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Linha São Luiz Geosite, Rio Grande do Sul State: 25 years of discoveries, and a unique window to the Brazilian Mesozoic

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Abstract

The Linha São Luiz Geosite is one of the most remarkable outcrops from the central region of Rio Grande do Sul state, southern Brazil. With more than 20 meters of vertical exposure, the locality preserves records of distinct sedimentary episodes, and one of the richest fossil assemblages known in southern Brazil. After a quarter of a century from the first expeditions to the site, the Linha São Luiz still yields new discoveries, registering exquisitely preserved fossils from micro and macrovertebrates, invertebrates, and plants, as well as trace fossils generated by these groups. In this contribution, we assembled representatives from distinct fields of paleontological study to provide a summary of the fossil assemblage from this site. We also briefly discuss the history of research and report geoconservation strategies which are being implemented at the locality, in order to preserve this important window to the Brazilian Mesozoic.

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1. Introduction

Located mere three kilometers away from the center of the Faxinal do Soturno municipality, the Linha São Luiz outcrop is a prominent locality. Over more than two decades of research by various specialist teams, the site has yielded a vast paleontological record, with hundreds of specimens being uncovered. The São Luiz Geosite is noteworthy, for its strata preserve a wide variety of fossil types, from microfossils to plant remains, micro and macro-invertebrates, tiny vertebrates to large dinosaurs, ranging from both somatofossils and ichnological remains. This turns the locality into a unique window to the past, specifically to the end of the Triassic Period, and perhaps even the beginning of the Jurassic. Thus, the outcrop documents part of important faunal and floristic turnovers that would shape the Earth's ecosystems in the following geologic stages. Despite the already abundant fossil record, the site still yields new fossils and species yet unknown to science, even a quarter of century after its discovery. In this contribution, we provide an overview of the known fossil record at the Linha São Luiz Geosite, trace the historical background of the prospections performed at the locality, and report efforts for the conservation of the area and promotion of its cultural importance as a heritage site.

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2. Geological Settings

The Paraná Basin, situated on continental crust, is filled with sedimentary and volcanic rocks ranging in age from the Ordovician to the Cretaceous periods (Figure 1A). Covering an area of 1,500,000 km², the basin extends across Brazil (1,100,000 km²), Uruguay, Argentina, and Paraguay, with a maximum sediment thickness of 8000 meters. This thickness results from polycyclic deposition events related to successive sedimentation episodes driven by tectonic activities affecting Southwestern Gondwana (Milani 1997; Milani et al. 1998). During the Paleozoic Era, the Paraná Basin functioned as an intracratonic basin, recording significant transgressive-regressive cycles linked to the stabilization of West Gondwana, the Andean active margin, climatic changes, Panthalassa paleo-ocean activity, and the formation of Pangea (Milani et al. 2007; Limarino et al. 2014). The Mesozoic breakup of Gondwana, and consequently Pangea, led to the formation of multiple rift and proto-oceanic basins, profoundly affecting the depocenters of adjacent intracratonic basins (Milani et al. 1998; Lovecchio et al. 2020). In the Paraná Basin, this context resulted in unconformities related to active margin tectonics of southwestern Gondwana and the South Atlantic rifting process, with repeated reactivation of NW-SE, NE-SW, and E-W fault systems driving sedimentation and preservation of stratigraphic units (Milani 1997; Zerfass et al. 2003, 2004).

Seven main continental Mesozoic successions have been identified in the Brazilian portion of the basin (Milani 1997; Scherer 2000; Scherer et al. 2023): (1) Sanga do Cabral Formation (Induan/Olenekian), consisting of fluvial, lacustrine and aeolian deposits; (2) Santa Maria and Caturrita formations (Ladinian to Norian) composed of fluvial-lacustrine deposits; (3) Mata Sandstone (which was originally recognized as part of the Caturrita Formation by Andreis (1980) and separated from it by later authors) deposits of braided fluvial system; (4) Pirambóia Formation, a wet aeolian system with cyclic fluvial incursions; (5) Guará Formation (Upper Jurassic), constituted by fluvial and fluvial-aeolian systems; (6) Botucatu Formation (Lower Cretaceous), recording dunes of dry aeolian system fossilized under the Serra Geral Formation volcanic lavas; and (7) Bauru Group (Upper Cretaceous) composed of fluvial and aeolian deposits.

This study focuses on the second succession (2), comprising the Santa Maria and Caturrita Formations, a continental deposit occurring only in the central block of Rio Grande do Sul State, South Brazil (Figure 1B; Zerfass et al. 2003; Scherer et al. 2023). In terms of sequence stratigraphy, the Santa Maria and Caturrita Formations comprise the Santa Maria Supersequence, a second-order continental sequence which is subdivided into third-order sequences, from base to top: Pinheiros-Chiniquá, Santa Cruz, Candelária and Mata (Figure 1C; Zerfass et al. 2003; Horn et al. 2014; Schultz et al. 2020). Each sequence begins with fluvial deposits (low-

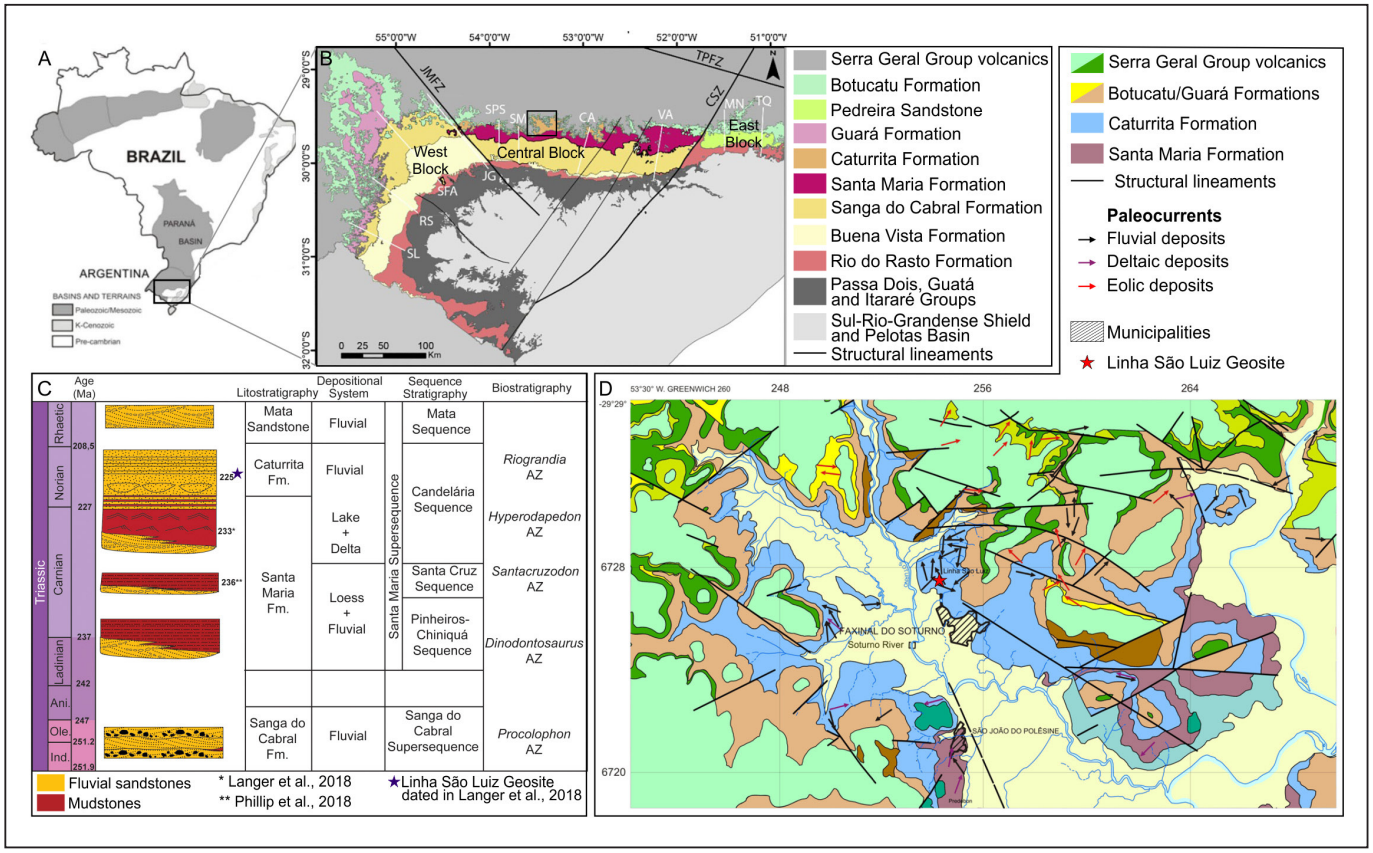

Figure 1. Location and geological context of the Linha São Luiz Geosite. A, Brazilian phanerozoic basins locating the study area at the southern portion of the Brazilian Paraná Basin in the Rio Grande do Sul State (rectangle). B, Geological context of the central portion of the Rio Grande do Sul State with the East, Central, and West Blocks of the Paraná Basin, locating the Faxinal do Soturno municipality and surroundings (rectangle). C, Stratigraphical chart of the Triassic layers from the Paraná Basin, including (Sanga do Cabral and Santa Maria Supersequences), with lithostratigraphic, depositional environments, and biostratigraphic information. D, Geology of Faxinal do Soturno and surroundings, locating the Linha São Luiz Geosite (star). Modified from modified from Crisafulli et al. (2016), Scherer et al. (2023) and Schultz et al. (2020). Abbreviations: Ani, Anisian; Ind, Induan; Ole, Olenekian.

sinuosity rivers) overlain by aeolian and shallow lacustrine deposits. This stratigraphic stacking is interpreted as cyclic basin subsidence induced by tectonic uplift of the source areas (Zerfass et al. 2004). The three first sequences contain a globally recognized and richly fossiliferous record of tetrapods divided into four successive faunal associations, or Assemblage Zones (AZ) that define a precisely dated biostratigraphy, aiding correlation, especially, with other South American and African faunas (Schultz et al. 2020).

The Candelária Sequence comprises the upper part of the Santa Maria Formation and the Caturrita Formation, including the *Hyperodapedon* and *Riograndia* Assemblage Zones, respectively (Figure 1C; Schultz et al. 2020). This sequence begins with white to reddish sandstones featuring planar and trough cross-stratification, occasional mudstone intraclasts, and plant fossils, interpreted as ephemeral braided river deposits (Zerfass et al. 2003). These are overlain by laminated reddish mudstones and very fine-grained massive or stratified sandstones with climbing and wave ripples, suggesting deposition in sheet deltas and ephemeral lakes under increased humidity (Horn et al., 2018b). The sequence transitions from dominant mudstones to interlayered fine-grained, massive sandstones and laminated mudstones, indicative of mass flows from seasonal downpours. Subordinate stratified sandstones show planar bedding, thick lamination, low-angle cross-stratification, and climbing ripples, interpreted as deposits from hyperconcentrated flows in ephemeral fluvial systems with lateral avulsions and frontal deconfinement, forming sheet-like channel deposits with lateral accretion macroforms (Faccini 2000; Faccini et al. 2003; Horn et al., 2018a).

The Linha São Luiz Geosite integrates the final part of the Candelária Sequence (Figure 1C, D), traditionally related to the Caturrita Formation (excluding the Mata Sequence), and integrating the *Riograndia* AZ (Bonaparte et al., 2010a; Soares et al. 2011; Schultz et al. 2020; Martinelli et al. 2021). The 25 years of research at the Linha São Luiz Geosite allowed excellent detailing of the facies, sedimentary structures, and fossil content. The outcrop, with *circa* 23 meters of vertical exposure (Figure 2), can initially be divided into at least two main parts: one predominantly fluvial and one predominantly lacustrine, overlain by a deltaic system.

The lower portion of the package (Figure 2A), approximately 11 meters in thickness, comprises facies Sh, Sr, and Sm at its base, characterized by paleocurrents predominantly directed eastward. These facies exhibit amalgamated layers indicative of deposition within a meandering fluvial system, with evidence of rhizobioturbation at certain levels and one level containing *Taenidium barreti* bioturbation (Jenisch et al. 2017). Overlying these facies and exhibiting greater thickness is facies Sm, which can be interpreted either as deposits from high-concentration sediment-gravity flows or as layers that have undergone post-depositional fluidization, leading to the loss of primary sedimentary structures (Jenisch et al. 2017). The coarser segment of this unit is a medium-grained sandstone, approximately 1 meter thick, containing vertebrate remains characteristic of the *Riograndia* AZ. This level has been dated using U-Pb radiometric techniques by Langer et al. (2018), yielding a maximum deposition age of ~225.42 ± 0.37 Ma (Early Norian), corroborated by relative dating within the AZ (Soares et al. 2011; Schultz et al. 2020). The top of these strata, capping the lower succession, is marked by extensive rhizobioturbation, including a piece of wood with roots in life position and additional *Taenidium barreti* bioturbation. These features suggest the establishment of larger vegetation within a stable, subaerially exposed substrate, indicative of a paleoenvironment conducive to biological activity (Crisafulli and Dutra 2009; Jenisch et al. 2017).

The upper portion of the Geosite (Figure 2B) is characterized by a coarsening-upward sequence, beginning with a mudstone package (facies Fl) measuring 2.20 meters in thickness. This unit contains the greatest diversity of fossil biota, including branchiopods, insects, wood fragments, leaves, shoots, and fish scales. Within these levels, occasional inputs of silt and very fine sand create two intervals of ferriferous symmetrical ripples, suggesting deposition in shallow yet perennial water bodies located on floodplains (Jenisch et al. 2017). This mudstone package is progressively replaced by a heterolithic succession, comprising tabular, lenticular, and occasionally sigmoidal beds of facies Sm, Sh, and St. It is common to observe facies Fl overlaying these sandy facies, primarily deposited through decantation processes. The association of these facies indicates the development of river mouth bars formed by the discharge of fluvial currents into water bodies and crevasse splay deposits within a fluvial floodplain. The presence of roots and desiccation cracks at the tops of individual layers signifies episodic subaerial exposure interrupted by occasional depositional events. The uppermost part of the sequence is capped by a fine-grained heterolithic package, ~1 meter in thickness, exhibiting abundant drying cracks and rhizoturbation, along with clusters of Branchiopoda. At one level, carapaces are associated with two theropod footprints (Silva et al. 2012; Jenisch et al. 2017). Overall, this upper package of the Linha São Luiz Geosite can be subdivided into an intermediate portion representing lacustrine deposits and an upper portion indicative of a fluvial system characterized by river mouth bars and crevasse splay deposition.

The two primary packages of the outcrop exhibit discordant ages, with accumulating evidence reinforcing this difference over the years. The lower portion has been radiometric dated and shows strong biostratigraphic correlation with other outcrops of the *Riograndia* AZ, characterized as Early Norian (Late Triassic) (Bonaparte et al. 2010a; Soares et al. 2011; Langer et al. 2018; Schultz et al. 2020; Martinelli et al. 2021). This also befits the observed vertebrate assemblage, including typically Triassic fossils, such as procolophonids, rhynchocephalians, and non-mammaliaform cynodonts, as well as lagerpetids and an early sauropodomorph. In contrast, the fossil content of the upper package suggests a younger age. For instance, the branchiopods are more closely related to Jurassic taxa (Cabral 2011; Rohn et al. 2014; Jenisch et al. 2017), and the plants are evolutionarily more complex, corresponding to the Upper Triassic to Lower Jurassic transition (Barboni and Dutra 2013). Footprints attributed to large theropods might also indicate affinity to Jurassic forms (Silva et al. 2012), though large-bodied saurischians are already present in Upper Triassic communities. Further evidence of the age discrepancy between the two levels includes the presence of prominent rhizoturbation, a trunk in life position, and *T. barretti* ichnofossils, indicating subaerial exposure and a period of non-deposition at the boundary of the two packages (Crisafulli and Dutra 2009; Jenisch et al. 2017). This evidence implies that the upper package might not belong to the Caturrita Formation (*sensu* Andreis et al. 1980), although it does not clearly align with other known Jurassic units of the Paraná Basin, requiring further investigations.

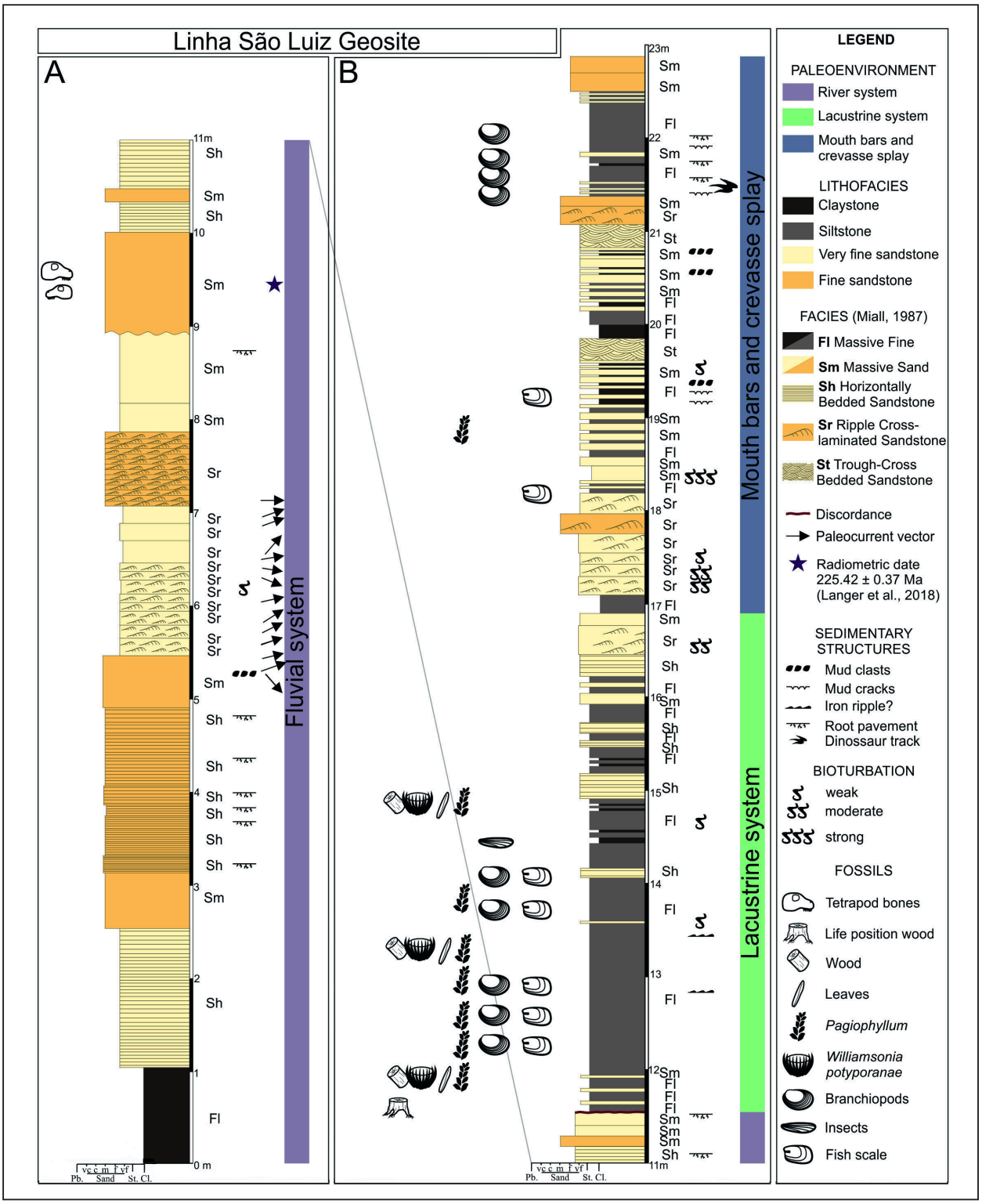

Figure 2. Stratigraphic section and fossil distribution at the outcropping areas of the Linha São Luiz Geosite. A, basal part of the outcrop. B, central and top of the outcrop. Modified from Barboni and Dutra (2013) and Jenisch et al (2017).

3. History of Research

Many of the fossil localities which characterize the *Riograndia* Assemblage Zone (Bonaparte et al. 2001, 2003, 2005, 2010a; Langer et al. 2007; Soares et al. 2011; Schultz et al. 2020), especially those containing a rich microvertebrate content, were discovered in the years of 1998 – 2000 in expeditions led by the former Fundação Zoobotânica do Rio Grande do Sul (FZB-RS) and Instituto de Geociências of the Universidade Federal do Rio Grande do Sul (IG-UFRGS), in collaboration with other institutions (Figure 3). A brief narrative detailing some of these discoveries was provided by Bonaparte and Migale (2010, 2015), from the point of view of the Argentine paleontologist José Fernando Bonaparte (1928-2020), who was employed by the former FZB-RS and then as a CNPq research fellow

at the IG-UFRGS and actively participated during these first expeditions in the search for vertebrate fossils. He also got financial support from the National Geographic Society (USA) to develop long-term fieldwork at the Faxinal do Soturno and Candelária regions during those years. Based on these accounts, the paleontologists were drawn to the locality of Linha São Luiz by Daniel Cargnin, a priest who resided in the region and who held a profound interest in fossil prospection and collection and who ultimately came to discover this fossil locality in Faxinal do Soturno (Figure 3). Though not an academic, Cargnin had a fundamental role in the development of paleontological studies, especially regarding vertebrate paleontology and paleobotany, for he and his brother Abraão were based in several municipalities of the Central Depression of Rio Grande do Sul, often collecting a vast number of Triassic fossils, and acting to raise the awareness of the locals to their importance.

Most vertebrate taxa discussed in the following section were collected in the interstice between 1998 and 2005, and less frequently since then, during several expeditions led by the aforementioned institutions (Figure 3). These fossils would be prepared and studied in the following years, and indeed, many still await proper assessment.

In turn, the study of fossil plants gained momentum following the discovery of vertebrates at the outcrop, leading to greater attention and systematic collections after 2004. A collaborative research team led by Pires and Guerra-Sommer (UFRGS, UNIVATES, and FZRS) named the first trunk morphotaxon *Sommerxylon* (Pires and Guerra-Sommer 2004). Jorge Ferigolo (FZRS) and Robson Tadeu Bolson (UFPR) also contributed to this work. New floral elements, including conifer stems, were described in 2009 (Crisafulli and Dutra 2009). This work attracted the interest of researchers such as Alexandra Crisafulli (Universidad Nacional del Nordeste, Argentina) and Tania Lindner Dutra (UNISINOS University, São Leopoldo), who would continue research at the São Luiz site over the next decade. Fieldwork and projects by the Geology undergraduate program at Unisinos University, led by Tânia Lindner Dutra, in the later part of that decade, resulted in the preliminary description of new conifer leaves and stems. Notably, the publication of the “flower-like” cycad cone *Williamsonia potyporanae* Barboni and Dutra (2013) provided evidence that the upper strata of the São Luiz outcrop, along with the tetrapod footprints, date to the Jurassic period (Barboni and Dutra 2013; Silva et al. 2012).

In the 2010s, records of invertebrates started to be reported in the upper strata, comprising a diverse and well-preserved assemblage of insects and abundant spinicaudatans (reports not published yet). From 2014 onwards, Spinicaudata received special attention for paleoenvironmental and taphonomic studies (Rohn et al. 2014; Jenisch et al. 2017). Following the retirement of paleobotanist Tânia Lindner Dutra from the MHGEO in 2017, curator Rodrigo Scalise Horodyski continued fieldwork at the São Luiz site. These ongoing efforts have resulted in the collection of over 730 fossil specimens, including undescribed vertebrates, invertebrates, and plants. Currently, research is being conducted to describe and interpret the

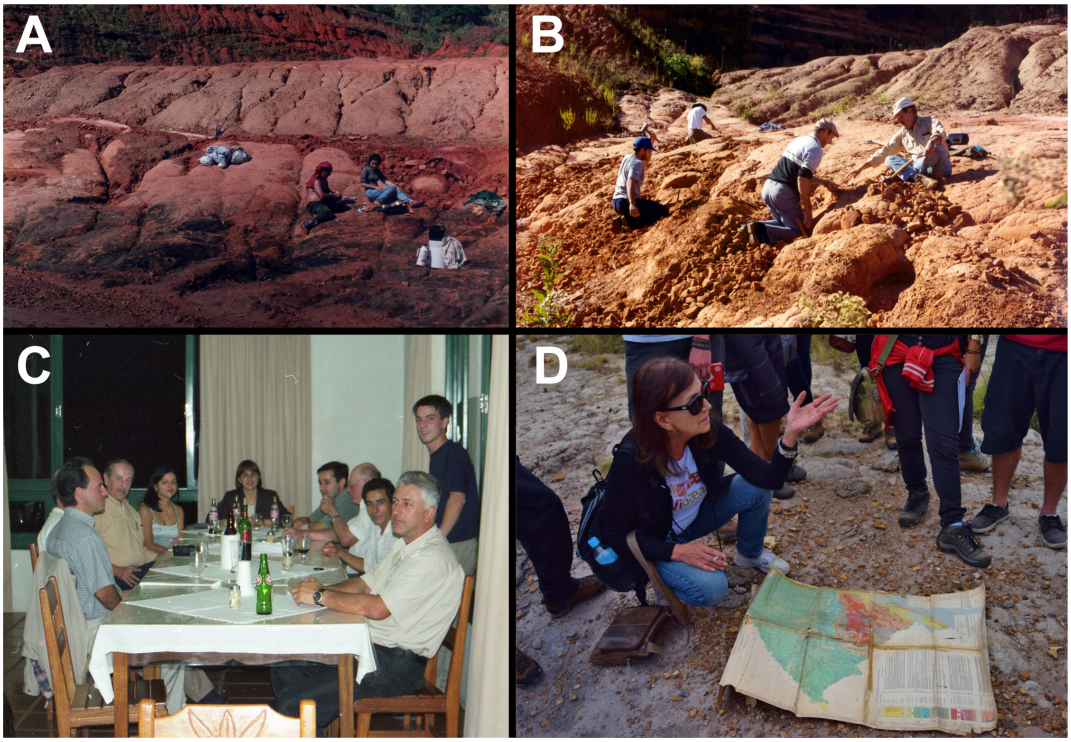

Figure 3. Early expeditions to the Linha São Luiz Geosite. A, fieldwork conducted by the former Fundação Zoobotânica do Rio Grande do Sul, with Jorge Ferigolo and Ana Maria Ribeiro excavating the outcrop in 1998. B, fieldwork by the Universidade Federal do Rio Grande do Sul, in 1999, with Rogerio Rubert, Daniel Hernández, Claudio Bortolas, and Mario Barberena. C, Dinner meeting at the Paleon Hotel in Mata where the UFRGS team joined Daniel Cargnin and municipal authorities before fieldwork at Linha São Luiz in 1999. In the picture can be seen Mario Barberena (left) and Daniel Cargnin, Daniel Hernández, Rogerio Rubert, Agustín Martinelli, and Adauto, driver of the UFRGS (right). Photograph taken by José Bonaparte. D, Tânia Lindner Dutra, during fieldwork conducted in 2015 by the UNISINOS team.

insect fossils and to integrate data from the assemblages of plants and carapaces.

Starting at the decade of 2010, other institutions intensified efforts of prospection at the site, and with the establishment of the Centro de Apoio à Pesquisa Paleontológica from the Universidade Federal de Santa Maria (CAPPA/UFSM), located 5.5 km from the outcrop, an intensified monitoring of the site became possible. The constant prospections and attention given to the site greatly reduced the loss of material due to erosion. Additionally, efforts conducted by the team at CAPPA/UFSM, in partnership with the public administration of Faxinal do Soturno and the administration of UNESCO Geopark Quarta Colônia led to the mitigation of important sources of vulnerability to the site, namely the accumulation of debris and the expansion of vegetational cover by exotic trees (see Geoconservation, below).

4. Fossil Record

4.1. Vertebrates

Fossil vertebrates are predominant at the top of the fluvial stage in the fine sandstones of facies Sm (Figure 2), which is dominated by small-sized tetrapods (Figure 4), microvertebrate of estimated skull lengths of 15 to 40 millimeters (Bonaparte et al. 2010a; Schultz et al. 2020). These fossils occur as isolated elements, semi-articulated skeletons and occasional clumps of disarticulated bones. This peculiar preservation

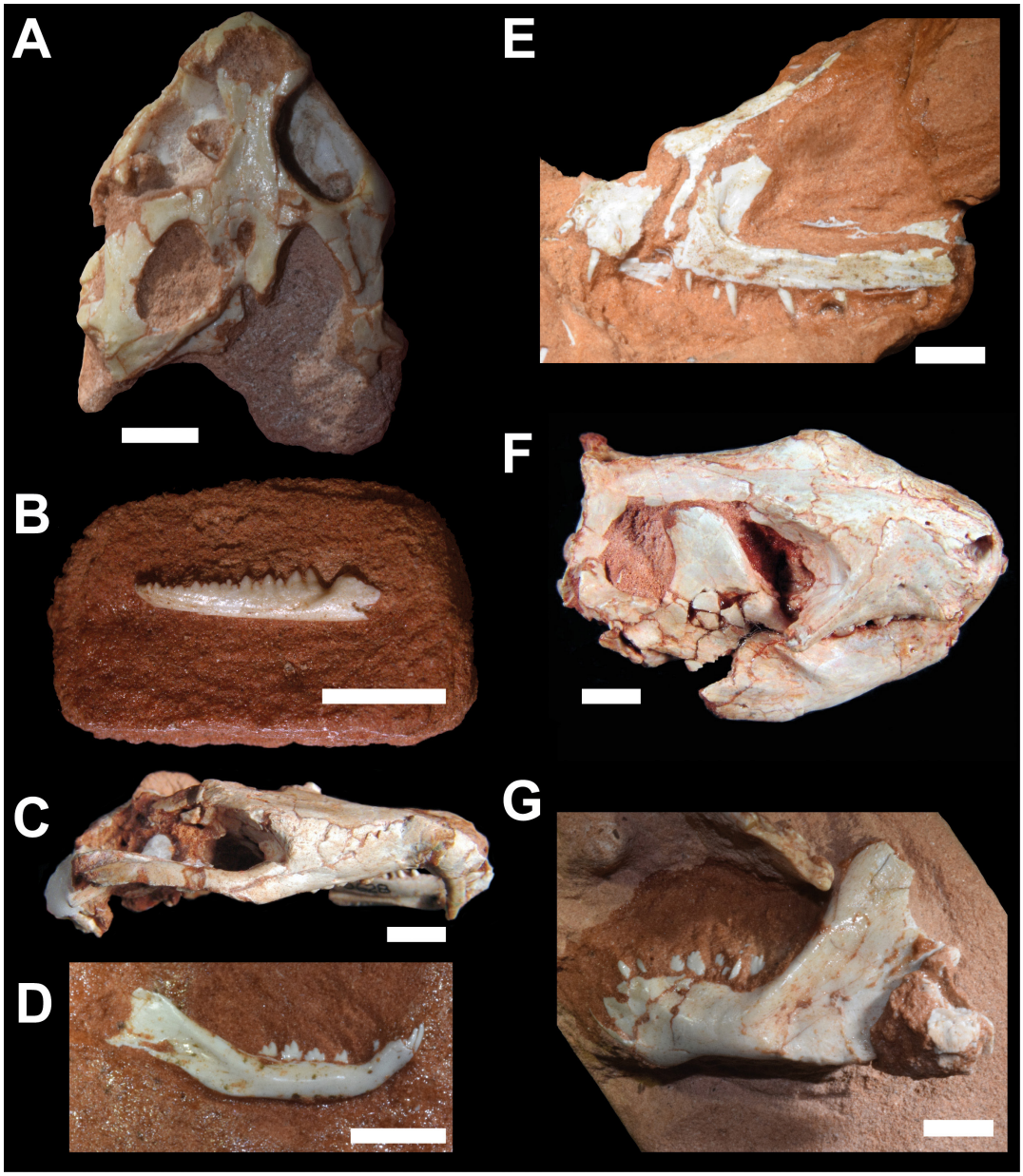

Figure 4. Microvertebrates of the Linha São Luiz Geosite. A, *Clevosaurus brasiliensis* skull (CAPPA/UFSM 0131) in dorsal view. B, *Lanceirosphenodon ferigoloi* left dentary (CAPPA/UFSM 0226, holotype). C, *Brasilodon quadrangularis* skull (UFRGS-PV-0628-T), skull in right lateral view. D, *B. quadrangularis* right mandibular ramus (CAPPA/UFSM 0424) in lateral view. E, *Maehary bonapartei* (CAPPA/UFSM 0300, holotype), partial skull in left lateral view. F, *Riograndia guaibensis* (UFRGS-PV-0596-T), skull in right lateral view. G, *R. guaibensis* (CAPPA/UFSM 0425) left mandibular ramus in lateral view.

of tiny microvertebrates has long intrigued paleontologists. Though suspicions were raised that some accumulations might represent regurgitalites (Arantes et al. 2008), the genesis of this taphocoenosis was never deeply investigated. Among the sample, the most abundant records are of sphenodontids, followed by cynodonts, archosauromorphs and procolophonids. Romo de Vivar et al. (2020a) provided an account on the relative abundance of tetrapod fossils at the Linha São Luiz Geosite.

The only macrovertebrates (Figure 5) in this assemblage are represented by an articulated skeleton of the saurischian dinosaur *Guaibasaurus candelariensis* (Bonaparte et al. 2007; Langer et al. 2011), and an isolated archosauromorph tooth (De-Oliveira et al. 2023). Apart from these, the lacustrine and yields occasional fish scales which still await detailed studies. Finally, a large set of footprints was recorded on the upper layers of the mouth bar system, those being referred to a theropod of moderately large size (Silva et al. 2012), though no tetrapod bones were yet recorded on these layers. A list of occurrences is provided below, followed by a brief description of the taxa.

4.1.1 Systematic Paleontology

CYNODONTIA Owen (1861)
PROBAINOGNATHIA Hopson (1990)
PROZOSTRODONTIA Liu and Olsen (2010)
ICTIDOSAURIA Broom, 1929 (sensu Martinelli and Rougier 2007)
Riograndia Bonaparte et al. (2001)
Riograndia guaibensis Bonaparte et al. (2001)

Riograndia guaibensis (Figure 4F, G; Electronic Supplementary File 1) is a small cynodont with faunivorous-omnivorous habits that is the guide taxon of the *Riograndia* AZ (Soares et al. 2011, see also Schultz et al. 2020; Martinelli et al. 2021). Although its holotype (MCN-PV2264, Bonaparte et al. 2001) comes from the Sesmaria do Pinhal site, at Candelária municipality, the Linha São Luiz Geosite has provided numerous and well-preserved specimens, being the most abundant cynodont at this locality. Several important specimens for understanding the taxon have been collected from this outcrop (Bonaparte et al. 2010a; Soares

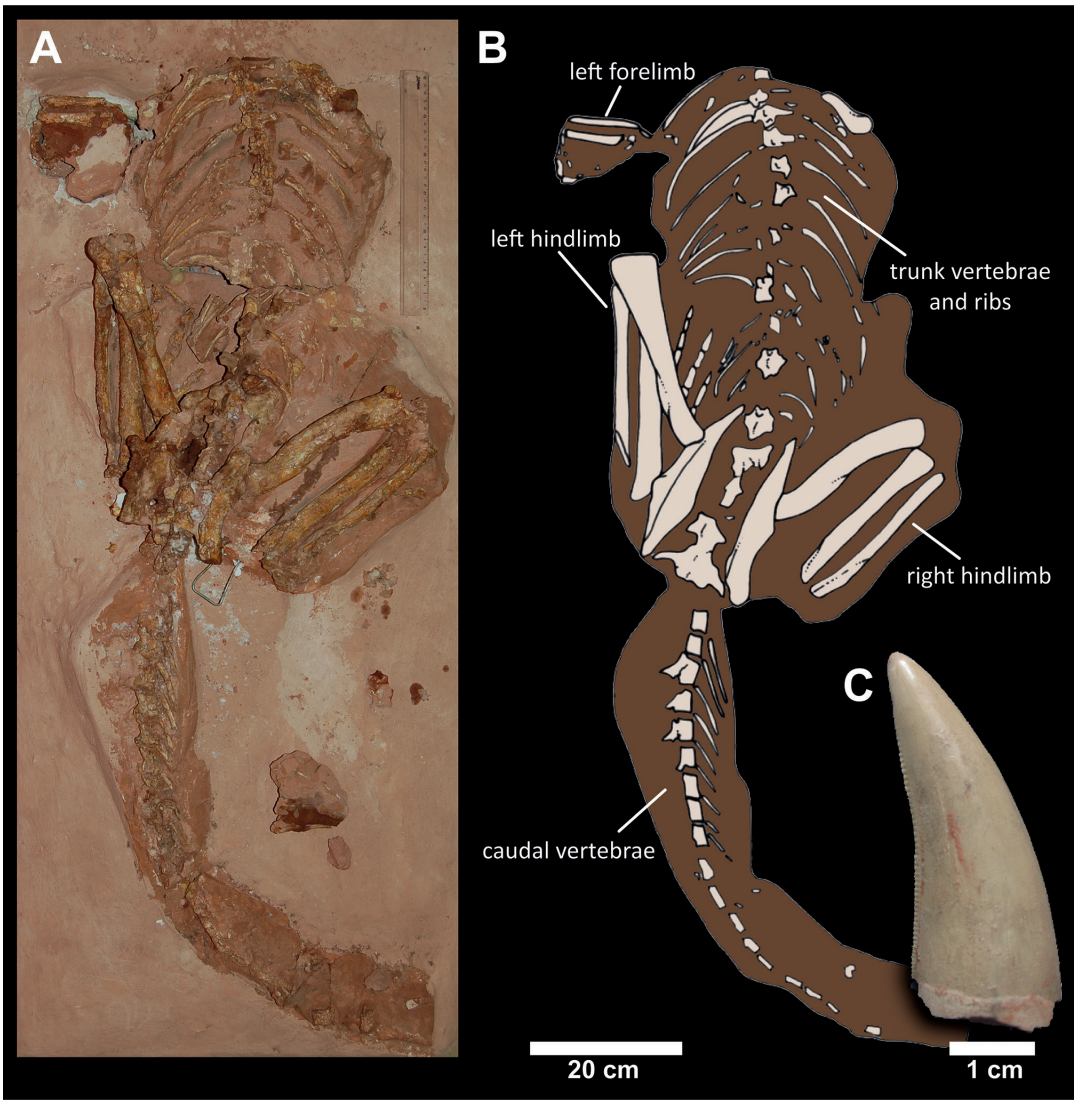

Figure 5. Macrovertebrate remains from the Linha São Luiz Geosite. A, B, articulate incomplete skeleton of *Guaibasaurus candelariensis* (UFRGS-PV-0725-T). C, isolated tooth of a carnivore archosauromorph (CAPPA/UFSM 0050). Line reconstruction in B modified from Bonaparte et al. (2007).

et al. 2011; Guignard et al. 2019a; Fonseca et al. 2024), as the specimen UFRGS-PV-0596-T (Fig. 4 F), mistakenly pointed out by Soares et al. (2011) as recovered from Sesmaria do Pinhal 1 site, Candelária. *Riograndia guaibensis* has a set of anatomical features that are important for understanding the evolution of prozostrodonts including a set of derived features in the dentition, braincase, cranial endocast, nasal cavity and postcranium (Bonaparte et al. 2001; Bonaparte et al. 2010a; Soares et al. 2011; Guignard et al. 2019a; Rodrigues et al. 2019; Kerber et al. 2021; Fonseca et al. 2024). Due to its abundance and wide distribution, it has allowed the correlation to other fossiliferous outcrops that can be associated with other Triassic faunas, establishing the *Riograndia* Assemblage Zone (Soares et al. 2011, see also Schultz et al. 2020; Martinelli et al. 2021).

TRITHELEDONTIDAE Broom, 1912 (sensu Martinelli and Rougier 2007)
Irajatherium Martinelli et al. (2005)
Irajatherium hernandezi Martinelli et al. 2005

Irajatherium hernandezi (Electronic Supplementary File 2) is the largest prozostrodont cynodont from the Faxinal do Soturno Fauna, slightly larger than *Riograndia* and *Brasilodon*. It exhibits upper postcanines with a main bulbous cusp, flanked by small mesial and distal cusps, whereas the lower postcanine teeth are sectorial (Figure 6), with a main cusp followed by distal cusps that decrease in size. It is considered the oldest member of the cynodont clade Tritheledontidae (Martinelli and Rougier 2007), although some phylogenies did not recover tritheledontids as monophyletic (e.g., Kerber et al. 2022). Similar to *Riograndia guaibensis*, the holotype of *I. hernandezi* comes from Sesmaria do Pinhal (holotype UFRGS-PV-0599-T). However, fossils of this cynodont have also been found in Linha São Luiz Geosite, represented by cranial, dental, and postcranial materials (Oliveira et al. 2011; Kerber et al. 2022), contributing to the knowledge of its anatomy. This taxon is one of the least known cynodonts from this site.

MAMMALIAMORPHA Rowe, 1988 (sensu Abdala 2021)
BRASILODONTIDAE Bonaparte et al. (2005)
Brasilodon Bonaparte et al. (2003)
Brasilodon quadrangularis Bonaparte et al. (2003)

Brasilodon quadrangularis (Figure 4 C, D) is an abundant cynodont at Linha São Luiz Geosite. It is represented by crania, mandibles, and postcranial remains (Bonaparte et al. 2003, 2005, 2010a, 2012; Martinelli and Bonaparte 2011; Guignard et al. 2019b). The upper postcanine teeth have a main central cusp and two mesial and two distal cusps forming a quadrangular shape in occlusal view, which served to name the species (Bonaparte et al. 2003). The lower postcanine has a “triconodont” pattern with discrete lingual accessory cusps. *Brasilitherium riograndensis* (holotype UFRGS-PV-0594-T), described together with *B. quadrangularis* in 2003, was differentiated from the latter mainly by its smaller size and different skull proportions, as well as the presence of a cusp d in lower postcanines (Bonaparte et al. 2003, 2005). However, subsequent works have considered this taxon as a junior synonym of *B. quadrangularis* (Liu and Olsen 2010; Guignard et al. 2019b; Martinelli 2017; Martinelli et al. 2019; Kerber et al. 2022). Another taxon described on the basis of a skull with jaws is *Minicynodon maieri* (Bonaparte et al. 2010a), which also has undistinguished features of those of present in the wide sample of *Brasilodon*, and thus is considered a junior synonym too (Martinelli 2017; Guignard et al. 2019b; Martinelli et al. 2019).

Brasilodon quadrangularis is an important cynodont in understanding the evolution of mammalian traits, being considered the sister group to Mammaliaformes (Liu and Olsen 2010; Martinelli et al. 2017a, b; Stefanello et al. 2023; Kerber et al. 2024). Besides having its anatomy well-documented through various specimens, within the evolutionary context of non-mammaliaform cynodonts, it exhibits a wide range of cranial, dental, postcranial, and neurological anatomical innovations, such as the presence of a promontorium, a trait shared with mammaliaforms (Martinelli and Bonaparte 2011; Rodrigues et al. 2013, 2014; Martinelli 2017; Martinelli et al. 2017a, b; Botha-Brink et al. 2018; Guignard et al. 2019b;

Figure 6. Artistic impression of the small cynodont *Irajatherium hernandezi*. Artwork by Márcio L. Castro.

Abdala et al. 2020; Stefanello et al. 2023; Kaiuca et al. 2024; Kerber et al. 2024).

PARAREPTILIA Olson, 1947
PROCOLOPHONIDAE Seeley, 1888
LEPTOPLEURONINAE Ivakhnenko, 1979
Soturnia Cisneros and Schultz (2003)
Soturnia caliodon Cisneros and Schultz (2003)

Soturnia caliodon is the only Late Triassic procolophonid known in South America (Cisneros and Schultz 2003) and is regarded as one of the latest known surviving members of Parareptilia, together with Norian and Rhaetian representatives of the Northern Hemisphere (Butler et al. 2024). It possesses the typical bicuspid distal teeth on the maxilla, which characterizes advanced procolophonids, whereas its incisiviforms present a single cusp (Zanchett et al. 2024), such as the dentary teeth. The bulbous teeth possessed a thick enamel layer and were firmly set in the dentigerous bones. This set of traits are suggested to have given the teeth stable occlusion and long useful life, adaptive features for its proposed diet of tough fibrous vegetation (Cabreira and Cisneros 2009). The taxon is known from several specimens, including a fairly complete skull (UFRGS-PV-1111-T) which shows two robust quadratojugal spines which were probably recovered by keratinous tissue in life (Melo et al. 2012). Nonetheless, only the holotype (MCN PV2738) has reported postcranial remains, including a segment of the axial skeleton and a right humerus (Cisneros and Schultz 2003).

LEPIDOSAUROMORPHA Gauthier, 1984 (sensu Gauthier et al. 1988)
Cargninia Bonaparte et al. (2010a)
Cargninia enigmatica Bonaparte et al. (2010a)

The holotype of *Cargninia enigmatica* (UFRGS-PV-1027-T) is known from a single left dentary, missing its rostral extremity. It was presented as having only 6-7 preserved teeth (Bonaparte et al. 2010a), though later authors recognized it originally preserved at least 14 teeth of an estimated total of more than 20 tooth loci (Romo de Vivar et al. 2020b). These authors also tentatively referred to a second specimen of the species in the same work while presenting lepidosauromorph maxillary remains (UFRGS-PV-0819-T) that could not be confidently referred to as *C. enigmatica* by the lack of overlapping elements. The teeth of *C. enigmatica* are homodont, with closely-spaced crowns that are finger-shaped. The presence of replacement pits in the lingual side of some teeth and partial ankylosis in some elements indicates that the taxon had a pleuroacrodont tooth attachment, differing from most rhynchocephalians, which are also markedly heterodont. The low tooth crowns also differ *Cargninia* from kuehneosaurids. Nonetheless, the fragmentary condition of the known materials allows only to refer the material as either a non-rhynchocephalian lepidosauromorph, or a basal lepidosaurian (Romo de Vivar et al. 2020b).

LEPIDOSAURIA Haeckel, 1866
RHYNCHOCEPHALIA Günter, 1867
SPHENODONTIA Williston, 1925
Clevosaurus Bonaparte and Sues (2006)
Clevosaurus brasiliensis Bonaparte and Sues (2006)

The first fossils of *Clevosaurus brasiliensis* were described by Bonaparte and Sues in 2006, based in two specimens, comprising a complete skull and an articulated mandible of an adult specimen (UFRGS-PV-0748-T, the holotype), and an incomplete skull and mandible of a juvenile specimen (UFRGS-PV-0613-T), which was later referred to another genus (see below). In the years following the description, dozens of specimens were added to the sample, making *C. brasiliensis* one of the most abundant taxa at the Linha São Luiz Geosite (Romo de Vivar et al. 2020a). Postcranial remains were described by Arantes et al. (2009), including the axial skeleton and limb elements such as tibia, fibula, and phalangeal elements. The extensive sample allowed several authors to conduct quantitative analyses. While Hsiou et al. (2015) regarded that the phylogenetic relationships of Clevosauridae were uncertain, even with the description of new specimens, other workers provided glimpses on the paleoautoecology of the animal. An assessment of the mandibular morphological variation (Romo de Vivar Martínez and Soares, 2015) indicated a dietary shift among the sample, with adult specimens probably adopting an omnivorous diet, with more plant material than other species of *Clevosaurus*. Furthermore, pathological mandibles suggested that *Clevosaurus* might exhibit agonistic behavior similar to that seen in *Sphenodon punctatus*, where individuals bite each other in intraspecific combats (Romo-de-Vivar-Martínez et al. 2017). A recent effort including micro-CT imaging (Chambi-Trowell et al. 2021) presented a detailed description of the craniomandibular anatomy of the taxon, reinforcing its diagnosis. *C. brasiliensis* is recognized by several cranial features, such as its short rostrum (Figure 4A; Electronic Supplementary File 3), characteristic palatal dentition with three rows of teeth, and a unique type of tooth implantation. Furthermore, the authors provided an extensive phylogenetic revision for Clevosauridae, and recovered *C. brasiliensis* closely related to the North American *C. bairdi*, from the Lower Jurassic of Canada. Finally, some of the specimens previously assigned to *C. brasiliensis* were recognized as an independent genus and species, *Microsphenodon bonapartei* (see below).

Microsphenodon Chambi-Trowell et al. (2021)
Microsphenodon bonapartei Chambi-Trowell (2021)

Originally recognized as a juvenile of *Clevosaurus brasiliensis* (Bonaparte and Sues 2006; Hsiou et al. 2015; Romo de Vivar Martínez and Soares 2015), the materials referred to *Microsphenodon bonapartei* allow the reconstruction of most of the skull and mandible (missing only the premaxillae, vomer and stapes). In addition to the skull, the first two cervical vertebrae are known from the holotype (Chambi-Trowell et al. 2021). *M. bonapartei* is generally smaller than adult specimens of *C. brasiliensis*, and among other features, has a dentition which is notoriously distinct from the latter. *M. bonapartei* has a pronounced tooth differentiation, with a marked caniniform both in the maxilla and the dentary. The parietal table is relatively wider than in *C. brasiliensis*, though the skull is generally narrower than in that taxon. It is remarkable that the combination of plesiomorphic and apomorphic traits shown by *Microsphenodon bonapartei* not only renders it easily distinguishable, but also affects its phylogenetic relationships. Indeed, Chambi-Trowell et al.

(2021) recovered the taxon as one of the earliest members of Eusphenodontia, and positioned outside of Clevosauridae.

Lanceirosphenodon Romo de Vivar et al. 2020a
Lanceirosphenodon ferigoloi Romo de Vivar et al. 2020a

Lanceirosphenodon ferigoloi (Figure 4B) is a small sphenodontian known only from its holotype (CAPPA/UFSM 0226), which consists of an almost complete left dentary, missing only its posteriormost portion. *L. ferigoloi* presents features shared with non-eusphenodontian rhynchocephalians and was regarded by the original authors as an early juvenile. Despite the early ontogenetic state, Romo de Vivar et al. (2020a) erected a combination of several diagnostic features to support the taxon. It possesses a remarkable dentition composed of two series of alternating teeth, and two modes of tooth attachment – whereas the posteriormost teeth show a degree of acrodonty, the successional teeth are markedly acrodont. The last two teeth are spearhead-shaped (hence the etymology of the genus), and located close to the low coronoid process, a feature distinct from *C. brasiliensis* and *M. bonapartei*, the other sphenodont taxa from the Linha São Luiz Geosite (Chambi-Trowell et al. 2021). Its piercing dentition was compatible with an insectivore diet similar to that inferred for *Microsphenodon*. While some of its anatomical differences to other Triassic sphenodontians may be related to ontogeny, several of the aforementioned features are age-independent. Therefore, the diversity and morphological disparity of Triassic Rhynchocephalia, such as attested by the taxa at the Linha São Luiz Geosite, among other triassic localities, might support the idea of a pre-Triassic origin for the group, as advanced by some authors (Simões et al. 2018; Hsiou et al. 2019).

ARCHOSAUROMORPHA von Huene, 1946
ARCHOSAURIFORMES Gauthier, 1986
ARCHOSAURIA Cope, 1869
Archosauria indet. De-Oliveira et al. 2023

Although the Linha São Luiz Geosite is remarkable for its microvertebrate fossil biodiversity, the record of larger animals is very scarce. Apart from footprints (Silva et al. 2012), the single record of an unequivocal large predator resides in an isolated tooth (Figure 5C). The assessment of the material, realized by De-Oliveira et al. (2023), recognized it as the tooth of a carnivorous archosaur, with distinct serrations and a robust shape. Its subcircular cross-section allows its shape as a pachydont morphotype, common in the mesial teeth of several Triassic carnivores, including (but not restricted to) dinosaurs. The tooth shows a large abrasion facet at its apex, extending in both medial and distal carinae, suggesting it may have been a shed tooth, replaced after being worn by predation. Though fragmentary, this fossil fills an ecological gap in the fossil record of the Linha São Luiz Geosite, with the recognition of archosaurs as the apex predators in the locality, such as in most Brazilian Triassic faunas (Schultz et al. 2020).

PTEROSAUROMORPHA Padian, 1997
LAGERPETIDAE Arcucci, 1986 (sensu Nesbitt et al. 2009a; Nesbitt et al. 2009b)
Faxinalipterus Bonaparte et al. (2010b)
Faxinalipterus minimus Bonaparte et al. (2010b) (emended by Kellner et al. 2022)

Among the microvertebrate fossils that abound in the Linha São Luiz Geosite, paleontologists found in 2002 a set of small, elongated, and hollowed bones of a small archosauromorph (UFRGS-PV-0927-T). Three years later, in 2005, the team found remains of a maxilla of peculiar morphology (UFRGS-PV-0769-T). Suggesting that all elements represented a single taxon, Bonaparte et al. (2010b) presented the specimen as an early pterosaur, *Faxinalipterus minima*. In a later study, Kellner et al. (2022) reevaluated the material and found it unlikely that the two specimens, collected in two distinct opportunities and lacking overlapping materials, could be referred to a single animal. Furthermore, the phylogenetic study of the holotype (UFRGS-PV-0927-T) allowed the authors to recognize it not as a pterosaur, but as a representative of Lagerpetidae, an earlier lineage of Pterosauromorpha. The preserved elements were reevaluated as pertaining to fragments of both humeri, as well as the proximal portion of a femur, tibia, fibula and two incomplete metatarsals. Finally, an amendment to the specific name was advanced, from *F. minima* to *F. minimus*.

GRACILISUCHIDAE Butler Sullivan, Ezcurra, Liu, Lecuona & Sookias, 2014
Maehary Kellner et al. 2022
Maehary bonapartei Kellner et al. 2022

In the same work that reassessed the phylogenetic positioning and the anatomy of *Faxinalipterus minimus*, Kellner et al. (2022) presented a second small purported ornithodiran from the Linha São Luiz Geosite. Specimen CAPPA/UFSM 0300 (Figure 4E; Electronic Supplementary File 4) comprises a partial skull, associated to a few vertebral centra and a partial scapula. Interestingly, the maxilla of the new material was anatomically compatible to the maxilla (UFRGS-PV-0769-T) originally proposed by Bonaparte et al. (2010b) to be part of *Faxinalipterus*. Contrary to those authors, Kellner et al. (2022) referred the specimens CAPPA/UFSM 0300 and UFRGS-PV-0769-T as representative of a new taxon, *Maehary bonapartei*. Among the features that allow the recognition of the taxon, are the maxilla with a tall dorsal process creating a wide antorbital fenestra, and the maxillary teeth, which were devoid of serrations, but ornated by two apicobasally oriented grooves, unique for the taxon. The slender jaw suggested *M. bonapartei* fed on small delicate insects, which it probably captured with its piercing teeth (Figure 7). In its original description, the taxon was recovered as the earliest-diverging member of Pterosauromorpha, but this positioning was defied recently by Müller et al. (2023), who recovered the taxon as a gracilisuchid.

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
GUAIBASAURIDAE Bonaparte et al. (1999)
Guaibasaurus Bonaparte et al. (1999)
Guaibasaurus candelariensis Bonaparte et al. (1999)

The type locality of *Guaibasaurus candelariensis* is an outcrop ca. 100 km far from the Linha São Luiz Geosite, in the municipality of Candelária. The species was originally known from a few vertebrae and some incomplete bones of the girdles and hindlimbs described by Bonaparte et al. (1999) as a saurischian of uncertain affinities. Even though no skull or dental remains of this dinosaur were ever found,

Figure 7. Artistic impression of the life habits of the small archosaur *Maehary bonapartei*, hunting an indeterminate Odonata over the branches of an Araucariaceae. Artwork by Márcio L. Castro.

the authors were inclined to postulate it was a carnivorous saurischian. Nonetheless, the remains, though well preserved, were too scarce to propose a phylogenetic position for the taxon confidently. Part of this scenario would change when a second, more complete skeleton was unearthed in the Linha São Luiz Geosite. Collected in 2002 and described five years later (Bonaparte et al. 2007), the specimen UFRGS-PV-0715-T (Figure 5A, B) preserved most of the postcranial elements in remarkable articulation but lacked cervical and skull elements. Therefore, though more completely known, the taxon remained entangled in phylogenetic uncertainty. Bonaparte et al. (2007) suggested that *Guaibasaurus* was a taxon closely related to the origin of Sauropodomorpha, but yet retained several features shared with Theropoda which could indicate its position as an early eusaurischian. Langer et al. (2011), on the other hand, advanced the phylogenetic hypothesis that *Guaibasaurus* was a theropod, this time supported by a numeric phylogenetic study, yet the authors emphasize that the support within Theropoda was weak and obscured by the several plesiomorphic traits retained by the taxon. Indeed, the taxon has a rogue distribution among independent phylogenetic approaches, floating from a basal position within Eusaurischia, or as an early theropod or sauropodomorph (Cabreira et al. 2016; Ezcurra 2010; Langer et al. 2011; Müller et al. 2018; Novas et al. 2021; Pol et al. 2021; Pretto et al. 2019). Much of this conundrum rests in the matter that, though an almost complete postcranium is known for *Guaibasaurus*, it lacks skull and neck elements, which differentiated early in the split between Theropoda and Sauropodomorpha (Leal et al. 2004; Müller et al. 2018; Pretto et al. 2019). It is, nonetheless, an unmistakable member of Saurischia, and the only dinosaur known from somatofossils in the entire Linha São Luiz Geosite.

4.2. Invertebrates

In the middle and upper sections of the Linha São Luiz stratigraphy (Figure 2), invertebrates represent the most prevalent body fossils (Figure 8). These invertebrates are often found in association with plant remains and fish scales within lacustrine facies, and with ichnofossils in the heterolithic upper strata.

Branchiopods (commonly referred to as 'conchostracans') constitute the most abundant fossils, typically preserved as remains and/or molds of entire carapaces, which may be either articulated or disarticulated (Rohn et al. 2014; Jenisch et al. 2017). Notably, these skeletons, which are poorly mineralized, lack evidence of bioerosion, encrustation, abrasion, or corrosion (Jenisch et al. 2017). The distribution of these fossils is facies dependent and ranges from dispersed to densely packed, consistently aligned parallel to the bedding plane. They occur in three distinct modes: at the interface of siltstones/heteroliths with mudstones (Ht), within the middle of mudstone strata (Fl), and within plane-parallel sandstones (Sm). Jenisch et al. (2017) identified two distinct taphofacies for branchiopods. The first taphofacies is characterized by a muddy matrix with a polymodal distribution of carapaces, which are dispersed to loosely packed. This distribution suggests episodes of flooding within the lake, leading to the decantation of fine sediments and the non-selective mortality of the autochthonous assemblage, with a short residence time in the taphonomically active zone. The second taphofacies is found within a heterolithic muddy matrix at specific lake body levels and within upper crevasse splay facies. This facies features a juxtaposition of dispersed articulated carapaces and densely packed lenticular groupings, with relative size selection and a mix of closed, open, and disarticulated valves. The internal structure of these layers indicates deposition through traction and traction-suspension processes, likely resulting from sporadic river overflow events. These events concentrate autochthonous (closed) valves alongside allochthonous or parautochthonous (open and isolated) valves (read more in Jenisch et al. 2017).

Insects are less abundant within these strata and are exclusively associated with lacustrine facies (Figure 2). They are typically found as isolated wing molds and occasionally as larvae, with the head, thorax, and abdomen preserved in mold form (Correa et al. 2019). Despite multiple insect reports from the Linha São Luiz Geosite, no publications have been released to date. However, new studies are underway, and preliminary details are presented below.

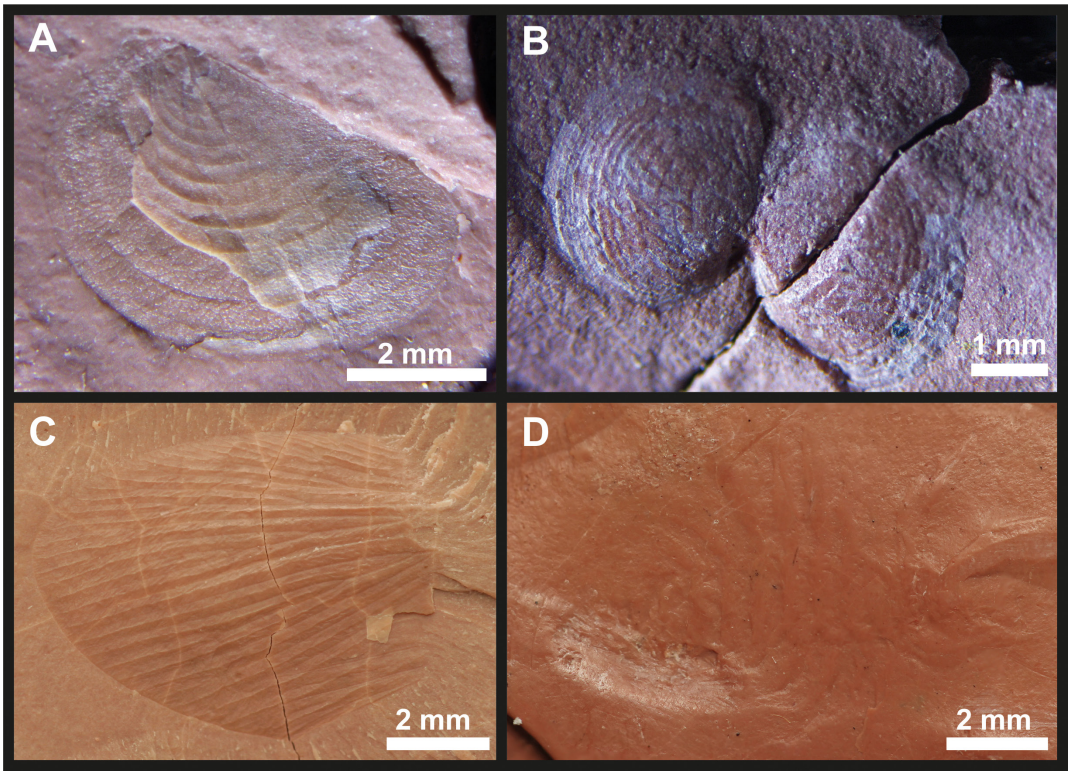

Figure 8. Invertebrate fossils of the Linha São Luiz Geosite. A, *Nothocarapacestheria soturnensis*, right isolated valve partially preserved (iridescent material) and external mold with growth lines and ornamentation. B, *Australestheria sp.*, articulated valves resting the bedding plane, rest preserved as whitish material. C, Blattodea indet. (ULVG13632) partial insect hindwing preserved as mold. D, mold of holometabolan larva (ULVG11209), showing anterior (thorax) and upper posterior (abdomen) regions.

4.2.1 Systematic Paleontology

ARTHROPODA Latreille, 1829
BRANCHIOPODA Latreille, 1817
DIPLOSTRACA Gerstecker, 1866
SPINICAUDATA Linder, 1945
EOSESTHERIOIDEA Zhang et al. 1976
EOSESTHERIIDAE Zhang et al. 1976
Nothocarapacestheria Rohn et al. 2014
Nothocarapacestheria soturnensis Rohn et al. 2014

Nothocarapacestheria soturnensis is a large Spinicaudata (Figure 8A) characterized by an oval carapace and a small larval valve with a submedial, marginal, and small umbo, featuring 18-27 growth bands (Rohn et al. 2014). The carapace ornamentation is complex, transitioning distally from isodiametric irregular reticles to elongated polygons, and finally to radial lirae in the most distal regions (Rohn et al. 2014). The microornamentation, distinguished by irregular mamelons, sets *N. soturnensis* apart from the genus *Carapacestheria* Shen (1994), found in the Lower Jurassic of Antarctica. The name *Nothocarapacestheria* reflects this distinction, as “Notho” implies “false” *Carapacestheria*. According to Rohn et al. (2014), the similarities between *N. soturnensis* and *Carapacestheria*, along with significant differences from other members of the Eosestheriidae family from the Upper Triassic of Argentina and Chile (Gallego et al. 2005; Gallego 2010), suggest that the Spinicaudata of the Linha São Luiz Geosite could indicate a Lower Jurassic age, at least for the lacustrine system of the outcrop. Recently, *N. soturnensis* was also described from the Sinemurian (Lower Jurassic) of China (Teng and Li 2024), reinforcing the hypothesis regarding the age of this geological package in southern Brazil.

FUSHUNOGRAPTIDAE Wang, 1974
Australestheria Chen in Zhang et al. 1976
Australestheria sp. Rohn et al. 2014

The specimens of *Australestheria* sp. from the Linha São Luiz Geosite are medium-sized and rounded, with a straight and short dorsal margin, and a small supramarginal submedial umbo (Figure 8B). They exhibit 12 to 19 growth lines, which are characterized by regular bands weakly ornamented with thin homogeneous punctuations that show slight orthogonal alignment (Rohn et al. 2014). The growth lines can be either continuous (straight) or slightly serrated (beaded structures) with discrete punctuations forming small arrow shapes (Rohn et al., 2014). This feature of very weak and smaller arrows distinguishes these specimens from the type species of the genus *Australestheria corneti* from the (Middle?) Jurassic of the Democratic Republic of the Congo (Zhang et al. 1976; see discussion in Rohn et al. 2014). Another species of *Australestheria*, *A. barbosai*, associated with *Pseudograpta mendesi* (Cabral 2011; Christofoletti et al. 2021), occurs in the Pirambóia Formation, an overlying unit in the Paraná Basin. A Middle Jurassic age has been suggested for this formation, again reinforcing the possible Jurassic age of the strata containing conchostracans at the Linha São Luiz Geosite (Cabral 2011; Rohn et al. 2014).

FUSHUNOGRAPTIDAE Wang, 1974
Fushunograptidae indeterminated Jenisch et al. 2017

This morphotype, identified by Jenisch et al. (2017), features medium to large carapaces with an oval to round shape, an inframarginal submedial umbo, and 15 to 25 growth lines. The ornamentation on the dorsal margin is irregularly reticulate, transitioning from the central part to a well-developed striate to radial lirae pattern with occasional transverse bars on the ventral margin (Jenisch et al. 2017). These characteristics distinguish it from *Australestheria sp.*, the other Funshunograptidae present at the outcrop (Rohn et al. 2014; Jenisch et al. 2017). Currently under investigation, this morphotype occurs exclusively in the second taphofacies. It is more common than *Australestheria sp.*, which is found only in the first taphofacies, but less frequent than *Nothocarapacestheria soturnensis*, which occurs in both taphofacies (Jenisch et al. 2017).

INSECTA Linnaeus, 1758
PTERYGOTA Brauer, 1885
BLATTODEA Latreille, 1810
Blattodea indeterminate unpublished

Although rare, these remains are important to highlight the diversity of invertebrate fossils at the Linha São Luiz Geosite. The site yielded isolated wings, a hindwing, and a forewing, tentatively related to cockroaches. The good preservation of these specimens in mold allows for detailed observation of the wing veins (Figure 8C). However, further studies are required to fully characterize the anatomy of the specimens and elucidate their taxonomic categorization.

HOLOMETABOLA Burmeister, 1835
Holometabola indeterminate unpublished

Correa et al. (2019) reported the occurrence of an adpressed three-dimensional mold of a holometabola larva slightly compressed, which exhibits the head, thorax, and abdomen (Figure 8D). Some anatomical details suggest a possible relationship with the subfamily Chauliodinae (Corydalidae) or to a larva of aquatic beetles (Coleoptera). The systematic affinity and paleoenvironmental significance of this specimen are still under further investigation. The larva, along with other insect wings, is found in association with plant remains and Branchiopoda carapaces within the lacustrine strata of the outcrop.

PTERYGOTA Brauer, 1885
Pterygota indeterminate unpublished

Three samples from the Linha São Luiz Geosite contain wings attributed to Pterygota. Two of these samples are fragments that are difficult to classify systematically. However, the third sample includes a forewing and hindwing that may be associated with either Odonata or Neuroptera, pending further examination. All these samples are still under study.

4.3 Paleobotany

The Linha São Luiz Geosite boasts a substantial record of plants, characterized by diverse forms of preservation, detail, and abundance (Figure 9). Paleosols and root pavements are present at specific levels within both the lower sandstone and upper crevasse splay deposits. Rhizoturbations manifest as large, fibrous impressions of homogeneous size, associated with shrub vegetation in unconfined river channels, or as thin, intensely branched undergrowth (Barboni and Dutra 2013; Dutra and Crisafulli 2022). Both types exhibit diagenetic halos that facilitate easy identification. In contrast, the lacustrine package contains the greatest abundance of fossil plants, both autochthonous and parautochthonous (Crisafulli and Dutra 2009). Trunks, shoots, and leaves are evenly distributed within the fine sediment strata, with approximately 90% of the paleobotanical assemblage consisting of conifer remains (Dutra and Faccini 2002; Pires and Guerra Sommer 2004; Wilberger 2009; Crisafulli and Dutra 2009).

The fossilized wood logs found at the Linha São Luiz Geosite are notably small compared to the large trunks of the Mata Sequence, which is renowned for its sizable trunks. These smaller trunks have a pith that allows for identification (Crisafulli and Dutra 2009). Among the trunks under study, two species have been reported: *Sommerxylon spiralosus* Pires and Guerra-Sommer 2004 and *Kaokoxylon zalesskyi* (Sahni) Maheshwari 1967 (in Crisafulli and Dutra 2009). The trunks are completely silicified, with some densely impregnated with iron oxides (Pires and Guerra-Sommer 2004; Pires et al. 2005; Crisafulli and Dutra 2009), ensuring excellent preservation of their features, including reproductive structures of ovules and seeds located near the trunk (Crisafulli et al. 2018; Dutra and Crisafulli 2022).

A diverse array of leaves, shoots, and reproductive structures is also preserved at the site (Figure 9), either as impressions or covered by coatings of oxides. Among the notable finds are Bennettitales such as *Pterophyllum* leaves (*sensu* Brongniart 1825 *apud* Barboni and Dutra 2013) and reproductive cones, with such excellent preservation that allows for the three-dimensional reconstruction of the structure of *Williamsonia potyporanae* Barboni and Dutra (2013). Additionally, leaves of *Pelourdea* and leaves and conifer branches of *Pagiophyllum* Heer 1881 (in Wilberger 2009) have been reported, which require further investigation.

Martins et al. (2022) detailed the presence of iron films on leaves and branches, identifying them as amorphous and acicular goethite, with spheroidal ferrihydrite associated with microfeatures of twisted and stalks. These features were possibly produced by microaerophilic and neutrophilic iron-synthesizing bacteria during eodiagenesis, ensuring the exceptional preservation of the micro-anatomical structures of plants from the Linha São Luiz Geosite (Martins et al. 2022).

The paleoassemblage, containing autochthonous to parautochthonous primitive conifers and paleosols preserved in a restricted lacustrine/deltaic context within a broader river system, supports a depositional environment characterized by a warm and seasonal climate with periods of intense rainfall, attested by wood dendrochronological data (Pires et al. 2005; Crisafulli and Dutra 2009). The periodic high-water supply ensured the preservation and seasonal renewal of woody and herbaceous vegetation, which was physiognomically similar to the vegetation currently covering modern rain shadow and continental areas at the boundary between tropical and subtropical climate belts (Barboni and Dutra 2013).

4.3.1 Systematic Paleontology

GYMNOSPERMAE Lindley, 1830
PINALES Gorozhankin, 1904
TAXACEA Gray, 1822
Sommerxylon Pires and Guerra-Sommer 2004
Sommerxylon spiralosus Pires and Guerra-Sommer 2004

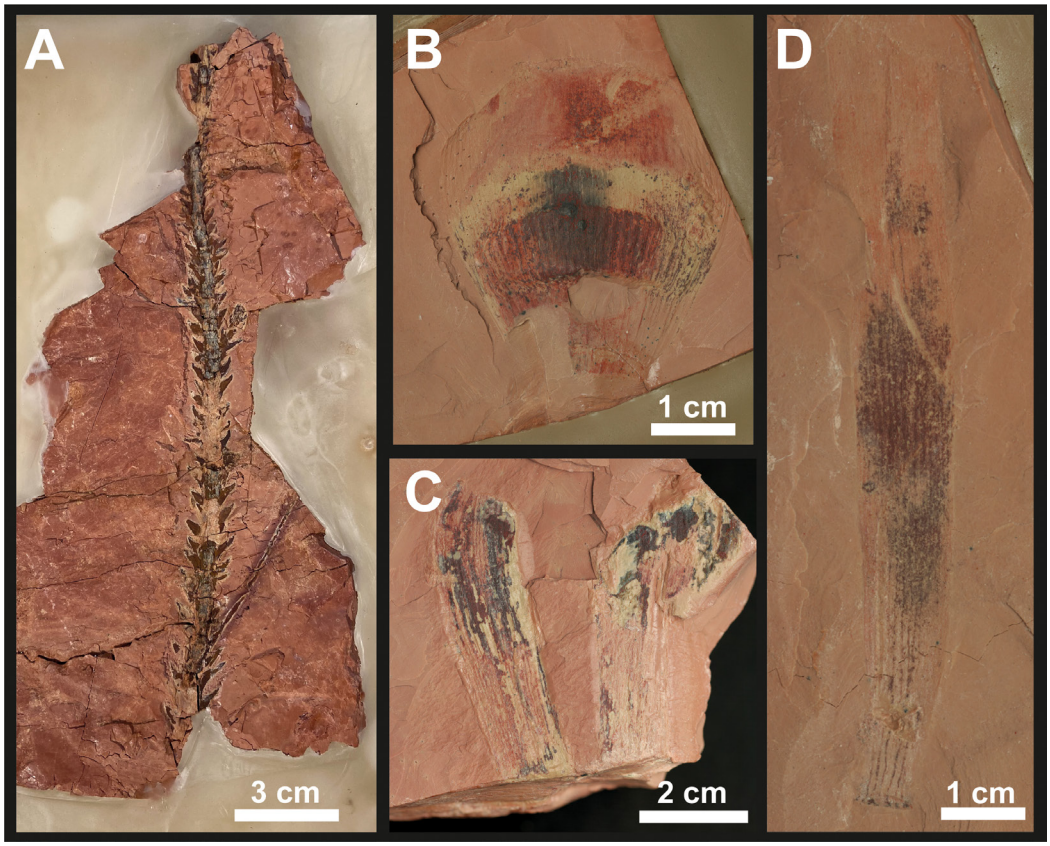

Figure 9. Examples of fossil plants of the Linha São Luiz Geosite. A, *Pagiophyllum sp.* (ULVG8266), stem with helicoidally arranged needle leaves preserved in 3D and partially covered by goethite. B, *Williamsonia potyporanae* (ULVG7186), complete cone with the receptacle and fertile and sterile rings of interseminal scales. C, cf. *Pelourdea* (ULVG13575a) leaf segments. D, *Pterophyllum?* (ULVG7326), impressions of coriaceous leaf segments.

This taxon is characterized by a heterocellular medulla with parenchymatic and sclerenchyma cells, endarch primary xylem and secondary xylem with dominance of uniseriate areolate pits, spiral thickenings on the radial walls of the tracheids, medullary ray homocellular, uniseriate and absence of resinous canals and axial parenchyma. The medullary parenchyma has thin-walled cells grouped in nests (Pires and Guerra-Sommer 2004). The growth rings of *Sommerxylon spiralosus* are distinct with a gradual transition from early to latewood suggesting that growth phase in each cycle developed at a slow rate, and the growing environment was relatively uniform with not very extensive periodic phases of growth restriction The different cycles of growth were affected by external factors as cyclic reduction of water supply (Pires et al. 2005).

CONIFERALES Engler, 1897

Kaokoxylon Kräusel 1956

Kaokoxylon zalesskyi (Sahni) Maheshwari, 1967

Kaokoxylon zalesskyi in Linha São luiz Geosite was described in Crisafulli and Dutra (2009) as a pycnoxylic homogeneous wood with wedge-shaped, endarch, and cuneiform primary xylem, and the secondary xylem with marked growth rings typically auraucarioid. In a subsequent work by Crisafulli et al. (2018), a seed was also identified, immersed in the lignified xylem tissue. This integument seems to be thick in texture, with well-developed nucellus, micropylar part and megagametophitic. Two nucellar cavities enclosed by a common integument which probably contain a sarcotesta and endotesta. Part of the peduncle of this seed is also preserved (Crisafulli et al. 2018). Crisafulli and Dutra (2009) highlight the presence of a *K. zalesskyi* trunk with roots in life position at the limit between the lower sandstone package and the intermediate lacustrine mudstones.

ARAUCARIACEAE Henckel and Hochstetter, 1865

Pagiophyllum Heer, 1881

Conifer leaves, branches, and shoots were preliminarily related to Pagiophyllum by Wilberger (2009) based on epidermal anatomy. Preserved mainly as three-dimensionally preserved (Figure 9A) shoots and twigs covered by goethite (Dutra and Crisafulli 2022; Martins et al. 2022), this material is abundant in the lacustrine layers of the Linha São Luiz Geosite. Alternatively, part of the materials assigned to the taxon may be referrable to *Agathoxylon* or *Brachyphyllum* (Crisafulli and Dutra 2009; Dutra and Crisafulli 2022).

BENNETTITALES Engler, 1892

WILLIAMSONIACEAE (Carruthers) Nathorst, 1913

Williamsonia (Carruthers) Harris, 1969

Williamsonia potyporanae Barboni and Dutra (2013)

Williamsonia potyporanae is a detailed isolated and pedunculate ovulate structure (Figure 9B), probably in the stage of seed maturity (seed cone) covered by two layers of elongated, parallel orientated, striate, hairy membranaceous bracts (Barboni and Dutra 2013). The advanced morphology

of ovulate structure suggest warm and wet conditions, but seasonally or irregularly distributed humidity, with short and intense rain episodes. These characteristics of *W. potyporanae* display affinities to taxa found in Jurassic and Cretaceous, as discussed by Barboni and Dutra (2013).

Pterophyllum? Brongniart, 1825

Described in Barboni and Dutra (2013), these impressions of coriaceous leaf segments have an elongate and ensiform shape, slightly curved with five to six veins that rarely bifurcate in the admedial part, with parallel and equidistant courses (Figure 9D). These give place to nearly ten veins in the mid portion of the segment, which contains two to three veins per millimeter. The affinity with *Pterophyllum* is supported by total length, smooth margins, parallel veins with few ramifications, as well as the constricted and decurrent base on both sides of the segment (Barboni and Dutra 2013). It is interesting to note that this genus is mostly composed of species from the Triassic/Jurassic boundary (Barboni 2010).

DIVISION UNKNOWN

Pelourdea Seward 1917 emend. Ash 1987

Pelourdea indeterminate unpublished

This vegetative structure is still under investigation and is represented by fragmented leaves with parallel venation (Figure 9C). If the taxonomic placement of the materials comes to be confirmed, the occurrence of yet another plant taxon may demonstrate the potential for continued research at the Linha São Luiz Geosite.

5. Geoconservation

The Linha São Luiz Geosite is located in a rural area, though the surroundings of the main outcropping are not employed in agriculture. Despite this, over the last fifteen years, the outcrop has been severely endangered by the proliferation of exotic pine trees, *Pinus* sp. (Ziemann and Figueiró 2017). Apart from covering fossil-bearing areas, the trees established especially over the fine and brittle

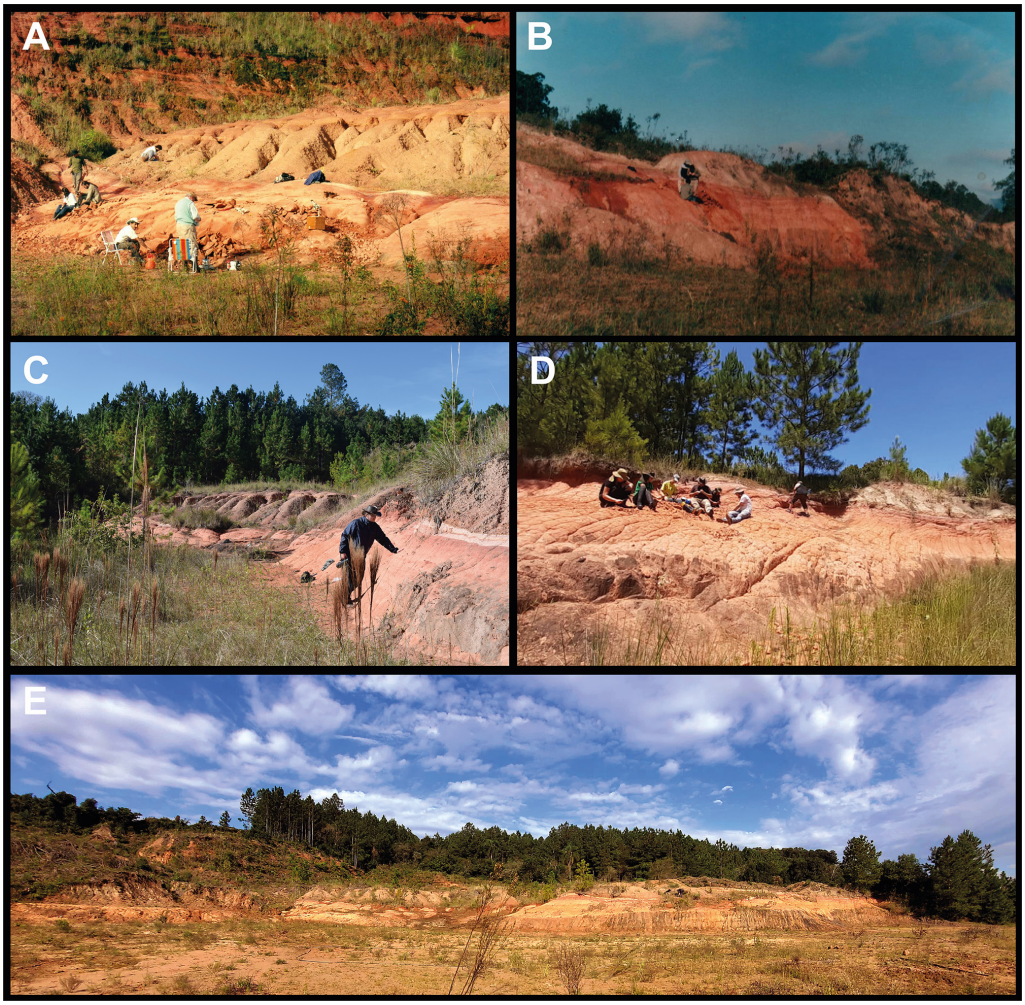

Figure 9. The Linha São Luiz Geosite over the years. A, B, fieldwork conducted during the early years of exploration, at the beginning of the decade of 2000. A, view of the ravine facing roughly S-SE, the most fossiliferous site with microremains of tetrapod at the time, taken in 2005, with Dr. José F. Bonaparte and technician Daniel Hernández near the middle of the photograph; B, view of the ravine facing roughly S-SW, where a partial skeleton of *Guaibasaurus candelariensis* was found. C, D, fieldwork conducted by the team of CAPPA/UFSM at the beginning of the decade of 2020. Shots taken in roughly the same views of A and B. Note the advance of pine trees over the outcrop, and the accumulation of sediment at the base of the outcrop, obscuring fossiliferous levels. E, current state of the outcrop (at 2024), after the removal of the accumulated sediment and of the pine trees that threatened the site.

mudstones of the lacustrine system deposition (Figure 10), degrading much of the area through root development. An evaluation of the vulnerability of fossiliferous sites (Figueiró et al. 2022) was developed during the establishment of the UNESCO Quarta Colonia Geopark with the Linha São Luiz Geosite figuring among the most relevant sites in terms of heritage value, and the most vulnerable locality with fossils in the territory.

Over the year of 2023, driven by the qualification of the territory in the UNESCO Global Geopark network, the municipality of Faxinal do Soturno undertook an important step in the maintenance of the locality, removing the main cover of exotic trees. In the same endeavor, accompanied by paleontologists, the municipal public administration removed the sediment accumulated by erosion at the base of the main vertebrate-bearing strata, re-exposing almost 2 meters of outcrop and restoring the exposure to conditions similar to those of the time of the first discoveries at this fossiliferous locality. This activity will not only allow the update of the status of this site as a locality under low risk of degradation in future vulnerability evaluations but also facilitate the access of the locality by researchers, bolstering the very activities of fossil prospection and collection, which originally gave the site its scientific and heritage relevance.

5.1. Digitalization

Geological formations are constantly changing through the eons, and their fossils are usually fragile and one of a kind. Since fossilized remains are the main study object of paleontology, one cannot afford to lose any data, especially considering the efforts and resources involved in collecting them. Digitalization is a great way of making perishable items eternal in the virtual realm, where they can be more easily shared, stored, and open to new types of analysis, made possible by computer algorithms (Falkingham 2012).

Based on our previous research (Almeida et al. 2023) in 3D reconstruction and virtualization of paleontological materials, we recreated several specimens found at this outcrop. Some fossils from the paleontological collection of CAPPA/UFSM are provided as 3D models for download in the Supplementary Files of this paper. Other specimens will be, in time, made available as QR codes and other sources of digital storage. This way, anyone interested in the locality can get to really know its flora and fauna. This effort not only gives the wider public direct access to science, but also protects this valuable cultural heritage.

Finally, joint efforts are being made to scan and recreate the complete Linha São Luiz Geosite in 3D. This site is being integrated into Virtual Reality and will be made available for digital exploration in a forthcoming endeavor.

6. Final Remarks – Perspectives

Along the 25 years passed since Daniel Cargnin first reported to paleontologists his discovery of a new fossil-bearing area, in the outskirts of Faxinal do Soturno, a rich history of research has unfolded. Several institutions, as well as renowned scientists from Brazil and abroad, focused their research on the ravines and beautifully preserved fossils from the Linha São Luiz Geosite, providing a rich account of several taxonomic groups and working together to elucidate the story told by its fossils and sedimentary layers. From the dawn of dinosaurs and stem-mammals in the Triassic, to the establishment of ancient Jurassic conifer forests, the Linha São Luiz Geosite is now not only a fossil-bearing area restricted to scientists, but a source of cultural heritage, protected by the people of the local communities. And after a quarter century of work and discoveries, there are still questions to be settled and new taxa to be uncovered from this which is one of the richest fossiliferous outcrops in Brazil.

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Authorship credits

Author	A	B	C	D	E	F
FAP						
LK						
AGM						
JPS						
RC						
RSH						
GCA						
HSB						
DSO						
DM						
CLS						

A - Study design/ Conceptualization **B** - Investigation/ Data acquisition
C - Data Interpretation/ Validation **D** - Writing
E - Review/Editing **F** - Supervision/Project administration

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