Paleoenvironment and Taphonomy of the Chañares Formation Tetrapod Assemblage (Middle Triassic), Northwestern Argentina: Spectacular Preservation in Volcanogenic Concretions

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The enigmatic concretionary exposures that typify the Chañares Formation (Ladinian, northwestern Argentina) long have defied precise paleoenvironmental characterization. Recent work indicates that the formation accumulated in an alluvial-to-lacustrine setting within an active rift basin that received sedimentary detritus from surrounding highlands, as well as copious amounts of volcanic ash. Ash-flow sheets were emplaced presumably as secondary mass flows on alluvial surfaces characterized by small fluvial channels and shallow lakes. Thin bentonite beds intercalated in the Chañares Formation indicate that ash also accumulated via direct airfall, although this mode of emplacement accounts for a very small fraction of the overall section. A shift to widespread lacustrine deposition is recorded by the superjacent Los Rastros Formation, which preserves at least six shallowing-upward hemicycles, five of which commenced amidst explosive volcanic activity as evidenced by intercalated bentonite beds.

Volcanism played an important role in the generation and preservation of the Chañares Formation's exceptional tetrapod fossil record. This is especially true of the classic Los Chañares locality, where more than 100 individuals representing a diverse array of taxa (archosaurs, cynodonts, dicynodonts) are entombed in volcanogenic concretions with matrices of relic glass shards diagenetically replaced by calcite. Taphonomic attributes of the Los Chañares locality are consistent with the scenario of mass mortality, and several clues hint at the nature of the event. The killing agent was lethal to a variety of taxa, killed both adults and juveniles, and led to the concentration of taxa that under normal circumstances would tend to dissociate, such as carnivores and their potential prey. It also produced a counter-intuitive bias against the preservation of large-bodied taxa, which may have been largely unsusceptible to the death event, or perhaps were excluded from the Los Chañares death assemblage via post-mortem sorting. The spatial arrangement of skeletal material in a small sample of concretions is consistent with the stranding of tetrapod carcasses along a strandline, and it is feasible that volcanism led to catastrophic flooding of the landscape via damming and/or diversion of local drainages. Uncompacted skeletal elements and relic outlines of glass shards indicate that carbonate concretions formed shortly after skeletal material was buried in reworked volcanic ash. The microbial decay of organic matter presumably catalyzed concretion diagenesis. There is no indication that bone hydroxyapatite diffused into the entombing glassy matrix and contributed to concretion formation. Bones entombed within early diagenetic concretions were safeguarded from subsequent destructive pedogenic and/or diagenetic processes, and were incorporated in exquisite quality into the fossil record.

INTRODUCTION

Fossils from the Chañares Formation (Middle Triassic, Argentina) span a pivotal stage in the evolution of terrestrial vertebrates and, arguably, represent the best single record of tetrapod evolution immediately prior to the Late

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Triassic diversification of dinosaurs, advanced cynodonts, and mammals (Romer, 1966, 1973; Bonaparte, 1982). The Chañares tetrapod assemblage includes a wide variety of archosauriform reptiles and synapsids. Some of the Chañares archosauriforms, such as the superficially crocodile-like proterochampsids (*Chañaresuchus, Gualosuchus,* Tropidosuchus: Romer, 1971a, 1972a; Arcucci, 1990), represent lineages that diverged prior to the split between crocodilian and bird clades. Other Chañares archosauriforms either represent early offshoots of the crocodilian line (*Gracilisuchus, Lewisuchus*: Romer, 1972b,c) or the oldest and most primitive members of the Ornithodira, the group that includes dinosaurs and birds. These small-bodied, bipedal predators are known exclusively from the Chañares Formation (*Marasuchus, Pseudolagosuchus, Lagerpeton*: Romer, 1971b, 1972d; Bonaparte, 1975; Arcucci, 1986, 1987; Sereno and Arcucci, 1993, 1994). The Chañares synapsids include representatives of a variety of lineages, including a large dicynodont known from an excellent skull (*Chañaria*: Cox, 1968), smaller herbivorous-omnivorous cynodonts known from many complete skeletons (*Massetognathus*: Romer, 1967; Jenkins, 1970; Abdala and Giannini, 2000), and rarer carnivorous cynodonts that have played an important role in understanding early stages in the evolution of mammals (*Probelesodon, Probainognathus*: Romer, 1969, 1970a; Rowe, 1988; Hopson, 1991; Martinez et al., 1996).

Romer and Jensen (1966) named and briefly described the Chañares Formation, which was promptly rejected as a valid stratigraphic unit by Bonaparte (1967). Since that time, there only has been cursory mention of the geology or taphonomy of the Chañares Formation, which is a stark contrast to the considerable body of work published during the past several decades on the unit's vertebrate paleontology. Existing sedimentologic descriptions of the formation are sketchy at best, with interpretations of the paleoenvironment ranging from eolian to lacustrine to fluvial (e.g., Romer and Jensen, 1966; Romer, 1971c; Stipanícic, 1983; López Gamundi et al., 1989; Bonaparte, 1997). The prominent role of volcanism in the depositional history of the Chañares Formation also has remained essentially unexplored. Along these same lines, taphonomically-oriented descriptions of the spectacular Chañares tetrapod fossils are virtually nonexistent. The taphonomic information that does exist is dispersed in old geologic reports (e.g., Romer and Jensen, 1966, mention the general distribution of fossiliferous concretions) and the occasional systematic paper (e.g., Sereno and Arcucci, 1994, provide a detailed map of a single fossiliferous concretion).

Here, the major exposures of the Chañares Formation, as well as the underlying Tarjados and the overlying Los Rastros Formations are described, and new data are presented pertaining to the paleoenvironment of the Chañares tetrapod fauna. The taphonomy of the concretion-hosted Chañares tetrapod assemblage also is described and the dynamics of tetrapod mortality and preservation in the lower lithologic unit of the Chañares Formation are explored. These findings provide the first detailed paleoenvironmental reconstruction for the Chañares tetrapods and offer new insights into the taphonomy and paleoecology of this important and exceptionally well-preserved Middle Triassic paleofauna.

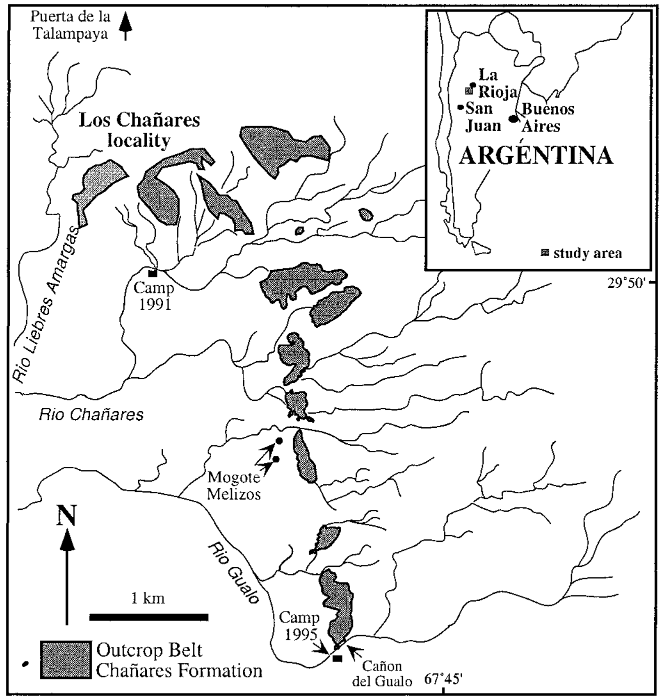

FIGURE 1—Outcrop belt (gray) of the Chañares Formation in La Rioja Province, Argentina. Exposures extend from the classic Los Chañares locality (see text for GPS coordinates) to the vicinity of Cañon del Gualo (see text for GPS coordinates). Modified from a topographic map produced by the Instituto Geográfico Militar (1987).

STUDY AREA AND METHODS

The most extensive and fossiliferous exposures of the Chañares Formation crop out in the arroyos of the Rio Chañares and Rio Gualo, which are located to the south of the steep-walled, picturesque canyons of the Puerta de la Talampaya (Fig. 1). The classic Los Chañares locality, where the majority of the vertebrate remains have been discovered, consists of low-relief badlands situated at the base of an east-west-trending escarpment capped by the Los Rastros Formation (29°49′8.9″S, 67°48′47.9″W). The outcrop belt continues to the southeast for approximately 5.5 km, to the vicinity of Cañon del Gualo (29°53′38.3″S, 67°46′21.2″W). Vertebrate fossils have been recovered from exposures near Cañon del Gualo, but not in the abundance that typifies Los Chañares. Other exposures of the Chañares Formation crop out to the south of the principal study area in the Arroyo de Agua Escondida and farther southwest along the southern edge of the Ischigualasto-Villa Unión Basin (Romer and Jensen, 1966). These southern exposures have failed to yield well-preserved vertebrate fossils.

Twelve stratigraphic sections measured along the outcrop belt from Los Chañares to the Cañon del Gualo serve as the basis for correlation and paleoenvironmental analysis, and provide a framework for sampling. Data pertinent to the taphonomy of the Chañares assemblage were collected both in the field and in the collections of the Museo de Paleontología, Universidad Nacional de La Rioja (ULR), the Fundación Miguel Lillo, Universidad Nacional de Tucuman (PVL), and the Museum of Comparative Zoology, Harvard University, Cambridge (MCZ). A total of

213 museum specimens were studied, including 23 fossil-bearing concretions, most of which are from the Los Chañares locality. Because these concretions preserve original taxonomic associations and spatial data (e.g., skeletal orientation and density patterns), they proved vital to the reconstruction of taphonomic history.

The mineralogy of concretions and surrounding facies was determined using both petrographic thin sections and standard x-ray powder diffraction (XRD) techniques. For the XRD analyses, both oriented and pressed samples were run on a Rigaku D/Max-B x-ray diffractometer set at 40 kV and 20 mA. Collected scans were processed using MDI Jade software. Major element concentrations were determined by x-ray fluorescence (XRF). Fused beads were analyzed on a Philips PW 2400 XRF spectrometer. The distribution of elements and mineral phases in selected fossil-bearing concretions were scrutinized further using a Zeiss DSM 960 scanning electron microscope (SEM) and an Oxford energy dispersive spectrometer (EDS) coupled with Oxford Link Isis software. Polished thin sections were coated with carbon and analyzed at 20 kV and 50 mA. Linescans were taken across bone-concretion interfaces tracking the elements Ca, P, Fe, Mn, Si, F, and Ti. Scanned regions were documented with high-resolution backscatter-electron images.

GEOLOGIC SETTING

The Chañares Formation crops out in the Ischigualasto-Villa Unión Basin, which is one of several small extensional basins that formed along the western margin of South America during the breakup of Gondwana (Uliana and Biddle, 1988; Ramos and Kay, 1991). Up to 4000 m of nonmarine Triassic strata are preserved within the Ischigualasto-Villa Unión Basin. These strata are subdivided into the Paganzo III Group and the overlying Agua de la Peña Group (de la Mota, 1946; Bossi, 1971; Stipanícic, 1983; Milana and Alcober, 1994). The Paganzo III Group includes the cliff-forming Talampaya and Tarjados Formations, both of which are characterized by red strata that preserve relatively few fossils (Romer and Jensen, 1966; Cox, 1968). A regional unconformity separates the Lower to Middle Triassic Paganzo III Group from the superjacent Agua de la Peña Group. Most workers recognize either four or five discrete units of formation-rank within the Agua de la Peña Group (Romer and Jensen, 1966; Bonaparte, 1967, 1969; Sill, 1969; Bossi, 1970; Herbst, 1970; Stipanícic, 1983; Milana and Alcober, 1994). These include, in ascending order, the Chañares, Ischichuca, Los Rastros, Ischigualasto, and Los Colorados Formations (Fig. 2).

Romer and Jensen (1966) recognized the unique lithological and paleontological features of the Chañares beds and proposed to formalize the unit as a formation. In their report on the geology of the Rio Chañares and Rio Gualo region, these authors provided a general description of the Chañares Formation and briefly described the nature of its lower and upper contacts. Subsequently, Bonaparte (1967) and Stipanícic and Bonaparte (1979) argued that the proposed elevation to formational status was inappropriate, and that the Chañares beds instead should be included as a basal member within the Ischichuca Formation of de la Mota (1946). These authors contended that

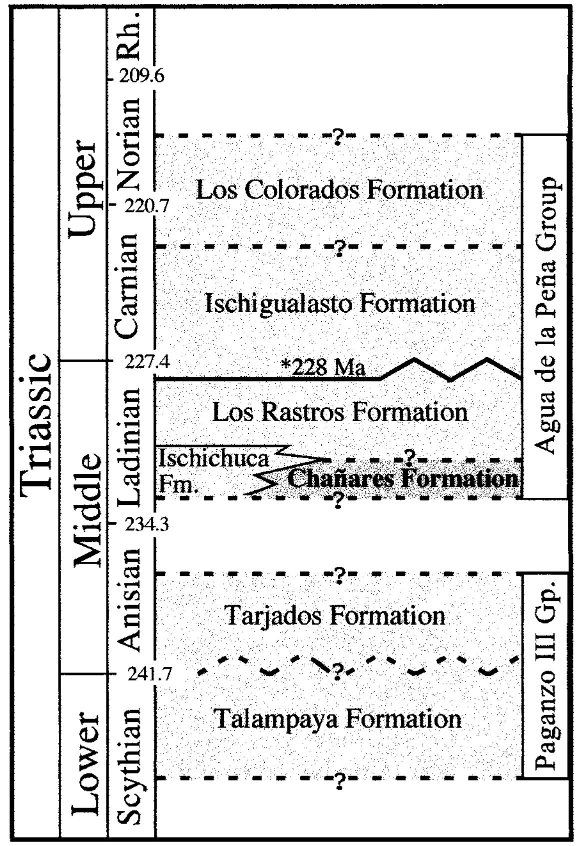

FIGURE 2—Triassic lithostratigraphy and chronostratigraphy in the Ischigualasto-Villa Unión Basin. The Paganzo III Group consists of the Talampaya and Tarjados Formations. An unconformity intervenes between the Tarjados Formation and the overlying Agua de la Peña Group. Units in the Agua de la Peña Group include, in ascending order, the Chañares, Ischichuca, Los Rastros, Ischigualasto, and Los Colorados Formations. The Ladinian age of the Chañares Formation is based upon the position of the unit in the local section and vertebrate biochronology (see text). The radioisotopic age in the Ischigualasto Formation was obtained via $^{40}Ar/^{39}Ar$ analyses of a bentonite intercalated near the base of the unit (Rogers et al., 1993). The Triassic time-scale is based on Gradstein et al. (1995).

the beds of the Chañares Formation and the basal beds of the Ischichuca Formation were lithologically very similar, and that the two formations also shared comparable tetrapod remains. Despite these early objections, the Chañares Formation has persisted as a viable lithostratigraphic unit in the geological literature (e.g., Bossi, 1970; Stipanícic, 1983; Arcucci, 1986, 1987, 1990; Milana and Alcober, 1994; Sereno and Arcucci, 1994; Bonaparte, 1997).

The age of the Chañares tetrapod fauna usually has been interpreted to be Middle Triassic (Anisian or Ladinian) because, in contrast to the Ischigualasto fauna of early Late Triassic age, dinosaurs and several other archosaurian subgroups (e.g., aetosaurs, ornithosuchids) are absent. However, the Chañares fauna is not especially similar to Middle Triassic terrestrial faunas from other continents, such as those from Europe, in which rhynchosaurs, prolacertiform lepidosauromorphs, and temnospondyl amphibians are particularly common (Bonaparte, 1966; Cox, 1968; Romer, 1970b; Benton et al., 1997). Great faunal similarities do exist, however, between the Chañares tetrapod assemblage and the *Dinodontosaurus* Assemblage from the Santa Maria Formation of Brazil (Barberena et al., 1985; Cox, 1991; Abdala et al., 1999). Four genera are shared by these faunas: *Dinodontosaurus, Massetognathus, Probelesodon* (Barberena et al., 1985; Cox, 1991), and *Chanaresuchus* (Dornelles, 1995). Recent biochronological analyses of Middle Triassic faunas from Africa and India (e.g., Cox, 1991; Battail, 1993) indicate that the *Dinodontosaurus* Assemblage of the Santa Maria Formation is considerably younger than the *Cynognathus* Assemblage Zone of South Africa, and is most likely Ladinian in age. Finally, an early Late Triassic age (latest Ladinian—early Carnian using the time scale of Gradstein et al., 1995) recently has been established based on $^{40}Ar/^{39}Ar$ analyses of a bentonite bed intercalated near the base of the Ischigualasto Formation (Rogers et al., 1993). Because the thick Los Rastros Formation intervenes between the Chañares and Ischigualasto Formations (Figs. 2, 3), it is unlikely that the latter is also Late Triassic in age. A late Middle Triassic age (Ladinian), therefore, is accepted provisionally for the Chañares tetrapod assemblage.

SEDIMENTOLOGY

Tarjados Formation

Red beds of the Tarjados Formation (Romer and Jensen, 1966) underlie the Chañares Formation in the study area (Fig. 3) and are well exposed to the east of the Cañon del Gualo camp (Fig. 4A). Fine- to coarse-grained sandstone, siltstone, and claystone comprise the unit. Sandstone beds are generally tabular in geometry, and locally display small- to large-scale trough and tabular cross-bedding (Fig. 4B). Directional measurements taken from axes of trough cross-bed sets ($n = 10$) located approximately 100 m below the top of the formation yield a vector mean of 333°. Rounded pebbles and cobbles of chert, quartzite, igneous rock fragments, rare silicified wood, and claystone rip-ups commonly mantle set boundaries and fill localized scours. A laterally persistent 20-to-30 cm-thick bed of extraformational clasts crops out ~30 m beneath the formation's upper contact. Intercalated beds of siltstone and claystone are typically massive, and preserve mudcracks, carbonate nodules (some of which are septarian), and silicified root traces. Sporadic bioturbation in the upper 50 m of the Tarjados Formation consists of small bedding plane traces and rare sub-vertical burrows (~1 cm diameter). The upper 50 cm of the formation exhibit irregular masses and layered stringers of chert interspersed with silicified root traces. Milana and Alcober (1994) interpreted the silicified cap of the Tarjados Formation as a silcrete horizon. The upper contact of the Tarjados Formation is a regional unconformity that locally exhibits up to 2 m of relief (Figs. 3, 4C, D).

Chañares Formation

Romer and Jensen (1966) distinguished two informal lithologic units in the Chañares Formation at the Los Chañares locality on the basis of color and fossil content. They described a lower "tuffaceous" unit characterized by a "bluish tinge," scattered concretions, and abundant tetrapod fossils, and an upper concretionary unit that is "nearly pure white" and devoid of fossils (Figs. 3, 5A). Their lower unit is traceable throughout most of the study area, where it varies from 20 to 35 m in thickness. Fine- to coarse-grained sandstones at the base of the lower unit drape the paleotopography of the silicified Tarjados surface (Fig. 4D) and, in contrast to underlying red Tarjados sandstones (7.5R 6/6 fresh, 7.5R 5/6 weathered), are relatively drab in color (5Y 6/1), poorly indurated, and very calcareous. Faint low-angle to horizontal lamination is locally preserved, as are small silicified root traces, and rare bedding planes exhibit meandering horizontal burrows. Thin stringers of claystone, chert and quartzite pebbles, and small-gray-and tan carbonate concretions (5–20 cm diameter) are scattered throughout these basal sandstone beds. The relatively small carbonate concretions that crop out near the base of the Chañares Formation preserve relic glass shards that have been replaced diagenetically by calcite in association with abundant subangular to rounded detrital grains of predominantly quartz (Fig. 5B).

Sandstones at the base of the Chañares Formation pass upsection into light bluish gray (10B 7/1) clay-rich strata that display a smooth weathering surface. In fresh exposures, these fine-grained beds appear predominantly nodular and massive (Fig. 5C), with only rare evidence of primary stratification in the form of localized planar lamination. In thin section, these rocks are characterized by matrix-supported grains of angular to subrounded feldspar and quartz, and relic glass shards set in a groundmass of microcrystalline silica and clay. X-ray diffraction analyses indicate that montmorillonite is the predominant clay mineral, with only minor amounts of illite. Brown carbonate concretions (2.5Y 7/1 fresh, 7.5YR 4/3 weathered) that are generally oblate (minor compression on z-axis) and have diameters ranging up to two meters crop out in considerable abundance in these fine-grained sediments starting at approximately 10 m above the Chañares—Tarjados contact (Fig. 5D). It is within these calcareous concretions that the vast majority of the tetrapod fossils are preserved (see below). Some of the concretions intercalated in the bluish-gray facies exhibit radiating vertical dikelets (Fig. 5E). In thin section, these concretions typically preserve scattered grains of quartz and plagioclase, and corroded lithic fragments set in a fine-grained matrix composed of cuspate relic glass shards that have been altered diagenetically to calcite and, more rarely, iron oxide (Fig. 5F). Concretions in the lower lithologic unit of the Chaña-

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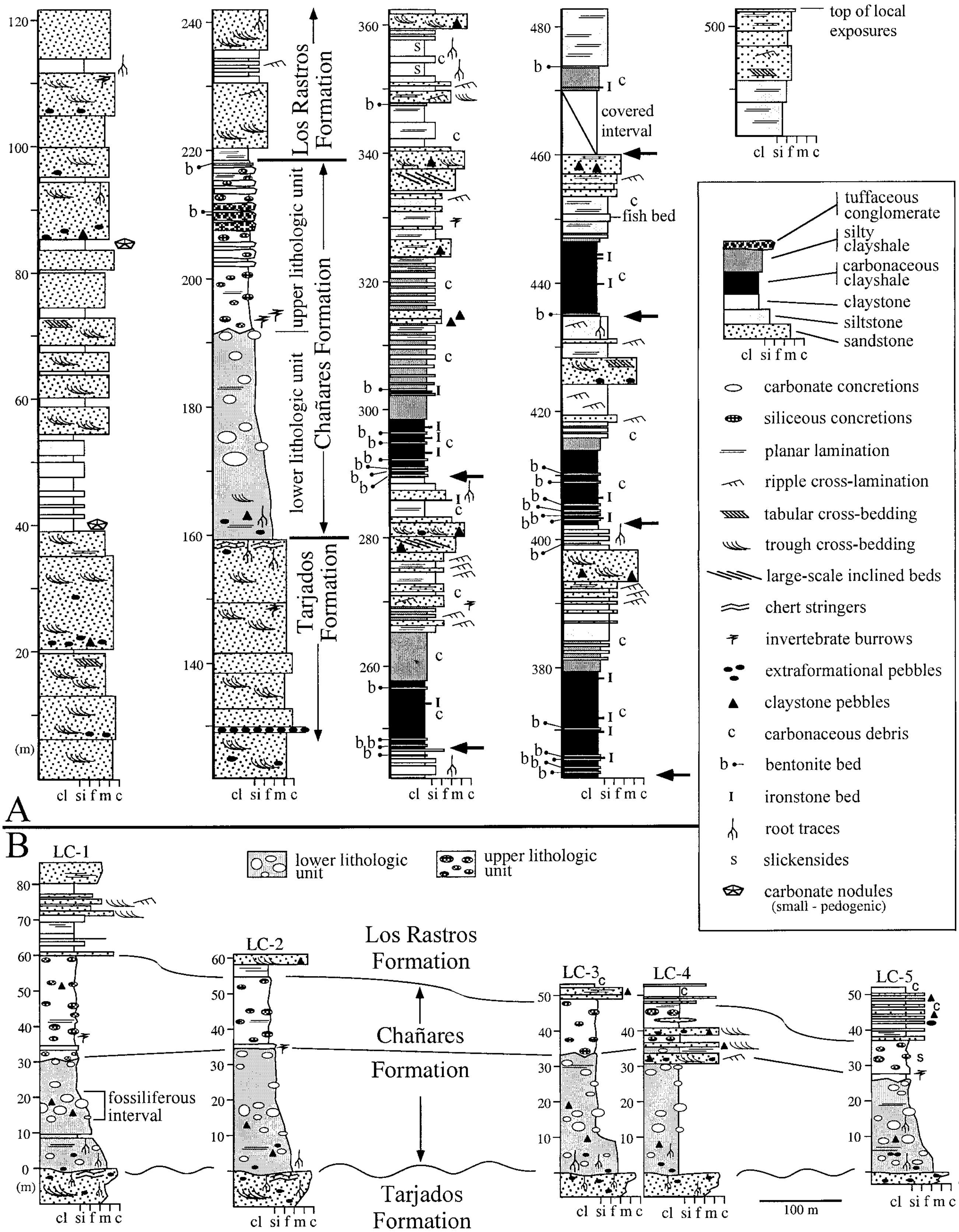
FIGURE 3—Graphic stratigraphic logs of Tarjados, Chañares, and Los Rastros Formations. (A) Composite section measured in the vicinity of Cañon del Gualo. Horizontal arrows indicate bases of six lacustrine hemicycles in the Los Rastros Formation. (B) Schematic cross-section spanning the Los Chañares locality from east (LC-1) to west (LC-5). The Los Chañares tetrapod assemblage was recovered from the fossiliferous interval in the vicinity of section LC-1. Grain size trends within the lower and upper lithologic units of the Chañares Formation can be ascertained from the rock texture abbreviations at the base of each log: cl = claystone, si = siltstone, f = fine-grained sandstone, m = medium-grained sandstone, c = coarse-grained sandstone. Munsell color notation is provided in text.



top of local exposures
Los Rastros Formation
upper lithologic unit
Chañares Formation
lower lithologic unit
Tarjados Formation
covered interval
fish bed
cl si f m c
(m)
A
B
LC-1
LC-2
LC-3
LC-4
LC-5
lower lithologic unit
upper lithologic unit
Los Rastros Formation
Chañares Formation
Tarjados Formation
fossiliferous interval
100 m
tuffaceous conglomerate
silty clayshale
carbonaceous clayshale
claystone
siltstone
sandstone
carbonate concretions
siliceous concretions
planar lamination
ripple cross-lamination
tabular cross-bedding
trough cross-bedding
large-scale inclined beds
chert stringers
invertebrate burrows
extraformational pebbles
claystone pebbles
carbonaceous debris
bentonite bed
ironstone bed
root traces
slickensides
carbonate nodules (small - pedogenic)

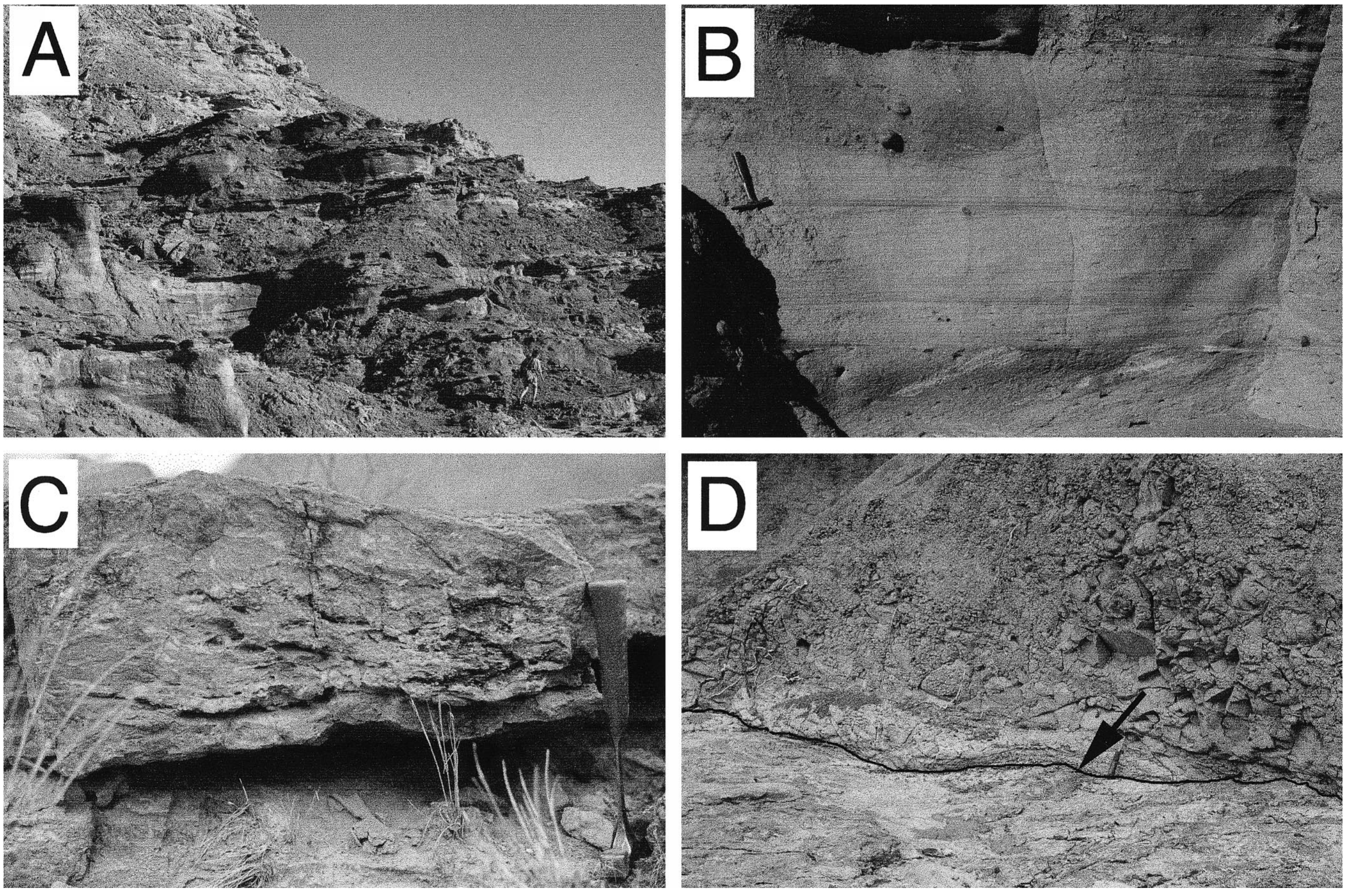


FIGURE 4—Exposures of the Tarjados Formation in the vicinity of the Cañon del Gualo. (A) The Tarjados Formation is well exposed to the east of the Cañon del Gualo, where approximately 160 m of the unit are accessible. (B) Typical cross-bedding and cut-and-fill in sandstones of the Tarjados Formation. (C) Abundant chert stringers and irregular chert masses in the upper 50 cm of the Tarjados Formation. (D) The contact between the Tarjados Formation and the overlying Chañares Formation (marked by arrow, black line added) is a regional unconformity that locally exhibits up to 2 m of relief.

res Formation do not appear to be associated with any particular surface or horizon, although it is difficult to ascertain their precise stratigraphy due to down-slope settling.

Three sandstone bodies crop out in the approximate middle of the Chañares Formation near the western end of the Los Chañares locality (Figs. 3, 6). The lowermost sandstone body attains a maximum thickness of 2.1 m. The middle sandstone lens, which crops out ~2 m above the lower sandstone body and is exposed in its entirety, is 0.7 m thick and ~150 m wide. The uppermost sandstone body crops out 1.9 m above the middle lens and is up to 2.0 m thick. Lower contacts of all three sandstone bodies exhibit erosional relief (up to 30 cm), and are mantled by deposits of rounded claystone pebbles (up to 10 cm long axis) and rounded to angular chert clasts (Fig. 6B). Basal conglomeratic facies pass up-section into fine- to coarse-grained calcareous sandstone characterized by small- to large-scale trough cross-bedding (sets range from 15–60 cm in thickness) and localized ripple cross-lamination (Fig. 6C). The sand fraction is dominated by quartz (mono- and polycrystalline), plagioclase, K-feldspar, and lithic fragments (microlitic volcanic rock fragments and chert grains). Paleocurrent measurements taken from trough cross-bed sets in the lower and upper sandstone bodies yield vector means of 199° (n = 7) and 183° (n = 8), respectively. Directional data derived from trough cross-beds in the middle sandstone lens yield a vector mean of 344° (n = 9).

The upper lithologic unit of the Chañares Formation (*sensu* Romer and Jensen, 1966) ranges from 10 m to 30 m thick in the area of study, and is predominantly light gray (10YR 6/1) to drab gray-green in color (Fig. 5A). The basal meter of the upper unit preserves abundant subvertical non-tapering burrows (0.5–1.0 cm diameter) that curve irregularly. Some burrows exhibit meniscate fills and are referable to *Taenidium,* which has been described in Tertiary lacustrine deposits (Toots, 1967; Smith and Mason, 1998). Strata overlying this bioturbated interval are generally massive and concretionary, and display "popcorn" weathering (Fig. 7A, B). The basal few meters of the upper lithologic unit are characterized by angular to subhedral grains of quartz, plagioclase, and biotite set in a microcrystalline matrix of silica and clay, with montmorillonite being the predominant clay mineral. Upper reaches of the upper lithologic unit display meter-scale horizontal bedding (Fig. 7C). In the vicinity of Rio Gualo, these bedded strata are conglomeratic, with rounded clasts of tuffaceous material ranging from granules to cobbles embedded in a fine-grained tuffaceous matrix that preserves relic glass shards (Fig. 7D). A few distinctive thin seams of white to light gray claystone, interpreted as air-fall ash beds that

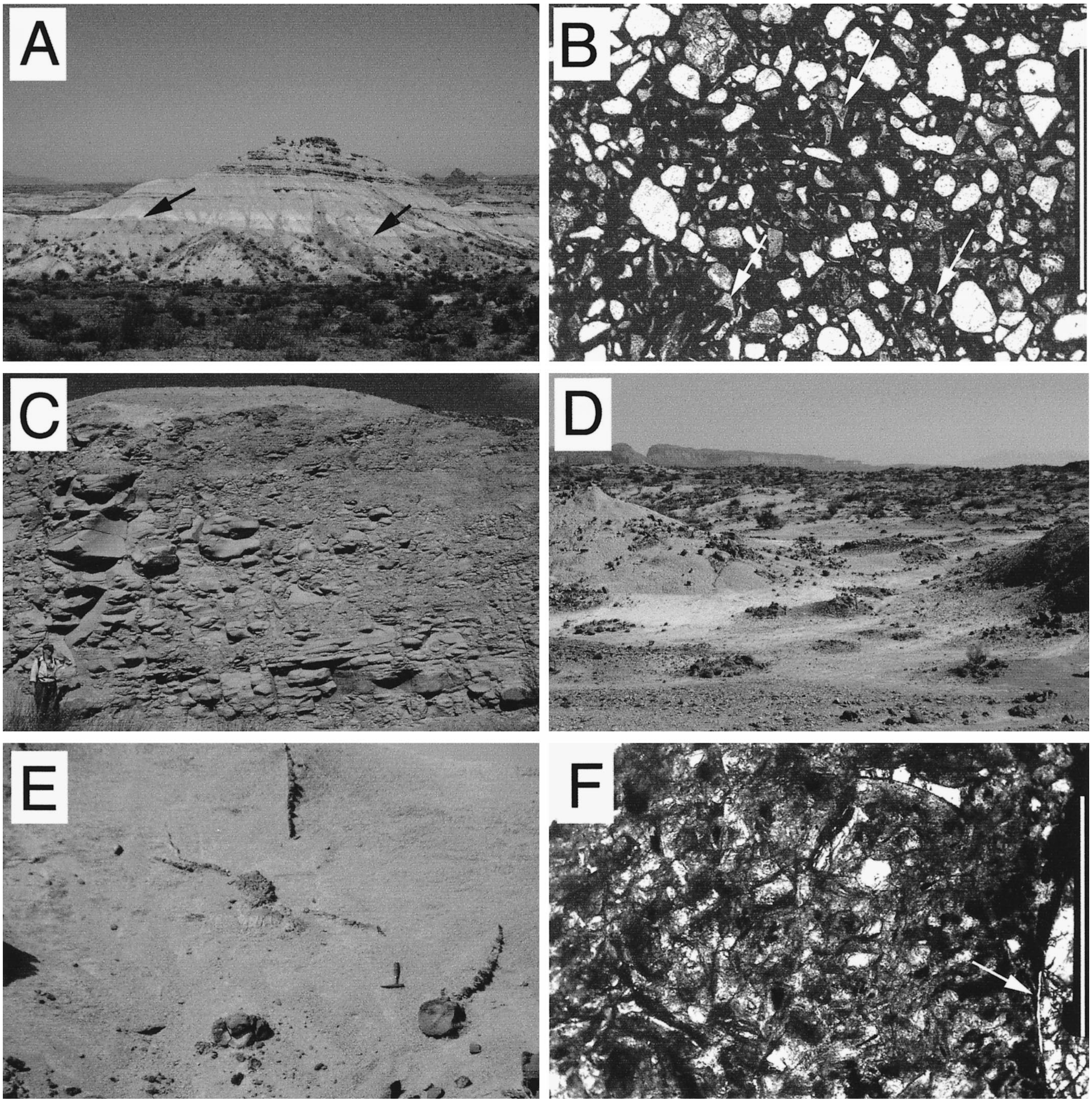


FIGURE 5—Lower lithologic unit of the Chañares Formation. (A) View of the Chañares Formation in the eastern sector of the Los Chañares locality. Tertiary volcanic plugs (Magote Melizos, see Fig. 1) are visible in the distance. Arrows separate the lower ''tuffaceous'' unit (Romer and Jensen, 1966), which is characterized by a ''bluish tinge'' and abundant tetrapod fossils, from the upper unit, which is characterized by a ''nearly pure white'' appearance and an apparent complete lack of vertebrate fossils. (B) Calcareous concretions intercalated in the basal few meters of the Chañares Formation preserve relic glass shards that have been replaced by $CaCO_3$ (arrows) amidst abundant grains of detrital quartz. Scale bar ≈ 2.5 mm. (C) Nodular exposures characteristic of the lower Chañares Formation. (D) Shattered carbonate concretions in the Los Chañares locality. These concretions were broken over the past several decades in the search for tetrapod fossils. The national park Talampaya forms the cliffs in the distance. (E) Vertical calcite dikelets emanate from some concretions in the lower lithologic unit. These dikelets may reflect a local or regional structural fabric. (F) Photomicrograph of a fossil-bearing carbonate concretion from the lower lithologic unit of the Chañares Formation. The concretion matrix consists of diagenetically replaced glass shards and rare detrital grains. Arrow points to bone margin. Scale bar ≈ 1 mm.

have been altered to clay (bentonites), are intercalated within the upper lithologic unit (Fig. 7E). Tuffaceous nodular beds of the upper lithologic unit pass upward and laterally into microlaminated clayshales and siltstones of the basal Los Rastros Formation (Figs. 3, 7F).

Los Rastros Formation

The Los Rastros Formation crops out throughout the study area, but is well-exposed in a series of ridges that lie immediately to the northwest of the Cañon del Gualo (Fig. 8A). Here, in beds that dip 15°–20° to the west, the basal contact with the Chañares Formation is exposed, as are approximately 280 m of overlying Los Rastros strata (Fig. 3). In exposures throughout the study area, the Chañares—Los Rastros contact is herein placed at the transition from concretionary beds with irregular surface weathering to more regularly-bedded clayshales and siltstones that exhibit a smoother weathering profile (Fig. 7F). This lithologic transition is accompanied typically by a shift in color from light gray to drab gray-green. The contact between the Los Rastros Formation and the overlying Ischigualasto Formation is not exposed in the outcrops situated to the northwest of the Cañon del Gualo. However, the upper contact can be observed in near-vertical beds exposed near the mouth of the Arroyo de Agua Escondida. Here, thinly-bedded, fine-grained, drab-gray and tan sandstones of the Los Rastros Formation are sharply overlain by variegated red and green siltstones and trough cross-stratified conglomeratic sandstones of the Ischigualasto Formation.

Six distinct depositional packages, each characterized by a similar succession of facies, are preserved in the Los Rastros Formation exposed to the northwest of the Cañon del Gualo (Figs. 3, 8B). A typical facies succession consists of basal dark gray to black carbonaceous clayshale (facies 1) that preserves conchostracans, plant debris, insect impressions (Gallego, 1997), and rare fish body fossils. Thin seams of tan to yellow bentonite (Figs. 3, 8C) and dark brown to orange beds of ironstone are intercalated in this microlaminated clayshale facies, which is sharply overlain by interbedded light gray silty clayshale and siltstone (facies 2). Siltstone interbeds have sharp lower and upper contacts, display planar and ripple lamination, and increase in thickness and abundance up-section. Beds of silty claystone and siltstone pass up section into fine-grained sandstones (facies 3) that are characterized by large-scale, low-angle (5°–10°) inclined beds with distal toes that interfinger laterally with finer-grained deposits of facies 2 (Fig. 8D). This fine-grained sandstone facies is typically in erosional contact with superjacent medium- to coarse-grained sandstone bodies characterized by trough and tabular cross-bedding (facies 4). These sandstone bodies are interstratified with fine-grained beds of siltstone and claystone (facies 5) that preserve silicified root traces and slickensides.

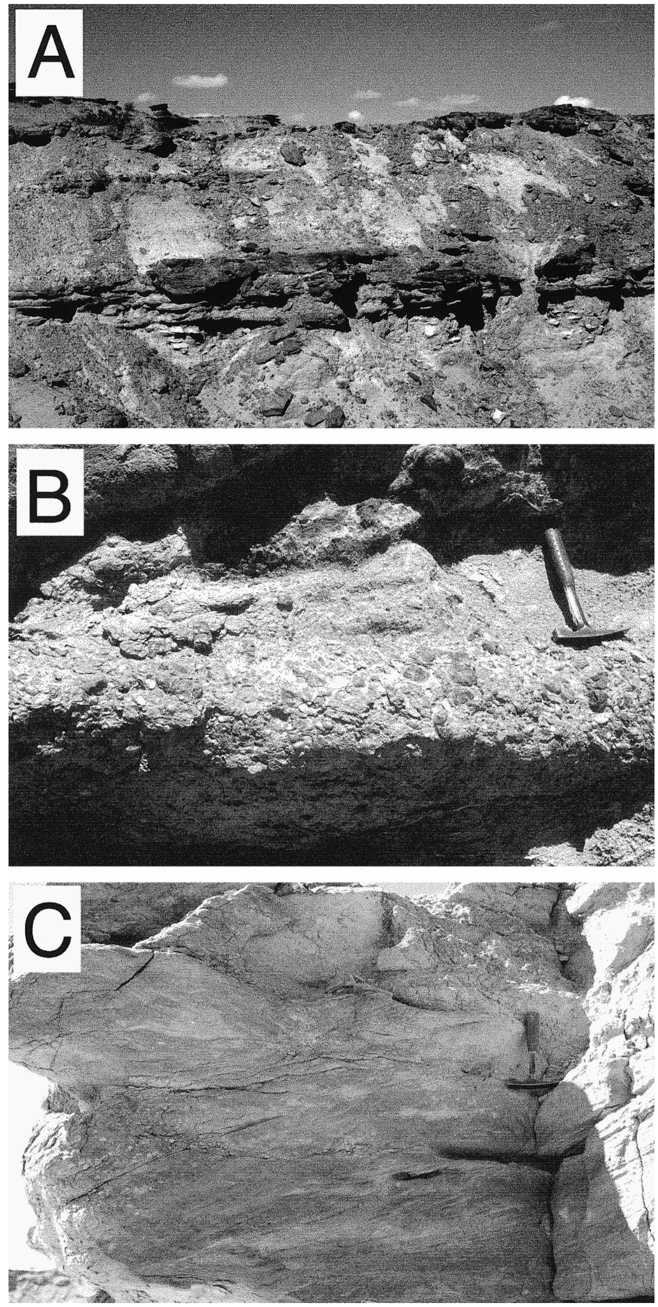


FIGURE 6—Sandstone bodies in the Chañares Formation. (A) View of sandstone bodies intercalated in the Chañares Formation near the western end of the Los Chañares locality. (B) Lower contacts of sandstone bodies exhibit erosional relief and are mantled by deposits of rounded claystone pebbles and rounded-to-angular chert clasts. (C) Basal conglomeratic facies pass up-section into fine- to coarse-grained calcareous sandstone characterized by small- to large-scale tabular and trough cross-bedding and ripple cross-lamination.

PALEOENVIRONMENTAL RECONSTRUCTION

Sedimentological data provide ample indication of the prevailing conditions during deposition of the Tarjados and Los Rastros Formations. The observations presented herein, coupled with the findings of Romer and Jensen (1966), indicate that the Tarjados Formation consists of alluvial deposits with facies reflecting deposition in high-energy fluvial channels and on adjacent floodplains. Previous work on the Los Rastros Formation (Romer and Jensen, 1966; Stipanícic, 1983; Milana and Alcober, 1994) indicates that this unit is primarily lacustrine in origin, with intercalated fluvial intervals. The present work on Los

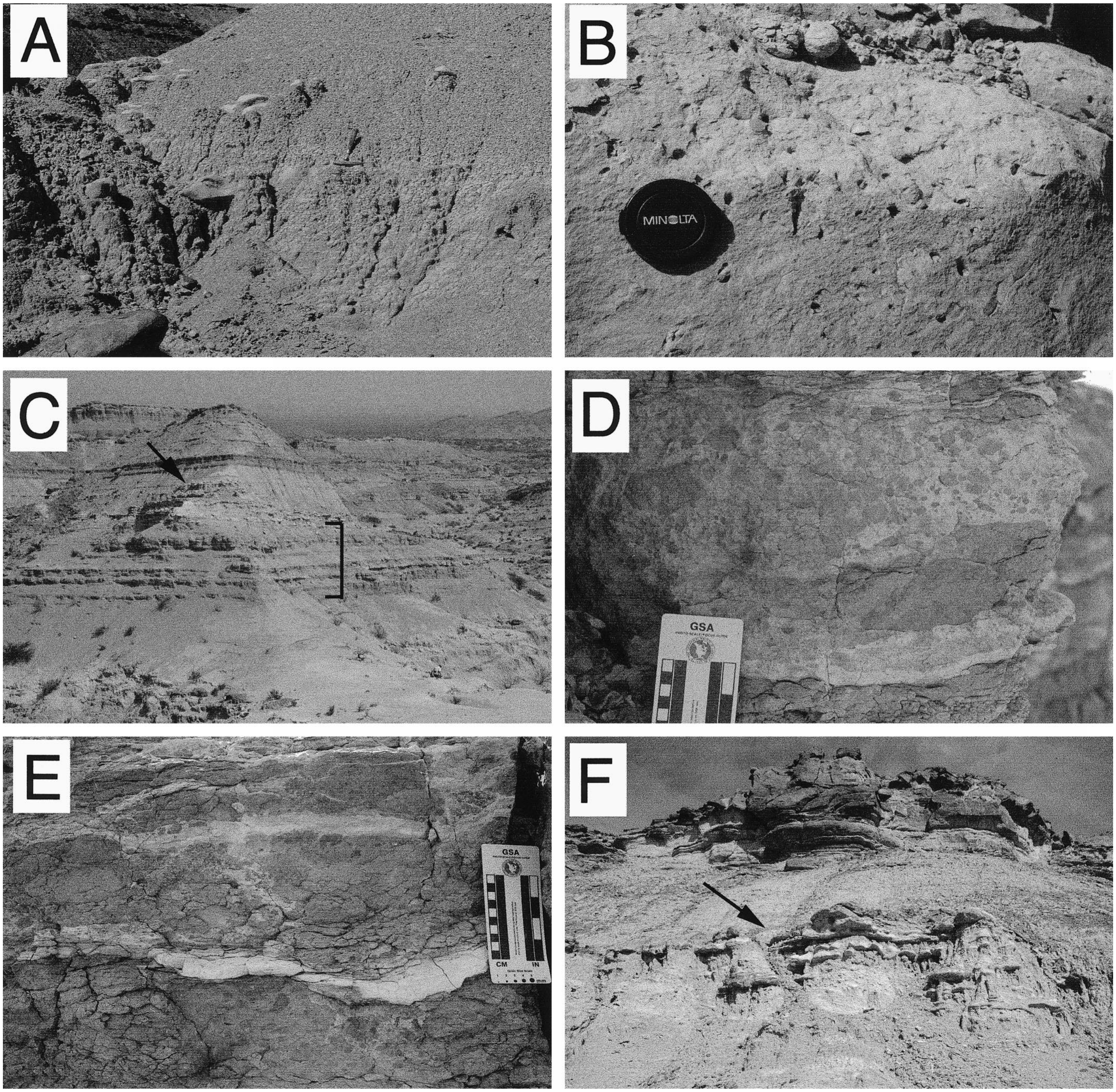


FIGURE 7—Upper lithologic unit of the Chañares Formation. (A) Outcrop view of the contact (marked by hammer) between the lower and upper lithologic units of the Chañares Formation. The upper unit is characterized by ''popcorn'' weathering. (B) The basal meter of the upper unit preserves abundant burrows, some of which are characterized by meniscate fills. (C) Upper reaches of the upper lithologic unit display meter-scale horizontal bedding (bracket). In the vicinity of the Cañon del Gualo, these bedded strata are conglomeratic. (D) Close-up of conglomeratic facies in the upper lithologic unit. Rounded clasts of tuffaceous material ranging from granules to cobbles are embedded in a fine-grained tuffaceous matrix. (E) Thin seams of white to light gray claystone are intercalated within the conglomeratic beds in the upper lithologic unit, and these distinctive layers are interpreted as bentonite beds. (F) Tuffaceous nodular beds of the upper lithologic unit grade rapidly upward and laterally into microlaminated clayshales of the basal Los Rastros Formation. This lithologic transition is typically accompanied by a shift in color from light gray to drab gray-green. Arrow marks contact.

Rastros exposures in the Cañon del Gualo region indicates that at least six episodes of lacustrine sedimentation occurred, each of which is capped by a relatively thin record of fluvial sedimentation. The microlaminated clayshale facies described above (facies 1) is interpreted to reflect open (distal) lake conditions, with only the finest clastic fraction settling from suspension amidst biological detritus (e.g., plant and insect debris). Overlying beds of silty claystone and siltstone (facies 2) are interpreted to reflect progressive filling of the large lake basin. Sedimentary structures preserved in siltstone interbeds indicate that traction currents and perhaps small-scale storm waves impinged

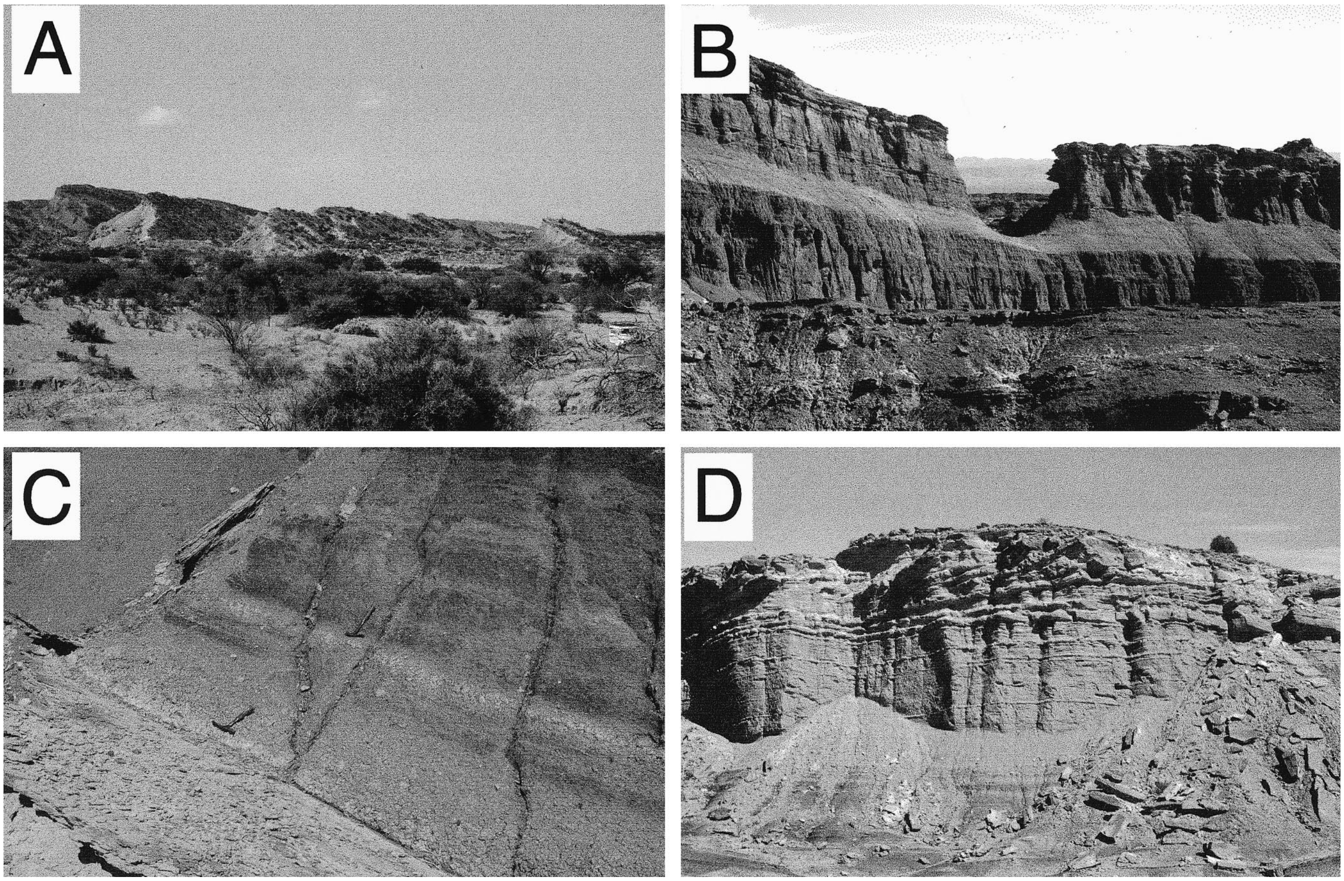


FIGURE 8—Exposures of the Los Rastros Formation in the vicinity of the Cañon del Gualo. (A) View of the Los Rastros Formation in the vicinity of the Cañon del Gualo. Here, the formation is exposed in a series of ridges and escarpments that dip 15°–20° to the west. (B) In the area of study, the Los Rastros Formation consists of six distinct depositional ''hemicycles,'' each characterized by a similar upward-shallowing succession of lacustrine to fluvial facies. One complete hemicycle is illustrated in this view (see text for details) (C) Thin beds of tan to yellow bentonite crop out at the base of five of the six recorded lacustrine hemicycles. Hammers rest upon two bentonite beds in this view. (D) Deltaic deposits cap lacustrine facies in the Los Rastros Formation. In this view, the deltaic sandstone body progrades to the left (south), with large-scale, low-angle inclined beds interfingering laterally with finer-grained deposits of the open lake.

upon the lake bottom. Inclined beds of fine-grained sandstone (facies 3) deposited by prograding Gilbert-type deltas mark the final stage of lacustrine sedimentation. Delta deposits in turn, are overlain by markedly coarser-grained fluvial deposits (facies 4) and associated floodplain strata (facies 5, paleosols and floodbasin ponds). The repetitive record of widespread lacustrine flooding in the Los Rastros Formation exposures near Cañon del Gualo is interpreted to reflect pulses of basin subsidence related to episodic movement on bounding faults. Contemporaneous episodes of explosive volcanism are indicated by numerous intercalated ash horizons: thin bentonite beds occur within the basal few meters of the microlaminated clayshale facies (facies 1) in five of the six recorded lacustrine hemicycles (Figs. 3, 8C; Rogers and May, 1996).

The depositional history of the Chañares Formation is more difficult to reconstruct because the unit is characteristically massive and concretionary. Previous workers generally concluded that this enigmatic unit represented an extremely thick accumulation of volcanic tuffs that were deposited in either eolian or lacustrine settings (e.g., Romer and Jensen, 1966; Stipanícic, 1983). The prevailing lack of primary stratification prompted Romer (1973) to further conclude that deposition in water was unlikely. Instead, Romer envisioned the catastrophic blanketing of the Chañares landscape "with tremendous quantities of volcanic ash in Pompeii-like fashion" (Romer, 1973, p. 6). These conclusions are understandable, given the generally massive appearance of the formation and its substantial volcaniclastic component. A more recent analysis by López Gamundi et al. (1989) concluded that the formation included deposits of muddy streams transporting abundant volcanic detritus.

A purely volcanic scenario fails to account for at least a few key sedimentological features of the Chañares Formation, such as the abundance of detrital sandstones and siltstones in the lower lithologic unit, and the presence of cross-bedded lenticular sandstone bodies in the western portion of the Los Chañares locality (see Fig. 6). Thus, the present results are in agreement with López Gamundi et al. (1989). The fossil-bearing facies of the lower lithologic unit is interpreted as fluvial and floodplain deposits of an alluvial setting, which is certainly consistent with the abundance of terrestrial tetrapods. Another paleoenvironmental refinement that is proposed concerns the likely deposition of at least part of the upper lithologic unit in la-

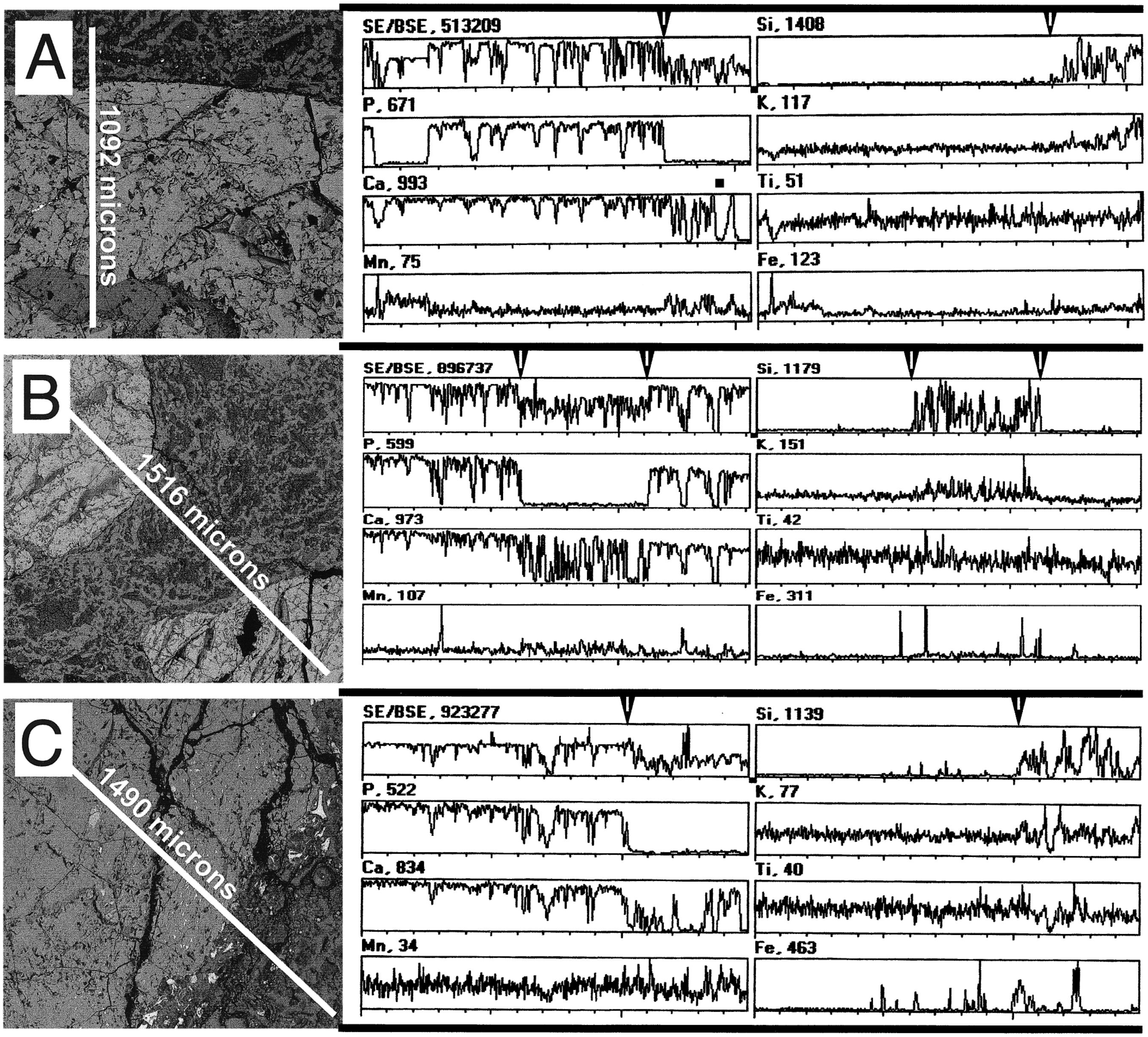


FIGURE 9—Backscatter-electron images and SEM/EDS linescans spanning bone-concretion interfaces. Arrows mark location of bone margin. All samples from Los Chañares locality. (A) Image and accompanying linescan show a sharp contact between fossil bone (light gray) and concretion matrix (mottled gray and dark gray). There is indication of weathering and leaching of bone mineral in the outer 100 microns. Scan extends from bottom of image, where it passes through a zone of calcite replacement (darker gray), to top of image. (B) Two fossil bones are intersected in this linescan, which extends from top left to bottom right. As in scan ''A'', there is indication of progressive loss of Ca and P in the vicinity of bone-concretion interfaces. Fe spikes occur in the vicinity of both bone-concretion interfaces. (C) Bone surface displays fracturing and microbrecciation. Oxidation (Fe spikes, white dots on image) penetrates ~500 microns into bone, and there is indication of progressive loss of both Ca and P. Oxidized material, including relic glass shards (top right), fringe fossilized bone. Scan extends from top left to bottom right.

custrine settings. This interpretation is consistent with the occurrence of the ichnogenus *Taenidium,* and lakes would provide an ideal setting for the preservation of the unit's thin but areally widespread air-fall ash beds. Moreover, in exposures in the Los Chañares locality and near the Cañon del Gualo, microlaminated lacustrine clayshales at the base of the Los Rastros Formation pass laterally across what are clearly diagenetic boundaries into massive concretionary beds at the top of the Chañares Formation. It is very likely that diagenetic overprinting has obscured lacustrine facies in the upper lithologic unit.

Finally, present observations regarding the pyroclastic nature of the Chañares Formation are generally in accord with the opinions of earlier workers. Much of the formation is composed of volcaniclastic material (confirmed through thin-section and SEM analyses; see Figs. 5, 9), although the exact mechanism(s) of emplacement remains debatable. The massive and essentially unsorted sediments that comprise the upper reaches of the lower lithologic unit and most of the upper lithologic unit probably represent, at least in part, devitrified pyroclastic flow deposits. The predominantly fine grain size (>50% ash-size particles by volume) is characteristic of ash-flow deposits (Fisher and Schmincke, 1984). Ash-flow sheets (including the tuffaceous conglomeratic beds in the upper unit, see Fig. 8C, D) potentially were emplaced as mass flows on subaerial alluvial surfaces and in lakes that occupied the Ischigualasto-Villa Unión basin. They may have been deposited as primary flows coeval with eruptions or as secondary flows related to over-steepening and slumping. The emplacement of secondary flows in either subaerial or subaqueous settings is consistent with the apparent absence of welded textures and distinct cooling units. A few altered ash beds of air-fall origin are interbedded within the Chañares Formation, but these laterally extensive beds of virtually pure claystone are thin and comprise only a minute fraction of the section.

CHAÑARES TETRAPOD ASSEMBLAGE

Taxonomic Overview

The Chañares vertebrate assemblage, as currently known, is composed of 16 tetrapod taxa: three cynodonts, three dicynodonts, and ten archosauriforms (Table 1). Minimum number of individual (MNI) counts (Badgley, 1986) in the collections of the Universidad Nacional de La Rioja, Universidad Nacional de Tucuman, and Harvard University indicate that cynodonts, dicynodonts, and archosauriforms comprise 81%, 7%, and 12% of the Chañares assemblage, respectively. More than half of the identified individuals (~58%) are the traversodont cynodont *Massetognathus.* This taxon was arguably one of the most abundant animals inhabiting the Chañares ecosystem. Another aspect of the assemblage worthy of note is the great diversity of the archosauriforms (Table 1), which is greater than that of the cynodonts and dicynodonts combined. Aquatic and semiaquatic taxa such as fish and amphibians are conspicuously absent from the assemblage.

TABLE 1—Tetrapods of the Chañares Formation, Middle Triassic (Ladinian), northwestern Argentina

Dicynodonts
Dinodontosaurus platiceps Cox 1968[1]
Dinodontosaurus platygnathus Cox 1968[2]
Dinodontosaurus brevirostris Cox 1968
Cynodonts
Probelesodon lewisi Romer 1969[3]
Massetognathus pascuali Romer 1967[4]
Probainognathus jenseni Romer 1970a
Archosauriforms
Luperosuchus fractus Romer 1971d
Lagerpeton chanarensis Romer 1971b
Chanaresuchus bonapartei Romer 1971a
Gualosuchus reigi Romer 1971a
Gracilisuchus stipanicicorum Romer 1972b
Lewisuchus admixtus Romer 1972c
Marasuchus lilloensis Romer 1972d[5,6]
Pseudolagosuchus major Arcucci 1987
Tropidosuchus romeri Arcucci 1990
Tarjadia ruthae Arcucci & Marsicano 1998

[1] Formerly *Chanaria platyceps,* proposed as *Dinodontosaurus platyceps* by Keyser and Cruickshank (1979).

[2] Formerly *Dinodontosaurus platygnathus* (Cox, 1968), proposed as *Jachaleria platygnathus* by Keyser and Cruickshank (1979) due to structure of lower jaw. However, the specimen in question apparently has tusks, and thus is not *Jachaleria.* We prefer to maintain this taxon as *Dinodontosaurus.*

[3] *Probelesodon minor* Romer 1973 is here considered a synonym of *Probelesodon lewisi* Romer 1969.

[4] *Massetognathus teruggii* Romer 1967, *Massetognathus major* Romer 1972e and *Megagomphodon oligodens* Romer 1972e are herein considered synonyms of *Massetognathus pascuali* Romer 1967 (Abdala and Giannini, 2000).

[5] Formerly *Lagosuchus lilloensis* Romer 1972d, proposed as *Marasuchus liloensis* by Sereno and Arcucci (1994).

[6] *Lagosuchus talampayensis* is considered nomina dubia (Sereno and Arcucci, 1994).

Taphonomy

Preservation of the Chañares Tetrapod Assemblage

To date, tetrapod fossils have been found only in the lower lithologic unit of the Chañares Formation, where they are preserved almost exclusively within carbonate concretions (Table 2). Fossiliferous concretions in the lower lithologic unit are segregated into local pockets that are separated by broad expanses of concretionary exposures that yield relatively few fossils. The richest pocket of fossil preservation by far in the Chañares Formation is the classic Los Chañares locality (Fig. 1, 29°49′8.9″S, 67°48′47.9″W), which has been a focal point of collection for almost 40 years (Romer and Jensen, 1966; Romer, 1967). Beyond the bounds of this extraordinary locality, which encompasses ~75 m^2, it is estimated that less than five percent of the concretions exposed at the ground surface preserve vertebrate skeletal material. Concretions devoid of skeletal debris occasionally preserve small chert or claystone pebbles at their core, but the majority of the concretions that have been examined in the field failed to exhibit any obvious center of nucleation.

The general quality of fossilized bone preserved in concretions is exceptional, with dark brown (10YR 2/2) to reddish-brown (2.5YR 3/1) bone surfaces exhibiting virtually no evidence of macroscopic weathering (*sensu* Behrensmeyer, 1978). However, backscatter-electron images of selected bones do indicate a degree of surficial oxidation and corrosion (Fig. 9). Moreover, linescans of bone-concretion interfaces that track a variety of elements indicate that bone hydroxyapatite is leached locally at bone margins, although the adjacent concretion matrix does not show any appreciable enrichment in phosphate (Fig. 9). Downing and Park (1998) used similar methods to demonstrate that bone hydroxyapatite had been leached and that P had diffused into diagenetic mammal-bearing concretions from the Miocene Sucker Creek Formation of Oregon. Original pore space and post-mortem fractures in bones preserved in Chañares concretions are filled with microcrystalline $CaCO_3$ cement, and some bone mineral is replaced by calcite (Fig. 9).

Fossils also are preserved outside of concretions in the lower lithologic unit of the Chañares Formation, but they are rare and usually intercalated in the basal sandstones

TABLE 2—Characteristics of 23 fossil-bearing concretions from the Chañares Formation of northwestern Argentina.

Specimen ID	MNI	Taxon/taxa represented	Taphonomic characteristics
ULR Nodule 1*	1	1	B, E, F, H, J
PVL Nodule 8[?]	1	1	B/C, D, F, H, J
PVL Nodule 12*	1	3	C, D, G, H, J, M?
PVL Nodule 4*	1	1	B/C, E, F, H, J
PVL Nodule 2*	1	1	B/C, E, G?, H, J
PVL Nodule 11*	1	4	B/C, E, F, H, J
MCZ 4232*	1	1	B/C, E, F, H, J
PVL Nodule 6*	1+	1	B/C, E, F, H, J
PVL Nodule 5*	2	1, 4	C, E, G?, H/I[4], J
PVL Nodule 12*	2	1, 4	B/C, E, F, H, J
MCZ 4220*	2	1	B, D, F, H, J
MCZ 4018*	2	1	B/C, E, F, H, J
MCZ 4000*	2	1	B/C, E, F, H, J
MCZ 4001*	2	1	C, E, F, H, J
MCZ 4102*	2	1, 2	B/C, E, F, H, J
MCZ 4036†	2	5	B/C, E, F, H, J
MCZ 3691[?]	2+	1	A/B/C, E, G?, H, J
PVL Nodule 10*	3	1, 4	B/C, E, F, H, J
PVL Nodule 3*	3	1	B/C, E, F, H, J
PVL Nodule 7*	3+	1, 4	B/C, E, G, H, J
PVL Nodule 1*	4	1	B/C, E, G, H, J
UPLF 08/09*	4	6, 7, 8	B/C, E, G, H, J
MCZ 4038‡	5	1, 4	B/C, E, F, H, J

Locality Data: *—Los Chañares locality, †—Far East locality (~10 km east of mouth of Rio Chañares), ‡—Hill ½ mi. East of abandoned puesto, ½ mi. east of Chañares plug, [?]—locality unknown

Taxonomic Designations: 1—*Massetognathus pascauli,* 2—*Probelesodon lewisi,* 3—Dicynodontia indeterminate, 4—Archosauriform indeterminate, 5—*Chanaresuchus bonapartei,* 6—*Marasuchus lilloensis,* 7—*Gracilisuchus stipanicorum,* 8—*Tropidosuchus romeri*

Taphonomic Observations:

Bone Articulation: A—fully articulated, B—articulated components, C—disarticulated but associated

Skeletal Parts: D—sorted, E—unsorted

Spatial Arrangement: F—random, G—preferred orientation

Breakage: H—complete elements, I—broken elements

Bone Modification: J—fresh surfaces, K—moderate degradation (pitting, flaking), L—advanced degradation (cortical bone removed), M—punctures/scratches/grooves

and siltstones below the tuffaceous horizons that yield fossiliferous concretions. There are no known concentrations of fossils preserved outside of concretions, and all discoveries appear to represent isolated individuals, to date. Interestingly, many of these fossils are larger than the typical material recovered within concretions, and they tend to be the remains of relatively large-bodied taxa. Specimens recovered outside of concretions include skulls of large archosaurs, skulls and postcrania of large dicynodonts, and occasional skulls of relatively large specimens of *Massetognathus* (e.g., the holotype of "*Megagomphodon oligodens*"). Material preserved outside of concretions tends to be characterized by a greater degree of compressional distortion, and often a more advanced weathering stage (Fig. 10). Bone surfaces tend to be rough, exhibit cracking and pitting, and generally are light pinkish gray (7.5YR 6/2), rather than the dark brown typical of concretion-hosted bone.

Preservational states vary among concretions, ranging from isolated bone fragments to concentrations of partially articulated skeletons. The vast majority of skeletal elements are intact, and those that are broken tend to display sharp fractures, with no indication of abrasion or rounding. Easily transported elements such as ribs and vertebrae are well represented, as are less mobile elements such as skulls and limb bones. Concretions exhibit a "two-dimensional" mode of preservation, with skeletal material distributed in a tabular fashion through a thickness of a few centimeters. Two large concretions (MCZ 3691, PVL Nodule 7) display a linear style of preservation, with skeletal material densely concentrated along 15-to-20-cm-wide swaths (Fig. 11). PVL Nodule 7 also shows an alignment of elongate elements with the long axis of the overall concentration (Fig. 11B). Several other concretions also show preferred orientations of skeletal debris (Table 2).

Three general modes of tetrapod association can be discerned within the sample of 23 prepared concretions. Eight concretions preserve the disarticulated to partially articulated skeletal remains of a single individual which, in most cases, is the gomphodont cynodont *Massetognathus* (Fig. 12A). Skeletal representation ranges from a few associated bones to nearly complete skeletons. Eight concretions in the sample preserve assemblages of two or more individuals of the same taxon. Seven of these concretions preserve skeletal elements of *Massetognathus,* while one preserves partial skeletons of the archosaur *Chañaresuchus.* One *Massetognathus*-bearing concretion preserves four skulls that show a strong alignment amidst a jumble of associated postcranial elements (Fig. 12B). The seven remaining concretions preserve assemblages of two or more taxa, with up to five individuals represented (Figs. 11, 12C, D). These taxonomically mixed assemblages include archosaurs, herbivorous and carnivorous cynodonts, and dicynodonts in various combinations.

Four concretions recovered from the Los Chañares locality preserve small fusiform coprolites averaging 1.5–2.5 cm in length (Fig. 13). The coprolites vary in color from gray to purple, and boundaries between coprolites and surrounding matrix are sharp. Coprolites are associated with disarticulated skeletal debris in three of the four concretions. One of these concretions yielded vertebrae, scutes, and ribs of a small archosaur, along with several bone-bearing coprolites. The minute skeletal elements preserved in these coprolites are the remains of an, as yet, unidentified tetrapod.

Interpretations of Taphonomic History: Two Pathways to Preservation

The concretion-based mode of preservation that typifies the Chañares Formation greatly facilitates the recovery of tetrapod fossils because the search image is clear—all concretions in the lower lithologic unit are potential targets, and only those that are too large to be broken with a sledge hammer escape scrutiny. Unfortunately, drawbacks also accompany this style of preservation. For example, many of the best-exposed concretions are already out of place at the time of discovery due to their tendency to roll downslope and/or settle as surrounding soft sediments erode (see Fig. 5). Thus, original stratigraphic associations and taphonomic patterns among concretions, such as local trends in concentration and orientation, are virtually impossible to ascertain. Another drawback is the potentially

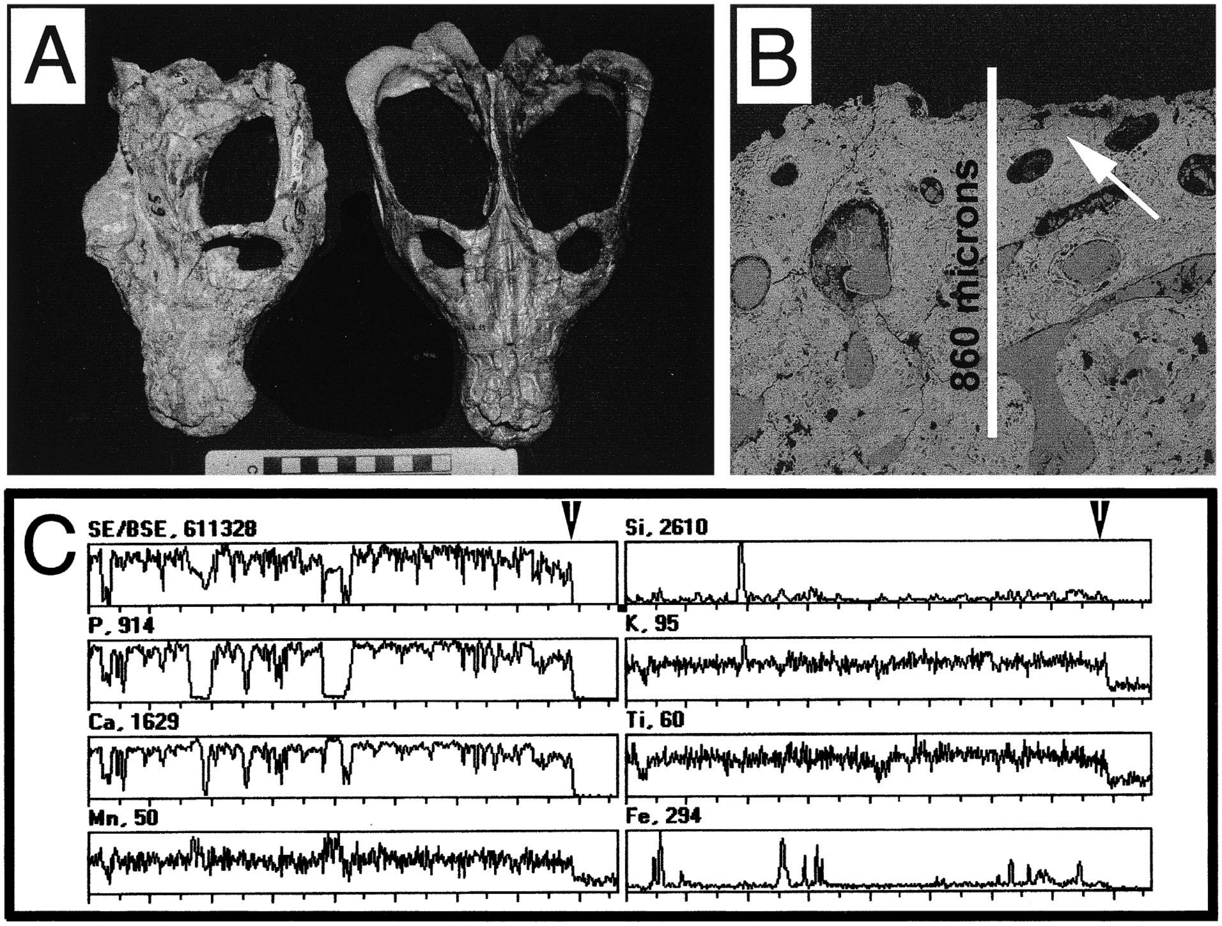


FIGURE 10—Comparison of tetrapod preservation inside and outside of concretions. (A) Skulls of *Massetognathus pascuali* showing a contrast in the quality of preservation. The light pinkish gray skull on the left was fossilized outside of a concretion, and shows dorso-ventral compression and displacement of the saggital crest. The dark brown skull on the right was fossilized within a concretion, and shows much less evidence of compaction. (B) Backscatter-electron image of a dicynodont rib fragment (MCZ 3455) fossilized outside of a concretion. This fragment exhibits an irregular bone surface, with apparent removal of cortical bone. The bone is permineralized with calcite (dark gray material in pores). A discontinuous zone of surficial discoloration that penetrates to a depth of 50–100 microns is indicated by arrow. (C) SEM/EDS linescan of dicynodont rib fragment figured in ''B'' shows indication of loss of P and Ca in outer 200 microns of bone. Oxidation is also apparent near bone margin. Arrow marks bone margin.

biased image of preservation that the concretions provide. Rich but extremely localized windows of preservation afforded by the concretions are separated by expanses of relatively unfossiliferous exposures. This renders it extremely difficult to reconstruct the original geometry and extent of fossiliferous horizons. Are the fossil-bearing concretions a random sampling of an originally very rich and more evenly distributed record, or do the scattered fossiliferous concretions closely track an originally patchy distribution of bone?

The distribution of fossils within the lower lithologic unit of the Chañares Formation is interpreted as indicative of at least two distinct taphonomic pathways to preservation. Isolated occurrences of tetrapods (both within and outside of concretions), either as solitary skeletal components or relatively intact single carcasses, probably represent attritional mortality within the Chañares ecosystem. Single individuals, of course, would have succumbed periodically to predation, disease, and old age, and their carcasses would have been distributed across the landscape. Taphonomic processes (scavenging, weathering, etc.) would have ensued at the time of death, and the nature and intensity of these processes, and their duration, would have varied. Taphonomic data indicate that some carcasses experienced only minor disarticulation prior to final burial, whereas others were disarticulated thoroughly and dissociated. Final burial presumably resulted from overbank flood events or perhaps the accumulation of wind-blown volcanic dust.

A second taphonomic pathway is suggested by the spectacular concentration of fossiliferous concretions preserved at the classic Los Chañares locality. This concentration is interpreted as indicative of mass mortality within the Chañares ecosystem. Unfortunately, the vagaries of diagenesis and gravitational settling, combined with decades of collection by a variety of field parties, render it impossible to determine whether or not all of the fossiliferous concretions recovered from Los Chañares originated from a single horizon. However, it seems most parsimonious to conclude that this unique and highly localized site, which differs from surrounding strata apparently only by virtue

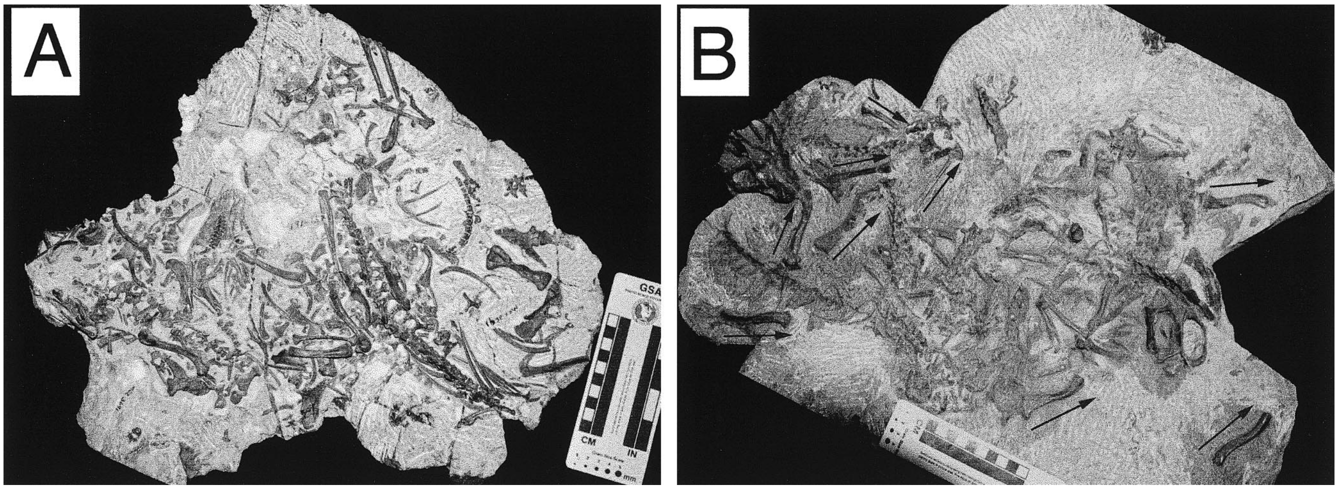


FIGURE 11—Two concretions that show linear concentrations of bone. (A) Concretion MCZ 3691 preserves the skeletal remains of at least two *Massetognathus.* Bones are concentrated most densely in the lower half of the concretion, extending in a swath from left to right. There is also a hint of alignment of elongate elements with the general trend of the concentration. (B) PVL Nodule 7 preserves the skeletal remains of at least 3 individuals (2 *Massetognathus* and an unidentified archosaur), with bones concentrated in a linear swath that extends from left to right. Arrows mark elongate elements that were presumably free to rotate. There is an arguable alignment of most of these elements with the general trend of the concentration.

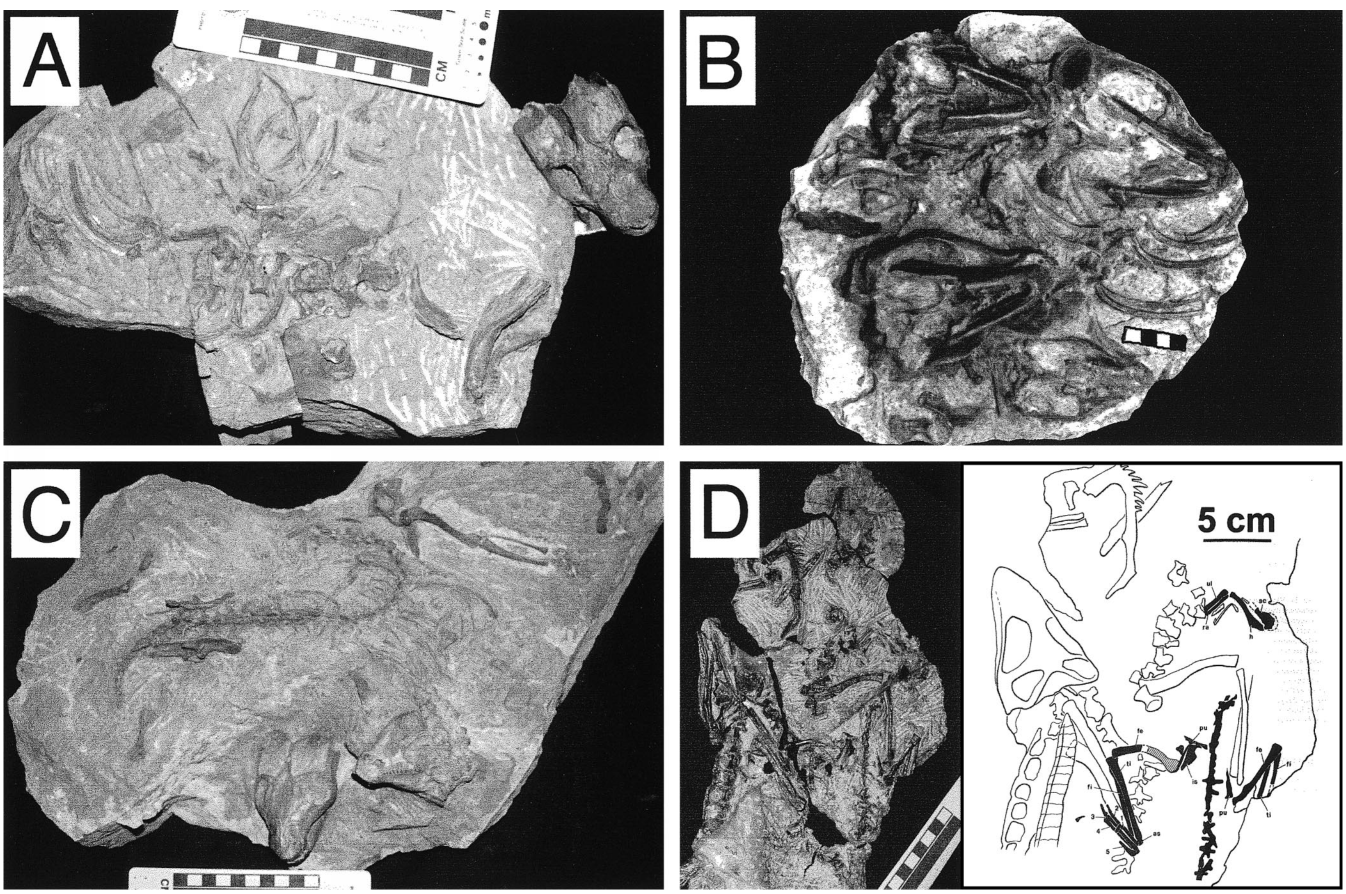


FIGURE 12—Three general modes of tetrapod association can be discerned in the sample of 23 prepared concretions studied in this report (see Table 2). (A) For example, PVL Nodule 2 preserves a single individual of *Massetognathus* that is disarticulated but remains closely associated. (B) PVL Nodule 1 preserves four *Massetognathus* skulls that show a strong alignment amidst a jumble of associated postcranial elements. (C) PVL Nodule 10 preserves two intact crania of *Massetognathus* in association with archosaur postcranial elements (including an articulated vertebral column and pelvis). (D) UPLR 08/09 provides another example of a multitaxic assemblage, with four individuals representing three different archosaur taxa preserved together. Interestingly, the long axes of the articulated vertebral segments are aligned almost perfectly. Line drawing of UPLR 08/09 modified from Sereno and Arcucci (1994).

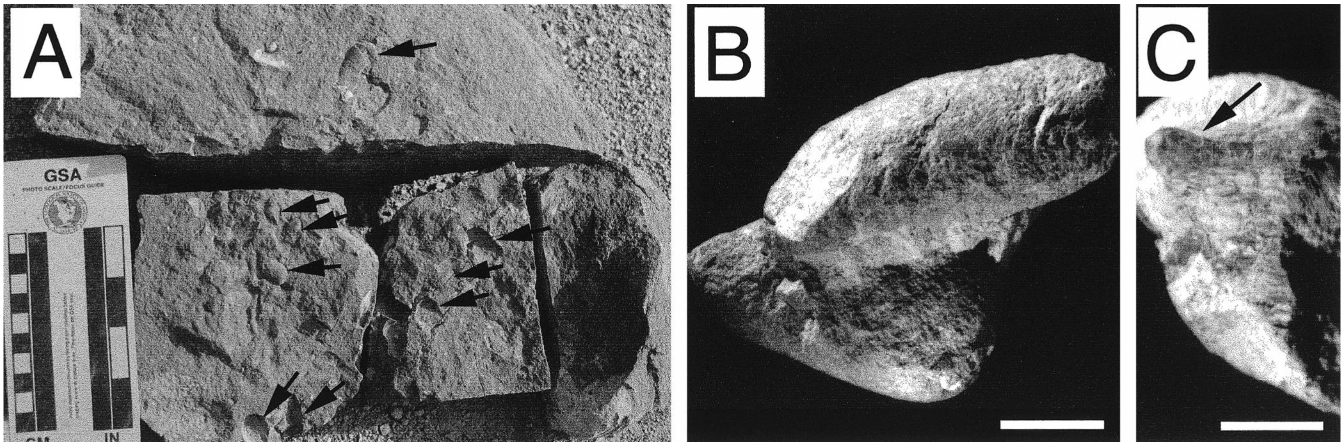


FIGURE 13—Coprolites from the Los Chañares locality. (A) Rare concretions recovered from the Los Chañares locality preserve small coprolites (marked by arrows) averaging 1.5–3 cm in length. (B) Close-up view of two fusiform coprolites (scale bar = 1 cm). (C) Coprolite preserving minute skeletal element (arrow) from an as yet unidentified tetrapod (scale bar = 5 mm).

of its amazing concentration of fossils, does record a single mode, if not event, of tetrapod mortality and preservation.

The scenario of mass mortality is consistent with many aspects of the Los Chañares assemblage. Well over 100 individuals representing a diverse array of taxa have been collected from Los Chañares, and the assemblage includes specimens of both adults and juveniles (e.g., Abdala and Giannini, 2000). Based on analysis of the MCZ, ULR, and PVL collections, a minimum of 94 cynodonts (68 *Massetognathus,* 18 *Probainognathus,* 8 *Probelesodon*), 2 dicynodonts, and 11 archosaurs (including *Marasuchus, Gracilisuchus,* and *Tropidosuchus*) are represented in the local assemblage, and this tally reflects only prepared concretions. Many more individuals undoubtedly are preserved in, as yet, unprepared concretions in La Rioja (ULR) and Tucuman (PVL), Argentina. Another feature indicative of mass mortality is the clustering of individuals within single concretions (Figs. 11, 12). This attribute is striking particularly when non-sympathetic taxa are found in close association, such as in the four concretions that preserve skeletal remains of carnivorous archosaurs co-mingled with those of small-bodied cynodonts (Table 2), with no indication of time-averaging. Still another feature consistent with the scenario of mass mortality is the general similarity of preservational attributes among taxa. Virtually all of the fossil bones from the Los Chañares locality are characterized by comparable low weathering stages (Behrensmeyer, 1978). Modes of skeletal articulation and association, although variable, also are comparable, in that the cynodont and archosaur taxa represented in the assemblage generally are preserved as either near-complete skeletons or concentrations of closely associated skeletal elements (Figs. 11, 12). Only the relatively large-bodied dicynodonts, which rarely are preserved at Los Chañares, show a variation from this theme, in that their fossils tend to occur as isolated specimens.

Delving deeper into the possibility of mass mortality, several aspects of the Los Chañares assemblage hint at the actual nature of the event, although there is no proverbial "smoking gun." The killing agent was clearly lethal to a variety of taxa, and it killed both adults and juveniles. The event also led to the concentration of animals that under normal circumstances would tend not to associate, specifically carnivores and their potential prey. Whether concentration occurred during life (albeit presumably very near the end of it) or post-mortem is unknown. The event also produced a counterintuitive bias against the preservation of large-bodied taxa (e.g., *Chanaria*), whose remains are preserved at a relatively greater frequency elsewhere in the Chañares Formation. The scarcity of large-bodied taxa in the Los Chañares fossil assemblage could reflect relative immunity of large animals to the death event, or perhaps the post-mortem sorting of carcasses. After death, the carcasses of an array of taxa lay exposed, and numerous concretions show evidence of partial to fairly advanced stages of disarticulation. There is no convincing evidence of scavenging, which may reflect a glut of carcasses and selective utilization (hence minimal bone processing) or maybe the local devastation of the vertebrate scavenger community. Close element association and limited weathering (from a macroscopic perspective) indicate that burial in reworked volcanic ash occurred shortly after mortality, possibly within weeks or months if decomposition and disarticulation transpired in a setting favorable to soft tissue decay (Schäfer, 1972; Coe, 1978; Hill, 1980; Weigelt, 1989; Behrensmeyer, 1991).

Two remaining lines of evidence help to narrow the focus. The first relates to the style of preservation exhibited by two of the larger concretions in the sample, MCZ 3691 and PVL Nodule 7. Although admittedly speculative, these concretions show a spatial arrangement of skeletal material consistent with the stranding of carcasses along the margin of a body of water (Fig. 11). The alignment of several elongate limb elements with the trend of the concentration in PVL Nodule 7 lends support to this hypothesis, as wave action presumably would have acted to align elements with roughly equidimensional ends more or less tangential to the shoreline (e.g., Weigelt, 1989; Leggitt and Buchheim, 1997). The four aligned *Massetognathus* skulls preserved in PVL Nodule 1 and the three aligned vertebral columns in UPLR 08/09 (Fig. 12D), among other less developed indications of preferred alignment (see Table 2), also might reflect wave activity along a strandline. In addition to the spatial arrangement of disarticulated

FIGURE 14—A near complete skeleton of *Massetognathus* that was separated from MCZ 3691 (see Fig. 11). This skeleton exhibits a reasonable approximation of a ''passive'' death pose (or ''water carcass'' of Weigelt, 1989), with no indication of vertebral or limb contortion that would typically accompany desiccation.

skeletal debris, a relatively intact carcass associated with concretion MCZ 3691 (Fig. 14) shows a "passive" death pose that is also consistent with an aqueous grave (Weigelt, 1989). The seminal report of Weigelt (1989) on the Smithers Lake carcass assemblage in southeast Texas provides a modern analog for this preservational scenario. Weigelt's detailed and richly illustrated report describes the taphonomy of a catastrophic carcass assemblage that formed in response to a "norther," a severe winter storm driven by north winds and characterized by a sudden drop in temperature. A diverse array of vertebrate taxa (alligator, turtles, fish, birds) and plant debris accumulated in a 1,300-m-long swath along the south shore of the lake. Many of the carcasses figured and/or discussed in Weigelt's report show preferred orientations relative to the lake shoreline.

The second clue is geological in nature, and it pertains to the indisputable volcanic character of the lower lithologic unit of the Chañares Formation. Specifically, the matrix that encases the fossils indicates that the Los Chañares tetrapod assemblage formed amidst the accumulation of copious amounts of volcanic ash. Hence, it certainly is plausible that lethal volcanic processes, such as catastrophic gas surges or inundation by ash, led to the demise of the local fauna (Voorhies, 1981; Lockley, 1990). Alternatively, and more in line with the preservational attributes of the assemblage outlined above, volcanism may have led to the catastrophic flooding of the landscape, possibly due to the diversion of upland drainage systems or the damming of local rivers. It is also possible that volcanic activity *per se* had little to no direct effect on the living tetrapod community, and that the influx of volcanic ash simply enhanced burial potential and generated favorable geochemical conditions for bone preservation (Lockley and Rice, 1990).

Taphonomic and sedimentologic characteristics of the Los Chañares tetrapod assemblage are consistent with volcanically-induced mass death followed by accumulation and eventual burial along a strandline. However, additional scenarios also were considered, including catastrophic drought (Rogers, 1990; Schwartz and Gillette, 1994), other severe weather-related events (e.g., sudden temperature drops; see Weigelt, 1989; Oliver and Graham, 1994), lethal mass wasting (Loope et al., 1999), and miring (Sander, 1992; Hungerbühler, 1998). Most alternative hypotheses effectively can be ruled-out due to the absence of diagnostic sedimentologic and taphonomic criteria. For example, mass wasting should favor the preservation of abundant articulated skeletons because, in this scenario, animals are overwhelmed and rapidly entombed within sediment gravity flows (e.g., sandslides, mudflows). An extraordinary example of this mode of mortality is provided by the Ukhaa Tolgod locality from the Upper Cretaceous of the Gobi Desert, Mongolia (Dashzeveg et al., 1995). Here, abundant articulated skeletons of a wide variety of tetrapod taxa are preserved within structureless beds of sandstone that apparently buried them alive (Loope et al., 1999). In contrast, virtually all of the tetrapods preserved in the Los Chañares assemblage show some degree of disarticulation, which indicates a period of exposure prior to final burial. Along these same lines, miring would presumably lead to the preservation of occasional subvertical limb elements and escape structures that reflect extrication efforts. None of the fossiliferous concretions in the Los Chañares assemblage exhibit either characteristic. Moreover, a vigorous struggle to gain freedom from a viscous substrate is inconsistent with the preferential orientations exhibited by skeletal elements in several concretions (Figs. 11, 12, Table 2).

Finally, Rogers et al. (1994) proposed the possibility of preservation within burrows in a preliminary taphonomic analysis of the Los Chañares tetrapod assemblage. Entombment within burrow casts has been documented for primitive South African synapsids comparable in size to *Massetognathus* (Smith, 1993), and this mode of preservation would explain the bias for small-bodied taxa that typifies the Los Chañares assemblage. The volcaniclastic sediments of the Chañares Formation also presumably would have provided an amenable substrate for the excavation and maintenance of burrows (Voorhies, 1975; Hunt, 1990). However, burrow casts, which would provide considerable support for this hypothesis, have not been identified within the Chañares Formation. Carbonate concretions in the lower lithologic unit which, on first inspection, might seem reasonable candidates, are too regular in geometry (oblate spheroids), too variable in size, and too evenly distributed to readily qualify as potential burrow casts. Moreover, the overall taphonomy of the Los Chañares assemblage generally is incompatible with preservation in burrows. Fossil-bearing concretions exhibit a two-dimensional mode of preservation suggestive of accumulation and disarticulation on flat surfaces rather than within subterranean chambers. Some of these same concretions also display evidence of preferential orientation that presumably would be difficult to generate within the confines of a burrow (but see Saunders and Dawson, 1998).

Role of Carbonate Concretions

The striking association of fossil bone and carbonate concretions at the Los Chañares locality and elsewhere in the Chañares Formation suggests that concretion formation played an important role in the overall preservation potential of Chañares tetrapods. The uncompacted condition of skeletal elements and coprolites found within concretions (Figs. 11, 12, 13) indicates that precipitation occurred shortly after material was incorporated into the sediment. Relic outlines of glass shards also suggest that concretions formed prior to the complete alteration of glassy matrix to clay (Figs. 5, 9). Precipitation presumably could have transpired in a few decades if Ca-bearing porewaters were mobile and organic matter was abundant (Allison and Pye, 1994).

Fossil-bearing concretions in the lower lithologic unit of the Chañares Formation are composed primarily of low-Mg calcite, which has replaced an original glassy matrix (Fig. 5F). Ca^{+2} presumably was derived from surrounding sediments, which have a present CaO concentration of less than 1% based on X-ray fluorescence analyses. In some concretions, it is clear that bone mineral served as a nucleation site for carbonate precipitation. In concretions that lack clear osseous cores, it is plausible that carbonate supersaturation and precipitation resulted from the microbial breakdown of non-refractory organic detritus, perhaps tetrapod soft tissues or fecal material, that created localized zones of high alkalinity (Canfield and Raiswell, 1991; Briggs et al., 1996). In contrast to the findings of Downing and Park (1998), there is no clear indication that bone hydroxyapatite contributed to the formation of concretions (Fig. 9). Bones engulfed by precipitating carbonate concretions were protected from destructive pedogenic and/or later diagenetic processes.

CONCLUSIONS

There is no better preserved or better dated (Rogers et al., 1993) sequence of fossiliferous strata that includes both dinosaur precursors (*Marasuchus, Lagerpeton, Pseudolagosuchus*) and indisputable primitive dinosaurs (*Herrerasaurus, Eoraptor, Pisanosaurus, Riojasaurus*) than the Agua de la Peña Group of northwestern Argentina. The Chañares Formation crops out at the base of the succession and includes excellently preserved examples of the above-mentioned dinosaur precursors, along with rare carnivorous cynodonts (*Probelesodon, Probainognathus*) that shed important light on the therapsid-mammal transition. With its pivotal assemblage of Middle Triassic archosaurs, cynodonts, and dicynodonts, the Chañares Formation offers an unparalleled opportunity to study tetrapod evolution leading up to the Late Triassic origination of dinosaurs and mammals. The work on the Chañares Formation presented herein suggests the following general conclusions with regard to paleoenvironment and taphonomic history.

(1) Chañares tetrapods inhabited an active rift basin that experienced synextensional effusive and explosive volcanism throughout the Middle and Late Triassic (Valencio et al., 1975; Uliana et al., 1989). The vertebrate paleofauna occupied an "upland" alluvial-to-lacustrine setting that received sedimentary detritus from surrounding highlands, in addition to copious amounts of volcanic ash. Ash-flow sheets presumably were emplaced as mass flows on subaerial alluvial surfaces and in shallow lakes, and these events of volcaniclastic sedimentation potentially would have been devastating to local tetrapod communities. Widespread lacustrine conditions were established in the basin with the deposition of the Los Rastros Formation. Exposures of the Los Rastros Formation in the vicinity of Cañon del Gualo indicate that at least six major episodes of lacustrine sedimentation occurred, five of which commenced amidst explosive volcanic activity, as evidenced by intercalated bentonite beds.

(2) The abundance of fossiliferous concretions preserved at the classic Los Chañares locality is consistent with the scenario of tetrapod mass mortality. Several taphonomic clues hint at the potential nature of the death event. The killing agent was lethal to a variety of taxa, and it killed both adults and juveniles. The event led to the concentration of carnivorous, omnivorous, and herbivorous taxa that under normal circumstances would tend not to co-occur. It also produced a counterintuitive bias against the preservation of large-bodied taxa, which may have been relatively invulnerable to the death event, or were perhaps removed from the Los Chañares death assemblage via post-mortem sorting. The spatial arrangement of skeletal material in a sample of well-preserved concretions is consistent with the stranding of tetrapod carcasses, perhaps along a shoreline, and the glassy volcaniclastic matrix that entombs most fossils is indicative of contemporaneous volcanic activity. Whether volcanism led directly to the extirpation of the local tetrapod community, or whether it simply enhanced preservation potential, remains unresolved.

(3) Early diagenetic concretions played an important role in the preservation of Chañares tetrapods. Uncompacted skeletal elements and relic diagenetically-replaced glass shards indicate that calcite precipitation took place shortly after skeletal material was incorporated into the sediment. The presence of organic matter presumably catalyzed calcite diagenesis. There is no indication that bone hydroxyapatite contributed to concretion formation. Bones entombed within early diagenetic concretions were protected from destructive pedogenic and/or later diagenetic processes, and were incorporated in exquisite quality into the vertebrate fossil record.

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3RD INTERNATIONAL LIMNOGEOLOGY CONGRESS

International Association of Limnogeologists (IAL) will be held from 29 March to 2 April, 2003, in Tucson, Arizona, USA at the Presidio Plaza Hotel. The organizing committee at the University of Arizona invites all interested participants to submit proposals for theme sessions and field trips. A first circular, describing the meeting venue and general plans for the Congress will be circulated by mailings and electronically later in 2001.

CONTACTS:

Theme session proposals should be sent to Andrew Cohen, *General Chair of the Congress.* Department of Geosciences, University of Arizona, Tucson, AZ 85721
Tel: 1-520-621-4691
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E-Mail: acohen@geo.arizona.edu

FIELD TRIP PROPOSALS:

Should be sent to David Dettman, *Field Trip Coordinator*
E-Mail: dettman@geo.arizona.edu

FURTHER INFORMATION:

Concerning housing and registration, please contact Noah Lopez.
E-Mail: noahl@u.arizona.edu