America (Romer, 1960a, 1960b, 1962; Reig, 1963; Bonaparte, 1973, 1982; Sereno and Novas, 1992).

Radioisotopic dating of volcanic ashbeds eventually provided absolute age constraints (Gonzalez and Toselli, 1971; Rogers et al., 1993; Shipman, 2004; Martínez et al., 2011b), largely supporting previous relative age interpretations. Ashbed samples for these dates were all derived from the most fossiliferous southern outcrops of the formation: the first near the base of the formation (Rogers et al., 1993); another from the basalt flows of Cerro Morado near the southeastern edge of the basin (Gonzalez and Toselli, 1971); and two near the top of the formation (Shipman, 2004; Martínez et al., 2011b). This distribution of samples within the section provides bracketing temporal constraints for deposition of the formation. Preliminary results of a magnetostratigraphic survey of southern outcrops of the overlying Los Colorados Formation (Santi Malnis et al., 2011) provide additional support for the upper age of the Ischigualasto Formation (ca. 227 Ma).

Ages Low in Section

Cerro Morado—A K–Ar date of 223 ± 4 Ma, the first radioisotopic age for the Ischigualasto Formation, was based on the thick basal basalt flow (Gonzalez and Toselli, 1971). The sample was taken from the top of a butte (Cerro Morado) located south of the main outcrops of the Ischigualasto Formation and thought to be stratigraphically below the Ischigualasto Formation (Fig. 1). This radioisotopic age, one of the first for a Triassic fossil-bearing formation in South America, has been widely cited (Valencio et al., 1975; Odin et al., 1982; Currie et al., 2009; Martínez et al., 2011b). Valencio et al. (1975) also reported a paleomagnetic pole from the same basalt with a paleopole position consistent with a Triassic age. Odin et al. (1982) cited this date without explanation as 229.0 ± 5 Ma rather than 223 ± 4 Ma. Currie et al. (2009) suggested that the basalt at Cerro Morado may be correlative with basalt flows in the lower part of the Ischigualasto Formation. Following Odin et al. (1982), they also cited this date as 229.0 ± 5 Ma.

We regard this date as flawed for the following reasons: (1) the sample comes from an unspecified region of a basalt flow that is 15 m thick and composed of at least three flow events of unknown duration (Gonzalez and Toselli, 1971; Page et al., 1997); (2) the sampled basalt overlies the Middle Triassic (Ladinian) Chañares Formation, which casts doubt on possible correlation with basalts within the Ischigualasto Formation (contra Currie et al., 2009); (3) the methods used for derivation of the age have never been clarified; and (4) no reason has been given for increasing the age and decreasing its accuracy from 223 ± 4 Ma, as originally reported (Gonzalez and Toselli, 1971), to 229.0 ± 5 Ma (Odin et al., 1982).

Herr Toba—Rogers et al. (1993) reported an $^{40}\text{Ar}/^{39}\text{Ar}$ age using incremental laser heating of fine-grained sanidine crystals extracted from a bentonite (Herr Toba) 20 m above the base of the formation (Fig. 1). Incremental heating analyses of the sanidine with well-defined spectra gave overlapping plateau ages of 228.06 ± 0.78 and 227.78 ± 0.30 Ma. The authors concluded that the lat-

ter date presented a more refined spectrum and considered it the more accurate of the two ages (227.78 ± 0.30 Ma).

Furin et al. (2006) recalibrated the age given by Rogers et al. (1993), adjusting for bias in the $^{40}\text{Ar}/^{39}\text{Ar}$ timescale that often results in ages ca. 1% too young (Min et al., 2000; Mundil et al., 2006; Kuiper et al., 2008). They recalculated the age of the Herr Toba as 229.2 Ma relative to an age for Fish Canyon Tuff of 28.02 ± 0.3 (originally 227.8 ± 0.3 Ma by $^{40}\text{Ar}/^{39}\text{Ar}$ relative to Fish Canyon Tuff of 27.84 Ma). Because $^{40}\text{Ar}/^{39}\text{Ar}$ dates are often 0.5–1.0% younger than U–Pb dates, their final estimate of the age of the Herr Toba was 230.3–231.4 Ma. Recently, Martínez et al. (2011b) recalculated the Herr Toba age as 231.4 ± 0.3 Ma, accounting for recent revisions of standard ages and the ^{40}K decay constant bias (Renne et al., 2010).

Ages High in Section

Las Cascadas—The first radioisotopic date for the upper Ischigualasto Formation was cited by Currie et al. (2009) based on an unpublished dissertation (Shipman, 2004). The sample was collected near the top of “section 3” in that study (Shipman, 2004:fig. B2), located 352 m above the base of the formation near Las Cascadas (Fig. 1). The date was determined by $^{40}\text{Ar}/^{39}\text{Ar}$ incremental laser heating of fine-grained sanidine crystals, yielding a date of 218 ± 1.7 Ma.

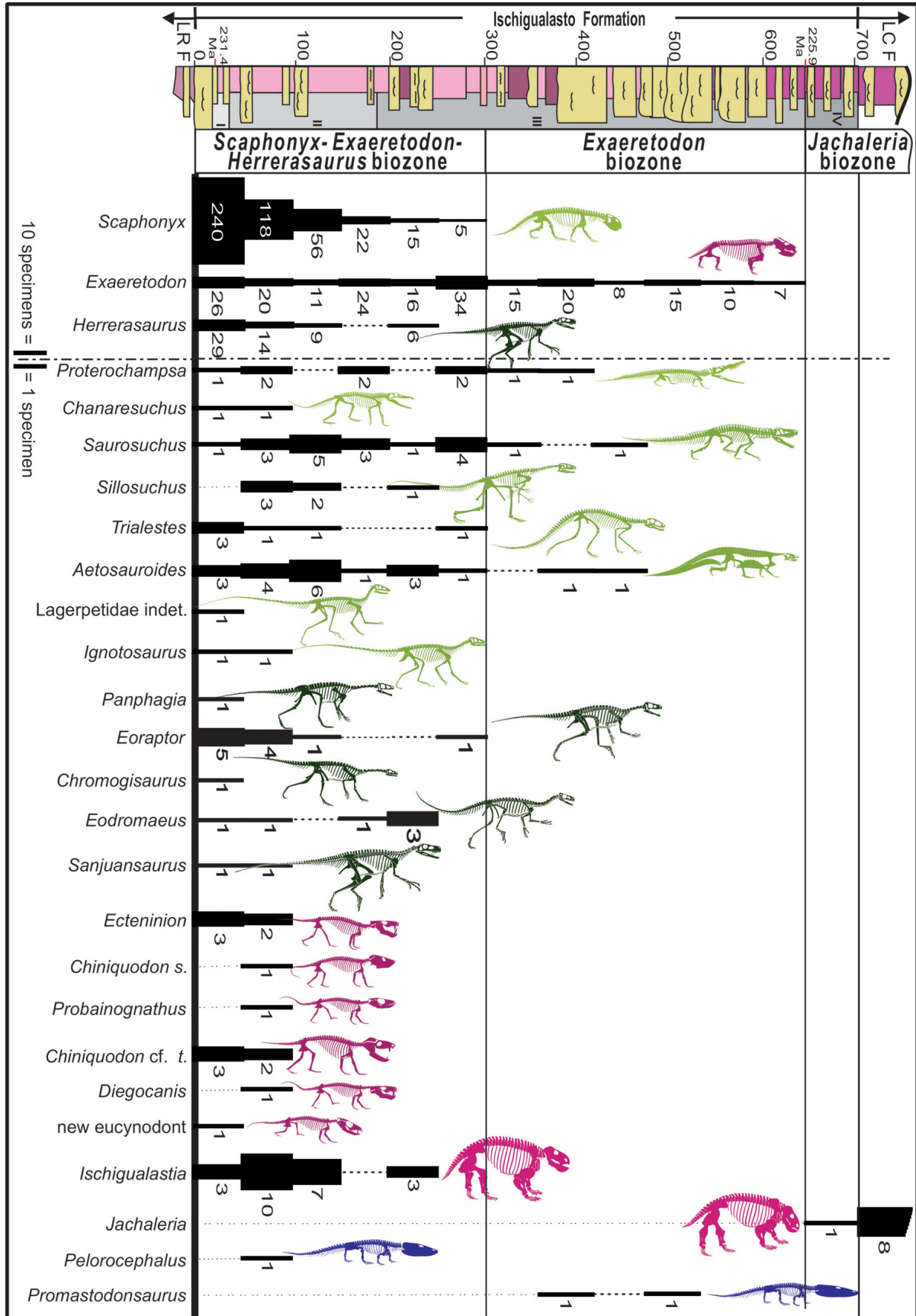
There are several potential problems with this age. ‘Section 3’ is located at the southeastern extremity of outcrops of the Ischigualasto Formation near a major fault zone (El Alto fault) (Fig. 1). As noted by the Shipman (2004), this was the only sample out of 14 from the locality that yielded a date. Two ashbeds near the top of the formation were dated to 223 and 218 ± 1.5 Ma, respectively (Shipman, 2004:126), although the author does not provide more details about these alternative dates or the methodology for age estimation. Finally, Shipman (2004) cited four different dates for the same stratigraphic level (Shipman, 2004:figs. B-5, C-7, date 220 Ma; fig. B-8, -9, -11, date 218.5 ± 1.7 Ma; and fig. B-10, date 222.1 ± 2.2 Ma), and it is not clear which one is the correct or preferred age.

ISCH-6-611—The second available age was determined by $^{40}\text{Ar}/^{39}\text{Ar}$ analysis of sanidine or anorthoclase crystals extracted from a bentonite (ISCH-6-611) located in the southern outcrops of the formation (section 1; Currie et al., 2009), 630 m above the base and 70 m below the top of the formation (Martínez et al., 2011b). Sixteen grains were analyzed by total fusion yielding a coherent population of eight grains of low-Ca/K (2.0–4.0) plagioclase with a nominal weighted age of 223.84 ± 0.88 Ma. Another analysis was attempted on an additional 24 crystals. Although some failed to yield useful results, five yielded nominal plateau ages from 218 ± 7 to 226 ± 6 Ma. Their combined uncorrected, weighted mean age is 223.10 ± 2.20 Ma. Combining the results of both type of measurements yielded an uncorrected age of 223.79 ± 0.87 Ma. Because of uncertainties in ^{40}K decay constants used to calculate these ages (Min et al., 2000), the method of Renne et al. (2010) was used to obtain a final age estimate of 225.9 ± 0.9 Ma (Martínez et al., 2011b).

Ramezani et al. (2011) conjectured that the sample upon which this age is based was contaminated with the crystals older than the true depositional age of the formation. Without any additional evidence to the contrary, however, we regard the sample as valid and the age estimate of 225.9 ± 0.9 Ma as reasonable.

Magnetostratigraphy of the Overlying Los Colorados Formation

Recently, Santi Malnis et al. (2011) published preliminary results from a magnetostratigraphic study of the overlying southern outcrops of the Los Colorados Formation. They obtained consistent remnant magnetization at 60 paleomagnetic sites distributed over 600 m of a complete section. The



magnetostratigraphic record of the Los Colorados Formation was correlated with the magnetostratigraphic section for the Late Triassic from the Newark Basin along the east coast of the North America (Kent et al., 1995; Kent and Olsen, 1999). According to these correlations, the section falls between magnetochron zones E7r and E14n in the Late Triassic (Kent et al., 1995), suggesting that deposition of the Los Colorados Formation began ca. 227 Ma and ended ca. 215 Ma during the early to middle Norian (Walker et al., 2013).

VERTEBRATE ASSEMBLAGES

The approximately 2000 vertebrate specimens collected from the Ischigualasto Formation probably represent less than 5% of the number of individuals preserved in at least a fragmentary manner on the outcrop. Most fossils are not collected because they consist of highly weathered, unrecognizable pieces. In addition, preservational potential is highly variable across the formation (Colombi et al., 2013). Among collected specimens, the Ischigualasto Formation yields a relatively high number (ca. 10%) of complete or partial articulated skeletons. A wide range of body sizes among vertebrates is preserved (15 cm to more than 10 m), and fossils also include soft-bodied invertebrates such as insects (Frenguelli, 1945; Gallego et al., 2004; Giuliano, 2010), coprolites (Hollocher et al., 2005), and large-diameter burrows (Colombi et al., 2008, 2012). The Ischigualasto Formation also preserves a rich paleobotanical record that includes impressions, cuticles, and palynomorphs (Zamuner, 1991; Spalletti et al., 1999; Artabe et al., 2001; Colombi and Parrish, 2008; Colombi et al., 2011) as well as the more common permineralized wood (Archangelsky and Brett, 1961, 1963; Bonetti, 1966; Archangelsky, 1968; Colombi and Parrish, 2008).

Fossil distribution is spatially and temporally heterogeneous within the formation. Previous work suggested that most of the fossils occur in the lower two-thirds of the formation (Bonaparte, 1982; Rogers et al., 1993). Recently, Martínez et al. (2011b) refined the abundance and diversity of vertebrate specimen distribution, arguing that fossil preservation is correlated with sedimentary paleoenvironments as captured in distinctive stratigraphic members (Martínez et al., 2011b).

The majority of the known tetrapod assemblage of the Ischigualasto Formation was found in southern outcrops of the formation. Exceptions include the ornithischian *Pisanosaurus* from Cerro Bola, a large specimen of *Herrerasaurus* originally described as '*Frenguellisaurus*' (Novas, 1986) from La Chilca Creek, and one specimen of *Triolestes* (Bonaparte, 1978) from Cerro Las Lajas. These specimens come from outcrops located north of El Salto (Fig. 1), and their stratigraphic positions relative to fossils from southern outcrops remain unknown.

Martínez et al. (2011b) divided the Ischigualasto Formation into three abundance-based biozones: (1) the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone; (2) the *Exaeretodon* biozone; and (3) the *Jachaleria* biozone. The *Scaphonyx-*

Exaeretodon-Herrerasaurus biozone spans the La Peña Member and the lower one-third of the Valle de la Luna Member, and it includes the majority of fossils and the highest diversity. It is characterized by a great predominance of the rhynchosaur *Scaphonyx*, the cynodont *Exaeretodon*, and the dinosaur *Herrerasaurus*. The *Exaeretodon* biozone, which includes the upper two-thirds of the Valle de la Luna Member, is characterized by low diversity and high relative abundance of the cynodont *Exaeretodon*. The *Jachaleria* biozone, spanning the Quebrada de la Sal Member and continuing into the lower section of the overlying Los Colorados Formation, is almost devoid of vertebrate fossils. Two principal transitions divide the formation into the three biozones. The end of the first biozone is marked by the disappearance of the rhynchosaur *Scaphonyx* and the simultaneous disappearance of dinosaur occurrences and most of the therapsid genera. The end of the second biozone is marked by the disappearance of the cynodont *Exaeretodon*.

The current census includes 848 vertebrate fossils, all of them mapped to the southern outcrops of the Ischigualasto Formation (Fig. 5; Table 2). In the area selected for the census (Fig. 1), the outcrops are homogeneously well exposed from the bottom to the top of the unit, and uniform sampling was done by the authors. To better understand the role of each taxon, we logged inferred diet, habitat, and body mass estimates, the latter divided arbitrarily into small (<25 kg), medium (25–250 kg), and large body masses (>250 kg).

The 29 known genera fall into three major clades: Amphibia, Diapsida, and Synapsida (Table 2; Appendix 2). Diapsida is the most diverse, constituting 71% of the specimens and 63% of generic diversity. Synapsida is second, constituting 37% of the specimens and 35% of generic diversity. Amphibia represents only 2% of abundance and generic diversity (Table 2). The major vertebrate subgroups, ranked according to decreasing abundance, include therapsids 35% (10 genera), dinosauromorphs 31% (nine genera), crurotarsans 17% (five genera), basal archosauriforms 7% (two genera), temnospondyls 7% (two genera), and basal archosauriforms 3% (one genus).

Faunal Composition of the *Scaphonyx-Exaeretodon-Herrerasaurus* Biozone

The *Scaphonyx-Exaeretodon-Herrerasaurus* biozone constitutes 91% of all collected fossils and 93% of genera (25 of 27). In this zone, the highly specialized, herbivorous, medium-sized *Scaphonyx* is the most abundant taxon (59.5%), followed by the other herbivore of similar size, the cynodont *Exaeretodon* (17%). The third-most abundant taxon is the mid- to large-sized carnivore *Herrerasaurus* (8%). The remaining 15.5% is distributed among 24 genera. The most abundant of these are the herbivorous dicynodont *Ischigualastia* (3.1%), aetosaur *Aetosauroides* (2.5%), the large 'rauisuchid' *Saurosuchus* (2.4%), the small saurischian dinosaur *Eoraptor* (1.4%), the basal archosauriform *Proterochampsia* (1%), the carnivorous cynodont *Ecteninion*

← FIGURE 5. Range chart indicating the stratigraphic distribution and relative abundance of 26 of the 29 known vertebrate taxa in the Ischigualasto Formation. The stratigraphic positions of the rare ornithischian *Pisanosaurus*, the ornithosuchid *Venaticosuchus*, and the non-mammalian cynodont *Ischnognathus* are poorly constrained stratigraphically and so are not included. Lower (231.4 Ma) and upper (225.9 Ma) radiometric ages and the three biozones are shown alongside a simplified, 700-m-thick section across the fossiliferous zone (modified from Martínez et al., 2011b). The sampling interval for the 848 fossil vertebrate specimens in our survey is 50 m in the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone and 60 m in the two overlying biozones. Species abundance is given graphically (bar thickness) and numerically for each interval. Due to scale problems, the most abundant taxa (*Scaphonyx*, *Exaeretodon*, and *Herrerasaurus*) are located at the right separated by a dot-dash line from the other taxa and their bar width is reduced by a factor of 10. Black dotted lines represent ghost lineages. Stratigraphic section is composed of gleyed vertisols and paleosols (purple), calcic vertisols and paleosols (pink), and channel sandstone (yellow). Vertebrates are divided into temnospondyl amphibians (blue), basal archosauriforms and crurotarsans (light green), basal dinosaurs (dark green), and basal synapsids (pink). **Abbreviations:** I, La Peña Member; II, Cancha de Bochas Member; III, Agua de la Peña Member; IV, Quebrada de la Sal Member; **LC F**, Los Colorados Formation; **LR F**, Los Rastros Formation.

TABLE 2. Characterization of the vertebrate fossil record within the Ischigualasto Formation, based on a mapped collection of 851 fossil vertebrates that record the presence of 29 extinct species.

Taxon	Quantity			Habit	Diet	Mass (kg)	References
	B1	B2	B3				
Temnospondyli							
<i>Promastodontosaurus bellmani</i>	0	2	0	Aquat	Carn	<25	Bonaparte, 1963a
<i>Pelorocephalus ischigualastensis</i>	1	0	0	Aquat	Carn	<25	Bonaparte, 1975
Archosauromorpha							
<i>Scaphonyx sanjuanensis</i>	456	0	0	Land	Herb	25–250	Sill, 1970
Archosauriformes							
<i>Proterochampsa barrionuevoi</i>	7	2	0	Aquat	Carn	25–250	Sill, 1967
<i>Chanaresuchus ischigualastensis</i>	2	0	0	Aquat	Carn	<25	Trotteyn et al., 2012
Crurotarsi							
<i>Saurosuchus galilei</i>	17	2	0	Land	Carn	>250	Reig, 1959, 1961
<i>Sillosuchus longicervix</i>	6	0	0	Land	Carn?	25–250	Alcober and Parrish, 1997
<i>Trialestes romeri</i>	6	0	0	Land	Carn	25–250	Reig, 1963
<i>Venaticosuchus rusconii</i>	0	?	0	Land	Carn	<25	Bonaparte, 1971
<i>Aetosauroides scagliai</i>	18	2	0	Land	Herb	25–250	Casamiquela, 1961, 1967a
Dinosauromorpha							
Lagerpetidae indet.	1	0	0	Land	Carn?	<25	This study
Dinosauriformes							
<i>Ignotosaurus fragilis</i>	1	0	0	Land	Herb?	<25	This study
Ornithischia							
<i>Pisanosaurus mertii</i>	0	0	1?	Land	Herb	<25	Casamiquela, 1967b
Sauropodomorpha							
<i>Panphagia protos</i>	1	0	0	Land	Omn?	<25	Martínez and Alcober, 2009
<i>Chromogisaurus novasi</i>	1	0	0	Land	Herb?	<25	Ezcurra, 2010
<i>Eoraptor lunensis</i>	10	0	0	Land	Omn?	<25	Sereno et al., 1993
Theropoda							
<i>Eodromaeus murphi</i>	6	0	0	Land	Carn	<25	Martínez et al., 2011b
<i>Herrerasaurus ischigualastensis</i>	59	0	0	Land	Carn	25–250	Reig, 1963
<i>Sanjuansaurus gordilloi</i>	2	0	0	Land	Carn	25–250	Alcober and Martínez, 2010
Dicynodontia							
<i>Ischigualastia jenseni</i>	23	0	0	Land	Herb	>250	Cox, 1962
<i>Jachaleria colorata</i>	0	0	1	Land	Herb	>250	Bonaparte, 1971
Cynodontia							
<i>Exaeretodon argentinus</i>	131	75	0	Land	Herb	25–250	Bonaparte, 1962
<i>Ischignathus sudamericanus</i>	1?	0	0	Land	Herb	25–250	Bonaparte, 1963b
<i>Ecteninion lunensis</i>	7	0	0	Land	Carn	<25	Martínez et al., 1996
<i>Chiniquodon sanjuanensis</i>	1	0	0	Land	Carn	<25	Martínez and Forster, 1996
cf. <i>Probainognathus</i> sp.	1	0	0	Land	Carn	<25	Bonaparte and Crompton, 1994
<i>Chiniquodon</i> cf. <i>theotonicus</i>	5	0	0	Land	Carn	25–250	Bonaparte, 1966
<i>Diegoanis elegans</i>	1	0	0	Land	Carn	<25	Martínez et al., 2013a
Unnamed eucyndont	1	0	0	Land	Carn	<25	Martínez et al., 2011a

Of these specimens, 848 are logged with confidence below into one of three biozones (B1–3). Three specimens of questionable biozone assignment are the holotypic and only specimens of the ornithischian *Pisanosaurus mertii* (Casamiquela, 1967b), the ornithosuchid *Venaticosuchus rusconii* (Bonaparte, 1971), and the traversodontid cynodont *Ischignathus sudamericanus* (Bonaparte, 1963b), the type localities of which are poorly known. *Pisanosaurus* and *Venaticosuchus* were found to the north in poorly fossiliferous outcrop near La Chilca Creek (Fig. 1). The number of specimens, habitat (aquatic, land), diet (herbivorous, carnivorous), estimated body mass (small is <25 kg; mid-sized is 25–250 kg; large is >250 kg), and original references are given for each of the 29 species. **Abbreviations:** **aquat**, aquatic; **B1**, *Scaphonyx-Exaeretodon-Herrerasaurus* biozone; **B2**, *Exaeretodon* biozone; **B3**, *Jachaleria* biozone; **carn**, carnivorous; **herb**, herbivorous.

(1%), the poposauroid *Sillosuchus* (0.8%), the basal crocodylomorph *Trialestes* (0.8%), the small theropod *Eodromaeus* (0.8%), and the carnivorous cynodont *Chiniquodon* (0.7%). The rest of the taxa are known by single specimens, constituting 0.6% of the fossils (Table 1).

In the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone, the secondary terrestrial consumers (carnivores) are more diverse, although less abundant, than the primary consumers (herbivores), constituting 58% of the genera. When pooling the terrestrial and aquatic genera (*Pelorocephalus*, *Proterochampsa*, and *Chanaresuchus*), carnivores constitute 63% of the genera. In the terrestrial habitat, the ratio between diversity of carnivores and herbivores is 1.0 for large species (>250 kg) and increases to 1.25 for mid-sized genera (25–250 kg) and 1.6 for small-bodied taxa (<25 kg). In contrast, the diversity of small carnivores is dispersed across a greater variety of clades, including crurotarsans (*Venaticosuchus*), dinosauromorphs (a lagerpetid PVSJ 883, *Eodromaeus*), and cynodonts (*Ecteninion*, *Probesodon*, *Probainognathus*, *Diegoanis*,

and an unnamed new eucynodont), whereas the small herbivores are all dinosauriforms (a silesaurid, *Panphagia*, *Chromogisaurus*, and *Eoraptor*).

In general, carnivores are less abundant than the herbivores (13.5%). Among the small-bodied vertebrates, in contrast, carnivores are more abundant (55%), even with the basal sauropodomorphs *Panphagia* and *Eoraptor* counted among herbivores. This high percentage of carnivores may indicate that some may prey upon aquatic taxa or terrestrial invertebrates or some may be tertiary consumers or scavengers.

Two aspects are important regarding vertebrate fossil distribution within the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone. First, abundance and diversity are not stratigraphically homogeneous; both decrease from older to younger levels. Second, the faunal shift between this biozone and the next (*Exaeretodon* biozone) occurs gradually rather than suddenly (Fig. 5).

More than 60% of the fossils in the biozone occur in the lower 100 m (515 specimens). Abundance decreases from the base of

the formation through the first 200 m. Thus, the first 50 m of the biozone records two-thirds (324) of the specimens. That number decreases by about one-third in the next 50 m of section (191 specimens) and by another one-third in the interval from 100–150 m (108 specimens). The number of specimens decreases even more in the next interval, with just 53 specimens from 150 to 200 m. After that, abundance is almost constant, with approximately 50 specimens every 50 m of section. The decline in fossil richness is heavily influenced by the progressive decline in the numbers of specimens attributable to *Scaphonyx* and *Herrerasaurus* (Fig. 5). On the other hand, most of the rest of the taxa seem to maintain their abundance along the same interval, although these are based on low sample sizes in each 50-m interval.

The broad exposure of the section in southern outcrops of the Ischigualasto Formation suggests that the aforementioned decrease of abundance and diversity of fossils within the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone is not the result of a decrease in outcrop. The disappearance of *Scaphonyx* and *Herrerasaurus* may be the result of environmental changes, including an increase of humidity, evidenced by the appearance of standing water bodies in thicker floodplain deposits, gradual transition from calcisols to argillisols, and preservation fossil plants (Tabor et al., 2006; Colombi and Parrish, 2008; Currie et al., 2009; Colombi et al., 2013). These changes may have affected the geochemical condition of the surface and subsurface. This is a gradual decline, although there is a conspicuous, laterally extensive 2-m-thick layer composed by reworked pink tuff located at the end of the biozone (Fig. 5). Volcanic activity may have killed off the rhynchosaurs, although their abundance in the formation was already in decline.

Vertebrate taxonomic diversity shows a different pattern from that of abundance. Diversity decreases in one step after the lowest 100 m of thickness of the formation. From 20 taxa present in the lowest 100 m, only 11 persist higher in section (Fig. 5). All of the taxa that disappear in the upper interval are small-bodied tetrapods, with the exception of the medium-bodied herrerasaurid dinosaur *Sanjuansaurus*. The absence of *Sanjuansaurus* could be related to its scarcity (only two specimens preserved) or that some of the fragmentary specimens attributed to *Herrerasaurus* in overlying layers may pertain to *Sanjuansaurus*.

In any event, the absence of 80% of the small-bodied taxa after the lowest 100 m of the formation is probably related to a taphonomic bias against the preservation of small, more fragile bones. In particular, there is a gradual decrease in abundance of layers with carbonitic nodules after the first 100 m that mark a change in pedogenesis, from dominant calcic soils in Cancha de Bochas Member to mainly argillic soils in the Valle de la Luna Member (Tabor et al., 2006; Currie et al., 2009). These pedogenic changes are also correlated with different types of fossil mineralization from calcite to hematite dominant (Colombi et al., 2013).

Faunal Composition of *Exaeretodon* Biozone

The *Exaeretodon* biozone includes the upper two-thirds of the Valle de la Luna Member (Martínez et al., 2011b). It is characterized by the numerical predominance of specimens of the cynodont *Exaeretodon* (90.3%) and rare presence (2.4% each) of the temnospondyl amphibian *Promastodontosaurus*, the 'rauisuchid' *Saurosuchus*, the aetosaur *Aetosauroides*, and the basal archosauriform *Proterochampsa*. Of the three eponymous taxa in the underlying *Scaphonyx-Exaeretodon-Herrerasaurus* biozone, only the herbivorous cynodont *Exaeretodon* remains unaffected, because the abundance of *Exaeretodon* is almost the same as in the underlying biozone. Specimens of other taxa, such as *Promastodontosaurus* and the survivors of the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (*Proterochampsa*, *Aetosauroides*, and *Saurosuchus*), are only found in the lower half of the biozone.

At the top of the Valle de la Luna Member, it seems there is a return to xeric conditions and continued volcanic activity, evidenced by the presence of root halos linked with the immature soils. A shift in the composition of the vertebrate fauna of the Ischigualasto Formation is marked by the final disappearance of the medium-sized herbivorous cynodont *Exaeretodon* (an abundant component of the two lower biozones and the only survivor of the diverse vertebrate fauna) and the appearance of the larger-bodied herbivorous dicynodont *Jachaleria* in the succeeding biozone.

Faunal Composition of *Jachaleria* Biozone

The *Jachaleria* biozone is located within the Quebrada de la Sal Member and is almost devoid of fossils. As noted before, the virtual absence of fossils in this biozone is probably not due to sampling efforts or limited exposure; it has been as intensively searched as the others. Nonetheless, only a single bone of the dicynodont *Jachaleria* and a couple of bones tentatively assigned to a non-dinosaurian archosaur have been discovered. Although this biozone is highly depauperate, due to a true scarcity of fauna or by taphonomic bias, the changes produced at the beginning of this biozone are remarkable. The final disappearance of the medium-sized herbivorous cynodont *Exaeretodon*, an abundant component of the two underlying biozones, and the appearance of the large-bodied herbivorous dicynodont *Jachaleria*, marks a shift in the composition of the vertebrate fauna of the Ischigualasto Formation. This poorly known new association persists across the formation boundary through the basal portion of the overlying Los Colorados Formation, where the fossils are more abundant (Fig. 5). The faunal replacement recorded in the *Jachaleria* biozone, coincident with the dated upper ash, ca. 225.9 Ma, is principally correlated to climate change, with a return to drier conditions.

The persistence of the same assemblage through the uppermost Ischigualasto Formation and the lower Los Colorados Formation is not surprising. The Quebrada de la Sal Member, coincident with the Ischigualasto portion of *Jachaleria* biozone, contains the same fluvial architecture (meandering) and immature soils as does the lower portion of Los Colorados Formation. The only true change between these formations is chromatic, from greenish-gray (Ischigualasto) to red (Los Colorados). The return to arid conditions is evidenced in the Quebrada de la Sal Member and basal portion of the overlying Los Colorados Formation by the presence of desiccation cracks and decrease in the deepness of root traces, as well as the absence of other fossil plant remains.

Vertebrate Succession

The vertebrate assemblage from the Ischigualasto Formation demonstrates that the faunal shift was a gradual process unfolding over approximately 5 million years. This gradual process involved (1) the extinction of the medium-sized herbivorous rhynchosaur *Scaphonyx* and the large-sized herbivorous dicynodont *Ischigualastia*; and (2) the subsequent extinction of the medium-sized herbivorous cynodont *Exaeretodon*. As noted previously (Martínez et al., 2011b), these events were not synchronous and did not result in a compensating increase in abundance or diversity of dinosaurs. During this interval, the rare temnospondyl amphibian *Promastodontosaurus* is the only new species to appear in the section. In the upper portion of the section, the rare dicynodont *Jachaleria* is the only new taxon to appear after the extinction of the cynodont *Exaeretodon*. Fossils in the *Jachaleria* biozone, however, are very scarce and the true faunal composition of this biozone is therefore poorly known. More fossil evidence is needed to understand the transition from this depauperate fauna to the diverse Norian assemblage of the upper Los Colorados Formation (Bonaparte, 1978; Arcucci et al., 2004), which includes abundant medium- to large-sized

herbivorous sauropodomorph dinosaurs, turtles, aetosaurs, carnivorous crurotarsans, and theropod dinosaurs.

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APPENDIX 1. Character state scorings of the lagerpetid PVSJ 883 and the silesaurid *Ignotosaurus fragilis*, gen. et sp. nov. (PVSJ 884), for the matrix of Nesbitt et al. (2010).

PVSJ 883

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Ignotosaurus fragilis

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APPENDIX 2. Tetrapod fossils from the Ischigualasto Formation, grouped in major clades.

Archosauromorpha

Scaphonyx sanjuanensis
Sill, 1970

Occurrence—La Peña and Cancha de Bochas members (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herreriasaurus* biozone (Martínez et al., 2011b).

Holotype—MACN 18185, a partial skull and postcranial skeleton.

Comments—Langer and Schultz (2000) combined *Scaphonyx sanjuanensis* from Argentina and *Scaphonyx fisheri* from Brazil as *Hyperodapedon sanjuanensis*. We do not accept this synonymy, because the South American genera remain poorly described and the synonymy was proposed without detailed comparison.

Archosauriformes

Proterochampsia barrionuevoi
Reig, 1959

Occurrence—Upper La Peña, Cancha de Bochas, and lower Valle de la Luna members (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herreriasaurus* and lower *Exaeretodon* biozones (Martínez et al., 2011b).

Holotype—MCZ 3408, a skull and cervical vertebrae with associated ribs and some dorsal vertebrae.

Comments—Although Reig (1959) and Sill (1967) initially regarded *Proterochampsia* as a primitive crocodylian, proterochampsids since have been positioned as an outgroup to Archosauria (Serenó and Arcucci, 1990; Sereno, 1991a; Dilkes and Sues, 2009; Nesbitt, 2009, 2011; Dilkes and Arcucci, 2013).

Chanaresuchus ischigualastensis
Trotteyn, Martínez, and Alcober, 2012

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herreriasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 567, an articulated partial skeleton including the skull with jaws, the vertebral column with the exception of the distal caudal vertebrae, most of both girdles and limbs, and some gastralia.

Comments—Romer (1971) originally described the genus *Chanaresuchus* (*C. bonapartei*) from the Chañares Formation (Ladinian). *Chanaresuchus ischigualastensis* was briefly described in recent publications (Trotteyn and Haro, 2012; Trotteyn et al., 2012), but the phylogenetic relationships of the new species were not analyzed. Both species share some features that may be derived and justify their inclusion in the same genus, such as the presence of longitudinal crests and depressions on the dorsal surface of the premaxillae, maxillae, and nasals, lateral fossae in the centra of presacral vertebrae, and a low deltopectoral crest. The new species *C. ischigualastensis* differs in other ways from *C. bonapartei*, suggesting that they are distinct (e.g., basal tubera wide, paroccipital processes distally expanded, caudal prezygapophyses with elliptical articular surfaces, astragalus without foramina in the posterior fossa, osteoderms with a longitudinal sulcus).

Crurotarsi

Saurosuchus galileigalilee
Reig, 1961

Occurrence—Cancha de Bochas and lower Valle de la Luna members (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herreriasaurus* and lower *Exaeretodon* biozones (Martínez et al., 2011b).

Holotype—PVL 2062, a nearly complete skull.

Comments—In all phylogenetic analyses, *Saurosuchus* has been shown to be closely related to *Prestosuchus* and *Ticinosuchus* (Parrish, 1993; Benton, 2004) and positioned as a stem taxon outside Crocodylomorpha. Braincase characters alone generated a more basal position outside a clade containing *Postosuchus*, *Tikisuchus*, *Batrachotomus*, aetosaurs, and crocodylomorphs (Gower and Walker, 2002). Brusatte et al. (2010a) recovered a clade called Prestosuchidae, which included *Saurosuchus*, *Batrachotomus*, and *Prestosuchus*, whereas Nesbitt (2011) positioned *Saurosuchus* at the base of a series of stem taxa (including the above mentioned genera) outside Crocodylomorpha.

Sillosuchus longicervix
Alcober and Parrish, 1997

Occurrence—Middle levels of the Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herreriasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 085, postcranium consisting of parts of five cervical vertebrae, an articulated series of four posterior dorsal vertebrae, sacral vertebrae 1–5, and caudal vertebrae 1–8, a partial right ilium, both pubes, both ischia preserved in articulation, both femora (complete), various pieces of ribs, and indeterminate fragments. A partial left coracoid and scapula, the proximal portion of the left humerus, and the proximal portions of both tibiae were also collected with the holotype but have not been described.

Comments—Brusatte et al. (2010a) positioned *Sillosuchus* within Poposauroidea, joining a polytomy with *Arizonasaurus*, *Bromsgroveia*, *Lotosaurus*, *Poposaurus*, and *Shuvosauridae*. Following the more recent analysis and taxonomy of Nesbitt (2011), *Sillosuchus* is positioned within Poposauroidea close to *Shuvosaurus* and *Effigia*.

Trialestes romeri (Reig, 1963)

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herreriasaurus* biozone (Martínez et al., 2011b).

Holotype—PVL 2561, a partial skull lacking the skull roof and braincase, portions of two forelimbs including scapula, humerus, radius, ulnae, radiale, and ulnare, and several cervical and 16 caudal vertebrae.

Comments—Originally described as *Triassolestes* (preoccupied) by Reig (1963), *Trialestes* was later proposed as a replacement (Bonaparte, 1982). Bonaparte (1978) and Clark et al. (2000) suggested that *Trialestes* exhibits a combination of dinosaurian and crocodylomorph features and may represent a mixed taxon. Ezcurra et al. (2008) and Nesbitt (2011) regarded *Trialestes* as a basal crocodylomorph.

Venaticosuchus rusconii
Bonaparte, 1971

Occurrence—Southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Stratigraphic position unknown, presumably from the middle or upper levels of the Ischigualasto Formation.

Holotype—PVL 2578, an incomplete skull with mandible, an incomplete anterior extremity, and some osteoderms.

Comments—*Venaticosuchus* is an ornithosuchid archosaur, a clade that recent analyses usually position near the base Crurotarsi (= Pseudosuchia) (Benton, 1990; Sereno, 1991a; Brusatte et al., 2010a; Nesbitt, 2011).

Aetosauroides scagliai
Casamiquela, 1967b

Occurrence—Cancha de Bochas and lower Valle de la Luna members (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herrerasaurus* and lower *Exaeretodon* biozones (Martínez et al., 2011b).

Holotype—PVL 2073, a nearly complete and articulated postcranial skeleton including one anterior cervical, 13 dorsal, two sacral, and seven caudal vertebrae; an almost complete right scapula; proximal portion of left scapula; coracoid, interclavicle, and clavicle; incomplete right humerus, complete left humerus, ulna, and radius; two metacarpals; articulated and complete ilia; incomplete pubes; almost complete and articulated ischia; complete right femur, fibula, astragalus, and distal tarsal; complete left femur; incomplete tibia; complete fibula; proximal tarsal?; two incomplete metatarsals; and two isolated metatarsals; non-terminal pedal phalanges; an ungual; cervical, dorsal, sacral, and caudal osteoderms; ventral armor; and several appendicular and fragments of indeterminate osteoderms (Desojo and Ezcurra, 2011).

Comments—Heckert and Lucas (1999, 2000) proposed that the genus *Aetosauroides* is a junior synonym of *Stagonolepis*, suggesting that there are no autapomorphies in the type specimen of *Aetosauroides* that justify generic distinction. However, that synonymy was not supported by the analyses of Parker (2008) and Desojo and Ezcurra (2011), who found a combination of characters that allow the diagnosis of *Aetosauroides* from all other aetosaurs, supporting it as a genus distinct from *Stagonolepis*. Parker (2008) proposed *Aetosauroides* as member of Aetosaurinae, one of the main clades of Aetosauria, whereas Desojo et al. (2012) suggested that *Aetosauroides* is a basal member of Aetosauria and sister taxon to Stagonolepididae.

Argentinosuchus bonapartei
Casamiquela, 1961

Occurrence—Cancha de Bocha Member (Currie et al., 2009), lower levels of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVL 2091, isolated plates of the dorsal, ventral, and appendicular armor, an almost complete humerus, proximal region of the articulated left radius and ulna, and four articulated caudal vertebrae.

Comments—*Argentinosuchus* was reinterpreted as a junior synonym of *Aetosauroides* by Casamiquela (1967ba). Subsequently, Heckert and Lucas (1998, 1999, 2000) proposed that *Argentinosuchus* is a junior synonym of *Stagonolepis*. Recently, Desojo and Ezcurra (2011) considered *Argentinosuchus* a nomen dubium because of the lack of autapomorphies and viewed PVL 2091 as an indeterminate aetosaurine aetosaur. We agree with Desojo and Ezcurra (2011) and did not include *Argentinosuchus* in the census.

Dinosauromorpha

Lagerpetidae indet.
Martínez et al., 2013b

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Material—PVSJ 883, distal end of the left femur.

Comments—PVSJ 883 was added to the data matrix of Nesbitt et al. (2010) and was positioned within Lagerpetidae along with *Lagerpeton chanarensis*, *Trilicosaurus rapax*, *Dromomeron romeri*, and *Dromomeron gregorii*. PVSJ 883 was positioned as the sister taxon to the two *Dromomeron* species (Martínez et al., 2013b).

Dinosauriformes

Ignotosaurus fragilis, gen. et sp. nov.
Martínez, Apaldetti, Alcober, Colombi, Sereno, Fernandez, Santi Malnis, Correa, and Abelin, 2013

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 884, a right ilium.

Comments—Using the matrix of Nesbitt et al. (2010), *Ignotosaurus fragilis* was recovered within a monophyletic Silesauridae. *Ignotosaurus* joins a polytomy with *Silesaurus*, *Sacisaurus*, and *Eucoelophysis*, with *Asilisaurus* as the sister taxon of this clade (Martínez et al., 2013b).

Dinosauria

Pisanosaurus mertii
Casamiquela, 1967a

Occurrence—Cerro Bola area in the northern outcrops of the Ischigualasto Formation, La Rioja Province, Argentina. Exact stratigraphic level unknown, although probably from upper levels of the Ischigualasto Formation, judging from available outcrop in the area of the locality.

Holotype—PVL 2577, a maxilla and lower jaw fragments bearing teeth, vertebrae, incomplete hind limb, and the impression of the pelvis.

Comments—*Pisanosaurus* is known from fragmentary materials, and it was originally proposed as the most basal ornithischian (Casamiquela, 1967a). None of the subsequent studies contradicted the original proposal, finding *Pisanosaurus* as the basal-most member of Ornithischia (Bonaparte, 1976; Weishampel and Witmer, 1990; Sereno, 1991b; Langer and Benton, 2006; Irmis et al., 2007a; Butler et al., 2007, 2008a, 2008b).

Panphagia protos

Martínez and Alcober, 2009

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 874, partial skull including the right nasal and prefrontal, left frontal, both parietals, both quadrates, right prootic, supraoccipital, anterior half of the left lower jaw, and right lower jaw, axial skeleton including one anterior and two posterior cervical vertebrae, four posterior dorsal neural arches, one dorsal centrum, first primordial sacral vertebra, three proximal and 15 distal caudal vertebrae, appendicular elements including the left scapula, left ilium, left pubic apron, left ischium, right tibia and astragalus, right metatarsal 3, proximal half of left metatarsal 4, and four pedal phalanges including one ungual.

Comments—*Panphagia* was originally proposed as the most basal sauropodomorph (Martínez and Alcober, 2009). Subsequent studies also positioned *Panphagia* among basal sauropodomorphs closely related either to *Guaibasaurus* (Ezcurra, 2010), *Pampadromaeus* (Cabreira et al., 2011), or *Eoraptor* (Martínez et al., 2013b).

Chromogisaurus novasi

Ezcurra, 2010

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 845, a partial skeleton including a proximal caudal vertebra, two mid-caudal vertebrae, anterior chevron, glenoid region of the left scapulocoracoid, right ilium, acetabular fragment of the left ilium, proximal and distal ends of the left femur, right femur lacking its proximal and distal ends, right tibia, proximal end of the left tibia, proximal end of the left fibula, right fibula lacking its proximal and distal ends, right pedal digit III, and some unidentified bone fragments (Martínez et al., 2013b).

Comments—Martínez et al. (2013b) re-identified some bones in the holotypic skeleton of *Chromogisaurus* and described some previously unidentified elements (e.g., fragment of the glenoid region of the scapulocoracoid, fragment of acetabular region of the left ilium, proximal and distal end of the left femur, proximal end of the right tibia, proximal end of left fibula). *Chromogisaurus* was originally positioned within the clade *Guaibasauridae* closely related to *Saturnalia* (Ezcurra, 2010). Martínez et al. (2013) also retrieved *Chromogisaurus* as a sister taxon of *Saturnalia*, but depicted *Guaibasaurus* as a basal theropod.

Eoraptor lunensis

Serenó, Foster, Rogers, and Monetta, 1993

Occurrence—Cancha de Bochas Member (Currie et al., 2009) of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 512, a nearly complete articulated skeleton lacking the distal caudal vertebrae (Serenó et al., 2013).

Comments—*Eoraptor* was initially considered a basal theropod, sister taxon to *Herrerasaurus* + Neotheropoda (Serenó et al., 1993; Rauhut, 2003; Nesbitt et al., 2009; Sues et al., 2011). Other studies positioned *Eoraptor* outside other saurischians, albeit on weaker grounds (Langer and Benton, 2006). More recently, Martínez et al. (2011b) presented new evidence for positioning *Eoraptor* among basal sauropodomorphs (e.g., enlarged narial opening, slender ventral process of the squamosal, inset position of the first dentary tooth, teeth with basal constriction and inclined denticles, medial rotation of the first phalanx of digit I, astragalus with an anteri-

orly projecting anteromedial corner). The sauropodomorph affinities of *Eoraptor* are examined in more detail elsewhere (Martínez et al., 2013b; Sereno and Martínez, in review).

Eodromaeus murphi

Martínez, Sereno, Alcober, Colombi, Renne, Montañez, and Currie, 2011b

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 560, an articulated skeleton including a crushed skull, most of the axial skeleton, scapular and pelvic girdles, appendicular skeleton almost complete including both humeri, radius and ulna, manus, tibiae, fibulae, and pes (Martínez et al., 2011b).

Comments—*Eodromaeus* was recovered as a basal theropod more derived than herrerasaurids but basal to Neotheropoda (Martínez et al., 2011b). The basal theropod position of *Eodromaeus* was supported by several derived character states in the skull (e.g., promaxillary fenestra, basisphenoid fossa) and postcranial skeleton (e.g., radioulnar shaft apposition, elongate penultimate phalanges, distally tapering pubic blade, pubic foot, femoral extensor depression) (Martínez et al., 2011b).

Herrerasaurus ischigualastensis

Reig, 1963

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVL 2566, an articulated skeleton including articulated vertebral column from seventh dorsal to the most distal caudal vertebrae, almost complete pelvis, nearly complete right hind limb, left astragalus, metatarsals, and several pedal phalanges.

Comments—*Herrerasaurus* has long been considered closely related to the Brazilian genus *Staurikosaurus* and placed within *Herrerasauridae* (Benedetto, 1973; Novas, 1992). The clade has been positioned among basal theropods (Reig, 1963; Sereno and Novas, 1992, 1994; Novas, 1994; Rauhut, 2003; Ezcurra and Novas, 2007; Nesbitt et al., 2009, 2010; Nesbitt, 2011; Sues et al., 2011), as outgroups to other saurischians (Langer, 2004; Langer and Benton, 2006; Irmis et al., 2007b), or as non-dinosaur dinosauriforms (Gauthier, 1986; Brinkman and Sues, 1987; Novas, 1992).

Freguellisaurus ischigualastensis

Novas, 1986

Occurrence—La Chilca Creek in northern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Exact stratigraphic level unknown, although probably from upper levels of the Ischigualasto Formation, judging from available outcrop in the area of the locality.

Holotype—PVSJ 053, a partial skull including right premaxilla, both maxillae, left jugal, and temporal, occipital, and basicranial regions, both mandibular rami, axis, fragments of cervical vertebrae, 25 articulated distal caudal vertebrae, right scapula and fragmentary coracoid, fragments of both humeri and ulnae, and distal end of radius.

Comments—*Freguellisaurus* was originally considered a primitive saurischian closely related to *Herrerasaurus* (Novas, 1986). Subsequently, Novas (1994) regarded *F. ischigualastensis* a junior synonym of *Herrerasaurus ischigualastensis*. The holotypic material of *Freguellisaurus* requires a detailed review in light of new herrerasaurid material from the Ischigualasto Formation. For now, we follow Novas (1994) and do not include this

specimen in the census, because it was found outside the census area.

Sanjuansaurus gordilloi
Alcober and Martínez, 2010

Occurrence—Upper levels of the La Peña Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 605, an incomplete skeleton including left maxilla, partial axial column, from the axis to the twelfth caudal vertebra, lacking the third, fourth, and anterior half of the fifth dorsal vertebrae, left and right scapulae, left ulna, ungual of manual digit III, preacetabular portion of the left ilium, proximal end of left pubis, complete right pubis, both femora and tibiae, right fibula, right astragalus and calcaneum, and left metatarsal 2.

Comments—Using the matrix of Langer and Benton (2006), *Sanjuansaurus gordilloi* was recovered as member of *Herrerasauridae* in an unresolved relationship with *Herrerasaurus* and *Staurikosaurus* (Alcober and Martínez, 2010).

Dicynodontia

Ischigualastia jenseni
Cox, 1962

Occurrence—Cancha de Bochas Member (Currie et al., 2009) of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—MCZ 18.055, a skull, lower jaw, and partial postcranial skeleton including vertebrae, ribs, and portions of forelimbs and hind limbs.

Comments—*Ischigualastia* is one of the most derived members within *Kannemeyeriiformes*. It is included in a group of tuskless dicynodonts, including *Angoniasaurus*, *Stahleckeria*, and *Jachaleria*. *Ischigualastia* shares many features with *Jachaleria*, whereas *Angoniasaurus* and *Stahleckeria* are regarded as their sister group (Vega-Dias et al., 2004). Based on analysis of postcranial characters, *Ischigualastia* is positioned in a polytomy with *Dinodontosaurus* and *Stahleckeria* (Surkov et al., 2005). Damiani et al. (2007) placed *Ischigualastia* within the clade *Kannemeyerioides* as sister taxon to *Stahleckeria*, whereas Kammerer et al. (2011) positioned *Ischigualastia* as the sister taxon to *Jachaleria*.

Jachaleria colorata
Bonaparte, 1970

Occurrence—Quebrada de la Sal Member (Currie et al., 2009) in southern outcrops of the Ischigualasto and Los Colorados Formations, Ischigualasto Provincial Park, San Juan Province, Argentina. *Jachaleria* biozone (Martínez et al., 2011b).

Holotype—PVL 3841, an almost complete skull with lower jaws.

Comments—*Jachaleria* was positioned close to *Ischigualastia*, *Stahleckeria*, *Angoniasaurus*, *Dinodontosaurus*, and *Placerias* among derived *Kannemeyeriiformes* (Vega-Dias et al., 2004). The most recent analysis positions *Jachaleria* as the sister taxon to *Ischigualastia* (Kammerer et al., 2011).

Cynodontia

Exaeretodon argentinus
Bonaparte, 1962

Occurrence—Middle levels of the Cancha de Bochas Member (Currie et al., 2009), Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-*

Herrerasaurus biozone through the *Exaeretodon* biozone (Martínez et al., 2011b).

Holotype—MLP 42-VII-14-3, a partial skull.

Comments—Cabrera (1943) described the first cynodont from Ischigualasto as *Exaeretodon frenguelli*. Bonaparte (1962) considered *Belesodon? argentinus*, *Exaeretodon frenguelli*, and *Theropis robusta* as belonging to the genus *Exaeretodon*. He recognized two species, *E. argentinus* and *E. frenguelli*, the latter being proposed as the synonym of *Theropis robusta*. In their review of cynodonts, Hopson and Kitching (1972) proposed the synonymy of *Exaeretodon argentinus*, *E. frenguelli*, and *Proxaeretodon vincei* under the species name *E. argentinus*, a proposal adopted by several later authors (Liu, 2007; Abdala and Ribeiro, 2010; Liu and Olsen, 2010). Battail (1991), Abdala et al. (2002), and Oliveira et al. (2007), however, have maintained *Exaeretodon frenguelli* as a valid species.

Ischignathus sudamericanus
Bonaparte, 1963b

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* and *Exaeretodon* biozones (Martínez et al., 2011b). Exact stratigraphic position unknown.

Holotype—PVL 2564, a partial skull.

Comments—*Ischignathus sudamericanus* (Bonaparte, 1963b) was regarded as a junior synonym of *Exaeretodon argentinus* by Liu (2007), based on cranial evidence and the presumption that *I. sudamericanus* may represent the upper end of a growth series of *E. argentinus*. Abdala and Ribeiro (2010) regarded it as a distinct taxon. *Ischignathus sudamericanus* is excluded from the census of stratigraphic distribution and relative abundance of vertebrate taxa because its stratigraphic position is unknown.

Proxaeretodon vincei
Bonaparte, 1963c

Occurrence—Middle levels of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b). Exact stratigraphic position unknown.

Holotype—PVL 2565, a partial skull.

Comments—Bonaparte (1963c) erected *Proxaeretodon vincei* with a very brief description. In their review of cynodonts, Hopson and Kitching (1972) proposed the synonymy of *Exaeretodon argentinus*, *E. frenguelli*, and *Proxaeretodon vincei* under the species name *E. argentinus*.

Ecteninion lunensis
Martínez, May, and Forster, 1996

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 422, a skull with lower jaws, lacking both zygomatic arches and partial postcranial skeleton.

Comments—*Ecteninion* was originally positioned as a cynodont more derived than *Chiniquodon* (Martínez et al., 1996). Martínez et al. (2013a) and other authors regarded it as a basal probainognathian (Hopson and Kitching, 2001; Martinelli and Rougier, 2007; Fernandez et al., 2010; Liu and Olsen, 2010) or

as the sister taxon to *Cynognathus* and *Gomphodontia* (Abdala, 2007).

Chiniquodon sanjuanensis (Martínez and Forster, 1996)

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 411, a skull with lower jaws and partial postcranial skeleton.

Comments—This taxon was originally described by Martínez and Forster (1996) as a new species of *Probesodon*, a genus previously known from the underlying (Ladinian) Chañares Formation. *Probesodon* is now regarded as a junior synonym of *Chiniquodon* (Abdala and Giannini, 2002). *C. sanjuanensis* was recognized as a cynodont similar in overall morphology and the presence of serrations on some crowns.

cf. *Probainognathus* sp.

Bonaparte and Crompton, 1994

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 410, a skull and articulated lower jaws. The specimen represents a very immature individual, with a skull length of 35 mm.

Comments—This specimen was described as juvenile cf. *Probainognathus* (Bonaparte and Crompton, 1994), based on similarities to *Probainognathus jenseni* Romer, 1970, from the underlying (Ladinian) Chañares Formation. It was recently proposed as a new probainognathian by Fernandez et al. (2011), given the distinctive features of its dentition and cranium (e.g., slender dentary and zygoma, absence of contact between the prefrontal and postorbital on the orbital margin, the alveolar level of the incisors positioned at a higher position than the level of the postcanines). Fernandez et al. (2011) positioned the as-yet-unnamed taxon as more derived than *Probainognathus* and *Prozoostrodon* and closer to *Therioherpeton cargnini*, tritheledontids, and more derived mammaliamorphs.

Chiniquodon cf. *theotonicus*
Bonaparte, 1966

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVL 2076, three fragments of the anterior region of the skull, one of them with mandible.

Comments—The hypodigm (PVL 2076, PVL 2077, PVL 2115) were originally referred to *Chiniquodon* cf. *theotonicus* by Bonaparte (1966). Abdala and Giannini (2002), in their review of the clade Chiniquodontidae, tentatively referred the specimens to *Chiniquodon sanjuanensis*. In this paper we follow Bonaparte (1966).

Diegoanis elegans

Martínez, Fernández, and Alcober, 2013

Occurrence—Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 881, a partial skull preserving most of the cranium and upper dentition.

Comments—*Diegoanis* is placed within Eucynodontia more derived than *Chiniquodon* and *Probainognathus* and allied with *Ecteninion* and *Trucidocynodon* in Ecteniniidae (Martínez et al., 2013a).

Unnamed eucynodont

Occurrence—Lower levels of Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 882, a cranium.

Comments—Preliminary phylogenetic analysis placed PVSJ 882 in an unresolved polytomy with *Brasilodon*, *Adelobasileus*, tritylodontids, and Mammaliaformes (Martínez et al., 2011a).

Amphibia

Promastodonsaurus bellmanni
Bonaparte, 1963a

Occurrence—Middle levels of the Valle de la Luna Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Exaeretodon* biozone (Martínez et al., 2011b).

Holotype—PVL 2092, left and posterior portions of the cranium, impression of right internal naris and posterior end of the lower jaw, partial left clavicle, and interclavicle.

Comments—Although *P. bellmanni* has often been cited as a mastodonsaurid (Bonaparte, 1963a), it exhibits features of a capitosaurid (Paton, 1974). Further description of this material is needed.

Pelorocephalus ischigualastensis
Bonaparte, 1975

Occurrence—Lower levels of the Cancha de Bochas Member (Currie et al., 2009) in southern outcrops of the Ischigualasto Formation, Ischigualasto Provincial Park, San Juan Province, Argentina. Middle *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011b).

Holotype—PVSJ 616 (formerly MCZ 4299), a skull with associated mandibles and interclavicle.

Comments—*Pelorocephalus ischigualastensis* was erected with a very brief description (Bonaparte, 1975). Later Bonaparte (1978) put all Argentine chigutisaurids in *P. mendozensis*. More recently, Marsicano (1993) reversed this decision, recognizing more than one taxon of chigutisaurid from Argentina. In a review of Brachyopoidea, *Pelorocephalus* was positioned as the sister taxon of *Siderops* (Warren and Marsicano, 2000).