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An oasis in Western Gondwana: A diverse Guadalupian paleoflora from South America

Joseane Salau Ferraz [a,*], Joseline Manfroi [b,c,**], Arielli Fabrício Machado [a], William Vieira Gobo [d,e], Margot Guerra-Sommer [d], Felipe L. Pinheiro [a]

[a] Laboratório de Paleobiologia, Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal do Pampa (UNIPAMPA), São Gabriel, Rio Grande do Sul, Brazil
[b] Centro de Investigación y Avance de la Paleontología e Historia Natural de Atacama - CIAHN Atacama, Prat 58, Atacama, Caldera, Chile
[c] Department of Biology, Paleontology Laboratory of Ribeirão Preto, Universidade de São Paulo - USP, São Paulo, Brazil
[d] Paleontology and Stratigraphy Department, Universidade Federal do Rio Grande do Sul - UFRGS, Porto Alegre, Rio Grande do Sul, Brazil
[e] Technological Institute of Paleoceanography and Climate Change, Universidade do Vale do Rio dos Sinos - UNISINOS, São Leopoldo, Rio Grande do Sul, Brazil

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ABSTRACT

The end of the Paleozoic Era was marked by intense climatic crises that not only annihilated much of the marine and terrestrial biodiversity but also acted as an evolutionary pressure, shaping the surviving lineages that thrived throughout the Mesozoic. The Guadalupian (Permian) is characterized by a gradual aridification, with the end of this epoch punctuated by a significant mass extinction event that profoundly impacted continental ecosystems. Guadalupian plant fossil localities are rare across Gondwana, usually preserving isolated material. In this study, we present a Guadalupian-aged outcrop in the southern Paraná Basin, Brazil, featuring a unique and remarkable taphoflora composed of a floristic association represented by different taxa: Lycopsida, Sphenopsida, Pteridospermae, Filicopsida, and Gymnospermae. This taphoflora not only represents an important record that broadens the paleoflora database of Gondwana during the Guadalupian but also demonstrates that arid conditions were not uniformly severe, allowing the persistence of forested humid latitudinal belts or small biodiversity hotspots, that served as sanctuaries for plant biodiversity of Gondwana in the lead-up to the Guadalupian extinction.

1. Introduction

The end of the Paleozoic was marked by significant global climatic changes, making this time interval an important opportunity to study the Earth's climatic and environmental dynamics (Griffis et al., 2018). During this time period, terrestrial vegetated ecosystems underwent an icehouse-greenhouse transition, with a notorious increase in global mean temperatures (Gastaldo et al., 1996; Isbell et al., 2008). Evidence of this significant climatic transition marking the end of the Paleozoic Era has been demonstrated by numerous authors through stratigraphic, paleontological, and paleoenvironmental data (e.g., López Gamundí et al., 1992; Gastaldo et al., 1996; Limarino et al., 1997; Rees et al., 2002; Retallack et al., 2006; Holz et al., 2008). Additionally, oxygen and carbon isotopic records have also shown a progressive transition toward global warming after the end of The Last Paleozoic Ice Age (LPIA) that was the longest-lived (c.370 to 260 Ma) and possibly the most extensive and intense of the icehouse periods during the Phanerozoic (Hyde et al., 2006; Montañez et al., 2007; Grossman et al., 2008; Montañez, 2022).

The Permian geological and paleontological record is thus a cornerstone to understanding the response of terrestrial and marine ecosystems to global crises, as it bears witness to a series of climatic and environmental changes that occurred worldwide (Benton and Newell, 2014). During this period, plant communities were heavily impacted by global warming and, consequently, by wildfire occurrences (e.g., Benton and Newell, 2014; Manfroi et al., 2015; Jasper et al., 2020).

The Permian stands out by having at least three mass extinction events, and two of which (the Guadalupian extinction and the Permian-Triassic extinction) are particularly significant in shaping the faunas and

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* Corresponding author.
** Corresponding author. Centro de Investigación y Avance de la Paleontología e Historia Natural de Atacama - CIAHN Atacama, Prat 58, Atacama, Caldera, Chile.
E-mail addresses: joseaneferraz98@gmail.com (J.S. Ferraz), joselinemanfroi@ciahn.cl (J. Manfroi), ariellifm@gmail.com (A.F. Machado), williamgobo@hotmail.com (W.V. Gobo), margot.sommer@ufrgs.br (M. Guerra-Sommer), felipepinheiro@unipampa.edu.br (F.L. Pinheiro).

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floras of the late Paleozoic and early Mesozoic. Severe environmental changes contributed to the aridification of terrestrial environments and the collapse of biodiversity in continental and marine ecosystems, culminating in the Permian-Triassic extinction event, which wiped out over 90 % of all known biodiversity (Gastaldo et al., 1996). This environmental and climatic crisis appears to have intensified from the Guadalupian onward (Metcalfe et al., 2015).

Guadalupian-aged outcrops with plant fossils are rare globally, especially in Gondwana (Rees et al., 2002). In the southern Paraná Basin, only a few records were reported (Manfroi et al., 2015; Cambria et al., 2021; Cisneros et al., 2021). However, these generally represent isolated fossils, failing to characterize the presence of a well-developed plant community, thus hindering effective ecological interpretations. This study presents the taphoflora of a Guadalupian-aged outcrop in the southern Paraná Basin, Brazil, revealing a unique paleofloristic assemblage for Gondwana. These new data contribute to a more detailed assessment of paleoenvironmental and climatic dynamics during the greenhouse cycle observed globally in the middle to late Permian (Gibbs et al., 2002; Limarino et al., 2014).

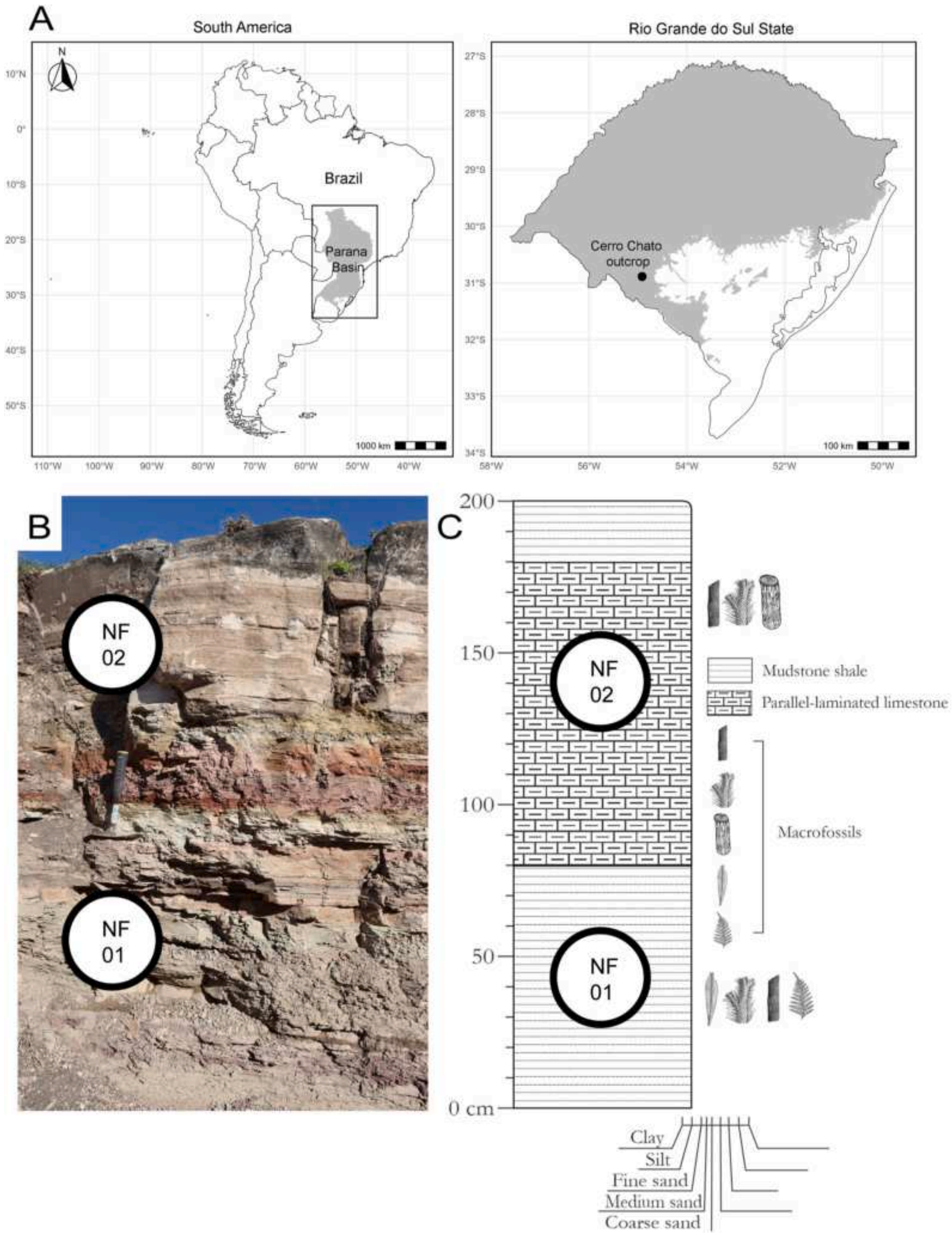

Fig. 1. A) Location of the Cerro Chato outcrop. B - C) Lithological facies of the outcrop. NF 01 corresponds to the basal fossiliferous level, composed of mudstone shale, and NF 02 corresponds to the upper fossiliferous level, composed of parallel-laminated limestone.

2. Material and methods

2.1. Geological context

Located in the municipality of Dom Pedrito, in the state of Rio Grande do Sul, Brazil, the Cerro Chato outcrop is situated in the southern Paraná Basin (Fig. 1), a significant sedimentary unit covering an area of approximately 1,500,000 km^2, the majority of which lies within Brazilian territory (Milani et al., 2007). The sedimentary fill of the Paraná Basin is divided into six depositional supersequences, with the Cerro Chato outcrop belonging to the Gondwana I Supersequence, which encompasses units deposited between the Carboniferous and the Early Triassic (Milani et al., 2007).

The Cerro Chato outcrop was first named and described in 1951 (Martins and Sena-Sobrinho, 1951) when the first fossil plants for the locality were discovered. Despite the importance of its fossiliferous content, information on its geographical location remained unknown for more than fifty years after its discovery. This fact was attributed to the limited geographical references available at the time and the disuse of rural roads that once provided access to the site (Ferraz et al., 2021). Recently, the Cerro Chato outcrop (30°53′16″ S, 54°54′50″ W) was rediscovered, enabling the resumption of studies and paleontological prospecting in this locality (Fig. 1, A).

The Cerro Chato outcrop, with deposits corresponding to the Guadalupian Series, belongs to the Passa Dois Group (Martins and Sena-Sobrinho, 1951). It was excavated at the top of a natural mound approximately 190 m above sea level. The outcrop has a lithology essentially composed of two distinct facies. The basal one consists of silt-rich mudstones in reddish, purplish, and greenish tones, containing fossils preserved throughout the entire section (Fig. 1, B). The upper facies is characterized by planar-parallel deposition of light grey to white limestone, with fossil content concentrated at its top and a thickness of approximately 80 cm (Fig. 1, C).

The attribution of the Cerro Chato outcrop to the Guadalupian Series is supported by the presence of *Lycopodiopsis derbyi* Renault (1890), a taxon previously reported for this site by Martins and Sena-Sobrinho (1951) and more recently by Ferraz et al. (2021). Holtz et al. (2010) mention that the *Lycopodiopsis derbyi* biozone does not extend beyond the transition between the Teresina and Rio do Rasto Formations (Guadalupian). However, the authors note that the lithological transition between these units, as observed in outcrops, is poorly defined, suggesting that it may not be separated by a significant unconformity. This ambiguity is also evident at the Cerro Chato outcrop, complicating its precise assignment to either of the two formations based on lithological or biostratigraphic criteria. Luiza De Lima et al. (2025) also indicate that the contact between the Teresina Formation and the lower Serrinha Member of the Rio do Rasto Formation is gradational, marked by a progressive change in the color of sediments (from grey to green, violet, or red). In this respect, the fine-grained sediments from the base of the Cerro Chato section may be more compatible with the Serrinha Member of the Rio do Rasto Formation.

2.2. Field collection and laboratorial processing procedures

The macrofossils presented in this study were collected during field expeditions conducted between 2020 and 2022. During these campaigns, the geological profile of the outcrop was measured, and new fossiliferous layers were accessed through the excavation of a trench approximately 2 m wide and 5 m long. The outcrop was divided into two distinct fossiliferous levels: the lower one, dominated by silt-rich shales, designated as NF 01, and the upper fossiliferous level, corresponding to planar-parallel laminated limestone, designated as NF 02 (Fig. 1B–C).

The NF 01 revealed new fossiliferous layers previously unknown for the outcrop (Martins and Sena-Sobrinho, 1951). This level contains macrofossils in greater abundance (Fig. 2), and their collection was carried out systematically and in stages, with each depositional layer being exposed and photographed prior to fossil collection. Cuts were made in quadrants using a saw with an appropriate rock-cutting disc, and the careful removal of blocks was performed to facilitate and optimize fossil collection without compromising their integrity.

In the laboratory, the collected samples were cataloged and stored in the paleontological collection of the Laboratório de Paleobiologia at the

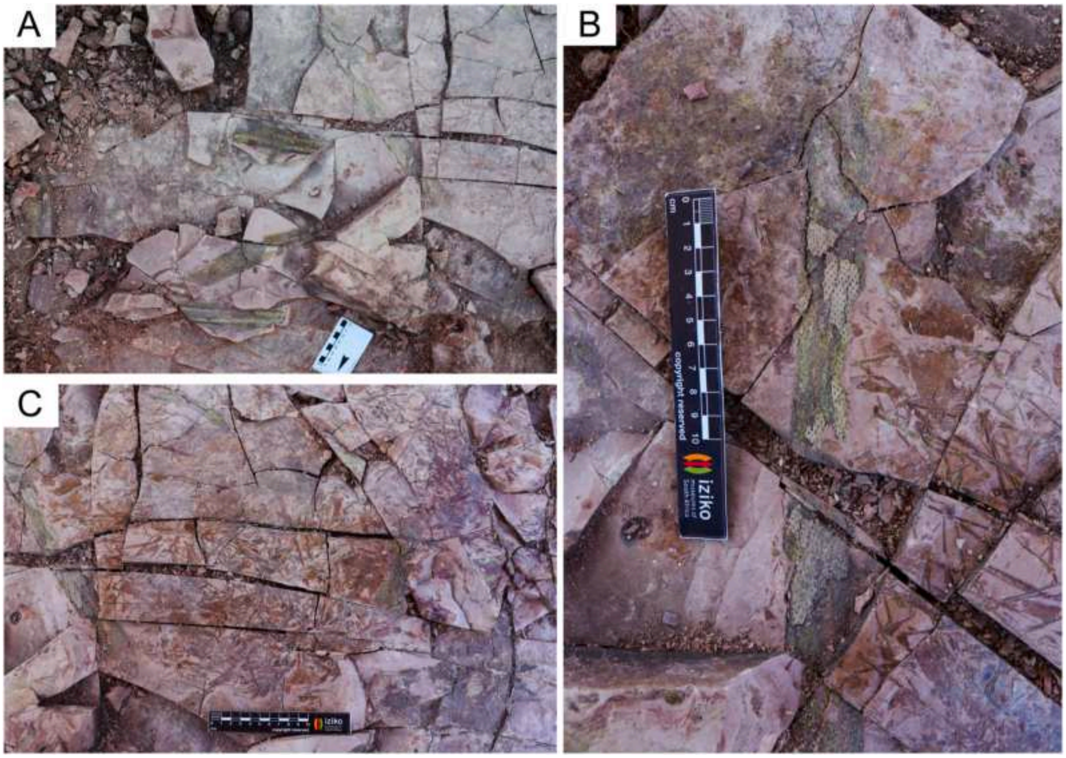

Fig. 2. Plant assemblage at the basal fossiliferous level (NF 01). A - C) Stems and disarticulated lycopsid microphylls.

Universidade Federal do Pampa, under the acronym “UNIPAMPA PBCC,” followed by the sequential sample number. Some samples containing plant fossils were mechanically prepared using air scribes (model Paleotools MicroJack 1) when necessary. To better visualize and identify the morpho-anatomical structures, a stereomicroscope (Zeiss, Model Stemi 2000-C, magnifications 10× - 40x) was used, coupled with a digital camera (Zeiss AxioCam ERC5s). Larger samples were photographed using a Canon EOS Rebel SL3 camera.

Based on the analyses conducted and the digitized photographs of the fossil material, measurements of the anatomical structures were taken using the ImageJ software for the diagnosis of plant fossils, primarily observing structures such as pinnae, pinnules, leaf blades, leaf cushions, and stems (Schneider et al., 2012). The taxonomic identification of the specimens was performed with the aid of and by comparing specialized literature (e.g., Tryon and Tryon, 1982; Meyen, 1987; Christenhusz et al., 2011a, b). After taxonomic identification, the data were tabulated. From this, the diversity of the plant groups was assessed, estimating the composition, abundance, and proportion of each taxon using the R v.4.4.0 software (R Core Team, 2024) and RStudio (Posit team, 2024). These estimates were represented for visualization through a bar chart using the barplot function from the base package of R v.4.4.0 (R Core Team, 2024). These analyses were conducted to demonstrate the paleofloristic composition of the elements belonging to this taphoflora. An anatomical analysis of fossil wood was performed using Scanning Electron Microscopy (SEM- Zeiss EVO LS15). In addition, petrographic slides were prepared and observed through thin sections (see standard methods in Jones and Rowe, 1999). Cross-sections were analyzed and described using a Zeiss AxioScope 5 microscope equipped with an AxioCam 305 color camera. The other sections (radial and tangential longitudinal) were too poorly preserved to be used. These analyses were conducted at Unisinos University (ittOceaneon – Technological Institute of Paleoceanography and Climate Changes).

3. Results and discussion

3.1. Taphoflora

A total of 200 plant macrofossil specimens (PBCC-001 to PBCC-200) were collected from the Cerro Chato outcrop, of which 103 specimens exhibited preserved and identifiable diagnostic features. These records correspond to impressions, compressions, and, more rarely, permineralizations of structures such as stems, leaves, fronds, and rhizomatic stem bases. Despite representing distinct depositional events, both facies (NF 01 and NF 02) preserve abundant fossil contents. However, NF 01 exhibits a significantly higher abundance and better-preserved fossils.

The fossiliferous level described by Martins and Sena-Sobrinho (1951) corresponds only to the limestone deposits exposed amidst low-lying vegetation (NF 02). This fossiliferous level contains important paleobotanical records, including the holotype of the lycophyte *Cyclodendron dolianitti* (Herbst, 1986). The presence of *Glossopteris* sp. and *Lycopodiopsis derbyi* (Martins and Sena-Sobrinho, 1951), among other paleobotanical records, was also reported (Beurlen et al., 1955; Sommer and Trindade, 1966).

The basal fossiliferous level (NF 01), previously unknown in the literature until recently, corresponds to the deposits of silt-rich mudstones that revealed a diverse and abundant taphoflora preserved across a surprising range of depositional layers (Fig. 2). Fossils recovered from this facies commonly exhibit excellent preservation, highlighting records of *Pecopteris* sp., *Glossopteris* sp., and *Lycopodiopsis* sp. (Ferraz et al., 2021). There is also a significant increase in the concentration of microphylls at this level, which is attributed to lycopsids.

Among the plant macrofossil specimens identified and analyzed from the Cerro Chato outcrop, it was possible to identify the presence of five distinct taxa that make up this taphoflora (Fig. 3), listed in order of abundance: Lycopsida (73 %), Sphenopsida (17 %), Pteridospermae (4 %), Filicopsida (4 %), and Gymnospermae (2 %).

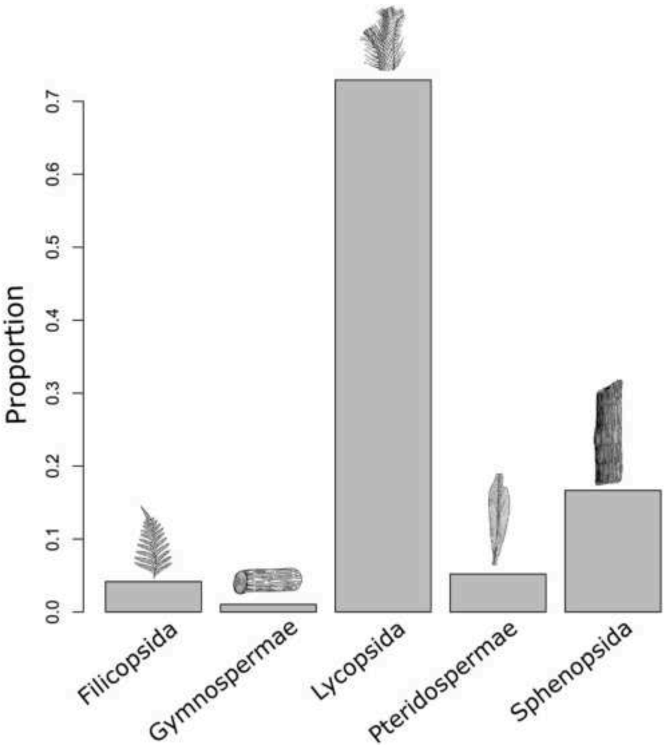

Fig. 3. Floristic composition of the taphoflora of the Cerro Chato outcrop and abundance of each taxon, significantly highlighting the dominance of lycopsids.

Lycopsids are the dominant elements of the taphoflora (Figs. 4 and 5). Their stems were found in abundance at the outcrop, some in excellent preservation, showing the plant’s vascular cylinder (Fig. 4A–B). The recovered vegetative structures include microphylls, stems preserving leaf cushions, and stem bases with rhizomes. The dominant preservation type of these structures is impression-compression and, less frequently, permineralization.

The diagnosis of lycopsids is mainly revealed through the external morphology of their stems (Spiekermann et al., 2021). It was possible to identify some of the plant macrofossils recovered from the Cerro Chato outcrop to the morphological pattern found in *Lycopodiopsis derbyi*, with rhomboidal leaf cushions measuring between 2.8 mm and 4 mm in length and a maximum width of 3.5 mm. These cushions exhibit rounded leaf insertion scars located on the superomedial part of the cushion and the absence of ligules and/or parichnos (Fig. 4C–D).

In the Paraná Basin, *Lycopodiopsis derbyi* is recorded from the Teresina and Corumbataí Formations. Isolated microphylls and stems are recorded for the units, and these structures are commonly associated with the same mother plant (Kräusel, 1961; Faria and Ricardi-Branco, 2010). To date, the only leaf-based species recorded for Brazil is *Lepidophylloides corumbataensis* Faria and Ricardi-Branco (2010). Despite the lack of a specimen that clearly shows the organic connection between *Lepidophylloides corumbataensis* and *Lycopodiopsis derbyi*, the authors suggest that both represent different organs of the same species, as the stems and microphylls are closely associated in the same assemblage (Faria and Ricardi-Branco, 2010).

At the Cerro Chato outcrop, as previously mentioned, isolated microphylls are frequently and abundantly found. However, in specimen PBCC-091, corresponding to *Lycopodiopsis derbyi*, a rare connection between the stem impression and microphylls is observed (Fig. 5A–B). However, due to the poor microphyll preservation, their morphological-anatomical details are not visible for taxonomic characterization. The presence of stems with true leaf scars observed in the analyzed material indicates that these plants underwent leaf abscission, and thus, the isolated microphylls observed throughout the Cerro Chato outcrop likely

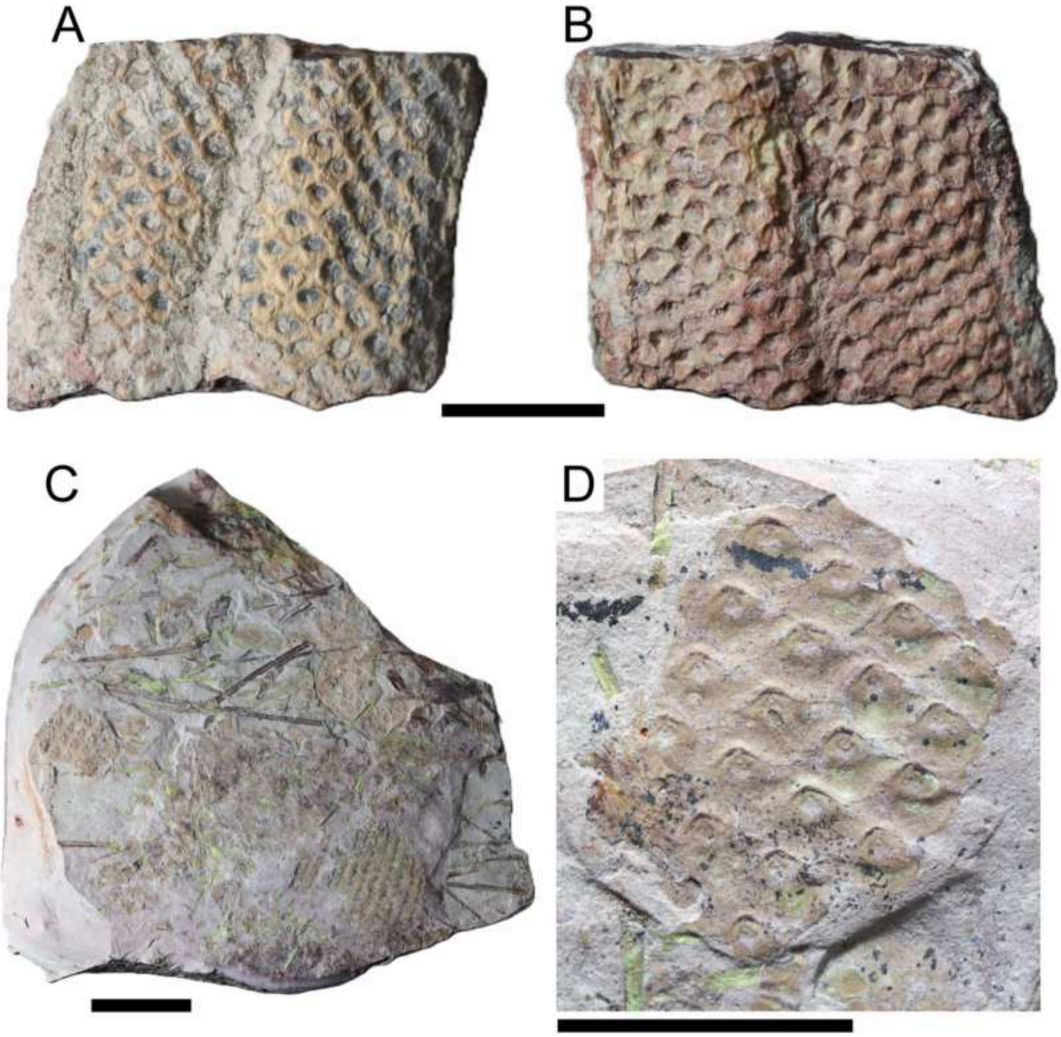

Fig. 4. A - B) Three-dimensional stem with leaf cushions preserving the vascular cylinder. Scale bar = 15 mm. C) Sedimentary matrix containing fragmented parts of plants. Scale bar = 20 mm. D) Details of the leaf cushions. Scale bar = 15 mm.

belong to the same plants or group of plants (Fig. 5C–D), as suggested for other specimens in the Paraná Basin (Kräusel, 1961).

Fragmented impressions of the basal parts of lycopsid stems were also identified, presenting rounded, bulbous structures (Fig. 5, E). The recorded plant bases for Gondwanan lycophytes are relatively scarce. Of the three sub-arborescent morphospecies recorded in Permian deposits in Brazil, *Brasilodendron pedroanum* (Chaloner et al., 1979), *Lycopodiopsis derbyi* and *Cyclodendron dolianitti* (Kräusel, 1961) Herbst (1986), only basal bulbs attributed to *Brasilodendron* are known (Jasper and Guerra-Sommer, 1998). Although a detailed description of the basal parts found at the outcrop cannot be provided at this time, the size of these structures suggests a sub-arborescent or arborescent habit.

It is important to highlight that, in other fossiliferous assemblages of the Paraná Basin that record Lycopsida, rarely are more than one organic structure of this group found in the same fossil site (e.g., Faria et al., 2009; De Carvalho et al., 2022). Furthermore, most outcrops reveal monospecific assemblages. However, the Cerro Chato outcrop preserves different organic structures of this group (leaves, stems, and basal stems/rhizomes) and, to date, records two morphospecies: *Cyclodendron dolianitti* and *Lycopodiopsis derbyi*. Unfortunately, we cannot include a comparison with *Cyclodendron dolianitii* at the moment. The description of the material from the Cerro Chato outcrop, initially assigned to *Lycopodiophloios dolianitii* by Kräusel (1961) and later recombined as *Cyclodendron dolianitii* by Herbst (1986), does not include information on the pattern of leaf cushions, nor does it provide illustrations that allow these structures to be observed.

As secondary elements, representing the remaining 27 % of the floristic composition of the Cerro Chato outcrop's taphoflora, are Pteridospermae, Sphenopsida, Filicopsida, and Gymnospermae. As representatives of Pteridospermae, the taphoflora reveals impressions of glossopterids. Fragmentary leaf impressions corresponding to *Glossopteris* sp. were recorded in both levels of the outcrop (Martins and Sena-Sobrinho, 1951; Ferraz et al., 2021). The most complete specimen recovered from the NF 01 level of the outcrop (PBCC-068) measures 93.90 mm in length and 17.75 mm in maximum width (Fig. 6A–B). The base of the leaf with its petiole is absent, suggesting that the leaf might have been longer than what is preserved. The leaf apex is oblong (and not lanceolate), and although the details of the veins are not completely visible macroscopically, the sample reveals a very thin central longitudinal bundle of veins that extends from the base to the apex of the blade, as well as secondary veins that extend to the leaf blade. The secondary veins are derived from the central vein. In the most distal part, the secondary veins are slightly straight to curved, increasing their curvature progressively as they approach the apex of the leaf. The venation patterns of this morphogenus are distinguished from other glossopterids, such as *Gangamopteris*, by the presence of a persistent midrib composed of multiple well-defined parallel veins that extend from the base to the apex of the leaf (Guerra-Sommer et al., 2020). Typically, *Glossopteris* leaves occur in large concentrations in taphofloras worldwide. However, the occurrence of few leaves in the Cerro Chato outcrop, as well as their

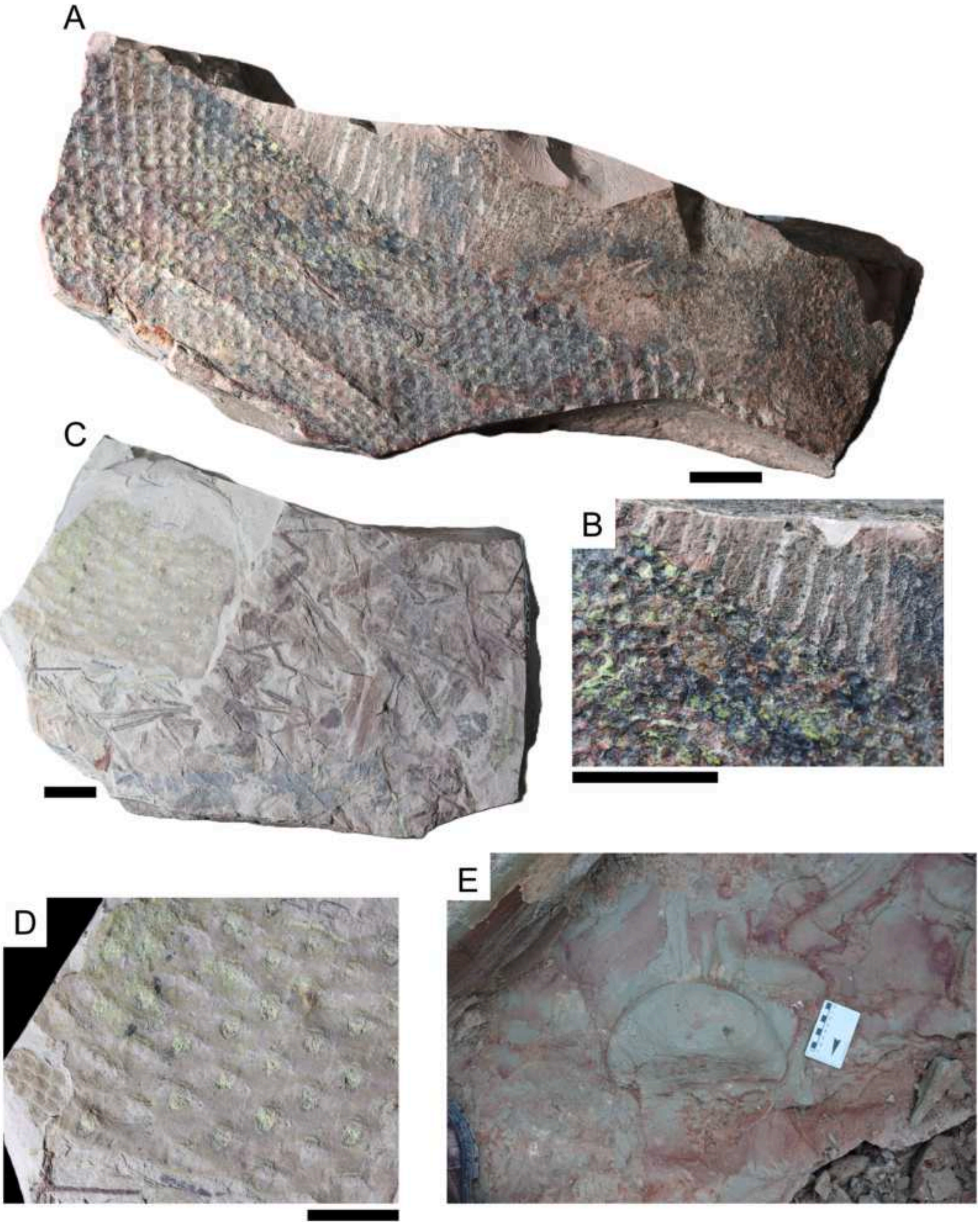

Fig. 5. Lycopsida from the Cerro Chato outrcop. A - B) Organic connection of the stem and microphylls. Scale bar = 10 mm. C) Isolated microphylls associated with a fragmentary stem. Scale bar = 10 mm. D) Details of the leaf cushions. Scale bar = 5 mm. E) Bulbous structure attributed to lycopsid bases.

fragmentation, may suggest that this genus's habitat was distant from the site of deposition, and the leaves underwent at least moderate transport before their final deposition.

The record of Sphenopsida occurs in both fossiliferous levels; however, it is more prevalent in the basal level of the outcrop (NF 01). Fragmentary stem impressions/compressions and permineralizations exhibit fine longitudinal striations along the entire length of the stems. Among the specimens analyzed, two present stem bifurcations (PBCC-052 and PBCC-030). The specimen PBCC-102, found in the upper fossiliferous level of the outcrop (NF 02), presents three-dimensional preservation (Fig. 6C–D). However, the absence of morpho-anatomical details in the specimens presented here prevents a more complete description and comparisons.

Sphenopsida had previously been recorded for the outcrop (Ferraz et al., 2021), as well as being documented in other localities of the Paraná Basin (e.g., Bortoluzzi, 1975; Rösler and Rohn, 1984). The most documented genera in the basin include *Phyllotheca*, *Schizoneura*, *Sphenophyllum*, and *Paracalamites*. Sphenopsids are frequent in Cisuralian-aged deposits, but their occurrence decreases significantly in Guadalupian-Lopingian-aged deposits (Neregato et al., 2021). It is suggested that the significant rise in sea level led to the flooding of extensive areas of the basin's coastal plain (Holz et al., 2010), creating taphonomic conditions unfavorable for sphenopsid preservation (Neregato et al., 2021).

The occurrence of Filicopsida is restricted to the basal fossiliferous level (NF 01) of the outcrop, where foliar impressions/compressions were found, representing organic structures such as pinnae, pinnules, and a possible crozier. Among the analyzed filicopsids (Fig. 7A–F),

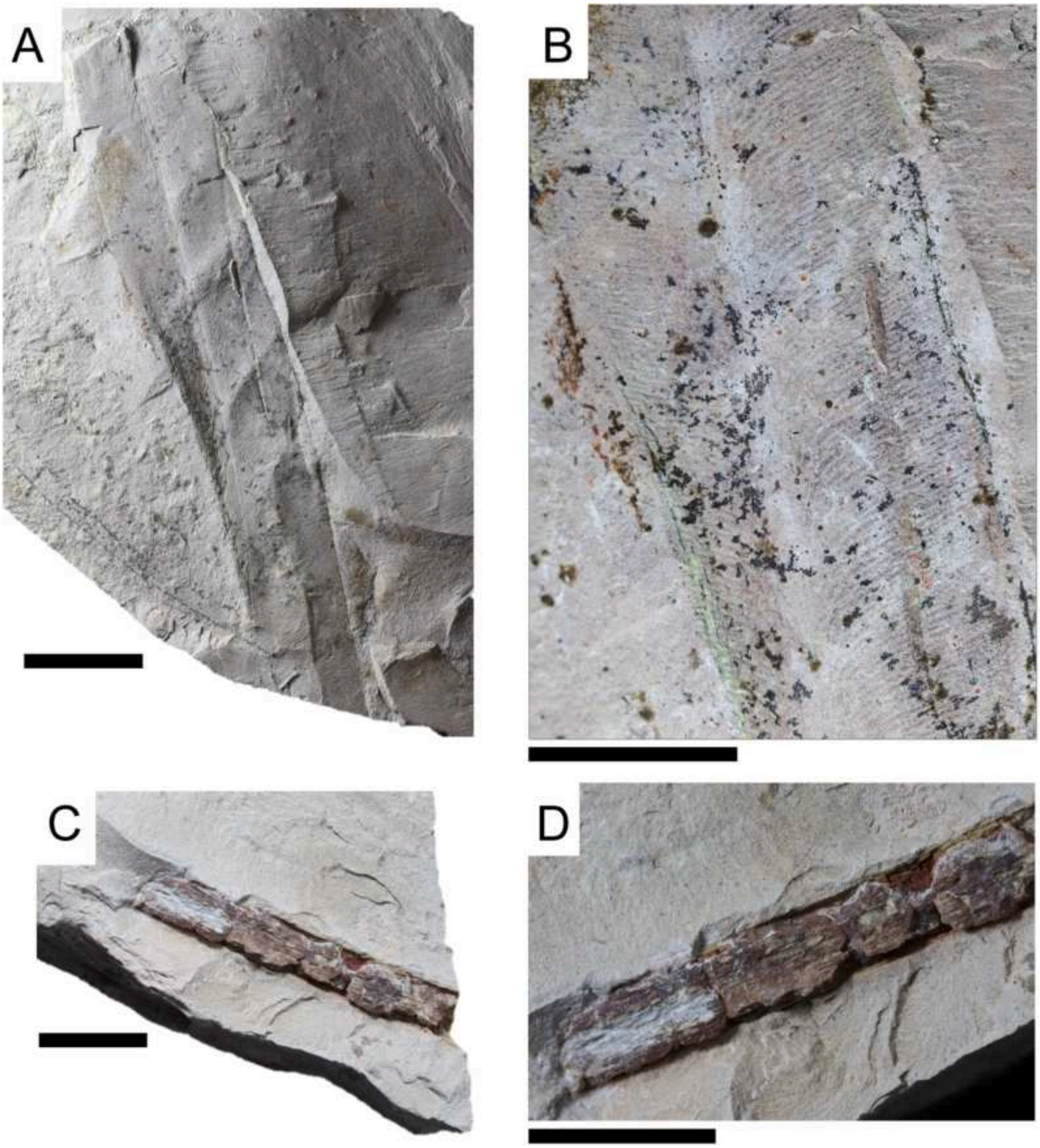

Fig. 6. A) Partially complete leaf impression corresponding to Pteridospermae (*Glossopteris* sp.) Scale bar = 20 mm. B) Details of the leaf venation. Scale bar = 10 mm. C) Three-dimensional stems recovered in NF 02, corresponding to the Sphenopsida group (PBCC-102). Scale bar = 10 mm. D) Details of stem. Scale bar = 5 mm.

specimen PBCC-001 shows the best preservation, consisting of an articulated pinna displaying morphological details of pinnules and foliar venation (Fig. 7, A and D). The specimen is 88.10 mm long and 21.50 mm wide. The rachis is 1.30 mm wide, with an angle of >90° at the apex of the pinna. It has pinnules alternately arranged on the rachis, which are in contact with each other or even imbricated, having an insertion angle between 63° and 85°. The pinna is formed by 41 pinnules, 20 pinnules arranged on the left side and another 21 pinnules arranged on the right side of the pinna.

The pinnules of specimen PBCC-001 (Fig. 7, A and D) are oblong and have rounded apexes, slightly curved towards the distal portion of the pinna. The pinnules are inserted into the pinna rach along the entire length of their bases and have entire, parallel margins. The length of the pinnules ranges from 6.20 mm to 11.24 mm. While the width of the pinnules varies from 3.10 mm to 4.16 mm. There are 2–3 pinnules per centimeter. It is visible that the pinnules have varying sizes as they approach the apex of the pinna, i.e., larger pinnules are concentrated in the proximal portion, while those concentrated in the distal portion are smaller. The venation composed of the middle vein is slightly curved towards the apex of the pinnule, sometimes oblique and undivided, with a thickness varying between 0.20 mm and 0.36 mm. The lateral veins are rectilinear towards the margins of the pinnule and start opposite on both sides of the middle vein so that the spacing between the lateral veins is up to 1 mm, at angles between 23° - 55°, with a density of approximately two pinnules per millimeter, resulting in approximately 10–12 pairs in each pinnule. On average, the length of the lateral veins is 1.5 mm, and the width is 0.20 mm. In some lateral veins, a "Y"-shaped dichotomization that extends to the margin of the pinnule, forming 50° angles, is visible.

The presence of small pinnules (Fig. 7, D) and the arrangement of venation with dichotomization, observed in specimen PBCC-001, are characteristic of *Pecopteris* (Cleal and Thomas, 2018). In addition, the morpho-anatomical features described above clearly show affinities with *Pecopteris* in a number of relevant diagnostic features, such as the opposite arrangement of pinnules, the alternate arrangement of pinnule bases, the apex angles of pinnae 63°–85°, pinnules with basis fused to the rachis, pinnules oblong in shape, the decurrent midvein and, finally, the dichotomized venation (Rohn et al., 2021). This genus is well documented in other Permian deposits of the Paraná Basin, such as the Teresina and Rio do Rasto Formations (Cazzulo-Klepzig, 1978; Rohn and

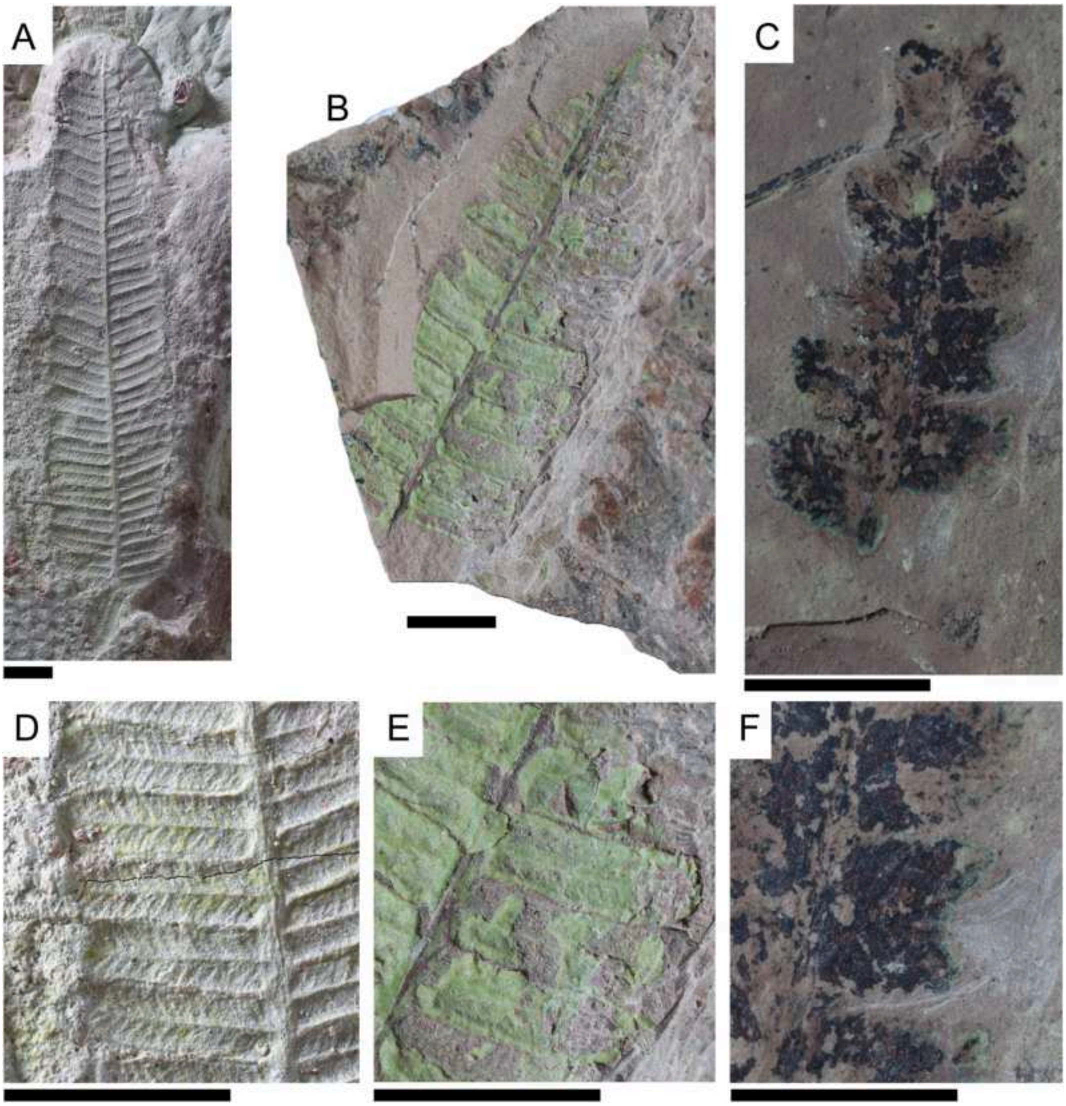

Fig. 7. Filicopsida specimens. A) Pinna (PBCC-001) with excellent preservation attributed to *Pecopteris* sp. Scale bar = 10 mm. B) Pinna attributed to *Pecopteris* sp. (PBCC-028). Scale bar = 10 mm. C) Indeterminate filicopsida (PBCC-040). Scale bar = 10 mm. D) Details of pinnule (PBCC-001). Scale bar = 10 mm. E) Details of pinnule (PBCC-028). Scale bar = 10 mm. F) Details of pinnule (PBCC-040). Scale bar = 5 mm.

Rösler, 1986; Cambria et al., 2021; Rohn et al., 2021). However, specimens with well-preserved morpho-anatomical features, such as PBCC-001 (Fig. 7, A and D), are poorly known from Guadalupian-aged deposits in the southern Paraná Basin.

Gymnospermae were recorded in the upper fossiliferous level (NF 02). A single silicified wood specimen (PBCC-050) was identified within a sedimentary layer corresponding to the upper fossiliferous level of the outcrop (Fig. 8A and B). The specimen was observed and described based on cross-section characteristics (Fig. 8C–H). Surprisingly, the major conductive tissues (xylem and phloem) of the stem are preserved (Fig. 8F–H), but also the medulla (Fig. 8, E) and cortex (Fig. 8, H). The secondary xylem is homoxylous pycnoxylic with compact and abundant tracheids associated with parenchymatous ray cells (Fig. 8, G). Tracheids are mainly rectangular to circular (Fig. 8, G). They have ca. 15–40 μm in diameter, and their walls ca. 4–7 μm in thickness. The pith measures 2.6 mm in cross-section. It is stellar, solid, heterocellular with parenchymatous cells and secretory canals. Canals are present at the periphery of the pith (Fig. 8, E). The phloem is clearly composed of fiber cells, and the cortex is most collapsed, but parenchymatous cells are clearly preserved (Fig. 8, H). Gymnospermic woods from the Permian preserving the pith tissue are relatively scarce in deposits of the Paraná Basin and, when preserved, constitute an important taxonomic element in inter-taxa differentiation (Dohms, 1976; Merlotti, 2009).

The presence of a heterogeneous pith, with secretory canals, sclerenchymatous, and parenchymatous cells, are characteristics present in a restricted group of morphogenera described for Gondwana. Considering the characteristics present in PBCC-050, we can relate the specimen to the following genera: *Solenoxylon* Kräusel (1956), *Solenopitys* Kräusel (1956), *Polysolenoxylon* Kräusel and Dolianiti (1958) and *Barakaroxylon* (Surange, Maithy) Kulkarni et al. (1970). PBCC-050 differs from *Polysolenoxylon* and *Barakaroxylon*, as both genera have as a diagnostic characteristic the presence of a central pith canal associated with secretory canals in the pith, with these being dispersed in *Polysolenoxylon* and concentrated at the periphery in *Barakaroxylon*. The specimen also differs from *Solenopitys*, which exhibits secretory cells either isolated or grouped in small, sparse clusters with a greater peripheral concentration. On the other hand, PBCC-050 resembles the pith pattern of *Solenoxylon*, displaying secretory cells exclusively located at the periphery (Mussa, 1986). However, we chose not to directly assign the specimen presented here to *Solenoxylon* due to the absence of additional diagnostic features described in the literature. Although gymnosperm woods are among the most frequently found plant

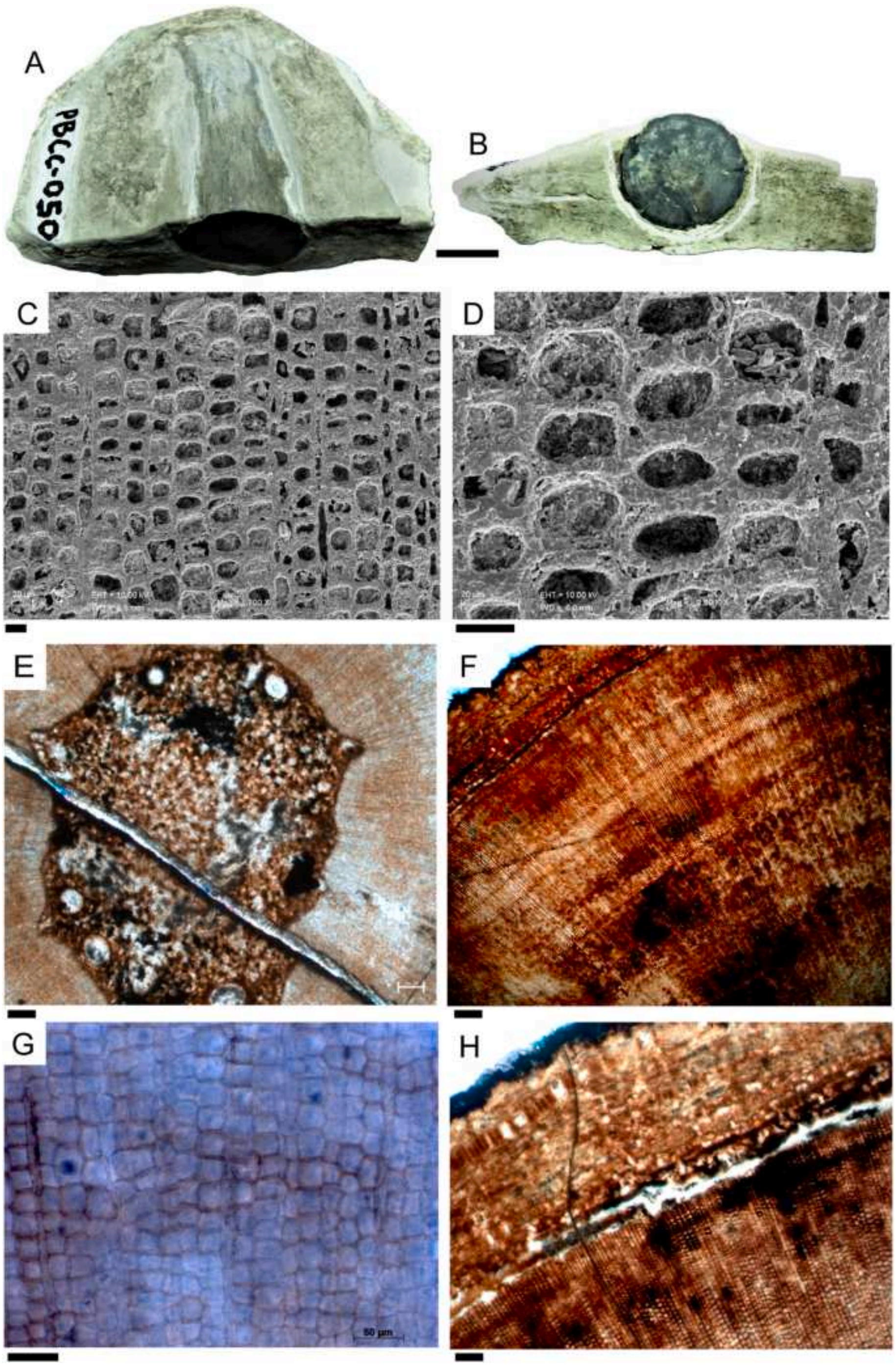

Fig. 8. Gymnospermae silicified wood. A - B) Macroscopic view. Scale bar = 15 mm. C - D) Details of the tracheids and parenchymatous ray cells seen by scanning electron microscopy. Scale bar = 20 μm. E – H) Transverse sections showing medullary, secondary xylem, phloem and cortical regions. E) Close-up of star-shaped pith. F) Pycnoxylic wood with indistinct growth rings. G) Details of tracheids and parenchymatous ray cells. H) Cortex. Scale bars = 50 μm.

elements in Permian deposits in Rio Grande do Sul (Dohms, 1976), and their occurrence has been recorded since the 19th century (De Andrade Ramos, 1986), recent studies on these structures in these deposits are rare. Most of the published works to date investigating wood anatomy come from the Irati and Serra Alta Formations (Cisuralian) (e.g., Guerra-Sommer, 1975; Dohms, 1976; Guerra-Sommer, 1976; Guerra-Sommer, 1978; Merlotti, 2002), and these are older works with few illustrations or clear figures indicating specific diagnostic features (Merlotti, 2009), making comparisons with other specimens difficult.

The plant diversity known for Gondwana during the Guadalupian is significantly low, especially during the Roadian and Capitanian (Rees et al., 2002). As a reflection of a global paleoclimatic crisis, changes in vegetation composition have been observed in different paleogeographic regions worldwide (Roscher et al., 2011). Guadalupian-aged plant associations in the Paraná Basin, particularly in the Teresina Formation (Passa Dois Group), can be easily differentiated from older Permian floras, such as those from the Early Permian, due to the presence of key taxonomic elements.

These paleofloras are characterized by the abundance of *Lycopodiopsis*, with representatives of glossopterids and pecopterids also being frequent (Rohn and Rösler, 2000), which is consistent with the paleobotanical records from the Cerro Chato outcrop. Christiano-de-Souza and Ricardi-Branco (2015) emphasize that no fossil plant assemblages have been recorded for the southern Paraná Basin during the Guadalupian. To date, the only paleobotanical records include isolated occurrences of charcoal (Manfroi et al., 2015), fragmentary impressions of *Glossopteris communis* Feistmantel (1876); sphenophytes (Cisneros et al., 2021), and pecopterids (Cambria et al., 2021).

Thus, considering the various aspects highlighted, the Cerro Chato outcrop's taphoflora can currently be regarded as one of the best windows of opportunity in the Paraná Basin for understanding environmental, climatic, and ecological aspects. The preserved ecosystem represents a kind of "oasis" prior to a major paleoclimatic crisis in Gondwana, the Guadalupian mass extinction.

3.2. *Taphonomy and paleoenvironmental significance*

The latter half of the Permian period, specifically the Guadalupian (approximately 273–259 million years ago), was marked by significant climatic and environmental transitions, both globally and regionally (Da Rosa et al., 2024). In the southern part of Gondwana, corresponding to the present-day state of Rio Grande do Sul, Brazil, the climate shifted from glacial conditions in the early Permian to a more arid and seasonal climate toward the end of the period (Holz et al., 2010). This climatic transition occurred within a range of depositional environments, including fluvial and lacustrine systems, which provided favorable conditions for fossilization in some sparse areas (e.g., Dentzien-Dias et al., 2012; Cisneros et al., 2021; Ferraz et al., 2021).

The fossiliferous deposits of the Cerro Chato outcrop indicate that favorable local environmental conditions facilitated the high concentration and diversity of preserved plant elements. The varied depositional environments, as witnessed by the limestone deposits (NF 02) and mudstones (NF 01), created ideal scenarios for fossilization, preserving both plant impressions/compressions and permineralizations. Generally, the recovered organ remains probably of the same taxon were not in organic connection, a fact that likely reflects distinct taphonomic processes throughout the deposition interval. A similar occurrence of an abundant life scenario during the Guadalupian has only been recorded in deposits from South Africa, but this refers to the fossil record of vertebrates and invertebrates and not to a plant community (Ronchi et al., 2023). The Cerro Chato outcrop "oasis" represents a unique window into the diverse paleoflora of the Guadalupian in South America.

The presence of lycopsid stem bases with rhizomes, preserved in the mudstone levels (NF 01), along with the high concentration of microphylls, some even articulated to the stem, suggests that these plants underwent limited or any transportation, meaning they were likely fossilized close to their original habitat. This interpretation is further reinforced by the random orientation of microphylls in these levels, (which rules out hydraulic transport) and the preservation of distinct organic structures (stem, stem bases, and microphylls) within the same fossiliferous level. Together, these evidences strongly support the autochthonous deposition of the lycopsids preserved in the outcrop. The other elements recovered from this taphoflora (Pteridospermae, Sphenopsida, Filicopsida, and Gymnospermae) show a lower diversity of fossilized structures but still demonstrate the preservation of delicate plant structures, such as pinnate leaves with articulated pinnae, also indicating limited transportation (autochthony/para-autochthony) before fossilization.

The taphoflora of Cerro Chato exhibits a dual preservation pattern, with Lycopsida fossils retained in an autochthonous state, while representatives of Pteridospermae, Sphenopsida, Filicopsida, and Gymnospermae are para-autochthonous. The autochthonous nature of Lycopsida is evidenced by the presence of stem bases with rhizomes, suggesting minimal displacement and direct burial within their original growth environment. Whereas the autochthonous/parautochthonous preservation of the other groups is evidenced by the occurrence of foliar delicate structures and stems belonging to Pteridospermae, Sphenopsida, Filicopsida, and Gymnospermae, plant groups typically associated with environments that had water availability, this fact is confirmed by the presence of fish scales and bivalve shells (Ferraz et al., 2021).

Furthermore, local environmental conditions enable the observation of unprecedented morpho-anatomical aspects of arborescent lycophytes in the fossil record of southern Gondwana. The specimen illustrated in Fig. 5 (A - B) is noteworthy for being the first attributed to *Lycopodiopsis derbyi* to exhibit an organic connection between the stem and microphylls. In the recovered stems, noticeable leaf scars provide direct evidence that the leaf abscission process was either a natural part of these plants' life cycle or occurred in response to local climatic variations. For lycopsids recorded in southern Gondwana, this biological process has already been discussed in studies by Faria et al. (2009), Faria and Ricardi-Branco (2010), and De Carvalho et al. (2022). Nevertheless, despite these earlier records, additional evidence such as that presented here contributes to advancing our understanding of the biology of *Lycopodiopsis derbyi*.

In deposits of Guadalupian age in the Paraná Basin, monospecific lycopsid assemblages are predominantly recovered, favoring the preservation of only one type of anatomical structure (De Carvalho et al., 2022). However, at the Cerro Chato outcrop, different lycopsid organs of the same taxon are preserved morphologically, sometimes in organic connection (microphylls, stems, and rhizomatic stem bases), offering a more comprehensive view of the morphology and biological aspects of these plants, in addition to the co-occurrence of other plant groups alongside vertebrate and invertebrate fragments. A detailed investigation into the morpho-anatomical aspects of the lycophytes recovered from the outcrop is underway, aiming to provide a more comprehensive systematic analysis and a deeper understanding of their taxonomy and biology.

The concentration of preserved plant material, many exhibiting excellent preservation, suggests a rapid final burial in lacustrine settings. Furthermore, this idea is reinforced by the presence of fish scales and bivalve shells, which attest to the existence of permanent water bodies. These factors and both fossiliferous layers' fine, laminated sedimentation are consistent with a calm-water depositional environment (Fig. 9). However, as in the present day, coastal lacustrine systems are subject to sporadic events, such as eustatic variations, which alter and define the landscape and its biodiversity. In this context, NF 02 of the Cerro Chato outcrop exemplifies one of these events, with the putative marine incursions disrupting the lacustrine system previously inhabited by lush vegetation, something that was also recorded in another Permian deposit in Rio Grande do Sul by Jasper et al. (2009).

In this context, it becomes evident that the depositional and taphonomic processes differed between the two fossiliferous levels of the Cerro Chato outcrop (NF 01 and NF 02), which also explains the variation in the diversity and preservation of the elements that composed the taphoflora in both levels. The taphonomic signatures observed at the Cerro Chato site thus reflect a complex depositional environment, locally distinct from other environmental scenarios common to the Permian in the southern Paraná Basin (e.g., Dentzien-Dias et al., 2012), which is characterized by Guadalupian/Lopingian-aged deposits indicative of semi-arid conditions (Holz et al., 2010).

4. Final considerations

The analysis of the fossiliferous deposits at the Cerro Chato outcrop reveals a unique and complex paleoenvironmental scenario. The combination of favorable environmental conditions, including deposition in a lacustrine setting, enabled the preservation of a remarkable diversity of plant material. In contrast to the rarity of Guadalupian localities in Gondwana, which often yield isolated plant fragments, Cerro Chato stands out for its abundant concentration of vegetation. This abundance provides a more comprehensive perspective on the taphoflora and biological aspects of Permian vegetation, particularly the arborescent

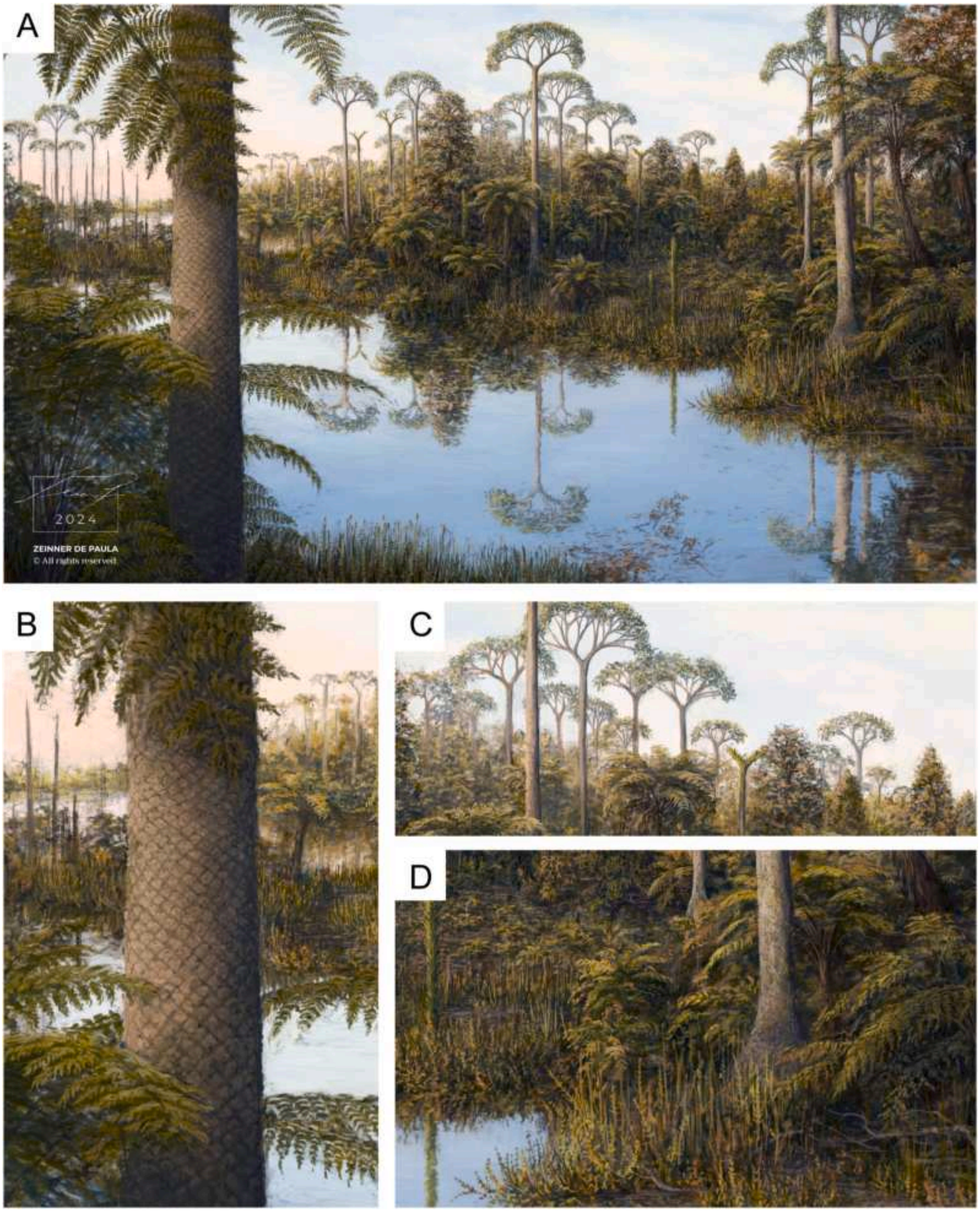

Fig. 9. A) Paleoenvironmental reconstruction of the Cerro Chato outcrop. B) Morphological details of the stem of Lycopsida, represented by *Lycopodiopsis derbyi*. C) Morphological details of the apex of arborescent lycopsids. D) Morphological details of the basal bulbs of arborescent lycopsids and undergrowth composed of Filicopsida and Sphenopsida. Artwork by: Zeinner de Paula.

representatives of the Lycopsida group, during a temporal interval that would culminate in the Guadalupian climatic crisis.

This taphoflora not only represents an important record that expands the paleofloral database of Gondwana during the Guadalupian but also demonstrates that the aridification conditions were not uniformly severe across all environments. On the contrary, the evidence suggests that small biodiversity hotspots, or even a forested humid latitudinal belt was present in Southern Gondwana, serving as a sanctuary for the flora in the lead-up to major climatic crises. The taphonomic and paleoenvironmental analysis of the Cerro Chato outcrop provides clear evidence that the plant groups recorded at the site occupied humid environments, being also adapted to drier conditions, as witnessed by representatives of these groups that are found in outcrops indicative of more arid settings within the Paraná Basin (e.g., Holz et al., 2010; De Carvalho et al., 2022). The adaptive plasticity of these groups reflects the significant climatic and environmental changes that occurred during the Late Permian, contributing to a deeper understanding of the ecological dynamics of the time. The presence of fish scales and bivalve shells reinforces the idea of permanent water bodies, further highlighting the uniqueness of Cerro Chato as a site of complex deposition and rich fossil content. The data presented here suggests that the landscape during the deposition of the Cerro Chato outcrop at the Guadalupian was composed dominantly of subarborescent lycopsids and understory ferns, pteridosperms, and horsetails, surrounding a coastal lacustrine system.

In summary, the exceptional nature of the Cerro Chato outcrop not only enriches our knowledge of the Permian plant biodiversity but also serves as a reference for future paleobotanical and paleoclimatic investigations in the site, highlighting the importance of conserving and studying this rare paleontological heritage.

CRediT authorship contribution statement

Joseane Salau Ferraz: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Joseline Manfroi:** Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Arielli Fabrício Machado:** Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Data curation. **William Vieira Gobo:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Margot Guerra-Sommer:** Writing – review & editing, Writing – original draft, Validation, Investigation, Conceptualization. **Felipe L. Pinheiro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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