DEEP AND INTENSE BIOTURBATION IN CONTINENTAL ENVIRONMENTS: EVIDENCE FROM MIOCENE FLUVIAL DEPOSITS OF BOLIVIA

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ABSTRACT: Continental ichnofaunas display a progressive increase in bioturbation depth and intensity through the Phanerozoic. Ichnologic data from Cenozoic fluvial deposits of the Chaco Basin, Subandean zone of Bolivia, indicate widespread colonization of deep infaunal ecospace by the Miocene. Trace fossils are described from the Tariquia Formation, which records deposition in anastomosed fluvial systems. Although the Tariquia ichnofauna is of low diversity and does not display significant compositional variations throughout the succession, ichnofabric analysis reveals some degree of variability linked to different taphonomic pathways that helps to understand depositional dynamics and environmental conditions during accumulation of this fluvial unit. Intense and deep bioturbation occurs in medium- to very fine-grained crevasse sandstone and overbank mudstone. Less pervasive bioturbation is recorded in deposits of abandoned main channels. The Tariquia ichnofauna is dominated by *Taenidium barretti*, representing an example of the *Scoyenia* ichnofacies. Overbank deposits are totally bioturbated (BI = 6), showing complete destruction of the primary sedimentary fabric. Main-channel and crevasse-splay sandstones display an upward increase in degree of bioturbation. The top of the channel and crevasse-splay sandstone represents colonization surfaces that allow direct measurements of maximum burrowing depth. *Taenidium barretti* extends up to 2.2 m into the crevasse sand sheets. Depth and intensity of bioturbation of the main-channel and crevasse sands seem to be a function of time between depositional events. Main-channel and crevasse sandstones underlying thick packages of bioturbated overbank mudstones are intensely bioturbated, recording prolonged periods of low-energy sediment fallout between crevassing events. Conversely, the lowest degree of bioturbation is found in amalgamated channel sandstone units underlying thin intervals of overbank mudstones, reflecting high-frequency depositional episodes.

INTRODUCTION

Continental ichnofaunas display secular changes in bioturbation through geologic time (Miller, 1984; Buatois and Mángano, 1993, 1998; Buatois et al., 1998; Miller et al., 2002; Miller and Labandeira, 2003; Braddy, 2004). One of these changes is the increase in degree and depth of bioturbation through the Phanerozoic. In particular, it has been suggested that the increase in bioturbation migrated from fluvial and lake-margin settings to permanent subaqueous lacustrine environments through time (Buatois et al., 1998). While Paleozoic continental ichnofaunas consist mostly of superficial to very shallow trails and trackways, reflecting the activity of epifaunal and near-surface infaunal organisms, Mesozoic and Cenozoic continental ichnofaunas contain a higher abundance of deeper burrows produced by middle-tier infaunal animals. In this paper we document ichnofaunas from Cenozoic fluvial deposits of the Chaco Basin, Subandean zone of Bolivia, which indicate widespread colonization of the deep infaunal ecospace by the Miocene. Detailed descriptions and interpretations of the associated facies are provided, and an ichnofabric analysis is performed. This reveals some degree of variability in the ichnofaunas that helps to understand depositional dynamics and environmental conditions during accumulation of this fluvial unit. This is particularly relevant because careful integration of sedimentologic and ichnologic data is essential to construct more robust depositional models and to understand patterns of trace-fossil distribution in continental depositional systems.

STRATIGRAPHIC FRAMEWORK

The Chaco basin is a retroarc foreland basin located in west-central South America. It is limited to the east by the Brazilian Shield and to the west by the Subandean Zone (Fig. 1). The basin formed in response to lithospheric loading and shortening by thin-skinned fold- and thrust-belt deformation, and its sedimentary architecture was influenced by Oligocene to Recent Andean tectonics (Sempere et al., 1990). Cenozoic sedimentation in the Chaco foreland basin commenced during the Late Oligocene to Middle Miocene with the deposition of densely packed calcrete horizons of
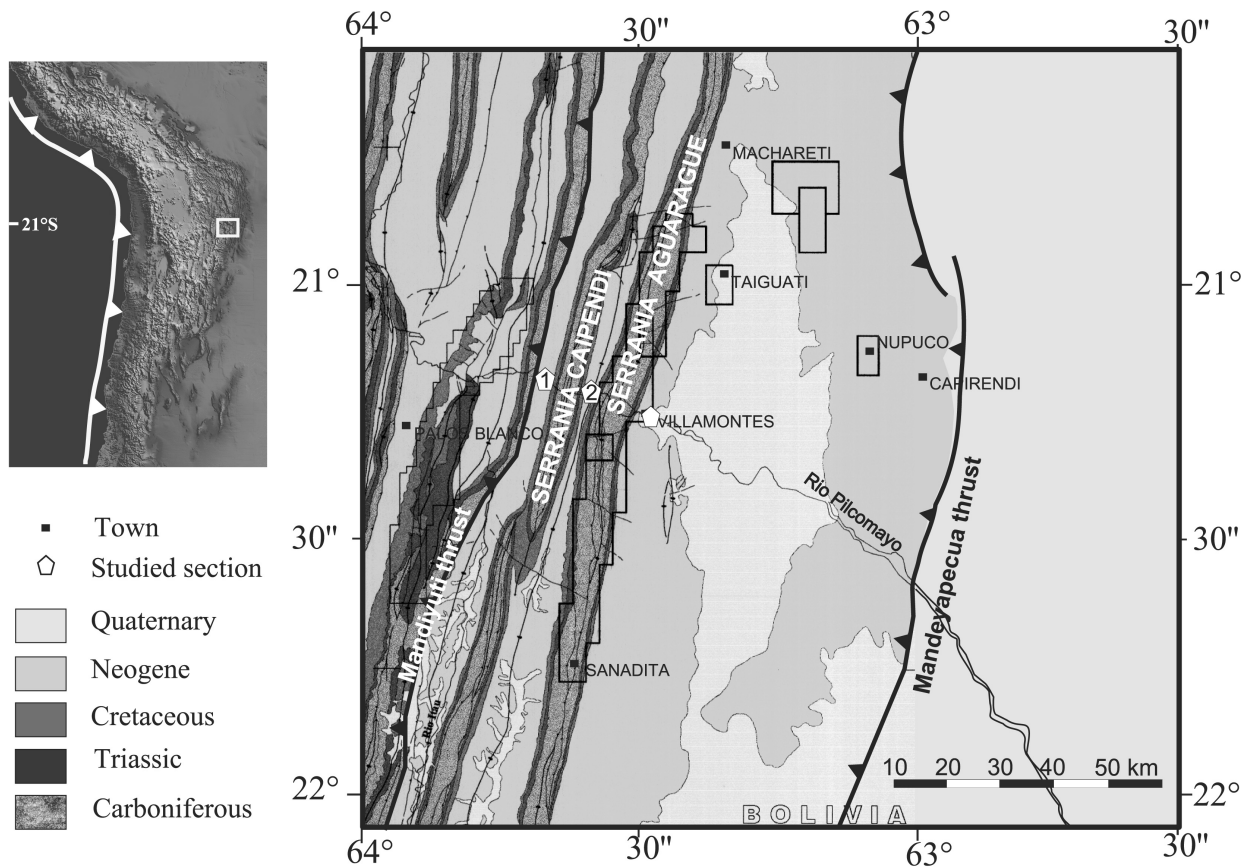
FIG. 1.—Geological map of the study area showing the major thrust faults, anticlinal and synclinal axes, petroleum industry concessions, and measured sections: 1, Zapaterimbia; 2, Puesto Salvacion.

the Petaca Formation (Gubbels et al., 1993; Sempere, 2000). The eastward-wedging Cenozoic strata are up to 7.5 km thick and are subdivided into five stratigraphic units (base to top): (1) the Petaca Formation, (2) the Yecua Formation, (3) the Tariquia Formation, (4) the Guandacay Formation, and (5) the Emborozu Formation. Figure 2 summarizes Cenozoic stratigraphy, including thickness and depositional environments of the various units.

Conformably overlying the Yecua Formation (Padula and Reyes, 1958) is the Upper Miocene Tariquia Formation (Chaco Inferior or Lower Chaco of Russo, 1959, and Ayaviri, 1964). This widespread and well-exposed unit is up to 4500 m thick and consists of fine- to medium-grained, red to brown sandstone and red to dark-red mudstone (Figs. 3, 4A). The Tariquia sediments were probably deposited in low-gradient fluvial systems in a semiarid to humid paleoclimate. Uba et al. (2004) attributed initial high accommodation and sediment supply to the onset of active basin subsidence and high denudation of the uplifted Andes during the deposition of the Tariquia successions. This paper focuses on intensely bioturbated strata of this unit that are exposed in the Zapaterimbia and Puesto Salvación localities (Fig. 3).

SEDIMENTARY FACIES ASSOCIATIONS

Three principal facies associations have been identified in the Tariquia Formation: (1) thick-bedded sandstone, (2) thin-bedded sandstone, and (3) interbedded mudstone and sandstone. Lithofacies and architectural elements follow those of Miall (1996).

Age (Ma)	Stage	Formation	Thickness (m)	Depositional environment
	Calabrian	Emborozu Fm	500 - 2000	Alluvial fan
	Gciasian			
	Piacenzian			
3.3	Zancican	Guandacay Fm	500 - 1500	Braided river
6	Messinian	Tariquia Fm	1200 - 4500	Anastomosed river
7	Tortonian	Yecua Fm	0 - 350	Shallow marine
	Serravalian			
14	Langhian	Petaca Fm	10 - 250	Braided river
	Burdigalian			
	Aquitanian			
	Chattian			
27				

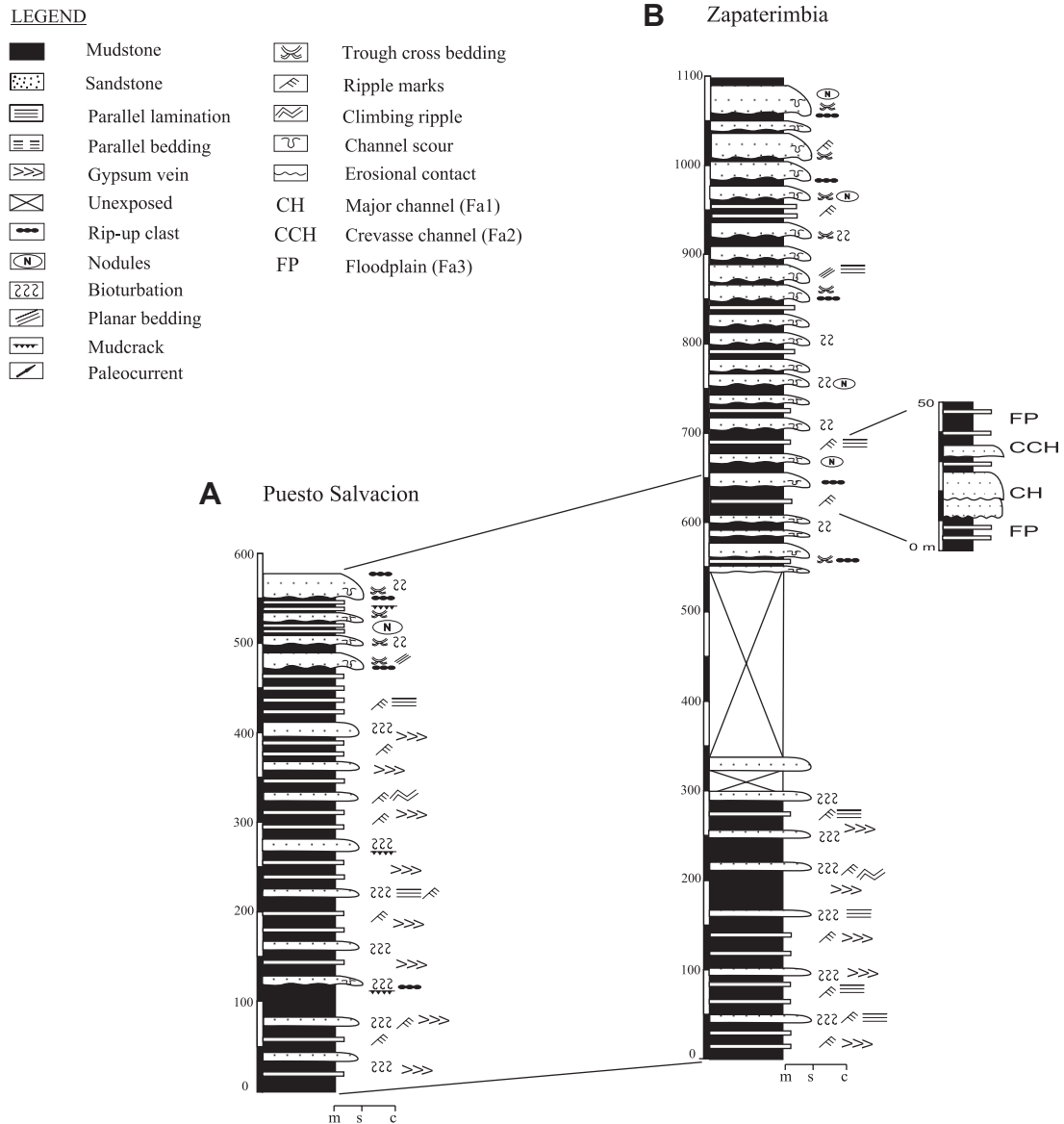FIG. 2.—Cenozoic stratigraphy of the Subandean Zone.

FIG. 3.—Sedimentologic log of the Tariquia Formation at the **A)** Zapaterimbia and **B)** Puesto Salvación sections.

FA 1. Thick-Bedded Sandstone Facies Association

Description.—

Light brown, light yellow, and light red, well sorted, medium- to very fine-grained sandstones 2 to 15 m thick characterize this facies association (Fig. 4B). They show ribbon-like geometries that may exceed 100 m width in cross section. Their bases are bounded by fifth-order sharp erosion surfaces (Miall, 1996), containing scour fills of red intraformational pebble-size mud chips (Se). The sand bodies show very subtle fining-upward tendencies, possibly due to the lack of grain-size variability. This facies association locally contains white to light brown calcareous nodules. Up-section, the sandstone exhibits increased vertically stacked and laterally continuous beds. Individual beds are 1.0 to 5.0 m thick and extend laterally for hundreds of meters. Grain size increases towards the west.

Small- to medium-scale trough cross-bedded (St), planar cross-bedded (Sp), massive (Sm), horizontally bedded (Sh), and ripple cross-laminated (Sr) lithofacies are present. Channel (CH) and sandy bedform (SB), bounded by fourth- or lower-order surfaces, are the most common architectural elements present. Limited plant fragments and trace fossils occur. Bioturbation locally disrupts the original sedimentary fabrics (ichnofabric 1). Small-scale soft-sediment deformation and a variety of dewatering structures are present locally. Paleocurrent patterns indicate a western-sourced (unimodal) drainage network. This facies association incises or grades upwards into the interbedded mudstone and sandstone facies association (FA3).

Interpretation.—

These laterally extensive and erosionally based sandstone units are interpreted as the deposits of major channels with mixed
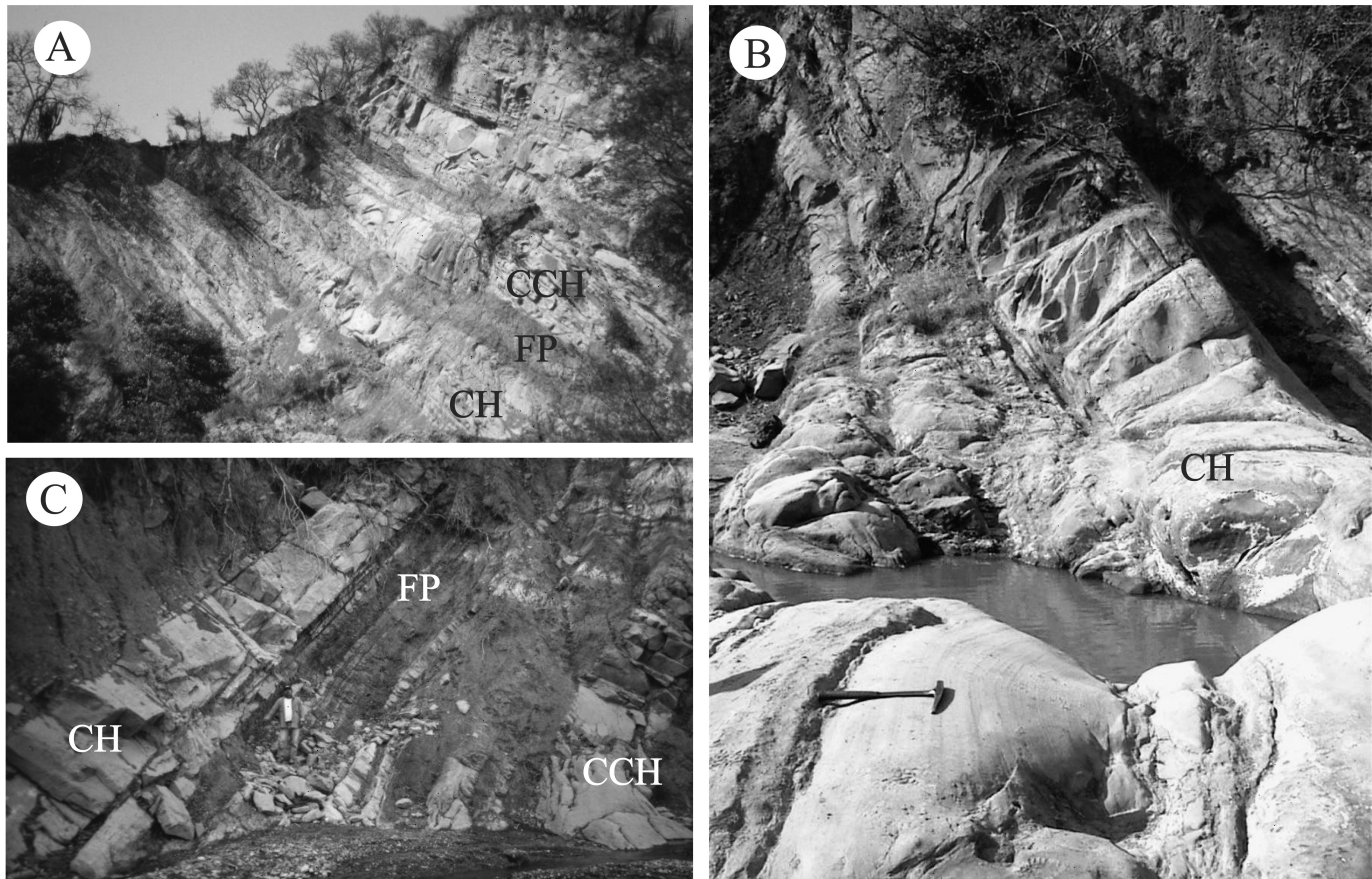
F<small>IG</small>. 4.—Outcrop photographs of the Tariquia Formation showing **A)** thick-bedded sandstones interbedded with mudstones, **B)** multistory channelized character of the thick-bedded sandstone facies association (see hammer for scale), and **C)** thick-bedded sandstone interbedded with floodplain deposits. The sandstone body on the right (arrow) is the thin-bedded sandstone facies association (FA2). The geologist is 1.78 m tall.

loads and fluctuating stream power. The relatively deep channels (CH) have low sinuosity, lateral channel migration was very limited to absent, and the floodplain was aggrading (e.g., McCarthy et al., 1997). The channel underwent scouring and bed-load transport and deposition. In addition, the dominance of vertically stacked channels and gradation of sandy bedforms (SB) into overbank deposits support the limited channel migration (e.g., Smith and Smith, 1980; Smith, 1983; Kirschbaum and McCabe, 1992; Makaske et al., 2002). This facies association is dominated by frequent crevassing and avulsion, which led to formation of new channels on the floodplain, while active channels were abandoned simultaneously (Smith, 1986; Smith et al., 1989; Makaske et al., 2002). Frequent channel abandonment, crevassing, subaerial exposure, post-flood bioturbation, and high seasonality are also indicated by the presence of mud chips, desiccation cracks, and weakly developed paleosols.

Up-section increase in vertically stacked, multistory, and channelized sandbodies indicates deposition during a period of decreasing subsidence (Ghosh, 1987; McCarthy et al., 1997). The abundant intraformational mudclasts, scour, and reactivation surfaces suggest erosion of significant amounts of mud from the overbank facies during flooding events. The ripple cross-lamination (Sr) locally found at bed tops indicates gradual waning in flow velocity and channel abandonment (Smith et al., 1989; Miall, 1996).

FA 2. Thin-Bedded Sandstone Facies Association

Description.—

This facies association consists of light brown to light yellow, well sorted, and very fine- to medium-grained sandstone (Fig. 4C), arranged in ribbon-shaped geometries. These are less than 5 m thick and extend laterally for tens of meters. Their bases have irregular, concave-up erosional and fourth-order bounding surfaces, containing pebble-size rip-up clasts (Se). The upper boundaries are mostly flat and transitional, and only occasionally sharp. The beds are massive (Sm), trough cross-bedded (St), horizontally bedded (Sh), and ripple cross-laminated (Sr). Sandy bedforms (SB) are the most common architectural element in this facies association. Fining- and coarsening-upward successions, moderate to intense bioturbation (ichnofabric 2), possible root traces, plant remains, and calcareous nodules characterize the thin sandstone bodies. Pedogenic alteration of the deposits is also common. This facies association incised into interbedded mudstone and sandstone facies.

Interpretation.—

The thin sand bodies are interpreted as the deposits of mixed-loaded, minor channels, with a fluctuating stream power, analo-

gous to crevasse channels. This interpretation is supported by the proximity to major channel sandstone bodies and concave-up channel geometry (e.g., Miall, 1996). Thickness and lateral extent of individual architectural-element groups indicate that the channels were shallow to moderately deep. The fining- and coarsening-upward trends may be a result of changes in flow velocity during deposition or gradual channel abandonment (Bristow, 1995; Miall, 1996). Facies characteristics indicate periodic reactivation, incision, and abandonment of the channel. This interpretation is supported by the upper finer sandy material, which consists mostly of climbing ripples and ripple cross-lamination. Abundant bioturbation suggests periods of channel abandonment or emergence between floods. Basal erosional surfaces are evidence for erosion and deposition by strong stream currents and reduction in deposition rate and flow velocity in subsequent floods (Deluca and Eriksson, 1989; McCarthy et al., 1997).

FA 3. Interbedded Mudstone and Sandstone Facies Association

Description.—

This facies association consists of bedsets of interbedded medium- to very fine-grained sandstone and mudstone (Fig. 4C). It is subdivided into a mudstone-dominated lower interval (more than 75% mudstone) and a sandstone-dominated upper interval (more than 70% sandstone). The red to light-brown sandstone forms units 0.5–3 m thick, having sheet and, more rarely, lenticular geometry. The sheet sandstones can be traced laterally for several hundreds of meters. These fine- to medium-grained sand sheets show fining- and coarsening-upward successions. The architectural-element groups consist mostly of massive (Sm), laminated (Sl), and ripple cross-laminated (Sr) units. The architectural elements are laminated sand sheets (LS) and sandy bedform (SB).

The laterally extensive mudstones are mostly red to dark brown and up to 10 m thick, and contain abundant micas. The common lithofacies in these fine-grained deposits are laminated mudstones (Fl) and massive mudstones (Fm). Rare, poorly developed nodular and patchy-colored deposits only show weakly developed paleosol horizons. Intense bioturbation (ichnofabrics 2 and 3), desiccation cracks (Fig. 5), and calcareous and rare ferruginous nodules occur in the sandstone and mudstone beds.
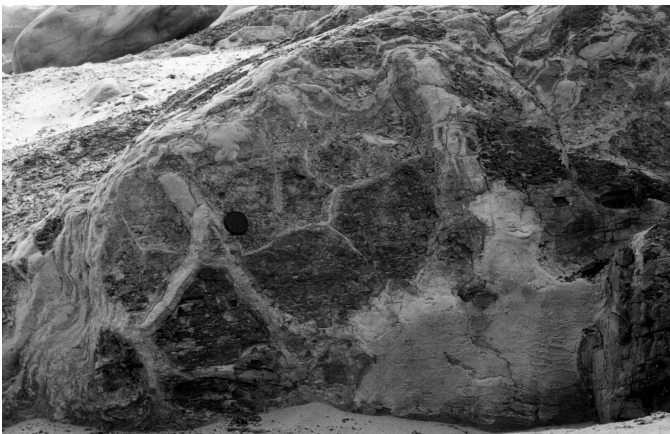

Fig. 5.—Desiccation cracks preserved at the base of a sandstone bed overlying floodplain mudstones. Puesto Salvación. Lens cap is 5.5 cm.

A high degree of disruption of the sedimentary structures by bioturbation is common in the sandstone beds, and total homogenization of the primary fabric occurs in the mudstone units.

Interpretation.—

This facies association is interpreted as mud-dominated overbank and floodplain deposits that accumulated in standing waters or waning streams, which were punctuated by frequent sand deposition as sheet floods through crevasse splays. The sand bodies with a lenticular shape are interpreted as crevasse-splay and levee deposits, on the basis of their proximity to major channels and occasional coarsening-upward trends (e.g., Smith et al., 1989; Bridge, 1993; Ferrell, 2001). They are probably distal-splay deposits because of the presence of SB elements and flat surfaces, which could be due to waning flow energy away from the channels (Miall, 1996). The upward-coarsening and -thickening trends suggest phases of crevasse-lobe migration into the floodplain (Ferrell, 2001) or a progressive change in location of the main channel (Bridge, 1993). The fining-upward successions imply abandonment of crevasse splays (Ghosh, 1987). Laminated mudstones (Fl) suggest suspended-load deposition and fallout from low-velocity flood. The occasional massive mudstone (Fm) was probably due to postdepositional sediment disruption by bioturbation and pedogenic processes, which is supported by the abundance of trace fossils and calcareous nodules. The red to dark brown colors of the mudstone suggest deposition in well-drained floodplains under oxidizing conditions (e.g., Mack and James, 1992; Retallack, 1997; Mack et al., 2003). The abundance of desiccation cracks, trace fossils, calcareous nodules, and iron oxide suggest periods of substantial aerial exposure in a seasonally wet/dry semiarid environment.

DEPOSITIONAL MODEL

Architectural elements and lithofacies associations suggest deposition on a rapidly aggrading floodplain, which was dissected by a network of low-gradient, well-defined channel networks separated by ponded areas. Accordingly, the Tariquia Formation is interpreted as the product of a highly sediment-loaded, anastomosed fluvial system (cf. Smith and Smith, 1980; Rust, 1981; Smith, 1986; Makaske et al., 2002; Bridge, 2003). This interpretation is further supported by a high degree of channel interconnection and a lack of limited lateral channel migration. The coarsening-upward sandstone bodies imply progradation of crevasse splays or levees onto the flood-basin areas over several flooding events. The Tariquia anastomosed rivers were long-lived, highly dynamic fluvial systems, with frequent avulsion and channel abandonment. The Tariquia anastomosed setting is comparable to the modern anastomosed rivers in the Columbia River of Canada (Makaske, 2001; Makaske et al., 2002), and the Copper Creek and the Marshall River of Australia (Rust, 1981; Tooth and Nanson, 1999, 2004).

Crevassing is an important process to compensate for channel aggradation (Smith et al., 1989). The lack of lateral channel migration points to channel stability, vertical aggradation, and probably straight courses of the channels (Rust, 1981; Schumm et al., 1996; Ferrell, 2001). The channel stability of the Tariquia anastomosed system might have resulted from fine sediment texture and protective vegetation (Rust, 1981; Tooth and Nanson, 2004). Brierley et al. (1993) attributed crevassing, avulsion, and pervasive oxidation to paucity of bank-stabilizing vegetation.

The semiarid paleoclimate is suggested by the abundance of desiccation cracks, mud chips, and red coloring (e.g., Stear, 1985), and high and fluctuating depositional rates are indicated by

sharp erosional bases, dewatering structures, and climbing ripples (e.g., Deluca and Eriksson, 1989). The contrast in color between the thin and thick sandstone units and interbedded mudstone and sandstone bodies suggests that coloring was probably formed during or after deposition, due to oxidation of organic matter and dehydration of ferric oxyhydroxides (Besly and Turner, 1983). The weakly developed paleosols point to a high rate of sedimentation and a high rate of floodplain aggradation (Kraus, 1996, 2002). Kraus (2002) showed that when avulsion frequency increases more than accumulation rate, an increase in sedimentation rate produces greater channel connectivity among sandstone bodies and a decrease in the fine-grained sandstone deposits.

Sediment supply increases up-section throughout the deposition of the Tariquia Formation. This interpretation is supported by substantial up-section thickness variations, decrease of reactivation surfaces, and condensed intervals. The percentage of channel sandstones increases westward in response to asymmetrical basin subsidence. In addition, up-section increase in channel size and low percentage of overbank deposits, coupled with increasing channel erosion, suggest initial rapid subsidence followed by subsequent reduced subsidence (Allen, 1978; Clemente and Pérez-Arlucea, 1993). This process probably led to the gradual increase in valley slope and flow competence, and promoted the accumulation of thick sandstone deposits in the upper Tariquia Formation. This asymmetric increase in basin subsidence created high accommodation space for the Tariquia strata (up to 4500 m thick). The variation in accommodation is reflected in the initial single-channel morphology and mudstone-dominated intervals of the lower Tariquia Formation, where the subsidence rate was relatively high in contrast to low avulsion. At this point, the slope of the valley decreases, favoring the deposition of fine-grained sediments (e.g., Smith and Smith, 1980; Blair, 1988). Densely interconnected channels and low overbank deposits in the upper Tariquia Formation indicate low subsidence and high avulsion. These reflect the adjustment of the fluvial system to increased valley gradient and decreased accommodation space (Schumm, 1993). There is consensus among fluvial sedimentologists (e.g., Rust, 1981; Smith, 1986) that avulsion and aggradation are probably caused by tectonic subsidence.

Frequent avulsion, crevassing, and channel abandonment in the Tariquia Formation point to multiple Subandean erosion pulses (Kley et al., 1997), which shed large amounts of siliciclastic sediment into the Chaco foreland basin during the Late Miocene. Paleoflow directions measured in the Tariquia strata show northeast-to-southeast dispersion patterns, thereby indicating a western source. The Tariquia anastomosed streams represent a distal foreland fluvial system that deposited Andes-derived sediments into the Chaco foreland basin (Uba et al., 2004).

DESCRIPTION AND COMPOSITION OF THE TARIQUIA ICHNOFAUNA

Trace fossils occur in medium- to very fine-grained sandstone and mudstone that are included in the three facies associations previously described. The Tariquia ichnofauna is of low diversity and dominated by monospecific assemblages of *Taenidium barretti*. Possible root trace fossils (Fig. 6F) have been observed in the Puesto Salvación section.

Taenidium barretti (Bradshaw, 1981)

Taenidium is distinguished from *Scoyenia* by the absence of wall striations and lining (D'Alessandro and Bromley, 1987). As noted by D'Alessandro and Bromley (1987) and Keighley and Pickerill (1994), the ichnogenus *Ancorichnus* has a structured

peripheral mantle surrounding the meniscate core and clearly differs from *Taenidium*. According to Keighley and Pickerill (1994), absence of a lining distinguishes *Taenidium* from the related ichnogenus *Beaconites*. However, the presence of a wall in *Beaconites* has been questioned by other authors (e.g., Goldring and Pollard, 1995, 1996; Morrissey and Braddy, 2004). The ichnogenus *Beaconites* was established by Vialov (1962), but trace-fossil material was not collected. Goldring and Pollard (1995, 1996) revised material from the type locality and noted that no lining is present. However, their view was questioned by Keighley and Pickerill (1996), who criticized the use of topotype material. Further complications result from the fact that the type material of *Taenidium* is lost, and at its type locality no true specimens of *Taenidium* have subsequently been found. However, *Nereites* specimens having the typical *Scalarituba* preservation with meniscate structure are common at that locality, which raises additional doubts about the taxonomic status of *Taenidium* (Bromley, written communication, 2004). The name *Taenidium* is provisionally adopted here, pending a comprehensive review of meniscate trace fossils. In particular, *Taenidium barretti* is characterized by its hemispherical and deeply arcuate menisci, which are tightly packed or stacked, forming a non-compartimentalized backfill of thin meniscate segments (Keighley and Pickerill, 1994). Two different forms of meniscate backfilled trace fossils have been recognized in the Tariquia Formation.

Taenidium barretti large form (Fig. 6A, B).—

This form consists of endichnial, horizontal, inclined to vertical meniscate trace fossils. The meniscate backfill comprises homogeneous, non-compartmentalized menisci, each meniscus consisting of very fine-grained sand. Small, elongated pellets oriented parallel to the menisci are present locally. In some cases, the meniscate backfill is not apparent and the fill appears structureless. A lining is absent. Specimens are straight to very rarely slightly curved and remain level with bedding planes. In transverse section, this form comprises circular to semicircular impressions. Overlap among specimens is rare. Trace width is 30.0–55.7 mm, and the maximum length observed on bedding planes is 235.0 mm. In cross section, meniscate trace fossils up to 0.5 m deep beneath the colonization or erosion surface have been observed. *Taenidium barretti* large form is present only in the Zapaterimbia section. The Zapaterimbia specimens are very similar to those illustrated from the Carboniferous of New Brunswick (Canada) by Keighley and Pickerill (1994, 1997) and from the Lower Devonian of Wales by Morrissey and Braddy (2004).

Taenidium barretti small form (Fig. 6C–E).—

This form consists of trace fossils with a morphology similar to that of the large form but of smaller size. The meniscate backfill is preserved as sediment segments of very fine-grained sand and silt, forming arcuate to curved menisci. Locally, the meniscate backfill is not apparent and the fill appears structureless. A lining is absent, but red to pink diagenetic haloes are present locally, particularly in intensely bioturbated intervals. Specimens are commonly straight or, more rarely, curved. Secondary successive branching may occur. Specimens remain level with the bedding plane or form weathered-out hollows. Overlap among different specimens is very common. Some specimens coalesce to form aggregates. Trace width is 2.0–8.5 mm. Maximum length observed on a single bedding plane is 95.5 mm. In cross section, meniscate trace fossils up to 2.2 m deep have been observed. *Taenidium barretti* small form occurs in both the Zapaterimbia and Puesto Salvación sections.
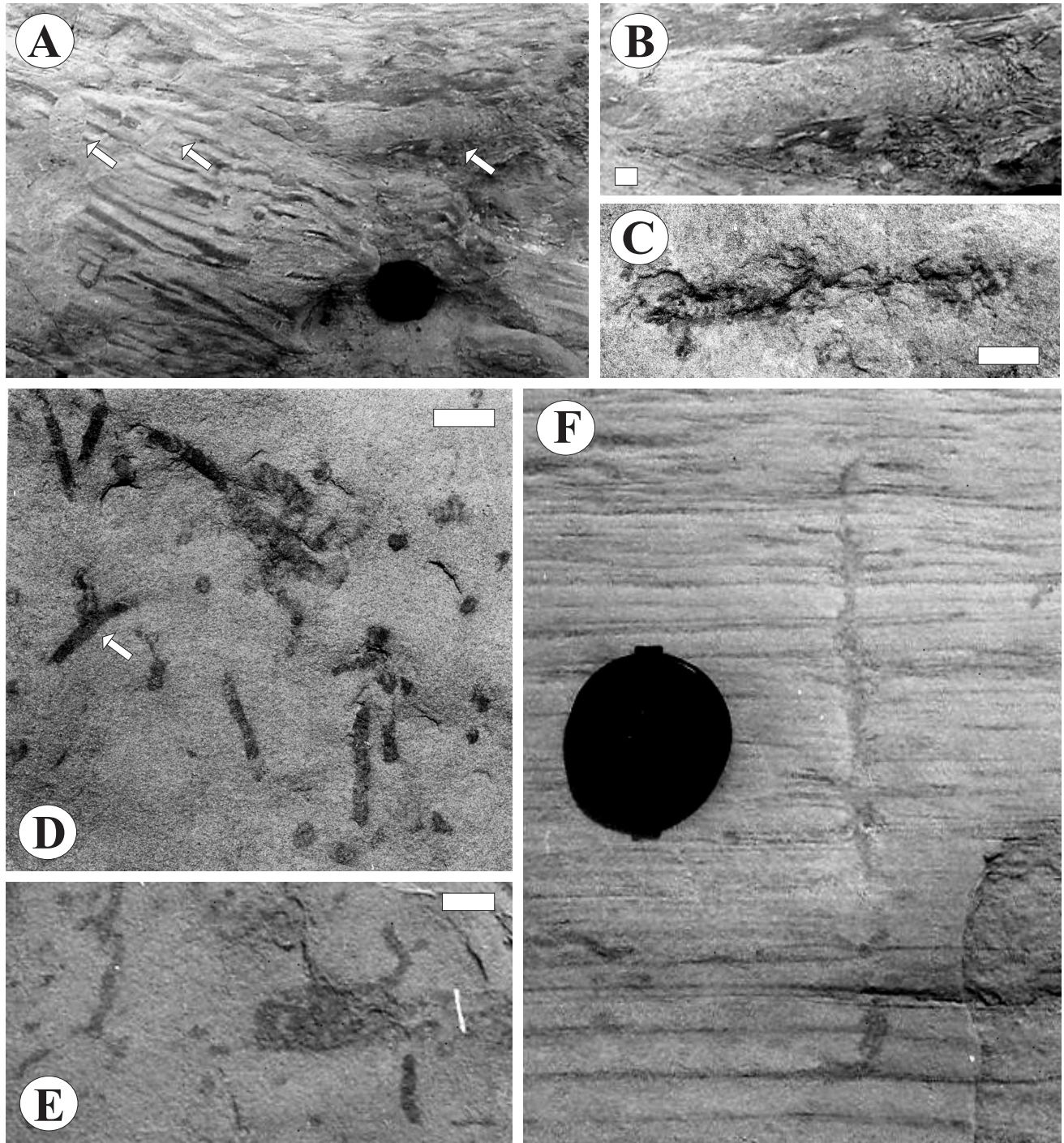
FIG. 6.—The Tariquia Formation ichnofauna. **A)** General view of a channel bed containing several specimens of *Taenidium barretti* large form (arrows) from Zapaterimbia. Note the circular cross section of one specimen. Lens cap is 5.5 cm. **B)** Close-up of specimen arrowed in Part A. Note the pelletoidal fill. Scale bar is 1 cm. **C)** *Taenidium barretti* small form from Zapaterimbia. Scale bar is 1 cm. **D)** General view of channel deposits containing several specimens of *Taenidium barretti* small form. Note secondary successive branching in one of the specimens (arrow) from Puesto Salvación. Scale bar is 1 cm. **E)** Coalescing *Taenidium barretti* small form. Scale bar is 1 cm. **F).** Possible root trace fossil from Puesto Salvación. Lens cap is 5.5 cm.

The meniscate structure of *Taenidium* is thought to result from sediment backfilling during excretion (D'Alessandro and Bromley, 1987; Keighley and Pickerill, 1994; Schlirf, 2000). Meniscate burrows most likely reflect the activity of vagile organisms moving into the substrate in search for food, revealing a combination of bypassing and ingestion. *Taenidium barretti* is a typical component of continental ichnofaunas (Keighley and Pickerill, 1994).

ICHNOFACIES

The Tariquia ichnofauna records an example of the *Scoyenia* ichnofacies. The *Scoyenia* ichnofacies was originally defined by Seilacher (1963, 1967), and subsequently was redefined by Frey et al. (1984) and Buatois and Mángano (1995). It is characterized by: (1) horizontal meniscate backfilled traces produced by mobile deposit feeders, (2) locomotion traces, including both trackways and trails, (3) vertical domiciles, (4) a mixture of invertebrate (mostly arthropod), vertebrate and plant traces, (5) low to moderate ichnodiversity, and (6) localized high abundance. Typical ichnotaxa include meniscate trace fossils (e.g., *Scoyenia, Beaconites, Taenidium*), arthropod trackways (e.g., *Umfolozia, Merostomichnites, Diplichnites, Stiaria, Hexapodichnus, Permichnium, Acripes*), bilobate locomotion (*Cruziana*) and resting (*Rusophycus*) structures, simple traces (e.g., *Planolites, Palaeophycus*), sinuous crawling traces (*Cochlichnus*), banana-shaped traces (*Fuersichnus*), and vertical burrows (e.g., *Skolithos, Macanopsis, Cylindricum, Camborygma*). Vertebrate tracks may be abundant locally (e.g., Gand and Haubold, 1984; Aramayo and Manera de Bianco, 1987a, 1987b, 1996; Lockley, 1991; Fuglewicz et al., 1996; Ptaszyński and Niedźwiedzki, 2004).

As noted by Frey et al. (1984), the *Scoyenia* ichnofacies is commonly represented by low-diversity ichnocoenoses of meniscate trace fossils, a situation illustrated here by the Tariquia ichnofauna. The *Scoyenia* ichnofacies commonly contains physical sedimentary structures indicative of periodic subaerial exposure and typifies low-energy deposits periodically exposed to air or periodically inundated, and intermediate between aquatic and nonaquatic environments (Frey and Pemberton, 1984, 1987). In fluvial systems, this ichnofacies is present in abandoned channels and overbank deposits, encompassing a wide variety of subenvironments, such as ponds, levees, and crevasse splays (Frey et al., 1984; Frey and Pemberton, 1984, 1987; Buatois and Mángano, 1995, 2002, 2004).

The importance of substrate consolidation in the *Scoyenia* ichnofacies has been emphasized in more recent studies (Bromley, 1996; Buatois et al., 1996; Savrda et al., 2000; Buatois and Mángano, 2002, 2004; Uchman et al., 2004). The *Scoyenia* ichnofacies can be subdivided into two distinct suites: one characterized by meniscate, backfilled structures without ornamentation (e.g., *Taenidium, Beaconites*) developed in a soft substrate and the second typified by striated traces (e.g., *Scoyenia gracilis, Spongeliomorpha carlsbergi*), crosscutting the former and developed in a firm substrate (Buatois and Mángano, 2002). Many examples of the *Scoyenia* ichnofacies, therefore, form palimpsest surfaces or composite ichnofabrics that reflect progressive desiccation of sediment. In the present case, no striations have been detected in the meniscate trace fossils (*Taenidium barretti*), suggesting emplacement in a relatively wet, soft substrate. Interestingly, sedimentologic evidence (e.g., desiccation cracks, red coloration) indicates widespread desiccation under semiarid conditions. The Tariquia ichnofauna may indicate preferential colonization of wet substrates as a way to avoid harsh conditions (i.e., desiccation) in a fluvial system developed under semiarid conditions (cf. MacNaughton and Pickerill, 1995). Deep bioturbation may in part reflect avoidance of stressful conditions caused by pervasive desiccation. For example, Morrissey and Braddy (2004) suggested that the *Beaconites* producer, most likely a myriapod, burrowed to the water table in search of moisture during the dry season. Absence of ichnofaunas emplaced subaqueously in freshwater ponds (i.e., depauperate *Mermia* ichnofacies) is also suggestive of semiarid conditions (Buatois and Mángano, 2004) during deposition of the Tariquia Formation.

ICHNOFABRICS

Although the Tariquia ichnofauna is of low diversity and does not display significant compositional variations throughout the succession, ichnofabric analysis reveals some degree of variability that helps to understand depositional dynamics and environmental conditions during accumulation of this fluvial unit. This variability is mostly linked to different taphonomic pathways leading to ichnofabric preservation. Three different *Taenidium* ichnofabrics, essentially characterized by contrasting bioturbation intensities and depths (Fig. 7A–C), can be distinguished in the Tariquia Formation. Bioturbation index (BI) is expressed following the scheme by Taylor and Goldring (1993).

ICHNOFABRIC 1
(MAJOR CHANNELS)

ICHNOFABRIC 2
(CREVASSE SPLAYS)
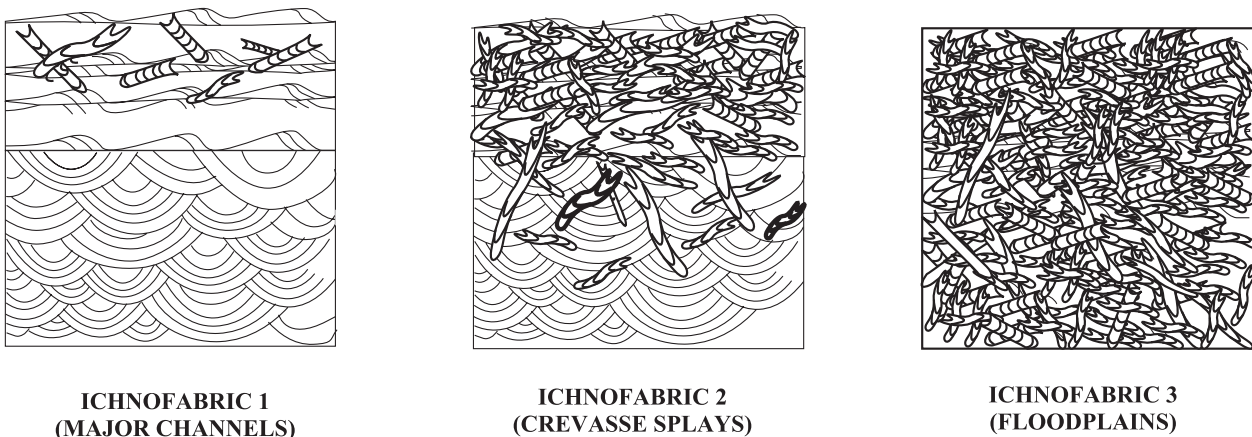
ICHNOFABRIC 3
(FLOODPLAINS)

FIG. 7.—Schematic reconstructions of fluvial ichnofabrics from the Tariquia Formation. Ichnofabric 1. This ichnofabric is characterized by a low degree of bioturbation and occurs in Facies Association 1 (thick-bedded sandstone), major-anastomosed-channel sandstones. Ichnofabric 2. This ichnofabric is characterized by moderate to high bioturbation intensities and occurs in sandstone units of Facies Association 2 (thin-bedded sandstone) and 3 (interbedded mudstone and sandstone), crevasse-splay sandstones. Ichnofabric 3. This ichnofabric is characterized by intense bioturbation and is present in mudstone units included in Facies Association 3 (interbedded mudstone and sandstone), floodplain mudstones.

Ichnofabric 1

Ichnofabric 1 is characterized by a low degree of bioturbation and occurs in facies association 1 (thick-bedded sandstone) (Fig. 7A). These deposits record sedimentation in major anastomosed channels. Bioturbation is absent in the thickest sandstone units of facies association 1, being restricted to the thinnest-bedded end member of this facies association (Fig. 8A, B). Bioturbation is less pervasive in facies association 1 than in facies associations 2 and 3. BI ranges from 0 to 1 at the lower interval of sandstone units to 3–4 at the upper interval, displaying an upward increase in bioturbation in these channel sandstones. The top of the anastomosed-channel sandstone represents colonization surfaces that allow direct measurements of maximum burrowing depth. Maximum bioturbation depth is 85 cm. Trace-fossil overlap is very rare, occurring only locally and towards the top of the sandstone unit.

Ichnofabric 2

Ichnofabric 2 is characterized by moderate to high bioturbation intensities and occurs in sandstone units of facies associations 2 (thin-bedded sandstone) and 3 (interbedded mudstone and sandstone) (Fig. 7B). This association represents deposition in crevasse-splay channels characterized by fluctuating stream flow, periodic reactivation, incision, and abandonment. Crevasse-splay sandstones display an upward increase in degree of bioturbation, ranging from BI 0–1 at the lower interval of sandstone units
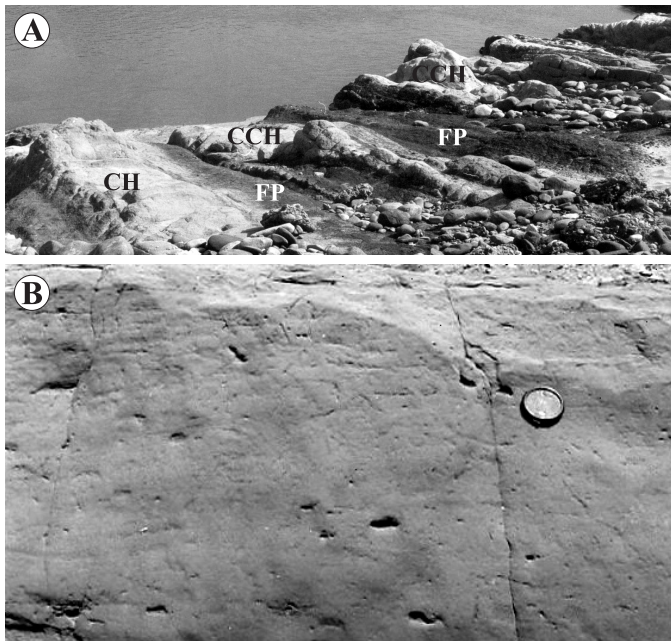

FIG. 8.—Facies associations and ichnofabrics at Puesto Salvación. **A)** General view of facies associations forming a fining-upward succession. CH = major channel (Facies Association 1). CCH = crevasse channel (Facies Association 2). FP = floodplain (Facies Association 3). Bioturbation is restricted to the uppermost part of the channelized sandstone bodies and is pervasive in the associated floodplain deposits. Outcrop width = 9 m. **B)** Top of a major channel deposit. Note the sparse bioturbation represented by scarce *Taenidium barretti* small form. Lens cap is 5.5 cm.
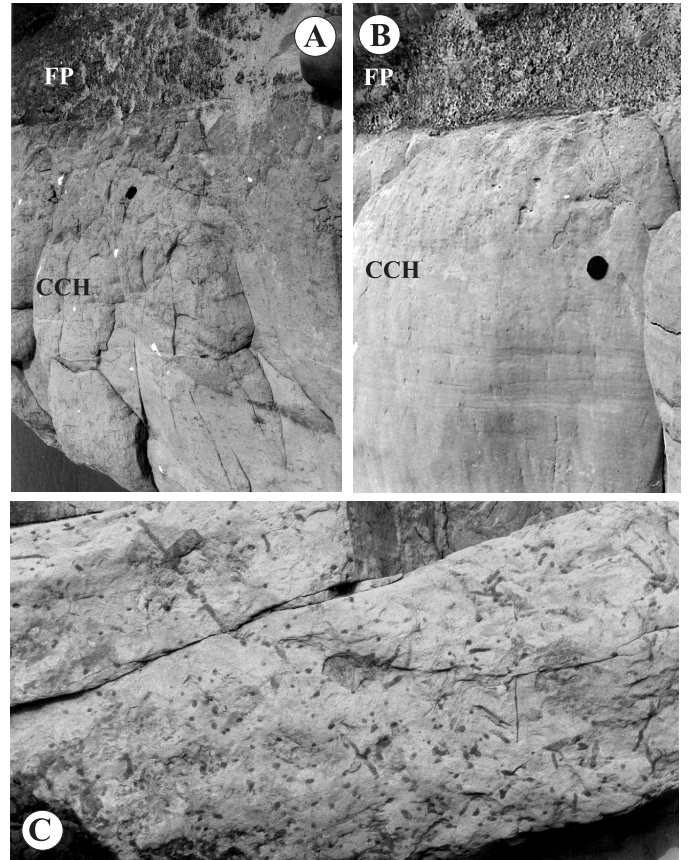

FIG. 9.—Examples of ichnofabrics 2 (crevasse channels) and 3 (floodplains) at Puesto Salvación. CCH = crevasse channel. FP = floodplain. Lens cap is 5.5 cm. **A)** General view of a crevasse channel sandstone that passes upwards into intensely bioturbated floodplain mudstone. Note upward increase in degree of bioturbation in crevasse-splay deposit. **B)** General view of a crevasse-channel sandstone and overlying totally bioturbated floodplain mudstone. Horizontal bedding is preserved only in the lower zone of the deposit. **C)** Close-up of top of a crevasse sandstone bed with overlapping specimens of *Taenidium barretti* small form.

to BI 4–5 at the upper interval of crevasse sheets (Fig. 9A, B). Specimens of *Taenidium barretti* commonly display overlap at the upper interval of the crevasse deposits (Fig. 9C). Preservation of physical sedimentary structures in crevasse sandstones is a direct function of bioturbation, with cross bedding and horizontal bedding preserved only in the lower, sparsely bioturbated zone of the deposit (Fig. 9B). As in the case of ichnofabric 1 from anastomosed-channel sandstones, the top of the crevasse-splay sandstone in ichnofabric 2 represents colonization surfaces, allowing precise estimation of maximum burrowing depth. Deep, vertical specimens of *Taenidium barretti* are relatively common (Fig. 10A) and extend for up to 2.2 m into the crevasse sand sheets.

Ichnofabric 3

Ichnofabric 3 displays intense bioturbation and is characteristic of mudstone units in facies association 3 (interbedded mudstone and sandstone) (Fig. 7C). These mudstone units record overbank deposition, representing the lower-energy correlatives

of the sandy crevasse channel fills during flooding events. Overbank deposits are totally bioturbated (BI = 6), showing complete destruction of the primary sedimentary fabric (Figs. 9A, B). Discrete specimens of *Taenidium barretti* are commonly difficult to recognize due to total homogenization of the sediment. The most common expression of this ichnofabric is a mottled texture reflected by red to pink haloes (Fig. 10B).

Fluvial channels are characterized by high to moderate energy, rapid fluctuations in rates of sedimentation and erosion, and coarser grain sizes than those typically deposited in adjacent environments. In the Tariquia Formation, depth and degree of bioturbation of both main-channel and crevasse sands seem to be a function of time between depositional events (Fig. 11). Thick packages of strongly erosional, amalgamated, main-channel sandstones included in facies association 1 are nonbioturbated. A low degree of bioturbation and shallow penetration characterize thinner sandstone units of facies association 1 (ichnofabric 1). These channel sandstone units may be amalgamated or more commonly occur below thin intervals of overbank mudstones, reflecting a high frequency of depositional episodes. Crevasse sandstones (facies associations 2 and 3) underlying thick packages of overbank mudstones are intensely bioturbated, recording prolonged periods of low-energy sediment fallout between crevassing events (ichnofabric 2). Ichnofabrics 1 and 2 reflect colonization of sandstone deposits after channel diversion ("abandonment") or, more rarely, during periods of low discharge virtually characterized by nondeposition ("inactive"). Finally, lower rates of sediment accumulation and lower-energy conditions that characterize overbank mudstones of facies association 3 were conducive to total sediment reworking by the *Taenidium barretti* producers (ichnofabric 3). The three ichnofabrics can be arranged according to their position with respect to the main channel, revealing proximal–distal trends (Fig. 12).

In a recent review, Buatois and Mángano (2004) compared the ichnology of active and abandoned fluvial channels and introduced the concept of taphonomic pathways. While the ichnofauna from active fluvial channels is characterized by low-diversity, typically monospecific suites of simple vertical burrows and escape traces, that of abandoned-channel or inactive-channel deposits is characterized by low-diversity assemblages dominated by meniscate trace fossils. The Tariquia ichnofabrics 1 and 2 correspond with this latter category of ichnofaunas. Similar ichnofaunas from abandoned channels have been documented elsewhere (e.g., Allen and Williams, 1981; Graham and Pollard, 1982; Bamford et al., 1986; Sarkar and Chaudhuri, 1992; Miller and Collinson, 1994; Goldring and Pollard, 1995; Miller, 2000; Morrissey and Braddy, 2004). Buatois and Mángano (2004) also noted that the composition of abandoned-channel ichnofaunas is similar to those from overbank deposits because abandoned channels lead to the formation of ponded areas, representing a process of floodplain construction. This view is supported by the Tariquia ichnofabric 3, which records bioturbation in floodplain settings and does not display any significant variation in taxonomic composition with respect to their channelized equivalents.

EVOLUTIONARY PALEOECOLOGY

Continental ichnofaunas display an overall increase in extent and depth of bioturbation through the Phanerozoic (Buatois et al., 1998; Miller et al., 2002; Miller and Labandeira, 2003). Comparative analysis of continental ichnofaunas in space and time suggests that bioturbation depth and intensity increased progressively through time, from fluvial and lake-margin settings to permanent subaqueous lacustrine environments (Buatois et al., 1998). This increase in depth and intensity of bioturbation strongly influenced the nature of the stratigraphic record of continental environments, producing increasing disturbance of primary sedimentary fabrics.

Paleozoic ichnofabrics are mostly simple and possess low bioturbation indices. Because surface and very shallow trails and trackways are dominant, primary fabric is commonly distinct and undisrupted. This is particularly true for Silurian to Carboniferous lacustrine and transitional alluvial–lacustrine deposits (e.g., Pollard et al., 1982; Walker, 1985; Pickerill, 1992; Buatois and Mángano, 1993). However, more intense bioturbation has been recorded in coeval fluvial deposits. In particular, large meniscate trace fossils, currently referred to in the literature indistinctly as *Beaconites* or *Taenidium*, are common in Paleozoic alluvial deposits, particularly fluvial-channel and overbank facies (e.g., Gevers et al., 1971; Allen and Williams, 1981; Bradshaw, 1981; Gevers and Twomey, 1982; Graham and Pollard, 1982; Bruck et al., 1985; Bamford et al., 1986; Gordon, 1988; Keighley and Pickerill, 1997; Draganits et al., 2001; Morrissey and Braddy, 2004). Maximum bioturbation depth recorded is 1.44 m (Lance Morrissey, written communication, 2004). Ichnodiversity is generally low, and in most cases this meniscate ichnotaxon is the only form present in these fluvial deposits. Although the ichnospecies *Taenidium* (*Beaconites*) *barretti* is present in Mesozoic–Cenozoic continental strata, large specimens (up to 250 mm wide) seem to be typical of Silurian to Carboniferous rocks (Keighley and Pickerill, 1994). On the basis of their recurrent association with large *Diplichnites* and their similar size range, Morrissey and Braddy (2004) argued convincingly for a myriapod (e.g., arthropleurid) producer for these large meniscate trace fossils.

Smaller meniscate backfilled trace fossils are relatively common in Permian, Mesozoic, and Paleogene floodplain and marginal lacustrine deposits. These meniscate structures seemed to have been restricted to shallow and middle tiers. Deep bioturbation was the result of crayfish burrowing during the Triassic, as suggested by the presence of crayfish galleries up to 1 m deep in floodplain and lake-margin deposits (Hasiotis et al., 1993). In-
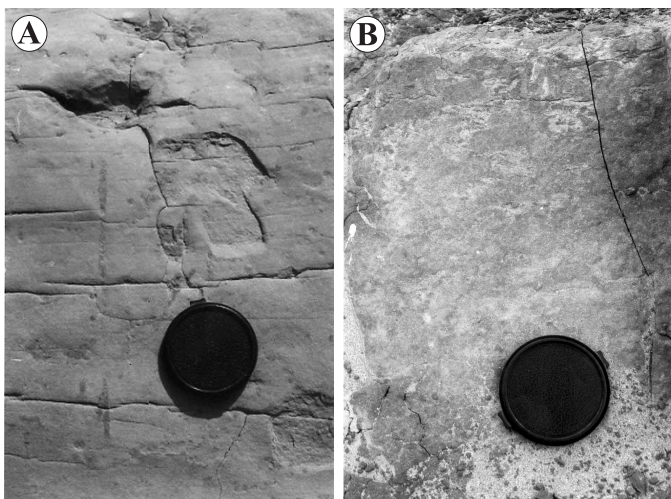

Fig. 10.—Contrasting bioturbation styles. **A)** Deep vertical *Taenidium barretti* in crevasse-splay sandstone. **B)** Floodplain deposit characterized by a mottled texture. Note abundant alteration haloes in these totally bioturbated deposits. Lens cap is 5.5 cm.
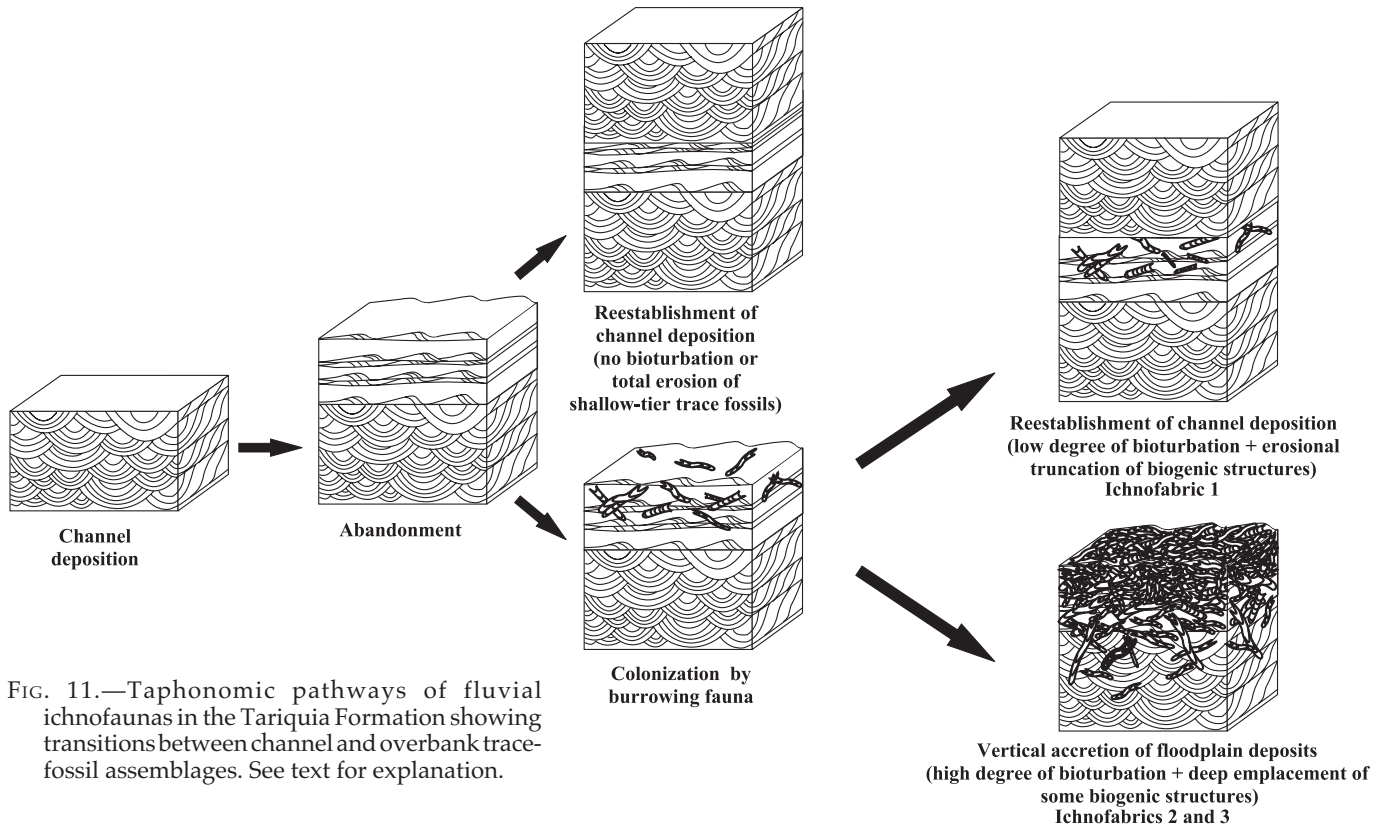
Fɪɢ. 11.—Taphonomic pathways of fluvial ichnofaunas in the Tariquia Formation showing transitions between channel and overbank trace-fossil assemblages. See text for explanation.
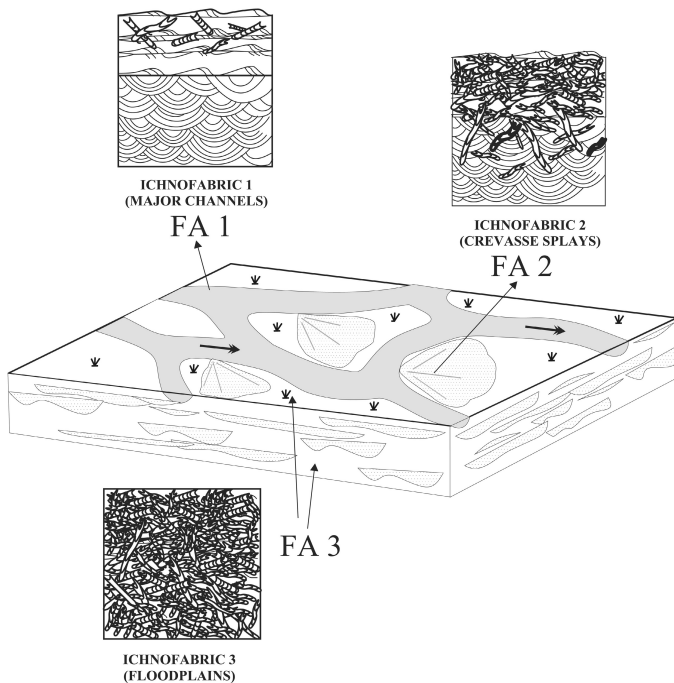

Fɪɢ. 12.—Ichnofabric distribution and depositional model of the Tariquia Formation.

tense bioturbation has been also documented in Jurassic continental deposits (Hasiotis, 2004), although the identity of the producers is still uncertain. In any case, meniscate trace fossils seem to have occupied a middle-tier position during the Mesozoic and most of the Cenozoic.

The Tariquia ichnofauna records bioturbation depths that suggest extensive colonization of the deep infaunal ecospace in continental environments by the Miocene. The maximum bioturbation depth recorded is 2.2 m. This indicates that the producers of backfilled burrows were able to reoccupy deep tiers in the same way as arthropleurids during the Paleozoic. A similar situation has been noted in Pleistocene floodplain deposits, where backfilled, meniscate *Taenidium* penetrates up to 2.5 m into the substrate (D'Alessandro et al., 1993). In the Pleistocene example, however, the *Taenidium* (probably produced by cicada nymphs; Bromley, written communication, 2006) is tightly clustered around large vertical roots. The establishment of deep meniscate backfilled trace fossils in overbank and abandoned-channel deposits led to a significant increase in bedding disruption.

CONCLUSIONS

1. Ichnologic data from fluvial deposits of the Tariquia Formation of the Chaco Basin, in Bolivia, indicates widespread colonization of the deep infaunal ecospace by the Miocene. Intense and deep bioturbation is recorded in medium- to very fine-grained crevasse sandstone and overbank mudstone that accumulated in anastomosed fluvial systems.

2. Three *Taenidium barretti* ichnofabrics have been recognized, essentially reflecting different degrees of bioturbation from

scarcely to moderately bioturbated main-fluvial-channel sandstones (ichnofabric 1), moderately to intensely bioturbated crevasse-channel sandstones (ichnofabric 2) and totally bioturbated overbank mudstones (ichnofabric 3).

3. Depth and degree of bioturbation of the main-channel and crevasse sands seem to be a function of time between depositional events. Main-channel and crevasse sandstones underlying thick packages of bioturbated overbank mudstones are intensely bioturbated, recording prolonged periods of low-energy sediment fallout between crevassing events. On the other hand, amalgamated channel sandstone units underlying thin intervals of overbank mudstones display the lowest degree of bioturbation, reflecting a high frequency of depositional episodes.

ACKNOWLEDGMENTS

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