FIRST ARGENTINE MICROFOSSIL BONEBED FROM THE UPPER TRIASSIC MARAYES—EL CARRIZAL BASIN, SAN JUAN PROVINCE

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ABSTRACT: The first Triassic microfossil bonebed found in Argentina is located 80 meters from the top of the Quebrada del Barro Formation in the Marayes-El Carrizal Basin, in the province of San Juan. It consists of specimens from at least 63 individuals from an anomalously high concentration of fossils distributed laterally and vertically in a meter-thick fine-grained deposit. Two new taxa from the genera *Sphenodontia* and *Eucynodontia* had previously not been found in Argentine Triassic quarries. The bonebed is preserved in a mudflow deposit interbedded with calcic-Argillisols in the medial-distal zone of a distributary fluvial system (DFS). The accumulation is characterized by small-sized skeletal fragments (skulls, jaws and vertebra; all less than 50 mm), low degree of articulation, variable degrees of subaerial exposure, tooth marks, surface dissolution, and an alkaline authigenic mineral suite. Detailed paleoenvironmental and taphonomic characterization indicate that this accumulation underwent three stages in its taphonomic history: (1) biogenic extrinsic concentration; (2) local transportation and re-deposition by a mudflow on a swampy floodplain; and (3) drying and pedogenesis. Additionally, the deposit highlights biogenic activity as a way to concentrate a paleofaunal assemblage that likely represents the original community, and mudflow deposits from crevasse splays in DFS as a potential facies for microfossil preservation.

INTRODUCTION

The Marayes-El Carrizal Basin, located in the southwest of San Juan, Argentina (Fig. 1), includes three Middle to Upper Triassic units: the Esquina Colorada, Carrizal and Quebrada del Barro formations (Borrello 1946; Bossi 1976). Following early studies by Bossi (1976), little work has been done on the Quebrada del Barro Formation. However, new vertebrate fossil discoveries have led to renewed interest in this formation and other fossil-bearing units in the upper portion of the Marayes Basin succession (Apaldetti et al. 2011; Abelín et al. 2012; Colombi et al., in press; Martínez et al. 2013a, 2013b).

Until recently, only a few isolated or associated bones of the basal sauropodomorph massospondylid *Leyesaurus* had been found in the floodplain and channel facies of the Quebrada del Barro Formation (Abelín et al. 2012). Recently, a high-density deposit of small vertebrate fossils, mostly less than 5 cm in length, was discovered in a single bed ~ 80 m from the top of the Quebrada del Barro Formation. These fossils represent at least five new taxa (Martínez et al. 2013a, 2013b), making this the first Triassic microfossil bonebed described from this region of Pangea (e.g., Wood et al. 1988; Behrensmeyer 1991; Eberth et al. 2007; Rogers and Kidwell 2007).

The importance of microfossil bonebeds lies principally in the fact that these deposits generally yield fossil remains of rarely recovered species, particularly those of small size or delicate morphology. These taxa provide fundamental information relating to the understanding of paleoecosystems (Fisher 1981; Brinkman et al. 1998). The study of the microfossil bonebed hosted in the Quebrada del Barro Formation is no exception. This discovery yields important new paleofaunal data from

strata positioned just below the Triassic–Jurassic mass extinction. This locality also affords insights into how sedimentary processes concentrate and preserve vertebrate microfossils in a single layer.

GEOLOGICAL AND PALEONTOLOGICAL CONTEXT AND AGE

The Marayes-El Carrizal Basin is located in the cratonic geological province of the Western Sierras Pampeanas, in the Northwestern Argentine province of San Juan. This basin, together with those of Ischigualasto-Villa Union and Cuyo, belongs to a series of continental rift basins developed along the southwestern margin of Pangea during the lower Mesozoic (Spalletti 1999). The Marayes-El Carrizal Basin was described by Bossi (1976), who defined the Marayes Group following Borrello (1946). Three units have been formalized: the Esquina Colorada, Carrizal, and Quebrada del Barro formations from base to top (Fig. 1). The Marayes Group rests unconformably on the crystalline basement of the Valle Fertil Group (Bossi 1976), which is mainly composed of amphibolites and other low to mid-grade metamorphic rocks. In turn, the Marayes Group is disconformably overlain by the Cretaceous El Gigante Group (Fig. 2).

The Quebrada del Barro Formation, which is the focus of this study, has a variable thickness ranging between 600 and 1400 m, and consists of coarse sandstones and conglomerates interbedded with sandy claystone with dispersed granule clasts (Fig. 2). The depositional environment was originally interpreted as an alluvial fan due to the large proportion of conglomerates (Bossi et al. 1975). Later, Rivarola et al. (2002) described the facies associations and interpreted the environment as a braided fluvial system. Our study of the facies associations leads us to re-interpret
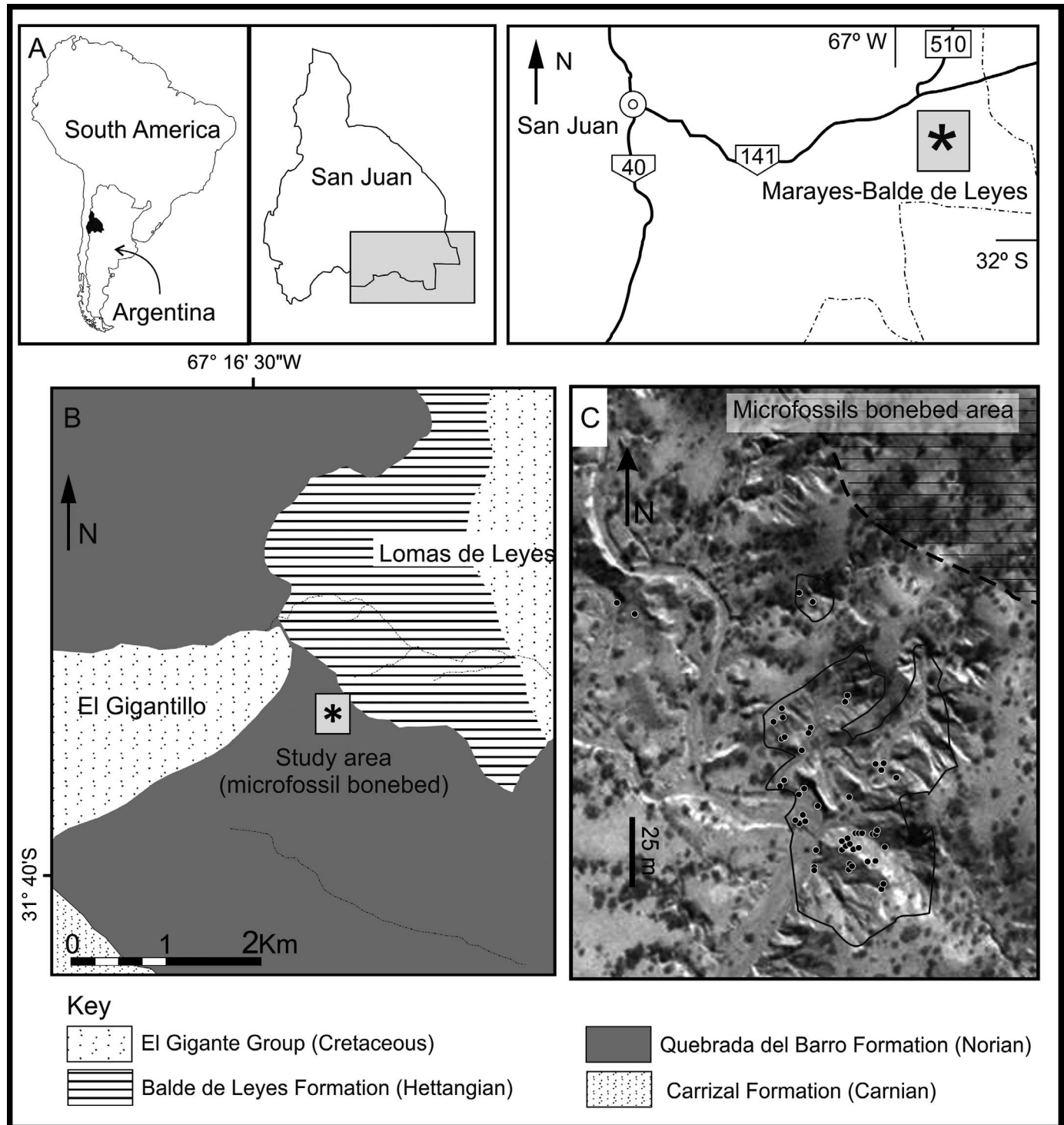
FIG. 1.—Location and geological map of the study area in the southern part of the Marayes-El Carrizal Basin. Map scale decreases from top to bottom and left to right, the area of each successive map is shown as a light gray rectangle. **A**) Location maps. **B**) Geological map of the study area. **C**) Panoramic photograph of the microfossil bonebed area showing density of fossil occurrences, marked by black dots. The lines demarcate Triassic rock outcrops. A line pattern represents the Balde de Leyes Formation, located on the top of the Quebrada del Barro Formation.

FIG. 2.—Stratigraphic section of the Quebrada del Barro Formation, with the location of the microfossil bonebed and facies associations (FA) indicated. Abbreviations: c = claystone; s = sandstone; g = conglomerate.
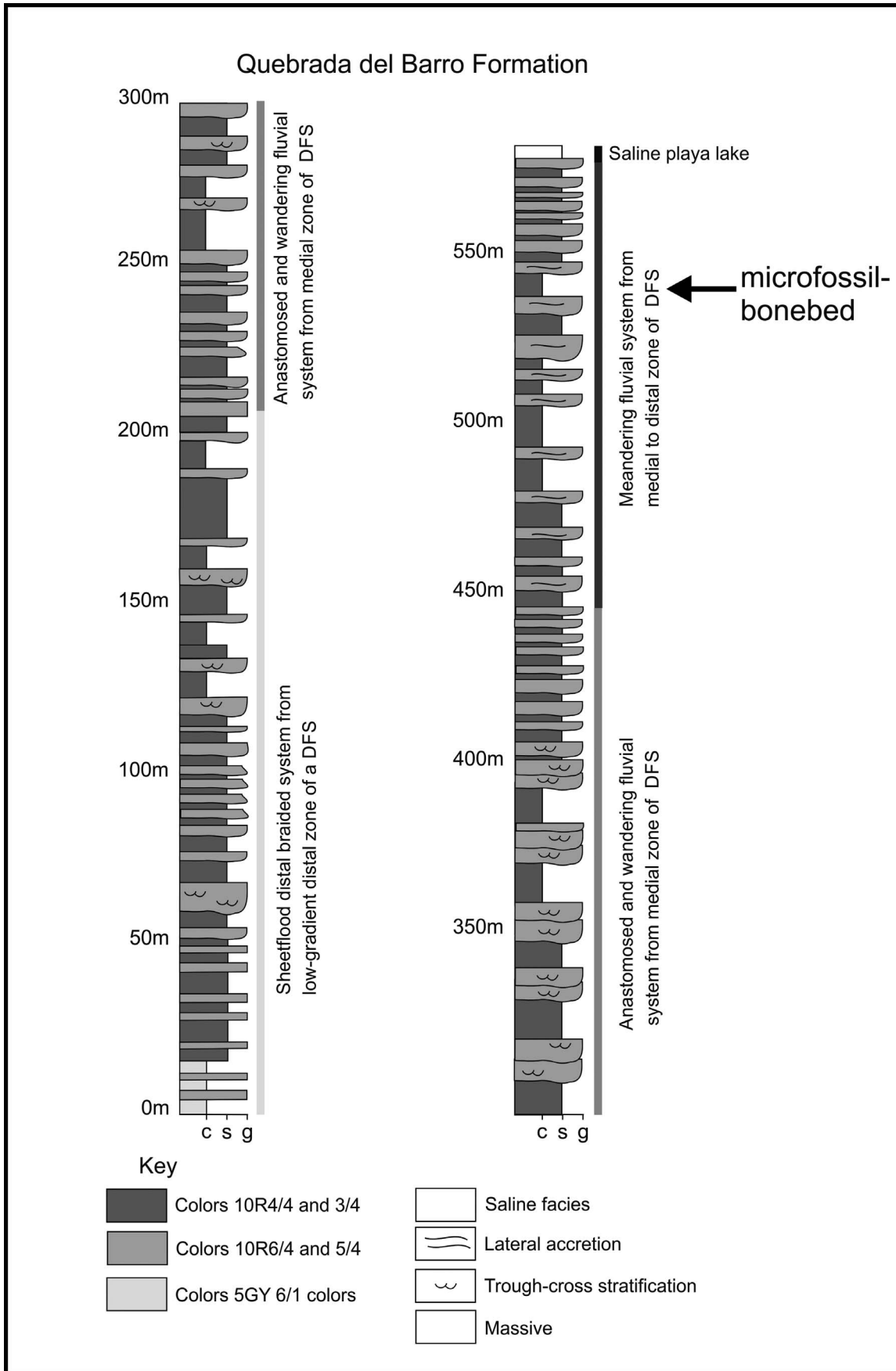
Quebrada del Barro Formation

Key

Colors 10R4/4 and 3/4

Colors 10R6/4 and 5/4

Colors 5GY 6/1 colors

Saline facies

Lateral accretion

Trough-cross stratification

Massive

TABLE 1.—*Facies asssemblages of the Quebrada del Barro Formation (Colombi et al. 2014)*

Facies associations	Description	Interpretation
FA-A—Sheetflood distal braided system from low-gradient distal zone of a distributary fluvial system	This facies association is dominated by muddy-fine sandstone and mudstone with abundant chaotically distributed granules interlayered with tabular gravel bedforms and channels. The channel/overbank facies proportion is 1:7. The fine facies have pedogenic features (Calcisols).	The facies association is interpreted as sheetflood distal braided system (Miall 1996) dominated by single-storey channels and abundant over-flooded deposits, corresponding to the low-gradient distal zone of a distributive fluvial system developed at some distance from the mountain front (Stanistreet and McCarthy 1993; Blair and McPherson 1994; Nichols and Fisher 2007). The type of soil indicates a seasonal semiarid to arid climate (Mack et al. 1993)
FA-B—Anastomosed and wandering fluvial system from medial zone of distributary fluvial system	This facies association is characterized by a cyclic succession formed by deep erosive multi-storey conglomerate and coarse sandy channels followed with minor proportion of fine deposits. The channel:floodplain ratio is 1.5:1. The fine facies are composed by muddy-fine sandstone and mudstone with abundant chaotically distributed granules. There are also heterolithic facies and sporadic conglomeratic lenses. The fine facies have scarce pedogenic features (immature Calcisols)	The facies association is interpreted as anastomosed and bedload wandering fluvial channels (Church 1983; Miall 1996; Makaske 2001) coincident with the medial facies of a distributive fluvial system (Stanistreet and McCarthy 1993; Blair and McPherson 1994; Nichols and Fisher 2007). The type of soil indicates a seasonal semiarid to arid climate (Mack et al. 1993).
FA-C—Meandering fluvial system from medial to distal zone of distributary fluvial system	This facies association is characterized by a succession of fining upward cycles that start with tabular single-storey conglomerate and sandy channels, followed by fine facies of the floodplain in similar proportion. The channel:floodplain ratio is 1:1. The fine facies are composed of massive muddy-fine sandstone and mudstone with abundant chaotically distributed granules. This facies has pedogenic features (argillic-Calcisols).	This facies association is interpreted as the deposits of gravel-sand meandering rivers (Miall 1996). Lateral overflows of mudflow dominate the floodplain formation, forming temporary abandoned channels. The high sinuosity of the rivers together with the appearance of abandoned channels indicate a low gradient and distal areas of the distributary fluvial system, probably indicating the outer edge of the medial zone (Stanistreet and McCarthy 1993; Nichols and Fisher 2007).
FA-D—Saline playa lake deposit	This facies association is formed by a tabular layer of 30 to 50 centimeters of salt minerals. This facies caps the Quebrada del Barro succession.	This facies association is interpreted as a subaqueous deposit of salts in a playa lake formed by ground water uplift or flooding after big storms (rainy season) followed by evaporation and the consequent precipitation of salts, assuming that the clastic component was deposited in the outer area of the basin. Thus, this deposit has been interpreted as a distal playa lake deposit.

the depositional environment as a distributary fluvial system, in which fluvial channels with a large range of sinuosity form a complex deposit with mudflow dominated floodplains, and terminal splays that are formed by heterolithic sandstone and mudstone accumulations (Table 1, Colombi et al. 2014).

Bossi and Bonaparte (1978) initially proposed the Quebrada del Barro Formation to be Norian in age based on a single specimen, an incomplete articulated right pes (PVL 4087) of a basal sauropodomorph. They referred to this specimen as *Riojasaurus* due to its similarities with *Riojasaurus incertus* (Bonaparte 1967) from the Norian Los Colorados Formation in the neighboring Ischigualasto-Villa Unión Basin. Recent studies, based on the correlation of many taxa from this microfossil bonebed with the Los Colorados paleofaunal assemblage, confirm a late Norian age for the Quebrada del Barro Formation (Martínez et al. 2015).

THE MICROFOSSIL BONEBED OF THE QUEBRADA DEL BARRO FORMATION

Sedimentology

Colombi et al. (2014) recognized four facies associations (FA) in the Quebrada del Barro Formation, described in Table 1 from A to D (Colombi et al. 2014).We interpreted the environment of the Quebrada del Barro succession as a gradual transition from the medial to distal zone of a distributary fluvial system (DFS), associated with saline playa lakes (Colombi et al. 2014). This environment is dominated by lateral and terminal splays produced by sheetfloods and high sinuosity rivers with

variable proportion of floodplain deposits, which mainly grow by lateral mudflows. This type of environment usually forms in basins that have warm and arid climates (Nichols and Fisher 2007).

The microfossil bonebed under study is positioned close to the top of the Quebrada del Barro succession (FA-C from Table 1), in facies association C (meandering fluvial system from medial to distal zone of DFS). This facies is derived from deposits of gravel-sand meandering rivers and associated floodplains.

The bonebed layer consists of a massive, reddish, tabular deposit of mudstone with abundant isolated granules (Figs. 2, 3). This 8-m-thick deposit corresponds to a crevasse-splay formed by a lateral mudflow from a distributive meandering channel in the medial-distal zone of a DFS. This layer has abundant pedogenic features including bioturbation, faint lamination, redoximorphic features (mottles and root halos), centimeter-scale calcareous nodules (1 cm) and rhizocretions, and weak clay cutans. The presence of these pedogenic features allows us to classify this soil as an argillic-Calcisol (a paleosol with a well-developed calcic horizon as its dominant feature and an overlying argillic horizon), following the criteria of Mack et al. (1993).

Taphonomic Characterization

Approximately 90% of the bones in the bonebed are less than 20 mm long (Fig. 4A). Only 5% of them were greater than 50 mm (mostly belonging to Sauropodomorpha), which coincides with the definition of a microfossil bonebed (e.g., Wood et al. 1988; Behrensmeyer 1991; Eberth et al. 2007; Rogers and Kidwell 2007).

c sf smsc g

Key

Colors 10R4/4 and 3/4

Colors 10R6/4 and 5/4

Granules

Root halos

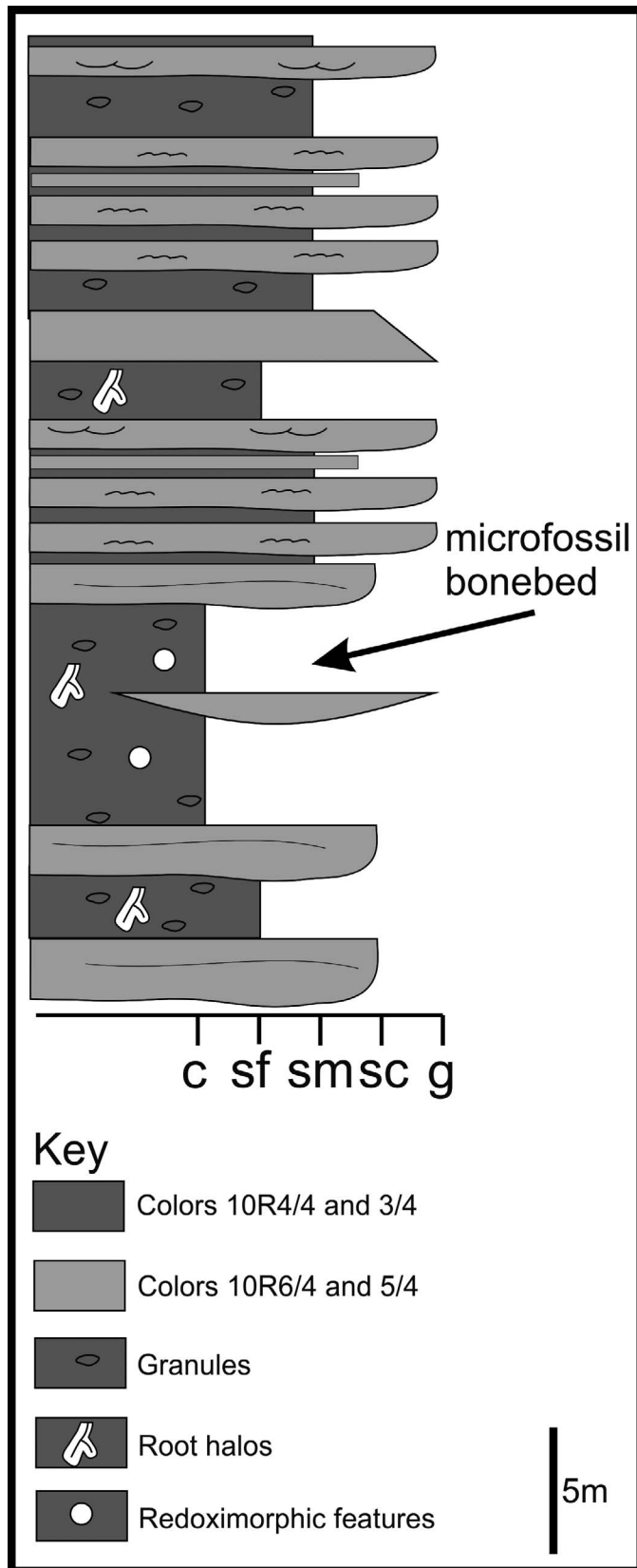Redoximorphic features

microfossil bonebed

5m

FIG. 3.—Detailed section of the microfossil bonebed showing texture of the different facies and major pedogenic features.

Spatial Density.—The Quebrada del Barro Formation preserves vertebrate fossils throughout its entire thickness but the fossils are relatively rare, except in the studied interval (Fig. 1C). The bonebed preserves a minimum number of individuals (MNI) of 63. Along this level, there are pockets of concentration where the density is approximately five specimens per square meter, and areas where the density falls to as low as one specimen per square meter (Fig. 1C). In this context, one specimen corresponds to an original individual, which can be represented by articulated, associated or isolated bones in the taphocoenosis. Exceptionally, two or more individuals have been found together in close association. These associations can be formed by individuals of the same taxa, with different or similar sizes, but with repeated bones (i.e., two left lower jaws)—or, more rarely, individuals of different taxa that include different feeding habits.

Based on the density of vertebrate bioclasts, this association can be classified as a "dispersed concentration" (sensu Kidwell and Holland 1991), characterized by the sparsely distributed, matrix-supported remains of paleovertebrates.

About 70% of the bone fragments were excavated and collected *in situ*, and these specimens were used for spatial density analyses. The remaining ~ 30% of the fossils were not recovered *in situ* and can be considered products of secondary concentration by means of present-day erosional processes, even though they most likely came from the same bed (Fig. 1C). They preserve similar taphonomic features as the *in situ* fossils, which indicate that modern processes are not a potential bias in the assemblage analyses.

Taxa Present.—In the Quebrada del Barro Formation, the most abundant fossils correspond to one or more species of Sauropodomorpha (95%) (Bossi and Bonaparte 1978; Martínez et al. 2013a). However, in the level studied, this group is relatively underrepresented (5%), and the most common remains represent a new species of *Sphenodontia* (Martínez et al. 2013a) (70%) (Fig. 4B). The relative abundance of this taxon is followed by a new species of small *Eucynodontia* (17%). Other taxa present include an indeterminate small Pseudosuchia (3%). The assignment of the other taxa to certain groups is based on personal observation using apomorphy-based comparisons.

Preserved Skeletal Parts and Fragment Size.—The association is dominated by skull fragments (46%), to which mandibular rami could be added (22%). However, we decided to analyze the latter as independent skeletal elements due to the ease of detachment from the skull and high mobility (Fig. 4C). These fragments are followed in abundance by vertebrae (16%), complete in some cases and without neural arches in others. Lastly, long bone fragments—corresponding to some of the appendicular elements—are significantly underrepresented and comprise only 6% of the assemblage.

Degree of Association and Articulation of the Skeleton.—About 230 bones and bone fragments were found in the studied level, of which only three are partially articulated (5%), and the remaining are either associated (55%) or isolated (40%) (Fig. 4D). Interestingly, the associated fragments are mainly skull fragments, while the isolated parts are mostly jaw fragments with teeth or dental plates. The bones frequently appear broken. Approximately half of the fracture edges are rough with uneven, jagged edges (Fig. 5A), indicating that these fractures occurred early in the taphonomic history of the remains. The other half have straight edges (Fig. 5B), probably corresponding to fractures that occurred after fossilization processes began (e.g., Behrensmeyer 1991).

Bone Surface Marks.—The remains in general show a high quality of preservation in relation to bone morphology, with very delicate processes
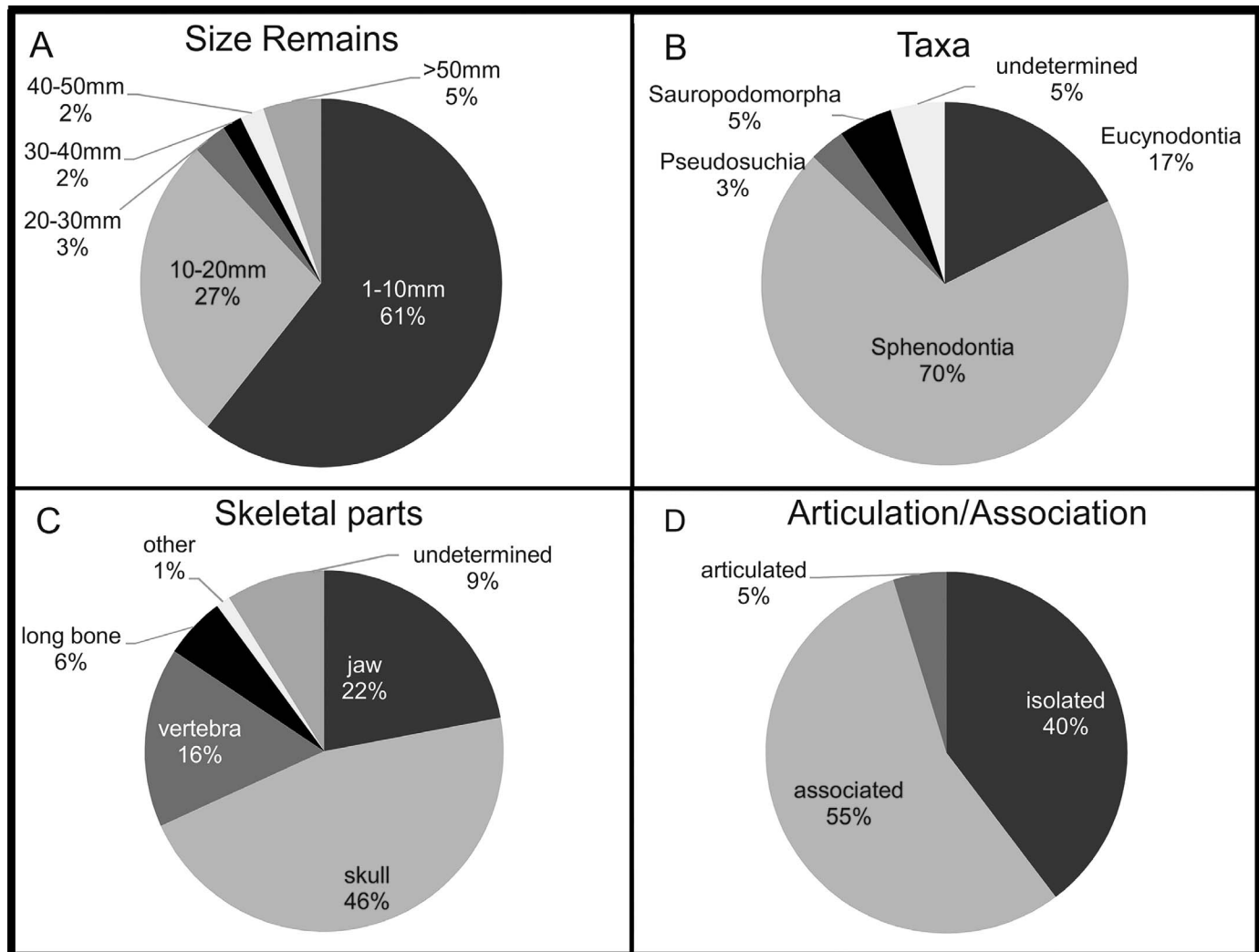
FIG. 4.—Pie charts indicating relative percentages of the taxa, preserved skeletal elements, size of remains, and the degree of articulation-association based on the MNI of 63 (see online Supplemental Data).

preserved in good quality (Fig. 6). However, cracks (Fig. 7A), flaking (Fig. 7B), and fractures parallel to bone fiber are present in both bones and teeth. Following the standard classification of weathering (Behrensmeyer 1978), approximately 60% of the specimens are fresh, without marks on the surface; 17% are slightly weathered, showing cracks and a low degree of surface flaking; and 23% of the remains are weathered, showing deep flaking that exposes deeper bone layers and splinter fractures (Fig. 8A). Weathering is variable in the assemblage, although most fossils appear fresh and relatively unweathered. Given the enormous quantity of jaws preserved, a remarkable feature is that all teeth remain in their alveoli.

In addition, approximately 30% of the bones exhibit $\sim$ 0.1 mm dendritic channels on the bone surface or penetrating into the internal bone tissue (Figs. 7C, 7D, 8B). These features are consistent with the marks left by root traces or boring organisms (Behrensmeyer 1991).

Further marks found in the assemblage, representing 10% of the whole, are parallel grooves or scrape marks, pitting, shallow oval perforations in bone surfaces, and cancellous bones that have had the bone tissue scooped out from the epiphyseal ends of limb bones (Figs. 8C, 9A–E). Each of these marks resembles varying stages of carnivore damage observed in the archeological and paleontological record, from simple gnawing to extreme furrowing (e.g., Maguire et al. 1980; Shipman 1981;

Binford 1981; Andrews and Evans 1983; Lyman 1994; Rogers et al. 2003).

Finally, calcareous submillimeter spheres are present on some bone surfaces (Fig. 9F). These modifications are present on approximately 30% of the bones, and are distributed in patches. They could represent the product of microbial alteration, as described by Truemen et al. (2004) for recent bones that have oval or circular foci surrounded by a densely mineralized apatite wall. Peterson et al. (2010) also describe similar structures as colonies of fungi and bacteria observed in biofilms developed on bone surfaces.

Surface Dissolution.—Dissolution of bone and tooth surfaces is the main feature observed in this microfossil association, and is evident in 80% of the specimens (Fig. 8D), including teeth that have lost most of their enamel. The dissolution has produced a rough appearance, with small punctae on the surfaces of bones and teeth (Fig. 10A–D). The extent of the dissolution is not the same along all surfaces. On some bones it is barely distinguishable and produces only the loss of the most external layer of bones and enamel in teeth. On other bones, all of the external layers have been dissolved, exposing the internal cancellous bone tissue. With regards to the degree of dissolution, four stages have been
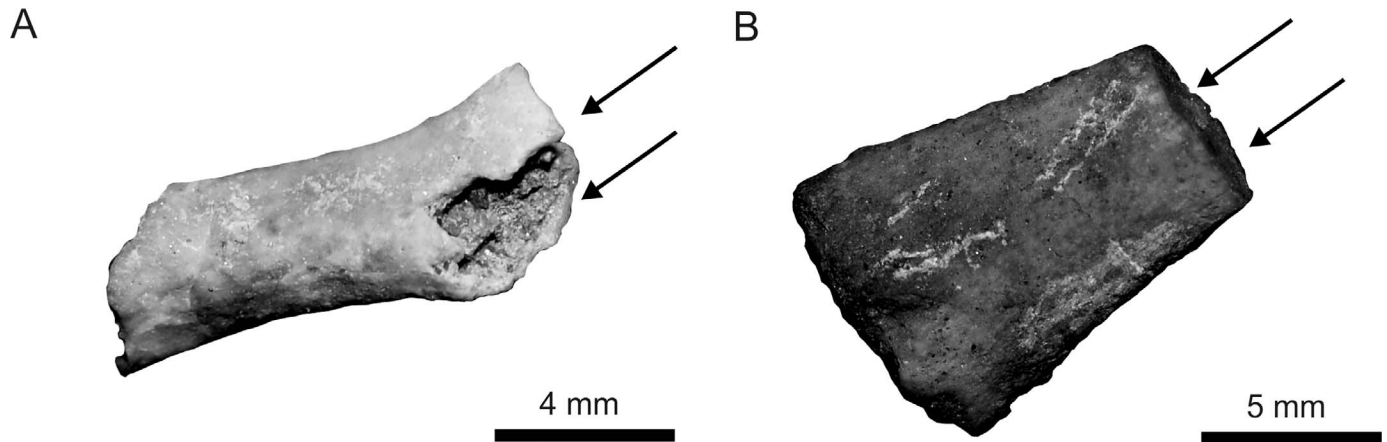
A

B

4 mm

5 mm

FIG. 5.—Photographs comparing fractures of bone fragments of the microfossil bonebed assemblage. **A)** Rough fractures with uneven and jagged edges, indicating that these fractures occurred early in taphonomic history. This bone corresponds to the *Sphenodontia* specimen with collection number PVSJ942 of the Collection of Paleovertebrates from the Institute and Museum of Natural Sciences, National University of San Juan (CPV-IMCN). **B)** Fractures with straight edges that probably correspond to fractures occurring after fossilization, potentially the result of present-day weathering processes. This bone (PVSJ951 CPV-IMCN) is unidentified.

differentiated: undissolved, slightly dissolved, moderately dissolved, and strongly dissolved; all of which are approximately equally represented (Fig. 8D). In some of the jaws, the observed dissolution is different on each side of the fragments, indicating that the burial position of the bones had some influence on this attribute. Moreover, dissolution of the surface in this assemblage increases as the fragment size decreases although the correlation between the two variables is not statistically strong (r^2 0.07; t (0.05, 60); 0.05), there is a noticeable trend of inverse correlation related to increased surface area to volume ratios for smaller particles. Detailed observations of the other surface marks and dissolution of bone and tooth surfaces indicate that dissolution occurred later than that of the other surface marks (Figs. 7A, 11). Consequently, the dissolution obscures previously generated modifications, giving a generally rough and rounded appearance around the entire surface,

while also expanding the natural foramina and the holes generated by root bioturbation or tooth marks (Fig. 10A–D).

Authigenic Minerals.—Sample PVSJ 897 was analyzed with a polarized light microscope and a scanning electron microscope, yielding the recognition of a suite of authigenic minerals: sparry calcite, dolomite, halite, clay, anhydrite, minor silica, and hematite (Fig. 12A, B). This suite of minerals is remarkably similar to the bone mineralization documented in the top of the Los Colorados Formation, which is the same age (Colombi and Rogers 2014). It is distinct from the authigenic mineralization in older paleofaunal assemblages from the Ischigualasto and Chañares formations, which are mainly dominated by hematite and calcite (Colombi and Rogers 2014), which are the most common authigenic minerals during bone fossilization (Smith 1993; Bao et al. 1998; Holz and Shultz 1998; Trueman et al. 2004).

DISCUSSION

According to Rogers and Kidwell (2007), skeletal concentrations arise principally from one of two main origins: biogenic or physical. Biogenic causes can be divided into two groups, intrinsic and extrinsic concentrations. Intrinsic concentrations are those in which the animals constituting the taphocoenosis, are responsible for the concentration on behalf of their own actions; included here are those related to reproductive events (Böttcher 1990; Emslie 1995; Chiappe et al. 2004) and those caused or prompted by disturbances or environmental hazards (Berger et al. 2001; Spencer et al. 2003; Capaldo and Peters 1995; Shipman et al. 1984; Fiorillo et al. 2000). Extrinsic concentrations, on the other hand, are those in which other animals, usually not present in the taphocoenosis, are responsible for the concentration. In general, these are related to different types of predation, such as coprocoenosis, serial predation, or intentional collection (Haynes 1988; Lam 1992; Terry 2004; Laudet and Selva 2005). The remaining concentrations are generated by physical processes—that is, concentrations where bones are introduced into the depositional environment as clasts, and as such are subject to the dynamics of the depositional, tectonic, and climatic environment of the basin (Beherensmeyer 1975). A microfossil bonebed may be the result of a single geological or ecological event or the interaction of multiple ecological and geological agents over a long period of time (Rogers and Kidwell 2007). The latter include many associations of mixed origin in
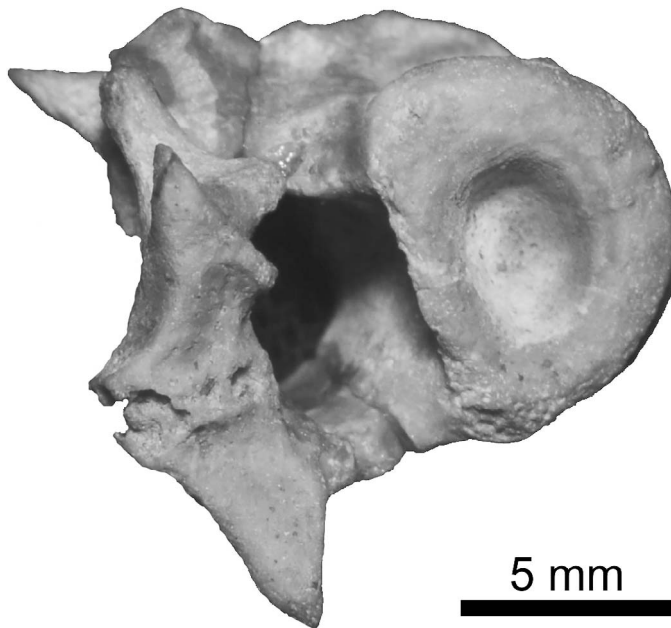
5 mm

FIG. 6.—Delicate remains preserved in the Quebrada del Barro microfossil bonebed. This bone is a vertebra of *Sphenodontia* specimen (PVSJ948 of the CPV-IMCN).
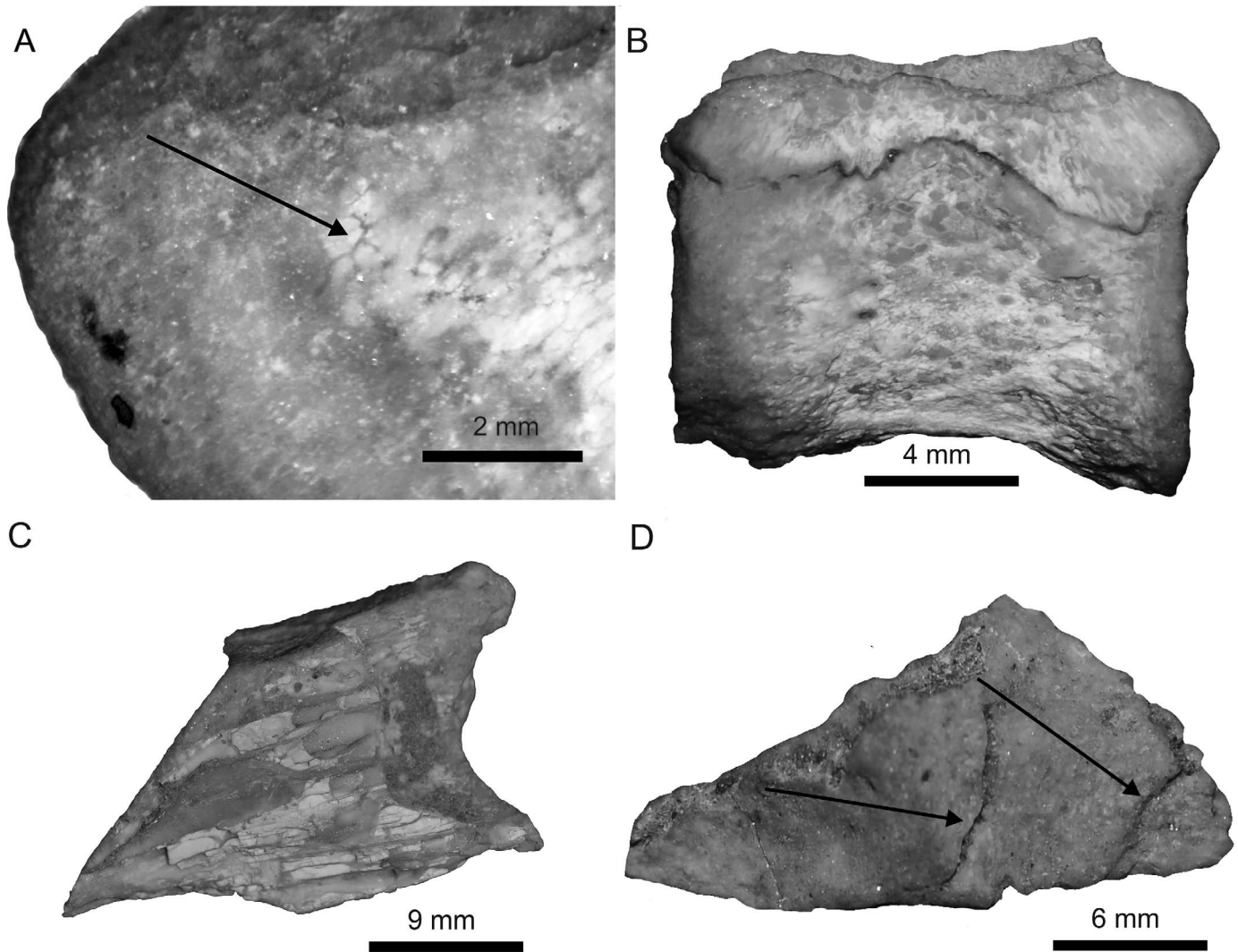
FIG. 7.—Photomicrographs of taphonomic modifications on bone surfaces. **A)** Cracks on the surface of a *Sphenodontia* specimen (PVSJ954 CPV-IMCN). **B)** Cracks and flaking of outer bone surface layers in a Pseudosuchian vertebrae (PVSJ912b-IMCN CPV). **C)** Deep flaking of the outer bone surface in a Pseudosuchian unidentified fragment (PVSJ912 CPV-IMCN). **D)** Root traces represented by millimeter-scale dendritic channels on the bone surface in *Sphenodontia* specimen PVSJ942-IMCN CPV.

which different components come into play at different points in time within the taphonomic history (Terry 2004; Rogers and Kidwell 2007).

The mechanism responsible for the Quebrada del Barro microfossil accumulation can be deduced by means of taphonomic characterization. Below we describe nine key taphonomic characteristics of the deposit that we then use to propose a scenario for the accumulation and preservation of the bonebed.

1. The microfossils were buried in a mudflow deposit corresponding to a crevasse splay in the floodplain of the medial-distal zone in a distributary fluvial system. The calcic-Argillisol, consistent with the typical climate associated with DFS, suggests that the climate during bonebed formation was seasonal arid to semiarid (Mack et al. 1993; Cecil and Dulong 2003; Tabor et al. 2006).

2. The fossils appear distributed in a one-meter thick level as a "dispersed concentration" (sensu Kidwell and Holland 1991). This vertical distribution of microfossils in the bonebed renders unlikely the possibility that final burial corresponded to the burial of a bone-rich surface by a mudflow deposit. The arrangement

implies at least local transportation and dispersion of the remains into the mudflow before final burial.

3. Most of the taxa present in the assemblage can be considered prey of larger animals. This is clear in the case of the *Sphenodontia* specimens, as they were herbivores; Sauropodomorpha were herbivorous as well, but their large size can explain the relative low abundance in which they were found. *Pseudosuchia* and *Eucynodontia* were probably insectivores or carnivores, however, the representatives of these groups preserved in the assemblage are small-sized specimens (ontogenetically, in the case of *Pseudosuchia*; genus size in the case of *Eucynodontia*). This suggests the action of carnivores or scavengers.

4. The assemblage also shows evidence of biased preservation of elements with a dominance of skulls, jaws with teeth, and vertebrae, as well as a clear size selection, with most of the remains smaller than 20 mm. However, the presence of the two dominant elements, vertebra and mandibles, demonstrate that the selection was not produced by fluvial transport, since these two main elements correspond to two different Voorhies Groups (i.e., sets of bones
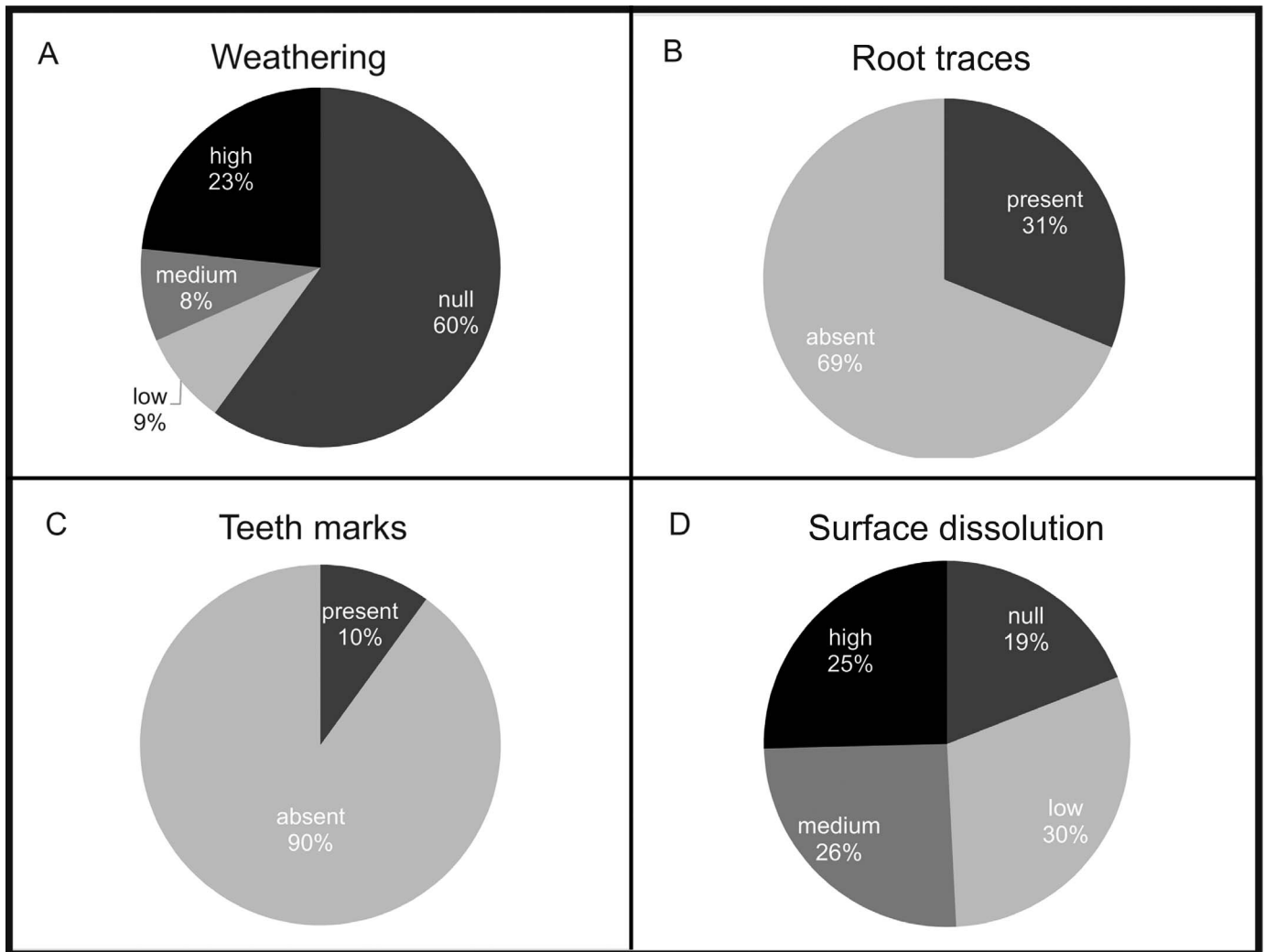
FIG. 8.—Pie charts that indicate the relative percentages of the main taphonomic attributes in the bone surfaces: weathering, root traces, tooth marks, and surface dissolution. Percentages based on MNI of 63 (see online Supplemental Data).

displaying varying probabilities of being moved by fluvial processes): vertebra belong to Group I (immediately moved, by floating or bouncing along a channel bottom) and mandible and skull remains belong to Group III or II-III (basal lag) (Voorhies 1969; Behrensmeyer 1975).

In addition, the sedimentological context is not consistent with fluvial sorting during transport due to the fact that mudflows are formed by the movement of sediment by laminar flow in mass movement, devoid of sorting capacity (Coussot 1997). Weathering and decomposition cannot explain the abundance of these pieces either, as such factors would more intensely affect elements containing a high proportion of compact bone and natural lines of weakness, such as skulls and jaws, while vertebra would remain intact. It is also likely that biological processes in soils would have affected the more porous bones, such as vertebrae, as opposed to those that are compact (Hanson and Buikstra 1987; Behrensmeyer 1991).

The fossil concentration could reflect a double origin, as was proposed for the bone accumulation of Quarry 9 of the Morrison Formation, where the concentration of jaws is explained based on their durability, and the concentration of the other pieces is based on their transportability

(Carrano and Velez-Juarbe 2006). An alternative, and potentially more likely explanation could be that skulls and vertebrae survived the attention of carnivores and scavengers because of their low nutritional value (Hill 1980).

5. Most of the remains are isolated and highly fragmented, with the exception of teeth in jaws. The low stage of articulation could indicate a long period of surface exposure. However, the extended fragmentation with irregular fractures could also indicate trampling and gnawing, with the high degree of fragmentation linked to predators (Hoffman 1988; Lyman 1994).

6. The assemblage has different weathering stages, although most bones are fresh (stage 0-1). In general, teeth are in their alveoli, which is further evidence of generally low weathering stage for most of the specimens. However, the bones that show evidence of weathering ($\sim$ 40%), including flaking and splintering, suggest extended surface exposure prior to final burial. This suggests that the accumulation preserves fossils that were exposed on the surface for variable periods of time after death and before burial. This in turn is consistent with moderate time-averaging of the deposit (Behrensmeyer 1978).
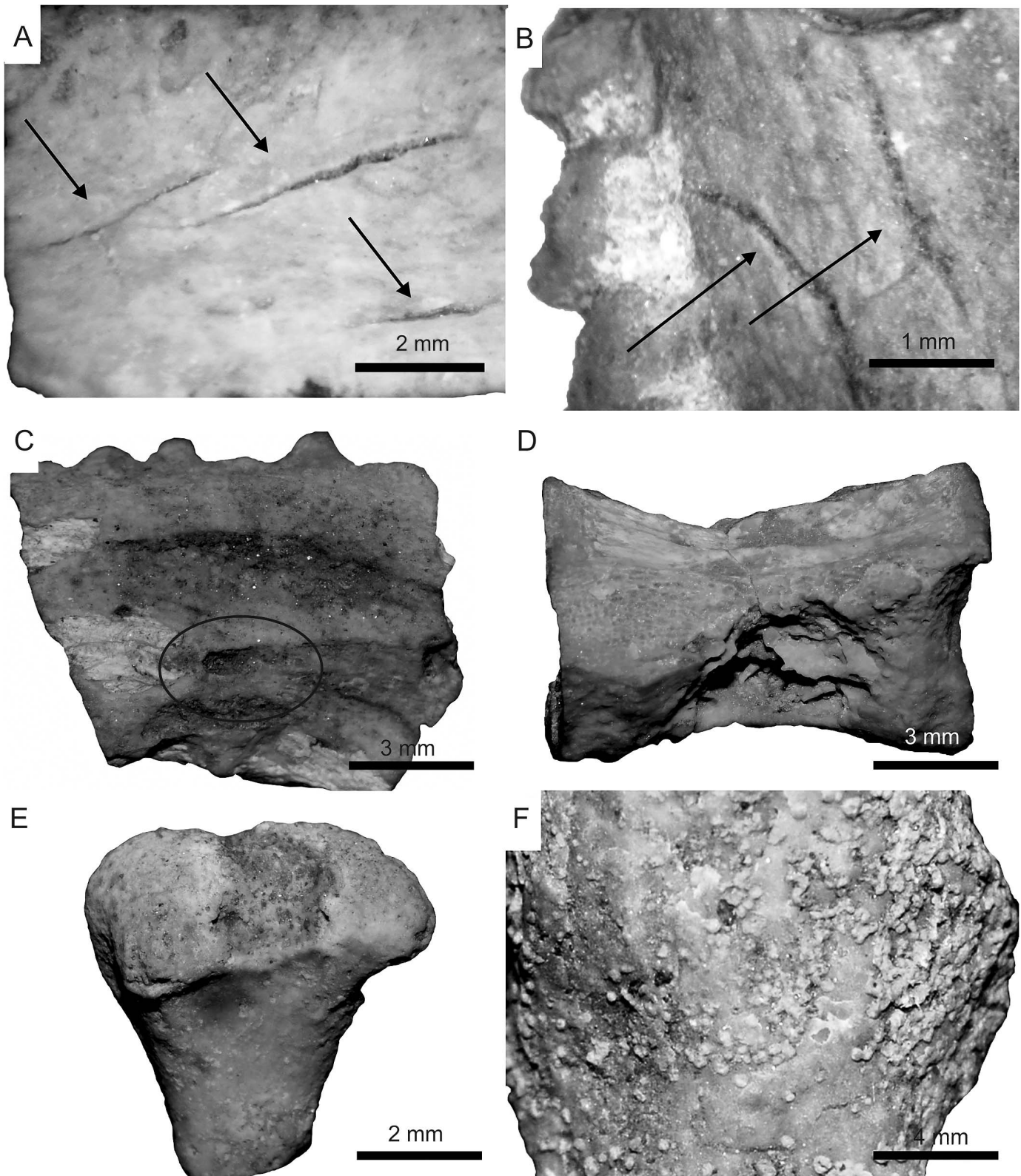
FIG. 9.—Photomicrographs of common taphonomic attributes in fragmentary bone assemblage. **A**) Three parallel grooves on the surface of *Sphenodontia* specimen PVSJ951-IMCN CPV. **B**) Two parallel grooves in *Eucynodontia* specimen PVSJ971-IMCN CPV. **C**) Isolated tooth mark on a skeletal fragment of *Sphenodontia* specimen PVSJ886 CPV-IMCN. **D**) Deep break, presumably due to impact in pseudosuchian vertebrae PVSJ912b-IMCN CPV. **E**) Cancellous bones with bone tissue removed by scooping from the epiphyseal ends of the limb bones, identified as *Sphenodontia* PVSJ951-IMCN CPV. **F**) Spherical calcareous walls that surround holes in the bone surfaces. They are potentially the result of organic activity (biofilms or microbial alteration). This photograph was taken of unidentified *Sphenodontia* specimen PVSJ951 from the CPV-IMCN.
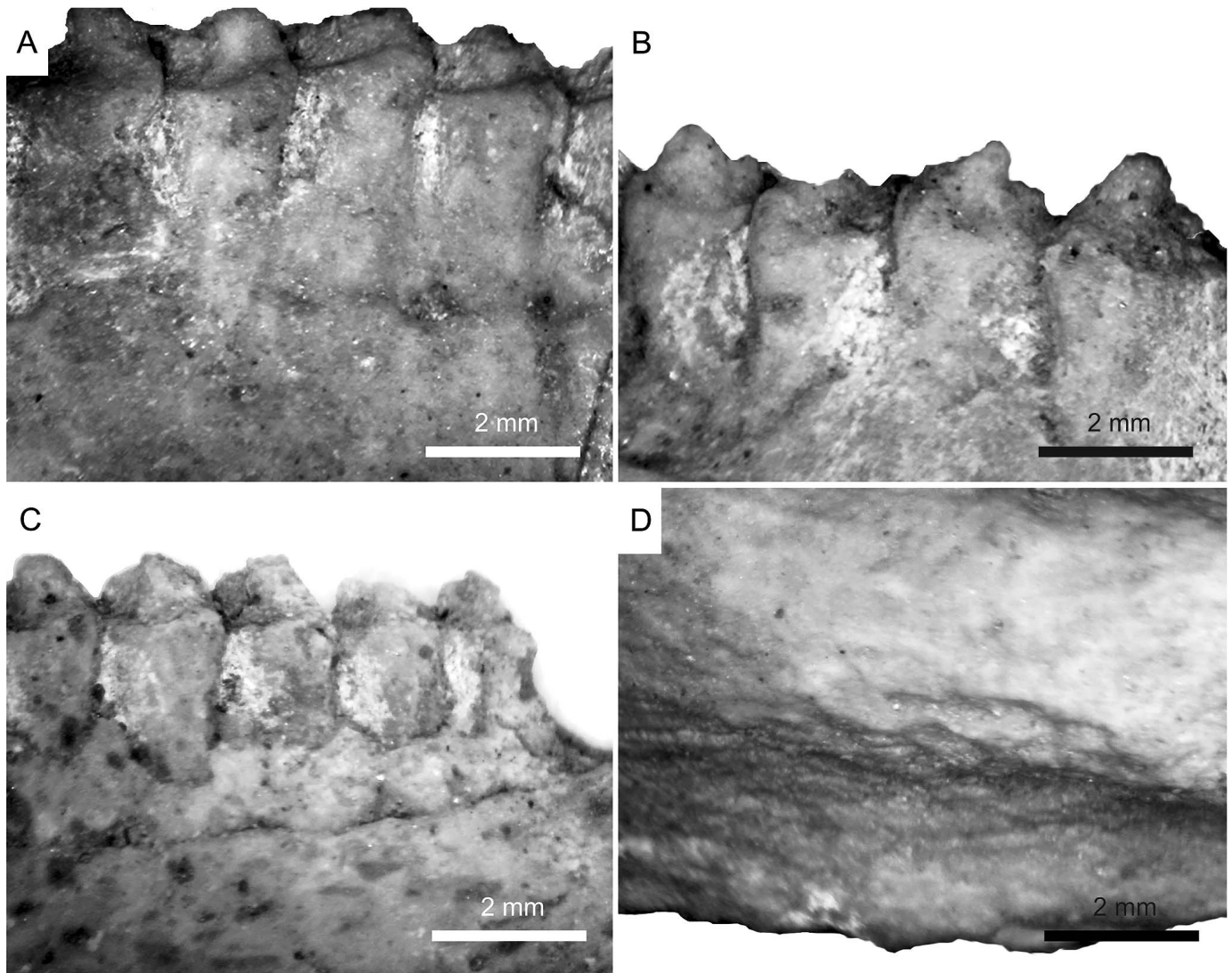
FIG. 10.—Photomicrographs of chemical corrosion, the main taphonomic attribute observed in approximately 80% of the preserved remains in the assemblage. The first three photographs correspond to a *Eucynodontia* mandibular fragment in which the effects of corrosion can be seen on bone and tooth surfaces. The specimens correspond to provisional numbers of CPV-IMCN: **A)** PVSJ928. **B)** PVSJ934. **C)** PVSJ932. **D)** Indeterminate fragment in which the roughness generated by chemical corrosion is visible.

7. The bones exhibit root etching and tooth marks. These are indicative of a period of exposure on the ground surface or in shallower water bodies. Evaluating the degree of carnivore processing is difficult because some species do not leave tooth marks (Haynes 1980, 1983; Kent 1981). In addition, evidence of feeding based on bone-tooth interaction may be limited because the abundance of available bones was high enough that the incidence of gnawing was consequently low (Brain 1981).

8. The vast majority of remains exhibit surface dissolution. Dissolution on bone and tooth surfaces can be linked to three causes: (1) dissolution by acidic soils (Gordon and Buikstra 1981; Rogers and Kidwell 2007); (2) dissolution by gastric digestion processes (e.g., Fisher 1981; Richardson et al. 1986; Lyman 1994; Andrews 1990; Liggett and Nelson 1993; Hockett 1996; Laudet 2005); and (3) dissolution by algal growth and invertebrate grazing in subaquatic environments (Behrensmeyer 1991, Rogers and Brady 2010). The effect of soil dissolution on the bones in this assemblage

cannot explain the rough, rounded aspect, since this type of bone dissolution only occurs in soils with low pH, such as spodosols (White and Hannus 1983). The type of paleosol associated with the bonebed, a calcic-Argillisol, is developed in a high pH alkaline environment (Mack et al. 1993; Tabor et al. 2006). Furthermore, the suite of authigenic minerals is indicative of alkaline conditions (Krystinik 1990). Digestive corrosion is an attribute consistent with a predatory origin; it occurs as a result of the effect of gastric acids and varies as a function of where the digestion takes place in different taxa (e.g., Fisher 1981). When digestive corrosion appears together with other marks on the surface of bones and teeth, it should be one of the temporally first observable attributes, forming immediately after fragmentation and tooth marks, but certainly prior to weathering and bioturbation. Such is the case in some existing deposits that underwent biogenic action followed by a prolonged time on the surface where the already fleshless bone weathered (Terry 2004). The association under study, however,
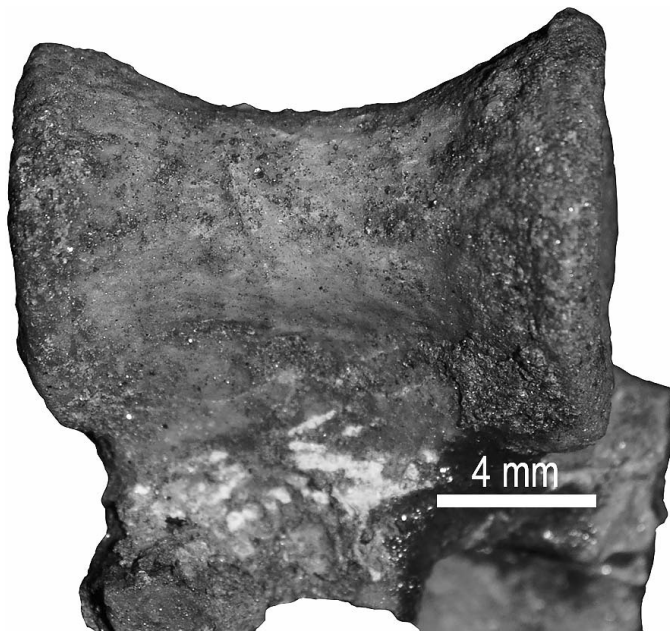
FIG. 11.—Photomicrographs of chemical corrosion in a vertebra over other surface marks (i.e., weathering, root traces and tooth marks). The specimen corresponds to provisional number CPV-IMCN PVSJ941.

shows evidence that the dissolution covers all other marks, enlarging or exaggerating the perforations and giving a rounded aspect to the surface of the bones, even those that are weathered, which eliminates gastric dissolution as a potential origin of this attribute. By process of elimination, dissolution by algal growth and invertebrate grazing in subaquatic environments is the most likely explanation (Behrensmeyer 1991; Rogers and Brady 2010). The observed root etching on some of the bone surfaces could also be the result of algal growth and invertebrate grazing. Even though the paleosols indicate well-drained floodplain deposits (Retallack 1990), after a splay occurred in the floodplain during the high discharge season, the impermeability of muddy sediments would

have initially favored the formation of temporary standing bodies of water (Fisher et al. 2006; Nichols and Fisher 2007). In this type of environment, water would be alkaline, therefore, algal and some invertebrates would have been able to attack the bone and tooth surfaces, without dissolving them.

9. The authigenic suite of minerals present in this assemblage coincides with early diagenetic suites of sandstone mineral cements in continental arid deposits. The presence of anhydrite suggests fossilization occurred in a low-lying area where sulphate was present in pore water (Krystinik 1990).

A Scenario for the Taphonomic History of this Deposit

Based on the observations outlined above, we suggest a three stage taphonomic model. The accumulation began with an extrinsic biogenic origin, where carnivores or scavengers trampled and gnawed bones at the ground surface. These actions produced fragmentation and yielded the concentration of small-sized remains along with skulls, jaws and vertebra because of their low nutritional value. At the same time, these actions produced different types of tooth marks on bone surfaces. An extended interval of surface accumulation accounts for the time-averaging of the assemblage as well as the differences in weathering among the elements.

The second stage in the taphonomic history of this accumulation relates to the re-working of the previously concentrated remains by a mudflow sourced from a distributary channel through the floodplain, forming a splay. The re-working and re-deposition is necessary to explain the vertical and lateral dispersion of the remains inside the one-meter thick massive mudflow deposit. The absence of evidence for current re-working in the remains and the lack of erosion at the base of the deposit suggest that the mudflow entrained the remains accumulated on the surface in the interchannel areas and transported them in a viscous flow without much internal contact between the remains and clasts before final deposition and burial. Water should have stagnated along the floodplain when the energy finally dissipated, thereby forming a temporary pond, characteristic of this environment (Moscariello, 2005). Vertebrate remains in ponds of stagnant water or in inundated soil were impacted by algal growth and invertebrate grazing that dissolved the bone and tooth surfaces, with roots boring into their tissues, and microbes or colonies of fungi and bacteria forming biofilms. Simultaneously, remains covered by sediment or water were
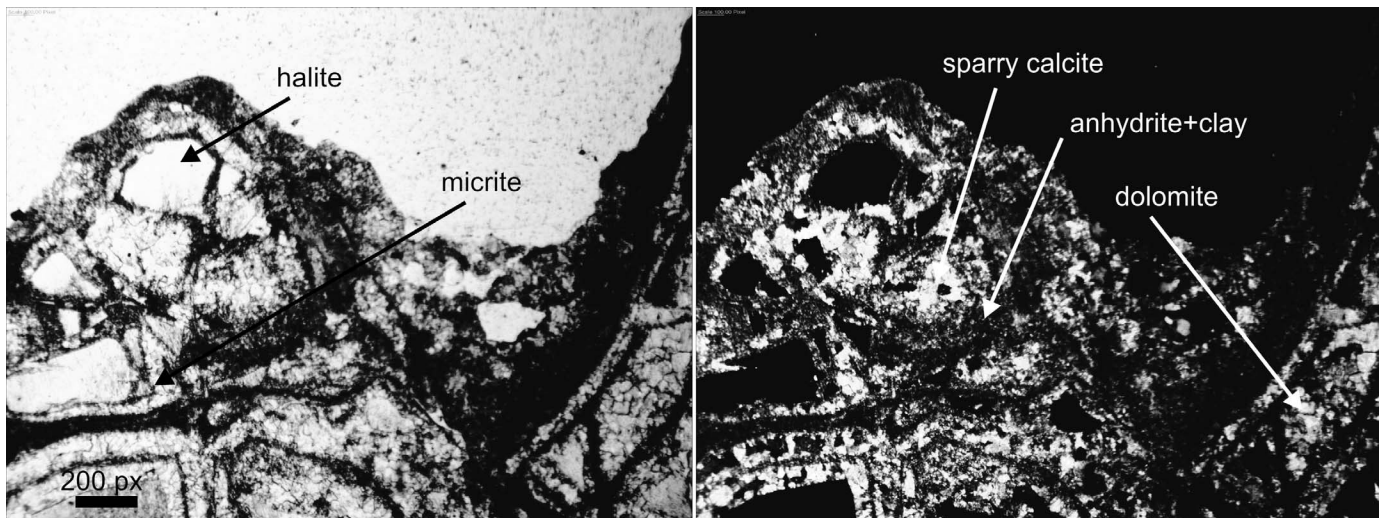

FIG. 12.—Thin section photographs of a Sphenodontian jaw, cataloged as PVSJ 897. A) Plain light. B) Polarized light. A suite of alkaline authigenic minerals can be identified: micrite, sparry-calcite, halite, anhydrite and clay.

protected from the subaerial conditions that normally destroy small bones and teeth. After the remains were buried, minerals started filling the original holes and altering the apatite, while the dry climate and consequently alkaline water precipitated a suite of alkaline minerals—including dolomite and hematite. Simultaneously, anhydrite—together with clay—altered the apatite, leaving just a ghost of the original bone tissue.

Finally, a third stage of preservation corresponds to the desiccation of the pond and the development of a calcic-Argillisol. During this stage, halite and sparry calcite probably completed the permineralization of the bones.

Comparable preservational scenarios were presented by Eberth (1990) and Badgley et al. (1998), who interpreted their assemblages as the result of bones that were concentrated previously in interchannel facies by different causes, then re-worked, and finally deposited and accumulated at the time of their final burial.

Importance and Implications

The Quebrada del Barro Formation preserves many vertebrates, including isolated sauropodomorphs and dispersed microfossils at other stratigraphic levels; however, there are no other layers with rich concentrations of fossil bones comparable to the bonebed described here. This extrinsic biogenic concentration is especially important since carnivores and scavengers opportunistically killed prey, resulting in a varied and random sample, allowing the preservation of taxa absent in assemblages that do not involve concentration by carnivores or scavengers. The microfossil bonebed of the Quebrada del Barro Formation preserves at least three new taxa (Abelín et al. 2012; Martínez et al. 2013a, 2013b). These new taxa enhance our understanding of the Upper Triassic faunal assemblage of the Quebrada del Barro Formation, which we now know includes riojasaurid sauropodomorphs, tritheledontid cynodonts, protosuchid and "sphenosuchid" pseudosuchians, and opisthodontian sphenodonts, allowing a stronger correlation with the known faunal assemblage from the Norian Los Colorados Formation (LCF) in the neighboring Ischigualasto-Villa Unión Basin (Bonaparte 1973; Kent et al. 2014). This diverse fauna is considered a transitional assemblage containing Late Triassic (e.g., "rauisuchids", "sphenosuchids", aetosaurs) and Early Jurassic elements (e.g., protosuchid crocodyliform, derived basal sauropodomorph). Most of the vertebrates found in the microfossil bonebed of the Quebrada del Barro Formation (QBF) have equivalents in the fauna from the Los Colorados Formation (e.g., QBF tritheledontid/LCF *Chaliminia*, QBF basal sauropodomorph/LCF *Riojasaurus*, QBF "sphenosuchid"/LCF *Pseudhesperosuchus*), and thus both faunas seem to be contemporary (Martínez et al. 2013b). Nevertheless, recent analysis of the Quebrada del Barro Formation faunal association suggests its late Norian age, younger than that of the Los Colorados Formation (Martínez et al. 2015).

In addition, the predominance of small taxa in the microfossil bonebed of the Quebrada del Barro Formation increases the faunal diversity of the Norian in this region of southwestern Pangea, previously known only by the fauna from the Los Colorados Formation, which is taphonomically biased against small vertebrates. This is especially interesting if we consider that most global models for faunal evolution in the Mesozoic, including the Triassic–Jurassic extinctions, are based in the fossil record of the Northern Hemisphere.

Finally, several others (Rogers 2005; Eberth et al., 2006) have previously called attention to the link between debris-flows in ancient alluvial systems and bonebeds, and this study has led to the recognition of mudflow deposits, related to splays in distributary fluvial systems as another likely paleoenvironment in the preservation of microfossils unmentioned in previous literature (e.g., Eberth 1990; Henrici and Fiorillo 1993; Rogers and Kidwell 2000, 2007). Thus, this study highlights

a new potential depositional setting for the preservation of vertebrate microfossils.

CONCLUSIONS

This work documents the first microfossil bonebed identified in Argentine Mesozoic outcrops. The scarcity of this type of fossil occurrence in Argentina is potentially related to the limited study of bonebeds in South America (Behrensmeyer 2007). However, in Argentina, there is good indication that bonebeds became more common in upper Mesozoic and Cenozoic basins (e.g., Porfiri et al. 2007; Bell and Coria 2013; Ibiricu et al. 2013; Fiorelli et al. 2013). This is partly due to the scarcity of Triassic outcrop as well as less potential for catastrophic gregarious mass death because social behaviors conducive to localized mass mortality were not yet widely established.

In spite of these potential biases against bonebed preservation, it is apparent that during the Upper Triassic (Norian) the physical and taphonomic conditions were in general favorable for the preservation of bonebeds, especially those influenced by biogenic concentration processes. The seasonality and aridity that characterized the Upper Triassic should have favored the preservation of bonebeds because even though precipitation was infrequent, it was likely higher in magnitude, generating the massive flow discharges that confer prompt burial of live animals and carcasses close to rivers (Newell et al. 1999; Cecil and Dulong 2003; Rogers 2005; Behrensmeyer 2007). Moreover, the extreme dry seasons of the Late Triassic could have heightened the likelihood of death due to drought, which is one of the main causes of bonebed formation, as evidenced by the abundant bonebeds in Permian basins (Behrensmeyer 2007). In addition, the arid climate favored alkaline conditions in soils, which likely encouraged the rapid mineralization of bones.

As part of this contribution we analyzed the origin of a microfossil bonebed at the top of the Quebrada del Barro Formation in the Marayes-El Carrizal Basin and explored its paleontological and geological implications. Sedimentological and taphonomic evidence suggest the taphonomic history of the assemblage followed at least three stages. First, a stage of biogenic extrinsic concentration; second, re-working and re-deposition via a mudflow in a temporarily flooded floodplain; and, third, a stage of drying and pedogenesis. Finally, this study highlights mudflow facies from floodplain splays in a distributary fluvial system as a potential paleoenvironment for the preservation of vertebrate microfossils.

SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: http://www.sepm.org/pages.aspx?pageid=332.

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