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The Río Loro Formation (Paleogene, northwestern Argentina) and its unique vertebrate fauna: Exploring paleoenvironmental and paleoecological aspects

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THE RÍO LORO FORMATION (PALEOGENE, NORTHWESTERN ARGENTINA) AND ITS UNIQUE VERTEBRATE FAUNA: EXPLORING PALEOENVIRONMENTAL AND PALEOECOLOGICAL ASPECTS

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Abstract. Paleoenvironmental and paleoecological aspects of the Río Loro Formation (Paleogene, northwestern Argentina) were analyzed. In the type locality, four main sedimentary facies were recognized. Facies 1 (coarse-grained to pebbly amalgamated sandstones) record sedimentation in braided channels. Facies 2 (structureless to faintly laminated mudstones) and Facies 3 (interbedded mudstones with sandstones) are ascribed to deposition in distal to proximal floodplain settings, respectively. Facies 4 (coarse to medium-grained sandstone) is interpreted as deposited in meandering channels. Insect trace fossils, ascribed to nesting structures, were recognised particularly in facies 1 and 4. The recognized facies were grouped in a main facies association which allows interpretating a deposition in a complex multi-channel fluvial system with relatively stable muddy floodplain areas. Within this system, seasonal humid to dryer conditions favored biota substrate colonization and soil-forming processes. Well-preserved mammalian and reptilian remains were recognized in sandy mudstone deposits of Facies 3, showing low weathering stages (mainly stages 1 and 2) and the absence of signs of abrasion. These aspects, along with the presence of some articulated remains and their integration with the paleoenvironmental framework, suggest that skeletal pieces suffered an early burial after partial disarticulation, possibly by splays during major floods. The inferred habits of some of the taxa recorded are consistent with proximity to freshwater sources, vegetated areas, and seasonality. This multidisciplinary approach contributes to the understanding of paleoenvironmental and paleontological attributes of the Río Loro Formation and represents a basis for future surveys on this unit and its remarkable fossil record.

Key words. Sedimentology. Fluvial system. Ichnofossils. Fossil herpetofauna. Paleoecology. Pan-Perissodactyla.

Resumen. LA FORMACIÓN RÍO LORO (PALEÓGENO, NOROESTE ARGENTINO) Y SU SINGULAR FAUNA DE VERTEBRADOS: EXPLORANDO ASPECTOS PALEOAMBIENTALES Y PALEOECOLÓGICOS. Se analizaron aspectos paleoambientales y paleoecológicos de la Formación Río Loro (Paleógeno, noroeste argentino). Se reconocieron cuatro facies sedimentarias. La Facies 1 (areniscas gruesas a guijarrosas amalgamadas) registran sedimentación en canales entrelazados. La Facies 2 (fangolitas masivas o débilmente laminadas) y la Facies 3 (fangolitas intercaladas con areniscas) reflejan depositación en planicies de inundación distales a proximales, respectivamente. La Facies 4 (areniscas gruesas a medias) documenta depositación en canales meandriformes. Trazas fósiles de insectos atribuibles a estructuras de nidificación fueron reconocidas en las facies 1 y 4. Las facies fueron agrupadas en una asociación de facies principal que refleja sedimentación en un sistema fluvial multicanalizado complejo con áreas de planicie de inundación fangosa relativamente estables, donde condiciones estacionales húmedas a más secas favorecieron la colonización del sustrato por parte de la biota y procesos de formación de suelo. Se reconocieron restos de mamíferos y reptiles bien conservados en depósitos de la Facies 3, con estadios bajos de meteorización (principalmente etapas 1 y 2) y ausencia de signos de abrasión. Asimismo, la presencia de restos articulados y su integración con el marco paleoambiental, sugieren desarticulación parcial y enterramiento temprano, posiblemente a partir de desbordes durante inundaciones. Los hábitos inferidos para los taxones registrados muestran consistencia con la proximidad a fuentes de agua dulce y áreas vegetadas, así como estacionalidad. Este enfoque multidisciplinario contribuye a la comprensión de los atributos paleoambientales y paleontológicos de la Formación Río Loro y representa una base para futuros estudios sobre esta unidad y su notable registro fósil.

Palabras clave. Sedimentología. Sistema fluvial. Icnofósiles. Herpetofauna fósil. Paleoecología. Pan-Perissodactyla.

Paleoenvironmental studies on Paleogene units from northwestern Argentina are represented by several contributions. These have been mainly focused on the Santa Bárbara Subgroup of the Salta Group (Tunal/Mealla, Maíz Gordo, and Lower Lumbrera formations; Salfity & Marquillas, 1994; del Papa & Salfity, 1999; del Papa *et al.*, 2002, 2022; del Papa, 2006; Andrews *et al.*, 2017). However, there are also surveys that were carried out on Upper Lumbrera (Lapiana *et al.*, 2016), Geste (Alonso, 1992; Carrapa & DeCelles, 2008; Ciancio *et al.*, 2016; de la Fuente *et al.*, 2022), Quebrada de los Colorados (del Papa *et al.*, 2013), and Casa Grande formations (Montero-López *et al.*, 2018; Tapia *et al.*, 2023).

Most of these Paleogene sequences have yielded an important record of fossil vertebrates and their study has acquired relevance since at least half a century (Pascual *et al.*, 1981; Vucetich *et al.*, 2007; Powell *et al.*, 2011; Babot *et al.*, 2017, 2018 and references therein). This relevance rests on many factors, being among the most conspicuous the geographical distribution of such deposits, bearing an important assemblage of mid-latitude vertebrates for the South American Paleogene. Moreover, these fossil communities illustrate a key span in the early evolutionary history of South American vertebrates, which took place in times of intense climate changes (hyperthermal warming events and subsequent and gradual cooling; Zachos *et al.*, 2008; Kiehl *et al.*, 2018).

Periodic and systematic studies recently resumed on the fossil-bearing levels of the Río Loro Formation (?middle Paleocene–early Eocene; see below) led to the discovery of new vertebrate morphotypes and also new specimens of already described species. These new sources of anatomical information allowed the reinterpretation of previously documented taxa in a more comprehensive phylogenetic framework and improved the knowledge on diversity and paleoecology of the Río Loro Formation (Gelfo *et al.*, 2020; Saade *et al.*, 2023a). Despite this increasing faunistic dataset, the paleoenvironmental context of the Río Loro Formation is still poorly documented and is only based on some early studies carried out when its relevant fossil vertebrate community was still scantily known (*e.g.*, Powell & Palma, 1981). The current state of knowledge provides a good opportunity to perform an integrated sedimentological and paleontological analysis on these deposits. This paper aims to improve the paleoenvironmental resolution of the Río Loro Formation, as well as investigate the taphonomical and paleoecological attributes of the paleovertebrate assemblage recovered from this unit.

GEOLOGICAL SETTING

Paleogene rocks analyzed in this work crop out in the northeast of Tucumán Province, northwestern Argentina (Fig. 1), and represent part of the Cenozoic sedimentary cover that flanks the Precambrian and early Cambrian metamorphic basement mountain blocks of the Northwestern Pampean Ranges tectonic province (Bossi *et al.*, 1998; González *et al.*, 2000; Mon *et al.*, 2014). These deposits were accumulated in the Cretaceous–Cenozoic Choromoro Valley depocenter, which is limited to the west and the east by N–S to NE–SW oriented basement highs mainly corresponding to Cumbres Calchaquíes and Sierra de Medina, respectively, and develop a filling that thickens towards the north merging with deposits of the Salta Basin (Bossi *et al.*, 1998; Abascal, 2005; Georgieff *et al.*, 2014; Mon *et al.*, 2014). Sedimentation within this basin began with alluvial deposits of the Cretaceous El Cadillal Formation (Bossi, 1969) and represents the synrift stage (Bossi & Moyano, 2014). These deposits are in turn intruded by volcanic rocks including traquites, andesites, and riolites belonging to the coeval Alto de las Salinas Complex (Bossi, 1969; Bossi & Wampler, 1969; González *et al.*, 2000). These rocks are unconformably overlain by the ?middle Paleocene–early Eocene Río Loro Formation (Bossi, 1969; Powell & Palma, 1981; Gelfo *et al.*, 2020), which records deposition in a fluvial setting preserving floodplains and corresponds to the postrift stage (Bossi & Peral, 1992; Bossi *et al.*, 1998). Postrift stage sedimentation continued during the Eocene with the establishment of ephemeral systems including mud flats deposits, represented by the Río Nío Formation (Bossi, 1984; Bossi & Peral, 1992; Georgieff *et al.*, 2014). Compression due to Andean orogenesis promoted basin inversion, developing a foreland basin which during the Neogene hosted sedimentation in lacustrine settings, particularly in shallow and ephemeral lakes, recorded in the Miocene Río Salí Formation (Abascal, 2005; Georgieff *et al.*, 2014; Zapata *et al.*, 2019). Neogene sedimentation continued with the development of fluvial settings, including ephemeral, braided, and meandering systems, documented by the overlying Miocene India Muerta Formation (Bossi *et al.*, 1998; Georgieff *et al.*, 2014; Zapata *et al.*, 2019; Armella *et al.*, 2024). Finally, these rocks are unconformably overlied by alluvial deposits of the Pliocene Ticucho Formation (Bossi, 1969; Zapata *et al.*, 2019).

The Río Loro Formation (Bossi, 1969) is 95 m thick and consists of brownish-red, violet to whitish medium to coarse-grained sandstones, which present intercalations of brownish-red mudstones and diamictites, with minor occurrences of conglomerates (Powell & Palma, 1981; Georgieff *et al.*, 2014). Petrographic classification indicates that the sandstone is mainly sublitharenite (Bossi *et al.*, 1998). These deposits are interpreted to reflect fluvial sedimentation (Bossi, 1969) in meandering systems (Powell & Palma, 1981) and in laterally mobile braided rivers with muddy floodplains (Bossi *et al.*, 1998). In the type locality, the unit rests over sandstones and conglomerates of the Cretaceous El Cadillal Formation and is in turn overlain by greenish to yellowish mudstone and marl deposits of the Miocene Río Salí Formation (Powell & Palma, 1981; Fig. 1). Although there are no references of absolute dating, the fossil mammal record first suggested a middle or late Paleocene age (Powell & Palma, 1981), although recent works favor a ?middle Paleocene–early Eocene age (Gelfo *et al.*, 2020; Saade *et al.*, 2023a).

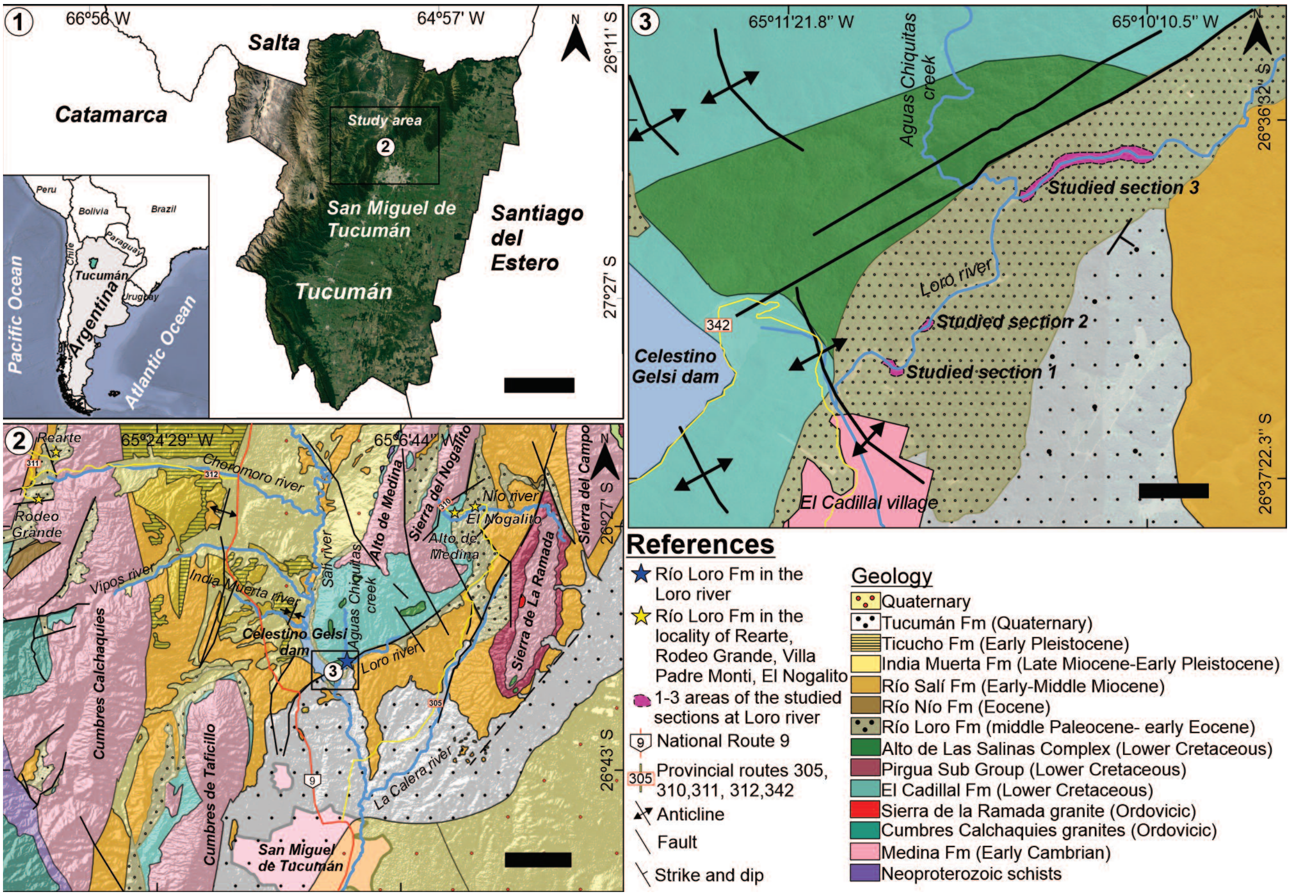


Figure 1. Geographic and geologic setting. **1,** General geographic location of Tucumán Province in southern South America. Scale bar= 40 km; **2,** Location and geologic map of the study area, modified from Gonzalez *et al.* (2000). Scale bar= 8 km. The blue star marks the Río Loro locality, whereas the yellow ones indicate the exposures of the unit at the localities of Nogalito and Alto de Medina (eastward), and Rearte (westward); **3,** Analyzed exposures of the unit along the Loro River margins, showing sections 1, 2, and 3 highlighted with solid purple lines. Scale bar= 400 m.

MATERIALS AND METHODS

This study was mainly carried out in the area of confluence of the Loro River and Aguas Chiquitas creek. This corresponds to the type locality of the Río Loro Formation, where the fossil-bearing levels are recognized (Fig. 1). Field data was collected along the succession cropping out on the eastern margins of the homonymous river in which, due to limited exposures, three sedimentary logs (namely 1, 2, and 3) were measured in order to obtain a continuous composite section (Fig. 2). The location of these studied sections coincides with part of the previously analyzed outcrop by Powell & Palma (1981). Sedimentary facies were characterized by their dominant lithology, internal arrangement, bed boundaries, geometry, and fossil content (including ichnofauna). Sedimentary facies attributes were also observed in exposures of the unit located westward (Rearte) and eastward (Nogalito and Alto de Medina) of the main study area (Fig. 1), in order to obtain complementary data and allow comparisons.

Taphonomical analysis mainly includes biostratinomical observations made on skeletal remains of recent findings and previous documented material for the Río Loro Formation. Each specimen was analyzed regarding their composition, the degree of articulation, and weathering stages, following Behrensmeyer (1978, 1991). This author established weathering stages based on superficial features produced by decomposition and environmental factors. The information was integrated with the paleoenvironmental data in order to provide a more comprehensive framework regarding preservational aspects of the fossil fauna. The fossil vertebrate specimens examined in this work are housed at the Colección Paleontología de Vertebrados Lillo (PVL) of the Facultad de Ciencias Naturales e Instituto Miguel Lillo (Universidad Nacional de Tucumán).

RESULTS

Sedimentary Facies Analysis

The deposits herein analyzed mainly correspond to those located on the margins of the Loro River and allowed the recognition of four main sedimentary facies, namely: Facies 1, coarse-grained to pebbly amalgamated sandstone beds; Facies 2, structureless to faintly laminated mudstones; Facies 3, interbedded mudstones with sandstones; and Facies 4, coarse to medium grained sandstone beds. Descriptions and interpretations of the facies are presented below, as well as in Figure 2 and Table 1.

TABLE 1 – Summary of sedimentary facies of the Río Loro Formation at the type locality

Facies	Lithologies, sedimentary structures, geometry and observed fossil content	Interpretation	Other localities with comparable attributes
1 Coarse-grained and pebbly amalgamated sandstones	Light reddish to pinkish brown coarse- to very coarse-grained lenticular sandstone and pebbly sandstone beds. Includes local occurrences of laminated to massive mudstones. Planar and trough and low angle cross-stratification, and horizontal bedding. Local presence of rhizoliths and insect traces. No skeletal remains were observed.	Braided channel belt deposits	Rearte and Nogalito
2 Structureless and faintly laminated mudstones	Reddish-brown mudstone. Mudstone beds may be structureless or exhibit a faint parallel lamination. Commonly include blocky and prismatic aggregates, irregularly shaped carbonate concretions, rhizoliths, and slickensides. Mottles and clastic dykes may be also present. No skeletal remains observed.	Distal floodplain (flood basin and paleosols)	Rearte and Nogalito
3 Interbedded mudstones and sandstones	Brown to reddish mudstones interbedded with pinkish to grayish fine to medium-grained sandstones. Sandy beds are structureless or exhibit low-angle cross-stratification, ripple cross-lamination, and (only locally) through cross-stratification. Common presence of carbonate concretions and bioturbation, including rhizoliths. Presence of vertebrate cranial and postcranial remains of snakes, turtles, crocodiles, and mammals.	Proximal floodplain (splays, levees, and paleosols)	Nogalito
4 Coarse to medium-grained sandstones	Pink to light grey coarse- to medium-grained sandstones and locally pebbly sandstones. Tabular to lentiform bodies with a roughly fining-upward trend. Planar and trough cross-stratification, and in minor proportion ripple cross-lamination. Cross stratification in some cases resting on inclined surfaces (accretion surfaces). Local presence of rhizoliths and insect traces. No skeletal remains observed.	Meandering channels	Alto de Medina

Facies 1. Coarse-grained to pebbly amalgamated sandstone beds. This facies is mainly composed of light reddish to pinkish brown, coarse- to very coarse-grained sandstones that are locally interbedded with gravelly (pebbly) sandstones (Fig. 3.1–2) forming laterally continuous amalgamated packages up to ~7 m thick. Only locally, scarce

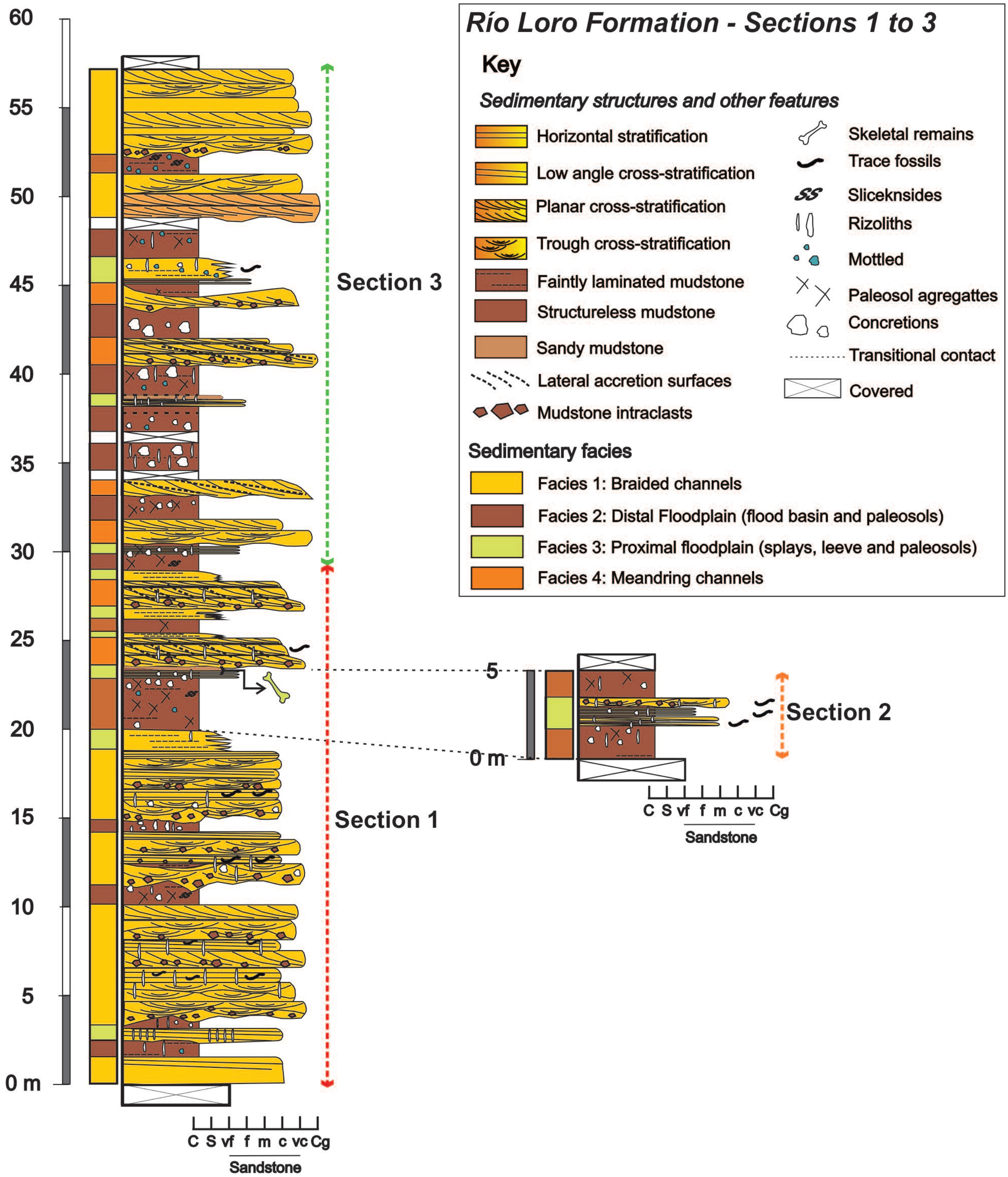


Figure 2. Composite section of the Río Loro Formation at the Río Loro River area. See Table 1 for a summary of facies.

decimetric (up to ~0.80 m thick) and laterally discontinuous reddish to reddish-brown structureless to faintly laminated mudstone interbeds (see also Facies 2 below) are present. Individual sandstone beds are erosionally based and present a poorly defined lenticular geometry that varies from ~0.3 m to ~1.7 m thick. Internally, these beds display planar and trough cross-stratification in sets that range from ~0.2 m to ~0.8 m thick (Fig. 3.1), in many cases characterized by alternating gravelly sand and sand layers (Fig. 3.2). Low-angle cross-stratification and horizontal bedding are also preserved, while structureless beds locally occur. Subangular to angular mudstone intraclasts (up to ~8 cm in diameter) are commonly dispersed within beds and in some cases they are relatively abundant together with pebble to cobble-sized volcanic and quartz clasts, overlying lower erosive bed surfaces. Insect trace fossils are ubiquitous in some sandstone beds and are mainly characterized by piled-up parallel to sub-parallel tabular to flat-lobate structures (up to ~1 cm in height and ~12 cm in width) interconnected by a central vertical burrow (of ~1 to ~3 cm in diameter) and/or minor shafts (Fig. 3.3–4), referable to the ichnogenus *Krausichnus* Genise & Bown, 1994. In addition, roughly cylindrical (~1 to ~3 cm in diameter) vertically oriented burrows (up to ~80 cm in length) that locally intercept slightly flattened and inclined bulbous-like structures (relatively similar to the ichnogenus *Daimoniobarax* Smith *et al.*, 2011; Fig. 3.5) also occur. This facies intercalates with Facies 2 and Facies 3 and its best exposures are located towards the base of the studied succession (Fig. 2). Comparable sedimentological attributes were observed in exposures of the unit located in the Nogalito and Rearte localities (Fig. 1). Particularly in the former locality, a sharp erosive basal surface separates coarse-grained sandy beds from underlying mudstones deposits. In the latter locality, amalgamated coarse-grained to pebbly sandstone beds (Fig. 3.6) are present, although these deposits are partially covered and its internal arrangement is poorly discernible due to weathering.

The erosive bases and lenticular geometry are consistent with deposition within channels. Amalgamated beds reflect the staking of single-event channel fills. The local occurrence of mudstone interbeds may be related to local channel abandonment (*e.g.*, Miall, 1985; Bridge, 2006), whereas the presence of mudstone intraclasts suggests erosion and rework of fine-grained interchannel deposits during channel migration (*e.g.*, Collinson, 1996). Basal gravel lags above the lower erosive base of some beds are deposited as channel lag accumulations. Planar and trough cross-stratification result from the migration of transverse bedforms, including straight-crested (2D) and sinuous-crested (3D) bars and subaqueous dunes, respectively (Miall, 1996; Collinson & Mountney, 2019). In this regard, the alternation of gravelly sand and sand layers within cross beds is related to the avalanching and falling clast process on the steep lee sides of bedforms during migration (*e.g.*, Lunt & Bridge, 2007; Collinson & Mountney, 2019). Low-angle cross-stratification and horizontal bedding in sandstone are related to sedimentation in upper-flow regime conditions, in which plane bed and possibly antidunes developed under shallow and fast flows (*e.g.*, Miall, 1996; Fielding, 2006). The lack of structures in some beds may indicate that the channel flow was in some cases heavily laden with sediment relative to its competence, favoring rapid deposition and suppressing bedform development (*e.g.*, Collinson, 1996; Fisher *et al.*, 2007). The absence of lateral accretion surfaces also points towards low sinuosity channels (*e.g.*, Miall, 1996). The presence of insect trace fossils representing nesting structures (*e.g.*, Genise, 2004; Smith *et al.*, 2011; Genise *et al.*, 2016) and rhizoliths in these deposits suggest colonization by biota possibly during minimum sedimentation intervals with subaerial bar exposure well above the seasonal low-water mark (*e.g.*, Collinson, 1996; Hasiotis, 2007; Tabor & Myers, 2015). Overall, this facies is interpreted as recording sedimentation in multistory channels, particularly in braided channel belts or complexes dominated by the migration of transverse sandy bars and locally subaqueous dunes (*e.g.*, Collinson, 1996; Miall, 1996; Gibling, 2006).

Facies 2. Structureless to faintly laminated mudstones. Facies 2 consists of mainly reddish-brown, silt to sand-bearing, claystone-rich mudstone beds, arranged in laterally extensive bodies that range from ~0.8 to ~3.5 m thick (Fig. 3.7). Mudstone beds are commonly structureless, although faint parallel lamination is preserved in some cases. Irregularly shaped carbonate concretions that vary from 1 to about 15 cm in diameter and centimeter to

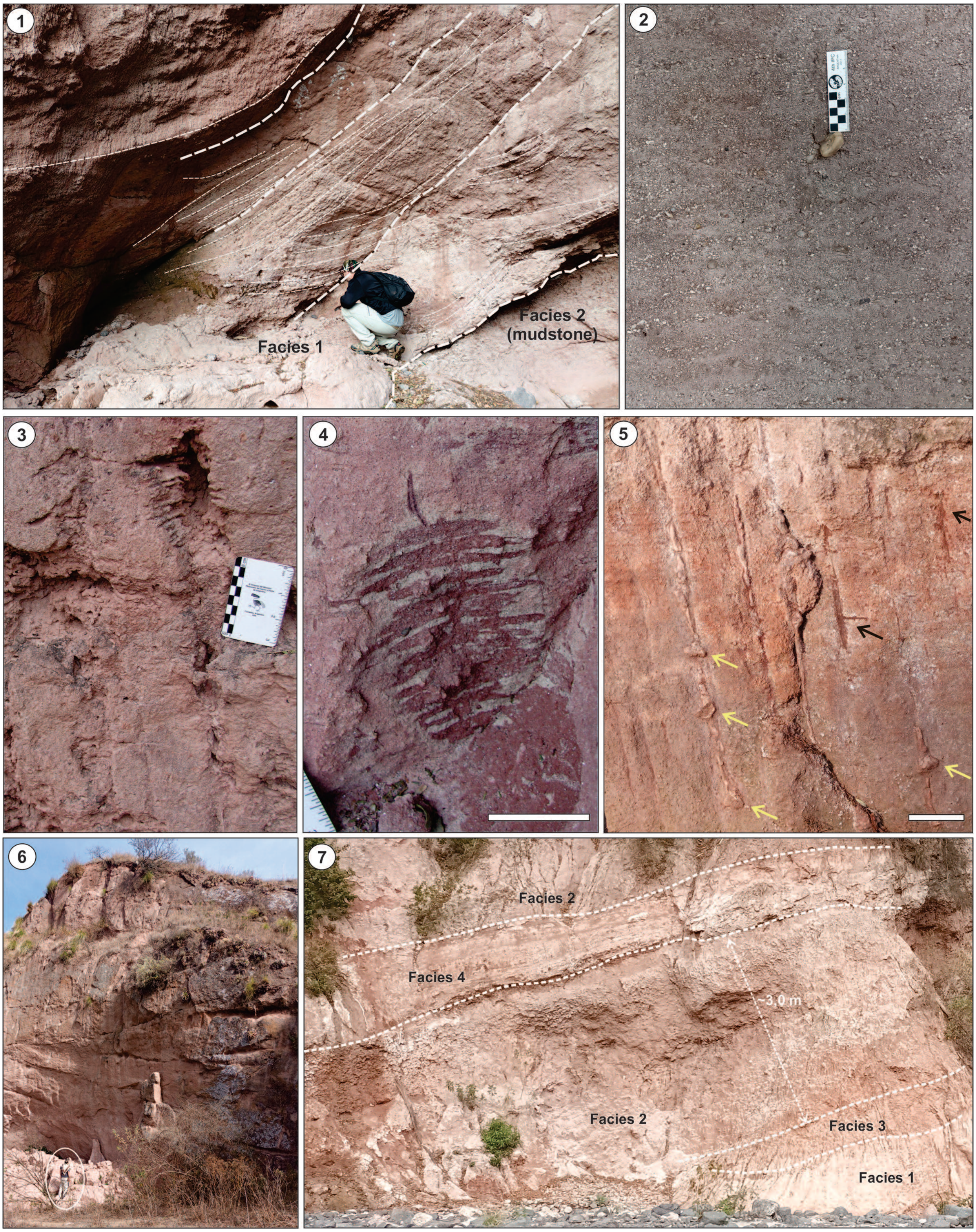


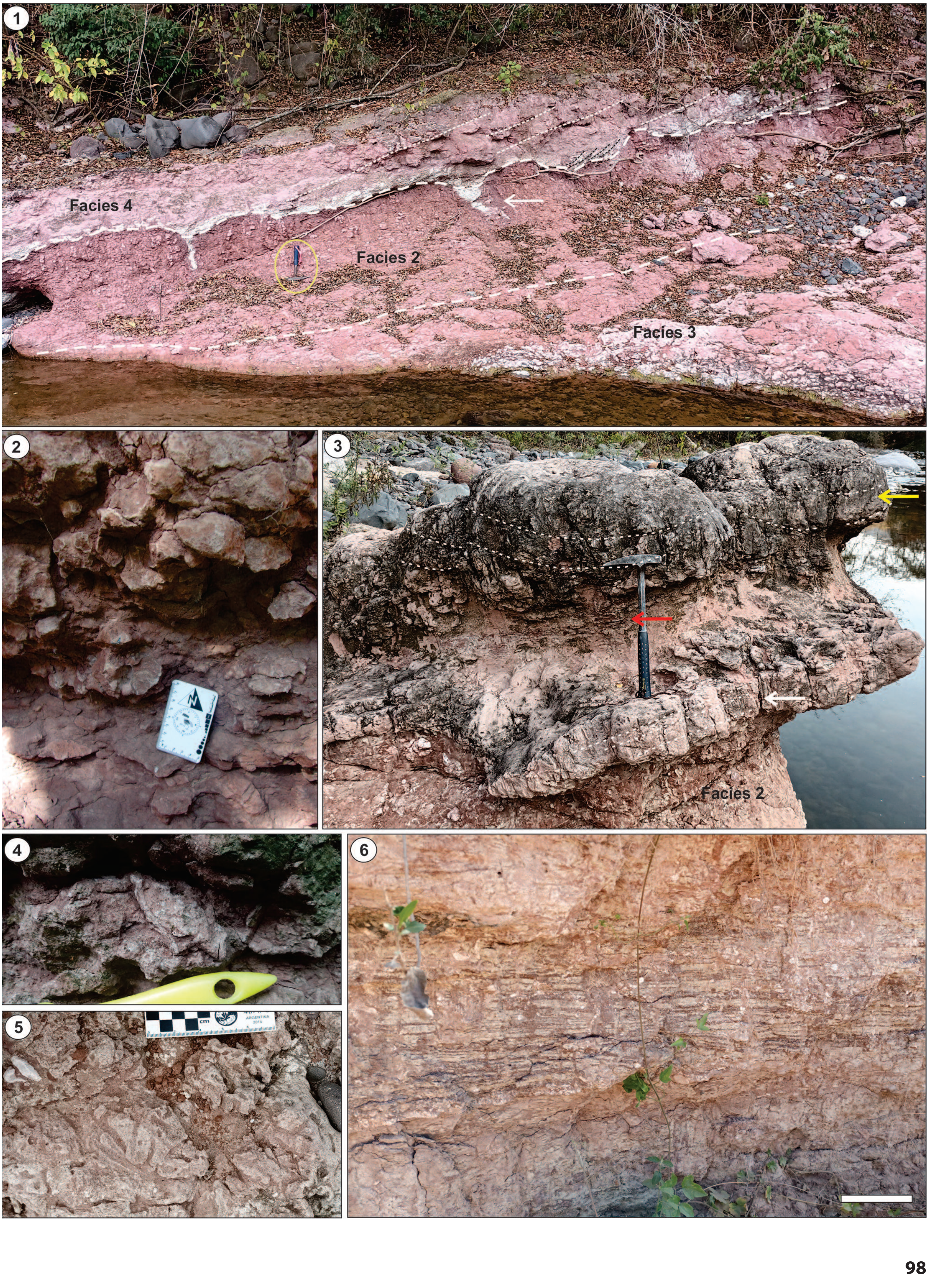
Figure 3. Field photographs. **1,** Facies 1, amalgamated sandstone deposits (person for scale). Note internal erosive surfaces (thick dashed lines) separating beds with cross-stratification; **2,** Facies 1, weathered exposure of pebbly sandstone deposits displaying alternation of gravely and sandy layers; **3–4,** Facies 1, coarse- to very coarse-grained sandstone bed with insect trace fossils refered to the ichnogenus ***Krausichnus***. Scale bar= ~5 cm; **5,** Facies 1, coarse-to very coarse-grained sandstone bed with slightly flattened and inclined bulbous-like structures (yellow arrows) intercepted/or connected by a vertical burrows adscribed to insect trace fossils and rizholiths (black arrows). Scale bar= ~10 cm; **6,** Weathered exposures of coarse-grained to pebbly amalgamated sandstone beds at the Rearte locality (person for scale); **7,** General aspect of Facies 2 mudstone deposits.

decimeter-long rhizoliths are commonly present (Fig. 4.1–2). In addition, blocky to prismatic peds (Fig. 4.1) and in minor proportion, laminar aggregates forming horizons of up to about 70 cm, are also observed among these beds. Moreover, these structures may be accompanied by slickensides, together with local occurrences of clastic dykes (Fig. 4.1) and, in some cases, greenish-gray and reddish-brown-colored mottles. This facies is erosionally overlaid by Facies 1 and Facies 4 and transitionally passes to Facies 3. Similar deposits ascribed to this facies were observed in the Nogalito and Rearte localities (Fig. 1).

Primarily, structureless and laminated mudstone deposits of this facies reflect overbank deposition in a low-energy setting, where suspension fall-out was the dominant sedimentation process (Collinson, 1996; Miall, 1996), followed by minor participation of low energy unconfined tractive currents that brought fine-grained sand to the system (*e.g.*, Burns *et al.*, 2019). The presence of carbonate concretions, rhizoliths, aggregates (or peds), slickensides, clastic dykes, and mottles is ascribed to soil-forming processes (Retallack, 1988; Miall, 1996). In this regard, the reddish coloration of mudstones and abundance of irregular carbonate concretions (calcretes) are related to oxidizing conditions, excess of alkaline solutes, and precipitation in a well-drained floodplain (*e.g.*, Kraus, 1996; Wright, 1999; Retallack, 2001). Rhizoliths are related to plant root instauration and indicate subaerial vadose conditions (Klappa, 1980; Tabor & Myers, 2015). The presence of slickensides is consistent with seasonal wetting and drying, whereas mottles suggest fluctuations in the water table that favored oxidizing and reducing conditions (*e.g.*, Wright, 1999; Kraus, 2002; Kraus & Hasiotis, 2006). The occurrence of some clastic dykes indicates the shrinkage and swelling of expandable clays (Tabor & Myers, 2015). In addition, the mentioned pedogenic features are comparable with vertisols and calcisols development (Mack *et al.*, 1993; Bossi *et al.*, 1998). This facies is interpreted to represent deposition in a distal (from the main channels) floodplain setting, which was temporarily inundated (flood basin) and developed well-drained soils (*e.g.*, Collinson, 1996; Wright, 1999; Retallack, 2001).

Facies 3. Interbedded mudstones and sandstones. This facies consists of reddish-brown to pinkish-orange mudstones interbedded with fine- to coarse-grained pinkish sandstones, forming intervals that range from ~0.3 to ~1.5 m thick (Fig. 4.1–3). Mudstone beds are up to ~50 cm thick and generally present similar attributes to those indicated for Facies 2. Structureless sandy-to-pebbly mudstone with matrix-supported clasts, including subangular mudstone intraclasts (Fig. 4.1–4), occur locally. The distinction among these mudstone deposits is not always straightforward, due to weathering patterns, similar color, as well as diffuse contacts and the presence of similar pedogenic structures (see also Facies 2). Sandstone interbeds range from ~2 to ~40 cm thick and are locally sheet-like, or to some degree flat lobe-shaped to flat lenticular, exhibiting slightly erosive bases (Fig. 4.3) that may include abundant subangular to angular mudstones (silty-claystone) intraclasts up to 20 cm in diameter. These beds present low-angle cross-stratification, in minor proportion trough cross-stratification (Fig. 4.3), poorly preserved ripple cross-lamination, or can also be structureless. In addition, vertically oriented centimeter to decimeter-long rhizoliths, horizontal to inclined burrows with a poorly defined meniscated fill ascribed to ?*Taenidium* Heer, 1877 (Fig. 4.5), and irregularly distributed small-sized (up to ~2 cm in diameter) carbonate concretions are locally present. This facies transitionally passes to Facies 2 and intercalates

Figure 4. Field photographs. **1,** Interval exhibiting facies 2, 3, and 4. From base to top, pinkish sandy-to-pebbly mudstone bed of Facies 3 passes upward to reddish to brown mudstone deposits of Facies 2, which is in turn erosivelly overlaid by sandstone beds of Facies 4 (rock hammer for scale). Note for Facies 2, the presence of concretions (calcretes), the local occurrence of vertically oriented rhizolits, and a clastic dyke (arrow) below the contact between the mudstone and the overlying sandstone (Facies 4); **2,** Facies 2, structureless mudstone deposits with concretions; **3,** Facies 3, interbedded mudstones and sandstones. Sandstone deposits exhibiting low-angle cross-stratification (lower white arrow) and trough cross-stratification (upper yellow arrow) are intercalated with a decimetric interval presenting sheet-like sandy beds (middle red arrow; rock hammer for scale). Note that all these structures are overprinted by bioturbation, including burrows together with vertically oriented rhizoliths; **4,** Facies 3, close view of sandy-to pebbly mudstone deposits (brush handle about 5 cm long). The bed also presents irregular concretions and a rhizolith; **5,** Plan view of a sandstone bed with burrows ascribed to ?***Taenidium***; **6,** Rhythmic alternations of sandstone and mudstone at the Nogalito locality. Scale bar= ~10 cm.


1
Facies 4
Facies 2
Facies 3
2
3
Facies 2
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5
cm
6

with Facies 4 and Facies 1. Similar facies attributes were recognized in outcrops of the unit located at the Nogalito locality (Fig. 1), in which a rhythmically stratified trend was also observed (Fig. 4.6).

Vertebrate fossils consisting of cranial and postcranial remains of turtles, crocodiles, and mammals (see below) were discovered in sandy-mudstone with dispersed granules of this facies. Particularly, crocodile bones were recently found in sandy mudstone deposits near the contact with the overlying sandy beds of Facies 4 (Figs. 2; 5.1). Although fossil remains are partially articulated, the different elements present in some cases slightly to moderately eroded surfaces and heavy breakage (see taphonomic observations below).

Interbedded sheet-like beds of structureless to rippled cross-laminated sandstones and mudstones may be related to the alternation of traction/suspension fall-out processes as a consequence of episodic overbank floods (*e.g.*, Collinson, 1996; Miall, 1996). In this regard, low-velocity unconfined flows favored ripple migration and deposition of fine particles from suspension occurred during waning conditions following the flood event. However, rapid deposition from decelerating heavily sediment-laden flows may have also occurred, producing structureless sandy beds (*e.g.*, Miall, 1996; Collinson & Mountney, 2019). Similarly, wedge-shaped sandy beds, exhibiting low-angle cross-stratification and/or through cross-stratification can be related with deposition from sporadic waning currents, in which plane beds developed over initially dipping surfaces and locally sinuous crested subaqueous dunes migration (*e.g.*, Miall, 1996; Burns *et al.*, 2019). In addition, the presence in these beds of slightly erosive bases and mudstone intraclasts reflects local erosion and rework by unconfined to weakly confined flows (*e.g.*, Burns *et al.*, 2017, 2019). Moreover, the observed sandy-to-pebbly mudstone deposits, in some cases containing muddy intraclasts, also referred to as diamictites (*e.g.*, Bossi, 1969; Powell & Palma, 1981; Bossi *et al.*, 1998), are interpreted to be deposited by debris flows and/or mudflows (Miall, 1996; Collinson & Mountney, 2019). Local occurrence of rhizoliths and concretions among these beds indicates subaerial exposure and pedogenesis (Retallack, 1988; Tabor & Myers, 2015). Particularly, the presence of burrows (?*Taenidium*) in sandy beds also suggests the instauration of ichnofauna on soft and wet substrates (*e.g.*, Buatois & Mángano, 2011), which in turn contributed to substrate particle mixing. Overall, this facies is interpreted as deposited in a floodplain setting relatively close to channels, in which crevasse channels and associated splays formed during floods and unconfined flows overtopping channel bank locally developed levee deposits (*e.g.*, Gosh *et al.*, 2006; Miall, 2010; Burns *et al.*, 2019). In this framework, debris flows and mudflows sporadically developed during major floods and expanded away from channel margins, in some cases through the breaking up of levees (*e.g.*, Powell & Palma, 1981; Miall, 1996; Eberth *et al.*, 2006).

Facies 4. Coarse to medium-grained sandstones. Facies 4 comprises erosive-based tabular to slightly lentiform bodies that vary from ~1 to ~2 m thick, of pinkish to light gray coarse- to medium-grained sandstones and only locally pebbly sandstones, that mostly develop roughly fining-upward trend (Figs. 3.7; 4.1; 5.1–2). Individual beds range from 20 to 80 cm in thickness and commonly display planar and trough cross-stratification in sets that vary from ~10 to ~50 cm thick (Fig. 5.3), in many cases associated with normal grading. Ripple cross-lamination is locally present, particularly towards the tops of sandstone bodies. In some good exposures, it is also possible to observe inclined surfaces with superimposed cross-stratification, ascribed to lateral accretion surfaces (Figs. 4.1; 5.1, 5.3, 5.5). Pebble-sized clast with a similar composition to that of Facies 1 and variable diameter (up to ~5cm) mudstone intraclast are locally present, particularly near or above the basal surfaces. In addition, insect trace fossils (similar to those indicated for Facies 1), as well as centimeter to decimeter long rhizoliths oriented perpendicular to the bedding plane, also occur in some beds. This facies may occur as isolated bodies, intercalating with metric to decimetric intervals of Facies 2 and Facies 3 (Figs. 4.1; 5.1) or as stacked roughly fining upward cycles separated by relatively thin (up to ~30 cm) intercalations of Facies 3 (Fig. 5.2). Deposits characterized by stacked and relatively thick (~2.5 m) tabular sandstone bodies (Fig. 5.6) also bearing some structures referable to insect trace fossils (Fig. 5.7) were observed in the unit near the Alto de Medina locality, at the side of provincial route 310 and the Nío River (Fig. 1).

Erosive bases and fining upward trends of this facies suggest channel deposition with a gradual reduction in depth and/or flow velocity. The tabular to lentiform geometry and the presence of lateral accretion surfaces are consistent with the migration of sinuous channels and point-bar development (Allen, 1963; Nanson, 1980; Miall, 1996). In

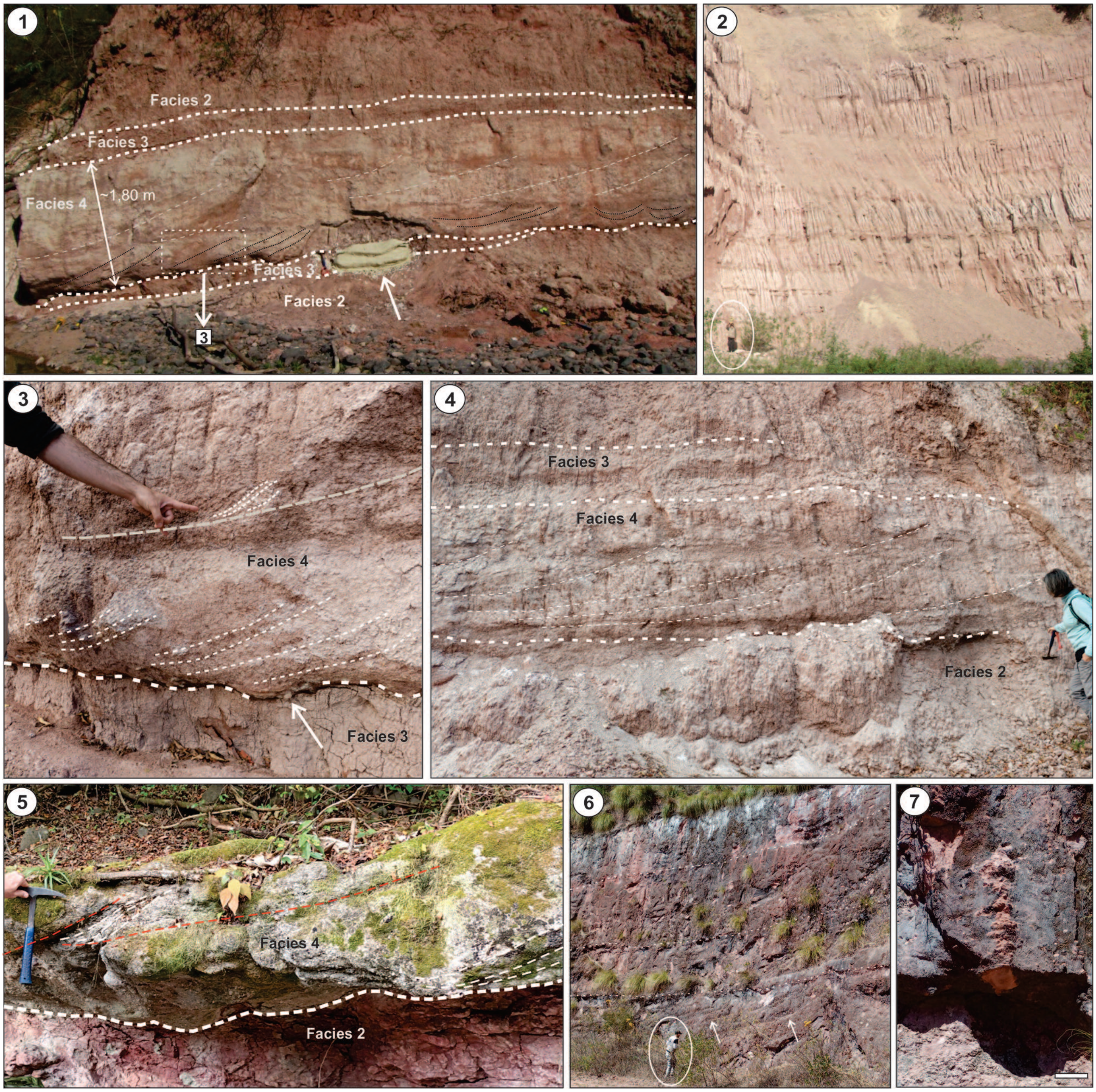

Figure 5. Field photographs. **1,** Overall view of the Facies 4 exhibiting quasi-tabular geometry. Observing from base to top of the facies, the basal cross-stratified beds (enhanced by black lines) are followed upward by faintly defined inclined surfaces (inferred as lateral accretion surfaces) marked with dashed grayish lines. Below the erosive contact that separates the facies from the underlying Facies 3, the "gypsum ball" shows the occurrence of the recent vertebrate findings; **2,** Overall view of stacked Facies 4 sandstone deposits separated by relatively thin intervals of facies 2 and 3 (person for scale); **3,** Detail of Fig. 5.1 displaying different sets of planar cross-stratification. Note the upper cross-stratified set (finger-pointed) above an inclined surface. The white arrow points toward a quartz pebble above the basal and erosive surface of the facies; **4,** Facies 4, sandstone body showing with inclined surfaces (enhanced by dashed lines) and common occurrences of vertical structures mainly ascribed to rhizoliths along the sandstone body; **5,** Facies 4, faintly preserved cross-stratification overlying inclined surfaces; **6,** Staked tabular sandstone bodies at the Alto de Medina locality. White arrows point towards faintly defined low-angle inclined surfaces (person for scale); **7,** Close-up view of a structure ascribed to an insect trace fossil. Scale bar= ~15 cm

this regard, the superimposed planar and trough cross-stratified beds represents subaqueous 2D and 3D dunes (respectively) that migrated in and towards the deeper parts of the channels, whereas ripple cross-lamination formed due to migration of ripples in shallower positions within the inner bank (*e.g.*, Miall, 1996; Nichols, 2009). In addition, dispersed pebbles and mudstone intraclasts on the lower erosive surfaces of the sandstone bodies are related to basal lag accumulations due to channel migration and overbank erosion. Moreover, the presence of rhizoliths and insect nesting traces suggests pauses in sedimentation and local subaerial exposure of sandy channel deposits (*e.g.*, Hasiotis, 2002, 2007; Tabor & Myers, 2015). This facies is interpreted to represent deposition in meandering channels.

Facies association and paleoenvironmental interpretation

Facies analysis mainly reveals the presence of fluvial channels and floodplain deposits (see also discussion below). Therefore, the facies 1, 2, 3, and 4 are integrated into a facies association that allows interpretating a multi-channel fluvial system with relatively stable muddy floodplain areas (*e.g.*, Miall, 1996, 2010; Makaske, 2001). In this scenario, braided and sinuous channel belts represented by the Facies 1 and Facies 4, respectively, were separated by fine-grained overbank areas characterized by Facies 2 and Facies 3. The channels were possibly interconnected enclosing floodplain areas. Proximal to distal floodplain settings (facies 2 and 3, respectively) were exposed to relatively prolonged periods of subaerial conditions, as well as reduced sediment supply, allowing instauration of vegetation and soil development (*e.g.*, Bossi *et al.*, 1998; Trendell *et al.*, 2013; Nascimento *et al.*, 2019). Similar conditions took place in certain areas of the channel belts, in which emerged parts of bars during low water table periods and low sedimentation rates favored local plant development and substrate colonization by insects (*e.g.*, Hasiotis, 2007; Tabor & Myers, 2015; Genise *et al.*, 2016; Nascimento *et al.*, 2017).

The Río Loro paleovertebrate assemblage: an updated overview

Vertebrate groups recorded in the Río Loro Formation include turtles, snakes, sebecid crocodyliforms, and different mammalian lineages (Tab. 2). This assemblage is

TABLE 2 – Fossil vertebrate assemblage of the Río Loro Formation

Podocnemididae, Testudines	"*Podocnemis*" cf. *P. argentinensis*	de Broin & de la Fuente (1993); Babot *et al.* (2017)
Testudines	Testudines indet.	This contribution
Sebecidae, Notosuchia, Crocodyliformes	*Lorosuchus nodosus*	Pol & Powell (2011)
Sebecidae, Notosuchia, Crocodyliformes	Sebecidae indet. (*Bretesuchus*-like form)	Bravo & García-López (2023)
Sebecidae, Notosuchia, Crocodyliformes	Sebecidae indet.	Bravo & García-López (2023)
Sebecidae, Notosuchia, Crocodyliformes	Sebecidae indet.	Bravo & García-López (2023)
Serpentes, Diapsida	Serpentes indet.	This contribution
Notonychopidae, ?Litopterna/Notopterna, Pan-Perissodactyla	*Notonychops powelli*	Soria (1989a)
Indaleciidae, ?Litopterna/Notopterna, Pan-Perissodactyla	*Indalecia* sp.	Powell & Ortiz (2014); Saade *et al.* (2023a)
Eoastrapostylopidae, ?Astrapotheria, Pan-Perissodactyla	*Eoastrapostylops riolorense*	Soria & Powell (1981); Kramarz *et al.* (2017); Saade *et al.* (2023b)
Carodniidae, Xenungulata, Pan-Perissodactyla	*Rodcania kakan*	Bergqvist *et al.* (2004); Gelfo *et al.* (2020)
Pan-Perissodactyla	*Satshatemnus bonapartei*	Soria (1989b); García-López *et al.* (2022)

The original version of this article contained an error in Table 2, which has been corrected in this version.

particularly interesting in the context of the early Paleogene mid-latitude units of South America, given the probable Paleocene age of the fossil-bearing levels and the singularities and endemic nature of most of the recorded taxa, whose affinities have recently been reinterpreted in a wide phylogenetic framework (Kramarz *et al.*, 2017; García-López *et al.*, 2022; Saade *et al.*, 2023a). Although the assemblage has two taxa that can be closely related to the records of the Santa Bárbara Subgroup (a *Bretesuchus*-like form and *Indalecia* sp., comparable to records of the Maíz Gordo and Lower Lumbrera formations, respectively), the high endemicity of the remaining species precludes, until now, further faunistic comparisons with other Paleogene units.

Herpetofauna. This is represented by turtles (Fig. 6.1), an isolated vertebra referred to a snake (Fig. 6.2), and crocodiles (Fig. 6.3–7). The presence of turtles was mentioned by de Broin & de la Fuente (1993), who documented the record of "*Podocnemis*" cf. *P. argentinensis* Cattoi & Freiberg, 1958 based on a specimen currently lost. Another record is represented by a partially preserved carapace and plastron (PVL 4746; Fig. 6.1) with associated postcranial remains, whose taxonomic identification is currently under way.

Among crocodyliforms, a singular record of the Río Loro Formation is *Lorosuchus nodosus* Pol & Powell, 2011 (Fig. 6.3). This species was considered as a basal sebecid, although recent phylogenetic analysis revealed ambiguous affinities for this very distinctive taxon. Most of the problematic status of the species is based on the presence of homoplastic cranial features related to aquatic habits that have profound implications for the possible ecological and morphological disparity within Sebecidae (Bravo *et al.*, 2021). The platyrostral skull of *Lorosuchus nodosus* contrasts with the oreinirostry of all other representatives of the family. This condition would indicate that *Lorosuchus* Pol & Powell, 2011 is the only member of this group with specializations typical of aquatic crocodyliforms (Pol & Powell, 2011). In contrast, a second possibility is considering *Lorosuchus* as part of a crocodyliform lineage different from Sebecidae that would have survived the K/Pg boundary extinction event (Bravo *et al.*, 2021). This interpretation would lead to a necessary reevaluation of crocodyliform diversity during the early Cenozoic and should be carefully addressed. Other three records of sebecids have been reported recently (PVL 7689, PVL 7690, and PVL 7694; Fig. 6.4–7). These new materials, currently under study, represent at least two new taxa that display a set of typical features related to terrestrial habits, including the nares anteriorly directed and an oreinirostral condition (*e.g.*, *Sebecus* Simpson, 1937; *Bretesuchus* Gasparini *et al.*, 1993). Thus, there are different ecological morphotypes of crocodyliformes (both terrestrial and aquatic, based on cranial anatomical features), among the reptiles recorded in the Río Loro Formation (Bravo & García-López, 2023).

Mammalian fauna. Mammals represent the bulk of the fossil vertebrate diversity within the Río Loro Formation. In the context of this unit, these vertebrates are represented entirely by genera of early diverging placental clades allied with South American native ungulates (Fig. 7.1–5). *Notonychops* Soria, 1989a, *Indalecia* Bond & Vucetich, 1983, *Eoastrapostylops* Soria & Powell, 1981, *Satshatemnus* Soria, 1989b, and *Rodcania* Gelfo *et al.*, 2020 were traditionally considered as part of Litopterna-Notopterna, Astrapotheria, Notoungulata, and Xenungulata, respectively. *Notonychops powelli* Soria, 1989a (Fig. 7.1) was described as a representative of the Notonychopidae by Soria (1984, 1989a), who included this family plus Amilnedwardsidae and Indaleciidae (originally regarded as Litopterna) within the order Notopterna. The taxonomic *status* of Notopterna was extensively discussed in Saade *et al.* (2023a), where opposing postures on the validity of this order were exposed. The current revision of *Notonychops* will determine its affinities with other putatively related forms, such as *Indalecia* (Fig. 7.2) and *Adiantoides* Simpson & Minoprio, 1949.

Currently represented by the most abundant specimens, *Eoastrapostylops riolorense* Soria & Powell, 1981 is one of the best-known taxa of the Río Loro Formation (Fig. 7.3), although its affinities remain unclear nowadays. Initially regarded as the most basal Astrapotheria (Soria & Powell, 1981; Cifelli, 1993), a recent survey based on an exhaustive anatomical and phylogenetic study led Kramarz *et al.* (2017) to consider *E. riolorense* in a basal position regarding Astrapotheria, Pyrotheria, and Notoungulata. Recent fieldwork carried out in the classic fossil-bearing levels of the Río Loro Formation and the identification of specimens previously collected, allowed increasing the number of

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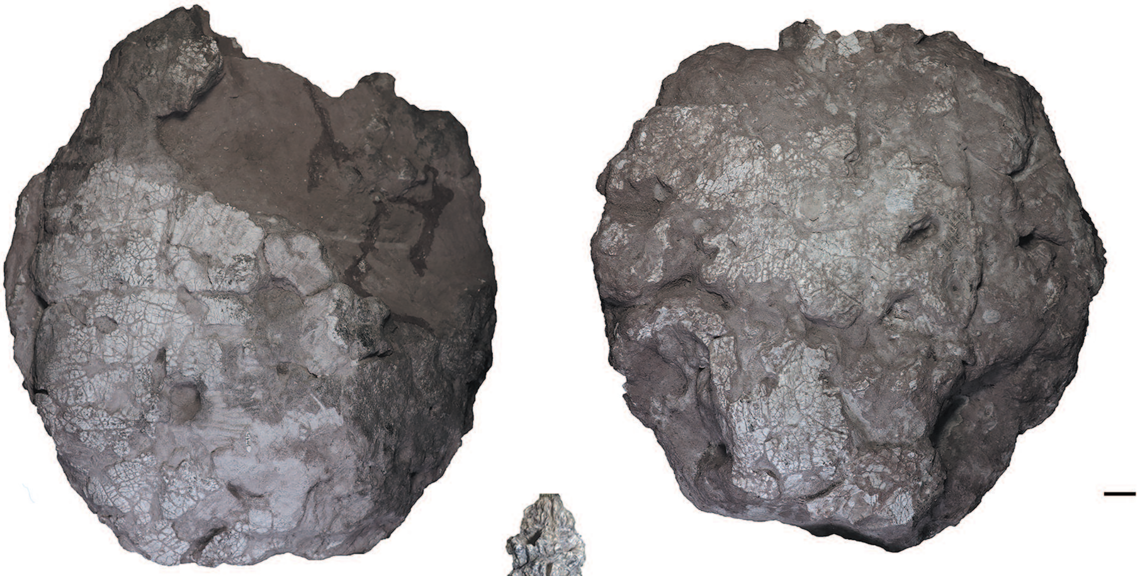

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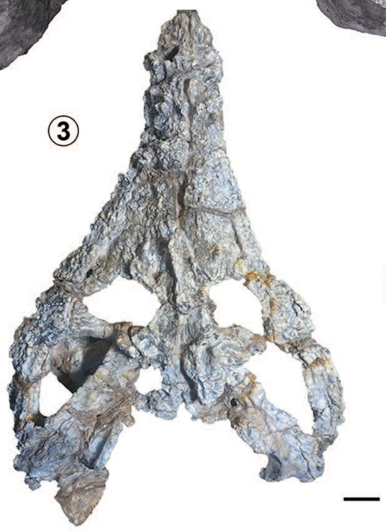

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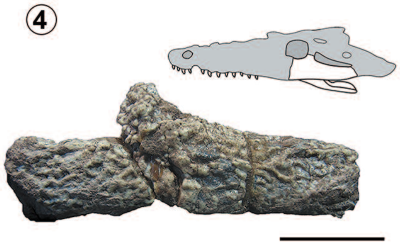

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known materials up to nine specimens. It is expected that the study of this new material will shed light on the affinities of this taxon, contrasting the different points of view about its relation to astrapotheres. Given its abundance, *E. riolorense* can be also considered the dominant form among the Río Loro mammalian assemblage and hence, its study is crucial for the understanding and characterization of this fauna. Among other traits, these new materials will allow recognizing intraspecific variation related to sexual dimorphism (Saade *et al.*, 2023b).

The enigmatic *Satshatemnus bonapartei* Soria, 1989b (Fig. 7.4) was traditionally considered the only representative of the order Notoungulata in the Río Loro Formation. The description of the type species was based on a very fragmentary specimen (Soria, 1989b) but currently *S. bonapartei* is represented by several new specimens, some finely preserved, which increased the morphological knowledge of the species and lead to discard its inclusion within the order Notoungulata, at least considering its usual definition. A first glimpse on the phylogenetic affinities of this species indicates that it represents a singular early radiation, outside the groups traditionally defined as the South American native ungulate orders, although probably close to Notoungulata, given the presence of some advanced dental features, such as the increased lophodonty and the basic eutheromorphic arrangement of the upper molars. These traits are shared between *Satshatemnus* and early-diverging species of Notoungulata and probably represent the conceptual basis for the original affinity hypothesis stated for this taxon (García-López *et al.*, 2022; Saade *et al.*, 2023a).

Finally, *Rodcania kakan*, included within Carodniidae (Xenungulata), represents the largest mammal currently known for the Río Loro Formation (Fig. 7.5). Given the sparse and scattered record of this order throughout South America (including low-latitude localities in Colombia and Peru and middle- to high-latitude localities in Brazil and Argentina), its presence in the Río Loro Formation is remarkable, as it widens the diversity and distributional spectrum for a relatively poorly-known but yet emblematic clade of South American fossil mammals (Gelfo *et al.*, 2020; Saade *et al.*, 2023a).

The general temporal and geographic background of the fossil mammals recovered from the Río Loro Formation is noteworthy given its particular circumstances. As mentioned before, although the chronology of these fossil-bearing levels is yet to be elucidated with higher precision, this assemblage certainly represents one of the earliest pulses of diversification among the South American native ungulates. Moreover, this important circumstance is underlined by the fact that it is highly possible that at least some of the conditions established by the thermal events of the first half of the Paleogene have had a strong influence on this fauna. Additionally, this evolutionary history took place in the South American middle-latitude strip, an area relatively under-represented regarding fossil communities, whose study has been historically biased toward Patagonian localities in the continent. These factors taken together raise the Río Loro assemblage as one of the most important Paleogene settlements of northern Argentina and one of the keys to understanding the early history of South American Cenozoic mammalian communities.

Biostratinomical aspects related to the vertebrate fauna

Fossils in the Río Loro Formation outcrops are often found as isolated and fragmentary elements but also include articulated specimens, such as complete skulls (joined cranium and dentary and in some cases also articulating with cervical vertebrae). Although most specimens are affected by recent weathering, preserved surfaces of the bones still allow analyzing pre-burial biostratinomic conditions. Following the scheme proposed by Behrensmeyer (1978), four stages of weathering were

Figure 6. Representatives of the fossil herpetofauna of the Río Loro Formation. **1, PVL 4746**, Testudines indet., incomplete carapace (left) and plastron (right); **2, PVL 7913**, Serpentes indet., dorsal vertebra in anterior (up) and posterior (down) view; **3, PVL 6219**, ***Lorosuchus nodosus*** (holotype), skull in dorsal view; **4, PVL 7694**, Sebecidae indet., schematic drawing (up) and cranial fragment corresponding to the left maxilla and left jugal (down); **5, PVL 7694**, Sebecidae indet., cervical (left) and dorsal (right) vertebrae in lateral view; **6, PVL 7689**, Sebecidae indet., rostral end of the premaxillae and a portion of the right hemimandible in occlusion (left) and schematic drawing (right); **7, PVL 7690**, Sebecidae indet. (***Bretesuchus***-like form), schematic drawing (up) and skull in right lateral view (down). Scale bar= 20 mm.

identified among vertebrate fossils recovered from the Río Loro Formation: Stage 0 to Stage 3 (Fig. 8). Most specimens fall into Stage 1 and Stage 2 (62.5% of the sample), with 15.63% corresponding to Stage 0, and 3.13% (representing a single individual) falling into Stage 3, the highest weathering recorded among the analyzed specimens (Tab. 3). Beyond this categorization, the pieces do not show evidence of abrasion due to transportation.

The conservation pattern, including the average low degree of weathering and fragmentation, as well as the absence of signs of abrasion, suggests that the pieces suffered an early burial after partial disarticulation of the

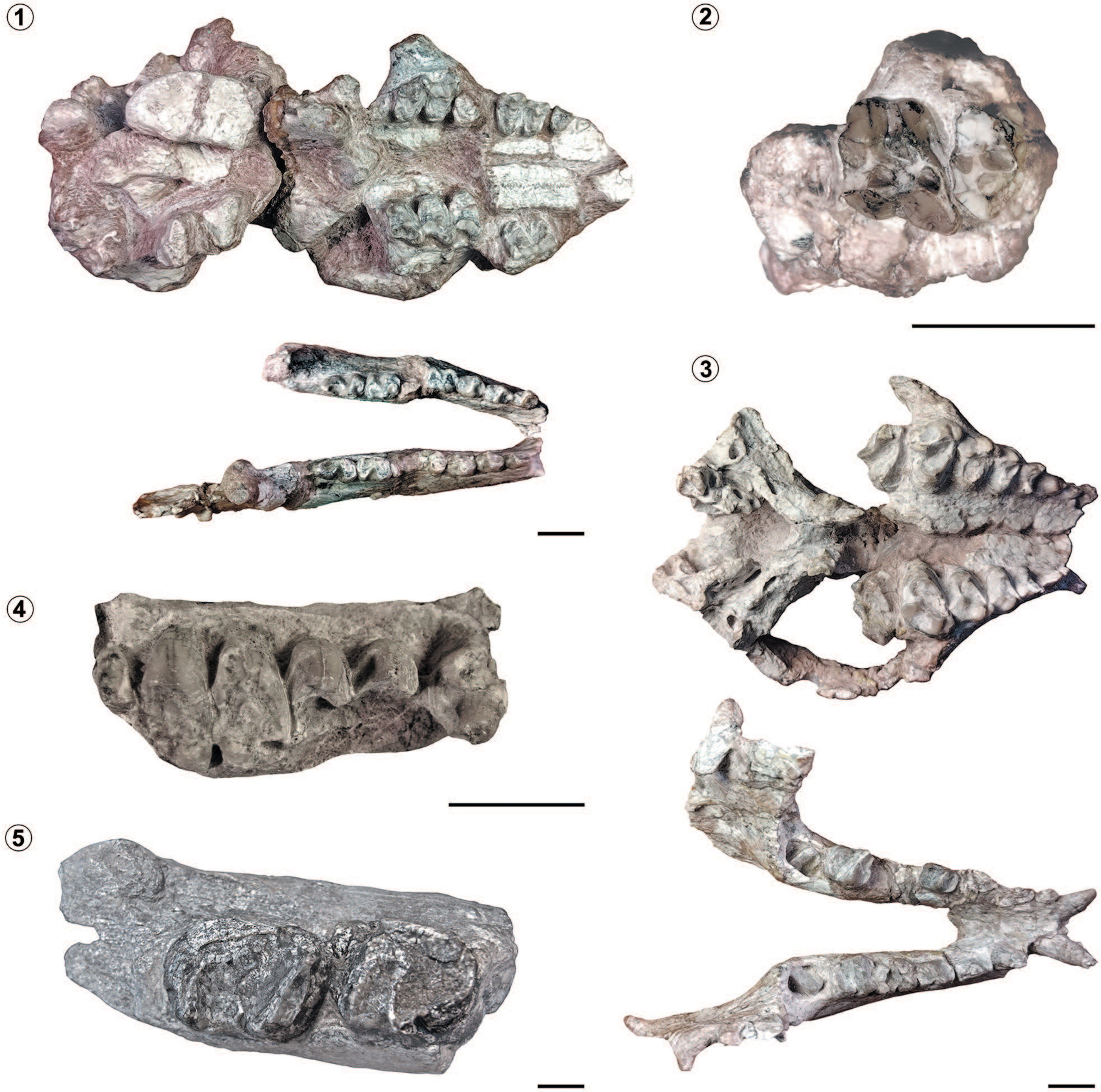


Figure 7. Representatives of the fossil mammal fauna of the Río Loro Formation. **1, PVL 4298**, ***Notonychops powelli*** (holotype), cranium in ventral view (up) and mandible in dorsal view (down); **2, PVL 5901**, ***Indalecia*** sp., left maxillary fragment with M1 (incomplete) and M2 in occlusal view; **3, PVL 4216**, ***Eoastrapostylops riolorense*** (holotype), cranium in ventral view (up) and mandible in dorsal view (down); **4, PVL 4297**, ***Satshatemnus bonapartei*** (holotype), left maxillary fragment with P2, P3–4 (incomplete), M1–2, and fragment of M3 in occlusal view; **5, PVL 7583**, ***Rodcania kakan*** (holotype), left mandibular fragment with m2–3 in occlusal view. Scale bar= 10 mm.

TABLE 3 – Main taphonomic attributes in fossil vertebrates recovered from distal floodplains of the Río Loro Formation

Bone weathering stages (*sensu* Behrensmeyer, 1978)	N	%
Stage 0	5	15.63
Stage 1	12	37.50
Stage 2	8	25.00
Stage 3	1	3.13
Stage 4	0	0.00
Stage 5	0	0.00
?	5	15.63
Total	32	100.00
Articulation	N	%
Articulated	16	50.00
Associated	1	3.13
Isolated	15	48.39
Total	32	100.00
Percentage of preserved skeleton	N	%
30%	28	87.50
30%–70%	4	12.50
70%	0	0.00
Total	32	100.00

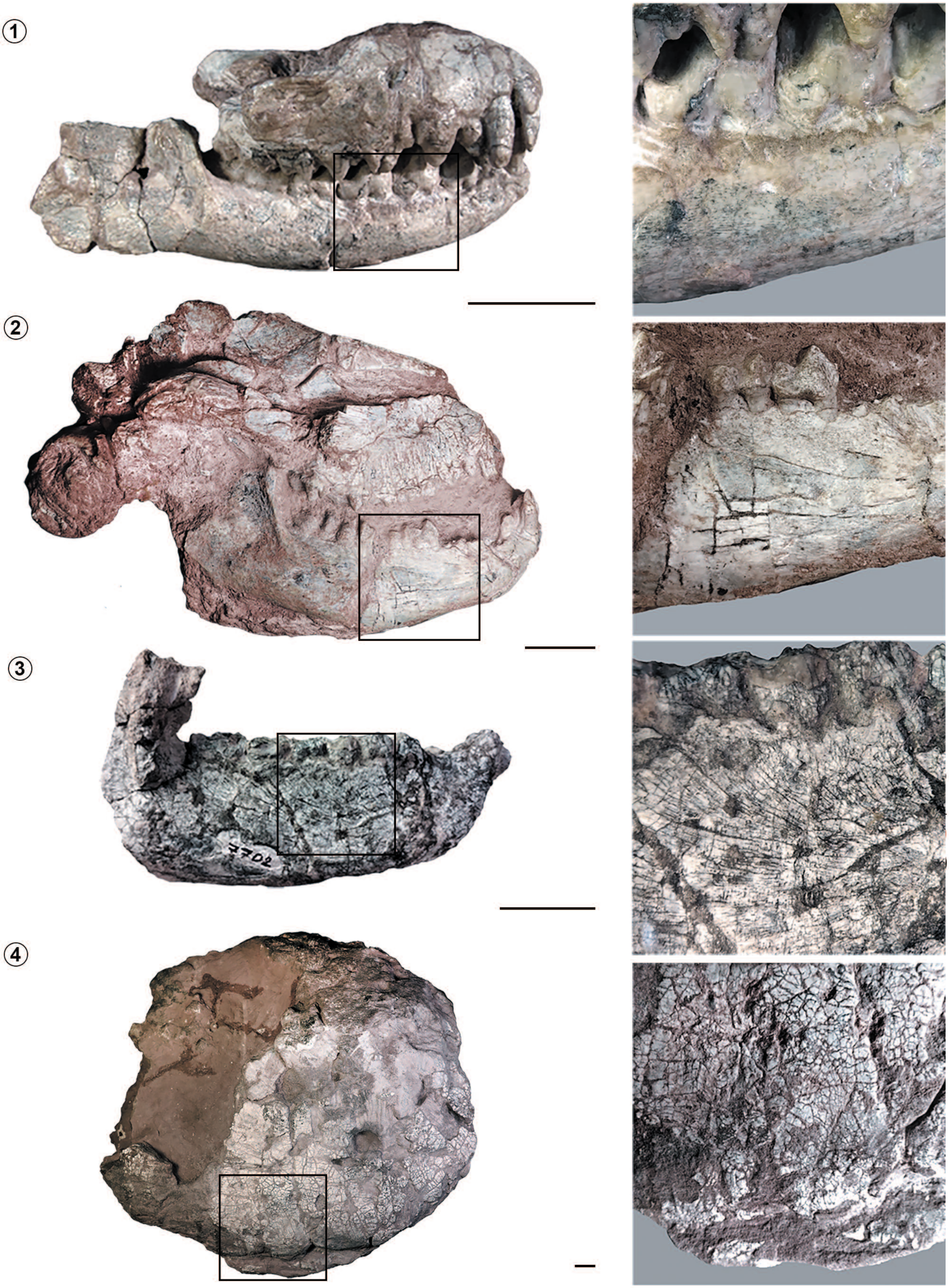
skeleton, with a relatively brief post-mortem subaerial exposure. In this sense, carcasses would have been exposed on the floodplain surfaces for a short to moderate pre-burial period, in which destructive processes (*e.g.*, carnivory, scavenging, trampling, and weathering) promoted relatively small disarticulation of the skeletons and the dispersion of the pieces from the source area (*e.g.*, Behrensmeyer, 1978, 1982; Behrensmeyer *et al.*, 1995). In addition to these aspects and considering some of the fossil occurrences related to Facies 3, it is also possible to suggest a short interval of transport of the skeletal remains and bone burial due to heavily sediment-laden overbank flows (*e.g.*, debris/mudflows).

DISCUSSION

Paleoenvironmental model and taphonomic insights

Since the study carried out by Bossi (1969) in which fluvial sedimentation is indicated for the Río Loro Formation deposits, scarce papers have been published regarding sedimentary facies and paleoenvironmental reconstructions of the unit. Powell & Palma (1981), in a short note communicating the first finding of fossil mammals in this formation, revised some general sedimentological aspects of the unit and interpreted deposition in a meandering fluvial system with floodplains affected by density currents. Later, Bossi *et al.* (1998), in a synthesis of the Cenozoic sedimentary record of the study area, briefly indicated that these deposits represent sedimentation in highly mobile braided rivers with floodplains. In addition, the authors also mentioned the presence of paleosol (vertisols) horizons in the interfluve deposits that supported a dense arbustive to arborescent vegetation cover.

Our results, in consistency with previous works (*e.g.*, Powell & Palma, 1981; Bossi *et al.*, 1998) reveal the presence of sandy fluvial channels as well as floodplain deposits. Moreover, the sedimentary facies analysis here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presented contributes to improving the paleoenvironmental resolution for the unit. To this extent, the facies association here recognized characterized a deposition in a multi-channel fluvial system, in which multi-story and multi-lateral channel bodies developed among floodplain areas (*e.g.*, Collinson, 1996; Miall, 1996, 2010; Makaske, 2001), allowing to envisage a paleoenvironmental model (Fig. 9) and further exploring its complexity. In this sense, the braided and meandering channel belts deposits of facies 1 and 4 (respectively) can be referred to two main fluvial channel sub-types that developed within the fluvial system, representing variations in discharges and different reaches of a possible anastomosing network. Moreover, the Facies 1 comprising thick intervals can be related to deposition within major trunk channels of the system, whereas Facies 4 characterized by relatively thinner bodies, in some cases intercalating with Facies 2 and Facies 3, may represent sedimentation in tributaries and probably in minor channels that developed divagating on floodplain areas (*e.g.*, Makaske, 2001; Bridge, 2006; Fig. 9). Both channel sub-types migrated along distal and proximal floodplain settings, typified by Facies 2 and Facies 3, respectively. Floodplains received sediment from the channels during episodic floods, mainly by crevassing and possibly levee over-topping. In this regard, during major floods, debris flows may have developed as part of splays that reached the floodplain, probably through breaches in the channel bank and/or levees. Suspension fall-out of sediment from floods mainly accumulated in temporary shallow water bodies (ponds) within lower and distal areas of the floodplain (flood basin). Inter-flood periods, possibly associated with semihumid to semiarid seasonal climate conditions, favored the formation of vertisols and calcisols in overbank settings (*e.g.*, Bossi *et al.*, 1998; Wright, 1999; Tanner, 2010; Tabor & Myers, 2015). Furthermore, dryer conditions together with a relatively low water table in certain areas of the fluvial system allowed the instauration of plants and development of insect nests (*e.g.*, Kraus & Hasiotis, 2006; Genise *et al.*, 2016; Nascimento *et al.*, 2017, 2019). The occurrence of abundant rhizoliths, exhibiting different sizes, may be related to the development of herbaceous to arbustive and possibly arboreous cover (*e.g.*, Bossi *et al.*, 1998; Retallack, 2001; Nascimento *et al.*, 2019).

Regarding taphonomic insights, it is interesting to recall that debris flow deposits accumulated in floodplain settings contain some well-preserved vertebrate remains, which are mainly represented by skulls but also by articulated postcranial elements. This suggests that the proximal floodplain setting developed a favorable preservational potential regarding other subenvironments within the system, possibly due to the participation of episodic flows and proper sedimentation rate. In this sense, the skeletal parts remained on the floodplain surface for a relatively short period, in which some selective dispersion of postcranial bones due to scavenger activity may have occurred. Then, possibly during major flood events, splays from the channels occasionally developing debris flows and mudflows, shortly mobilized and buried the skeletal parts in the system (*e.g.*, Smith, 1993; Ebert *et al.*, 2006; Casal *et al.*, 2023). Moreover, considering the associated pedogenic features of the related facies, it is probable that warmer conditions favored early permineralization processes (by carbonate and possibly iron deposits), contributing to the preservation of the skeletal remains (*e.g.* Smith, 1993; Behrensmeyer *et al.*, 1995; Collinson, 1996). However, additional data are necessary to confirm this last aspect.

Finally, considering the inferred paleoenvironmental framework from a broader context, the observations made for the Río Loro Formation in the surrounding localities (Fig. 1) allow some general and preliminary inferences regarding sedimentary facies prediction and paleovertebrate

Figure 8. Weathering indicia on Río Loro Formation vertebrate specimens. **1, PVL 7686**, ***Satshatemnus bonapartei***, rostral half of skull in right lateral view and detail of mandible showing weathering Stage 0 (bone surface shows no sign of cracking of flaking due to weathering); **2, PVL 7697**, ***Eoastrapostylops riolorense***, skull in right lateral view and detail of mandible showing weathering Stage 1 (bone shows cracking, normally parallel to the fiber structure); **3, PVL 7702**, ***Eoastrapostylops riolorense***, incomplete mandible in right lateral view and detail of mandibular body showing weathering Stage 2 (outermost layers of bone show flaking, usually associated with cracks); **4, PVL 4746**, Testudines indet., incomplete plastron in ventral view and detail showing weathering Stage 3 (homogeneously weathered compact bone, presenting a fibrous texture). Weathering stages established following Behrensmeyer (1978). Scale bar= 20 mm (details on boxes not to scale).

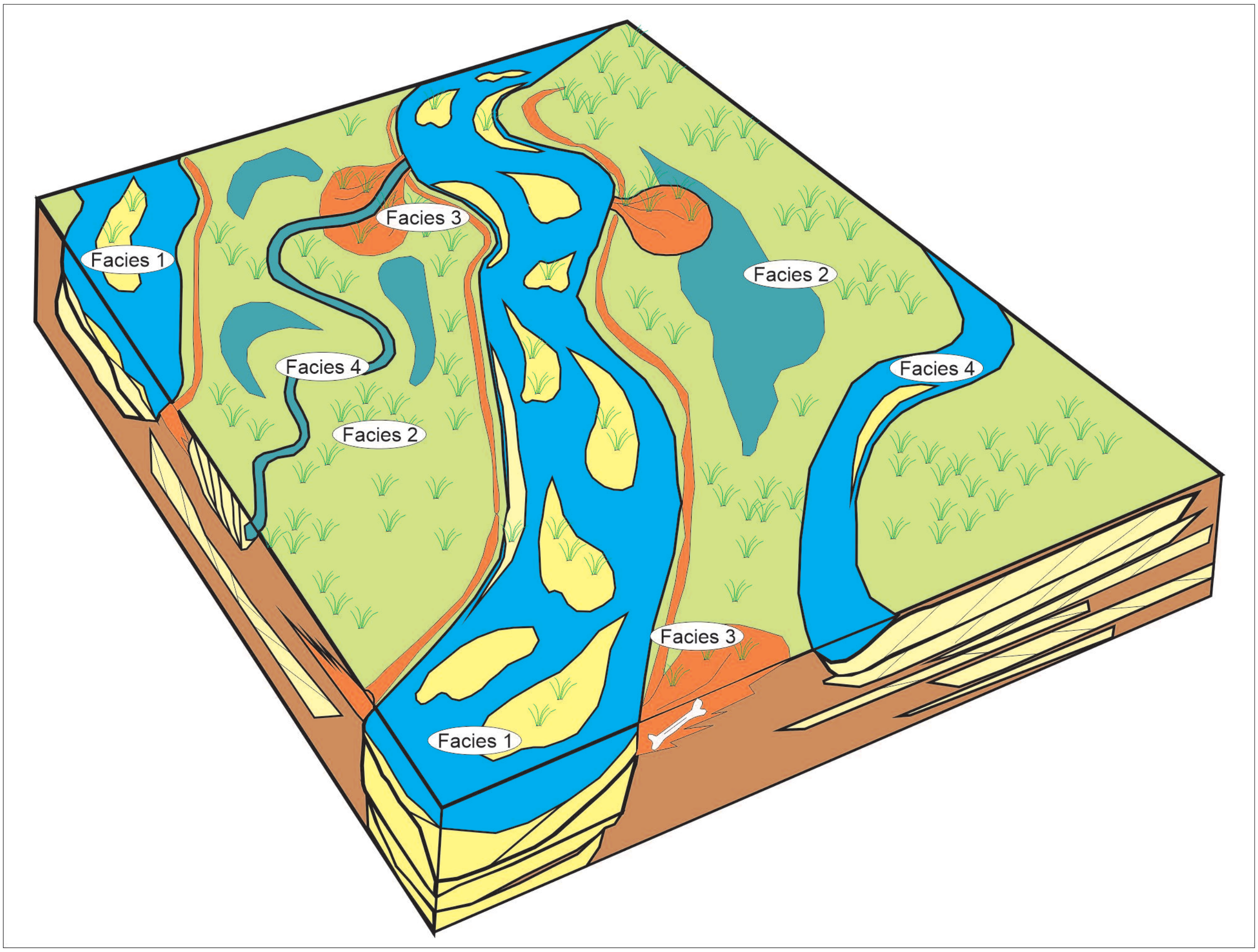

Figure 9. Inferred paleoevironmental model for the Río Loro Fromation at the type locality, showing a multi-channel fluvial system with floodplains and related facies distribution (see Tab. 1 for a summary of facies).

prospection. At Rearte, Nogalito, and Alto de Medina localities, sedimentary attributes of Facies 1 and Facies 4 preliminary suggest the presence of braided and meandering fluvial channel deposits for the unit. Similarly, the occurrence of intervals that can be referred to facies 2 and 3 at Rearte and Nogalito localities indicates that fine-grained floodplain sedimentary facies were widely distributed across the region, which in turn also promotes a favorable framework concerning fossil preservation and future prospection. However, it should be indicated that these deposits may represent sedimentation in a different fluvial setting with respect to the one interpreted at the Río Loro and Aguas Chiquitas localities.

Paleovertebrate association and paleoecological implications

Although limitations must be considered (see below), the record of fossil vertebrates of the Río Loro Formation provides some significant paleoecological proxies. Integration of these data can be used to elucidate the habitat preferences of this fossil community and improve the paleoenvironmental resolution obtained solely based on sedimentological attributes.

Given the main habits of such organisms (at least considering extant counterparts), turtles and crocodyliforms with aquatic adaptations among the Río Loro fauna (see Herpetofauna above) indicate at least a temperate environment and the development of relatively extensive freshwater bodies (Martin, 2008).

In mammals, dental morphology is usually examined in order to infer feeding habits and environmental preferences among herbivore species (Fortelius & Solounias, 2000; Schap & Samuels, 2020). Within the Río Loro faunal assemblage, all ungulates recorded show brachydont teeth with high-relief cusps (*i.e.*, low mesowear rates). This is traditionally indicative of browsing habits among mammals (MacFadden, 2000; Ortiz-Jaureguizar & Cladera, 2006; Madden, 2015; Schap & Samuels, 2020). Browsing ungulates usually feed in forested (closed) environments (Bro-Jørgensen, 2008; Croft *et al.*, 2020); therefore, in a general sense, dental morphology among the Río Loro mammals would indicate that these species were adapted to warm and moist conditions, in which closed vegetation was developed. Additionally, the body size distribution of the mammalian assemblage can be interpreted as part of the same line of evidence. Most of the Río Loro mammals represent small to medium-sized forms (*Notonychops*, *Satshatemnus*, *Indalecia*, and *Eoastrapostylops*; Gelfo *et al.*, 2020; Prevosti *et al.*, 2021). Even *Rodcania kakan*, the largest mammal of this assemblage, would have reached an average body mass of no more than 170 kg, which is less than the typical body mass inferred for larger xenungulates (Gelfo *et al.*, 2020) and even less than that of most tapir species (considered as typical browsers; Schap & Samuels, 2020). This size distribution of small to medium forms among the ungulates of the Río Loro Formation also relates to the development of closed and forested habitats (Quin *et al.*, 1996; Bro-Jørgensen, 2008). Nevertheless, a more complete paleoecological framework could be obtained by integrating other lines of evidence (*e.g.*, cranial and postcranial functional morphology analysis, meso and microwear dental studies, as well as palinological and geochemical analyses of the unit). The exploration of these additional data will certainly enrich the state of knowledge of the studied community.

Hence, the current knowledge of the Río Loro community matches with a scenario in which the fauna thrived under a warm climate with fluctuating humidity conditions, in association with freshwater sources (*e.g.*, rivers and ponds) and near well-vegetated areas. Moreover, even though the chronological context of the Río Loro Formation is currently not completely certain, this unit has been most probably deposited in a warm interval characterized by global maximum and optimum thermal conditions of the first half of the Paleogene (Zachos *et al.*, 2008; Kiehl *et al.*, 2018).

Overall, the integration of paleoenvironmental data with biostratinomical features of the fauna and their paleoecological affinities show consistency and allows us to envisage a fluvial setting in which floodplains with ponds and minor channels would have provided a suitable environmental scenario for the vertebrate fauna, particularly during dryer seasons (Fig. 10).

CONCLUSIONS

The following conclusions can be drawn from the analyses and observations presented here:

The sedimentary succession analyzed is composed of four main facies (1 to 4) that represent sedimentation in pebble-sandy to sandy fluvial channels and muddy floodplains. Facies 1 characterize deposition in braided channels, facies 2 and 3 typify sedimentation in distal to proximal floodplain settings, respectively, while Facies 4 records deposition in meandering channels.

A main facies association comprising the four facies is interpreted to reflect sedimentation in a complex multichannel fluvial system with relatively stable floodplain areas. Within this system, seasonal humid to dryer conditions favored biota substrate colonization, including insect nests development, and soil formation.

The abundance of articulated remains and low weathering stages for most of the recorded specimens indicates relatively rapid burial of skeletal parts by splays from the channels, mainly debris flows and mudflows that reached proximal floodplain settings.

The habits inferred for some of the vertebrate species recorded, as long as mammal dentitions and size distribution goes, match with a community developed close to fresh water sources and well-vegetated areas. This paleoenvironmental framework can be further characterized by certain seasonality (as evidenced by the sedimentological insights) and possibly warm conditions (considering the global temperature increase during the Paleocene and part of the Eocene).

This work contributes significantly to a most complete

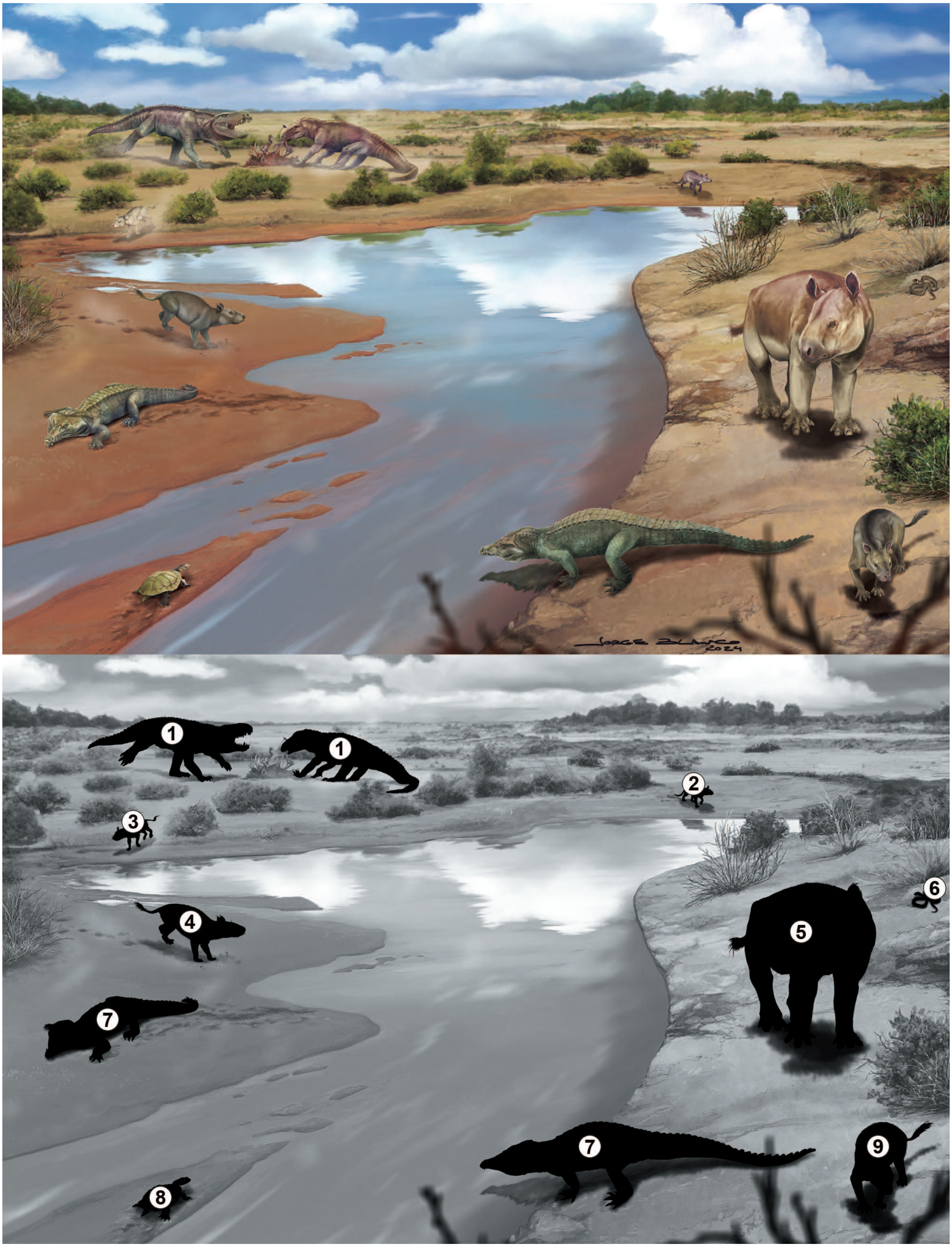

Figure 10. Hypothetical reconstruction sketching the environmental context and analyzed paleovertebrate fauna of the Río Loro Formation. **1,** Sebecidae indet. (***Bretesuchus***-like form); **2**, ***Indalecia*** sp.; **3**, ***Satshatemnus bonapartei***; **4**, ***Eoastrapostylops riolorense***; **5**, ***Rodcania kakan***; **6,** Serpentes indet.; **7,** ***Lorosuchus nodosus***; **8,** Testudines indet.; **9,** ***Notonychops powelli***. Drawings by Jorge Blanco.

and multidisciplinary approach to the general characterization of the Río Loro Formation and increases the knowledge of this unit regarding previous contributions that were published decades ago. This novel information will certainly represent a long-needed basis for future surveys focused on this unit and its remarkable fossil record.

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