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INTERPRETED DEPOSITIONAL CONDITIONS OF BALANCED-FILL LAKE BASIN STRATA INCORPORATING VERTEBRATE AND INVERTEBRATE TRACE FOSSILS, TRIASSIC SANTA CLARA SUB-BASIN, CUYANA RIFT BASIN, ARGENTINA

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ABSTRACT: **The Santa Clara Abajo and Santa Clara Arriba formations host a diverse assemblage of trace fossils that record a wide range of behaviors and a broad array of ecological niches during the Middle Triassic—a critical period in the evolution of continental fauna with the diversification of both synapsids (cynodont and dicynodont) and archosauromorphs (dinosaurs, pterosaurs, and crocodilians) that represent post-Permian faunal recovery. The Santa Clara formations are part of the continental infill of the Cuyana rift basin in Argentina and represent a lacustrine system with fluvial input and delta development. Sedimentological characteristics of these units as well as their stacking patterns characterize a "fluctuating profundal" facies association typical of a balanced-fill lake basin. The lacustrine and associated terrestrial environments preserve a rich record of invertebrate traces with 26 ichnogenera from ethological classes of fodichnia, domichnia, repichnia, pascichnia, and cubichnia occupying all continental tiers (subaerial and subaqueous, surficial, and/or very shallow, shallow, mid, and deeper) and ecological niches (epiterraphilic, terraphilic, hygrophilic, and hydrophilic). In association with invertebrate traces, two taphonomic modes of tetrapod footprints have been found: a moderate-fidelity mode and a high-fidelity mode. Physical sedimentary features, burrows, trails, and tracks, and their stratigraphic positions are integrated to interpret the main factors involved in footprint preservation in these subsettings. The most significant and variable preservational factor found is water-table fluctuation controlled by the paleohydrology of a balanced-fill lake system. These data show that in balanced-fill lake systems, diverse trace assemblages occur in the lake and associated subsettings such as delta plains and lake-margin settings, whereas trace fossils can be totally absent in coeval lake-center strata, particularly if anoxic lake-bottom conditions occur, as probably occurred in the meromictic Santa Clara lake system.**

INTRODUCTION

The variety and temporal variations of depositional conditions characteristic of balanced-fill lake basins result in wide ranges of ecological niches and promote faunal diversity (e.g., Gierlowski-Kordesch and Park 2004; Bohacs et al. 2000). The trace-fossil record of invertebrate and vertebrate faunas in balanced-fill lake basins is correspondingly diverse. Such records can provide detailed insights into depositional conditions, especially when integrated with their sedimentary and stratigraphic context (e.g., Buatois and Mángano 1995, 2004, 2009; Hasiotis et al. 2012; Scott and Smith 2015). Most attention, however, has been focused on traces attributed to invertebrates (but see Mancuso et al. 2022a, for an exception). In this contribution, we analyze the co-occurrence and taphonomy of vertebrate tracks and invertebrate traces found in sections of the Middle Triassic Santa Clara Abajo and Santa Clara Arriba formations in an integrated sedimentological, stratigraphic, geochemical, and paleogeographic framework. These formations host a diverse assemblage of trace fossils that record a critical period in the recovery of land fauna from the Permo-Triassic extinction, when both synapsids (cynodont and dicynodont) and archosauromorphs (dinosaurs, pterosaurs, and crocodilians) diversified significantly.

Recurrent assemblages of continental trace fossils can be found in all lake-basin types (*sensu* Carroll and Bohacs 1999; Bohacs et al. 2000). The occurrences of these assemblages have been found to be systematically related to lake-basin type (e.g., Bohacs et al. 2007; Buatois and Mángano 2009; Hasiotis et al. 2012; Scott et al. 2012). Most of these observations and integrations concentrate on traces that are interpreted to have been made by invertebrates. In contrast, although tetrapod trackways are found in all three lake-basin types (e.g., Hitchcock 1858; Van Dijk et al. 1978; Gillette and Lockley 1991; Melchor and De Valais 2006; Bohacs et al. 2007; Minter et al. 2007; Scott et al. 2012; Klein et al. 2016), their occurrences and characteristics have not been comprehensively integrated with their associated invertebrate traces and depositional context. There are some detailed integrated studies of tetrapod tracks in underfilled lake basins (Mancuso et al. 2020, 2022a, 2022b), but few from balanced-fill lake basins (Mancuso et al. 2022b). Studies of tetrapod track taphonomy addressing their paleobiological implications or the paleoenvironmental

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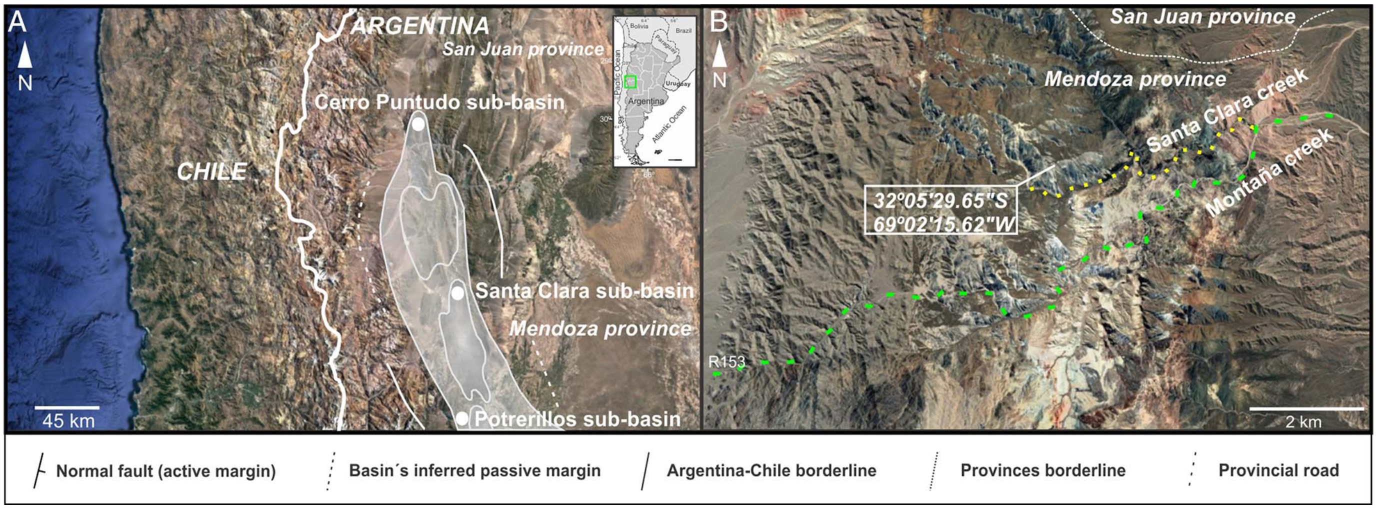


FIG. 1.—**A)** Location map of the Santa Clara sub-basin in the Cuyana rift Basin in the west-central region of Argentina showing the location of the master fault bounding the half grabens of the rift. **B)** Location of the Santa Clara sub-basin.

context are scarce (e.g., Cohen et al. 1991; Marsicano et al. 2010; Scott et al. 2012; Melchor 2015).

Vertebrate trackways, especially of dinosaurs and their ancestors, attract great attention but are often interpreted in isolation or focused on providing an effectively instantaneous snapshot of substrate consistency (e.g., Razzolini et al. 2014; Souza Carvalho and Leonardi 2021). This approach does not make use of the many valuable insights into depositional conditions available from sedimentology, stratigraphy, chemistry, and other trace fossils (commonly made by invertebrates; Mancuso et al. 2020, 2022a, 2022b).

Strata in the Santa Clara sub-basin, Argentina, record continental-interior conditions during a critical time in the evolution of land fauna—the Middle Triassic—and contain diverse and abundant vertebrate and invertebrate traces. There was, however, no published record of ichnofossil assemblages for the Santa Clara sub-basin, despite their abundance and richness. There are only few mentions of the vertebrate tetrapod footprints in the Santa Clara sub-basin (Romer 1966) or in the Las Peñas succession (interpreted as the southward extension of the Santa Clara outcrops; Romer 1966; Rolleri and Criado Roque 1968; Baldoni 1972). The Santa Clara formations were interpreted as fluctuating-profundal lake facies associations (*sensu* Carroll and Bohacs 1999) that accumulated in a balanced-fill lake basin based on their lithologies, sedimentary structures, stratigraphic stacking patterns, body and trace fossils, and organic, inorganic, and isotopic geochemistry (Benavente et al. 2021a).

Our approach considers that tetrapod tracks provide evidence about the sedimentological conditions of the substrate at the time of their imprinting, which controls their final morphology, preservation, and spatial and stratigraphic distributions. Therefore, detailed studies of the different taphonomic modes of tetrapod track preservation observed in a succession can be used as sensitive indicators of the environmental conditions of the track-bearing beds in lacustrine systems during deposition and imprinting (e.g., Cohen et al. 1991; Scott et al. 2010; Mancuso et al. 2020, 2022a, 2022b).

Other associated trace fossils (burrows, trails, etc.) also provide information about many aspects of their depositional environment (sediment and/or media consistency and moisture content, oxygen levels, food availability, and ecosystem trophic structure); therefore, integrating tracks and other trace fossils with physical and chemical observations (sedimentology, stratigraphy, mineralogy, and stable isotopes) enables the most robust and detailed interpretations of depositional conditions and their short- and long-term changes (Buatois and Mángano 2009; Scott et al. 2012; Hasiotis et al. 2012, 2013; Buatois et al. 2020).

The aims of this contribution are to: a) characterize the vertebrate and invertebrate trace-fossil assemblages of the Santa Clara Abajo and Arriba formations; b) characterize tetrapod footprint preservation and ichnofauna taphonomic pathways in a balanced-fill paleolake system represented by these formations; c) place the assemblages into stratigraphic and sedimentological context; d) consider the interrelations of those data in their regional paleoclimatic and paleohydrological setting; and e) provide further insights into the continental paleoenvironmental conditions of the Middle Triassic in the central Cuyana rift basin, southwest Gondwana.

GEOLOGICAL SETTING

Global and Regional Context

The Santa Clara Abajo and Santa Clara Arriba formations accumulated during the Middle Triassic in southwestern Pangea in the Santa Clara sub-basin, located in the central part of the Cuyana rift basin. The Cuyana rift basin formed in a continental intraplate setting at the southwestern margin of Gondwana during the Triassic earliest extensional phase of the opening of the South Atlantic Ocean (Uliana and Biddle 1988). Adjacent sub-basins are the Barreal, Rincón Blanco, and Cerro Puntudo to the north and the Potrerillos to the south. The Cuyana rift basin spans 30,000 km^2 across the San Juan, Mendoza, and San Luis provinces of Argentina, trends NNW–SSE, and comprises several asymmetric half-grabens whose master faults alternate between the western and eastern sides (Legarreta et al. 1992; Kokogian et al. 1993; Barredo et al. 2012) (Fig. 1). The master fault of the Santa Clara sub-basin is located on its eastern margin (Benavente et al. 2018). The lake basin was asymmetric throughout deposition of the Santa Clara formations, with a steep eastern margin and gently sloping margins to the west, north, and south. Basement rocks are dominantly the volcanics of the Permian–Triassic Choiyoi Group (Llambías 2001) (Fig. 2). Paleozoic sedimentary rocks were also widespread in the catchment area of the basin (Harrington 1971) (Fig. 2). The age of the strata in the Santa Clara sub-basin has been constrained to the Middle Triassic by the paleontological content (tetrapod tracks and fish remains) of the Santa Clara Abajo Formation (Bordas 1944; López-Arbarello and Zavattieri 2008; López-Arbarello et al. 2010; Benavente et al. 2021a).

In the Triassic, the global climate mode was changing from warm to extreme hot with high-latitude ice-free areas (Parrish 1993; Sellwood and Valdes 2006; Holz 2015; Retallack 2013). The wide extent of Pangea, however, spanning from about 85° N to 90° S (Ziegler et al. 1983; Parrish 1993; Torsvik et al. 2012; Torsvik and Cocks 2013; Holz 2015), has been interpreted to have had extraordinary effects on global climate (Parrish et al.

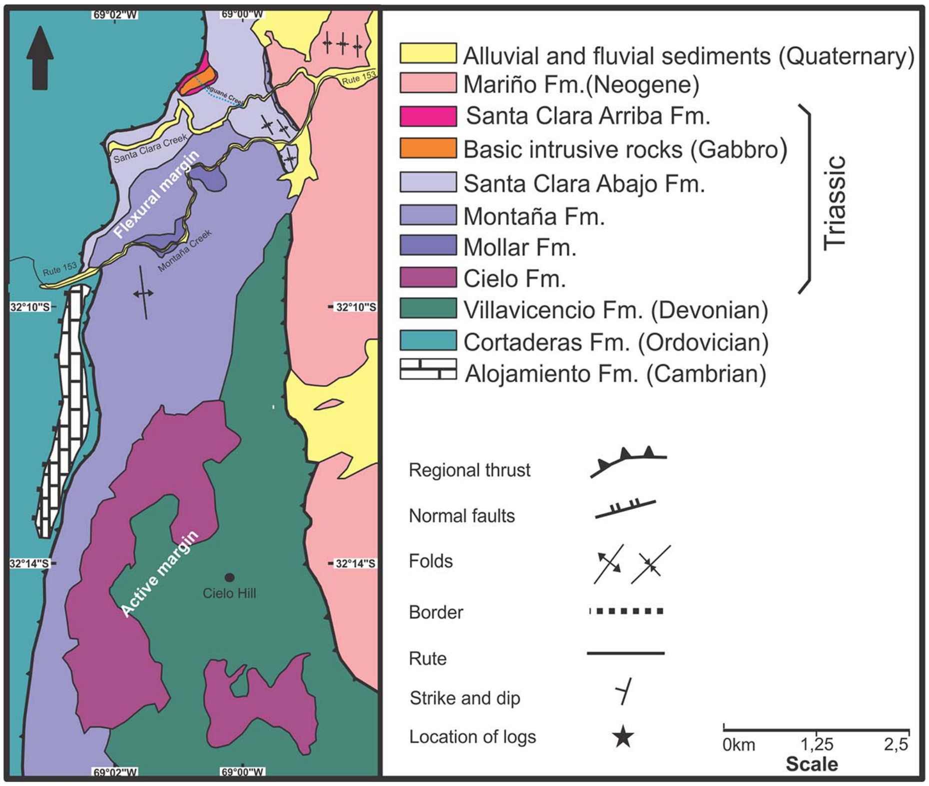


FIG. 2.—Geologic map of the Triassic Santa Clara sub-basin of the Cuyana rift Basin.

1986). Global atmospheric circulation models propose a mega-monsoonal regime that led to highly marked seasonality, a displacement of the climatic belts poleward, and a decrease of the precipitation/evaporation rate in the mid-latitude interior of Pangea during the entire Triassic (Kent and Tauxe 2005; Sellwood and Valdes 2006). Globally, primary aquatic producers of organic carbon were cyanobacteria and chlorophytae (e.g., Miller and Labandeira 2002; Knoll et al. 2007; Buatois et al. 2016). Land-plant assemblages during the Triassic were dominated by conifers, with subsidiary gingkoes, sphenopsids, ferns, seed ferns, and cycadophytes (e.g., Gensel and Edwards 2001; Gibling and Davies 2012). Land vertebrate faunal assemblages were dominated by Archosauromorpha with subordinate Amphibia and Synapsida (e.g., Padian and Sues 2015). All major present-day tetrapod classes were present (except for birds). Inland areas of Pangea were occupied by a fauna that comprised temnospondyls, synapsids (cynodonts and dicynodonts), and archosauromorphs (e.g., Pseudosuchia, erythrosuchids, proterosuchids, proterochampsids, rhyncosaurs) (Sereno 1991; Benton 2004); all these were potential trackmakers in the strata we studied. Other potential trackmakers included such insects as Diptera (including fruit flies and mosquitoes), Coleoptera (beetles), Ephemeroptera (mayflies), Hemiptera (bugs), Odonata (dragonflies, damselflies), and Plecoptera (stoneflies), as well as oligochaete annelids, bivalves, ostracods, gastropods, and nematodes (e.g., Labandeira 1998; Benton and Donoghue 2007).

In terms of paleogeography, our study area was about 800 km to 1,000 km from the southwest coast of Pangea (Markello et al. 2008) and occupied paleolatitudes between 44° S and 52° S (calculated using Hinsbergen et al. 2015) during the Middle Triassic. Paleoaltitudes are estimated to have ranged from 500 m to 1,000 m above sea level by analogy with the elevation of present-day lake systems in the East Africa Rift (Moernaut et al. 2010; Benavente et al. 2021a, 2021b).

The lake system represented by the Santa Clara Abajo and Santa Clara Arriba formations was in a mid-latitude paleoclimate that varied seasonally from warm semiarid to warm subhumid with frost-free winters; indeed, minimum air temperatures were probably well above 4°C based on local stable-isotope data and fish taphonomy (Benavente et al. 2020), along with the occurrence of ephemeral-stream strata, subaerial-exposure features, and clay-mineral assemblages dominated by illite with minor content of smectite and kaolinite (Benavente et al. 2021a). Paleobotanical studies of broadly coeval strata in adjacent Barreal and Potrerillos sub-basins confirm this interpretation (Spalletti et al. 2003; Bodnar et al. 2018; Ruffo Rey 2021).

Basin-Scale Context

The Santa Clara sub-basin (Fig. 1B) occupies a position in the Cuyana rift that is equidistant among the Potrerillos, Sorocayense–Hilario, and Barreal sub-basins. It has an active margin on the east and a flexural margin on the west (Fig. 1A), similar to the Cerro Puntudo sub-basin (Benavente et al. 2018). The Santa Clara sub-basin contains a thick succession of Triassic continental strata designated as the El Peñasco Group (Stappenbeck 1910; Stipanicic 1947; Groeber and Stipanicic 1953; Spalletti 2001; Cortés et al. 2003; Spalletti and Zavattieri 2009). This group includes five units from base to top: 1) Cielo Formation: thickly bedded coarse-grained sandstone and structureless conglomerate with sandstone matrix (alluvial-fan setting; Harrington 1971); 2) Mollar Formation: fine-grained, stratified to structureless sandstone alternating with organic-carbon-rich black mudstone (fluctuating lacustrine system; Harrington 1971; Spalletti and Zavattieri 2009); 3) Montaña Formation: coarse-grained stratified sandstone interbedded with thinly stratified siltstone (fluvial and vegetated floodplain system; Harrington 1971; Artabe et al. 2009); 4) Santa Clara Abajo Formation: siltstone, fossiliferous mudstone (fish remains), sandstone, and subordinate conglomerate (fluvio-deltaic–lacustrine system; Harrington 1971; López-Arbarello and Zavattieri 2008; Benavente et al. 2020); 5) Santa Clara Arriba Formation: thin clayey tuffaceous fine-grain sandstone alternating with laminated limestone, mudstone, and siltstone

TABLE 1.—*Bioturbation and Trace Fossil categories.*

	BI	Verbal BI	Description
Bioturbation Index (after Lazar et al. 2015)	0	Not bioturbated	No visible burrows; all original sedimentary structures preserved.
	1	Weakly bioturbated	Beds continuous, a few burrows visible.
	2	Sparsely bioturbated	Beds discontinuous, some burrows visible.
	3	Moderately bioturbated	Remnant bedding, common burrows, individual burrows mostly recognizable.
	4	Strongly bioturbated	Minimal bed continuity, abundant burrows, some distinct burrows recognizable.
	5	Churned	No remnant bedding, fully disrupted and mixed, difficult to recognize individual burrows.
Ecological Categories (after Hasiotis 2002, 2007)	Epibenthic: living on a sediment surface under free-surface water (lake, pond, stream).		
	Epiterraphilic: living on a subaerially exposed surface (*syn.* epigeal).		
	Hydrophilic: living in sediment below the water table in the phreatic zone.		
	Hygrophilic: living in sediment in the lower vadose zone, where sediment is persistently moist.		
	Terraphilic: living in sediment in the upper vadose zone, where sediment moisture varies substantially.		
Ethological Categories (after Seilacher 1953, 1964; Simpson 1975; Ekdale et al. 1984; Bromley 1990)	Agrichnia: "farming" or "gardening" traces.		
	Calichnia: breeding or reproduction structures (nest, brood chamber, bee cell).		
	Cubichnia: resting, hiding, or ambush traces on sediment surface.		
	Domichnia: dwelling traces in sediment.		
	Equilibrichnia: adjustment traces that record an organism's response to sediment accumulation or removal, usually by spreiten.		
	Fodichnia: deposit feeding and dwelling traces formed by organisms moving sediment or tunneling while seeking food.		
	Fugichnia: escape traces in response to episodes of sudden sediment accumulation.		
	Pasichnia: grazing traces, generally two-dimensional on or near sediment surface.		
	Praedichnia: predation traces.		
	Repichnia: locomotion traces, commonly in trackways.		
Tiers (after Ausich and Bottjer 1982; Bromley 1990, 1996)	Epifaunal: on or above the sediment surface.		
	Surface layer ("mixed layer"): uppermost interval, within approximately 6 cm of the sediment surface.		
	Shallow: next deeper interval, typically between 6 and 12 cm (generally) below the sediment surface.		
	Mid or Intermediate: interval between shallow and deep tiers.		
	Deep: deepest layer occupied by metazoan infauna, about 12 cm or more below the sediment surface.		

interpreted as a low-gradient deltaic–lacustrine system (Harrington 1971; Benavente et al. 2018).

The Santa Clara sub-basin hosted a range of depositional environments from alluvial fans through lake-margin fluvial-floodplain, littoral, and sublittoral, to lake-center profundal environments (Benavente et al. 2021a). At its maximum extent, the Santa Clara paleolake could have been as large as 6100 km^2, which is approximately the size of present-day tectonic lakes Lake Issyk–Kul in Asia and Lake Albert (Mwitanzige) in Africa. The hydrography (surface flow) of the Santa Clara Arriba paleolake appears to have been intermittently open; its groundwater flow (hydrology) was likely open but rather slow-flowing with long water residence times, according to sedimentological, stratigraphic, mineralogical, and C and O stable isotope data (Benavente et al. 2021a). The Santa Clara formations have been interpreted to have accumulated in balanced-fill lake systems based on their sedimentologic and stratigraphic attributes, body and trace fossils, organic-matter content, and stable-isotope geochemistry (Benavente et al. 2018, 2021a).

METHODS

Three high-resolution sedimentary logs (1 cm = 20 cm) of the Santa Clara Abajo and Santa Clara Arriba formations were measured along a transect at Santa Clara Creek and Yaguané Hill (Pedernal, Mendoza Province, Argentina), and facies and facies associations were identified. Color descriptions follow the Rock Color Chart of the Geological Society of America. Hand samples were taken for further mineralogical analyses.

Invertebrate trace fossils were assigned to an ichnotaxon based on their key characteristic architectural and surficial morphologies and fill pattern (e.g., Hasiotis and Mitchell 1993; Bromley 1996). Ichnological information was documented describing the abundance of trace fossils and evaluating how common were occurrences of each ichnotaxa on bedding planes per m^2 and in vertical profiles of individual bedsets per 10 cm^2 sectors. We used descriptors such as not observed (in 0% of bedsets and stratal levels), very sparse (up to 10%), sparse (11 to 20%), few (21 to 40%), common (41 to 60%), abundant (61 to 80%), and very abundant (81 to 100%) (after cf. Miller and Smail 1997; Lazar et al. 2015). Ichnofossil diversity was defined based on the number of ichnotaxa observed; since a total of 26 ichnotaxa were observed across all facies, we subdivided diversity into five categories: absent (0 ichnotaxa), low (1 to 5), moderate (6 to 10), high (11 to 15), and very high ($\geq$ 16 ichnotaxa). We assessed the bioturbation index (BI) using a 0-to-5 scale following the usage of Lazar et al. (2015) (their Table 9.2) that was devised to apply to all sedimentary rock types and reconcile the various classic classification systems: Potter et al. (1980), Droser and Bottjer (1986), Taylor and Goldring (1993), Miller and Smail (1997), Aplin and Macquaker (2010), Reineck and Singh (2012). The degree of bioturbation varies from no visible burrows (BI 0) to no remnant bedding preserved when a mudstone is fully churned (BI 5). See Table 1 for details of all the categories.

Vertebrate footprints were described by their number of digits, character of contact between the appendage and the sediment (complete manus or ped to distal phalanges only), track width and length, digit-impression lengths, and the angles between digit impressions (see Fig. 4 in Mancuso et al. 2016; Krapovickas et al. 2015) Tetrapod-track taphonomic modes are defined according to the fidelity of the trackmaker's pedal anatomy to evaluate the source of such variation of the physical and morphological traits in footprints (see Gatesy and Falkingham 2017). The presence or absence of different morphological and extra-morphological features such as palm-sole pads, digit impressions, claw marks, and marginal rims, among others were documented (e.g., Mancuso et al. 2016, 2020, 2022a, 2022b).

The assignment of particular traces to specific tiers and ecological niches is based on our observations of their crosscutting relations, preservation quality, and sedimentary-stratigraphic context in the strata studied as well as on a review of previous usages in the literature on fluvial, paleosol, and lacustrine deposits. Tier categories are after Ausich and Bottjer (1982), Bromley (1990, 1996), Buatois and Mángano (2009), and Buatois et al. (2016). Trace fossil categories for interpreted ecological niches follow the usage of Hasiotis (2002, 2007): epiterraphilic, terraphilic, hygrophilic, and hydrophilic (subdivided by tiers: hydrophilic-epibenthic (made by organisms on the sediment surface) and hydrophilic-endobenthic shallow, intermediate, and deep (made by organisms at various depths within the sediment). The ecological niches generally correspond to these tiers in the sediment (and are used as a shorthand for the tiers in this paper; Table 1): epiterraphilic, subaerial epifaunal to surface layer (surficial to very shallow); terraphilic, subaerial shallow; hygrophilic, subaerial mid-tier; hydrophilic-epibenthic, epifaunal to surface layer (surficial to very shallow) in sediments with water-filled pores; hydrophilic-endobenthic shallow, intermediate, and deep, subaqueous shallow, intermediate, and deep, respectively. Ethological categories are after Seilacher (1953, 1964), Simpson (1975), Ekdale et al. (1984), Bromley (1990, 1996), and Vallon et al. (2016). See Table 1 for a listing of these categories and the ichnotaxa. The term "suite" is used in the sense of Mancuso et al. (2020) for recurrent assemblages of trace fossils with similar ethologies and diversity interpreted as ichnocoenoses that vary as a function of substrate rheology and humidity. As defined by Mancuso et al. (2020), Suite 1 is characterized by a moderate-diversity assemblage of mostly pascichnia and repichnia emplaced in a soft substrate under standing water (in a lake, pond, or stream—that is, a limnic or lotic setting); Suite 2 is a lower-diversity assemblage dominated by domichnia emplaced in a soft substrate with saturated pores; Suite 3 is a lower-diversity assemblage of mostly fodichnia emplaced in a firm substrate with varying humidity.

RESULTS

Sedimentology and Ichnology

The Santa Clara Abajo and Santa Clara Arriba formations contains 13 distinct lithofacies and six facies (Figs. 3–9; Tables 2, 3). Table 2 contains details of each lithofacies. Table 3 contains detailed lists of ichnotaxa and their tiers and ecological niches by facies and key environmental processes and conditions. The following sections describe the facies and interpret their vertical relations, stratigraphic trends, and trace-fossil content.

Facies A

Facies A (FA) comprises a range of sandstone and siltstone in seven lithofacies (Fig. 4, Table 2). The dominant lithofacies is structureless siltstone (Fm) with reddish and greenish coloration (Fig. 4A, B). Fm intervals alternate vertically with subordinate lenticular sandstone bodies that are isolated or laterally amalgamated by erosion (Fig. 4C) and with minor intervals of mudstone (Fl). These sandstone bodies contain trough-cross bedding (St), planar-cross bedding (Sp), asymmetric ripple-cross lamination (Sra) (Fig. 4D), planar bedding (Sh), and structureless sandstone (Sm). These structures measure 20 cm long and 0.5 cm wide (Fig. 4E). The sandstones occur mostly as isolated bedsets with minimally erosive bases interbedded with drab colored Fm layers in the section at 0 to 18 m, 93 to 103 m, and 330 to 338 m (Fig. 3). Other such sandstone bedsets are interbedded with reddish- and greenish-colored intervals of Fm, have more obviously erosional bases, and are closely vertically stacked or laterally amalgamated in the section at 285 to 307 m and 348 to 372 m (Fig. 3). FA overlies facies E (delta plain) (Fig. 4F) and underlies facies B (lake margin) and facies E (delta plain).

Ichnology.—FA contains a moderate-diversity assemblage of invertebrate and plant traces (six ichnogenera) mainly in intervals of Fm (e.g., ca. 364 m in Fig. 5). Lithofacies Fm contains horizontal, inclined, and vertical traces including abundant *Planolites*, common occurrences of Naktodemasis (cf. *Taenidium*), *Palaeophycus*, *Skolithos*, *Spongeliomorpha* (see note in Supplemental Material on this ichnotaxa), and a few occurrences of *Edaphichnium* (Table 3) (there are sparse occurrences of a trace that somewhat resembles *Eatonichnus*, which would be one of the earliest reported occurrences, but the examples and currently available data do not permit a definitive diagnosis). Lithofacies Sm contains abundant tubular vertical structures that branch and taper in diameter downwards and have drab-colored haloes (Fig. 4E). Completely churned layers (BI 5) are common.

Interpretation.—The most abundant lithofacies Fm (structureless siltstone facies) is interpreted as due to suspension settle-out from waning overbank flows (cf. Makaske 2001; cf. Nichols and Fisher 2007; Stoner and Holbrook 2010) in a fluvial floodplain, as modified by pedogenic processes and bioturbation. The predominantly lenticular, erosionally-based, and laterally amalgamated sandstone bedsets with abundant primary sedimentary structures representing high- and moderate-energy tractive flows (St, Sp, Sra, and Sh) are interpreted as fluvial channel fills (James and Dalrymple 2010). Tubular tapering vertical structures observed in Sm are interpreted as rhizoliths that record colonization by land plants as the groundwater table lowered (cf. Kraus and Hasiotis 2006). The resulting rhizoturbation in those Sm intervals most likely contributed to the structureless fabric of Sm beds. The moderate diversity of preserved discrete invertebrate trace fossils in mostly structureless facies is fairly typical of a floodplain setting with net sediment accumulation rates less than the rates of reworking by plant and animal activity and pedogenic processes (e.g., Buatois and Magano 2002; Hasiotis 2004, 2007, 2008). The ethological classes of the ichnogenera in this facies span fodichnia and domichnia (in order of decreasing abundance). The traces all appear to have occupied terraphilic or hygrophilic ecological niches (subaerial shallow to mid tiers).

Facies A represents a fluvial system and its floodplain where sediment accumulated from tractive flows during episodic floods and suspension settle-out during waning phases, with subsequent land-plant growth. The variability in fluvial-channel stacking among stratigraphic intervals can be interpreted as recording changes in the ratio of accommodation to sediment supply (A/S; e.g., Leeder 1978): Intervals of isolated sandstone bedsets interbedded with drab-colored Fm record higher A/S as crevasse-splay sandstones isolated vertically in poorly drained (drab) floodplain mudstone. Intervals of vertically and laterally amalgamated erosionally-based sandstone bedsets associated with reddish to greenish Fm containing exclusively terraphilic traces record lower A/S in intercutting channel-fill sandstones associated with well-drained floodplain mudstone.

Facies B

Facies B (FB) comprises a range of sandstone and siltstone, along with calcareous carbonate in six lithofacies: planar bedded sandstone (Sh), symmetric rippled sandstone (Srs), structureless sandstone (Sm), planar bedded siltstone (Fh), laminated carbonate (Cl), and laminated mudstone (Fl). Lithofacies Fm and Cl occur in recurrent alternation with beds of Sh, Sm, and Fm (Table 2; Figs. 3, 6A–F).

This facies overlies FA (fluvial system) gradationally and underlies FC (lake center). The transition between FA and FB is recognized where the dominant Fm lithofacies of FA turns minor upwards and repetitively alternates with planar bedded (Sh), structureless (Sm), and rippled sandstones (Srs), carbonates (Cl), and mudstones (Fl). A distinct feature is that Fm in FB contains very fragmented land-plant remains, mud cracks, and raindrop marks, and there is no evidence of rhizolith development as in FA. Also, Fl is light gray in color, unlike FC, where

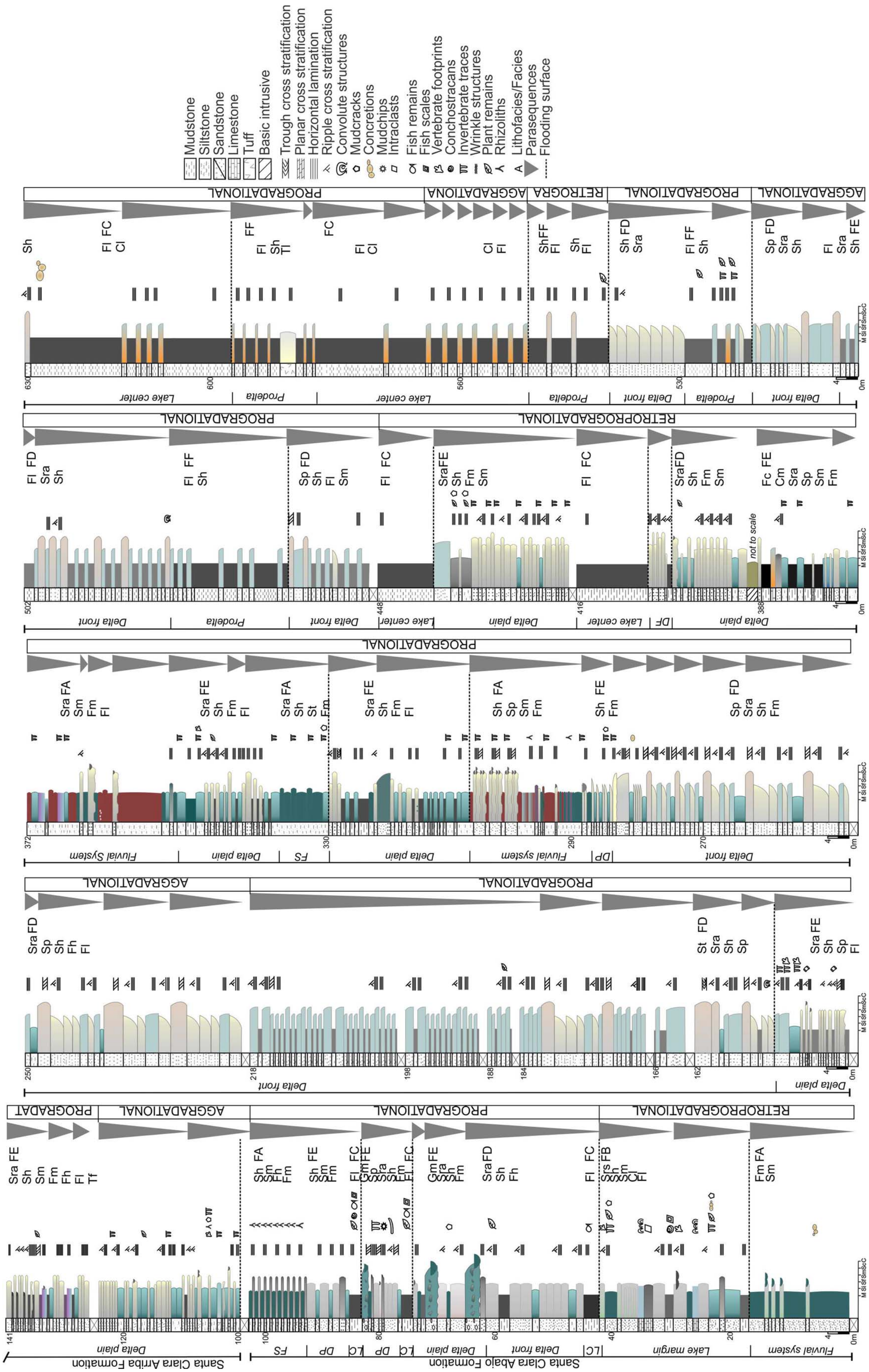


FIG. 3.—High-resolution sedimentary log of the Santa Clara Abajo and Santa Clara Arriba formations at the Santa Clara creek and Yaguané hill respectively.

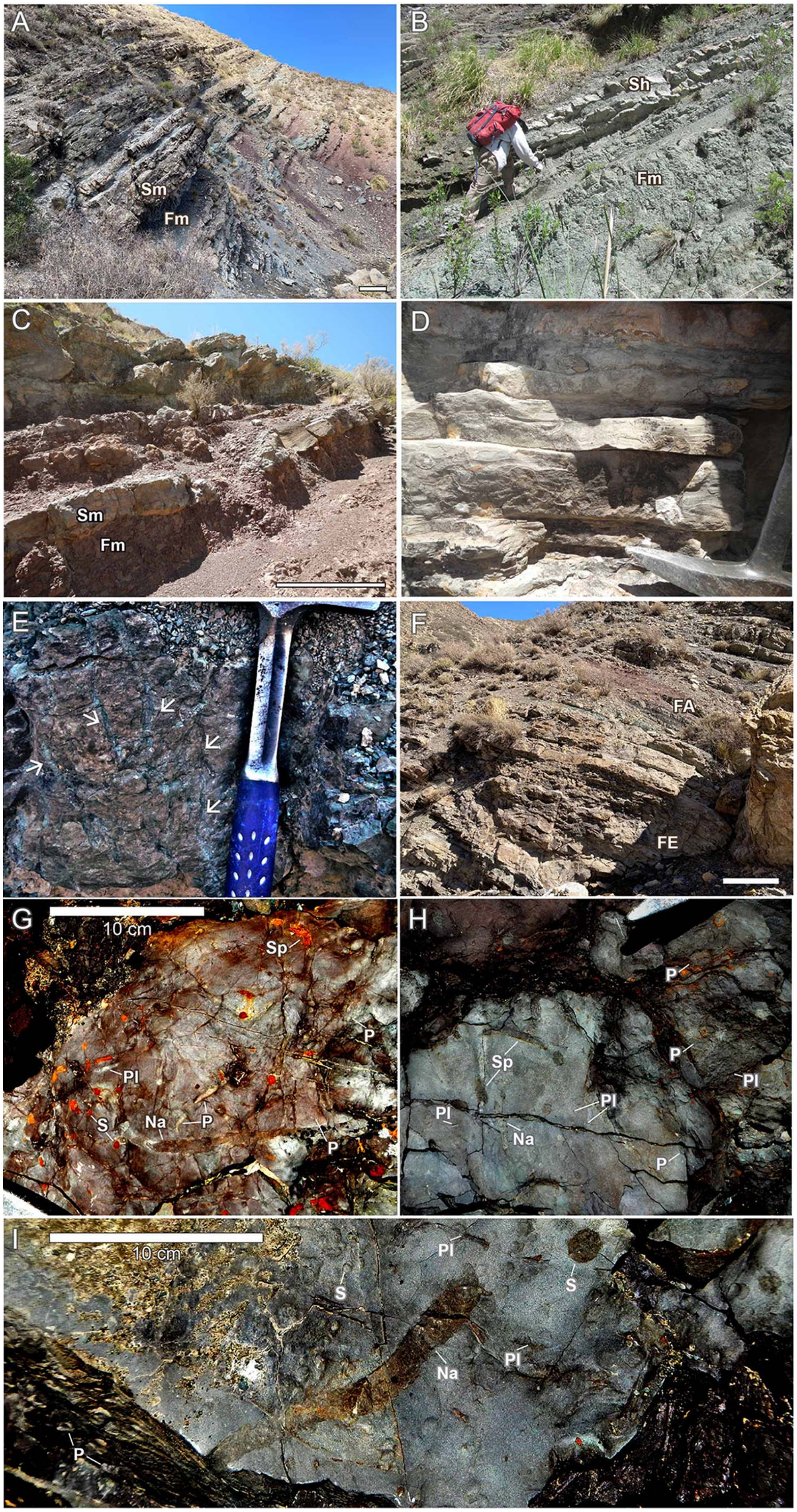


FIG. 4.—Field photographs of the facies and facies associations of the Santa Clara Abajo Formation, Fluvial facies (FA). **A)** Package of dominant reddish and greenish structureless siltstone (Fm) with structureless sandstone beds. Scale is 1 m. **B)** Tabular laterally amalgamating sandstones with faint planar bedded (Sh) and pale blue green (5BG 7/2) structureless siltstone (Fm). **C)** Detail of lenticular sandstone (Sm) with erosional base and reddish structureless siltstone (Fm). Scale is 0.25 m. **D)** Detail of asymmetric-ripple cross-stratified sandstone (Sra). Tip of hammer is 10 cm. **E)** Tubular vertical structures interpreted as rhizoliths (white arrows). Hammer is 35 cm. **F)** Fluvial facies deposits (FA) overlying delta-plain beds (FE). Scale is 0.5 m. **G)** Top view of a bed of the structureless siltstone facies (Fm) with *Palaeophycus*, *Planolites*, *Steneinichnus* and *Scoyenia*. Head of hammer is 20 cm. **H)** Top view of a bed of the structureless siltstone facies (Fm) with *Palaeophycus*, *Planolites*, and *Steneinichnus*. The tip of the hammer is 5 cm. **I)** Zoom in on a top and lateral view of a bed of the structureless siltstone facies (Fm) with *Steneinichnus* and *Scoyenia*. Scale is 10 cm.

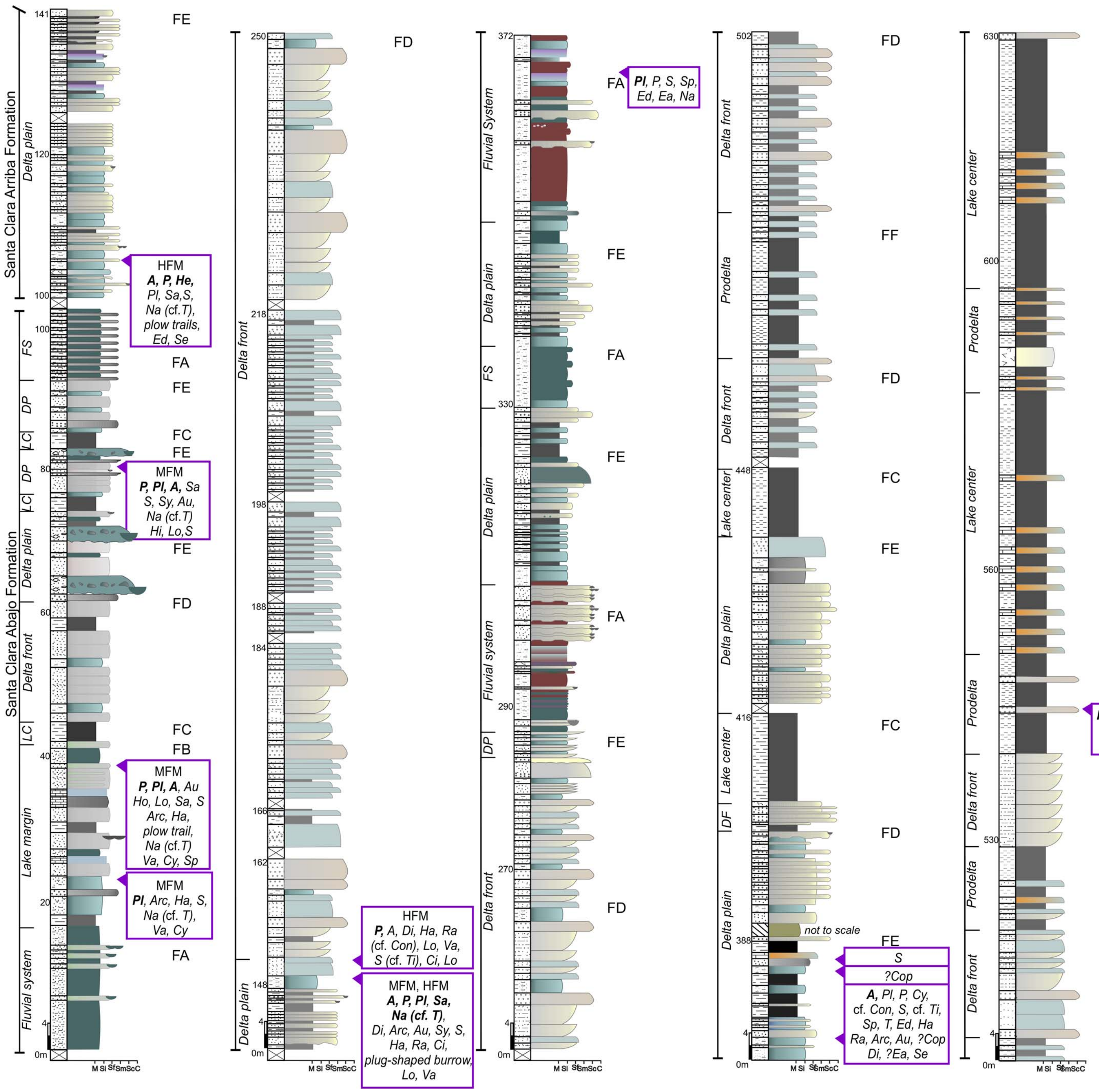


FIG. 5.—Sedimentary log of the Santa Clara Arriba and Santa Clara Abajo formations with ichnological assemblages and footprint preservation modes in stratigraphic position. Bold letters indicates the most common ichnological components in each assemblage.

mudstones are very dark gray to black. In FB the sandstones are tabular (Fig. 6A), no lenticular bed geometry is observed as in FA and, like Fm, contains very fragmented land plant remains (Fig. 6B). The most diagnostic lithofacies in FB is the symmetric rippled sandstone (Srs) which occurs below Cl and Sh beds and above Fm and Fl beds (Fig. 6C). Also diagnostic is Fl with raindrop marks and mud cracks (Fig. 6D). The laminated to domal carbonates contain domes 15 cm wide and 10 cm thick with an intraclastic component.

Ichnology.—FB contains vertebrate footprints of moderate-fidelity mode (MFM) as well as a very high-diversity assemblage of invertebrate traces (16 ichnogenera in aggregate) that vary systematically among the lithofacies. Lithofacies Fm (e.g., ca. 22 m in Fig. 5) contains vertebrate footprints with moderate-fidelity mode (MFM) and a moderate-diversity assemblage (seven ichnogenera) of horizontal, inclined, and vertical traces including common occurrences of *Planolites*, few *Archaeonassa*, *Haplotichnus* (see Supplemental Material for taxonomic discussion), plow trails, linear clusters of *Skolithos* (cf. *Tigillites*), and *Vagorichnus*, and sparse *Cylindricum* ("plow trails" resemble *Scolicia* but with much simpler internal organization: mm-scale-wide furrows on bedding planes with narrow central V-shaped groove and relatively wide lateral ridges. See Supplemental Material). Lithofacies Sm (ca. 39 m in Fig. 5) contains vertebrate footprints with moderate-fidelity mode (MFM; Fig. 6E, F)

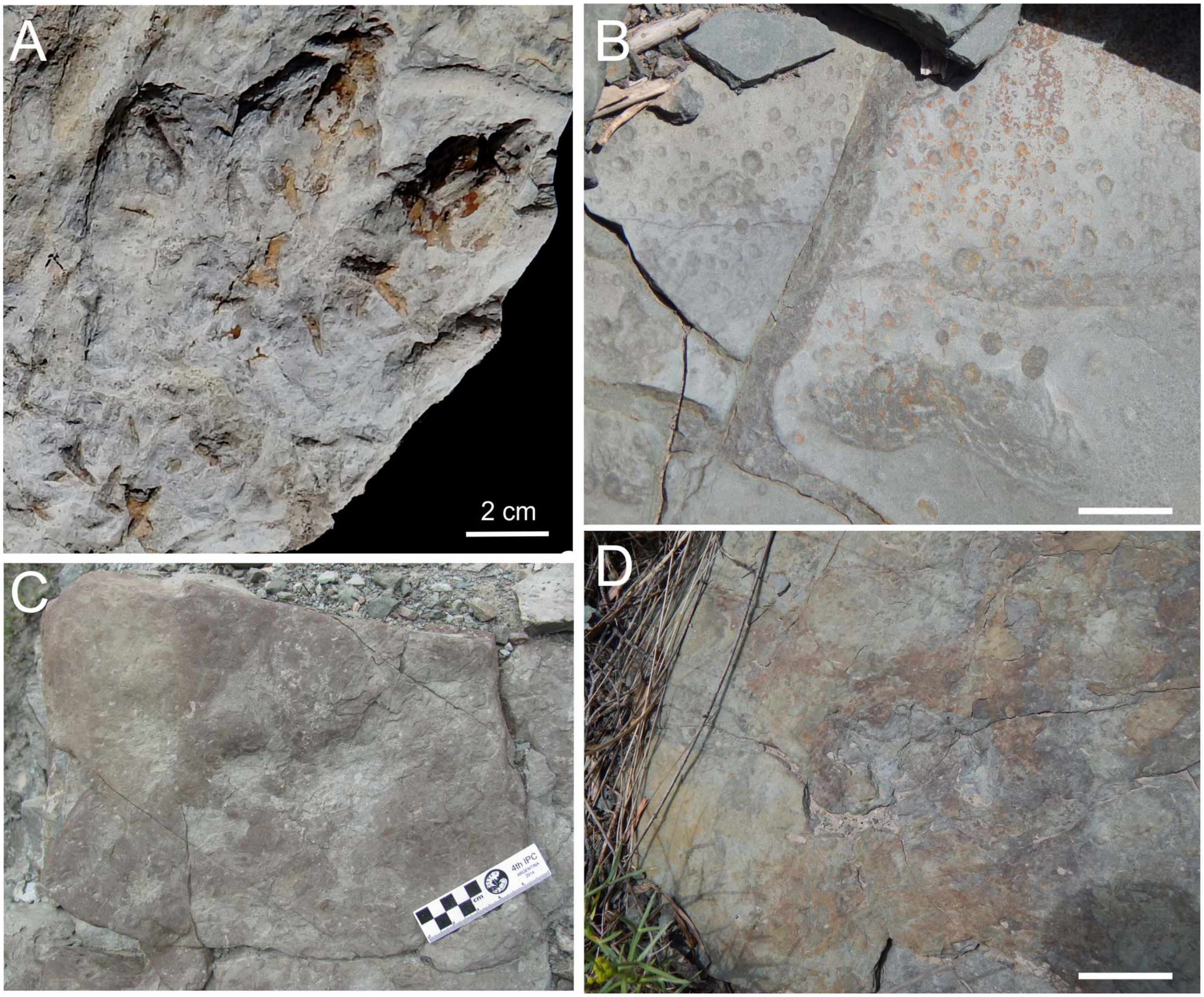


FIG. 6.—Field photographs of the lake-margin facies (FB) of the Santa Clara Abajo Formation. **A)** Tabular planar bedded sandstone with land-plant remains and footprints with moderate-fidelity-mode preservation (MFM). Scale is 5 cm. **B)** Structureless siltstone facies (Fm) with mud cracks and rain-drop marks. Scale is 10 cm. **C)** Structureless sandstone lithofacies (Sm) with vertebrate footprints with moderate-fidelity-mode preservation (MFM) at the tops of bedsets. Scale is 10 cm. **D)** Structureless-sandstone facies (Sm) with vertebrate footprints with moderate-fidelity-mode preservation (MFM) at the tops of bedsets. Scale is 10 cm.

and a highly diverse assemblage of 16 ichnogenera: vertical, inclined, and horizontal traces, including very abundant *Palaeophycus* and *Planolites*, abundant *Arenicolites*, common *Sagittichnus* (see Supplemental Material SM2 for taxonomic discussion), and *Skolithos* (mostly as isolated individuals, with a few in linear clusters (cf. *Tigillites*)), few *Archaeonassa*, *Aulichnites*, *Haplotichnus*, *Helminthoidichnites*, *Lockeia*, *Naktodemasis* (cf. *Taenidium*), plow trails, and *Vagorichnus*, and sparse *Cylindricum* and *Spongeliomorpha* (Fig. 6G–I; Table 3). Completely churned layers (BI 5) are common, and trampled surfaces are very sparse (Table 3).

Interpretation.—The association of sedimentary features indicate a complex lake-margin environment that spanned supralittoral to upper littoral settings, and frequent changes of lake level and consequent depositional conditions. Episodic inundation by flowing water (Sh, Sm) and subsequent standing waters (Srs) alternated with frequent subaerial exposure and desiccation (mud cracks, raindrop impressions) recorded in Fm. The sedimentary structures of the sandstone lithofacies (Sh, Sp, Sm) indicate unidirectional tractive flows at relatively high velocities (upper flow regime) and their tabular bed geometry points to unconfined flows (Middleton and Southard 1984). Particularly, Sm beds were likely the result of high rates of sedimentation in response to a rapid decrease in flow velocity (cf. Fisher et al. 2007). The presence of Srs lithofacies is interpreted as oscillatory tractive flows commonly developed by wave reworking in marginal and coastal subenvironments at the end of and in between storms (cf. Nadon 1994). Lithofacies Cl shows a combination of subaqueous precipitation with intraclastic supply. The presence of very fragmented land-plant remains in the sandstone lithofacies as well as in Fm indicates transported lant-plant material from adjacent vegetated subenvironments like the one represented by FA in which rhizoturbation indicators have been identified (Benavente et al. 2020). Moreover, the

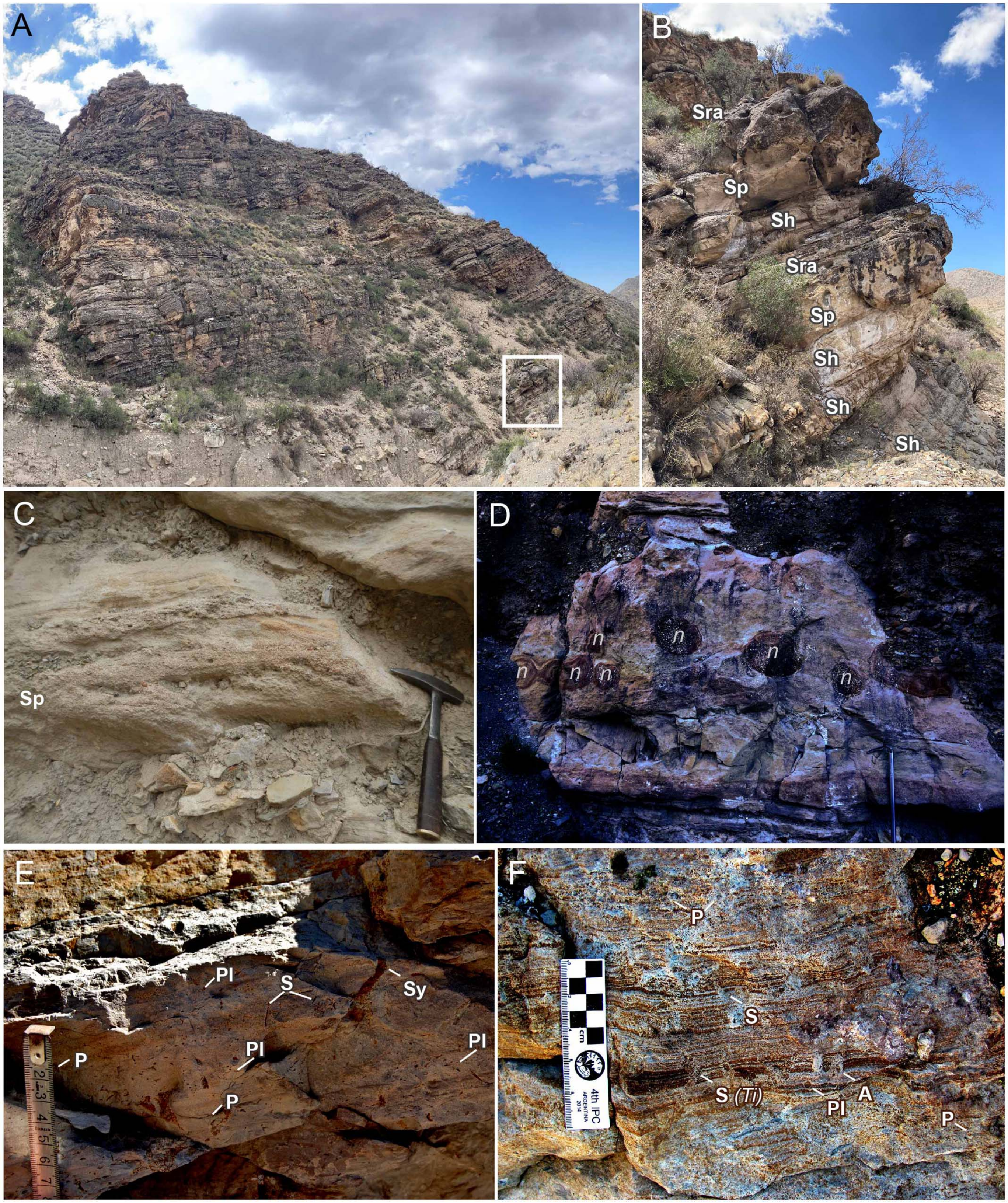
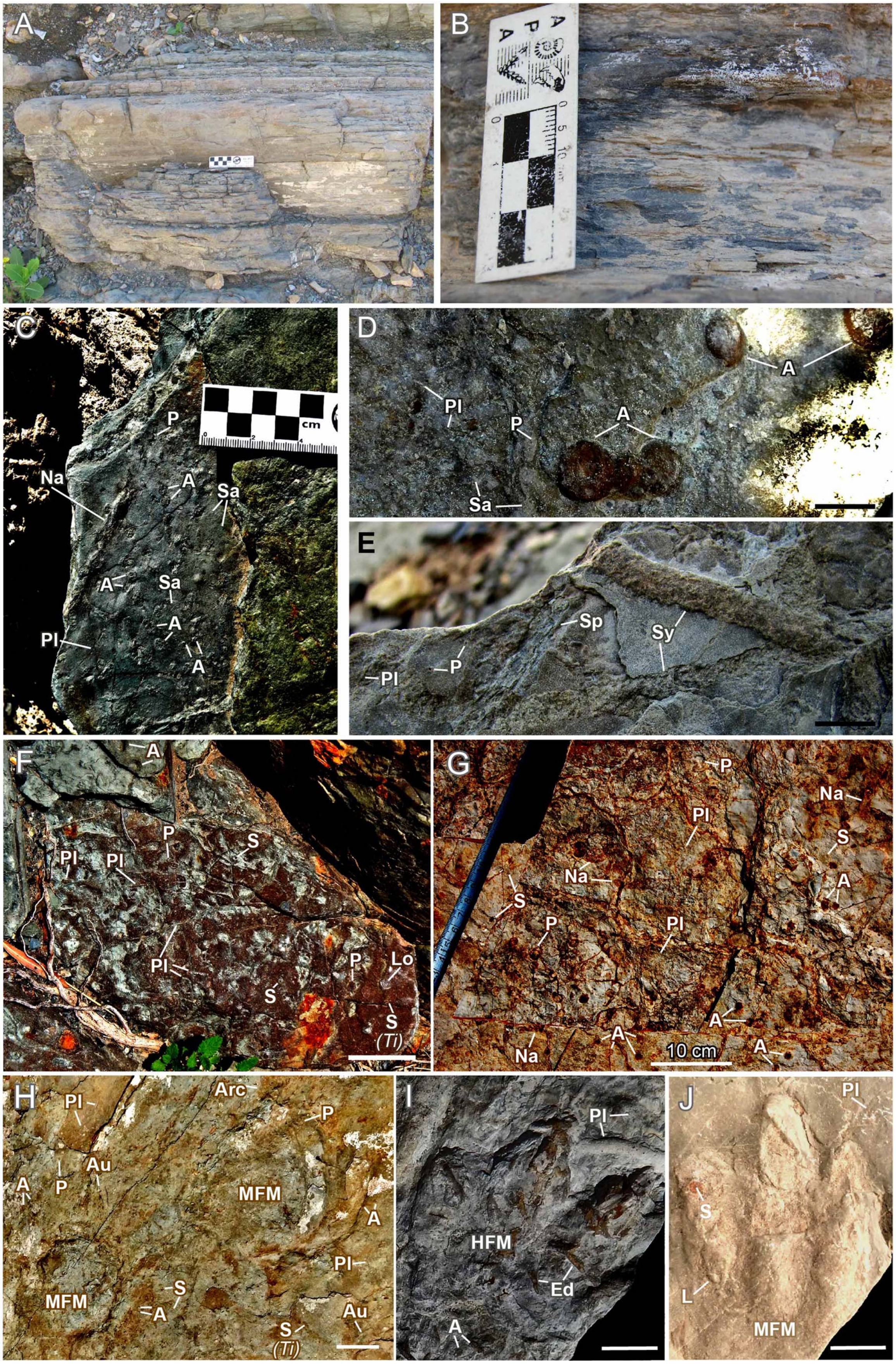


FIG. 7.—Field photographs of the delta-plain facies (FD) of the Santa Clara Arriba Formation. **A)** Approximately 50 m of exposure of the FD packages. Green rectangle is 10 m. **B)** Detail of the package inside the rectangle in Part A) showing the stacking of planar bedded sandstone (Sh), planar-cross-stratified sandstone (Sp), and asymmetrical-ripple-cross-stratified sandstone (Sra). **C)** Detail of a very coarse-grained to pebbly sandstone with planar cross bedding overlain by a medium-grained planar bedded sandstone. Hammer is 35 cm. **D)** Detail of a medium-grained planar bedded to massive sandstone. Hammer is 1.1 m. **E)** Ichnological taxa identified in Sh beds: P, *Palaeophycus*; Pl, *Planolites*; S, *Skolithos*; Sy, *Scoyenia*. **F)** Sh beds with P, *Palaeophycus*, Pl, *Planolites*, S, *Skolithos*, and A, *Arenicolites*.


A
B
C
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indicators of subaerial exposure found in Fm such as mud cracks and raindrop marks support their deposition in a marginal lacustrine (or palustrine) subenvironment (Renaut and Gierlowski-Kordesch 2010; Benavente et al. 2020). Cl shows a combination of subaqueous precipitation with intraclastic supply, which points to a mix of processes very likely to occur in a marginal lacustrine subenvironment, most likely developed laterally to main clastic fluvial input (Benavente et al. 2020). The ethological classes of the ichnogenera in this facies span domichnia, fodichnia, pascichnia, repichnia, and cubichnia (in order of decreasing abundance). The traces are interpreted to have occupied hydrophilic-endobenthic shallow, hygrophilic, terraphilic, hydrophilic-epibenthic, hydrophilic-endobenthic intermediate, and epi-terraphilic ecological niches (Table 1).

The wide range of trace-fossil tiers (subaqueous, shallow and mid tiers; subaerial, epifaunal and/or surface layer, shallow and mid tiers) and ecological niches (hydrophilic-endobenthic intermediate to terraphilic) record episodic inundation alternating with frequent subaerial exposure, groundwater-table withdrawal, and desiccation of the lake-margin surface. Vertebrate tracks were emplaced shortly after short-term lake-level falls, and the shallow and mid tiers under subaerial surfaces were occupied during periods of lake-level withdrawal and associated groundwater-table lowering.

Facies C

Facies C (FC) is dominantly composed of thinly laminated argillaceous mudstone (Fl) with subordinate laminated carbonate (Cl) lithofacies (Table 2), and sparse concretions. Lithofacies Fl contains very abundant articulated fish remains, variable organic-matter content associated with pyrite, and sparse land-plant remains. Lithofacies Cl comprises planar laminated to domal limestone with occasional subangular carbonate sand-size intraclasts and occurs in tabular beds. FC occurs in intervals 2 to 16 m thick that overlie FB (lake margin) in the Santa Clara Abajo Formation and overlie and underlie FD (delta front), FE (delta plain), and FF (prodelta) in the upper part of the Santa Clara Arriba Formation (Fig. 3).

Ichnology.—No vertebrate or invertebrate trace fossils were observed, only the laminae of Cl beds that can be interpreted as traces of microbial activity (e.g., Hasiotis and Brake 2019).

Interpretation.—Fl lithofacies indicates sedimentation dominated by suspension settling with possible traction reworking (Benavente et al. 2020; Schieber et al. 2007). The well preserved laminae suggest low-oxygen conditions, probably due to stable water-column stratification (meromictic conditions; e.g., Bohacs et al. 2000; Scott and Smith 2015). Lithofacies Cl likely resulted from subaqueous precipitation mediated by biofilms on the lake floor (Hasiotis and Brake 2019; Benavente et al. 2020). This lithofacies, along with the very abundant articulated fish remains in the Fl facies indicates minimal influx of clastic sediments. FC is interpreted to record persistently low energy and sediment-accumulation rates under persistent standing water distal from shore.

Integrating all lines of evidence indicates a distal sublittoral to profundal setting persistently inundated and subjected to sparse episodic clastic influx, suspension settle-out, and minimal benthic reworking. This environment was hostile to metazoan infaunal activity, probably due to some combination of dysoxic to anoxic bottom waters, elevated bottom-water salinity, benthic turbidity, and unfavorable sediment rheology. The absence or sparse occurrence of trace fossils in such settings is commonly reported in other balanced-fill lake examples and is ascribed to persistent meromixis and resultant low-oxygen bottom waters and elevated bottom-water salinities (e.g., Bohacs et al. 2000; Buatois and Mángano 2009; Loewen and de Gibert 1999; Martin et al. 2010; Hasiotis et al. 2012; Scott and Smith 2015).

Facies D

Facies D (FD) comprises a range of sandstone, siltstone, and mudstone in six lithofacies: trough cross stratified sandstone (St), planar-tabular cross bedded sandstone (Sp), asymmetric ripple sandstone (Sra), planar bedded sandstone (Sh), horizontally stratified to structureless siltstone (Fh-Fm), and laminated mudstone (Fl) (Fig. 7A–D).

This facies mostly overlies FC (lake center) or FF (prodelta) strata, and underlies FE (delta plain) in the lower 300 m of the stratigraphic section and mostly underlies FC or FF strata in the upper 330 m of the section. FD is recognized by its dominance of coarse-grained lithofacies arranged in thickening- and coarsening-upwards packages of exclusively tabular beds laterally persistent for tens of meters (Fig. 7A). Each package has a trend upwards from thinner and finer lithofacies (Fh/Fl) to sandy beds with planar bedding to asymmetric ripple cross lamination (Fig. 7B) to planar-cross-lamination (Fig. 7C) with concretions (Sh-Sra-Sp) (Fig. 7D). The packages are 5 to 30 m thick and their overall trend in the log is thickening upwards as well, with the thickest interval identified between approximately 150 and 286 m of the log (in which these stratal packages stack aggradationally and then thin upward, probably related to progradation and bypass; Fig. 3). No indicators of subaerial exposure such as desiccation cracks or raindrop marks have been identified in this facies. The sandstones contain abundant land-plant debris and wood fragments.

Ichnology.—FD contains a moderately diverse assemblage of invertebrate traces (six ichnogenera) including abundant occurrences of *Planolites*, common *Diplichnites*, *Haplotichnus*, plough trails, and *Skolithos* (mostly as isolated individuals, and a few in linear clusters (cf. *Tigillites*)) (Figs. 5, 7E; Table 3). Completely churned layers (BI 5) are sparse and trampled surfaces were not observed.

Interpretation.—FD is interpreted to record frequent, relatively long-duration episodes of high energy and sedimentation rates under river influence with intervening pauses in sedimentation in a permanently subaqueous delta-front environment. Lithofacies St, Sp, Sh, and Sra all record the influence of unidirectional tractive flows. Sp and Sh represent upper plane bedding that records tractive transport under higher flow velocities (upper flow regime) and longer-duration flows (hours to days; cf. Middleton and Southard 1984; Fielding 2006), nearer the peak of flood hydrographs. Sra records relatively persistent (minutes to hours) tractive transport under relatively slow flow velocities (cf. Southard and Boguchwal 1990; Fielding 2006) most likely during the falling limbs of flood hydrographs. Fh records suspension settle-out from waning flows and reworking as bed load (Scheiber et al. 2007). Ethological classes of these ichnogenera span domichnia, repichnia, fodichnia, and pascichnia (in order of decreasing abundance). The

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FIG. 8.—Field photographs of the delta-plain facies (FE) of the Santa Clara succession. **A)** Package of planar bedded sandstone lithofacies (Sh) with 5 cm thick structureless siltstone intervals (Fm). **B)** Detail of coaly mudstone facies (Fc). **C)** Ichnological taxa identified in FE: A, *Arenicolites*; P, *Palaeophycus*; Pl, *Planolites*; Sa, *Sagittichnus*. **D)** A, *Arenicolites*; P, *Palaeophycus*; Pl, *Planolites*; Sa, *Sagittichnus*. Scale is 2 cm. **E)** A, *Arenicolites*; P, *Palaeophycus*; Pl, *Planolites*; Sy, *Scoyenia*. Scale is 2 cm. **F)** A, *Arenicolites*; P, *Palaeophycus*; Pl, *Planolites*; Lo, *Lockeia*; S, *Skolithos* (linear cluster). Scale is 10 cm. **G)** A, *Arenicolites*; P, *Palaeophycus*; Sy, *Scoyenia*; Na, *Nakollites*. **H)** Vertebrate footprints of the moderate-fidelity-mode (MFM) and A, *Arenicolites*; Arc, *Archeonassa*; Au, *Aulichnites*; S, *Skolithos*. Scale is 5 cm. **I)** Va, *Vagorichnus*. Scale is 2 cm. **J)** Vertebrate footprints of the moderate-fidelity-mode (MFM). Scale is 2 cm.

FIG. 9.—Field photographs of the delta-plain (FE) and prodelta (FF) facies and facies of the Santa Clara succession. **A)** Representative ichnotaxa identified in FE: Pl, *Planolites*; P, *Palaeophycus*; Cy, *Cylindricum*; Na, *Naktodemasis* (cf. *Taenidium*); Ha, *Haplotichnus*; Se, *Selenichnites*. Scale is 5 cm. **B)** P, *Palaeophycus*; S, *Skolithos*; Na, *Naktodemasis* (cf. *Taenidium*); Cy, *Cylindricum*; Ho, *Helminthoidichnites*. **C)** Representative ichnotaxa identified in the prodelta facies (FF): Pl, *Planolites*; Arc, *Archeonassa*; P, *Palaeophycus* (cf. *Siphonites*); Tr, *Treptichnus*; Sa, *Sagittichnus*. Scale is 10 cm.

traces occupied various hydrophilic/subaqueous tiers: epibenthic, endobenthic shallow, and endobenthic intermediate.

Thickening- and coarsening-upwards multi-meter-thick packages composed of bedsets with high-energy indicators at the base capped by thin and finer-grained deposits are interpreted as parasequences, consistent with the interpretation of this facies as a delta-front subenvironment (e.g., Van Wagoner et al. 1990). The common occurrence of land-plant debris in the lithofacies indicates recurrent river influx. The type, abundance, and diversity of trace fossils as well as lack of subaerial exposure indicators suggest permanently subaqueous deposition. Occurrences of such ichnotaxa have been reported in similar settings by Buatois and Mángano (1998).

Facies E

Facies E (FE) comprises a range of polymictic conglomerate, sandstone, siltstone, and mudstone in eight lithofacies: clast-supported conglomerate (Gm), asymmetric-ripple sandstone (Sra), planar-tabular cross-bedded sandstone (Sp), planar bedded sandstone (Sh), laminated siltstone (Fh-Fc)

TABLE 2.—*Facies associations and their characteristics defined for the Santa Clara Abajo and Santa Clara Arriba formations (Middle Triassic) at the Santa Clara sub-basin, Central area of the Cuyana Basin, Mendoza, Argentina. See Table 3 for detailed lists of trace fossils. FA, facies association; MHF, high-fidelity preservation; MLF, low-fidelity preservation; SCAb, Santa Clara Abajo Formation; SCAr, Santa Clara Arriba Formation (trace-fossil ethological classes are listed in descending order of abundance).*

Facies	Lithofacies	Sedimentary Structures	Bed Geometry	Vertical and Lateral Relations	Fossil Content	Processes	Facies Interpretation
A	Planar cross-bedded sandstone Sp	Coarse- to medium-grained moderately to poorly sorted light bluish grey (5B7/1) sandstone, Sp: 1 cm sets in 5 cm cosets.	Tabular to lenticular, 0.15–0.30 m thick, erosional base, laterally amalgamated	Underlies facies Sh and overlies facies Sh and Fl	--------------------------------------	Tractive flows	Confined and unconfined tractive flows representing a **fluvial system**
	Assymmetric-ripple sandstone Sra	Coarse- to medium-grained, moderately sorted yellowish gray (5Y8/1) sandstone. Sra: asymmetric-ripple cross-lamination, 5-cm-thick ripple forms, spacing is 10 cm.	Tabular to lenticular, 1.5 m thick, inclined upper contacts, convex bases	Underlies facies Sh and Sp and overlies facies Sh	--------------------------------------	Tractive flows	
	Planar bedded sandstone Sh	Very fine- to fine-grained, moderately sorted dusky yellow green (5GY 5/2) sandstone. Clasts are angular. Sh: 0.01–0.5 cm laminae, mud drapes.	Tabular to lenticular, 0.5 m thick, erosive base	Underlies and overlies Fm (FA)	Land-plant remains.	Tractive flows	
	Structureless sandstone Sm	Very coarse to medium-grained, poorly to moderately sorted structure less sandstone. Greenish gray (5GY 6/1), yellowish gray (5Y 7/2) and very pale orange (10YR 8/2) with grayish pink (5R 8/2) mottling colors.	Lenticular, laterally amalgamated, sharp bases, 0.15–0.30 m thick, irregular tops	Underlies and overlies Fm (FA)	Sparse faint rhizoliths with mottling. Rhizoliths are 0.5 cm in diameter at the top of the strata and 0.5 cm downwards and extend vertically for 20 cm.	Unconfined tractive flows followed by plant colonization	
	Siltstone Fm	Structureless pale blue green (5BG 7/2) siltstone, sparse spherical light brown (5 YR 6/4) carbonate nodules ~ 4 cm in diameter.	Tabular, 0.5–2.0 m thick	Underlies and overlies Sh and Sm (FA)	Sparse rhizoliths of 1 cm in diameter at the top of the strata and 0.5 cm downwards and extend vertically for 20 cm. Invertebrate traces: 6 ichnogenera representing fodichnia and domichnia.	Suspension settle-out from waning flows followed by plant colonization	
	Finely laminated argillaceous mudstone Fl	Thinly laminated medium dark gray (N4) mudstone: laminae are 1 mm thick. Clay assemblage dominated by illite and minor smectite and kaolinite.	Tabular 0.05–2.5 m thick	Underlies and overlies facies Sh and Tl	Land-plant remains, fish scales.	Suspension settle-out and tractive transport	
	Tuffaceous sandstone Tl	Very fine-grained-massive tuff.	Tabular, 0.4 m thick	Underlies and overlies facies Fl	--------------------------------------	Ash fall	
B	Planar bedded sandstone Sh	Medium-grained, moderately sorted dusky yellow green (5GY 5/2) sandstone. Clasts are angular. Sh: 1 cm laminae in sets of 5 cm and cosets 10 cm thick, sometimes muddy, silt drapes.	Tabular, 0.5–2 m thick	Underlies and overlies Fm (FB)	Sparse to common land-plant remains.	Tractive flows	**Lake margin**
	Rippled sandstone Srs	Fine- to very fine-grained, well-sorted greenish gray (5G 6/1) sandstone alternating with muddy silty layers of 1 cm thick. Muddy silty layers are 1 cm thick. Ripple cross-lamination shows 1–10 cm-high symmetric ripples with 7–45 cm spacing, present only at the top of the strata. Cut-and-fill structures.	Tabular to laterally amalgamated lenses, 0.1–0.5 m thick, sharp bases	Underlies facies Cl and Sh (FB), overlies Fm and Fl (FC)	----------------------------	Waves and wave reworking	
	Structureless sandstone Sm	Medium-grained, poorly to moderately sorted structure less moderate red (5R 4/6), greenish gray (5GY 6/1), yellowish gray (5Y 7/2) and very pale orange (10YR 8/2) arkosic sandstone.	Tabular, sharp bases, 0.15–0.30 m thick	Underlies and overlies Fm (FB)	Common land-plant remains. Vertebrate footprints (MFM), Invertebrate traces: 16 ichnogenera representing domichnia, fodichnia, pascichnia, repichnia, and cubichnia.	Unconfined tractive flows	
	Siltstone Fm	Structureless siltstone with abundant mud cracks and raindrop marks.	Tabular, very thin levels (0.5 cm) forming deposits of 0.5–1.5 m thick	Underlies facies Sh, Srs, and Sm and overlies facies Cl, Sh, and Sm	Land-plant remains, vertebrate footprints (MFM). Invertebrate traces: 7 ichnogenera representing domichnia, fodichnia, repichnia, pascichnia.	Suspension settle-out from waning flows and subsequent exposure	
	Laminated carbonates Cl	Planar to domal laminated moderate blue (5B 5/6) limestone, sometimes with subangular carbonate intraclasts of 1 mm.	Tabular, 0.40–0.75 m thick	Underlies Fm and Sm (FB) and overlies Srs (FB)	-------------------	Subaqueous precipitation and minor clastic input	
	Thinly laminated argillaceous mudstone Fl	Mudstone, light gray (N4) with Fl: laminae are 1 mm, thick.	Tabular 0.25–0.5 m	Overlies and underlies Fm and Sm	Land-plant remains.		
C	Thinly laminated argillaceous mudstone Fl	Mudstone, dark gray (N3) with Fl: laminae are 1 mm, thick, Fe concretions 5–20 cm in diameter, variable organic matter content associated with pyrite.	Tabular 0.25–11 m thick	Overlies and underlies Cl, and Srs (Delta front) and Sh (Lake margin) and Sh (Floodplain overbank splay); overlies facies Cl and Sm and Sh (Lake margin) and Srs (Delta front)	Land-plant remains, fish remains.		Suspension settle-out and current transport in the profundal zone of the **lake center**
	Laminated carbonate Cl	Structureless to faintly laminated carbonate of dominant dolomite composition.	Tabular, 0.05–0.5 m thick	Underlies and overlies facies Fl	Laminae can be interpreted as traces of microbial activity.		
D	Trough cross-stratification St	Coarse- to medium-grained moderately to poorly sorted yellowish gray (5Y8/1) sandstone. St: 5 cm sets in 15 cm cosets.	Tabular to lenticular, 3 m thick	Overlies facies Sra	--------------------------------------	Tractive flows	Unconfined and confined erosive (channel) tractive flows in the **delta front** representing inflow of sediment and water supply from the distributary system to the lacustrine system
	Planar-cross-bedded sandstone Sp	Coarse to medium-grained moderately to poorly sorted light bluish gray (5B7/1) sandstone. Sp: 1 cm sets in 5 cm cosets.	Tabular to lenticular, 0.50 m thick	Underlies facies Sh and overlies facies Sh and Fl	--------------------------------------	Tractive flows	
	Assymmetric-ripple sandstone Sra	Medium-grained, moderately sorted yellowish gray (5Y8/1) sandstone. Sra: asymmetric ripple cross-lamination, 5–7-cm-thick ripple forms, spacing is 10–15 cm.	Tabular, 1.5 m thick, inclined upper contacts, convex bases	Underlies facies Sh and Sp and overlies facies Sh	--------------------------------------	Tractive flows	

TABLE 2.—*Continued.*

Facies	Lithofacies	Sedimentary Structures	Bed Geometry	Vertical and Lateral Relations	Fossil Content	Processes	Facies Interpretation
	Planar bedded sandstone Sh	Medium-grained, moderately sorted dusky yellow green (5GY 5/2), very pale orange (10YR 8/2) and yellowish gray (5Y 8/1) sandstone. Clasts are angular. Sh: 0.5 to 5 cm laminae in sets of 2 to 10 cm and cosets of 10 to 30 cm thick. Rip-up clasts and convolute structures. Muddy and silty drapes.	Tabular to lenticular, 0.5–2 m thick, inclined tops, convex to erosive bases	Underlies facies Srs, Sra and Sp overlies facies Fl (lake center), Fh, Sp and Sra		Tractive flows	
	Planar bedded to massive siltstone Fm Fh	Massive or structureless to planar bedded muddy pale blue green (5BG7/2) to light bluish gray (5B7/1) siltstone, laminae are 1 cm thick.	Tabular, 0.1–0.5 m thick	Underlies Sh and overlies facies Sp	Invertebrate traces: six ichnogenera representing domichnia, repichnia, fodichnia, pascichnia.	Suspension settle-out	
	Thinly laminated argillaceous mudstone Fl	Mudstone, light gray (N4) with Fl: laminae are 1 mm, thick.	Tabular 0.25–0.5 m	Overlies Sr and underlies Sh			
E	Clast-supported conglomerate Gm	Grain-supported conglomerate. Matrix is coarse sandstone. Volcanic and siliciclastic clasts of 1–15 cm, subangular to rounded, poorly sorted. Colors are grayish green (10G 4/2) and pale blue green (5BG 7/2).	Lenticular 1.85 m thick, erosional base	Underlies facies Fm overlies facies Sh	------------------------	Erosive tractive flows	**Delta plain**
	Assymmetric-ripple sandstone Sra	Coarse- to medium-grained, moderately sorted yellowish gray (5Y8/1) sandstone. Sra: asymmetric ripple cross-lamination, 5–7-cm-thick ripple forms, spacing is 10–15 cm. Mud chips.	Tabular to lenticular, 0.5 m thick	Underlies facies Sh and Sp and overlies facies Sh and Fh	Plant remains, possible root traces. Invertebrate traces: one ichnogenus representing domichnia.	Tractive flows	
	Planar-tabular cross-bedded sandstone Sp	Coarse- to medium-grained moderately to poorly sorted yellowish gray (5Y8/1) sandstone, planar cross stratification is 1 cm thick.	Tabular to lenticular, 0.50 m thick	Underlies facies Sh and overlies facies Sra	Invertebrate traces: seven ichnogenus representing domichnia, repichnia, fodichnia, cubichnia, and praedichnia.	Erosive tractive flows	
	Planar bedded sandstone Sh	Very fine- to medium-grained, moderately to well sorted grayish yellow (5Y8/4) sandstone. Clasts are angular. Sh: 0.5 cm laminae in sets of 2 cm and cosets 6 cm thick, muddy, silt drapes. Mud cracks with 10 cm wide polygons in muddy silt drapes.	Tabular to lenticular, 0.5 m thick	Underlies facies Sra, Fc and Fh overlies facies Fh, Sra, Sp and Fc	Common land-plant remains Santa Clara Abajo: Invertebrate traces: 11 ichnogenera representing domichnia, fodichnia, Pasichnia, cubichnia, repichnia. Santa Clara Arriba: Vertebrate footprints (HFM), Invertebrate traces: 8 ichnogenera representing domichnia, fodichnia, repichnia, cubichnia.	Tractive flows	
	Siltstone Fh Fm	Massive or structure-less to planar bedded muddy pale blue green (5BG7/2) siltstone, laminae are 1 cm thick, muddy component with mud cracks.	Tabular, 0.1–0.5 m thick	Underlies Sh, Sra, and Fc and overlies facies Sh	Land-plant remains, common. Santa Clara Arriba: Very abundant vertebrate footprints: MFM, Invertebrate traces: 19 ichnogenera representing domichnia, fodichnia, pascichnia, repichnia, cubichnia.	Suspension settle-out	
	Coaly mudstone Fc	Structureless black (N1) mudstone rich in OM.	Tabular, 0.2–2 m thick	Underlies facies Sh and overlies facies Fh	--------------------------------------	Suspension settle-out	
	Finely laminated argillaceous mudstone Fl	Thinly laminated medium dark gray (N4) mudstone: laminae are 1 mm thick.	Tabular to lenticular 0.05–0.5 m thick	Underlies and overlies facies Sh and Tl	--------------------------------------	Suspension settle-out	
	Tuffaceous sandstone Tf	Very fine-grained-massive tuff.	Tabular, 0.4 m thick	Underlies and overlies facies Fl	--------------------------------------	Ash fall	
F	Horizontally stratified sandstone Sh	Fine- to very fine-grained, moderately sorted light bluish gray (5B7/1) sandstone. Clasts are angular. Sh: 0.5 cm laminae in sets of 2 cm. Mud drapes.	Tabular to lenticular, 0.1-0.5 m thick	Underlies and overlies facies Fl, and Tl	Land-plant remains; five ichnogenera representing fodichnia, domichnia, cubichnia, and repichnia.	Tractive flows	Sandstone sheets at the **prodelta** with major contribution of fine deposits of the lacustrine system. Ash-fall contribution.
	Finely laminated argillaceous mudstone Fl	Thinly laminated medium dark gray (N4) mudstone: laminae are 1 mm thick. Clay assemblage dominated by illite and minor smectite and kaolinite.	Tabular 0.05–2.5 m thick	Underlies and overlies facies Sh and Tl	Land-plant remains, fish scales.	Suspension settle-out and tractive transport	
	Tuffaceous sandstone Tl	Very fine-grained-tuff, single layer, containing angular quartz (70%) and K-feldspar (5%) crystals up to 1 mm long and 0.5 mm crystals of opaque minerals in a structureless texture in the upper 85 cm with faint horizontal laminae (5 mm thick) of silty sandstone in the lowermost 15 cm.	Tabular 1 m thick	Underlies and overlies facies Fl	--------------------------------------	Ash fall	

TABLE 3.—*Facies with ichnological and vertebrate track content and their biogenic characteristics, Santa Clara Abajo and Santa Clara Arriba formations (Middle Triassic), Santa Clara sub-basin, central Cuyana basin, Mendoza, Argentina.*

Facies	Lithofacies	Ichnofossils	Ichnofossil Tiers (ecological niches)	Physical Processes	Paleoenvironmental Conditions and History
A	Sh Sm Fm	Rhizoliths (common); *Planolites* (abundant); *Naktodemasis* (cf. *Taenidium*), *Palaeophycus* (isolated individuals), *Skolithos* (isolated individuals), *Spongeliomorpha* (common); *Edaphichnum* (few).	Subaerial, shallow, and mid tiers (terraphilic, hygrophilic)	Tractive flows, unconfined tractive flows, suspension settle-out from waning flows.	• Floodplain inundation by overbank flow of the proximal distributary system. • Subsequent subaerial exposure and colonization by land plants.
B	Sh Srs Sm Fm Cl	Vertebrate footprints (MFM); *Palaeophycus*, *Planolites* (very abundant); *Arenicolites* (abundant); *Sagittichnus*, *Skolithos* (isolated individuals) (common); *Archaeonassa*, *Aulichnites*, *Haplotichnus*, *Helminthoidichnites*, *Lockeia*, *Naktodemasis* (cf. *Taenidium*), plough trails, cf. *Tigillites* (linear clusters of *Skolithos*), *Vagorichnus* (few); *Cylindricum*, *Spongeliomorpha* (sparse).	Subaqueous, shallow, and mid tiers, subaerial, epifaunal/surface layer, shallow and mid tiers; (hydrophilic-endobenthic shallow >> hydrophilic-epibenthic, hygrophilic, terraphilic > hydrophilic-endobenthic intermediate, epi-terraphilic)	Subaerial exposure and groundwater table withdrawal, unconfined tractive flows, waves, suspension settle-out, subaqueous precipitation.	• Intermittent standing water with frequent subaerial exposure. • Alternating high- and low-energy episodes. • Occasional fast sedimentation rates, with frequent pauses.
D	Sp Sra Fm Fh Sh	*Planolites* (abundant); *Diplichnites*, *Haplotichnus*, plough trails, and *Skolithos* (mostly as isolated individuals, and a few in linear clusters (cf. *Tigillites*)) (common)	Subaqueous, epifaunal, surface layer, shallow, and mid tiers. (Hydrophilic-epibenthic, hydrophilic-endobenthic shallow > hydrophilic-endobenthic intermediate)	Erosive and non-erosive tractive flows, suspension settle out from waning flows and reworking.	• Persistent inundation. • Alternating high-, moderate-, and low-energy episodes. • Fast sedimentation rates. • Turbid waters.
E	Gm Sp Sra Sh Fl Fc	Santa Clara Abajo Formation: *Arenicolites*, *Helminthopsis*, *Palaeophycus* (isolated individuals) (very abundant); *Planolites*, *Sagittichnus*, *Scoyenia* (abundant); *Skolithos* (isolated individuals) (common); *Aulichnites*, *Naktodemasis* (cf. *Taenidium*) (few); *Lockeia*, *Spongeliomorpha* (sparse). Santa Clara Arriba Formation: Vertebrate footprints (MFM); *Archaeonassa*, *Cylindricum*, *Diplichnites, Haplotichnus,* plough trails (common); cf. *Tigillites* (linear clusters of *Skolithos*), *Circulichnus, Edaphichnium, Radulichnus* (few); plug-shaped burrows (cf. *Conichnus*) *Selenichnites* (very sparse).	Subaqueous, epifaunal, surface layer, shallow, and mid tiers; subaerial, epifaunal/surface layer, shallow and mid tiers (hydrophilic-endobenthic shallow >> hydrophilic-epibenthic, terraphilic, hygrophilic > hydrophilic-endobenthic intermediate)	Tractive flows, suspension settle-out and tractive transport.	• Erosion related to high-energy episodes of the delta-distributary system. • Frequent exposure with infrequent flooding to intermittent subaerial exposure with frequent flooding, persistently high groundwater table, and persistent standing water in ponds. • Dominantly low energy, with infrequent, episodic high-energy events. • Dominantly low net sedimentation rates: frequent pauses with intermittent high-sed-rate episodes.
F	Fl Cl Sh Tl	*Planolites, Sagittichnus* (common); *Archaeonassa*, cf. *Siphonites* (clusters of Palaeophycus), and cf. *Treptichnus* (few)	Subaqueous, epifaunal, surface layer, shallow, and mid tiers (hydrophilic-endobenthic shallow > hydrophilic-epibenthic, hydrophilic-endobenthic intermediate)	Tractive flows, suspension settle-out, precipitation and ash fall.	• Persistent standing water. • Alternating high and low energy episodes • Intermittently fast sedimentation rates, with frequent pauses

(Fig. 8A), laminated mudstone (Fl), coaly mudstone (Fc), and tuffaceous sandstone (Tf) (Table 2). The most diagnostic lithofacies is Fc, which occurs in 0.2–2-m-thick beds very rich in land-plant debris (Fig. 8B).

This facies is characterized by repetitive alternating packages of sandstone beds, siltstone, and mudstone in equal proportions. Predominant bed geometry is tabular. The lower part of the section, however, contains lenticular conglomerate beds with erosional bases between approximately 60 and 82 m of the log (Fig 3). Siltstone beds contain very abundant bioturbation and cracks in muddy drapes and plant fragments; sandstone beds are bioturbated as well, although less intensely. Sandstone and siltstone packages thin upwards and can be capped by Fc facies (Fig. 3).

Ichnology.—FE contains a high- to very high-diversity ichnofauna that varies among lithofacies and between the Santa Clara Abajo (11 ichnogenera) and Santa Clara Arriba (2 ichnogenera) formations, the highest-diversity assemblage of trace fossils in both formations; Table 3).

In the Santa Clara Abajo Formation, lithofacies Sh (e.g., ca. 80 m in Fig. 5) contains a high-diversity assemblage of horizontal and vertical traces including 11 ichnogenera: very abundant *Arenicolites*, *Helminthopsis*, and *Palaeophycus*, abundant *Planolites*, *Sagittichnus*, and *Scoyenia* (Fig. 8C–E; Table 3), common *Skolithos* (Fig. 8F), few *Naktodemasis* (cf. *Taenidium*), and *Aulichnites* (Fig. 8G, H), and sparse *Lockeia* (Fig. 8F) and *Spongeliomorpha* (Table 3).

The Santa Clara Arriba Formation contains invertebrate trace fossils and vertebrate tracks in three lithofacies. Lithofacies Fh at approximately 148 m of the log (Fig. 5) contains vertebrate tracks with high-fidelity mode (HFM) (Fig. 8I) as well as moderate-fidelity mode (MFM) (Fig. 8H, J). The very highly diverse assemblage of invertebrate traces (15 ichnogenera) contains horizontal, inclined, and vertical forms that include very abundant *Arenicolites*, abundant *Palaeophycus*, *Planolites*, *Sagittichnus*, and *Naktodemasis* (cf. *Taenidium*), common *Archaeonassa*, *Aulichnites*, *Scoyenia*, and *Skolithos* (mostly as isolated individuals, and a few in linear clusters (cf. *Tigillites*)) (Fig. 8F, H), few *Diplichnites*, *Haplotichnus*, and *Radulichnus*, sparse *Circulichnus*, and very sparse "plug-shaped burrows" (cf. *Conichnus*), and *Lockeia* (Fig. 8F, I; Table 3). At other stratigraphic levels, lithofacies Fh contains these plus four additional ichnotaxa in varying abundances: commonly observed *Cylindricum* (Fig. 9A), *Spongeliomorpha* (Fig. 9B), and *Edaphichnium*, and very sparse *Selenichnites* (Fig. 9A) (Table 3) (there are very sparse occurrences of traces that somewhat resemble *Eatonichnus* and *Coprinisphaera*, which would be some of the earliest reported occurrences, but the examples and currently available data do not permit a definitive diagnosis). Lithofacies Sh at approximately 108 m of the log (Fig. 5) contains vertebrate footprints and a highly diverse assemblage of horizontal and vertical traces (eight ichnogenera). Vertebrate footprints correspond to the high-fidelity mode (HFM). Invertebrate traces include very abundant *Arenicolites*, abundant *Palaeophycus*, common *Sagittichnus*, *Skolithos* (mostly as isolated individuals, and a few in linear clusters (cf. *Tigillites*)), *Planolites*, and plow trails, and sparse *Edaphichnium* and *Selenichnites* (Table 3). Lithofacies Sp at approximately 150 m on the log (Fig. 5) contains vertebrate footprints and a moderately diverse assemblage of horizontal and vertical traces (7 ichnogenera). Footprints represent the high-fidelity mode (HFM) and invertebrate traces include abundant *Palaeophycus*, common *Arenicolites*, *Diplichnites*, *Haplotichnus*, and linear clusters of *Skolithos*, few *Circulichnus*, sparse isolated *Skolithos*, and very sparse *Lockeia* (Table 3). Lithofacies Sra contains sparse poorly preserved isolated *Skolithos* (or possible root traces). Completely churned layers (BI 5) are common, whereas trampled surfaces are sparse.

All 11 ichnogenera found in the Santa Clara Abajo Formation were found in the Santa Clara Arriba Formation (Table 3). The 11 additional traces found in the Santa Clara Arriba Formation include common *Archaeonassa*, *Cylindricum*, *Diplichnites*, *Haplotichnus*, and plough trails, few cf. *Tigillites* (linear clusters of *Skolithos*), *Circulichnus*, *Edaphichnium*, and *Radulichnus*, and very sparse plug-shaped burrows (cf. *Conichnus*) and *Selenichnites*. This is the only facies in which *Circulichnus*, plug-shaped burrows (cf. *Conichnus*), *Edaphichnium*, *Helminthopsis*, *Radulichnus*, and *Selenichnites* were observed.

Interpretation.—FE is interpreted to record a variety of settings with relatively short episodes of high energy and sedimentation rates with subsequent pauses in sedimentation and laterally variable withdrawal of the groundwater table. The lenticular geometry of the Gm beds, their erosional bases, and clast sizes suggests episodes of high-energy tractive flows confined in distributary channels (e.g., Giosan and Bhattacharya 2005; James and Dalrymple 2010; Renaut and Gierlowski-Kordesch 2010; Baganz et al. 2012). Lithofacies Sra records relatively persistent (minutes to hours) unidirectional traction transport under relatively slow flow velocities (cf. Southard and Boguchwal 1990; Fielding 2006) during the rising or falling limbs of flood hydrographs in both confined (channel) and unconfined (levee, overbank, crevasse splay) settings. Sp also records unidirectional tractive transport but under higher flow velocities and longer-duration flows (hours to days; cf. Middleton and Southard 1984; Fielding 2006), nearer the peak of flood hydrographs, most probably in such confined settings as stream and crevasse channels and proximal crevasse splays. Sh records the influence of tractive flows under relatively high flow velocities or shallow water depths or both (i.e., upper-plane-bed conditions; Fielding 2006) which occur in confined and unconfined settings. Fh facies record suspension settle-out and benthic transport during waning flows (Schieber 2011) in both confined and unconfined settings. Fm with abundant bioturbation, cracks, and plant fragments suggests intermittent subaerial exposure and invertebrate colonization as well as plant material washed in from the surroundings, most likely in overbank and floodplain settings. Fc records significant accumulation of allochthonous (or parautochthonous) land-plant debris in standing bodies of water (e.g., abandoned channels, delta-plain ponds, backswamps). The presence of fluvial channels and exposure indicators along with ponded subenvironments (backswamps, delta-plain ponds) that accumulated large amounts of OM suggests the record of a delta plain (Giosan and Bhattacharya 2005).

The ethological classes of the ichnogenera observed in the facies span domichnia, fodichnia pascichnia, repichnia, and cubichnia (in order of decreasing abundance). The traces occupied epi-terraphilic, terraphilic, hygrophilic, and hydrophilic (epibenthic and endobenthic shallow and intermediate) ecological niches and subaerial epifaunal to deeper tiers and subaqueous epifaunal to mid tiers. This facies comprises the most diverse trace-fossil assemblage in the formation, comprising 22 ichnogenera in all, befitting the intricate facies mosaics typical of such settings. The wide range of trace-fossil types and ecological niches and tiers record a corresponding variety of environmental conditions, from standing water and saturated sediments to prolonged subaerial exposure and deep groundwater tables.

Integrating all lines of evidence indicates a delta-plain environment (epilittoral setting) that comprised a variety of subenvironments including distributary channels and coaly swamps. In those subenvironments conditions ranged from frequent subaerial exposure with infrequent overland flooding by river waters, through intermittent subaerial exposure with frequent overland flooding and persistently high groundwater table, to persistent standing water with intermittent local anoxia in delta-plain ponds. Overall, the setting had dominantly low energy, with infrequent, episodic high-energy events with subsequent epifaunal and infaunal activity. Highly diverse and abundant trace-fossil content is commonly reported in other balanced-fill lake examples and is ascribed to the variety of ecological niches, abundance of food and oxygen, and changes in groundwater levels and soil moisture characteristic of a delta plain in a balanced-fill lake basin (e.g., Bohacs et al. 2007; Hasiotis 2007; Scott 2010; Scott and Smith 2015; Buatois and Mángano 2009).

Facies F

Facies F (FF) comprises three lithofacies: thinly laminated argillaceous mudstone (Fl), planar bedded sandstone (Sh), and tuffaceous sandstone (Tl) (Table 2). This facies underlies or overlies facies D (delta front) in most of the section (lower 542 m) and underlies or overlies or facies C (lake center) in the upper 100 m of the section. It is characterized by the dominance of Fl and minor content of Sh in very thin tabular beds. Only one occurrence of Tl lithofacies is identified (at 580 m approximately on Fig. 3).

Ichnology.—FF contains a low-diversity assemblage of horizontal and inclined traces (five ichnogenera) in lithofacies Sh, including commonly occurring *Planolites* and *Sagittichnus*, and few *Archaeonassa*, clusters of *Palaeophycus* (cf. *Siphonites*), and cf. *Treptichnus* (Fig. 9C; Table 3). This is the only facies association in which clusters of *Palaeophycus* (cf. *Siphonites*) and cf. *Treptichnus* were observed. No completely churned layers or trampled surfaces were observed.

Interpretation.—Fl indicates sedimentation dominated by suspension settling with some possible tractive reworking (Schieber et al. 2007; Schieber 2011) and Sh records unidirectional tractive flows under relatively high flow velocities (i.e., upper flow regime; Middleton and Southard 1984). The sparse content contribution of Sh forming very thin tabular beds suggests that this facies resulted from accumulation in an area that was distal to the supply of sediment into the lacustrine system. The bed of Tl records volcanic ash fall with possibly some current reworking in its basal 15 cm. Ethological classes of these ichnogenera span fodichnia, domichnia, cubichnia, and repichnia. The traces are interpreted to have occupied exclusively hydrophilic ecological niches: shallow endobenthic, epibenthic, and intermediate endobenthic. Facies F is interpreted to represent episodic sediment accumulation in an overall low-energy, standing-water setting in a prodelta subenvironment (river-influenced sublittoral zone) with frequent pauses in sedimentation that allowed epifauna and infauna to occupy the recently deposited sediment. The dominance of hydrophilic trace fossils records persistent free-surface water or saturated sediment pores, as does their three-tier distribution (subaqueous epibenthic, endobenthic shallow, and endobenthic intermediate). That the trace-fossil assemblages observed in FF overlap significantly with those of FD is consistent with the genetic relation of the prodelta (FF) strata to delta-front (FD) strata. That trace fossils are more commonly observed in these prodelta strata than in distal sublittoral to profundal (FC) strata that were probably laterally equivalent can be attributed to the intermittent influx of fresh and oxygenated waters due to floods characteristic of a prodelta setting.

Santa Clara Succession Stacking Pattern

The main stacking pattern identified in the Santa Clara succession is aggradational to progradational to retrogradational with distinctly expressed parasequences (Fig. 3). Parasequences are shoaling-upward stratal packages bounded by flooding surfaces identified at the contact of relatively distal environments over proximal environments: fluvial system facies (FA) is overlain by lake margin (FB), lake center (FC) overlies lake margin (FB), delta plain (FE) is overlying lake center (FC), and fluvial system (FA) overlies delta plain (FE). Also, delta front (FD) overlies delta plain (FE) and is overlain by lake center (FC), or prodelta (FF) (Fig. 3). Prodelta (FF) parasequences are delimited by shoaling-upward packages capped by carbonate-cemented sandstone (Fig. 3).

The base of the stratigraphic section studied is characterized by a retrogradational interval with diminishing parasequence thicknesses between 0 and 42 m approximately in the succession; this section marks the transition upward from the fluvial facies (FA) to the lake-margin facies (FB). Overlying the retrogradation a progradational interval is identified between 43 and 102 m with thickening-upwards parasequences marked by the delta front (FD) up into delta plain (FE) facies progression, the lake center (FC) up into delta-plain (FD) facies progression, and the delta-plain (FE) to fluvial-system (FA) progradation. Between 102 and 125 m an aggradational pattern is identified in the delta-plain facies (FE) with repetition of similar-thickness parasequences; between 126 and 153 m the stacking changes to progradational in the delta plain facies (FE). From 153 to 218 m of the log the stacking pattern is progradational and represented by thickening-upwards parasequences of the delta-front facies (FD); between 219 and 248 m the pattern changes to aggradational in FD (Fig. 3).

A progradational pattern is identified between 250 and 372 m; it is characterized by progression from delta-front (FD) to delta-plain (FE) to fluvial-system (FA) facies. A retrogradational interval is observed from 372 to 448 m in which the delta-plain (FE) is overlain by delta-front (FD) and then lake-center (FC) facies. From 448 up to 502 m a progradational stacking pattern is observed in which delta front (FD) passes upward to prodelta facies (FF), indicating a flooding event. Between 502 and 520 m an aggradational pattern is recognized in FD. Between 520 and 544 m a retrogradational stacking pattern is characterized by prodelta (FF) overlain by lake center (FC) facies. The lake-center interval between 544 and 572 m presents an aggradational stacking pattern formed by parasequences with similar thickness capped by carbonates. The uppermost section between 572 and 630 m consists of a progradational pattern (Fig. 3).

Major flooding surfaces, marked by delta-plain (FE) strata abruptly overlain by lake-center (FC) facies, are identified at approximately 74, 84, and 443 m. This contrasts with the general stepwise progression of facies in which intermediate subenvironments are expected to be represented and therefore suggest a tectonic control of deposition in this lake basin. Similar changes have been interpreted as recording tectonic control on other lake basins (e.g., Gore 1988; Benavente et al. 2021b; Wood and Clemens 2002; Pietras et al. 2003).

The facies identified, their progression and lateral and vertical relations, and their stacking pattern suggest a fluctuating profundal facies association for the Santa Clara succession (Carroll and Bohacs 1999; Benavente et al. 2021a). Furthermore, the diagnostic characteristics proposed by Bohacs et al. (2000) for balanced-fill lake basins including interbedded siliciclastic and biochemical lithofacies, presence of both subaqueous and subaerial exposure indicators, and relatively thick intervals with aggradational and retrogradational stratal stacking (compared to progradational intervals) are in agreement with what we have found in the Santa Clara succession. Another key aspect for lake-basin-type classification is content and nature of organic matter (Bohacs et al. 2000), which, in balanced-fill lakes is usually enriched and mixed terrestrial and algal in composition. The lake-center facies (FC) of the Santa Clara succession is of moderate to high organic-matter content, and the palynofacies are dominated by mixed terrestrial–algal components with few exclusively algal lacustrine components at the top (Benavente et al. 2018; Siderac et al. 2022). This is in agreement with the classification scheme as well. All these observations point to a balanced-fill lake type basin and the relatively thin parasequence development in the succession most likely indicates a shallow balanced-fill lake-basin type (Carroll and Bohacs 1999; Bohacs et al. 2000).

Tetrapod Footprint Taphonomy

Two taphonomic modes of tetrapod footprint preservation are present in the Santa Clara formations: moderate fidelity (MFM) and high fidelity (HFM). The modes are defined on their fidelity to the trackmaker's pedal anatomy, including the presence or absence of different morphological and extra-morphological features such as palm pad, digit impressions, claw marks, and marginal rims, among others. The tetrapod footprints are represented by isolated prints, and isolated manus–pes sets.

Moderate-Fidelity Mode (MFM)

Moderate fidelity to the trackmaker's pedal anatomy is characterized by impressions of digits and palms that have little detail. Tracks are poorly defined, being preserved as oval to somewhat irregular outline impressions with a relatively deep shaft. There is no clear evidence of digits or consistent palm or sole dimensions, and they lack deformational structures. The footprints included in this category are preserved in the Fm and Sm facies of the lake-margin facies of the Santa Clara Abajo Formation and on the top of planar bedded muddy siltstone beds (Fh) of the delta-plain facies of the Santa Clara Arriba Formation.

Interpretation.—MFM tracks were made on relatively soft, moderate- to high-plasticity surfaces (sandy and muddy deposits of the delta-plain and lake-margin environments). This interpretation is evidenced by the poorly defined and relatively deep footprint impressions and the absence of deformational structures but with the occurrence of some crosscutting invertebrate traces of soft-substrate suites during subsequent lowering of the groundwater table.

The lithofacies with MFM vertebrate tracks (Sm, Fm, and Fh) are interpreted to have been the result of high rates of sediment accumulation. Beds in these facies were likely to have been poorly packed, with high pore-water content and soft rheologies for some time after deposition. The moderate-fidelity mode of footprints in this setting is probably due to imprinting shortly after deposition, while an elevated groundwater table or shallow standing water and high pore-water content resulted in a moderate-plasticity surface and extensive reworking under a variety of conditions subsequent to final burial (cf. Mancuso et al. 2020, 2022).

High-Fidelity Mode (HFM)

The high-fidelity mode of the trackmaker's pedal anatomy is typified by sharp and detailed impressions of the digits and palms, with clear impression of walls. The palm or sole impressions are separated from those of the digits. The digits are generally associated with claw drag marks. The marks are usually relatively long, sharply incised grooves with well-defined borders. The footprints included in this category are preserved on the top of the muddy siltstone, very fine- to medium-grained, moderately sorted sandstone with planar bedding, coarse to medium-grain moderately to poorly sorted sandstone with planar-cross-bedded sandstone, and siltstones of the delta plain (FE) of the Santa Clara Arriba Formation (facies Sh, Sp, and Fh).

Interpretation.—HFM tracks were imprinted in relatively firm, low- to moderate-plasticity substrates (sandy and muddy deposits in the delta-plain facies), This is evidenced by the well-defined and shallow-depth footprint impressions and the absence of deformational structures and crosscutting invertebrate traces in soft-substrate suites.

The three lithofacies with HFM vertebrate tracks (Sh, Sp, and Fh) are interpreted to have been the result of moderate rates of sediment accumulation under relatively fast and persistent unidirectional currents. Beds in these facies were likely to have been at least moderately well packed and sufficiently permeable to allow relatively rapid drainage during subsequent subaerial exposure and withdrawal of the groundwater table. This would have resulted in an appropriate sediment rheology for high-fidelity preservation of tracks.

Taphonomic Pathways of Balanced-Fill Lake Basin Ichnofaunas

Recurring successions of ichnological assemblages (or suites, *sensu* Mancuso et al. 2020) are associated with specific track preservation modes in particular facies and characterize particular taphonomic paths along a continuum of ichnological processes (Fig. 10). The taphonomic pathways are summarized by key indicator ichnotaxa described in the text and shown in Figure 10, for clarity not all ichnotaxa are described in this section or shown in the figure. The recurrent suites observed in the Santa Clara formations are interpreted to represent snapshots of various ichnocoenoses and their successions in response to changes in substrate humidity and rheology (Supplemental Table 1). Thus, Suite 1 records tracks, trails, and burrows of epibenthic and shallow endobenthic fauna on and in a softground substrate under standing water. Suite 2 represents tracks, grazing and deposit-feeding traces, and dwelling structures of hydrophilic and organisms in a softground to firmground substrate. Suite 3 hosts dwelling and reproduction structures along with deposit-feeding and locomotion traces of hygrophilic and terraphilic taxa in a firmground substrate. Recognition of these assemblages and the quality of burrow preservation and their crosscutting relations enables more detailed characterization of depositional conditions and recognition of subdivisions of the main facies (Buatois and Mángano 2004).

In the lake-margin environment (FB) one taphonomic pathway has been identified (Fig. 10). Taphonomic Pathway A contains MFM vertebrate tracks found only in beds of the structureless sandstone (Sm) and siltstone (Fm) facies. The ichnofossil content records a taphonomic path that spans all three suites and ecological niches (tiers) from hydrophilic-endobenthic intermediate to terraphilic, but with decreasing ichnofaunal diversity. The initial recorded ichnocoenosis comprised hydrophilic-epibenthic and shallow endobenthic traces (most commonly *Sagittichnus*, with few *Lockeia*, *Haplotichnus*, *Helminthoidichnites*, and plow trails) made in soft substrates (Suite 1) under standing waters following the deposition of the Sm and Fm beds. Next, burrows, tracks, and trails of hydrophilic shallow and intermediate endobenthic organisms (mostly *Skolithos*, with a few *Aulichnites*, *Archaeonassa*, *Vagorichnus*, *Diplichnites*, and sparse *Cylindricum*) along with MFM vertebrate footprints, followed by *Arenicolites* and *Planolites*, were made in relatively soft media with saturated pore waters (or, perhaps, under very shallow or intermittent standing water; Suite 2; Fig. 10A). With continuing desiccation, hygrophilic and terraphilic organisms that made very abundant *Skolithos* and a few *Spongeliomorpha* next colonized the firmground substrate (Suite 3; Fig. 10A) and eventually, terraphilic organisms that made sparse *Naktodemasis* (cf. *Taenidium*) occupied the upper vadose zone of the sediment (Fig. 10A). Subsequent subaerial exposure was sufficiently long to accumulate desiccation cracks, rain-drop impressions, and land-plant remains, but apparently the duration of groundwater withdrawal was too short (or other conditions unfavorable) to permit more extensive colonization by a diverse set of terraphilic organisms before the strata were buried beyond the limit of burrowing. In addition, although the sediment was relatively well-drained, this taphonomic pathway probably records subaerial exposure of short duration ("normal" subaerial exposure)—that is, this pathway is not associated with sequence boundaries (erosional unconformities or omission surfaces of climatic or tectonic origin) between successive sedimentation episodes (Van Wagoner et al. 1990; Bohacs 1998; Mancuso et al. 2020).

This taphonomic pathway suggests that the MFM tracks were emplaced in the eulittoral zone of the Lake Margin environment (that is, between seasonal high and low lake-water levels), a zone likely to be quite wide because it occurs in a balanced-fill lake basin (e.g., Bohacs et al. 2000, 2007). This pathway is quite consistent with the interpretation of Facies B as accumulating in a lake-margin setting based on the physical attributes of symmetric-rippled sandstone (Srs), planar bedded sandstone and siltstone (Sh, Fh), laminated carbonate (Cl), desiccation cracks, and raindrop impressions.

In the delta-plain facies (FD) four other taphonomic pathways have been recognized: two with MFM tracks (B, D) and two with HFM tracks (C, E; Fig. 10). These pathways are probably associated with particular subenvironments or depositional episodes on the delta plain with different histories of changes in sediment saturation, rheology, and accumulation.

Taphonomic Pathway B contains HFM footprints in the planar bedded sandstone (Sh) lithofacies as well as the planar-tabular cross-bedded sandstone (Sp) and laminated siltstone (Fh) lithofacies (Fig. 10B). The ichnofossil content records a taphonomic path that spans hydrophilic-endobenthic intermediate to

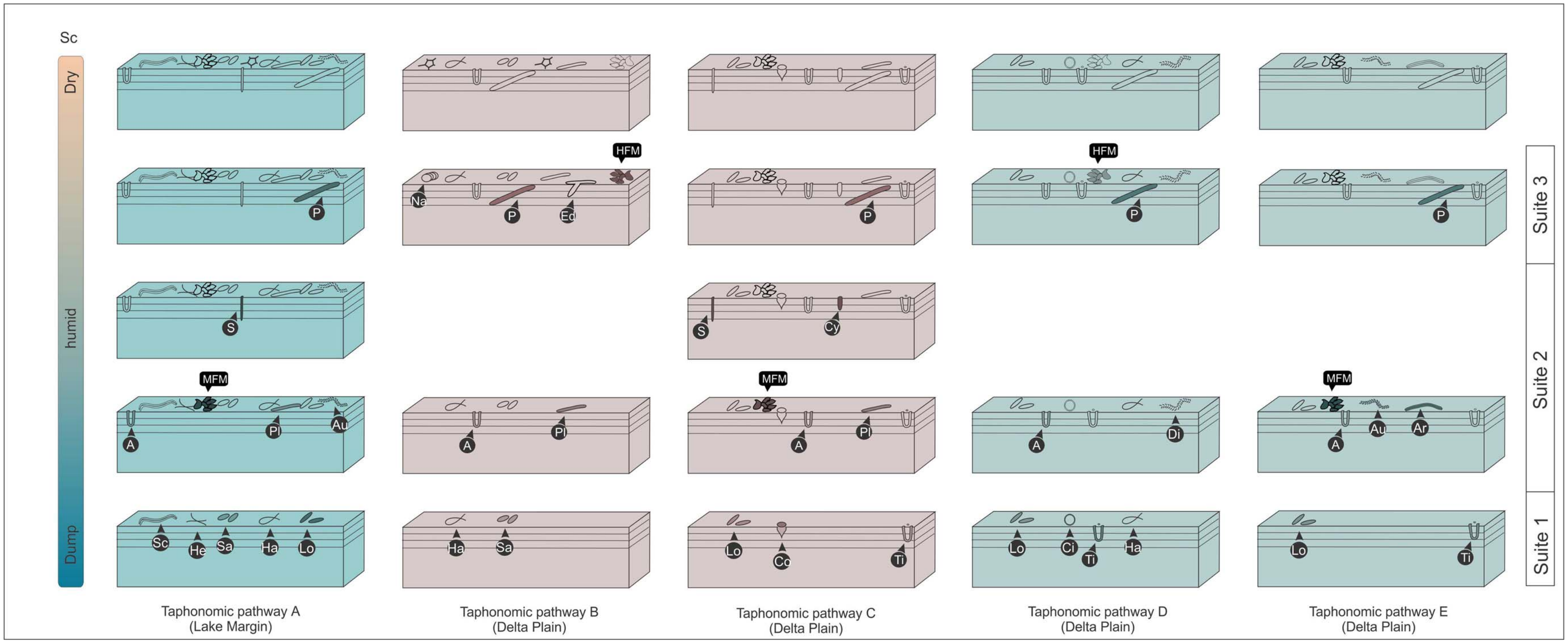

FIG. 10.—Block diagrams of taphonomic pathways illustrating the most diagnostic and abundant invertebrate traces and the tetrapod-tracks taphonomic modes for each suite identified. A, *Arenicolites*; D, *Diplichnites*; Di, *Diplocraterion*; E, *Edaphichnium*; Hi, *Helminthoidichnites*; Ho, *Helminthopsis*; N, *Naktodemasis* (cf. *Taenidium*); P, *Palaeophycus*; S, *Skolithos*.

terraphilic tiers and Suites 1, 2, and 3. The first recorded ichnocoenosis comprised subaqueous epibenthic and shallow-endobenthic traces (common *Haplotichnus* and *Sagittichnus*) which formed in soft substrates under standing waters (Suite 1; Fig. 10B). Subsequently, burrows of hydrophilic shallow and intermediate endobenthic organisms (abundant *Planolites* and *Arenicolites*) formed in moderately soft to firm substrates (Suite 2) with saturated pore waters (or, perhaps, under very shallow or intermittent standing water; Fig. 10B). Next, and with continuing desiccation, hygrophilic and terraphilic organisms that made such traces as *Palaeophycus*, *Naktodemasis* (cf. *Taenidium*), and *Edaphichnium* colonized the subaerial firmground substrate (Suite 3) and are associated with HFM tracks (Fig. 10B). Subsequent subaerial exposure was sufficiently long to accumulate desiccation cracks, but apparently, groundwater withdrawal was too short to permit extensive colonization by a diverse set of terraphilic organisms before burial deeper than biogenic reworking. As with Taphonomic Pathway A, although the sediment was somewhat well drained, this taphonomic pathway probably records "normal" subaerial exposure of short duration, not a major break in sediment accumulation (Van Wagoner et al. 1990; Bohacs 1998; Mancuso et al. 2020). The attributes of this taphonomic pathway, along with the physical attributes and sedimentary structures of the host lithofacies (Sh, Sp, Fh) suggests that such HFM tracks were emplaced in a proximal crevasse-splay subenvironment on the delta plain (e.g., Giosan and Bhattacharya 2005; James and Dalrymple 2010; Renaut and Gierlowski-Kordesch 2010; Banganz et al. 2012).

Taphonomic Pathway C, also on the delta plain (Facies E), contains MFM footprints in the Siltstone (Fh) lithofacies (Fig. 10C). The ichnofossil content records a taphonomic path that spans hydrophilic-endobenthic intermediate to hygrophilic tiers and Suites 1, 2 and 3. The initial recorded ichnocoenosis comprise hydrophilic shallow and intermediate traces (*Lockeia*, plug-shaped burrows (cf. *Conichnus*), and linear clusters of *Skolithos* (cf. *Tigillites*) which formed in soft media under standing waters (Suite 1; Fig. 10C). Subsequently, additional burrows of hydrophilic shallow and intermediate organisms formed in several phases (*Planolites* and *Arenicolites* then crosscut by *Skolithos* and *Cylindricum*) in moderately soft to firm substrates (Suite 2) with saturated pore waters or under shallow standing water, along with MFM tracks (Fig. 10C). Following this phase, and with continuing desiccation, hygrophilic organisms (that made *Palaeophycus*) colonized the firmground substrate (Suite 3; Fig. 10C). In contrast to Taphonomic Pathways A and B, Pathway C does not appear to have been particularly well drained: seven of the eight key indicator ichnotaxa are most probably hydrophilic, only one ichnotaxon is hygrophilic (to possibly terraphilic), and no desiccation cracks were observed. The biogenic attributes of this taphonomic pathway, as well as its physical attributes, bedding (Fh), and stratigraphic context suggest that the MFM tracks were emplaced in a distal crevasse-splay subenvironment on the delta plain (e.g., Giosan and Bhattacharya 2005; James and Dalrymple 2010; Renaut and Gierlowski-Kordesch 2010; Banganz et al. 2012).

Taphonomic Pathway D contains HFM footprints in the planar bedded sandstone (Sh) lithofacies as well as the planar-tabular cross-bedded sandstone (Sp) and laminated siltstone (Fh) lithofacies of the delta plain (Facies E; Fig. 10D). The ichnofossil content records a taphonomic path that spans Suites 1 and 2 almost exclusively. The first recorded ichnocoenosis comprised hydrophilic-epibenthic and shallow and intermediate endobenthic traces (common *Haplotichnus*, and linear clusters of *Skolithos* (cf. *Tigillites*), few *Circulichnus*, and very sparse *Lockeia*) which formed in soft media under standing waters (Suite 1; Fig. 10D). Subsequently, burrows and trails of hydrophilic shallow and intermediate endobenthic organisms (abundant *Planolites*, and common *Arenicolites* and *Diplichnites*) formed in moderately soft to firm substrates with saturated pore waters or under intermittently very shallow standing water (Suite 2; Fig. 10D). Finally, vertebrate footprints with high-fidelity mode (HFM) were emplaced on a firm substrate (Suite 3; Fig. 10D); the associated traces are only one hygrophilic ichnogenus (*Palaeophycus*) but with very abundant individuals. In addition, there is no evidence of prolonged subaerial exposure (terraphilic traces, desiccation cracks) associated with the vertebrate tracks. Thus, it appears that the substrate was persistently water saturated with only episodic and short-lived exposure and drainage. Although the ichnofaunal content of Pathway D is similar to Pathway E (which is associated with MFM footprints), Pathway D has a higher diversity of hydrophilic traces (seven vs. five ichnotaxa) and only one hygrophilic trace (Fig. 10D). This setting was probably similar to that interpreted for Pathway B (the other path with HFM tracks) but not as well drained nor subaerially exposed for as long—the sediment remained more persistently moist (the one non-hydrophilic ichnotaxon is interpreted as hygrophilic and no desiccation cracks were observed). The ichnological associations and successions of this taphonomic pathway, as well as its physical attributes, bedding (Sh, Sp, Fh), and stratigraphic context suggests that the HFM tracks were emplaced in a proximal crevasse-splay subenvironment on the delta plain (e.g., Giosan and Bhattacharya 2005; James and Dalrymple 2010; Renaut and Gierlowski-Kordesch 2010; Banganz et al. 2012).

Taphonomic Pathway E (Fig. 10E) contains MFM vertebrate tracks that were found only in the planar bedded muddy siltstone (Fh) lithofacies in the delta plain (Facies E; 10E). The initial recorded ichnocoenosis comprised hydrophilic-endobenthic shallow and intermediate traces (linear clusters of *Skolithos* (cf. *Tigillites*) and *Lockeia*) which formed in soft substrates under standing waters (Suite 1; Fig. 10E). Next, burrows of hydrophilic shallow and intermediate endobenthic organisms (abundant *Arenicolites*, common *Archaeonassa* and *Aulichnites*), along with MFM vertebrate footprints were made in relatively soft media (Suite 2) with saturated pore waters (or, perhaps, under very shallow or intermittent standing water; Fig. 10E). The last phase is represented by a few individuals of one hygrophilic ichnogenus (*Palaeophycus*; Suite 3), and no terraphilic traces or mud cracks were observed in association with the vertebrate tracks. Thus, it appears that the substrate was the most persistently soft and water saturated of all the taphonomic pathways. This setting was probably similar to that interpreted for Pathway C (the other path with MFM tracks on the delta plain (FE)) but even more persistently poorly drained and subaerially exposed for shorter periods—perhaps in or around a delta plain that was at most seasonally dry (e.g., Cohen et al. 2005; Giosan and Bhattacharya 2005; James and Dalrymple 2010; Renaut and Gierlowski-Kordesch 2010; Banganz et al. 2012). In addition, the lower diversity of its ichnofossil assemblage (six ichnotaxa, the lowest of all taphonomic pathways) and the predominance of hydrophilic traces (five of six ichnotaxa) with only one hygrophilic trace in the same lithofacies and general setting as Pathway C also suggests that strata that exhibit Pathway E were buried below the zone of bioturbation reworking more quickly (e.g., Buatois and Magano 2002; Hasiotis 2004, 2007, 2008).

Among all the taphonomic pathways, nine ichnotaxa are found associated with both HFM and MFM: *Arenicolites*, *Haplotichnus*, *Lockeia*, *Naktodemasis* (cf. *Taenidium*), *Palaeophycus*, *Planolites*, *Sagittichnus*, plow trails, and *Skolithos* (as isolated individuals and linear clusters (cf. *Tigillites*)). Their primary ecological niches (tiers) are three hydrophilic-endobenthic shallow, two hydrophilic-epibenthic, two hygrophilic, one hydrophilic-endobenthic intermediate, and one terraphilic. Eight additional ichnotaxa are found only associated with MFM tracks: *Archaeonassa*, *Aulichnites*, *Cylindricum*, *Helminthoidichnites*, *Helminthopsis*, *Scoyenia*, *Spongeliomorpha*, and *Vagorichnus* (Supplemental Table 1). Their primary ecological niches (tiers) are five hydrophilic-endobenthic shallow, two hygrophilic, and one hydrophilic-epibenthic. Thus, MFM tracks are associated with a total of 13 hydrophilic out of 18 ichnotaxa (three epibenthic, nine shallow, and one intermediate), along with four hygrophilic and only one terraphilic traces—consonant with the generally soft and saturated substrate envisioned for MFM preservation mode. Four other ichnotaxa are found only associated with HFM tracks: *Circulichnus*, *Diplichnites*, *Edaphichnium*, and *Selenichnites*. Their primary ecological niches (tiers) are two hydrophilic-endobenthic shallow, and one each hydrophilic-epibenthic and terraphilic. Thus, HFM tracks are associated with a total of 10 of 14 hydrophilic (three epibenthic, six shallow, and one intermediate), two hygrophilic, and two terraphilic traces.

Overall, a common pattern of ichnological succession is evident in these facies associations. The initial ichnocoenoses comprises hydrophilic-epibenthic and shallow endobenthic traces, probably of dipteran larvae and other arthropods, oligochaete annelids, bivalves, ostracods, gastropods, and nematodes, in soft media beneath shallow and relatively stable standing waters (Suite 1). Next, as the standing water withdrew, the sediment surface was exposed (at least intermittently), and water content of the substrate fluctuated, the sediment was occupied by such hydrophilic shallow and intermediate endobenthic organisms as gastropods, semiaquatic insects and their larvae (beetles, centipedes, mayflies, millipedes, wasps), and polychaete and oligochaete annelids that produced the grazing, deposit-feeding, and locomotion traces and dwelling structures of Suite 2. Eventually, when the sediment surface was persistently exposed, the groundwater table withdrew for longer periods, and soil moisture varied substantially, hygrophilic and terraphilic organisms of Suite 3 (such as beetles and their larvae, cicadas, mole crickets, oligochaete annelids, and wasps) colonized the firmground substrate, making dwelling and reproduction structures as well as deposit-feeding and locomotion traces. What influences the footprint taphonomic mode appears to be the time span between substrate deposition and track emplacement, speed of pore water drainage, duration of subaerial exposure following track emplacement, and recurrence interval of subsequent sediment-accumulation events that buried the tracks.

DISCUSSION

Paleoichnology and Paleolimnology of the Santa Clara Abajo and Santa Clara Arriba Formations

The character and distribution of ichnofossils in these formations is quite typical of terrestrial and lacustrine settings, with ichnofossil occurrence, diversity, and abundance increasing away from the lake center. The delta-plain setting (FE) contains the most diverse invertebrate trace-fossil assemblages in the formations (22 ichnogenera), with six ichnogenera that are seen only in the delta plain. This is in accordance with the intricate facies mosaics typical of such settings that provided many ecological niches within and among the laterally varying subenvironments (e.g., Bohacs et al. 2007; Scott et al. 2012). The distribution of modern biota vertically and laterally is influenced strongly by their physiological needs or tolerance of water, soil moisture, salinity, and ecological interactions with other organisms (e.g., Aber and Melilo 1991). Based on these factors, ichnofossils made by such organisms can be placed into one of four ecological categories (or tiers) that indicate their use of the soil profile and groundwater moisture zones occupied (Table 1; Hasiotis 2002). The lateral and vertical distribution (or tiering) of ichnofossils also reflects the evolution of the ancient soil-moisture levels and groundwater tables during and after the deposition (Hasiotis 2004, 2007, 2008; Buatois and Mángano 2009; Scott et al. 2012; Hasiotis et al 2012).

Conditions in the lake that influenced the biota also varied between the time periods recorded by the Santa Clara Abajo and Santa Clara Arriba formations. In the Santa Clara Abajo Formation, with a mix of wave- and river-influenced shorelines, ichnogenera were widely distributed in all facies except for FC. This may indicate relatively hospitable (in terms of oxygen, food, and turbidity) and stable environmental conditions. In contrast, in the Santa Clara Arriba Formation, with river-dominated shorelines, ichnotaxa were more restricted in their distribution: six ichnogenera were found only in the delta plain (FE), one only in proximal delta front (FD), one only in distal delta front (FE), and two only in prodelta facies (FF). These restricted occurrences suggest more stressed conditions in the lake associated with the variable turbidity, salinity, and energy levels of its river-dominated environments.

Vertebrate tracks can provide additional insights about the tempo of sedimentation and groundwater changes. HFM results from relatively slow and organized sediment accumulation from traction transport (Sh, Sp, Fh facies for Santa Clara Arriba Fm.), relatively rapid exposure and drainage of newly deposited sediment with track imprinting soon thereafter, and relatively short subaerial exposure until the next sediment-accumulation event and burial. MFM results from relatively rapid sediment accumulation from upper-flow-regime or mass flows (Sm and Fm lithofacies for Santa Clara Abajo Fm. and Fh lithofacies for Santa Clara Arriba Fm.), relatively slow exposure and drainage with track imprinting on soggy substrates, and relatively long exposure and biogenic reworking until the next sedimentation event and burial.

The intermittently open hydrography and hydrology of the system likely kept the lake waters relatively fresh with only moderate changes in salinity (cf. Horsfield et al. 1994; Bohacs et al. 2000). During periods of closed hydrography, lake salinity would increase somewhat, which concentrated nutrients, enhanced the production of aquatic organic matter, and provided abundant food for fish and other aquatic metazoans (e.g., Ryder 1965; Matuszek 1978; Smith 1979), but not elevated enough for salinity be a significant stressor.

Footprint Preservation

Although invertebrate traces are found in the fluvial system and deltaic subenvironments of the Santa Clara Abajo and Santa Clara Arriba formations, vertebrate tracks are recorded exclusively in the lake-margin and delta-plain subenvironments (Fig. 5). This indicates that only these two subsettings provided a suitable initial moist surface in which the tracks could be imprinted that later experienced short subaerial exposure producing a firm, erosion-resistant substrate that was subsequently buried (cf. Mancuso et al. 2020). The taphonomic modes identified in this study indicate that two main sets of conditions can be identified for footprint preservation in the succession: MFM tracks are associated with high-water content sediment whereas HFM tracks indicate relatively low moisture content.

Other significant factors in track preservation are the clay-mineral amount and type. No swelling clays have been identified through XRD in the Santa Clara Abajo and Arriba formations, with assemblages being dominated by illite, except for one sample from the Fl lithofacies of the Santa Clara Arriba Formation showing minor expandable clay smectite-group contribution (Benavente et al. 2021a). The predominance of non-swelling clays in the succession is linked to the moderate- and high-fidelity modes of footprints (HFM, MFM), as opposed to sediments with swelling clays which tend to produce low fidelity mode of preservation (MFM) due to plastic collapse of the footprints, and shrinking and swelling during subsequent subaerial exposure (cf. Scott et al. 2010; Mancuso et al. 2020, 2022a, 2022b). This absence of swelling clays in the Santa Clara formations explains the lack of MFM footprints.

Humidity and the proportion of clay versus sand in the beds are defining factors in preservation as well. Beds that preserve footprints have approximately equal proportions of clay- and sand-size components, and this is consistent throughout the succession (Benavente et al. 2021a). This grain-size mix also leads to two possible taphonomic modes, moderate or high fidelity, same as with the type of clay present. Therefore, in the Santa Clara succession footprints, the key determinant factor between the development of HFM or MFM is the humidity of the substrate. As shown in Figure 10, ichnofossil assemblages dominated by diverse hydrophilic traces (Suite 2) associated with persistently high moisture content bears MFM tracks, whereas ichnofossil assemblages with significant content of hygrophilic and terraphilic traces (Suite 3) associated with low moisture content preserves HFM tracks. Similar influences on MFM and HFM track preservation have been observed in the delta-plain facies of the Triassic Los Rastros Formation, Ischigualasto–Villa Unión Basin (an overfilled lake-basin system; Mancuso et al. 2022b).

Integrated Characterization of the Santa Clara System

In previous work on the Santa Clara formations (Benavente et al. 2020, 2021a), we have been able to reconstruct large-scale paleohydrological trends integrating sedimentology, stratigraphy, mineralogy, C and O stable isotopes, and taphonomy. These lines of evidence reveal fluctuating thermal conditions of the water column for the Santa Clara Abajo Formation and a generally long water-residence time for the Santa Clara Arriba Formation with a shorter residence time upwards in the succession. Both proxies, geochemistry and taphonomy, indicate that the paleohydrology of the Santa Clara balanced-fill system was controlled by climate fluctuations (Benavente et al. 2018, 2020, 2021a). In addition, ichnoassemblages provide a much higher-resolution record of paleohydrological fluctuations. Traces provide an essentially instantaneous record that is not altered or reworked, in contrast with organic and inorganic chemical attributes that are a record integrated over the time of precipitation, preservation, and postdepositional alteration (e.g., Tissot and Welte 1984; Horsfield et al. 1994; Buatois et al. 2020). Ichnofossil analyses can refine the time-averaged picture obtained from stable isotope data. Each trace fossil records the animal's response to synoptic conditions. Trace-fossil assemblages record the interactions among the members of an ecological community and the changes in substrate conditions over relatively short periods—the time required for the sedimentary layer to be buried beyond the deepest zone of active bioturbation (Droser and Bottjer 1993; Hasiotis 2007; Hasiotis et al. 2013).

Integrating all lines of evidence enable us to consider the relative influences of climate, tectonics, and hydrology on this lake system. Mixed progradational–aggradational–retrogradational stratal stacking and sediment character indicate intermittently open surface-water flow whereas stable isotopes suggest long groundwater residence time with stratigraphic trend upwards to shorter residence time linked to a change from an aggradational to a progradational stratal stacking pattern (Benavente et al. 2021a). The active rift-basin setting, broader-scale stratal stacking, and the occurrence of three abrupt major flooding surfaces suggest the possibility of tectonic influences on hydrography and lake level changes through changes in spill-point elevation and basin bathymetry (cf. Bohacs et al. 2003).

Lake-Basin-Type Context

The Santa Clara Abajo and Santa Clara Arriba formations were deposited during the Middle Triassic and represent a balanced-fill lake-basin system in which we have identified fluvial, wave-influenced (lake margin), and river-influenced (deltaic) shorelines, and lake-center paleoenvironments. The ichnological record found comes from the lake-margin areas whereas the lake center is devoid of traces. This was most likely caused by persistent water-column stratification and anoxia in the bottom waters (Benavente et al. 2018, 2020). Lake-margin areas bearing the traces studied record abundant features of subaerial exposure such as desiccation cracks, raindrop impressions, mud drapes, and HFM tracks in close association with indicators of lake-level rise and standing water, such as laminated carbonate beds, carbonate intraclasts, planar bedded and structureless sandstone beds, wave-rippled beds, structureless siltstone beds, and scour surfaces (Table 1). Those characteristics and the aggradational–progradational–retrogradational stratal stacking pattern support our interpretation of the fluctuating hydrology of the system between contraction and expansion of the lake, typical in balanced-fill lake basins (Bohacs et al. 2000).

Model of Balanced-Fill Ichnological Preservation

The distribution and preservation of ichnofossils in the Santa Clara lacustrine system is characteristic of balanced-fill lake basins (e.g., Bohacs et al. 2007; Buatois and Mángano 2009; Hasiotis et al. 2012): absent or depauperate ichnoassemblages in permanently subaqueous lake-center facies and abundant soft to firmground assemblages, composite ichnofabrics, and crosscutting relations among traces in lake-margin facies. Trace fossils were absent in the lake-center facies of the Santa Clara formations because the lake was likely meromictic with anoxic bottom waters (Benavente et al. 2018, 2020). The richest, most diverse ichnofossil assemblages in the Santa Clara formations occur in the lake-margin areas. The diversity and distribution of ichnotaxa resembles those found in modern (e.g., Lake Tanganyika; Hasiotis et al. 2012) and ancient (e.g., Laney member, Green River Formation; Bohacs et al. 2007; Buatois and Magano 2009; Scott and Smith 2015) balanced-fill lake systems, prone to develop meromixis.

Balanced-fill lake basins appear to be prone to preserving high-fidelity-mode tetrapod tracks only during certain time periods, when lake level is falling or low. In the case of the Santa Clara succession, we have found several levels that preserve footprints. These levels contain a high-diversity ichnofossil assemblage representing all ecological niches, tiers, and suites. Such diversity is related to the rather wide range of lake and substrate conditions (from submerged to subaerially exposed) that occur in a typical balanced-fill lake basin (Carroll and Bohacs 1999; Bohacs et al. 2000, 2007). The stratal record of balanced-fill lake basins (the fluctuating profundal facies association) is characteristically a mixture of aggradational to progradational stacking of both clastic and biogenic–chemical lithologies, The accumulation of biogenic–chemical lithofacies is enhanced by concentration of solutes during closed-hydrography periods. Such lake systems have a closed hydrography during lowstands that results in lowered groundwater tables and more saline lake waters. During lake-level highstands, such lake systems have an open hydrography resulting in freshened lake waters and higher groundwater tables. This typically results in highly diverse trace-fossil assemblages that contain ichnogenera typical of overfilled lake basins (persistent standing water and high-water-content sediments) during lake-level high stands and ichnogenera characteristic of underfilled lake basins (subaerial exposure, low groundwater tables, and low-water-content sediments) during lake-level low stands (e.g., Bohacs et al. 2007; Buatois and Mángano 2009; Hasiotis et al. 2012; Scott and Smith 2015; Scott et al. 2012).

CONCLUSIONS

In balanced-fill lake basins, hydrology is generally a complex factor, involving groundwater fluctuations and surficial inflow that can be intermittent, that drives expansions and contractions of the water body. Stratigraphic stacking and geochemical proxies are time-averaged records of paleohydrology and therefore are limited in their resolution of hydrological dynamics during the existence of a lake basin. In contrast, trace-fossil analysis can provide an effectively instantaneous synoptic record of hydrological fluctuations; such analyses are especially powerful when integrated with detailed data sets of sedimentology, geochemistry, paleontology, and other stratal attributes. Furthermore, integrating vertebrate and invertebrate trace data sets with sedimentological and stratigraphical analysis provides another perspective on how hydrology shifted in a depositional layer (the shortest time span).

The Santa Clara Abajo and Santa Clara Arriba formations host a diverse assemblage of trace fossils that record a wide range of behaviors and occupied a broad array of ecological niches during the Middle Triassic—a critical period in the evolution of land fauna. We recognized 26 ichnogenera from ethological classes of fodichnia, domichnia, repichnia, pascichnia, and cubichnia (in decreasing order of occurrence). The trace fossils occupied all continental ecological niches (epiterraphilic, terraphilic, hygrophilic, and hydrophilic; Fig. 11); no hydrophilic-endobenthic deep were observed.

The vertebrate footprints studied from the Santa Clara Formation represent two modes: a moderate-fidelity mode associated with a high-diversity trace-fossil assemblage from a wide range of ethological classes, along with a moderate range of trace-fossil ecologies and tiering relations suggesting a setting with initial inundation and subsequent episodic subaerial exposure and groundwater-table withdrawal resulting in a relatively long period of faunal activity by a highly diverse community. Footprints with high-fidelity mode preservation are associated with a moderate-diversity trace-fossil assemblage from a moderate range of ethological classes and wide range of trace-fossil ecologies, from standing water through episodic exposure. The taphonomic

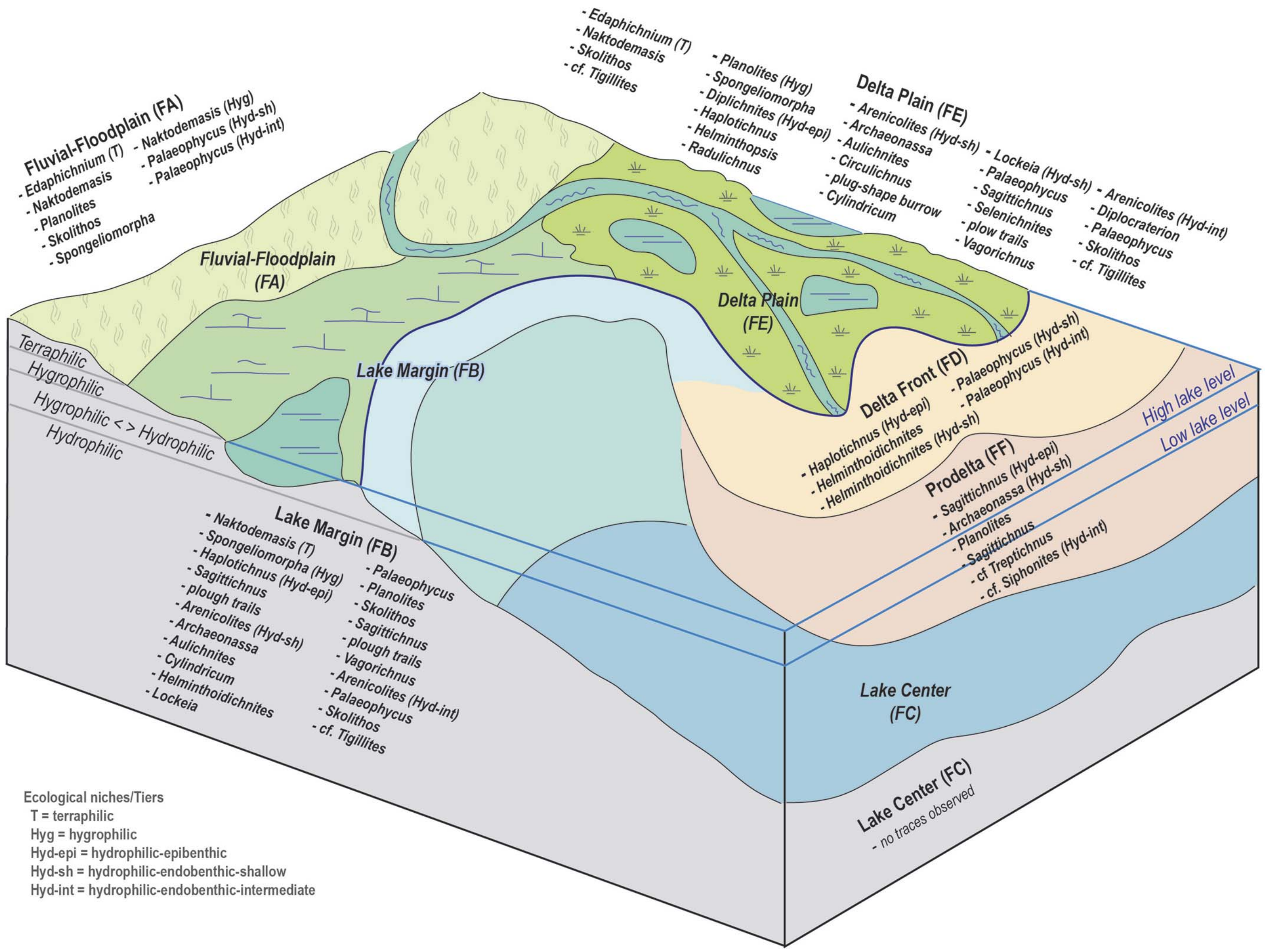

FIG. 11.—Block diagram (not to scale) representing the ichnological assemblages, the ecological niches and tiers in the facies context of the Santa Clara succession.

pathways recognized allow interpretation of three hydrological situations (damp, humid, dry) for the lake-margin and delta-plain subenvironments, linked to ecological preferences of trace producers and preservation of vertebrate footprints.

This approach provides detailed insights into the Santa Clara lacustrine system, showing that all ecological niches were probably fully exploited under highly variable hydrological conditions (lake level and groundwater level fluctuations). This allows reflection on what were common and/or strong evolutionary drivers of biotic distribution and evolution in such balanced-fill lake basins with rapid and frequent hydrological fluctuations and varying availability of water. Perhaps widely varying lake levels isolated breeding populations around the margins of the basin or perhaps rapidly and frequently varying availability of a key resource (water holes) stressed certain faunal groups—and both conditions resulted in evolutionary pressure that contributed to the diversification of land animals during this critical time period.

SUPPLEMENTAL MATERIALS

Supplemental files are available from the SEPM Data Archive: https://www.sepm.org/supplemental-materials.

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