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A glimpse of a Gondwanan postglacial fossil forest

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ABSTRACT

The rooted nature of vegetation allows for individual plants or entire communities to be buried in life position under exceptional geological conditions, thereby preserving their ecology and spatial distribution in the stratigraphic record. Upright lycopsids are not uncommon within paleoequatorial Carboniferous coal-bearing deposits, but they are rare in mid- to high-paleolatitude Gondwana, where they have only been found in lower Permian strata. An exceptionally well preserved in situ *Brasilodendron*-like lycopsid forest is described from an early Permian postglacial paleolandscape of western Gondwana (Paraná Basin, Brazil). The forest depicted here is unique given its extratropical location, as well as the exceptional preservation of abundant specimens and their morphological and paleoecological aspects. Over 150 lycopsid stumps, with a clustered spatial organization, were mapped. The host succession, overlying glaciomarine diamictites by a few tens of meters, captures the terminal deglaciation in the Paraná Basin, and shows that these forests could establish dense communities on poorly developed soils in postglacial times. Sedimentological data suggest that the death and burial of these lycopsids in life position were caused by crevasse splay progradation over the colonized interdistributary bay areas as a consequence of a major river flooding event.

1. Introduction

The late Paleozoic was a key interval in geological history because it preserves a complete transition from icehouse to greenhouse states on a vegetated Earth (Montañez and Poulsen, 2013). Continental glaciers, which expanded out from multiple ice centers in Gondwana through the Pennsylvanian and earliest Permian (e.g., Isbell et al., 2003, 2012; Le Heron et al., 2021), underwent stepwise deglaciation concomitant with rising atmospheric pCO_2 (Griffis et al., 2019), providing suitable conditions for widespread colonization by arborescent lycopsids in mid- to high-paleolatitudes of Gondwana.

Lycopsids, early basal vascular plants, were a dominant and widespread constituent of Pennsylvanian tropical forests, and often buried in situ (Bateman, 1996; DiMichele and Falcon-Lang, 2011; Fig. 1A). In the paleotropics, arborescent lycopsids reached their acme in the first half of the Pennsylvanian and experienced near extinction just before the Middle to Late Pennsylvanian boundary (DiMichele et al., 2009). In contrast, at higher paleolatitudes, arborescent lycopsids radiated in the early Permian (e.g., McLoughlin et al., 2015; Spiekermann et al., 2020). These temporal disparities reflect differences in paleogeography and paleoclimatic conditions (Ryberg et al., 2012), as well as there being different evolutionary lineages of lycopsids in the Euramerican and Gondwanan floral provinces.

Although preserved lycopsid forests of Pennsylvanian age are moderately common in the Euramerican strata (DiMichele and Falcon-Lang, 2011), such communities preserved in growth position are extremely rare from mid- to high-paleolatitude regions of Gondwana. To date, there are only two reports of specimens preserved in growth position, in the lower Permian of Argentinean Patagonia (Cúneo and Andreis, 1983; Fig. 1A) and at the Quitéria outcrop in southern Brazil (Jasper et al., 2006; Fig. 1A-B). The root system morphology and/or the spatial distribution of individual plants was not documented in detail at either locality.

In this paper we investigate a new and exceptionally well-preserved lycopsid forest that occupied an early Permian coastal plain landscape of western Gondwana, and present new ecological inferences about the vegetation. The fossil forest is preserved within the coal-bearing, lower Permian Rio Bonito Formation of the Paraná Basin, southern Brazil

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(Fig. 1). The deposit lies ca 30 m above the uppermost glaciomarine diamictite in the region (Fig. 2A), providing a unique opportunity to examine a fossil forest that lived at the onset of postglacial conditions in western Gondwana.

2. Geological background

The newly discovered lycopsid fossil forest was recently exposed by road and railroad construction in the Ortigueira municipality (Fig. 1; Latitude 24°15′46”S, Longitude 50°44′38”W), central region of the Paraná State, southern Brazil. The host sedimentary succession is assigned to the lower-middle part of the Rio Bonito Formation, base of the Guatá Group, to which an early Permian age is attributed based in both palynological and radiometric ages (Souza, 2006; Griffis et al., 2018). The coal-bearing Rio Bonito Formation was deposited in the intracratonic Paraná Basin, following late Paleozoic glaciation, and records a definitive change to postglacial conditions. The uppermost glacial deposits underlying the Rio Bonito Formation in this region are referred to as the Taciba Formation (upper Itararé Group; França and Potter, 1988), whose succession is dominated by diamictites, sandstones and dropstone-bearing heterolithics deposited mostly in glaciomarine environments (Mottin et al., 2018).

The Rio Bonito Formation abruptly rests on the uppermost glaciomarine diamictite of the Taciba Formation by means of a subaerial unconformity (e.g., Zacharias and Assine, 2005; Mottin et al., 2018). The surface underlying the Rio Bonito Formation is topographically undulating due to paleovalley development and marked by a well-developed paleosol level, thus involving a hiatus between its development and the infilling of valleys by fluvial and estuarine sediments of the lower Rio Bonito Formation (Zacharias and Assine, 2005; Mottin and Vesely, 2021). The lowermost valley-fill deposits are assigned to the Triunfo Member, which includes fluvial conglomerates and poorly sorted, quartz-feldspathic sandstones. These facies grade upward to coal-bearing estuarine and deltaic deposits of the Paraguaçu Member (Schneider et al., 1974; Zacharias and Assine, 2005).

The newly discovered plant fossil-bearing sedimentary succession of Ortigueira is stratigraphically placed in an interval spanning the upper Triunfo to lower Paraguaçu members (Fig. 2A). This is the same interval from which the Figueira and São João do Triunfo plant-fossil localities were previously described in northeastern and southeastern Paraná State, respectively (Rösler, 1978; Zacharias and Assine, 2005; Iannuzzi, 2010). The plant fossil content of Figueira and São João do Triunfo is very similar, consisting of abundant pecopteroid fern fronds (*Pecopteris* spp., *Asterotheca* spp., *Asterotheca derbyi*), abundant to common sphenopsid stems and foliage (*Sphenophyllum brasiliensis*, *Annularia* spp.), and glossopteroid leaves (*Glossopteris* spp., *Glossopteris communis*, *Gangamopteris obovata*) (Iannuzzi, 2010). The Figueira paleoflora presents relatively abundant lycopsid stems (*Brasilodendron* sp.), conifer leaf shoots (*Paranocladus* spp., *Buriadia figueirensis*) and seeds (*Paranospermum cambuiense*), whereas lycopsid stems (*Brasilodendron pedroanum*) are less common in the São João do Triunfo flora (Iannuzzi, 2010).

3. Methods

The study site consists of four closely spaced outcrops, hereafter referred to as “transects”. Field study of exposed lycopsid casts included analysis of their morphology, diameter and vertical extent, mode of preservation, sediment fill, and subsurface tissues (roots and lateral lobes). Associated facies were described through the construction of bed-by-bed sedimentological logs, photomosaics and paleocurrent measurements.

A total of 115 lycopsid casts in original life position were mapped on the four transects using a Real-Time Kinematic (RTK; *GNSS STONEX S8 Plus*) positioning to collect accurate position data. This high precision method of acquisition was required because the distance between adjacent trunks can be as short as 25 cm. UTM coordinates for the position of the measured lycopsid casts is found in the data supplement (Supplementary Material 1).

Considering that transects only provided a two-dimensional spatial

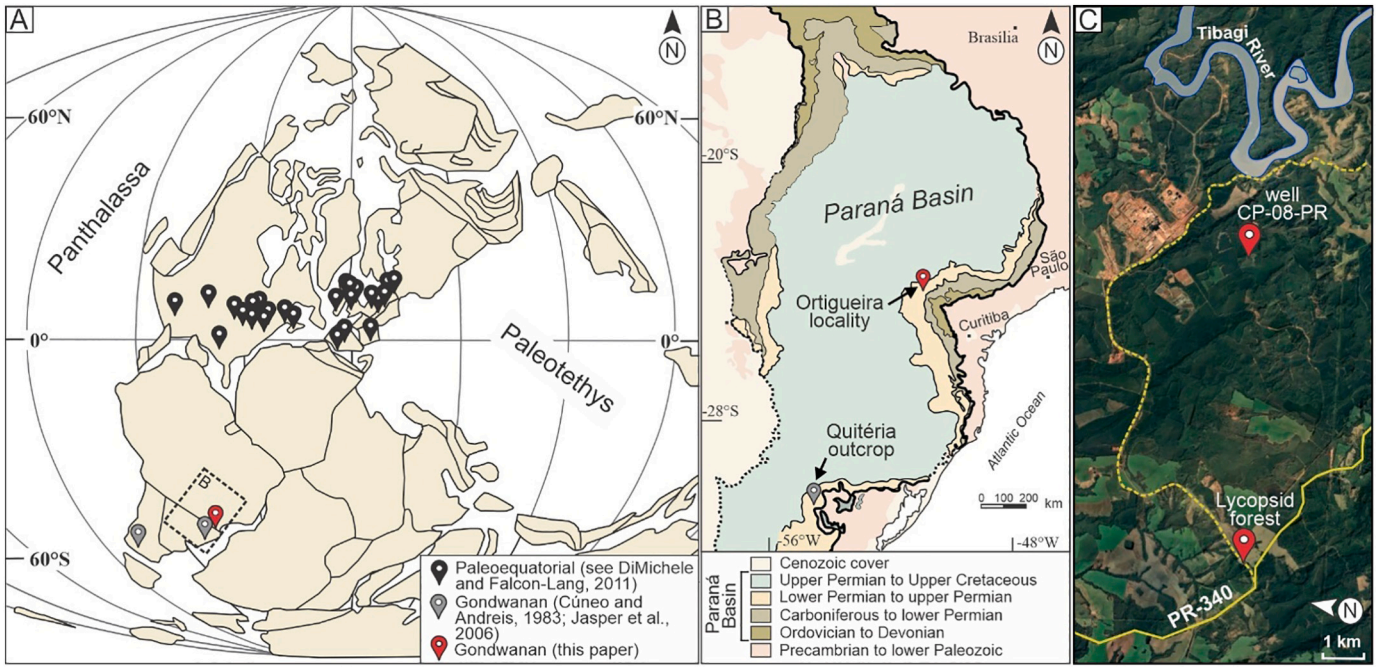

Fig. 1. In-situ lycopsids of the late Paleozoic landmasses. (A) Late Carboniferous-early Permian paleogeography (after Domeier and Torsvik, 2014), with distribution of reported paleoequatorial (black symbols) and Gondwanan upright lycopsids (grey symbols), including the new locality reported here (red symbol). (B) Location of the Quitéria outcrop (Jasper et al., 2006) and the newly discovered lycopsid forest (Ortigueira locality; red symbol) in the lower Permian outcrop belt of the Paraná Basin. (C) Map containing the location of the well CP-08-PR and the lycopsid forest in Ortigueira locality, northeast Paraná State, south Brazil. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

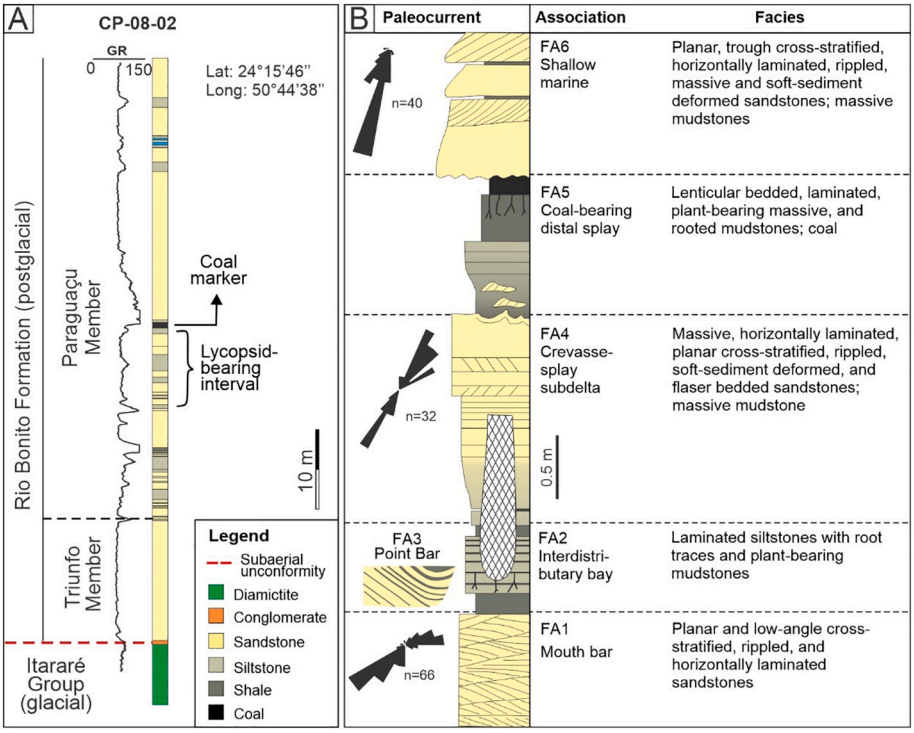

Fig. 2. Stratigraphic setting. (A) Position of the lycopsid-bearing interval in the glacial-postglacial stratigraphy represented in the well CP-08-02, Ortigueira locality. (B) Representative sedimentological log of the middle Rio Bonito Formation (Paraguaçu Member) in Ortigueira locality, showing the exact stratigraphic position of the lycopsid forest.

structure of the trunks, we also performed high-resolution Ground Penetrating Radar (GPR) mapping ($n = 64$) in a 20 m^2 polygon in between transects to evaluate the density and three-dimensional distribution of buried stumps. This was achieved using an ASIR3000 GPR System (GSSI) with a 400 MHz shielded antenna. The GPR survey produced 20 parallel sections, spaced 0.1 m apart and oriented in a northeast-southwest direction, which resulted in a high-resolution pseudo-3D radargram. Data processing and interpretation was executed in ReflexW 7.0 software (Sandmeier, 2010) using 2D and 3D data analysis mode. Radargram interpretation was conducted in vertical sections and depth slices.

The original heights of the living lycopsid trees were estimated from their diameters using the equation that Niklas (1994) developed based on the allometric relationship between diameter and height in extant woody trees. Trunk diameter values were recorded for 111 specimens along the four transects concurrently with the RTK survey. Self-thinning was calculated using the relationship between volume (m^3/ha) and density (trees/ha). Spatial distribution pattern was evaluated by two different methods in the composite transect (5 m wide x 380 m long) and in the 20 m^2 polygon: the method of Hayek and Buzas (2010), as adapted by DiMichele et al. (1996), and the method of Haining (1993).

4. Results

4.1. Host sedimentary succession

The fossil tree-bearing succession is 5.5 m thick and comprises six distinct facies associations, from base to top: FA1-Mouth bar, FA2-Interdistributary bay, FA3-Point bar, FA4-Crevasse-splay subdelta, FA5-Coal-bearing distal splay, and FA6-Shallow marine (Fig. 2B). However, here we focus on the interval between FA2 and FA5, which is directly related to the sedimentary processes that supported the initiation and growth of the lycopsid forest, and then provided the burial conditions for its preservation. The sedimentary succession containing the fossil forest lies ca 30 m above the glaciomarine diamictites of the Taciba Formation based on correlation with the CP-08-02 well drilled nearby the studied outcrops (Figs. 1C; 2A).

4.1.1. Description

Lycopsids are rooted in their original clastic immature soil, which developed in a 0.4 m thick bed of laminated, coarse-grained siltstone of FA2 (Figs. 2-4; 8A). In addition to the laminated siltstone, the association comprises plant-fossil-bearing claystones totaling 0.6 cm thick. Inclined heterolithic beds (3 m thick; Fig. 3B) consisting of horizontally laminated and rippled fine-grained sandstones interbedded with massive siltstones, corresponding to FA3, occur laterally to FA2 (Fig. 2B).

The mudstones of FA2 pass gradually upwards to a coarsening- and thickening-upward 1.65 to 1.9 m thick succession ascribed to FA4 (Fig. 2B). Massive coarse-grained siltstones pass into very fine- to fine-grained, massive, laminated, and rippled sandstones. Bidirectional ripples and organic-rich drapes on ripple foresets are characteristics of this interval, along with pyrite concretions, commonly nucleated from plant remains. The upper portion of FA4 encloses fine-grained sandstones with soft-sediment deformation, consisting of load, flame and water-escape structures, and contorted lamination.

The interaction of sediments of FA4 and the standing stumps produced a variety of structures, mainly present in the upper half of the association and in the boundary between FA4 and mudstones of FA5. We identified ca 0.5 m thick bodies of fine-grained sandstone filling in depressions centered on lycopsid stumps, where the laminae dip towards the tree on one or both sides of the exposed tree (Fig. 3F). Other common structures around individual plants include upturned and downturned beds, and cone-shaped depressions filled in by mudstones centered on the tops of stumps (Fig. 3G).

Fine-grained sandstones at the top of FA4 are in abrupt contact with mudstones of FA5. The latter is characterized by a 1 m thick fining-upward trend, with lenticular bedded coarse-grained siltstones passing upwards to laminated, massive and rooted mudstones. The stacking of FA5 is completed by a 10 cm thick coal bed whose upper limit is

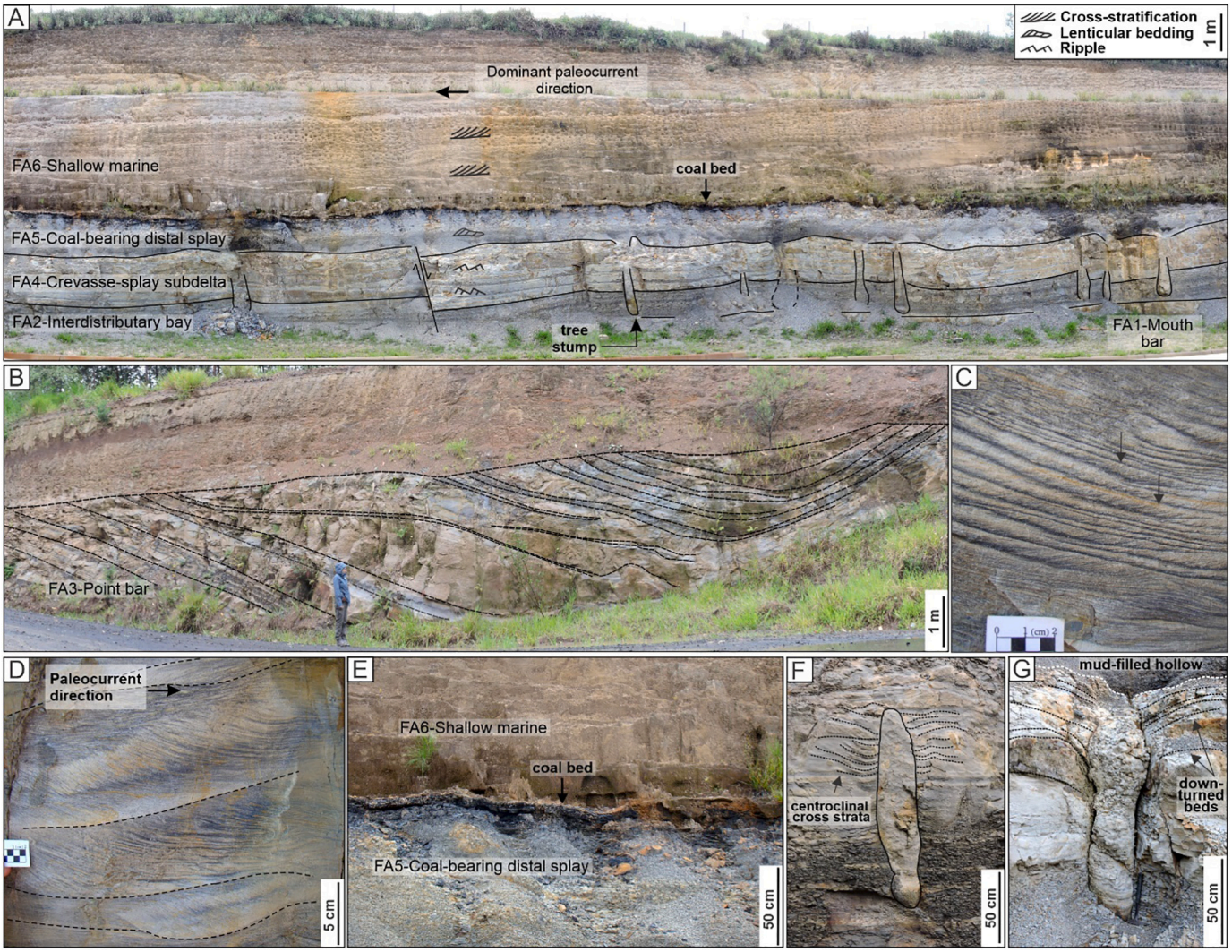

Fig. 3. Sedimentary characteristics of the lycopsid-bearing succession. (A) Photomosaic of the sedimentary succession hosting the fossil forest in part of transect 1, showing the facies associations, main sedimentary structures, dominant paleocurrent direction and the lycopsid casts. (B) Laterally accreted bedsets of a fluvial point-bar deposit (FA3) lateral to FA2. (C—D) Mud-draped, tide influenced sandstone facies (FA1). (E) Detail of the coal marker bed (FA5) in erosive contact with shallow marine association (FA6). (F) Example of centroclinal cross-stratification (FA4) and (G) associated downturned beds and mud-filled hollow around individual upright tree casts (FA4 and FA5).

truncated by an erosive surface that marks the contact with shallow marine sandstones of FA6 (Figs. 2B; 3A; 3E).

4.1.2. *Interpretation*

The inclined heterolithic beds (FA3) lateral to the in situ stumps are interpreted as lateral accretion packages (point bars). This interpretation implies that the mudstones of FA2 were deposited in overbank zones of sinuous channels. Bidirectional paleocurrents (Fig. 2B) and rhythmic mud drapes in cross-laminated sandstones (Fig. 3C-D) below (FA1) and above (FA4) the lycopsid-bearing siltstones (FA2) point to tidal reworking. Collectively, these features indicate that the lycopsid community occupied an interchannel, lowland environment subject to seawater incursions, most likely an interdistributary zone of a lower delta (or bay-head delta) plain.

Mudstones of FA2 gradually pass upward into coarse-grained siltstones and fine-grained sandstones of FA4. The characteristic coarsening-upward stacking pattern (Fig. 2B), presence of facies indicative of traction-plus-fallout hydraulic processes, and signals of the interaction of river currents with marine processes in FA4 suggest a crevasse-splay subdelta environment (e.g., Elliot, 1974; Gugliotta et al., 2015).

The structures observed around the standing lycopsids in FA4 are interpreted as vegetation induced sedimentary structures (VISS; Rygel et al., 2004), which result from the interaction of clastic sediment with in situ plants. Laminae of fine-grained sandstone dipping towards the stumps (centroclinal and uniclinal cross-stratifications; Figs. 3F; 4B) and upturned beds are considered as primary sedimentary structures produced by hydrodynamic processes around a vegetative obstacle. These features are commonly associated with downturned beds and mud-filled hollows (Figs. 3G; 4B), which are generated by soft-sediment deformation due to decay of an entombed plant (Rygel et al., 2004).

4.2. *Spatial organization of lycopsid stumps*

We assessed the spatial distribution of lycopsid stumps by using the two positioning data sets separately: a map of 115 georeferenced casts along with the 111 respective diameters along transects (from the RTK survey), and a radargram displaying 64 buried casts within the 20 m^2 polygon (GPR survey).

The radargram was interpreted by observing the geometry, amplitude and frequency of reflectors in vertical sections and depth slices. The lycopsid casts were identified in the subsurface based on their

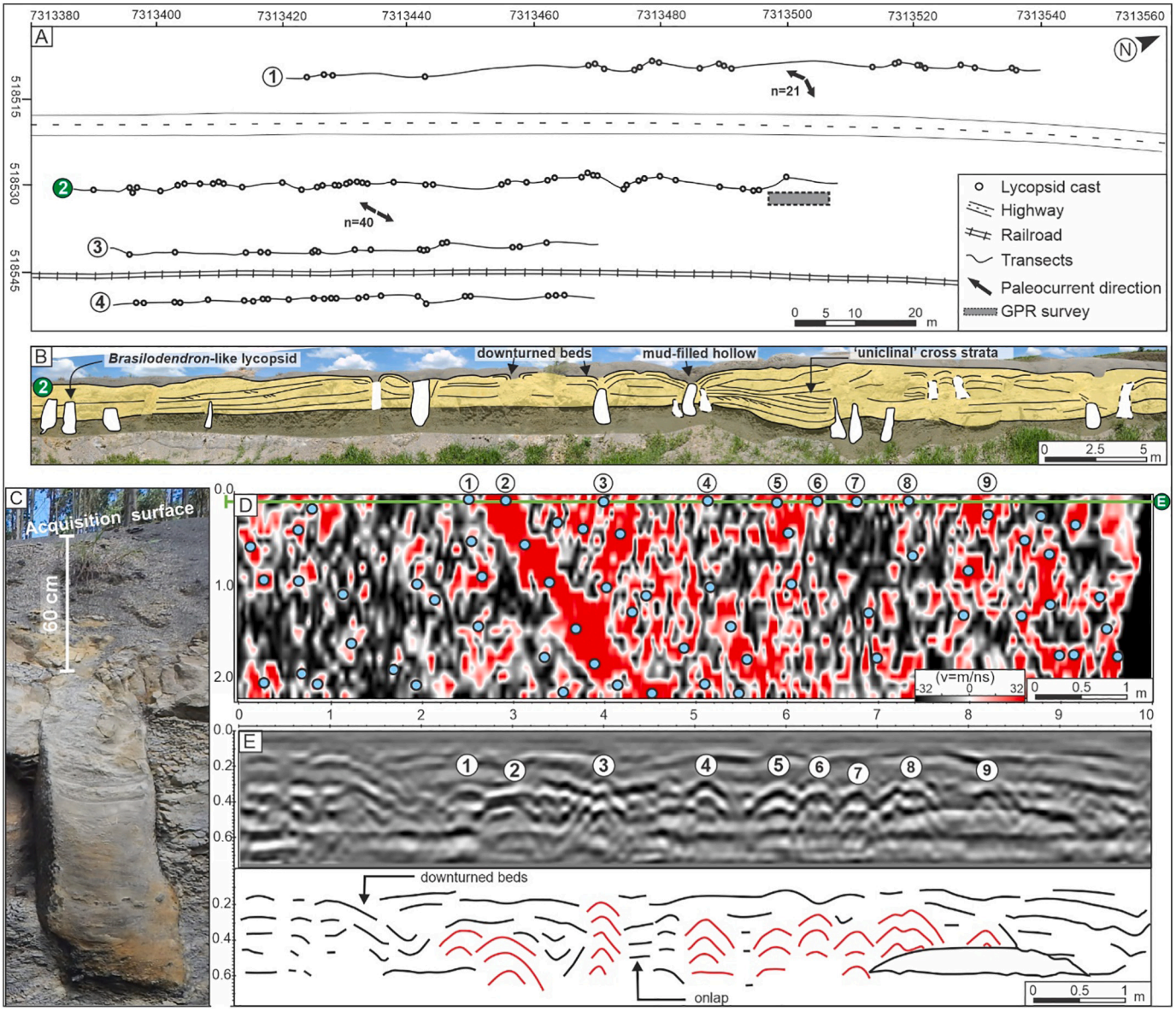

Fig. 4. Spatial distribution of lycopsid casts. (A) Map-view of high precision positioning (RTK) of the 115 stumps exposed in the four transects. (B) Photomosaic of part of transect 2 showing the clustered organization of lycopsids and indications of VISS, i.e., downturned beds, 'uniclinal' cross-strata and mud-filled hollows (Rygel et al., 2004). Dashed white areas represent non-georeferenced, partially covered casts. (C) Outcrop photo showing the vertical distance between the top of the investigated object and the GPR acquisition surface. (D) GPR depth-slice, i.e., map view, where blue dots correspond to lycopsid stumps identified simultaneously in depth slices and intercepting vertical sections. Transverse line indicates the location of section shown in E. (E) GPR cross-section and its interpretation (location in D). Convex-up anomalies interpreted as stems are indicated by red lines; bedding of the host sedimentary succession is represented by black lines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

characteristically high to moderate amplitude and convex-up anomalies found at the same depth as those casts observed in outcrops (Fig. 4C; 4E). The mapping of 64 individual lycopsid stumps in plan view across the GPR survey was done by tying depth slices with anomalies seen in intercepting vertical sections. The result was a 3D positioning of stumps (Fig. 4D).

The pseudo-3D radargram displayed anomalies with widths between 0.3 and 0.7 m at depths between 0.3 and 0.6 m. (Fig. 4E). These anomalies are interpreted as sediment-filled casts of lycopsids because: (i) their depths are the same as those in the transects (Fig. 4C); (ii) anomaly spacings match that of the exposed casts; (iii) the same geometric relationships between casts and adjacent beds were found in outcrops and GPR profiles (i.e., onlap, centroclinal cross-strata, upturned beds, downturned beds). Depth-slice sections denote lycopsid casts as near circular spots with anomalous high-amplitude reflections (Fig. 4D).

The distribution of exposed casts suggests that the fossil forest has a minimum lateral extent of 600 m. Qualitative analysis indicates the presence of small clusters (pairs or trios) frequently characterized by an oversized tree surrounded by smaller ones. Individual clusters are spaced on average 5.1 m from one another (Fig. 6A-B), with an average in-cluster distance between stumps of 0.7 m.

We investigated whether the lycopsid community presents evidence for self-thinning, the natural ecological process whereby the density of trees decreases as average tree size increases over time. Self-thinned communities tend to be distributed around a line with an average slope of 1.5 (White and Harper, 1970). Average tree densities, diameters, heights, volumes, and basal areas were calculated for 11 subareas within transects (Table 1), for which we have positioning data associated with diameter measurements. Fig. 5A shows the distribution

Table 1
Descriptive data for the 11 transect subareas. Volume was calculated by multiplying the value of tree basal area by the mean tree height in each of the subareas.

Subarea	Number of trees	Area (m^2)	Tree density/m^2	Tree density/ha	Tree diameter range (cm)	Mean tree diameter (cm)	Tree basal area (m^2/ha)	Tree height range (m)	Mean tree height (m)	Volume (m^3)
1	12	34.28	0.35	3500.28	17.5–44	33.19	302.77	6.27–12.22	9.96	8620.21
2	12	35.89	0.3344	3343.55	29–75	47.54	593.48	9.04–17.96	12.92	22,932.28
3	7	21.49	0.3257	3256.85	22–62	42.57	463.45	7.4–15.65	11.93	16,977.13
4	8	16.81	0.4759	4758.64	23–60	38.38	550.57	7.64–15.65	11.07	12,803.62
5	8	22.03	0.3631	3631.38	18–43	33.5	319.92	6.4–12.01	10.03	8841.22
6	12	18.91	0.6346	6344.77	21–43	33.21	549.46	7.16–12.01	9.97	8634.36
7	5	15.51	0.3224	3222.94	23–43	31.8	255.90	7.64–12.01	9.66	7672.27
8	10	20.09	0.4978	4976.77	15–61	34.85	474.78	5.61–15.47	10.32	9845.4
9	10	21.49	0.4653	4652.52	23–56	37.6	516.43	7.64–14.54	10.90	12,107.4
10	5	23.19	0.2156	2155.70	31–69	42.6	307.19	9.48–16.91	11.93	17,009.73
11	9	20.48	0.2238	4393.86	18–63	40.22	558.02	6.4–15.84	11.45	14,544.9

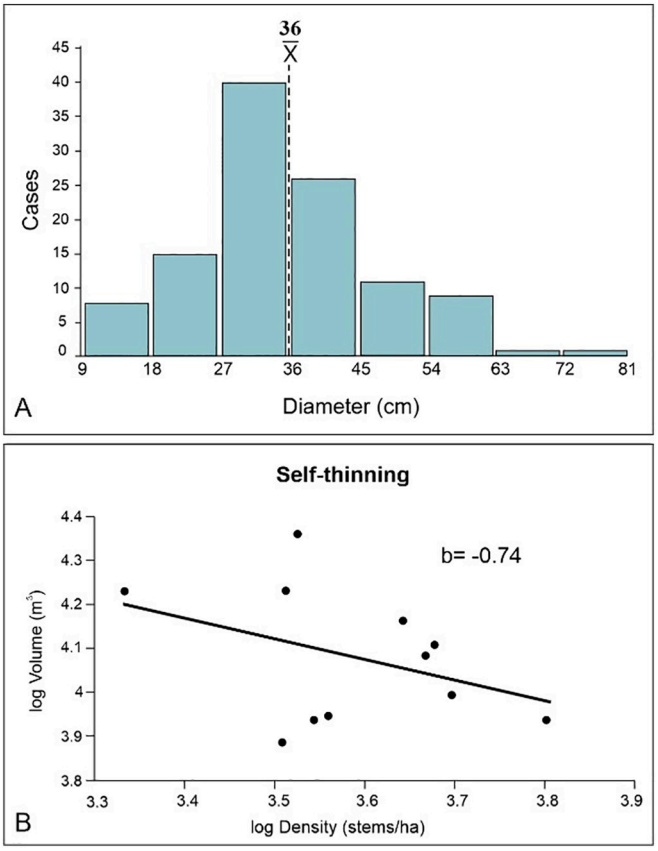

Fig. 5. Diameter relationships. A) Distribution of diameters of 111 upright stems measured along transects. B) Plot of the log-transformed mean volume against the log-transformed mean density of the 11 subareas. Slope of the line equals 0.74, well below the 1.5 self-thinning threshold.

of measured diameters of the 111 exposed stems along transects; the average diameter is 36 cm. As for the self-thinning calculation, a moderate inverse relationship (ca 0.75; Fig. 5B) between tree volume (m^3/ha) and tree density (trees/ha) indicates that the Ortigueira fossil forest did not reach the natural self-thinning threshold of 1.5 that leads to mortality caused by competition for growing space. Tests conducted with smaller and larger subareas show quite similar results to that presented here. Furthermore, the distribution of tree diameters is unimodal and right-skewed (Fig. 5A), which suggests that the lycopsids were mostly immature when they were buried.

Tree density estimated from the 20 m^2 polygon indicates a forest density of c. 3200 trees per hectare (Fig. 4D). A similar average density (4000 trees/ha) was obtained from the transect area. In addition, the combined basal area of trees in the Ortigueira forest is ca 500 m^2 per hectare (Table 1), indicating that approximately 5% of the lycopsid forest was occupied by trees.

The spatial organization pattern of stumps was analyzed separately for transect and 20 m^2 polygon data, following the method proposed by Hayek and Buzas (2010), as adapted by DiMichele et al. (1996), which consists of dividing a plot map into a series of ever smaller quadrats. The four transects were combined to form a composite transect totaling 380 m in length, with a standard width of 5 m. The surveyed areas (composite transect and 20 m^2 polygon) were subdivided four times, each time using a different quadrat size with standard widths. Means and variances of tree occurrences were calculated for each of the quadrat sizes (Table 2) and then plotted with means on the abscissa and variances on the ordinate. The values of mean and variance were log transformed, to produce a straight line whose slope indicates the spatial distribution pattern of stems (Hayek and Buzas, 2010).

Values of 1.3 for the composite transect (Fig. 6A) and of 1.1 for the polygon (Fig. 6B) suggest a clumped organization of stumps along transects and in the 20 m^2 polygon area. In this method, the amount by which the $\sigma 2/\mu$ ratio (variance/mean) deviates from 1 (randomness) dictates the organization pattern of the population: if $\sigma 2 > \mu$, the spatial distribution is clumped, and if $\sigma 2 < \mu$, then the distribution is considered regular or ordered (Hayek and Buzas, 2010; DiMichele et al., 1996).

The spatial organization pattern obtained by the method above is reinforced by a second method (adapted from Haining, 1993) that compares the average number of stumps in adjacent quadrats against that in a target quadrat. The clear inverse relationship of the number of stumps per 1.8 m quadrat and the average number of stumps in the two adjacent 1.8 m quadrats in the composite transect indicates a clear clumped pattern (Fig. 7A). Stumps in the 20 m^2 polygonal also exhibit an inverse relationship, but less pronounced than in the composite transect (Fig. 7B).

4.3. Characteristics and identification of the lycopsid stumps

The lycopsid stumps occur in a single stratigraphic level, ca. 2 m beneath a coal marker bed (Figs.3A; 4B) that is laterally persistent. The stumps are preserved as unbranched external stem molds or casts (Schopf, 1975) in their growth position, extending upward for up to 2 m and onlapped by younger strata (Fig. 8). Casts were filled by the same sediment in which the stems were entombed, a poorly sorted mixture of silt and sand with mudstone rip-up clasts (Fig. 8E).

Diameters measured above the basal flare zone are on average 36 cm (Fig. 5A; range of 9 to 75 cm), indicating that the lycopsids in the Ortigueira fossil forest could have reached heights of 4 to 18 m (mean = 11 m), using the equation of Niklas (1994). The stumps lack any internal tissue preservation, except for rare casts of collapsed stele (Fig. 8D). Although leaf cushions lack leaves, they occur as adpressions (Fig. 8G) in the surrounding sediment, along with rare and highly fragmented adpressed remains of *Paracalamites* sp. and *Pecopteris* sp. The scarcity and fragmented nature of the leaves of the latter two species indicate an allochthonous origin.

Table 2
Summary statistics for four different quadrat sizes in the composite transect and the 20 m^2 polygon area.

Composite transect				20 m^2 polygon			
Quadrat size (m x m)	Total stumps	Mean	Variance	Quadrat size (m x m)	Total stumps	Mean	Variance
5 × 38	115	11	18.33	2 × 2	64	6	2.8
5 × 19	115	5.57	5.96	2 × 1.43	64	4	2
5 × 9.5	115	2.75	2.12	2 × 1	64	3.2	1.87
5 × 6.3	115	1.63	1.54	2 × 0.5	64	1.8	1.12

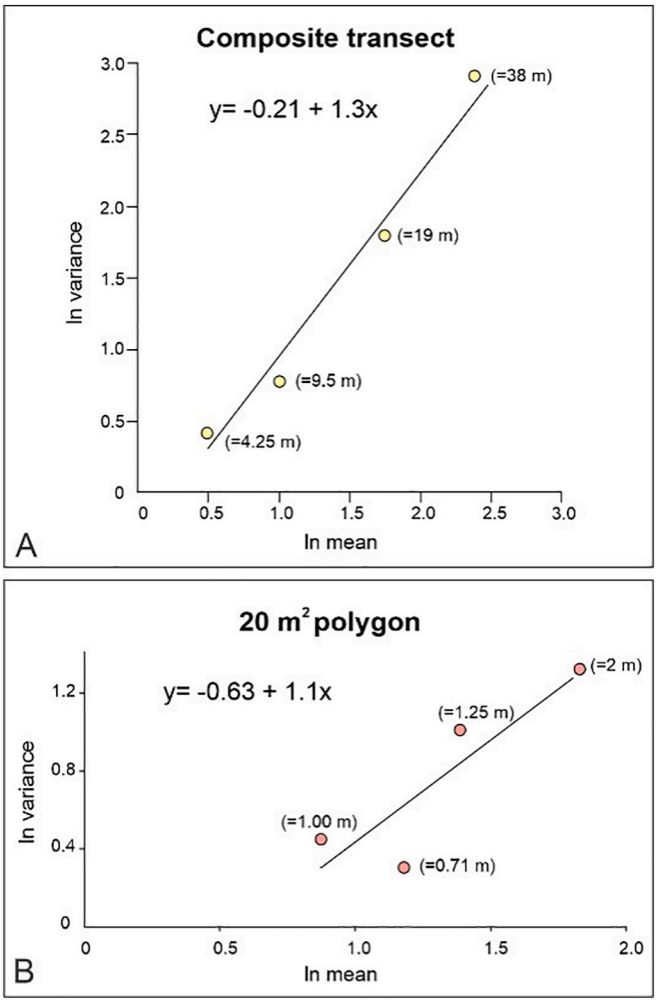

Fig. 6. Plot of the log-transformed mean vs. log-transformed variance for number of tree stumps per quadrat at four quadrat sizes along the composite transect (A) and in the 20 m^2 polygon (B). The slope of the line is greater than 1 in both areas, indicating a clumped organization.

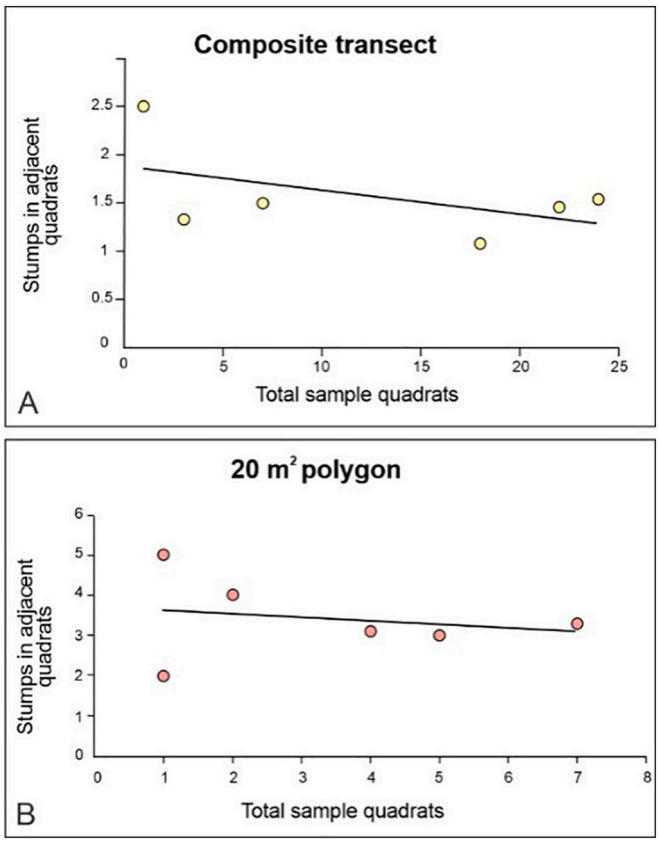

Fig. 7. Plot of the average number of stumps in adjacent quadrat pair against the total sample quadrats for the composite transect (A) and 20 m^2 polygon area (B), following the method of Haining (1993).

The lycopsid stumps in the study locality have bulging bases indicating a cormose-based tree. Small lobes extend laterally downwards giving an undulated appearance to the lower fringes of the stump bases (Figs. 8-9). Each lobe extends subhorizontally, forming a short appendage that curves slightly downwards distally, like the tips of semi-closed fingers (Fig. 8C). Thin roots extend downwards from the lobes and dichotomize repeatedly through the underlying strata (Figs. 9A-B), forming an isotomously branched pattern. Beds with root traces frequently present soft-sediment deformation in the form of folds and displaced laminae (Figs. 9E-F).

The external surface of standing stumps is not well-preserved but displays spirally arranged fusiform to rhombic leaf cushions. In addition, some cushions can be observed on compressed bark remains within surrounding sediment. Leaf cushions lack evidence of ligule and parichnos traces and the leaves were attached in their upper third, as shown by the small rounded and rhombical leaf scars observed (Fig. 8H). We interpret the change in outermost tissues that occurs as stems increase in diameter to record various decortication stages. Slender stems show closely spaced, rhombic leaf cushions representing less decorticated specimens, whereas thicker stems displaying widely spaced leaf cushions or characterized by irregular, longitudinally oriented ridges are assigned to higher degrees of decortication. Abundant compressed remains of lycopsid leaves, typically long and linear with a single vein and fimbriate to spiny margins, were found within enclosing strata. Collectively, these characteristics are comparable to those of the genus *Brasilodendron* (Chaloner et al., 1979; Ricardi-Branco and Ricardi, 2003). However, the absence of morpho-anatomical information for the leaves and of the megaspores preclude the identification with the type species *Brasilodendron pedroanum* Chaloner et al. (1979). Thus, we tentatively assign the lycopsids to *Brasilodendron*-like stems until additional diagnostic features are identified.

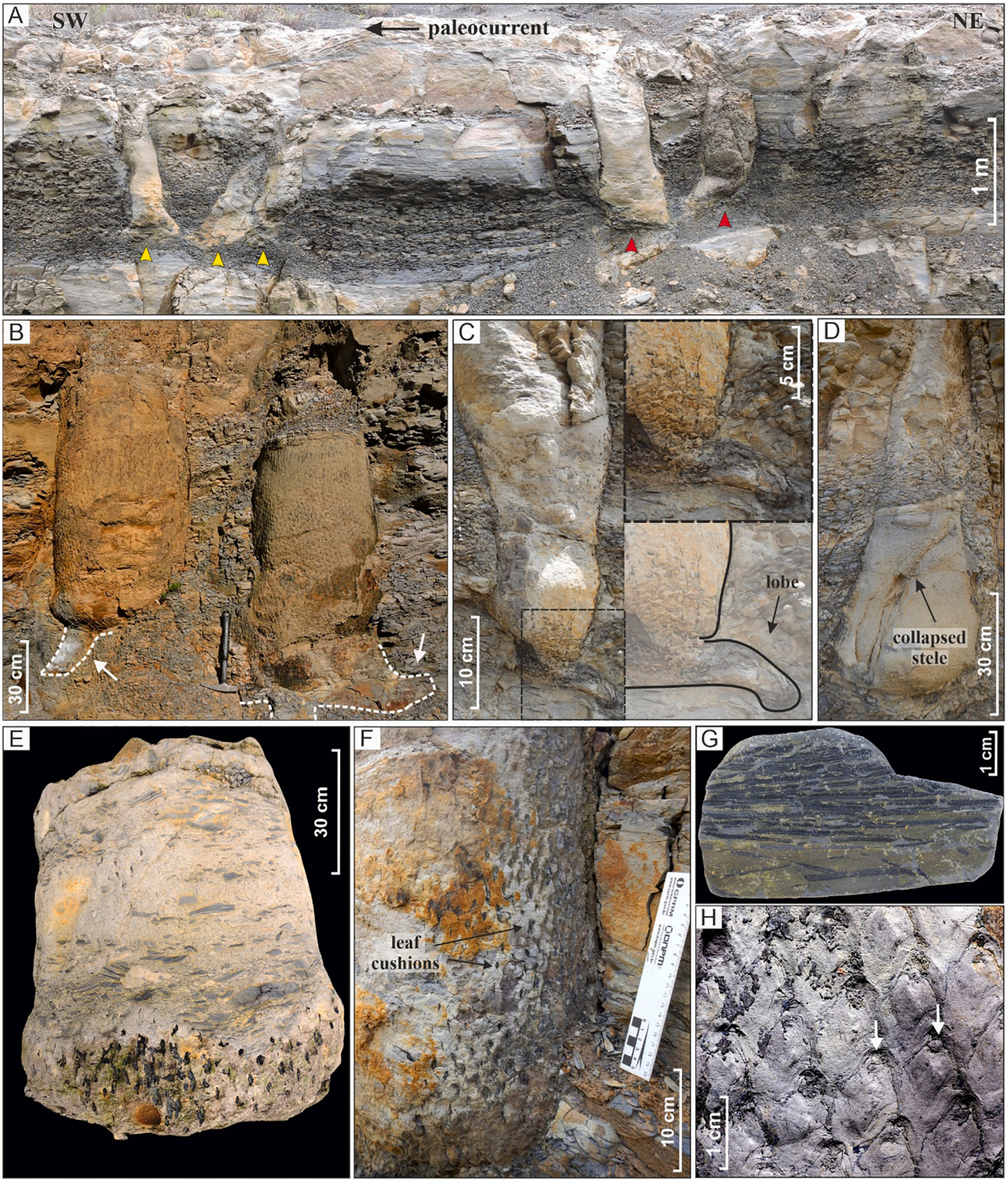

Fig. 8. Examples of upright *Brasilodendron*-like lycopsids in Ortigueira. (A) Arrows indicate five lycopsid casts, grouped into two clusters (yellow and red arrows). (B) Lycopsid casts endowed with appendages (white arrows). (C) Overview and detail of an appendage curving slightly downwards at the base of a lycopsid cast. (D) Cast of stump with additional cast of collapsed central stele inside. (E) Lower section of a stump exemplifying the infilling siliciclastic material. (F) Partially decorticated bark with elongated leaf cushions. (G) *Brasilodendron*-like leaves compressed in rock matrix. (H) Bark compression covered by *Brasilodendron*-like leaf cushions; white arrows indicate the superior position of leaf scars. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

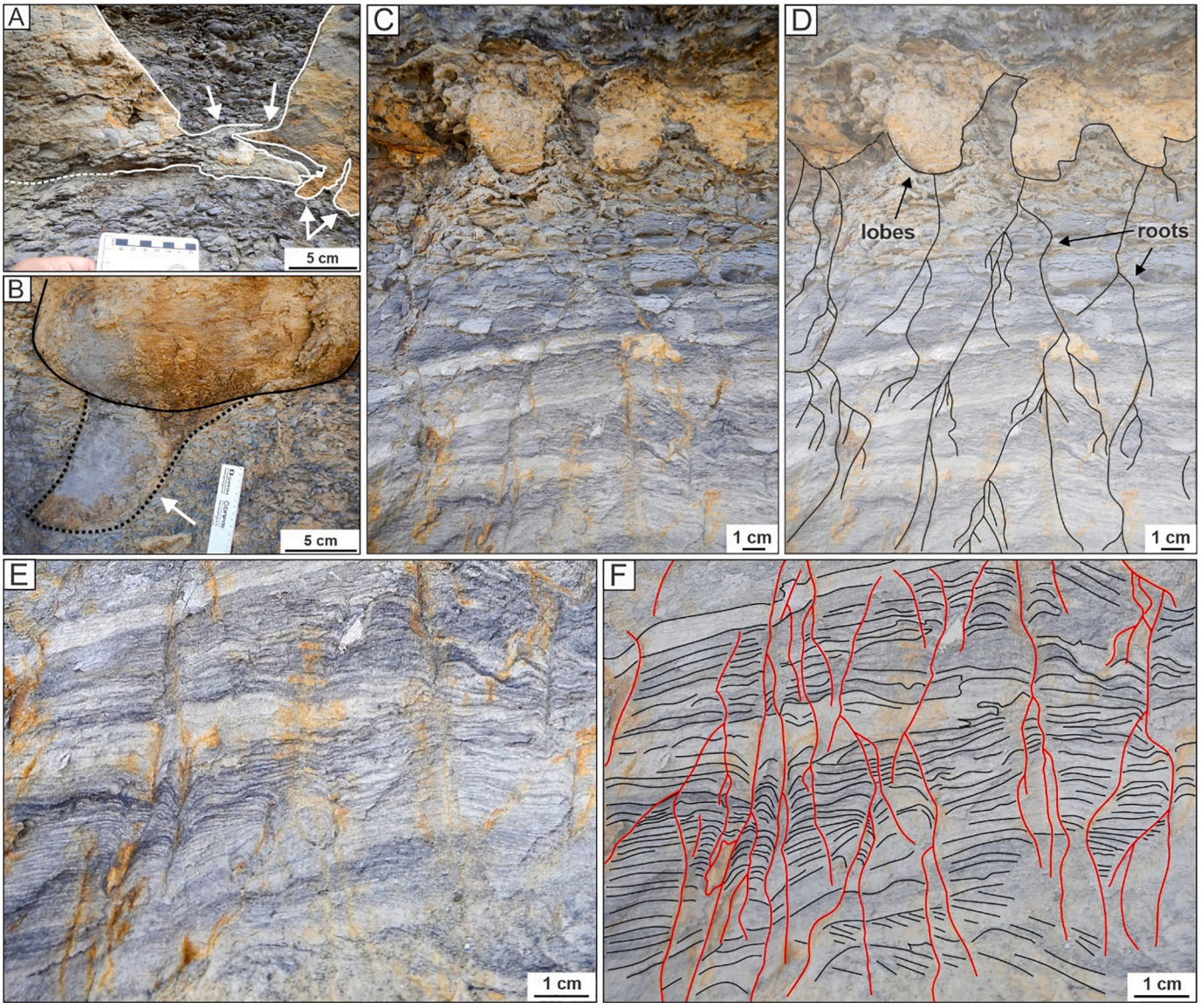

Fig. 9. Details of the *Brasilodendron*-like lycopsid root system. (A-B) Stem bases with lobes extending laterally and/or downwards (white arrows). (C) Small lobes and thin, repeatedly divided roots extending downward from the lycopsid base. (D) Drawing highlighting lobes and roots seen in C. (E) Detail of rooted beds seen in C and D showing an isotomously branched pattern and soft-sediment deformation around the roots. (F) Interpretation of roots (red lines) and deformed sediments (black lines) evidenced in E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Discussion

5.1. Life and burial setting

Our results show that *Brasilodendron*-like lycopsids colonized poorly developed soils, which formed in muds deposited on floodplains flanking sinuous distributary channels of a river-dominated, tidally-influenced delta (Fig. 10A). These trees formed dense communities that withstood regular physiological stress and disturbances. Early Permian in situ lycopsid forests from Gondwana are mostly associated with floodplains of prograding, river-dominated deltas (e.g., Cúneo and Andreis, 1983; Cariglino et al., 2012). This environment is, however, far less representative of Carboniferous paleoequatorial lycopsid forests (e.g., Calder et al., 2006; Rygel et al., 2006), where most communities have been interpreted as buried in tidal deposits (e.g., Archer et al., 2016; Elrick et al., 2017; Nelson et al., 2020).

In order for the trees to be exceptionally preserved in an upright posture, the *Brasilodendron*-like forest must have been rapidly buried to prevent remobilization by erosion or complete decay. The creation of long-term accommodation space, in addition to short-term burial below the water table is essential for the preservation of in situ fossil plants (e.g., Gastaldo and Demko, 2011; Looy et al., 2014; DiMichele et al., 2020). Preservation of considerable tree heights, as reported here, implies the occurrence of substantial and sudden accommodation events (Gastaldo et al., 2004; DiMichele and Falcon-Lang, 2011). Many Late Quaternary drowned forests, for example, were preserved owing to sea-level rise caused by glacial melting (e.g., Fedje and Josenhans, 2000), in combination with the existence of flat cratonic surfaces (DiMichele and Falcon-Lang, 2011).

In a postglacial coastal environment, such as that which prevailed in Ortigueira in the early Permian, the creation of accommodation space could have been triggered by several local (e.g., coal bed compaction, mud diapirism, earthquake-induced subsidence) or global (eustatic sea-level rise) mechanisms (DiMichele and Falcon-Lang, 2011). We do not disregard local processes as contributing mechanisms to generate the necessary accommodation space. However, given the substantial evidence for early Permian transgression following the demise of late Paleozoic glaciation throughout the Paraná Basin (e.g., Lavina and

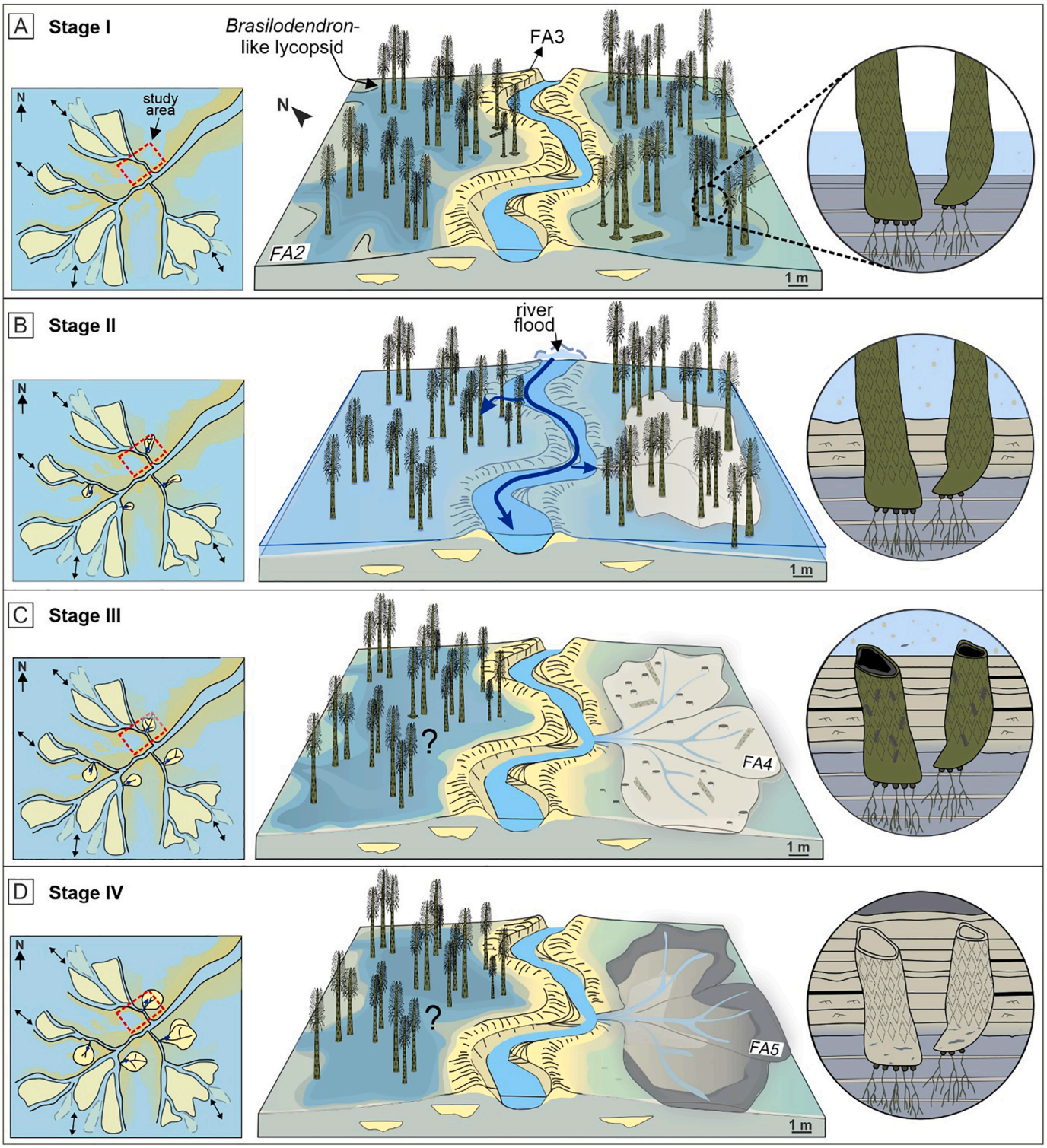

Fig. 10. Schematic paleoenvironmental model depicting life and burial of the Ortigueira fossil forest. A) The plant community colonized a tidally influenced interdistributary zone of a delta plain. B) Onset of crevasse splay progradation following a major river flood and progressive burial of *Brasilodendron*-like lycopsids. Death of the plant community occurred between stages II and III. C) Collapse of lycopsid trunks and creation of hollow cylinders prone to be filled with sediments. D) Progressive sedimentation and complete filling of the casts.

Lopes, 1987; Milani et al., 2007; Griffis et al., 2019), the hypothesis of eustatic sea-level rise being the main mechanism to produce the accommodation space seems more likely.

The rate of sediment accumulation around the upright plants is, however, the crucial factor to preserve them in the stratigraphic record (DiMichele and Falcon-Lang, 2011). The burial rate must exceed, at some point in time, the decay rate of the entombed plant remains (Gastaldo, 1994; Gastaldo and Demko, 2011). The Rio Bonito Formation represents a regressive phase interrupting the general transgressive pattern that followed the late Paleozoic deglaciation (Milani et al., 2007). The subaerial unconformity underlying the Rio Bonito Formation has been interpreted to result from tectonically induced base-level fall

because of uplifting in the northern flank of the basin (Milani et al., 2007; Zacharias and Assine, 2005). This uplifting would have caused denudation, increased sediment input and leading to sedimentation rates that outpaced the effects of eustatic rise. This early Permian tectonic readjustment also redirected sediment transport to the south, a major change compared to the northward sediment dispersion observed during most of the Carboniferous in the Paraná Basin (e.g., Zacharias and Assine, 2005; Mottin et al., 2018). However, the inferred increased sedimentation could also be a response to changes in regional hydroclimate, with a shift from glacial to interglacial conditions. This would have caused an increased weathering and erosion of exposed terrains at high latitudes during the interglacial periods and, ultimately, higher sedimentation rates (e.g., Griffis et al., 2021).

Thus, in terms of external factors, the rapid burial of the Ortigueira forest was favored by a combination of eustatic-driven accommodation and the increase of sediment supply to the basin in response to tectonic uplifting or changes in regional hydroclimate.

The regressive phase was punctuated by shorter-term marine transgressions that inundated the interdistributary areas (Fig. 10A), as evidenced by several indicators of tidal action. However, these incursions probably were not the cause of death of the lycopsids, as these trees could tolerate standing water conditions ranging from fresh to saline (e.g., Gastaldo, 1986a; DiMichele et al., 2009). Instead, burial probably began while the trees were still living, perhaps by means of a major river flood and increasing accumulation of sediment, leading to asphyxiation and compression of the roots and stem bases (Fig. 10B). In river-dominated delta plains, the rapid progradation of a crevasse-splay subdelta over the interdistributary zone, with abrupt breaching of levees, could provide an effective mechanism for rapid burial (e.g., Gastaldo, 1986a; Falcon-Lang, 2004; Calder et al., 2006). The alternation of rippled sandstone beds encasing the trees (Figs. 2B; 3A) supports the idea of burial by episodic but continuous pulses of sedimentation, rather than by a single catastrophic burial event, reinforcing the interpretation of a crevasse splay subdelta progradation.

Decomposition of the lycopsids would have occurred more rapidly in their exposed parts than in those that were already buried. As the plants died, their aerial portions that remained above the crevasse deposits decomposed and fell onto the sands and silt, and are preserved as compressions found in the beds surrounding the standing bases (Fig. 10C). After the downfall of aerial parts increased the exposure of the upright trees, decay of the inner soft parenchymatous and cortical tissues was accelerated in the lycopsid bases, creating a hollow cylinder surrounded by water-resistant sclerenchymatous bark (Fig. 10C; e.g., Gastaldo, 1986b; Phillips and DiMichele, 1992; DiMichele et al., 1996; DiMichele and Falcon-Lang, 2011). Subsequent sediment-laden flows infilled the cylindrical voids, either by entering the top opening, or through lateral fissures in the bark. The existence of lateral gaps is suggested by the presence of parallel lamination and ripples within some casts, and by the entombment and partial preservation of the bark (10D). During this process, the steles (woody central cylinders) could become preserved as individual casts, as the presence of lignin in the walls of their xylem cells made them more resistant to decay than were surrounding tissues. Therefore, differences in decaying and infilling rates between soft stem tissues and stele tissues could explain the preservation of the latter as collapsed casts inside some stem base casts (Fig. 8D).

Above the buried lycopsid-dominated forest, occur mudstones and rare sandstones of FA5, corresponding to distal portions of the crevasse splay. Alternating periods of flooding and subaerial exposure is indicated by the presence of interbedded rooted and massive mudstones, all of which are capped by an interval of peat accumulation, now preserved as the coal marker bed.

5.2. Structure of the Ortigueira forest

The immaturity of the host paleosol is suggested by the absence of alteration, except for being extensively rooted, and by the presence of pervasive soft-sediment deformation caused by lycopsid rooting within the hydroplastic sediments while still unconsolidated (Figs. 9E-F). This characteristic corroborates the low values of self-thinning (0.74) for the studied forest, and indicates that the lycopsids were able to colonize relatively newly deposited sediments in disturbance-prone environments. In this case, disturbance was caused by river floods introducing large amounts of sediment-laden water into the colonized interdistributary areas. Repeated disturbance of the interdistributary areas colonized by the *Brasilodendron*-like lycopsids either did not allow the forest to surpass the self-thinning threshold, or the community was buried and smothered by introduced sediment before reaching maturity.

The values of tree density (stems/ha) of the studied community are higher than those described for Pennsylvanian paleoequatorial lycopsid forests with similar diameters (e.g., Gastaldo, 1986a; DiMichele and DeMaris, 1987; DiMichele et al., 1996; Table 3), but lower than the values described for some Mississippian forests, whose average tree diameters are remarkably smaller (e.g., Falcon-Lang et al., 2004; Rygel et al., 2006; Table 3). The *Brasilodendron*-like lycopsids had a monopodial stem growth form without apical branching (Chaloner et al., 1979; Spiekermann et al., 2020), and thus would have formed a forest with much reduced crowns and an extremely open canopy, similarly to forms like *Pleuromeia* or *Chaloneria*. Such a forest could have supported a higher tree density than those tropical forests dominated by arborescent lycopsids that had multiple lateral branches and/or with much-divided apical crowns during terminal reproductive phases (DiMichele and DeMaris, 1987; Phillips and DiMichele, 1992; DiMichele et al., 1996; Opluštil et al., 2009).

The monospecific character of the forest depicted here probably reflects an ecophysiological tolerance to environments prone to periodic saline water incursion and repeated sediment introduction. The monospecificity or extreme low diversity in communities that colonize these transitional mixohaline subenvironments is expected, and has occurred since the late Paleozoic and up to the present day, as seen in mangroves growing within modern estuaries. In situ lycopsid forests from paleoequatorial regions might exhibit low diversity, frequently consisting of one identifiable species and rare co-occurrences of calamitaleans and pteridosperms (e.g., Wnuk and Pfefferkorn, 1987; DiMichele et al., 1996; Falcon-Lang et al., 2004), but more diversified lycopsid-dominated forests also occurred, consisting of pteridosperms, sphenopsids, cordaites and ferns (DiMichele and Philips, 1994).

5.2.1. Spatial organization of lycopsid communities

Lycopsid forests occupying peat-clastic transitional settings in the paleoequatorial belt are mostly associated with a random spatial organization (e.g., Gastaldo, 1986a; DiMichele and DeMaris, 1987; DiMichele et al., 1996). The random pattern is attributed to paleoenvironmental characteristics, but also to the life-history strategies of these plants. Peat swamps are nearly uniform environments with very low nutrient and acidic conditions, which implies minimal or an absence of intraspecific competition for resources (DiMichele et al., 1996). Some lycopsid trees were opportunistic and early-colonizers, allowing them to establish randomly in open sites (DiMichele and DeMaris, 1987; DiMichele and Phillips, 1994). The competition for sunlight in paleoequatorial lycopsid forests with equal-age distribution of the trees would be minimal and apparently not control the spatial distribution of individuals, since they were characterized by low crown volumes for most of their growth period (DiMichele and Phillips, 1985; DiMichele and DeMaris, 1987).

The lycopsids of the Ortigueira forest show a clumped organization pattern both in qualitative and quantitative analyses. However, the statistical analysis conducted in the 20 m^2 polygon area surveyed with the GPR shows a tendency to approach a random distribution. Populations characterized by a general clumped distribution may appear randomly organized if the quadrat size adopted in the sampling is small enough (Hayek and Buzas, 2010). Accordingly, we consider that the small area of the GPR survey, due to methodological limitations and

Table 3
Summary of paleoecological aspects of paleoequatorial (Mississippian and Pennsylvanian) and Gondwanan (early Permian) lycopsid forests.

Author	Growth substrate	Underground part	Diameter (cm)	Density (trees/ha)	Spatial distribution
Early Permian (Gondwanan)					
Cúneo and Andreis (1983)	Clastic - alluvial plain	Conical appendages in organic connection	25–60	N.D.	Clumped*
Jasper et al. (2006)	Clastic (organic-rich) - lagoon	Corm-like bases associated with roots in radial disposition	9–20	N.D.	Random
This study	Clastic - delta plain	Protostigmarian-type	9–75	2155–6344	Clumped
Pensylvannian (Paleoequatorial) - lepidodendrid					
Beckett (1845)	Organic + clastic	Stigmarian	30[§†]	763[†]	Random
Gastaldo (1986a)	Clastic - lower delta plain	Stigmarian	20.8[†]	87[†]	Random and contagious
DiMichele and DeMaris (1987)	Organic - coal swamp	Stigmarian	98[†]	1769[†]	Random
DiMichele et al. (1996)[†]	Organic - coal swamp	Stigmarian	60.2	573	Random
Calder et al. (2006)	Organic - interdistributary bay	Stigmarian	25–50	N.D.	N.D.
Archer et al. (2016)	Organic - coal swamp	Stigmarian	$\leq$ 2 m	N.D.	N.D.
Thomas and Seyfullah (2015)	Clastic - lake	Stigmarian	$\leq$ 1.5 m	N.D.	N.D.
Mississippian (Paleoequatorial) - *Lepidodendropsis*					
Falcon-Lang (2004)	Clastic - interdistributary flood-basin	Protostigmarian	0.9–22	10,746–29,060	Clumped
Rygel et al. (2006)	Clastic - coastal wetland	Protostigmarian	3.8–62.2	1846–37,000	N.D.

N.D. = no data; * Inferred from the spatial distribution map; [§] Estimated by DiMichele et al. (1996); [†] Data compiled by DiMichele et al. (1996).

consequently the small quadrat sizes, may have resulted in an inaccurate trend to approach the random distribution.

In western Gondwana, the upright arborescent lycopsids mapped by Cúneo and Andreis (1983) in the lower Permian Nueva Lubecka Formation of the Central Patagonia of Argentina show an apparent clumped distribution along a ca 300 m long transect, although those authors did not discuss this matter. The clusters are usually composed of two to three individuals, spaced between 5 and 9 m apart, and thus similar to the forest analyzed here. In addition, as in the Ortigueira forest, the Argentinean lycopsids are rooted in a clastic paleosol formed in a floodplain setting (Cúneo and Andreis, 1983). A distinct structure was proposed for the Quitéria lycopsids, in the southernmost part of the Paraná Basin (Fig. 1B), which are randomly distributed along a single clastic paleosol level (Jasper et al., 2006). However, the methods and results presented by those authors do not contain the relevant details needed for an accurate comparison with the Ortigueira record.

Lastly, the spatial organization of lycopsids in clusters in the study site can be explained by two possible coexisting factors. The first concerns the probable reproductive strategy of some arborescent lycopsids, which involves the dispersal of megaspores over limited distances (e.g., Falcon-Lang, 2004). Putative megaspores of *Brasilodendron*-like lycopsids are frequently found as impressions in the strata between individual upright trees, or together with bark impressions, suggesting an inherent proximity with the individuals or clusters. The second factor may be related to the laterally diverse configuration of landforms in the clastic depositional environment that could lead to a heterogeneous distribution of resources and intraspecific competition (e.g., Hayek and Buzas, 2010).

5.3. Root system adaptations

Our study provides the first evidence of lobate bases in Permian Gondwanan arborescent lycopsids. Extinct lycopsids with similar lobate bases were rare and occurred in the Late Devonian, Mississippian and Triassic as small to moderate-sized trees, besides species of the extant genus *Isoetes* (Jennings et al., 1983). It is assumed that these lobate bases were adapted to some extent to provide anchorage and mechanical support in hydroplastic sediments. The wavy fringe formed by the short and downwardly curved lobes probably helped in the fixation of the tree bases through a differential suction pressure exerted on the substrate. This feature, reminiscent of a "vintage cork lined soda bottle cap" type system, would be very efficient in unconsolidated sediments, as existed at the Ortigueira locality. The fine roots that extend downwards from the lobes form an isotomously branched pattern (Fig. 9D-F) that would be specialized in for water uptake. The isotomously branched root pattern of *Brasilodendron*-like lycopsids observed at the locality resembles that described by Hetherington and Dolan (2017) as a root architecture conserved over time from the earliest to modern lycopsids. Furthermore, the lobate bases would be an adaptive innovation acquired independently (=homoplasy) by the *Brasilodendron*-like lycopsids and other arborescent lycopsid lineages (Jennings et al., 1983; Hetherington and Dolan, 2017) in order to solve problems of settlement on unconsolidated substrates.

The underground parts of the lycopsids analyzed here are remarkably similar to those defined by Jennings et al. (1975) as the genus *Protostigmaria*, first described in the Price Formation (Virginia), but also occurring in other Mississippian deposits of the paleoequatorial belt (e.g., Falcon-Lang et al., 2004; Rygel et al., 2006). The underground system of the lycopsids from the Ortigueira forest resembles the protostigmarian forms regarding the presence of corm-like bases, short downward extensions (rhizomorphs/lobes), roots (water-absorbing "true" roots/rootlets) attached to the lobes, and furrows present between the extensions with rootlets (Jennings, 1975). The lycopsids of Ortigueira and the original specimens of *Protostigmaria* of the Price Formation, differ, however, in the size of the rooting structures (diameter of corm-like bases and size of downward extensions), in which the Gondwanan structures are a few times larger.

In comparison with other lower Permian records from Gondwana, the lycopsid bases observed in the Nueva Lubecka Formation of Patagonia (Fig. 1A) present conical appendages (up to 30 cm long x 1 cm wide), sometimes in organic connection, perpendicularly arranged and parallel to each other (Cúneo and Andreis, 1983). These plants are rooted in mudstones and sandstones interpreted as floodplain and meandering channel deposits of an alluvial plain. The conical appendages in the root system of this Argentinean lycopsid were considered to have an anchorage function, ensuring that the plant remained fixed in a clastic depositional environment subject to higher energy flood events (Cúneo and Andreis, 1983). Accordingly, these bases resemble those found in the lycopsids from Ortigueira, as they support shortened appendages, also interpreted as adaptive structures for fixing the plant to the substrate, but apparently differing in shape. As for the lycopsids preserved in the Quitéria outcrop, in the southern Paraná Basin (Fig. 1B;

Jasper and Guerra-Sommer, 1998), i.e., *Brasilodendron pedroanum*, the root system is formed by rounded corm-like bases associated with thin, elongated, acicular roots which are mostly parallel to the bedding planes (Jasper et al., 2006), differing noticeably from the lobate bases studied here.

In summary, Gondwanan lycopsids rooted in clastic substrates lack the stigmarian-type root system characteristic of most large paleoequatorial arborescent lycopsids (Table 3). Stigmarian rooting structures are described in a variety of paleoenvironments in the paleoequatorial lycopsid forests, as coal swamps and associated clastic wetland environments (Table 3). Nonetheless, a few taxa associated with clastic environments in the paleotropics exhibit lobed bases (e.g., Falcon-Lang, 2004; Rygel et al., 2006; Taylor et al., 2009) assigned to the genus *Protostigmaria* (Jennings, 1983). This may indicate that distinct root system architectures in the lycopsids were directly related to paleoecological conditions, but also to independent evolution of similar root structures in distinct lineages.

6. Conclusions

Fossil forests may be preserved in growth position in a geological instant under exceptional circumstances, mainly related to high rates of sediment accumulation combined with the creation of accommodation space. In the Paraná basin of Brazil, accommodation space created by postglacial eustatic sea-level rise following the early Permian deglaciation, combined with increased sediment influx, played an important role in the development of extensive coastal plains that could be colonized by arborescent lycopsids. However, tectonic control and/or changes in regional hydroclimate and corresponding increases in sediment input to the basin could also have played a relevant role in creating favorable habitats for lycopsid-dominated forests.

Relatively dense, lycopsid-dominated communities (3000–4000 trees per hectare), showing a clumped spatial organization, occupied relatively newly deposited sediments in interdistributary bay areas, which were prone to saltwater incursions and river floods. The death and burial of these forests were promoted by crevasse-splay progradation following a major river flood. The low value of self-thinning calculated for the studied population (0.74), which is below the 1.5 threshold, records the immaturity of this forest at the time of its burial. The higher density of trees in the Ortigueira forest in relation to many in paleotropical regions can be attributed in part to the reduced canopy present in the *Brasilodendron*-type lycopsids, which apparently had a monopodial architecture without apical branching, being similar in this sense to Euramerican forms such as *Pleuromeia* and *Chaloneria*.

There is a clear correspondence between the environments colonized by lycopsids from western Gondwana with those that inhabited in paleotropical lineages, which indicates a conservation of occupied niches regardless of paleogeographic position and paleoclimatic differences. However, the strategies of how to colonize and live in these same environments varied from group to group and from taxon to taxon, as seen here through the development of lobate bases for substrate anchorage by the Ortigueira lycopsids.

In order to better understand the ecology and evolution of lycopsids in Gondwana, it is necessary to greatly expand the knowledge of the taxonomy and environmental preferences of this group during the Carboniferous-Permian interval. This contribution is an initial attempt aimed at stimulating future work in this direction.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110814.

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