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Article

NEW OCCURRENCES OF LATE PALEOZOIC SEEDS IN THE PALEOVALLEY OF MARIANA PIMENTEL, RIO GRANDE DO SUL: TAXONOMY, DISPERSAL SYNDROMES AND BIOSTRATIGRAPHY

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ABSTRACT – Seeds are crucial for understanding plant life cycles and environmental adaptation. This study analyzed fossil seeds from the Cocuruto outcrop (upper Itararé Group, Paraná Basin) in the Mariana Pimentel (MP) Paleovalley, identifying three genera: *Cordaicarpus*, *Cornucarpus*, and *Samaropsis*. A new species, *Samaropsis sulriograndensis* sp. nov., was erected, along with occurrences of *Cordaicarpus cerronegrensis*, *C. brasilianus*, *C. truncatus*, *Samaropsis moreirana*, *S. kurtzii*, and *S. seixasii*. *Cornucarpus* was identified only at the genus level. The diagnosis of *Samaropsis seixasii* was emended. The dispersal syndrome of each species was proposed based on size, volume, and the presence of dispersal features, with anemochory and barochory being the most common. Notably, *Cordaicarpus brasilianus* showed a clear affinity with glossopterids, found in connection to *Arberia*-type fructifications. The stratigraphic ranges of these species in the MP Paleovalley were established for the first time, highlighting *S. kurtzii* as a key taxon for long-distance biostratigraphy in the latest Gzhelian–earliest Asselian interval.

Keywords: seed taxonomy, dispersal syndromes, phytostratigraphy, Paraná basin, Carboniferous–Permian transition.

INTRODUCTION

Seeds play a crucial role in understanding plant life cycles, assisting in the elucidation of their reproductive strategies, as well as expanding the knowledge regarding the ecology of plant communities. In the outcrops of the Late Paleozoic rocks from Rio Grande do Sul State, in southern Paraná Basin, Brazil, a great diversity of seeds has been recorded (Souza & Iannuzzi, 2007, 2009, 2012), in the meantime, studies about these fossils and their dispersal syndromes are still scarce.

The taxonomic analysis of the seeds in the Paraná Basin was based mainly on the previous works of Millan (1967a, b, 1974, 1977a, b, 1980, 1994, 1995), Rigby (1972), Archangelsky (2000), Bernardes-de-Oliveira *et al.* (2007) and Souza & Iannuzzi (2007, 2009, 2012). These works have addressed seeds from three genera, *i.e.* *Samaropsis*, *Cordaicarpus* and *Cornucarpus*. The genus *Samaropsis* Goeppert, 1984 is characterized, mainly, by the differentiated and well-developed testa, usually called "winged seed". The genus *Cordaicarpus* Geinitz, 1862 does not feature the differentiated testa, characterized by its oval shape and thin testa. Finally, the genus *Cornucarpus* Arber emend. Archangelsky, 2000 includes seeds with bilateral symmetry, with a bifurcated apex into two projections, similar to spikes or horns that are basically apical extensions of the sclerotesta. The external part of the testa, the sarcotesta, when present, is very thin. Other features, such as the presence or absence of a medial ridge, detailed characteristics of the bifurcated apex and the general outline of seed, allow for the differentiation of the seeds at a specific level.

On the other hand, studies about seed dispersal are common in the ecology of modern plants. Still, they are underexplored in paleontology even though they are essential tools for paleoecological and paleoenvironmental reconstructions. Key ecological functions of seed dispersal include: (i) escaping competition, (ii) colonizing suitable sites, and (iii) relocating seeds to favorable environments (Howe & Smallwood, 1982; Hughes *et al*., 1994; Willson & Traveset, 2000; Tiffney, 2004). These strategies transform the environment and shape the landscape. Through the taxonomic analysis made with seed fossils from the Lower Permian of the Paraná Basin, it was noticed that such dispersal structures could be used as tools for the paleoecology analysis due to the abundance and quality of the material (Souza & Iannuzzi, 2012).

The main goal of this contribution is to describe and identify unpublished seed fossils previously recovered from the Cocuruto outcrop, located in the State of Rio Grande do Sul, southern Paraná Basin, that is, for the first time, published here. Based on the considerations previously discussed, an analysis will be conducted to determine the probable dispersal syndrome of the seeds studied here, along with an evaluation of their botanical affinities, where applicable. Finally, considerations will be made about the stratigraphic range of seed taxa in the Morro do Papaléo locality and their value for biostratigraphic purposes.

MATERIAL AND METHODS

Geological setting

The Paraná Basin comprises a thick, widespread, sedimentary–magmatic sequence located in central-eastern South America, extending through southern Brazil, Uruguay, Argentina, and Paraguay. According to Milani & Zalán (1999), the basin fill can be divided into six supersequences: Rio Ivaí (Rio Ivaí Group, Ordovician–Silurian), Paraná (Paraná Group, Devonian), Gondwana I (Tubarão Supergroup and Passa Dois Supergroup, Carboniferous–Permian), Gondwana II (Triassic units), Gondwana III (São Bento Group, Jurassic–Cretaceous) and Bauru Supersequence (Bauru Group, Cretaceous). This paper focuses on the post-glacial deposits of the uppermost Itararé Group and the Rio Bonito Formation (Tubarão Supergroup, Gondwana I Supersequence) exposed at the Morro do Papaléo area, located in the municipality of Mariana Pimentel, southern of the Paraná Basin (Figure 1).

Two sections called Morro do Papaléo (Mine) and Faxinal (Outcrop) within the proximal area of Mariana Pimentel (**MP**) Paleovalley (Iannuzzi *et al*., 2010) are known. The Morro do Papaléo Section is the thickest and most complete, being better studied (Iannuzzi *et al*., 2006; Iannuzzi, 2010) and, therefore, serves as the reference section for understanding the succession of the sedimentary rock package exposed in this locality. The lower portion of the Morro do Papaléo Section is assigned to the uppermost Itararé Group, and the upper to the Rio Bonito Formation (Iannuzzi *et al*., 2006).

A paleoenvironmental model shows that during the initial deglaciation period, the MP Paleovalley was filled with fine-grained sediments assigned to the Itararé Group (Iannuzzi, 2010; Fedorchuk *et al*., 2019). This part of the section mainly comprises of lacustrine and lagoonal deposits associated towards the top with prodelta and delta front deposits. The overlying coal-bearing sequence, deposited under alluvial plain-fan deltaic and fluvial conditions, is assigned to the Rio Bonito Formation (Iannuzzi, 2010; Fedorchuk *et al*., 2019).

Cocuruto outcrop

Cocuruto outcrop is also situated in the Morro do Papaléo locality, in the Municipality of Mariana Pimentel, around 100 km southwest of Porto Alegre (Figure 1). This outcrop is about 300 m east of the Morro do Papaléo Section described by Iannuzzi *et al.*

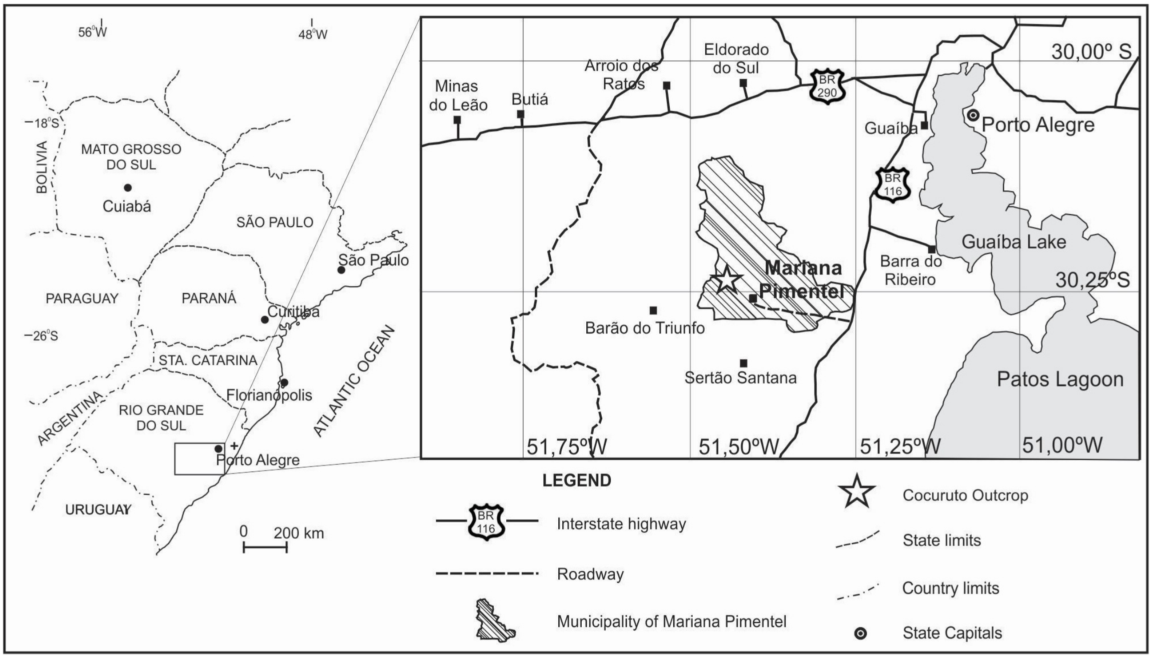

Figure 1. Localization map of the Morro do Papaléo locality and Cocuruto outcrop, Mariana Pimentel town, Rio Grande do Sul State (modified from Iannuzzi *et al*., 2006).

(2006). It is essential to point out that the Cocuruto outcrop was preliminarily reported by Marques-de-Souza (2013) in her doctoral thesis but was never formally published. Therefore, the following description represents this outcrop's first in a journal.

The analyzed section of Cocuruto (Figure 2) measures around 3.6 m and is composed, at the bottom, of 1.1 m of brown/yellow and massive claystone that sometimes contains rare sandy-silt lenses and evidence of roots. The top of this clayish package is cut by a lens of thin-to-middle grained sandstone that has wavy surfaces and internally climbed stratifications. After that, there is a 1.2 m thick grain-decreasing heterolytic package that starts off as a very thin grained sandstone and ends as a claystone. Internally, there is a presence of truncating wavy lamination through the package. From the lower to middle portions of section, there is internally a dominance of wavy and ripple laminations with flaser, varying towards the upper portion, to the wavy lamination and linsen, as the granulometry becomes thinner. There are evidences of rare plant remains in this interval (N1). Above, there is a bed of middle grained sandstone around 20–30 cm thick, showing ripple lamination. At the top of this bed, roots can be found as evidence of the presence of a paleosol (N2). At the top of the section, there are two heterolithic grain-decreasing sandstones, around 40 cm thick, interspaced with a bed of massive claystone, with evidence of paleosol at the top. These two sandy packages are similar to the heterolith described in the middle portion of the section, presenting the same sedimentary structures (*i.e.*, wavy bedding, cavalcading cross-stratification, truncating wavy lamination, linsen bedding). However, they are richer in terms of plant remains. In the first heterolithic package, there are wavy heteroliths and truncating wavy laminations, and there is a dominance of cavalcading cross-stratification at the bottom, and linsen at the top (N3). After the layer of massive claystone, the second package shows wavy heteroliths and laminations, also possessing cavalcading cross-stratification at its bottom and linsen at its top (N4). On top of this last package, there is a 20 cm thick bed of conglomerate sandstone with cross-stratification (Figure 2).

According to the lithological correlation with the Morro do Papaléo Section (Iannuzzi *et al*., 2006), the section of Cocuruto outcrop corresponds to the interval between the uppermost Itararé Group (fine-grained rocks) and the lowermost Rio Bonito Formation (conglomerate sandstone). The uppermost portion of the Itararé in the Morro do Papaléo Section are interpreted as having been generated in a lacustrine environment (Iannuzzi *et al*., 2006; Iannuzzi, 2010; Fedorchuk *et al*., 2019) while the conglomerate sandstone represents a channel deposit of a fluvial system that characterizes the most basal part of Rio Bonito Formation (Iannuzzi *et al*., 2006; Iannuzzi, 2010). The occurrence of many plants remains, a few paleosols and the sedimentary structures such as wavy, truncating wavy lamination, linsen, and flaser, suggest that the fossiliferous levels (N1–N4) were generated in marginal settings of a lentic environment.

Palynological analysis at the base of the Morro do Papaléo Section furnished elements that characterize the *Vittatina costabilis* Palynozone (Iannuzzi *et al*., 2006), considered to be early Permian in age. However, radiometric dating performed

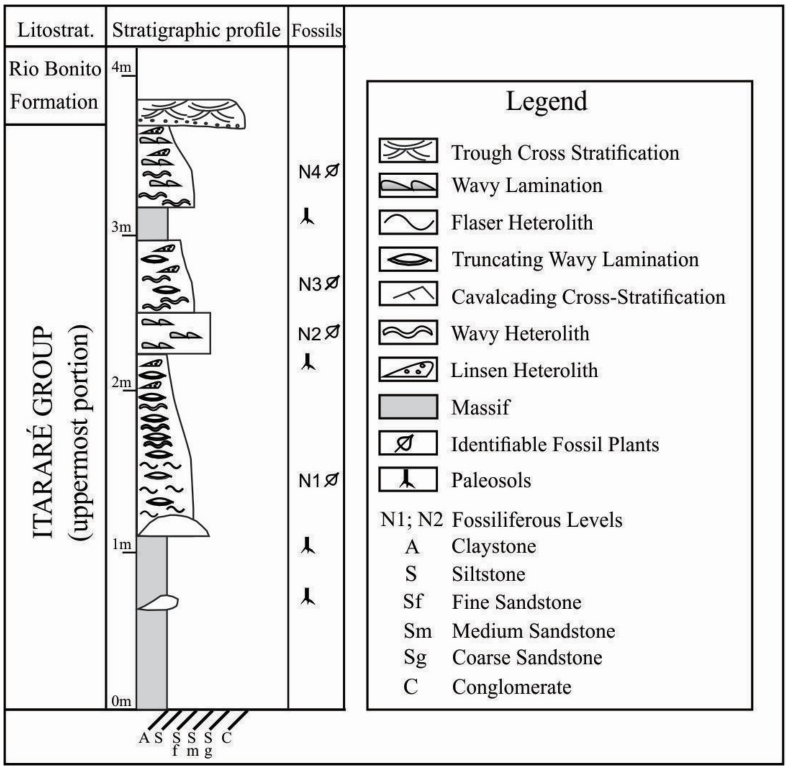

Figure 2. Stratigraphic profile of the Cocuruto outcrop, situated at the Morro do Papaléo locality, in Mariana Pimentel town, Rio Grande do Sul State. Note the fossiliferous levels (N1 to N4) very close to each other (modified from Marques-de-Souza, 2013).

on strata located in the central region of Rio Grande do Sul State indicated an age of the latest Pennsylvanian for the upper portion of the Itararé Group (Cagliari *et al*., 2023). Unfortunately, the rock exposure that was dated does not contain any macro- or microfossils preserved, which prevents a biostratigraphic correlation with the outcropping sections of the Morro do Papaléo area. Other radiometric dating of deposits in the southern part of the state shows that the overlying Rio Bonito Formation begins in the earliest Permian (Griffis *et al*., 2018, 2019). Therefore, an age in between the latest Pennsylvanian and earliest Permian can be assumed for the deposits at the top of the Itararé Group in the Morro do Papaléo locality, both for the Morro do Papaléo Section and the Cocuruto outcrop.

Material

The plant material was previously collected on different heterolithic levels (*i.e*., N1–N4) positioned very close to each other along the Cocuruto Outcrop (Figure 2). Thus, this collection will be treated as only one association of seeds that coexisted in the same plant communties. The seeds preserved as impressions and compressions are housed in the Paleobotany Collection of the Paleontology Museum of the Paleontology and Stratigraphy Department (**DPE**) of the Federal University of Rio Grande do Sul (**UFRGS**), Brazil, under the prefix MP-Pb.

In addition to the seeds that will be described later, the fossiliferous levels of the Cocuruto outcrop record a large quantity of glossopterid leaves, with *Gangamopteris* McCoy (1875) predominating over *Glossopteris* Brongniart (1982). Stems and leaf whorls of sphenophytes (*i.e*., *Paracalamites* Zalessky, 1927; *Phyllotheca* Brongniart, 1828; and *Stephanophyllites* Millan & Dolianiti emend. Rohn & Lages, 2000) are common. *Arberia*-type fructification occurs eventually.

Morphometric analysis

The seed's morphology was analyzed and described according to the following criteria: (i) axis of symmetry: platyspermic, radiospermic; (ii) shape and testa differentiation (sarcotesta, sclerotesta, and endotesta); (iii) shape and surface of the nucellus; (iv) the relation between the testa thickness and nucellus width (according to Oliveira & Pontes, 1976); (v) presence or not of a median ridge along the nucellus; (vi) surface of the sarcotesta (smooth, striated, ornate) and (vii) shape of the micropyle (Millan, 1994; Archangelsky, 2000).

The terms length, width, and thickness were utilized for the measurement analysis, the latter directly characterizing the maximum extension of the testa thickness. Considering that the samples analyzed in this work are impressions, the studied seeds appear as flattened fossils, with a two-dimensional preservation tendency.

The taxonomic design of *Samaropsis* or *Cordaicarpus* is based on the testa differentiation, in which the genus *Samaropsis* has thicker and differentiated testa, while *Cordaicarpus* has seeds with thinner testa. To determine that more precisely, a relation between testa thickness and nucellus width is used (Tt/Nw). The seeds that show a relation of testa thickness/nucellus width (Figure 3) higher or equal to 0.22 mm (1/4.5) are classified as *Samaropsis*, and the ones with the relation with a value lower than that will be considered *Cordaicarpus* (Oliveira & Pontes, 1976).

Seed dispersal

Seed dispersion is crucial for understanding a plant's habit and habitat. This study examines three criteria: (i) seed size, (ii) the presence and role of dispersal structures, and (iii) the relationship between dispersal method and seed size, focusing on morphological characteristics unaffected by fossilization.

Seed size provides insights into a species' ecological group and local distribution. Larger seeds, with greater nutritional reserves, offer more autonomy before germination, allowing for wider dispersal and germination in shaded, nutrient-rich areas. In contrast, smaller seeds are linked to pioneer species that germinate in well-lit environments, enabling faster independence (Harper *et al*., 1970; Tiffney, 1984, 1986, 2004; Coomes & Grubb, 2003).

The seed size was interpreted by the seed volume in mm^3 (Tiffney, 1984). To measure the *volume* of the seeds (total and nucellus only), the formula

$$V = 4/3\pi ab^2 \quad (1)$$

where a = seed length/2; b = (seed width + seed thickness)/4 – was applied. This formula, used to obtain the volume of ellipsoid structures, was used by Eriksson *et al*. (2000) and Sims (2012).

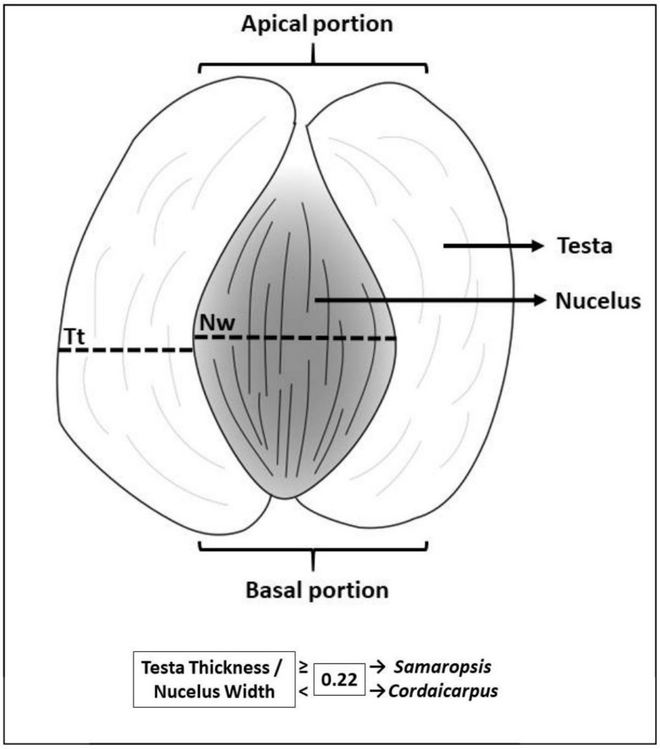

Figure 3. Schematic drawing of a specimen of *Samaropsis kurtzii* (MP-Pb 5480), showcasing the testa and nucellus, two fundamental parts to determine the seed's genus. The dotted lines represent the measures (**Tt**, testa thickness, and **Nw**, nucellus width) utilized in the relation between testa thickness and nucellus width (**Tt/Nw**), established by Oliveira & Pontes (1976): if the value is equal or higher than 0.22 a particular seed belongs to the genus *Samaropsis*, but if the value is below 0.22 it is classified into the genus *Cordaicarpus*.

When the seeds are preserved as impressions and compressions, Tiffney (1984) suggests that the thickness be estimated by the formula

$$thickness = width\ x\ 0.66 \quad (2)$$

assuming the Power Law governing the relationship between surface area and volume. The total volume was used for seeds with narrow, fibrous testa, while the nucellus volume was used for winged, membranous testa to avoid overestimation.

Dispersal syndromes are categorized as biotic or abiotic. Biotic dispersal involves organisms (*e.g.*, birds, insects), while abiotic dispersal involves non-living agents (*e.g.*, wind, water). Major abiotic forms include anemochory (by wind), hydrochory (by water), barochory (by action of gravity), and autochory (self-dispersal). Biotic dispersal includes epizoochory (transport of animals), fish dispersal, saurochory (by reptiles), ornithochory (by birds), and mammal dispersal. These syndromes can be combined, leading to complex seed transport (Van der Pjil, 1969).

SYSTEMATIC PALEONTOLOGY

GYMNOSPERMAE

Semina Incertae sedis

Cornucarpus Arber emend. Archangelsky, 2000

Cornucarpus sp. 1

(Figure 4A–B)

Study material. MP-Pb 4982 A–B (Figure 4A–B).

Description. Small platyspermic and elliptical seed with a length of 5.8 to 6.2 cm and a width between 2.4 and 2.6 cm, and a nucellus smooth, but covered by a very few fine longitudinal grooves. The apex is bifurcated into two into two thin, incomplete horns, and the base is flattened, sometimes trucated showing occasionally two tiny projections laterally arranged (Figure 4B). The testa is narrow (thickness less than 1 mm), undifferentiated, and follows the general contour of the seed. The nucellus follows the shape of the seed and is smooth, with 5 mm in length and around 2.0–2.2 mm of width.

Volume estimated. The range of total volume of these specimens varies between 12.0–15.1 mm^3.

Discussion and comparison. The specimens studied represent small seeds, with a narrow testa and apices bifurcated into two small and thin horns or processes. According to the amendment proposed for this genus by Archangelsky (2000), they can be included in the fossil genus *Cornucarpus*.

Particularly, the main diagnostic characteristic of fossil-genus *Cornucarpus* is the presence of two delicate projections at the apex (micropylar region) of the seed, especially to differentiate from those specimens normally included in *Cordaicarpus*. However, these small apical structures cannot always be clearly seen in fossils, depending on the state of preservation of each specimen. Therefore, it is quite fearful to indicate the presence of forms attributable to the genus from a single specimen or from specimens that are not well preserved (see discussions in Archangelsky, 2000). Because of this, the initial record of forms attributed to the seed genera has been contested by researchers later re-examined. This was the case of the species *Cornucarpus cerquilhensis* Millan (1977b), transferred to *Samaropsis* by Bernardes-de-Oliveira *et al*. (2007), who established a new combination, i.e. *Samaropsis cerquilhensis* (Millan) Bernardes-de-Oliveira et al (2007).

The material described is comparable to the common *Cornucarpus* species already described for Gondwana, but it appears morphologically distinct from all of them. The specimens studied herein differ from *Cornucarpus striatus* Walkom, 1935, from the Permian of Australia by clearly presenting two apical projections, whereas Walkom's species has only a strongly emarginate apex and lacks any projections. Therefore, this species does not fit the accepted definition of *Cornucarpu*s (according to the diagnosis amended by Archangelsky, 2000) and should be removed from this genus in the future.

In South America, two known species: *Cornucarpus patagonicus* (Feruglio), Corrêa da Silva & Arrondo (1977) ex. A. Archangelsky and *Cornucarpu*s *furcata* (Surange & Lele) Maithy (1965) are known. The seed under study differs from *C. patagonicus*, from the Lower Permian of Argentina, due to its more elongated and elliptical shape, the absence of striations regularly distributed along the seed surface and, mainly, because it has more prominent apical projections, being longer and better defined than in the Argentinean species. *C. furcata*, originally established from specimens from Lower Permian strata in India, was later recognized in the Lower Permian (Rio Bonito Formation) of the Paraná Basin, in Brazil, by Bernardes-de-Oliveira & Yoshida (1981). Our material is close to *C. furcata* in terms of dimensions (length-width) and the presence at the apex (micropylar region) of two relatively long and thin horns that project beyond the seed body. However, it is distinguished by its more elliptical and elongated shape, less oval, and by the smooth nucellus and, especially, by the two tiny projections that occur at the base of the seed. Another small difference that can be noted is that the two apical horns do not come together at the base, forming like a short "neck" from the seed body. In our specimens, the horns depart side by side, without showing any basal connection or junction with each other. Considering the above, it is preferred to keep the studied specimens classified only at a generic level and simply named them as *Cornucarpus* sp. 1.

Cordaicarpus Geinitz, 1862

Cordaicarpus cerronegrensis Souza et Iannuzzi, 2009

(Figure 4C–D)

Study material. MP-Pb 5059 (Figure 4C), MP-Pb 5475 (Figure 4D).

Description. Small platyspermic and lance-ovate/ovate (drop-shaped) seed with striated surface with elongated and acute apex and rounded base (Figure 4C–D). It measures 6–7.2 mm in length and 3–4 mm in width. At the base (as seen in specimen MP-Pb 5475, Figure 4D), an insertion point is evidenced by a rounded "scar". The testa is narrow, undifferentiated, and striated and follows the general contour of the seed, but its thickness is slightly variable, being thinner on both sides and the basal region of the seed, while it is thicker on the apical region (reaching up to 0.5 mm). The nucellus follows the shape of the seed, except for the apex where it does not follow the

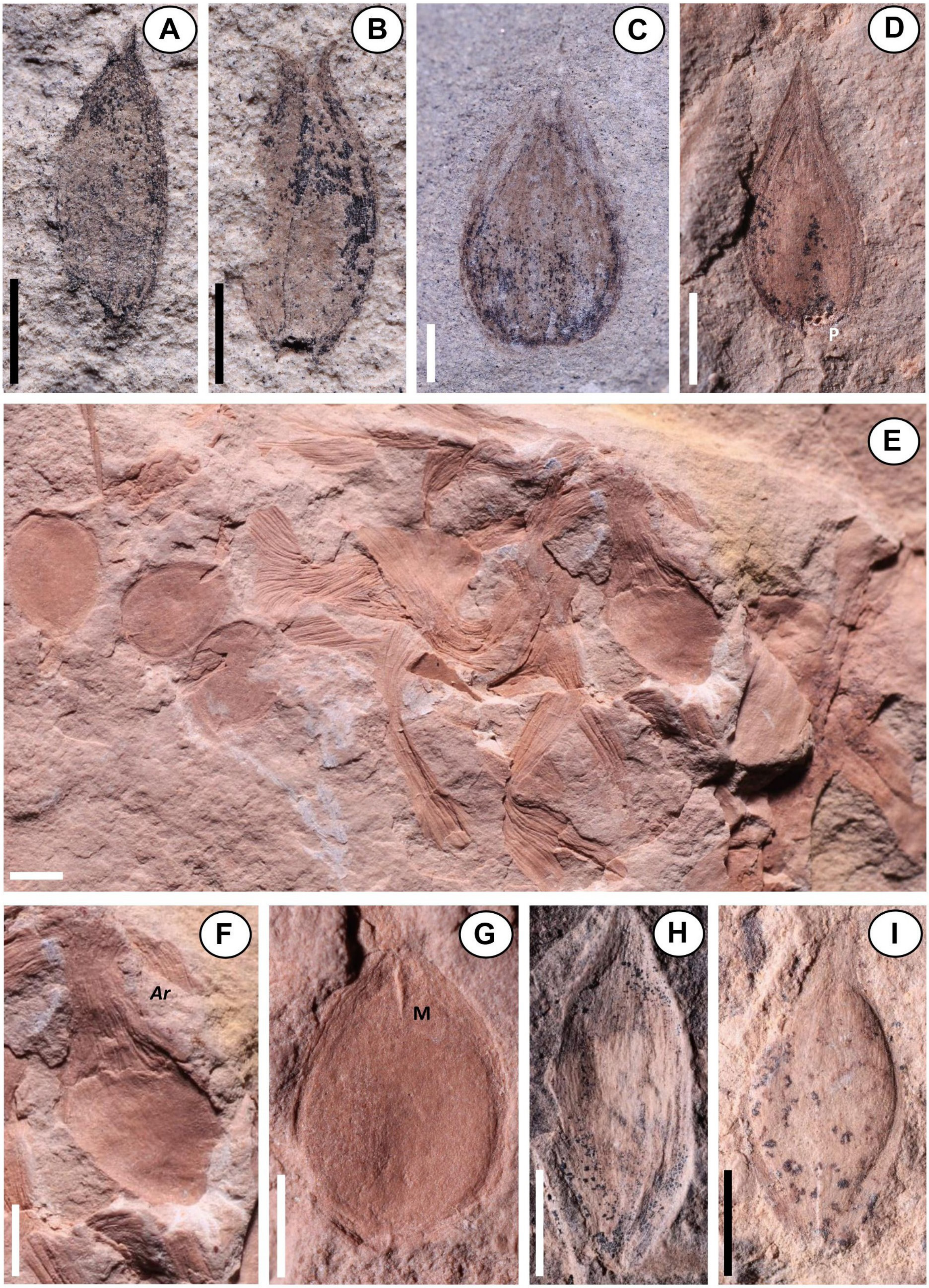

Figure 4. A–B, *Cornucarpus* sp. 1, **A**, MP-Pb 4982a; **B**, MP-Pb 4982b. **C–D**, *Cordaicarpus cerronegrensis*, **C**, MP-Pb 5059; **D.** MP-Pb 5475, the base of the seed has a strong peduncular mark; **E–G**, *Cordaicarpus brasilianus,* **E**, MP-Pb 4462; general view of specimen, **F**, shows, in detail, the connection between the *Arberia*-like fructification and one of the seeds, in **G**, there is a micropyle mark at the top of the seed. **H–I**, *Cordaicarpus truncatus*, **H**, MP-Pb 5473; **I**, MP-Pb 3970. **Abbreviations: P**, peduncular mark; **Ar**, *Arberia*-like fructification; **M**, micropyle mark. Scale bars: A–B, E–G = 2 mm; C–D, H–I = 3mm.

testa until the end, being shorter. The nucellus is 5.7–6.0 mm in length and 2.5–3.5 mm in width. The relation between testa thickness and nucellus width results in values of 0.14–0.17.

Volume estimated. The range of total volume of this species varies between 23.4–34.6 mm^3.

Discussion and comparison. The Tt/Nw relations obtained from the specimens allows us to include them in the genus *Cordaicarpus*. Specimens with similar morphology were described by Souza & Iannuzzi (2009). In that study, the authors compared that morphotype with other platyspermic species from Gondwana that possessed an obtuse to acute or acuminate apex and a striated surface without a median ridge. These species include *Cordaicarpus acuminatus* Gutierrez *et al.*, 1992; *C. chicariensis* Lele, 1962; *C. emarginatus* Walkom, 1935; *C. irapuensis* Oliveira (Oliveira & Pontes, 1976); *C. mucronatus* Höeg & Bose, 1960; *C. prolatus* Walkom, 1935; *C. ovatus* Walkom, 1935; *C. rocha-camposii* Oliveira (Oliveira & Pontes, 1976); and *C. zeillerii* Maithy, 1965.

As highlighted by Souza & Iannuzzi (2009), despite their structural simplicity, all these species exhibit differences in apex shape, base morphology, and overall seed outline (see Souza & Iannuzzi, 2009, for details). Consequently, the authors described a new species, *Cordaicarpus cerronegrensis*, emphasizing its drop-shaped body, striated surface, and the presence of insertion scars at the base. These characteristic features are also observed in our material and support its classification as *Cordaicarpus cerronegrensis*.

Other occurrences. Cerro Negro Outcrop and Faxinal Section-Morro do Papaléo (both at the uppermost the Itararé Group), in Mariana Pimentel Municipality, Rio Grande do Sul State (in Souza & Iannuzzi, 2009).

Cordaicarpus brasilianus Bernardes-de-Oliveira, De Castro-Fernandes, Tewari et Ricardi-Branco, 2007

(Figure 4E–G)

2009. *Cordaicarpus* aff. *C. brasilianus* Souza & Iannuzzi, p.11, fig. 5.

Study material. MP-Pb 3970 C–E, 4462 A–E (Figure 4E–G), 4467 A–T, 4482 A–H, 5456 A–D, 5468 A–G, 5473, 5477 A–C, 5487, 5488, 5553 A–I, 5562 A–D, 5564 A–H.

Description. Small seeds with smooth surfaces and widely elliptic shapes, almost circular, and a rounded base and obtuse apex. The length varies between 3.0–4.5 mm and the width between 2.0–3.7 mm. The seeds have an undifferentiated testa that outlines the nucellus with almost the same thickness. The nucellus follows the same shape pattern as the seed; it has an incipient medium ridge, its length varies between 3.0–4.0 mm, and its width between 2.5–3.0 mm. The micropyle is visible in some samples, in a "V" shape (Figure 4G). The relation between the maximum testa thickness and nucellus width (Tt/Nw) is approximately 0.08–0.12.

Volume estimated. This species' total volume range varies between 9.7–27.9 mm^3.

Discussion and comparison. The studied material is classified as part of the genus *Cordaicarpus*. Souza & Iannuzzi (2009) described the same morphotype from the Morro do Papaléo Section. In that study, the authors compared the morphotype with *Cordaicarpus prolatus* Walkom, 1935, *C. ovatus* Walkom, 1935, *C. chicariensis* Lele, 1962, *C. irapuensis* Oliveira (Oliveira & Pontes, 1976), *C. rocha-camposii* Oliveira (Oliveira & Pontes, 1976) and, *Cordaicarpus brasilianus* Bernardes-de-Oliveira *et al.* (in Bernardes-de-Oliveira *et al.*, 2007). The authors concluded that the material had an affinity with *Cordaicarpus brasilianus*, classifying it as *Cordaicarpus* aff. *C. brasilianus* (Souza & Iannuzzi, 2009).

Here, we describe specimens from the Cocuruto outcrop that share the same morphology as *Cordaicarpus* aff. *C. brasilianus* and, as observed by Souza & Iannuzzi (2009), are also found in association or connection with *Arberia*-type fructifications (Figure 4E–F). By examining the holotype of *Cordaicarpus brasilianus*, we observed that, despite its structural simplicity, there is a strong morphological resemblance to our material. The occasionally striated seed surface, which led Souza & Iannuzzi (2009) to classify the specimens from the Morro do Papaléo Section as C*ordaicarpus* aff. *C. brasilianus*, is now understood to be a characteristic that, in this species, depends on the degree of preservation of the seed coat covering the nucellus.

Considering the above, the material from the Cocuruto outcrop is identified here as belonging to *Cordaicarpus brasilianus*. Furthermore, the specimens from the Morro do Papaléo described by Souza & Iannuzzi (2009) are also definitively included in *C. brasilianus*.

Other occurrences. Levels N4 (uppermost Itararé Group), N7 and N8 (Rio Bonito Formation) at the Morro do Papaléo Section, in Mariana Pimentel Municipality, Rio Grande do Sul State (in Souza & Iannuzzi, 2009); "Toca do Índio" Ranch (uppermost Itararé Group), in Cerquilho Municipality, São Paulo State (*in* Bernardes-de-Oliveira *et al*., 2007, 2016); Probst Outcrop (Rio Bonito Formation), in the Municipality of Alfredo Wagner, Santa Catarina State, southern Brazil (Rischbieter *et al*., 2022).

Cordaicarpus truncatus Souza et Iannuzzi, 2009

(Figure 4H–I)

2009. *Cordaicarpus truncata* Souza & Iannuzzi, p.11, fig. 5.

Study material. MP-Pb 3970A–B (Figure 4I), 5473B (Figure 4H).

Description. Seeds with bilateral symmetry, ovate, and striated surface possess acute apex and truncated base. In the better-preserved specimen (MP-Pb 3970) the length is 9.5 mm, and its width is 4.7 mm. The nucellus basal portion follows the shape of the seed, but the apical portion is more obtuse in format. The nucellus surface presents a prominent striation and the micropyle does not become very noticeable; the medium ridge is poorly preserved. The narrow testa is thin on the sides and thicker on the tips, an irregular margin forms on the base and possibly indicates the point of connection with the mother plant.

Volume estimated. the total volume of these seeds varies between 39.5–75.6 mm^3.

Discussion and comparison. The specimens analyzed were classified as part of the genus *Cordaicarpus*, due to the low values presented in the Tt/Nw relations (0.11–0.14). Several Paleozoic seed species, including *Cordaicarpus acuminatus* Gutiérrez *et al*. (1992), *C. mucronatus* Höeg & Bose, 1960, and *C. prolatus* Walkom, 1935, exhibit bilateral symmetry, a narrow and undifferentiated testa lacking a median ridge, and an obtuse, acute, or acuminate apex. However, none of these species exhibit the truncated base observed in our material.

Cordaicarpus cerronegrensis established based on specimens from the Cerro Negro outcrop (Souza & Iannuzzi, 2009) and Faxinal Section in Morro do Papaléo locality (Pimentel Municipality, Rio Grande do Sul State) and identified among the specimens analyzed in this study, differs in its drop-shaped body (elongated acute apex and rounded base) as well as in size.

Another morphotype, *Cordaicarpus truncata* Souza & Iannuzzi, 2009, was described from the Level N2 of Morro do Papaléo Section (see Souza & Iannuzzi, 2009). The authors emphasized its distinctive seed outline, particularly the truncated base, which appears to correspond to a broad point of attachment to the fructification, as well as its prominent apex. These defining characteristics are also observed in our specimens.

Considering all the morphological traits analyzed, the material from the Cocuruto outcrop is identified here as belonging to *Cordaicarpus truncata*. In accordance with international rules of botanical nomenclature, to ensure agreement of the species epithet with the genus gender, the species name is here changed to *Cordaicarpus truncatus*.

Other occurrences. Level N2 of Morro do Papaléo Section, in Mariana Pimentel Municipality, Rio Grande do Sul State (in Souza & Iannuzzi, 2009).

Samaropsis Goeppert, 1864

Samaropsis sulriograndensis Prado, Marques-de-Souza & Iannuzzi sp. nov.
(Figure 5A–B)

Holotype. MP-Pb 5464 (Figure 5A).

Paratypes. MP-Pb 2586, 5058a, 5060ab, 5466, 5472, 5656ab (Figure 5B).

Etymology. The specific epithet *sulriograndensis* derives from the name of the state the species was found, Rio Grande do Sul.

Type locality. Cocuruto outcrop, Morro do Papaléo site, in Mariana Pimentel Municipality, Rio Grande do Sul State.

Stratigraphic horizon. uppermost Itararé Group, Paraná Basin.

Age. Latest Carboniferous–earliest Permian (Gzhelian–Asselian).

Diagnosis. Platyspermic seeds of overall reniform outline with emarginate apex and reniform base. Nucellus finely striated, lacking a median ridge, ovate to widely ovate, and surrounded by two testae: an innermost narrow and fibrous sclerotesta and an outer well developed and reticulated sarcotesta. Sarcotesta enlarged in the median and basal portions of the seed, and interrupted at the base.

Volume estimated. The nucellus' volume measures around 360.5–670.2 mm^3.

Description. Total length varies around 14–17 mm and the width measures around 13–22.6 mm. We could observe three distinct structures, the more internal one was interpreted as the central body (nucellus) with an ovate or widely ovate outline, obtuse apex, rounded base and finely striated surface. The size of the nucellus varies around 10–12 mm (N= 7) in length and 10–13.94 mm (N= 7) in width. The intermediary layer, when preserved, is interpreted as sclerotesta: it covers the whole nucellus and is thin (0.31–0.37 mm; N= 6) and fibrous. The sarcotesta (external last layer), is well-developed, forming two structures that resemble wings. It possesses a finely reticulated striation; it has a variable width of 3–5.6 mm (N= 7) and has an improved development on the median and basal portions of the seed corresponding to ½ of the seed's total width. The sarcotesta is interrupted in the most basal portion of the seed.

Discussion and comparison. Among the described seeds for the Carboniferous–Permian interval of Gondwana, the specimens described here fit in the morphological types of the winged seeds, with differentiated testa and sarcotesta with sinus. In the Paganzo Basin, northern Argentina, two species resemble morphologically and morphometrically to the ones studied here, possessing a prominent lateral expansion of the sarcotesta, they are: *Samaropsis kurtzii* Leguizamon, 1971 and *S. tasacunensis* Archangelsky, 2000. They differ from our in the basal recession observed in our samples that interrupts the sarcotesta and shapes the seed in an overall reniform outline. Furthermore, the shape of the nucellus in our specimens is oval, while both Argentinean species are elliptical (see Table 1).

This recession that interrupts the sarcotesta in the basal portion of the seed is also observed in specimens included in different species from the Paraná Basin, namely: *Samaropsis criciumensis* Millan, 1967b, *S. bainhensis* Millan, 1967b, *S. rygbyi* Millan, 1977b, *S. rugata* Bernardes-de-Oliveira *et al.*, 2007 and *S. rohnii* Bernardes-de-Oliveira *et al.*, 2007. These species, however, exhibit greater development in their longitudinal axis (which gives them an overall elliptical shape), as well as a greater development of the sarcotesta in the basal portion, differing therefore from the analyzed material.

In the other regions of Gondwana, the species *Samaropsis ganjirensis* Saksena, 1956, *Samaropsis goraiensis* Surange & Lele, 1956, both from India, and *S. boutakoffi* Höeg & Bose, 1960, from Congo, differ by having an elliptic shape and greater development of the distal portion of the testa, an overall size of the seed smaller, and having a pointed apex respectively.

Samaropsis seixasii (White) Seward, 1917 emend. Prado, Marques-de-Souza & Iannuzzi
(Figure 5C–D)

1908. *Cardiocarpon* (*Samaropsis*) *seixasi* White, p. 558, est. X, figs. 5 and 8.
1917. *Samaropsis seixasi* (White) Seward, p. 351, fig. 502, F.
1967b. *Samaropsis seixasi* (White) Seward. Millan, p. 3, fig 2.
1972. *Samaropsis seixasii* (White) Seward. Rigby, p. 284, pl. 4, figs. 24, 25.
1977. *Samaropsis seixasi* (White) Seward. Corrêa da Silva et Arrondo, est. II, figs. 6, 7.
1977a. *Samaropsis seixasii* (White) Seward. Millan, p. 41, est. 1, fig. 9.

Study material. USMN 32012 (holotype, Figure 5D); MP-Pb 4470A–C, 4944, 5015, 5018 (Figure 5C), 5455, 5486, 5489A–B, 5490, 5553.

Original diagnosis. Lower nucellus, convex, finely and irregularly striated, oval, or rarely elliptical, measuring 8–10 mm in length and 5 mm in width, distinctly apiculate, sometimes acuminate and

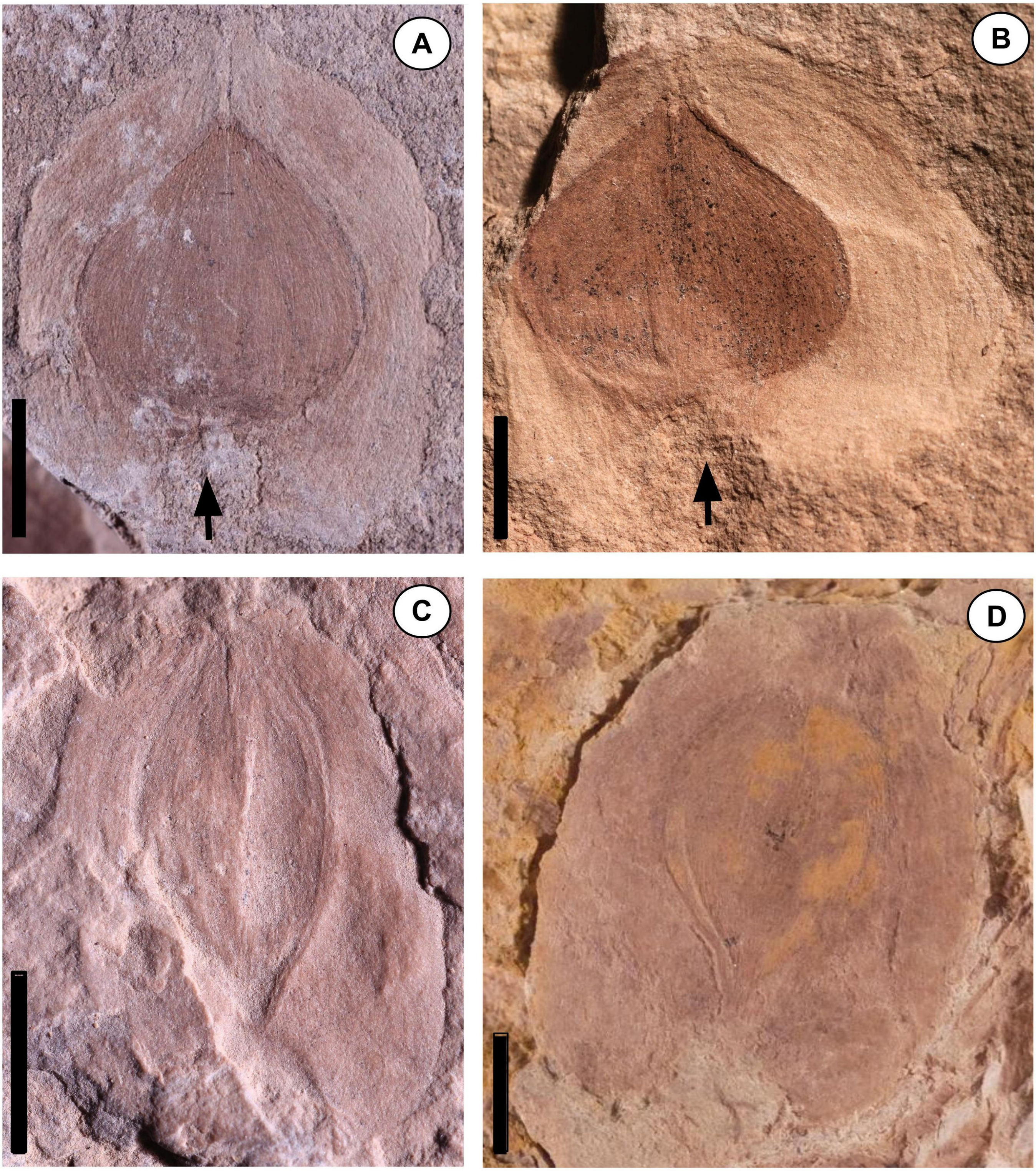

Figure 5. A–B, *Samaropsis sulriograndensis* sp. nov. **A**, MP-Pb 5464, holotype; **B**, MP-Pb 5656ab, paratype. **C–D**, *Samaropsis seixasii*. **C**, MP-Pb 5018; **D**, USMN 32012, holotype. The arrows in pictures A and B indicate the basal recession that interrupts the sarcotesta in *S. sulriograndensis* sp. nov. Scale bars = 5mm.

Table 1. Morphometric comparison of *Samaropsis sulriograndensis* sp. nov., *Samaropsis kurtzii* and *Samaropsis tasacunensis.*

Species	n	Seed size (mm)	Nucellus	Testa (mm)	Apice	Base	References
S. sulriograndensis nov. sp.	7	14–17 (length) 13–22 (width)	ovate	3.0–5.6	emarginate	reniform	This paper
S. kurtzii	3	16–22 (length) 14–20 (width)	elliptic with acuminate extremities	3.0	emarginate	cordate	Leguizamón (1971) Archangelsky (2000)
S. kurtzii	5	15 (length) 16 (width)	elliptic with acuminate extremities	4.6	emarginate	cordate	Leguizamón (1972)
S. kurtzii	2	23–24 (length) 21–23 (width)	elliptic with acuminate extremities	5.0–7.0	emarginate	cordate	Souza & Iannuzzi (2007)
S. kurtzii	5	12.8–20.4 (length) 11.8–21.6 (width)	elliptic with acuminate extremities	3.0–5.8	emarginate	cordate	This paper
S. tasacunensis	1	13.5–17 (length) 14–19 (width)	elliptic with acuminate extremities	not informed	bifurcated	cordate	Archangelsky (2000)

slightly tapering wedge-like at the base towards the truncated line of attachment, which is about one-third of the maximum transverse diameter, near the middle of the nucellus. The sclerotesta is thin, 25 to 26 mm in width along the edge in flattened specimens, but narrower at the top, wider at the base, and sometimes very clearly defined. The sarcotesta is probably thin, laterally expanded along the entire length of the nucellus, forming a thin wing, very finely lined, whose shape varies somewhat, 2–4 mm in width on each side, usually slightly narrower just below the middle, where it tapers along the nucellus and sometimes a short distance below the line of separation. It is generally wider towards the apex, where it extends on each side into a very broadly angled lobe that curves slightly inward, towards the apical sinus, which opens widely at an angle (White, 1908, p. 558).

Emended diagnosis. Platyspermic elliptical seed with differentiated testa. Winged sarcotesta emarginate on the apical region and well-developed on the lateral-bottom region of the seed forming a sagittate basal sinus. Narrow and continuous sclerotesta surrounding the nucellus being interrupted at the micropyle. Obovate, striated nucellus with a slightly emarginate apex (or V-shaped) and cuneate base.

Description. Platyspermic elliptical seed, with differentiated testa and thinly striated surface, measuring 10–12 mm in length and 8–10 mm in width (N=7). Well-developed winged sarcotesta measuring on the lateral-bottom region of the seed about 3.6–4.0 mm in thickness, forming a sagittate basal sinus. Obovate, striated nucellus with a slightly emarginate apex and cuneate base, measuring around 4.2–5.3 mm in width and 6.8–9.2 mm in length (N=7).

Volume estimated. The nucellus' volume measures around 43.2–77 mm^3.

Discussion and comparison. The Tt/Nw (=0.5) relation indicates that the specimens belong to the genus *Samaropsis*. The differentiated testa, and the presence of sinus on both extremities (base and apex), suggest a morphological similarity between some known species from Paraná Basin, like *S. cerquilhensis* (Millan, 1977b; Bernardes-de-Oliveira *et al*., 2007), *S. rugata* Bernardes-de-Oliveira *et al*., 2007, *S. rohnii* Bernardes-de-Oliveira *et al*., 2007, *S. rigbyi* Millan, 1977b and *S. seixasii* (White) Seward (1917).

Samaropsis cerquilhensis is bigger than our specimens with a poorly developed lobed basal sinus (Bernardes-de-Oliveira *et al*., 2007). *Samaropsis rugata* has a triangular, rounded to oval nucellus with a rounded base and sarcotesta roughly striated differing morphologically from our material (Bernardes-de-Oliveira *et al*., 2007). *S. rigbyi* is distinguished by having an ovate nucellus, with a rounded base, median ridge and embryonic structure at its base (Millan, 1977b). *Samaropsis rohnii* and *S. seixasii* are very similar to the material described here.

Access to high-quality photographs of both species' type material allowed us to verify that what differs *Samaropsis rohnii* from the material analyzed here is the shape of the nucellus and basal sinus of the testa. In *S. rohnii*, the nucellus is elliptic and the basal sinus of the testa is reniform, while our specimens have an obovate nucellus with cuneate base and a sagittate basal sinus (Bernardes-de-Oliveira *et al*., 2007). These last two features are shared between the studied specimens and those included in *S. seixasii*, which allows us to establish a similarity between them. However, this similarity can only be confirmed if we reinterpret White's (1908) original description considering current knowledge of Paleozoic seeds from Gondwana. It seems that White (1908) described the type-specimen of *S. seixasii* in an inverted way, considering the basal region as being the micropylar region and vice versa (Figure 5D). So, if we consider the correct positioning of the base and the top of this seed, the sarcotesta of *S. seixasii* has its biggest development in the basal region, where it projects itself in two well-developed wings, which gives the seed basis a sagittate shape. Likewise, the distal portion of the nucellus, where the micropyle is, appears, at times, marked with a V-shaped opening. This reinterpretation grants our specimens total similarity with *S. seixasii*. To correct the type specimen's positioning and appropriately indicate and describe its proximal and distal regions, the original diagnosis of *S. seixasii* is emended here.

Other occurrences. Volpe Ranch, in Monte Mor Municipality (middle Itararé Group), São Paulo State (in Millan, 1977a);

Morro do Papaléo Section (uppermost Itararé Group), in Mariana Pimentel Municipality, Rio Grande do Sul State (in Corrêa da Silva & Arrondo, 1977); Lauro Müller Municipality (Siderópolis Member, upper Rio Bonito Formation), in Santa Catarina State (in White, 1908; Millan, 1967b; Rigby, 1972).

Samaropsis moreirana (White) Millan, 1965
(Figures 6A–B)

Study material. USMN 30019 (holotype, Figure 6B); MP-Pb 2498 (Figure 6C), 2572AB.

Description. Small seed with general rounded/widely elliptic outline, total length measures approximately 5.5 mm and width measures 5 mm on average (N= 2). Fibrous testa, thicker on the middle-upper regions, where it reaches up to 0.9 mm in thickness, ending on the micropyle region in an acute/acuminate shape, marking an opening on the region in a "V" shape (MP-Pb 2572). Nucellus with rounded based, slightly truncated, and acute/acuminate apex, measuring around 3.8 mm in width and 4.5 mm in length (including the acute/acuminate projection). The testa thickness/nucellus width relation result is 0.23.

Volume estimated. the total volume of the studied seeds varies between 44.02–54.07 mm^3.

Discussion and comparison. The Tt/Nw relation Oliveira & Pontes (1976) of 0.23 leads to the inclusion of this seed into the genus *Samaropsis*. Considering the lack of a medial ridge, the presence of an apical *sinus*, and the general morphological similarity comparisons can be drawn with the following Gondwanan species: *Samaropsis surangei* Lele, 1962, *S. srivastavae* Lele, 1955, *S. raniganjensis* Seward & Sahni, 1920, *S. yoshidae* Rigby, 1972, *S. barcellosa* (White) Millan & *S. moreirana* (White) Millan (1965).

Samaropsis surangei differs by possessing a sarcotesta of uniform thickness through the whole outline of the seeds (Lele, 1962). *S. srivastavae* (Lele, 1955) differs by its apical region with two acute projections like hooks; *S. raniganjensis* has a retuse apical sinus (Seward & Sahni, 1920); *S. yoshidae* (Rigby, 1972) has a bigger size compared to our material (17 mm width and 23 mm length); *S. barcellosa* is also bigger in its dimensions, having an expansion of the sarcotesta in the apical region that can reach around 5 mm (Millan, 1967b).

Finally, after analyzing the type-material of *Samaropsis moreirana* (Figure 6B), as well as its dimensions presented in the original diagnosis of this species, we concluded that it had enough similarities with our material. Despite the specimens analyzed not showing a clear presence of a differentiated testa (sarcotesta and sclerotesta), the morphology and the general dimensions match with the ones of the type-material (Figure 6B) suggesting that the absence of a differentiated testa is consequence of preservational conditions. As a result, the studied material can be considered morphologically and morphometrically similar to *S. moreirana*, hence its inclusion in this species.

Other occurrences. "Toca do Índio" Ranch (uppermost Itararé Group), in Cerquilho Municipality, São Paulo State (in Bernardes-de-Oliveira *et al*., 2007, 2016), and Lauro Müller Municipality (Siderópolis Member, upper Rio Bonito Formation), in Santa Catarina State (White 1908; Rigby 1972; Bernardes-de-Oliveira *et al*., 2007).

Samaropsis kurtzii Leguizamón, 1971
(Figure 6C–D)

Study material. MP-Pb 4437, 5454, 5476, 5480 (Figure 6C), 5485 (Figure 6D).

Description. Striated seeds, with bilateral symmetry and sub-circular outline. Its length varies between 12.8–20.47 mm and the width is around 11.8–21.66 mm (N= 2). The nucellus has an acute apex and base, its length varies between 8–13.4 mm and the width around 5–11.4 mm (N=5). There is no evidence of medium ridge in the studied material. The sarcotesta of the seeds are striated and form two well-developed wings with a bigger development in the proximal region, the striation marks that involve the seeds are connected, forming a tenuous reticle.

Volume estimated. The nucellus volume range varies between 75–432 mm^3.

Discussion and comparison. Considering these specimens have a well-developed sarcotesta and are known as "winged seeds" there is no need to use the Tt/Nw relation (=0.3–0.74) as a mean to determine their inclusion into the genus *Samaropsis*. The specimens characterize themselves by their well-defined orbicular/circular shape, by their extensions present on the apical and basal regions of the nucellus and by the significant development of the sarcotesta. The study material resembles morphologically and morphometrically two species from Gondwana: *Samaropsis kurtzii* Leguizamón, 1971 and *Samaropsis tasacunensis* Archangelsky, 2000.

The two Argentinean species are very similar, and the low quality of the illustrations does not allow us to clearly observe the differences between the two taxa (Leguizamón, 1971, 1972; Archangelsky, 2000). According to the description provided, we can observe that the more complete specimens from our collection (MP-Pb 5480, Figure 6C; 5485, Figure 6D) differentiate from the Argentinean species *Samaropsis tasacunensis* because they have a sarcotesta better developed in the proximal region of the seed, as well as seen in *S. kurtzii* (Table 1), while in *S. tasacunensis* the better development of the sarcotesta is observed in the medial region.

The specimens (except MP-PB 5485, Figure 6D) from this study present smaller dimensions than the material from Argentina, however, as described by Leguizamón (1971) and Archangelsky (2000), one of the characteristics of *Samaropsis kurtzii* is its quite variable size.

Other occurrences. Bajo de Véliz, San Luis Province (Bajo de Véliz Formation), Argentina (*in* Leguizamón, 1971); Faxinal Section-Morro do Papaléo (uppermost Itararé Group), in Mariana Pimentel Municipality, Rio Grande do Sul State (in Souza & Iannuzzi, 2007, 2012).

REMARKS

Dispersal structures

Seeds can be categorized according to their size and the existence or not of "facilitating structures" to their dispersion

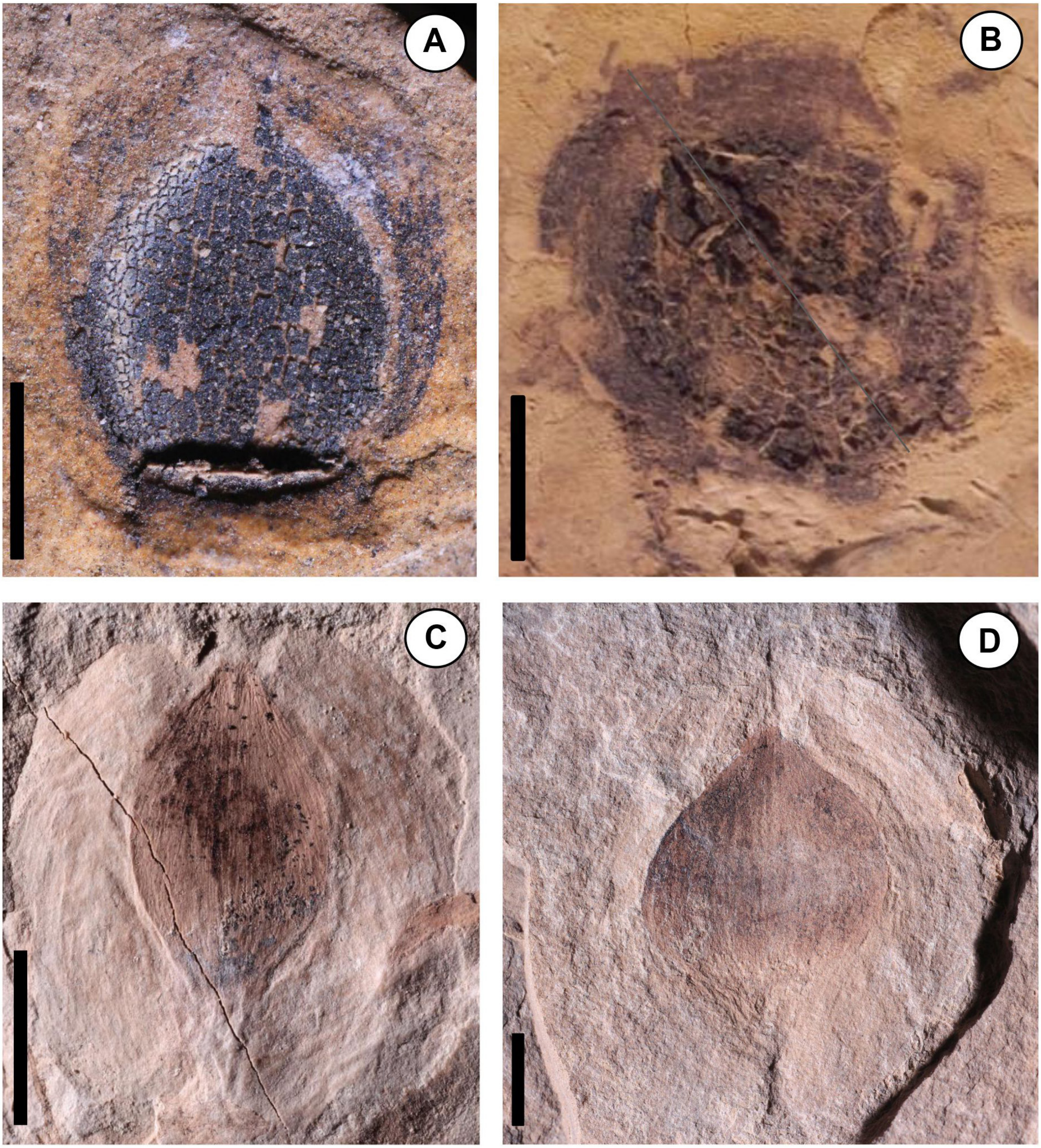

Figure 6. A–B, *Samaropsis moreirana*. **A**, MP-Pb 2498; **B**, USMN 30019; holotype; **C–D**, *Samaropsis kurtzii*, **C**, MP-Pb 5480; **D**, MP-Pb 5485. Scale bars: A–B = 2 mm; C–D = 5 mm.

(Marques-de-Souza, 2013). Below there is a brief description of each one of these categories and the dispersion analysis of each taxon described in this study.

- Small unassisted dispersal. Seeds smaller than 10 mm^3. In this volume interval, there is a bigger frequency of anemochory (= dispersion by wind) or unassisted dispersion (Hughes *et al*., 1994; Moles *et al*., 2005). The morphological simplicity of the seeds prevents us to have a more conclusive answer about the real dispersal agent of this morphotype, given that its smaller size favors the wind regardless of having adaptive structures such as wings or plumes, as well as the unassisted dispersion. In this work, we do not have any specimens that could fit this category. However, as an example, there is a very small seed associated with *Ottokaria minor* Marques-de-Souza & Iannuzzi, 2016a (reproductive structure of glossopterids), which was described as *Cordaicarpus* by Marques-de-Souza & Iannuzzi (2016a) and fits the criteria of this category (volume of 2 mm^3). Considering there is no investment in the production of dispersal specialized structures, the mother-plant tends to invest in the production of a large quantity of seeds. The absence of those seeds in the Cocuruto outcrop could be the consequence of selection by size, due to the selection by transport in a depositional environment dominated by currents and waves (see item Cocuruto outcrop).

- Medium unassisted dispersal (volume = 10–100 mm^3). In this interval, according to Hughes *et al*. (1994), "every type of dispersion is possible", given that those are all relatively small seeds (Sims, 2012). However, studies indicated a reduction in the occurrence of the unassisted dispersion in this group (Hughes *et al*., 1994; Moles *et al*., 2005). The action of vertebrates, as dispersal agents, also begins to appear. The birds, reptiles and fish are the main responsible to disperse seeds of this size Moles *et al*. (2005). *Cordaicarpus brasilianus* has the lowest value of volume in this category, the seeds do not present adaptations to be dispersed by the wind and, probably, are not dispersed by it considering that these seeds are commonly found agglomerated and next to *Arberia*-like fructifications. Therefore, the most likely scenario for this species is that they disconnect from the fructifications that fall really close to the mother-plant, not necessarily being transported (barochory). *Cordaicarpus cerrenogrensis*, *C. truncatus*, *Cornucarpus* sp. and *Samaropsis moreirana* have an intermediate volume within this interval as well as narrow and fibrous testa, suggesting protection against the ingestion of these seeds by vertebrate animals (fishes?). Here the dispersal by wind without auxiliary structures is not viable anymore. This is further supported by the analysis of the winged taxa which fits this category: *Samaropsis seixasii*. This type of seed has wings, most likely membranous ones, which clearly aid them to be carried by the wind. In this category, it is possible to notice the transition between small seeds that are produced in a larger scale and have no auxiliary structures to those with a more well-developed nucellus with adaptations to anemochory or biotic dispersals.

- Large, assisted dispersal (volume = 100–1.000 mm^3). In this category, structures that can support determined strategies of dispersion start to be frequent, such as "wings" from seeds with a nucellus big enough that demands a structural change to aid in the dispersion. Among the possible dispersion syndromes (Hughes *et al*., 1994; Moles *et al*., 2005), prevail the dispersion by water (= hydrochory) and the dispersion by vertebrates (= zoochory), following the logic of the previous category, but with the presence of a well-differentiated testa. *Samaropsis kurtzii* and *S. sulrigrandensis* are the most appropriate examples for this category. The presence of big and well-developed testa allows us to infer something about the type of dispersion adopted by these seeds. Being apparently thin, the wings can indicate an initial dispersion by anemochory, which does not prevent that the seed can also be transported (posteriorly) through water, for a while (Van der Pjil, 1969; Howe & Smallwood, 1982). The aerodynamic morphology that these wings proportionate to the seeds allows them to occupy and establish themselves in other places to germinate.

- Massive, assisted dispersal (volume > 1.000 mm^3). According to Willson & Traveset (2000), larger seeds have more difficulty to be dispersed compared to the smaller ones, given that they would need more efficient agents, such as larger animals, strong winds and water currents or, if that is the case, a powerful propulsion (in cases of auto dispersion). The authors also affirmed that for those seeds to be dispersed by wind, big, winged structures would be necessary and, when absent, the biotic dispersion becomes the most likely type of dispersion. None of our specimens can be categorized here, however, a good example of a species which would fit the criteria of this category would be *Samaropsis mendesii* Rigby emend. Marques-de-Souza & Iannuzzi, 2016b, a very large seed that has spongy/fibrous endotesta, which together with a protection and expanded surface area provided by the well-developed sarcotesta, would allow its flotation (Marques-de-Souza & Iannuzzi, 2016b). Thus, in the case of *S. mendesii* the most likely dispersal type would be hydrochory.

Botanical affinities

In general, studies have been showing that small seeds have the tendency to survive and germinate on open and sunny environments (Harper *et al*., 1970; Tiffney, 1984), due to their little nutritive reserve it is essential that the seedling becomes photosynthetically active as soon as possible to guarantee its survival after the total consumption of the reserve (Harper *et al*., 1970; Coomes & Grubb, 2003).

According to Gastaldo *et al*. (1996), the Sakmarian age corresponds to the relative interval of climate amelioration and domain of glossopterids on Gondwana, which appeared, primarily, at the top of the Itararé Group (=Taciba Formation), where the leaves of *Gangamopteris* predominated (Iannuzzi & Souza, 2005; Iannuzzi, 2013). Later, during the deposition of the Rio Bonito Formation, the genus *Glossopteris* became to dominate constituting up to 50% of the plant remains recorded in the outcrops of the "Irapuá Bed", Santa Catarina, according to Bernardes-de-Oliveira (1980).

In the literature (Taylor & Taylor, 1993), the large seeds are always related to cordaitaleans, even though they were never found, on Gondwana, any sort of organic connection with leaf structures capable of clarifying their botanical affinity. On the other hand, the smaller seeds are frequently assigned to conifers and glossopterids. Regarding the latter, there are records of fertile reproductive structures, some of which still carry seeds, as well as the connection with leaves of glossopterids, elucidating the botanical affinity of some types of small seeds such as, for instance, *Ottokaria santa-catharinae* Dolianiti (1971) and *Ottokaria minor* Marques-de-Souza & Iannuzzi (2016a). From Cocuruto outcrop *Cordaicarpus brasilianus* is the only taxon found attached to *Arberia*-type fructification (Figure 4E–F).

Cordaicarpus brasilianus has already been reported in a close association with a *Arberia*-type fructification by Souza & Iannuzzi (2009), on the level N8 of the Morro do Papaléo Section (upper Rio Bonito Formation). Now, in this study, we found the same species in close association to the *Arberia*-type fructification on top of the uppermost Itararé Group. Furthermore, in our sample (MP-Pb 4462, Figure 4E–F), one of the seeds is still in an organic connection with the reproductive structure. Thus, this indicates a clear connection of *C. brasilianus* and this type of fructification. Fructifications of the type *Arberia* do not possess a well-defined systematic position (Bernardes-de-Oliveira, 1977). According to Andendorff (2005), this type of fructification was never found attached to a leaf or another organ that could indeed link them to the glossopterids. However, in the literature, these fructifications are commonly associated with glossopterids (Bernardes-de-Oliveira *et al*., 2000), most likely being considered as basal forms of reproductive structures from this group (Andendorff, 2005). Therefore, it is assumed that *C. brasilianus* has a botanical affinity with glossopterids, in addition to that, some studies (Iannuzzi *et al*., 2006) registered leaves of glossopterids intimately associated with these types of fructification. However, it is important to continue searching for fertile structures in close association or connected, to clarify which groups of mother-plants the seeds are part of and to amplify our comprehension about the paleoecology of Paleozoic plants.

Unfortunately, due to the lack of precise information and more evidence of connected structures, the other seeds from this study could not be directly associated with any plant groups we know of. We could only infer about some of their botanical affinities, but nothing conclusive that would add to the knowledge we have of those seeds up to date (see Souza & Iannuzzi, 2012).

Biostratigraphic significance

The new seed association established for the Cocuruto outcrop lets the geographic or/and stratigraphic extension of the occurrence of taxa to the Morro do Papaléo locality, in Mariana Pimentel. As discussed above (in item Cocuruto outcrop), the fossiliferous interval of the Cocuruto outcrop is equivalent to Level N3 of the Morro do Papaléo Section, as proposed by Iannuzzi *et al.* (2006, 2010). To establish the stratigraphic distribution of the seeds described here in this locality, Figure 7 presents, for the first time, a synthesis of the stratigraphic distribution of the seed taxa described for both the Cocuruto outcrop and the Morro do Papaléo Section until the present.

The Figure 7 shows that the new occurrences of the Cocuruto outcrop allowed extending the range of some previously described taxa to other horizons of the Morro do Papaléo Section. *Cordaicarpus cerronegrensis* and *C. truncatus*, previously restricted to Level N2 (Souza & Iannuzzi, 2009), now also occur in a horizon above (i.e., in Cocuruto Outcrop), equivalent to Level N3, positioned in the uppermost portion of the Itararé Group (Figure 7). *C. brasilianus*, a species that extended from Level N4, top of the Itararé Group, up to Levels N7 and N8, top of the Rio Bonito Formation (Souza & Iannuzzi, 2009), now also appears in a slightly lower horizon, considering the records described here (Figure 7). *Samaropsis kurtzii*, previously assigned to Faxinal Section at Morro do Papaléo locality, by Souza & Iannuzzi (2012), approximately equivalent to the Level N2 of Iannuzzi *et al*. (2006, 2010), is now also occurring in a horizon above, equivalent to Level N3, positioned in the uppermost portion of the Itararé Group.

The species *Samaropsis seixasii* had previously been mentioned for Morro do Papaléo by Corrêa da Silva & Arrondo (1977). However, it is not possible to precisely determine the position of the specimen collected in relation to the stratigraphic distribution scheme of plant fossils established much later by Iannuzzi *et al*. (2006). Based on the present study, the distribution of this species is restricted to Level N3 (Figure 7). Thus, it is noteworthy that, for the first time, *S. seixasii* is reported in a well-defined stratigraphic position. Furthermore, the species *Samaropsis moreirana* is recorded for the first time not only at the Morro do Papaleo, but also in the state of Rio Grande do Sul. Previously, this species had been recorded for the top of the Itararé Group, in the state of São Paulo, Bernardes-de-Oliveira *et al*. (2007, 2016), and for the top of the Rio Bonito Formation, in the state of Santa Catarina (White, 1908; Rigby, 1972; Bernardes-de-Oliveira *et al*., 2007). Therefore, with the record presented here there is an extension of the geographic distribution of this species to the southernmost portion of the Paraná Basin.

From the point of view of biostratigraphic significance, most of the species recorded in the Cocuruto Outcrop have a wide range, when considering all their records throughout the Paraná Basin (Table 2), except for *Cordaicarpus truncatus*, *C. cerronegrensis* and *Samaropsis kurtzii*, which are species restricted to the top of the Itararé Group. However, *C. truncatus* and *C. cerronegrensis* are species with a geographic occurrence limited to the area of the municipality of Mariana Pimentel, where the localities of Morro do Papaléo and Cerro Negro are situated. Therefore, they can be considered as guide fossils of only regional range.

In biostratigraphic terms, the most relevant species found is *Samaropsis kurtzii*. Although *S. kurtzii* was previously recorded for the Morro do Papaléo Section and other surrounding exposures (Souza & Iannuzzi, 2007, 2012), the recovery of more specimens belonging to this species at another stratigraphic level helps to confirm its presence at the top of the Itararé Group in the southern Paraná Basin. The material-type of *S. kurtzii* described by Leguizamón (1971) was recovered in Bajo de los Véliz Formation, northwestern Argentina. In recent times, this unit has been dated within the latest Ghzelian–earliest Asselian interval, based on its palynological and paleofloristic content and stratigraphic positioning (Césari & Chiesa, 2017). In association with *Botrychiopsis plantiana* (Carruthers) Archangelsky & Arrondo, 1971 and *Stephanophyllites sanpauloensis* Millan & Dolianiti emend. Rohn & Lages, 2000, *Samaropsis kurtzii* can be considered a guide fossil for this time interval in the Paganzo Basin (Césari *et al*., 2007). *Botrychiopsis plantiana* and *Stephanophyllites sanpauloensis* were also found in association with *S. kurtzii* at the Level N2 in the Morro do Papaléo Section (unpublished data), reinforcing the correlation between the Argentinean strata of the Bajo de Véliz Formation and those

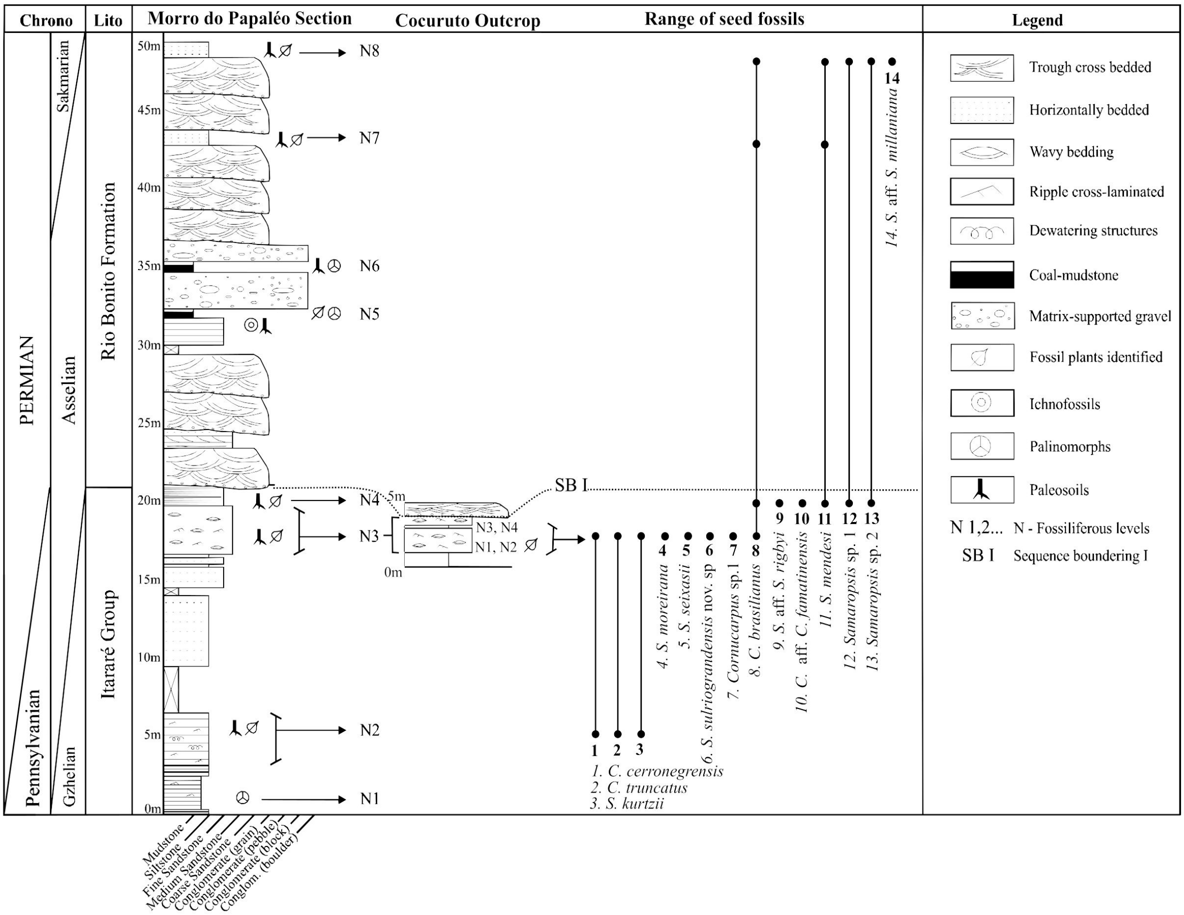

Figure 7. Stratigraphic range of seed fossils at the Morro do Papaléo Section, including the new occurrences from the Cocuruto outcrop presented here. Note that the fossiliferous interval of the Cocuruto outcrop corresponds to the fossiliferous Level N3 of the Morro do Papaléo Section, top of the Itararé Group, while the top shows the contact with the Rio Bonito Formation, represented by the conglomeratic sandstone that lies discordantly on the fine sediments of the Itararé Group. Most of the taxa identified in the Cocuruto Outcrop are new for the Morro do Papaléo locality. Morro do Papaléo Section based on the profiles by Iannuzzi *et al.* (2006, 2010).

Table 2. Stratigraphic distribution of fossil seed taxa recovered from the Cocuruto Outcrop through the Paraná Basin, Brazil. The localities-outcrops are arranged in stratigraphic order, from left to right. Localities/outcrops/fossiliferous levels: **MOR**, Monte Mor (Volp Ranch); **CER**, Cerquilho (Toca do Índio site – Itapema Farm); **MP-1**, lowermost part of the Morro do Papaléo outcrop (Cerro Negro, Morro do Papaléo-Faxinal Section = Level N2); **COC**, Cocuruto outcrop; **MP-2**, lower part of the Morro do Papaléo outcrop (Morro do Papaléo- Level N4); **PRO**, Probst outcrop; **MPA**, uppermost part of the Morro do Papaléo outcrop (Levels N7 and N8); **CBB**, Barro Branco Coal (Sideròpolis Member). **Time-scale abbreviations: Penn.**, middle-to-late Pennsylvanian; **Penn.–Cis.**, latest Pennsylvanian–earliest Cisuralian interval.

Species	Penn	Penn.–Cis.				Cisuralian			References
		Itararé Group				Rio Bonito Formation			
	MOR	CER	MP-1	COC	MP-2	PRO	MPA	CBB	
Cordaicarpus brasilianus		■		■	■	■	■		Bernardes-de-Oliveira *et al.* (2007, 2016); Souza & Iannuzzi (2009); Rischbieter *et al.* (2022)
Cordaicarpus cerronegrensis			■	■					Souza & Iannuzzi (2009)
Cordaicarpus truncatus			■	■					Souza & Iannuzzi (2009)
Cornucarpus sp. 1				■					This paper
Samaropsis kurtzii			■	■	■				Souza & Iannuzzi (2007, 2012)
Samaropsis moreirana		■		■				■	White (1908); Rigby (1972); Bernardes-de-Oliveira *et al.* (2007, 2016)
Samaropsis seixasii	■			■	■			■	White (1908); Millan (1967b; 1977a); Corrêa da Silva & Arrondo (1977); Rigby (1972)
Samaropsis sulriograndensis				■					This paper

positioned at the top of the Itararé Group, in Rio Grande do Sul. As a result, it can be assumed that *Samaropsis kurtzii* is a useful taxon for long-distance biostratigraphic correlation purposes.

Finally, it is interesting to note that seed species morphologically similar to *Samaropsis kurtzii*, such as *S. tasacunensis* and *S. riograndensis* sp. nov., are also restricted to the same chronostratigraphic interval. *S. tasacunensis* was originally described from the Tasa Cuna Formation of the Paganzo Basin, Argentina (Leguizamón, 1971, 1972). This formation was considered chrono-correlated with the Bajo de Véliz Formation based on palynostratigraphy (Balarino & Gutiérrez, 2006). On the other hand, *S. riograndensis* sp. nov., the species proposed here, has so far been limited to the strata of the Cocuruto outcrop. All these four seed species share a medium-sized central body (=nucellus) and symmetrical well-developed wings, with membranaceous appearance and disposed longitudinally in relation to the nucellus, making them very closely related forms. Therefore, seeds with this set of morphological features appear to have been relatively common from northwestern Argentina to southern Brazil during the Carboniferous–Permian transition.

CONCLUSIONS

In this study, we identified at the Cocuruto Outcrop: (i) seven seeds in specific level, i.e. *Cordaicarpus cerronegrensis*, *C. brasilianus*, *C. truncatus*, *Samaropsis moreirana*, *S. kurtzii*, and *S. seixasii*, besides genus *Cornucarpus*; (ii) the species *S. moreirana* for the first time in the State of Rio Grande do Sul; (iii) a new species named as *Samaropsis sulriograndensis*; (iv) anemochory, barochory and hydrochory as the most common dispersion syndromes, however we did not discard the possibility of some species suffering dispersion by zoochory due to the presence of auxiliary structures, strong striations on the seeds or due to the locations they were found; (v) glossopterids as the mother-plant of the species *Cordaicarpus brasilianus* based on the proven connection between this type of seed and *Arberia*-type fructification; (vi) *S. kurtzii* as a useful taxon for long-distance biostratigraphy within the latest Ghzelian–earliest Asselian interval, while *C. truncatus* and *C. cerronegrensis* as guide fossils only for the same interval at regional level, all of them being stratigraphically restricted to the upper Itararé Group, (vii) furthermore, the section of Cocuruto outcrop is described and stratigraphically positioned in relation to Morro do Papaléo Section for the first time.

The study of seeds is vital to the understanding of life habits of a plant, through this analysis it is possible to discover innumerous relations and strategies of these organisms to their survival. This contribution focused on the identification and analysis of dispersion syndromes of each species and, through literature, as well as checking the potential of these seeds for biostratigraphic purposes. We hope that contributions like this will encourage further studies with seed fossils across Paleozoic strata of Gondwana in the future.

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AUTHOR CONTRIBUTIONS

Raul Santos do Prado: writing – original draft, editing, visualization, investigation, formal analysis, revision. Juliane Marques-De-Souza: data curation, review, conceptualization. Roberto Iannuzzi: data curation, review, conceptualization. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

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

REFERENCES

Andendorff, R. 2005. *A revision of the ovuliferous fructifications of Glossopteris from the Permian of South Africa*. University of the Witwtersrond, D.Sc. Thesis.

Archangelsky, A. 2000. Estudio sobre semillas neopaleozoicas de Argentina. *Boletín de la Academia Nacional de Ciencias*, **64**:79–115.

Balarino, M.L. & Gutiérrez, P.R. 2006. Palinología de la Formación Tasa Cuna (Pérmico Inferior), Córdoba, Argentina: sistemática y consideraciones bioestratigráficas. *Ameghiniana*, **43**:437–460.

Bernardes-de-Oliveira, M.E.C. 1977. *Tafoflora eogondwanica da camada Irapuá, Formação Rio Bonito (Grupo Tubarão), SC*. Instituto de Geociências, Universidade de São Paulo, D.SC Thesis, vol. I, 301 p., vol. II, 32 p.

Bernardes-de-Oliveira, M.E.C. 1980. Tafoflora eogondvânica da Formação Rio Bonito ("Camada Irapuá"), Bacia do Paraná, Brasil. *In*: CONGRESO ARGENTINO DE PALEONTOLOGIA, BLOESTRATIGRAFIA, 2, CONGRESO LATINOAMERICANO DE PALEONTOLOGIA, 1, 1978. *Actas*, Buenos Aires, tomo IV, p. 69–88.

Bernardes-de-Oliveira, M.E.C. & Yoshida, R. 1981. Coniferófitas da 'Tafoflora Irapuá', Formação Rio Bonito, Grupo Tubarão em Santa Catarina. *Boletín de la Asociación Latinoamericana de Paleobotánica y Palinología*, **8:39**–55.

Bernardes-de-Oliveira, M.E.C.; Ricardi-Branco, F. & Rösler, O. 2000. As estruturas reprodutivas de Glossopterídeas na sucessão das tafofloras Permianas da Bacia do Paraná, Brasil. *Geociências*, **5**:62–68.

Bernardes-de-Oliveira, M.E.C.; Castro-Fernandes, M.C.; Tewari, R. & Ricardi-Branco, F. 2007. Platyspermic seeds from the Early Permian of Paraná Basin, Brazil. *Palaeobotanist*, **56**:1–19. *doi:10.54991/jop.2007.59*.

Bernardes-de-Oliveira, M.E.C. *et al*. 2016. Pennsylvanian – Early Cisuralian interglacial macrofloristic succession in Paraná Basin of the State of São Paulo. *Journal of South American Earth Sciences*, **72**:351–374. *doi:10.1016/j.jsames.2016.09.004*.

Cagliari, J.; Schmitz, M.D.; Tedesco, J.; Trentin, F.A. & Lavina, E.L.C. 2023. High-precision U-Pb geochronology and Bayesian age-depth modeling of the glacial-postglacial transition of the southern Paraná Basin: detailing the terminal phase of the Late Paleozoic Ice Age on Gondwana. *Sedimentary Geology*, **451**:106397. *doi:10.1016/j.sedgeo.2023.106397*.

Césari, S.N. *et al*. 2007. Paleozoico Superior de Argentina: un registro fosilífero integral para el Gondwana occidental. *Asociación Paleontológica Argentina*, **11**:35–54.

Césari, S.N. & Chiesa, J. 2017. Palynology of the Bajo de Veliz Formation, central-western Argentina: implications for Carboniferous-Permian transition biostratigraphy. *Journal of South American Earth Sciences*, **78**:238–249. *doi:10.1016/j.jsames.2017.07.004*.

Coomes, D.A. & Grubb, P.J. 2003. Colonization, tolerance, competition and seed size variation within functional groups. *Trends in Ecology & Evolution*, **8**:283–291. *doi:10.1016/S0169-5347(03)00072-7*.

Corrêa da Silva, Z.C. & Arrondo, O.G. 1977. Tafoflora Permiana de Mariana Pimentel, Município de Guaíba, Rio Grande do Sul. *Pesquisas*, **7**:27–44.

Eriksson, O.; Friis, E. M. & Löfgren, P. 2000. Seed size, fruit size, and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. *American Naturalist*, **156**:47–58. *doi:10.1086/303367*.

Fedorchuk, N.D. *et al*. 2019. Origin of paleovalleys on the Rio Grande do Sul Shield (Brazil): Implications for the extent of late Paleozoic glaciation in west-central Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **531**:108738. *doi:10.1016/j.palaeo.2018.04.013*.

Gastaldo, R.A.; Dimichele, W.A. & Pfefferkorn, H.W. 1996. Out of the icehouse into the greenhouse: a Late Paleozoic analog for modern global vegetation change. *GSA Today*, **6**:1–7.

Griffis, N.P.; Mundil, R.; Montañez, I.P.; Isbell, J.; Fedorchuk, N.; Vesely, F.; Iannuzzi, R. & Yin, Q.-Z. 2018. A new stratigraphic framework built on U-Pb single-zircon TIMS ages and implications for the timing of the penultimate icehouse (Paraná Basin, Brazil). *Geological Society of America Bulletin*, **130**:848–858. *doi:10.1130/B31775.1*.

Griffis, N.P. *et al.* 2019. Coupled stratigraphic and U–Pb zircon age constraints on the Late Paleozoic Icehouse-to greenhouse turnover in southcentral Gondwana. *Geology*, **47**:1146–1150. *doi:10.1130/G46740.1*.

Gutiérrez, P.R.; Ganuza, D.G.; Morel, E. & Arrondo, O.G. 1992. Los géneros *Cordaicarpus* Arber y *Samaropsis* Goeppert (Semillas Platispérmicas) en el Neopaleozoico argentino. *Ameghiniana*, **29**:49–68.

Harper, J.L.; Lovell, P.H. & Moore, K.G. 1970. The shapes, and sizes of seeds. *Annual Review of Ecology and Systematics*, **1**:327–356. *doi:10.1146/annurev.es.01.110170.001551*.

Höeg, O.V. & Bose, M.N. 1960. The *Glossopteris* Flora of the Belgian Congo, with a note on some fossil plants from the Zambesi Basin (Mozambique). *Annales du Musée du Congo Belge, Sciences Géologiques*, **32**:1–107.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**:201–228. *doi:10.1146/annurev.es.13.110182.001221*.

Hughes, L.; Dunlop, M.; French, K.; Leishman, M.R.; Rice, B.; Rodgerson, L. & Westoby, M. 1994. Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. *Journal of Ecology*, **82**:933–950. *doi:10.2307/2261456*.

Iannuzzi, R. *et al*. 2006. Afloramento Morro do Papaléo, Mariana Pimentel, RS. Registro ímpar da sucessão pós-glacial do Paleozoico da Bacia do Paraná *In*: M. Winge *et al.* (eds.) *Sítios Geológicos e Paleontológicos do Brasil*, CPRM.

Iannuzzi, R. 2010. The flora of Early Permian coal measures from the Paraná Basin in Brazil: a review. *International Journal of Coal Geology*, **83**:229–247. *doi:10.1016/j.coal.2010.05.009*.

Iannuzzi, R. 2013. The Carboniferous-Permian floral transition in the Paraná Basin. *Bulletin New Mexico Museum of Natural History and Science*, **60**:32–136.

Iannuzzi, R. & Souza, P.A. 2005. Floral succession in the Lower Permian deposits of the Brazilian Paraná Basin: an up-to-date overview. *New Mexico Museum of the Natural History and Science*, **30**:144–149.

Iannuzzi, R.; Souza, P.A. & Holz, M. 2010. Stratigraphic and paleofloristic record of the Lower Permian Post-glacial succession in the Southern Brazilian Paraná Basin. *Geological Society of America. Special Paper*, **468**:113–132. *doi:10.1130/2010.2468(05)*.

Leguizamón, R.R. 1971. Paleophytologia Kurtziana III. 6. Revisión de las semillas platispermicas de Bajo de Los Vélez (San Luis), ilustradas en el "Atlas de Plantas Fosiles de La Republica Argentina" (F. Kurtz, 1921). *Ameghiniana*, **8**:259–264.

Leguizamón, R.R. 1972. Estudio paleobotánico de la Formación Tasa Cuna, Permico Inferior de la Provincia de Cordoba. *Ameghiniana*, **4**:305–342.

Lele, K. 1955. Plant fossils from Parsora in the South Rewa Gondwana Basin, India. *Journal of Palaeosciences*, **4**:23–34. *doi:10.54991/jop.1955.466*.

Lele, K. 1962. Studies in the Indian Middle Gondwana Flora: 3. Platyspermic seeds and Megaspore impressions from the South Rewa Gondwana Basin. *Journal of Palaeosciences*, **11**:13–18. *doi:10.54991/jop.1962.615*.

Maithy, P.K. 1965. Studies in the Glossopteris flora of India: 18. Gymnospermic seeds and seed-bearing organs from the Karharbari beds of the Giridih coalfield, Bihar. *Palaeobotanist*, **13**:45–56.

Marques-de-Souza, J. 2013. *Análise taxonômica, estratigráfica e ecológica de sementes e estruturas reprodutivas do Permiano Inferior da Bacia do Paraná*. Programa de Pós-Graduação em Geologia, Universidade Federal do Rio Grande do Sul, D.Sc. Thesis, 247 p.

Marques-de-Souza, J. & Iannuzzi, R. 2016a. New occurrences of the genus *Ottokaria* Zeiller (Cisuralian, Paraná Basin, Brazil). *Review of Palaeobotany and Palynology*, **234**:1–10. *doi:10.1016/j.revpalbo.2016.08.001*.

Marques-de-Souza, J. & Iannuzzi, R. 2016b. Revaluation of the *Samaropsis mendesii* Rigby, 1972 from Paraná Basin lower Permian. *Geologia USP - Serie Cientifica*, **16**:33–40. *doi:10.11606/issn.2316-9095.v16i4p33-40*.

Milani, E.J. & Zalán, P.V. 1999. An outline of the geology and petroleum systems of the Paleozoic interior basins of South America. *Episodes*, **22**:199–205. *doi:10.18814/epiiugs/1999/v22i3/007*.

Millan, J.H. 1965. *Considerações sobre as sementes do Carbonífero do Brasil*, Rio de Janeiro, Departamento Nacional da Produção Nacional, Divisão de Geologia e Mineralogia, 18 p. (Boletim 123).

Millan, J.H. 1967a. *Novas frutificações na Flora Glossopteris do Gonduana Inferior do Brasil*, Rio de Janeiro, Departamento Nacional da Produção Nacional, Divisão de Geologia e Mineralogia, 27 p. (Boletim 140).

Millan, J.H. 1967b. *O gênero* Samaropsis *na flora do Gondwana do Brasil e de outros países*. Rio de Janeiro, Museu Nacional, 11 p. (Boletim 32).

Millan, J.H. 1974. As sementes platispérmicas do Gondwana face ao Esquema Maithy. *Anais da Academia Brasileira de Ciências*, **46**:538–547.

Millan, J.H. 1977a. Sementes platispérmicas da florula gondwanica de Monte Mor, Estado de São Paulo, Brasil. *Ameghiniana*, **14**:33–44.

Millan, J.H. 1977b. Sementes platispérmicas do eogondwana de Cerquilho, São Paulo, (Bacia do Paraná). *Anais da Academia Brasileira de Ciências*, **49**:581–595.

Millan, J.H. 1980. Sobre uma possível utilização estratigráfica de sementes gondvânicas. *Anais da Academia Brasileira de Ciências*, **52**:353–358.

Millan, J.H. 1994. O esquema de identificação e classificação das sementes gondvânicas: reatualização e análise crítica. *Anais da Academia Brasileira de Ciências*, **66**:475–488.

Millan, J.H. 1995. Novas ocorrências de sementes platispérmicas em tafofloras associadas a camadas carbonosas do Grupo Tubarão, eogondwana da Bacia do Paraná, no Estado de São Paulo. *Anais da Academia Brasileira de Ciências*, **67**:117–128.

Moles, A.T.; Ackerly, D.D.; Webb, C.O.; Tweddle, J.C.; Dickie, J.B.; Pitman, A.J. & Westoby, M. 2005. Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences of the United States of America*, **102**:10540–10544. *doi:10.1073/pnas.0501473102*.

Oliveira, M.E.C.B. & Pontes, C.E.S. 1976. Algumas observações sobre cordaitófitas da Formação Rio Bonito. Grupo Tubarão Bacia do Paraná Brasil. *In*: CONGRESSO GEOLÓGICO CHILENO, 1, 1976. *Actas*, Santiago do Chile, vol. 3, p. L22–L81.

Rigby, J.F. 1972. The Upper Palaeozoic Flora at Lauro Müller, Santa Catarina, southern Brazil. *Anais da Academia Brasileira de Ciências*, **44**:279–293.

Rischbieter, M.; Neregato, R.; Iannuzzi, R.; Di Pasquo, M.M.; Alvarenga, R. & Freitas, J. 2022. A new flora from the Rio Bonito Formation (late Asselian) and its implications for the biostratigraphy of the southern Paraná Basin, Brazil. *Journal of South American Earth Sciences*, **119**:104010. *doi:10.1016/j.jsames.2022.104010*.

Rohn, R. & Lages, L.C. 2000. Lower Permian sphenopsids from Cerquilho, northestern Paraná Basin, Brazil. *Revue Paléobiologie*, **19**:359–379.

Saksena, S. 1956. On two new species of *Samaropsis* from the South Rewa Gondwana Basin, Central India. *Palaeobotanist*, **4**:73–76.

Seward, A.C. 1917. *Fóssil plants*, London, Cambridge Biology Series, 656 p.

Seward, A.C. & Sahni, B. 1920. Indian Gondwana plants: a revision. *Memoirs of the Geological Survey of India, Palaeontologia Indica, New Series*, **7**:1–54.

Sims, H.J. 2012. The evolutionary diversification of seed size: using the past to understand the present. *Evolution; International Journal of Organic Evolution*, **66**:1636–1649. doi:10.1111/j.1558-5646.2011.01527.x.

Souza, J.M. & Iannuzzi, R. 2007. Sementes do gênero *Samaropsis* Goeppert no Permiano Inferior da Bacia do Paraná, Sul do Brasil. *Revista Brasileira de Paleontologia*, **10**:95–106. *doi:10.4072/rbp.2007.2.03*.

Souza, J.M. & Iannuzzi, R. 2009. The genus *Cordaicarpus* Geinitz in the Lower Permian of the Paraná Basin, Rio Grande do Sul, Brazil. *Revista Brasileira de Paleontologia*, **12**:5–16. *doi:10.4072/rbp.2009.1.01*.

Souza, J.M. & Iannuzzi, R. 2012. Dispersal syndromes of fossil seeds from Lower Permiano f Paraná Basin, Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências*, **84**:43–68. *doi:10.1590/S0001-37652012000100006*.

Surange, K.R. & Lele, K.M. 1956. Studies in the Glossopteris flora of India – 6. Plant fossils from Talchir beds of South Rewa Gondwana Basin. *Palaeobotanist*, **5**:82–90. *doi:10.54991/jop.1956.491*.

Taylor, T.N. & Taylor, E.L. 1993. *The biology and evolution of fossil plants*, New Jersey, Prentice Hall, 982 p.

Tiffney, B.H. 1984. Seed size, dispersal syndromes and the rise of the angiosperms: evidence and hypothesis. *Annals of the Missouri Botanical Garden*, **71**:551–576. *doi:10.2307/2399037*.

Tiffney, B.H. 1986. Evolution of seed dispersal syndromes according to the fossil record. *In*: D.R. Murray (ed.) *Seed dispersal*, Academic Press. *doi:10.1016/B978-0-12-511900-9.50012-7*.

Tiffney, B.H. 2004. Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution, and Systematics*, **35**:1–29. *doi:10.1146/annurev.ecolsys.34.011802.132535*.

Van Der Pjil, L. 1969. *Principles of dispersal in higher plants*; New York, Springer-Verlag, 153 p. *doi:10.1007/978-3-662-00799-0*.

Walkom, A.B. 1935. Some fossil seeds from the upper Paleozoic rocks of the Werrie Basin, N.S.W. *Proceedings of the Linnean Society of New South Wales*, **60**:459–463.

White, D. 1908. Fossil flora of the coal measures of Brazil. *In*: I.C. White (ed.); *Comissão de Estudos das Minas de Carvão de Pedra do Brasil: relatório final*, Rio de Janeiro, p. 558–568.

Willson, M.F. & Traveset, A. 2000. The ecology of seed dispersal. *In*: M. Fenner (ed.) *Seeds: the ecology of regeneration in plant communities*, CABI Publishing. *doi:10.1079/9780851994321.0085*.

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