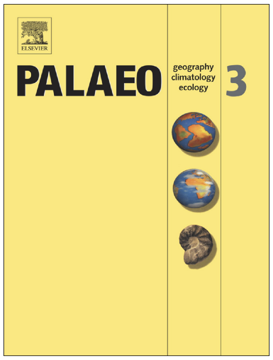

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An early Permian Euramerican plant assemblage in northwestern Gondwana: the plant-arthropod interactions of the Costela Mine locality, northeastern Brazil.

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ABSTRACT

The Costela Mine locality (CM), situated in southern Maranhão State, Brazil, exposes deposits of the Pedra de Fogo Formation (Parnaíba Basin) that preserve an early Permian plant assemblage of notable phytogeographic importance. The assemblage is dominated by callipterid peltasperms, represented by *Rhachiphyllum*, *Auritifolia*-like foliage, and *Autunia*-like reproductive structures. From 525 plant specimens examined, 27 specimens show evidence of plant-arthropod interactions and plant disease. These interactions encompass eight functional feeding groups (FFGs) attributed to arthropod herbivory and one FFG representing plant disease, with a total of 15 distinct damage types (DTs). Among these, *Rhachiphyllum* sp. hosted the highest frequency and diversity of interactions. For the plant assemblage, the FFG spectrum includes hole feeding, margin feeding, skeletonization, oviposition, piercing and sucking, galling and borings, together with pathogen-induced damage. Such diversity of FFGs suggests an advanced stage of plant–herbivore associations, compared to earlier stages, in the early Permian tropics of Gondwana. Non-metric multidimensional scaling (NMDS) analysis indicate that the CM assemblage is most closely related to the Sanzenbacher Ranch assemblage of Texas, USA, revealing a strong paleoecological tie with Euramerican plant assemblages. In contrast, contemporaneous southwestern Gondwanan floras were dominated by glossopterids that hosted a markedly different FFG spectrum. These findings demonstrate CM represents a key site for understanding the biogeographic links between northwestern Gondwana and southwestern Euramerica, extending the boundary between the Euramerican and Gondwanan Realms southward to present-day central Brazil. This region, corresponding to northwestern Gondwana, currently represents the southernmost and most inland record of the callipterids known from this continent.

Keywords: Callipterid peltasperm; Damage Types; Euramerica; Functional Feeding Groups; Gondwana; Herbivory

1. Introduction

The plant composition and biogeographic patterns of Gondwana during the Permian reveal a complex interplay among regional floras, with distinctive plant assemblages reflecting varying climatic and geographic conditions (Rees et al., 2002). For instance, the south-central parts of Gondwana were characterized by the dominance of the *Glossopteris* Flora as a phytogeographical hallmark of this region (Brongniart, 1828; Archangelsky, 1986; Cúneo et al., 1993; Anderson et al., 1999; Iannuzzi, 2010; Saxena et al., 2018; Guerra-Sommer et al., 2024). However, other areas in Gondwana present a markedly different phytogeographical scenario. Notably, the northwestern part of Gondwana, including basins in northern and northwestern South America, and northern Africa, hosted plants from the Euramerican Realm. These plants are represented by medullosans (fronds of *Odontopteris* Brongniart), the gigantopterid *Delnortea* Mamay, Miller, Rohr et Stein, callipterid fronds designated as *Rhachiphyllum* (Doubinger and Roy-Dias, 1985; Ricardi-Branco, 2008; Iannuzzi et al., 2018; Mazouar et al., 2024), the filicalean fern *Grammatopteris* Renault (Rößler and Galtier 2002), calamitalean wood (Neregato et al., 2017), gymnosperm wood assigned to *Cordaixylon* Grand'Eury and *Europoxylon* Vogellehner (Conceição et al., 2020a, 2022), along with the absence of *Glossopteris* Brongniart (Dolianiti, 1972). The distribution of these plants suggests a linkage between the southwestern Euramerican and northwestern Gondwana floral realms (Rees et al., 2002). To conceptualize these occurrences, some authors have proposed a new paleophytogeographic unit, the Mid-North Brazilian Region, buttressed by the presence of calamitaleans and gymnosperms that were endemic to the Parnaíba Basin situated largely within Maranhão state of Brazil (Neregato et al., 2017). Nevertheless, this hypothesis of a new floristic province should be re-examined in the near future based on new data from advances in taxonomic studies of Permian plants from this and the broader region of Central and South America. Recent fossil discoveries and advances in taxonomy have revealed an increasing number of taxa shared with the Euramerican Realm (Conceição et al., 2020a, 2022, and ongoing studies).

Based on this understanding of floristic distribution, studies have also highlighted records of Permian plant-arthropod and pathogen interactions across Gondwana. These interactions are documented in basins such as the Lambert Graben in Antarctica (Slater et al., 2012), the Paganzo Basin in Argentina (Cariglino and Gutiérrez, 2011; Cariglino, 2018; Fernández and Chiesa, 2020), the Lafonia Basin in the Falkland Islands (McLoughlin et al., 2024), the Sydney and Bowen Basins in Australia (Beattie, 2007; McLoughlin, 2011), the Paraná Basin in Brazil (Adami-Rodrigues et al., 2004a, 2004b; Pinheiro et al., 2024), the Damodar Basin in India (Srivastava, 1988, 1996; Srivastava and Agnihotri, 2011), and the Karoo Basin in South Africa (Prevec et al., 2009; McLoughlin et al., 2021). These interactions from these basins occur primarily on foliage, seeds, and woods (McLoughlin et al., 2021). In Brazil, records of these interactions have been published by Adami-Rodrigues et al. (2004a, 2004b), Pinheiro et al. (2012a, 2012b, 2015), and Dos Santos et al. (2020), among others. However, all previous studies have focused on plant assemblages of the Paraná Basin in southern Brazil, leaving northern basins poorly known for Permian plant assemblages and their biotic interactions.

Previous analyses of specimens from the Parnaíba Basin have highlighted the potential for understanding paleoecology of plants and their arthropod and pathogen interactions on fossil leaves, woods, and seeds (Dos Santos et al., 2024a). Based on this framework, the present study aims to document a plant assemblage recovered from the lowermost part of the Pedra de Fogo Formation, situated in the northwestern region of Gondwana, and provide the first record of Permian plant-arthropod and pathogen interactions from the Parnaíba Basin. These findings aim to enhance our understanding of the paleoecology of this region during the early Permian. Given this context, we have examined the plant composition, recorded the functional feeding groups and damage types to assess herbivory patterns, and compared the diversity and intensity of interactions in this locality with other latest Pennsylvanian to Cisuralian plant assemblages.

2. Geological Setting

The samples analyzed in this study were collected from an outcrop of the Pedra de Fogo Formation, one of the richest fossiliferous units from the Parnaíba Basin (Santos and Carvalho, 2004), situated in northeastern Brazil (Fig. 1). This basin is an intracratonic crustal sag structure covering approximately 600,000 km² in northwestern to central Gondwana, with a stratigraphic record spanning the Silurian to Cretaceous (Góes and Feijó, 1994; Santos and Carvalho, 2004; Vaz et al., 2007).

The Pedra de Fogo Formation is exposed extensively across the central part of the Parnaíba Basin. It overlies Middle Pennsylvanian deposits of the Piauí Formation and is overlain by Permian strata of the Motuca Formation (Plummer, 1948; Abrantes et al., 2019). This formation belongs to the Balsas Group, a sedimentary succession marking the terrestrialization of the Parnaíba Basin, which was deposited between the upper Carboniferous (Pennsylvanian) and Lower Triassic, based on the work of Vaz et al. (2007). The Pedra de Fogo Formation is characterized by cyclic sedimentation with diverse lithologies, including carbonates, claystones, shales, silicified sandstones, evaporites, and significant chert beds. No volcanic ash has been identified in the Permian units, including the Pedra de Fogo and Motuca formations, of this basin. The cherts and fossil-related diagenetic silicification are interpreted as resulting from continental chemical weathering combined with sedimentological processes (Matysová et al., 2010; Andrade and Nogueira, in press). Additionally, the basin features stromatolitic, oolitic, and pisolitic structures (Plummer, 1948; Vaz et al., 2007). Góes and Feijó (1994) mentioned that the deposition of this formation began in a shallow marine to paralic system characterized by broad mudflats and coastal plains. The basin later transitioned into an extensive lacustrine system with inland areas composed of sabkhas and aeolian dunes (Andrade et al., 2014; Conceição et al., 2016). Nevertheless, the precise age of the Pedra de Fogo Formation remains a topic of debate. Biostratigraphic studies based on fossil botanical and vertebrate evidence have considered this deposit as Cisuralian in age (Cisneros et al., 2015, 2020; Iannuzzi et al., 2018). Recent palynological results obtained from samples throughout the formation also indicate ages constrained to the Cisuralian (early Permian) (Oliveira, 2024).

Widely distributed across the states of Piauí, Maranhão, and Tocantins, the outcrops of the Pedra de Fogo Formation preserve a rich paleontological record. This record includes macrofossils of aquatic vertebrates, such as fish and amphibians, along with uncommon terrestrial, reptilian-grade vertebrates (Cisneros et al., 2015, 2020; Figueroa and Gallo, 2017; Richter et al., 2022). The formation has also yielded exceptionally well-preserved fossil plant assemblages that include marattialean tree-ferns, arborescent calamitaleans, and gymnosperms, such as basal pinopsids (including cordaitaleans and early conifers), cycadaleans, and seed ferns, which are commonly preserved as permineralized stems (Iannuzzi et al., 2018; Conceição et al., 2020b; Kurzawe et al., 2024). Although the Pedra de Fogo Formation is best known for its petrified forests (Conceição et al., 2016), rare outcrops of this unit also contain impression-compression plant fossils (Iannuzzi et al., 2018). Among the latter, one of the most significant localities, namely the Costela Mine, has yielded material that is the subject of this contribution and is described below (Fig. 2).

2.1. The Costela Mine Plant Assemblage

The Costela Mine is situated at the Costela locality, near the margins of the artificial lake formed by the Boa Esperança Dam, in the municipality of Nova Iorque, approximately 550 km southeast of São Luís, capital of the state of Maranhão (Fig. 1). The Costela Mine is an open pit limestone-bearing mine exposing layers containing plant fossils reported by Iannuzzi and Langer (2014). The documented plants include callipterid foliage associated with tree-fern (pecopterid) fronds, leaflet whorls of *Sphenophyllum* Brongniart, seeds, and a larger number of small stems. However, those authors did not describe or illustrate the outcrop stratigraphically. The following geological profile with descriptions represents the exposed section of the limestone quarry and is published here for the first time.

The analyzed section of the Costela Mine (Fig. 2) is approximately 6.5 m thick, and is composed of a basal 20 cm of brown and massive claystone rich in plant remains that are examined in this contribution (Fig 2.). This bed is overlain by a 70-

cm-thick, massive, and yellowish dolomitic limestone that includes centimeter-scale calcite crystals indicating a recrystallization process (Fig. 2). This limestone is the lithology/unit that is exploited economically. The succeeding 1.8-m-thick sandstone containing planar laminations is, in turn, overlain by a thin layer of massive brownish claystone (Fig. 2). This bed is succeeded by a massive bed of 5-cm-thick fine-grained sandstone that is in turn overlain by a relatively thick package of pelitic strata about 2.7 m thick, consisting of a massive dark brown mudstone (Fig. 2) that grades into dispersed, very thin lenses of siltstone to fine-grained sandstone at the top, forming incipient lenticular bedding. Towards the top of the section, the uppermost 1.2 m are characterized by mudstone facies interdigitating with two beds of fine-grained sandstone, one 45 cm thick and the other 15 cm thick (Fig. 2). These sandstone beds contain ripple cross lamination, wavy laminations, some of which are truncated, and mud drapes that form flaser bedding (Fig. 2). This mudstone–sandstone association constitutes an interval of heterolithic bedding. Above, there are fragmented, transported and loose permineralized stems occurring as float that are randomly scattered on the ground. Among the identifiable stems, those attributable to the marattialean tree-fern genus *Psaronius* Cotta are predominant. This float corresponds to an association whose rock matrix has been locally eroded and consequently the permineralized axes are found in an *ex situ* condition.

The presence of plant remains, heterolithic bedding containing sedimentary structures, such as wavy lamination, truncated wavy lamination, lenticular and flaser bedding, suggests that the deposit was generated in a marginal setting of a lentic aquatic environment. Unfortunately, it was not possible to recover microfossils, particularly palynomorphs, from the stratigraphic section that could attest to the nature of the aqueous environment, i.e., whether it was lagoonal or lacustrine.

Based on geological maps (http://geosgb.cprm.gov.br) of the area, the Costela Mine exposes rocks of the Pedra de Fogo Formation. Indeed, the basal portion of the unit is rich in confined deposits of exploitable dolomitic limestones and permineralized stems. These beds are exposed over an extensive area, ranging from the south of Maranhão State to the center of Tocantins State (Faria Jr. and Truckenbrodt, 1980), confirming the position of our studied section near the base of the Pedra de Fogo Formation.

3. Material and methods

3.1. Collections and specimens

Specimens from two collections were analyzed. The first collection belongs to the University of São Paulo (USP), Ribeirão Preto campus. The material is housed in the Laboratório de Paleontologia de Ribeirão Preto collection, under prefix LPRP/USP. The second collection belongs to the Museum of Archaeology and Paleontology (MAP) at the Federal University of Piauí (UFPI), under the prefix MAP-PAB.

3.2. Macrofossil Data Collection

One hundred and fifty-three hand slabs (52 from UFPI and 101 from LPRP/USP) were evaluated taxonomically by using a hand lens, a steromicroscope where needed, and macrophotography. These slabs represent 525 plant specimens that were examined. Photos were taken using a Canon EOS Rebel T3 equipped with Canon EF-S 60 mm and a Sigma EF-S 100 mm macro lenses. The paleoecological analysis was based on a quantitative evaluation of the Costela Mine plant remains, using the ‘quadrat’ method of Pfefferkorn et al. (1975), which is appropriate for obtaining data from fossil collections. Originally for this method, each hand-sized rock sample was treated as a 'quadrat' in which every preserved fossil/taxon is counted just once, and their abundance is recorded as the number of 'quadrats' in which they occur. Here, we applied the slightly modified methodology of Bashforth et al. (2016), in which each slab face is treated as a 'quadrat' and a fossil/taxon is recorded as 'present' regardless of the number of specimens on the face. We further used a variation of this method, establishing a 'quadrat' size of 10×10 cm. Most of the rock samples encompass a single 'quadrat', whereas a few larger specimens included two quadrats, providing a more reliable estimate of abundance and biomass.

3.3. Sampling Coverage

Specimens were analyzed using a stereomicroscope to verify the presence or absence of herbivory damage and to classify these traces into functional feeding groups (FFGs) and damage types (DTs) (Labandeira et al., 2007; unpublished updates). The first category, the FFG, is based largely on the classification of the type of mouthparts that arthropods use to feed on a plant or the use of an ovipositor for insertion of eggs into a plant substrate. FFGs are classified into five groups: ectophytic (hole feeding, margin feeding, skeletonization, and surface feeding); stylophytic (oviposition, and piercing and sucking); endophytic (mining, galling, seed predation, and borings); plant disease (pathogens); and domatia (Labandeira and Wappler, 2023). The category subsumed under a FFG is the damage type, or DT, which is a style of herbivore damage that occurs in time and space and is recognized by defining features, such as the position on a plant, the size, shape, and fine structural details that includes avoidance of vascular elements, frass trails, tumor-like features, and necrotic tissue. These features are based on the *Guide to Insect (and*

Other) Damage Types on Compressed Plant Fossils (Labandeira et al., 2007) and addenda in subsequent publications.

Four metrics were used to assess arthropod and pathogen herbivory on plants, including DT richness, DT frequency (Schachat et al., 2018, 2020), feeding event occurrences (Xiao et al., 2022a, 2022b), and herbivorized surface area (Beck and Labandeira, 1998). Damage type richness is a metric used to evaluate the diversity of DTs within a plant assemblage and has been employed in other Paleozoic studies (Labandeira and Allen, 2007; Schachat et al., 2014, 2015; Xu et al. 2018; Maccracken and Labandeira, 2020; Dos Santos et al. 2024b). Damage type frequency is used to verify how many cases of the DT were present in a plant assemblage or on a particular plant taxon (Labandeira and Allen, 2007). Feeding event occurrence is a metric for assessing how many examples of a DT are recorded on a plant organ, a plant taxon, or a plant assemblage, providing the finest-grained measure of herbivory intensity and distribution (Xiao et al., 2022a, 2022b, 2022c). The last metric, herbivorized surface area, is used to evaluate the extensiveness of herbivory in plants by measuring the amount of foliar surface area removed during feeding (in cm^2). This metric can show the preference for particular areas of foliage removed by a plant or for specific plants herbivorized within a plant assemblage. Calculation of this metric uses the total surface area (TSA) of the plant and its total herbivorized surface area (THSA) (Beck and Labandeira, 1998; Xu et al., 2018; Dos Santos et al., 2024b). Both types of data were collected using the software *ImageJ* 1.53t (Image processing and analysis in Java (Wayne Rasband and contributors, National Institutes of Health, USA). The data collected for the TSA and THSA is used to establish the herbivory index (HI) for the entire plant assemblage and for each plant taxon.

We ran a non-metric multidimensional scaling (NMDS) ordination analysis in R software (R Development Core Team, 2013) using the package vegan (Oksanen et al., 2013). This ordination method was used to understand the relationship between functional feeding groups and their plant host taxa from different Pennsylvanian–Asselian plant localities in Euramerica and Gondwana (Schachat et al., 2015; Xu et al., 2018; MacCracken and Labandeira, 2020; Dos Santos et al., 2024b).

To provide a standardized comparison of insect damage type (DT) diversity between the Sanzenbacher Ranch and Costela Mine assemblages, we performed sample-based rarefaction analyses (Supplementary Data). These analyses were conducted in the software R using the vegan package. Comparisons were made at multiple levels: between the entire assemblages of each locality, and between specific, dominant plant hosts. For the primarily dominant host analyses, we compared *Autunia conferta* from Sanzenbacher Ranch against *Rhachiphyllum* sp. from Costela Mine, and we also plotted this for *Rhachiphyllum schenkii* (SR) and *Rhachiphyllum* sp. (CM). For each comparison, a presence/absence matrix was constructed from the raw data, with individual specimens as rows and the observed DTs as columns. Rarefaction curves were then computed using the *specaccum* function with the "random" method, which generates a smoothed curve by averaging 100 random permutations of specimen accumulation. For comparing herbivory in the fossil record, we generated two distinct sets of rarefaction curves for each of these comparisons to ensure robust conclusions (Schachat et al., 2018). Rarefaction curves were standardized against two metrics: the number of specimens and the cumulative leaf surface area (cm^2), the latter correcting for biases in specimen size and fragmentation. All curves were plotted with 95% confidence intervals.

4. Results

4.1. Plant Assemblage Composition

The plant remains from the Costela Mine are preserved as impressions, although many specimens have an iron oxide coating, which is, usually only partially removed. The taphonomical signature of Costela Mine plant assemblage is reminiscent of the Colwell Creek Pond assemblage of north-central Texas (Schachat et al., 2014). Because of this, the state of preservation commonly prevents clear observation of leaflet venation, which can be obliterated or degraded, especially for callipterid fronds. Furthermore, most fossil plant specimens are in a fragmentary state, particularly those of pecopterid ferns and sphenophylls. Consequently, the taxonomic identifications were generally restricted to the generic level, sufficient for the study proposed herein that focused on the arthropod and pathogen interactions with the plant groups. A more in-depth study involving taxonomic classification of the plant specimens to species level will be presented in a subsequent contribution.

The plant assemblage recovered from the Costela Mine is depauperate, with identified plant groups limited to three primary taxa: sphenopsids, ferns, and peltasperms. Sphenopsids are represented only by sphenophylls. Among these, specimens attributable to *Sphenophyllum* are less common, usually consisting of isolated triangular leaflets, except for one specimen in which the leaflets form whorls that are still attached to nodes that join two continuous articulated stem segments (Taylor et al., 2009) (Fig. 3A). Some leaflets have a clearly dissected apical margin that forms a fringe with long teeth resembling specimens assigned to *Sphenophyllum thonii* von Mahr (DiMichele et al., 2018). However, the presence of more than one *Sphenophyllum* species needs to be verified. Additionally, small, smooth, relatively long, and quite narrow aerial stems that expand at their ends (clearly representing internodes of an articulated branching system) are attributable to sphenophylls and are frequently found in isolation. These remains are designated here as sphenophyll stems (Table 1).

Fossil fern fronds are as common as leaves of sphenopsids and are all attributable to *Pecopteris* (Brongniart) Sternberg, due to their regularly positioned, finger-shaped pinnules, each which consists of a central main vein that originates from the base and continues rectilinearly to the pinnule apex, and from which secondary lateral veins emerge alternately and usually bifurcate once or twice (Cleal, 2015) (Fig. 3B). Typically, only the ultimate pinnae are found, whereas bipinnate fronds are rare. These *Pecopteris*-type pinnules that are borne on fronds are normally referred to marattialean ferns (Taylor et al., 2009). However, it seems that there are two distinct species of “*Pecopteris*” among the specimens examined, one with shorter pinnules, thick laminae, and more robust major veins, and the other with larger pinnules, thinner laminae, and more delicate major veins. Future study of this material may confirm this hypothesis. A few fertile fronds bear poorly preserved, circular synangia and have been attributed to *Asterotheca* Presl (Fig. 3C), a fossil genus typically linked worldwide to Paleozoic marattialean ferns (Taylor et al., 2009; Cleal, 2015). Lastly, Cleal (2015) recommended abandoning the name *Pecopteris* for sterile foliage in favor of adopting the nomenclature applied to fertile foliage. However, for the present study, it is not possible to link most of the fragmentary sterile specimens analyzed here confidently to poorly preserved synangia-bearing fronds. Consequently, we have chosen to refer to the sterile specimens as pecopterid fronds and the fertile ones as *Asterotheca* sp. (Table 1).

The Costela Mine plant assemblage is dominated by callipterid fronds. The fronds (compound leaves) are relatively complete, with the rachises, pinnae and pinnules remaining attached to each other, unlike the condition of the pecopterid fronds. The callipterid fronds are incomplete, with preserved lengths averaging 8.54 cm (n = 10) and widths averaging 5.92 cm (n = 10) (Fig. 3D). The pinnules are oblong to elliptical, with entire margins, decurrent, and inserted obliquely on the rachis, slightly contracted at the base, and becoming slightly lobed to pinnatifid apically. The venation is not well preserved, and only a few pinnules are partially visible. From what can be observed, there is not a strong or sunken main vein in the pinnule lamina; all veins are of the same rank. More than one vein emerges decurrently at the base of the pinnule and continues rectilinearly toward the most distal margin of the lamina, dividing two or more times along their lengths (Fig. 3E). Intercalary pinnules resemble the other pinnules, except are of smaller size and in some cases shortened (Fig. 3D). Considering the morphological features described herein, these fronds can be attributed to *Rhachiphyllum* Kerp (Kerp, 1988; Kerp and Haubold, 1988). Due to their extreme rectilinearity of the veins running along the pinnule blades, it is possible that the form studied here constitutes a new species, very similar to *Rhachiphyllum schenkii* (Heyer) Kerp, 1988, a very common taxon in assemblages from Euramerica (Kerp, 1988; DiMichele et al., 2018, 2019). At present, these fronds will be assigned simply to *Rhachiphyllum* sp. (Table 1).

A few very fragmentary fronds have a continuous leaf lamina along the ultimate rachises (Fig. 3F) and are tentatively assigned to *Auritifolia* Chaney, Mamay, DiMichele & Kerp, according to the criteria applied by DiMichele et al. (2018) to distinguish between *Supaia* White and *Auritifolia*. Due to the poor preservation of the veins, which makes it difficult to verify the fasciculate venation pattern of the pinnules, the specimens studied here are attributed with caution to *Auritifolia*-like foliage (Table 1).

Rare fragmentary specimens comprising isolated portions of reproductive organs are assigned to Peltaspermales. These specimens have morphological features of polleniferous and ovuliferous organs that resemble those associated with *Autunia* Krasser emend. Kerp (Kerp, 1988; Kerp and Haubold, 1988). One of the more complete specimens resembles a centimeter-size, flabelliform megasporophyll with robust ribs radiating from the central area, where it should be connected to an axis (petiole). This structure is closely associated with one or two ovules, with an overlap between these elements (Fig. 3G). This structure is interpreted as a fragmented megasporophyll belonging to an ovuliferous organ of *Autunia*, as established by Kerp (1988). Another relatively complete specimen consists of a small, cup-shaped structure bearing laterally elongate, rod-shaped bodies fused at their bases and extending to the distal margin, where they are held together by a membrane along their length (Fig. 3H). This structure is interpreted as a polleniferous organ, in which each elongate body corresponds to a sporangium. Such structures being typically are associated with species of *Autunia*. Given the fragmentary state and scarcity of these structures (both female and male) and the goal of the present contribution, we have chosen to refer to them simply as *Autunia*-like reproductive structures (Table 1).

Small platyspermic seeds (ovules) are scattered sparsely among the callipterid foliage (Fig.3I). These seeds are elliptical to ovate with a central body (nucellus) and an outer layer (testa). The nucellus is finely striated and elliptical to elongate–elliptical. The testa is undifferentiated and comprises the outer layer considered herein as the sarcotesta. This sarcotesta is finely striated, relatively wide and becomes wider along the median-to-basal portions of the seed (Fig 3I). These seeds have a testa width/nucellus width ratio greater than or equal to 0.22 (ranging from 0.4 to 0.55), and are, therefore, assigned to *Samaropsis*, according to the criteria established by Oliveira and Pontes (1976). Future taxonomic studies may clarify whether these seeds correspond to a single fossil species. The seeds are similar in size and morphology to those recorded in close association with callipterid leaves in other plant assemblages from Euramerica (Kerp, 1988; DiMichele et al., 2018, 2019). Due to the absence of other types of seed plants in the plant assemblage, these seeds are tentatively attributed to callipterids that are preserved in the same deposit. For the purposes of our analyses, they will be referred to as *Samaropsis*-like seeds.

Lastly, woody stems preserved as impressions/compressions and iron oxide replacements are common in the Costela Mine plant assemblage (Fig. 3J). Because such stems could only have been produced by seed plants, they are tentatively associated with callipterid fronds. Nevertheless, for the purposes of this study, these stems are designated simply as wood impressions/compressions (Table 1).

4.2. Quantitative Analysis of the Plant Assemblage

The Costela Mine plant assemblage is of low diversity (Table 1). The assemblage includes callipterid peltasperm foliage and reproductive structures, putative marattialean ferns, sphenopsids, platyspermic seeds, and wood impressions/compressions. The quantitative data collected using the quadrat counting method shows the callipterid peltasperm *Rhachiphyllum* sp. to be the most abundant identifiable taxon (Table 1). This genus occurs at a frequency of 51% (n=181). The second peltasperm present in this assemblage was *Auritifolia*-like foliage with a frequency of 1.4%, with only five specimens (Table 1). Fern foliage was represented by sterile fronds bearing *Pecopteris*-like pinnules and fertile foliage included in *Asterotheca* sp., both constituting 5.6% of the specimens (Table 1). In addition, sphenopsid remains, i.e., whorls bearing *Sphenophyllum*-like leaflets or isolated leaflets, occur at a frequency of 5.5%, represented by 16 specimens. Stems associated with sphenophylls occur in greater numbers (n=43), reaching a frequency of 12% (Table 1). *Samaropsis*-like platyspermic seeds were also noticeable, with a frequency of 4.2% (Table 1). Peltasperm reproductive structures (ovuliferous and polleniferous organs), referred to *Autunia*-like reproductive structures, are scarce at a frequency of 1.1% (Table 1). A large number of wood impressions/compressions were observed (n=71), but these were not identified owing to the lack of anatomical detail and the absence of attached leaves or other organs; they occur at a frequency of 20% (Table 1).

4.3. Composition of Arthropod and Plant Disease Interactions

We emphasize that the methods proposed to account for interactions (see section 3.3 above) are distinct from those used to account for the frequency of plant remains (see item 3.2 above). Therefore, the results obtained for the frequencies of taxa and plant organs are numerically distinct (see Tables 1 and 2). However, these results regarding the dominance ranking of plant taxa and organs from both counting methods maintain a proportionality between them, as will be seen below. (Compare Tables 1 and 2).

The data collected for arthropod and pathogen damage also shows the callipterid peltasperm *Rhachiphyllum* sp. to be the most abundant, identifiable taxon in the plant assemblage (Table 2). This genus represented 32% of the total plant assemblage (168 specimens). The second most abundant foliage taxon in the CM assemblage with only five specimens (0.95%) was the peltasperm, *Auritifolia*-like foliage (Table 2). Fern sterile foliage was represented by pecopterid fronds and the fertile *Asterotheca* foliage; both totaled 3.81%. The 15 leaflet whorls or isolated leaflets of

Sphenophyllum sp. represented 2.86% of the total plant assemblage. Platyspermic seeds and other *Autunia*-like reproductive structures, were also comparatively common. A relatively high number of wood impressions/compressions also was observed.

4.4. Composition of the Herbivory at the Costela Mine Plant Assemblage

Among the 525 plant specimens from the Costela Mine (CM) plant assemblage, our search showed that only 27 specimens hosted arthropod herbivory or plant disease damage (Table 2). Herbivory was observed in 22 *Rhachiphyllum* sp. fronds (81.48% of the total), four wood impressions/compressions (14.81% of the total) and one *Sphenophyllum* sp. leaflet (3.7% of the total). Damage types (DTs) were documented from the FFGs of hole feeding, margin feeding, skeletonization, surface feeding, oviposition, piercing and sucking, galling, borings and plant disease (Table 3). The CM plant assemblage hosted a richness of 15 DTs, a frequency of 32 DTs (Table 3), and 72 feeding event occurrences. The total surface area of plants from the CM plant assemblage was 4956.03 cm^2, with *Rhachiphyllum* sp. representing the taxon with the greatest measured area. Only one side of each specimen – the impression without its counterpart – was measured, resulting in a total area of 3369.03 cm^2 for Rhachiphyllum sp. The total herbivorized surface area recorded was 2.16 cm^2. This amounts to a low herbivory index of 0.044%.

Rarefaction analyses (Supplementary Data Figure 1) indicate that damage type (DT) diversity at Costela Mine (CM) and Sanzenbacher Ranch (SR) did not reach stabilization when standardized by either the number of specimens or the total sampled surface area (Supplementary Data Figure 1A, B). The rarefaction analysis based on specimen count shows the lowest sampling completeness, suggesting that additional material could reveal higher DT diversity. Although sampling at CM does not indicate sufficiency, the number of DTs is much lower, and the curves show a tendency toward stabilization at lower values, suggesting that this plant assemblage was approaching (asymptotic) stability with fewer damage types. When comparing the most herbivorized taxa, *Rhachiphyllum* sp. from CM and *Autunia conferta* from SR, DT diversity curves standardized by leaf area reveal that *A. conferta* has a lower richness trajectory than *Rhachiphyllum* sp., indicating that herbivory on *Rhachiphyllum* sp. was closer to stabilization in terms of DT diversity compared to *A. conferta* in SR (Supplementary Data Figure 1C, D).

4.4.1. Hole Feeding

Plant hosts: *Rhachiphyllum* sp. (Fig. 4A–E)

Damage types present: DT03, in MAP-PAB 072.4a and LPRP/USP 0110a.

Production: Arthropods with mandibulate mouthparts that damage plants by making incisions in the leaf lamina interior, creating rounded, irregular, and polylobate holes.

Occurrence: In this study, hole feeding consisted of one DT, representing 6.67% of the total DT richness (Table 3). Two specimens hosted damage, and the frequency recorded was two instances (6.25%), making it the fourth FFG in frequency rank. Thirteen feeding event occurrences (FEO) were recorded (18.06%), the second highest number after piercing and sucking (Table 3). The herbivorized area measured was 0.151 cm^2 (7.0%), placing it in fifth position among the FFGs represented (Table 3).

This FFG was found in two specimens of *Rhachiphyllum* sp. (Table 4). These circular holes were observed near the margin and at the center of the leaves (pinnules). One specimen hosted 11 feeding event occurrences (FEOs)

(MAPPAB072.4a), and the second specimen had two such occurrences (LPRP/USP 0110a). Reaction tissue surrounded the damaged areas (Fig. 4A–E).

4.4.2. Margin Feeding

Plant hosts: *Rhachiphyllum* sp. (Fig. 4F–I)

Damage types present: DT012, in MAP-PAB 184b, LPRP/USP 0061Da and LPRP/USP 0127b; DT013, in LPRP/USP 0084Dc, LPRP/USP 0091, LPRP/USP 0085b, LPRP/USP 0142b and LPRP/USP 137a; DT014, in LPRP/USP 0087b.

Production: The continuous removal of the leaf blade along the margin is caused by arthropods with mandibulate mouthparts that chew a cuspate excision from the edge of a foliage component.

Occurrence: Margin feeding was the FFG with the highest DT richness with three DTs representing 20.00% of the total. Nine occurrences represented a DT frequency of 28.13%. The 12 occurrences of this FEO ranked it third highest for this DT metric, and the herbivorized surface area was 0.77 cm^2, or 35.77% of the total (Table 3).

Nine specimens of *Rhachiphyllum* sp. had at least one occurrence of herbivory, represented by DT012 (three occurrences), DT013 (five), and DT014 (one). Reaction tissue surrounded the incisions (Fig. 4F–I, M).

4.4.3. Skeletonization

Plant hosts: *Rhachiphyllum* sp. (Fig. 4J–L)

Damage type present: DT016, in MAP-PAB 200Bb.

Production: Arthropods that cause skeletonization consume tissues of the entire leaf blade, leaving the primary, secondary, and occasionally tertiary veins intact, forming a lattice pattern.

Occurrence: The single DT of this category found in the CM plant assemblage, represents 6.67% of the total DT frequency and was represented by two FEOs (Table 3). Skeletonization was second among FFG, with the highest herbivorized surface area, representing 14.37% of the total.

One specimen of *Rhachiphyllum* sp. had two instances of consumption. These tissue removals are close to the leaf margin and represented by two areas near secondary veins (Fig. 4J, L).

4.4.4. Surface Feeding

Plant hosts: *Rhachiphyllum* sp.

Damage types present: DT103, in MAP-PAB 165a and MAP-PAB 200Ba.

Production: Surface feeders remove one or more but not all tissue layers on the abaxial or adaxial surface of a leaf, thus engaging in partial consumption of the leaf thickness. This type of herbivory leads toward delamination or abrasion of some tissue layers. Insects, in many cases possessing specialized mouthparts, such as modified mandibles, maxillae, or labia are commonly specialized for the abrasion and delamination of live plant tissue.

Occurrence: DT richness and frequency for surface feeding recorded in the CM plant assemblage is based on two damage occurrences. The scarcity of the FEOs and small herbivorized surface area (0.097% cm^2) indicates that this type of feeding was at a low level. This FFG was found in two *Rhachiphyllum* sp. specimens and represented by DT103.

4.4.5. Oviposition

Plant hosts: wood impression

Damage types present: DT072, in MAP-PAB 077c.

Production: Insects lay their eggs on plant tissues, producing exophytic oviposition, or more commonly, insert their ovipositors into plant tissues, generating endophytic oviposition that results in lesions within and on the surface of a plant’s tissue typically surrounded by prominent bordering scar.

Occurrence: DT richness, DT frequency and FEO for this herbivory category were represented by a single occurrence. The total herbivorized area is 0.13 cm^2. The wood fragment hosted oviposition DT072, an elliptical lesion on a stem.

4.4.6. Piercing and Sucking

Plant hosts: *Rhachiphyllum* sp. (Fig. 5A–C); wood impressions (Fig. 5D–F).

Damage types present: DT046, in MAP-PAB 199a; DT048, in MAP-PAB 165a and MAP-PAB 199a; and DT183, in MAP-PAB 161a.

Production: Insects with stylate mouthparts insert their stylet bundle into plant tissues to consume its fluids through piercing-and-sucking feeding. Plant fluids, such as sap contain proteins, carbohydrates, and lipids in varying amounts. In addition, piercing-and-sucking (P&S) damage can also be indicated by the presence of a scale insect carapace or its impression on the plant surface commonly leaving distinctive scars or other forms of deformation on the plant indicating access by a piercing-and-sucking insect.

Occurrence: Together with margin feeding, P&S was the FFG with the highest DT richness of three (Table 3), and DT frequency of six. The number of FEOs is 15, making it the highest in rank of this parameter. By contrast, this FFG has the lowest value overall for herbivorized area, at 0.05 cm^2, attributable to miniscule surface areas formed from stylet punctures. Six specimens hosted P&S damage. Two specimens of *Rhachiphyllum* sp. and one stem bored DT046, whereas two *Rhachiphyllum* sp. specimens featured DT048. DT183 was found in one wood sample. DT046 was the most abundant, with three occurrences; DT048 had two occurrences, and DT183 had one.

4.4.7. Galling

Plant hosts: *Rhachiphyllum* sp. (Fig. 5G, G), *Sphenophyllum* sp.

Damage types present: DT80, in MAP-PAB 074.2d, MAP-PAB 163, MAP-PAB 190a, MAP-PAB 199a, LPRP/USP 0063 and LPRP/USP 0055A; DT87, in LPRP/USP 0063; and DT247, in MAP-PAB 074.2e.

Production: Some organisms can stimulate plants to produce teratologic tissue, using it as a shelter and nutriment for their offspring. Insects and mites are the most common organisms that cause galling, but galls are also caused by nematodes and pathogens, such as viruses, bacteria and fungi.

Occurrence: Galling is the FFG with the third highest DT richness, expressed by three DTs representing 20.00% of the total. The DT frequency was eight, placing it second in the rank of frequency, and the number of FEOs was nine. The recorded herbivorized surface area was 0.30 cm². Eight specimens hosted DTs. Six specimens of *Rhachiphyllum* sp. were recorded with DT080, and one with DT087. *Sphenophyllum* sp. was the only taxon to have DT274.

4.4.8. Borings

Plant hosts: wood compressions (Fig. 5K, L)

Damage types present: DT284, in MAP-PAB 077c and LPRP/USP 0143a.

Description: Terrestrial arthropods can excavate channels, tunnels, and galleries on dead tissues, such as wood and bark, and live plant tissues including collenchyma, sclerenchyma and cambia.

Borings are caused by arthropod feeding and pupation and symbioses with fungi. The most common arthropods to cause damage on wood are mites, termites and beetles. Much of this damage can be identified by differences in boring size, shape, and trajectory, together with the presence ofdistinctive coprolites and other frass features.

Occurrence: A boring was recorded based on a single DT, with a recorded DT frequency of two. This FFG was recorded 13 times, the second highest number of occurrences together with hole feeding (Table 3). The herbivorized surface was 0.118 cm^2. Two wood compressions hosted one DT each.

4.4.9. Plant Disease

Plant hosts: *Rhachiphyllum* sp. (Fig. 5I, J).

Damage types present: DT174, in LPRP/USP 0134.

Production: Pathogens can cause plant diseases and other disorders. The major agents responsible for plant disease blotches are viruses, bacteria, oomycetes, fungi and nematodes.

Occurrence: This FFG was found in one specimen, and the DT richness and DT frequency was one. We counted four FEOs, and the herbivorized surface area was 0.24 cm^2 (Table 3). The plant disease was present in a single specimen of *Rhachiphyllum* sp. Such damage is characterized by pathogen blotches dispersed on a leaf, each measuring approximately 0.25 mm in width and 0.26 mm in length. These blotches have a central fructification.

5. Discussion

5.1. Plant assemblage composition and comparisons

It is evident that the callipterid peltasperm *Rhachiphyllum* represents the dominant taxon in the Costela Mine assemblage, with approximately 50% frequency of occurrence (Table 1). However, if the other plant remains probably related to peltasperms are considered, such as *Auritifolia*-like foliage, *Autunia*-like reproductive structures, *Samaropsis*-like seeds, and even woody stems found in close association, the dominance of this group of seed plants reaches a frequency of ca. 78% in the plant assemblage (Table 1). This indicates that this assemblage is dominated by peltasperm seed plants, with spore-producing plants, such as sphenophylls and pecopterid ferns, as secondary elements that total ca. 22% of the plant assemblage (Table 1).

The Costela Mine plant assemblage can be considered a depauperate assemblage, consisting only of three plant groups —sphenopsids, ferns, and peltasperms—represented by fewer than ten identified taxa or morphotypes (Table 1). Despite this low diversity, the assemblage contains sufficient taxa to allow comparison with other plant assemblages distributed throughout the Pennsylvanian to Cisuralian. The absence of any evidence of glossopterids and the widespread dominance of the callipterid peltasperm *Rhachiphyllum* prevents close comparisons of the Costela Mine plant assemblage with geographically adjacent (South American) Gondwanan floras (Wnuk, 1996; Cúneo, 1996; Cariglino and Gutiérrez, 2011; McLoughlin et al., 2024) or even with the "mixed floras" that contain elements from Euramerican and Cathaysian regional floras that occur marginally in the area occupied by the "*Glossopteris* Flora" (Srivastava and Agnihotri, 2010). The studied plant assemblage is clearly affiliated with the Euramerican flora where peltasperms were dominant (Fig. 6).

Several plant assemblages dominated by callipterid peltasperms occur in North America (DiMichele et al., 2013, 2018, 2019; Labandeira and Allen, 2007; Schachat et al., 2014; Purens et al., 2025) and Europe (Kerp, 1988; Opluštil et al., 2013, 2022; Šimůnek and Martínek, 2009; Galtier and Broutin, 1995; Wagner and Álvarez-Vázquez, 2010), particularly in lower Permian strata. In these plant assemblages, callipterid fronds are commonly associated with stems of *Calamites* (Kerp, 1988; Galtier and Broutin, 1995; Opluštil et al., 2013, 2022; DiMichele et al., 2018, 2019; Mazouar et al., 2024). Also common is an association with pecopterid ferns (Kerp, 1988; Opluštil et al., 2013, 2022; DiMichele et al., 2018, 2019; Purens et al., 2025) and, sporadically, with stems of Sphenophyllales (Galtier and Broutin, 1995; Opluštil et al., 2013, 2022; DiMichele et al., 2018, 2019; Purens et al., 2025). Leafy shoots of walchian conifers, cordaitaleans, and fronds of medullosan pteridosperms rose to co-dominance in younger assemblages (Kerp, 1988; Galtier and Broutin, 1995; Labandeira and Allen, 2007; Wagner and Álvarez-Vázquez, 2010; Opluštil et al., 2013, 2022; Schachat et al., 2014; DiMichele et al., 2018, 2019; Purens et al., 2025). The last of these three groups of plants, along with Calamitaceae, were not recorded in the Costela Mine plant assemblage (see Table 1). This low diversity limits comparisons with richer Euramerican plant assemblages, and is necessarily based primarily on *Rhachiphyllum*, pecopterid fronds, and Sphenophyllales.

Comparable Euramerican plant assemblages recovered from localities in the Saar-Nahe Basin in Germany can be considered most similar to those of the Costela Mine plant assemblage (Kerp, 1988). In particular, the ‘*Pecopteris* Horizon’ from the Sobernheim plant fossil assemblage, Germany, resembles the Brazilian assemblage based on the dominance of the *Rhachiphyllum schenkii* (Heyer) Kerp–*Calamites gigas* Brongniart association co-preserved with pecopterid fronds (Kerp, 1988). The absence of *Calamites* from the Costela Mine plant assemblage is notable – sphenopsids are instead represented by sphenophyllaleans. However, there is undeniably a general similarity between these two geographically distant assemblages based on the composition of the plant groups and their relative abundances.

Of those plant assemblages studied for plant-arthropod interactions, the most similar to the Costela Mine plant assemblage by plant composition are those from the Coprolite Bone Bed (CBB) (Labandeira and Allen, 2007) and Sanzenbacher Ranch (SR) (DiMichele et al., 2018). The CBB plant assemblage is dominated largely by callipterid peltasperms, followed by cordaitaleans, conifers and cycadopsids as secondary elements. Pecopterid ferns and *Annularia*-like sphenopsids constitute an insignificant fraction of total abundance of taxa (Labandeira and Allen, 2007). Callipterids are represented solely by *Autunia conferta*, which comprises over 55% of the assemblage (Labandeira and Allen, 2007). Based on the absence of *Rhachiphyllum* and sphenophyllaleans, and the low abundance of pecopterids, the CBB plant assemblage is somewhat dissimilar to that of the Costela Mine plant assemblage. At SR, callipterid peltasperms are also dominant elements, with *Autunia conferta* having an average frequency of more than 20%, whereas *Rhachiphyllum schenkii* has a frequency of 5% (DiMichele et al., 2018). Furthermore, walchian conifers, the lyginopterid pteridosperm *Sphenopteridium germanicum* (Weiss) Kerp et DiMichele (DiMichele et al., 2022*),* marattialean (pecopterid) ferns, medullosan pteridosperms, and calamitaleans are common elements in the SR plant assemblage, with average frequencies between 5% and 10% (DiMichele et al., 2018). All remaining plant groups – sphenophyllaleans, sphenopterids, cordaitaleans, noeggerathialeans and putative cycadopsids – occur at less than 5% frequency. The SR plant assemblage is markedly more diverse, comprising 38 identified taxa. Although they differ significantly in diversity, there are similarities between the SR and Costela Mine plant assemblages in sharing *Rhachiphyllum*, *Sphenophyllum*, and *Pecopteris* and in the dominance of callipterid peltasperms.

5.2. General pattern of functional feeding group and damage composition

The Costela Mine plant assemblage hosts herbivore damage attributable to eight functional feeding groups (FFGs) (Fig. 7) but lacked evidence for mining and seed predation. Mining is recorded from the earliest Permian of Germany, at the Crock locality in Thuringia (Laaß et al., 2025) and seed predation is present in other Permian assemblages from Gondwana (Pinheiro et al., 2012a; Dos Santos et al., 2020) and Euramerica (Schachat et al., 2014, 2015; Mcloughlin et al., 2022; Dos Santos et al., 2024b). The composition of FFGs at Costela Mine is similar to that of late Pennsylvanian and early Permian Euramerican plant assemblages, such as Williamson Drive (WD), Sanzenbacher Ranch (SR), and Colwell Creek Pond (CCP) (Fig. 7).

Differences are evident in FFG composition and host distribution between northwestern Gondwana and Euramerica, as compared to southwestern Gondwana (Figures 6 and 7). Plant assemblages from Euramerica and northwestern Gondwana yield a greater diversity of FFGs than those from southwestern Gondwana. This pattern likely is influenced by climatic differences. Euramerica experienced a tropical climate through the Carboniferous and Permian (Ziegler et al., 1990), which may have facilitated the establishment and diversification of a more complex array of herbivore strategies. Northwestern Gondwana, specifically the Parnaíba Basin, was subject to seasonally alternating wet and dry conditions, with climate models suggesting a tropical, warm, semi-arid environment (Iannuzzi et al., 2018). In contrast, southwestern Gondwana underwent a climatic transition from cold-wet to warm-wet temperate conditions throughout the late Carboniferous to early Permian, which influenced arthropod composition and feeding strategies. This shift is reflected in the increasing number of FFGs from the older Papaléo Mine–Faxinal plant assemblages (Asselian) to the younger Papaléo Mine L7/L8 assemblage (Sakmarian), in the Paraná Basin (Pinheiro et al., 2012a).

Hole feeding and margin feeding are the most common and diverse FFGs in late Paleozoic plant assemblages, except for Minas do Leão, where hole feeding is absent (Fig. 7). Skeletonization remains a very rare FFG in Paleozoic plant assemblages, recorded in low abundance for the few localities of Williamson Drive (WD), Coprolite Bone Bed (CBB), and Taint, all of which occur in Euramerica, and Papaléo Mine L7/L8, present in Gondwana. Several DTs previously recorded from other localities were not observed in the present study. DT17, for example, was documented at CBB and WD on host plants, such as the callipterid peltasperm *Autunia* cf. *conferta* (Stemberg) Kerp, the noeggerathialean *Russellites taeniata* Mamay, and *Lilpopia raciborskii* (Lilpop) Conert et Schaarschmidt. DT23 was reported on *Glossopteris communis* Feistmantel and *Glossopteris occidentalis* White emend. Tybusch et Iannuzzi from Papaléo Mine L7/L8. Conversely, DT16, which is present in this study, was recorded previously at WD on the medullosan *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute and Zodrow and at Taint on the gigantopterid *Gigantopteridium americanum* White. The occurrence of DT016 on *Rhachiphyllum* sp. in the Costela Mine plant assemblage extends the known host range of this damage type to include callipterid peltasperms and expands its geographical range from western Euramerica to northwestern Gondwana.

Piercing-and-sucking damage is well-documented in Euramerican Paleozoic plant assemblages, with its earliest occurrence in the Early Pennsylvanian (Knecht et al., 2024). This feeding strategy was later recorded in early Permian plant assemblages such as SR, CCP, and MCF (Mitchell Creek Flats) in Euramerica. In Gondwana, Adami-Rodrigues et al. (2004a) initially described piercing perforations on *G. communis* and *Cordaites hislopii* (Bunbury) Seward & Leslie, in the Paraná Basin of southern Brazil, but Pinheiro et al. (2014) later reinterpreted these as hole feeding (DT001). Subsequently, true piercing and sucking was identified at Bajo de Véliz, northwestern Argentina, dating to the Gzhelian–Asselian transition (Fig. 7). The present study expands the record of piercing and sucking to northwestern Gondwanan plant assemblages of Cisuralian age.

The oldest evidence for oviposition is from the Early Pennsylvanian (Knecht et al., 2024). Oviposition has a distribution pattern similar to piercing and sucking, with records from both older (WD, SR, MCF, CCP) and younger (Bajo de Véliz, Papaléo Mine L7/L8) plant assemblages. Oviposition damage has been found on a broad range of Permian glossopterid leaves (Srivastava & Agnihotri, 2011; McLoughlin, 2011; Prevec et al., 2009, 2010; Srivastava and Srivastava, 2016; Gallego et al., 2016; Cariglino, 2018; McLoughlin et al., 2021, 2024). In the Costela Mine plant assemblage, oviposition is represented by DT072, preserved on a stem fragment.

Galling was especially abundant in some Permian plant assemblages. The MCF plant assemblage yielded six galling DTs associated with cycadopsids and gigantopterids, and the SR plant assemblage had nine galling DTs on peltasperms, including *A. conferta*, *Rhachiphyllum* sp. and cf. *Lodevia* sp. The Costela Mine plant assemblage also hosts galling, sharing some DTs with SR (Table 4).

Borings are widely distributed in late Paleozoic assemblages, including WD and SR, where DT284 was documented. This same DT was identified in the Costela Mine plant assemblage on a fragment of unidentified wood. Previous studies reported small perforations in *Calamites* sp. stems and medullosans associated with DT284.

Lastly, damage from plant disease was documented in Euramerican plant assemblages from WD, SR and CCP. In particular, *R. schenkii* from SR hosted DT174, a damage type also represented in the Costela Mine plant assemblage (Table 4).

The NMDS analysis (Fig. 8) indicates that the Costela Mine plant assemblage is most closely associated with the Sanzenbacher Ranch (SR) plant assemblage. This similarity likely reflects shared patterns in the prevalence of margin feeding, piercing and sucking, and galling; these localities shared six DTs. These results suggest that similar paleoenvironmental conditions, possibly seasonally dry climates, based on the relative similarity in the composition of the two plant assemblages, with a broad dominance of callipterids over other elements (see item 5.1.), influenced the composition of functional feeding groups in these regions. The weaker association of Costela Mine with other plant assemblages, such as Williamson Drive and Mitchell Creek Flats, highlights how plant-insect interactions were possibly shaped by local environmental and floristic differences during the Cisuralian. Additionally, the Costela Mine plant assemblage is clearly distinct from southwestern Gondwanan plant fossil suites, such as from Faxinal Mine, Papaléo Mine - Faxinal, and Papaléo Mine L7/8 of southeastern Brazil, which have yielded glossopterid-dominated plant assemblages typical of the high-paleolatitude Gondwanan Realm. This difference highlights the unique floristic and ecological composition of northwestern Gondwana, where glossopterids are absent and replaced by floristic elements more typical of the Euramerican Realm.

5.3. Patterns of Herbivory across Major Plant Groups

Damage on the callipterid peltasperm *R. schenkii* has been recorded on Asselian plants from the Sanzenbacher Ranch plant assemblage (Dos Santos et al., 2024b). The authors documented the presence of the following FFGs on this taxon: hole feeding, margin feeding, surface feeding, piercing and sucking, oviposition, galling and plant disease. Our study recorded some of these FFGs; however, the presence of skeletonization notably was documented on *Rhachiphyllum* sp., which was not previously observed in Euramerican plant assemblages. By contrast, the callipterid peltasperm *A. conferta* hosted skeletonization damage in the Coprolite Bone Bed plant assemblage. The oldest records of skeletonization in Euramerican floras are associated with sphenopsids and medullosans from the Williamson Drive locality (Xu et al., 2018). This damage type, albeit rare, was also reported in greater abundance on gigantopterids from the Taint locality.

Sphenopsids were recorded in the Sanzenbacher Ranch (SR) and Williamson Drive (WD) plant assemblages, with evidence of margin feeding, surface feeding, skeletonization, oviposition, piercing and sucking, galling and plant disease damage. *Sphenophyllum* spp. from SR and *Sphenophyllum* sp. 1 from WD hosted a substantially higher diversity of DTs compared to the Costela Mine assemblage, with three and one DTs, respectively. In contrast, the only DT identified on *Sphenophyllum* sp. in the present study was the gall DT247, differing from DTs recorded on this genus from SR, namely DT034, DT121, and DT415, and from WD, DT106.

Sphenopsids comprise ca. 30% of the WD plant assemblage (Xu et al., 2018), with herbivory recorded on 183 specimens and a DT frequency of 239 occurrences. Of the sphenopsid fraction, stems (primarily *Calamites*) accounted for 85.51% of plant surface area, whereas calamitalean foliage constituted only 10.39% of this measure. *Sphenophyllum* foliage represented 3.46% of the total surface area. Similarly, in the present study, sphenopsid stems accounted for 77.88% of the total surface area, and leaves represented 22.11%, reflecting a relatively higher proportion of leaves compared to the WD plant assemblage (Xu et al., 2018), though stems were still predominant. This difference likely influenced the observed differences in damage type richness and organ representation. Consequently, this contrast underscores the importance of considering organ representation, sampling size, and taphonomic biases when comparing herbivory patterns between fossil plant assemblages.

For late Paleozoic assemblages, borings have corresponded to DT284 reported in *Calamites* sp. stems from the latest Pennsylvanian of Williamson Drive (Xu et al., 2018). The Asselian plant assemblage from Sanzenbacher Ranch also included borings DT160 and DT284 in stems of *Walchia* sp. 1, *Calamites* sp. 1, and an unidentified stem. In the present study, DT284 was identified in two specimens belonging to two unidentified wood fragments. The occurrence of DT284 in these three plant assemblages demonstrates the persistence of this damage type throughout the late Paleozoic, from the latest Pennsylvanian to the Asselian, at least in Euramerican plant assemblages.

Additionally, the Costela Mine plant assemblage shares six other DTs with SR, including margin feeding (DT012, DT013, DT014), piercing and sucking (DT046), galling (DT080), and plant disease damage (DT174). Moreover, other peltasperms from SR, such as *A. conferta* and cf. *Lodevia* sp. 1, also hosted margin feeding (DT012, DT013, DT014), piercing and sucking (DT046), and galling (DT080). Surface feeding damage (DT108) was recorded both in *A. conferta* from SR and *Rhachiphyllum* sp. from the Costela Mine assemblages.

Studies conducted in the Paraná Basin have focused primarily on analyzing Glossopteridales and Cordaitales from the early Permian (Adami-Rodrigues et al., 2004; Pinheiro et al., 2012a). The scarcity of information on other plant groups, such as sphenopsids, ferns and conifers, is likely due to the absence of comprehensive analyses encompassing entire plant assemblages. A brief report by Adami-Rodrigues et al. (2017) demonstrated the great potential for detecting the plant-arthropod interactions in other taxa from the middle Permian (Wordian) of the Paraná Basin.

5.4. Phytogeographic Significance

The callipterid peltasperms, consisting of the callipterids *sensu stricto* of *Autunia*, *Rhachiphyllum*, and *Peltaspermum* first emerged in the tropical areas of Euramerica, between east- and west-central Pangea corresponding to Central and Western Europe as opposed to the Midwestern United States during the late Carboniferous (Kerp, 1988; Pšenička et al., 2011). During the Carboniferous–Permian transition, callipterid peltasperms diversified and expanded within the tropical belt toward the west, east and south and became common and/or locally dominant elements in plant assemblages from Europe, southwestern United States, Angara, the North China block and North Africa, colonizing mainly the peri-Tethyan lowlands (Wang et al., 2013; Bashforth et al., 2021). During this interval, tropical Pangea underwent a long-term drying trend resulting in the disappearance of extensive wetlands and expansion of well-drained habitats under new seasonally dry climatic conditions (Bashforth et al., 2021; Opluštil et al., 2022). Consequently, wetland biomes colonized by free-sporing plants, including lepidodendroid and sigillarian lycopsids, were reduced significantly, possibly acting as refugia for archaic plant and animal groups, and were replaced by drought-tolerant plant biomes dominated by gymnosperms, such as callipterid peltasperms, cordaitaleans, and walchian conifers during the early Permian (Bashforth et al., 2021; Opluštil et al., 2022).

Despite the wide geographic distribution achieved by callipterid peltasperms from the early Permian onward, their occurrence in Gondwana was traditionally limited to plant assemblages found in present-day Morocco in northwestern Africa (Mazouar et al., 2024). Only more recently, Iannuzzi and Langer (2014) and Iannuzzi et al. (2018) reported the first record of callipterid peltasperms for northeastern South America, documenting *Rhachiphyllum* from the Parnaíba Basin in northeastern Brazil (the material studied here). This occurrence extends the presence of this plant group, and probably the southern limit of the tropical Euramerican flora (Wang et al., 2013; Mazour et al., 2024) to the west-central portion of Gondwana.

In Venezuela, Ricardi-Branco (2008) reported a late Carboniferous–early Permian plant assemblage containing taxa typically found in Europe and especially in the United States. Based on this data, the author claimed that this region should be included in the Euramerican Realm rather than Gondwanan Realm. Furthermore, Ricardi-Branco (2008) argued in favor of this proposition based on the absence of any typical Gondwanan elements in the Venezuelan plant assemblages, in particular glossopterids, and the positioning of this part of the South American continent at low latitudes within the equatorial-tropical belt from 0° to 15° S during the time interval in question. These same arguments also justify linking the Costela Mine plant assemblage to the Euramerican Realm, except for the fact that the Parnaíba Basin was positioned approximately at 30° S, which would correspond to the southern limit of the tropical belt during the Cisuralian (Neregato et al., 2017). For the early Permian, the northernmost known record of glossopterids in South America corresponds to the report by Iannuzzi et al. (2004) from Lake Titicaca, in the Bolivian Altiplano, in western Bolivia (Fig. 6). In addition to the plant composition of the Costela Mine assemblage, paleoecological data from plant-arthropod interactions obtained here reveal damage patterns similar to those evident in early Permian plant assemblages from North America, particularly those from Texas, such as Sanzenbacher Ranch; this is supported by the NMDS analysis (Fig. 8).

This conclusion does not necessarily apply to the younger floristic record of the Parnaíba Basin. Cluster analyses performed by Neregato et al. (2017) of younger, anatomically preserved plant assemblages of permineralized wood plant fossils from stratigraphically higher beds of the Permian Pedra-de-Fogo and Motuca formations indicate that these plant assemblages had a highly endemic composition, but also shared roughly half of their genera with floras from Euramerica, Cathaysia, and southern Gondwana (Neregato et al., 2017). Based on these results, the authors proposed a new phytogeographic unit for this part of Gondwana, the Mid-North Brazilian Region that existed under conditions of a tropical summerwet climate. Recently, Conceição et al. (2020b, 2022) described fossil woods that corresponded to gymnosperm genera common in Euramerica, such as *Cordaixylon*, and *Europoxylon*, thereby increasing the number of extra-Gondwanan elements in the Parnaíba Basin plant assemblages and suggesting closer affiliation with the Euramerican Realm in this part of Gondwana. Indeed, the degree of endemism seems to increase from the base towards the top of Pedra-de-Fogo Formation strata and/or to the base of the overlying Motuca Formation.

6. Conclusions

We provide the following five conclusions from our examination of the Costelo Mine plant assemblage.

1. The Costela Mine plant assemblage of the Pedra de Fogo Formation includes representatives from the Euramerican Floristic Realm, such as the callipterid peltasperms *Rhachiphyllum* sp. and *Auritifolia*-like foliage, highlighting a floristic composition in the northwestern Gondwanan region, distinct from the more southerly Glossopterid Floristic Realm during the Cisuralian. The assemblage demonstrates significant biogeographic and paleoecological characteristics. In addition, the observed diversity of herbivory supports this biogeographic distinction.
2. Herbivory recorded at the Costela Mine plant assemblage is represented by eight functional feeding groups, 15 damage types, and 72 recorded feeding event occurrences. This represents the first comprehensive analysis of Permian plant-arthropod interactions in Brazil integrating those metrics.
3. The most common FFGs were margin feeding, piercing and sucking and galling, with three associated DTs each; other FFGs, such as hole feeding, surface feeding, skeletonization, borings, and possible mining, were sparse.
4. *Rhachiphyllum* sp. was the most herbivorized taxon in the assemblage, hosting seven FFGs and 12 DTs. The total analyzed leaf surface area of this taxon was 3,369.03 cm^2, with a herbivorized surface of 1.87 cm^2, yielding a herbivory index of 0.04. This value is considerably lower than other Permian plant assemblages, likely

reflecting a combination of adverse environmental conditions, biotic factors, and taphonomic constraints.

5. A non-metric multidimensional scaling (NMDS) analysis revealed that the herbivory patterns of the Costela Mine plant assemblage are compositionally distinct but overlap partially with a few Cisuralian Euramerican plant assemblages, particularly Sanzenbacher Ranch of north-central Texas. This floristic similarity reinforces the biogeographic link between the northwestern Gondwanan Realm and the southwestern Euramerican Realm during the early Permian.

Credit authorship contribution statement

T.B. Dos Santos: Conceptualization, Formal analysis, Investigation, Writing – Original draft, Writing - Review & Editing, Funding acquisition. **C.C. Labandeira**: Conceptualization, Writing – Original draft, Writing - Review & Editing. **R. Iannuzzi**: Conceptualization, Fieldwork, Writing – original draft, Writing - Review & Editing, Supervision. **E.R.S. Pinheiro**: Writing – Original draft. **D.M. Conceição**: Fieldwork, Writing – Original draft, Writing - Review & Editing. **J.C. Cisneros**: Fieldwork, Funding acquisition, Writing - Review & Editing. **M. C. Langer**: Fieldwork, Funding acquisition, Writing - Review & Editing.

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Figure Captions

Figure 1. Map of the Parnaíba Basin. (a) General view of South America at upper left, showing the location of the Parnaíba Basin. (b) Detail highlighting the outcrop areas of the Pedra de Fogo and Motuca formations. The yellow star marks the location of the outcrop analyzed in this study. Modified from Conceição et al. (2020).

Figure 2. Profile of the exposed section at the Costela Mine in the municipality of Nova Iorque, state of Maranhão. The plant-arthropod and pathogen associations were recovered from the mudstone located in the basalmost portion of the section (red arrow). Above the section, in the terrain surrounding the mine pit, mineralized stems (including ferns, calamitaleans, and gymnosperms) are scattered as float (*ex-situ*), and are not discussed here.

Figure 3. Composition of the Costela Mine plant assemblage. A, *Sphenophyllum* sp., leaflets are still attached to the stem node that form a leaf whorl. B, *Pecopteris* pinna with secondary veins emerging alternately from pinnule midveins, typically bifurcating once or twice. C, *Asterotheca* sp., the ultimate pinnae bearing fertile *Pecopteris*-type pinnules showing poorly preserved, small, circular synangia. D–E, *Rhachiphyllum* sp., a bipinnate frond bearing intercalary pinnules on the main rachis (arrow) and elliptical pinnules on the ultimate pinnae; the venation is characterized by more than one vein arising decurrently at the base of the pinnule and continuing toward the distal margin of the lamina, dividing two or more times (detail in E). F, *Auritifolia*-like foliage consisting of a frond fragment having a continuous leaf lamina margin along the rachis. G–H, *Autunia*-like reproductive structures, with isolated portions of a

flabelliform megasporophyll (ovuliferous organ) with strong ribbing radiating from the central area in (G), associated with one or two partially preserved ovules (arrows) and a cup-shaped polleniferous organ that laterally bears elongate, rod-shaped sporangia fused at their bases in (H). I, *Samaropsis*-like seeds, consisting of two small platyspermic seeds or ovules, showing a well-differentiated nucellus (n) and sarcotesta (s). J, A compressed, woody stem. Scale bars: A = 25 mm; B, E, G, H = 5 mm; C, D, F, J = 10 mm; I = 25 mm.

Figure 4 – Examples of ectophytic feeding, including hole feeding, margin feeding, and skeletonization on *Rhachiphyllum* sp. from the Costela Mine plant assemblage of the Pedra de Fogo Formation. A–C, Specimen MAP-PAB 72.4a with hole feeding DT003. D, E, Specimen LPRP/USP 110a showing DT003. F, G, Specimen LPRP/USP 127b with margin feeding DT012. H, I, Specimen LPRP/USP 137a with symmetrically positioned margin-feeding excisions of DT013. J–L, Specimen MAP-PAB 200 with skeletonization DT016 and possible adjacent surface feeding. M, Additional specimen of *Rhachiphyllum* sp. with extensive margin-feeding damage consisting of DT012 and DT013. Scale bars: black = 10 mm; white = 5 mm; black and white = 1 mm.

Figure 5 – Examples of piercing and sucking, galling, boring, and plant disease damage from the Costela Mine plant assemblage of the Pedra de Fogo Formation. A–C, *Rhachiphyllum* sp. (specimen PAB 199a) hosting DT046 (piercing and sucking) and DT048. D–F, A woody stem (specimen LPRP/USP 0083f) with DT046. G, H, *Rhachiphyllum* sp. (specimen LPRP/USP 0063) bearing gall damage DT080. I, J, *Rhachiphyllum* sp. (specimen LPRP/USP 0134) with pathogen damage DT174. K, L,

A woody stem (specimen LPRP/USP 0143) with evidence of DT284 borings. Scale bars: black = 10 mm; white = 5 mm; black and white = 1 mm.

Figure 6 – Floristic Realms during the early Permian (Cisuralian). Colored areas represent the geographic distribution of the four Permian floristic realms, i.e., Euramerican, Cathaysian, Gondwanan, and Angaran. The colored dots represent the regions containing plant assemblages from the western portion of Pangea, i.e., North and South America, which are relevant to the present study; they are: yellow dots from north to south Texas, U.S.A (1). (DiMichele et al., 2018, 2019); southern Mexico (2) (Flores-Barragan et al., 2024); Venezuelan Andes (3) (Ricardi-Branco, 2008); orange dot, northwestern Brazil, the Costela Mine plant assemblage (4); and red dots Bolivian Altiplano (5) (Iannuzzi et al., 2004); northwestern Argentina (6) (Cúneo, 1996); Argentinean Patagonia (7) (Cúneo, 1996); and southern Brazil (8) (Holz et al., 2010; Iannuzzi, 2010). Modified map from Scotese (1999) and delimitations of the realms according to Neregato et al. (2017).

Figure 7 – Occurrence of functional feeding groups from plant assemblages during the late Pennsylvanian to Cisuralian in Euramerica and Gondwana. Rio da Estiva, Papaléo Mine (L7/L8, L3/4, and Faxinal), Minas do Leão, Faxinal Mine and Quitéria – Pinheiro et al. (2012); Bajo de Véliz – Pinheiro et al. (2015); Fernández and Chiesa (2020); Colwell Creek Pond – Schachat et al. (2014); Mitchell Creek Flats – Schachat et al. (2015); Taint – Beck and Labandeira (1998); Coprolite Bone Bed – Labandeira and Allen (2007); Sanzenbacher Ranch – Dos Santos et al. (2024); Williamson Drive – Xu et al. (2018); Emma Pit – Knecht et al. (2023). Abbreviations: Art, Artinskian;

Ass., Asselian; Gzhe., Gzhelian; Kung, Kungurian; Moscov., Moscovian; Sak., Sakmarian.

Figure 8 – A non-metric multidimensional scaling (NMDS) ordination shows the similarity/dissimilarity relationships among the functional feeding groups from various latest Pennsylvanian to early middle Permian localities. Abbreviations: OV – Oviposition; P&S – Piercing and Sucking; GA – Galling; EF – Ectophytic Feeding (hole feeding, margin feeding, and skeletonization); WD – Williamson Drive; SR – Sanzenbacher Ranch; CCP – Cowell Creek Pond; MCF – Mitchell Creek Flats; SAP – South Ash Pasture; COS – Costela Mine; PML3/4 – Papaléo Mine L3/4; PMFX – Papaléo Mine Faxinal; QUI – Quitéria.

Table 1. Quantification of macrofossils from manually sampled quadrats from the Costela Mine plant assemblage of the Pedra de Fogo Formation.

Table 2. Total specimen data from the early Permian Costela Mine plant assemblage, Pedra de Fogo Formation, indicating total and herbivorized specimens analyzed, total surface area (TSA).

Table 3. Functional Feeding Groups (FFGs), each of which shows their damage type richness, damage type frequency, feeding event occurrences, and herbivorized surface area from the Costela Mine plant assemblage of the Pedra de Fogo Formation.

Table 4. Classification of damage type frequency for each plant taxon or morphotype from the Costela Mine plant assemblage of the Pedra de Fogo Formation.

		USP Collection	UFPI Collection	Total (sum taxon)	Percentage (%)
Quadrats-informative		181	107	288	
Quadrats barren		9	14	23	
Quadrats total		190	121	311	
	Taxon or morphotype				
Sphenopsids					
	Sphenophyllum sp.	5	11	16	4.51
	sphenophyll stems	30	13	43	12.11
Ferns					
	pecopterid fronds	7	8	15	4.22
	Asterotheca sp.	2	3	5	1.41
Pteridosperms					
	Rhachiphyllum sp.	126	55	181	50.99
	Auritifolia-like foliage	5		5	1.41
	Samaropsis-like seeds	13	2	15	4.22
	Autunia-like reproductive structures	3	1	4	1.13
Others	wood impressions/compressions	44	27	71	20
Total (specimens)		235	120	355	100

Plant taxon or morphotype	Examined specimens		Herbivorized specimens		Total surface area (TSA)		Herbivorized SA		Herbivory index
	No	PT (%)	No	PT (%)	S (cm²)	PT (%)	S (cm²)	PT (%)	PT (%)
Asterotheca sp.	5	0.95	0	0	33.09	0.67	0	0	0
Auritifolia-like foliage	5	0.95	0	0	28.63	0.58	0	0	0
Pecopterid fronds	15	2.86	0	0	41.94	0.85	0	0	0
Autunia-like reproductive structures	3	0.57	0	0	5.52	0.11	0	0	0
Rhachiphyllum sp.	168	32	22	81.48	3373.68	68.07	1.87	86.65	0.05
Samaropsis-like seeds	21	4	0	0	3.33	0.07	0	0	0
Sphenophyllum sp.	15	2.86	1	3.7	19.33	0.4	0.01	0.42	0.05
Sphenophyll stems	68	12.95	0	0	68.08	1.37	0	0	0
Wood impres./comp.	225	42.86	4	14.81	1382.44	27.89	0.28	12.93	0.02
Grand Total	525	100	27	99.99	4956.04	100	2.16	100	0.044

Abbreviations for No, number; PT, percent; S, summarized value; impres,impressions; comp., compressions.

FFGs	DT richness	PT (%)	Rank	DT frequency	PT (%)	Rank	FEO	PT (%)	Rank	Herbivorized area (cm^2)	PT (%)	Rank
Hole feeding	1	6.67	**2**	2	6.25	**4**	13	18.06	**2**	0.15	7	**5**
Margin feeding	3	20	**1**	9	28.13	**1**	12	16.67	**3**	0.77	35.77	**1**
Skeletonization	1	6.67	**2**	1	3.13	**5**	2	2.78	**7**	0.31	14.37	**2**
Surface feeding	1	6.67	**2**	2	6.25	**4**	3	4.17	**6**	0.1	4.47	**8**
Oviposition	1	6.67	**2**	1	3.13	**5**	1	1.39	**8**	0.13	5.89	**6**
Piercing and sucking	3	20	**1**	6	18.75	**3**	15	20.83	**1**	0.05	2.36	**9**
Galling	3	20	**1**	8	25	**2**	9	12.5	**4**	0.3	13.72	**3**
Borings	1	6.67	**2**	2	6.25	**4**	13	18.06	**2**	0.12	5.47	**7**
Pathogen	1	6.67	**2**	1	3.123	**5**	4	5.56	**5**	0.24	10.94	**4**
Totals	**15**	**100**		**32**	**100**		**72**	**100**		**2.157**	**99.99**	

Abbreviations for PT, percent.

FFGs	DTS	Plant taxon/morphotype	Damage frequency
HF	DT03	*Rhachiphyllum* sp.	2
HF Total			2
MF	DT012	*Rhachiphyllum* sp.	3
	DT013	*Rhachiphyllum* sp.	5
	DT014	*Rhachiphyllum* sp.	1
MF Total			9
SK	DT016	*Rhachiphyllum* sp.	1
SK Total			1
SF	DT103	*Rhachiphyllum* sp.	2
SF Total			2
PS	DT046	*Rhachiphyllum* sp.	2
		Wood impression	1
	DT048	*Rhachiphyllum* sp.	2
	DT183	Wood impression	1
PS Total			6
OV	DT72	Wood impression	1
OV Total			1
GA	DT080	*Rhachiphyllum* sp.	6
	DT87	*Rhachiphyllum* sp.	1
	DT247	*Sphenophyllum* sp.	1
GA Total			8
WB	DT284	Wood compressions	2
WB Total			2
PA	DT174	*Rhachiphyllum* sp.	1
PA Total			1
Grand Total			**32**

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Research highlights

- The early Permian flora from Costela Mine, Parnaíba Basin, is described as a callipterid-dominated flora.
- Herbivory includes eight functional feeding groups from arthropods and one pathogen; a total of 15 damage types.
- *Rhachiphyllum* shows the highest diversity of arthropod–plant interactions.
- A NMDS analysis reveals paleoecological affinities with Euramerican floras.
- The Costela plant assemblage differs from coeval Gondwanan assemblages dominated by glossopterids.