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VERTEBRATE TAPHONOMY OF THE ISCHIGUALASTO FORMATION

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ABSTRACT—Trends of preservation are established on the basis of 385 fossil occurrences in the Ischigualasto Formation. The distribution and preservational quality of vertebrate fossils are related to sedimentary facies and stratigraphic position and follow trends in basin evolution and paleoclimate. Fossils in the Ischigualasto Formation are mainly concentrated along the margins of the basin. Floodplain deposits preserve ca. 88% of fossils, which range from unidentifiable fragments to articulated skeletons. The remaining fossil occurrences (ca. 12%) come from coarser-grained fluvial channel deposits and exhibit variable preservational quality, including some well-preserved cynodont skulls. Fossils in the basal La Peña Member (ca. 4% of occurrences) are generally highly weathered and disarticulated with hematitic permineralization. The majority of collected specimens (ca. 65% of occurrences) come from the overlying Cancha de Bochas Member and range from isolated bones to articulated skeletons. Calcite, rather than hematite, is the predominant agent of permineralization. The succeeding Valle de la Luna Member (ca. 30% of occurrences) preserves an association between vertebrate fossils and plant remains. Fossil preservation suggests prolonged exposure prior to burial under wetter conditions with superficial and penetrating precipitation of hematite. The uppermost Quebrada de la Sal Member of the Ischigualasto Formation is nearly barren of fossil remains.

RESUMEN—Se establecieron las tendencias en la preservación de restos de paleovertebrados a lo largo de la Formación Ischigualasto en base a 385 fósiles. La distribución y la calidad de preservación de los fósiles de vertebrados en esta unidad está relacionada con las facies sedimentarias y la posición estratigráfica de los mismos, variando según la evolución de la cuenca y del paleoclima. Los fósiles en la Formación Ischigualasto están principalmente concentrados en los márgenes de la cuenca. Paleoambientalmente, los depósitos de llanura de inundación preservan alrededor del 88% de los fósiles de la unidad, los cuales van desde fragmentos inidentificables hasta esqueletos articulados. Las restantes ocurrencias de fósiles (alrededor del 12%) provienen de depósitos de canal de grano grueso y también exhiben variables calidades de preservación, incluyendo algunos pequeños cráneos de cinodontes en excelente estado de preservación. Estratigráficamente, los fósiles en el miembro basal La Peña (alrededor del 4% de los hallazgos) están generalmente muy meteorizados, desarticulados y permineralizados con hematita. La mayoría de los especímenes colectados (alrededor del 65% de los hallazgos) provienen del suprayacente Miembro Cancha de Bochas, los cuales van desde huesos aislados hasta esqueletos articulados completos. Estos restos están permineralizados principalmente con calcita en lugar de hematita. En el siguiente, Miembro Valle de la Luna (alrededor del 30% de los hallazgos), se preserva una peculiar asociación de restos fósiles de vertebrados y plantas. La preservación de los fósiles en esta unidad sugiere una prolongada exposición bajo un clima más húmedo, con la consecuente precipitación de abundante hematita en la superficie y en el interior. Por último, en el techo de la Formación Ischigualasto, el Miembro Quebrada de la Sal carece casi completamente de restos fósiles.

INTRODUCTION

The Ischigualasto-Villa Unión Basin, located in San Juan Province in northwestern Argentina, preserves a thick fossiliferous sequence of continental Triassic rocks (Fig. 1). Perhaps most notably, the basin includes extensive exposures of the Upper Triassic Ischigualasto Formation, which has yielded a diverse and well-preserved assemblage that includes the earliest-known dinosaurs (see Rogers et al., 1993; Martínez et al., 2011, 2013), basal archosauromorphs, crurotarsal archosaurs, therapsids, and amphibians. The fossil record of the Ischigualasto Formation is complemented by a wealth of associated data that relate to the sedimentology, paleoclimate, and geochronology (Rogers et al., 1993; Milana and Alcober, 1994; Shipman, 2004; Tabor et al., 2006; Colombi, 2007; Colombi and Parrish, 2008; Currie et al., 2009; Colombi et al., 2011; Martínez et al., 2011). The Ischigualasto Formation offers one of our best opportunities to study terrestrial vertebrate evolution during the Late Triassic, during which important faunal turnovers occurred, including the emergence of both dinosaurs and mammals (e.g., Simms and Ruffel, 1989, 1990; Martínez et al., 2011).

Despite the overarching significance of the Ischigualasto Formation paleofauna to studies of vertebrate evolution, there has been little published on the vertebrate taphonomy of this unit. In this report, we describe the preservation of the vertebrate fossils of the Ischigualasto Formation at different scales. First, we describe the relationship between sedimentary facies and vertebrate taphonomy, identifying recurrent modes of preservation in a facies context. Second, we explore the stratigraphic distribution of tetrapod fossils and their preservational features, based on numerous sections measured from the base to the top of the unit (spanning the La Peña, Cancha de Bochas, Valle de la Luna, and Quebrada de la Sal members). General basin-scale taphonomic features were also analyzed, with the goal of identifying fossiliferous vs. non-fossiliferous areas within the basin.

GEOLOGIC AND PALEONTOLOGIC CONTEXT

The Ischigualasto-Villa Unión Basin is part of a system of continental rift basins that developed during the early Mesozoic along the southwestern margin of Pangea due to regional extension related to large-scale plate interactions (Uliana and

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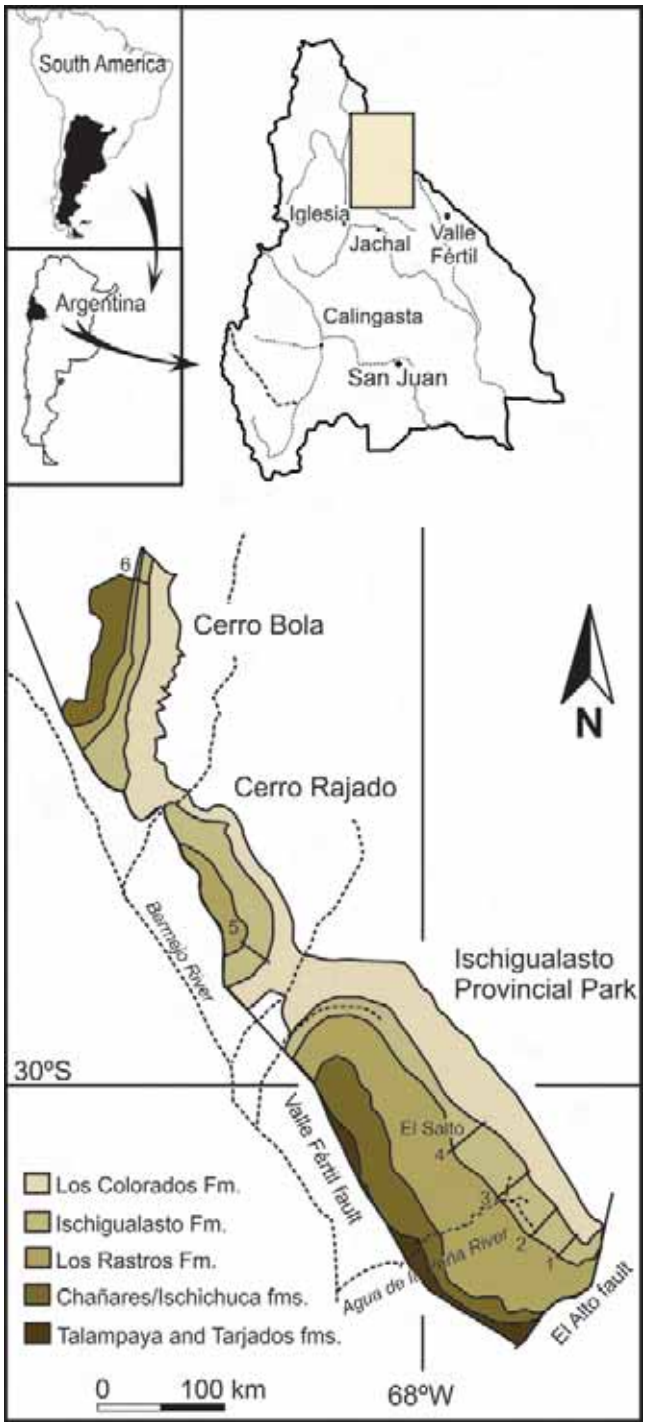

FIGURE 1. Map of the Ischigualasto-Villa Unión Basin, showing the main outcrop belts of Triassic rocks and the distribution of the measured sections. The stratigraphic sections are numbered on the map as follows: **1**, Valle Pintado; **2**, La Gallinita; **3**, Agua de la Peña; **4**, El Salto; **5**, Cerro Rajado; **6**, Cerro Bola (see Fig. 3).

Biddle, 1988; Ramos and Kay, 1991; López-Gamundi et al., 1994). Infilling of the Ischigualasto-Villa Unión Basin began during the Early Triassic and persisted throughout the remainder of the Triassic. Miocene compressional tectonics related to the uplift of the Andes reactivated faults and generated extensive outcrops of Triassic rocks in a homoclinal succession (Milana and Alcober, 1994; Fig. 1).

The Ischigualasto Formation is underlain by the Los Rastros Formation (Fig. 2), a predominantly lacustrine unit characterized by carbonaceous shales, siltstones, and sandstones arranged in repeated coarsening-upward packages that represent the

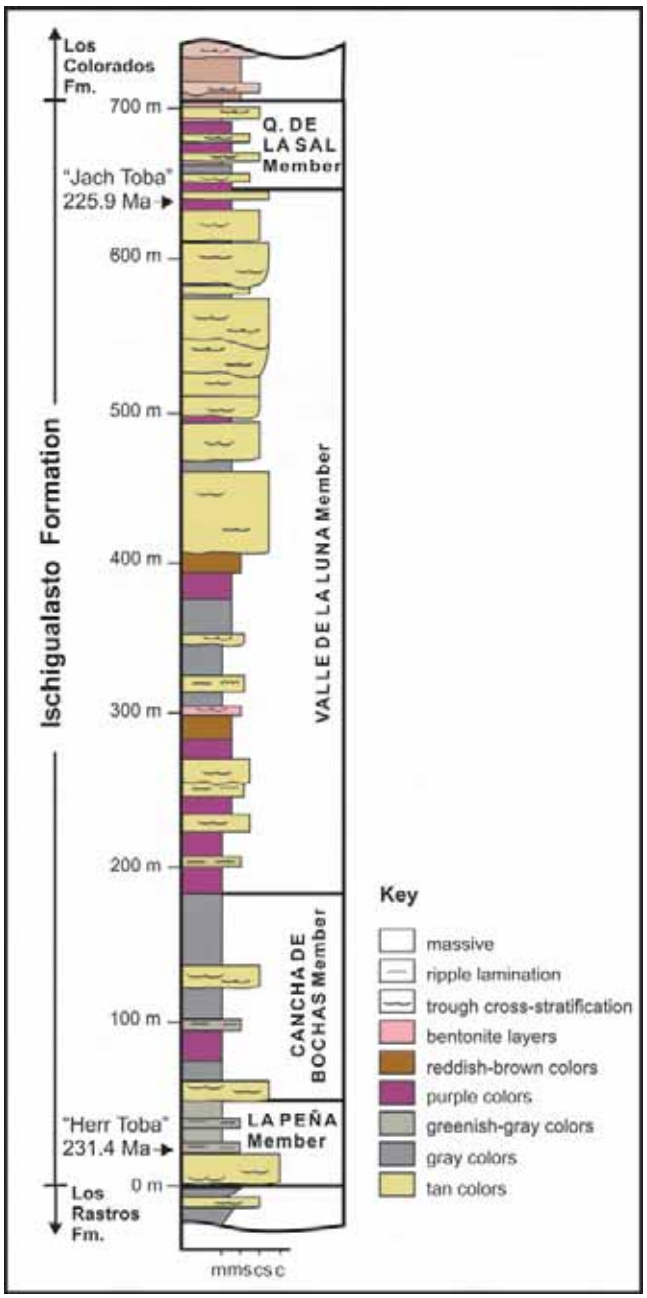

FIGURE 2. Stratigraphic section of the Ischigualasto Formation measured at Agua de la Peña (Fig. 1). Lithofacies, general colors of the rocks, member distribution, and the stratigraphic position of two radiometric ages (arrows) are indicated. The estimated age range of ca. 231.4 to ca. 225.9 Ma (Rogers et al., 1993; Renne et al., 2010; Martínez et al., 2011) corresponds to the Carnian–Norian stages of the Late Triassic (Walker et al., 2012). **Abbreviations**: **c**, conglomerate; **cs**, coarse sandstone; **m**, mudstone; **ms**, medium sandstone.

deposits of Gilbert-type deltas (Rogers et al., 2001) and overlain by terrestrial fluvial red beds of the Los Colorados Formation (Stipanicic and Bonaparte, 1979; Milana and Alcober, 1994; Milana, 1998; Fig. 2). The contact with the Los Rastros Formation is conformable in most parts of the basin (Milana and Alcober, 1994; Colombi et al., 2010), except in the Agua de la Peña Canyon area, where it is marked by an angular unconformity related to a slump structure at the top of the lacustrodeltaic succession of the Los Rastros Formation (Currie et al., 2006). In most of the basin, the contact between these two formations is marked by an incised fluvial surface capped by amalgamated fluvial channels that mark the beginning of the deposition in the Ischigualasto Formation. The transition to the superjacent Los Colorados Formation is apparently conformable throughout the basin and coincides with a regional change in alluvial architecture and a shift from the grayish Ischigualasto beds to characteristic red beds (Milana and Alcober, 1994).

Thickness of the Ischigualasto Formation ranges from 300 m on the margin of the basin, near the El Alto fault, to more than 700 m in the basin depocenter, in the El Salto area (Figs. 1, 2). The formation includes the deposits of fluvial channels characterized by massive and trough cross-stratified sandstones and conglomerates, intercalated with finer-grained proximal and distal floodplain facies (Fig. 2). The proximal floodplain deposits are represented by fine-grained sandstones and mudstones characterized by horizontal lamination and ripple cross-lamination, which is frequently disturbed by paleosol development. The distal floodplain facies, in contrast, is formed by massive or finely laminated siltstones and mudstones that are typically overprinted by paleosol development. This distal floodplain facies also tends to include abandoned channel deposits, which are characterized by laminated mudstone deposits intercalated with abundant seams of compressed plant cuticles (Currie et al., 2009). The paleosols in the Ischigualasto Formation have been studied in detail (Tabor et al., 2006), and eight different types have been identified that reflect changing landscape stability, variations in sedimentation rates, diverse soil drainage conditions, and shifts in humidity through time.

The Ischigualasto Formation can be subdivided into four members, which from base to top comprise (Fig. 2) La Peña, Cancha de Bochas, Valle de la Luna, and Quebrada de la Sal (Currie et al., 2009). These members are distinguished by variations in sedimentary architecture, paleosol development, and plant taphonomy (Tabor et al., 2006; Colombi, 2007; Colombi and Parrish, 2008; Currie et al., 2009). Brief descriptions of the four members of the Ischigualasto Formation are provided in Table 1. In addition to these distinct members, laterally extensive outcrop belts have also allowed the documentation of geomorphic variation along the basin transect. Geomorphic variation is represented by differences in stratal thickness, shifts in channel vs. floodplain ratios, and paleosol types (Tabor et al., 2006; Currie et al., 2009), along with variation in the preservation of the paleoflora (Colombi and Parrish, 2008). This variation is particularly well developed in the La Peña and Cancha de Bochas members, but it is more subdued in the Valle de la Luna Member. Moving from the margin (Section 1) to the center of the basin (Section 4), the La Peña and Cancha de Bochas members show an increase in channel thickness and channel amalgamation, accompanied by a decrease in the thickness of overbank packages and increase in the abundance of thin lacustrine deposits (Colombi et al., 2010; Figs. 1, 3). Paleosol development also changes in these two members from the margin to the center of the basin, with paleosols in the basin center typically thinner and more poorly drained than their margin counterparts (Tabor et al., 2006; Currie et al., 2009). In the Valle de la Luna Member, the fluvial architecture and paleosols remain more or less consistent from margin to center of the basin, but there are changes in the taphonomic attributes of the paleoflora, with plant cuticles, tree trunks, and palynomorphs more abundant in the center of the basin.

The climate during the deposition of the Ischigualasto Formation has been reconstructed based on a variety of observations (i.e., fluvial architecture, paleosols, plant taphonomy), all of which imply an overall seasonal paleoclimate with respect to rainfall regime (Stipanicic and Bonaparte, 1979; Tabor et al., 2006; Colombi and Parrish, 2008; Currie et al., 2009; Colombi et al., 2011). In the basal La Peña Member, paleoclimatic inference is complicated due to the transition from lacustrine facies of the Los Rastros Formation to fluvial depositional systems of the Ischigualasto Formation. In the Cancha de Bochas Member, an arid to semiarid climate is suggested by the presence of calcic paleosols (Tabor et al., 2006) and the absence of fossil plant remains other than root halos (Colombi and Parrish, 2008). In the Valle de la Luna Member, a change in paleoclimate reflecting an increase in humidity (i.e., rainfall) is indicated by the shift from calcic paleosols to argillic paleosols (Tabor et al., 2006), the preservation of abundant fossil plant remains, including mummified cuticles, petrified tree trunks, and palynomorphs (Colombi and Parrish, 2008), and a positive carbon isotope composition of fossil plant cuticle relative to that of younger fossils (Colombi et al., 2011). Finally, a return to xeric conditions in the Quebrada de la Sal Member is suggested by the absence of fossilized plant remains (Colombi and Parrish, 2008), a change in fluvial architecture, and the presence of desiccation cracks.

The Ischigualasto Formation vertebrate fauna includes early dinosaurs, archosauromorphs, crurotarsan archosaurs, therapsids, and amphibians (Table 2). The rhynchosaur *Scaphonyx* (Sill, 1970) is the most abundant vertebrate in the fauna, representing ca. 60% of the recovered fossils. Therapsid cynodonts are particularly abundant and diverse, although dicynodonts are recovered rarely as well. Early dinosaurs, including representatives of sauropodomorph, theropod, and ornithischian clades, and crurotarsan archosaurs are represented by a very diverse, although less abundant, assemblage. The Ischigualasto Formation has also yielded amphibians, which are very rare (e.g., Martínez et al., 2011).

Finally, with regard to age control, the Ischigualasto Formation is one of very few continental Triassic successions that have yielded reliable radioisotopic ages. Dated horizons positioned near the bottom and top of the formation constrain the age of the Ischigualasto Formation to be between ca. 231.4 and ca. 225.9 Ma (Rogers et al., 1993; Renne et al., 2010; Martínez et al., 2011), which corresponds to the Carnian–Norian stages (Walker et al., 2012).

METHODS

Six detailed sedimentological sections were measured along the outcrop belts of the Ischigualasto Formation in the Ischigualasto-Villa Unión Basin. These were designated the Ischisaurus, La Gallinita, Agua de la Peña, El Salto, Cerro Rajado, and Cerro Bola sections (Figs. 1, 3). Data that pertain to bed thickness, lithology, sedimentary structures, rock color, and pedogenic features were collected for each section. Data sets related to vertebrate taphonomy were collected from exposures extending ca. 100 meters lateral from each section (i.e., each set contains information from ca. 200-m-wide swaths). Taphonomic data collection followed the methods outlined in Behrensmeyer (1991), and included features such as bone weathering, articulation state, skeletal representation, various surface modifications (e.g., tooth marks, scratch marks, corrosion), breakage, and mineralization state (including perimineralization and replacement). During the course of this study, 385 individual fossil occurrences

TABLE 1. Summary of the main features that distinguish each member of the Ischigualasto Formation (Currie et al., 2009).

Member	Thickness (m)	Channel facies (%)	Sinuosity of channels	Paleosols	Plant taphonomy	Description and paleoenvironmental interpretation
La Peña	45	49	Low and high	Protosols Argillisols	Floodplain facies characterized by root halos of herbaceous plants and silicified root traces restricted to fluvial sandstones.	Lower part of member is characterized by amalgamated sandstone and conglomeratic multistory channel belt facies, representing low-sinuosity rivers. Upper part of member is characterized by greenish-gray and gray fine-grained floodplain facies interbedded with crevasse-splay and rare single-story tabular sandstone bodies.
Cancha de Bochas	125	12	High	Calcic vertisols Calcisols Argillic calcisols Protosols Gleyed vertisols	Floodplain facies characterized by root halos of herbaceous plants and silicified root traces restricted to fluvial sandstones.	This member is characterized by variegated reddish-brown, greenish-gray, and mottled gray fine-grained overbank facies, including levee and crevasse-splay deposits. Overbank facies are interbedded with rare high-sinuosity sandstone bodies (meandering and anastomosing rivers). This succession also contains basalt and bentonite beds.
Valle de la Luna	450	55	High	Argillisols Protosols Gleyed vertisols Calcisols Argillic calcisols	Proximal floodplain characterized by root halos of herbaceous plants, distal facies characterized by abandoned channels and marsh facies that preserve leaf cuticles, palynomorphs, and in situ silicified stems and tree trunks. Channel facies preserve transported silicified trunks of riparian trees, charcoal (burned wood), and transported leaf cuticles.	The lower portion of member is characterized by thick variegated fine-grained overbank facies intercalated with high-sinuosity sandstone bodies (anastomosing and meandering rivers). In the upper portion of this member, the proportion of channel deposits increases and results in an amalgamated channel belt associated with abandoned channels and minor fine-grained floodplain deposits. This unit also includes a notable increase in altered ash layers.
Quebrada de la Sal	65	41	High	Protosols Gleyed vertisols Argillisols Calcisols	Floodplain facies characterized by root halos of herbaceous plants.	This member is characterized by similar proportions of variegated fine-grained facies of the overbank environment and tabular, single-story, high-sinuosity sandstone bodies (meandering rivers). Abundant altered ash layers are present in this member.

TABLE 2. Ischigualasto paleovertebrate assemblage.

Archosauromorpha	Rhynchosauria		*Scaphonyx* (Sill, 1970)
Archosauriformes	Proterochampsidae		*Proterochampsa* (Reig, 1959)
Archosauria	Dinosauria	Ornithischia	*Pisanosaurus* (Casamiquela, 1967)
		Sauropodomorpha	*Eoraptor* (Sereno et al., 1993)
			Panphagia (Martínez and Alcober, 2009)
			Chromogisaurus (Ezcurra, 2010)
		Theropoda	*Eodromaeus* (Martínez et al., 2011)
			Herrerasaurus (Reig, 1963)
			Sanjuansaurus (Alcober and Martínez, 2010)
	Pseudosuchia	Sphenosuchia	*Trialestes* (Bonaparte, 1982)
		Ornithosuchia	*Venaticosuchus* (Bonaparte, 1971)
		Aetosauria	*Aetosauroides* (Casamiquela, 1960)
		'Rauisuchidae'	*Saurosuchus* (Sill, 1974)
Therapsida	Cynodontia		*Exaeretodon* (Bonaparte, 1962)
			Ischignathus (Bonaparte, 1963a)
			Ecteninion (Martínez and Forster, 1996)
			Probelesodon (Martínez et al., 1996)
			cf. *Probainognathus* (Bonaparte and Crompton, 1994)
	Dicynodontia		Ischigualastia (Cox, 1962)
			Jachaleria (Bonaparte, 1970)
Amphibia	Temnospondyli		*Promastodonsaurus* (Bonaparte, 1963b)
			Pelorocephalus (Bonaparte, 1975)

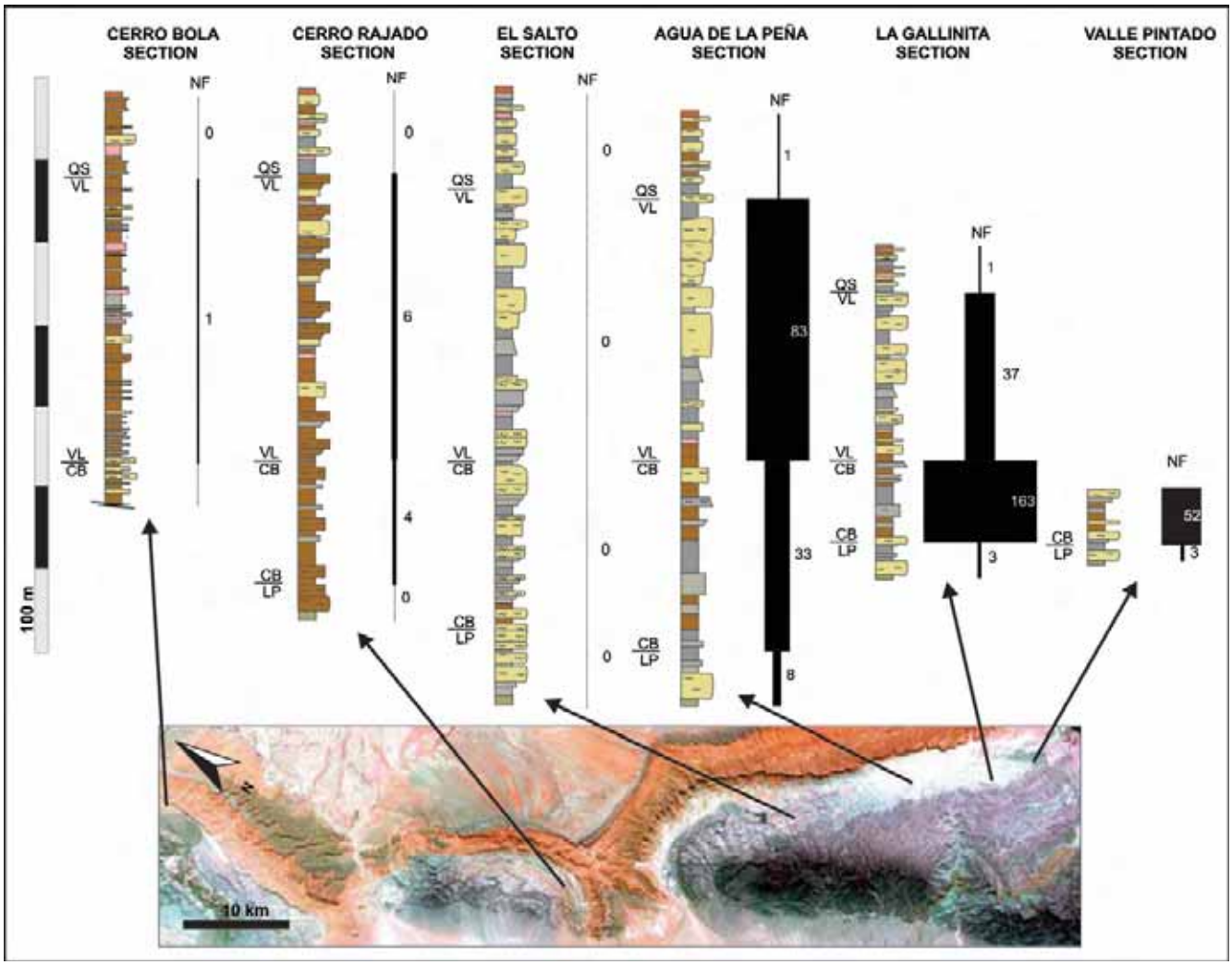

FIGURE 3. Location of the six stratigraphic sections measured in the Ischigualasto Formation. Stratigraphic sections follow the same organization as in Figure 2. The number of vertebrate fossils collected (**NF**) is represented by the width of the black line and specified by the adjacent numbers. A greater density of fossils is observed along the margin of the basin (from Agua de la Peña to Valle Pintado) and in the Cancha de Bochas Member. **Abbreviations**: **CB**, Cancha de Bochas Member; **LP**, La Peña Member; **QS**, Quebrada de la Sal Member; **VL**, Valle de la Luna Member. The color key is explained in Figure 2. (Color figure available online.)

were analyzed. All fossil bones encountered were added to the data set, including taxonomically indeterminate specimens. Some of these specimens have been collected and preserved in the repository of the Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan. However, most of them have not been collected because their importance mostly resides in their taphonomic features and their paleoenvironmental implications.

The mineralization history of Ischigualasto bones was analyzed using polarized light microscopy and scanning electron microscopy. Images and mineral analyses were obtained using a JEOL 6610LV scanning electron microscope (SEM) and an Oxford Instruments energy-dispersive X-ray detector and Inca Energy software. Thin sections were carbon coated prior to analysis. Qualitative X-ray spectra for mineral identification were obtained at a 10 mm working distance for approximately 20 seconds live time with an accelerating voltage of 15 kV.

PRESERVATION OF THE ISCHIGUALASTO VERTEBRATE ASSEMBLAGE

Vertebrate fossils from the Ischigualasto Formation are characterized by highly variable preservation quality. In our effort to characterize the taphonomy of the Ischigualasto vertebrate assemblage and discern general patterns in preservation, we focused on four readily discernable attributes: (1) percentage of skeleton preserved in each specimen; (2) articulation state of each specimen; (3) weathering stage (following Behrensmeyer, 1978); and (4) mineralization of the bones. We describe them in two ways—in terms of facies/depositional environment (Table 3) and member/taphonomic mode (Table 4).

Facies Associations and Taphonomic Modes

The Ischigualasto Formation consists of mudstones, siltstones, and sandstones that represent deposits of channels and associated floodplains that accumulated in an ancient fluvial setting (Currie et al., 2009). With regard to the floodplain deposits, it is possible to distinguish proximal and distal facies, as well as rare abandoned channel facies. The ancient channel and associated floodplain facies are characterized by a suite of sedimentary processes and ecological parameters that together serve to define the availability of remains, the causes of death, and the potentials for transport, burial, and diagenesis of vertebrate skeletons (Behrensmeyer, 1991). Consequently, each alluvial facies should have particular preservational attributes that make them distinctive from a taphonomic perspective.

Active Channels—Deposits of once-active channels constitute approximately 34% of the thickness of the alluvial suite in the Agua de la Peña section of the Ischigualasto Formation and more than the 60% of the succession in the El Salto section (Fig. 3). Channel facies in all sections are characterized by tabular to lenticular bodies with erosive bases that consist of light yellow coarse- to medium-grained sandstone and minor conglomerates. They vary from massive to pervasively trough cross-stratified. The La Peña Member is characterized by low-sinuosity amalgamated channels that were located within an incised valley. The Cancha de Bochas Member, in contrast, is characterized by highly sinuous channel deposits that are typically amalgamated in the depocenter and isolated in other parts of the basin. The Valle de la Luna Member is characterized throughout the entire basin by mostly isolated high-sinuosity channel deposits at the base of the unit that pass up section into amalgamated channels that show minimal indication of incision. Finally, the Quebrada de la Sal Member is characterized by isolated tabular channel deposits that exhibit high sinuousity.

Channel facies preserve ca. 11.7% of the vertebrate fossils included in this study (Fig. 4; Table 3). Vertebrate fossils are not evenly distributed through the entire succession, but are mostly concentrated in the channel deposits along the margin of the basin in the Cancha de Bochas Member. This member includes both channels that are rich in fossils as well as channels that are devoid of fossils. Fossil bones occur both as isolated specimens and as associated occurrences, and the preserved percentage per individual usually does not exceed 30% of the skeleton (Table 3). There is a predominance of highly weathered specimens (Fig. 5A; Table 3), although there are many isolated and even fragile elements that are preserved in very good condition (Fig. 5B). For example, many small cynodont skulls (<10-cm-long axis) or parts of skulls have been recovered from channel facies in pristine condition, without evidence of weathering or abrasion.

TABLE 3. Summary of the main taphonomic attributes in channel, proximal and distal floodplain, and abandoned channel facies of the Ischigualasto Formation.

	Channel		Proximal floodplain		Distal floodplain		Abandoned channel	
Taphonomic attributes/facies	N	%	N	%	N	%	N	%
Weathering								
Fresh	2	4.4	20	7.7	6	7.9	2	66.7
Slightly weathered	15	33.3	88	33.7	20	26.3	1	33.3
Weathered	28	62.2	153	58.6	50	65.8	0	0
Articulation								
Articulated	3	6.7	40	15.4	8	10.6	1	33.3
Associated	20	44.4	102	39.0	27	35.5	1	33.3
Isolated	22	48.9	119	45.6	41	53.9	1	33.3
% of skeleton preserved								
>70%	4	8.9	15	5.7	6	7.9	0	0
70–30%	6	13.3	47	18.0	6	7.9	1	33.3
<30%	35	77.8	199	76.3	64	84.2	2	66.7
Permineralization (authigenic minerals)								
Calcite		X		X		—		—
Calcite + hematite		X		X		X		—
Hematite		—		X		—		X
Total	45	11.7	261	67.8	76	19.7	3	0.8

N is the number of fossils recorded with taphonomic attributes (total number of fossil samples = 385). The 'X' indicates that a certain type of permineralization is present; the dash (—) indicates that it is not.

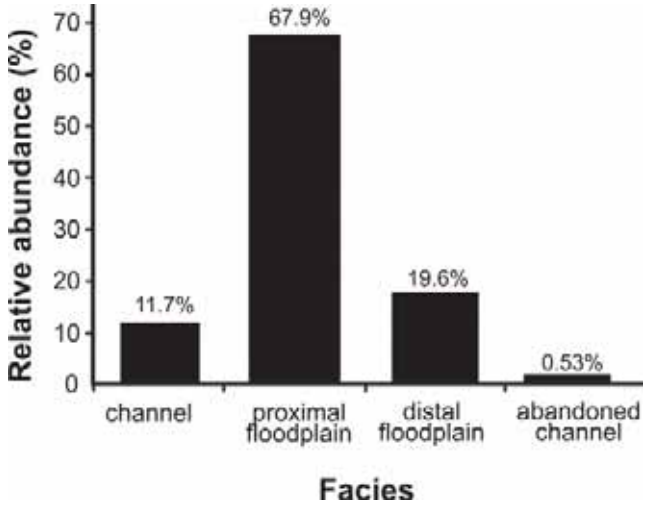

FIGURE 4. Relative abundances of vertebrate fossils in the four different facies of the Ischigualasto Formation.

Interestingly, these isolated skulls are unique to this facies within the Ischigualasto Formation, and channel deposits have become the primary target in the search for small cynodont skulls. Vertebrate fossils in channel facies are typically permineralized with calcite, and are often encased in sandy calcite concretions.

Proximal Floodplains—Floodplain facies are the predominant deposits in the Ischigualasto alluvial suite, and they crop out throughout the basin. Proximal floodplain deposits represent ca. 39% of the thickness of the Ischigualasto Formation. They are characterized by fine- to medium-grained sandstones, which range from massive or ripple cross-laminated, and are intercalated with finer-grained mudstones. In general, proximal floodplain facies form tabular heterolithic sheet-like deposits. There are two main types of proximal floodplain facies. One includes reddish to reddish-brown calcic or argillic soils, which indicates oxidized environments (Tabor et al., 2006). The other includes greenish-gray argillic soils (i.e., protosols) or no soil development, which suggests reducing environments and poor drainage (Tabor et al., 2006).

Proximal floodplain deposits preserve well over half of the fossils in our study sample (67.9%) (Fig. 4; Table 3). These fossils are distributed along the margin of the basin in the three lower members. Of these, the proximal floodplain facies of the Cancha de Bochas Member preserves the vast majority of the fossils, with the most productive beds yielding more than one fossil per square meter. The quality of preservation in this sedimentary facies is highly variable. Most of the beds host isolated skeletons, some completely articulated, whereas others yield disarticulated but still associated as well as isolated remains (Fig. 6). Rare layers preserve multi-individual concentrations of vertebrate bones (i.e., bonebeds), with complete articulated skeletons preserved alongside more degraded skeletons that exhibit various degrees of disarticulation (Fig. 7). The bone weathering signature is also variable. Most of the specimens are highly weathered (Fig. 6A), although close to 40% of the fossils appear fresh or are only slightly weathered (Fig. 6B, C; Table 3). The chemical variability in the postmortem environment in the proximal Ischigualasto floodplain produced a wide range of mineralization in fossil bones. Bones recovered from calcic paleosols tend to be permineralized with calcite and trace amounts of hematite, with some bones entombed in calcite rinds. Bones recovered from drab-colored floodplain facies tend to be permineralized with hematite, barite, and secondary calcite, and usually exhibit hematite coatings.

Distal Floodplains—Distal floodplain deposits share many sedimentological and taphonomic attributes with proximal floodplain facies, although distinctions emerge as the distance from the active channel increases. Distal floodplain deposits comprise ca. 26% of the thickness of the Ischigualasto Formation succession. These deposits are characterized by tabular bodies of massive muddy sandstone and silty mudstone that show deep development of paleosols. Like the proximal facies, they can be separated into two types: reddish to reddish-brown floodplain deposits and drab dark gray to greenish-gray floodplain deposits. The former is typically characterized by calcic soils or argillisols, whereas the latter are characterized by argillic soils or, in some cases, incipient soil development (Tabor et al., 2006). These deposits preserve ca. 19.6% of the study sample (Fig. 4; Table 3), most of which was recovered along the margin of the basin in the Cancha de Bochas Member.

The distal floodplain facies association is characterized by highly weathered specimens (Fig. 8A, B), although contrary to

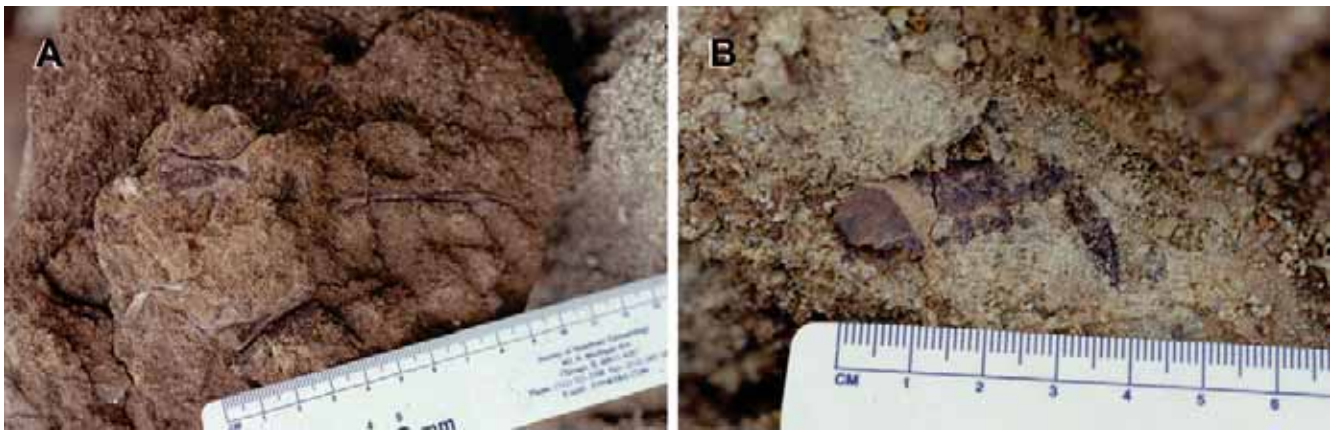

FIGURE 5. Characteristic fossil preservation in the paleochannel facies of the Ischigualasto Formation. Fossil bones occur as isolated specimens or fragmentary associations of a few elements. **A**, associated highly weathered specimen (not collected); **B**, isolated and disarticulated lower jaw of *Ecteninion lunensis* (PVSJ 694) preserved in very good quality, an example of delicate elements preserved in this facies. (Color figure available online.)

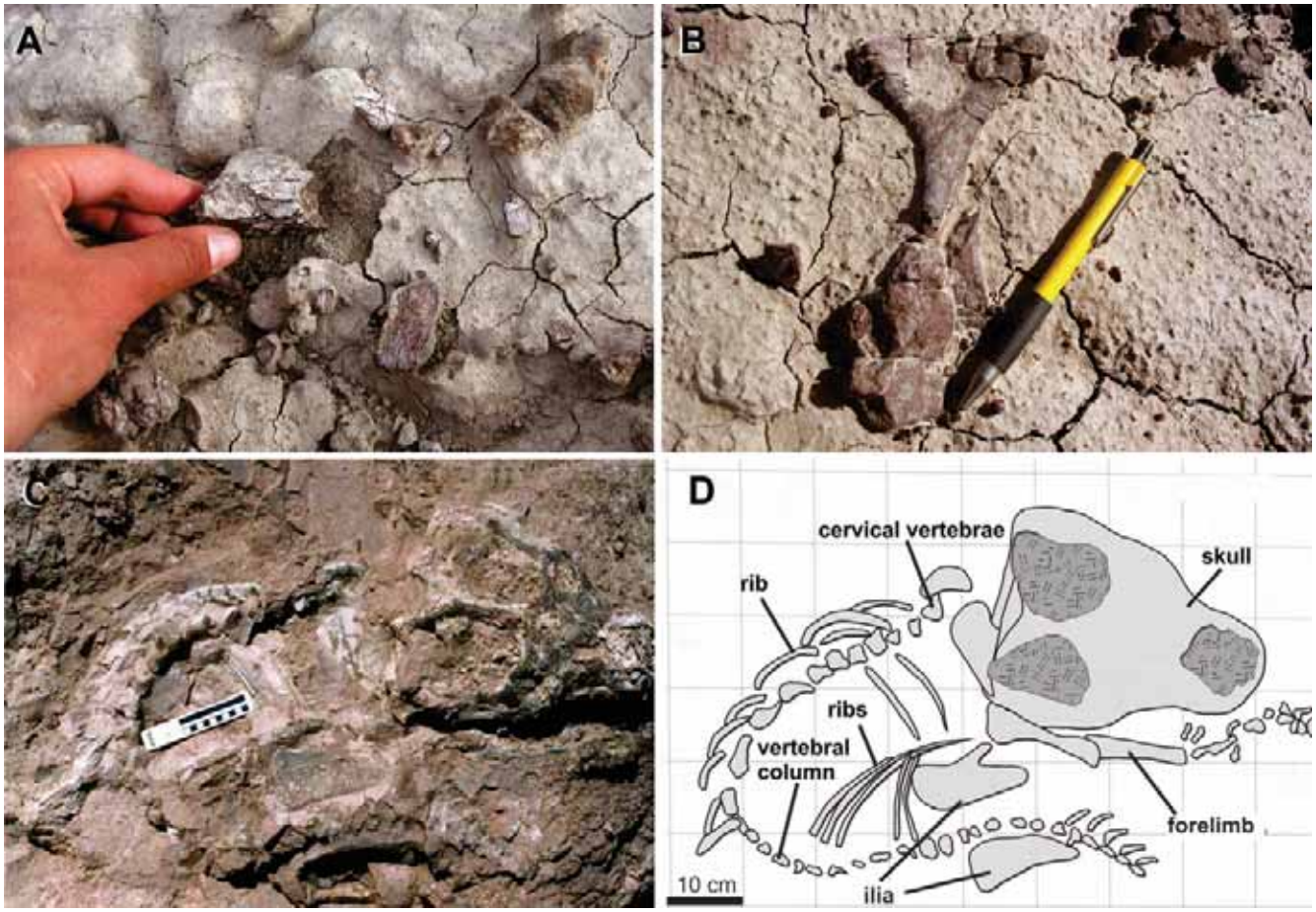

FIGURE 6. Characteristic fossil preservation in proximal floodplain facies of the Ischigualasto Formation. **A**, unidentified fragments of highly weathered bones that were not collected; **B**, isolated slightly weathered rhynchosaur humerus that was not collected; **C**, **D**, photograph and map of a complete skeleton of *Exaeretodon frenguelli* (PVSJ 713), providing an example of high-quality preservation in the proximal floodplain facies of the Ischigualasto Formation. Bone surfaces appear fresh and exhibit no evidence of post-mortem damage. The animal is oriented perpendicular to the paleocurrent direction of a nearby paleochannel deposit. Presumably the animal died of natural causes on the floodplain and was quickly buried by an overbank deposit shortly after its death. (Color figure available online.)

expectation given low rates of sedimentation, minimally weathered specimens also occur (Table 3). Interestingly, specimens with a relatively high percentage of skeletal element representation and articulation also typify this facies (Fig. 9; Table 3). One unusual aspect of the distal floodplain facies is that many of the articulated skeletons occur in multi-individual monotaxic associations (Fig. 8C, D).

Abandoned Channel—The abandoned channel facies association in the Ischigualasto Formation succession is characterized by lenticular bodies on the order of a few meters thick that consist of thinly laminated black to dark gray mudstones with intercalated horizons of plant cuticles (mainly represented by the *Dicroidium* flora). These lenticular bodies are usually associated with sandstone channel deposits.

The abandoned channel facies association hosts only 0.53% of the sample of vertebrate fossils examined in this study (Fig. 4; Table 3), and all occur in the Valle de la Luna Member. Fossil bones in this facies are generally black with a vitrine aspect (Fig. 10), and they tend to be only slightly weathered. None of the recovered skeletons are complete, and only one of the specimens is partially articulated, represented by the skull and a few articulated cervical vertebrae (Fig. 10A). All other specimens observed in this facies are disarticulated, although they tend to remain in association (Fig. 10B). Two of the three specimens recovered have been identified as an amphibian, which is consistent with the aquatic nature of this facies. The permineralization of the fossils in this facies is characterized by recrystallized apatite with sulfur and secondary uranium oxides. Finally, it is important to note that the abandoned channel facies is unique in that it preserves vertebrate remains together with abundant plant cuticle and palynomorphs.

Stratigraphic Distribution of Ischigualasto Vertebrate Fossils

As clarified above, the fluvial architecture of the Ischigualasto Formation exhibits stratigraphic changes from the base to the top of the formation that support division into four formal stratigraphic members (Currie et al., 2009). Along the margins of the basin, where most of the fossils have been recovered, these four members exhibit variations in the amount of fossils preserved, as

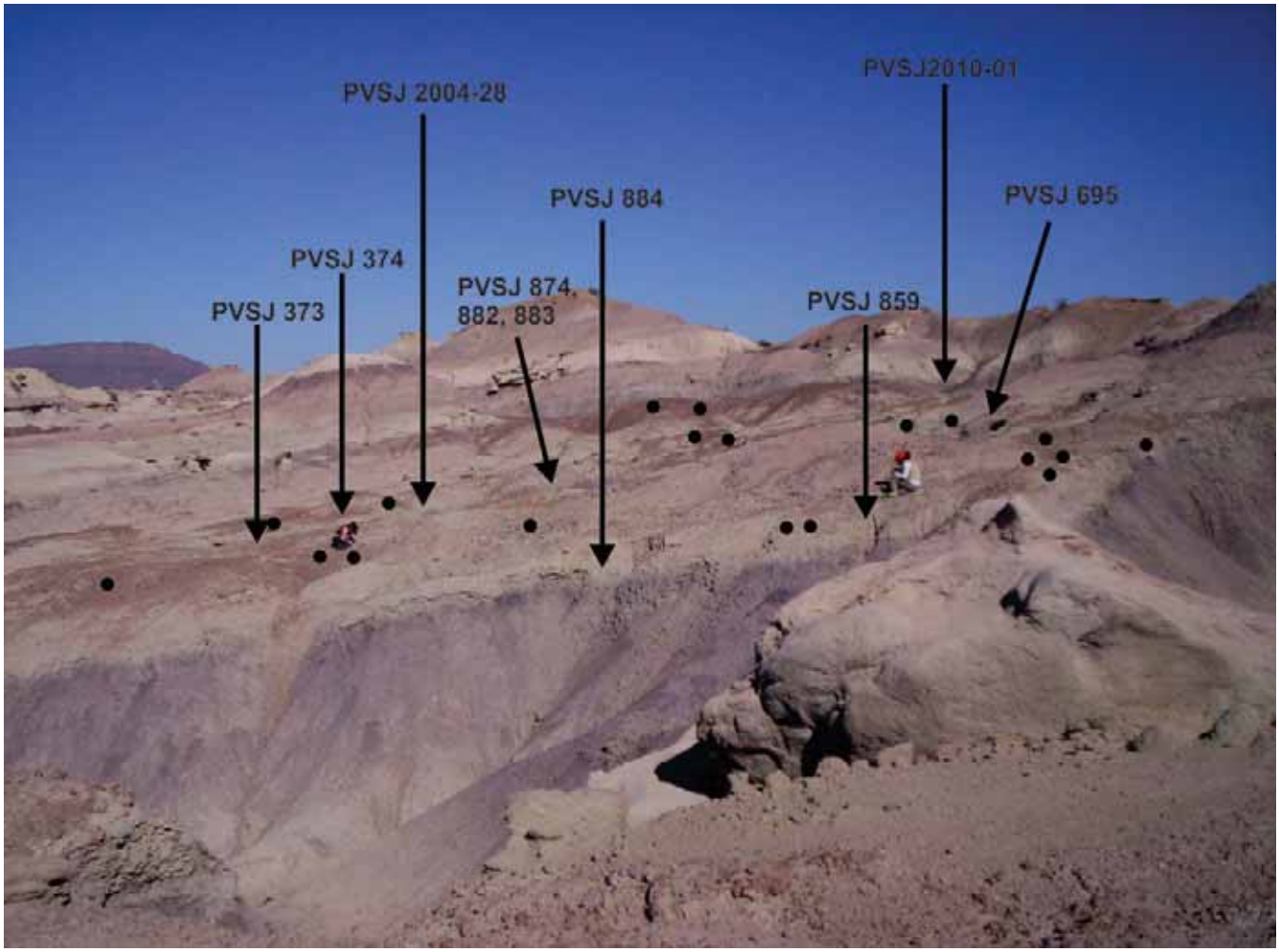

FIGURE 7. Multi-individual concentrations of animals (i.e., bonebeds) in a proximal floodplain facies in the Valle Pintado area. The host lithosome consists of greenish-gray sandy mudstone with ripple lamination. The arrows indicate each of the individual animals collected in the bonebed; together with specimens and coprolites that were not collected (Hollocher et al., 2005) marked with black dots. (Color figure available online.)

TABLE 4. Summary of the main taphonomic attributes in the La Peña, Cancha de Bochas, Lower and Upper Valle de la Luna, and Quebrada de la Sal members of the Ischigualasto Formation.

	La Peña		Cancha de Bochas		Lower Valle de la Luna		Upper Valle de la Luna		Quebrada de la Sal	
Taphonomic attributes/facies	N	%	N	%	N	%	N	%	N	%
Weathering										
Fresh	3	20	17	6.8	9	9	2	10	0	0
Slightly weathered	8	53.3	71	28.6	41	41	3	15	0	0
Weathered	4	26.7	160	64.5	50	50	15	75	2	100
Articulation										
Articulated	3	20	37	14.9	10	10	2	10	0	0
Associated	9	60	105	42.3	33	33	3	15	1	50
Isolated	3	20	106	42.7	57	57	15	75	1	50
% of skeleton preserved										
>70%	2	13.3	16	6.4	6	6	1	5	0	0
70–30%	4	26.7	44	17.7	8	8	4	20	0	0
<30%	9	60	188	75.8	86	86	15	75	2	100
Permineralization (authigenic minerals)										
Calcite		—		X		—		—		—
Calcite + hematite		X		X		X		—		—
Hematite		X		—		X		X		X
Total	15	3.9	248	64.4	100	26.0	20	5.2	2	0.5

N is the number of fossils recorded with taphonomic attributes (total number of fossil samples = 385). The 'X' indicates that a certain type of permineralization is present; the dash (—) indicates that it is not.

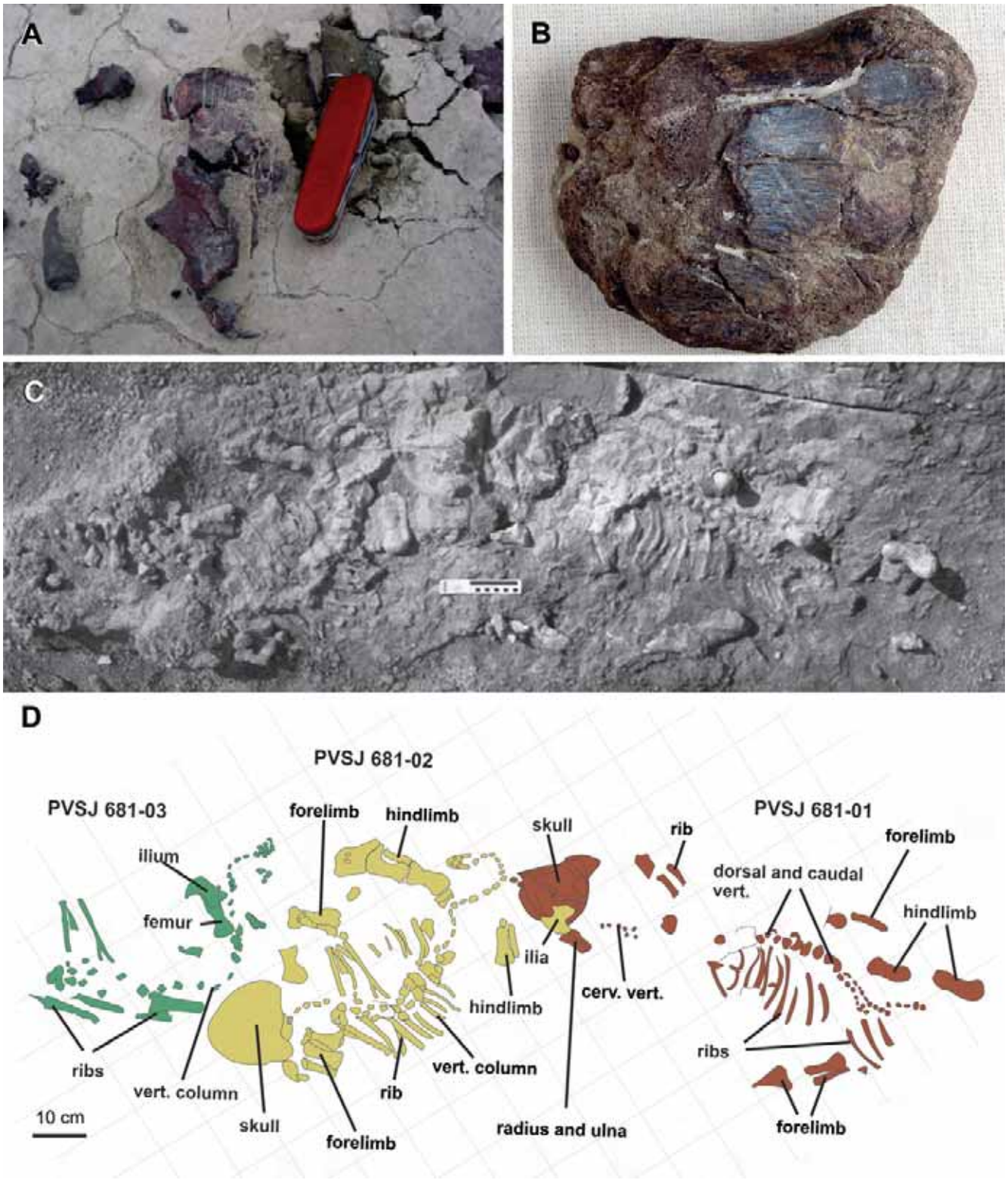

FIGURE 8. Characteristic preservation in distal floodplain facies of the Ischigualasto Formation. **A**, rhynchosaur scapula and coracoid (not collected) in a thick coating of hematite; **B**, highly weathered fragmentary bone (not collected) of indeterminate affinity (element is approximately 4 cm long); **C**, **D**, photograph and map of a multi-individual association of three articulated skeletons of juvenile rhynchosaurs (PVSJ 681 01-03) found in the distal floodplain facies of Cancha de Bochas Member. The skeletons are similar in size, exhibit minimal evidence of weathering, and are aligned oblique to local bedding. The bones exhibit no evidence of scavenging by large predators, although some displacement did occur, likely due to the activity of small necrophagous animals. This assemblage is interpreted to reflect the mortality of three juvenile animals in a burrow or den that was either filled with sediment-laden floodwaters or collapsed. In either case, rapid entombment would have protected carcasses from carnivore activity and atmospheric conditions. (Color figure available online.)

FIGURE 9. Characteristic facies associations and modes of preservation in the Cancha de Bochas Member of the Ischigualasto Formation. **A**, poorly drained floodplain in the depocenter area (El Salto); **B**, well-drained floodplain facies with calcisols that preserve most of the vertebrate fossils in this member; **C**, typical preservational quality of fossils in the Cancha de Bochas Member. Fossil fragments bear a thick calcareous coating; **D**, articulated skeleton (not collected) premineralized with hematitie and calcite; **E**, complete, articulated skeleton of cynodont (PVSJ 2004-33) exhibiting minimal weathering, consistent with the hypothesis of rapid burial; **F**, SEM image of typical permineralization of the Cancha de Bochas Member, with vertebrate bones permineralized by calcite or calcite plus hematite.

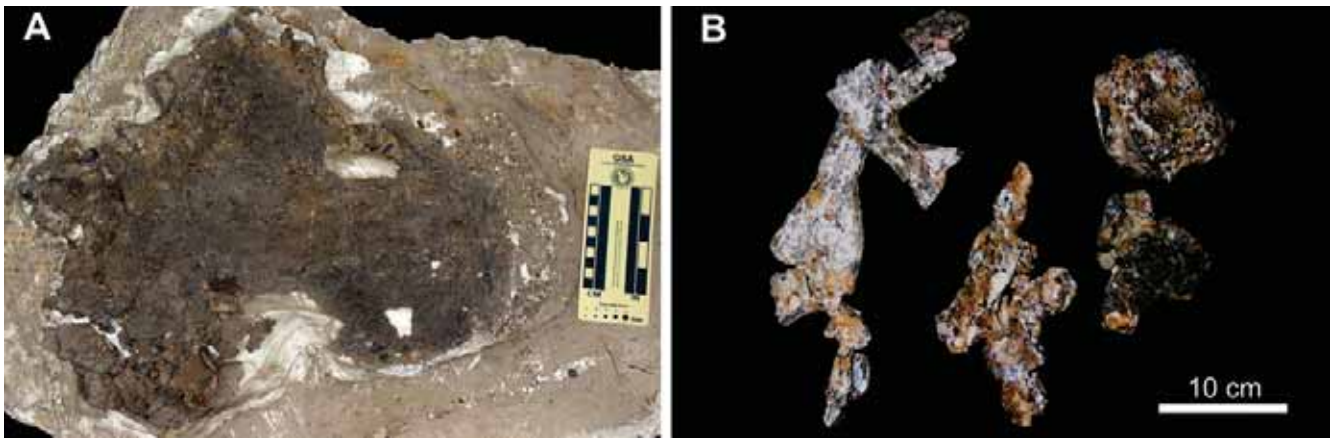

FIGURE 10. Characteristic preservation in abandoned channel facies of the Ischigualasto Formation. **A**, amphibian skull (PVSJ 840); **B**, partially articulated and slightly weathered black postcranial bones (PVSJ 1994-88). (Color figure available online.)

well as in the specific taphonomic attributes of fossils (Figs. 3, 11; Table 4).

Five distinct modes of taphonomic occurrence can be recognized from the base to the top of the formation. The first mode corresponds to the basal La Peña Member, which is characterized by amalgamated conglomeratic sandstone channels and poorly drained drab-colored floodplain mudstones (Currie et al., 2009; Fig. 12A; Table 1). Along the southern margin of the basin (from Valle Pintado to Agua de la Peña section), the La Peña Member yielded 15 fossil occurrences representing 3.9% of the samples we analyzed (Fig. 3; Table 4). No fossils were encountered in the depocenter of the basin, or in the Cerro Rajado region. The La Peña fossil assemblage is predominated by highly altered specimens that exhibit a low percentage of skeletal representation (Table 4). Fossils exhibit cracking/splintering and surficial exfoliation, and they typically occur as disarticulated multi-element occurrences or, more rarely, as partially articulated specimens (Fig. 12B, C). However, 20% of the fossil occurrences documented in the La Peña Member exhibit minimal weathering (stages 0–1 sensu Behrensmeyer, 1978) and preserve all or most of the skeleton. From a mineralogical perspective, the fossils of this member are characterized by recrystallized apatite, and permineralized by hematite and to a lesser degree barite and calcite. Hematite coats most of the bones (Fig. 12D).

The second mode of occurrence corresponds to the Cancha de Bochas Member, which is characterized by vertically stacked channel sandstone bodies with incised bases intercalated with poorly drained floodplain mudstones in the depocenter (Fig. 9A), and well-drained reddish-brown and gray floodplain mudstone deposits that exhibit mature calcisols on the margin of the basin (Tabor et al., 2006; Currie et al., 2009; Fig. 9B; Table 1). This member preserves most of the fossils in the Ischigualasto Formation, and includes 64.7% of our taphonomic sample (Fig. 3; Table 4). Like the La Peña Member, the Cancha de Bochas Member yields fossils primarily along the basin margins. The Cancha de Bochas fossil assemblage analyzed for this report (N = 248) is characterized by considerable variability in taphonomic attributes, even within single fossiliferous beds (Table 4). Again there is a predominance of isolated and disarticulated multi-element specimens that exhibit deep exfoliation and splinters (Fig. 9C). The unit also yields partial or complete articulated skeletons (Figs. 6C, 8C, 9D, E). Approximately 10% of the fossils documented in this package are in excellent condition and exhibit minimal post-mortem degradation (Figs. 6C, 8C, 9E). The bulk of the collection at the Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, was recovered from this member. From a mineralogical perspective, the fossils of the Cancha de Bochas Member often have calcite coatings and infills (Fig. 9C, F), and carbonate concretions jacket many bones (Fig. 9C). Calcite permineralization is particularly well developed in the calcic paleosols. Hematite and barite also occur as coatings on the outer surface of some bones (Fig. 9D). Some bones are coated with both calcite and hematite, with hematite typically in contact with the bone, and calcite forming a second rind on the outer surface (Fig. 9F).

The third mode of occurrence corresponds to the lowermost one-third of the Valle de la Luna Member (ca. 300 m from the base). This part of the member is characterized by isolated tabular channel sandstone deposits and thick reddish-brown and gray floodplain mudstone deposits that preserve calcisols and argillisols (Tabor et al., 2006; Fig. 13A; Table 1). This member yielded 26.1% of the vertebrate fossils treated in this report, which were recovered at both margins of the depocenter, but especially along the southern margin (Fig. 3; Table 4). The fossils of the lower Valle de la Luna Member (N = 100) are characterized by a predominance of isolated highly altered specimens that occur as disarticulated or partially articulated specimens, with a low percentage of skeletal representation (Fig. 13B). Only 6% of the fossil occurrences from this unit can be categorized as good quality (minimally weathered), and these occurrences tend to be complete, articulated skeletons (Fig. 13C). This mode is characterized by an abundance of hematite that permineralizes the bone, fills primary and secondary voids and cracks, and coats most specimens. Calcite rarely occurs as coatings or infills in bones (Fig. 13D).

The fourth taphonomic package treated in this report corresponds to the upper Valle de la Luna Member (upper two-thirds), which is characterized by amalgamated tabular channel belt sandstones interlayered with reddish-brown and greenish-gray floodplain fines that preserve abundant argillisols (Tabor et al., 2006; Fig. 14A; Table 1). This portion of Valle de la Luna Member, unlike the rest of the unit, preserves abundant plant cuticles, palynomorphs, and tree trunks in channel facies, abandoned channel facies, and floodplain marsh facies (Colombi and Parrish, 2008). This section is also characterized by an increase in altered volcanic ash (bentonite) layers compared with the lower part of the section. This package is relatively depauperate in vertebrate

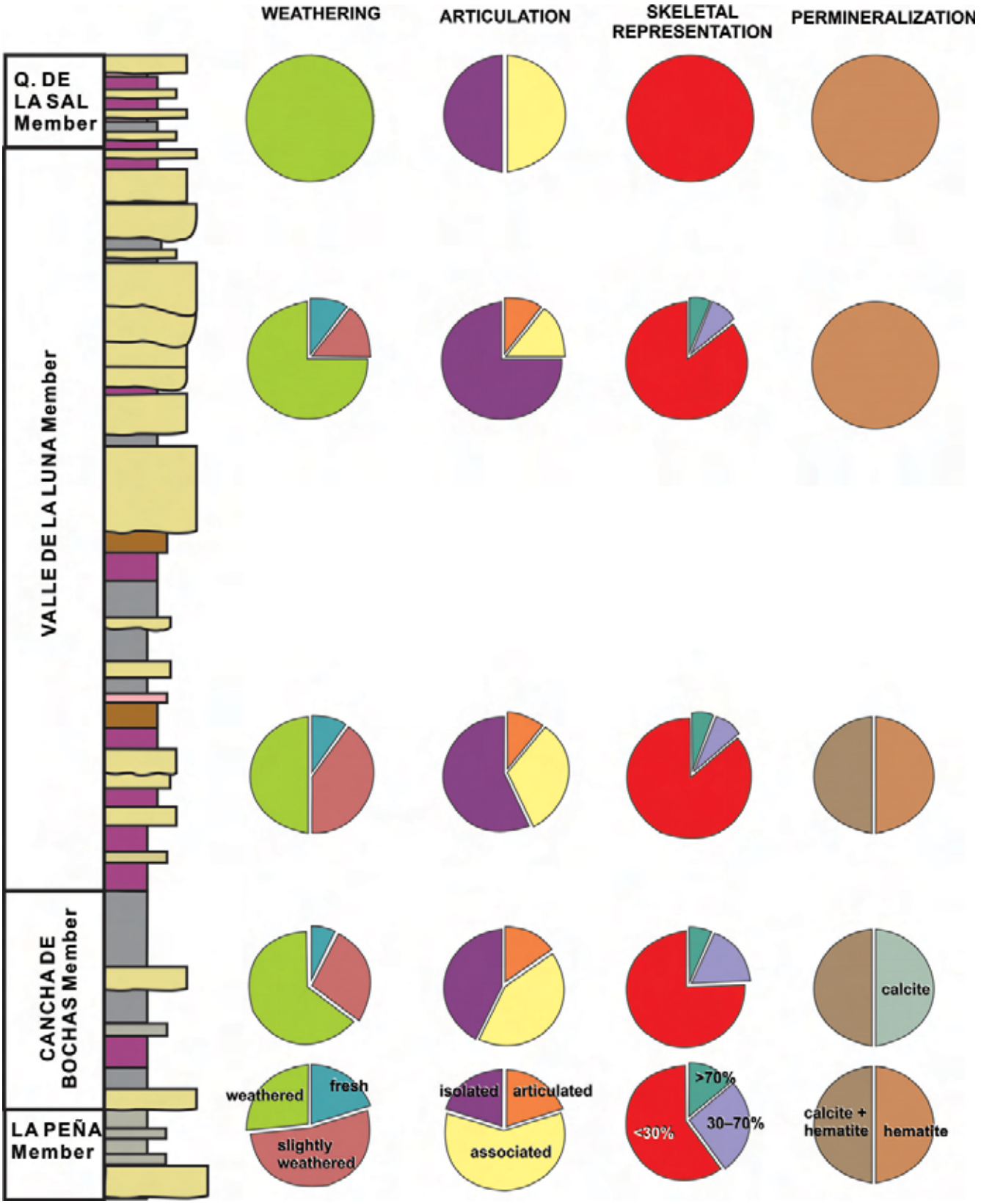

FIGURE 11. General taphonomic characteristics of each of the four members of the Ischigualasto Formation. The main taphonomic attributes analyzed in 385 specimens within the Ischigualasto Formation fossil assemblage are weathering, articulation, skeletal preservation, and permineralization (see Table 4 for more details).

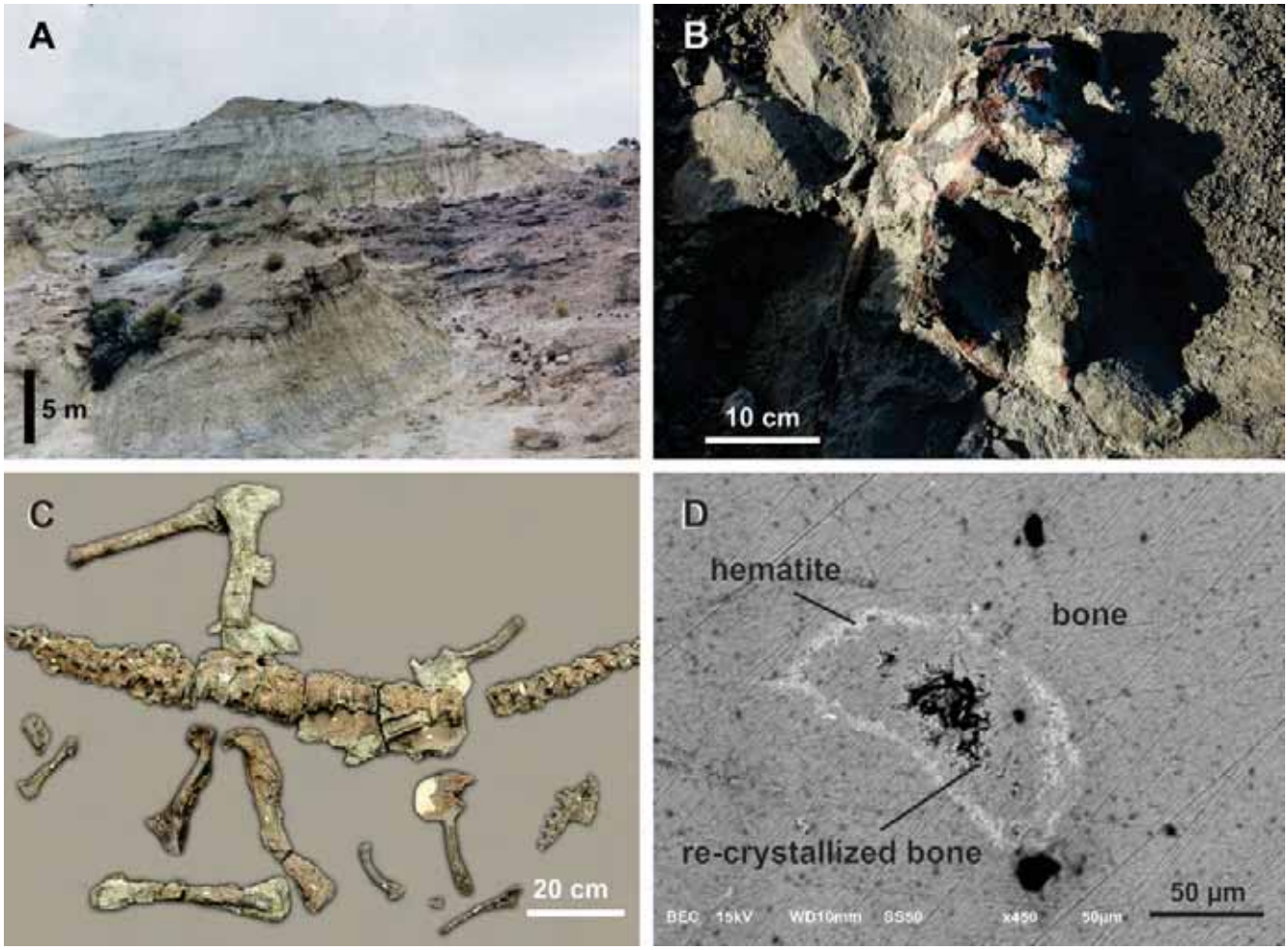

FIGURE 12. Exposures and characteristic preservation of the La Peña Member of the Ischigualasto Formation. **A**, poorly drained, drab-colored floodplain mudstones capping amalgamated channel sandstones; **B**, isolated complete cynodont skull with surficial exfoliation (not collected); **C**, partially articulated skeleton of *Sanjuansaurus* (PVSJ 605); **D**, SEM image of unidentified bone with typical permineralization found in the La Peña Member, where bones exhibit recrystallized apatite, and are typically permineralized with hematite. (Color figure available online.)

fossils, and it only yielded 5% (N = 20) of the fossils analyzed in this study (Fig. 3; Table 4). Fossils of the upper Valle de la Luna Member are generally highly degraded incomplete specimens (Fig. 14B, C). The predominant permineralizing mineral in the Valle de la Luna Member is hematite, with occasional barite permineralization (Fig. 14D). The rare well-preserved specimens found in this interval are interpreted to be the result of rapid burial on flooded floodplains (Fig. 14E, F).

The last mode corresponds to the fossils preserved in Quebrada de la Sal Member, which preserved only two specimens. They are isolated bones that are intensely weathered, strongly permineralized by hematite, and covered by a centimeter-thick jacket of hematite.

DISCUSSION

Studies of fluvial architecture (Currie et al., 2009), paleosols (Tabor et al., 2006), and plant taphonomy (Colombi and Parrish, 2008) indicate that the vertebrates that roamed the rift valley of the Ischigualasto-Villa Unión Basin did so under variable tectonic and climatic conditions (Tabor et al., 2006; Colombi and Parrish, 2008; Currie et al., 2009; Colombi et al., 2011; Martínez et al., 2011). The large-scale variations in taphonomic attributes detailed in this study are coincident with the variability in the alluvial system produced by tectonism and climate, which control accommodation space (i.e., aggradation and erosion) and the degree of confinement of the fluvial system. Similar large-scale controls on taphonomic patterns were identified by Behrensmeyer (1987) in the fluvial Miocene facies of Pakistan and by Smith and Swart (2002) in the terrestrial facies of a Triassic Karoo rift valley succession in Namibia, and others (e.g., Behrensmeyer and Hook, 1992; Aslan and Behrensmeyer, 1996; Rogers and Kidwell, 2000; Holz and Simoes, 2005).

Sedimentological data indicate that the Ischigualasto Formation was initially deposited on a surface that marks a basin-wide transition from lacustrine Los Rastros paleoenvironments to fluvial Ischigualasto paleoenvironments (Milana and Alcober, 1994). Basal fluvial facies of the Ischigualasto Formation accumulated in a confined valley, under conditions of low accommodation. Braided channel belt facies amalgamated into thick sandstone packages. The ecological and preservational conditions of this facies tract are generally not conducive to the preservation of vertebrate

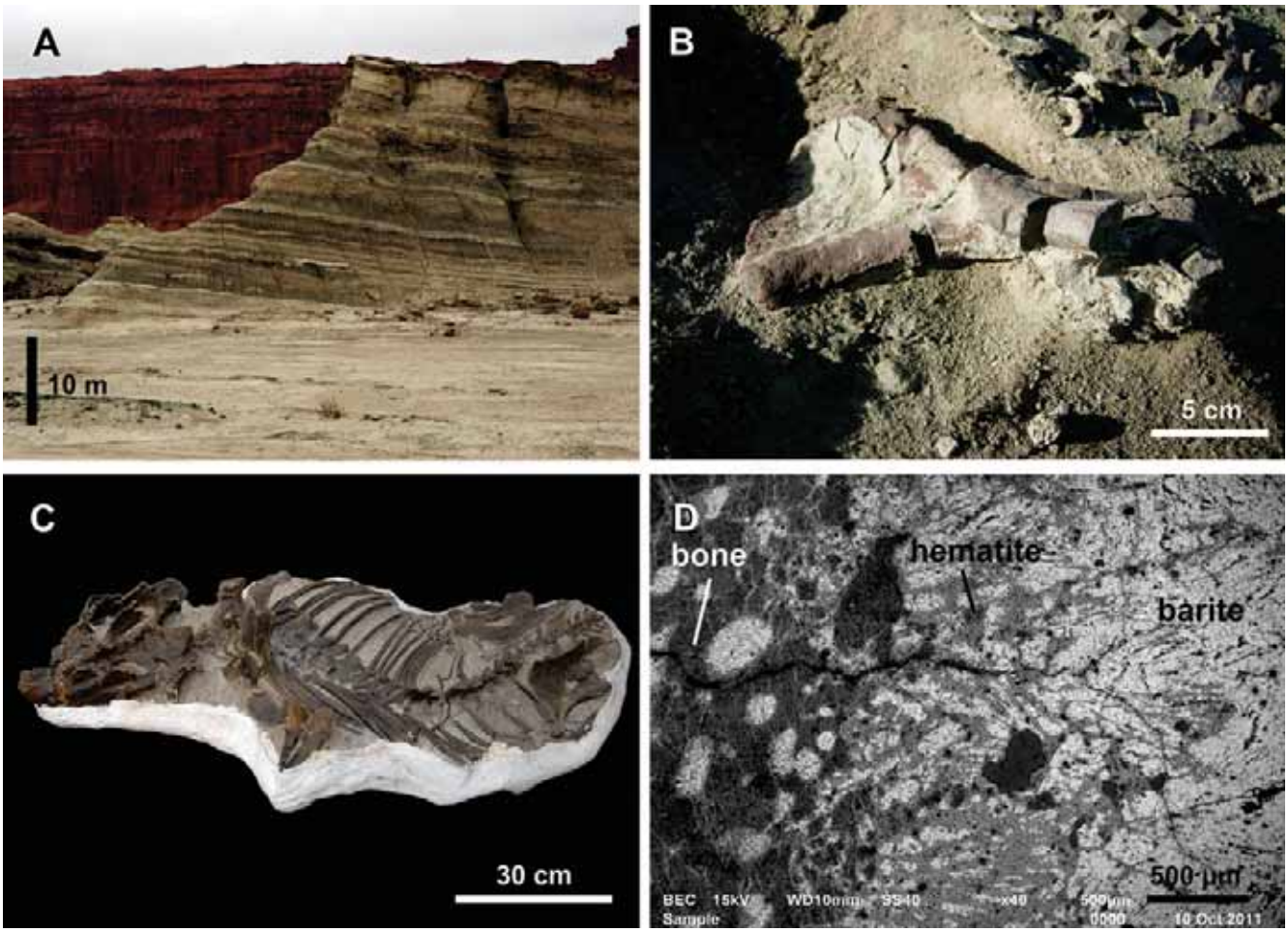

FIGURE 13. Exposures and characteristic preservation of the Lower Valle de la Luna Member of the Ischigualasto Formation. **A**, isolated tabular channel sandstone deposits and thick reddish-brown and gray floodplain mudstone deposits that host calcisols and argillisols; **B**, isolated highly altered humerus of rhynchosaur (not collected); **C**, complete articulated skeleton of cynodont (PVSJ 565) with unweathered bone surfaces; **D**, SEM image of typical permineralization of the lower portion of Valle de la Luna Member, with bones permineralized by hematite and barite. (Color figure available online.)

remains (Koster, 1987), and this holds true in the Ischigualasto Formation.

Rifting at approximately 231.6 Ma (Martínez et al., 2011) led to subsidence and the generation of accommodation (especially along the margins of the basin). The fluvial system shifted to a more sinuous pattern (Table 1), and floodplain facies began to accumulate, hosting the first remains of vertebrates in the Ischigualasto Formation in the La Peña Member. Sedimentological data indicate that the floodplains were poorly drained, as evidenced by drab colors in protosol and argillosol paleosols (Tabor et al., 2006; Currie et al., 2009; Table 1). The abundance of fossil occurrences represented by relatively few associated bones indicates that vertebrate carcasses were exposed on floodplain surfaces for prolonged periods and were exposed to surface processes that disarticulated and dispersed skeletal material (Behrensmeyer, 1975). The abundance of specimens exhibiting relatively minor weathering stages potentially reflects the accumulation of the carcasses under generally wet conditions and/or abundant vegetation, which protected the remains from destructive surface fluctuations in temperature and humidity (Behrensmeyer, 1975). There is no indication that the vertebrate carcasses were transported by currents on these hydromorphic floodplains. Decay of the carcasses both pre- and post-burial under anoxic poorly drained conditions led to the precipitation of iron minerals, most notably hematite, in the La Peña Member (Bao et al., 1998; Downing and Park, 1998).

The next stage in basin fill history, at approximately 231.1 Ma (Martínez et al., 2011), is characterized by tectonic instability that generated episodic periods of erosion (concentrated in the depocenter) or non-deposition (basin margin) followed by periods of increased aggradation (Colombi et al., 2011). These conditions, together with a seasonally arid climate, inferred on the basis of paleosol characteristics and plant taphonomy (Tabor et al., 2006; Colombi and Parrish, 2008), apparently led to optimal conditions for vertebrate fossil preservation along the margins of the basin in the Cancha de Bochas Member. Extended periods of very low net sedimentation rates, manifested by mature calcic paleosols, promoted the attritional accumulation of abundant vertebrate remains in basin margin settings (Leeder, 1975; Bown and Kraus, 1981; Behrensmeyer, 1982; Retallack, 1984; Kraus and Bown, 1986; Behrensmeyer, 1988; Willis and Berhensmeyer, 1994). Many animals probably concentrated

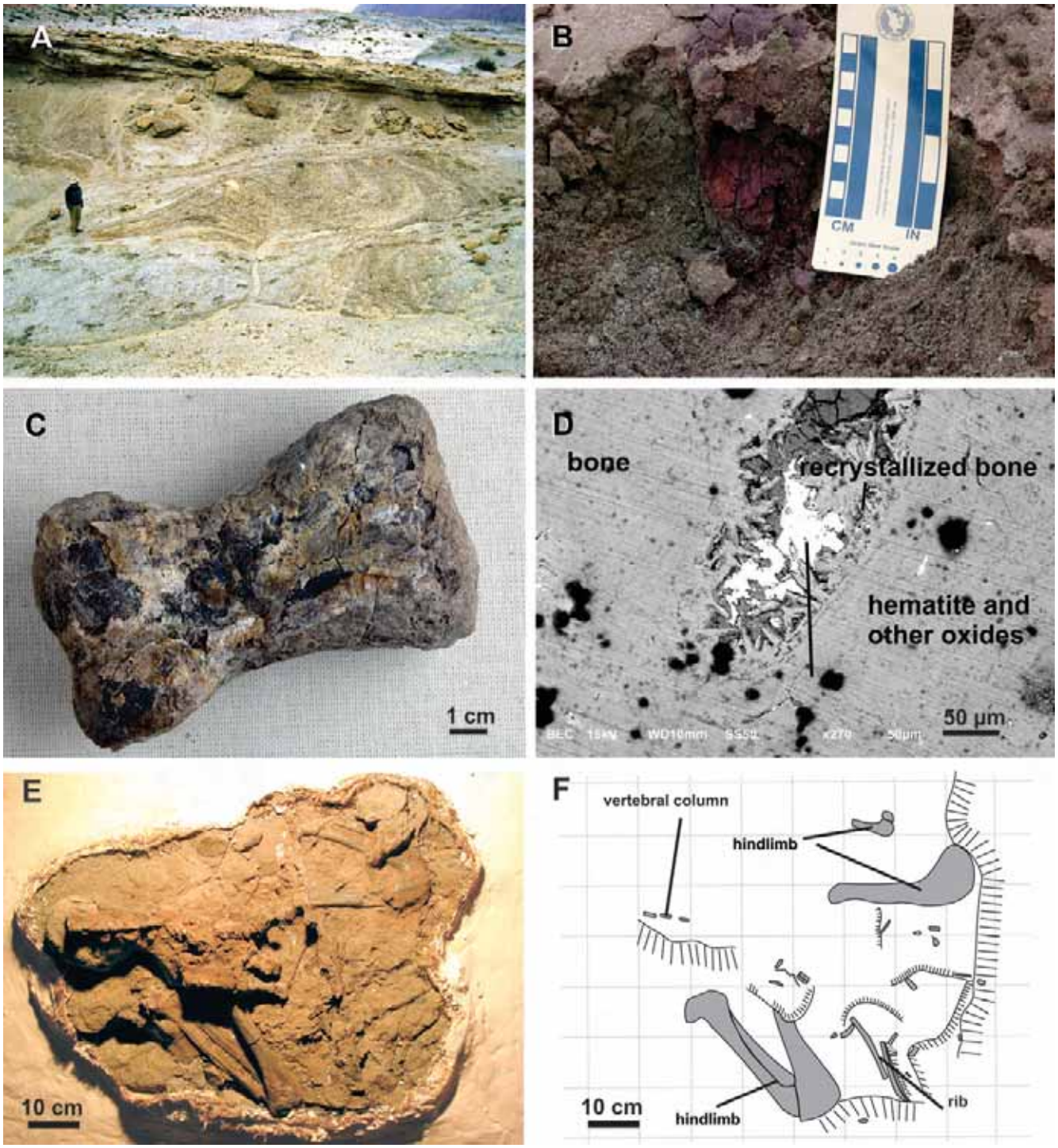

FIGURE 14. Exposures and characteristic preservation of the Upper Valle de la Luna Member of the Ischigualasto Formation. **A**, amalgamated tabular channel belt sandstones interstratified with abandoned paleochannels composed of dark gray mudstone and plant cuticles; **B**, typical fragmentary bone highly mineralized with hematite in Cerro Rajado area; **C**, typical black unidentified bone (not collected) found in the abandoned channels of this member; **D**, SEM image showing advanced recrystallization of apatite that show crystals growing inside one of the original bone canals. Hematite and other oxides (including Uranium oxide) permineralize the bone; **E**, **F**, well-preserved herrerasurid (PVSJ 714) preserved in Upper Valle de la Luna Member of the Ischigualasto Formation. This specimen consists of the posterior portion of the axial column and hind limb skeleton in a vertical position. The front half of the animal was not preserved, but there were abundant millimeter-scale bone fragments with sharp borders found near the skeleton that might belong to it. Bones are fresh, without any indication of weathering or carnivore activity. The animal was potentially trapped in mud, with the front half of the animal possibly removed by scavengers post-mortem. (Color figure available online.)

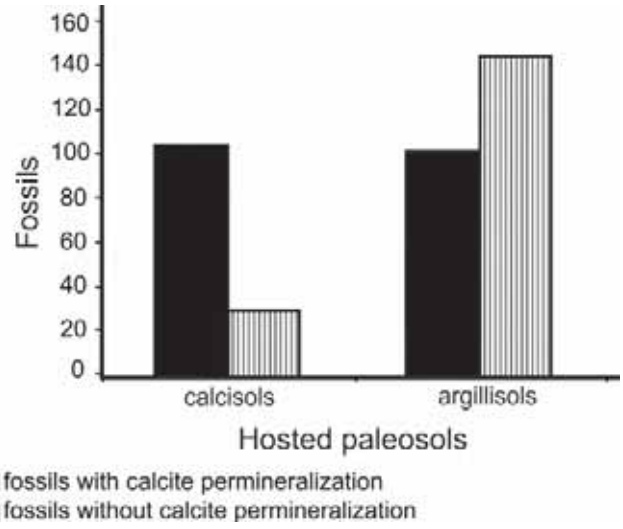

FIGURE 15. Histogram showing the number of fossils preserved in paleosols with and without calcite permineralization. There is an abundance of calcite-permineralized bones in calcisols, whereas hematite is the dominant permineralizing agent in argillisols.

looking for water sources during the dry seasons, comparable to the scenario reconstructed for the Middle Triassic Santa Maria Formation in Brazil (Holz and Barberena, 1994). During the dry season, droughts would presumably cause episodes of mass death, thereby increasing the likelihood of preserving intact skeletons due to the glut of carcasses (Behrensmeyer, 1975). In addition, many of the carcasses could have been mummified, which is consistent with the high number of pristine complete skeletons (Toots, 1965; Behrensmeyer, 1975; Holz and Barberena, 1994). Periods of low net deposition would have also favored the accumulation of time-averaged assemblages in this particularly fossiliferous part of the formation, mixing fossils with different stages of alteration and potentially different overall taphonomic histories. Finally, the seasonal dry weather during deposition of the Cancha de Bochas Member provided one last necessary condition to preserve an abundance of fossils, namely an alkaline geochemical environmental that promoted the widespread calcite mineralization of bone characteristic of this portion of the formation (Bao et al., 1998). This mineralization was presumably contemporaneous with pedogenesis, which is suggested by the close relation between the calcic mineralization of bones and mineralized features in associated calcic paleosols (Fig. 15). A similar early diagenetic situation was proposed by Smith (1993), who found that the calcite of fossil bones had comparable texture and composition to surrounding calcareous features in the pedogenic record.

A gradual regional increase in the humidity at around 230.2 Ma, as evidenced by the replacement of calcisols by argillisols (Tabor et al., 2006) and a coincident increase in the preservation of plant remains (Colombi and Parrish, 2008) in the Valle de la Luna Member, resulted in a dramatic decrease in the abundance of vertebrate fossils preserved in the Ischigualasto Formation and a drastic change in their preservation. The increase in humidity within the basin coincides with higher aggradation rates and the preservation of thick floodplain deposits at the base of the Valle de la Luna Member and amalgamated channel belt sandstones at the top. With higher sedimentation rates, vertebrate carcasses tended to accumulate as isolated specimens as indications of time-averaging diminished. The basin-wide increase in accommodation space also favored the preservation of distal floodplain facies, where lower rates of sedimentation translated to longer residence time for carcasses on the surface. Accordingly, carcasses in distal floodplain facies in this part of the section show abundant evidence of disarticulation and weathering, reflecting prolonged exposure to biotic (e.g., scavenging, trampling; Toots, 1965; Holz and Barberena, 1994) and abiotic (e.g., ultraviolet [UV] light, daily temperature variation; Behrensmeyer, 1978) agents. The fossils preserved in the proximal facies exhibit variable weathering stages and varying states of disarticulation and association. The hydromorphic and potentially somewhat acidic conditions associated with prolonged wet seasons apparently led to the partial dissolution of some bones (Behrensmeyer, 1975) and prompted permineralization with iron complexes (Bao et al., 1998; Downing and Park, 1998).

Finally, at the top of the Ischigualasto Formation (Quebrada de la Sal Member), biologic and geologic conditions were apparently unsuitable for vertebrate fossil preservation, and to date only two specimens, which are highly altered, have been recovered. The reasons for the paucity of vertebrate fossil remains in the uppermost Ischigualasto Formation are unknown, but could potentially be linked to the decrease in slope and sediment supply during the final stages of rifting in the basin (Milana and Alcober, 1994).

CONCLUSIONS

The Upper Triassic Ischigualasto Formation of northwestern Argentina hosts an abundance of vertebrate fossils that afford an unparalleled opportunity to study tetrapod evolution during the emergence and diversification of dinosaurs and mammals. The vast fossiliferous exposures that typify the Ischigualasto Formation also afford an outstanding opportunity to explore relationships among basin evolution, paleoclimate, sedimentary facies, and fossil preservation. In this report we delineated general taphonomic patterns in the formation based on a sample of 385 fossil occurrences (ranging from isolated elements to intact skeletons) documented during organized stratigraphic transects in selected portions of the basin. Trends in vertebrate preservation elucidated here, ranging from the basin scale to the local scale, are summarized below.

1. Vertebrate fossils are most abundant along the margins of the Ischigualasto-Villa Unión Basin (Valle Pintado, La Gallinita, Agua de la Peña) and are relatively rare in the basin depocenter (El Salto). This spatial pattern presumably reflects differences in sedimentary processes (aggradation vs. incision), duration of non-deposition, geochemical subsurface conditions (e.g., position of the water table relative to the surface) subsidence-driven facies distinctions between these two regions, and the predominance of amalgamated high-energy channel sandstone bodies, which are not particularly fossiliferous, in the basin depocenter. Floodplain facies, which preserve the majority of fossils in the Ischigualasto Formation, constitute more of the overall section along the flanks of the basin.
2. The basal La Peña Member yielded 15 fossil occurrences, representing 3.9% of the taphonomic sample. The La Peña fossil assemblage is dominated by highly weathered disarticulated, fragmentary specimens. Approximately 20% of the occurrences exhibit minimal weathering but preserve a low percentage of the skeleton. Fossils are typically permineralized by hematite. Taphonomic data suggest that vertebrate carcasses probably accumulated via attritional processes and were generally exposed on floodplain surfaces for prolonged periods under generally humid conditions and /or abundant vegetation.

Anaerobic conditions in the burial environment encouraged the precipitation of hematite.

3. The vast majority of Ischigualasto vertebrate fossils in museum collections have been recovered from the Cancha de Bochas Member of the Ischigualasto Formation, and almost 65% of the fossil occurrences analyzed in this report are derived from this unit. Cancha de Bochas fossils are characterized by considerable variability in taphonomic attributes, ranging from poorly preserved isolated specimens to well-preserved articulated skeletons. Calcite is the predominant (although not exclusive) permineralizing agent. Fossils in this unit apparently represent both attritional assemblages and mass mortality assemblages that presumably accumulated in response to ancient droughts. Alkaline burial environments in calcic paleosols promoted widespread calcite permineralization of bone.
4. Lower portions of the Valle de la Luna Member yielded ca. 26% of the fossil occurrences treated in this report. These occurrences are predominantly isolated specimens that exhibit considerable degradation. A small fraction of the fossil occurrences in the lower Valle de la Luna Member are complete, articulated skeletons.
5. The upper two-thirds of the member, which are rich in plant remains, preserve a sparse record of fossil bone and yielded only 5% of the fossil occurrences analyzed in this study. Fossils in the upper part of the unit are generally highly degraded, isolated specimens. The dominant authigenic mineral is hematite. The Valle de la Luna Member accumulated under more humid conditions than underlying strata, and there is indication that sedimentation rates also increased during deposition of this unit. Fossils generally exhibit features consistent with prolonged exposure to destructive taphonomic agents prior to burial. Hydromorphic conditions in the burial environment led to the precipitation of hematite on and within bone.
6. The Quebrada de la Sal Member, which is the uppermost member of the Ischigualasto Formation, yielded only two highly degraded specimens that were permineralized and enclosed within hematite. Taphonomic explanations for the fossil-poor nature of this unit are difficult to provide, but may relate to the tectonic evolution of the Ischigualasto-Villa Unión Basin and an attendant decrease in sediment supply.
7. Finally, at the local scale, it is possible to observe the influence of the fluvial context on vertebrate preservation. Floodplain deposits (divided herein into proximal and distal components) preserve the vast majority of fossils in the Ischigualasto Formation and yielded approximately 88% of the fossil occurrences included in this study. The quality of fossil preservation in the Ischigualasto floodplain complex is highly variable, from isolated highly weathered specimens to complete well preserved skeletons. Coarser-grained deposits of ancient fluvial channels preserve just under 12% of the fossil occurrences examined in this study. Interestingly, many small cynodont skulls preserved in pristine condition have been recovered from channel sandstone facies. Vertebrate fossils are exceptionally rare in abandoned channel facies of the Ischigualasto Formation. This at least in part reflects the scarcity of this particular facies context in the unit as a whole, but may also reflect generally low rates of sedimentation and acidic geochemical conditions.

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